Journal of Mycology and Truffle
Journal homepage: www.mycotruffle.org
Volume: 1 Issue: 1 (2026) Pages: 43-55 ISSN: 3136-4209

Review Article

Aquatic Fungi and Mushrooms: Ecology, Applications, and Future Prospects

Waill ELKHATEEB [1,*], **Atsushi ISHIHARA** [2], **Ghoson DABA** [1]

[1] *Chemistry of Natural and Microbial Products Department, National Research Centre, Dokki, Giza 12622, Egypt.*
[2] *Faculty of Agriculture, Tottori University, 4–101 Koyama-Minami, Tottori 680–8553, Japan.*

* Corresponding author: waillahmed@yahoo.com

Received: **2026-08-28** Revised: **2026-10-14** Accepted: **2026-10-24** Published: **2026-11-07** **DOI:** 10.65999/mycotruffle.2026.41

ABSTRACT: Most mycology research focuses on land mushrooms, but aquatic species form a remarkable and ecologically valuable group that deserves more scientific attention. Fungi contribute roughly 38% of all known biologically active metabolites, making them a rich reservoir of compounds valuable to the pharmaceutical industry and human health. Although fungi are widespread, aquatic species are emerging as a particularly promising source of new molecules for various biotechnological applications. Numerous fungi isolated from marine environments have yielded novel substances with important biological activities. Likewise, mushrooms as macrofungi are common in our environment and play an important role in human life by providing nutrition and bioactive constituents. Several aquatic fungi and mushrooms have been identified as valuable sources of secondary metabolites with diverse biological effects. Recently, *Psathyrella aquatica* was described from the Rogue River in Oregon, USA. This species represents a new taxon within the family Psathyrellaceae and the large, polyphyletic genus *Psathyrella*. It is currently the only known aquatic gilled mushroom. Such underwater Basidiomycetes are of special interest because of their rarity. This review highlights the potential of aquatic fungi in general, and aquatic mushrooms in particular, as sources of new bioactive compounds. It also discusses the ecology and distribution of unique aquatic gilled mushrooms and summarizes available data on the novel species *Psathyrella aquatica*.

Keywords: Agaricales; Aquatic Fungi; Aquatic Mushrooms; Biotechnology; Secondary Metabolites.
Cite this article: ELKHATEEB, W.; ISHIHARA, A.; & DABA, G. (2026). Aquatic Fungi and Mushrooms: Ecology, Applications, and Future Prospects. *Journal of Mycology and Truffle* *1*(1): 43-55. https://doi.org/10.65999/mycotruffle.2026.41

1. INTRODUCTION

While terrestrial fungi dominate the field of mycology, their aquatic counterparts represent a captivating and ecologically important assemblage. The genus *Psathyrella aquatica* is unique as the only single-gilled fungus known to fruit underwater, and marine genera like Nia and Halocyphina show how Basidiomycota expanded into water environments. However, little is known about their life cycles and ecology. These mushrooms inhabiting freshwater, marine, and brackish systems play key roles as nutrient recyclers, wood decomposers, and ecological partners, yet their biology and ecological functions remain largely understudied (Elkhateeb et al., 2021). This review summarizes existing knowledge on the diversity of aquatic fungi, their evolutionary traits, including floating spores, salt-tolerant enzymes, and water-repellent fruiting structures and their promise for biotechnological use. Marine mushroom species produce bioactive compounds with antimicrobial and anti-inflammatory effects, and their specialized enzymes could support bioremediation in saline or aquatic settings. As climate change accelerates, studying aquatic mushrooms matters both to protect biodiversity and to explore their use in green technologies. This review synthesizes current data to support targeted research and conservation of aquatic mushrooms, knowledge essential for both biodiversity science and biotech innovation.

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Fungi are multicultural and occur throughout the terrestrial biosphere, ranging from polar regions and hot deserts to tropical rainforests and estuarine zones. Although most described fungal species are terrestrial, some taxa are restricted to aquatic environments. Most fungi adopt a saprotrophic lifestyle in soil or on decaying organic material, yet many form symbiotic relationships with plants, animals, or other fungi. In all cases, fungi perform essential functions in ecosystem processes (Elkhateeb and Daba, 2018). Fungi are also prolific sources of bioactive secondary metabolites from diverse chemical classes, and these compounds have been harnessed as biotechnological tools in agriculture and the pharmaceutical sector (Elkhateeb et al., 2019a, 2019b). They are highly efficient degraders and help rapidly restore ecosystems impacted by pollutants from industrial activity and human behaviour. This capacity largely stems from the sophisticated array of enzymes produced by different fungal species (Daba et al., 2018; Yadav, 2019; Meyer et al., 2020). In terrestrial systems, fungi together with soil bacteria serve as the main decomposers of organic matter (Taylor et al., 2016; Gulis et al., 2019; Lustenhouwer et al., 2020). The breakdown of dead organisms is fundamental to ecosystem function, as it recycles nutrients back into soil and the environment (Elkhateeb, 2005; Elkhateeb et al., 2016; Elkhateeb & Daba, 2018). Fungi may have originated in aquatic environments. The oldest known fungal microfossils come from Canada, in estuarine sediments dated to 1.0–0.9 billion years ago. These fossils, assigned to *Ourasphaira giraldae*, indicate an estuarine habitat, though the organism could have been transported from terrestrial or deeper marine settings (Loron et al., 2019). Marine fungi are now considered widespread and have been detected in nearly every marine habitat examined, including hydrothermal vents, deep-sea sediments, and Arctic sea ice (Gladfelter et al., 2019). They also parasitize primary producers such as diatoms (Gutiérrez et al., 2016; Kagami et al., 2021). It is estimated that less than 1% of marine fungi have been described. Among those identified, excluding yeasts, many belong to Ascomycotina, Basidiomycotina, Mastigomycotina (zoosporic fungi), Deuteromycotina, and some Zygomycotina (Kohlmeyer & Kohlmeyer, 2013; Gladfelter et al., 2019). Whether a large proportion of marine fungi are truly amphibious remains unresolved. Many species occur both above and below the high-tide mark. Nevertheless, evidence and expectations suggest that some fungi complete their entire life cycle in water, function aquatically during one life stage, or are genuinely amphibious (Amend et al., 2019; Grossart et al., 2019). In addition, some fungi detected as "marine" via DNA may in fact be terrestrial forms deposited into aquatic systems by wind or flooding.

This appraisal inspects the potential of aquatic fungi as promising sources of novel bioactive compounds. It also addresses the ecology and distribution of rare aquatic gilled mushrooms and summarizes current information on the newly described species *Psathyrella aquatica*. Our planet is 71% water, mostly oceanic (saltwater), with 96.5% in oceans and seas. Freshwater accounts for only 2.5% of Earth's water, with a scant 0.6% in surface freshwater in wetlands, rivers, and lakes (Tarasova & Gulevets 2022; Mishra 2023). Both freshwater and marine environments, despite their variations, are essential to global biodiversity and ecological balance and contain a wide array of species and processes (Tockner 2021). These aquatic habitats are home to ubiquitous and diverse fungi whose roles in organic matter and nutrient cycling, and in food web dynamics, are vital (Bahram and Netherway 2022). Fungi in aquatic ecosystems play a very important role in ecosystem processes, from stream habitats in mountainous areas to the ocean floor. Nonetheless, among these fungi, Basidiomycota remain disproportionately underinvestigated relative to their Ascomycota relatives, despite their specializations for submerged environments. This underrepresentation stems from historical research biases toward land-dwelling fungi, challenges in culturing aquatic Basidiomycota, and the often cryptic fruiting bodies of these organisms (Vatova et al., 2022; Pang et al., 2023; Ochs et al., 2025).

This overview discusses how aquatic Basidiomycota overcome evolutionary challenges in waterlogged environments, including oxygen deficiency, salinity stresses, and hydrodynamic stress, and why their biotechnological potential remains largely unexploited. In addition to their ecological roles, aquatic fungi are a rich source of secondary metabolites with antibacterial, antifungal, anticancer, and other activities. However, Basidiomycota have not been extensively utilized for drug discovery. Recent studies increasingly demonstrate that this group produces pharmacologically distinct compounds (Elkhateeb et al., 2021; Wang et al., 2023; Bharathi & Lee, 2024; Shi et al., 2025).

2. AQUATIC AND MARINE FUNGI

Fungi in aquatic ecosystems play a very important role in ecosystem processes, from stream habitats in hilly areas to the ocean floor. Aquatic Basidiomycota display significant evolutionary modifications for life in water. For classification purposes, three ecological types were observed. Obligate aquatic species conduct all life stages underwater, exemplified by *Psathyrella aquatica*. Aquatic-adapted species occur primarily in riparian and waterlogged settings, where they are important for nutrient cycling yet are not exclusively aquatic, such as *Gloiocephala* sp. Finally, some

terrestrial Basidiomycota are isolated from aquatic substrates but lack adaptations to submerged conditions (Barros and Seena 2022; Vatova et al., 2022; Pang et al., 2023; Ochs et al., 2025).

Freshwater fungal communities are frequently dominated by representatives of Oomycota and Chytridiomycota, along with asexual forms of Ascomycota and Basidiomycota, commonly referred to as aquatic hyphomycetes (Jones et al., 2015; Pang et al., 2019). Most aquatic fungi are microscopic and grow as mycelia, with hyphae colonizing submerged organic matter of plant or animal origin. Obligate aquatic species can complete their entire life cycle in freshwater and typically possess specialized traits for growth, spore production, and dispersal in water (Manoharachary et al., 2005). Hyde et al. (2007), estimated global fungal diversity at approximately 1.5 million species. Of these, only about 3000 have been recorded from aquatic environments, and just 465 are known from marine systems. Many aquatic fungi are microscopic and reproduce asexually without forming conspicuous fruiting bodies; these are termed anamorphic fungi (Raghukumar 2017). In aquatic ecosystems, fungi perform essential functions. In transitional zones their roles parallel those of terrestrial fungi, including nutrient cycling, decomposition of organic material, and symbiosis with semi-aquatic plants. In other habitats, such as coral reefs and deep-sea sediments, their ecological functions are less clear. Still, they likely contribute to organic matter breakdown and to pathogenic interactions with organisms ranging from algae to mammals. Such pathogenic associations may be important for nutrient turnover in marine environments (Gladfelter et al., 2019).

Marine fungi occupy diverse ecological niches, from sand grains and plankton to algae, sediments, and the plastisphere. As discussed earlier, they are also found on estuarine plants and on wood submerged in seawater (Jones 2011; Overy et al., 2019). The latter substrate is especially conducive to colonization by Halosphaeriaceae and taxa within Torpedosporales and Lulworthiales, groups predominantly distributed in open ocean areas (Elkhateeb et al., 2021). Marine fungi have developed various strategies to thrive and disperse spores in marine habitats (Musa et al., 2018; Rafiq et al., 2019). In arenicolous fungi, a common trait is the absence of long-necked ascomata, while their ascospores frequently become entrapped in sea foam. By comparison, ascomata associated with submerged wood are often found embedded within the host material.

A current research focus is the capacity of marine fungi to produce unique secondary metabolites of medical, industrial, and agricultural value. Beyond the search for new antibiotics and anticancer drugs, these organisms show promise for environmental applications such as bioremediation of wastewater pollutants and plastic degradation, which could help tackle major oceanic pollution issues. Fungi are undeniably significant members of aquatic microbial communities. Despite this, microbial ecologists are only now starting to characterize how aquatic fungi influence biodiversity and ecosystem services, and many aspects remain largely unstudied (Zhang et al., 2016; Kan et al., 2015). Furthermore, aquatic fungi provide a substantial source of natural compounds, most of which originate from secondary metabolic pathways. Recently many studies have demonstrated the biosynthetic capacity of marine Ascomycota, Basidiomycota, and Zoopagomycota, highlighting them as important sources of novel secondary metabolites (Kenshole et al., 2021; Elkhateeb et al., 2021).

2.1. Aquatic and Marine Fungi as Sources of Bioactive Metabolites for Biotechnological Applications

Beyond their ecological importance, aquatic fungi have been shown to produce bioactive secondary metabolites with diverse biological activities. Up to now, Basidiomycota have received limited attention for drug discovery. Although aquatic fungi are less numerous in terms of described species than terrestrial fungi, they have yielded several notable compounds of aquatic origin (Butler et al., 2014; Shin, 2020). Secondary metabolites from aquatic fungi display a wide range of pharmacological activities such as antibacterial, antifungal, antiviral, anticancer, anti-inflammatory, and antioxidant functions (Bovio et al., 2019; Sajjad et al., 2020; Hagestad et al., 2020). Thus, aquatic fungi are regarded as potent reservoirs of diverse chemical classes, including peptides, polyketides, terpenes, and alkaloids (Youssef et al., 2019; Elkhateeb et al., 2021; Zhang et al., 2020). Up to 2002, approximately 272 metabolites from marine fungi were documented and described (Overy et al., 2014). However, apart from cyclosporine A, none of these compounds have progressed to commercial products or market availability (Langdon & Pearce, 2017; Shin, 2020).

Several natural products have been reported from marine ascomycetous fungi. Examples include aigialomycins A–G, aigialospirol and its derivatives, and aigialone, all isolated from *Aigialus parvus* (Isaka et al., 2009). Likewise, the marine ascomycete *Halorosellinia oceanica* (syn. *Hypoxylon oceanicum*) was found to produce three novel lipodepsipeptides, five new macrocyclic polyethers, and five new linear polyesters. An isolate of *Alternaria alternata* from the soft coral Litophyton arboreum yielded five previously undescribed secondary metabolites: alternariol-9-methyl ether 3-O-sulfate, alternariol-9-methyl ether, alternariol, maculosin, and maculosin-5. These compounds exhibited notable

antimicrobial and anticancer activity, as well as strong inhibition of HCV NS3/NS4A protease (Hawas et al., 2015; Hawas et al., 2016). In addition, zofimarin, a potent antifungal sordarin derivative, was obtained from Zopfiella marina. More recently, sordarin analogs and sordarin-inspired scaffolds have been evaluated in vivo for activity against a broad range of susceptible pathogens (Chakraborty et al., 2016; Wu and Dockendorff, 2018). Conversely, *Aspergillus versicolor* strain XZ-4, isolated from a hydrothermal vent crab collected off Taiwan, was found to produce versicomides A–D along with several cyclopenin derivatives, including 7-methoxycyclopeptin, 7-methoxydehydrocyclopeptin, 7-methoxycyclopenin, and 9-hydroxy-3-methoxyviridicatin (Pan et al., 2017). In addition, the marine fungus *Phaeosphaeria spartinae*, obtained from the internal tissues of the marine alga *Ceramium* sp., yielded eight previously undescribed natural products, such as spartinoxide and spartinol C. These compounds showed inhibitory activity against human leukocyte elastase and may be relevant to cystic fibrosis treatment (Elsebai et al., 2009; Elsebai et al., 2010).

Fungi of the genus *Aspergillus* originating from marine habitats represent important reservoirs of bioactive natural products. Preussins C–K from *Aspergillus flocculosus* 16D-1 were shown to possess anti-inflammatory properties targeting IL-16 (Gu et al., 2018). Compounds such as asperversiamides B, C, F, and G isolated from A. versicolor inhibited inducible nitric oxide synthase. Furthermore, luteoride E, lovastatin, versicolactone G, territrem A, brasilanone A, brasilanone E, and methyl 3,4,5-trimethoxy-2-(2-(nicotinamido)benzamido)benzoate, each obtained from distinct marine *Aspergillus terreus* isolates, demonstrated NO-suppressing activity (Liu et al., 2018a; Wu et al., 2018). Additional anti-inflammatory constituents reported from various Aspergillus species include dihydrobipolaroxins B–D, dihydrobipolaroxin, aspertetranones A–D, diorcinol, cordyol C, and 3,7-dihydroxy-1,9-dimethyldibenzofuran (Wang et al., 2015; Wang et al., 2016). In parallel, marine *Penicillium* species have been identified as producers of diverse bioactive compounds such as methylpenicinoline, citrinin H1, penicillinolide A, penstyrylpyrone, chrysamide C, viridicaol, and brevicompanines E and F (Chen et al., 2016; Ngan et al., 2017). Several other marine fungi have also been cited as sources of bioactive substances, namely *Eurotium* sp., *Graphostroma* sp., *Chondrostereum* sp., *Hypocreales* sp., *Phoma* sp., *Acremonium* sp., and *Alternaria* sp. (Zhu et al., 2013; Chen et al., 2015; Hsiao et al., 2017).

Certain fungi can survive in deep-sea environments at depths exceeding 1 km, where conditions are highly extreme (Deshmukh et al., 2018). Indeed, fungi isolated from deep-sea samples are promising sources of bioactive compounds, likely because of the structural diversity of their secondary metabolites, which can be exploited for drug discovery and pharmaceutical applications. For instance, researchers isolated five novel benzophenone derivatives from the aquatic fungus *Phomopsis lithocarpus*, along with a new eremophilane derivative and two known compounds (Xu et al., 2018). Among these, tenellone H exhibited cytotoxic effects against HepG-2 and A549 cell lines. Similarly, from the marine-derived fungus *Phialocephala* sp., two new sorbicillinoids (Sorbicillassins A and B), a new 3,4,6-trisubstituted α-pyrone derivative (scirpyrone K) with antioxidant activity, and two known biosynthetically related polyketides were obtained (Zhang et al., 2018).

Fungi associated with marine sponges also produce diverse secondary metabolites (Bovio et al., 2018). An *Alternaria* species from sponge tissue provided seven new polyketide derivatives and 21 known compounds (Pang et al., 2018). Altertoxin VII exhibited anticancer effects on K562, SGC-7901, and BEL-7402 cells. From *Aspergillus* sp. isolated from *Ligia oceanica* gut, two new aspochalasins — tricochalasin A and aspochalasin A2 — were identified along with three known analogs (Li et al., 2018). *Myrothecium* sp. yielded eight novel meroterpenoids and isocoumarinoids (Xu et al., 2016). *Sporendonema casei* from marine sediment afforded five new anthraquinones (auxarthrols D–H) with cytotoxic and antitubercular properties (Ge et al., 2019). *Aspergillus versicolor* from sediment was a source of six new diketopiperazines and three pairs of new brevianamides (Hu et al., 2019). Six novel phenalenone derivatives were reported from sediment-derived *Penicillium* sp., among which 4-hydroxysclerodin and a triketone acetone adduct showed anti-angiogenic and anti-inflammatory activities, respectively (Park et al., 2019). *Fusarium solani* from mangrove sediment produced the new alkenoic acid fusaridioic acid A, three new bis-alkenoic esters (fusariumesters A1, A2, and B), and three known compounds (Liu et al., 2018b). In summary, although terrestrial fungi have historically provided many well-known bioactive compounds, fungi in aquatic saline environments are important sources of novel, biologically active natural products (Elkhateeb et al., 2021).

2.2. From Land to Water: Exploring Terrestrial and Aquatic Mushrooms as Bioactive Producers

Mushrooms represent the above-ground fruiting bodies of terrestrial fungi. Lacking both cellulose and chlorophyll, they exhibit a nutritional strategy distinct from that of non-motile organisms such as plants. Because they cannot synthesize sugars via photosynthesis, mushrooms depend on living or dead organic matter from plants and animals for their nutritional requirements. While we typically observe only the visible portion of mushrooms, commonly re-

sembling an umbrella- or tree-like form, their fruiting structures display a wide range of shapes, colors, and sizes. The classic morphology consists of a stalk (stipe) supporting a cap (pileus) that bears the spores (Sridhar, 2020). The underlying fungal mycelium, which gives rise to these fruiting bodies, often extends across a considerable area.

Mushroom-forming fungi belong to the Basidiomycetes and Ascomycetes and include both edible and non-edible taxa. In many Basidiomycetes, spores (Basidiospores) are produced at the apices of club-shaped basidia located along the gills (Elkhateeb et al., 2019; Elkhateeb, 2020; Kamalakannan et al., 2020). For centuries, mushrooms have been valued as food and in traditional medicine because of their rich content of nutrients and bioactive metabolites, with applications in agriculture, food technology, pharmaceuticals, cosmetics, and related industries (Ali El-Hagrassi et al., 2020; Daba et al., 2020). Nutritionally, they function as saprotrophs, parasites, or symbionts such as mycorrhizal fungi. The visible mushroom is the reproductive stage, while the vegetative mycelium constitutes the main body of the fungus.

Edible mushroom species are generally low in calories and provide proteins, flavonoids, amino acids, minerals, trace metals, volatile oils, carotenoids, lipids, phenolics, vitamins, and ergosterol, the latter serving as a precursor for vitamin D2 (Rathee et al., 2012; Xu & Beelman, 2015). They have also been used extensively in traditional Asian medicine to manage various ailments (Rahi & Malik, 2016; Elkhateeb et al., 2019). Mushroom cultivation is land-efficient and does not require prime agricultural land, as production can occur on waste substrates and marginal areas. Indoor systems also allow vertical farming to increase yield. Agricultural and forestry residues can be recycled as growth substrates to generate nutritious food. Beyond nutrition, mushrooms are recognized for health-promoting properties, with recent research supporting their role in enhancing vitality and adaptive responses. Their chemical diversity makes them a valuable source of novel compounds. Some constituents act as Host Defence Potentiators (HDPs) with immunomodulatory effects (Kamalakannan et al., 2020). Depending on the genus, mushrooms produce different metabolites associated with anticancer, anti-inflammatory, hypoglycemic, antimicrobial, antioxidant, immunomodulatory, antiviral, hepatoprotective, neuroprotective, anti-angiogenic, and hypocholesterolemic activities (Sánchez, 2017; Elkhateeb et al., 2018).

3. AQUATIC MUSHROOMS

Aquatic mushrooms not only play ecological roles but also hold promise for bioremediation, medical, and biotechnological applications. Among freshwater fungi, mushrooms constitute the most compelling and functionally important subgroup. Aquatic mushroom taxa are widely distributed, occurring in freshwater lakes, rivers, wetlands, and marine habitats. Their activities are central to nutrient dynamics, decomposition of organic material, and sustaining ecological equilibrium (Ali et al., 2024; Cicero et al., 2025). Aquatic mushrooms are equipped with specific adaptations to thrive in water-saturated habitats characterized by changing water levels, hypoxic conditions, and shifting salinity. Certain species bear fruiting bodies that endure long-term submersion, and some disperse spores through water flow (Shearer et al., 2007). As saprotrophs, they degrade submerged wood, aquatic plants, animals, and organic remains, which supports nutrient turnover (Shen et al., 2025). Aquatic mushrooms also form mutualistic relationships with aquatic plants. (Dash et al., 2021).

The review integrates information on their diversity, evolutionary innovations, and applications. It synthesizes current findings, identifies knowledge gaps, and informs future research on their use. Our focus is on lignicolous and mushroom-forming aquatic members of the Agaricomycetes within Basidiomycota, referred to throughout as aquatic mushrooms.

3.1. Biotechnological Tools for Aquatic Basidiomycota

Marine-derived Basidiomycota show promise for environmental biotechnology. Experimental evidence demonstrates that selected strains can degrade polycyclic aromatic hydrocarbons under saline conditions, supporting their potential application in bioremediation (Vieira et al., 2018). Aquatic Basidiomycota often contain enzyme systems evolved for submerged, oxygen-limited conditions, potentially enhancing the degradation of pollutants such as dyes, hydrocarbons, and endocrine-disrupting chemicals. Compared to terrestrial fungi grown in submerged culture, their natural aquatic adaptations likely offer greater ecological compatibility and durability for in situ bioremediation. These fungi and their enzymes therefore hold strong promise for green biotechnological solutions to combat pollution in freshwater and marine ecosystems (Frank et al., 2010). Aquatic Basidiomycota are also gaining recognition in industrial biotechnology due to their resilient enzyme systems and chemically diverse metabolites. Prominent examples include the aquatic basidiomycetes *Clavariopsis aquatica* and *Tetracladium marchalianum*, which have been extensively studied

for their production of lignocellulolytic enzymes such as laccases and peroxidases. These enzymes help break down plant biomass in aquatic habitats. Such enzymatic capabilities are especially valuable for bioenergy and bioremediation, where effective lignocellulose degradation is critical (Raghukumar 2017; Heeger et al., 2021).

Aquatic fungi also support aquaculture indirectly by decomposing organic material, improving water quality and potentially reducing pathogen levels. For example, *Tetracladium* sp. have been reported to perform ecological functions in stream ecosystems that promote microbial equilibrium and nutrient turnover. These traits suggest potential applications for Tetracladium in aquaculture systems (Raghukumar, 2017). Members of aquatic Basidiomycota, is *Wallemia* sp., have shown the capacity to produce melanin and antioxidant metabolites with UV-shielding and anti-aging effects. These properties position them well for the cosmeceutical market, where natural active ingredients are increasingly sought (Budzianowska et al., 2025). Overall, the literature points to aquatic Basidiomycota as promising sources of enzymes, antifouling agents, and cosmetic bioactives. Future studies and industrial upscaling may unlock their potential for sustainable biotechnology solutions.

3.2. Aquatic Basidiomycota as Pharmaceutical Potential

Aquatic Basidiomycota from freshwater and marine ecosystems are gaining attention as a source of secondary metabolites with strong pharmaceutical potential. To survive submerged, these fungi have evolved specialized metabolic pathways that facilitate biosynthesis of bioactive compounds, including those with antimicrobial, antioxidant, anti-inflammatory, and anticancer effects (Frank et al., 2010; Heeger et al., 2021).

A variety of bioactive compounds have been isolated from marine Basidiomycota with notable bioactivities. Among them are the cytotoxic sterol EP produced by *Fulvifomes* sp., the antibacterial diketopiperazine siccayne from *Halocyphina villosa*, and the anti-parasitic sesquiterpenoid villosane A from the same species. These compounds show cytotoxicity against tumour cells, antibacterial action, and potent antiplasmodial effects, indicating their promise as leads for pharmaceutical discovery (Elkhateeb et al., 2021).

4. ADAPTATION OF GILLED MUSHROOMS TO AQUATIC HABITATS: MORPHOLOGICAL AND PHYSIOLOGICAL INSIGHTS

Certain aquatic ascomycete fungi have been documented to produce fruiting bodies on submerged wood in freshwater habitats, with reports from Japan, Thailand, and Costa Rica (Pinruan et al. 2004; Ferrer et al. 2008). In contrast, the discovery of an aquatic gilled mushroom, *Psathyrella aquatica* (Figure 1), reported in the mid-2000s, represents one of the few known basidiomycetes with gills adapted to aquatic life. Researchers first encountered the species in 2005 when they incidentally observed it in the Rogue River. The presence of a submerged, gilled basidiomycete was unexpected, as such fruiting structures are uncommon in aquatic settings. Most fungi recorded from underwater environments belong to the Ascomycetes or mitosporic Hypomycetes. The basidiocarps of *P. aquatica* were observed growing underwater, typically colonizing wood as a substrate while remaining submerged in the water column rather than within the benthic sediment (Frank et al., 2010). Phylogenetic analyses suggest that the aquatic gilled mushrooms from southern Oregon constitute a novel lineage within the Psathyrellaceae and the polyphyletic genus *Psathyrella* (Padamsee et al., 2008).

Additional records of Ascomycota fruiting on submerged wood in lakes have also been reported from Japan, Thailand, and Costa Rica (Pinruan et al., 2004; Ferrer et al., 2008). Nevertheless, *Psathyrella aquatica* is not unique in forming mushroom-like structures underwater. Other basidiomycetes, *Gloiocephala aquatica* Desjardin, Martinez-Peck & Rajchenberg, *Nia vibrissae* (Figure 1), and *Halocyphina villosa* (Marine mushroom), which develop submerged basidiocarps with a smooth hymenium, have been described from lakes and ponds in southern Argentina. Furthermore, basidiocarps of 11 species of homobasidiomycetes have been documented from marine ecosystems (Larsson and Örstadius, 2008; Hibbett and Binder, 2001).

The marine basidiomycete *Nia vibrissa* has been described as a species complex, possibly including several species, because morphological variation in fruitbodies, spores, and spore appendages has been observed in materials from worldwide collections. More than 50 monosporic isolates of *Nia vibrissa* were used, mostly obtained from Japanese beaches. Mating tests of monokaryotic strains showed mating compatibility within clades and incompatibility between clades. Consequently, each clade was recognized as a different *Nia* species phylogenetically, morphologically, and biologically. Remarkably, the type specimen of *Nia vibrissa* revealed a tiny T-shaped apical structure of spore appendages. Culture-based studies have shown that *Nia* species have both sexual and asexual morphs that produce morphologically similar fruiting bodies (Basidiomata and conidiomata) and spores (Basidiospores and conidia). Be-

cause it has both morphs forming appendaged waterborne basidiospores and conidia, *Nia vibrissa* is the most well-adapted marine basidiomycete (Nakagiri et al., 2024).

The marine basidiomycete *Halocyphina villosa* grows submerged on mangrove roots and wood in the brackish water of tropical/subtropical mangrove swamps. To date, only material from the natural habitat of *Halocyphina villosa* has been investigated, mainly for morphological and systematic purposes. Basidiocarp structure and development in the aquatic basidiomycete *Halocyphina villosa* were observed. *Halocyphina villosa* produces completely closed gasteroid basidiocarps at an early developmental stage and shows cyphelloid hymenium distribution and ballistosporic basidiospore formation. Basidia and basidiospores are gasteroid and nonballistosporic and are distributed on a loosely formed hymenium (Nakagiri and Ito, 1991).

Gloiocephala aquatica was collected near Esquel, Chubut, Argentina. The taxon is characterized by tiny, acystidiate basidiomata developing from circular pseudosclerotial plates, with lateral stipes, smooth hymenophores, and gelatinous tissue. It inhabits submerged culms of *Schoenoplectus californicus* in eutrophic lake and pond littoral zones. Outstanding, basidioma development and spore release occur submersed, usually underneath thin ice. The psychrophilic aquatic ecology of *Gloiocephala aquatica* is the first of its kind reported for the Agaricales (Desjardin et al., 1995).



Figure 1. Aquatic Mushrooms. A: *Psathyrella aquatic*; Cited in: *https://www.novaforma.hu/psathyrella-aquatica*. B: *Nia vibrissae*; Cited in: *https://www.gbif.org/occurrence/search?view=GALLERY&taxonKey=63VZ&entity=o_4921915506*

5. *PSATHYRELLA AQUATICA* AS A NOVEL AQUATIC GILLED MUSHROOM TAXON

Psathyrella aquatica is characterized by submerged basidiomata 4.5–10 cm tall. The cap is 0.8–1.5 cm wide, with a brown to gray-brown pigmentation. Its basidiospores are smooth, ellipsoid, brown, 10–14 × 6–8 µm, and possess a germ pore. Both cheilocystidia and pleurocystidia occur in the hymenium; they are morphologically similar, ventricose, and measure 25–45 × 10–18 µm. Gills are adnate, while the stipe shows a porrect arrangement of hyphae (Frank et al., 2010).

51. *Psathyrella aquatica* macromorphology

Basidiomata immersed, 4.5–10 cm tall; pileus 0.8–1.5 cm diam, broadly parabolic to campanulate, light brown to brownish gray, sometimes with central orange-brown disk, sometimes mottled or striate, smooth, hygrophanous; pileus context thin above gills, light tan to orange-brown; odor not distinctive; lamellae adnate, thin, light tan, densely speckled with dark brown spores, extending to pileus margin, lamellulae in two ranks and extending from one-half to one-fourth of the radius; stipe 4.0–9.5 cm long, diameter expanding from 1.0–2.2 mm at apex to 1.8–3.2 mm at base, white to pale yellow, hollow, lacking annulus, fibrous, surface fibrillose covered with wefty white to gray-white mycelium, and with cottony rhizomorphs and mycelial tomentum emanating from base (Frank et al., 2010).

5.2. *Psathyrella aquatica* micromorphology

Basidiospores 10–14 × 6–8 µm, ave. 12.3 × 6.9 µm, elliptical with a germ pore, smooth, dark reddish brown in water and in Melzer's, fading to gray-brown in KOH and to lilac in H_2SO_4, spore print purple-black; basidia 4-spored, clavate, 32–40 × 10–13 µm, hyaline; cheilocystidia 25–45 × 10–18 µm ventricose, apex subacute to elongate, thin walled, colourless, hyaline; pleurocystidia 25–40 × 10–13 µm, ventricose, apex subacute, scattered, thin-walled, colourless, hyaline; caulocystidia 32–40 × 10– 13 µm, cylindrical to ventricose, in fascicles, apex obtuse; pileipellis cellular, suprapellis a single layer of spherical to isodiametric, inflated cells, 25–35 µm diam, on 30–50 × 3–5 µm peduncles that extend into the pileus trama, clamp connections absent; pileus trama thin-walled hyphae 8– 15 µm diam, interwoven; stipe hyphae 35–70 × 8–14 µm, parallel; clamp connections present in mycelium at stipe base, absent elsewhere. Because the mycelium of *Psathyrella aquatica* inhabits river substrates, the fruiting body of the mushroom is fully submerged under the water. This leads scientists to speculate about how the spores of this underwater mushroom are dispersed (Frank et al., 2010).

6. CONCLUSION AND FUTURE PROSPECT

The study of marine and freshwater Basidiomycota is approaching a turning point with strong potential as biotechnological tools, but practical exploitation is limited by key knowledge gaps. The major bottleneck is rarity, as most aquatic fungi depend on habitat-specific factors and exhibit slow growth and physiological fragility. These constraints impede in vitro biomass production, limiting their availability for experimental and commercial use (Hyde et al., 2019). This should be overcome by laboratory cultivation. Ecologically, the role of aquatic Basidiomycota in ecosystem processes and nutrient cycling remains poorly understood compared to land-dwelling fungi. Hence, further studies are needed to fill this gap and maximize environmental benefits. On the other hand, studying adaptation mechanisms is important; aquatic colonization occurs across freshwater, brackish, and marine fungi, each with unique adaptations, including hydrophobic fruiting structures, spores adapted for flotation, and enzymes tolerant of high salinity that facilitate growth in submerged settings. Their ecological importance lies in driving nutrient turnover, breaking down organic substrates, and maintaining aquatic trophic networks through multifaceted symbiotic associations.

Expanding biodiversity surveys through systematic sampling across lakes, rivers, and coastal habitats is essential, especially in geographically unexplored locations. Sampling should cover different seasons to distinguish resident taxa from transient species and reveal the impact of environmental conditions such as temperature, humidity, nutrient load, pollution, and pH on community composition. Whole-genome sequencing and genome mining to detect biosynthetic gene clusters may reveal the genetic capacity of aquatic mushrooms to produce specific chemical classes, including polyketide terpenoids and peptides. Moreover, linking genomic predictions with metabolic profiles under different conditions will help activate silent or weakly expressed pathways.

Further investigations are essential to evaluate the potency of metabolites secreted by aquatic mushrooms, identify novel compounds, elucidate their mechanisms of action, and assess their safety. Future assessments, molecular ecology, and genome mining will help unlock the full ecological and biotechnological potential of aquatic mushrooms.

Ethical Statement

Not Applicable.

Conflicts of Interest

The authors declare no competing interests.

Funding

No funding was received for this research.

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