#### **Bioluminescence**

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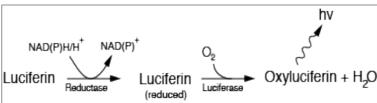
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#### What is Bioluminescence?

Bioluminescence is the emission of light by an organism as a result of a biochemical reaction. In contrast to fluorescence and phosphorescence, bioluminescence reactions do not require the initial absorption of sunlight or other electromagnetic radiation by a molecule or pigment to emit light. Bioluminescent systems produce light through the oxygenation of a substrate, generically called *luciferin* (lat. *lucifer*, the light-bringer), and an enzyme, *luciferase*. Bioluminescent reactions vary greatly among organisms but can generally be described as a luciferase catalyzed production of an excited intermediate from oxygen and luciferin that emits light when returning to its ground state. Additionally, many bioluminescence systems involve cofactors such as FMNH<sub>2</sub>, ATP, additional enzymes and intermediate steps for the light production (Figure 1). In some bioluminescence systems special types of luciferases, photoproteins, bind and stabilize the oxygenated luciferin and emit light only in the presence of cations, such as Mg<sup>2+</sup> or Ca<sup>2+</sup>, which acts as an mechanism for the host to precisely control the timing of the light emission.

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Figure 1 - Schematic of the fungal bioluminescence reaction as proposed by Oliveira et al., Evidence that a single bioluminescent system is shared by all known bioluminescent fungal lineages. Photochem. Photobiol Sci, 2012, 11:848.

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## How does bioluminescent light differ among organisms?

Light production in bioluminescence has a remarkable range of emission patterns such as continuous glow (Figure 2 A,C), single flashes of light, e.g. in dinoflagellates, or repetitive pulse patterns that are often species-specific (Figure 2B). Bioluminescent light is emitted in wavelengths between 400-720nm, from violet into the near-infrared. The majority of bioluminescent marine organisms emit blue light (410-550nm) which correlates with the peak sensitivities of the opsins of many marine organisms. Interestingly, wavelengths of bioluminescent light seem to shift based on the habitat of the organism: from violet and blue (420-500nm) in the deep sea to blue-green (460-520nm) in shallow waters to green-yellow (520-580nm) on land, and its hue is often correlated with the optical characteristics of the environment (Figure 2D). The color of the bioluminescent light is dependent on multiple factors such as the luciferins and luciferases that are involved in the

bioluminescent reaction or the conformation of the luciferase. In some bioluminescent systems fluorescent pigments, e.g. the green fluorescent protein (GFP), act as secondary emitters that affect the emitted color of the light. In addition to variations of the light emitting molecules some organisms alter the original color of the bioluminescence through anatomical structures that act as biological filters and can refract or reflect the emitted light.

## How is bioluminescence distributed among taxa?

To date, bioluminescence has been reported in nearly 700 prokaryotic and eukaryotic genera. The majority of bioluminescent organisms inhabit marine environments including bacteria, dinoflagellates, molluscs, custraceans, bony fish and sharks. In contrast to marine species bioluminescence has not been confirmed in any fresh water organisms. On land, bioluminescence is less common and almost exclusively found in the kingdoms Fungi and Animalia. Approximately 70 species of fungi in four lineages of order Agaricales are bioluminescent. In Animalia, bioluminescence has been reported in two phyla, Nematoda and Arthropoda. Phylum Arthropoda includes one of the best-known groups of terrestrial bioluminescent organisms, the fireflies (order: Coleoptera).

# How diverse are bioluminescence systems and what are their evolutionary origins?

Bioluminescent systems are as diverse as their host organisms. Few bioluminescence systems are conserved among related taxa with the exception of fungi which are thought to share one conserved bioluminescence system. Generally, luciferins are more widely conserved than luciferases. For example, the luciferin *coelenterazine* is found in the bioluminescent systems of at least nine different marine phyla. In contrast, the luciferases used are highly diverse and often species specific. It is currently estimated that bioluminescence has independently evolved more than 30 times which suggests that the molecular building blocks of bioluminescence systems are ubiquitous. Nevertheless, their evolutionary origins remain mysterious. One hypothesis is that bioluminescence evolved from detoxification systems as some luciferins show characteristics of strong antioxidants. Additional hypotheses propose mixed-function oxygenases or, in case of the beetle luciferase, certain types of ligases as the origins of luciferases.

### What are the ecological functions of bioluminescence?

Despite the ubiquity of bioluminescence and the fact that early reports of bioluminescence date back to ancient Greece (Aristotle, 384 – 322 BC and Pliny the Elder, 23-79 AC), evidence for its ecological functions is scarce. Suggested functions of bioluminescence in organisms are diverse and include: camouflage via counter-illumination, escape-mechanisms through dazzling predators, aposematism (warning colouration), prey luring, and courtship. However, outside of animal taxa the possible functions of

bioluminescence are less clear, e.g. in bioluminescent bacteria, or in fungi that only possess luminescent mycelium. For bacteria one hypothesis is that bioluminescence promotes beneficial interactions with host organisms as several bioluminescent bacteria are found as symbionts in the light organs of organisms that lack the ability to emit light themselves. Another hypothesis is that bioluminescence may be incidental in some organisms and that the emission of light is merely a byproduct of another essential metabolic function. However, the repeated evolution of bioluminescence suggests that it may directly or indirectly provide its producer with a selective advantage over its non-luminescent counterparts.



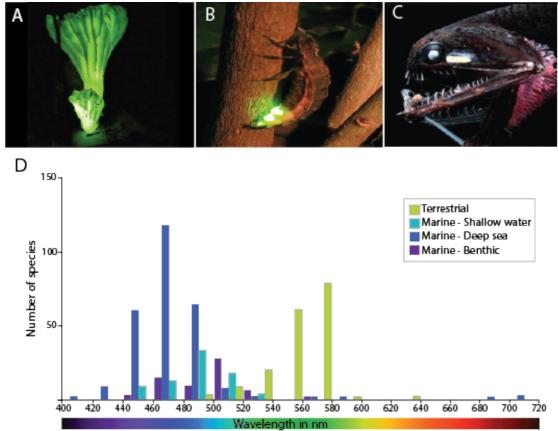


Figure 2 – Bioluminescence patterns and distribution among different species: continuously green ( $\lambda_{\rm max}$  530nm) glowing fungus *Neonothopanus gardneri* (A); green-yellow ( $\lambda_{\rm max}$  ~550nm) pulsing light organ of the common glowworm (*Lampyris noctiluca*) (C); glowing light organ of a dragonfish *Photostomias guernei* continuously emitting blue ( $\lambda_{\rm max}$  530nm) light (C). Wavelengths of bioluminescent organisms in different habitats. Number of species are approximated for intervals of 20nm redrawn from Widder *et al.* 2010 and Hastings 1996 . [Photo credits: A from "A. G. Oliveira, C. V. Stevani, H. E. Waldenmaier, V. Viviani, J. M. Emerson, J. J. Loros, and J. C. Dunlap, "Circadian Control Sheds Light on Fungal Bioluminescence," *Curr. Biol.*, vol. 25, no. 7, pp. 964–968, Mar. 2015"; B from "Lampyris noctiluca: "Lampyris noctiluca". Licenced under CC BY-SA 2.0 de by Wikimedia Commons"; C from "Widder E.A., "Bioluminescence in the Ocean: Origins of Biological, Chemical and Ecological Diversity", Science, 7 May 2010, Vol. 328 no. 5979 pp. 704-°© -708,DOI:.10.1126/science.1174269]

**Further reading** J. C. Day, L. C. Tisi, and M. J. Bailey, "Evolution of beetle bioluminescence: the origin of beetle luciferin," *Luminescence*, vol. 19, no. 1, pp. 8–20, Jan. 2004. D. E. Desjardin, A. G. Oliveira, and C. V. Stevani, "Fungi bioluminescence revisited," Photochem. Photobiol. Sci., vol. 7, no. 2, p. 170, 2008. M. Dubuisson, C. Marchand, and J.-F. Rees, "Firefly luciferin as antioxidant and light emitter: the evolution of insect bioluminescence," Luminescence, vol. 19, no. 6, pp. 339-344, Nov. 2004. S. H. D. Haddock, M. A. Moline, and J. F. Case, "Bioluminescence in the sea," Annu. Rev. Mar. Sci., vol. 2, pp. 443-493, 2010. J. W. Hastings, "Chemistries and colors of bioluminescent reactions: a review," *Gene*, vol. 173, no. 1 Spec No, pp. 5-11, 1996. C. V. Stevani, A. G. Oliveira, L. F. Mendes, F. F. Ventura, H. E. Waldenmaier, R. P. Carvalho, and T. A. Pereira, "Current Status of Research on Fungal Bioluminescence: Biochemistry and Prospects for Ecotoxicological Application," *Photochem. Photobiol.*, vol. 89, no. 6, pp. 1318–1326, Nov. 2013. V. R. Viviani, "The origin, diversity, and structure function relationships of insect luciferases," Cell. Mol. Life Sci. CMLS, vol. 59, no. 11, pp. 1833-1850, Nov. 2002. Widder E.A., "Bioluminescence in the Ocean: Origins of Biological, Chemical and Ecological Diversity", Science, 7 May 2010, Vol. 328 no. 5979 pp. 704-°© - 708,DOI:.10.1126/science.1174269