

Review

Fungal Hydrophobins: Taxonomic Distribution, Functional Roles, Physicochemical Properties, and Biotechnological Applications

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Abstract

Hydrophobins are small, cysteine-rich amphipathic proteins predominantly produced by filamentous fungi, known for their ability to self-assemble at hydrophobic–hydrophilic interfaces. These proteins are essential for fungal development, surface interactions, pathogenicity, and environmental adaptation, and they have attracted growing interest for biotechnological applications. In this work, we provide a narrative review of fungal hydrophobins, based on a systematic literature search and manual curation of eligible studies integrated with protein database records from Ascomycota and Basidiomycota. Information was compiled from peer-reviewed publications selected according to predefined eligibility criteria and complemented with UniProt records, covering taxonomic distribution, functional and biophysical properties, and physiological and pathogenic roles. Significant diversity in molecular features and physicochemical profiles was observed, indicating functional specialization across different ecological niches and lifestyles. Additionally, the compiled data highlight various biotechnological applications, such as surface modification, enzyme immobilization, drug delivery systems, biomaterial development, and environmentally sustainable technologies. By consolidating molecular, functional, and applied information across a wide range of fungal species, this review provides a comprehensive reference framework for hydrophobin research and biotechnological innovation.

Keywords: hydrophobins; filamentous fungi; physicochemical properties; amphipathic proteins; surface-active biomolecules



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1. Introduction

Hydrophobins are small amphipathic proteins predominantly produced by fungi of the phyla Ascomycota and Basidiomycota, characterized by their ability to self-assemble at hydrophobic–hydrophilic interfaces, forming structured layers that alter surface properties. As surface-active molecules, they play essential roles in fungal growth and development, contributing to the formation of aerial hyphae, spore adhesion to surfaces, evasion of host immune responses, and interactions with the environment (Figure 1) [1].

Hydrophobin genes have also been identified in dimorphic fungi such as *Paracoccidioides brasiliensis* and *Ustilago maydis*, where their expression is predominantly associated with the filamentous growth phase rather than the yeast morphotype [2,3]. This observation reinforces the link between hydrophobin production and filamentous development and suggests that fungi restricted to yeast-form growth lack these proteins.

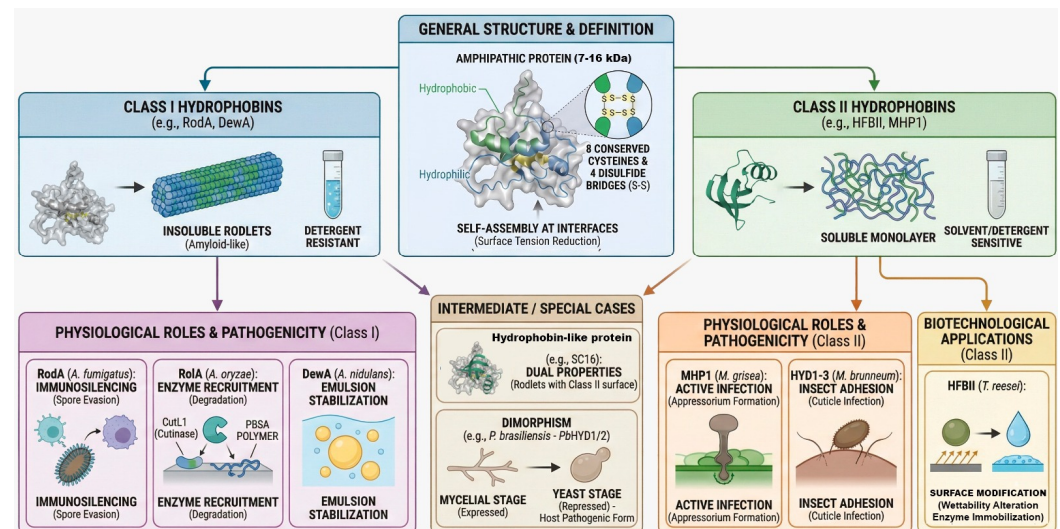


Figure 1. Main structural classification, functional diversity, and applications of fungal hydrophobins. Typically, the molecular mass of hydrophobins ranges from 7 to 16 kDa, but there are hydrophobin-like proteins with higher molecular masses, containing additional protein domains or extended sequence insertions (See Supplementary Tables S1 and S2).

Typically ranging from 7 to 16 kDa and composed of approximately 70 to 130 amino acid residues, these proteins are stabilized by four conserved intramolecular disulfide bridges formed by eight cysteine residues. Many structurally characterized hydrophobins adopt a compact β -barrel-like fold, although structural variations occur among different classes and species. Despite their small size, they exhibit structural stability and surface activity, driven by the spatial segregation of hydrophobic and hydrophilic regions that define their amphipathic character. These molecular features underpin their ability to assemble at hydrophilic–hydrophobic interfaces, a property central to their roles in both natural and technological applications [1,4].

Based on structural and physicochemical properties, hydrophobins can be classified into two major groups. The Class I hydrophobins form highly stable, insoluble rodlet layers that resist chemical and thermal disruption, whereas Class II hydrophobins are more soluble, forming flexible monolayers at interfaces [1,5]. Both classes share the conserved cysteine pattern but differ in solubility and aggregation behavior [6].

Hydrophobins that cannot be assigned to either Class I or Class II represent a subset of proteins with atypical biophysical and self-assembly properties, but exhibiting cysteine patterns, disulfide bond topologies, and surface activity consistent with the hydrophobin functional paradigm. These unconventional hydrophobins exhibit variable aggregation behaviors that differ from the canonical rodlet layers typical of Class I and from the soluble, reversible films observed for Class II. Although some authors have proposed classifying it as Class III (or pseudo-Class I), this is not universally accepted. Their structural organization and surface assembly are often highly responsive to environmental conditions, including pH, ionic strength, and the presence of amphiphilic molecules such as lipids or polysaccharides [7].

The growing interest in these proteins reflects their multifaceted roles in fungal biology, development, and pathogenesis, as well as their biotechnological applications. Hydrophobins have been studied as stabilizers in emulsions, for coating nanoparticles, for immobilizing enzymes, and for improving the solubility and bioavailability of hydrophobic compounds [8,9]. Understanding the structural diversity and ecological functions of hydrophobins provides a foundation for expanding their use in medicine, materials science, and environmental biotechnology [10]. Therefore, a comprehensive and up-to-date review

of fungal hydrophobins contributes not only to understanding their biological relevance but also to advancing the development of efficient and sustainable technologies.

2. Review Design

This study presents a curated narrative review based on a literature search, focusing on fungal hydrophobins and emphasizing their taxonomic distribution, functional roles, physicochemical characteristics, and biotechnological applications across the phyla Ascomycota and Basidiomycota. A literature search was conducted in PubMed, Web of Science, and Scopus, complemented by protein records retrieved from UniProt. The search included articles published up to February 2026 using combinations of the terms hydrophobin, fungal hydrophobin, Ascomycota, Basidiomycota, structure, function, and biotechnology.

Eligible studies included original research articles reporting (i) gene identification and annotation, (ii) expression evidence, (iii) biochemical characterization, (iv) structural and self-assembly properties, and/or (v) functional validation *in vivo* or *in vitro*. After screening titles, abstracts, and full texts for relevance, the references meeting these criteria were used as the primary source for selecting hydrophobin entries included in the compiled tables. Hydrophobin entries were subsequently curated and integrated with protein database information to generate the comparative datasets.

All data generated in this study consist of curated information derived from publicly available peer-reviewed publications and public protein databases (e.g., UniProt). The curated dataset is fully reported in the manuscript tables. Protein identifiers and accession numbers are provided whenever available to ensure reproducibility and traceability. For some hydrophobins, accession numbers could not be included because these proteins were identified only in the original publications and are not currently annotated in the UniProt database. For each hydrophobin, the following metadata were compiled, when available: UniProt entry, organism name, taxonomic placement, gene name and synonyms, reported functional and biophysical properties, experimental evidence described in the literature, and accession identifiers (including nucleotide accessions when reported in UniProt) (Supplementary Tables S1 and S2).

The curated protein sequences were subsequently used for sequence alignment and phylogenetic analyses to investigate the evolutionary relationships among fungal hydrophobins. Sequence alignments were performed using the MUSCLE algorithm [11] with default gap penalties (gap open penalty -2.90 , gap extension penalty 0.00) and the UPGMA clustering method, implemented in the MEGA 12 software [12]. To minimize statistical noise generated by highly divergent terminal regions, a partial deletion approach was applied with a 95% site coverage cutoff. This strict filtering parameter resulted in final alignments comprising 45 conserved amino acid positions for the Ascomycetes dataset (191 sequences) and 89 positions for the Basidiomycetes dataset (115 sequences).

Evolutionary analyses were conducted using the Maximum Likelihood (ML) method based on the Jones-Taylor-Thornton (JTT) matrix-based substitution model [13] with uniform rates among sites. The initial trees for the heuristic search were generated automatically by applying Neighbor-Joining [14] and Maximum Parsimony (MP) algorithms to a matrix of pairwise distances computed using the p-distance model [15], subsequently selecting the topology with the superior log-likelihood value.

Statistical support for the clades was evaluated using an adaptive standard bootstrap test, which achieved convergence at 120 replicates for the Ascomycetes tree and 128 replicates for the Basidiomycetes tree. All phylogenetic computations were performed in MEGA 12 utilizing up to 7 parallel computing threads. The resulting original ML trees, conserving branch lengths and bootstrap support values, were exported in Newick format and graphi-

cally rendered using the Interactive Tree Of Life (iTOL) web platform [16]. The resulting phylogenetic analyses are presented in Supplementary Figures S1 and S2.

3. Hydrophobins in Ascomycota

The phylum Ascomycota comprises a genomically diverse group of fungi occupying a broad range of ecological niches, including saprotrophic, symbiotic, and pathogenic lifestyles [5,17–42]. Members of this phylum are also of considerable industrial importance due to their production of enzymes, antibiotics, and fermented products. Within Ascomycota, hydrophobins constitute one of the most extensively characterized protein families, displaying remarkable structural diversity and functional specialization associated with fungal development, environmental adaptation, host interactions, and biotechnological applications [43]. To organize and contextualize the available data, Table S1 compiles hydrophobins identified in Ascomycota, integrating taxonomic information with molecular and physicochemical features, including amino acid length, molecular weight, solubility, isoelectric point, GRAVY score, Pfam domain classification, subcellular localization, and accession identifiers. Also lists hydrophobins not deposited in the UniProt platform and includes proteins annotated as putative hydrophobins. Additionally, to complement the molecular and physicochemical dataset, Supplementary Figure S1 presents a phylogenetic analysis of Ascomycota hydrophobins, which are described throughout this review. Collectively, these data provide a comprehensive overview that emphasizes the broad functional diversity of Ascomycota hydrophobins, which are involved in processes such as fruiting body formation, hyphal organization, surface attachment, environmental resilience, and interactions with hosts.

3.1. Physiological Roles of Ascomycota Hydrophobins

The hydrophobins play essential roles in fungal morphogenesis and in modulating surface properties, serving as key determinants of the transition between submerged and aerial growth, substrate adhesion, and the stability of reproductive structures. A previous comparative genomic analysis of seven *Aspergillus* species identified 50 putative hydrophobins based on cysteine motifs, protein size, secretion signals, and hydropathy profiles, although most remain experimentally uncharacterized [44]. These data were subsequently integrated into functional genomics analyses, enabling a deeper understanding of regulatory and gene expression mechanisms within the genus [45].

In *A. nidulans*, six hydrophobin genes (*RodA*, *DewA–E*) have been identified and characterized. *RodA* is the main structural component of the conidial rodlet layer, responsible for hydrophobicity and resistance to environmental stresses, while *DewA–E* act in a complementary manner to protect against desiccation and ultraviolet radiation and to promote adhesion to substrates [46,47]. The *RodA* gene (AN8803), which encodes a 157-amino-acid protein, is transcriptionally regulated by *BrlA* and localized exclusively in the conidial wall, functioning synergistically with *DewA* to ensure spore hydrophobicity [48,49]. In vitro assays show that AnRodA and DewA can form fibrillar structures similar to those seen in vivo. Additionally, *RodF* and *RodG* display intermediate characteristics and cannot be classified as either Class I or Class II, which may be linked to spore adhesion and dispersal [43,50,51].

Hydrophobin structural conservation among *Aspergillus* species is evident in *A. fumigatus*, where the hydrophobin HYP1 can restore the rodlet phenotype in *RodA*-deficient strains. *A. fumigatus* also possesses at least seven hydrophobin genes (*RodA–RodG*), with *AfRodA* functionally similar to its homologues in *A. nidulans* [43,52]. In *A. oryzae*, the Class I hydrophobin *RolA* (*HypA*) forms Langmuir films and stable fibrillar assemblies through hydrophobic interactions mediated by Cys–Cys loops and zeta potential. This

property confers amphipathic properties that support aerial hyphae formation, adhesion, and biofilm stability [4,46,51]. Another *A. oryzae* hydrophobin, HsbA, contributes to spore hydrophobicity and adhesion [43,53,54].

In *Neurospora crassa*, the Class I hydrophobin EAS is among the most extensively studied examples. Its ability to form rodlets and amphipathic layers confers resistance to spores and facilitates aerial dispersal, demonstrating remarkable stability under varying pH and temperature conditions [55,56].

The following table summarizes the physiological roles of hydrophobins from other Ascomycota members (Table 1):

Table 1. Physiological Roles of Ascomycota Hydrophobins.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Aspergillus fumigatus</i>	RodA (P41746), RodB (E9QT94), RodC (Q4WBR8) and RodE (Q4WC31): Class I. RodD (Q4WE22), RodF (Q4WEK0) and RodG (Q4X055): hydrophobin-like protein.	Involvement on Surface/spore hydrophobicity, fungal growth and development, and environmental stress tolerance. <i>RodA</i> forms rodlets on the conidial surface. <i>RodB-G</i> do not participate in rodlet formation.	[7,57–62]
<i>Aspergillus nidulans</i>	DewA (P52750), DewB (Q5BC93), DewC (Q5AZ79), DewE (Q5AVZ1) and RodA (P28346): Class I. DewD (Q5BEU0): hydrophobin-like protein.	Involvement in surface/spore hydrophobicity and fungal dispersal. <i>DewD</i> and <i>DewE</i> are expressed in hyphae; <i>DewA</i> , <i>DewB</i> and <i>DewC</i> are mainly associated with conidial surfaces. <i>DewC</i> contributes to growth on lignocellulose. <i>RodA</i> is essential for the formation of hydrophobic rodlet layers on asexual spores and for conidial transfer. <i>RodA</i> indirectly enhances lignocellulose utilization by promoting close substrate–enzyme–fungus interactions.	[43,46,47,50, 63–67]
<i>Beauveria bassiana</i>	Hyd1A (J4KPV6), Hyd1B (J4W2A8), Hyd 1C (J5JJC1), Hyd 1D (J4VS95), Hyd 1E (J4UGK4) and Hyd 1F (J4UJ50): Class I. Hyd 2A (J4WDT5), Hyd2B (J5JTB1) and Hyd2C (J4WMI6): Class II.	Involvement in cell wall hydrophobicity and fungal development. <i>Hyd1A</i> and <i>Hyd1B</i> form and coregulate the spore coat rodlet layer essential for conidial hydrophobicity, whereas <i>Hyd1C-F</i> and <i>Hyd2A-B</i> are not required for conidial hydrophobicity. <i>Hyd1B</i> participates in pre-penetration or surface conditioning processes, and <i>Hyd2C</i> contributes to asexual fungal development.	[68,69]
<i>Botryotinia fuckeliana</i>	Bhp1 (A0A384JA57), Bhp2 (A0A384JW35) and Bhp3 (A0A384JJM8): Class II.	<i>Bhp1</i> is required for maintaining conidial and hyphal hydrophobicity and for normal conidiation. <i>Bhp3</i> contributes to conidial morphology and chain formation. <i>Bhp2</i> shows no detectable role in hydrophobicity, growth or sporulation, suggesting a redundant or condition-specific function.	[70,71]

Table 1. Cont.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Cladosporium fulvum</i>	Hcf-1 (Q00367), Hcf-2 (O94217), Hcf-3 (Q7Z9L5) and Hcf-4: Class I. Hcf-5 (O94203) and Hcf-6 (Q9C2X0): Class II.	Involvement in surface hydrophobicity, conidial development, germination and fungal adhesion. <i>HCF-1</i> forms part of the rodlet layer and conidial hydrophobicity and water-mediated spore dispersal. <i>HCF-2</i> cell surface hydrophobicity. <i>HCF-3</i> involved in maintenance of hyphal integrity in planta. <i>HCF-4</i> may assist adhesion within the apoplast. <i>HCF-5</i> is strongly upregulated during sporulation under nutrient-depleted conditions and shows stage- and environment-dependent regulation, whereas <i>HCF-6</i> is involved in fungal adhesion.	[72,73]
<i>Claviceps fusiformis</i>	TH1 (Q9UVI4): Class II.	Involvement in the reduction of water surface tension at the water–air interface and contribution to aerial hyphae formation.	[74]
<i>Cordyceps militaris</i>	CmHyd1 (A0A2H4SBS0) and CmHyd2 (A0A2H4SHM4): Class II. CmHyd3 (A0A2H4SKW2) and CmHyd4 (A0A2H4SI69): Class I.	Involvement in conidiation, aerial hyphae formation, stress tolerance and fruiting body development. <i>CmHYD1</i> contributes to osmotic, oxidative and thermal stress tolerance. <i>CmHYD4</i> negatively regulates aerial mycelial growth, carotenoid and adenosine synthesis and oxidant-stress resistance. <i>CmHYD2</i> and <i>CmHYD3</i> contribute to fruiting body development, and <i>CmHYD2</i> contributes to the formation of aerial hyphae.	[75–77]
<i>Fusarium graminearum</i>	FgHyd1-4 (N/A): Class I. FgHyd5 (N/A): Class II.	Involvement in conidiation, secondary metabolism and modulation of aerial structure properties. <i>FgHyd1</i> , <i>FgHyd2</i> and <i>FgHyd4</i> are expressed in aerial and submerged structures. <i>FgHyd3</i> is exclusively expressed in aerial hyphae on solid surfaces. <i>FgHyd2</i> and <i>FgHyd3</i> contribute to hyphal penetration. <i>FgHyd5</i> specifically affects aerial mycelial hydrophobicity.	[78–80]
<i>Magnaporthe grisea</i>	Mhp1 (N/A): Class II.	Involvement in conidial hydrophobicity, conidiation, appressorium induction, plant colonization. and fungal development.	[81]
<i>Neurospora crassa</i>	Eas (Q04571): Class I.	Self-assembly into cross- β amyloid rodlets, promotion of spore formation and dispersal, and adaptation to environmental and circadian cues.	[55,82]

Table 1. Cont.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Penicillium expansum</i>	HfbA (A0A0A2K7M3), HfbB (A0A0A2JSZ6), HfbC (A0A0A2IC94), HfbD (A0A0A2K253), HfbE (A0A0A2KI06) and HfbF (A0A0A2JK41): Class I. HfbG (A0A0A2J434): Class II.	Involvement in surface hydrophobicity, conidiophore development and spore dispersal. <i>HfbA</i> is uniquely expressed in spores and is essential for hydrophobicity, spore morphology and both air and water dispersal. <i>HfbB</i> is expressed during conidiophore development and influences hydrophobicity. <i>HfbC–HfbF</i> are expressed during hyphal growth. <i>HfbG</i> is expressed during hyphal growth.	[83]
<i>Trichoderma guizhouense</i>	Hfb2 (N/A), Hfb3 (A0A1T3CWR1), Hfb4 (A0A1T3C949) and Hfb10 (A0A5P8PB18): Class II.	Involvement in light-responsive regulation and modulation of spore-surface hydrophobicity during asexual development. All are induced by blue light in a BLR1 and ENV1-dependent manner. <i>hfb2</i> is moderately expressed during development. <i>hfb3</i> shows low basal expression and indirect light-mediated induction. <i>hfb4</i> is more expressed during development and plays a prominent role in spore-surface hydrophobicity. <i>hfb10</i> is the most expressed gene and uniquely depends on the HOG1 MAPK pathway in addition to BLR1 and ENV1, positioning it centrally in light-responsive hydrophobin production.	[84,85]
<i>Trichoderma harzianum</i>	Qid3 (P52755), Srh1 (P79072), Hfb2 (N/A), Hfb 2-a2 (N/A), Hfb3 (A0A2N1LQG4), Hfb4 (A0A2N1LTE2), Hfb7 (A0A0B5H3H0) and Hfb10 (A0A5P8PAX6): Class II or hydrophobin-like protein.	Involvement in plant interaction, adhesion, spore formation, stress response, and dispersal regulation. <i>Qid3</i> is induced by chitin and nutrient deprivation, influencing cytokinesis. <i>Srh1</i> is associated with sporulation. <i>HFB2</i> and <i>HFB3</i> exhibit low basal expression, suggesting condition-specific roles. <i>HFB2-a2</i> shows enhanced adsorption to hydrophobic surfaces. <i>HFB4</i> and <i>HFB10</i> regulate aerial spore dispersal. <i>HFB7</i> likely functions in oxidative-stress tolerance and environmental establishment.	[86–93]
<i>Trichoderma reesei</i>	hfb1 (P52754), hfb2 (P79073) and hfb3 (G0RVE5): Class II.	Involvement in hyphal development, aerial mycelium formation, sporulation and surface hydrophobicity. <i>hfb1</i> is central to aerial hyphae formation. <i>hfb2</i> is required for efficient sporulation. <i>Hfb3</i> contributes to vegetative growth and asexual development.	[94–98]

Table 1. Cont.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Xanthoria ectaneoides</i>	XEH1 (Q9HFD2): Class I.	Involvement in rodlet formation and species delimitation, with pronounced sequence polymorphism among Mediterranean populations providing a molecular signature for distinguishing <i>Xanthoria</i> species.	[99,100]
<i>Xanthoria parietina</i>	XPH1 (Q9HFD1): Class I.	Involvement in rodlet-layer formation and maintenance of population cohesion, with high genetic conservation supporting its use as a marker for species boundary assessments.	[99–101]

3.2. Pathogenicity Roles of Ascomycota Hydrophobins

Comparative genomic analyses of *A. fumigatus*, *A. nidulans*, and *A. oryzae* have revealed substantial genetic diversity among these species, providing an evolutionary framework for understanding the diversification of hydrophobin functions and their adaptation to distinct ecological niches [102–104]. In *A. fumigatus*, hydrophobins form densely organized fibrillar structures that act as both physical and immunological barriers, masking epitopes recognized by the host immune system. Their expression is induced during sporulation, and deletion of the *RodA* gene results in conidia that lose hydrophobicity, exhibit increased permeability, and are more susceptible to antifungal agents, highlighting their protective function and importance in pathogenicity [7,105].

Δ *RodA* mutants in *A. fumigatus* exhibit structurally disorganized conidia that are more vulnerable to antifungal compounds and phagocytosis, confirming their role as an immune barrier [106]. The Class I hydrophobin RodB is expressed in biofilms and appears to participate in hyphal adhesion and cohesion, although it is not involved in rodlet formation in *A. fumigatus* [43]. The cysteine-rich proteins RodC, RodD, and RodE are also expressed during sporulation and likely play complementary roles in protecting and maintaining the cell wall, under conditions relevant to environmental adaptation and host interaction [7].

Functional diversity among hydrophobins in Ascomycota is further evidenced by the coexistence of multiple classes within the same organism. In *C. fulvum*, six hydrophobins (HCF-1 to HCF-6) have been identified, each with complementary functions and distinct structural distributions [72,73,107]. The first four belong to Class I and are located in conidia and aerial hyphae, whereas HCF-5 and HCF-6, both Class II, are associated with surface growth and adhesion during infection [108–110]. Among these, *C. fulvum* HCF-1 participates in conidial dispersal in aqueous environments, while HCF-6 is involved in adhesion and penetration into plant tissues; they contribute to the species’ pathogenicity. Constitutive expression of HCF-6 in mycelia, which decreases under carbon limitation, suggests that hydrophobin regulation depends on physiological and metabolic factors, reinforcing their adaptive character in mediating fungal–environment interactions [111].

In the genus *Trichoderma*, many species are mycoparasitic and widely used as biological control agents against plant pathogens. Species of *Trichoderma* possess one of the largest repertoires of hydrophobin-encoding genes among fungi, particularly Class II members [112], supporting roles in development, dispersal, and plant-associated interactions [85,113]. A Class I hydrophobin identified in *T. asperellum* is involved in root colonization and rhizosphere interaction [113], while hydrophobins such as HYTLO1 from *T. longibrachiatum* contribute to early plant–fungus signaling [114].

In the dermatophyte *Arthroderma benhamiae*, a causative agent of superficial mycoses in humans and animals [115], the hydrophobin HypA is the dominant cell-surface protein. HypA forms the rodlet layer that maintains conidial hydrophobicity and modulates host immune recognition. Deletion of HypA increases neutrophil activation and immune mediator release, indicating that this hydrophobin contributes to immune evasion during infection [116].

Among phytopathogenic fungi, the genus *F. harbours* multiple Class I and II hydrophobins. In *F. graminearum*, proteins such as FgHyd1–5 are regulated by G-protein complexes and the velvet system, participating in conidiogenesis, secondary-metabolite production, and host colonization [79]. In *F. culmorum*, the hydrophobin FcHyd3p facilitates adhesion to plant tissues and initiates infection [117].

In the genus *Cladosporium*, the species *C. fulvum* is an important biotrophic pathogen of tomato and a model for plant–microbe interactions. In the mango pathogen *Colletotrichum asianum*, hydrophobins contribute to early infection processes. The hydrophobin gene 14730 is involved in spore germination on hydrophobic plant surfaces and is regulated by CaGα1 signaling, suggesting a role in surface sensing and host penetration during infection [118].

In *Penicillium expansum*, the causal agent of blue mold in pome fruits, the hydrophobin HfbA is a major determinant of conidial surface hydrophobicity and promotes spore dispersal through both air and water. Deletion of *hfbA* alters conidial and conidiophore morphology, reducing dispersal efficiency and highlighting its essential role in fungal dissemination and environmental fitness [83].

In the *Magnaporthe* genus, hydrophobins play essential roles in morphological differentiation and plant infection. In *M. grisea*, the Class I hydrophobin MPG1 is required for appressorium formation, a penetration structure used to invade leaf tissues and that functions as a morphogenetic signal for surface recognition [119]. The Class II hydrophobin MHP1 is involved in conidial germination and the maintenance of virulence, and is expressed during infectious growth [81].

In entomopathogenic fungi such as *M. anisopliae* and *B. bassiana*, hydrophobins are directly linked to insect infection. In *M. anisopliae*, the Class I hydrophobin Hyd1 is a key mediator for cuticle adhesion, environmental stress resistance, and virulence, while Hyd2 and Hyd3 perform complementary functions [120,121]. In *B. bassiana*, Hyd1 and Hyd2 are structural components of the conidial wall and influence germination, conidiogenesis, and symbiotic interaction with plant roots [122,123].

Another entomopathogenic fungus, *Beauveria bassiana*, is used as a biological control agent against insect pests and disease vectors. Nine hydrophobins have been identified, including six Class I (Hyd1A–F) and three Class II proteins (Hyd2A–C). These proteins localize mainly on the cell walls of aerial hyphae and conidia, while accumulating in vacuoles and vesicles in submerged hyphae and blastospores, suggesting roles in surface hydrophobicity and developmental differentiation [68,69].

In the *Ophiostoma* genus, cerato-ulmin (CU), a Class II hydrophobin, is associated with Dutch elm disease. Although its toxic effects remain controversial, CU has been proposed to facilitate disease development by moving freely through the aqueous environment of the xylem in infected elm trees, where it may contribute to host damage. In addition, CU promotes the formation of hydrophobic biofilms at air–water interfaces, enhancing fungal growth and adhesion to plant tissues [124].

In *Verticillium dahliae*, a soilborne pathogen responsible for vascular wilt in numerous crops, the hydrophobin VdHP1 contributes to fungal morphogenesis and host interaction. VdHP1 influences surface hydrophobicity and can induce plant immune responses and cell death. It also participates in fungal adaptability and regulation of pathogenicity during plant colonization [125].

Among dimorphic fungi, *P. brasiliensis* expresses the Class I hydrophobins PbHyd1 and PbHyd2 during the mycelial phase. Both are related to the formation of aerial structures and adhesion of hyphae to hydrophobic surfaces, processes that are fundamental to the initiation of infection [126].

Extremophilic species such as *S. alkalinus* produce hydrophobins adapted to alkaline environments. The Class II hydrophobin Sa-HFB1 exhibits antifungal activity against opportunistic pathogens, including *C. neoformans*, suggesting a defensive role and potential pharmaceutical application for this protein [127]. In the following table, the pathogenicity-related roles of hydrophobins in Ascomycota members are summarized (Table 2):

Table 2. Pathogenicity Roles of Ascomycota Hydrophobins.

Organism	Gene (Accession) and Class	Pathogenicity Roles	References
<i>Arthroderma benhamiae</i>	HypA (D4ARW0): Class I.	Masks fungal cell wall components and prevents recognition by the host immune system, thereby influencing disease progression by reducing immune detection of pathogen-specific biopolymers.	[116]
<i>Aspergillus flavus</i>	-	Associated with corneal infection	[128]
<i>Aspergillus fumigatus</i>	RodA (P41746), RodB (E9QT94), RodC (Q4WBR8) and RodE (Q4WC31): Class I. RodD (Q4WE22): RodF (Q4WEK0) and RodG (Q4X055): hydrophobin-like protein.	<i>RodA</i> can mask immunogenic cell-wall components and prevents early Dectin-1 and Dectin-2 recognition, allowing germination prior to immune detection; its removal promotes recognition by dendritic cells and alveolar macrophages, highlighting <i>RodA</i> secretion as a potential antifungal target. <i>RodB</i> -G contribute to rodlet-layer integrity, and defects or alterations in these proteins increase fungal sensitivity to antifungal agents, supporting their relevance for the development of targeted antifungal therapies.	[7,57–62]
<i>Aspergillus nidulans</i>	RodA (P28346): Class I.	Provides immune evasion, while acting as a virulence factor by masking conidial recognition by the host receptors Dectin-1 and Dectin-2.	[57,59,60]
<i>Cladosporium herbarum</i>	HCh-1 (Q8NIN9): Class I.	Exhibits IgE-binding allergenic properties, and recombinant forms of this fungal allergen improve the sensitivity and specificity of fungal allergy diagnosis.	[129]
<i>Colletotrichum asianum</i>	Gene 14730 (A0A8H3W1T0): Class not informed	Proposed to mediate germination on hydrophobic surfaces, acting downstream of CaGα1-dependent GPCR signaling and enabling sensing of hydrophobic cues and initiating pathogenicity-related germination responses.	[118]

Table 2. Cont.

Organism	Gene (Accession) and Class	Pathogenicity Roles	References
<i>Colletotrichum siamense</i>	CsHydr1 (A0A6G6VYL3): Class I.	Required for full virulence on rubber tree leaves.	[130]
<i>Cordyceps militaris</i>	CmHYD1 (A0A2H4SBS0): Class II.	Regulates conidiation and cuticle-bypassing infection by modulating frq and vosA transcription and by influencing primordium formation through MAPK signaling. It also contributes to osmotic, oxidative, and thermal stress tolerance, acts as a defensive barrier against <i>Calcarisporium cordycipiticola</i> , and controls AreA transcription via a developmental positive feedback loop.	[75,76]
<i>Cryphonectria parasitica</i>	Cryparin (P52753): Class II.	The most abundant protein produced in liquid culture and plays a key role in the fitness of this plant pathogen by enabling the eruption of fungal fruiting bodies through the host tree bark.	[131,132]
<i>Fusarium verticillioides</i>	Hyd1 (Q6YF32), Hyd 2 (Q6YF31) and Hyd 3 (Q6YF30): Class I. Hyd 4 (Q6YF29) and Hyd 5 (Q6YD93): Class II.	Microconidial chain formation, spore–surface interaction, and adhesion to hydrophobic epicuticles are compatible with insecticides. and insect-associated virulence. <i>HYD1</i> contributes to attachment to waxy epicuticles. <i>HYD2</i> supports proper chain architecture and adhesion to hydrophobic surfaces. <i>HYD3</i> participates in cuticle adhesion and supports epizootic spread in insect hosts. <i>HYD4</i> contributes to spore attachment to insect cuticles. <i>HYD5</i> regulates hydrophobic spore–epicuticle interactions and enhances insect-related virulence.	[133,134]
<i>Magnaporthe grisea</i>	MPG1 (P52751): Class I.	Highly expressed during early host infection and appressorium morphogenesis, with expression dependent on CPKA and NPR1 regulatory pathways.	[119,135,136]
<i>Metarhizium acridum</i>	HYD3 (E9DZB1): Class I.	It is located on the conidial surface and specifically activates humoral and cellular immunity in <i>Locusta migratoria manilensis</i> , enhancing resistance to fungal pathogens without affecting non-host insects.	[137]
<i>Metarhizium anisopliae</i>	ssgA (P52752): Class I.	Hydrophobic-surface sensing, infection structure differentiation and secretion of penetration enzymes during insect infection. It is induced by nutrient deprivation and late conidiation and is expressed across the pH range typical of insect cuticles.	[120,138,139]

Table 2. Cont.

Organism	Gene (Accession) and Class	Pathogenicity Roles	References
<i>Metarhizium robertsii</i>	hyd1 (E9FDE9) and hyd2 (E9FBT2): Class I. Hyd3 (E9EN44): Class II.	Conidial hydrophobicity, adhesion to insect cuticle, sporulation, stress tolerance and pathogenicity. <i>Hyd1</i> is essential for insect virulence, with deletion causing reduced sporulation, increased hydrophilicity, impaired stress tolerance and disorganized rodlet bundles, although it has a negligible role in hyphal growth and asexual development. <i>Hyd2</i> and <i>Hyd3</i> show no significant role.	[121]
<i>Oidiodendron maius</i>	OmSSP1 (A0A0C3D4E3): Class I hydrophobin-like.	Symbiosis establishment and promotion of ericoid mycorrhiza formation, acting as an effector required for efficient colonization of <i>Vaccinium myrtillus</i> roots.	[140]
<i>Ophiostoma novo-ulmi</i>	Cerato-ulmin (CU) (Q06153): Class II.	Increases surface hydrophobicity and adhesion of yeast-like propagules, protects infectious cells against desiccation, and may induce Dutch elm disease-like wilt symptoms when expressed in nonpathogenic strains, functioning as a parasitic fitness factor whose contribution to virulence depends on the genetic background.	[141–144]
<i>Paracoccidioides brasiliensis</i>	Pbhyd1 (Q8NJJQ1) and Pbhyd2 (Q6T935): Class I-like hydrophobins.	Regulation of morphological switching and early dimorphism-associated remodeling. Both are mycelium-specific and strongly induced during the early mycelium-to-yeast transition, suggesting involvement in growth and differentiation processes.	[126]
<i>Penicillium camembertii</i>	RodA (Q1I187): Class I.	ACTS in cell surface hydrophobicity, promotion of conidiation under aerial conditions and formation of a rodlet layer that masks airborne conidia from immune recognition.	[145,146]
<i>Pyricularia oryzae</i>	MPG1 (P52751): Class I. MHP1 (N/A): Class II.	Rodlet-layer assembly, hydrophobic-surface sensing, conidiation, pathogenicity and surface-associated enzyme retention. <i>MPG1</i> is highly induced during appressorium formation, plant infection and nutrient starvation, directing rodlet formation on conidia and mediating surface sensing for appressorium development. <i>MHP1</i> assembles into a non-fibrillar film and participates in retention of cutinase 2 at hydrophobic interfaces.	[119,135,147,148]

Table 2. Cont.

Organism	Gene (Accession) and Class	Pathogenicity Roles	References
<i>Trichoderma virens</i>	TVHYDII1 (N/A): Class II.	Functions as an effector protein, promoting plant root colonization and antagonism against <i>Rhizoctonia solani</i> , likely aiding immune evasion, protection from plant defenses, and establishment of beneficial fungus–plant interactions.	[149]
<i>Verticillium dahliae</i>	VdHP1 (N/A): Class II.	Triggers plant cell death and immune activation. Acts as a negative regulator of virulence, modulating development, adaptability, and pathogenicity.	[125]

3.3. Biotechnological Applications of Hydrophobins from Ascomycota

The industrial species *A. oryzae* produces the Class I hydrophobin RolA, which plays a unique role in polymer degradation and in the interface between biocatalysis and surface engineering. When cultivated in media containing the biodegradable polyester PBSA (polybutylene succinate-co-adipate), RolA is highly expressed and localized at the fungal cell wall, where it binds to hydrophobic surfaces and recruits the cutinase CutL1, catalyzing polymer hydrolysis. This cooperative mechanism between RolA and CutL1 exemplifies how hydrophobins can function not only as structural elements but also as mediators of enzymatic localization and interfacial catalysis [53].

Subsequent studies deepened the understanding of the RolA and CutL1 system. Specific ionic interactions between acidic residues, such as Asp142, Asp171, and Glu31, in CutL1, and basic residues, such as His31 and Lys34, in RolA that regulate enzymatic anchoring, are modulated by physicochemical parameters such as pH and ionic strength [4,150].

The ability of RolA to form organized films and alter surface properties also makes it relevant in biomedical and nanotechnological applications. Hydrophobin coatings enhance cellular uptake and the antitumor efficacy of curcumin nanoparticles without altering the drug-release profile [151]. Similarly, the functionalization of clay nanotubes with hydrophobins has yielded more efficient sustained-release systems for doxorubicin, improving dispersion and in vitro cytotoxicity [152].

In more complex therapeutic systems, the hydrophobin GLP-1 complexes extend the half-life of bioactive peptides by protecting them from enzymatic degradation, an effect associated with the high conformational stability of Class I hydrophobins, such as those from *A. fumigatus* [153]. The ability of these proteins to form stable amphipathic films and to modulate wettability (assessed by contact angle measurements) has been explored in the design of water-responsive surfaces and gas-exchange control devices [9]. In lipid-based systems, coating liposomes and niosomes with hydrophobins such as RodA from *A. fumigatus*, which represents a promising alternative to PEGylation, provides greater selectivity and biocompatibility to drug formulations such as doxorubicin, while reducing immune recognition [154].

On an applied scale, simple techniques such as dip-casting with RolA enable the stable anchoring of enzymes, antibodies, and other biomolecules on solid surfaces, creating robust platforms for biosensors, implant coatings, and diagnostic devices [155]. Comparative mapping of hydrophobins among *Aspergillus* species therefore provides a valuable set of structural targets for the rational design of coatings and nanosystems with predictable performance [43–45].

In *Trichoderma*, a genus widely exploited for its biotechnological potential, Class II hydrophobins predominate, including HFBI, HFBII, HFBIII, HFB4, and HFB7, which are involved in biocontrol, adhesion, and emulsion stabilization. HFBI and HFBII, in particular, display a high capacity for self-assembly at air–water interfaces and have been used for nanoparticle functionalization and recombinant protein purification systems [5,85,112].

Beyond their established biotechnological roles, hydrophobins have recently been implicated in environmental remediation, particularly in the removal of microplastics. Klauer et al. (2025) [156] demonstrate that hydrophobins mediate strong fungal–microplastic interactions, enabling efficient flocculation and particle removal from aqueous systems, even in the absence of fungal cells. These findings highlight the potential of surface-active hydrophobins, such as HFBI and HFBII, for engineered strategies to decontaminate microplastic pollution. In the following table, the biotechnological applications of hydrophobins in Ascomycota members are summarized (Table 3):

Table 3. Biotechnological Applications of Ascomycota Hydrophobins.

Organism	Gene (Accession) and Class	Biotechnological Applications	References
<i>Aspergillus nidulans</i>	DewA (P52750), DewC (Q5AZ79), DewE (Q5AVZ1) and RodA (P28346): Class I. DewD (Q5BEU0): hydrophobin-like protein.	<i>DewA</i> is a promising candidate for orthopedic implant coatings, promoting cell adhesion and tissue integration, and also functions as an emulsifier for biotechnological uses. <i>DewC-E</i> have been explored for surface modification, stabilization of emulsions and foams, enhancement of enzyme activity and antifouling strategies. The <i>RodA</i> rodlet layer contributes to immune evasion, biofilm formation and efficient lignocellulosic substrate deconstruction.	[43,46,47,50, 63–67]
<i>Aspergillus oryzae</i>	RolA (Q2U3W7): Class I.	Overall roles include binding to hydrophobic polymer surfaces, recruitment of hydrolytic enzymes and enhancement of polymer degradation. <i>RolA</i> binds to polymers such as PBSA and PET, recruits and increases the activity of cutinases and PETases, and promotes polymer hydrolysis at the liquid–solid interface. Its interaction with PETase highlights its potential for eco-friendly PET recycling and for improving hydrolytic reactions on hydrophobic solid substrates.	[43,53,157]
<i>Beauveria bassiana</i>	Hyd1A (J4KPV6), Hyd1B (J4W2A8), Hyd 1C (J5JJC1), hyd1D (J4VS95), Hyd 1E (J4UGK4) and Hyd1F (J4UJ50): Class I. Hyd 2A (J4WDT5), Hyd 2B (J5JTB1) and Hyd2C (J4WMI6): Class II.	In entomopathogenic fungi such as <i>Beauveria bassiana</i> , these hydrophobins (<i>hyd1A-F</i> , <i>hyd2A-C</i>) contribute to traits associated with insect infection, supporting their potential use as biological alternatives to chemical pesticides due to the organism’s insecticidal activity.	[68,69]

Table 3. Cont.

Organism	Gene (Accession) and Class	Biotechnological Applications	References
<i>Clonostachys rosea</i>	Hyd1 (W8P1J0), Hyd2 (W8NXX4) and Hyd3 (W8NQ71): Class II.	Conidial hydrophobicity, biocontrol mechanisms and regulation of germination under stress conditions. <i>HYD1</i> is induced during conidiation and contributes to stress-mediated inhibition of germination. <i>HYD3</i> restricts premature germination under abiotic stress and is required for effective root colonization of <i>Arabidopsis thaliana</i> . <i>HYD2</i> shows constitutive basal expression, and its function remains unresolved, suggesting a potentially essential role.	[158]
<i>Fusarium culmorum</i>	FcHyd3p (N/A): Class I. FcHyd5p (N/A): Class II.	<i>FcHyd3p</i> exhibits weak foam-stabilizing activity and is not associated with gushing in beer. In contrast, <i>FcHyd5p</i> modifies surface hydrophobicity to increase wettability, stabilizes air bubbles in aqueous solutions, and acts as a potent gushing-inducing factor in carbonated beverages.	[117,159]
<i>Metarhizium brunneum</i>	Hyd1 (N/A) and Hyd 3 (N/A): Class I. Hyd 2 (N/A): Class II.	Sporulation, pigmentation, surface hydrophobicity and virulence. <i>HYD1</i> is strongly expressed in mycelia and conidiophores and weakly in conidia. <i>HYD2</i> is primarily expressed in blastospores. <i>HYD3</i> contributes to conidiogenesis and pathogenicity.	[160]
<i>Neurospora crassa</i>	NC2 (Q7S3P5): Class II.	Stabilizes air bubbles and forms ordered molecular networks on hydrophobic substrates, supporting applications such as biocompatible nanodevices and drug delivery systems.	[56,161]
<i>Paecilomyces farinosus</i>	PfaH1 (N/A); PfaH2 (N/A): Class I.	Modulation of surface hydrophobicity through increased water contact angles. <i>PfaH1</i> is abundantly produced in mycelium under diverse growth conditions, whereas <i>PfaH2</i> is constitutively expressed.	[162,163]
<i>Sodiomyces alkalinus</i>	Sa- Hfb1 (A0A3N2PQC3): Class II.	Isolated from the alkaliphilic fungus <i>Sodiomyces alkalinus</i> that exhibits antifungal activity, with MIC values ranging from 1 to 8 µg/mL against opportunistic and clinically relevant pathogens, including inhibition of <i>Cryptococcus neoformans</i> , suggesting a role in the organism's antimicrobial defense and highlighting its potential as a promising antifungal lead compound.	[164]

Table 3. Cont.

Organism	Gene (Accession) and Class	Biotechnological Applications	References
<i>Trichoderma asperellum</i>	TasHyd1 (A0A6V8R0V1): Class I hydrophobin-like protein. Hfb 2-1 (A0A2T3ZKC8), Hfb 2-2 (A0A2T3ZC06), Hfb 2-3 (A0A2T3Z3L3), Hfb 2-4 (A0A2T3ZJV9), Hfb 2-5 (A0A2T3ZCF4), Hfb 2-6 (I7AQQ9) and Hfb 2-7 (A0A2T3YYV2): Class II. Hfb2-8 (A0A2T3ZJ73): Hydrophobin-like gene lacking a signal peptide.	Root attachment and colonization, plant interaction, stress responsiveness and environmental sensing. <i>TasHyd1</i> is required for conidial wettability and colonization and is induced during plant interaction and carbon limitation. <i>HFB2-1</i> is selectively induced by woody plant extracts. <i>HFB2-5</i> and <i>HFB2-6</i> are strongly induced by plant-derived substrates and stress-related cues, whereas <i>HFB2-7</i> shows broader but lower-level induction. <i>HFBII-4</i> enhances plant defense. <i>HFB2-2</i> and <i>HFB2-3</i> are predicted to participate in stress-responsive and plant-associated processes. <i>HFB2-8</i> likely represents a nonfunctional pseudogene.	[113,165,166]
<i>Trichoderma atroviride</i>	Hfb-1b (N/A), Hfb-1c (N/A), Hfb-2a (N/A), Hfb-2b (N/A), Hfb-2c (N/A), Hfb-5a (N/A), Hfb-6a (N/A), Hfb-6b (N/A), and Hfb-6c (N/A): Class II; hfb-22a (N/A): Hydrophobin-like gene. Hfb4 (A0A7D5LZ09) and <i>srh1</i> (N/A): hydrophobin-like protein.	Participate in light and stress-responsive regulation, surface interaction, and environmental adaptation. <i>hfb-1b</i> , <i>hfb-1c</i> , <i>hfb-2a</i> , <i>hfb-6a</i> , and <i>hfb-6b</i> are induced by BLR1/BLR2-dependent light signaling, whereas <i>hfb-2c</i> is BLR-independent and upregulated during early plant–host interaction. <i>hfb-2b</i> shows constitutive expression, including during host confrontation, while <i>hfb-6a</i> and <i>hfb-6b</i> are repressed during self-confrontation. The gene <i>hfb-22a</i> is likely a pseudogene due to lack of detectable expression. <i>HFB4</i> binds to diverse surfaces and enhances PET hydrolysis by cutinase, and <i>srh1</i> is predicted to contribute to surface interaction and environmental responsiveness.	[112,167–169]
<i>Trichoderma harzianum</i>	ThHyd1 (A0A219TTW8) and ThHyd2 (A0A1B1RVB9): Class II.	Involved in plant interaction, adhesion, spore formation, stress response, and dispersal regulation. <i>ThHyd1</i> acts as an elicitor of induced systemic resistance via brassinosteroid and JA/ET pathways, enhancing plant resistance without growth penalties, whereas <i>ThHyd2</i> shows limited ability to activate host defenses.	[86,87]
<i>Trichoderma longibrachiatum</i>	Hytlo1 (N/A): Class II.	Activation of plant defense signaling, induction of systemic resistance, antifungal activity and promotion of plant growth. It functions as a multifunctional MAMP that triggers rapid Ca ²⁺ influx via a NAADP-dependent pathway, localizes as a surface film on plant cell walls, and is required for full antagonistic activity and plant-growth promotion during <i>Trichoderma</i> –plant interactions.	[114,170]

Table 3. Cont.

Organism	Gene (Accession) and Class	Biotechnological Applications	References
<i>Trichoderma reesei</i>	Hfb1 (P52754): Class II.	Surface modification and biotechnological applications, showing strong potential for technical and medical uses, particularly in the development of implant coatings.	[94–98]
<i>Trichoderma virens</i>	Hfb9a (N/A) and Hfb9b (N/A): Class I.	Plant root colonization, antagonistic activity and interfacial self-assembly. <i>HFB9a</i> and <i>HFB9b</i> self-assemble into ordered monolayers that modify surface wettability, and in combination with EPL1 form hybrid interfacial layers with altered wetting properties distinct from pure hydrophobin films.	[171,172]

4. Hydrophobins in Basidiomycota

The phylum Basidiomycota comprises a diverse group of fungi, including mushrooms, rusts, smuts, and basidiomycetous yeasts. Sexual reproduction in this phylum is characterized by the formation of basidiospores on specialized structures called basidia, which in many species are organized into complex fruiting bodies known as basidiocarps [5]. Within Basidiomycota, hydrophobins contribute to fungal morphogenesis and ecological fitness by regulating processes such as fruiting body development, aerial hyphae formation, surface adhesion, and host interactions. Comprehensive genomic and biochemical studies have also highlighted their functional diversity and their importance in environmental adaptation and fungal colonization [6,43,173–185].

Hydrophobins characterized in Basidiomycota species display considerable diversity in structural features and physiological functions, reflecting their participation in complex developmental and ecological processes. To integrate UniProt data on characterized hydrophobins, Table S2 presents all the biophysical properties of hydrophobins in Basidiomycota and includes putative hydrophobins identified through sequence-based prediction from the UNIPROT database. Additionally, to complement the molecular and physicochemical dataset, Supplementary Figure S2 presents a phylogenetic analysis of Basidiomycota hydrophobins, which are described throughout this review.

4.1. Physiological Roles of Basidiomycota Hydrophobins

Basidiomycota hydrophobins allow the fungus to regulate surface interactions, facilitating the transition from submerged to aerial growth and providing structural integrity to reproductive tissues [5,186]. In *Schizophyllum commune*, the hydrophobin SC3 is among the most extensively studied examples. It self-assembles into highly ordered, fibrillar films at the air–water interface, promoting the formation of aerial hyphae and conferring hydrophobicity to the hyphal surface [187,188]. These assemblies also protect spores and hyphae against desiccation and environmental stress [1].

In *Agaricus bisporus*, several hydrophobins, such as ABH1, ABH2, ABH3, and HYPA, are expressed at specific stages of fruiting body development [189]. ABH1 forms hydrophobic rodlet layers in the cap tissues, protecting the fruiting body from mechanical and water stress, while ABH4 displays a unique self-assembly pattern that modulates surface tension at hydrophilic–hydrophobic interfaces [190]. Differential gene expression of HypA and hypB reveals functional specialization. HypA predominates in undifferentiated hyphae, whereas hypB is expressed during primordium differentiation [189,191].

In *Pleurotus ostreatus*, hydrophobins Vmh2, Vmh3, and Hydph16 contribute to cell wall formation, lignin degradation, and adaptation to stress conditions such as oxidative or detergent exposure [192–194]. The deletion of *Hydph16* results in thinner aerial hyphal walls, confirming its role in morphogenesis [194]. Some of these hydrophobins are light and temperature-inducible, mediating the formation of aerial mycelium and primordia in response to environmental triggers [195].

Fruiting body initiation and tissue differentiation in *Flammulina velutipes* are also tightly linked to hydrophobin expression. Genes such as *fov1* and *Hyd9* are specifically expressed after induction of fruiting, controlling the formation of aerial hyphae knots and primordia. Their temporal regulation underscores the importance of hydrophobins as developmental markers in mushroom morphogenesis [196–198].

Similarly, *Lentinula edodes* produces multiple hydrophobins, including Le.hyd1 and Le.hyd2, whose expression patterns differ across developmental stages [199,200]. Le.hyd1 transcripts are abundant in primordia and pre-hymenial regions, while Le.hyd2 predominates in the dikaryotic mycelium. Electrical stimulation of the substrate increases hydrophobin secretion, linking these proteins to electrophysiological signaling during primordium induction [201,202].

In *Coprinopsis cinerea*, the hydrophobins CoH1 and CoH2 are developmentally regulated, with expression confined to monokaryotic vegetative hyphae [203]. Their absence in oid-1 mutants correlates with the loss of aerial growth, indicating a requirement for these proteins in fruiting initiation. Recent evidence suggests that regulatory miRNAs (*cci-milR-12c*, *cci-milR-13e-5p*) fine-tune hydrophobin expression during the transition from vegetative to reproductive stages [204].

Hydrophobins also contribute to environmental sensing and morphogenetic regulation in genera such as *Pholiota* and *Agrocybe*. In *P. nameko*, hydrophobin genes *pnh1–3* are induced under phosphate deficiency and electrical stimulation, linking environmental stress to morphogenesis [205]. In *A. cylindracea*, hydrophobins act as surface modifiers, altering the wettability of glass and Teflon and enabling the formation of aerial hyphae even in nutrient-rich conditions [206].

In symbiotic basidiomycetes like *Pisolithus tinctorius*, hydrophobins such as HydPt-1, HydPt-2, and HydPt-3 mediate hyphal adhesion and ectomycorrhiza formation. Their expression peaks during the early stages of plant–root interaction, assisting in hyphal aggregation and water exclusion at the symbiotic interface [207,208]. Finally, in *Tricholoma vaccinum*, hydrophobin Hyd8 is strongly induced during aerial mycelium formation and ectomycorrhizal symbiosis, where it contributes to surface structuring and compatible host recognition [209].

In the following table, the physiological roles of hydrophobins in Basidiomycota are summarized (Table 4):

Table 4. Physiological Roles of Basidiomycota Hydrophobins.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Agaricus bisporus</i>	HypA (P49072), HypB (O43122) and HypC (O13300): Class I.	Fruiting-body development, tissue differentiation and surface adhesion. <i>HypA</i> accumulates during cap expansion and self-assembles into rodlets that generate protective hydrophobic coatings on the cap, veil and stipe. <i>hypC</i> is enriched in fruit bodies, particularly at the pin stage. <i>hypB</i> is highly expressed during early fruiting-body differentiation, especially in developing cap tissues.	[186,189,190, 210]

Table 4. Cont.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Agrocybe aegerita</i>	Aa-Pri2 (Q9Y8F0): Class I.	Fruiting-body development and developmental regulation. <i>Aa-Pri2</i> encodes a secreted protein specifically expressed during basidiocarp differentiation, with promoter architecture indicating tight developmental control and conserved homologs across several basidiomycete species, supporting a role in reproductive structure formation.	[211]
<i>Coprinopsis cinerea</i>	CoH1 (P78601) and CoH2 (P78602): Class I.	Aerial mycelial growth and light-regulated developmental transitions during fruiting-body formation. <i>CoH1</i> and <i>CoH2</i> are predominantly expressed in monokaryotic mycelia and contribute to aerial hyphal growth.	[203]
<i>Dictyonema glabratum</i>	Dgh1 (Q8WZJ3), Dgh2 (Q8WZJ2) and Dgh3 (Q8WZJ1): Class I.	Formation of hydrophobic hyphal wall coatings, maintenance of gas-filled interhyphal spaces, water translocation, and structural organization of the fruiting body. <i>DGH1</i> forms rodlet layers that maintain hydrophobic cavities within the photobiont layer and support tissue stratification. <i>DGH2</i> produces similar hydrophobic coatings in both photobiont and lower strata, contributing to basidiocarp structural integrity. <i>DGH3</i> shows developmentally regulated expression and participates in hydrophobic wall formation and compartmentalization in mature fruiting-body tissues.	[212,213]
<i>Flammulina velutipes</i>	fvh1 (Q9HDD5), Hyd-1 (Q75T84), Hyd-2 (A0A1I9QLC3), Hyd-3 (A0A1I9QLC4), Hyd-4 (A0A1I9QLC5), Hyd-5 (A0A1I9QLC6), Hyd-6 (A0A1I9QLC7), Hyd-7 (A0A1I9QLC8), Hyd-8 (A0A1I9QLC9), Hyd-9 (A0A1I9QLD0) and Hyd-10 (A0A1I9QLD1): Class I.	Regulation of fruiting-body development, hyphal behavioral transition, and structural differentiation during mushroom morphogenesis. <i>Fvh1</i> is strongly expressed immediately after fruiting induction in substrate-associated mycelia. <i>Hyd-1</i> is light-induced and highly expressed from the primordial stage through mature fruiting bodies. <i>Hyd-2-10</i> show low expression in vegetative mycelia and reduced transcription in fruiting bodies, suggesting specialized functions restricted to early or tissue-specific stages of morphogenesis.	[198,214]
<i>Laccaria bicolor</i>	LbH1 (B0CX61), LbH5 (B0DG11), LbH6 (N/A), LbH11 (B0E003) and LbH14 (B0E2E5): Class I.	Overall roles include fruiting-body development and host-dependent regulation. <i>LbH1</i> is induced specifically in Douglas fir-associated fruiting bodies, <i>LbH5</i> and <i>LbH14</i> are upregulated in fruiting bodies from both Douglas fir and poplar, <i>LbH6</i> is repressed during fruiting-body formation, and <i>LbH11</i> shows host-specific regulation, being repressed in Douglas fir but induced in poplar fruiting bodies.	[215]
<i>Lentinula edodes</i>	Le.hyd1 (Q9P8T0) and Le.hyd2 (Q9P8S9): Class I.	Fruiting-body development, mating-type-dependent regulation, and stage-specific hyphal growth. <i>Le.hyd1</i> is transcribed during the primordial stage and functions primarily in fruit body initiation. <i>Le.hyd2</i> is expressed in dikaryotic mycelia.	[199,201]

Table 4. Cont.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Paxillus involutus</i>	hydA (Q4G2I6), hydB (A9X617), hydC (A9X618), hydD (A9X619), hydE (A9X668), hydF (A9X669) and hydG (A9X622): Class I.	Coordinated developmental regulation and differential transcriptional specialization during fungal growth. <i>hydA</i> – <i>C</i> and <i>hydE</i> show similar expression profiles, indicating shared regulatory control within the dominant hydrophobin module, with <i>hydE</i> displaying relatively stronger induction. <i>hydD</i> and <i>hydF</i> exhibit lower expression and distinct regulatory patterns, suggesting functional divergence and increased tissue specificity. <i>hydG</i> likely represents an allelic variant of <i>hydD</i> .	[216]
<i>Pholiota nameko</i>	pnh1 (Q8X1T9) and pnh2 (Q8X1T8); pnh3 (pnh3): Class I.	Adaptive responses to inorganic phosphate (Pi) deficiency, extracellular protein secretion and nutrient acquisition from wood substrates. <i>PNH1</i> is upregulated under Pi limitation. <i>PNH2</i> is induced during Pi deficiency. <i>PNH3</i> shows expression patterns similar to <i>PNH2</i> , being expressed under low Pi.	[205,217]
<i>Pisolithus tinctorius</i>	hydPt-1 (P52748), hydPt-2 (P52749) and hydPt-3 (O93917): Class I.	Early ectomycorrhizal development, root colonization, and aerial hypha formation. <i>HYDPT-1</i> accumulates on hyphal cell walls and is abundant across ectomycorrhizal tissues. <i>HYDPT-2</i> shows elevated expression in early eucalypt symbiotic tissues, is abundant in aerial hyphae, and follows a regulatory pattern similar to <i>HYDPT-1</i> and <i>HYDPT-3</i> . <i>HYDPT-3</i> is upregulated during ectomycorrhiza formation, co-regulated with the other two hydrophobins.	[208,218–220]
<i>Pleurotus ostreatus</i>	vmh1 (Q9Y7G9), Vmh2 (A0A067N4H9), Vmh3 (A0A067N648), Poh1 (O13502), Poh2 (O13503), Poh3 (O60048), fbh1 (O60047), Hydph6 (A0A067PCX8), Hydph7 (A0A067P1E6), Hydph8 (A0A067NFU6), Hydph12 (A0A067N4P3), Hydph13 (A0A067P494), Hydph15 (A0A067NHW8), Hydph16 (A0A067P943), Hydph17 (A0A067NHE1), Hydph18 (A0A067NEJ5), Hydph19 (A0A067NRJ8), Hydph20 (A0A067N7P3), Po.hyd1 (N/A), Po.hyd2 (N/A), Po.hyd3 (N/A), Po.hyd4 (N/A), Po.hyd5 (N/A), Po.hyd7 (N/A), Po.hyd8 (N/A), Po.hyd9 (N/A), Po.hyd10 (N/A), Po.hyd16 (N/A) and Po.Hyd1–10: Class I. Hydph5 (A0A067N582), Hydph9 (A0A067N4P7), Hydph11 (A0A067P0I9) and Hydph14 (A0A067NRQ5): hydrophobin-like protein.	Vegetative development, fruiting-body differentiation, surface structuring, aerial mycelium formation and environmental adaptation. <i>Vmh1</i> and <i>Vmh2</i> are restricted to vegetative mycelium, supporting surface interaction and stable coating formation, with <i>Vmh2</i> additionally enabling protein immobilization, biosensor applications and nanomaterial functionalization. <i>Vmh3</i> is glycosylated and expressed in both vegetative and reproductive stages, contributing to structural development. <i>POH1</i> and <i>fbh1</i> are fruiting-body-specific hydrophobins involved in rodlet formation and tissue specialization, whereas <i>POH2</i> and <i>POH3</i> function mainly during vegetative growth and extracellular surface assembly. <i>Hydph6</i> – <i>8</i> , <i>Hydph15</i> , <i>Hydph17</i> and <i>Hydph20</i> support vegetative growth, substrate colonization and aerial hypha formation, while <i>Hydph16</i> is essential for proper cell wall architecture and resistance to wall-targeting stress. Intermediate hydrophobins (<i>Hydph5</i> , <i>Hydph9</i> , <i>Hydph11</i> and <i>Hydph14</i>) contribute to developmental regulation and structural surface modulation. <i>Hydph12</i> , <i>Hydph13</i> and several <i>Po.Hyd</i> proteins (<i>Po.Hyd1</i> – <i>5</i> , <i>Po.hyd8</i>) are expressed during primordia and young fruiting bodies, supporting primordium initiation, fruit-body differentiation and pileus air-channel formation, whereas <i>Po.hyd7</i> , <i>Po.Hyd9</i> and <i>Po.hyd10</i> are associated with substrate colonization, dikaryotic growth and surface adaptation. <i>Po.hyd16</i> shows monokaryon-specific expression linked to early developmental specialization.	[194,195,221–232]

Table 4. Cont.

Organism	Gene (Accession) and Class	Physiological Roles	References
<i>Schizophyllum commune</i>	SC1 (P04158), SC4 (P16934), SC6 (O74300), SC16 (D8QCG9), Hyd3 (D8PTH5), Hyd4 (D8PU87) and Hyd6 (D8Q897): Class I.	Aerial hypha development, fruiting-body differentiation, hydrophobic surface structuring and biointerface formation through amphipathic self-assembly. <i>SC1</i> is a weakly expressed dikaryon-specific hydrophobin likely involved in auxiliary wall structuring and surface coating formation. <i>SC4</i> accumulates in fruiting-body hyphae, lining gas channels with hydrophobic membranes that maintain gas exchange and prevent water infiltration. <i>SC6</i> likely acts as a secondary structural component in fruiting tissues. <i>SC16</i> exhibits increased conformational flexibility due to the absence of one disulfide bond, enabling aeration-dependent rodlet formation and controlled self-assembly. <i>Hyd3</i> shows stable expression independent of <i>thn1</i> regulation, <i>Hyd4</i> displays moderate repression with limited regulatory responsiveness, and <i>Hyd6</i> is strongly <i>thn1</i> -dependent.	[233–236]
<i>Suillus luteus</i>	HydSI1 (A0A0C9ZLX1), HydSI3 (A0A0D0AYW4), HydSI4 (A0A0D0BGG3), HydSI5 (A0A0D0AM44), HydSI6 (A0A0D0B5N3), HydSI7 (A0A0D0ALE0), HydSI8 (A0A0D0AMA6), HydSI9 (A0A0C9ZII0) and HydSI10 (A0A0D0AZF5): Class I.	Surface attachment, interface adaptation, adhesion, and structural coating functions.	[237]
<i>Tricholoma terreum</i>	Hyd1 (Q8TFP0): Class I.	Coating vegetative mycelium and aerial hyphae, forming the dominant surface layer in ectomycorrhizal tissues (mantle and Hartig net), contributing to hyphal hydrophobicity, supporting interface architecture for nutrient exchange, and displaying host-dependent regulation indicative of a role in symbiotic recognition and specificity.	[238]
<i>Ustilago maydis</i>	Hum2 (A0A0D1BZL3) and Hum3 (A0A0D1CKI0): Class I.	Aerial hyphae formation, surface hydrophobicity, and early cell-wall-associated morphogenesis. <i>Hum2</i> is strongly expressed during dikaryotic filamentous growth and acts as a key determinant of aerial hyphae, while <i>Hum3</i> , a chimeric hydrophobin–Rep1 fusion, plays a minor or redundant role, contributing to surface hydrophobicity and supporting redundancy with other wall-modifying proteins.	[239–241]

4.2. Roles of Basidiomycota Hydrophobins in Fungal–Host Interactions

Hydrophobins in pathogenic and symbiotic Basidiomycota act as molecular interfaces between fungal cells and their environments, regulating adhesion, recognition, and immune evasion. In the phytopathogenic fungus *U. maydis*, which causes corn smut disease, the hydrophobins Hum2 and Hum3 were initially implicated in host adhesion and the formation of hydrophobic aerial hyphae. However, subsequent functional and genetic analyses demonstrated that these hydrophobins are dispensable for pathogenic development and are functionally replaced by repellents, a distinct family of secreted amphipathic proteins that assemble at the cell surface, reduce wettability, and ensure the maintenance of hydrophobicity during host colonization [239].

In ectomycorrhizal Basidiomycetous species that establish mutualistic or semi-pathogenic relationships with plants, also exploit hydrophobins to mediate attachment and colonization. In *P. tinctorius*, an ectomycorrhizal fungus forming symbiotic associations with tree roots, hydrophobins HydPt-1, HydPt-2, and HydPt-3 are transcriptionally up-regulated during the early stages of root colonization [207,208]. Likewise, Hyd8 from *T. vaccinum* is highly expressed during ectomycorrhiza formation with *Picea abies*, where it participates in fungal surface organization and host recognition [209]. These proteins promote hyphal aggregation and facilitate adhesion to root epidermal cells, forming hydrophobic barriers that limit desiccation and microbial invasion while stabilizing the mycorrhizal sheath. Although primarily symbiotic, these interactions share functional parallels with pathogenesis, including controlled penetration and defense modulation at the host–fungus interface [242].

In *C. neoformans*, a pathogenic yeast that infects humans, hydrophobin-like proteins contribute to virulence and biofilm formation by providing a hydrophobic barrier that shields the fungal surface from immune detection [164].

Regarding pathogenicity roles in Basidiomycota, the hydrophobins Hah1 (Q3HS86) and Hah2 (Q3HS87) from *H. annosum* belong to Class I and are involved in the regulation of aerial mycelial development and environmental responsiveness to gas composition. HAH1 is expressed in aerial hyphae but is only weakly expressed in submerged mycelia and during seedling infection, with its transcription reduced under antagonistic interactions and low-oxygen conditions. HAH2 exhibits greater sensitivity to atmospheric composition, showing increased expression under ambient conditions and repression under oxygen-limited conditions [243,244].

Similarly, the hydrophobins Pgh1 (Q2VTP0) and Pgh2 (Q2VTN9) from *Phlebiopsis gigantea* belong to Class I and play roles in hyphal development and antagonistic interactions during wood colonization. Pgh1 is strongly expressed during early hyphal growth and in barrage zones, with late-stage upregulation supporting aerial hyphae formation, sporulation, and enhanced antagonistic performance. Pgh2 exhibits basal expression under nutrient-rich conditions, is induced during the early stages of confrontation, but is down-regulated in barrage zones and at later stages. Together, these hydrophobins contribute to the biological control potential of *P. gigantea*, enabling it to outcompete *Heterobasidion* spp. on conifer stumps and thereby assisting in the management of pine root and butt rot caused by *H. annosum* [245,246].

4.3. Applications of Hydrophobins from Basidiomycota in Biotechnology

Hydrophobins from Basidiomycota have properties that make them candidates for surface functionalization, nanostructure design, and biomaterial engineering, bridging natural biological interfaces with technological applications [5]. The Class I hydrophobin SC3 from *S. commune* is a well-established model for biotechnological surface modification. Its amphipathic films, which self-assemble into stable rodlet layers, can be immobilized on metals, glass, polymers, and biological membranes [188]. The surface-modifying capacity of SC3 is reversible under controlled conditions, allowing reactivation and regeneration of biofunctional surfaces without structural degradation [6].

In environmental and materials biotechnology, ABH3 from *A. bisporus* has been used to create self-cleaning, anti-fouling, and moisture-regulating materials [247]. These hydrophobins can reduce surface energy and adjust wettability, serving as biological alternatives to fluorinated coatings in sustainable manufacturing. Their ability to immobilize enzymes such as laccases or cellulases further expands their use in bioremediation and biocatalysis, particularly in aqueous or multi-phase systems [190].

Hydrophobins from *P. ostreatus* (Vmh2 and Vmh3) also show promise in nanobiotechnological applications. Their ordered films exhibit distinct electrical and mechanical properties, making them suitable as biotemplates for nanowire formation and in biosensor design [193]. In the following table, the biotechnological applications of hydrophobins from Basidiomycota members are summarized (Table 5):

Table 5. Biotechnological Applications of Basidiomycota Hydrophobins.

Organism	Gene (Accession) and Class	Biotechnological Applications	References
<i>Agaricus bisporus</i>	ABH3 (Q9HGX0): Class I.	Expressed exclusively in vegetative mycelium; Substrate attachment, aerial hyphae emergence, and adhesion to hydrophobic surfaces. <i>ABH3</i> has potential biotechnological applications in enhancing adhesion and hydration of lignocellulosic materials, improving processes for lignin biodegradation and bioconversion.	[248]
<i>Coprinopsis cinerea</i>	Hyd1 (A8P9W4), Hyd2 (A8PA37) and Hyd3 (D6RQ66): Class I.	<i>Hyd1</i> is required for hyphal knot and primordium formation and is directly regulated by CcNsdD2, showing strong light-dependent induction. <i>Hyd2</i> is upregulated during early light-induced developmental initiation, while <i>Hyd3</i> is activated under light/dark rhythms and depends on CcNsdD2 for expression during early reproductive development, thereby enhancing yields in the edible mushroom industry.	[249]
<i>Ganoderma lucidum</i>	Hyd1 (A0A9E8S4N7): Class I.	Overall roles include primordium formation, developmental regulation, and stress tolerance. <i>Hyd1</i> is expressed during primordium initiation, and its silencing prevents primordium formation, demonstrating an essential role in early development. Its expression is negatively regulated by AreA, increases under nitrate conditions, and contributes to tolerance against heat, cell-wall, and salt stresses.	[250]
<i>Grifola frondosa</i>	Hgfl (A4LAR6) and HgflI (A0A8A5N547): Class I.	Surface modification, self-assembly at interfaces, and biotechnological applications. <i>HGFI</i> forms interfacial nanolayers enabling antibody immobilization, enhances PET hydrolysis, supports antibacterial surface formation via nisin adsorption, and functions as an adhesive amphiphilic modifier promoting hyphal growth. <i>HGFII</i> is expressed in mycelia, self-assembles into rodlet-like nanostructures with increased β -sheet content, and exhibits stronger surface hydrophobicity and superior emulsifying capacity, enabling the formation of highly stable oil-in-water emulsions.	[152,251–255]
<i>Pleurotus ostreatus</i>	Vmh1 (Q9Y7G9), Vmh2 (A0A067N4H9), Vmh3 (A0A067N648), Fbh1 (O60047): Class I.	<i>Vmh1-3</i> and <i>fbh1</i> overall roles include surface immobilization, biocatalysis, wood degradation, and biotechnological applications. <i>Vmh1</i> , <i>Vmh2</i> and <i>Vmh3</i> support lipase immobilization via interfacial activation, with <i>Vmh2</i> additionally enabling GST-based biosensors for pesticide detection and chimeric antimicrobial surfaces when fused to LL-37. <i>fbh1</i> contributes to wood and lignin-derived compound degradation and supports production of secondary metabolites with pharmaceutical potential.	[221–232]

Table 5. Cont.

Organism	Gene (Accession) and Class	Biotechnological Applications	References
<i>Schizophyllum commune</i>	SC3 (P16933): Class I.	Forms highly insoluble rodlet layers that reduce surface tension and mediate adhesion to hydrophobic and hydrophilic interfaces, supporting stable surface coatings and biomaterial functionalization.	[233,234,256–260]
<i>Serpula lacrymans</i>	Slh1 (N/A) and Slh4 (F8NJA2): hydrophobin-like protein.	Rodlet formation, β -sheet assembly, and interfacial coating. <i>SL1</i> can be overexpressed in <i>E. coli</i> , refolded into an active conformation, and forms rodlets with strong thioflavin-T fluorescence, suitable for functional and biophysical assays. <i>SLH4</i> assembles efficiently at air–water interfaces, forming small, densely clustered rodlets with pH- and ionic-strength-dependent conformational changes, supporting controlled interfacial coatings and nanostructure formation.	[261,262]

5. Conclusions

Altogether, hydrophobins from both Ascomycota and Basidiomycota represent an example of functional convergence between fungal biology and applied sciences. Across these phyla, hydrophobins play essential physiological roles in fungal growth and development, including the formation of aerial structures, spore dispersal, surface adhesion, and adaptation to environmental stresses. In addition, they are key determinants in fungal–host interactions, contributing to pathogenicity through mechanisms such as immune evasion, surface masking, host colonization, and infection structure formation.

Beyond their biological significance, the unique physicochemical properties of hydrophobins, particularly their ability to self-assemble at hydrophobic–hydrophilic interfaces, have positioned them as versatile molecules for biotechnological applications. These proteins have been successfully explored in areas such as surface functionalization, enzyme immobilization, drug delivery, biomaterial engineering, and environmentally sustainable technologies, including biocontrol and pollutant remediation.

Therefore, integrating structural, functional, and ecological knowledge across both fungal phyla highlights hydrophobins as multifunctional proteins with broad relevance. Continued investigation into their diversity and mechanisms of action will not only deepen our understanding of fungal biology but also expand their potential as natural building blocks for innovative and sustainable biotechnological solutions.

Supplementary Materials: The following supporting information can be downloaded at: <https://www.mdpi.com/article/10.3390/jof12080587/s1>, Methodology for Sequence Alignment and Phylogenetic Analysis. Supplementary Figure S1. Maximum Likelihood phylogenetic tree of Ascomycota hydrophobins. Supplementary Figure S2. Maximum Likelihood phylogenetic tree of Basidiomycota hydrophobins. Supplementary Table S1. Biophysical Properties of Hydrophobins from Ascomycota. Supplementary Table S2. Biophysical Properties of Hydrophobins from Basidiomycota.

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Abbreviations

The following abbreviations are used in this manuscript:

GLP-1	Glucagon-like peptide-1
GPCR	G protein-coupled receptor
GRAVY	Grand Average of Hydropathy
IgE	Immunoglobulin E
kDa	kilodalton
MAPK	Mitogen-Activated Protein Kinase
PBSA	Poly(butylene succinate-co-adipate)
PEG	Polyethylene glycol
PET	Poly(ethylene terephthalate)
Pfam	Protein families database
pH	potential of hydrogen
UniProt	Universal Protein Resource

References

- Berger, B.W.; Sallada, N.D. Hydrophobins: Multifunctional Biosurfactants for Interface Engineering. *J. Biol. Eng.* **2019**, *13*, 10. [\[CrossRef\]](#) [\[PubMed\]](#)
- Felipe, M.S.S.; Andrade, R.V.; Petrofeza, S.S.; Maranhão, A.Q.; Torres, F.A.G.; Albuquerque, P.; Arraes, F.B.M.; Arruda, M.; Azevedo, M.O.; Baptista, A.J.; et al. Transcriptome Characterization of the Dimorphic and Pathogenic Fungus *Paracoccidioides brasiliensis* by EST Analysis. *Yeast* **2003**, *20*, 263–271. [\[CrossRef\]](#) [\[PubMed\]](#)
- Kämper, J.; Kahmann, R.; Bölker, M.; Ma, L.-J.; Brefort, T.; Saville, B.J.; Banuett, F.; Kronstad, J.W.; Gold, S.E.; Müller, O.; et al. Insights from the Genome of the Biotrophic Fungal Plant Pathogen *Ustilago maydis*. *Nature* **2006**, *444*, 97–101. [\[CrossRef\]](#) [\[PubMed\]](#)
- Terauchi, Y.; Tanaka, T.; Mitsuishi, M.; Yabu, H.; Yoshimi, A.; Nantani, K.; Abe, K. Analysis of the Self-Assembly Process of *Aspergillus oryzae* Hydrophobin RolA by Langmuir–Blodgett Method. *Biosci. Biotechnol. Biochem.* **2020**, *84*, 678–685. [\[CrossRef\]](#) [\[PubMed\]](#)
- Wösten, H.A.B.; Scholtmeijer, K. Applications of Hydrophobins: Current State and Perspectives. *Appl. Microbiol. Biotechnol.* **2015**, *99*, 1587–1597. [\[CrossRef\]](#) [\[PubMed\]](#)
- Bayry, J.; Aïmanianda, V.; Guijarro, J.I.; Sunde, M.; Latgé, J.-P. Hydrophobins—Unique Fungal Proteins. *PLoS Pathog.* **2012**, *8*, e1002700. [\[CrossRef\]](#) [\[PubMed\]](#)
- Valsecchi, I.; Dupres, V.; Stephen-Victor, E.; Guijarro, J.I.; Gibbons, J.; Beau, R.; Bayry, J.; Coppee, J.Y.; Lafont, F.; Latgé, J.P.; et al. Role of Hydrophobins in *Aspergillus fumigatus*. *J. Fungi* **2018**, *4*, 2. [\[CrossRef\]](#) [\[PubMed\]](#)
- Khalesi, M.; Gebruers, K.; Derdelinckx, G. Recent Advances in Fungal Hydrophobin Towards Using in Industry. *Protein J.* **2015**, *34*, 243–255. [\[CrossRef\]](#) [\[PubMed\]](#)
- Rojas-Osnaya, J.; Nájera, H. Assembly of Hydrophobin Class I from *Agaricus bisporus* Produced Different Amyloid-like Fibrils. *Biochim. Biophys. Acta (BBA)-Proteins Proteom.* **2024**, *1873*, 141048. [\[CrossRef\]](#) [\[PubMed\]](#)
- Salve, A.; Apotikar, S.; Muddebihalkar, S.V.; Joshi, K.; Kulkarni, S. Applications of Hydrophobins in Medical Biotechnolog. *J. Sci. Res.* **2022**, *66*, 86–94. [\[CrossRef\]](#)
- Edgar, R.C. MUSCLE: Multiple Sequence Alignment with High Accuracy and High Throughput. *Nucleic Acids Res.* **2004**, *32*, 1792–1797. [\[CrossRef\]](#) [\[PubMed\]](#)

12. Kumar, S.; Stecher, G.; Suleski, M.; Sanderford, M.; Sharma, S.; Tamura, K. MEGA12: Molecular Evolutionary Genetic Analysis Version 12 for Adaptive and Green Computing. *Mol. Biol. Evol.* **2024**, *41*, msae263. [\[CrossRef\]](#) [\[PubMed\]](#)
13. Jones, D.T.; Taylor, W.R.; Thornton, J.M. The Rapid Generation of Mutation Data Matrices from Protein Sequences. *Bioinformatics* **1992**, *8*, 275–282. [\[CrossRef\]](#) [\[PubMed\]](#)
14. Saitou, N.; Nei, M. The Neighbor-Joining Method: A New Method for Reconstructing Phylogenetic Trees. *Mol. Biol. Evol.* **1987**, *4*, 406–425. [\[CrossRef\]](#) [\[PubMed\]](#)
15. Nei, M.; Kumar, S. *Molecular Evolution and Phylogenetics*; Oxford University Press: New York, NY, USA, 2000.
16. Letunic, I.; Bork, P. Interactive Tree Of Life (ITOL) v5: An Online Tool for Phylogenetic Tree Display and Annotation. *Nucleic Acids Res.* **2021**, *49*, W293–W296. [\[CrossRef\]](#) [\[PubMed\]](#)
17. Futagami, T.; Mori, K.; Kadooka, C.; Niihara, H.; Tashiro, K.; Tamaki, H.; Tanaka, T. Chromosome-Level Genome Sequence of *Aspergillus puulaauensis* MK2, a Fungus Isolated from a Dead Hard Tick. *Microbiol. Resour. Announc.* **2021**, *10*, e0037221. [\[CrossRef\]](#) [\[PubMed\]](#)
18. Wortman, J.R.; Gilson, J.M.; Joardar, V.; Deegan, J.; Clutterbuck, J.; Andersen, M.R.; Archer, D.; Bencina, M.; Braus, G.; Coutinho, P. The 2008 Update of the *Aspergillus nidulans* Genome Annotation: A Community Effort. *Fungal Genet. Biol.* **2009**, *46*, S2–S13. [\[CrossRef\]](#) [\[PubMed\]](#)
19. Xiao, G.; Ying, S.-H.; Zheng, P.; Wang, Z.-L.; Zhang, S.; Xie, X.-Q.; Shang, Y.; St. Leger, R.J.; Zhao, G.-P.; Wang, C.; et al. Genomic Perspectives on the Evolution of Fungal Entomopathogenicity in *Beauveria bassiana*. *Sci. Rep.* **2012**, *2*, 483. [\[CrossRef\]](#) [\[PubMed\]](#)
20. Van Kan, J.A.L.; Stassen, J.H.M.; Mosbach, A.; Van Der Lee, T.A.J.; Faino, L.; Farmer, A.D.; Papasotiriou, D.G.; Zhou, S.; Seidl, M.F.; Cottam, E.; et al. A Gapless Genome Sequence of the Fungus *Botrytis cinerea*. *Mol. Plant Pathol.* **2017**, *18*, 75–89. [\[CrossRef\]](#) [\[PubMed\]](#)
21. Staats, M.; van Kan, J.A.L. Genome Update of *Botrytis cinerea* Strains B05.10 and T4. *Eukaryot. Cell* **2012**, *11*, 1413–1414. [\[CrossRef\]](#) [\[PubMed\]](#)
22. Amselem, J.; Cuomo, C.A.; van Kan, J.A.L.; Viaud, M.; Benito, E.P.; Couloux, A.; Coutinho, P.M.; de Vries, R.P.; Dyer, P.S.; Fillinger, S.; et al. Genomic Analysis of the Necrotrophic Fungal Pathogens *Sclerotinia sclerotiorum* and *Botrytis cinerea*. *PLoS Genet.* **2011**, *7*, e1002230. [\[CrossRef\]](#) [\[PubMed\]](#)
23. Meng, Y.; Ren, Y.; Wang, W.; Gleason, M.L.; Zhang, R.; Sun, G. A Genome Sequence Resource for the Geographically Widespread Anthracnose Pathogen *Colletotrichum asianum*. *Plant Dis.* **2020**, *104*, 2044–2047. [\[CrossRef\]](#) [\[PubMed\]](#)
24. Kramer, G.J.; Nodwell, J.R. Chromosome Level Assembly and Secondary Metabolite Potential of the Parasitic Fungus *Cordyceps militaris*. *BMC Genom.* **2017**, *18*, 912. [\[CrossRef\]](#) [\[PubMed\]](#)
25. Spanu, P. HCF-1, a Hydrophobin from the Tomato Pathogen *Cladosporium fulvum*. *Gene* **1997**, *193*, 89–96. [\[CrossRef\]](#) [\[PubMed\]](#)
26. Mey, G.; Correia, T.; Oeser, B.; Kershaw, M.J.; Garre, V.; Arntz, C.; Talbot, N.J.; Tudzynski, P. Structural and Functional Analysis of an Oligomeric Hydrophobin Gene from *Claviceps purpurea*. *Mol. Plant Pathol.* **2003**, *4*, 31–41. [\[CrossRef\]](#) [\[PubMed\]](#)
27. Zhang, L.; Villalon, D.; Sun, Y.; Kazmierczak, P.; van Alfen, N.K. Virus-Associated down-Regulation of the Gene Encoding Cryparin, an Abundant Cell-Surface Protein from the Chestnut Blight Fungus, *Cryphonectria parasitica*. *Gene* **1994**, *139*, 59–64. [\[CrossRef\]](#) [\[PubMed\]](#)
28. Bettini, P.P.; Frascella, A.; Comparini, C.; Carresi, L.; Pepori, A.L.; Pazzagli, L.; Cappugi, G.; Scala, F.; Scala, A. Identification and Characterization of GEO1, a New Class II Hydrophobin from *Geosmithia* spp. *Can. J. Microbiol.* **2012**, *58*, 965–972. [\[CrossRef\]](#) [\[PubMed\]](#)
29. Frascella, A.; Bettini, P.P.; Kolařík, M.; Comparini, C.; Pazzagli, L.; Luti, S.; Scala, F.; Scala, A. Interspecific Variability of Class II Hydrophobin GEO1 in the Genus *Geosmithia*. *Fungal Biol.* **2014**, *118*, 862–871. [\[CrossRef\]](#) [\[PubMed\]](#)
30. Gao, Q.; Jin, K.; Ying, S.-H.; Zhang, Y.; Xiao, G.; Shang, Y.; Duan, Z.; Hu, X.; Xie, X.-Q.; Zhou, G.; et al. Genome Sequencing and Comparative Transcriptomics of the Model Entomopathogenic Fungi *Metarhizium anisopliae* and *M. acridum*. *PLoS Genet.* **2011**, *7*, e1001264. [\[CrossRef\]](#) [\[PubMed\]](#)
31. Saud, Z.; Kortsinoglou, A.M.; Kouvelis, V.N.; Butt, T.M. Telomere Length de Novo Assembly of All 7 Chromosomes and Mitogenome Sequencing of the Model Entomopathogenic Fungus, *Metarhizium brunneum*, by Means of a Novel Assembly Pipeline. *BMC Genom.* **2021**, *22*, 87. [\[CrossRef\]](#) [\[PubMed\]](#)
32. Hu, X.; Xiao, G.; Zheng, P.; Shang, Y.; Su, Y.; Zhang, X.; Liu, X.; Zhan, S.; St. Leger, R.J.; Wang, C. Trajectory and Genomic Determinants of Fungal-Pathogen Speciation and Host Adaptation. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 16796–16801. [\[CrossRef\]](#) [\[PubMed\]](#)
33. Galagan, J.E.; Calvo, S.E.; Borkovich, K.A.; Selker, E.U.; Read, N.D.; Jaffe, D.; FitzHugh, W.; Ma, L.-J.; Smirnov, S.; Purcell, S.; et al. The Genome Sequence of the Filamentous Fungus *Neurospora crassa*. *Nature* **2003**, *422*, 859–868. [\[CrossRef\]](#) [\[PubMed\]](#)
34. Bell-Pedersen, D.; Dunlap, J.C.; Loros, J.J. The *Neurospora* Circadian Clock-Controlled Gene, Ccg-2, Is Allelic to Eas and Encodes a Fungal Hydrophobin Required for Formation of the Conidial Rodlet Layer. *Genes Dev.* **1992**, *6*, 2382–2394. [\[CrossRef\]](#) [\[PubMed\]](#)

35. Ballester, A.-R.; Marcet-Houben, M.; Levin, E.; Sela, N.; Selma-Lázaro, C.; Carmona, L.; Wisniewski, M.; Droby, S.; González-Candelas, L.; Gabaldón, T. Genome, Transcriptome, and Functional Analyses of *Penicillium expansum* Provide New Insights into Secondary Metabolism and Pathogenicity. *Mol. Plant-Microbe Interact.* **2015**, *28*, 232–248. [\[CrossRef\]](#) [\[PubMed\]](#)
36. Cheeseman, K.; Ropars, J.; Renault, P.; Dupont, J.; Gouzy, J.; Branca, A.; Abraham, A.-L.; Ceppi, M.; Conseiller, E.; Debuchy, R.; et al. Multiple Recent Horizontal Transfers of a Large Genomic Region in Cheese Making Fungi. *Nat. Commun.* **2014**, *5*, 2876. [\[CrossRef\]](#) [\[PubMed\]](#)
37. Grum-Grzhimaylo, A.A.; Falkoski, D.L.; van den Heuvel, J.; Valero-Jiménez, C.A.; Min, B.; Choi, I.; Lipzen, A.; Daum, C.G.; Aanen, D.K.; Tsang, A.; et al. The Obligate Alkalophilic Soda-lake Fungus *Sodiomyces alkalinus* Has Shifted to a Protein Diet. *Mol. Ecol.* **2018**, *27*, 4808–4819. [\[CrossRef\]](#) [\[PubMed\]](#)
38. Ribitsch, D.; Herrero Acero, E.; Przylucka, A.; Zitzenbacher, S.; Marold, A.; Gamerith, C.; Tscheließnig, R.; Jungbauer, A.; Rennhofer, H.; Lichtenegger, H.; et al. Enhanced Cutinase-Catalyzed Hydrolysis of Polyethylene Terephthalate by Covalent Fusion to Hydrophobins. *Appl. Environ. Microbiol.* **2015**, *81*, 3586–3592. [\[CrossRef\]](#) [\[PubMed\]](#)
39. Nakari-Setälä, T.; Aro, N.; Kalkkinen, N.; Alatalo, E.; Penttilä, M. Genetic and Biochemical Characterization of the *Trichoderma reesei* Hydrophobin HFBI. *Eur. J. Biochem.* **1996**, *235*, 248–255. [\[CrossRef\]](#) [\[PubMed\]](#)
40. Martinez, D.; Berka, R.M.; Henrissat, B.; Saloheimo, M.; Arvas, M.; Baker, S.E.; Chapman, J.; Chertkov, O.; Coutinho, P.M.; Cullen, D.; et al. Genome Sequencing and Analysis of the Biomass-Degrading Fungus *Trichoderma reesei* (Syn. *Hypocrea jecorina*). *Nat. Biotechnol.* **2008**, *26*, 553–560. [\[CrossRef\]](#) [\[PubMed\]](#)
41. Chung, D.; Kwon, Y.M.; Yang, Y. Telomere-to-Telomere Genome Assembly of Asparaginase-Producing *Trichoderma simmonsii*. *BMC Genom.* **2021**, *22*, 830. [\[CrossRef\]](#) [\[PubMed\]](#)
42. Mukherjee, M.; Horwitz, B.A.; Sherkhane, P.D.; Hadar, R.; Mukherjee, P.K. A Secondary Metabolite Biosynthesis Cluster in *Trichoderma virens*: Evidence from Analysis of Genes Underexpressed in a Mutant Defective in Morphogenesis and Antibiotic Production. *Curr. Genet.* **2006**, *50*, 193–202. [\[CrossRef\]](#) [\[PubMed\]](#)
43. Tanaka, T.; Terauchi, Y.; Yoshimi, A.; Abe, K. *Aspergillus* Hydrophobins: Physicochemical Properties, Biochemical Properties, and Functions in Solid Polymer Degradation. *Microorganisms* **2022**, *10*, 1498. [\[CrossRef\]](#) [\[PubMed\]](#)
44. Jensen, B.G.; Andersen, M.R.; Pedersen, M.H.; Frisvad, J.C.; Søndergaard, I. Hydrophobins from *Aspergillus* Species Cannot Be Clearly Divided into Two Classes. *BMC Res. Notes* **2010**, *3*, 344. [\[CrossRef\]](#) [\[PubMed\]](#)
45. de Vries, R.P.; Riley, R.; Wiebenga, A.; Aguilar-Osorio, G.; Amillis, S.; Uchima, C.A.; Anderluh, G.; Asadollahi, M.; Askin, M.; Barry, K.; et al. Comparative Genomics Reveals High Biological Diversity and Specific Adaptations in the Industrially and Medically Important Fungal Genus *Aspergillus*. *Genome Biol.* **2017**, *18*, 28. [\[CrossRef\]](#) [\[PubMed\]](#)
46. Grünbacher, A.; Throm, T.; Seidel, C.; Gutt, B.; Röhrig, J.; Strunk, T.; Vincze, P.; Walheim, S.; Schimmel, T.; Wenzel, W.; et al. Six Hydrophobins Are Involved in Hydrophobin Rodlet Formation in *Aspergillus nidulans* and Contribute to Hydrophobicity of the Spore Surface. *PLoS ONE* **2014**, *9*, e94546. [\[CrossRef\]](#) [\[PubMed\]](#)
47. Winandy, L.; Hilpert, F.; Schlebusch, O.; Fischer, R. Comparative Analysis of Surface Coating Properties of Five Hydrophobins from *Aspergillus nidulans* and *Trichoderma reesei*. *Sci. Rep.* **2018**, *8*, 12033. [\[CrossRef\]](#) [\[PubMed\]](#)
48. Breakspear, A.; Momany, M. *Aspergillus nidulans* Conidiation Genes *DewA*, *FluG*, and *StuA* Are Differentially Regulated in Early Vegetative Growth. *Eukaryot. Cell* **2007**, *6*, 1697–1700. [\[CrossRef\]](#) [\[PubMed\]](#)
49. Stringer, M.A.; Dean, R.A.; Sewall, T.C.; Timberlake, W.E. Rodletless, a New *Aspergillus* Developmental Mutant Induced by Directed Gene Inactivation. *Genes Dev.* **1991**, *5*, 1161–1171. [\[CrossRef\]](#) [\[PubMed\]](#)
50. Morris, V.K.; Kwan, A.H.; Sunde, M. Analysis of the Structure and Conformational States of *DewA* Gives Insight into the Assembly of the Fungal Hydrophobins. *J. Mol. Biol.* **2013**, *425*, 244–256. [\[CrossRef\]](#) [\[PubMed\]](#)
51. Valsecchi, I.; Lai, J.I.; Stephen-Victor, E.; Pillé, A.; Beaussart, A.; Lo, V.; Pham, C.L.L.; Aimanianda, V.; Kwan, A.H.; Duchateau, M.; et al. Assembly and Disassembly of *Aspergillus fumigatus* Conidial Rodlets. *Cell Surf.* **2019**, *5*, 100023. [\[CrossRef\]](#) [\[PubMed\]](#)
52. Parta, M.; Chang, Y.; Rulong, S.; Pinto-Dasilva, P.; Kwon-Chung, K.J. *HYPI*, a Hydrophobin Gene from *Aspergillus fumigatus*, Complements the Rodletless Phenotype in *Aspergillus nidulans*. *Infect. Immun.* **1994**, *62*, 4389–4395. [\[CrossRef\]](#) [\[PubMed\]](#)
53. Takahashi, T.; Maeda, H.; Yoneda, S.; Ohtaki, S.; Yamagata, Y.; Hasegawa, F.; Gomi, K.; Nakajima, T.; Abe, K. The Fungal Hydrophobin *RolA* Recruits Polyesterase and Laterally Moves on Hydrophobic Surfaces. *Mol. Microbiol.* **2005**, *57*, 1780–1796. [\[CrossRef\]](#) [\[PubMed\]](#)
54. Ohtaki, S.; Maeda, H.; Takahashi, T.; Yamagata, Y.; Hasegawa, F.; Gomi, K.; Nakajima, T.; Abe, K. Novel Hydrophobic Surface Binding Protein, *HsbA*, Produced by *Aspergillus oryzae*. *Appl. Environ. Microbiol.* **2006**, *72*, 2407–2413. [\[CrossRef\]](#) [\[PubMed\]](#)
55. Macindoe, I.; Kwan, A.H.; Ren, Q.; Morris, V.K.; Yang, W.; Mackay, J.P.; Sunde, M. Self-Assembly of Functional, Amphipathic Amyloid Monolayers by the Fungal Hydrophobin *EAS*. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 5152. [\[CrossRef\]](#) [\[PubMed\]](#)
56. Ren, Q.; Kwan, A.H.; Sunde, M. Solution Structure and Interface-Driven Self-Assembly of NC2, a New Member of the Class II Hydrophobin Proteins. *Proteins Struct. Funct. Bioinform.* **2014**, *82*, 990–1003. [\[CrossRef\]](#) [\[PubMed\]](#)

57. Carrion, S.d.J.; Leal, S.M.; Ghannoum, M.A.; Aimanianda, V.; Latgé, J.-P.; Pearlman, E. The RodA Hydrophobin on *Aspergillus fumigatus* Spores Masks Dectin-1– and Dectin-2–Dependent Responses and Enhances Fungal Survival In Vivo. *J. Immunol.* **2013**, *191*, 2581–2588. [[CrossRef](#)] [[PubMed](#)]
58. Subroto, E.; van Neer, J.; Valdes, I.; de Cock, H. Growth of *Aspergillus fumigatus* in Biofilms in Comparison to *Candida albicans*. *J. Fungi* **2022**, *8*, 48. [[CrossRef](#)] [[PubMed](#)]
59. Gupta, L.; Sen, P.; Bhattacharya, A.K.; Vijayaraghavan, P. Isoeugenol Affects Expression Pattern of Conidial Hydrophobin Gene *RodA* and Transcriptional Regulators *MedA* and *SomA* Responsible for Adherence and Biofilm Formation in *Aspergillus fumigatus*. *Arch. Microbiol.* **2022**, *204*, 214. [[CrossRef](#)] [[PubMed](#)]
60. Hu, X.; Zhou, Y.; Liu, R.; Wang, J.; Guo, L.; Huang, X.; Li, J.; Yan, Y.; Liu, F.; Li, X.; et al. Protein Disulfide Isomerase 1 Is Required for *RodA* Assembling-Based Conidial Hydrophobicity of *Aspergillus fumigatus*. *Appl. Environ. Microbiol.* **2024**, *90*, e0126023. [[CrossRef](#)] [[PubMed](#)]
61. Beauvais, A.; Latgé, J.-P. *Aspergillus* Biofilm In Vitro and In Vivo. *Microbiol. Spectr.* **2015**, *3*, 149–161. [[CrossRef](#)] [[PubMed](#)]
62. Paris, S.; Debeaupuis, J.P.; Crameri, R.; Carey, M.; Charlès, F.; Prévost, M.C.; Schmitt, C.; Philippe, B.; Latgé, J.P. Conidial Hydrophobins of *Aspergillus fumigatus*. *Appl. Environ. Microbiol.* **2003**, *69*, 1581–1588. [[CrossRef](#)] [[PubMed](#)]
63. Dynesen, J.; Nielsen, J. Surface Hydrophobicity of *Aspergillus nidulans* Conidiospores and Its Role in Pellet Formation. *Biotechnol. Prog.* **2003**, *19*, 1049–1052. [[CrossRef](#)] [[PubMed](#)]
64. Boeuf, S.; Throm, T.; Gutt, B.; Strunk, T.; Hoffmann, M.; Seebach, E.; Mühlberg, L.; Brocher, J.; Gotterbarm, T.; Wenzel, W.; et al. Engineering Hydrophobin *DewA* to Generate Surfaces That Enhance Adhesion of Human but Not Bacterial Cells. *Acta Biomater.* **2012**, *8*, 1037–1047. [[CrossRef](#)] [[PubMed](#)]
65. Stringer, M.A.; Timberlake, W.E. *DewA* Encodes a Fungal Hydrophobin Component of the *Aspergillus* Spore Wall. *Mol. Microbiol.* **1995**, *16*, 33–44. [[CrossRef](#)] [[PubMed](#)]
66. Girardin, H.; Paris, S.; Rault, J.; Bellon-Fontaine, M.-N.; Latgé, J.-P. The Role of the Rodlet Structure on the Physicochemical Properties of *Aspergillus conidia*. *Lett. Appl. Microbiol.* **1999**, *29*, 364–369. [[CrossRef](#)] [[PubMed](#)]
67. Brown, N.A.; Ries, L.N.A.; Reis, T.F.; Rajendran, R.; Corrêa Dos Santos, R.A.; Ramage, G.; Riaño-Pachón, D.M.; Goldman, G.H. RNAseq Reveals Hydrophobins That Are Involved in the Adaptation of *Aspergillus nidulans* to Lignocellulose. *Biotechnol. Biofuels* **2016**, *9*, 145. [[CrossRef](#)] [[PubMed](#)]
68. Zhang, S.; Xia, Y.X.; Kim, B.; Keyhani, N.O. Two Hydrophobins Are Involved in Fungal Spore Coat Rodlet Layer Assembly and Each Play Distinct Roles in Surface Interactions, Development and Pathogenesis in the Entomopathogenic Fungus, *Beauveria bassiana*. *Mol. Microbiol.* **2011**, *80*, 811–826. [[CrossRef](#)] [[PubMed](#)]
69. Feng, J.R.; Li, M.; Ying, S.H.; Feng, M.G. Deciphering Roles of Nine Hydrophobins (*Hyd1A–F* and *Hyd2A–C*) in the Asexual and Insect-Pathogenic Lifecycles of *Beauveria bassiana*. *Microbiol. Res.* **2025**, *292*, 128029. [[CrossRef](#)] [[PubMed](#)]
70. Mosbach, A.; Leroy, M.; Mendgen, K.W.; Hahn, M. Lack of Evidence for a Role of Hydrophobins in Conferring Surface Hydrophobicity to Conidia and Hyphae of *Botrytis cinerea*. *BMC Microbiol.* **2011**, *11*, 10. [[CrossRef](#)] [[PubMed](#)]
71. Terhem, R.B.; van Kan, J.A.L. Functional Analysis of Hydrophobin Genes in Sexual Development of *Botrytis cinerea*. *Fungal Genet. Biol.* **2014**, *71*, 42–51. [[CrossRef](#)] [[PubMed](#)]
72. Lacroix, H.; Spanu, P.D. Silencing of Six Hydrophobins in *Cladosporium fulvum*: Complexities of Simultaneously Targeting Multiple Genes. *Appl. Environ. Microbiol.* **2009**, *75*, 542–546. [[CrossRef](#)] [[PubMed](#)]
73. de Wit, P.J.G.M.; van der Burgt, A.; Ökmen, B.; Stergiopoulos, I.; Abd-El Salam, K.A.; Aerts, A.L.; Bahkali, A.H.; Beenen, H.G.; Chettri, P.; Cox, M.P.; et al. The Genomes of the Fungal Plant Pathogens *Cladosporium fulvum* and *Dothistroma septosporum* Reveal Adaptation to Different Hosts and Lifestyles But Also Signatures of Common Ancestry. *PLoS Genet.* **2012**, *8*, e1003088. [[CrossRef](#)] [[PubMed](#)]
74. De Vries, O.; Moore, S.; Arntz, C.; Wessels, J. Identification and Characterization of a Tri-Partite Hydrophobin from *Claviceps fusiformis*. A Novel Type of Class II Hydrophobin. *Eur. J. Biochem.* **1999**, *262*, 377–385. [[CrossRef](#)] [[PubMed](#)]
75. Li, X.; Wang, F.; Liu, M.; Dong, C. Hydrophobin *CmHYD1* Is Involved in Conidiation, Infection and Primordium Formation, and Regulated by GATA Transcription Factor *CmAreA* in Edible Fungus, *Cordyceps militaris*. *J. Fungi* **2021**, *7*, 674. [[CrossRef](#)] [[PubMed](#)]
76. Li, X.; Wang, F.; Xu, Y.; Liu, G.; Dong, C. Cysteine-Rich Hydrophobin Gene Family: Genome Wide Analysis, Phylogeny and Transcript Profiling in *Cordyceps militaris*. *Int. J. Mol. Sci.* **2021**, *22*, 643. [[CrossRef](#)] [[PubMed](#)]
77. Li, X.; Liu, M.; Dong, C. Hydrophobin Gene *Cmhyd4* Negatively Regulates Fruiting Body Development in Edible Fungi *Cordyceps militaris*. *Int. J. Mol. Sci.* **2023**, *24*, 4586. [[CrossRef](#)] [[PubMed](#)]
78. Quarantin, A.; Hader, B.; Kröger, C.; Schäfer, W.; Favaron, F.; Sella, L.; Martínez-Rocha, A.L. Different Hydrophobins of *Fusarium graminearum* Are Involved in Hyphal Growth, Attachment, Water-Air Interface Penetration and Plant Infection. *Front. Microbiol.* **2019**, *10*, 751. [[CrossRef](#)] [[PubMed](#)]

79. Shin, Y.K.; Kim, D.W.; Lee, S.W.; Lee, M.J.; Gi Baek, S.; Lee, T.; Yun, S.H. Functional Roles of All Five Putative Hydrophobin Genes in Growth, Development, and Secondary Metabolism in *Fusarium graminearum*. *Fungal Genet. Biol.* **2022**, *160*, 103683. [[CrossRef](#)] [[PubMed](#)]
80. Minenko, E.; Vogel, R.F.; Niessen, L. Significance of the Class II Hydrophobin *FgHyd5p* for the Life Cycle of *Fusarium graminearum*. *Fungal Biol.* **2014**, *118*, 385–393. [[CrossRef](#)] [[PubMed](#)]
81. Kim, S.; Ahn, I.P.; Rho, H.S.; Lee, Y.H. *MHP1*, a *Magnaporthe grisea* Hydrophobin Gene, Is Required for Fungal Development and Plant Colonization. *Mol. Microbiol.* **2005**, *57*, 1224–1237. [[CrossRef](#)] [[PubMed](#)]
82. Chang, H.J.; Lee, M.; Na, S. Investigation of the Structural Conformation and Surface Interaction of Desired Chimeric Hydrophobin: Interface Simulation via Molecular Dynamics. *Colloids Surf. B Biointerfaces* **2019**, *173*, 128–138. [[CrossRef](#)] [[PubMed](#)]
83. Luciano-Rosario, D.; Eagan, J.L.; Aryal, N.; Dominguez, E.G.; Hull, C.M.; Keller, N.P. The Hydrophobin Gene Family Confers a Fitness Trade-off between Spore Dispersal and Host Colonization in *Penicillium expansum*. *mBio* **2022**, *13*, e0275422. [[CrossRef](#)] [[PubMed](#)]
84. Li, Y.; Sun, T.; Guo, D.; Gao, J.; Zhang, J.; Cai, F.; Fischer, R.; Shen, Q.; Yu, Z. Comprehensive Analysis of the Regulatory Network of Blue-light-regulated Conidiation and Hydrophobin Production in *Trichoderma guizhouense*. *Environ. Microbiol.* **2021**, *23*, 6241–6256. [[CrossRef](#)] [[PubMed](#)]
85. Cai, F.; Gao, R.; Zhao, Z.; Ding, M.; Jiang, S.; Yagtu, C.; Zhu, H.; Zhang, J.; Ebner, T.; Mayrhofer-Reinhartshuber, M.; et al. Evolutionary Compromises in Fungal Fitness: Hydrophobins Can Hinder the Adverse Dispersal of Conidiospores and Challenge Their Survival. *ISME J.* **2020**, *14*, 2610–2624. [[CrossRef](#)] [[PubMed](#)]
86. Yu, C.; Dou, K.; Wang, S.; Wu, Q.; Ni, M.; Zhang, T.; Lu, Z.; Tang, J.; Chen, J. Elicitor Hydrophobin *Hyd1* Interacts with Ubiquitin1-like to Induce Maize Systemic Resistance. *J. Integr. Plant Biol.* **2020**, *62*, 509–526. [[CrossRef](#)] [[PubMed](#)]
87. Ma, A.; Zhang, D.; Wang, G.; Wang, K.; Li, Z.; Gao, Y.; Li, H.; Bian, C.; Cheng, J.; Han, Y.; et al. *Verticillium dahliae* Effector VDAL Protects MYB6 from Degradation by Interacting with PUB25 and PUB26 E3 Ligases to Enhance *Verticillium wilt* Resistance. *Plant Cell* **2021**, *33*, 3675–3699. [[CrossRef](#)] [[PubMed](#)]
88. Lora, J.M.; de la Cruz, J.; Benítez, T.; Llobell, A.; Pintor-Toro, J.A. A Putative Catabolite-Repressed Cell Wall Protein from the Mycoparasitic Fungus *Trichoderma harzianum*. *Mol. Gen. Genet.* **1994**, *242*, 461–466. [[CrossRef](#)] [[PubMed](#)]
89. Guo, R.; Wang, Z.; Zhou, C.; Liu, Z.; Zhang, P.; Fan, H. Transcriptomic Analysis Reveals Biocontrol Mechanisms of *Trichoderma harzianum* ACCC30371 under Eight Culture Conditions. *J. For. Res.* **2020**, *31*, 1863–1873. [[CrossRef](#)]
90. Rosado, I.V.; Rey, M.; Codón, A.C.; Govantes, J.; Moreno-Mateos, M.A.; Benítez, T. QID74 Cell Wall Protein of *Trichoderma harzianum* Is Involved in Cell Protection and Adherence to Hydrophobic Surfaces. *Fungal Genet. Biol.* **2007**, *44*, 950–964. [[CrossRef](#)] [[PubMed](#)]
91. Muñoz, G.; Nakari-Setälä, T.; Agosin, E.; Penttilä, M. Hydrophobin Gene *Srh1*, Expressed during Sporulation of the Biocontrol Agent *Trichoderma harzianum*. *Curr. Genet.* **1997**, *32*, 225–230. [[CrossRef](#)] [[PubMed](#)]
92. Riveros, G.; Shokribousjein, Z.; Karla, M.; Riveros, D.; Shokribousjein, Z.; Losada-Pérez, P.; Khalesi, M.R.; Cordova, K.; Michiels, C.; Delcour, J.A.; et al. Comparison of Structure, Sequence, Physical Interactions and Its Effects on Primary Gushing among Several Class II Hydrophobins. *Monatsschrift Brauwiss* **2015**, *68*, 38–45.
93. Przylucka, A.; Akcapinar, G.B.; Chenthamara, K.; Cai, F.; Grujic, M.; Karpenko, J.; Livoi, M.; Shen, Q.; Kubicek, C.P.; Druzhinina, I.S. *HFB7*—A Novel Orphan Hydrophobin of the *Harzianum* and *Virens* Clades of *Trichoderma*, Is Involved in Response to Biotic and Abiotic Stresses. *Fungal Genet. Biol.* **2017**, *102*, 63–76. [[CrossRef](#)] [[PubMed](#)]
94. Lohrasbi-Nejad, A.; Torkzadeh-Mahani, M.; Hosseinkhani, S. Heterologous Expression of a Hydrophobin *HFB1* and Evaluation of Its Contribution to Producing Stable Foam. *Protein Expr. Purif.* **2016**, *118*, 25–30. [[CrossRef](#)] [[PubMed](#)]
95. Kottmeier, K.; Günther, T.J.; Weber, J.; Kurtz, S.; Ostermann, K.; Rödel, G.; Bley, T. Constitutive Expression of Hydrophobin *HFB1* from *Trichoderma reesei* in *Pichia pastoris* and Its Pre-Purification by Foam Separation during Cultivation. *Eng. Life Sci.* **2012**, *12*, 162–170. [[CrossRef](#)]
96. Askolin, S.; Penttilä, M.; Wösten, H.A.B.; Nakari-Setälä, T. The *Trichoderma reesei* Hydrophobin Genes *Hfb1* and *Hfb2* Have Diverse Functions in Fungal Development. *FEMS Microbiol. Lett.* **2005**, *253*, 281–288. [[CrossRef](#)] [[PubMed](#)]
97. Nakari-Setälä, T.; Aro, N.; Ilmén, M.; Muñoz, G.; Kalkkinen, N.; Penttilä, M. Differential Expression of the Vegetative and Spore-Bound Hydrophobins of *Trichoderma reesei*: Cloning and Characterization of *Hfb2* Gene. *Eur. J. Biochem.* **1997**, *248*, 415–423. [[CrossRef](#)] [[PubMed](#)]
98. He, R.; Li, C.; Feng, J.; Zhang, D. A Class II Hydrophobin Gene, *Trhfb3*, Participates in Fungal Asexual Development of *Trichoderma reesei*. *FEMS Microbiol. Lett. Adv. Access* **2017**, *364*, fnw297. [[CrossRef](#)] [[PubMed](#)]
99. Scherrer, S.; Honegger, R. Inter- and Intraspecific Variation of Homologous Hydrophobin (*H1*) Gene Sequences among *Xanthoria* spp. (Lichen-Forming Ascomycetes). *New Phytol.* **2003**, *158*, 375–389. [[CrossRef](#)]
100. Scherrer, S.; De Vries, O.M.H.; Dudler, R.; Wessels, J.G.H.; Honegger, R. Interfacial Self-Assembly of Fungal Hydrophobins of the Lichen-Forming Ascomycetes *Xanthoria parietina* and *X. ectaneoides*. *Fungal Genet. Biol.* **2000**, *30*, 81–93. [[CrossRef](#)] [[PubMed](#)]

101. Scherrer, S.; Haisch, A.; Honegger, R. Characterization and Expression of *XPH1*, the Hydrophobin Gene of the Lichen-Forming Ascomycete *Xanthoria parietina*. *New Phytol.* **2002**, *154*, 175–184. [\[CrossRef\]](#)
102. Fedorova, N.D.; Khaldi, N.; Joardar, V.S.; Maiti, R.; Amedeo, P.; Anderson, M.J.; Crabtree, J.; Silva, J.C.; Badger, J.H.; Albarraq, A.; et al. Genomic Islands in the Pathogenic Filamentous Fungus *Aspergillus fumigatus*. *PLoS Genet.* **2008**, *4*, e1000046. [\[CrossRef\]](#) [\[PubMed\]](#)
103. Nierman, W.C.; Pain, A.; Anderson, M.J.; Wortman, J.R.; Kim, H.S.; Arroyo, J.; Berriman, M.; Abe, K.; Archer, D.B.; Bermejo, C.; et al. Genomic Sequence of the Pathogenic and Allergenic Filamentous Fungus *Aspergillus fumigatus*. *Nature* **2005**, *438*, 1151–1156. [\[CrossRef\]](#) [\[PubMed\]](#)
104. Machida, M.; Asai, K.; Sano, M.; Tanaka, T.; Kumagai, T.; Terai, G.; Kusumoto, K.-I.; Arima, T.; Akita, O.; Kashiwagi, Y.; et al. Genome Sequencing and Analysis of *Aspergillus oryzae*. *Nature* **2005**, *438*, 1157–1161. [\[CrossRef\]](#) [\[PubMed\]](#)
105. Beauvais, A.; Schmidt, C.; Guadagnini, S.; Roux, P.; Perret, E.; Henry, C.; Paris, S.; Mallet, A.; Prévost, M.-C.; Latgé, J.P. An Extracellular Matrix Glues Together the Aerial-Grown Hyphae of *Aspergillus fumigatus*. *Cell. Microbiol.* **2007**, *9*, 1588–1600. [\[CrossRef\]](#) [\[PubMed\]](#)
106. Thau, N.; Monod, M.; Crestani, B.; Rolland, C.; Tronchin, G.; Latgé, J.P.; Paris, S. Rodletless Mutants of *Aspergillus fumigatus*. *Infect. Immun.* **1994**, *62*, 4380–4388. [\[CrossRef\]](#) [\[PubMed\]](#)
107. Whiteford, J.R.; Lacroix, H.; Talbot, N.J.; Spanu, P.D. Stage-Specific Cellular Localisation of Two Hydrophobins during Plant Infection by the Pathogenic Fungus *Cladosporium fulvum*. *Fungal Genet. Biol.* **2004**, *41*, 624–634. [\[CrossRef\]](#) [\[PubMed\]](#)
108. Segers, G.C.; Hamada, W.; Oliver, R.P.; Spanu, P.D. Isolation and Characterisation of Five Different Hydrophobin-Encoding CDNAs from the Fungal Tomato Pathogen *Cladosporium fulvum*. *Mol. Gen. Genet.* **1999**, *261*, 644–652. [\[CrossRef\]](#) [\[PubMed\]](#)
109. Whiteford, J.R.; Spanu, P.D. The Hydrophobin *HCF-1* of *Cladosporium fulvum* Is Required for Efficient Water-Mediated Dispersal of Conidia. *Fungal Genet. Biol.* **2001**, *32*, 159–168. [\[CrossRef\]](#) [\[PubMed\]](#)
110. Lacroix, H.; Whiteford, J.R.; Spanu, P.D. Localization of *Cladosporium fulvum* Hydrophobins Reveals a Role for *HCF-6* in Adhesion. *FEMS Microbiol. Lett.* **2008**, *286*, 136–144. [\[CrossRef\]](#) [\[PubMed\]](#)
111. Nielsen, P.S.; Clark, A.J.; Oliver, R.P.; Huber, M.; Spanu, P.D. *HCF-6*, a Novel Class II Hydrophobin from *Cladosporium fulvum*. *Microbiol. Res.* **2001**, *156*, 59–63. [\[CrossRef\]](#) [\[PubMed\]](#)
112. Espino-Rammer, L.; Ribitsch, D.; Przylucka, A.; Marold, A.; Greimel, K.J.; Acero, E.H.; Guebitz, G.M.; Kubicek, C.P.; Druzhinina, I.S. Two Novel Class II Hydrophobins from *Trichoderma* spp. Stimulate Enzymatic Hydrolysis of Poly(Ethylene Terephthalate) When Expressed as Fusion Proteins. *Appl. Environ. Microbiol.* **2013**, *79*, 4230–4238. [\[CrossRef\]](#) [\[PubMed\]](#)
113. Huang, Y.; Mijiti, G.; Wang, Z.; Yu, W.; Fan, H.; Zhang, R.; Liu, Z. Functional Analysis of the Class II Hydrophobin Gene *HFB2-6* from the Biocontrol Agent *Trichoderma asperellum* ACCC30536. *Microbiol. Res.* **2015**, *171*, 8–20. [\[CrossRef\]](#) [\[PubMed\]](#)
114. Moscatiello, R.; Sello, S.; Ruocco, M.; Barbulova, A.; Cortese, E.; Nigris, S.; Baldan, B.; Chiurazzi, M.; Mariani, P.; Lorito, M.; et al. The Hydrophobin *HYTLO1* Secreted by the Biocontrol Fungus *Trichoderma longibrachiatum* Triggers a NAADP-Mediated Calcium Signalling Pathway in *Lotus japonicus*. *Int. J. Mol. Sci.* **2018**, *19*, 2596. [\[CrossRef\]](#) [\[PubMed\]](#)
115. Burmester, A.; Shelest, E.; Glöckner, G.; Heddergott, C.; Schindler, S.; Staib, P.; Heidel, A.; Felder, M.; Petzold, A.; Szafranski, K.; et al. Comparative and Functional Genomics Provide Insights into the Pathogenicity of Dermatophytic Fungi. *Genome Biol.* **2011**, *12*, R7. [\[CrossRef\]](#) [\[PubMed\]](#)
116. Heddergott, C.; Bruns, S.; Nietzsche, S.; Leonhardt, I.; Kurzai, O.; Kniemeyer, O.; Brakhage, A.A. The *Arthroderma benhamiae* Hydrophobin *HypA* Mediates Hydrophobicity and Influences Recognition by Human Immune Effector Cells. *Eukaryot. Cell* **2012**, *11*, 673–682. [\[CrossRef\]](#) [\[PubMed\]](#)
117. Lutterschmid, G.; Muranyi, M.; Stübner, M.; Vogel, R.F.; Niessen, L. Heterologous Expression of Surface-Active Proteins from Barley and Filamentous Fungi in *Pichia pastoris* and Characterization of Their Contribution to Beer Gushing. *Int. J. Food Microbiol.* **2011**, *147*, 17–25. [\[CrossRef\]](#) [\[PubMed\]](#)
118. Kao, C.Y.; Wu, C.T.; Lin, H.C.; Hsieh, D.K.; Lin, H.L.; Lee, M.H. The G Protein Subunit A1, CaGα1, Mediates Ethylene Sensing of Mango Anthracnose Pathogen *Colletotrichum asianum* to Regulate Fungal Development and Virulence and Mediates Surface Sensing for Spore Germination. *Front. Microbiol.* **2022**, *13*, 1048447. [\[CrossRef\]](#) [\[PubMed\]](#)
119. Talbot, N.J.; Ebbole, D.J.; Hamer, J.E. Identification and Characterization of *MPGI*, a Gene Involved in Pathogenicity from the Rice Blast Fungus *Magnaporthe grisea*. *Plant Cell* **1993**, *5*, 1575–1590. [\[CrossRef\]](#) [\[PubMed\]](#)
120. St Leger, R.; Staples, R.; Roberts, D. Cloning and Regulatory Analysis of Starvation-Stress Gene, *SsgA*, Encoding a Hydrophobin-like Protein from the Entomopathogenic Fungus, *Metarhizium anisopliae*. *Gene* **1992**, *120*, 119–124. [\[CrossRef\]](#) [\[PubMed\]](#)
121. Zhang, J.G.; Xu, S.Y.; Ying, S.H.; Feng, M.G. Only One of Three Hydrophobins (*Hyd1–3*) Contributes to Conidial Hydrophobicity and Insect Pathogenicity of *Metarhizium robertsii*. *J. Invertebr. Pathol.* **2023**, *201*, 108006. [\[CrossRef\]](#) [\[PubMed\]](#)
122. Cho, E.-M.; Kirkland, B.H.; Holder, D.J.; Keyhani, N.O. Phage Display cDNA Cloning and Expression Analysis of Hydrophobins from the Entomopathogenic Fungus *Beauveria (Cordyceps) bassiana*. *Microbiology* **2007**, *153*, 3438–3447. [\[CrossRef\]](#) [\[PubMed\]](#)
123. Moonjely, S.; Keyhani, N.O.; Bidochka, M.J. Hydrophobins Contribute to Root Colonization and Stress Responses in the Rhizosphere-Competent Insect Pathogenic Fungus *Beauveria bassiana*. *Microbiology* **2018**, *164*, 517–528. [\[CrossRef\]](#) [\[PubMed\]](#)

124. Bowden, C.G.; Hintz, W.E.; Jeng, R.; Hubbes, M.; Horgen, P.A. Isolation and Characterization of the *Cerato-ulmin* Toxin Gene of the Dutch Elm Disease Pathogen, *Ophiostoma ulmi*. *Curr. Genet.* **1994**, *25*, 323–329. [\[CrossRef\]](#) [\[PubMed\]](#)
125. Zhang, X.; Zhao, L.; Liu, S.; Zhou, J.; Wu, Y.; Feng, Z.; Zhang, Y.; Zhu, H.; Wei, F.; Feng, H. Identification and Functional Analysis of a Novel Hydrophobic Protein VdHP1 from *Verticillium dahliae*. *Microbiol. Spectr.* **2022**, *10*, e0247821. [\[CrossRef\]](#) [\[PubMed\]](#)
126. Albuquerque, P.; Kyaw, C.M.; Saldanha, R.R.; Brigido, M.M.; Felipe, M.S.S.; Silva-Pereira, I. *Pbhyd1* and *Pbhyd2*: Two Mycelium-Specific Hydrophobin Genes from the Dimorphic Fungus *Paracoccidioides brasiliensis*. *Fungal Genet. Biol.* **2004**, *41*, 510–520. [\[CrossRef\]](#) [\[PubMed\]](#)
127. Carresi, L.; Comparini, C.; Bettini, P.P.; Pazzagli, L.; Cappugi, G.; Scala, F.; Scala, A. Isolation of the Orthologue of the *Cerato-ulmin* Gene in *Ophiostoma quercus* and Characterization of the Purified Protein. *Mycol. Res.* **2008**, *112*, 1245–1255. [\[CrossRef\]](#) [\[PubMed\]](#)
128. Mohammed, M.R.; Balamurugan, M.; Amrathlal, R.S.; Kannan, P.; Jayapal, J.M.; Namperumalsamy, V.P.; Prajna, L.; Kuppamuthu, D. Identification of the Proteoforms of Surface Localized *RodA* of *Aspergillus flavus* and Determination of the Mechanism of Proteoform Generation. *J. Proteom.* **2019**, *193*, 62–70. [\[CrossRef\]](#) [\[PubMed\]](#)
129. Weichel, M.; Schmid-Grendelmeier, P.; Rhyner, C.; Achatz, G.; Blaser, K.; Cramer, R. Immunoglobulin E-Binding and Skin Test Reactivity to Hydrophobin HCh-1 from *Cladosporium herbarum*, the First Allergenic Cell Wall Component of Fungi. *Clin. Exp. Allergy* **2003**, *33*, 72. [\[CrossRef\]](#) [\[PubMed\]](#)
130. Wang, N.; Wang, J.; Lu, J.; Liu, Y.; Xi, Y.; Song, M.; Guan, X.; Li, Z.; Li, X.; Zhang, Y.; et al. The *Colletotrichum siamense* Hydrophobin CsHydr1 Interacts with the Lipid Droplet-Coating Protein CsCap20 and Regulates Lipid Metabolism and Virulence. *J. Fungi* **2022**, *8*, 977. [\[CrossRef\]](#) [\[PubMed\]](#)
131. So, K.K.; Kim, D.H. Role of MAPK Signaling Pathways in Regulating the Hydrophobin *Cryparin* in the Chestnut Blight Fungus *Cryphonectria parasitica*. *Mycobiology* **2017**, *45*, 362–369. [\[CrossRef\]](#) [\[PubMed\]](#)
132. Kazmierczak, P.; Dae, H.K.; Turina, M.; Van Alfen, N.K. A Hydrophobin of the Chestnut Blight Fungus, *Cryphonectria parasitica*, Is Required for Stromal Pustule Eruption. *Eukaryot. Cell* **2005**, *4*, 931–936. [\[CrossRef\]](#) [\[PubMed\]](#)
133. Fuchs, U.; Czymmek, K.J.; Sweigard, J.A. Five Hydrophobin Genes in *Fusarium verticillioides* Include Two Required for Microconidial Chain Formation. *Fungal Genet. Biol.* **2004**, *41*, 852–864. [\[CrossRef\]](#) [\[PubMed\]](#)
134. Prajapati, D.; Patel, N.; Gohel, N. A Review on Entomopathogenic Facet of *Fusarium verticillioides*. *Environ. Ecol.* **2023**, *41*, 2365–2374. [\[CrossRef\]](#)
135. Talbot, N.J.; Kershaw, M.J.; Wakley, G.E.; H de Vries, O.M.; H Wessels, J.G.; Hamer, J.E. *MPG1* Encodes a Fungal Hydrophobin Involved in Surface Interactions during Infection-Related Development of *Magnaporthe grisea*. *Plant Cell* **1996**, *8*, 985–999. [\[CrossRef\]](#) [\[PubMed\]](#)
136. Soanes, D.M.; Kershaw, M.J.; Cooley, R.N.; Talbot, N.J. Regulation of the *MPG1* Hydrophobin Gene in the Rice Blast Fungus *Magnaporthe grisea*. *Mol. Plant Microbe Interact.* **2002**, *15*, 1253–1267. [\[CrossRef\]](#) [\[PubMed\]](#)
137. Jiang, Z.Y.; Ligoxygakis, P.; Xia, Y.X. *HYD3*, a Conidial Hydrophobin of the Fungal Entomopathogen *Metarhizium acridum* Induces the Immunity of Its Specialist Host Locust. *Int. J. Biol. Macromol.* **2020**, *165*, 1303–1311. [\[CrossRef\]](#) [\[PubMed\]](#)
138. Bidochka, M.J.; De Koning, J.; Leger, J.S. Analysis of a Genomic Clone of Hydrophobin (*SsgA*) from the Entomopathogenic Fungus *Metarhizium anisopliae*. *Mycol. Res.* **2001**, *105*, 360–364. [\[CrossRef\]](#)
139. Fang, W.; Pei, Y.; Bidochka, M.J. A Regulator of a G Protein Signalling (RGS) Gene, *Cag8*, from the Insect-Pathogenic Fungus *Metarhizium anisopliae* Is Involved in Conidiation Virulence and Hydrophobin Synthesis. *Microbiology* **2007**, *153*, 1017–1025. [\[CrossRef\]](#) [\[PubMed\]](#)
140. Casarrubia, S.; Daghighi, S.; Kohler, A.; Morin, E.; Khouja, H.R.; Daguerre, Y.; Veneault-Fourrey, C.; Martin, F.M.; Perotto, S.; Martino, E. The Hydrophobin-like *OmSSP1* May Be an Effector in the Ericoid Mycorrhizal Symbiosis. *Front. Plant Sci.* **2018**, *9*, 546. [\[CrossRef\]](#) [\[PubMed\]](#)
141. Del Sorbo, G.; Scala, F.; Parrella, G.; Lorito, M.; Comparini, C.; Ruocco, M.; Scala, A. Functional Expression of the Gene *Cu*, Encoding the Phytotoxic Hydrophobin *Cerato-ulmin*, Enables *Ophiostoma quercus*, a Nonpathogen on Elm, to Cause Symptoms of Dutch Elm Disease. *Mol. Plant Microbe Interact.* **2000**, *13*, 43–53. [\[CrossRef\]](#) [\[PubMed\]](#)
142. Sherif, S.; Jones, A.M.P.; Shukla, M.R.; Saxena, P.K. Establishment of Invasive and Non-Invasive Reporter Systems to Investigate American Elm-*Ophiostoma novo-ulmi* Interactions. *Fungal Genet. Biol.* **2014**, *71*, 32–41. [\[CrossRef\]](#) [\[PubMed\]](#)
143. Temple, B.; Horgen, P.A.; Bernier, L.; Hintz, W.E. *Cerato-ulmin*, a Hydrophobin Secreted by the Causal Agents of Dutch Elm Disease, Is a Parasitic Fitness Factor. *Fungal Genet. Biol.* **1997**, *22*, 39–53. [\[CrossRef\]](#) [\[PubMed\]](#)
144. Zhang, X.; Kirby, S.M.; Chen, Y.; Anna, S.L.; Walker, L.M.; Hung, F.R.; Russo, P.S. Formation and Elasticity of Membranes of the Class II Hydrophobin *Cerato-ulmin* at Oil-Water Interfaces. *Colloids Surf. B Biointerfaces* **2018**, *164*, 98–106. [\[CrossRef\]](#) [\[PubMed\]](#)
145. Boualem, K.; Waché, Y.; Garmyn, D.; Karbowiak, T.; Durand, A.; Gervais, P.; Cavin, J.F. Cloning and Expression of Genes Involved in Conidiation and Surface Properties of *Penicillium Camemberti* Grown in Liquid and Solid Cultures. *Res. Microbiol.* **2008**, *159*, 110–117. [\[CrossRef\]](#) [\[PubMed\]](#)

146. Aimanianda, V.; Bayry, J.; Bozza, S.; Kniemeyer, O.; Perruccio, K.; Elluru, S.R.; Clavaud, C.; Paris, S.; Brakhage, A.A.; Kaveri, S.V.; et al. Surface Hydrophobin Prevents Immune Recognition of Airborne Fungal Spores. *Nature* **2009**, *460*, 1117–1121. [\[CrossRef\]](#) [\[PubMed\]](#)
147. Pham, C.L.L.; Rey, A.; Lo, V.; Soulès, M.; Ren, Q.; Meisl, G.; Knowles, T.P.J.; Kwan, A.H.; Sunde, M. Self-Assembly of MPG1, a Hydrophobin Protein from the Rice Blast Fungus That Forms Functional Amyloid Coatings, Occurs by a Surface-Driven Mechanism. *Sci. Rep.* **2016**, *6*, 25288. [\[CrossRef\]](#) [\[PubMed\]](#)
148. Anjago, W.M.; Zeng, W.; Chen, Y.; Wang, Y.; Biregeya, J.; Li, Y.; Zhang, T.; Peng, M.; Cai, Y.; Shi, M.; et al. The Molecular Mechanism Underlying Pathogenicity Inhibition by Sanguinarine in *Magnaporthe oryzae*. *Pest Manag. Sci.* **2021**, *77*, 4669–4679. [\[CrossRef\]](#) [\[PubMed\]](#)
149. Guzmán-Guzmán, P.; Alemán-Duarte, M.I.; Delaye, L.; Herrera-Estrella, A.; Olmedo-Monfil, V. Identification of Effector-like Proteins in *Trichoderma* spp. and Role of a Hydrophobin in the Plant-Fungus Interaction and Mycoparasitism. *BMC Genet.* **2017**, *18*, 16. [\[CrossRef\]](#) [\[PubMed\]](#)
150. Takahashi, T.; Tanaka, T.; Tsushima, Y.; Muragaki, K.; Uehara, K.; Takeuchi, S.; Maeda, H.; Yamagata, Y.; Nakayama, M.; Yoshimi, A.; et al. Ionic Interaction of Positive Amino Acid Residues of Fungal Hydrophobin RolA with Acidic Amino Acid Residues of Cutinase CutL1. *Mol. Microbiol.* **2015**, *96*, 14–27. [\[CrossRef\]](#) [\[PubMed\]](#)
151. Sun, L.; Xu, H.; Xu, J.H.; Wang, S.N.; Wang, J.W.; Zhang, H.F.; Jia, W.R.; Li, L.S. Enhanced Antitumor Efficacy of Curcumin-Loaded PLGA Nanoparticles Coated with Unique Fungal Hydrophobin. *AAPS PharmSciTech* **2020**, *21*, 171. [\[CrossRef\]](#) [\[PubMed\]](#)
152. Wang, X.; Liu, F.; Zhang, Y.; Zhu, D.; Saris, P.E.J.; Xu, H.; Qiao, M. Effective Adsorption of Nisin on the Surface of Polystyrene Using Hydrophobin HGFI. *Int. J. Biol. Macromol.* **2021**, *173*, 399–408. [\[CrossRef\]](#) [\[PubMed\]](#)
153. Zhao, L.; Xu, H.; Li, Y.; Song, D.; Wang, X.; Qiao, M.; Gong, M. Novel Application of Hydrophobin in Medical Science: A Drug Carrier for Improving Serum Stability. *Sci. Rep.* **2016**, *6*, 26461. [\[CrossRef\]](#) [\[PubMed\]](#)
154. Barani, M.; Mirzaei, M.; Torkzadeh-Mahani, M.; Lohrasbi-Nejad, A.; Nematollahi, M.H. A New Formulation of Hydrophobin-Coated Niosome as a Drug Carrier to Cancer Cells. *Mater. Sci. Eng. C* **2020**, *113*, 110975. [\[CrossRef\]](#) [\[PubMed\]](#)
155. Pitocchi, R.; Stanzione, I.; Illiano, A.; Amoresano, A.; Tarallo, O.; Cicatiello, P.; Piscitelli, A.; Giardina, P. Evidence of Small Fungal Cysteine-Rich Proteins Acting as Biosurfactants and Self-Assembling into Large Fibers. *Int. J. Mol. Sci.* **2023**, *24*, 13843. [\[CrossRef\]](#) [\[PubMed\]](#)
156. Klauer, R.R.; Silvestri, R.; White, H.; Das, M.; Hayes, R.D.; Riley, R.; Lipzen, A.; Barry, K.; Grigoriev, I.V.; Talag, J.; et al. Hydrophobins from *Aspergillus* Mediate Fungal Interactions with Microplastics. *Environ. Sci. Technol.* **2025**, *59*, 14528–14539. [\[CrossRef\]](#) [\[PubMed\]](#)
157. Puspitasari, N.; Tsai, S.L.; Lee, C.K. Fungal Hydrophobin RolA Enhanced PETase Hydrolysis of Polyethylene Terephthalate. *Appl. Biochem. Biotechnol.* **2021**, *193*, 1284–1295. [\[CrossRef\]](#) [\[PubMed\]](#)
158. Dubey, M.K.; Jensen, D.F.; Karlsson, M. Hydrophobins Are Required for Conidial Hydrophobicity and Plant Root Colonization in the Fungal Biocontrol Agent *Clonostachys rosea*. *BMC Microbiol.* **2014**, *14*, 18. [\[CrossRef\]](#) [\[PubMed\]](#)
159. Stübner, M.; Lutterschmid, G.; Vogel, R.F.; Niessen, L. Heterologous Expression of the Hydrophobin FcHyd5p from *Fusarium culmorum* in *Pichia pastoris* and Evaluation of Its Surface Activity and Contribution to Gushing of Carbonated Beverages. *Int. J. Food Microbiol.* **2010**, *141*, 110–115. [\[CrossRef\]](#) [\[PubMed\]](#)
160. Sevim, A.; Donzelli, B.G.G.; Wu, D.; Demirbag, Z.; Gibson, D.M.; Turgeon, B.G. Hydrophobin Genes of the Entomopathogenic Fungus, *Metarhizium brunneum*, Are Differentially Expressed and Corresponding Mutants Are Decreased in Virulence. *Curr. Genet.* **2012**, *58*, 79–92. [\[CrossRef\]](#) [\[PubMed\]](#)
161. Chang, H.J.; Choi, H.; Na, S. Predicting the Self-Assembly Film Structure of Class II Hydrophobin NC2 and Estimating Its Structural Characteristics. *Colloids Surf. B Biointerfaces* **2020**, *195*, 111269. [\[CrossRef\]](#) [\[PubMed\]](#)
162. Lunkenbein, S.; Takenberg, M.; Nimtz, M.; Berger, R.G. Characterization of a Hydrophobin of the Ascomycete *Paecilomyces farinosus*. *J. Basic Microbiol.* **2011**, *51*, 404–414. [\[CrossRef\]](#) [\[PubMed\]](#)
163. Zelena, K.; Takenberg, M.; Lunkenbein, S.; Woche, S.K.; Nimtz, M.; Berger, R.G. PfaH2: A Novel Hydrophobin from the Ascomycete *Paecilomyces farinosus*. *Biotechnol. Appl. Biochem.* **2013**, *60*, 147–154. [\[CrossRef\]](#) [\[PubMed\]](#)
164. Kuvarina, A.E.; Rogozhin, E.A.; Sykonnikov, M.A.; Timofeeva, A.V.; Serebryakova, M.V.; Fedorova, N.V.; Kokaeva, L.Y.; Efimenko, T.A.; Georgieva, M.L.; Sadykova, V.S. Isolation and Characterization of a Novel Hydrophobin, Sa-HFB1, with Antifungal Activity from an Alkaliphilic Fungus, *Sodiomyces alkalinus*. *J. Fungi* **2022**, *8*, 659. [\[CrossRef\]](#) [\[PubMed\]](#)
165. Viterbo, A.; Chet, I. TasHyd1, a New Hydrophobin Gene from the Biocontrol Agent *Trichoderma asperellum*, Is Involved in Plant Root Colonization. *Mol. Plant Pathol.* **2006**, *7*, 249–258. [\[CrossRef\]](#) [\[PubMed\]](#)
166. Zhang, H.; Ji, S.; Guo, R.; Zhou, C.; Wang, Y.; Fan, H.; Liu, Z. Hydrophobin HFBII-4 from *Trichoderma asperellum* Induces Antifungal Resistance in Poplar. *Braz. J. Microbiol.* **2019**, *50*, 603–612. [\[CrossRef\]](#) [\[PubMed\]](#)
167. Mikus, M.; Hatvani, L.; Neuhofer, T.; Komoń-Zelazowska, M.; Dieckmann, R.; Schwecke, T.; Druzhinina, I.S.; Von Döhren, H.; Kubicek, C.P. Differential Regulation and Posttranslational Processing of the Class II Hydrophobin Genes from the Biocontrol Fungus *Hypocrea atroviridis*. *Appl. Environ. Microbiol.* **2009**, *75*, 3222–3229. [\[CrossRef\]](#) [\[PubMed\]](#)

168. Kubicek, C.P.; Baker, S.; Gamauf, C.; Kenerley, C.M.; Druzhinina, I.S. Purifying Selection and Birth-and-Death Evolution in the Class II Hydrophobin Gene Families of the Ascomycete *Trichoderma/Hypocrea*. *BMC Evol. Biol.* **2008**, *8*, 4. [[CrossRef](#)] [[PubMed](#)]
169. Neuhof, T.; Dieckmann, R.; Druzhinina, I.S.; Kubicek, C.P.; Nakari-Setälä, T.; Penttilä, M.; Von Döhren, H. Direct Identification of Hydrophobins and Their Processing in *Trichoderma* Using Intact-Cell MALDI-TOF MS. *FEBS J.* **2007**, *274*, 841–852. [[CrossRef](#)] [[PubMed](#)]
170. Ruocco, M.; Lanzuise, S.; Lombardi, N.; Woo, S.L.; Vinale, F.; Marra, R.; Varlese, R.; Manganiello, G.; Pascale, A.; Scala, V.; et al. Multiple Roles and Effects of a Novel *Trichoderma* Hydrophobin. *Mol. Plant-Microbe Interact.* **2015**, *28*, 167–179. [[CrossRef](#)] [[PubMed](#)]
171. Seidl-Seiboth, V.; Gruber, S.; Sezerman, U.; Schwecke, T.; Albayrak, A.; Neuhof, T.; Von Döhren, H.; Baker, S.E.; Kubicek, C.P. Novel Hydrophobins from *Trichoderma* Define a New Hydrophobin Subclass: Protein Properties, Evolution, Regulation and Processing. *J. Mol. Evol.* **2011**, *72*, 339–351. [[CrossRef](#)] [[PubMed](#)]
172. Bonazza, K.; Gaderer, R.; Neudl, S.; Przylucka, A.; Allmaier, G.; Druzhinina, I.S.; Grothe, H.; Friedbacher, G.; Seidl-Seiboth, V. The Fungal Cerato-Platanin Protein EPL1 Forms Highly Ordered Layers at Hydrophobic/Hydrophilic Interfaces. *Soft Matter* **2014**, *11*, 1723–1732. [[CrossRef](#)] [[PubMed](#)]
173. Morales, P.; Thurston, C.F. Efficient Isolation of Genes Differentially Expressed on Cellulose by Suppression Subtractive Hybridization in *Agaricus bisporus*. *Mycol. Res.* **2003**, *107*, 401–407. [[CrossRef](#)] [[PubMed](#)]
174. Stajich, J.E.; Wilke, S.K.; Ahrén, D.; Au, C.H.; Birren, B.W.; Borodovsky, M.; Burns, C.; Canbäck, B.; Casselton, L.A.; Cheng, C.K.; et al. Insights into Evolution of Multicellular Fungi from the Assembled Chromosomes of the Mushroom *Coprinopsis cinerea* (*Coprinus cinereus*). *Proc. Natl. Acad. Sci. USA* **2010**, *107*, 11889–11894. [[CrossRef](#)] [[PubMed](#)]
175. Olson, Å.; Aerts, A.; Asiegbu, F.; Belbahri, L.; Bouzid, O.; Broberg, A.; Canbäck, B.; Coutinho, P.M.; Cullen, D.; Dalman, K.; et al. Insight into Trade-off between Wood Decay and Parasitism from the Genome of a Fungal Forest Pathogen. *New Phytol.* **2012**, *194*, 1001–1013. [[CrossRef](#)] [[PubMed](#)]
176. Martin, F.; Aerts, A.; Ahrén, D.; Brun, A.; Danchin, E.G.J.; Duchaussoy, F.; Gibon, J.; Kohler, A.; Lindquist, E.; Pereda, V.; et al. The Genome of *Laccaria Bicolor* Provides Insights into Mycorrhizal Symbiosis. *Nature* **2008**, *452*, 88–92. [[CrossRef](#)] [[PubMed](#)]
177. Wright, D.P.; Johansson, T.; Le Quéré, A.; Söderström, B.; Tunlid, A. Spatial Patterns of Gene Expression in the Extramatrical Mycelium and Mycorrhizal Root Tips Formed by the Ectomycorrhizal Fungus *Paxillus involutus* in Association with Birch (*Betula pendula*) Seedlings in Soil Microcosms. *New Phytol.* **2005**, *167*, 579–596. [[CrossRef](#)] [[PubMed](#)]
178. Larraya, L.M.; Pérez, G.; Peñas, M.M.; Baars, J.J.P.; Mikosch, T.S.P.; Pisabarro, A.G.; Ramírez, L. Molecular Karyotype of the White Rot Fungus *Pleurotus ostreatus*. *Appl. Environ. Microbiol.* **1999**, *65*, 3413–3417. [[CrossRef](#)] [[PubMed](#)]
179. Riley, R.; Salamov, A.A.; Brown, D.W.; Nagy, L.G.; Floudas, D.; Held, B.W.; Levasseur, A.; Lombard, V.; Morin, E.; Otilar, R.; et al. Extensive Sampling of Basidiomycete Genomes Demonstrates Inadequacy of the White-Rot/Brown-Rot Paradigm for Wood Decay Fungi. *Proc. Natl. Acad. Sci. USA* **2014**, *111*, 9923–9928. [[CrossRef](#)] [[PubMed](#)]
180. Ma, A.; Shan, L.; Wang, N.; Zheng, L.; Chen, L.; Xie, B. Characterization of a *Pleurotus ostreatus* Fruiting Body-specific Hydrophobin Gene, *Po.Hyd. J. Basic Microbiol.* **2007**, *47*, 317–324. [[CrossRef](#)] [[PubMed](#)]
181. Dons, J.J.M.; Mulder, G.H.; Rouwendal, G.J.A.; Springer, J.; Bremer, W.; Wessels, J.G.H. Sequence Analysis of a Split Gene Involved in Fruiting from the Fungus *Schizophyllum commune*. *EMBO J.* **1984**, *3*, 2101–2106. [[CrossRef](#)] [[PubMed](#)]
182. Schuren, F.H.J.; Wessels, J.G.H. Two Genes Specifically Expressed in Fruiting Dikaryons of *Schizophyllum commune*: Homologies with a Gene Not Regulated by Mating-Type Genes. *Gene* **1990**, *90*, 199–205. [[CrossRef](#)] [[PubMed](#)]
183. Ohm, R.A.; de Jong, J.F.; Lugones, L.G.; Aerts, A.; Kothe, E.; Stajich, J.E.; de Vries, R.P.; Record, E.; Levasseur, A.; Baker, S.E.; et al. Genome Sequence of the Model Mushroom *Schizophyllum commune*. *Nat. Biotechnol.* **2010**, *28*, 957–963. [[CrossRef](#)] [[PubMed](#)]
184. Eastwood, D.C.; Floudas, D.; Binder, M.; Majcherczyk, A.; Schneider, P.; Aerts, A.; Asiegbu, F.O.; Baker, S.E.; Barry, K.; Bendiksby, M.; et al. The Plant Cell Wall-Decomposing Machinery Underlies the Functional Diversity of Forest Fungi. *Science* **2011**, *333*, 762–765. [[CrossRef](#)] [[PubMed](#)]
185. Schirawski, J.; Mannhaupt, G.; Münch, K.; Brefort, T.; Schipper, K.; Doehlemann, G.; Di Stasio, M.; Rössel, N.; Mendoza-Mendoza, A.; Pester, D.; et al. Pathogenicity Determinants in Smut Fungi Revealed by Genome Comparison. *Science* **2010**, *330*, 1546–1548. [[CrossRef](#)] [[PubMed](#)]
186. Lugones, L.G.; Bosscher, J.S.; Scholtmeyer, K.; De Vries, O.M.H.; Wessels, J.G.H. An Abundant Hydrophobin (*ABHI*) Forms Hydrophobic Rodlet Layers in *Agaricus bisporus* Fruiting Bodies. *Microbiology* **1996**, *142*, 1321–1329. [[CrossRef](#)] [[PubMed](#)]
187. Wösten, H.A.; de Vries, O.M.; van der Mei, H.C.; Busscher, H.J.; Wessels, J.G. Atomic Composition of the Hydrophobic and Hydrophilic Membrane Sides of Self-Assembled *SC3p* Hydrophobin. *J. Bacteriol.* **1994**, *176*, 7085–7086. [[CrossRef](#)] [[PubMed](#)]
188. De Vocht, M.L.; Reviakine, I.; Wosten, H.A.B.; Brisson, A.; Wessels, J.G.H.; Robillard, G.T. Structural and Functional Role of the Disulfide Bridges in the Hydrophobin *SC3*. *J. Biol. Chem.* **2000**, *275*, 28428–28432. [[CrossRef](#)] [[PubMed](#)]
189. De Groot, P.W.J.; Roeven, R.T.P.; Van Griensven, L.J.L.D.; Visser, J.; Schaap, P.J. Different Temporal and Spatial Expression of Two Hydrophobin-Encoding Genes of the Edible Mushroom *Agaricus bisporus*. *Microbiology* **1999**, *145*, 1105–1113. [[CrossRef](#)] [[PubMed](#)]

190. Paslay, L.C.; Falgout, L.; Savin, D.A.; Heinhorst, S.; Cannon, G.C.; Morgan, S.E. Kinetics and Control of Self-Assembly of ABH1 Hydrophobin from the Edible White Button Mushroom. *Biomacromolecules* **2013**, *14*, 2283–2293. [\[CrossRef\]](#) [\[PubMed\]](#)
191. Morin, E.; Kohler, A.; Baker, A.R.; Foulongne-Oriol, M.; Lombard, V.; Nagye, L.G.; Ohm, R.A.; Patyshakuliyeve, A.; Brun, A.; Aerts, A.L.; et al. Genome Sequence of the Button Mushroom *Agaricus bisporus* Reveals Mechanisms Governing Adaptation to a Humic-Rich Ecological Niche. *Proc. Natl. Acad. Sci. USA* **2012**, *109*, 17501–17506. [\[CrossRef\]](#) [\[PubMed\]](#)
192. Han, J.; Kawauchi, M.; Terauchi, Y.; Yoshimi, A.; Tanaka, C.; Nakazawa, T.; Honda, Y. Physiological Function of Hydrophobin *Vmh3* in Lignin Degradation by White-Rot Fungus *Pleurotus ostreatus*. *Lett. Appl. Microbiol.* **2023**, *76*, ova048. [\[CrossRef\]](#) [\[PubMed\]](#)
193. Han, J.; Kawauchi, M.; Schiphof, K.; Terauchi, Y.; Yoshimi, A.; Tanaka, C.; Nakazawa, T.; Honda, Y. Features of Disruption Mutants of Genes Encoding for Hydrophobin *Vmh2* and *Vmh3* in Mycelial Formation and Resistance to Environmental Stress in *Pleurotus ostreatus*. *FEMS Microbiol. Lett.* **2023**, *370*, fnad036. [\[CrossRef\]](#) [\[PubMed\]](#)
194. Han, J.; Kawauchi, M.; Terauchi, Y.; Tsuji, K.; Yoshimi, A.; Tanaka, C.; Nakazawa, T.; Honda, Y. Physiological Function of Hydrophobin *Hydph16* in Cell Wall Formation in Agaricomycete *Pleurotus ostreatus*. *Fungal Genet. Biol.* **2025**, *176*, 103943. [\[CrossRef\]](#) [\[PubMed\]](#)
195. Xu, D.; Wang, Y.; Keerio, A.A.; Ma, A. Identification of Hydrophobin Genes and Their Physiological Functions Related to Growth and Development in *Pleurotus ostreatus*. *Microbiol. Res.* **2021**, *247*, 126723. [\[CrossRef\]](#) [\[PubMed\]](#)
196. Ando, A.; Harada, A.; Miura, K.; Tamai, Y. A Gene Encoding a Hydrophobin, *Fvh1*, Is Specifically Expressed after the Induction of Fruiting in the Edible Mushroom *Flammulina velutipes*. *Curr. Genet.* **2001**, *39*, 190–197. [\[CrossRef\]](#) [\[PubMed\]](#)
197. Tao, Y.; Chen, R.; Yan, J.; Long, Y.; Tong, Z.; Song, H.; Xie, B. A Hydrophobin Gene, *Hyd9*, Plays an Important Role in the Formation of Aerial Hyphae and Primordia in *Flammulina filiformis*. *Gene* **2019**, *706*, 84–90. [\[CrossRef\]](#) [\[PubMed\]](#)
198. Yamada, M.; Sakuraba, S.; Shibata, K.; Inatomi, S.; Okazaki, M.; Shimosaka, M. Cloning and Characterization of a Gene Coding for a Hydrophobin, *Fv-Hyd1*, Specifically Expressed during Fruiting Body Development in the Basidiomycete *Flammulina velutipes*. *Appl. Microbiol. Biotechnol.* **2005**, *67*, 240–246. [\[CrossRef\]](#) [\[PubMed\]](#)
199. Ng, W.L.; Ng, T.P.; Kwan, H.S. Cloning and Characterization of Two Hydrophobin Genes Differentially Expressed during Fruit Body Development in *Lentinula edodes*. *FEMS Microbiol. Lett.* **2000**, *185*, 139–145. [\[CrossRef\]](#) [\[PubMed\]](#)
200. Suizu, T.; Zhou, G.-L.; Oowatari, Y.; Kawamukai, M. Analysis of Expressed Sequence Tags (ESTs) from *Lentinula edodes*. *Appl. Microbiol. Biotechnol.* **2008**, *79*, 461–470. [\[CrossRef\]](#) [\[PubMed\]](#)
201. Nishizawa, H.; Miyazaki, Y.; Kaneko, S.; Shishido, K. Distribution of *Hydrophobin 1* Gene Transcript in Developing Fruiting Bodies of *Lentinula edodes*. *Jpn. Biosci. Biotechnol. Biochem.* **2002**, *66*, 1951–1954. [\[CrossRef\]](#) [\[PubMed\]](#)
202. Takaki, K.; Yoshida, K.; Saito, T.; Kusaka, T.; Yamaguchi, R.; Takahashi, K.; Sakamoto, Y. Effect of Electrical Stimulation on Fruit Body Formation in Cultivating Mushrooms. *Microorganisms* **2014**, *2*, 58–72. [\[CrossRef\]](#) [\[PubMed\]](#)
203. Ásgeirsdóttir, S.A.; Halsall, J.R.; Casselton, L.A. Expression of Two Closely Linked Hydrophobin Genes of *Coprinus cinereus* Is Monokaryon-Specific and Down-Regulated by Theoid-1 Mutation. *Fungal Genet. Biol.* **1997**, *22*, 54–63. [\[CrossRef\]](#) [\[PubMed\]](#)
204. Lau, A.Y.T.; Cheng, X.; Cheng, C.K.; Nong, W.; Cheung, M.K.; Chan, R.H.-F.; Hui, J.H.L.; Kwan, H.S. Discovery of MicroRNA-like RNAs during Early Fruiting Body Development in the Model Mushroom *Coprinopsis cinerea*. *PLoS ONE* **2018**, *13*, e0198234. [\[CrossRef\]](#) [\[PubMed\]](#)
205. Tasaki, Y.; Ohata, K.; Hara, T.; Joh, T. Three Genes Specifically Expressed during Phosphate Deficiency in *Pholiota nameko* Strain N2 Encode Hydrophobins. *Curr. Genet.* **2004**, *45*, 19–27. [\[CrossRef\]](#) [\[PubMed\]](#)
206. Pothiratana, C.; Fuangsawat, W.; Jintapattanakit, A.; Teerapatsakul, C.; Thachepan, S. Putative Hydrophobins of Black Poplar Mushroom (*Agrocybe cylindracea*). *Mycology* **2021**, *12*, 58–67. [\[CrossRef\]](#) [\[PubMed\]](#)
207. Tagu, D.; Nasse, B.; Martin, F. Cloning and Characterization of Hydrophobins-Encoding CDNAs from the Ectomycorrhizal Basidiomycete *Pisolithus tinctorius*. *Gene* **1996**, *168*, 93–97. [\[CrossRef\]](#) [\[PubMed\]](#)
208. Duplessis, S.; Sorin, C.; Voiblet, C.; Palin, B.; Martin, F.; Tagu, D. Cloning and Expression Analysis of a New Hydrophobin CDNA from the Ectomycorrhizal Basidiomycete *Pisolithus*. *Curr. Genet.* **2001**, *39*, 335–339. [\[CrossRef\]](#) [\[PubMed\]](#)
209. Sammer, D.; Krause, K.; Gube, M.; Wagner, K.; Kothe, E. Hydrophobins in the Life Cycle of the Ectomycorrhizal Basidiomycete *Tricholoma vaccinum*. *PLoS ONE* **2016**, *11*, e0167773. [\[CrossRef\]](#) [\[PubMed\]](#)
210. De Groot, P.W.J.; Schaap, P.J.; Sonnenberg, A.S.M.; Visser, J.; Van Griensven, L.J.L.D. The *Agaricus bisporus* *HypA* Gene Encodes a Hydrophobin and Specifically Accumulates in Peel Tissue of Mushroom Caps during Fruit Body Development. *J. Mol. Biol.* **1996**, *257*, 1008–1018. [\[CrossRef\]](#) [\[PubMed\]](#)
211. Santos, C.; Labarère, J. *Aa-Pri2*, a Single-Copy Gene from *Agrocybe aegerita*, Specifically Expressed during Fruiting Initiation, Encodes a Hydrophobin with a Leucine-Zipper Domain. *Curr. Genet.* **1999**, *35*, 564–570. [\[CrossRef\]](#) [\[PubMed\]](#)
212. Trembley, M.L.; Ringli, C.; Honegger, R. Hydrophobins *DGH1*, *DGH2*, and *DGH3* in the Lichen-Forming Basidiomycete *Dictyonema glabratum*. *Fungal Genet. Biol.* **2002**, *35*, 247–259. [\[CrossRef\]](#) [\[PubMed\]](#)
213. Trembley, M.L.; Ringli, C.; Honegger, R. Differential Expression of Hydrophobins *DGH1*, *DGH2* and *DGH3* and Immunolocalization of *DGH1* in Strata of the Lichenized Basidiocarp of *Dictyonema glabratum*. *New Phytol.* **2002**, *154*, 185–195. [\[CrossRef\]](#)

214. Kim, H.I.; Lee, C.S.; Park, Y.J. Further Characterization of Hydrophobin Genes in Genome of *Flammulina velutipes*. *Mycoscience* **2016**, *57*, 320–325. [\[CrossRef\]](#)
215. Plett, J.M.; Gibon, J.; Kohler, A.; Duffy, K.; Hoegger, P.J.; Velagapudi, R.; Han, J.; Kües, U.; Grigoriev, I.V.; Martin, F. Phylogenetic, Genomic Organization and Expression Analysis of Hydrophobin Genes in the Ectomycorrhizal Basidiomycete *Laccaria bicolor*. *Fungal Genet. Biol.* **2012**, *49*, 199–209. [\[CrossRef\]](#) [\[PubMed\]](#)
216. Rajashekar, B.; Samson, P.; Johansson, T.; Tunlid, A. Evolution of Nucleotide Sequences and Expression Patterns of Hydrophobin Genes in the Ectomycorrhizal Fungus *Paxillus involutus*. *New Phytol.* **2007**, *174*, 399–411. [\[CrossRef\]](#) [\[PubMed\]](#)
217. Kudo, T.; Sato, Y.; Tasaki, Y.; Hara, T.; Joh, T. Heterogeneous Expression and Emulsifying Activity of Class I Hydrophobin from *Pholiota nameko*. *Mycoscience* **2011**, *52*, 283–287. [\[CrossRef\]](#)
218. Tagu, D.; De Bellis, R.; Balestrini, R.; De Vries, O.M.H.; Piccoli, G.; Stocchi, V.; Bonfante, P.; Martin, F. Immunolocalization of Hydrophobin HYDPT-1 from the Ectomycorrhizal Basidiomycete *Pisolithus tinctorius* during Colonization of *Eucalyptus globulus* Roots. *New Phytol.* **2001**, *149*, 127–135. [\[CrossRef\]](#) [\[PubMed\]](#)
219. Martin, F.; Laurent, P.; de Carvalho, D.; Voiblet, C.; Balestrini, R.; Bonfante, P.; Tagu, D. Cell Wall Proteins of the Ectomycorrhizal Basidiomycete *Pisolithus tinctorius*: Identification, Function, and Expression in Symbiosis. *Fungal Genet. Biol.* **1999**, *27*, 161–174. [\[CrossRef\]](#) [\[PubMed\]](#)
220. Acioli-Santos, B.; Sebastiana, M.; Pessoa, F.; Sousa, L.; Figueiredo, A.; Fortes, A.M.; Baldé, A.; Maia, L.C.; Pais, M.S. Fungal Transcript Pattern during the Preinfection Stage (12 h) of Ectomycorrhiza Formed between *Pisolithus tinctorius* and *Castanea sativa* Roots, Identified Using cDNA Microarrays. *Curr. Microbiol.* **2008**, *57*, 620–625. [\[CrossRef\]](#) [\[PubMed\]](#)
221. Peñas, M.M.; Rust, B.; Larraya, L.M.; Ramírez, L.; Pisabarro, A.G. Differentially Regulated, Vegetative-Mycelium-Specific Hydrophobins of the Edible Basidiomycete *Pleurotus ostreatus*. *Appl. Environ. Microbiol.* **2002**, *68*, 3891–3898. [\[CrossRef\]](#) [\[PubMed\]](#)
222. Palomo, J.M.; Peñas, M.M.; Fernández-Lorente, G.; Mateo, C.; Pisabarro, A.G.; Fernández-Lafuente, R.; Ramírez, L.; Guisán, J.M. Solid-Phase Handling of Hydrophobins: Immobilized Hydrophobins as a New Tool to Study Lipases. *Biomacromolecules* **2003**, *4*, 204–210. [\[CrossRef\]](#) [\[PubMed\]](#)
223. Longobardi, S.; Gravagnuolo, A.M.; Rea, I.; De Stefano, L.; Marino, G.; Giardina, P. Hydrophobin-Coated Plates as Matrix-Assisted Laser Desorption/Ionization Sample Support for Peptide/Protein Analysis. *Anal. Biochem.* **2014**, *449*, 9–16. [\[CrossRef\]](#) [\[PubMed\]](#)
224. Gravagnuolo, A.M.; Longobardi, S.; Luchini, A.; Appavou, M.S.; De Stefano, L.; Notomista, E.; Paduano, L.; Giardina, P. Class I Hydrophobin *Vmh2* Adopts Atypical Mechanisms to Self-Assemble into Functional Amyloid Fibrils. *Biomacromolecules* **2016**, *17*, 954–964. [\[CrossRef\]](#) [\[PubMed\]](#)
225. Rea, I.; Giardina, P.; Longobardi, S.; Porro, F.; Casuscelli, V.; Rendina, I.; De Stefano, L. Hydrophobin *Vmh2*-Glucose Complexes Self-Assemble in Nanometric Biofilms. *J. R. Soc. Interface* **2012**, *9*, 2450–2456. [\[CrossRef\]](#) [\[PubMed\]](#)
226. Piscitelli, A.; Pennacchio, A.; Longobardi, S.; Velotta, R.; Giardina, P. *Vmh2* Hydrophobin as a Tool for the Development of “Self-Immobilizing” Enzymes for Biosensing. *Biotechnol. Bioeng.* **2017**, *114*, 46–52. [\[CrossRef\]](#) [\[PubMed\]](#)
227. Sorrentino, I.; Gargano, M.; Ricciardelli, A.; Parrilli, E.; Buonocore, C.; de Pascale, D.; Giardina, P.; Piscitelli, A. Development of Anti-Bacterial Surfaces Using a Hydrophobin Chimeric Protein. *Int. J. Biol. Macromol.* **2020**, *164*, 2293–2300. [\[CrossRef\]](#) [\[PubMed\]](#)
228. Politi, J.; De Stefano, L.; Longobardi, S.; Giardina, P.; Rea, I.; Methivier, C.; Pradier, C.M.; Casale, S.; Spadavecchia, J. The Amphiphilic Hydrophobin *Vmh2* Plays a Key Role in One Step Synthesis of Hybrid Protein-Gold Nanoparticles. *Colloids Surf. B Biointerfaces* **2015**, *136*, 214–221. [\[CrossRef\]](#) [\[PubMed\]](#)
229. Kulkarni, S.S.; Nene, S.N.; Joshi, K.S. Identification and Characterization of a Hydrophobin *Vmh3* from *Pleurotus ostreatus*. *Protein Expr. Purif.* **2022**, *195–196*, 106095. [\[CrossRef\]](#) [\[PubMed\]](#)
230. Asgeirsdóttir, S.A.; de Vries, O.M.H.; Wessels, J.G.H. Identification of Three Differentially Expressed Hydrophobins in *Pleurotus ostreatus* (Oyster Mushroom). *Microbiology* **1998**, *144*, 2961–2969. [\[CrossRef\]](#) [\[PubMed\]](#)
231. Peñas, M.M.; Aranguren, J.; Ramírez, L.; Pisabarro, A.G. Structure of Gene Coding for the Fruit Body-Specific Hydrophobia *Fbh1* of the Edible Basidiomycete *Pleurotus ostreatus*. *Mycologia* **2004**, *96*, 75–82. [\[CrossRef\]](#) [\[PubMed\]](#)
232. Peñas, M.M.; Ásgeirsdóttir, S.A.; Lasa, I.; Culiñez-Macià, F.A.; Pisabarro, A.G.; Wessels, J.G.H.; Ramírez, L. Identification, Characterization, and *In Situ* Detection of a Fruit-Body-Specific Hydrophobin of *Pleurotus ostreatus*. *Appl. Environ. Microbiol.* **1998**, *64*, 4028–4034. [\[CrossRef\]](#) [\[PubMed\]](#)
233. Wessels, J.G.H.; De Vries, O.M.H.; Ásgeirsdóttir, S.A.; Schuren, F.H.J. Hydrophobin Genes Involved in Formation of Aerial Hyphae and Fruit Bodies in *Schizophyllum*. *Plant Cell* **1991**, *3*, 793–799. [\[CrossRef\]](#) [\[PubMed\]](#)
234. Van Wetter, M.A.; Wösten, H.A.B.; Wessels, J.G.H. SC3 and SC4 Hydrophobins Have Distinct Roles in Formation of Aerial Structures in Dikaryons of *Schizophyllum commune*. *Mol. Microbiol.* **2000**, *36*, 201–210. [\[CrossRef\]](#) [\[PubMed\]](#)
235. Gandier, J.A.; Langelan, D.N.; Won, A.; O'Donnell, K.; Grondin, J.L.; Spencer, H.L.; Wong, P.; Tillier, E.; Yip, C.; Smith, S.P.; et al. Characterization of a Basidiomycota Hydrophobin Reveals the Structural Basis for a High-Similarity Class I Subdivision. *Sci. Rep.* **2017**, *7*, 45863. [\[CrossRef\]](#) [\[PubMed\]](#)

236. Wirth, S.; Kunert, M.; Ahrens, L.M.; Krause, K.; Broska, S.; Paetz, C.; Kniemeyer, O.; Jung, E.M.; Boland, W.; Kothe, E. The Regulator of G-Protein Signalling Thn1 Links Pheromone Response to Volatile Production in *Schizophyllum commune*. *Environ. Microbiol.* **2018**, *20*, 3684–3699. [\[CrossRef\]](#) [\[PubMed\]](#)
237. Sillo, F.; Zampieri, E.; Giordano, L.; Lione, G.; Colpaert, J.V.; Balestrini, R.; Gonthier, P. Identification of Genes Differentially Expressed during the Interaction between the Plant Symbiont *Suillus luteus* and Two Plant Pathogenic Allopatric *Heterobasidion* Species. *Mycol. Prog.* **2015**, *14*, 106. [\[CrossRef\]](#)
238. Mankel, A.; Krause, K.; Kothe, E. Identification of a Hydrophobin Gene That Is Developmentally Regulated in the Ectomycorrhizal Fungus *Tricholoma terreum*. *Appl. Environ. Microbiol.* **2002**, *68*, 1408–1413. [\[CrossRef\]](#) [\[PubMed\]](#)
239. Teertstra, W.R.; Deelstra, H.J.; Vranes, M.; Bohlmann, R.; Kahmann, R.; Kämper, J.; Wösten, H.A.B. Repellents Have Functionally Replaced Hydrophobins in Mediating Attachment to a Hydrophobic Surface and in Formation of Hydrophobic Aerial Hyphae in *Ustilago maydis*. *Microbiology* **2006**, *152*, 3607–3612. [\[CrossRef\]](#) [\[PubMed\]](#)
240. Müller, O.; Schreier, P.H.; Uhrig, J.F. Identification and Characterization of Secreted and Pathogenesis-Related Proteins in *Ustilago maydis*. *Mol. Genet. Genom.* **2008**, *279*, 27–39. [\[CrossRef\]](#) [\[PubMed\]](#)
241. Fukada, F.; Rössel, N.; Münch, K.; Glatter, T.; Kahmann, R. A Small *Ustilago maydis* Effector Acts as a Novel Adhesin for Hyphal Aggregation in Plant Tumors. *New Phytol.* **2021**, *231*, 416–431. [\[CrossRef\]](#) [\[PubMed\]](#)
242. Tagu, D.; Marmeisse, R.; Baillet, Y.; Rivière, S.; Palin, B.; Bernardini, F.; Méreau, A.; Gay, G.; Balestrini, R.; Bonfante, P.; et al. Hydrophobins in Ectomycorrhizas: Heterologous Transcription of the *Pisolithus HydPt-1* Gene in Yeast and *Hebeloma cylindrosporum*. *Eur. J. Histochem.* **2009**, *46*, 23. [\[CrossRef\]](#) [\[PubMed\]](#)
243. Kern, L.; Linkies, A. Influence of O₂ and CO₂ on Fungal Development and Hydrophobin Expression during the Interaction between *Heterobasidion parviporum* and *Phlebiopsis gigantea*. *For. Pathol.* **2019**, *49*, e12511. [\[CrossRef\]](#)
244. Karlsson, M.; Stenlid, J.; Olson, A. Two Hydrophobin Genes from the Conifer Pathogen *Heterobasidion annosum* Are Expressed in Aerial Hyphae. *Mycologia* **2007**, *99*, 227–231. [\[CrossRef\]](#) [\[PubMed\]](#)
245. Mgbeahuruike, A.C.; Karlsson, M.; Asiegbu, F.O. Differential Expression of Two Hydrophobin Genes (*Pgh1* and *Pgh2*) from the Biological Control Agent *Phlebiopsis gigantea*. *Fungal Biol.* **2012**, *116*, 620–629. [\[CrossRef\]](#) [\[PubMed\]](#)
246. Adomas, A.; Eklund, M.; Johansson, M.; Asiegbu, F.O. Identification and Analysis of Differentially Expressed CDNAs during Nonspecific-Competitive Interaction between *Phlebiopsis gigantea* and *Heterobasidion parviporum*. *FEMS Microbiol. Ecol.* **2006**, *57*, 26–39. [\[CrossRef\]](#) [\[PubMed\]](#)
247. Linder, M.B.; Szilvay, G.R.; Nakari-Setälä, T.; Penttilä, M.E. Hydrophobins: The Protein-Amphiphiles of Filamentous Fungi. *FEMS Microbiol. Rev.* **2005**, *29*, 877–896. [\[CrossRef\]](#) [\[PubMed\]](#)
248. Lugones, L.G.; Wosten, H.A.B.; Wessels, J.G.H. A Hydrophobin (*ABH3*) Specifically Secreted by Vegetatively Growing Hyphae of *Agaricus bisporus* (Common White Button Mushroom). *Microbiology* **1998**, *144*, 2345–2353. [\[CrossRef\]](#) [\[PubMed\]](#)
249. Liu, C.; Kang, L.; Lin, M.; Bi, J.; Liu, Z.; Yuan, S. Molecular Mechanism by Which the GATA Transcription Factor CcNsdD2 Regulates the Developmental Fate of *Coprinopsis cinerea* under Dark or Light Conditions. *mBio* **2022**, *13*, e0362621. [\[CrossRef\]](#) [\[PubMed\]](#)
250. Qiao, J.; Liu, H.; Xue, P.; Hong, M.; Guo, X.; Xing, Z.; Zhao, M.; Zhu, J. Function of a Hydrophobin in Growth and Development, Nitrogen Regulation, and Abiotic Stress Resistance of *Ganoderma lucidum*. *FEMS Microbiol. Lett.* **2023**, *370*, fnad051. [\[CrossRef\]](#) [\[PubMed\]](#)
251. Wang, B.; Duan, S.; Zhang, H.; Xu, H.; Liu, B.; Qiao, M. A Label-Free Lateral Offset Spliced Coreless Fiber MZI Biosensor Based on Hydrophobin *HGFI* for TNF- α Detection. *Optoelectron. Lett.* **2022**, *18*, 263–268. [\[CrossRef\]](#) [\[PubMed\]](#)
252. Puspitasari, N.; Tsai, S.L.; Lee, C.K. Class I Hydrophobins Pretreatment Stimulates PETase for Monomers Recycling of Waste PETs. *Int. J. Biol. Macromol.* **2021**, *176*, 157–164. [\[CrossRef\]](#) [\[PubMed\]](#)
253. Song, D.; Gao, Z.; Zhao, L.; Wang, X.; Xu, H.; Bai, Y.; Zhang, X.; Linder, M.B.; Feng, H.; Qiao, M. High-Yield Fermentation and a Novel Heat-Precipitation Purification Method for Hydrophobin *HGFI* from *Grifola frondosa* in *Pichia pastoris*. *Protein Expr. Purif.* **2016**, *128*, 22–28. [\[CrossRef\]](#) [\[PubMed\]](#)
254. Wang, Z.; Feng, S.; Huang, Y.; Qiao, M.; Zhang, B.; Xu, H. Prokaryotic Expression, Purification, and Polyclonal Antibody Production of a Hydrophobin from *Grifola frondosa*. *Acta Biochim. Biophys. Sin.* **2010**, *42*, 388–395. [\[CrossRef\]](#) [\[PubMed\]](#)
255. Yu, L.; Zhang, B.; Szilvay, G.R.; Sun, R.; Jänis, J.; Wang, Z.; Feng, S.; Xu, H.; Linder, M.B.; Qiao, M. Protein *HGFI* from the Edible Mushroom *Grifola frondosa* Is a Novel 8 KDa Class I Hydrophobin That Forms Rodlets in Compressed Monolayers. *Microbiology* **2008**, *154*, 1677–1685. [\[CrossRef\]](#) [\[PubMed\]](#)
256. Schuur, T.A.; Schaeffer, E.A.M.; Wessels, J.G.H. Homology-Dependent Silencing of the *SC3* Gene in *Schizophyllum commune*. *Genetics* **1997**, *147*, 589–596. [\[CrossRef\]](#) [\[PubMed\]](#)
257. Tillotson, R.D.; Wösten, H.A.B.; Richter, M.; Willey, J.M. A Surface Active Protein Involved in Aerial Hyphae Formation in the Filamentous Fungus *Schizophyllum commune* Restores the Capacity of a Bald Mutant of the Filamentous Bacterium *Streptomyces coelicolor* to Erect Aerial Structures. *Mol. Microbiol.* **1998**, *30*, 595–602. [\[CrossRef\]](#) [\[PubMed\]](#)

258. Lumsdon, S.O.; Green, J.; Stieglitz, B. Adsorption of Hydrophobin Proteins at Hydrophobic and Hydrophilic Interfaces. *Colloids Surf. B Biointerfaces* **2005**, *44*, 172–178. [[CrossRef](#)] [[PubMed](#)]
259. Fan, H.; Wang, X.; Zhu, J.; Robillard, G.T.; Mark, A.E. Molecular Dynamics Simulations of the Hydrophobin SC3 at a Hydrophobic/Hydrophilic Interface. *Proteins Struct. Funct. Genet.* **2006**, *64*, 863–873. [[CrossRef](#)] [[PubMed](#)]
260. Akanbi, M.H.J.; Post, E.; Van Putten, S.M.; De Vries, L.; Smisterova, J.; Meter-Arkema, A.H.; Wösten, H.A.B.; Rink, R.; Scholtmeijer, K. The Antitumor Activity of Hydrophobin SC3, a Fungal Protein. *Appl. Microbiol. Biotechnol.* **2013**, *97*, 4385–4392. [[CrossRef](#)] [[PubMed](#)]
261. Kenward, C.; Vergunst, K.L.; Langelaan, D.N. Expression, Purification, and Refolding of Diverse Class IB Hydrophobins. *Protein Expr. Purif.* **2020**, *176*, 105732. [[CrossRef](#)] [[PubMed](#)]
262. Vergunst, K.L.; Kenward, C.; Langelaan, D.N. Characterization of the Structure and Self-Assembly of Two Distinct Class IB Hydrophobins. *Appl. Microbiol. Biotechnol.* **2022**, *106*, 7831–7843. [[CrossRef](#)] [[PubMed](#)]

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