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REVIEW

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Bioluminescent Mushrooms: Boon for Environmental Health

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Abstract
Mushrooms contain secondary metabolites in their fruit bodies, cultured mycelium, and cultured broth which are higher Basidiomycetes and Ascomycetes. Mushrooms have been used in many sides of human activity for many years. Bioluminescence mushrooms gained more attention. Researchers focused on the ecological role of bioluminescence mushrooms as attracting insects for spore dispersal, which may be beneficial for fungi growing on the forest floor where wind flow is low. In this review, we will focus on some famous bioluminescent mushrooms, their ecology, bioluminescence mechanisms and their ecological benefits.

Keywords: Bioluminescence fungi; Mushroom; *Omphalotus; Neonothopanus; Armillaria; Favolaschia; Mycena*

Introduction
Mushrooms are those macrofungi that are known from centuries for their nutritional and medicinal benefits. Thanks to the richness of mushrooms in bioactive compounds that belong to different chemical classes such as phenols, terpenes, proteins, fatty acids, flavonoids, polysaccharides, polyketides, alkaloids, steroids, and other compounds. Ascomycota and Basidiomycota, the two phyla of fungal organisms that include mushrooms, are each known to have both edible and toxic species. Majority of mushrooms are saprophytes, but some are insect parasites, which extend the environmental application of mushrooms as agents that clean environment and recycle essential elements among food chain (ALKolaibe et al., 2021; Daba et al., 2019; Daba et al., 2020; El-Hagrassi et al., 2020; Elkhateeb and Daba, 2020a, b). Also, as clean and efficient biocontrol agents that help in getting rid of many harmful insects and nematodes (Soliman et al., 2022).

On the other hand, many studies have described the activities of the fruiting bodies, crude extracts, and purified compounds originated from mushrooms (Elkhateeb et al., 2019a, b, c, d, e; Elkhateeb and Daba, 2019; Elkhateeb, 2020; Elkhateeb et al., 2020a, b, c, d). These activities include antimicrobial, antiviral, anticancer, antioxidant, antitumor, anti-inflammatory, immuno-suppressant, hypocholesterolemic, and hypoglycaemic effects. It should be noted that different species under the same genus may show different biological potentials (Thomas et al., 2019; Thomas et al., 2021; Zhang et al., 2021; Elkhateeb et al., 2021a, b, c, d, e, f). This can be attributed to the change in environmental and growing conditions which are critically affecting the chemical profile of different species. Understanding the importance of mushrooms and their originated compounds encourages for increasing the efforts to discover new species, and study currently identified ones (Elkhateeb and Daba, 2021a, b, c, d, e). There are other mushroom genera that are not edible or even dangerous in addition to the known edible mushroom species. These mushrooms are also generous sources of bioactive compounds that have pharmaceutical and industrial applications. Also, some of these mushrooms can contribute in bio-control of different insects (Elkhateeb et al., 2022a, b; Elkhateeb and Daba, 2022a, b, c, d, e). Natural bioluminescence is the emission of visible lights from a living organism due to a chemical reaction (Haddock et al., 2010). It is widely found across the ocean and terrestrial environments as well as across diverse groups of organisms, including unicellular algae, bacteria (Tanet et al., 2019), multicellular fungi (Karunarathna et al., 2020; Mishra and Srivastava, 2021) and animals (Mensinger 2011).

As currently understood, bioluminescence is the consequence of the oxidation of the light-emitting molecule luciferin, which is oxidised by the enzyme luciferase or photoproteins, producing an intermediate high-energy material that then transforms into oxyluciferin (Moline et al., 2013). In this review, we will focus on some famous bioluminescence mushrooms, their ecology, bioluminescence mechanisms of the luminescent fungi, and their benefits.

Bioluminescence phenomenon and Bioluminescent mushrooms

Bioluminescence has been known since ancient times (Weinstein et al., 2016). The phenomenon is most common in marine environments, and a number of theories have been put forward to account for its apparent selective advantage in the dark of the deep ocean (Rees et al., 1998). Hastings (1983) studied the putative ecological functions of bioluminescence and listed defence, offence, and communication; fungal bioluminescence was not covered. A total of 140,000 terrestrial fungus have been found, with about 100 species belonging to four distantly related lineages namely Armillaria, Lucentipis, Mycenoid, and Omphalotus, have been recognized as bioluminescent fungi (Kotlobay et al., 2018). Bioluminescent mushrooms emit green light (530 nm) from their fruiting bodies or mycelium when luciferins break down. Oliveira et al. (2012) have found that a single biochemical process is involved across all four bioluminescent monophyletic lineages due to the shared luciferin compound and luciferase enzyme. Numerous studies have suggested that the ecological function of bioluminescence in fungi is to attract insects for spore dispersal, which may be beneficial for fungi growing on the forest floor where wind flow is low (Oliveira et al., 2015).

According to recent experimental research conducted in the Neotropics by Oliveira et al. (2015) for *Neonothopanus garderni*, it has been hypothesised that the selection advantage offered by bioluminescent fungi (mushroom) can be attributed to the attraction of possibly spore disseminating insects (Agaricales, Marasmiaceae). Alternative explanations might involve warning signals, fungivore deterrence, fungivore predator attraction, or as an unintended byproduct of detoxification or other metabolic processes. Bioluminescence could still have a thermodynamic cost and the ability to attract fungivores. In recent years, the world's known species of bioluminescent fungi (order Agaricales) has dramatically increased. Desjardin et al., (2008), established a list of 64 species of bioluminescent fungi. Chew et al., (2015), revised the list to 81 species. Mihail (2015), discovered five known *Armillaria* species which were bioluminescent. Desjardin et al. (2016), reported two new and two known species of bioluminescent mushrooms from Brazil. Terashima et al. (2016) reported eight new species of bioluminescent mushrooms from Japan. Chew et al. (2011) reported that in Malaysia 71 species of fungi recognised to be luminescent, all Basidiomycetes and belonging to three distinct lineages; Mycenaceae, Omphalotaceae and Physalacriaceae. In China, macrofungi have long been an important part of culture and medicine, and macrofungal diversity in mainland China is becoming more widely studied. However, there have been relatively few reported encounters of bioluminescent mushrooms in the country (Dauner et al., 2021).

Up until recently, a key question has concerned whether molecular oxygen or hydrogen peroxide oxidizes a luciferin substrate in the presence of the enzyme luciferase. Alternatively, it was possible that light emission is a by-product of some metabolic process such as lignin degradation. To create the electrically excited product (oxyluciferin), which decays to the ground state through photon emission, almost all known bioluminescent species utilise oxygen. Thus, the visible and 'cold' light emission results from efficient conversion of energy from chemical bonds to light without heat dissipation (Bechara, 2015). According to a study, the *Neonothopanus garderni* mushrooms, which are native to the coconut woods of northern Brazil, emit green light under the direction of a circadian clock. Additionally, since light attracts insects, it's possible that bioluminescence aids in the spreading of spores and the spread of fungi (Bechara, 2015). Enchantment and curiosity are immediately suggested when, entering humid woods under a new moon, one sees green, shining mushrooms popping up on the surface of rotten logs. The reader should be able to better appreciate these unusual and beautiful

Agaricomycetes by looking at the picture of a colony of *Mycena lucentipis* mushrooms. Seventy-one out of thousands of fungus species occurring mainly in tropical and temperate zones of the globe are documented to be bioluminescent, of which twenty-six species belong to the genus *Mycena*. As reported in this issue of Current Biology by Oliveira *et al.* (2012), light emission by *Neonothopanus garderni* mushrooms found in Brazilian coconut forests is controlled by a circadian clock and serves to attract insects for spore dispersal.

Even though the temperate south of the continent is home to various bioluminescent species, including the ubiquitous *Omphalotus nidiformis* (ghost fungus; Agaricales, Marasmiaceae), Weinstein et al. (2016) reported that no studies on bioluminescent fungi have focused on the ecological role of bioluminescence. Fungal (Mushroom) bioluminescence uses an enzymatic pathway where a 'luciferin' is oxidised in the presence of 'luciferase' (Desjardin et al., 2008). This process has been tested in several extract-based experiments (Desjardin et al., 2008). In order to show that diverse evolutionary lineages of luminous mushrooms share comparable luciferin-luciferase mechanisms of bioluminescence, Oliveira et al. (2012) combined extracts from a variety of species. Basidiomycetes make up all 64 of the mushrooms known to produce bioluminescence (Matheny et al., 2006), but belong to three distinct lineages; the *Omphalotus*, *Armillaria* and the mycenoid lineages (Desjardin et al., 2008). Thus, despite the similarity of the molecular pathways, bioluminescence may have diverse ecological roles in different lineages. According to Weinstein et al. (2016), data from several fungus lineages and presumably various growth settings supports both the attraction of spore-dispersing insects and the incidental by-product of metabolism theories for bioluminescence in mushrooms. One possible explanation for such a situation would be that bioluminescence in fungi arose as an incidental by-product of metabolism, and that some fungi such as *Omphalotus nidiformis* remained in this condition. Others, like *Neonothopanus garderni*, gained a fitness advantage by modifying their bioluminescence to increase their appeal to potential spore-dispersing insects.

***Favolaschia* (Pat.)**

Favolaschia (Pat.) is a saprobic, often tiny, mushroom-like genus of the Basidiomycetes family Mycenaceae, which has a wide range of species. It was reported from a lowland warm-temperate to subtropical and tropical zone (Fig. 1). The genus *Favolaschia* comprises 109 species (Nimalrathna et al., 2022). Hymenial pores, a gelatinous trama, and the presence of gloeocystidia and acanthocystida are characteristics of this genus (Gillen et al., 2012). To date, *F. manipularis* (Audrey et al., 2015) and *F. peziziformis* (Bodensteiner et al., 2004) have been reported to have bioluminescence.

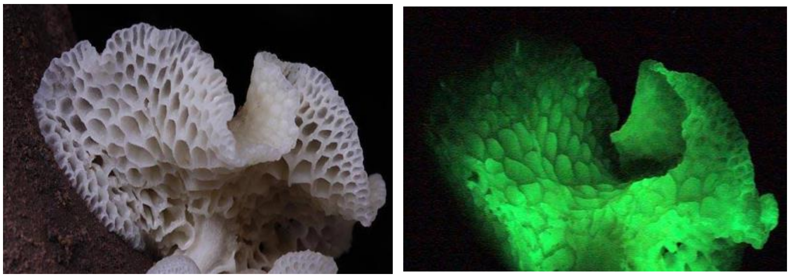

Fig. 1. *Favolaschia* mushroom showing bioluminescent in the dark.
Cited in: https://imgur.com/gallery/KPzbH

Omphalotus nidiformis

Omphalotus nidiformis is an Australian basidiomycete from the temperate zone that is typically found around or close to the foot of eucalyptus trees. Its basidomes range in colour from cream to brown and are typically between 20 and 40 cm in diameter (Weinstein et al., 2016). In the

Southern Hemisphere winter (June to July), it develops basidomes and continuously gives off a flimsy white-blue glow (Fig. 2).

Fig. 2. *Omphalotus nidiformis* showing bioluminescent in the dark
Cited in: https://texasmycology.com/shop/ols/products/mushroom-fruiting-kit-beech-hypsizygus-tesselatus

Neonothopanus gardneri

Neonothopanus gardneri is a species of bioluminescent fungus belonging to the order Agaricales (Marasmiaceae) found in South America. Its existence was first reported in 1840 by George Gardner in his travels to Brazil, where it is popularly called "coco flower" (Weinstein et al., 2016). Recently, N. *gardneri* had some of its bioactives separated and their corresponding structures clarified. It is mostly found in decomposing leaves and in the trunk of dwarf palm trees such as "pindoba" (*Attalea oleifera*) or "babaçu" (*Orbignya phalerata*) (Fig. 3).

Fig. 3. *Neonothopanus gardneri* showing bioluminescent in the dark
Cited in: https://www.sciencenews.org/article/how-mushroom-gets-its-glow

Mycena lucentipis

Mycena is a large genus of small saprotrophic mushrooms that are rarely more than a few centimeters in width. They are characterized by a white spore print, a small conical or bell-shaped cap, and a thin fragile stem. Most are gray or brown, but a few species have brighter colors. Most have a translucent and striate cap, which rarely has an incurved margin. The gills are attached and usually have cystidia (Fig. 4).

According to reports, seven species of *Mycena*, representing specimens gathered in Belize, Brazil, the Dominican Republic, Jamaica, Japan, Malaysia, and Puerto Rico are luminous. Four of them represent new species (*Mycena luxaeterna*, *M. luxarboricola*, *M. luxperpetua* and *M. silvaelucens*) and three represent new reports of luminescence in previously described species (*M. aff. abieticola*, *M. aspratilis* and *M. margarita*). The genus *Mycena* includes about 500 known species of gilled mushrooms. More than 58 species are known to be bioluminescent (Desjardin et al., 2010).

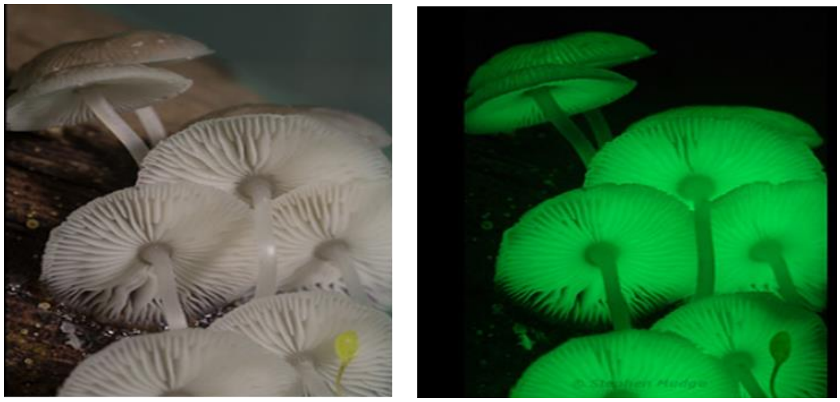

Fig. 4. *Mycena* sp. showing bioluminescent
Cited in: https://www.flickr.com/photos/stephenmudge/39774574525

Armillaria

Armillaria is one of the most important genera of fungal root pathogens worldwide. It attacks hundreds of tree species in both timber (Abies, Picea, Pinus and Pseudotsuga). *Armillaria* genus belonging to Basidiomycota, (Physalacriaceae) (Baumgartner et al., 2011). The honey fungus species *Armillaria mellea*, which inhabits trees and woody bushes, belongs to the genus *Armillaria* of fungi. It includes about 10 species formerly categorized summarily as *Armillaria mellea*. The largest known species is *Armillaria ostoyae*. Some species of *Armillaria* display bioluminescence, resulting in foxfire. *Armillaria* can be a destructive forest pathogen. It causes "white rot" root disease of forests. *Armillaria* can kill its host because it is a facultative saprophyte that also consumes dead plant matter, as opposed to parasites that must control their growth to prevent host death (Kirk et al., 2008). The properties and mechanisms of bioluminescence in fungi are also of interest to mycological research (Fig. 5).

Fig. 5. ***Armillaria*** showing bioluminescent in the dark
Cited in: https://www.sciencelearn.org.nz/images/3717-armillaria-novae-zelandiae-te-harore

Unlike the blue light of marine organisms and the yellow light of fireflies, bioluminescent fungi emit greenish-bluish light at a wavelength of 520–530 nm (Ilondu & Okiti 2016). In Omphalotus and Mycenaceae fungi, luminescence often occurs in both the fruiting bodies and the mycelia, but *Armillaria*, curiously, exhibit luminescence only in the mycelia, producing the “foxfire” effect of glowing wood that has been described for millennia (Desjardin et al., 2008).The biochemical mechanism of bioluminescence in *Armillaria*, *Favolaschia*, *Omphalotus*, *Neonothopanus* and *Mycena* (Basidiomycetes) remains unclear but most research theories proposed both enzymatic and non-enzymatic reaction (Baumgartner et al., 2011).

Benefits and application for bioluminescent fungi

Many different applications for bioluminescent fungi have been formulated, including using them as an indicator for low concentrations of environmental pollutants (Wan et al., 2014) and expanding the use of luminescent markers in biomedicine and biotechnology (Ilondu and Okiti, 2016).

Conclusion

Bioluminescence has been known since ancient times from different living organisms (Marine Fish, plant, bacteria, fungi and others). Bioluminescence fungi (Mushroom) gained more attention from the researchers. Many scientific researches focused on the ecological role of bioluminescence and their benefits. The most famous bioluminescence mushroom were *Armillaria*, *Favolaschia*, *Omphalotus*, *Neonothopanus* and *Mycena* all belonging to Basidiomycetes. Now many researchers discovered many new different mushroom genera. Further studies are required to explore the additional applications of this phenomenon.

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WAE and GMD conceived the concept, wrote and approved the manuscript.

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Competing interest
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