Bioluminescent Diversity: From Microbes to Insects

Abstract

Bioluminescence is a remarkable biological phenomenon where living organisms produce light through a chemical reaction, primarily involving the enzyme luciferase and the substrate luciferin. This process serves various ecological functions, including predation, communication and defense across different taxa such as bacteria, fungi and insects. Bioluminescent bacteria, predominantly found in marine environments, use this capability for symbiotic relationships, with species like *Vibrio fischeri* providing light to host organisms. Fungi display bioluminescence in a limited number of species, suggesting an evolutionary link across diverse lineages. In insects, bioluminescence plays roles in mating and predation, with fireflies showcasing intricate signalling systems that vary among species. Click beetles exhibit bioluminescence for communication and defense, while glowworms utilize light to attract prey. Recent advancements in genetic engineering, particularly using fluorescent proteins like Green Fluorescent Protein (GFP) in pest management, highlight the potential for bioluminescence in ecological monitoring and targeted pest control strategies. This review showcases bioluminescence in both microbes and insects that offers invaluable insights into the ecological roles and functions of these luminous organisms in their respective ecosystems.

Keywords: Bioluminescence, communication, luciferase, Green Fluorescent Protein, symbiotic

Introduction

Bioluminescence, the natural phenomenon of light emission by living organisms, has fascinated scientists and laypeople alike for centuries. Dioscorides and Pliny the Elder, were the one who documented bioluminescent organisms, with Pliny even attributing medicinal properties to some of these organisms (Dybas, 2019). The practical applications of bioluminescence are evident in accounts of coal-miners using dried fish skins and bottled fireflies as safe sources of light (Fordyce, 1973). Charles Darwin mentioned the glowing oceans in their travels, emphasizing the widespread presence and fascination with bioluminescence. Earlier in 19th century, a renowned zoologist, E. N. Harvey, also called as the “Dean of Bioluminescence” (1887-1959) detailed bioluminescence in his book “*A History of Luminescence”*(Johnson, 1967). The ideologies from Osamu Shimomura (1928–2018) and John Woodland (Woody) Hastings in the 20^{th} century for the role of luceferin, luciferase and calcium ions in light property paved the further research (Wilson and Hastings, 2012).While insects such as fireflies and glowworms have long captured our imaginations with their mesmerizing glow, it is important to acknowledge that microbes also exhibit bioluminescence. From bioluminescent bacteria in the ocean to glowing fungi in decaying wood, these microorganisms add another layer of complexity to the study of bioluminescence in nature. Bioluminescence is a fascinating phenomenon that occurs when living organisms produce light through a chemical reaction within their bodies. This light emission is often the result of a specific enzyme, luciferase, acting on a light-emitting molecule, luciferin, in the presence of oxygen. This phenomenon serves various purposes for different organisms. In some cases, it is used for predation, where organisms such as deep-sea fish or certain types of bacteria use bioluminescence to attract prey or communicate with each other. The most well-known example of bioluminescence is perhaps the firefly (Hosseinkhani, 2011), whose flashing light serves a role in mating and communication. In marine environments, bioluminescent organisms are common, with certain species of plankton, shark and jellyfish displaying beautiful light displays (Kahlke and Umbers, 2016).This process primarily involves two components: luciferin, a light-emitting molecule, and luciferase, an enzyme that catalyzes the reaction. When luciferin is oxidized in the presence of luciferase and oxygen, light is produced which is a spectrochemistry molecule called as firefly oxyluciferin (Al-Handawi et al., 2022). This reaction can occur in various forms across different organisms, including fungi, bacteria, and of course, insects.Unlike fluorescence, where substances absorb light and re-emit it, bioluminescence is a chemical reaction that generates light, making it one of nature's most fascinating phenomena.

Bioluminescence in Bacteria

Bioluminescent bacteria are prevalent and widely distributed in various habitats (both terrestrial and aquatic environments). These are also residents of beach detritus and uncooked seafood (Haddock et al., 2010). Additionally, it references the glowing oceans created by these microorganisms, noting their mention in Darwin's work and their observation in different locations worldwide. Bioluminescent bacteria primarily belong to the class Gammaproteobacteria and are limited to three genera: *Vibrio*, *Photobacterium*, and *Xenorhabdus*. Among these genera, *Vibrio* and *Photobacterium* are predominantly found in marine environments, while *Xenorhabdus* thrives in terrestrial habitats (Mahajan and Phatak, 2019). New strains of bioluminescent bacteria continue to be discovered (Gentile et al., 2009). The terrestrial bioluminescent bacteria are not common and are typically associated with infecting nematodes that parasitize glowworm larvae. When the glowworm larva dies, predators and scavengers consume the carcasses. This consumption process disperses both the bioluminescent bacteria and the nematode into the environment. The diverse relationships of bioluminescent bacteria, which can exist as free-living, symbiotic or pathogenic forms (Labella et al., 2017). For example, *Vibrio fischeri* colonizes specialized light organs in the fish *Monocentris japonicus* (Engebrecht and Silverman, 1984) and has a mutualistic relationship with the Hawaiian squid *Euprymniascolopes* (Mahajan and Phatak, 2019). Various species from the genus *Photobacterium* exhibit symbiosis (Moreira et al., 2014) with different fish and mollusks while causing diseases in other species (Labella et al., 2017). Such symbiotic relationships with bioluminescent bacteria have evolved specialized modifications like light organs, indicating a co-evolutionary process between the host and the bacteria (Haddock et al., 2010). This suggests that the ability of bacteria to produce light might play a crucial role in establishing and maintaining symbiotic relationships with host organisms, potentially enhancing the fitness of both parties involved in the symbiosis (Kahlke and Umbers, 2016).

Biochemistry of bacterial bioluminescence

The enzyme responsible for catalyzing light emission in bacteria is a uniquely bacterial luciferase, which is a heterodimeric protein consisting of approximately 80 kDa. This protein is composed of two subunits, a (40 kDa) and b (37 kDa), and shows homology to long-chain alkane monooxygenases (Li et al., 2008; Hastings, 2012). The enzyme functions by mediating the oxidation of reduced flavin mononucleotide (FMNH2) in the presence of a long-chain aliphatic (fatty) aldehyde (RCHO) and oxygen (O2). This reaction ultimately leads to the production of blue-green light as a result of the oxidation process. The specific reaction involved in this light emission process may vary slightly depending on the bacterial species and luciferase enzyme involved.

$$\mathbf{FMNH_2 + O_2 + RCHO \overset{\textit{luciferase}}{\Rightarrow} FMN + H_2O + RCOOH + light\,(490\,nm)}$$

In the bacterial luminescence reaction, the substrates FMNH2 and long-chain fatty aldehyde, are specific to this process. Unlike bioluminescent eukaryotes, which employ different luciferases and chemistries, bacterial luminescence relies on the interaction of these specific substrates with the bacterial luciferase (Hastings, 2012). The binding of FMNH2 by the enzyme precedes the interaction with O2, resulting in the formation of a flavin-4a-hydroperoxide. This complex then interacts with the aldehyde to form a stable intermediate, leading to the oxidation of the FMNH2 and aldehyde substrates and the subsequent emission of light (Hastings and Nealson, 1981; Hastings, 2012). The quantum yield for this reaction has been estimated at 0.1–0.2 photons, indicating the efficiency of light emission. The specificity of the reaction for FMNH2 suggests the importance of this substrate in the luminescence process and in vivo, the aldehyde substrate is likely to be tetradecanal. The FMNH2 necessary for the reaction is provided by the activity of an NADH:FMN oxidoreductase (flavin reductase), which utilizes reductant from NADH generated in cellular metabolism such as glycolysis and the citric acid cycle. The transfer of reductant from FMNH2 to luciferase occurs via free diffusion. Synthesis of the long-chain aldehyde is catalyzed by a fatty-acid reductase complex, which comprises three polypeptides: an NADPH-dependent acyl protein reductase (54 kDa), an acyl transferase (33 kDa), and an ATP-dependent synthetase (42 kDa). This complex plays an essential role in the production of light in the absence of exogenously added aldehyde (Hastings et al., 1985; Meighen, 1991; Tinikul et al., 2013). Furthermore, the substantial amino acid residue and nucleotide sequence identity observed in luciferases from different species of luminous bacteria indicate a common evolutionary origin of luminescence in bacteria, consistent with the shared ancestry of these light-producing mechanisms.

Bioluminescence in Fungi

There is limited exploration of fungal bioluminescence compared to other bioluminescent systems, despite fungi being the only terrestrial eukaryotes, apart from animals, that exhibit bioluminescence (Kahlke and Umbers, 2016). Initial attempts to understand the enzymatic nature of fungal bioluminescence were unsuccessful, but more recent research has successfully confirmed these mechanisms (Oliveira et al., 2012). This shift has led to an increased interest in studying fungal bioluminescence, with the development of a genetically encodable bioluminescent system for eukaryotes being a significant advancement (Kotlobay et al., 2018). Earlier attempts to understand fungal bioluminescence were likely unsuccessful for several reasons. Out of all the documented fungal species, only around 71 (Desjardin et al., 2010) to 80 (Chew et al., 2015) have been identified as bioluminescent. These bioluminescent species have been unequally classified into four distinct lineages that are not closely related (Kotlobay et al., 2018). For example, "Honey Mushrooms" from the Armillaria lineage, which cause the foxfire phenomenon and "Jack-o-Lantern Mushrooms" from the Omphalotus lineage are common examples of bioluminescent fungi. Despite their diverse lineages, evidence suggests that the origin of fungal bioluminescence can be traced back to a single evolutionary ancestry. The proof for this lies in the ability of luciferins and luciferases from distant lineages to cross-react and produce light successfully (Oliveira et al., 2012). This indicates a common evolutionary origin for the bioluminescent capabilities observed across these diverse fungal lineages. The emergence of fungal bioluminescence continues to puzzle researchers, as its exact purpose remains elusive. Speculations by Oliveira et al., 2012 suggest that it may function as a means of attraction for insects, aiding in the entomophilous dispersal of spores, a phenomenon observed in certain species of *Neonothopanus*. This revealed the evidence of circadian control over bioluminescence, potentially making this process more energy efficient by increasing light emission at night. However, not all fungal species exhibit this behavior and for some, bioluminescence may be simply a luminous by-product of metabolism, lacking a clear, defined purpose (Weinstein et al., 2016). The evolutionary implications of these different cases are yet to be fully understood, leaving the exact reasons and underlying mechanisms for fungal bioluminescence an ongoing area of investigation.

Bioluminescence in Insects

Bioluminescence can be noticed in various insects, beetles, click beetles, glowworms, railroad worms and fireflies (Viviani and Bechara, 1997). The biochemical mechanism of luminescence is similar across these insects (Wood, 1995), despite emitting a diverse range of wavelengths (Wilson and Hastings, 1998). Insects such as lantern flies and springtails also display bioluminescence, expanding the scope beyond just beetles and fireflies. In the case of springtails, only two families display bioluminescence upon mechanical stimulation, particularly during sexual phases for sperm transfer. Lantern flies, exemplified by *Fulgora lanternaria*, emit bright white light when both male and female individuals are in flight together, likely playing a role in their mating behavior (Hoffmann, 1984). On the other hand, glowworms and fungus gnats from the order Diptera showcase bioluminescence primarily during their larval stages. In these stages, the glow emitted by these insects serves the purpose of attracting prey, which they then capture using webs (Lloyd, 1983). The larvae of *Arachnocampaluminosa* are specifically highlighted as a prime example of this behavior

(Meyer□Rochow, 2007). Interestingly, female glowworm pupae also emit light to attract males (Hoffmann, 1984), indicating the multifaceted roles that bioluminescence plays in the life cycles and behaviors of these insects.

Fireflies

Fireflies, particularly the *Photinus pyralis* species, are extensively studied for their bioluminescent properties (Marques and Esteves da Silva, 2009) where all life stages of fireflies exhibit luminescence, with firefly larvae specifically using their glow for defensive purposes (McElroy, 1974; Lloyd, 1983). The illumination patterns of fireflies can differ, even among individuals of the same species and these patterns are highly encodable, indicating the potential for variation and specificity in their bioluminescent signals (McElroy, 1974; Hoffmann, 1984). Fireflies possess specialized organs known as lanterns in their abdominal segments. These lanterns are controlled by the firefly's nervous system (Wilson and Hastings, 1998). The bioluminescence produced by these lanterns plays a crucial role in various complex interactions both between different species (interspecific) and within the same species (intraspecific) (Lall et al., 1980). Fireflies have evolved visual sensitivity in parallel with their bioluminescence capabilities (Lall et al., 1980). This visual sensitivity is influenced by factors such as the environment they inhabit, the time of their activity, and other parameters. This adaptation allows fireflies to effectively utilize their bioluminescence in response to different circumstances, enhancing their communication, mating rituals, and defensive strategies. The signalling systems in fireflies are highly encodable, indicating that the patterns and characteristics of their flashes can convey specific and detailed information. These signals are species-specific, meaning that different species of fireflies may have unique patterns to differentiate themselves from others. Additionally, it highlights the crucial timing of these displays for maximum efficiency. Synchronous flashes being observed in various firefly species, sometimes in swarms spanning significant distances, such as up to 30 meters (Hoffmann, 1984). The spectacular nature of these displays, citing a specific example at the Chaophraya river in Bangkok. Despite the impressive nature of these displays, the biological significance of such synchronized flashing behaviors is still not fully understood (Lloyd, 1983). Uniqueness exists in firefly signalling mechanisms, noting that some species have evolved to mimic the specific signals of other species. For example, female fireflies of the genus *Photuris mimic* the female signal of *Photinus macdermotti* to attract and prey upon their males (Hoffmann, 1984). This illustrates the complexity of firefly signalling and the evolutionary strategies they employ for survival and reproduction.

Mechanism of bioluminescence in insects

A. fireflies

1. **Biosynthesis of Luciferin:**

The process starts with the biosynthesis of luciferin, the substrate responsible for generating light in fireflies. Fireflies are able to synthesize luciferin from a precursor molecule, arbutin (Oba et al., 2013). Through a series of enzymatic reactions involving hydrolase and oxidase enzymes, arbutin is converted into benzoquinone. Addition of cysteine to the hydroxybenzothiazole intermediate results in the formation of luciferin. It is important to note that only the D form of luciferin is utilized as a substrate for the bioluminescence reaction. The correct form of the structure is crucial for carrying out biological reactions effectively.

2. **Luciferin Catalyzed by Luciferase:**

In the presence of ATP and Mg, D-luciferin undergoes a reaction catalyzed by the enzyme luciferase. This enzymatic reaction results in the formation of an intermediate compound. Subsequent oxidation of the intermediate compound, in the presence of oxygen, leads to the generation of a cyclic dioxetanone ring structure. This structure is highly energy-rich and serves as the precursor for light emission. The energy-rich cyclic dioxetanone ring is further converted into an unstable oxyluciferin molecule, which exists in two forms: enol tautomer and keto tautomer. These tautomeric forms possess activated oxygen atoms that release photons in the form of light at varying wavelengths. The bioluminescent reaction in fireflies, catalyzed by luciferase in the presence of oxygen, is a complex biochemical process where the activated oxygen atoms within oxyluciferin release energy in the form of light (Marques and Esteves Da Silva, 2009).

B. Click beetles

Click beetles exhibit bioluminescence throughout their life cycle (Day et al., 2004), using it for purposes such as attracting prey, defense, mating communication, and general illumination (Hoffmann, 1984). Earlier reports implicated, click beetles also show intraspecific interactions. In elaterids, the bioluminescence of the abdominal lantern serves as an optical signal for intraspecific sexual communication, while the signals from the prothoracic lanterns are proposed to serve as warnings to predators and may also provide illumination during flight. This suggests that elaterids may utilize a similar strategy of spectral correspondence between visual sensitivity and bioluminescence emission from their multiple lanterns for various ecological and behavioural functions. (Lall et al., 2010). Current research explored the genomic cause of bioluminescence and its evolution with firefly, *Aquatica lateralis* as a model organism for beetle bioluminescence study (Oba and Schultz, 2022). Some of the elaterid beetles (Jamaican click beetle, *Pyrophorus plagiophthalamus*) show light colour polymorphism for predation, mating, communication and for thermoregulation (Stolz et al., 2003). Click beetle, *Pyrearinustermitilluminans* commonly found in termite mounds in central Brazil (Baldwin, 1996). These beetles have adapted to their environment and developed unique behaviors to thrive in their ecosystem. The larvae are found within illuminated termite mounds, where they extend their heads and emit an exceptionally green light from their prothoracic lanterns out of the tunnel mouths during the rainy season when ants and termites go on their alate flights (Bechara and Stevani, 2018). This behavior is used to attract flying adult termites and other insects.

Luciferases in beetles- Advantages and disadvantages

The process of bioluminescence in beetles involves the enzyme luciferase catalyzing a chemical reaction that generates light as a result. Beetle luciferases derived from insects require the cofactors ATP and Mg2+ in addition to the specific substrate and molecular oxygen (O2) for bioluminescence (BL) emission. These luciferases catalyze the oxidation of the substrate luciferins, leading them to an excited state. As these excited intermediates relax to the ground state, they emit photons, resulting in the characteristic bioluminescent glow. Researchers have been leveraging this mechanism to enhance the optical intensity and expand the color range of bioluminescence by making modifications to the luciferase and/or luciferin structures (Carrasco-Lopez et al., 2023). Conflicts exists between beetle luciferases and marine luciferases. There are some unique characteristics of beetle luciferases make them advantageous compared marine luciferases in various applications:

1. **Red-shifted BL spectra**: Beetle luciferases exhibit bioluminescence (BL) spectra at longer wavelengths compared to marine luciferases. This red-shifted emission property is beneficial because longer-wavelength light tends to undergo less attenuation in physiological samples and animal tissues. This feature allows for better penetration of the

emitted light, improving the visibility and detectability of the bioluminescent signal in biological systems.

2. BL signal stability: Beetle luciferases are known for producing stable BL signals. The stability of the bioluminescent signal generated by beetle luciferases is crucial for maintaining the accuracy and reliability of bioassays over an extended period. This stability ensures consistent and reliable results, making beetle luciferases suitable for long-term experiments and studies.

3. Low autoluminescence: Beetle luciferase systems have lower autoluminescence compared to marine luciferase systems. Autoluminescence refers to the background or unwanted signal generated by the luciferase system itself in the absence of the specific substrate or under certain conditions. The requirement of ATP and Mg2+ in addition to O2 for the beetle luciferase-luciferin reaction sets a high threshold for bioluminescent emission, reducing the likelihood of nonspecific signal generation. This low autoluminescence background in beetle luciferase systems enhances the signal-to-noise ratio and specificity of the bioluminescent output, making them advantageous for sensitive and precise detection applications.

C. Glowworms

Glowworms primarily use bioluminescence as a secondary trait for pheromone-mediated communication, with males being rarely bioluminescent and females being very luminescent. Additionally, the railroad worm *Phrixothrix* is noted for its aposematic nature, featuring bright green glowing patches and rare red headlights, which are used for defense and potentially as a warning to predators (Viviani and Bechara, 1997). The dipteran family Keroplatidae(Babu and Kannan, 2002) has wide range of bioluminescent glowworms. *Arachnocampaluminosa* deploys this luminescence via the distal ends of the Malpighian tubules located at the posterior end of its body (Viviani et al., 2018; Falaschi et al., 2019). the larvae of this species construct a horizontal web around a ribbon-like gallery in caves and banks within the bush, where humidity is high and they are protected from the wind (Viviani et al., 2002; Meyer□Rochow, 2007). The larvae are observed to suspend up to 30 small, sticky, vertical fishing lines, while continuously emitting blue-green light to lure flying insects, which serve as their prey (Viviani et al., 2002; Meyer□Rochow, 2007; Viviani et al., 2018). *Orfeliafultoni*, found in North America produces luminescence, notably from the black bodies of the anterior and posterior lanterns, as well as displaying diffuse bioluminescence throughout the body and its larvae inhabit moss rock cavities and sandstone caves, where they construct sticky webs and emit blue luminescence to capture flying prey (Viviani et al., 2018). The larvae of *Keroplatus*sps. emit blue light from their entire bodies (Osawa et al., 2014), a trait that is facilitated by the presence of proteinaceous granules in the fat bodies. Furthermore, it also exhibits a specialized feeding behavior, as they exclusively consume fungal spores that are trapped by horizontal mucilaginous webs beneath the fungus (Osawa et al., 2014). The luminescence emitted by the larvae can serve as a warning signal, potentially repelling negatively phototropic enemies. The larvae of *Neoceroplatusbetaryiensis* emits blue bioluminescence, which is visible in the first thoracic segment and the last abdominal segment (Falaschi et al., 2019). They are typically found on tree trunks and fallen branches that are lodged between wood, surrounded by their secreted mucus. When disturbed, these larvae move quickly within their mucus, but interestingly, they stop emitting light when touched after a few minutes (Falaschi et al., 2019). Apart from these insects, bioluminescence is also evident in lantern fly, *Fulgora laternaria* (Fulgoridae, Hemiptera) (Oba and Schultz, 2022).

Other Bioluminescent arthropods

The diversity of bioluminescence within the Arthropoda phylum, extending beyond insects to include certain species of centipedes and millipedes. Few luminous species of centipedes and millipedes, such as *Motyxia*, have been shown to exhibit bioluminescence (Oba et al., 2017). Millipedes are known to exhibit aposematic signalling, which serves as a warning to potential predators about their toxicity (Marek et al., 2011).

Bioluminescence in pest management

The use of bioluminescence, such as the green fluorescent protein (GFP) derived from the jellyfish, in pest management is an innovative and promising approach. A study by Pavan et al., 2023 where the genetic material of the pink bollworm was modified with GFP. The GFP transgenic pink bollworm strain fluoresces strongly green in its larval stage. This fluorescent marker can be used for various purposes in pest management:

1. **Mapping Organism Distribution Patterns**: The fluorescent marker allows researchers to map the distribution of the pest. This can be valuable in understanding the spread of the pest population and identifying areas that require targeted pest management strategies.

2. **Field Performance Studies**: The GFP-marked strain of pink bollworm can be utilized for field performance studies. This hepls to track the movement and behavior of the pest in agricultural settings, providing insights into its ecological interactions and enabling the evaluation of pest management strategies.

3. **Potential for Enhanced Pest Management**: The future objective is to add a temperature-sensitive lethal gene along with the GFP gene into the pink bollworm. This would create a strain of the pest that is not only fluorescent but also potentially susceptible to temperature-based control measures. By introducing a temperature-sensitive lethal gene (Chapman, 2014) it may be possible to develop a method for targeted pest control, where the modified pests would be susceptible to specific temperature conditions, allowing for population control without widespread environmental impact.

Conclusion

Bioluminescence is a captivating convergence of evolutionary adaptation and biochemical innovation found in diverse organisms, from bacteria and fungi to insects and arthropods. This phenomenon serves various ecological purposes, including attracting mates, luring prey, deterring predators and facilitating symbiotic relationships. In bacteria, luminescence plays a vital role in mutualistic interactions, particularly with marine organisms, while fungi contribute to spore dispersal in a limited number of species. In insects, especially fireflies and click beetles, bioluminescence is crucial for communication, mating and defense, reflecting complex interactions within and between species. Glowworms further demonstrate diverse ecological strategies linked to luminescence. Additionally, bioluminescence research has led to innovative pest management applications, such as genetically modified organisms with luminescent markers, which improve understanding of pest behavior and offer environmentally friendly control methods. As research progresses, the significance of bioluminescence as a key component of ecological interactions and evolutionary success becomes increasingly evident, promising further insights into its functions and applications in both nature and science.

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