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Bioluminescence: Fundamentals and Applications in Biotechnology– Volume 1

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Bioluminescence: Fundamentals and Applications in Biotechnology–Volume 1

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Contents

Part I
Fundamentals of Bioluminescence

Eco-Evo Bioluminescence on Land and in the Sea

Yuichi Oba and Darrin T. Schultz

Abstract This review discusses the evolution of bioluminescence organisms that inhabit various environments based on the current understanding of their unique ecologies and biochemistries. As shown here, however, there are still many unanswered questions regarding the functions and mechanisms of bioluminescence, which should be investigated in further studies. To facilitate future research in this field, we introduce our recent attempt, the bioluminescent organism DNA barcode initiative. This genetic reference library will provide resources for other scientists to efficiently identify unstudied bioluminescent organisms, focus their biochemical and genetic research goals, and will generally promote bioluminescence as a field of scientific study.

Keywords Aposematism · Coelenterazine · Counter-illumination · Cypridinid luciferin · DNA barcoding · Ecology · Evolution · Symbiotic luminescence

Contents

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1 Introduction

Bioluminescent organisms occur in a wide variety of habitats, from tropical jungles to barren fields, from sunny beaches to dark caves, and from oceanic surface waters to abyssal depths. Those species that are aquatic are largely confined to the oceans whereas only a few occur in freshwater. Bioluminescent taxa have been reported from bacteria to vertebrates, in fact from most branches on the tree of life. However, some branches are species-rich, such as teleosts, crustaceans, cnidarians, and coleopterans, whereas others contain few or, like plants, tetrapods, arachnids, and lepidopterans, have no known bioluminescent representatives (Fig. 1). The biological and ecological functions of bioluminescence vary from species to species, but it seems likely that counter-illumination is predominant in marine species, and aposematism is abundant in terrestrial species. Coelenterazine, a substance involved in the luminescence reaction, is commonly used by disparate marine taxa, whereas firefly luciferin is used only in the terrestrial elateroid beetles. In this chapter, we review the ecology and evolution of luminous organisms, and discuss the possible reasons why some functions, habitats, chemical substrates, and taxa are preferred or avoided in the world of bioluminescence.

2 Function of Bioluminescence

2.1 Self-defense

Many different biological and ecological functions have been proposed for bioluminescence [1, 2], but the most parsimonious explanation is that it is used as an antipredator defensive device. Here we categorize the various defensive reactions by luminous organisms aimed at predators into three types: startling (or deterring), misdirection (or distraction/obstruction of sight), and aposematism (warning display).

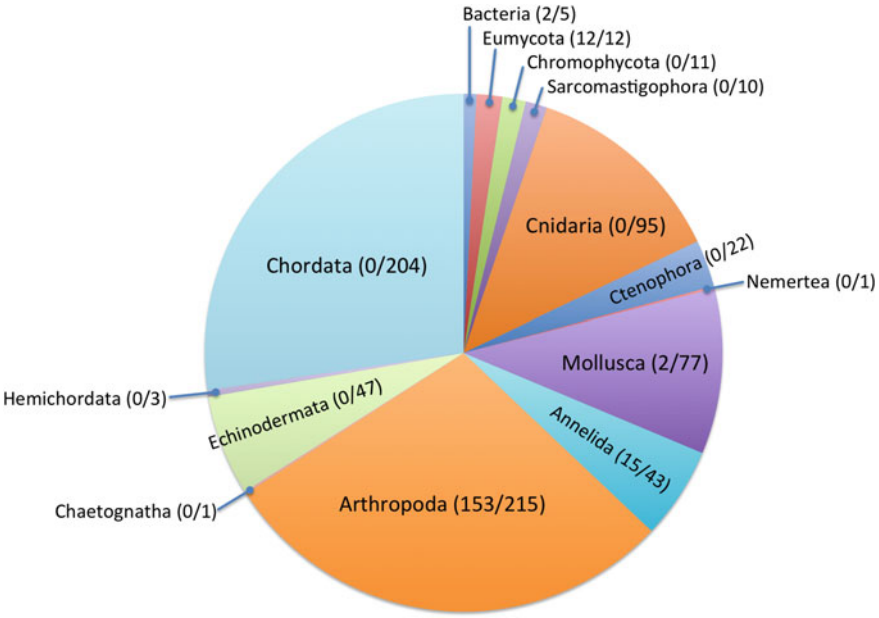

Fig. 1 The diversity of bioluminescent organisms as proportions of the named 746 genera. The fraction indicates the number of terrestrial genera relative to the total number of genera. Numbers are based on Herring [1] and the supplemental material in Haddock et al. [2]. The genera not certain to be luminous in Herring [1], and "doubtfully" luminous genera of sponge and bryzoan [2] are excluded. Numbers of genera in some groups are modified according to recent publications: Bacteria [139], Lampyridae [173], Phengodidae [8], Rhagophthalmidae [174], Gastropoda [109], Oligochaeta [102], Homalisidae (Omalisidae) [81], and Fungi [97]. Nematode *Heterorhabditis* is excluded because symbiotic luminous bacteria *Photorhabdus* does not emit visible light in the nematode [100]. For compatibility with the list by Herring [1], the classification of Division and Phylum is followed in the systematics by Parker [95]

Sudden flashes in dark surroundings have been shown to startle, deter, and stun or temporarily blind predators regardless of the prey's palatability. For example, the mesopelagic squid, *Taningia danae,* uses its arm-tip photophores to flash in bursts while attacking bait rigs [3]. Moreover, in the firefly squid *Watasenia scintillans* (Fig. 2), the nervous-system controlled arm-tip photophores are thought to flash in bursts when attacked by predators [4, 5]. This seems to be similar to cases in which the eye-spots on the surfaces of the hind wings of some Lepidoptera startle predators by their sudden exposure [6], an example of Batesian mimicry in which reflective owl eyes are the model. However, startling bioluminescence is probably not Batesian mimicry, as it does not imitate any predator models. The exceptions include some phengodid beetle larviform female adults, and the adults of click beetles. The female phengodids *Diplocladon* and *Rhagophthalmus* curl their bodies around their eggs to protect the brood, and when disturbed emit light from small circular photophores lining the body (Fig. 3).

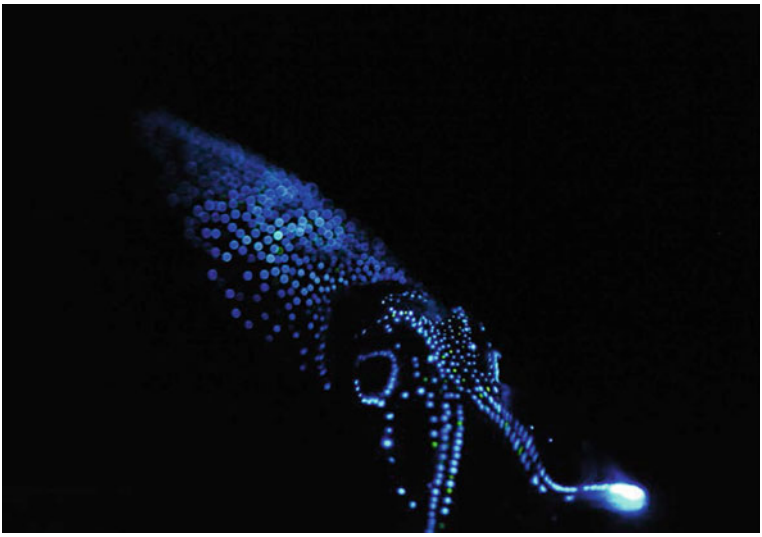

Fig. 2 Firefly squid *Watasenia scintillans* collected in Toyama Bay, Japan. This picture shows the interspersed photophores on the ventral side of the mantle that face down as the creature swims. The larger light organ on the tip of arms is assumed to be used for stunning predators. Photo courtesy of So Yamashita

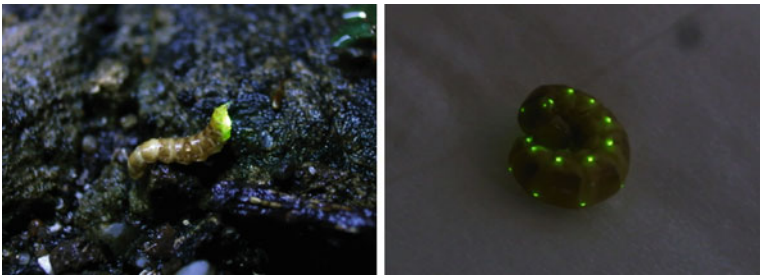

Fig. 3 Luminescence of the phengodid beetle *Rhagophthalmus ohbai* female adult at Ishigaki Island, Japan. Attracting a male (*left*) and after copulation (*right*)

Ohba [7] hypothesized that the light emission may function to startle predators by mimicking the shining eyes of nocturnal birds. The adults of the luminous click beetles (e.g., Jamaican *Pyrophorus* species) possess a pair of oval photophores at the outward-angled posterior margins of the prothorax [8], and the luminescence looks like the shining eyes of nocturnal animals found in forests at night (VB Meyer-Rochow, personal communication). Thus, the luminescence of phengodid and click beetles may be an example of a startling function evolved in the presence of a sympatric predator model.

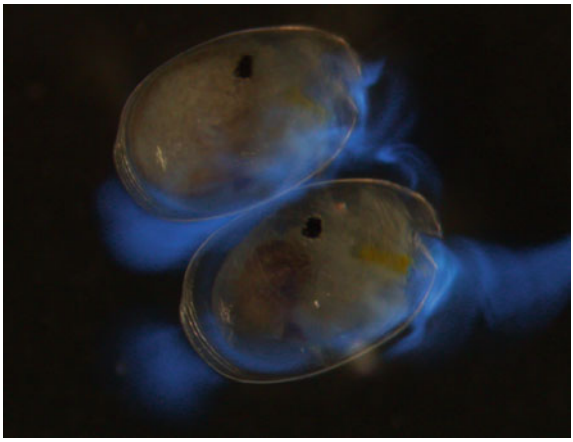

Fig. 4 Coastal ostracod *Vargula hilgendorfii* collected at Seto Inland Sea, Japan. This blue luminous cloud was discharged upon electro-stimulation. Photo courtesy of Ken-ichi Onodera

Luminescent secretion clouds discharged by agitated bioluminescent organisms in aphotic or very dim seawater are assumed to cause predators to lose sight of the prey or become distracted while the creature escapes. This is similar to the squid, octopus, and other cephalopod behavior of releasing a "smokescreen" of dark ink to obscure its position from predators when disturbed. Some luminous squid, shrimp, and ostracods (Fig. 4) discharge luminous clouds into the seawater, primarily to act as a smoke screen against predators while making an escape [2]. Some luminous species discharge luminous droplets or mucus as decoys and flee when attacked, for example, terrestrial centipedes [9], freshwater limpet *Latia* (see Sect. 3.4), and copepods [10, 11]. These behaviors will make predators lose track of the prey's path, allowing it to escape safely. However, this strategy is sometimes indistinguishable from that of creating a smokescreen of luminous material in marine environments.

Aposematism is a signal displayed to potential predators to warn of toxicity and/or noxiousness. For example, firefly larvae and adults are both noxious and toxic for various predators, including insects, centipedes, spiders, fish, amphibians, reptiles, and mammals [12–16], thus a function of firefly luminescence has been considered to be an aposematic display [17–19]. All known larvae of lampyrid species are luminous, but the adults of some species are nonluminous [20]. Therefore, it seems that aposematism was a contributing factor in the evolution of bioluminescence in the Lampyridae, and subsequently became a part of the courtship behavior in adults [18, 21].

All known phengodid beetles are also luminous in at least the larval stages and as adult females [8]. Grimaldi and Engel [22] suggested that their bioluminescence functions as an aposematic signal in most species, but as a courtship signal in only some species. A brownish substance discharged from *Phrixothrix* larva is inflammatory to human skin upon contact [23], and *Rhagophthalmus* secretes a caustic odor by stimulation [7, 24]. Toxicity and distastefulness have not been reported in click beetles, including luminous species. Therefore, luminescence in these species is not likely to be aposematic in function.

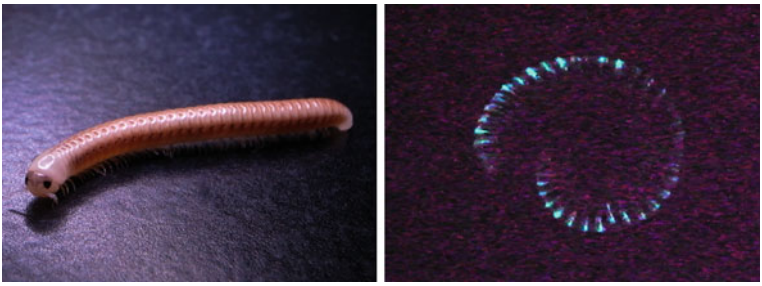

Fig. 5 Luminous millipede *Paraspirobolus lucifugus* collected in Okinawa, Japan. *Blue-green* luminescence was elicited by stimulating with chloroform vapor

The function of the luminescence in millipedes and centipedes has been interpreted as aposematism [25, 26]. The luminous millipedes *Motyxia* spp. gradually intensify the glow of their entire bodies and discharge noxious cyanide-containing secretions when stimulated [26, 27], and a species of *Salpidobolus* similarly sprays caustic substances [28]. When the author stimulated the luminous millipede *Paraspirobolus lucifugus* with forceps, the millipede emitted luminescence from gaps between the body segments along with an unpleasant smell (Fig. 5). Luminous secretions of the centipede *Otostigmus aculeatus* induced erythema and blisters on human skin [29].

Aposematic coloration, as in the cases of poisonous and colorful butterflies of the genus *Heliconius*, usually allows the evolution of palatable mimics (Batesian mimicry) and/or unpalatable mimics (Müllerian mimicry) [30]. It has been known that some cantharid and lycid beetles as well as other insects (at least 20 species belonging to 11 families and four orders of insects) share color patterns with Papua New Guinea lampyrids, *Pteroptyx effulgens* [31]. The mimicry involved in these cases has been interpreted as a combination between Mertensian and Müllerian mimicry; fireflies may usually be distasteful, but not lethal, whereas numerous species especially those belonging to the family Lycidae are considerably more toxic [18, 32]. However, none of firefly-mimics have yet evolved luminescence properties, and there is the possibility that fireflies mimicked some lycids [31] (VB Meyer-Rochow, personal communication).

Brightly colored mushrooms are sometimes poisonous: an aposematic display [33]. Similarly, the persistent glow of bioluminescent mushrooms may be an aposematic signal of unpalatability toward nocturnal fungivores. However, this hypothesis has not been proven [34]. The Japanese luminous mushroom *Omphalotus japonicus* is toxic to humans, but the author (YO) has observed staphylinid beetles frequently consuming this mushroom. On the Japanese island of Hachijo, the luminous mushroom *Mycena chlorophos* is an economically important tourist attraction, but the damage to fruiting bodies by land snails and ants is a problem (Fig. 6).

Although aposematic luminescence occurs in many terrestrial species, this strategy seems to be rare in the ocean. One probable example is the luminous

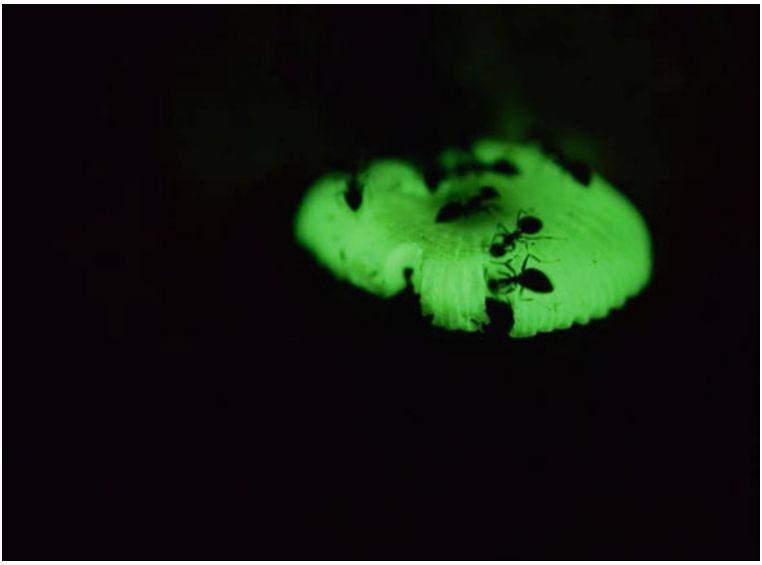

Fig. 6 Luminous fungus *Mycena chlorophos* fruiting body damaged by ants at nighttime in situ on Hachijo Island, Japan. Photo courtesy of Masashi Naito

brittle star *Ophiopsila* (Ophiuroidea, Echinodermata) [35]. Found in shallow reefs, the brittle star *O. riisei* is unpalatable for some potential predacious crabs, and when disturbed by predators it flashes rapidly from its arm-tips. In repeated laboratory trials, the crabs showed increases in avoidance behavior in response to brittle star luminescence [36]. Wilson and Hastings mentioned in their book [37] that ostracods are distasteful, thus the luminescence might also function as an aposematic display. On the other hand, one study showed that ostracods comprised 3–6 % of the gut contents of gobiid fish collected at Odawa Bay of Japan [38], which suggests that ostracods are palatable for some predators. Haddock et al. [2] hypothesized that luminescence in cnidarians also plays a role as an aposematic display, but it has not yet been demonstrated.

In our observations, the Japanese fireworm *Odontosyllis* released luminous mucus when attacked by gobiid fish in the aquarium. Lastly, some specimens were observed breaking off brightly luminescent posterior body segments. A similar behavior was observed during rough handling (Fig. 7). We also observed that some gobiid fishes regurgitated the fireworms, whereupon they began to luminesce brightly. These observations suggest that *Odontosyllis* employs several of these luminescent self-defense tactics: startling, decoy, and aposematism.

Fig. 7 Luminous fireworm *Odontosyllis* sp. after autotomy by stimulation. Detached tail tip glows continuously. Specimens were collected in Toyama Bay, Japan. Photo courtesy of Masashi Naito

2.2 Light Organ Lure

Deep-sea anglerfish, such as *Himantolophus,* are known to attract prey with a light organ created by cultivating symbiotic luminous bacteria in the tips of their escas, that is, the lure-like structure created from the modified first spine of the dorsal fin. However, anglerfish have not been observed in situ luring prey using luminescence. Using bioluminescence to attract prey has also been suggested for other marine animals, such as stomiid dragonfish, *Chiroteuthis* squid, *Stauroteuthis* octopus, and Siphonophores [2].

There are some hypotheses as to why prey are attracted to luminescence in the ocean. One plausible explanation is that luminescent particles in the sea visually indicate food. For example, deep-sea marine snow contains organic detritus and fecal pellets that host glowing bacteria. Small zooplanktons and fry detect the luminescence and consume the luminous material [39], and consequently, zooplankton are attracted to the luminescence. Zarubin et al. [39] suggests that the luminescence of nonsymbiotic bacteria enables them to find a host and to propagate in the nutrient-rich intestines of zooplankton and fish. Previous studies corroborate the high level of nonsymbiotic luminous bacteria in fecal pellets [40, 41].

The caves and riverbanks of Australia and New Zealand are home to larvae of fungus gnats, *Arachnocampa* spp., that attract small phototactic insects with luminescent posterior light organs into nonluminescent snares of vertical threads (termed “fishing-lines”) coated with mucous [42–44] (Fig. 8). A similar behavior

Fig. 8 Luminescence of the carnivorous fungus gnat *Arachnocampa luminosa* on a riverbank near Auckland, New Zealand. Photo courtesy of So Yamashita

Fig. 9 Luminescence of spore-feeding fungus gnat *Keroplatus nipponicus* on Hachijo Island

was also reported from the North American fungus gnat *Orfelia fultoni* [45, 46]. Interestingly the larvae of fungus gnats of the genus *Keroplatus* (Fig. 9), are also luminescent, despite that these species are likely to be spore-feeders [47]. The luminescence function of *Keroplatus* is unclear [9].

Most fireflies do not feed in adult stages. By contrast, it is very unique and exceptional that female adults of the North American fireflies *Photuris* and *Bicellonycha* mimic flash patterns of other fireflies, for example, *Photinus* and *Pyractomena* females, thereby attracting the males of the latter as prey [48]. *Photuris* cannot produce toxins by themselves, so they obtain the toxins, rather than nutrition, from prey fireflies and use them for aposematic display [49–51]. Larvae of the luminous click beetle *Pyrearinus termitilluminans* reside in termite mounds in Central America, and emit light from their prothorax to attract alate ants and termites as prey [52].

One of the roles of luminescence in mushrooms may be the attraction of spore-dispersing organisms. This hypothesis has been widely accepted for many years, but has never clearly been demonstrated [34].

Luminescence intended for prey sometimes attracts predators instead. The cave harvestmen *Megalopsalis* and *Hendea* possess prominent eyes to detect the luminescence of larval *Arachnocampa luminosa,* which are their major prey [53]. It is hypothesized that some large-sized marine predators such as sperm whales and leatherback turtles may use bioluminescent cues in their search for their food ([2], and references therein).

2.3 Intraspecific Communication

On land, it is well known that some adult fireflies use luminescence signals for sexual communication between males and females [51, 54, 55]. Larviform females of *R. ohbai* display their dorsal photophore toward males with continuous luminescence (Fig. 3), suggesting the function of luminescence is sexual communication [55]. The luminescence of the females of other phengodid beetles, *Dioptoma* and *Diplocladon*, also functions to attract their respective males [54, 56]. The function of luminescence in luminous click beetles has also been suggested as a means of sexual communication between males and females [4, 57]. Indeed, the male adults are sometimes attracted to artificial lights, including cigarettes [58]. The adults of the New Zealand fungus gnat *Arachnocampa luminosa* may use luminescence for sexual communication [42, 59, 60]; this has been challenged by Broadley [61], who provides evidence in support of pheromonal attraction.

In the ocean, bioluminescence in some ostracods, including the genus *Vargula* and the polychaete genus *Odontosyllis* has been suspected to possess a role in sexual communication based on observations of their behavior in the wild [4, 10, 38]. Luminescence of certain shallow water fish, such as leiognathid ponyfish and the flashlight fish *Photoblepharon palpebratus*, may function as a means of intraspecific communication (for mating, dominance display, and/or schooling) [62–64]. Based on some sexual dimorphism in photophores (light organs) it has been suggested that various midwater organisms use luminescence for sexual communication [65, 66].

2.4 Camouflage

Many organisms use bioluminescence to camouflage themselves in the open from potential predators in a strategy called “counter-illumination.” This strategy is most prevalent in the marine midwater, a depth down to which dim blue light still penetrates.

In the open ocean it is rare to find objects to hide in or behind, so mesopelagic animals become silhouetted against the seawater-penetrating sun and moonlight to observers below. This silhouette is less advantageous for large animals, such as

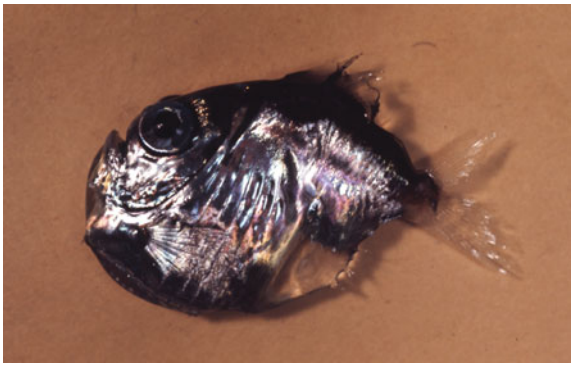

Fig. 10 Midwater hatchetfish *Sternoptyx pseudobscura*, with ventral photophores for counter-illumination and large eyes for finding the silhouettes of prey by looking up. Photo courtesy of Laboratory of Marine Biology, Kochi University

turtles, whales, and sharks. On the other hand, smaller animals are at risk of attack for many predators look up to find prey (Fig. 10).

Dahlgren [67] first suggested that ventral light organs in luminous squid are used to negate their silhouette by shining at ambient brightness levels. This counter-illumination hypothesis has also been used to explain luminescence in various luminous fish and shrimp; some of their downward-pointing light organs were shown to dynamically match background light intensity in laboratory studies [68, 69].

Counter-illumination is common in marine mesopelagic dwellers [70] but not supported in terrestrial and freshwater species. The myriad shelters and hiding spots on land as well as in the shallow or cloudy waters of rivers, ponds, and lakes may in the course of evolution have led to alternatives to bioluminescence as a survival strategy.

2.5 Searchlight

Species in three genera of deep-sea dragonfish, *Malacosteus, Aristostomias*, and *Pachystomias,* emit red light from a pair of photophores under the eyes. This unusual red, postorbital luminescence is considered to be akin to "night-vision" illumination. Because most deep-sea organisms are adapted to blue-light sensitivity for dim, blue downwelling light and bioluminescence detection [71], they are essentially blind to the red light projected by dragon fish. Indeed the vision of *Malacosteus niger* is red light sensitive, so it can seek and find unsuspecting prey [72, 73]. The anomalopid flashlight fish possess a pair of large suborbital light organs under their eyes, for which Morin et al. [62] have suggested a function to find and/or attract prey and Meyer-Rochow et al. [74] have reported an increased light emission activity in *Anomalops katoptron* during feeding. However, it is difficult to distinguish whether the photophores located near the eyes and the mouth function biologically as decoys or searchlights.

2.6 Functionless Bioluminescence

Visible light from some organisms may not have any significance in itself. Bioluminescence is considered to be an energetically low-cost mechanism [75, 76], and thus can potentially evolve as a metabolic byproduct unless the light emission is disadvantageous. For example, it has been proposed that fungal luminescence is a byproduct of some unknown metabolic process [34, 77]. Luminescence of organisms emitting very weak light, such as the Japanese fungus gnat *Keroplatus nipponicus*, or glowing underground, such as the annelid *Microscolex phosphoreus*, may also be functionless.

3 Terrestrial Taxa

Because of its accessibility to observers, bioluminescence in terrestrial habitats has received a great deal more attention ecologically and taxonomically than that of aquatic habitats. Terrestrial environments are varied, and in the following we discuss various luminous organisms' life histories and physiologies related to their habitats: land, air, underground, and freshwater.

3.1 On Land

Terrestrial luminous organisms comprise arthropods and fungi. One exception is the world's only known luminous terrestrial mollusk *Quantula striata* (syn. *Dyakia striata*) of Southeast Asia [78]. These land snails, especially the young snails, produce intracellular light on or near the mouthparts, but do not respond to disturbance. The biological and ecological significance of the luminescence in these land snails is uncertain, but it has been proposed to facilitate aggregation behavior [79]. In the Plantae, no luminous species have been discovered. *Schistostega pennata* (syn. *Gymnostomum pennatum*), generally called "luminous moss," is not autoluminescent: it appears to glow emerald green or gold on cave floors, but the glow is actually a directional reflection of dim light by a particular cell structure of the protonema [80]. No luminous species are known from tetrapods (amphibians, reptiles, birds, and mammals), instead they can use many other remote sensory and communication systems; sound, odor, vibration, color vision, UV, thermal radiation, ultrasonic, and even electricity.

Among the arthropods, the Myriapoda and Hexapoda contain luminous species, but no luminous species are found in another large arthropod subgroup that includes spiders and scorpions, the Chelicerata. Given that the larvae of the fungus gnat, *Arachnocampa*, lure positively phototactic prey into their curtains of sticky

vertical threads using luminescence, it seems strange that no luminous spider has been reported to date.

In the subphylum Myriapoda, some millipedes (Diplopoda) and centipedes (Chilopoda) emit light, with 24 known species altogether [25]. In the subphylum Hexapoda, luminous species are only found in elateroid beetles (Coleoptera), fungus gnats (Diptera), and springtails (Collembola) [9, 81].

Coleoptera are the largest order in the class Insecta, containing about 350,000 species in over 160 families worldwide [22]. Luminescent species of beetles are found in three elateroid families: Lampyridae, Phengodidae, and Elateridae [81, 82]. All species of the Lampyridae and Phengodidae (roughly 2,000 and 200 species worldwide, respectively) are luminous, and of the approximately 10,000 elaterid species worldwide, approximately 200 are luminous [83].

The Diptera (true flies) are the fourth largest order in the Insecta, containing 150 families and 150,000 species [84]. Despite their huge diversity, only a small number of luminous species ($\sim$15 species) are known from a single family, the Keroplatidae [9]. The bioluminescence mechanism of *Arachnocampa* fungus gnats is considered to be different from that of *Orfelia* [85], but the details are still unknown.

In Collembola, luminescent species have been recognized in the families Neanuridae and Onychiuridae [4, 56], but the observation records are limited. The author (YO) observed the luminescence of *Lobella* sp. (Neanuridae), in which the specimens emitted a continuous weak light from the body after stimulation with forceps. The function of luminescence in *Lobella* sp. is uncertain but it seems too faint to deter predators or to use for intraspecific communication [9].

Recently luminescence was claimed to occur in some South American cockroaches (Blattodea) [86, 87], but the veracity of these reports is highly dubious [88].

It is interesting that Lepidoptera, the second largest order in Insecta [22] apparently possess no luminous species. Most adult moths are nocturnal and some are poisonous; thus bioluminescence would seem a suitable tool for communication by moths. However, lepidopteran insects do not seem to have evolved any bioluminescence and instead widely use pheromones for their nocturnal communications. It seems worth noting that some nonluminous fireflies also use pheromones for intraspecific communication, but in contrast to the moths, the beetles are diurnal. In Hemiptera, the fifth largest insect order [22], the elongated head of the lantern fly *Fulgora laternaria* in South America had long been believed to be luminescent, but this has now become very doubtful [89].

Luminous species of the three elateroid beetle families use the same luciferin molecule in their luminescence mechanism, (4*S*)-4,5-dihydro-2-(6-hydroxy-2-benzothiazolyl)-4-thiazolecarboxylic acid, and a homologous luciferase sharing over 48 % amino acid identity [90]. Phylogenetic relationships among these families have been studied in the context of the evolution of bioluminescence [18, 91], but are still not fully resolved. Recent molecular analysis based on the mitochondrial genome revealed that Lampyridae and Phengodidae are sister groups in the cantharoid beetles [92], suggesting a single origin of their luminescence. Although Elateridae are also closely related to the Lampyridae–Phengodidae clade [92],

phylogenetic analyses of Elateridae showed that luminous click beetles are deeply nested within the nonluminous species, thus bioluminescence may have arisen independently in Elateridae [93, 94]. These results indicate that bioluminescence in beetles may have evolved once or twice [81].

Bioluminescence mechanisms of the land snail *Quantula*, millipedes, centipedes, fungus gnats, and springtails are still unknown in detail ([9], and references therein), but probably are independent from each other. Therefore, this author (YO) suspects that bioluminescence has evolved at least seven times among terrestrial organisms, including the case of luminous fungi described hereafter.

Luminous fungi are found only in the phylum Basidiomycota (Division Eumycota, sensu Parker [95]), that is, the taxon of fungi that produces large, apparent fruiting bodies referred to as "mushrooms" (approximately 32,000 species [96]). About 70 species of luminescent fungi have been recognized worldwide, and they belong to three different subclades: *Omphalotus*, *Armillaria*, and the mycenoid fungi [97]. Although all fungal luminescence is intracellular, some species glow only in the mycelia (e.g., *Armillaria* species), whereas others luminesce in both mycelia and fruiting bodies (e.g., *O. japonicus* and *M. chlorophos*). Even though the bioluminescence mechanism of the luminous fungi is not fully understood [98], the reaction mechanism is known to be identical in all species [99]. The function of bioluminescence in fungi has long been questioned, and remains unconfirmed experimentally.

Terrestrial luminescent bacteria of the genus *Photorhabdus* adhere to the intestine of a *Heterorhabditis* nematode worm: the nematode burrows into its insect host and regurgitates *Photorhabdus* into the hemocoel; the bacteria grow in the insect body and finally kill the insect. The Nematode feeds exhaustively on the bacteria or products of bacterial degradation of the hemolymph then leaves the cadaver in search of a new host insect. The luminescence of *Photorhabdus* is observed only when it grows in the insect cadaver. The ecological functions of the cadaver luminescence has been uncertain, but one suggestion was that it may represent an aposematic warning to nocturnal scavenging animals or act as a lure to attract further insect prey [100].

3.2 In the Air

Some lampyrid beetles are well known for luminescing during flight, and are rightly commonly called fireflies. However, not all luminous beetles are capable of flight. Some phengodid (e.g., *Rhagophthalmus*) and lampyrid beetles (e.g., *Lampyris*) have luminous but flightless wingless females (Fig. 3) and are commonly called glow-worms, whereas the males are capable of flight (winged) but are nonluminous or only very dimly luminescent [20, 55]. Male and female adults of some lampyrid genera are able to fly but are nonluminous, such as *Lucidota*, *Pyropyga*, and *Pristolycus* [101]. The manipulation of luminescence in some winged fireflies, such as in *Luciola* and *Photinus*, is very sophisticated: they use

species-specific flash signals to recognize conspecific males and females [51, 82, 101]. All luminous click beetles are likely capable of flight as adults, and it has been suggested that these males and females use the light for sexual communication while flying [57, 101].

3.3 Underground: Why in Soil?

In the Oligochaeta (earthworms and potworms), luminous species have been reported from 16 genera worldwide [9, 102]. Why do these underground dwellers produce light? The answer remains unclear, but it is considered to play a defensive role against predators [102]. Luminous earthworms discharge luminescent mucus from the mouth, the anus, and/or the body wall upon mechanical stimulation [102]. These earthworms are potentially palatable: *M. phosphoreus* was consumed by various potential predators, such as an earwig, a spider, a mole cricket [103], a topminnow, a newt, and a lizard (Oba, unpublished). The New Zealand giant luminous earthworm *Octochaetus multiporus* was eaten by a kiwi bird without ill effect (VB Meyer-Rochow cited in [102], and personal communication); *M. phosphoreus* captured by a centipede (Lithobiidae gen. sp.) was observed at nighttime in nature (Fig. 11; H Yoshida, personal communication).

These observations indicate that the light of luminous earthworms may be to startle, but not to aposematically warn predators in the darkness underground. Sivinski and Forrest [103] fed *M. phosphoreus* to mole crickets, an underground-dweller that feeds on earthworms. A mole cricket immediately captured the worm, but dropped the worm from its grasp and drew away when the worm discharged luminous mucus. Finally, this mole cricket attacked the worm again and consumed it, but this observation suggests that the luminescence of earthworms may provide the prey with some opportunity to escape from the predator.

Pupae of some lampyrid species, such as *Luciola*, produce underground mud cocoons and emit a dim green light from their entire body. When disturbed, they also emit an intense yellow light from their ventral photophore (Fig. 12). The biochemical mechanism of the dim glow in lampyrid pupae is understood [104], but the biological advantage of the dual colored luminescence remains unknown.

3.4 Fresh Water: Why so Rare?

Compared with the rich diversity of luminous organisms in the sea, luminous freshwater dwellers are quite rare. Fish and crustaceans make up a large percentage of the list of luminous organisms [1, 105], but there are apparently no luminescent freshwater fish and crustacean species.

The limpet *Latia neritoides* (Latiidae, Mollusk) found in streams of New Zealand's North Island is the world's only luminous freshwater gastropod species.

Fig. 11 Luminous earthworm *Microscolex phosphoreus*, attacked by the lithobiid centipede at night. Photo courtesy of Hiroshi Yoshida

Fig. 12 Luminescence of the Japanese firefly *Luciola lateralis* male pupa. The light organ on the abdominal segments VI and VII emits *yellow light* upon stimulation. The rest of the body continuously emits *green light*. Two independent luciferases are involved in this phenomenon

This small basommatophoran snail clings to the surface of submerged stones (Fig. 13) and discharges green-yellow, brightly luminescent mucus when disturbed. Meyer-Rochow and Moore [106] reported that the luminescent mucus was released into the stream when the limpet was attacked by predators, such as fish,

Fig. 13 Luminous freshwater snail *Latia neritoides* discharging luminescent mucus by stimulation at the river near Auckland, New Zealand (same as the place for Fig. 8). Photo courtesy of So Yamashita

crayfish, or dragonfly larvae, and suggested "the predators may chase after luminescent droplets washed away from *Latia* instead of attacking *Latia* itself".

Most of the lampyrid species are terrestrial for all phases of their lifecycle, but only a few *Luciola* species (~10 species) are known to be aquatic during the larval stage [107]. They adapt well to the aquatic environment where they locate and overpower freshwater snails in order to feed on them. Most, but not all, of the aquatic species' larvae respire in water using tracheal gills [16, 107]. These aquatic larvae project white glands from abdominal segments that emit a fetid smell, suggesting that the luminescence of some aquatic larvae is also an aposematic display to predators, such as freshwater goby and dragonfly larvae [14].

4 Marine Taxa

Although there are various terrestrial luminous organisms, they nevertheless belong to only a few taxonomic groups. This contrasts with marine taxa, in which luminous species are distributed across most of the large taxonomic groups, except for diatoms, marine macro-algae, and sponges (see [2]). In total, about 80 % of the genera containing luminous species are marine dwellers [1, 105].

4.1 Intertidal Zone

The intertidal area between the sea and land, called the littoral zone, is regularly exposed to variable conditions: rain causes low salinity, and sunlight causes heat, desiccation, strong UV/visible light, and high salinity. Only a few shellfish and an earthworm are reported as luminous in this environmentally challenging zone.

Some tiny luminous gastropod snails, *Angiola* and *Hinea* (Planaxidae), can be found under rocks in tide pools at low tide and on stony beaches [108–111]. The luminous bivalve *Pholas dactylus* inhabits the shallow sublittoral zone of soft-rock coasts, typically gneiss [4]. It is of interest that the luminous bivalves and

Fig. 14 Luminous marine snail *Angiola zonata* at stony beach of Hachijo Island, Japan. These specimens were found aggregated after upturning the pictured stone

gastropod snails are found only in the harsh intertidal zone, given that there are many thousands of related species that inhabit almost every depth of the ocean. One possible exception is the eulimid gastropod snails *Melanella luminosa,* which was found as a parasite on the scarlet sea cucumber at a depth of 10–238 m; Marshall [112] has described its yellow glow.

In the snail *Angiola zonata* (syn. *Angiola longispira*) (Fig. 14), a patch on the mantle (or hypobranchial gland, [109]) emits a weak blue-green light when the animal is stimulated mechanically or exposed to high salinity ([108], S Yamashita, personal communication). Houbrick [109] reported that all species in *Angiola* appear to be nocturnal and suggested that the light in "*Angiola* species may have a startling effect on predators". Deheyn and Wilson [111] suggested that an aposematic function "is less probable considering the gregarious and cryptic behaviour" of planaxid snails. The author (YO) observed in aquaria that fry of the intertidal teleost *Kuhlia mugil* consumed the soft bodies of *A. zonata* with no apparent ill effect, suggesting the snail's luminescence is not for aposematic display. In *Pholas*, luminescent mucus is discharged from the siphon when disturbed, and as Harvey suggested, "the best guess is that the light masses scare away predacious animals" [4], but the actual function remains uncertain [37].

The luminous earthworm *Pontodrilus litoralis* (syn. *P. matsushimensis*, *P. bermudensis*) inhabits the littoral zone of sandy beaches. The function of bioluminescence in *P. litoralis* remains unclear, likewise in other luminous earthworms. In Japan, this species is sometimes used as bait for fishing [113]. Furthermore, a crab and goby immediately fed on living *P. litoralis* when introduced into aquaria, and no apparent ill effects in the predators were observed after consuming the luminescent earthworm, suggesting it is neither distasteful nor toxic for potential predators. The author (YO) has observed carnivorous insects such as earwigs (Dermaptera) and staphylinid beetles (Staphylinidae) occurring sympatrically with *P. litoralis*. These observations suggest that the function of *P. litoralis* luminescence might be to startle, but not as an aposematic display. On the other hand, as luminous fluid is discharged only when *P. litoralis* specimens are severely stimulated, such as being cut, squeezed, and/or beaten [9, 114], the startling hypothesis will need to be verified.

4.2 Coastal Water

In the neritic zone, the number of luminescent species is relatively low, a reported 1–2 % of all coastal species [115]. However, each luminous species often occurs in high density in its environment. This situation is in contrast to those in oceanic waters where species diversity is very high, but population density of individual species is usually low (see Sect. 4.3). Luminous species usually make up only a small proportion of a phylum's total number of species, but there are two exceptions: the Cnidaria (jellyfish) and the Ctenophora (comb jelly). A large proportion of the former phylum and nearly all of the latter are luminous [4], and these two groups are common members of the coastal planktonic dwellers. As for the biological function of luminescence in coastal dwellers, Morin [115] suggested that these species primarily use fast flashes of luminescence to deter prey or continuously glowing decoys to distract predators, giving the prey an opportunity to escape.

Dinoflagellates (Division Chromophycota, sensu Parker [95]) are important primary producers in coastal waters. Some of the free-living species are luminous, and most of these are autotrophic and therefore live in shallow waters where they can photosynthesize. The luminous dinoflagellate *Noctiluca scintillans* is an obligate heterotroph, but it also lives in shallow water to feed on autotrophic diatoms, other dinoflagellates, and even small zooplankton [37]. For the enzymatic bioluminescence reaction, luminous dinoflagellates use open-chain tetrapyrrole luciferin [116], which is structurally related to chlorophyll. Interestingly, luminous krill (Euphausiidae) also use the tetrapyrrole luciferin, which is structurally very similar to the luciferin of dinoflagellates [117, 118]. Accordingly, it is expected that krill consume luminous dinoflagellates and chemically modify the dinoflagellate luciferin as a precursor to their own luciferin [119]. To date, other luminous taxa that use dinoflagellate luciferin or its derivatives as a luminous substrate have not been reported.

4.2.1 Cypridinid Luciferin

In ostracods, luminous species in the genera *Vargula* and *Cypridina* are coastal, whereas species in the genus *Conchoecia* are midwater dwellers [120]. The two former genera use cypridinid luciferin (also called Cypridina luciferin) as a bioluminescent substrate [98, 121], whereas *Conchoecia* use coelenterazine [98, 122]. These findings are consistent with the fact that no midwater fish are known that use cypridinid luciferin as a bioluminescent substrate (see below).

Coastal fish with nonbacterial luminescence rely on cypridinid luciferin in bioluminescence reactions [123, 124]. These types of luminous fish are found in three distantly related families of the orders Perciformes and Batrachoidiformes [123–128]: *Parapriacanthus ransonneti* (syn. *P. beryciformes* [129]) and *Parapriacanthus dispar* (Pempheridae); *Pempheris ypsilychnus* (Pempheridae [130]);

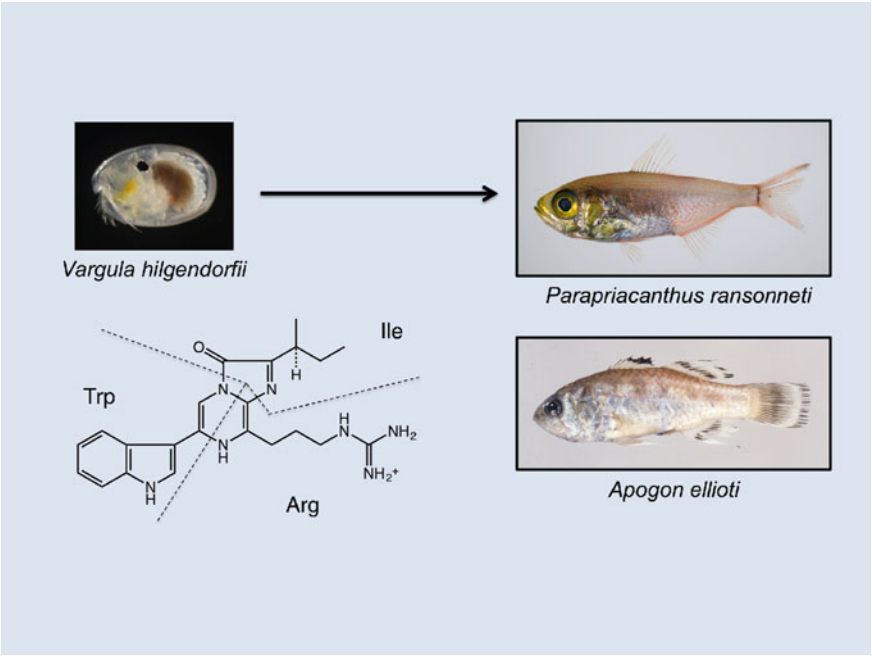

Fig. 15 In the marine coastal zone, cypridinid luciferin is biosynthesized by ostracods. It is considered that some coastal fish consume the ostracods and obtain the cypridinid luciferin for their own bioluminescence reactions. Photos courtesy of Ken-ichi Onodera (*Vargula*), and the Laboratory of Marine Biology of Kochi University (*Parapriacanthus* and *Apogon*)

Apogon ellioti (syn. *Jaydia ellioti*) and *Apogon poecilopterus* (syn. *Jaydia poecilopterus*) (Apogonidae); midshipman fish *Porichthys* spp. (*P. notatus*, *myriaster*, and *porosissimus;* Batrachoididae); and presumably some *Archamia* and *Rhabdamia* species (Apogonidae).

It has been suggested that these coastal fish obtain cypridinid luciferin by consuming *Cypridina* and *Vargula* ostracods [37]. In fact, ostracod specimens have been discovered from the stomach of *P. ransonneti* ([131], Oba and Hiruta, unpublished), and a nonluminous form of *P. notatus* recovered its luminescent ability following injection of cypridinid luciferin [132]. Recently, the author (YO) and colleagues demonstrated that cypridinid luciferin is biosynthesized from three amino acids (Ile, Arg, Trp) in *Vargula hilgendorfii* (Fig. 4) and *Cypridina noctiluca* [133–136]. These findings indicate that cypridinid luciferin produced by coastal ostracods partly contributes to the species' richness of luminous fish in the coastal environment (Fig. 15). Indeed, cypridinid luciferin chemiluminesces strongly in certain solvents, such as diglyme, dimethyl sulfoxide, and detergent-water solution, without an enzymatic catalyst [137]. This high reactivity suggests that cypridinid luciferin is potentially a good bioluminescent substrate by nature. Therefore, it may not be difficult to evolve luciferase from an extant protein, if organisms are able to obtain cypridinid luciferin by diet.

4.3 Midwater: Why so Species-Rich?

Previous research suggests that nearly all of the luminescent species known to occur in the midwater of oceans. Beebe [138] estimated that based on a study in Bermuda that luminous mesopelagic fish collected below a depth of 600 m represent 81 % of the families, 66 % of the species, and 97 % of all the individuals. Calanoid copepods, krill, and *Cyclothone* fish represent a large part of total macro- and microzooplanktonic marine biomass, and these taxa contain particularly many luminous species [4].

Haddock et al. [2] listed hypotheses of why most luminescent taxa are ocean dwellers: they suggested that the sea is favorable for the evolution of bioluminescence because it is (1) a stable environment, (2) optically clear relative to other aqueous habitats, (3) continuously dark or very dim, and (4) highly diversified taxonomically with complex interspecific relationships. We suggest that there are additional factors that favor the evolution or acquisition of bioluminescent capabilities in marine organisms: namely "symbiotic luminescence" and "dietary supply of coelenterazine".

4.3.1 Symbiotic Luminescence

Luminous bacteria are common in seawater, especially in temperate and coastal oceans, but they are rarely found in freshwater or on land [139]. Accordingly, marine animals constantly contact, ingest unintentionally, or feed on luminous bacteria. Therefore, it is reasonable to assume that symbiotic luminescence could have evolved independently several times in various fish and squid.

There are at least seven orders of fish and two orders of squid (orders Sepiolida and Teuthida) that employ luminous bacteria in both coastal shallow water and midwater [139–141] (Fig. 16).

Species of luminous bacteria found in symbiotic hosts living in shallow water are different from those in midwater. Shallow-water fish, such as leiognathid ponyfish and pinecone fish, and bobtail squid *Euprymna* and *Sepiola* use *Photobacterium leiognathi*, *P. mandapamensis, Aliivibrio fischeri*, *A.* "*thorii*," or *A. wodanis* (formerly *Vibrio fischeri* and *V. logei* [139, 142]). In contrast, midwater species, such as chlorophthalmid and macrourid fish, predominantly use *Photobacterium kishitanii* (formerly included in nonsymbiotic *P. phosphoreum*) [139–141]. The symbiotic bacteria obtain essential nutrients from their hosts and begin to luminesce less and less, or even die, when the host is starved [143].

Considering the advantages of bioluminescence for marine life forms, it is surprising that only fish and squid evolved mutual symbioses with luminescent bacteria. It has been suggested that the bioluminescence of one species of the pelagic colonial tunicate *Pyrosoma* is due to bacterial symbiosis, but details are not available [98].

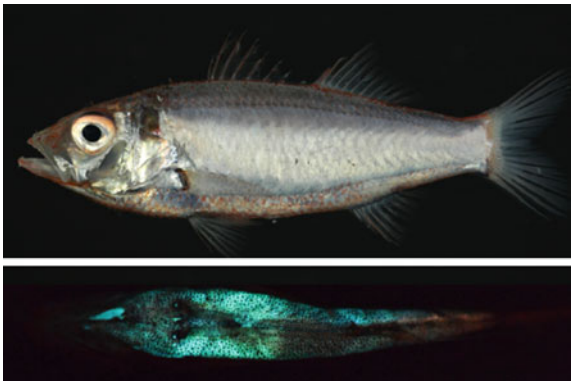

Fig. 16 Luminous coastal fish *Acropoma japonicum* (Acropomatidae) harboring the luminous bacteria *Photobacterium leiognathi* and *P. mandapamensis*, and its ventral bioluminescence. Photo courtesy of Laboratory of Marine Biology of Kochi University

4.3.2 Coelenterazine

Coelenterazine was originally named for the bioluminescent substrate found in coelenterates (Cnidaria and Ctenophore), but the term is still used despite the wide variety of marine taxa that use the same molecule for their bioluminescence reactions [98]. Organisms that use coelenterazine or its derivatives for their bioluminescence are scattered at least in five phyla: the Cnidaria, Ctenophora, Mollusca (e.g., the squid *W. scintillans* and *Symplectoteuthis luminosa*), Arthropoda (e.g., ostracod *Conchoecia*, copepods, and the decapod shrimps), Chordata (e.g., myctophid lanternfish [98]), and putatively in the Echinodermata (the benthic brittle star *Amphiura filiformis* [98]), Chaetognatha (the bathypelagic arrowworm *Caecosagitta macrocephala* [144]), and the Radiolaria (solitary spumellarian *Thalassicolla* sp. [145]; Phylum Sarcomastigophora, sensu Parker [95]). In midwater, fish of the family Myctophidae are very abundant, and Beebe [138] found in study of Bermuda that approximately one-quarter of the fish species caught by net below 600-m depth were in the Myctophidae. From the view of total specimen quantity, the gonostomatid *Cyclothone* is extremely abundant in midwater [138, 146], and the involvement of coelenterazine in their luminescence has been suggested [147]. On the other hand, there are no freshwater or terrestrial organisms that use coelenterazine or its analogues in bioluminescence. This unusually widespread and abundant recruitment of coelenterazine in marine bioluminescent systems may be a key to understanding the species richness of marine luminescent organisms, and pose questions as to its biosynthetic origin.

Some luminous animals that use coelenterazine in their luminescent systems are not capable of biosynthesizing it. For example, the mysid shrimp *Gnathophausia ingens* and the jellyfish *Aequorea victoria* lost their luminescence after a prolonged period of a coelenterazine-free diet, but recovered luminescence when fed food containing coelenterazine [148, 149]. These findings suggest that some luminous organisms need a supply of coelenterazine from their diet for their luminescence abilities. Thomson et al. [150] concluded that the luminous midwater shrimp *Systellaspis debilis* is capable of coelenterazine biosynthesis on the basis of their

observation that the content of coelenterazine increased during the time in development between newly laid eggs and just before hatching. As Shimomura [98] mentioned, however, their analysis cannot eliminate the possibility that coelenterazine is sequestered as an inactive form in the eggs and converted to active coelenterazine during development; thus coelenterazine may not be biosynthesized de novo in the egg.

Buskey and Stearns [151] showed that the bioluminescence potential of the marine calanoid *Metridia longa* was not reduced even after starvation for 3 weeks. Furthermore, they demonstrated that the bioluminescence potential in *M. longa* fully recovered within 10 h after luminescent substances were exhausted by mechanical stimulation. As luminous copepods use coelenterazine for their luminescence, these findings strongly suggested that *M. longa* can biosynthesize coelenterazine. Recently, we demonstrated for the first time that coelenterazine is biosynthesized in the midwater calanoid *Metridia pacifica* from three amino acids (Tyr, Tyr, Phe) by feeding specimens stable isotope-labeled compounds and analyzing the incorporation of the labeled compounds in coelenterazine by LC-ESI-TOF/MS analysis [152].

Calanoids are one of the most abundant biomass components in the sea and are important prey for marine carnivorous organisms [153], including luminous "coelenterazine-users," such as chaetognaths, myctophid, and gonostomatid fish [154]. Another luminous coelenterazine-user *Thalassicolla* is a unicellular radiolarian, which is known to capture and ingest living copepods [155]. Unknown copepods were found in the stomach of the myctophid lanternfish *Diaphus watasei* (Oba, unpublished). Species of the genus *Metridia* are widely distributed in the oceans and occur in Antarctic waters [156] as well as in the subarctic Pacific Ocean [154], where *Metridia pacifica* is known as a substantial member of the zooplankton biomass. In Toyama Bay in the southern Sea of Japan, *M. pacifica* contributed 37 % (annual mean) to the total copepod biomass [157], and is one of the major prey items for the luminous firefly squid *W. scintillans* (Fig. 2) [158]. Coelenterazine was also present in various nonluminous marine plankton-feeding fish and shrimps but was not detected in benthic scavengers, such as lobsters and crabs [98]. Taken together, it is conceivable that various marine luminous organisms obtain coelenterazine by consuming *M. pacifica* and other copepods, and for this reason, luminous organisms are abundant in the ocean, especially in midwater (Fig. 17).

It has been known that coelenterazine exhibits chemiluminescence in various substances, including egg yolk, BSA, and surfactants [98, 159], indicating that coelenterazine has innate beneficial properties as a bioluminescent substrate. Indeed, coelenterazine-type luciferases and photoproteins have been identified from deep-sea shrimp *Oplophorus*, copepods, the sea pansy *Renilla*, and jellyfish, but do not share significant amino acid sequence homologies [98]. This suggests that luciferases or photoproteins using coelenterazine as a substrate or chromophore have independently evolved from unrelated proteins several times in an example of convergent evolution.

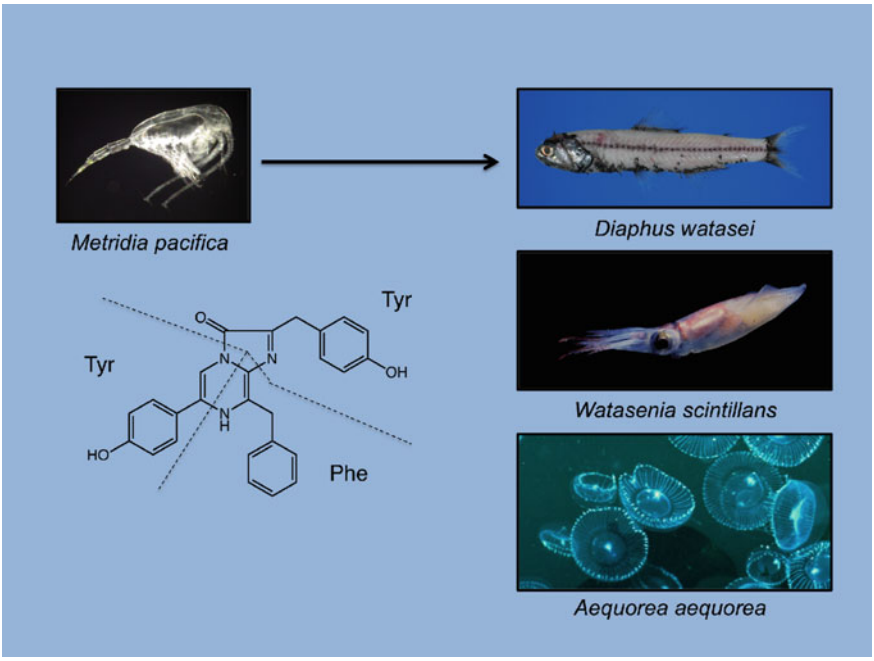

Fig. 17 In the marine midwater, coelenterazine is biosynthesized by copepods. It is considered that various midwater organisms consume the copepods and obtain the coelenterazine for their own bioluminescence reactions. Photos courtesy of Ken-ichi Onodera (*Metridia*), the Laboratory of Marine Biology of Kochi University (*Diaphus*), the Uozu Aquarium (*Watasenia*), and Osamu Shimomura (*Aequorea*)

4.4 Deep-Sea Benthos

Based on a recent study in the Bahamas, the benthic zone of the deep sea (500–1,000 m depth) is not as species-rich in luminous organisms as the midwater zone: less than 20 % of the collected species emitted light [160]. Johnsen et al. [160] explain that visibility in benthic water is obstructed by particulate matter stirred by a bottom current, which is in contrast to the optically clear midwater that facilitates the evolution of bioluminescence [2].

In the deep-sea benthos, luminous species are found mostly in bamboo corals, sea anemones, sea pens, sea cucumbers, and brittle stars [160]. Because it is extremely difficult to observe natural behavior of the organisms, the functions of their luminescence are still unclear. There are many bottom dwellers in crabs, hermit crabs, lobsters, and isopods, but no luminous species have been reported in these groups. An unidentified luminous sea anemone was found on the shell inhabited by a hermit crab [160]. It is known that some sea anemones and hermit crabs engage in a mutualistic symbiosis [161]. If the deep-sea hermit crab positively selects luminous sea anemones as a symbiont, the hermit crab should be

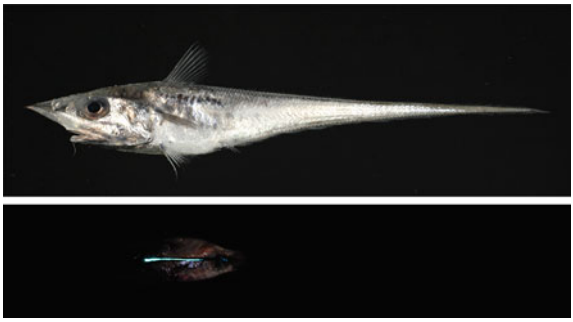

Fig. 18 The deep-sea benthic rattail fish, *Coelorhynchus kamoharai*. The ventral *midline* glows *blue-green* by harboring the luminous bacterium *Photobacterium kishitanii* inside photophores there. Photo courtesy of the Laboratory of Marine Biology of Kochi University

regarded as a luminous organism, as other taxa with luminous symbiotic bacteria are themselves considered luminous organisms.

The rattail fish (Macrouridae) are a large family of teleosts that generally inhabit deep-sea benthic habitats. Most of the species are luminous [162] and have saclike photophores containing luminous bacterial cultures around the anus and along the midline of the abdomen (Fig. 18).

The morphological features of the photophores are an important characteristic for identifying species in the Macrouridae, but whether they use the light of their ventral photophores for intraspecific recognition and communication in the dark is unknown.

As the deep-sea benthos remains a largely unexplored frontier, the story of bioluminescent life there is likely still hidden in the depths.

5 Conclusion

World-leading authorities of bioluminescence, including Newton Harvey (1887–1959), as well as the Japanese pioneers, Sakyo Kanda (1874–1939) and Yata Haneda (1907–1995), focused in their comprehensive works on species lists, habitat, morphology, histology, physiology, biochemistry, biophysics, and evolution of the world's luminous organisms, but scarcely worked on the biological significance of the light [4, 56, 163]. This may be simply due to the difficulty of assigning a definite biological function to the light [164]. However, in some cases the luminescent functions of some organisms are exceptionally well identified. For example, the flash signals of fireflies used for sexual communication [51, 54, 55], the continuous glow of the cave glowworm *Arachnocampa* for prey attraction [165], and the counter-illumination of various midwater dwellers [65] are all well understood. Even in the case of fireflies, however, the functions of synchronous flashing in South Asian species [166, 167], the weak luminescence in diurnal species [55], and the glowing of eggs and pupae [104] are still not resolved. The significance of bioluminescence has sometimes been presumed to be for self-defense, because light emission can be produced by prodding or other forms of

physical stimulation, or the light may be for sexual communication given that morphological variations of photophores between sexes are rather common. It is, however, best to be wary of cursory postulations: for example, stimulation-induced lights may be too weak to startle predators and photophore sexual dimorphism may be involved in behaviors other than mating. Meanwhile, some luminous organisms possess highly sophisticated light organs (equipped with lenses, color filters, reflectors, diffusers), and are neuronally controlled [168], suggesting that the light must have some biological significance, albeit poorly understood. Moreover, some unique hypotheses such as "predatory counter-illumination" for luminous sharks [169], and "luminescent burglar alarms" [115, 164] for luminous dinoflagellates and luminous fungi ([170] and [34], respectively) may illuminate wealthiness of bioluminescence when tested experimentally in future.

6 Perspectives

This chapter has presented an ecological and evolutionary overview of the many divergent bioluminescent taxa found in the world. One important observation has been the great diversity of bioluminescent substrates and enzymes that has arisen during the evolution of the varied taxa. Moreover, the paths of convergent evolution have yielded a wide variety of ecological behaviors that utilize bioluminescence.

Although the luciferin structures of many organisms were resolved between the 1960s and 1980s, many luciferase or photoprotein genes remain unknown, such as those of euphausiid krill *Euphausia pacifica*, the firefly squid *W. scintillans* (Fig. 2), the midwater lanternfish of the family Myctophidae, the shallow water fish *Parapriacanthus* and *Porichthys*, the earthworm *Diplocardia longa*, and the freshwater limpet *L. neritoides*. Several taxa still have eluded identification of both their luciferin and their luciferase, including the millipedes *Paraspirobolus* and *Motyxia*, the polychaete *Odontosyllis*, and the brittle star *Ophiopsila* (summarized in [98]). In the case of luminous fungi, enzymatic involvement in light production is still unresolved [98, 171].

To facilitate future research of bioluminescent organisms, my group is proceeding with a DNA barcoding initiative to create a genetic reference library for bioluminescent organisms, per Hebert et al. [172]. The database will provide a resource for other scientists in the identification of luminous organisms with unresolved bioluminescent systems. Given the many applications of bioluminescent systems using only a few well-characterized protein families, elucidating currently unknown proteins, genes, and substrates will expand the toolkit of molecular science and bioengineering. As there are likewise many species for which the biological and ecological function of bioluminescence is poorly understood or disputed in the literature, this same principle will apply to ecologists who seek to study bioluminescent organisms.

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