Fungi bioluminescence revisited†

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A review of the research conducted during the past 30 years on the distribution, taxonomy, phylogeny, ecology, physiology and bioluminescence mechanisms of luminescent fungi is presented. We recognize 64 species of bioluminescent fungi belonging to at least three distinct evolutionary lineages, termed *Omphalotus*, *Armillaria* and mycenoid. An accounting of their currently accepted names, distributions, citations reporting luminescence and whether their mycelium and/or basidiomes emit light are provided. We address the physiological and ecological aspects of fungal bioluminescence and provide data on the mechanisms responsible for bioluminescence in the fungi.

Introduction

Harvey's *A History of Bioluminescence* covers the physics, chemistry, and biology of diverse luminescence phenomena, including a detailed description of bioluminescence.[1] Therein we learn that light emission by living organisms has been noticed and documented since ancient times by many philosophers and scientists.[1] According to Harvey, Aristotle (384–322 BC) first described light emission from rotten wood and distinguished this living light from fire.[1] Pliny the Elder (23–79) mentioned in his *Historia Naturalis* that bioluminescent white fungi, sweet in taste and with pharmacological properties, could be found in France on decaying trees. Interestingly, G. E. Rumph (1637–1706), a Dutch physician, merchant and consul of Amboine (Moluccas, Indonesia), reported in his *Herbarium Amboiense* that natives were able to illuminate their path in the dark forest carrying bioluminescent fruiting bodies in their hands. Harvey pointed out uncommon uses of luminous mushrooms 200 hundred years later in Micronesia, where natives used them on their head as ornaments in ritual dances or crushed them on their face in order to scare their enemies. Curiously, these mushrooms were frequently destroyed as they were considered a bad omen.[1]

Despite Aristotle's and Pliny's writings on bioluminescent mushrooms and reports by botanists on the distribution of luminous mushrooms, early attention was focused mainly on

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the light emitted from rotten wood instead on the fungi. Light emission was only directly linked to the fungi in the first half of the nineteenth century.[1] J. F. Heller (1813–1871), professor at Vienna University, was the first to correlate cause and effect attributing to fungi and bacteria the light exhibited by decaying wood and animals, respectively. A modern appraisal of this subject was provided by W. Pfeffer (1845–1920),[1] who applied to bioluminescent fungi the terms *luciferin* and *luciferase* coined by Dubois for the thermo-stable (substrate) and labile (enzyme) factors.[2,3]

In this work we revisit, expand and update Wassink's 1978[4] review of the taxonomy and bioluminescence mechanisms in fungi. The number of reported bioluminescent fungus species in the world is reevaluated to include the many new species that we discovered since 2005. In addition, we discuss evolutionary aspects of bioluminescence in the fungi and raise hypotheses on the molecular mechanisms underlying the bioluminescent pathway based on the literature and our own observations. Our revision is focused on fungi bioluminescence defined as a chemical reaction that occurs in fungi leading to constant light emission with maximum intensity in the range 520–530 nm whose chemiexcitation step is catalyzed by an enzyme generally called luciferase. This phenomenon should not be confused with transient, low-level or ultraweak chemiluminescence that often increases in response to oxidative stress (*e.g.*, elevated O_2 concentrations or introduction of ROS-generating compounds) wherein light may be emitted from singlet oxygen, triplet excited states, reactions of $ONOO^-$, lipoxygenase activity, heme protein-peroxide reactions and Fenton chemistry.[5] The latter phenomenon, reported from some yeasts and other fungi,[4] will not be treated herein.

Taxonomy and evolutionary aspects of fungi bioluminescence

In 1978,[4] Wassink updated his review of luminescent fungi published in 1948[6] and that of Harvey,[7] wherein he treated 42 *taxa* with verified or questionable luminescent properties. His review included a reevaluation of the taxonomic status, synonymy, and luminescent characteristics of all species reported before 1945 (19 species), and detailed accounts of newly described or rediscussed luminous species reported between 1946 and 1978 (23 species). In addition he provided lists of species of uncertain taxonomic position (16 epithets) and of doubtful bioluminescent capabilities (17 epithets). Many of the new accounts represented species described from Malaysia, Japan and the South Pacific, but unfortunately many of these epithets were invalidly published.[8,9] In addition, the protologues provided only limited morphological data making identification of subsequent collections difficult, and consequently, vouchered reports of most of the Asian species have not been published since.

Significant strides have been made in the past 30 years in augmenting our knowledge of the occurrence, distribution, ecology, taxonomy and phylogeny of luminescent fungi. For most fungi, populations are delimited into species based on a suite of shared morphological features, with distinctions between species often being subtle differences in the macro- and micromorphological characteristics of their sexual reproductive structures. Because macromorphological features are quite plastic and easily influenced by environmental factors, comprehensive descriptions that include data on all cell and tissue types that comprise the reproductive structures of individuals from numerous populations are necessary for accurate species diagnoses. These micro-data are usually absent from most descriptions published prior to the 1950s. Consequently, many synonyms have been published and many of the species listed by Wassink[4] remained poorly known until recently. Concerted efforts by a number of fungal taxonomists to study exsiccati (type or authentic specimens) and to recollect and redescribe luminescent species has lead to the clarification of many species concepts.[10–13] In addition, Desjardin and colleagues[14–16] have discovered a number of new species and new luminescence accounts of species from Brazil to add to the growing list of luminescent fungi (Fig. 1).

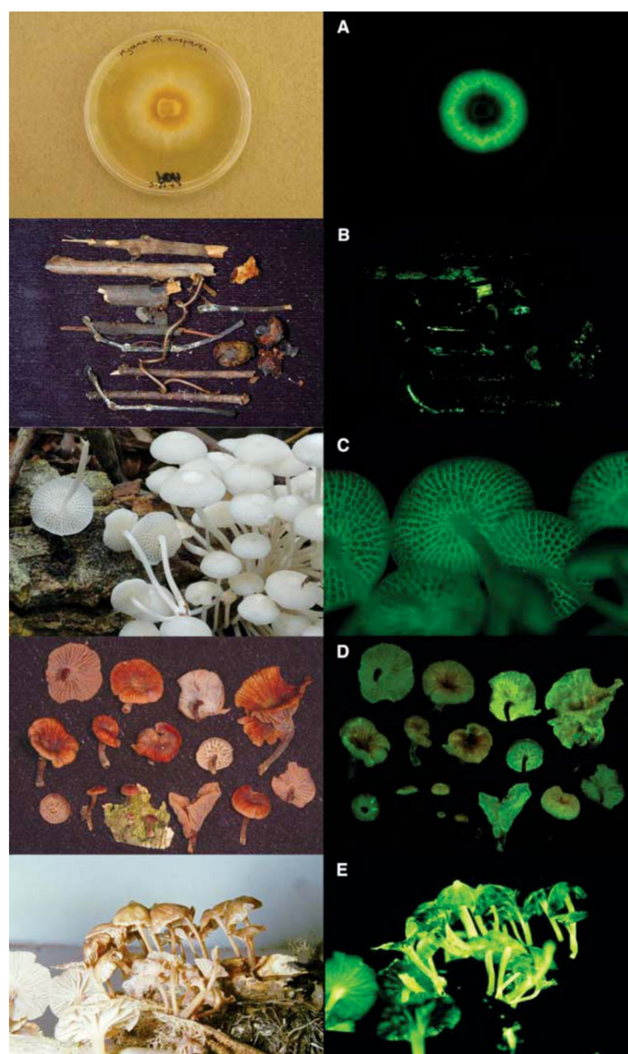

Fig. 1 Images of bioluminescent fungi taken in natural light (left) and in the dark (right). (A) Culture of *Mycena* aff. *euspeirea* on agar isolated from basidiomes collected in the El Verde Research Area, Puerto Rico. (B) Naturally bioluminescent twigs inhabited by mycelium of undetermined basidiomycetous fungi collected in Parque Estadual Turístico do Alto Ribeira (PETAR), São Paulo State, Brazil. (C) *Filoboletus manipularis* collected in Negeri Sembilan Prov., Malaysia. (D) *Gerronema viridilucens* collected in PETAR, São Paulo State, Brazil. (E) *Mycena lucentipes* collected in PETAR, São Paulo State, Brazil.

A biological species concept can be applied to species that cooperate *in vitro.* For many saprotrophic fungal species, single spores can be isolated, mated on select media, and their ability to dikaryotize and develop into new individuals can be evaluated. Hence, interbreedability and genetic exchange can be tested. An evolutionary species concept may be applied when molecular sequences datasets are generated and clades of terminal *taxa* in resultant phylogenetic analyses are used to inform taxonomic decisions. The application of these new techniques of mating system studies[17–21] and phylogenetic analyses[22–26] are helpful in delimiting the taxonomic boundaries of species and have been used to clarify species concepts in a number of luminescent fungi.

Phylogenetic analyses of multiple *loci* datasets have greatly advanced our understanding of relationships amongst the fungi and have allowed a first glimpse at the phylogenetic placement of bioluminescent fungi. After extensive searches of pertinent literature, examination of numerous exsiccati specimens, fieldwork throughout the world, and analyses of the nomenclature, taxonomy and phylogeny of reported species, we recognize no fewer than 64 species of luminescent fungi (Table 1). If we couple these data with the seminal research published by Moncalvo *et al.*[27] and Matheny *et al.*[28] it is clear that all known bioluminescent fungi are Basidiomycetes and represent white-spored euagarics once placed in the polyphyletic family Trichomolataceae sensu Singer.[29] They are mushroom-forming, saprotrophic or rarely plant pathogenic species belonging to three distinct lineages. Twelve species belong to the *Omphalotus* lineage (Omphalotaceae), five species to the *Armillaria* lineage (Physalacriaceae), and the majority 47 species belong to the mycenoid lineages (mostly Mycenaceae). We will address each of these lineages separately.

Omphalotus lineage

The luminescent properties of the large and conspicuous mushrooms in this lineage have been documented at least since the time of Pliny the Elder. The group includes the Jack-o-Lantern mushrooms of Europe and eastern North America (*Omphalotus olearius* and *O. illudens*), the Western Jack-o-Lantern mushroom of western North America (*O. olivascens*), the Moon Night mushroom or Tsukiyotake of Japan (*O. japonicus*), and the Ghost Fungus of Australasia (*O. nidiformis*). Most species in this group are well-characterized by morphological and chemotaxonomical,[13,30] intercompatibility,[17] restriction enzyme,[22] and molecular datasets,[24–26] and are currently accepted in the genera *Omphalotus* and *Neonothopanus.* Historically they were placed in the genera *Clitocybe*, *Omphalotus*, *Lampteromyces*, *Pleurotus*, *Panus*, and *Nothopanus.* A recent phylogeny of *Omphalotus* based on sequences from the ITS1-5.8S-ITS2 rDNA region included worldwide coverage of eight species, five of which are known as luminescent, and confirmed that *Lampteromyces* is a synonym of *Omphalotus.*[23] *Omphalotus mangensis* and *Lampteromyces luminescens* were not included in the analyses although they have been verified as luminescent.[31,32] We suspect that all species of *Omphalotus* form luminescent basidiomes (fruit bodies). Luminescent mycelium has been confirmed only in three species (*O. illudens, O. japonicus, O. olearius*), whereas the mycelium of *O. olivascens* has been reported as non-luminescent (Table 1).[33] Although reported as forming luminescent basidiomes, very little is currently known about the biology of the Malesian species *Nothopanus noctilucens*, *Pleurotus decipiens* and *Pleurotus eugrammus* var. *radicicolus*, and the Brazilian species *Pleurotus gardneri.* In the most current and comprehensive phylogeny of euagaric lineages,[28] the luminescent *Omphalotus* lineage is sister to the non-luminescent gymnopoid fungi (*Gymnopus*, *Marasmiellus*, *Lentinula* and others *sensu* Wilson and Desjardin)[34] and distantly related to any of the other known luminescent fungi.

Armillaria lineage

Armillaria species, commonly called the Honey Mushroom, are well-known edible fungi that are saprotrophs or problematical forest tree root pathogens. They form creamy-white mycelial fans and coarse black rhizomorphs as infection, exploratory and transport organs. It is the mycelium, mycelial fans and rhizomorphs that are luminescent as first proven by Guyot in 1927.[35] The luminous phenomenon of these asexual hyphae, known as "foxfire", has been known for millennia and the earliest accounts of glowing wood probably document the effects of *Armillaria* mycelia. It has been shown that the mycelia *in vitro* can sustain bright luminescence for up to 10 weeks.[36] Interestingly, the basidiomes of *Armillaria* species have never been reported as luminescent. Currently, the taxonomy of the worldwide members of *Armillaria* is well-known with *ca.* 40 species recognized based on morphological,[12,37] intercompatibility[20,21] and molecular datasets.[24–26] Because many species are serious forest tree pathogens, much is known about their biology, genetics and ecology,[38,39] although only five species have been verified as being luminescent (Table 1). It must be remembered, however, that until the late 1970s when mating studies and genetic research intensified, most currently recognized species of *Armillaria* were lumped into an admittedly morphologically variable *A. mellea.* Hence, the many early reports of luminescent mycelium from around the world that were attributed to *A. mellea* most likely represent different species currently accepted in the *A. mellea* species complex. We suspect that the mycelium of most (if not all) *Armillaria* species is luminescent. In the most current and comprehensive phylogeny of euagaric lineages,[28] the luminescent *Armillaria* lineage is sister to the remainder of the Physalacriaceae, all of which are non-luminescent, and distantly related to any of the other known luminescent fungi

One final note, it was a species of *Armillaria* (reported as *A. bulbosa*, now known as *A. gallica*) that received headlines and the nickname "humungous fungus" for being one of the world's largest organisms. A single individual (*i.e.*, mycelial genet) in Michigan covered 15 hectares and was estimated to weigh at least 9 700 kg and be 1 500 years old![40] This discovery stimulated the search for even larger *Armillaria* individuals and in 2003 researchers in Oregon reported a single individual of *A. ostoyae* covering 900 hectares (9 km^2) and estimated to be between 2 000 and 8 500 years old.[41] One wonders if the entire forest floor is aglow at night?

Mycenoid lineages

Most known luminescent fungi were described in the genus *Mycena* or in closely allied genera and belong to what we have termed the mycenoid lineages. They are nearly all saprotrophic, white-rot decomposers that form small mushrooms with lamellate (gills) or poroid (tubes) spore-bearing surfaces. A few are plant

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Table 1 Species of fungi reported as bioluminescent in the literature

Taxon[a]	Mycelium	Basidiomes	Distribution[b]	Citations[c]
Omphalotus lineage				
Lampteromyces luminescens M. Zang	?	+	CH	Zang 1979[31]
Neonothopanus nambi (Speg.) Petersen & Krisai-Greilhuber	?	+	SA, CA, MS, AU	Corner 1981[86]
= *Nothopanus eugrammus* (Mont.) Singer *sensu* Corner *non sensu* Singer				
Nothopanus noctilucens (Lév.) Singer	?	+	JP	Léveillé 1844;[87] Haneda 1955[8]
= *Pleurotus noctilucens* Lév.				
Omphalotus illudens (Schwein.) Bresinsky & Besl.	+	+	EU, NA	Wassink 1948,[6] 1978;[4] Berliner 1961[36]
= *Clitocybe illudens* Schwein.				
= *Panus illudens* (Schwein.) Fr.				
= *Pleurotus facifer* Berk. & M. A. Curtis				
Omphalotus japonicus (Kawam.) Kirchm. & O. K. Mill.	+	+	JP	Kawamura 1915;[88] Bermudes *et al.* 1992;[44] Singer 1947[89]
= *Lampteromyces japonicus* (Kawam.) Singer				Singer 1947[89]
= *Pleurotus japonicus* Kawam.				
Omphalotus mangensis (J. Li & X. Hu) Kirchm. & O. K. Mill.	?	+	CH	Li and Hu 1993[32]
= *Lampteromyces mangensis* J. Li & X. Hu				
Omphalotus nidiformis (Berk.) O. K. Mill.	?	+	AU	Berkeley 1844;[90] Miller 1994[62]
= *Pleurotus nidiformis* (Berk.) Sacc.				
= *Pleurotus candescens* (F. Muell. & Berk.) Sacc.				
= *Pleurotus illuminans* (Berk.) Sacc.				
= *Pleurotus lampas* (Berk.) Sacc.				
= *Pleurotus phosphorus* (Berk.) Sacc.				
Omphalotus olearius (DC.: Fr.) Singer	+	+	EU	Wassink 1948[6]
= *Pleurotus olearius* (DC.) Gillet				
Omphalotus olivascens H. E. Bigelow, O. K. Mill. & Thiers	—	+	NA	Bigelow *et al.* 1976[33]
Pleurotus decipiens Corner	?	+	MS	Corner 1981[86]
Pleurotus eugrammus var. radicicolus Corner	?	+	MS, JP	Corner 1981[86]
= *Pleurotus lunaillustris* Kawam. *nom. inval*.				
Pleurotus gardneri (Berk.) Sacc.	?	+	SA	Saccardo 1887[91]
[Predicted to have luminescent basidiomes: *Omphalotus mexicanus* Guzmán & V. Mora - CA; *Omphalotus olivascens* var. *indigo* Moreno, Esteve-Rav., Pöder & Ayala - CA; *Omphalotus subilludens* (Murrill) Bigelow - NA; *Pleurotus olivascens* Corner - MS]				
Armillaria lineage				
Armillaria fuscipes Petch	+	—	MS	Wassink 1948,[6] 1978;[4] Berliner 1961[36]
Armillaria gallica Marxm. & Romagn.	+	—	EU, NA	Mihail and Bruhn 2007[63]
Armillaria mellea (Valh.) P. Kumm. *sensu stricto*	+	—	EU, NA	Mihail and Bruhn 2007[63]
= *Armillariella mellea* (Valh.) P. Karst.				
Armillaria ostoyae (Romagn.) Henrik	+	—	EU, NA	Risbeth 1986[64]
Armillaria tabescens (Scop.) Emel	+	—	EU, NA	Mihail and Bruhn 2007[63]
= *Collybia tabescens* (Scop.) Fr.				
Mycenoid lineages				
***Gerronema* species**				
Gerronema viridilucens Desjardin, Capelari & Stevani	+	+	SA	Desjardin *et al.* 2005[14]
***Mycena* species**				
Sect. *Aspratiles*				
M. lacrimans Singer	?	+	SA	Desjardin and Braga-Neto 2007[16]
Sect. *Basipedes*				
M. illuminans Henn.	?	+	MS, JP	Haneda 1939;[92] Corner 1954,[9] 1994[93]
= *M. bambusa* Kawam. *nom. inval.*				
M. stylobates (Pers.: Fr.) P. Kumm.	+	—	EU, NA, JP, AF	Bothe 1931[94]
= *M. dilitata* (Fr.: Fr.) Gillet				
Sect. *Calodontes*				
M. pura (Pers.: Fr.) P. Kumm.	+	—	EU, NA, SA, JP	Treu and Agerer 1990[46]
M. rosea (Bull.) Gramberg	+	—	EU	Treu and Agerer 1990[46]
Sect. *Citricolores*				
M. citricolor (Berk. & M. A. Curtis) Sacc.	+	—	SA, CA	Buller 1934;[48] Berliner 1961[36]
= *Omphalia flavida* Maubl. & Rangel				
Sect. *Diversae*				
M. lucentipes Desjardin, Capelari & Stevani	+	+	SA, CA	Desjardin *et al.* 2007[15]
Sect. *Euspeireae*				
M. species	+	+	SA	Desjardin *et al.* 2007;[15] unpublished data
Sect. *Exornatae*				
M. chlorophos (Berk. & M. A. Curtis) Sacc.	+	+	MS, JP, PA	Corner 1954[9]
= *M. cyanophos* (Berk. & M. A. Curtis) Sacc.				
M. discobasis Métrod	?	+	SA, AF	Desjardin *et al.* 2007[15]

Table 1 (*Contd.*)

Taxon[a]	Mycelium	Basidiomes	Distribution[b]	Citations[c]
Sect. *Fragilipedes*				
M. polygramma (Bull.: Fr.) S. F. Gray	+	—	EU, NA, JP, AF	Bothe 1931;[94] Berliner 1961;[36] Treu and Agerer 1990[46]
= *M. parabolica* (Fr.) Quél. *sensu* Ricken				
M. zephirus (Fr.: Fr.) P. Kumm.	+	—	EU	Bothe 1931;[94] Treu and Agerer 1990[46]
Sect. *Galactopoda*				
M. haematopus (Pers.: Fr.) P. Kumm.	+	+	EU, NA, JP	Treu and Agerer 1990;[46] Bermudes *et al.* 1992[44]
Sect. *Hygrocyboideae*				
M. epipterygia (Scop.: Fr.) S. F. Gray	+	—	EU, NA, JP	Bothe 1931[94]
Sect. *Lactipedes*				
M. galopus (Pers.: Fr.) P. Kumm.	+	—	EU, NA, JP	Bothe 1931;[94] Berliner 1961;[36] Treu andAgerer 1990[46]
Sect. *Mycena*				
M. inclinata (Fr.) Quél.	+	—	EU, NA, AF	Wassink 1948[6]
= *M. galericulata* var. *calopus* (Fr.) P. Karst.				
M. maculata P. Karst.	+	EU, NA, AF		Treu and Agerer 1990[46]
M. tintinnabulum (Fr.) Quél.	+	—	EU	Bothe 1930[95]
Sect. *Roridae* (= *Roridomyces* Rexer 1994[96])				
M. irritans E. Horak	—	+	AU	Horak 1978[45]
M. lamprospora (Corner) E. Horak	—	+ (spores)	MS, AU	Corner 1950,[97] 1994;[93] Horak 1978[45]
= *M. rorida* var. *lamprospora* Corner				
M. pruinoso-viscida Corner	?	+	MS	Corner 1954,[9] 1994[93]
M. pruinoso-viscida var. *rabaulensis* Corner	?	+ (spores)	AU	Corner 1954,[9] 1994[93]
M. rorida (Fr.) Quél.	+	—	EU, NA, SA, JP	Josserand 1953[98]
M. sublucens Corner	—	+	MS	Corner 1954[9]
Sect. *Rubromarginatae*				
M. lux-coeli Corner	?	+	JP	Corner 1954[9]
M. noctilucens Kawam. ex Corner	?	+	MS, PA	Corner 1954,[9] 1994[93]
M. noctilucens var. *magnispora* Corner	?	+	PA	Corner 1994[93]
M. olivaceomarginata (Massee apud Cooke) Massee	+	—	EU, NA	Wassink 1948[6]
= *M. avenacea* (Fr.) Quél.				
M. singeri Lodge	?	+	SA, CA	Desjardin *et al.* 2007[15]
M. species	?	+	SA	Desjardin *et al.* 2007[15]
Sect. *Sacchariferae*				
M. asterina Desjardin, Capelari & Stevani	+	+	SA	Desjardin *et al.* 2007;[15] unpublished data
Sect. *Sanguinolentae*				
M. sanguinolenta (Alb. & Schwein.: Fr.) P. Kumm.	+	—	EU, NA, JP	Bothe 1931[94]
Sect. *Supinae*				
M. fera Maas Geest. & de Meijer	?	+	SA	Desjardin *et al.* 2007[15]
Incertae Sedis				
Mycena daisyogunensis Kobayasi	?	+	JP	Kobayasi 1951[99]
Mycena pseudostylobates Kobayasi	+	?	JP	Kobayasi 1951[99]
Manipularis-group				
Filoboletus pallescens (Boedijn) Maas. Geest.	?	+	MS	Maas Geesteranus 1992[42]
Poromycena pallescens Boedijn				
Filoboletus yunnanensis P. G. Liu	?	+	CH	Liu and Yang 1994[100]
Mycena manipularis (Berk.) Métrod *nom. inval*. [non *M. manipularis* (Berk.) Sacc.]	+	+	MS, PA, AU	Corner 1954[9]
= *Poromycena manipularis* (Berk.) Heim				
= *Filoboletus manipularis* (Berk.) Singer				
= *Polyporus mycenoides* Pat.				
Mycena manipularis var. *microporus* Kawam. ex Corner *nom. inval.*	?	+	PA	Corner 1954[9]
= *Polyporus microporus* Kawam. *nom. inval*.				
Poromycena hanedai Kobayasi	?	+	JP	Kobayasi 1951[99]
= *Polyporus hanedai* Kawam. *sensu* Kobayasi *nom. inval.* (not *Polyporus hanedai* A. Kawam.)				
Panellus/dictyopanus species				
Dictyopanus foliicolus Kobayasi	+	+	JP	Kobayasi 1951,[99] 1963[101]
Dictyopanus pusillus var. *sublamellatus* Corner	?	+	SA	Corner 1954[9]
Panellus gloeocystidiatus (Corner) Corner	?	+	JP, MS	Corner 1954,[9] 1986;[102] Kobayasi 1963[101]
= *Dictyopanus gloeocystidiatus* Corner				
Panellus luminescens (Corner) Corner	?	+	MS	Corner 1950,[97] 1986[102]
= *Dictyopanus luminescens* Corner				
Panellus pusillus (Pers. ex Lév.) Burdsall & O. K. Mill.	+	+	NA, SA, MS, AU, AF	Haneda 1955;[8] Burdsall and Miller 1975[103]
= *Dictyopanus pusillus* (Pers. ex Lév.) Singer				
= *Polyporus rhipidium* Berk.				

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Table 1 (*Contd.*)

Taxon[a]	Mycelium	Basidiomes	Distribution[b]	Citations[c]
Panellus stipticus (Bull.: Fr.) Karst.	+	+	EU, NA, SA, JP, AU, AF	Buller 1924;[50] Berliner 1961;[36] Wassink 1948[6]
= *Panus stipticus* (Bull.) Fr.				
Excluded, doubtful or insufficiently known taxa				
Collybia cirrhata (Schumach.) P. Kumm.	?	+	EU, NA, JP	Wassink 1948[6]
Collybia tuberosa (Bull.) P. Kumm.	?	+	EU, NA, JP	Wassink 1948[6]
Flammulina velutipes (Curtis) Singer	+	—	EU, NA, JP	Airth and Foerster 1964[104]
= *Collybia velutipes* (Curtis) P. Kumm. [a non-luminescent species]				
Fungus igneus Rumph. *nom. inval.*	?	+	MS	Wassink 1948[6]
Gerronema glutinipes Pegler	?	+	AF	Liu 1995[105]
Locellina illuminans Henn. (not *Mycena illuminans* Henn.)	?	+	MS	Hennings 1900;[106] Wassink 1948[6]
Locellina noctilucens Henn. (not *Mycena noctilucens* Henn.)	?	+	AU	Hennings 1898;[107] Wassink 1948[6]
Marasmius phosphorus Kawam. *nom. inval.*	?	+	JP	Haneda 1939[108]
Mycena bambusa Kawam. *nom. inval.*	?	+	JP	Haneda 1939[108]
Mycena citrinella var. *illumina* Kawam. *nom. inval.*	?	+	JP	Haneda 1955[8]
Mycena microillumina Kawam. *nom. inval.*	?	+	JP	Haneda 1939[108]
Mycena phosphora Kawam. *nom. inval.*	?	+	JP	Haneda 1939,[108] 1955[8]
Mycena photogena Komin. *nom. inval.*	?	+	JP	Haneda 1955[8]
Mycena yapensis Kawam. *nom. inval.*	?	+	JP	Haneda 1939[108]
Omphalia martensii Henn.	?	+	MS	Wassink 1948[6]
Omphalia noctilucens Rick	?	+	SA	Rick 1930[109]
Panus incandescens Berk. & Broome	?	+	AU	Wassink 1948[6]
Pleurotus emerci Berk. *nom. inval.*	?	+	?	Wassink 1948[6]
Pleurotus lux Hariot	?	+	PA	Wassink 1948[6]
Pleurotus prometheus Berk. & M. A. Curtis	?	+	CH	Wassink 1948[6]
= *Pleurotus djamor* (Rumph. ex Fr.) Boedijn [a non-luminescent species]				
Polyporus noctilucens Lagerh.	?	+	AF	Wassink 1948[6]
All brown-spored agarics, boletes, polypores, corticioid fungi, gasteromycetes and ascomycetes reported in Table III of Wassink 1948,[6] and parts A.2–A.3 of Wassink 1978.[4]				

[a] Taxonomic synonyms are listed only if they were reported as luminescent in published literature. [b] Distributions reported in the literature. If we consider a report unreliable we have not included it. Europe (EU), North America (NA), South America (SA), Central America and the Caribbean region (CA), Pacific islands (PA), China (CH), Japan (JP), Malaysia, South Asia and Southeastern Asia (MS), Australasia including Papua New Guinea and New Caledonia (AU), Africa (AF). [c] Citations where bioluminescence was reported. These are not necessarily the first or only reports of luminescence.

pathogens, such as *M. citricolor* (syn. *Omphalia flavida*) that causes the American Leaf Spot disease of coffee. There are currently over 500 species of *Mycena sensu lato* and the genus has been subdivided into 60 sections.[10,11,42,43] Out of this tremendous diversity, only 35 *Mycena* species have been reported as luminescent, but these belong to 17 different sections of the genus (Table 1). Additional bioluminescent mycenoid fungi include five species traditionally placed in *Filoboletus* or *Poromycena* that form putrescent poroid basidiomes, and six species traditionally placed in *Panellus* or *Dictyopanus* that form tough and persistent, lamellate or poroid basidiomes. Phylogenetic analyses reveal that *Mycena s.l.* is not monophyletic, although which infrageneric groups represent distinct genus-rank lineages remains uncertain.[27,28] Multiple *loci* molecular sequences datasets are currently being generated in the Desjardin lab to help elucidate phylogenetic relationships in the mycenoid fungi. We can state that all but two of the luminescent mycenoid species listed in Table 1 belong to the Mycenaceae (excluded: *Gerronema viridilucens, Mycena lucentipes*), that *Panellus* is the correct name for taxa once named *Dictyopanus*, and that the luminescent species listed under *Manipularis*-group represent a distinct lineage that requires a new generic name (none are closely related to the type species of *Filoboletus* or *Poromycena*). Most of the *Mycena* epithets added to the list after Wassink[4] were the result of our recent fieldwork in Brazil where we discovered eight luminescent taxa from a single site in primary Atlantic Forest habitat in São Paulo State,[14,15] and *M. lacrimans* from Amazonas State.[16] Nocturnal collecting protocols and the use of photometers and digital cameras to capture light emitted at intensities not visible by dark-adapted human eyes have also increased the number of known luminescent mycenoid fungi. We contend that many of the described *Mycena* species have bioluminescent properties that are currently undetected. For example, most literature classifies *M. haematopus* as non-luminescent, but when studied photometrically, both the mycelium and basidiomes emit light.[44]

The components of the life cycle that luminesce are variable in the mycenoid lineages and this surely influences the ecological roles and adaptive significance of bioluminescence. In many species, only the mycelium is luminescent (Table 1), whereas in others both the mycelium and basidiomes emit light. Very rarely has the basidiome been reported as luminescent while the mycelium is non-luminescent (*M. irritans, M. lamprospora, M. sublucens*).[9,45] Treu and Agerer[46] confirmed earlier reports of luminescent mycelium in *Mycena* spp. and added several more species to the list. For many species, however, pure cultures have not been studied so no data are available documenting the luminescent properties of their mycelia. There is also variability in which components of the basidiomes glow. For example, in *M. lamprospora* and *M. pruinoso-viscida* var. *raboulensis* only the spores are known to emit light,[9,45] in *G. viridilucens* only the lamellae glow,[14] in *M. chlorophos* and *M. asterina* the pilei and lamellae are luminescent,[15,47] whereas in *M. lucentipes* only the stipes glow.[15] Clearly more qualitative

observations of fresh basidiomes and mycelia *in situ* and *in vitro* are needed to clarify the bioluminescent properties of mycenoid fungi.

One of the more interesting luminescent mycenoid fungi is the coffee leaf pathogen *M. citricolor.* Its mycelium produces asexual reproductive structures called gemmifers that are tiny (2 mm tall), mushroom-shaped structures with a sterile (non-sporulating) cap that disarticulates and acts as a dispersal propagule.[48] These modified sterile caps are the primary infecting *inoculum* of new *Coffea* host plants and they are luminescent. Whether the luminous propagules attract arthropod dispersal vectors thereby aiding the fungus in infecting new hosts is unknown. To avoid confusion in the use of the misapplied name *Stilbum flavida* for this stage in the life cycle, Redhead *et al.*[49] created the name *Decapitatus* for the anamorphic dispersal stage of *M. citricolor.*

In the most current and comprehensive phylogeny of euagaric lineages,[28] the luminescent mycenoid fungi in the Mycenaceae belong to the Tricholomatoid clade whose other members are all non-luminescent. The Tricholomatoid clade is distantly related to the Marasmioid clade in which the Omphalotaceae (*Omphalotus* lineage) and Physalacriaceae (*Armillaria* lineage) belong.

In summary, recent multi-gene molecular sequences datasets suggest at least 3 independent origins of bioluminescence in the fungi: in the Omphalotaceae, the Physalacriaceae and the Mycenaceae. The phylogenetic placement of *G. viridilucens* and *M. lucentipes* outside of the Mycenaceae (unpublished data) may indicate a fourth independent origin but more work needs to be done to support this contention. Within the Mycenaceae, the 45 recognized luminescent taxa belong to 18 different taxonomic groups (genera or sections within *Mycena*). Whether this indicates a single early origin of luminescence in the family followed by multiple losses, or multiple independent origins is currently unknown but under investigation in our labs.

Physiology of luminescent fungi

Wassink provided an excellent review of the literature on the physiology and biochemical aspects of luminescent fungi up to 1978.[4] Since then, limited research has been conducted on luminescent fungi in pure culture and none *in situ.* A few examples are presented here.

As early as 1924[4] it was known that there are luminescent and non-luminescent strains of *Panellus stipticus*, and interfertility studies by Macrae[51,52] confirmed that non-luminescent populations from Europe were sexually compatible with luminescent populations from eastern North America. More recent research by Petersen and Bermudes[18,19] indicated that populations of *P. stipticus* from eastern Russia, Japan, New Zealand, and eastern North America were all sexually compatible, and they confirmed with photometric analyses that the species is non-luminescent in Eurasia, but that both non-luminescent and luminescent strains of *P. stipticus* occur in eastern North America. The effects of various environmental and nutritional conditions on the growth and bioluminescence of mycelia of *P. stipticus* indicated that optimal conditions included: darkness; 28 °C; pH 3.8; cellobiose, glucose, maltose, pectin, or trehalose as the carbon source; and ammonia or asparagine as the nitrogen source.[53] Studies on the localization of bioluminescent tissues in *P. stipticus*[54,55] indicated a 10- to 50-fold increase in luminescence emission during basidiome development and that luminescence in the basidiomes was restricted primarily to the pileus margin and lamellar edges. In addition it was shown that in both cultures and basidiomes, the wavelength of maximum bioluminescence was at 525 nm.[56] In *in vitro* antagonism studies, it was shown that bioluminescence emissions in *P. stipticus* and *O. olearius* were reduced over six orders of magnitude when grown with the mycopathogenic fungus *Trichoderma harzianum.*[57]

Some early work was published on laboratory cultivation of *Omphalotus japonicus* (syn. *Lampteromyces japonicus*)[58] as a prelude to investigations on the mechanism of bioluminescence, and subsequent research resulted in the proposition of riboflavin as the putative light emitter.[59,60] Other than a few papers elucidating the cultural conditions for optimal mycelial growth,[61] and the production of degradative enzymes, toxins (illudoids), nematophagous compounds, and biomedically active (antibiotic, antitumor) compounds (not cited here), only limited research has been published on the biology of the Moon Night mushroom, *O. japonicus.*

In Miller's[62] redescription on the Australian Ghost Fungus, *O. nidiformis*, he noted different color-morphs that had variable luminescent properties, with a dark form that luminesced rather weakly and a light form with very strong luminescence. Culture analyses and interfertility studies amongst the two forms indicated that they belong to a single morphologically and physiologically variable species.

The dynamics of bioluminescence in three sympatric species of *Armillaria* (*A. gallica, A. mellea, A. tabescens*) was examined in response to environmental illumination and mechanical disturbance.[63] The data revealed consistent differences in expression of bioluminescence among the three species, confirming earlier work,[64] and among intragenet cultures. They found no evidence in support of diurnal periodicity of bioluminescence in the mycelial cultures *in vitro.* Similar results indicating that bioluminescence does not vary between night and day were reported recently from mycelia of an undetermined tropical fungus inhabiting natural wood substrate *in situ.*[65] Earlier reports suggested a diurnal–nocturnal oscillation[66,67] and seasonal variation[68] of light emissions in *A. mellea* and *P. stipticus.* Weitz *et al.*[69] studied the effects of temperature, light and pH on mycelial growth and luminescence in *A. mellea*, *O. olearius*, *M. citricolor* and *P. stipticus* and found that temperature and pH had a significant effect on both aspects but that light did not.

Bermudes and colleagues[44] were some of the first to systematically use photometers to measure light emission from fungi, and as a consequence discovered that *Mycena haematopus*, previously thought to be non-luminescent, actually emitted light but at intensity not perceived by the human eye. Measurements of total luminescence of single-spore (monokaryon) or dikaryon cultures of six species of fungi revealed a significant difference in luminescence between different species and between monokaryon and dikaryon cultures of the same species (*P. stipticus*, *O. japonicus*).

Recently, the optimal conditions for the growth of mycelia and the production of basidiomes in *Mycena chlorophos* have been published.[47,70] Optimal temperature for mycelial growth and primordium formation were 27 °C and 21 °C respectively, optimal pH of the medium was 4.0, and light was required for primordium initiation. Basidiomes of this species are typically short-lived, but luminescence at a maximum wavelength of 522 nm was emitted continuously for three days. In an unpublished report, basidiomes

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of *M. lux-coeli* emitted relatively strong light for 2–3 days *in situ* in Japan.[71] The mechanism of luminescence in *M. chlorophos* has not been elucidated although it was assumed by those authors[70] to be the same as that reported by Shimomura[72] for other mycenoid fungi (*M. citricolor, M. lux-coeli P. stipticus*).

To summarize, most of the published research on the physiology of bioluminescent fungi has focused on determining the conditions for optimal mycelial growth and basidiome production, the conditions for maximum light emission, the effects of environmental conditions and mechanical disturbance on bioluminescence, and the variability in the quality and quantity of light emission amongst different luminescent species under different growth conditions. Nearly all of the published research has been conducted on fungi grown in pure culture. There is considerable variability amongst luminescent fungi in the optimal growth conditions for maximum light emission and in the various environmental factors that impact bioluminescence. All reports agree that luminescent fungi have a bioluminescence emission peak in the range 520–530 nm.

Ecological functions of luminescent fungi

The potential ecological functions and adaptive significance of bioluminescence in the fungi have been reviewed recently,[44,73,74] reiterating the ideas of numerous earlier workers.[75–78] It has been suggested that bioluminescent basidiomes attract invertebrates to aid in fungal spore dispersal.[79,80] In an elegant experiment, Sivinski[79] showed that more arthropods were attracted at night to luminous forest litter containing mycelia of a *Mycena* species encapsulated in closed glass test tubes (to allow visual recognition but practically eliminate olfactory detection) than to glass test tubes containing non-luminous forest litter. In addition, subsequent research has confirmed that fungivorous insects are positively phototactic to relatively low light emissions of wavelengths in the range 300–650 nm.[81] Hence, for those fungal species that form luminous basidiomes that sporulate at night, emitting light may have a selective advantage over non-luminous species in attracting potential spore-dispersing arthropods, especially in areas where wind dispersal is inhibited (*e.g.*, dense, closed canopy tropical forests). Given that luminous and non-luminous basidiomes can each produce millions of spores per night that are easily wind-dispersed, the significance of supplemental insect dispersal is unknown.

Bioluminescence as an adaptation to enhance spore dispersal, however, cannot be used to explain the ecological function of light emissions from mycelia. In most luminescent fungi, the mycelium does not form dispersal propagules, except for the enigmatic *M. citricolor* (see above). Fungal mycelia are a major or sole source of nutrition for myriad invertebrates, and the fungi have evolved a number of ways to counter predation, including the production of noxious compounds.[82,83] Sivinski[79] also suggested that luminescence might serve as a warning signal to repel nocturnal fungivores, or might attract predators or parasitoids of fungivores. These hypotheses are worthy of further study.

As pointed out by Weitz,[74] luminescence may not confer selective advantage because there are both luminescent and non-luminescent sympatric strains of the same species,[19] and may have no ecological value. Some published data indicate that light emission involves little energy expenditure, implying that the luminous reaction involves a readily available by-product compound or secondary metabolite.[39,65,73] This has been observed in luminous bacteria where reduced flavin mononucleotide ($FMNH_2$), a continuously available by-product of respiration, is the substrate of the luminous reaction.[65] Luminous fungi may be emitting light instead of heat as an energy by-product of enzyme mediated oxidation reactions.[74] Bioluminescence is an oxygen-dependant metabolic process. Lingle[84,85] and Bermudes *et al.*[44] have hypothesized that fungal bioluminescence is involved in lignin degradation through the detoxification of peroxides formed during ligninolysis. As far as we know, all luminescent basidiomycetes are white-rot fungi capable of lignin degradation. We favor the hypothesis that fungal bioluminescence is an advantageous process that provides antioxidant protection against deleterious effects of reactive oxygen species (ROS) produced mainly by mitochondria during respiration.[15]

Bioluminescence mechanism

Early accounts

Although significant advances have occurred in the past 30 years to augment our knowledge of the occurrence, taxonomy, phylogeny and ecology of bioluminescent fungi, only limited progress have been made in understanding the biochemistry involved in fungal light emission. Mechanistic studies of fungal bioluminescence reported until now are incomplete and often misleading. A chronological and critical compilation of published data is here presented.

The first attempts to elucidate the chemistry of fungal bioluminescence were based on the classic “cold” and “hot” extract procedure proposed by Dubois in 1885.[110] Dubois reported that light emission *in vitro* could be observed as soon as the “cold” and the “hot” extracts prepared from either luminous organs of the bivalve mollusk *Pholas dactylus* or from an Indian click-beetle, *Pyrophorus* sp., were mixed. Dependence of light emission on molecular oxygen was already known. Usually light emission from extracts is too dim to be perceived by the naked eye and a sensitive photometer or photocounter must be employed. Perhaps this explains the unsuccessful attempts by Ewart in 1907 and by Kawamura in 1915 to detect light using “cold” and “hot” extracts from the fungi *Pleurotus candescens* and *O. japonicus*, respectively.[76,111] Some years later, Harvey applied Dubois’ procedure to *A. mellea*, *O. olearius* and *P. stipticus*,[7,112] but did not observe any light emission, which was then attributed to a low concentration and instability of luciferin or luciferase in the extracts.

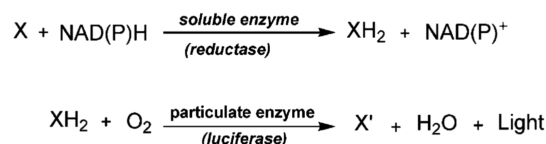
Buller tried to extract the luciferin/luciferase system from *P. stipticus* by pressing basidiomes between two glass slides.[50] As the mushrooms were gradually squeezed, the light emission diminished until total extinction. Light could be visually detected if water was dripped onto dried and whole mushrooms; however, if dried mushrooms had been pulverized, light could not be observed upon water addition. Buller interpreted these results to represent a chemical inactivation of the substances involved in the bioluminescent reaction, such as oxidation of luciferin and/or luciferase by substances previously confined in cell compartments.

In 1959, Airth and McElroy[113,114] finally accomplished a successful experiment using the “cold” and “hot” extract procedure.

These authors ascribed the failure of prior attempts to a low concentration of luciferase in the extracts, eventual presence of inhibitors, and/or the lability of luciferin in "hot" extracts. Importantly, light emission could only be detected if NAD(P)H was added to the reactive medium, suggesting reversibility of any oxidation process that affected the native components.

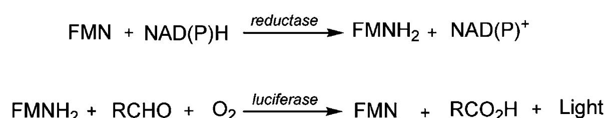
Airth and Foerster's proposal

Airth and Foerster performed several experiments using the "hot" extract of *A. mellea* (source of luciferin) and the "cold" extract of *Collybia velutipes* (source of luciferase).[115] Clearly, the authors used a luminous culture identified erroneously as *C. velutipes*, because that species has been shown to be non-luminescent.[4] Some modifications to the classic Dubois's procedure were also introduced by the authors. The "hot" extract was obtained from dried mycelium cultures of *A. mellea* by prior preparation of fungus homogenate in phosphate buffer and centrifugation, followed by heating the supernatant in boiling water. The homogenate of "cold" extract, obtained from dried mycelium cultures of "*C. velutipes*", was first separated by centrifugation at 3 000 *g*, followed by ultracentrifugation of the supernatant at 198 000 *g*, yielding a soluble protein fraction and a membrane protein fraction (pellet). Light emission was observed as the hot extract (luciferin/oxiluciferin) was mixed with the soluble protein fraction in the presence of NADPH, followed by addition of the pellet (re-suspended in buffer) some minutes after incubation. The protein nature of both ultracentrifugation fractions was suggested by the fact that they precipitated upon addition of ammonium sulfate, were non-dialyzable, and became inactive under heating. The experiment also provided clear-cut evidence that the soluble protein fraction contained a NADPH-dependent reductase while the membrane protein fraction contained the fungal luciferase. Based on this experiment, Airth and Foerster proposed a two-step bioluminescent mechanism involving (i) an initial reduction of the luciferin precursor (X) present in the "hot" extract by a NADPH-dependent reductase, leading to the formation of the fungal luciferin (XH_2), and (ii) the reaction of reduced luciferin with luciferase in the presence of molecular oxygen yielding light and oxyluciferin (X′) (Scheme 1).



Scheme 1

Although Airth and Foerster's proposal resembles the mechanism of bacterial bioluminescence (Scheme 2), the fungal system is not stimulated by the addition of reduced flavin mononucleotide ($FMNH_2$), flavin adenine dinucleotide ($FADH_2$) or dodecanal.[114]



Scheme 2

Moreover, the maximum wavelength emission observed for fungi bioluminescence is around 530 nm[15,56] whereas for bacteria, it is *ca.* 490 nm.[114] In addition, Airth and Foerster repeated successfully their experiment with any possible enzyme/substrate combinations of extracts obtained from *A. mellea*, "*C. velutipes*", and the North American bioluminescent variety of *P. stipticus*, suggesting that both enzyme and substrate are essentially the same for all bioluminescent fungi species.[104]

The structural characterization of the chemical components remained to be accomplished. All efforts conducted to purify protein fractions using ammonium sulfate precipitation, dialysis, different types of chromatography and differential centrifugation resulted in loss of activity and protein degradation.[116] With regard to the luciferin purification, its lability especially in basic medium and the presence of oxygen complicate the adoption of purification procedures and consequent structural characterization.

In 1966, Kuwabara and Wassink were able to isolate 12 mg of a crystalline fluorescent substance from 15 kg of *Mycena citricolor* cultivated mycelium.[117] The compound was unstable in basic conditions, in the presence of light and oxygen, and at high temperatures, similar to what has been reported for other luciferins isolated from different bioluminescent organisms (Scheme 3).[118–123] Additionally, a visible green light emission with a spectrum similar to that of the fungal bioluminescence was observed in the presence of NaOH and H_2O_2 or when the substance was subjected to the Airth and Foerster's procedure. Unfortunately, these authors never reported any structural or physical properties of the fluorescent crystalline substance.

Between the early 1970s and middle 1990s, some authors claimed to be able to isolate and characterize the chemical structure of fungal luciferin.[58–60,124–126] Several molecules were then assigned as the actual luciferins, among them: lampterol (illudin S), ergosta-4,6,8(14),22-tetraen-3-one, riboflavin and lampteroflavin, all extracted and purified from *O. japonicus* (Scheme 4). Notwithstanding the similarity of their fluorescent spectra to the fungal bioluminescence, no further evidence has ever been provided to support the involvement of any of these molecules in the mechanism of fungal light emission *in vivo*.

Shimomura's proposal

During that same period, Shimomura isolated a sesquiterpene from fruiting bodies of *P. stipticus* possibly involved in the bioluminescent pathway, which was named panal. In fact, panal is present in that fungus in the form of its decanoic and dodecanoic esters, PS-A and PS-B, respectively (Scheme 4).[127,128] When panal was incubated with ammonium salts or primary amines for 1 to 24 h, the putative pyrrolic derivative that formed (our assumption) exhibited light emission upon Fe^{2+}/H_2O_2 addition at pH 7–8. The emission maximum wavelength (485–585 nm) was dependent on added surfactant.[129] The author did not observe any light emission from the fungus *P. stipticus*[128] using the procedure of Airth and Foerster.[104]

Based on these findings, Shimomura proposed a non-enzymatic mechanism to account for the fungal bioluminescence, where no luciferase was involved and panal (in fact PS-A and PS-B) was the luciferin precursor. It must be emphasized that there is no report of *in vivo* reactions of panal with nitrogen compounds. This idea was conceived with basis on the reaction between polygodial,

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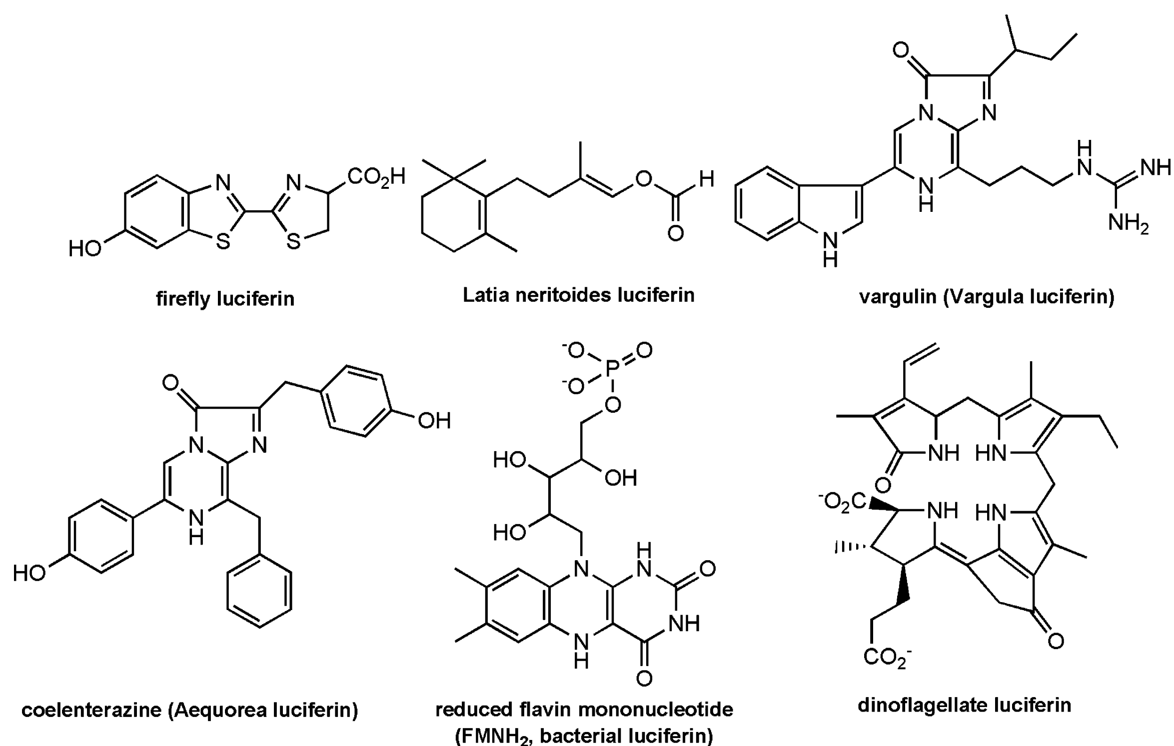
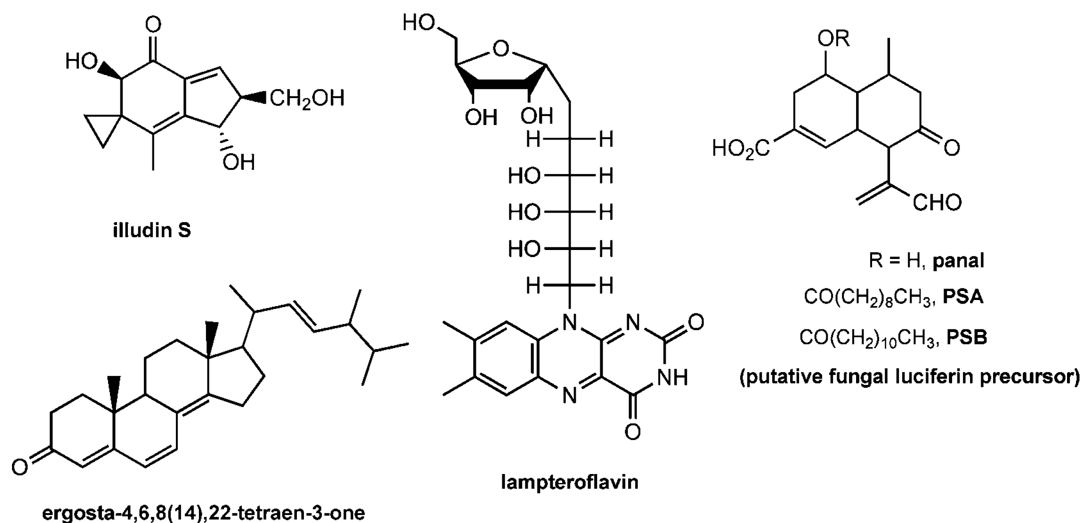


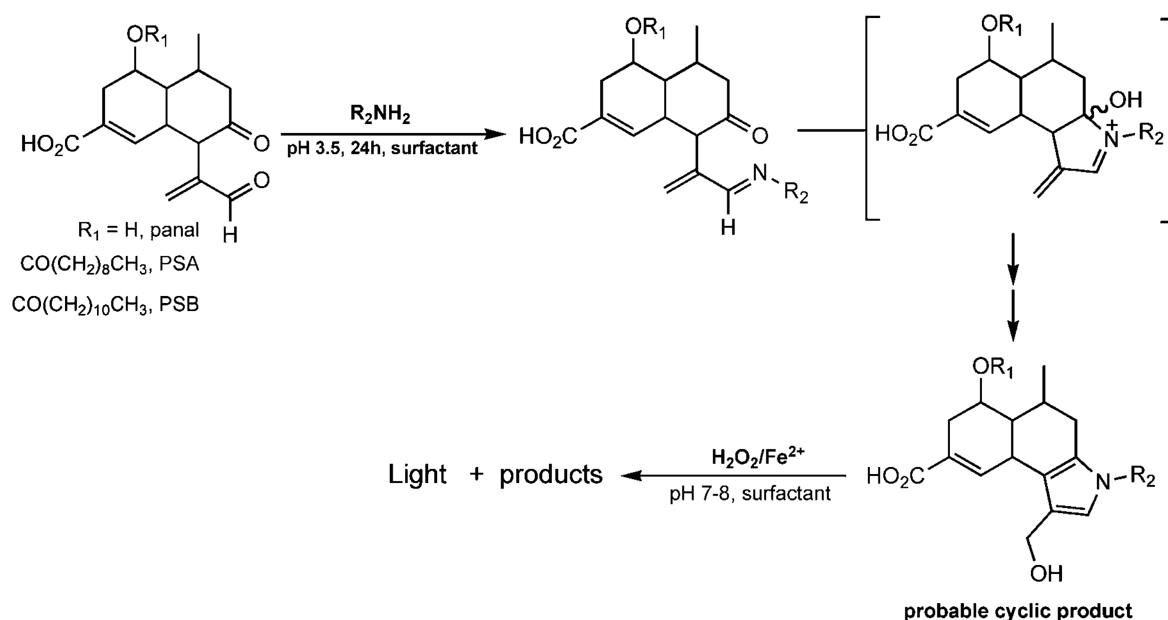
Scheme 3



Scheme 4

a phytoalexin obtained from the plant *Polygonum hydropiper*, and nitrogen compounds.[130] Actually, panal is endowed with low conjugation and high flexibility requiring a cyclization reaction in order to become more rigid and consequently to increase its fluorescence quantum yield (Scheme 5). Moreover, it is widely known that the hydroxyl radical produced by the Fenton's reaction (Fe^{2+} in the presence of H_2O_2) is a highly oxidizing reagent, which argues against its use in model studies of bioluminescence, in which the main objective is to resemble physiological plausible conditions. The hypothesis of a non-enzymatic pathway involved in fungal bioluminescence requires further investigations to be seriously considered.

We have been able to observe light emission using the classic "cold" and "hot" extract procedure in the presence of either NADH or NADPH with cultures of the recently described Brazilian bioluminescent species *G. viridilucens* and *M. lucentipes.*[14,15] To our knowledge, aside from Kuwabara[117] and Kamzolkina's group,[131] we are the only ones to successfully observe light with the aid of a photometer using either Dubois's or Airth and Foerster's procedure carried out with cultivated mycelium extracts under physiologically plausible conditions. Moreover, we were also able to detect light emission with any possible enzyme/substrate combinations of extracts obtained from *G. viridilucens* and *M. lucentipes* as performed earlier with other bioluminescent fungi



Scheme 5

(*i.e.*, *A. mellea* and *P. stipticus*).[104] Based on our own findings we are very much inclined to favor Airth and Foerster's proposal against Shimomura's mechanism. We are currently employing Dubois's and Airth and Foerster's procedure to guide us in the isolation of the luciferin and enzymes involved in fungi bioluminescence.

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