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REVIEW

Melanin in *Auricularia auricula*: biosynthesis, production, physicochemical characterization, biological functions, and applications

Jiaying Wang[1] · Zihui Ma[1] · Chengtao Wang[1] · Wei Chen[1]

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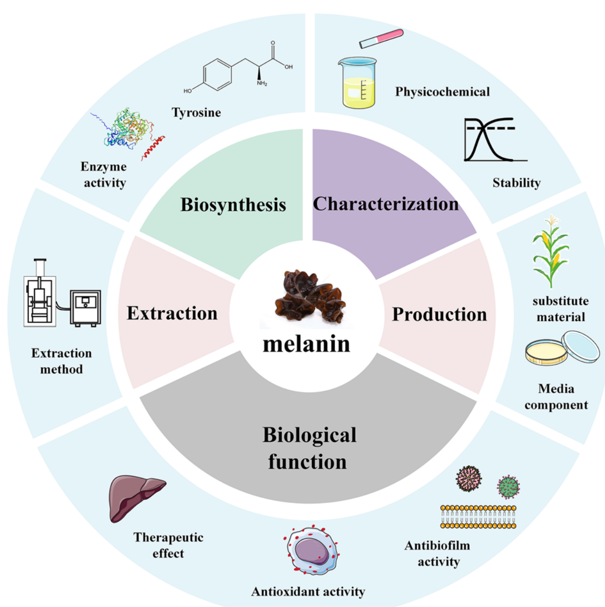
Abstract
Auricularia auricular (*A. auricula*), a nutritious fungus and traditional medicinal resource, is known for melanin. This review aims to summarize the research progress on melanin in *A. auricula*, specifically focusing on biosynthesis, fermentation production, extraction processes, physicochemical characterization, biological functions, and applications. The biosynthesis of melanin in *A. auricula* primarily involves the oxidative polymerization reaction of phenolic compounds. To enhance melanin production, strategies such as deep fermentation culture, selection of optimal fermentation materials, and optimization of the culture medium have been employed. Various extraction processes have been compared to determine their impact on the physicochemical properties and stability of melanin. Moreover, the antioxidant and antibiofilm activities of *A. auricula* melanin, as well as its potential beneficial effects on the human body through in vivo experiments, have been investigated. These findings provide valuable insights into the application of *A. auricula* melanin and serve as a reference for future research in this field.

Graphical abstract



Keywords *Auricularia auricular* · Biosynthesis · Fermentation production · Extraction process · Physicochemical characterization · Biological function

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Introduction

Auricularia auricula, a macro-fungus widely utilized as both a food and medicinal resource, has gained significant popularity in Asia. Its applications span a range of fields including traditional medicine, fermented foods, noodles, antibiotic oxidants, and other valuable resources (Liu et al., 2021). *Auricularia auricula* contains various bioactive components, including melanin, polysaccharides (Aili and Mixia, 2015) and phenolic compounds. Polysaccharides and melanin in *A. auricula* exhibit distinct structural features depending on their origin and isolation methods (Pak et al., 2021). Melanin, a secondary metabolite composed of complex heterogeneous polymers, is prevalent in animal cells, bacteria, fungi, and plants (Toledo et al., 2017). Different classifications of melanin, such as eumelanin, pyomelanin, pheomelanin, neuromelanin, and allomelanin, exist based on polymerization pathways, building blocks, and enzymes involved (Choi, 2021). Melanins derived from various sources share functional properties such as antioxidant effects (Ma et al., 2023, 2022; Wu et al., 2018), antimicrobial membrane activity (Li et al., 2012), hypoglycemic properties (Pak et al., 2021), antitumor properties (Ye et al., 2019), anti-HIV activity (Montefiori and Zhou, 1991; Manning et al., 2003), and immunomodulatory effects (Sava et al., 2001). Consequently, melanin has significant potential applications in medicine, pharmacology, and cosmetics.

However, the preparation process of melanin in *A. auricula* is intricate and costly. Microbial fermentation methods for melanin production are considered effective and natural alternatives, replacing expensive enzymatic or complex chemical extraction methods from plant or animal tissues while reducing experimental costs (Zou and Hou, 2017). Furthermore, the use of corn stalks as a substitute material for sawdust cultivation in the fermentation production of melanin has demonstrated reduced environmental impact and improved melanin production capacity through optimized fermentation medium (Yao et al., 2019). In this work, we consolidate the existing knowledge on analytical methods applicable to melanin analysis workflows, encompassing extraction, purification, and high-throughput techniques such as matrix-assisted laser desorption/ionization mass spectrometry or pyrolysis gas chromatography (Pralea et al., 2019). Ma et al., (2022) investigated the pathway of melanin biosynthesis in *A. auricula* using enzyme inhibitor assays and intermediate determination, evaluating its functional activity. Singh et al., (2021) reported that the enzymes responsible for melanin synthesis primarily belong to the tyrosinase, laccase, and polyketide synthase families. Recent studies have also revealed the medicinal potential and numerous health-promoting properties of *A. auricula* (Islam et al., 2021). With its emerging status as a novel antioxidant, *A. auricula* melanin holds promise for various applications in the food industry. This comprehensive review presents the research progress on the biosynthesis, fermentation production, extraction process, physicochemical characterization, biological functions, and applications of *A. auricula* melanin, providing a solid foundation for the future development and utilization of *A. auricula* melanin.

Biosynthesis

Melanin, a natural pigment found in various organisms, including fungi and bacteria, is synthesized through the oxidative polymerization of phenolic compounds. In fungi and bacteria, this process occurs via two main pathways (Fig. 1): 1,8-dihydroxynaphthalene (DHN) or 3,4-dihydroxyphenylalanine (DOPA), resulting in different types of melanin such as eumelanin, pheomelanin, allomelanin, pyomelanin, and neuromelanin (Singh et al., 2021). In the case of *A. auricula*, a traditional medicinal resource in China, the biosynthesis pathways of melanin have been investigated through enzyme inhibitor assays and intermediate determination (Ma et al., 2022). It has been observed that environmental stimuli can influence melanin production in *A. auricula*. For instance, proteomic analysis of *A. auricula* subjected to freezing treatment revealed that proteins involved in glycolysis/gluconeogenesis, tyrosine metabolism, ribosome, and arginine biosynthesis might contribute to color differences (Li et al., 2021).

Production

The production of melanin in *A. auricula* through submerged culture has been studied extensively. Various factors have been identified to significantly impact melanin biosynthesis, including glucose, tyrosine, peptone, and $CaCO_3$. Optimization of these factors using experimental designs and response surface methodology has been conducted (Zhang et al., 2015). Tyrosine has been found to stimulate melanin synthesis, and the deficiency of tyrosine in the medium leads to reduced melanin secretion (Sun et al., 2016a, 2016b). Therefore, precise control of the nutritional composition in the fermentation medium is crucial for achieving efficient melanin production by *A. auricula*. Recent studies have explored different approaches to enhance melanin production. For instance, Zou et al. investigated the fermentative production of melanin using wheat bran extract as a major nutrient source and optimized the concentrations of wheat bran extract, L-tyrosine, and $CuSO_4$ to enhance tyrosinase activity and increase melanin yield while reducing costs (Yu

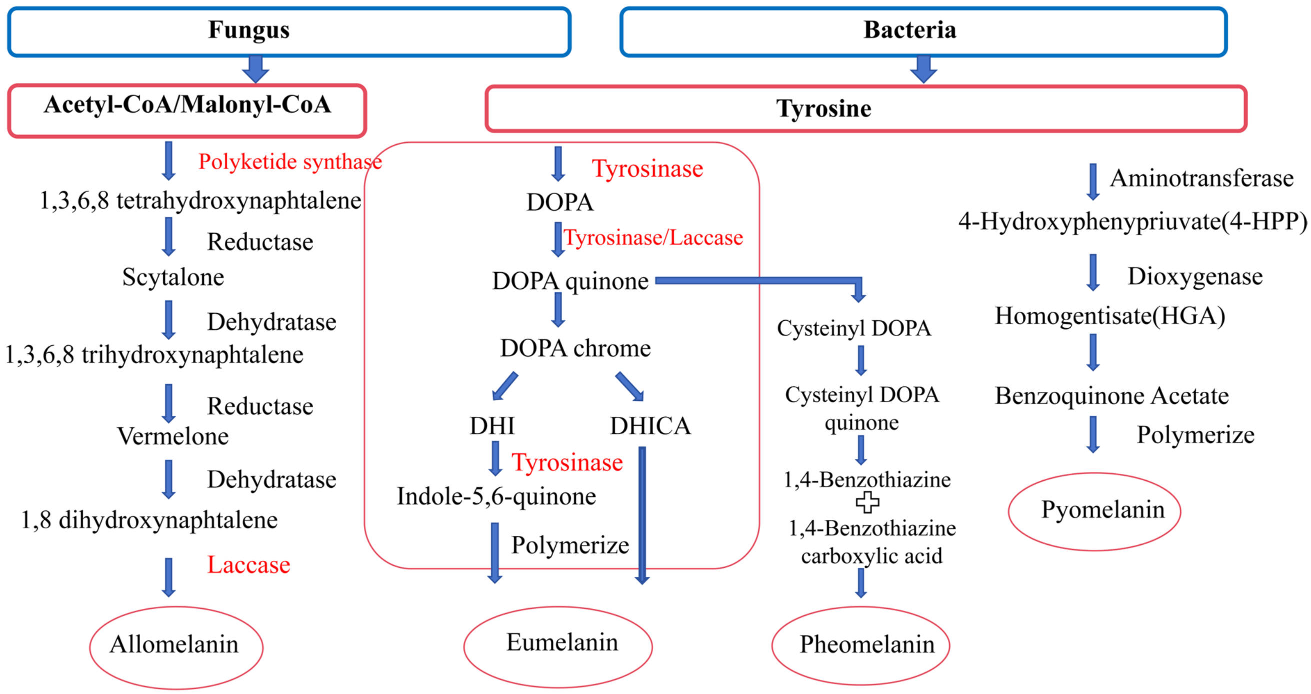

Fig. 1 Biosynthetic pathways of different species of melanin in fungi and bacteria: eumelanin, pheomelanin, allomelanin, and pyomelanin. Red text indicates key enzymes in the pathway

and Tian, 2017; Zou et al., 2017). Yao et al. analyzed the use of corn stalks as a substitute material for sawdust in fermentation, which significantly improved nutrient content in *A. auricula* and had a minimal impact on melanin production (Yao et al., 2019). Furthermore, Zou et al. screened three strains of *A. auricula* to identify a strain with higher pigment production capacity (Zou and Ma, 2018). Wu et al. studied the composition of the medium for submerged culture of *A. auricula* and found that specific additions such as 1% methanol, 0.25% peanut oil, 1.0% stearic acid, or 0.5% palmitic acid were beneficial for melanin biosynthesis, while Tween 80 had a significant inhibitory effect on melanin formation (Wu et al., 2018; Zou and Hou, 2017). Detailed information on factors affecting melanin biosynthesis in *Auricularia auricula* is shown in Fig. 2.

Extraction

The extraction of melanin from *A. auricula* provides an avenue for fully utilizing this resource. Current studies have explored various extraction methods to enhance the efficiency of melanin extraction. Zou et al. employed ultrasound-assisted extraction (UAE) to extract melanin from the fruiting bodies of *A. auricula*, optimizing the extraction conditions using single-factor experiments and response surface methodology. It can increase extraction rate and shorten extraction time (Ma et al., 2018; Zou et al., 2010). Chen et al. utilized a biological enzymatic method to break the cell wall of *A. auricula* and extract melanin (Chen et al., 2021). The cell wall of the *A. auricula* was thick and tough, which was broken by using mannanase and the extraction conditions were optimized, and the highest extraction rate was found at enzyme substrate ratio of 1.1%, pH 4.4, 50℃and 52 min. Yin et al. employed an ultra-high pressure(UHP)-assisted extraction method to isolate melanin from wild *A. auricula* (Yin et al., 2022), advantages that count are shorted extraction time, and low energy consumption and can improve the performance and function of the target product. Another method is microwave-assisted extraction of melanin from *A. auricula*, which increases the cost but improves the quality of the final product compared to the traditional method (Ma et al., 2023). Zou et al. utilized Sephadex G-100 column chromatography to separate melanin fractions from *A. auricula* fruiting body (Zou et al., 2015a, 2015b, 2015c). Additionally, Liu et al. investigated the extraction process and physicochemical properties of melanin from *A. auricula* waste residue using an ultrasonic-assisted extraction method, contributing to the utilization of *A. auricula* waste (Liu et al., 2019). Details about different Extraction Methods of *A. auricula* are given in Table 1.

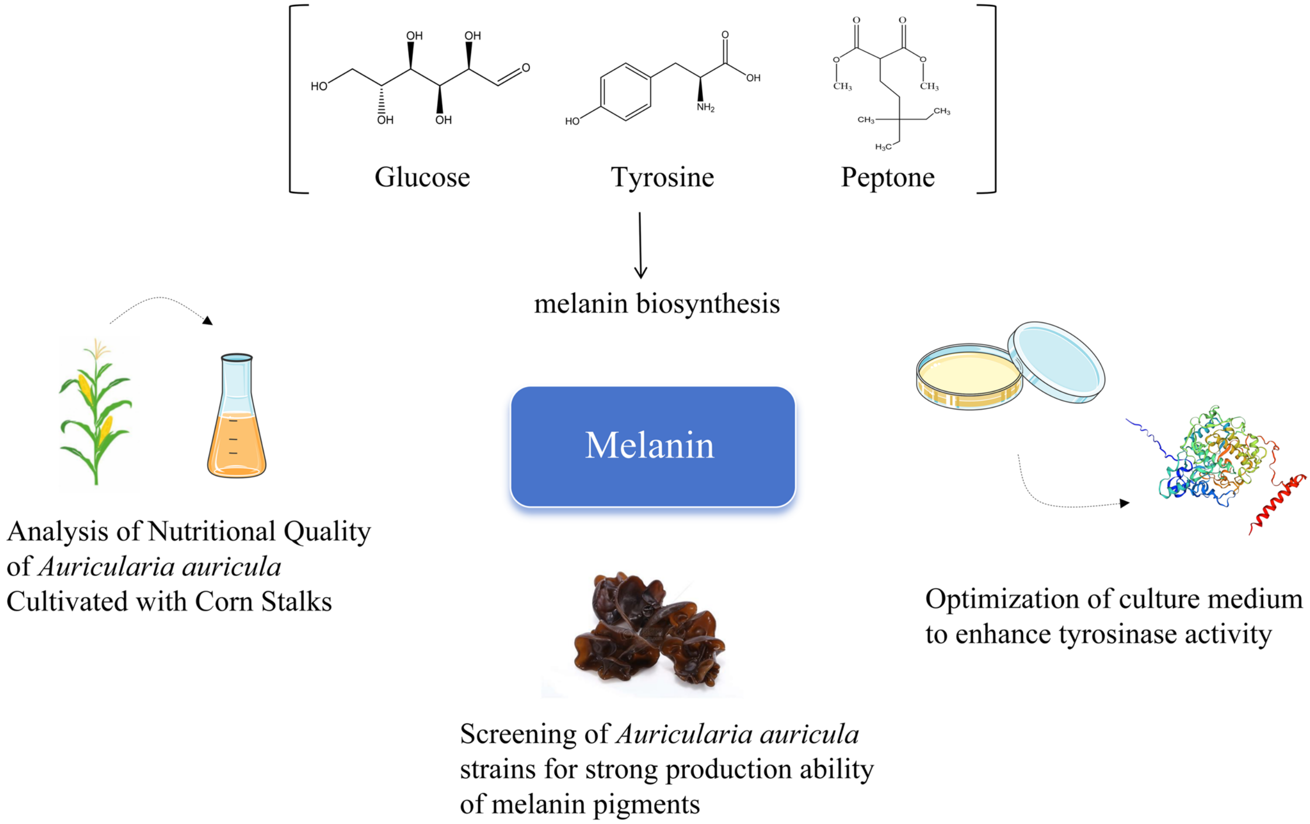

Fig. 2 Schematic diagram of factors affecting melanin biosynthesis in *Auricularia auricula*

Physicochemical properties characterization

Apart from extracting melanin from dried *A. auricula* fruiting bodies, the extraction of melanin from *A. auricula* fermentation broth has gained significant attention in recent years. Understanding the physicochemical properties and stability of melanin is crucial for its potential applications in the food industry. Studies by Zou et al. have shown that melanin extracted from *A. auricula* dried fruit and *A. auricula* fermentation broth exhibit similar solubility, redox properties, and spectroscopic characteristics, with melanin from the fermentation broth displaying a darker coloration (Zou et al., 2013). Zou et al. also investigated the physicochemical properties of melanin in *A. auricula* fermentation broth, revealing its insolubility in water and common organic solvents. It only dissolves in alkali aqueous solutions and precipitates in acidic aqueous solutions (pH < 3). The melanin in the fermentation broth undergoes gradual oxidative bleaching when exposed to oxidants but remains stable in reducing conditions. Moreover, it exhibits strong optical absorbance across a wide Ultraviolet–visible spectroscopy (UV–VIS) spectral range (Feng et al., 2015). Elemental composition and amino acid analyses conducted by Zou on melanin from *A. auricula* fruiting bodies indicated a high content of amino acids and metal elements (Zou et al., 2015a, 2015b, 2015c). Prados-Rosales et al. characterized commercial *A. auricula* fruiting bodies preparations for melanin content and performed structural characterization of isolated insoluble melanin materials using advanced spectroscopic and physical/imaging techniques, and found that this melanin has physicochemical properties consistent with those of eumelanins, including hosting a stable free radical population (Prados-Rosales et al., 2015). Yin et al. observed that wild *A. auricula* melanin lacked structural order on the surface but exhibited strong absorption at a wavelength of 210 nm, displaying characteristic absorption peaks. Furthermore, it demonstrated good stability to heat, light, and low concentrations of reducing and oxidizing agents (Yin et al., 2022).

Biological function

Antioxidant activity

Auricularia auricula melanin has demonstrated antioxidant activity in several studies. Melanin extracted from *A. auricula* fruiting bodies exhibited strong scavenging activities

Table 1 Different extraction methods of *Auricularia auricula*

Source	Method	Optimal extraction parameters	Extraction yield (%)	Merit and demerit	Reference
The fruiting bodies of *A. auricula*	Ultrasound-assisted extraction (UAE)	Ultrasonic power(250 W); Temperature(63 °C); liquid–solid ratio(43 mL/g); duration(36 min)	0.12005	As increasing extraction yield, reducing solvent usage, economizing power consumption and shortening extraction duration	Zou et al. (2010), Ma et al. (2018)
A. auricula	Biological enzymatic method	Enzyme(Mannanase); E/S(1.1%);time(150 min); pH(4.4); temperature(50 °C)	0.0221 ± 0.03	Its walls are thick, tough, and difficult to break by conventional methods, the cell wall can be better disrupted by using a bio-enzymatic method	Chen et al. (2021)
Wild *A. auricula*	Ultra-high pressure (UHP)-assisted extraction method	Solid/liquid ratio(1:30); UHP(450 MPa); Pressure holding time(22 min); NaOH concentration(1 mol/L); acid precipitation(8 h)	7.9 ± 0.16	UHP extraction has a high yield, short extraction time, and low energy consumption and can improve the performance and function of the target product	Yin et al. (2022)
A. auricula fermentation	Microwave-assisted extraction	Power(300 W); alkali-soluble pH (12.3); acidprecipitation pH (3.1); microwave time (53 min)	0.4042	Reduced extraction time,high yield, and improved quality of end products	Ma et al. (2023)
A. auricula waste	Ultrasonic-assisted extraction method	Ultrasonic power(450 W); NaOH concentra-tion (0.58 mol/L); solid–liquid ratio (1:44); extraction time (50 min); extraction temperature (70 °C)	11.99 ± 0.13	Extracting melanin from the waste residue of *A. auricula* can make maximum use of *A. auricula* and reduce the waste of resources	Liu et al. (2019)

against DPPH radical, superoxide radical, and hydroxyl radical (Zou et al., 2015a, 2015b, 2015c). *Auricularia auricula* melanin also displayed free radical scavenging activity (Yin et al., 2022). Liu et al. compared the antioxidant activity of melanin from *Auricularia auricula* and waste residue, finding no significant difference in ABTS, DPPH, and hydroxyl radical scavenging activity, indicating strong antioxidant activity in *A. auricula* waste melanin as well (Liu et al., 2019). In addition, Zou et al. evaluated the Fe^{2+} chelating ability, DPPH radical scavenging activity, and superoxide radical scavenging activity of melanin obtained from *A. auricula* fermentation, and observed strong antioxidant activity (Zou et al., 2013) (Fig. 3A).

Therapeutic effect

Recent studies have explored the therapeutic effects of *A. auricula* melanin through in vivo experiments. Hou et al. investigated the hepatoprotective effect of melanin on mice with acute alcoholic liver injury, observing improved antioxidant enzyme levels and activation of nuclear factor E2-related factor 2 (Nrf2) and its downstream antioxidant enzymes (Hou et al., 2019). Melanin treatment for alcoholic liver injury resulted in enhanced cell viability, improved cell morphology, reduced ROS, and increased GSH/GSSG levels in ethanol-pretreated L02 cells. The therapeutic effect of melanin may be attributed to the inhibition of CYP2E1 expression and activation of Nrf2 and its downstream antioxidase (Hou et al., 2021). Lin et al. studied the effect of oral administration of *A. auricula* on the intestinal flora in mice ingesting alcohol and found significant regulatory effects of *A. auricula* melanin on liver metabolites involved in various pathways, as well as mRNA levels of genes related to lipid metabolism and inflammatory response in the liver (Lin et al., 2021) (Fig. 3B).

Antibiofilm activity

Melanin from *A. auricula* has also demonstrated antibiofilm activity. Li et al. reported that *A. auricula* melanin significantly inhibits biofilm formation of *E. coli* K-12, *P. aeruginosa* PAO1, and *P. fluorescens* P-3 without affecting their growth (Li et al., 2012). The antibiofilm activity of *A. auricula* melanin was confirmed through crystal violet and LIVE/DEAD BacLight staining as well as confocal laser scanning microscopy (CLSM) (Fig. 3A).

Applications

Auricularia auricula, commonly renowned in Eastern countries as both an edible and medicinal fungus, contains melanin as a pivotal active ingredient. Melanin, a ubiquitous substance produced by animals, plants, and microorganisms, serves not only as a natural colorant (Ma et al., 2023) but also exhibits diverse biological activities (Liu et al., 2019). Notably, melanin demonstrates robust antimicrobial properties (Li et al., 2012), offering significant potential for application in infection pathology and biomedical contexts, particularly in the functionalization of biomaterials (Kunwar et al., 2012). The edible and safe nature of *A. auricula* makes the isolated melanin an advantageous alternative to potentially toxic compounds for human use. These findings underscore the promising potential of *A. auricula* melanin in clinical medicine and the food industry.

In summary, this review has effectively summarized the current knowledge on the biosynthesis, production, and

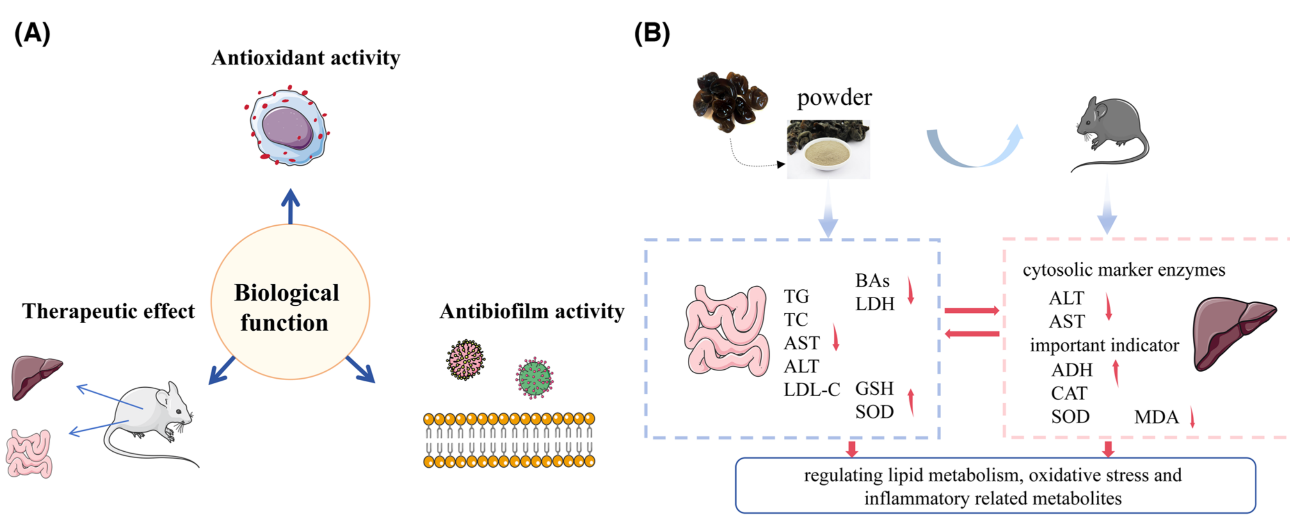

Fig. 3 Biological function study of *Auricularia auricula.* (**A**) Biological function of *Auricularia auricula*; (**B**) Protective effect of *A. auricula* melanin on liver injury and its effect on intestinal microorganisms

properties of *A. auricula* melanin, highlighting its significant potential in various applications. Although promising, further research is needed to deeply understand its physicochemical characteristics and optimize its biosynthesis and extraction processes. As these challenges are addressed, *A. auricula* melanin holds great promise for new discoveries and applications.

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Data availability All raw data and materials will be made available following a reasonable request.

Declarations

Competing interests The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Authors and Affiliations

Jiaying Wang[1] · Zihui Ma[1] · Chengtao Wang[1] · Wei Chen[1]

✉ Chengtao Wang
wangchengtao@th.btbu.edu.cn

✉ Wei Chen
weichen@btbu.edu.cn

Jiaying Wang
2230202145@st.btbu.edu.cn

Zihui Ma
15233760605@163.com

[1] Key Laboratory of Geriatric Nutrition and Health, Ministry of Education, Beijing Advanced Innovation Center for Food Nutrition and Human Health, Beijing Engineering and Technology Research Center of Food Additives, School of Food and Health, Beijing Technology and Business University, Beijing 100048, People's Republic of China