Chapter

The Ecology of Bioluminescence

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Abstract

Bioluminescence, or the ability to emit light biologically, has evolved multiple times across various taxa. As fascinating as the phenomenon is, various studies have been undertaken to harness this phenomenon for human use. However, the origins, distribution and ecology of bioluminescence still remain obscure. The capability to produce biological light is found in various species, ranging from tiny bacteria to huge fishes like lantern sharks. Many organisms that do not possess this ability partake in symbiotic relationships, resulting in a variety of anatomical and behavioral modifications. The ecological interactions resulting from bioluminescence are even more interesting and diverse, but many of them are still shrouded in mystery because of a lack of *in-situ* study. As agreed by many, bioluminescence conferred certain evolutionary advantages which still remain unclear. In spite of the lack of understanding, many spectacular ecological interactions like offence, defense, courtship or intra-specific synchrony have been observed, studied and documented, and their significance understood. As far as humans are concerned, efforts are being made to channel this capability to the best of our use, though some of these are still in their infancy. This chapter explores the origins, ecology and future prospects of bioluminescence in detail.

Keywords: Bioluminescence, Ecology, Bioluminescent organisms, Firefly, Deep-sea fauna, Fungi

1. Introduction

'Bioluminescence' refers to the phenomenon of chemically induced emission of light (or other electromagnetic radiations) by a living organism. It is a common occurrence frequently observed in various organisms, ranging from simple ones like bacteria to complex animals like deep-sea fish or fireflies, and even some fungi. The first accounts of bioluminescence are found in the works of Dioscorides and even Pliny the Elder, who believed that certain bioluminescent organisms had medicinal properties [1]. There are accounts of coal-miners using dried fish skins, and even bottled fireflies as safe light sources [2]. Charles Darwin also wrote about the glowing oceans in his travails. E. N. Harvey conducted extensive studies on this phenomenon, and wrote the first detailed account of all natural bioluminescent forms. In biochemical terms, the phenomenon of bioluminescence occurs due to an interaction of a substrate luciferin with an enzyme luciferase. Shimomura et al. were the first to obtain crystalline luciferin from the sea firefly *Vargula hilgendorfii* [3].

In this chapter, we explore the origins of bioluminescence in nature, its distribution, and the many ecological roles that it plays. Furthermore, the harnessing of this phenomenon for human use and the future prospects have also been discussed in brief.

2. The evolution of bioluminescence

Since bioluminescence has proven to be an energy-expensive process, the evolution of bioluminescence in nature must be of some ecological or biological significance, or must offer some evolutionary advantage to the organism. This is certainly true, because there are multiple incidences of the evolution of bioluminescence, all completely independent from each other, and showing a convergent evolution pattern [4, 5]. This trait is found in multiple species spanning different phyla. Some even show symbiotic association with microbes. All these species use this phenomenon for a diverse range of applications including evasion of predators, luring prey and even attracting mates [6–8].

Since bioluminescence is so widespread in nature, scientists have been speculating the cause of its origin and selection in the first place. The first speculation was made by E. N. Harvey himself, who believed that it had something to do with respiratory chain proteins, some of which may have had fluorescent groups or side chains [9]. Owing to the extensive research that he conducted, his theory gained some attention and credibility. It was, however, soon disproved. Some even state that bioluminescence may have merely evolved as a by-product of other metabolic functions, having no importance of its own. However, the repetitive and independent origins of bioluminescence in nature must mean that this trait does confer a significant evolutionary advantage to the species that exhibits it [10].

One theory, proposed by Seliger et al. in 1993, stated that luciferases were actually a group of mixed function oxygenases [11]. According to him, bioluminescence evolved primarily as a means of intra-specific or inter-specific interaction in the dark, deep sea biome.

Rees et al. conducted an independent study on coelentrazine, which is a marine luciferin [12]. They came to the conclusion that bioluminescence may have evolved as a biochemical pathway, mainly for the disposal of peroxide, superoxide, and other harmful oxygen species produced in the course of metabolism. This may have additionally been favored by the acute absence of illumination in the dark depths of the ocean. Bioluminescence may have undergone natural selection as these species may have progressed deeper in the dark depths of the ocean, where the selective pressure for anti-oxidant defense naturally subsided.

As is clear from the above discussion, there was a unanimous agreement among many that bioluminescence may have evolved in the deep sea ecosystem. Even today, the vast depth of the ocean abounds in various species that exhibit this trait. These may range from microbes like bacteria and dinoflagellates to complex organisms like crustaceans, molluscs, jellyfish, various bony fish, and even cartilaginous fish like sharks [10].

As of today, bioluminescence has many more purposes apart from free radical disposal, like camouflage, counter-illumination, warning colouration, predation or courtship, [10] which have been discussed in further subsections.

3. Distribution

As stated earlier, bioluminescence has emerged independently in nature on multiple occasions. Nearly 700 to 800 genera spanning 13 phyla, including both prokaryotic as well as eukaryotic species, have been reported to exhibit this trait [10, 13]. The evolutionary trends of bioluminescence show exemplary convergent evolution in many cases, because of the almost similar purposes this trait serves in various species, or because of the similarity in the biochemistry of the molecules involved.

Bioluminescent organisms are found in both terrestrial as well as aquatic habitats. However, the aquatic species are exclusively limited to marine ecosystems, and a freshwater bioluminescent system is yet to be reported [10].

For the sake of simplicity, the distribution of this trait has been discussed separately for bacteria, fungi and protists, and higher animals have been discussed separately.

3.1 Bacterial bioluminescence

It is a common belief that bacterial bioluminescent systems were among the first to originate in nature. Bioluminescent bacteria are present in both terrestrial as well as aquatic habitats, and can be found all over the world. In fact, these bacteria can easily be sourced from any tissue or detritus lying on beaches, or even from uncooked seafood [4]. The glowing oceans, which are a spectacular result of these microorganisms, have been described in detail in the travails of Darwin, and can be observed, or rather enjoyed at various locations all over the world.

Bioluminescent bacteria mainly belong to the class *Gammaproteobacteria*, and are confined to three genera, namely *Vibrio*, *Photobacterium* and *Xenorhabdus*. Out of these, *Vibrio* and *Photobacterium* are mostly found in marine ecosystems, whereas *Xenorhabdus* inhabits terrestrial habitats [14]. New strains of bioluminescent bacteria are still being discovered [15]. A remarkable fact about bacterial bioluminescence is that all bacterial bioluminescent systems are exactly alike in terms of biochemistry, i.e., they all rely on flavin mononucleotide (FMN), myristic aldehyde and NADH, and also oxygen [16].

Bioluminescent bacteria may exist as free-living, symbiotic or even pathogenic forms. However, a completely obligate bacterial symbiotic system is yet to be observed in nature [8]. For example, *Vibrio fischeri* has been known to colonize specialized "light organs" [17] in the fish *Monocentris japonicus* [18], and also exhibits mutualistic relationship with Hawaiian squid *Euprymnia scolopes* [10, 14], and various species from the genus *Photobacterium* have been known to exhibit symbiosis with various fish, molluscs, etc. [19] and even cause diseases in some others [8]. However, there has been no genetic alteration in the bacterial genome for the said symbiosis. Though the animals showing the said symbiosis have developed exclusive modifications like light organs, they do not show any endosymbiotic behavior. The development of the said specialized organs may even be influenced by the presence of the symbiotic bacterial population [4]. One hypothesis accounts for the emergence of bioluminescence in bacteria because it promotes such symbiotic behavior, conferring a survival advantage to the microbes [10]. The symbiotic behavior may further be promoted because of the fact that the luminescent machinery of the bacteria is instrumental in getting rid of the reactive oxygen species produced in the host tissue [20]. The symbiotic microbes are obtained externally, and the hosts show some degree of selectivity towards the symbiont [8]. It appears that the host organisms 'choose' the colonizing symbiont according to the availability as per the depth which they inhabit. Furthermore, the said hosts can even dump the symbiont cells in order to keep their population in check [20].

Terrestrial bioluminescent bacteria are rare, and are known to infect nematodes that parasitize glowworm larvae. Upon the death of the larva, predators and scavengers ingest the carcasses, hence dispersing the bacteria as well as the nematode. Other than that, bioluminescent bacteria have been observed to inhabit various depths of the ocean, and are found even in sediments, seawaters, saline lakes, etc.

3.2 Fungal bioluminescence

Of all the bioluminescent systems that have been studied, fungal bioluminescence remains by far the most poorly investigated of them all, even though fungi are the only terrestrial eukaryotes that exhibit bioluminescence, besides animals [10]. This might be owing to the fact that most initial attempts at determining the enzymatic nature of fungal bioluminescence were failures, and have only recently been confirmed successfully [21]. The study of fungal bioluminescence has thus gained sudden prominence [22], and a genetically encodable bioluminescent system for eukaryotes has been developed [23]. Kaskova et al. conducted an extensive study of the fungal bioluminescence and colour modulation mechanisms [24].

Out of all the fungal species that have been documented till date, only about 71 [25] to 80 [26] fungal species have been known to exhibit bioluminescence. All of the said species have been unequally classified into four distinct lineages that are not so closely related [23]. "Honey Mushrooms" of the Armillaria lineage, the causative species for foxfire phenomenon, and the "Jack-o-Lantern Mushrooms" from the Omphalotus lineage are common examples of bioluminescent fungi. The origin of fungal bioluminescence can be attributed to a single evolutionary ancestry, the proof of which has been given by cross-reactions between the luciferins and luciferases of distant lineages to yield light successfully [21].

The purpose behind the emergence of fungal bioluminescence still remains elusive. Speculations have been made by Oliveira et al. that it may serve as a mode of attraction for insects, facilitating entomophilous spore dispersal, as seen in some species of *Neonothopanus* [27]. Furthermore, the same study revealed that there is some semblance of circadian control to make this entire affair more energy efficient by increasing bioluminescence at night. However, this is not true for all fungal species, wherein this trait may simply be a luminous by-product of metabolism, without a definite purpose [28]. The evolutionary feasibility of such cases is yet to be determined.

3.3 Bioluminescence in protists

Among protists, the chief groups that exhibit bioluminescence are Radiolaria (or Radiozoa), and Dinoflagellates, which are both exclusively marine. Both of these are described as follows:

3.3.1 Bioluminescent radiolaria

Among all the radiozoa, only two genera, namely *Collozoum* and *Thalassicola* are known to exhibit bioluminescence. Both of these belong to the order Collodaria, and use coelenterazine as substrate [4].

Bioluminescence has also been reported in some other deep sea species like *Aulosphaera* spp. and *Tuscaridium cygneum* [4].

3.3.2 Bioluminescence in dinoflagellates

Dinoflagellates are a group of cosmopolitan protistan organisms [29] having an ancient evolutionary history, which form one of the most important groups of phytoplankton in the aquatic ecosystems [30]. They are the only photosynthetic organisms that are capable of bioluminescence [30], and are the most dominant contributors to the occurrence of this phenomenon in the upper ocean [31]. Common phenomena like the "Red Tides" and the bioluminescent bays of Jamaica are because of the dramatic increase in the population of *Gonyaulax* and other dinoflagellate species. *Gonyaulax polyedra* is supposedly the most studied dinoflagellate species [20]. Other common bioluminescent genera are *Ceratium*, *Protoperidinium*, *Pyrocystis*, *Noctiluca*, [31] and *Alexandrianum* [29]. There have been inaccurate records of bioluminescent dinoflagellate species in the past, because of the presence of both bioluminescent as well as non-bioluminescent strains belonging to the same species. Difference in the ability has been observed even between cells of the same strain [31].

The chemical structure of dinoflagellate luciferin (sourced from *Pyrocystis lunula*) is remarkably unique [20], similar only to that found in euphausiids (krill). This perhaps is an example of dietary linkage, as krill are known to source their luciferin from the food they consume [4]. Dinoflagellate luciferin is believed to be a derivative of chlorophyll [20]. Unlike most species that are autotrophic in nature, some heterotrophic species even supplement their luciferin synthesis with chlorophyll-rich diets [4].

Dinoflagellates produce bioluminescence with the help of specialized cell organelles called "scintillons", which enable them to glow only in response to shear or physical disturbance/turbulence in the surrounding water [31]. This glow is not persistent, but occurs in brief flashes. The intensity of these flashes may be affected by various factors like exposure to prior illumination, nutritional state of the cell, or even because of a diurnal rhythm [31]. There are evidences of a circadian rhythm that is operational in dinoflagellates, and also photoinhibition of bioluminescence during daytime [29]. The synthesis and destruction of luciferin is not the only method of regulation though; cellular redistribution of luciferin has been reported to be affected by the said circadian rhythm [20]. The intensity of the flashes also differs from species to species. Dinoflagellates prioritize bioluminescence second only to reproduction, to an extent that there have been reports of cannibalism under nutritional stress in order to support bioluminescence [31].

As far as the ecological purpose of bioluminescence in dinoflagellates is concerned, we are still unclear as to why these organisms take such measures to sustain it. The exact ecological context of this trait still remains unclear, maybe because of a lack of *in-situ* studies [29]. Some studies show that the flashes of light have a startling effect on copepods (the prime predators of dinoflagellates), which dart away from the prey [32]. Another speculation, called the "Burglar Alarm" hypothesis, states that the brief flashes produced by the cells upon coming in contact with a grazer (for example, a copepod) in turn attracts a predator of higher trophic level, hence protecting the cell from its own predator. This hypothesis is widely accepted, although there are no sufficient evidences of the same [4]. Furthermore, this hypothesis does not point out any clear advantage to the dinoflagellate [31].

To conclude, bioluminescence in dinoflagellates seems to be a useful but unnecessary evolutionary trait, as an accurate ecological context is yet to be determined [30]. In order to gain more knowledge on the same, coastal blooms can be harnessed as natural laboratories to study dinoflagellate bioluminescence in further detail [29].

4. Bioluminescence in animals: distribution and ecological significance

As it is expected, the complexity of bioluminescence certainly upgrades as we proceed upwards in the tree of life. There are no plants (terrestrial or aquatic) that exhibit bioluminescence. Fungal bioluminescence is rare, and has been discussed in the previous sections. Coming to bioluminescence in animals, there is a strong agreement that the evolution of bioluminescence first occurred in the ocean, as the oceanic ecosystem offers many favorable conditions like optical homogeneity, stability of environment, large areas that are almost or completely perpetually dark and a large diversity of organisms that can engage in a variety of ecological interactions [4]. This, and the fact that both luminous as well as non-luminous prey in the ocean are rich in luciferins ensures that the emergence of bioluminescence in the ocean must have been a comparatively easy process [4, 33, 34]. The phenomenon of bioluminescence is so significant in the oceanic ecosystem, that it serves as the predominant source of illumination in many parts of the ocean [35]. Furthermore, courtships involving bioluminescence have been reported to show higher species accumulation rates than those without bioluminescence [36]. The presence of many independent coelenterazine-mediated bioluminescent systems, nine different phyla to be exact [10], indicates dietary linkage, as coelenterazine is procured by most species mainly through their diet [16]. Bioluminescence is encountered most commonly in the topmost 1 kilometer layer of the ocean, and is doubtlessly the most efficient mode of communication in the oceanic ecosystem [35]. The ability to glow is strongly habitat dependent because of various selection forces described earlier, and it is observed that there is a marked difference in the occurrence of this trait as we go deeper in the ocean [35].

Bioluminescence is also common in the terrestrial ecosystems, though it is nowhere as abundant as in the ocean. Various worms and arthropods are known to exhibit complex behaviors related to this phenomenon. It is clear that bioluminescence has a powerful impact on behavioral and ecosystem dynamics [4].

In this section, bioluminescence has been followed as a trait through various animal phyla, both terrestrial and aquatic, and its ecological significance is simultaneously discussed.

4.1 Bioluminescence in ctenophores

Comb jellies are the phylogenetically the most basic examples of bioluminescence in animals. Many species like *Mnemiopsis* [20, 37] use calcium activated coelenterazine as their bioluminescent substrate [4]. Some species, for example *Beroe forskalii* are known to produce myriad, cascading wave-patterns of intrinsic glow on their bodies, and some even emit a haze of glowing particles to startle the predator as a defensive measure, coupled with an escape response [38]. A majority of pelagic species are likely to exhibit bioluminescence [35]. The photo-proteins involved in bioluminescence in various genera like *Mnemiopsis* and *Beroe* have been studied, and are known to depend on calcium ions for their activity [39, 40].

Many comb jellies like *Pleurobrachia* and some species of the genus *Beroe* also show a startling display of rather colorful lights, in various wavelengths found in the visible spectrum. This was mistakenly believed as bioluminescence in the past. However, the said lights were not actually "produced" in the organism itself, as was evident in some studies [41, 42]. This iridescence was rather found to be a result of refraction of ambient light through the moving combs as the organism swims around [43].

4.2 Bioluminescence in cnidarians

Cnidarians in both pelagic as well as benthic zones, including corals, anemones, hydroids and medusae are known to exhibit bioluminescence. All of them use the luciferin coelenterazine as the substrate for their biochemical pathways (hence the name "coelenterazine"). Most of the pelagic siphonophores encountered show bioluminescence [4, 35]. The most common examples of bioluminescent coelenterates is the shallow-living hydrozoan Crystal Jelly (*Aequorea victoria*), the sea pansy *Renilla* and also the bamboo corals from the pelagic zone [44]. Anatomically, light producing centers, or photocytes, may be clustered or widely scattered all over the body, located around the endodermal layer [20]. The bioluminescent system of *Renilla* has been studied extensively, and attempts have been made to triangulate and engineer the genes from the source into various eukaryotic (plant) systems [45].

Cnidarians use bioluminescence for various defensive, agressive as well as warning purposes. Some jellyfish show glowing wave patterns on their umbrellas, and even emit clouds of glowing particles as a part of their escape response [4]. Siphonophores use bioluminescence to attract prey within reach of their cnidocytes. Some jellyfish are also known to show aposematic glow, which is indicative of distastefulness. Cnidarians can gain a lot from aposematic bioluminescence, as it would not only warn the predators of the unpalatability of the individual, but also protect them from any physical injuries [4]. However, many predator species like leatherback turtles use this to their advantage, and easily locate prey like jellyfish.

4.3 Bioluminescence in annelids

Bioluminescence in annelids has independently emerged in several lineages [46], resulting in a rich taxonomic diversity [36] spanning across 45 different genera in 13 lineages of clitellates and polychaetes [7]. They are found in diverse terrestrial and aquatic habitats all across the globe.

Clitellates are the only terrestrial annelids known, including potworms and earthworms from families Lumbridae [47] and Megascolidae [48]. Most of them emit brief flashes, and secrete a slimy coelomic fluid packed with bioluminescent granules [47, 49] under mechanical, chemical [50] or electrical stimulation. The same trend is seen in benthic species from the family Chaetopteridae [46, 51]. This is basically a form of aposematism or advertisement of distastefulness or toxicity [52], due to which predator species avoid such individuals from a distance [7].

In the marine ecosystems, polychaetes are the predominant annelid species in both pelagic as well as benthic zones [53]. Unlike their terrestrial counterparts, marine annelids show an interesting diversity of adaptations of bioluminescence, which they use for a variety of functions. The swarming behaviors of *Chaetopterus* and *Odontosyllis* spp. [51] and their flashing patterns [54] have been studied in detail. The bioluminescent "bombs" of the deep-sea genus *Swima* are detonated upon the slightest disturbance, facilitating an almost ninja-like distraction while the animal swims to safety [55]. Several members of the family Tomopteridae are known to produce golden yellow light, which is quite rare in aquatic ecosystems [56]. Scale worms (family Polynoidae) emanate flashes when disturbed, and even break off one or more bioluminescent scales or even whole parts of the body [57] as decoys or sacrificial lures for the predator while they flee [46]. Some species even shoot sticky glowing mucus at the predators to hamper their mobility, distracting them while making them even more conspicuous [58]. Arrow worms (Chaetognatha) are also known to adapt similar defensive measures. Light production also wards of symbiotic bacteria that overcrowd the tubules of some annelids [59]. Bioluminescence is also used as a mode of intraspecific communication in annelids [7]. Some members of the families Syllidae and Cirratulidae exhibit bioluminescence as a part of their mating behaviors. Elaborate bioluminescent courtship displays of the genus *Odontosyllis* are even known to align with lunar cycles [52, 60].

4.4 Bioluminescence in molluscs

Bioluminescence in molluscs is represented by many unusual taxa, for example the bivalve *Pholas*, the biochemical machinery of which has been extensively studied. Also, the sea-firefly *Cypridina* is a specimen of significance, as its bioluminescent system was among the first to be studied and analysed in detail [3, 61]. The only bioluminescent organism from freshwater ecosystem, the snail *Latia* *neritoides*, is also a mollusc [62]. Also, the terrestrial snail *Dyakia striata* is another bioluminescent organism that has been studied in great detail [63, 64]. Also, the snail *Hinea brasiliana* uses flashes of blue light as an aposematic signal to ward off predators [65].

Cephalopods are the prominent representatives of bioluminescent molluscs, and some of these may have been the source behind the fables of the mythical Kraken. Among squids alone, there are about 70 bioluminescent genera, both symbiotic and intrinsic [66]. Most luminescent cephalopods use coelenterazine as substrate for bioluminescence [67]. Squids are almost flamboyant in their exhibition of bioluminescence. *Euprymna* is known to be symbiotic with the bioluminescent bacteria *Vibrio fischerii* to form exclusive light organs [10] which it uses for counter illumination [68]. The vampire squid *Vampyroteuthis* has light organs all over its body, and it even shoots glowing particles from the tips of its tentacles. The squid *Taningia danae* has light organs on the tips of its arms, which it uses for intraspecific communication as well as to lure, stun and baffle prey [69]. Even some octopods are known to use bioluminescence to lure prey into their glowing suckers [4]. Cephalopods are also known to autotomize entire glowing arms as decoys if threatened. Some species of octopus also use bioluminescence in courtship displays.

An interesting fact about sperm whales is that they hunt squid by triggering the burglar alarm mechanism around themselves to attract unsuspecting squids.

4.5 Bioluminescence in insects

Insects are the most predominant terrestrial organisms that exhibit the phenomenon of bioluminescence. A majority of the bioluminescent insects are beetles (Coleoptera), click beetles (Elateridae), glowworms & railroad worms (Phengodidae), and fireflies (Lampyridae) [70]. The biochemical mechanism of luminescence is similar in all of these [71], even though each of them emit a diverse palette of wavelengths [20]. Other insects like lantern flies (Homoptera), springtails (Collembola), etc. also show bioluminescence.

Among springtails, only two families exhibit bioluminescence upon mechanical stimulation. Bioluminescence occurs only during sexual phases, and is crucial for sperm transfer. Lantern flies, for example *Fulgora lanternaria*, emit bright white light when both the sexes fly together [72]. Glowworms and Fungus gnats from the order Diptera show bioluminescence only in the larval stages, where they use their glow to attract prey and snare them in webs [73]. The larvae of *Arachnocampa luminosa* are a prime example of such behavior [74]. Female glowworm pupae also glow to attract males [72].

Click beetles show bioluminescence in all stages of life [75]. In the larval stage, bioluminescence serves as a tool to attract prey, as well as for defense. The pupae also glow when illuminated, and adults use bioluminescence for various functions like defense, mating communication and even general illumination [72]. In glowworms, on the other hand, bioluminescence is only secondary to pheromone-mediated communication. Males are rarely bioluminescent, only in the sexual stages for seductive purposes, whereas larvae and females are very luminescent. The railroad worm *Phrixothrix* is highly aposematic, as its body is lined with bright green glowing patches, while it has red headlights, which is very rare among all animals [70].

Fireflies are among the most studied bioluminescent systems, especially the north American *Photinus pyralis* [76]. All life stages in fireflies are luminescent, and firefly larvae are known to use their glow for defensive purposes [73, 77]. Illumination patterns of fireflies may differ even for different individuals of the same species, and are highly encodable [72, 77]. Fireflies have specialized organs called lanterns in their abdominal segments, which can be controlled by the nervous system [20]. Since bioluminescence in fireflies forms the basis of various complex interspecific as well as intraspecific interactions, visual sensitivity according to the environment, time of activity and other parameters has evolved in parallel [78]. The signaling systems in firefly species are highly encodable, species specific, and crucially timed for maximum efficiency. Synchronous flashes are seen in various species, sometimes in swarms spanning 30 meters [72], producing spectacular displays like the ones at Chaophraya river, Bangkok. The biological significance of such displays are still not understood [73]. Due to the uniqueness of the signaling mechanism, some species have evolved to mimic other species specific signals. For example, female fireflies of the genus *Photuris* mimic the female signal of *Photinus macdermotti* to attract and prey upon their males [72]. Fireflies are also highly distasteful to predators, which is exhibited by their aposematic signals, a necessary counter measure to compensate for their high conspicuousness. Today, fireflies are adversely affected by the growing numbers of artificial lighting systems, which hamper their signaling and even cause direct mortality in some cases [79].

4.6 Bioluminescence in crustaceans

The evolutionary pathway of crustaceans reveals that bioluminescence has emerged multiple times. Many krill (euphausiids) are bioluminescent, showing biochemical pathways similar to diatoms [4]. Sergestids use bioluminescence for counter-illumination purposes. Cypridinids are known to release puffs of bioluminescent particles, and also have elaborate mating behaviors involving bioluminescence [4].

4.7 Bioluminescence in other Arthropods

Few luminous species of centipedes (Chilopoda) and millipedes (Diplopoda eg. *Motyxia*) have also been shown to exhibit bioluminescence [50]. Millipedes are also known to show aposematic signaling as a warning for toxicity [80].

4.8 Bioluminescence in echinoderms

Four out of the five classes of echinoderms, namely Ophiuroidea (brittle stars), Asteroidea (starfishes), Holothuroidea (sea cucumbers) and Crinoidea (sea lilies) are bioluminescent [50]. Echinoderms mostly use coelenterazine dependent bioluminescent systems, although some of them also use a novel photoprotein [4]. Bioluminescence is more commonly exhibited by echinoderms inhabiting deep seas. Many new bioluminescent taxa are still being discovered, and 70 ophiuroid species have been recognized to exhibit bioluminescence till date [81, 82].

4.9 Bioluminescence in tunicates

Many species of tunicates are known to exhibit bioluminescence, though planktonic tunicates are not as frequent exhibitors of the trait as planktonic larvacean Appendicularia. However, it cannot be ascertained accurately because some filter feeders (like *Pyrosoma*) may ingest and trap luminescent microbes and appear to be bioluminescent [50]. Species like *Balanoglossus* (Acorn worms) and *Ptychodera* of the class Enteropneusta are also known to be bioluminescent. Also, the sessile adult *Clavelina miniata* glows green when stimulated.

4.10 Bioluminescence in fish

Among vertebrates, fish are the only taxa that have the ability of bioluminescence. This trait is found in fish inhabiting all the depths of the ocean, but is most frequently encountered in specimens from the deepest recesses of the ocean [6]. Bioluminescence is found in about 1500 species of marine bony fish spanning 43 families in 11 different orders [4, 5, 83], out of which some like the anglerfish, flashlight-fish (*Photoblepharon*) and pony-fish (*Leiognathus*) harbor symbiotic bacteria in discrete, specialized light organs, while others produce glow intrinsically [84]. On the other hand, only a handful of shark species in three families of cartilaginous fish are known to exhibit bioluminescence [83]. Unlike bony fish species, cartilaginous fishes do not rely on symbionts for bioluminescence [85], but use an altogether different, unknown bioluminescent system [86]. Some other species like the midshipman fish *Porichthys* and various lantern-fish obtain their respective luciferins from dietary sources [13].

Fish use the ability of bioluminescence for a variety of applications like communication, evading predators, luring prey. The latter is highly expressed in various taxa inhabiting the deep seas. Various anatomical modifications (like the light organs in various bony fish and the esca of anglerfish) harbor symbiotic bacteria, which enable the fish to use the bacterial emission with ample control on the intensity as well as distribution of the emission [4]. Fish of the order Stomiiformes (like dragon-fish, etc.) have evolved most elaborately arranged photophores, including those emitting red light [4]. Cookie-cutter sharks are interesting examples of both counterillumination and mimicry, as they bait their prey with non-luminescent patches on their bodies that look like small fish.

Bioluminescence may also prove disadvantageous to some species in certain cases. For example, elephant seals follow bioluminescence to track down prey populations. Some studies have shown that seals prefer to hunt in locations where there are more bioluminescent individuals [4].

5. Future prospects

Even though we still need to understand the dynamics and biochemistries of many bioluminescent systems in nature, humans have already begun to put bioluminescence to various applications. Bioluminescent mechanisms have been used in the diagnosis of various pathological conditions in the form of Green Fluorescent Proteins (GFP) [20]. Furthermore, attempts are being made to incorporate bioluminescent systems into plants to supplement illumination [87–89]. However, these prospects are still in their developmental stages, and there are various challenges and issues that need to be tackled.

6. Conclusion

The emergence of bioluminescence in nature has occurred independently on multiple occasions, which certainly means that it confers some significant evolutionary advantage(s) which we are yet to understand fully. This is bolstered by the fact that there are so many species that exhibit this trait, and show a plethora of behavioral, anatomical and ecological trends so as to survive and thrive in various habitats. With a better understanding of these systems and their interactions, we will certainly be able to use this phenomenon to our advantage. However, there are some challenges that keep us from fully exploring certain bioluminescent systems.

For example, the deep sea bioluminescent systems are very hard to access, and thus *in-situ* observations are few and far between. With the advent of new tools and techniques, we shall be able to gain a better insight into the dynamics of these systems.

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