Biodiversity Journal, 2022, 13 (2): 409–416 https://doi.org/10.31396/Biodiv.Jour.2022.13.2.409.416

Ecology and Diversity of Lampyridae (Firefly): Checklist, State of Knowledge, and Priorities for Future Research and Conservation in the Philippines

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ABSTRACT Lampyridae commonly known as fireflies, glow worms, or lightning bugs are a very diverse taxon that is known to be distributed globally. They have the ability to emit light through bioluminescence and have attracted public interest because of this. Though bioluminescence in insects is not restricted to this group, the family of fireflies (Lampyridae) contains more bioluminescent species compared to other families. This diverse and easily accessible group is well suited for studies focusing on the function and evolution of bioluminescence. Lampyrids are beneficial to ecosystems around the world and are often keystone species and serving as bioindicator in their habitat. They also play a role in medical and evolutionary science as important study organisms in biotechnology, behavioral ecology, evolution of communication systems, responses to climate change, and conservation biology. This paper presents the ecology and diversity of Lampyridae as well as the state of knowledge globally and in the Philippines. This paper also presents some priority area for future research and conservation.

KEY WORDS Fireflies; Bioluminiscence; Lampyridae; diversity.

Received 12.12.2021; accepted 26.02.2022; published online 03.06.2022

INTRODUCTION

Lampyridae commonly known as fireflies, glow worms, or lightning bugs are a very diverse taxon which includes over 2,000 species in approximately 100 genera of eight subfamilies worldwide, comprising about 40% of the Class Insecta (Shahara et al., 2017). The Lampyridae are characterized by small to medium-sized bodies, with an average of 10-15 mm in most species and usually not longer than 3cm, though some larviforms of females may reach up to 8cm in length. Adult lampyrids have an elongate, soft and flattened oval body form, with their head being partly concealed. Lampyrids have short antennae varying from filiform to serrate (Ballantyne, 2010). Their forewings are generally dark gray or brown and relatively soft compared to most beetles. The prothorax is broad and plate-like, concealing most of the head, and is usually edged with yellow, red, or orange color (Cranshaw, 2019).

DISTRIBUTION OF THE FAMILY LAMPYRIDAE

Members of the family Lampyridae are known to be globally distributed but are more diversely found in warm and humid environments (Jeng et al., 2007), with the richest fauna being found in South America and Asia (Viviani, 2001). They are one of the charismatic fauna that attract public interest due to their ability for bioluminiscence (Shahara et al., 2017). The congregations and synchronous flashing lights in wetland areas were reported as early as 1680 by Dutch physician Engelbert Kaempfer. This phenomenon was recorded in Southern Asia and the western Pacific, from East India through Thailand, Malaysia and Indonesia to the Philippines and Papua New Guinea. Most of their light displays occur in trees or shrubs along tidal rivers in mangrove swamps. Nowadays, the luminiscent activities of lampyrids are an integral part of the biological diversity and tourism activities in Asian Countries that provide a valuable commodity in some communities contributing to ecotourism that generates local income (Nallakumar, 2011; Dawood & Saikim, 2016;).

THE FUNCTION AND EVOLUTION OF BIOLUMINESCENCE IN LAMPYRIDAE

Lampyridae classified as beetles (Coleoptera) represents the highest diversity of bioluminescent organisms in terrestrial ecosystems. Though bioluminescence in insects is not restricted to the order Coleoptera, the Lampyridae contains more bioluminescent species compared to the other families (Branham, 2017). Bioluminescence is a phenomenon wherein living organisms were able to emit light and this is best understood in the lampyrids (Babu & Kannan, 2002). Most of them are capable of emitting bioluminescence wherein they chemically produce a cold light without infrared or ultraviolet frequencies from the lower abdomen that may appear as yellow, green, or pale red, with wavelengths from 510 to 670 nanometers (Branchini et al., 2017). This bioluminescence is an attractive characteristic, though it is not unique among Lampyridae, and not all lampyrid species glow (Park et al., 2007). There are also non-luminescent species such as *Pyropyga minuta*, *Ellychnia corrusca* which are much more abundant (Park et al., 2007; Cranshaw, 2009).

All of the members of the family Lampyridae emit light at some stage during their life cycle from the larval stage that might extend to the adult stage. All of the known larvae produce a faint glow through the use of a paired organ located in their eighth abdominal segments, while in adults, it varies greatly in the presence, location, and the use of light organs (Stanger-Hall et al., 2007). On a study conducted by Ohba et al. (2004), it was found out that lampyrids have a dual luciferase gene that originated by a gene duplication event. One paralog of the gene is known to be expressed and used in the luminescence of larval and adult lanterns, while the other one is used in glowing eggs and pupae. The study also revealed that luciferin is biosynthesized from one molecule of hydroquinone and two molecules of cysteine and that the toxic hydroquinone is stored in firefly as a glycosylated, less toxic form known as arbutin. As such, it was demonstrated that the luciferin-luciferase system evolved from the genes and compounds of existing metabolic pathways and that luciferase evolved from a basic enzyme for fatty acid metabolism, fatty acyl-CoA synthetase, by gene duplication and subsequent mutations.

Bioluminescence in lampyrids serves multiple functions. They may utilize light as a mating signal, to attract their prey, or to defend themselves from enemies. Each species belonging to the family Lampyridae has a unique flashing frequency and their courtship involves an exchange of flashing signals at dusk or once it is dark. In general, they can be divided into three different groups, which are: 1) the congregating synchronous flashing type; 2) the congregating non-synchronous flashing type; and 3) the solitary fireflies. (Dawood et al., 2018). Both male and female fireflies use species-specific light signals in order to communicate in an interactive visual "morse-code" identifying the sex and species of the signaler (Stanger-Hall et al., 2007; Luk et al., 2011). The flashing pattern vary between species and sexes, some species emit light in a short single flash, some hold the flash for a full second, while some tropical species flash as a congregate and in unison. In some species the light emission attracts individuals of the same species to aggregate indirectly improving the chances of mating, while in some species, the females are sedentary and wingless, thus they utilize the light for them to attract the winged males. In contrast, in species where females are winged, the flashes are usually from the males seeking mates. The females climb a blade of grass, and then males flash within 10-12 feet of the females. Exchange of signals is repeated 5 to 10 times until they start mating. The characteristic flashes and glows of these adult lampyrids show intraspecific variation in color, duration, and frequency for species-specific courtship dialogs in habitats that contain multiple and simultaneously signaling species (Fallon et al., 2017).

In connection to light signaling, it was also suggested that lampyrids have the capacity to detect flashing colors at night. In a study conducted by Lall (2014), he made use of Electroretinographic

(ERG) determination of spectral sensitivity [S(λ)] of the dark- and chromatic-adapted compound eyes of a certain firefly species (*Photinus pyralis)*. It was revealed that there were three spectral mechanisms in the green (λmax= 550 nm), blue (λmax= 435 nm), and near-uv (λmax= 380 nm). They demonstrated that a spectral tuning exists between ERG S(λ) and species bioluminescence (BL) emission. "*The action spectrum of the Photinus pyralis female's behavioral response to simulated male yellow flash matched the ERG S(λ) as well the species BL emission. However when blue light was added to the yellow flash simulating the male BL, there was a marked inhibition of flashing response in the female. Similar inhibition of flashing in the female was observed when the yellow simulated flash was superimposed on a blue adaptation light."* (Lall, 2014). In a phototactic experiment done with a different species, *Lampyris noctiluca,* inhibition was observed in the males when blue (λmax= 485 nm) light was added to the simulated green (λmax= 555 nm) BL of the female. Among invertebrates generally, the blue (-) and the green (+) receptor systems are antagonistic to one another to facilitate color vision. In addition to serving as a mating signal, bioluminescence has also been used as an aposematic signaling as warning signals for predators that they are unpleasant to eat. The sudden flashes can repel potential predators (Babu and Kannan, 2002)**.** The predators have incorporated flashing signals of the larvae to their reflex bleeding and emission of toxic substances called lucibufagins (Luk et al., 2011). Most of the lampyrids produce these distasteful chemicals that help protect them from predators. They may also reflex bleed when disturbed, exposing droplets of blood containing these defensive materials (Cranshaw, 2009).

LAMPYRIDS' DEPENDENCE ON THEIR HABITAT

The life cycle of the Lampyrids shows the complexity of relationships between the firefly species and their habitat. Each stage in their life cycle is dependent upon different environment and environmental conditions (Fig. 3). Adult mostly occupy the canopies of mangrove and other trees and would only descend on the moist soil further from their mating site to lay their eggs. The eggs are laid on the ground or on mosses, and as the egg hatched into larvae, they then become mobile on the ground to feed on their prey. It will then become inactive as it reached the pupal stage that may stay on the ground or on logs or other plants for protection before it emerge gain into an adult firefly.

Lampyrids are relatively sensitive to environmental changes in the habitat and the species distribution appeared to be largely associated to habitat type (Tan, 2018). In terms of the display trees of the adults, it was found out that *Pteroptyx* sp. used the same display trees within a period of 5 years (Murray, 1984; Motuyang, 1995), but this was not supported by Ohba & Wong (2004) who observed that a certain firefly species *Phyrophanes* sp. from Indonesia migrates every week, as well as with the findings of Jusoh et al. (2010) where in *Pteroptyx* sp. switched on display trees in a certain time. Among the factor that is considered with regard to tree species is the preference of lampyrids to tree characteristics or an individual trees traits such as height, crown size, leaf density, and trunk diameter as suggested by Nallakumar (2002) who found out that some members of the lampyrids only used the young *S. caseolaris* trees in Kuala Selangor in Malaysia. Other factors that are being evaluated are: "*1. The display tree must be located near to the water's edge as it make easier for fireflies to communicate, 2. Leaf arrangement of each display tree must be suitable for mating purposes, 3. If adult fireflies do eat, the display tree must have the nectaries or sap, 4. The display tree must be near to larval prey food plant and 5. The display tree must be in healthy condition*." (Jusoh et al., 2010).

Aside from the display tree as preference of lampyrids, habitat conditions also play a role in the distribution and diversity of lampyrids. Disturbed habitat affects the larval life and may affect the whole lifecycle of fireflies (Hazmi & Sagaff, 2017). Their abundance is highly dependent on the environmental factor such as water quality where there is a positive relationship between the water quality and abundance where it acts as a direct determinant of larval habitat quality. The abundance was also found to be decreasing with the increasing concentration of heavy metal in the water. There is also a positive linear relationship on the abundance and the percentage of silt in the soils since the egg and larva of fireflies are suitable with the soils condition due to the presence of sufficient water, however, too much water may restrict the foraging activities of small larvae and may also adversely affect populations of the larvae's prey (Hazmi & Sagaff, 2017).

Ecological conditions are also recorded to have indirect effects on the number of lampyrids as they cause changes in vegetation. The availability of vegetation is necessary as mating site and resting site. In addition, some specific features of plant leaves, like broader leaves, may be a crucial factor in enabling them to escape the attention of predators. Members of the family Lampyridae may also be affected by seasonal changes. During rainy season, the abundance of several fauna in mangrove and wetland areas increases therefore increases the amount of food resources for larva (Wattanachaiyingcharoen & Nak-eiam, 2016). In Asia, the peak abundance of adult lampyrids occurs between June and August and a less distinct peak between December and February. Seasonal variation affects diversity where in most species occurred in wet condition, from late summer to rainy season which resulted from availability of vegetation. Temperature and relative humidity did not appear to influence trends in the abundance of adult lampyrids if it is in a relative stable condition (Khoo et al., 2012).

STUDIES AND STATE OF KNOWLEDGE ON THE FAMILY LAMPYRIDAE

Lampyridae did not have a clear definition until recently. The taxonomic classification including family-group compositions and boundaries were frequently altered during the past century (Jeng et al., 2007). On the course of these taxonomic modifications, the classification of Lampyridae was fundamentally built on the basis of Olivier (1907, 1910), then modified and improved by Green (1948, 1959), Crowson (1955, 1972), McDermott (1964, 1966), Wittmer (1979), Nakane (1991), Lawrence and Newton (1995), Lawrence et al. (1999), and Branham and Wenzel (2001),and Jeng et al. (1998a, 2006a, 2006b). It was on 1907 that Olivier published the first lampyrid catalogue. Based on the catalogue, the Lampyridae was classified using a nine-subfamily system, largely based on antennal and head morphology. This was modified into seven-subfamily system (McDermott, 1964, 1966) by reducing the previous subfamilies into to subordinate units of Lampyrinae and added Matheteinae, Rhagophthalminae, and Pterotinae. Ototretinae. In 1972, Crowson clarified the separation of Lampyridae from the other cantharoid families by removing Rhagophthalminae to Phengodidae and Matheteinae to Omethidae, and by transferring many genera of Drilidae to Ototretinae, and established Cyphonocerinae and Ototretadrilinae based on former drilid genera. Crowson did not address much on the content of each subfamily but gave a tentative key to the eight lampyrid subfamilies he suggested. Across these three classifications, there were a total of 23 family-group taxa based on different type genera that have been proposed (Olivier, 1907; McDermott, 1964; Crowson, 1972).

Currently, the classification of Lampyridae that is being used is a mix of McDermott's and Crowson's systems where in it adopted Crowso's eight subfamily system and followed McDermot's generic composition of each subfamily. But based on the findings of some phylogenetic analysis (like that of Branham & Wenzel, 2001), the definitions of Lampyridae and the sub units of classifications needs a comprehensive revision (Jeng et al., 2007). Using the above mentioned classifications, some studies on distribution and abundance of lampyrids have been conducted. Results were summarized in Table 1 below.

Aside from the survey on the Lampyrid distribution and abundance, over the years, most of the studies have been focused on the genus *Pteroptyx* Olivier, 1902 which are the congregating or synchronous fireflies (Table 2). The synchronous flashing lights in wetland areas were reported as early as 1680 by Dutch physician Engelbert Kaempfer. This phenomenon was recorded in Southern Asia and the western Pacific, from East India through Thailand, Malaysia and Indonesia to the Philippines and Papua New Guinea (Dawood & Saikim, 2016).

LAMPYRID STUDIES IN THE PHILIPPINES

In the Philippines, comprehensive sampling of the beetles (Coleoptera) that includes the Lampyrids started in 1990s, but many species are still not described and undiscovered, and many islands still remain poorly explored. A total of fifty (50) species/subspecies is estimated to be in the Philippines (Fig. 1 and Table 3). Sixteen (16) species of

Location	N. of species	Genera/Species	Habitat Type	Author
Spain	7	*Nyctophila reichii, Lampyris* (1) *Lampyris iberica, Lamprohiza* (1), *Lamprohiza patulinoi, Lamprohiza mulsanti*	mountainous and semi-arid regions	Alvarez & De Cock, 2011
Brazil	26	*Cratomorphus* (5), *Aspisoma* (5), *Photinus* (3), *Macrolampis* (1), *Bicellonychia* (3), *Pyrogaster* (3), *Photuris* (1), *Amydetes* (3), *Lamprocera* (1), *Lucidota* (1)	Mesophyl tropical forests, Secondary growths, marshy areas, and open fields	Viviani, 2001
Northern Thailand	19	*Diaphanes, Lamprigera, Pyrocoelia, Abscondita, Asymmetricata, Curtos, Luciola, Pygoluciola, Trisinuata,* 1 unknown genus	Lower montane, coniferous forests, and upper montane forests	Wattanachaiyingcharoen et al., 2016
Eastern Canada	23	*Pyractomena, Ellychnia, Lucidota, Phosphaenus, Photinus, Pyropyga, Photuris*, *Pollaclasis*	Not mentioned (Review paper)	Luk et al., 2011
Pulau Ubin Singapore	6	*Pteroptyx valida, Diaphanes* spp., *Colophotia praeusta, Curtos* sp.	All encounters were in or near mangroves	Tan, 2018
Dyke Marsh Wildlife Preserve (DMWP),Virginia	6	*Ellychnia corrusca, Lucidota atra Photinus pyralis, Photuris* spp., *Pyractonema lucifera, Pyropyga decipiens*	Low forest, freshwater tidal marsh, and the forest-marsh ecotone	Barrows et al., 2008

Table 1. Some studies on the distribution and abundance of Lampyrids.

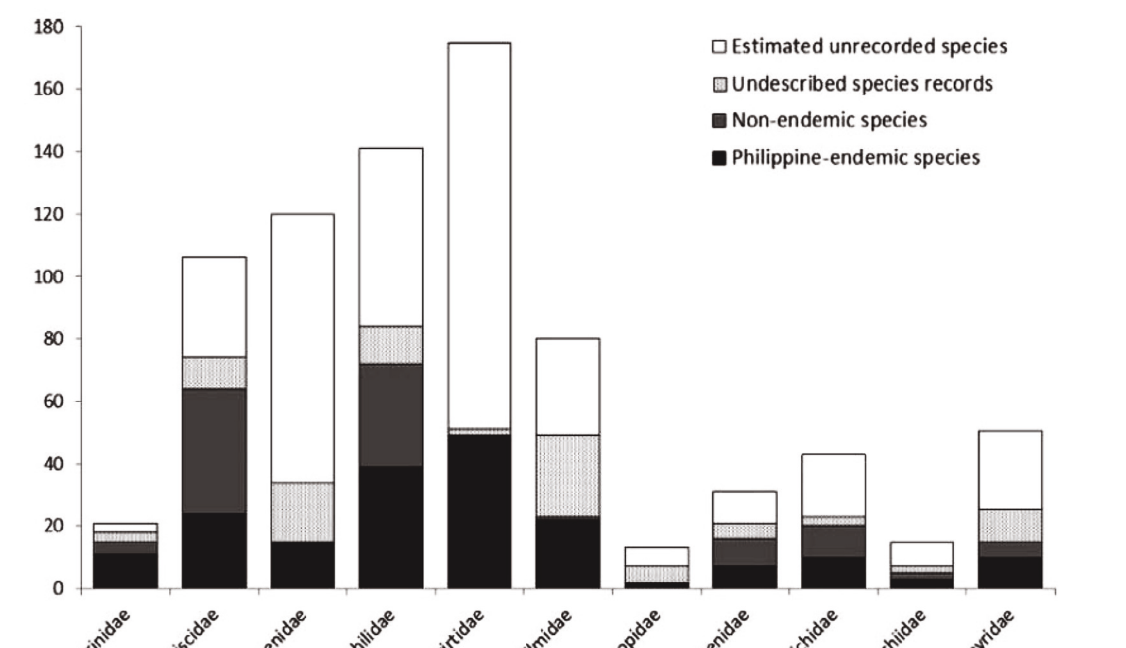

Figure 1. Estimated Coleoptera per Family in the Philippines (source: Freitag et al., 2016).

Location	Congregating Firefly Species	Habitat Type/Display Tree	Author
Thailand	*Pteroptyx malaccae* *Pteroptyx valida*	*Sonneratia caseolaris* and *Terminalia catappa*	Prasertkul, 2018
Malaysia	*Pteroptyx* sp.		Jusoh et al., 2010
Peninsular and East Malaysia (Sabah and Sarawak)	*Pteroptyx tener*	Mangroves growing along tidal rivers	Jusoh et al., 2013
Sabah, Malaysia	*Pteroptyx*	Seven mangrove species: *Excoecaria indica, Hibiscus tiliaceus, Nypa fruticans, Rhizophora apiculata*, *Avicennia alba*, *Excoecaria agallocha L., and Sonneratia alba*	Foo & Dawood, 2017
Sungai Sepetang, Kampung Dew, Perak, Malaysia	*Pteroptyx tener*	*Sonneratia caseolaris*	Hazmi & Sagaff, 2017
Selangor, peninsular Malaysia	*Pteroptyx tener*	*Sonneratia caseolaris* and *Ficus* sp.	Shahara et al., 2017
Selangor River, Malaysia	*Pteroptyx tener*	Adults on *Sonneratia caseolaris*. Larvae on sago palms (*Metroxylon sagu*), nibong (*Oncosperma tigillarium*), figs (*Ficus* spp.) and betel nut palms (*Areca catechu*)	Khoo et al., 2012
Kota Kinabalu, Sabah Malaysia	*Pteroptyx bearni* *Pteroptyx malaccae*	*Rhizophora mucronata, Aegiceras floridum, Lumnitzera littorea*	Foo & Dawood, 2016
Kerteh River, Terengganu Malaysia	*Pteroptyx tener* *Pteroptyx bearni*	Different species: *G. velutina, Barringtonia* sp., *S. caseolaris, N. fruticans, B. gymnorrhiza, H. tiliaceus, Excoecaria agallocha, X. granatum, A. alba, R. apiculata, F. microcarpa*	Jusoh et al., 2011
Sabah Malaysia	*Pteroptyx tener* *Pteroptyx bearni* (formerly known as *P. similis* in Sabah) *Pteropty gelasina* *Pteroptyx valida* *Pteroptyx malaccae*	Mangrove species; *Sonneratia caseolaris, Lumnitzera littorea, Aegiceras floridum, Avicennia alba, Rhizophora apiculata, Scyphiphora hydrophyllacea* and *Xylocarpus granatum*, *Ficus microcarpa, Clerodendrum inerme, Glochidion littorale, Bruguiera parviflora, Nypa fruticans, Excoecaria indica, Ficus benjamina* and *Hibiscus tiliaceus*	Dawood & Saikim, 2016

Table 2. Survey on congregating Fireflies genus *Pteroptyx*.

these have been recorded, ten (10) of which are endemic, and eleven (11) species are undescribed or unidentified (Freitag et al., 2016).

The enumerated studies above focused on taxonomy and systematics, specifically on species identification. Assessment of distribution of the existing Lampyridae within a specific area was also undertaken in relation to their habitat but most of the available data on lampyrid is limited on distribution. There are only a few published studies of lampyrid communities in particular habitats. Research undertakings involving Lampyridae has been poorly funded and given insufficient priority but is greatly needed since it forms the basis for our understanding of their diversity and is crucial for the development of other aspects of research. Because of this, their global diversity is still poorly understood, and studies on their physiology and behaviour have focused on small number of species. Accurate understanding of the distribution, abundance & habitat requirements of fireflies is essential towards the effective conservation of firefly population (Takeda et al., 2006).

Species	Location
Atyphella abdominalis Olivier, 1886*	Luzon
Luciola angusticollis Olivier, 1886*	Mindanao
Luciola apicalis Eschscholtz, 1822*	Luzon
Luciola bicoloriceps Pic, 1924*	Philippines
Luciola infuscate Erichson, 1834*	Bohol Luzon and Mindanao
Luciola rugiceps Olivier, 1886*	Philippines
Luciola truncata Olivier, 1886	Mindoro
Pteroptyx macdermotti McLean, 1970*	Leyte, Palawan, Samar
Pteroptyx testacea Motschulsky, 1854	Luzon
Pygoluciola hamulate Olivier, 1885	Philippines
Pygoluciola satoi Ballantyne, 2008*	Mindanao
Pyrophanes appendiculata Olivier, 1885	Bongao (Sulu) Islands, Luzon, Mindanao
Pyrophanes elongate Ballantyne, 2015*	Luzon, Negros, Palawan
Pyrophanes quadrimaculata Olivier, 1886*	Leyte, Mindanao, Samar
Pyrophanes semilimbata Olivier, 1883	Mindanao
Pyrophanes similis Olivier, 1885	Luzon, Mindanao, Palawan

Table 3. Lampyrids in the Philippines (source: Freitag et al., 2016); * =endemic.

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