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# A review on bioluminescent fungus *Neonothopanus gardneri*

## Uma revisão sobre o fungo bioluminescente *Neonothopanus gardneri*

## Revisión sobre el hongo bioluminiscente *Neonothopanus gardneri*

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**Abstract**
*Neonothopanus gardneri* (N. *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". Found mainly in decaying leaves and in the trunk of dwarf palm trees called "pindoba" (*Attalea oleifera*) or babaçu (*Orbignya phalerata*), recently N. *gardneri* had some of its bioactives isolated and their respective structures elucidated. Thus, this paper aims to present and discuss the findings of the works produced involving this theme. Thus, for the development of this literature review, books and scientific articles were searched in the following databases: Scopus, PubMed, Science Direct, web of science, Royal Society of Chemistry (RSC) Publishing and Google Scholar (1990-2021). The following keywords were used to filter the productions: "Neonothopanus", "Neonothopanus gardneri", "Bioactivities", "Bioprospecting", "Secondary metabolite", "Endophytic" and "bioluminescence". Finally, it is possible to observe that studies involving this species of bioluminescent fungus have focused on explaining the mechanism of light production and its potential biological activities, among them, antitumor, antioxidant, antimicrobial and antileishmanial effects.
**Keywords:** Bioluminescence fungus; *Neonothopanus gardneri*; Flor de coco; *Agaricales.*

**Resumo**
A *Neonothopanus gardneri* (N. *gardneri*) é uma espécie de fungo bioluminescente pertencente à ordem *Agaricales* (*Marasmiaceae*) encontrada na América do Sul. Sua existência foi reportada pela primeira vez em 1840 por George

Gardner em suas viagens ao Brasil, onde é popularmente chamada de "flor de coco". Encontrada principalmente em folhas em decomposição e no tronco de palmeiras-anãs chamadas “pindoba” (*Attalea oleifera*) ou babaçu (*Orbignya phalerata*), recentemente a N. *gardneri* teve alguns de seus bioativos isolados e suas respectivas estruturas elucidadas. Sendo assim, este trabalho tem como objetivo apresentar e discutir os achados das obras produzidas envolvendo este tema. Sendo assim, para desenvolvimento dessa revisão da literatura foram realizadas buscas de livros e artigos nas seguintes bases de dados: Scopus, PubMed, Science Direct, web of science, Royal Society of Chemistry (RSC) Publishing e Google Scholar (1990-2021). Para filtragem das produções utilizou-se as seguintes palavras-Chaves: “Neonothopanus”, “Neonothopanus gardneri”, “Bioatividades”, “Bioprospecção”, “Metabolito secundário”, “Endofitico” e “bioluminescência”. Por fim, é possível observar que os estudos envolvendo essa espécie de fungo bioluminescente tem se concentrado em explicar o mecanismo de produção de luz e seus potenciais atividades biológicas, dentre elas, os efeitos antitumorais, antioxidantes, antimicrobianos e antileishmania.
**Palavras-chave:** Fungo de bioluminescência; *Neonothopanus gardneri*; Flor de coco; *Agaricales.*

**Resumen**
Neonothopanus gardneri (N. gardneri) es una especie de hongo bioluminiscente perteneciente al orden Agaricales (Marasmiaceae) que se encuentra en Sudamérica. Su existencia fue reportada por primera vez en 1840 por George Gardner en sus viajes a Brasil, donde se le llama popularmente "flor de coco". Encontrada principalmente en las hojas en descomposición y en el tronco de las palmeras enanas llamadas "pindoba" (Attalea oleifera) o babaçu (Orbignya phalerata), recientemente se han aislado algunos de sus bioactivos y se han dilucidado sus respectivas estructuras. Así, este trabajo tiene como objetivo presentar y discutir las conclusiones de los trabajos realizados en torno a este tema. Así, para el desarrollo de esta revisión bibliográfica, se buscaron libros y artículos en las siguientes bases de datos: Scopus, PubMed, Science Direct, web of science, Royal Society of Chemistry (RSC) Publishing y Google Scholar (1990-2021). Se han utilizado las siguientes palabras clave para filtrar las producciones: "Neonothopanus", "Neonothopanus gardneri", "Bioactividades", "Bioprospección", "Metabolito secundario", "Endofítico" y "bioluminiscencia". Por último, es posible observar que los estudios sobre esta especie de hongo bioluminiscente se han centrado en explicar el mecanismo de producción de luz y sus potenciales actividades biológicas, entre ellas, los efectos antitumorales, antioxidantes, antimicrobianos y antileishmania.
**Palabras clave:** Hongo de la bioluminiscencia; *Neonothopanus gardneri*; Flor de coco; *Agaricales.*

## 1. Introduction

Living organisms that emit light, such as plants and animals, have long attracted the interest and curiosity of man (Olivei et all., 2013). There are mentions of some descriptions that corroborate with this statement, such as Chinese songs and poetry that quote “night travelers”, which is credited treat of fireflies (Lee, 2008). Although in this period records on the luminescence of these beings are fragmented and scarce, partly attributed to technologies and rustic writing techniques, it was from the time of Aristotle (384-322), who recognized and recorded observations about the self-luminosity of these organisms. In recent years, there has been a growing interest of the researchers in the light emitted by organic beings (Shimomura, 2006; Lee, 2008; Oliveira et al., 2013; Puzyr et al., 2019).

The term luminescence was proposed by Wiedemann (1888), who felt the need of a uniform designation for bodies with cold light emission. The use of the word “bioluminescence”, refers to the living beings that emit this type of light as a result of chemical reactions, may have been used for the first time by Harvey (1916) and is present in several species of bacteria, dinoflagellates, fungi, marine and land animals (Shimomura, 2006).

Bioluminescence has been observed mainly in aquatic marine organisms. It is present in around 700 genera of eukaryotes and prokaryotes of 16 phyla (Stevani et al., 2013). Although much less common in terrestrial environment, this phenomenon is confirmed almost exclusively in animals, reported in the genera of *Nematoda* and *Arthropoda*, and in fungi, present in about 71 species of the order *Agaricales* (Kahlke & Umbers, 2016). In spite of the fact that there is no apparent specific relationship for its distribution, fungi are one of the few taxa by which it is believed to have a conserved system of this characteristic (Shimomura, 2006; Oliveira et al., 2013; Stevani et al., 2013; Kahlke & Umbers, 2016).

Until recently, there were some controversies about the green light emanated by bioluminescent fungi due to the ultra-weak emission of photons. However, oxygen is fundamental and extremely important in the process, it should not be confused with the emission of light generated from oxidative stress, that is, with chemiluminescence (Sivinski et al., 1998; Oliveira et al.,

2013; Kahlke & Umbers, 2016). A justification for the production of light in fungi can be directly linked to communication, predation, mating, repulsion, etc. It is believed that light works as a way for the body to get rid of reactive oxygen species (ROS) and attract spore-dispersing insects (Paley & Prescher, 2014; Waldenmaier et al., 2015).

In 2013, there were approximately 71 species of known terrestrial bioluminescent fungi belonging to four bloodlines evolutionary found in different parts of the world: *Micenoide* (Asia, Europe, Americas, Africa, Caribbean, Australia and Pacific Islands), *Omphalotus* (Asia, Europe, Americas, Caribbean and Australia), *Armillaria* (one native from South / Southeast Asia and four from Europe / North America) *Lucentipes* (Brazil) (Lloyd & Gentry, 2009; Oliveira et al., 2012, 2013).

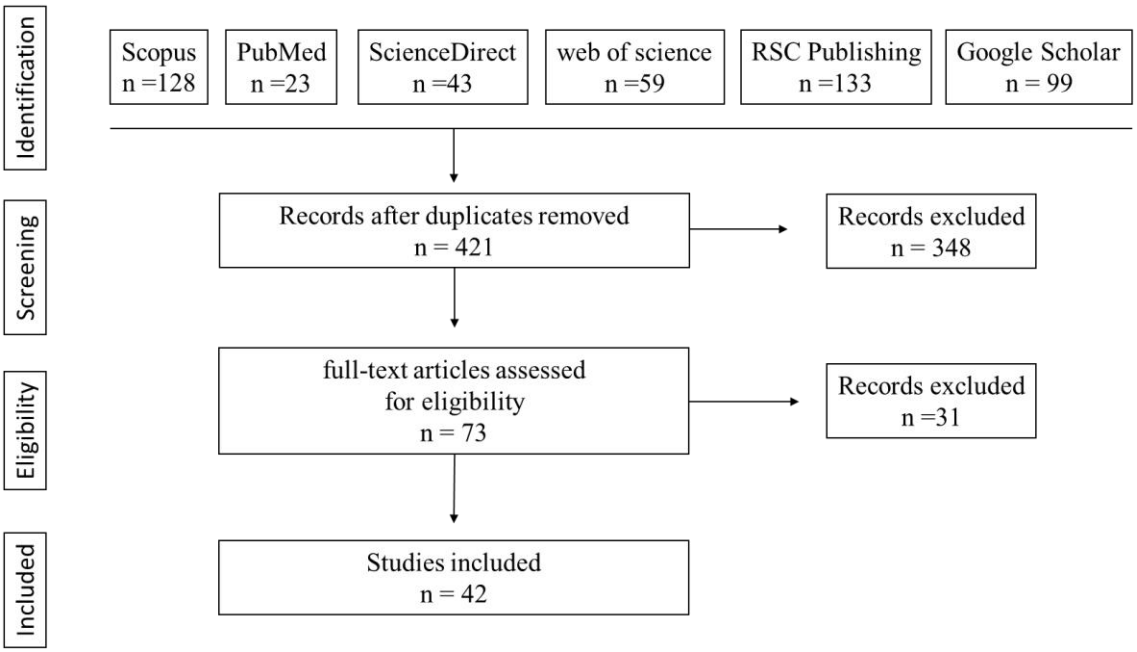
Bioluminescent fungi, in general, are saprophytes, that is, they feed on decomposing organic matter, "white rot" *agaricus*, and due to the high humidity and hot climate, are found mainly in tropical areas. The emission of light by these organisms is not evenly distributed throughout their structure and may be present in the mycelium, fruiting body or both. Although popular for their continuous brightness, they are much less studied than other bioluminescent organisms. Among the slightly more than 71 species reported, 12 of them can be found in Brazilian territory (Deheyn & Latz, 2007; Oliveira et al., 2013; Stevani et al., 2013). This review describes an interesting fungal species *Neonothopanus gardneri*; the largest bioluminescent mushroom in Brazil and one of the largest reported to date (Waldenmaier, 2015).

## 2. Methodology

As stated by Gonçalves (2021), the methodology is the detailed, rigorous and exact explanation of every action developed in the research work. In the case of literature review articles, their data collection is based on the search for descriptors that make up the topic addressed in database, books and scientific articles. Thus, in order to achieve the objective of the work, an integrative review was chosen because it allows a broader investigation and considers a diverse sample of studies with different approaches and methodologies, resulting in a diversified and understandable panorama of the investigated study object.

Thus, this integrative review article is a qualitative bibliographical study that aims to discuss what has been reported and studied about the bioluminescent fungus of the species *Neonothopanus gardneri* in studies published between 1990 to 2021. For this purpose, searches were made for books and articles scientific in the following databases: Scopus, PubMed, ScienceDirect, web of science, Royal Society of Chemistry (RSC) Publishing and Google Scholar. For filtering the productions, the following keywords were used: "Neonothopanus", "*Neonothopanus gardneri*", "Bioactivities", "Bioprospection", "Secondary Metabolite", "Endophytic" "Bioluminescence". We used as inclusion criteria the works in Portuguese and English that presented in the title or abstract at least one of the used descriptors. As exclusion criteria those that did not fit the theme (Figure 1).

**Figure 1.** Flowchart of identification and selection of found.




Source: Authors (2022).

## 3. Results and Discussion

As shown in the flowchart (figure 1), after the search, screening and selection of records, 42 studies were considered relevant to the discussion of the theme. Thus, after reading them in their entirety, we collected those exposed in chart 1.

**Chart 1.** Studies located in the databases Scopus, PubMed, ScienceDirect, web of science, Royal Society of Chemistry (RSC) Publishing and Google Scholar (1990-2021).

| Reference | Title | Objective | Results |
|---|---|---|---|
| (Baker & Dunlap, 2012). | The circadian clock of *Neurospora crassa* | It presents a review focused on the contributions to the field of chronobiology obtained from the study of the circadian system in *Neurospora crassa.* | Introduces the fundamentals of circadian rhythms, the filamentous fungus model *Neurospora crassa*, and provides an overview of the molecular components and regulation of the circadian clock. |
| (Blunt, 2006) | Marine natural products. *Natural* | Literature review on marine natural products. | review of the literature for 2007 and describes 961 new compounds from 350 articles |
| (Bondar et al., 2011) | The luminescent system of the luminous fungus *Neonothopanus nambi* | Investigate the luminescent system of the luminous fungus *Neonothopanus nambi*, which was found in the rainforests of South Vietnam. | in this study, primary data were obtained on the structural and functional organization and physical-chemical properties of the luminescence system has the superior tropical luminous fungus N. *nambi.* |
| (Bondar et al., 2013) | On the mechanism of luminescence of the fungus Neonothopanus nambi | Investigate the luminescent system of the luminous fungus *Neonothopanus nambi*, which was found in the rainforests of South Vietnam. | It has been shown that the mycelial globules transferred to a measuring cuvette from the nutrient medium display no luminescence; that is, the luminescence level does not significantly differ from the background noise of the measurement system. the incubation of N. *nambi* mycelial globules in DI water for 12–24 h leads to a considerable increase in the luminescence. |
| (Bondar et al., 2014) | Isolation of Luminescence System from the Luminescent Fungus *Neonothopanus nambi* | Investigate the luminescent system of the luminous fungus *Neonothopanus nambi*, which was found in the rainforests of South Vietnam. | It was found that supernatants isolated from the mycelium of the luminous fungus N. *nambi* by the method described emitted long luminescence. This fact allowed us to conclude that a selfsufficient luminescent system that ensures luminescence in vitro was isolated from this fungal species. |

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| (Capelari et al., 2011). | *Neonothopanus gardneri*: A new combination for a bioluminescent agaric from Brazil | Re-evaluation of its taxonomic affinities. | *Agaricus gardneri* was transferred to the genus *Neonothopanus* based on a combination of morphological and molecular data. |
| (Desjardin et al., 2008) | Fungi bioluminescence revisited | To present a review of the research carried out during the last 30 years on the distribution, taxonomy, phylogeny, ecology, physiology and mechanisms of bioluminescence of luminescent fungi. | We recognized 64 species of bioluminescent fungi belonging to at least different evolutionary lineages, named Omphalotus, Armillaria and mycenoid. |
| (Dubois, 1885) | Note sur la physiologic des pyrophores | Verified the chemical nature of the bioluminescence reaction. | Identification of enzymes generically called luciferase and the substrate as luciferin |
| (Dunlap, 1999) | Molecular bases for circadian clocks | Detail the molecular basis of circadian systems | Described central aspects of the circadian basis<br>time in at least four of these groups - cyanobacteria, fungi, insects and mammals. |
| (Fagg et al., 2015). | Useful Brazilian plants listed in the manuscripts and publications of the Scottish medic and naturalist George Gardner (1812-1849) | To present data recorded by Gardner in his manuscript *Catalogue of Brazilian Plants* regarding the use of native plants by Brazilian people and evaluate the extent to which they have been explored. | A total of 63 useful plants was recorded from the *Catalogue* and a further 30 from Gardner's book *Travels in the Interior of Brazil* (Gardner, 1846). Of the recorded names in the *Catalogue*, 46 (73%) could be identified to species by consulting specimens collected by Gardner and held at Kew. |
| (Gomes, 2019). | Toxicogenética e os efeitos antitumorais de extratos obtidos do *neonothopanus gardneri*: potencial biotecnológico e farmacêutico | Iwdentify some of the chemical compounds by phytochemistry, liquid chromatography and magnetic resonance; in addition to evaluating the toxicogenetic and antitumor effects of methanolic and ethyl acetate extracts obtained from N. gardneri, in Saccharomyces cerevisiae, murine models for Sarcoma 180 and for breast cancer. | Antitumor effects of the extract were observed by mechanisms associated with DNA damage and induction of apoptosis, possibly with the inclusion of oxidative damage induced by its bioactives. |
| (Hevia et al., 2016). | Circadian clocks and the regulation of virulence in fungi: Getting up to speed | Comment on the overall importance of clocks, what is known in Neurospora and what has been described in other fungi including new insights on the evolution of fungal clock components. | Showed the molecular description of the fungal circadian system, general importance of clocks, what is known in Neurospora and what has been described in other fungi, including new insights into the evolution of fungal clock components. |
| (Ilondu & Okiti, 2016) | Bioluminescence in Mushroom and Its Application Potentials | Compile information on fungal bioluminescence. | It presented bases to assist among biochemists, chemists and physicists in the isolation and purification of Luciferin compounds present in these mushrooms and other possible potentials in the production of light. |
| (Jayakumar et al., 2009) | *In-vitro* antioxidant activities of an ethanolic extract of the oyster mushroom, *Pleurotus ostreatus* | To investigate the antioxidant potential of an ethanolic extract of the oyster mushroom, *Pleurotus ostreatus*. | The data generated by this study strongly suggest that an ethanolic extract of the oyster mushroom, *P. ostreatus*, has potent antioxidant activity. |
| (Johnson & Haneda, 1966). | Bioluminescence in Progress | To isolate, characterize, and synthesize the reactants that are involved directly and indirectly in the light-emitting process; to understand the kinetics and mechanism of their reactions; and to interpret the action of various factors that influence light emission | lists the types of bioluminescence systems that have been extracted from various kinds of luminescent organisms, together with the minimal requirements for a light-emitting reaction in vitro, and some of the spectrographic properties of the systems |
| (Kanokmedhakul et al., 2012) | Cytotoxic sesquiterpenes from luminescent mushroom *Neonothopanus nambi* | isolation and characterization of substances from the bioluminescent fungus *Neonothopanus nambi* | Isolation of six new compounds along with a known compound, aurisin A. |
| (Kaskova et al., 2017) | Mechanism and color modulation of fungal bioluminescence | Report the structure of fungal oxyluciferin, investigate the mechanism of fungal bioluminescence, and describe the use of simple synthetic α-pyrones as luciferins to produce multicolor enzymatic chemiluminescence | Provides insight into the mechanism of fungal bioluminescence by characterizing the oxyluciferin of 3-hydroxyhispidin and expanding the knowledge on how styryl-3-hydroxy-α-pyrones are chemiexcited *in vivo*. |

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| (Kirk, 2008) | Dictionary of the Fungi | Present taxonomic data. | Contains the consensus on the fungal taxonomic hierarchy to the rank of genus. |
| (Lee, 2008) | Bioluminescence: The First 3000 Years (Review) | Describes the many investigations of animal luminescence up to the end of the 19th Century. | Presents relevant aspects in 300 years of research on bioluminescence. |
| (Love & Prescher, 2020) | Seeing (and using) the Light: Recent Developments in Bioluminescence Technology | Highlights recent advance in bioluminescent probe development that are driving new directions in biomedical research. | Show how new luciferins and engineered luciferases are expanding the scope of optical imaging. also highlight how bioluminescent systems are being leveraged not just for sensing-but also controlling-biological processes. |
| (Menolli et al., 2014) | The genus Pleurotus in Brazil: A molecular and taxonomic overview | Present for the first time a discussion on the recognition of at least five species of Pleurotus in Brazil | Presents a list of all epithets that have been recorded for Brazil and the current update of their taxonomic status. |
| (Min et al., 2017) | Theoretically obtained insight into the mechanism and dioxetanone species responsible for the singlet chemiexcitation of Coelenterazine | Determine what the dioxetanone species responsible for efficient chemiexcitation are, in the luminescent reactions of Coelenterazine. | Efficient chemiexcitation of Coelenterazine results from a neutral dioxetanone; is achieved without significant electron/charge transfer;The thermolysis of anionic dioxetanones leads to less efficient chemiexcitation occurs albeit significant electron and charge transfers. |
| (Montenegro-Montero et al., 2015) | Aro und the Fungal Clock: Recent Advances in the Molecular Study of Circadian Clocks in Neurospora and Other Fungi | discuss the circadian system of the filamentous fungus *Neurospora crassa* | Provided additional insights into the physiological impact of the clock and potential additional functions of clock proteins in fungi and speculate on the presence of FRQ or FRQ-like proteins in diverse fungal lineages. |
| (Oba et al., 2017). | Identification of hispidin as a bioluminescent active compound and its recycling biosynthesis in the luminous fungal fruiting body | Check the presence of hispidin as a bioluminescent active compound at 25-1000 pmol g-1 in the fruiting bodies of *Mycena chlorophos*, *Omphalotus japonicus*, and *Neonothopanus gardneri.* | The results suggest that luminous mushrooms contain hispidin as a luciferin precursor and the non-luminous "young" fruiting bodies exhibited luminescence by hispidin treatment. |
| (Olivei et all., 2013). | Bioluminescência de fungos: Distribuição, função e mecanismo de emissão de luz. | To discuss the distribution of bioluminescent fungi on Earth, attempts to elucidate the mechanism involved in light emission, and presents preliminary results on the evolution and ecological role of fungal bioluminescence. | It contributes to the discussion about the bioluminescence mechanism in fungi for new perspectives of academic and applied studies. |
| (Olivei et all., 2012). | Evidence that a single bioluminescent system is shared by all known bioluminescent fungal lineages | verify if the bioluminescence mechanism is the same in all four evolutionary lineages suggesting a single origin of luminescence in fungi, or if each lineage has a unique light emission mechanism implying independent origins. | The results support the hypothesis that all four lineages of luminescent fungi share the same type of luciferin and luciferase, that there is a single luminescent mechanism in the Fungi, and that fungal luciferin is not a ubiquitous molecule in fungal metabolism. |
| (Oliveira & Stevani, 2009). | The enzymatic nature of fungal bioluminescence | Enzymatically obtain in vitro light emission from the assay of cold and hot extracts using different species of fungi. | Kinetic data suggest a consecutive two-step enzymatic mechanism and corroborate the enzymatic proposal of Airth and Foerster. |
| (Oliveira & Stevani, 2015). | Circadian control sheds light on fungal bioluminescence | Influence and relationship of circadian control on fungal bioluminescence | Report that bioluminescence from the mycelium of Neonothopanus gardneri is controlled by a temperature compensated circadian clock, the result of cycles in content/activity of the luciferase, reductase, and the luciferin that comprise the luminescent system. |
| (Pegler, 1988) | Agaricales of Brazil Described by M. J. Berkeley | To evaluate fifty-five species of agaricoid fungi described from Brazil by M. J. Berkeley between 1840 and 1876. | He following new combinations are proposed: *Eccilia vespertilio* (Berk.) Pegler (*Agaricus vespertilio* Berk.), *Gymnopilus panurensis* (Berk.) Pegler (*Agaricus panurensis* Berk.), G. *psamminus* (Berk.) Pegler (*Agaricus psamminus* Berk.), and *Pleurotus submembranaceus* (Berk.) Pegler (*Lentinus submembranaceus* Berk.). |
| (Petersen & Krisai-Greilhuber, 1999) | Type specimen studies in Pleurotus | to identify the epithets of the Pleurotus species that did not have their type specimens documented | Report on three additional species, *P. cornucopiae, P. eugrammus.and P. opuntiae* |

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|---|---|---|---|
| (Petushkov et al., 2014) | A novel type of luciferin from the Siberian luminous earthworm Fridericia heliota: structure elucidation by spectral studies and total synthesis | The structure elucidation and synthesis of the luciferin from the recently discovered luminous earthworm *Fridericia heliota.* | The novel luciferin was found to have an unusual extensively modified peptidic nature, thus implying an unprecedented mechanism of action. UV, fluorescence, NMR, and HRMS spectroscopy studies were performed in the isolated substance and revealed four isomeric structures that conform to spectral data. |
| (Petushkov et al., 2018) | Isolation and Purification of Fungal Luciferase from Neonothopanus nimbi. | The aim of this study was to isolate and purify the luciferase of the luminous fungus *Neonothopanus nambi* for its subsequent sequencing. | Have for the first time obtained a high-purity fungal luciferase suitable for Edman sequencing (N-terminal sequencing) and mass spectrometric sequencing. |
| (Petushkov et al., 2015) | Components of the luminescent system of the luminous fungus Neonothopanus nambi. | The aim of this work was to separate the protein and nonprotein components of the light emitting system of the fungus *Neonothopanus nambi* and to study some of their properties. | The results obtained in this study indicate that the luminescent system of luminous fungus *N. nambi* includes at least four components that ensure light emission *in vitro.* |
| (Queiroz, 2017) | Composição fitoquímica e atividades antileishmania, citotóxica, imunomoduladora e genotóxica de *Neonothopanus gardneri*: um cogumelo bioluminescente | Identify bioactive compounds and their respective biological activity, in addition to elucidating their chemical structures. | He obtained positive results for metabolites such as alkaloids, reducing sugars, tannins, depsides, among others. Antileishmanial, cytotoxic and immunomodulatory activity were found. |
| (Ronzhin, 2020) | Extracellular Oxidases of Basidiomycete Neonothopanus nambi: Isolation and Some Properties | Isolate extracellular oxidases from the mycelium of the basidiomycete *Neonothopanus nambi* by treating its biomass with β-glucosidase and to the study of some of their properties. | Two protein fractions were isolated from the extracts, which contained enzymes with oxidase activity conventionally called F1 and F2. |
| (Samuel et al., 2011) | Antibacterial activity of marine derived fungi collected from South East Coast of Tamilnadu, India | To study the antibacterial activity of the marine fungi, collected from the south east coastal area of Tamilnadu, India. | Among the used fungal species, Geotrichum candidum was found to be active against all human pathogenic bacterial strains. |
| (Shimomura, 2006) | Bioluminescence: Chemical principles and methods. | Provide a comprehensive overview of the biochemical aspects of all currently known luminous organisms | It is the first book to provide chemical information on all known bioluminescence systems. |
| (Smetanina et al., 2007) | Indole Alkaloids Produced by A Marine Fungus Isolate Of Penicillium Janthinellum Biourge. | To describe the isolation and structural elucidation of new alkaloids produced by the marine fungus P. janthinellum. | Three new indole alkaloids, shearinines D, E, and F, together with the known shearinine A were isolated from the marine-derived strain of the fungus *Penicillium janthinellum* Biourge. |
| (Stevani et al., 2013) | Current status of research on fungal bioluminescence: Biochemistry and prospects for ecotoxicological application | To present an overview of the current state of the study of fungal luminescence and the application of bioluminescent fungi as versatile tool in ecotoxicology. | It contributes to studies related to fungal bioluminescence, presenting a recent overview of research in the area. |
| (Ventura, 2021) | Toxicity of metal cations and phenolic compounds to the bioluminescent fungus Neonothopanus gardneri | To describe a toxicological bioassay that relies on a 24-h variation of total light emitted by the mycelium of the bioluminescent fungus *Neonothopanus gardneri* when exposed to a toxicant. | Among the compounds tested, found that N. *gardneri* presents a predictable bioluminescence and growth pattern, and is highly sensitive to these compounds. |
| (Waldenmaier et al., 2015) | Circadian rhythm in fungal bioluminescence: nature's bright idea | Present a mini review on the circadian rhythm in fungal bioluminescence. | Contributes to studies related to the chemical basis of bioluminescence and reports about N. *gardneri.* |
| (Wilson & Hastings, 1998) | Bioluminescence | To present a broad overview of the chemistry and cellular control of bioluminescence with deeper discussions of selected topics. | Contributes to interest and importance of bioluminescence to a reader unfamiliar with the field. |

Source: Authors (2022).

### 3.1 Discovery and classifications attributed to *Neonothopanus gardneri*

George Gardner, a Scottish naturalist and surgeon, is among the scientists who traveled the most in Brazil cataloging information about biodiversity in the early 19th century. Although the Brazilian flora has already been extensively studied, few ventured into the interior of the country as Gardner did, mainly in the northeast region (Fagg et al., 2015). In 1840, in his work ‘‘*Description of a new phosphorescent species of Agaricus*’’ the naturalist, after observing children playing with a luminous object and performing a careful inspection, first identified an *Agaricus* species belonging to the required tribe *Pleurotus of Fries* (Capelari et al., 2011).

It is popularly known as "coconut flower" (flor de coco) because of its resemblance to a flower growing at the base of a palm tree. The species was formally named in 1840 in an article written by G. Gardner as *Agaricus gardneri* Berk. Later Berkeley, in his 1843 work titled ‘‘*Notices of some Brazilian fungi’’*, refers to the species as *Agaricus (Omphalia) gardneri*. Shortly thereafter, in 1887, Saccardo reclassified it as *Pleurotus gardneri*. However, Pegler (1988), after carrying out an analysis, found that although it had characteristics typical of *Omphalotus olearius*, it was one of its variants, but to distinguish *A. gardneri* as a different species, it required to study with fresh material in which it had no access (Capelari et al., 2011).

More recently, after studies of molecular and morphological data of material collected in the states of Tocantins and Piauí (Brazil), the species of *Agaricus gardneri* was transferred to *Neonothopanus gardneri*. This mushroom has greater incidence in the North and Northeast regions of Brazil. It is distributed in coconuts forests, a transitional biome between the Amazon Forest and the Caatinga, in the states of Maranhão, Piauí, Tocantins and Goiás. They are found mainly in decomposing leaves and in the trunk dwarf palms popularly called “pidomba” (*Attalea oleifera*) or babassu (*Orbignya phalerata*) (Capelari et al., 2011; Menolli et al., 2014).

### 3.2 Taxonomic classification

In the order *Agaricales*, most of the bioluminescent fungi belong to the families *Mycenaceae* and *Marasmiaceae.* This last one is characterized by the presence of basidiomycetes which in general presents resistant stems (stipe) and, during dry periods, have the ability to collect, wither, as a way to cross the drought and recover later (Kaskova et all., 2019; Johnson & Haneda, 1966).

The genus *Neonothopanus* was proposed in 1999 after the need for a new classification for *Lentinus (Pleurotus) eugrammus* once the categorization of *Nothopanus* was based on a misinterpretation, given that not match the type specimen of that species. In addition, the term was attributed a taxonomically distinct concept, although later it was found to be correct. Horak, in 1968, classified the specimen as *Pleurotus* using *Nothopanus* with a synonym of that genus. The impasse between such concepts arose the need for a new nomenclature: *Neonothopanus* (Kirk, 2008).

In Latin America the main representative of the *Neonothopanus* (*Marasmiaceae*) is *Neonothopanus gardneri* species, found mainly in Brazilian ecotones territory, the cocal forests. A molecular study carried out by Capelari et al. (2011) demonstrated that the species did not present in any analysis a monophyletic lineage with any of the *Omphalotus* family, but that it resembled *Neonothopanus nambi*, differing mainly in size of the basidiospore, stature and its pigmentation (Waldenmaier, 2015).

Although *N. nambi* has been relatively more studied in recent years (Bondar et al., 2011, 2013, 2014; Purtov, 2015, 2018; Ronzhin, 2020), presenting itself as a rich source of cytotoxic sesquiterpenes used against cancer cells. The studies have rarely gone deeper to investigate the metabolites and possible biological activities of *N. gardneri* that can be observed by a few reports present in the literature (Kanokmedhakul et al., 2012).

Among the main characteristics of the fungus *Neonothopanus gardneri* is the presence of strong bioluminescent basidiomas, omphalotoid basidiomes with a coloration strain ranging from white to yellow and size around 10 - 90 mm, wide

lamellae, well-developed stipe, hyaline basidospores, smooth and globular as well as elongated - fusoid to sinuous-cylindrical cheilocystidia (Johnson & Haneda, 1966).

Recently, a study was published describing a toxicological bioassay based on a 24-hour variation of the total light emitted by the mycelium of the bioluminescent fungus *Neonothopanus gardneri* when exposed to a toxicant. It was found that *N. gardneri* has a predictable bioluminescence and growth pattern, and is highly sensitive to the compounds Cd (II), 4-nitrophenol, phenol and Cu (II). According to the authors, these characteristics offer valuable advantages and make *N. gardneri* the ideal candidate for toxicological studies with basidiomycetes (Ventura, 2021).

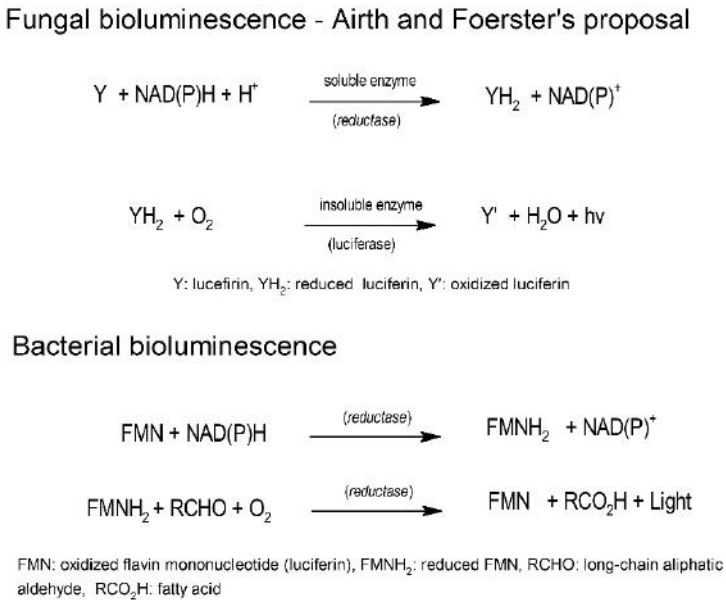
### 3.3 Light emission mechanism

With the discovery of the organic nature of the reactions of mixtures outside living organisms that resulted in luminescence and the oxidation reaction of lophine, the first chemiluminescent reaction discovered in 1877, the idea was born that bioluminescence is reaction chemistry that occurs within these organisms. Raphael Dubois was the first to study bioluminescence based on this idea in addition to trying to elucidate the chemical nature of light emission by fungi (Lee, 2008).

In his classic experiments, Dubois used "hot" and "cold" extracts obtained from organs of the beetle *Pyrophorus noctilucus* or bivalve mollusc *Pholas dactylus* to study the luminescence of these organisms, and observed that the extract prepared in cold water produced a brilliant solution that it gradually lost its intensity, while the preparation in hot water had its shine extinguished. When the two solutions were mixed, the light emission was restored and Dubois thus verified the chemical nature of the bioluminescence reaction. In addition, he observed that the cold extract contained thermolabile enzymes necessary for light emission, while the hot extract contained heat-stable enzymes. These enzymes were generically called luciferase and the substrate as luciferin (Dubois, 1885; Desjardin et al., 2008; Oliveira, 2012, 2013).

An experiment carried out by Airth and Foerster (Desjardin et al., 2008) using hot (*A. mellea*) and cold (*Collybia velutipes*) extracts, that is, sources of luciferase and luciferin confirmed that the fungal bioluminescence process depends on two enzymes: a soluble substrate dependent on nicotinamide adenine dinucleotide (NADPH) or nicotinamide adenine dinucleotide reduced (NADH), responsible for the reduction of luciferin. When reacting with luciferase in the presence of molecular oxygen, light emission is produced. That is, in synthesis, bioluminescence occurs through the oxidation of a substrate (luciferin) by luciferase (enzyme) generating an excited by-product where the emission of light occurs, similar to the mechanism present in bacteria, although they are distinguished by the lack of stimulation in the presence of reduced flavin mononucleotide (FMNH 2) or adenine flavin dinucleotide (FADH 2) (Figure 2) (Wilson & Hastings, 1998; Desjardin et al., 2008; Oliveira et al., 2013; Stevani et al., 2013).

**Figure 2:** Light emission mechanism in fungi and bacteria.




Source: Adapted from Oliveira et al., (2013).

In a bioluminescent reaction, the enzyme (luciferase) requires the presence of oxygen in the system with luciferin (a small molecule that generates light), acting as a catalyst and can be recycled. The total amount of light produced in the reaction is directly linked to the amount of substrate (luciferin) available. Looking at the chemical level, the vast majority of light emissions by living organisms occur as a result of the decomposition of a four-membered dioxetone ring. Thus, although these peroxides require little energy to break the bonds and open the ring, they result in a molecule in the electronically excited state that seeks stability, returning to its fundamental state and the energy is released in the form of light in the visible range (Min et al., 2017; Waldenmaier et al., 2015).

Oliveira et al. (2012), when studying bioluminescence in four different strains of fungi obtained results that corroborate the idea of a common mechanism for light emission by these organisms, where it is believed to share the same luciferin / luciferase or a similar one. Furthermore, when performing cross tests with hot / cold extracts on seven species that represented the four bioluminescent strains, including *N. gardneri*, and comparing them with non-bioluminescent species, the emission of light was observed only in the first, suggesting a single pathway bioluminescent in the evolution of the order *Agaricales.*

At different stages of their life cycle, bioluminescent fungi emit greenish tint light in a wavelength range (λ) between 520 to 530 nanometers (Shimomura, 2006; Ilondu & Okiti, 2016). This emission occurs mainly in certain periods of its development. In 2009, a study reported based on *in vitro* tests that the light emission of the fungus species *Neonothopanus gardneri* occurs continuously with $\lambda_{max} = 533$ nanometers (Oliveira & Stevani, 2009). Bioluminescence in this species is mainly governed by a circadian clock, that is, a molecular mechanism with a rhythm around 24 hours that allows organisms to perform an infinite number of biological processes in sync with the daily cycles of the environment (Waldenmaier, 2015).

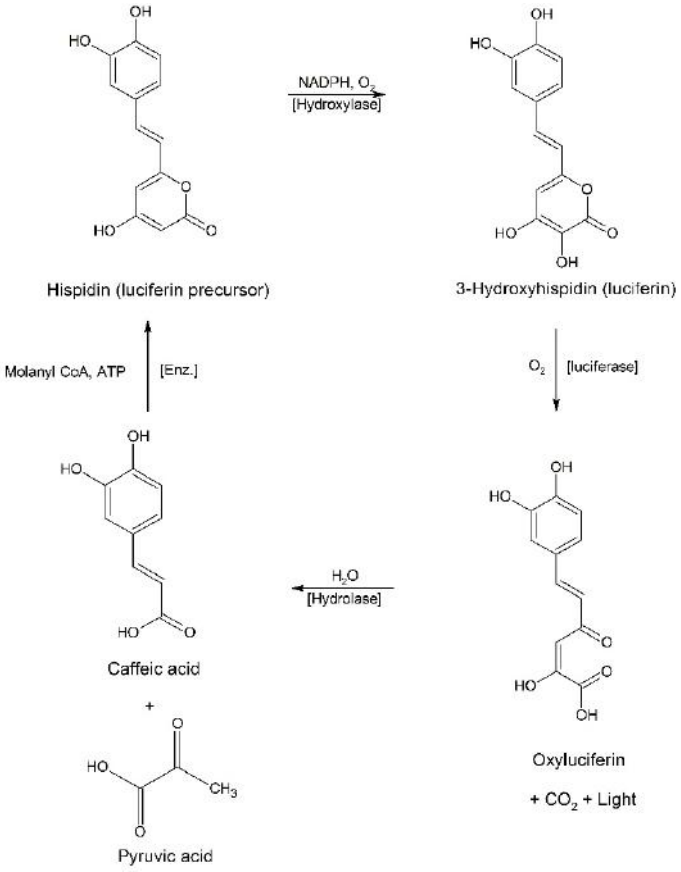
This species of central clock has been described in several organisms, having in common an internal, autonomous negative feedback oscillator with rhythms that is basically the same at different temperatures, in addition to responding according to information it receives from the environment, such as light and light (Dunlap, 1999; Montenegro-Montero et al., 2015).

*N. gardneri*, as described by Oliveira et al. (2015) in a study with agar plates freshly inoculated with the mycelium of the species, the light emission oscillates in a circadian rhythm of approximately 22 hours, reaching its peak at night. A curious fact lies in *Neurospora crassa*, a species of non-bioluminescent fungus from the phylum *Ascomycota*, present a circadian period

also less than 24 hours (22.5 hours) (Baker & Dunlap, 2012). Furthermore, the establishment of rhythmic bioluminescence, that is, a circadian clock, provided for the first time a basis for explaining the presence of luminescence in these organisms. Although unknown, bioluminescence can have a range of biological and ecological functions, not only as an improbable metabolic by-product but with an adaptive meaning, such as attracting insects and thus dispensing spores providing an evolutionary advantage compared to non-luminescent fungi (Hevia et al., 2016).

Knowing the basic pillars of the bioluminescent chemical reaction in living organisms, that occurs in the presence of a substrate (luciferin), a reductase dependent on soluble NAD(P)H, membrane-bound oxygen (luciferase) and oxygen (Petersen & Krisai-Greilhuber, 1999; Wilson & Hastings, 1998; Oliveira et al. 2015) the light emission in *N. gardneri* was explained by hydrolysis catalyzed by the oxyluciferin (caffeylpyruvic acid), which emits light in this system from enzymatic hydrolysis resulting in the production of caffeic acid (Figure 3) (Hevia et al., 2016).

**Figure 3:** Chemical reaction of fungal bioluminescence**.**



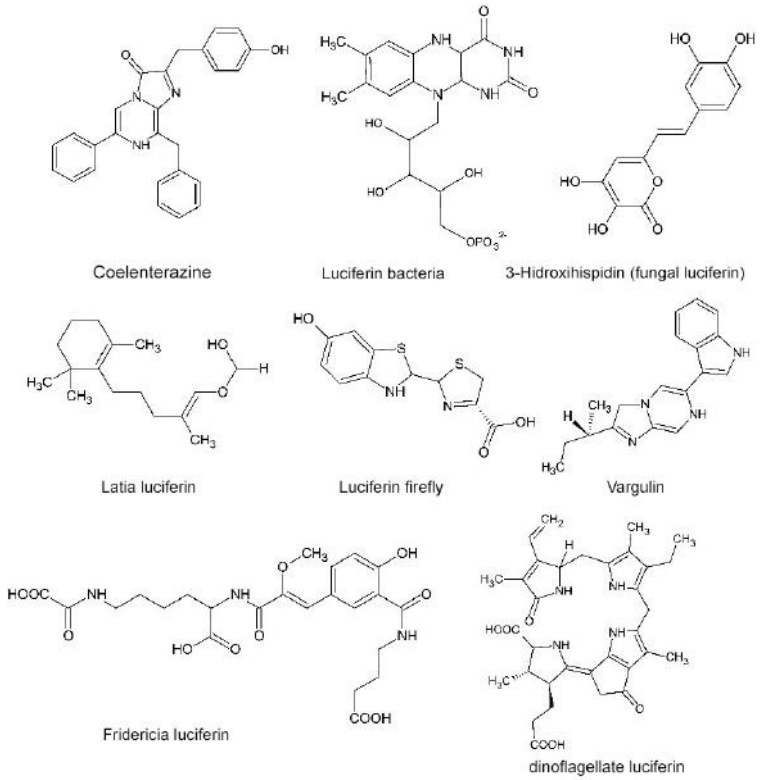

Source: Adapted from Oba et al. (2017).

Purtov et al. (2015), while studying the mechanism of bioluminescence in fungi using the mycelium *N. nambi*, reported hispidin as a precursor of fungal luciferin, 3 - hydroxyspidine, and in this way, has turned to isolation, elucidation and characterization of luciferin structures. Although it is present in nature, few of these molecules had their chemical structure determined and many of them are still unknown.

In 2014, Petushkov et al. (2014) reported the chemical structure of a luciferin present in a bioluminescent earthworm *Fridericia heliota* and thus elucidates the eighth structure of bioluminescent molecules present in organisms (**Figure 4**), as well as coelenterazine and its derivatives (used by many taxonomically unrelated species), firefly luciferins, crustacean (Dinoflagellata) (Cypridina and Latia lapa) and a worm (*Diplocardia longa).* However, it is worth noting the fact that *N. gardneri*

has not yet had its luciferin structure elucidated.

**Figure 4:** Chemical structures of luciferins identified in different species of organisms so far in literature.




Source: Authors (2022).

### 3.4 Biological activity

Fungi belonging to the phylum *Basidiomycota* are among the sources of obtaining new natural products most used by the industry in recent years, mainly due to their wide range of biological activities due to the bioactive compounds isolated from these organisms such as alkaloids, terpenoids, steroids, phenolic compounds, and flavonoids. Investigations on the bioactive compounds and secondary metabolites present in the species that make up the genus *Neonothopanus* are mainly focused on *N. gardneri* and *N. nambi*, with almost all studies focused on the latter - *N. nambi* (Blunt, 2006; Smetanina et al., 2007; Jayakumar et al., 2009: Samuel et al., 2011; Love & Prescher, 2020).

In an attempt to identify bioactive compounds that are responsible for biological activity, in addition to elucidating their respective chemical structures, some scholars have dedicated themselves to studying *N. gardneri* extensively, mainly due to its promising characteristics against some neglected diseases (Queiroz, 2017; Gomes, 2019).

Queiroz (2017) evaluated cytotoxicity, genotoxicity, immunomodulatory, and antileishmania activity in extracts of *N. gardneri and* became one of the pioneers in the search to identify the bioactivities. of this species. In this study, by performing qualitative phytochemical characterization with ethyl acetate extract (AcOEt), methanolic extract (MeOH) and ethanolic extract (EtOH) from *N. gardneri*, he obtained positive results for metabolites such as alkaloids, reducing sugars, tannins and depsides among others as shown in Table 1.

**Table 1:** Phytochemical screening of the extracts AcOEt, MeOH and EtOH of *N. gardneri.*

| | Extracts | | | | |
|---|---|---|---|---|---|
| **Metabolites** | **AcOEt** | **MeOH** | **EtOH** | **Main biological activities** | **Reference** |
| **Alkaloids** | present | present | present | anticholinergic, antihypertensive, antimalarial, antitumor, antitussive, antiviral, among others. | (QUEIROZ, 2017) |
| **Reducing sugars** | present | present | present | - | |
| **Proteins/ amino acids** | absent | present | present | showed antitumor effects by inducing apoptosis | |
| **catechins** | absent | present | present | antioxidant | |
| **Tannins** | absent | present | Absent | antioxidant activity, astringent properties,potencial citotóxico contra parasita. | |
| **Depsídeos/ depsidonas** | absent | present | present | antioxidants, antivirals, antitumor, analgesics and antipyretics. | |

Source: Adapted from (Gomes, 2019).

The analysis of antileishmanial, cytotoxic and immunomodulatory activity justified mainly by virtue of natural products, such as the tannins found in the extracts of *N. gardneri* as shown in Table 1, present potential biological activities mentioned before. Queiroz (2017) while evaluating extracts and isolates of *N. gardneri in vitro*, observed a significant potential antileishmanial activity causing death of promastigote forms of *Leishmania amazonenses* in approximately 80, 91 and 81% in the concentration of 3,200 µg / mL and 74; 85; 59% at 1,600 µg / mL of the EtOH, MeOH and AcOEt extracts. While assessing cytotoxicity, antileishmanial activity must have greater selectivity in relation to the parasite and less toxicity to host cells, Queiroz (2017) described how the extracts obtained from *N. gardneri* have been shown to be more selective for the parasite than for mammalian cells, to be able to increase the phagocytosis capacity of murine peritoneal macrophages in addition to their lysosomal volume and to induce nitric oxide synthesis (NO).

When evaluating for the first time the cytotoxic, genotoxic and mutagenic potential of *N. gardneri* ethyl acetate and methanolic extracts in meristematic cells of *Allium cepa*, an ability to reduce the mitotic index was observed, resulting in a cytotoxic effect. Furthermore, the extracts did not cause a significant increase in the frequency of chromosomal changes, that is, they did not result in genotoxicity (Queiroz, 2017).

Recently, Gomes (2019) studied the antitumor activity of methanolic extracts and ethyl acetate from *N. gardneri* in Sarcoma 180 cells and breast cancer using murine models, in addition to possible toxicogenic effects. The extracts showed antioxidant effects in *Saccharomyces cerevisiae* at low concentrations (500 and 1000 µg / mL). Furthermore, the author was able to isolate and evaluate two natural substances with antitumoral potential, 7,8-Dihydroxy-13-oxo-heneicosa-9,11-dienamide (2) and 7,8-Di-hydroxy-13-oxo- octadeca-9,11-dienamide isolated from the methanolic extract of *N. gardneri*.

In the analysis of the extracts, it was observed that the methanolic extract significantly interfered in the cell viability in cells of the ascitic liquid of Sarcoma 180, presenting cytotoxic effects in the concentrations of 1000, 1500 and 2000µg / mL. Furthermore, the extracts also showed genotoxicity at all concentrations tested (Gomes, 2019). According to Gomes (2019) genotoxic damage may be directly linked to the *N. gardneri* bioluminescence mechanism, since it occurs under oxidative stress due to the production of hydrogen peroxide ($H_2O_2$), which also causes damage to DNA.

Moreover, Gomes (2019) reported for the first time the antitumor effect in breast carcinoma, obtaining reduction in the breasts of female mice, after treatment with *N. gardneri* methanolic extract (10 mg / kg). In addition, characterized by mechanisms associated with DNA damage, the methanolic extract showed a cytotoxic effect on breast carcinoma cells culminating in a percentage increase in aptitude, due to nuclear dissolution and fragmentation, in neoplastic breast cells. The tests of mutagenic tests in liver cells and bone marrow, according to the author's data, did not induce mutagenicity due to the formation of micronuclei.

## 4. Final Considerations

Reports on the metabolites and biological activities of *Neonothopanus gardneri* are rare in the literature. The reported bioactivities, such as: antitumor and antileishmania effect investigated by some researchers, show the importance and the need to carry out more detailed studies for this species of bioluminescent fungus, since Basidiomycota is a source of compounds with different applications and important pharmacological activities. The few in-depth reports on the species described here aim to study its bioluminescent mechanism to identify luciferin. In addition, it is extremely important to carefully analyze the extracts to understand the bioactive substances and their respective biological activities.

Based on our results, it is observed that most of the studies have been dedicated to the elucidation of the substances involved in the bioluminescence mechanism of N. gardneri. Only in the last few years some interest in its biological activities has been observed, resulting in a promising field of studies that should be explored. Therefore, studies for this purpose are necessary.

## Conflict of Interest

The authors declare that there are no conflicts of interest.

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