

Hericium erinaceus: Combining traditional uses with modern biotechnology to develop nutraceuticals

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Edible and medicinal macromycetes are capable of synthesizing a unique complex of biologically active metabolites with significant antioxidant, immunomodulatory, neuroprotective and other properties. Today, mushrooms are recognized as functional foods with significant culinary, nutritional and pharmacological value. Modern biotechnology is actively introducing innovative methods for creating therapeutic agents, including those based on mushroom raw materials. Thanks to multi-stage screening and the development of biotechnology, the cultivation of highly productive producer strains with a high ability to synthesize natural pharmacologically active compounds has significantly increased the possibilities of their use in the food industry, pharmacology and medicine. *Hericium erinaceus* is a valuable edible and medicinal macrofungus, which is considered a promising food product and is increasingly attracting the attention of consumers. The fruiting bodies and mycelial biomass of this species are rich in biologically active substances, particularly polysaccharides, triterpenes, phenolic compounds, and glycoproteins. Due to its high levels of essential fatty acids, amino acids, minerals, and vitamins, *H. erinaceus* is considered a low-calorie product and falls into the category of functional foods. The review presents a comprehensive analysis of the modern literature on *H. erinaceus* with an emphasis on its mycochemical composition, traditional use, pharmacological potential, in particular, data on the immunomodulatory, anticancer, antioxidant, prebiotic effects of *H. erinaceus* extracts. However, the main effect that makes this mushroom unique is its neuroprotective, neuroregenerative properties. Data on the pharmacological use of both fruiting bodies and mycelial mass and the possibilities of its further use in the production of functional products are analyzed. Taking into account the nutritional and pharmacological value of this species, the review considers sustainable cultivation strategies, in particular, maintaining highly productive producer strains, provides a description of the micro- and macromorphological properties, data on the ecology and distribution of the fungus, and presents the results of targeted regulation of biosynthetic activity using the light factor. The analysis of literature data confirms the significant potential of *H. erinaceus* for obtaining mycelial biomass and valuable metabolites in modern mycobiotechnologies.

Keywords: Lion's mane; edible macrofungi; nutraceutical; polysaccharides; bioactive compounds and properties.

Introduction

In recent years, the considerable attention paid by biotechnologists and pharmacists to edible and medicinal mushrooms is due primarily to the diverse content of biologically active substances, which determines their multidirectional effect on the human body (Chang & Buswell, 2023; Pinar & Rodríguez-Couto, 2024). Thanks to modern biotechnological methods, such as the cultivation of mushrooms in pure culture conditions, and the isolation and identification of active components, it is becoming possible to develop new effective drugs and food additives (Hyde et al., 2019; Berovic et al., 2024). Thus, mushrooms are becoming a promising source of new natural products for maintaining health and treating various diseases (Niego et al., 2021; Kour et al., 2022). A significant number of experimental and review works are devoted to the study of the nutritional value, mycochemical composition, pharmacological and therapeutic properties of edible and medicinal mushrooms (González et al., 2020; Rangel-Vargas et al., 2021; Martínez-Burgosa et al., 2024; Lomberg et al., 2025).

Nowadays, *Hericium erinaceus* is among the most commercially significant cultivated species, the fruiting bodies of which have been an integral element of various cuisines and food cultures of mankind since ancient times and were used in traditional medicine in many countries of the world (Tan et al., 2024). Numerous literature data of the last decade are devoted to various bioactive compounds within *H. erinaceus* fruiting bodies and mycelium, collecting information on actual and potential secondary metabolites for prevention or treatment

of chronic, cognitive and human neurological diseases (Chong et al., 2020; Limanaqi et al., 2020; Qi et al., 2024; Contato & Conte, 2025). The composition of *H. erinaceus* includes various metabolites such as β -glucans (Spano et al., 2024) and secondary metabolites such as terpenoids (hericenones, erinacine), sterols, isoindolinones (Wang et al., 2019). It is reported that *H. erinaceus* extracts exert immunomodulatory, anticancer, anti-inflammatory, gastroprotective, cytoprotective, antioxidant, antibacterial, hypoglycemic, and hepatoprotective effects but the main effect that makes this fungus unique is its neuroprotective, neurotrophic, and neuro-regenerative properties (Hetland et al., 2020; Valu et al., 2020; Bizjak et al., 2024). Currently, this species is a promising object of modern clinical and pharmacological research (Kumar et al., 2021; Tan et al., 2024).

Hericium erinaceus is a popular culinary medicinal mushroom cultivated in many European countries, North America, and Asia. *Hericium erinaceus* is a good source of proteins and carbohydrates, low in fat. Also, the mushroom composition includes dietary fibers, essential amino and unsaturated fatty acids, minerals, vitamins, and ergosterol (provitamin D₂) making it a high-quality, low-calorie food (Das et al., 2021; Díaz-Godínez & Téllez-Téllez, 2021).

Unlike most reviews that predominantly focus on the ecology, distribution, and conservation status of *H. erinaceus* in natural ecosystems, as well as the technological aspects of cultivating its fruiting bodies on plant substrates or its pharmacological properties, this article systematizes information on the biologically active compounds found in both the fruiting bodies and the mycelium of the fungus. It also analyses their chemical nature and mechanisms of action. Special

attention is given to the neuroprotective potential, summarizing recent data from *in vitro*, *in vivo*, and clinical studies that demonstrate the effects of individual metabolites on neurogenesis, nerve growth factor (NGF) synthesis, and cognitive functions. The paper presents original data on the biological characteristics of producer strains cultivated on various agar nutrient media, focusing on the morphological and micromorphological features of the vegetative mycelium. Additionally, innovative approaches to enhancing the biosynthetic activity of promising strains are considered, including the use of low-intensity laser and LED irradiation during submerged cultivation. The significance of *H. erinaceus* is highlighted in the context of sustainable development due to its high nutritional, nutraceutical, and ecological value.

Thus, the objectives of this review are to summarize contemporary data regarding the chemical composition, pharmacological and biotechnological potential of cultivating *H. erinaceus* and evaluate its neuroprotective properties and biosynthetic activity under controlled conditions.

Mycology, distribution, and ecology

Hericium erinaceus (Fig. 1) is a basidiomycete from the family Hericiaceae. It is commonly known as Lion's mane, Pom Pom, Hedgehog Fungus, Monkey's Head mushroom, etc, all related to the conspicuous macromorphology of the basidiomes. *Hericium erinaceus* is characterized in a mature stage to have basidiomes consisting of numerous single, typically long, dangling, fleshy spines, which are at first white, becoming yellowish, then brownish with age (Thongbai et al., 2015). *Hericium erinaceus* has been commonly recorded in nature in Asia and North America, and more rarely in Europe.



Fig. 1. Fruiting bodies of *Hericium erinaceus* in Ukraine (Oleksandr Balagura's photo)

It is a saprotroph that grows on living (facultative parasite) and dead deciduous trees, mainly on oak and beech trees, less often on hornbeam, horse chestnut, aspen, plane tree, etc. It occurs in natural forests (deciduous and mixed) and artificial plantations (gardens and parks) from August to November. Fruiting bodies develop singly or in clusters of several pieces, up to 15 cm in diameter, woody, fleshy, hemispherical, rounded or flattened pillow-like, single or sitting or with a short eccentric leg, completely covered with a spiny hymenophore, white, later yellowish-ochre to reddish-ochre (Tkachenko et al., 2021). The spines in bundles, length of spines is 1–4 cm. The spore powder is white. Basidiospores are short ellipsoid to subglobose, size 5.0–6.5 × 4.0–5.0 μm (Hallenberg et al. 2013) and 5.5–6.2 × 5.0–5.5 μm (Tkachenko et al. 2021). The fungus rarely occurs in nature but is easily cultivated on industrial scales for edible and medicinal purposes (Thongbai et al., 2015).

Micromorphology, cultural characteristics of *H. erinaceus* pure cultures

Xylotrophic macromycetes play an important role in many fields of science and industry due to their unique properties and wide range

of applications (Bakratsas et al., 2021; Kour et al., 2022; Xv et al., 2024). Current literature indicates that the mycelium and basidiomes of *H. erinaceus* are sources of important nutrients and biologically active compounds that possess significant therapeutic potential (Chong et al., 2020; Qi et al., 2024; Tan et al., 2024). Information on the main biological characteristics of high-yield producer strains is extremely important for producers, since it is the correct selection of such strains that determines the success of the cultivation process and ensures high quality and quantity of the final product. In this regard, the complex analysis and evaluation of the biological characteristics of potential producer strains, as well as multi-stage screening for the selection of the most promising of them, becomes particularly relevant. In this context, a significant role is played by certified collections of mushroom cultures, which store a significant number of strains in an active physiological state in their funds and provide information support through modern databases (Bakratsas et al., 2021; Berovic et al., 2022; Cartabia et al., 2022).

To verify and confirm the taxonomic status of the culture at the species level, a complex of molecular-genetic and morphological-cultural methods are used, in particular, micromorphological characteristics using light and scanning electron microscope (SEM), physiological and biochemical characteristics of the cultures from the IBK Mushroom Culture Collection (Kyiv, Ukraine) (Buchalo et al., 2009; Bisko et al., 2016). According to research by Buchalo et al. (2009) *H. erinaceus* strains were characterised by the presence of micromorphological features, such as numerous medallion-type clamp connections – 1.2–2.4 × 4.0–6.8 μm in size (Fig. 2a, 2b, 2c), anastomoses between hyphae and stamps; apical and intercalary ellipsoid chlamydo spores – 5.6–6.4 × 8.8–14.5 μm (Fig. 2c). Numerous cubic, rectangular, and polygonal crystals were formed on the hyphae (Fig. 2a, d). The vegetative mycelium of *H. erinaceus* consisted of branched, regularly septated, colorless generative hyphae with a diameter of 1.3–4.5 μm. In the zone of mycelium growth, branched thin (width ≤ 1 μm) hyphae – dichohyphidia are formed (Mykchaylova et al., 2019).

The morphology and density of the colonies are varied. Mycelial colonies appear whitish and become cream or brownish over time, forming patterns of interconnected mycelial strands radiating from a dense center. The colonies of *H. erinaceus* strains are mostly felt or cottony, dense, and fluffy. The reverse darkens over time and is yellow. The edge of the colony is uneven and slightly raised above the substrate. The mycelium has a pleasant mushroom aroma. There is no exudate. It easily forms the teleomorph stage in the light, which serves as a reliable criterion for their identification in culture. We observed that strains actively formatted primordia and fruiting bodies on the vast majority of nutrient media, which allowed us to confidently verify them as strains of Lion's mane (Fig. 3) (Mykchaylova et al., 2019; Dotsenko et al., 2024).

As highlighted by Cheng et al. (2021) the potato dextrose agar supports the fastest growth rate of *H. erinaceus* mycelia. In our study, this nutrient medium also performed well, but the most selective media were found to be wort agar, also supplemented with decoctions of 3% oak sawdust and 5% fir needles. The strains grew at maximum growth rates on these media – up to 6 mm/day, depending on the strain and nutrient medium, and the densest woolly colonies were observed. However, the colonies were silky with mycelial strands in some slower-growing strains. The first fruiting bodies appeared on these media starting from the 20th day of cultivation (Dotsenko et al., 2024). The study of morphological and cultural features of strains on agarized nutrient media makes it possible to reveal additional taxonomic characteristics of mushroom culture, as well as to choose optimal nutrient media for cultivation and preservation of strains in a proper physiological state (Buchalo et al., 2009; Mykchaylova et al., 2019).

Bioactive metabolites of *H. erinaceus* with proven pharmacological activities

Research on the mycochemical composition of fungi as a new functional product has, until recently, focused mainly on certain classes of compounds, namely proteins, carbohydrates, fatty acids, fiber

or individual metabolites, which are considered responsible for specific biological properties.

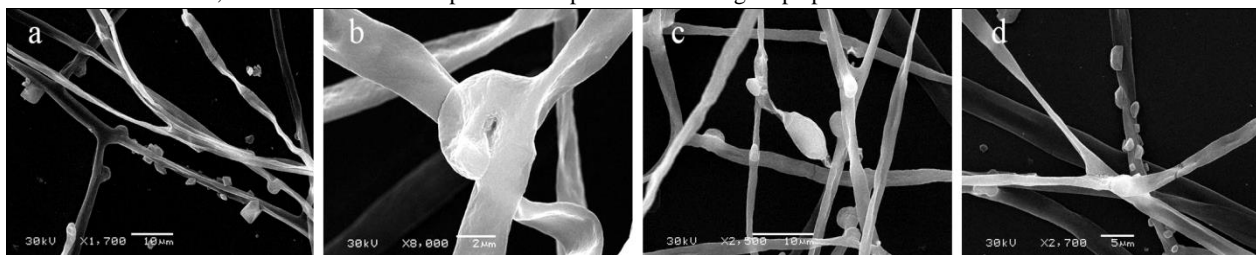


Fig. 2. The IBK Mushroom Culture Collection (Kyiv, Ukraine) *Hericium erinaceus* strain 1609 micromorphology: *a* – vegetative mycelium with clamp connections and crystals (SEM, $\times 1700$); *b* – clamp connection (SEM, $\times 8000$); *c* – vegetative mycelium with clamp connections and intercalary chlamydospore (SEM, $\times 2500$); *d* – hyphae with crystals (SEM, $\times 2700$); compiled from the authors' materials

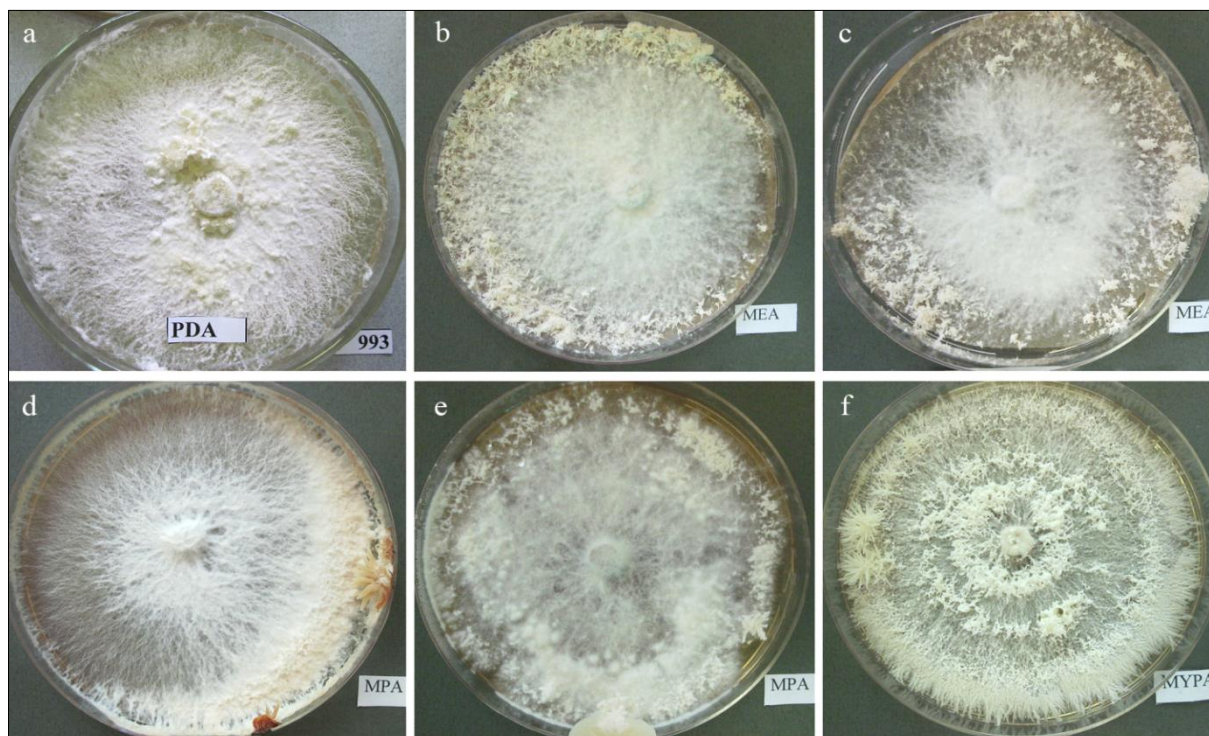


Fig. 3. Primordia and teleomorph formation of *Hericium erinaceus* strains from the IBK Mushroom Culture Collection (Kyiv, Ukraine) on agar media: *a* – potato-dextrose agar (PDA), strain IBK 993; *b* – malt extract agar (MEA), strain IBK 2016 and *c* – strain IBK 963; *d* – malt extract-peptone agar (MPA), strain IBK 991 and *e* – strain IBK 1606; *f* – malt extract-peptone-yeast agar (MYPA), strain IBK 2239; compiled from the authors' materials

However, to assess the potential of the food and medicinal matrix of a promising producer, it is necessary to have its detailed chemical profile. Friedman (2015), in a review article, reported that Lion's mane cultivars contain more than 50 characterized organic compounds many of which are bioactive. Qiu et al. (2024) have already reported that approximately 150 small molecules from *H. erinaceus* have been separated and identified. Among them, the two most recognized categories are hericenones and erinacines, as many possess neurotrophic and neuroprotective activities (Deshmukh et al., 2021). The bioactive metabolites found in *H. erinaceus* can be classified into two groups: high molecular weight compounds, including polysaccharides and proteins, and low molecular weight compounds, such as terpenoids and polyketides (Yang et al., 2021; Lazur et al., 2024). *Hericium erinaceus* extracts show some dominant compounds: terpenoids (erinacines), phenols (hericenone AE), pyrones (erinapyrones AC), sterols (erinanol, hericerins, hericenones), and fatty acids. The representative chemical compounds of *H. erinaceus* are described in Table 1. They also demonstrated various biological activities, which are explored in greater depth below and summarized in Table 2.

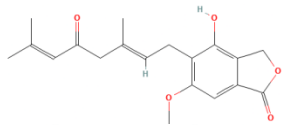
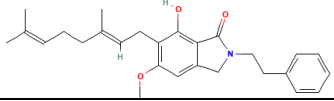
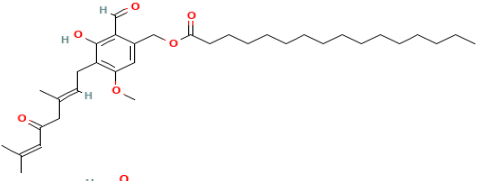
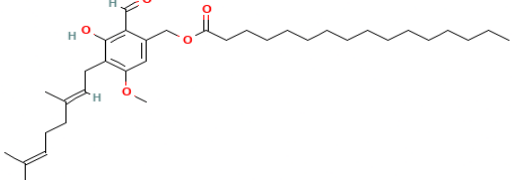
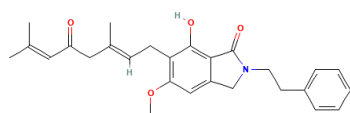
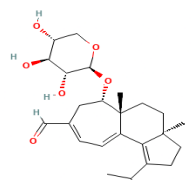
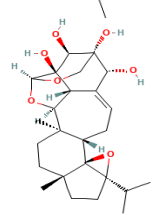
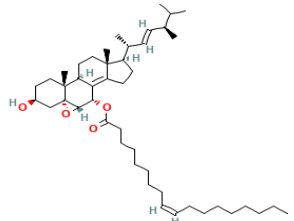
Polysaccharides

Numerous studies have focused on establishing the structural, physicochemical, and biological properties of mushroom biopolymers. Currently, only a small quantity of mushroom polysaccharides is produced on an industrial scale. The limited production is primarily due to high costs associated with production and purification, low final product yields, and the polysaccharides' unstable chemical characteristics. Such problems occur mainly during the production of these biopolymers from fruiting bodies. However, modern technologies for cultivating mycelial biomass using submerged cultivation under controlled processing conditions have significantly improved both the yield and quality of the desired products. Therefore, there is an ongoing need to identify promising producer strains and develop methodologies to regulate biosynthetic activity effectively. Polysaccharides derived from edible and medicinal mushrooms are emerging as valuable biomolecules with potential applications in pharmaceuticals, nutraceuticals, and functional foods. Their various therapeutic properties have been extensively studied, confirming their significant potential for use in developing functional food products (Rauf et al., 2023; Navarro-Simarro et al., 2024; Mayirmao et al., 2025). As of 2025, more than 35 different polysaccharides have already been isolated from the mycelium of *H. erinaceus* (Spelman et al., 2017; Łysakowska et al., 2023; Kostanda et al., 2024). These polysaccharides have many therapeutic effects: antitumor, antibacterial, antiviral, he-

patoprotective, immunostimulating, hypolipidemic, prebiotic effects (Fernandes et al., 2023).

Table 1

Structure of some representative bioactive compounds derived from *Hericium erinaceus* fruiting bodies, mycelia and cultures

Class and name of compounds	Example	Structure
Hericenones A, I, J, H, G, and F	Ketones	
	Hericenone A	
	Erinacerins A-N	Erinacerin B
Hericerin, Hericerin A	Hericerin	
Hericenones C, D, E, and I	Phenols	
	Hericenone C	
Hericenes A-D	Hericenes A	
Hericenone B	Alkaloid	
Hericenone B	Hericenone B	
Erinacines A-Z2	Terpenoids	
	Erinacine A	
Hericinoids A-C	Hericinoid A	
Erinarol A-G	Sterols:	
Erinarol A	Erinarol A	

Note: compiled by the authors based on data from <https://pubchem.ncbi.nlm.nih.gov>.

The review by Yu et al. (2023) shows that polysaccharide fractions isolated from this mushroom show significant potential for stimulating the immune system, in particular through the activation of the production of interleukins, macrophages and other components of the body's defence system. Kour et al. (2022) confirm their effectiveness in this direction in animal studies and human clinical studies. Anti-cancer and immunostimulating effects of polysaccharides from *H. eri-*

naceus are primarily associated with the activation of many immune cells (T-cells, macrophages, cytokines, etc.), as well as increasing the ability of the immune system cells to find and destroy migrating cancer cells in the human body (Jiang et al., 2014; Zhang et al., 2022). Unlike synthetic drugs used in chemotherapy, these polysaccharides do not have a toxic effect, on the contrary, they can activate the N-terminal c-Jun kinases (JNK), which participate in the processes of

apoptosis, enhancing intracellular apoptotic signals. The research by Ren et al. (2017) demonstrates that the polysaccharide fraction of ethanolic extracts of *H. erinaceus* exhibits immunomodulating properties, contributes to the maturation of dendritic cells, their production of cytokines and proliferation of T cells, activation of macrophages, and an increase in tumor necrosis factor. For example, the review by Wang et al. (2019) indicates that both extracellular and intracellular

polysaccharides demonstrate a protective effect against oxidative hepatotoxicity in mice. In general, the review by Tan et al. (2024) confirms that numerous tests were conducted *in vitro* and *in vivo* showed significant therapeutic potential of metabolites of the *H. erinaceus* mushroom (aqueous and ethanol extracts of fruiting bodies and mycelial mass) with promising results against a variety of cancers, including those in the breast, blood, colon, liver, lungs, sarcoma, stomach.

Table 2

Some important bioactive metabolites of *Heridium erinaceus* and their biological activities

Bioactive compounds	Type of sample	Test model	Mechanism of action
Polysaccharides, beta-glucan, lipopolysaccharide	FB, M	<i>in vitro</i> , <i>in vivo</i> , pre-clinical, clinical	Anticancer, antioxidant, immunomodulatory, anti-inflammatory, antimicrobial, anti-ageing, neurotonic, gastroprotective (lactogenic effect, which positively affects the intestinal microbiota), hepatoprotective, anti-asthmatic, hypoglycemic, hypocholesterolemic effects
Glycoprotein, protein, glycolipids, lectin protein (agglutinin)	FB	<i>in vitro</i>	Anticancer, immunomodulatory effect, hemagglutinating activity, antimicrobial action
Erinacines	M	<i>in vitro</i> , <i>in vivo</i> , pre-clinical, clinical	Neuroprotective properties, anti-neurodegenerative, anti-aging, protection against brain ischemia injury induced neuronal cell death, life-prolonging activity, antidepressant-like effects
Erinacerins	FB, SC	<i>in vitro</i>	Anticancer, brain protective agents for preventing dementia disease
Hericenones	FB	<i>in vitro</i> , <i>in vivo</i> , pre-clinical, clinical	Neuroprotective, anticancer, cytotoxic, reduces platelet aggregation, anti-aging, anti-inflammatory, antioxidants, prevention of neurodegenerative disorders, improve neurocognitive impairment
Hericerins	FB	<i>in vitro</i>	Reduction of pro-inflammatory mediators and cytokines, pollen growth inhibitor
Hericenens	FB, M	<i>in vivo</i>	Effects of oral supplementation on cognitive decline
Hericenals	M	<i>in vitro</i>	Anti-hyperglycemic and anti-hypocholesterolemic
Sterols	FB, M	<i>in vitro</i>	Antioxidative, anti-inflammatory and antiproliferative properties
Phenolic compounds	FB, M	<i>in vitro</i>	Antioxidative properties

Note: FB – fruiting body; M – mycelium; SC – solid culture; compiled by the authors based on data from Inanaga (2012), Ma et al. (2012), Reis et al. (2012), Cui et al. (2014), Jiang et al. (2014), Lee et al. (2014), Li et al. (2014), Wang et al. (2014), Dai et al. (2015), Friedman (2015), Lee et al. (2015), Thongbai et al. (2015), Wang et al. (2015), Zan et al. (2015), Sokół et al. (2016), Diling et al. (2017), Li et al. (2017), Ren et al. (2017), Sheng et al. (2017), Spelman et al. (2017), Zhang et al. (2017), Tzeng et al. (2018), Ashour et al. (2019), Li et al. (2019), Ratto et al. (2019), Bailly & Gao (2020), Chong et al. (2020), Liu et al. (2020), Mitsou et al. (2020), Valu et al. (2020), Zhang et al. (2020), Alkin et al. (2021), Niego et al. (2021), Roda et al. (2021), Wang et al. (2021), Chang & Buswell (2023), Kopylchuk et al. (2023), Lomberg et al. (2023), Narmuratova et al. (2023), Bizjak et al. (2024), Qi et al. (2024), Qiu et al. (2024), Tan et al. (2024), Wang et al. (2024), Contato & Conte (2025).

Mushroom polysaccharides can stimulate the immune response in the intestine through interaction with certain receptors or with microorganisms that produce butyrate or propionate molecules, which in turn affect the expression of cytokines associated with various inflammatory substances. In addition, they improve the assimilation of some food components (Sawangwan et al., 2018; Liu et al., 2020). A study by Sheng et al. (2017) demonstrates that the polysaccharide fraction of *H. erinaceus* stimulates the intestinal immune system through the activation of natural killer cells. In addition, β -glucans from the fruiting bodies of *H. erinaceus* have a pronounced lactogenic effect, which positively affects the intestinal microbiota (Mitsou et al., 2020). A scheme of the mechanism of action of *H. erinaceus* polysaccharides in the gastrointestinal tract is presented in Figure 4.

Chitin, mannans, galactans, xylans, glucans, and hemicelluloses found in mushrooms have potential as probiotics (Cheung, 2013; Sawangwan et al., 2018). Ma et al. (2021) also considered the edible mushroom polysaccharides as prebiotics as they can be selectively fermented by colonised microbiota in the gastrointestinal tract. Experimental studies have confirmed that the polysaccharides of *Lentinula edodes*, *Pleurotus ostreatus*, *P. eryngii*, *Ganoderma lucidum*, *Flammulina velutipes* are composed of short-chain sugars that resist digestion in the intestines and selectively enhance the growth and metabolic activity of beneficial gut bacteria. In addition, the high potential of antimicrobial action of these species against some pathogens, such as *Bacillus cereus*, *Staphylococcus aureus*, and *Salmonella typhimurium*, has been demonstrated (Aida et al., 2009; Fernandes et al., 2023). However, Liu et al. (2020) argued that it is important that these polysaccharides retain their prebiotic properties in the conditions of the human gastrointestinal tract, even in the presence of salivary amylase, gastric juice or bile extract, activating microflora beneficial to human health.

The effects of *H. erinaceus* on the microbiota have been investigated in various studies, including *in vitro* experiments (Mitsou et al., 2020), animal models (Diling et al., 2017; Yang et al., 2021), and several short-term pilot clinical studies (Xie et al., 2021; Bizjak et al., 2024). According to the investigations by Xie et al. (2021), short-term supplementation with *H. erinaceus* increased alpha diversity and the relative abundance of bacteria that produce short-chain fatty acids,

while also downregulating some pathobionts. Despite these findings, only a few changes in gut microbiota composition were observed after the intervention. It is well established that gut microbiota significantly influences mental health by impacting the gut-brain axis, primarily through the regulation of various neuroactive modulators, such as brain-derived neurotrophic factor. Bizjak et al. (2024) demonstrated that modifying gut microbiota composition through the consumption of *H. erinaceus* may lead to longevity-promoting effects and provide protection against age-related cognitive decline. In a randomized study, the effects of *H. erinaceus* supplementation on the composition of gut microbiota were found to be influenced by the age and gender of the participants. Additionally, the activity level of chitinase 3-like-1 appeared to play a role, suggesting a potential mechanism for the increased bioavailability of the active ingredients in mushrooms.

Thus, polysaccharides of edible medicinal mushroom *H. erinaceus* have significant potential for use in pharmaceuticals, nutraceuticals and functional products. Modern technologies for obtaining cultivated mycelial biomass under submerged controlled conditions of the technological process can significantly increase the yield and quality of the target product. Due to the significant pharmacological potential of polysaccharides from *H. erinaceus*, studies have been conducted to explore how light affects biomass formation and polysaccharide synthesis. Based on the conducted research, Mykchaylova et al. (2023) developed methods of photoactivation of the inoculum with the aim of its further use to increase the efficiency of biotechnological processes of obtaining mycelial mass, biologically active compounds (polysaccharides, fatty acids, melanins, derivatives of phenolic substances), reducing the duration of cultivation. It has been established that the most effective *H. erinaceus* inoculum irradiation dose is 240 mJ/cm². It has been shown that using light-emitting diodes (LED) and laser light sources is expedient because, in the specified modes, it promotes significant growth stimulation in *H. erinaceus*. Activation of the seed mycelium in the selected modes allows the duration of cultivation to be reduced and increase in the amount of the obtained mycelial mass and biologically active substances of the *H. erinaceus* species. The most effective irradiation regimens that

stimulate the synthesis of extracellular and intracellular polysaccha-

rides are shown in Table 3.

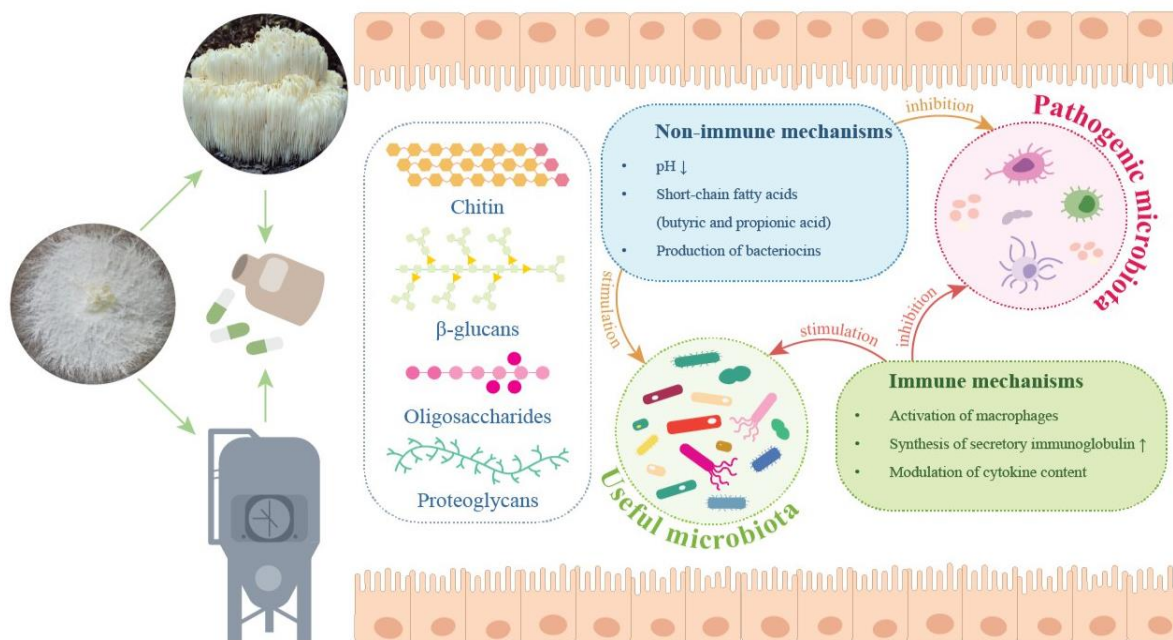


Fig. 4. Schematic representation of the mechanism of action of *Hericium erinaceus* polysaccharides in the gastrointestinal tract: designed by the authors

Table 3

Increase in the amount of biomass, extracellular and intracellular polysaccharides during irradiation of the inoculum of *Hericium erinaceus* IBK 977 under submerged cultivation (% control)

Parameters studied	Irradiation modes, nm			
	LED $\lambda = 470$	Laser $\lambda = 488$	LED $\lambda = 530$	LED $\lambda = 650$
Biomass	98.1	132.1	66.0	100.1
EPS	57.1	42.8	9.0	19.1
IPS	75.6	53.6	41.9	24.3

Note: EPS – extracellular polysaccharides, IPS – intracellular polysaccharides; compiled by the authors based on data from Mykchaylova et al. (2023).

Therefore, the search for promising producer strains and the development of conditions and methods of regulation of biosynthetic activity remain a relevant direction of research in this field.

Terpenoids

Various diterpenes are present in *H. erinaceus*. To date, numerous low molecular weight secondary metabolites have been isolated from the mycelium and fruit bodies of *H. erinaceus*. The most interesting are two classes of terpenoid compounds: hericenones and erinacines obtained from fruiting bodies and cultivated mycelium, respectively. Hericenones, a class of aromatic compounds, were isolated from the *H. erinaceus* fruiting body by Kawagishi et al. (1990). They pointed out the perspective of using hericenones as natural remedies against Alzheimer's disease, assuming the possibility of their passing through the blood-brain barrier and inducing the production of neurotrophic growth factor (NGF) in the brain. Hericenones A and B showed significant cytotoxicity against HeLa cells. In their further research Kawagishi et al. (1996) proved that hericenone B effectively inhibits platelet aggregation, preventing thrombosis, heart attacks, and strokes. However, hericenones C, D, E and H showed a stimulating effect activity in the synthesis of NGF *in vitro*. On the other hand, hericenones F and G did not stimulate NGF synthesis under the same conditions, but 3-hydroxyhericenone F protected against neuronal death. Ma et al. (2012) noted that in addition, hericenones I, J and L showed cytotoxic activity against EC109 tumor cells. It is still controversial whether all hericenones are active components in stimulating NGF biosynthesis. Phan et al. (2014) investigated the stimulation of

NGF synthesis by hericenone E cells in rat pheochromocytoma (PC12) using several pharmacological inhibitors. Instead, some researchers have shown that hericenones C, D, and E did not increase NGF biosynthesis in the 1321N1 cell line (Mori et al., 2008). Chen et al. (2018) also reported that the isolation of three cyathane-type diterpenoids – hericinoids A–C from the fermentation broth of *H. erinaceus*, could not enhance NGF-induced neurite outgrowth in PC12 cells.

In addition, another class of terpenoid compounds, a group of cyathane-type diterpenoids, named erinacines (A–I), was obtained from cultivated mycelium (Jiang et al., 2014; Spelman et al., 2017). Erinacines are low-molecular substances that stimulate synthesis of NGF through interaction with mitogen-activated protein kinase of neurons and can overcome hematoencephalic barrier. Erinacine derivatives are potential drugs for degenerative disorders of neurons and peripheral regeneration nerves. Thus, Venturella et al. (2021) noted that the cyanine-diterpenoid erinacine A, obtained from the *H. erinaceus* mycelium, demonstrated inhibitory activity against a wide range of cancer cells associated with the gastrointestinal tract and has been proven to have an effective protective effect against Parkinson's disease. Some studies were conducted with *H. erinaceus* extracts regarding the mechanisms involved in the process of brain neuroprotection (Mori et al., 2008; Phan et al., 2014; Kushairi et al., 2019). Thongbai et al. (2015) reported that erinacine A can prevent ischemic injury to neurons and acts as an anti-inflammatory agent. Bizjak et al. (2024) examined the effects of erinacine A-enriched *H. erinaceus* supplement on cognitive function and serum biochemical markers (Brain-Derived Neurotrophic Factor and Neuropeptide Y), faecal levels of chitinase 3-like-1, and gut microbiota composition in healthy adults (aged 62.9 ± 7.1). In 8-week double-blind, placebo-controlled clinical trial 33 subjects were randomly assigned to either a group receiving a diet supplemented with *H. erinaceus* or a placebo group. Two non-verbal speed tests were used to assess cognitive function. The group that received the *H. erinaceus* supplementation showed a significant improvement in cognitive ability when taking into account baseline cognitive scores, chitinase 3-like-1 level, age, and gender. Additionally, this group exhibited a notable increase in gut microbiota diversity, which was positively correlated with neuropeptide Y levels. The study found that dietary supplementation with *H. erinaceus* is safe, well-tolerated, and provides neurocognitive benefits (Bizjak et al., 2024).

Erinacerins

Wang et al. (2015) from a Lion Mane mushroom fermented on rice isolated ten new isoindoline-1-ones, named erinacerins C–L. This represents another class of secondary metabolites produced by *H. erinaceus*. The authors suggest that the described solid-state fermentation technique seems to be a useful method to stimulate the biosynthesis of secondary metabolites. Some of these compounds inhibited the growth of cancer cells, as described before. Four novel isoindolinone compounds with neurotrophic activity isolated by Ryu et al. (2018) from the *H. erinaceus* fruiting bodies were named as hericerin, isohericerinol A, N-de-phenylethyl isohericerin and corallocin. Erinacerins A–N are a series of isoindolinone compounds, with erinacerins A, B, M, and N being derived from the fruiting bodies of *H. erinaceus*, while erinacerins C–L are isolated from the solid culture of *H. erinaceus* and exhibit α -glucosidase inhibitory activity (Qiu et al., 2024).

Sterols

Qui et al. (2024) reported that erinarol A–G is a group of sterol fatty acid esters isolated from the methanol extract of the fruiting bodies of *H. erinaceum*. In the fruiting body of *H. erinaceus*, ten erinarols A–J, five ergostane-type sterol fatty acid esters, and ten ergostane-type sterols have been identified. Sterols, such as ergosterol confer antioxidative properties. As Spelman et al. (2017) highlight, *H. erinaceus* has been identified as the most potent *in vitro* inhibitor of both low-density lipoprotein (LDL) oxidation and HMG-CoA reductase activity, indicating its potential therapeutic value in preventing vascular diseases associated with oxidative stress. Dai et al. (2015) evaluated the biomass and ergosterol content of *H. erinaceus* mycelium using plant-derived compounds supplementation into liquid culture and obtained the highest ergosterol content of 2.33 mg/g after 6 days of cultivation with 100 $\mu\text{mol/L}$ salicylic acid. In another instance of sterol identification, Li et al. (2017) compared the sterol composition found in both ethanol and water extracts of *H. erinaceus*, and showed that sterols were primarily concentrated in the ethanol extracts. The research outlined the isolation and structural characterization of six new compounds, named erinarols A–F, as well as five known ergostane-type sterol fatty acid esters. Additionally, ten known ergostane-type sterols and erinarols G–J were also identified from methanol extracts of the dried fruiting bodies of *H. erinaceum*. Some of these compounds also exhibit anti-inflammatory and antiproliferative properties in cell assays (Cui et al., 2014; Friedman, 2015).

Glycoprotein and glycolipids

Interestingly, *H. erinaceus* is not just a source of low molecular weight biologically active compounds, but as well as some proteins that have a considerable tumor suppressive potential. As observed by Diling et al. (2017), the HEP3 protein isolated from *H. erinaceus* exhibited immunomodulatory activity in lipopolysaccharide-activated macrophages by decreasing the overproduction of tumor necrosis factor- α , interleukin (IL)-1 β , and IL-6, and downregulating the expression of inducible nitric oxide synthase and nuclear factor- κB p65. The further immunomodulatory effect was caused by the stimulation of intestinal microbiota with protein, which included activation of proliferation and differentiation of T cells and stimulation of antigen-presenting cells of the intestine. Another example of a biologically active protein isolated from fermented mycelia of *H. erinaceus* – is a glycoprotein HEG-5, which was able to induce apoptosis in the gastric cancer cell line SGC-7901, stimulating expression of some proapoptotic factors (Cui et al., 2014; Zan et al., 2015). The compound has a molecular weight of 14.4 kDa and was shown to have hemagglutinating activity. Analysis using FT-IR and NMR showed that HEG-5 contains the protein and carbohydrate parts with (1 \rightarrow 4)-linked β -galactose and β -glucose residues, and circular dichroism showed that the HEG-5 is a predominantly β -sheet glycoprotein.

Cerebrosides are natural organic compounds from the group glycolipids, another class of compounds found in mushrooms. It is shown that cerebroside E, isolated from *H. erinaceus* fruiting bodies, exhibited a significant inhibitory effect on angiogenesis in HUVECs.

As highlighted by Lee et al. (2015), this compound has also been shown to have antitoxic properties, and attenuated cisplatin-induced nephrotoxicity in LLC-PK1 cells, which is sufficient to propose its use in a cancer chemotherapy protocol.

Fatty acids

Heridium erinaceus also contains fatty acids with unique properties, including octadecenoic acid derivatives identified by Kawagishi et al. (1990). These compounds exhibit growth-inhibitory effects on tea pollen and demonstrate cytotoxicity toward HeLa cells (Qiu et al., 2024).

The research results by Mykchaylova et al. (2023) have demonstrated that low-intensity LED and laser light within the visible spectrum can influence the lipid composition of *H. erinaceus* mycelial mass. Light exposure also induced alterations in the fatty acid profile in the mycelial mass. The lipid fraction analysis of the *H. erinaceus* mycelial mass revealed a reduction in saturated fatty acid content in response to exposure to various wavelengths of light. For *H. erinaceus* mycelium optimal regimes of irradiation were established: blue laser light ($\lambda = 488$ nm) demonstrated the greatest effect on the fatty acid profile of the mycelial mass and the synthesis of monounsaturated oleic (C18:1 ω -9) acid. Green ($\lambda = 530$ nm) and red ($\lambda = 650$ nm) LED irradiation induced the synthesis of polyunsaturated fatty acids: linoleic (C18:2 ω -6), eicosadiene (C20:2 ω -6), cis-11,14,17-eicosatriene (C20:3 ω -6), arachidonic (C20:4 ω -6) acids that belong to the group of essential fatty acids and were absent in the control samples. This opens up new opportunities for the development of effective technologies for the cultivation of mushrooms to increase their biological value.

Phenolic compounds

Recently, xylophilic macromycetes have been considered a natural source of phenolic compounds with high antioxidant activity (Kozarski et al., 2015; Rašeta et al., 2020). Reactive oxygen species react with many molecules in the body, causing oxidative damage that requires antioxidants to neutralize. As Rašeta et al. (2020) notes, the biological activity of phenolic compounds is related to their ability to chelate metals, inhibit lipoxygenase, and scavenge free radicals, which is the main cause of endogenous damage to the body that leads to aging. Exogenous food antioxidants or natural products based on medicinal mushrooms, including *H. erinaceus*, are promising for use as a nutraceutical in chronic diseases (Reis et al., 2012; Niego et al., 2021). According to the scientific literature, the synthesis of various phenolic compounds in fruiting bodies and mycelium of xylophilic macromycetes is a protective reaction to the influence of various adverse environmental factors, including light (Zhou et al., 2022).

A review of the literature data on the total phenol content in the mycelium of *H. erinaceus* indicates a significant influence of cultivation conditions on these indicators. For example, Valu et al. (2020) reported that the content of total phenolics in the mycelial mass of *H. erinaceus*, using ultrasonic extraction, ranged from 11.1 mg/g to 23.2 mg/g, depending on the type of solvent and extraction technique. Based on the results of the data analysis, the general content of phenolic compounds in aqueous and methanolic extracts of *H. erinaceus* ranges from 1.96 to 6.31 mg/g (Alkin et al., 2021). Extracts obtained with n-hexane, chloroform, ethyl acetate, n-butanol and water had concentrations ranging from 4.36 to 35.18 mg/g (Li et al., 2012). Further investigation by Kopylchuk et al. (2023) showed that the ethanolic extract of *H. erinaceus* had a total phenolic content of 41.28 mg/g. This is supported by the study of Sevindik et al. (2024), who demonstrated that, obtained under optimized conditions, the ethanolic extract of *H. erinaceus* had a concentration of 59.75 ± 1.82 mg/g. Therefore, *H. erinaceus* is a valuable natural resource for pharmacological applications.

Effects and mechanisms of action of biologically active compounds

Neuroprotective and neurotrophic effects. It is reported above that the fruiting bodies and mycelia of *H. erinaceus* produce several classes of biologically active molecules, including polysaccharides, proteins, lectins, phenols, and terpenoids. A significant part of the recent research was focused on the neuroprotective properties of the mushroom, which are currently widely described (Chong et al., 2020; Venturella et al., 2021).

As Thongbai et al. (2015) highlighted, erinacin A causes potent restoration of nerves, strengthens their properties and effectively inhibits death of neuronal cells. It can enhance the synthesis of NGF by increasing the secretion of norepinephrine and catecholamines. Cyanate-xyloside of erinacin P and its biochemical transformations in erinacin A as well as erinacin B induced NGF synthesis. A number of studies were conducted with by *H. erinaceus* extracts regarding the mechanisms involved in brain neuroprotection (Mori et al., 2008; Kushairi et al., 2019). An effect of erinacin A is reported to have been found which can prevent ischemic injury to neurons and act as an anti-inflammatory agent. The use of hericenone C and erinacine A has been recommended for improving memory functions and improvement teaching. It has been proven that these compounds can significantly affect synthesis of NGF *in vitro* or *in vivo* (Jiang et al., 2014; Thongbai et al., 2015).

A natural agent has been isolated from *H. erinaceus* extracts – amycenone (amyloban), which is an activator of brain function and can exert a protective effect on brain cells in culture, protecting them from damage by amyloid peptides. As Inanaga's (2012) further studies have shown, hericenones and amyloban, are effective against damage to the human brain. Due to its anti-inflammatory properties and its ability to promote the expression of nerve growth factor genes and support neurite outgrowth, *H. erinaceus* is used for the treatment of Alzheimer's as well as Parkinson's diseases (Deshmukh et al., 2021). As Chong et al. (2020) reported, bioactive compounds extracted from the mycelia and fruiting bodies of *H. erinaceus* may be used as a potential alternative medicine for the treatment of depression. Authors have confirmed that using Lion's mane does not result in any negative consequences. The clinical studies with with amyloban indicate its promising results for use against dementia and Alzheimer's disease, primarily due to the absence of any side effects (Thongbai et al., 2015). Another actual use of amycenone, an active substance extracted from *H. erinaceus* mushrooms, is to fight excess weight. Kudo et al. (2022) clarified the effects and mechanisms of action of amycenone *in vivo*. The authors reported that amycenone reduces excess body weight and attenuates hyperlipidaemia in mice by inhibiting lipogenesis and promoting lipolysis through lipid metabolism pathway stimulation and fatty acid β -oxidation acceleration.

Thus, *H. erinaceus* has numerous biological activities. Hericenones and erinacines stimulate NGF, which suggests that *H. erinaceus* has a certain influence on the functioning of the brain and the autonomic nervous system. Research by Limanaqi et al. (2020) shows that consuming *H. erinaceus* can reduce symptoms of depression and anxiety. Cheng et al. (2016) demonstrated that treatment of rat pheochromocytoma cells PC12 with two high-molecular purified *H. erinaceus* polysaccharides increases antioxidant activity and has neuroprotective properties effects against A β -induced neurotoxicity. That is, *H. erinaceus* polysaccharides protected PC12 cells from A β -induced cell apoptosis. Thus, polysaccharides from *H. erinaceus* with different molecular weights not only play a role in the immunomodulation of dendritic cells but also demonstrate neuroprotective effects for neurons.

Antimicrobial effect and antioxidant activity

Various researchers have confirmed the antimicrobial effect of fresh *H. erinaceus* fruiting bodies (Jiang et al., 2014; Thongbai et al., 2015; Song et al., 2020). According to research by Kim et al. (2019), the *H. erinaceus* mycelium inhibits bacterial growth. The results of the study provided by Lomberg et al. (2023) and Narmuratova et al. (2023), who investigated the antimicrobial activity of culture fluid and mycelial mass of selected *Hericium* strains, confirm the ability of the studied *Hericium* species to produce antibacterial metabolites with a

wide and narrow spectrum of action that might have potential health benefits and could be recommended for further analysis, isolation, and identification of antibacterial compounds potentially promising in pharmacology.

Ryu et al. (2018) conducted a comparative study of the content of ergothioneine and polyphenols in fruiting bodies of different *H. erinaceus* and *H. coralloides* strains to evaluate their antioxidant properties. It is known that ergothioneine, which humans are unable to synthesize, is a unique sulphur-containing amino acid, an antioxidant, cytoprotective, and anti-inflammatory element, with therapeutic potential, approved by World Food Agencies (Bell et al., 2022). In general, the content of ergothioneine and polyphenols differed by strain, but the ratio of the two compounds did not much differ in the studied species.

Hericium erinaceus has demonstrated the highest content of antioxidant compounds and the strongest inhibition of hydroxyl activity among investigated ethanol extracts of four wild edible mushrooms (*H. erinaceus*, *Laetiporus sulphureus*, *Polyporus umbellatus*, *Sparassis nemecii*). Consequently, it can be a valuable source of substances with significant antioxidant potential. The antioxidant compounds present in *H. erinaceus* may act as promising protective agents in preventing and treating diseases related to oxidative stress (Kopylchuk et al., 2023). Malinowska et al. (2009) found that the selenium-containing extracellular polysaccharides obtained under submerged cultivation of *H. erinaceum*, demonstrate excellent antioxidant activity as evidenced by reducing power, inhibition of lipid peroxidation and free radicals scavenging assays. Optimizing the extraction parameters from *H. erinaceus* was a method to achieve the best possible antioxidant potential of this fungus. Obtained extracts exhibit high antioxidant, antiproliferative, and antimicrobial properties (Sevindik et al., 2024).

Therefore, *H. erinaceus* is considered one of the most highly regarded edible mushrooms due to its production of neuroprotective biomolecules. Its traditional use for chronic ailments, coupled with the findings of current studies, indicates that *H. erinaceus* is safe and holds significant potential as a neuroprotective and neurotrophic therapeutic agent for neurological conditions. Its rich myconutrient composition suggests that utilizing the entire fungus could be the most beneficial approach clinically. Thus, preparations from *H. erinaceus* are already available today to prevent and improve conditions with Alzheimer's disease, Parkinson's disease, and dementia, as well as in sports medicine. Despite all the variety of neurotrophic effects of macromycetes on the human body, functional changes in the nervous system, which are the basis of the described effects, have been insufficiently studied, the vast majority of the results described in the review were carried out on cell lines and experimental animals (*in vitro* and *in vivo*), and require further observations.

Conclusion

The cultivation of mushrooms, particularly *H. erinaceus*, presents a promising opportunity to contribute significantly to the Sustainable Development Goals (SDGs) set by the United Nations. The edible medicinal mushroom *H. erinaceus* contains high levels of protein and fiber in its fruiting bodies and mycelium while being low in fat and calories. It offers a complete profile of essential amino acids and fatty acids, as well as macro and microelements, making it a desirable addition to any diet. Due to their non-toxic bioactive compounds, Lion's mane mushrooms hold promise in preventing and treating neurodegenerative diseases and others. They can also serve as a source of health-promoting products for future use in functional foods, dietary supplementation, and nutraceuticals.

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