

## Acquisition of bioluminescent trait by non-luminous organisms from luminous organisms through various origins

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### Abstract

Bioluminescence is a natural light emitting phenomenon that occurs due to a chemical reaction between luciferin and luciferase. It is primarily an innate and inherited trait in most terrestrial luminous organisms. However, most luminous organisms produce light in the ocean by acquiring luminous symbionts, luciferin (substrate), and/or luciferase (enzyme) through various transmission pathways. For instance, coelenterazine, a well-known luciferin, is obtained by cnidarians, crustaceans, and deep-sea fish through multi-level dietary linkages from coelenterazine producers such as ctenophores, decapods, and copepods. In contrast, some non-luminous *Vibrio* bacteria became bioluminescent by obtaining *lux* genes from luminous *Vibrio* species by horizontal gene transfer. Various examples detailed in this review show how non-luminescent organisms became luminescent by acquiring symbionts, dietary luciferins and luciferases, and genes. This review highlights three modes (symbiosis, ingestion, and horizontal gene transfer) that allow organisms lacking genes for autonomous bioluminescent systems to obtain the ability to produce light. In addition to bioluminescence, this manuscript discusses the acquisition of other traits such as pigments, fluorescence, toxins, and others, to infer the potential processes of acquisition.

**Keywords:** Dietary luciferin, acquired luminescence, light organs, deep-sea organisms, coelenterazine.

## Introduction

Acquiring bioluminescent trait from other organisms is one of the fascinating topics in marine biology and ecology. Several prokaryotes and eukaryotes lacking innate bioluminescent traits are reported to obtain them from organisms bearing this trait through mechanisms such as prey ingestion or gene acquisition. The acquisition increases the ecological fitness of the organisms in many ways, such as for defense, predation, or communication <sup>1,2</sup>. These incidences are common in the ocean, although cases are not disseminated widely in the literature beyond the initial reports. We gathered literature describing various examples of organisms obtaining bioluminescent traits through three different modes to increase awareness of these natural events.

Bioluminescence is the natural phenomenon of light emission by living organisms. Individual luminous organisms primarily use an enzyme and a substrate (and co-factors in some cases) to generate light through an oxidation reaction. These organisms produce light upon stimulation or under certain conditions <sup>3</sup>. Various bioluminescent chemical reactions are known so far <sup>2,4,5</sup>. The mechanisms involved in obtaining the trait of bioluminescence are well studied <sup>6-8</sup>, especially in fireflies by focusing on the mutation on an ancestral gene toward a luciferase <sup>9,10</sup>. Here, we detailed three alternative mechanisms that are involved in the acquisition of bioluminescence or other traits from closely or distantly related organisms:

HGT: In the first mechanism, horizontal gene transfer (HGT), a process where non-luminous organisms obtain mobile genes to become bioluminescent <sup>11</sup>.

Ingestion: In the second case, several marine organisms in the ocean obtain either luciferin <sup>2,12</sup> or both luciferin and luciferase <sup>8</sup> from their diet to produce light.

Symbiosis: In the third case, ingestion of or colonization by luminous bacteria results in the host macro-organism acquiring bioluminescence <sup>13-19</sup>.

Bioluminescence is widespread in the ocean, present in about 76% of macroscopic organisms in water column <sup>20</sup> and 24-40% of benthic macrofaunal environments <sup>21</sup>. In many animals, bioluminescent courtship causes species diversification<sup>22</sup>. One mechanism of the acquisition of bioluminescent traits is accomplished by the dietary uptake of luciferins. However, the source organisms, biosynthesis, and dietary acquisition pathways of even the most common marine luciferin, coelenterazine, are not yet fully understood <sup>2</sup>. The transfer of dietary luciferins and genes within closely related or non-related organisms is rarely known in the ocean. Distribution patterns and acquisition pathways of intact forms of exogenous luciferins (e.g., euphausiids via dinoflagellate prey) in the food web are yet to be demonstrated <sup>2</sup>. The presence of vargulin, also known as

cypridinid luciferin, in luminous fishes like *Parapriacanthus* and *Apogon*; and coelenterazine in various cnidarians, shrimps, squids, and fishes indicate the importance of studying the origin, biosynthesis, and dietary pathways of these luciferins<sup>23</sup>. In the case of cnidarians such as the crystal jelly, *Aequorea* must continuously obtain coelenterazine from dietary sources for light emission<sup>12</sup>.

This review primarily deals with organisms emitting light upon acquiring luciferins, luciferases, and genes via dietary sources, horizontal gene transfer, and colonization by bacteria. This review aims to help researchers aware of gaps in our understanding of evolutionary processes, bioluminescence function, luciferin synthesis and transfer pathways, and the role of luciferins in food webs, even for non-luminous members.

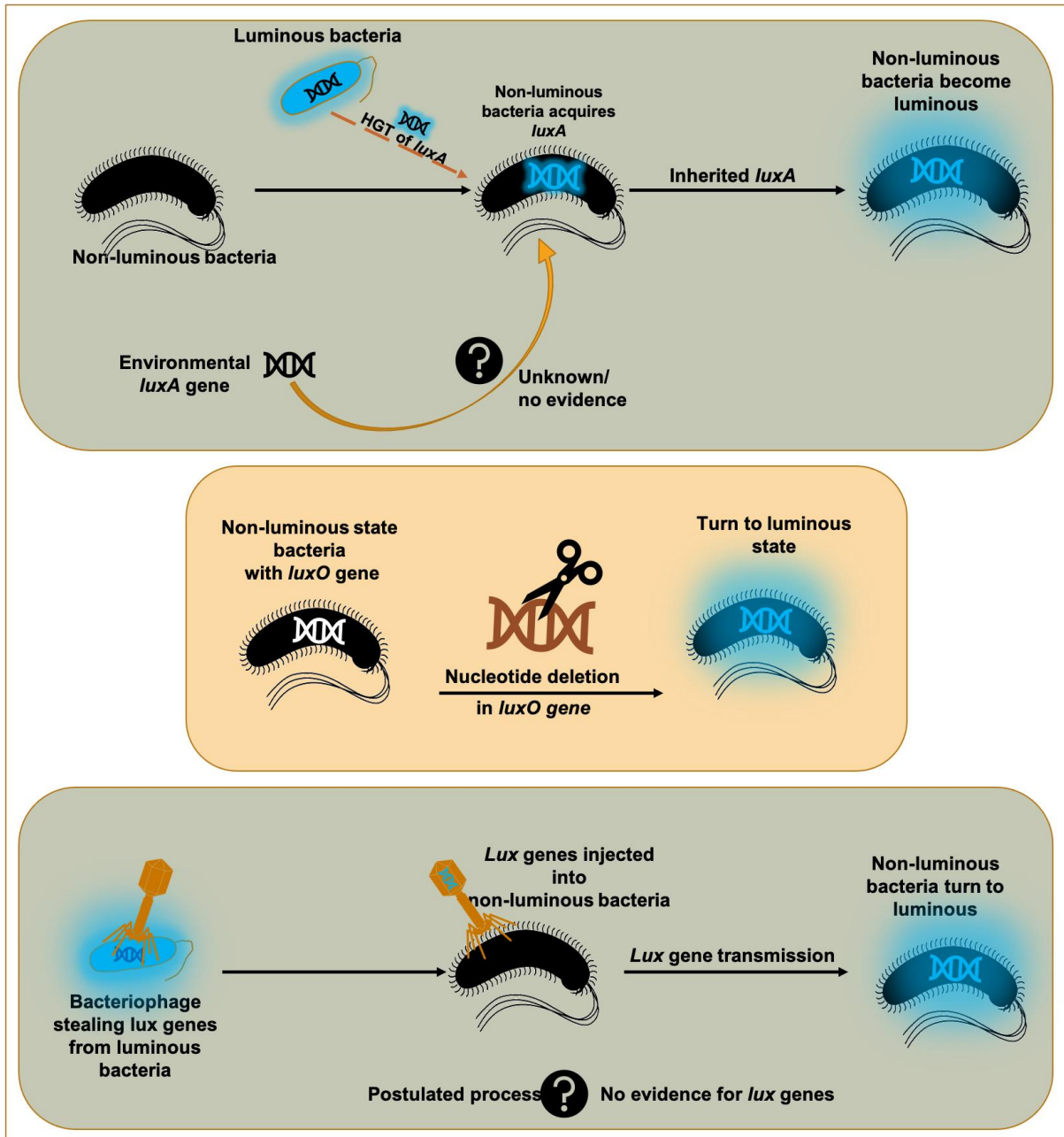
## 1. Horizontal gene transfer mediated luminescence

During the course of evolution, organisms rarely integrate exogenous DNA into their genome resulting in an acquisition of a trait, such as antibiotic resistance, virulence, pigments, and bioluminescence: this mechanism is known as horizontal gene transfer (HGT). In the last two decades, there have been reports of acquired traits through HGT in prokaryotes<sup>24</sup> and metazoans<sup>25</sup> (Table 1; Table S1). For example, many pathogenic bacteria share their antibiotic genes and virulence genes within closely related or distantly related bacteria<sup>26,27</sup>. *Collimonas*, a Gram-negative bacterium, produces blue pigments due to pigment gene acquisition via HGT, probably from *Janthinobacterium lividum* or *Duganella* sp.<sup>28</sup>. These acquired genes impart defensive function to these bacteria to fight against other microbes.

Likewise, luminescence trait acquisition via HGT has been reported in bacteria. The bacterial family Vibrionaceae comprises three major luminous bacterial genera such as *Aliivibrio*, *Vibrio*, and *Photobacterium*<sup>29,30</sup>; while the genus *Photorhabdus* belongs to the Enterobacteriaceae<sup>31</sup>, and *Shewanella* to Shewanellaceae family<sup>32</sup>. Luminescence in members of *Aliivibrio*, *Vibrio*, and *Photobacterium* is primarily due to vertical transmission (parent to progeny). In these bacteria, *lux* genes encode luciferases (*luxA* and *luxB*) and luciferin biosynthesis enzymes (*luxC*, *luxD*, and *luxE*), altogether composing a *lux* operon. Many non-luminous bacterial strains of *Vibrio* and *Photobacterium* are known to acquire a *lux* operon for bioluminescence through HGT<sup>11,30</sup> (Figure 1). This type of luminescence is reported in non-luminous members related to luminous bacteria. These bacteria are known to display bright, dim, undetectable, or no-luminescence (dark mutants)<sup>5,33</sup>. In the case of dark mutants carrying *lux* genes, which are often encountered on culture media, their failure to emit luminescence is due to insertion, deletion, and mutation in *lux* gene sequences<sup>34–36</sup>. HGT of *lux* genes from luminous members to non-luminous bacterial members of Vibrionaceae

remains an unanswered question <sup>11,30</sup>. Without a regular cell division process, the mobile genetic elements were reported to transfer as individual genes or entire operons into recipients (other bacteria) <sup>37-39</sup>. These mobile genetic elements facilitate evolution in these microbes (Frost et al., 2005). The *lux* gene cluster has been suggested to be transferred from *Vibrio cholerae* to other luminous bacterial species <sup>40</sup>. Natural vertical inheritance of *lux-rib* operon (*rib* genes are involved in regulating riboflavin synthesis and luminescence) and horizontally acquired *lux-rib* operon from *Photobacterium mandapamensis* was also observed in luminescent strains of *Photobacterium aquimaris* <sup>41</sup>. In contrast, for certain *Vibrio* and *Photobacterium* strains, the HGT process (recruitment time of *lux* genes) under certain unknown environmental factors is not understood <sup>11</sup>. In the natural merodiploid state, strains of *Photobacterium leiognathi* carry single or multiple *lux-rib* operons obtained via HGT <sup>42</sup>.

Non-luminous strains of *Vibrio alginolyticus*, *Vibrio anguillarum*, *Vibrio owensii*, and *Photobacterium damsela*, produce light upon acquiring *lux* genes <sup>11</sup>. The *Photobacterium toruni* also might obtain *lux* genes via HGT. Non-luminous bacterial strains of *Kosakonia* <sup>43</sup> and *Kurthia* sp. are thought to acquire *lux* genes through HGT to emit luminescence <sup>44</sup>. In all these cases, acquiring light-emitting genes resulted in non-luminous bacterial members producing luminescence in the natural environment. Acquisition of bioluminescent genes by non-luminous *Vibrio* species was postulated through bacteriophage infection, but no evidence has been found so far <sup>45</sup>. Leaky vertical transmission mode <sup>46</sup> has not been encountered so far in luminous bacteria (i.e., acquiring *lux* genes from both parent and environment). Members of Vibrionaceae are well known to display HGT of mobile genetic elements, which are involved in host range expansion, pathogenesis, and evolution <sup>47</sup>. Analyzing the flanking regions of the *lux* operon is a possible way to trace the origin of acquired genes in various bacterial phylogenies <sup>40</sup>. Once received, the trait of bioluminescence helps defend the bacteria from predators so that the luminous population may be favored and propagated.



**Figure 1.** Acquisition of bioluminescence trait through HGT, nucleotide deletion, and possibly through bacteriophage injection in non-luminous bacteria.

In contrast to luminous bacteria, metazoans are also presumed to acquired luciferase proteins or genes through HGT. For example, sea pansy *Renilla* luciferase (RLuc) shows an unexpected sequence similarity of 49-62% with haloalkane dehalogenases of bacteria and 40% similarity with a protein (possibly luciferase) from sea urchin *Strongylocentrotus purpuratus*<sup>48</sup>. The catalytic triad sequences of dehalogenases of bacteria and protein of *S. purpuratus* displayed a conserved homology with catalytic sites D120, E144, and H285 in RLuc sequence. For this reason, it is postulated that such incidents could occur via horizontal gene transfer<sup>48</sup>. However, no evidence has been reported

so far to confirm that this haloalkane dehalogenases-like protein has luciferase activity in *Renilla* and *S. purpuratus*. These conserved catalytic residues are required for the activity of dehalogenases in bacteria but not in luciferase activity in sea urchin and *Renilla* <sup>48</sup>. Similarly, another study has also found such homologous sequences of luciferase of the ophiuroid *Amphiura filiformis* with *Renilla* luciferase <sup>49</sup>. Thus, haloalkane-dehalogenase function was hypothesized to shift to luciferase activity in octocorals and brittle stars <sup>49</sup>. These studies suggest HGT as a possible process responsible for acquired traits in prokaryotes and metazoans.

## 2. Dietary source based luminescence

In this section, the various taxonomic groups of organisms showing dietary based luminescence are detailed. Some animals are also known to acquire poison characteristics by feeding on other animals and plants. For example, firefly *Photuris* females obtain lucibufagins from *Photinus* preys <sup>50</sup>; while firefly *Ellychnia corrusca* synthesizes or acquires lucibufagins <sup>51</sup>. Bright skin coloration and toxic lipophilic skin alkaloids in some poison dart frogs are probably obtained from the diet (e.g., various insects) <sup>52,53</sup>. Similarly, monarch butterflies also acquire cardenolid toxic molecules from their milkweed host plants, *Asclepias* spp., to defend themselves from predators <sup>54</sup>. Those small organic compounds are broadly known to be passed through predation. In fact, luciferin molecules are acquired through the dietary pathway to predators.

### 2.1. Dietary acquisition of organic molecules

Food sources are key factors that regulate the morphological appearance, biochemical and metabolic processes, gene expression, and survival of nearly all heterotrophic life forms. As we humans need vitamins from dietary sources for our health, most organisms obtain essential chemical compounds for their biological functions from other organisms which can synthesize them. Many terrestrial (bacteria, fungi, beetle, etc.) and marine (bacteria, dinoflagellates, ctenophores, decapods, copepods, and ostracods) luminous organisms are known to produce their luciferin <sup>2,4,55</sup>. However, many more, even most marine luminous animals, rely their luciferin molecules on their diets <sup>56-63</sup>. The supplementation of luciferins from prey creates higher probabilities for predators to become bioluminescent. Luciferin-containing food becomes a preferred element of the diet, since dietary luciferin dependent luminous organisms need a steady supply to maintain luminescence.

Dinoflagellates are single-cell phytoplankton, which often causes bioluminescent blooms in the coastal waters associated with elevated temperature and nutrient availability. Their luminescence is usually triggered by mechanical disturbance via vacuolar proton channels <sup>64</sup>. The biosynthetic process of dinoflagellate luciferin has not been resolved <sup>65</sup>, but the chemical structure of

dinoflagellate luciferin highly resembles the chlorophyll molecule of photosynthetic organisms, indicating that dinoflagellate luciferin might be originated from the chlorophyll molecule (i.e., photosynthetic organisms) <sup>55,66,67</sup>. *Euphausia* (krill) luciferin possesses the same structural backbone as dinoflagellate luciferin <sup>68-70</sup>. It is believed that *Euphausia* obtains dinoflagellate luciferin and modifies it for euphausia's bioluminescence, but no evidence of luciferin uptake has been reported in *Euphausia*. Since dinoflagellate luciferin is structurally similar to krill luciferin and cross-reacts with the krill luminous system, studies suggested that krill luciferin may be obtained via diet <sup>2,71,72</sup>. Also, there is no evidence of the biosynthesis of krill's luciferin.

Coelenterazine, a luciferin originally discovered in coelenterates (former taxonomic classification including Cnidaria and Ctenophora), plays a significant role in many organisms' light emission, especially in the deep-sea <sup>12</sup>. Coelenterazine is also found in many non-luminous marine organisms (e.g., some fish, shrimps, and sponges) and was thought to be obtained via dietary pathways <sup>73,74</sup>. An experimental study demonstrated the dietary requirement of coelenterazine in luminous Cnidarians. Hydromedusae, *Aequorea victoria*, and *Eutonia indicans* failed to emit light when fed a diet containing no coelenterazine <sup>12</sup>. However, feeding *A. victoria* and *E. indicans* with diets containing coelenterazine or supplements of coelenterazine reagent in water tanks containing hydromedusa specimens resulted in luminescence <sup>12</sup>. Since these cnidarians subsist mainly on gelatinous planktonic organisms <sup>12</sup>, research needs to focus on these gelatinous organisms to understand the actual source of coelenterazine and its transfer within the food web. In other experiments, the bioluminescent lophogastrid shrimp *Gnathophausia ingens* could produce luminescent secretions when tested with various luminous food types, including *Triphoturus*, *Cyclothone*, *Atolla*, *Sergestes*, and *Gaussia*, which contains coelenterazine. However, the shrimp failed to luminesce when fed on euphausiid or *Porichthys*, which do not contain coelenterazine but different luciferins <sup>75</sup>. Digestive tracts of various shrimps, including *G. ingens* possessed exogenous dietary luciferin responsible for luminescence <sup>75</sup>. The luminescence capabilities of brittle star, *Amphiura filiformis* (Ophiuroidea) was observed by feeding *A. filiformis* with a coelenterazine-free diet and coelenterazine supplemented food. Experimental results showed depleted luminescence with coelenterazine-free diet and recovered luminescence when fed with coelenterazine supplemented food, suggesting that *A. filiformis* obtain a dietary coelenterazine to maintain luminescence capability <sup>76</sup>. Lantern sharks in the genus *Etmopterus* also use coelenterazine for light emission. Those sharks probably obtain coelenterazine from fishes, crustaceans, and copepods based on their stomach contents <sup>77</sup>. These incidences indicate that some bioluminescent animals lack the capability of luciferin biosynthesis but can produce light upon obtaining luciferins through diet. Only a few

animals are known to possess the capability of coelenterazine biosynthesis, such as copepod, shrimp, and ctenophore<sup>6,7,78-81</sup>. These animals must therefore serve as a primary dietary source for coelenterazine dependent luminous organisms. Noteworthy, some coelenterazine users such as *Vampyrotheuthis*, Oikopleutidae, and *Amphiura* feed on detritus (marine snow or mud) materials in which coelenterazine is not protected in cells from oxidation. Because free coelenterazine molecules are highly unstable, coelenterazine in the detritus is likely to be autooxidized and to form non-active reactant, coelenteramide, or coelenteramine. It is unknown how those animals can obtain active coelenterazine from such diets.

The stable forms of coelenterazine such as enol-sulfate and dehydrocoelenterazine were detected in the tissues of few myctophid species, which are hypothesized to be derived from the diet<sup>74</sup>. Detection of coelenterazine in the gonads of few myctophid species<sup>74,82</sup> and presence of ventral photophores in the late embryonic stage of the lantern shark *Etmopterus spinax*<sup>77,83</sup>, suggests the maternal transfer of bioluminescent substrates to offspring. Several deep-sea non-luminous cephalopods and octopods contained luminous substrates in their tissues and organs, apparently due to ingestion and accumulation of a coelenterazine and a de-hydrocoelenterazine<sup>13</sup>. However, the possibility that the cephalopods can biosynthesize those luciferins is not addressed. Coelenterazine was extracted from an enoploteuthid squid *Watasenia scintillans*, a myctophid fish, an oplophorid shrimp, and cnidarians, indicating that coelenterazine may be of dietary origin in the midwaters<sup>13</sup>.

Despite the well-known dietary pathway of coelenterazine acquisition among different organisms, the actual biosynthetic mechanism remains unknown, although the total chemical synthesis of coelenterazine has been reported<sup>84-91</sup>. Although there could be alternative synthetic mechanisms in various luminous or non-luminous organisms in the ocean<sup>57</sup>. Coelenterazine was detected in the eggs of *Argyropelecus hemigymnu*, supporting the hypothesis of a maternal transfer of luminous capabilities<sup>60</sup>. In another observation, increasing coelenterazine concentrations were detected during the development of eggs to adults for the decapod crustaceans, *Stellaspis debilis*, *Oplophorus spinosus*, and *Acanthephyra purpurea*<sup>78,79</sup>. However, there is no evidence for the specific biosynthesis mechanism of coelenterazine throughout development in these species.

The biosynthesis of coelenterazine luciferin using two molecules of L-tyrosine and one molecule of L-phenylalanine has been documented for two deep-sea copepod *Metridia pacifica*<sup>80</sup>, and *M. lucens*<sup>92</sup>. Earlier studies postulated a mechanism in which mutation in the peptide serine-tyrosine-glycine (SYG) to form the tripeptide phenylalanine-tyrosine-tyrosine (FYY) could be involved in coelenterazine biosynthesis in cnidarians and decapod crustaceans<sup>78</sup>. The comparative transcriptomic analysis found an isopenicillin-N-synthase with FYY sequence on the C-terminus in



luminous ctenophores, but the homologs in non-luminous ctenophores lacked FYY sequence <sup>93</sup>. Luminous ctenophores *Mnemiopsis leidyi* and *Bolinopsis infundibulum* were shown to be capable of coelenterazine biosynthesis, but the non-luminous ctenophore *Hormiphora californensis* lacked the capability <sup>7</sup>. However, the involvement of the FYY gene in coelenterazine biosynthesis lacks experimental evidence <sup>7</sup>. Thus, further research is needed to identify and prove the chemical mechanism for tripeptide-based coelenterazine synthesis in coelenterazine dependent decapods, ctenophores, and other organisms <sup>78</sup>. Investigations on transcriptome data of luminous and non-luminous organisms and gene-knockout experiments would unveil the coelenterazine biosynthetic pathways in the near future <sup>93</sup>.

Vargulin, a luciferin originally found from the luminous ostracod *Vargula hilgendorffii* (previously *Cypridina hilgendorffii*), is also acquired by predators for bioluminescence. The midshipman fish *Porichthys notatus* was observed to have dim, undetectable, or no luminescence depending on collection location <sup>94</sup>. *P. notatus* gained luminescence capability upon being given pure vargulin or after feeding on luminous ostracod *Vargula tsujii* and *V. hilgendorffii* <sup>94</sup> or gelatin capsules containing dried *Vargula* or intraperitoneal injection of luminous *Porichthys* tissue extracts <sup>95</sup>. The absence of dietary luciferin in food <sup>96</sup> or a diet of other luminous organisms did not result in any luminescence in *P. notatus* <sup>94</sup>. Similar cases have been observed for the cardinalfish *Jayadia ellioti* (= *Apogon ellioti*) <sup>97</sup> and golden sweepers *Parapriacanthus ransonneti*, whose luminescence was produced upon feeding on exogenous luciferin diet from a sympatric ostracod *Vargula hilgendorffii* <sup>57,97,98</sup>.

The ability to synthesize vargulin has been demonstrated in *V. hilgendorffii* <sup>99</sup>. Three amino acids L-arginine, L-isoleucine, and L-tryptophan are the required substrates <sup>100</sup>. Similar to coelenterazine biosynthesis, cyclization of the tripeptide is thought to be involved, but the detailed pathway remains unknown <sup>2,93</sup>. There is little detail about the mechanism of synthesis of coelenterazine in decapod crustaceans <sup>78</sup>, deep-sea copepod *Metridia pacifica* <sup>80</sup> and ctenophores <sup>7</sup>. A recent study postulated that pyrosomes might obtain coelenterazine-like luciferin from dietary sources <sup>101</sup>, although the actual source in its diet of phytoplankton is unclear. Thus, further research is required on the dietary origin of coelenterazine and vargulin luciferin in crustaceans and other organisms to identify their biosynthetic pathways and substrate flow through the food web. In most marine organisms, the acquired bioluminescence is thought to be used in defensive functions.

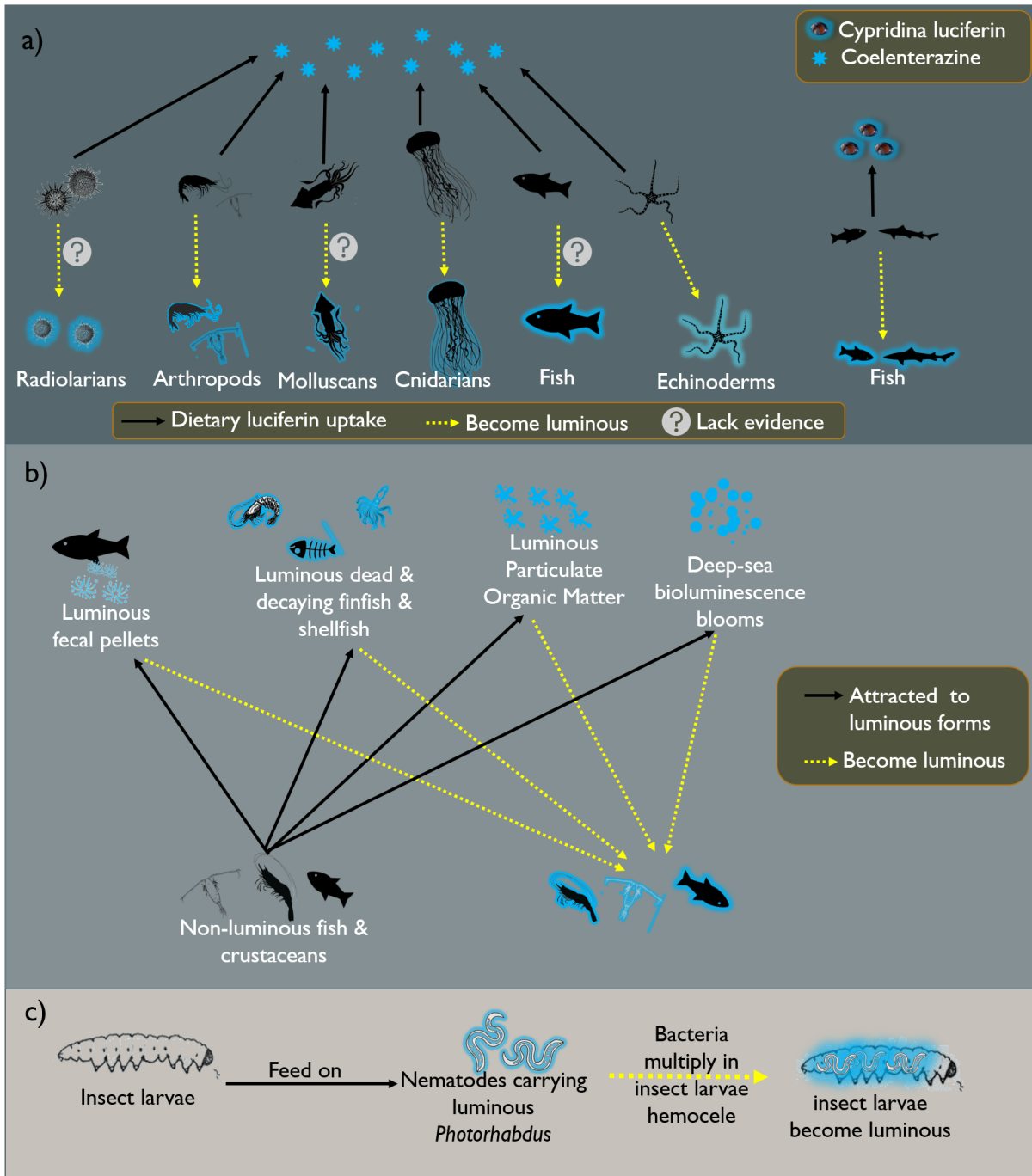
## 2.2. Dietary acquisition of protein or larger functional module

Aside from small organic compounds, larger molecules and cellular components such as proteins and cell organelles are generally vulnerable to digestion. There have been a few reports of the exceptions, for example, sacoglossan sea slugs can sequester chloroplasts from their algal food and maintain their photosynthetic function. The maintenance of the acquired chloroplast (kleptoplast) is independent of HGT, but some involvement of kleptoproteins from the algae has been postulated <sup>102</sup>. Sequestered cnidocytes (kleptocnidae) are known from the comb jelly *Haeckelia* (Ctenophora), nudibranchs (Mollusc), flatworms (Platyhelminthes), and *Acoelomorpha* <sup>103</sup>. In addition to small compounds, these cell organelles are rarely but certainly integrated into the predators, but protein uptake has not been known until recent.

The golden sweeper, *Parapriacanthus ransonneti*, obtains and uses not only luciferin but also luciferase by consuming the ostracod, *Cypridina noctiluca* <sup>8</sup>. This study was the first report of sequestration of a protein with its function intact, and it was termed a kleptoprotein system. *P. ransonneti* is also capable of sequester luciferase of *V. hilgendorffii*, showing 84% amino acid identity to the luciferase of *C. noctiluca*, if fed in the laboratory condition. The fish uses kleptoprotein bioluminescence for counterillumination, so it needs to supplement vargulin and cypridinid luciferase constantly. As many marine animals utilize coelenterazine, it is possible that some of them also use a kleptoprotein for their bioluminescence. The molecular mechanisms involved in protein uptake, as well as kleptoplastids and kleptocnidids, from diets are not understood.

## 2.3. Dietary acquisition of individuals

A few observations have recorded the occurrence of temporary luminescence from non-luminous organisms due to feeding on luminous organisms. Certain amphibians, lizards, spiders, ants, birds, and mammals are reported to be the predators of fireflies <sup>104</sup>. These predators are attracted to firefly light, prey on them, as a result, flashes of temporary luminescence are observed in predators with soft-bodied tissues. Light ceases as the firefly digests in the stomach. We hypothesize that regular or occasional predation on bioluminescent organisms by predators might facilitate the potential for evolutionary processes to develop a prototype luminous system (having either luciferin or luciferase in their body) or kleptoprotein system.



**Figure 2.** Acquisition of luminescence through dietary source, ingestion, colonization, and chemical triggering in different organisms. (a) Dietary luciferin uptake by various groups of organisms. (b) Some non-luminous crustaceans and fish are attracted to various luminous forms (colonized by luminous bacteria and to less extent dinoflagellates) such as fecal pellets, dead and decaying finfish, and shellfish, particulate organic matter, and deep-sea bioluminescence blooms feed on them and display a temporary luminescence. (c) Ingestion of luminous *Photorhabdus* by insect larvae. Silhouette icons were obtained from PhyloPic.org and iconfinder.com. Other images (copepods and radiolarians) are courtesy of anonymous artists.

### 3. Symbiosis-mediated luminescence

Visual appearance is usually innate character well known as cases of pigment. However, the literature suggests that the dissemination of pigment traits may also be imparted through symbiotic organisms. Dolastatin, an antitumor yellow molecule and other molecules isolated from sea hares and other molluscs, is originally biosynthesized by their symbiotic cyanobacteria<sup>105,106</sup>. Pigment molecules produced by different seagrasses, sponges, corals, molluscs, and tunicates are produced by their epibiotic bacteria<sup>107</sup>. Tambjamine pigments characterized from bryozoans, *Bugula dentata* and *Sessibugula translucens*, nudibranchs, and ascidian, *Atapozoa* sp. are produced by endobiotic or epibiotic *Streptomyces* sp., *Pseudoalteromonas tunicata*, and *Serratia marcescens*<sup>108–111</sup>.

Similarly, the association between luminous bacteria and host organisms results in symbiosis-mediated luminescence (Figure 3). Host organisms lack genetic sources to produce light; therefore, without the luminous symbionts, the host organisms remain non-luminous. Most vertebrates and molluscs, which display luminescence with the aid of symbiotic luminous *Vibrio* and *Photobacterium* species, have specific organs to harbor luminous bacteria, so-called “light organs”<sup>112</sup>. Symbiotic bioluminescence in the Hawaiian bobtail squid *Euprymna scolopes* has been well studied. *E. scolopes* harbors luminous bacteria in its light organ located below the eyes and ejects *Aliivibrio fischeri* as a cloud of light into surrounding waters to escape from predators. The expelled free-swimming luminous bacteria colonize on a new host (e.g., the symbiosis between *Aliivibrio fischeri* and *Euprymna scolopes*)<sup>116</sup>. The leftover luminous bacterial cells present in the light organs will again proliferate to requisite cell density by nightfall. *A. fischeri* in the light organ do not possess flagella, but once the bacteria are ejected into the ocean, they transform to have flagella and freely move through the water<sup>34,117</sup>. Those bacteria again colonize on the juvenile squids as a cyclical process of symbiosis via (1) a series of reciprocal chemical communication between host and symbiont<sup>116</sup>, (2) flagellum based motility towards the light organ<sup>118</sup> and (3) their attachment to mucus secreted by the ciliated epithelia of the squid light organ<sup>119</sup>.

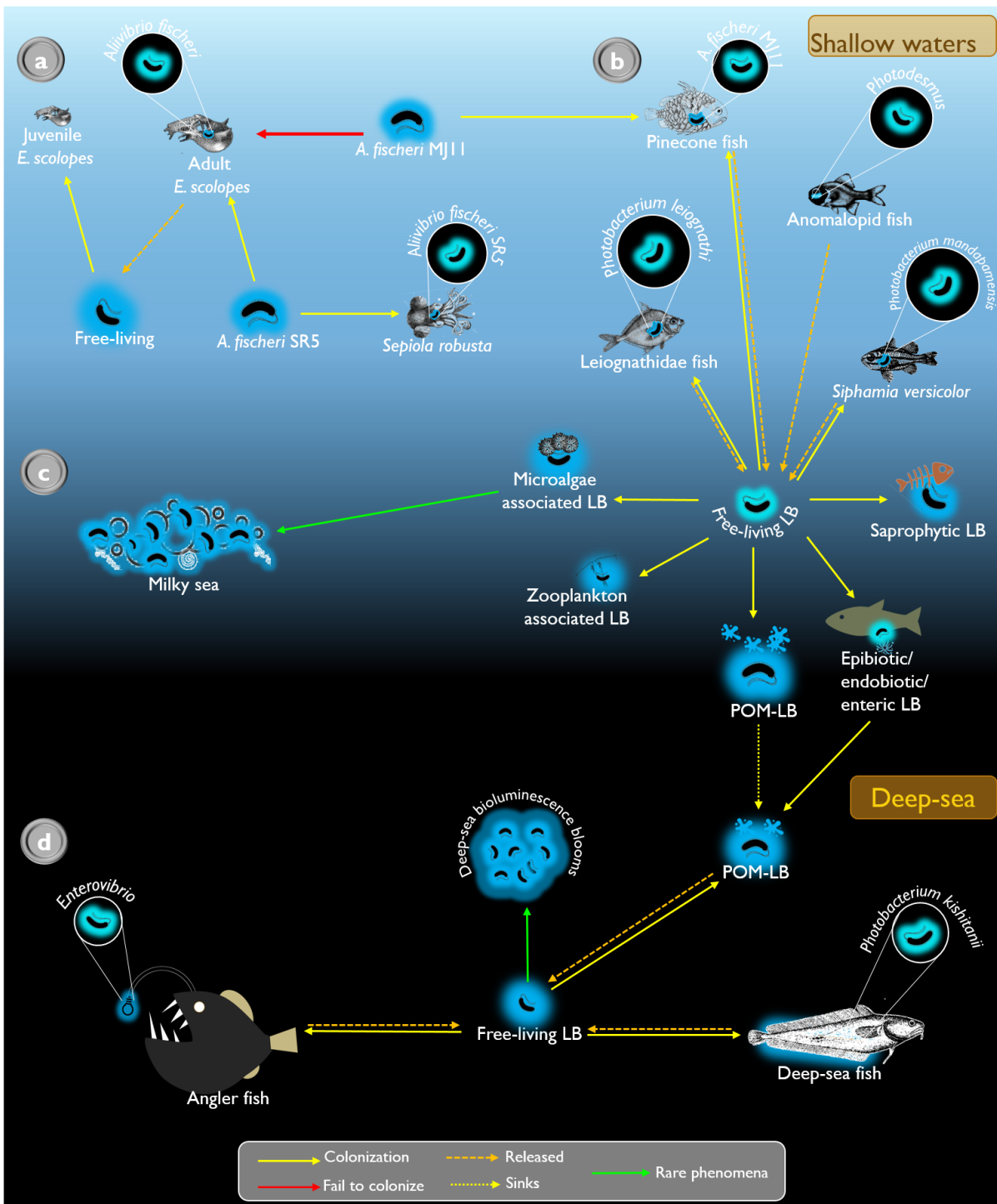
The process of how free-living bacteria initiate colonization on the host is partially understood in the shallow waters (Figure 3a-c). Luminous bacteria are ubiquitous in the ocean and can be seen in various forms such as saprophytic, enteric (surviving or growing in gut tracts of animals), and light organ symbionts<sup>120</sup>. Depending on the host, luminous symbionts use surface-binding pilin proteins and secretion proteins for colonizing the new host<sup>121</sup>.

A study reported the colonization of *A. fischeri* SR5 on its natural host squid, *Sepiolo robusta*, and heterologous squid host, *E. scolopes*<sup>122</sup>. In contrast, the monocentrid fish luminous

symbiont, *A. fischeri* MJ11 failed to colonize heterologous host *E. scolopes*, indicating the strain-host specific colonization<sup>122,123</sup> (Figure 3a). A recent study identified the diketopiperazine molecule required for a symbiotic relationship between the microbial symbiont *A. fischeri* and its host *Euprymna scolopes*<sup>124</sup>. But the same bacterial species failed to colonize other potential hosts, like monocentrid fish (Figure 3b). This indicates that research is needed on symbiont-specific colonization of luminous bacteria with different fishes. Some marine fishes produce light with the aid of luminous bacteria. These fish culture luminous bacteria in their light organs and release them into seawater when they proliferate to the excessive densities. And, the released bacteria recolonize new generations of the same host<sup>128</sup>, or may colonize other luminous and non-luminous organisms<sup>120,125,129</sup>. Anomalopidae, monocentrid fish, and angler fish are known to release luminous bacteria from their light organs and intestine excretions into the external environment and maintain the bacterial count in their light organs<sup>125,126</sup>. Cardinal fish *Siphamia* releases luminous feces composed of luminous bacteria cultured in the light organ, connected to its digestive tract<sup>127</sup>. Some zooplankton and fishes are also attracted to bacterial bioluminescence primarily associated with particulate organic matter (Figure 2b). The bacterial bioluminescence in the gut of those planktons and small fish can be seen through the transparent bodies, which become vulnerable to nocturnal fish or coprophagic organisms by attracting them to light<sup>16,130</sup>. These bacteria survive during digestion, grow in the nutrient rich intestinal tracts<sup>130</sup>, and are released back into the environment through the predators' feces, which results in the propagation of the luminous bacteria<sup>16</sup>. The dispersion and propagation of luminous bacteria through the attraction of light associated with fecal pellets and sediment particles is also supported by a previous study on copepods<sup>17</sup>. Fresh fecal pellets of copepods were found with a high count of luminous bacteria, which are known to be involved in the decomposition of fresh fecal pellets during egestion<sup>17</sup>. Subsequently, these bacteria are again released back into the seawater through feces. However, it is not yet known whether such association could be transient or permanent<sup>129</sup>, indicating a promising area for future research.

In the deep-sea environment, the cosmopolitan free-living luminous bacteria, *Photobacterium kishitanii*, is associated with skins and light organs of diverse deep-dwelling fishes<sup>131</sup>. Many deep-sea animals display host-specific colonization by luminous bacteria<sup>120</sup>. The genomes of deep-sea angler fish luminous symbionts, *Candidatus* Enterovibrio escacola, and *Candidatus* Enterovibrio luxaltus were observed to be reduced to 50% from actual genome size after colonization, compared to free-living luminous symbionts<sup>132</sup>. Similarly, such incidents of reduced genome contents after colonization were reported in flashlight fish symbionts. The genome content of pseudo-vertically transmitted flashlight fish luminous symbionts such as *Candidatus* Photodesmus blepharus, and

*Candidatus Photodesmus katoptron* were reduced to moderate or extreme levels <sup>121,128,133</sup>. The same species of symbionts were observed to colonize the light organs of a majority of the deep-sea angler fish, except *Cryptosaras couesii* that colonized *Candidatus Enterovibrio luxaltus* <sup>134</sup>. Adult stage angler fish acquire free-living luminous bacteria, while these symbionts are absent in larval specimens <sup>135</sup>. Unlike the known colonization mechanism of luminous bacteria with bobtail squid <sup>116</sup>, the actual mechanism of colonization and transmission of luminous bacteria with anglerfish is not yet understood. Based on 16S rDNA, luciferase operon, and other housekeeping genes analysis, HGT is proposed as a possible mechanism involved in the colonization of enterovibrio bioluminescent symbionts from the environment to the light organs of anglerfish <sup>134,135</sup>. However, based on the luminous bacterial genomes, recent studies suggest that motility and chemotaxis are perhaps important for luminous bacteria to colonize angler fish <sup>121,133,134</sup>.



**Figure 3.** Colonization of free-living luminous symbionts by different host organisms. **a.** Luminous bacteria (LB)-Squid colonization; **b.** LB-fish colonization; **c.** LB-non-luminous organisms or LB-organic matters colonization in shallow water; **d.** LB-Deep-sea fish colonization. POM-LB: particulate organic matter associated LB.

Rare phenomena such as the formation of milky sea<sup>136,137</sup> and deep-sea bioluminescent blooms<sup>138</sup> are large-scale examples of quorum-sensing mediated luminescence. Milky sea and deep-sea bioluminescent blooms are the two luminescent phenomena observed in surface water and deep-sea waters, correspondingly. In both events, luminous bacteria are involved. In the former event,

luminescence is triggered by autoinducer molecules, whereas in the latter event, nutrients and other chemical elements are thought to be involved. A satellite captured an area of about 15,400 km<sup>2</sup> luminescing, known as milky sea, in the Arabian Sea, which has been linked to luminous bacteria *Vibrio harveyi* associated with microalga *Phaeocystis* blooms in the surface waters (Figure 3c). This bacteria releases enormous quantities of quorum sensing autoinducer molecules with *Phaeocystis* bloom to form milky sea<sup>136</sup>. The microalga *Phaeocystis* is not luminescent, but the enormous load of *V. harveyi* on this alga generates intense luminescence. Milky seas are sometimes exceeding 100,000 km<sup>2</sup> in size and continues for days to weeks<sup>137</sup>. It is unknown whether or not fish and crustaceans feed on milky sea. In contrast, deep-sea bioluminescence blooms were suggested to occur due to luminous bacterial densities triggered by nutrient availability through open-sea convection<sup>138</sup>. The actual factors triggering the development of these two phenomena have not yet been investigated experimentally *in situ* only surmised from *in vitro* comparisons. The ecological roles of milky sea and bioluminescent bloom, how this enormous luminescence benefits on the luminous bacteria, remain unknown.

In contrast to symbiosis, saprophytic luminous bacteria are often reported to colonize and spread on dead organisms. A dead specimen of seabream kept in a refrigerator produced light from its surface skin after a couple of days due to the proliferation of epibiotic marine luminous bacteria. In this case, it is not due to symbiotic bacteria in it but saprophytic luminous bacterial proliferation. The brackish water amphipod, *Pontogammarus maoticus*, was reported to emit a steady green light from its whole body, postulated to be of bioluminescent bacterial origin<sup>139</sup>. However, luminescence in these amphipods is not because of symbiotic colonization but thought to be due to the aggregation and proliferation of pathogenic luminous bacteria. It is yet to be confirmed whether this incident is occasional or recurrent and whether these amphipods obtained luminous bacteria through diet or natural infection. A previous study suggested that the fluids of crustaceans are often infected with luminous bacteria, which might be possibly pathogens or merely opportunists<sup>129</sup>. Marine saprophytic luminous bacteria were reported to cause luminescence in different fish, meat, and eggs<sup>30</sup>. Similarly, many terrestrial samples such as a variety of insects, eggs of chicken and lizards, mutton, decaying bodies of marine and terrestrial organisms, human wounds, and corpses were reported to luminesce, which is attributed to the colonization of terrestrial luminous bacterial species belonging to the genus *Photobacterium*<sup>30,140</sup>.

The terrestrial bioluminescent *Photobacterium* bacterial species is reported to be a human pathogen and a symbiont of the nematode family *Heterorhabditidae*<sup>141</sup>. When insect larvae feed on nematodes carrying *Photobacterium*, nematodes release these luminous bacteria into the insect larva



hemocoel, where luminous bacteria replicate, produce toxins, and kill the insect larva for nutrients for themselves and the nematodes. At this stage, the dead specimens of insect larvae begin to glow because of light production from proliferating luminous bacteria in the hemocoel <sup>141,142</sup> (Figure 2). Luminescence emitted from the dead insect larvae would possibly help newly reproduced nematode larvae attract and infect new insect larvae <sup>143,144</sup>. The ecological role of this luminescence in the dead insect body is not understood.

**Table 1.** Details of various organisms acquiring bioluminescence from luminous organisms through various modes. Other phenotypic traits acquired by several organisms are detailed in the supplementary file (Table S1).

Acquired gene/molecule/any	Receiving organism	Acquired from	Acquired via	Reference
Coelenterazine	Hydromedusae, <i>Aequorea Victoria</i> , and <i>Eutonina indicans</i>	Coelenterazine containing diet	Diet	12
Coelenterazine	Mysid, <i>Gnathophausia ingens</i>	Coelenterazine containing diet	Diet	75
Coelenterazine	Radiolarians, copepods, Cnidaria, Ctenophora, Arthropoda, Mollusca, and fishes	Coelenterazine containing diet	Diet	57–59, 60,61, 62,63, 145
Coelenterazine	Ophiuroid, <i>Amphiura filiformis</i>		Diet	76
Dinoflagellate luciferin	Dinoflagellates	Probably photosynthetic organisms	Unknown	55
Dinoflagellate luciferin	Krill	Dinoflagellates (Possibly)	Diet (Possibly)	68
Coelenterazine as squid luciferin precursor	Cephalopods and octopods	Luminous organisms	Diet	13
<i>Cypridina</i> luciferin	Midshipman fish, <i>Porichthys notatus</i>	Ostracod, <i>Vargula hilgendorfi</i>	Diet	55,94
<i>Cypridina</i> luciferin	Cardinalfish, <i>Apogon</i> ,	Ostracod, <i>Vargula</i>	Diet	57,97,98

	and sweepers, <i>Parapriacanthus</i> , and <i>Pempheris</i>	<i>hilgendorffii</i>		
Luciferase	Sweeper, <i>Parapriacanthus</i> <i>ransonneti</i>	Ostracod, <i>Cypridina</i> <i>noctiluca</i>	Diet	8
<i>luxA</i>	<i>Vibrio</i> species	<i>Vibrio cholerae</i>	HGT	40
<i>luxA</i>	Non-luminous <i>Vibrio</i> species	Luminous <i>Vibrio</i> species	HGT	11
<i>lux-rib</i> operon	<i>Photobacterium</i> <i>leioognathi</i>	Interspecies or <i>Photobacterium</i> strains	HGT	42
<i>lux-rib</i> operon	<i>P. mandapamensis</i>	Interspecies or <i>Photobacterium</i> strains	HGT	146
<i>lux-rib</i> operon	<i>P. aquimaris</i>	<i>Photobacterium</i> <i>mandapamensis</i>	HGT	41
<i>Aliivibrio fischeri</i>	Juvenile <i>Euprymna</i> <i>scolopes</i>	<i>Aliivibrio fischeri</i>	Colonization	116
Luminous bacteria	Zooplankton & fish	Particulate organic matter	Feeding	16
<i>Photorhabdus</i> spp.	Insect larvae	Nematodes of <i>Heterorhabditidae</i> family	Feeding	142
Firefly	Rhacophoridae Frog	Firefly	Predation	104

## Conclusion

As detailed above, there have been few studies showing that some non-luminous organisms may become luminescent via various dietary, HGT, or symbiotic pathways. Since many of these pathways are not well understood, research on these aspects would provide new insights on convergent evolutionary pathways<sup>82</sup>. Analyzing the luminescence activity of various animals' gut contents will help determine the chemistry and genetics behind the dietary flow of luciferins and luciferases

through the food web. Studying the milky sea and deep-sea bioluminescent bloom events using satellites and deep-sea bathyphotometers, respectively, would provide a deeper understanding of the occurrence and impact of these phenomena. The mechanisms and ecological functions of acquired genes and foods in non-luminous organisms also need further investigation. The ability to luminesce by non-luminous organisms is linked with evolutionary mechanisms. Thus, studies are required on two aspects: 1) how light organs (or related tissues) of the organisms are specialized to sense and integrate foreign molecules, genes, or microbes from donor organisms; 2) how the molecules, genes, or bacteria avoid host immune system or digestive system before integrating into the host organism.

### **Conflict of Interest**

The authors do not have any conflict of interest to declare.

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**Table S1.** Details of other phenotypic traits acquired by various organisms.

Acquired trait	Acquired gene/molecule /any	Receiving organism	Acquired from	Acquired via/ influencing factor	Function/specific activity	Reference
Fluorescence	GFP-like (non-fluorescent protein)	Ctenophore	Cnidarian prey	Predation	Tissues fluoresce	1,2
	GFP	Amphioxus	Bilaterians	HGT	Body fluorescence	3
Pigments	Dolastatin	Sea hare & molluscs	Cyanobacteria	Symbiosis		4
	Tambjamine	Invertebrates	Associated bacteria	Symbiosis		5,6
	Tambjamine	<i>Nembrotha</i> spp.	Ascidian <i>Atapozoa</i> sp.	Diet	Yellow pigment	7
	Violacein	<i>Collimonas</i> CT	<i>Janthinobacterium</i> and/or <i>Duganella</i> sp.	HGT	Blue pigment	8
	Lipophilic skin alkaloids	Poison dart frogs	Arthropods	Diet	Aposematism	9,10
Toxins/virulence	Lipophilic skin alkaloids	Poison dart frogs	Arthropods	Diet	Toxins	9,10
	Cardenolides	Monarch butterflies	Milkweed plant, <i>Asclepias</i> spp.	Diet	Toxins for defence	11
	Lucibufagins	Female firefly <i>Photuris</i>	Male firefly <i>Photinus</i>	Diet	Defence	12
	Virulent & antibiotic resistance genes	Microbes, plants, & animals	Microbes, plants, & animals	HGT	Virulence, survival, & evolution	13-19

	Cholera toxins	<i>Vibrio cholerae</i>	CTX $\phi$ bacteriophage	Bacteriophage injection	Survival, evolution, pathogenesis	20,21
Others	16s rRNA	Bacteria	Bacteria	HGT		22
	Autotrophs	Tubeworms & clams	Free-living bacteria	Colonization	Nutrition and metabolism	23,24
	Chloroplasts	Sea slug <i>Elysia viridis</i> & <i>Plakobranc hus Ocellatus</i>	Multiple Algal Species	Kleptoplasty	Photoautotroph or mixotroph	25–27
	Cnidocysts	Ctenophore, Nudibranchs, turbellarian flatworms	Cnidarians, Coelenterates	Kleptocnidiae	Defense	28–30
	Cnidocysts	<i>Tremoctopus violaceus</i>	<i>Physalia</i>	Predation	Defense and offense	31
	Symbionts	<i>Rimicaris exoculata</i> and <i>R. chacei</i>	Bacteria	Possibly colonization	Nutrients & mineral supply	32,33

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