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[REVIEW]

The Terrestrial Bioluminescent Animals of Japan

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Light production by organisms, or bioluminescence, has fascinated not only scientists but also ordinary people all over the world, and it has been especially so in Japan. Here we review the biological information available to date for all luminous terrestrial animals known from Japan, particularly focusing on their diversity and systematics, their biology and ecology in Japan, and putative function and biochemistry of their luminescence. In total 58 luminous terrestrial animals have been described from Japan, which consist of 50 fireflies (Coleoptera: Lampyridae), one glowworm beetle (Coleoptera: Phengodidae), two fungus gnats (Diptera: Keroplatidae), one springtail (Collembola), one millipede (Diplopoda), one centipede (Chilopoda) and two earthworms (Oligochaeta). For all except some firefly species, the DNA “barcode” sequences of a cytochrome oxidase subunit I region are provided. We also introduce how intricately the seasonal appearance and glimmering of luminous insects, in particular those of fireflies, have been interwoven into the culture, art, literature and mentality of Japanese people.

Key words: bioluminescence, Japan, firefly, glowworm beetle, fungus gnat, springtail, millipede, centipede, earthworm

INTRODUCTION

Oh, this firefly! — seen by daylight, the nape of its neck is red!

A Haiku versicle by Bashō Matsuo (1644–1694); translated by Lafcadio Hearn (1902).

In summer the nights (is the most beautiful time of the day). Not only when the moon shines, but on dark nights too, as the fireflies flit to and fro, and even when it rains, how beautiful it is!

The Pillow Book (“Makura no Sōshi”, the oldest Japanese essay) by Sei Shōnagon (early 11th century); translated by Ivan Morris (1967).

In the legend of the opening remark for the 1st Conference on Luminescence in Asilomar, California (March 28–April. 2, 1954), Edmund Newton Harvey (1887–1959; a biography by Johnson, 1967), the world’s leading authority on bioluminescence of his time, mentioned that “Japan is like a treasure box of luminous organisms” (Haneda, 1972). Harvey visited Japan in 1916, with his bride, and then again in 1917 to study Japan’s luminous organisms (Johnson, 1967).

While the biology of luminous organisms in Japan has been extensively studied by both Japanese and foreign researchers (Kanda, 1923, 1935; Hasama, 1943; Harvey, 1952; Haneda, 1972, 1985; Ohba, 2009), Sakyō Kanda (1874–1939; biographies by Takasuna, 2005 and Konishi, 2007) (Fig. 1A) and Yata Haneda (1907–1995; biographies by Buck, 1995 and Somiya, 1995) (Fig. 1B) remain important pioneers in this area. Their pioneering efforts have been continued by Nobuyoshi Ohba (1945–; an autobiography by Ohba, 2009), especially in the study of luminescent beetles, and many other contemporary Japanese researchers. Through their ceaseless efforts, the luminous organisms of Japan are well documented. However, since the comprehensive review by Haneda (1955), no review of the luminous organisms of Japan has been published in English.

Here we provide an updated comprehensive review of all luminescent terrestrial animals ever described from Japan, which we expect may be useful to biologists as well as amateur naturalists who are interested in bioluminescence.

Luminous animals from terrestrial habitats

Luminous animals (excluding luminescent bacteria and fungi) are known from some 11 phyla and more than 600 genera (Hastings and Morin, 1991), and most (about 80% of the genera) are oceanic (Haddock et al., 2010; Widder, 2010). By contrast, terrestrial luminous animals have been described from only three phyla (Annelida, Mollusca and Arthropoda) and some 140 genera (Hastings and Morin,

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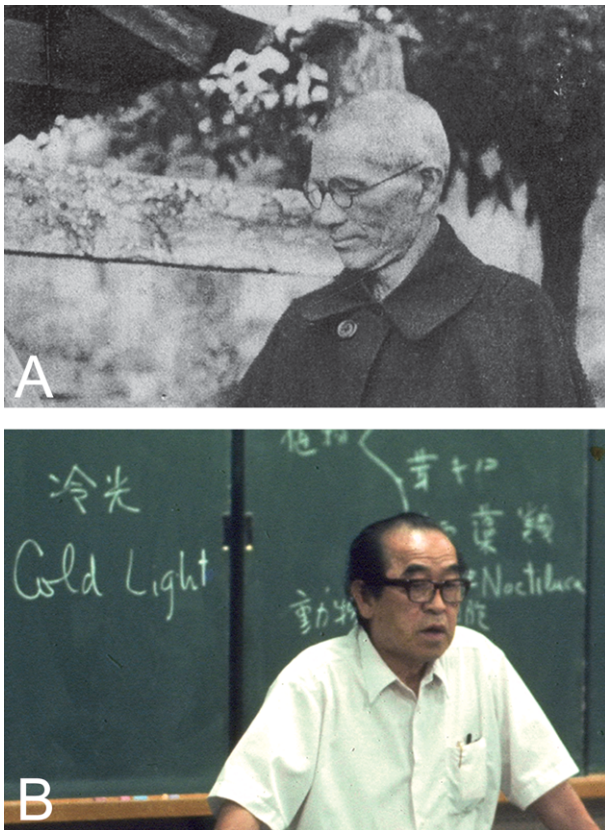


Fig. 1. (A) Sakyo Kanda (copied from Okada, 1939). (B) Yata Haneda (Photo by courtesy of N. Ohba).

1991). As for mollusks, the land snail *Quantula striata* (= *Dyakia striata*; Dyakiidae) in Sundaland is the world's only known terrestrial luminous species (Haneda, 1946, 1963, 1985), and the limpet *Latia neritoides* (Latiidae) in New Zealand is the only freshwater luminous species (Bowden, 1950; Meyer-Rochow and Moore, 1988, 2009). Of these terrestrial luminous animals, 58 species representing 16 genera and two phyla (Arthropoda and Annelida) have been reported from Japan (Table 1).

The Firefly, or “Hotaru”, intricately interwoven into Japanese culture

Luminous beetles of the family Lampyridae, also called fireflies in English and “Hotaru” in Japanese, are traditionally well-known and loved by the Japanese people (Takeda, 2010). Fireflies are prominently featured in the folklore of Japan. Many of these stories have been collected and compiled into several volumes (Watase, 1902; Kanda, 1935; Hara, 1940; Minami, 1961). However, most of these folktales are written in Japanese and have yet to be translated into English. Patrick Lafcadio Hearn (1850–1904), who is known for his books about Japan, collected many Japanese legends and ghost stories. To our knowledge, his essay “Fireflies” (Hearn, 1902) is the only example of Japanese folklore about fireflies that is available in English.

“There are many places in Japan which are famous for fireflies, – places which people visit in summer merely to enjoy the sight of the fireflies” (Hearn, 1902). This description applies to the habit of Japanese people even today (Figs. 2, 3). Firefly species in this context are definitely either *Luciola cruciata* (Figs. 2, 4A, B) or *Luciola lateralis* (=

Table 1. List of the terrestrial luminous animals in Japan (58 species).

	Distribution
Class INSECTA	
Order Coleoptera	
Family Lampyridae	
Subfamily Psilocladinae (Cyphonocerinae)	
1. <i>Cyphonocerus inelegans</i> Nakane, 1967	Honshu (Mie Pref., Wakayama Pref.)
2. <i>Cyphonocerus marginatus</i> Lewis, 1895	Shikoku, Kyushu
3a. <i>Cyphonocerus okinawanus okinawanus</i> Nakane, 1983	Ryukyu Isls. (Okinawa Isl.)
3b. <i>Cyphonocerus okinawanus amamianus</i> Jeng, Yang et M. Satō, 1998	Amami Isls. (Amami Isl.)
4. <i>Cyphonocerus ruficollis</i> Kiesenwetter, 1879	Honshu, Shikoku, Kyushu, Izu Isls.
5. <i>Cyphonocerus watarii</i> M. Satō, 1991	Kyushu (Fukuoka Pref.)
6. <i>Cyphonocerus yayeyamensis</i> M. Satō, 1976	Ryukyu Isls. (Ishigaki Isl., Iriomote Isl.)
Subfamily Otoretinae	
7. <i>Drilaster akakanajai</i> Kawashima, Satou et M. Satō, 2005	Ryukyu Isls. (Iheya Isl.)
8. <i>Drilaster akusekianus</i> Nakane, 1983	Tokara Isls. (Akuseki Isl.)
9. <i>Drilaster axillaris</i> Kiesenwetter, 1879	Hokkaido, Honshu, Shikoku, Kyushu
10. <i>Drilaster bicolor</i> M. Satō, 1968	Amami Isls. (Amami Isl.)
11. <i>Drilaster flavocephalicus</i> Kawashima, Satou et M. Satō, 2005: Syn. <i>Drilaster flavicollis</i> Nakane, 1977	Ryukyu Isls. (Yonaguni Isl.)
12a. <i>Drilaster fuscicollis fuscicollis</i> Nakane, 1977	Ryukyu Isls. (Okinawa Isl.)
12b. <i>Drilaster fuscicollis keramensis</i> Kawashima, Satou et M. Satō, 2005	Ryukyu Isls. (Tokashiki Isl.)
13. <i>Drilaster iokii</i> M. Satō, 1968	Amami Isls. (Tokunoshima Isl.)
14. <i>Drilaster kumejimensis</i> Kawashima, Satou et M. Satō, 2005	Ryukyu Isls. (Kumejima Isl.)
15. <i>Drilaster nigroapicalis</i> Kawashima, Satou et M. Satō, 2005	Amami Isls. (Tokunoshima Isl.)
16. <i>Drilaster ohbayashii</i> M. Satō, 1968	Ryukyu Isls. (Ishigaki Isl., Iriomote Isl.)
17. <i>Drilaster okinawensis</i> Nakane, 1977	Ryukyu Isls. (Okinawa Isl.)
18. <i>Drilaster ruficollis</i> Kawashima, Satou et M. Satō, 2005	Ryukyu Isls. (Ishigaki Isl.)
19. <i>Drilaster shibatai</i> M. Satō, 1968: Syn. <i>Drilaster anomalus</i> Nakane, 1977	Amami Isls. (Amami Isl.)
20. <i>Drilaster tenebrosus</i> Kawashima, Satou et M. Satō, 2005	Ryukyu Isls. (Okinawa Isl.)
21. <i>Drilaster unicolor</i> Lewis, 1895	Kyushu (Kumamoto Pref., Kagoshima Pref., Yaku Isl.)

Continued

Table 1. Continued.

22. <i>Stenocladius azumai</i> Nakane, 1981	Ryukyu Isls. (Okinawa Isl.)
23. <i>Stenocladius flavipennis</i> Kawashima, 1999	Ryukyu Isls. (Kumejima Isl.)
24. <i>Stenocladius yoshikawai</i> Nakane, 1981: Syn. <i>Stenocladius shirakii</i> Nakane, 1981	Ryukyu Isls. (Ishigaki Isl., Iriomote Isl.)
25. <i>Stenocladius yoshimasai</i> Kawashima, 1999 Subfamily Luciolinae	Amami Isls. (Amami Isl.)
26. <i>Luciola cruciata</i> Motschulsky, 1854	Honshu, Shikoku, Kyushu, Tsushima Isls.
27. <i>Luciola filiformis yayeyamana</i> Matsumura, 1918: Syn. <i>Luciola yayeyamana</i> Matsumura, 1918	Ryukyu Isls. (Ishigaki Isl., Iriomote Isl.)
28. <i>Luciola kuroiwae</i> Matsumura, 1918	Amami Isls. (Amami Isl.), Okinawa (Okinawa Isl., Kumejima Isl.)
29. <i>Luciola lateralis</i> Motschulsky, 1860: Syn. <i>Aquatica lateralis</i> (Motschulsky, 1860)	Hokkaido, Honshu, Shikoku, Kyushu, Tsushima Isls., Korea, Siberia
30. <i>Luciola owadai</i> M. Satō et M. Kimura, 1994	Ryukyu Isls. (Kumejima Isl.)
31. <i>Luciola parvula</i> Kiesenwetter, 1874: Syn. <i>Hotaria parvula</i> (Kiesenwetter, 1874)	Honshu, Shikoku, Kyushu, Goto Isls.
32. <i>Luciola tsushimana</i> Nakane, 1970: Syn. <i>Hotaria tsushimana</i> (Nakane, 1970)	Tsushima Isls.
33. <i>Curtos costipennis</i> (Gorham, 1880)	Tokara Isls., Amami Isls., Ryukyu Isls., Taiwan, South East China
34. <i>Curtos okinawanus</i> Matsumura, 1918 Subfamily Lampyrinae	Amami Isls., Ryukyu Isls.
35. <i>Pyrocoelia abdominalis</i> Nakane, 1977	Ryukyu Isls. (Ishigaki Isl., Iriomote Isl., Kohama Isl.)
36. <i>Pyrocoelia atripennis</i> Lewis, 1896	Ryukyu Isls. (Yaeyama Isls.)
37. <i>Pyrocoelia discicollis</i> (Kiesenwetter, 1874)	West Honshu, Shikoku, Kyushu
38. <i>Pyrocoelia fumosa</i> (Gorham, 1883)	East Honshu
39. <i>Pyrocoelia iriomotensis</i> Nakane, 1985	Ryukyu Isls. (Iriomote Isl.)
40a. <i>Pyrocoelia matsumurai matsumurai</i> Nakane, 1963	Ryukyu Isls. (Okinawa Isl.)
40b. <i>Pyrocoelia matsumurai kumejimensis</i> (Chūjō et M. Satō, 1972)	Ryukyu Isls. (Kumejima Isl.)
41. <i>Pyrocoelia miyako</i> Nakane, 1981	Ryukyu Isls. (Miyako Isls.)
42. <i>Pyrocoelia oshimana</i> Nakane, 1985	Amami Isls. (Amami Isl.)
43. <i>Pyrocoelia rufa</i> E. Olivier, 1886	Tsushima Isls., Korea, Jeju, China
44. <i>Lucidina accensa</i> Gorham, 1883	Honshu, Shikoku, Kyushu
45. <i>Lucidina biplagiata</i> (Motschulsky, 1866)	Hokkaido, Honshu, Shikoku, Kyushu, Korea, Kuril Isls., Sakhalin
46. <i>Lucidina natsumiae</i> Chūjō et M. Satō, 1972	Ryukyu Isls. (Iriomote Isl.)
47. <i>Lucidina okadai</i> Nakane et Ohbayashi, 1949	Honshu (Mie Pref., Gifu Pref.)
48a. <i>Pristolytus sagulatus sagulatus</i> Gorham, 1883	Hokkaido, Honshu, Kyushu, Kuril Isls.
48b. <i>Pristolytus sagulatus adachii</i> M. Satō, 1986	West Honshu, Shikoku, Kyushu
48c. <i>Pristolytus sagulatus amami</i> Nakane, 1961	Amami Isls. (Amami Isl.)
49. <i>Pristolytus shikokensis</i> Ohbayashi et M. Satō, 1963	Shikoku (Ehime Pref.)
50. <i>Pyropyga</i> sp. Family Phengodidae Subfamily Rhagophthalminae	Honshu (Tokyo, Saitama, Kanagawa), North America (?)
51. <i>Rhagophthalmus ohbai</i> Wittmer, 1994	Ryukyu Isls. (Ishigaki Isl., Iriomote Isl., Kohama Isl.)
Order Diptera Family Keroplatidae Subfamily Keroplatinae	
52. <i>Keroplatus nipponicus</i> (Okada, 1938)	Hokkaido, Honshu, Izu Isls. (Hachijo Isl.)
53. <i>Keroplatus biformis</i> (Okada, 1938): Syn. <i>Ceroplatus testaceus</i> Dalman, 1818 f. <i>biformis</i> Okada, 1938	Hokkaido, Honshu, Russia Far East
Class ENTOGNATHA	
Order Collembola Family Neanuridae	
54. <i>Lobella</i> sp.	Honshu (Tokyo)
Class DIPLOPODA	
Order Spirobolida Family Spirobolellidae	
55. <i>Paraspirobolus lucifugus</i> (Gervais, 1836): Syn. <i>Spirobolellus phosphoreus</i> Takakuwa, 1941; <i>Spirobolellus takakuwai</i> Wang, 1961	Tropical cosmopolitan (incl. Okinawa Isl., Taiwan)
Class CHILOPODA	
Order Geophilomorpha Family Oryidae	
56. <i>Orphnaeus brevilabiatus</i> (Newport, 1845)	Tropical and Subtropical cosmopolitan (incl. Okinawa Isl., Taiwan)
Class OLIGOCHAETA	
Order Haptotaxida Family Acanthodrilidae	
57. <i>Microscolex phosphoreus</i> (Dugès, 1837)	Cosmopolitan (incl. Honshu, Shikoku, Kyushu, Europe, North and South America)
Family Megascolecidae	
58. <i>Pontodrilus litoralis</i> (Grube, 1855): Syn. <i>Pontodrilus bermudensis</i> Beddard, 1891; <i>Pontodrilus matsushimensis</i> Iizuka, 1898	Cosmopolitan (incl. Honshu, Kyushu)

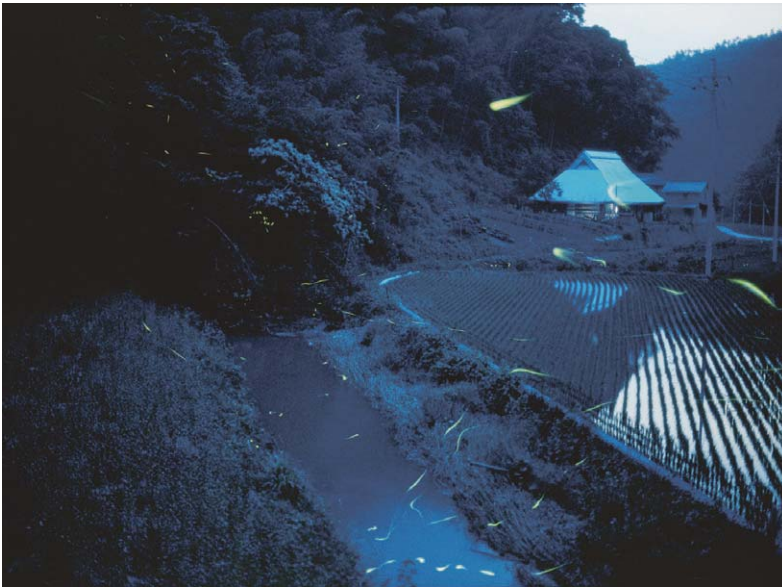


Fig. 2. Glimmering adult insects of the Genji-botaru firefly, *Luciola cruciata*, swarming over a stream flowing across rice paddies in a Satoyama area at Takahashi, Okayama Pref., Japan. Photo by courtesy of R. Ohara.



Fig. 3. Fireflies in Japanese arts. Ukiyo-é pictures depicting the activity of “Hotaru-gari” or firefly hunting: **(A)** “Fireflies in Summerhouse” (datable to ca. 1890) by Yōshū (Hashimoto) Chikanobu, 330 × 670 mm; and **(B)** “Negishi Village” (1872) by Shōsai Ikkei, 330 × 225 mm. **(C)** A small “Imari” Saké cup (height, 62 mm) (late 17-early 18 century). Fireflies on grasses are drawn in front (top), and a Chinese poem by Hsü Hun in the “Wakan Rōei Shū” (compiled in ca. 1013) is printed behind (bottom). The poem means: “A single song of the mountain bird beyond the clouds of dawn; ten thousand water-fireflies, points in autumnal grass” (translated by Rimer and Chaves, 1997). **(D)** A traditional firefly cage woven with straws (height, 130 mm).

Aquatica lateralis; Fu et al., 2010) (Fig. 4C, D), the most common and popular luminous insects in the mainland Japan. The larger species, *L. cruciata*, is called “Genji-botaru” in Japanese, which comes from “The Tale of Genji” (or “Genji Monogatari” in Japanese). This tale, which is rated among the world’s oldest novels (Tyler, 2006), describes the life of a fictitious character, the second son of the emperor named “Hikaru Genji (= Shining Genji)” (Kanda, 1935; Minami, 1961; Konishi, 2007). On the other hand, the lesser species, *L. lateralis*, called “Héiké-botaru” in Japanese, after the name of the major clan “Héiké” in the 11th century that was defeated by another major clan “Genji” in the Genpei War (1180–1185) (Kanda, 1935; Minami, 1961; Konishi, 2007). The name “Héiké-botaru” probably reflects the smaller body size of *L. lateralis* in comparison with *L. cruciata* (Kanda, 1935; Minami, 1961; Konishi, 2007).

Here, for non-Japanese readers, we point out a euphonic change between “Hotaru” and “-botaru” in the Japanese language. The same word is pronounced as “Hotaru” when it stands alone, whereas the pronunciation changes into “-botaru” with a prefix, like “Genji-botaru”.

Impressively, these two firefly species, *L. cruciata* and *L. lateralis*, have been frequently depicted as essential items in a number of Japanese traditional verses “Waka” (mainly from 8th to 12th century) and “Haiku” (from 17th century and on) (Blyth, 1963), drawn in old Japanese woodblock pictures “Ukiyo-é” (from 17th to 19th century; Kobayashi, 1992) (Fig. 3A, B), and painted on sophisticated porcelains such as “Imari” (from 17th century and on; Nagatake, 2003) (Fig. 3C).

William Elliot Griffis (1843–1928), an American orientalist as well as a prolific writer, compiled the book “The Fire-fly’s Lovers and Other Fairy Tales of Old Japan” (Griffis, 1908), wherein the first chapter “The Fire-fly’s Lovers” narrates a fairy tale as to why young Japanese girls love to catch fireflies. Indeed, not only girls but also boys, as well as adults have traditionally enjoyed chasing and catching fireflies in Japan (Fig. 3A, B), and the activity is called “Hotaru-gari” (= firefly hunting). Adult fireflies, mainly *L. cruciata*, have been commercially available in Japan since the late 17th century (Konishi, 2007), and people purchased the insects in order to enjoy their bioluminescent displays (Fig. 3D). This tradition remains, as one can easily find a number of companies online that mass-culture and sell fireflies. All Japanese people must remember a traditional children’s song “Hotaru Koi” (= Come, fireflies):

Ho, ho, ho, firefly.

Come, there's some water that's bitter to taste.

Come, here's some water that's sweet to your taste.

Ho, ho, ho, firefly.

(Translated by David Larson; Ongaku no Tomo Sha Co., 1979)

Why are these two firefly species so popular in Japan? *L. cruciata* (Fig. 4A, B) and *L. lateralis* (Fig. 4C, D) are distributed throughout the Japanese main islands, Honshu, Shikoku, and Kyushu (and also Hokkaido for *L. lateralis*). The larvae of both species are aquatic and inhabit streams and rice paddies. The adults can be seen flying over these aquatic habitats, emitting bright yellow-green flashes of light in the evening during early mid-summer (Fig. 2). Traditionally, most Japanese people have lived in a suburb-like environment called "Satoyama" (Takeuchi, 2003), where they

cultivate paddy rice using water from nearby streams. Perhaps for this reason, the glimmering lights of fireflies have been deeply imprinted in the Japanese mind, signaling a seasonal change (Fig. 2).

Since the larvae of *L. cruciata* and *L. lateralis* require clean water environments, populations have been decreasing in recent years due to land development and water pollution. Today the charming tradition of capturing fireflies is in decline due to the increasing need to conserve local populations. Numerous volunteers and organizations are actively assisting efforts to protect and rehabilitate firefly populations and their habitats. Several areas that serve as good habitats for *L. cruciata*, where the beauty of the firefly swarming is reputed to be outstanding, have been designated as natural monuments (Nagaoka, Shiga Pref. and Ishinoyu, Nagano Pref., Japan, etc.) by the Japanese government. On the other hand, these activities have caused a new problem –

the genetic contamination of local firefly populations. It is clear that good-intentioned individuals and organizations have introduced fireflies from remote localities into local streams for the purpose of population recovery. Recently, however, experts are warning of the risk that the original genetic structure of the local firefly populations could be disturbed by such activities (Ohba, 2006). In Japan, few other insects attract such a high level of attention by ordinary people. In this context, *L. cruciata* and *L. lateralis* can be regarded as "flagship species" (Maeda, 1996), which, like giant pandas and mountain gorillas, generate profound interest and strong emotional reactions in many people (Cunningham and Cunningham, 2009).

Luminous beetles (Insecta: Coleoptera)

The insect order Coleoptera contains the greatest number of species in the animal kingdom. Some 350,000 species have been described worldwide (Grimaldi and Engel, 2005), and many luminous species are known from the families Elateridae, Lampyridae and Phengodidae, which are placed in the superfamily Elateroidea. We note that a recent taxonomic treatise regarded the Rhagophthalminae, a subfamily of the Phengodidae, as comprising a distinct family Rhagophthalmidae (Lawrence et al., 2010; Kawashima et al., 2010). Although there are sporadic reports of luminous beetles belonging to species in the Omalidae (Berkau, 1891), the Eucnemidae (Costa, 1984) and the Staphylinidae (Costa et al., 1986), these reports need to be confirmed (Burakowski, 1988; Grimaldi and Engel, 2005; Bocakova et al., 2007; Oba, 2009). Members of the Elateridae, known as click beetles, are widespread throughout

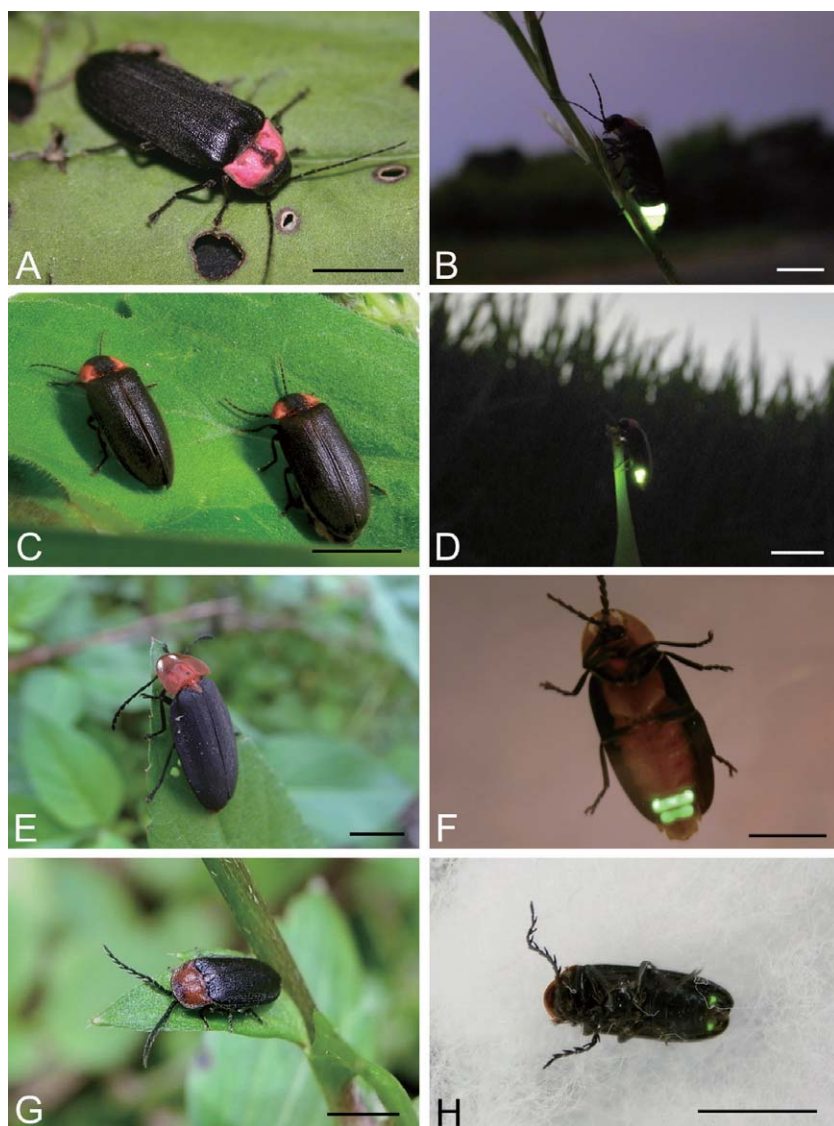


Fig. 4. Luminous adult fireflies of the Lampyridae. (A, B) *Luciola cruciata* (adult males). (C, D) *Luciola lateralis* (right of panel C, adult female; left of panel C and panel D, adult males). (E, F) *Pyrocoelia atripennis* (adult males). (G, H) *Cyphonocerus ruficollis* (adult males). Bars show 5 mm.

the world with ~9,000 described species; the luminous species of this family (~200 species) being restricted to tropical and subtropical America and Melanesia (Costa, 1975; Lloyd, 1978). By contrast, all known species of the Lampyridae and the Phengodidae are luminous, at least during their larval stages (Crowson, 1972; Branham and Wenzel, 2003). To date, 50 lampyrid and one phengodid species have been recorded from Japan (Table 1).

Fireflies (Lampyridae)

Diversity and systematics. The monophyly of the Lampyridae was supported by recent molecular phylogenetic analyses on the basis of nuclear 18S ribosomal RNA gene sequences (Sagegami-Oba et al., 2007; Bocakova et al., 2007). By contrast, the monophyly was not supported by phylogenetic analyses of mitochondrial 16S ribosomal RNA gene sequences, where a phengodid genus *Rhagophthalmus* was placed within the lampyrid clade (Suzuki, 1997; Li et al., 2006; Stanger-Hall et al., 2007). The Lampyridae contains eight subfamilies, ~100 genera and ~2,000 species worldwide (Crowson, 1972; Lawrence and Newton, 1995; Lawrence, 1982), of which four subfamilies, nine genera and 50 species have been reported from Japan (Kawashima et al., 2003, 2005; Ohba, 2004a, 2009; Table 1).

Biology of luminous species in Japan. Among the 50 Japanese lampyrids, 30 species are endemic to southwestern remote islands such as Tokara, Amami, and Ryukyu Islands (Kawashima et al., 2003; Ohba, 2004a, 2009). Fireflies are famous for the bright, flashing, luminous displays of the adults, but only 12 Japanese species are brightly luminous in both sexes of the adult stage. Nine of these species are assigned to the genera *Luciola* (Fig. 4A–D) and *Curtos* in the Luciolinae and produce blinking flash patterns, while *Pyrocoelia rufa*, *Pyrocoelia miyako*, and *Pyrocoelia atripennis* (Fig. 4E, F) produce continuously glowing emissions (Ohba, 2009). The remaining species are weakly luminous or non-luminous in the adult stage. For the species of *Cyphonocerus* spp. (male and female) (Fig. 4G, H), *Pyrocoelia* spp. (other than *P. rufa*, *miyako* and *atripennis*; male and female) and *Stenocladus* spp. (female), a weak but continuous luminescence can be detected. The luminescence in adult males and females of the genera *Lucidina* (Fig. 5A), *Pristolytus* and *Drilaster* (Fig. 5B) as well as *Stenocladus* males (Fig. 5C) are undetectable by the human eye (Ohba, 2004a). Bright larval luminescence has been recognized in *L. cruciata*, *L. lateralis* and many other species. It is thought that all lampyrid species are luminous at the larval stage, which probably functions as a warning display (Sivinski 1981; Branham and Wenzel, 2003). For *L. cruciata* and other species, their eggs and pupae are also known to be luminous (Ohba, 2004a; Oba et al., 2010a). There is a putatively invasive firefly species in Japan, whose name and origin have yet to be established (Fig. 5D). This species, listed as *Pyropyga* sp. in Mito and Uesugi (2004), has been collected from the sides of the



Fig. 5. Non-luminous adult fireflies of the Lampyridae. (A) *Lucidina biplagiata* (adult male). (B) *Drilaster ohbayashii* (adult female?) (Photo by courtesy of T. Fukaiishi). (C) *Stenocladus yoshikawai* (adult male). (D) *Pyropyga* sp. (adult female?). Bars show 5 mm.

Edogawa, Arakawa, and Tamagawa rivers around the Tokyo area. In 1986, one of the authors (T. F.) collected unknown firefly specimens at a pier on Tokyo Bay and sent the specimens to Dr. N. Ohba, who recognized them as new in Japan (Ohba, 2004a). An earlier specimen was found in a 1983 insect collection at Tamagawa river (Kaneko, 1997), suggesting that the species had already been introduced to Tokyo in the early 1980's. The adults of this species are approximately 5 mm long (Fig. 5D) and apparently non-luminous.

Most Japanese people regard fireflies as aquatic insects, probably due to their familiarity with *L. cruciata* and *L. lateralis*, which they observe flying and flashing around riversides. Actually, the larvae of most lampyrid species are terrestrial and feed on land snails, earthworms, and other animals (McDermott, 1964), while some larvae are known to be subterranean or arboreal (Branham, 2010). Only three Japanese species, *L. cruciata*, *L. lateralis* and *Luciola owadai*, and a few other species in Southeast Asia are known to be aquatic at the larval stage and feed exclusively on freshwater snails (Ohba, 1999, 2004a).

One of the most spectacular events involving luminescent animals in Japan is the large number of flying males of *L. cruciata* flashing in synchrony (Ohba, 1984, 2009) (Fig. 2). Synchronous flashing is also observed in several other Luciolinae species in the genera *Pteroptyx* and *Pyrophanes* in Southeastern Asia, which gather on trees in dense swarms (Buck, 1938; Ohba, 1984; Ohba and Shimoyama, 2009).

Among Japanese local populations of *L. cruciata*, distinctive geographical variations have been identified in the flash patterns of flying adult males (Kanda, 1935; Ohba, 1984, 2001, 2004b; Tamura et al., 2005). The flash intervals are generally about 4 seconds (slow-flash type) in populations of the northern Japan (to the north of the Fossa Magna region of Honshu), and about 2 seconds (fast-flash type) in

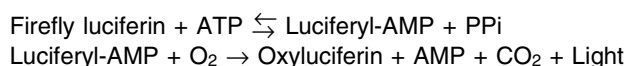
the southern Japan (to the south of the Fossa Magna region of Honshu, and Shikoku and Kyushu). Analysis of their mitochondrial cytochrome oxidase II gene revealed three major haplotype groups, namely northern Honshu group, southern Honshu and Shikoku group, and Kyushu group. Among these, the former two groups are more closely related, suggesting the possibility that the populations of the slow-flash type may be derived from the populations of the fast-flash type (Suzuki et al., 2002).

Function of luminescence. Previous studies have shown that the major functions of adult luminescence in fireflies are sexual communication and aposematic display (Branham and Greenfield, 1996; Branham and Wenzel, 2003; Ohba, 2004a; Lewis and Cratsley, 2008; Lewis, 2009). The adult fireflies of luminous species have comparatively large eyes. By contrast, non-luminous and weakly luminous species have well-developed male antennae (see Fig. 5A, C) and mainly use pheromones for sexual communication (Lloyd, 1972; Ohba, 2004a, b; De Cock and Matthysen, 2005). Aggressive mimicry involving bioluminescent signals is known in some North American *Photuris* and *Bicellonycha* fireflies, whose females mimic the flash patterns of *Photinus* or *Pyraclomena* females, thereby attracting males of these species as prey (Lloyd, 1975). Based on luminescence characters (flash, glow or non-luminescent) and pheromone usage, Ohba (1983, 2004a, b) classified the sexual communication behaviors of Japanese fireflies into six types. On the basis of morphological and molecular data, the evolution of communication systems in the Lampyridae has been inferred and discussed by several authors (Branham and Wenzel, 2003; Suzuki, 1997; Stanger-Hall et al., 2007). These studies consistently suggest that the loss of adult luminescence has occurred multiple times during the evolution of the Lampyridae. In some “non-luminous fireflies,” a very weak luminescence has been measured, as in the adults of *Lucidina biplagiata* (Ohba, 1983; Oba et al., 2010b) (Fig. 5A).

Cantharoid beetles, representing the families Cantharidae, Lycidae, Lampyridae and Phengodidae, are characterized by their leathery soft elytra, soft-bodies, their conspicuous color and/or their luminescence, and many of them are known to contain defensive chemicals (Grimaldi and Engel, 2005). In the Lampyridae, many species exhibit reflex bleeding, and the excreted fluid is stinky, distasteful and repellent to predators (Lloyd, 1973; Ohba and Hidaka, 2002). Eisner et al. (1978) demonstrated that fireflies possess defensive steroids in effective quantities to deter predation. Lizards, birds and mice quickly learn to associate bioluminescence with a distasteful organism (Underwood et al., 1997; De Cock and Matthysen, 1999, 2003; Knight et al., 1999). Hence, it has been suggested that their luminescence may be for aposematic display (Lloyd, 1973; Ohba and Hidaka, 2002), akin to the conspicuous coloration of non-luminous cantharoids (Sagegami-Oba et al., 2007). Larval luminescence of lampyrid species seems to be also for aposematic display (Sivinski, 1981; Underwood et al., 1997; De Cock and Matthysen, 2003; Branham and Wenzel, 2003). Based on the fact that all known lampyrid species are luminous as larvae (Branham and Wenzel, 2003), it has been argued that bioluminescence in the Lampyridae had first evolved as an aposematic signal and was subsequently co-opted as a

courtship signal (Branham and Wenzel, 2003).

Biochemistry of luminescence. The North American firefly *Photinus pyralis* and the Japanese firefly *L. cruciata* (Fig. 4A, B) have been the main subjects of studies into the mechanisms of bioluminescence. In general, bioluminescence is produced through chemical reactions in which substrates, called luciferins, and enzymes, called luciferases, are involved in the production of light (Shimomura, 2006). Biochemical studies revealed that the firefly luciferin, (4S)-4,5-dihydro-2-(6-hydroxy-2-benzothiazolyl)-4-thiazolecarboxylic acid, is structurally identical between *P. pyralis* and *L. cruciata* (White et al., 1961; Kishi et al., 1968). It is believed that the luciferin structure is the same among all lampyrid species (Seliger and McElroy, 1964). The lampyrid luciferase gene was isolated for the first time from *P. pyralis* (de Wet et al., 1985, 1987) and then from *L. cruciata* (Tatsumi et al., 1989). To date, luciferase genes have been isolated from over 20 firefly species, including 10 Japanese species: *L. cruciata*, *L. lateralis*, *Luciola parvula*, *Luciola tsushima*, *P. miyako*, *P. rufa*, *L. biplagiata*, *Cyphonocerus ruficollis*, *Drilaster axillaris* and *Stenocladus azumai*. From *L. cruciata*, two types of luciferase genes were detected (Oba et al., 2010a). The identities of amino acid sequences (about 550 residues) among firefly luciferases are > 53%. The luciferin-luciferase reaction in fireflies is represented by a common two-step reaction:



The colors of lampyrid luminescence vary from green to yellow depending on species, and the spectra of luminescence in vivo are in agreement with those of the luciferin-luciferase reaction in vitro under optimal pH conditions (pH around 7.8) (Seliger and McElroy, 1964). Accordingly, the color of luminescence is determined by the excited state of oxyluciferin depending on the active site structure of the luciferase enzyme (Nakatsu et al., 2006). This reaction is generally considered to have the highest known quantum yield (0.41) of any bioluminescence system based on the conversion of substrate (luciferin) into photons (Ando et al., 2008).

Glowworm beetles (Phengodidae)

Diversity and systematics. Crowson (1972) recognized the family Phengodidae as consisting of the subfamilies Phengodinae and Rhagophthalminae (Rhagophthalmidae *sensu* Wittmer and Ohba, 1994). The Phengodinae and the Rhagophthalminae are geographically restricted to the New World and the Old World, respectively (Lawrence, 1982). Based on a phylogenetic analysis of morphological characters, Branham and Wenzel (2001) recovered rhagophthalmine taxa as being distinct from the Phengodidae and on the basis of this finding, restored the Rhagophthalmidae to family status, thereby removing *Rhagophthalmus*, *Diptotoma*, *Menghuoius*, *Mimochotyra*, *Dodecatoma* and *Diplocladon* from the Phengodidae (Kawashima et al., 2010). Meanwhile, recent molecular phylogenetic analyses suggested sister relationships between the Phengodinae and the Rhagophthalminae (Sagegami-Oba et al., 2007; Bocakova et al., 2007). Here we conservatively regard the Rhagophthalminae as a subfamily of the Phengodidae. The Phengodidae

embraces about 35 genera and 200 species in the world (Lawrence, 1982), of which a single species, *Rhagophthalmus ohbai*, has been recorded from Iriomote, Ishigaki and Kohama Islands, Japan (Ohba, 2004a, 2009) (Fig. 6; Table 1).

Biology of luminous species in Japan. Larviform adult females of *Rhagophthalmus ohbai* (Fig. 6B–D) were found at Iriomote Island for the first time in 1985 (Ohba, 2009). Adult males (Fig. 6A) were later discovered by using a living female as lure (Ohba, 2009), and described as new species (Wittmer and Ohba, 1994). Larvae and adult females possess a median dorsal and two post lateral light organs on each body segment from the mesothorax to the 8th abdominal segment (Ohba et al., 1996). Adult females also possess a single large ventral light organ on the 8th abdominal segment (Ohba et al., 1996), which emits a blight yellow light (Wittmer and Ohba, 1994) (Fig. 6C). Adult males have no light organs, but a weak luminescence was observed in the ventral surface of the abdomen (Ohba, 2004a).

Function of luminescence. The function of luminescence in the phengodid larvae has been suggested as an aposematic signal (Viviani and Bechara, 1997; Grimaldi and Engel, 2005). A discharge of colored, non-luminous fluid has been observed in several species representing different genera (Sivinski, 1981), including *R. ohbai* (Ohba, 2004a). A brownish substance with inflammatory activity was identified from *Phrixothrix* larvae (Sivinski, 1981), and a caustic odor was reported to be characteristic of *Rhagophthalmus* larvae (Raj, 1957; Ohba, 2004a). The luminescence of adult females of *R. ohbai* is apparently for sexual communication: females display their ventral light organs on the 8th abdominal segment upwards into the air for attracting males (Ohba, 2004a) (Fig. 6C). After oviposition, females encircle their eggs with their body, emitting light from their dorsal and lateral light organs (but not from the ventral light organ used for attracting males), especially when disturbed (Fig. 6D). Ohba (2004a) suggested that this luminescent behavior may function as an aposematic display.

Biochemistry of luminescence. The chemical structure of the luciferin in phengodid species is suggested to be the same as that in lampyrids (Viviani and Bechara, 1993). Luciferase genes have been isolated from four phengodid species, *Phengodes* sp., *Phrixothrix vivianii*, *Phrixothrix hirtus* and *R. ohbai*, whose luminescence spectra in vitro at pH 8.0 showed a peak at 549 nm, 549 nm, 622 nm and 554 nm, respectively (Gruber et al., 1996; Viviani et al., 1999; Ohmiya et al., 2000). The amino acid identities among phengodid luciferases are 67–72%, and those between phengodids and lampyrids are 47–57%. Interestingly, the luminescence spectra of phengodid luciferases are not influenced by pH conditions in vitro (Viviani et al., 2008), which is in contrast to the observation that the spec-

tra of the lampyrid luciferases are shifted to red under acidic pH conditions (but LcLuc2 newly identified from *L. cruciata* exceptionally lacks such pH dependency; Oba et al., 2010a). These data suggest that the mechanism of lumines-

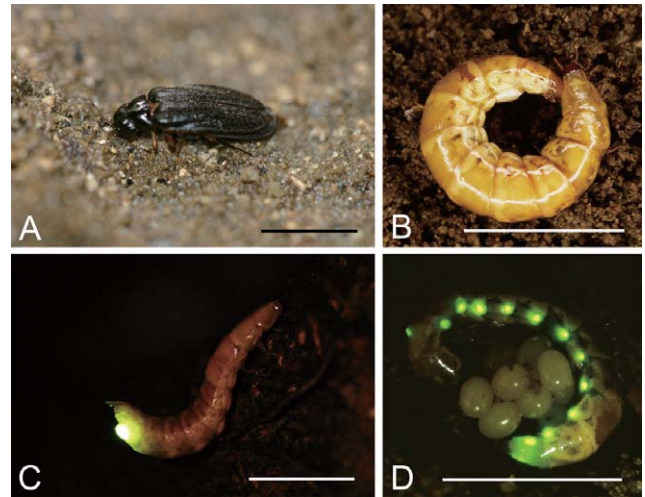


Fig. 6. The luminous glowworm beetle, *Rhagophthalmus ohbai*, of the Phengodidae. (A) A beetle-form adult male. (B) A larviform adult female. (C) An adult female raising the caudal photophore and emitting light for attracting male. (D) An adult female protecting her eggs. Photos by courtesy of N. Ohba. Bars show 5 mm.

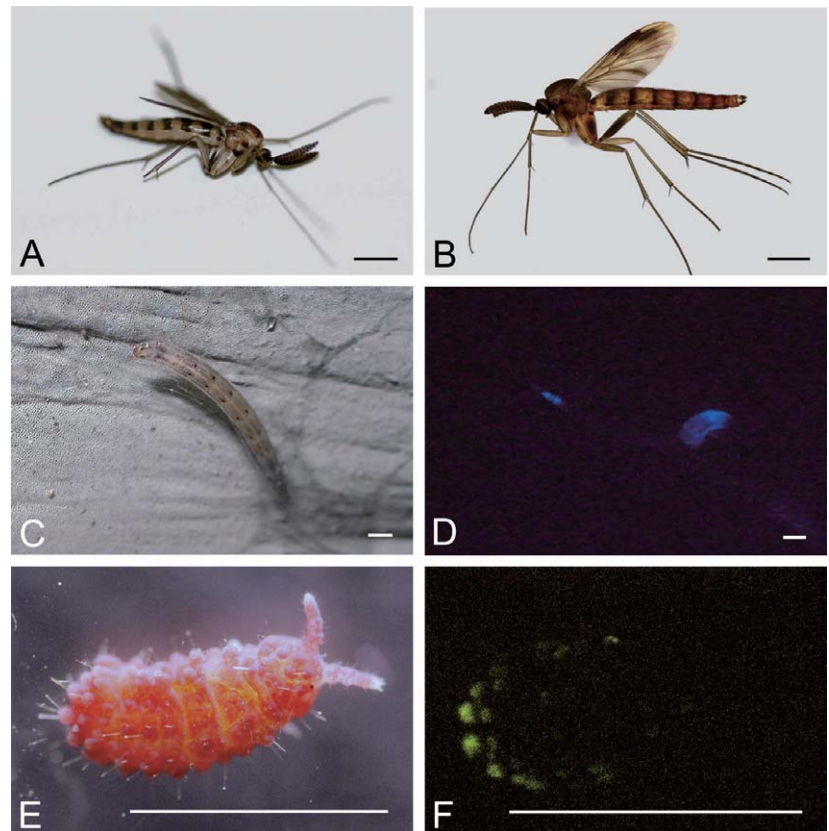


Fig. 7. The luminous true flies of the Keroplatidae (A–D) and the luminous springtail of the Collembola (E, F). (A) An adult male of *Keroplatus nipponicus*. (B) An adult male of *Keroplatus bififormis*. (C, D) Larvae of *K. nipponicus*. (E, F) *Lobella* sp. Photos by courtesy of S. Yamashita (A), K. Ichige (B) and Y. Minagoshi (E, F). Bars show 2 mm.

cence in the Phengodidae is basically the same as the mechanism in the Lampyridae, although the active sites of the enzymes may have different properties. Molecular phylogenetic analyses did not support a sister group relationship between the Lampyridae and the Phengodidae (Sagegami-Oba et al., 2007; Bocakova et al., 2007; Arnoldi et al., 2007), except for a recent mitochondrial genome analysis (Timmermans et al., 2010). Therefore, whether or not the same bioluminescence system has independently evolved in the Lampyridae and the Phengodidae is an open question deserving future studies (Oba, 2009).

Luminous true flies (Insecta: Diptera)

Diversity and systematics. The order Diptera (true flies) contains about 150 families and 150,000 species (Yeates et al., 2007). Despite the huge diversity, only a small number of luminous species are known from a single family Keroplatidae (Sciarioidea, fungus gnats). The Keroplatidae consists of 86 genera and about 1,000 species (Evenhuis, 2006), of which the genera *Arachnocampa* (Arachnocampinae), *Keroplatus* (Keroplattini, Keroplatinae), and *Orfelia* (*O. fultoni*, = *Neoplatyura fultoni* and *Platyura fultoni*; Orfeliini, Keroplatinae) contain luminous species (Fulton, 1941; Baccetti et al., 1987; Matile, 1997; Evenhuis, 2006). The presence of luminescence in *Mallochinus* (*M. mastersi*, formerly *Ceroplatus mastersi*; Keroplattini, Keroplatinae) is uncertain, and an unknown luminous species was found in New Guinea (Lloyd, 1978). The genus *Arachnocampa* currently comprises 9 species, with 8 species distributed in Australia (including Tasmania) and a single species, *A. luminosa* in New Zealand (Baker, 2009, 2010). A related species was found in the Fiji Islands but the species name has not been identified (Harvey, 1952). Larvae of all *Arachnocampa* species live and glow on the ceiling of caves or overhanging riverbanks, and are well known as “glowworms” for tourism. Pupae of *A. luminosa* were reported to be luminous, and the light intensity was stronger in females than in males (Richards, 1960; Meyer-Rochow, 2007). The Tama Zoological Park, Tokyo, Japan, has been successfully maintaining the Australian luminous keroplatid *Arachnocampa richardsae* since 1987 (Takaie, 1997; Meyer-Rochow, 2007; H. Takaie, personal communication). The genus *Keroplatus* contains 26 species worldwide, of which the following 5 species have been reported to produce faint light at the larval and pupal stages: *K. nipponicus* (distributed in Japan; “Nippon-Hirata-Kinoko-Bae” or “Mitsuboshi-Hirata-Kinoko-Bae” in Japanese) (Fig. 7A, C, D), *K. biformis* (formerly *Ceroplatus testaceus* f. *biformis*) (distributed in Japan and Russia Far East; “Mesuguro-Hirata-Kinoko-Bae” in Japanese) (Fig. 7B), *K. testaceus* (in Europe), *K. tipuloides* (formerly called *Ceroplatus sesioides*; in Europe) and *K. reaumurii* (in Europe) (Baccetti et al., 1987).

Biology of luminous species in Japan. Two *Keroplatus* species (*K. nipponicus* and *K. biformis*) have been recorded from Japan (Evenhuis, 2006) (Table 1) and their larvae and pupae were described as luminous. *K. nipponicus* is known from Hokkaido, Honshu and Hachijo Island in Japan (Okada, 1938). Mature larvae are ~20 mm long and 2 mm wide (Esaki, 1949; Ogino, 1987) (Fig. 7C, D) and adults are 7–10 mm long (Okada, 1938) (Fig. 7A). *K. biformis* is distributed from Hokkaido to Honshu in Japan (Okada, 1938).

Adults are 10–12 mm long (Okada, 1938) (Fig. 7B), while the size of larvae is not described. Haneda (1955, 1985; Fig. 1B) provided a detailed description on the discovery of luminous fungus gnats in Japan. In brief, the larvae of *K. nipponicus* were found emitting light on the brown rot fungus *Poria vaporaria* in 1948 by a Japanese mycologist Daisuke Shimizu at Mt. Ryogami, Saitama Pref. (Esaki, 1949; Kato, 1953a, b), and then *K. biformis* was collected at the same place (Kato, 1953a, b). Larval luminosity in these species was confirmed by Kato (1953b). In 1951, Haneda observed the larval luminescence of *K. nipponicus* on the artist's fungus *Ganoderma applanatum* at Hachijo Island (Haneda, 1955, 1957). Since these observations, however, reports on the luminescence of *K. nipponicus* have been limited until recently (Ogino, 1987; Takaie, 1996). In 2005, Hachijo islanders found many luminescent larvae of *K. nipponicus* gleaming on the polypore fungus *Grammothele fuligo* (gray structure in Fig. 7C) and *Gloeocystidiellum* sp. formed on fan palm (*Livistona chinensis*) woods. One of the authors (Y. O.) observed at Hachijo Island that faint blue light was emitted continuously from the entire body of the larvae, and intensity of the luminescence was stronger in the head and tail regions than in the middle (Fig. 7D). The luminescence of pupae was also described (Kato, 1953a, b; Haneda, 1957). Eggs and adults are not luminous (Haneda, 1957). The larval luminescence of *Keroplatus* species is due to fat body cells around the gut (Kato, 1953a, b; Baccetti et al., 1987), which differs from the luminescence of *Arachnocampa* species, wherein the luminous organs are located at the Malpighian tubules (Wheeler and Williams, 1915). In *O. fultoni*, the luminescence is due to “binucleate-giant-black” secretory cells (Fulton, 1941; Bassot, 1978). Based on the morphological variation in the light organs among fungus gnats, Sivinski (1998) suggested several independent evolutionary origins of bioluminescence in the Keroplatidae.

Function of luminescence. The larvae of *Arachnocampa* spp. and *O. fultoni* attract and prey on phototactic invertebrates by emitting luminescence and catching prey insects in sticky threads excreted by the larvae (Fulton, 1941; Meyer-Rochow, 2007). By contrast, the Keroplattini species (including luminous and non-luminous species of *Keroplatus* and *Mallochinus*) are spore-feeders, constructing a sheet web at the surface of fungi and feed on spores (Kato, 1953a; Matile, 1997) (Fig. 7C). The function of bioluminescence in these sporophagous species is unclear. A closely related species, *Heteropterna* sp. (Keroplattini, Keroplatinae) occurs sympatrically with *K. nipponicus* in Hachijo Island, also feeds on spores (Matile, 1997), and is non-luminous. On the other hand, non-luminous Orfeliini species are generally predatory (Matile, 1997; Evenhuis, 2006), and some of them are reported to trap prey with vertical sticky threads like *Arachnocampa* and *O. fultoni* (Jackson, 1974; Gould, 1991; Meyer-Rochow, 2007). A phylogenetic analysis based on morphological characters suggested that the ancestral state of the Keroplatidae was predaceous and the sporophagy in the Keroplattini was acquired secondarily (Matile, 1997). In these contexts, the biological function of the luminosity in sporophagous *K. nipponicus* is of ecological and evolutionary interest. Sivinski (1998) speculated that the luminescence of sporophagous fungus gnats might function by

repelling negatively phototropic enemies or as an aposematic display. The luminescence of *K. nipponicus* larva is very faint and not enhanced by stimulation (Haneda, 1957), and thus its startling function against predators seems unlikely. The sheet web of *K. nipponicus* larva (Fig. 7C) is sticky and very acidic (pH ~1, measured by pH test paper) as known in some luminous and non-luminous fungus gnats (Matile, 1997). Ants and other invertebrates, such as snails and spiders, wandered around but never intruded into the sheet web (Ohba and Oba, unpublished). These observations support the aposematic display hypothesis of Sivinski (1998). On the other hand, as suggested by Sivinski (1998), the production of light may aid parasitic hymenopterans in locating fungus gnat hosts. One of the authors (Y. O.) and Yohsuke Tagami found a parasitoid, *Megastylus* sp., emerging from a pupa of *K. nipponicus*, but their host searching behavior is not studied. Richards (1960) suggested that the luminescence in female pupae and adults of *A. luminosa* may act as a sexual signal for attracting males. Meyer-Rochow and Eguchi (1984) supported this hypothesis by their electrophysiological studies on the eyes of male adults: the second response peak of the optical sensitivity (460 nm) corresponded to the luminescence spectrum.

Biochemistry of luminescence. The mechanisms of bioluminescence have been studied on *Arachnocampa* species and *O. fultoni* (Shimomura et al., 1966; Lee, 1976; Wood, 1993; Viviani et al., 2002) but the details remain unclear. The luciferin-luciferase reaction using a cold-water extract and a hot-water extract was positive in each of *Arachnocampa* spp. (Wood, 1993) and *O. fultoni* (Viviani et al., 2002), but the luminescent mechanisms seemed different between the genera, because the cross-reactions between these luciferin-luciferase systems were negative (Viviani et al., 2002). The luminescent reaction in *Arachnocampa* spp. was ATP dependent like that in fireflies (Shimomura et al., 1966; Lee, 1976), but did not cross-react with the firefly luminescence system (Wood, 1993). The mechanism of luminescence in *K. nipponicus* remains unknown. The dried larvae and pupae emit luminescence when the specimens were ground and wet with water (Haneda, 1957; Y. Oba, unpublished). The luciferin-luciferase reaction was negative (Haneda, 1955, 1957). In our experiments, the luminescence maximum of *K. nipponicus* larva in vivo was 460 nm, which is the same as that of *O. fultoni* (λ_{\max} in vitro = 460 nm; Viviani et al., 2002) but different from those of *A. luminosa* (λ_{\max} in vitro = 487 ± 5 nm; Shimomura et al., 1966), *A. richardsae* (λ_{\max} in vivo and in vitro = 488 nm; Lee, 1976) and *Arachnocampa flava* (λ_{\max} in vitro = 484 nm; Viviani et al., 2002).

Luminous springtails (Entognatha: Collembola)

The order Collembola (springtails) consists of 20 families and over 1,000 species (Fрати et al., 1997), and the numbers are rapidly increasing (Deharveng, 2004). Here we note that the Collembola has historically been placed in the class Insecta, but based on new data, many researchers now regard it as a non-insect taxon belonging to the class Entognatha (Wheeler et al. 2001; Grimaldi and Engel, 2005). Luminescent species have been recognized in the families Neanuridae and Onychiuridae (Harvey, 1952; Haneda, 1985), but the observations are quite limited.

Harvey (1952) suspended judgment as to whether the collembolan luminescence is a true bioluminescence or an accidental luminescence due to infection with luminous bacteria or by their feeding on luminous fungi. Haneda (1985) suggested the possibility of collembolan self-luminescence. Here we list a Japanese species *Lobella* sp. (Neanuridae) as probably self-luminous (Fig. 7E, F; Table 1). This species is ~3 mm long, found under litter, emits a continuous weak green light from abdominal tubercles by stimulation, and the luminescence is not secretory (Kashiwabara, 1997; Konishi, 2007; Y. Minagoshi, personal communication).

The biological function and mechanism of this luminescence are completely unknown. Lloyd (1978) suggested the function may be either for defense or sexual communication, since the luminescence was emitted upon stimulation and also occurred in the sexual phase.

Luminous millipedes (Diplopoda)

Diversity and systematics. In the class Diplopoda, luminous species have been recorded from three genera, *Motyxia* (= *Luminodesmus*) (Xystodesmidae), *Paraspirobolus* (Spirobolellidae) and *Salpidobolus* (= *Dinematocricus*) (Rhincrocricidae) (Causey and Tiemann, 1969; Haneda, 1985; Herring, 1987). Their entire body emits light, and no luminous material is ejected (Harvey, 1952; Haneda, 1985).

Biology of luminous species in Japan. In 1937, Haneda found a luminous millipede at Chuuk Islands in Micronesia and sent the specimens to a myriapod researcher, Yosioki Takakuwa (Haneda, 1972, 1985), which was described as a new species *Spirobolellus phosphoreus* (Takakuwa, 1941). In 1997, Shinohara and Higa (1997) found a luminous millipede in Okinawa, Japan. This species was identified as *Spirobolellus takakuwai* (Fig. 8A, B), which had been recorded only from Taiwan (the genus name *Spirobolellus* by Wang in 1961 is incorrect). The species names *S. phosphoreus* and *S. takakuwai* have recently been identified as junior synonyms of a circumtropical ubiquitous species *Paraspirobolus lucifugus* (Korsós, 2004, and references therein) (Table 1). In Japanese we call this species "Takakuwa-Kaguya-Yasude": "Takakuwa" is after the name of Y. Takakuwa; "Kaguya" is the name of the shining princess in one of the oldest Japanese fairy tales "Taketori-Monogatari" (~mid 10th century); "Yasude" means millipede. The body size is 12–20 mm long and 1.5–2.0 mm wide (Wang, 1961; the body width, 4.5 mm, in this paper is incorrect). Wang (1961) suggested this species as non-luminous in the evening (Wang, 1961), but Shinohara and Higa (1997) observed a weak glow induced by mechanical stimulation at night. One of the authors (Y. O.) also observed a weak glow of *P. lucifugus* by stimulating with forceps or pouring chloroform on it (Fig. 8B).

Function of luminescence. The biological function of the luminescence in diplopods remains uncertain, but is probably used as an aposematic signal (Haneda, 1967; Rosenberg and Meyer-Rochow, 2009). Aposematic coloration is widely found among non-luminous millipedes (Whitehead and Shelley, 1992): *Motyxia* species discharge repugnatorial secretions upon stimulation (Causey and Tiemann, 1969) and a species of *Salpidobolus* sprays caustic substances from paired repugnatorial glands (Hudson and Parsons, 1997). A variety of defensive chemicals have been detected

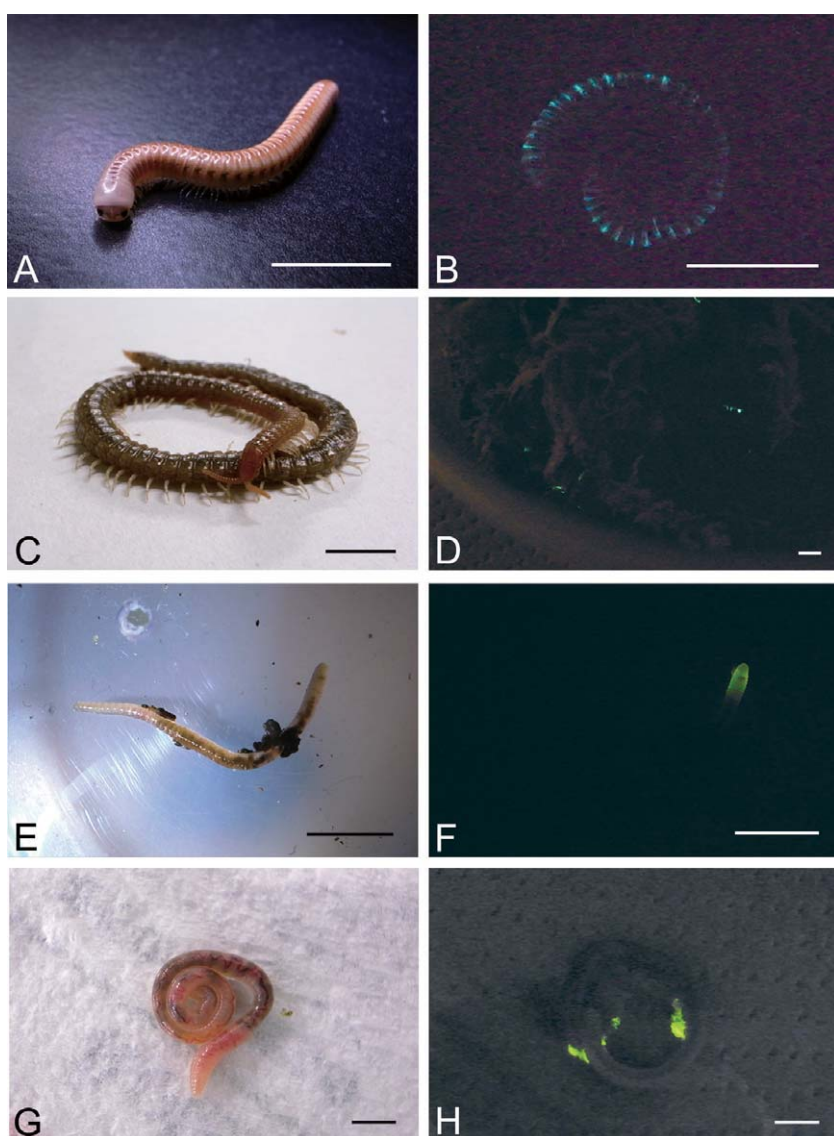


Fig. 8. The luminous millipede (A, B), centipede (C, D) and earthworms (E–H). (A, B) *Paraspilobolus lucifugus*. (C, D) *Orphnaeus brevilabiatius*. (E, F) *Microscolex phosphoreus*. (G, H) *Pontodrilus litoralis*. Bars show 5 mm.

from various millipedes, including those from *P. lucifugus* (Kuwahara et al., 2002). The luminescence of *P. lucifugus*, and *Salpidobolus* sp. become brighter upon stimulation (Haneda, 1955, 1967, 1985; Shinohara and Higa, 1997). When one of the authors (Y. O.) stimulated *P. lucifugus* with forceps, a noxious smell was discharged. It is unlikely that bioluminescence in *Motyxia* species is used for interspecific communication, as the species in the order Polydesmida, including the luminous genus *Motyxia*, do not possess eyes (Hopkin and Read, 1992; Shelley, 1997). On the other hand, *P. lucifugus* has developed eyes (Fig. 8A), but the involvement of bioluminescence in intraspecific communication has not been examined.

Biochemistry of luminescence. Shimomura (1981) studied the mechanism of luminescence in the North American sequoia millipede *Motyxia sequoiae* (= *Luminodesmus sequoiae*), and suggested involvement of photoprotein, ATP and Mg^{2+} . “Photoprotein” is a term for a bioluminescent pro-

tein that emits light in proportion to its amount, like luciferin, but its light-emitting reaction does not require a luciferase (Shimomura, 1985). Kuse et al. (2001) identified the chemical structure of a fluorescent compound, 7,8-dehydropterin-6-carboxylic acid, from *M. sequoiae*, which may be involved in the bioluminescence as an in vivo light emitter to some extent (Shimomura, 2006). The mechanisms of luminescence in other luminous millipedes have not been studied.

Luminous centipedes (Chilopoda)

Diversity and systematics. In the Chilopoda, luminous species have been reported from five families: the Himantariidae, the Oryidae, the Geophilidae, the Linotaeniidae (Geophilomorpha) and the Scolopendridae (Scolopendromorpha) (Lewis, 1981; Haneda, 1985; Herring, 1987). The genera *Stigmatogaster* (Himantariidae), *Geophilus* (Geophilidae), *Strigamia* (Linotaeniidae) and *Otostigmus* (Scolopendridae) contain luminous species, but luminescence of the congeneric species found in Japan (Takakuwa, 1940a) has not been reported.

Biology of luminous species in Japan. *Orphnaeus brevilabiatius* (Oryidae) (Fig. 8C, D) is broadly distributed in the tropical and subtropical regions throughout the world, including Taiwan and Japan (Yatsu, 1912; Takakuwa, 1940b; Harvey, 1952; Haneda, 1939) (Table 1). Many books and references misspelled the generic name as “*Orphaneus*” (Haneda, 1939; Takakuwa, 1940b; Harvey, 1952; Haneda, 1972, 1985; Ohmine, 2006; Shimomura, 2006), “*Orphaneus*” (Yatsu, 1912) or “*Orphaneous*” (Anderson, 1980). In Japan, this species is found in Okinawa, Miyako, and Yaeyama Islands, and is listed in the Red Data Book Okinawa edition (Ohmine, 2006) at the LP rank (threatened local population). The body size is 60–65 mm long and ca. 1 mm wide (Haneda, 1985) or ~90 mm long (Takakuwa, 1940b). We call this species “Hirata-Hige-Jimukade” in Japanese. This species secretes droplets of clear viscous liquid from body segments, where the pores of the sternal gland for the production of defensive chemicals are located (Rosenberg and Meyer-Rochow, 2009), upon mechanical, chemical and electrical stimuli (Haneda, 1939; Anderson, 1980). These secretions produce green luminescence. One of the authors (Y. O.) observed the luminous secretion from the body segments by stimulating the organism with forceps; even after the centipede escaped from the forceps, the mucus stuck to the soil and emitted bright green light for several seconds (Fig. 8D).

Function of luminescence. The function of luminescence in centipedes remains unclear, although the possibility of use for an aposematic signal has been suggested

(Harvey, 1952; Lewis, 1981; Rosenberg and Meyer-Rochow, 2009). Geophilomorphan species, including *O. brevilabiatus*, generally possess venomous forcipules (jaws), although the venom of *O. brevilabiatus* is not so harmful to humans (Takakuwa, 1940b; Haneda, 1955). Houdemer (1926) observed that a luminescent secretion of *Otostigmus aculeatus* induced erythemata and blisters on human skin. Intraspecific bioluminescent communication is unlikely, as all species in the order Geophilomorpha are blind (Edgecombe and Giribet, 2007).

Biochemistry of luminescence. The luminescent secretion from *O. brevilabiatus* obtained by an electrical stimulus showed a λ_{\max} at about 510 nm with a second λ_{\max} at 480 nm (Anderson, 1980), which might indicate the involvement of energy transfer from a 480 nm light-emitter to a 510 nm light-emitter (Shimomura, 2006). The bioluminescence of *O. brevilabiatus* was characterized as an oxygen-dependent luciferin-luciferase reaction: mixture of a heat treated-extract and an anaerobic cold buffer-extract resulted in light emission in vitro (Anderson, 1980). The optimal pH for this bioluminescent reaction was unusually low (pH 4.6) (Anderson, 1980), like that of certain luminous fungi (Shimomura, 2006). Biochemical studies on other luminous centipedes have not been reported.

Luminous earthworms (Oligochaeta)

Diversity and systematics. Among the phylum Annelida, the only known terrestrial luminous species belong to the class Oligochaeta (earthworms and potworms) (Harvey, 1952; Herring, 1978). In the Oligochaeta, luminous species have been reported from 16 genera: *Diplocardia*, *Diploptrema*, *Megascolex*, *Microscolex*, *Parachilota* (Acanthodrilidae), *Eutyphoeus*, *Ramiella*, *Octochaetus* (Octochaetidae), *Digaster*, *Fletcherodrilus*, *Lampito*, *Pontodrilus*, *Spenceriella* (Megascolecidae), *Eisenia* (Lumbricidae), *Fridericia* and *Henlea* (Enchytraeidae) (Herring, 1978, 1987; Petushkov and Rodionova, 2005; Rota, 2009). A current revision lists approximately 80 earthworm species in seven families and 15 potworm species in the family Enchytraeidae from Japan (Nakamura, 2000; Blakemore, 2003), of which two species of earthworms are known to be luminous (Haneda, 1972, 1985) (Table 1). Although some species of the genera *Eisenia*, *Fridericia* and *Henlea* are found in Japan, their luminescence has not been reported. Bioluminescence of *Eisenia fetida* (Shima-mimizu in Japanese), a common “compost worm” in Japan, has been reported, but the question remains as to whether the observed luminescence was self-luminosity (see Rota, 2009). *Henlea ventriculosa* (Marukobu-Hime-Mimizu in Japanese) is common and widespread in Japan (Nakamura, 2000). Walter (1919) described luminescence of *H. ventriculosa*, but there has been no further report on its luminescence (Rota, 2009).

Biology of luminous species in Japan. *Microscolex phosphoreus* (Acanthodrilidae) (Fig. 8E, F) is broadly distributed throughout the world (Gates, 1972), and its distribution in Japan is probably due to an accidental introduction (Blakemore, 2003). The body size is 10–35 mm long (or longer; H. Yoshida, personal communication) and 1.0–1.5 mm wide (Gates, 1972). We call it “Hotaru-Mimizu” in Japanese, which means firefly-earthworm. In Japan, the luminescence of *M. phosphoreus* was first recognized in 1934 at Ôiso,

Kanagawa Pref. (Yamaguchi, 1935). Since then, this species has been reported from many localities across the Honshu, Shikoku, and Kyushu areas (Kobayashi, 1941; Okada, 1965; Easton, 1980; Haneda, 1985). In Japan, *M. phosphoreus* has been sporadically observed only in the winter, which surprised people and were sometimes reported by newspapers, although the habitat and life cycle of this species are still unknown (Haneda, 1972, 1985; H. Yoshida, personal communication). *Pontodrilus litoralis* (Acanthodrilidae *sensu* Gates, 1959; Megascolecidae *sensu* Blakemore, 2000) (Fig. 8G, H) is distributed along the tidal line in the Atlantic, Pacific and Indian Oceans, including the shorelines in Japan (Yamaguchi, 1953; Okada, 1965; Easton, 1980; Blakemore, 2003) (Table 1). The body size is 32–120 mm long and 2–4 mm wide (Easton, 1984). We call it “Iso-Mimizu” in Japanese, which means shore-earthworm. The luminescence in this littoral earthworm was first discovered at Tomioka, Yokohama in Japan. At that time, this species was identified as *P. matsushimensis* (Kanda, 1938), but it was later reduced to a synonym of *P. litoralis* (Easton, 1984). The mucus of *M. phosphoreus* and *P. litoralis* emits a faint yellowish-green luminescence, which is the coelomic fluid discharged from mouth, anus and/or body wall upon mechanical, chemical or electrical stimuli (Kanda, 1938; Haneda and Kumagai, 1939; Gates, 1972; Herring, 1978; Wampler, 1982). One of the authors (Y. O.) collected *M. phosphoreus* at Kashiba (Nara Pref., Japan) and Nagoya (Aichi Pref., Japan), and observed luminescent mucus discharged from the anus upon chloroform vapor or pinching with forceps. The luminescence lasted for a few minutes (Fig. 8F). The author (Y. O.) also collected specimens of *P. litoralis* at Fukutsu (Fukuoka Pref., Japan). As Kanda (1938) and Haneda (1939b) reported, luminescence was not observed after a simple touch or tap. Only after the animals were cut, squeezed, or otherwise handled roughly, luminescent fluid was discharged from the body (Fig. 8H).

Function of luminescence. The function of bioluminescence in earthworms and potworms remains unclear (Rota, 2009). Sivinski and Forrest (1983) reported that a mole cricket (*Scapteriscus acletus*) dropped *M. phosphoreus* and rapidly withdrew upon its luminescence, although the earthworm is potentially palatable to various carnivorous insects. Based on this observation, they suggested that bioluminescence in earthworms may be for startling predators in the darkness underground (Sivinski and Forrest, 1983). One of the authors (Y. O.) observed that, in an aquarium, *P. litoralis* was immediately consumed by a crab (*Hemigrapsus sanguineus*) and a goby (*Eviota abax*). Furthermore, *P. litoralis* is sometimes used as bait for fishing in Japan (Yamaguchi, 1970), suggesting that this littoral earthworm is neither distasteful nor toxic for shallow-sea predators.

Biochemistry of luminescence. The mechanism of earthworm luminescence was best studied in the North American earthworm *Diplocardia longa*, wherein the luciferin was identified as *N*-isovaleryl-3-aminopropanal (Ohtsuka et al., 1976), the luciferase was purified as 300 kDa heterotrimeric metalloprotein containing Cu^{2+} (Bellisario and Cormier, 1971; Bellisario et al., 1972), and the luminescence was stimulated by hydrogen peroxide (Bellisario and Cormier, 1971; Bellisario et al., 1972). The mechanisms of luminescence in *M. phosphoreus* and *P.*

bermudensis (= *Pontodrilus litoralis*; Easton, 1984) were suggested to be similar to that of *D. longa*, on the grounds that their luminescence was stimulated by hydrogen peroxide, the luciferin of *D. longa*, and the luciferase of *D. longa* (Wampler and Jamieson, 1980; Wampler, 1982). Emission maxima of the luminescent reaction in vitro for *M. phosphoreus* and *P. bermudensis* were 538 nm and 540 nm, respectively (Wampler, 1982; Wampler and Jamieson, 1980, 1986).

The bioluminescence mechanism of potworm *F. heliota* has been studied (Rota, 2009 and references therein). The system involves a luciferin-luciferase reaction, which is H₂O₂ independent and does not cross-react with the luciferin of earthworm *Diplocardia*. The reaction requires O₂, ATP and Mg²⁺, which is similar to the firefly luminescence but cross-reacts neither with the luciferin of fireflies nor with the luciferase of *P. pyralis* (Petushkov and Rodionova, 2007). The luminescent system in another luminous potworm, *Henlea*

sp., also involves a luciferin-luciferase reaction, but does not cross-react with the luminescent systems of *Fridericia* and *Diplocardia* (Petushkov and Rodionova, 2005). Chemical structure of the luciferin and primary structure of the luciferase have not yet been determined for the luminous potworms (Rota, 2009; Marques et al., 2011).

DNA barcode of the Japanese terrestrial luminous animals

It has been proposed that the DNA sequence of a cytochrome oxidase I subunit (COI) fragment (DNA "barcode") is practically useful for identifying and discriminating species (Hebert et al., 2003). Here we list the barcode sequences for 29 of 58 terrestrial luminous animals in Japan. For the Lampyridae, the data of 21 of 50 species representing all 9 genera are shown, while all Japanese luminous species of the Phengodidae, Keroplatidae, Collembola, Diplopoda,

Table 2. DNA Barcode (COI) of the Japanese terrestrial luminous animals.

Species	Collection location	GenBank number
Lampyridae		
<i>Cyphonocerus marginatus</i>	Japan: Shikoku, Ehime Pref., Saijo, Mt. Kamegamori	AB608754
<i>Cyphonocerus ruficollis</i>	Japan: Shikoku, Ehime Pref., Imabari, Ohnishi, Yamanouchi	AB608755
<i>Drilaster axillaris</i>	Japan: Honshu, Tokyo (Mt. Mitake)	AB608756
<i>Drilaster ohbayashii</i>	Japan: Ryukyus, Okinawa Pref., Ishigaki Is., Takeda-rindou	AB608757
<i>Drilaster okinawensis</i>	Japan: Ryukyus, Okinawa Pref., Kunigami	AB608758
<i>Stenocladus yoshikawai</i>	Japan: Ryukyus, Okinawa Pref. Ishigaki Is.	AB608759
<i>Luciola cruciata</i>	Japan: Kyushu, Fukuoka Pref., Fukutsu	AB608760
<i>Luciola filiformis yayeyamana</i>	Japan: Ryukyus, Okinawa Pref., Ishigaki Is.	AB608761
<i>Luciola lateralis</i>	Japan: Honshu, Aichi Pref., Okazaki, Kuwabara	AB608762
<i>Luciola parvula</i>	Japan: Honshu, Aichi Pref., Anjo, Higashibata	AB608763
<i>Curtos costipennis</i>	Japan: Ryukyus, Okinawa Pref., Ishigaki Is.	AB608764
<i>Curtos okinawanus</i>	Japan: Ryukyus, Okinawa Pref., Uruma, Suzaki	AB608765
<i>Pyrocoelia abdominalis</i>	Japan: Ryukyus, Okinawa Pref., Ishigaki Is., Omoto	AB608766
<i>Pyrocoelia atripennis</i>	Japan: Ryukyus, Okinawa Pref., Ishigaki Is., Yoshihara	AB608767
<i>Pyrocoelia discicollis</i>	Japan: Honshu, Okayama Pref., Niimi, Toyonagaakouma	AB608768
<i>Pyrocoelia fumosa</i>	Japan: Honshu, Aichi Pref., Okazaki, Yatsugi	AB608769
<i>Pyrocoelia matsumurai matsumurai</i>	Japan: Ryukyus, Okinawa Pref., Kunigami, Yona-rindou	AB608770
<i>Lucidina accensa</i>	Japan: Honshu, Aichi Pref., Shinshiro, Tsukude	AB608771
<i>Lucidina biplagiata</i>	Japan: Honshu, Aichi Pref., Shinshiro, Kameyamajo	AB608772
<i>Pristolycus sagulatus sagulatus</i>	Japan: Honshu, Aichi Pref., Kitashitara, Shitara, Dando-uradani	AB608773
<i>Pyropyga</i> sp.	Japan: Honshu, Saitama Pref., Misato (Edogawa)	AB608774
Phengodidae		
<i>Rhagophthalmus ohbai</i>	Japan: Ryukyus, Okinawa Pref., Ishigaki Is., Kabira	AB608775
Keroplatidae		
<i>Keroplatys nipponicus</i>	Japan: Honshu, Tokyo, Hachijo Is., Nakanogou	AB608776
<i>Keroplatys biformis</i>	Japan: Hokkaido, Sapporo, Maruyama	AB608777
Collembola		
<i>Lobella</i> sp.	Japan: Honshu, Tokyo, Tama	AB608778
Diplopoda		
<i>Paraspirobolus lucifugus</i>	Japan: Ryukyus, Okinawa Pref., Shimajiri, Yaese	AB608779
Chilopoda		
<i>Orphnaeus brevilabiatus</i>	Japan: Ryukyus, Okinawa Pref., Kunigami	AB608780
Oligochaeta		
<i>Microscolex phosphoreus</i>	Japan: Honshu, Nara Pref., Kashiba, Mamigaoka	AB608781
<i>Pontodrilus litoralis</i>	Japan: Kyushu, Fukuoka Pref., Fukutsu, Tsuyazaki	AB608782

DNA was extracted using QIAamp DNA mini kit (Qiagen, Hilden, Germany). PCR reactions were performed using the primer pair of LCO1490 and HCO2198 as previously described (Hebert et al., 2003). The amplicon was directly sequenced using BigDye terminator v3.1 cycle sequencing kit (Applied Biosystems, Foster City, CA) with an ABI Prism 3130 sequencer (Applied Biosystems).

Chilopoda and the Oligochaeta are included. The nucleotide sequence data (658 bp) were deposited in the DNA Data-bank with the accession numbers AB608754–AB608782 (Table 2). These data will be useful for those who are interested in and would like to study these luminous animals in the future.

Perspectives

Here we reviewed the biological information available to date for all 58 species of terrestrial luminous animals in Japan, particularly focusing on their diversity and systematics, their biology and ecology, and putative function and biochemistry of their luminescence. We point out that these luminous animals and their luminescence have been, in general, very poorly investigated: for most of them, only taxonomic description and basic biological notes are available. The only exception is the “Genji-botaru” firefly *L. cruciata* (Ohba, 1988): its vision (Gleadall et al., 1989; Hariyama et al., 1998; Oba and Kainuma, 2009) and morphological and behavioral variations (Ohba, 2001) have been intensively studied; its luciferin and luciferases, including their structural interaction by X-ray crystallography (Nakatsu et al., 2006) have been identified, and utilized, together with *L. lateralis* luciferase, for such purposes as sensitive microbial detection and scientific education (Nakano, 1991; Hattori et al., 2003; Murakami et al., 2004); ecological information has been extensively compiled for conservation, educational, and eco-tourism applications (Yajima, 1978; Ohba, 1988, 2004c, 2006, 2009; Tokyo Fireflies Ecology Institute, 2004); and protocols for rearing it have been established (Ohba, 1988; Tokyo Fireflies Ecology Institute, 2004). There is no doubt that *L. cruciata* serves as the model organism for the study of bioluminescence and promises to further contribute to our understanding of bioluminescence.

Future studies of luminous animals and their luminescence should be directed toward the chemical, physiological, ecological and evolutionary aspects of this phenomenon, as well as commercial applications of this knowledge. What luciferins, luciferases and chemical reactions are involved in their luminescence? How is light emission regulated physiologically and biochemically? What biological and ecological roles does bioluminescence play? What are the evolutionary origins of bioluminescent systems? Considering that most luminous animals are oceanic (Haddock et al., 2010; Widder, 2010), marine luminous animals in Japan represent a much wider and totally untouched research field to be explored in future studies.

In 2008, Osamu Shimomura was awarded the Nobel Prize for his pioneering works on the luminous jellyfish *Aequorea aequorea* (or *Aequorea victoria*) (Shimomura, 2006, 2009). In 1960’s–70’s, he and his colleagues identified a luminescent protein, named aequorin, and a green fluorescent protein known as GFP (see Shimomura, 2006; Tsuji, 2010). Aequorin has enabled the development of extremely sensitive Ca²⁺ indicators (Blinks, 1990; Mithöfer and Mazars, 2002), and GFP and its derivative fluorescent proteins are widely utilized as molecular markers of general use in a wide variety of genetic, biological and medical applications (Zimmer, 2005). Shimomura’s investigations of the luminous jellyfish were driven simply by his scientific curiosity about the mechanism of bioluminescence (Pieribone and

Gruber, 2005; Shimomura, 2009, 2010). However, these basic biological studies eventually led to the development of highly successful biotechnological applications. This episode is symbolic of the multi-disciplinary nature of bioluminescence studies, which embrace natural history, biology, chemistry and physics, and highlights the biodiversity of bioluminous organisms as a treasure box of biological and genetic resources.

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