Original article / Оригинальная статья
УДК 582.287.236 (470.67) : 57.012.3 : 577.15 : 574.9
DOI: 10.18470/1992-1098-2026-1-7

Ecology and cultural characteristics of the tooth fungi genus *Hericium* (Russulales, Basidiomycota) in the Republic of Dagestan, Russia

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How to cite this article
Volobuev S.V., Ivanushenko Yu.Yu., Shakhova N.V. Ecology and cultural characteristics of the tooth fungi genus *Hericium* (Russulales, Basidiomycota) in the Republic of Dagestan, Russia. *South of Russia: ecology, development.* 2026; 21(1):63-80. DOI: 10.18470/1992-1098-2026-1-7

Received 20 November 2025
Revised 13 December 2025
Accepted 25 December 2025

Abstract
The current work is aimed to provide data on the first finding of *Hericium cirrhatum* in the Republic of Dagestan, new localities of *Hericium coralloides* in the region, their ecological features, as well as to analyze the cultural characteristics of new *Hericium* strains *in vitro*.
The authors collected the original material during own field mycological inventories of forest ecosystems in the Republic of Dagestan in 2023–2025. Fungal specimens and strains were studied by techniques of light microscopy, solid-phase cultivation, molecular analysis of nrDNA, as well as qualitative evaluation of enzymatic activity. All samples are deposited at the LE Mycological herbarium and the LE-BIN culture collection (St. Petersburg).
The first data on the record of *Hericium cirrhatum* in the Samursky National Park and new locations of the red-listed species *H. coralloides* in the Kazbekovsky and Magaramkentsky districts of the Republic of Dagestan are presented. The cultural and morphological features of three new dikaryotic strains of *H. cirrhatum* and *H. coralloides* are described. Pure culture analyses have been performed to assess the lignocellulolytic and degradation potential of these white-rot xylotrophic species.
The data obtained can contribute to nature conservation practice, including the preservation of the gene pool of rare and little-known fungal species.

Key Words
Biodiversity, cellulases, fungal conservation, hydnoid fungi, ligninases, North-Eastern Caucasus, pure culture, Red Data Book.

Экология и культуральные особенности грибов рода *Hericium* (Russulales, Basidiomycota) в Республике Дагестан, Россия

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Формат цитирования
Volobuev S.V., Ivanushenko Yu.Yu., Shakhova N.V. Ecology and cultural characteristics of the tooth fungi genus *Hericium* (Russulales, Basidiomycota) in the Republic of Dagestan, Russia // Юг России: экология, развитие. 2026. Т.21, N 1. C. 63-80.
DOI: 10.18470/1992-1098-2026-1-7

Получена 20 ноября 2025 г.
Прошла рецензирование 13 декабря 2025 г.
Принята 25 декабря 2025 г.

Резюме
Цель работы – представить сведения о первой находке *Hericium cirrhatum* в Республике Дагестан, новых местонахождениях *Hericium coralloides* в регионе, их экологических особенностях, а также провести анализ культуральных характеристик новых штаммов *Hericium* в условиях *in vitro*.
Авторами собран оригинальный материал в ходе собственных полевых микологических обследований лесных экосистем в Республике Дагестан в 2023–2025 годах. Гербарные образцы и штаммы грибов были изучены с помощью методов световой микроскопии, твердофазного культивирования, молекулярного анализа ярДНК, а также качественной оценки ферментативных активностей. Все изученные образцы хранятся в Микологическом гербарии Ботанического института им. В.Л. Комарова РАН (LE) и Коллекции культур базидиомицетов LE-BIN (Санкт-Петербург).
Впервые для Республики Дагестан отмечен *Hericium cirrhatum*, выявленный в национальном парке «Самурский», установлены новые местонахождения охраняемого в регионе вида *H. coralloides* на территории Казбековского и Магарамкентского районов. Описаны культурально-морфологические признаки трех новых дикариотических штаммов *H. cirrhatum* и *H. coralloides*. Проведена качественная оценка их лигноцеллюлолитического и деградационного потенциала.
Полученные данные могут быть использованы в природоохранной практике, в том числе мероприятиях по сохранению генофонда редких и малоизвестных видов грибов.

Ключевые слова
Биологическое разнообразие, целлюлазы, охрана грибов, ежовиковые грибы, лигниназы, Северо-Восточный Кавказ, чистые культуры, Красная книга.

INTRODUCTION

Fungi of the genus *Hericium* Pers. are among the most impressive xylotrophic macromycetes, as they develop large, whitish and easily visible basidiomata with a toothed hymenophore. These species cause a white rot, growing on wood of both deciduous trees and conifers. Despite of large quantities of basidiospores producing by *Hericium* species, in the experimental study their poor germination has been shown and considered as a factor contributing to the rarity of recorded fruiting bodies in the field [1].

Representatives of the genus *Hericium* are valuable edible mushrooms known for their medicinal properties and possessing a unique set of biologically active compounds [2]. Currently, among *Hericium* species, *Hericium erinaceus* (Bull.) Pers., named in Europe and North America as Lion's mane or bearded hedgehog, is the most extensively studied. This species, known as the monkey head mushroom in China, the deer butt mushroom in Korea and as Yamabushitake in Japan [3], is actively used in East Asian countries as a potential alternative or complementary treatment due to the bioactive compounds synthesised by this fungus.

Extracts from the basidiomata and mycelium of *H. erinaceus* contain secondary metabolites such as polysaccharides (in particular, β-glucans), terpenoids (hericenones and erinacines), polyphenols, and peptides, which have notable physiological functions, including immunomodulatory, antioxidant, anti-inflammatory, and antimicrobial effects [4]. In the clinical study carried out by Bizjak et al. [5], a dietary supplement containing *H. erinaceus* was found to be beneficial for improving cognitive function and modulating the gut microbiota in elderly people. Extracts and purified bioactive metabolites from the basidiomata or mycelium of *H. erinaceus* have antimicrobial activity against a number of bacterial and fungal pathogens, opening up further opportunities for combating antibiotic-resistant infections [4; 6]. In addition, experimental analyses of the *H. erinaceus* mycelium chemical composition have revealed no side effects and confirmed the safety of using this fungus for drug development [7].

Despite the long-standing research interest in the therapeutic and nutritional potential of *Hericium* fungi, there is significantly less information available on the secondary metabolites produced by other species of the genus. The presence of biologically active substances have been demonstrated in the mycelium of *Hericium coralloides* (Scop.) Pers. with antitumour [8], immunomodulatory [9], antioxidant [10], anticoagulant, and cholesterol-lowering activities [11]. In addition, the preparation containing the polysaccharide galactan isolated from the basidiomata of *H. coralloides* was able to alleviate Alzheimer's disease and cognitive impairment by activating the Nrf2 signalling pathway [12; 13]. Song with colleagues [14] have developed optimized protocols for the extensive cultivation and fruiting of *H. coralloides* strains for commercial use in the food industry.

In the study by Narmuratova et al. [6], it was shown that extracts from pure cultures of *Hericium cirrhatum* (Pers.) Nikol., along with *H. coralloides* and *H. erinaceus*, demonstrated strong antibacterial activity against Gram-positive bacterial test cultures, such as *Staphylococcus aureus* and *Bacillus subtilis*, which suggests the potential for application of these fungal strains as antibacterial agents.

The registered *Hericium* species diversity varies greatly between different regions and countries. In Russia, a total of six species of the genus are known as *Hericium alpestre* Pers., *H. cirrhatum*, *H. coralloides*, *H. erinaceus*, *H. fimbrillatum* (Iwade) R. Sugaw., N. Maek. et N. Endo, *H. ptychogasteroides* Nikol. [15–18]. Two latter species are recorded only in the Russian Far East from Sakhalin Oblast [15] and Primorsky Krai [17]. One species, *H. alpestre* (as *H. flagellum* (Scop.) Pers.) is included in the Red Data Book of the Russian Federation with category 3 – “Rare species” and “Vulnerable” (VU D1) according to IUCN criteria in Russia [19].

In the Caucasus, four *Hericium* species have been recorded to date. Among them, *H. alpestre* and *H. erinaceus* are found in the Western Caucasus, where they are rare and also listed in the regional Red Data Books [20–22]. Ecologically, the species differ in their substrate preferences: *H. alpestre* grows on coniferous wood (*Abies*, *Larix*, *Picea*, *Pinus*), while *H. erinaceus* develops on deciduous trees (*Aesculus*, *Alnus*, *Carpinus*, *Fagus*, *Populus*, *Quercus*, *Tilia*, etc.). Recently, *H. erinaceus* has also been noted in Stavropol Krai [23]. The species *H. cirrhatum* is registered only from the Republic of North Ossetia – Alania based on the almost century-old finding [24]. The most distributed species of the genus *Hericium* is *H. coralloides* revealed in all Caucasian regions of Russia. This species is also well-known in the European part of Russia alongside other wood-inhabiting fungi such as *Bjerkandera adusta* (Willd.) P. Karst., *Fomes fomentarius* (L.) Fr., and *Oxyporus populinus* (Schumach.) Donk [18]. *Hericium coralloides* is red-listed species in Krasnodar Krai [21], the Republic of Adygea [22], Stavropol Krai [25], the Kabardino-Balkarian Republic [26], the Republic of North Ossetia – Alania [27], the Chechen Republic [28], and the Republic of Dagestan [29].

In the Republic of Dagestan, the genus *Hericium* was previously known based on the only location of *H. coralloides* in vicinity of the Yersi settlement of Tabasaransky District [29].

The current work is aimed to provide data on the first finding of *H. cirrhatum* in the Republic of Dagestan, new localities of *H. coralloides* in the region, their ecological features, as well as to analyze the cultural characteristics of newly obtained *Hericium* strains *in vitro*.

MATERIAL AND METHODS

Field studies

Fresh basidiomata were collected and observed by the authors during field mycological inventories of forest ecosystems in the Republic of Dagestan. Field surveys were carried out both in the previously studied territory of the Samursky National Park within the “Delta Samura” site in Magaramkentsky District [30–36] and in the mycologically unexplored “Ozero Gorenzho” planned protected nature area in vicinity of the Dylym settlement of Kazbekovsky District. Geographic coordinates (WGS-84) were measured using the Garmin 64st GPS-navigator. Photographs of basidiomata were made *in situ* using a digital camera.

Morphological identification of herbarium specimens

Microscopic identification of four dried specimens was performed by light microscopy technique using a LOMO Mikmed-6 microscope (Russia) and an Axio Imager.A1 ZEISS microscope (Germany) equipped with Axiocam 506 color digital camera (Carl Zeiss) based on the monograph of Bernicchia & Gorjón [37]. A standard set of chemicals (5 %

aqueous solution of KOH, Melzer's reagent, 0.1 % Cotton Blue) was used for fungal slide preparation. The examined specimens have been deposited at the Mycological herbarium of the Komarov Botanical Institute RAS, St. Petersburg (LE).

Isolation and verification of fungal pure cultures

Three dikaryotic strains were isolated *ex situ* using the solid-phase cultivation method, as described in Shakhova and Volobuev [38]. The macro- and micromorphological characteristics of the isolates were described using cultural and morphological parameters based on the method and terminology of Stalpers [39]. Verification of the strains was carried out using molecular genetic methods. Genomic DNA was amplified from a 14-day-old culture grown on standard malt extract agar (MEA), containing 1.5 % Conda malt extract (Madrid, Spain) and 2 % Difco agar (Kansas City, USA) in the dark in a thermostat at 25°C, using the Phire Plant Direct PCR Master Mix Kit (Thermo Fisher Scientific, USA), in accordance with the manufacturer's instructions. Amplification of the ITS nrDNA region was performed using the ITS1F/ITS4B primer set, as described in Volobuev and Shakhova [40]. The strains were deposited in the Komarov Botanical Institute Basidiomycetes Culture Collection (LE-BIN, St. Petersburg) and are stored using subculture, disc culture and cryopreservation methods [41].

Growth measurement and detection of enzymatic activity

Measurements of growth rate dynamics, as well as the characterisation of the strain macro- and micromorphological features, were carried out on three agarised nutrient media: BWA (4 % beer wort (Svoya kruzhka Ltd., Tolyatti, Russia), pH 5.8, and 2 % Difco agar), MEA and PDA (potato dextrose agar, Panreac, Germany). The activity of ligninases and cellulases in the strains investigated was assessed by the application method, as described in Volobuev and Shakhova [40; 42]. The degradation potential of the strains was analysed using a modified method involving the polyphenolic dye Azure B [43].

Herbarium specimens studied:

Hericium cirrhatum — Russia, Republic of Dagestan, Magaramkentsky District, Samursky National Park, "Delta Samura" site, in 1.5 km south-eastward from the course of the Karasu River, 41.87907º N, 48.5191º E, on fallen trunk of *Populus alba* in poplar forest with hornbeam, lianas and wood spurge, 08.05.2023, coll. E.A. Dunaev, det. S.V. Volobuev, LE F-352273. — *ibid.*, vicinity of the ecological route close to Visit-center, 41.81469º N, 48.52933º E, on fallen trunk of *Carpinus betulus* in hornbeam forest with wood spurge (*Euphorbia amygdaloides*), 05.06.2025, coll. Yu.Yu. Ivanushenko, det. S.V. Volobuev, LE F-352269.

Hericium coralloides — Russia, Republic of Dagestan, Magaramkentsky District, Samursky National Park, "Delta Samura" site, in 3 km northward from the Samur settlement, on fallen trunk of *Carpinus betulus* in hornbeam forest with oak and wood spurge, 26.10.2023, coll. N.V. Shakhova and S.V. Volobuev, det. S.V. Volobuev, LE F-352270. — *ibid.*, in 1 km south-eastward from the course of the Karasu River, on fallen trunk of *Ulmus* sp. in poplar forest with elm and lianas, 28.10.2023, coll. N.V. Shakhova and S.V. Volobuev, det. S.V. Volobuev, LE F-352271. — *ibid.*, Kazbekovsky District, vicinity of the Dylym settlement, "Ozero Gorenzho" planned protected nature area, on fallen trunk of *Fagus orientalis* in herb-rich beech forest with hornbeam, 06.11.2025, coll. and det. S.V. Volobuev, LE F-352272.

Fungal strains studied:

Hericium cirrhatum — LE-BIN 5192: *ex basidioma*, voucher specimen LE F-352273, introduced by N.V. Shakhova.

Hericium coralloides — LE-BIN 5238: *ex basidioma*, voucher specimen LE F-352270, introduced by N.V. Shakhova. — LE-BIN 5254: *ex basidioma*, voucher specimen LE F-352271, introduced by N.V. Shakhova.

RESULTS

Based on macro- and micromorphological features, the tiered tooth fungus *H. cirrhatum* has been identified. This species is recorded by the authors for the first time for the Republic of Dagestan from the territory of the Samursky National Park within the "Delta Samura" site in Magaramkentsky District in 2023 and 2025. The description of this basidiomycete fungus based on our original collections is presented below.

Hericium cirrhatum (Pers.) Nikol., Acta Inst. Bot. Acad. Sci. USSR, Plantae Cryptogamae, Ser. II, Fasc. 5: 343 (1950).

Basionym: *Hydnum cirrhatum* Pers. [as '*cirratum*'], Neues Mag. Bot. 1: 109 (1794).

Basidiomata annual, pileate, dimidiate to semicircular, consisting of overlapping pilei that are fused at the base, up to 40 mm wide, initially white, then turning yellowish cream with a pinkish tint, and later becomes dirty-ochre to brownish when dry. Context thick, soft and fleshy, white or slightly pinkish, with sweetish-fruity odour when fresh, then gently corky, yellowish with a pinkish tint, non-fibrous. Upper sterile surface rough, granulose to echinulate, covered with compressed conical or sometimes flattened sterile spines, more densely arranged near the edge of pileus. Margin obtuse or thin and sharp, and then bend over when drying. Hymenophore hydnoid with tapering conical aculei up to 10–12 mm long, whitish yellow and creamy apricot to dirty rusty and brownish beige on drying.

Hyphal system monomitic. Hyphae hyaline, thin-walled or with thickened walls, interwoven, frequently inflated, variable in diameter, 3–15 µm wide, with clamps. Gloeocystidia abundant, swollen fusiform or club-shaped, multiple constricted towards the apex, embedded in the hymenial layer, 5–6.5 µm wide, with granular contents. Basidia hyaline, clavate, clamped at the base, 18–28 × 4–5 µm, with four sterigmata. Basidiospores hyaline in KOH, broadly ellipsoid to subglobose, (3.2–) 3.4–3.9 (–4.1) × (2.4–) 2.5–3.1 (–3.2) µm, L = 3.62 µm, W = 2.79 µm, Q = 1.3, guttulate, amyloid.

As a result of continuing monitoring studies [32] of fungal protected species included in the Red Data Book of the Republic of Dagestan [29], three new locations of *H. coralloides* have been revealed. In 2023, two populations of this species have been registered in the territory of the Samursky National Park within the "Delta Samura" site in Magaramkentsky District. In 2025, one more population of *H. coralloides* have been found in the "Ozero Gorenzho" planned protected nature area in vicinity of the Dylym settlement of Kazbekovsky District. Morphological features of basidiomata observed are fully corresponded to the description of the species presented in the Red Data Book of the Republic of Dagestan [29].

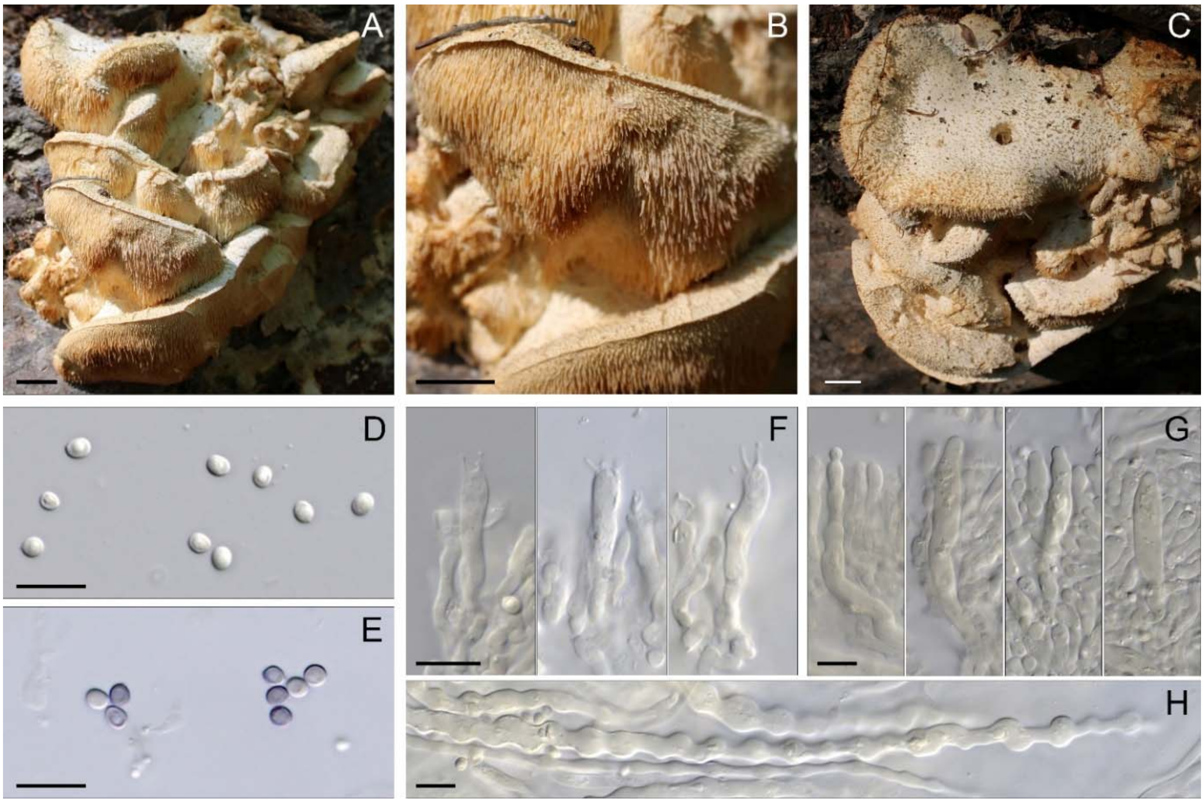

Figure 1. *Hericium cirrhatum*: A — habitus of basidiomata *in situ*, B — hydnoid hymenophore; C — upper sterile surface of basidioma; D — basidiospores in KOH; E — basidiospores in Melzer reagent (amyloid reaction); F — basidia; G, H — gloeocystidia. Scale bars: A–C — 1 cm, D–H — 10 µm

Рисунок 1. *Hericium cirrhatum*. A — внешний вид плодовых тел в природе; B — гидноидный гименофор; C — верхняя стерильная поверхность базидиомы; D — базидиоспоры в KOH; E — базидиоспоры в реактиве Мельцера (амилоидная реакция); F — базидии; G, H — глеоцистиды. Масштабные линейки: A–C — 1 см, D–H — 10 мкм

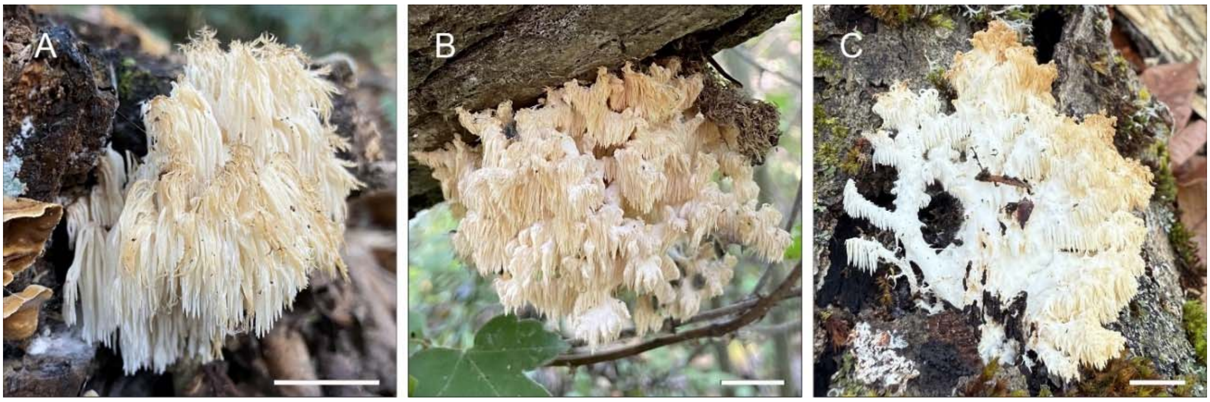

Figure 2. Habitus of *Hericium coralloides* basidiomata *in situ*: A — LE F-352270; B — LE F-352271; C — LE F-352272. Scale bars — 1 cm

Рисунок 2. Внешний вид плодовых тел *Hericium coralloides* в природе: A — LE F-352270; B — LE F-352271; C — LE F-352272. Масштабные линейки — 1 см

Among the main conservation activities provided by maintaining regional Red Data Books there are obtaining and preserving of wild species strains in the pure culture collections. For these purposes, we introduced one strain of *Hericium cirrhatum* and two strains of *H. coralloides* in pure culture. These strains were verified by molecular analysis of ITS nrDNA sequences generated in this study and deposited in GenBank (Table 1).

Table 1. Information on the studied strains and voucher specimens
Таблица 1. Сведения об изученных штаммах и ваучерных образцах

Species	Strain	GenBank accession no.	Voucher specimen	Collection date
Hericium cirrhatum	LE-BIN 5192	PZ179913	LE F-352273	08.05.2023
Hericium coralloides	LE-BIN 5238	PZ179914	LE F-352270	26.10.2023
Hericium coralloides	LE-BIN 5254	PZ179912	LE F-352271	28.10.2023

Newly obtained *Hericium* strains have been estimated in terms of mycelial growth rate, macro- and micromorphology of colonies on three different nutrient media, as well as lignocellulolytic enzymes activies.

The study of the growth rates of *Hericium* spp. colonies on various nutrient media revealed that the strains investigated belong to the group of slow-growing pure cultures. The *H. cirrhatum* LE-BIN 5192 strain exhibited the slowest growth rate among the strains studied. Cultivation of this strain for 29 days did not result in complete coverage of Petri dishes (90 mm in diameter) by mycelium on any of the nutrient media explored. When the *H. cirrhatum* LE-BIN 5192 strain was cultured on BWA, the colony diameter exceeding 50 mm was observed only on the 25th day, after which there was a noticeable decrease in growth rate, and the colony had reached 67.2 mm in diameter by the 29th day. MEA proved to be the most favourable for the growth of *H. cirrhatum* LE-BIN 5192; the colony diameter was 54.5 mm by the 25th day, and it was 75.5 mm by the 29th day. When *H. cirrhatum* was cultured on PDA, the colony diameter was 57.8 mm; the mycelium diameter was 69.3 mm by the 29th day (Fig. 3, A).

The *H. coralloides* strains exhibited a faster growth rate than *H. cirrhatum*. The *H. coralloides* LE-BIN 5238 strain demonstrated the highest growth rate when cultured on PDA: the colony diameter exceeded 50 mm by the 11th day of growth, and complete coverage of Petri dishes with mycelium was observed after 17 days. When this strain was grown on BWA, the colony diameter was 62 mm by the 11th day of growth; however, mycelial growth had completely ceased by the 15th day, and Petri dishes were not completely overgrown. The slowest growth rate was observed when *H. coralloides* LE-BIN 5238 was cultured on MEA: the fungal mycelium had reached 53.5 mm in diameter by the 15th day, but the colony growth rate had slowed significantly by the 21st day and the mycelium diameter was 80 mm by the 29th day (Fig. 3, B).

When the *H. coralloides* LE-BIN 5254 strain was cultured on PDA, the colony diameter exceeded 50 mm by the 11th day of growth, and Petri dishes were completely covered with mycelium by the 19th day. The slowest growth rate was observed when this strain was grown on BWA: the colony diameter was 51.3 mm on the 15th day, and the strain growth had completely ceased (diameter 69.5 mm) by the 25th day. When *H. coralloides* LE-BIN 5254 was grown on MEA, the colony diameter exceeded 50 mm on the 15th day; however, a decrease in growth rate was noted from the 17th day, and the mycelium diameter was 86.2 mm by the 29th day (Fig. 3, C).

Characteristics of *Hericium cirrhatum* LE-BIN 5192:

Colonies on BWA medium — Macromorphology. Growth rate – slow, 22.8 mm in 14 days. The colour is white. The mycelium becomes cream-coloured with age. The colony reverse is darkened. The outline is fringed, strongly fractured. Growing edge is submerged, sparse. The mycelial mat is plumose: mycelial tufts with short or long hyphae or groups of hyphae radiating from the central axis, often in fan-like arrangement. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 1.8–3.6 µm wide, straight, septate, rarely branching. Clamps are weakly curved to steeply curved, simple, 4.3–9.4 µm. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.2.3.9.14(2).15(2).23.30(1).31.36(0).38(2).39(2).44.52–53.

Colonies on MEA medium — Macromorphology. Growth rate – slow, 17.4 mm in 14 days. The colour is creamy. The colony reverse is unchanged. The outline is wavy. Growing edge is submerged, sparse diffuse. The mycelial mat is powdery-plumose: mycelial tufts with short or long hyphae or groups of hyphae radiating from the central axis, in fan-like arrangement. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 1.5–3.9 µm wide, straight, septate, rarely branching. Clamps are slightly curved to steeply curved, simple, 5.2–10.0 µm. Hyphal swellings are frequently observed, 9.4(12.7) × 14.2(16.6) µm. Cystidia are observed at the ends of hyphae, spinde-shaped or swollen club-like, with frequent constrictions towards apex, 6.1(8.8) × 17.5 (24.6) µm. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.2.3.9.14(2).15(1). 18(1).23(1).31.36(0).37(0).38(0).39(2).44.52–53.65.72.

Colonies on PDA medium — Macromorphology. Growth rate – slow, 16.1 mm in 14 days. The colour is creamy-white. The colony reverse is unchanged. The outline is wavy. Growing edge is pressed down. The mycelial mat is floccose-plumose: small hyphal tufts, standing out radiating from the central axis. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 1.5–3.5 µm wide, straight, septate, rarely branching. Clamps are slightly curved to steeply curved, simple, 4.5–9.3 µm. Hyphal swellings are frequently observed, 9.9(13.5) × 16.0(18.4) µm. Cystidia are rare observed at the ends of hyphae, spinde-shaped or swollen club-like, with frequent constrictions towards apex, 6.0(9.0) × 18.2 (25.5) µm. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.2.3.9.14(2).15(1).19(1).23(1). 30.36(0).37(0).38(0).39(2).44.52–53.65.72(1).

Characteristics of *Hericium coralloides* LE-BIN 5238

Colonies on BWA medium — Macromorphology. Growth rate – slow, 68.5 mm in 14 days, but stagnation of growth in 15–29 days. The colour is white. The mycelium becomes cream-coloured with age. The colony reversum is darkened. The outline is wavy. Growing edge is submerged, sparse. The mycelial mat is flaky-plumose: mycelial tufts with short or long hyphae or groups of hyphae radiating from the central axis, in fan-like arrangement. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 1.5–4.9 µm wide, straight, septate, rarely branching. Clamps are weakly curved to steeply curved, simple, 5.5–10.7 µm. Multiple clamps are rarely observed on hyphae. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.3.7.14(2).15(1).23.30.(31).36(0). 38.39.44.52–53.

Colonies on MEA medium — Macromorphology. Growth rate – slow, 53.5 mm in 14 days, but stagnation of growth in 21–29 days. The colour is cream-coloured. The colony reversum is darkened. The outline is severely fractured. Growing edge is submerged, sparse diffuse. The mycelial mat is powdery-plumose: mycelial tufts with short or long hyphae or groups of hyphae radiating from the central axis, in fan-like arrangement. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 2.2–6.8 µm wide, straight, septate, rarely branching. Clamps are slightly curved to steeply curved, simple and medallion-shaped, 5.8–11.0 µm. Hyphal swellings are frequently observed, 10.5(13.7) × 15.1 (18.0) µm. Cystidia are often observed at the ends of hyphae, somewhat irregular, acute, with yellowish contents, 5.9(9.4) × 19.2 (29.9) µm. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.3.7.14(2).15(2).18.23.31.36(0).38.39.44.52–54.72(2).80(2).

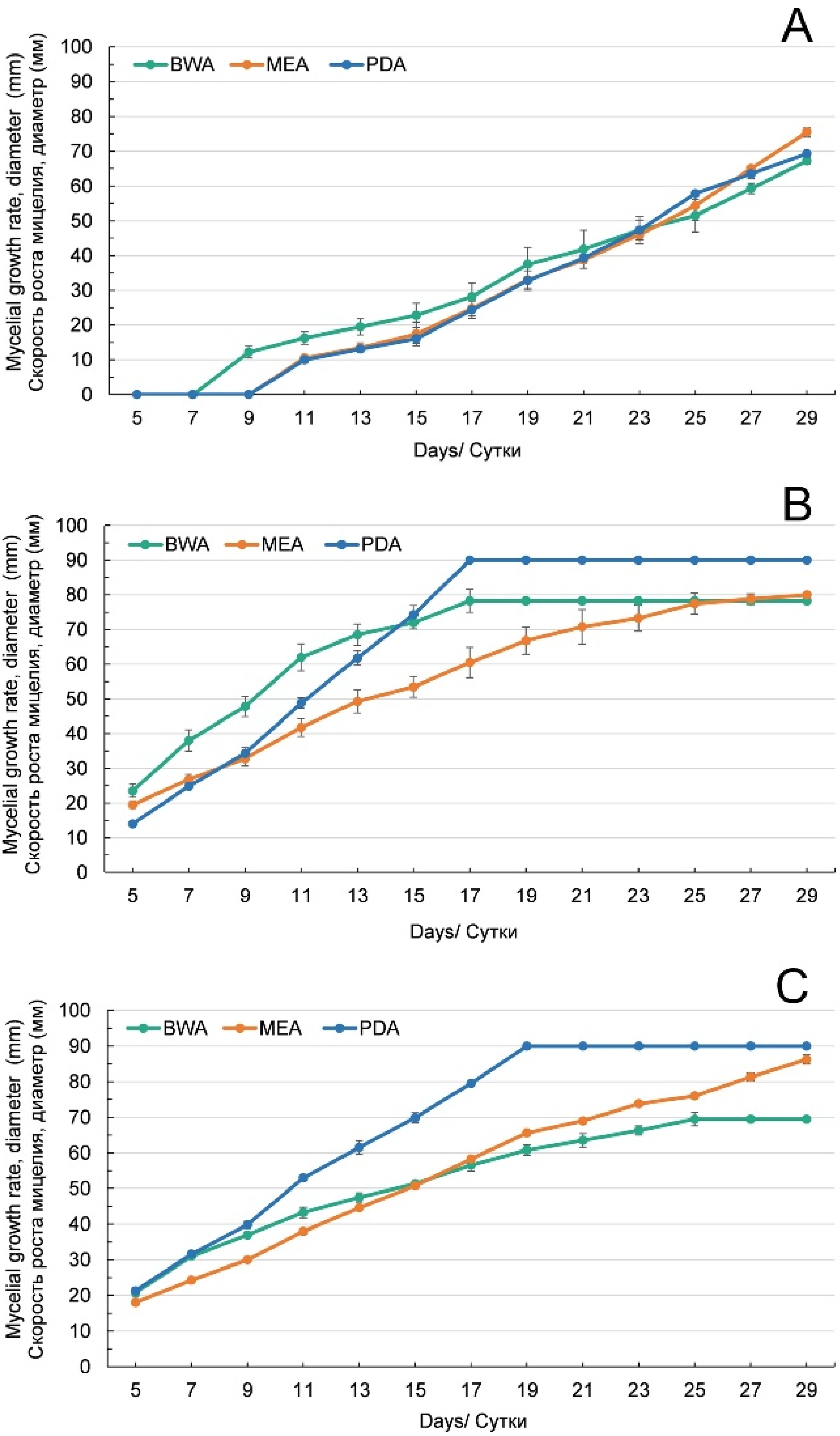

Figure 3. Mycelial growth rate of the *Hericium cirrhatum* LE-BIN 5192 (A), *H. coralloides* LE-BIN 5238 (B), and *H. coralloides* LE-BIN 5254 (C) strains on BWA, MEA and PDA nutrient media

Рисунок 3. Скорость роста мицелия штаммов *Hericium cirrhatum* LE-BIN 5192 (A), *H. coralloides* LE-BIN 5238 (B) и *H. coralloides* LE-BIN 5254 (C) на питательных средах BWA, MEA и PDA

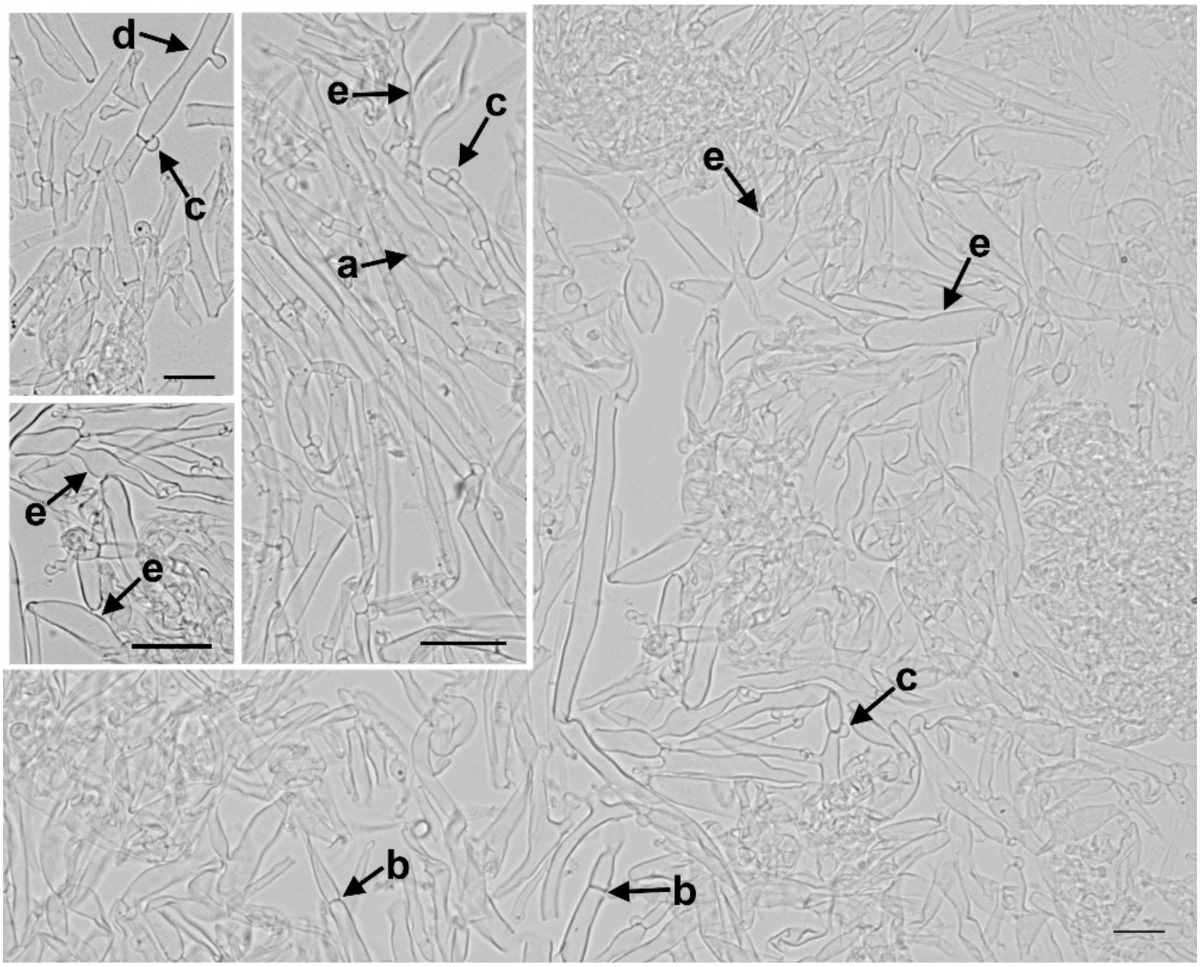

Figure 4. Microscopic features of *Hericium cirrhatum* LE-BIN 5192: a — swellings on generative hyphae; b, c — clamped hyphae; d — wart-like structure on generative hypha; e — cystidia. Scale bars — 10 µm

Рисунок 4. Микроскопические особенности *Hericium cirrhatum* LE-BIN 5192: a — вздутия на генеративных гифах; b, c — гифы с пряжками; d — бородавковидная структура на генеративной гифе; e — цистиды. Масштабные линейки — 10 мкм

Colonies on PDA medium — Macromorphology. Growth rate – moderate, 74.3 mm in 14 days. The colour is pale. The colony reversum is unchanged. The outline is wavy. Growing edge is submerged, sparse. The mycelial mat is powdery-floccose: small hyphal tufts, standing out from the agar or from the aerial mycelium. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 2.3–7.2 µm wide, straight, septate, rarely branching. Clamps are slightly curved to steeply curved, simple and medallion-shaped, 6.1–11.8 µm. Hyphal swellings are frequently observed, 12.7(15.1) × 16.5 (22.5) µm. Cystidia are often observed at the ends of hyphae, somewhat irregular, acute, with yellowish contents, 7.5(10.5) × 26.3 (34.0) µm. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.3.6.14(2).15(1).18.23.31.36(0).37(0).39.44.52–54.72(2).80(2).

Characteristics of *Hericium coralloides* LE-BIN 5254

Colonies on BWA medium — Macromorphology. Growth rate – slow, 51.3 mm in 14 days, but stagnation of growth in 25–29 days. The colour is cream-coloured. The colony reversum is unchanged. The outline is flat. Growing edge is submerged, sparse. The mycelial mat is flaky-plumose: mycelial tufts with short or long hyphae or groups of hyphae radiating from the central axis, in fan-like arrangement. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 1.5–6.0 µm wide, straight, septate, rarely branching. Clamps are weakly curved to steeply curved, simple, 7.5–10.0 µm. Multiple clamps are rarely observed on hyphae. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.3.7.14(2).15(1).23.30.(31).36(0).37(0).38.39.44.52–53.

Colonies on MEA medium — Macromorphology. Growth rate – slow, 50.8 mm in 14 days, but stagnation of growth in 17–29 days. The colour is cream-coloured. The colony reversum is unchanged. The outline is wavy. Growing edge is submerged, sparse, diffuse. The mycelial mat is powdery-plumose: mycelial tufts with short or long hyphae or groups of hyphae radiating from the central axis, in fan-like arrangement. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 2.0–6.5 µm wide, straight, septate, rarely branching. Clamps are slightly curved to steeply curved, simple and medallion-shaped, 4.2–12.2 µm. Hyphal swellings are frequently observed, 7.5(9.9) × 16.5 (18.5) µm. Cystidia are often observed at the ends of hyphae, somewhat irregular, acute, with yellowish contents, 5.5(6.4) × 15.5 (19.6) µm. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.3.6.14(2).15(1).18.23.31.36(0).37(0).39.44.52–54.72(2).80(2).

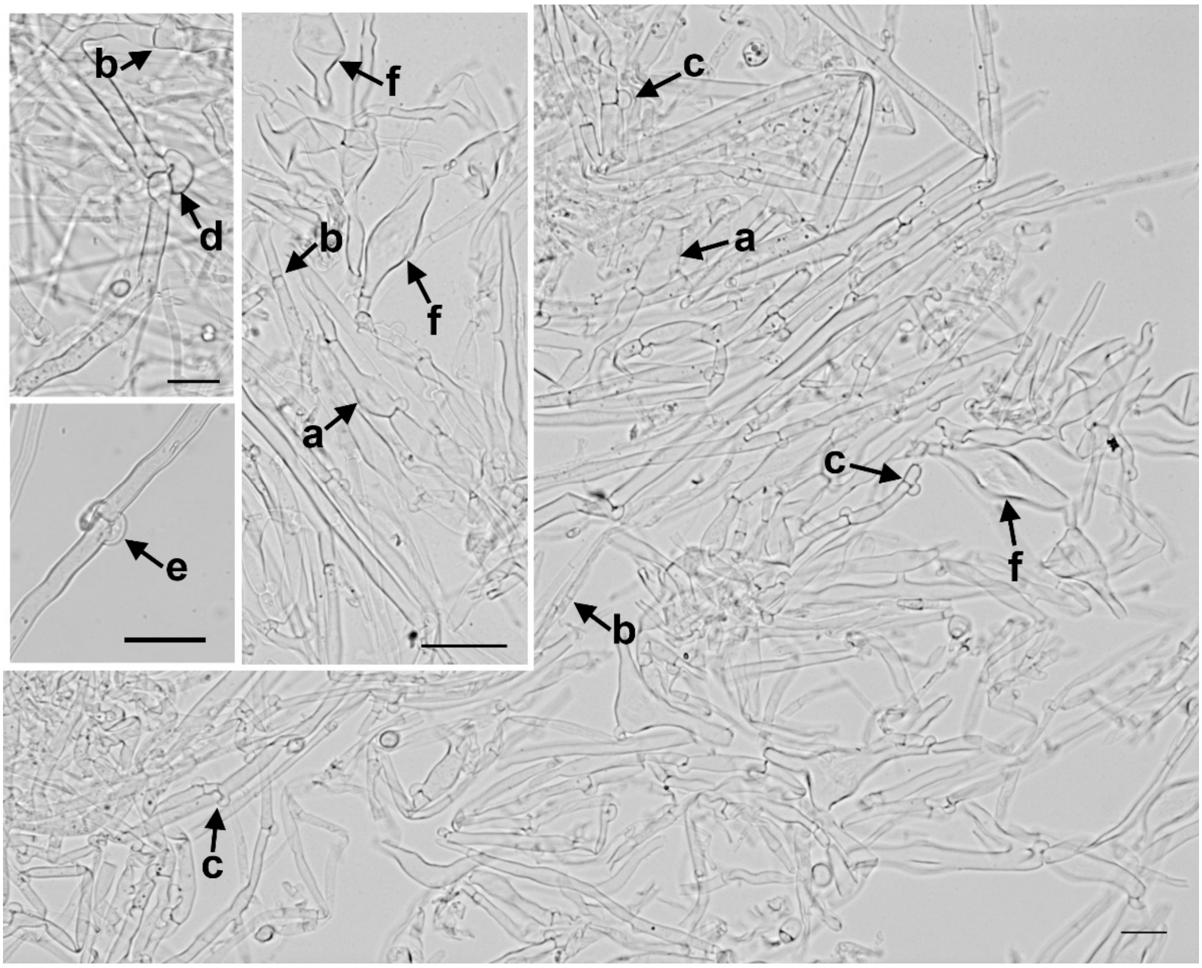

Figure 5. Microscopic features of *Hericium coralloides* in pure culture: a — swellings on generative hyphae; b — hyphae with septa; c — clamped hyphae; d — medallion-shaped clamp; e — multiple clamps; f — cystidia. Scale bars — 10 µm

Рисунок 5. Микроскопические особенности *Hericium coralloides* в чистой культуре: a — вздутия на генеративных гифах; b — гифы с перегородками; c — гифы с пряжками; d — медальонная пряжка; e — множественные пряжки; f — цистиды. Масштабные линейки — 10 мкм

Colonies on PDA medium — Macromorphology. Growth rate – slow, 69.9 mm in 14 days. The colour is pale. The colony reversum is unchanged. The outline is wavy. Growing edge is submerged, sparse, diffuse. The mycelial mat is powdery-floccose: small hyphal tufts, standing out from the agar or from the aerial mycelium. It is odourless. — Micromorphology. Hyphal system is monomitic. Mycelium consists of thin-walled hyaline hyphae, 2.5–7.5 µm wide, straight, septate, rarely branching. Clamps are slightly curved to steeply curved, simple and medallion-shaped, 6.4–14.8 µm. Hyphal swellings are frequently observed, 6.5(10.0) × 15.0 (20.8) µm. Cystidia are often observed at the ends of hyphae, somewhat irregular, acute, with yellowish contents, 6.6(8.0) × 17.9 (20.5) µm. Chlamydospores, arthro- and blastoconidia were not found. — Code: 1.3.6.14(2).15(1).18.23.31.36(0).37(0).39.44.52–54.72(2). 80(2).

Due to the genus *Hericium* belongs to xylotrophic basidiomycetes causing a white rot, they possess extracellular enzymes of the ligninolytic and cellulolytic complexes. We investigated the lignocellulolytic potential of *Hericium cirrhatum* and *H. coralloides* using pure cultures. The assessment of oxidative enzymes was carried out using a method based on the ability of producer strains to oxidise the ABTS substrate (2,2'-azino-bis(3-ethylbenzothiazoline-6-sulfonic acid)) to ABTS+. However, in the analysis of oxidoreductases in the *H. cirrhatum* LE-BIN 5192 strain, oxidised ABTS changed colour around the inocula from transparent to purple-red, but not to emerald green (Fig. 7, A). The most likely explanation for the formation of the purple-red colour is the attachment of the free radical 2,2'-azino-bis(3-ethylbenzothiazoline-6-sulphonate) (ABTS ●) to tyrosine residues in proteins [44]. It was found that the *H. cirrhatum* LE-BIN 5192 strain was characterised by a high level of ligninase activity, with the diameter of the stained zone reaching 26.8±1.6 mm. At the same time, this strain exhibited low production of cellulolytic enzymes, with the diameter of the clearing zone being 7.0 ± 0.1 mm.

When assessing the enzymatic activities of *H. coralloides* LE-BIN 5238 and *H. coralloides* LE-BIN 5254 (Fig. 7, B, C), it was found that the strains exhibited moderate oxidative enzyme activity; with the diameter of the coloured zone being 18.7±0.8 mm for the *H. coralloides* LE-BIN 5238 strain, and 18.0±0.6 mm for the *H. coralloides* LE-BIN 5254 strain. The activity of the cellulolytic complex enzymes in these strains was similar and low; the zone of clearing observed in *H. coralloides* LE-BIN 5238 was 13.0±0.9 mm, and 12.0±0 mm in *H. coralloides* LE-BIN 5254 (Fig. 8).

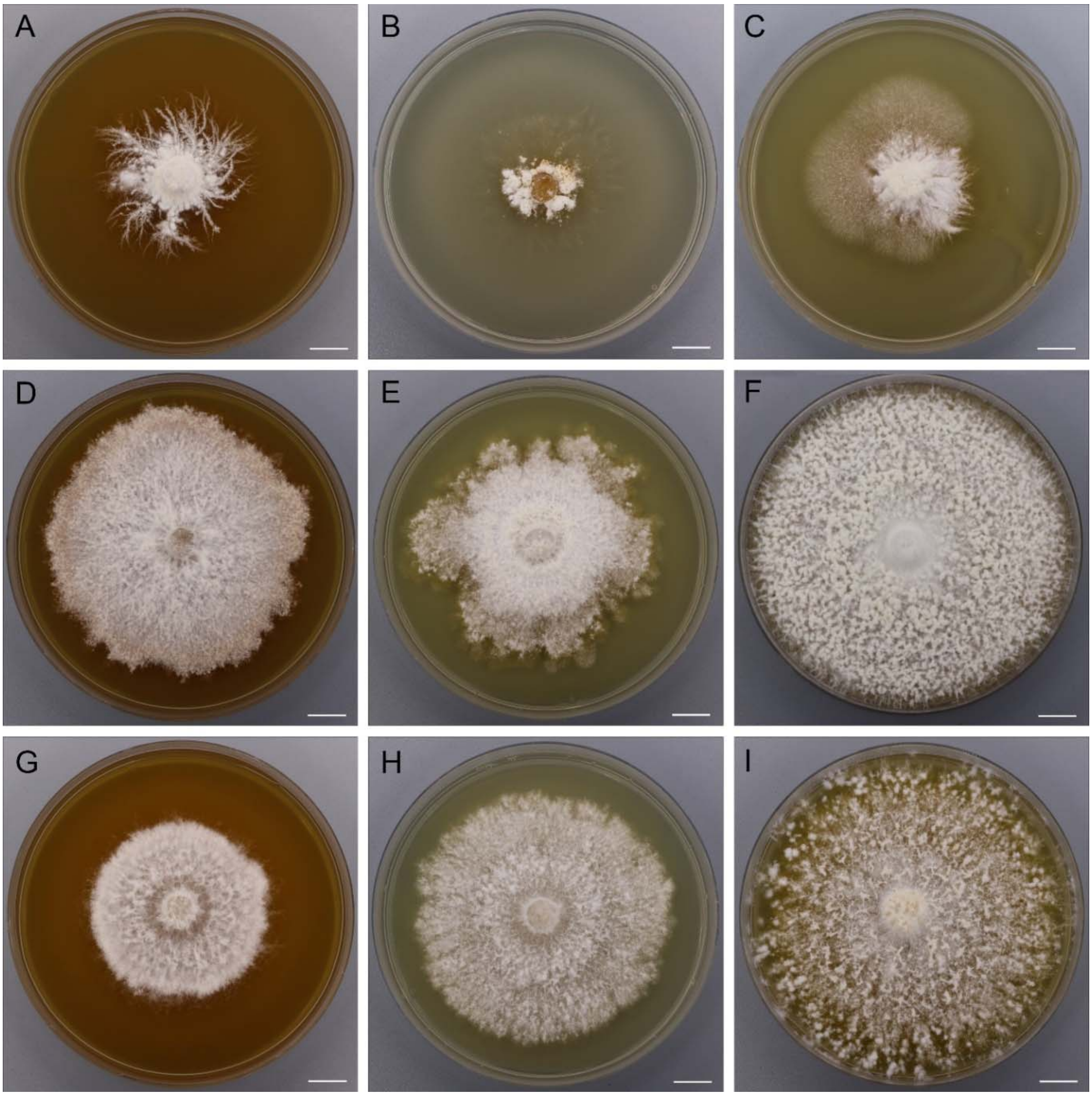

Figure 6. The colony appearance of the *Hericium cirrhatum* LE-BIN 5192 (A, B, C), *H. coralloides* LE-BIN 5238 (D, E, F), and *H. coralloides* LE-BIN 5254 (G, H, I) strains at 23 days of cultivation on BWA (A, D, G), MEA (B, E, H), and PDA (C, F, I). Scale bars – 1 cm

Рисунок 6. Внешний вид колоний штаммов *Hericium cirrhatum* LE-BIN 5192 (A, B, C), *H. coralloides* LE-BIN 5238 (D, E, F) и *H. coralloides* LE-BIN 5254 (G, H, I) на 23 сутки культивирования на питательных средах BWA (A, D, G), MEA (B, E, H) и PDA (C, F, I). Масштабная линейка – 1 см

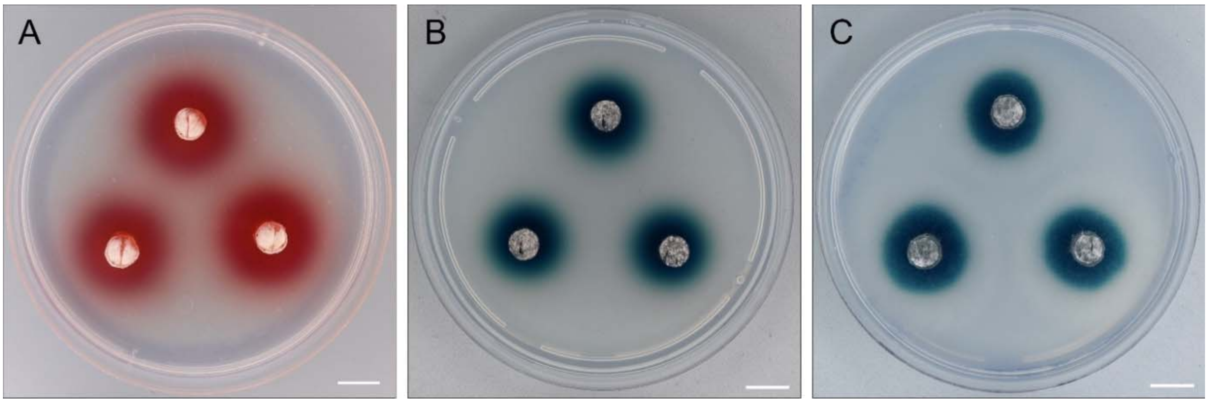

Figure 7. Extracellular ABTS-oxidizing activity on agar plates of the *Hericium cirrhatum* LE-BIN 5192 (A), *H. coralloides* LE-BIN 5238 (B), and *H. coralloides* LE-BIN 5254 (C) strains. Scale bars – 1 cm

Рисунок 7. Активность внеклеточных окислительных ферментов на агаризованной среде с ABTS у штаммов *Hericium cirrhatum* LE-BIN 5192 (A), *H. coralloides* LE-BIN 5238 (B) и *H. coralloides* LE-BIN 5254 (C). Масштабная линейка — 1 см

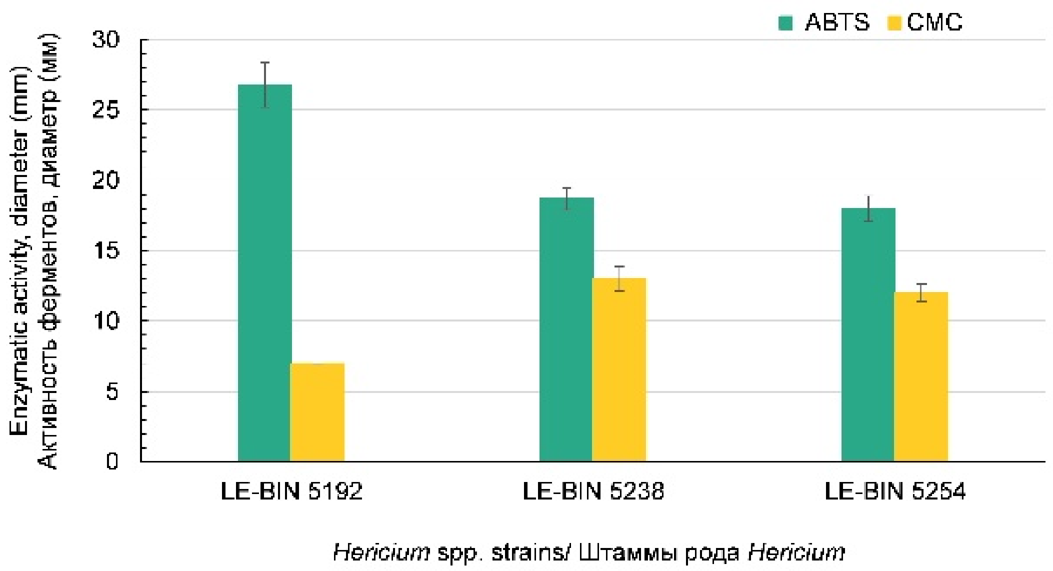

Figure 8. Extracellular enzymatic activities of the *Hericium cirrhatum* LE-BIN 5192, *H. coralloides* LE-BIN 5238, and *H. coralloides* LE-BIN 5254 strains: ABTS — ABTS-oxidizing activity on agar plates, CMC — cellulase activity on carboxymethyl cellulose agar plates
Рисунок 8. Активность внеклеточных ферментов у штаммов *Hericium cirrhatum* LE-BIN 5192, *H. coralloides* LE-BIN 5238 и *H. coralloides* LE-BIN 5254: ABTS — окислительная активность на агаризованной среде с ABTS, CMC — целлюлолитическая активность на агаризованной среде с карбоксиметилцеллюлозой

As an additional physiological and biochemical characteristic, the degradation potential of the *Hericium* strains was assessed using a test based on the decolourisation of the nutrient medium with added azo dye Azure B. No one studied strains showed any positive result in the Azure B decolourisation test. Meanwhile, the *H. cirrhatum* LE-BIN 5192 strain was found to be capable of primordia formation (Fig. 9) when the mycelium was cultured for three months on the medium containing Azure B. The primordia of *H. cirrhatum* were odourless, 2–5 cm in diameter, characterised by a felt-like, white- and yellow-coloured surface of pilei, which were fused at the elongated base, and a hymenophore with whitish-cream spines.

DISCUSSION

The species *Hericium cirrhatum* has been revealed from two different localities in the "Delta Samura" site of the Samursky National Park. The fungus was growing on fallen trunks of *Carpinus betulus* and *Populus alba*. These trees were previously known as hosts of *H. cirrhatum* according to data from the European part of Russia, where this fungal species also grows on wood of *Alnus*, *Betula*, *Fagus*, *Quercus*, *Salix*, *Sorbus* [16; 18]. *H. cirrhatum* is proposed for consideration and assessment as globally rare species within the IUCN Global Fungal Red List initiative. The species is threatened by the loss of habitat due to logging of old forests with long continuity of native ecosystem and trees of various ages and their replacement by the same-aged monocultures. According to experts' estimations, the decline in habitat quality is ongoing and expected to continue over the next 50 years. This allowed to categorised *H. cirrhatum* as "Near Threatened" (NT) under A2c+3c+4c criteria [45]. In Russia, this species is included in regional Red Data Books of Lipetsk Oblast [46], Udmurt Republic [47], Republic of Komi [48], Khanty-Mansi Autonomous Okrug – Yugra [49], Krasnoyarsk Krai [50], and Amur Oblast [51]. The main population-limiting factors in each region are following: undisturbed habitat preferences of the species, irregular and rare fructification, logging of old-growth and successional forests, removal of coarse woody debris, as well as wildfires. In the Republic of Dagestan, the revealed habitats of *H. cirrhatum* may also be affected by anthropogenic impact, including the removal of large-sized dead wood and forest fires. We recommend monitoring the state of the discovered populations at least one time per year.

Hericium coralloides included in the Red Data Book of the Republic of Dagestan [29] with the category 3 (VU) – rare, vulnerable species – was previously known for the region from Tabasaransky District only. This saprobe species was growing on large fallen and dry standing trunks of *Fagus orientalis*. Our record of *H. coralloides* from Kazbekovsky District has also been collected on fallen trunk of beech. At the same time, this fungus is able to develop on dead wood of other deciduous trees. In particular, new findings from "Delta Samura" site of the Samursky National Park in Magaramkentsky District have been made on fallen trunks of *Carpinus betulus* and *Ulmus* sp. The species *Hericium coralloides* prefers old-growth broad-leaved forests with constant moisture level and the presence of large woody debris. The ecological features of earlier recorded populations of this xylotrophic fungus in the Republic of Dagestan correlates with newly observed habitats. Basidiomata of *H. coralloides* were found together with several widespread species of wood-inhabiting fungi on the same woody substrate unit. In Kazbekovsky District, *Auricularia mesenterica* (Dicks.) Pers. and *Bjerkandera adusta* (Willd.) P. Karst. were noted as neighboring species with *Hericium coralloides* jointly involved in wood decomposition of *Fagus orientalis* dead trunk. In Magaramkentsky District, *Stereum hirsutum* (Willd.) Pers. accompanied with *Hericium coralloides* on the common fallen trunk of *Carpinus betulus*. Remarkably, all registered fungal species growing together with *Hericium coralloides* belong to white-rot fungi.

Figure 9. The teleomorph formation by the *Hericium cirrhatum* LE-BIN 5192 strain on agarized medium, containing the polyphenol dye Azure B. Scale bar – 1 cm
Рисунок 9. Образование телеоморфы штаммом *Hericium cirrhatum* LE-BIN 5192 на агаризованной питательной среде, содержащей полифенольный краситель Азур Б. Масштабная линейка – 1 см

The strains studied *in vitro* were characterised by a slow growth rate, typical of *Hericium* representatives [52; 53; 54]. The *H. cirrhatum* LE-BIN 5192 strain showed the slowest growth rate among the pure cultures tested. The MEA proved to be the most suitable for the cultivation of this strain. Strains of *H. coralloides* LE-BIN 5238 and *H. coralloides* LE-BIN 5254 exhibited some variability in growth parameters when cultured on different nutrient media. The growth rate dynamics of both *H. coralloides* strains when grown on BWA and MEA were similar; the stable mycelial growth was observed during the initial stages of cultivation, but from 15–25 days (depending on the strain), a complete cessation of mycelial growth was observed. Both strains demonstrated the fastest growth and the ability to completely colonise a Petri dish (90 mm in diameter) when grown on PDA, which does not correspond to some literature data. Thus, Gonkhom et al. indicated that MEA supplemented with yeast extract was the best suited for the cultivation of *H. coralloides* mycelium [55]. According to Nguyen et al., PDA supplemented with yeast extract was optimal for the growth of *H. erinaceus* mycelium [56]. The results obtained in our study can likely be explained by the fact that the optimal culture media and nutrient requirements for mycelial growth vary depending on the specific strains of *Hericium* spp.

The macromorphological colony characteristics of all three strains exhibited considerable variability during growth on the test media. The texture of *H. cirrhatum* LE-BIN 5192 colonies varied from feathery on BWA to mealy-feathery on MEA and flaky-feathery on PDA. The mycelial mat of *H. coralloides* LE-BIN 5238 and *H. coralloides* LE-BIN 5254 was characterised by a flaky-feathery texture on BWA to mealy-feathery on MEA and mealy-flaky on PDA. Colony colour ranged from white (on BWA for *H. coralloides* LE-BIN 5238) to cream and pale beige (on PDA for *H. coralloides* LE-BIN 5254). The colony outline varied from smooth (on BWA for *H. coralloides*

LE-BIN 5254) to wavy and highly irregular (on MEA for *H. coralloides* LE-BIN 5238). It should be noted that the cultivation of *H. coralloides* LE-BIN 5238 on all the media studied led to darkening of the reverse side in the later stages of cultivation. Whereas prolonged cultivation of *H. coralloides* LE-BIN 5254 did not resulted in darkening of the culture media.

The micromorphological characteristics of the strains studied, both *H. cirrhatum* and *H. coralloides*, remained largely stable. However, in *H. coralloides* strains, when cultured on MEA and PDA, some changes in hyphal structure were observed, manifested by the appearance of cystidia and more frequent occurrence of hyphal swellings than when grown on BWA. It is also worth noting the loss of medallion-shaped clamps and, in general, a lower frequency of clamps in the mycelium of strains grown on BWA compared to MEA and PDA.

It is known that the efficiency of the wood biodegradation process by white-rot basidiomycetes depends on the activity of the ligninolytic complex enzymes. The enzymes responsible for the modification and subsequent degradation of lignin are primarily lignin peroxidases (LiP; EC 1.11.1.14), which catalyse the oxidation of both phenolic and non-phenolic compounds, as well as manganese peroxidases (MnP; EC 1.11.1.13) and laccases (Lac; EC 1.10.3.2), which oxidise phenolic compounds [57]. The *H. cirrhatum* LE-BIN 5192 strain exhibited high levels of oxidoreductase production and low levels of cellulases, which is consistent with the literature data for *Hericium erinaceus*. Furthermore, based on the analysis of transcripts of putative polyphenol oxidases, Van La et al. identified at least six different laccase genes expressed at different growth stages of *H. erinaceus*, which may be involved in the enzymatic oxidation of phenolic compounds [58].

The assessment of the ligninase activity of the *H. cirrhatum* LE-BIN 5192 strain revealed the appearance of a red-purple ABTS adduct. It was known that the formation of stable tyrosine-ABTS adducts as a result of tyrosyl radical reactions. Kut et al. established that the presence of pre-formed ABTS ● led to a transformation of blue laccase obtained from ascomycete fungus *Sclerotinia sclerotiorum* (Lib.) de Bary to a dark violet colour [59]. Wood-decaying basidiomycetes, in addition to n-diphenol oxidase (laccase; EC 1.10.3.2), can also produce o-diphenol oxidase (tyrosinase; EC 1.14.18.1). Tyrosinase is a copper-containing oxidase with mixed functions, capable of various oxidative modifications, including one-electron oxidation [60]. Moreover, tyrosinase is associated with the formation of brown pigments (melanins) in fungi. Thus, the origin of a purplish-red colour in the inoculum of *H. cirrhatum* LE-BIN 5192 may indicate the production of highly active tyrosinase by this strain.

Both strains of *H. coralloides* demonstrated moderate oxidative enzyme activity, which is consistent with data we previously obtained for the *H. coralloides* LE-BIN 3594 strain, isolated from the "Bryanskiy les" State Biosphere Nature Reserve (Bryansk Oblast, European part of Russia) [54]. Simultaneously, Popa et al. showed that a liquid potato-dextrose medium was optimal for the production of highly active laccase in *H. coralloides* [61]. The medium level of ligninase activity in *H. coralloides* LE-BIN 5238 and *H. coralloides* LE-BIN 5254 strains investigated in our study is probably related to the choice of MEA as the culture medium for the inoculum.

Extracellular enzymes produced by basidiomycetes play an important role not only in the depolymerisation of natural lignocellulosic substrates, but also possess the ability to decolourise resistant dyes and degrade non-polymeric compounds, such as polyhydroxyaromatic hydrocarbons, nitrotoluene and pentachlorophenol under *in vitro* conditions [62]. Despite the fact that our studied strains proved no capable of decolourising Azure B in the medium, there known the ability of *H. coralloides* to bleach azo dyes. Earlier, Nicolcioiu et al. found that a 70 % ethanol extract containing oxidative enzymes (lignin peroxidase, manganese peroxidase and laccase) from *H. coralloides* was capable of depigmenting the azo dye Bemacid Rot N-TF [63]. The process of dye decolourisation by fungi is highly complex and is associated with the presence of extracellular peroxidases in basidiomycetes, particularly manganese peroxidases [64]. Furthermore, the decolourisation process involves not only individual enzymes and multi-enzyme complexes, but also a multitude of other factors (various mediators, radicals, hydrogen peroxide, etc.) [57]. Thus, the inability of the studied strains to decolourise Azure B may be due to MnP genes being in an inactive state or the incompleteness of bleaching enzyme set. Furthermore, the toxic azo dye Azure B in the culture medium could be present in too high concentration that have inhibited mycelial growth and the production of enzymes responsible for the degradation of the dye in *Hericium* strains.

CONCLUSION

The study has yielded new data on the species richness, ecological features and cultural characteristics of the genus *Hericium* within the Republic of Dagestan. *Hericium cirrhatum* has been recorded for the first time in the North-Eastern Caucasus, whilst new localities have been identified for *H. coralloides*, a protected species in the region. Both species are preserved as herbarium specimens in the Mycological herbarium of the Komarov Botanical Institute RAS (LE) and at the mycelial stage in the Komarov Botanical Institute Basidiomycetes Culture Collection (LE-BIN). The isolated pure cultures enable the preservation of the gene pool of rare and little-known species *in vitro*. The data obtained can be used to characterise the physiological traits of strains having various geographical and ecological origins, and may be utilised in conservation practice for the reintroduction of xylotrophic species of basidiomycetes.

ACKNOWLEDGMENT

1. The authors are grateful to Dr. A.B. Ismailov (Mountain Botanical Garden, DFRC RAS, Makhachkala) and to the administration of the "Dagestansky" State Nature Reserve for help in the organisation of field studies.
2. This research was carried out within the framework of the institutional research project of the Komarov Botanical Institute RAS (project no. 124013100829-3, "Taxonomic, ecological and structural-functional diversity of fungi and fungus-like protists") using the equipment of the Core Facility Centre "Cell and Molecular Technologies in Plant Science" at the Komarov Botanical Institute, RAS (St. Petersburg, Russia).

БЛАГОДАРНОСТЬ

1. Авторы благодарят к.б.н. А.Б. Исмаилова (Горный ботанический сад ДФИЦ РАН, Махачкала)

и администрацию Государственного природного заповедника «Дагестанский» за помощь в организации полевых исследований.
2. Работа выполнена в рамках государственного задания БИН РАН по теме №124013100829-3 «Таксономическое, экологическое и структурно-функциональное разнообразие грибов и грибообразных протистов» с использованием оборудования Центра коллективного пользования научным оборудованием «Клеточные и молекулярные технологии изучения растений и грибов» Ботанического института им. В.Л. Комарова РАН (Санкт-Петербург).

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AUTHOR CONTRIBUTIONS

Sergey V. Volobuev undertook study conceptualization, carried out microscopic and molecular studies, data analysis and visualization, collected voucher specimens, wrote the original draft and participated in the manuscript editing. Yuliya Yu. Ivanushenko collected voucher specimens and participated in the manuscript editing. Nataliya V. Shakhova carried out cultural, molecular and biochemical studies, data analysis, introduced fungal pure cultures, wrote the original draft and participated in the manuscript editing. All authors are responsible for plagiarism, self-plagiarism and other ethical transgressions.

КРИТЕРИИ АВТОРСТВА

Сергей В. Волобуев разработал концепцию исследования, провел микроскопические и молекулярные исследования, анализ и визуализацию данных, собрал ваучерные образцы, написал первоначальный вариант и участвовал в редактировании рукописи. Юлия Ю. Иванушенко собрала ваучерные образцы и участвовала в редактировании рукописи. Наталия В. Шахова провела культуральные, молекулярные и биохимические исследования, анализ данных, получила чистые культуры грибов, написала первоначальный вариант рукописи и участвовала в редактировании. Все авторы в равной степени несут ответственность при обнаружении плагиата, самоплагиата и других неэтических проблем.

NO CONFLICT OF INTEREST DECLARATION

The authors declare no conflict of interest.

КОНФЛИКТ ИНТЕРЕСОВ

Авторы заявляют об отсутствии конфликта интересов.

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