



## INVITED REVIEW

# Glowing Worms: Biological, Chemical, and Functional Diversity of Bioluminescent Annelids

Aida Verdes<sup>1,\*,\dagger,\ddagger</sup> and David F. Gruber<sup>1,\*,\dagger</sup>

\*Baruch College and The Graduate Center, PhD Program in Biology, City University of New York, 365 5th Ave, New York, NY 10010, USA; <sup>\dagger</sup>Sackler Institute for Comparative Genomics, American Museum of Natural History, Central Park West at 79th Street, New York, NY 10024-5192, USA; <sup>\ddagger</sup>Departamento de Biología (Zoología), Facultad de Ciencias, Universidad Autónoma de Madrid, C/Darwin 2, Cantoblanco, Madrid, 28049, Spain

<sup>1</sup>E-mail: averdes@gradcenter.cuny.edu; david.gruber@baruch.cuny.edu

**Abstract** Bioluminescence, the ability to produce light by living organisms, has evolved independently in numerous lineages across the tree of life. Luminous forms are found in a wide range of taxonomic groups from bacteria to vertebrates, although the great majority of bioluminescent organisms are marine taxa. Within the phylum Annelida, bioluminescence is widespread, present in at least 98 terrestrial and marine species that represent 45 genera distributed in thirteen lineages of clitellates and polychaetes. The ecological diversity of luminous annelids is unparalleled, with species occupying a great variety of habitats including both terrestrial and marine ecosystems, from coastal waters to the deep-sea, in benthic and pelagic habitats from polar to tropical regions. This great taxonomic and ecological diversity is matched by the wide array of bioluminescent colors—including yellow light, which is very rare among marine taxa—different emission wavelengths even between species of the same genus, and varying patterns, chemical reactions and kinetics. This diversity of bioluminescence colors and patterns suggests that light production in annelids might be involved in a variety of different functions, including defensive mechanisms like sacrificial lures or aposematic signals, and intraspecific communication systems. In this review, we explore the world of luminous annelids, particularly focusing on the current knowledge regarding their taxonomic and ecological diversity and discussing the putative functions and chemistries of their bioluminescent systems.

## Introduction

The phylum Annelida, more commonly known as segmented or bristle worms, is an ancient and ecologically important lineage of Lophotrochozoans, with around 17,000 described species (Struck et al. 2011; Weigert and Bleidorn 2016). Annelids are present in a wide variety of environments ranging from terrestrial and freshwater to marine habitats, including species that are highly specialized to occupy unique ecological niches such as hydrothermal vents or whale falls (Rouse and Pleijel 2001; Struck et al. 2011; Purschke et al. 2014; Weigert and Bleidorn 2016). Subsequent adaptive radiations within Annelida have led to the remarkably high species diversity we see today and have also resulted in an extraordinary variety of body types, life strategies, feeding mechanisms and striking adaptations. One of these adaptations is bioluminescence.

Bioluminescence, the ability to produce light by living organisms, is a biological property that has evolved independently in many lineages across the tree of life (Harvey 1952; Haddock et al. 2010). Bioluminescent light results from a chemical reaction involving the oxidation of a light-emitting molecule—luciferin—by a specific enzyme—luciferase (Shimomura 2012). In some organisms, the luciferin is tightly bound to luciferase and oxygen forming a photoprotein, and light production is triggered when the photoprotein binds to a co-factor (Deheyn and Latz 2009). There are several types of photoproteins based on their chemical identity and the cofactor they require. For example, in coelenterates, ctenophores, and radiolarians, calcium is required to trigger luminescence, whereas the photoproteins of the bivalve *Pholas* and some polychaetes seem to bind to superoxide radicals, and the millipede *Motyxia*

requires ATP and magnesium to produce light (Shimomura 1985).

It is estimated that bioluminescence has originated independently at least 40 times (Haddock et al. 2010), but the evolutionary origins of most systems remain unclear. The strong antioxidative properties of luciferin and its high reactivity with ROS (reactive oxygen species) like superoxides and peroxides (Devillers et al. 1999; Haddock et al. 2010), has led to a prominent evolutionary theory suggesting that bioluminescence first originated as a mechanism for reducing oxidative stress (Rees et al. 1998; Labas et al. 2001). Because exposure to oxidative stress is reduced in the deeper layers of the ocean, a functional shift might have occurred from its antioxidative to its light-emitting function, when marine organisms began to colonize the deep ocean and the selective pressure for antioxidative defense mechanisms was decreased (Rees et al. 1998).

Bioluminescent forms are found in a wide range of taxonomic groups from bacteria to vertebrates, but despite this broad phylogenetic diversity, the great majority of light-producing organisms are marine taxa. More than 80% of the approximately 700 bioluminescent genera known to date are marine organisms (Shimomura 2012, Widder 2010). Bioluminescence is nearly absent in freshwater taxa, with the exception of the limpet *Latia* (Meyer-Rochow and Moore 1988; Ohmiya et al. 2005) and some insect larvae, and it is rare within terrestrial ecosystems. Fireflies are the most prominent group of bioluminescent terrestrial taxa, but there are other examples, such as the gastropod *Dyakia striata* (Isobe et al. 1988; Copeland and Daston 1989), millipedes of the genus *Motyxia* (Marek et al. 2011), and several beetles (Wood 1995; Day et al. 2004), earthworms (Wampler and Jamieson 1979; Rota et al. 2003) and fungi (Weitz 2004; Desjardin et al. 2008; Purtov et al. 2015). However, bioluminescence in terrestrial organisms is dwarfed when compared to marine environments. In the water column, Martini and Haddock (2017) recently reported that 76% of more than 350,000 observed individuals are bioluminescent, with 93% of the identified polychaetes (~9.8% of the total individuals examined) exhibiting bioluminescence.

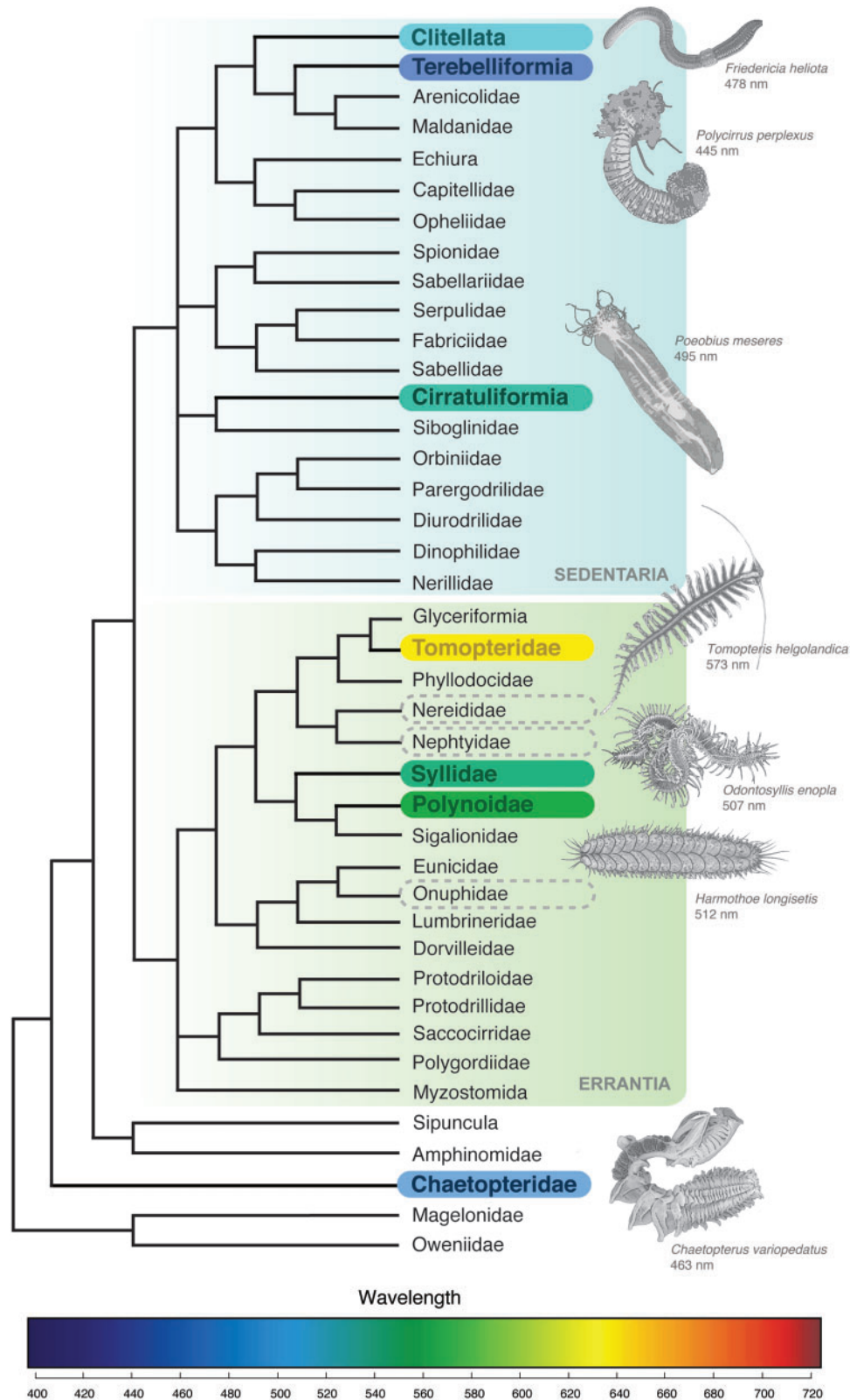
Light production is closely related with different vital functions such as reproduction, feeding, defense, or communication and therefore, the light produced by different luminous organisms has varying wavelengths, intensities and patterns, based on the function associated to light production and the physical properties of the environment they occupy (Morin 1983; Widder 2001; Haddock 2006). For

example, in terrestrial environments bioluminescent light is generally yellow, whereas it has a green hue in shallow waters and it is usually blue in deep-sea habitats, corresponding to the wavelengths that propagate best in these environments (Haddock et al. 2010; Widder 2010). In a similar way, bioluminescent glows are thought to function as a lure or attraction signal, whether directed to prey or potential mates, whereas sudden flashes are generally associated with defensive functions, used to startle and confuse predators (Haddock et al. 2010).

Within Annelids, bioluminescence has evolved independently in several lineages (Fig. 1) (Haddock et al. 2010; Shimomura 2012) possibly contributing to the high taxonomic diversity we observe today (Ellis and Oakley 2016) with almost 100 luminous species distributed in thirteen families (Fig. 1, Table 1). Their ecological diversity is also unparalleled, with species occupying a wide range of habitats including both terrestrial and marine ecosystems from coastal waters to the deep-sea, and both benthic and pelagic habitats from polar to tropical regions. Their taxonomic and ecological diversity is matched by the wide array of bioluminescent colors (Figs. 1 and 2, Table 1), including yellow light emitters which are extremely rare among marine taxa (Fig. 2E) (Widder 2010), and widely varying patterns, chemical reactions, and kinetics. We present the current state of knowledge regarding luminous annelids, particularly focusing on their taxonomic and ecological diversity and discussing the putative functions and chemistries of their bioluminescent systems.

## Diversity of luminous annelids: which worms glow?

Approximately 98 luminous annelid species representing 45 genera have been reported so far, distributed in five clitellate families including Acanthodrilidae, Enchytraeidae, Lumbricidae, Megascolecidae, and Octochaetidae, and eight polychaete families, namely Acrocirridae, Chaetopteridae, Cirratulidae, Flabelligeridae, Polynoidae, Syllidae, Terebellidae, and Tomopteridae (Fig. 1, Table 1) (Harvey 1952; Herring 1978, 1987; Shimomura 2012). Among these, there are species that occupy an incredible variety of habitats and ecological niches and show a corresponding diversity of bioluminescent colors and patterns. In this section, we review the diversity of luminous annelids both in terms of taxonomic and ecological diversity and provide information about their bioluminescent displays and patterns.

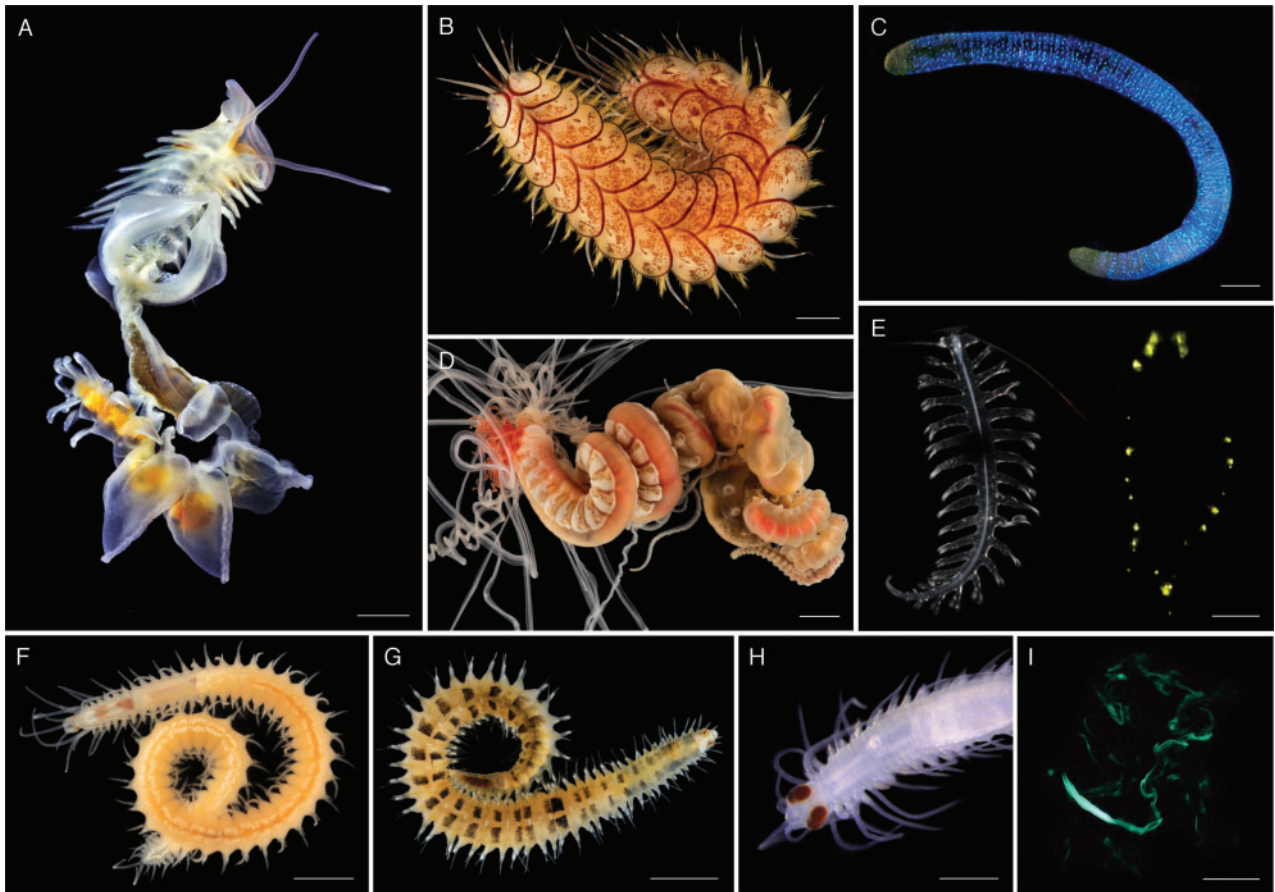


**Fig. 1** Distribution and spectral diversity of bioluminescence in the phylum Annelida. Lineages surrounded by ovals include bioluminescent species. Color of the oval indicates the bioluminescence emission maxima of a representative species; the corresponding wavelength, species name, and a schematic representation are shown to the right. Ovals with a dashed-line contour indicate lineages with dubious reports of bioluminescent species. Cladogram based on phylogenetic reconstruction from Weigert and Bleidorn (2016). Visible light spectrum is shown at the bottom for reference.

**Table 1** Biochemical characteristics of annelid bioluminescence. Peak emission wavelengths and components necessary for bioluminescence reaction in luminous clitellates (top half) and polychaetes (bottom half). Shaded rows correspond to terrestrial species and clear rows indicate marine species. Bioluminescent species for which none of these characteristics are known are not included in the table.

Species	$\lambda$ max (nm)	Components of bioluminescence system	References
Family Acanthodrilidae			
<i>Diplocardia alba</i>	501	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>D. eigeni</i>	505	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>D. longa</i>	507	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub> /O <sub>2</sub> /Cu <sup>2+</sup>	Bellisario et al. (1972)
<i>Diplotrema heteropora</i>	545	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>Microscolex phosphoreus</i>	538	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler (1982)
Family Enchytraeidae			
<i>Fridericia heliota</i>	478	Luciferin/luciferase/ATP/Mg <sup>2+</sup> /O <sub>2</sub>	Rodionova et al. (2003)
<i>Henlea</i> sp.	464	Luciferin/luciferase/O <sub>2</sub> /Ca <sup>2+</sup>	Rodionova et al. (2002)
Family Lumbricidae			
<i>Eisenia lucens</i>	493	Riboflavin/luciferase/aldehyde/O <sub>2</sub>	Pes et al. (2016)
Family Megascolecidae			
<i>Fletcherodrilus fasciatus</i>	–	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>F. unicus</i>	–	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>Pontodrilus bermudensis</i>	540	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1986)
<i>Spenceriella cormieri</i>	–	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>S. curtisi</i>	535	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>S. minor</i>	531	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
<i>S. noctiluca</i>	–	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
Family Octochaetidae			
<i>Octochaetus multiporus</i>	>570	Luciferin/luciferase/H <sub>2</sub> O <sub>2</sub>	Wampler and Jamieson (1979)
Family Flabelligeridae			
<i>Flota flabelligera</i>	497	–	Francis et al. (2016)
<i>Poeobius meseres</i>	495	–	Francis et al. (2016)
Family Chaetopteridae			
<i>Chaetopterus variopedatus</i>	463	Riboflavin/luciferase/H <sub>2</sub> O <sub>2</sub> /Fe <sup>2+</sup>	Nicol (1957a), Rawat and Deheyn (2016)
Family POLYNOIDAE			
<i>Gattyana cirrhosa</i>	517	–	Nicol (1957b)
<i>Harmothoe longisetis</i>	512	–	Nicol (1957b)
<i>Harmothoe extenuate</i>	515	–	Nicol (1957b)
<i>Malmgrenia lunulata</i>	510	Polynoidin/superoxide anions/O <sub>2</sub>	Bassot and Nicolas (1995)
<i>Polynoe scolopendrina</i>	511	–	Nicol (1957b)
Family Syllidae			
<i>Odontosyllis enopla</i>	507	Luciferin/luciferase/Mg <sup>2+</sup> /cyanide/O <sub>2</sub>	Shimomura et al. (1963)
<i>Odontosyllis phosphorea</i>	494	Photoprotein/co-factor	Deheyn and Latz (2009)
Family Terebellidae			
<i>Polycirrus perplexus</i>	445	–	Huber et al. (1989)
Family Tomopteridae			
<i>Tomopteris</i> sp.	565	Aloe-emodin/luciferase	Francis et al. (2014)
<i>Tomopteris</i> sp.	493	–	Francis et al. (2016)
<i>T. carpenter</i>	574	–	Gouveneaux et al. (2016)
<i>T. helgolandica</i>	573	–	Gouveneaux and Mallefet (2013)
<i>T. nisseni</i>	565	–	Latz et al. (1988)
<i>T. pacifica</i>	549	–	Gouveneaux et al. (2016)
<i>T. planktonis</i>	450	–	Gouveneaux et al. (2016)
<i>T. septentrionalis</i>	557	–	Gouveneaux et al. (2016)





**Fig. 2** Bioluminescent annelids. (A) *Chaetopterus variopedatus*, scale bar 2 mm; (B) *Harmothoe imbricata*, scale bar 2 mm; (C) *Fridericia heliota* bioluminescence, scale bar 1 mm; (D) *Thelepus cincinnatus*, scale bar 2 mm; (E) *Tomopteris helgolandica* photographed under natural light (left) and in the dark after KCl-induced bioluminescence (right), scale bar 500  $\mu$ m; (F) *Eusyllis blomstrandii*, scale bar 2 mm; (G) *Odontosyllis fulgurans*, scale bar 2 mm; (H) Close-up of *Odontosyllis enopla* male, scale bar 1 mm; (I) *Odontosyllis enopla* female bioluminescent display, still frame from Supplementary Video S1, scale bar 2 cm. Images courtesy of Alexander Semenov (A, C), Fredrik Pleijel (B, D, F, G), Anaïd Gouveneaux (E) and John Sparks (I). Image E was adapted with permission from The Journal of Experimental Biology (Gouveneaux and Mallefet 2013).

### Terrestrial taxa

The only known terrestrial luminous annelids identified to date are several earthworm species in the class Clitellata. Clitellates, which include earthworms, branchiobdellids, and leeches, comprise around one-third of all annelid species currently described, and are characterized by the clitellum, a glandular epidermal structure with the shape of a ring involved in reproduction (Erséus 2005; Erséus et al. 2010).

Bioluminescent clitellates are found in five families of earthworms and potworms: Acanthodrilidae, Enchytraeidae, Lumbricidae, Megascolecidae, and Octochaetidae. With few exceptions, bioluminescent clitellates secrete a luminescent coelomic fluid under mechanical, chemical or electric stimulation. The bioluminescent system is located in granules packed in cells of the secreted coelomic fluid (Wampler and

Jamieson 1979, 1986; Petushkov et al. 2002, 2014; Rota et al. 2003; Pes et al. 2016).

### Enchytraeidae

Enchytraeids or potworms are probably the most ubiquitous taxon of clitellates, with around 700 species distributed throughout the world (Erséus 2005; Erséus et al. 2010). Bioluminescent terrestrial enchytraeids are found in the genera *Fridericia* and *Michaelseniella* and usually inhabit soils rich in organic matter. The majority of luminescent enchytraeids produce flashes of light after stimulation triggers the release of a luminous coelomic slime (Wampler and Jamieson 1986; Petushkov and Rodionova 2005), with the exception of *Fridericia heliota* (Fig. 2C), whose bioluminescent system is located under the cuticle, in a region of epidermal

glandular cells not related to coelomic cells. The luminescent granules are scattered throughout the body, being most abundant in the prostomium and pygidium (Petushkov et al. 2003, 2014; Rota et al. 2003; Petushkov and Rodionova 2007).

#### Lumbricidae

Lumbricid earthworms are essential members of the soil biota playing a major role in biogeochemical cycles (Edwards and Bohlen 1995). There are around 300 described species of lumbricids, generally characterized by the presence of a multilayered clitellum (Pérez-Losada et al. 2012).

All records of bioluminescence in the Lumbricidae refer to species currently classified in *Eisenia*, probably limited to only two or three species, including *Eisenia fetida* and *E. lucens* (Pes et al. 2016). Luminescence in lumbricids is reported from the coelomic fluid which contains the granular coelomocytes with the luminescent compounds and is secreted through the dorsal pores in response to strong mechanical or chemical stimulation (Rota et al. 2003).

#### Megascolecoidea

The majority of luminescent clitellates belong to the earthworm superfamily Megascolecoidea, with around 30 luminous species distributed in 13 genera in the families Ancanthodrilidae, Megascolecidae, and Octochaetidae (Rota et al. 2003). Luminescence in megascolecoideans is reported after mechanical, chemical, or electrical stimulation from the coelomic fluid discharged through either the dorsal pores or the mouth and anus (Wampler and Jamieson 1979, 1986; Wampler 1982), although light production varies among species. The ubiquitous earthworm *Microscolex phosphoreus* has a quick bright response even upon disturbance of the surrounding soil, while in other species the response is much slower and light emission is weaker. Interestingly, in others like *Digaster keasti* mechanical stimulation does not elicit light production, which is only obtained after exposure to hydrogen peroxide (Harvey 1952; Jamieson 1977, Jamieson and Wampler 1979; Wampler 1982; Rota et al. 2003).

#### Marine taxa

All marine bioluminescent annelids reported to date are polychaetes, except for a handful of clitellates including the potworms *Henlea* and *Enchytraeus* (Enchytraeidae) and the earthworm *Pontodrilus* (Megascolecidae) which are found in different intertidal habitats (Wampler and Jamieson 1979, 1986; Healy and Coates 1999) (Table 1). The term

Polychaeta refers to a paraphyletic group of annelids, characterized by having parapodia with chitinous chaetae. Despite being an artificial grouping, the term is commonly used to distinguish non-clitellate annelids from clitellates (Weigert and Bleidorn 2016).

Bioluminescence in polychaetes is widespread, present in numerous species distributed in eight families including Acrocirridae, Chaetopteridae, Cirratulidae, Flabelligeridae, Polynoidae, Syllidae, Tomopteridae, and Terebellidae (Harvey 1952; Herring 1987; Haddock et al. 2010; Shimomura 2012). Light production in polychaetes is very diverse, with emission wavelengths ranging from 445 nm in Terebellidae to 573 nm in Tomopteridae (Fig. 1, Table 1) and varying patterns and kinetics, suggesting it serves many different functions. For example, *Chaetopterus* and swarming females of *Odontosyllis* show long glows emitted from secretions (Hastings and Morin 1991; Fischer and Fischer 1995; Gaston and Hall 2000; Deheyn and Latz 2009; Deheyn et al. 2013), whereas polynoids and swarming males of *Odontosyllis* produce flashes of light via intracellular bioluminescence (Bassot and Nicolas 1995; Fischer and Fischer 1995; Deheyn and Latz 2009; Martin and Plyuscheva 2009). Bioluminescent polychaetes are found in a wide range of marine habitats from intertidal and shallow waters to the deep-sea, both in the benthic and pelagic zones, from polar to tropical regions (Raymond and DeVries 1976; Gaston and Hall 2000; Francis et al. 2016).

#### Pelagic taxa

##### *Acrocirridae and Flabelligeridae*

Acrocirridae and Flabelligeridae are sister families of cirratuliform pelagic and benthopelagic polychaetes that share several features including gelatinous sheathes, transparent bodies, and the capability to produce light (Osborn and Rouse, 2010). Luminous acrocirrids include species of the deep-sea genus *Swima*, which carry luminescent “bombs” that are released upon disturbance, rapidly lighting up and glowing intensely for many seconds (Osborn et al. 2009, 2011). These bioluminescent structures are in fact four pairs of modified branchiae that immediately produce green light when autotomized. Mechanical stimulation of any part of the body results in the detachment of a bomb (Osborn et al. 2011). Among the Flabelligeridae, there are also bioluminescent swimming species, such as *Poeobius meseres* and several species of the genus *Flota* which produce flashes of light as spots near the bristle junctions (Francis et al. 2016).

### Tomopteridae

Tomopterids are dorsoventrally flattened holopelagic polychaetes mainly characterized by their modified parapodia, conspicuous palps, and long parapodial cirri on the second segment (Halanych et al. 2007). Most species are transparent or have little pigmentation and a number of them are capable of producing light. Bioluminescence in tomopterids was first reported in the parapodial rosettes (glandular organs) of *Tomopteris mariana* (Greeff 1882, 1885; Dales 1971). Most tomopterids produce a golden yellow bioluminescent light that is under nervous control (Fig. 2E) (Dales 1971; Latz et al. 1988; Haddock et al. 2010; Gouveneaux and Mallefet 2013) but interestingly, species that emit blue light have also been reported recently (Francis et al. 2016; Gouveneaux et al. 2016).

### Benthic taxa

#### Chaetopteridae

Chaetopterids are a basal branching lineage of marine, filter-feeding annelids, mainly benthic and tube-dwelling worms with the body divided in three distinct regions—anterior, middle, and posterior—(Osborn et al. 2007; Weigert et al. 2014). Two genera, *Chaetopterus* and *Mesochaetopterus* have bioluminescent representatives (Harvey 1952; Herring 1987). Bioluminescence is common among *Chaetopterus* species, which secrete a steadily luminous slime from various parts of the body and emit a flash of light from the posterior segments lasting a few seconds (Nicol 1952; Osborn et al. 2007; Shimomura 2012; Branchini et al. 2013; Deheyn et al. 2013). *Chaetopterus variopedatus*, for example (Fig. 2A), emits transitory undispersed light and secretes luminescent mucus that is scattered in the surrounding water when direct mechanical stimulation or freshwater are applied to the peristomial palps, feeding structures, dorsal surface or notopodia (Nicol 1952), while *Chaetopterus gregarious* produces weak bluish luminous mucus through the palps and notopodia (Nishi et al. 2000).

An unusual pelagic deep-water chaetopterid, *Chaetopterus pugaporcinus*, emits light in two forms: it produces bright blue light around the peristomium and prostomium during 3–6 s that extinguishes abruptly, and releases minute green bioluminescent particles from the mid-dorsal ciliated groove and posterior end, that are dispersed throughout a mucous cloud and glow intensely for 1–2 s before slowly fading (Osborn et al. 2007).

#### Cirratulidae

Cirratulids typically burrow in soft sediments and have a large number of elongate filaments along

the body, some of which occur as an anterior cluster of grooved tentacles for deposit feeding (Blake 1996). There are several species of bioluminescent cirratulids in the genera *Caulleriella* and *Chaetozone* whose epitokous forms (sexually mature individuals) become bioluminescent (Petersen 1999; Rouse and Pleijel 2001; Gibbs 2009). For example, sexually mature individuals of *Caulleriella fragilis* and also atokous (not sexually mature) specimens of *Caulleriella parva* produce a bluish light when disturbed (Petersen 1999). *Chaetozone caputesocis* has also been observed to emit a greenish light from photophores found mainly in the epidermis of abdominal segments (Gibbs 2009). There are some additional reports of bioluminescent cirratulids in the genera *Cirratulus*, *Dodecaceria*, and *Tharyx* (Harvey 1952; Herring 1987).

#### Polynoidae

Polynoids are the largest family of scale worms, which occur in all marine benthic habitats from the intertidal zone to the deep sea (Norlinder et al. 2012). Polynoids are characterized by a series of paired scales or elytra covering the dorsal surface of the body (Fig. 2B). Upon disturbance, some species emit flashes of light from the ventral epithelium of the scales. If the stimulus is strong, one or more glowing scales might be detached while the animal swims away (Nicol 1953; Bassot and Nicolas 1995; Shimomura 2012; Martin and Plyuscheva 2009). Bioluminescence has been reported in several species including *Harmothoe imbricata* (Fig. 2B), *Harmothoe lunulata* and *Acholoe astericola*. In the luminous species, the ventral epithelium of the elytra has a layer of luminescent cells or photocytes, which are modified epidermal cells not present in the non-luminous species (Nicol 1953; Martin and Plyuscheva 2009).

#### Syllidae

The family Syllidae is a highly diverse family of polychaetes present in nearly all marine benthic habitats and characterized by a specialization of the digestive tube named proventricle (Rouse and Pleijel 2001; Aguado et al. 2012). Syllids are known for their striking reproductive modes, which involve strong physical, morphological, and behavioral modifications, in some cases linked to bioluminescent displays. There are several luminescent species in the genera *Odontosyllis* (Fig. 2G, H, I), *Eusyllis* (Fig. 2F), and *Pionosyllis* mainly found in shallow coastal waters (Zörner and Fischer 2007; Deheyn and Latz 2009; Haddock et al. 2010). The behavioral aspects of the bioluminescence display linked to swarming and



spawning in *Odontosyllis* have been thoroughly studied, but little is known about the molecular mechanisms or chemistry of the bioluminescent system (Galloway and Welch 1911; Potts 1913; Huntsman 1948; Markert et al. 1961; Tsuji and Hill 1983; Fischer and Fischer 1995; Gaston and Hall 2000).

The first record of a bioluminescent *Odontosyllis* was likely by Christopher Columbus in November of 1492 when the Santa María was approaching the Bahamas (Crawshaw 1935). It was first assumed that the species was the Bermudian *O. enopla*, but it is more likely the species was *O. luminosa*, later described by San Martín (1990) from Cuba (Gaston and Hall 2000). The first account of *Odontosyllis* reproduction and bioluminescent display comes from Galloway and Welch (1911). The authors recorded the spawning periodicity of *O. enopla* (Fig. 2H, I) from Bermuda, reporting its correlation with the lunar cycle and daily periodicity. In this species, females appear first at the surface showing a bright continuous glow while swimming rapidly in small circles (Fig. 2H, Supplementary Video S1). The males swim directly to the females, emitting flashes of light, and they both rotate together releasing gametes in the water column. Later authors added more information, reporting the display lasts roughly half an hour, beginning around 55 min after sunset, each month after a full moon. Females glow for 3–8 s, while males give 2–3 quick flashes of light when approaching a female (Huntsman 1948; Markert et al. 1961). The species *O. octodentata* from Puerto Rico and *O. luminosa* from Belize have similar swarming and bioluminescent displays the second night after a full moon, around 75 min and 55–65 min after sunset, respectively, more frequently during the summer months (Erdman 1965; Gaston and Hall 2000).

Potts (1913) described the reproductive behavior of another bioluminescent species, *O. phosphorea* from British Columbia and reported its swarming periodicity, which takes place during the last quarter or beginning of first quarter of the moon, about half an hour after sunset. Tsuji and Hill (1983) studied the spawning of the same species in southern California and described its strong seasonality. The authors reported that the bioluminescent display and spawning are correlated with the monthly lunar cycles and occur shortly after sunset at fortnightly intervals from June through October, lasting around 30 min. Unlike the rest of *Odontosyllis* species, in *O. phosphorea* the first flashes of light are usually from males. The females appear shortly after, swimming in circles, flashing and secreting a bright green luminous mucus along with the gametes (Potts 1913; Tsuji and Hill 1983).

Other syllids also produce light, most notably the species *Eusyllis blomstrandii* (Figure 2F), which has paired epidermal luminescent regions in each segment that produce light upon stimulation. Light emission is usually localized on a posterior group of segments, where it seems to be intracellular and can be turned on and off very rapidly (Zörner and Fischer 2007).

### Terebellidae

Terebellids are tubicolous polychaetes that usually inhabit soft substrates worldwide. They are selective deposit feeders that use their numerous buccal tentacles to collect organic matter from the sea floor (Garraffoni and Lana 2008). Bioluminescence in terebellids was first described by Dahlgren (1916) when he observed the production of a bright violet-blue luminous secretion in the tip of the tentacles of *Polycirrus auranticus*. Harvey (1926) also reported bioluminescence as a luminous secretion in *Thelepus cincinnatus* (Fig. 2D). The extracellular nature of bioluminescence has also been suggested in other terebellids, including *P. auranticus* and *P. caliendrum*. However, Huber et al. (1989) argued that the extremely rapid flashes of light produced by *P. perplexus* in response to stimulation are inconsistent with the hypothesis that light production is extracellular and concluded that bioluminescence in this species is not secretory.

### Other reports

There are additional, less detailed and sometimes dubious reports of bioluminescent annelids in the literature (Herring 1978, 1987). For example, the planktonic genera *Alciopina* and *Rhynchonereella* (Alciopidae) have been reported to be luminescent (Dales 1971). An unidentified species of *Onuphis* (Onuphidae) was reported to have pairs of lateral luminous spots in each segment that emit a bluish-green light when stimulated (Haneda 1955). A survey of bioluminescence organisms in Antarctica described the bioluminescence of *Aglaophamus foliosus* (Nepthyidae) (Raymond and DeVries 1976) and early authors reported light production in Nereididae species including *Nereis noctiluca*, *N. pelagica*, and *N. radiata* (Harvey 1952). But in general, these reports are questionable as they are based in single observations in which the actual source of the light was uncertain. In addition, the identification of the species is sometimes doubtful, such as in the case of the nereid species which were probably misidentified and most likely correspond to syllids (Harvey 1952).



## Functions of bioluminescence in Annelida: why do worms glow?

The biological significance of light production is poorly understood in most systems mainly because of the difficulty of linking bioluminescence to a specific biological or ecological function (Oba and Schultz 2014). There are a few instances in which the function of light production is well understood such as in fireflies that use flash signals for sexual communication (Lewis and Cratsley 2008) or mid-shipman fish and lantern sharks that use bioluminescence for camouflage through counterillumination (Claes et al. 2010; Harper and Case 1999). In other cases, the highly complex neurally controlled light organs and light-associated behaviors (Ancil and Case 1977; Gouveneaux and Mallefet 2013) indicate bioluminescence must serve an important biological role (Oba and Schultz 2014).

As a general rule in annelids, bioluminescence is poorly understood and this lack of knowledge makes it extremely difficult to link light production to a specific function. Within clitellates, for example, the diverse bioluminescent systems and chemistries displayed by different species suggest that light production might be associated to a variety of functions, yet in species that do not produce light immediately upon stimulation it is thought to be a functionless byproduct of other metabolic processes (Jamieson 1977; Oba and Schultz 2014).

Despite the differences observed in the bioluminescence characteristics and light emission patterns in the different groups of luminous annelids, in most cases, light production has been associated with a defensive function (Harvey 1952; Herring 1978; Huber et al. 1989; Deheyn and Latz 2009; Osborn et al. 2009; Haddock et al. 2010; Shimomura 2012; Gouveneaux and Mallefet 2013) and in a few instances, it has been linked to intraspecific communication (Dales 1971; Harvey 1952; Latz et al. 1988; Fischer and Fischer 1995; Gaston and Hall 2000; Gouveneaux and Mallefet 2013). It is important to mention that as far as we know, there have been no published studies that provide experimental evidence to support any of the hypothesized functions of light production in annelids. The suggested functions are based on inferences from morphological and physiological characteristics and in the best-case scenario, supported by *in situ* behavioral observations (i.e., Gaston and Hall 2000; Zörner and Fischer 2007; Deheyn and Latz 2009). In this section, we discuss the putative functions associated with light production in annelid worms.

## Defense

### Startle mechanism

Tubicolous species of Chaetopteridae and Terebellidae exude glowing particles from their tube when disturbed and it has been hypothesized that bioluminescence acts as a startle mechanism against predators and commensals (Harvey 1952; Morin 1983; Shimomura 2012). The glowing mucus of *Chaetopterus* has also been proposed to have a defensive function by sticking to the predator, interfering with its locomotion and making it more visible and vulnerable to its own predators (Rawat and Deheyn 2016).

In *Odontosyllis* species (Fig. 2G and H), it is well known that bioluminescence is used for intraspecific communication during reproduction (see Section “Intraspecific communication”) but light production has also been observed in juveniles and in adults that had returned to benthic life after spawning, suggesting that it might serve additional functions (Fischer and Fischer 1995; Gaston and Hall 2000; Deheyn and Latz 2009). For example, internal bioluminescence in *O. enopla* has been observed during the nocturnal foraging behavior of adults and following mechanical stimulation (Fischer and Fischer 1995). Intense flashes of light have also been reported from adults and juveniles *O. phosphorea* after mechanical stimulation, indicating bioluminescence might be used for predator deterrence acting as a startle mechanism (Deheyn and Latz 2009).

### Sacrificial lure

In scale worms (Polynoidae), bioluminescence has been suggested to serve as a warning or distracting mechanism (Nicol 1953; Herring 1978; Bassot and Nicolas 1995; Martin and Plyusheva 2009; Oba et al. 2016). Polynoids emit light from the dorsal scales or elytra (Fig. 2B), which are easily autotomized in response to a strong stimulus and flash brightly from some time, acting as a sacrificial lure that allows the animal to escape (Nicol 1953; Herring 1978). A similar mechanism has been proposed to explain the function of the bioluminescent “bombs” released by the deep-sea acroirid *Swima bombiviridis*, which glow intensely for many seconds distracting the predator while the animal swims away (Osborn et al. 2009).

In the syllid *Eusyllis blomstrandii* (Fig. 2F), a similar, albeit more extreme behavior has been observed. Light emission in this species is localized in the posterior end of the body, which upon strong stimulation becomes autotomized and glows extremely

brightly for a few seconds, while the anterior non-luminescent end swims away (Zörner and Fischer 2007). The anterior end of the worm is capable of regenerating the lost segments while the posterior fragment can survive for some time, but it is unable to regenerate the head and feeding structures and thus, it might serve as a decoy or sacrificial lure attracting the attention of predators while the anterior fragment escapes (Zörner and Fischer 2007).

#### Aposematic signal

Both terebellids and chaetopterids produce short wavelength luminescence at around 440 nm, which has been suggested to function as an aposematic signal, specifically in the terebellid *Polycirrus perplexus* where it might indicate the distastefulness and toxicity of its tentacles (Dahlgren 1916; Morin 1983; Huber et al. 1989). Similarly, flashes of light of *O. luminosa* may also represent an aposematic signal indicating distastefulness or toxicity as predators have been observed to regurgitate recently ingested worms (Gaston and Hall 2000).

#### Intraspecific communication

Probably the only case in which annelid light production can be unquestionably associated with a particular function is in the courtship displays of *Odontosyllis* worms. Bioluminescent light is used for mate attraction, acting as a swarming cue. In most species, the females swim to the surface first and swim in circles releasing gametes and producing a steady bright green light (Fig. 2I, Supplementary Video S1) that attracts the males, which swim towards the females and also release gametes (Galloway and Welch 1911; Markert et al. 1961). Luminescence in the cirratulid *Chaetozone caputesocis*, has also been suggested to serve an intraspecific communication role during reproduction, to maintain cohesion during the pelagic swarming events (Petersen 1999; Gibbs 2009).

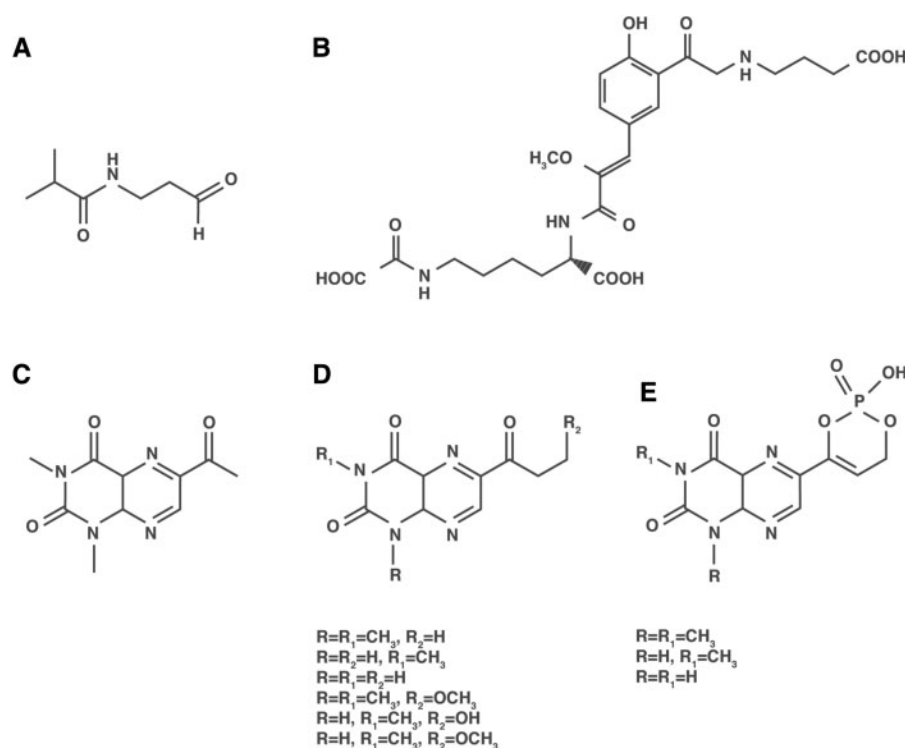
In other species, light production is thought to function as a mechanism for intraspecific communication but not necessarily related to reproduction. For example, the species-specific distribution of the luminous organs and the atypical emission of yellow light in Tomopteridae has led several authors to suggest that bioluminescence provides a private communication channel (Harvey 1952; Dales 1971; Latz et al. 1988; Gouveneaux and Mallefet 2013). Because contact between planktonic organisms in the open ocean is difficult, other bioluminescent annelids with a pelagic lifestyle, such as the chaetopterid *C. pugaporcinus*, may also use bioluminescence as an intraspecific communication system. This hypothesis

is not restricted to the open ocean, as the bioluminescent system of the terrestrial annelid *Digaster keasti* is thought to function as an intraspecific recognition tool (Jamieson 1977; Herring 1978).

### Chemistry of bioluminescent systems: how do worms glow?

Although knowledge on the chemistry of annelid luminescent systems is scarce, there is a recognized wide diversity of chemical reactions and kinetics among the different species. The luminescent system of most clitellates requires luciferin, luciferase, hydrogen peroxide, oxygen, and an activator that varies among different species (Table 1) (Petushkov et al. 2002; Shimomura 2012). For example, the bioluminescence of *Diplocardia longa* (Megascolecidae) is triggered by copper, while in *Henlea* sp. (Enchytraeidae) the activator is calcium and *Fridericia heliota* (Enchytraeidae) requires magnesium and ATP as a co-substrate (Petushkov et al. 2002, 2003, 2014; Petushkov and Rodionova 2005). In the megascolecid earthworm *Diplocardia longa* the luciferin has been identified as *N*-isovaleryl-3-amino-propanal (Fig. 3A) and the luciferase isolated and characterized as a 300 kDa heterotrimeric copper metalloprotein (Bellisario and Cormier 1971; Bellisario et al. 1972; Ohtsuka et al. 1984; Oba et al. 2016). Bioluminescence in other megascolecid genera is also triggered by hydrogen peroxide and the reaction can be activated with the addition of *D. longa* luciferin or luciferase suggesting the chemistry of light production is equivalent (Wampler and Jamieson 1979; Wampler 1982; Oba et al. 2016). Although there is spectral and biochemical data that might support that bioluminescence in clitellates requires hydrogen peroxide, the relevant studies provided experimental evidence *in vitro*, and thus this hypothesis has to be considered with caution (Bellisario and Cormier 1971; Rudie et al. 1976; Wampler and Jamieson 1979, 1986).

More recently, different luminescent systems have been described in clitellates with the structural characterization of a novel luciferin in *Fridericia heliota* (Fig. 3B) (Petushkov et al. 2002, 2003, 2014) and studies on the bioluminescence system of the European earthworm *Eisenia lucens* (Pes et al. 2016). The structure of the *F. heliota* luciferin has an unusual modified peptidic nature and represents a novel mechanism of luminescence with the oxidation of an oxalate moiety and a fluorescent CompX moiety as the light emitter (Petushkov et al. 2014). The coelomic fluid of *E. lucens* has a high content of riboflavin which suggests that light production



**Fig. 3** Chemical structures of annelid luciferins and lumazines. (A) *Diplocardia longa* luciferin; (B) *Fridericia heliota* luciferin; (C–E) *Odontosyllis undecimdonga* lumazines.

involves the oxidation of riboflavin by atmospheric oxygen (Pes et al. 2016).

The chemistry of bioluminescence in parchment tubeworms has been mainly studied in *Chaetopterus variopedatus* (Shimomura and Johnson 1966; Anctil 1979; Martin and Anctil 1984; Zinner 1986; Shimomura 2012; Branchini et al. 2013; Deheyn et al. 2013; Rawat and Deheyn 2016). The luminous system includes a photoprotein that emits blue light in presence of hydrogen peroxide and iron and the amount of light emitted is proportional to the amount of photoprotein that reacts (Shimomura and Johnson 1966; Shimomura 2012). The luminous mucus of *Chaetopterus* has been recently studied in detail, suggesting that riboflavin or a structurally related derivative is the light emitter in this species and revealing that ferritin is involved in light production possibly storing iron to facilitate light production (Branchini et al. 2013; Rawat and Deheyn 2016).

In scale worms, the bioluminescent system involves a membrane photoprotein of about 65 kDa called polynoidin which is specifically triggered by superoxide radicals that result from the oxidation of reduced riboflavin in the presence of calcium (Nicolas et al. 1982; Bassot 1987; Bassot and Nicolas 1995; Martin and Plyuscheva 2009). The polynoid photoprotein seems to contain a tightly bound

cofactor or alternatively, it may function using its conformational change to transfer the energy from the superoxide radicals to the light emitter directly (Martin and Plyuscheva 2009). Interestingly, polynoidin is also present in non-luminescent scale worms suggesting that bioluminescence might have originated from a mechanism able to quench superoxide radicals (Martin and Plyuscheva 2009).

In Syllidae, the bioluminescent systems of *O. enopla* and *O. phosphorea* have been briefly investigated. The luciferin of *O. enopla* has been partially purified showing that light emission requires the presence of magnesium, molecular oxygen, and crude luciferase, although its chemical structure has not yet been determined (Table 1) (Shimomura et al. 1963; Trainor 1979). More recently, analyses of the bioluminescent mucus of *O. phosphorea* revealed that the reaction appears to involve a photoprotein (Table 1) instead of a luciferin-luciferase reaction, therefore representing an alternative mechanism in this species (Deheyn and Latz 2009). Additionally, several lumazines and lumazine derivatives (Fig. 3C–E) have been isolated from the metabolites of the luminescent Japanese species *O. undecimdonga* although their connection to the bioluminescence system remains unclear (Inoue et al. 1991; Sato and Fukuya 2000; Oba et al. 2016).

The light emitting substance in the bioluminescence system of the holopelagic Tomopteridae is thought to be a membrane-bound photoprotein tightly associated with small particles (Shimomura 2012; Francis et al. 2014). A recent study isolated the fluorescent yellow–orange pigment found in the luminous exudate and body of *Tomopteris* and identified the compound as aloxe-emodin, suggesting it might act as the light emitter in *Tomopteris* (Francis et al. 2014).

## Conclusions and future prospects

Numerous lineages of annelids have independently evolved a wide diversity of bioluminescence systems, making Annelida a very interesting phylum for bioluminescence research. However, annelid luminescent systems are currently poorly understood, with luciferin structures known for only two earthworm species and no luciferases or photoproteins characterized so far. Likewise, little is known regarding the biological or ecological functions of bioluminescence in annelids or the evolutionary origins of the bioluminescent systems in the different lineages.

Nonetheless, the development of new instruments and technological devices like remotely operated vehicles (ROVs) and low-light underwater cameras has already led to the discovery of new bioluminescent annelids (Osborn et al. 2009) and provided important observations regarding species interactions and distribution of bioluminescent taxa (Gouvenaux et al. 2016; Phillips et al. 2016; Martini and Haddock 2017). These technologies will continue to progress and improve our understanding of the diversity and functions of bioluminescence in annelids in the future. Likewise, the recent advances in Next-Generation sequencing technologies and bioinformatics methods, as well as biochemical analytical tools will lead to an exponential increase in our knowledge on the molecular basis of bioluminescence and the chemistry of light-producing molecules. The ocean seems full of unknown, and likely novel, annelid systems that may also provide illuminating insights and opportunities for the development of new biomedical and biotechnological applications.

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## References

- Aguado MT, San Martín G, Siddall ME. 2012. Systematics and evolution of syllids (Annelida, Syllidae). *Cladistics* 28:23450.
- Ancil M. 1979. The epithelial luminescent system of *Chaetopterus variopedatus*. *Can J Zool* 57:1290–310.
- Ancil M, Case JF. 1977. The caudal luminous organs of lanternfishes: general innervation and ultrastructure. *Am J Anatomy* 149:1–21.
- Bassot JM. 1987. A transient intracellular coupling explains the facilitation of responses in the bioluminescent system of scale worms. *J Cell Biol* 105:2235–43.
- Bassot JM, Nicolas MT. 1995. Bioluminescence in scale-worm photosomes: the photoprotein polynoidin is specific for the detection of superoxide radicals. *Histochem Cell Biol* 104:199–210.
- Bellisario R, Cormier MJ. 1971. Peroxide-linked bioluminescence catalyzed by a copper-containing, non-heme luciferase isolated from a bioluminescent earthworm. *Biochem Biophys Res Commun* 43:800–5.
- Bellisario R, Spencer TE, Cormier MJ. 1972. Isolation and properties of luciferase, a non-heme peroxidase, from the bioluminescent earthworm, *Diplocardia longa*. *Biochemistry* 11:2256–66.
- Blake JA. (1996) Family Cirratulidae Ryckholdt, 1851. Including a revision of the genera and species from the eastern North Pacific. In: Blake JA, Hilbig B, Scott PH, editors. *Taxonomic Atlas of the Benthic Fauna of the Santa Maria Basin and Western Santa Barbara Channel*. 6 - The Annelida Part 3. Polychaeta: Orbiniidae to Cossuridae. Santa Barbara: Santa Barbara Museum of Natural History. p. 263–384.
- Branchini BR, Behney CE, Southworth TL, Rawat R, Deheyn DD. 2013. Chemical analysis of the luminous slime secreted by the marine worm *Chaetopterus* (Annelida, Polychaeta). *Photochem Photobiol* 90:247–51.
- Claes JM, Aksnes DL, Mallefet J. 2010. Phantom hunter of the fjords: camouflage by counterillumination in a shark (*Etmopterus spinax*). *J Exp Mar Bio Ecol* 388:28–32.
- Copeland J, Daston MM. 1989. Bioluminescence in the terrestrial snail *Quantula (Dyakia) striata*. *Malacologia* 30:317–24.
- Crawshaw LR. 1935. Possible bearing of a luminous syllid on the question of the landfall of Columbus. *Nature* 136:559–60.



- Dahlgren U. 1916. The production of light by animals. *J Franklin Inst* 181:805–43.
- Dales RP. 1971. Bioluminescence in pelagic polychaetes. *J Fish Res Board Canada* 28:1487–9.
- Day JC, Tisi LC, Bailey MJ. 2004. Evolution of beetle bioluminescence: the origin of beetle luciferin. *Luminescence* 19:8–20.
- Deheyn DD, Enzor LA, Dubowitz A, Urbach JS, Blair D. 2013. Optical and physicochemical characterization of the luminous mucus secreted by the marine worm *Chaetopterus* sp. *Physiol Biochem Zool* 86:702–5.
- Deheyn DD, Latz ML. 2009. Internal and secreted bioluminescence of the marine polychaete *Odontosyllis phosphorea* (Syllidae). *Invertebr Biol* 128:31–45.
- Desjardin DE, Oliveira AG, Stevani CV. 2008. Fungi bioluminescence revisited. *Photochem Photobiol Sci* 7:170–82.
- Devillers I, de Wergifosse B, Bruneau MP, Tinant B, Declercq JP, Touillaux R, Rees JF, Marchand-Brynaert J. 1999. Synthesis, structural characterization and antioxidative properties of aminopyrazine and imidazolopyrazine derivatives. *J Chem Soc Perkin 1* 2:1481–8.
- Edwards CA, Bohlen PJ. 1995. Biology and ecology of earthworms, 3rd edn. London: Springer.
- Ellis EA, Oakley TH. 2016. High rates of species accumulation in animals with bioluminescent courtship displays. *Curr Biol* 26:6–1.
- Erdman DS. 1965. Lunar periodicity in the swarming of luminescent worms, *Odontosyllis octodentata* Treadwell (Annelida) off La Parguera, P.R. *Caribb J Sci* 5:103–7.
- Erséus C. 2005. Phylogeny of oligochaetous Clitellata. *Hydrobiologia* 357–72.
- Erséus C, Rota E, Matamoros L, De Wit P. 2010. Molecular phylogeny of Enchytraeidae (Annelida, Clitellata). *Mol Phylogenet Evol* 57:849–58.
- Fischer A, Fischer U. 1995. On the life-style and life-cycle of the luminescent polychaete *Odontosyllis enopla* (Annelida: Polychaeta). *Invertebr Biol* 114:236–47.
- Francis WR, Powers ML, Haddock SHD. 2014. Characterization of an anthraquinone fluor from the bioluminescent, pelagic polychaete *Tomopteris*. *Luminescence* 29:1135–40.
- Francis WR, Powers ML, Haddock SHD. 2016. Bioluminescence spectra from three deep-sea polychaete worms. *Mar Biol* 163:255.
- Galloway TW, Welch PS. 1911. Studies on a phosphorescent bermudian annelid, *Odontosyllis enopla* Verill. *Trans Am Microsc Soc* 30:13–39.
- Garraffoni ARS, Lana PC. 2008. Phylogenetic relationships within the Terebellidae (Polychaeta: Terebellida) based on morphological characters. *Invertebr Syst* 22:605–26.
- Gaston GR, Hall J. 2000. Lunar periodicity and bioluminescence of swarming *Odontosyllis luminosa* (Polychaeta: Syllidae) in Belize. *Gulf Caribb Res* 12:47–51.
- Gibbs PE. 2009. A comparative study of reproductive cycles in four polychaete species belonging to the family Cirratulidae. *J Mar Biol Assoc UK* 51:745.
- Gouveneaux A, Flood PR, Mallefet J. 2016. Unexpected diversity of bioluminescence in planktonic worms. *Luminescence* 32:394–400.
- Gouveneaux A, Mallefet J. 2013. Physiological control of bioluminescence in a deep-sea planktonic worm, *Tomopteris helgolandica*. *J Exp Biol* 216:4285–9.
- Greeff R. 1882. Ueber die rosettenförmigen leuchtorgane der tomopteriden und zwei neue arten von *Tomopteris*. *Zool Anz* 5:384–7.
- Greeff R. 1885. Ueber die pelagische fauna an der kusten der Guinea-Inseln. *Z Wiss Zool* 42:423–58.
- Haddock SH. (2006) Luminous marine organisms. In: Daunert S, Deo S, editor. *Photoproteins in bioanalysis*. New York: Wiley. p. 25–47.
- Haddock SH, Moline MA, Case JF. 2010. Bioluminescence in the sea. *Annu Rev Mar Sci* 2:443–93.
- Halanych KM, Cox LN, Struck TH. 2007. A brief review of holopelagic annelids. *Integr Comp Biol* 47:872–9.
- Haneda Y. 1955. Luminous organisms of Japan and Far East. In: Johnson FH (editor). *The luminescence of biological systems*. Washington (DC): American Association for the Advancement of Science. p. 335–85.
- Harper RD, Case JF. 1999. Disruptive counterillumination and its anti-predatory value in the plainfish midshipman *Porichthys notatus*. *Mar Biol* 134:529–40.
- Harvey E. 1952. Bioluminescence. New York: Academic Press.
- Harvey EN. 1926. Bioluminescence and fluorescence in the living world. *Am J Physiol* 77:555–61.
- Hastings JW, Morin JG. 1991. Bioluminescence, 4th edn. In: Prosser CL, editor. *Neural and integrative animal physiology*. New York: Wiley. p. 131–70.
- Healy B, Coates KA. 1999. Finding enchytraeid oligochaetes (Clitellata) in hot climates: species occurrence on the shores of Bermuda. *Hydrobiologia* 406:111–7.
- Herring PJ. 1978. Bioluminescence in action. London: Academic Press.
- Herring PJ. 1987. Systematic distribution of bioluminescence in living organisms. *J Biolumin Chemilumin* 1:147–63.
- Huber ME, Arneson AC, Widder EA. 1989. Extremely blue bioluminescence in the polychaete *Polycirrus perplexus* (Terebellidae). *Bull Mar Sci* 44:1236–9.
- Huntsman AG. 1948. *Odontosyllis* at Bermuda and lunar periodicity. *J Fish Res Board Canada* 7b:363–9.
- Inoue S, Okada K, Tanino H, Kakoi H, Ohnishi Y, Horii N. 1991. New lumazines from the marine polychaete, *Odontosyllis uncecimdongta*. *Chem Lett* 20:563–4.
- Isobe M, Uyakul D, Goto T, Counsilman JJ. 1988. *Dyakia* bioluminescence—1. Bioluminescence and fluorescence spectra of the land snail, *D. striata*. *J Biolumin Chemilumin* 2:73–79.
- Jamieson BGM. 1977. Bioluminescent Australian earthworms, I. *Digaster keasti* sp. nov., (Megascolecidae), the first record of an oligochaete from Fraser Island. *Proc R Soc Qld* 88:83–8.
- Jamieson BGM, Wampler JE. 1979. Bioluminescent Australian earthworms II. Taxonomy and preliminary report of bioluminescence in the genera *Spenceriella*, *Fletcherodrilus* and *Pontodrilus* (Megascolecidae: Oligochaeta). *Aust J Zool* 27:483–99.
- Labas YA, Matz MV, Zakhartchenko VA. (2001) On the origin of bioluminescent systems. In: Case JF, Herring PJ, Robinson BH, Haddock SHD, Kricka LJ, Stanley PE, editors. *Bioluminescence and chemiluminescence*. Singapore: World Scientific Publishing Company. p. 91–94.

- Latz MI, Frank TM, Case JF. 1988. Spectral composition of bioluminescence of epipelagic organisms from the Sargasso Sea. *Mar Biol* 98:441–6.
- Lewis SM, Cratsley CK. 2008. Flash signal evolution, mate choice, and predation in fireflies. *Annu Rev Entomol* 53:293–321.
- Marek P, Papaj D, Yeager J, Molina S, Moore W. 2011. Bioluminescent aposematism in millipedes. *Curr Biol* 21:680–1.
- Markert RE, Markert BJ, Vertrees NJ. 1961. Lunar periodicity in spawning and luminescence in *Odontosyllis enopla*. *Ecology* 42:414–5.
- Martin D, Plyuscheva M. 2009. On the morphology of elytra as luminescent organs in scale-worms (Polychaeta, Polynoidae). *Zoosymposia* 2:379–89.
- Martin N, Anctil M. 1984. Luminescence control in the tube-worm *Chaetopterus variopedatus*: role of nerve cord and photogenic gland. *Biol Bull* 166:583–93.
- Martini S, Haddock SHD. 2017. Quantification of bioluminescence from the surface to the deep sea demonstrates its predominance as an ecological trait. *Sci Rep* 7:45750.
- Meyer-Rochow VB, Moore S. 1988. Biology of *Latia neritoides* Gray 1850 (Gastropoda, Pulmonata, Basommatophora): the only light-producing freshwater snail in the world. *Int Rev Hydrobiol* 73:21–42.
- Morin J. 1983. Coastal bioluminescence: patterns and functions. *Bull Mar Sci* 33:787–817.
- Nicol JAC. 1952. Studies on *Chaetopterus variopedatus* (Renier). II. Nervous control of light production. *J Mar Biol Assoc UK* 30:433–52.
- Nicol JAC. 1953. Luminescence in polynoid worms. *J Mar Biol Assoc UK* 32:65–84.
- Nicol JAC. 1957a. Spectral composition of the light of *Chaetopterus*. *J Mar Biol Assoc the UK* 36:629–42.
- Nicol JAC. 1957b. Spectral composition of the light of polynoid worms. *J Mar Biol Assoc UK* 36:529–38.
- Nicolas MTT, Bassot JMM, Shimomura O. 1982. Polynoidin: a membrane photoprotein isolated from the bioluminescent system of scale worms. *Photochem Photobiol* 35:201–7.
- Nishi E, Arai H, Sasanuma S. 2000. A new species of *Chaetopterus* (Polychaeta, Chaetopteridae) with comments on its bioluminescence. *Actinia* 13:1–12.
- Norlinder E, Nygren A, Wiklund H, Pleijel F. 2012. Phylogeny of scale-worms (Aphroditiformia, Annelida), assessed from 18SrRNA, 28SrRNA, 16SrRNA, mitochondrial cytochrome c oxidase subunit I (COI), and morphology. *Mol Phylogenet Evol* 65:490–500.
- Oba Y, Schultz DT. (2014) Eco-Evo bioluminescence on land and in the sea. In: Thouand G, Marks R, editors. *Bioluminescence: fundamentals and applications in biotechnology* - volume 1. Berlin, Heidelberg: Springer. p. 3–36.
- Oba Y, Stevani CV, Oliveira AG, Tsarkova AS, Chepurnykh TV, Yampolsky IV. 2016. Selected least studied but not forgotten bioluminescent systems. *Photochem Photobiol* 93:405–15.
- Ohmiya Y, Kojima S, Nakamura M, Niwa H. 2005. Bioluminescence in the limpet-like snail, *Latia neritoides*. *Bull Chem Soc Japan* 78:1197–205.
- Ohtsuka H, Rudie NG, Wampler JE. 1984. Structural identification and synthesis of luciferin from the bioluminescent earthworm, *Diplocardia longa*. *North* 15:1974–7.
- Osborn KJ, Haddock SHD, Pleijel F, Madin LP, Rouse GW. 2009. Deep-sea, swimming worms with luminescent “bombs”. *Science* 325:964.
- Osborn KJ, Haddock SHD, Rouse GW. 2011. *Swima* (Annelida, Acrocirridae), holopelagic worms from the deep Pacific. *Zool J Linn Soc* 163:663–78.
- Osborn KJ, Rouse GW. 2010. Phylogenetics of Acrocirridae and Flabelligeridae (Cirratuliformia, Annelida). *Zoologica Scripta* 40:204–19.
- Osborn KJ, Rouse GW, Goffredi SK, Robison BH. 2007. Description and relationships of *Chaetopterus pugaporcinus*, an unusual pelagic polychaete (Annelida, Chaetopteridae). *Biol Bull* 212:40–54.
- Pérez-Losada M, Bloch R, Breinholt JW, Pfenninger M, Domínguez J. 2012. Taxonomic assessment of Lumbricidae (Oligochaeta) earthworm genera using DNA barcodes. *Eur J Soil Biol* 48:41–7.
- Pes O, Midlik A, Schlaghamersky J, Zitnan M, Taborsky P. 2016. A study on bioluminescence and photoluminescence in the earthworm *Eisenia lucens*. *Photochem Photobiol Sci* 15:175–80.
- Petersen ME. 1999. Reproduction and development in Cirratulidae (Annelida: Polychaeta). *Hydrobiologia* 402:107–28.
- Petushkov VN, Dubinnyi MA, Tsarkova AS, Rodionova NS, Baranov MS, Kublitski VS, Shimomura O, Yampolsky IV. 2014. A novel type of luciferin from the siberian luminous earthworm *Fridericia heliota*: structure elucidation by spectral studies and total synthesis. *Angew Chem Int Ed* 53:5566–8.
- Petushkov VN, Rodionova NS. 2005. New types of luminescent systems of soil enchytraeids (Annelida: Clitellata: Oligochaeta: Enchytraeidae). *Dokl Biochem Biophys* 401:115–8.
- Petushkov VN, Rodionova NS. 2007. Purification and partial spectral characterization of a novel luciferin from the luminous enchytraeid *Fridericia heliota*. *J Photochem Photobiol B Biol* 87:130–6.
- Petushkov VN, Rodionova NS, Bondar' VS. 2003. Study of the luminescence system of the soil enchytraeid *Fridericia heliota* (Annelida: Clitellata: Oligochaeta: Enchytraeidae). *Dokl Biochem Biophys* 391:204–7.
- Petushkov VN, Rodionova NS, Purtov KV, Bondar' VS. 2002. The luminescence system of soil enchytraeids, *Henlea* sp., (Annelida: Clitellata: Oligochaeta: Enchytraeidae). *Dokl Biol Sci* 310–2.
- Phillips BT, Gruber DF, Vasan G, Roman CN, Pieribone VA, Sparks JS. 2016. Observations of in situ deep-sea marine bioluminescence with a high-speed, high-resolution sCMOS camera. *Deep-Sea Res A* 111:102–9.
- Potts FA. 1913. The swarming of *Odontosyllis*. *Proc Camb Philos Soc* 17:193–200.
- Purschke G, Bleidorn C, Struck T. 2014. Systematics, evolution and phylogeny of Annelida – a morphological perspective. *Mem Mus Vic* 71:247–69.
- Purtov KV, Petushkov VN, Baranov MS, Mineev KS, Rodionova NS, Kaskova ZM, Tsarkova AS, Petunin AI, Bondar VS, Rodicheva EK, et al. 2015. The chemical basis of fungal bioluminescence. *Angew Chem Int Ed* 54:8124–8.

- Rawat R, Deheyn DD. 2016. Evidence that ferritin is associated with light production in the mucus of the marine worm *Chaetopterus*. *Sci Rep* 6:36854.
- Raymond JA, DeVries AL. 1976. Bioluminescence in McMurdo Sound, Antarctica. *Limnol Ocean* 21:599–602.
- Rees JF, De Wergifosse B, Noiset O, Dubuisson M, Janssens B, Thompson EM. 1998. The origins of marine bioluminescence: turning oxygen defence mechanisms into deep-sea communication tools. *J Exp Biol* 201:1211–21.
- Rodionova NS, Bondar' VS, Petushkov VN. 2003. ATP is a cosubstrate of the luciferase of the earthworm *Fridericia heliota* (Annelida: Clitellata: Oligochaeta: Enchytraeidae). *Dokl Biochem Biophys* 392:253–5.
- Rodionova NS, Bondar VS, Petushkov VN. 2002. Ca(2+)-activator of the luminescence system of the earthworms *Henlea* sp., (Annelida: Clitellata: Oligochaeta: Enchytraeidae). *Dokl Biochem Biophys* 386:260–3.
- Rota E, Zaleskaja NT, Rodionova NS, Petushkov VN. 2003. Redescription of *Fridericia heliota* (Annelida, Clitellata: Enchytraeidae), a luminous worm from the Siberian taiga, with a review of bioluminescence in the Oligochaeta. *J Zool* 260:291–9.
- Rouse G, Pleijel F. (2001) Polychaetes. New York (NY): Oxford University Press.
- Rudie NG, Ohtsuka H, Wampler JE. 1976. Purification and properties of luciferin from the bioluminescent earthworm, *Diplocardia longa*. *Photochem Photobiol* 23:71–5.
- San Martin G. 1990. Eusyllinae (Syllidae, Polychaeta) from Cuba and Gulf of Mexico. *Bull Mar Sci* 46:590–619.
- Sato N, Fukuya S. 2000. Studies on pyrazines. Part 37. Synthesis of 6-propionylpteridine-2,4(1H,3H)-dione and its 1- and/or 3-methyl derivatives from marine natural products. *J Chem Soc Perkin 1* 4:89–95.
- Shimomura O. 1985. Bioluminescence in the sea: photoprotein systems. *Symp Soc Exp Biol* 39:351–72.
- Shimomura O. 2012. Bioluminescence: chemical principles and methods. Hackensack, New Jersey: World Scientific Publishing Company.
- Shimomura O, Johnson FH. (1966) Partial purification and properties of the *Chaetopterus* luminescence system. In: Johnson FH, Haneda Y, editors. Bioluminescence in progress. Princeton: Princeton University Press. p. 495–521.
- Shimomura O, Johnson FH, Saiga Y. 1963. Partial purification and properties of the *Odontosyllis* luminescence system. *J Cell Comp Physiol* 61:275–92.
- Struck TH, Paul C, Hill N, Hartmann S, Hosel C, Kube M, Lieb B, Meyer A, Tiedemann R, Purschke G, et al. 2011. Phylogenomic analyses unravel annelid evolution. *Nature* 471:95–U113.
- Trainor GL. 1979. Studies on the *Odontosyllis* bioluminescence system. Cambridge (MA): Harvard University.
- Tsuji FI, Hill E. 1983. Repetitive cycles of bioluminescence and spawning in the polychaete, *Odontosyllis phosphorea*. *Biol Bull* 165:444–9.
- Wampler JE. 1982. The bioluminescence system of *Microscolex phosphoreus* and its similarities to those of other bioluminescent earthworms (Oligochaeta). *Comp Biochem Physiol Physiol* 71:599–604.
- Wampler JE, Jamieson BGM. 1979. Earthworm bioluminescence: comparative physiology and biochemistry. *Comp Biochem Physiol* 66b:43–50.
- Wampler JE, Jamieson BGM. 1986. Cell bound bioluminescence from *Pontodrilus bermudensis*, and its similarities to other earthworm bioluminescence. *Comp Biochem Physiol* 84:81–7.
- Weigert A, Bleidorn C. 2016. Current status of annelid phylogeny. *Org Divers Evol* 16:345–62.
- Weigert A, Helm C, Meyer M, Nickel B, Arendt D, Hausdorf B, Santos SR, Halanych KM, Purschke G, Bleidorn C, et al. 2014. Illuminating the base of the annelid tree using transcriptomics. *Mol Biol Evol* 31:1391–401.
- Weitz WHJ. 2004. Naturally bioluminescent fungi. *Mycologist* 18:4–5.
- Widder EA. 2001. Marine bioluminescence: why do so many animals in the open ocean make light?. *Harbor Branch Oceanogr Inst* 1:1–9.
- Widder EA. 2010. Bioluminescence in the ocean: origins of biological, chemical, and ecological diversity. *Science* 328:704–8.
- Wood KV. 1995. The chemical mechanism and evolutionary development of beetle bioluminescence. *Photochem Photobiol* 62:662–73.
- Zinner K, Vani YS. 1986. Some characteristics of the mucus of the bioluminescent polychaete *Chaetopterus variopedatus*. *Bol Fisiol Anim* 10:7–14.
- Zörner SA, Fischer A. 2007. The spatial pattern of bioluminescent flashes in the polychaete *Eusyllis blomstrandii* (Annelida). *Helgoland Mar Res* 61:55–66.