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Bioluminescence

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8 What is Bioluminescence?

9 Bioluminescence is the emission of light by an organism as a result of a biochemical reaction. In contrast to fluorescence and phosphorescence, 10 11 bioluminescence reactions do not require the initial absorption of sunlight or other electromagnetic radiation by a molecule or pigment to emit light. 12 13 Bioluminescent systems produce light through the oxygenation of a substrate, 14 generically called *luciferin* (lat. *lucifer*, the light-bringer), and an enzyme, *luciferase*. Bioluminescent reactions vary greatly among organisms but can 15 16 generally be described as a luciferase catalyzed production of an excited intermediate from oxygen and luciferin that emits light when returning to its 17 18 ground state. Additionally, many bioluminescence systems involve cofactors 19 such as FMNH₂, ATP, additional enzymes and intermediate steps for the light 20 production (Figure 1). In some bioluminescence systems special types of luciferases, photoproteins, bind and stabilize the oxygenated luciferin and 21 emit light only in the presence of cations, such as Mg²⁺ or Ca²⁺, which acts as 22 an mechanism for the host to precisely control the timing of the light emission. 23 24

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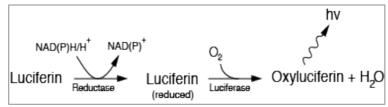


Figure 1 - Schematic of the fungal bioluminescence reaction as proposed by Oliveira et al., Evidence that a single bioluminescent system is shared by all known bioluminescent fungal lineages, Photochem. Photobiol Sci, 2012, 11:848.

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How does bioluminescent light differ among organisms? 30

31 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 32 33 dinoflagellates, or repetitive pulse patterns that are often species-specific

34 (Figure 2B). Bioluminescent light is emitted in wavelengths between 400-

35 720nm, from violet into the near-infrared. The majority of bioluminescent

marine organisms emit blue light (410-550nm) which correlates with the peak 36 37 sensitivities of the opsins of many marine organisms. Interestingly,

38 wavelengths of bioluminescent light seem to shift based on the habitat of the

39 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 40
- 41 hue is often correlated with the optical characteristics of the environment
- 42 (Figure 2D). The color of the bioluminescent light is dependent on multiple
- 43 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
- 46 protein (GFP), act as secondary emitters that affect the emitted color of the
- 47 light. In addition to variations of the light emitting molecules some organisms
- 48 alter the original color of the bioluminescence through anatomical structures
- that act as biological filters and can refract or reflect the emitted light.
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52 How is bioluminescence distributed among taxa?

53 To date, bioluminescence has been reported in nearly 700 prokaryotic and eukaryotic genera. The majority of bioluminescent organisms inhabit marine 54 55 environments including bacteria, dinoflagellates, molluscs, custraceans, bony 56 fish and sharks. In contrast to marine species bioluminescence has not been 57 confirmed in any fresh water organisms. On land, bioluminescence is less 58 common and almost exclusively found in the kingdoms Fungi and Animalia. Approximately 70 species of fungi in four lineages of order Agaricales are 59 60 bioluminescent. In Animalia, bioluminescence has been reported in two phyla, Nematoda and Arthropoda. Phylum Arthropoda includes one of the best-61 62 known groups of terrestrial bioluminescent organisms, the fireflies (order: 63 Coleoptera).

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How diverse are bioluminescence systems and what are theirevolutionary origins?

Bioluminescent systems are as diverse as their host organisms. Few 68 69 bioluminescence systems are conserved among related taxa with the 70 exception of fungi which are thought to share one conserved bioluminescence 71 system. Generally, luciferins are more widely conserved than luciferases. For 72 example, the luciferin *coelenterazine* is found in the bioluminescent systems 73 of at least nine different marine phyla. In contrast, the luciferases used are 74 highly diverse and often species specific. It is currently estimated that 75 bioluminescence has independently evolved more than 30 times which 76 suggests that the molecular building blocks of bioluminescence systems are 77 ubiguitous. Nevertheless, their evolutionary origins remain mysterious. One 78 hypothesis is that bioluminescence evolved from detoxification systems as 79 some luciferins show characteristics of strong antioxidants. Additional 80 hypotheses propose mixed-function oxygenases or, in case of the beetle luciferase, certain types of ligases as the origins of luciferases. 81 82 83

84 What are the ecological functions of bioluminescence?

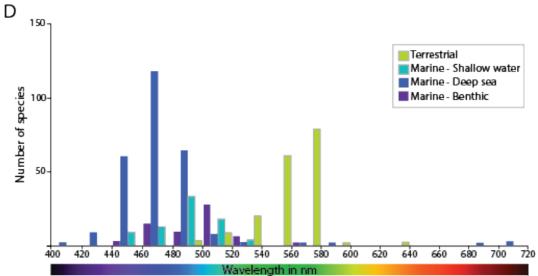
Despite the ubiquity of bioluminescence and the fact that early reports of
bioluminescence date back to ancient Greece (Aristotle, 384 – 322 BC and
Pliny the Elder, 23-79 AC), evidence for its ecological functions is scarce.
Suggested functions of bioluminescence in organisms are diverse and
include: 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

92 bioluminescence are less clear, e.g. in bioluminescent bacteria, or in fungi 93 that only possess luminescent mycelium. For bacteria one hypothesis is that 94 bioluminescence promotes beneficial interactions with host organisms as 95 several bioluminescent bacteria are found as symbionts in the light organs of organisms that lack the ability to emit light themselves. Another hypothesis is 96 97 that bioluminescence may be incidental in some organisms and that the 98 emission of light is merely a byproduct of another essential metabolic function. 99 However, the repeated evolution of bioluminescence suggests that it may 100 directly or indirectly provide its producer with a selective advantage over its non-luminescent counterparts. 101 102

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Figure 2 - Bioluminescence patterns and distribution among different species: continuously 107 green (λ_{max} 530nm) glowing fungus *Neonothopanus gardneri* (A); green-yellow (λ_{max} 108 109 ~550nm) pulsing light organ of the common glowworm (Lampyris noctiluca) (C); glowing light organ of a dragonfish *Photostomias guernei* continuously emitting blue (λ_{max} 530nm) light (C). 110 Wavelengths of bioluminescent organisms in different habitats. Number of species are 111 112 113 114 115 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, 116 117 Chemical and Ecological Diversity", Science, 7 May 2010, Vol. 328 no. 5979 pp. 704-°© -708,DOI:.10.1126/science.1174269]

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