Chapter 5
Bioluminescence and Pigments

José Paitio and Yuichi Oba

Abstract Bioluminescence is present in organisms across the tree of life and inhabiting diverse environments on the planet. Light emissions are used for specific communication purposes such as camouflage, attracting preys, and mating. The light produced in a chemical reaction is often modulated by pigmented tissues in the light organs. Although the chemical compounds vary, pigments can be categorized according to functions of light shields, control of light intensity, and spectral modification. In this chapter, we discuss the diversity of pigments present in different tissues of the light organs and their role in the alteration of the light emitted from bioluminescent organisms.

Keywords Bioluminescence · Pigment · Communication · Photophore · Reflection · Fluorescence

5.1 Introduction

Diurnal animals manipulate sunlight and utilize pigments to display colorful patterns in visual communication, e.g., butterflies and tropical fishes. Animals that live in dark environments have to produce their own light to present such displays. Bioluminescence is the production of light by organisms through an oxidative chemical reaction, which generally consists of three players: a substrate, "luciferin"; an enzyme, "luciferase"; and a cofactor, oxygen (Shimomura 2006). Chemical structures of the luciferins have been determined from various marine and terrestrial luminous organisms (Fig. 5.1); however, the structures of several luciferins remain a mystery in some invertebrates, teleosts, and sharks.

Photocytes are cells responsible for light production (Morin 1983; Thompson and Rees 1995; Haddock et al. 2010). Simple bioluminescent structures consist of solely

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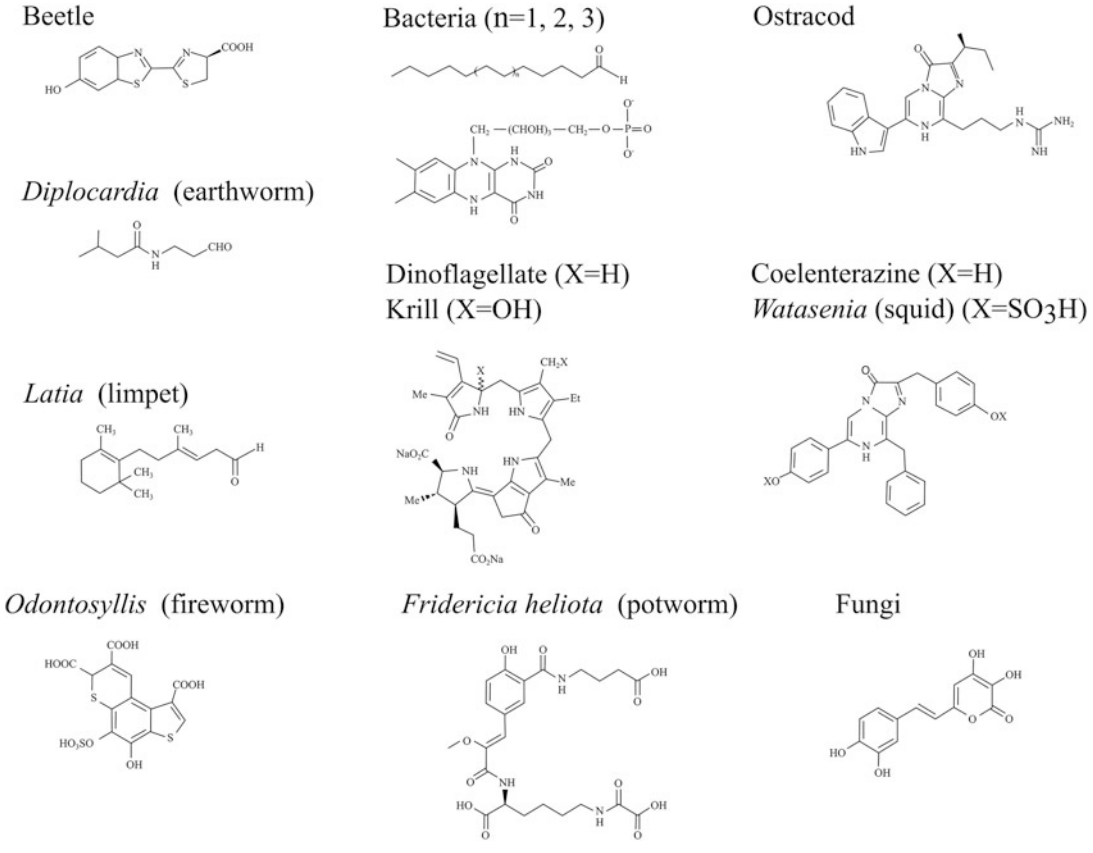

Fig. 5.1 Examples of luciferins from diverse taxa of terrestrial and marine animals and their respective molecular structures

these cells, such as in ctenophores (Harvey 1952), cnidarians (Harvey 1952; Morin 1974; Morin and Reynolds 1974), scale worms (Harvey 1952; Bassot 1966b), springtails (Sano et al. 2019), amphipods (Herring 1981a), and brittle stars (Deheyn et al. 2000); however, other animals utilize complex organs (Morin 1983; Kotlobay et al. 2019; Tsarkova et al. 2016). The structures of these organs are greatly diverse among various taxa; however, they exhibit certain common characteristics: photocytes in a matrix, which is covered by an inner reflector and a pigment layer, and an outer lens (Clarke 1963; Denton et al. 1985). The reflector ensures minimal loss of the light produced via redirecting photons to outside of the organ, while the pigmented layer prevents the light from penetrating into the tissues surrounding the organ. Some species possess colored reflectors, filters, or lenses to adjust the spectra of light emission. Because the terminology used for lenses and filters varies among authors (Haneda 1949, 1951, 1966; Bassot 1966a; Lawry 1973; Denton et al. 1985; Cavallaro et al. 2004), we adopted the following definitions for lenses and filters (Haneda 1949, 1951, 1952): Filters are internal tissues with light-absorbing pigments for spectral selection, while lenses are outer tissues that perform the primary dioptric function (Denton et al. 1970; Lawry 1973), i.e., refract light on a ventral angle. Bioluminescent organs are called light organs or photophores (Morin 1983; Thompson and Rees 1995; Haddock et al. 2010). Light organs are symbiotic and open to outside, while photophores, including photocytes, are closed organs, except in blackchin fishes of the genus *Neoscopelus* for unknown reasons (Herring and Morin 1978; Karplus 2014; Paitio et al. 2016).

Most luminous organisms produce their own light—intrinsic bioluminescence; however, some squids and fishes maintain cultures of glowing bacteria in their light organs—symbiotic bioluminescence (Morin 1983; Karplus 2014). These symbionts can be either facultative or obligatory; however, the biotic relationship provides them nutrition and growing conditions in exchange for light emission. Rare exceptions are certain anglerfishes of the *Centrophryne* and *Linophryne* genera that, in addition to the symbiotic escal light, possess intrinsic luminous barbels (Karplus 2014).

Luminous organisms are spread throughout the web of life from bacterial unicellular life forms to vertebrates (Fig. 5.2). The apparently random dispersion of light-emitting taxa has been debated for decades. It is difficult to determine the number of times that bioluminescence has evolved independently since its rise likely 400 million years ago; however, estimations indicate that this number is most likely more than 50 times (Haddock et al. 2010). This estimation is even more challenging in the case of hosts of symbiotic bacteria, such as squids or fishes, considering the evolution of the hosts and the symbionts.

Our planet is inhabited by light-emitting organisms either living in terrestrial or aquatic habitats. Several luminescent species live on land in the most diverse habitats, such as the flying fireflies, fungus, snails, and millipedes on the vegetation and soil and the earthworms below the soil. In freshwater, apart from the firefly larval forms and certain brackish water bacteria, the only bioluminescent species known so far is the limpet *Latia* (Harvey 1956). In contrast to freshwater, seawater exhibits the highest number of bioluminescent species, which inhabit the seas from shallow

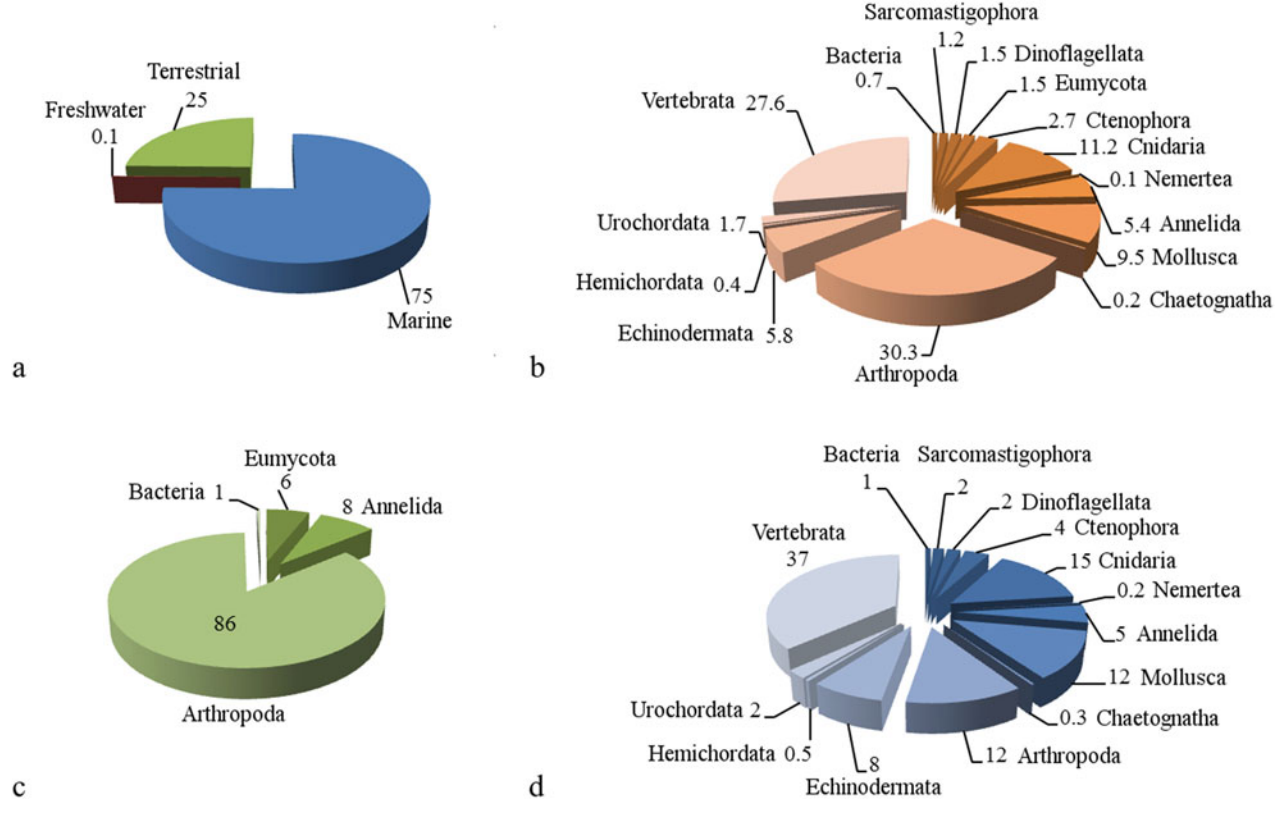

Fig. 5.2 Biodiversity of bioluminescent genera in diverse habitats (%). (**a**) according to habitat; (**b**) globally; (**c**) among terrestrial organisms, per phyla; (**d**) and among marine organisms, per phyla. Adapted from Oba (2019), Haddock et al. (2010), Oba and Schultz (2014), and Paitio et al. (2016)

coasts to deep-sea floors. Approximately 80% of bioluminescent organisms are estimated to be marine species (Shimomura 2006; Widder 2010), living in the upper 1000 m depth (Widder 2001). Some researchers (Young 1983) claim that the mesopelagic zone (200–1000 m depths) is the primary domain of bioluminescence in the planet, in terms of species diversity and abundance. Additionally, the most complex bioluminescence systems exist at these depths (Young 1983). The high richness of bioluminescent creatures is derived from the light parameters of this environment (Young 1983; Widder 2001). This region, which is also known as twilight zone, contains no visual obstacles, and only low-intensity light penetrates it, allowing luminous signals to be easily seen at large distances (Young 1983; Widder 2001). Most light is absorbed by the shallow waters, and only a narrow wavelength of blue-green light reaches the mesopelagic zone (Warrant and Locket 2004; Johnsen 2014) in a highly directional manner at a vertical angle (Widder 2001; Warrant and Locket 2004; Johnsen 2014), which explains the development of bioluminescent camouflage in several species in this zone (Widder 2001; Johnsen 2014).

Bioluminescence is primarily an ecological "tool" for interspecific communication. The primordial purpose of bioluminescence is believed to be defense against predators (Morin 1983). The ecological roles of light emission are highly diverse, as well as multifunctional in some animals that exhibit different light signals (Haddock et al. 2010) and/or different light organs or photophores (Young 1983). The ecological functions of bioluminescence can be classified as interspecific functions, for attracting prey and protecting against predators; intraspecific functions, for reproduction or recognition; and functions for illumination of the surroundings (Table 5.1).

5.2 Pigments in Bioluminescent Tissues

Light organs and photophores are similar with respect to their function, irrespective of their organic differences, as indicated by the similarity in the basic structure of the light organ in animals from different phyla. Convergent evolution of tissues has clearly provided a vast variety of light organs and photophores that work in astonishingly similar manners. This is only possible through the organization of tissues with the same functions, despite the difference in the organic composition of these tissues. In contrast, luminous structures are dependent on their functions and the complexity of the organism (Fig. 5.3). Single-cell life forms such as bacteria and dinoflagellates possess specific organelles as light-emitting structures (Morin 1983). Animals, which represent most luminous organisms, have developed photogenic tissues in complex light organs and photophores (Morin 1983). This complexity is characterized by organs containing differentiated tissues for specific functions. Some

Table 5.1 Ecological functions of bioluminescence among diverse luminous organisms (Morin 1983; Haddock et al. 2010; Dunlap and Urbanczyk 2013; Oba and Schultz 2014; Paitio et al. 2016)

Ecological role			Taxonomic group
Interspecific	Defense	Aposematism	Fungi, Cnidaria, Arthropoda, Annelida, Echinodermata,[a] Chordata
		Illumination	Chordata
		Camouflage	Arthropoda, Mollusca, Chordata
		Startle	Dinoflagellata, Arthropoda, Annelida, Mollusca, Chordata
		Smokescreen	Ctenophora, Cnidaria, Arthropoda, Annelida, Mollusca, Chaetognatha, Chordata
		Distraction	Cnidaria, Annelida, Mollusca, Echinodermata
		Burglar alarm	Dinoflagellata, Cnidaria
		Decoy	Cnidaria, Arthropoda, Annelida, Mollusca, Echinodermata
	Offense	Attraction (hosts and feeders)	Proteobacteria
		Attraction (prey)	Fungi,[a] Cnidaria, Arthropoda, Mollusca, Chordata
		Stun	Mollusca, Chordata
		Illumination (prey)	Chordata
Intraspecific		Recognition	Arthropoda, Annelida, Mollusca, Chordata
		Mating	Arthropoda, Mollusca, Chordata
		Schooling	Chordata
Illumination of surroundings			Chordata

[a]Uncertain

tissues are responsible for the modulation of the primordial light produced in the photocytes, namely the pigmented layer, reflector,[1] and filter.

For this purpose, several chemical compounds are used (Table 5.2), such as melanin for light shielding (Nicol 1957, 1964; Karplus 2014), guanine for reflection (Bassot 1966a; Best and Bone 1976; Karplus 2014), and carotenoids for spectral absorption (Herring 1972; Herring and Locket 1978; Denton et al. 1985), beyond taxonomical groups (Fig. 5.4). Pigments limited by function and animal taxon are observed as well, e.g., uric acid in the reflectors of fireflies (Goh et al. 2013), porphyrins in the filters of fishes (Denton et al. 1985), and lumazine in a blue-luminescent strain of bacteria (Koka and Lee 1979; Visser and Lee 1980; Vervoort et al. 1982).

[1]According to Bagnara (1966), Bagnara and Hadley (1974), and Kelsh (2004), pigmentation in animals is achieved by all chromatophore types, including melanophores and iridophores. Additionally, the same authors state that iridophores are pigment reflective cells. On the basis of these descriptions, we include reflectors with iridophores as pigmented tissues.

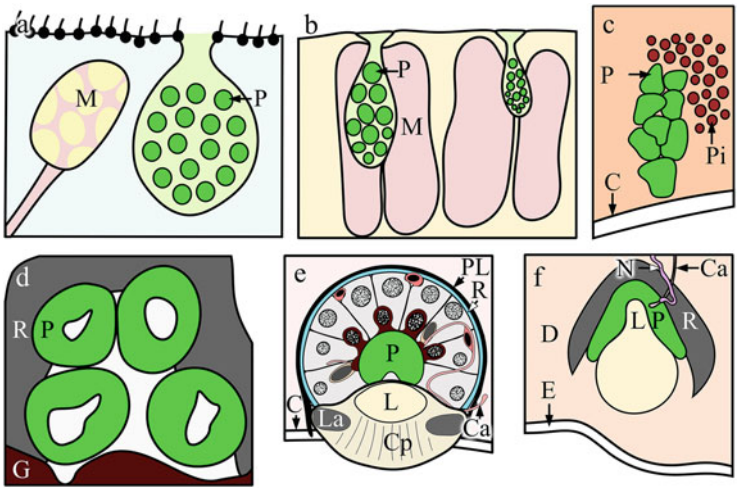

Fig. 5.3 Schematic illustrations of the diversity of bioluminescent structures. (**a**) Cnidaria *Pelagia*. (**b**) Tubeworm *Chaetopterus.* (**c**) Amphipod *Parapronoe.* (**d**) Larvae of fungus gnat *Arachnocampa.* (**e**) General Euphausiidae. (**f**) Midshipman fish *Porichthys*. *M* mucous cell, *P* photocyte, *Pi* pigment cells, *C* cuticle, *R* reflector, *G* gut, *PL* pigment layer, *L* lens, *La* laminar ring; *Cp* cap, *Ca* capilar, *N* nerve, *D* dermis, *E* epidermis. Adapted from Dahlgren (1916), Harvey (1952), Nicol (1957), Herring and Locket (1978), Herring (1981a), and Rigby and Merritt (2011)

5.2.1 Light Shields

Bioluminescence is undoubtedly an ecological advantage; however, without the right structure, light organs and photophores can become a disadvantage for the user. A light signal has the potential to attract preys and predators as well; thereby, if an organism glows constantly it is putting itself in danger. Thus, it is not surprising that the light organs and photophores of amphipods, mysids, euphausiids, decapods, cephalopods, and certain fishes are internally covered by a pigmented layer that acts as a "light wall" (Haneda 1952; Nicol 1964; Herring and Locket 1978; Herring and Morin 1978; Herring 1981c). This layer is primarily composed of chromatophores that absorb the produced light that is not emitted outside the organ; thus, it prevents the light from reaching the inner body tissues and exposing the animal. The amphipods *Parapronoe*, *Megalanceola*, *Chevreuxiella*, and *Dannaela* have been reported to possess photocytes covered with brownish pigment (Herring 1981a). Secretory bioluminescence of the mysid *Gnathophausia* is attributed to pigmented photophores on the maxilla (Herring 1985; Meland and Aas 2013). The pigmentation coating the light organs and photophores is usually black or dark-brown and composed of melanophores, such as in fishes (Fig. 5.5) (Nicol 1957; Denton et al. 1985; Karplus 2014) and squids (Nicol 1964). The outer pigment layer in the photophores of certain squids can be reddish-brown, such as in *Pterygioteuthis* (Arnold et al. 1974), *Pyroteuthis* (Butcher et al. 1982), and *Histioteuthis* (Dilly and Herring 1981). Euphausiids possess photophores that are covered with

Table 5.2 Pigments in light organs, classified according to function, chemistry, and organisms

Functions	Pigment group	Taxonomic group
Light shield	Melanin	Mollusca (Nicol 1964) Chordata (Nicol 1957; Denton et al. 1985; Karplus 2014)
	Astaxanthin	Arthropoda (Euphausiacea) (Herring and Locket 1978), (Decapoda)[a] (Dennell 1955; Herring 1981b)
Reflection	Uric acid	Arthropoda (Coleoptera) (Buck 1948; Goh et al. 2013)
	Lipid[a]	Arthropoda (Decapoda) (Herring 1981b)
	"Proteinaceous"	Mollusca (Arnold et al. 1974; Herring 2000)
	Collagen	Mollusca (Herring 2000)
	Guanine	Mollusca (Denton et al. 1985; Herring 2000), Chordata (Bassot 1966a; Denton et al. 1985; Karplus 2014)
Spectra	Lipochrome[a]	Arthropoda (Decapoda) (Kemp 1910b, Dennell 1955)
	Carotenoprotein[a]	Arthropoda (Euphausiacea) (Herring and Locket 1978), (Decapoda) (Herring 1972; Denton et al. 1985)
	Protoporphyrin[a]	Mollusca (Dilly and Herring 1981; Denton et al. 1985)
	Porphyrin[a]	Chordata (Stomiidae; *Malacosteus*, *Chaulodius*, *Stomias*) (Denton et al. 1985)
	Cytochrome *c*[a]	Chordata (Sternoptychidae, *Argyropelecus*) (Denton et al. 1985)
	Dicarboxylic porphyrin	Chordata (Sternoptychidae, *Valenciennellus*) (Denton et al. 1985)
Fluorescence	FMN	Proteobacteria (Daubner et al. 1987; Macheroux et al. 1987)
	6,7-Dimethyl-8-(1-D-ribityl)lumazine	Proteobacteria (Koka and Lee 1979; Visser and Lee 1980; Vervoort et al. 1982)
	Porphyrin[a]	Cnidaria (Haddock et al. 2005)
	7,8-Dihydropterin-6-carboxylic acid	Arthropoda (Kuse et al. 2001)
	Riboflavin	Annelida (*Odontosyllis*) (Deheyn et al. 2013; Branchini et al. 2014; Rawat and Deheyn 2016)
	Phycobiliprotein[a]	Chordata (Stomiidae) (Campbell and Herring 1987)

[a]Uncertain

chromatophores containing astaxanthin (Fig. 5.6a, b) (Herring and Locket 1978). As this pigment is present in many decapods (Herring 1972), the red carotenoid pigmented outer layer observed on the photophores (Fig. 5.6d, e, g) (Nowel et al. 1998) is possibly astaxanthin as well (Dennell 1955; Herring 1981b). In a previous report, although it is not stated by the author, the description of the photophores of the fungus gnat *Orfelia* as "black bodies" might indicate cover pigmentation (Fulton 1941). In cnidarians, neither chromatophores nor reflectors have been reported to be associated with photocytes (Harvey 1952; Morin 1974; Morin and Reynolds 1974).

Intrinsic bioluminescence is under neural or hormonal control, and it cannot be achieved in symbiotic luminous animals because of the impossibility of directly regulating the constant light produced by the bacterial symbionts (Nicol 1959). To control the intensity of the light emitted by the bacteria cultures, hosts have

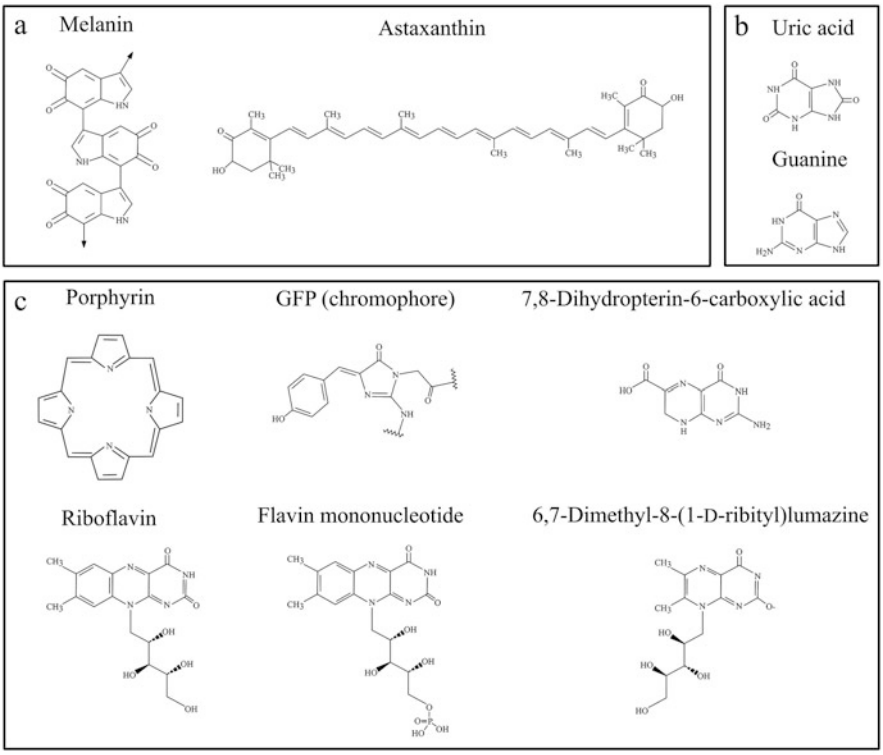

Fig. 5.4 Examples of pigments present on bioluminescent organs, with their respective molecular structures, by function: (**a**) light shields; (**b**) reflection; (**c**) colored filters and fluorescence. Arrows indicate the position where the polymer continues. Adapted from Koka and Lee (1979), Delgado-Vargas et al. (2000), Kuse et al. (2001), Lubczak et al. (2002), Nuevo et al. (2009), Schweitzer-Stenner (2014), and Shinoda et al. (2018)

developed accessory structures for light organs—pigmented shutters. These structures are similar to Venetian blinds, which are used for controlling the sunlight illuminating living rooms; however, they act on outgoing light instead of incoming light. Similar to blinds and curtains, the shutters for light organs occur as diverse structures to achieve the same purpose.

Squids can control emissions from symbiotic light organs via tissues densely pigmented with melanophores, shutters, and ink sacs. In certain species, colored chromatophores on the skin absorb visible light ranging from purple to green and may act as screens for spectral selection to the underlying photophores (Nicol 1959). Chromatophores present on the organs can act as movable screens in *Spirula*, *Vampyroteuthis* (Schmidt 1922; Pickford 1949), and *Histioteuthis* (Dilly and Herring 1981). Additionally, researchers have observed that light output is controlled via contraction and expansion of the brown chromatophores covering the photophores in *Watasenia* (Fig. 5.7) (Berry 1920) and that of purple red chromatophores in *Bathothauma* (Dilly and Herring 1974). In *Uroteuthis*, the rectum is flanked by

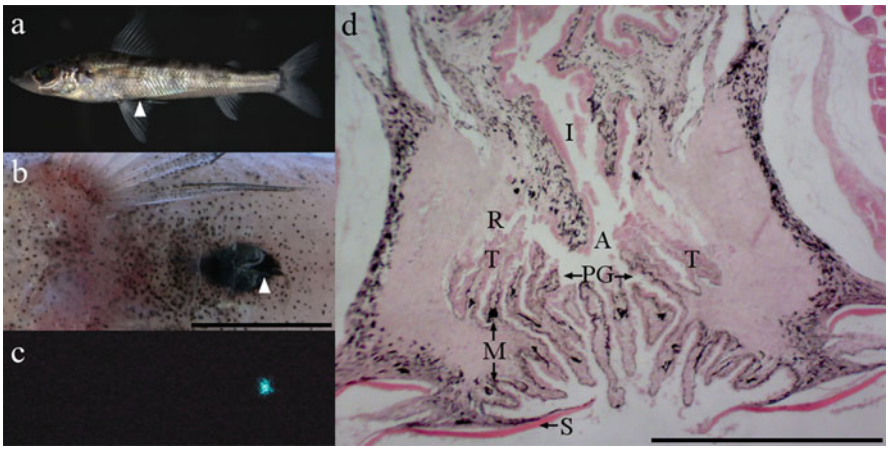

Fig. 5.5 Melanophores on the circumanal light organ of the green-eye fish *Chlorophthalmus*. (**a**) Lateral view of the full body of the fish. (**b**) Ventral view of the light organ under white light. (**c**) Ventral view of bioluminescence from the light organ in the dark. Arrowheads indicate the position of the light organ. (**d**) Histological section of the light organ. *I* intestine, *R* reflector, *A* anus, *PG* perianal groove, *T* tubules with luminous bacteria, *M* melanophore layers, *S* scale. Scale bars: (**b**) 1 cm; (**d**) 500 μm. Photography: whole fish, courtesy of Hiromitsu Endo; the light organ and bioluminescence, by Yuichi Oba; histological section, by José Paitio

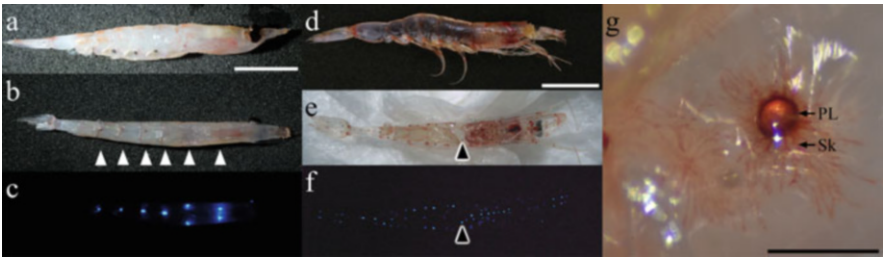

Fig. 5.6 Red chromatophores on photophores of the euphausiid *Euphausia* and decapod *Lucensosergia*. (**a**) Lateral and (**b**) ventral views of the full body of *Euphausia* under white light and (**c**) ventral view of bioluminescent light emissions in the dark. (**d**) Lateral and (**e**) ventral views of the full body of *Lucensosergia* under white light, (**f**) ventral view of bioluminescent light emissions in the dark, and (**g**) close view of red-pigmented chromatophore layers on the skin and around the photophore. *PL* chromatophores in photophores pigment layer. *Sk* Chromatophores in skin. White arrowheads indicate the position of photophores in *Euphausia*. Black arrowheads indicate the position of the photophore of (**g**) on *Lucensosergia.* Scale bars: (**a**–**f**) 1 cm; (**g**) 500 μm. Photography by Yuichi Oba and José Paitio

two light organs, which are covered by a black membrane that acts as a diaphragm and regulates the light emission enabling the light to fade away (Haneda 1963). Pigmented muscular flaps can rapidly block the photophores of *Leachia* (Young 1975). The bobtail squid *Euprymna* is a special case; it controls light emissions through movements of the ink sac and reflector (McFall-Ngai and Montgomery 1990).

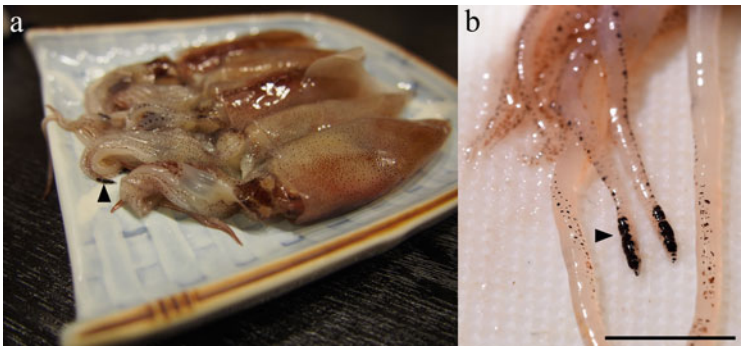

Fig. 5.7 Arm-tip photophores on the squid *Watasenia.* (**a**) Full body showing darkened area on arm-tip. (**b**) High concentration of chromatophores on arm-tip photophores. Arrowheads indicate the photophore position. Scale bar = 1 cm. Photography by Yuichi Oba

Although several squids possess photophores positioned near the ink sac, till date, control over the light emission by this organ has been proven only in the bobtail squid.

Symbiotic luminous fishes with internal luminescence share the feature of melanophores in the skin surrounding light organs, which leads to the theory that these fishes regulate light output through aggregation and dispersion of melanocytes on the outer tissue layer. Chromatophores on the skin of non-luminous fishes are under neural, paracrine, and hormonal control (Fujii 2000; Sköld et al. 2016). A similar mechanism is assumed to be utilized in luminous organs even though all existing reports are based on observations and suppositions. Regulation of light emission via chromatophores, on the skin or internally surrounding the light organs or photophores, have been proposed for the families Acropomatidae (Fig. 5.8), Pempheridae, Trachichthyidae, Macrouridae (Fig. 5.9), Apogonidae, Leiognathidae, Monocentridae, Chlorophthalmidae, Evermannellidae, Merluciidae, and Moridae, (Haneda 1949, 1951; Haneda and Johnson 1962; Cohen 1964; Herring 1977; Herring and Morin 1978; Tebo et al. 1979; Somiya 1981; McFall-Ngai and Dunlap 1983). Chromatophore patterns around the light organ in *Lumiconger* (Congridae) is similar to that in Gadiformes (Castle and Paxton 1984); although the function is not clearly stated, it should achieve a similar purpose. In Opisthoproctidae species, the chromatophores are located on the ventral–lateral body scales in a species-specific pattern, and they may be additionally used for intraspecific recognition (Bertelsen 1958; Poulsen et al. 2016).

Accessory structures are common on light organs, and shutters in symbiotic bioluminescent fishes are no exception. In contrast to the chromatophores in the skin that are adapted to a specific function, shutters must have developed because of the necessity to control bioluminescent emissions. Evolution facilitated the development of these structures, allowing a faster and precise regulation of light emissions and possibly introducing time-lapse signals for communication. Thus, shutters opened the doors to the eco-ethological roles of luminescence in fishes. Besides camouflage, owing to the versatility of light signals using shutters, new roles and multipurpose luminescence may have been introduced at that time for intra- and interspecific communication. It is difficult not to provide such a hypothesis,

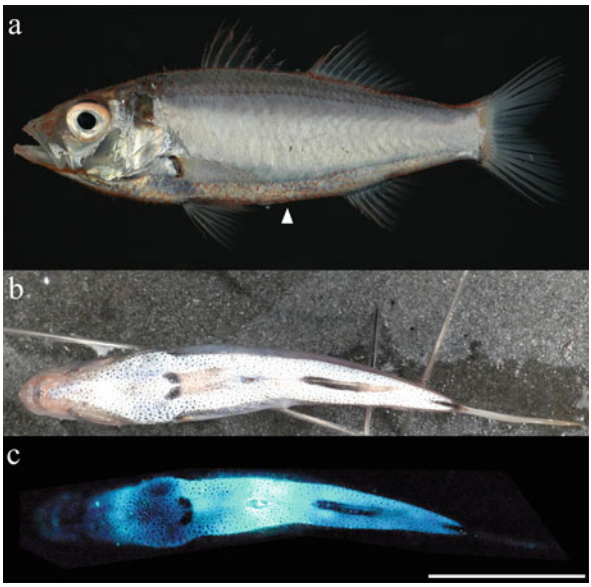

Fig. 5.8 Internal bioluminescence in *Acropoma*. (**a**) Lateral view of fish, chromatophores visible on ventral skin (arrowhead). (**b**) Ventral view exhibiting chromatophore pattern on all luminous areas, under white light. (**c**) Ventral view of bioluminescent emission in the dark. Scale bar = 1 cm. Photography: lateral view, courtesy of Hiromitsu Endo; others, by Yuichi Oba

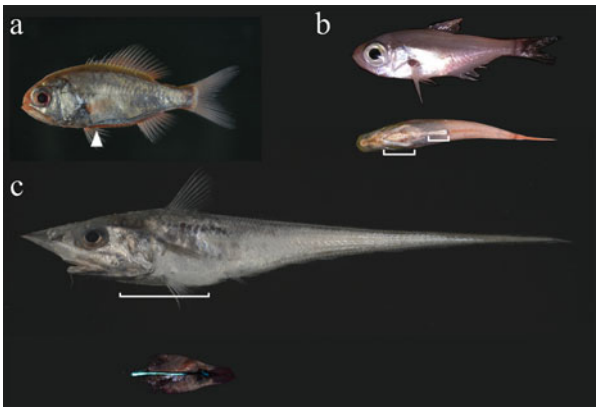

Fig. 5.9 Light organs in roughy (Trachichthyidae), sweeper (Pempheridae), and grenadier (Macrouridae) fishes. (**a**) Lateral view of the roughy *Aulotrachichthys*. (**b**) Lateral view of the sweeper *Parapriacanthus* under white light (upper) and bioluminescence in the dark (lower). (**c**) Lateral view of the grenadier *Coelorinchus* under white light (upper) and bioluminescence in the dark (lower). White arrowheads or bracket lines indicate the position and extension of the bioluminescent organs. Photography: *Aulotrachichthys*, courtesy of Hiromitsu Endo; *Parapriacanthus*, courtesy of Manabu Bessho-Uehara; *Coelorinchus*, by Yuichi Oba

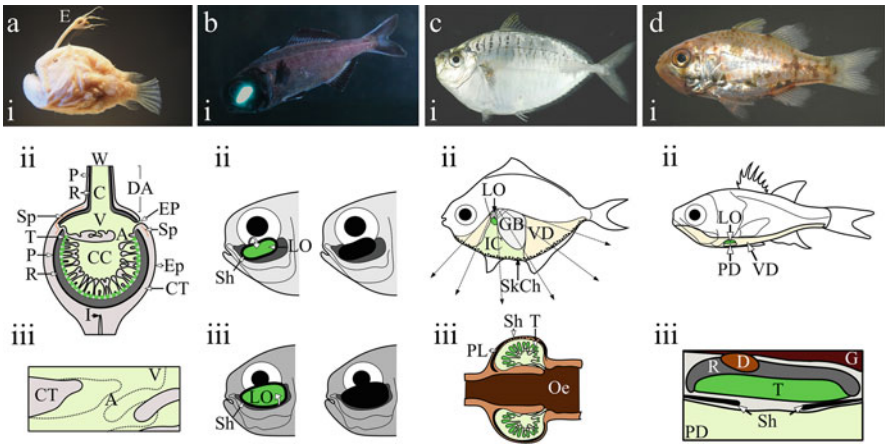

Fig. 5.10 Shutters on symbiotic bioluminescent organs of fishes. (**a**) The anglerfish *Himantolophus* (i), diagrams of generic structure of esca (ii), and shutter mechanism (iii). (**b**) The flashlight fish *Anomalops* (i), scheme of shutter mechanisms in *Anomalops* (ii), and *Photoblepharon* (iii). (**c**) The ponyfish *Secutor* (i), illustrations of the bioluminescence system (ii), and light organ (iii) of *Gazza*. (**d**) The cardinalfish *Siphamia* (i), schematics of the light emission system (ii), and light organ (iii). *E* esca, *P* pigment layer, *R* reflector, *Sp* sphincter, *T* tubules with luminous bacteria, *W* window, *C* light guide core, *V* vestibule, *A* central escal aperture, *CC* central escal cavity, *I* illicium, *DA* distal appendage, *EP* escal pore, *Ep* epiderm, *LO* light organ, *Sh* shutter, *GB* gas bladder, *VD* ventral diffuser (transparent muscle), *SkCh* skin chromatophores, *Oe* esophagus, *PD* primary diffuser, *D* duct (link light organ to gut), *G* gut. Dashed line on Aiii represents aperture under contraction by the sphincter. Dashed arrows on Cii indicates the direction of light emission. Photography: *Himantolophus*, by Yuichi Oba; *Anomalops*, courtesy of Takehito Miyatake; *Secutor* and *Siphamia*, courtesy of Hiromitsu Endo. Schemes adapted from Haneda (1949), McCosker (1977), Munk (1999), Sparks et al. (2005), and Dunlap and Nakamura (2011)

considering the best known cases of ponyfishes and flashlight fishes. Besides these two families of shallow-water fishes, only deep-sea anglerfishes present shutters on their light organs. The structures of the light organs are slightly different among these fishes primarily because anglerfishes are deep-sea creatures, and between the shallow-water fish groups, ponyfishes exhibit internal luminescence, while flashlight fishes exhibit external light organs (Karplus 2014). Despite their differences, all three groups of fishes use shutters in the same manner: smooth muscles control a dark-pigmented tissue to cover or uncover the emission window of the light organ (Karplus 2014).

Anglerfishes are one of the strangest creatures in the world, and their luminous species share the characteristic of the light organ—the esca—that looks like a fishing rod (Fig. 5.10a), generally hanging from their heads (Munk 1999). The luminous structures are species-specific, and their emissions illuminate the dark deep-sea and act as torches to attract preys. On the frontal top, the light organs possess an aperture for light emission, which can be completely shut through contracting a sphincter-like muscle that works similar to a curtain (Herring and Munk 1994; Munk 1998, 1999). In addition to the shutter, oxygen depletion on the light organ has also been proposed

to regulate light flashes; however, this theory remains to be confirmed (Karplus 2014).

Flashlight fishes appear as "blinking schools" on moonless nights around shallow coral reefs (Fig. 5.10b) (Morin et al. 1975). These small animals use light emissions to avoid predators, attract and search for preys, illuminate the surroundings, schooling, and mating. Distinct structures, shutter mechanism, and even bacterial species differentiate the two defined types of sub-ocular large light organs for *Anomalops* and *Photoblepharon* (McCosker 1977; Hendry et al. 2016). The ancestral light organ had been smaller and shut off by a primitive system of rotation, which was derived first and refined by *Anomalops* to fully rotate downwards into a pouch (Rosenblatt and Johnson 1991). Later, the primitive rotatable small organ developed a shutter-like structure that upwardly encloses the light organ, similar to an eyelid (Johnson et al. 1988; Baldwin et al. 1997). The evolutionary stages from the ancient archetype light organ to the light organ in *Photoblepharon* are represented in the genera *Protoblepharon*, *Parmops*, *Phthanophaneron*, and *Kryptophanaron*, in the order of evolution. Finally, at the edge of this family phylogenetic tree is *Photoblepharon*, which completely lost the ancestral rotation character and sophisticated the eyelid membrane. Presently, flashlight fishes are possibly the best living case study on bioluminescence evolution in shallow-water fishes.

Ponyfishes are possibly the zenith of multifunctional bioluminescence systems among fishes (Fig. 5.10c). The meticulous regulation of light signals involves the skin, shutters, and swim bladder; all these tissues and the light organ itself possess chromatophores for light intensity control (Herring and Morin 1978; Sparks et al. 2005). The circumesophageal light organ exhibits translucent windows covered by muscular shutters that are filled with melanophores, which together with the skin chromatophores regulate bioluminescent signals (Herring and Morin 1978; McFall-Ngai and Dunlap 1983). The light organ morphology and pattern of melanophores is species-specific and even sexually dimorphic, which appears to correlate with variations in bioluminescent behavior (McFall-Ngai and Dunlap 1984). The light organ in *Gazza* and *Leiognathus* are heavily covered with chromatophores, which allow a gradual control of light intensity compared to that in other species (McFall-Ngai and Morin 1991). The luminous tissue and overlap shutter are restricted to the dorsal area of the esophagus; however, some species possess two additional lateroventral bacterial pouches and independent shutters (McFall-Ngai and Dunlap 1983; Sparks et al. 2005) *Photoplagios* has a non-identified dark-blue pigmented patch along the median lateral area of the body that may regulate and absorb the blue-green luminescence to prevent lateral light emissions when necessary (Sparks et al. 2005).

In addition to ponyfishes, flashlight fishes, and anglerfishes, another example of fishes with shutters is Apogonidae, which is one of the most puzzling and astonishing cases of evolution in bioluminescent fishes; in this family, some genera are symbiotic, while others produce their own light (Thacker and Roje 2009). The symbiotic genus *Siphamia* possess an eyelid shutter covering the ventral face of the internal light organ (Fig. 5.10d) (Dunlap and Nakamura 2011). The tissue consists of two halves intercepting on the midline of the anterior–posterior axis of

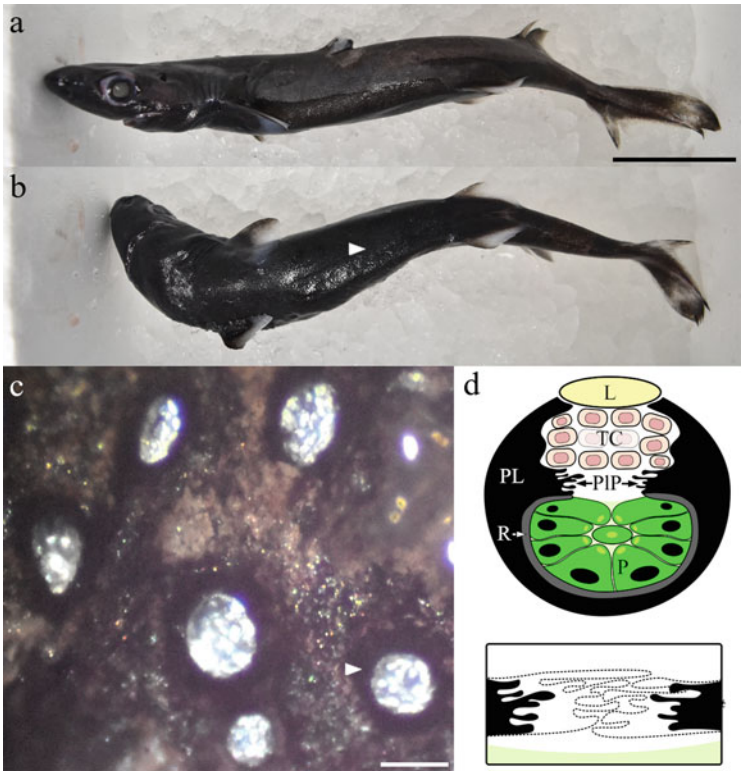

Fig. 5.11 Photophores on the lanternshark *Etmopterus.* (**a**) Lateral view of full body. (**b**) Ventral view of full body presenting the photophore patterns (arrowhead indicates photophores area of **c**). (**c**) Photophores surrounded by a pigmented layer (arrowhead). (**d**) Schemes representing photophore structure (upper) and "pseudopodia-like" projections when the iris-like ring is opened (filled) or closed (dashed outline). *L* lens, *TC* transition cells, *PL* pigment layer, *PlP* "parapodia-like" projections, *R* reflector, *P* photocyte. Scale bars: (**a**) 5 cm; (**c**) 100 μm. Photography by José Paitio. Schemes adapted from Claes and Mallefet (2010) and Renwart et al. (2014)

the body of the fish. Mediated by adrenalin neuromuscular control, both halves of the shutter retract or contract laterally to expose or cover the light emission from the symbiotic bacteria.

Luminous sharks developed a specific mechanism to control the light intensity (Fig. 5.11). The photocytes of Etmopteridae are surrounded by a dark iris-like ring tissue in which lie chromatophores with "pseudopodia-like projections" (Ohshima 1911). The pigmented projections spread across the organ, covering the luminous tissue below. Under hormonal control, the iris-like structure uncovers the photocytes through contraction of the chromatophore projections, enhancing the light output (Claes and Mallefet 2010). Additionally, two types of cell layers between the photocytes and the lens have been suggested to be involved in the light control; however, this theory has not been confirmed till date (Renwart et al. 2014).

The role of melanin for light regulation involves diverse structures spread throughout a wide variety of fishes, either in terms of habitats or phylogeny. In the authors' opinion, this can be an example of evolutionary convergence, which illustrate per se not only the crucial importance of bioluminescence signal regulation for the survival and reproductive success of fishes but also the evolutionary pressure.

5.2.2 Colored Filters

Mesopelagic animals use ventral light emissions to match the blue-green spectra, intensity, and angle of the downwelling sunlight (Clarke 1963). Body silhouette of the camouflaged organism is concealed from the eyes of the predators lying below. This bioluminescence camouflage is called counterillumination and used by euphausiids, decapods, cephalopods, and fishes (Herring 1983; Haddock et al. 2010). The spectra of light produced in the photogenic tissues do not perfectly match the downwelling sunlight (under 250 m depth, approximately 475 nm); therefore, filters and reflectors are used to optimize camouflage (Denton et al. 1985).

Marine invertebrates possess light organs and photophores with colored filters. The photophores of the euphausiids *Nematobrachion*, *Thysanopoda*, and *Euphausia* contain purple-blue pigmentation on the chitin overlying the photophores or in its center, which has been characterized as carotenoproteins (Kemp 1910b; Herring and Locket 1978). Decapods include different photophores, the organs of Pesta of sergestiids and general dermal photophores (Kemp 1910b; Dennell 1955). Filters on both types present violet to blue color (Kemp 1910a; Herring 1972, 1981b; Nowel et al. 1998) The deep-violet-blue pigment in *Systellaspis* is likely to be a lipochrome (Kemp 1910b; Dennell 1955), while those in *Sergestes*[2] and *Oplophorus* appear to be a carotenoprotein (Denton et al. 1985). The blue filters in *Sergestes* have been reported to cut out long wavelengths to match the downwelling sunlight (Denton et al. 1985). The filters appear to fulfill the same purpose in *Oplophorus* and *Systellaspis*, as the light spectra of the photophores differ with respect to the excreted fluid (Herring 1983; Latz et al. 1988). *Histioteuthis* is the only reported cephalopod to have developed pigmented purple-reddish filters, which appear to be protoporphyrins (Dilly and Herring 1981). The absence of filters on the arm-tip photophores (Dilly and Herring 1981) might be explained by their role other than counterillumination (Denton et al. 1985).

Deep-sea fishes commonly use pigmented filters to alter the spectra of emitted light. Researchers have demonstrated the achievement of camouflage through filters in the photophores of these fishes; removing the filters broadens the spectra of

[2]The analyzed specimens of *Sergestes* (Herring 1981b; Denton et al. 1985) were identified up to the genus taxon. Since this publication in 1985, according to the genera alteration of *Sergestes* species (Vereshchaka et al. 2014), the species cited as *Sergestes* (Herring 1981b; Denton et al. 1985) may now belong to a different genus.

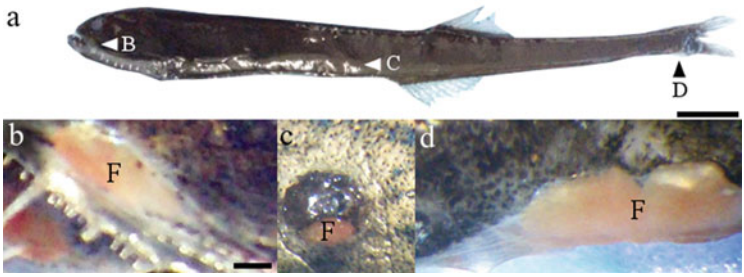

Fig. 5.12 Red-pigmented filter in photophores of the bristlemouth fish *Sigmops*. (**a**) Full body. (**b**) Sub-ocular photophore. (**c**) Ventral–lateral body photophore. (**d**) Caudal photophore. *F* pigmented filter. Arrowheads indicate the photophores in photographs **b–d**. Scale bars: (**a**) 1 cm; (**b–d**) 1 mm. Photography by José Paitio

emitted light (Widder et al. 1983; Denton et al. 1985). Pigmented orange-red filters (Fig. 5.12, pers. obs.) on *Sigmops* may be used for spectral alteration (Copeland 1991). Green filters have been reported in the photophores of the lightfish *Photichthys* (Haneda 1952). Red filters have been observed in other lightfishes, *Polymetme* (Fig. 5.13a), *Yarrella*, and *Ichthyococcus* (Haneda 1952, 1985; Herring 1981c; Denton et al. 1985), and the bristlemouths *Vinciguerria*, *Margrethia*, and *Bonapartia* (Denton et al. 1985; Haneda 1985). Reddish-purple filters have been observed in the hatchetfishes *Maurolicus* (Fig. 5.13b), *Sternoptyx*, *Argyropelecus*, and *Polyipnus*, and red filters in *Valenciennellus* (Haneda 1952, 1985; Herring 1981c; Denton et al. 1985). Red filters in the lightfishes *Ichthyococcus* and *Polymetme* and the hatchetfish *Valencienellus* have been reported to be similar to porphyrins (Herring 1981c; Denton et al. 1985). The reddish-purple pigment on the hatchetfish *Argyropelecus* appears to be similar to cytochrome *c* (Denton et al. 1985), which contains a covalently bound heme group (Schweitzer-Stenner 2014). All fishes in the family Stomiidae exhibit lilac-red-pigmented ventral photophores and lilac, blue, or yellow barbels (Herring 1981c; Denton et al. 1985; Haneda 1985). *Chauliodus* and *Stomias* dragonfishes possess lilac filters in body photophores that appear similar to porphyrin (Herring 1981c; Denton et al. 1985). As adult stomiids live in the bathypelagic zone, where light does not penetrate, counterillumination would have no significance; therefore, it has been suggested (Herring 1981c; Denton et al. 1985) that the pigmentation in the photophores has remained since juvenile forms migrated from the surface, where the larvae used counterillumination to avoid predators. The stomiid fishes *Pachystomias*, *Malacosteus*, and *Aristostomias* possess red-light-emitting sub-ocular photophores. In contrast to most deep-sea animals, the red-light-emitting dragonfishes *Aristostomias*, *Malacosteus*, and *Pachystomias* are visually sensitive to red, which indicates the possibility that this "private bandwidth" is used for intraspecific communication and illumination of preys (Widder et al. 1984; Denton et al. 1985). The dark-red suborbital photophores in *Malacosteus* emit far-red light with a red-brown filter that absorbs all wavelengths below 650 nm; they appear to contain a porphyrin pigment (Widder et al. 1984; Denton et al. 1985).

Fig. 5.13 Ventral view of pigmented filters in ventral–lateral photophores in lightfish, hatchetfish, and blackchin fish. (**a**) Red-pigmented filters of the lightfish *Polymetme*. (**b**) Purple filters on the photophores of the hatchetfish *Maurolicus* under white light (upper) and bioluminescent emission in the dark (lower). (**b**) Orange-pigmented filters in the photophores of the blackchin *Neoscopelus*. Scale bars = 1 cm. Photography by Yuichi Oba

Light absorption by filters appears to be lacking in red photophores in other genera of dragonfishes (Denton et al. 1985; Campbell and Herring 1987; Herring and Cope 2005). The slickhead fishes *Xenodermychthys* and *Photostylus* possess small photophores with reddish-violet filters, which can be used to match ambient light (Best and Bone 1976). Orange-colored filters have been reported in another slickhead fish, *Bathytroctes* (Haneda 1952); these filters may be used for counterillumination as proposed for other species of Alepocephalidae. Blackchin *Neoscopelus* (Fig. 5.13c) possess photophores with internal filters exhibiting faint orange coloration (Kuwabara 1953), similar to the filters in Stomiiformes species.

Filters are present in symbiotic luminous fishes as well. The barreleyes *Opisthoproctus* possesses a violet filter between the luminous bacteria and the ventral sole, which ensures that the bandwidth of all light produced is narrowed (Denton et al. 1985). The pinecone fish *Cleidopus* (Fig. 5.14) possesses a pigmented filter on the bacterial light organ that alters the spectra of light produced by the

Fig. 5.14 School of the pinecone fish *Monocentris*. Arrowhead indicates the position of the lower-lip light organ. Photography by Yuichi Oba

symbionts to longer wavelengths, i.e., from blue to blue-green color, after the light passes through the orange-reddish filter (Haneda 1966; Widder et al. 1983).

5.2.3 Reflection

Internal reflectors are a widespread characteristic of light organs and photophores; they ensure that the light produced by the photocytes is emitted effectively to the environment (Herring 2000). Additional reflective tissues peripheral to the inner reflector act as light guides, conducting the light through a precise path inside the organ. For reflecting the entire light spectrum produced by the photocytes, the coloration of the reflector is generally silver or white. Specular structural colored reflectors are also used to alter the spectra of the luminous output. An angle-dependent constructive interference is produced by alternating layers of materials with different refractive indexes—high for the reflective substance and low for the cytoplasm, in which the reflective layers are perfectly positioned and spaced, resulting in colored reflectors (Herring 2000).

On firefly photophores, immediately behind the photogenic tissue, one can easily discriminate the thick white reflective layer (Buck 1948). The reflector is composed of uric acid spherulites (Goh et al. 2013), which function as a diffusive mirror (Herring 2000). The presence of a reflective layer is not restricted to the adult phase; it is observed in the firefly larvae as well (Fig. 5.15) (Okada 1935). The reflector is observed on the photophores of another bioluminescent larval form on land; the swollen distal tips of the Malpighian tubules form the light organ of the larvae of the fungus gnat *Arachnocampa*, and the ventral air-filled tracheal layer supplies oxygen and functions as a reflector as well (Green 1979; Rigby and Merritt 2011).

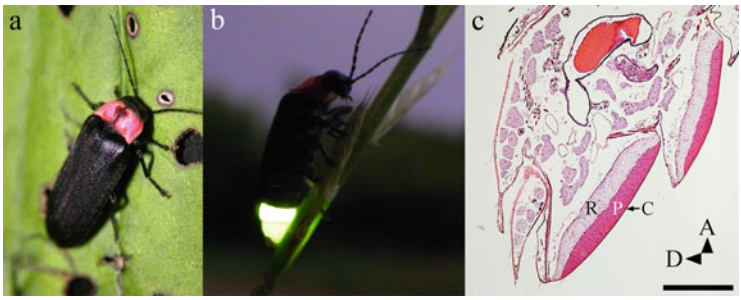

Fig. 5.15 Photophores of the firefly *Luciola*. (**a**) Full body dorsal view under white light. (**b**) Lateral view of full body in twilight, showing light emission from photophores. (**c**) Lateral view of histological section of light organs. *R* reflector, *P* photocytes, *C* cuticle, *A* anterior, *D* dorsal. Scale bar = 500 μm. Photography of full body, by Ken-ichi Onodera and Yuichi Oba; histological section, courtesy of Keisuke Kawano

The mesopelagic zone is a "bioluminescent hotspot," where most luminous organisms on this planet live (Young 1983); therefore, it is not surprising that the light organs and photophores of the organisms in this habitat exhibit high complexity. In mesopelagic crustaceans, the photophores are highly complex and widespread throughout the taxa in euphausiids than in decapods (Kemp 1910b; Yaldwyn 1957). The photophores of some euphausiids exhibit blue-green multilayered reflectors, which act as light interference (Herring and Locket 1978). Colored reflectors have been observed in the body photophores of *Thysanopoda*, *Nematobrachion*, and *Euphausia*, as well in the eye-stalk photophores of *Thysanopoda*. In contrast, *Meganyctiphanes* has a red inner reflector that might enable spectral modification through light interference (Bassot 1966a). In addition to the inner reflectors, euphausiids possess an iridescent lamellar ring on the proximal side of the photophores that narrow the angle of blue light emission and limit lateral emissions of light (Bassot 1966a; Herring and Locket 1978). Although several researchers have observed the structure of colored reflectors in euphausiids, there is no report on the chemical composition.

Granular diffuse reflectors on decapods have been observed in a wide range of species; however, the reflective material remains unknown (Herring 1981b; Nowel et al. 1998). Nevertheless, the reflectors in the organs of Pesta of *Sergestes* appear to be lipidic spheres and non-lipidic in the hepatic organs of *Plesionika*,[3] *Thalassocaris*, and *Chlorotocoides* (Herring 1981b). A crustacean sea-firefly *Vargula hilgendorfii*, known to produce a brilliant secretion of luminous cloud from the upper lip, is a coastal species; however, it possesses reflector structure posterior to the anus. (Abe et al. 2000) suggested that the function might be related to their bioluminescence.

[3] *Parapandalus richardi* in the original reference (Herring 1981b) is accepted as *Plesionika richardi* (WoRMS 2019).

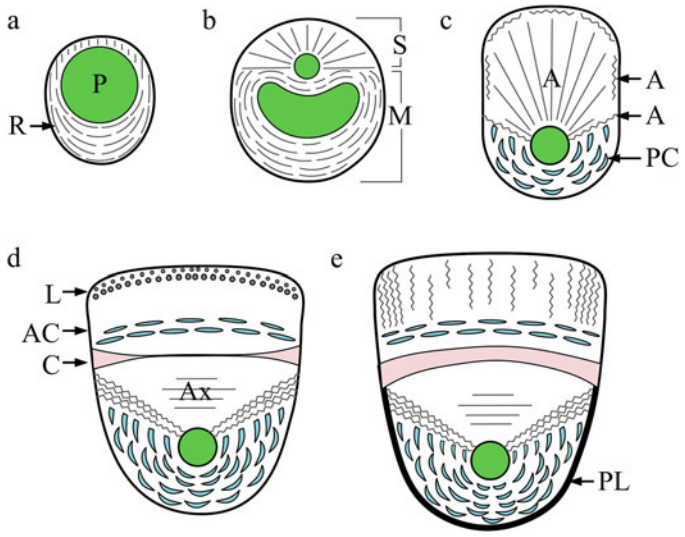

Fig. 5.16 Schematic representation of the variability of the reflective structure of the photophores in the squid *Pyroteuthis*. The silver reflectors are represented in silver and light interference colored reflectors in blue. (**a**) Individual photophores of tentacles. (**b**) Double photophores on tentacles. (**c**) Mantle photophores. (**d**) Ocular photophores. (**e**) Anal photophores. *P* photocytes, *R* reflector; *S* small outer photophore of double photophore, *M* main photophore of double photophore, *A* accessory reflector, *PC* posterior cup, *L* lens, *AC* anterior cap, *C* connective tissue, *Ax* axial reflector, *PL* pigmented layer. Adapted from Butcher et al. (1982)

Reflectors in the light organs and photophores of cephalopods are generally composed of collagen fibers, such as in *Abralia* (Young and Arnold 1982), *Spirula* (Herring et al. 1981), and *Pyroteuthis* (Butcher et al. 1982). Other specific materials can be found, such as the endoplasmic reticulum in *Sepiola* and *Selenoteuthis* (Herring et al. 1981; Herring 2000), the proteinaceous platelets in Sepiolidae and Octopoteuthidae (Dilly and Herring 1981; Herring et al. 1992), and guanine in *Histioteuthis* (Denton et al. 1985). The structure of the photophores and their reflectors vary according to different body parts in Octopoteuthidae (Herring et al. 1992), Sepiolidae (Dilly and Herring 1978, 1981), and Pyroteuthidae (Arnold et al. 1974). The squid *Pyroteuthis* possesses collagenous reflective systems that include photophores along the tentacle and mantle and ocular and anal photophores (Fig. 5.16) (Butcher et al. 1982). The tentacles contain individual and double photophores, the latter consisting of a major elongated organ and an outer smaller one (Butcher et al. 1982). The tentacle and mantle photophores contain green-colored main reflectors and accessory silver reflective tissues as light diffusers (Butcher et al. 1982). The violet to green hue of the ocular and anal photophores of *Pyroteuthis* (Butcher et al. 1982) is imparted by one of the most complex reflective structures in all photophores known to date. The inner reflector—the posterior cup—has a central aperture where lies the axial reflector, covered by another reflective layer—the anterior cap—and the outer lens, which also integrates

reflective fibers (Butcher et al. 1982). While the posterior cup and anterior cap are colored tissues for spectral selection, the axial reflector and lens act as light guides (Butcher et al. 1982).

The direction of light emission is controlled by iridophores, generally for dispersion purposes, acting as diffusers (Herring et al. 1981, 1992, 2002; Herring 2000). The reflector can be used for light collimation (*Pterygioteuthis*) (Arnold et al. 1974). Additionally, the symbiotic photophores attached to the ink sac of *Heteroteuthis* have a blue distal cap with additional lateral collar-like reflectors and a proximal main reflector that may be multifunctional, both for diffusion and interference reflection (Dilly and Herring 1978, 1981).

In addition to the spectral selective function of the reflectors (Arnold et al. 1974; Dilly and Herring 1974, 1981; Butcher et al. 1982; Herring 2000; Herring et al. 2002), some species went one step further, not only matching the bioluminescence color to the ambient light but also controlling the emitted spectra. Spectral manipulation via changing the platelet spacing or muscular contraction has been observed in *Abralia* (Young and Arnold 1982), *Pyroteuthis* (Butcher et al. 1982; Latz et al. 1988), and *Leachia* (Latz et al. 1988). Bioluminescence color variation in *Abraliopsis* and *Abralia* is triggered by the water temperature, corresponding to the light phenomena encountered during vertical migration (Young and Mencher 1980).

The major material in the photophore's reflectors is assumed to be guanine in sharks and teleosts (Bassot 1966a; Herring 2000); however, few studies have confirmed this assumption, similar to that for flashlight fishes (Watson et al. 1978), midshipman (Nicol 1957), and pearlsides (Barraud et al. 1959). However, slickhead fishes appear to be an exception. According to a previous report (Best and Bone 1976), blue-green specular reflectors are not composed of guanine platelets but closely and regularly spaced flattened cells.

Guanine is commonly present in light organs and photophores to guide light emissions for different purposes. The flashlight fish *Anomalops* has a thick internal diffusive guanine reflector lined behind the photocytes and a thin external ventral oblique reflector to enhance the dorsal output and reduce the downward emission (Watson et al. 1978). The internal reflector of the esca of anglerfishes covers the entire core of the bacterial space, except for an aperture where it extends distal from the organ toward the tubular appendages to output the bacterial light through one or multiple windows (Munk 1998, 1999).

Only comparable to that in squids, the complex light guidance systems in luminous fishes ensure adequate light emission angle for camouflage. Simple reflectors lined along the sole tube of barreleyes allow specular reflection of light from the posterior light organ through the entire ventral side of the body (Bertelsen 1958; Poulsen et al. 2016).

The bristlemouth *Sigmops* possesses double glandular photophores with reflectors that are thicker on the ventral-median region but lacking on its lower surface and auxiliary reflectors that concentrate and guide the light to the lens (Copeland 1991). The pearlside fish *Maurolicus* possesses ventral photophores with a specular inner reflector and a lamellar ring composed of flat cells with guanine, which act as light

guides to limit the wide angle of lateral emission (Barraud et al. 1959; Bassot 1966a). A similar inner reflector has been observed in *Yarrella* and *Polyipnus* (Haneda 1952), and (Denton et al. 1969) described the structure and function in the hatchetfish *Argyropelecus*. Each side of the ventral surface contains a tubular photogenic chamber aligned on the anterior–posterior axis of the body (Denton et al. 1969). The chamber is internally covered with guanine crystal, excluding the bottom apertures, where the light is directed to each individual wedge-shaped photophore (Denton et al. 1969). Elongated crystals aligned vertically in each tubular photophore, in a randomly positioned short axis, direct light from the photogenic chamber and spread it anterior–posteriorly (Denton et al. 1969). Additionally, the front surface of each organ is half-silvered, containing broad crystals parallel to its surface with long axes obliquely positioned for higher reflection at an oblique incidence, allowing the ventral angular light emitted to match the downwelling sunlight (Denton et al. 1969).

The body photophores of myctophids are a rare exception among fishes, lacking pigmented filters but incorporating a colored inner reflector (Fig. 5.17) (Denton et al. 1985). The outer portion of the photocytes is covered by a thick silver reflector, which ensures that the light produced by these cells reaches the inner reflector before being emitted to the environment (Lawry 1973). The inner blue-green reflector of *Diaphus*, which is composed of a regular hexagonal arrangement of iridophores, exhibits a mathematically parabolic shape that allows all light to be simultaneously reflected ventrally from the photophore while minimizing light loss (Paitio et al. 2020). This reflective system ensures that light is emitted at the same angle as that of the ambient light below 200 m (Warrant and Locket 2004; Paitio et al. 2020). Each iridophore is composed of stacked guanine crystals that induce colored light interference (Paitio et al. 2020). The light produced from the photocytes is modulated by the reflector to longer wavelengths and directed outside the organ. The reflected light output matches the downwelling light spectra at mesopelagic depths for successful camouflage (Denton et al. 1985; Johnsen 2014; Paitio et al. 2020). The ability of these fishes to regulate color, along with the variation of the reflection spectra (Young 1983), suggests that the iridophores can be modulated by the fishes to adapt a camouflage color during diel migrations (Paitio et al. 2020).

In addition to photophores, accessory reflective tissues have been reported in ponyfishes and sabertooths. Iridophores between the esophagus and the light organ direct light through the light organ windows of ponyfishes, which is reflected by the swimbladder to the outer tissues (Herring 2000). The swimbladder exhibits a species-specific spatial orientation of guanine, allowing different patterns of light to be reflected through the skin patches, which contains guanine as well (Herring 2000). The reflective accessory system of concentric multilayered guanine-like platelets is present exceptionally on the photophores of the isthmus on the sabertooth fish *Coccorella* (Herring 1977). The reflector surrounds all internal organs except for the ventral aperture directing the light to the translucent muscle below, which itself contains additional dorsolateral reflective layers.

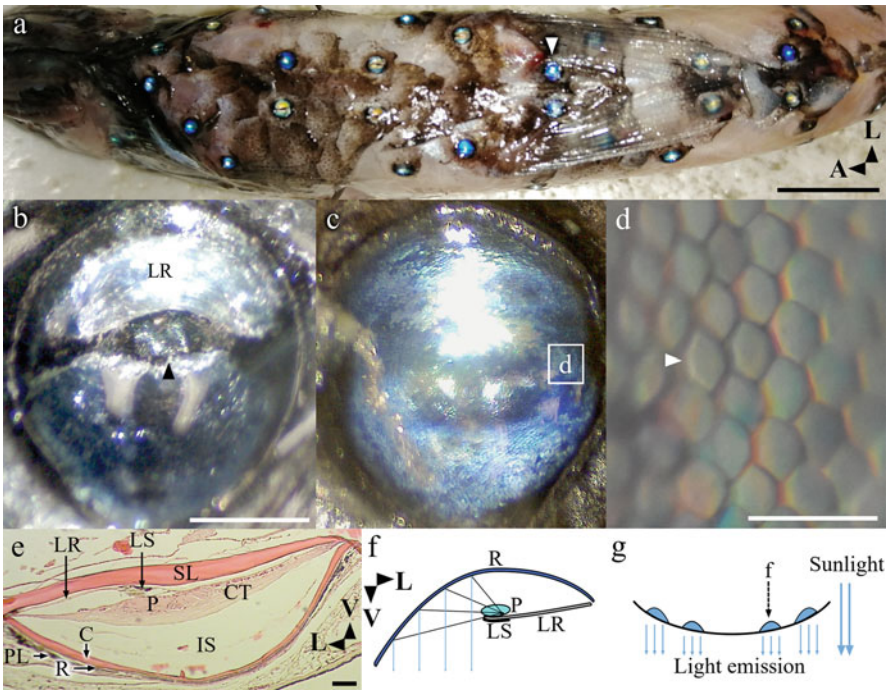

Fig. 5.17 Colored reflector in body photophores of lanternfishes. (**a**) Ventral view of *Diaphus* showing reflection spectra variation in photophores and position of photophore in **b**, **c** (arrowhead). (**b**) Ventral view of photophore. (**c**) Photophore without tissues between photocytes layer and scale lens (outlined white square indicates iridophores area in **d**). (**e**) Regular hexagonal arrangement of iridophores in photophore inner reflector. (**e**) Histological section of photophore. (**f**) Schematic view of light projection of body photophore. (**g**) Position of photophore on **f** (dashed black arrow) on ventral body of the fish and their light emission vertical angle relative to the downwelling sunlight. *L* lateral, *A* anterior, *V* ventral, *LR* lens reflector, *LS* lens septum, *SL* scale lens, *P* photocytes, *CT* connective tissue, *IS* internal space, *C* cup, *PL* pigment layer with melanocytes, *R* inner reflector. (**d**) Iridophore. Scale bars = (**a**) 1 cm, (**b**) 500 μm, (**d**) 50 μm; (**e**) 100 μm. Adapted from Paitio et al. (2020)

5.2.4 Fluorescence

The spectra of light produced by bioluminescent reaction can additionally be altered by the presence of fluorescent proteins. Perhaps the most famous example is the green fluorescent protein (GFP) in a luminous jellyfish, *Aequorea victoria*, (Hastings 1996; Shimomura 2006). Cnidarians commonly emit blue-green light; however, when GFP is present near the photoprotein it gets excited by the energy produced by the bioluminescent reaction and emits green photons. This mechanism is explained as follows: the light energy from aequorin (photoprotein, donor) is transferred to the GFP (fluorescent protein, acceptor) via fluorescence resonance energy transfer (FRET), defined by the closeness (less than 100 Å) and significant

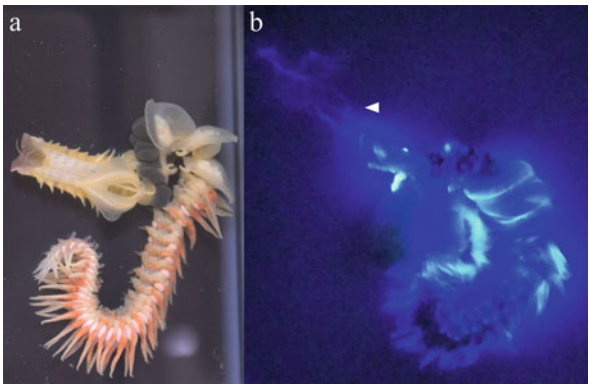

Fig. 5.18 Bioluminescence of the tubeworm *Chaetopterus.* (**a**) Under white light. (**b**) Body bioluminescence and mucus secretion (arrowhead), in the dark. Photographs: courtesy of Ikuhiko Kin

spectral overlap between the donor (emission) and acceptor (excitation) (Morin and Hastings 1971; Shimomura 2006). In contrast to GFP, fluorescent proteins on bioluminescent systems that do not meet the requisitions for FRET are considered as accessory emitters, as described in the following cases.

Millipedes and tubeworms are probably some of the most unknown animals that exhibit bioluminescence. The fluorescent cuticle of the millipede *Motyxia* is close to the bioluminescent spectra (Shimomura 1984; Kuse et al. 2001). The fluorescent spectra and bioluminescence spectra of the luminous slime of the tubeworm *Chaetopterus* (Fig. 5.18) are very similar; riboflavin is proposed as the light emitter in this case (Deheyn et al. 2013; Branchini et al. 2014; Rawat and Deheyn 2016). This observation suggests the involvement of fluorescent compounds in the luminous systems of the millipede and tubeworm; however, this theory has not been confirmed yet.

Luminous bacteria often emit blue-green light from the luciferin–luciferase reaction. The spectra may change because of fluorescent proteins that do not bind themselves to the luciferase molecules (Hastings 1996). Some strains of *Photobacterium* emits bluer light compared to other species of the same genera because of the presence of the fluorescent "lumazine protein," a protein that binds to with 6,7-dimethyl-8-(1-D-ribityl)lumazine, which shifts the emission wavelength and enhances the emission intensity (Koka and Lee 1979; Visser and Lee 1980; Vervoort et al. 1982). *Vibrio* Y-1 strain contains a fluorescent protein with a flavin mononucleotide ligand that is responsible for its yellow bioluminescent glow (Daubner et al. 1987; Macheroux et al. 1987). Although the alteration of the blue hue appears to be related to the sunlight spectrum in the sea where these bacteria live, the reason for the alteration of the yellow color in the bioluminescent spectra is unknown.

Juveniles of the *Erenna* siphonophores exhibit photophores on the tentacles with a photoprotein that emits blue-green light (Haddock et al. 2005). The adults possess an additional pigment that alters the bioluminescence color to red, for attracting prey. The fluorescent material involved in the alteration of the bioluminescence color appears similar to porphyrin-bound proteins.

The dragonfish *Malacosteus*, in addition to the lenticular red-light-absorbing pigment, possesses light-sensitive fluorophores described as phycobiliprotein-like (Campbell and Herring 1987). Similar fluorescent proteins extracted from the red-emitting photophores of the dragonfishes *Aristostomias* and *Pachystomias* suggest the involvement of related chemical compounds (Campbell and Herring 1987).

5.3 Perspectives

This chapter is, as far as the authors are aware, the first description that is focused solely on the diversity and role of pigments for bioluminescence. Although the phylogeny of organisms and chemistry of luminous reaction are quite diverse among bioluminescence organisms across the tree of life, it appears that the pigments and pigmented tissues exhibit a lower level of diversification. Considering the function of photophores and light organs to produce light, photogenic tissues would be the first to be developed, fulfilling the primary role for bioluminescence. Pigmented tissues must have developed later to modulate the light emitted by the photogenic tissues. One may then consider that pigmented tissues evolved secondarily and that they have a secondary function in the light organ, relative to the photogenic tissues. This might be explained by the low diversity of pigments in the light organs and photophores compared to the diversity of molecules involved in bioluminescent reactions. However, one should not discard the lack of clarity on this subject, as only a few reports are available on these pigments and several more studies need to be conducted.

The biological and ecological roles of pigments for bioluminescence are well studied. In contrast, few studies have focused on the chemical composition and microscopic arrangement of the pigments, and almost all available reports provide approximated suggestions. Such studies are needed to understand the physiological operation of the pigmented tissues, not only individually but also with an integrative perspective, because most light organs and photophores possess various pigmented tissues. Only this strategy will enable full comprehension of the role of each pigment in the entire functional light system that is a photophore.

Evolution of pigments and their functional roles remain unknown in bioluminescent animals. Modern technology such as molecular biology analyses should be utilized in the study of pigments on luminous species. The “When? How? Why?” for pigmentation tissues in light organs or photophores could then be answered.

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