J.Mycopathol.Res. 64(1) : 13-27, 2026, ISSN : 0971-3719 (Print), 2583-6315 (Online) 10.57023/JMycR.64.1.2026.013
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REVIEW

From Fungal taxonomy to Biotechnological applications: Structural and Functional insights into Melanin from *Curvularia*

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Received : 24.02.2026 Accepted : 05.03.2026 Published : 30.03.2026

Fungi represent one of the most taxonomically diverse and ecologically significant kingdoms, occupying a central position in biodiversity, ecosystem functioning, and applied biological sciences. Advances in morphotyping, molecular systematics, and multilocus phylogenetics have substantially refined fungal taxonomy and classification, revealing extensive cryptic diversity within recognized phyla and highlighting a global species richness estimated at 2.2–3.8 million taxa, of which only a fraction has been formally described. Beyond their taxonomic importance, fungi are prolific producers of structurally diverse secondary metabolites with wide-ranging biotechnological applications. In India alone, approximately 30,000 species have been documented, underscoring the vast yet underexplored potential of the fungal bioresource. Among fungal metabolites, melanin is a ubiquitous, multifunctional biopolymer synthesized by the oxidative polymerization of phenolic and indolic precursors. In fungi, melanin confers protection against ultraviolet radiation, oxidative stress, extreme environmental conditions, and host defences, while contributing to cell wall integrity, ecological fitness, and pathogenicity. Dematiaceous members of the genus *Curvularia* are distinguished by darkly pigmented hyphae and conidia resulting from melanin deposition; however, despite their ecological, agricultural, and clinical relevance, the structural and functional attributes of melanin in *Curvularia* remain insufficiently characterized. Research progress has been constrained by the inherent structural heterogeneity, low solubility, complex polymerization dynamics, and incomplete elucidation of biosynthetic and degradative pathways associated with fungal melanins.This review complies current knowledge on the taxonomy-to-technology continuum in *Curvularia*, integrating insights into melanin biosynthesis pathways, genetic and molecular regulation, physicochemical properties, and functional roles in stress tolerance and virulence. Advances in fermentation strategies, extraction and analytical characterization techniques, and emerging biomedical, agricultural, and industrial applications of fungal melanin are critically examined. Comparative perspectives with established melanized fungi are presented to delineate unique attributes and identify key research gaps. Collectively, this work provides a comprehensive framework to advance fundamental understanding and foster translational exploitation of *Curvularia*-derived melanin in biotechnology.

Keywords : Fungal diversity, fungal taxonomy, molecular systematics, bioprospecting, melanin

INTRODUCTION

Fungi represent one of the most taxonomically diverse and ecologically significant groups of organisms, occupying a pivotal position in biological classification and ecosystem functioning.

As a kingdom distinct from plants and animals, fungi exhibit remarkable morphological, physiological, and metabolic diversity, making them important for advances in taxonomy, phylogenetics, and evolutionary biology. Modern fungal taxonomy, increasingly based on molecular systematics and multilocus phylogenetic analyses, has revealed extensive cryptic diversity and led to the reclassification and refinement of numerous genera and species (Madrid *et al.* 2014). Accurate taxonomic delimitation is therefore essential not only for understanding fungal biodiversity and ecological roles but also for disease diagnosis, bioresource

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22nd Sir E.J.Butler Award Lecture organized by Indian Mycological Society delivered on 15th November 2025 during National Conference jointly organized by Regional Research Station (Hill Zone), UBKV, Kalimpongand IMS held at Kalimpong Science Centre, Kalimpong, West Bengal

management, and biotechnological exploitation. Current classifications recognize approximately 19 fungal phyla, over 1,200 families, and more than 10,000 genera, reflecting substantial phylogenetic refinement. Although about 1,60,000- 1,80,000 fungal species have been formally described worldwide, estimates suggest that global fungal diversity may range from 2.2 to 3.8 million species, highlighting a vast unexplored taxonomic frontier. An ongoing programme of exploration of fungal diversity and their selective isolation of novel, unusual or rare fungi from the forests of the Western Ghats and other regions in India was set up under the umbrella of the National Fungal Culture Collection of India (DST-National Facility), and several novel genera and species of fungi were discovered, described & identified and conserved (Table 1).

Beyond their taxonomic importance, fungi play indispensable roles in global biogeochemical cycles as primary decomposers and symbionts and are prolific producers of structurally diverse secondary metabolites. This metabolic versatility has established fungi as cornerstone organisms in biotechnology, with wide-ranging applications in pharmaceuticals, agriculture, food industries, environmental remediation, and materials science (Gadd 2007). In India, systematic taxonomic efforts since the beginning of the last century have documented about 30,000 fungal species, representing only a fraction of the country's true fungal diversity. Review of recent literature reveals that several novel genera and species of different taxonomic group of fungi

Among fungal-derived biomolecules, melanin has attracted considerable interest due to its multifunctional physicochemical and biological

Table 1: Details of fungal taxa described recently

Name of Fungal Taxa Described	Reference
Srinivasanomyces kangrensis	Rana & Singh (2020)
Kamalia indica	Rana & Singh (2019)
Neoacladium indicum	Singh & Singh (2019)
Trichomerium bhatii	Rana *et al.* (2019)
Coniochaeta simbalensis	Rana & Singh (2019)
Strelitziana sarbhoyi	Rana & Singh (2019)
Paraconiothyrium ajrekarii	Rana & Singh (2021)
Fusicolla hughesii	Singh *et al.* (2020)
Fusarium indicum	Rana & Singh (2023)
Fusarium kamalianum	Rana & Singh (2023)
Alanomyces manoharacharyi	Rana & Singh (2024)
Trichoderma indica	Lagashetti *et al.*(2023)
Nigrograna sunildeshmukhii	Rana & Singh (2025)
Keithomyces indicus	Lagashetti *et al.*
Synnemellisia punensis	Pawar *et al.* (2024)
Agaricus agharkarii	Singh *et al.* (2024)
Waitea akhanpalii	Rana & Singh (2025)
Conidiobolus srinivasanii	Pawar *et al.* (2025)

properties. Melanin is a high-molecular-weight, heterogeneous, negatively charged, and hydrophobic biopolymer produced by organisms across multiple kingdoms, including fungi (Riley 1997; Butler & Day 1998). In fungi, melanin is synthesized through oxidative polymerization of phenolic or indolic precursors and is deposited within the cell wall or extracellular matrices, imparting characteristic brown to black pigmentation (Gomez & Nosanchuk 2003; Eisenman and Casadevall, 2012). Functionally, fungal melanin enhances tolerance to a broad range of environmental stresses, including ultraviolet and ionizing radiation, oxidative damage, temperature extremes, enzymatic degradation, heavy metals, and toxic compounds (Dadachova & Casadevall, 2008).

Melanized fungi are ubiquitous in nature, particularly in soil, plant debris, decaying organic matter, and extreme or polluted environments, where melanin significantly improves ecological fitness and survival (Jacobson, 2000). In pathogenic fungi, melanization is widely recognized as a virulence-associated trait that contributes to immune evasion, antifungal resistance, and persistence within host tissues (Revankar & Sutton, 2010; Cordero & Casadevall, 2017). These adaptive properties have further stimulated interest in fungal melanin for biomedical, agricultural, and environmental applications, including antimicrobial, antioxidant, radioprotective, and wound-healing formulations (Eisenman *et al.* 2020; Suthar *et al.* 2023).

The genus *Curvularia* (family Pleosporaceae, order Pleosporales) comprises a taxonomically complex group of melanized filamentous fungi exhibiting saprophytic, endophytic, and pathogenic lifestyles. Approximately 160–200 *Curvularia* species have been described to date, with members widely distributed in tropical and subtropical regions and commonly isolated from soil, air, seeds, and plant surfaces (Madrid *et al.* 2014). Many species are economically important plant pathogens causing leaf spots, blights, root rots, and seedling diseases in cereals and grasses, while several are also recognized as opportunistic human pathogens, particularly in immune compromised individuals (Pombeiro *et al.* 2017; Revankar & Sutton, 2010). A defining morphological feature of the genus is the brown to black pigmentation of conidia and hyphae, implicating melanin as a central factor in its taxonomy, ecology, and pathogenic potential (Manamgoda *et al.* 2015).

Despite extensive research on melanin in other dematiaceous fungi such as *Cryptococcus*, *Aspergillus*, *Alternaria*, *Bipolaris*, and *Exophiala*, studies focusing specifically on melanin in *Curvularia* remain fragmented and limited (Langfelder *et al.* 2003; Eisenman and Casadevall 2012). Existing reports are largely dispersed across taxonomic and pathogenicity studies, with minimal integration of molecular, biochemical, and functional perspectives. This review therefore aims to synthesize current knowledge on melanin biosynthesis in *Curvularia*, elucidate its roles in stress tolerance, ecological adaptation, and host–pathogen interactions, and highlight the emerging biotechnological potential of *Curvularia*-derived melanin in comparison with other well-studied melanized fungi (Suthar *et al.* 2023). A graphical representation of approaches outline in this review in given in Fig.1.

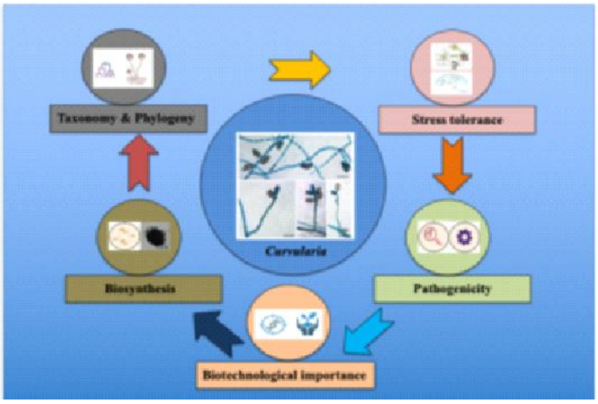

Fig 1: Graphical presentation of approaches outlined in this review

TYPES OF MELANIN IN FUNGI

Fungal melanins are a diverse group of dark, insoluble, and chemically heterogeneous pigments that vary in their biosynthetic origins, molecular organization, and biological functions. Unlike animal melanins, which are synthesized through relatively conserved tyrosine-dependent pathways, fungal melanins arise from multiple, evolutionarily distinct metabolic routes. Consequently, fungal melanins are broadly classified based on their primary biosynthetic precursors and enzymatic pathways rather than their final polymeric structure **(**Eisenman *et al.* 2020).

The three major types of melanin reported in fungi are 3,4-dihydroxyphenylalanine (DOPA)-melanin, 1,8-dihydroxynaphthalene (DHN)-melanin, and pyomelanin. Among these, DHN-melanin is the most prevalent pigment in filamentous ascomycetes, particularly in melanized or dematiaceous fungi, where it is responsible for the characteristic brown to black pigmentation of hyphae and conidia **(**Langfelder *et al*. 2003). Differences in melanin type are often correlated with fungal taxonomy, ecological niche, and pathogenic strategy, underscoring the importance of melanin biosynthesis in fungal adaptation and evolution.

DHN-Melanin

DHN-melanin is synthesized via the polyketide pathway and represents the dominant melanin type in filamentous ascomycetes, including most dematiaceous fungi (Bell & Wheeler 1986). This pathway is independent of L-tyrosine and instead originates from acetyl-CoA and malonyl-CoA units, which are condensed by non-reducing polyketide synthases (PKSs) to form the precursor 1,3,6,8-tetrahydroxynaphthalene (1,3,6,8-THN). 1,3,6,8-THNsubsequently undergoes a series of enzymatic reductions and dehydrations mediated by specific reductases and dehydratases, yielding intermediates such as scytalone and vermelone before being converted to 1,8-dihydroxynaphthalene (1,8-DHN) (Fig. 2) **(**Liu *et al*. 2022).

The final step involves oxidative polymerization of 1,8-DHN, typically catalyzed by laccases or peroxidases, resulting in the formation of an amorphous, highly cross-linked melanin polymer that is deposited primarily in the fungal cell wall (Agustinho & Nosanchuk 2017). Functionally, DHN-melanin enhances cell wall rigidity, reduces permeability, and protects fungal cells from ultraviolet radiation, oxidative stress, hydrolytic enzymes, and toxic compounds **(**Suthar *et al*. 2021). In plant-pathogenic fungi, DHN-melanin has been shown to play a critical role in appressorium formation and host penetration, whereas in opportunistic human pathogens it contributes to immune evasion and antifungal resistance **(**Belozerskaya *et al*. 2015).

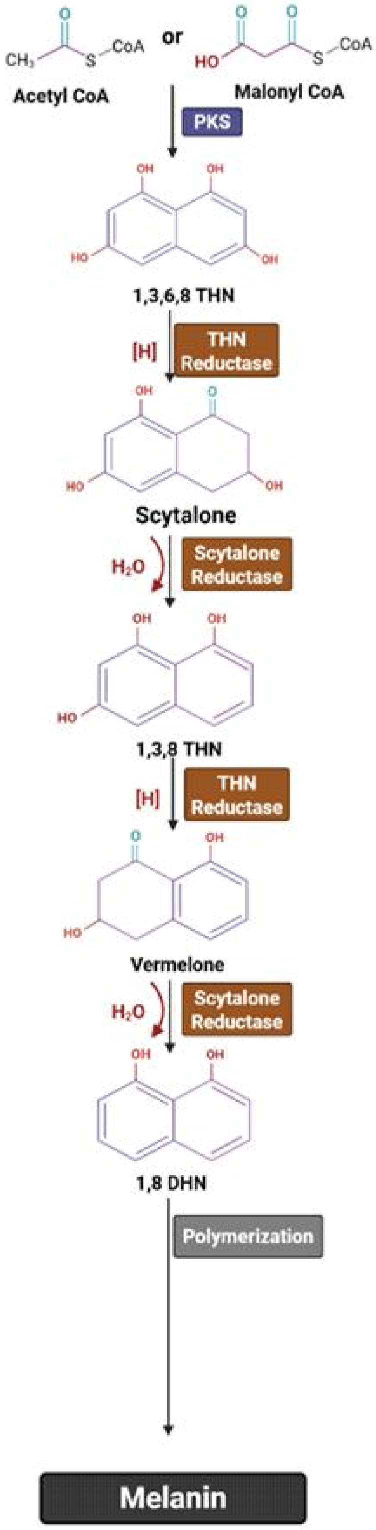

Fig 2 : Schematic representation of the DHN-melanin biosynthetic pathway in *Curvularia*

In the genus *Curvularia*, the presence of intensely pigmented conidia and hyphae strongly suggests the production of DHN-melanin. Although comprehensive genetic characterization of melanin biosynthesis in *Curvularia* remains limited, the genus shares close phylogenetic relationships with other DHN-melanin-producing genera within the *Pleosporales*, such as *Bipolaris* and *Alternaria* **(**Gomez, 2023**)**. The conservation of polyketide synthase genes among members of this order further supports DHN-melanin as the predominant pigment in *Curvularia* species.

Other Melanin Types

In contrast to DHN-melanin, DOPA-melanin is synthesized through the oxidation of L-tyrosine or L-DOPA and is predominantly associated with basidiomycetous fungi, most notably *Cryptococcus neoformans* **(**Belozerskaya*et al.* 2015**)**. This pathway relies on laccase-mediated oxidation of diphenolic substrates, leading to polymerization and deposition of melanin within the cell wall or extracellular matrix **(**Cordero, 2017**)**. DOPA-melanin is a well-established virulence factor in *C. neoformans*, where it protects fungal cells from oxidative killing, antimicrobial peptides, and phagocytosis by host immune cells **(**Nosanchuk & Casadevall, 2006).

Pyomelanin represents another distinct type of fungal melanin and is derived from homogentisic acid, an intermediate of tyrosine catabolism (Bell & Wheeler 1986**)**. Unlike DHN- and DOPA-melanins, pyomelanin is often secreted into the extracellular environment rather than being tightly associated with the cell wall. This pigment has been implicated in resistance to oxidative stress, iron acquisition, and environmental persistence in both fungal and bacterial systems **(**Mattoon *et al.* 2021).

To date, there is no convincing biochemical or genetic evidence indicating that *Curvularia* species synthesize DOPA-melanin or pyomelanin under natural or laboratory conditions. Available morphological, physiological, and taxonomic data consistently support DHN-melanin as the dominant pigment type in this genus, in agreement with its placement among filamentous ascomycetes **(**Manamgoda *et al.* 2015**)**. Nevertheless, the possibility of conditional activation of alternative melanin pathways under specific environmental or stress-related conditions remains an open avenue for future research.

MELANIN BIOSYNTHESIS IN *CURVULARIA*

Genetic and Enzymatic Basis

Although comprehensive molecular and functional studies specifically targeting melanin biosynthesis in *Curvularia* are still limited, accumulating genomic, biochemical, and comparative evidence strongly supports the operation of a DHN-melanin biosynthetic pathway in this genus. Comparative analyses with closely related dematiaceous genera within the order *Pleosporales*, such as *Bipolaris*, *Alternaria*, and *Exserohilum*, reveal a high degree of conservation in melanin-associated gene clusters, suggesting a shared evolutionary origin and similar regulatory mechanisms **(**Langfelder *et al.* 2003).

The DHN-melanin gene cluster typically encodes a non-reducing polyketide synthase (PKS), which catalyzes the initial condensation of acetyl-CoA and malonyl-CoA units to produce 1,3,6,8-tetrahydroxynaphthalene (1,3,6,8-THN) (Bell & Wheeler 1986). Subsequent enzymatic steps involve the action of T4HN reductase, scytalone dehydratase, and 1,3,8-trihydroxynaphthalene (1,3,8-THN) reductase, ultimately leading to the formation of 1,8-dihydroxynaphthalene (1,8-DHN), the immediate precursor of DHN-melanin. Oxidative polymerization of 1,8-DHN, mediated by laccases or peroxidases, results in the deposition of the final melanin polymer within the fungal cell wall (Eisenman *et al.* 2020).

Indirect but compelling functional evidence for DHN-melanin biosynthesis in *Curvularia* has been obtained through the application of pathway-specific inhibitors such as tricyclazole and pyroquilon. These fungicides selectively inhibit reductase enzymes involved in the DHN pathway, thereby blocking melanin synthesis and causing the accumulation of characteristic reddish-brown or orange intermediates, including flaviolin and scytalone **(**Cordero & Casadevall, 2017**)**. Experimental treatment of *Curvularia lunata* and

Curvularia geniculata with these inhibitors has resulted in marked alterations in colony pigmentation, providing strong biochemical evidence for the presence of a functional DHN-melanin pathway in these species **(**Pralea *et al.* 2019).

CELLULAR LOCALIZATION OF MELANIN

In *Curvularia*, as in other dematiaceous fungi, melanin is primarily localized within the cell wall of both hyphae and conidia, where it plays a central role in structural integrity and environmental protection **(**El-Naggar & Saber, 2022**)**. Ultrastructural studies using transmission electron microscopy in melanized fungi have consistently demonstrated that melanin is deposited as electron-dense, granular or lamellar material embedded within the polysaccharide-rich cell wall matrix. These melanin deposits are often closely associated with chitin and β-glucan layers, forming a rigid and chemically resistant barrier around the fungal cell **(**Caldas *et al.* 2020).

This strategic localization enables melanin to function as an effective physical and chemical shield, reducing cell wall permeability and protecting *Curvularia* cells against lytic enzymes, reactive oxygen species, ultraviolet radiation, and toxic environmental compounds (Dadachova & Casadevall, 2008**)**. In conidia, melanin deposition is particularly evident, contributing to spore longevity, resistance to desiccation, and enhanced survival during dispersal and dormancy **(**Keller, 2019).

In pathogenic contexts, cell wall–associated melanin has been shown to interfere with host recognition and immune responses by masking immunogenic cell wall components and scavenging host-derived reactive oxygen species **(**Jacobson, 2000). Although direct ultrastructural studies on melanin localization in *Curvularia* remain limited, observations from closely related dematiaceous fungi strongly support a conserved pattern of melanin deposition and function within this genus (Gomez & Nosanchuk, 2003).

ECOLOGICAL AND APPLIED SIGNIFICANCE OF MELANIN IN *CURVULARIA*

Melanin is a key adaptive trait underlying the ecological success and applied potential of *Curvularia* species. In natural environments, melanization enhances tolerance to diverse abiotic and biotic stresses, while the same physicochemical properties render *Curvularia*-derived melanin an attractive multifunctional biopolymer.

A primary ecological function of fungal melanin is protection against ultraviolet and ionizing radiation through efficient energy absorption and dissipation (Dadachova and Casadevall, 2008). *Curvularia* propagules inhabiting soil and aerial environments are frequently exposed to intense sunlight, temperature fluctuations, and desiccation, conditions under which melanin provides a substantial survival advantage. Melanin also mitigates oxidative stress by scavenging reactive oxygen species generated during microbial competition, plant root interactions, and abiotic stress **(**Gadd, 2007**)**. Incorporation of melanin into the cell wall enhances structural integrity, reduces permeability, and protects against thermal stress, toxic compounds, and heavy metals commonly encountered in soil environments **(**Cordero & Casadevall, 2017).

In phytopathogenic *Curvularia* species, melanin contributes to host infection by reinforcing penetration structures and increasing cell wall rigidity, thereby facilitating breaching of plant cuticles (Borovansky & Riley, 2011**)**. Similar melanin-dependent mechanisms have been described in related dematiaceous fungi such as *Bipolaris* and *Alternaria* **(**Mattoon *et al.* 2021). Melanin-mediated reinforcement supports turgor pressure generation during host invasionand protects invasive hyphae from plant-derived antimicrobial compounds and oxidative defences **(**Borovansky & Riley, 2011).

Melanin further enhances ecological competitiveness in soil ecosystems by conferring resistance to extracellular lytic enzymes and microbial antagonism, while its metal-binding capacity influences nutrient availability and persistence under nutrient-limited conditions (Gadd, 2007; Mattoon *et al*. 2021**)**. These combined effects likely contribute to the widespread distribution of melanized *Curvularia* species across diverse habitats **(**Manamgoda *et al.* 2015).

Beyond ecological functions, fungal melanins exhibit broad-spectrum UV absorption, antioxidant activity, redox behaviour, metal-chelating capacity, and exceptional chemical stability, enabling applications in cosmetics, pharmaceuticals, bioelectronics, drug delivery, and environmental remediation (Solano, 2016). DHN-based melanins from dematiaceous fungi, including *Curvularia*, are particularly attractive due to their cell wall association and resistance to degradation (d'Ischia *et al*. 2013; Cordero & Casadevall, 2017). Functional properties and application potential of fungal melanin has been outlined in Fig. 3.

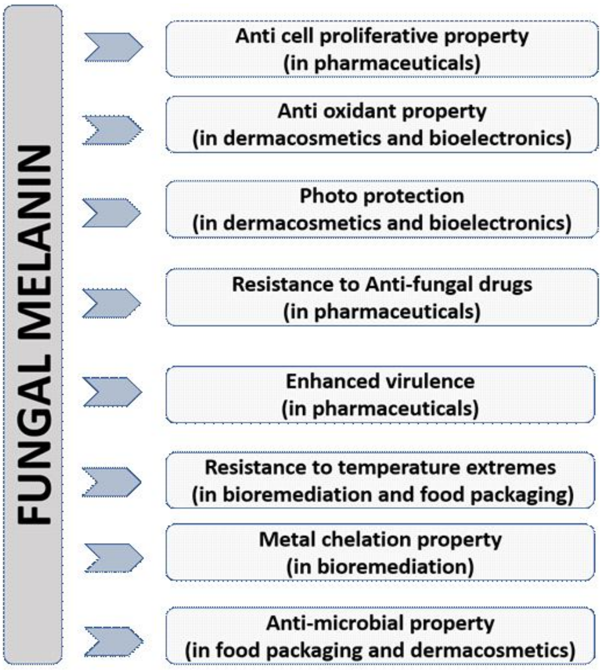

Fig 3: Functional properties and application potential of fungal melanin

Environmental remediation represents a promising application, as melanin efficiently binds metal ions and radionuclides, reducing their bioavailability and toxicity (Fogarty & Tobin 1996). In biomedical contexts, fungal melanins have been explored as antioxidant, radioprotective agents and drug carriers (Tran-Ly *et al.* 2020). Although *Curvularia*-specific studies remain limited, its DHN-melanin composition suggests comparable functional potential.

From a biotechnological perspective, *Curvularia* offers practical advantages for sustainable melanin production due to its rapid growth, low-cost cultivation, and compatibility with scalable fermentation systems. Optimization of culture conditions and stress induction strategies could further enhance yields, positioning *Curvularia* as a viable platform for commercial melanin production.

MELANIN AND PATHOGENICITY

Several species of *Curvularia*, including *C. lunata*, *C. pallescens*, *C. aeria*, and related taxa, have been increasingly recognized as opportunistic human pathogens, particularly in immuno compromised individuals or following traumatic implantation (Fogarty & Tobin 1996). These infections range from superficial and localized conditions, such as keratitis and allergic fungal rhinosinusitis, to invasive diseases, including sinusitis, cerebral infections, and phaeohy phomycosis. A defining feature shared by these pathogenic *Curvularia* species is their pronounced melanization, which has been widely implicated as a key virulence determinant in dematiaceous fungi.

In clinical contexts, melanin is considered an important fungal virulence factor due to its ability to interfere with host immune defenses. One of the most well-characterized roles of melanin is its capacity to neutralize reactive oxygen species (ROS) generated during the oxidative burst of phagocytic cells such as macrophages and neutrophils (Mattoon *et al.* 2021). By scavenging free radicals and reactive intermediates, melanin protects fungal cells from oxidative damage and enhances intracellular survival following phagocytosis. Studies on melanized fungi have demonstrated that melanin-containing cell walls can significantly reduce oxidative killing, thereby promoting persistence within host tissues (Polak *et al.* 1990).

In addition to modulating host immune responses, melanin has been shown to reduce susceptibility to antifungal drugs. Melanin can bind antifungal agents, including amphotericin B and azoles, thereby decreasing their effective concentration at the fungal cell membrane and limiting drug penetration. In several dematiaceous fungi, melanized cells exhibit increased tolerance to commonly used antifungal therapies compared to non-melanized or melanin-deficient mutants, contributing to treatment failure or prolonged infection. These protective effects are further enhanced by the localization of melanin within the cell wall, where it acts as both a physical and chemical barrier to antifungal compounds (Gessler *et al.* 2014).

Experimental studies in melanized pathogenic fungi such as *Cryptococcus neoformans*, *Exophiala dermatitidis*, and *Fonsecaea* spp. have demonstrated that melanin enhances survival within macrophages, increases resistance to antifungal drugs, and correlates with increased virulence in animal models. Although direct genetic or in vivo virulence studies focusing specifically on melanin-deficient *Curvularia* mutants are currently scarce, the strong conservation of DHN-melanin biosynthetic pathways among dematiaceous fungi strongly supports a similar role in *Curvularia* pathogenicity (Cordero, 2017).

Furthermore, melanin may contribute to immune evasion by masking pathogen-associated molecular patterns (PAMPs) such as â-glucans and chitin, thereby reducing recognition by host pattern recognition receptors and dampening inflammatory responses. This immune-modulatory effect, combined with enhanced resistance to oxidative stress and antifungal agents, likely underpins the ability of melanized *Curvularia* species to establish opportunistic infections and persist in host tissues (Gessler *et al.* 2014).

Taken together, available evidence strongly suggests that melanin plays a multifaceted role in the pathogenicity of *Curvularia*, contributing to immune evasion, antifungal resistance, and intracellular survival. While direct experimental validation in *Curvularia* remains limited, insights from closely related melanized fungi provide a compelling framework for understanding the contribution of melanin to virulence in this genus and highlight the need for targeted molecular and functional studies in future research.

SPECIES – SPECIFIC INSIGHTS INTO MELANIN PRODUCTION IN *CURVULARIA*

Curvularia lunata

Curvularia lunata is the most extensively studied species within the genus and is widely regarded as a representative model for understanding melanization in *Curvularia*. It is a well-known phytopathogen responsible for leaf spot and blight diseases in cereals and grasses, particularly maize and sorghum, and has also been implicated in opportunistic human infections, including keratitis, sinusitis, and phaeohyphomycosis (Manamgoda *et al.* 2015).

The characteristic dark brown to black pigmentation of *C. lunata* conidia and hyphae has been attributed to the accumulation of DHN-melanin within the fungal cell wall. Inhibitor-based studies employing specific DHN-melanin pathway blockers such as tricyclazole and pyroquilon have demonstrated marked reductions in pigmentation accompanied by the accumulation of shunt metabolites, including flaviolin and scytalone derivatives, providing functional evidence for the operation of a DHN-melanin biosynthetic pathway in this species (Wheeler & Bell, 1988). These findings are consistent with the presence of polyketide synthase (PKS)-mediated melanin biosynthesis, a trait commonly observed in dematiaceous fungi.

Functionally, melanin in *C. lunata* has been linked to enhanced tolerance to ultraviolet (UV) radiation, oxidative stress, and exposure to fungicidal compounds, underscoring its importance in both environmental persistence and pathogenicity (Langfelder *et al.* 2003). In plant–pathogen interactions, melanization is believed to facilitate survival on exposed leaf surfaces and may indirectly contribute to virulence by improving resistance to host-derived reactive oxygen species during infection. Although direct gene knockout studies targeting melanin biosynthetic genes in *C. lunata* remain limited, available physiological and inhibitor-based evidence strongly supports a central role for DHN-melanin in stress adaptation and pathogenic fitness.

Curvularia pallescens

Curvularia pallescens is primarily recognized as a plant-associated fungus but has also been reported in human infections, particularly in immuno compromised individuals (Revankar & Sutton, 2010). Melanin production in this species is thought to contribute to its ability to withstand host-derived oxidative stress and antifungal defenses, paralleling observations made in other melanized opportunistic pathogens.

Interestingly, *C. pallescens* often exhibits comparatively lighter pigmentation than *C. lunata*, suggesting intraspecific variability in melanin content. This variability may be influenced by environmental factors such as nutrient availability, light exposure, and oxidative stress, or by genetic differences affecting the regulation of PKS gene expression and downstream melanin biosynthetic enzymes (Eisenman & Casadevall 2012**)**. Such phenotypic plasticity in melanization may reflect adaptive modulation of melanin synthesis in response to ecological or host-associated conditions, although targeted experimental studies are required to validate these hypotheses.

Curvularia soli

Curvularia soli AS21 (ON076460) is an underexplored species capable of producing extracellular melanin with notable biological activities. It is septate, hyaline to lightly pigmented hyphae bearing simple conidiophores with sympodial proliferation are shown. Conidia are characteristically curved, ellipsoidal to obclavate, smooth-walled, brown to dark brown, and transversely septate, with a slightly enlarged central cell typical of the genus *Curvularia* (Fig. 4). Melanin production was optimized using the Plackett–Burman design, and low-dose gamma irradiation (1.0 kGy) significantly enhanced pigment yield (3.376 mg/L), indicating irradiation as a novel and economic stimulus for melanogenesis. The extracted melanin exhibited strong antimicrobial activity, particularly against *Klebsiella pneumoniae* and *Penicillium digitatum*, as well as significant antiviral efficacy against HSV-1 (77% inhibition). Additionally, the pigment showed potent antioxidant activity, selective cytotoxicity toward breast (MCF-7) and skin (A431) cancer cell lines with minimal effects on normal fibroblasts, and supported in vitro wound healing. These findings highlight *C. soli* AS21 as a promising fungal source of multifunctional melanin with biomedical potential (Abd *et al.* 2024).

Curvularia aeria and other emerging species

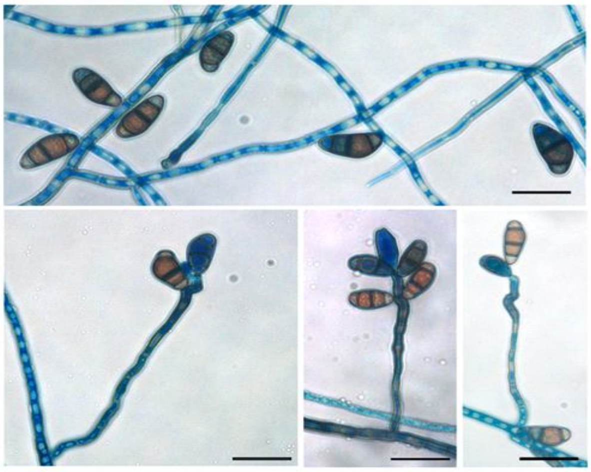

Fig 4. Micromorphological features of *Curvularia soli* observed under light microscopy, showing septate hyphae and typical conidia [Scale bars = 20 µm.]

Recent taxonomic revisions, supported by multilocus phylogenetic analyses, have led to the description of several new *Curvularia* species, including *C. aeria*, which has been isolated from air, soil, and plant substrates. These emerging species typically display melanized conidia, implying a conserved and possibly ancestral role for melanin across the genus (Suthar *et al.* 2023).

Despite these observations, experimental validation of melanin biosynthetic pathways in *C. aeria* and other newly described *Curvularia* taxa is largely absent. The presence of melanized structures suggests the operation of DHN-melanin pathways similar to those characterized in *C. lunata* and other dematiaceous fungi, but direct biochemical, genetic, and functional studies are needed. Investigating melanin production in these emerging species represents a promising avenue for future research, with potential implications for fungal ecology, taxonomy, and pathogenicity (Liu *et al*. 2022).

The relationships among different species of *Curvularia* has been shown in Fig. 5, which depicts multigene phylogenetic tree showing relationships among the species inferred from Maximum likelihood (ML) analysis based on combined ITS, *tef 1* - α and GAPDH.

MOLECULAR GENETICS AND REGULATION OF MELANIN BIOSYNTHESIS IN *CURVULARIA*

Polyketide Synthase Gene Clusters

DHN-melanin biosynthesis in filamentous fungi is governed by conserved secondary metabolite gene clusters encoding a non-reducing polyketide synthase (NR-PKS) and associated tailoring enzymes. In dematiaceous ascomycetes, these clusters are typically responsible for catalyzing the stepwise condensation of acetyl-CoA and malonyl-CoA units to generate 1,3,6,8-tetrahydroxynaphthalene (1,3,6,8-THN), the first committed intermediate in DHN-melanin synthesis (El-Naggar & Saber, 2022).

Although comprehensive functional genomics studies in *Curvularia* remain limited, genome mining and comparative analyses have revealed the presence of PKS genes with strong homology to ALB1/PKS1 genes characterized in *Bipolaris*, *Alternaria*, and *Magnaporthe oryzae* **(**Kimura & Tsuge 1993). These NR-PKSs possess characteristic domains, including ketosynthase (KS), acyltransferase (AT), acyl carrier protein (ACP), and product template (PT) domains, which together orchestrate the formation and cyclization of the polyketide backbone required for 1,3,6,8-THN production.

The conservation of these PKS clusters across phylogenetically related genera strongly suggests that *Curvularia* species utilize a homologous DHN-melanin biosynthetic machinery. Given the central role of PKS genes in fungal melanization, they represent promising molecular markers for investigating species-specific differences in pigment production, regulation, and ecological adaptation.

Tailoring Enzymes and Regulatory Elements

Following 1,3,6,8-THN synthesis, DHN-melanin biosynthesis proceeds through a series of reduction and dehydration reactions mediated by key tailoring enzymes, including 1,3,6,8-THN reductase, scytalone dehydratase, and 1,3,8-THN reductase. These enzymes convert 1,3,6,8-THN sequentially into scytalone, 1,3,8-trihydroxynaphthalene (1,3,8-THN), vermelone, and ultimately 1,8-dihydroxynaphthalene (DHN), which undergoes oxidative polymerization to form melanin (Keller, 2019**)**.

In *Curvularia*, direct molecular characterization of these enzymes is scarce; however, strong functional evidence for their activity has been obtained through the use of pathway-specific inhibitors such as tricyclazole and pyroquilon. These inhibitors block reductase steps in the DHN pathway, leading to the accumulation of reddish-brown shunt metabolites such as flaviolin—a diagnostic feature of DHN-melanin inhibition (Wheeler & Klich, 1995**)**. Such observations strongly support the presence and functionality of the complete enzymatic cascade in *Curvularia* species.

At the regulatory level, transcriptional control of melanin biosynthetic genes is likely mediated by global regulatory systems conserved among filamentous fungi. Studies in other melanized ascomycetes have demonstrated the involvement of the velvet complex (VeA, VelB, LaeA) in coordinating secondary metabolism, development, and stress responses, including melanin production (Bayram & Braus, 2012). In addition, stress-responsive transcription factors, such as Yap1- and PacC-like regulators, have been implicated in oxidative stress tolerance and pH-dependent regulation of melanin biosynthesis **(**Pralea *et al*. 2019). While these regulatory networks have not yet been experimentally validated in *Curvularia*, their conservation across related taxa strongly suggests a similar mode of control.

ENVIRONMENTAL REGULATION AND SIGNAL INTEGRATION

Melanin biosynthesis in *Curvularia* is highly responsive to environmental cues, reflecting its role as a multifunctional adaptive trait. Factors such as light exposure, nutrient limitation, pH, temperature, and oxidative stress have been shown to modulate melanization in dematiaceous fungi. In *Curvularia*, increased pigmentation is frequently observed under conditions of ultraviolet radiation and reactive oxygen species (ROS) exposure, suggesting that melanin synthesis is tightly linked to stress-response signalling pathways **(**Caldas *et al.* 2020).

Despite these insights, the precise molecular mechanisms underlying environmental signal integration in *Curvularia* remain poorly understood. Transcriptomic, epigenetic, and chromatin-level regulation of melanin gene clusters—such as histone modifications and

LaeA-mediated chromatin remodelling—represent critical knowledge gaps. Addressing these gaps through omics-based approaches will be essential for elucidating how *Curvularia* fine-tunes melanin production in response to diverse ecological and host-associated environments.

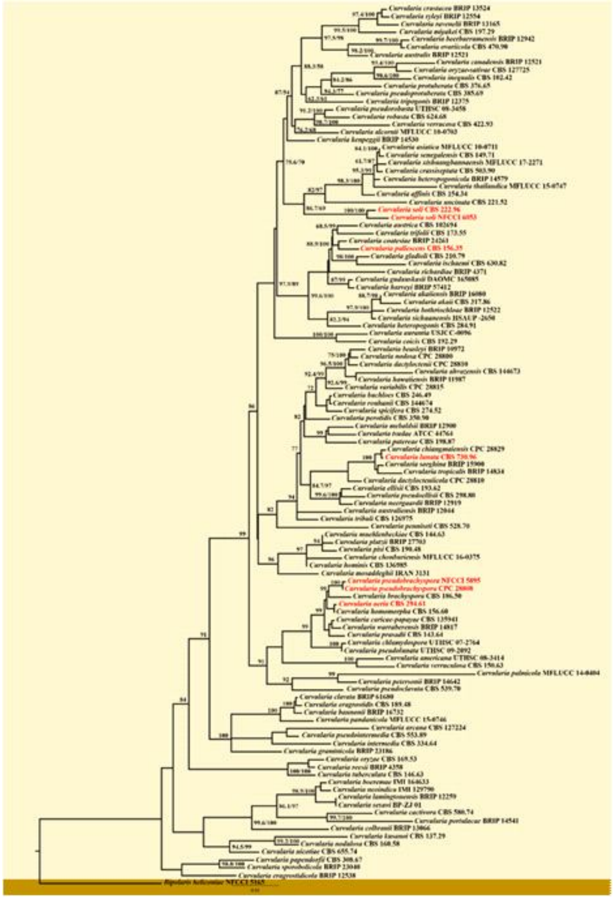

Fig. 5 : Multigene phylogenetic tree showing relationships among *Curvularia* species inferred from Maximum likelihood (ML) analysis based on combined ITS, *tef 1 - β* and GAPDH. Taxa reported to produce melanin are highlighted in **red**, indicating their distribution across multiple lineages within the genus. Numbers on the branches represent ML bootstrap.

COMPARISON OF MELANIN BIOSYNTHESIS AND FUNCTION IN *CURVULARIA* AND OTHER FUNGI

Melanin production in *Curvularia* shares core biochemical and genetic features with other dematiaceous fungi, particularly Pleosporales members such as *Alternaria*, *Bipolaris*, *Exserohilum*, and *Cladosporium*. In these fungi, melanin is predominantly synthesized via the 1,8-dihydroxynaphthalene (DHN) pathway, a polyketide synthase–dependent route independent of L-tyrosine (Table 2). Comparative genomic studies indicate strong conservation of DHN-melanin gene clusters across these genera, reflecting their close phylogenetic relationships and shared plant-associated and soil-inhabiting lifestyles (Kimura & Tsuge, 1993).

Despite this common biosynthetic pathway, melanin distribution and function vary among fungi. In *Curvularia*, melanin is deposited in both conidia and vegetative hyphae, resulting in uniformly melanized mycelia, whereas in *Aspergillus fumigatus*, melanization is largely restricted to conidia, serving primarily to protect spores from environmental and immune stresses. In contrast, basidiomycetous fungi such as *Cryptococcus neoformans* synthesize melanin via the DOPA pathway using host-derived phenolic substrates oxidized by laccases, a strategy closely linked to host adaptation and virulence (Nosanchuk & Casadevall 2006**)**. These differences illustrate the evolutionary flexibility of fungal melanization, with DHN-melanin supporting environmental persistence in *Curvularia* and related ascomycetes, while DOPA-melanin facilitates host-specific survival in pathogenic basidiomycetes (Suthar *et al.* 2021).

FUTURE PERSPECTIVES AND RESEARCH GAP

Despite the clear ecological importance and emerging biotechnological potential of melanin in *Curvularia*, our current understanding of its biosynthesis, regulation, and functional diversity remains fragmented. In contrast to well-studied melanized fungi such as *Cryptococcus neoformans*, *Aspergillus fumigatus*, and *Magnaporthe oryzae*, detailed molecular and genetic investigations of melanin pathways in *Curvularia* are notably scarce. Addressing this imbalance represents a critical priority for advancing both fundamental fungal biology and applied research.

A major research gap lies in the molecular characterization of DHN-melanin gene clusters in *Curvularia*. Although comparative genomics strongly suggests the presence of conserved polyketide synthase–based pathways, functional validation through targeted gene deletion, Table **2** : Comparative overview of Melanin characteristics in *Curvularia* and other selected fungi

Fungal species	Melanin type	Biosynthetic pathway / key enzymes	Biological roles	Cellular localization	References
Curvularia lunata	DHN-melanin	Polyketide pathway; NR-PKS, T4HN reductase, scytalone dehydratase	UV and oxidative stress tolerance, fungicide resistance, plant and human pathogenicity	Cell wall of hyphae and conidia	Jacobson (2000)
Curvularia geniculata	DHN-melanin	PKS-mediated DHN pathway (inferred from inhibitor and comparative genomic studies)	Environmental persistence, resistance to desiccation and enzymatic lysis	Predominantly conidial cell wall	Gadd (2007)
Curvularia pallescens	DHN-melanin (variable levels)	Putative PKS-dependent pathway	Tolerance to host-derived oxidative stress, opportunistic pathogenicity	Conidia and hyphae	Manamgoda *et al.* (2015)
Curvularia aeria	DHN-melanin (predicted)	PKS-based DHN pathway (genus-level conservation)	Survival in air- and soil-associated habitats	Melanized conidia	Madrid *et al.* (2014)
Curvularia verruculosa	DHN-melanin	PKS-dependent	Stress tolerance, saprophytic survival	Conidia	Jacobson (2000)
Curvularia soli	DHN-melanin	PKS-dependent	UV protection, Virulence, immune modulation, oxidative stress resistance	Conidia	Abd *et al.* (2024)
Alternaria alternata	DHN-melanin	Polyketide pathway; ALM1/PKS1 cluster	UV protection, ROS detoxification, plant virulence	Cell wall of hyphae and conidia	Kimura &Tsuge (1993)
Bipolaris sorokiniana	DHN-melanin	PKS-mediated DHN pathway	Appressorial rigidity, host penetration, virulence	Appressoria, conidia	Howard & Valent (1996)
Exserohilum rostratum	DHN-melanin	Polyketide pathway (PKS homologs)	Environmental stress tolerance, pathogenicity	Cell wall	Revankar & Sutton (2010)
Cladosporium cladosporioides	DHN-melanin	PKS-based DHN pathway	Extreme stress resistance, airborne survival	Heavily melanized cell wall	Gadd (2007)
Aspergillus fumigatus	DHN-like melanin	PKS-based conidial melanin cluster (Alb1, Arp1, Arp2)	Immune evasion, UV protection	Conidia (not hyphae)	Langfelder *et al.* (2003)
Magnaporthe oryzae	DHN-melanin	PKS1-dependent DHN pathway	Appressorial turgor generation, plant infection	Appressoria	Howard & Valent (1996)
Cryptococcus neoformans	DOPA-melanin	Laccase-mediated oxidation of host-derived phenolics	Virulence, immune modulation, oxidative stress resistance	Cell wall and extracellular matrix	Eisenman & Casadevall (2012)

overexpression, or CRISPR-based genome editing is largely absent. Future studies integrating genome mining with reverse genetics will be essential to confirm gene function, uncover species-specific regulatory features, and resolve potential diversification of melanin pathways within the genus.

Equally important is the need to elucidate the regulatory networks controlling melanization. Transcriptomic and proteomic analyses under defined environmental and stress conditions—such as UV exposure, oxidative stress, nutrient limitation, and host-mimicking environments—could reveal how melanin biosynthesis is integrated into broader cellular signalling and stress-response systems. The roles of global regulators, chromatin remodelling factors, and epigenetic modifications in governing melanin gene cluster expression remain virtually unexplored in *Curvularia* and represent fertile ground for future investigation.

From a methodological standpoint, the lack of standardized protocols for melanin extraction, purification, and characterization poses a significant barrier to cross-study comparisons. Variations in extraction solvents, hydrolysis methods, and analytical techniques often yield melanins with differing physicochemical profiles, complicating interpretation and reproducibility. Establishing standardized workflows—coupled with advanced analytical approaches such as solid-state NMR, FTIR, Raman spectroscopy, and mass spectrometry—will be crucial for defining structure–function relationships of *Curvularia*-derived melanins.

Finally, the applied potential of Curvularia melanin remains largely untapped. Systematic evaluation of yield optimization, scalability, and functional performance in industrially relevant contexts is required to translate laboratory observations into practical applications. Integrating fungal biology with materials science, environmental engineering, and biomedical research will be key to realizing the full value of *Curvularia* as a sustainable source of functional melanin biopolymers.

In summary, *Curvularia* offers a compelling yet underexplored model for studying fungal melanization at the intersection of ecology, pathogenicity, and biotechnology. Focused efforts to close existing knowledge gaps will not only deepen our understanding of melanin biology but also open new avenues for innovation and application.

CONCLUSION

Melanin is a critical adaptive trait in fungi, contributing to environmental resilience, ecological success, and pathogenicity. In the genus *Curvularia*, melanin is a defining biological feature, evident in the characteristic pigmentation of conidia and hyphae and closely associated with the genus's ecological versatility and pathogenic range. This review provides a genus-focused synthesis of melanin research in *Curvularia*, integrating biochemical, genetic, ecological, and applied perspectives that have previously been addressed only in a fragmented manner.

Current evidence supports the predominance of DHN-melanin biosynthesis in *Curvularia*, mediated by conserved polyketide synthase–based pathways shared with related dematiaceous fungi. Inhibitor studies, comparative genomics, and phenotypic observations collectively indicate a functional and evolutionarily conserved melanization machinery, with melanin extensively distributed in both hyphae and conidia, suggesting a broad protective role.

Functionally, melanin enhances tolerance to environmental stress, promotes persistence in soil ecosystems, and contributes to plant and human pathogenicity by facilitating host interactions and resistance to oxidative and antifungal stress. Beyond its biological roles, *Curvularia*-derived melanin represents a promising yet underexplored biotechnological resource, with potential applications in environmental remediation, biomaterials, and biomedicine.

Despite these insights, significant gaps remain in understanding the molecular regulation of melanization in *Curvularia*. Future studies integrating functional genomics, transcriptomics, and standardized analytical approaches will be essential to advance both fundamental knowledge and applied exploitation. Overall, *Curvularia* occupies a unique position among melanized fungi, linking ecological adaptability, pathogenic potential, and emerging biotechnological value.

DECLARATION

Conflict of Interest. Authordeclares no conflict of interest

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