

Terrestrial and marine bioluminescent organisms from the Indian subcontinent: A review

Chatragadda Ramesh

Biological Oceanography Division (BOD)
CSIR-National Institute of Oceanography (CSIR-NIO)
Dona Paula, Goa-403004, India
Email:chramesh@nio.org

Abstract

The inception of bioluminescence by Harvey (1952) has led to a Nobel Prize to Osamu Shimomura (Chemistry, 2008) in biological research. Consequently, in recent years, bioluminescence-based assays to monitor toxic pollutants as a real-time marker, to study various diseases and their propagation in plants and animals are developed in many countries. The emission ability of bioluminescence is improved by gene modification, and also search for novel bioluminescent systems are underway. Over 100 species of organisms belong to different taxa are known to be luminous in India. However, the diversity and distribution of luminous organisms and their applications are studied scarcely in the Indian scenario. In this context, the present review provides an overview of the current understanding of various bioluminescent organisms, functions, and applications. A detailed checklist of known bioluminescent organisms from India's marine, terrestrial, and freshwater ecosystems is detailed. This review infers that Indian scientists are needed to extend their research on various aspects of luminescent organisms such as biodiversity, genomics, and chemical mechanisms for conservation, ecological, and biomedical applications.

Keywords: Luciferins, luciferase, photophores, fluorescent proteins, luminescence applications.

Introduction

Bioluminescence is an innate natural light emitting phenomena displayed by some species of bacteria, fungi, dinoflagellates, sponge, jellyfish, deep-sea corals, annelids, shrimp, squids, gastropods, brittle stars, tunicates, and fishes. In this phenomenon, the molecular oxygen reacts with luciferin in the presence of luciferase enzyme and forms oxyluciferin molecule responsible for cold light emission. This natural enigma is widely distributed in aerial, terrestrial, marine, and freshwater ecosystems. Globally, around 686 (Björn and Ghiradella 2008), or 700 (Shimomura 2006), or 746 (Oba and Schultz, 2014) luminous genera are known to be luminescent from terrestrial and marine environments.

Currently, around 71 (Desjardin et al. 2010; Stevani et al. 2013) or 83 species of fungi (Vydryakova et al. 2011), 50 species of bacteria (C. H. Ramesh and Mohanraju 2019), 18 genera of dinoflagellates (Baker et al. 2008), 70 genera of squids (P J Herring 1977), 66 species of brittle stars (Jones and Mallefet 2012), 11 orders of bony fishes under 42 fish families (Paitio et al. 2016; Suntsov et al. 2008) are known to be luminescent. Except plants, amphibians, reptiles, birds, and mammals, all other taxonomic lineages are luminescent (Haddock et al. 2010). Considerably, 80% of the deep-sea organisms are known to be luminous (Widder 2010), and 90% of planktonic comb jellies (but not benthic jellies) and 91% of planktonic siphonophore genera are bioluminescent (Haddock et al. 2010).

The biochemistry and mechanism of some of the well-known bioluminescent organisms, such as bacteria, jellyfish, firefly, and *Renilla*, have been well established (Shimomura 2006). While many organisms are known to display luminescence only upon stimulation via chemical and mechanical stimulants (Ramesh, Pers. Comm.). Many bioluminescent organisms with novel chemical mechanisms and different chemistry are yet to be discovered from protected forest areas and deep-sea. The chemistry of well-known bioluminescent organisms has boosted the biomedical research enormously to discover several applications of luminescence. To emphasize the importance of luminous organisms, this review provides current status on India's luminescent organisms to influence Indian researchers to explore India's hidden luminous organisms and get acquainted with the current knowledge.

India is the third-largest country in Asia and seventh-largest in the world, with an area of 3.29 million square km. India is well diverse, with 44,500 species of plants (Botanical Survey of India, 2019) and 97,514 species of Protista+Animalia (Zoological Survey of India, 2016). So far, 20,444 species of marine organisms have been recorded from India (Dash 2018). However, the

bioluminescence phenomenon has not been investigated in these organisms. There are no accounts of Indian bioluminescent organisms found along the mainland and island ecosystems, including terrestrial and marine milieus. Many luminous organisms hide during the day and come out for foraging as soon as the sun goes down. Therefore, this review is written prudently to encourage the young students and researchers to explore new and hidden bioluminescent organisms found across India.

Spectral hues of bioluminescence

All the known luminous organisms from different environments are observed to produce luminescence with spectra ranging between 400 nm to 700 nm. Many benthic, shallow, and deep-water organisms produce blue luminescence (Verdes and Gruber 2017; Widder 2010). However, in many exceptional cases, some luminous organisms produce different colors. Various colours of luminescence are known, including red (e.g., railroad-worms, *Phrixothrix hirtus*, *P. heydeni*, *P. viviani*, and dragonfish, *Malacosteus niger*) (Wilson and Hastings 2013), blue (e.g., ctenophores, hydromedusae, *Tomopteris planktonis*, fishes, luminous bacteria), green (*Renilla*, *Aequorea*, *Swima*, *Odontosyllis phosphorea*, *Mycena fera*), yellow (*Aliivibrio fischeri* strain Y-1, *Tomopteris*, fireflies, *Bolitaena pygmaea*) (Bechara and Stevani 2018; W R Francis et al. 2014; P. Herring 2002), orange (e.g., *Pyrophorus angustus*, and *P. plagiophthalmus*, *Cyphocaris*) (Amaral et al. 2016; Haddock et al. 2010), purple blue (e.g., *Actinoscyphia* sp.), pink in *Photonectes waitti* (Wilson and Hastings 2013), and violet (e.g., *Obelia longissimi*) (Deng et al. 2001). Fireflies exhibit a wide range of species-specific luminescence colors, including yellow, green, yellow-green, and red (Seliger and Mcelroy 1964). The rainbow colour displayed by comb jellies is not bioluminescence but related to iridescence. Photoreceptors of many deep-sea creatures (e.g., black-belly dragon fish *Stomias*) show red fluorescence under blue light illumination (Haddock et al. 2010; Wilson and Hastings 2013).

Emission types and modes of luminescence

Bioluminescence falls into two types based on biochemical origins: primary bioluminescence in which organisms generate their own light; and secondary bioluminescence in which light is produced by symbiotic microorganisms (primary bioluminescants) (Schoenemann et al. 2015). These two types of luminescence include three modes of luminescence emission: intracellular (e.g., jellyfish *Aequorea victoria* & fireflies), extracellular (e.g., marine polychaete worm *Odontosyllis* & ostracods), and buried (e.g., luminous bacteria in anglerfish lure). The intracellular and buried emission types are also known as non-secretion type (many terrestrial and marine organisms), whereas the extracellular emission type known as secretion type (e.g., limpet *Latia* sticky slime,

copepod *Gaussia* sp., ostracods, *Cypridina*, certain shrimp like *Acanthephyra purpurea* and some squids) (Wilson and Hastings 2013). Some reviews on bioluminescence literature preferentially used intrinsic and extrinsic luminescence. The emission of luminescence is classified as: (i) intrinsic bioluminescence when the animal can produce its own light, Some fish families possess the ability to emit their own light like the Myctophidae or Stomiidae (Barnes and Case 1974; Case et al. 1977; Duchatelet et al. 2019; Mallefet et al. 2019); (ii) others display extrinsic bioluminescence as for the Anomalopidae, Monocentridae or Ceratiidae (Nealson and Hastings 1979), where light is produced by symbiotic bacteria (Haddock et al. 2010; Haneda and Tsuji 1971; Widder 2010).

Emission patterns of bioluminescence have particular relevance for ecological and evolutionary studies. These emission patterns appear to play essential roles in the physiological functions and survival of luminous organisms. Different modes of luminescence are detailed in table (Table 1): Most bioluminescent organisms display short duration of light emission in flashes, but mucus oozed from *Chaetopterus* tube worms show continuous glow lasting up to 16 to 72 hours (De Meulenaere et al. 2020). The NOAA team recently observed luminescence emission from two lemon sized photophores situated on two tentacles of octopus squid, *Taningia danae* (Kubodera et al. 2007) during an expedition near the deep ocean at Hawaii. Train of bioluminescence pattern was recently observed in deep-sea sea pens by IceAGE3 cruise near Iceland.

Table 1. Types of luminescence emission patterns and mode of luminescence.

Emission pattern of luminescence	Some examples	Mode of luminescence	References
Continuous glow	Firefly larvae	Intracellular	(Desjardin et al. 2008; Haddock et al. 2010; P J Herring and Widder 2004; Lynch and Hobbie 1988; C. H. Ramesh and Mohanraju 2019; Shimomura 2006; Sitarski 2007; Wilson and Hastings 2013)
	Millipede, <i>Motyxia</i>	Intracellular	
	Limpet, <i>Latia</i>	Extracellular	
	Luminous bacteria	Intracellular	
	Luminous fungi	Intracellular	
Blinking	Luminous bacteria	Intracellular	
Brief flashes	Fireflies (e.g., <i>Photuris</i>)	Intracellular	
	Squids	Buried & Extracellular	
	<i>Odontosyllis</i>	Extracellular	
Flash and glow	Scale worms	Extracellular	

	Other marine annelids	Intracellular & Extracellular
	<i>Eusyllis</i>	Extracellular
	Luminous bacteria	Intracellular
Steady glow	Fire beetle <i>Pyrophorus noctilucus</i>	Intracellular
Shooting or squirting or spew	Ostracod, <i>Vargula hilgendorffii</i>	Extracellular
	vampire squid, <i>Vampyroteuthis infernalis</i>	Buried & Extracellular
	Jellyfish	Intracellular
	Deep-sea shrimp, <i>AcanthePHYra purpurea</i> , <i>Oplophorus</i> sp.	Extracellular
Wavy	Sea pansy, <i>Renilla</i>	Intracellular
	Deep-sea, scyphozoans	Intracellular
Pulses	Cypridinids	Extracellular
	<i>Photeros annecohenae</i>	Extracellular
Switch on and off	Flash light fish	Buried
	<i>Pyrosoma atlanticum</i>	Intracellular
	Angler fishes	Buried
	Luminous bacteria	Intracellular
Luminescence bombs	<i>Swima bombiviridis</i>	Extracellular
	Deep sea bacterial bioluminescent blooms	Intracellular
Frenzy	<i>Beroe forskalii</i>	Intracellular
	<i>Pannychia moseleyi</i>	Intracellular
	Deep-sea scyphozoans	Intracellular
Train of bioluminescence	Sea pen, <i>Halipteris californica</i>	Intracellular

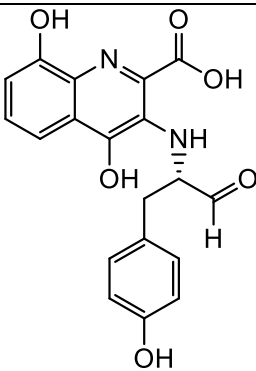

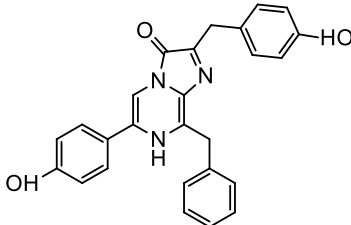
Luciferins, luciferase, and associated fluorescent proteins

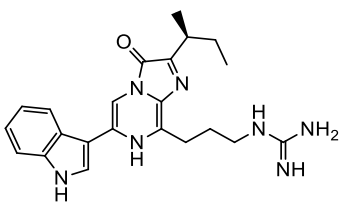
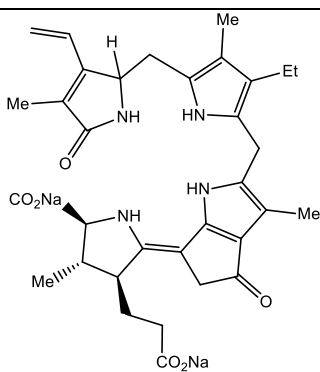
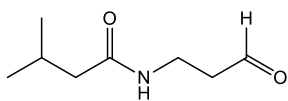
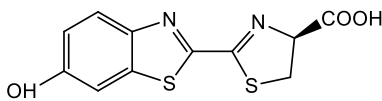
Luciferin and luciferase are the two fundamental components that generate bioluminescence through a biochemical reaction. In nature, around 30 different bioluminescent systems are known, of which 9 chemical reaction mechanisms are well established (Kaskova et al. 2016). Although mostly luciferases are homologous and diverse in many luminous organisms, luciferins are not well known so far. The best known luciferins are bacterial luciferin (Kuwabara et al. 1965), fungal luciferin (Purtov et al. 2015), D-luciferin and firefly luciferin (Bitler and McElroy 1957), dinoflagellate & krill luciferin (Nakamura et al. 1989), *Fridericia heliota* luciferin (Petushkov et al. 2014), *Diplocardia* luciferin (Ohtsuka et al. 1976), *Cypridina* or vargulin luciferin (Shimomura et al. 1957), coelenterazine (Inoue et al. 1976), *Latia* luciferin (Shimomura and Johnson 1968) and Furimazine (*Oplophorus graciliro* luciferin or NanoLuc) (Haddock et al. 2010; Hall et al. 2012; Kaskova et al. 2016; Widder 2010). Whereas, luciferase enzymes discovered are many, including *Aequorea* photoprotein (apoAequorin), *Renilla* luciferase, *Amphiura* luciferase, copepod luciferase, bacterial luciferase, *Stenoteuthis* photoprotein, *Obelia* photoprotein, *Mnemiopsis* photoprotein, *Watasenia* luciferase, insect luciferase, *Suberites* luciferase, ostracoda luciferase, *Oplophorus* luciferase, and dinoflagellate luciferase (Delroisse et al. 2017). These known bioluminescent systems have some limitations for the developing bioluminescence based analytical and imaging methods, therefore, search for the structurally and functionally unique bioluminescent systems is a current research interest (Kaskova et al. 2016). A demosponge, *Suberites domuncula* is reported to possess a different luminous mechanism consisting of an inorganic light converting silica spicules and organic luciferase enzyme (Wang et al. 2012).

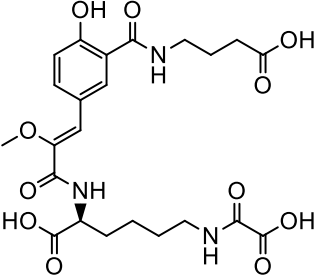
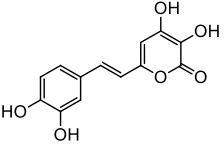
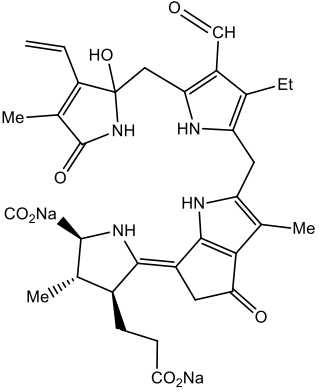
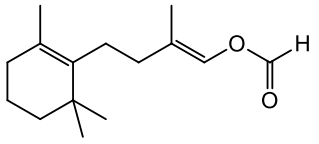
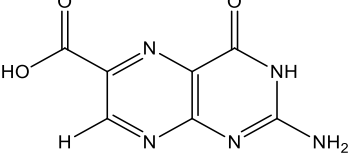
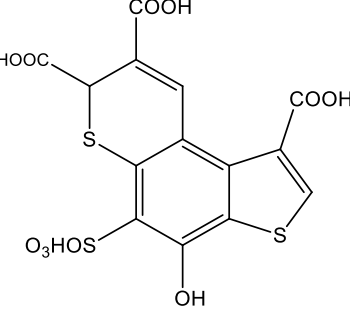
The intensity and wavelength of bioluminescence emission may be altered in the presence of fluorescent proteins (FPs) or photoproteins, which are stable enzyme–substrate complexes. Photoproteins are triggered by metal ions like Ca^{2+} and Fe^{2+} for light emission (Kaskova et al. 2016; Shimomura 2006). Although FPs are prevalent in bioluminescent and non-bioluminescent coelenterates like comb jellies, ctenophores, and jellyfishes, many luminous organisms are known to possess no fluorescent proteins. Some very well-known fluorescent molecules present or associated with luminous and non-luminous members of different taxa are include: flavin mononucleotide in luminous bacteria (Wilson and Hastings 2013), yellow fluorescent protein (YFP) in luminous *Aliivibrio sifiae* (*A. sifiae* strain Y1 formerly known as *Vibrio fischeri* strain Y1) (Yoshizawa et al. 2012), green fluorescent protein (GFP), YFP, and red fluorescent protein (RFP) in non-luminous anthozoans (Matz et al. 1999), aloe-emodin in *Tomopteris* (W R Francis et al. 2014), RFP in luminous *Latia* (Kaskova et al. 2016), blue fluorescent protein (BFP) (lumazine) in luminous

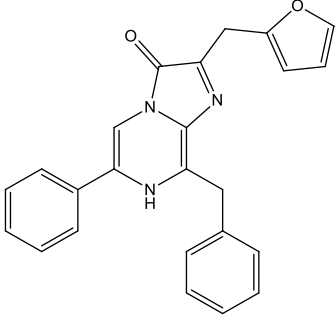
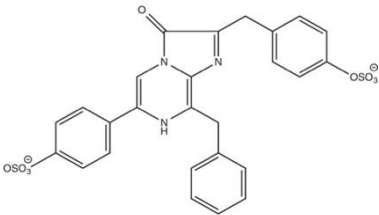
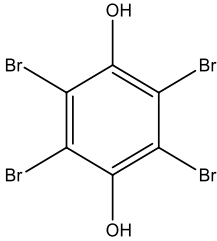
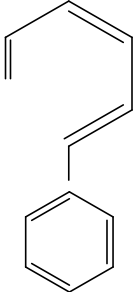
Photobacterium phosphoreum, *P. leiognathi* (O’Kane et al. 1985), *P. kishitanii* (Sato et al. 2010), and *Vibrio azureus* (Yoshizawa et al. 2012), green fluorescent protein (GFP) in luminous *Renilla reniformis*, and *Aequorea victoria* (Shimomura 2006), GFP in non-luminous cnidarians (Chudakov et al. 2010), and RFPs in non-luminous anthozoans and fishes (C. H. Ramesh 2020a) (Table 2; Fig. 1 & 2). Currently, three different types of photoproteins are known, 1) Ca^{2+} sensitive photoproteins which are present in coelenterates (aequorin, obelin, mnemiopsin) and protozoa (thalassicolin); 2) peroxide activation type photoprotein found in scaleworm (polynoidin) and freshwater clam *Pholas* (pholasin); and 3) ATP activation type found in Sequiola millipede *Luminodesmus* (Shimomura and Yampolsky 2019).

Table 2. Details of luciferins and FPs found across different taxa (Gimenez et al. 2016; Haddock et al. 2010; Kaskova et al. 2016; Kotlobay et al. 2019; Watkins et al. 2018; Widder 2010).

Luciferin	Chemical structure	λ_{max} range (nm) & light color	Observed in	Associated FPs
<i>Arachnocampa</i> luciferin		487-490 nm & Blue light	Glowworm <i>Arachnocampa luminosa</i>	
Bacterial luciferin		490 nm & Blue light	Bacteria, Some squids, Some fish, Pyrosomes?	BFP YFP Flavin Mononucleotide
Coelenterazine		454 nm, 480-493 nm & Blue light	Radiolarians, Cnidarians, Ctenophores, Squid, Some	GFP

			ostracods, Copepods, Decapod shrimp, Mysid shrimp, Some ophiuroids, Chaetognaths, Larvaceans, Some fish	
<i>Cypridina</i> luciferin		448-463 or 465-475 nm & Blue light	Some ostracods, Midshipman fish, Some other fish	GFP
Dinoflagellate luciferin		475 nm & Blue light	Dinoflagellates	
<i>Diplocardia</i> luciferin		500 nm & Green light	Earthworm, <i>Diplocardia</i> <i>longa</i>	
Firefly luciferin (D-luciferin)		536-630 nm & Yellow light	Fireflies	

<p><i>Fridericia</i> luciferin</p>	 <p>The structure shows a central benzene ring with a hydroxyl group at the top. A propyl chain is attached to the ring via an amide bond. Another propyl chain is attached to the ring via a methylene bridge. A third propyl chain is attached to the ring via a methylene bridge. A fourth propyl chain is attached to the ring via a methylene bridge.</p>	<p>478 nm & Blue light</p>	<p>Earthworm, <i>Fridericia heliota</i></p>	
<p>Fungal (<i>Neonothopanus gardneri</i>) luciferin</p>	 <p>The structure shows a central benzene ring with two hydroxyl groups at the top. A propyl chain is attached to the ring via a methylene bridge. Another propyl chain is attached to the ring via a methylene bridge.</p>	<p>530 nm & Yellow greenish light</p>	<p>Fungal mycelia and fruiting bodies</p>	
<p>Krill luciferin</p>	 <p>The structure shows a complex polycyclic system with multiple nitrogen atoms and various substituents including methyl, ethyl, and sodium carboxylate groups.</p>	<p>475 nm & Blue light</p>	<p>Euphausiid shrimps</p>	
<p><i>Latia</i> luciferin</p>	 <p>The structure shows a central benzene ring with two methyl groups at the top. A propyl chain is attached to the ring via a methylene bridge. Another propyl chain is attached to the ring via a methylene bridge.</p>	<p>536 nm & Yellow- green light</p>	<p>Limpet, <i>Latia neritoides</i></p>	<p>RFP (purple protein)</p>
<p><i>Luminodesmus</i> photoprotein (not luciferin)</p>	 <p>The structure shows a purine-like ring system with a carboxylic acid group and an amino group.</p>	<p>500 nm & Blue-green</p>	<p>Millipede, <i>Luminodesmus sequoiae</i></p>	<p>7,8- Dihydropterin- 6-carboxylic Acid</p>
<p><i>Odontosyllis</i> luciferin</p>	 <p>The structure shows a complex polycyclic system with multiple sulfur atoms and various substituents including carboxylic acid, hydroxyl, and sulfonic acid groups.</p>	<p>410 nm & Green light</p>	<p>Polychaetes <i>Odontosyllis undecimdongata</i></p>	<p>Oxyluciferin produces green and pink fluorescence</p>

<p><i>Oplophorus</i> luciferin (Furimazine) or NanoLuc [artificial luciferin]</p>		<p>460 nm & Blue light</p>	<p>Deep sea shrimp, <i>Oplophorus gracilirostris</i></p>	
<p><i>Watasenia scintillans</i> luciferin</p>		<p>470 nm & Blue light</p>	<p>Japanese firefly squid</p>	
<p><i>Ptychodera</i> luciferin</p>		<p>528 nm & Green light</p>	<p>Hemichordate worm, <i>Ptychodera flava</i></p>	
<p>Unknown</p>			<p>Some polychaetes, Bivalves, Hemichordates, Amphipods, Nemertean worms, Tunicates, doliolids, Echinoderms, Other polychaetes</p>	

Functions of bioluminescence

Despite the known functions of bioluminescence such as defence and offense, mate attraction, and intra and inter-specific interactions (Haddock et al. 2010), some of the ecological applications of bioluminescence phenomenon are explored. Deep-sea bioluminescence is used as real-time biomarker to study biological activities in the deep ocean (Craig et al. 2011a; Gillibrand et al. 2007a; Martini et al. 2014; Tamburini et al. 2013). This ecological trait also utilised to study the spatial, seasonal or diurnal biomass patterns and community composition changes of dominant pelagic organisms found at different depths (Craig et al. 2011a, 2011b; Cronin et al. 2016; Martini et al. 2019; Martini and Haddock 2017; Messié et al. 2019). Bioluminescence also utilised to study the vertical migration of pelagic organism like dinoflagellates (Shulman et al. 2012)(Geistdoerfer and Cussatlegras 2001), copepods (Cronin et al. 2016); and distributional structural patterns of species (presence & absence), abundance, and interactions of planktonic dinoflagellate and zooplanktons (Craig et al. 2015; Marcinko et al. 2013; Moline et al. 2009; Piontkovski et al. 1997; Valiadi et al. 2014). This trait is also utilised to identify deep-sea biodiversity hotspots (Craig et al. 2011a; Martini et al. 2019), whale falls and food falls at different depths and substrata (Gillibrand et al. 2007b), and substratum types (rocky, sediment) (Craig et al. 2011a). Stimulated bioluminescence of planktonic forms has a great advantage for fishermen to identify the fishery resources in the coastal waters (V. Balan 1961, 1963; Daniel et al. 1979). Bioluminescence trait is also utilised to identify the algal bloom dynamics and interactions between algae and luminous bacteria (Miller et al. 2005). Bioluminescence trait was utilised to identify the upwelling events, water current transport, and water quality & pollution (Shulman et al. 2012; Tamburini et al. 2013). In Lake Baikal, luminescence is utilised to correlate the depth gradient chlorophyll fluorescence (Dobrynin 2011). Stimulated luminescence has also been used to determine seawater's optical properties (Shulman et al. 2011).

From underneath earthworms to flying fireflies and marine organisms, bioluminescence has been an evolutionary language of multiple functions. The arrangement of light organs and emission patterns of light in different organisms are some of the taxonomical signatures which allowing taxonomist and scientist to identify them up to genus level, and to study their behavioural and evolutionary studies. The arrangement of light organs, size, shape, orientation, emission patterns, emission time & frequency, specific function, and organism's flyways or movements in terrestrial and marine organisms have significance evolutionary roles (Fig. 3). Light organ signatures are more diverse in deep-sea bioluminescent organisms. Thus identification of deep-sea organisms in the darkness is somewhat easier due to light emission patterns. In contrast, understanding the functions

of bioluminescence in several marine (e.g., deep-sea organisms) and terrestrial animals (e.g., earthworms) remain unknown as the maintenance of animals in live conditions is arduous in the laboratory (Haddock et al. 2010).

Applications of luminous organisms

Globally, luminous organisms such as bacteria, fungi, *Renilla*, *Aequorea*, fireflies, and earthworm are being used extensively for biotechnological applications (Thouand and Marks 2014). Although the chemistry of dozens of luciferins from different organisms known, many luminous organisms with unknown and novel chemistry are yet to be investigated. In the 21st century, luminescence based bioassays are reaching extraordinarily different approaches using various bioluminescent organisms. Bacterial bioluminescence (Krichevsky et al. 2010) and fungal bioluminescence systems (Khakhar et al. 2019) are being used to develop glowing plants. Dinoflagellates luminescence systems are employed to detect membrane protein expressions in mammalian cell surfaces (Kato et al. 2011). Development of bioluminescent lamps, trees, directing signs (LuxBrick) (Sanderson et al. 2020), and glowing light bulbs by PHILIPS (Philips 2011) are being improved greatly using genetically engineered bacterial bioluminescence (Reeve et al. 2014). Several other applications, including peroxidase activities, toxicity assays, immunoassays, mapping metabolic activities, gene transcriptional activities, bioimaging, tumour and disease progressions, and others are proven using different luminescent systems (Kaskova et al. 2016). Currently, a French based company –GLOWEE is working on the development of natural lights using luminous bacteria (Sandra 2020). Promega is developing luminescence based bioassay kits (e.g., ENLITEN[®] ATP Assay). Non-toxic dinoflagellates based luminous toys such as BioGlo, Dino Pet, BioPop DinoSphere, Bio-Orb, and others products BioToy-SplashLight (ReLumes) are available in the markets. Prolume is making various glowing food, beverages, personal care, cosmetics products, and bioassay kits (NanoLight & LucArray), and medical imaging (BioLume) products. The UK based fashion designer Victoria Geaney has demonstrated the use of luminous bacteria, *Photobacterium* for developing luminous dress. A fashion designer from India is trying to develop luminous jackets for coal mine workers using bacterial bioluminescence. At present, in our lab, we are developing bioluminescence energy harvesting devices similar to a solar panel for various applications (e.g., bioluminescence dependent underwater rovers and BIOLUM energy batteries) (Fig. 4).

In Indian scenario, applications of luminous organisms are not well demonstrated, except for luminous bacteria and fireflies. Therefore, other luminescent organisms are needed to be investigated for potential novel chemistry, biotechnological, and genetic engineering studies. The ecological roles of luminous bacteria are observed as cellulolytic activity (A. Ramesh and Venugopalan 1988), chitin

degradation in fishes (A. Ramesh and Venugopalan 1989), and agar digestion (Fukasawa et al. 1987). Industrial applications of luminous bacteria include production of L-asparaginase (Ramaiah and Chandramohan 1992a), esterases (Mohankumar and Ranjitha 2010), L-glutaminase (Kiruthika and Saraswathy 2013), other extracellular enzymes (Ramina et al. 2014), exopolysaccharides (Bramhachari and Dubey 2006), antimicrobial compounds (Arulmoorthy et al. 2014; C. H. Ramesh and Mohanraju 2017a, 2017b) antibiotics and pigments (Singh et al. 2012), and toxicity assays (Balachandar et al. 2010; A. K. Kumar 2010; C. H. Ramesh 2016; Thakre and Shanware 2014). While luciferase enzymes extracted from Indian fireflies, *Luciola praeusta* is suggested for assaying biochemical metabolites (Muthukumaran et al. 2014), and photonic applications (U. Sharma et al. 2018). Based on the literature survey on bioluminescence applications, luminous organisms could offer numerous biotechnological and medical applications; therefore, research on the diversity, distribution, chemistry and genetics of luminous organisms are gaining importance in the current research.

Historical note on bioluminescence in India

Decades ago, people witnessed that luminescent organisms were more prevalent in the Indian continent than now. A childhood memory of an older man from Mandapam, southeast coast of Tamil Nadu revealed the prevalence of fungal bioluminescence in a coconut plantation. He said that several decades ago, he was scared when he saw the eerie light emitting from gathered coconuts left for a long-time. However, later they realized that it was due to some fungal mycelia. In Nicobar group of Islands, the indigenous Nicobarese tribal people were surprised by the mysterious enigma of fungal bioluminescence in the forest during monsoon and firefly luminescence on mangroves and forest during pre-monsoon. Every year, along the mainland India and Island coasts, many people have been sighting luminous waves caused by dinoflagellates and ostracods seasonally. In Barrankula, a village near the Bay of Bengal in Andhra Pradesh, four decades ago my father has witnessed a strange incidence of massive luminescence in *Panaeus monodon* culture ponds around 4 AM, and startled by seeing luminous water moving like a ghost. Many Indian Navy people, especially the submarine crew also observed the bioluminescence in the Sea. Considerably, firefly festival is one of the well-known events that takes place every year from May to July at Purushwadi, a village situated about 220 km away from Mumbai. The most popular firefly sighting destinations in India are Bhandardara, Kothaligad, Panshet, Prabalmachi, Rajmachi, etc. Some luminous organisms observed in India are shown in the figure (Fig. 5&6).

Indian bioluminescent organisms

Bacteria

A total of seventeen different luminous bacterial species such as *Vibrio alginolyticus*, *V. azureus*, *V. campbellii*, *V. cholerae*, *V. fischeri*, *V. harveyi*, *V. owensii*, *V. orientalis*, *V. rotiferianus*, *V. splendidus* biotype1, *V. vulnificus*, *Photobacterium leiognathi*, *P. phosphoreum*, *P. damsela*, *Photorhabdus luminescens*, *Shewanella hanedai* and *Kurthia* sp. have been reported from India (Abraham and Sasmal 2014; Azizunnisa and Sreeramulu 2013; S. S. Balan et al. 2013; Ramaiah et al. 2000; Shanware et al. 2013; Vishwakarma et al. 2014). Among these luminous bacterial species, *V. harveyi*, *V. campbellii*, and *P. phosphoreum* are considered as cosmopolitan species due to their ubiquitous distribution in aquaculture systems and coastal waters (*V. harveyi* and *V. campbellii*), and pelagic waters (*P. phosphoreum*). *Photorhabdus luminescens* is found in terrestrial environment merely, and *V. cholerae* is also occurred in estuarine environments (C. H. Ramesh 2016).

Association and quantitative abundance of luminescent bacteria with 15 different groups of zooplankton were examined and found that the large number of luminous bacteria were associated with myctophids, dolioidids, hydromedusae, anthozoans, stomatopods and ctenophores (Director 1992). Symbiotic association of luminous *Photobacterium leiognathi* was observed with light organs of ponyfishes *Eubleekeria splendens* and *Photopectoralis bindus* (Sivasankar and Jayabalan 1991), frogfish *Antennarius hispidus* (Ramaiah and Chandramohan 1992b); and *V. harveyi* with *Gazza minuta*, *G. achlamys*, *Secutor ruconius*, *E. splendens*, *P. bindus*, and *Karalla dussumieri* (Jayabalan and Ramamoorthi 1982). Symbiotic association of *V. harveyi* with blue swimmer crab, *Portunus pelagicus* was also reported (Govindasamy and Srinivasan 2012). A recent study revealed the widespread distribution and diversity of luminous bacteria in several marine floral and faunal samples examined from the Andaman Islands (C. H. Ramesh 2016).

More often, luminous bacteria were isolated from aquaculture settings found along Indian coast. Occurrence of luminous *V. harveyi* (94.86%), *V. splendidus* biotype1 (4.57%) and *V. fischeri* (0.57%) were observed from various samples collected from *Penaeus monodon* culture ponds in West Bengal (Abraham et al. 2007). Luminous bacteria *Photobacterium leiognathi*, *V. fischeri*, *V. harveyi*, *V. orientalis*, and *V. splendidiis* biotype1 were identified from seawater fed ponds in Tuticorin (Abraham et al. 2008). Luminous *V. harveyi* was isolated from *P. monodon* larvae reared in hatchery systems from Andaman Islands (Shome et al. 1999). The dominance distribution of *V. fischeri* and *V. harveyi* followed by *P. leiognathi* and *P. phosphoreum* was reported from the coast of the Gulf of Mannar (Karthikeyan and Balasubramanian 2006).

Fungi

Reportedly, during monsoon, various species of epiphytic fungi observed on the trees in Bhimashankar Wildlife Sanctuary, Western Ghats Zone was found to display bioluminescence (Director 2009). A recent study from Kerala shows that mycelium of Basidiomycota fungi, *Mycena deeptha* produced faint greenish bioluminescence on natural substratum or on malt extract agar (Aravindakshan et al. 2012). Some other unidentified luminous fungal species are also recorded from the Nicobar group of Islands (Author Pers. Comm.). In Goa, *Mycena* species growing (21 to 27°C) on coconut plantations during rainy season are recorded at near Mollem, Bhagwan Mahavir, and Mhadei wild life sanctuaries.

Planktonic forms

Early reports had evidenced the presence of planktonic luminescent organisms such as radiolarian *Thalassicolla* sp. from Andaman Islands (Alcock 1902) and Gangetic delta (Prashad 1923), *Peridinium granii* from Visakhapatnam harbor (Ganapati et al. 1959), *Peridinium* sp. and *Pyrocystis* sp. from pools near Mandapam (Nair et al. 1967), and dinoflagellate *Noctiluca miliaris* from Tuticorin (Gopinathan et al. 1989). Recently, the bioluminescence bloom of *N. scintillans* was observed in the Chennai coast. Stimulated bioluminescence in *Noctiluca* swarms was observed during the movement of shoals of flying fish and dolphins in the Arabian sea (Daniel et al. 1979). Other animals from the estuarine environment of Gangetic delta were also observed (Prashad 1921). Calanoids are the major group of planktonic forms found in the coastal waters. The metridinid calanoids are known to be strongly bioluminescent during the nauplius stage to the adult stages of both sexes, whereas all species of Lucicutiidae copepods are possibly bioluminescent, even in the nauplii stage (P J Herring 1988). Although many studies have carried out various aspects of zooplanktons in India, luminescence activity of calanoids, Lucicutiidae and other zooplanktons are not studied so far in India.

Coelenterates

Luminescence in bloom-forming jellyfish *Pelagia noctiluca* was observed from the Chennai coast (Menon 1930), and estuarine waters of Rushikulya River, Odisha coast (Baliarsingh et al. 2015). The deep-sea luminous medusa, *Atolla wyvillei* was recorded from Krishna and Gangetic deltas, Andaman Sea, and Lakshadweep sea (H. S. Rao 1931). The luminous jellyfish, *Aequorea* sp. and another luminous medusa were recently recorded from Andaman Islands (Author Pers. Comm.).

Annelids

Interestingly, a previous study revealed that the coelomic cells of earthworm, *Lampito mauritii* produced greenish light emission upon stimulation with various stimulants such as dilute solution of ammonia or with 4-volt electric shock, and Hydrogen peroxide (Ismail and Kaleemurrahman 1981), glucose oxidase and glucose in phosphate buffer (Haram et al. 1996), or by pulse voltage, Tris-buffer and guanosine (Santhanam 1993; Santhanam and Haram 1992). This bioluminescent *L. mauritii* was observed by Kaleemurrahman (1981) at National College, Madras (Director 1991). Maximum intensity of bioluminescence in *L. mauritii* was also achieved upon injection of 50 mM Fe²⁺ ions to the cells in the coelomic fluid (Santhanam and Limaye 1989). The luminous earthworms, *Eutyphoeus peguanus*, *Eutyphoeus foveatus*, *Eutyphoeus rarus* and *Megascolex mauritii* which had exuded a glowing slimy substance were reported from Rangoon (Gates 1925). Gates also noted that luminous Oligochaeta belongs to the genera *Allolobophora* (*Eisenia*), *Enchytraeus*, *Lumbricus*, *Microscolex*, and *Octochaetus* are also found in India. Brilliant luminescence from slime of earthworms *Eutyphoeus incommodus*, *Eutyphoeus nicholsoni*, *Eutyphoeus waltoni* and *Ramiella nainiana* collected in Allahabad (Prayagraj) was observed in ammonia solution (Gates 1944). Comparatively, the bioluminescence of *L. mauritii* was intense than the Allahabad earthworm species (Gates 1944). Distribution of bioluminescent *Odontosyllis* sp. on various seaweeds was recorded from south Andaman (C. H. Ramesh et al. 2017).

Arthropods

Luminescence in decapod species such as *Chlorotocus spinicauda* and *Chlorocurtis miser* from Andaman, and *Thalassocaris lucida* and *Thalassocaris crinita* from the Christmas Island of East Indian Archipelago (de Man) and Maldives (Borradaile) were recorded earlier (Kemp 1925). Among Caridea, luminous species are only known from deep-sea species belonging to the family Hoplophoridae (Kemp 1925). Observations on ostracods luminescence in India began in the mid 18th century (Morin 2019). Ostracods are well known to attract their mates in the night using their bioluminescent displays (Morin and Cohen 1991; Parker 1997). Bioluminescence was observed in ostracodes, *Cypridina* sp. from Maldives (Angel 1968) (Zoological Survey of India enews-2012), swarms of *Cypridina dentata* from northern Arabian Sea (Daniel and Jothinayaoam 1979), and *Cypridina hilgendorffii* from Kavaratti Lagoon, Lakshadweep (R. M. Kumar et al. 2016). The zooplankton standing stock off the Karwar coast, Karnataka was reportedly higher (524 ml/100 m³) due to the presence of bioluminescent ostracods (Director 1980). The luminosity of midges (Chironomidae) and *Talitrus* (Amphipoda) were reportedly caused by parasitic luminous microorganisms (might be luminous bacteria or luminous planktonic forms) (Distant 1906).

Luminescence from photophores of *Hymenopenaeus debilis* was recorded during 1938 (Ramadan 1938). Luminescence ability in ostracods (Purushothaman 2015) and deep-sea shrimps (R. D. Chakraborty et al. 2018; Karuppasamy et al. 2006; Kuberan et al. 2018; Shanis 2014) was not investigated by earlier researchers, but reports from other geographical areas evidence that many ostracods (Cohen and Morin 2003) and deep-sea shrimps are luminous (Peter J. Herring 1976; Wong et al. 2015).

Fireflies are widely distributed luminous insect groups around the world. In India, flash patterns of different fireflies, including *Photinus pyralis*, *Phengodes lacticollis*, *Phoruris pennsylvanica* (Saikia et al. 2001), *Pyrophorus noctilucus* (Barua et al. 2007), *Luciola praeusta*, *Asymmetricata circumdata* (Goswami et al. 2019), and *Diaphanes* sp. (Rabha et al. 2020) were studied using time-resolved measurement spectra. Several species of fungus gnats belonging to family Mycetophilidae are known to be luminescent (Director 1991). A beetle *Diaphanes simulator* was found to produce luminescence from large transverse eburated spots in the middle of the fifth and sixth ventral plate (Oliver 1913). The luminosity of glow worms *Harmatelia bilinea*, *Diptoma adamsi*, and yellow-edged black larvae of *Lamprophorus tenebrosus* had been recorded in 1900 AD from Ceylon (Gravelly 1915). Some species of pyrophoric elaterids are also observed to display luminescence (P. Chakraborty and Samiran 2006). The luminous glow-worm, *Lamprophorus tenebrosus* was also reported from the Ganjam district of the Madras Presidency in August, 1917 (Paiva 1918). Recent study reports evidences that luminous fireflies are declining at local and global scales due to global warming, light pollution, and use of various toxic pollutants in agriculture fields (P. Kumar et al. 2019; C. H. Ramesh 2020b). Thus conservation of fireflies has been one of the current ecological research interests around the world.

A species of Trilobite larvae were known to emit luminescence from a pair of phosphorescent organs on the penultimate segment of the abdomen (Gravelly 1901). The first recorded luminous spider from Burma had greyish abdomen with thumb sized whole abdomen light (Brown 1925). The second luminous spider was reported from Shillong, Assam, produced luminescence from 6 to 8 spots under abdomen to frighten predators (Brown 1926). Recently, in our investigations a new luminous spider emitting yellow light was observed from northeast hill region (Author Pers. Comm.). This is the first observation made on this rare unidentified luminous spider in India. Whole-body of this specimen produced intense luminescence like fireflies. Whole specimen was in lime yellow colour. In these three cases, observations indicated the evolutionary specific functions of bioluminescence via species specific light organs position. Unfortunately, in all three cases, specimens were not caught and thus identification was unsuccessful.

Echinoderms

Although many luminous echinoderms (Holothuroidea, Asteroidea, Ophiuroidea, and Crinoidea) are reported from elsewhere (Mallefet 2005, 2009), but no attempts are made so far observe luminous echinoderms in India. The genus *Amphiura* is well known for luminescence emission, but India, genus *Amphiura*, *Ophiopsila* and others (Usha et al. 2018) are not investigated for luminescence abilities. For instance, brittle star, *Ophiopsila* sp. is found in Andaman Islands but luminescence was not investigated. Many deep-sea luminous echinoderm species have not been explored in India due to lack of facilities as well as specific focus on bioluminescence. Thus this is a huge research gap to be filled in India.

Salps

Reportedly, several specimens of salps *Cyclosalpa pinnata* collected from Nankauri Harbour and Revello Channel, Nicobars had displayed luminescence in four pairs of lateral luminous organs (S. R. B. Sewell 1926). Many other salp species found in Indian waters are not investigated for their bioluminescence capabilities. Thus many species are not recorded as luminous.

Fishes

Reef associated luminous pinecone fish, *Monocentris japonica* was recorded from Andaman and Nicobar Islands (D. V Rao 2003). Luminescence in two deep sea fish species *Chauliodus pammelas* and *Chauliodus sloani* from Bay of Bengal (Misra 1952) and some other fishes from Bombay region (Haneda 1961) was reported. A luminous bristlemouth, *Triplophos hemingi* collected from Bay of Bengal was known to produce luminescence (Lloyd 1909). Species specific light organ morphology was observed for luminous pony fish species such as *Secutor insidiator*, *S. ruconius*, *Gazza minuta*, *G. achlamyss*, *Leiognathus equulus*, *E. splendens*, *L. dussumieri*, *L. herbis*, *L. lineolatus*, *Karalla daura*, and *Leiognathus* sp. collected from Bay of Bengal off Parangipettai (Port Novo) (Jayabalan 1989). A report also mentioned that shoals of *P. bindus* observed in Kozhikode (Calicut) coast had displayed bright luminescence during dark phase of the moon (V. Balan 1963). Seasonal studies and length group based changes on the development of light organs of pug-nose ponyfish, *Secutor insidiator* revealed larger light organs in males than females of the same length groups (Sebastian and Inasu 2012). The catches of silverbellies using bottom trawlers was varied during day and night due to ventral bioluminescence (Jayabalan and Ramamoorthi 1979).

Whereas, many coastal and deep sea fishes of the families Ceratidae, Leiognathidae, Salmiformes, Myctolphiformes, Pempheridae, Gonostomatidae, Sternoptychidae, Photichthyidae, Monocentridae, Clupeiformes, Alepocephalidae (Genus *Xenodermichthys*, *Leptoderma*),

Chauliodontidae, Dolichopterygidae, Idiacanthidae, Astronesthidae, Sudidae, Melanostomiidae, Stomiidae, Platytroctidae, Trachichthyidae, Evermannellidae, and Myctophidae are known to emit luminescence (Bineesh et al. 2010; Director 1991; Meera et al. 2019; Misra 1976; M. P. Rajeeshkumar 2018). Several studies have been conducted on deep-sea fisheries (Akhilesh et al. 2010; Akhilesh 2013, 2014; Catul et al. 2011; Karuppasamy et al. 2006; K. V. K. Kumar et al. 2016; M. Rajeeshkumar et al. 2018; Sajeevan et al. 2009; Sebastine et al. 2013; Sileesh et al. 2020; Venu 2013; Venu et al. 2016; Venu and Kurup 2002), however these studies did not observe luminescence in these animals. Thus, further investigation are needed to confirm the luminescence ability in list of deep-sea fishes and other organisms in Indian waters.

Misidentified groups

Some non-luminous organisms are misidentified as luminous organisms in some parts of India. Although oil sardine species *Sardinella longiceps* are not bioluminescent, but previous reports documented luminescence exhibition by shoals of *S. longiceps* from inshore area off Calicut. These *S. longiceps* shoals displayed moderate to strong luminescence patterns. These fish were easily caught in net during moderate luminescence, and unsuccessful during intense luminescence due to high visibility of fishing gears (V. Balan 1961). Luminescence generated from shoals of *S. longiceps* is due to the presence of dense luminous planktonic forms (e.g., *Noctiluca*, *Ceratium*, Copepods etc.) or dinoflagellates associated luminous bacteria in water column. The Bombay duck *Harpodon nehereus* was also reported to be brilliantly luminous over its whole surface (Kemp 1917). Indeed, *H. nehereus* is not a luminous fish and its luminescence on body surface is bacterial to luminescence (Dewi et al. 2018).

A rare luminous rock gecko *Cyrtodactylus madarensis* was reported from the Madar foothills near Ajmer, Rajasthan (R. C. Sharma 1980). But later it was thought that luminescence from gecko perhaps due to preying on luminous fireflies that make them to glow in the night. In 1999, a bioluminescent gecko, *Velicham thoovunna* was also observed (Radhakrishnan 1999). However, recent evidences infers that geckos display fluorescence under blue light but not luminescence (Sloggett 2018; Top et al. 2020). In a rare incident, barn Owl species *Tyto alba*, in England and Australia, scurrying around their milieus were known to emit luminescence in the dark (Silcock 2003). This evidence indicates that perhaps luminous gecko's may be existing, but needed to be reinvestigated to confirm whether they display luminescence or fluorescence or iridescence.

A note by Col. D. D. Cunningham (1903) had indicated that the eyes of Indian toddy-cats (*Paradoxurus hermaphroditus*) appeared to strangely luminous in dim light (R. B. S. Sewell 1939).

However, it is due to reflection caused by tapetum lucidum, but not luminescence. In 1920, E.N. Harvey, in his book “Nature of Animal Light” had attributed bioluminescence in mammalian eyes to tapetum lucidum (Table 3).

Table 3. List of terrestrial and marine luminous organisms reported from India.

S. No	Organism type	Species/family	Environment	Remark
Bacteria				
1.		<i>Kurthia</i> sp.	Marine	Luminous; Needs taxonomic reverification
2.		<i>Vibrio alginolyticus</i>	Marine	Luminous
3.		<i>Vibrio azureus</i>	Marine	Luminous
4.		<i>Vibrio campbellii</i>	Marine	Luminous
5.		<i>Vibrio cholerae</i>	Marine	Luminous
6.		<i>Vibrio fischeri</i>	Marine	Luminous
7.		<i>Vibrio harveyi</i>	Marine	Luminous
8.		<i>Vibrio owensii</i>	Marine	Luminous
9.		<i>Vibrio orientalis</i>	Marine	Luminous
10.		<i>Vibrio rotiferianus</i>	Marine	Luminous
11.		<i>Vibrio splendidus</i> biotype1	Marine	Luminous
12.		<i>Vibrio vulnificus</i>	Marine	Luminous
13.		<i>Photobacterium. leiognathi</i>	Marine	Luminous
14.		<i>Photobacterium phosphoreum</i>	Marine	Luminous
15.		<i>Photobacterium damsela</i>	Marine	Luminous
16.		<i>Photorhabdus luminescens</i>	Terrestrial	Luminous
17.		<i>Shewanella hanedai</i>	Marine	Luminous
Fungi				
18.		<i>Mycena deeptha</i>	Terrestrial	Luminous
19.		Unidentified species	Terrestrial	Luminous
Planktonic forms				
20.		<i>Gonyaulax spinifera</i>	Marine	Luminous
21.		<i>Noctiluca miliaris</i>	Marine	Luminous
22.		<i>Noctiluca scintillans</i>	Marine	Luminous
23.		<i>Peridinium granii</i>	Marine	Luminous
24.		<i>Peridinium</i> sp.	Marine	Luminous
25.		<i>Pyrocystis</i> sp.	Marine	Luminous
26.		<i>Thalassicolla</i> sp.	Marine	Luminous
Coelenterates				
27.		<i>Atolla wyvillei</i>	Marine	Luminous
28.		<i>Aequorea</i> sp.	Marine	Luminous
29.		<i>Beroe ovata</i>	Marine	Luminous
30.		<i>Eirene</i> sp.	Marine	Luminous
31.		<i>Pelagia noctiluca</i>	Marine	Luminous
33.		<i>Pleurobrachia</i> sp.	Marine	Luminous
34.		Unidentified medusa	Marine	Luminous

Annelids				
35.		<i>Allolobophora (Eisenia)</i>	Terrestrial	Luminous
36.		<i>Enchytraeus</i>	Terrestrial	Luminous
37.		<i>Eutyphoeus foveatus</i>	Terrestrial	Luminous
38.		<i>Eutyphoeus incommodus</i>	Terrestrial	Luminous
39.		<i>Eutyphoeus nicholsoni</i>	Terrestrial	Luminous
40.		<i>Eutyphoeus peguanus</i>	Terrestrial	Luminous
41.		<i>Eutyphoeus rarus</i>	Terrestrial	Luminous
42.		<i>Eutyphoeus waltoni</i>	Terrestrial	Luminous
43.		<i>Lampito mauritii</i>	Terrestrial	Luminous
44.		<i>Lumbricus</i>	Terrestrial	Luminous
45.		<i>Megascolex mauritii</i>	Terrestrial	Luminous
46.		<i>Microscolex</i>	Terrestrial	Luminous
47.		<i>Octochaetus</i>	Terrestrial	Luminous
48.		<i>Odontosyllis</i> sp.	Marine	Luminous
49.		<i>Pontodrilus litoralis</i>	Marine	Probably luminous
50.		<i>Ramiella nainiana</i>	Terrestrial	Luminous; taxonomic uncertainty
Arthropods				
51.		<i>Acanthephyra fimbriata</i>	Marine	Luminous
52.		<i>Asymmetricata circumdata</i>	Terrestrial	Luminous
53.		Chironomidae	Terrestrial	Luminous
54.		<i>Chlorocurtis miser</i>	Marine	Luminous
55.		<i>Chlorotocus spinicauda</i>	Marine	Luminous
56.		<i>Cypridina</i> sp.	Marine	Luminous
57.		<i>Cypridina dentata</i>	Marine	Luminous
58.		<i>Cypridina hilgendorffii</i>	Marine	Luminous
59.		<i>Diaphanes simulator</i>	Terrestrial	Luminous
60.		<i>Diophtoma adamsi</i>	Terrestrial	Luminous
61.		Elateridae	Terrestrial	Luminous
62.		<i>Harmatelia bilinea</i>	Terrestrial	Luminous
63.		Hoplophoridae	Marine	Luminous
64.		<i>Hymenopenaeus debilis</i>	Marine	Luminous
65.		<i>Lamprophorus tenebrosus</i>	Terrestrial	Luminous
66.		<i>Luciola praeusta (Abscondita chinensis)</i>	Terrestrial	Luminous
67.		Mycetophilidae	Terrestrial	Luminous
68.		<i>Phengodes lacticollis</i>	Terrestrial	Luminous
69.		<i>Phoruris pennsylvanica</i>	Terrestrial	Luminous
70.		<i>Photinus pyralis</i>	Terrestrial	Luminous
71.		<i>Pyrophorus noctilucus</i>	Terrestrial	Luminous
72.		<i>Talitrus</i>	Marine	Luminous
73.		<i>Thalassocaris crinita</i>	Marine	Luminous
74.		<i>Thalassocaris lucida</i>	Marine	Luminous
75.		Unidentified spider	Terrestrial	Luminous
Echinoderms				

76.		<i>Amphiura</i> sp.	Marine	Probably luminous
77.		<i>Ophiopsila</i> sp.	Marine	Probably luminous
	Salps			
78.		<i>Cyclosalpa pinnata</i>	Marine	Luminous
	Fishes			
79.		Alepocephalidae	Marine	Luminous
80.		<i>Antennarius hispidus</i>	Marine	Luminous
81.		Astronesthidae	Marine	Luminous
82.		Ceratidae	Marine	Luminous
83.		<i>Ceratias uranoscopus</i>	Marine	Luminous
84.		<i>Chauliodus pammelas</i>	Marine	Luminous
85.		<i>Chauliodus sloani</i>	Marine	Luminous
86.		Clupeiformes	Marine	Luminous
87.		<i>Cryptopsaras couesi</i>	Marine	Luminous
88.		Dolichopterygidae	Marine	Luminous
89.		<i>Diaphus coeruleus</i>	Marine	Luminous
90.		<i>Diaphus garmani</i>	Marine	Luminous
91.		<i>Equulites lineolatus</i> (<i>Leiognathus lineolatus</i>)	Marine	Luminous
92.		<i>Eubleekeria splendens</i> (<i>Leiognathus splendens</i>)	Marine	Luminous
93.		Evermannellidae	Marine	Luminous
94.		<i>Gazza achlamyss</i>	Marine	Luminous
95.		<i>Gazza minuta</i>	Marine	Luminous
96.		Gonostomatidae	Marine	Luminous
97.		Idiacanthidae	Marine	Luminous
98.		<i>Karalla daura</i>	Marine	Luminous
99.		<i>Karalla dussumieri</i>	Marine	Luminous
100.		<i>Leiognathus</i> sp.	Marine	Luminous
101.		<i>Leiognathus equulus</i>	Marine	Luminous
102.		<i>Leiognathus herbis</i>	Marine	Luminous
103.		Melanostomiidae	Marine	Luminous
104.		<i>Monocentris japonica</i>	Marine	Luminous
105.		<i>Etmopterus</i>	Marine	Probably luminous
106.		Myctolphiformes	Marine	Luminous
107.		Myctophidae	Marine	Luminous
108.		Pempheridae	Marine	Luminous
109.		Photichthyidae	Marine	Luminous
110.		<i>Photopectoralis bindus</i> (<i>Leiognathus bindus</i>)	Marine	Luminous
111.		Salmoformes	Marine	Luminous
112.		Platytroutidae	Marine	Luminous
113.		<i>Secutor insidiator</i>	Marine	Luminous
114.		<i>Secutor ruconius</i>	Marine	Luminous
115.		Sternoptychidae	Marine	Luminous

116.		Stomiidae	Marine	Luminous
117.		Suidae	Marine	Luminous
118.		Trachichthyidae	Marine	Some are luminous
119.		<i>Triplophos hemingi</i>	Marine	Luminous
Misidentified groups				
120.	Fish	<i>Harpodon nehereus</i>	Marine	Non-luminous
121.		<i>Sardinella longiceps</i>	Marine	Non-luminous
122.	Reptile	<i>Eublepharis macularius</i> (<i>Cyrtodactylus madarensis</i>)	Terrestrial	Non-luminous
123.		<i>Velicham thoovunna</i>	Terrestrial	Probably not luminous; & taxonomic uncertainty
124.	Mammal	<i>Paradoxurus hermaphroditus</i>	Terrestrial	Non-luminous

How to photograph & measure luminescence

Live and undamaged luminous organisms have the more luminous capability; thus, handling luminous organisms is essential for best photography. Captured animals are always left in darkness to rest for 10 to 15 minutes, without any external stimulants (e.g., mechanical or light stimulation). Acclimate your eyes to darkness, observe the luminescence ability of animals, and proceed for photography. A dim red light is used to adapt our vision to the dark for checking bioluminescence. Exposure time shall be longer than the luminescent emission to ensure capturing the event (Warren R. Francis et al. 2016). Terrestrial bioluminescent organisms like earth worms and railroad worms are placed under red light or infrared light illumination for best capture of bioluminescence activity. If the animal does not produce any light, stimulate its body with a gentle touch or mechanical or photostimulation; and take photographs using low light sensitive cameras (Bessho-Uehara et al. 2020). Currently, many photographic equipment companies (e.g., Canon ninja, Nikon, etc.) have the advanced equipment to capture minute amounts of light, such as bioluminescence using high ISO performance, e.g., ISO of 4,560,000 (Gruber et al. 2018).

Deep-sea bioluminescence blooms caused by the main contributors like luminous bacteria were documented using ANTARES underwater “telescope,” a non-imaging array of sensitive light detectors (Tamburini et al. 2013). Whereas, massive bioluminescence blooms like “milky seas” (~15,400 km² area) caused by luminous *V. harveyi*, presumably in association with microalga *Phaeocystis* was captured using satellites (Miller et al. 2005). Among different bioluminescence bathyphotometers (Herren et al. 2005), HIDEX bathyphotometers have excellent efficiency to pump

seawater up to 44 L s^{-1} (Widder et al. 1993). Low light radiometer system with high-speed silicon photomultipliers are reported to offer a robust spectral analysis of deep-sea bioluminescence (Haag et al. 2014). Luminescence activity of fragile bodied deep-sea luminous organisms such as several zooplankton groups, hydromedusae, and pelagic worms like *Tomopteris* sp. was recorded using a high resolution scientific complementary-metal-oxide-semiconductor (sCMOS) microscopy camera (Phillips et al. 2016). Development of advanced remote and automated satellites and bathyphotometers will help to understand the spatial-temporal variations of harmful algal blooms and other planktonic populations as well as marine ecosystem dynamics (Haddock et al. 2010).

Research gaps

There are thousands of unexplored animals whose luminescence is yet to be determined naturally or using stimulation techniques. In the current scenario of global climate change, horizontal gene transfer (HGT) of *lux* genes from luminous bacteria to non-luminous bacterial members of Vibrionaceae is remaining a question mark (Urbanczyk et al. 2008). Specially, the various factors responsible for intense, weak, and dim luminescence patterns in bacteria and fungi are not well understood. Therefore, understanding these concepts are important for analysing ecological and biological influences on luminescence.

The origin, biosynthesis pathway, and acquirement of coelenterazine by the Cnidarians are yet to be determined (Haddock et al. 2010). Distribution patterns and acquirement pathways of luciferins exogenously (ex. euphausiids feed on zooplankton) through food web is yet to be demonstrated (Haddock et al. 2010). Presence of *Cypridina* luciferin in luminous fishes like *Parapriacanthus* and *Apogon*; and coelenterazine luciferin in various coelenterates, shrimps, squids and fishes indicating the importance of studying origin, synthesis and dietary pathways of these luciferins (Shimomura and Yampolsky 2019). The bioluminescence mechanisms of various species of dinoflagellates and krill are yet to be fully characterized (Kaskova et al. 2016). Luciferase like *Diplocardia* luciferase, fungal luciferase, are yet to be cloned (Kaskova et al. 2016). The chemical structures of *Latia* purple protein, and unknown luciferins of cnidarians, *Chaetopterus*, *Harmothoe*, *Henlea*, some echinoderms, sea salps and others (Haddock et al. 2010; Kaskova et al. 2016) are to be unveiled for potential biotechnological and biomedical applications.

Conclusion

This review represents that India has all most all taxonomic group of luminous organisms. The role of taxonomical researchers is also plays a major role in confirming the bioluminescence trait in many organisms as they encounter almost all organism in different environments. Also, many unexplored

areas of India are under protection, so not many researchers are unable to access such rich biodiversity areas. Thus, researchers who have official permits to access protected areas shall extend their night-time odysseys on bioluminescence. Therefore, exploring these luminous organisms is of great interest in biotechnology and genetic engineering research. Considerably, many known luminous organisms are least studied in Indian scenario, therefore, redirecting the basic research on bioluminescent organisms will certainly fetch great revival in Indian science and technology. Research on luminous organism would certainly improve our understanding of known bioluminescence systems, as well as to identify and characterize novel bioluminescent systems for developing new bioluminescence based monitoring tools. Luminescence of toddy-cats and rock gecko needs to be reconfirmed. Besides, the stimutable luminescence of echinoderms is yet to be explored from Indian waters. The deep-sea luminescence of several fish and another taxonomic group of organisms are to be explored. Conversely, it is a serious condition that some terrestrial luminous organisms (e.g., fireflies) are disappearing due to artificial light and air pollutions. Since their occurrence indicates a healthy environment, these indicator organisms shall be conserved. Significantly, the biodiversity hotspot regions such as the Bay of Bengal, the Arabian Sea, the Indian Ocean, Himalayan regions, and Andaman and Nicobar Islands needs to be explored for luminous organisms. Since the genes responsible for light emission have a great demand in commercial and industrial applications, the molecular characterization of these organisms is to be studied in detail. The applications of the known luminous organism are yet to be extended in various biotechnological fields, including toxicology, disease propagation, imaging, and biosensors.

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Figure legends

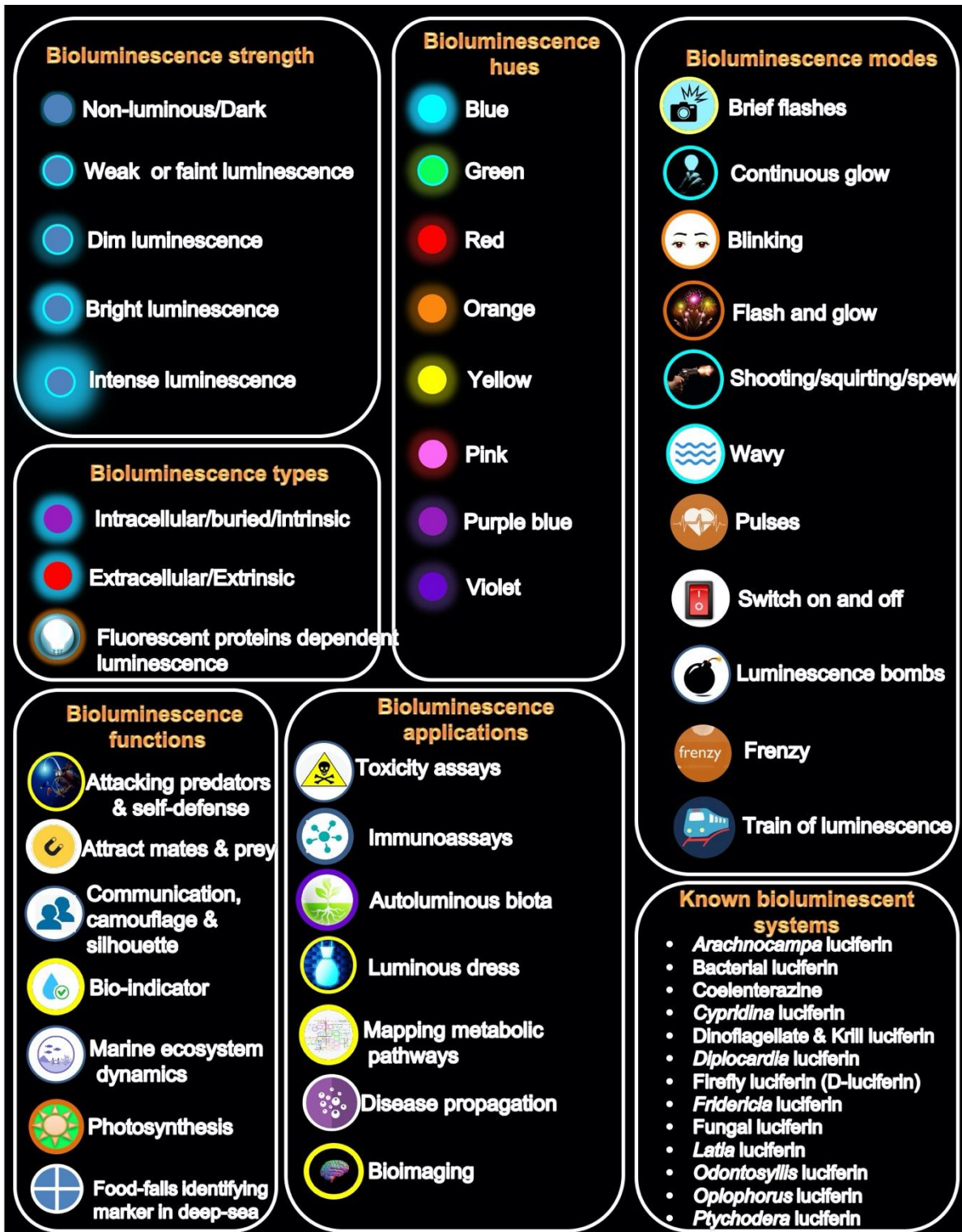


Fig. 1. An overview about bioluminescent phenomena.

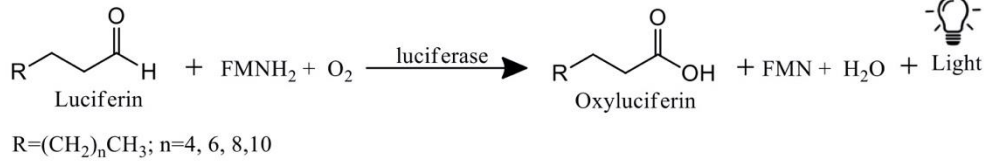
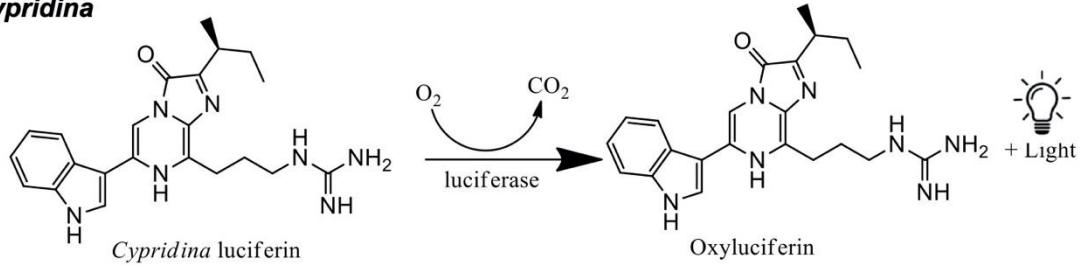
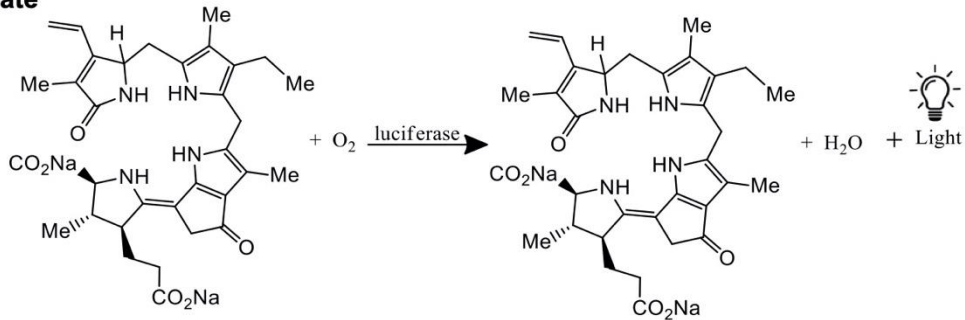
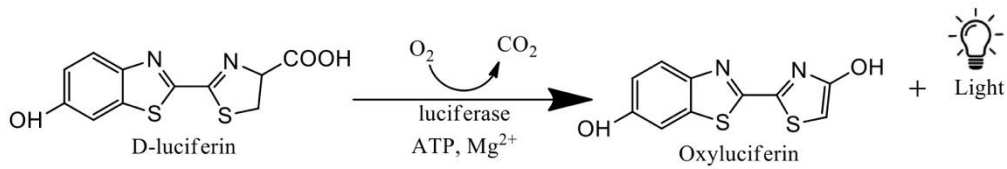
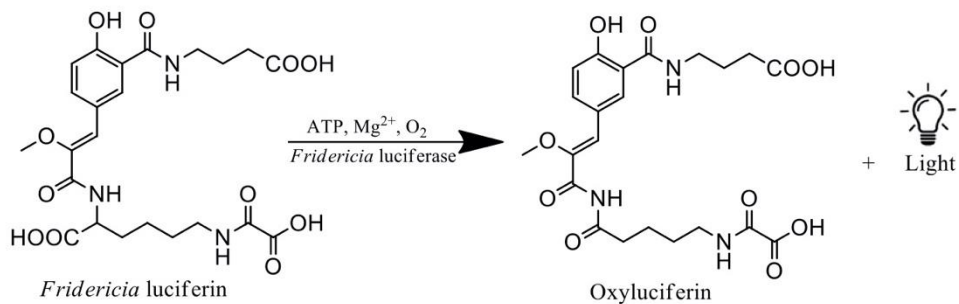
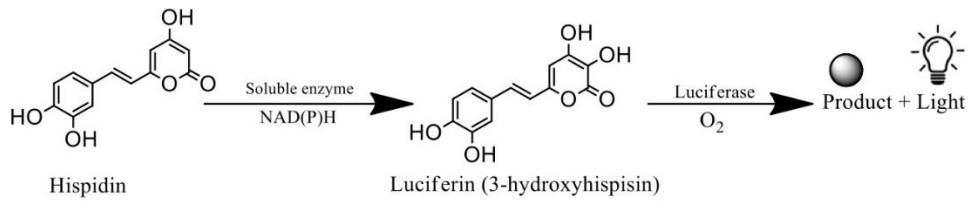
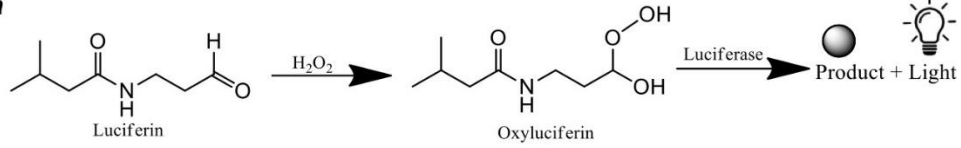
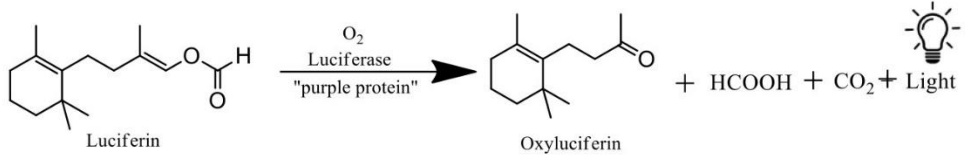
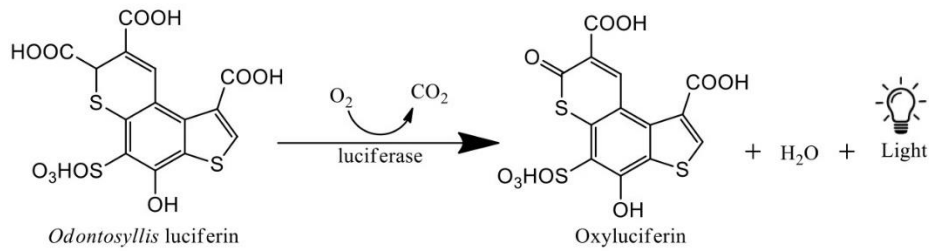
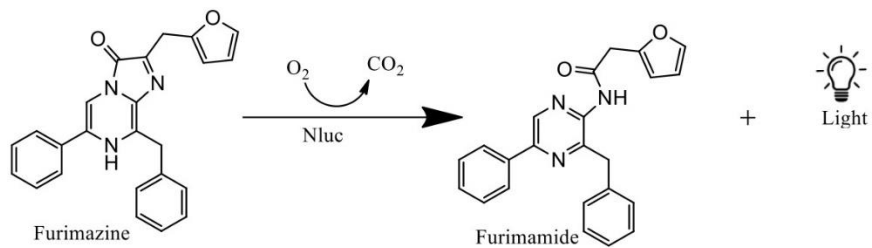
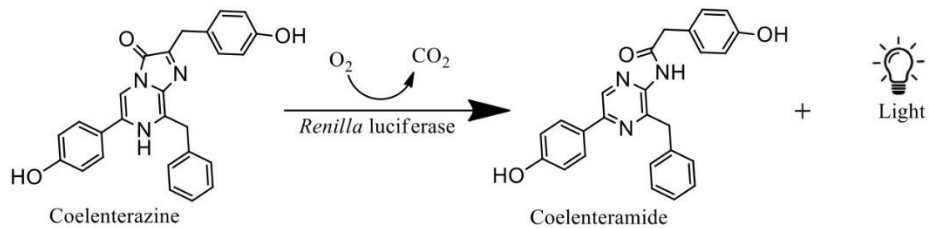
Bacterial**Cypridina****Dinoflagellate****Firefly****Fridericia**

Fig. 2. Chemical reactions of known bioluminescent systems (Brodl et al. 2018; Dubinnyi et al. 2015; Hall et al. 2012; Kaskova et al. 2016; Kotlobay et al. 2019; Lee 2017).

Fungal**Diplocardia****Latia****Odontosyllis****Oplophorus****Renilla****Fig. 2.** Continued.

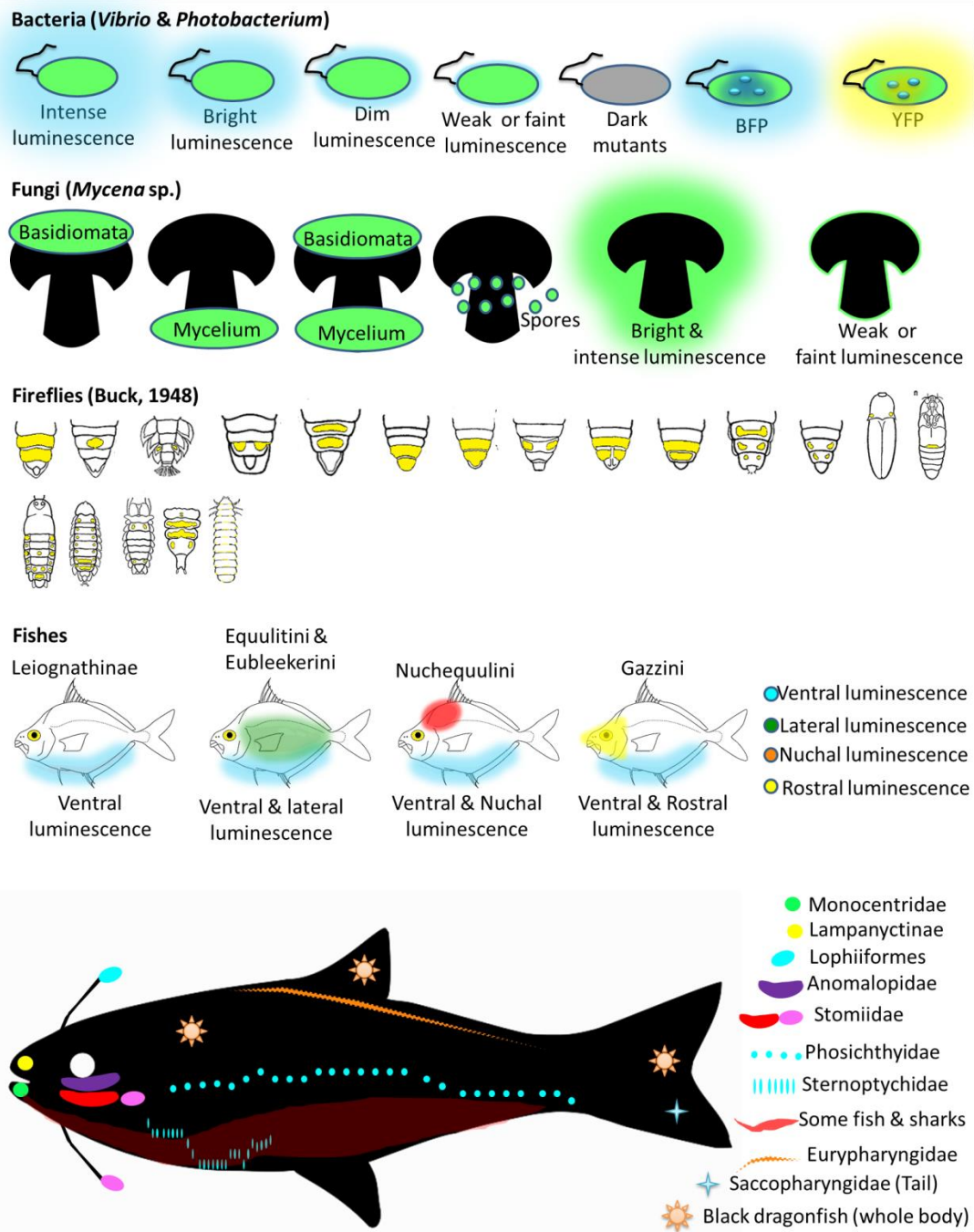


Fig. 3. Illustration showing some examples on light organ arrangement and emission patterns in specific group of luminous organisms. Image was created based on the references: (Aravindakshan et al. 2012; Buck 1948; Chakrabarty et al. 2011; Davis et al. 2014; Leavell et al. 2018; McDermott and Buck 1959; Paitio et al. 2016; C. H. Ramesh and Mohanraju 2019; Wilson and Hastings 2013).






	 Glowing plants	 Light Bulb	 Toxicity assays	 Bio imaging	 Naval studies
Bacterial luminescence	✓	✓	✓	✓	✓
Fungal luminescence	✓	✗	✓	✓	✗
Dinoflagellate luminescence	✗	✓	✓	✓	✓
Coelenterate luminescence	✗	✗	✓	✓	✗
Firefly luminescence	✗	✗	✓	✓	✗

Fig. 4. Applications of various known bioluminescence systems. Note: bacterial and dinoflagellate luminescence are known to hinder Naval operations in marine, thus studies on these organisms are great concern for Navy.

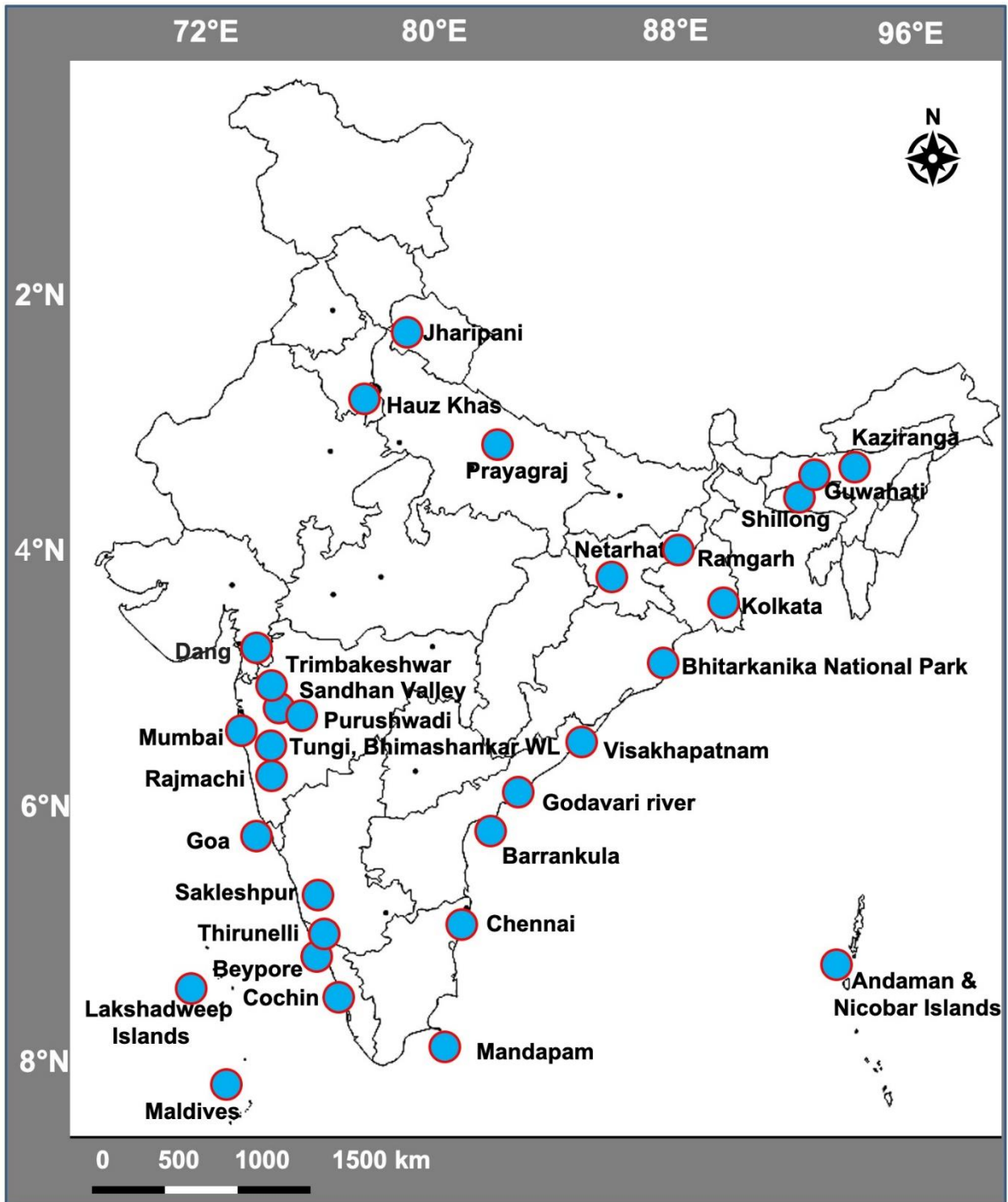


Fig. 5. Map showing luminous organisms distribution in different parts of India.

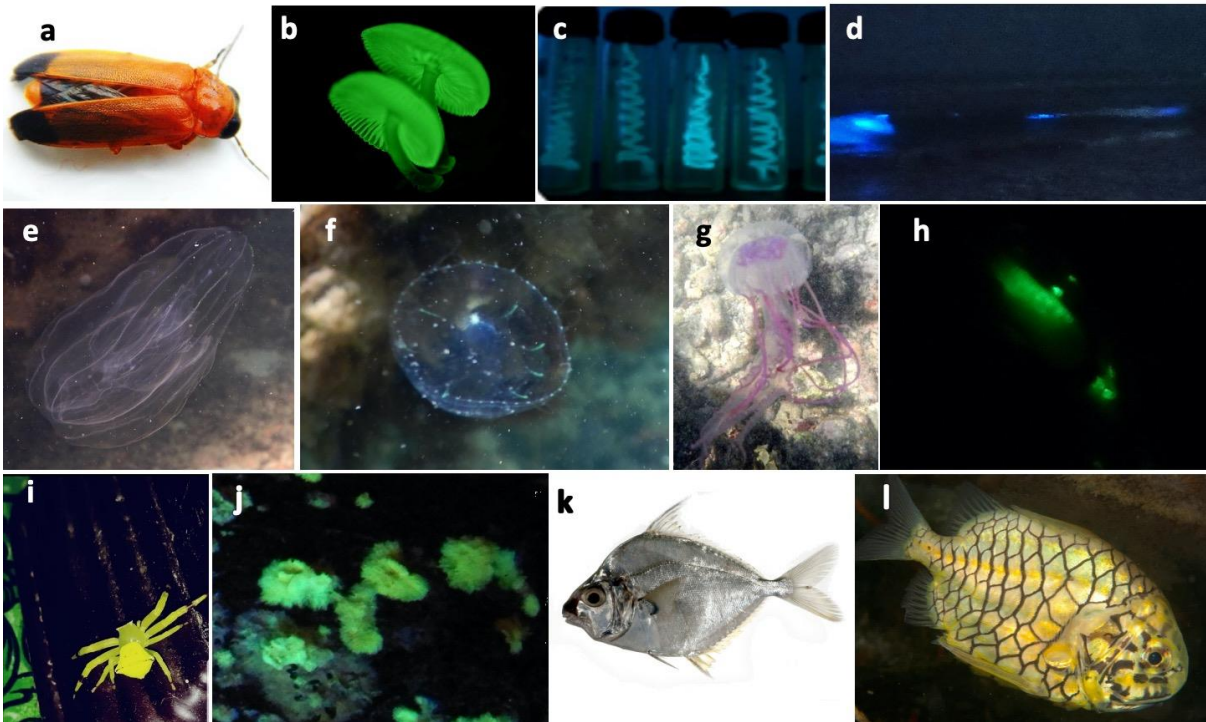


Fig. 6. Some of the luminous organisms of India. Firefly, *Abscondita perplexa* (a); basidiomycota fungi, *Mycena* sp. (b); luminous bacteria, *Vibrio* & *Photobacterium* (c); dinoflagellate, *Noctiluca scintillans* (d); comb jelly, *Beroe ovata* (e); hydroid, *Eirene* sp. (f); jellyfish *Pelagia noctiluca* (g); fireworm, *Odontosyllis* sp. (h); unidentified yellow luminous spider (i); unidentified luminous fungi (j); leiognathid fish, *Leiognathus equulus* (k); and pinecone fish, *Monocentris japonica* (l).