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Molecular Mechanism Underlying Intestinal Epithelial Cell Pinocytosis-Mediated Absorption of Auricularia auricula Polysaccharide-Iron Complex

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Abstract: *Iron deficiency anemia is a globally prevalent micronutrient deficiency disorder. Conventional inorganic and low-molecular-weight organic iron supplements are absorbed via the specific active transport pathway mediated by divalent metal transporter 1 (DMT1). This pathway has inherent drawbacks: strong dependence on intestinal microenvironment, susceptibility to interference from dietary antagonists, low iron bioavailability, and high risk of gastrointestinal oxidative damage. The Auricularia auricula polysaccharide-iron complex (designated Auricul-F®) is a core-shell macromolecular colloidal complex that is coordinately synthesized by chelating ferric ions with natural polysaccharides extracted from Auricularia auricula. It possesses excellent gastrointestinal stability, water solubility and biocompatibility. In vitro cellular experiments, simulated gastrointestinal digestion models and in vivo animal metabolic studies have confirmed that Auricul-F® breaks the single ion transport mode of traditional iron agents. It achieves complete macromolecular internalization through clathrin-independent fluid-phase pinocytosis in intestinal epithelial cells, forming a dual absorption pathway dominated by pinocytosis and supplemented by DMT1-mediated transport. The core pinocytotic absorption process is not inhibited by intestinal pH fluctuations, phytic acid or competing metal ions. Meanwhile, vesicles inside cells can realize controlled slow release of iron ions, which greatly reduces gastrointestinal irritation and significantly improves iron bioavailability. This paper systematically elaborates the spatial structural characteristics, gastrointestinal homeostasis mechanism, hierarchical molecular cascade of pinocytotic absorption, key regulatory signaling proteins, intracellular iron metabolic reprogramming and vesicle recycling mechanism of Auricul-F®. A comparative analysis of core differences between the pinocytotic pathway and the classical DMT1 transport pathway is carried out to clarify the molecular essence of Auricul-F® for efficient and safe iron supplementation. This study aims to improve the theoretical system of intestinal absorption of natural fungal polysaccharide-iron complexes, and provide solid theoretical and data support for its industrial application in functional fortified foods, foods for special medical purposes and novel iron-supplement formulations.*

Keywords: *Auricularia auricula polysaccharide-iron complexes; pinocytosis; intestinal epithelial cells; iron absorption mechanism; vesicular transport; iron metabolism; bioavailability*

1. Introduction

Iron is an essential trace element for human bodies, participating in hemoglobin and myoglobin synthesis, mitochondrial electron transport, cellular redox balance, differentiation and proliferation of immune cells. Long-term insufficient iron intake, impaired iron absorption or disordered iron metabolism will directly induce iron deficiency anemia, accompanied by pathological symptoms such as fatigue, decreased immunity, retarded growth and development and mucosal injury. It is one of the most prevalent nutritional diseases among pregnant women, infants and the elderly [1]. Epidemiological data show that the prevalence of latent iron deficiency and iron deficiency anemia among Asian residents remains high, and the application limitations of traditional iron supplements are important inducements for the intractable iron deficiency problem [1].

At present, iron raw materials commonly used in clinical practice and food industry, such as ferrous sulfate, ferrous fumarate and ferrous gluconate, rely on the specific active transport of Fe^{2+} mediated by DMT1 on the apical membrane of small intestinal duodenal epithelial cells [2–3]. This classical transport pathway has inherent technical bottlenecks. First, the activity of DMT1 strictly depends on the weakly

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acidic microenvironment of the proximal intestine; the increase of intestinal pH will directly cause conformational inactivation of the transporter and a sharp drop in absorption efficiency. Second, divalent metal ions such as calcium and zinc, as well as anti-nutritional factors in diets including phytic acid, tannins and oxalic acid, will competitively antagonize iron ions and significantly inhibit transmembrane iron transport [4]. Third, free iron ions in the gastrointestinal lumen are prone to trigger stress reactions and generate a large number of reactive oxygen species (ROS), which destroy the integrity of intestinal mucosal barrier and cause typical adverse reactions such as nausea, abdominal pain, constipation and melena, leading to poor tolerance after long-term supplementation [5].

Auricularia auricula is a high-quality medicinal and edible fungus resource. Its water-soluble acidic heteropolysaccharides are rich in a large number of active polar functional groups such as carboxyl groups, hydroxyl groups and ether bonds, which can form stable chelation reactions with Fe^{3+} through coordinate bonds, hydrogen bonds and electrostatic interactions to form structurally regular macromolecular polysaccharide-iron complexes without precipitated free iron [6]. Different from low-molecular-weight iron supplements, Auricul-F® exists in the form of intact colloidal macromolecules, with highly stable structure under gastric acid environment. It can avoid dissociation loss and oxidative inactivation in the stomach and be completely delivered to the main absorption segments of the small intestine [7].

In recent years, studies in nutrition and molecular biology have confirmed that high-molecular-weight polysaccharide-metal complexes cannot cross membranes through ion channels or carrier protein pathways, and fluid-phase pinocytosis is the core pathway for their intestinal absorption [8]. As a non-specific fluid-phase endocytosis mode of eukaryotic cells, pinocytosis can continuously take up extracellular soluble macromolecules and colloidal particles without specific receptors or transporters. It has no transport saturation effect and is not disturbed by microenvironment, which is a key pathway for macromolecular functional nutrients to cross the intestinal epithelial barrier [9]. Existing studies mostly focus on the optimization of preparation processes, structural characterization, antioxidant and anti-anemia pharmacodynamic verification of Auricul-F®. There is still a lack of systematic and in-depth sorting out of the complete molecular mechanisms and hierarchical regulatory networks of its pinocytotic internalization, vesicular transport, intracellular iron release and signal regulation.

Based on the above background, combined with in vitro cell models, simulated gastrointestinal digestion tests, in vivo animal metabolism experiments and the latest literature results, this paper systematically analyzes the structural basis of Auricul-F® adapting to pinocytotic absorption, the complete molecular mechanism of pinocytosis, key regulatory targets and intracellular iron metabolism rules, clarifies its core advantages compared with traditional iron agents, and provides a theoretical basis for the development and clinical transformation of novel natural high-efficiency iron fortificants.

2. Structural and Physicochemical Basis of Auricularia auricula Polysaccharide-Iron Complexes for Pinocytotic Absorption

The pinocytosis-specific absorption of Auricul-F® is not a random process. Its unique core-shell spatial structure, colloidal physicochemical properties and gastrointestinal stability are prerequisites for realizing fluid-phase pinocytotic internalization and avoiding the bottlenecks of traditional iron absorption, which are also the core characteristics distinguishing it from low-molecular-weight iron ions.

2.1 Molecular Structure and Coordination Characteristics

Purified polysaccharides from Auricularia auricula are mainly composed of glucuronic acid, glucose, mannose and xylose, with a high proportion of acidic groups and moderately branched molecular chains, showing strong metal chelating capacity [6]. During the chelation reaction, carboxyl and hydroxyl groups on the polysaccharide molecular chains act as main coordination sites to form multinuclear chelating coordination structures with Fe^{3+}, constructing core-shell macromolecular complexes with hydrophilic polysaccharide shells and iron ion cores. Its relative molecular weight reaches 3.783×10^5 Da, and the optimal iron binding rate is 28.40% under optimal preparation processes [7].

This coordination structure has extremely high structural stability. The high bond energy of coordinate bonds eliminates loosely bound free iron ions, completely eradicating oxidative stress and

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gastrointestinal irritation caused by free iron. Meanwhile, the hydrophilic polysaccharide shell endows the complexes with excellent water solubility, which can form homogeneous and well-dispersed colloidal solutions in intestinal fluid with particle sizes concentrated at 100–200 nm, fully meeting the substrate particle size uptake threshold of fluid-phase pinocytosis in intestinal epithelial cells [9].

2.2 Mechanism of Gastrointestinal Environmental Stability

Simulated human gastrointestinal digestion model experiments have verified that Auricul-F® has dynamic homeostasis characteristics of resisting gastric acid degradation and slow intestinal dissociation [7]. In the strong acidic gastric environment (pH 1.2–2.0), the coordination structure of the complexes is almost undissociated with zero precipitation of iron ions, which can completely resist gastric hydrolysis and oxidative damage. After entering the absorption segment of the proximal small intestine (pH 5.5–6.5), the coordination bonds slowly activate and break with a mild increase of environmental pH. The iron release rate reaches 83.1% within 90 min, and stable iron release is basically completed at 120 min [7].

This characteristic enables most intact Auricul-F® macromolecules to reach intestinal absorption sites, providing sufficient substrates for efficient initiation of pinocytosis, and avoiding the problems of premature dissociation, loss and oxidative failure of traditional iron agents in the stomach, which is the key prerequisite for the pinocytotic pathway to play a leading role in absorption.

2.3 Cell Membrane Affinity and Biocompatibility

The polysaccharide shell of Auricul-F® is rich in hydrophilic polar groups, which can produce non-specific hydrogen bond adsorption and hydrophobic interactions with the phospholipid bilayer of intestinal epithelial cell membranes, membrane surface mucins and glycosylated modification sites, showing excellent cell membrane affinity [8]. At the same time, natural fungal polysaccharides have no cytotoxicity and immunogenicity, will not destroy the integrity of cell membrane structure, can safely trigger cytoskeleton remodeling, and continuously initiate fluid-phase pinocytosis, providing a biocompatibility basis for macromolecular internalization and absorption.

3. Hierarchical Molecular Absorption Mechanism of Auricul-F® via Pinocytosis

Auricul-F® is mainly absorbed through clathrin-independent fluid-phase pinocytosis in epithelial cells of duodenum and jejunum. The whole process is divided into seven hierarchical stages: enrichment and adsorption on the cell membrane surface, cytoskeleton remodeling and membrane invagination, formation of primary pinocytic vesicles, acidification, maturation and intracellular directional transport of pinosomes, controlled iron release inside vesicles, activation and reduction of iron ions and transport across the basolateral membrane into the systemic circulation, and recycling and regeneration of empty pinosomes. Each link is precisely regulated by specific signaling proteins to form a complete macromolecular absorption and metabolic pathway.

3.1 Specific Enrichment and Adsorption on the Surface of Intestinal Epithelial Cell Membranes

Intact Auricul-F® colloidal macromolecules flow to the intestinal brush border with intestinal chyme. Relying on the polar groups of the polysaccharide shell, reversible non-specific adsorption occurs with membrane surface glycoproteins and mucopolysaccharide layers, forming high-concentration substrate accumulation areas outside the cell membrane [8]. This process does not consume ATP, does not require specific receptor recognition, and is independent of ion concentration gradients, which is completely different from the competitive specific binding process mediated by DMT1.

Meanwhile, Auricul-F® can slightly upregulate the expression of mucins on the surface of intestinal epithelial cells, enhance the adsorption capacity of cell membranes and further improve substrate enrichment efficiency, providing sufficient material basis for subsequent initiation of pinocytosis. Moreover, this adsorption process will not be interfered by dietary phytic acid, calcium ions, zinc ions and other antagonistic factors [10].

ISSN 2616-5910 Vol. 7, Issue 1: 41-47, DOI: 10.25236/AJALS.2026.070107

3.2 Cytoskeleton Remodeling and Cell Membrane Invagination to Initiate Pinocytosis

Auricul-F® colloidal particles enriched on the cell membrane surface trigger mechanical signal responses of cell membranes and activate the Rho GTPase family signaling pathway to regulate dynamic polymerization and remodeling of actin microfilament cytoskeletons [9]. The ordered assembly and contraction of actin drive local arc-shaped depressions and fold wrapping of cell membranes to gradually wrap the extracellular liquid matrix containing Auricul-F®.

This process is typical clathrin-independent fluid-phase pinocytosis, which does not rely on specific vesicle assembly proteins such as clathrin and caveolin, with no substrate specificity and no activation threshold. As long as stable Auricul-F® colloidal substrates exist outside cells, continuous initiation of cell membrane endocytosis can be realized, completely breaking the saturation limit of traditional iron absorption [9].

3.3 Closure of Primary Pinocytic Vesicles and Detachment from Cell Membranes

After continuous invagination of cell membranes to wrap the liquid matrix, the edges of membrane structures automatically fuse and close to form primary pinocytic vesicles with diameters of 100–500 nm, which completely wrap Auricul-F® macromolecular complexes and extracellular liquid matrix. Driven by microfilament contraction power, primary pinocytic vesicles are completely separated from cell membranes and distributed in the superficial layer of cytoplasm [8].

At this stage, Auricul-F® still maintains an intact core-shell coordination structure, and the iron core is completely isolated by membranous vesicles without release of free iron ions, which thoroughly avoids oxidative stress damage of cytoplasm and intestinal lumen, realizing isolated and safe internalization and absorption.

3.4 Acidification and Maturation of Pinosomes and Directional Intracellular Transport

After primary pinocytic vesicles detach from cell membranes, vesicular membrane proton pumps are gradually activated, and a large amount of H^+ actively flows in, which reduces the intraluminal pH of vesicles from neutral to 5.0–5.5 to complete acidification and maturation of pinosomes [9]. Mature secondary pinosomes after acidification bind to the cytoplasmic microtubule transport system and are stably transported directionally from the apical side to the basolateral membrane of cells under the traction of motor proteins, avoiding disordered diffusion of contents.

Mild acidification inside vesicles is the core trigger for controlled cleavage of Auricul-F® coordination bonds. Compared with drastic acid-base reactions in the intestinal lumen, precise acidification inside vesicles can realize sequential and controllable iron release, which is a key molecular mechanism for Auricul-F® to have better safety than traditional iron agents.

3.5 Cleavage of Coordination Bonds and Controlled Iron Release Inside Vesicles

With the stable increase of acidification degree in pinosomes, coordination bonds and hydrogen bonds between polysaccharides and Fe^{3+} are gradually broken, the core-shell structure of Auricul-F® disintegrates, and high-activity Fe^{3+} is slowly released inside vesicles [7]. The whole iron release process is closed inside vesicular membrane structures, and iron ions will not be directly exposed to cytoplasm, eliminating ROS burst and cellular oxidative damage caused by cytoplasmic overload of free iron.

The iron release rate is highly coupled with the acidification degree of vesicles, showing slow, continuous and stable iron release characteristics, which can match the iron metabolic demand of the body, avoid metabolic disorders caused by transient high concentration of iron ions, and realize accurate and mild iron supplementation.

3.6 Reduction of Activated Iron Ions and Transport Across the Basolateral Membrane into the Systemic Circulation

Fe^{3+} released inside vesicles can be rapidly reduced to bioavailable Fe^{2+} by endogenous reducing substances such as ascorbic acid and glutathione in vesicles and cytoplasm [10]. The reduced active iron ions are divided into two metabolic pathways:

ISSN 2616-5910 Vol. 7, Issue 1: 41-47, DOI: 10.25236/AJALS.2026.070107

Intracellular metabolic pathway: a small amount of Fe^{2+} directly enters the iron metabolic pool of intestinal epithelial cells to participate in cytochrome synthesis and mitochondrial energy metabolism and maintain normal physiological functions of intestinal cells.

Systemic circulatory pathway: most Fe^{2+} are exported across the basolateral membrane of intestinal epithelial cells via ferroportin 1 (FPN1) to interstitial tissue fluid, enter the systemic circulation, and are transported to target organs such as liver, bone marrow and spleen via transferrin to participate in hemoglobin synthesis and regulation of whole-body iron homeostasis [3].

The dissociated polysaccharide skeletons of Auricularia auricula can be degraded into small molecular monosaccharides and oligosaccharides by intracellular lysosomes. On the one hand, they participate in cellular energy metabolism; on the other hand, they exert auxiliary activities such as anti-oxidation, regulation of intestinal flora and repair of mucosal barriers, realizing synergistic benefits of iron supplementation, intestinal protection and anti-oxidation [6].

3.7 Recycling and Regeneration of Empty Pinosomes for Continuous Absorption

After iron release and degradation of internal contents, empty pinosomes flow back to the apical membrane of intestinal epithelial cells along microtubules in reverse direction, and fuse with cell membranes to complete recycling and regeneration of membrane structures and proton pump proteins [9]. The vesicle recycling mechanism enables the pinocytotic system of intestinal epithelial cells to continuously and repeatedly take up Auricul-F® macromolecules without transport fatigue and dose saturation, realizing long-term efficient iron supplementation, which is the core mechanism for the significantly higher iron bioavailability of Auricul-F® than traditional iron supplements (4%–10%) [2].

4. Differential Comparison Between Auricul-F® Pinocytotic Pathway and Traditional DMT1-Mediated Iron Absorption Pathway

Traditional low-molecular-weight iron supplements completely rely on DMT1-mediated specific active transport, while Auricul-F® adopts a dual absorption mode dominated by pinocytosis and supplemented by DMT1-mediated transport. The two pathways have fundamental differences in transport essence, regulatory mechanism, environmental adaptability, safety and absorption efficiency. The detailed comparative analysis is as follows:

4.1 Transport Substrates and Molecular Forms

The classical DMT1 pathway only recognizes and transports free low-molecular-weight Fe^{2+} with single substrates limited to ionic dissociation state. The pinocytotic pathway can completely take up intact Auricul-F® colloidal macromolecular complexes and complete transmembrane internalization with intact core-shell structures without pre-dissociation of iron ions [3,8].

4.2 Transport Dependence and Anti-Interference Capacity

The activity of DMT1 pathway strictly depends on the weakly acidic pH environment of intestinal tract and the activity of specific transporters, which is highly susceptible to competitive antagonism of divalent metal ions such as calcium and zinc as well as anti-nutritional factors such as phytic acid and tannins in diets, resulting in poor absorption stability [4]. The pinocytotic pathway does not require transporters or specific receptors, and will not be affected by intestinal pH fluctuations, dietary antagonistic factors or competitive metal ions, showing extremely strong anti-interference ability and significantly improved absorption stability.

4.3 Transport Saturation and Dose Effect

The expression level of DMT1 protein on cell membranes is limited, with an obvious transport saturation threshold. High-dose iron supplements cannot improve absorption efficiency, which easily causes iron waste and accumulation risks [3]. Pinocytosis relies on dynamic membrane endocytosis and vesicle recycling without an upper saturation limit. The absorption capacity can be continuously increased with the rise of extracellular substrate concentration, showing better dose responsiveness [9].

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4.4 Absorption Safety and Cellular Injury Mechanism

Traditional iron supplements dissociate a large amount of free iron in the gastrointestinal lumen, trigger stress responses to generate ROS, destroy the integrity of intestinal mucosal barrier, and cause gastrointestinal irritation and oxidative damage [5]. Auricul-F® realizes controlled iron release inside vesicles via pinocytosis, without release of free iron in the gastrointestinal lumen from the source, eliminating oxidative stress and mucosal injury and showing excellent tolerance after long-term supplementation.

4.5 Iron Bioavailability and Metabolic Efficiency

The bioavailability of inorganic iron and low-molecular-weight organic iron supplements is only 4%–10%, with large absorption loss and low utilization efficiency [2]. Relying on the dual pinocytosis-dominated absorption pathway, the iron bioavailability of Auricul-F® reaches 23.7%, close to the absorption level of natural heme iron, which greatly improves iron utilization rate and iron supplementation efficiency [2,7].

5. Biological Advantages and Application Value of Auricul-F® Pinocytotic Absorption Mode

5.1 Breaking the Bottleneck of Environmental Antagonism of Traditional Iron Supplementation

The non-specific internalization mechanism of pinocytosis completely decouples iron absorption from intestinal microenvironment and dietary conditions. For iron-deficient populations with complex diet structure, disordered intestinal microecology or unbalanced trace elements, Auricul-F® can stably maintain efficient iron uptake efficiency, solving the industry pain point of unstable iron supplementation effect of traditional iron agents easily affected by diet [8].

5.2 Realizing Long-Term Iron Supplementation with Low Irritation and High Safety

The compartmentalized iron release mode inside vesicles avoids gastrointestinal oxidative damage and mucosal irritation, without adverse reactions such as nausea, constipation and abdominal pain. It meets the demand of long-term mild iron supplementation for sensitive groups such as pregnant women, infants, patients with gastrointestinal diseases and the elderly, with significantly higher safety than chemically synthesized iron fortificants [7].

5.3 Synergistic Bioactivity of Polysaccharides and Iron

Polysaccharides extracted from Auricularia auricula have excellent biological activities including anti-oxidation, anti-inflammation, intestinal mucosal barrier repair and intestinal flora regulation [6]. During pinocytotic absorption, polysaccharide skeletons enter cells synchronously to exert physiological functions, offset slight oxidative loss during iron metabolism, improve intestinal absorption microenvironment, and form triple synergistic effects of efficient iron supplementation, mucosal repair and anti-oxidative stress to realize functional gain.

5.4 Adaptation to Diversified Industrial Application Scenarios

Auricul-F® has stable structure, acid and alkali resistance, heat resistance, high absorption efficiency and excellent safety. It can be widely applied to ordinary functional iron-fortified foods, children's nutritional fortified foods, exclusive nutritional products for pregnant women, foods for special medical purposes and other fields, making up for the shortcomings of traditional iron agents such as limited application scenarios and poor tolerance, and possessing extremely high industrial transformation value [10].

6. Conclusions and Future Perspectives

The unique core-shell colloidal structure, sustained-release stability in gastrointestinal tract and excellent cell membrane affinity of Auricul-F® constitute the structural basis for its initiation of intestinal epithelial pinocytotic absorption. The hierarchical molecular processes including Rho GTPase-regulated cytoskeleton remodeling, acidification and maturation of pinosomes, controlled iron

ISSN 2616-5910 Vol. 7, Issue 1: 41-47, DOI: 10.25236/AJALS.2026.070107

release inside vesicles and recycling of empty pinosomes jointly form the core absorption mechanism of Auricul-F® with high efficiency, safety and anti-interference performance.

Compared with the single and easily restricted DMT1-mediated transport pathway of traditional iron supplements, the novel absorption mode of Auricul-F® dominated by clathrin-independent fluid-phase pinocytosis completely breaks the efficiency bottleneck and safety shortcomings of traditional iron supplementation. With the advantages of no antagonism, no transport saturation, low gastrointestinal irritation and high bioavailability, it shows unique superiority as a natural macromolecular iron fortificant.

Current research on Auricul-F® pinocytotic absorption is mainly based on in vitro cell models, simulated gastrointestinal digestion and animal experiments. Follow-up research can focus on three directions: first, deeply excavate key regulatory genes and signal pathway networks in the pinocytotic process to clarify the regulatory mechanism of core targets; second, carry out large-sample human clinical trials to improve data on human iron metabolic kinetics, bioavailability and long-term safety; third, optimize complex particle size, coordination structure and preparation processes based on pinocytotic absorption mechanism to further improve pinocytotic internalization efficiency. With continuous improvement of molecular mechanism and clinical research, Auricul-F® is expected to replace traditional synthetic iron agents as a new generation of natural, safe and high-efficiency iron fortificant, and be widely applied in the fields of nutritional health and clinical iron supplementation.

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