Review

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The Luminous Fungi of Japan

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Review

The Luminous Fungi of Japan

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Abstract: Luminous fungi have long attracted public attention in Japan, from old folklore and fiction to current tourism, children's toys, games and picture books. At present, 25 species of luminous fungi have been discovered in Japan, which correspond to approximately one-fourth of the globally recognized species. This species richness is arguably thanks to the abundant presence of mycophiles looking to find new mushroom species and the tradition of night-time activities, such as firefly watching, in Japan. Bioluminescence, a field of bioscience focused on luminous organisms, has long been studied by many Japanese researchers, including the biochemistry and chemistry of luminous fungi. A Japanese Nobel Prize winner, Osamu Shimomura (1928-2018), has primarily focused on the bioluminescence system of luminous fungi in the latter part of his life, and the total elucidation of the mechanism was finally accomplished by an international research team with representatives from Russia, Brazil, and Japan in 2018. In this review, we focused on multiple aspects related to luminous fungi of Japan, including myth, taxonomy, and modern sciences.

Keywords: bioluminescence; fungi; mushroom; Japan

1. Introduction

The occurrence of dim-glowing mycelia on fallen twigs, which was first recognized as unknown 'shining wood', and luminous mushrooms on rotten trees have fascinated people around the world (Figure 1), and Japan is no exception. The special interest in bioluminescent fungi in Japan is probably related to the richness of fungal diversity, which has led to a love of mushrooms and mushroom consumption in this country. In addition, the tradition of night-time activities can also be a factor.

The climate of mainland Japan (Hokkaido, Honshu, Shikoku, and Kyushu) ranges from subarctic in the northern part to temperate in the southern part; it is typically characterized by a cold winter and humid summer. The peripheral Izu Islands, Bonin Islands (Ogasawara Islands), and Ryukyu Archipelago (including Amami and Okinawa Islands) have subtropical oceanic climates with mild winters and hot humid summers. Because of wide-ranging climates with high humidity and species richness in woods and mountainous areas, Japan has a high biodiversity of fungi. Currently, approximately 13,000 described species of fungi have been reported from Japan, with possibly even more undescribed species [1]. Mycophagy has been popular in Japanese food culture, probably since Japan's Jomon Period (-10th BCE) [2]. Various species of mushrooms have been cultivated and are always available on the market, such as *Lentinula edodes* (*Shii-také*, in Japanese), *Flammulina filiformis* (*Enoki-také*, formerly recognized as *F. velutipes*), *Hypsizygus marmoreus* (*Buna-shimeji*, also known as *H. tessulatus*) and *Pholiota microspora* (*Nameko*), which are indispensable for ordinary Japanese cuisines [2,3]. Many amateur mycologists have been devoted to the understanding of Japanese fungal diversity, and several new mushroom species are found and described every year all across Japan by amateur and professional Japanese mycologists.

Figure 1

Figure 1. Luminous mushroom stamps. (from left to right) *Mycena chlorophos*/West Samoa, 1985; *Mycena manipularis*/Việt Nam, 1996; *Mycena lucentipes*/USA, 2018. There are no luminous mushroom stamps in other countries, including Japan. Yuichi Oba's personal collections.

Since the old days, especially after the Edo Period, when people had more free time to enjoy their lives, there have been Japanese traditions of enjoying nature at night-time, including watching the moon (*Tsukimi*) and fireflies (*Hotaru-gari*), listening to insect calls (*Mushi-kiki*), and night hiking (*Kōchū-tozan*) [4]. Thus, it is not surprising that people accidentally witnessed bioluminescent mushrooms or glowing mycelia in the dark, and sometimes this glowing was thought to be caused by *Yōkai*: creatures, presence, or phenomena that could be described as mysterious or eerie [5]. In Japan, many terrestrial bioluminescent organisms have often been discovered by ordinary people or amateur naturalists based on sporadic observations. Examples of such organisms include the bioluminescent earthworms *Microscolex phosphoreus* [6] and *Pontodrilus litoralis* [7], the millipede *Paraspirobolus lucifugus* [8], the springtail *Lobella* sp. [9], the tiny mushroom *Marasmiellus lucidus* [10], and the scarlet mushroom *Cruentomycena orientalis* [11].

In this paper, we attempt to review bioluminescent mushrooms in Japan and their related topics, such as folklore, taxonomy, and some recent research results on bioluminescent fungi in Japan. For this purpose, we intentionally cite many studies written in Japanese to note hidden achievements from Japan to the world.

2. Folklores

There are many folkloric stories about strange glows around the world [12], including Japan. Some kinds of *Yōkai*, called *Kitsune-bi* (Meaning fox-fire; it is very curious coincidence with European fox-fire that old Japanese called an unknown glow on the ground as fox's fire) and *Mino-bi* (*Mino* is Japanese traditional raincoat made out of rice straw, *bi* is fire or glow, and a folklore about mysterious glow of wet *Mino* was called as *Mino-bi*), are partly considered to be responsible for the luminous mycelia growing on the rotten wood or straw of *Mino* [13,14]. *Mino-bi* was sometimes believed to be the work by foxes [15]. Figure 2 is a masterpiece *Ukiyo-é* woodblock by Hiroshige Utagawa at the end of Japan's Edo Period, showing foxes bearing fire on their mouths under a large Japanese hackberry tree. Of note, Sakyo Kanda (1874-1939), the author of the book "*Shiranui, Hitodama, and Kitsune-bi*" which sheds light on the mysterious luminescence, was a biologist of luminous organisms, and he believed that people mistaking simple lanterns for supernatural phenomena was the primary cause of the Japanese fox-fire phenomena [14].

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Figure 2

Figure 2. Foxfire at Ōji (*Ōji Shōzoku Enoki Ōmisoka no Kitsune-bi*) by Hiroshige Utagawa (recarved edition, original print in 1857). Yuichi Oba's personal collection.

The glowing of old pine trees was known as the mysterious phenomenon of *Hikari-matsu* (luminescent pine tree [16]; originally written in 1765) or *Ryū-tō* (dragon's lantern [17]), and these supernatural phenomena can most likely be explained by the luminescence of *Armillaria*'s mycelia [18]. *Armillaria* are known to be one of the common pathogens that cause wood rot in *Pinus* pine trees (*Armillaria* root rot, *Narataké-byō* in Japanese), which does occur in Japan [19].

Until recently (approximately 50 years ago), people on Hachijo Island (an island located in the Izu Islands) called the glow of the luminous mushrooms in the woods *Hato-no-hi*, meaning the fire of pigeons [20]. On this subtropical island, more than 7 bioluminescent mushroom species are distributed, of which *Mycena lux-coeli* and *Mycena chlorophos* exhibit especially strong glows [21]. The Japanese wood pigeon *Columba janthina* is also distributed in the island woods. Most likely, people made a connection between the unidentifiable glow of luminous mushrooms in the night-time forest and the unsettling night call of the wood pigeon [22,23].

3. The Tale of the Bamboo Cutter

It is believed that luminescence of mycelia appeared as early as in a description by Aristotle (4th BCE) [12,24]. This roughly corresponds to the end of the Jomon Period in Japan, when people in mainland Japan were primarily hunter-gatherers and no written records were available. The first appearance of luminous fungi in Japanese literature was in the ancient tales in Japan's Heian Period (6-12th century).

The Tale of the Bamboo Cutter "*Taketori Monogatari*" was written by an unknown Japanese author in the late 9th or early 10th century and is recognized as the oldest Japanese work of fiction [25,26]. In the first part of this tale, there is an impressive scene in which a man called the Old Bamboo Cutter finds a glowing bamboo in the field.

"*One day he noticed among the bamboos a stalk that glowed at the base*" (translated by Keene, 1998 [25])

When he examines it, he finds a lovely little girl approximately three inches tall, named Shining Princess (*Kaguya-himé* in Japanese). She grows to be an adult, and she refuses several proposals of marriage from noble men, including the Emperor, and finally returns to the moon. As it turns out, she was a princess from the Moon.

What was causing the bamboo to glow? A Japanologist, Katsumi Masuda (1923-2010), hypothesized that the cause of the glowing was the luminous fungus *Panellus pusillus* (*Suzume-také* in Japanese) [27], and a historian, Michihisa Hotate, agreed with that idea [26]. This species also grows on the rotten culm (ringed stem) of Japanese bamboo [28,29]. The distribution records of *P. pusillus* were mainly in the southern part of Japan; Bonin Isls., Matsuyama (Ehime Prefecture) [28], Hachijo Isl. [22,30] but also in the central Japan [28]. Shidei reported the growth of *P. pusillus* on bamboo in Kyoto [29]. As the story is probably set in Kyoto, and at that time, many bamboo craftworkers originating from the southern Kyushu region worked there [26], it can be speculated that the author of the tale had learned of the phenomenon of bamboo glowing from the craftworkers' experiences, inspiring the famous opening scene [27]. *Mycena chlorophos* (*Yakō-také* in Japanese) is another candidate; it is distributed mainly in the southern islands, such as Hachijo Isl. and Bonin Isls. [30,31], but is also found in various localities in mainland Japan (Honshu Kanto west to Kyushu, incl. Kyoto) [31,32], and it sometimes grows on bamboo. Of course, we do not exclude the possibility of the glow being caused by luminous mycelia of unknown identity on rotten bamboo [14] (Figure 3) or nonfungal organisms, such as the princess firefly *Luciola parvula* (*Himé-botaru*), which sometimes appears in bamboo groves [33,34].

Figure 3

Figure 3. Mycelia of *Mycena stellaris* growing on bamboo. Photo by Yoshinori Nishino at Ishigaki Isl., Okinawa Prefecture.

4. Current commercialization

Currently, the luminescence phenomena of mushrooms are familiar to many people in Japan. For example, there are the characters of the Pokémon Card Game (a card game that appeared in Japan in 1996 and is now a worldwide phenomenon) (Figure 4), capsule toys (small toys in vending machines packaged in a plastic capsule) (Figure 5), and picture books that focus on luminous mushrooms [22,35,36] (Figure 6). TV programs featuring mushrooms often include the topics of luminescence of some mushroom species. Artificial cultivation methods of *M. chlorophos* have been established [37,38], and the species has been used for special exhibitions in several local museums and botanical gardens (e.g., Hachijo Visitor Center, Tokyo; Yumenoshima Tropical Greenhouse Dome, Tokyo; Nagoya City Science Museum, Aichi). The culture kit is available online [39]. Night-time hiking ecotours to watch glowing *M. chlorophos* are one of the most economically significant tour activities in Hachijo Isl. and Bonin Isls [22,40] and trips to watch glowing *M. lux-coeli* have occasionally been held at various localities in southern Japan, such as the Amami Islands (Kagoshima Prefecture), Mt. Yokokura (Kochi Prefecture), and Ukui Peninsula (Wakayama Prefecture).

Figure 4

Figure 4. Pokémon cards. English names (from left to right), Morelull (basic), Shinotic (stage 1), Glimwood Tangle (stadium), produced by The Pokémon Company. Yuichi Oba's personal collections.

Figure 5

Figure 5. Capsule toy "luminous mushroom magnet" (2015-), produced by Ikimon Co. Diameter of the model of *Mycena chlorophos* (center) is approximately 30 mm, which is close in size to the largest specimens found in the wild.

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Figure 6

Figure 6. Picture books of luminous mushrooms. (From left to right) Nishino & Oba, 2013; Oba & Miyatake, 2015; Miyatake, 2023.

5. Taxonomy

5.1. Bioluminescent species in Japan

In Japan, scientific surveys of fungi started around the 18th century when Japanese scholars were emancipated from the Chinese herbalism *Honzō-gaku* and began genuine native studies on Japanese flora. For example, a Japanese herbalism scholar Tomohiro Ichioka (1739-1808) compiled a monograph of local fungi, "*Shin-you Kinpu,"* in 1799 and mentioned (probably) *Omphalotus japonicus* as *Kumahira* with illustration and remarks "luminescence at night and poisonous." Another Japanese herbalism scholar, Konen Sakamoto (1800-1853), compiled a monograph of the Japanese fungi "*Kinpu,"* in 1835 and described *O. japonicus* as "*Tsukiyo-také*" with illustration and remarks "this mushroom is called *Tsukiyo-také* because of luminescence at night". Though based on pre-Linnean classification, they probably are the earliest scientific references about the bioluminescent mushroom in Japan. However, other luminous species were not described until the 20th century. This is partially because of the climate diversity of Japan. Mainland Japan, where most Japanese people including scholars are located, is characterized by a subarctic to temperate climate, while many luminous mushroom species, especially of the *Mycena* group, are distributed in tropical and subtropical regions. In other words, *O. japonicus* is the one and only bioluminescent mushroom species commonly (frequently) observed in Japan.

Indeed, *O. japonicus* is the first luminous mushroom species described scientifically under the Linnean system, that was in 1915 by a mycologist, Seiichi Kawamura (1881-1946) [41]. The second piece of scientific evidence of luminescent fungi from Japan was reported by Yosio Kobayasi (1907-1993), who reported the luminescence of four known (currently three) species: *Favolaschia peziziformis, Panellus pusillus, Mycena chlorophos* (from Bonin Isl.), and *Mycena cyanophos* (= *M. chlorophos*) (Bonin Isl., also from Hachijo Isl.) [42].

Before and during the Second World War, a Japanese researcher of bioluminescent organisms, Yata Haneda (1907-1995), extensively surveyed luminous mushrooms when he stayed at Palao Tropical Biological Station in Palau as a researcher under the mandate of Japan (during 1937-1942) and as Army Civil Administrator of Shonan Museum (the present National Museum of Singapore) in Singapore (during 1942-1945). After the Second World War, he returned to Japan and continued his luminous-mushroom survey at Hachijo Island, Japan, and described several luminous mushrooms from Japan with assistance by the British mycologist/botanist Edred John Henry Corner (1906-1996) [43]. Of note, at the end of the Second World War, Corner was a captive prisoner of Japan.

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Thus, the official relationship between Haneda and Corner was that of enemies, but they struck a scientific friendship during and after the war [44]. Although many of these species names described by Haneda and Corner were invalidly published, which unfortunately caused taxonomic confusion [45,46], their contributions paved the way for understanding the diversity of luminous mushrooms in Japan after the Second World War; *Mycena lux-coeli* (*Shiino-tomoshibi-také*) was collected by Haneda on Hachijo Island and described by Corner, and the species name remains valid.

Even recently, many new localities of luminescence mushroom species have been recorded, and Terashima and her colleagues described 8 new luminescent species from southwestern Japan in their book [47]. Currently, approximately 100 species of luminous fungi have been recognized [48,49], of which 25 species are distributed in Japan [22,46,47].

In this section, all luminescent fungal species recognized in Japan are listed with remarks. Species that were "excluded, doubtful or insufficiently known" [46] were not included. Of note, *Nothopanus noctilucens* is sometimes listed as a luminescent species distributed in Japan [46]. However, the Japanese *Pleurotus noctilucens* (= *Nothopanus noctilicens*) *sensu* Inoko is an invalid name [50], and the true *Pleurotus noctilucens* Lév. (Syn. *Nothopanus noctilucens*) has not been reported in Japan [51]. *Mycena illuminans* has been reported as a luminescent species distributed in Japan [46]. However, this species is often considered a synonym of *M. chlorophos* [52] and thus is not included in the following list. The Japanese names were adopted from the list by Katumoto, 2010 [53], unless they have a more recent name.

Family Mycenaceae

Cruentomycena orientalis Har. Takah. & Taneyama

Japanese name: *Gahnetto-ochiba-také* [47]

Remarks: 'Gahnetto' means garnet in Japanese. This species was described from Ishigaki Island, southern Japan [47]. The luminescence of the mycelium and fruitbody of this species and other similar species collected in Fukuoka, Miyazaki, and Miyagi Prefectures was reported [11,54,55]. The luminescence of the fruitbody was weak compared to that of the mycelium and detected only by a long-exposure CCD camera.

Dictyopanus foliicola Kobayasi

Japanese name: *Konoha-suzume-také* [53]

Remarks: The Japanese *konoha* and *suzume* mean leaf and sparrow, respectively ("sparrow" represents a small creature in Japanese [56]). Mycelia and fruitbodies are luminous. This species has not been officially reported since the original description by Kobayasi from Miyazaki Prefecture [57]. The taxonomic status of this species warrants further study.

Favolaschia peziziformis (Berk. & M. A. Curtis) Kuntze (Figure 7)

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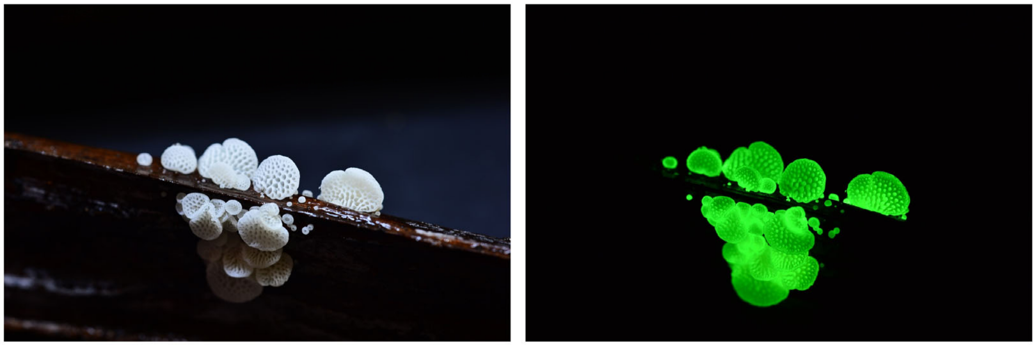

Figure 7

Figure 7. Fruitbody of *Favolaschia peziziformis.* Photo by So Yamashita at Hachijo Island, Tokyo.

Japanese name: *Enashi-rasshi-také* [53]

Remarks: This species was originally described from the Bonin Islands but is also known from Hachijo Island, Okinawa and other countries in Australasia [58]. Whole fruitbodies are reported to be bioluminescent. *Enashi* means the lack of a stipe. *Rasshi* derives from the genus name *Laschia* in honor of German mycologist Wilhelm Gottfried Lasch (1787-1863) [56].

Mycena chlorophos (Berk. & M. A. Curtis) Sacc. (Figure 8)

Figure 8

Figure 8. Fruitbody of *Mycena chlorophos*. Photo by So Yamashita at Hachijo Island, Tokyo.

Japanese name: *Yakō-také* [53]

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Remarks: The Japanese *Yakō-také* means 'night-illuminating mushroom'. This species is distributed in Honshu (probably from Aomori, the northernmost prefecture [59]), Shikoku, Kyushu, Izu Islands, and Bonin Islands [60]. In addition, the species is widely recorded from the Southern Pacific islands, e.g., Polynesia and Micronesia [60]. This species is listed in the Japanese Red Data as endangered in Fukushima, Chiba, and Miyazaki Prefectures [61]. Bioluminescence of the fruitbody is considered brighter than many other known luminous mushrooms, but some strains, such as a strain in Miyazaki and Aomori Prefectures, seem darker compared to those in Hachijo and Bonin Islands [10,36]. The draft genome sequence of this species (Hachijo Isl. strain) has been assembled [62]. We consider *Mycena cyanophos* (Berk. & M.A. Curtis) Sacc. to be a synonym.

Mycena daisyogunensis Kobayasi

Japanese name: *Hyūga-yakō-také* [53]

Remarks: This species was collected from Daisyogun Cave in Miyazaki Prefecture in Kyushu (*Hyūga* is an old name of Miyazaki Prefecture) [57], but no further collections have been made since the original description. The taxonomic status of this species warrants further study.

Mycena flammifera Har. Takah. & Taneyama

Japanese name: *Mori-no-ayashi-bi* [47]

Remarks: The Japanese *Morino-ayashi-bi* means 'forest ghost-fire'. This species was described from Ishigaki Island, southern Japan [47]. The morphological differences from the better-known bioluminescent species, *M. manipularis* (Berk.) Sacc. are subtle, and the taxonomic status of this species warrants further study.

Mycena lazulina Har. Takah., Taneyama, Terashima & Oba (Figure 9)

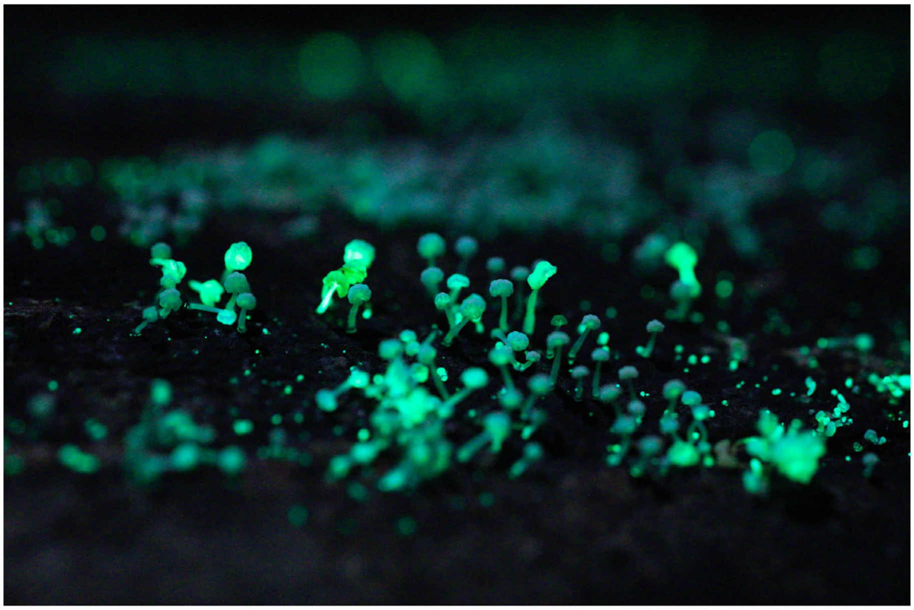

Figure 9

Figure 9. Fruitbody of *Mycena lazulina*. Photo by Yoshinori Nishino at Iriomote Island, Okinawa Prefecture.

Japanese name: *Konruri-kyūban-také* [47]

Remarks: The Japanese *Konruri-kyūban-také* means 'ultramarine-colored sucker mushroom' because of the presence of vivid blue (*Konruri*) disk-like (*Kyūban*) base. This species was described from the Yaeyama Islands, southern Japan [47]. Although its morphological characteristics seem to

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indicate that it belongs to the genus *Mycena*, the phylogenetic tree presented by Terashima et al. [47] has a very long branch leading to this species. The quality of DNA sequence data warrants further investigation.

Mycena lux-coeli Corner (Figure 10)

Figure 10

Figure 10. Fruitbody of *Mycena lux-coeli*. Photo by So Yamashita at Hachijo Island, Tokyo.

Japanese name: Shiino-tomoshibi-také, Hachijo-yakō-také [53]

Remarks: The Japanese *Shiino-tomoshibi-také* means '*Castanopsis* tree's lantern mushroom'. This species was originally described from Hachijo Island, but it is currently known from wider areas of central to southern Japan, mostly along the Pacific Ocean [58]. This species is listed in the Red Data as endangered in Mie Prefecture and as vulnerable in Miyazaki Prefecture [61].

Mycena luxfoliata Har. Takah., Taneyama & Terashima

Japanese name: *Kareha-yakō-také* [47]

Remarks: This species was described from Ishigaki and Iriomote Islands, southern Japan [47]. Its bioluminescence was observed from mycelia on fallen leaves (*Kareha* means fallen leaves).

Mycena manipularis (Berk.) Sacc. (Figure 11)

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Figure 11

Figure 11. Fruitbody of *Mycena manipularis*. Photo by Yoshinori Nishino at Ishigaki Island, Okinawa Prefecture.

Syn. Filoboletus manipularis (Berk.) Singer, Polyporus hanedai Kawam.

Japanese name: *Ami-hikari-také* [53]

Remarks: The Japanese *Ami-hikari-také* means 'reticulated luminous mushroom'. This species is known from central to southern Japan and has also been recorded in many other countries, including Indonesia and Australia [58]. It is listed in the Red Data as endangered in Chiba Prefecture and as near threatened in Miyazaki Prefecture [61]. The unique feature of this species is that its stems, rather than caps, are brightly luminous (Figure 12). The bioluminescent property seems erratic; it has been reported for the strain in Okinawa Island that non-luminescent and weak-luminescent fruitbodies sometimes appeared when cultivated in the laboratory [63]. Bioluminescence of the local strain in Miyazaki Prefecture seemed weaker [10]. Currently, the species is often called *Filoboletus manipularis* (Berk.) Singer.

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Figure 12

Figure 12. Fruitbody of *Mycena stellaris*. Photo by Yoshinori Nishino at Kunigami, Okinawa Isl., Okinawa Prefecture.

Mycena pseudostylobates Kobayasi

Japanese name: *Kyūbantaké-modoki* [53]

Remarks: The Japanese *Kyūbantaké-modoki* means 'pseudo sucker-mushroom'. This species was recorded from Miyazaki Prefecture, but no definitive collections have been made since the original description by Kobayasi, 1951 [57]. The taxonomic status of this species warrants further study. The mycelium is bioluminescent, but the luminosity of the fruitbody is unknown [57].

Mycena stellaris Har. Takah., Taneyama & A. Hadano (Figure 12)

Japanese name: *Hoshino-hikari-také* [47]

Remarks: The Japanese *Hoshino-hikari-také* means 'starlight mushroom'. This species was described from Ishigaki and Okinawa Islands, southern Japan [47]. The bioluminescence of the whole fruitbodies was recorded.

Panellus pusillus (Pers. ex Lév.) Burds. & O. K. Mill. (Figure 13)

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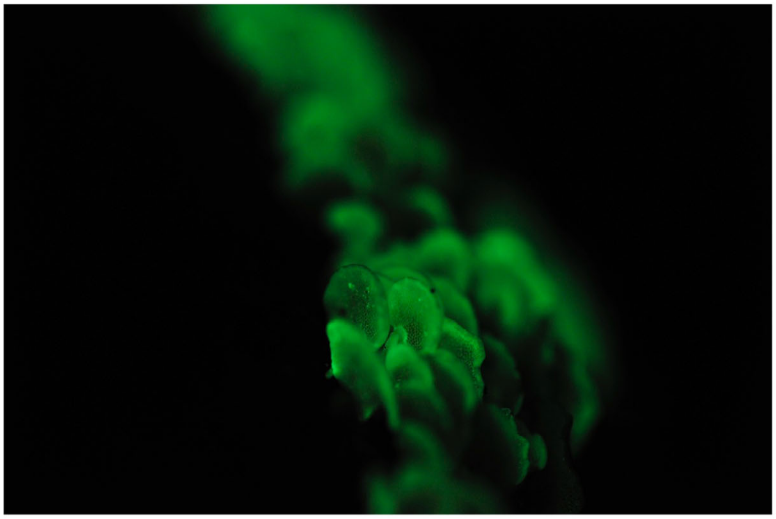

Figure 13

Figure 13. Fruitbody of *Panellus pusillus.* Photo by So Yamashita at Hachijo Island, Tokyo.

Japanese name: Suzume-také, Hinano-uchiwa [53]

Syn. *Panellus gloeocystidiatus* (Corner) Corner (Japanese name, *Suzume-také-modoki* [53])

Remarks: The Japanese name *Hinano-uchiwa* means 'princess fan'. This species is known from central to southern Japan but is also widely reported from North and South America and Australasia [58,60]. It often grows on bamboo.

Resiomycena fulgens Har. Takah., Taneyama & Oba (Figure 14)

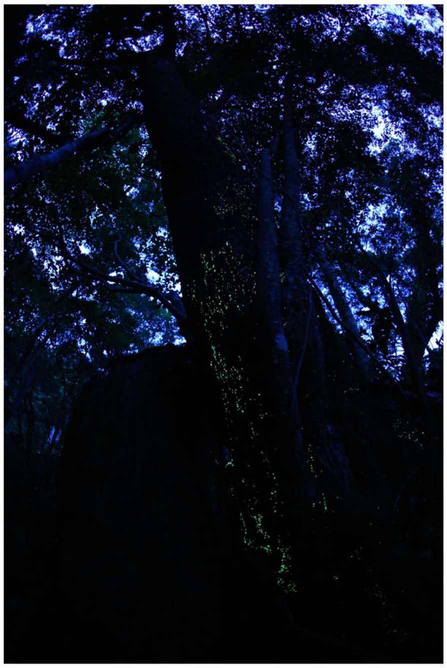

Figure 14

Figure 14. Fruitbody of *Resiomycena fulgens.* Photo by Takehito Miyatake at Hachijo Island, Tokyo.

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Japanese name: *Ginga-také* [47]

Remarks: This species is known from Yaku Isl. (Kagoshima Prefecture), Hachijo Isl., and Kochi Prefecture [47]. The fruitbodies are small (up to ca. 3 mm), but they often grow in large numbers on the standing timber of *Castanopsis*, visually evoking an image of the Milky Way (*Ginga* means the Galaxy or Milky Way). Whole fruitbodies were reported to be bioluminescent [47].

Roridomyces sp.

Japanese name: *Aya-hikari-také*

Remarks: Its taxonomic status has not been thoroughly studied, but it presumably represents a new species of the genus based on several morphological characteristics. Bioluminescence of Japanese samples (spores) was reported by Kurogi, 2015 [10]. The Japanese name *Aya* is derived from the fact that the species was discovered from Aya, Miyazaki Prefecture [10]. This species is listed in Red Data as endangered in Miyazaki Prefecture [61].

Family Omphalotaceae

Marasmiellus lucidus Har. Takah., Taneyama & S. Kurogi

Japanese name: *Himé-hotaru-také* [47]

Remarks: *Hotaru* means firefly in Japanese. This species was discovered in Miyazaki Prefecture [47] during a survey of the *Himé-botaru* firefly (*L. parvula*) [10]. The whole fruitbodies were reported to be bioluminescent.

Marasmiellus venosus Har. Takah., Taneyama & A. Hadano

Japanese name: *Himé-hikari-také* [47]

Remarks: The Japanese *Himé-hikari-také* means 'princess luminous mushroom'. This species was described from Oita Prefecture in Kyushu [47]. Whole fruitbodies and mycelia are both reported to be bioluminescent. This and the previous species belong to the genus *Marasmiellus,* but their taxonomic treatment warrants further investigation. Currently, no other species are known to be bioluminescent in the genus *Marasmiellus,* and their accurate phylogenetic relationship to other bioluminescent species will give important insight into the evolution of bioluminescence in fungi.

Omphalotus japonicus (Kawam.) Kirchm. & O. K. Mill. (Figure 15)

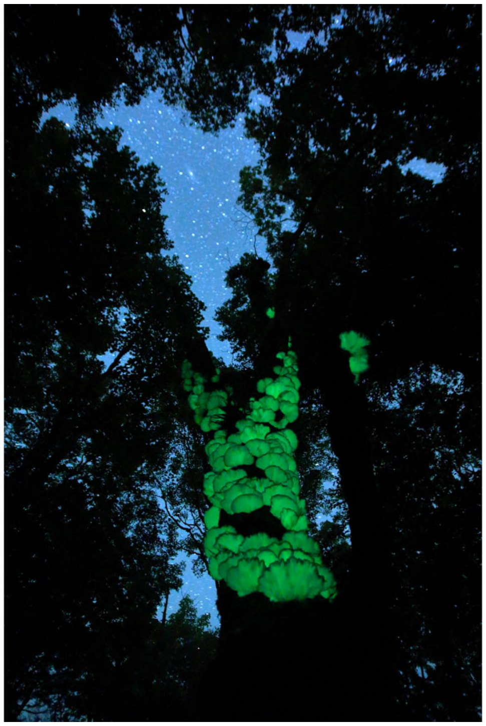

Figure 15

Figure 15. Fruitbody of *Omphalotus japonicus*. Photo by Yoshinori Nishino at Mt. Odaigahara, Nara Prefecture.

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Syn. Lampteromyces japonicus (Kawam.) Sing.

Japanese name: Tsukiyo-také (old name: Watari, Bunano-kataha, Kumahira, Hikari-goke, Hotaru-také) [53].

Remarks: The Japanese *Tsukiyo-také* means 'moonlit-night mushroom' (the suffix '*-také*' means mushroom). This species is distributed widely in mainland Japan and is thus arguably one of the most well-known bioluminescent mushrooms in Japan. An anecdote in the mid-Edo Period (ca. 1800s), "*Zoku Sanshū Kidan*" introduced a story called "*Nanao Kōrin*" where there was a bright luminescent mushroom, called *Yamiyo-také* meaning black-night mushroom, in Nanao (current Nanao City in Ishikawa Prefecture); it claimed that the luminescence was strong enough to illuminate 1 m square by holding 2-3 pieces, "like noon" [64].

Of course, this story most likely contains some hearsay exaggeration (the true luminescence of *O. japonicus* is such as "the fungi of different sizes could be easily recognized at a distance of thirty meters" in pitch dark, and of course not like noon, [41]), but this mushroom could possibly be *O. japonicus* because the story also introduces its gastrointestinal toxicity for humans, which is a characteristic property of this species [65]. The poisonousness of this species is well recognized in Japan because the fruitbody is similar to several Japanese edible species, including *Pleurotus ostreatus* (*Hira-také*, in Japanese), *Pleurotus pulmonarius* (*Usu-hirataké*), *Lentinula edodes* (*Shii-také*), and *Sarcomyxa edulis* (*Muki-také*), such that it is often consumed mistakenly [40,66]. In the 12th century tale "*Konjaku Monogatarishū*", there is a story where a priest in Nara planned to kill his old supervisor to obtain the supervisor's position by serving cooked *O. japonicus* (old Japanese name, *Watari*) under the guise of the edible mushroom *P. ostreatus*. Eventually, the old supervisor ate all of the mushroom dishes and said, "For years, this old priest has never had such deliciously cooked *watari*"; the old supervisor knew all along, but he was of a special constitution such that he never got affected by the toxin [67].

Currently, Japan experiences approximately 30 cases of mushroom poisoning annually, and the cases of *O. japonicus* are among the highest every year, accounting for approximately 50% of the cases [68]. The primary toxic substance was isolated and identified as illudin S (lampterol) by two Japanese organic chemists, Koji Nakanishi (1925-2019) and Takeshi Matsumoto (1923-2014) [69,70]. The major symptoms of the toxin are vomiting, diarrhea, and stomach ache. In one case, curiously, "They felt dizzy and everything around them appeared blue to their eyes. Moreover, they experienced a feeling as if a number of fire-flies were flying around them" [41]. The draft genome sequence of this species (Korean cultivar) was assembled, and bioluminescence-related genes were identified [71]. Haneda reported weak luminescence of the spore mass on moist paper based on specimens collected from Akita Prefecture [30]. This species has an essential role in beech log decomposition in cool temperate forest floors in Japan [72], and because of the recent decline in natural beech forests, it is listed in some prefectural Red Data as a threatened species (e.g., Mie, Osaka and Shimane Prefectures) [61]. *Tsukiyo-také* is one of the seasonal terms of the Japanese short poetry *Haiku* for mid-autumn [73].

Wolves wander along/mountain trails, their ways lit by/moonlit-night mushrooms

Kansuke Naka (1885-1965, a Japanese novelist, essayist, and poet) (translated by Nathaniel Guy [3], and his personal communication)

Family Physalacriaceae (Figure 16)

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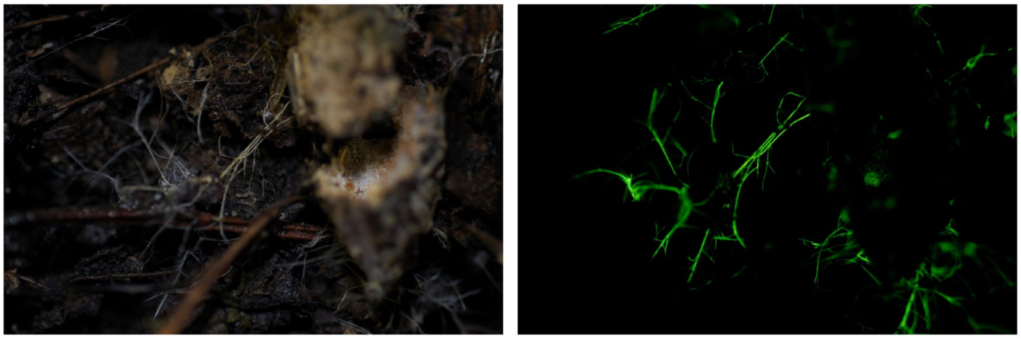

Figure 16

Figure 16. Rhizomorphs of *Armillaria* sp. Photo by So Yamashita at Hachijo Island, Tokyo.

Armillaria cepistipes Velen.

Japanese name: *Kuroge-naratаké* [53]

Remarks: Bioluminescence of Japanese samples (mycelium) was reported by Hiroi, 2006 [18]. Japanese *Kuroge* means black hair.

Armillaria gallica Marxmuller & Romagn.

Japanese name: Yawa-naratаké or Watage-naratаké [53]

Remarks: Bioluminescence of Japanese samples (mycelium) was reported by Hiroi, 2006 [18]. Luminescence of the rhizomorphs has been reported elsewhere [74] but not from the Japanese samples. The fruitbodies of several *Armillaria* species, including *A. gallica* and *A. mellea*, are popular in Japan as a tasty edible mushroom species [60]. Japanese *Naratаké* means 'oak mushroom', although *Armillaria* species also grow on other various trees. *Watage* means fluff because the veil of this mushroom is covered by a fluff-like structure [21]. *Yawa* means soft.

Armillaria mellea (Vahl) P. Kumm.

Japanese name: Naratаké or Harigane-také or Kuri-také [53]

Remarks: Bioluminescence of Japanese samples (mycelium), which are sometimes called *Armillaria mellea* subsp. *nipponica* J.Y. Cha & Igarashi, were reported by Hiroi, 2006 [18]. Luminescence of young rhizomorphs is also reported [60]. Japanese *Harigane* and *Kuri* mean wire and chestnut tree, respectively.

Armillaria nabsnona T. J. Volk & Burds.

Japanese name: *Yachi-naratаké* [53]

Remarks: Bioluminescence of Japanese samples (mycelium) was reported by Hiroi, 2006 [18]. Japanese *Yachi* means marsh land because this species appears in marsh areas [66].

Armillaria ostoyae (Romagn.) Herink

Japanese name: Oni-naratаké or Tsuba-naratаké [53]

Remarks: Bioluminescence of Japanese samples (mycelium) was reported by Hiroi, 2006 [18]. Japanese *Oni* and *Tsuba* mean a *Yōkai* ogre and mushroom ring (annulus) [56]. The mushroom possesses an obvious veil. Rough scales on the cap evoke the image of violent *Oni* [21].

Armillaria sp.

Japanese name: *Kitsubu-naratаké* [75]

Remarks: Its taxonomic status has not been thoroughly studied, but it presumably represents a new species of the genus based on several morphological characteristics. Bioluminescence of Japanese

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samples (mycelium) was reported by Hiroi, 2006 [18]. In Japanese, *kitsubu* means yellow dots, referring to this characteristic of its the cap surface.

Desarmillaria tabescens (Scop.) R. A. Koch & Aime

Syn. Armillaria tabescens (Scop.) Emel

Japanese name: *Narataké-modoki* [53]

Remarks: Luminescence intensities of the fruitbody measured by chemiluminescence detector largely depend on the specimens, but even in the most luminescent specimen, the light was too weak to be observed by human eyes [18,76]. Luminescent intensities of the mycelia also vary, but some could be clearly observed by human eyes [18,76]. The luminescence intensities are correlated with the strains of fruitbody and mycelium, suggesting that the luminescence characteristics are hereditary [18,76]. The species has long been known as *Armillaria tabescens* but was recently transferred to a newly established genus *Desarmillaria* [77]. Japanese *-modoki* means pseudo, because this mushroom is similar to that of *Narataké* (*A. mellea*), but it possesses no veil [21]. This mushroom is regarded as edible but can cause gastrointestinal disorders when consumed in large quantities [10].

Family Pleurotaceae

Pleurotus nitidus Har. Takah. & Taneyama (Figure 17)

Figure 17

Figure 17. *Pleurotus nitidus.* Photo by Yoshinori Nishino at Ishigaki Island, Okinawa Prefecture.

Japanese name: *Shiro-hikari-také* [47]

Remarks: The Japanese *Shiro-hikari-také* means 'white luminescent mushroom'. This species was described from Ishigaki and Iriomote Islands, southern Japan, as new [47]. However, it probably needs to be transferred to other genera containing bioluminescent species, such as *Neonothopanus* or *Nothopanus,* based on its morphological characteristics. Currently, no bioluminescent species are known from the genus *Pleurotus* and closely related genera. The only exception can be seen in *Pleurotus eugrammus* [46], but it is now treated as *Nothopanus eugrammus*, a species more closely related to *Omphalotus* and only distantly related to *Pleurotus* [78].

5.2. Nonbioluminescent species based on samples collected from Japan

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Panellus stipticus (Bull.) P. Karst.

Japanese name: Wasabi-také or Himé-kawaki-také [53]

Remarks: The Japanese name is *Wasabi-také* because of the strong pungent taste of the fruitbody, similar to 'wasabi', a spicy green paste served with sushi [31,60]. It is widely distributed in the world [58,60]. The North American population of this species is luminescent, but the European and Japanese strains are nonluminescent. The North American and European strains have interfertility, and luminosity was dominant over nonluminosity [79]. The samples from Turkey (nonbioluminescent) lacked the genes related to bioluminescence (luciferase, hispidin-3-hydroxylase, and hispidin synthetase) in the genome [80]. Fruitbodies are frequently attacked by slugs, which may be important agents in the dispersal of their spores [81], but their involvement in bioluminescence for the attraction of dispersers is unknown (see Section 7). Japanese *Kawaki-* means 'dried-'.

5.3. Potentially bioluminescent species in Japan

There are several fungal species that have been reported to be bioluminescent elsewhere but not in Japan. Some (probably most) of these species are bioluminescent at least in mycelial stages. According to Desjardin et al., "mycelium of most (if not all) *Armillaria* species is luminescent" [46], thus the *Armillaria* species, in which bioluminescence has not been reported in Japan, might also be bioluminescent; for example, *A. jezoensis* Cha & Igarashi (Japanese name, *Kobari-naratak*é [53]), *A. singula* J. Y. Cha & Igarashi (*Hitori-naratak*é [53]) and *A. tympanitica* (Berk. & M. A. Curtis) Sacc. (no Japanese name. collected once from Bonin Isl. [82], but Ito suggested its species identification doubtful [83]). Since bioluminescence of *Gerronema viridilucens* mycelia and fruitbodies has recently been reported from Brazil [84], the congeneric species recorded from Japan (such as *G. holochlorum* and *G. nemorale*) may also be bioluminescent. Table 2 summarizes the species reported to be bioluminescent elsewhere but not in Japan.

Table 2. Potentially bioluminescent species in Japan.

Taxon	**Japanese name** (*1)	**Bioluminescence (references)** (*3)
Family Mycenaceae		
Mycena epipterygia (Scop.) S.F. Gray	*Nameashi-také*	Mycelium (Bothe, 1931 [85]; Wassink, 1978 [74], 1979 [45]; Desjardin et al., 2008 [46])
Mycena galopus (Pers.) P. Kumm.	*Nise-chishio-také*	Mycelium (Bothe, 1931 [85]; Berliner, 1961 [86]; Wassink, 1978 [74], 1979 [45]; Treu & Agerer, 1990 [87]; Desjardin et al., 2008 [46])
Mycena haematopus (Pers.) P. Kumm.	*Chishio-také*	Mycelium (Treu & Agerer, 1990 [87]; Bermudes et al., 1992 [88]; Desjardin et al., 2008 [46]): Basidiomes (weak) (Bermudes et al., 1992 [88]; Desjardin et al., 2008 [46])
Mycena inclinata (Fr.) Quél.	*Sembon-ashinaga-také*	Mycelium (Wassink, 1978 [74], 1979 [45]; Desjardin et al., 2008 [46])
Mycena olivaceomarginata (Massee) Massee	*Fuchidori-kunugitaké* (*3)	Mycelium (Wassink, 1978 [74], 1979 [45]; Desjardin et al., 2008 [46])
Mycena pura (Pers.) P. Kumm. (*4)	*Sakura-také*	Mycelium (Treu & Agerer, 1990 [87]; Desjardin et al., 2008 [46]): gill of basidiome (Bothe, 1931 [85]; Wassink, 1978(?) [74], 1979(?) [45])
Mycena rosea (Bull.) Gramberg	*Sakurairo-také* [66]	Mycelium (Treu & Agerer, 1990 [87]; Desjardin et al., 2008 [46])
Mycena sanguinolenta (Alb. & Schwein.) P. Kumm.	*Himé-chishio-také*	Mycelium (Bothe, 1931 [85]; Wassink, 1978 [74], 1979 [45]; Desjardin et al., 2008 [46])
Mycena stylobates (Pers.) P. Kumm.	*Kyūban-také*	Mycelium (Bothe, 1931 [85]; Wassink, 1978 [74], 1979 [45]; Desjardin et al., 2008 [46])
Roridomyces roridus (Fr.) Rexer	*Nunawa-také*	Mycelium (Josserand, 1953 [89]; Wassink, 1978(?) [74], 1979(?) [45]; Desjardin et al., 2008 [46])
Family Physalacriaceae		

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Armillaria fuscipes Petch (*5)	*Ashiguro-narataké* [90]	Mycelium (Wassink, 1978 [74], 1979 [45]; Berliner, 1961 [86]; Desjardin et al., 2008 [46]): Rhizomorph (Wassink, 1978 [74])
Armillaria sinapina Berube & Dessur.	*Hotei-narataké*	Mycelium (Mihail, 2015 [91])
Desarmillaria ectypa (Fr.) R.A. Koch & Aime	*Yachihiro-hidataké*	Mycelium, rhizomorph, basidiomes (Ainsworth, 2004 [92])

*1. The Japanese names were adopted from the list by Katumoto, 2010 [53], unless they have a more recent name. *2. Question marks represent the references showing that luminescence is doubtful or worth further investigation. Wassink (1948) [93] was not referenced in this list because his recent review papers [45,74] are considered updated versions of it. *3. Hongo (1989) [94] suggested that *Mycena neoavenacea* may be the same species as *Mycena olivaceomarginata*. *4. Molecular analysis suggests that the current *M. pura* morphospecies represent the species complex [95], and the bioluminescent ability of each phylospecies is unknown. *5. The morphological characteristics of this mushroom (named *Ashiguro-narataké* in Japanese, from Amami-Oshima) appeared indistinguishable from those of *A. fuscipes*, but the species name was not confirmed [96].

6. Bioluminescence

Chemical research on luminous fungi began in the 17th century, coinciding with the Scientific Revolution. Sir Robert Boyle (1627-1691), a founder of modern chemistry, examined luminous mycelia on rotten wood, called 'shining wood', using his newly invented vacuum pump and showed the involvement of air in luminescence [97]. Although Boyle did not know that the luminescence of 'shining wood' was caused by the mycelia of luminous fungi, his elegant experiments were recognized as a pioneering study leading the chemical understanding of bioluminescence. Jean-Henri Fabre (1823-1915), a French entomologist, demonstrated the requirement of oxygen for the luminescence of the 'jack-o'-lantern' mushroom growing on the olive tree, *Omphalotus olearius* [98]. In contrast, Japan had a late start in modern science, which is also true for the chemistry of fungal bioluminescence. In the days of Boyle and Fabre, Japan's Edo Period, Japanese people still believed in the story of *Yamiyo-také* (see above) or simply composed *Haiku* poems on the luminescence of mushrooms [99].

In Japan, modern science started in the Meiji Revolution in 1868. Most likely, S. Kawamura was the first Japanese individual who studied the bioluminescence of fungi. In his description paper of *O. japonicus*, he also reported the effects of nitrogen, hydrogen and oxygen gasses on the luminosity of *O. japonicus* fruitbodies, showing that the luminescence did not fade when it was treated with oxygen [41,100]. These results are basically the same as those using *O. olearius* by Fabre [98], as described above. Kawamura also observed that the juice squeezed out from the luminous gills had no luminosity [41,65].

Bioluminescence reactions *in vitro* using extracts of luminous fungi had not yet been achieved despite decades of trials (Harvey, 1952 [24], and references therein), but Airth and McElroy finally succeeded using the extracts of 'luminous fungi' species [101]. They detected luminescence when the hot-water extract from the mycelia of the luminous fungus *Armillaria mellea* and the cold-water extract from the mycelia of the luminous fungus '*Collybia velutipes*' were mixed in the presence of NADH or NADPH [101,102]. Airth and Foerster showed that this reaction consists of at least two steps, involving the reduction of unidentified dehydro- or oxyluciferin (luciferin precursor) by NADH or NADPH with a soluble enzyme (approximately 25 kDa [103]) and light-emitting oxidation of luciferin by molecular oxygen with an insoluble membrane-bound enzyme [102,104]. Airth and Foerster also showed that a cold-water extract from *Panellus stipticus* (*Panus stipticus*, in their paper) mycelia (luminescent strain) exhibited luminescence activity for a hot-water extract from *A. mellea* mycelia with NADH [105]. Based on these results, they suggested that fungal luminescence is explained as a luciferin-luciferase reaction, and the presence of reduced pyridine nucleotides in the reaction mixture is key to reproducing the luminescence *in vitro* [103]. Regarding the species '*Collybia velutipes*', the authors of this paper wrote that the mycelia of '*C. velutipes*' used for cold-water extraction was "luminous" [105], but this species is currently recognized as nonluminous *Flammulina velutipes* [46,74]. We confirmed that the cold-water extract of the *F. velutipes* (or *F. filiformis*) fruitbody has no

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luminescence activity by mixing the hot-water extract of the *M. chlorophos* fruitbody and NADPH. Interestingly, on the other hand, strong luminescence activity was detected in the hot-water extract of the *F. velutipes* fruitbody by mixing the cold-water extract of the *M. chlorophos* fruitbody and NADPH [106]. Accordingly, we conclude that Airth's research group misidentified unknown luminous mycelia as '*C. velutipes*', and true *F. velutipes* has no enzymatic activity but unexpectedly contains a luciferin precursor. Later, we realized that several nonluminous fungi contain a large amount of the luciferin precursor hispidin [107], as described below.

Candidates of luciferin or compounds involved in fungal luminescence have been proposed by several research groups. Airth et al. [102] showed that the luciferin precursor is soluble in phosphate buffer (pH 7.5) with 2% Tween 80 rather than in organic solvents, including acetone, chloroform, benzene and diethyl ether [102]. In 1966, Kuwabara and Wassink reported the purification and crystallization of the 'active substance' (luciferin or dehydroluciferin) from the mycelia of the luminous fungi *Mycena citricolor* (*Omphalia flavida*, in the paper); this substance had enzymatic luminescent activity for "Dr. Airth's fungal luciferase system" and nonenzymatic chemiluminescent activity in the presence of H_2O_2 [108]. The crystal was a brownish-orange 'microcrystalline solid' (needle-like crystalline, see Kuwabara & Wassink, 1966 [108]). The UV, IR and fluorescence of this 'active substance' were measured, but the chemical structure was not determined. Later, Airth himself examined the enzymatic activity of this crystal shipped from Kuwabara using the cold-water extract of '*C. velutipes*' with NADH or NADPH. However, the result was negative: "Since the possibility of inactivation during transport has not been disproved, the question as to whether Kuwabara and Wassink (1966) did crystallize fungal luciferin remains unanswered" [103]. Wassink suggested that there remains some doubt whether this crystallized compound was indeed fungal luciferin [74]. From the current viewpoint, it is believed that the basic optical properties (UV and fluorescent spectra) of the 'active substance' correspond neither with the candidate precursors of luciferin (hispidin and caffeic acid); both have luminescence activities to the crude buffer extract of the luminescent fungi [107,109]. Of note, Seishi Kuwabara, the first author of the paper about crystallization of the 'active substance' is a Japanese biologist. His biography is uncertain, but he also worked on bacterial luciferase with a bioluminescence researcher, Milton Cormier, in the 1960s (see Kuwabara et al., 1965 [110]).

Nakanishi and his colleague isolated fluorescent compounds illudin S and ergosta-4,6,8(14),22-tetraen-3-on, which showed emission maxima close to those of fungal luminescence, from the mycelia and fruitbody of *O. japonicus* as potential substances involved in the bioluminescence of fungi [111]. Illudin S is a compound responsible for the toxicity of *O. japonicus,* as shown above. The bioluminescence and chemiluminescence activities of these compounds have not been examined.

Lampteroflavin is a pentofuranosyl riboflavin compound isolated from *O. japonicus* that possesses green fluorescence (λmax = 524 nm) identical to the bioluminescence spectrum [112,113]. Minoru Isobe, a Japanese organic chemist, and his colleagues suggested that this compound is the light emitter of *O. japonicus* luminescence because it was the only fluorescent compound that showed an identical fluorescence spectrum to the *in vivo* bioluminescence detected in the lamellae of this mushroom [113]. Several chemicals, including flavins, exhibit chemiluminescence in Fenton's reagent (Fe^{2+} and H_2O_2) [114], and Isobe showed that the chemiluminescence of lampteroflavin in Fenton's reagent was significantly stronger than that of other flavins (lumiflavin, riboflavin, FMN and FAD). Based on this result, Isobe expected that lampteroflavin would also be involved in the luminescence reaction itself [115]. On the other hand, O'Kane et al. suggested that flavin could not be the light emitter because luminous mushrooms are pigmented, and the 'corrected' bioluminescence spectrum of *O. japonicus* mycelia, which do not have the filter effect by pigmentation, did not match the fluorescence spectrum of flavin [116].

Nobel Prize winner Osamu Shimomura (1929-2018), a Japanese chemist/biochemist living in the USA, also contributed to research on fungal bioluminescence. He won the prize by finding the green fluorescent protein from luminous jellyfish *Aequorea aequorea*, and he also studied fungal bioluminescence using a *Panellus stipticus*; he was fascinated by this luminous mushroom, which appeared on an oak stump cut for building his new house at Falmouth in the 1980s [117]. He

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cultivated the fruitbody himself by applying his *Shii-také* (*L. edodes*) cultivation experience [118,119]. Using those cultivated *P. stipticus* mushrooms, Shimomura isolated panal, a sesquiterpene aldehyde, and its derivatives, PS-A and PS-B, as possible candidates for luciferin precursors from the fruitbody [120–122]. After activation with primary amine, these panal derivatives exhibited chemiluminescence in the presence of Fe^{2+} and H_2O_2. The emission spectral peak of the chemiluminescence depends on the reaction conditions, some of which were close to the luminescence spectra *in vivo*. The same chemiluminescence was also observed for various other luminous fungi, such as *Armillaria* mycelia and *Mycena* fruitbodies [123]. Based on these results, Shimomura suggested that the bioluminescence of fungi might be a nonenzymatic reaction, which is inconsistent with Airth's suggestion.

Other candidate compounds for luciferin or its precursor of fungal luminescence were isolated from the mycelia of *M. citricolor* by O. Shimomura (see Shimomura, 2006 [118]), and the chemical structure was analyzed by a Japanese organic chemist, Hideshi Nakamura (1952-2000). He suggested that all luciferin precursors contain a common catechol-derived group (4-(3,4-dihydroxyphenyl)-3-buten-2-carbonyl group) in the structures (personal communication from Dr. H. Nakamura, 1998, as referred to in Shimomura, 2006 [118]). To our surprise, this partial structure and UV absorption peak of the luciferin precursor (369 nm; see Shimomura, 2006 [118]) match those of hispidin (Figure 2), which we currently think is a true luciferin precursor of fungal bioluminescence [107].

The enzymatic reaction proposed by Airth's group has been verified using several species of luminous fungal fruitbodies and mycelia, including the genera representing all four bioluminescent fungal lineages, *Gerronema*, *Mycena, Armillaria* and *Neonothopanus* [124–127]. Oliveira et al. also examined cross-reactions between species, including the nonluminous fungi *Filoboletus gracilis* and *Mycena singeri*, and the results were all negative when nonluminous species were used for the assay [127]. Based on these results, they suggested that all luminous fungi share the same or similar luciferin and luciferase, whereas these components are absent in nonluminous species [127].

The luminescence mechanism of Japanese *M. chlorophos* was recently investigated by two independent Japanese research groups [128,129]. Mori et al. showed that Dubois' classical luciferin-luciferase test was negative, bioluminescent components are insoluble in various surfactants, and the luminescence is heat unstable and thus will be an enzymatic reaction [128]. Hayashi et al. isolated an unknown compound that exhibited a UV absorption spectrum similar to that of flavins from the fruitbody, and the fluorescence peak almost matched both riboflavin and the bioluminescence of *M. chlorophos* [129]. Based on these findings, the authors concluded that this flavin-like compound is a factor in fungal bioluminescence. The bioluminescence or chemiluminescence activity of this compound was not examined in this report.

In 2015, we eventually identified the chemical structure of fungal luciferin and its precursor as 3-hydroxyhispidin and hispidin, respectively, using the mycelium of the Vietnamese luminous fungus *Neonothopanus nambi* [107]. In 2017, we reported the whole mechanism of fungal bioluminescence by determining the chemical structure of the reaction product as caffeylpyruvic acid as a light emitter [130]. In 2017, we also determined the presence of hispidin as an active compound for the NADPH-dependent bioluminescence reaction in the fruitbodies of Japanese *M. chlorophos*, *O. japonicus*, and Brazilian *N. gardneri* [109].

Katsunori Teranishi, a Japanese organic chemist, proposed a conflicting suggestion of light emitter compounds of luminescence in the *M. chlorophos* mushroom as riboflavin, riboflavin 5'-monophosphate, and/or flavin adenine dinucleotide [131]. He stated that 3-hydroxyhisidin can produce light by partially purified luciferase from *M. chlorophos*, but it remains unclear whether the compound actually produces light in the natural tissue of luminous fungi [132].

In 2018, we identified the luciferase gene, as well as luciferin-regenerating enzymes from *N. nambi*; these genes were clustered on the fungal genome and the molecular size of the luciferase (Luz) was approximately 28.5 kDa [80]. When these genes were transferred to yeast, the strain emitted the same green light. Currently, bioluminescent gene clusters have been identified in various luminous fungal species [71,80,133], suggesting that basic bioluminescence mechanisms are common in all luminous fungi; thus, bioluminescence in fungi has a single evolutionary origin [133]. In 2020, a self-luminescent plant was genetically produced using fungal luminescence genes [134]. Indeed, this

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bioengineering was realized because a common compound produced by all plants, caffeic acid, is coincidentally a precursor of fungal luciferin. This finding has the potential to advance plant science as a novel tool for bioimaging technology. To date, no natural bioluminescent higher plant has ever been reported [23], but in the future, fungal luminescent genes may illuminate the city as glowing street trees [135].

7. Biological function

For the biological function of fungal bioluminescence, many hypotheses have been proposed [136] but are not yet conclusive [137]. Arguably the most plausible hypothesis is that light attracts insects as a spore vector [138]. In Japan, we observed various animals visiting the fruitbodies of *M. chlorophos* (Figure 18) at night. Undescribed Japanese species *Roridomyces* sp. (*Aya-hikari-také*) has luminescent spores, suggesting the presence of spore dispersal function by light-attracted animals [10]. Aposematism is another strong hypothesis [136]. However, for example, *O. japonicus* is toxic to humans, but many insect species visit and consume the fruitbody [139] (Figure 18).

Figure 18

Figure 18. Fruitbodies of *Mycena chlorophos* with collembolas gathering under the gills (left) and *Omphalotus japonicus* with millipede and land snail grazing (right). Photo by Yoshinori Nishino at Bonin Isls. Tokyo (left) and by Takehito Miyatake at Tokushima Prefecture (right).

8. Conclusions

In this review, we demonstrated the enthusiasm for luminous fungi in Japan, from old folklore and taxonomic surveys to current popular entertainment and life sciences. Luminous mushrooms activate ecotourism, and the biotechnology born from the science of luminous fungi has the potential to change our urban life.

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References

1. Hosoya, T. History and the current status of fungal inventory and databasing in Japan. In *Proceedings of the 7th and 8th Symposia on Collection Building and Natural History Studies in Asia and the Pacific Rim*; Tomida, Y. et al. Eds.; National Science Museum Monographs: Ibaraki, Japan, 2006; pp. 51-61.
2. Sugahara, T. Japanese and mushrooms. *J. Cookery Sci. Jpn.* **2001**, *34*, 313-320.
3. Guy, N. *Kinoko: A window into the mystical world of Japanese mushrooms*; Amazon on demand (ISBN 979-8987537671), 2023.
4. Nakano, J. *Primer of Yamigaku (Study of dark)*; Shueisha: Tokyo, Japan, 2014. (in Japanese)
5. Komatsu, K. *Introduction to Yokai Culture: Monsters, Ghosts, and Outsiders in Japanese History*; Japan Publishing Industry Foundation for Culture: Tokyo, Japan, 2018.
6. Yamaguchi, H. Occurrence of the luminous oligochæte *Microscolex phosphoreus* (Dug.). *Annot. Zool. Japon* **1935**, *15*, 200-202.
7. Kanda, S. On the luminous earthworm Hikari-umi-mimizu. *Rigakukai* **1938**, *36*, 1-7. (in Japanese)
8. Shinohara, K.; Higa, Y. New record of the luminous millipede from Okinawa. *Edaphologia* **1997**, 59, 61-62. (in Japanese with English abstract)
9. Kashiwabara, S. An origin of firefly luminescence?: Luminescence of Collembola. *SCIaS* **1997**, *2*, 10. (in Japanese)
10. Kurogi, S. *Mushrooms in Miyazaki Prefecture (Miyazaki no Kinoko)*; Komyakusha: Miyazaki, Japan, 2015. (in Japanese)
11. Iwama, A. An unexpected finding of the luminescent *Cruentomycena*. *Mycologist Circle of Japan* **2020**, *No. 213*, 2-3. (in Japanese)
12. Harvey, E.N. *A History of Luminescence. From the Earliest Times Until 1900*; Am. Phil. Soc.: Philadelphia, USA, 1957.
13. Watasé, S. *On the Fireflies (Hotaru no Hanashi)*; Kaiseikan: Tokyo, Japan, 1902. (in Japanese)
14. Kanda, S. *Shiranui, Hitodama, and Kitsune-bi*; Shunyodo: Tokyo, Japan, 1931. (in Japanese)
15. Togawa, A. Haguro-san Yobanashi (or Haguro-san Yawa). *Tabi to Densetsu* **1944**, *193*, 13-24. (in Japanese)
16. Sakai, T. Nankou Chawa. In *Nihon Zuihitsu Taisei*; Yoshikawakobunkan: Tokyo, Japan, 1977; pp. 413-448. (in Japanese)
17. Takahashi, T. Yamagata-ken ni okeru Torimono no Keifu. *Seikou Minzoku* **1991**, *135*, 36-37. (in Japanese)
18. Hiroi, M. On the luminescence of mushrooms. *Kinoko-ken Dayori* **2006**, *28*, 10-20. (in Japanese)
19. Hasegawa, E.; Ota, Y.; Hattori, T.; Sahashi, N.; Kikuchi, T. Ecology of *Armillaria* species on conifers in Japan. *For. Path.* **2011**, *41*, 429-437.
20. Dan, I. *The Smoke of a Pipe, Still*; Asahi Shimbun Co.: Tokyo, Japan, 1972. (in Japanese)
21. Nakajima, A. *Kinoko Zukan*; Natsume Pub.: Tokyo, Japan, 2017. (in Japanese)
22. Nishino, Y.; Oba, Y. *Luminous Mushrooms with Night Forests*; Iwanami Shoten Pub.: Tokyo, Japan, 2013. (in Japanese)
23. Oba, Y. *Luminous Organisms of the World: Diversity, Ecology, and Biochemistry*; The University of Nagoya Press: Nagoya, Japan, 2022. (in Japanese)
24. Harvey, E.N. *Bioluminescence*; Academic Press: New York, USA, 1952.
25. Keene, D. *The Tale of the Bamboo Cutter*; Kodansha International: Tokyo, Japan, 1998.
26. Hotate, M. *Shining Princess and the Sovereign myth (Kaguya-himé to Ouken-shinwa)*; Yosensha: Tokyo, Japan, 2010. (in Japanese)
27. Masuda, K.; Suzuki, H. The origins of fiction. *Kokubungaku* **1993**, *38*, 6-24. (in Japanese)
28. Yasuda, A. Miscellaneous notes on fungi. *Bot. Mag. Tokyo* **1920**, *34*, 194-196. (in Japanese)
29. Shidei, T. Report of fungal flora in bamboo forest. *Trans. Mycol. Soc. Japan* **1974**, *15*, 251-257. (in Japanese)
30. Haneda, Y. *Luminous Organisms*; Kouseisha-Kouseikaku: Tokyo, Japan, 1985. (in Japanese)
31. Imazeki, R.; Otani, Y.; Hongo, T. *Mushrooms in Japan*; Yama-Kei Pub.: Tokyo, Japan, 1988. (in Japanese)
32. Kyoto Prefecture. *The List of Biological and Geological Components of the Natural Environment 2015, Red Data Book of Kyoto Prefecture 2015, Supplementary*; Kyoto Prefecture: Kyoto, Japan, 2015. (in Japanese)
33. Kanda, S. *Fireflies*; Nippon Hakkō Seibutsu Kenkyu Kai: Tokyo, Japan, 1935 (in Japanese)
34. Ohba, N. *Mystery of Fireflies*; Yokosuka City Mus.: Yokosuka, Japan, 2004 (in Japanese)
35. Oba, Y.; Miyatake, T. *Luminous Creatures, Mushrooms*; Kumon Pub: Tokyo. Japan, 2015. (in Japanese)
36. Miyatake, T. *Luminous mushrooms (World of Wonders)*; Fukuinkan Shoten: Tokyo, Japan, 2023. (in Japanese)
37. Niitsu, H.; Hanyuda, N.; Sugiyama, Y. Cultural properties of a luminous mushroom, *Mycena chlorophos*. *Mycoscience* **2000**, *41*, 551-558.

doi:10.20944/preprints202305.0223.v1

38. Niitsu, H.; Hanyuda, N. Fruit-body production of a luminous mushroom, *Mycena chlorophos*. *Mycoscience* **2000**, *41*, 559-564.
39. Ise Shimbun. *Enjoy luminous mushroom. Iwade Research Institute of Mycology Group in Tsu City sells the culture kit*. (2021, May 24). *The Ise Shimbun Chusei Local*, Japan. (in Japanese)
40. Neda, H. *Kinoko Museum*; Yasaka Shobo: Tokyo, Japan, 2014. (in Japanese)
41. Kawamura, S. Studies on the luminous fungus, *Pleurotus japonicus* sp. nov. *J. Coll. Sci. Tokyo Imp. Univ.* **1915**, *35*, 1-29.
42. Kobayasi, Y. Seven luminous mycomycetes from Bonin Islands. *Bull. Biogeographic. Soc. Jpn.* **1937**, *7*, 1-7.
43. Corner, E.J.H. Further description of luminous agarics. *Trans. Br. Mycol. Soc.* **1954**, *37*, 256-271.
44. Corner, E.J.H. *The Marquis: A Tale of Syonan-to*; Heinemann Asia: Kuala Lumpur, Singapore, 1981.
45. Wassink, E.C. *On fungus luminescence*; Mededelingen Landbouwhogeschool, Wageningen, H. Veenman & Zonen: Wageningen, Nederland, 1979.
46. Desjardin, D.E.; Oliveira, A.G.; Stevani, C.V. Fungi bioluminescence revisited. *Photochem. Photobiol. Sci.* **2008**, *7*, 170-182.
47. Terashima, Y.; Takahashi, H.; Taneyama, Y. *The Fungal Flora in Southwestern Japan: Agarics and Boletes*; Tokai Univ. Press: Kanagawa, Japan, 2016.
48. Cortés-Pérez, A.; Desjardin, D.E.; Perry, B.A.; Ramírez-Cruz, V.; Ramírez-Guillén, F.; Villalobos-Arámbula, A.R.; Rockefeller, A. New species and records of bioluminescent *Mycena* from Mexico. *Mycologia* **2019**, *111*, 319-338.
49. Chang, C.-C.; Chen, C.-Y.; Lin, W.-W.; Kao, H.-W. *Mycena jingyinga*, *Mycena luguensis*, and *Mycena venus*: three new species of bioluminescent fungi from Taiwan. *Taiwania* **2020**, *65*, 396-406.
50. Tanaka, N. On the report about Japanese poisonous mushrooms part 1 by Kichindo Inoko. *J. Plant Res* **1889**, *3*, 47-51. (in Japanese)
51. Haneda, Y. Luminous Organisms of Japan and the Far East. In *The Luminescence of Biological Systems*; Johnson, F.H., Ed): Am. Assoc. Adv. Sci.: Washington DC, USA, 1955, pp. 335-385.
52. Chew, A.L.C.; Tan, Y.-S.; Desjardin, D.E.; Musa, Md.Y.; Sabaratnam, V. Taxonomic and phylogenetic re-evaluation of *Mycena illuminans*. *Mycologia* **2013**, *105*, 1325-1335.
53. Katumoto, K. *List of Fungi Recorded in Japan*; The Kanto Branch of the Mycological Society of Japan: Tokyo, Japan, 2010. (in Japanese)
54. Takahashi, H. An impact on the finding of the luminescent *Cruentomycena* by Ami Iwama. *Mycologist Circle of Japan* **2020**, *No. 213*, 4. (in Japanese)
55. Taneyama, Y. *Cruentomycena* was bioluminescent! *Mycologist Circle of Japan* **2020**, *No. 213*, 5. (in Japanese)
56. Okuzawa, Y.; Okuzawa, M. *Mushroom Etymology and Dialect Dictionary*; Yama-Kei Pub.: Tokyo, Japan, 1998. (in Japanese)
57. Kobayasi, Y. Contributions to the luminous fungi from Japan. *J. Hattori Bot. Lab.* **1951**, *5*, 1-6.
58. GBIF.org. GBIF Home Page. Available from: https://www.gbif.org. 2023 (accessed on 19 Apr 2023).
59. Kawai, D. *Handbook of Mushrooms in Oirase Stream (Oirase Keiryu, Kinoko Handbook), spring – early summer*; NPO Oiken: Aomori, Japan, 2022. (in Japanese)
60. Imazeki, R.; Hongo, T. Colored Illustrations of Mushrooms of Japan, Vol. I; Hoikusha: Osaka, Japan, 1987. (in Japanese)
61. Search System of Japanese Red Data; Association of Wildlife Research and EnVision (accessed on 15 Apr 2023), http://jpnrdb.com/index.html
62. Tanaka, Y.; Kasuga, Y.; Oba, Y.; Hase, S.; Sakakibara, Y. Genome sequence of the luminous mushroom *Mycena chlorophos* for searching fungal bioluminescence genes. *Luminescence* **2014**, *29*, 47-48.
63. Miyagi, G. Notes on luminous fungi, *Filoboletus manipularis*, on Okinawa. *Bull. Coll. Sci. Univ. Ryukyus* **1960**, *4*, 77-87. (in Japanese)
64. Hioki, K. (Ed.) *Sanshu Kidan*; Ishikawa Prefecture Library Association: Ishikawa, Japan, 1933. (in Japanese)
65. Kawamura, S. Studies on a luminous fungus, *Pleurotus japonicus* sp. nov. Bot Mag Tokyo **1910**, *24*, 165-177.
66. Kudo, S. *Macrofungi of Aomori*; Access 21 Pub.: Aomori, Japan, 2017. (in Japanese)
67. Dykstra, Y.K. (translation) *The Konjaku Tales. Japanese section (Honcho-Hen)(III) from a Medieval Japanese Collection*; Kansai Gaidai Univ. Pub.: Osaka, Japan, 2003.
68. Watari, T.; Tachibana, T.; Okada, A.; Nishikawa, K.; Otsuki, K.; Nagai, N.; Abe, H.; Nakano, Y.; Takagi, S.; Amano, Y. A review of food poisoning caused by local food in Japan. *J. Gen. Fam. Med.* **2021**, *22*, 15-23.
69. Nakanishi, K.; Ohashi, M.; Tada, M.; Yamada, Y. Illudin S (lampterol). *Tetrahedron* **1965**, *21*, 1231-1246.
70. Matsumoto, T.; Shirahama, H.; Ichihara, A.; Fukuoka, Y.; Takahashi, Y.; Mori, Y.; Watanabe, M. Structure of lampterol (illudin S). *Tetrahedron* **1965**, *21*, 2671-2676.
71. Kim, J.; Park, M.-J.; Shim, D.; Ryoo, R. *De novo* genome assembly of the bioluminescent mushroom *Omphalotus guepiniiformis* reveals an *Omphalotus*-species lineage of the luciferase. *Genomics* **2022**, *114*, 110514.

Preprints (www.preprints.org) | NOT PEER-REVIEWED | Posted: 4 May 2023 doi:10.20944/preprints202305.0223.v1

72. Fukasawa, Y.; Osono, T.; Takeda, H. Beech log decomposition by wood-inhabiting fungi in a cool temperate forest floor: a quantitative analysis focused on the decay activity of a dominant basidiomycete *Omphalotus guepiniformis*. *Ecol. Res.* **2010**, *25*, 959-966.
73. Ooka, M. *Easy-Access Index of Haiku Seasonal Words (Autumn)*; Yushikan: Tokyo, Japan, 2005. (in Japanese)
74. Wassink, E.C. Luminescence in Fungi. In *Bioluminescence in Action*; Herring, P.J. Ed.; Academic Press: New York, USA, 1978; pp. 171-197.
75. Kudo, S.; Tezuka, Y.; Yonaiyama, H. *Fungi of Aomori*; Graph Aomori: Aomori, Japan, 1998. (in Japanese)
76. Hiroi, M. Light emission of *Armillaria tabescens* (Scop.:Fr.) Emel –Measurement of light emission of mushrooms using chemiluminescence detector–. *Bull. Koriyama Women's Univ.* **2013**, *49*, 179-189.
77. Koch, R.A.; Wilson, A.W.; Séne, O.; Henkel, T.W.; Aime, M.C. Resolved phylogeny and biogeography of the root pathogen *Armillaria* and its gasteroid relative, *Gyanogaster*. *BMC Evol. Biol.* **2017**, *17*, 33.
78. Moncalvo, J.-M.; Lutzoni, F.M.; Rehner, S.A.; Johnson, J.; Vilgalys, R. Phylogenetic relationships of agaric fungi based on nuclear large subunit ribosomal DNA sequences. *Syst. Biol.* **2000**, 49, 278-305.
79. Macrae, R. Interfertility studies and inheritance of luminosity in *Panus stypticu*s. *Can. J. Res.* **1942**, *20c*, 411-434.
80. Kotlobay, A.A.; Sarkisyan, K.S.; Mokrushina, Y.A.; Marcet-Houben, M.; Serebrovskaya, E.O.; Markina, N.M.; Somermeyer, L.G.; Gorokhovatsky, A.Y.; Vvedensky, A.; Purtov, K.V.; Petushkov, V.N.; Rodionova, N.S.; Chepurnyh, T.V.; Fakhranurova, L.I.; Guglya, E.B.; Ziganshin, R.; Tsarkova, A.S.; Kaskova, Z.M.; Shender, V.; Abakumov, M.; Abakumova, T.O.; Povolotskaya, I.S.; Eroshkin, F.M.; Zaraisky, A.G.; Mishin, A.S.; Dolgov, S.V.; Mitiouchkina, T.Y.; Kopantzev, E.P.; Waldenmaier, H.E.; Oliveira, A.G.; Oba, Y.; Barsova, E.; Bogdanova, E.A.; Gabaldón, T.; Stevani, C.V.; Lukyanov, S.; Smirnov, I.V.; Gitelson, J.I.; Kondrashov, F.A.; Yampolsky, I.V. Genetically encodable bioluminescent system from fungi. *Proc. Natl. Acad. Sci. USA* **2018,** *115*, 12728-12732.
81. Dickinson, C.; Lucas, J. (Eds.). The Encyclopedia of Mushrooms; G. P. Putnam's Sons: New York, USA, 1979.
82. Berkeley, M.J.; Curtis, M.A. Characters of new fungi, collected in the North Pacific Exploring Expedition by Charles Wright. *Proc. Amer. Acad. Arts Sci.* **1860**, *4*, 111-130.
83. Ito, S. *Mycological Flora of Japan. Vol. II. Basidiomycetes No. 5. Agaricales, Gasteromycetales*; Yokendo: Tokyo, Japan, 1959. (in Japanese)
84. Desjardin, D.E.; Capelari, M.; Stevani, C.V. A new bioluminescent agaric form São Paulo, Brazil. *Fung. Div.* **2005**, *18*, 9-14.
85. Bothe, F. Über das Leuchten verwesender Blätter und seine Erreger. *Planta* **1931**, *14*, 752-765. (in Germany)
86. Berliner, M.D. Studies in fungal luminescence. *Mycologia* **1961**, *53*, 84-90.
87. Treu, R.; Agerer, R. Culture characteristics of some *Mycena* species. *Mycotaxon* **1990**, *38*, 279-309.
88. Bermudes, D.; Petersen, R.H.; Nealson, K.H. Low-level bioluminescence detected in *Mycena haematopus* basidocarps. *Mycologia* **1992**, *84*, 799-802.
89. Josserand, M. Sur la luminescence de "*Mycena rorida*" en Europe occidentale. *Bull. Mens. Soc. Linn. Lyon* **1953**, *22*, 99-102.
90. Neda, H.; Sato, H. New record of *Armillaria fuscipes* Petch from Japan. In *Abstract of Papers Presented at the 53th Annual Meeting of the Mycological Society of Japan*; 2009; p. 48. (in Japanese)
91. Mihail, J.D. Bioluminescence patterns among North American *Armillaria* species. *Fungal Biology* **2015**, *119*, 528-537.
92. Ainsworth, M. Searching for luminous mushrooms of the marsh fungus *Armillaria ectypa*. *Field Mycol.* **2004**, *5*, 142-144.
93. Wassink, E.C. Observations on the luminescence in fungi, I, including a critical review of the species mentioned as luminescent in literature. *Recueil Trav. Bot. Neerl.* **1948**, *41*, 150-212.
94. Hongo, T. New taxa of the Agaricales published by T. Hongo from 1973 to 1988. *Trans. Mycol. Soc. Jpn.* **1989**, *30*, 499-504.
95. Harder, C.B.; Laæssøe, T.; Frøslev, T.G.; Ekelund, F.; Rosendahl, S.; Kjøller, R. A three-gene phylogeny of the *Mycena pura complex* reveals 11 phylogenetic species and shows ITS to be unreliable for species identification. *Fungal Biol.* **2013**, *117*, 764-775.
96. Ota, Y.; Kim, M.-S.; Neda, H.; Klopfenstein, N.B.; Hasegawa, E. The phylogenetic position of an *Armillaria* species from Amami-Oshima, a subtropical island of Japan, based on elongation factor and ITS sequences. *Mycoscience* **2011**, *52*, 53-58.
97. Boyle, R. Observations and tryals about the resemblances and differences between a burning coal and shining wood. *Philos. Trans. Royal Soc.* **1668**, *2*, 605-612.
98. Fabre, J.–H. Recherches sur la cause de la phosphorescence de l'agaric de l'olivier. *Ann. Sci. Nat. Bot.* **1855**, *4*, 179-197. (in French)
99. Goto, Y. Luminous organisms appeared in Edo-period literatures. *Bull. Firefly Mus. Toyota Town* **2022**, *14*, 81-86. (in Japanese)

100. Kawamura, S. Studies on a Luminous fungus, *Pleurotus japonicus* sp. nov. (Continued from p. 213). *Bot. Mag. Tokyo* **1910**, 24, 249-260.
101. Airth, R.L.; McElroy, W.D. Light emission from extracts of luminous fungi. *J. Bacteriol.* **1959**, *77*, 249-250.
102. Airth, R.L.; Foerster, G.E.; Behrens, P.Q. The luminous fungi. In *Bioluminescence in Progress*; Johnson, F.H., Haneda, Y., Eds.; Princeton University Press: Princeton, USA, 1966; pp. 203-223.
103. Airth, R.L.; Foerster, G.E.; Hinde, R. Bioluminescence. In *Photobiology of Microorganisms*; Halldal, P., Ed.; John Wiley & Sons: London, UK, 1970; pp. 417-446.
104. Airth, R.L.; Foerster, G.E. The isolation of catalytic components required for cell-free fungal bioluminescence. *Arch. Biochem. Biophys.* **1962**, *97*, 567-573.
105. Airth, R.L.; Foerster, G.E. Enzymes associated with bioluminescence in *Panus stypticus luminescence* and *Panus stypticus non-luminescence*. *J. Bacteriol.* **1964**, *88*, 1372-1379.
106. Oba, Y. Bioluminescent mechanism of luminous mushroom. *Kinoko-ken Dayori* **2017**, *40*, 18-25. (in Japanese)
107. Purtov, K.V.; Petushkov, V.N.; Baranov, M.S.; Mineev, K.S.; Rodionova, N.S.; Kaskova, Z.M.; Tsarkova A.S.; Petunin, A.I.; Bondar, V.S.; Rodicheva, E.K.; Medvedeva, S.E.; Oba, Y.; Oba, Y.; Arseniev, A.S.; Lukyanov, S.; Gitelson, J.I.; Yampolsky, I.V. The chemical basis of fungal bioluminescence. *Angew. Chem. Int. Ed.* **2015**, *54*, 8124-8128.
108. Kuwabara, S.; Wassink, E.C. Purification and properties of the active substance of fungal luminescence. In *Bioluminescence in Progress*; Johnson, F.H., Haneda, Y. Eds.; Princeton University Press: Princeton, USA, 1966; pp. 233-245.
109. Oba, Y.; Suzuki, Y.; Martins, G.N.R.; Carvalho, R.P.; Pereira, T.A.; Waldenmaier, H.E.; Kanie, S.; Naito, M.; Oliveira, A.G.; Dörr, F.A.; Pinto, E.; Yampolsky, I.V.; Stevani, C.V. Identification of hispidin as a bioluminescent active compound and its recycling biosynthesis in the luminous fungal fruiting body. *Photochem. Photobiol. Sci.* **2017**, *16*, 1435-1440.
110. Kuwabara, S.; Cormier, M.J.; Dure, L.S.; Kreiss, P.; Pfuderer, P. Crystalline bacterial luciferase from *Photobacterium fischeri*. *Proc. Natl. Acad. Sci. USA* **1965**, *53*, 822-828.
111. Endo, M.; Kajiwara, M.; Nakanishi, K. Fluorescent constituents and cultivation of *Lampteromyces japonicus*. *Chem. Commun.* **1970**, 309-310.
112. Isobe, M.; Uyakul, D.; Goto, T. *Lampteromyces* bioluminescence-2. Lampteroflavin, a light emitter in the luminous mushroom, *L. japonicus*. *Tetrahedron Lett.* **1988**, *29*, 1169-1172.
113. Uyakul, D.; Isobe, M.; Goto, T. Lampteromyces bioluminescence 3. Structure of lampteroflavin, the light emitter in the luminous mushroom, *L. japonicus*. *Bioorg. Chem.* **1989**, *17*, 454-460.
114. Zeng, J.; Jewsbury, R.A. Chemiluminescence of flavins in the presence of Fe(II). *J. Photochem. Photobiol.* **1995**, *A91*, 117-120.
115. Isobe, M. New bioluminescent systems in fungi, plant and animals. *Nippon Nōgeikagaku Kaishi* **1992**, *66*, 736-741. (in Japanese)
116. O'Kane, D.J.; Fuhrer, B.; Lingle, W.L. Spectral studies on fungal bioluminescence. In *Bioluminescence and Chemiluminescence: Fundamentals and Applied Aspects*; Campbell, A.K. Ed.; John Wiley & Sons: Chichester, UK, 1994; pp. 552-555.
117. Shimomura, O. *Learning from Jellyfish (Kurage ni Manabu)*; Nagasaki Bunken Sha: Nagasaki, Japan, 2010. (in Japanese)
118. Shimomura, O. *Bioluminescence: Chemical Principles and Methods*; World Scientific: Toh Tuck Link, Singapore, 2006.
119. Shimomura, O.; Shimomura, S.; Bringer, J.H. *Luminous Pursuit: Jellyfish, GFP, and the Unforeseen Path to the Nobel Prize*; World Scientific: Toh Tuck Link, Singapore, 2017.
120. Nakamura, H.; Kishi, Y.; Shimomura, O. Panal: a possible precursor of fungal luciferin. *Tetrahedron* **1988**, *44*, 1597-1602.
121. Shimomura, O. Superoxide-triggered chemiluminescence of the extract of luminous mushroom *Panellus stipticus* after treatment with methylamine. *J. Exp. Bot.* **1991**, *42*, 555-560.
122. Shimomura, O. Structure and non-enzymatic light emission of two luciferin precursors isolated from the luminous mushroom *Panellus stipticus*. *J. Biolumin. Chemilumin.* **1993**, *8*, 201-205.
123. Shimomura, O. The role of superoxide dismutase in regulating the light emission of luminescent fungi. *J. Exp. Bot.* **1992**, *43*, 1519-1525.
124. Kamzolkina, O.V.; Danilov, V.S.; Egorov, N.S. On the nature of luciferase from the bioluminescent fungus *Armillariella mellea*. *Doklady Akademii Nauk SSSR* **1983**, *3*, 750-752. (in Russian)
125. Kamzolkina, O.V.; Bekker, Z.E.; Egorov, N.S. Luciferin-luciferase system of the mushroom *Armillariella mellea*. *Biologicheskie Nauki* **1984**, *1*, 73-77. (in Russian)
126. Oliveira, A.G.; Stevani, C.V. The enzymatic nature of fungal bioluminescence. *Photochem. Photobiol. Sci.* **2009**, *8*, 1416-1421.
127. Oliveira, A.G.; Desjardin, D.E.; Perry, B.A.; Stevani, C.V. Evidence that a single bioluminescent system is shared by all known bioluminescent fugal lineages. *Photochem. Photobiol. Sci.* **2012**, *11*, 848-852.

 doi:10.20944/preprints202305.0223.v1

128. Mori, K.; Kojima, S.; Maki, S.; Hirano, T; Niwa, H. Bioluminescence characteristics of the fruiting body of *Mycena chlorophos*. *Luminescence* **2011**, *26*, 604-610.
129. Hayashi, S.; Fukushima, R.; Wada, N. Extraction and purification of a luminiferous substance from the luminous mushroom *Mycena chlorophos*. *Biophysics* **2012**, *8*, 111-114.
130. Kaskova, Z.M.; Dörr, F.A.; Petushkov, V.N.; Purtov, K.V.; Tsarkova, A.S.; Rodionova, N.S.; Mineev, K.S.; Guglya, E.B.; Kotlobay, A.; Baleeva, N.S.; Baranov, M.S.; Arseniev, A.S.; Gitelson, J.I.; Lukyanov, S.; Suzuki, Y.; Kanie, S.; Pinto, E.; Di Mascio, P.; Waldenmaier, H.E.; Pereira, T.A.; Carvalho, R.P.; Oliveira, A.G.; Oba, Y.; Bastos, E.L.; Stevani, C.V.; Yampolsky, I.V. Mechanism and color modulation of fungal bioluminescence. *Sci. Adv.* **2017**, *3*, e1602847.
131. Teranishi, K. Identification of possible light emitters in the gills of a bioluminescent fungus *Mycena chlorophos*. *Luminescence* **2016**, *31*, 1407-1413.
132. Teranishi, K. Bioluminescence and chemiluminescence abilities of trans-3-hydroxyhispidin on the luminous fungus *Mycena chlorophos*. *Luminescence* **2018**, *33*, 1235-1242.
133. Ke, H.–M.; Lee, H.–H.; Lin, C.–Y.I.; Liu, Y.–C.; Lu, M.R.; Hsieh, J.–W.H.; Chang, C.–C.; Wu, P.–H.; Lu, M.J.; Li, J.–Y.; Shang, G.; Lu, R.J.–H.; Nagy, L.G.; Chen, P.–Y.; Kao, H.–W.; Tsai, I.J. *Mycena* genomes resolve the evolution of fungal bioluminescence. *Proc. Natl. Acad. Sci. USA* **2020**, *117*, 31267-31277.
134. Mitiouchkina, T.; Mishin, A.S.; Somermeyer, L.G.; Markina, N.M.; Chepurnyh, T.V.; Guglya, E.B.; Karataeva, T.A.; Palkina, K.A.; Shakhova, E.S.; Fakhranurova, L.I.; Chekova, S.V.; Tsarkova, A.S.; Golubev, Y.V.; Negrebetsky, V.V.; Dolgushin, S.A.; Shalaev, P.V.; Shlykov, D.; Melnik, O.A.; Shipunova, V.O.; Deyev, S.M.; Bubyrev, A.I.; Pushin, A.S.; Choob, V.V.; Dolgov, S.V.; Kondrashov, F.A.; Yampolsky, I.V; Sarkisyan, K.S. Plants with genetically encoded autoluminescence. *Nat. Biotechnol*. **2020**, *38*, 944-946.
135. Strack, R. Harnessing fungal bioluminescence (research highlights). *Nat. Methods* **2019**, *16*, 139-145.
136. Sivinski, J. Arthropods attracted to luminous fungi. *Psyche* **1981**, *88*, 383-390.
137. Weinstein, P.; Delean, S.; Wood, T.; Austin, D. Bioluminescence in the ghost fungus *Omphalotus nidiformis* does not attract potential spore dispersing insects. *IMA Fungus* **2016**, *7*, 229-234.
138. Oliveira, A.G.; Stevani, C.V.; Waldenmaier, H.E.; Viviani, V.; Emerson, J.M.; Loros, J.J.; Dunlap, J.C. Circadian control sheds light on fungal bioluminescence. *Curr. Biol.* **2015**, *25*, 964-968.
139. Makihara, H.; Takeno, K.; Chûjô, M. Check list of the insects collected from *Lampteromyces japonicus* (Kawam.) Sing. on Mt. Hiko. *Sci. Bull. Fac. Agr. Kyushu Univ.* **1972**, *26*, 595-600. (in Japanese with English title)