INTERNATIONAL SOCIETY FOR MEDICINAL MUSHROOMS

国际药用菌学会

International Society for Medicinal Mushrooms （ISMM）was founded in Vancouver, Canada. As a global non-profit organization, ISMM promotes the development of research, education, production, transportation, marketing and cultivation of medicinal mushrooms to have people to work towards common aspirations and goals. The integration will increase the impact of the international medicinal mushroom industry and benefit the health of people in the world.

Honorable President: Prof. S.T.Chang, Prof.S.P. Wasser
President: Academician Li Yu
Executive President: Mr. Chen Hui
Secretary General: Mr. Liu Ziqiang

国际药用菌学会（International Society for Medicinal Mushrooms），简称ISMM，在加拿大温哥华注册成立，由从事药用菌产业的科研、教学、生产、流通、市场、文化及相关产业链的单位、团体和个人自愿组成的为实现共同意愿的非营利性国际组织。本学会致力于促进国际药用菌产业各个领域的融合与发展，以提升药用菌行业在全球的影响力，造福人类健康。

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NEWSLETTER OF THE INTERNATIONAL SOCIETY FOR MEDICINAL MUSHROOMS

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News Reports

Dutch Mushroom Days 2026

From 22 to 24 April 2026, the 37th edition of the Mushroom Days took place at the Brabanthallen in ’s-Hertogenbosch. This leading international trade fair for the mushroom industry was once again a great success.

A total of 124 exhibitors from 21 countries participated, creating an impressive exhibition floor with their professionally presented stands. With 4,800 admissions over the three days and visitors from 97 countries, the event can rightly be described as a truly global mega-event, unrivalled within the mushroom industry.

The Networking Party was also well attended, attracting 900 participants. During the evening, five winners of the Ambassador of the Mushroom Industry Award were announced. During the Mushroom Days 2026, this prestigious prize was awarded to five people.

Ambassador of the Mushroom Industry Award – from left to right – Mel O’Rourke (spawn / mushroom promotion), Helen Grogan (research / crop protection), Gerard van de Wijdeven (mushroom production), Ger Hendriks (mushroom substrate) and Hans van den Boomen (mushroom grower).

The organisers look back on a flawlessly run edition and greatly appreciate the pleasant interactions with both exhibitors and visitors. Surveys have now been sent to participants and visitors, and the initial results confirm the organising committee’s positive impression. The full survey results will be published on this website shortly.

The next edition of the Mushroom Days is scheduled to take place from 13 to 15 June 2029 at the Brabanthallen in ’s-Hertogenbosch.

Source: https://champignondagen.nl/home-eng/

Ameliorating the Brownfield Burden with Help from Mushrooms

Brownfields, or abandoned and contaminated former industrial sites, pose many challenges for cleanup and redevelopment efforts. For example, common remediation methods can amount to the onerous task of relocating tons of soil and debris. However, in a new project, Department of Plant Science and Landscape Architecture researchers including Ph.D. student Paulette Goyes and assistant professor Mia Maltz are exploring if bioremediation using mushrooms is a viable strategy for cleaning up contaminated soil at brownfield sites in Connecticut.

Goyes working in a lab. (Jason Sheldon/UConn Photo)

"Fungi have been noted for their capacity to degrade hazardous compounds or mobilize them," says Goyes. "We are interested in analyzing where the fungi move these hazardous compounds and what's happening, for example, how the fungi interact with the microbial communities with these pollutants."

Maltz explains that some species of mushrooms can also hyperaccumulate metals or make the compounds less bioavailable, or able to enter the food web. Therefore, the right mushroom in the right context can help simplify cleanup efforts. This project explores a way to reduce the hazardous waste burden and ideally treat the soil in place and eliminate the need to dig up the contaminated soil and dump it at a hazardous waste facility.

In a previous study focused on a brownfield site in California, Maltz says they found that mushrooms helped decrease polycyclic aromatic hydrocarbons (PAH) levels, but before deploying this promising fungal amendment strategy here, they need to understand how mesic conditions in Connecticut might lead to different outcomes.

"That location in California has a very dry climate. Here in Connecticut, we have a lot more rain and we're not sure how these water events are going to affect the mycelial process. Is it going to amplify the mycelial growth, and then they're going to be even more effective, or are these high-water events leaching pollutants out of the soil faster than the mushrooms can mobilize it? We're checking that in this more humid environment," says Maltz.

The current project, funded with the help of an Office of Sustainability Environmental and Social Sustainability Grant (ESSG), focuses on a location in Collinsville at the site of a former ax factory. The factory was active until the 1960s and over the course of its operation, industrial processes introduced very high quantities of lead into the soil that now need to be remediated before any new development projects can begin.

For the initial, laboratory-based phase of the study, Goyes says they collected soil samples from the site that they inoculated with fungi.

If the mushrooms accumulate heavy metals in their biomass, there is an opportunity to harvest and concentrate the biomass via anaerobic digestion to reduce the footprint of the hazardous waste at the site. (Contributed photo)

"We characterized what fungi were in some of the high lead sites. We decided to use two different types of mushrooms, the native tiger sawgill, *Lentinus tigrinus*, and a common oyster mushroom *Pleurotus ostreatus* that have historically been known as bioremediators," says Maltz.

Following the experimental phase, Goyes is now analyzing the data from the samples, including details about organopollutants like PAHs and PCBs with the help of the UConn Center of Environmental Sciences and Engineering (CESE), and genetic details with help from the Center for Genome Innovation (CGI). Goyes is also analyzing the physical properties of the soil, including pH, organic matter content, and soil aggregates as these qualities can impact how the metals move within the soil.

"If we use fungi, are we doing a good thing rather than mobilizing and remobilizing what was already in the soil? Metals have a behavior of small particles where they can move toward the surface, and they don't travel a lot in the soil, because the organic matter or other properties of the soil, they have this behavior of getting attached to the soil," says Goyes. "Their movement requires biological activity, for example, or physical movement for them to be displaced, remobilized, or turned into more reactive species."

It is important to understand how these mushrooms impact the bioavailability and mobility of the lead, Maltz explains, because they also need to understand what happens when it rains, and whether the lead leaches out into waterways or if it stays in the soil, and how the addition of mushrooms or mushroom compost impacts these processes.

They are also investigating how these two species of mushrooms accumulate lead.

"If the heavy metals are extracted by the mushrooms and are in the fruit body of the mushroom, that mushroom then becomes hazardous waste," says Goyes. "We don't want it to go through the food chain, so that poses another management question."

If the mushrooms accumulate heavy metals in their biomass, Maltz says, there is an opportunity to harvest and concentrate the biomass via anaerobic digestion to reduce the footprint of the hazardous waste at the site.

"So far, all treatments have increased soil pH, perhaps leading to less bioavailable lead species. Lead mobilization was significatively higher in the compost treatment, overpassing the mushroom treatments. The implications of these mobilizations need to be further scrutinized through bioavailability analyses," says Goyes.

This remediation method reduces industrial waste in other innovative ways, Maltz explains, since they were able to use mushroom mycelium that was a waste product from a food production company.

"It is very circular in terms of industrial ecology. We were able to use a byproduct of one industry to try to clean up an environmental issue," says Maltz.

Maltz and Goyes are planning to work on similar projects with other groups like the Hartford Land Bank to help with brownfield cleanup efforts at municipal sites in Hartford by reducing the amount of dig and dump needed for those efforts.

This project explores a way to reduce the hazardous waste burden and ideally treat the soil in place and eliminate the need to dig up the contaminated soil and dump it at a hazardous waste facility. (Contributed photo)

Goyes recently presented on this work in Portland, Oregon, at the Mycological Society of America meeting, and will present in Quito, Ecuador, at the Latin American Mycological Congress. The researchers plan to write a grant to restore the site in Collinsville using the treatment that was most successful in the experiment.

“I think the community is really excited about the idea,” says Maltz. “They would have liked us to jump in and just start with the field experiment right away, but we wanted to do more of a controlled experiment to see what the mechanisms are, how is it working, and what are some of the risks associated with using these mycotechnologies.”

Source: https://today.uconn.edu

Up-coming Events

International Mushroom Days, China 2026

20–22 September 2026

Xiamen Fliport Conference & Exhibition Center, Xiamen, China

By Douglas Zhao, Deputy Secretary-General, Mushroom and Mushroom Products Sub-chamber, China Chamber of Commerce of Import & Export of Foodstuffs, Native Produce & Animal By-products (CFNA)

Medicinal mushroom research is advancing rapidly worldwide. However, transforming scientific discoveries into commercially viable products requires more than promising laboratory results. It also depends on reliable strains, scalable cultivation systems, processing technologies, quality control, product development, market access and cooperation across the value chain.

Medicinal mushroom research is advancing rapidly worldwide. However, transforming scientific discoveries into commercially viable products requires more than promising laboratory results. It also depends on reliable strains, scalable cultivation systems, processing technologies, quality control, product development, market access and cooperation across the value chain.

International Mushroom Days, China 2026—officially known as the 2026 Mushroom Whole Industry Chain Innovation Expo (Xiamen)—will bring these different parts of the industry together from 20 to 22 September at the Xiamen Fliport Conference & Exhibition Center in China.

The exhibitor list released as of 9 August includes more than 100 confirmed participating organizations across approximately 20 industry categories. It provides a useful picture of the breadth and depth of China's mushroom industry: from breeding and production inputs to intelligent equipment, processing, branding and international trade.

A Whole-Industry-Chain Platform

China is widely recognized for the scale and diversity of its mushroom production. Yet production volume alone does not fully represent the transformation now taking place within the industry.

Chinese mushroom enterprises are increasingly investing in better genetics, standardized cultivation, automation, energy efficiency, intelligent environmental control, deep processing, functional products and new market channels. The Xiamen Expo has therefore been developed as a whole-industry-chain platform rather than a conventional exhibition focused primarily on fresh or processed products.

Confirmed exhibitors cover key areas including:

- mushroom strains, breeding and biotechnology;

- substrates, growing materials and production inputs;

- mushroom farm planning and factory design;

- cultivation systems and production equipment;

- environmental control, refrigeration and clean-room engineering;

- automation, robotics and intelligent production management;

- harvesting, sorting, drying and freeze-drying technologies;

- food processing, packaging and product development;

- mushroom growers, processors and trading companies;

- regional production areas, industry organizations and international partners.

For researchers and enterprises working with medicinal mushrooms, this integrated structure is particularly relevant. It makes it possible to examine not only individual species or products, but also the industrial conditions required to move from research and experimental cultivation to standardized production and market application.

Connecting Medicinal Mushroom Research with Industrial Capacity

Medicinal mushrooms occupy an increasingly important position at the intersection of agriculture, biotechnology, food science and health-related product development.

China has extensive production experience with species such as "*Ganoderma*/ lingzhi", "*Hericium erinaceus*", "*Cordyceps militaris*", "*Poria cocos*" and "*Sanghuangporus*" species. At the same time, the sector continues to face practical questions concerning strain stability, active-compound consistency, cultivation standardization, processing methods, quality evaluation and the responsible communication of product benefits.

These challenges cannot be addressed by researchers, growers or product companies working independently.

The Xiamen Expo will create opportunities for scientific institutions, technology suppliers, cultivation enterprises, processors and market partners to meet within the same industrial setting. For members of the International Society for Medicinal Mushrooms, the event offers a window into how research findings may connect with China's production capacity, engineering expertise, processing infrastructure and consumer market.

The objective is not to present the Expo as a specialized medicinal mushroom conference. Rather, its value lies in placing medicinal mushrooms within a broader and highly developed mushroom value chain—one capable of supporting scientific collaboration, pilot production, technology transfer, commercial manufacturing and international market development.

Innovation Focused on Practical Industry Needs

Technology will be a central theme in Xiamen, but the emphasis will remain firmly on practical application.

The Expo will examine how artificial intelligence, machine vision, robotics, production data and intelligent

environmental systems can help mushroom enterprises improve consistency, reduce labour dependence, manage energy use and lower unit production costs.

AI will not be treated as an isolated concept or promotional label. It will be considered alongside the equipment, biological processes and operational knowledge required for successful mushroom production.

This approach is relevant to medicinal mushrooms, where cultivation conditions and post-harvest processing can significantly influence product consistency and quality. Better monitoring, traceability and data-supported production may help connect scientific standards with industrial practice.

The wider innovation agenda will also include automated harvesting, factory production systems, energy-saving technologies, drying and extraction-related equipment, product formulation, packaging and value-added applications.

An Access Point to China and Asia

For international participants, Xiamen offers more than an opportunity to observe new equipment and products. It provides direct access to Chinese growers, manufacturers, regional industry clusters, technology providers and business decision-makers.

The Expo is being promoted through international industry events and professional media. Its international outreach has already included presentations and exchanges at mushroom industry events in the Netherlands and Russia, together with advertising and communication through the European trade publication “Mushroom Business”.

These activities are part of a broader effort to establish more consistent links between China’s mushroom industry and the international community.

International companies and institutions may participate through exhibition, professional visits, technical presentations, business matchmaking and industry exchanges. The Organizing Committee is also working to facilitate communication and local coordination for overseas participants.

For organizations seeking partners in China, the event can provide opportunities to:

- identify manufacturing and supply-chain partners;

- explore joint research and technology-transfer possibilities;

- assess cultivation and processing technologies;

- meet potential distributors, customers and investors;

- better understand the structure and direction of China’s mushroom market;

- introduce international technologies, products and services to Chinese industry counterparts.

We warmly invite members of the International Society for Medicinal Mushrooms, research institutions, medicinal mushroom enterprises and industry professionals from around the world to visit Xiamen, meet their Chinese counterparts and explore opportunities for scientific and commercial cooperation.

EXHIBIT IN XIAMEN 2026

- Connect with China's Mushroom Industry Decision-Makers
- Join Asia's Leading International Mushroom Industry Gathering
- Your Gateway to China and Asia's Mushroom Market

International Mushroom Days, China 2026 20–22 September 2026 | Xiamen, China

Asia's Leading Platform for Mushroom Production, Technology and Trade

300+	5000+	20+	20+
Exhibitors	Professional Visitors	Countries & Regions	Industry Conferences

Meet: Producers · Spawn Companies · Equipment Suppliers · Compost Producers · Casing Suppliers · Researchers · Traders · Investors




Why Exhibit?

- Meet China's largest mushroom producers
- Reach key decision makers and buyers
- Generate qualified business leads
- Explore Asia's fastest-growing markets
- Build long-term strategic partnerships

Discover What Makes China Different

- World's Largest Mushroom Industry
- Leading Exotic Mushroom Production
- Highly Automated Production Systems
- Complete Supply Chain Integration
- Fast-Growing Consumer Demand

Register Now
Learn More

For further information, please contact:
Edible Fungi Chamber, CFNA

Mr. Douglas Zhao; Ms. Naixuan Xu
WhatsApp: +86-13910657921; 18210918176
E-mail: mushroomdays@hotmail.com

CONNECTING EUROPE AND ASIA

13th International Medicinal Mushroom Conference (IMMC13)

We are pleased to announce the upcoming 13th International Medicinal Mushrooms Conference (IMMC13), which will take place in the beautiful city of Bragança, Portugal, from 22 - 25 September 2026.

Under the theme *Medicinal Mushrooms for a Sustainable Future in Food & Health*, the conference will bring together researchers, representatives from the mushroom industry, and key stakeholders to share recent scientific advances and discuss current challenges and opportunities in unlocking the full potential of medicinal mushrooms for health, sustainability, and innovation.

CONFERENCE VENUE

The IMMC13 will take place at two venues in Bragança, Portugal.

22th September (Tuesday)

The opening day of the conference, including the Opening Ceremony and scientific sessions, will be held at the **Teatro Municipal de Bragança**.

Teatro Municipal de Bragança

Praça Professor Cavaleiro Ferreira

5300-252 Bragança, Portugal

23th to 25th September (Wednesday–Friday)

The remaining conference programme, including scientific sessions, poster presentations, exhibition area, and closing activities, will take place at the **Salão Armindo Correia**, located within the **Exe São Lázaro Hotel**.

Salão Armindo Correia – Exe São Lázaro

Avenida do Sabor, 2

5300-367 Bragança, Portugal

ACCOMODATION

As the conference venue, the Exe São Lázaro Hotel is our recommended accommodation option. For participants wishing to stay at the hotel, we are pleased to inform you that a special accommodation rate has been arranged for

IMMC13 participants:

• Single room: € 59

• Double room: € 69

Reservations should be made directly by email to reservas@exesaolazaro.com, indicating that you are an IMMC13 participant.

HOTEL SÃO LÁZARO

Avenida do Sabor, Lote 24. 5300-111 Bragança, Portugal.

(+351) 273 310 070

reservas@exesaolazaro.com

CONFERENCE TOPICS

Sustainable Innovation in Mushroom

Personalized Nutrition & Precision Medicine

Therapeutic Potential of Psychedelic Mushrooms

Microbiome-Mycotherapy Interactions

AI & Omics in Medicinal Mushroom Research

Climate Resilience via Ecosystem Services

Cultural Heritage & Biocultural Conservation

Public Health & Policy Applications

Ethics, Safety & Regulatory Foresight

Agro-food Systems & Circular Integration

REGISTRATION

Opening of registration: 1st January 2026

Early bird registration deadline: 15th May 2026

Closing date for registrations: 31st August 2026

*Individual registrations can ONLY be made by using the Official Platform.

Registration Platform: https://immc13.sci-meet.org/register/IMMC13

Registration Category	Early Bird Fee	Standard Rate Fee
Regular Attendees	600€	650€
PhD Students, Research Fellow*	300€	350€
Master Students and Research Fellow*	200€	250€
Accompanying Persons (with lunches)	350€	380€
Accompanying Persons (without lunches)	200€	250€
One-day Registration	200€	250€
Lower Income Countries	400€	400€

*Student registration forms must be accompanied by a signed letter from the Head of Department attesting to student status. The fees do not include accommodation costs.

Registration Is Open - Until 31 August!

If you have not yet registered, now is the time to secure your place. Registration closes on 31 August 2026.

Do not miss the opportunity to learn from leading experts in medicinal mushroom research, discover emerging scientific and industrial perspectives, and connect with an international community of researchers, research centers, companies and professionals.

IMMC13 SPEAKERS

We are honored to welcome an outstanding group of internationally recognized Reflective, Plenary, Keynote, and Industrial Speakers.

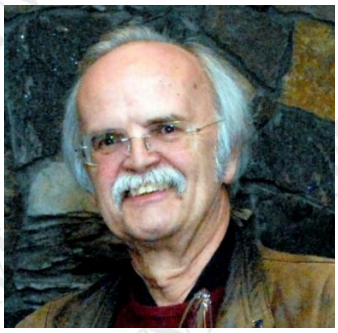
Below, we highlight the speakers featured throughout the four days of IMMC13.

Day 1 | 22 September

Sustainable Innovation in Mushrooms

REFLECTIVE SPEAKER
Giuseppe Venturella
University of Palermo, Italy
Medicinal Mushrooms: Multidisciplinary Approaches to Studying Therapeutic Potential
15:00 – 15:45

PLENARY SPEAKER
Paul Stamets
Fungi Perfect, United States of America
Can Polypore Mycelium be Useful in Defending Against Viral Storms?
15:45 – 16:30



PLENARY SPEAKER

Marin Berovič

Academy of Engineering, Slovenia

Redox Potential Scale-up of *Ganoderma lucidum* Submerged Cultivation from Laboratory to Higher Pilot Scale

16:30 – 17:15

Day 2 | 23 September

Personalized Nutrition & Precision Medicine

PLENARY SPEAKER

Alfredo Martínez

IMDEA Nutrition, Spain

Individualized Nutrition, Health, and Artificial Intelligence: Opportunities for Precision Metabolomic Dietary Intake Assessment

09:00 – 09:40

KEYNOTE SPEAKER

Liudmila Kalitukha

Good Feeling Products, Germany

Fungal Wisdom Meets OMICS-TECH

09:40 – 10:05

Agro-food Systems & Circular Integration

PLENARY SPEAKER

Manuela Pintado

Universidade Católica Portuguesa, Portugal

Medicinal Mushroom Biomass: From Bioactive Characterization and Bioaccessibility to Gut Microbiota Modulation and Neuroprotection

14:00 – 14:40

PLENARY SPEAKER

John Holliday

Highland Mushrooms, United States of America

Hericium erinaceus as a Neuroregenerative Medicinal Mushroom: Bioactive Compounds, Clinical Evidence and Emerging Production Technologies

14:40 – 15:20

KEYNOTE SPEAKER

Omon Isikhuemhen

North Carolina A&T State University, United States of America

Medicinal Mushrooms as Functional Additives in Animal Health and Production

15:20 – 15:45

KEYNOTE SPEAKER

Georgios Zervakis

Agricultural University of Athens, Greece

An Update of the Worldwide Diversity of the Genus *Pleurotuos*

16:15 – 16:40

Day 3 | 24 September

AI & Omics in Medicinal Mushroom Research

PLENARY SPEAKER

Boris Jakopović

Dr Myko San, Croatia

New Advances in Medicinal Mushroom Proteomics: From Complex Bioactives to Therapeutic Protein Networks

09:00 – 09:40

KEYNOTE SPEAKER

Eva Tejedor Calvo

Agrifood Research and Technological Centre of Aragón, Spain

Decoding Truffle Aroma, Bioactivity and Quality through Omics and Data-Driven Approaches

09:40 – 10:05

Climate Resilience via Ecosystem Services

KEYNOTE SPEAKER

Dennis Walker

Mycopreneur, United States of America

Cultural Heritage & Biocultural Conservation of Mushrooms Around the World

09:40 – 10:05

Cultural Heritage & Biocultural Conservation

KEYNOTE SPEAKER

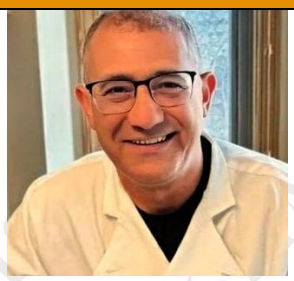
José Antonio Bonet

Center of Research in Agrotechnology, Spain

Can Mycosilviculture Optimize the Ecosystem Services Provided by Fungi in the Context of Climate Change?

10:15 – 10:40

Ethics, Safety & Regulatory Foresight



KEYNOTE SPEAKER

Ayman Daba

Doctor's Data, United States of America

Mushroom-Derived Polysaccharides: Translational Challenges in Efficacy, Safety, and Regulatory Standardization

11:30 – 11:55

Public Health & Policy Applications

PLENARY SPEAKER

Ulrike Lindequist

University of Greifswald, Germany

Safety Aspects of Medicinal Mushrooms

14:00 – 14:40

KEYNOTE SPEAKER

Ángel Trigos

University of Veracruz, Mexico

Microsterols: Beyond their Function and Regulation in Membrane Fluidity and Structure

14:40 – 15:05

Day 4 | 25 September

Therapeutic Potential of Psychedelic Mushrooms

PLENARY SPEAKER

Albino Oliveira-Maia

Champalimaud Foundation, Portugal

Beyond Trials in Psychedelic Medicine: Ethics, Implementation, and Equity

09:00 – 09:40

Round Table Industry & Innovation

Scientific and Industrial Perspectives on Medicinal Mushroom Research and Innovation

CHAIR
Eric Puro
KÄÄPÄ Biotech,
Finland

INDUSTRIAL SPEAKER
Chris Fields
Applied Food Sciences,
United States of America

INDUSTRIAL SPEAKER
Per Björk
Cien por Cien Natural,
Spain

INDUSTRIAL SPEAKER
John Holliday
Highland Mushrooms,
United States of America

INDUSTRIAL SPEAKER
William Ahern
Mycology Research
Laboratories, United Kingdom

INDUSTRIAL SPEAKER
Rojison Koshy
Ujala Life Sciences,
India

AWARDS

To recognize excellence and innovation, IMMC13 will include awards for the STUDENT AWARDS and RESEARCHER AWARDS for:

Best Poster Presentation

Best Oral Presentation

For details on conference website: https://immc13.com/awards/.

INVITATION TO SPONSORS

The Organizing Committee of the 13th International Medicinal Mushroom Conference (IMMC13) invites companies, institutions, and stakeholders to support this global event dedicated to scientific excellence, innovation, and sustainability in the medicinal mushroom field.

IMMC13 will gather leading researchers, industry experts, and professionals from around the world to share state-of-

the-art advancements and strengthen collaboration between academia and industry.

Your participation as a sponsor will enhance your visibility, promote your brand, and reinforce your commitment to scientific progress and innovation.

CONTACTS

Conference Website: https://immc13.com/

Registration Platform: https://immc13.sci-meet.org/register/IMMC13

Participant Access Area: https://immc13.sci-meet.org/login

E-mail: info@immc13.com

11th ICMBMP Oct. 13-17, 2026, Accra, Ghana

Second Announcement

The 11th International Conference on Mushroom Biology and Mushroom Products

Oct. 13-17, 2026

Accra, Ghana.

We are pleased to invite you to join us in Accra, Ghana, from October 13–17, 2026, for the 11th International Conference on Mushroom Biology and Mushroom Products (11th ICMBMP 2026). This milestone conference hosted for the first time on African soil will take place in Accra, Ghana under the theme ***"Fungal Frontiers: Mushrooms for Food Security, Health, and Sustainability."***

The 11th ICMBMP offers a unique opportunity for global experts to share the latest research and innovations in fungal biology, mushroom cultivation, functional food development, and sustainability. The conference will feature keynote lectures, scientific sessions, technical presentations, posters, exhibitions, and field visits, complemented by rich cultural programming.

The 11th ICMBMP meetings will foster vibrant scientific exchange and multi-sectoral collaboration among researchers, entrepreneurs, educators, policymakers, and development partners. This edition will showcase Africa's growing contributions to mushroom science and catalyze cross-continental partnerships for transformation.

Organizers of the 11th ICMBMP 2026

World Society for Mushroom Biology and Mushroom Products (WSMBMP)

CSIR-Food Research Institute (CSIR-FRI), Ghana

Accra Technical University (ATU), Ghana

Ho Technical University (HTU), Ghana

Co-organizers

Ministry of Environment Science and Technology (MEST), Ghana

Ministry of Food and Agriculture (MoFA), Ghana

University of Ghana, Institute for Environment and Sanitation Studies (IESS), Ghana

Institute of Edible Fungi, Shanghai Academy of Agricultural Sciences (SAAS), China

National Engineering Research Center of Edible Fungi, China

Mushroom Branch of the Chinese Agricultural Society (MBCAS), China

International Society for Mushroom Science (ISMS)

Organizing Committees of the 11th ICMBMP

WSMBMP Executive Committee

Qi Tan (China)

András Geösel (Hungary)

Manjit Singh (India)

Jingsong Zhang (China)

Johan Baars (Netherlands)

Yoichi Honda (Japan)

Mary Obodai (Ghana)

Hui Chen (China)

Local Organizing Committees

Scientific Committee

Finance and Sponsorship Committee

Technical and Logistics Committee

Publicity and Marketing Committee

Social Committee

Secretariat

Language

Working languages for the conference are English, French and Chinese. Simultaneous translation will be provided for conference oral presentations.

Scientific Program

The 11th ICMBMP will incorporate the latest advances in mushroom biology and mushroom products through keynote lectures, oral presentations, poster displays, and technical workshops.

Panel topics will include:

1) Biodiversity, Systematics, and Taxonomy;

2) Omics and Bioinformatics;

3) Genetics, Breeding and Engineering;

4) Physiology, Developmental Biology and Mushroom Cultivation;

5) Myco-Molecules: Nutritional and Therapeutic Potential;

6) Processing Technologies;

7) Pest and Disease Management;

8) Product Quality, Safety, and Regulation;

9) Mushroom Economics, Culture, and Policy

Registration

All registered participants will have access to the full scientific program, the mushroom innovation expo, field excursions, conference materials, and networking events. Registration includes the conference kit, program booklet (E copy), book of abstracts, and access to proceedings.

Online registration will be available at https://icmbmp11.foodresearchgh.org.

Registration rates are as follows:

Regular Participant: 500 USD before (including) July 31, 2026; 600 USD after July 31, 2026

Student*: 300 USD before (including) July 31, 2026; 400 USD after July 31, 2026

Accompanying Guest#: 400 USD

* Proof of student status is required upon registration

Accompanying Guest registration includes access to cultural events and the exhibition hall.

Refund Policy: Full refunds (less 50 USD administration fee, excluding bank charges) will be issued for cancellations received by Aug 15, 2026. A 50% refund applies for requests received by Sep 15, 2026. No refunds after that date.

Call for Abstracts and Papers

Participants are invited to submit abstracts for oral or poster presentations. Full papers may also be submitted for consideration in the conference proceedings.

Abstracts should include the title, authors, affiliations, and a 300–350 words summary of the research. Full manuscripts should follow standard scientific format.

Important dates

- 31 JUL Early bird registration
- 4 SEP Abstract submission closes

- 20 SEP Acceptance notification
- 25 SEP Full paper submission

Pre-Conference Activities

Hands-on technical training: Spawn production, quality control, alternative substrates, cultivation systems and strain maintenance.

Educators' forum: Curriculum development, e-learning, virtual laboratories and institutional collaboration.

Youth & women enterprise summit: Founder stories, business-model coaching, innovation labs, financial literacy and market access.

Abstract & poster bootcamp: Scientific writing, visual storytelling, peer review and one-to-one mentoring.

Programme

Day 1 13 OCT

Opening & global exchange

- Opening ceremony
- Scientific sessions and technical tracks
- Plenary and keynote presentations
- Poster exhibition and media interactions
- Global Mushroom Educators Roundtable
- Welcome dinner and cultural celebration

Day 2 14 OCT

Science, awards & communiqué

- Scientific and technical sessions continue
- Research exchange across thematic tracks
- Awards ceremony
- Closing ceremony
- Conference communiqué

Day 3 15 OCT

Field learning & next steps

- Field excursion and foraging experience
- Advocacy engagements with policymakers

- Masterclass planning
- Networking and follow-on initiatives

Accommodation

Special conference rates will be available through the official registration portal at [https://icmbmp11.foodresearchgh.org]. Early booking is strongly encouraged due to limited availability.

Contact

Secretariat, 11th ICMBMP 2026

CSIR–Food Research Institute

P.O. Box M20, Accra, Ghana

Phone: +233 (0) 244 711 860 / +233 (0) 207 930 703

Email: icmbmp11@foodresearchgh.org

Website: [https://icmbmp11.foodresearchgh.org]

World Society for Mushroom Biology and Mushroom Products (WSMBMP)

Conference Announcement Date: October 2025

Research progress

The Effect of the Lingzhi or Reishi Medicinal Mushroom *Ganoderma lucidum* (Agaricomycetes) Administration on the Functional State of Erythrocytes in Rats with Experimental Metabolic Syndrome

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[b] *Institute of Evolution and Department of Evolutionary and Environmental Biology, Faculty of Natural Science, University of Haifa, Mt. Carmel, Haifa 31905, Israel*

[c] *Department of Biochemistry, Faculty of Biology, Ivan Franko National University of Lviv, Lviv 79005, Ukraine; Collegium Medicum, Faculty of Biotechnology, University of Rzeszow, Rzeszow 35-601, Poland*

Abstract: The research examined how the extract of *Ganoderma lucidum* mushroom mycelium affects the functional state of erythrocytes in rats with fructose-induced metabolic syndrome (MetS). MetS was induced by a high-carbohydrate diet: for 42 d, the animals consumed a 10% fructose solution instead of drinking water. Following the induction of MetS, the rats were treated with *G. lucidum* mycelium extract for 14 d at a dose of 1 g/kg of body weight. It was found that administration of the extract to animals with MetS resulted in a gradual reduction in body weight and a 13.2% decrease in blood plasma glucose levels. Additionally, the extract normalized erythrocyte count, hemoglobin concentration, and both the number and daily production of reticulocytes. It also reduced lactate concentration and lactate dehydrogenase activity in blood plasma, increased the resistance of erythrocyte membranes to acid hemolysis, and decreased hemoglobin's affinity for oxygen. Treatment with the extract led to a 41.8% decrease in fetal hemoglobin content and a 17.0% reduction in plasma sialic acid concentration, while also normalizing its level in erythrocytes. These findings indicate a corrective effect of the *G. lucidum* mycelium extract on the functional state of erythrocytes.

Keywords: *Ganoderma lucidum*, metabolic syndrome, hyperglycemia, medicinal mushrooms, erythrocytes, hemoglobin

International Journal of Medicinal Mushrooms, Volume 28, Issue 5, pp. 47-62

DOI: 10.1615/IntJMedMushrooms.2026063253

Variations in elemental and isotopic compositions of Cu, Zn, and Cd in mushrooms: are they site- or species-dependent?

Alexandre V. Andronikov, Irina E. Andronikova, Eva Martinkova, Ondrej Sebek, Anna Vynnychuk, Marketa Stepanova

Division of Geochemistry and Laboratories, Czech Geological Survey, Geologicka 6, Prague, 15200, Czech Republic

Abstract: We studied the elemental and isotopic systematics of Cu, Zn, and Cd in *Imleria badia* mushroom and the related soil samples from six sites underlain by granite, amphibolite, and peridotite bedrock. The soils contain varying amounts of Cu, Zn, and Cd and exhibit a wide range of δ^{65}Cu (−0.85 to +0.67‰), δ^{66}Zn (−0.06 to +0.25‰), and δ^{114}Cd (−0.73 to −0.37‰) values. Mushrooms show site-dependent concentrations only in the case of Cd. Isotopes of Cd, Cu, and Zn fractionate to different degrees during both uptake from the substrate and within-mushroom translocation. Mushrooms display higher uptake of isotopically heavier Zn ($\Delta^{66}Zn_{FB\text{-}soil}$ = 0.33 to 1.03‰) and Cd ($\Delta^{114}Cd_{FB\text{-}soil}$ = 0.17 to 0.47‰), and predominantly isotopically heavier Cu ($\Delta^{65}Cu_{FB\text{-}soil}$ = −0.08 to 1.47‰). The degrees of within-mushroom isotopic fractionation are insignificant: Δ^{65}Cu had a total range of values of 0.38‰; Δ^{66}Zn, of 0.53‰; and Δ^{114}Cd, of 0.15‰ for the mushroom samples. Individual samples show the extent of within-mushroom isotopic fractionation (Δ^{x}E) from −0.29 to 0.13‰ for different elements. The study suggests that some elemental and isotopic differences in the analyzed mushrooms are more species-dependent than site-dependent.

Keywords: Cu, Zn, and Cd isotopes; Growing substrate; Isotopic fractionation; Mushrooms; Translocation; Uptake

Fungal BiologyOctober 2026, Volume 130, Issue 6

10.1016/j.funbio.2026.101812

Alginate-based edible coating incorporating green tea extract for preserving postharvest quality and safety of white mushrooms (*Agaricus bisporus*)

Jade Morais Alves [a], Bruna Heloiza Gomes da Silva [a 1], Adma Nadja Ferreira de Melo [b 1], Louise Iara Gomes de Oliveira [a], André Ulisses Dantas Batista [d], Marcos dos Santos Lima [c], Ruthchelly Tavares da Silva [a], Maria Manuela Pintado [b], Marciane Magnani [a]

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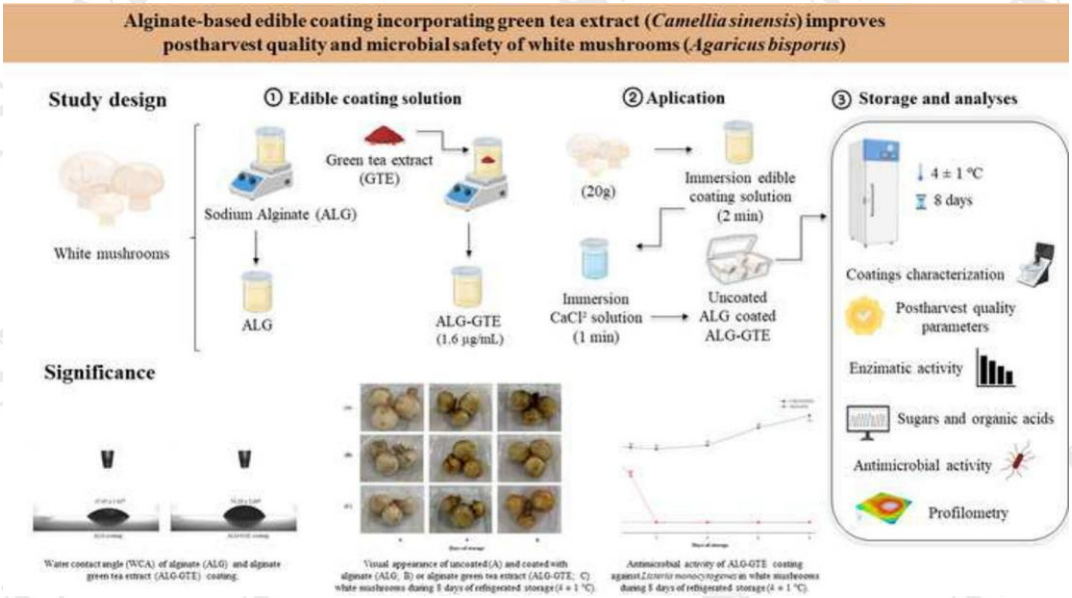
[c]*Laboratory Beverages and Liquid Chromatography, Instituto Federal do Sertão, Pernambucano, Petrolina, PE, Brazil.*

[d]*Integrated Biomaterials Laboratory, Department of Restorative Dentistry, Health Sciences Center, Federal University of Paraíba, João Pessoa, Paraíba, Brazil.*

Abstract: This study aimed to evaluate the effects of a sodium alginate based edible coating incorporated with green tea extract (GTE) (*Camellia sinensis*) on the postharvest quality attributes and antimicrobial activity against *Listeria monocytogenes* in white mushrooms during refrigerated storage. The phenolic profile of GTE was characterized, and its minimum inhibitory concentration (MIC) against L. *monocytogenes* (1.6 mg/mL) was determined. Sodium alginate coatings, with (ALG-GTE) or without GTE (ALG) at MIC (1.6 mg/mL), were characterized (functional groups, solubility in water, moisture, thickness, water contact angle and color) for their chemical and physical properties. The effects of

ALG-GTE coatings on quality parameters (firmness, weight loss, color, pH, sugars and organic acids), enzymatic activity [polyphenol oxidase (PPO), peroxidase (POD) and pectin methylesterase (PME)], antimicrobial activity against L. *monocytogenes* (5 log CFU/g), and surface characteristics (3D optical profilometry) were assessed in white mushrooms (*Agaricus bisporus*) during refrigerated storage (8 days, 4 ± 1 °C, 90–95% RH). The ALG-GTE coatings preserved sugar composition, particularly rhamnose, reduced organic acids accumulation and delayed weight and firmness loss, reduced color changes, and decreased PME activity in coated white mushrooms. *L. monocytogenes* counts decreased by 1.4 log CFU/g after 1 day, and no viable cells were detected after 2 days (< 1.5 log CFU/g) in ALG-GTE coated white mushrooms. In addition, ALG-GTE coated white mushrooms exhibited smoother surfaces than uncoated samples. These findings highlight the potential of ALG-GTE coatings as a sustainable alternative capable of improving the microbiological safety and delaying the postharvest changes in fresh mushrooms.

Graphical abstract



Keywords: Sustainable edible coating; Fresh mushrooms; *Listeria monocytogenes*; Antimicrobial activity

Food Research International, 31 October 2026, Volume 242, Part 3

10.1016/j.foodres.2026.120051

Clinical utility of bioactive metabolites of medicinal mushrooms in colorectal cancer

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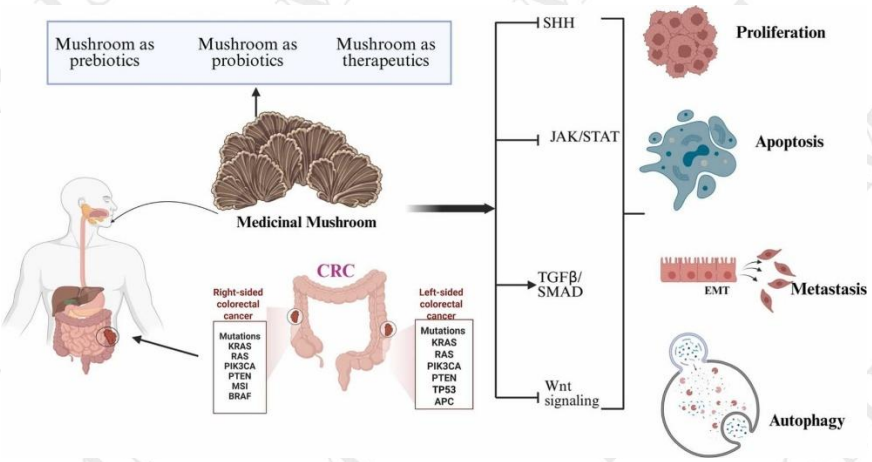
[b]*Faculty of Medical Research, Academy of Scientific & Innovative Research (AcSIR), Ghaziabad, India*

Abstract: Despite the availability of multimodal treatment strategies for colorectal cancer (CRC), their therapeutic efficacy is limited because of their resistance, with grade 3–4 side effects. CRC is the third most common cancer type,

and only 35% of patients diagnosed in the last stage still do not have satisfactory life expectancies. The major risk factors for CRC include an unhealthy lifestyle, junk and processed food, tobacco use, alcohol consumption, and dysbiosis of the gut microbiome. Edible mushrooms are being used in traditional medicine and have tremendous precision potential. Different phytochemicals of medicinal mushrooms have diverse pharmacological properties that may relieve CRC. Preclinical and clinical research has endorsed the antitumoral and immunomodulatory potential of many medicinal mushrooms in cancer therapy. *Ganoderma lucidum*, and other species of medicinal mushrooms (*Agaricus blazei*, *Lentinula edodes*, *Pleurotus eryngii*, *Phellinus linteus*, *Agaricus bisporus*) and their metabolites have been reported to be largely nontoxic and to act as potential inhibitors of multiple targets involved in oncogenesis with potent immunomodulation. The key components of metabolites such as terpenoids, carotenoids, quinolones, steroids, terpenes, anthraquinones, and benzoic acid derivatives are suggested to modulate cell signaling pathways (Wnt, SHH, TGF/SMAD and JAK/STAT pathways) involved in the regulation of aberrant cell growth associated with cancer. Additionally it can inhibit carcinogenesis and microbial growth to improve the gut flora. In this editorial review, emphesized on the components of medicinal mushrooms and their metabolic pathways involved in colorectal cancer treatment are highlighted to aid in the CRC treatment.

Graphical Abstract



Pharmacological Research - Natural Products, Volume 11, June 2026, 100758

https://doi.org/10.1016/j.prenap.2026.100758

Synthetic Biology Approaches for Representative Bioactive Metabolites of Medicinal Mushrooms

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Abstract: Medicinal mushrooms represent valuable sources of high-value bioactive molecules. However, these valuable active ingredients exhibit low yield in their natural sources, and their structural complexity presents significant

challenges for their extraction and isolation. Synthetic biology addresses these limitations by enabling the green and efficient synthesis of bioactive molecules through engineered microbial cell factories, offering a sustainable approach to utilizing rare mushroom-derived compounds. This review summarizes recent advances in the biosynthesis and heterologous microbial production of key bioactive constituents, including cordycepin, ganoderic acid, ergothioneine, pachymic acid, blazeispirols, erinacines and *Sanghuang* polysaccharide. Furthermore, it provides methodological strategies based on synthetic biology to produce other rare bioactive constituents from medicinal mushrooms.

Keywords: medicinal mushrooms, biosynthesis, biosynthetic pathways, heterologous expression

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DOI: 10.1615/IntJMedMushrooms.2026064068

Quality deterioration and its molecular basis in postharvest Flammulina filiformis: Insights from physiological and transcriptomic profiling under simulated storage environments

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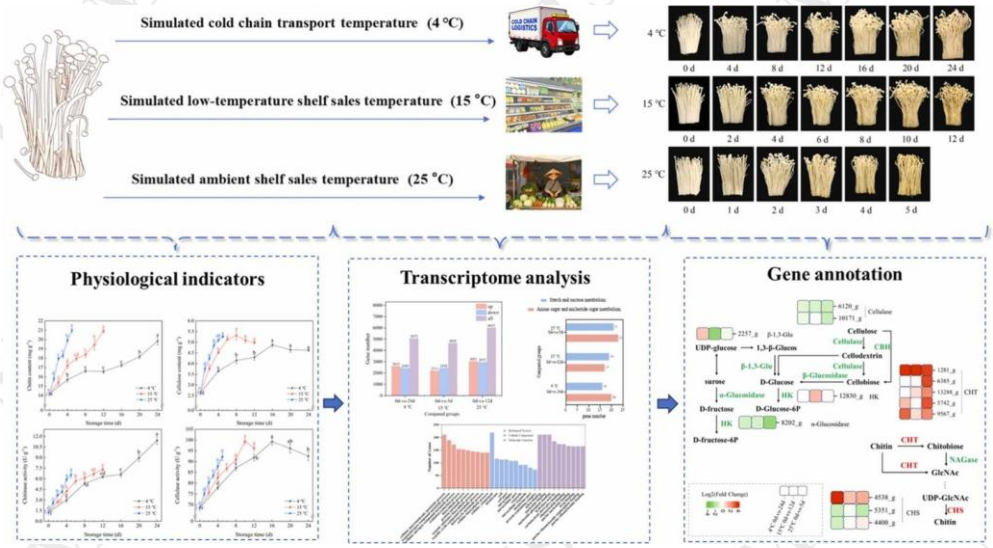
Abstract: This study simulated three postharvest supply chain environments: cold chain (4 °C), low-temperature shelf (15 °C), and room temperature shelf (25 °C), to investigate their impact on the quality deterioration of *Flammulina filiformis*. Results indicated that storage at 4 °C effectively maintained sensory quality and significantly delayed the accumulation of rigid cell wall components (lignin, cellulose, chitin). After 4 days of storage, the contents of lignin, cellulose, and chitin in samples stored at 4 °C were 2.57%, 19.24%, and 8.72% lower than those stored at 15 °C, respectively, and 10.41%, 28.43%, and 21.10% lower than those stored at 25 °C. This was consistent with the strong inhibition of related enzyme activities, including phenylalanine ammonia-lyase (PAL), cinnamyl alcohol dehydrogenase (CAD), peroxidase (POD), chitinase and cellulase. Transcriptomic and qRT-PCR analyses revealed that storage temperatures profoundly affected the expression of cell wall metabolism-related genes (e.g., *FfCHT3*, *FfCHS1*, *FfCHS3*, *FfEG-A*, *FfEG-B*, *FfECH-B*, *Ffβ-1,3-Glu-A*), potentially by modulating the supply of energy and precursors like UDP-glucose. In conclusion, 4 °C storage delays postharvest quality loss in *F. filiformis* primarily by downregulating the expression of key genes in cell wall metabolic pathways, whereas 25 °C storage promotes it. These findings provide crucial insights for developing targeted strategies to manage critical logistical nodes and extend the shelf life of *F. filiformis*.

Graphical Abstract



Keywords: *Flammulina filiformis*; Chitin; Temperature; Transcriptome; Postharvest quality

Postharvest Biology and Technology, September 2026, Volume 239

10.1016/j.postharvbio.2026.114390

Morphological and molecular characterization of Mexican *Hericium erinaceus* strains

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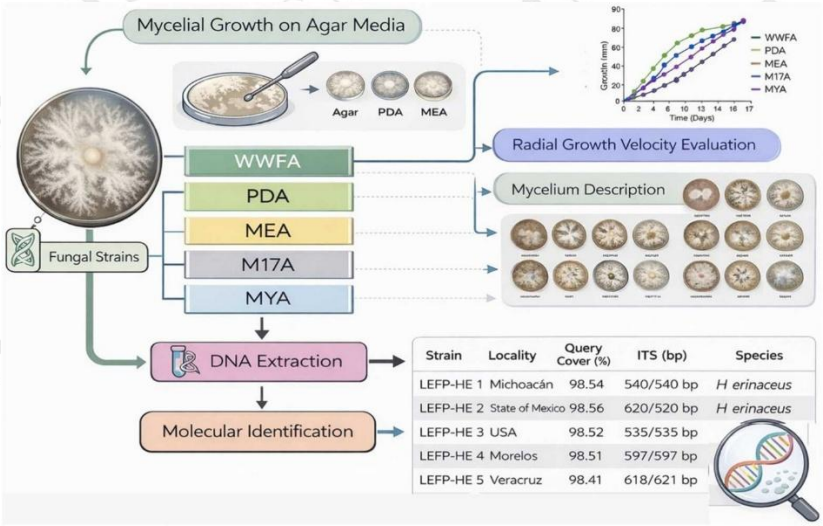
[b]*Department of Medical Microbiology and Immunology, University of Alberta, Edmonton, AB, Canada*

[c]*Laboratory of Protein Structure, Function and Engineering, Biotechnology Research Center, Universidad Autonoma del Estado de Morelos, Mexico*

Abstract: *Hericium erinaceus* is an edible and medicinal fungus recognized for its antimicrobial, antioxidant, anticancer, neuroprotective, and immunomodulatory properties. Despite its biological and biotechnological relevance, reports of this species in Mexico remain limited, with only one previous molecularly confirmed record from Durango state. Here, we present the second formal report of *H. erinaceus* in Mexico, based on four isolates obtained from different states and identified by sequencing of the internal transcribed spacer (ITS) region. Molecular analysis confirmed their taxonomic identity as *H. erinaceus*. The strains are maintained in the Laboratory of Protein Structure-Function and Engineering collection as LEFIP-HE mycelial strains. To characterize their growth performance, mycelial radial growth rate (RGR) and colony morphology were evaluated across different culture media. Growth responses varied among isolates: LEFIP-HE 1 exhibited the highest RGR on potato dextrose agar (PDA), LEFIP-HE 2 and LEFIP-HE 4 on Maca yeast agar (MYA), LEFIP-HE 3 on Medium 17 agar (M17A), and LEFIP-HE 5 on Whole wheat flour agar (WWFA). Colony morphology also differed depending on medium composition, ranging from hyaline to white pigmentation and from sparse aerial growth to dense cottony mycelium. These findings confirm the presence of *H. erinaceus* in multiple regions

of Mexico and demonstrate significant medium-dependent variation in mycelial physiology. This work provides a foundation for optimizing cultivation strategies and advancing future biotechnological applications of this species in the country.

Graphical Abstract



Keywords: Mushrooms; Sequencing; Biodiversity

Journal of Biotechnology,September 2026, Volume 417, 49-57

10.1016/j.jbiotec.2026.04.016

Hericium erinaceus Extract Relieves Depression by Targeting the Microbiota–Metabolite–Neurotrophic Axis

Pin Gong [1 2 3], Jiating Wang [1 2 3], Hui Long [1 2 3], Wenjuan Yang [1 2 3], Xuefeng Chen [1 2 3], Jing Wang [1 2 3], Nan Li [1 2 3], Fuxin Chen [4], Yuxi Guo [1 2 3]

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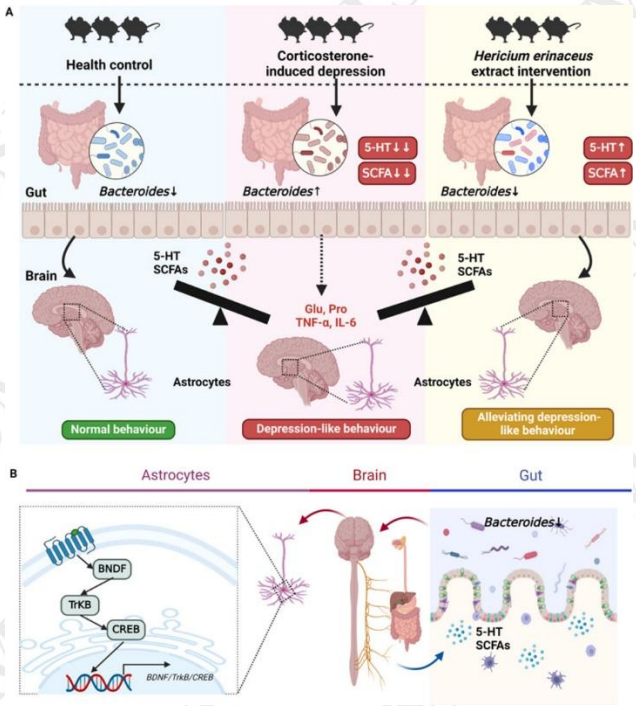
Abstract: Depression is increasingly recognized as a disorder driven by complex interactions among the gut microbiota, host metabolism, and neuroplasticity. In this study, we demonstrated that *Hericium erinaceus* extract (HEE) alleviates depressive-like behaviors in corticosterone (CORT)-induced mice by orchestrating a novel microbiota–metabolite–brain signaling cascade. HEE intervention reversed CORT-induced disruptions in amino acid homeostasis, notably normalizing serum glutamate and proline levels. Simultaneously, HEE remodeled gut microbiota composition, suppressing the overgrowth of *Bacteroides* associated with glutamate dysregulation. Fecal microbiota transplantation (FMT) experiments confirmed the causative role of HEE-modulated microbiota in alleviating depressive symptoms. At the

neurochemical level, HEE significantly restored 5-hydroxytryptamine (5-HT) levels and reactivated the BDNF/TrkB/CREB signaling axis in the hippocampus and BV2 microglial cells. Mechanistically, our findings suggest HEE as a potent natural agent capable of reprogramming the *Bacteroides*–glutamate–BDNF/TrkB/CREB axis to promote neuroprotection and emotional resilience. This work provides new insight into gut–brain axis interventions and highlights the therapeutic potential of HEE in depression management.

Graphical abstract



Keywords: Metabolomics; intestinal flora; BDNF/TrkB/CREB signaling pathway

Journal of Future Foods, Available online 11 March 2026

https://doi.org/10.1016/j.jfutfo.2026.03.014

A novel physical hurdle technology by combining plasma-activated water and ultrasound for long-term stored shiitake mushrooms

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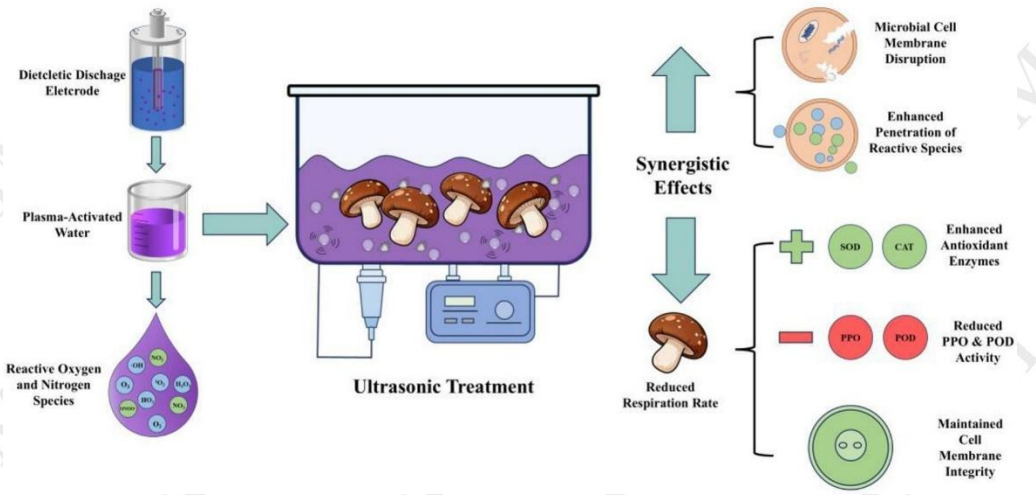
[e]*School of horticulture, Ludong University, Yantai 264025, Shandong Province, China*

Abstract: The shiitake mushrooms are perishable due to microbial infection and water loss during storage. This study

investigated the effect of plasma-activated water (PAW) combined with ultrasound (US) treatment to microbes and the postharvest quality of shiitake mushrooms. For combined treatments, fresh shiitake mushrooms were soaked in PAW for 10 min while being simultaneously sonicated at 110, 220, or 330 W for 10 min (PAW-US_{110}, PAW-US_{220}, and PAW-US_{330}, respectively). The results unveiled that the PAW combined with US (PAW-US) treatment significantly reduced nearly 0.85–1.09 log natural microorganisms at 14 d of storage. The results showed that PAW-US treatment contributed to suppressing the respiration rate, inhibiting softening and browning, enhancing antioxidant capacity, and maintaining membrane integrity. Among all the groups, PAW-US_{220} treatment yielded the most pronounced effects, highlighting the potential of this hurdle technology for postharvest preservation of shiitake mushrooms.

Graphical abstract

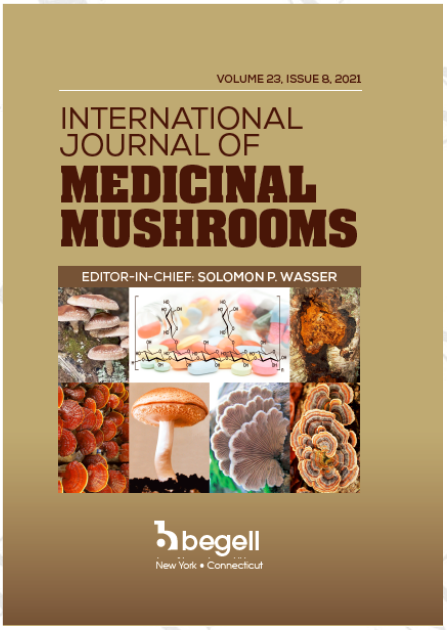


Keywords: Plasma-activatedwater treatment; Ultrasound treatment; Postharvest quality; Combined treatment; Shiitake mushrooms

Ultrasonics Sonochemistry,June 2026, Volume 129

10.1016/j.ultsonch.2026.107840

International Journal of Medicinal Mushrooms Call for Papers



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International Journal of
Medicinal Mushrooms

2026, Vol. 28, Issue no.6

International Journal of
Medicinal Mushrooms

2026, Vol. 28, Issue no.7

International Journal of
Medicinal Mushrooms

2026, Vol. 28, Issue no.8

International Journal of
Medicinal Mushrooms

2026, Vol. 28, Issue no.9

Points and Reviews

Altered Stereostructures of the DNA-Binding Domains of Variant Mating Proteins of *Ophiocordyceps sinensis* and the Wild Insect–Fungal Complex (Part I)

Xiu-Zhang Li [1], Yu-Ling Li [1], Wei Liu [2] and Jia-Shi Zhu [1,*]

[1] *State Key Laboratory of Plateau Ecology and Agriculture, Qinghai Academy of Animal and Veterinary Sciences, Qinghai University, Xining 810016, China; xiuzhang11@163.com (X.-Z.L.); yulingli2000@163.com (Y.-L.L.)*

[2] *Institute of Immunology, Army Medical University, Chongqing 400038, China; weiliu@tmmu.edu.cn*

*Correspondence: zhujosh@163.com

Simple Summary

The *Cordyceps sinensis* insect–fungal complex, comprising the *Ophiocordyceps sinensis* fruiting body and the remains of a *Hepialidae* moth larva, is a highly valued therapeutic agent intraditional Chinese medicine. The sexual reproduction of *O. sinensis* is controlled bythe tertiary structures of functional domains of the MAT1-1-1 and MAT1-2-1 proteins. This study reveals the primary structures of MAT1-1-1 and MAT1-2-1 protein variantsderived from numerous wild-type *C. sinensis* isolates. The protein sequences exhibitedvarious amino acid substitutions in the functional domains and clustered into severalBayesian clades associated with altered secondary and tertiary structures of the functional domains. In combination with data on the alternative splicing and differential occurrence and transcription of the *MAT1-1-1* and *MAT1-2-1* genes, the altered 3D structures of thefunctional domains of mating proteins refute the hypothesis that *O. sinensis* can self-fertilize via homothallic mating and instead suggest that *O. sinensis* is self-sterile and requires amating partner for sexual reproduction under heterothallism or hybridization during the sexual life of the *C. sinensis* insect–fungal complex. This conceptual shift in reproductionmode provides a new perspective on *O. sinensis* and the *C. sinensis* insect–fungal complex and will guide future r

Abstract

The MATα_HMGbox and HMG-box_ROX1-like domains of the MAT1-1-1 and MAT1-2-1 proteins, respectively, play essential roles in DNA binding and the subsequent regulation of gene transcription, controlling *Ophiocordyceps sinensis* sexual reproduction. Alternative splicing, differential occurrence and transcription of the *MAT1-1-1* and *MAT1-2-1* geneshave been demonstrated in *Hirsutella sinensis* (GC-biased Genotype #1 of the 17 *O. sinensis* genotypes), suggesting self-sterility under heterothallic or hybrid outcrossing. In thisstudy, the MATα_HMGbox domains of MAT1-1-1 proteins

in wild-type *Cordyceps sinensis* isolates were shown to cluster into 5 clades in the Bayesian clustering tree and belong to diverse stereostructure morphs under 19 AlphaFold codes. The HMG-box_ROX1-likedomains of MAT1-2-1 proteins, on the other hand, were shown to cluster into 2 branched Bayesian clades and belong to stereostructure morphs under 25 AlphaFold codes. Correlation analysis revealed that 1–3 amino acid substitutions in the DNA-binding domains of the mating proteins resulted in altered hydrophobicity and secondary and tertiary structures of the DNA-binding domains of the proteins, especially altered stereostructures of thehydrophobic cores formed by 3 critical α- helices within the functional domains of the proteins. Fungal origin analysis revealed possible heterospecific fungal sources ofmating proteins with stereostructure variations in wild-type *C. sinensis* isolates, suggesting thatalterations in DNA binding function and the subsequent regulation of mating-relatedgene transcription are involved in ensuring the accuracy and genetic diversity of heterothallic and hybrid reproduction of *O. sinensis* during the lifecycle of the *C. sinensis* insect–fungal complex.

Keywords: MATα_HMGbox domain of the MAT1-1-1 protein; HMG-box_ROX1-like domain of the MAT1-2-1 protein; heteromorphic protein structures; wild-type *Cordycepssinensis* isolates; sexual reproduction of *Ophiocordyceps sinensis*; *Cordyceps sinensis* insect–fungal complex

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1.Introduction

Cordyceps sinensis is one of the most expensive therapeutic agents in traditional Chinese medicine (TCM) and has a rich history of clinical use over several centuries for health maintenance, disease amelioration, post-illness and postoperative recovery, and antiaging therapy [1–3]. This natural therapeutic agent consists of the *Ophiocordyceps sinensis*(Hypocreales) fruiting body and the remains of a *Hepialidae* moth larva containing anintact, thick larval body wall with numerous bristles, an intact larval intestine, head tissues, and fragments of other larval tissues [4–10]. Studies of *C. sinensis* have demonstrated itsmulticellular heterokaryotic microscopic structures and genetic heterogeneity, including17 genomically independent genotypes of *O. sinensis* fungi, >90 other fungal species spanning at least 37 fungal genera, and larval genes [4,7,10–29]. Thus, the Chinese Pharmacopoeia defines natural *C. sinensis* as an insect–fungal complex classified as a LEVEL-IIendangered natural species [30].

Among the numerous fungal species [15,21,26], *Hirsutella sinensis* has been postulated to be the sole anamorph of *O. sinensis* [31]. However, ten years later, in an artificial cultivation study conducted in an industrial product-oriented setting, Wei et al. [32] reported aspecies contradiction between anamorphic inoculants (GC-biased Genotype #1 *H. sinensis* strains) on *Hepialidae* moth larvae and the sole teleomorph (the genomically independent AT-biased Genotype #4 of *O. sinensis*) in the fruiting body of cultivated *C. sinensis*.

Notably, the Latin name *Cordyceps sinensis*, which was originally given to the intrinsic fungus, has been indiscriminately used since the 1840s to refer to both the teleomorph/holomorph of the fungus *C. sinensis* and the wild insect–fungal complex. Thefungus was renamed *O. sinensis* in 2007, with the use of the *H. sinensis* strain EFCC 7287as the nomenclatural reference [4,7,33–35]. Zhang et al. [36] proposed improper implementation of the “One Fungus = One Name” nomenclature rule set by the InternationalMycological Association [37], disregarding the findings of multiple genomically independent genotypes of *O. sinensis* fungi and inappropriately replacing the anamorphic name *H. sinensis* with the teleomorphic name *O. sinensis* [7,9,10]. In this work, we continue to use the anamorphic name *H.*

sinensis for GC-biased Genotype #1 of the 17 *O. sinensis* genotypes that may share a common evolutionary ancestor [17] and refer to the genomically independent Genotypes #2–17 fungi as *O. sinensis* according to the taxonomic descriptions that are used in several public depository databases, such as the GenBank and AlphaFold databases,before the systematic positions of these evolutionarily related genotypes are individually determined and differentiated, regardless of whether they are GC- or AT-biased genetically. In this study, we continue to use the customary name *C. sinensis* to refer to the wild orcultivated insect–fungal complex because the renaming of *C. sinensis* to *O. sinensis* in 2007 using the *H. sinensis* strain EFCC 7287 as the nomenclatural reference did not involve the indiscriminately used Latin name for the insect–fungal complex [7,33]. However, weunderstand that this practice will likely be revised in the future by the differential use ofproprietary and exclusive Latin names for the multiple genome-independent *O. sinensis*genotypic fungi and the insect–fungal complex.

The sexual reproductive behavior of ascomycetes is strictly regulated by transcription factors encoded at the mating-type (*MAT*) locus. These transcription factors constitute the core mechanism that determines mating compatibility, regulates mating type recognition, and controls the development of fruiting bodies and reproductive structures, e.g., ascocarps and ascospores [38–46]. Like other fungi in Ascomycota, the reproductive behavior of *O.sinensis* relies on the synergistic interaction of 2 mating proteins, the *MAT1-1* and *MAT1-2* idiomorphs. These proteins contain 2 types of critical domains that specifically regulate the expression of genes related to sexual reproduction: (1) the mating-type alpha high mobility group box (MATα_HMGbox) domain in the MAT1-1-1 protein and (2) the high mobilitygroup box ROX1-like (HMG-box_ROX1-like) domain in the MAT1-2-1 protein [41,47–50]. However, differential occurrence, alternative splicing, and differential transcription ofmating-type and pheromone receptor genes and heteromorphic stereostructures of the entire MAT1-1-1 and MAT1-2-1 proteins in *H. sinensis* strains and wild-type *C. sinensis* isolates have been observed, invalidating the self-fertilization hypothesis under homothallism and pseudohomothallism for *H. sinensis*, which was postulated to be the sole anamorph of *O. sinensis*, and instead suggesting that the self-sterile *O. sinensis* requires sexual partners to accomplish heterothallic or hybrid reproduction within the lifecycle of the *C. sinensis* insect–fungal complex [31,50–55].

Mutations of the 2 critical DNA-binding domains of mating proteins that result in a few amino acid substitutions may cause conformational changes in the core stereostructures of the domains, thereby affecting the synergistic interaction of the mating proteins, probably through the regulation of the expression of complementary downstream genes of the2 idiomorphic mating proteins. Our previous study [50] showed variations in the 3Dstructures of complete mating proteins. This study continues from our previous study,focusing on amino acid substitutions within the MATα_HMGbox and HMG-box_ROX1-like domains of the full-length MAT1-1-1 and MAT1-2-1 proteins, respectively, and theimpact of the variable primary structures of the DNA-binding domains on the changesin the hydrophobic properties and the secondary and tertiary structures of the functional domains in wild-type *C. sinensis* isolates. Correlations between changes in hydrophobicity and the primary and secondary structures of the DNA-binding domains of mating proteins encoded by the genome, transcriptome and metatranscriptome assemblies of *H. sinensis*and *C. sinensis* insect–fungal complexes were also analyzed.

2.Materials and Methods

2.1.The MAT1-1-1 and MAT1-2-1 Protein Sequences of the Wild-Type C. sinensis Isolates

The AlphaFold database lists the AlphaFold-predicted 3D structures for 138 MAT1- 1-1 proteins and 74 MAT1-2-1 proteins [50]. These proteins were produced by differentsample sources: *O. sinensis* strains of different genotypes (including GC-biased Geno-type #1 *H. sinensis* strains), wild-type *C. sinensis* isolates, and *C. sinensis* insect-fungal complexes (Table S1). Among these proteins, 118 MAT1-1-1 proteins and 69 MAT1-2-1proteins are full-length proteins, as shown in Tables S2 and S3. Three full-length MAT1-1-1 proteins (ALH24945, AGW27560, and EQK97643) and 2 full-length MAT1-2-1 proteins(AEH27625 and EQL04085) were derived from *H. sinensis* strains (bolded and underlined in Tables S2 and S3). All other full-length mating proteins were derived from wild-type *C. sinensis* isolates that were collected from various production areas on the Qinghai–Tibet Plateau [5,34,36,49,50,52,56,57]. The internal transcribed spacer (ITS) sequence information is available in the GenBank database for the full-length MAT1-1-1 and MAT1-2-1 protein variants derived from 34 wild-type *C. sinensis* isolates and aligned with the reference ITS sequences of the 7 GC-biased genotypes of *O. sinensis* (Table S4).

The remaining 20 MAT1-1-1 proteins (AGW27517–AGW27536) and 5 MAT1-2-1 proteins (AGW27543, AGW27548, AGW27552, AGW27554, and AGW27555), which were derived from *O. sinensis* strains [23,48], are truncated at the N- and/or C-termini and will be analyzed elsewhere.

2.2.Genome, Transcriptome, and Metatranscriptome Assemblies of H. sinensis Strains and C. sinensis Insect–Fungal Complexes

The GenBank database lists 5 genome assemblies, LKHE00000000, NGJJ00000000, ANOV00000000, JAAVMX000000000, and LWBQ00000000, of the *H. sinensis* strains 1229, CC1406-20395, Co18, IOZ07, and ZJB12195, respectively, and a transcriptome assembly,GCQL00000000, of the *H. sinensis* strain L0106 [49,58–62].

The metatranscriptome assembly GAGW00000000 for the *C. sinensis* insect–fungal samples (unknown maturation stages) collected from Kangding County, Sichuan Province, China [63], is available in the GenBank database.

Another metatranscriptome assembly was derived from mature *C. sinensis* samples collected from Deqin, Yunnan Province, China, and was uploaded to a repository database, http://www.plantkingdomgdb.com/Ophiocordyceps_sinensis/ (accessed from 18 May 2017) [64]. Although this database is currently inaccessible, it was accessed from 18 May 2017 to 18 January 2018, and a cDNA file was downloaded.

The genome, transcriptome, and metatranscriptome assemblies were used to analyze the MATα_HMGbox and HMG-box_ROX1-like domains of the MAT1-1-1 and MAT1-2-1 proteins, respectively.

2.3.Alignment of the DNA-Binding Domain Sequences of the Mating Proteins

The amino acid sequences of the MATα_HMGbox domains of the MAT1-1-1 proteins and the HMG-box_ROX1-like domains of the MAT1-2-1 proteins of the wild-type *C. sinensis* isolates and *C. sinensis* insect–fungal complexes were aligned using the GenBank Blastp program (https://blast.ncbi.nlm.nih.gov/ (Bethesda, MD, USA), accessed from 18 October 2024 to 10 July 2025).

2.4.Bayesian Clustering Analysis of the DNA-Binding Domains of the Mating Proteins

Multiple sequence alignment of the DNA-binding domains of the mating proteins of the wild-type *C. sinensis* isolates

and *C. sinensis* insect–fungal complexes was performedusing the auto mode of MAFFT (v7.427; Osaka, Japan). The intron regions were removed using trimAl (v1.4. rev15; Barcelona, Spain). Based on the Bayesian information criterion, ProtTest v3.4.2 (University of Vigo and University of La Coruña, Spain) was used todetermine the optimal amino acid substitution model. Bayesian clustering trees of the DNA- binding domain sequences of the MAT1-1-1 and MAT1-2-1 proteins were then inferredusing MrBayes v3.2.7 software (Markov chain Monte Carlo [MCMC] algorithm; Uppsala, Sweden) at a sampling frequency of 100 iterations after discarding the initial 25% ofthe samples from a total of 1 million iterations. This process yielded final majority ruleconsensus trees for the MATα_HMGbox domains of the MAT1-1-1 proteins and the HMG- box_ROX1-like domains of the MAT1-2-1 proteins [7,50,54,55,65,66]. Clustering analysiswas conducted by Nanjing Genepioneer Biotechnologies Co. (Nanjing, China).

2.5.Amino Acid Properties and Scale Analysis

The amino acid sequences of the DNA-binding domains of the mating proteins were scaled on the basis of the general chemical characteristics of their side chains (Table S5), as reported at https://web.expasy.org/protscale/ (Basel, Switzerland), accessed from 18 October 2024 to 20 May 2025 [50,55,67–71]. The MATα_HMGbox domain of MAT1-1-1proteins (amino acids 51→225 of the reference sequence AGW27560 derived from the *H.sinensis* strain CS68-2-1229 (Table S2) [48]) and the HMG-box_ROX1-like domain of MAT1- 2-1 proteins (amino acids 127→197 of the reference sequence AEH27625 derived from the *H. sinensis* strain CS2 (Table S3) [56]), with an additional 9 amino acid residues extending upstream and downstream of the domains, were plotted sequentially with a window size of 9 amino acid residues using the linear weight variation model of the ExPASy ProtScale algorithms [50,55,67–71] to generate ExPASy ProtScale plots that display and compare the topology and waveform changes in hydrophobicity and the 2D structures for α-helices, β-sheets, β-turns, and coils of the DNA-binding domains of the mating proteins.

2.6.AlphaFold-Based Predictions of the 3D Structures of the Mating Proteins

For heteromorphic stereostructure analysis, the 3D structures of the MAT1-1-1 and MAT1-2-1 proteins from the wild-type *C. sinensis* isolates were computationally predicted from their amino acid sequences using the artificial intelligence (AI)-based machine learning technology AlphaFold (https://alphafold.com/, Cambridgeshire, UK), which was downloaded from the AlphaFold database (accessed from 18 October 2024 to 10 November 2025) [50,72–82].

The AlphaFold database provides per-residue model confidence, predicts scores between 0 and 100 for the local distance difference test (pLDDT), and provides a per-residue score that is assigned to each individual residue [73–76,78,79]. The model's confidencebands are used to color-code the residues in the 3D structures: residues with very highconfidence (pLDDT > 90) are shown in dark blue, those with high confidence (90 > pLDDT

> 70) are shown in light blue, residues with low confidence (70 > pLDDT > 50) are shown in yellow, and residues with very low confidence (pLDDT < 50) are shown in orange [50,80,83]. The AlphaFold database provides an average pLDDT score for each of the AI-predicted 3D structural models.

The main reasons for low-confidence region AlphaFold predictions include the following: (1) There are insufficient supporting data because the AlphaFold-based prediction relies on the quality of multiple sequence alignment (MSA). If few homologous sequences are available in a certain region of the MSA, the model will lack sufficient evolutionary information to infer the structure, resulting in low confidence. (2) Some protein regionsare naturally flexible under physiological conditions, such as the activation domains oftranscription factors, which do not have a fixed 3D

structure, leading to low predictionconfidence assigned by AlphaFold. (3) In terms of special structural regions, such as small- molecule binding sites and artificial linkers in fused proteins, the AlphaFold system mayhave limited prediction power, leading to low confidence in the prediction of complexstructures. Thus, the low-confidence regions in AlphaFold predictions are informative flags for highlighting prediction challenges and should not be interpreted too confidently.

2.7.Correlations of the Primary, Secondary, and Tertiary Structures of the DNA-Binding Domains of the MAT1-1-1 and MAT1-2-1 Proteins

The AlphaFold-predicted 3D structures of the MATα_HMGbox domains of the MAT1- 1-1 proteins and the HMG-box_ROX1-like domains of the MAT1-2-1 proteins were magnified at the sites of amino acid substitutions. The locally magnified 3D structures at themutation sites were correlated with the amino acid substitutions to obtain the primary structures and the changes in topology and waveform via ExPASy ProtScale plotting, which revealed hydropathy, α-helices, β-sheets, β-turns, and coils for altered hydrophobicity and the 2D structures of the DNA-binding domains of the MAT1-1-1 and MAT1-2-1 proteins.

3.Results

3.1.Primary Structures of the MATα_HMGbox Domains of the Full-Length MAT1-1-1 Proteins

Among the 138 MAT1-1-1 proteins in the AlphaFold database, 118 (85.5%) are full- length proteins containing 372 amino acid residues. These proteins contribute to 15 hetero- morphic 3D structure morphs belonging to 5 Bayesian clusters (Table S2) [50]. Twenty-nine (24.6%) of the 118 full-length MAT1-1-1 proteins derived from wild-type *C. sinensis* isolates contain variable amino acid substitutions.

The MAT1-1-1 proteins contain a MATα_HMGbox domain that is located at amino acids 51→225 (shown in blue and underlined in Figure S1), as represented by the reference MAT1-1-1 protein AGW27560 derived from the *H. sinensis* strain CS68-2-1229 (Table S2) [48]. Other MAT1-1-1 proteins derived from wild-type *C. sinensis* isolates or encoded by the genome assemblies of the *H. sinensis* strains and the metatranscriptome assemblies of *C. sinensis* insect–fungal complexes contain various amino acid substitutions (Figure S1). The MATα_HMGbox domains of 10 (34.5%) of the 29 variant proteins are 100% identical tothe domain sequence of the query protein AGW27560 when the amino acid substitutions outside the domains are not considered. Each of the remaining 19 proteins (65.5%) contains a mutation or mutations that results in 1 or 2 amino acid substitutions at various siteswithin the MATα_HMGbox domains, as shown in red in Figure S1.

Figure S1 also shows the MATα_HMGbox domains of the MAT1-1-1 proteins encoded by the genome assemblies ANOV01017390 (794←1129 & 1280←1396), LKHE01001116(4183←4620 & 4667←4759), and JAAVMX010000001 (6,699,061→6,699,153 & 6,699,203 →6,699,637) of the *H. sinensis* strains Co18, 1229, and IOZ07, respectively [49,60,62]. (Note: the arrows "→" and "←" indicate sequences in the sense and antisense strands of thegenomes, respectively; "&" refers to the removed intron portion.) These genome-encoded MAT1-1-1 proteins are truncated at their C-termini; the truncated segments are located far downstream of the MATα_HMGbox domains.

The genome assemblies LWBQ00000000 and NGJJ00000000 and the transcriptome assembly GCQL00000000 of the *H. sinensis* strains ZJB12195, CC1406-20395, and L0106, respectively, do not contain the genes or transcripts that encode the MAT1-1-1 proteins [58–60].

The metatranscriptome assemblies GAGW01008880 (300←1127) and OSIN7648 (1→1065) of natural *C. sinensis* insect–fungal complexes encode MAT1-1-1 proteins(Figure S1) [63,64]. The MAT1-1-1 protein OSIN7648 contains an 18 amino acid truncation in the middle sequence (SMQREYQAPRFFYDYSVS) between residues 863 and 864; thetruncated segment is located downstream of the MATα_HMGbox domain (151→675). The N-terminus of the MATα_HMGbox domain (741←1127) of the MAT1-1-1 protein encoded by GAGW01008880 is truncated by 46 amino acid residues (AAASRATRQTKEASCDRAKR- PLNAFMAFRSYYLKLFPDVQQKTASG).

3.2.Primary Structures of the HMG-Box_ROX1-like Domains of theFull-Length MAT1-2-1 Proteins

Among the 74 MAT1-2-1 proteins listed in the AlphaFold database, 69 (93.2%) are full- length proteins, each of which contains 249 amino acid residues; these proteins contribute to 17 heteromorphic AlphaFold tertiary structure morphs belonging to 5 Bayesian clusters (Table S3) [50]. Among the 69 full-length proteins, 39 (56.5%) are 100% identical to therepresentative MAT1-2-1 protein AEH27625, which was derived from the *H. sinensis* strain CS2 (Table S3) [56]. The remaining 30 full-length proteins (43.5%) contain amino acidsubstitutions at various sites, as shown in red in Figure S2. The HMG-box_ROX1-likedomains of the MAT1-2-1 proteins are located at amino acid residues 127→197, as shown in blue and underlined in Figure S2, whereas the 9 external amino acid residues upstream and downstream of the domain are shown in blue but not underlined. The HMG-box_ROX1- like domain sequences of 3 of the 30 variable MAT1-2-1 proteins are 100% identical to the domain sequence of the query protein AEH27625, although the amino acid substitutionsoccur outside the functional domains, whereas the domains of the remaining 27 proteinscontain 1–3 amino acid substitutions at various sites inside and/or outside the functional domains, as shown in red in Figure S2.

The MAT1-2-1 proteins encoded by the genome assemblies ANOV01000063, LKHE01001605, LWBQ01000021, and NGJJ01000619 of the *H. sinensis* strains Co18, 1229,ZJB12195, and CC1406-20395, respectively, are shown in Figure S2 [49,59–61]. An S-to-A substitution occurred in each of the HMG-box_ROX1-like domains of the genome- encoded MAT1-2-1 proteins ANOV01000063 (9759→9851 & 9907→10,026), LKHE01001605 (14,016←14,135 & 14,191←14,283), LWBQ01000021 (239,029←239,148 & 239,204←239,269), and NGJJ01000619 (23,186←23,305 & 23,361←23,453). An additional Y-to-H substitution occurred in the HMG-box_ROX1-like domains of LKHE01001605, LWBQ01000021 and NGJJ01000619 but not in the HMG-box_ROX1-like domain of ANOV01000063, resultingin 97.2–98.6% similarity to the sequence of the HMG-box_ROX1-like domain of the query protein AEH27625 [56].

The genome assembly JAAVMX000000000 of the *H. sinensis* strain IOZ07 and the metatranscriptome assembly GAGW00000000 of the *C. sinensis* insect–fungal complex do not contain genes or transcripts encoding MAT1-2-1 proteins [62,63].

The protein sequences encoded by the MAT1-2-1 transcripts of the transcriptome assembly GCQL01020543 (397←1143) of the *H. sinensis* strain L0106 and the metatran- scriptome assembly OSIN7649 (1→747) of the mature *C. sinensis* insect–fungal complex are shown in Figure S2 [59,64]. The HMG-box_ROX1-like domains (553←765 of GCQL01020543 and 379→591 of OSIN7649) of these proteins contain Y-to-H substitutions, resulting in98.6% similarity to the sequence of that domain in the query protein AEH27625 [36].

3.3.Bayesian Analysis of the MATα_HMGbox Domains of the Full-Length MAT1-1-1 Proteins

The sequences of the MATα_HMGbox domains of 19 full-length MAT1-1-1 proteins that display various amino acid substitutions were subjected to Bayesian clustering analysis and compared with the sequences of 6 authentic MAT1-1-1

proteins as reference sequences (Figure 1). The MATα_HMGbox domains of the full-length MAT1-1-1 proteins were clustered into 5 Bayesian clusters (Figure 1), among which Clusters a and d were branched. The functional domains of the 19 proteins with various amino acid substitutions wereclustered into Clusters/Branches a2, b, d, and e1–e2 in the Bayesian clustering tree. Cluster d has a longer clustering distance than some of the other clusters, and Branch e2 has thelongest clustering distance.

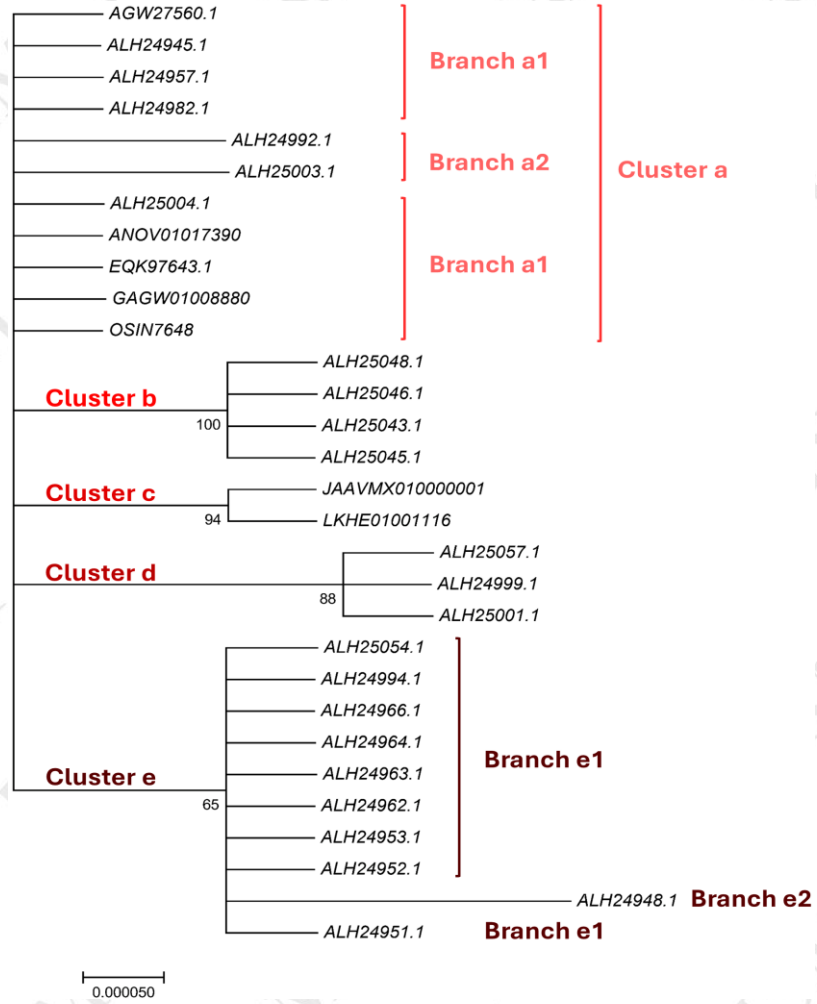

Figure 1. A Bayesian majority rule consensus clustering tree inferred using MrBayes v3.2.7 software for the MATα_HMGbox domain sequences of the 25 full-length MAT1-1-1 proteins of the wild-type *C. sinensis* isolates and the corresponding domain sequences encoded by the genome andmetatranscriptome assemblies of the *H. sinensis* strains and *C. sinensis* insect–fungal complexes.

The MATα_HMGbox domains encoded by the genome assemblies JAAVMX010000001 (6,699,061→6,699,153 & 6,699,203→6,699,637) and LKHE01001116 (4183←4620 & 4667←4759) of the *H. sinensis* strains 1229 and IOZ07 contain Y-to-M substitutions (Figure S1) [60,62]. The domains encoded by the genome assembly ANOV01017390 (794←1129 & 1280←1396) of *H. sinensis* strain Co18 and the metatranscriptome assembly OSIN7648 (151→675) of the *C. sinensis* insect–fungal complex contain no altered amino acid residues [49,64]. The domain encoded by the metatranscriptome assembly GAGW01008880 (714←1127) of the *C. sinensis* insect–fungal complex is truncated at the N-terminus (Figure S1) [63]. The MATα_HMGbox domains encoded by the genome assembly ANOV01017390 and metatranscriptome assemblies OSIN7648 and GAGW01008880 cluster into Branch a1 in the Bayesian clustering tree, together with the 6 authentic MAT1-1-1 proteins (Figure 1). Tables S6 and S7 summarize the amino acid substitutions

and deletions in the MATα_HMGbox domains of the MAT1-1-1 proteins derived from wild-type *C. sinen- sis* isolates and encoded by the genome and metatranscriptome assemblies of *H. sinensis* strains and *C. sinensis* insect–fungal complexes, respectively, which resulted in different Bayesian clustering results and changes in the predicted 3D structures under various AlphaFold codes.

3.4.Bayesian Analysis of the HMG-Box_ROX1-like Domains of the Full-Length MAT1-2-1 Protein Sequences

Thirty full-length MAT1-2-1 proteins that are present in wild-type *C. sinensis* isolates or encoded by the genome and transcriptome assemblies of *H. sinensis* strains and by the metatranscriptome assembly of the *C. sinensis* insect–fungal complex and that have various amino acid substitutions in their HMG-box_ROX1-like domains were subjected to Bayesian clustering analysis and compared with the HMG-box_ROX1-like domains of 6 authentic MAT1-2-1 proteins as references. Figure 2 shows 2 branched clusters (a and b). Branches b2–b3 have longer clustering distances than some of the other branches, and Branch b2βhas the longest clustering distance.

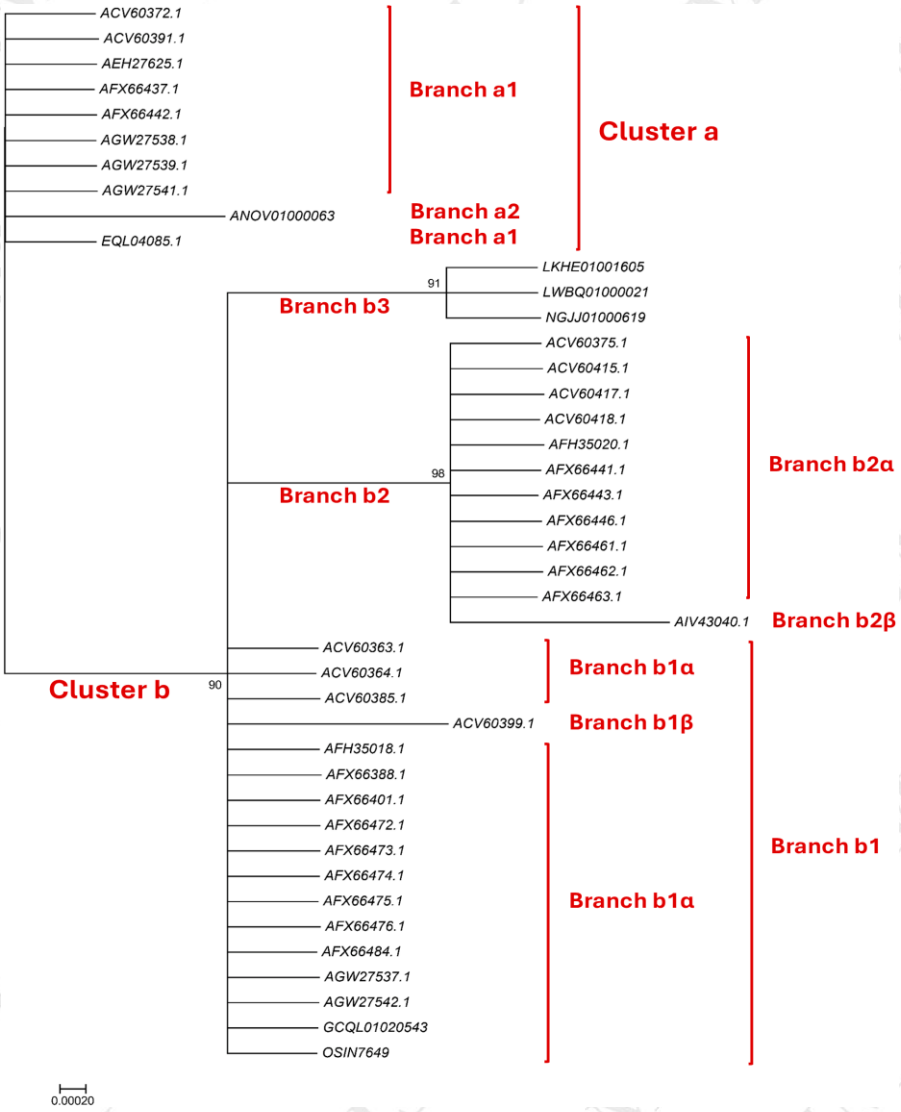

Figure 2. Bayesian majority rule consensus clustering tree inferred using MrBayes v3.2.7 software for the HMG-box_ROX1-like domain sequences of 35 full-length MAT1-2-1 proteins of the wild-type *C. sinensis* isolates and the corresponding domain segments of the translated genome, transcriptome,and metatranscriptome assemblies of the *H. sinensis* strains and *C. sinensis* insect–fungal complexes.

The HMG-box_ROX1-like domain encoded by the genome assembly ANOV01000063 (9759→9851 & 9907→10,026) of *H. sinensis* strain Co18 contains an S-to-A substitutionand is clustered into Branch a2 with a slightly longer clustering distance (Figure 2) [49].The domains encoded by other genome assemblies [LKHE01001605 (14,016←14,135 & 14,191←14,135 & 14,191←14,283), LWBQ01000021 (239,029←239,148 & 239,204←239,269), and NGJJ01000619 (23,186←23,305 & 23,361←23,453) of the *H. sinensis* strains 1229, ZJB12195, and CC1406-20395, respectively] [59–61] contain Y-to-H and S-to-A substitu-tions and are clustered into Branch b3 in the Bayesian clustering tree (Figure 2). TheHMG-box_ROX1-like domain of the MAT1-2-1 protein encoded by the transcriptomeassembly GCQL01020543 (553←765) of the *H. sinensis* strain L0106 contains a Y-to-H sub- stitution [58]. The domain of the MAT1-2-1 protein encoded by the metatranscriptomeassembly OSIN7649 (379→591) of the *C. sinensis* insect–fungal complex is 100% identical to that of the reference MAT1-2-1 protein AEH27625 [56,64]. The domains of the MAT1-2-1proteins encoded by the transcriptome and metatranscriptome assemblies were clustered into Branch b1α in the Bayesian clustering tree (Figure 2).

Tables S8 and S9 summarize the amino acid substitutions and deletions in the HMG- box_ROX1-like domains of MAT1-2-1 proteins derived from wild-type *C. sinensis* isolates and encoded by the genome, transcriptome, and metatranscriptome assemblies of *H.sinensis* strains and *C. sinensis* insect–fungal complexes, respectively, which resulted indifferent Bayesian clustering results and changes in the predicted 3D structures undervarious AlphaFold codes.

3.5.Heteromorphic Stereostructures of the MATα_HMGbox Domains of Full-Length MAT1-1-1 Proteins Derived from Wild-Type C. sinensis Isolates

Section 3.5 presents analyses of the correlations between the changes in the structure and hydrophobicity of the MATα_HMGbox domains of full-length MAT1-1-1 proteins(under 7 AlphaFold 3D structure codes; Table S6) derived from wild-type *C. sinensis*isolates compared with the reference MAT1-1-1 proteins represented by AGW27560 (under AlphaFold code U3N942) derived from the *H. sinensis* strain CS68-2-1229 (Table S2) [48].The MATα_HMGbox domain sequences (amino acid residues 51→225) were extendedby 9 amino acid residues both upstream and downstream of the domains because of thesetting of the sequential ExPASy ProtScale plotting for hydropathy, α-helices, β-sheets, β-turns, and coils at a window size of 9 amino acid residues (Section 2.5 of the Materialsand Methods).

Figure 3 compares the hydrophobicity and structure of the MATα_HMGbox domain of the mutant MAT1-1-1 protein ALH24992 (under AlphaFold code A0A0N9R5B3) derived from the wild-type *C. sinensis* isolate SC09_65 (Tables S2 and S6) [52] with those of theMATα_HMGbox domain of the reference protein AGW27560 (under AlphaFold code U3N942) derived from the *H. sinensis* strain CS68-2-1229 (Table S2) [48]. Panel (A) ofFigure 3 shows an A-to-T substitution (aliphatic alanine to threonine with polar side chains; hydropathy indices changed from 1.8 to −0.7). This substitution reduces the hydrophobicity (the larger the hydropathy value is, the stronger the hydrophobicity, whereas negative values indicate hydrophilicity [67]), as illustrated by the topological structure and waveform changes in the hydropathy plot shown in Panel (B). These changes alter the secondarystructure of the protein in the area surrounding the mutation site in the MATα_HMGbox domain of the mutant MAT1-1-1 protein ALH24992, as illustrated by the changes in thetopology and waveform in the ExPASy ProtScale plots for α-helices, β-sheets, β-turns, and coils shown in Panels C–F, respectively.

Panel A: Alignment of amino acid sequences

```
AGW27560 42   ADVLTPVSTAAASRATRQTKEASCDRAKRPLNAFMAFRSYYLKLFPDVQQKTASGFLTTL 101
ALH24992 42   ---------T---------------------------------------------------- 101

AGW27560 102 WHKDPFRNKWALIAKVYSFVRDQIGKDKVSLSYFMSLACPTMTIIEPAAYLNALGWCVQD 161
ALH24992 102 ------------------------------------------------------------ 161

AGW27560 162 DDAGSQKLFQDESSANLDQSSLLSAEYPSTEIELLSALVNIGYFPDHGADLVERMGSSHS 221
ALH24992 162 ------------------------------------------------------------ 221

AGW27560 222 GIMAPRAANCTPP                                                 234
ALH24992 222 -------------                                                 234
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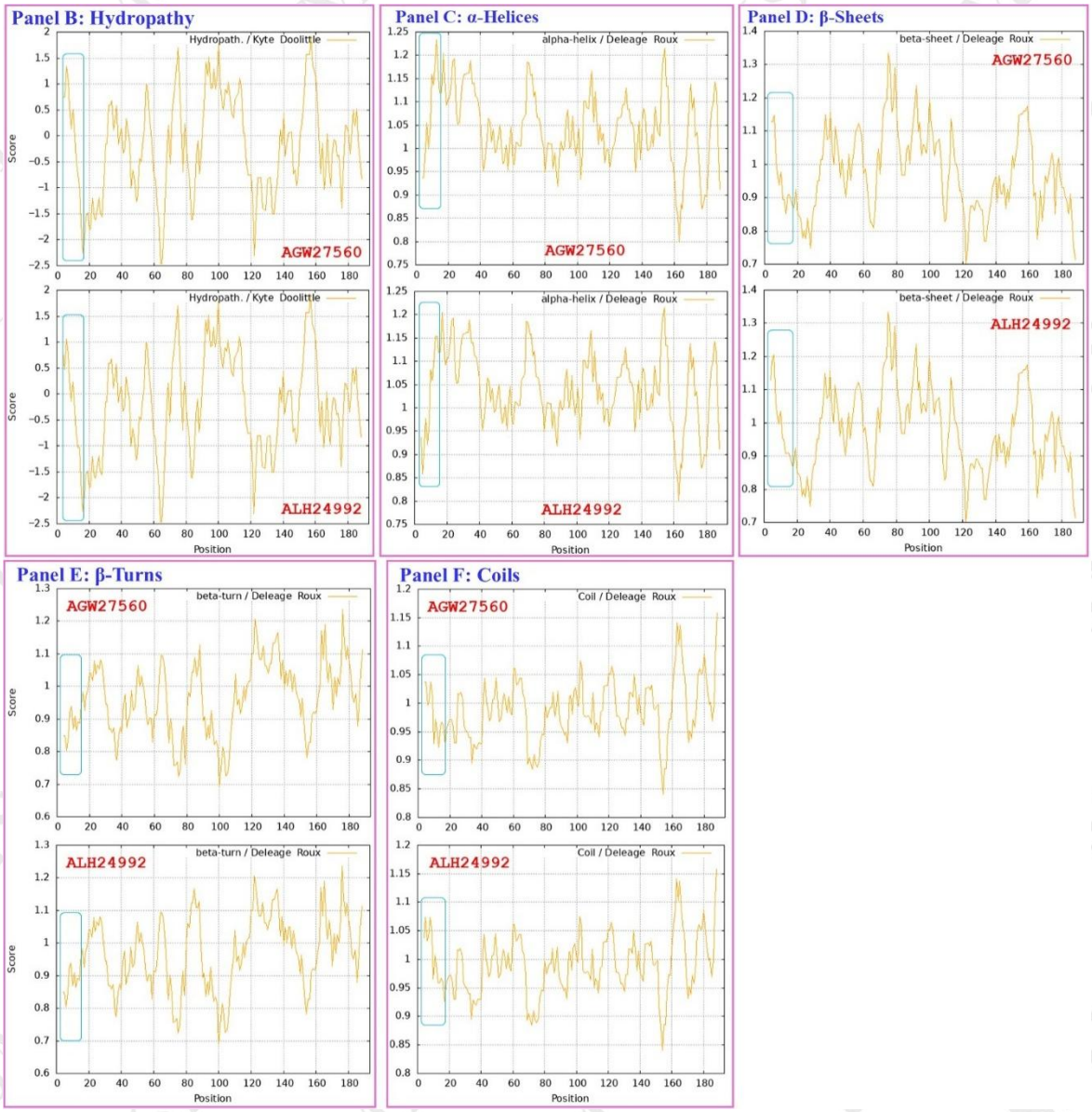

Figure 3. *Cont*.

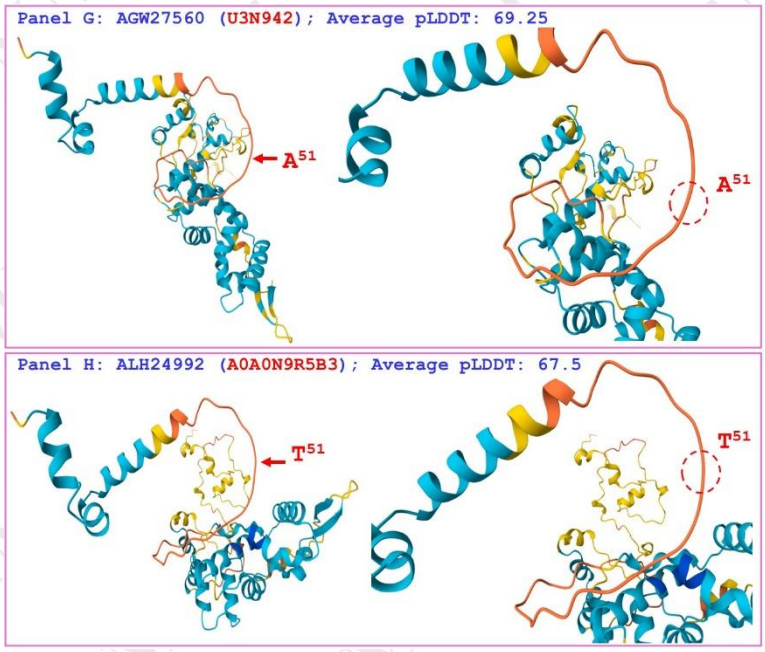

Figure 3. Correlations of the changes in hydrophobicity and the primary, secondary, and tertiary structures of the MATα_HMGbox domains of the reference MAT1-1-1 protein AGW27560 derived from the *H. sinensis* strain CS68-2-1229 [48] and the variant MAT1-1-1 protein ALH24992 derived from the wild-type *C. sinensis* isolate SC09_65. Panel (**A**) shows the alignment of the amino acid sequences of the MATα_HMGbox domains of the proteins; the amino acid substitution is shown in red, whereas the hyphens indicate identical amino acid residues. The ExPASy ProtScale plots show the changes in hydrophobicity (Panel (**B**)) and in the 2D structures (Panels (**C**–**F**) for α-helices, β-sheets, β-turns, and coils, respectively) of the proteins; the open blue rectangles highlight the topological structure and waveform changes of the ExPASy plots. Panels (**G**,**H**) show the 3D structures of the full-length proteins on the left and the locally magnified structures surrounding the mutation site on the right. The model confidence values for the AlphaFold-predicted 3D structures are as follows: ☐ very high (pLDDT > 90); ☐ high (90 > pLDDT > 70); ☐ low (70 > pLDDT > 50); and ☐ very low (pLDDT < 50).

As shown in Panels (G and H) of Figure 3, which illustrate the 3D structures of the proteins, the substitution is located upstream of the core structure of 3 α-helices and may not directly participate in stabilizing the hydrophobic core structure of the DNA-binding domain [84,85]. However, the replacement of alanine with a threonine residue with reduced hydrophobicity altered the stereostructure of the MATα_HMGbox domain of the MAT1-1-1 protein ALH24992 under AlphaFold code A0A0N9R5B3, possibly through long-range spatial interactions. The variant MATα_HMGbox domain clustered into Branch a2 in the Bayesian clustering tree (Figure 1, Table S6).

Figure 4 compares the hydrophobicity and structure of the MATα_HMGbox domain of the MAT1-1-1 protein ALH24948 (AlphaFold code A0A0N9QUF3) derived from the wild-type *C. sinensis* isolate GS09_143 (Table S2) [52] with those of the MATα_HMGbox domain of the reference protein AGW27560 (AlphaFold code U3N942) derived from the

H. sinensis strain CS68-2-1229 (Table S2) [48]. Panel (A) of Figure 4 shows substitutions of two adjacent residues, Q-to-S (glutamine to serine, both of which have polar side chains; hydropathy indices changed from −3.5 to −0.8 [67]) and I-

to-F (aliphatic isoleucine to aro- matic phenylalanine; hydropathy indices changed from 4.5 to 2.8), causing bidirectionally changed hydrophobicity, as illustrated by the topological structure and waveform changes in the hydropathy plot in Panel (B). These changes alter the secondary structure surround- ing the mutation sites in the MATα_HMGbox domain, as illustrated by the topologicalstructure and waveform changes in the ExPASy ProtScale plots for α-helices, β-sheets,β-turns, and coils shown in Panels (C–F). As shown in the diagrams of the 3D structuresin Panels (G and H), the adjacent amino acid substitutions are located at the end of oneof the 3 α-helices that form the hydrophobic core stereostructure [84,85], and they alterthe tertiary structure of the MATα_HMGbox domain of the variant protein ALH24948 under AlphaFold code A0A0N9QUF3. The variant MATα_HMGbox domain clustered into Branch e2 in the Bayesian clustering tree (Figure 1, Table S6).

Panel A: Amino acid sequence alignment

```
AGW27560 42  ADVLTPVSTAAASRATRQTKEASCDRAKRPLNAFMAFRSYYLKLFPDVQQKTASGFLTTL 101
ALH24948 42  ------------------------------------------------------------ 101

AGW27560 102 WHKDPFRNKWALIAKVYSFVRDQIGKDKVSLSYFMSLACPTMTIIEPAAYLNALGWCVQD 161
ALH24948 102 ----------------------SF------------------------------------ 161

AGW27560 162 DDAGSQKLFQDESSANLDQSSLLSAEYPSTEIELLSALVNIGYFPDHGADLVERMGSSHS 221
ALH24948 162 ------------------------------------------------------------ 221

AGW27560 222 GIMAPRAANCTPP                                                 234
ALH24948 222 -------------                                                 234
```

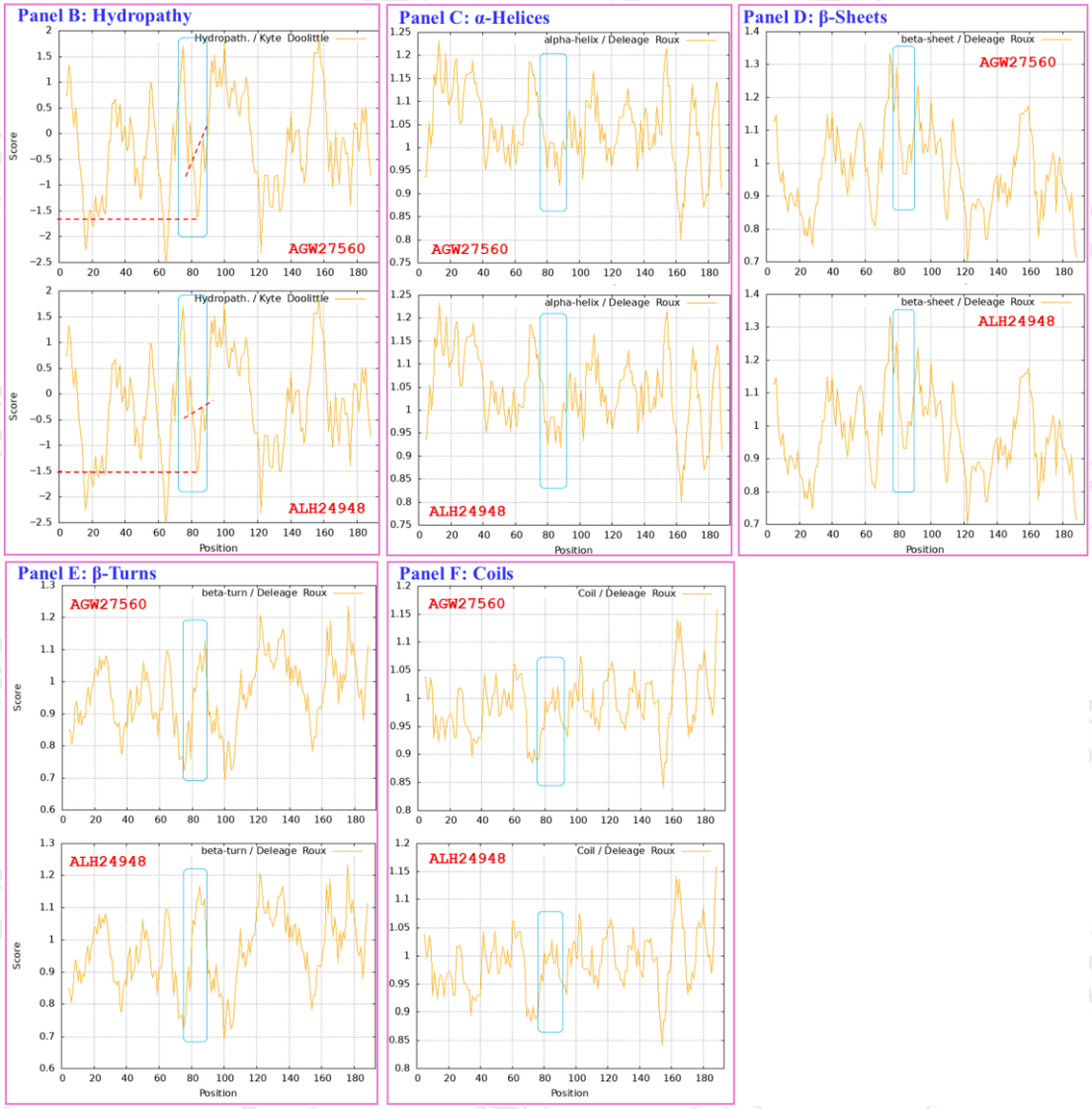

Figure 4. *Cont*.

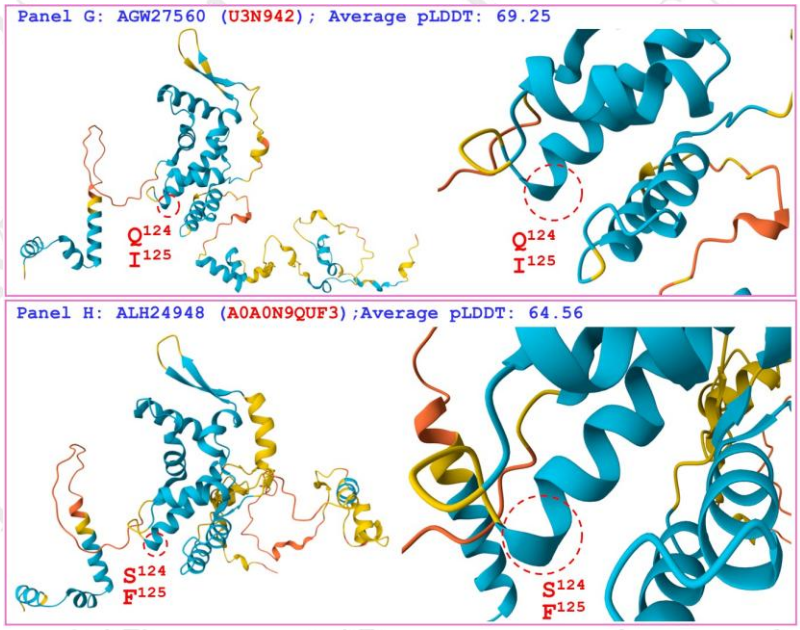

Figure 4. Correlations among the changes in the primary, secondary, and tertiary structures of the MATα_HMGbox domains of the reference MAT1-1-1 protein AGW27560 derived from the *H. sinensis* strain CS68-2-1229 [48] and the variant MAT1-1-1 protein ALH24948 derived from the wild-type *C. sinensis* isolate GS09_143. Panel (**A**) shows an alignment of the MATα_HMGbox domain sequences of the proteins; amino acid substitutions are shown in red, whereas the hyphens indicate identical amino acid residues. The ExPASy ProtScale plots show the changes in hydrophobicity (Panel (**B**))and in the 2D structures (Panels (**C**–**F**) for α-helices, β-sheets, β-turns, and coils, respectively) of the proteins; the open blue rectangles highlight the topological structure and waveform changes shown in the ExPASy plots. Panels (**G**,**H**) show the 3D structures of the full-length proteins on the left and the locally magnified structures at the substitution sites on the right. The model confidence valuesfor the AlphaFold-predicted 3D structures are as follows: □ very high (pLDDT > 90); □ high (90 > pLDDT > 70); □ low (70 > pLDDT > 50); and □ very low (pLDDT < 50).

Figure 5 compares the hydrophobicity and the structures of the MATα_HMGbox domains of the MAT1-1-1 proteins ALH25043, ALH25045, ALH25046, and ALH25048(AlphaFold code A0A0N9QMS9) derived from the wild-type *C. sinensis* isolates YN09_22, YN09_51, YN09_6, and YN09_64, respectively (Table S2) [52], with those of theMATα_HMGbox domain of the reference protein AGW27560 (AlphaFold code U3N942)derived from the *H. sinensis* strain CS68-2-1229 (Table S2) [48]. Panel (A) of Figure 5 shows substitutions of R-to-I (basic arginine to aliphatic isoleucine; hydropathy indices changed from −4.5 to 4.5 [67]) and P-to-T (proline to threonine, both of which possess polar neutral side chains; hydropathy indices changed from −1.6 to −0.7). These substitutions resultin increased hydrophobicity, as illustrated by the topological structure and waveformchanges that are apparent in the hydropathy plot in Panel (B). They also alter the secondary structure surrounding the mutation sites in the MATα_HMGbox domains of the MAT1-1-1 proteins ALH25043, ALH25045, ALH25046, and ALH25048, as illustrated by the topolog- ical structure and waveform changes shown in the ExPASy ProtScale plots for α-helices,β-sheets, β-turns, and coils in Panels (C–F). As shown in the diagrams of the 3Dstructure in Panels (G and H), the sites of the R-to-I and P-to-T substitutions are inside and outside, respectively, the hydrophobic core formed by the 3 α-helices, and the substantial increase in hydrophobicity alters the tertiary structures of the MATα_HMGbox domains of theMAT1-1-1 proteins under AlphaFold code A0A0N9QMS9. The variant

MATα_HMGboxdomain clustered into Cluster 2 in the Bayesian clustering tree (Figure 1, Table S6).

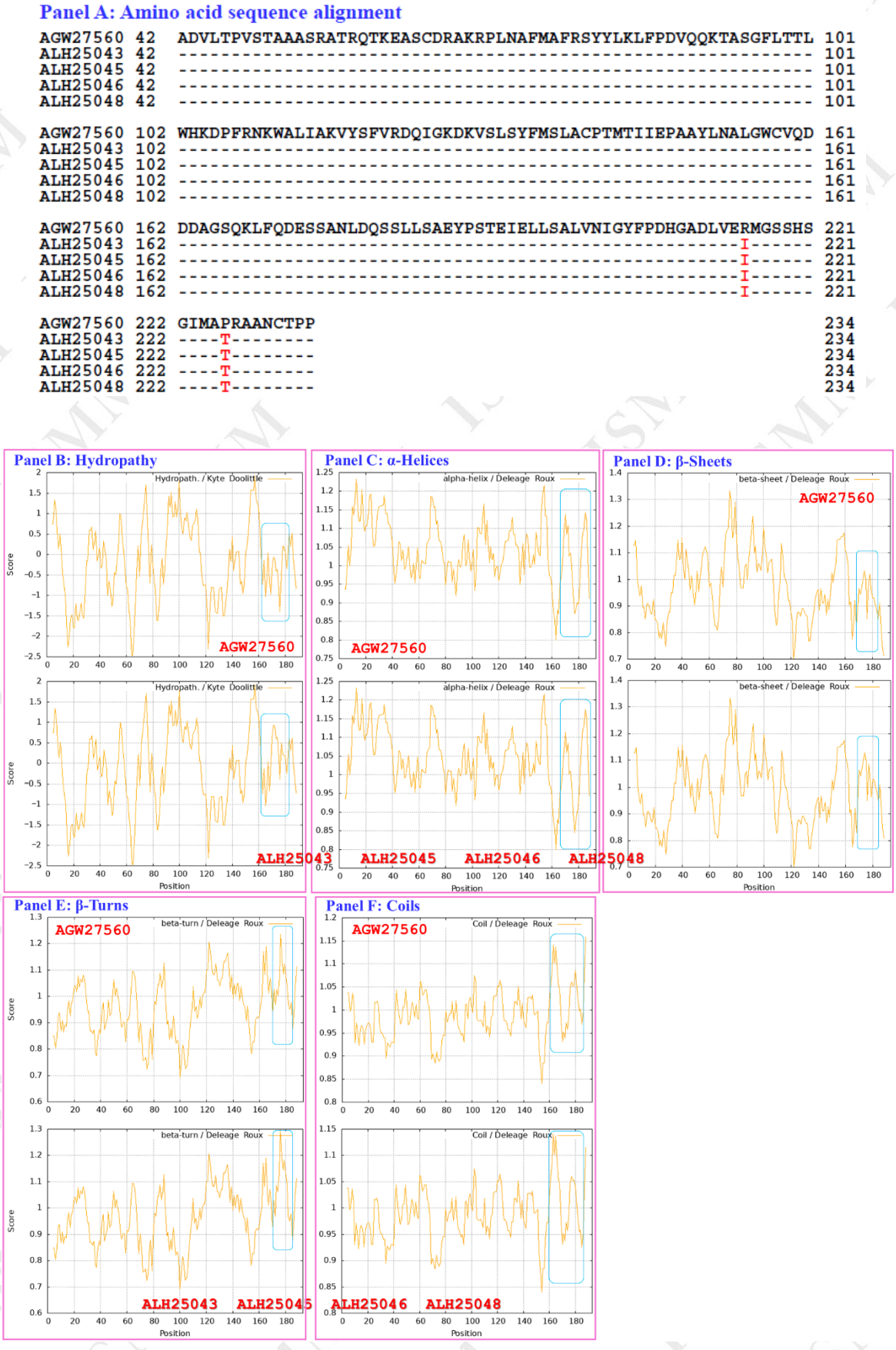

Figure 5. *Cont*.

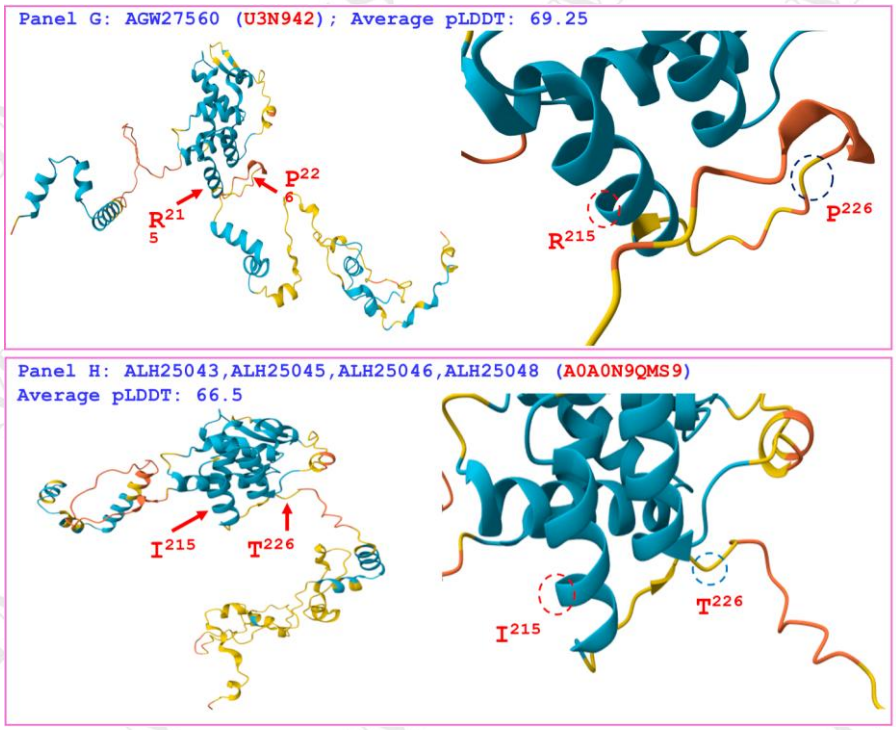

Figure 5. Correlations of changes in the primary, secondary, and tertiary structures of the MATα_HMGbox domains of the reference MAT1-1-1 protein AGW27560 derived from the *H. sinensis* strain CS68-2-1229 [48], and the variant MAT1-1-1 proteins ALH25043, ALH25045, ALH25046, and ALH25048 derived from the wild-type *C. sinensis* isolates YN09_22, YN09_51, YN09_6, and YN09_64, respectively. Panel (**A**) shows an alignment of the amino acid sequences of the MATα_HMGboxdomains of the proteins; amino acid substitutions are shown in red, whereas the hyphens indicate identical amino acid residues. The ExPASy ProtScale plots show the changes in hydrophobicity (Panel (**B**)) and in the 2D structures (Panels (**C**–**F**) for α-helices, β-sheets, β-turns, and coils, respectively) of the proteins; the open blue rectangles highlight the topological structure and waveform changes of the plots. Panels (**G**,**H**) show the 3D structures of the full-length proteins on the left and thelocally magnified structures at the substitution sites on the right. The model confidence values for the AlphaFold-predicted 3D structures are as follows: ☐ very high (pLDDT > 90); ☐ high (90 > pLDDT > 70); ☐ low (70 > pLDDT > 50); and ☐ very low (pLDDT < 50).

Figure 6 compares the hydrophobicity and structures of the MATα_HMGbox do- mains of the MAT1-1-1 proteins ALH25054, ALH24951, ALH24952, ALH24953, ALH24962, ALH24963, ALH24964, ALH24966, and ALH24994 (AlphaFold code A0A0N7G845) derived from the wild-type *C. sinensis* isolates GS09_311, GS09_229, GS09_281, GS10_1, QH09_164, QH09_173, QH09_201, QH09_210, and SC09_87, respectively (Table S2) [52], with those of the reference protein AGW27560 (AlphaFold code U3N942) derived from the *H. sinensis* strain CS68-2-1229 (Table S2) [48]. Panel (A) of Figure 6 shows I-to-L substitutions (aliphatic isoleucine to aliphatic leucine, hydropathy indices changed from 4.5 to 3.8 [67]); these sub- stitutions resulted in reduced hydrophobicity, as illustrated by the topological structure and waveform changes shown in the hydropathy plot in Panel (B). As shown in Panels (C–F), the secondary structure of the proteins near the mutation sites in the MATα_HMGbox do- mains of the MAT1-1-1 proteins ALH25054, ALH24951, ALH24952, ALH24953, ALH24962, ALH24963, ALH24964, ALH24966, and ALH24994 (Table S2) was altered, as illustratedby the topological structure and waveform changes in the ExPASy ProtScale plots for α-helices, β-sheets, β-turns, and coils, respectively. As shown in the representations of the 3D structures presented in Panels (G and H), the substituted amino acid residues are located within the core structures of the 3 α-helices, and they destabilize the hydrophobic core of the protein [84,85],

altering the tertiary structures of the MATα_HMGbox domains of the MAT1-1-1 proteins under AlphaFold code A0A0N7G845, which cluster into Branch e1 in the Bayesian clustering tree (Figure 1, TableS6).

Panel A: Amino acid sequence alignment

```
AGW27560  42  ADVLTPVSTAAASRATRQTKEASCDRAKRPLNAFMAFRSYYLKLFPDVQQKTASGFLTTL  101
ALH25054  42  ------------------------------------------------------------  101
ALH24951  42  ------------------------------------------------------------  101
ALH24952  42  ------------------------------------------------------------  101
ALH24953  42  ------------------------------------------------------------  101
ALH24962  42  ------------------------------------------------------------  101
ALH24963  42  ------------------------------------------------------------  101
ALH24964  42  ------------------------------------------------------------  101
ALH24966  42  ------------------------------------------------------------  101
ALH24994  42  ------------------------------------------------------------  101

AGW27560  102 WHKDPFRNKWALIAKVYSFVRDQIGKDKVSLSYFMSLACPTMTIIEPAAYLNALGWCVQD  161
ALH25054  102 ----------------------L-------------------------------------  161
ALH24951  102 ----------------------L-------------------------------------  161
ALH24952  102 ----------------------L-------------------------------------  161
ALH24953  102 ----------------------L-------------------------------------  161
ALH24962  102 ----------------------L-------------------------------------  161
ALH24963  102 ----------------------L-------------------------------------  161
ALH24964  102 ----------------------L-------------------------------------  161
ALH24966  102 ----------------------L-------------------------------------  161
ALH24994  102 ----------------------L-------------------------------------  161

AGW27560  162 DDAGSQKLFQDESSANLDQSSLLSAEYPSTEIELLSALVNIGYFPDHGADLVERMGSSHS  221
ALH25054  162 ------------------------------------------------------------  221
ALH24951  162 ------------------------------------------------------------  221
ALH24952  162 ------------------------------------------------------------  221
ALH24953  162 ------------------------------------------------------------  221
ALH24962  162 ------------------------------------------------------------  221
ALH24963  162 ------------------------------------------------------------  221
ALH24964  162 ------------------------------------------------------------  221
ALH24966  162 ------------------------------------------------------------  221
ALH24994  162 ------------------------------------------------------------  221

AGW27560  222 GIMAPRAANCTPP                                                 234
ALH25054  222 ------------                                                 234
ALH24951  222 ------------                                                 234
ALH24952  222 ------------                                                 234
ALH24953  222 ------------                                                 234
ALH24962  222 ------------                                                 234
ALH24963  222 ------------                                                 234
ALH24964  222 ------------                                                 234
ALH24966  222 ------------                                                 234
ALH24994  222 ------------                                                 234
```

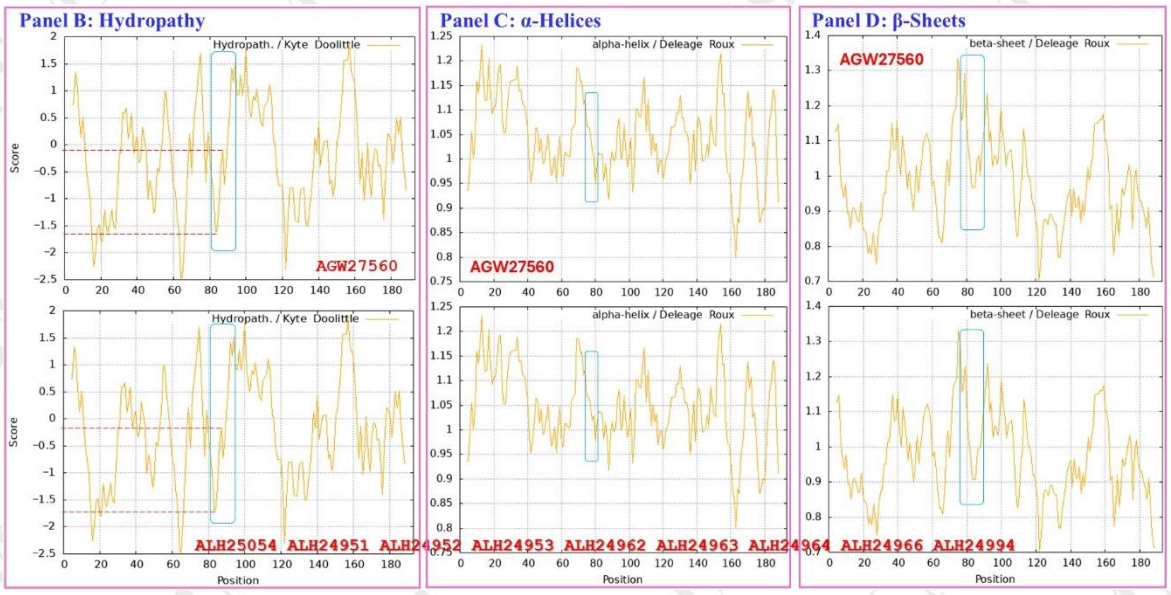

Figure 6. *Cont*.

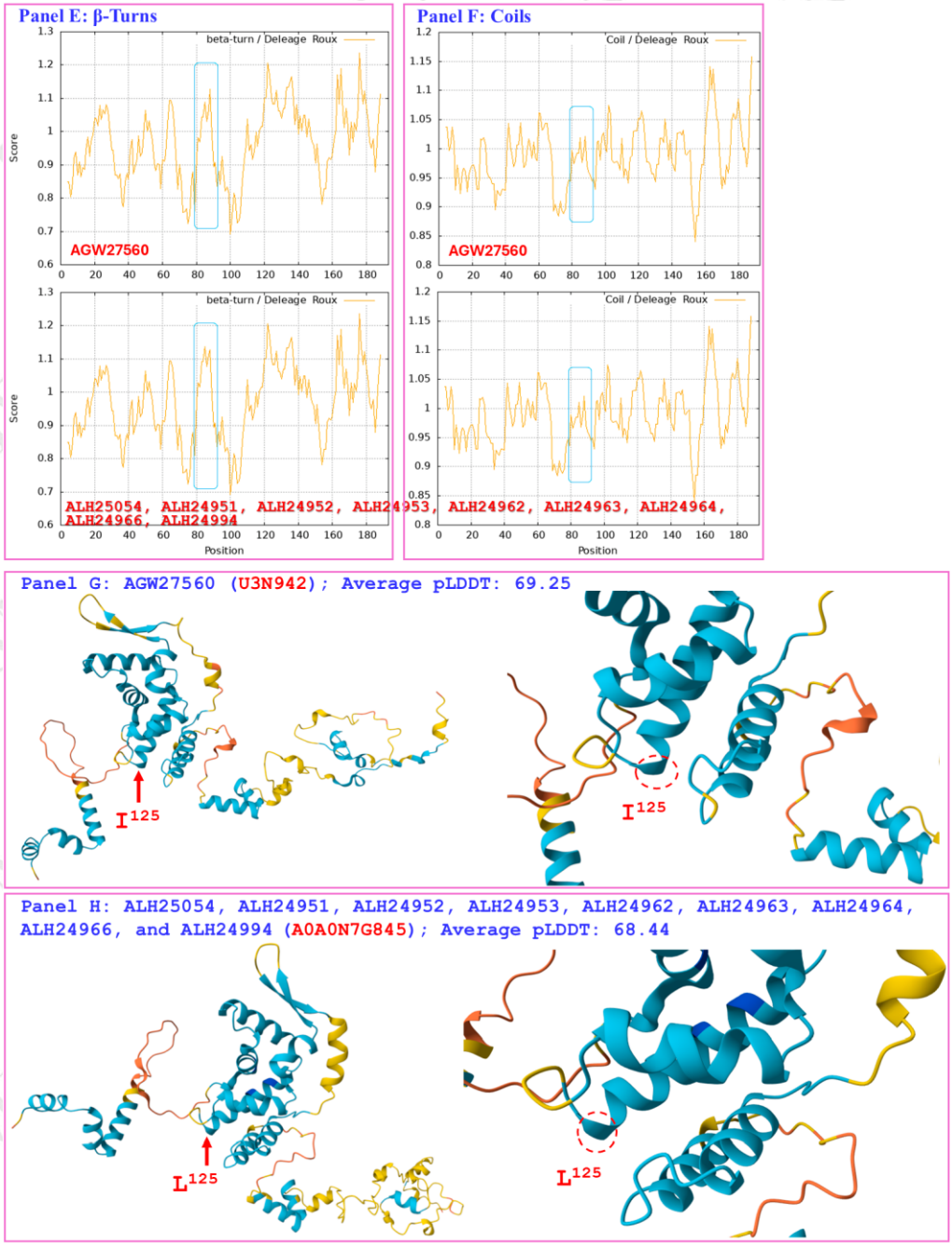

Figure 6. Correlations of changes in the primary, secondary, and tertiary structures of the MATα_HMGbox domains in the reference MAT1-1-1 protein AGW27560 derived from the *H. sinen- sis* strain CS68-2-1229 [48], and the mutant MAT1-1-1 proteins ALH25054, ALH24951, ALH24952,ALH24953, ALH24962, ALH24963, ALH24964, ALH24966, and ALH24994 derived from the wild-

type *C. sinensis* isolates GS09_311, GS09_229, GS09_281, GS10_1, QH09_164, QH09_173, QH09_201, QH09_210, and SC09_87, respectively. Panel (**A**) shows the alignment of the amino acid sequences of the MATα_HMGbox domains of the proteins; amino acid substitutions are shown in red, whereasthe hyphens indicate identical amino acid residues. The ExPASy ProtScale plots show the changes in hydrophobicity (Panel (**B**)) and in the 2D structures (Panels (**C**–**F**) for α-helices, β-sheets, β-turns,and coils, respectively) of the proteins; the open blue rectangles highlight the topological structureand waveform changes shown in the plots. Panels (**G**,**H**) show the 3D structures of the full-lengthproteins on the left and the locally magnified structures at the substitution sites on the right. Themodel confidence values for

the AlphaFold-predicted 3D structures are as follows: ☐ very high (pLDDT > 90); ☐ high (90 > pLDDT > 70); ☐ low (70 > pLDDT > 50); and ☐ very low (pLDDT < 50).

Figure 7 shows the hydrophobicity and structures of the MATα_HMGbox domains of the MAT1-1-1 proteins ALH24999 and ALH25057 (AlphaFold code A0A0N9QMT4)and the MAT1-1-1 protein ALH25001 (AlphaFold code A0A0N9R4Q4) derived from thewild-type *C. sinensis* isolates XZ07_H2, XZ12_16, and XZ05_2, respectively (Table S2) [52], compared with the reference protein AGW27560 (AlphaFold code U3N942) derivedfrom the *H. sinensis* strain CS68-2-1229 (Table S2) [48]. Panel (A) of Figure 7 shows A-to-V(aliphatic alanine to aliphatic valine; hydropathy indices changed from 1.8 to 4.2 [67]) and A-to-T (aliphatic isoleucine to threonine, an amino acid that contains polar neutral sidechains; hydropathy indices changed from 1.8 to −0.7) substitutions. These substitutionsaltered the hydrophobicity of the protein, as illustrated by the topological structure andwaveform changes shown in the hydropathy plot in Panel (B). These changes altered thesecondary structure surrounding the mutation sites in the MATα_HMGbox domain of the MAT1-1-1 proteins ALH24999, ALH25057, and ALH25001, as illustrated by the topological structure and waveform changes in the ExPASy ProtScale plots for α-helices, β-sheets,β-turns, and coils shown in Panels (C–F), respectively. As shown in the 3D structurespresented in Panels (G–I), the mutation sites are located upstream of the hydrophobic core structure of 3 α-helices in the MATα_HMGbox domains, and mutations at these sites alter the tertiary structures of the MATα_HMGbox domains of MAT1-1-1 proteins underAlphaFold codes A0A0N9QMT4 and A0A0N9R4Q4, which are clustered into Cluster d in the Bayesian clustering tree (Figure 1, TableS6).

Panel A: Amino acid sequence alignment

```
AGW27560 42  ADVLTPVSTAAASRATRQTKEASCDRAKRPLNAFMAFRSYYLKLFPDVQQKTASGFLTTL 101
ALH24999 42  ---------V----T---------------------------------------------- 101
ALH25057 42  ---------V----T---------------------------------------------- 101
ALH25001 42  ---------V----T---------------------------------------------- 101

AGW27560 102 WHKDPFRNKWALIAKVYSFVRDQIGKDKVSLSYFMSLACPTMTIIEPAAYLNALGWCVQD 161
ALH24999 102 ------------------------------------------------------------ 161
ALH25057 102 ------------------------------------------------------------ 161
ALH25001 102 ------------------------------------------------------------ 161

AGW27560 162 DDAGSQKLFQDESSANLDQSSLLSAEYPSTEIELLSALVNIGYFPDHGADLVERMGSSHS 221
ALH24999 162 ------------------------------------------------------------ 221
ALH25057 162 ------------------------------------------------------------ 221
ALH25001 162 ------------------------------------------------------------ 221

AGW27560 222 GIMAPRAANCTPP                                                 234
ALH24999 222 -------------                                                 234
ALH25057 222 -------------                                                 234
ALH25001 222 -------------                                                 234
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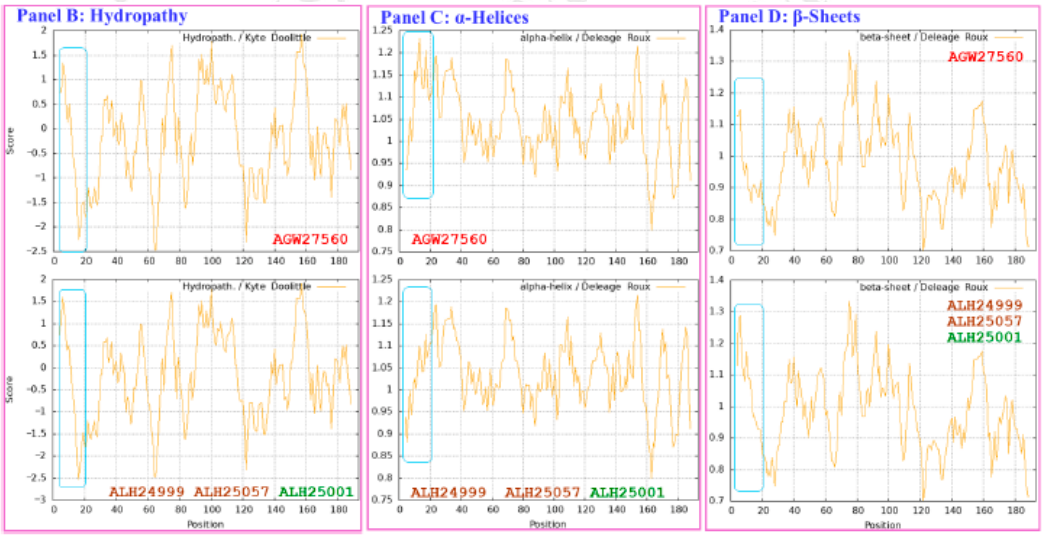

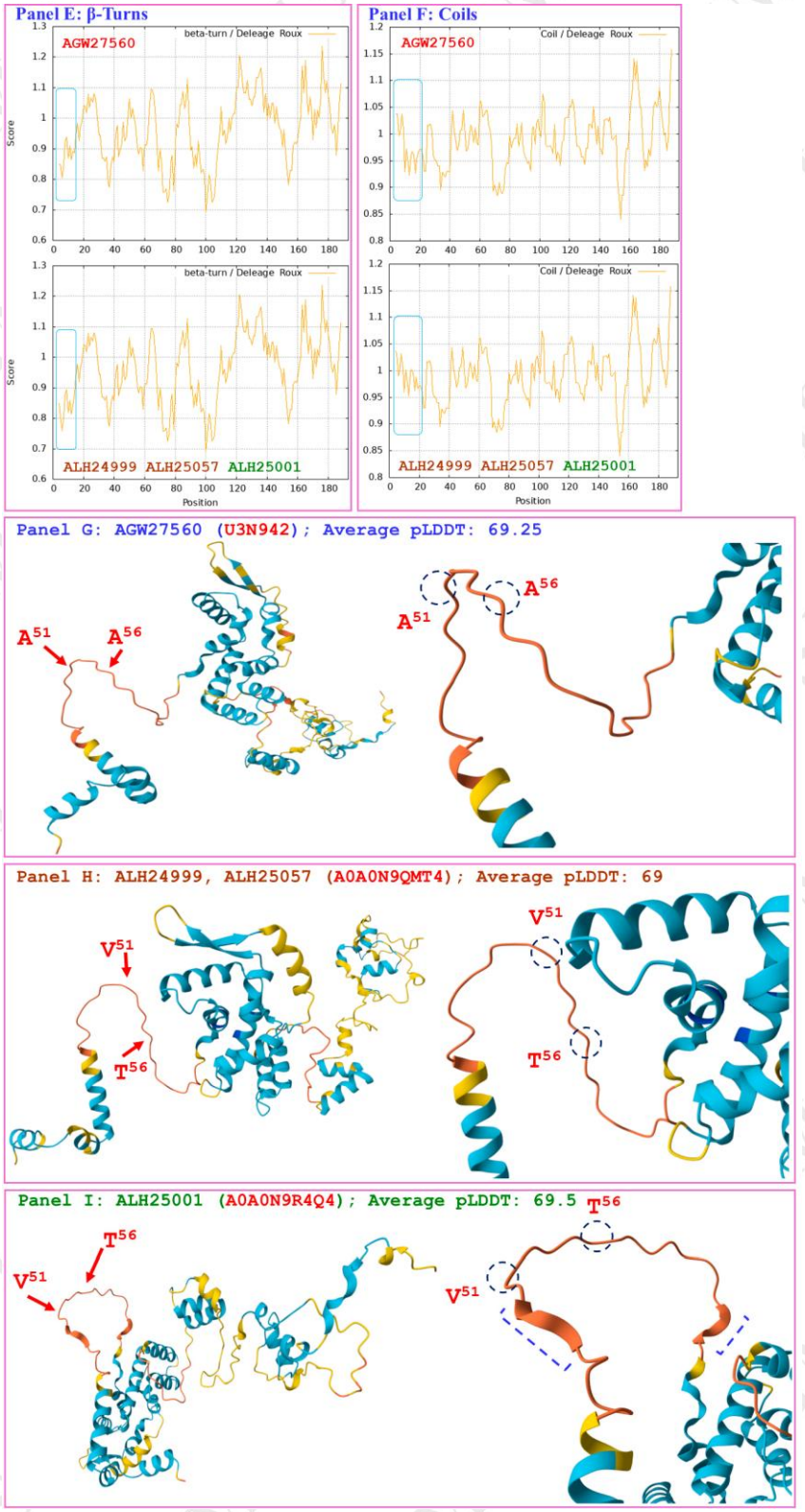

Figure 7. Correlations of the changes in the primary, secondary, and tertiary structures of the MATα_HMGbox domains in the reference MAT1-1-1 protein AGW27560 derived from the *H. sinensis* strain CS68-2-1229 [48], the mutant MAT1-1-1 proteins ALH24999 and ALH25057 (AlphaFold code A0A0N9QMT4), and the protein ALH25001 (AlphaFold code A0A0N9R4Q4) derived from the wild- type *C. sinensis* isolates XZ07_H2, XZ12_16, and XZ05_2, respectively. Panel (**A**) shows an alignment of the amino acid sequences of the MATα_HMGbox domains of the proteins; amino acid substitutions are shown in red; the sequences displayed in brown and green represent the MAT1-1-1 proteins under the AlphaFold codes A0A0N9QMT4 and A0A0N9R4Q4, respectively; and the hyphens indicate identical amino acid

residues. The ExPASy ProtScale plots show the changes in hydrophobicity (Panel (**B**)) and in the 2D structures (Panels (**C**–**F**), which display the α-helices, β-sheets, β-turns, and coils, respectively) of the proteins. The open blue rectangles highlight the topological structure and waveform changes shown in the plots. Panels (**G**–**I**) show the 3D structures of the full-length proteins on the left and the locally magnified structures at the substitution sites on the right. The model confidence values for the AlphaFold-predicted 3D structures are as follows: ☐ very high (pLDDT > 90); ☐ high (90 > pLDDT > 70); ☐ low (70 > pLDDT > 50); and ☐ very low (pLDDT < 50).

Although Panel (A) of Figure 7 shows the same substitutions of A-to-V and A-to- T in the MATα_HMGbox domains of the variant proteins ALH24999, ALH25057, andALH25001 [52], Panels (H and I) show different tertiary structures for the MATα_HMGbox domains of the MAT1-1-1 protein variants under the AlphaFold codes A0A0N9QMT4 and A0A0N9R4Q4. Specifically, the protein ALH25001 contains 2 short β-sheet structures upstream and downstream of the mutation sites in the MATα_HMGbox domain shownin Panel (I); these structures are marked with dashed half brackets in blue. In contrast,the distinct tertiary structures of the mutant proteins ALH24999 and ALH25057 withoutsimilar β-sheet structures are shown in Panel (H).

Figure 8 compares the hydrophobicity and structures of the MATα_HMGbox domain of the MAT1-1-1 protein ALH25003 (AlphaFold code A0A0N7G850) derived from the wild- type *C. sinensis* isolate XZ05_6 (Table S2) [52] with those of the reference protein AGW27560 (AlphaFold code U3N942) derived from the *H. sinensis* strain CS68-2-1229 (Table S2) [48]. Panel (A) of Figure 8 shows an S-to-G substitution (serine, which has polar neutral sidechains, is replaced by the unique amino acid glycine; hydropathy indices changed from −0.8 to −0.4 [67]). This substitution resulted in a slight increase in hydrophobicity, as illustrated by the topological structure and waveform changes shown in the hydropathyplot in Panel (B). These changes altered the secondary structure of the mutant MAT1-1-1protein ALH25003 in the region surrounding the mutation site in the MATα_HMGboxdomain, as illustrated by the topological structure and waveform changes in the ExPASyProtScale plots for α-helices, β-sheets, β-turns, and coils shown in Panels (C–F). As shown in the representations of the 3D structures of the proteins in Panels (G and H), the aminoacid residue (serine), which is located at the end of one of the 3 α-helices that form the hy- drophobic core structure of the MATα_HMGbox domain [84,85], was replaced by glycine, which became the first residue after the α-helix in the domain. This single-residue substitu- tion plus additional E-to-K and Y-to-H substitutions downstream of the MATα_HMGbox domain (Figure S1) significantly altered the tertiary structure of the protein ALH25003under the unique AlphaFold code A0A0N7G850. The mutant MATα_HMGbox domainclustered into Branch a2 in the Bayesian clustering tree (Figure 1, Table S6).

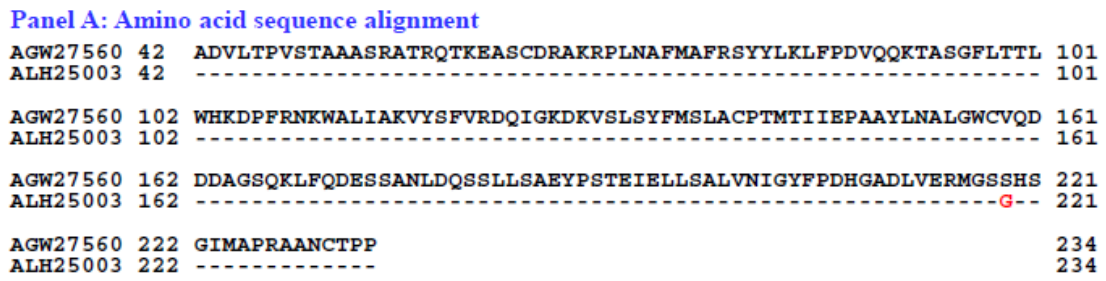

Figure 8. *Cont*.

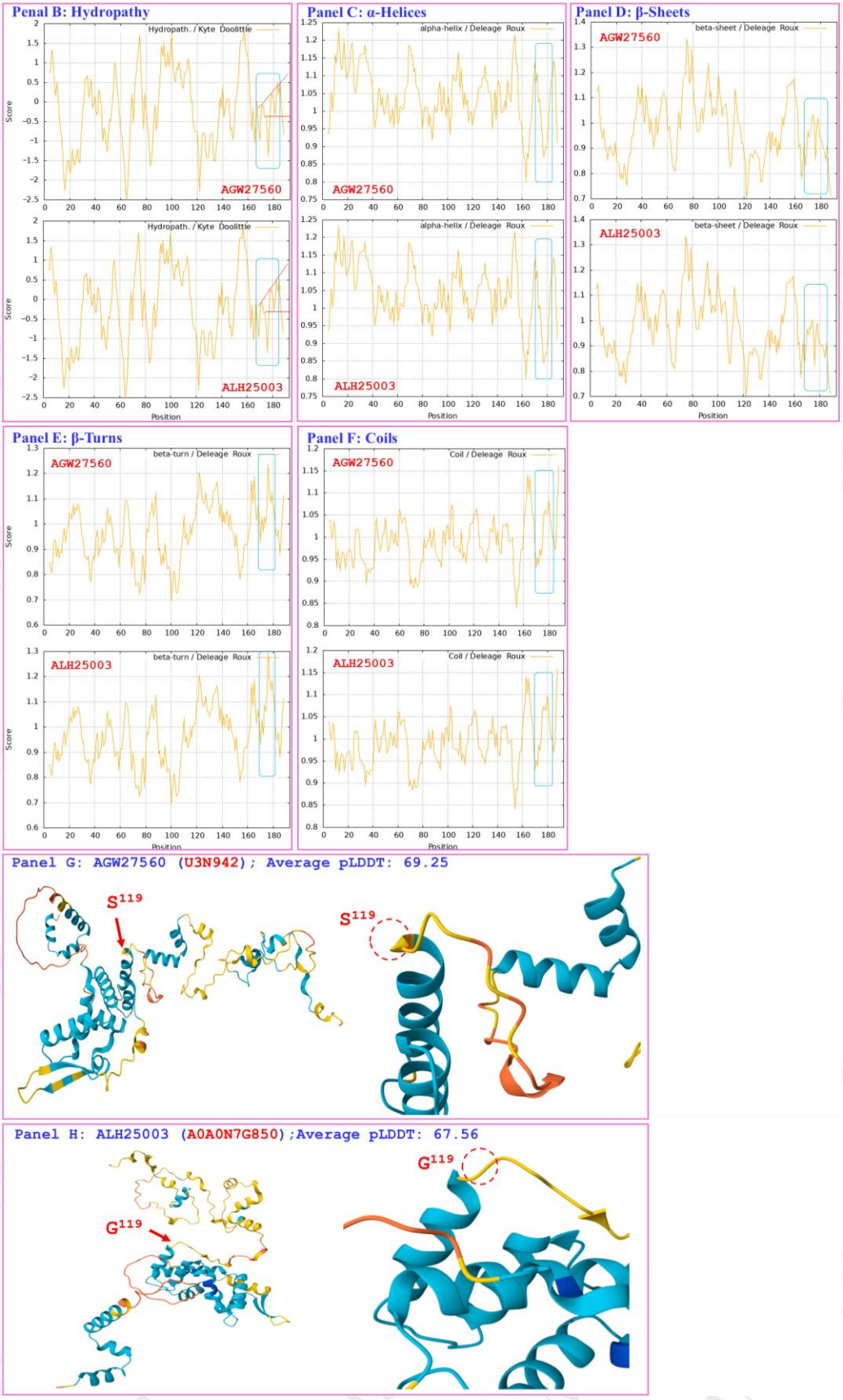

Figure 8. Correlations of the changes in the primary, secondary, and tertiary structures of the MATα_HMGbox domains of the reference MAT1-1-1 protein AGW27560 derived from the *H. sinensis* strain CS68-2-1229 [48] and the mutant MAT1-1-1 protein ALH25003 derived from the wild-type *C. sinensis* isolate XZ05_6. Panel (**A**) shows an alignment of the amino acid sequences of theMATα_HMGbox domains of the MAT1-1-1 proteins; the amino acid

substitution is shown in red,whereas the hyphens indicate identical amino acid residues. The ExPASy ProtScale plots show thechanges in the hydrophobicity (Panel (**B**)) and in the 2D structures (Panels (**C**–**F**) for the α-helices,β-sheets, β-turns, and coils, respectively) of the proteins, and the open blue rectangles highlight the topological structure and waveform changes shown in the plots. Panels (**G**,**H**) show the 3D structures of the full-length proteins on the left and the locally magnified structures at the substitution sites on the right. The model confidence values for the AlphaFold-predicted 3D structures are as follows: ☐ very high (pLDDT > 90); ☐ high (90 > pLDDT > 70); ☐ low (70 > pLDDT > 50); and ☐ very low (pLDDT < 50).

Aggregating the data presented in Section 3.5, Panel (A) in Figures 3–8 depicts the 1–2 amino acid substitutions in the MATα_HMGbox domains of MAT1-1-1 pro-teins under various AlphaFold 3D structure codes derived from wild-type *C. sinensis*isolates compared with the reference MAT1-1-1 protein AGW27560 under AlphaFold code U3N942 [48]. The substitutions within the MATα_HMGbox domains caused topologicalstructure and waveform changes shown in the ExPASy ProtScale plots in Panels (B–F) ofFigures 3–8. These changes indicate differences in the hydrophobicity and secondary struc- tures (α-helices, β-sheets, β-turns, and coils) of the variant full-length proteins. The changes in hydrophobicity and in the primary and secondary structures of the MATα_HMGboxdomains altered the AlphaFold 3D structures of the domains of the proteins under various AlphaFold codes (Panels (H) in Figures 3–8 and Panel (I) of Figure 7). The mutant domain sequences containing 1 or 2 amino acid substitutions were clustered into different clades in the Bayesian clustering tree (Figure 1, Table S6), and the altered 3D structures of the proteins may ultimately affect the DNA binding affinities and the regulation of the transcription of genes related to the sexual reproduction of *O. sinensis*.

(To be continued)

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