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FUNGI-PRODUCERS OF BIOGENIC MAGNETIC NANOPARTICLES: PROSPECTS FOR USE IN NANOSYNTHESIS

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Biogenic magnetic nanoparticles (BMNs) — products of biologically controlled mineralization — have been detected in organisms from all three domains of life, indicating the existence of a single evolutionarily conserved genetic mechanism of their formation. Fungi of the divisions Ascomycota and Basidiomycota are part of this universal biological phenomenon: genomic analysis has confirmed the presence of homologs of essential magnetosome island proteins of magnetotactic bacteria in fungal genomes, while mycogenic BMNs combine magnetically responsive properties with natural biocompatibility, opening broad prospects in nanosynthesis and nanomedicine.

Aim. To systematize current data on fungi as BMN producers, to characterize the mechanisms of their synthesis, and to substantiate the prospects for practical applications in biotechnology and medicine.

Materials and Methods. Scientific publications indexed in PubMed, Web of Science, and Scopus databases, primarily from the past twenty years, together with key historical works, were analyzed. Comparative analysis, systematization, and generalization of data on the taxonomic composition of producing fungi, molecular mechanisms of synthesis, and physicochemical properties of the obtained nanoparticles were applied.

Results. It was established that representatives of Ascomycota and Basidiomycota are capable of synthesizing a broad spectrum of nanoparticles — from iron oxides (Fe_3O_4, Fe_2O_3) to silver, gold, and other metallic particles. A key role in the properties of synthesis products is played by the "biocorona" — an organic coating of proteins and polysaccharides of the producer organism — which ensures colloidal stability, biocompatibility, and ease of functionalization of the nanoparticles. It was found that the vast majority of active fungal strains perform extracellular synthesis, which substantially simplifies product isolation.

Conclusions. Fungi are natural producers of BMNs whose biomineralization mechanism is evolutionarily conserved and genetically related to the corresponding mechanisms in prokaryotes. Mycogenic BMNs carry a natural "biocorona" that ensures biocompatibility and ease of functionalization without additional chemical manipulations, and represent promising multifunctional agents for targeted drug delivery, magnetic hyperthermia, MRI diagnostics, and antimicrobial and antitumor therapy.

Key words: biogenic magnetic nanoparticles, fungal producers, biomineralization, mycogenic synthesis, biocorona, magnetosome island, *Ascomycota, Basidiomycota*, biocompatibility, targeted drug delivery.

Biogenic magnetic nanoparticles (BMNs) — products of biologically controlled mineralization — have been detected in organisms from all three domains of life: Bacteria, Archaea, and Eukarya, including humans [1, 2]. These findings suggest the possibility of an evolutionarily conserved genetic mechanism underlying biomineralization, potentially involving homologs of proteins encoded by the magnetosome island of magnetotactic bacteria [1–4]. Fungi belonging to the phyla Ascomycota and Basidiomycota may also produce BMNs. Comparative genomic analyses have identified homologs of the corresponding proteins in

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fungal genomes, while atomic force microscopy (AFM), magnetic force microscopy (MFM), and high-gradient magnetic separation (HGMS) have provided evidence for the presence of BMNs in macromycete tissues [5, 6].

Research on biogenic magnetic nanoparticles (BMNs) spans more than six decades. In 1962, H. A. Lowenstam discovered biogenic magnetite in the denticle cappings of chitons (Polyplacophora), providing the first evidence that living organisms can synthesize this mineral [7]. In 1975, R. Blakemore described magnetotactic bacteria [8], and shortly thereafter, Frankel et al. identified their intracellular magnetic inclusions, known as magnetosomes, as magnetite crystals [9]. Over the following decades, BMNs were reported in the tissues of numerous animals, including the human brain [10], as well as in plants [11]. These findings contributed to the hypothesis that BMN biomineralization may involve evolutionarily conserved genetic mechanisms across different domains of life [1, 2].

In parallel, around the turn of the century, the use of living organisms for the targeted production of nanostructures, including magnetic nanoparticles, emerged as a potentially more environmentally friendly alternative to conventional chemical synthesis involving toxic reagents [12, 13]. Fungi were investigated as nanoparticle producers later than some other organisms. One of the early demonstrations of fungal nanoparticle synthesis was the intracellular formation of gold nanoparticles by *Verticillium* sp., reported in 2001 [13]. In 2006, the synthesis of magnetite by *Fusarium oxysporum* and *Verticillium* sp. was demonstrated [14].

Subsequent studies identified potential BMN-producing fungi belonging to Ascomycota and Basidiomycota through comparative genomic analyses [6]. Magnetically responsive biosorbents based on the macromycetes *Agaricus bisporus* and *Lentinula edodes* were also developed [15], and BMNs were directly detected in fungal tissues [5]. Thus, the study of fungi as potential BMN producers represents a relatively recent but rapidly developing area of nanobiotechnology.

Conventional chemical and physical methods for synthesizing magnetic nanoparticles may involve toxic reagents, generate hazardous waste, and require additional surface functionalization to improve biocompatibility [12, 16]. Mycogenic synthesis offers a distinct approach: fungal-derived nanoparticles may possess a naturally formed biological coating — a *biocorona* composed of proteins and polysaccharides derived from the producing organism — that can contribute to colloidal stability and biocompatibility and facilitate further functionalization [17–19]. The principal iron oxide phases of magnetic nanoparticles include magnetite (Fe_3O_4) and maghemite (γ-Fe_2O_3). Although biological control of mineralization may influence nanoparticle formation and structural properties, the degree of crystallinity and the occurrence of superparamagnetic behavior depend on factors such as particle size, morphology, and composition [2, 16, 20]. Superparamagnetic nanoparticles can exhibit minimal remanent magnetization in the absence of an external magnetic field, potentially reducing magnetic aggregation under appropriate conditions.

Despite the substantial body of research on mycogenic nanoparticle synthesis [21–23], a systematic review focusing specifically on fungi as natural producers of biogenic magnetic nanoparticles (BMNs), with particular emphasis on the potential evolutionary conservation of the underlying biomineralization mechanisms, appears to be lacking. The aim of this review is to synthesize and systematize current knowledge of fungi as BMN producers, characterize the mechanisms underlying BMN synthesis, and evaluate their potential applications in biotechnology and medicine.

1. Fungi as BMN producers

1.1. Genomic and experimental evidence for bmn biomineralization in fungi

Comparative genomic analyses of representatives of the phyla Ascomycota and Basidiomycota have identified fungi as potential producers of biogenic magnetic nanoparticles (BMNs) [6]. This hypothesis is based on reported sequence homology between fungal proteins and functionally characterized magnetosome proteins of magnetotactic bacteria (MTB), in which the mechanisms of BMN biomineralization have been studied in detail [3, 4]. MTB biomineralize intracellular, membrane-bound magnetic crystals composed of magnetite (Fe_3O_4) or greigite (Fe_3S_4) [1, 3]. These particles are characterized by high crystallinity, a narrow size distribution, well-defined morphology, and an enclosing lipid–protein membrane [24].

Experimental evidence for the presence of BMNs in fungi has been obtained using atomic force microscopy (AFM), magnetic

force microscopy (MFM), and high-gradient magnetic separation (HGMS) [5]. BMNs arranged in chain-like aggregates, resembling those reported in animals and plants, have been detected in the tissues of *Agaricus bisporus* (button mushroom) and *Lentinula edodes* (shiitake) [5]. Of particular significance, these particles have been reported in association with the transport system and localized in the walls of vessel-like hyphae. Similar localization has been described for BMNs in animal capillary walls and plant phloem sieve tubes [25, 26]. The reported localization of BMNs in conducting tissues across different biological kingdoms may provide additional evidence for similarities in their biomineralization mechanisms.

Experimental evidence supporting the presence of magnetically responsive material in fungi is provided by the study reported in [15], in which a magnetically responsive fraction was isolated from the biomass of *Agaricus bisporus* and *Lentinula edodes* using high-gradient magnetic separation (HGMS). The proportion of the magnetically responsive fraction was higher in shiitake (3.3–4.8%) than in button mushroom (1.05–1.8%) [15]. The removal efficiency for Fe^{3+} ions using *A. bisporus* biomass exceeded 90% within 30 min. Furthermore, using biomass cultivated on a substrate supplemented with magnetic fluid reduced the sorbent saturation time sixfold, from 30 to 5 min, highlighting the potential for technological applications that exploit the magnetic properties of fungi [15].

1.2. Species diversity of nanoparticle-producing fungi

Fungal cultures representing diverse taxonomic groups are promising producers of nanoparticles (NPs) with a wide range of chemical compositions, from iron oxides to silver, gold, and other metallic nanoparticles [12, 27]. The advantages of fungi stem from their ability to secrete a broad range of enzymes and metabolites that facilitate the extracellular reduction of metal ions and the formation and stabilization of nanoparticles [21, 22]. However, although these mechanisms underpin the broad nanosynthetic capabilities of fungi, their relationship to the proposed evolutionarily conserved mechanisms of biomineralization underlying fungal BMN production remains to be elucidated [1, 2, 6]. Table 1 provides a systematic overview of fungal species with documented nanoparticle-producing capabilities.

1.3. Current evidence on the use of fungi for magnetic nanoparticle synthesis

Species of the genus *Aspergillus*, which predominate among the iron oxide nanoparticle producers listed in Table 1, are among the most extensively characterized fungal producers of iron oxide nanoparticles. Two of the best-documented examples, *Aspergillus niger* and *Aspergillus elegans*, are discussed in detail below.

1.3.1. Aspergillus niger as a Model Producer of Mycogenic Iron Oxides

Abosharaf et al. [47] and El-Shanshoury et al. [48] demonstrated the capacity of Abosharaf et al. [47] and El-Shanshoury et al. [48] demonstrated that *Aspergillus niger* can synthesize iron oxide nanoparticles extracellularly using cell-free culture filtrates. In both studies, nanoparticle formation was characterized using a range of physicochemical techniques. UV–Vis spectroscopy revealed characteristic absorption peaks at 320 nm [47] and 410 nm [48]. These differences in absorption maxima may reflect differences in the phase composition of the synthesized products, as hematite (α-Fe_2O_3) and magnetite (Fe_3O_4) exhibit distinct optical properties associated with differences in their electronic structures and iron oxidation states.

Fourier-transform infrared spectroscopy (FTIR) confirmed the presence of Fe–O bonds and indicated the presence of fungal proteins and carbohydrates on the nanoparticle surfaces [47, 48]. These findings suggest that fungal biomolecules may contribute both to iron ion transformation and particle nucleation and to the formation of an organic coating that stabilizes the resulting nanoparticles. X-ray diffraction (XRD) confirmed the crystalline nature of the synthesized materials [47, 48]. Scanning electron microscopy (SEM) revealed particle sizes of 36–44 nm [47] and 36–47 nm [48]. In addition, transmission electron microscopy (TEM) in [48] revealed a substantially smaller mean diameter for individual primary crystallites (7 ± 2 nm). Differences between SEM- and TEM-derived size estimates may reflect the distinction between larger particles or aggregates observed by SEM and individual primary crystallites resolved by TEM.

El-Shanshoury et al. [48] also demonstrated the potential application of the synthesized nanoparticles in nanobioremediation, particularly for removing heavy metals from industrial wastewater. The reported removal efficiencies were 92.47% for Cu^{2+}, 84.76%

Table 1

Fungi as producers of nanoparticles of diverse chemical composition

Fungal species	Synthesized NPs	Synthesis type	Application	Reference
Iron oxides (Magnetite, Hematite)				
Aspergillus flavipes	Fe_3O_4 NPs	Extracellular	Antifungal activity against *Alternaria solani*	[28]
Fusarium oxysporum	Fe_3O_4 NPs	Extracellular	First demonstration of extracellular magnetite synthesis by fungi	[14]
Trichoderma harzianum	α-Fe_2O_3 NPs	Extracellular	Control of brown rot of apple	[29]
Aspergillus terreus	Fe_3O_4 NPs	Extracellular	Antimicrobial activity	[30]
Aspergillus niger	Fe_3O_4 NPs	Extracellular	Sorption of Cr(VI) from wastewater	[31]
Silver nanoparticles (AgNPs)				
Agaricus bisporus	Ag NPs	Extracellular	Antibacterial activity	[32]
Aspergillus niger	Ag NPs	Extracellular	Antitumor and antimicrobial activity	[33]
Ganoderma neo-japonicum	Ag NPs	Extracellular	Cytotoxicity against breast cancer cells	[34]
Aspergillus fumigatus	Ag NPs	Extracellular	Antibacterial and cytotoxic activity	[35]
Penicillium chrysogenum	Ag NPs	Extracellular	Antibiofilm activity against *Acinetobacter baumannii*	[36]
Rhizopus oryzae	Ag NPs	Extracellular	Antibacterial activity against *E. coli* and *P. aeruginosa*	[37]
Trametes versicolor	Ag NPs	Extracellular	Synergism with phytocompounds against pathogens	[38]
Gold nanoparticles (AuNPs)				
Aspergillus oryzae	Au NPs	Extracellular	Green synthesis from industrial waste	[39]
Verticillium sp.	Au NPs	Intracellular	First demonstration of intracellular fungal AuNP synthesis	[13]
Volvariella volvacea	Au NPs	Extracellular	Noble metal synthesis using an edible mushroom	[40]
Aureobasidium pullulans	Au NPs	Extracellular	Bioconjugates with amylase for catalytic applications	[41]
Other nanoparticles				
Aspergillus terreus	CuO NPs	Extracellular	Antibacterial and anticandidal activity	[42]
Pleurotus citrinopileatus	CuO NPs	Extracellular	Antibacterial and anticancer activity	[43]
Pleurotus sajor-caju	ZnO NPs	Extracellular	Antibacterial activity	[44]
Aspergillus sp.	TiO_2 NPs	Extracellular	Anticancer effect	[45]
Penicillium expansum	Se NPs	Extracellular	Antimicrobial, antioxidant, and anticancer activity	[46]

for Mn^{2+}, and 80.79% for Cr^{3+}. Notably, despite using the same fungal species, Abosharaf et al. [47] obtained hematite (α-Fe_2O_3) at a precursor concentration of 6 mM and a pH of 9.0, whereas El-Shanshoury et al. [48] synthesized magnetite (Fe_3O_4) at a precursor concentration of 1 mM and near-neutral pH. These findings suggest that the phase composition of the resulting iron oxide nanoparticles depends on synthesis conditions and is not determined solely by the identity of the biological agent.

1.3.2. Aspergillus elegans as an Alternative Producer: A Quantitative Comparison of Mycogenic and Chemical Synthesis

Alongside the findings for *A. niger*, important quantitative data have also been reported for *A. elegans*. Mhammedsharif et al. (2024) [49] demonstrated that the mycogenic synthesis of Fe_3O_4 using this species yielded nanoparticles with mean sizes ranging from 13.96 to 21.18 nm, depending on the type of fungal extract used. These particles were substantially smaller than their chemically

synthesized counterparts, which had a mean size of 27.9 nm. The saturation magnetization of the mycogenic nanoparticles ranged from 43.5 to 48.3 emu/g, compared with 35.4 emu/g for the chemically synthesized analogues. Their zeta potential was also substantially more negative (–69 mV versus –9.8 mV), suggesting greater electrostatic repulsion and potentially improved colloidal stability.

Further evidence was reported by Mohammed et al. (2024) [50], whose comparative study showed that Fe_3O_4 nanoparticles synthesized using *A. elegans* (19.2 nm) exhibited higher photocatalytic degradation efficiency for synthetic dyes, including methyl violet, methyl orange, and Bengal rose, than commercial nanoparticles with a mean size of 60 nm. The authors attributed this difference to the greater specific surface area of the mycogenic nanoparticles and the presence of functional groups associated with their biocorona, which may facilitate the adsorption of dye molecules [50].

1.4. Conditions, formation mechanisms, and properties of mycogenic nanoparticles

The properties of mycogenic nanoparticles depend on both the synthesis conditions and the biochemical mechanisms involved in metal ion reduction and nanoparticle stabilization by the producing organism. These interrelated aspects are therefore discussed together.

1.4.1. Factors Governing the Physicochemical Properties of Nanoparticles

The physicochemical properties of nanoparticles depend not only on their chemical composition and crystal structure but also on their size and morphology, including particle shape, surface topography, and microstructural features [51].

For many practical applications, key requirements include a narrow particle size distribution, uniform morphology, and resistance to aggregation in suspension. The properties of biogenic nanoparticles depend on several factors, including the species and strain of the producing microorganism; the composition of the extracts and metabolites involved; the nature and concentration of the ionic precursor; the composition of the growth medium; and process parameters such as stirring rate, incubation time, temperature, and pH. Adjusting these parameters can help control nanoparticle morphology and other physicochemical characteristics [52].

Developing methods for precise control over nanoparticle size, shape, and other properties remains a major objective of contemporary nanobiotechnology. Furthermore, understanding the natural conditions under which BMN biomineralization occurs in fungi—including physiological pH, moderate temperatures, and specific ionic compositions—may help guide the optimization of mycosynthesis protocols to produce nanoparticles with properties that more closely resemble those of naturally formed biogenic particles [1, 2].

1.4.2. Mechanisms of Mycogenic Nanoparticle Synthesis: Enzymatic Basis and the Role of Metal Resistance

Understanding the biochemical mechanisms underlying mycogenic nanoparticle synthesis is essential for the rational design and optimization of production processes. In their comprehensive review, ebesta et al. (2022) [21] examined the relationship between fungal metal resistance and nanoparticle synthesis. The authors discussed several strategies employed by fungi to tolerate toxic metal concentrations, including chelation, biomineralization, biosorption, compartmentalization, and active efflux, some of which may also contribute to nanoparticle formation. NADH-dependent nitrate reductase has been implicated in nanoparticle synthesis, as it may facilitate electron transfer from NADH to metal ions, promoting their reduction under appropriate conditions [21].

In a subsequent review, Šebesta et al. (2023) [22] examined mycogenic nanoparticle synthesis in representatives of Ascomycota and Basidiomycota and highlighted potential differences in their biosynthetic capabilities. Ascomycetes, including *Aspergillus*, *Fusarium*, and *Penicillium*, are frequently associated with enzyme-mediated extracellular nanoparticle synthesis. Basidiomycetes, in turn, exhibit diverse secondary metabolic capabilities that may influence nanoparticle formation, morphology, and surface properties. However, these characteristics vary among species and strains and should not be regarded as universal distinctions between the two fungal phyla [22].

2. Interactions within the “producer fungus–mycogenic nanoparticle” system

this section examines the biochemical and cellular aspects of the interactions between producer fungi and mycogenic nanoparticles. It addresses the genetic basis

of BMN biomineralization, the putative physiological functions of endogenous BMNs, the applicability of this concept to fungi, the effects of magnetic nanoparticles on the producer organism, and the potential role of endogenous BMNs in determining fungal responses to external magnetic fields.

2.1. A conserved genetic basis for BMN biomineralization and homologs of magnetosome island proteins across the three domains of life

The reported occurrence of biogenic magnetic nanoparticles (BMNs) in representatives of all three domains of life—Bacteria, Archaea, and Eukarya, including fungi, plants, and animals—has prompted hypotheses concerning an evolutionarily conserved genetic basis for their biomineralization [1, 2]. Of particular relevance to this hypothesis are comparative genomic studies reporting homologs of essential magnetosome island (MI) proteins from magnetotactic bacteria (MTB) in representatives of diverse taxonomic groups [1, 2].

In MTB, magnetite biomineralization within magnetosome vesicles is a genetically regulated process involving specialized proteins encoded by genes in the magnetosome island. These include MamA, MamB, MamE, MamK, MamM, MamO, and other proteins that contribute to magnetosome formation, organization, and mineralization. Homologs of several magnetosome-associated proteins have also been reported in fungi, plants, animals, and archaea [1, 2]. Of particular interest, MamK, an actin-like protein involved in magnetosome chain organization in MTB, has been reported to have a homolog in the human proteome [53]. This observation is consistent with reports of chain-like BMN aggregates in human tissues. However, the extent to which the organization, size, morphology, and abundance of these particles are genetically regulated in humans remains unclear [53].

The hypothesis of a conserved genetic basis for BMN biomineralization [1, 2] has also been discussed in the context of the experimental findings of Van de Walle et al. (2019), published in *Proceedings of the National Academy of Sciences* [54]. The authors demonstrated that human mesenchymal stem cells (MSCs) can exhibit de novo formation of magnetic nanoparticles following the intracellular degradation of previously internalized synthetic iron oxide nanoparticles. This remagnetization phenomenon was observed during specific differentiation pathways, including osteogenesis and adipogenesis, but not during chondrogenesis. The findings implicated ferritin in the process and suggested that human cells may be capable of forming magnetic nanoparticles from iron released during the degradation of internalized particles. Although these results provide experimental evidence for cellular magnetic nanoparticle formation in humans, they do not, by themselves, establish that the underlying mechanism is genetically identical to the magnetosome biomineralization pathway in MTB [54].

2.2. The proposed physiological role of BMNs as intracellular magnetic separators

The physiological role of BMNs in organisms that do not exhibit magnetotaxis remains a subject of ongoing debate. One hypothesis, supported by theoretical analysis, proposes that BMNs may function as intracellular high-gradient magnetic separators, facilitating the sorting of vesicles and granules [2].

The proposed mechanism is based on the ability of BMNs to generate strong local magnetic fields with steep gradients, thereby exerting magnetic gradient forces on intracellular structures. The magnitude and direction of these forces depend on the effective magnetic susceptibility of the structures relative to that of the surrounding cytoplasm. This mechanism could potentially facilitate the directed transport and sorting of vesicles involved in normal cellular metabolism [2].

Further theoretical support for this hypothesis comes from the study reported in [55], in which calculations suggested that the introduction of artificial or biogenic magnetic nanoparticles can alter the intensity and dynamics of vesicular transport within cells.

2.3. The predictive value of the concept and its support from experimental studies of extracellular magnetite synthesis by fungi

The possibility of extracellular magnetite synthesis by fungi was proposed theoretically [1, 6] before being investigated experimentally. This prediction was based on reports of homologs of essential magnetosome island proteins from magnetotactic bacteria (MTB) in fungal genomes, together with the hypothesis that certain aspects of biomineralization may be evolutionarily conserved. Subsequent studies by Bharde et al. (2006) [14] and Abdullah (2022) [28] provided experimental evidence that fungi can synthesize crystalline iron-containing nanoparticles extracellularly,

supporting the proposed possibility of fungal extracellular biomineralization.

Taken together, these findings suggest that fungi may represent an important component of the broader biological phenomenon of biomineralization observed across diverse groups of organisms. The contribution of the aforementioned theoretical studies lies in their attempt to integrate several aspects of this phenomenon, from its proposed molecular and genetic foundations and the reported localization of BMNs in conducting tissues to hypotheses concerning their physiological functions and potential biomedical applications (Section 3) [1, 2, 6, 53–57]. The findings on BMN-producing fungi belonging to Ascomycota and Basidiomycota, summarized in the present review, provide further evidence of the relevance of fungal systems to nanobiotechnology and support continued investigation of the mechanisms underlying mycogenic BMN formation.

2.4. The effects of magnetic nanoparticles on fungal growth and physiology

In the context of mycosynthesis, an important practical question concerns the effects of the reaction products—magnetic nanoparticles—on the physiology of the producer fungi themselves. Understanding these effects is essential for optimizing mycosynthesis conditions and maintaining the productivity of the producing organisms.

Magnetic nanoparticles may affect fungal cells through physicochemical interactions with the cell wall [58] and by inducing oxidative stress [59]. At the same time, the endogenous formation of magnetic nanoparticles may represent an adaptive response that enables cells to sequester potentially toxic metal ions in less reactive forms, thereby protecting cellular structures. This possibility is consistent with the reported relationship between fungal metal resistance and nanoparticle synthesis [21].

Shi et al. [58] investigated the size-dependent effects of Fe_3O_4 nanoparticles from three size fractions (10, 20, and 200 nm) on the growth and sporulation of *Aspergillus niger*. None of the fractions exerted a pronounced inhibitory effect on mycelial growth. However, 20 nm nanoparticles (MNP20) at a concentration of 500 mg/L significantly inhibited sporulation, an effect accompanied by chitin accumulation in the cell wall, which may indicate changes in cell wall structure. The observed effect was not attributed to increased reactive oxygen species (ROS) generation or iron dissolution, as the addition of Fe^{2+} and Fe^{3+} ions in the absence of nanoparticles did not reproduce the phenomenon. These findings have direct implications for biotechnology: when developing mycosynthesis processes, both precursor concentrations and the size of the resulting nanoparticles should be carefully controlled to minimize adverse effects on the growth and productivity of the producer organism [58].

Findings reported in [5] concerning the effects of magnetic nanoparticles on fungal cells provide additional context. The introduction of both synthetic and biogenic magnetic nanoparticles altered the intensity and dynamics of vesicular transport. These observations are consistent with the hypothesis that BMNs may function as intracellular magnetic separators involved in vesicle transport and sorting [2]. However, further experimental evidence is required to establish whether this mechanism accounts for the observed changes in fungal cellular activity.

2.5. Endogenous BMNs as potential mediators of fungal responses to external magnetic fields

Unlike magnetic nanoparticles, external magnetic fields act as physical stimuli that can penetrate cells and mycelial structures. The effects of magnetic fields on fungal growth and physiology constitute a distinct research area that lies beyond the scope of the present review. Here, the focus is restricted to findings that may indicate a role for endogenous BMNs in fungal responses to magnetic fields. One proposed hypothesis is that endogenous magnetic nanoparticles increase the sensitivity of cells to external magnetic fields, thereby altering their responses to this physical stimulus [2].

Anaya et al. [60] reported that exposure to a 60 Hz alternating magnetic field (AMF; 1–5 mT for 2 h) stimulated colony growth in *Aspergillus niger*, *Cladosporium cladosporioides*, and *Penicillium citrinum* and altered pigmentation, conidiogenesis, and exudate production. Although the authors interpreted these effects as an adaptive stress response, the reported presence of BMNs in fungal tissues [5], together with genomic evidence suggesting the potential for their formation [6], raises the possibility that endogenous magnetic inclusions may act as targets of the applied field. This hypothesis was subsequently discussed explicitly by the same research group [61].

Further insights into fungal responses to magnetic fields come from studies of medicinal and edible fungi. Li et al. (2021)

[62] reviewed the potential applications of ultrasound and magnetic fields in the cultivation and fermentation of medicinal and edible fungi. Their review described findings suggesting that low-frequency alternating magnetic fields can stimulate mycelial growth and the production of polysaccharides and triterpenoids in *Grifola frondosa* and *Antrodia camphorata*. These effects have been associated with changes in ion exchange, electron transport, and cell membrane fluidity. Although such findings may be consistent with the reported effects of magnetic nanoparticles on vesicular transport in fungal cells [5], a direct mechanistic link to endogenous BMNs or their proposed role as intracellular magnetic separators remains to be established [2].

In a subsequent study, Anaya et al. (2023) [61] reported magnetotropism in the pathogenic fungus *Candida guilliermondii*. Following 2 h of exposure to a 60 Hz AMF at 3 mT, the authors observed growth rates reported to be 3–60 times higher than those of the controls, together with the alignment of pseudohyphae along the magnetic field lines. They proposed that these effects might result from interactions between the applied field and endogenous ferrimagnetic inclusions in fungal cells. This interpretation is consistent with the hypothesis that BMNs could influence intracellular processes in response to external magnetic fields [2]. The possibility of modulating fungal growth through magnetic stimulation therefore warrants further investigation, particularly in the context of optimizing fermentation and mycosynthesis processes.

Taken together, studies of fungal responses to magnetic fields [60–62], considered alongside hypotheses concerning the physiological roles of endogenous BMNs [2], suggest a promising direction for future research. Rather than viewing fungi solely as biological platforms for nanoparticle production, this perspective emphasizes their potential to respond actively to magnetic stimuli through changes in cellular physiology and metabolism. However, the specific contribution of endogenous BMNs to these responses remains to be demonstrated experimentally.

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3.2. Targeted drug delivery systems

The magnetic properties of BMNs, combined with the functionalizable biocorona described in Section 3.1, make mycogenic BMNs promising candidates for targeted drug delivery applications [64, 65]. The application of an external magnetic field gradient may enable the localized accumulation of BMN–therapeutic agent complexes at pathological sites. When combined with pH- or enzyme-responsive drug release, this approach could improve delivery to target tissues and potentially reduce systemic toxicity [64, 65].

The potential for magnetic dipole interactions between endogenous BMNs in target cells and artificially engineered, magnetically responsive carriers, such as magnetoliposomes, has also been investigated theoretically [56]. The calculated magnetic dipole interaction forces may exceed those associated with specific molecular recognition mechanisms, such as antigen–antibody binding, suggesting a possible alternative mechanism for enhancing carrier–cell interactions and cellular uptake. The reported elevation of BMN levels in tumor tissues further suggests that this approach may warrant investigation for oncological applications [53, 56].

3.3. Magnetic hyperthermia: mechanisms and therapeutic potential

Magnetic hyperthermia exploits the ability of magnetic nanoparticles to dissipate energy from an alternating magnetic field as heat. The efficiency of this process is commonly quantified by the specific absorption rate (SAR) [65]. The heating performance of mycogenic Fe_3O_4-based BMNs depends on their crystallinity, particle size, magnetic anisotropy, aggregation state, and the frequency and amplitude of the applied magnetic field. Heat generation may occur through Néel and Brownian relaxation, as well as other magnetic loss mechanisms, depending on the physicochemical properties of the particles and the experimental conditions. Under suitable conditions, these processes may enable temperatures in the therapeutic range of 42–45 °C to be reached [65].

The magnetic properties of these particles may also be relevant to their potential use as contrast agents in magnetic resonance imaging (MRI), which is discussed in the following section. However, direct experimental evidence supporting the use of mycogenic BMNs specifically in drug delivery and magnetic hyperthermia systems remains limited. The studies reviewed in Sections 3.2 and 3.3 provide a theoretical and physicochemical rationale for these applications, but further experimental validation in vitro and in vivo is needed to establish their therapeutic efficacy and safety.

3.4. Bmns as contrast agents in magnetic resonance imaging

Magnetic nanoparticles can act as T_2-weighted negative contrast agents in magnetic resonance imaging (MRI). Owing to their magnetic properties, they generate local magnetic field inhomogeneities that accelerate the transverse relaxation of water protons, thereby reducing signal intensity in T_2-weighted images [66]. The transverse relaxivity (r^2) of mycogenic BMNs is an important parameter determining their potential as MRI contrast agents. If sufficiently high r^2 values and appropriate biodistribution can be achieved, these nanoparticles may offer potential for the detection of small metastatic lesions and early inflammatory foci [66].

3.5. Synergistic antimicrobial and antitumor activity

The intrinsic biological activity associated with fungal metabolites represents a potential additional advantage of mycogenic nanoparticles over their chemically synthesized counterparts. In addition to the generation of reactive oxygen species (ROS) at the iron oxide nanoparticle surface, which may contribute to bacterial cell damage, mycogenic BMNs may retain fungal

metabolites on their surfaces, potentially enhancing their antibacterial and antifungal activity through synergistic interactions [59]. In particular, Fe_3O_4 nanoparticles synthesized using *Aspergillus terreus* have demonstrated pronounced activity against the reference strain *Staphylococcus aureus* ATCC 6538 [30].

3.6. Agricultural applications of mycogenic iron-containing nanoparticles

In addition to their biomedical and technological applications, mycogenic iron-containing nanoparticles show considerable potential for agricultural use. Akbar et al. [29] reported that α-Fe_2O_3 nanoparticles (17.78 nm) synthesized using *Trichoderma harzianum* effectively suppressed brown rot in apples, reportedly without affecting their ascorbic acid content or organoleptic properties. A complementary proteomic study of the *T. harzianum* secretome by Gallo et al. (2025) [67] identified key secreted oxidoreductases and heat shock proteins potentially involved in the synthesis and stabilization of iron and zinc oxide nanoparticles. These findings provide a basis for further investigation of targeted genetic engineering strategies to improve nanoparticle yield and uniformity.

4. Current trends, prospects, and barriers to the development of mycogenic nanotechnologies

A recent review by Sidhu et al. (2025) [23] summarized current research on multimetallic nanoparticles (MMNPs) synthesized using fungi. These nanoparticles comprise two or more metallic components arranged in core–shell, alloy, or cluster-in-cluster configurations and may exhibit enhanced catalytic, antimicrobial, and magnetic properties compared with their monometallic counterparts. Of particular relevance to the present review are mycogenically synthesized Fe_3O_4–Ag and Fe_3O_4–ZnO nanocomposites, in which the iron oxide component provides magnetic functionality, while silver or zinc oxide may enhance antimicrobial activity [23]. Given the growing threat of antimicrobial resistance, such multifunctional systems represent an important area of applied nanobiotechnology.

A critical review published in the *Journal of Fungi* in 2026 [68], which assessed mycogenic nanotechnologies using a "Promise vs. Barrier" framework, identified several major challenges to progress in the field: (1) the lack of standardized synthesis protocols, which limits interlaboratory comparability; (2) an incomplete understanding of the molecular mechanisms underlying mycogenic iron oxide synthesis, particularly in comparison with the extensively characterized biomineralization pathways of magnetotactic bacteria; (3) difficulties in scaling up production and maintaining reproducibility in industrial reactors; and (4) regulatory challenges associated with clinical translation. The authors suggest that genetic engineering of fungal strains, including strategies to enhance the activity of key oxidoreductases or modify biocorona composition, may help address some of these challenges [68].

In this context, the reported presence of homologs of essential magnetosome island proteins from bacteria in fungal genomes [6] provides a rationale for investigating whether endogenous fungal genes can be harnessed to regulate iron biomineralization. However, the functional roles of these homologs in fungal BMN formation remain to be established. Elucidating their functions could help bridge fundamental research on biomineralization [1, 2] and the development of controlled, reproducible mycosynthesis processes.

Conclusions

Fungi belonging to the phyla Ascomycota and Basidiomycota are promising candidates for the production of biogenic crystalline magnetic nanoparticles. Comparative genomic analyses have identified fungal homologs of essential magnetosome island proteins from magnetotactic bacteria, including MamA, MamB, and MamM. These findings suggest a potential evolutionary relationship between fungal biomineralization and bacterial magnetosome formation, although the functional roles of these homologs in fungi remain to be established.

Many characterized fungal strains synthesize nanoparticles extracellularly, offering an important technological advantage by facilitating product recovery and purification and potentially simplifying scale-up for industrial applications.

The natural biocorona, composed of proteins and polysaccharides derived from the producer organism, may contribute to the colloidal stability and biocompatibility of mycogenic BMNs and provide functional groups for further modification. These properties may reduce the need for additional surface functionalization, although the extent of these benefits depends on nanoparticle composition and synthesis conditions.

Mycogenic BMNs are promising candidates for multifunctional applications, including targeted drug delivery, magnetic hyperthermia, magnetic resonance imaging (MRI), and antimicrobial and antitumor therapy. However, their therapeutic efficacy and safety require further experimental validation.

Exogenous magnetic nanoparticles can affect fungal physiology through physicochemical interactions with cellular structures, whereas endogenous BMNs may contribute to fungal responses to external magnetic fields. Both effects should be considered when optimizing mycosynthesis conditions, although the mechanisms underlying these interactions require further investigation.

Priority areas for future research include developing methods for precise control of the physicochemical properties of mycogenic BMNs, elucidating the molecular mechanisms underlying fungal biomineralization, and conducting comprehensive safety assessments of the resulting nanoparticles, including *in vivo* studies.

Use of artificial intelligence

During the preparation of this work, the authors used an artificial intelligence tool (Claude, developed by Anthropic) to assist with the search for and systematization of scientific literature, as well as with linguistic editing of the manuscript. All scientific statements, interpretations, and conclusions were independently formulated by the authors and verified against primary sources. The authors bear sole responsibility for the accuracy and integrity of the article's content.

Conflict of interest

The authors declare no conflict of interest.

Author contributions

A.O. Hudzovskyi — conceptualization, data collection, manuscript writing, and preparation of the original draft; S.V. Gorobets — critical review, manuscript editing, translation editing, and final approval of the manuscript.

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ГРИБИ-ПРОДУЦЕНТИ БІОГЕННИХ МАГНІТНИХ НАНОЧАСТИНОК: ПЕРСПЕКТИВИ ВИКОРИСТАННЯ У НАНОСИНТЕЗІ

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Біогенні магнітні наночастинки (БМН) — продукт біологічно контрольованої мінералізації — виявлені в організмах усіх трьох доменів живої природи, що свідчить про існування єдиного еволюційно консервативного генетичного механізму їхнього утворення. Гриби відділів *Ascomycota* та *Basidiomycota* є частиною цього загальнобіологічного феномену: геномний аналіз підтвердив наявність у них гомологів незамінних протеїнів магнітосомного острівця магнітотаксичних бактерій, а мікогенні БМН поєднують магнітокеровані властивості з природною біосумісністю, що відкриває широкі перспективи в наносинтезі та наномедицині.

Мета. Систематизувати сучасні дані про гриби-продуценти БМН, охарактеризувати механізми їхнього синтезу та обґрунтувати перспективи практичного застосування в біотехнології й медицині.

Матеріали й методи. Проведено аналіз наукових публікацій, індексованих у базах даних *PubMed, Web of Science* та *Scopus*, переважно за останні двадцять років, а також ключових історичних праць. Застосовано методи порівняльного аналізу, систематизації та узагальнення даних про таксономічний склад грибів-продуцентів, молекулярні механізми синтезу та фізико-хімічні властивості одержаних наночастинок.

Результати. Встановлено, що представники відділів *Ascomycota* та *Basidiomycota* здатні синтезувати широкий спектр наночастинок — від оксидів заліза (Fe_3O_4, Fe_2O_3) до срібних, золотих та інших металічних наночастинок. Ключову роль у властивостях продуктів синтезу відіграє «біокорона» — органічне покриття з протеїнів і полісахаридів продуцента, що забезпечує колоїдну стабільність, біосумісність та функціоналізованість наночастинок. Виявлено, що переважна більшість активних грибних штамів здійснює позаклітинний синтез, що суттєво спрощує виділення продукту.

Висновки. Гриби є природними продуцентами БМН, механізм біомінералізації яких еволюційно консервативний і генетично споріднений із відповідними механізмами прокаріотів. Мікогенні БМН несуть природну «біокорону», що забезпечує біосумісність і функціоналізованість без додаткових хімічних маніпуляцій, і є перспективними мультифункціональними агентами для адресної доставки ліків, магнітної гіпертермії, МРТ-діагностики та антимікробної і протипухлинної терапії.

Ключові слова: біогенні магнітні наночастинки, гриби-продуценти, біомінералізація, мікогенний синтез, біокорона, магнітосомний острівець, *Ascomycota, Basidiomycota*, біосумісність, адресна доставка ліків.

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