

Diversity of Bioluminescent Insects and Their Threats: Status and Struggles

ABSTRACT

Bioluminescence, a mesmerizing natural phenomenon, bridges the gap between the living and the luminous. In class Insecta, various species of insects show bioluminescence to attract their partners, to defend themselves and to snare their prey. Among the bioluminescent insect orders (Collembola, Diptera and Coleoptera), Coleoptera has the most diverse bioluminescent terrestrial insects. However, their unique abilities have led to innovations in lighting technology. Bioluminescent insects face significant threats from habitat destruction, light pollution, and pesticide use and these anthropogenic factors jeopardize their populations and disrupt their ecological roles. Conservation efforts are urgently needed to mitigate these threats and ensure the survival of these remarkable organisms, which are essential for maintaining ecosystem's health and biodiversity.

Keywords: *ALAN, bioluminescence, conservation, firefly, glowworm, habitat loss, and lighting insects.*

1. INTRODUCTION

Bioluminescence is the phenomenon wherein living organisms generate and emit light through a chemical reaction called "bioluminescence" (Shukla, 2022). Bioluminescent insects play crucial roles in attracting mates, deterring predators, and communicating within species (Zimmer, 2015; Navizet, 2021). In this process, chemical energy is converted into light energy by an enzyme (luciferase), hence, it is also called an enzyme-catalyzed chemoluminescence reaction. Earlier Aristotle documented the glowing dead fish and flesh (from bacteria), light from agitating seawater with a rod (from dinoflagellates), fireflies and glowworms (John, 2008). Bioluminescence can be found in nearly all kingdoms of life with a variety of luciferases and luciferins, the enzymes and light-emitting molecule involved in light emission, respectively (Brodli et al., 2018).

Bioluminescence is found in almost 700 genera, spanning various life forms (Kahlke & Umbers, 2016). Among animals, about 12-13 out of 25 phyla exhibit bioluminescence (Harvey, 1952). Most bioluminescent organisms live in marine environments, with rare instances in terrestrial fungi and animals (Kahlke & Umbers, 2016). In the animal kingdom, bioluminescence is reported in two phyla: Nematoda and Arthropoda. Within the arthropods, the subphyla Myriapoda and Hexapoda contain luminous species, while another significant arthropod subgroup, Chelicerata (including spiders and scorpions), lacks such species. In the Myriapoda subphylum, some millipedes (Diplopoda) and centipedes (Chilopoda) emit light, with a total of 24 known species (Rosenberg & Meyer-Rochow, 2009). Within the Hexapoda subphylum, bioluminescent species are found exclusively in elateroid beetles

(Coleoptera), fungus gnats (Diptera), and springtails (Collembola) (Oba et al., 2011; Oba, 2009).

The majority of coleopteran beetles with the ability for bioluminescence belong to the Elateroidea superfamily, encompassing various families such as Lampyridae (comprising around 200 species), Phengodidae (with approximately 200 species), Rhagophthalmidae (comprising about 100 species), and Elateridae (with over 100 species) (Kusy et al., 2021). In Collembola, luminescent species exist in the Neanuridae and Onychiuridae families, with limited records (Harvey, 1952). There are questionable claims of luminescence in South American cockroaches (Blattodea) (Zompro&Fritzsche, 1999). However, Lepidoptera, the second-largest insect order, lacks known luminous species (Grimaldi & Engel, 2005). So far, the brightest insect discovered is the very large *Pyrophorusnoctilucus*(Linnaeus) (Elateridae), with a brightness of 45 milli lamberts. This insect is also known as the 'Jamaican Click beetle' and the 'Cucujo beetle' of the West Indies (Babu & Kannan, 2002). Delving into the mysteries of their behaviour and conservation, the secrets of this natural wonder are uncovered, and efforts are required to ensure the continued existence of these extraordinary insects. With the above in mind, this review unveils the diversity of bioluminescent insects and their associated challenges.

2. DIVERSITY OF BIOLUMINESCENT INSECTS

2.1 COLLEMBOLA (SPRINGTAILS)

Certain species of springtails (Collembola) possess the intriguing ability to emit light, as detailed in Table 1. Notably, *Lipuranociluca* (Macartney), *Anuridasp.* (Guérin-Méneville), *Anuridagranaria*(Nicolet) from the Neanuridae family, *Anurophorusfimetareus* (Nicolet) from the Isotomidae family, and *Onychiurusarmatus* (Tullberg) from the Onychiuridae family exhibit a continuous and pervasive glow throughout their bodies. In contrast, *Neanuramuscorum* (Templeton) and *N. quadrioculata*(Tullberg), also part of the Neanuridae family, emit intermittent flashes of light upon stimulation (Barber, 1913). The emitted light varies in colour across these species, ranging from bluish-green to greenish-yellow. However, the exact source of this luminosity in springtails remains a subject of inquiry, with possibilities including self-luminescence, consumption of luminous fungi, or accidental infection by luminous bacteria (Jiang et al., 2012; Sano et al., 2019).

Furthermore, within the realm of luminous springtails, *Lobella* sp., a member of the Neanuridae family, radiates yellowish-green light with a wavelength of 540 nm. This luminescence emanates from specific tubercles located on the thorax (segments II and III) and abdomen (segments I–VI) which can be observed through a low-light imaging system. Although this luminescence persists for several seconds, it occasionally displays oscillations. In *Lobella* sp., fat bodies housing eosin-positive granules exist beneath the integument of the tubercles on the tergum. Notably, these fat bodies are also present in the non-luminous springtail, *Vitronurasp.*, but devoid of eosin-positive granules. The fat bodies within *Lobellasp.* are believed to function as photo-cytes similar to the firefly's lantern, and the presence of eosin-positive granules strongly suggests that these granules are the primary origin of bioluminescence. This implies that springtails have the capacity for self-generated luminescence (Sano et al., 2019).

2.2DIPTERA (GLOWWORMS)

Glowworms represent the larval stage of fungus gnats within the genus, *Arachnocampa*. There are eight species of these glowworms found exclusively in Australia, along with a single species unique to New Zealand (Table 1). The New Zealand glowworm, scientifically known as *Arachnocampaluminosa* (Skuse) (Diptera: Keroplatidae), inhabits damp forest areas, stream sides, and caves (Von-Byern et al., 2016). These larvae use a specialized light organ at their rear, formed from modified Malpighian tubules, to emit blue-green light and attract prey. Notably, the luciferin substrate responsible for this light production differs entirely from that of fireflies and other bioluminescent organisms and is synthesized from xanthurenic acid and tyrosine (Watkins et al., 2018). Glowworms exhibit luminescence in all the instars, except during the egg stage, with the larval phase producing the brightest light. In cave environments, these insects can emit light at any time of day or night. When disturbed, a glowworm's light may appear to abruptly extinguish. Each light line they construct consists of silk threads adorned with sticky, bead-like droplets of mucus. Much of the larva's time is dedicated to creating and repairing these lines, generating 15–25 lines per night, with approximately 15 minutes spent on each one. Flying insects are drawn to the glowworm's light, mistaking it for moonlight filtering through trees. Tragically, they become ensnared in the sticky silk threads rather than finding freedom (Faust, 2017).

Whereas, *Neoceroplatusbetaryiensis* Falaschi larvae inhabit fallen branches and tree trunks, concealed in secreted mucus. They may be found on trunks approximately one meter above the ground, displaying nocturnal activity. When disturbed, they retreat beneath their mucus. Before pupation, they create cocoons on logs beneath moss or fungi. Pupae also emit bioluminescence. The bioluminescence serves as a predatory mechanism to aid in feeding by luring prey close enough to be captured (Falaschi et al., 2019). *Orfeliafultoni* Fisher and *Arachnocampa* sp. are two similar brownish larvae, measuring approximately 10–20 mm in length and 1–2 mm in diameter (Amaral et al., 2021). They both create impressive webs in comparable environments, such as crevices along moist stream banks. However, *Orfelia* is rarely found on cave roofs and doesn't use "fishing lines" like *Arachnocampa* (Meyer-Rochow, 2007). Both species are carnivorous and may even exhibit cannibalistic behaviour. Despite their names, there is little evidence of fungi in their diets. *Orfelia* has blue bioluminescence that contrasts with blue-green as in *Arachnocampa*. *Arachnocampa* has one caudal lantern, whereas *Orfelia* has unique bilateral lanterns (Wilson & Hastings, 2012). These larvae thrive in early spring, even in cold temperature. When they are disturbed, they emit luminescent material, either as a secretion or due to injury (Meyer-Rochow, 2007; Ramesh & Meyer-Rochow, 2021).

2.3 COLEOPTERA (click beetle, leather winged beetle, firefly, glowworm beetles, rove beetle)

Bioluminescent click beetles belonging to family, Elateridae have two sets of light organs, one on the dorsal surface of the head that emits long flashes at rest, while a ventral organ emits during flight and this flash is extinguished on the ground due to closure of the cleft. Most emit longer wavelengths from the ventral organ. A large number of luminescent click beetle species, such as *Pyrophorus* and *Pyrearinus*, are found in Brazil (Table 1).

Table 1. Brief Inventory of insects exhibiting bioluminescence

Taxa	Distribution	Glowing instars	Colour variation	Significance	References*
Springtails (Neanuridae: Collembola)					
<i>Lobellasp.</i>	Japan	All instars and adults	Yellowish green	Not known (may be defence or courtship)	Sano et al. (2019)
<i>Lipuranoclituca</i> , <i>Anurida</i> sp., <i>Anuridagranaria</i>	cosmopolitan distribution				
Springtails (Isotomidae: Collembola)					
<i>Anurophorusfimetareus</i>	Europe and Northern America	All instars and adults	Bluish green to greenish yellow	Not known	Sano et al. (2019)
Springtails (Onychiuridae: Collembola)					
<i>Onychiurusarmatus</i>	Cosmopolitan distribution	All instars and adults	Bluish green to greenish yellow	Not known	Sano et al. (2019)
Glowworm flies (Keroplatidae: Diptera)					
<i>Arachnocampaluminosa</i>	New Zealand and Australia	Maggot	Blue green	Snaring prey	Watkins et al. (2018)
<i>Neoceroplatusbetaryiensis</i>	South America	Maggot and pupa	Blue	Snaring prey	Falaschi et al. (2019)
<i>Orfeliafultoni</i>	North America	Maggot	Blue	Predation	Viviani et al. (2002)
Click beetle (Elateridae: Coleoptera)					
<i>Pyrophorus</i> spp., <i>Pyrearinus</i> spp., <i>Conoderus</i> spp., <i>Hapsodrilus</i> spp., <i>Fulgeochlizus</i> spp., etc.	Brazil and Jamaica	Larva	Green	Predation	Arnoldi et al. (2007)
		Adults	Green to orange	Courtship	
<i>Sinopyrophorusschimmeli</i>	Southwest China	Adult	Yellowish green light	Unknown	Bi et al. (2019)
Leather winged beetle (Phengodidae: Coleoptera)					
<i>Phengodess</i> spp., <i>Phrixotrixhirtus</i> , <i>Pseudophengodes</i> spp., <i>Phrixothrix</i> spp., <i>Euryopa</i> spp., <i>Brasilocerus</i> spp.	Nearctic and Neotropical	Larva	Yellowish-green	Defence and predation	Viviani et al. (2007); Bevilaqua et al. (2019)
		All Female adults (larviform) and few males	Green and red	Warning signal (Aposematism)	
Firefly (Lampyridae: Coleoptera)					
<i>Photuris</i> spp. (femme fatale), <i>Macrolampis</i> spp., <i>Amydetes</i> spp., <i>Bicellonycha</i> spp., <i>Aspisoma</i> spp., <i>Lucidota</i> spp., <i>Cratomorphus</i> spp., <i>Photinus</i> spp., <i>Pyractomena</i> spp., etc.	Temperate and tropical climates	Larva	Yellow or green light	Predation	Copeland et al. (2008)
		Adult (female)	Yellow or green light	Predation / Deceptive signals (some shows aggressive mimicry)	
<i>Phausis reticulata</i> (Blue ghost)	Eastern and central United States	Males display a steady glow	Bluish-white	Spotting glowing females for mating	Frick-Ruppert et al. (2008)
Glowworm beetles (Rhagophthalmidae: Coleoptera)					
<i>Diplocladon</i> spp., <i>Dodecatoma</i> spp., <i>Pseudothilmanus</i> spp., <i>Rhagophthalmus</i> spp., etc.	Eastern Palearctic and Oriental	larvae and females	Yellowish-green	Courtship and mating	Branham and Wenzel (2003)
Rove beetles (Staphylinidae: Coleoptera)					
<i>Xantholinus</i> spp.	Brazil	Larvae	Green-bluish	The larvae glowed when disturbed and the tiny light could be observed only in the complete darkness.	Rosa (2010)

Jamaican large click beetle, *Pyrophorus plagiophthalmus* Germar produces two varied lights in its body with dorsal light ranging from green (548 nm) to yellow-green (565 nm), and ventral light from green (547 nm) to orange (594 nm) (Wood et al., 1989). Whereas in the click beetle, *P. termitilluminans* Costa exhibits the blue coloured bioluminescence with the peak wavelength of 534 nm. Among the click beetles, *Fulgeochlizus bruchi* Candeze relies only on the functioning abdominal lantern to produce a vibrant green bioluminescence without any thoracic lanterns and this abdominal lantern displays the most pronounced blue-shifted bioluminescence (Amaran et al., 2012).

Fireflies belong to the family Lampyridae with 2400 described species in 11 subfamilies globally (Martin et al., 2019; Riley et al., 2021) (Table 1). About 45 species have been recorded from India. Each firefly species in their larval stage displays bioluminescence in order to signal their potential predators about the presence of defensive chemicals in them (unpleasant to consume) (Powell et al., 2022). Based on the habitat preferences, fireflies are categorized into terrestrial groups (such as genera *Lychnuris*, *Asymmetricata* and *Pteroptyx*), aquatic species (*Aquatica* and *Luciola*), and semi-aquatic species (*Pygoluciola*) (Fu et al., 2012). Most of the firefly larvae prey actively on slugs and snails, by their sharp jaws which injects a potent toxin to paralyze them. Finally, they feed on the prey which are hundred times larger in size than themselves (Dreisig, 1978). *Lampyrus noctiluca* Linnaeus prefers brown, banded yellow, and unbanded yellow snails whereas, *Phosphaenus hemipterus* Goeze prefers to feed on earthworms (De-Cock & Matthysen, 2005). They spend their entire larval stage as dedicated hunters and prey voraciously. Most of the species, such as *Lampyrus sardinae* Geisthardt, *L. noctiluca* Linnaeus, *Phosphaenus hemipterus* Geoffroy, *Nyctophilareichii* Du Val and *Luciola lusitanica* (Charpentier) go through the pupation stage beneath various forms of cover, including leaf litter, stones, bark fragments, soil crevices, or within moss. Few species, like *Pelaniamauritanica* Linnaeus, choose ant nests as pupation sites. However, *Luciola* species build pupal mud chambers underground, while *Lamprohiza* species seem to form cells using tiny fragments of deceased leaf litter (Riley et al., 2021).

Leather winged beetles belong to the family Phengodidae, in which the larviform females exhibit bioluminescence from the paired organs on the body segments and sometimes on dorsal luminous bands (Branham, 2005). Males are typical beetles having shorter elytra, and plumose antennae for detecting female pheromones. Females hide during the day but emerge on warm, wet nights in June, displaying lights to attract males with keen eyes (Dahlgren, 1917). They are commonly referred to as "railroad-worms" due to the luminescent spots on the female's body, which resemble the internally illuminated windows of train cars at night. This distinctive feature is highly prominent in South American *Phrixothrix*. Eastern US *Phengodes* females retain larval characteristics and remain inactive during the day (Atkinson, 1887). At night, they display glowing dots and bands, producing greenish-yellow light through luciferin oxidation in gland cells (Burbanck & Lower, 1946). Some South American *Pseudophengodes* males possess firefly-like photic organs for finding its mate (Branham, 2005).

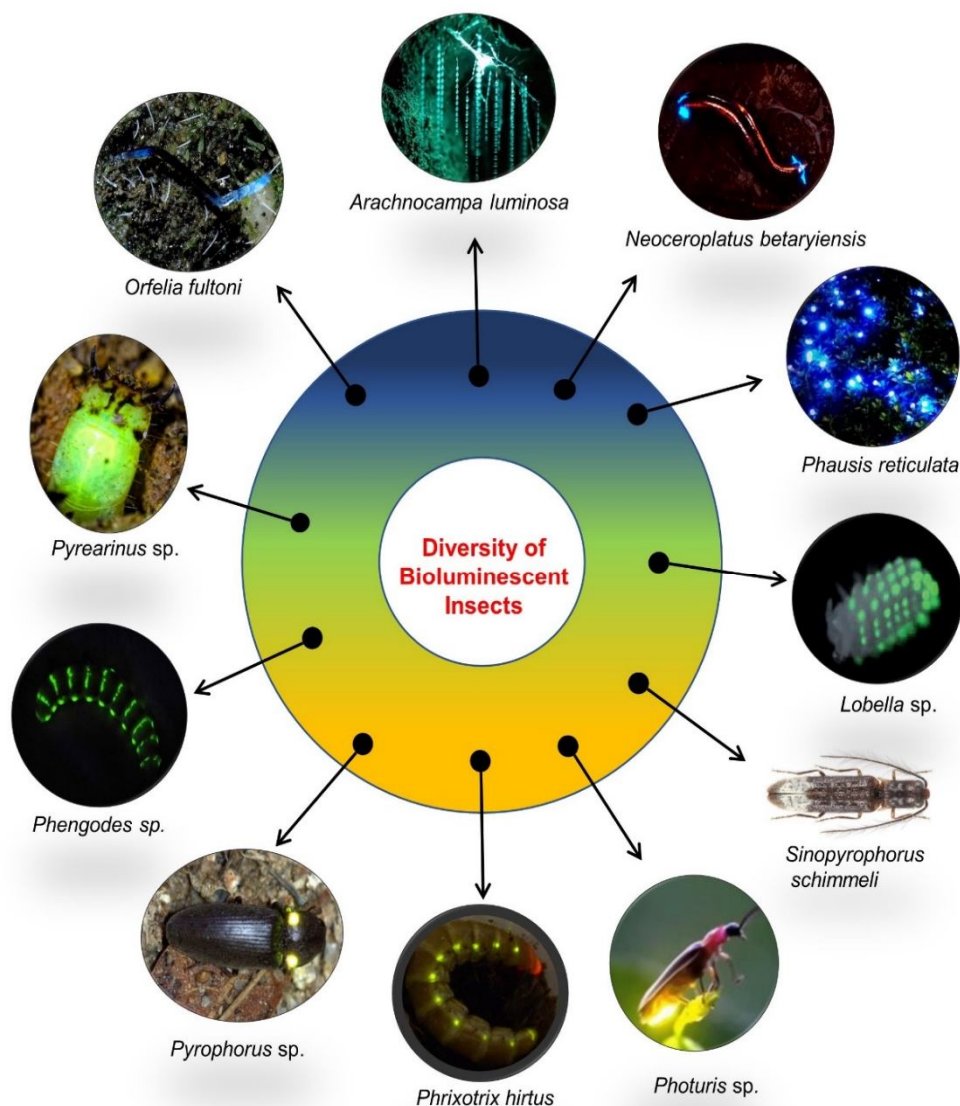


Fig. 1. Diversity of Bioluminescent insects.

Glowworm beetles belong to the family Rhagophthalmidae and the males are soft-bodied and capable of flight, whereas all known females are strongly paedomorphic and remain larva-like as adults. Predatory larvae can be found in the soil and leaf litter, where they primarily prey on millipedes. Both the larvae and adults of these species exhibit bioluminescence, although the biology and ecology of the majority of these species remain largely unexplored (Li & Liang, 2008; Kawashima et al., 2010).

The larvae and larviform females in the genus *Diplocladon* colloquially named as “Starworms” (Napompeth, 2009). This name is derived from the presence of three distinct rows of lights – one dorso-central and two on the lateral sides. These rows are created by three small light organs located on adjacent body segments, which emit a continuous yellowish-green glow (Li & Liang, 2008). Even though *Diplocladon* was reported by Gorham

in 1883, India and Indonesia have only two reported species within the genus, namely, *D. hasseltii* Gorham and *D. indicum* Gorham (Lawrence et al., 2000). In India, *Pseudothilmanus alatus* Pic has been recorded from Uttar Pradesh, and *Pseudothilmanus marginatus* Pic from Darjeeling (Li & Liang, 2008; Roza, 2020).

Some of the rove beetle species under the family Staphylinidae are bioluminescent. In Brazil, Costa et al. (1986) found the greenish-yellow light on the 8th abdominal segment of *Xantholinus* sp. with the peak wavelength around 568 nm. Later, Rosa (2010) described the greenish-blue bioluminescence from the pronotum along the mid-dorsal line emitting the brightest light. This luminosity gradually diminished over time and visible again only under absolute darkness.

3. THREATS TO BIOLUMINESCENT INSECTS

3.1 Habitat fragmentation

Habitat fragmentation is the process by which a single large area of habitat gets divided into several smaller patches that are isolated from one another by a matrix of habitats that is different from the original environment (Wilcove et al., 1986). Habitat loss can occur due to three primary factors: the disappearance of resident species, the reduction in available food resources, and the deterioration of ecosystem services provided by the habitat (Airoldi et al., 2008). However, anthropogenic activities such as habitat destruction and fragmentation have led to the loss of insect populations and altered their natural habitats, including the bioluminescent insects (Table 2).

3.2 Human interferences and ALAN

Tourism can negatively impact firefly populations by destroying their habitats used for egg laying, larval prey capture, growth, development, and pupation sites. This adverse effect is compounded by soil compaction, erosion, disruption of leaf litter, water pollution, and light pollution, which can indirectly contribute to habitat deterioration (Buckley & Pannell, 1990). Environmental activists have initiated a campaign opposing firefly festivals across the globe as like the firefly festivals in villages near the Bhandardara dam in Maharashtra, India. New Zealand's Waitomo Glowworm Cave draws 500,000 visitors annually to witness *Arachnocampaluminosa* Skuse (De-Freitas, 2010). Australia's glowworm viewing hubs include Marakoopa Cave in Tasmania, Natural Bridge in Springbrook National Park, Queensland, and Mount Tamborine in Queensland (Hall, 2012). Because of ecotourism, expert opines that the breeding season of these fireflies extends from May to June. However, visitors inadvertently harm female fireflies that remain underground, due to trampling (Figure 2). Trampling can also directly harm firefly survival by killing off ground-dwelling eggs, larvae, and pupae (Lloyd, 2008). Fireflies face human-induced threats, including disturbances such as handling larvae or their webs, as well as harmful activities like igniting fires (Merritt et al., 2013).

The specific lighting of night-time surroundings by human-created light sources such as streetlamps, walkway illumination, and vehicle headlights is commonly known as artificial light at night (ALAN) which is expected to disturb populations of crepuscular and nocturnal insect species residing in these impacted habitats (Davies & Smyth, 2018) (Figure 2). When cave-dwelling *A. luminosa* Skuse were subjected to white light at an intensity of 800 lux for five minutes, their bioluminescence diminished, and it took approximately one hour for them to recover (Meyer-Rochow & Waldvogel, 1979). Research conducted in Sorocaba, Brazil, revealed that artificial night lighting harms the population density of *Photinus* sp. (Hagen et al., 2015). The courtship behaviour of fireflies can be interrupted by a range of portable light

sources, including headlights, boat lights, flashlights, smartphones, and camera flashes (Thancharoen&Masoh, 2019).

Table 2. Habitat factors contributing to the threat faced by fireflies

Taxa	Causes for the threat	Country	Reference
<i>Lampyrisspp.</i> , <i>Nyctophila spp.</i> , <i>Luciola spp.</i>	Urbanization, industrialisation and intensification of agriculture	Europe	De-Cock (2009)
<i>Lampyrisnoctiluca</i>	Decline in pasture land	United Kingdom	Gardiner (2011)
<i>L. noctiluca</i>	Drought	United Kingdom	Atkins et al. (2017)
<i>Nyctophilareichii</i> , <i>Lampyrisiberica</i> , and <i>Lamprohizapaulinoi</i>	Orchards converted to xeric places which decreased snail population (primary prey).	Spain	Lewis et al.(2020)
<i>Pteroptyxtenor</i>	Decline in mangrove cover	Malaysia	Fuzi et al. (2022)

3.3 Pesticide usage

The widespread use of broad-spectrum insecticides has a direct impact on a wide range of arthropods. Clothianidin exposure significantly reduced long-term firefly survival at high concentrations (Pearsons et al., 2021). Residual insecticides, such as highly toxic imidacloprid and other neonicotinoids, have been shown to indirectly impact firefly populations by reducing the abundance of their primary prey, earthworms (Figure 2). This prey reduction affects *Photinus* fireflies in North America (Pisa et al., 2015). Pesticide exposure on Japanese fireflies (*Nipponoluciola cruciate* Motschulsky) revealed that the 5% emulsion of organophosphate insecticides (fenitrothion and difenphos) showed minimal toxicity to both *Nipponoluciola cruciate* Motschulsky larvae and their snail prey (Tabaru et al.,1970). The primary factor causing the decline in the population of *Abseonditachinensis*Linnaeus, the luminous firefly in Barrankula, Andhra Pradesh, India, seems to be the extensive use of chemical pesticides in paddy cultivation (Chatragadda, 2020). The combination of organophosphates (e.g., fenitrothion, phenthoate, Acephate, Fenthion, and Diazinon) with certain neonicotinoids led to 80-100% mortality in both larvae and adult of *Aquatica lateralis*Motschulsky (Lee et al.,2008).

3.4 Other environmental factors

Winter floods in Waitomo Glowworm Cave were documented to wash away a large number of firefly larvae (Richards, 1960). This decline is exacerbated by alterations in water quality and shifts in the cave's microclimate. Firefly population abundance in the Cherating River, Malaysia, was found to be influenced by five water quality parameters viz., water temperature, dissolved oxygen (DO), biochemical oxygen demand (BOD), chemical oxygen demand (COD), and ammonia nitrogen. Furthermore, Faudzi et al. (2021) unveiled a correlation indicating that regions with elevated water temperatures tend to harbor fewer fireflies. During the summer, the water levels in the Bhandardara dam's backwater (standing water) drop alarmingly, leading to complete drying. This in turn, results in the destruction of the habitat for firefly larvae, consequently causing a significant reduction in the population of *Ascondita* sp. fireflies (Pawar et al., 2023).



Fig. 2. Reasons for population decline of bioluminescent insects.

A. Natural habitat for bioluminescent insects: Negative impact of tourism on bioluminescent insects by B. light pollution, C. Trampling; D. Insecticide residues affecting the primary prey of bioluminescent insects; E. ALAN affects the mating of bioluminescent insects; F. Habitat destruction leading to population decline.

4. CONSERVATION OF BIOLUMINESCENT INSECTS

The conservation of bioluminescent insects are critical aspects of preserving these unique and ecologically important creatures. Additionally, these insects play vital roles in ecosystems and serving as indicators of environmental health. Habitat loss and degradation are critical threats to fireflies, necessitating conservation strategies that protect and manage habitats to support their full life cycle. This includes safeguarding areas for adult courtship, suitable oviposition and pupation sites, and habitats where larvae and their prey thrive. Many threatened fireflies are habitat specialists, so active management of these sites is essential to mitigate threats and prevent further degradation. Effective management involves legal protection, reducing light pollution, controlling insecticide use, and preventing disturbance of vulnerable life stages.

In Southeast Asia, *Pteroptyx* fireflies are vital for tourism revenue. After mating, females lay eggs in muddy river margins, and larvae hunt snails in the intertidal zone. To protect firefly tourism, the Selangor State Government and the Selangor Water Management Board established a river reserve in 2009, covering over 1000 hectares along 40 km of the Sungai Selangor. This reserve limits activities like land clearing and preserves 150–400 m of habitat on each riverbank (Wong, 2022). Though the tourism is a major threat for fireflies in Southeast Asia, the Selangor State Government and the Selangor Water Management Board established a river reserve to preserve the habitat of *Pteroptyx* fireflies.

In US, a budding movement is emerging among local conservation organizations and land trusts to establish Firefly Sanctuaries, which should be encouraged to follow published guidelines for best management practices (Fallon et al., 2019). In Japan, the Genji firefly has long been central to summertime firefly-watching, but it declined by the early 20th century due to water pollution and habitat degradation (Lewis, 2016). Hence, in 1970s, communities-initiated projects to clean rivers and restore habitats, leading to breeding programs and the release of captive-bred larvae. Citizens and school-children enthusiastically joined these efforts, and the Japanese government designated several high-quality habitats as National Natural Monuments. Today, conservation of Genji fireflies continues to receive widespread public support (Oba et al., 2011).

In India, to protect the *Abscondita* firefly population in the Bhandardara region, it is imperative that access to the Kalsubai Harishchandra Wildlife Sanctuary, Maharashtra be restricted to all tourists, particularly during the critical period from the end of May to the middle of June. It is advisable to limit entry into the forest area for local villagers only until evening hours. This precautionary measure helps minimize disturbances to the ecosystem during the night-time when the fireflies are most active. To mitigate light pollution in the area, it is recommended to exclusively employ low-intensity red lighting. This approach is specifically designed to reduce the adverse effects of artificial light on the local environment, especially in areas inhabited by fireflies (Pawar et al., 2023). In 2018, the Fireflyers International Network and the Malaysia Nature Society launched World Firefly Day on the first weekend in July, to raise awareness about firefly ecology and conservation. This event now attracts thousands of participants and it also include various activities like firefly-watching festivals, live demonstrations, webinars, art exhibits, night walks, and creative contests like haiku-writing and origami-folding (Kirton et al., 2012).

The IUCN SSC (International Union for Conservation of Nature's Species Survival Commission) Firefly Specialist Group has been assessing the extinction risks of around 2200 firefly species worldwide. Starting in 2020, they compiled data on the distribution, habitats, life history, behaviours, and threats for 130 firefly species and 2 subspecies in the

US and Canada, determining their conservation status using Red List criteria (Fallon et al., 2021).

5. CONCLUSION

Bioluminescent insects hold significant ecological and economic importance, playing vital roles in courtship, predation, and defense. This review has highlighted the remarkable diversity of these insects, from well-known fireflies and glowworms to the lesser-known railroad worms and click beetles. However, their survival is increasingly threatened by habitat loss, pesticide use, climate change, and light pollution, underscoring the urgent need for conservation. Protecting these extraordinary creatures requires a multifaceted approach, including habitat preservation, reduction of light pollution, pesticide regulation, public awareness, protection of breeding sites, policy implementation, and collaboration with NGOs. To address these challenges, sustained investment in research and conservation is crucial. Future studies should focus on species-specific vulnerabilities, the impacts of environmental stressors, effective conservation strategies, and the molecular mechanisms of bioluminescence to support both ecological protection and biotechnological advancements. These efforts not only protect biodiversity but also make sure that the enchanting glow of these insects continues for many more years.

Disclaimer (Artificial intelligence)

Option 1:

Author(s) hereby declare that NO generative AI technologies such as Large Language Models (ChatGPT, COPILOT, etc.) and text-to-image generators have been used during the writing or editing of this manuscript.

REFERENCES

- Airoidi L., Balata D. & Beck M.W. (2008). The gray zone: relationships between habitat loss and marine diversity and their applications in conservation. *J. Exp. Mar. Biol. Ecol.* 366(1-2): 8-15.
- Amaral D.T., Johnson C.H. & Viviani V.R. (2021). RNA-Seq analysis of the blue light-emitting *Orfelia fultoni* (Diptera: Keroplatidae) suggest photoecological adaptations at the molecular level. *Comp. Biochem. Physiol. Part D Genomics Proteomics.* 39: 100840.
- Amaral D.T., Prado R.A. & Viviani V.R. (2012). Luciferase from *Fulgeochlizus bruchi* (Coleoptera: Elateridae), a Brazilian click-beetle with a single abdominal lantern: molecular evolution, biological function and comparison with other click-beetle luciferases. *Photochem. Photobiol. Sci.* 11: 1259-1267.
- Arnoldi F.G.C., Ogoh K., Ohmiya, Y., & Viviani, V.R. (2007). Mitochondrial genome sequence of the Brazilian luminescent click beetle *Pyrophorus diversgens*

(Coleoptera: Elateridae): mitochondrial genes utility to investigate the evolutionary history of Coleoptera and its bioluminescence. *Gene*, 405(1-2): 1-9.

Atkins V., Bell D., Bowker A., Charig M., Crew J., Dale M. & Tyler, J. (2017). The status of the glowworm *Lampyrinoctiluca* L. (Coleoptera: Lampyridae) in England. *Lampyrid*, 4: 20-35.

Atkinson G.F. (1887). Observations on the female form of *Phengodes laticollis* Horn. *J. Elisha Mitchell Sci. Soc.* 4(2): 92-95.

Babu B.G. & Kannan, M. (2002). Lightning bugs. *Resonance*, 7(9): 49-55.

Barber, H.S. (1913). Luminous Collembola. *Proceedings of the Entomological Society of Washington*. 15:46-50.

Bevilaqua V.R., Matsushashi T., Oliveira G., Oliveira P.S.L., Hirano T. & Viviani, V.R. (2019). Phrixotrix luciferase and 6'-aminoluciferins reveal a larger luciferin phenolate binding site and provide novel far-red combinations for bioimaging purposes. *Scientific reports*, 9(1): 89-98.

Bi W.X., He J.W., Chen C.C., Kundrata R. & Li X.Y. (2019). Sinopyrophorinae, a new subfamily of Elateridae (Coleoptera, Elateroidea) with the first record of a luminous click beetle in Asia and evidence for multiple origins of bioluminescence in Elateridae. *ZooKeys*, 864: 79.

Branham M. (2004). Glow-Worms, Railroad-Worms (Insecta: Coleoptera: Phengodidae). *UF/IFAS Features Creatures*. EENY, 332: 1-5.

Branham M.A. & Wenzel J.W. (2003). The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics*, 19(1): 1-22.

Brodl, E., Winkler, A., & Macheroux, P. (2018). Molecular mechanisms of bacterial bioluminescence. *Computational and structural biotechnology journal*, 16, 551-564.

Buckley R. & Pannell J. (1990). Environmental impacts of tourism and recreation in national parks and conservation reserves. *J. Tour. Stud.* 1(1): 24-32.

Burbanck W.D. & Lower G.G. (1946). The American Railroad Worm: A Luminescent Insect Larva. *Bios*, 198-200.

Chatragadda R. (2020). Decline of luminous firefly *Absconditachinensis* population in Barrankula, Andhra Pradesh, India. *Int. J. Trop. Insect Sci.* 40(2): 461-465.

Copeland J., Moiseff A. & Faust L. (2008). Landing distance in a synchronic North American firefly. *Physiological Entomology*, 33(2): 110-115.

Costa C., Vanin S.A. & Colepicolo P. (1986). Larvae of neotropical coleoptera. Xiv. First record of bioluminescence in the family staphilinidae (xantholinini). *Rev. Bras. Entomol.* 30(1): 101-4.

Dahlgren U. (1917). The production of light by animals. *J. Frank. Inst.* 183(5): 593-624.

- Davies T.W. & Smyth, T. (2018). Why artificial light at night should be a focus for global change research in the 21st century. *Glob. Chang. Biol.* 24(3): 872-882.
- De-Cock R. & Matthysen E. (2005). Sexual communication by pheromones in a firefly, *Phosphaenushemipterus* (Coleoptera: Lampyridae). *Animal behaviour*, 70(4): 807-818.
- De-Cock R. (2009). Biology and behaviour of European lampyrids. In Victor B. & Meyer-Rochow (eds.): *Bioluminescence in Focus - A Collection of Illuminating Essays*, Research signpost, Trivandrum, Kerala, India, pp. 161-200.
- De-Freitas C.R. (2010). The role and importance of cave microclimate in the sustainable use and management of show caves. *Acta carsologica*, 39(3).
- Dreisig H. (1978). The circadian rhythm of bioluminescence in the glowworm, *Lampyrinoctiluca* L. (Coleoptera, Lampyridae). *Behav. Ecol. Sociobiol.* 3: 1-18.
- Falaschi R.L., Amaral D.T., Santos I., Domingos A.H., Johnson G.A., Martins A.G. & Stevani C.V. (2019). *Neoceroplatus betaryiensis* nov. sp. (Diptera: Keroplatidae) is the first record of a bioluminescent fungus-gnat in South America. *Scientific Reports*, 9(1): 11291.
- Fallon C., Hoyle S., Lewis S., Owens A., Lee-Mäder E., Black S.H. & Jepsen S. (2019). *Conserving the jewels of the night: Guidelines for protecting fireflies in the United States and Canada*. Portland, OR: The Xerces Society for Invertebrate Conservation, 56.
- Fallon C.E., Walker A.C., Lewis S., Cicero J., Faust L., Heckscher C.M. & Jepsen, S. (2021). Evaluating firefly extinction risk: Initial red list assessments for North America. *PLoS One*, 16(11): e0259379.
- Faudzi R., Abas A., Othman N.W. & Mazlan S.M. (2021). Effect of Water Quality on the Abundance of Firefly Populations at Cherating River, Pahang, Malaysia. *Environment Asia*, 14(1).
- Faust L.F. (2017). *Fireflies, glowworms, and lightning bugs: identification and natural history of the fireflies of the eastern and central United States and Canada*. University of Georgia Press.
- Frick-Ruppert J.E. & Rosen J.J. (2008). Morphology and behavior of *Phausis reticulata* (Blue ghost firefly). *J. NC. Acad. Sci.* 139-147.
- Fu X., Ballantyne L. & Lambkin C. (2012). The external larval morphology of aquatic and terrestrial *Luciolinae* fireflies (Coleoptera: Lampyridae). *Zootaxa*, 3405(1): 1-34.
- Fuzi N.F.A., Abd Rahman A. & Marzukhi F. (2022). Mangroves are Home to Fireflies (*Pteroptixtener* sp.) in Malaysia: A Review. *Social Sciences*, 12(7): 1592-1605.
- Gardiner T. (2011). *Glowing, Glowing, Gone? The Plight of the Glowworm in Essex*. British Naturalists' Association.
- Grimaldi D. & Engel M.S. (2005). *Evolution of the Insects*. Cambridge University Press.

- Hagen O., Santos R.M., Schlindwein M.N. & Viviani V.R. (2015). Artificial night lighting reduces firefly (Coleoptera: Lampyridae) occurrence in Sorocaba, Brazil. *Adv. Entomol.* 3(1): 24.
- Hall M. (2012). Glowworm tourism in Australia and New Zealand: commodifying and conserving charismatic micro-fauna. In Lemelin R.H. (ed): *The management of insects in recreation and tourism, Part III Insects and tourism*. Cambridge University Press, Canada. pp. 217-232.
- Harvey E.N. (1952). *Bioluminescence*. Academic Press, New York, pp. 649.
- Jiang J., Luan Y. & Yin W. (2012). *Paralobellapalustris* sp. nov. (Collembola: Neanuridae: Neanurinae) from China, with remarks and key to species of the genus. *Zootaxa*, 3500(1): 70-76.
- John L. (2008). *Bioluminescence: the first 3000 years*. J. Sib. Fed. Univ. Biol. 1(3): 194-205.
- Kahlke T. & Umbers K.D. (2016). *Bioluminescence*. *Current Biology*, 26(8): R313-R314.
- Kawashima I. (2010). A New Species of the Lampyrid Genus *Lamellipalpus* (Coleoptera, Lampyridae) from Myanmar, Indochina. *Elytra*, 38(1): 35-41.
- Kirton L.G., Lim G.T. & Day J.C. (2012). *Proceedings of the Second International Firefly Symposium*, Selangor, Malaysia, 5th August, 2010, Brazen Head Publishing, pp. 218.
- Kusy D., He J.W., Bybee S.M., Motyka M., Bi W.X., Podsiadlowski L. & Bocak L. (2021). Phylogenomic relationships of bioluminescent elateroids define the 'lampyroid' clade with clicking Sinopyrophoridae as its earliest member. *Systematic Entomology*, 46(1): 111-123.
- Lawrence J.F., Hastings A.M., Dallwitz M.J. & Paine Z.E. (2000). *Elateriformia (Coleoptera): descriptions, illustrations, identification, and information retrieval for families and subfamilies*. Version: 9th October 2005.
- Lee K.Y., Kim Y.H., Lee J.W., Song M.K. & Nam S.H. (2008). Toxicity of firefly, *Luciola lateralis* (Coleoptera: Lampyridae) to commercially registered insecticides and fertilizers. *Korean J. Appl. Entomol.* 47(3): 265-272.
- Lewis S. (2016). *Silent sparks: the wondrous world of fireflies*. Princeton University Press.
- Lewis S.M., Wong C.H., Owens A.C., Fallon C., Jepsen S., Thancharoen A. & Reed, J.M. (2020). A global perspective on firefly extinction threats. *BioScience*, 70(2): 157-167.
- Li X.Y. & Liang X.C. (2008). A gigantic bioluminescent starworm (Coleoptera: Rhagophthalmidae) from northwest Yunnan, China. *Entomological News*, 119(2): 109-112.
- Lloyd J.E. (2008). Fireflies (Coleoptera: Lampyridae). In J. L. Capinera (Ed.), *Encyclopedia of entomology*, New York: Springer, pp. 1429–1452.

- Martin G.J., Stanger-Hall K.F., Branham M.A., Da Silveira L.F., Lower S.E., Hall D.W., ... & Bybee S.M. (2019). Higher-level phylogeny and reclassification of Lampyridae (Coleoptera: Elateroidea). *Insect Syst. Diver.* 3(6): 11.
- Merritt D.J. & Clarke A.K. (2013). The impact of cave lighting on the bioluminescent display of the Tasmanian glowworm *Arachnocampa tasmaniensis*. *J. Insect Conserv.* 17: 147-153.
- Meyer-Rochow V.B. & Waldvogel H. (1979). Visual behaviour and the structure of dark and light-adapted larval and adult eyes of the New Zealand glowworm, *Arachnocampaluminosa* (Mycetophilidae: Diptera). *J. Insect Physiol.* 25(7): 601-613.
- Meyer-Rochow V.B. (2007). Glowworms: a review of *Arachnocampa* spp. and kin. *Luminescence.* 22(3): 251-265.
- Napompeth B. (Ed.). (2009). Diversity and conservation of fireflies. Queen Sirikit Botanic Garden, Botanical Garden Organization.
- Navizet I. (2021). QM/MM Study of Bioluminescent Systems. QM/MM Studies of Light-responsive Biological Systems, 227-270.
- Oba Y. (2009). On the origin of beetle luminescence. *Bioluminescence in focus-A collection of illuminating essays.* Research Signpost, Kerala, 277-290.
- Oba Y., Branham M.A. & Fukatsu T. (2011). The terrestrial bioluminescent animals of Japan. *Zoological science*, 28(11): 771-789.
- Pawar C., Patil S. S. & Gharge M.N. (2023). In-Situ conservation of *Abscondita* sp. (close perplexa) program-Policies and perspectives for Kalsubai Harishchandragad wildlife sanctuary in Maharashtra, India. *J. Surv. Fish. Sci.* 192-198.
- Pearsons K.A., Lower S.E. & Tooker J.F. (2021). Toxicity of clothianidin to common Eastern North American fireflies. *PeerJ*, 9: e12495.
- Pisa L.W., Amaral-Rogers V., Belzunces L.P., Bonmatin J.M., Downs C.A., Goulson D. & Wiemers M. (2015). Effects of neonicotinoids and fipronil on non-target invertebrates. *Environ. Sci. Pollut. Res. Int.* 22: 68-102.
- Powell G.S., Saxton N.A., Pacheco Y.M., Stanger-Hall K.F., Martin G.J., Kusy D. & Bybee, S.M. (2022). Beetle bioluminescence outshines extant aerial predators. *Proc. R. Soc. B-Biol. Sci.* 289(1979): 20220821.
- Ramesh C. & Meyer-Rochow V.B. (2021). Bioluminescence in aquatic and terrestrial organisms elicited through various kinds of stimulation. *Aquatic Ecology*, 55(3): 737-764.
- Richards A.L.M. (1960). Observations on the New Zealand glowworm *Arachnocampaluminosa* (Skuse). *Trans. Proc. R. Soc. N. Z.* 88: 559-574.
- Riley W.B., Rosa S.P. & da Silveira L.F.L. (2021). A comprehensive review and call for studies on firefly larvae. *PeerJ*, 9: e12121.

- Rosa S.P. (2010). Second record of bioluminescence in larvae of *Xantholinus* Dejean (Staphylinidae, Xantholinini) from Brazil. *Rev. Bras. Entomol.* 54: 147-148.
- Rosenberg J. & Meyer-Rochow V.B. (2009). Luminescent myriapoda: A brief review. *Bioluminescence in focus—a collection of illuminating essays*. Research Signpost, Trivandrum, 139-146.
- Roza A.S. (2020). Notes on the morphology and distribution of the Himalayan genus *Pseudothilmanus*, including the first record of the genus from Nepal (Coleoptera: Rhagophthalmidae). *Trans. Am. Entomol. Soc.* 146(2): 421-426.
- Sano T., Kobayashi Y., Sakai I., Ogoh K. & Suzuki H. (2019). Ecological and histological notes on the luminous springtail, *Lobella* sp. (Collembola: Neanuridae), discovered in Tokyo, Japan. In *Bioluminescence-Analytical Applications and Basic Biology*. IntechOpen.
- Shukla, U. (2022). Bioluminescence: Biologically Living Organism. *International Journal of Optical Sciences*, 8(2), 9-19.
- Tabaru Y., Kouketsu T., Oba M. & Okafuji S. (1970). Effects of some organophosphorus insecticides against the larvae of Genji firefly, *Luciola cruciata* Motschulsky (Lampyridae: Coleoptera) and their prey, Japanese melania snail, *Semislucospirabensoni* Phillipi (Pleuroceridae; Mesogastropoda). *Jpn. J. Sanit. Zool.* 21(3): 178-181.
- Thancharoen A. & Masoh S. (2019). Effect of camera illumination on flashing behavior of *Pteroptyx malacca* (Coleoptera: Lampyridae). In *Bioluminescence-Analytical Applications and Basic Biology*. IntechOpen.
- Viviani V.R., Arnoldi F.G., Ogawa F.T. & Brochetto-Braga M. (2007). Few substitutions affect the bioluminescence spectra of *Phrixotrix* (Coleoptera: Phengodidae) luciferases: a site-directed mutagenesis survey. *Luminescence*. 22(4): 362-369.
- Viviani V.R., Hastings J.W. & Wilson T. (2002). Two Bioluminescent Diptera: The North American *Orfelia fultoni* and the Australian *Arachnocampa flava*. Similar Niche, Different Bioluminescence Systems. *J. Photochem. Photobiol.* 75(1): 22-27.
- Von-Byern J., Dorner V., Merritt D.J., Chandler P., Stringer I., Marchetti-Deschmann M. & Grunwald I. (2016). Characterization of the fishing lines in Titiwai (= *Arachnocampa luminosa* Skuse, 1890) from New Zealand and Australia. *PLoS One*, 11(12): e0162687.
- Watkins O.C., Sharpe M.L., Perry N.B. & Krause K.L. (2018). New Zealand glowworm, (*Arachnocampa luminosa*) bioluminescence is produced by a firefly-like luciferase but an entirely new luciferin. *Scientific reports*, 8(1): 3278.
- Wilcove D.S. (1986). Habitat fragmentation in the temperate zone. *Conservation biology*, 237-256.
- Wilson T. & Hastings J.W. (2012). *Bioluminescence: living lights, lights for living*. Harvard University Press.

- Wong C.H. (2022). Congregating Firefly Zones (CFZ) in Malaysia: Conservation of Mangrove Congregating Fireflies. MNS Conservation Publication: Kuala Lumpur, Malaysia.
- Wood K.V., Lam Y.A. & McElroy W.D. (1989). Introduction to beetle luciferases and their applications. *Luminescence*. 4(1): 289-301.
- Zimmer M. (2015). Bioluminescence: Nature and Science at Work. Twenty-First Century Books.
- Zompro O. & Fritzsche I. (1999). *Lucihormeticafenestrata* n. gen., n. sp., the first record of luminescence in an orthogteroid insect (Dictyoptera: Blaberidae: Blaberinae: Brachycolini). Volume 15, fascículo 3/4, 1999, página 211-21.