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O gênero *Resupinatus* (Resupinataceae, Agaricales): taxonomia, ecologia e avaliação antimicrobiana

São Gabriel

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LAURA AMÁLIA MIRANDA COSTA

Dissertação apresentada ao Programa de Pós-graduação em Ciências Biológicas da Universidade Federal do Pampa, como requisito parcial para obtenção do Título de Mestre em Ciências Biológicas.

Orientador: Professor Dr. Jair Putzke

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RESUMO

Os fungos desempenham papéis fundamentais nos ecossistemas em que estão inseridos, apresentando uma ampla diversidade morfológica e funcional. Dentro do grupo dos Basidiomycota, os Agaricomycetes se destacam, com espécies capazes de degradar madeira e influenciar o ciclo de nutrientes. O gênero *Resupinatus* é um exemplo relevante, conhecido por sua distribuição ampla, mas ainda pouco explorado cientificamente. Apesar dos avanços recentes no estudo da taxonomia e ecologia de *Resupinatus*, lacunas permanecem em relação à sua diversidade, interações ecológicas e aplicações biotecnológicas. Um melhor entendimento dessas questões é essencial para a conservação de espécies e o aproveitamento de seu potencial biológico. O objetivo geral deste estudo foi analisar aspectos ecológicos e taxonômicos dos fungos pertencentes aos Basidiomycota, com ênfase no gênero *Resupinatus* da ordem Agaricales, com o intuito de agregar informações sobre sua diversidade, taxonomia, interações ecológicas e preferências de substrato. Para isso, o trabalho foi estruturado em três capítulos. No primeiro, foi realizada uma revisão sistemática sobre *Resupinatus*, integrando dados existentes e identificando lacunas no conhecimento. O segundo capítulo descreveu uma nova espécie do gênero, ampliando o conhecimento sobre sua distribuição no Brasil. O terceiro capítulo investigou o crescimento micelial e a atividade antimicrobiana de *Resupinatus* e *Hericium erinaceus*, visando explorar possíveis aplicações biotecnológicas. Os resultados obtidos reforçam a importância dos estudos taxonômicos e ecológicos para a compreensão da biodiversidade fúngica e suas interações. Além disso, a investigação do potencial antimicrobiano e do crescimento micelial amplia as perspectivas para o uso de *Resupinatus* em aplicações biotecnológicas. Assim, este estudo contribui para o avanço do conhecimento sobre fungos e reforça a necessidade de estudos futuros sobre sua diversidade e aplicações.

Palavras-Chave: Macrofungo, crescimento micelial, nova espécie, biodiversidade, atividade biológica.

ABSTRACT

Fungi play fundamental roles in the ecosystems they are found, presenting a wide morphological and functional diversity. Within the Basidiomycota group, Agaricomycetes stand out, with species capable of degrading wood and influencing the nutrient cycle. The genus *Resupinatus* is a relevant example, known for its wide distribution, but still little explored scientifically. Despite recent advances in the study of the taxonomy and ecology of *Resupinatus*, gaps remain regarding its diversity, ecological interactions, and biotechnological applications. A better understanding of these issues is essential for the conservation of species and conserving species and exploiting addition, fungi can function as environmental bioindicators, contributing to the monitoring and preservation of habitats. The general objective of this study was to analyze ecological and taxonomic aspects of fungi belonging to the Basidiomycota, with emphasis on the genus *Resupinatus* of the order Agaricales, to aggregate information on their diversity, taxonomy, ecological interactions, and substrate preferences. For this purpose, the work was structured in three chapters. First, a systematic review of *Resupinatus* was conducted, integrating existing data and identifying gaps in knowledge. The second chapter described a new species of the genus, expanding the knowledge of its distribution in Brazil. The third chapter investigated the mycelial growth and antimicrobial activity of *Resupinatus* and *Hericium erinaceus*, aiming to explore possible biotechnological applications. The results obtained reinforce the importance of taxonomic and ecological studies for the understanding of fungal biodiversity and its interactions. Furthermore, the investigation of the antimicrobial potential and mycelial growth broadens the perspectives for the use of *Resupinatus* in biotechnological applications. Thus, this study contributes to the advancement of knowledge about fungi and reinforces the need for future studies on their diversity and applications.

Keywords: Macrofungus, mycelial growth, new species, biodiversity, biological activity.

LISTA DE FIGURAS

- Figure 1** Representation of the morphological diversity of the genus. a *Resupinatus merulioides* (McDonald 2015), b *Resupinatus porosus* (mushroomobserver.org), c *Resupinatus applicatus* (nahuby.sk. 2013), and d *Resupinatus poriaeformis* (Yatoo and Sheikh 2022)..... 31
- Figure 2** Diversity of the genera characteristic of *Resupinatus* compared with other groups. RStudio version 4.4.1 (Csardi and Nepusz 2006; Pedersen 2020), adapted from Bodensteiner et al. 2004; Moncalvo et al. 2002 and Silva-Filho et al. 2023..... 34
- Figure 3** Internal transcribed spacer (ITS) sequence containing ITS1 and ITS4. Source the author 38
- Figure 4** Points of occurrence from works analyzed with geographical distributions available . 44
- Figure 5** Sequences in PhyML v3.1, employing the GTR+G+I substitution model. The aLRT SH-like support values are indicated at the nodes and represent the branch support probabilities. aLRT SH-like values ≥ 0.70 are shown at the nodes and indicate strong support for the branch. The species analyzed are highlighted. *H. flabelliformis*, *H. lageniformis*, and *H. thornii* were used as outgroups..... 70
- Figure 6** Maximum likelihood (ML) phylogenetic tree constructed using nrLSU sequences in PhyML v3.1, employing the TN93 substitution model. aLRT SH-like values ≥ 0.70 are shown at the nodes and indicate strong support for the branch. The species analyzed are highlighted. *H. flabelliformis*, *H. lageniformis*, and *H. thornii* were used as outgroups..... 71
- Figure 7** *Resupinatus brunneus*: (LFPAMPA005). a–b) Basidiomata, c) Pleurocystidia and hymenophore trama showing metuloids d) metuloid, e) Basidiospores. Scale bars: a = 9 cm, b = 2cm, c = 20 μm d = 30 μm , e = 10 μm 73
- Figure 8** Plates with treatments after 10 days. The first line is from *Hericium* and the second is from *Resupinatus* 84

LISTA DE TABELAS

Table 1 Species of the genus following the Index Fungorum 2025	23
Table 2 Principal macro- and microscopic features of <i>Resupinatus</i> species reported in the literature	26
Table 3 Country/region relationships and records of the species found.....	40
Table 4 Relationships among species and the type/preference of substrate. Reference with signal: - are about just Index Fungorum information	45
Table 5 GenBank accession numbers of sequences used in the phylogenetic analyses (newly-generated sequences are indicated in bold).....	68
Table 6 <i>Hericium erinaceus</i> and <i>Resupinatus brunneus</i> , species H and R, respectively. Standard deviation (sd - mm), Standard error of the mean (se - mm) and Confidence interval (ci):	84
Table 7 p-values of the statistical comparison between means using the t-test, verifying whether there was a significant difference in mycelial growth between the different treatments for each species	85

SUMÁRIO

1 INTRODUÇÃO.....	11
2 OBJETIVOS.....	15
2.1 Objetivo geral	15
2.2 Objetivos específicos	15
3 RESULTADOS	16
3.1 Artigo 1 Exploring the Genus <i>Resupinatus</i> (Agaricales, Resupinataceae): A Review	17
3.2 Artigo 2 A new species of <i>Resupinatus</i> (Agaricales, Resupinataceae) with metuloid cystidia in the hymenium found in the south of Brazil	64
3.3 Artigo 3 Evaluation of mycelial growth and antimicrobial activity of <i>Resupinatus brunneus</i> (Resupinataceae) and <i>Hericium erinaceus</i> (Herinaceae)	79
CONCLUSÃO	94
REFERÊNCIAS BIBLIOGRÁFICAS.....	95

1 INTRODUÇÃO

Dentre os microrganismos que desempenham papéis importantes no ecossistema em que estão inseridos, os fungos são amplamente difundidos. Este grupo pertence aos Eukarya que se encontra subdividido em outras categorias. Dykarya é uma das ordens pertencentes aos Eukarya, onde os Basidiomycota se enquadram e caracterizam como fungos que produzem basidiomas conhecidos como cogumelos (GERKE *et al.*, 2020).

Mesmo diante de ampla quantidade de espécies estimadas sobre os fungos, em torno de 1.4-4.2 milhões, os Basidiomycota apresentam uma estimativa em torno de 41.270 registros. Esses números podem variar dependendo do método de análise utilizado, todavia estipula-se que este número seja ainda maior (HYDE *et al.*, 2019; HE *et al.*, 2019, 2022, 2024). A presença fúngica é relatada no mundo há cerca de 1,8 bilhões de anos. Eles compreendem formas diversas e podem se apresentar como seres unicelulares, que incluem as leveduras, por exemplo. Outra forma existente é como seres filamentosos, que abrangem diversas morfologias, onde estão incluídos os Agaricomycetes (HASAN & GUPTA, 2012; SARBHOY, AGARWAL & VARSHNEY, 1996).

Os fungos apresentam diversas funções fundamentais em diferentes áreas. Estas funções podem variar desde propriedades contra doenças humanas e em plantas, melhoramento de culturas, produção de alimentos e bebidas, commodities, remediação de efluentes, produção de biocombustíveis e eliminação de resíduos (HYDE *et al.*, 2019). Os Agaricomycetes compreendem cerca de oito ordens e dentre elas encontramos os Agaricales, um grupo diverso e que engloba muitas espécies. Estas espécies possuem a capacidade de degradar de madeira e grande parte do material disponível, dentre outros potenciais (GOODELL, WINANDY & MORRELL, 2020; VIRÁGH *et al.*, 2022).

Resupinatus é um exemplo de gênero dentro de Agaricales que apresenta capacidade de degradar material lenhoso, possui ampla distribuição e algumas espécies são consideradas raras e inexploradas. Estudos recentes têm agregado informações sobre o gênero a partir de dados moleculares, descrições taxonômicas e contribuições sobre suas associações com hospedeiros, além da complementação de dados sobre a distribuição geográfica. Diante das informações disponíveis sobre *Resupinatus*, as associações com outros grupos e hospedeiros ainda seguem descritas de forma isolada (MCDONALD, 2015; HE *et al.*, 2019; CARPOURON *et al.*, 2024). Apesar dos avanços sobre dados taxonômicos e de diversidade sobre o gênero, ainda existe muito

a ser explorado. Este fato se estende a outros gêneros de fungos e reforçam a necessidade de mais estudos sobre a biodiversidade e potenciais aplicações (HYDE *et al.*, 2019).

Além da capacidade de degradação de celulose e lignina, os fungos são considerados bioindicadores de fatores ambientais. Como indicadores biológicos são utilizados para acompanhamento e monitoramento de fatores físicos e químicos, que sinalizam a qualidade do ambiente (GERHARDT, 2002; SOARES *et al.*, 2022). O acompanhamento de fatores ambientais auxilia no monitoramento de ecossistemas, contribuindo para o fornecimento de dados sobre espécies muitas vezes consideradas raras. Essas espécies em geral, se desenvolvem em determinados locais onde existe uma combinação específica e favorável de suas preferências ecológicas (BRANCO *et al.*, 2022).

Para que a conservação de diversas espécies ocorra, além da combinação de fatores bióticos e abióticos, estudos taxonômicos e sistemáticos são indispensáveis. A realização de estudos interdisciplinares colabora para a identificação de novas espécies raras ou inexploradas, além de contribuir com o fornecimento de dados ecológicos e possíveis aplicações biotecnológicas (ZHOU & MAY, 2022). A presença dos cogumelos em determinados locais está associada à presença de matéria orgânica. Durante o processo de desenvolvimento, os fungos degradam o material lenhoso e realizam um processo de conversão, conseguindo decompor diversos compostos e absorver toxinas, metais pesados entre outros e transformando-os em nutrientes favoráveis ao seu crescimento (WARNASURIYA *et al.*, 2023).

Dentre os substratos onde os fungos podem ser encontrados, a madeira é um dos mais abundantes. A produção de esporos acontece de forma eficaz e a partir disso os fungos desenvolvem estruturas conhecidas como hifas. Estas são células alongadas que favorecem o crescimento e sucesso na colonização. Com o crescimento avançado das hifas, essas estruturas agrupadas e em grande quantidade recebem forma de micélio. Conforme o desenvolvimento aumenta, o micélio pode se espalhar da superfície até o interior do material e iniciar a produção de biomassa fúngica (GOODELL, WINANDY & MORRELL, 2020).

Através deste potencial que os fungos apresentam, eles recebem a denominação de saprotróficos e constituem um grupo responsável pela regulação da estrutura do ecossistema onde se encontram. Essa regulação acontece por meio da degradação de madeira e material orgânico, que são transformados e reaproveitados pelos fungos e outras espécies em diferentes níveis. A partir da decomposição, a biomassa gerada favorece a produção de enzimas extracelulares, por

exemplo, que são importantes indicadores da dinâmica e ciclo de nutrientes disponíveis (MIDGLEY & PHILIPS, 2019).

Muitos gêneros têm sido estudados também pelo amplo potencial de utilização em áreas com atividade biológica promissora. Estas espécies podem exibir capacidade de produção e liberação de enzimas extracelulares, bem como propriedades antimicrobianas. Um exemplo é o gênero *Hericium* mundialmente conhecido e que tem sido amplamente estudado devido as suas aplicações. Possui efeito terapêutico, através da produção e liberação de metabólitos secundários com efeitos contra bactérias, células tóxicas e doenças que atingem o sistema nervoso (THONGBAI *et al.*, 2015; SANDARGO *et al.*, 2019; QIU *et al.*, 2024).

Embora *Hericium* seja estudado numa escala maior, gêneros como *Resupinatus* apresentam poucos estudos, por exemplo, sobre a produção e liberação de metabólitos secundários e outras atividades biológicas (SUNDIN *et al.*, 1993; EILBERT *et al.*, 2000; HARMS *et al.*, 2023). A avaliação e descrição de dados sobre gêneros distintos e pouco analisados são essenciais para o fornecimento de informações mais precisas e concretas sobre a biodiversidade fúngica e o ecossistema onde estão inseridos.

As associações podem indicar preferências e por consequência ajudar na preservação de espécies, além de indicar as características ambientais por meio de espécies de árvores e fungos presentes. Compreender as interações ecológicas viabiliza a análise de condições climáticas e auxilia na conservação do habitat. Com isso, estudos sobre fungos envolvendo taxonomia e biodiversidade são extremamente valiosos para uma melhor compreensão de suas interações e características, podendo proporcionar análises sobre suas propriedades biológicas e aplicações em diversas áreas. Existem diversas lacunas presentes sobre dados como a distribuição geográfica, associações com outros organismos e descrições taxonômicas precisas envolvendo gêneros como *Resupinatus*.

Portanto, o presente trabalho teve como objetivo compreender melhor os dados taxonômicos e ecológicos do gênero *Resupinatus*, bem como a diversidade fúngica e suas interações. Para isso o trabalho foi subdividido em três capítulos. A primeira parte foi desenvolvida a partir de uma revisão sistemática realizada sobre o gênero, buscando compreender melhor as informações disponíveis, ressaltar e unificar análises, e preencher lacunas existentes sobre *Resupinatus*. Posteriormente a descrição de uma nova espécie e ocorrência para o Brasil sobre o gênero foi delineada, através da descrição taxonômica e análise molecular. Por fim, a fim de

disponibilizar novos dados e possíveis aplicações, a análise do crescimento micelial em diferentes tratamentos e a atividade antimicrobiana foram realizadas com *Resupinatus brunneus* e *Hericium erinaceus*.

2 OBJETIVOS

2.1 Objetivo geral

Analisar os aspectos ecológicos e taxonômicos dos fungos pertencentes aos Basidiomycota, com ênfase no gênero *Resupinatus* da ordem Agaricales, com o intuito de agregar informações sobre sua diversidade, taxonomia, interações ecológicas e preferências de substrato.

2.2 Objetivos específicos

- Realizar uma revisão sistemática sobre o gênero *Resupinatus*, englobando informações sobre suas características, dados geográficos e moleculares, a fim de contribuir para o seu conhecimento taxonômico e ecológico;
- Descrever uma nova espécie de *Resupinatus*, com base nas características taxonômicas e moleculares;
- Avaliar o crescimento micelial em diferentes meios de cultura e a atividade antimicrobiana de uma nova espécie de *Resupinatus* e *Hericiium erinaceus*.

3 RESULTADOS

Os resultados que compõem este estudo estão dispostos em três capítulos. O primeiro foi submetido à revista *Biodiversity and Conservation* (Fator de Impacto: 3.0, ISSN: 0960-3115, conceito A2 - Qualis Capes - 2020). O segundo foi submetido à revista *Phytotaxa* (Fator de Impacto: 1.1, ISSN 1179-3155, conceito A4 - Qualis Capes - 2020). O terceiro será submetido à revista *Current Microbiology* (Fator de Impacto: 2.6, ISSN: 1432-0991, conceito B1 - Qualis Capes - 2020).

3.1 Artigo 1 Exploring the Genus *Resupinatus* (Agaricales, Resupinataceae): A Review

Artigo submetido à revista Biodiversity and Conservation, ISSN: 0960-3115, Fator de Impacto: 3,0, conceito A2 - Qualis Capes-2020.

Exploring the Genus *Resupinatus* (Agaricales, Resupinataceae): A Review

Abstract

Fungal research is significant in various domains, and biodiversity conservation is often initiated through regional surveys that enhance our understanding of fungal dynamics and their ecological contexts. The classification of *Resupinatus* (tribe *Resupinateae sensu stricto*) remains ambiguous. Like other Basidiomycetes genera, *Resupinatus* can degrade recalcitrant components such as leaf litter. Their interactions with woody materials range from decomposition to the development of specific pathogenicity in these environments. The genus *Resupinatus* has numerous knowledge gaps that require further investigation. This review aims to summarize the existing research on this genus and supplement this information. A literature search was conducted via primary databases, and selected studies were aligned with the keywords and subtopics of interest. This study was organized into four main sections, with classification, taxonomic description, and phylogeny being the most extensively researched areas, followed by geographical distribution and host associations. A discussion of the species nomenclature followed these methods. Morphological variations contribute to the diversity of the genus and complicate efforts to determine its precise taxonomic position. Consequently, questions regarding ecological interactions and host associations remain unanswered. A broader dataset enhances species descriptions and provides insights into these interactions. Expanding our knowledge of fungal communities is therefore essential.

Keywords: Biodiversity, taxonomic, conservation, morphology, ecological interactions, wood-inhabiting.

Introduction

Fungi are important in many ways and are present in most environments. These are key players in the ecosystem in which they are found. Their existence in certain locations, associated with their development, helps in monitoring and preserving biodiversity (Bazzicalupo et al. 2022).

Studies have revealed the existence of approximately 155,000 described fungal species. This number is extremely low compared with the estimated 2–3 million species that have not yet been fully described (Kirk et al. 2008; Niskanen et al. 2023).

The conservation of fungal biodiversity is something that the authors point out, given the important role they play in different areas such as medicine, the pharmaceutical industry, and cooking, among others. Therefore, the need to include fungi in conservation measures more systematically is essential (Cao, Wu and Yu 2021; Gonçalves et al. 2021). Fungi can take different forms depending on the type of nutrition, resulting in different basidiomes. Nutrition is also related to the lifestyle of fungi, which can be directly associated with the food used. Thus, they can be classified as saprophytes or biotrophs (Niskanen et al. 2023).

Resupinatus Nees ex Gray (1821:617) pertains to the tribe *Resupinateae*, family Pleurotaceae, Agaricales, Agaricomycetes, is a saprophytic and cosmopolitan genus with external morphological characteristics similar to those of *Hohenbuehelia* Schulzer (1866) and *Pleurotopsis* Henn. The genus is dark-colored (grayish), small, pendent or resupinate, and wood-inhabiting, with diverse hymenophore types. New species have been described on the basis of morphological and molecular analyses in recent years; for example, other species within this genus have been redistributed (Singer 1962; Pegler 1986; Redhead and Nagasawa 1987; He et al. 2019; Yattoo and Sheikh 2022; He et al. 2024).

Currently, the genus is characterized by 49 species (Liu et al. 2024; Species Fungorum 2025). Furthermore, some members of *Resupinateae*, such as *Asterotus* Singer and *Resupinatus*, have been classified within Tricholomataceae, but recent molecular studies have led *Resupinatus* to a new classification for Pleurotaceae (Thorn et al. 2000; Consiglio and Setti 2018; Liu et al. 2024; He et al. 2024).

This study aimed to review the literature on *Resupinatus* and analyze recently described species, focusing on their taxonomic implications, ecological preferences, and host associations. A review of the genus is essential, as several species have been reclassified owing to advances in molecular biology. Understanding its diversity can contribute to the conservation of sites and habitats with rare and threatened species. Therefore, a comprehensive synthesis is needed to consolidate this information.

Materials and methods

To conduct this literature review, the terms “*Resupinatus* Nees ex Gray; fungal conservation; diversity; taxonomy; *Hohenbuehelia*; phylogeny; molecular analysis; Agaricales; ” were consulted in the following databases: ScienceDirect (<https://www.sciencedirect.com>), PubMed (<https://pubmed.ncbi.nlm.nih.gov>), Scopus (<https://www.scopus.com>), ResearchGate (<https://www.researchgate.net>), SciFinder (<https://www.cas.org>), academic google (<https://scholar.google.com.br/?hl=pt>), and Web of Science (<https://access.clarivate.com>). The data collection took place from April 12, 2024, to February 28, 2025. The articles selected for the review were chosen on the basis of the evaluation of abstracts and keywords, and those that fit the criteria were evaluated according to the subthemes and aspects addressed.

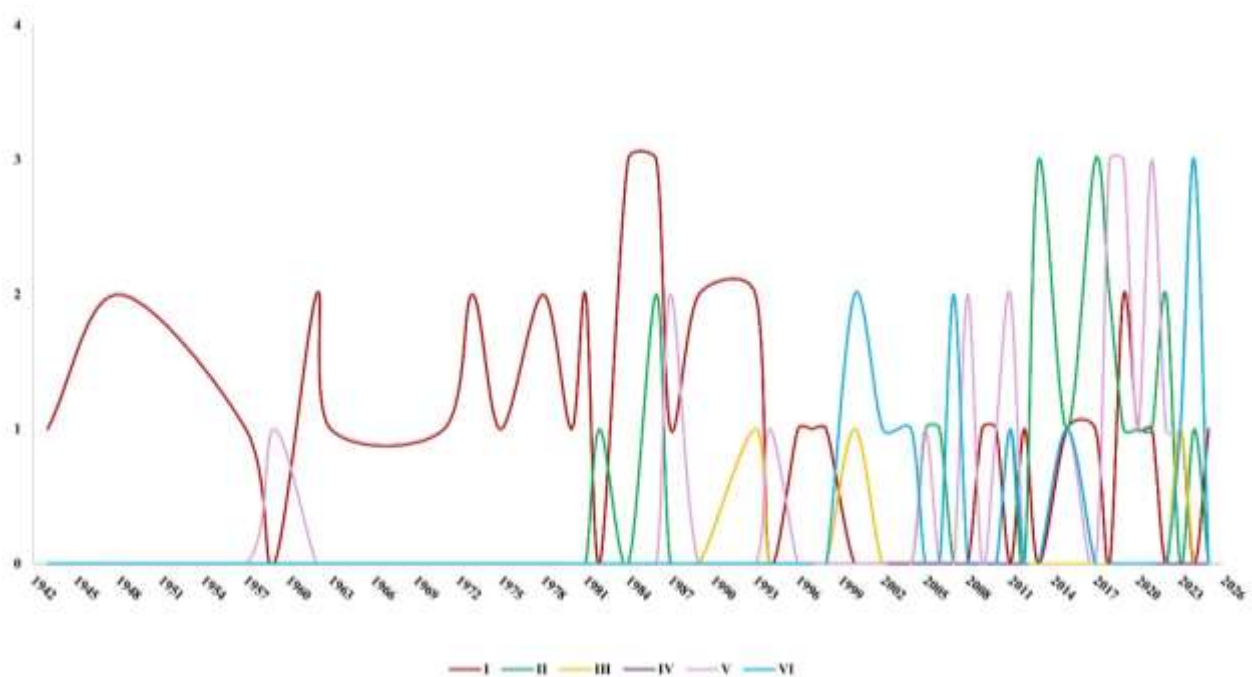
The R libraries `igraph` and `ggraph` were used to construct the network. First, the data were organized into a data frame containing two sets of information: fungal genera and their respective characteristics. The characteristics were stored in a list, allowing the association of multiple characteristics with each genus. From this data frame, an additional data frame was constructed that contained the graph edges, where each edge represented the relationship between a genus and a characteristic. Using the `graph_from_data_frame` function of the `igraph` package, a graph object is created from the generated edge data frame. The `ggraph` package was used to visualize the network, which allowed the intuitive creation of graph graphs. A circular layout was chosen to represent the connections between genera and their characteristics. The nodes were colored according to their category (genera or features), and the labels were adjusted to avoid overlaps via the `geom_node_label` function with the `repel` option (Csardi and Nepusz 2006; Pedersen 2020).

Results and discussion

Most of the analyzed articles focused on phylogenetic and molecular studies, whereas others addressed the description of new species or emphasized the need for more practical biodiversity assessments. Some studies contained only one citation of the genus, presented in tables, or listed various species, with the first record appearing after years. This finding may indicate that species that require further analysis on the basis of their ecological role in the

ecosystem. After analyzing these studies, we identified areas with more available information about the genus. Figure 1 illustrates these areas, showing a significant increase in contributions and studies across different segments after 2000.

However, many gaps remain that require further investigation. Importantly, some studies overlap in focus, correlating with multiple areas. For this analysis, however, we grouped them on the basis of their primary study area. Some works address two or more topics simultaneously, for example, phylogenetic analysis is often linked to studies on classification and nomenclature or the description of new species. A deeper understanding is necessary in both cases to provide more detailed insights into the genus and related taxa.



Graph 1 Study area of the works analyzed, where I = morphogenesis and taxonomic classification, II = geographical distribution and host associations, III = metabolite analysis, IV = nematophagous activity, V = new description/addition/record, and VI = molecular

To better exemplify their descriptions on the basis of the themes of the works, the present work is organized into sections that reflect the main aspects of the analysis. This manuscript provides a better understanding of taxonomic contributions (overviews, evolutionary studies, relationships, and molecular and morphological systematics), new descriptions and records (such

as first records, reclassifications, and newly discovered species or genera), and geographical distributions (including first records and checklists, biodiversity contributions, and host associations).

Morphogenesis and taxonomic classification

Basidiomas within Basidiomycota have diverse morphologies and can be naked lawns of basidia, coralloid, or even more complex forms (pileate-stipitate). Another form found is resupinate and characterized by a flattened appearance such as crusts more adhered to the substrate, which may be a disadvantage of a common ancestral form of the best known within the Agaricomycetes. During the process of evolution, which has occurred quickly, the structures known as the pileus, stipe, and hymenophore have differentiated (Varga et al. 2019; Nagy et al. 2023).

The type species of the genus is *Resupinatus applicatus* (Batsch. ex Fr.) S. F. Gray, and the absence of metuloids separates *Resupinatus* from *Hohenbuehelia*. The dark coloration also helps distinguish it from other pleurotoid genera, where 'resupinatus' is derived from the Latin *resupinus*, meaning 'bent backward' or 'inverted', referring to the growth habit of the basidiome, with the hymenium facing downward. The genus has pleurotoid basidiomes. Small, sessile, or nearly sessile pileus, discoid or cup shaped, attached to the substrate dorsally or laterally, with a dark coloration, brown to black. Lamellae radiating from a lateral or eccentric point. Stipes are usually absent or lateral and very short, inconspicuous, and sometimes form a pseudostipe. White spore print. Basidiospores are subglobose to ellipsoid or elongated, sometimes allantoid, inamyloid, smooth, and thin walled. The lamellar edge is sterile and sometimes gelatinized.

Cheilocystidia are generally abundant and sometimes inconspicuous. Pleurocystidia and metuloids are absent. Hymenophoral trams are regular and sometimes gelatinized. Pileus cortical layer with an asterostromelloid structure. Pileus context gelatinized, with extremely thin, clamp-connected hyphae. Lignin is sometimes found on small branches and even on palms (Putzke and Putzke 2025).

Following the Index Fungorum 2025 register names, the genus has 78 records with 49 valid species, including 4 variations and 29 synonyms in the world (Table 1).

Table 1 Species of the genus following the Index Fungorum 2025

Specie	Author	Synonym
<i>Resupinatus alboniger</i>	(Pat.) Singer 1978	-
<i>Resupinatus alboniger</i> var. <i>bisporus</i>	Singer 1978	<i>Resupinatus alboniger</i>
<i>Resupinatus algidus</i>	(Fr.) M. Lange 1955	-
<i>Resupinatus algidus</i> var. <i>dendrocystis</i>	M. Lange 1955	<i>Resupinatus algidus</i>
<i>Resupinatus americanus</i>	Consiglio and Setti 2018	-
<i>Resupinatus applicatus</i>	(Batsch) Gray 1821	-
<i>Resupinatus applicatus</i> f. <i>kavinae</i>	(Pilát) Pilát 1935	<i>Resupinatus kavinae</i>
<i>Resupinatus applicatus</i> var. <i>trichotis</i>	(Pers.) Krieglst. 1992	<i>Resupinatus trichotis</i>
<i>Resupinatus approximans</i>	(Peck) Murrill 1915	<i>Hohenbuehelia approximans</i>
<i>Resupinatus argentinus</i>	(Singer) Singer 1973	<i>Resupinatus alboniger</i>
<i>Resupinatus atrocoeruleus</i>	(Fr.) Murrill 1912	<i>Hohenbuehelia atrocoerulea</i>
<i>Resupinatus atropellitus</i>	(Peck) Murrill 1915	-
<i>Resupinatus bicolor</i>	(Mont.) Singer 1973	<i>Resupinatus dealbatus</i>
<i>Resupinatus campanulatus</i>	(Peck) Murrill 1915	-
<i>Resupinatus chilensis</i>	Singer 1948	-
<i>Resupinatus cinerascens</i>	(Cleland) Grgur. 1997	-
<i>Resupinatus cinereus</i>	(Pat.) McDonald and Thorn 2019	-
<i>Resupinatus conglobatus</i>	(Burt) McDonald and Thorn 2019	-
<i>Resupinatus conspersus</i>	(Pers.) Thorn, Moncalvo and Redhead 2006	-
<i>Resupinatus crawfordiae</i>	G. Stev. 1964	<i>Panellus crawfordiae</i>
<i>Resupinatus cubensis</i>	Murrill 1915	<i>Hohenbuehelia cubensis</i>
<i>Resupinatus cupuliformis</i>	(Berk. and Ravenel) McDonald and Thorn 2019	-
<i>Resupinatus cyatheae</i>	Comer 1996	-
<i>Resupinatus cyphelliformis</i>	(Berk.) Singer 1951	<i>Hohenbuehelia cyphelliformis</i>

<i>Resupinatus daedalea</i>	(Schwein.) McDonald and Thorn 2019	-
<i>Resupinatus dealbatus</i>	(Berk.) Singer 1973	-
<i>Resupinatus dorotheae</i>	G. Stev. 1964	<i>Delicatula dorotheae</i>
<i>Resupinatus europaeus</i>	Consiglio and Setti 2018	-
<i>Resupinatus graminum</i>	(Singer) Singer 1973	-
<i>Resupinatus griseopallidus</i>	(Weinm.) Knudsen and Elborne 2008	-
<i>Resupinatus griseus</i>	(Peck) Murrill 1915	<i>Hohenbuehelia grisea</i>
<i>Resupinatus hausknechtii</i>	Consiglio and Setti 2017b	-
<i>Resupinatus huia</i>	(G. Cunn.) Thorn, Moncalvo and Redhead 2006	-
<i>Resupinatus hyalinus</i>	(Singer) Thorn, Moncalvo and Redhead 2006	-
<i>Resupinatus incanus</i>	(Kalchbr.) Thorn, Moncalvo and Redhead 2006	-
<i>Resupinatus kavinae</i>	(Pilát) Moser 1978	-
<i>Resupinatus leightonii</i>	(Berk.) Orton 1960	<i>Hohenbuehelia leightonii</i>
<i>Resupinatus merulioides</i>	Redhead and Nagas.1987	-
<i>Resupinatus multilamellatus</i>	Corner 1996	-
<i>Resupinatus niger</i>	(Schwein.) Murrill 1915	<i>Hohenbuehelia nigra</i>
<i>Resupinatus odoratus</i>	Pradeep, Bijeeesh and Kumar 2020	-
<i>Resupinatus omphalioides</i>	Singer 1965	-
<i>Resupinatus orizabensis</i>	Murrill 1915	<i>Pleurotus orizabensis</i>
<i>Resupinatus pahangensis</i>	Corner 1996	-
<i>Resupinatus petaloides</i>	(Bull.) Kühner 1980	<i>Hohenbuehelia petaloides</i>
<i>Resupinatus physaroides</i>	Malençon 1975	-
<i>Resupinatus plectocomiae</i>	Corner 1996	-
<i>Resupinatus poriaeformis</i>	(Pers.) Thorn, Moncalvo and Redhead 2006	-
<i>Resupinatus porosus</i>	MP Martín, Lodge and Thorn 2006	-
<i>Resupinatus porrigens</i>	Xu and Li 2024	-

<i>Resupinatus purpureo-olivaceus</i>	G. Stev. 1964	<i>Pleurotus purpureo-olivaceus</i>
<i>Resupinatus reviviscens</i>	Carpouren and Raspé 2024	-
<i>Resupinatus rhacodium</i>	(Berk. and MA Curtis) Singer 1951	<i>Resupinatus trichotis</i>
<i>Resupinatus rickii</i>	Trierv-Per. and Espinho 2019	-
<i>Resupinatus rouxii</i>	Consiglio and Setti 2018	-
<i>Resupinatus rubrhacodium</i>	Singer 1952	-
<i>Resupinatus silvanus</i>	(Sacc.) Singer 1951	<i>Hohenbuehelia silvana</i>
<i>Resupinatus sordulentus</i>	(Berk. and Broome) G. Stev. 1964	-
<i>Resupinatus stictoides</i>	(Speg.) Nakasone 2008	-
<i>Resupinatus striatulus</i>	(Pers.) Murrill 1915	-
<i>Resupinatus striatulus</i> var. <i>prolificans</i>	Lib.-Barnes 1981	<i>Resupinatus striatulus</i>
<i>Resupinatus subapplicatus</i>	(Cleland) Grgur. 1997	-
<i>Resupinatus subbarbatulus</i>	Murrill 1915	<i>Pleurotus subbarbatulus</i>
<i>Resupinatus subbarbatus</i>	(Berk. and MA Curtis) Murrill 1915	<i>Hohenbuehelia subbarbata</i>
<i>Resupinatus subrhacodium</i>	Singer 1952	-
<i>Resupinatus subvinaceus</i>	Comer 1996	-
<i>Resupinatus taxi</i>	(Lév.) Thorn, Moncalvo and Redhead 2006	-
<i>Resupinatus trichotis</i>	(Pers.) Singer 1961	-
<i>Resupinatus tristis</i>	G. Stev. 1964	<i>Campanella tristis</i>
<i>Resupinatus unguicularis</i>	(Fr.) Singer 1951	<i>Hohenbuehelia unguicularis</i>
<i>Resupinatus urceolatus</i>	(Wallr. ex Fr.) Thorn, Moncalvo and Redhead 2006	-
<i>Resupinatus urceoloides</i>	McDonald and Thorn 2019	-
<i>Resupinatus ursinus</i>	(Fr.) Murrill 1915	<i>Lentinellus ursinus</i>
<i>Resupinatus vetlinianus</i>	(Domański) MM Moser 1979	<i>Lignomyces vetlinianus</i>
<i>Resupinatus vinosolidus</i>	(Segedin) Cooper 2012b	-

<i>Resupinatus violaceofulvus</i>	(Batsch) Murrill 1915	<i>Panellus violaceofulvus</i>
<i>Resupinatus violaceogriseus</i>	G. Stev. 1964	<i>Marasmiellus violaceogriseus</i>
<i>Resupinatus yunnanensis</i>	Yang and Zhao 2023	-

Resupinatus species are mostly found in Pleurotaceae, but some species have synonyms and have been described in different families, such as *Resupinatus crawfordiae* (G. Stev.) as *Panellus crawfordiae* (Segedin, Buchanan and Wilkie 1995) and *Resupinatus violaceofulvus* ((Batsch) Murrill) as *Panellus violaceofulvus* in Mycenaceae, *Resupinatus porrigens* (Xu and Li) in Thricolomataceae, *Resupinatus tristis* (G. Stev.) as *Campanella tristis* in Marasmiaceae (Horak 1971; Segedin 1993), *Resupinatus ursinus* ((Fr.) Murrill) as *Lentinellus ursinus* in Auriscalpiaceae, and *Resupinatus violaceogriseus* (G. Stev.) as *Marasmiellus violaceogriseus* in Omphalotaceae. *Resupinatus purpureo-olivaceus* (now in *Pleurotus* (Segedin, Buchanan and Wilkie 1995), *Resupinatus dorotheae* now in *Delicatula* (Horak 1971) and *Resupinatus sordulentus* now as *Conchomyces bursiformis* (Horak 1981) (Index Fungorum 2025; McDonald 2015).

To better exemplify some of the actual species of the genus, some macro- and micromorphological features were placed together (Table 2), following the traditional characteristics that distinguish them from each other. Various species present similar characteristics in terms of macromorphology but differ in micromorphology, as we described below.

Table 2 Principal macro- and microscopic features of *Resupinatus* species reported in the literature

Specie	Macroscopic features	Basidiospores (μm)	Observations	Reference (s)
<i>R. applicatus</i> (Batsch) Gray	Basidiocarps 10-20 mm with cap surface tomentose. Blackish when fresh and dry grayish. Stipe rudimentary to absent	Smaller subglobose $4.2-5.1(-5.5) \times 3.7-4.5(-5)$	Considered very similar to <i>R. striatulus</i> and <i>R. trichotis</i> (Pers.) Singer	Gonou-Zagou et al. 2011; Thorn and Barron 1986; Akçay 2021; Bijeesh, Kumar and Pradeep 2020; Consiglio and Setti 2018; He et al. 2019
<i>Resupinatus trichotis</i> (Pers.) Singer	Basidiocarps larger than 10 mm with cap surface with prominent, shaggy, and blackish hairs	Subglobose to ovate basidiospores $4.8-5.6 \times 4.3-5.2$	It is considered similar to <i>R. striatulus</i> in general appearance and presents a clavate to ventricose cheilocystidia	Gonou-Zagou et al. 2011; Thorn and Barron 1986; McDonald 2015; Akçay 2021; Consiglio and Setti 2018
<i>Resupinatus striatulus</i> (Pers.) Murrill	Basidiomata sessile, smaller than 10 mm with cap surface striate and glabrous. First dark cream to ocher, dark brown to almost black when dry	Hyaline, inamyloid, smooth-walled, globose to subglobose, $(4.2-4.7-5.4(-5.7) \times (4-)4.7-5.3(-5.6)$	Turkish suggested name: "Çizgili cüceyanak". It has a vesiform cheilocystidia and is considered similar and a variation of <i>R. applicatus</i>	Gonou-Zagou et al. 2011; Thorn and Barron 1986; McDonald 2015; Akçay 2021; Lotz-Winter et al. 2021
<i>Resupinatus odoratus</i> Pradeep, Bijeesh and Kumar sp. nov.	Larger basidiomata (Pileus: 3-26 mm), present a fragrant spicy odor and turn blackish and hard on drying. Surface fawn brown, which varies to young and old form. Stipe absent, sessile, and coralloid hyphae	Globose to subglobose basidiospores $5.2-6.4 \times 5.2-6$	It is very close to <i>R. merulioides</i> and resembles <i>R. porrigens</i> , but has differences in the pileus and the hymenium	Bijeesh, Kumar and Pradeep 2020; Liu et al. 2024
<i>Resupinatus merulioides</i> Redhead and Nagas.	Coralloid hyphae, pileus 2-19 mm, lacking stipe, brownish-gray to darker gray-brown, and surface hairs	Inamyloid subglobose $5.2-6.4 \times 5.2-6.0$	It is a unique hymenophore feature within the genus. Absence of metuloidal cystidia	Bijeesh, Kumar and Pradeep 2020; Redhead and Nagasawa 1987; Cooper 2012b
<i>Resupinatus porosus</i> M.P. Martín, Lodge and Thorn	Basidiomas are pubescent to pruinose, gregarious to imbricate with a surface orange gray, grayish orange, or brownish orange to light brown, 0.5-1.4 x 0.2-0.6 cm. Hymenophore pale orange to grayish orange and heavily encrusted pileipellis hyphae	Smaller subglobose basidiospores $4.6-5.4 (-5.8) \times (3) 4.0-5.0 (-5.2)$ with a distinct apiculus nondextrinoid and nonamyloid	Resembles <i>R. odoratus</i> but differs in pileus and hymenophore type, basidiospore size, and <i>R. applicatus</i> but differs in hymenophore type	Bijeesh, Kumar and Pradeep 2020; Thorn et al. 2005; Triervelier-Pereira, Prado-Elias and Baltazar 2024

<i>Resupinatus vinosolividus</i> (Segedin) Cooper	Livid vinaceous and floccose pileus, alveolate and livid hymenium	Larger 6.0–7.0 × 3.5–4.0 (6.0 × 3.6) elliptic-oblong to ovoid basidiospores	Recently, transferred to <i>Resupinatus</i> . Resembles <i>R. merulioides</i> , but differs in gills, and spores form	Bijeesh, Kumar and Pradeep 2020; Cooper 2012b; Liu et al. 2024; McDonald 2015
<i>Resupinatus reviviscens</i> Carpouren and Raspé, sp. nov	Yellowish basal hairs and clavate pleurocystidia. Brownish gray to dark gray, astipitate, and pileus 3–7 mm. Ability basidiomas to withstand desiccation	Broadly ellipsoid to ellipsoid basidiospores (3.8–)4.4–5.7–6.8(–7.6) × (2.8–)3.2–3.9–5(–5.8)	Most resemble <i>R. applicatus</i> , <i>R. striatulus</i> , and <i>R. trichotis</i> in basidiome color, size, and shape.	Carpouren et al. 2024
<i>Resupinatus niger</i> (Schwein.: Fr.) Murrill	Basidiomata are small to medium with dorsolateral pseudostipe, gray–brown surface, and black in mature basidiocarps. Pileus 3–5 mm with stipe rudimentary to absent and pleurocystidia metuloid	Hyaline, inamyloid, ellipsoid to elongate-ellipsoid or phaseoliform, smooth, 6.2–7.6 × 3.7–4.5	Sister position to <i>R. conspersus</i> and <i>R. europeus</i> in which the form basal, but <i>R. niger</i> in types of spores and black basidiocarps	Demirak and Kaygusuz 2021; Thorn and Barron 1986; Consiglio, Setti and Thorn 2018
<i>Resupinatus alboniger</i>	Stipe absents and pileus 3.5–7 mm with surface heavily pruinose. Fuscous black when fresh and drying grayish	Ellipsoid-phaseoliform (5.5–)6–7.3(–9) × 2.7–3.5(–4.0)	Morphologically similar to certain species, especially the group <i>H. nigra</i>	Gonou-Zagou et al. 2011; Watling and Gregory 1989
<i>Resupinatus poriaeformis</i> (Pers.) Thorn, Moncalvo and Redhead	Basidiomata with 0.5–1.5 mm. Hymenial cystidia absent; cap surface with branched dendrohyphidia covered with pale yellowish crystals	Has globose to subglobose spores (5–5.5 × 4.5–5)	Considered <i>R. urceolatus</i> a separate taxon from <i>R. poriaeformis</i> because of the lack of a subiculum. Resembles <i>R. hyalinus</i> in basidiomas size and hymenial surface	Elborne 2008; Nogueira-Melo, Ryvarden and Gibertoni 2011; Thorn et al. 2005; Yattoo and Sheikh 2022
<i>Resupinatus rickii</i> Trierv-Per. and Thorn, nom. nov.	Basidiomas with 0.15–0.25 mm, sessile to subsessile, grayish yellow to gray with hymenial surface yellow to brownish, difficult to observe. External surface with dendrohyphidia and external hairs completely encrusted	Subglobose (4–5 × 3.5–4) with distinct apiculus nondextrinoid and nonamyloid	Described a new variety for the species (<i>H. minimus</i> var. <i>venezuelae</i> Reid)	Trierveiler-Pereira, Thorn and Gugliotta 2019
<i>Resupinatus porrigens</i> Xu and Li, sp. nov.	Basidiomes are small and sessile, with pileus up to 7 mm and surface beige to red brown with margin incurved	Globose to subglose (3.8–)4.1–4.6(–4.9) × (3.0–)3.3–4.0(–4.3)	The pileus beige resembles <i>R. merulioides</i> , but it is differentiated by a taupe alveolate hymenium	Redhead and Nagasawa 1987; Liu et al. 2024

<i>Resupinatus taxi</i> (Lév.) Thorn, Moncalvo and Redhead	Basidiomatas with 0.5-1 x 0.5-1.2 mm, whitish to gray with hymenial surface smooth and whitish. Stipe absent or reduced	Elliptical and smooth (4.7- 5.7 × 4.5- 5.2)	Placed in <i>Rhodocyphella</i> , but was synonymized as <i>R. griseopallidus</i> and requires a new name	Uzun et al. 2018; McDonald 2015
<i>Resupinatus stictoides</i> (Speg.) Nakasone	Discoid basidiome up to 2 mm, brownish orange and became ceraceous rehydrated. Hymenial surface smooth	Broadly ellipsoid, 7.5-9 (-10) × 4-5 (-5.5)	It has similarities with <i>R. porrigens</i> in basidia type, and the basidiome color and size are not the same as the early description	Liu et al. 2024; Thorn et al. 2005; Nakasone 2008
<i>Resupinatus silvanus</i> (Sacc.) Singer	Hourglass-shaped adhesive cells are produced on the hyphae, which is similar to the hyphae produced by <i>Nematoctonus</i>	-	Represents <i>Hohenbuehelia silvana</i> (Sacc.) now	Thorn and Barron 1986; Bijeesh, Kumar and Pradeep 2020
<i>R. kavinii</i> (Pila't) M.M. Moser	Small cups, 1-2 mm, with few reduced lamellae	Hyaline, inamyloid, smooth-walled, globose to subglobose (4.0-)4.2-5.0(-5.2) x (4.0-)4.2-4.9(-5.1)	Similar to <i>R. applicatus</i> , but has basidiomas that are much smaller than observed in	Thorn et al. 2005; McDonald 2015
<i>Resupinatus griseopallidus</i> (Weinm.) Knudsen and Elborne	Cup-shaped, 0.5-1.5 mm x 0.5-1 mm, pale gray, cap surface with branched dendrohyphidia covered with pale yellowish crystals, and entire margin	Subglobose to broadly elliptical, smooth-walled, inamyloid, hyaline, 4.5-5.5 x 4-5	Confused with the North American taxon <i>Rhodocyphella cupuliformis</i>	Knudsen and Elborne 2008; McDonald 2015
<i>Resupinatus yunnanensis</i> Yang and Zhao	Basidiomata cupulate to resupinate, grayish brown hymenophore	Ellipsoid (4.5–9 × 3.5–7)	Grouped like a sister to <i>R. conspersus</i>	Yang et al. 2023
<i>Resupinatus hyalinus</i> (Singer) Thorn, Moncalvo and Redhead	Cupulate, light tan to brown, nearly transparent when rehydrated. Cups sessile, 0.5-1 x 0.3-0.5 mm, in a ticked subiculum, creamy-white	Elliptical (6–6.5 × 3–3.4)	Collected just once in Brazil	Nogueira-Melo, Ryvardeen and Gibertoni 2011; McDonald 2015
<i>Resupinatus dealbatus</i> (Berk.) Singer	Surface hairs highly branched, some appearing nearly asterostromelloid. Grows supine on the top surface of the substrate	Cylindrical (5–8 × 2.5–3)	The hymenium was facing down. Considered a synonym for <i>R. bicolor</i>	Thorn et al. 2005; Nogueira-Melo, Ryvardeen and Gibertoni 2011; McDonald 2015
<i>Resupinatus urceolatus</i>	Basidiomata grayish, globose to vase-shape with	Globose to subglobose (4.5–6.0)	Frequently confused with <i>R.</i>	Thorn et al. 2005; Cooper

(Wallr. ex Fr.) Thorn, Moncalvo and Redhead	0.3-1.5 mm. Externally farinaceous with short incrusted hairs, subiculum sparse and wispy or lacking		<i>poriaeformis</i> but differs in color and basidiomata type, resembling a crustose lichen	2012b; Nogueira-Melo, Ryvarden and Gibertoni 2011;
<i>Resupinatus cinerascens</i> (Cleland) Grgur.	Basidiomata up to 15 mm, grayish black and drying darker (almost darker), cupulate or convex. Dense hairs around the margin and the surface	Subglobose to ellipsoid spores (5.8-)6.1-7.1(-7.5) x (3.5-)3.8-4.6(- 5.0)	Resembles <i>R. violaceogriseus</i> , now <i>Marasmiellus violaceogriseus</i>	Cooper 2012b; McDonald 2015
<i>Resupinatus</i> <i>violaceogriseus</i> G. Stev.	Basidiomata up to 25 mm, tinged violet margin	Oblong to cylindrical spores	Placed in <i>Marasmiellus</i> (/marasmioid clade)	Moncalvo et al. 2002; Horak 1971; McDonald 2015
<i>Resupinatus urceoloides</i> McDonald and Thorn, sp.nov.	Basidiomes 0.2–1.5 mm with wispy subiculum	Globose, hyaline, nonamyloid (4.4– 4.8–5.5 (–6.4) x (4.0–) 4.4–5.2 (–5.6)	-	McDonald and Thorn 2019
<i>Resupinatus conspersus</i> (Pers.: Fr.) Thorn, Moncalvo and Redhead	Dark gray, encrusted cups with a darker (brownish) hymenium and smooth, dense white surface hairs	Hyaline, inamyloid, smooth-walled, angular, oblong or cylindrical-elliptic, 6.0-8.0 x (2.5-)2.7-3.5(-4.0)	Very rare species placed in <i>Resupinatus</i> by Thorn et al. 2005	Yatoo and Sheikh 2022; McDonald 2015; Demirak Kaygusuz 2021
<i>Resupinatus huia</i> (G. Cunn.) Thorn, Moncalvo and Redhead	Cyphelloid, globose or depressed-globose, small (250-550 µm), and presents dense hairs. Cups black to dark brown	Ellipsoid, hyaline, inamyloid, smooth- walled, oblong 7-9 x 5-6.5	Similar to <i>Stigmatolemma incanum</i> , but differs in collected location	Cooper 2012b; McDonald 2015
<i>Resupinatus incanus</i> (Kalchbr.) Thorn, Moncalvo and Redhead	Cupulate, sessile, gray to nearly black/dark brown with 175-350 µm. Cups with hyaline diverticulate hairs	Hyaline, inamyloid, smooth-walled, oblong, (6.0-)6.5-8.0(-8.8) x (3.5-)4.4- 5.2	Lacks a true subiculum and has a dense mat of white hair when removed from the substrate	McDonald 2015
<i>Resupinatus</i> <i>subapplicatus</i> (Cleland) Grgur	Gray to dark gray–black when fresh, with a tomentose. Pileus 6-16 mm with coralloid- diverticulate surface hairs dark brown to gray	Hyaline, inamyloid, smooth-walled, globose to subglobose, (4.5-)5-6(-6.2) x (4.4-)4.8-5.9	Considered a synonym for <i>R.</i> <i>applicatus</i> , but differs in the basidiospores form	McDonald 2015

Some species of *Cellypha*, *Rimbachia* and *Resupinatus* present morphological similarities with others of the Discomycetes; however, spores are found on basidia (Uzun et al. 2018). *Resupinatus* and *Hymenochaete* are examples of genera that present morphological variety. This diversity (Figure 1) is represented through hymenophores with lamellae (*Resupinatus applicatus*), poroid forms (*Resupinatus porosus* Martin, Lodge and Thorn), cyphelloid forms (*Resupinatus poriaeformis*) or merulioid forms (*Resupinatus merulioides* Redhead and Nagas) (Kalichman, Kirk and Mathney 2020).

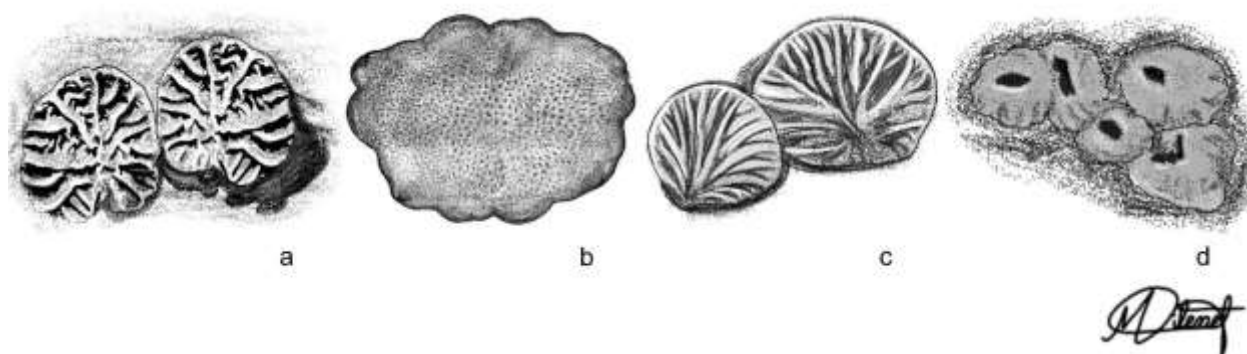


Figure 1 Representation of the morphological diversity of the genus. a *Resupinatus merulioides* (McDonald 2015), b *Resupinatus porosus* (mushroomobserver.org), c *Resupinatus applicatus* (nahuby.sk. 2013), and d *Resupinatus poriaeformis* (Yatoo and Sheikh 2022)

The morphological evolution within *Resupinatus* can be understood from four main genetic regions, where *R. applicatus* and *R. trichotis* appear closer on one side and *R. striatulus* is shown on the other (Consiglio and Setti 2018; Lotz-Winter et al. 2021). Both the poroid and cyphelloid hymenophores, which some species of the genus present, seem to have evolved from ancestors with lamellae (Moncalvo et al. 2002). *R. porosus*, as its name suggests, has a poroid hymenophore and has been included in the tribe *Resupinatus* owing to its resemblance in micro- and macromorphology to *R. applicatus*, despite its lamellar hymenophoral trama. Phylogenetic analyses, including those of Moncalvo et al. 2002, confirmed its placement within the *Resupinatus* clade, with a 55-taxa data matrix supporting its monophyly (100% Bayesian posterior probability, 70% bootstrap support). The discovery of a poroid *Resupinatus* species highlights the extreme plasticity of hymenophoral arrangement within the *Resupinatus* clade, showing that classification

on the basis solely of hymenophoral structure is artificial and lacks phylogenetic support (Thorn et al. 2005).

Species with poroid and cyphelloid hymenophores, such as *R. merulioides*, *R. porosus*, *R. alboniger*, *R. applicatus*, *R. striatulus* and *Resupinatus urceoloides* sp. nov, have been included in the clade and described *Resupinatus* as a monophyletic genus with greater diversity in the hymenophore variations inside the euagarics group in addition to the best-known species characterized by a lamellate hymenophore (Redhead and Nagasawa 1987; Hibbett et al. 1997; Thorn et al. 2005; Gonou-Zagou et al. 2011; McDonald and Thorn 2019).

The distribution of poroid species can be grouped into two main groups, where they are aligned in larger clades with lamellate genera (Hibbett, Murakami and Tsuneda 1993; Virágh et al. 2021). Poroid forms appear as a reduction from pileate gills and are related to crust-like species. Various studies have proposed the recognition of these features in Agaricales (Moncalvo et al. 2002; Thorn et al. 2005; Matheny et al. 2007).

Inside Agaricales, spores are produced in the pileus on the gilled surface, whereas Boletales and Polyporales produce spores inside the caps with the hyphal sheath around the pores, which are unclosed (Kües and Navarro-González 2015). Hibbett, Murakami and Tsuneda (1993) analyzed the hymenophore evolution between *Panus* and *Lentinus*, revealing characteristics of convergence. They are placed together by Singer (1986) in Polyporaceae, despite being gilled mushrooms. *Panus* and *Lentinus* (lamellae genera close to poroid clades) have evolved hymenophores that are distinct from those of other genera, such as *Poromyцена*, *Favolaschia*, and *Dictyopanus* (poroid genera close to gilled clades) (Bijeesh, Kumar and Pradeep 2020; Virágh et al. 2021).

Poroid hymenophores and gelatinized tissues are common features of genera such as *Campanella* and *Marasmiellus*. Although *Marasmiellus* can have gelatinized tissues, it does not have poroid hymenophores. These characteristics are present in *R. porosus* and *R. merulioides*. They share poroid (merulioid) hymenophores and are placed in *Resupinatus* because of their micromorphology, similar to that of gelatinized tissues, in addition to being globose in amyloid basidiospores, the absence of metuloidal cystidia and the presence of coralloid pileipellis with tibiiform cystidioids (Redhead and Nagasawa 1987; Cooper 2012b; Bijeesh, Kumar and Pradeep 2020).

Cyphelloid genera such as *Stigmatolemma* present basidiomes that are gelatinous and more or less cupulate, and the external cuticle is formed by irregularly diverticulate hyphae. In addition,

they also present pigmented hyphae, major spore sizes, globules in different parts of the basidium, similarities in mode of life, and putative parasitism shared with *Resupinatus*. While they share this characteristic, they also have different structures. The hymenophore is smooth on the *Stigmatolemma* and the *Resupinatus* but becomes gilled in the latter. The arrangement of the basidiomes of *Resupinatus* appeared to be solitary or growing in scattered groups, whereas *Stigmatolemma* was generally found in compound aggregates. Therefore, on the basis of its anatomical morphology, this cyphelloid genus was placed in the /resupinatus clade, which was better described in other recent studies with phylogenetic analyses (Agerer 1978a, 1978b; Cooke 1962; Donk 1962; Singer 1986; Thorn and Barron 1986).

Among the cyphelloid species, the phylogenetic relationships of the *Resupinatus* sister clades of *Stigmatolemma* Kalchbr. has been considered in some molecular studies, which are defined as reduced taxa present in the *Resupinatus* clade (becoming paraphyletic). *Stigmatolemma* has a well-supported clade (91% BS, 1.0 BPP) with sequences from *R. alboniger* (MK278432) and *Resupinatus conspersus* (AY570994).

On the other hand, *Calyptella* Quél. a well-supported clade (78% BS, 0.99 BP) also appears with a sister clade but is not well supported (Moncalvo et al. 2002; Bodensteiner et al. 2004; Silva-Filho et al. 2023). In Brazil, for example, studies of cyphelloid species are scarce, where the small size of some basidiomes and the small number of samples deposited in the herbarium contribute to this phenomenon (Trierveiler-Pereira, Thorn and Gugliotta 2019).

The differences between the cyphelloid and poroid forms appear to result in a larger surface area, resulting in an efficient distribution of reproductive material, especially in countries and temperate regions with tropical climates, where high humidity can interfere. *Resupinatus* has lamellae that can be widely distributed and could indicate an evolutionary mechanism that helps in dispersion and survival (Thorn et al. 2005). *Resupinatus* establishes a broad connection with groups that present poroid and cyphelloid hymenophores and other common morphological characteristics (Figure 2).

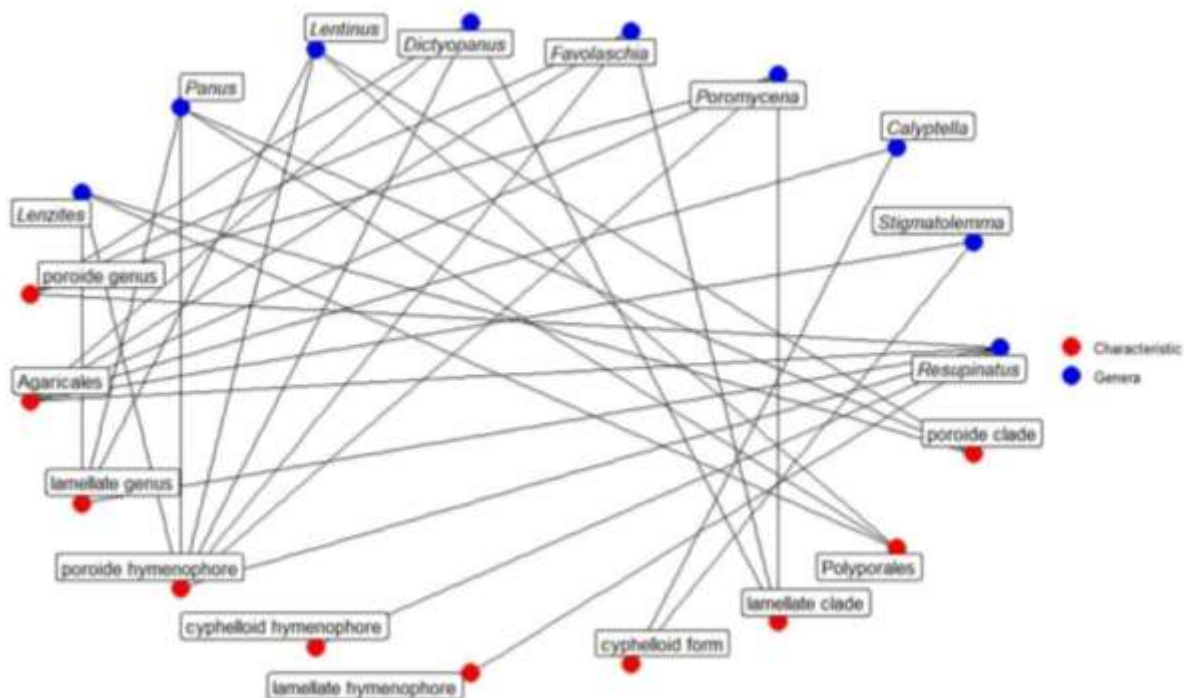


Figure 2 Diversity of the genera characteristic of *Resupinatus* compared with other groups. RStudio version 4.4.1 (Csardi and Nepusz 2006; Pedersen 2020), adapted from Bodensteiner et al. 2004; Moncalvo et al. 2002 and Silva-Filho et al. 2023.

Like *Hohenbuehelia*, *Resupinatus* is a genus that is macromorphological. Some species may present very similar characteristics, such as the presence of elliptical to allantoid basidiospores; for this reason, they have been very closely related for many years (Singer 1986; Thorn and Barron 1986; Henrici 2009). Smaller individuals of *Hohenbuehelia* can easily be confused with *R. applicatus* (Harms et al. 2023).

Hohenbuehelia has a gelatinous layer in the pileus tissue or the hair web. Members of *Resupinatus* do not have this characteristic but instead have lamellae on the surface that contain spores, and the basidiomes are dark/black in color, small in size, resupinate or cupulate, and have clamped hyphae without the asexual morph discovered (Watling and Gregory 1989; Thorn and Barron 1986; He et al. 2019).

Resupinatus does not have metuloids and does not produce a *Nematoctonus* anamorph. It has diverticulated cheilocystidia and may have cystidia with apical projections that are similar to those of *Hohenbuehelia* and *Pleurotus* (Fr.) P. Kumm. (1871), but it does not capture nematodes, and the morphology of its asexual phase is unknown. It has tapered spines, which may have a small adhesive drop at the tip, and its hyphae are cuticular and assimilative. The cortical layer of the

pileus is globular or amorphous and, if present, has an hourglass-shaped secretory structure surrounded by a mucoid ball (Singer 1986; Thorn and Barron 1986; Watling and Gregory 1989; Thorn et al. 2005; Henrici 2009).

Although it does not capture nematodes, nematophagous activity has been described for some species of *Resupinatus*. The mechanism of action of *Resupinatus silvanus* (Sacc.) Singer, which occurs through hourglass-shaped adhesive cells, where the nematodes adhere, causing their infection and subsequent death (Thorn and Barron 1984), but was replaced and is now *Hohenbuehelia silvana* (Sacc.) OK Mill (1986:131) (Bijeesh, Kumar and Pradeep 2020). For *R. applicatus*, the nematophagous potential was also evaluated and presented positive results, but the capture method was not fully outlined (Ishizaki, Nomura and Watanabe 2015).

For many years, studies have reported the proximity of *Resupinatus* and *Hohenbuehelia*, but molecular analyses have demonstrated that, despite their similarity, they are distinct. These studies do not point to a common ancestry; rather, the similarities show convergence on the evolutionary scale over time (Thorn et al. 2000, 2005; Moncalvo et al. 2002; Gonou-Zagou et al. 2011). In recent decades, they have been considered very close, with *Hohenbuehelia* being considered a subgenus of *Resupinatus*. This association involves different aspects, such as morphology, in hymenophore development because they present a gelatinous layer or because of the presence of ramified hyphae (in the pileipellis) (Singer 1948, 1962, 1975, 1986; Reijnders 1948, 1963; Kühner 1980; Moore 1987; Consiglio and Setti, 2017b).

Later, *Asterotus* was considered a synonym and was reduced to a subgenus of *Resupinatus*; initially, species without metuloids were grouped with *Resupinatus*, and others that presented these features were placed in *Hohenbuehelia* (Singer 1973b, 1975; Miller 1984). Therefore, a few years ago, *Resupinatus* was included in the tribe *Resupinatae* of *Pleurotaceae* by Kühner (1980). After this, Jülich (1981) and Singer (1986) defined the family *Resupinataceae* and established the tribe *Resupinateae* (Tricholomataceae), and after phylogenetic analysis, *Asterotus*, *Lignomyces*, *Rhodocyphella*, *Stigmatolemma*, and *Stromatocyphella* were considered synonymous from *Resupinatus* (Thorn et al. 2000, 2005; McDonald 2015; Consiglio and Setti 2018; McDonald and Thorn 2019).

Nomenclature and phylogeny

In previous studies by Moncalvo et al. (2000, 2002) and Thorn et al. (2000), the proposal to separate *Resupinatus* from the family, keeping *Hohenbuehelia* and *Pleurotus* together, had already been considered but was not established. This occurred because *Pleurotus* and *Hohenbuehelia* present a nematophagous ability that *Resupinatus* does not have. Therefore, this feature can indicate evidence of morphological synapomorphies. However, the existence of a monophyletic family, Pleurotaceae, was indicated via six genetic regions grouped within the pluteoid clade, but strong support was not obtained. One factor that may have influenced this was the use of a few representatives of the genera in the analysis (Matheny et al. 2007; Koziak, Cheng and Thorn 2007; Justo et al. 2011). Despite the previous phylogenetic studies, McDonald (2015) and Consiglio, Setti and Thorn (2018) considered the *Resupinatus* position closely but not within Pleurotaceae, as Demirak and Kaygusuz (2021) considered recent studies with support for monophyletic recognition of *Resupinatus* and *Hohenbuehelia*.

Thus, differences between other genera, such as *Pleurotus* and *Nematoctonus*, and the existence of weak support already obtained do not reinforce their origin through a monophyletic family. *Resupinatus* (tribe *Resupinateae sensu stricto*) is described with an uncertain classification. Despite the various analyses over the years, many of them have little significant support. Recent suggestions indicate the restoration of *Resupinataceae* as an independent clade belonging to *Pleurotineae*, which also includes *Fistulinaceae*, *Pleurotaceae*, and *Schizophyllaceae* (Koziak, Cheng and Thorn 2007; Vizzini et al. 2024; Carpouren et al. 2024).

Like other families *sensu lato* (*Brauniella*, *Chromocyphella*, *Hemigaster*, *Lenzitopsis*, and *Mycospongia*), *Resupinatus* can be directly named with legitimate names. However, owing to a lack of molecular evidence or the recent definition of names, some studies on nomenclature and phylogeny do not consider these monotypic families. This results in the neglect of basal lineages and species that are important for establishing more concrete connections at the evolutionary scale (Kalichman, Kirk and Matheny 2020; Nagy et al. 2023; Vizzini et al. 2024).

Factors such as those described above contribute to the classification of *Resupinatus* as *incertae sedis* and reinforce the need for new analyses on the order Agaricales. Another factor that influences this classification is the scarcity of available rDNA sequences, which makes data processing a complex process, with several datasets and gaps (Nagy et al. 2023). Aligning taxonomic information with the sequences of described species is necessary to help fill these gaps

effectively (Haelewaters et al. 2018).

Changes in nomenclature and taxonomic identification included several species of the genus, some of which were made recently, indicating that there are still gaps to be filled regarding the diversity of this genus and many other genera. Many studies have performed phylogenetic analyses and were re-evaluated later on the basis of new records or identification via molecular studies. *Resupinatus niger* (Schwein. Fr.) Murrill is considered a true representative of the genus that was initially identified as *Hohenbuehelia grisea* (Schulzer) (VT1324; KY679143) or *Hohenbuehelia nimueae* (Consiglio, Setti and Thorn) (RGT 871128/01), and *Hohenbuehelia nigra* (Schwein) (RLG 10761), which in the 1980s was not a conidial anamorph of *Nematoctonus* and was identified as *Resupinatus* sp. (AF042499) (Thorn and Barron 1984, 1986; Moncalvo et al. 2002; Consiglio, Setti and Thorn 2018).

Second, Lotz-Winter et al. 2021 reported the disappearance of descriptions by *R. striatulus* and the permanence of data just for *R. applicatus* in Germany. Owing to the absence of correct morphological demarcation, works with correct new citations could be lost. Description of morphological features helps to define the precise classification. In a recent study performed by Carpouren et al. (2024), phylogenetic analyses strongly supported (MLBS (93%) and BIPP (1.0)) *R. reviviscens* and the American specimens *Resupinatus* sp. “*trichotis*” (iNaturalist numbers 39114228, 57471425, and 129942182) and *R. aff. trichotis* (TENN-F-63042) in a larger clade and highlighted the possibility of the existence of a unique species with intraspecific variation. Thus, the taxonomic position of this American specimen is still uncertain but shows a close relationship with *R. reviviscens* despite having some genetic differentiation. Another species was analyzed, but when it is placed in a distinct position, it can indicate another level, and more samples are needed for confirmation.

For correct names to be established in collections such as *Resupinatus* sp., literature records from locations such as North America and Europe require data processing with more complex meta-analyses and consensus definitions that can encompass data from different geographic regions (Haelewaters et al. 2018). These factors can help expand the knowledge of species of the genus and their ecological preferences and specificities (Demirak and Kaygusuz 2021). An example of this was the primary identification of *Resupinatus* sp. 1 by Haelewaters et al. (2018), which was redescribed one year later by McDonald and Thorn (2019), as *Resupinatus urceoloides* on the basis of Canadian material and presented a new geographic record in the United States

(Mortier et al. 2024). The difference between the basidiospores of *Resupinatus alboniger* (Pat.) Singer (ellipsoid), *R. dealbatus* (cylindrical), and *R. applicatus* (subglobose) are other characteristics that help distinguish the species (Singer 1943, 1962; Thorn et al. 1986).

Correct identification facilitates the differentiation and verification of the proximity between groups. In the case of *Resupinatus* and *Hohenbuehelia*, similar morphological characteristics may generate confusion in identification. *Resupinatus* and *Hohenbuehelia* exhibit similar characteristics. Both share gelatinized trama and amyloid basidiospores (McDonald 2015; Thorn et al. 2005). In *Resupinatus*, the pileipellis and assimilative hyphae are diverticulate and possess tapering pegs, a feature not found in *Hohenbuehelia*. Additionally, *Resupinatus* lacks a nematophagous asexual morphology (Consiglio, Setti and Thorn 2018; Thorn et al. 2005).

Owing to these morphological similarities, molecular analyses, such as DNA barcoding, are essential for the accurate identification and differentiation of *Resupinatus* and *Hohenbuehelia* DNA sequences, particularly ribosomal genes, which are powerful tools for the taxonomy and phylogeny of fungi, including *Resupinatus* (Consiglio, Setti and Thorn 2018).

Analyses involving the comparison of specific genes, especially the internal transcribed spacer (ITS) region, are used to construct phylogenetic trees that reveal the evolutionary history of *Resupinatus* and its relationships with other taxa. The ITS region is located between the 18S and 28S rDNA genes (Figure 3) and exhibits sequence variation between species, which can be used to distinguish morphologically similar species (Thorn et al. 2005; Bijeeesh, Kumar and Pradeep 2020).

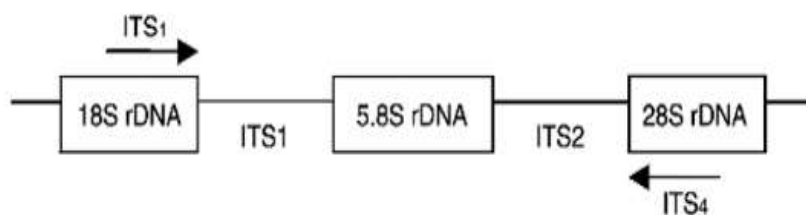


Figure 3 Internal transcribed spacer (ITS) sequence containing ITS1 and ITS4. Source the author

Bijeeesh, Kumar and Pradeep (2020) described a new species of *Resupinatus* found in India, *Resupinatus odoratus*, in which ITS sequences were used to confirm its identity. The phylogenetic

relationships within the genus can also be clarified through ITS sequences. Thorn et al. (2005) investigated the genetic diversity of *Resupinatus porosus* from Puerto Rico, providing insights into its evolution and geographical distribution. Additionally, on the basis of analyses of the ITS region, Petersen et al. (2015) demonstrated that the species originally described as *Resupinatus violaceogriseus*, in phylogenetic analysis, appears to be a sister species to *Lignomyces*.

Furthermore, diverticulate pileus cuticle hyphae and cheilocystidia, as well as their geographical distributions, suggest the taxonomic separation of these species, providing strong reasons to consider *R. violaceogriseus* as a potential new and distinct genus (Petersen et al. 2015). These and other studies demonstrate that ribosomal DNA, particularly the ITS region, is a valuable molecular tool for the taxonomy and systematics of *Resupinatus*, enabling the elucidation of diversity and evolutionary relationships within this group.

Phylogenetic analyses of *Resupinatus sp.* are essential for understanding the evolutionary relationships within the species group and for identifying characteristics that may differentiate them from related genera, such as *Hohenbuehelia*. The nomenclature of some species is confusing and erroneous, which may be due to the scarcity of records and/or very old descriptions. These incorrect applications may occur in the absence of holotype samples or where only a single original material is available with representations of macroscopic characteristics. In other cases, such as synonymous species that have not been adequately studied, nomenclature was defined on the basis of comprehensive concepts. These factors have contributed to the incorrect definitions of names for *Hohenbuehelia* and *Resupinatus* for a long time (Consiglio, Setti and Thorn 2018).

The classification of *Resupinatus* within Agaricales still requires adequate resolution. The definition of its taxonomic position remains complex due to the lack of molecular identification of several taxa, resulting in a compromise in the association and establishment of connections with clades close to the genus (Demirak and Kaygusuz 2021).

Geographical distribution

Differences in species characteristics can suggest either a similarity or divergence in taxonomic status, such as the presence of hairs at the base of the basidiomes. Geographical distribution is a factor that involves diverse characteristics of the genus, related taxonomy,

morphology, and substrate preferences. These descriptions improve specimen identification and contribute to more accurate data collection. These data can be used to distinguish between specimens in distinct places (McDonald 2015; Consiglio and Setti 2018; Carpouren et al. 2024). This species is found in different countries/regions (Table 3) and could be a synapomorphy; thus, the correct classification is necessary and useful for better understanding this genus.

Table 3 Country/region relationships and records of the species found

Country/Region	Species found	References
Argentina	<i>R. applicatus</i> (Batsch) Gray, <i>R. striatulus</i> (Pers.) Murrill and <i>R. niger</i> (Schwein.) Murr	Albertó, Fazio and Wright 1998; Niveiro, Popoff and Albertó 2010
Australia	<i>Resupinatus cinerascens</i> (Cleland) Grgur., <i>R. subapplicatus</i> (Cleland) Grgur and <i>R. vinosolidus</i> (Segedin) Cooper	Cooper 2012b; McDonald 2015
Brazil	<i>R. applicatus</i> (Batsch) Gray, <i>R. dealbatus</i> (Berk.) Singer, <i>R. stictoideus</i> (Speg.) Nakasone, <i>Resupinatus subrhacodium</i> Singer, <i>R. hyalinus</i> (Singer) Thorn, Moncalvo and Redhead, <i>R. alboniger</i> (Pat.) Singer, <i>R. poriaeformis</i> (Pers.) Thorn, <i>R. rickii</i> Trierv-Per. and Thorn, and <i>Resupinatus porosus</i> Martin, Lodge and Thorn	Singer 1943, 1973, 1989; Pegler 1987; Cooke 1957; Donk 1959; Thorn and Barron 1986; Putzke 1994; Meijer 2006; Nogueira-Melo, Ryvarden and Gibertoni 2011; Trierveiler-Pereira, Thorn and Gugliotta 2019; Trierveiler-Pereira, Prado-Elias and Baltazar 2024
Canada	<i>R. dealbatus</i> (Berk.) Singer	Bazzicalupo et al. 2022
China	<i>Resupinatus</i> sp., <i>Resupinatus yunnanensis</i> Yang and Zhao, and <i>Resupinatus porrigens</i> Xu and Li, sp. nov.	Yuan et al. 2017; Yang et al. 2023; Liu et al. 2024
Denmark	<i>Resupinatus griseopallidus</i> (Weinm.) Knudsen and Elborne	Knudsen and Elborne 2008; McDonald 2015
Germany	<i>R. applicatus</i> (Batsch) Gray, <i>R. striatulus</i> (Pers.) Murrill and <i>R. trichotis</i> (Pers.) Singer	Lotz-Winter et al. 2021
Greece	<i>R. applicatus</i> (Batsch) Gray (2), <i>R. striatulus</i> (Pers.) Murrill (1), <i>R. silvanus</i> (Sacc.) Singer (1) and <i>R. alboniger</i> (Pat.) Singer	Gonou-Zagou et al. 2011
India	<i>R. odoratus</i> (Pradeep, Bijeeesh and Kumar) and <i>R. applicatus</i> (Batsch) Gray	Bijeeesh, Kumar and Pradeep 2020; Gogoi and Prakash 2015
Japan	<i>R. merulioides</i> Redhead and Nagas	Redhead and Nagasawa 1987
South Korea	<i>R. applicatus</i> (Batsch) Gray and <i>R. trichotis</i> (Pers.) Singer	Jo et al. 2013
Kosovo	<i>R. striatulus</i> (Pers.) Murrill	Ramshaj et al. 2022

Country/Region	Species found	References
Argentina	<i>R. applicatus</i> (Batsch) Gray, <i>R. striatulus</i> (Pers.) Murrill and <i>R. niger</i> (Schwein.) Murr	Albertó, Fazio and Wright 1998; Niveiro, Popoff and Albertó 2010
Australia	<i>Resupinatus cinerascens</i> (Cleland) Grgur., <i>R. subapplicatus</i> (Cleland) Grgur and <i>R. vinosolidus</i> (Segedin) Cooper	Cooper 2012b; McDonald 2015
Brazil	<i>R. applicatus</i> (Batsch) Gray, <i>R. dealbatus</i> (Berk.) Singer, <i>R. stictoideus</i> (Speg.) Nakasone, <i>Resupinatus subrhacodium</i> Singer, <i>R. hyalinus</i> (Singer) Thorn, Moncalvo and Redhead, <i>R. alboniger</i> (Pat.) Singer, <i>R. poriaeformis</i> (Pers.) Thorn, <i>R. rickii</i> Trierv-Per. and Thorn, and <i>Resupinatus porosus</i> Martin, Lodge and Thorn	Singer 1943, 1973, 1989; Pegler 1987; Cooke 1957; Donk 1959; Thorn and Barron 1986; Putzke 1994; Meijer 2006; Nogueira-Melo, Ryvarden and Gibertoni 2011; Trierveiler-Pereira, Thorn and Gugliotta 2019; Trierveiler-Pereira, Prado-Elias and Baltazar 2024
Canada	<i>R. dealbatus</i> (Berk.) Singer	Bazzicalupo et al. 2022
China	<i>Resupinatus</i> sp., <i>Resupinatus yunnanensis</i> Yang and Zhao, and <i>Resupinatus porrigens</i> Xu and Li, sp. nov.	Yuan et al. 2017; Yang et al. 2023; Liu et al. 2024
Denmark	<i>Resupinatus griseopallidus</i> (Weinm.) Knudsen and Elborne	Knudsen and Elborne 2008; McDonald 2015
Germany	<i>R. applicatus</i> (Batsch) Gray, <i>R. striatulus</i> (Pers.) Murrill and <i>R. trichotis</i> (Pers.) Singer	Lotz-Winter et al. 2021
Greece	<i>R. applicatus</i> (Batsch) Gray (2), <i>R. striatulus</i> (Pers.) Murrill (1), <i>R. silvanus</i> (Sacc.) Singer (1) and <i>R. alboniger</i> (Pat.) Singer	Gonou-Zagou et al. 2011
India	<i>R. odoratus</i> (Pradeep, Bijeeesh and Kumar) and <i>R. applicatus</i> (Batsch) Gray	Bijeeesh, Kumar and Pradeep 2020; Gogoi and Prakash 2015
Japan	<i>R. merulioides</i> Redhead and Nagas	Redhead and Nagasawa 1987
South Korea	<i>R. applicatus</i> (Batsch) Gray and <i>R. trichotis</i> (Pers.) Singer	Jo et al. 2013
New Zealand	<i>R. vinosolidus</i> (Segedin) Cooper, <i>Resupinatus cinerascens</i> (Cleland) Grgur., <i>Resupinatus huia</i> (G. Cunn.) and <i>R. subapplicatus</i> (Cleland) Grgur	Bijeeesh, Kumar and Pradeep 2020; Cooper 2012b; Liu et al. 2024; McDonald 2015
Paraguay	<i>R. alboniger</i> (Pat.) Singer, <i>R. applicatus</i> (Batsch) Gray, <i>R. striatulus</i> (Pers.) Murrill and <i>R. stictoideus</i> (Speg.) Nakasone	Spegazzini 1886, 1919; Campi et al. 2013; McDonald 2015
Puerto Rico	<i>Resupinatus porosus</i> (Martin, Lodge and Thorn)	Thorn et al. 2005
South Africa	<i>Resupinatus incanus</i> (Kalchbr.) Thorn, Moncalvo and Redhead	McDonald 2015
South America	<i>R. alboniger</i> (Pat.) Singer, <i>R. applicatus</i> (Batsch) Gray, <i>R. dealbatus</i> (Berk.) Singer, <i>Resupinatus graminum</i> (Singer) Singer and <i>R. hyalinus</i> (Singer) Thorn, Moncalvo and Redhead	Nogueira-Melo, Ryvarden and Gibertoni 2011; Rivas and Niveiro 2019

Country/Region	Species found	References
Argentina	<i>R. applicatus</i> (Batsch) Gray, <i>R. striatulus</i> (Pers.) Murrill and <i>R. niger</i> (Schwein.) Murr	Albertó, Fazio and Wright 1998; Niveiro, Popoff and Albertó 2010
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China	<i>Resupinatus</i> sp., <i>Resupinatus yunnanensis</i> Yang and Zhao, and <i>Resupinatus porrigens</i> Xu and Li, sp. nov.	Yuan et al. 2017; Yang et al. 2023; Liu et al. 2024
Denmark	<i>Resupinatus griseopallidus</i> (Weinm.) Knudsen and Elborne	Knudsen and Elborne 2008; McDonald 2015
Germany	<i>R. applicatus</i> (Batsch) Gray, <i>R. striatulus</i> (Pers.) Murrill and <i>R. trichotis</i> (Pers.) Singer	Lotz-Winter et al. 2021
Greece	<i>R. applicatus</i> (Batsch) Gray (2), <i>R. striatulus</i> (Pers.) Murrill (1), <i>R. silvanus</i> (Sacc.) Singer (1) and <i>R. alboniger</i> (Pat.) Singer	Gonou-Zagou et al. 2011
India	<i>R. odoratus</i> (Pradeep, Bijeeesh and Kumar) and <i>R. applicatus</i> (Batsch) Gray	Bijeeesh, Kumar and Pradeep 2020; Gogoi and Prakash 2015
Japan	<i>R. merulioides</i> Redhead and Nagas	Redhead and Nagasawa 1987
South Korea	<i>R. applicatus</i> (Batsch) Gray and <i>R. trichotis</i> (Pers.) Singer	Jo et al. 2013
Thailand	<i>Resupinatus</i> sp. and <i>R. reviviscens</i> Carpouron and Raspé, sp. nov.	Harms et al. 2023; Carpouron et al. 2024
Türkiye	<i>R. applicatus</i> (Batsch) Gray, <i>R. trichotis</i> (Pers.) Singer, <i>R. taxi</i> (Lév.) Thorn and <i>R. striatulus</i> (Pers.) Murrill	Sümer 1982; Uzun et al. 2018; Sesli et al. 2020; Akçay 2021
United States	<i>Resupinatus urceoloides</i> McDonald and Thorn	McDonald and Thorn 2019; Mortier et al. 2024

Resupinatus is considered cosmopolitan, but despite this description, some species appear to show preferences for more specific geographic regions. This specificity may help distinguish between species on the basis of their occurrence location (McDonald 2015). *R. poriaeformis*,

which was collected in North America, was shown to differ from *Resupinatus urceolatus* (Wallr. ex Fr.) Thorn, Moncalvo and Redhead, on the basis of their different geographic distributions, where *R. urceolatus* has a European continental distribution (Donk 1962). The species was considered equal because of the feature subiculum by Cooke (1957), but Donk (1959) and Thorn et al. (2005) do not consider this synonym (Yatoo and Sheikh 2022). McDonald (2015) performed a phylogenetic analysis with support and suggested that the North American clade needs to be reviewed.

The presence of common characteristics is also common with *R. conspersus*, which has macromorphological similarity with *R. poriaeformis* but differs in morphology and habitat. While *R. conspersus* appears in softwood and has encrusted cups with a darker (brownish) hymenium, *R. poriaeformis* is found in hardwood and has a (brown) hymenium with a dense subiculum (Yatoo and Sheikh 2022). Lotz-winter et al. (2021) reported a different classification by *R. striatulus* in Germany, where this species was considered distinct in countries such as Canada, France, and the United States. The classification of this species was previously performed, with *R. applicatus* and *R. trichotis* as synonyms.

However, other authors related different features in your habitat. Karadelev et al. (2018), Akçay (2021), and Ramshaj et al. (2021) reported this species in the rotten wood of *Pinus* sp. (*Pinus heldreichii*) in Turkey, whereas Niveiro, Popoff and Albertó (2010) reported the decomposition of *R. striatulus* in palm wood (*Butia yatay*) in Argentina. This finding may indicate that the species probably does not have the right identification and classification or addiction to their substrate preference, which results in a necessary review of these data.

Bijeesh, Kumar and Pradeep (2020) reported the difference between *R. odoratus*, which is located close to *R. applicatus*, and *R. striatulus*, which is in the nrITS and has a relatively high ML bootstrap, but the *R. odoratus* sequence available from India differs from other geographical sequences available. *R. niger* and *R. conspersus* are similar in morphology; however, they exhibit different habitats in which *R. conspersus* is usually found in trees that are coniferous trees (*Abies*) and collected in South America, the Czech Republic, France and Switzerland, and *R. niger* is found on dead or very rotten wood *Quercus* sp. with a worldwide distribution but is concentrated in the Northern Hemisphere, in countries such as the United States, China, Italy and Norway (Bodensteiner et al. 2004; Demİrak and Kaygusuz 2021; McDonald 2015).

R. niger has metuloid cystidia and is similar to *R. alboniger*, which does not have metuloid

cystidia, in terms of spores and basidiomes. They share the same habitat preferences and grow on deciduous trees. Nonetheless, *R. alboniger* was also found on coniferous trees in Greece and could be an addition to their substrate preferences (Thorn 1986; Watling and Gregory 1989; Gonou-Zagou et al. 2011; Demırak and Kaygusuz 2021). *R. niger* also shares genetic proximity with *Resupinatus europaeus* Consiglio and Setti, but *R. niger* has a gray–brown surface and is black in mature basidiocarps, whereas *R. europaeus* has more grayish or grayish-white pileus with blackish tints (Thorn and Barron 1986; Consiglio, Setti and Thorn 2018; Demırak and Kaygusuz 2021)

Diverse studies with data concerning *Resupinatus* species have not been published (Carpouren et al. 2024), which reveals a major problem. Considering the large number of fungal specimens we have in global ecosystems, unpublished works seem to turn biodiversity data into a question that need attention. These works often provide discrepant information about taxonomic and ecological preferences. The works found are distributed in certain regions but are intercontinental (Figure 4). Thus, geographical information will help to complete and generate more robust and precise works, and points of occurrence are important to correlate the existing knowledge and fill in the gaps in fungal diversity.

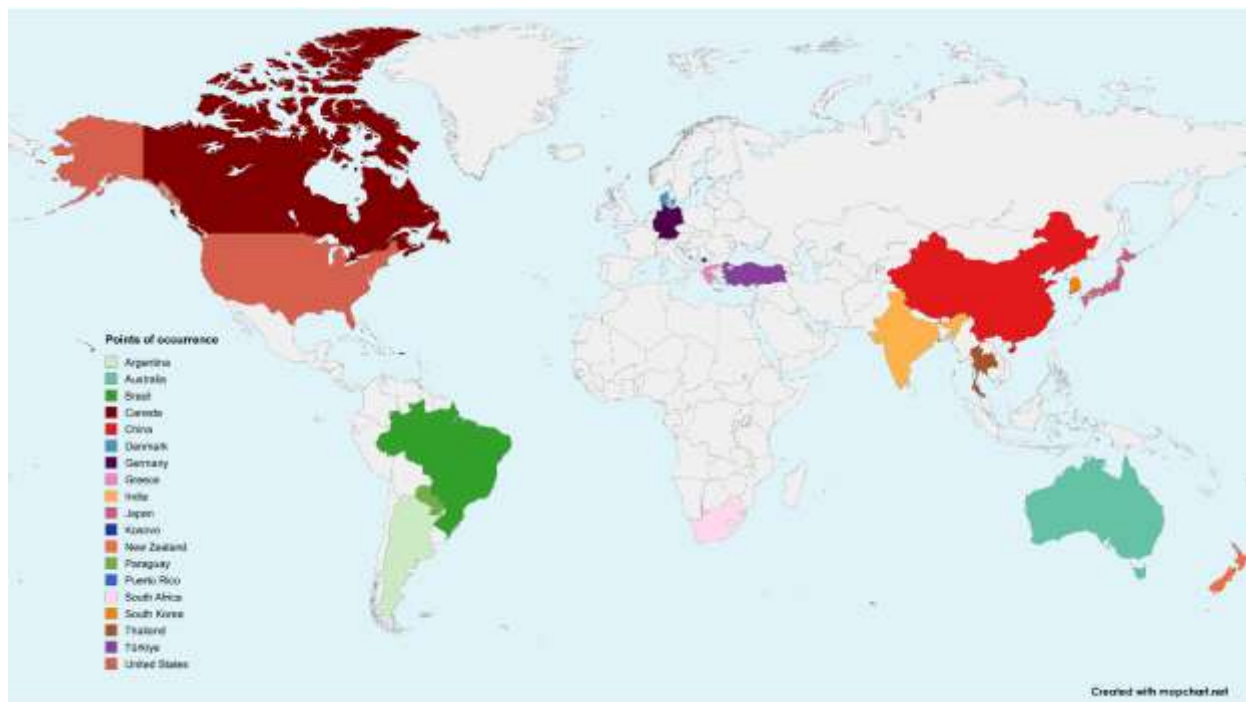


Figure 4 Referenced worldwide distribution of *Resupinatus* computed in this revisional study. Data collected and elaborated by the author

Geographic information is crucial for maintaining biodiversity and explains the associations between fungi and forests. This can be a key to better understanding how wood-decaying fungal degradation is performed and revealing more local data, which provides practical insights and better utilization of available resources (Wang, Yang and Zhao 2024).

Ecological relationships and host associations

For fungal conservation, we cannot analyze just one parameter at a time. It is necessary to gather as much data as possible. These data complement each other rather than contradict one another. Evaluating studies and data can reveal species abundance and associations, contributing to a better understanding of fungal resources and ecosystems. For example, *R. striatulus* is cited as a very rare species, and its presence in forests reveals the ecological requirements of fungi. The association between fungi and trees, such as *P. heldreichii* (Karadelev 2018), may indicate a mutualistic preservation relationship between both. In practical conservation efforts, we not only preserve fungi but also extend this protection to other groups. This indicator needs to be further explored and can help us obtain more detailed information about deadwood-dependent fungi (Mair et al. 2017).

Generally, the species are found on wood or decaying litter (Nogueira-Melo, Ryvardeen and Gibertoni 2011), and similar to other genera within Basidiomycetes, *Resupinatus* can degrade recalcitrant components, such as leaf litter. Its relationship with woody materials ranges from its ability to decompose to the development of specific pathogenicity in these locations. This may be due to the presence of large amounts of lignin, such as in abandoned areas (Bonanomi et al. 2022). The data presented below (Table 4) show the interactions of some species with trees with distinct characteristics, indicating diverse substrate preferences at different locations.

Table 4 Relationships among species and the type/preference of substrate. Reference with signal: - are about just Index Fungorum information

Species	Substrate/Forest	References
<i>R. applicatus</i> (Batsch) Gray	Oak wood and <i>Quercus pubescens</i> : fallen granch	Pryltsky 2013; Ramshaj et al. 2021
<i>R. trichotis</i> (Pers.) Singer	<i>Acer saccharinum</i> , <i>Ailanthus altissima</i> , <i>Gleditsia ferox</i> , <i>Maclura pomifera</i> and <i>Salix x rubens</i>	Benkert 2005
<i>R. conspersus</i> (Pers.) Thorn, Moncalvo and Redhead	<i>Abies</i> spp. and noble wood	Yatoo and Sheikh 2022; Nogueira-Melo, Ryvarden and Gibertoni 2011
<i>R. poriaeformis</i> (Pers.) Thorn	<i>Abies</i> spp. and noble wood. Scattered on the bark of <i>Juniperus</i> , <i>Taxus</i> , <i>Syringa</i> , <i>Lonicera</i> , <i>Vitis</i> , <i>Clematis</i> , <i>Populus</i> , and <i>Quercus</i> sp.	Thorn et al. 2005; Elborne 2008; Nogueira-Melo, Ryvarden and Gibertoni 2011; Yatoo and Sheikh 2022;
<i>R. striatulus</i> (Pers.) Murrill	<i>Pinus heldreichii</i> and on the rotting wood residue of <i>Pinus</i> sp.	Ramshaj et al. 2022; Akçay 2021
<i>Resupinatus</i> sp.	<i>Pinus tabulaeformis</i>	Yuan et al. 2017
<i>R. dealbatus</i> (Berk.) Singer	Eastern deciduous forest endemic	Bazzicalupo et al. 2022
<i>R. reviviscens</i> Carpouren and Raspé, sp. nov.	Dead bamboo branches suspended or still attached to bamboo culms	Carpouren et al. 2024
<i>R. niger</i> (Schwein.) Murrill	On dead branches or very rotten wood of <i>Quercus</i> , <i>Ulmus</i> or <i>Alnus</i> sp., (deciduous trees)	Singer 1986; Thorn and Barron 1986; Thorn et al. 2005; Watling and Gregory 1989; Consiglio et al. 2018; Demİrak and Kaygusuz 2021
<i>Resupinatus alboniger</i> (Pat.) Singer	Deciduous and coniferous trees (<i>Abies</i> and <i>Pinus</i>)	Thorn 1986; Watling and Gregory 1989; Gonouzagou et al. 2011
<i>Resupinatus americanus</i>	On fallen branch	Consiglio and Setti 2018
<i>Resupinatus chilensis</i>	On rotten wood	Singer 1948
<i>Resupinatus crawfordiae</i> G. Stev.	On fallen <i>Nothofagus menziesii</i>	-
<i>Resupinatus cubensis</i> Murrill	On dead sticks	-
<i>Resupinatus dorotheae</i> G. Stev.	On fallen twigs	-
<i>Resupinatus europaeus</i>	Associated with <i>Cedrus deodara</i> and <i>Cupressus arizonica</i>	Consiglio and Setti 2018

<i>Resupinatus merulioides</i>	On rotten log of <i>Zelkova</i>	Redhead and Nagasawa 1987
<i>Resupinatus multilamellatus</i>	On dead sticks, trunks and roots in wood	Corner 1996
<i>Resupinatus purpureo-olivaceus</i>	On fallen wood	-
<i>Resupinatus striatulus</i> var. <i>prolificans</i>	On the decorticated log of <i>Thuja plicata</i>	-
<i>Resupinatus subbarbatulus</i> Murrill	On dead trunk, associated with <i>Coffea</i>	-
<i>Resupinatus subrhacodium</i> Singer	On wood of <i>Salix humboldtiana</i> and <i>Phoebe porphyria</i>	-
<i>Resupinatus tristis</i> G. Stev.	On standing dead <i>Beilschmiedia</i>	-
<i>Resupinatus urceoloides</i>	On rotting wood of <i>Acer saccharum</i>	McDonald and Thorn 2019
<i>Resupinatus violaceogriseus</i> G. Stev.	On fallen <i>Nothofagus menziesii</i>	-
<i>Resupinatus yunnanensis</i> Yang and Zhao	On dead branches of <i>Angiospermae</i>	Yang and Zhao 2023
<i>Resupinatus cinerascens</i> (Cleland) Grgur.	On rotting wood and bark of living deciduous and coniferous trees; one specimen on <i>Banksia</i> cone scales, <i>Eucalyptus</i> and <i>Pinus</i>	Cooper 2012b; McDonald 2015
<i>Resupinatus huia</i> (G. Cunn.)	On rotting wood of dicot trees; observed on <i>Leptospermum</i> and <i>Nothofagus</i>	Cooper 2012b; McDonald 2015
<i>Resupinatus incanus</i> (Kalchbr.) Thorn, Moncalvo and Redhead	On rotting wood of unidentified dicot	McDonald 2015
<i>Resupinatus porrigens</i> Xu and Li, sp. nov.	On the rotting coniferous trunk	Liu et al. 2024
<i>Resupinatus rickii</i> Trierv-Per. and Thorn, nom. nov	Growing on rotten wood	Trierweiler-Pereira, Thorn and Gugliotta 2019
<i>R. stictoides</i> (Speg.) Nakasone	On rotting wood in the tropics	McDonald 2015
<i>R. subapplicatus</i> (Cleland) Grgur	On rotting wood of dicot trees; on <i>Eucalyptus</i> and	McDonald 2015
<i>R. taxi</i> (Lév.) Thorn, Moncalvo and Redhead	Pine forest, on dead plant remains with moss	Uzun et al. 2018

R. vinosolidus (Segedin) Cooper

On fallen rotting wood of unidentified dicotyledonous trees

Cooper 2012b; McDonald 2015

Previous studies have described the possible substrate preferences of various species within the genus (Thorn and Barron 1986; Consiglio and Setti 2018; Miller and Bates 2017). Most species have been found in one or more types of substrates, such as hardwood, softwood, rotting hardwood, or dead wood. Other examples include bamboo and trees such as *Junglans bark* and *Quercus* sp., which prefer selective deciduous substrates (Demirak and Kaygusuz 2021; Carpouren et al. 2024).

The presence of *Resupinatus* in certain forest areas may be related to variations in the C/N ratio as the decomposition stage progresses and is considered a secondary decay organism. These changes result in the release of nitrogen and other compounds in advanced stages, which are essential for fungal community development and serve as indicators of nutrient preference (Thorn and Barron 1986; Rajala et al. 2011).

Some species are considered rare and have been found either in specific localities or during the decomposition succession of fallen trees. The presence of fungal communities in these environments often shows a high similarity of species in the initial decomposition stages. However, in the later stages, this composition changes significantly. This highlights the variability of the fungal community, which can be extensive and influenced by physical and chemical factors. These factors impact not only the diversity of species found in fallen wood samples but also those present in other forest ecosystems. The observation of the presence of these rare species in such localities underscores the importance of understanding the specific ecological requirements and particularities of fungi, which requires further study (Yuan et al. 2017; Karadelev 2018; Ramshaj et al. 2022; Bazzicalupo et al. 2022).

Surveying macrofungi can help bridge existing knowledge gaps, contributing to the preservation of species worldwide and the establishment of priority conservation practices. These findings highlight the need for more urgent actions to ensure the conservation of endangered or rare species, such as *R. dealbatus* (Bazzicalupo et al. 2022). A deeper understanding of the habitat preferences of this group and others, which play key roles in the species preservation process, is essential. To achieve this goal, integrating data processing with effective conservation practices is crucial. Additionally, valuable data are often underutilized in literature, a factor that needs to be reconsidered to support biodiversity conservation (Binley et al. 2023).

Many records do not have a full description of the species. Various registers are from the 19th century and are the only ones available with a very simple description; the material was not adequately conserved or appears just like a citation in a checklist, for example. This lack makes

the true description of the genus difficult in some cases because the primary description is extremely necessary for the real classification of the genus.

Conclusions

Considering analyses such as secondary metabolites (Sundin et al. 1993; Eilbert et al. 2000; Harms et al. 2023) and nematophagous activity (Ishizaki, Nomura and Watanabe 2015), we found only a few studies in these areas. This highlights the potential for further exploration with other species of the genus and with different research approaches.

The analyzed studies demonstrated that there is little recent material available on this genus. Most analyses report new occurrences or records for specific countries and include only taxonomic descriptions of the species, often as the only existing record. This genus has significant potential for further exploration, from its role in the degradation process and nutrient uptake to the collection of data on host associations. However, current analyses remain limited and lack a more in-depth definition of nutrient cycling and relative abundance in forests, which are factors that are essential for establishing conservation measures and should be considered with greater emphasis.

Morphological variations make the genus diverse and increase the complexity of determining a more precise taxonomic position. Measures that integrate these aspects, encompassing both taxonomy and phylogeny, are necessary for proper delimitation. Thus, the availability of more robust data will lead to improvements beyond species descriptions, fostering a much-needed enrichment of knowledge regarding fungal communities.

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3.2 Artigo 2 A new species of *Resupinatus* (Agaricales, Resupinataceae) with metuloid cystidia in the hymenium found in the south of Brazil

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A new species of *Resupinatus* (Agaricales, Resupinataceae) with metuloid cystidia in the hymenium found in the south of Brazil

Abstract

The genus *Resupinatus* has a wide worldwide distribution and some species with distinctive characteristics have been added in recent years. The present work presents a new species for the genus and Brazil. This specie has metuloids in the hymenium, described so far in only one species of the genus and which serve to distinguish *Resupinatus* from *Hohenbuehelia*. It has *basidiomata* resupinate, small, gregarious, attached eccentrically, hard when dry; basidioma cup-shaped when young, becoming spatula-like with an irregular edge and larger as it grows. *Pileus* 1.7-cm x 2.5 cm, conchate, gray, stipe absent and context gelatinous. Found growing on the trunk of a living tree *Ligustrum lucidum* at a preservation area Sanga da Bica - São Gabriel, Rio Grande do Sul, Brazil. The observed genetic distance justifies its recognition as a new specie based on significant molecular differences. Statistical support indicates strong confidence in the observed phylogenetic relationships. The phylogenetic position shows proximity to *R. reviviscens*, but the presence of basal hairs and pleurocystidia size differs. *R. reviviscens* has a brownish-gray to dark-gray basidiome (Carpouron *et al.* 2024). In terms of the color of basidiomas, *Resupinatus brunneus* does not resemble any species described, and in drying basidiomes present a light grey color near the base and the central region with edges of dark gray color. This new record helps to increase data with different features for the genus.

Keywords: Biodiversity, cyphelloid mushrooms, taxonomy, subtropical fungal diversity, phylogeny, macrofungi, new record.

Introduction

The association between fungi and other groups occurs based on their ecological roles and life modes. We can observe that soil fungi enhance plant growth, soil-borne root pathogens, or saprotrophic fungi. This is the biggest group and is important in many aspects of vital complex

biological processes (Frąc *et al.* 2018). The estimated number of fungal species distributed in the world is about 2,5 million, where the total value, which has been studied, does not exceed 10% of that (Niskanen *et al.* 2023).

The genus *Resupinatus* Nees ex Gray 1821 (Agaricales, Resupinataceae) belongs to the euagaric clade and is characterized by saprotrophic habits which can be found in dead, rotting, or decomposing wood (Binder *et al.* 2005, McDonald 2015, Consiglio *et al.* 2018, Vizzini *et al.* 2024). Over 49 species are described in the genus (Index Fungorum 2025). Species of *Resupinatus* have different characteristics, but generally, they are small in size, can be dark-colored, and resupinate or cupulate basidiomata. The pileal trama presents a gelatinous zone with hyaline, amyloid, and smooth basidiospores. Another factor that helps the determination of species in the genus is the absence of metuloid cystidia, which is found in species of the genus *Hohenbuehelia* Schulzer (Singer 1986, Thorn & Barron 1986, Watling & Gregory 1989).

In the last years, your classification has been modified under different groups and families, but recent studies have considered the classification in Pleurotaceae based on molecular and phylogenetic analysis (Consiglio & Setti 2018, Demirak & Kaygusuz 2021, Liu *et al.* 2024, He *et al.* 2024). Although Jülich (1981) has suggested the placement of Resupinataceae and some new studies considered *Resupinatus* such as a family with a direct name based on recent molecular analyses (Kalichman *et al.* 2020, Vizzini *et al.* 2024, Carpouren *et al.* 2024). This study presented a new record species to the genus from Brazil and suggested the restoration of Resupinataceae based on the position obtained with phylogenetic analyses.

Materials and methods

Morphological analysis

Resupinatus specimens were collected in the preservation area in São Gabriel, Rio Grande do Sul, Brazil (-30°20'36.9816" S -54°19'18.49512" W) characterized as a late regenerative forest. The specimens were photographed in their natural habitat and the following proceedings were conducted at the Laboratório de Taxonomia de Fungos (LATAF) from Universidade Federal do Pampa (UNIPAMPA) - São Gabriel, Rio Grande do Sul, Brazil.

The macro morphological identification was determined, and the microscopic description was analyzed using a biological stereomicroscope Olympus SZ51, and a microscope Zeiss Axio Scope A1. Microscopic structures were made from slide preparations with dried specimens rehydrated in distilled water (Kirk *et al.* 2008). The measurement analysis includes Lm and Wm, which indicate the mean length and width of basidiospores, Q shows the length/width ratios, and Qm is the average of the 20 basidiospores measured (Demirak & Kaygusuz 2021) with HAYEAR microscope camera measure software version x64. The materials examined were deposited at the Bruno Edgar Irgang Herbarium of Universidade Federal do Pampa (UNIPAMPA), with the identifying number 137.

DNA extraction, PCR amplification, and sequencing

Dehydrated samples of *Resupinatus* were used for DNA extraction using the Quick-DNA Fungal/Bacterial Miniprep kit (Zymo Research) following the protocol specifications. Subsequently, PCR amplification of the ITS region (ITS1-5.8S-ITS2) was performed using the primers ITS1 (5'-CTTGGTCATTTAGAGGAAGTAA-3') and ITS4 (5'-TCCTCCGCTTATTGATATGC-3') (Sappington and Taylor 1990, White *et al.* 1990), and the 28S nuclear ribosomal DNA (nrLSU) was amplified using the primers LR0R (5'-ACCCGCTGAACTTAAGC) and LR5 (5'-TCCTGAGGGAACTTCG-3') (Vilgalys and Hester, 1990).

Polymerase Chain Reaction (PCR) was conducted in a final volume of 25 μ L, comprising 25 ng of genomic DNA (1 μ L), 20 mM of each primer (0.25 μ L), 10 mM of dNTP mix (2 μ L), 50 mM of MgCl₂ (0.75 μ L), 10 \times PCR buffer (2.5 μ L), Taq polymerase at 5 U/ μ L (0.25 μ L) (Ludwig Biotechnology), and ultrapure water (Milli-Q®) to complete the reaction volume. The PCR cycling conditions for ITS were as follows: initial denaturation at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 40 s, extension at 72 °C for 1 min, and a final extension step at 72 °C for 1 min. For nrLSU, the PCR conditions were as follows: initial denaturation at 94 °C for 2 min, followed by 35 cycles of denaturation at 94 °C for 30 s, annealing at 51 °C for 40 s, extension at 72 °C for 1 min, and a final extension step at 72 °C for 1 min.

The resulting PCR product fragments were verified on a 1% agarose gel, using the 100 bp Ladder (Ludwig Biotechnology). Amplicon purification and sequencing were performed by the

ATCGene Molecular Analyses Service (Rio Grande do Sul, Brazil). The sequences obtained in this study were submitted to GenBank under accession numbers PV246211 for nrLSU and PV246188 for ITS.

Phylogenetic analysis

For the phylogenetic analysis, a BLAST search (NCBI; <https://www.ncbi.nlm.nih.gov/>) was conducted, where sequences closely related to the ITS and nrLSU regions generated in this study were downloaded from GenBank (Table 5). Those genes were aligned individually using Mafft v. 7.220 (Kato *et al.* 2019) with default parameters. Phylogenetic reconstruction was performed by maximum likelihood using the PhyML 3.0 webserver (<http://www.atgc-montpellier.fr/phyml/>) (Guindon *et al.* 2010). Branch support was evaluated using the aLRT SH-like method, where branch support > 0.70 is considered well-supported. Sequences from *Hohenbuehelia flabelliformis* Phonemany & Raspé (2023:115), *H. lageniformis* Phonemany & Raspé (2023:118), and *H. thornii* Consiglio & Setti (2017a:1) were used as outgroups.

Table 5 GenBank accession numbers of sequences used in the phylogenetic analyses (newly-generated sequences are indicated in bold)

Species	Voucher	Location	GenBank Accession		Reference
			ITS	LSU	
<i>H. flabelliformis</i> *	MFLU22 0008	Thailand	OP236779	OM521957	Phonemany <i>et al.</i> (2023)
<i>H. lageniformis</i> *	MFLU22 0010	Thailand	OP236781	OM521958	Phonemany <i>et al.</i> (2023)
<i>H. thornii</i> *	AMB 18086	Italy	NR_166381	KU355400	Consiglio & Setti (2018)
<i>Resupinatus brunneus</i>	LFPAMPA005	Brazil	PV246188	PV246211	In this study
<i>R. applicatus</i>	AMB 18075	Italy	KU355368	KU355411	Consiglio & Setti (2018)
<i>R. conspersus</i>	C61852	Ecuador	AY 571061	AY 571024	Bodensteiner <i>et al.</i> (2004)
<i>R. europaeus</i>	AMB 18077	Italy	KU355366	KU355410	Consiglio & Setti (2018)
<i>R. griseopallidus</i>	Blasco	Spain	MG553642	MG553649	Consiglio & Setti (2017b)
<i>R. hausknechtii</i>	WU 7659	Austria	KU355370	KU355412	Consiglio & Setti (2018)
<i>R. kavinae</i>	AVM 3128	Spain	MG553643	MG553650	Consiglio & Setti (2017b)
<i>R. niger</i>	MCVE 10781	Italy	KU355331	KU355395	Consiglio & Setti (2018)
<i>R. niger</i>	AMB 18095	Italy	KU355371	KU355413	Consiglio & Setti (2018)
<i>R. niger</i>	Roux 3740	NA*	KU355372	KU355414	Consiglio & Setti (2018)
<i>R. poriformis</i>	CBS 327 91	Canada	AY571062	AY571025	Bodensteiner <i>et al.</i> (2004)
<i>R. reviviscens</i>	MFLU24-0230	Thailand	PQ036933	PQ036939	Carpouron <i>et al.</i> (2024)
<i>R. reviviscens</i>	MFLU24-0231	Thailand	PQ036934	PQ036940	Carpouron <i>et al.</i> (2024)

<i>R. rouxii</i>	Z ZT 971	Switzerland	MH168326	MH190787	Consiglio & Setti (2018)
<i>Resupinatus sp.</i>	ALV 5614	Italy	KU355376	KU355415	Consiglio & Setti (2018)
<i>Resupinatus sp.</i>	OR1781	Thailand	PQ475810	PQ036943	Carpouron <i>et al.</i> (2024)
<i>R. striatulus</i>	Wilhelm 5316	France	MH137831	MH169342	Consiglio & Setti (2018)
<i>R. trichotis</i>	AMB 18074	Italy	KU355378	KU355416	Consiglio & Setti (2018)
<i>R. yunnanensis</i>	CLZhao 8651	China	OP901839	OP904197	Yang <i>et al.</i> (2023)

Note: The specimens with * were utilized as outgroup and NA* means Not Available.

Results

Phylogenetic analysis

The phylogenetic analysis was performed using the PhyML program based on ITS (ITS1-5.8S-ITS2) and nrLSU sequences from 22 species of the order Agaricales, including 19 specimens of *Resupinatus* spp. and 3 specimens of *Hohenbuehelia* spp. *Hohenbuehelia flabelliformis*, *H. lageniformis*, and *H. thornii* were used as an outgroup. A total of 896 nucleotide positions were analyzed for ITS and 1442 for nrLSU. Both phylogenetic trees, resulting from the ITS (Figure 5) and nrLSU (Figure 6) sequences and generated using the maximum likelihood approach, position *Resupinatus brunneus* close to previously identified *Resupinatus* spp. specie. However, the observed genetic distance is sufficient to justify its recognition as a new specie based on significant molecular differences. Statistical support indicates strong confidence in the observed phylogenetic relationships.

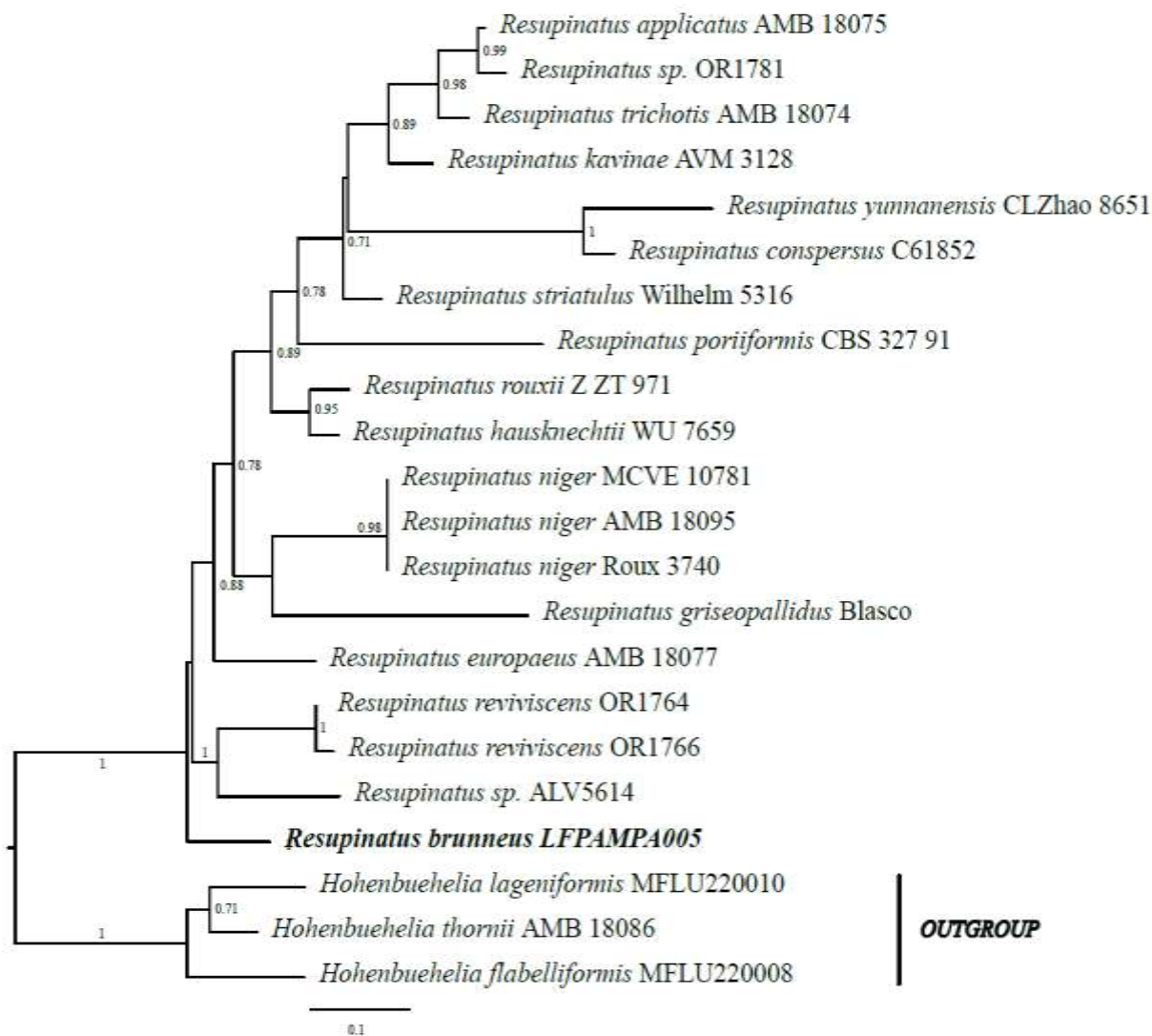


Figure 5 Sequences in PhyML v3.1, employing the GTR+G+I substitution model. The aLRT SH-like support values are indicated at the nodes and represent the branch support probabilities. aLRT SH-like values ≥ 0.70 are shown at the nodes and indicate strong support for the branch. The species analyzed are highlighted. *H. flabelliformis*, *H. lageniformis*, and *H. thornii* were used as outgroups.

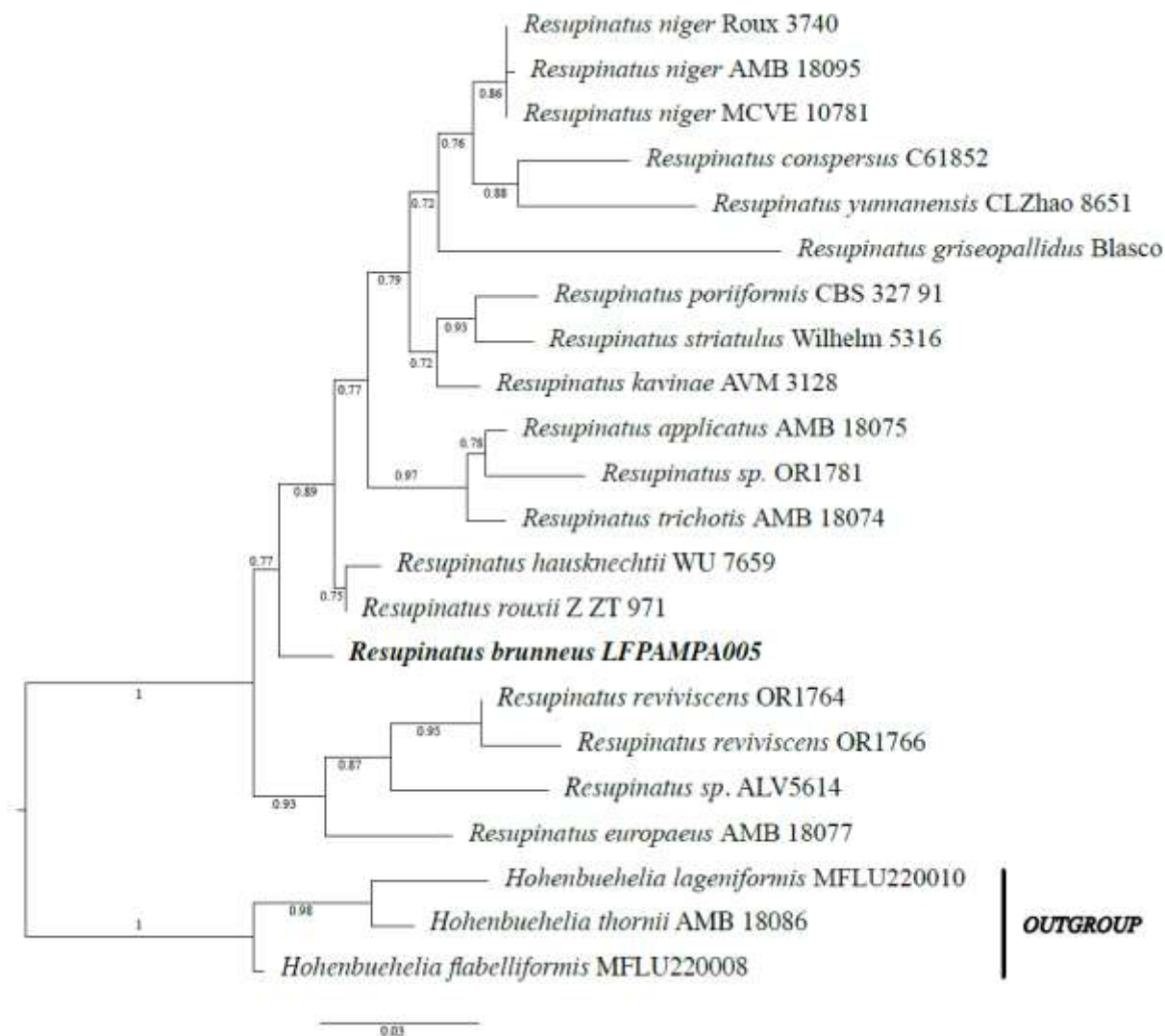


Figure 6 Maximum likelihood (ML) phylogenetic tree constructed using nrLSU sequences in PhyML v3.1, employing the TN93 substitution model. aLRT SH-like values ≥ 0.70 are shown at the nodes and indicate strong support for the branch. The species analyzed are highlighted. *H. flabelliformis*, *H. lageniformis*, and *H. thornii* were used as outgroups

Taxonomy

Resupinatus brunneus Costa et al., *sp. nov.* FIGURE 7

Etymology: The specific epithet “*brunneus*”, from Latin, refers to the brown color basidiomata when they are fresh.

Holotype: BRAZIL. Sanga da Bica, São Gabriel, Rio Grande do Sul, 14 April 2024. *Laura Costa* (LFPAMPA005).

Diagnosis: *Resupinatus brunneus* resembles *Resupinatus reviviscens* Carpouren & Raspé, *sp. nov.* in their ability of basidiomes to withstand drying but differs in basidiospores and pileus size, nonbasal hairs, and basidiomata color. Also resembles *Resupinatus niger* (Schwein.) Murrill for the presence of the metuloid cystidia but differs in mature basidiocarps color, pileus, and basidiospores size.

Mycobank: 858449

Basidiomata resupinate, small, gregarious, attached eccentrically, hard when dry; basidioma cup-shaped when young, becoming spatula-like with an irregular edge and larger as it grows. *Pileus* 1.7-cm x 2.5 cm, conchate, gray, stipe absent and context gelatinous. The *external surface* presents a wet and shiny appearance; light off-white when young, turning to cream and reaching brown, then becoming brownish to black in the central region and brown lighter towards the edge. *Lamellae* concurrent, moderately close to sub-distant, thick, with 1–4 unequal and weave regular. The *hymenial surface* is light off-white when young, turning to cream and reaching brown when fresh; when well developed, the basidiomata acquire a dark brown color at the base and central region, while the edge remains light brown, turning to black before starting to dry; when drying, it presents a light gray color near the base and in the central region, the edges have a dark gray color.

Basidiospores (5.9-) 6.8 – 7.29 (7.8) x (3.1) 3.2 – 3.71 (3.9) μm {N=20}, yellowish under the microscope, subreticulate with thick wall, ellipsoid, smooth, inamyloid. *Pleurocystidia* present of the metuloid type (39.3-) 43.28 – 49.6 (57) x (8-) 7.8 – 12.7 (16) Apex width (4.8-) 5.9 – 6.9 (8.1) μm {N=20}. A *cortical layer* of the tricothecium-type pileus up to the lamella; is continuous and covers the pileus and presents rounded structures, similar to crusts/shells, but it is not continuous throughout the layer, it appears in some points. *Hyphae* with fibulae present.

Habitat and distribution: Growing on the trunk of a living tree *Ligustrum lucidum* at a preservation area Sanga da Bica - São Gabriel, Rio Grande do Sul, Brazil.

Ecology: The species was found on the trunk of *Ligustrum lucidum*, within the Sanga da Bica preservation area. In this location, the tree had a large crown, which was covered by other smaller crowns of other trees. The incidence of sunlight was partial, due to the large number of crowns around the tree.



Figure 7 *Resupinatus brunneus*: (LFPAMPA005). a–b) Basidiomata, c) Pleurocystidia and hymenophore trama showing metuloids d) metuloid, e) Basidiospores. Scale bars: a = 9 cm, b = 2cm, c = 20 μm d = 30 μm , e = 10 μm .

Discussion

In Brazil, some species have been described until this moment. *Resupinatus applicatus* (Batsch) Gray 1821, *Resupinatus dealbatus* (Berk.) Singer 1973 (Singer 1943, 1973, 1989, Pegler 1997, Thorn & Barron 1986), *Resupinatus alboniger* (Pat.) Singer (Meijer 2006), *Resupinatus hyalinus* (Singer) Thorn, Moncalvo & Redhead (Singer 1989), *Resupinatus poriaeformis* (Pers.) Thorn, Moncalvo & Redhead (Cooke 1957, Nogueira-Melo *et al.* 2011), *Resupinatus porosus* and *Resupinatus rickii* (Triervelier-Pereira *et al.* 2019, 2024), *Resupinatus stictoides* (Speg.) Nakasone (Donk 1959) and *Resupinatus subrhacodium* Singer (Putzke 1994, Meijer 2006).

The presence of metuloids is a morphological characteristic that helps identify and differentiate *Hohenbuehelia* and *Resupinatus*. *Hohenbuehelia* has metuloids, which can be sterile cells with thick lanceolate walls and could be present in crystal-encrusted cells in the hymenium. *Resupinatus* species described until now do not have this characteristic (McDonald, 2015).

Resupinatus brunneus share the metuloid cystidia presence with *R. niger* and is the only species in the genus that presented this feature and also shares the form and size of spores similarities. *R. niger* also shares proximity with *Resupinatus europaeus* Consiglio & Setti, but *R. niger* features a gray-brown exterior and turns black when the basidiocarps mature, whereas *R. europaeus* displays a more grayish or grayish-white cap with blackish tints (Thorn & Barron 1986, Consiglio, Setti & Thorn 2018, Demırak & Kaygusuz 2021).

The phylogenetic position shows proximity to *R. reviviscens*, but the presence of basal hairs and pleurocystidia size differs. *R. reviviscens* has a brownish-gray to dark-gray basidiome (Carpouren *et al.* 2024). In terms of the color of basidiomas, *Resupinatus brunneus* does not resemble any species described, and in drying basidiomes present a light grey color near the base and the central region with edges of dark gray color.

Most species of the genus have color variations in shades of gray and black. The size and shape of the basidioma are other characteristics that differentiate this new record from other species of the genus. This way, this new record helps to increase data with distinctive features for the genus. The taxonomic descriptions are confirmed by molecular analysis.

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3.3 Artigo 3 Evaluation of mycelial growth and antimicrobial activity of *Resupinatus brunneus* (Resupinataceae) and *Hericiium erinaceus* (Herinaceae)

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**Evaluation of mycelial growth and antimicrobial activity of *Resupinatus brunneus*
(Resupinataceae) and *Hericium erinaceus* (Herinaceae)**

ABSTRACT

Resupinatus and *Hericium* are worldwide fungi. While *Resupinatus* does not have data about mycelial growth and antibacterial activity, *Hericium* is a commercial species worldwide. Evaluating these potentials is very important to help in implementing new data in different analyses for both the genus. Mycelial growth was performed for 10 days, and the 04 treatments were in quintuplicate. We propose analysis with 03 conventional treatments and a different one. After 10 days, the measurements were submitted for statistical analysis. For *H. erinaceus*, the mean mycelial growth was statistically significant for all treatments when compared to the control treatment (TC). For *R. brunneus*, TC differed significantly at the 5% significance level from T2, with no significant difference when compared to T1 and T3. The antimicrobial activity was performed against the strain *Escherichia coli* (Gram-negative, standard ATCC 10536) and we utilized Yeast malt agar (YMA) and Luria Bertani (LB). The measurements were taken in a total of 24 hours and the average were analyzed. The data obtained show some bacteriostatic effects after 12 hours of exposition. *Resupinatus* 1:1 has something that makes it become a catalyst/nutrient, but apparently, at a concentration of 1:2 it has a bacteriostatic effect from 6 hours. *Hericium erinaceus* with concentration 1:2 from 6 hours onwards showed a bacteriostatic effect. The results obtained are preliminary but positive. The existence of this data elucidated the need for further analysis in different concentrations and times of evaluation.

Keywords: Medicinal mushroom, basidiomycetes, growth rate, different culture media, antimicrobial effect.

INTRODUCTION

Fungi are one of the most species-rich groups that predominantly inhabit terrestrial

ecosystems and play an important role in ecosystems like decomposition, host specificity, and symbiotic relationships. The diversity of fungi is estimated to be approximately 2 to 11 million species, and only a part of that, about 150.000 species, are known. If we consider metabarcoding data, the value is 11.7-13.2 million species (Hawksworth and Lücking 2017; Wu et al. 2019; Phukhamsakda et al. 2022).

The presence of vegetative mycelia and a basidium in Agaricomycetes turns beneficial fungi applicable in diverse areas. The wood-decaying fungi, which includes utilization in culinary and remediation of pollutants, is based on their potential nutritional and therapeutic (Bhagarathi et al. 2023; Shin et al. 2025). In addition, industrial applications and biotechnology have widely explored the ecological importance of fungi. In the food industry, mushroom cultivation and food fermentation through yeasts stand out as important in producing fermented drinks and baked goods (Trierveiler-Pereira et al. 2018). In the pharmaceutical and medicine industry, many species have produced secondary bioactive metabolites with the potential for the fabrication of drugs, including antibiotics, immunosuppressants, and compounds with anticancer properties (Meyer et al. 2020).

Within the species studied as promising cultivation and pharmaceutical analyses, *Hericium erinaceus* (*Hericiaceae* - Basidiomycota) known as the mushroom “lion’s mane”, has been utilized in culinary and medicine, because of its medicinal properties in the mycelium and the basidiome, showing a larger amount bioactive compound, and influenced studies about different potential investigations uses (Kirk et al. 2008; Bolaño-Campos and Romero-Bautista 2025).

Species such as *Hericium erinaceus* have been studied in several areas, but some of them still with few studies carried out, such as their potential for antimicrobial activity and mycelial growth. *Resupinatus brunneus* is a new record available in Brazil, and the evaluation of mycelial growth and antimicrobial activity enables the increase of new data on this genus. Thus, this study intends to evaluate the mycelial growth in different treatments and the antimicrobial activity of *Resupinatus brunneus* and *Hericium erinaceus* in different culture mediums and concentrations.

MATERIAL AND METHODS

Obtaining samples

Pure cultures of *Resupinatus brunneus* were obtained from the Laboratório de Taxonomia de Fungos (LATAF) at Universidade Federal do Pampa (Unipampa), São Gabriel, Rio Grande do Sul, Brazil, and Mycobank number 858449. *Hericium erinaceus* was obtained from Laboratório Muschária localized in Caxias do Sul, Rio Grande do Sul, Brazil. The procedures were realized in the previously mentioned laboratory LATAF and Laboratório de Microbiologia from Unipampa. Cultures were isolated initially in Potato Dextrose Agar (PDA) in Petri plates 09 mm and incubated at room temperature until the mycelial colonization was complete.

Mycelial growth

Three commercial culture media (Potato dextrose agar (PDA), Sabouraud dextrose agar (SDA), and Yeast malt agar (YMA)) and a media with PDA + 5% sawdust filtrate of *Eucalyptus* sp. (PDA + SE). were utilized to evaluate the mycelial growth of *Resupinatus brunneus* and *Hericium erinaceus*. The sequence of treatments used was Treatment Control (PDA), T1 (YMA), T2 (SDA), and T3 (PDA + SE). The experiment was performed and realized based on the methodology described by Julian et al. (2018).

The media were sterilized at 121°C for 20 min and distributed in sterile Petri plates with 05 replicates per treatment. Approximately 05 mm of mycelial disc from each species was aseptically inoculated in the center of sterile culture plates, sealed with plastic film, and incubated at 28-30°C for 10 days. The diameter of mycelial growth was measured in mm every 24 hours using a digital Vernier caliper, and statistical analyses were performed.

Data processing and statistical analysis were performed using the R and RStudio software programs (R Core Team, 2024). The Shapiro-Wilk test (Royston 1982a, 1982b, 1995) was used to verify normality assumption. If the data followed a normal distribution ($p\text{-value} > 0.05$), the t-test was used to compare the means between the different treatments. The growth means were obtained in RStudio (R Core Team, 2024) using the summarySE tool of the Rmisc package (HOPE, 2022). Figures were created using the ggplot2 package (Wickham, 2016), within the RStudio program (R Core Team, 2024).

Evaluation of antimicrobial activity

The antimicrobial effect of *Resupinatus brunneus* and *Hericiium erinaceus* were tested against the strain *Escherichia coli* (Gram-negative, standard ATCC 10536) belonging to Laboratório de Microbiologia, Universidade Federal do Pampa (UNIPAMPA), São Gabriel, Rio Grande do Sul. *Escherichia coli* was cultivated in media liquid Luria Bertani. The incubation period was realized at 37°C, *overnight*. The experiment *in vitro* was performed and adapted following the protocol established by Jacques (2024) and adapted from Patton et al. (2006). A 96-well plate was organized in sections for tests with *Escherichia coli* in triplicate. Each well was filled with different treatments, and the sterilization control consisted of just liquid Luria Bertani until the growth control was the bacterial inoculum.

In the preparation of wells, the plates were incubated at 36°C and the growth curve was monitored, with measurements during a total period of 24 hours. This measurement was made using a plate reader Perkin Elmer Enspire 2300, which was adjusted to 630 nm of wavelength. Analysis of the wavelength of bacterial growth was performed in Microsoft Excel®. The data obtained were expressed as the Mean Standard Error of the Mean.

RESULTS AND DISCUSSION

Mycelial growth

The measurements were taken after 48 hours of growing. Figure 8 represents the mycelial growth after 10 days of experiment.



Figure 8 Plates with treatments after 10 days. The first line is from *Hericium* and the second is from *Resupinatus*. The sequence of treatments used was Treatment Control = TC (PDA), T1 (YMA), T2 (SDA), and T3 (PDA + SE), and the measurements were taken in mm.

The data on daily mycelial growth in mm, when subjected to the Shapiro-Wilk test, showed a result indicating that it is possible to state that the sample set comes from a population that follows a normal distribution ($p\text{-value} > 0.05$). In this sense, it was decided to use the t-test to compare the growth means (Table 6) for each treatment.

Table 6 *Hericium erinaceus* and *Resupinatus brunneus*, species H and R, respectively. Standard deviation (sd - mm), Standard error of the mean (se - mm) and Confidence interval (ci):

Sp	Treatment	Mean	sd	se	ci
H	T1	1.8195	0.591563	0.264555	0.734523
H	T2	2.1655	0.228457	0.102169	0.283667
H	T3	2.279075	0.224166	0.10025	0.278339
H	TC	0.923194	0.623284	0.278741	0.77391
R	T1	2.712	0.607779	0.271807	0.754657
R	T2	0.34375	0.556323	0.248795	0.690766

R	T3	3.648676	0.4091	0.182955	0.507964
R	TC	3.257	0.29845	0.133471	0.370574

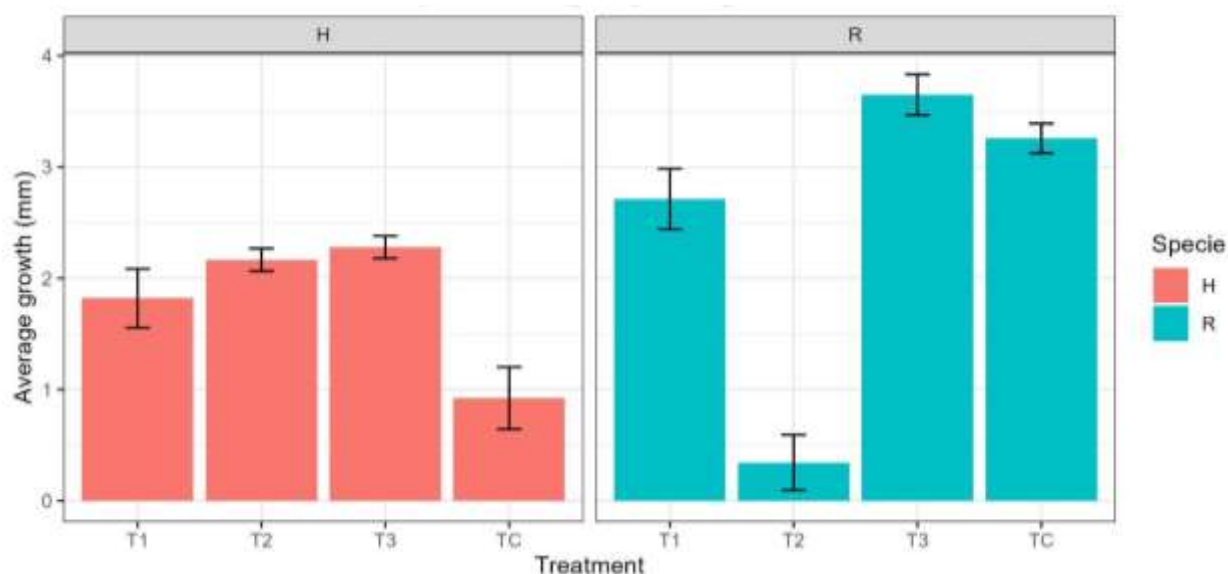
For species *H. erinaceus*, the mean mycelial growth was statistically ($\alpha = 5\%$) higher (Table 2, p-value < 0.05) for all treatments (T1, T2, and T3) when compared to the control treatment (TC). The three alternative treatments (T1, T2, and T3) did not have significant differences in their mean growths when compared to each other (Table 2, p-value > 0.05). For species *R. brunneus*, TC differed significantly at the 5% significance level from T2, with no significant difference when compared to T1 and T3 (Table 2, p-value > 0.05). When comparing the alternative treatments (T1, T2, and T3), only T2 differed from T1 and T3 (Table 7, p-value < 0.05).

Table 7 p-values of the statistical comparison between means using the t-test, verifying whether there was a significant difference in mycelial growth between the different treatments for each species

<i>H. erinaceus</i>				
	T1	T2	T3	TC
T1		0,275	0,163	0,048*
T2			0,450	0,008*
T3				0,005*
<i>R. brunneus</i>				
T1		0,000*	0,024*	0,123
T2			0,000*	0,000*
T3				0,125

*there is a significant difference.

The genus *Resupinatus* has not had mycelial growth evaluated until now, so this is the first data obtained about an evaluation of different media utilized to observe the mycelial growth in plates. Some previous studies have analyzed secondary metabolites (Sundin et al. 1993; Eilbert et al. 2000; Harms et al. 2023) but without data about mycelial growth or antimicrobial activity. When we observe the average graphic generated (Graph 2), it is possible to see the difference in the media.



Graph 2 Average mycelial growth of *Hericium erinaceus* and *Resupinatus brunneus*, species H and R, respectively

Resupinatus is generally found growing on softwood and hardwood or in wood decay (Carpouren et al. 2024), and this could influence the fact that T3 shows the biggest value obtained over TC. The presence of a sawdust filtrate can be attributed to optimizing the mycelial growth. Several studies have linked lignin presence to changes in the carbon-to-nitrogen ratio and the later stages of decomposition, which are associated with the emergence of *Resupinatus* in certain areas (Thorn and Barron 1986; Rajala et al. 2011; Bonanomi et al. 2022).

Hericium has a habit similar to *Resupinatus* and can grow mostly on dead or dying wood (Ko et al. 2005). This can indicate a similarity with the results described, where T3 appears to be an available media for the cultivation of commercial species or noncommercial. PDA is one of the most utilized media for the analysis and inoculation of species and the composition of media influences the nutritional requirements of fungi (Odds, 2009).

Akata et al. (2012) utilized homokaryotic mycelium from germinated *H. erinaceus* to determine the mycelium growth rate in different microbiological media. The media PDA was utilized and presented faster spore germination but was not the culture media chosen in comparison with Malt Extract Agar (MEA) and Minimal Agar (MA) analyzed. Gonkhom et al. (2022) evaluated

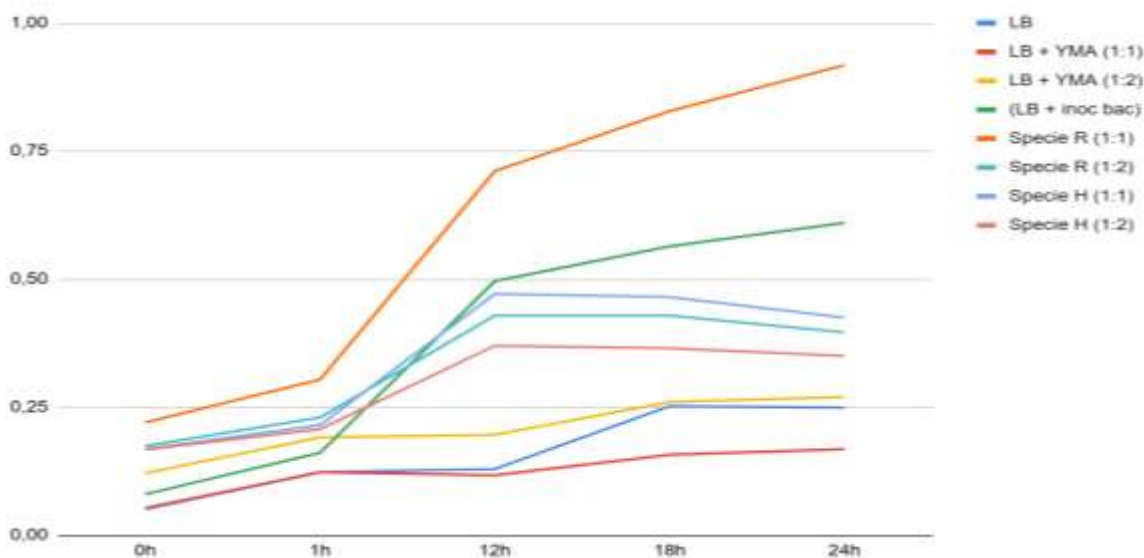
the mycelial growth in different *Hericium* species with nine culture media. PDA and SDA were utilized during the 15-day experiment, but the media most effectively was indicated as oatmeal yeast agar (OMYA) and carrot dextrose agar (CDA) to *H. erinaceus*.

Early studies by Julian et al. (2018), described PDA as appropriate to *H. erinaceus*. Nguyen et al. (2018) indicated PDA but with addition to fresh mushroom extract being the most suitable medium for the mycelial growth of *H. erinaceus*. Imtiaj et al. (2008) also indicated that PDA, and YM (yeast and malt extract) were the media more effective for mycelial growth in 4 strains of *H. erinaceus*. In this study, PDA is not the most indicated to *H. erinaceus*. SDA and PDA + SE appear to be the most appropriate.

To *R. brunneus* PDA shows a good value obtained, but when compared with PDA + SE we observe a better performance. In both species, PDA with sawdust of *Eucalyptus* sp. shows potential and could be considered an alternative media with the reuse of sawdust.

Evaluation of antimicrobial activity

The evaluation of antimicrobial activity had an average concentration obtained and was expressed in a graph (Graph 3). After up to 12 hours of measurements, the treatments show compartment, and after this period a change can be observed.



Graph 3 Average concentration from different treatments observed after 24 hours

The potential antimicrobial activity was described in many studies for *Hericium* species, especially for *H. erinaceus* against diverse bacteria. The presence of different compounds is elucidated and acts against diverse species. The time of appearance was indicated as a factor that interferes with the action model, as well as the concentration of the sample (Zhang et al. 2015; Whong et al. 2009; Jianzhao et al. 2024).

Hericium erinaceus with concentration 1:2 from 6 hours onwards showed a bacteriostatic effect below the control with the inoculum. It was far from the controls without the inoculum and was in an intermediate position between the growth patterns and the negative control. This made us repeat the experiment and extend it for a few hours to check and reinforce the behavior again. After 12 hours, it decreased again, between 12 and 24 hours, falling well below the growth control and getting close to control without the inoculum. So, there was a decrease in growth and a stabilization/reduction. It has had a bacteriostatic effect on this concentration.

R. brunneus also shows a decrease after 12 hours, a slower effect on bacterial growth, but it does have a bacteriostatic effect. *R. brunneus* 1:1 has something that makes it become a catalyst/nutrient, but apparently, at a concentration of 1:2 it has a bacteriostatic effect from 6 hours onwards and lasts until 12/24 hours. It is an effect that takes time, it is slow to start acting, but after 12 hours they can perform a bacteriostatic effect compared to the growth control.

For *Resupinatus* species, the evaluation of antimicrobial activity was the first described in this work. Preliminary results require more repetitions but have a good indication of a bacteriostatic effect after 12 hours. Dependent concentration and time are variable, considering that fungi take longer to grow than bacteria, however with strong positive indications.

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CONCLUSÃO

Através da revisão sistemática foi possível aprofundar características e informações importantes que se encontravam dispostas em trabalhos distintos e que necessitavam de uma conexão interdisciplinar de forma abrangente.

A descrição da nova espécie para o gênero contribuiu para a adição de informações sobre a biodiversidade fúngica brasileira e local. Também, importante para o gênero em si na sua classificação por relacionamentos filogenéticos. Por meio deste novo registro considerações importantes foram apresentadas e que podem vir a ser muito úteis no delineamento correto do gênero em futuros trabalhos. Auxiliando a ressaltar a importância da taxonomia, as associações de espécies dentro de um ecossistema, que são fundamentais para sua coexistência e ajudando no fornecimento de novos dados para corroborar com a preservação da biodiversidade fúngica.

Os resultados obtidos a partir das análises do crescimento micelial e atividade antimicrobiana também foram promissores. Elucidando a importância de análises como esta, que podem servir como indicadores de meios alternativos e o estudo de compostos em concentrações diferentes úteis para o ecossistema e a sociedade em que estamos inseridos. Por fim, estes resultados reforçam a importância dos estudos taxonômicos e ecológicos para a compreensão da biodiversidade fúngica e suas interações. Além disso, a investigação do potencial antimicrobiano e do crescimento micelial amplia as perspectivas para o uso de *Resupinatus* em aplicações biotecnológicas. Desta forma, este estudo contribui para o avanço do conhecimento sobre fungos e reforça a necessidade de estudos futuros sobre sua diversidade e aplicações.

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