

Review Article

Fireflies in South East Asia: Species Diversity, Distribution, and Habitat (2015-2021)

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ABSTRACT

Fireflies are one of the most famous luminous insects that emit bioluminescence. The most famous fireflies in Southeast Asia are *Pteroptyx*, of the order Coleoptera and the Lampyridae family. This review paper combined the data on the species diversity and firefly distribution in Southeast Asian countries such as Malaysia, the Philippines, Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Papua New Guinea, Laos, Thailand, and Vietnam published in 2015-2021. Some countries have limited data and no studies to identify firefly species and their habitat from 2015 to 2021; the data before 2015 was used. Furthermore, the lack of studies by Southeast Asian researchers regarding the richness of firefly species has been reviewed. Malaysian and Thailand researchers are among the forerunners in the study related to fireflies in the Southeast Asian region compared to other Southeast Asian countries. Lastly, not much is known about the display trees or habitat of fireflies in many

areas such as the Philippines, Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Papua New Guinea, Laos, Thailand, and Vietnam. More studies are warranted to be conducted in the future on firefly species and their habitat.

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INTRODUCTION

Insects include about 5.5 million species that have been documented based on the projected richness of species on a global scale (Stork, 2018). Beetles belong to the Coleoptera insect order, in which there are approximately 350,000 identified species (Slipinski et al., 2011). Beetles first started to evolve around about 297 million years old (Zhang et al., 2018) and account for insects makeup 38% of all recognised species presently (Stork, 2018). Coleoptera is also the most significant insect order, and fireflies belong to this order (Mckenna & Farrell, 2009). The beetles/insects in this Coleoptera order are also the most numerous and most prosperous insects on this earth (Slipinski et al., 2011). Although the number of beetles identified is almost 25% of all animal species living on earth, many more species are unidentified (Grove & Stork, 2000). McDonald (2003) estimates that 12 million of the 30 million Arthropod species found on earth are beetle species. However, according to Nielsen and Mound (1999), the number of beetle species described is unclear, but the species may be between 300,000 and 450,000.

Fireflies are not ‘flies,’ but rather beetles belonging to the Lampyridae family. Flies have one pair of wings, whereas all other winged insects have two or four pairs of wings (Dawood & Saikim, 2016). Coleoptera fireflies, which belong to the Lampyridae family, are widely known for their bioluminescent courtship sign used by the adults of several species (Lloyd, 2008) believed that synchronisation enhances the female’s ability to distinguish the male’s flash patterns in particular (Buck & Buck, 1968). Bioluminescence lampyrid in fireflies originates from the larval stage (Martin et al., 2017), where it acts as an aposematic signal (De Cock & Matthysen, 2003; Marek et al., 2011) that tells predators that they are unpalatable (Vencl et al., 2016). It could also be a possible tactic to attract prey (Bechara & Stevani, 2018). Attested per Moiseff and Copeland (2010), synchronous flashing is a behavioural technique to reduce visual clutter. In contrast, the the current study indicates that bioluminescence created by flying adult fireflies is often used to deter bat predators (Leavell et al., 2018). Bioluminescence is the result of the conversion of chemical energy into photons (Figure 1).



Figure 1. Bioluminescence process (Bechara & Stevani, 2018)

Note. Luciferin: Oxidation of a substrate; O₂ (Luciferase): Catalysed molecular oxygen; Oxyluciferin: Singlet excited-state product

Thus, using identical chemical routes involving the luciferin compound, Elateridae, Rhagophthalmidae, Phengodidae, and Lampyridae emit light, as do various structurally alike to luciferases (Day et al., 2009). Therefore, fireflies of the Coleoptera order in the Lampyridae family are among the night's most attractive and majestic insects. These fireflies look enticing because they have a special bioluminescent (Lewis & Cratsley, 2008; Ohba, 2004) display that emits flickering light, which makes them a potentially significant insect conservation species (Jusoh et al., 2018; Lewis et al., 2020) and sustainable ecotourism attraction (Jusoh et al., 2018). Bioluminescence is created when an enzyme called luciferase catalyses the reaction, which manifests as a flashing light emitted by fireflies (Nur Khairunnisa et al., 2016). *Pteroptyx* fireflies can produce sharp flashes with an average flashing duration of 320 milliseconds per flash, including several species of fireflies that possess 'perfect synchronisation' (Abdul Razak & Sulaiman, 2016). Foo and Dawood (2016) reported that the *Pteroptyx bearni* is the dominant firefly species found in the mangrove forest of Kawang in Sabah, Malaysia, which can be a firefly tourism spot.

Unfortunately, there was a reduction in the incidence and abundance of numerous species of fireflies in the last few decades (Lauff, 2017; Lloyd, 2018). The vast areas of mangroves on the river banks in South East Asia have been cleared for shrimp farming, flood mitigation, or oil palm plantations. These affected areas have become ill-

sued for the growth and reproduction of *Pteroptyx* firefly larvae and its snail prey (Jusoh et al., 2010b; Jusoh & Hashim, 2012; Thancharoen, 2012; Wong & Yeap, 2012). Plants play an essential role in an insect's life-cycle because it is used as a stage for insect mating and food or egg-laying (Kaiser et al., 2017). However, there are also other factors, such as habitat change (Sánchez-Bayo & Wyckhuys, 2019), use of pesticides (Disque et al., 2019) as well as light pollution (Firebaugh & Haynes, 2016), that cause a decrease in the variety and quantity of fireflies. Since 2007, the firefly population has declined by 42 per cent over ten years due to land clearing along the river (Nadirah et al., 2020).

Prasertkul (2018) stated that Malaysian researchers have begun to perform various large-scale surveys, and *Pteroptyx* (especially *Pteroptyx tener*) studies have been conducted along some Malaysian rivers including, those in Selangor, Rembau, Linggi, Kerteh, and Kuala Sepetang. These studies provide valuable information on firefly abundance, distribution, seasonal variation, and the connection between plant species and fireflies. However, according to Prasertkul (2018), researchers in Thailand are less interested in studying *Pteroptyx* congregations since most recent studies have only focused on biodiversity surveys, conservation approaches, life cycle studies, and detailed habitat descriptions. Although, as Jusoh et al. (2020) stated, synchronous flashing fireflies of the genus *Pteroptyx* are found all across Southeast Asia, although little is known about

their biodiversity. According to them, recent investigations in Malaysia have shown the well-known population-level phylogeographic structure of the *P. tener* and *P. bearni*, implying the existence of crypto species. Second, morphological and genetic similarities between *Pteroptyx balingiana* and *Pteroptyx malacca* have prompted debate over the former's validity as a different species. Consequently, they recommended that research be conducted to expand the geographical, taxonomic, and genetic sampling of Southeast Asian fireflies to understand the species biodiversity better. Similarly, according to Chen et al. (2019), basic information regarding biodiversity and its evolutionary history is still insufficient.

This review has gathered and analysed data/list, species diversity, and firefly distribution in Southeast Asia countries, such as Malaysia, Philippines, Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Papua New Guinea, Laos, Thailand, and Vietnam papers published from 2015 to 2021. Meanwhile, this paper also collected data on display trees and firefly habitat areas and factors that influence selecting certain trees as their habitat and display trees.

FIREFLY LIST AND SPECIES DIVERSITY IN SOUTHEAST ASIAN COUNTRIES

Lampyridae is a cosmopolitan family made up of seven sub-families, 67 genera, and more than 2,000 species of fireflies that have been described worldwide (Da Silveira & Mermudes, 2014; Hu & Fu, 2018; Mu et al., 2016), most of which are found in tropical regions around the world (Hu &

Fu, 2018). More than 400 species have been identified in Southeast Asia and the Indo-Pacific regions, most of which belong to the Luciolinae family (Ballantyne et al., 2015). There is only one species of *Pteroptyx* Olivier (*Maipo* sp. nov.) firefly identified in Hong Kong (Ballantyne et al., 2011), but Southeast Asia is the home to this species (Ballantyne et al., 2019; Jusoh et al., 2018). The firefly species primarily found in Southeast Asian countries, such as Malaysia, Thailand, Indonesia, Vietnam, and the Philippines, are *P. malacca*, *Luciola pupilla*, and *P. tener* (Abdul Razak & Sulaiman, 2016). In addition, *Pteroptyx* is an East Asian and Southeast Asian descent genus with 18 species found from Hong Kong (Ballantyne et al., 2015, 2019; Jusoh et al., 2018), south to Southeast Asia (Ballantyne, 2001), and west to the Madras region of India (Ballantyne et al., 2011; Ballantyne & McLean, 1970).

The *P. tener* population was first discovered in Thailand mangrove forest in 2015 (Sriboonlert et al., 2015). They also mentioned that this was an uncommon occurrence for this species compared to the other main species in the area (*Pteroptyx malacca* and *Pteroptyx valida*). Therefore, they suggested that extensive research utilising molecular data, morphology and behaviour, such as lightning analysis, is needed to learn more about *P. tener*'s distribution and boundaries over the Thai-Malay peninsula. It is because morphological differences in *P. tener* may come to light of variances in geographical location. Whereas in southern Thailand, there are nine species of *Pteroptyx*, once recorded in Peninsular Malaysia (Jusoh et

al., 2018) (Figure 2 for *Pteroptyx* species distribution in Thailand), of which *P. tener* was one of the most widely recorded species (Foo & Dawood, 2017). Jaikla et al. (2020) found *P. tener* only found at one site in Surat Thani province in Thailand. The identification of this species in Surat Thani validated the findings by Sartsanga et al.

(2018) and Sriboonlert et al. (2015). The *P. tener* is found to be prevalent in Peninsular Malaysia, such as in Sungai Sepetang, Perak (Hazmi & Sagaff, 2018; Sulaiman et al., 2017), Sungai Bernam, Selangor (Shahara et al., 2017), Sungai Johor, Johor (Sulaiman et al., 2016), and Sungai Chukai, Kemaman (Mahmod et al., 2018).

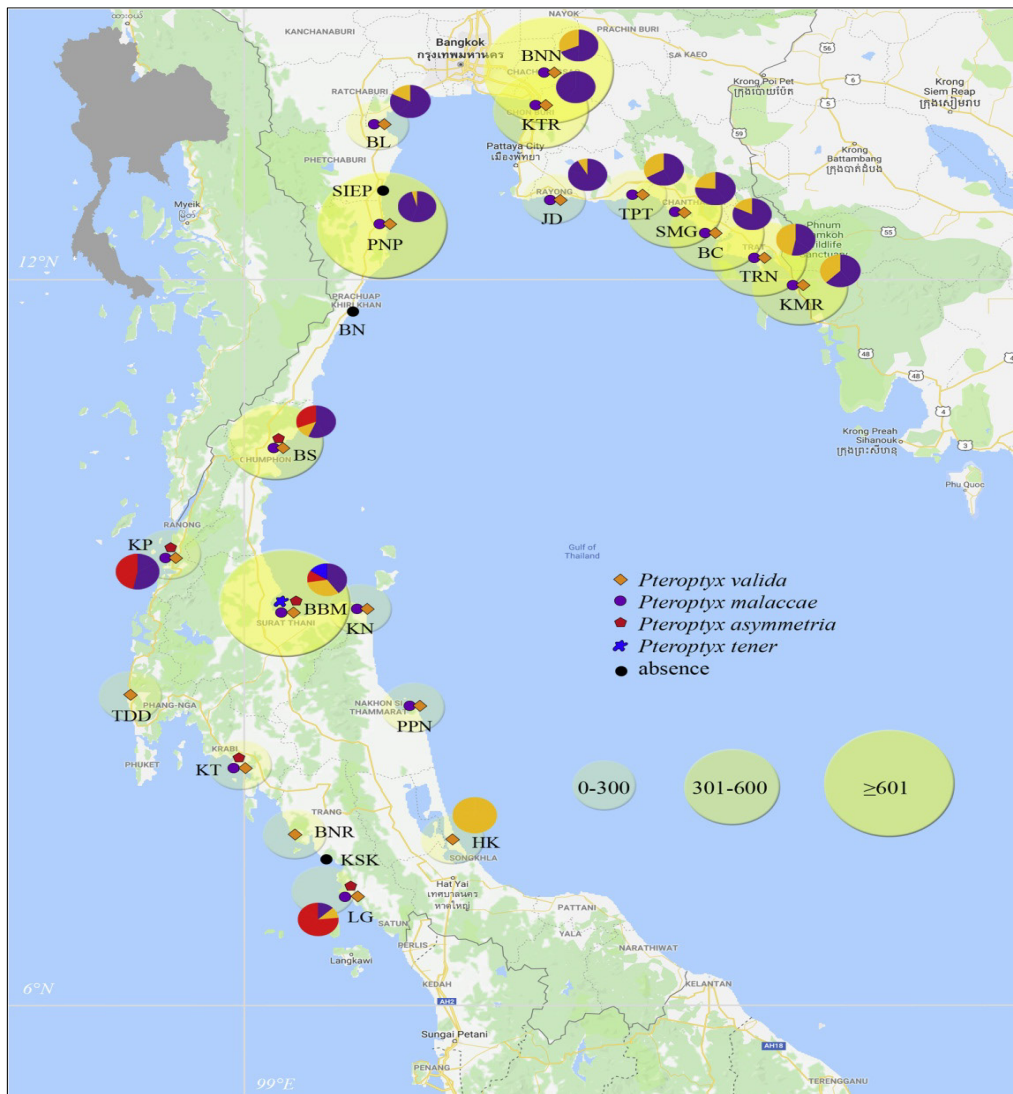


Figure 2. *Pteroptyx* species distribution in Thailand (Jaikla et al., 2020)

Sriboonlert et al. (2015) have also examined *Pteroptyx* museum specimens from two major insect museums in Thailand. From the examination, they discovered 319 *P. malacca* and 53 *P. valida* specimens collected from 47 locations in ten provinces between 1993 and 2005, including Chanthaburi, Nakhon Pathom, and Nakhon Si Thammarat, Pathum Thani, Phang Nga, Phetchaburi, Samut Sakhon, Samut Songkhram, Sukho Thai, and Trat. The examination again discovered that 117 specimens were *P. malacca* and 15 were *P. valida*, taken from 11 locations in six provinces between 1999 and 2008, including Chanthaburi, Nakhon Si Thammarat, Pattani, Phetchaburi, Samut Songkhram, and Trat. Using a range of species boundary analyses, Jusoh et al. (2020) discovered that *P. tener* populations along the west coast of Peninsular Malaysia differ from those on the east coast and in Borneo, although no physical differences. However, the investigation was unable to differentiate *P. bearni* from Borneo and eastern Peninsular Malaysia or distinguish *P. balingiana* and *P. malacca* as distinct species, suggesting that these populations may be specific or indicative of a new species.

According to Jaikla et al. (2020), *P. valida* was the first to be detected in 11 provinces in Thailand, namely in Chachoengsao, Chon Buri, Chumphon, Songkhla, Krabi, Phang Nga, Phetchaburi, Prachuap Khiri Khan, Ranong, Rayong, and Trang. The study also discovered the first species of *Pteroptyx asymmetria* in Chumphon and *P. malacca* in Krabi province. In Malaysia,

P. malacca has only been found once in Sarawak, in Limbang (Jusoh et al., 2018). However, Abdullah et al. (2020) recently found this species along the Niah River in Miri, Sarawak. This species has been identified in Sabah (Foo & Dawood, 2015) and in Muar (Johor), Chukai (Terengganu), and Pahang Tua River (Pahang) (Jusoh et al., 2018). *Pteroptyx malacca* was found in Malaysia in smaller populations, generally in sympathy with *P. tener*, found in much larger groups (Jusoh et al., 2011, 2018). In contrast to what happened in Thailand, *P. malacca* developed enormous assemblages in trees along river banks in sympathy with *P. valida* Olivier (Prasertkul, 2018).

In the meantime, *P. asymmetria* has only been found in Malaysia's western peninsula (Jusoh et al., 2018). Thus, Jaikla et al. (2020) found that *P. asymmetria* is restricted to locations on the southern coast of Thailand, which has a climate similar to Malaysia. The research on firefly abundance, distribution, seasonal variation, and the relationship between plant species and fireflies is very significant since, based on the findings by Dawood and Saikim (2016), the occurrence of *P. bearni* has been reviewed in Sabah, as well as an alarming decrease in the population of some fireflies in Likas, triggered by the loss of mangroves. One study found that *P. bearni* no longer exists in Likas (Dawood & Saikim, 2016). Apart from *P. bearni*, *Pteroptyx gelasina* is also no longer found in Likas (Dawood & Saikim, 2016). However, most fireflies remain a mystery; even relevant information is practically similar to the distribution of

the species (Mobilim & Dawood, 2020). Geographically and genetically, *P. bearni* Olivier was divided into two groups: one in the eastern Malaysian Peninsula and another one in Borneo, showing colour differences between the two groups (Jusoh et al., 2014). Figure 3 shows the geographical distribution of the *Pteroptyx* samples used by Jusoh et al. (2020) in their study covering Peninsular Malaysia (East and West), Borneo, and Thailand. While, Table 1 below lists the species of fireflies found in several countries in Southeast Asia, including Malaysia, the Philippines, Indonesia, Cambodia, Myanmar, Vietnam, Laos, Brunei, Papua New Guinea, Singapore, and Thailand, from 2015-2021.

Not much is known about the fauna of fireflies in many parts of Southeast Asia, such as Laos, Cambodia, Philippines, Indonesia, Vietnam, Timor-Leste, Myanmar, Singapore, and Brunei, where many species are less known due to lack of studies on the abundance and identification of firefly species-flashes compared to Thailand and Malaysia. The majority of the firefly genera found in Indonesia are endemic fireflies found in Sumatra, Kalimantan, and Papua, although some, such as *Diaphanes javanus*, may be found on Java island (Puspitaningrum et al., 2017). In Vietnam, an unusual genus of lampyrids has been found by Jeng et al. (2007), namely *Oculogryphus fulvus* Jeng. Later, Jeng et al. (2011) have discovered a second species of the enigmatic lampyrid genus *Oculogryphus* known as *Oculogryphus bicolor* sp. in Huong Son, Ha Tinh Province, Vietnam. The Philippines is the first country outside Malaysia (Sabah

and Sarawak) to record a new rare Southeast Asian firefly *Pygoluciola Satoi* (Ballantyne, 2008). Ballantyne and Lambkin (2009, 2013) and Ballantyne et al. (2015) include essential references that are partly linked to the Luciolinae fireflies present in the Philippines. Ohba and Meyer-Rochow (2012) have recorded the existence of a Guinea firefly known as *Pteroptyx effulgens* occur on the same tree (unknown species) at Open Bay (New Britain) and Kaw (New Ireland) in Papua New Guinea. Similarly, the study conducted by Iamba et al. (2021) in the Balsa plantations area of East New Britain Province, Papua New Guinea, in 2020 have found the same species, namely *P. effulgens*.

Electromethes gen. n. (Omethidae) and *Electotreta* gen. n. (Lampyridae), as well as two species, (*Electromethes alleni* sp. n. and *Electotreta rasnitsyni* sp. n.), were discovered in Baltic amber in Myanmar (Kazantsev, 2012a). Both taxa appear to be linked to the East Asian omethid (*Electromethes*) and ototretin (*Electotreta*). Again fossils of the genus of *Eoluciola* gen. n., and species *Eoluciola varang* sp. n., are described from the same place (Baltic amber), Myanmar. The taxa are placed in between Luciolini and Pristolycini, i.e. Luciolinae (Kazantsev, 2012b). The fossil genus of firefly, *Protoluciola* gen. n., and a new species, *Protoluciola albertalleni* Kazantsev sp. n., have been discovered Cretaceous Burmese amber, Myanmar (Kazantsev, 2015). While Jeng et al. (2003) reported the distribution of *Luciola substriata* in Myanmar.

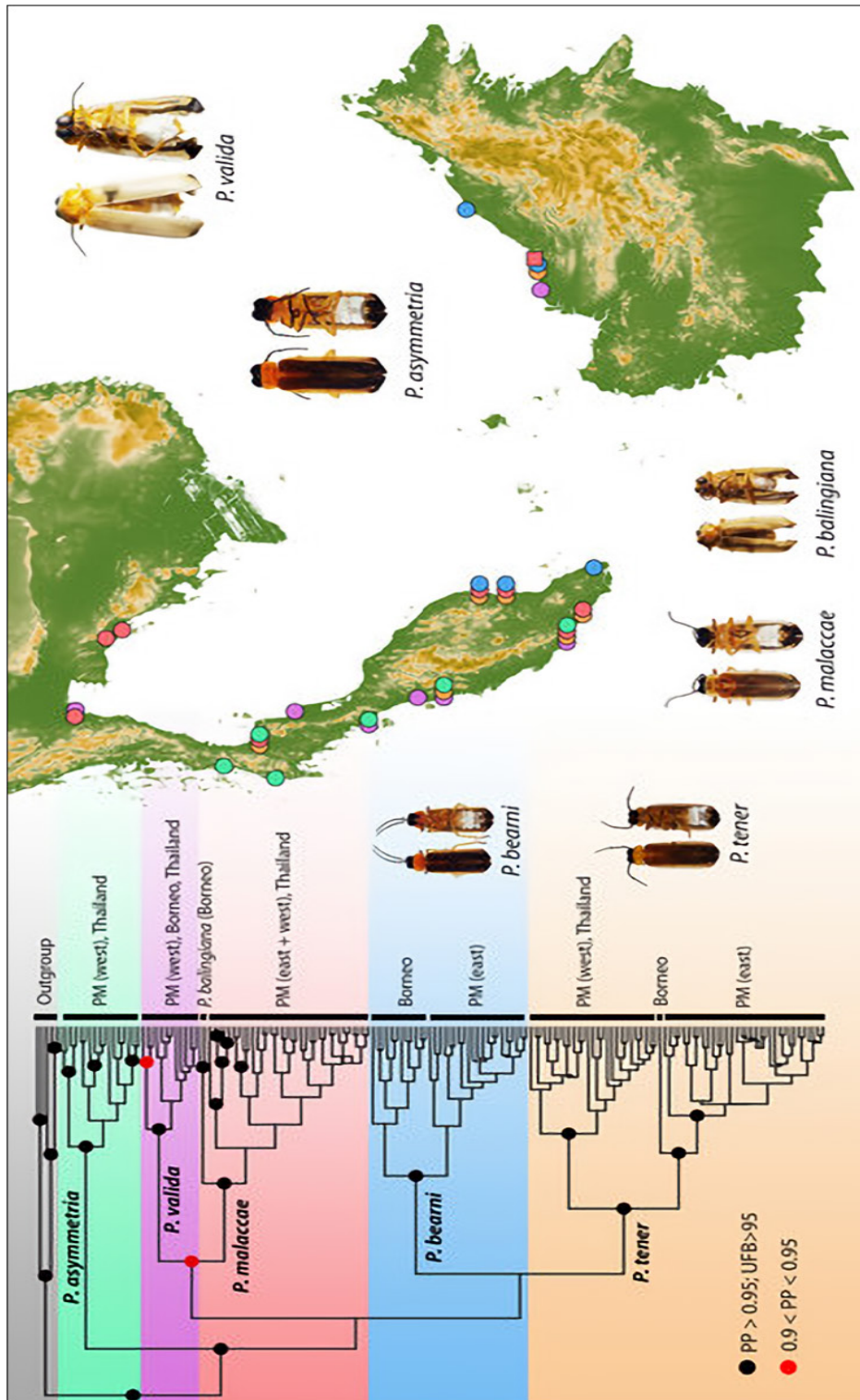


Figure 3. The geographical distribution of *Pteropyx* samples used by Jusoh et al. (2020) in their study

Tan (2018) documented five genera of fireflies on Pulau Ubin, Singapore, including *P. valida*, *Diaphanes* sp., *Colophotia* c.f. *praeusta*, *Curtos* sp., and presumably *Stenocladus* sp. and *Diplocladon* sp. in a study performed from 2012 to 2016. While, *Curtos* sp., which he discovered in his research, might be the first to be found in Singapore. Figure 4 shows the distribution of many species related to habitat type in the western and eastern parts of Pulau Ubin, Singapore, with *Curtos* sp. only found in secondary forests at one location in Bukit Tinggi, and *Diaphanes* sp. occurring in secondary forests in the eastern and western parts of Pulau Ubin (Tan, 2018). From

February 2009 to April 2010, Chan et al. (2012) conducted a nationwide survey in Singapore to determine the species richness, distribution, and abundance of fireflies at 14 sites across five habitats. The survey discovered three genera in the Luciolinae family, two in the Lampyrinae family, one in the Ototretinae family, one in the Rhagophthalmidae family, and 11 species (some of them are unknown), including *Luciola* sp. 2. *Luciola* sp. 2 is noteworthy because specimens were collected from freshwater swamp forests in Singapore's central catchment region and do not align with recognised *Luciola* species' characterisation.

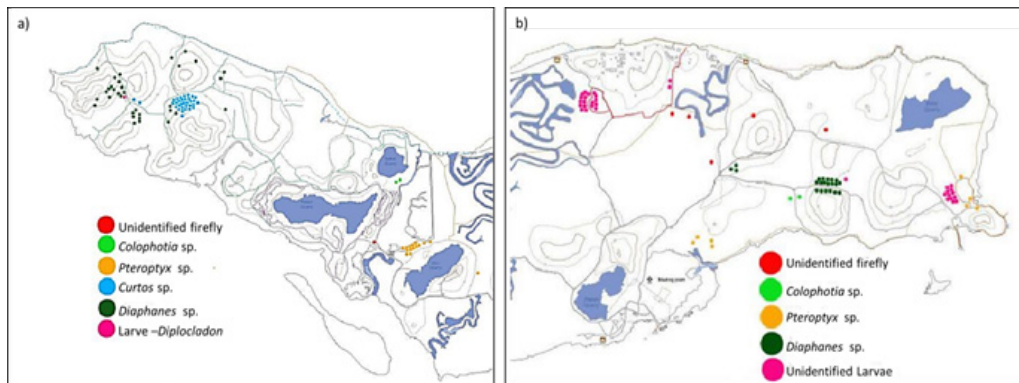


Figure 4. Records of fireflies in Pulau Ubin, Singapore; a) Western; b) Eastern (Tan, 2018)

Pteroptyx valida Olivier, *Stenocladus* sp., and *Diplocladon* sp. were all verified in the same research; however, *Pteroptyx bearni* Olivier and *Lucidina wallacei* Pic were not. While, throughout a survey performed by Jusoh et al. (2021) in the Nee Soon Swamp Forest (NSSF) on October 9, 2018, October 11, 2018, January 11, 2019,

and January 18, 2019, targeting specimens that fit the description of *Luciola* sp. 2 sensu have documented four specimens (three males and one female) were collected (all discovered on January 2019). Figure 5 displays a map of Singapore that illustrates the location of *Luciola singapura* Jusoh & Ballantyne sp. nov. in the Nee Soon Swamp

Forest (NSSF), as well as other *Luciola* species in Asia and the Pacific islands that were examined and evaluated in a study conducted by Jusoh et al. (2021).

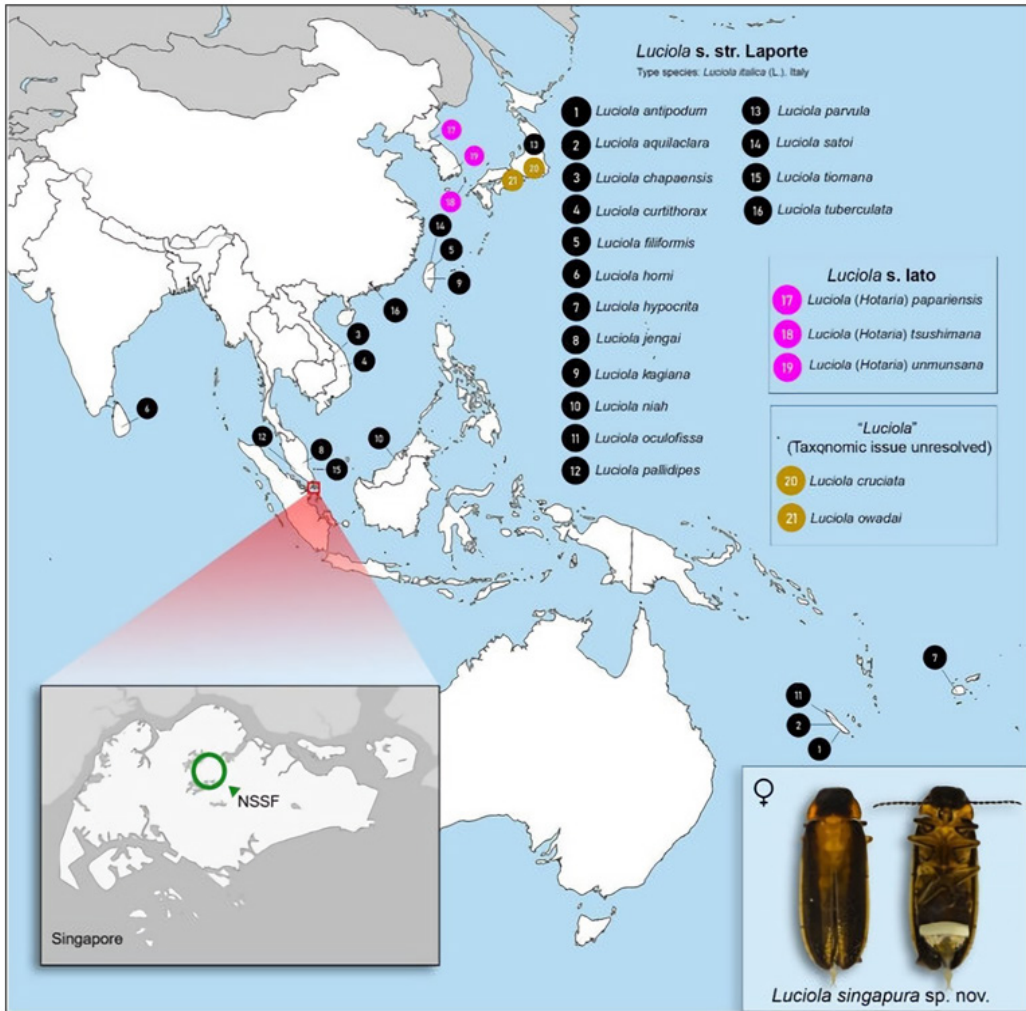


Figure 5. *Luciola Singapura* Jusoh & Ballantyne sp. nov. in the Nee Soon Swamp Forest (NSSF) as well as other localities of *Luciola* species in Asia and the Pacific Islands (Jusoh et al., 2021)

In Sri Lanka, the study of the taxonomy of fireflies for the first time began in the early 18th century (Wijesekara & Wijesinghe, 2003). Wijekoon et al. (2012) conducted a study on the regional diversity of fireflies of the subfamily Luciolinae in 2010 in Sri

Lanka, covering grassland areas in Uva and Sabaragamuwa and Central, North-Central, West, South, East, North, and North regions-West. The findings of this study revealed that there are nine different species of firefly, all of which are *Luciola* species

(*Luciola antennalis*, *Luciola candezei*, *Luciola chinensis*, *Luciola horni*, *Luciola humeralis*, *Luciola intricata*, *Luciola melaspis*, *Luciola nicollieri*, and *Luciola vespertina*) (Figure 6 and Table 1). The survey was conducted by Wijekoon (2013) from 2010 to 2012 in nine provinces in Sri Lanka [same as the study area in Wijekoon et al. (2012)] showed 13 species of fireflies belonging to six genera (*Asymmetricata*, *Curtos*, *Diaphenes*, *Lamprigera*, *Luciola*, and *Stenocladus*) were recorded. The species recorded were *Asymmetricata humeralis*, *Curtos costipennis*, *Diaphenes lutescens*, *Diaphenes vitrifera*, *Luciola*

cerata, *Luciola cingulata*, *Luciola dubia*, *Luciola extricans*, *Luciola horni*, *Luciola melaspis*, *Luciola praeusta*, *Lamprigera tenebrosa*, and *Stenocladus* sp. Wijekoon et al. (2016) classified specimens in the National Sri Lankan collection in Colombo as *Abcondita chinensis*, *Abcondita perplexa*, and *Abcondita promelaena*, as well as documenting *Luciola doriae* without commenting on its probable position. They also validated the presence of *Luciola humeralis* and *Luciola impressa* in Sri Lanka, classifying both as *Asymmetricata* genus (Figure 6).



Figure 6. Firefly species discovered in nine provinces of Sri Lanka in 2010 (Wijekoon et al., 2012)

Table 1

Firefly species found in Southeast Asian countries from 2015-2021

No.	Species	Country	References
1	<i>Abscondita anceyi</i>	Thailand	Wattanachaiyingcharoen et al. (2016)
2	<i>Abscondita anceyi</i> (Olivier 1883)	Myanmar	Ballantyne et al. (2016); Olivier (1883)
3	<i>Abscondita berembun</i> Nada sp. nov.	Malaysia	Ballantyne et al. (2019)
4	<i>Abscondita chinensis</i>	Sri Lanka, Thailand	Wattanachaiyingcharoen et al. (2016); Wijekoon et al. (2016)
5	<i>Abscondita chinensis</i> (L. 1767)	Cambodia, Myanmar, Thailand, Vietnam	Ballantyne et al. (2016); Linnaeus (1767)
6	<i>Abscondita jerangau</i> Nada sp. nov.	Malaysia	Ballantyne et al. (2019)
7	<i>Abscondita pallescens</i>	Indonesia, Malaysia	Ballantyne et al. (2019)
8	<i>Abscondita perplexa</i>	Sri Lanka	Wijekoon et al. (2016)
9	<i>Abscondita perplexa</i> (Walker 1858)	Cambodia	Ballantyne et al. (2016); Walker (1858)
10	<i>Abscondita promelaena</i>	Sri Lanka	Wijekoon et al. (2016)
11	<i>Abscondita promelaena</i> (Walker 1858)	Myanmar	Ballantyne et al. (2016)
12	<i>Abscondita promelaena</i> (Walker) comb. nov.	Myanmar	Ballantyne et al. (2013)
13	<i>Asymmetricata circumdata</i>	Thailand	Pronak et al. (2018); Wattanachaiyingcharoen et al. (2016)
14	<i>Asymmetricata ovalis</i>	Thailand	Pronak et al. (2018); Wattanachaiyingcharoen et al. (2016)
15	<i>Atripennis</i> Pic 1934	Malaysia	Ballantyne et al. (2019); Pic (1934)
16	<i>Atyphella testaceolineata</i> Pic, 1939	Indonesia	Ballantyne and Lambkin (2009); Pic (1939)
17	<i>Australoluciola</i> sp.	Thailand	Sartsanga et al. (2017)
18	<i>Australoluciola baduria</i> sp. nov.	Indonesia	Ballantyne and Lambkin (2013)

Table 1 (Continued)

No.	Species	Country	References
19	<i>Australoluciola jappenensis</i> sp. nov.	Indonesia	Ballantyne and Lambkin (2013)
20	<i>Baolacus lajoyei</i> Pic, 1915	Laos, Malaysia, Vietnam	Janisova and Bocakova (2013); Pic (1915)
21	<i>Ceylanidrilus bipartitus</i> Pic, 1911	Sri Lanka	Janisova and Bocakova (2013); Pic (1911)
22	<i>Colophotia brevis</i>	Malaysia	Jusoh et al. (2018)
23	<i>Colophotia</i> c.f. <i>praeusta</i>	Singapore	Tan (2018)
24	<i>Colophotia praeusta</i>	Malaysia	Jusoh et al. (2018)
25	<i>Curtos cerea</i>	Indonesia, Thailand	Annisa (2016); Wattanachaiyingcharoen et al. (2016)
26	<i>Curtos</i> sp.	Singapore	Tan (2018)
27	<i>Curtos</i> sp. 1	Indonesia	Annisa (2016)
28	<i>Curtos</i> sp. 2	Indonesia	Annisa (2016)
29	<i>Diaphanes javanus</i>	Indonesia	Annisa (2016); Puspitaningrum et al. (2017)
30	<i>Diaphanes</i> sp.	Indonesia, Singapore	Puspitaningrum et al. (2018); Tan (2018)
31	<i>Diaphanes</i> sp.2	Thailand	Wattanachaiyingcharoen et al. (2016)
32	<i>Diaphanes</i> sp.3	Thailand	Wattanachaiyingcharoen et al. (2016)
33	<i>Diaphanes</i> sp.4	Thailand	Wattanachaiyingcharoen et al. (2016)
34	<i>Diplocladon</i> sp.	Singapore	Jusoh et al. (2021); Tan (2018)
35	<i>Drilaster (Apodrilus) agcoensis</i> n. sp.	Philippines	Janisova and Bocakova (2013)
36	<i>Drilaster axillaris</i> Kiesenwetter, 1879	Borneo, Indonesia, Malaysia, Philippines, Sri Lanka, Thailand, Vietnam	Janisova and Bocakova (2013)
37	<i>Drilaster (Kerincius) medioniger</i> n. sp.	Indonesia	Janisova and Bocakova (2013)
38	<i>Electromethes alleni</i> sp. n.	Myanmar	Kazantsev (2012a)

Table 1 (Continued)

No.	Species	Country	References
39	<i>Electotreta rasnitsyni</i> sp. n.	Myanmar	Kazantsev (2012a)
40	<i>Emasia</i> gen. nov.	Borneo	Bocakova and Janisova (2010)
41	<i>Emasia dentata</i> sp. n.	Borneo	Bocakova and Janisova (2010)
42	<i>Eoluciola varang</i> sp. n.	Myanmar	Kazantsev (2012b)
43	<i>Eugeusis nigripennis</i> Pascoe, 1887	Myanmar, Thailand, Vietnam	Janisova and Bocakova (2013); Pascoe (1887)
44	<i>Eugeusis palpator</i> Westwood, 1853	Sri Lanka	Janisova and Bocakova (2013); Westwood (1853)
45	<i>Falsophaeopterus fruhstorferi</i> Pic, 1911	Indonesia	Janisova and Bocakova (2013); Pic (1911)
46	<i>Hyperstoma marginata</i> Wittmer, 1979	Sri Lanka	Janisova and Bocakova (2013); Wittmer (1979)
47	<i>Inflata indica</i>	Thailand	Sriboonlert and Wonnapijit (2019)
48	<i>Inflata indica</i> (Motschulsky 1854) comb. nov.	Thailand	Ballantyne et al. (2015); Motschulsky (1854)
49	<i>Lamellipalpodes annandalei</i> Maulik, 1921	Myanmar, Thailand	Janisova and Bocakova (2013); Maulik (1921)
50	<i>Lamprigera tenebrosa</i>	Thailand	Pronak et al. (2018)
51	<i>Lamprigera yunnana</i>	Thailand	Wattanachaiyingcharoen et al. (2016)
52	<i>Lampyrus noctiluca</i>	Indonesia	Ratnawulan et al. (2020)
53	<i>Lloydiella japonensis</i> sp. n.	Indonesia	Ballantyne and Lambkin (2009)
54	<i>Luciolinae angusticollis</i> Olivier 1886	Philippines	Ballantyne et al. (2016); Olivier (1886)
55	<i>Luciola antennalis</i>	Sri Lanka	Wijekoon et al. (2012)
56	<i>Luciolinae apicalis</i> (Eschscholtz 1822)	Philippines	Ballantyne et al. (2016); Eschscholtz (1822)
57	<i>Luciola aquatilis</i> Thancharoen	Thailand	Sumruayphol and Chaiphongpachara (2019)
58	<i>Luciola candezei</i>	Sri Lanka	Wijekoon et al. (2012)
59	<i>Luciola chinensis</i>	Sri Lanka	Wijekoon et al. (2012)
60	<i>Luciola curtithorax</i>	Thailand	Wattanachaiyingcharoen et al. (2016)
61	<i>Luciola doriae</i>	Sri Lanka	Wijekoon et al. (2016)

Table 1 (Continued)

No.	Species	Country	References
62	<i>Luciola horni</i>	Sri Lanka	Wijekoon et al. (2012)
63	<i>Luciola humeralis</i>	Sri Lanka	Wijekoon et al. (2012, 2016)
64	<i>Luciola impressa</i>	Sri Lanka	Wijekoon et al. (2016)
65	<i>Luciola indica</i>	Thailand	Wattanachaiyingcharoen et al. (2016)
66	<i>Luciola intricata</i>	Sri Lanka	Wijekoon et al. (2012)
67	<i>Luciola melaspis</i>	Sri Lanka	Wijekoon et al. (2012)
68	<i>Luciola nicollieri</i>	Sri Lanka	Wijekoon et al. (2012)
69	<i>Luciola picea</i>	Indonesia	Annisa (2016)
70	<i>Luciola singapura</i> Jusoh & Ballantyne sp. nov.	Singapore	Jusoh et al. (2021)
71	<i>Luciola</i> sp.	Malaysia	Mobilim and Dawood (2020)
72	<i>Luciola</i> sp.1	Indonesia	Annisa (2016)
73	<i>Luciola</i> sp.2	Indonesia	Annisa (2016)
74	<i>Luciola</i> sp.3	Thailand	Wattanachaiyingcharoen et al. (2016)
75	<i>Luciola trilucida</i>	Thailand	Wattanachaiyingcharoen et al. (2016)
76	<i>Luciola vespertina</i> (<i>Luciola praeusta</i> complex)	Sri Lanka	Wijekoon et al. (2012)
77	<i>Luciola</i> WFA	Malaysia	Jusoh et al. (2018)
78	<i>Luciolinae bicoloriceps</i> Pic 1924	Philippines	Ballantyne et al. (2016); Pic (1924)
79	<i>Luciolinae bicoloripes</i> Pic 1927	Vietnam	Ballantyne et al. (2016); Pic (1927)
80	<i>Luciolinae brahmina</i> Bourgeois 1890	Cambodia	Ballantyne et al. (2016); Bourgeois (1890)
81	<i>Luciolinae delauneyi</i> Bourgeois 1890	Vietnam	Ballantyne et al. (2016); Bourgeois (1890)
82	<i>Luciolinae deplanata</i> Pic 1929	Vietnam	Ballantyne et al. (2016); Pic (1929)
83	<i>Luciolinae infuscata</i> (Erichson 1834)	Philippines	Ballantyne et al. (2016); Erichson (1834)
84	<i>Luciolinae maculipennis</i> Olivier	Malaysia	Ballantyne et al. (2016)
85	<i>Luciolinae reticulata</i> Olivier 1900	Indonesia	Ballantyne et al. (2016); Olivier (1900)

Table 1 (Continued)

No.	Species	Country	References
86	<i>Luciolinae sordida</i> Olivier 1909	Indonesia	Ballantyne et al. (2016); Olivier (1909)
87	<i>Luciolinae substriata</i> Gorham 1880	Indonesia, Myanmar	Ballantyne et al. (2016); Gorham (1880)
88	<i>Luciolinae succincta</i> Bourgeois 1890	Cambodia	Ballantyne et al. (2016); Bourgeois (1890)
89	<i>Luciolinae varia</i> Olivier 1908	Indonesia	Ballantyne et al. (2016); Olivier (1908)
90	<i>Medeopteryx amilae</i> (Satô) comb. nov.	Philippines	Ballantyne and Lambkin (2013)
91	<i>Medeopteryx flagrans</i> (Ballantyne) comb. nov.	Indonesia	Ballantyne and Lambkin (2013)
92	<i>Medeopteryx fulminea</i> (Ballantyne) comb. nov.	Indonesia	Ballantyne and Lambkin (2013)
93	<i>Medeopteryx</i> sp.	Thailand	Pronak et al. (2018)
94	<i>Mimophaeopterus jacobsoni</i> Pic, 1930	Indonesia	Ballantyne and Lambkin (2013); Pic (1930)
95	<i>Ototreta drescheri</i> Pic, 1937	Indonesia	Janisova and Bocakova (2013); Pic (1937)
96	<i>Oculogryphus fulvus</i> Jeng	Vietnam	Jeng et al. (2007)
97	<i>Ototreta subvittata</i> Pic, 1943	Indonesia, Malaysia	Janisova and Bocakova (2013); Pic (1943)
98	<i>Ototreta weyersi</i> E. Olivier, 1900	Borneo, Indonesia, Malaysia, Philippines, Sri Lanka, Thailand, Vietnam,	Janisova and Bocakova (2013); Olivier (1900)
99	<i>Poluninius selangoriensis</i> (<i>Pteroptyx testacea</i>)	Malaysia	Jusoh et al. (2018)
100	<i>Protoluciola albertalleni</i> sp. n.	Myanmar	Kazantsev (2015)
101	<i>Pteroptyx asymmetria</i>	Thailand, Malaysia	Abdullah et al. (2019); Asri et al. (2020); Jaikla et al. (2020); Jusoh et al. (2018); Sartsanga et al. (2018)
102	<i>Pteroptyx balingiana</i>	Malaysia	Jusoh et al. (2018)
103	<i>Pteroptyx bearni</i> Ballantyne	Malaysia	Foo and Dawood (2017)

Table 1 (Continued)

No.	Species	Country	References
104	<i>Pteroptyx bearni</i> or <i>Pteroptyx similis</i>	Malaysia	Abdullah et al. (2020); Chey (2008, 2010, 2011); Dawood and Saikim (2016); Foo and Dawood (2015); Foo et al. (2017); Jusoh et al. (2018)
105	<i>Pteroptyx effulgens</i>	Papua New Guinea	Iamba et al. (2021); Ohba and Meyer-Rochow (2012)
106	<i>Pteroptyx galbina</i>	Malaysia	Ballantyne et al. (2015); Jusoh et al. (2018)
107	<i>Pteroptyx gelasina</i>	Malaysia	Chey (2008, 2011); Dawood et al. (2018)
108	<i>Pteroptyx gombakia</i> sp. nov.	Malaysia	Ballantyne et al. (2015)
109	<i>Pteroptyx malaccae</i>	Malaysia, Thailand	Abdullah et al. (2019, 2020); Chey (2010); Dawood and Saikim (2016); Foo and Dawood (2015); Jaikla et al. (2020); Sartsanga et al. (2018)
110	<i>Pteroptyx malaccae</i> Gorham	Malaysia, Thailand	Asri et al. (2020); Foo and Dawood (2017); Sumruayphol and Chaiphongpachara (2019)
111	<i>Pteroptyx malaccae</i> Group 2	Malaysia	Jusoh et al. (2018)
112	<i>Pteroptyx malaccae</i> Group 3	Malaysia	Jusoh et al. (2018)
113	<i>Pteroptyx malaccae</i> Group 4	Malaysia	Jusoh et al. (2018)
114	<i>Pteroptyx sayangia</i> sp. nov.	Malaysia	Ballantyne et al. (2015)
115	<i>Pteroptyx surabaya</i> sp. nov.	Indonesia	Ballantyne et al. (2015)
116	<i>Pteroptyx tener</i>	Indonesia, Malaysia, Thailand	Abdullah et al. (2019); Chey (2010); Dawood and Saikim (2016); Foo and Dawood (2015); Hazmi and Sagaff (2018); Jaikla et al. (2020); Jusoh et al. (2018); Othman et al. (2018); Sari et al. (2014); Sartsanga et al. (2018); Shahara et al. (2017); Sriboonlert et al. (2015)
117	<i>Pteroptyx tener</i> Olivier	Indonesia, Malaysia	Asri et al. (2020); Ballantyne and Lambkin (2013); Foo and Dawood (2017); Salleh et al. (2019)

Table 1 (Continued)

No.	Species	Country	References
118	<i>Pteroptyx valida</i>	Malaysia, Singapore, Thailand	Abdullah et al. (2019); Dawood and Saikim (2016); Foo and Dawood (2015); Jaikla et al. (2020); Sartsanga et al. (2018); Tan (2018)
119	<i>Pteroptyx valida</i> Group 2	Malaysia	Jusoh et al. (2018)
120	<i>Pteroptyx valida</i> Olivier	Malaysia, Singapore, Thailand	Foo and Dawood (2017); Jusoh et al. (2021); Sumruayphol and Chaiphongpachara (2019)
121	<i>Pygatyphella huonensis</i> (Ballantyne, 1968)	Indonesia	Ballantyne (1968); Ballantyne and Lambkin (2009)
122	<i>Pygatyphella japenensis</i> sp. n.	Indonesia	Ballantyne and Lambkin (2009)
123	<i>Pygatyphella nabiria</i> sp. n.	Indonesia	Ballantyne and Lambkin (2009)
124	<i>Pygoluciola satoi</i>	Philippines	Ballantyne (2008)
125	<i>Pygoluciola dunguna</i>	Malaysia	Nada and Ballantyne (2018)
126	<i>Pygoluciola</i> sp.1	Thailand	Wattanachaiyingcharoen et al. (2016)
127	<i>Pyrocoelia analis</i>	Indonesia, Malaysia, Thailand	Annisa (2016); Jusoh et al. (2018); Wattanachaiyingcharoen et al. (2016)
128	<i>Pyrocoelia</i> <i>praetexta</i> Olivier	Thailand	Sumruayphol and Chaiphongpachara (2019)
129	<i>Pyrocoelia</i> sp.	Malaysia	Roslan and Sulaiman (2015)
130	<i>Pyrocoelia</i> sp.2	Thailand	Wattanachaiyingcharoen et al. (2016)
131	<i>Pyrophanes appendiculata</i> Olivier	Indonesia, Philippines	Ballantyne et al. (2015)
132	<i>Pyrophanes beccarii</i> Olivier	Indonesia	Ballantyne et al. (2015)
133	<i>Pyrophanes elongata</i> Ballantyne sp. nov.	Philippines	Ballantyne et al. (2015)

Table 1 (Continued)

No.	Species	Country	References
134	<i>Pyrophanes quadrimaculata</i> Olivier	Philippines	Ballantyne et al. (2015)
135	<i>Pyrophanes semilimbata</i> (Olivier)	Indonesia, Malaysia, Philippines	Ballantyne et al. (2015)
136	<i>Pyrophanes similis</i> Olivier	Indonesia, Philippines	Ballantyne et al. (2015)
137	<i>Pyrophanes similisimma</i> sp. nov.	Indonesia	Ballantyne et al. (2015)
138	<i>Pygoluciola wittmeri</i>	Malaysia	Mobilim and Dawood (2020)
139	<i>Sclerotia aquatilis</i>	Thailand	Pronak et al. (2018)
140	<i>Stenocladus</i> sp.	Singapore	Jusoh et al. (2021); Tan (2018)
141	<i>Trisinuata</i> sp.	Thailand	Pronak et al. (2018)
142	<i>Trisinuata</i> sp. 2	Thailand	Wattanachaiyingcharoen et al. (2016)
143	<i>Trisinuata microthorax</i> (Olivier) comb. nov.	Indonesia	Ballantyne and Lambkin (2013)
144	<i>Trisinuata similispapuae</i> (Ballantyne) comb. nov.	Indonesia	Ballantyne and Lambkin (2013)
145	<i>Vesta menetriesi</i>	Indonesia	Annisa (2016)

DISPLAY TREES/HABITAT OF FIREFLIES ACROSS SOUTHEAST ASIAN COUNTRIES

According to Buck and Buck (1966), tree species used by fireflies as a gathering/convergence area are known by several terms, such as ‘mangrove fireflies’ or ‘firefly trees’. Meanwhile, Chey (2004) and Jusoh et al. (2010a, 2010b) called these trees ‘display trees’. Fireflies often randomly pick their spot to converge (Buck & Buck, 1966). However, they often like display trees for a number of reasons, such as proximity to larval prey food, arrangement of leaves conducive for mating, and nectar-

like or rubber-like food-providing trees for adults to feed (Jusoh et al., 2010a, 2010b). Sriboonlert et al. (2015) previously associated the volatile distribution of *P. tener* in southern Thailand with the cleavage of mangrove forests. However, Cheng et al. (2020) argued that there was a lack of efforts to consider or clarify how the species had achieved its current distribution in selected river systems in Southeast Asia.

Fireflies have a wide range of habitats, including mangroves, rivers, and inland highlands (Ballantyne et al., 2011). *Pteroptyx* species that inhabit mangroves are mostly in *Sonneratia caseolaris* (L.)

Engler (Sonneratiaceae), *Nypa fruticans* Wurm. (Arecaceae), *Acanthus ilicifolius* L. (Acanthaceae), *Rhizophora apiculata* Blume (Rhizophoraceae), *Rhizophora mucronata* Lamarck, and *Bruguiera gymnorrhiza* (L.) Lamarck (Rhizophoraceae) (Jusoh et al., 2010a, 2010b; Ohba & Wong, 2004). A study conducted by Prasertkul (2018) on the occurrence of fireflies (*P. malacca* and *P. valida*) at a park surrounded by an urban area in Samut Prakan Province found that the fireflies were in several tree species including *Sonneratia caseolaris*, *Hibiscus tiliaceus*, *Terminalia catappa*, *Ficus* sp. 1 (Banyan tree), *Ficus* sp. 2 (Fig tree), *Cerbera odollam*, *Albizia procera*, *Bambusa* sp., *Tamarindus indica*, *Pterocarpus indicus*, and *Erythrina variegata*. Of all the plant species, fireflies often use *Sonneratia caseolaris* as a pilgrimage platform, while *Terminalia catappa* (an exotic ornamental plants) are also often used mainly during the rainy season.

According to Jusoh et al. (2018), *P. bearni*, which is found in mangrove areas in Peninsula Malaysia, is restricted to the East Coast in areas bathed in saltwater, while in Miri, Sarawak, this species has been carried far into the river system, which is about 16 km from Mat Shah Jetty, to Maloi, 1 km past the Taniku jetty. The collection of this species in Likau and Niah is located near the estuary. Jusoh (2015) found that *P. galbina* had gathered around the river area but was not limited to mangrove forests. This species was spotted about 30 kilometres from the sea, flying from Niah alone along the forest trail near the river (Jusoh et al.,

2018). Meanwhile, *Pteroptyx* Olivier, from the subfamily Luciolinae, is found in many mangrove swamps shrub trees (Jusoh et al., 2018). See Table 2 for a list of firefly species identified in Southeast Asian countries.

Of all 23 study locations located in 16 provinces along the Thai coast, it was found that there were three dominant (90%) mangrove species [*Sonneratia caseolaris* (L.) Engl., *Avicennia* sp. and *Rhizophora* sp.] selected by fireflies as display trees. Recent findings indicate that there are six mangrove species from three families, namely *Acanthaceae*, *Lythraceae*, and *Rhizophoraceae*, which constitute 92.5 per cent of all display trees, while 7.5% are associated with mangrove trees (Jaikla et al., 2020). *Pteroptyx* fireflies like trees with a higher proportion of openings or open spaces in the canopy, whereas trees surrounded by open areas of 0-25% are seldom as display trees. *Pteroptyx* fireflies never occupy a tree covered by a thick canopy (Jaikla et al., 2020). In Peninsular Malaysia, fireflies were discovered congregating on several tree species along the downstream riparian zone, especially the *Sonneratia* spp. (Jusoh et al., 2018; Shahara et al., 2017; Sulaiman et al., 2016, 2017). They are found associated with some riparian flora, such as *Sonneratia caseolaris*, *Hibiscus tiliaceus*, *Nypa fruticans*, *Acrotichum aureum*, *Areca catechu*, *Ficus* spp., and *Oncosperma tigillarum* (Juliana et al., 2012; Khoo et al., 2012), which are also found in Thailand (Prasertkul, 2018).

Table 2

Firefly display trees in Malaysia and Thailand

No.	Species	Country	References
1	<i>Acacia auriculiformis</i> A. Cunn.	Thailand	Jaikla et al. (2020)
2	<i>Albizia procera</i>	Thailand	Prasertkul (2018)
3	<i>Aegiceras floridum</i>	Malaysia	Foo and Dawood (2016)
4	<i>Avicennia</i> sp.	Thailand; Malaysia	Abdullah et al. (2020); Foo and Dawood (2016, 2017); Jaikla et al. (2020)
5	<i>Bambusa</i> sp.	Thailand	Prasertkul (2018)
6	<i>Barringtonia</i> sp.	Malaysia	Mahmod et al. (2018)
7	<i>Bruguiera</i> sp.	Thailand; Malaysia	Abdullah et al. (2020); Jaikla et al. (2020)
8	<i>Bruguiera parviflora</i>	Malaysia	Abdullah et al. (2020)
9	<i>Ceriops</i> sp.	Thailand	Jaikla et al. (2020)
10	<i>Cerbera odollam</i>	Thailand	Prasertkul (2018)
11	<i>Cocos nucifera</i> L.	Thailand	Jaikla et al. (2020)
12	<i>Cyperus involucratus</i> Rottb.	Thailand	Jaikla et al. (2020)
13	<i>Derris</i> sp.	Malaysia	Abdullah et al. (2020)
14	<i>Excoecaria agallocha</i>	Malaysia	Foo and Dawood (2017)
15	<i>Excoecaria indica</i> L.	Malaysia	Foo and Dawood (2017)
16	<i>Ficus benjamina</i> L.	Thailand	Jaikla et al. (2020)
17	<i>Ficus</i> sp. 1	Thailand	Prasertkul (2018)
18	<i>Ficus</i> sp. 2	Thailand	Prasertkul (2018)
19	<i>Guilandina bonduc</i> L.	Malaysia	Mahmod et al. (2018)
20	<i>Hibiscus</i> sp.	Thailand; Malaysia	Abdullah et al. (2020); Foo and Dawood (2016, 2017); Jaikla et al. (2020); Prasertkul (2018)
21	<i>Lumnitzera</i> sp.	Thailand	Jaikla et al. (2020)
22	<i>Lumnitzera littorea</i>	Malaysia	Foo and Dawood (2016)
23	<i>Nypa fruticans</i>	Thailand; Malaysia	Foo and Dawood (2017); Prasertkul (2018)
24	<i>Pandanus</i> sp.	Malaysia	Abdullah et al. (2020)
25	<i>Rhizophora</i> sp.	Thailand; Malaysia	Abdullah et al. (2020); Foo and Dawood (2016, 2017); Jaikla et al. (2020)
26	<i>Rhizophora apiculata</i>	Malaysia	Foo and Dawood (2017)

Table 2 (Continued)

No.	Species	Country	References
27	<i>Sonneratia caseolaris</i> (L.) Engl.	Thailand; Malaysia	Cheng et al. (2017); Hazmi and Sagaff (2018); Jaikla et al. (2020); Mahmud et al. (2018); Prasertkul (2018)
28	<i>Sonneratia ovata</i> Backer	Thailand	Jaikla et al. (2020)
29	<i>Tamarindus indica</i>	Thailand	Prasertkul (2018)
30	<i>Terminalia catappa</i>	Thailand	Prasertkul (2018)
31	<i>Thespesia populnea</i> (L.) Sol.	Thailand	Jaikla et al. (2020)
32	<i>Thespesia populnea</i>	Malaysia	Abdullah et al. (2020)
33	Unidentified species from the family Poaceae	Thailand	Jaikla et al. (2020)
34	<i>Xylocarpus granatum</i>	Malaysia	Abdullah et al. (2020)
35	<i>Xylocarpus</i> sp.	Thailand	Jaikla et al. (2020)

CONCLUSION

The study successfully identified a total of 145 different species of fireflies throughout Southeast Asian countries (such as Malaysia, Philippines, Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Papua New Guinea, Laos, Thailand, and Vietnam. While the authors also failed to find studies in Brunei) based on studies conducted by previous researchers. Data on the species of fireflies found in countries such as the Philippines, Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Borneo, Papua New Guinea, Laos, and Vietnam are incredibly outdated due to the lacking of research undertaken in the country.

This review has managed to find at least 34 tree species and one unidentified species (Poaceae family) of display trees or habitat by fireflies in Malaysia and

Thailand. For other countries such as Indonesia, Cambodia, Myanmar, Singapore, Sri Lanka, Borneo, Papua New Guinea, Laos, Thailand, and Vietnam, there are no studies were found to identify tree species inhabited by fireflies. The studies conducted in those countries only focused on firefly species and did not study the habitat areas and display trees chosen by fireflies. More research regarding fireflies, including species richness, abundance, distribution, seasonal variation, and habitat, should be conducted in Southeast Asia.

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