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Semi-Intrinsic Luminescence in Marine Organisms

Jeremy Mirza and Yuichi Oba

Abstract

Light emission is widespread in the oceans, with over three quarters of all observed marine species exhibiting bioluminescence. Several organisms such as the copepod *Metridia pacifica* and the ostracod *Vargula hilgendorfii* have been proven to synthesise their luciferin and luciferase to facilitate light emission. However, many luminescent species lack the capability to do this and instead it is possible that they acquire some of the components for their luminescence through predation or filter feeding on organisms that produce luciferins or precursors to these molecules. This has resulted in many organisms using certain luciferins, such as coelenterazine, as their substrate without possessing a clear mechanism to synthesise these. This chapter will review several examples of these semi-intrinsic luminescent systems and how the substrates and enzymes can be obtained for these reactions. Moreover, it will look at why particular luciferins, such as coelenterazine, are more widespread and utilised in this manner compared to other substrates.

Keywords: Bioluminescence, Semi-Intrinsic, Luciferin, Coelenterazine, Imidazopyrazinone

1. Introduction

Bioluminescence is a chemical process numerous organisms utilise to produce light. This reaction has been studied in a wide range of taxa, in terms of its chemistry, evolutionary history and purpose in ecology [1]. This ability to emit light via a chemical reaction can be found in a diverse range of phyla, ranging from simple unicellular bacteria and protists to more complex organisms such as cephalopods and elasmobranchs [1]. Generally, this is a chemical reaction that involves the oxidation of a luciferin compound in the presence of a luciferase enzyme. This produces an unstable intermediate (usually a cyclic peroxide) that breaks down to produce a compound generically called oxyluciferin and gives off a large amount of energy as light [2, 3].

This phenomenon has evolved independently at least 94 and potentially over 100 times [4] across both marine and terrestrial genera, and around 80% of bioluminescent genera occur in the oceans [5, 6]. In marine ecosystems, it is estimated that up to 95% of organisms that dwell below 200 m depth are able to emit light [7–9]. Given the widespread utilisation of this phenomenon, there are a diverse array of luminescent systems that exist with several different substrates and a wide variety of associated enzymes.

Unlike the enzymatic component of the reaction where individual species are capable of expressing unique enzymes, luciferins are more conserved, and the same structures can be found across multiple distinct phyla. As of now at least 10 natural

luciferins have been identified in terms of their chemical structure [4, 10]. Of those, the four main marine groups of luciferins are bacterial luciferin, tetrapyrrole used by dinoflagellates and krill, cypridinid luciferin used by several species of fish and ostracods and coelenterazine which is used by luminescent organisms in at least 9 different phyla [11].

Despite being a critical component for light emission, many marine organisms do not produce their own luciferins, and obtain these small organic compounds from their diet by grazing or predating on other luminescent organisms [1]. These species exhibit semi-intrinsic luminescence, as they still express their own luciferase enzymes, however they can obtain the substrates and potentially precursors to luciferin needed for luminescence through their diets [12]. Some have even shown the capacity to obtain the enzymatic component of the luminescent reaction through their diet as well [13]. With regards to this phenomenon the most notable examples of semi-intrinsic luminescence involve coelenterazine and cypridinid luciferin [14].

This chapter will review the prevalence of known semi-intrinsic luminescent systems and how these organisms have attained light emission. Moreover, it will look at why these reactions and predator–prey relationships have evolved over time and discuss why certain substrates are more commonly observed in semi-intrinsic luminescence.

2. Sources of luminescence in semi-intrinsic systems

Identifying the presence of luminescence in an organism is well established and involves identifying the luciferin and luciferase involved in the reaction and separating them. The basic technique for luciferin and luciferase separation, developed by Dubois [15, 16] is termed "hot-cold extract". In this method, two water extracts of luminogenic tissue are prepared [3, 16]. The use of cold extract allows to preserve the activity of the enzyme (luciferase), while the heated fraction destroys the proteins and yields the luciferin, and when both extracts are mixed together an *in vitro* luminescence is produced [3, 16]. Each extract can be purified to allow for the identification of the amino acid sequence corresponding to the luciferase and the chemical structure of the luciferin [3, 17].

However, this in of itself does not establish how the luminescent organism obtained these components. A possible method to identify this is by constructing the transcriptome of an organism to prove the luciferase enzyme was expressed and not obtained through diet [3, 18]. However, this is a lot more difficult when it comes to identifying whether an organism can synthesise its own luciferin, as very few biosynthetic pathways have been established.

Despite this, it has been shown by controlling the diet of a number of higher taxa that their luminescence is dependent on the consumption of particular organisms [12, 19]. Subsequently, it has been possible to identify several organisms at lower trophic levels that can produce their own luciferin, including the ostracod *Vargula hilgendorfii* [20] and the copepod *Metridia pacifica* [14], both shown in **Figure 1**.

2.1 Cypridinid luciferin

Cypridinid luciferin was the first marine luminescent substrate to be identified in terms of its chemical structure. This compound was first isolated and crystallised by Shimomura and colleagues [21, 22], and the structure was determined by Kishi et al. [23], allowing for the detailed study of the biochemistry of this reaction [1]. The ostracod *V. hilgendorfii* was shown to secrete a luminescent mucus when disturbed, emitting a bright blue light at a peak wavelength of 453–455 nm [24]. The

Figure 1.
Photographs of luminescent organisms known to synthesise their luciferins. The ostracod Vargula hilgendorfii *(upper) synthesises cypridinid luciferin and the copepod* Metridia pacifica *(lower) synthesises coelenterazine. Photos taken by ken-ichi Onodera, and Yuichi Oba.*

luminescent cloud of mucus is emitted from specialised glands from two types of cell, one producing the luciferin and the other the luciferase [25].

   Kato and colleagues [26, 27] showed that ostracod luciferin is synthesised from tryptophan, isoleucine, and arginine, via a currently unknown pathway. This was

observed by labelling the amino acid L-tryptophan with deuterium before feeding the ostracod *V. hilgendorfii* with this to confirm incorporation into the cypridinid luciferin [20]. *V. hilgendorfii* was shown to be the first example of a species that could use free amino acids to synthesise its imidazopyrazinone-type substrate, cypridinid luciferin. While this is used by several bioluminescent species, it makes up a small component of total systems in marine environments [20, 28].

2.2 Coelenterazine

The majority of luminescent organisms in marine environments with known or partially studied light emission systems utilise coelenterazine. Coelenterazine is an imidazopyrazinone compound (3,7-dihydroimidazopyrazin-3-one structure) that occurs exclusively in marine organisms in a wider range of phyla (at least nine) than any other luciferin [4]. These include radiolarians, ctenophores, cnidarians, molluscs, multiple arthropods, and some fish [29]. A large proportion of these organisms are assumed to have taken up this luciferin through their diet with only a few organisms shown to synthesise their own substrate [30–32]. The coelenterazine molecule was originally given its name due to the initial discovery of its presence in coelenterates, namely *A. victoria* and *Renilla reniformis* [33]. *A. victoria* is a hydrozoan jellyfish that emits a green light at 508 nm from a ring of photocytes on the peripheral regions of its umbrella [3]. Variants of this substrate exist in several species of squid either as a coelenterazine disulphate [34] or as dehydrocoelenterazine [35, 36].

Whilst coelenterazine has been found in a diverse array of phyla, a biosynthetic pathway and origin has not yet been determined for the majority of species, which are thought to obtain coelenterazine through their diet [12]. Coelenterazine has been shown to be synthesised in the deep-sea copepod, *Metridia pacifica,* via a similar mechanism to that observed for cypridinid luciferin in *Vargula hilgendorfii* wherein free amino acids are biosynthesised to form the coelenterazine luciferin [20, 26]. By labelling L-tyrosine and L-phenylalanine with deuterium it was proven that *M. pacifica* was able to incorporate these amino acids into its diet and that it was able to synthesise coelenterazine from two molecules of L-tyrosine and one molecule of L-phenylalanine [14]. Given that *M. pacifica* is at a lower trophic level it is likely to be predated upon by several higher taxa, many of which exhibit their own luminescent reactions [14, 37].

Recently it has been proposed that luminescent ctenophores are also able to produce their own luminescent components. The phylum Ctenophora or comb jellies are similar to the coelenterates in their morphology and apart from the family Pleurobrachiidae, all are presumed to be luminescent [38]. Ctenophores had previously been considered to be a source of coelenterazine synthesis in the oceans as there are reports of bioluminescence at early developmental stages [39]. When fed a coelenterazine-free non-luminescent diet, ctenophores were still shown to possess this substrate via mass spectrometry [40]. This recent study has implications that a number of other marine organisms, in addition to *M. pacifica* and Ctenophora, have the capacity to synthesise luciferin, which can provide a clear source of coelenterazine for a number of semi-intrinsic luminescent organisms.

3. Semi-intrinsic luminescent systems

3.1 Luminescence in fish

Most notable semi-intrinsic luminescence occurs in higher trophic levels such as among fishes. Several species have been shown to utilise the imidazopyrazinone type

substrates cypridinid luciferin and coelenterazine in luminescent reactions [1, 3, 41], though they are shown to express their own luciferase enzymes [6]. Often these have evolved to harbour luminescence in specialised regions of the body that allow for particular behaviours and functions for luminescence [1, 42].

3.1.1 Cypridinid luciferin in the midshipman fish

Several species of midshipman fish have been shown to utilise cypridinid luciferin as a substrate in their own luminescent reactions, despite showing no identifiable capability to synthesise their own luciferin [43]. A notable example of this has been observed consistently in the species *Porichthys notatus*, which can be found along the Pacific coast of the North American continent [44]. This species is characterised by an array of over 700 dermal photophores distributed along its head and body [45, 46]. Whilst light emission is restricted to specific organelle structures and can be stimulated mechanically, this is not sufficient to constitute a wholly intrinsic luminescent system. Moreover, non-luminescent individuals of the species have been identified when caught in the North Pacific off the coast of Oregon, where despite possessing the photophores in the same pattern, they did not exhibit luminescence [47]. This lack of luminescence was attributed to these animals not having a source of luciferin available from their diet at all of their life stages [48].

By adding small amounts of cypridinid luciferin to *P. notatus*, either by feeding them ostracods, or by intraperitoneal doses of as little as 6 μg of luciferin it was possible to induce luminescence [44]. This also was shown to be possible for completely non-luminescent individual midshipman fish and confirmed cross-reactivity of *P. notatus'* luciferase with cypridinid luciferin led to light emission [43]. It was identified that following consumption of ostracods, *P. notatus* is able to absorb the cypridinid luciferin through its gut. From here the substrate is believed to be able to bind non-specifically to erythrocytes in the blood plasma, possibly preventing autooxidation as it is transferred to the organelles of *P. notatus* where it can be oxidised in the presence of the luciferase enzyme to result in an emission of blue light [43, 49]. Light emission from the addition cypridinid luciferin to non-luminescent *P. notatus*, was indistinguishable from naturally luminescent Californian *P. notatus* [49].

The midshipman fish is a visually active nocturnal predator, that can utilise this acquired cypridinid luciferin to facilitate its hunting strategies. It has been speculated that the array of photophores on its body can mimic the light emission seen in euphausiid swarms, attracting unsuspecting prey [43, 50, 51]. This ability in combination with its highly evolved eyesight have allowed for it to be an effective nocturnal predator, feeding on both luminescent and non-luminescent organisms [52]. Cypridinid luciferin is not isolated to this species and has been found in several other luminescent coastal fishes including in the families, Pempheridae and Apogonidae [53]. Apogonids, or cardinalfishes are mostly reef dwelling with several species exhibiting visceral light organs that produce luminescence [54]. Similarly, Pempheridae commonly known as sweeper fishes, also have photophores along the length of their bodies and tend to be found in shallow marine and brackish waters [54]. It is likely that these species acquire their luminescence from ostracods, in a similar manner to the midshipman fish, though this is still to be confirmed experimentally.

3.1.2 Coelenterazine in Myctophid and Stomiid fishes

Cypridinid luciferin accounts for the luminescence observed in only a few species of bony fish as well as within ostracods, meaning it does not encompass a large amount of the total luminescence in marine environments. The most ubiquitous luciferin found in marine organisms is coelenterazine with species across multiple

phyla utilising this as their substrate for light emission [12, 40]. Among the fishes, numerous species of Myctophidae and Stomiiformes have been shown to utilise coelenterazine for bioluminescence, which is obtained through their diet, either by predating directly on coelenterazine producing copepods such as *Metridia pacifica*, or indirectly by predating on the consumers of these copepods [55, 56].

Myctophids, commonly known as lanternfish, are one of the most widespread and abundant families of mesopelagic fish in the oceans. They are distributed globally, with over 250 species identified across 33 genera and 2 subfamilies [56, 57]. Lanternfish are taxonomically distinguished by specific patterns of luminescent photophores that have allowed for a diverse array of strategies for both prey detection and predator avoidance [58, 59]. Generally, Lanternfish have two kinds of photophores, one along the body with the other proximal to their eyes (**Figure 2**). These two sets of photophores are able to illuminate independently from one another allowing for a variety of ecological functions. Photophores arranged on the ventral surface produce a constant dim blue luminescent glow and can allow for counter-illumination similar to other luminescent fishes, which would allow lanternfish to blend into the surrounding water column [56]. This would facilitate an ability to ambush prey as well as to hide from potential predators in the water column. These arrays of photophores form species specific patterns, which may allow for them to be used in intraspecific recognition [56, 60]. In addition to this array of photophores on the body, most lanternfish have one or more larger photophores on their head, usually positioned sub-orbitally or in the direct vicinity of their eyes [61]. Unlike the photophores on the ventral surface, these emit light in brief intermittent brilliant flashes. This is thought to allow either for predation by illuminating their prey, as well as being used to avoid predators by flashing and startling any larger organisms [56, 62]. Given that these suborbital photophores have sexual dimorphism, it is also possible that their main role is in communication within the species [56, 63].

Lanternfish feed predominantly on a variety of zooplankton including copepods such as *M. pacifica*, which would facilitate a source of coelenterazine luciferin for their luminescence, although it is difficult to assess this given the difficulties of maintaining deep sea fish such as myctophids in aquaria for sufficient amounts of time [55]. Lanternfishes are a major food source for a number of marine predators, including whales and dolphins. More importantly, they are also predated upon by squid and other larger lanternfishes, that also possess luminescence using coelenterazine or one of its derivatives [59]. Therefore, these potentially provide a key link in food webs by facilitating the transfer of coelenterazine from zooplankton to megafauna.

Stomiiform fishes include four families comprising of Gonostomatidae (bristlemouths), Phosichthyidae (lightfishes), Sternoptychidae (hatchetfishes), and the Stomiidae (dragonfishes) [64]. Among the dragonfishes, all species identified within this group have been shown to be bioluminescent, harbouring their light emission within specialised arrays of photophores. Apart from the Arctic Ocean, Stomiidae fishes are distributed globally, residing in the mesopelagic zone of the ocean between 200 and 1000 m depth, with some species recorded to a depth more than 4000 m [64, 65]. Luminescence may well be derived from the coelenterazine in their diets, with several species showing cross reactivity with coelenterazine in a similar way to some lanternfish [3]. However, it has been difficult to determine whether these animals are capable of synthesising their own luciferin, given that it is not yet possible to collect and maintain stomiid fishes in aquaria for any length of time. Dragonfishes are predators, utilising their bioluminescent emissions both as lures and as means to illuminate prey in order to facilitate prey capture [64]. Most feed on squid, shrimps and other fishes including lanternfishes, which may facilitate a source for coelenterazine in a number of these species [64].

Figure 2.
Photographs of Diaphus *sp. captured from a lateral (upper) and ventral view (middle). Displaying the photophores that produce a blue luminescent light (lower). Photographs taken by Yuichi Oba.*

Support for a dietary origin for luciferin in a number of stomiids is supported by their ability to uptake other small molecules to utilise in light emission. An example of this is shown in several species of loose-jaw dragonfish (*Malacosteus* spp.), that have a rare ability to emit longer wavelengths of luminescence that is red in colour, as opposed to blue light which is more ubiquitous in the oceans [1]. *Malacosteus* can also detect red wavelengths of light using a distinct mechanism requiring derivatives of bacteriochlorophylls *c* and *d* that enhance its sensitivity to these longer wavelengths [66]. As vertebrates are unable to synthesise chlorophyll, *Malacosteus* could obtain this through a diet, predominantly of grazers such as copepods that will contain phytoplankton derived pigments in their guts [64]. This strongly supports the concept that other small organic compounds such as luciferins can be taken up by dragonfishes, as well as other Stomiiformes to utilise in their bioluminescent reactions.

3.2 Other Coelenterazine utilising systems

Semi-intrinsic luminescence is clearly present in several marine vertebrates that utilise either cypridinid luciferin or coelenterazine as their substrate. However, this alone does not account for the diverse array of marine phyla that use coelenterazine in their bioluminescent behaviours. Many organisms previously considered to synthesise coelenterazine have since been shown to obtain this through their diet, including in the cnidarians where this was first discovered.

3.2.1 Cnidaria (Coelenterates)

Bioluminescence within the phylum Cnidaria has been studied more than in any other marine invertebrate. Most notably the hydromedusa *A. victoria* which emit light via the enzymatic oxidation of coelenterazine in the presence of calcium [12]. Unlike most coelenterazine utilising organisms that emit blue light, in *A. victoria*, light emission is green due to a green fluorescent protein. This emits green light via resonance energy transfer from the aequorin photoprotein [67]. According to Shimomura [3], photoproteins can be distinguished from luciferases by two general means, not requiring molecular oxygen for light emission and being capable of emitting light proportional to the amount of protein present [68]. Isolated aequorin can appear to emit light only by adding Ca^{2+}, and once the reaction is complete the protein does not appear to immediately be available for further reactions [69].

By controlling the diet of *A. victoria* in the lab it was possible to show that they are dependent on a dietary supply for their luciferin. When provided with an external source of luciferin to uptake after this, *A. victoria* was able to regain its luminescence [12]. The diet of *A. victoria* will consist of a variety of zooplankton, including luminescent copepods such as *M. longa* as well as luminescent cteno-phores, which could provide a dietary source for their luminescence. Several other notable examples of luminescent coelenterates are presumed to obtain coelenterazine from their diet including the sea pansy, *Renilla* sp. and the sea cactus *Cavernularia obesa* [70, 71]. These anthozoans are found predominantly in tropical waters and may be able to obtain coelenterazine by feeding on suspended detrital matter that may contain the substrate.

3.2.2 Crustacea

Among the crustacea there is proven case of a fully intrinsic luminescent system in the copepod *Metridia pacifica*, and a probable case in the decapod shrimp *Systellaspis debilis* which appears to have the ability to synthesise the molecule from free amino acids [72]. Zooplanktonic species such as these potentially provide a source for a lot of the coelenterazine utilised in semi-intrinsic luminescent systems found in many marine organisms. However not all crustacea are able to perform this, and some such as the lophogastrid shrimp, *Neognathophausia ingens*, have been shown to require coelenterazine from their diet [31, 73].

These shrimp use bioluminescence to evade predators as they emit a brilliant blue cloud of luminescence when agitated that acts as a smoke screen [74]. Given that deep water visual predators have highly sensitive eyes, the bioluminescent ink cloud will have a much greater effect in startling nearby predators than the ink clouds produced by most cephalopods [75]. It is possible that producing this amount of luminescent material has a high energetic so it may be easier from an evolutionary perspective to obtain this through their diet instead of via an internal biosynthetic pathway.

3.2.3 Radiolaria

An assumption may be that as the majority of coelenterazine in the ocean is produced and utilised by eukaryotes, that organisms such as protists would synthesise their own source of luciferin rather than obtain it through their diets. However even protozoa such as several radiolarian species are not only capable of bioluminescence but obtain coelenterazine through their diet [1]. For example, bioluminescence has been found in several species of *Thalassicolla* and *Sphaerozoum* [29]. As protists they may appear to be unable to possess semi-intrinsic luminescence, however

these species are heterotrophic, and capable of consuming and digesting larger prey including zooplanktonic copepods [76]. As to the function of luminescence in these organisms it remains poorly understood, although given their dietary acquisition of luciferin, light emission may assist in prey attraction and capture [1].

3.2.4 Chaetognatha

Other smaller marine organisms are able to acquire luminescence through predation, such as at least two species of chaetognaths. This phylum comprises of small, elongated worms that are between 2 and 120 mm in length [77]. Commonly known as "arrow worms" at least two species have been shown to be luminescent and can be found at depths greater than 700 m in marine systems ranging from tropical to polar regions [78]. Luminescence in all of these species is emitted as a blue cloud of light and may facilitate a role in stunning their prey to assist with their hunting strategies giving the lack of visible light that will attenuate down to these depths. Despite being from evolutionarily distinct lineages within the chaetognaths, luminescent species such as *Caecosagitta macrocephala* [79] and *Eukrohnia fowleri*, have a relatively uncommon trait among chaetognaths, in that they have an orange-pigmented gut lining [80]. Digestive systems in semi-transparent organisms that are orange in colour, have the capacity to mask any luminescence produced by ingested prey [78].

This provides strong evidence that some species will predate on luminescent organisms such as copepods in order to provide a dietary source of coelenterazine for their luminescent reaction as shown in a number of other marine organisms [12, 48]. Once absorbed, coelenterazine would be able to be passed through to their luminescent organs that harbour the light reaction, which tend to be found on the lateral and dorsal fins as well as along the sides of the body of these species [78].

3.2.5 Ophiuroidea

Most species that exhibit semi-intrinsic bioluminescence acquire their luciferin via predation, most notably on luminescent copepods or on their predators. However, it is also feasible that filter feeders will be able to acquire coelenterazine and other luciferins through their diet. One such example is seen in the ophiuroids or brittle stars where many species have been shown to emit light [81, 82]. One such example is the brittle star *A. filiformis*, whose bioluminescence has been studied from a biochemical perspective for the past decade. This species feeds on suspended organic matter by extending its arms into the water column [83, 84]. Each of its arms are covered with light-emitting cells called photocytes that have been shown to be dependent on coelenterazine as a source of luciferin [81, 84, 85]. Additionally, the enzyme involved in its luminescent reaction was shown to be homologous to *Renilla* luciferase, which is a coelenterate also thought to acquire its luciferin from its diet [81, 86].

A recent study monitored *A. filiformis* kept in an aquarium for several months whilst controlling its diet [82]. Over five months a depletion in *A. filiformis'* luminescence was observed when fed a coelenterazine-free diet, strongly suggesting it acquired components for luminescence through filter feeding [82]. This was validated as there was a quick recovery in its luminescent capabilities once the brittle star was fed coelenterazine supplemented food. This animal signifies that semi-intrinsic luminescent systems are not simply found among tertiary consumers. This also supports the notion that numerous other filter and detrital feeding organisms that exhibit luminescence, acquire their substrates via their diet.

3.2.6 Tunicata

While it has not fully been confirmed yet, it is possible a large number of other filter feeding marine organism can acquire luminescent components from their diet. Within the chordates the subphylum Tunicata, comprises of a number of species shown to produce luminescence, although compared with other luminescent organisms these remain poorly studied. Within the tunicates, luminescence is well represented among the appendicularians with several species being confirmed to produce luminescence. One such example within this group is the larvacean *O. dioica*, which is a free-swimming tunicate that dwells in the photic zone of the ocean [87]. The animal has transparent body and a tadpole-like appearance throughout its life cycle, ranging in size from 0.5 to 1 mm. Light emission occurs as blue flashes of light from its body that can be induced by mechanical stimulation [88]. This animal has also been reported to emit light in the presence of coelenterazine, so it is possible that these are able to acquire coelenterazine from exogenous sources [87]. Larvaceans like *O. dioica* can secrete their luminescence as a mucus that will capture and collect particulate organic matter whilst the animals are filter feeding [89]. These secretions form luminescent "houses" or clusters of organic matter which can harbour all of the components for the bioluminescent reaction. On mechanical stimulation, these "houses" emit blue light showing that the components luminescence are all present in a way such that coelenterazine does not undergo autooxidation. This display of luminescence supports coelenterazine being utilised by this and other filter feeders for semi-intrinsic luminescence as stable luciferins can potentially be found in particulate organic matter that these organisms can feed on [87, 88, 90].

Another example of luminescence in tunicates is found in pyrosomes which are pelagic tunicates known for their sustained bright blue luminescence as well as their capacity to form sporadic and yet massive blooms such as those observed in this region [91]. There is currently a lack of consensus on the origin of luminescence in this species. A recent study has shown that light emission occurs in the presence of coelenterazine for the species *Pyrosoma atlanticum* [92]. Moreover, using transcriptomic analysis, an enzymatic sequence was identified as being similar to the luciferase found in the Cnidarian *Renilla reniformis* that uses coelenterazine as its light emitter. Subsequent expression of this gene showed that light emission occurred in the presence of coelenterazine strongly supporting that this is the luciferase involved in pyrosome bioluminescence [92]. Coelenterates and some echinoderms have been shown to utilise luciferases with a similar structure to *Renilla*, and a number of these are thought to acquire coelenterazine through their diets. Therefore, it is entirely feasible that pyrosomes such as this species attain coelenterazine through filter feeding, which may also occur for various other luminescent tunicates. However, it should also be noted that recent studies have identified and characterised potentially luminescent bacterial symbionts within *P. atlanticum* [93] which supports several previous studies on this system. Determining how this organism obtains its luminescence will rely on further confirmation what the source of light emission is in this tunicate.

3.2.7 Mollusca

Like previously mentioned phyla, some luminescent molluscs are able to acquire coelenterazine through their diet. This includes the clam *Pholas dactylus*, as well as several species of squid that have been shown to possess coelenterazine in their livers [94]. However, these animals do not use coelenterazine directly as their source of luciferin for bioluminescence. Instead, they use modified forms of this substrate, for example the firefly squid utilises a disulphate form of coelenterazine
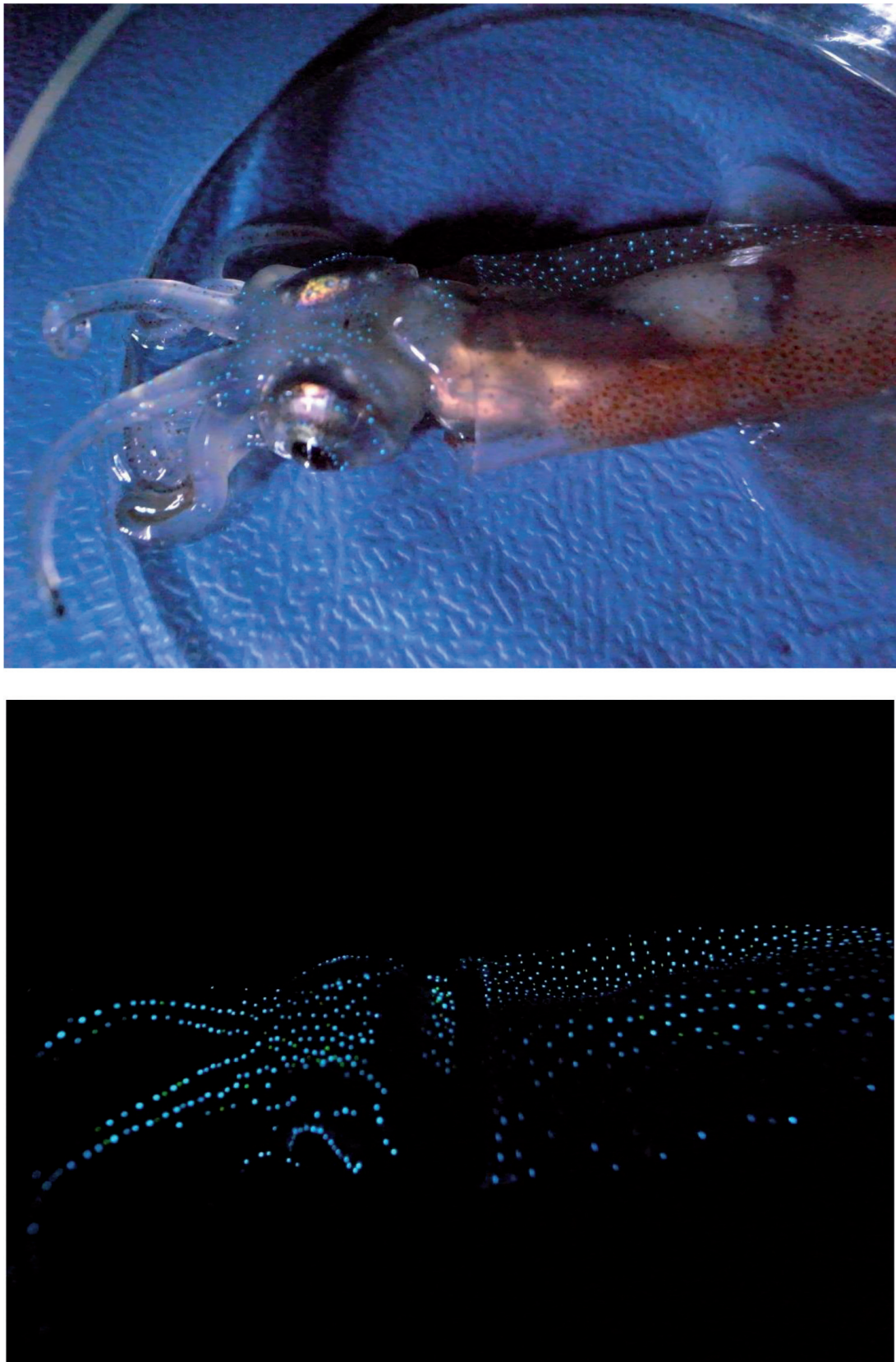
Figure 3.
Photograph of Watasenia scintillans *taken under natural light (upper) and in a dark room (lower) showing the luminescent photophores along its body. Photographs taken by Yuichi Oba.*

in its luminescent reaction [95]. These produce a dim continuous blue biolumi-
nescence from ventral photophores, as well as a bright blue flash of luminescence
(470 nm) from light organs on its arm tips after being mechanically stimulated
[96]. The flashing ability may be used as a means of intra-specific communication
and recognition although this has not yet been defined. The enzymatic oxidation of

coelenterazine disulphate [luciferin] in the presence of Mg^{2+} has led to emissions of blue light, however how or why obtained coelenterazine is modified remains undetermined [95, 97].

Another derivative found in several molluscs is dehydrocoelenterazine. This is an oxidised form of coelenterazine and was identified as the luciferin required in the luminescence of the clam *P. dactylus*, the purple back flying squid *Sthenoteuthis oualaniensis* and recently the Humboldt squid *Dosidicus gigas* [98]. In *D. gigas*, a blue bioluminescent light is emitted from an array of photophores on their body [39]. These structures are small, ovoid rice-like granules that are embedded in the muscle all over the squid on the mantle, fins, head, arms and tentacles [99]. It is entirely possible that this and other squids can obtain coelenterazine from lanternfishes which they are known to predate on. This coelenterazine may undergo an enzymatic oxidation to form dehydrocoelenterazine which is then utilised in its light emission (**Figure 3**).

3.3 Non imidazopyrazinone substrates

All examples of semi-intrinsic luminescence so far have involved either coelenterazine or cypridinid luciferin as the substrate. Dinoflagellate luciferin has also been shown be required by several heterotrophic organisms that appear to not be able to synthesise this luciferin. Dinoflagellates are unicellular organisms that account for the majority of bioluminescence observed in the surface ocean [100, 101]. The compounds involved with luminescence are regulated on a diurnal circadian rhythm, along with photosynthetic components. This means that dinoflagellates conduct primary production during the day and only produce bioluminescence at night, when this would be most effective. The structure of this luciferin was originally determined from *Pyrocystis lunula*. The compound is a linear tetrapyrrole which is very sensitive to non-enzymatic oxidation and is most likely to have derived from chlorophyll [102]. Within different species of dinoflagellates there is variation in the intensity and duration of light emission but in general light is emitted from organelles known as scintillons [101].

Dinoflagellate luciferin shows no similarities to other luciferins and is found in forms, one within dinoflagellates and another with two hydroxyl moieties in euphausiids (krill). This similarity suggests that there is some form of dietary link [102, 103]. Studies have shown luminescent euphausiids occurred in high densities which coincided with large populations of dinoflagellates during late spring [104]. Additionally, heterotrophic species of dinoflagellate, such as *Noctiluca scintillans* have been shown to feed on luminescent dinoflagellates such as *P. lunula*. When their diet was controlled in the lab to exclude luminescent dinoflagellates and all other phytoplankton, they were shown to lose their capacity to emit light [101]. Moreover, when fed other non-dinoflagellate phytoplankton, luminescence was maintained, suggesting that *N. scintillans* can synthesise the tetrapyrrole luciferin from chlorophyll [105]. These examples suggest other luciferins and their precursors may be taken up in the diets and utilised by consumers that already express the required luciferases for other non-imidazopyrazinone luciferins.

4. "Kleptoprotein" luminescence

A general consensus among semi-intrinsic luminescent systems is that the components of the light emission utilised by other organisms are the substrates rather than enzymes. As most of these animals acquire luminescence through their diets, any exogenous components would need to be able to withstand digestion and

potentially transport through the blood plasma to the luminogenic organs. Given this it seems unlikely that the enzymatic component of luminescence would be able to be obtained in this manner, as they would likely be denatured and completely broken-down during digestion [13].

However, a recent study on the *Parapriacanthus* fish, has shown that it is able to obtain both its luciferin and luciferase from its prey. Like midshipman fish, *Parapriacanthus ransonneti* predates on ostracods, which provide a source of cypridinid luciferin that is used in its light emission [13]. When *P. ransonneti* was fed on the ostracod *Cypridina noctiluca,* the luciferase identified from its light organs was identical to the luciferase of this species. When a different species of luminescent ostracod, *Vargula hilgendorfii* was identified in another individual fish, the identified luciferase was now the same as this ostracod, demonstrating the ability to specifically uptake luciferases from its diet to the fish's light organs [13]. Transcriptomic analysis of *P. ransonneti*, showed no transcripts corresponding to an ostracod-type luciferase, further highlighting that this was acquired via the diet (**Figure 4**).

This is the first reporting of this type of phenomenon in bioluminescence, and up until now it was assumed that any consumed luciferase enzyme would be broken down into amino acids or oligopeptides before being absorbed via the gut wall as nutrients [13]. However, the possibility of protein uptake without being fully broken down and retaining activity has been reported in several vertebrate immune systems. An example of this is seen in M cells within the mammalian intestinal epithelia as these have an important role in the immune system by transporting macromolecules and microbes into the cell via pinocytosis [106]. Similar examples of this have been observed in cyprinid fishes so it is feasible these or similar structures could facilitate the transfer of ostracod luciferase to the photophores of this animal [13].

This example of a "kleptoprotein" form of luminescence where both the substrate and the enzyme are provided through the diet, provides an additional novel category of luminescent reactions, as of yet not considered. Moreover, this highlights the possibility that other luminescent species may utilise this capability to obtain active exogenous luciferase from their gut. Potentially, this may include several species of fishes that predate on ostracods, whose light organs are often connected to their digestive tracts. This research may suggest that semi-intrinsic and "kleptoprotein" luminescent behaviours may be more widespread than previously considered, with proteins associated with other biological processes potentially being able to be attained via diet as opposed to gene expression.

Figure 4.
Ventral view of Parapriacanthus ransonneti *taken in a dark room to capture the light emission from these body regions. Photos by Okinawa Commemorative National Government Park (Ocean Expo Park), Okinawa Churaumi Aquarium.*

5. Why semi-intrinsic luminescence occurs?

Semi-intrinsic luminescence has been shown to exist in a number of organisms and is hypothesised to exist in several others. Cypridinid luciferin and dinoflagellate luciferin have been shown to be taken up by predators of ostracods and dinoflagellates respectively, notably several species of fishes, and euphausiid shrimp. However, the majority of semi-intrinsic luminescence, in addition to the majority of bioluminescence in the oceans involves using coelenterazine. Dietary uptake of coelenterazine has been shown in coelenterates, echinoderms, and decapod shrimp, while it is also strongly supported to be the source of luciferin in myctophid and stomiid fishes, chaetognaths, tunicates and several species of squid. Moreover, coelenterazine can be modified via oxidation or di-sulfonation, once it is taken up by species, allowing for a variety of different light reaction mechanisms to occur with this molecule. It is important to understand why some animals use semi-intrinsic luminescence, and the potential evolutionary origins of this, and how coelenterazine may spread across the food web and be the most common light emission system in the oceans. It is useful to consider whether this phenomenon along with "kleptoprotein" luminescence is a lot more widespread in other biological processes and systems.

There are two main groups of hypotheses on why bioluminescence evolved originally; one based around changes in the luciferin (substrate-centric hypothesis) [5, 107] and another that suggests changes occurred in what became the luciferase enzyme (enzyme-centric hypothesis) [108]. The first hypothesis suggests that the luciferin substrate evolved in order to protect organisms from reactive oxidative species (*e.g.*, hydrogen peroxide) in the water column [108]. Luminescent animal migrated to deeper water to evade visual predators and at these depths there was no longer significant oxidative stress. Therefore, the active selection pressure switched to the luminescent, communicative properties of luciferins, leading to more specific adaptations to predation, survival, and communication [1].

The alternate hypothesis focuses on the enzyme luciferase and that these molecules were originally less specific oxygenase enzymes [108]. The oxygenase enzymes mutated as a result of animals migrating to deeper waters to either evade visual predators, or to predate on organisms that have migrated to deeper water [5]. The mutation in oxygenase enzymes associated with display functions would result in external luminescence being exhibited [109]. These display pigments would previously have been associated with warning colourations or patterns to both recognise species and attract potential mates. There is evidence for enzyme-based hypotheses in terms of enhancement of visual signals [5]. However, there is no biochemical or genetic evidence that would support this hypothesis, and the mutation of the luciferase enzyme alone would not explain the convergent evolution of the bioluminescent reaction in multiple phyla [1, 5].

Whether one or a combination of both hypotheses are more viable for the origins of luminescence, both allow for the possible co-evolution of predators and prey that may utilise the same source of luminescence. Convergent evolution caused by environmental factors may have allowed for the presence of various enzymes that were compatible with the same substrate resulting in coelenterazine being utilised by both animals that can synthesise it as well as their predators. Moreover, given the energetic costs associated with synthesising luciferins, it may simply be more efficient for some of these organisms to acquire exogenous sources instead.

Semi-intrinsic luminescent organisms, particularly those that harbour coelenterazine, have shown the potential spread and dispersal across the food web for not just luciferins, but other molecules that may be involved in biological processes. A major source of coelenterazine is found in the copepod *M. pacifica* which is grazed

upon by a variety of organisms including coelenterates, lanternfishes, euphausiids, and radiolarians. Additionally, these animals, particularly lanternfishes are predated upon by tertiary consumers such as squid, stomiid fishes and luminescent sharks [110]. The consumption of copepods by zooplankton and higher taxa can lead to particulate organic matter or marine snow forming and descending to the depths of the ocean. These aggregates will contain detritus, plankton and larvacean houses, meaning that it is highly likely for free-available coelenterazine to be present. The coelenterazine within this particulate organic matter can then be taken up by filter feeders such as echinoderms and tunicates, allowing for them to utilise coelenterazine in their luminescent displays.

In a number of these organisms, luciferin has been identified in a sulfonated form. The most notable example of this is in the firefly squid, however sulfonated luciferins have been identified in *V. hilgendorfii* and *Renilla reniformis* [3]. This form is more stable than free forms of coelenterazine, and it is possible this is a stored form of luciferin that may prevent auto-oxidation that can occur. This more stable form may prevent breakdown and oxidation of the substrate when it is in the water column or during digestion. Potentially, a lot of these semi-intrinsic luminescent organisms will obtain their luciferins in this form, and then have the capability to de-sulfonate the luciferin to make it available for luminescence.

6. Conclusions

Luminescence has evolved and been prevalent in a wide variety of marine species being utilised for a number of predative, defensive and communicative functions. Some organisms have developed predator–prey relationships where the predator is able to acquire and utilise luciferin with its own luciferase to emit light. This chapter has reviewed many of the species that exhibit this type of behaviour and utilise semi-intrinsic luminescence, in addition to describing the sources of luciferin in these systems and how this molecule is able to be taken up by consumers. Although this has only been experimentally tested in a few species, it is highly likely that a number of other luminescent organisms utilise this, especially as it is a lot easier from an evolutionary perspective to obtain luciferins from the diet, compared with synthesising them from amino acids or other unknown biosynthetic pathways. This phenomenon raises the question of whether small molecules and enzymes involved in other biological processes are able to be taken up in this manner as well which could provide an evolutionary selection process that is an alternative to molecular evolution.

Notes/thanks/other declarations

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