



Evolution and Diversity of Bioluminescent Fungi

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Abstract

Bioluminescence is one of the most fascinating features of basidiomycetes. In this chapter, we have reviewed a total of 105 bioluminescent fungi that have been documented to date. We show that these species are restricted to three major lineages, including mycenoid, *Armillaria*, and *Omphalotus*, and display different bioluminescent patterns and geographical distributions. A global phylogeny shows that these species also exhibit patchy phylogenetic placement with their non-bioluminescent

relatives. We review previous work on their genomes, which contain the fungal luciferin biosynthetic cluster. The dynamics of this cluster provide an evolutionary scenario since the last common ancestor of the family Mycenaceae and the marasmioid clade of Agaricales. Finally, we discuss potential functions and possible research directions of bioluminescence in these fungi.

Keywords

Basidiomycetes, Fungal evolution, Bioluminescence, Luciferase, Mycena

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12.1 Introduction

Bioluminescence is the emission of light by a living organism, generated by a chemical reaction that involves proteins called luciferases that catalyze the oxidation of substrates called luciferins. It is a trait that has evolved at least 94 times independently across the tree of life (Lau and Oakley 2021), with over 700 genera of bioluminescent organisms recorded from freshwater, terrestrial, and marine environments (Haddock et al. 2010; Widder 2010; Lau and Oakley 2021; Delroisse et al. 2021). Bioluminescence can be further categorized into two types, autogenic and bacteriogenic, in which light is produced either by the organism itself or bioluminescent bacterial symbionts, respectively (Lau and Oakley 2021).

Bioluminescence in fungi is autogenic, which means fungi emit light using their own luciferin and luciferase (Oliveira et al. 2012; Oliveira and Stevani 2009; Airth and Mc 1959). Fungal luciferin is different from the other 13 known luciferins (Lau and Oakley 2021; Purtov et al. 2015) and all fungal luciferases are homologous and distinct from other known luciferases used by other organisms based on sequence similarity (Delroisse et al. 2021; Kotlobay et al. 2018).

All bioluminescent fungi belong to the Agaricales of Basidiomycetes, which is a major order comprising around 13,000 gilled mushrooms (Kirk et al. 2008). These fungi belong to ten different unrelated genera although some of which have taxonomic synonyms. The apparent patchy phylogenetic distribution of bioluminescence in fungi and the conserved genetic mechanisms underlying phenotype can be explained by either convergent evolution or an intricate loss/gain history. Recent phylogenomic progress has resolved the phylogenetic relationships among species and helps us answer those questions.

This review focuses on the evolution of bioluminescence in mushrooms in the Agaricales order. The recent identification of the luciferin biosynthetic pathway genes and new phylogenomic analyses of bioluminescent fungi and their sister taxa have shown that fungal bioluminescence occurred in the last common ancestor of the mycenoid and the marasmioid clade. We will review the features of bioluminescent fungi, the known genes involved in the bioluminescence, and their evolutionary history.

12.2 Diversity of Bioluminescent Fungi

Bioluminescence has long captured the imagination of scientists. The taxonomy and evolution of bioluminescent fungi was first compiled and discussed 70 years ago (Wassink 1978; Harvey 1952). The number of taxonomically reported bioluminescent fungi continues to increase with improvement over higher sensitivity in light detection initially from the naked eye to digital

camera, luminometer, or photomultiplier. Two reviews have updated the accounts to 64 luminescent species in 2008 (Desjardin et al. 2008) and 81 species in 2015 (Chew et al. 2015). We have removed the phylogenetically uncertain species and merged synonyms where possible, as well as compiled and assigned a list of 28 additional bioluminescent species (Mihail 2015; Desjardin et al. 2016; Cortes-Perez et al. 2019; Chang et al. 2020; Karunarathna et al. 2020; Dauner et al. 2021; Terashima et al. 2016). The current number of recorded bioluminescent fungi is 105. In recent years, molecular data were generated using barcode DNA sequences including rRNA ITS (Internal transcribed spacer), large subunit rRNA (LSU), and RNA polymerase II (*rpb2*) to revise the phylogenetic positions of these species, which can be classified into three lineages (Fig. 12.1): 80 in the mycenoid (78 Mycenaceae and two from the Lucentipes lineage) (Table 12.1), 11 in the *Armillaria* lineage and 13 in the *Omphalotus* lineage, and one species (*Pleurotus niitidus* Har. Takah. & Taneyama) with uncertain position (Table 12.2). With the availability of molecular markers, the term mycenoid was originally intended to describe various morphological features that are now coherently grouped in species belonging to the Mycenaceae family. A fourth lineage (Lucentipes) containing the bioluminescent *Gerronema viridilucens* Desjardin, Capelari & Stevani (Desjardin et al. 2005) and *Mycena lucentipes* Desjardin, Capelari & Stevani (Desjardin et al. 2007) which were classified as mycenoid species is excluded in this review because of the lack of available marker sequences. The three lineages shared a common origin in the last common ancestor of Mycenaceae and the marasmioid clade. For more details on the relationships, see Ke et al. 2020. Here, we summarize the properties of these three major bioluminescent fungal lineages.

12.2.1 Mycenaceae Family

The Mycenaceae family contains most species originally part of the mycenoid lineage (Desjardin et al. 2008), which are a type of mushrooms

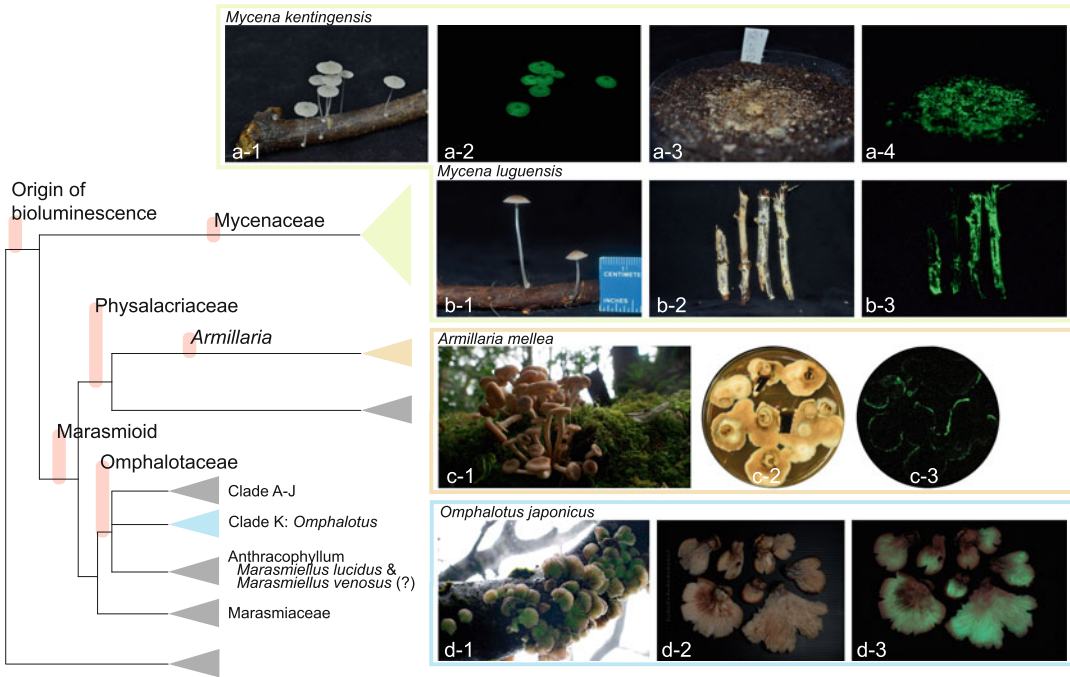


Fig. 12.1 Overview of bioluminescent fungi lineages and their sister groups. Basidiomes of *Mycena kentingensis* in light (a-1) and dark (a-2) exposures and its mycelium in light (a-3) and dark (a-4) cultured in compost. Basidiomes of *Mycena luguensis* (b-1) and its mycelium in light (b-2)

and dark (b-3) grown on wood. Basidiomes of *Armillaria mellea* (c-1) and its cultured mycelium in light (c-2) and dark (c-3). Basidiomes of *Omphalotus japonicus* on natural host tree (d-1) and the fruiting body in light (d-2) and dark (d-3)

whose gills adhere to cartilaginous and central stipes and lack a ring or volva (Ulloa and Hanlin 2017). The mycenoid lineage includes the majority of recorded bioluminescent fungi (80) belonging to the Mycenaceae family with the exception of two species (*Gerronema viridilucens* and *Mycena lucentipes*; Desjardin et al. 2008). In this review, we focus on the diversity of Mycenaceae. Mycenaceae contains over 600 species including *Atheniella*, *Dictyopanus*, *Favolaschia*, *Mycena*, *Mycenoporella*, *Panellus*, *Resinomyces*, *Roridomyces*, and *Xeromphalina* (Redhead et al. 2012; Kirk et al. 2008). Members of this family are known primarily to colonize leaves or wood as litter- or wood-decaying saprophytes (Moncalvo et al. 2002). Still, other members of this family were reported to use different nutritional strategies such as orchid mycorrhizae (Ogura-Tsujita et al. 2009; Martos et al. 2009; Zhang et al. 2012), the coffee

pathogen *Mycena citricolor* (Rao and Tewari 1987; Quesada-Chanto and Jimenez-Ulate 1996), a plant root invader (Harder et al. 2021), and tissues in moss and root system in healthy plant (Davey et al. 2013; Liao et al. 2014; Botnen et al. 2014; Lorberau et al. 2017; Kernaghan and Patriquin 2011). ITS is the most common marker used in this lineage. We downloaded available ITS sequences (>500 bp) from the National Center for Biotechnology Information (NCBI) according to taxId including Mycenaceae, *Favolaschia*, *Filoboletus*, *Dictyopanus*, and *Roridomyces*. We constructed a phylogenetic tree of 287 non-redundant sequences with species information using IQ-TREE (Nguyen et al. 2015). An alignment length of 1220 bp (last updated 2022.09.11; <https://github.com/HueiMien/bioluminescent-fungi.git>) was produced with MAFFT (Katoh and Standley 2013) and trimming with trimal (Capella-Gutierrez et al. 2009). (Fig. 12.2).

Table 12.1 Bioluminescent fungi recorded in the Mycenaceae

Section ^a	Scientific name ^b	Mycelium ^c	Fruiting body ^c	Stipe ^c	Cap ^c	Spore ^c	Reference ^d
Aspratiles	<i>Mycena lacrimans</i> Singer	–	+	+	–	–	(Desjardin and Braga-Neto 2007)
Aspratiles	<i>Mycena aspratilis</i> Maas Geest. & de Meijer	?	+	–	+	?	(Desjardin et al. 2010)
Basipedes	<i>Mycena illuminans</i> Henn.	+	+	–	+	–	(Corner 1954; Chew et al. 2015; Chew et al. 2013)
Basipedes	<i>Mycena stylobates</i> (Pers.: Fr.) P.Kumm.	+	–	–	–	–	(Bothe 1931)
Basipedes	<i>Mycena kentingensis</i> Y.S. Shih, C.Y. Chen, W.W. Lin & H.W. Kao	+	+	–	+	–	(Shih et al. 2014)
Basipedes	<i>Mycena nocticaelum</i> A.L.C. Chew & Desjardin	+	+	–	+	?	(Chew et al. 2015)
Calodontes	<i>Mycena pura</i> (Pers.: Fr.) P. Kumm.	+	–	–	–	–	(Treu and Agerer 1990)
Calodontes	<i>Mycena rosea</i> (Bull.) Gramberg	+	–	–	–	–	(Treu and Agerer 1990)
Calodontes	<i>Mycena cahaya</i> A.L.C. Chew & Desjardin	+	+	+	+	?	(Chew et al. 2014)
Calodontes	<i>Mycena seminau</i> A.L.C. Chew & Desjardin	+	+	–	+	?	(Chew et al. 2014)
Calodontes	<i>Mycena sinar</i> A.L.C.Chew & Desjardin	+	+	+	+	–	(Chew et al. 2014)
Calodontes	<i>Mycena sinar</i> var. tangkaisinar A.L.C.Chew & Desjardin	?	+	+	+	?	(Chew et al. 2014)
Citricolores	<i>Mycena citricolor</i> (Berk. & M.A.Curtis) Sacc.	+	–	–	–	–	(Berliner 1961a)
Crocatae	<i>Mycena luxfoliicola</i> Cortés-Pérez, Desjardin & Ram.-Cruz	+	+	+	+	?	(Cortes-Perez et al. 2019)
Exornatae	<i>Mycena chlorophos</i> (Berk. & M.A.Curtis) Sacc.	+	+	+	+	–	(Corner 1954)
Exornatae	<i>Mycena discobasis</i> Metrod	?	+	+	+	–	(Desjardin et al. 2007)
Exornatae	<i>Mycena margarita</i> (Murrill) Murrill	?	+	+	+	?	(Desjardin et al. 2010)
Exornatae	<i>Mycena deeptha</i> Aravind. & Manim.	+	–	–	–	–	(Aravindakshan et al. 2012)
Fragilipedes	<i>Mycena polygramma</i> (Bull.: Fr.) S.F.Gray	+	–	–	–	–	(Berliner 1961a; Treu and Agerer 1990)
Fragilipedes	<i>Mycena zephrus</i> (Fr.: Fr.) P.Kumm.	+	–	–	–	–	(Bothe 1931; Treu and Agerer 1990)
Fragilipedes	<i>Mycena silvaelucens</i> B.A. Perry & Desjardin	?	+	+	+	?	(Desjardin et al. 2010)
Fragilipedes	<i>Mycena flammifera</i> Har. Takah.& Taneyama	+	+	+	+	?	(Terashima et al. 2016)

(continued)

Table 12.1 (continued)

Section ^a	Scientific name ^b	Mycelium ^c	Fruiting body ^c	Stipe ^c	Cap ^c	Spore ^c	Reference ^d
Fragilipedes	<i>Mycena stellaris</i> Har. Takah., Taneyama & A. Hadano	+	+	+	+	?	(Terashima et al. 2016)
Fragilipedes	<i>Mycena jingyinga</i> C.C. Chang, C.Y. Chen, W.W. Lin & H.W. Kao	+	–	–	–	–	(Chang et al. 2020)
Fragilipedes	<i>Mycena luguensis</i> C.C. Chang, C.Y. Chen, W.W. Lin & H.W. Kao	+	–	–	–	–	(Chang et al. 2020)
Fragilipedes	<i>Mycena venus</i> C.C. Chang, C.Y. Chen, W.W. Lin & H.W. Kao	+	–	–	–	–	(Chang et al. 2020)
Galactopoda	<i>Mycena haematopus</i> (Pers.: Fr.) P.Kumm.	+	+	?	?	?	(Bermudes et al. 1992; Treu and Agerer 1990)
Hygrocyboideae	<i>Mycena epipterygia</i> (Scop.: Fr.) S.F.Gray	+	–	–	–	–	(Bothe 1931)
Incertae Sedis	<i>Mycena daisyogunensis</i> Kobayasi	?	+	?	?	?	(Kobayasi 1951)
Incertae Sedis	<i>Mycena pseudostylobates</i> Kobayasi	+	?	?	?	?	(Kobayasi 1951)
Lactipedes	<i>Mycena galopus</i> (Pers.: Fr.) P.Kumm.	+	–	–	–	–	(Berliner 1961a; Bothe 1931; Treu and Agerer 1990)
Manipularis-group	<i>Filoboletus pallescens</i> (Boedijn) Maas Geest.	?	+	?	?	?	(Maas Geesteranus 1992)
Manipularis-group	<i>Panellus yunnanensis</i> P.G. Liu = <i>Filoboletus yunnanensis</i>	?	+	?	?	?	(Liu 1995)
Manipularis-group	<i>Filoboletus manipularis</i> (Berk.) Teng = <i>Favolaschia manipularis</i>	+	+	+	?	?	(Corner 1954)
Manipularis-group	<i>Filoboletus manipularis</i> var. <i>microporus</i> Kawam. ex Corner nom. inval. = <i>Polyporus microporus</i> Kawam. nom. inval.	?	+	+	?	?	(Corner 1954)
Manipularis-group	<i>Filoboletus Hanedae</i> Kobayasi = <i>Poromyces hanedai</i>	?	+	+	?	?	(Kobayasi 1951)
Mycena	<i>Mycena inclinata</i> (Fr.) Quél.	+	–	–	–	–	(Wassink 1948)
Mycena	<i>Mycena maculata</i> P.Karst.	+	–	–	–	–	(Treu and Agerer 1990)
Mycena	<i>Mycena tintinnabulum</i> (Fr.) Quél.	+	–	–	–	–	(Bothe 1930)
Mycena	<i>Mycena gombakensis</i> A.L.C. Chew & Desjardin	+	+	+	+	?	(Chew et al. 2015)

(continued)

Table 12.1 (continued)

Section ^a	Scientific name ^b	Mycelium ^c	Fruiting body ^c	Stipe ^c	Cap ^c	Spore ^c	Reference ^d
Nodosae	<i>deformis</i> Maas Geest. & de Meijer	+	–	–	–	–	(Desjardin et al. 2016)
Panellus	<i>Panellus luxfilamentus</i> A.L.C. Chew & Desjardin	+	–	–	–	–	(Chew et al. 2015)
Panellus	<i>Dictyopanus foliicola</i> Kobayasi	+	+	?	?	?	(Kobayasi 1951)
Panellus	<i>Panellus pusillus</i> var. <i>sublamellatus</i> Corner	?	+	?	?	?	(Corner 1954)
Panellus	<i>Panellus luminescens</i> (Corner) Corner	+	+	+	+	+	(Chew et al. 2015; Corner 1950)
Panellus	<i>Panellus pusillus</i> (Pers. ex Lév.) Burdsall & O.K.Mill	+	+	?	+	?	(Corner 1954; Desjardin et al. 2008)
Panellus	<i>Panellus stipticus</i> (Bull.: Fr.) P.Karst.	+	+	–	+	?	(Berliner 1961a; Wassink 1948)
Resinomycena	<i>Resinomycena fulgens</i> Har. Takah., Taneyama & Oba	?	+	+	+	?	(Terashima et al. 2016)
Resinomycena	<i>Resinomycena petarensis</i> Desjardin, B.A. Perry & Stevani	+	–	–	–	–	(Desjardin et al. 2016)
Roridiae	<i>Roridomyces irritans</i> E. Horak = <i>Mycena irritans</i>)	–	+	–	+	–	(Horak 1978)
Roridiae	<i>Roridomyces lamprosporus</i> (Corner) Rexer = <i>Mycena lamprospora</i> (Corner) E. Horak	–	+	–	–	+	(Horak 1978; Corner 1950)
Roridiae	<i>Roridomyces pruinosoviscida</i> Corner = <i>Roridomyces pruinosoviscidus</i> (Corner) A.L.C. Chew & Desjardin	+	+	+	+	?	(Chew et al. 2015; Corner 1954)
Roridiae	<i>Roridomyces pruinosoviscidus</i> var. <i>rabaulensis</i> (Corner) Blanco-Dios	?	+	?	?	?)	(Corner 1954)
Roridiae	<i>Roridomyces roridus</i> (Fr.) Rexer = <i>rorida</i> (Fr.) Que l.	+	–	–	–	–	(Josserand 1953)
Roridiae	<i>Roridomyces sublucens</i> Corner	–	+	+	+	–	(Corner 1954)
Roridiae	<i>Roridomyces phyllostachydis</i> Karun., Mortimer and Axford	+	+	+	–	?	(Karunaratna et al. 2020)
Roridiae	<i>Roridomyces viridiluminus</i> L.A.P. Dauner, Karunaratna & P.E. Mortimer	+	+	+	+	?	(Dauner et al. 2021)
Rubromarginatae	<i>Mycena lux-coeli</i> Corner	?	+	+	+	–	(Corner 1954)
Rubromarginatae	<i>Mycena noctilucens</i> Kawam. ex Corner = <i>Mycena noctilucens</i> var. <i>magnispora</i> Corner	+	+	+	+	?	(Chew et al. 2015; Corner 1954)

(continued)

Table 12.1 (continued)

Section ^a	Scientific name ^b	Mycelium ^c	Fruiting body ^c	Stipe ^c	Cap ^c	Spore ^c	Reference ^d
Rubromarginatae	<i>Mycena olivaceomarginata</i> (Masseé apud Cooke)	+	–	–	–	–	(Wassink 1979)
Rubromarginatae	<i>Mycena singeri</i> Lodge	?	+	+	+	–	(Desjardin et al. 2007)
Rubromarginatae	<i>Mycena coralliformis</i> A.L.C. Chew & Desjardin	+	–	–	–	–	(Chew et al. 2015)
Rubromarginatae	<i>Mycena fulgoris</i> Cortés-Pérez, Desjardin	–	+	+	–	?	(Desjardin et al. 2016)
Rubromarginatae	<i>Mycena lumina</i> Cortés-Pérez, Desjardin	+	+	+	+	?	(Cortes-Perez et al. 2019)
Sacchariferae	<i>Mycena asterina</i> Desjardin, Capelari & Stevani	?	+	–	+	–	(Desjardin et al. 2007; Desjardin et al. 2008)
Sacchariferae	<i>Mycena lazulina</i> Har. Takah., Taneyama, Terashima & Oba	+	+	+	+	?	(Terashima et al. 2016)
Sacchariferae	<i>Mycena perlae</i> Cortés-Pérez, Desjardin & Rockefeller	–	+	–	+	?	(Cortes-Perez et al. 2019)
Sanguinolentae	<i>Mycena sanguinolenta</i> (Alb. & Schwein.: Fr.) P. Kumm.	+	–	–	–	–	(Desjardin et al. 2007)
Sanguinolentae	<i>Mycena nebula</i> Cortés-Pérez, Desjardin & Rockefeller	?	+	+	–	?	(Cortes-Perez et al. 2019)
Supinae	<i>Mycena fera</i> Maas Geest. & de Meijer	?	+	+	+	–	(Desjardin et al. 2007)
Supinae	<i>Mycena luxarboricola</i> B. A.Perry & Desjardin	?	+	+	+	?	(Desjardin et al. 2010)
Supinae	<i>Mycena globulispورا</i> Maas Geest. & de Meijer	?	+	+	–	?	(Desjardin et al. 2016)
Similar to Euspeireae/Aspratiles	<i>Mycena guzmanii</i> Cortés-Pérez, Desjardin	+	+	+	+	?	(Cortes-Perez et al. 2019)
Similar to Hygrocyboideae/Insignes/Euspeireae	<i>Mycena luxaeterna</i> B.A. Perry & Desjardin	+	+	+	–	?	(Desjardin et al. 2010)
Similar to Insignes/Euspeireae	<i>Mycena luxperpetua</i> B.A. Perry & Desjardin	+	+	+	+	?	(Desjardin et al. 2010)
Uncertain	<i>Mycena</i> aff. <i>abieticola</i> Singer	?	+	+	+	?	(Desjardin et al. 2010)
Uncertain	<i>Mycena luxfoliata</i> Har. Takah., Taneyama & Terashima	+	–	–	–	–	(Terashima et al. 2016)
Uncertain	<i>Mycena oculisymphae</i> Desjardin, B.A. Perry & Stevanir	?	+	+	+	?	(Desjardin et al. 2016)

^a The “Uncertain” section means there is no assignment according to the reference

^b Use current name of the species in Index Fungorum, and their synonyms are listed as well.

^c +, –, and? denote the structure with, without, and uncertain illumination, respectively

^d Citations which report the bioluminescence feature

Table 12.2 Bioluminescent fungi in *Armillaria* and *Omphalotus* lineage

Lineage	Taxon	Mycelium	Fruiting body	Reference
<i>Armillaria</i> lineage	<i>Armillaria fuscipes</i> Petch	+	–	(Wassink 1978; Wassink 1948; Berliner 1961a)
	<i>Armillaria gallica</i> Marxm. & Romagn	+	–	(Mihail and Bruhn 2007)
	<i>Armillaria mellea</i> (Valh.) P.Kumm.	+	–	(Mihail and Bruhn 2007)
	<i>Armillaria ostoyae</i> (Romagn.) Henrik	+	–	(Rishbeth 1986)
	<i>Armillaria tabescens</i> (Scop.) Emel	+	–	(Mihail and Bruhn 2007)
	<i>Armillaria calvescens</i> Bérubé & Dessur.	+	–	(Mihail 2015)
	<i>Armillaria cepistipes</i> Velen.	+	–	(Mihail 2015)
	<i>Armillaria gemina</i> Bérubé & Dessur.	+	–	(Mihail 2015)
	<i>Armillaria nabsnona</i> T.J. Volk & Burds.	+	–	(Mihail 2015)
	<i>Armillaria sinapina</i> Bérubé & Dessur.	+	–	(Mihail 2015)
<i>Omphalotus</i> lineage	<i>Desarmillaria ectypa</i> (Fr.) R.A. Koch & Aime = <i>Armillaria ectypa</i> (Fr.) Lamoure	+	+	(Ainsworth 2004)
	<i>Omphalotus guepiniformis</i> (Berk.) Neda = <i>Lampteromyces luminescens</i> M. Zang = <i>Omphalotus japonicus</i> (Kawam.) Kirchm. & O.K. Mill.	+	?	(Zang 1979; Kawamura 1910; Bermudes et al. 1992; Singer 1947)
	<i>Neonothopanus nambi</i> (Speg.) Petersen & Krisai-Greilhuber	+	?	(Corner 1981; Chew et al. 2015)
	<i>Nothopanus noctilucens</i> (Lé v.) Singer = <i>Pleurotus noctilucens</i> Lé v.	+	?	(Léveillé 1844; Haneda 1955)
	<i>Omphalotus illudens</i> (Schwein.) Bresinsky & Besl. = <i>Clitocybe illudens</i> Schwein. = <i>Panus illudens</i> (Schwein.) Fr. = <i>Pleurotus facifer</i> Berk. & M. A. Curtis	+	+	(Berliner 1961b, a; Wassink 1948)
	<i>Omphalotus mangensis</i> (J. Li & X. Hu) Kirchm. & O. K. Mill. = <i>Lampteromyces mangensis</i> J. Li & X. Hu	+	?	(Li and Hu 1993)
	<i>Omphalotus nidiformis</i> (Berk.) O. K. Mill. = <i>Pleurotus nidiformis</i> (Berk.) Sacc. = <i>Pleurotus candescens</i> (F. Muell. & Berk.) Sacc. = <i>Pleurotus illuminans</i> (Berk.) Sacc. = <i>Pleurotus lampas</i> (Berk.) Sacc. = <i>Pleurotus phosphorus</i> (Berk.) Sacc.	+	?	(Berkeley 1844; Miller Jr. 1994)
	<i>Omphalotus olearius</i> (DC.) Singer = <i>Pleurotus olearius</i> (DC.) Gillet	+	+	(Wassink 1948)
	<i>Omphalotus olivascens</i> H.E.Bigelow, O.K.Mill. & Thiers	+	–	(Bigelow et al. 1976)
	<i>Pleurotus decipiens</i> Corner	+	?	(Corner 1981)
	<i>Nothopanus eugrammus</i> (Mont.) Singer 1944 = <i>Pleurotus eugrammus</i> var. <i>radicolus</i> Corner	+	?	(Corner 1981)
	<i>Neonothopanus gardneri</i> (Berk.) Capelari, Desjardin, B.A. Perry, T. Asai & Stevani	+	?	(Capelari et al. 2011; Saccardo 1887)
	<i>Marasmiellus lucidus</i> Har. Takah., Taneyama & S. Kurogi	+	?	(Terashima et al. 2016)
<i>Marasmiellus venosus</i> Har. Takah., Taneyama & A. Hadano	+	+	(Terashima et al. 2016)	
Uncertain	<i>Pleurotus nitidus</i> Har. Takah. & Taneyama	+	?	(Terashima et al. 2016)

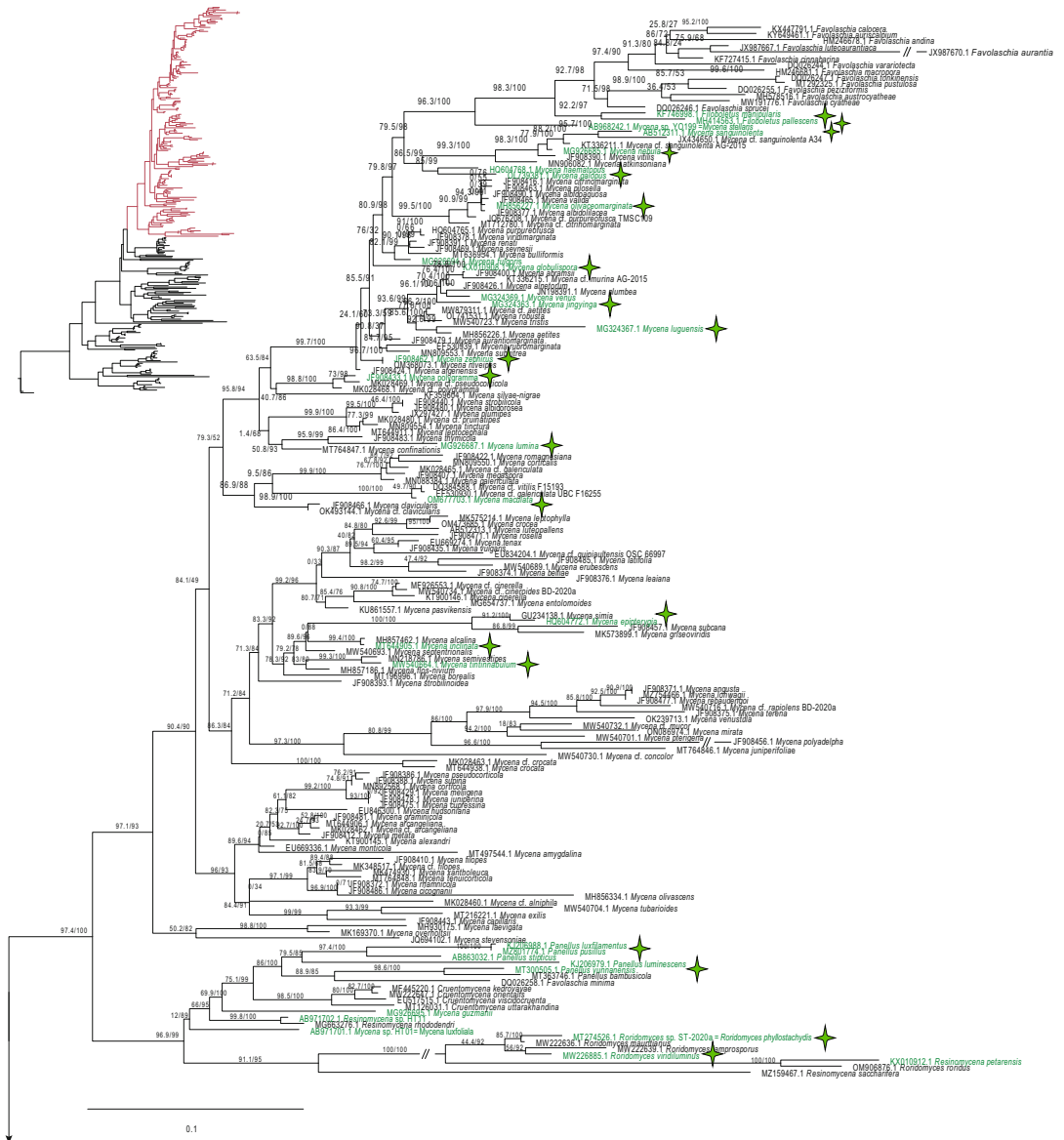


Fig. 12.2 ITS tree of 287 Mycenaceae sequences with two *Armillaria* species as outgroup which was constructed by IQ-TREE (Nguyen et al. 2015) with an alignment length of 1220 bp without redundant species downloaded from NCBI. Numbers on each branch denote support values (SH-aLRT support (%) / ultrafast bootstrap support (%)). Dark green nodes annotated with a star denote the

bioluminescent species. Note that the sequences are not necessary the same as the holotype, and not all bioluminescent Mycenaceae species were listed here since not all of them have been recorded in NCBI. The inset indicates the lineage with species belong to sect. Calodontes

We found that the bioluminescent trait was scattered along the Mycenaceae phylogeny and did not group to a specific genus. This

observation is consistent with previous patchy distributions observed in smaller datasets using different molecular markers and focusing on

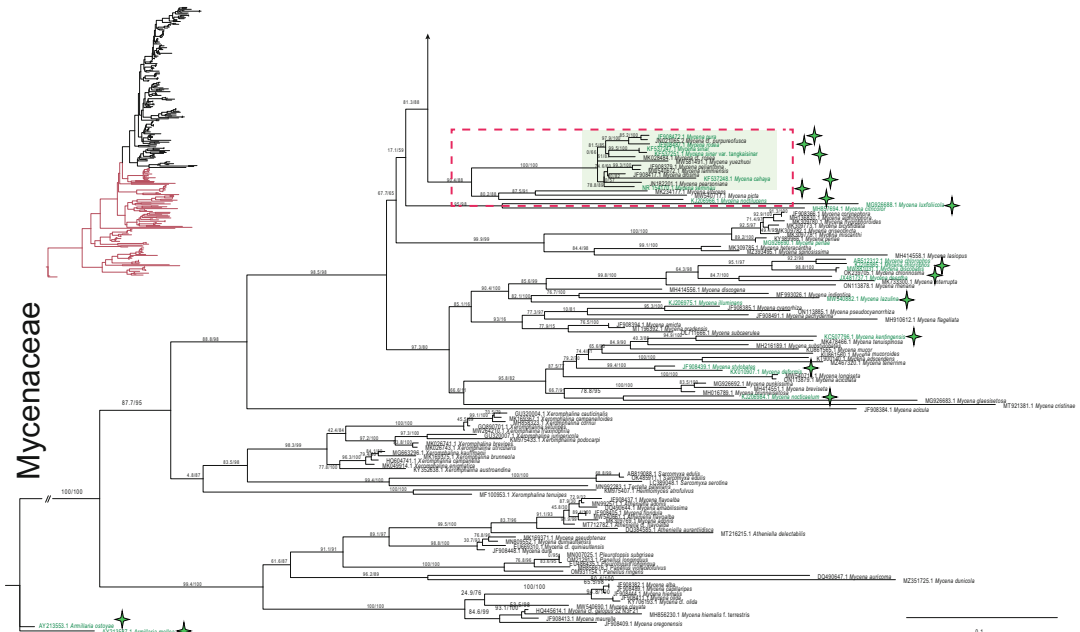


Fig. 12.2 (continued)

different closely related species (Chew et al. 2015; Karunarathna et al. 2020; Dauner et al. 2021; Shih et al. 2014; Chang et al. 2020).

Among different species, luminescence also showed diverse patterns in different tissues, including bioluminescent mycelia, caps and stipes of basidiomes (Table 12.1).

Our revision was consistent with the observations of Desjardin et al. 2008. Overall, the species with bioluminescent basidiomes mostly have bioluminescent mycelia (26/32) but some have non-bioluminescent mycelia (6/32). The variations can usually be found between closely related species, indicating that the expression of bioluminescent is not restricted to specific tissues. An example was the *Mycena* sect. *Calodontes* shown in Fig. 12.2. These 13 species with >85.8 ITS nucleotide identity form a monophyletic clade with seven non-bioluminescent species and six bioluminescent species, including two species with bioluminescent mycelia but non-bioluminescent fruiting bodies, as well as four species with bioluminescent fruiting bodies with different intensity in the stipes and caps. Different species also displayed different degrees of endemism (Fig. 12.3). *M. pura* is the most widely distributed across different continents.

By contrast, *M. chlorophos* is restricted in Asia, and *M. kentingensis* has only been found in Taiwan so far.

12.2.2 *Armillaria* lineage

This lineage includes all members of genus *Armillaria* comprising more than 40 species (Baumgartner et al. 2011; Anderson and Stasovski 1992; Piercey-Normore et al. 1998; Coetzee et al. 2001; Koch et al. 2017). The *Armillaria* lineage and its sister group, the physalacrioid lineage (all of which are non-bioluminescent), form the family Physalacriaceae (Moncalvo et al. 2002), which includes 11 genera and 169 species (Kirk et al. 2008). Most of them can decompose organic material as saprotrophs and infect plants as necrotrophic pathogens when they are in a suitable environment (Sipos et al. 2018; Shaw et al. 1991; Smith et al. 1992; Kedves et al. 2021). Some of them are associated with orchid mycorrhizas (Martos et al. 2009; Cha and Igarashi 1995; Sekizaki et al. 2008; Guo et al. 2016).

Eleven species in the *Armillaria* lineage have been confirmed to have a luminescent property in

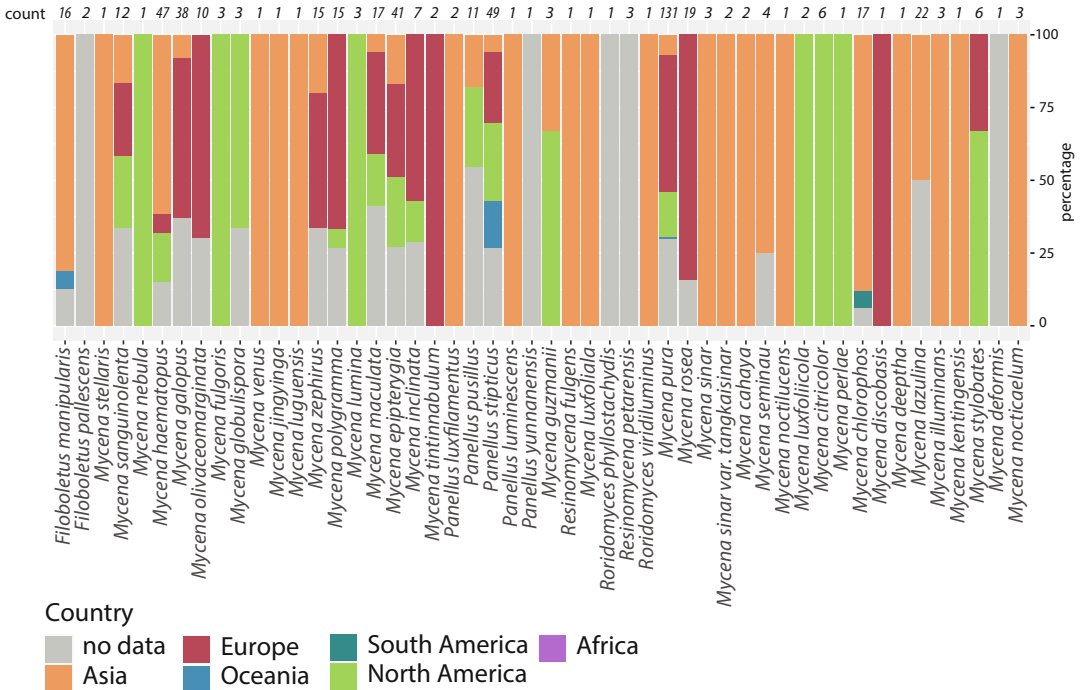


Fig. 12.3 The geographic distribution of bioluminescent fungi in Mycenaceae lineage recorded by extracting ITS (Internal transcribed spacer) from NCBI and converting the collected country to six continents

their mycelium (Table 12.2), and it has been believed that the mycelium of most *Armillaria* species is luminescent (Desjardin et al. 2008). Among them, only *Desarmillaria ectypa* (Synonym *A. ectypa*) emit light in both mycelium and

fruitbodies (mainly from the gills) so far in report. Based on the classification of a 2018 review using a translation elongation factor subunit 1-alpha (*tef-1α*) (Coetzee et al. 2018), nine sub-lineages were proposed (Fig. 12.4). Most of the known

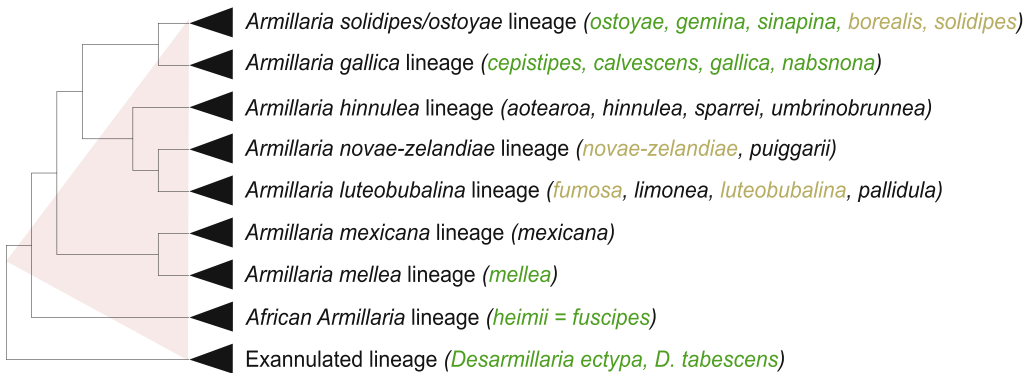


Fig. 12.4 The abbreviation of a phylogeny from (Coetzee et al. 2018), created using *tef-1α* sequences. Species with dark green denote the bioluminescent fungi according to observation of light emission, those with light green

denotes the bioluminescent fungi with prediction of luciferase cluster in genome. The figure was adapted with permission and redrawn

luminescent species according to phenotypic observations belong to the Holarctic lineages including the *A. gallica*, *A. solidipes/ostoyae*, *A. mellea*, *A. mexicana*, and Exannulated (subgenus *Desarmillaria*) lineages. In addition, based on the recent genomic content analysis, all of the analyzed 14 species have conserved luciferin biosynthetic pathway genes (mentioned later), which extend bioluminescence to two more lineages of *Armillaria* (*A. luteobubalina* and *A. novaezelandiae* Lineages).

Even when based just on those recorded bioluminescent fungi, it does not seem that the ability to emit light is related to geographic distribution. For example, the known luminescent species include *A. gemina* which is confined to North America, *A. fuscipes* which is confined to Africa, and *A. ostoyae* which has transcontinental distribution across Europe, North America, and Asia. Light emission was recorded in *Desarmillaria ectypa* and *D. tabescens*, which belongs to the monophyletic group of the Exannulated lineage basal to all *Armillaria* species, but no light emission has been recorded in the closely related genus *Guyanagaster*. Interestingly, the genome of *G. necrorhizus* maintains the luciferase cluster but with a truncated luciferase gene (Sect. 12.3).

12.2.3 *Omphalotus* Lineage

The *Omphalotus* lineage includes the genera *Omphalotus* and *Neonothopanus* (Kirchmair et al. 2004). According to a 2019 review (Oliveira et al. 2019) and Mycobank and Index Fungorum, in addition to *Omphalotus* and *Neonothopanus*, Omphalotaceae includes the other nine genera (*Anthracoephyllum*, *Connopus*, *Gymnopanella*, *Gymnopus*, *Lentinula*, *Marasmiellus*, *Marasmius*, *Mycetinis*, *Pusillomyces*, and *Rhodocollybia*). It has been suspected that all species from the *Omphalotus* lineage form luminescent fruiting bodies but that their mycelia can be either luminescent or non-luminescent. They are known for large mushrooms and *Neonothopanus gardneri* and *N. nambi* were well-characterized by bioluminescent mechanisms (Oliveira et al. 2015) and the relevant enzyme activity (Kotlobay et al. 2018).

Three new species, *Marasmiellus lucidus*, *M. venosus*, and *Pleurotus nitidus*, with bioluminescent fruiting bodies were recently discovered outside the current three major bioluminescent lineages (Terashima et al. 2016). We successfully amplified and sequenced the ITS sequences of *Marasmiellus lucidus* and *M. venosus* (submitted to NCBI; accession pending) and found both of them were part of *Anthracoephyllum* lineage which is sister to the *Omphalotus* lineage (Fig. 12.5). As it stands, *Pleurotus nitidus* remains the only record of bioluminescent fungus in the entire Pleurotaceae family. We speculate it may be misclassified that warrants further investigation as this family often was confused with species belonging in the *Omphalotus* lineage.

12.3 Genes Responsible for Bioluminescence; Luciferase Cluster: Luz and Luciferin Biosynthesis Genes

Green light (~530 nm) emission in fungi was confirmed to be a result of an enzyme-mediated reaction in which a hot extract containing heat-stable substrates (e.g., luciferin) mixed with a cold extract containing enzymes (e.g., luciferase) (Oliveira and Stevani 2009).

Later, one single bioluminescent system shared by all known bioluminescent fungal lineages was validated by detecting bioluminescence from combinations of substrate/enzyme extract from bioluminescent species from four lineages (*Gerronema viridilucens* from Lucentipes lineage, *Armillaria mellea* from *Armillaria* lineage, *Mycena luxaeterna* from Mycenaceae lineage, and *Neonothopanus gardneri* from *Omphalotus* lineage) and comparing them to nonluminescent species (Oliveira et al. 2012). The structure of fungal luciferin and its precursor were identified in 2015 as 3-hydroxyhispidin and hispidin in the bioluminescent *Neonothopanus nambi*, *Mycena citricolor*, *Panellus stipticus*, and *Armillaria borealis* (Purtov et al. 2015). In 2017, the light-emitting process was demonstrated by reporting the structure of the emitter, oxyluciferin, and oxyluciferin is enzymatically hydrolyzed yielding

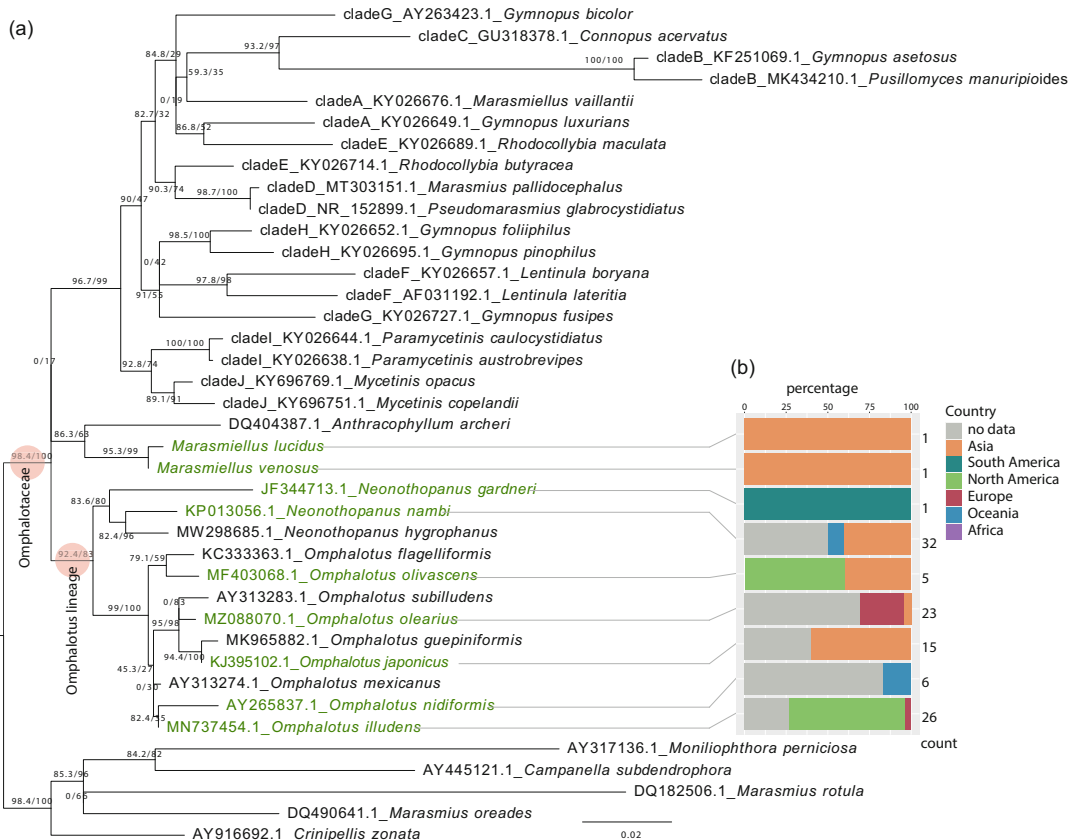


Fig. 12.5 (a), ITS tree of 34 Omphalotaceae sequences with five species of Marasmiaceae as an outgroup. The tree was constructed by IQ-TREE (Nguyen et al. 2015) with an alignment length of 1373 bp and without redundant species downloaded from NCBI. Numbers on each branch denote support values (SH-aLRT support (%) / ultrafast bootstrap support (%)). Nodes with dark green color denote bioluminescent species. Note that the sequences

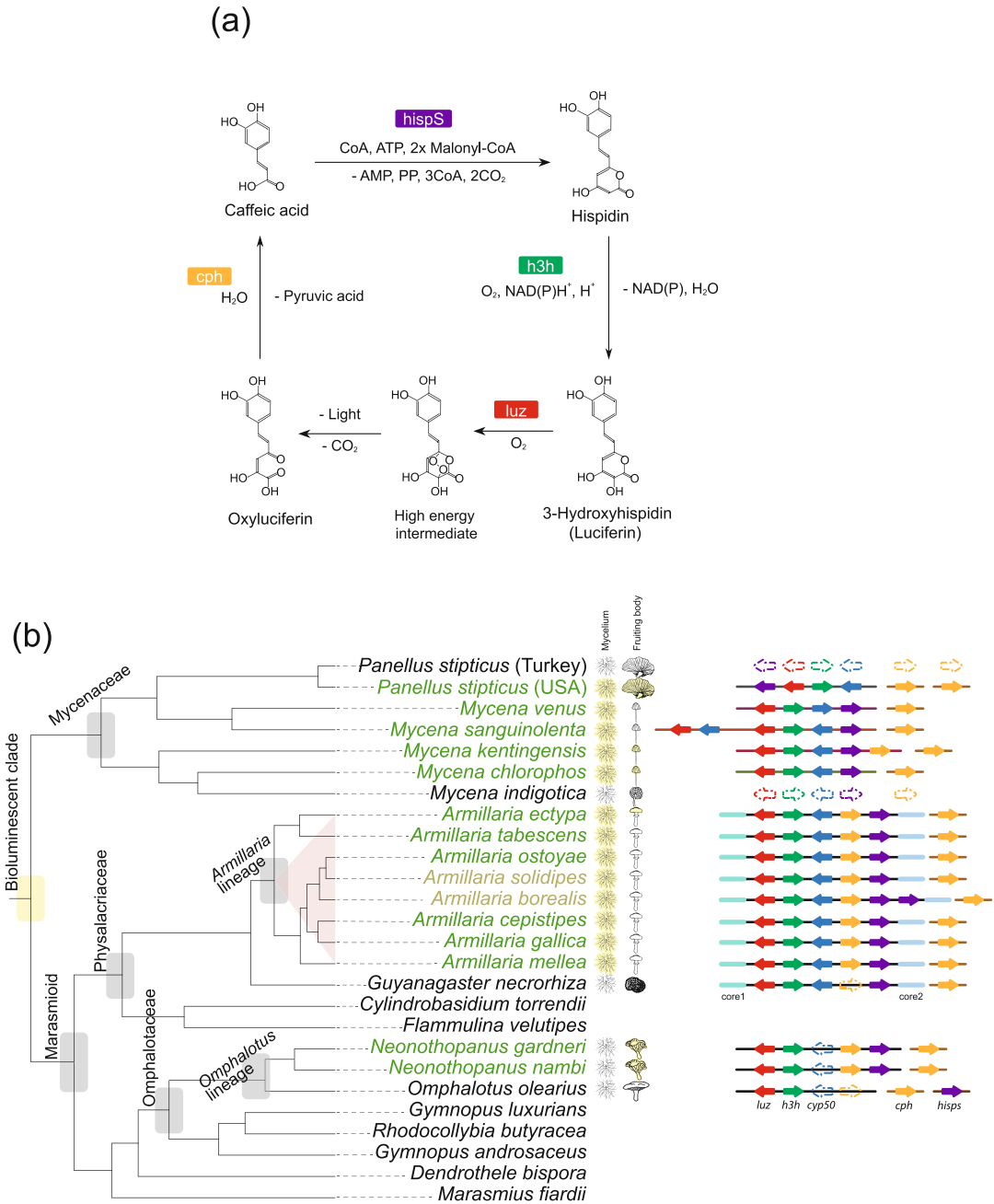
not necessary the same as the holotype, and not all bioluminescent species were listed here since not all of them have been recorded in NCBI. The clade name in the front of species name according to previous review (Oliveira et al. 2019). (b), The geographic distribution of bioluminescent fungi recorded by extracting ITS (Internal transcribed spacer) from NCBI and converting the collected country to six continents

caffeic acid (Kaskova et al. 2017). The biosynthetic cycle was finalized and the four enzymes involved were identified in *N. nambi* (Fig. 12.6a): Hispidin synthase (*hispS*) converts caffeic acid to hispidin; hispidin-3-hydroxylase (*h3h*) hydroxylates hispidin to give 3-hydroxyhispidin, the fungal luciferin; and the oxidation of luciferin by luciferase (*luz*) yields an unstable high-energy intermediate, which emits light while turning into oxyluciferin, a substance that can be recycled to caffeic acid by caffeylpyruvate hydrolase (*cph*) (Kotlobay et al. 2018). The *luz*, *h3h*, and *hispS*

were introduced in yeast *Pichia pastoris* for autoluminescence.

12.4 The Origin of Fungal Bioluminescence

Like other bioluminescent species, the discovery of bioluminescent fungi, with their minor presence and patchy phylogenetic placement in gilled mushrooms, initially suggested they evolved independently multiple times in a convergent manner. However, recent advances in the genome



their orientation. The dashed block arrows denote the loss of a gene. All the species with dark green are bioluminescent species with records in the literature. The species with light green are the species believed to illuminate

sequencing of Agaricales have pointed to an alternative scenario. One study found that the genes responsible for luciferin biosynthetic cycles were physically adjacent in genomes (luciferase cluster; Fig. 12.6b) by comparing genomes from ten bioluminescent fungi and their sister species (Kotlobay et al. 2018). By generating reference genomes of bioluminescent fungal genomes from five Mycenaceae (Ke et al. 2020), eight *Armillaria* lineages, and two *Omphalotus* lineages, we were able to investigate the evolutionary dynamics around the luciferase cluster. Members of the luciferase cluster were clearly homologous across distant bioluminescent fungi, suggesting that bioluminescence was not independently evolved. Both studies concluded that bioluminescence originated from the last common ancestor of the Mycenaceae family and marasmioid clade of Agaricales, although the species trees in these two studies were not congruent. The latter showed that the Schizophyllaceae was the closest lineage with the bioluminescent clade and had a genome encoding a homologous luciferase. Through phylogenetic reconciliation, it was found that the species tree was congruent to the gene trees in the luciferase cluster, suggesting the patchy distribution was a result of a loss of the luciferase cluster in the majority of Agaricales rather than horizontal gene transfer (Ke et al. 2020). However, the origin of these luciferin biosynthetic pathway genes within Schizophyllaceae is still unknown. Our experiment of adding hispidin (luciferin precursor) to *Schizophyllum commune* (unpublished data) showed that it could not be converted to light.

A fungal gene cluster can be differentially maintained due to differences in genome plasticity (Marcet-Houben and Gabaldon 2019). The luciferase cluster was located in different low synteny regions of *Mycena* genomes, which may suggest that they were dispensable and could be lost in most species in the Mycenaceae lineage. In contrast, the luciferase cluster was located in the conserved syntenic region in all eight of the bioluminescent fungal genomes from the *Armillaria* lineage. Ke et al. proposed an evolutionary

scenario that the luciferase cluster was originally located at the dispensable region of the last common ancestor and the cluster was translocated to different genomic locations through rearrangement (Ke et al. 2020). In the *Armillaria* lineage, the luciferase cluster was translocated to the core region and became more conserved.

12.5 Biological Function of Bioluminescent Fungi

The roles of bioluminescence in various organisms have been extensively studied (for review please see (Lau and Oakley 2021)), and often involve mating, luring prey or defense. At the molecular level, negative selection was detected on the luciferase cluster, and it could explain why the luciferase cluster had been maintained across hundreds of millions of years (Ke et al. 2020) suggesting that bioluminescence may play a role in environmental adaptation but in a species-specific way. Several pieces of evidence support different possible hypotheses for the function of bioluminescence. First, several studies proposed that fungal bioluminescence may facilitate spore dispersal by attracting potential vectors. More recently, in the Brazilian forest, a biological circadian control of luminescence was found by measuring the profiles of the luciferase-, reductase-, and luciferin-rich extract from mycelia of *N. gardneri*, as well as insects captured using an artificial mushroom with light similar to the bioluminescence of dark mushrooms (Oliveira et al. 2015). It was proposed that the bioluminescent *N. gardneri* of the *Omphalotus* lineage increased spore dispersal by attracting arthropods in the evening. However, the insects' attraction has not been proven in other bioluminescent species in the same lineage, such as *Omphalotus nidiformis* (Weinstein et al. 2016).

Second, fungal bioluminescence is a by-product of an unknown biological process. This hypothesis has been proposed two decades ago according to the existence of luminous and nonluminous populations of the same species or

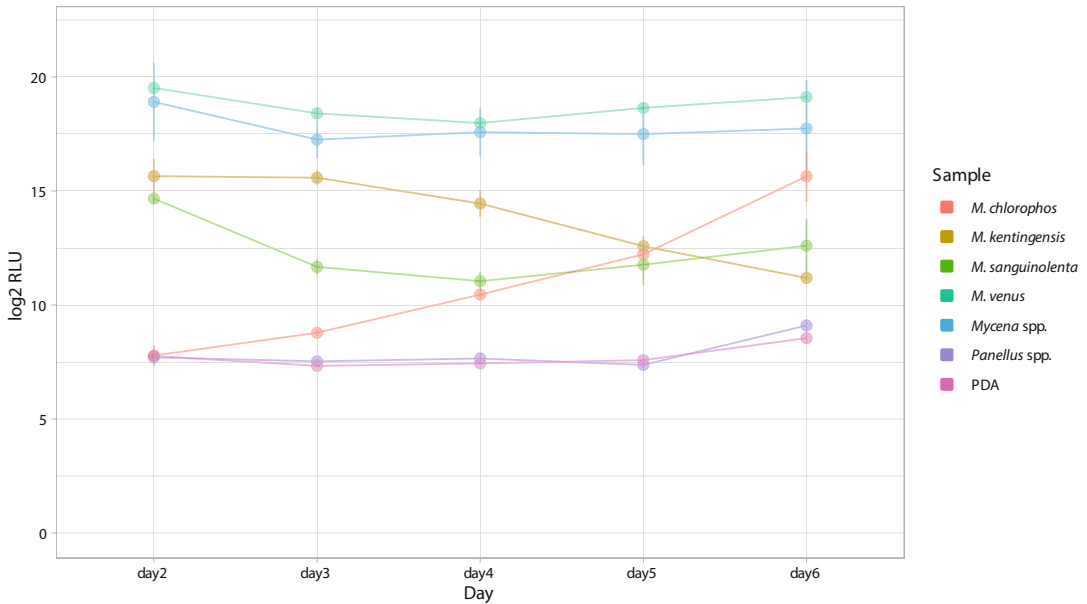


Fig. 12.7 Bioluminescence patterns were measured for 6 days after inoculation of mycelium on potato dextrose agar (PDA). The control was PDA only

the continuous light production in bioluminescent fungi (Herring 1994; Deheyn and Latz 2007). Recent studies revealing the expression of bioluminescence also indicate a biological function. It has been found that the synthesis of luciferin precursors and H3H was inhibited during the *Armillaria* development from mycelium to mushroom (Purtov et al. 2017; Mihail et al. 2018; Puzyr et al. 2017). This suppression resulted in decreased luminescence indicating a possible form of regulation and biological role. There is a divergent intensity in cap, stipe, or mycelium of species of Mycenaceae lineage. Several genes that could be responsible for this regulation were enriched when investigating the differential expression of genes among different stages of *Mycena kentingensis* (Ke et al. 2020). In addition, a diversity of intensities was also found in cultured mycelium among species in the Mycenaceae lineage (Fig. 12.7). Since regulation implies an adaptive function, these observations and analyses provide indirect evidence for a biological role. However, further validation will be necessary to clear up the biological role for each species.

12.6 Conclusions

Bioluminescence in fungi is an intriguing feature restricted to gilled mushrooms that utilizes a single type of biochemical reaction. We have been able to understand the evolution of bioluminescent mushrooms better recently thanks to the accumulated record of which fungi are bioluminescent, molecular studies on luciferin biosynthetic pathways, and genome research. When the first fungal luciferase gene cluster of *Neonothopanus nambi* was identified in 2018, this successfully heterogeneously expressed biosynthetic pathway advanced the further study and application of fungal bioluminescence ((Kotlobay et al. 2018); for a detailed review on potential applications see (Ke and Tsai 2021)). The homologous luciferase found from the genomic sequencing of several bioluminescent fungi and their sister groups allowed us to trace the evolutionary history to a last common ancestor of the Mycenaceae family and the marasmioid clade within Agaricales. Despite a great deal of progress, many important questions still remain. Important goals for future work include

developing a more complete understanding of bioluminescent features, ecological function and its gene regulation.

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