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A new genus for two species of Japanese fireflies having aquatic larvae (Coleoptera, Lampyridae) and a definition of *Luciola* s. str.

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Abstract. A new genus *Nipponoluciola* Ballantyne, Kawashima, Jusoh & Suzuki is proposed and described from males, females and larvae for two species of Japanese fireflies (Coleoptera, Lampyridae, Luciolinae) which have aquatic larvae. The famous Genji-botaru, the Genji firefly, formerly *Luciola cruciata* Motschulsky, 1854, now stands under *Nipponoluciola cruciata* (Motschulsky) gen. et. comb. nov. It is proposed that the original designation of this species from Java was in error and that the species is only known from Japan. The lesser known Kumejima-botaru, formerly *Luciola owadai* Satô & Kimura, 1994, now stands under *Nipponoluciola owadai* (Satô & Kimura) gen. et comb. nov. A neotype for *Luciola cruciata* is designated. Keys to adult males and larvae of Luciolinae genera with aquatic larvae are given. An overview of the status of the genus *Luciola* s. str. is given. Supplementary file addresses 1. Mitogenome analyses of the Luciolinae; 2. List of species of *Luciola* s. str.; 3. List of Japanese Luciolinae; 4. The identity of *Luciola lateralis* Motschulsky.

Keywords. Lampyridae, Luciolinae, females, Japanese Luciolinae, aquatic larvae.

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Table of contents

Introduction

Of all the countries that have a fascination for fireflies that of Japan's is exceptional (Oba *et al.* 2011; Takada 2011, 2012). The firefly fauna is extensive and varied. Kawashima (2018, 2021) and Kawashima *et al.* (2003, 2005) recorded 52 species from four subfamilies of Lampyridae Rafinesque, 1815 as well as a species of Rhagophthalmidae Olivier, 1907. Certain fireflies ("H(b)otaru" in Japanese), especially *Luciola cruciata* Motschulsky, 1854 (Genji-botaru) and *Aquatica lateralis* (Motschulsky, 1860) (Heike-botaru) are the most common and most popular luminous insects in mainland Japan. Not unsurprisingly some of the best efforts in the world for bioremediation of firefly habitats occurs in Japan (Ohba 2012).

This paper concerns taxonomy, the science of naming, describing and classifying living things. It is taxonomy that gives us the scientific name by which the Genji firefly has been known until now viz. *Luciola cruciata*. In the furtherance of taxonomy, zoological nomenclature is provided with a well-defined set of procedures and rules to follow, and adherence to those rules led our investigation to an unexpected course of action with regard to how the Genji firefly in particular should be named (International Code of Zoological Nomenclature 1999; ICZN). This paper also supports the rule that, however written descriptions may be phrased, ultimately a species name is defined by its holotype specimen.

We are proposing a change to the generic name of the most famous firefly in Japan. The need for a new generic category arose from several factors, the first of which is the taxonomic placement of *Hotaria* Yuasa, 1937. Yuasa erected a new genus, *Hotaria*, by comparing the morphology and ecology of *Luciola cruciata*, *L. lateralis* Motschulsky, 1860, and *L. parvula* Kiesenwetter, 1874, and transferred *L. parvula* to *Hotaria* (Yuasa 1937). Subsequently *Hotaria* was recognised as a valid genus by many Japanese and Korean entomologists (e.g., Satô 1974; Suzuki 1997; Choi *et al.* 2003; Kim *et al.* 2004; Han *et al*. 2019).

Kawashima *et al.* (2003) compared features of specimens of the type species of *Luciola*, *L. italica* (Linnaeus, 1758), and *H. parvula*, treated *Hotaria* as a junior synonym of *Luciola*, and returned *parvula* to *Luciola*, as they considered the morphological characteristics of *parvula* were traits of *Luciola*. However, they did not address the other two Asian species, *L. cruciata* and *L. lateralis*. While subsequently *L. lateralis* was transferred by Fu *et al.* (2010) to a new genus *Aquatica* Fu, Ballantyne & Lambkin, 2010 and *L. cruciata* has remained in the genus *Luciola.*

The other issue arises from phylogenetic analyses which have consistently recognised the distinctiveness of *Luciola cruciata* and *L. owadai* Satô & Kimura, 1994. Early molecular phylogenetic analyses using mitochondrial DNA (mtDNA) (Suzuki 1997) showed a monophyletic group of fireflies with aquatic larvae (*L. cruciata*, *L. owadai*, and *L. lateralis*) among the species of Luciolinae Lacordaire, 1857 from Japan. Ballantyne & Lambkin (2009) first included *Luciola cruciata* and *L. owadai* in their morphological analyses of the Luciolinae with their results indicating the two species belonged to a distinct clade, separate from *Luciola* s. str. Subsequent analyses where a *Luciola* s. str. clade was defined (Fu *et al.* 2010; Ballantyne *et al.* 2013, 2015, 2016, 2019) continued to infer a distinct *cruciata/owadai* clade, with Jusoh *et al*. (2018), incorporating molecular data, identifying both a *Luciola* s. str. clade and a separate *cruciata/owadai* clade allied to *Aquatica*. Analyses by Ballantyne *et al.* (2015, 2016, 2019) also including the rare monotypic New Guinean genus *Missimia* Ballantyne, 2009 suggested a sister relationship to *cruciata/owadai.* Common to all these analyses were two inferences concerning *Luciola cruciata* and/or *L. owadai*: 1. at no point were they included in *Luciola* s. str.; 2. the analyses always supported a separate group close to the genus *Aquatica* for both.

Despite the clear indications of the distinctiveness of the two Japanese species, both *L. cruciata* and *L. owadai* were placed under "Taxonomic issues unresolved" by Ballantyne *et al.* (2019).

Jusoh *et al.* (2021) addressed 16 species of *Luciola* s. str., and formally removed *L. cruciata* and *L. owadai* from *Luciola*, including them under species incertae. Thus, in the light of the prevailing ambiguous and unresolved systematics of *Luciola*, the need to formalise the placement of both these species arose.

Molecular studies that have included *Luciola*, especially those based on mtDNA only, tend to provide few answers regarding *Luciola* s. str. as they include too few species. The situation is further confused when those analyses use scientific names that have since changed. For example Maeda *et al.* (2017) used *Luciola lateralis* (now *Aquatica*), and *Luciola substriata* Gorham, 1880 (now *Sclerotia flavida* (Hope, 1845); Hu & Fu 2018), while showing a close relationship between *L. cruciata* and three species of *Aquatica* (and *Luciola lateralis*) (see Supp. file 1: 1).

We investigated the history of the specific epithet, *cruciata*, of the Genji-botaru, arising from a convoluted set of mistakes relating to incorrect identification, and the original locality for *cruciata*, which was supposedly Java. In the absence of a type, and not being able to locate any specimens identified as *cruciata* and bearing a Java locality label, we justify our suggestion of mistaken locality, or incorrect labelling, and consider that the species *cruciata* has always been from Japan.

Here, we describe a new genus *Nipponoluciola* for two species which are transferred from *Luciola*. *Nipponoluciola cruciata* gen. et comb. nov. is the new generic epithet for the Genji-botaru, which previously stood under *Luciola cruciata. Nipponoluciola owadai* gen. et comb. nov. is the new generic epithet for the Kumejima-botaru which previously stood under *Luciola owadai* (Figs 1A–B, 2G–H).

Genus and species are addressed from morphological characters of males, females and larvae, and include variability in aedeagal patterns for *Nipponoluciola cruciata* gen. et comb. nov. that relate to differences in male flash patterns and geographical incidence.

In this study, we also attempt to resolve *Luciola* taxonomy insofar as it relates to a definition of *Luciola* s. str., which is essential to our argument, and allows us to define a position for *Luciola cruciata* and *L. owadai*. Two possible options are addressed (see Results) following recommendations by Jusoh *et al.* (2021). Our choice of what we consider the best option is discussed, and we provide taxonomic amendments based on extensive revision, literature review and morphological characters to resolve this long-standing problem (see Supp. file 1: 2). Also included is a list of species currently assigned to *Luciola* s. str.

The dimensions and composition of *Luciola* s. lat. (sensu Ballantyne *et al.* 2019) are also addressed. Supp. file 1 that indirectly addresses and enhances material covered here includes: 1. Mitogenome analyses of the Luciolinae; 2. Species included within *Luciola* s. str.; 3. A list of Japanese Luciolinae; 4. The identity of *Luciola lateralis* Motschulsky.

Material and methods

Historical information

Taxonomic literature reporting *Luciola* from Japan was collated, translated (where possible), and interpreted to build a chronology of species descriptions and detect nomenclatural issues. Curators in charge of collections where the type specimens are deposited (see the list and names under Abbreviations for repositories for insect specimens) were contacted in an attempt to locate the types.

Morphology

We follow the descriptions of characters of males, females and larvae of the Luciolinae in Ballantyne *et al.* (2015; 438 characters). Interpretation of internal female reproductive anatomy follows Ballantyne *et al.* (2011). Larval morphology follows Fu *et al.* (2012b) who defined larval types, expanded certain larval characters, and defined terms such as aquatic and semiaquatic as they refer to larvae. We follow their terminology, with some exceptions outlined below. The aquatic larvae Itsuro Kawashima examined were very soft bodied and it was difficult to determine subdivisions of the ventral surface in particular.

Lawrence & Ślipiński (2013) discussed the numbers of palpomeres in the larval maxillary palps and the possible confusion that can arise if a palpifer is enlarged and articulated. For conformity with previous descriptions, we describe the maxillary palp here as being composed of four segments.

Fu *et al.* (2012b) referred to the ventral areas of the meso and metathorax in larvae as an anterior presternum and a posterior sternum. We now follow Lawrence & Ślipiński (2013) and call the anterior area the basisternum and the posterior area the sternellum. Lawrence & Ślipiński (2013) addressed the

division of tergites by a narrow median ecdysial line and the occurrence which we see here of a much broader division leading to the formation of much smaller, paired tergites. This wide line is referred to as a median area in descriptions. These aquatic larvae split open the cuticle along the lateral margins and not along the dorsal median cleavage line when moulting.

Subsequent to Ballantyne *et al.* (2015) a certain conformity of generic and specific descriptions was adhered to, thus enabling more direct comparisons. Ballantyne *et al.* (2019) expanded this to develop a method of generic description to cope with situations where not all the characters are necessarily of significance e.g., not all species have deflexed elytral apices. For the sake of simplicity, we have eliminated from both generic and specific descriptions selected characters which were scored as not present in Ballantyne *et al.* (2015).

Certain characters specify what seem to be subjective degrees of development as 'gently', 'moderately', etc., and the objective extent of these descriptions is either given in Ballantyne *et al.* (2015) or here by reference to figures.

Dissections of males and females either follow Ballantyne *et al.* (2019: 8) for dry specimens, and Ballantyne & Lambkin (2009) for ethanol preserved specimens, or the following for Kawashima, who used a different process. Pinned specimens were softened in hot water and the last 4 abdominal segments removed, immersed in 10% NaOH solution for 24 hours at room temperature, and dissected

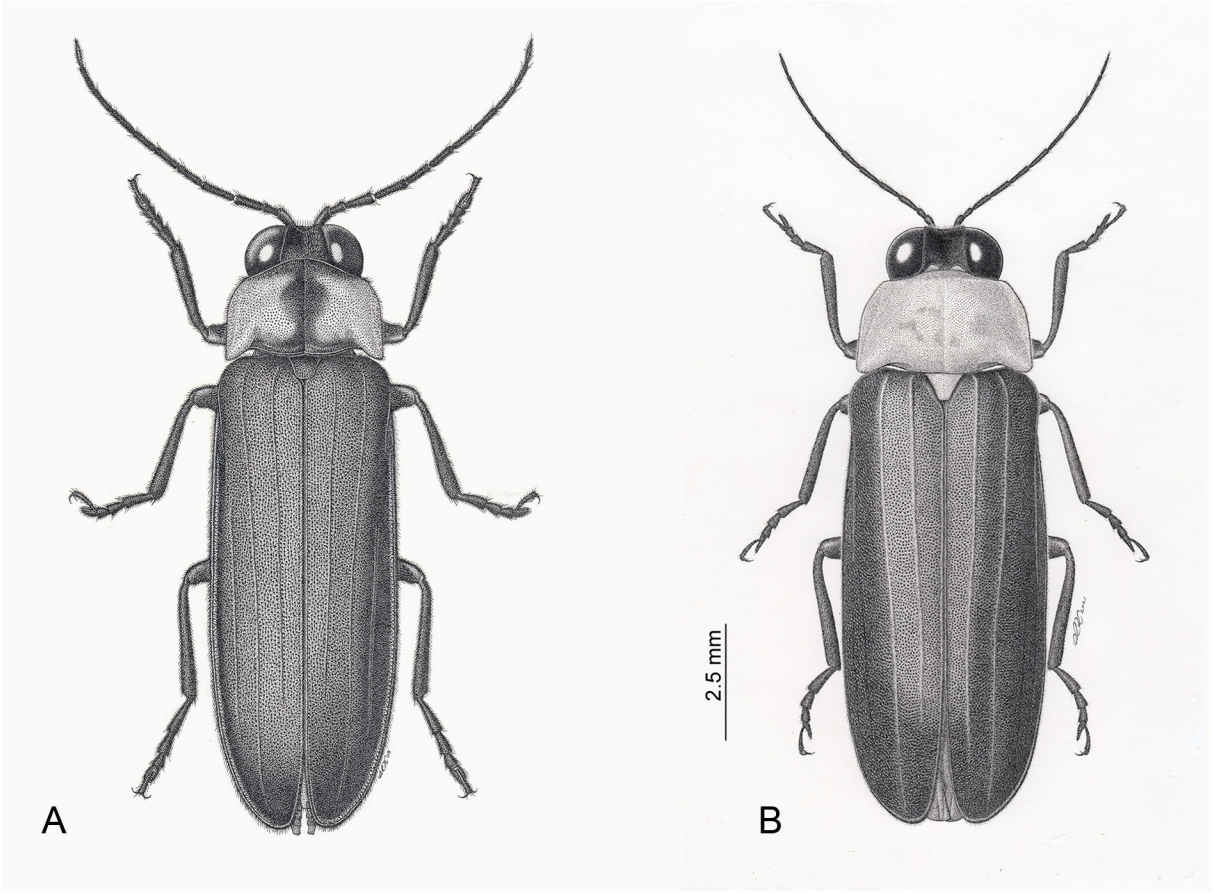

Fig. 1. Dorsal habitus males. **A**. *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. **B**. *Nipponoluciola owadai* (Satô & Kimura, 1994) gen. et comb. nov. Drawings by I. Kawashima (A–B).

to remove sheath and aedeagus. These were mounted on a glass slide in glycerin, observed through an optical microscope (Olympus BH-2, max magnification × 1000) and sketched with the aid of a drawing tube. The dissected parts were either immersed directly in glycerin in microvials or dried and stored on mounts. Whole specimens were observed under a stereo Olympus SZH10 microscope (maximum magnification × 140) fitted with a drawing tube (Kawashima 2019).

Orientation of aedeagi in repose within the aedeagal sheath is variable and assigning ventral and dorsal surfaces may be artificial. We follow Ballantyne *et al.* (2019) in referring to that side of the median lobe having the ejaculatory orifice as the ventral surface. The aedeagal sheath has clearly defined dorsal and ventral surfaces by comparison.

All aedeagi and aedeagal sheaths are depicted in illustrations either with the anterior end towards the top of the page, or the anterior end is specified in the figure legend.

Certain figures are arranged to allow comparisons between features (e.g., Figs 3–5) and are not to scale.

Ballantyne used an Olympus SC100 camera mounted on an Olympus SZX12 stereo microscope. Kawashima used an Olympus SZH10 stereo microscope with drawing tube, and his drawings were drafted first with a 0.2–0.3 mm mechanical pencil and drawn in ink using a 0.1–0.3 mm drafting pen (rapidograph) and round pen.

We continue to follow both the interpretations and the terminology of Lawrence & Ślipiński (2013) for male genitalia as follows: the male copulatory organ, the aedeagus, consists of four parts 1. the basal piece (phallobase); 2. paired lateral lobes (parameres); 3. median lobe (penis); 4. endophallus (internal sac). The external opening of the endophallus is referred to as the ejaculatory orifice in diagrams.

We use the abbreviations Fig. or Figs to refer to diagrams in this paper; fig. or figs refers to diagrams in already published work as referenced.

Abbreviations for taxonomic characters

Abbreviations follow Ballantyne *et al.* (2015, 2019) and are repeated here for convenience.

A	=	pronotal dimension measured from above; width across anterior third
ASD	=	distance between antennal sockets
ASW	=	antennal socket greatest diameter
B	=	pronotal dimension measured from above; width across middle
BP	=	basal piece
C	=	pronotal dimension measured from above; width across posterior third
FS	=	antennal flagellar segments
GHW	=	greatest head width (across eyes, measured parallel to ASD)
L	=	length
LL	=	lateral lobes
LO	=	light organ
MFC	=	metafemoral comb
ML	=	median lobe
MN	=	mesonotal plates
MO	=	median oviduct
MOP	=	median oviduct plate
MPP	=	median posterior projection ventrite 7 male only
MS	=	mesoscutellum
PLP	=	posterolateral projections ventrite 7 male only
SDG	=	spermatophore digesting gland

SIW = smallest interocular width (measured horizontally, may be on the same level as ASD, ASW, above it if the eyes are closer there)
T7, 8 etc. = abdominal tergites
V6, 7 etc. = abdominal ventrites, referred to by actual, not visible number
W = width

Abbreviations for repositories for insect specimens (curator)

AKPM = The collection of Akita Prefectural Museum, Akita (Kazushi Umetsu, now Yumi Fujinaka)
ANIC = Australian National Insect Collection, Canberra
CIK = The collection of Itsuro Kawashima, Yokosuka, Kanagawa
HZNHM = Natural History Museum Huazhong Agricultural University, Wuhan
KPM = Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa (Kyohei Watanabe)
MZLU = Biological Museum (Entomology), Lund, Sweden (Christoffer Fägerström)
MNHN = Muséum nationale d'histoire naturelle, Paris (Antoine Mantilleri)
NHMUK = Natural History Museum, London (Maxwell Barclay, Michael Geiser)
NSMT = Natural Museum of Nature and Science, Tsukuba, Ibaraki (Shuhei Nomura)
YCM = Yokosuka City Museum, Yokosuka, Kanagawa (Nobuyoshi Ohba, but now Toshiki Uchifune)
ZIN = Zoological Institute of the Russian Academy of Sciences, St. Petersburg (Alexander Kirejtshuk)
ZMMU = Zoological Museum of Moscow University (Aleksey Gusakov)
ZRC = Zoological Reference Collections, Lee Kong Chian Natural History Museum, Singapore

Results

Chronology of species descriptions and naming issues concerning the Genji botaru

Type locality of *Luciola cruciata* is Java

The original specimens of *Luciola cruciata* on which the description was based were recorded from "Iava" (Motschulsky 1854), or in modern parlance, Java [Article 58.3 of the ICZN (1999) deems the use of i or j for the same Latin letter to be identical]. This was confirmed by examination of the type label (Fig. 2A), but not the type specimen which no longer exists (Kazantsev & Nikitsky 2008; Aleksey Gusakov, Curator of Coleoptera ZMMU March 2021, pers. com.; Alexander Kirejtshuk, Curator of Coleoptera ZIN 19 March 2021, pers. com.). We have been unable to locate any specimens labelled both *cruciata* and Java.

Authorships

Confusion for us arose almost immediately as Motschulsky (1854), despite being the author of the description, listed the species as *Luciola cruciata* de Haan, and again in Motschulsky (1866). We know that he received the specimens from a conservator of the Rijksmuseum van Natuurlijke Historie, Wilhem de Haan (1801–1855) (Holthuis 1993) who had labelled them as '*cruciata*', and it is probable that Motschulsky in choosing to use this name also wanted to acknowledge de Haan (von Harold 1877). However, it was also Motschulsky (1866) who first recorded *Luciola cruciata* from Japan (again appearing to attribute the authorship to de Haan and also acknowledging the receipt of specimens collected in Japan until 1864). And apparently not obviously aware of any differences between the Java and Japanese specimens.

However here our obligations to adhere to a code of rules (ICZN) are juxtaposed against a time of taxonomic endeavours where such rules did not necessarily prevail (apart from the binomen advocated by Linnaeus). We believe that ICZN article 50.1 allows us to determine that Motschulsky is the sole author of the species *Luciola cruciata*.

We rely on accurate labelling of specimens in taxonomy. But this exercise is also about how we cope when those labels may be based on incorrect information.

Historical overview, alternative interpretations and a litany of errors

Following Motschulsky (1854), Lacordaire (1857) listed *Luciola cruciata* from Java but did not describe it. Kiesenwetter (1874) was the first, after Motschulsky, to describe a new species (from Japan) which was coloured like the description of *cruciata* Motsch., and which he named *Luciola picticollis* (Fig. 2B). However, while Motschulsky had described the femoral base as yellow, Kiesenwetter did not, suggesting to us the possibility that these were different species. Kiesenwetter (1874) also described as new *L. vitticollis* (Fig. 2C), but the wrong measurements were attributed to both. *Luciola picticollis* (which is the larger species) was recorded by Kiesenwetter as 7–9 mm long, and *L. vitticollis* (the smaller species) as 12–15 mm long. [Our interpretation of the Kiesenwetter descriptions suggest that the only error he made was in the size differences, and that all other features are consistent with the species he described]. It was von Harold (1877) and Heyden (1879) who first noted the discrepancies, with von Harold considering *picticollis* a synonym of *cruciata.* Heyden (1879) examined four specimens collected in Japan, naming them *L. cruciata*, and appeared confused about the identification of these four as well as *L. vitticollis* (based on an issue of size).

Lewis (1879) recorded both *L. cruciata* and *L. picticollis* from Japan, and from this point on we examined closely any references to any species with either name recorded from Japan, and any possible misidentifications of *L. lateralis* as well. Is the Genji-botaru *cruciata* or *picticollis*?

While Gorham (1880: 102) alluded to von Harold (1877) synonymising *picticollis* with *cruciata*, he considered *picticollis* and *cruciata* distinct from each other, noting the discrepancies in the colour of the femur base (yellow in the Motschulsky description and not yellow in the specimens he examined). He commented (Gorham 1880: 102–103) "it is scarcely likely that either = a species which is from Java". He also recorded that members of the *picticollis*/*cruciata* complex were considerably larger ("7 lines") than specimens he attributed to *Luciola vitticollis* ("3.5 lines"). He did not mention the misrepresentation of sizes for these species which Kiesenwetter (1874) had made. He examined a variety of material, including that of a Mr Norris, of the Brussels museum, and Japanese specimens from Lewis, which were now in his own collection. However, what he did next confused subsequent researchers. From the information in Gorham (1883) it appears he was at the British Museum in London examining the Lewis collection of Japanese fireflies. Under the heading *Luciola picticollis* Kiesenwetter Gorham lists *L. cruciata* sensu (LB's interpretation) von Harold and with the addition of "nec Mots.", equivalent to his interpretation of *picticollis* in Gorham (1880) (Fig. 2D). Again he appears to be recognising two different species, confirming his previous (Gorham 1880) opinion that the *cruciata* defined by von Harold was different to Motschulsky's *cruciata*. There is no mention of femoral colour. However, Gorham (1883) appears to completely denigrate the integrity of his own observations (in the eyes of researchers who followed him) by referring to *Luciola vitticollis* "this is the larger species, according to Kiesenwetter's description", thus accepting the errors of measurement in Kiesenwetter (1874). He did not mention how this conflicted with the differences in size for these two species he had already pointed out in Gorham (1880). The treatments of *picticollis* and *vitticollis* in Gorham (1880) and Gorham (1883) are essentially interchanged. Further examination of two of the sites Gorham (1883) listed on Hokkaido (as "Hakodaté" and "Junsai"), which is not an area from where *cruciata* is known, and the months when males were active, led both IK and HS to conclude that Gorham's (1883: 409) *picticollis* is actually

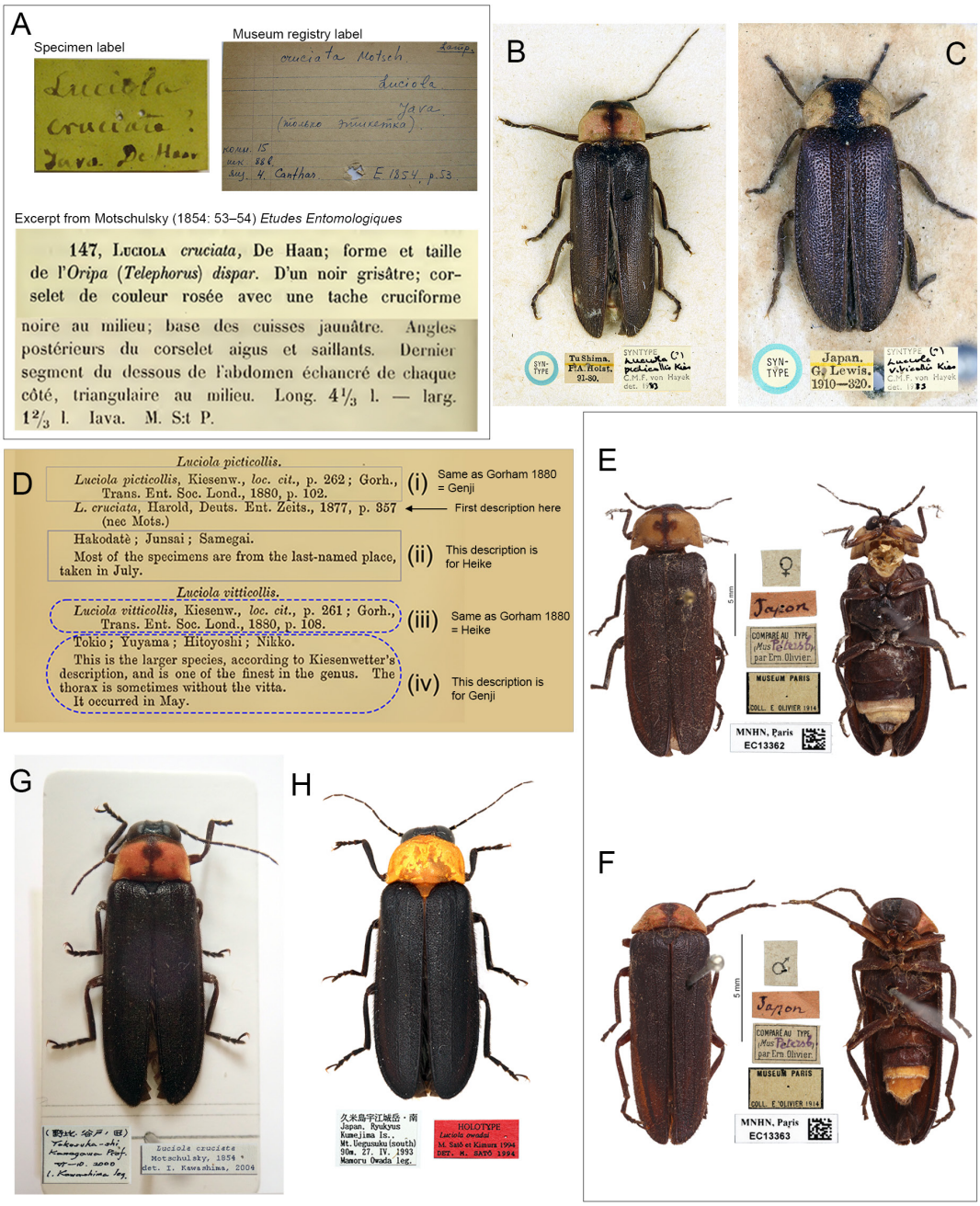

Fig. 2. Background information. **A**. Type specimen label, museum registry label, and excerpt of original description of *Luciola cruciata* Motschulsky, 1854 in ZMMU. **B**. *Luciola picticollis* Kiesenwetter, 1874, ♂, syntype (NHMUK). **C**. *Luciola vitticollis* Kiesenwetter, 1874, ♂, syntype (NHMUK). **D**. Excerpt from Gorham (1883) annotated by H. Suzuki and I. Kawashima. **E–F**. Dorsal (left) and ventral aspects specimens of *Luciola cruciata* from E. Olivier collection in MNHN compared with types. **G**. *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov., neotype (KPMNH). **H**. *Luciola owadai* Satô & Kimura, 1994 holotype (NSMT). Image A specimen label and registry by Aleksey Gusakov (ZMMU); excerpt of original description from Biodiversity Heritage Library; images B–C *Luciola picticollis* by Keita Matsumoto (NHMUK) https://www.flickr.com/; image D reproduced from Biodiversity Heritage Library; images E–F by Christophe Rivier (MNHN); image G by I. Kawashima; image H by H. Yoshitomi (Entomological Laboratory of Ehime University).

A. lateralis, while his reference on the same page to *L. vitticollis* is to *cruciata* (Fig. 2D). This conforms with Okada's (1931: 146) determination discussed below.

Olivier (1902b: 189) appears to have misinterpreted the width of the median dark pronotal band in *L. vitticollis* and synonymised *L. vitticollis* with *L. cruciata* ("la bande noire du prothorax ne se dilate pas au milieu pour former une sorte de croix comme dans le type *cruciata* Motsch."). However, the specimens in his collection, which were compared with the types, are correctly identified (Fig. 2E–F). Subsequently Olivier's catalogues (1902a, 1907, 1910) listed *vitticollis* as a variety of *cruciata*; and *picticollis*, following von Harold's (1877) interpretation of *cruciata*, as a synonym. The continued misinterpretation of *L. vitticollis* (as *cruciata*, or not) and the poor description or interpretation of the median pronotal dark colouration, suggested to us that it might be possible that the original Java specimen was *lateralis*. Blair (1927) had recorded an aquatic lampyrid larva with lateral gills along the sides of abdominal segments 1–8 from the S. Celebes [Sulawesi], identifying it as a possible *Pyrophanes* sp. [Ballantyne *et al.* (2015) indicated there were no reliable records of aquatic swimming larvae for any *Pyrophanes* sp.]. We have found no evidence to suggest that *lateralis* has ever been collected in Java.

Possible substantiation or further misidentification?

Okada (1931: 132, 146) further investigated, indicating the errors in the Kiesenwetter text, and examined cotypes of *L. cruciata* and *L. lateralis* which had been donated by Motschulsky to what is today the MNHN in Paris. Okada confirmed that, in his opinion, the specimens he saw were "the Genji- and Heike-botaru respectively" (*cruciata* and *lateralis*), while indicating that *picticollis* and *vitticollis* were synonyms of *cruciata* and *lateralis* respectively. His suggestions that *L. vitticollis* sensu Gorham (1883) is a synonym of *cruciata*, was also confirmed by examination of localities and times of emergence by both IK and HS. Okada also examined specimens of *L. picticollis* and *L. vitticollis* at what was then the British Museum in London, and confirmed the errors in body length in Kiesenwetter (1874) between *picticollis* and *vitticollis* (*picticollis* being the larger) (Fig. 2B–C). He did not, however, mention the colour of the femora. On the basis of his investigations, Okada (1931) explained that in his previous (Okada 1928) larval descriptions the Genji firefly is *cruciata* (with *picticollis* as a synonym), and the Heike firefly is *lateralis* (with *vitticollis* as a synonym). *Luciola vitticollis* presently stands under the genus *Aquatica* as *Aquatica lateralis*.

More recently Jeng *et al.* (2003: 542) were the first to suggest that the Java label for the type *cruciata* was simply a case of mislabelling. They did not provide any substantiation for their opinion. They synonymised *cruciata*, *picticollis* and *vitticollis* (following Okada). It appears that their table of synonymies was attempting to indicate which references to *vitticollis* were actually those that should have been attributed to *L. lateralis*, as they subsequently (Jeng *et al.* 2003: 546) again synonymised *vitticollis* with *lateralis*. McDermott (1966) recognised both *cruciata* and *picticollis* as valid species while also synonymising *vitticollis* with *cruciata*.

Our dilemma

Can we accept Okada's suggestions without being able to confirm the identity of the specimens he examined? What further information do we need? Are there actually two different species from Japan with different colouration of the femoral base? If so, should "*cruciata*" really be named *picticollis*?

Motschulsky was the original author. Should we not be able to trust his identifications of Japanese specimens as being the same as those he had previously recorded from Java? He was the first to have the original material at his disposal. But he made no mention of any conflict in locality, nor in the morphology of specimens examined when he recorded *cruciata* from Japan. All that remains of the Motschulsky types of *cruciata* is a label, and further syntypes cannot be located. The trust can be placed in a type specimen but not necessarily in the taxonomist who designated it.

Apart from Motschulsky, few have actually examined type material of *cruciata*. The treatments of Olivier and Gorham are confusing. Olivier indicates he saw type material (Fig. 2E–F) but in his publications he confused both *cruciata* and *lateralis* with his misinterpretation of the median pronotal marking, and thus any further reference by Olivier to either of these species could be to one or both (see table of synonymy subsequently). Apart from specimens he compared with types, we cannot reliably relocate any of the specimens he examined. Gorham examined specimens of *picticollis* and *vitticollis* in the Lewis collection in London, and because he accepted the incorrect measurements in Kiesenwetter (1874) where *vitticollis* (the smaller species) was recorded as the larger, his suggestions were ignored. However the Lewis collection itself may well contain specimens which were incorrectly recorded from Japan (Ballantyne *et al.* 2019: 158). Kawashima *et al.* (2003) unravelled the complicated situation, not dissimilar to what we face here, of the identity of *Luciola japonica*, described by Thunberg (1784), which they felt had been erroneously recorded from Japan. They presented a picture of a type (female) which cannot be assigned to a genus (Ballantyne *et al.* 2019).

We considered that determining the meaning that Motschulsky and de Haan might have attributed to the word '*cruciata*' could help and a search of translation services on the internet revealed the modern day usage of 'cruciatus' from 'crux' (genitive 'crucis') meaning 'cross'; alternatively cross shaped, having the form of a cross with equal arms. Neither interpretation fits our (modern day) impression of the median pronotal markings (https://www.etymonline.com › word › cruciate accessed 28 June 2021).

While Jeng's suggestion, that the Java record was simply a mistake, has no justification, it may be correct.

The issue of the differing femoral colouration was resolved by the second author, who noted from his extensive observations of specimens, (see subsequent list), that while freshly caught specimens of *L. cruciata* have black femoral bases, aged pinned specimens fade, and this area becomes brownish. In ethanol preservation the same is noted. Thus the differences noted previously could be attributed to differing ages of specimens.

While we cannot reliably relocate any of these specimens (except for those in the Olivier collection Fig. 2E–F) to confirm identification, the literature in the table of synonymies was assessed for any clues that might determine accurate species identity (using locations and local knowledge, format of description and especially diagrams if such were present).

A consideration of biogeography aided our decision. Java is one of the Greater Sunda Islands in the Orient, a region which is not shared with Japan except for the Ryukyu Islands, SW Japan in the east (where the dispersal of insects from the southwest via land bridges formed during glacial period was deemed possible) (Toussaint & Balke 2016; Tojo *et al*. 2017). However, *L. cruciata* has never been reported from the Ryukyu islands. No recent sighting report of *L. cruciata* from Java or any parts of Indonesia exists except for what was written in the original description. Furthermore, aquatic insects like *L. cruciata* have limited dispersal abilities and specialised habitat requirements (Takeda *et al.* 2006; Tojo *et al*. 2017). The possibility of this species occurring in both areas was, therefore, deemed highly unlikely.

We decided to accept the most recent published recommendation of Okada (1931) who had examined syntype material in MNHN and NHMUK. Only Okada gave a reasoned explanation while correctly (in our opinion) interpreting the placement for *L. vitticollis.* An extensive search in MNHN for any Motschulsky cotypes of *Luciola cruciata* was undertaken in late November 2021 by Antoine Mantilleri. No cotypes were found. The designation of a neotype male for *L. cruciata* was deemed necessary (Fig. 2G).

See also Supp. file 1: 3–4.

Table 1 (continued on next page). Comparison of morphological features of *Missimia* Ballantyne, 2009 and *Nipponoluciola* gen. nov.

***Missimia* Ballantyne, 2009**	***Nipponoluciola* gen. nov.**
Ballantyne *et al.* 2009: figs 21–22, 27, 29–30, 32–34, 246–254; Figs 3, 4E–H	This study
New Guinea Highlands	Japan
Rare genus known only from 2 males and 2 females	Well known in Japan from males, females and larvae
Colour: elytra pale brown	Colour: elytra black
Pronotum pale brown without darker markings	Pronotum pinkish with median dark markings
Body outline: elongate slender L/W 3.5/1	Body outline: heavier bodied L/W 3/1
Pronotum: width less than humeral width	Pronotum: width subequal to humeral width
Lateral margins sinuate with posterolateral corners narrowed and apically pointed	Lateral margins slightly divergent along length, not sinuate, and posterolateral corners apically rounded
Elytron: Either one or two elytral interstitial lines	Elytron: with at least two well defined interstitial lines
Base of epipleuron narrow (as in Fig. 3)	Base of epipleuron narrow (Fig. 3)
Humerus visible from beneath	Humerus widely visible from beneath
Viewed from above the epipleuron visible at elytral margins level with posterior margin of MS	Epipleuron visible at elytral margins well behind posterior margin of MS
Head: without clypeolabral suture	Head: with clypeolabral suture
Labrum well sclerotised inflexibly joined to rest of head	Labrum not well sclerotised, flexibly joined to rest of head
GHW 2–3 × SIW	GHW 3.7–4.5 × SIW
Apical labial palpomere lunate inner margin entire not dentate	Apical labial palpomere shaped like a broad triangle with inner margin dentate
Antennal length 3–4 × GHW	Antennal length 2 × GHW
FS 2–8 expanded at anterior apical angle	FS 2–8 not expanded at anterior apical angle
Abdomen: LO in V7 retracted from lateral margins of V7, with posterior margin rounded, not reaching into MPP, and LO occupies less than half total area of V7	Abdomen: LO in V7 reaches lateral margins and into MPP and occupies all but a narrow clear portion of posterior margin of V7
V7 with angulate corners; MPP elongate with rounded truncated apex	V7 with angulate corners; MPP shorter, with widely rounded MPP
T8 with elongated anterolateral arms longer than posterior entire portion of T8	T8 with anterolateral corners very short, barely produced and apically acute
T8 narrowed along posterior margin	T8 not narrowed along posterior margin
T8 ventral surface with median longitudinal trough with fine lateral margins	T8 ventral surface without trough
Aedeagal sheath (Fig. 4G): posterior area of sheath sternite shallowly emarginated on right side from point of tergite attachments; not emarginated on left side; apex of sternite broadly rounded	Aedeagal sheath: posterior area of sheath sternite widely emarginated on both sides from point of tergite attachments; apex of sternite narrowly rounded

Table 1 (continued).

***Missimia* Ballantyne, 2009**	***Nipponoluciola* gen. nov.**
Ballantyne *et al.* 2009: figs 21–22, 27, 29–30, 32–34, 246–254; Figs 3, 4E–H	This study
Aedeagus (Fig. 4H): BP wide, hooded, not emarginated along anterior margin and appearing to be in a single piece	Aedeagus: BP narrower, not hooded, usually with well defined emargination along anterior margin which divides BP into halves
Dorsal base of LL with median acute projection	Dorsal base of LL without projection
Inner preapical margins of LL with an elongate narrowly emarginated hair bearing area	Inner preapical margins of LL without any elongated hair bearing area
LL obliquely truncated along their preapical inner and outer margins	LL not obliquely truncated along their preapical inner and outer margins
LL apices bluntly acute	LL broadly rounded at apex

Aquatica or a new genus? Where to place *Missimia*?

The rare New Guinean highland genus, *Missimia*, known from only four specimens, also grouped alongside the *cruciata*/*owadai* complex in Ballantyne *et al.* (2013, 2015, 2016, 2019), probably because of the synapomorphy relating to the narrow base of the elytral epipleuron (Ballantyne & Lambkin 2009: fig. 33). Larvae are unknown, and the genus otherwise has the unique feature in the Luciolinae of a missing clypeolabral suture, and solid labrum, fused with the clypeus in both males and females (Ballantyne & Lambkin 2009: figs 27, 29–30, 32). We consider the rarity of the species, the occurrence of these few (four) specimens in the New Guinean highlands, the distinctive head characteristics, and absence of information about larvae to be sufficient to retain the genus in its present state and we eliminated it from our considerations (see Table 1).

Following Ballantyne *et al.* (2015, 2016), Jusoh *et al.* (2021: fig. 3), and Ballantyne *et al.* (2019) and references therein, and retaining *Missimia* as a distinct generic category, there are three options for considering a placement for *Luciola cruciata*/*L. owadai*, given that the analyses, mentioned previously, have clearly indicated they are not *Luciola* s. str.:

1) Merge the two species with *Aquatica*, which then has 7 species and no subgenera.

2) Merge the two species with *Aquatica* and erect two new subgenera.

3) Erect a new genus for *cruciata* and *owadai*.

Based on the distinctiveness of adult specimens revealed in morphological phylogenetic analyses we choose option 3, and erect a new genus, clearly closely affiliated with *Aquatica*, to accommodate *L. cruciata/owadai* (see Table 2).

Nipponoluciola gen. nov. is distinguished from the genus *Aquatica*, with which it shares similar aquatic larvae bearing abdominal gills, by the following features (features of *Aquatica*): elytra are black (Figs 1–2) (species of *Aquatica* may have pale margined elytra Fig. 4A); the elytral epipleuron at its base is narrow (wide Fig. 3); the LO in V7 is not much retracted from the posterior margin (Fig. 2E–F) (usually retracted from the posterior margin Fig. 4B); the lateral margins of V7 are angulated (Fig. 2E–F) (not angulate Fig. 4B); both left and right margins of the posterior area of the sheath sternite are smooth with no pointed projections Fig. 5 A–B, E, I–J) (both left and right margins of the posterior area of the sheath sternite have pointed projections Fig. 4C); the aedeagal basal piece often has a median notch Fig. 5C–D, G–H, M–P (the aedeagal basal piece is not notched Fig. 4D).

Table 2. Comparison of morphological features of *Aquatica* Fu *et al*., 2010 and *Nipponoluciola* gen. nov.

***Aquatica* Fu *et al*., 2010** (Fig. 4A–D)	***Nipponoluciola* gen. nov.**
Recorded from China, Korea and Russia with one species from Japan	Recorded only from Japan
Elytra black, may have fine paler margins, or elytra yellow	Elytra black
Pronotal width slightly less than humeral width	Pronotal width subequal to humeral width
Pronotal lateral margins divergent along length or subparallel-sided in posterior half	Pronotal lateral margins slightly divergent along length
Elytra with no well defined interstitial lines	Elytra with at least two well defined interstitial lines
Base of epipleuron wide	Base of epipleuron narrow
Humerus narrowly visible or not visible from beneath	Humerus widely visible from beneath
Epipleuron visible at elytral margins level with or anterior to posterior margin of MS	Epipleuron visible at elytral margins well behind posterior margin of MS
Male V7 without angulate corners	V7 with angulate corners
Male LO retracted to anterior half of V7	LO occupies most of V7
Aedeagal BP without median notch	Aedeagal BP usually with median notch
ML of aedeagus with apical area much narrower than rest	ML of aedeagus with apical area not much narrower than rest
Lateral margins of posterior area of aedeagal sheath sternite with toothed projections	Lateral margins of posterior area of aedeagal sheath sternite without toothed projections
Posterior area of aedeagal sheath sternite about as wide as anterior area except for *A. lateralis*	Posterior area of aedeagal sheath sternite much narrower than anterior area
Female with thin apically acute bursa plates	Female no bursa plates
Female MO plate elongated may project into vagina	Female MO plate short, not much wider than long, not projecting into vagina

Taxonomy of the Luciolinae with description of a new genus Nipponoluciola gen. nov.

Key to genera of Luciolinae using males

Keys to genera of the Luciolinae, beginning with Ballantyne & McLean (1970), addressed increasing numbers of genera as the taxonomy expanded, but have never included either *Luciola cruciata* or *L. owadai* (see review in Ballantyne *et al.* 2019). It is possible to distinguish *Nipponoluciola* gen. nov. from other Luciolinae genera by the following, without the need for a complicated generic key.

Of those Luciolinae genera with LL visible at the sides of the ML, only two genera have a narrow base to the elytral epipleuron such that the elytral humerus is visible from beneath if the specimens are held horizontally (Fig. 3), *Missimia* and *Nipponoluciola* gen. nov. *Missimia* (Figs 4E–H; Table 1) is a rare genus known from four specimens collected in the New Guinea highlands, distinguished most obviously from *Nipponoluciola* by its pale brown dorsal colouration, its distribution in the New Guinea highlands,

the acute posterolateral corners of the pronotum in males, the inflexible nature of the clypeolabral suture, the absence of a median notch in the aedeagal basal piece, and the presence of a well-defined and depressed area on the outer margins of the lateral lobes of the aedeagus bearing setae (Ballantyne & Lambkin 2009: figs 21–22, 27, 29–30, 32–34, 246–254). The two species of *Nipponoluciola* have black elytra, are known only from Japan including the Ryukyu Islands, the posterolateral corners of the pronotum are rounded, the clypeolabral suture is flexible, most aedeagi examined have a median notch in the basal piece, and there is no depressed setae bearing area on the outer margins of the lateral lobes of the aedeagus (Figs 1, 2G–H, 5).

List of genera of Luciolinae having aquatic larvae

Fu *et al.* (2010) noted that verified records of aquatic firefly larvae are rare, and given that original descriptions rarely give any indication of any larval associations or accurate habitat data, that adults are often described without knowledge of the larval types. It is thus possible that the incidence of aquatic Luciolinae will ultimately be shown to be wider than the range we address here.

Fu *et al.* (2012b) defined aquatic larvae as possessing either gills along the sides of the abdomen*, or having spiracles only at the end of the abdomen# (metapneustic). Those marked with superscript J are from Japan.

The following list includes genera and species for which confirmation of aquatic larval status exists.

Aquatica Fu *et al.*, 2010*
- *A. ficta* (Olivier, 1909)
- *A. hydrophila* (Jeng *et al.*, 2003)
- *A. lateralis* (Motschulsky, 1860)J
- *A. leii* (Fu & Ballantyne, 2006)
- *A. wuhana* Fu & Ballantyne, 2010

Sclerotia Ballantyne, 2016#
- *S. aquatilis* (Thancharoen, 2007)
- *S. flavida* (Hope, 1845)
- *S. fui* Ballantyne, 2016

Nipponoluciola gen nov.*
- *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov.J
- *Nipponoluciola owadai* (Satô & Kimura, 1994) gen. et comb. nov.J

Key to genera of Luciolinae having aquatic larvae using males

1. In horizontal specimen, viewed from beneath, elytral epipleuron narrow at base and elytral humerus clearly visible (Fig. 3A); elytra very dark brown to black with no paler margins; at least two interstitial lines well defined; elytral punctation not subparallel-sided; aedeagal sheath with both left and right sides of sheath sternite posterior to tergite articulations smoothly emarginated (Figs 1–3, 5) ..... ***Nipponoluciola*** gen. nov.

– In horizontal specimen, viewed from beneath, elytral epipleuron wide at base and elytral humerus not visible (as in Fig. 3D); elytral colour variable, often pale brown with black tips; interstitial lines well defined or not; elytral punctation may be subparallel-sided; aedeagal sheath sternite either little emarginated on both sides, and approximately subparallel-sided (Fig. 4M) or quite deeply emarginated more on right than left side, with both sides of sheath sternite posterior to the tergite articulations bearing short toothlike projections (Fig. 4C) 2

2. Dorsal colouration usually brownish-yellow, with or without dark brown elytral apices (Fig. 4I); one species has mid brown elytra with pale coloured interstitial lines and margins; elytra with subparallel-sided punctation (Fig. 4I); interstitial lines either evanescent or up to four well defined lines present; light organ in ventrite 7 with anterior median emargination, lateral and posterior margins of light organ usually almost reaching the lateral and posterior margins of ventrite 7 (Fig. 4J); tergite 8 with elongated slender anterolateral projections; lateral margins of abdominal tergite 8 usually enfold the sides of ventrite 7 (Fig. 4M); set of three sclerites (two lateral and one ventral) surrounding the aedeagal sheath in a ring of muscle, may be visible from above through the terminal abdominal tergites (Fig. 4L–N show two of the three sclerites); aedeagus short and squat (L/W < 3) (Fig. 4K); basal piece long, narrow, reaching posteriorly at the sides of the lateral lobes for about 0.4–0.6 aedeagal length, and not medially emarginated; aedeagal sheath asymmetrical in posterior half where sheath sternite inclines to the left; sternite not angulated on either side, posterior area subparallel-sided, and posterior margin either emarginated, truncated, or prolonged on one side (Fig. 4M) .....***Sclerotia*** Ballantyne, 2016 (Ballantyne *et al*. 2016: figs 17–38); Fig. 4 I–N
– Dorsal colouration with brownish-yellow pronotum, often with median dark markings, and dark brown elytra which may be pale margined (e.g., Fig. 4A); one species has mid brown elytra with pale margins; elytra without subparallel-sided punctation; interstitial lines not well defined; light organ in ventrite 7 without anterior median emargination, reaching sides but not posterior margin of ventrite 7 (light organs usually retracted to anterior half of ventrite 7) (Fig. 4B); tergite 8 anterolateral projections either very short or absent; lateral margins of abdominal tergite 8 do not enfold the sides of ventrite 7; no sclerites surrounding the aedeagal sheath (Fig. 4C); aedeagus longer than wide (L/W ≥ 3) (Fig. 4D); basal piece not narrow, not reaching posteriorly at the sides of the lateral lobes for about 0.4–0.6 aedeagal length, usually in two pieces and not medially emarginated; aedeagal sheath asymmetrical in posterior half where sheath sternite does not incline to the left, and may be irregularly emarginated on both sides with both sides bearing at least one toothed projection; sternite appears angulated on each side in two species; posterior margin of sternite either rounded or very shallowly medially emarginated .... ***Aquatica*** Fu *et al.*, 2010 (Fu *et al.* 2010: figs 2–24, 27–29, 32–43); Fig. 4A–D

Key to aquatic larvae in the Luciolinae

Fu *et al.* (2012b) keyed the genera listed above from larvae. They addressed five species of *Aquatica* (Fu *et al.* 2012b: figs 1–24, 61–62, 67–68, 73–80, 91), two species of *Sclerotia* which were still attributed to *Luciola* (Fu *et al.* 2012b: figs 31–42, 70, 83–86), and two species of *Nipponoluciola* gen. nov. which were also still attributed to *Luciola* (Fu *et al.* 2012b: figs 25–30, 69, 81–82). See also Fu *et al*. (2010: figs 25–26, 30–31, 44–49) for *Aquatica* larvae.

Description of a new Luciolinae genus

Class Insecta Linnaeus, 1758
Order Coleoptera Linnaeus, 1758
Family Lampyridae Rafinesque, 1815
Subfamily Luciolinae Lacordaire, 1857

Nipponoluciola gen. nov.
urn:lsid:zoobank.org:act:BD75E8CA-BC67-4597-A0A5-6BCEF5BA7B4F
Figs 1–3, 5–12

Type species

Luciola cruciata Motschulsky, 1854, designated here.

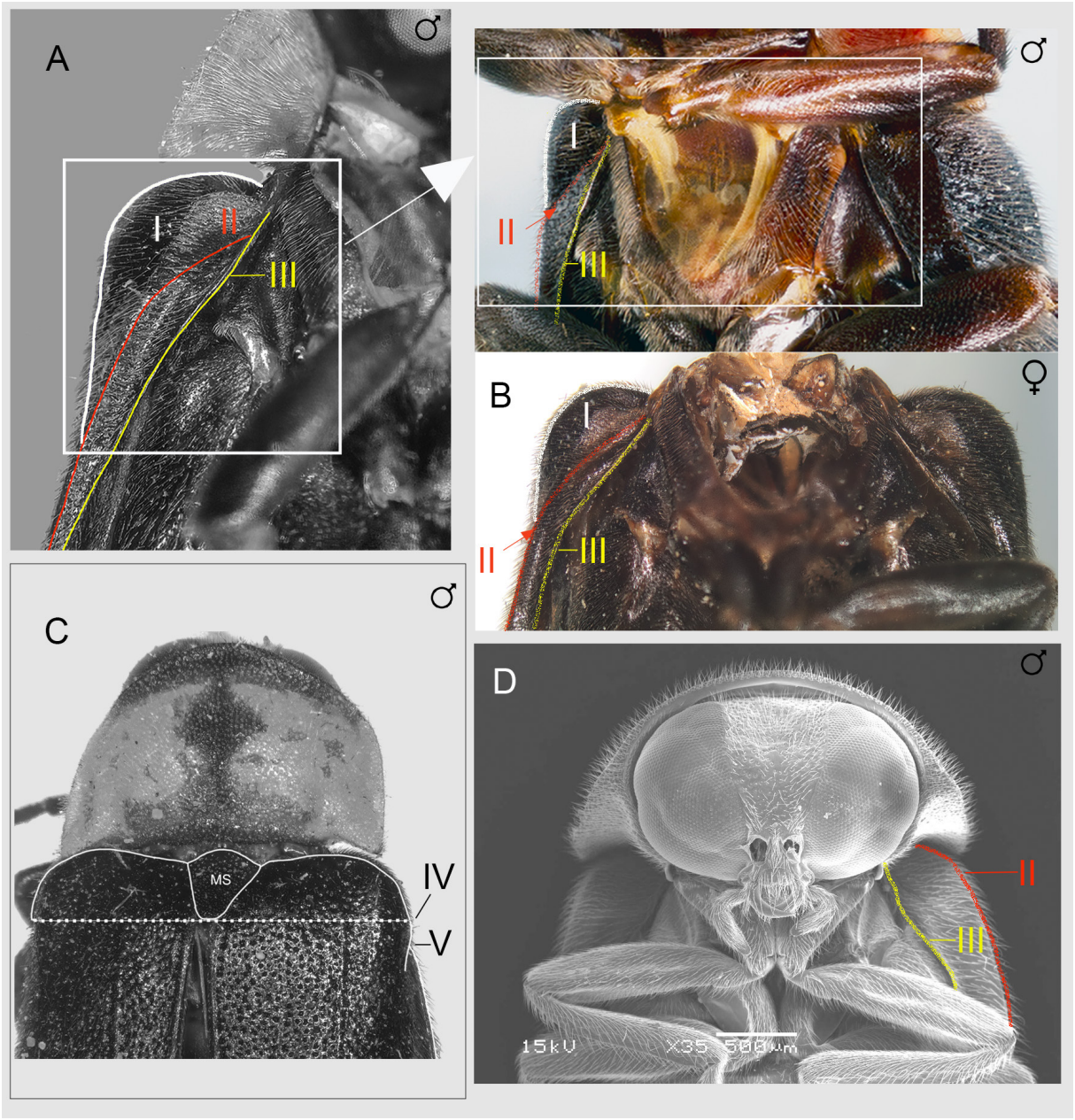

Fig. 3. Nature of epipleuron. **A, C**. *Luciola cruciata* Motschulsky, 1854, ♂ (Osugi, Japan; ANIC); inset A: Hayama, Japan; ZRC. **B**. *Luciola cruciata* ♀ (Doubaru, Japan; ANIC). **D**. *Aquatica lateralis* (Motschulsky, 1860) (Japan; XH Fu collection). **A**. Ventro-lateral thorax and elytron (inset: slightly oblique view of ventro-lateral thorax and elytron). **B**. Ventral anterior portion of mesothorax and elytral bases. **C**. Dorsal pronotum and elytral base of A. **D**. Ventral anterior body including head. Images by L. Ballantyne (A–C), W.F.A. Jusoh (inset A) and X.H. Fu (D, ex N. Ohba). Figure legends: I = humerus; II = outer edge of epipleuron; III = inner edge of epipleuron; IV = dotted line is posterior margin of MS; V = epipleuron first visible at side of elytron behind posterior margin of MS. Not to scale.

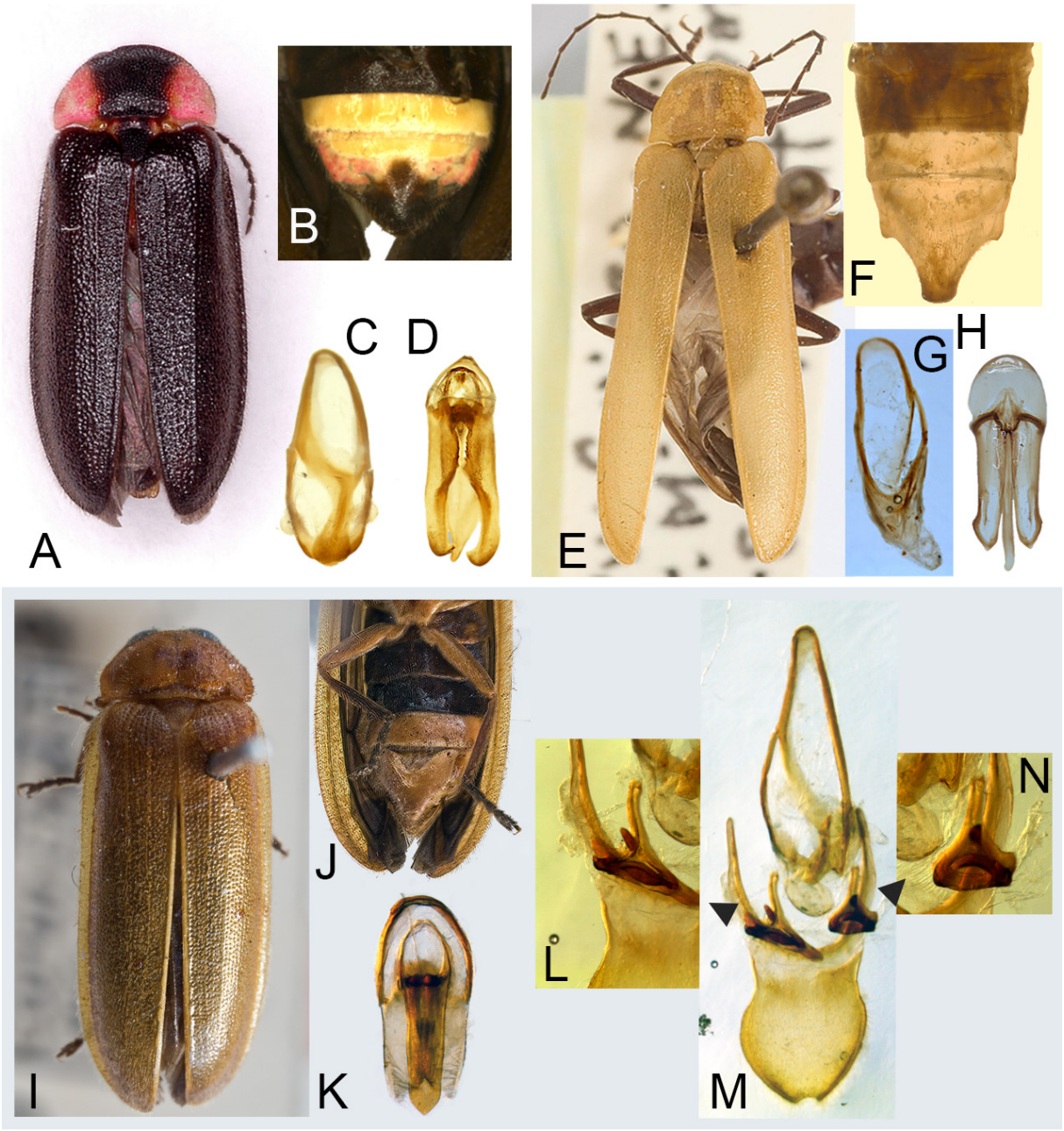

Fig. 4. Generic features. **A–D**. *Aquatica* Fu *et al.* 2010, specimen is *Aquatica lateralis* (Motschulsky, 1860), ♂, Tokyo (HZNHM). **E–H**. *Missimia* Ballantyne, 2009, specimen is *Missimia flavida* Ballantyne, 2009, holotype, ♂ (BPBM). **I–N**. *Sclerotia* Ballantyne, 2016, specimen is *Luciola seriata* Olivier, 1891, holotype, ♂ (MCSN). **A, E, I**. Habitus, dorsal view. **B, F, J**. Terminal abdomen with ventrites 3–7 visible, ventral view. **D, H, K**. Aedeagus, ventral (K) and dorsal (D, H) views. **C, G**. Aedeagal sheath, ventral (C) and dorsal (G) view. **L–N**. Aedeagal sheath, tergite 8 and lateral sclerites. **L, N**. Detail right (L) and left (N) sclerite. **M**. Aedeagal sheath, sclerites and T8, aedeagal sheath to top of page,T8 to foot of page with left and right sclerites (arrowed), ventral view. All images by L. Ballantyne.

Diagnosis

Nipponoluciola gen. nov. is a genus of Japanese Luciolinae fireflies and consists of two species both of which have aquatic larvae with abdominal gills. While *Nipponoluciola* belongs to that group of 18 genera of Luciolinae where the aedeagus in the male has the LL widely visible at the side of the ML (Ballantyne *et al.* 2019), it is one of only two genera in this group of 18 (the other is *Missimia*) where the elytral epipleuron at its base is very narrow and when viewed from beneath in a horizontal specimen the humerus is widely visible in both males and females (Fig. 3A–C). In the other genera of Luciolinae with LL visible at the sides of the ML the base of the elytral epipleuron is expanded, and the humerus is not visible from below in a horizontal specimen (example in Fig. 3D). It is distinguished from *Missimia* by distribution (*Missimia* is a rare genus known only from four specimens taken in the New Guinean highlands), and the unique feature of *Missimia*, where the labrum and clypeus are immovably joined (Fig. 4E; Table 1; Ballantyne & Lambkin 2009: figs 27, 29–30, 32). The clypeolabral suture in *Nipponoluciola* is flexible. It is distinguished from the genus *Aquatica*, with which it shares similar aquatic larvae bearing abdominal gills, by the following features: *Aquatica* species adult males may have pale margined elytra (Fig. 4A), the elytral epipleuron at its base is wide (Fig. 3D), the LO in V7 is usually retracted from the posterior margin (Fig. 4B), the lateral margins of V7 are not angulated, both left and right margins of the posterior area of the sheath sternite have pointed projections, the aedeagal basal piece is not notched (Fig. 4C–D). Females have thin paired bursa plates (Fu *et al*. 2010). See Table 2.

Males have black elytra and the pronotum may have median dark brownish to blackish markings and an underlying pink fat body (in *N. cruciata*) (Figs 1, 2G, 6), or have no dark markings and underlying yellowish orange fat body (in *N. owadai*) (Figs 1, 2H). Females are coloured like males, and are larger, macropterous, with spermatophore digesting gland, no obvious bursa plates and a small transverse median oviduct plate in *N. cruciata* (Fig. 7). Larvae (Figs 8–9) are aquatic, have forked gills along the sides of the abdominal segments 1–8 and apical sense organs on maxillary and labial palpomeres. Distinguished most obviously from *Aquatica* larvae by the differences in the markings of protergum (outlined subsequently); distinguished from *A. lateralis* by the unbranched setae on the dorsal surface of the mandibles, and the absence of microspines on pale areas of paired tergites of meso- and metathoraces, and abdominal segments 1–8 (Okada 1928: figs 2–3, 2–4 depicted but did not name these microspines; IK confirmed their presence in *A. lateralis*).

Etymology

The generic name seeks to honour the country of origin of these two species and their status as celebrated icons. ‘Nippon’ is the Japanese name for Japan, and *Luciola* represents the genus to which these species were formerly assigned. Gender: feminine.

Description

Male (Figs 1–3, 5–6, 10–12)

Pronotum (Figs 1–2). Punctation dense; anterior margin broadly rounded and projecting beyond rounded obtuse anterolateral corners, slightly so in *owadai*; lateral margins slightly divergent, the pronotum being wider across its posterior area than elsewhere (C >A, B), width (C) subequal to humeral width; posterolateral corners narrowed, apically rounded, slightly less than 90°, projecting posteriorly slightly beyond median posterior margin, which is not emarginated, and separated from it by well-defined emarginations. Pronotal colour variations depicted in Fig. 6 are discussed under *Nipponoluciola cruciata* gen. et comb. nov.

Hypomera. Not well flattened; pronotal width/GHW 1.43–1.47.

Elytron (Figs 1–3). Punctation dense, not linear, not as large as that of pronotum, nor widely and evenly spaced; apices not deflexed, nor emarginated; epipleuron and sutural ridge extend beyond mid-point, almost to apex but not extending around apex, neither thickened in apical half; with three interstitial lines of which the inner two interstitial lines are well defined; in horizontal specimen viewed from below epipleuron at elytral base narrow with humerus visible; viewed from above in horizontal specimen anterior margin of epipleuron arises well behind the posterior margin of MS (Fig. 3A, C); epipleuron

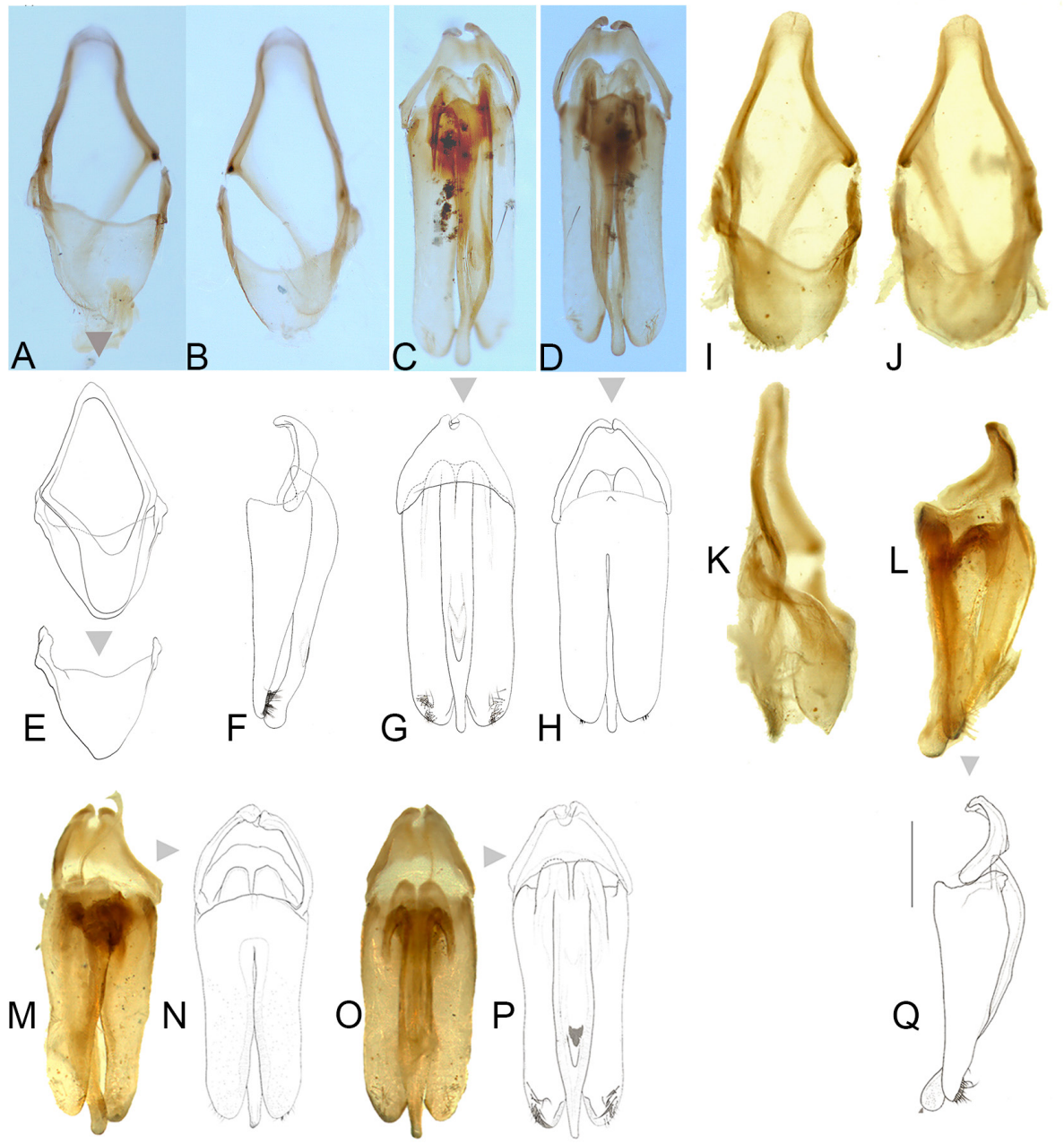

Fig. 5. Features of male genitalia. **A–H**. *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. **I–Q**. *Nipponoluciola owadai* (Satô & Kimura, 1994) gen. et comb. nov. **A–B, E, I–K**. Aedeagal sheath: dorsal (A, lower portion of E shows tergite alone; I), ventral (B, upper portion of E; J), and left lateral (K) views. **C–D, F–H, L–Q**. Aedeagus: ventral (C, G, O, P), dorsal (D, H, M, N), and right lateral (F, L, Q) views. Images by L. Ballantyne (A–D, I–M, O) and I. Kawashima (E–H, N, P–Q).

developed as a lateral ridge along most of length; sutural margins approximate along most of length in closed elytra; lateral margins parallel-sided.

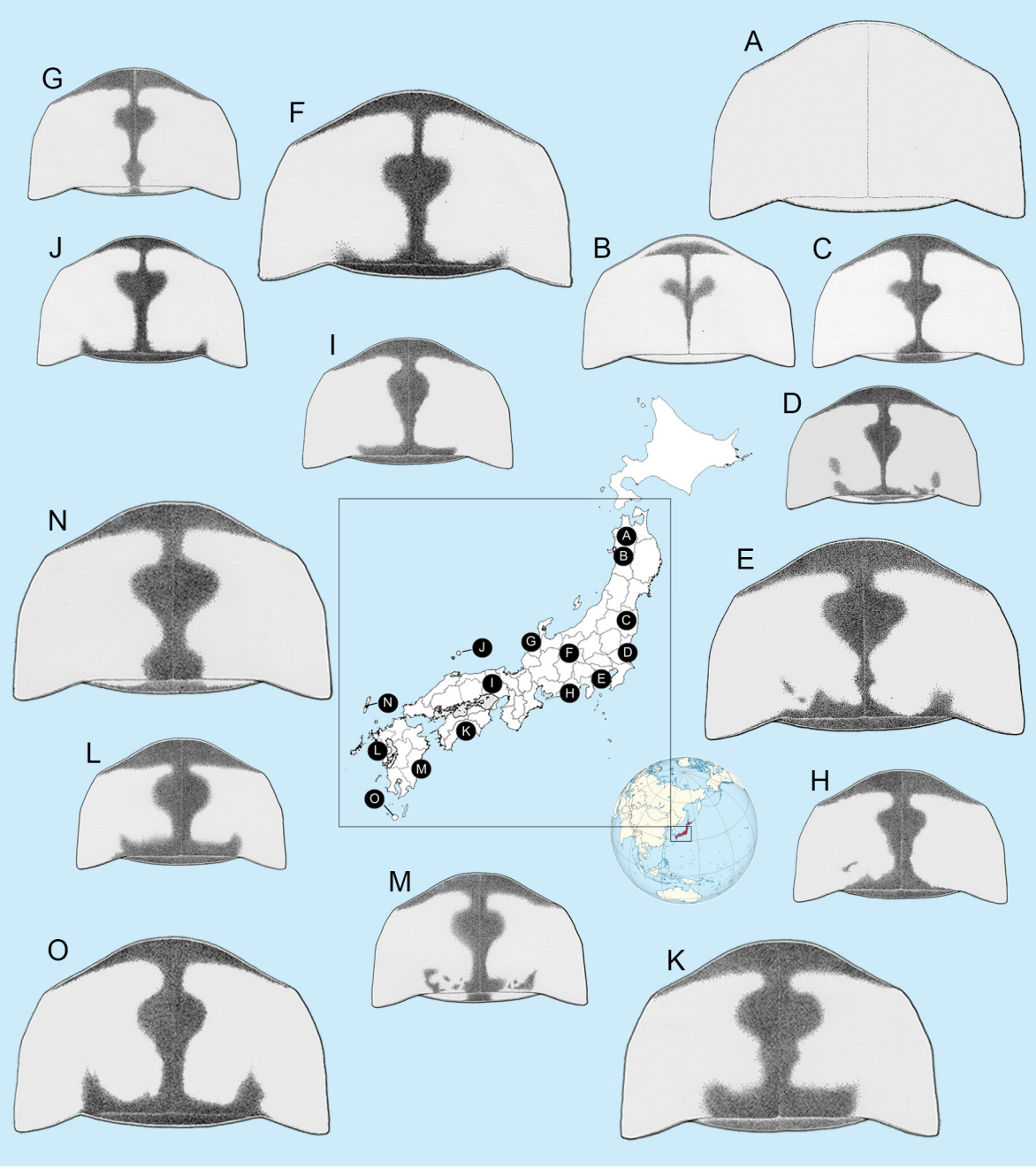

Fig. 6. Distribution of pronotal marking patterns of *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. in the Japanese islands. Images by I. Kawashima. Map by W.F.A. Jusoh (map of Japan using base maps obtained from Wikimedia Commons - Maximilian Dörrbecker and Connormah, CC BY-SA 3.0). Not to scale. Figure legend: **A**. Aomori (based on Nakane 1987). **B**. Akita. **C**. Fukushima. **D**. Ibaraki. **E**. Kanagawa. **F**. Nagano. **G**. Ishikawa. **H**. Shizuoka. **I**. Hyogo. **J**. Oki Islands. **K**. Kochi. **L**. Nagasaki. **M**. Miyazaki. **N**. Tsushima Island**. O**. Yakushima Island.

Head (Figs 1–2). Gently depressed between eyes; at least anterior portion exposed in front of pronotum, not capable of complete retraction within prothoracic cavity at rest; eyes moderately separated beneath at level of posterior margin of mouthpart complex; frons-vertex junction not defined this area rounded, posterolateral eye excavation not developed; antennal sockets on head between eyes, close but not contiguous, ASD subequal to ASW; clypeolabral suture present, flexible, not in front of anterior eye margin when head viewed with labrum horizontal; outer edges of labrum reach inner edges of closed mandibles. Mouthparts: functional; apical labial palpomere flattened, shaped like a broad triangle, longer than wide, with inner edge dentate. Antennae (Fig. 1) 11 segmented; approximately 2 × GHW; FS simple elongate; GHW/SIW 3.70–4.50.

Legs (Figs 1–2). Without MFC; no legs with curved or expanded femora or tibiae; no basitarsi expanded or excavated.

Abdomen (Fig. 2F). No ventrites with curved posterior margins nor extending anteriorly into emarginated posterior margin of anterior segment. LO in V7 entire, LO present in V6, occupying almost all V6 (Jeng *et al.* 2003: figs 7, 9). V7 with elongate apically rounded MPP and angulate lateral areas which are not prolonged and correspond to where PLP would originate in other species. T7 without prolonged anterolateral corners; T8 not heavily sclerotised; no concealed anterolateral arms of T8 and the anterolateral corners scarcely produced (see Jeng *et al.* 2003: figs 21–22); lateral margins subparallel sided; posterior margin evenly rounded and entire; T8 ventral surface smooth even without any ridges or projections.

Aedeagal sheath (Fig. 5). Approx. 1.94–2.12 times as long as wide; without bulbous paraprocts; symmetrical in anterior half where sheath sternite tapers evenly to a broadly rounded apex; lateral arms of sheath tergite widely visible from below on left, narrowly on right; posterior area of sternite (posterior to the articulation of the tergite arms) narrow, emarginated on both sides (depending on orientation it may appear to be more deeply emarginated on right side) with margin even, without projections, and sternite apex rounded; tergite broad with anterior margin slightly and evenly emarginated; no obvious subdivision into more than one segment observed; posterior margin entire and evenly rounded; tergite projecting about as far as apex of sternite.

Aedeagus (Figs 5, 10–12). Subparallel sided; basal piece well defined and usually with distinctive, asymmetrical median notch; LL widely visible beside ML; LL of similar length, slightly shorter than ML; width across LL, (measured from beneath), much wider than width across widest part of median lobe (3–3.3); ML slender gradually narrowing in apical 1/7; apices of LL with ventral surfaces broad, slightly curved and hairy. Differences in aedeagal patterns in *Nipponoluciola cruciata* gen. et comb. nov. are addressed under that species in Figs 10–12.

Female (Fig. 7)

Macropterous and flight capable.

Body length. 14.0–18.4 mm (Jeng *et al.* (2003) listed a range of 15.0–18.6 mm long).

Colour (Fig. 7A, C–D). As for male except white LO restricted to V6, pinkish fat bodies beneath V7 in *cruciata*, or V7 completely black and underlying fat body not visible in *owadai*; black V8 with paired semitransparent areas; all tergites black except for T7 which has a median dark band and semitransparent lateral areas under which pink fat bodies are visible in *cruciata*.

Pronotum (Fig. 7). Outline as for male; pronotal width/GHW 1.88–2.20.

Head. GHW/SIW 2.67–2.90.

Abdomen (Fig. 7C–D, I). Lateral margins of V8 taper posteriorly, V8 with shallow median posterior emargination; anterior apodeme of V8 well sclerotised and separated from posterior area of V8 by clear transparent cuticle (Fig. 7I).

Reproductive system (Fig. 7E–H, J). Spermatophore digesting gland well defined usually with particulate remnants inside; spermatheca with expanded non sclerotised base; no obvious bursa plates;

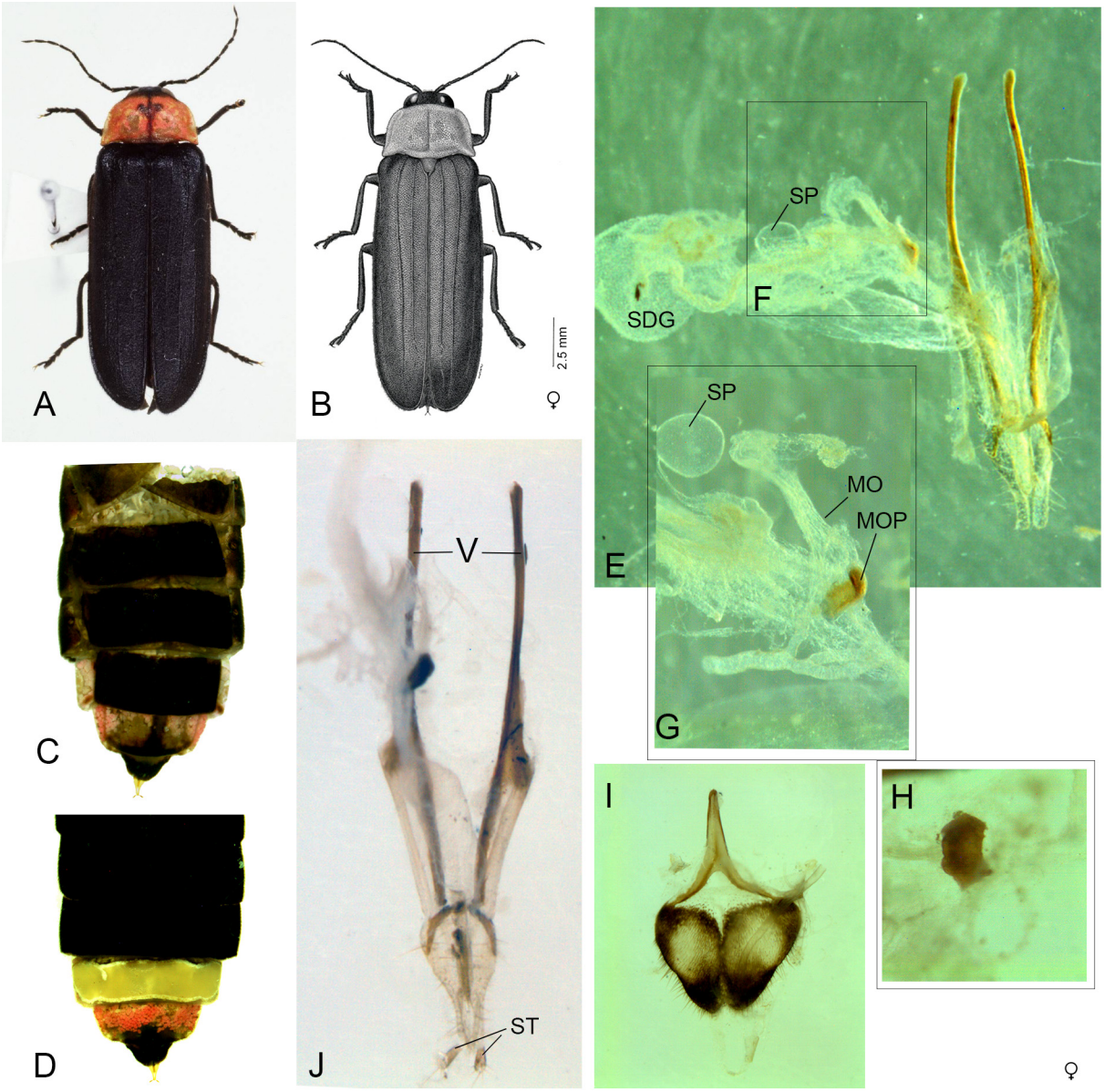

Fig. 7. Female morphology. **A, C-J**. *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. ♀ (Doubaru, Japan; ANIC). **B**. *Nipponoluciola owadai* (Satô & Kimura, 1994) gen. et comb. nov. **A–B**. Habitus, dorsal view. **C–D**. Abdomen, dorsal (C) and ventral (D) view. **E–G**. Female reproductive tract. **E**. With ovipositor to right and SDG to left. **F**. Area of bursa. **G**. Spermatheca to left. **H**. MO plate posterior end to right. **I**. V8 ventral surface. **J**. Ovipositor. Abbreviations: MO = median oviduct; MOP = median oviduct plate; SDG = spermatophore digesting gland; SP = spermatheca; ST = styli; V = valvifers. Images by I. Kawashima (A–B) and by L. Ballantyne (C–J).

median oviduct plate well defined (Fig. 7G–H), anterior margin curved and irregular, lateral margins straight and converging slightly posteriorly, posterior margin slightly and broadly emarginated; lying transversely in the median oviduct and curved possibly to accommodate to the outline of the duct. Ovipositor: elongate slender (Fig. 7J).

Larva (Figs 8A–B, 9A–H) (see also Fu *et al.* 2012b: figs 81–82)

Dorsal surface (Figs 8–9). With 3 thoracic and 9 obvious abdominal segments of which abdominal segments 1–8 bear lateral tracheal gills which are forked and compound, with a non-functional spiracle located at the end of the shorter branch. A narrow ring of cuticle at the posterior end of segment 9 has been attributed to segment 10 (Ballantyne & Menayah 2002: figs 2–3; Nada *et al.* 2021) and may be completely covered and concealed by the posterior margin of segment 9 from above in aquatic species, but visible from beneath. Lawrence & Ślipiński (2013) consider that segment 10 has been transformed into the holdfast organ (pygopodia) at the end of the abdomen. We refer to abdominal terga 1–9 only as these are clearly visible. Elongate, tapering at front and behind, membranous and very soft bodied, and somewhat flattened. The thorax and abdomen are almost membranous, with ventral sclerites degenerate and extent barely demarcated by wrinkles or folds, except for a single coloured dorsal plate on both the prothorax and abdominal segment 9, and paired well sclerotised and coloured tergites on the meso and metathorax, and abdominal segments 1–8. A wide membranous area/line extends from the anterior margin of the mesothorax to the posterior margin of abdominal segment 8. Without laterally explanate tergal margins thus laterotergites and gills visible from above.

Ventral surface (Fig. 9B, D, F). The extent of the following areas in very soft bodied aquatic larvae is often difficult to determine. A lateral pleural suture delimits laterotergites above in the thorax and abdomen (e.g., Ballantyne & Menayah 2002: fig. 1; Fu *et al*. 2012b: figs 81–82). In the thorax the median ventral surface of both meso and metathorax is subdivided into two areas by a sternocostal suture running anterior to the coxae, an anterior basisternum with laterotergites at the sides in the mesothorax; (in terrestrial larvae these mesothoracic laterotergites bear functional spiracles, but spiracles were not clearly visible in the larvae examined); a posterior median subrectangular sternellum bears the legs and is margined laterally by laterotergites; the episterna and epimera of both the meso and metathorax are visible above the coxae of the meso and metathoracic legs as thin dark sclerotised plates (see interpretation in Fu *et al.* 2012b: 5). This subdivision does not extend to the dorsal surface. In the abdominal segments 1–8 a median subrectangular area is attributed to the sternum; this is margined laterally by elongate narrow paired laterosternites, which are delimited by folds from the median sternal plate below, and the laterotergites above; in this aquatic genus the absence of any additional colour on the ventral surface makes interpretation of these areas difficult, and they may be incompletely distinguished only by folds in the membrane; laterotergites of segments 1–8 bear branched gills. Eversible branched defensive organs arise at the sides of the meso and metathorax, and abdominal segments 1–8, in the membrane at the sides of the terga of those segments and above the laterotergites of the abdomen (see below).

Head (Fig. 8C) (Kanda 1935: fig. 13; Hara 1962: figs 1, 5; Fu *et al.* 2012b: figs 25–30, 69). Subparallel sided, dorsoventrally flattened, prognathous, well sclerotised, with an ocellus at each side; not visible when retracted into the prothoracic cavity; extensible neck membrane forming two layered envelope around retracted head; capable of considerable extension beyond the anterior protergal margin; head capsule divisible into median dorsal frontoclypeus, bounded laterally by the U shaped frontal arms of the ecdysial line (= epicranial suture); lateral parietal plates at the sides of the frontoclypeus are separated behind by the epicranial stem and are reflexed ventrally but not meeting; maxillae and labium fused forming a maxillolabial complex covering most of ventral head area.

Antennae (Fu *et al.* 2012b: figs 27–29). Slender, cylindrical, 3 segmented, with elongated scape and pedicel, and apical very short (3rd) segment (the flagellum), with apical sensilla, subequal in length to adjacent sense cone; elongate ‘articulating membrane’ forms two layered envelope around retracted antenna.

Mouthparts (Fu *et al*. 2012b: figs 25, 29, 69). Well developed; mandibles falcate, strongly sclerotised; densely covered in fine hair along outer margins; densely pubescent along basal half of inner margins; perforated along length by a fine canal that opens on the outer margin just behind the apex; without a basal retinaculum; fine reticulate sculpture on the dorsal surface; with a row of elongate curved setae arising in a line just inside the outer margin. Maxillae with short, squat, four segmented palp bearing sense organs at the apex of segment 4; basal segment (which may be interpreted as the palpifer) large and well defined, segments 2 and 3 very short and diminishing in width towards apex, apical segment longer and narrower than palpomere 3, with apical sense organs; palp may obscure galea, which is long, thin, two segmented, bearing long and short setae at apex, and on its inner margin an elongate, flattened, dense profusion of anteromedially directed hairs (lacinia); cardo well defined, articulating

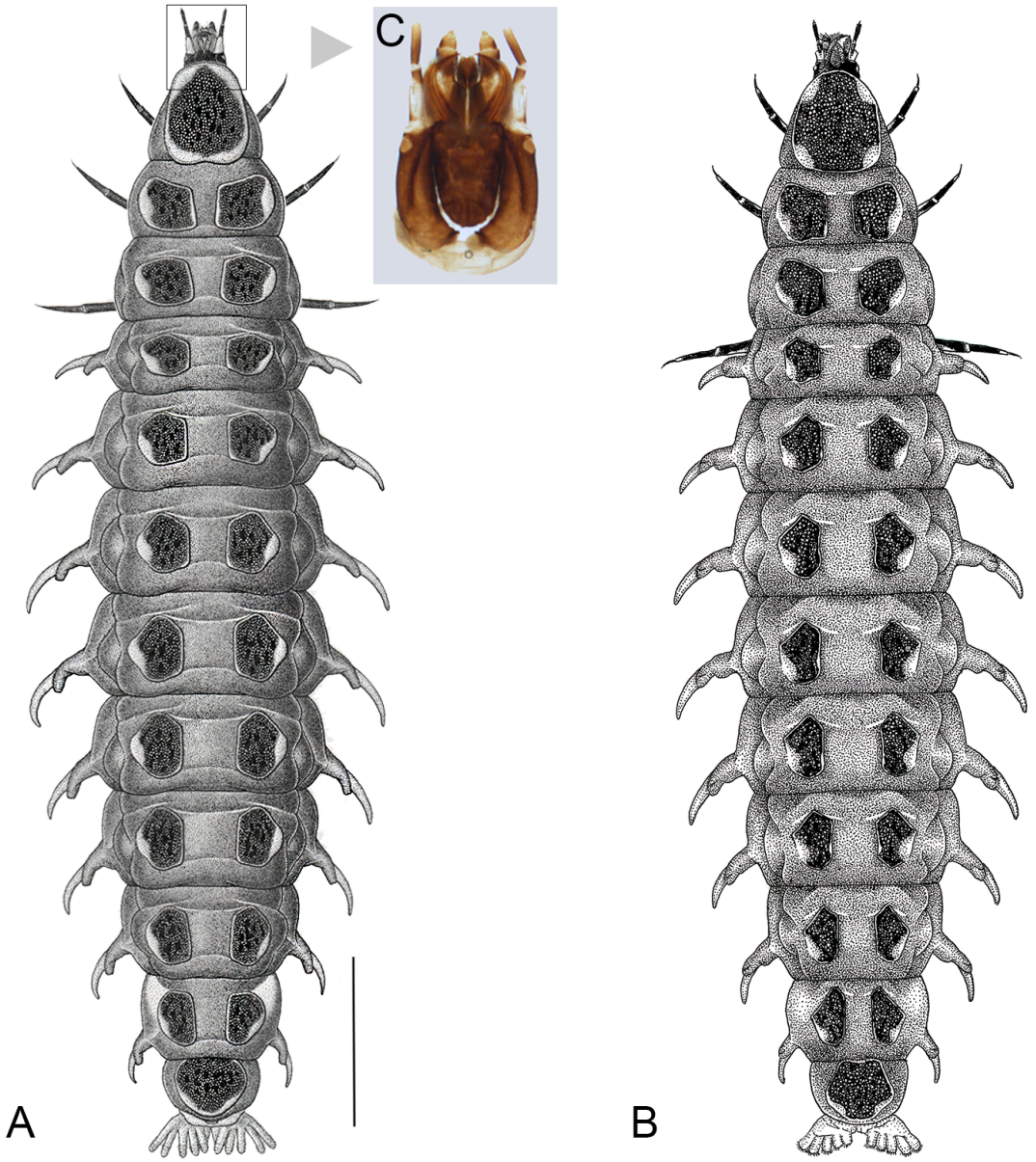

Fig. 8. Dorsal habitus larvae. **A**. *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. **B**. *Nipponoluciola owadai* (Satô & Kimura, 1994) gen. et comb. nov. (Ohba *et al.* 1994). **C**. Head, dorsal view of A. Images by I. Kawashima (A–B) and L. Ballantyne (C). Scale bar = 5 mm.

with broad elongate stipes; fused along its outer edges with the reflexed head margins, and along its inner margins with the median labium. Labium with two segmented labial palpi, bearing sense organs at the apex of segment 2, and arising at anterolateral corners of small prementum which lacks a ligula; apical palpomere elongate conical with two or three peg-like sensilla on the sides; anterior area of prementum densely covered by minute spines on both sides of dorsal surface; postmentum elongate, not well sclerotised and colourless, and joined along sides by membrane to the cardines.

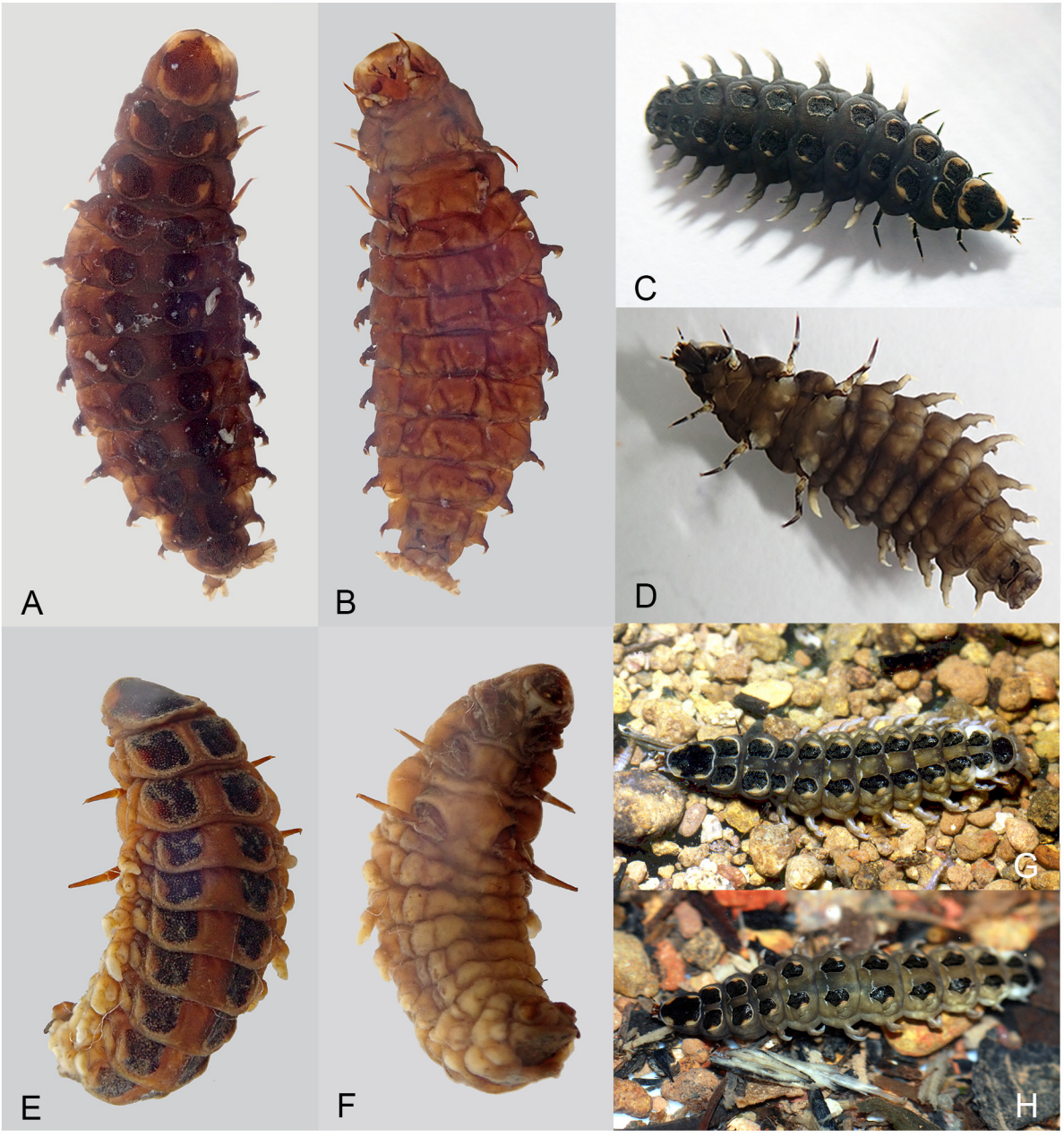

Fig. 9. Larvae. **A–D**. *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. **E–H**. *Nipponoluciola owadai* (Satô & Kimura, 1994) gen. et comb. nov. **A, C, E, G–H**. Dorsal view. **B, D, F**. Ventral view. Images by I. Kawashima (A–F) and F. Satou (Kumejima Firefly Museum) (G–H).

Thorax (Figs 8–9) (Fu *et al.* 2012b: figs 81–82). Prothorax longer than wide, and containing retracted head within; with ventral surface little differentiated. Protergum elongate or elliptical, with lateral margins arcuate and shallowly expanded laterad, divergent posteriorly; anterior and posterior margins rounded and widely arcuate, connecting directly to lateral margins without forming corners. Each tergite of meso- and metathorax as are those of abdominal segments 1–8 separated from each other as a pair of plates, subequal in size; the shape more or less round pentagonal; any corners more or less rounded; the margins lightly pale margined, broadened at the lateral margins to form pale spots; lateral margins arcuate, expanded to laterad; hind margins also arcuate; inner margins straight and parallel-sided to each other. Legs are four segmented – short cylindrical coxae with bases widely separated; elongate trochanters joining femora obliquely; tibiotarsus terminated by a single claw. In contrast with previous treatments the leg segments are attributed to coxa, trochanter, femur and tibiotarsus.

Abdomen (Figs 8–9) (Fu *et al.* 2012b: figs 81–82). Each tergite of abdominal segments 1–8, as are those of the meso- and metathorax, is separated as a pair of plates, similar form to those of meso- and metathoracic terga, more or less round pentagonal, diminishing slightly in both length and width toward posterior ones, not forming any corners; the margins lightly pale margined, broadened at the lateral margins to form pale spots; segment 9 has a single round tergal plate, with the margin also lightly pale margined as in segments 1–8; pale posterior margin often widens slightly to form a narrow pale spot; abdominal tergal width decreasing a little towards posterior end, ventral surface of all but terminal abdominal segment (segment 9) with paired laterotergites bearing gills at the sides (visible along sides of body as lateral projections); median sternal element in each of abdominal segments 1–8 margined by elongate slender laterosternites but these areas difficult to discern in soft bodied larvae; (laterosternites appear membranous on segment 8 which houses the light organs).

Defensive organs. With 10 pairs of similar pale white, forked eversible defensive organs (Okada 1928: fig. 1a; Kanda 1935: 57–58, pl. 5-5; Trice *et al.* 2004: 2; Fu *et al.* 2009: fig. 4; 2012b: figs 7–12) located laterally on the meso- and metathorax, and above the tracheal gills on each of the 8 abdominal segments; these organs arise in the thorax in folds of membrane on the upper side of the laterotergites and just below the lateral margins of the tergal plates, and in the abdomen above the abdominal laterotergites and below the lateral margins of the tergal plates; organs have protuberances on their external surface, each composed of a well-developed globular body attached to a long thick stalk; globular bodies consist of secretory cells.

Pygopodia (Fig. 8, partly visible in Fig. 9A). On the external surfaces of the tubular larval eversible holdfast organs, numerous hook-shaped protuberances grow in circular rows on each tube.

List of species of *Nipponoluciola* gen. nov.

Nipponoluciola cruciata (Motschulsky, 1854) gen. et comb. nov.
Nipponoluciola owadai (Satô & Kimura, 1994) gen. et comb. nov.

Key to species of *Nipponoluciola* gen. nov. using males

1. Widely distributed in Japan; pronotum usually with pinkish fat body visible through cuticle, and variable median blackish marking which may be expanded in the median area to assume a cross like formation; MS and elytra black (Figs 1–2) .... ***N. cruciata*** (Motschulsky, 1854) (Honshu, Shikoku, Kyushu and their sub-islands)
– A rare and protected species known only from the Okinawa Islands group; pronotum yellowish orange, without median dark markings, and fat body without pinkish colour; MS yellowish orange and elytra black (Figs 1–2) .... ***N. owadai*** (Satô & Kimura, 1994) (only Kume-jima Is. of the Okinawa Isls, Middle Ryukyus)

Description of species of *Nipponoluciola* gen. nov.

Nipponoluciola cruciata (Motschulsky, 1854) gen. et comb. nov.
Figs 1–3, 5–12

Luciola cruciata Motschulsky, 1854: 53. Type specimen represented by label only, ZMMU.
Luciola picticollis Kiesenwetter, 1874: 262. Series of syntype males. NHMUK. **Syn. nov.**
Luciola cruciata towadensis Nakane, 1987: 173.

Luciola cruciata PARTIM – Lacordaire 1857: 338. — Heyden 1879: 350. — Gorham 1880: 102. — Olivier 1902a: 77; 1902b: 188; 1907: 51; 1910: 41. — McDermott 1962: 24; 1966: 102. — Takakura 1977: 7. — Jeng *et al.* 2003: 541. — Kawashima *et al.* 2003: 247.
Luciola cruciata – Motschulsky 1866: 167. — von Harold 1877: 357. — Lewis 1879: 17. —Matsumura 1918: 86, 87. — Okada 1928: 102; 1931: 134, 146. — Kanda 1935:31. — Kishida 1936: 12, 20, 21. — Hasama 1942a: 366; 1942b: 378; 1943: 23; 1944: 155. — Nakane *et al.* 1959: 170. — Nakane 1960: 36, 118; 1968: 5; 1970: 285; 1983: 111; 1987: 173. — Minami 1961: 21–106, 152–238. — Bertrand 1972: 599; 1973: 107. — Satô 1974: 133; 1978: 17; 1985: 121; 1989: 352. — Ohba 1978: 25; 1983: 24; 1984: 23; 2001: 45; 2004a: 228; 2005: 240; 2012: 13. — Yuma 1981: 57. — Ohba *et al.* 1994: 13. — Suzuki *et al.* 1996a: 191; 1996b: 682; 2004: 297. — Suzuki 1997: 1; 2001: 99. — Sawada 2000: 93. — Branham & Wenzel 2003: figs 1–2, 4–5, 8. — Takeda *et al.* 2006: 177. — Ballantyne & Lambkin 2009: 21; 2013: 9. — Oba *et al.* 2011: 771. — Ballantyne *et al.* 2015: 8; 2016: 204; 2019: 163. — Fu & Ballantyne 2009: 243. — Fu *et al.* 2009: 155; 2010: 3; 2012a: 6; 2012b: 14. — Jusoh *et al.* 2018: 14; 2021: 1. — Kato *et al.* 2020: 1.
Luciola picticollis – Von Harold 1877: 357. — Lewis 1879: 17. — Olivier 1902a: 85; 1902b: 189; 1907: 54; 1910:45. — Matsumura 1918: 87. — Okada 1931: 130. — McDermott 1966: 111 (partim). — Nakane 1983: 111.
Luciola vitticollis – Sensu Gorham 1883: 409. — Okada 1931: 146.
Luciola cruciata vitticollis – Okamoto 1924: 182–183, 226 (incorrect record from Korea). — Matsumura 1928: 59 (misidentification).
Luciola cruciata towadensis – Kawashima *et al.* 2003: 247 (synonymy).
Luciola cruciata cruciata – Geisthardt & Satô 2007: 232.

non *Luciola picticollis* – Gorham 1883: 409 (= *lateralis*).
non *Luciola vitticollis* – Sensu Gorham 1883: 409. — Okada 1931: 146 (= *lateralis*).
non *Luciola cruciata* var. *vitticollis* – Olivier 1902a: 71; 1902b: 188; 1907: 54; 1910: 42. — McDermott 1966: 111 (= *lateralis*).
non *Lueiola erciata* – Matsumura 1918: 86 (misspelling, typographical error).
non *Luciola Cxuca'a* var. *vitticollis* – Matsumura 1918: 82 (misspelling, typographical error).
non *Luciola cruciata vitticollis* – Matsumura 1928: 59, pl. 5 fig. 15, pl. 6 figs 5–6, pl. 7 fig. 14.
non *Luciola cruciata* – Thapa 2000: 115 (incorrect record).

Diagnosis

One of the most famous fireflies in Japan, distinguished most obviously from the only other species in the genus, *N. owadai* gen. et comb. nov., by the pinkish pronotum with median blackish markings (that of *owadai* is yellowish orange without dark markings), and black MS and elytra (*owadai* has yellow MS and black elytra). Widely distributed throughout the main islands of Japan in contrast with *owadai*, which is restricted to a part of the Ryukyu islands, Kume-jima Island, and presently considered endangered in the locality. Macropterous females coloured as for males, except for white LO in V6, semitransparent anterior ⅔ of V7, with underlying pink fat body, and median posterior area black; V8 largely black.

Type material

Neotype of *Luciola cruciata* Motschulsky, 1854 (here designated)
JAPAN • ♂; Kanagawa Pref., Yokosuka-shi, Nobi (Aza-Yatonota); 10 Jun. 2000; Itsuro Kawashima leg.; registration number: KPM-NK 80923.

Remarks
This designation fulfils the requirements of the ICZN neotype designation as follows: 75.3: in the absence of a type specimen there is a need to designate a neotype to preserve the existing taxonomy; 75.3.1: having established that the type locality given in Motschulsky (1854) as Java is incorrect, we designate a specimen from mainland Japan; 75.3.2: characters differentiating the neotype from other genera in the Luciolinae, and the other species in this new genus, *owadai*, are given in the generic description and key to species; 75.3.3: the specimen is fully labelled (outlined below) and given an identifying number in the type depository below; 75.3.4: introductory sections of this paper outline the steps taken to establish that no type specimen could be found; 75.3.5: this paper outlines all the references to this species including the original description by Motschulsky (1854), and we believe the morphological features of this specimen are consistent with all; 75.3.6: we established that the original type specimen could not have come from Java, but Japan; the locality chosen for this neotype designation is an area of high density of the species; 75.3.7: upon publication of this paper the neotype specimen, already lodged in the Kanagawa Prefectural Museum of Natural History, Odawara, Kanagawa, will be permanently lodged there and become the property of that museum.

Notes
Labels attached to the neotype are as follows (from top to bottom, a slash indicates a line break): (Nobi, Yatonota (in Japanese "Kanji" characters)) / Yokosuka-shi/ Kanagawa Pref. / VI–10, 2000 / I. Kawashima leg. (original white label, hand written in black ink); *Luciola cruciata* / Motschulsky, 1854 / det. I. Kawashima, 2004 (white determination label, printed in black ink); NEOTYPE / *Luciola cruciata* / Motschulsky, 1854 / = *Nipponoluciola cruciata* / (Motschulsky, 1854) / Ballantyne, Kawashima, Jusoh & Suzuki, 2021 (designated) (pink neotype label, printed in black ink).

Other material examined

JAPAN – **Akita Prefecture** • 1 ♂; Higashi, Kawabe-machi; 39°39′ N, 140°12′ E; 25 Jun. 1994; K. Umetsu leg.; AKPM • 1 ♂; Sunakobuchi, Kawabe-machi; 39°44′ N, 140°33′ E; 25 Jun. 1994; K. Umetsu leg.; AKPM • 1 ♂; Yunosato, Akita-shi; 39°48′ N, 140°13′ E; Jul. 1995; K. Umetsu leg.; AKPM • 1 ♂; Noda, Taihei, Akita-shi; 39°43′ N, 140°20′ E; 25 Jun. 1994; K. Umetsu leg.; AKPM. • 1 ♂; Mt Ôtaki-yama, Akita-shi; 39°43′ N, 140°16′ E; 12 Jul. 1988; F. Satô leg.; AKPM • 1 ♀; Kawabe-machi; 13 Jun. 2002; collector unknown; CIK. – **Niigata Prefecture** • 1 ♂; Yomogihira, Nagaoka-shi; 37°36′ N, 138°53′ E; Jul. 1994; N. Harayama leg.; CIK. – **Ishikawa Prefecture** • 2 ♂♂; Kamitokuyama, Nomi-shi; 36°43′ N, 136°54′ E; 3 Jul. 2012; H. Fukutomi leg.; CIK. – **Fukushima Prefecture** • 1 ♀; Arakawa; 37°42′ N, 140°35′ E; Jun. 1993; K. Matsumoto leg.; CIK • 2 ♂♂; Jikiri-onsen Spa., Nagasaki, Iwaki-shi; 36°96′ N, 140°93′ E; 3 Jun. 1998; I. Kawashima leg.; CIK. – **Ibaraki Prefecture** • 2 ♀♀; Ishizuka, Jôhoku-machi, Higashi-ibaraki-gun; 36°47′ N, 140°38′ E; Jun. 1988; K. Nakayama leg.; CIK • 4 ♂♂; same collection data as for preceding; 30 May 1990; CIK • 1 ♂; same collection data as for preceding; 1 Jun. 1992; CIK • 1 ♂; same collection data as for preceding; 20 Jun. 1995; CIK • 2 ♂♂; same collection data as for preceding; 25 Jun. 1998; CIK • 2 ♂♂; same collection data as for preceding; 8 Jun. 1999; CIK • 3 ♂♂; same collection data as for preceding; 10 Jun. 1999; CIK • 4 ♂♂, 2 ♀♀; same collection data as for preceding; 6 Jun. 2000; CIK • 1 ♂, 1 ♀; same collection data as for preceding; 6–7 Jun. 2002; CIK • 1 ♂, 1 ♀; same collection data as for preceding; 3 Jun. 2009; CIK. – **Saitama Prefecture** • 2 ♂♂; Shôgun-sawa Riv., Ranzan-machi; 36°01′ N, 139°33′ E; 5 Jun. 1997; S. Arai leg.; CIK. – **Chiba Prefecture** • 13 ♂♂, 1 ♀; Hirasawa-gawa Riv., Ôtaki-machi; 35°23′ N, 140°22′ E; Jun. 2019; S. Nishihara and I. Kawashima leg.; CIK • 1 ♂; Tsutsumori, Ôtaki-machi; 35°22′ N, 140°14′ E;

13 Jun. 2018; I. Kawashima leg.; CIK. – **Tokyo Metropolitan** • 10 larvae; Hamura-shi; 35°45′ N, 139°31′ E; 2001; T. Sano leg.; CIK. – **Kanagawa Prefecture** • 3 ♂♂; Kurokawa, Asao-ku, Kawasaki-shi; 35°36′ N, 139°45′ E; 9 Jun. 1990; Y. Goto leg.; CIK • 6 ♂♂; Inukura, Miyamae-ku, Kawasaki-shi; 35°58′ N, 139°56′ E; 9 Jun. 1991; T. Arikawa leg.; CIK • 3 ♂♂; Nobi (Aza-Yatonota), Yokosuka-shi; 35°21′ N, 139°41′ E; 10 Jun. 2000; I. Kawashima leg.; KPM • 3 ♂♂; same collection data as for preceding; CIK • 18 ♂♂; same collection data as for preceding; 11 Jun. 2001; CIK • 1 ♂; same collection data as for preceding; 26 Jun. 2021; CIK • 5 ♂♂; Morito-gawa Riv., Sakurayama-Ôyama Pass, Hayama-machi; 35°28′ N, 139°59′ E; 15 Jun. 2000; I. Kawashima leg.; CIK. – **Shizuoka Prefecture** • 1 ♂; Katasumata-gawa Riv., Kanaya, Haibara-gun; 34°49′ N, 138°13′ E; 15 Jun. 1995; Y. Sato leg.; CIK • 3 ♂♂; Shizuoka-shi; 34°58′ N, 138°38′ E; 6 Jun. 1998; Y. Sato leg.; CIK. – **Yamanashi Prefecture** • 1 ♂, 1 ♀; Yamanashi; 35°41′ N, 138°41′ E; 16 Jun. 1978; unknown leg.; (id N. Ohba); ANIC. – **Nagano Prefecture** • 2 ♂♂; Sanozaka, Hakuba-mura; 36°37′ N, 137°50′ E; 13 Jul. 1986; M. Takakuwa leg.; CIK • 5 ♂♂, 1 ♀; Matsumoto-shi; 36°23′ N, 137°58′ E; 5 Jul. 1990; Y. Sato leg.; CIK. – **Mie Prefecture** • 1 ♂; Osugi; 34°21′ N, 136°15′ E; 6 Jun. 1932; N. Tamu leg.; (id T. Nakane); ANIC. – **Gifu Prefecture** • 4 ♂♂; Gujôhachiman, Gujo-shi; 35°44′ N, 136°58′ E; 5 Jun. 1988; H. Kuwano leg.; CIK • 4 ♂♂, 1 ♀; Kitaogi, Tajimi-shi; 35°33′ N, 137°11′ E; 18 Jun. 1994; H. Suzuki leg.; CIK. – **Hyogo Prefecture** • 1 ♂; Kawanishi-shi; 34°49′ N, 135°41′ E; 1 Jul. 1992; K. Matsuda leg.; CIK • 3 ♂♂, 3 ♀♀; same locality data as for preceding; 6 Jul. 1996; T. Ochi leg.; CIK. – **Shimane Prefecture, Oki Islands (off W Honshu)** • 1 ♂; Mt Akahage-yama, Chiburi Is.; 36°01′ N, 133°03′ E; 26 Jul. 2003; T. Shimada leg.; CIK • 7 ♂♂; Araki-gawa Riv., Saigo-chô, Dogo Is.; 36°20′ N, 133°32′ E; 13 Jun. 2003; T. Shimada leg.; CIK. – **Ehime Prefecture** • 1 ♂; Nakayama, Omogo-mura, Kami-ukena-gun (Kumakôgen-chô at present); 33°39′ N, 133°06′ E; 3 Jul. 1999; Y. Goto leg.; CIK. – **Kochi Prefecture** • 1 ♂; Amikawa, Tosayama-mura; 33°39′ N, 133°50′ E; 19–20 Jun. 1999; Y. Goto leg.; CIK • 11 ♂♂; Shimotsui, Shimanto-chô; 33°29′ N, 132°55′ E; 17 Jun. 2006; I. Kawashima leg.; CIK. – **Fukuoka Prefecture** • 1 ♂, 2 ♀♀; Doubaru, Kitakyushu-shi; 33°46′ N, 130°49′ E; Jun. 1978; M. Nakamura leg.; (id by N. Ohba); ANIC. – **Nagasaki Prefecture** • 6 ♂♂, 1 ♀; Tsushima Is. (off N. Kyushu), Kyôzuka, Izuhara-chô (Tsushima-shi at present); 33°46′ N, 129°55′ E; 18 Jun. 1990; Y. Goto leg.; CIK; 9 ♂♂; Urakami-gawa Riv., Azebettô-chô, Nagasaki-shi; 32°48′ N, 129°55′ E; 20 May 2018; K. Tanaka leg.; CIK. – **Kumamoto Prefecture** • 3 ♂♂, 1 ♀; Yubune, Kyokushi-mura (Kikuchi-shi at present); 32°55′ N, 130°52′ E; 29 May 1991; Y. Goto leg.; CIK. – **Miyazaki Prefecture** • 10 ♂♂; Kita-gawa Riv., Kitagawa-chô; 32°43′ N, 131°39′ E; 3 Jun. 1993; Y. Goto leg.; CIK. – **Kagoshima Prefecture** • 7 ♂♂, 4 ♀♀; Yaku-shima Is. (off S. Kyushu), Miyanoura to Ryûjinsugi-tozanguchi, Yakushima-chô; 30°37′ N, 130°52′ E; 29 May 2021; A. Ueno leg.; CIK. – **Without locality** • 7 ♀♀, pupa; reared by Y. Haneda; ANIC.

Description

Male (Figs 1–3, 5–6, 10–12)

Body Length. 10.5–15.8 mm (Jeng *et al.* (2003) listed a range of 10.5–16.5 mm long).

Colour (Figs 1–2, 6). Entirely black except for pale pronotum with underlying pink fat body, and usually with a series of black markings extending narrowly across the anterior margin, continuous with a narrow median band that expands just anterior to midsection into short arms (the median cross) which may be wide or narrow, and continuing to posterior area where there may be a wide expansion across the posterior margin (Fig. 6). Aged pinned and ethanol preserved specimens may fade and the femoral base may appear brownish. A few specimens have very reduced pronotal colour patterns, and even fewer have no dark pronotal markings at all. IK observed many individual variations in pronotal colour among specimens from the same locality (see Pronotal colouration variations below).

Abdomen (Fig. 2). Jeng *et al.* (2003: fig. 7) illustrated a narrow MPP on V7 with well-defined posterolateral corners which were not prolonged.

Aedeagal sheath (Fig. 5). Anterior margin of sheath tergite entire and slightly and broadly emarginated; sternite emarginated strongly on right side. Jeng *et al.* (2003: fig. 27) depict the same stronger emargination of the sheath sternite on its right side as we do here.

Aedeagus (Figs 5, 10–12). L/W 3/1; either subparallel-sided or with lateral margins converging slightly; maximum width across LL/maximum width of ML 2.57–3.57; LL separated along the dorsal surface longitudinally by $^{7}/_{9}$ of their length; LL apex width considerably wider than width of apex of ML; dorsal base of LL symmetrical, somewhat irregularly rounded; ML symmetrical, expanding slightly along its length to a maximum width around the ejaculatory orifice then narrowing in apical $^{1}/_{6}$ or less where it is approximately $^{2}/_{7}$–$^{2}/_{9}$ the width of the more anterior portion; with rounded apex; BP well sclerotised, not hooded, emargination along anterior margin, may be absent. Jeng *et al.* (2003: figs 33–34) show an anterior median notch in the BP and the ML narrowing towards the apex.

Aedeagal patterns (Figs 10–12). For the first time we are able to demonstrate intraspecific variation in the aedeagal patterns of *N. cruciata*. Aedeagal patterns corresponded with the areas of east Honshu, west Honshu and the island of Kyushu. In E Honshu the lateral margins of the LL converge slightly; the apices of the LL are slightly narrowed; the ML is broader (LL/ML range: 2.57–2.78), becoming widest around ⅓ of its length from the apex; when viewed from the side, the apex of the ML is not flattened vertically, but becomes thin and stick-like; the emargination of the anterior margin of the BP is more pronounced (Figs 10–12, A–E). In W Honshu and Kyushu the lateral margins of the LL are subparallel-sided; the apices of the LL are broader and more rounded; the ML is narrower (LL/ML range: 2.66–3.57); when viewed laterally, the tip of the ML is depressed along both sides and becomes slightly wider vertically in lateral view; the emargination of the anterior margin of the BP is less pronounced (Figs 10–12, F–P). In populations in E Honshu, from the north to the Pacific coast (Fig. 12A–E), aedeagus is generally upturned towards the ventral side when viewed from the side. In contrast, populations from Hokuriku to western Honshu, Shikoku and Kyushu (Fig. 12F–P) are generally straight.

Depictions of the aedeagus from line figures only are sometimes difficult to interpret. The figures in Jeng *et al*. (2003) are the exception. Assuming McDermott (1962: 24, fig. 20c) is left lateral then despite the absence of a basal piece, the ML can be interpreted as having a thin apex and curving strongly dorsally, similar to what we depict here for the E. Honshu pattern. Ohba's (2004b: 91, fig. 3) depiction of the aedeagus shows a basal piece with median notch. Takakura's (1977: fig. 2l) interpretation of the aedeagus may show a dorsal view but does show narrowing of the apex of the ML.

Female (Fig. 7)

Body length. 14.0–18.4 mm (Jeng *et al.* (2003) listed a range of 15.0–18.6 mm long).

Colour (Fig. 7). Coloured as for male except for abdomen; abdominal ventrites black except for white LO in V6 occupying all but a narrow transparent posterior margin; V7 (Fig. 7D) semitransparent with pink fat body granules visible beneath cuticle and clustered around anterior ⅔; median posterior area of V7 is largely devoid of fat bodies and appears black mainly due to the underlying black V8; V8 (observed when removed from intact specimen; Fig. 7I) black with lateral areas light brown; dorsal surface of basal tergites (up to T5), and dorsally reflexed margins of V2–V5 black; T6 (Fig. 7C) black with dorsally reflexed margins of V6 white, semitransparent; T7 (Fig. 7C) semitransparent with median dark stripe, dorsally reflexed margins of V6 appearing pink due to underlying fat body granules; T8 black (Fig. 7C).

Abdomen (Fig. 7C–D, I). V8: lateral margins converge posteriorly; median posterior margin shallowly and narrowly emarginated; anterior apodeme and narrow anterior margin of V8 well sclerotised, pale coloured, appearing separate to posterior area of V8 because of intervening transparent area (Jeng *et al*. 2003: fig. 15, depict the posterior margin of V7 with a broad shallow emargination).

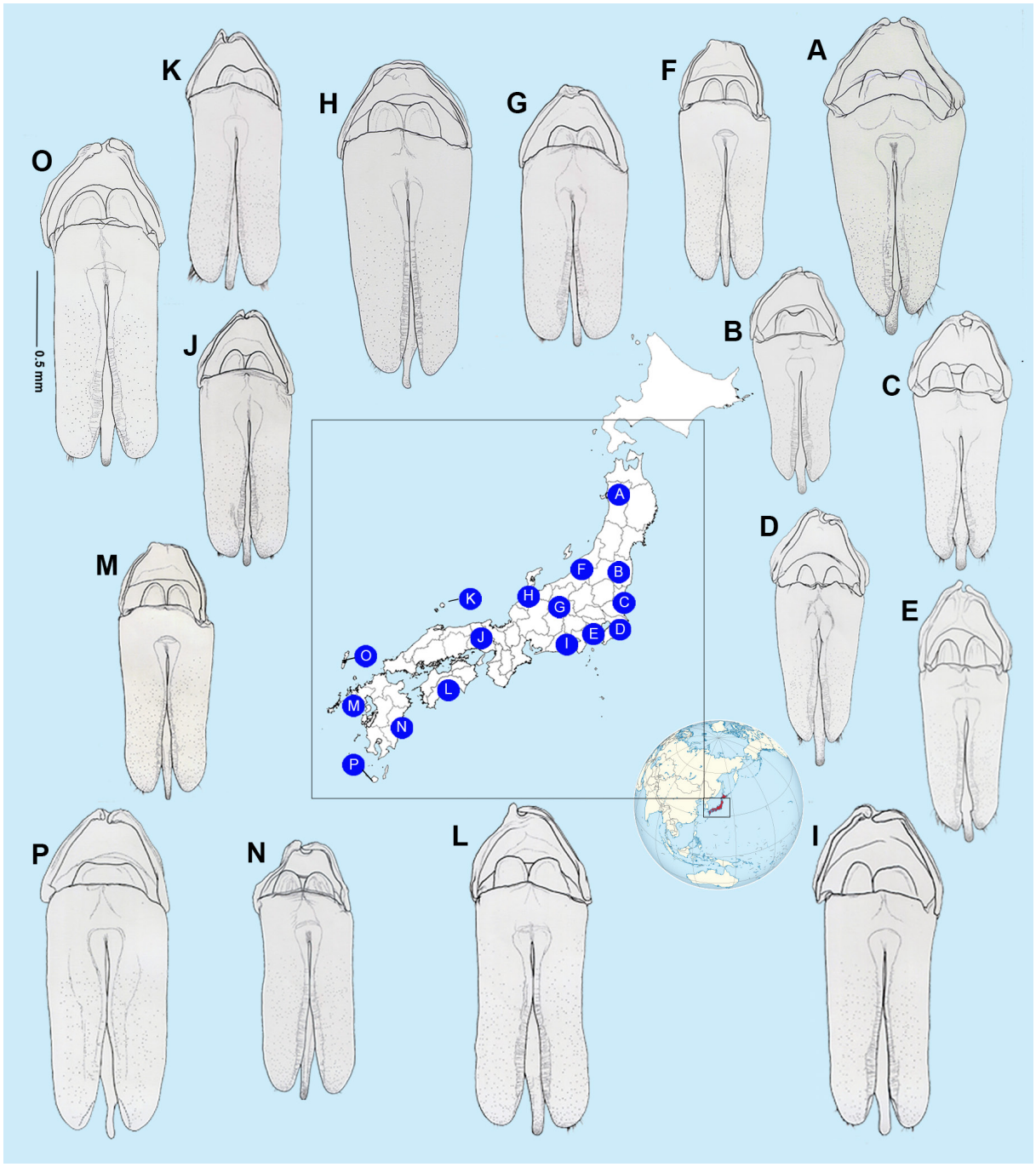

Fig. 10. Distribution of aedeagal patterns of *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. in the Japanese islands; aedeagus dorsal view. Images by I. Kawashima. Map by W.F.A. Jusoh (Map of Japan using base maps obtained from Wikimedia Commons - Maximilian Dörrbecker and Connormah, CC BY-SA 3.0). **A**. Akita. **B**. Fukushima. **C**. Ibaraki. **D**. Chiba. **E**. Kanagawa. **F**. Niigata. **G**. Nagano. **H**. Ishikawa. **I**. Shizuoka. **J**. Hyogo. **K**. Oki Islands. **L**. Kochi. **M**. Nagasaki. **N**. Miyazaki. **O**. Tsushima Island. **P**. Yakushima Island.

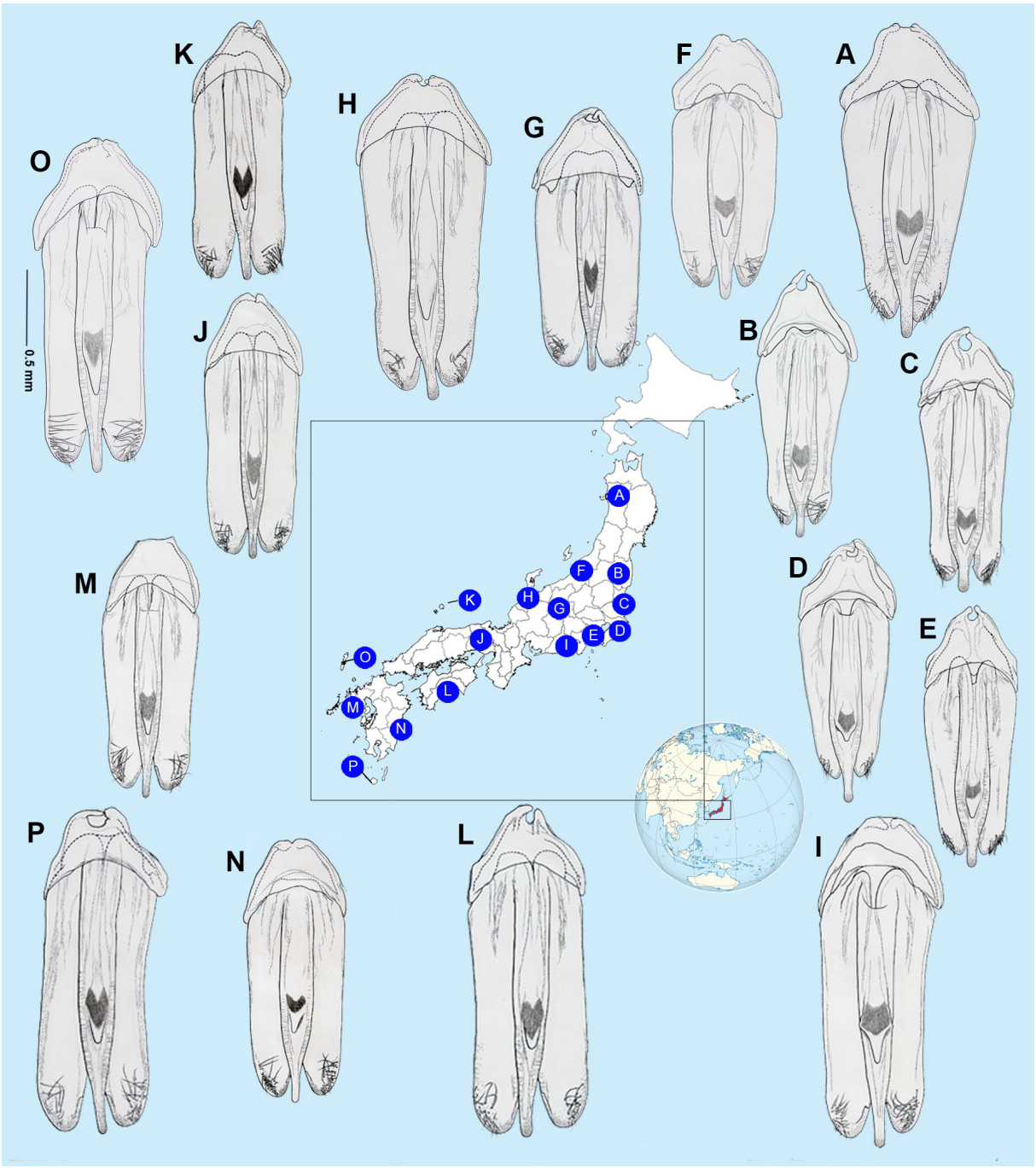

Fig. 11. Distribution of aedeagal patterns of *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. in the Japanese islands; aedeagus ventral view. Images by I. Kawashima. Map by W.F.A. Jusoh (Map of Japan using base maps obtained from Wikimedia Commons - Maximilian Dörrbecker and Connormah, CC BY-SA 3.0). **A**. Akita. **B**. Fukushima. **C**. Ibaraki. **D**. Chiba. **E**. Kanagawa. **F**. Niigata. **G**. Nagano. **H**. Ishikawa. **I**. Shizuoka. **J**. Hyogo. **K**. Oki Islands. **L**. Kochi. **M**. Nagasaki. **N**. Miyazaki. **O**. Tsushima Island**. P**. Yakushima Island.

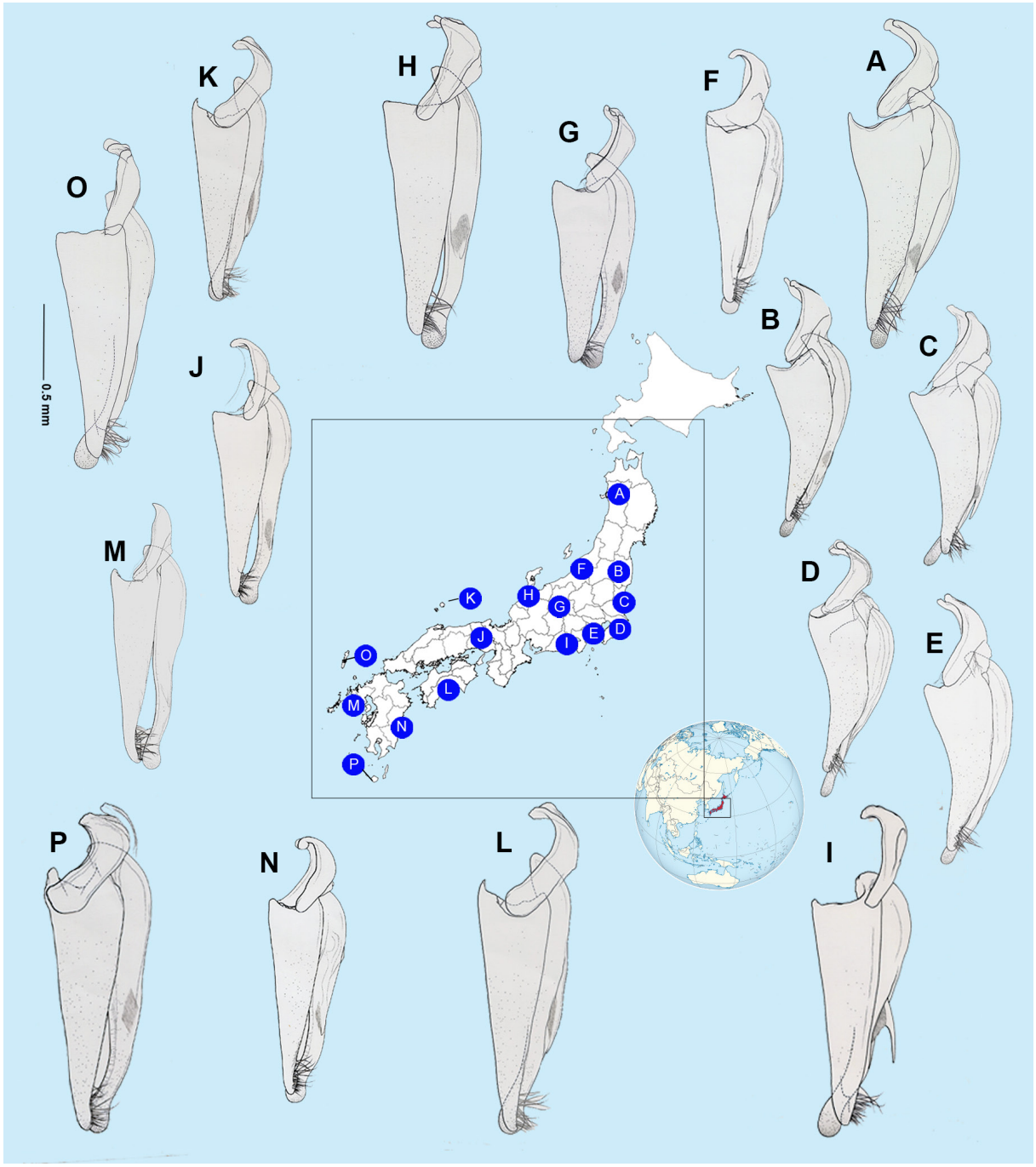

Fig. 12. Distribution of aedeagal patterns of *Nipponoluciola cruciata* (Motschulsky, 1854) gen. et comb. nov. in the Japanese islands; aedeagus right lateral view. Images by I. Kawashima. Map by W.F.A. Jusoh (Map of Japan using a base map obtained from Wikimedia Commons - Maximilian Dörrbecker and Connormah, CC BY-SA 3.0). **A**. Akita. **B**. Fukushima. **C**. Ibaraki. **D**. Chiba. **E**. Kanagawa. **F**. Niigata. **G**. Nagano. **H**. Ishikawa. **I**. Shizuoka. **J**. Hyogo. **K**. Oki Islands. **L**. Kochi. **M**. Nagasaki. **N**. Miyazaki. **O**. Tsushima Island. **P**. Yakushima Island.

Reproductive system (Fig. 7E–H). No intact spermatophores observed but spermatophore digesting gland may contain white particulate material which may represent digested spermatophore; median oviduct plate filling half of the median oviduct, anterior margin slightly irregular, lateral margins straight, posterior margin evenly shallowly emarginated. Ovipositor elongate slender (Fig. 7J).

Larva (Figs 8–9)

Final instar larvae were examined. Approx. body length 25–29 mm; maximum (median) length of protergum 3.2–3.4 mm; maximum width of protergum 2.6–2.9 mm. The following is modified and expanded from Fu *et al.* (2012b: 8). Living in shallow well oxygenated water, cannot swim. Similar to larvae of *Aquatica* spp. distinguished from *A. hydrophila* by the pale marginal markings of the protergum (that of *A. hydrophila* has no paler marginal markings); from *A. lateralis* in that the pale markings on both side of protergum are not divided anteriorly and posteriorly, but are more or less continuous, and in that the pale marked areas in lateral margins of each tergite are not covered with minute spines which occur in *A. lateralis*; from *N. owadai* in having remarkably paler ground colour of membranous body and in the tendency of the pale markings on the lateral margins of pronotum to separate anteriorly and posteriorly into four independent ones (in *cruciata*, the pale markings on the lateral margins of pronotum are more or less continuous anterior and posterior, becoming pale ones along the entire lateral margins). Defensive organs in this species emit a mint-like scent when the larva is disturbed. Organs are transparent when everted, and their colour reflects the amount of haemolymph in them. The protuberances on their surface may have 6 or more irregular apical spines arranged like a crown (Fu *et al.* 2009: fig. 4; 2012b: figs 81–82; Hara 1962: figs 2–4; Okada 1928: fig. 1a, pl. viii e). In the pygopodia (caudal legs) there are two rows, dorsal and ventral with each row divided into left and right pairs; each of the two dorsal basal stalks branch into two on each side with a single median strand for a total of ten individual strands; the two ventral stalks branch into two, for a total of 14 individual "legs" (Kanda 1933: 237; 1935: 57; Hara 1962).

Larvae can climb up the riverbank or canal edges to pupate on rainy nights (Yuma 1981). Larvae when moulting split their larval cuticle along the sides of the body and not along any ecdysial cleavage line (Kuribayashi 1979). During the day they hide under stones on the river bottom, but at night they walk around the river bottom, emitting light (IK observations).

Misidentifications

In the absence of specimens, we cannot substantiate all the listings in the table of synonymies above. However all literature, especially that including any pictorial depictions, was reassessed for accuracy of identification. References for which we feel there is the possibility of more than one species are listed as PARTIM. Local knowledge (co-authors IK, HS) of species occurrence permitted us to readdress records in Gorham (1883). He listed *L. picticollis* from localities in Hokkaido where *L. cruciata* has not been recorded; together with the adult flight period of July both IK and HS considered this species would have been *A. lateralis*. Gorham's reference to *L. vitticollis* as a larger species, with or without the median pronotal vitta, and a flight period of May suggested this reference is to *cruciata* (Fig. 2D). While the Olivier collection in MNHN revealed correctly identified specimens (Fig. 2B–C), we consider that in his catalogues spanning 1902–1910 he still misidentified some specimens. HS & IK considered that Matsumura's (1918) reference to *L. picticollis* is most probably to *Luciola lateralis.* The reference to *cruciata* (with typological errors, but recognisable) is to *cruciata* adult but not the larva (Matsumura 1918: 83, fig. 2–2), which HS & IK considered could be a *Pyrocoelia* larva. This error is evidenced by the fact that Matsumura (1928) illustrated *Pyrocoelia* larvae as those of *Luciola cruciata vitticollis* (= *N. cruciata*, pl. 7 fig. 14) and *L. picticollis* (= *Aq. lateralis*, pl. 7 fig. 16), respectively. McDermott (1966: 108) incorrectly annotated, under a listing of *L. lateralis* for Kishida (1936), that this reference addressed the introduction of *lateralis* into Jehol (it was *cruciata* which was introduced).

Pronotal colour variations (Fig. 6)

Ohba (1988) had described 4 different pronotal colour patterns but did not indicate any geographical distributional bias suggesting intraspecific variation. Variation within populations from the same locality was noted. IK noted a subjective impression that markings tend to become thinner and lighter from SW to NE. He did not find any evidence of the thicker and darker markings in the NE, while these markings were common in the SE. Neither did he observe any individuals in the SE with markings that were either faintly outlined, or completely absent (Nakane 1987), as he had observed in the NE (Fig. 6).

Flash communication

Nipponoluciola cruciata males flash synchronously when flying, and recognise the females by their irregular flashes (Ohba 1979, 1984, 2001, 2004a). There is no female response with fixed delay as in other species.

Ohba (1983, 2004a) classified mating behaviour of the Japanese fireflies into six systems. The LC (complex) system observed in *N. cruciata* is described in several phases: after sunset, the males began to fly and seek females with synchronous or semi-synchronous flashing light; the females emit single-pulsed flashes of light (not synchronised) on grasses; when a male finds the female's flash of light, the male approaches the female; the male emits flashes with various patterns while approaching and walking around the female; thereafter, they copulate.

Synchronous flashing was first described by Watasé (1902), with 26 flashes per minute (2.3 sec cycle) at 60°F (16°C). Kanda (1935) was the first to notice the difference in the flashing intervals and described synchronous flashing as a 3.7 sec cycle at 16°C and 21°C in Kofu, east area of Honshu, and a 1.8 sec cycle at 18°C in Gifu, west area of Honshu.

Ohba (1984) focussed on synchronous flashing in males swarming while seeking females of the LC system and analysed the flash intervals from video-recorded images of five populations (Yokosuka and Yokohama in east Honshu, Tatsuno in central Honshu, and Kyoto and Toyota in west Honshu). He determined the flash interval was about 2 sec and 4 sec in the west and east area of Honshu, respectively, and the two ecological types, 2 sec type (fast flash type) and 4 sec type (slow flash type) were recognised. The border between the two types was noted in the central area of Honshu. Subsequently, Ohba (1988) through the analysis of 30 populations, confirmed that the border of the two types was the central region of Honshu, and it was speculated that the formation of the Fossa Magna, which divides Honshu into eastern and western areas, may be a factor in the generation of the two types.

Since then, many researchers and amateur researchers observed the synchronous flashing. The relationships between temperature and flash interval, and an intermediate-flash type (3 sec type) were reported. However, the state of observations was not constant. In some cases, flash interval was confused with flash duration, and in other cases, flash interval was measured not in swarming but in solo flight.

Ohba (2001) summarised the geographic variation in morphology and flash patterns in 50 populations through almost all distributional areas of Japan and recognised three flash types: 1) flash interval of about 2 sec and flash duration of about 0.6 sec, 2) flash interval of about 3 sec and flash duration of about 1 sec, 3) flash interval of more than 4 sec and flash duration of about 2 sec. However, it has been observed that some populations have extremely short flash intervals, or that even in western Japan, the flash interval was of the 3 sec type, or that the flash intervals differ locally even in the same population. Iguchi (2010) reported three types (the fast-flash, slow-flash, and intermediate types) from five populations in the Kanto and Chubu regions, but whether the intermediate type is the progeny of a cross between the fast- and slow-flash types is not known. Ohba *et al.* (2020) reported a quick-flash type in the Goto Islands that is even faster than the fast-flash type, resulting in four types, slow, intermediate, fast and quick.

Genetic analysis

As the flash intervals of males did not change even when *N. cruciata* from west Japan were transplanted to east Japan and reared in succession, it was speculated that *N. cruciata* had already differentiated genetically. Therefore, populations of *N. cruciata* were investigated at allozyme, mt DNA, and genome DNA level.

On the allozyme level, Suzuki *et al*. (1996a) showed genetic differentiation among east and west Japan based on 17 loci of 13 enzymes in 15 populations. The two genetically differentiated groups corresponded to the synchronous flashing pattern of slow-flash and fast-flash types. The degree of the genetic differentiation was considered as subspecies level based on the comparison of Nei's genetic distances of other species groups. On the mt DNA level, Suzuki *et al.* (2002) analysed the COII gene of 62 populations of 494 individuals covering almost all distributional areas and showed three groups, east Honshu, west Honshu-Shikoku, and Kyushu. The east Honshu and west Honshu-Shikoku groups were the most closely related, followed by the Kyushu group. Flash interval of the east Honshu group and the west Honshu-Shikoku and Kyushu groups were slow-flash and fast-flash types, respectively. Furthermore, the three genetic groups divided into six subgroups and the distributional border of the subgroups corresponded to the geological structure of Japanese islands. They proposed a vicariant speciation scenario in which regional differentiation has occurred along with the formation of the Japanese archipelago. On the genome DNA level, Kato *et al.* (2020) also confirmed the three genetic groups and the vicariant scenario by RAD-Seq analysis, however, relationships among the groups differed from the mitochondrial DNA results in that the west Honshu and Kyushu groups were the most closely related, followed by the east Honshu group. As they could not find any individuals with genome composition between the east Honshu and west Honshu-Kyushu populations, they raised the possibility that mating would not occur between the slow- and fast-flash types.

Flying activity of males

In east Japan, swarming activity decreased after 21:00, but in west Japan, it continued through to midnight, with occasional breaks (Ohba 1988, 2001). The time difference between Aomori (northern part of Honshu) and Kagoshima (southern part of Kyushu) at sunset is about 15 minutes. Furthermore, flying speed of males in east Japan is slower than that in west Japan (Ohba 1988).

Spawning behaviour

In west Japan, females fly in a straight line at high speed over the river surface after swarming, and gather on the moss near water one after another. Then females lay their eggs on the moss, and that continues until dawn. On the other hand, in east Japan, females lay eggs alone on the moss without any flight behaviour to search for egg-laying sites (Kuribayashi 1979; Yuma & Hori 1981; Ohba 1988).

Female recognition by males

In general, flashing is believed to contain information that shows 'species', 'sex' and 'position'. However, Kawano (2013) found flashing contained little information other than 'position' in this species. He suggested that the factors influencing female recognition by males in the mating behaviour are the position (height), flashing and orientation of females in the long distance stage, while factors other than flashing such as an odorous substance operated during the direct contact stage.

Male approach to artificial flash light

The female responds to the synchronous flashing of the males with single-pulsed flashes of light, which the male detects and he then approaches her. Tamura *et al.* (2005) examined whether males approach artificial single-pulsed flashes of light at any flash interval, and found that males from east Japan (Aomori and Sendai populations) approached artificial single-pulsed flashes of light with an flash interval of 4 or 5 sec rather than 2 or 3 sec, and males from west Japan (Otsu population) approached artificial light with

an flash interval of 2 or 3 sec rather than 4 or 5 sec. Males from the central Japan (Inuyama) showed no particular preference for any flash interval (2, 3, 4, or 5 sec intervals). They proposed pre-mating isolation between the two ecological types.

Factors affecting life cycle and development

Light irradiation affects spawning. In the laboratory using reared specimens, yellow light-emitting diode (LED) irradiation at 0.11 lx inhibited spawning as did LED irradiation of other colours (white, blue and green) at 20 lx (Miyashita, 2011).

The sex ratio at emergence in this species is male-biased. Last instar larvae were captured (543 and 952 individuals in 2006 and 2007) in the field and emerged in the laboratory at 82.1 and 56.3% emergence rate in 2006 and 2007. Male emergence rate was significantly higher than female, 60.3 and 64.7% in 2006 and 2007 (Moriya *et al*. 2009).

Egg size is related to hatching rate and larval growth in this species. Egg size (as weight) decreased with aging of a female, and also seasonally through oviposition period. Heavy and light eggs showed high hatching rates at low (ca 20°C) and high temperature (ca 30°C), respectively. If eggs developed at the favourable temperature, they maximised their larval size and the tolerance of the larvae for starvation (Yuma 1984). One third of the larvae hatched from the light eggs produced females (Yuma 1986).

Brightness of the adult habitat at night affects its population density. The borderline for light intensity between the high and low densities (5 individuals per 10 m is boundary) was 0.05–0.2 lx (Yuma 2001). Frequent rainfall during rainy and typhoon seasons caused considerable decreases in emergence of adult fireflies, and a decrease in their foraging activity (Yuma 2007).

Several population characteristics were estimated by Richard and Waloff method. In Kyoto (West Japan), survival rate of adults was 0.76–0.88 per day, mean life span was 47 days, total number emerging 3200–3400 (Yuma & Ono 1985).

Adult males are observed either resting near ground, on trees, or in flight. The proportion of these three behavioural categories was constant through adult life of males, and the season. Seasonal and age-related changes of adult female behaviour were observed. Newly emerged females remained near ground level and copulated there. With increasing age, females changed their resting sites onto broad-leaved trees, and the proportion of females resting on trees increased with the season progression (Yuma & Hori 1990).

Seasonal variation of body size was observed in both sexes. Daily mean body size of male and female decreased from 12.7 to 12.0 mm and 15.1 to 13.5 respectively, as the season progressed (Iguchi 2001).

Fireflies intentionally introduced from the Lake Biwa area (West Japan) into Tatsuno area (Central Japan), exhibited a flash interval distinct from populations native to Tatsuno area, but similar to populations native to Lake Biwa area (Iguchi 2009a, 2009b).

Abundance of both gravel deposit covering the streambed and of freshwater snails significantly affected the firefly population. On the other hand, channel width, flow velocity, dissolved oxygen, and bank height did not always act as environmental factors (Tomita *et al*. 2006).

Colour of light organ emissions

Oba *et al.* (2010) discovered *N. cruciata* could possess two luciferase isotopes and Oba *et al* (2013) found these different isotopes of luciferase were responsible for the yellow luminescence in larval and adult light organs, and the dim greenish glow of eggs and whole pupae respectively, in both *A. lateralis* and *N. cruciata*.

Table 3. Summary of ecological and morphological characters of the slow- and fast-flash types.

Ecological type	**slow-flash type** (4 sec type)	**fast-flash type** (2 sec type)
Distributional area	east Honshu	west Honshu, Shikoku, Kyushu
Synchrony of male swarming	unclear	clear
Flash interval of male	about 4 sec	about 2 sec
Flying activity of male	decreased after 21:00	continued after 21:00
Flying speed of male	slow	fast
Male approach for artificial flash light	4 or 5 sec interval	2 or 3 sec interval
Spawning behaviour	solitary spawning	gregarious spawning
Lateral margins of ML	converging slightly	not coverging, subparallel-sided
Apices of LL	narrowed and apically rounded	broadly rounded
Emargination along anterior margin of BP	pronounced	not pronounced or absent

Occurrence outside Japan?

Specimens of *cruciata* from Osaka were introduced into Chih-feng (now known as Ulandad, Inner Mongolia), and were seen there for 1–2 years after introduction, but not since (Kishida 1936).

Remarks

Nipponoluciola cruciata is distributed throughout mainland Japan with the northern limit of its distribution in Honshu, it never crosses the Braxton line, and is not found in Hokkaido. The southern limit of its distribution is Yakushima Island of Ôsumi Islands, off Kyushu. The genetic differentiation of this species in mainland Japan seems to be influenced by the geological structure, e.g., the Fossa Magna and the Median Tectonic Line. Its habits (e.g., interval period of flashing behaviour and oviposition behaviour) are largely divided between eastern and western Japan, with the boundary near the Fossa Magna. *Nipponoluciola owadai* is distributed as relict populations on Kume-jima Island of the Okinawa Islands in the central part of Ryukyus, located in the southwestern part of Japan.

Since the recognition of two ecological types differing in flash interval, genetic differentiation has been confirmed, but no morphological characters distinguishing the two types have been reported until now, and they are summarised below.

We attempted unsuccessfully to determine if there is correlation between the extent of the pronotal markings and flash patterns as we have been able to show for certain aedeagal patterns (Figs 5, 10–12). Ohba (2001) depicted 50 examples of males and females showing variability in pronotal pattern but could not distinguish any relationship. It is difficult to determine the extent of the anterior broad pronotal marking in his figures, one of which is surely *A. lateralis* (Ohba 2001: fig. 12). In Ohba (2004b) the extent of the median darker marking on the pronotum varied, although females (Ohba 2004b: figs 10, 16, 48) and males (Ohba 2004b: fig. 48) have a narrow median pronotal stripe. Ohba's (2004b) illustrations on page 104 show a gradation depicting a progressive loss of the wide posterior area to pronota having no colour at all, but at no time did he depict the wide anterior marking we show here. Ohba (1988) described four patterns of the pronotum: 1) black cruciate marking thick and clear, 2) cross is thin,

3) cross is traceable, 4) no marking, but there were no corresponding geographic distributional biases suggesting intraspecific variation. Nakane (1987) proposed subspecies *L. cruciata towadensis* based on two female specimens with no pronotal marking collected at Aomori pref. (northern limit of distribution). Later, Ohba (2001) indicated a geographic distributional separation for the marking patterns; the black cruciate marking is thick and clear in Kyushu (southern limit of distribution), gradually becoming thin to Shikoku, Kinki (central distribution), Kanto, and it is traceable and no marking from Kanto to north east Honshu. However, Kawashima *et al.* (2003) synonymised the subspecies as interspecific variation. We could not detect any clear cut geographical distributional biases relating to the different marking patterns as we had for aedeagi.

Nipponoluciola owadai (Satô & Kimura, 1994) gen. et comb. nov.
Figs 1–2, 5, 8–9

Luciola owadai Satô & Kimura, 1994: 159.

Luciola owadai – Ohba *et al*. 1994: 13–26. — Ohba 1996: 17; 2004b: 10; 2005: 240. — Suzuki 1997: 19. — Jeng *et al*. 2003: 543, 550–551, 553–556. — Kawashima *et al*. 2003: 248. — Suzuki *et al*. 2004: 297. — Geisthardt & Satô 2007: 232.

Diagnosis

Distinguished from *Nipponoluciola cruciata* gen. et comb. nov. by the yellowish orange pronotum, (where the underlying fat body is yellowish), MS and MN (the pronotum of *N. cruciata* has underlying pink fat body and a median dark marking in most specimens, and the MS is black) (Figs 1–2).

Material examined

JAPAN – **Kume-jima Is., Okinawa Isls, Middle Ryukyus** • 1 ♀; Mt Uegusuku-dake; 25 Apr. 1993; I. Kawashima leg.; CIK • 4 ♂♂, 1 ♀; Ôta-gawa Riv.; 25 Apr. 1993; I. Kawashima leg.; CIK • 2 larvae; Shirase-gawa Riv.; 27 Dec. 1993; Y. Goto leg.; CIK • 20 ♂♂, 8 ♀♀ (paratypes); same collection data as for preceding; 26 Apr. 1994; Y. Goto leg.; YCM • 7 ♂♂, 1 ♀ (paratypes); Shimajiri; 28 Apr. 1994; Y. Goto leg.; YCM.

Notes

Locality labels on the type specimen were incorrectly quoted in Satô & Kimura (1994) and are repeated here in their correct form (Fig. 2H) as follows (from top to bottom, a slash indicates a line break): Kumejima-Uegusuku-dake, Minami (in Japanese "Kanji" characters) / Japan, Ryukyus / Kumejima Is. / Mt. Uegusuku (south) / 90 m. 27. IV. 1993 / Mamoru Owada leg. (original white label, printed in black ink); HOLOTYPE / *Luciola owadai*/ M. Satô et Kimura, 1994 / DET. M. SATÔ 1994 (red holotype label, printed in black ink).

Description

Male (Figs 1–2)

Body length. 9.5–15.8 mm.

Colour (Figs 1–2). All of body including head, mouthparts and antennae, ventral thorax, legs and abdomen, black, except for yellowish orange pronotum (with underlying yellowish fat body), having no median darker markings, yellowish MN and MS, and white LO in V6, 7. Pronotal width/GHW 1.39–1.46. GHW/SIW: 4–4.8.

Abdomen. As depicted in Jeng *et al.* (2003: fig. 8), with a short broad apically rounded MPP.

Aedeagal sheath (Fig. 5). Sheath sternite widely emarginated on right side, and scarcely so on left (see also Jeng *et al.* 2003: fig. 28).

Aedeagus (Fig. 5). BP well sclerotised; median anterior margin of BP with deep and well-defined notch (see also Jeng *et al.* 2003: fig. 34); lateral margins of ML subparallel-sided in basal $^{7}/_{10}$, gradually narrowing in apical $^{3}/_{10}$. LL/ML 2.81; LL apex width considerably wider than width of apex of ML; dorsal base of LL symmetrical; apex of ML depressed on both sides; the outline of apex rounded when viewed from either side.

Aedeagal patterns. Since the distribution of this species is limited to the small island Kume-jima Is., there is little individual variation in the shape of the aedeagus.

Female (Fig. 7B)

Macropterous and flight capable.

Body length. 13.1–15.7 mm.

Colour (Fig. 7B). Colouration as in male except for whitish LO in V6 (Satô & Kimura 1994 describe this as the 5th abdominal segment) occupying all but a narrow transparent posterior margin; V7 mostly black, not transparent as that of female of *N. cruciata*, and no underlying fat bodies visible; basal portion of V7 may have irregular and indistinct pale patches where the blackish pigmentation appears to be lost; V8 black; dorsal surface of all tergites (up to T8) and dorsally reflexed margins of ventrites (to V5, and V7, V8) dark brown to black; T6 black with outer margins of dorsally reflexed parts of V6 white and semitransparent.

Pronotum. Pronotal width/GHW 1.74–1.86.

Head. GHW/SIW 2.78–2.90.

Abdomen. Posterior margin of V7 shallowly and narrowly emarginated as in Jeng *et al*. (2003: fig. 16). Lateral margins of V8 converge posteriorly; with the median posterior margin very shallowly and narrowly emarginated. Jeng *et al.* (2003: fig. 16) depict the posterior margin of V7 with a shallow and narrow emargination.

Reproductive system. Well defined thin walled SDG; MOP trapezoidal, filling half of the median oviduct, with the anterior margin almost straight; lateral margins straight and convergent toward the posterior margin; posterior margin nearly straight but slightly irregular. Ovipositor elongate slender.

Larva (Figs 8B, 9E–H)

Approx. body length 13 mm (specimens measured were severely shrunken due to ethanol fixation); maximum (median) length of protergum 2.7 mm; maximum width of protergum 2.3 mm. Penultimate instar larvae were examined. The larvae of this species closely resemble those of *N. cruciata*, and are not clearly distinguishable from each other in general appearance and morphological characteristics. However, the ground colour of the membranous body of *N. owadai* is much paler (Ohba *et al.* 1994), light to greyish brown, while that of *N. cruciata* is dark to blackish brown, and it differs from *N. cruciata* in the tendency of the pale markings on the lateral margins of pronotum to separate anteriorly and posteriorly into four independent spots. Ohba *et al*. (1994) recorded 12 abdominal pygopodia in what was possibly the last instar larva. Jeng *et al*. (2003) considered the basal row of pygopods was composed of four retractable filaments.

Flash communication

The flash pattern of both sexes of this species is very similar to that of *N. cruciata*, and the communication system is the same as that of *N. cruciata*. Synchronous flashing of the males is similar to that of east Japan populations of *N. cruciata*, but the flash interval gets shorter over time, from 4 sec to 3 and 2 sec. However, unlike the west Japan populations of *N. cruciata*, the synchronous flashing does not last for a long time but continues intermittently through the night. Thus, it has characteristics of both east and west Japan *N. cruciata*.

Spawning behaviour

Females gather and lay eggs on the moss near water as in the western Japanese form of *N. cruciata*. However, they gather all at once just before dawn, not one after another in the night.

Remarks

This species is designated both a natural monument of Okinawa Prefecture and an endangered species of wild fauna and flora under the Law for the Protection of Cultural Properties and the Act on Conservation of Endangered Species of Wild Fauna and Flora, respectively. It is now difficult if not impossible to obtain specimens of this endangered species in the locality, Kume-jima Is. The few specimens examined by IK are listed above. All other remarks about this species are referenced. Ohba *et al.* (1994) addressed life history, behaviour and morphology. Ohba (2004b) depicted various aspects of morphology of this species including flashing patterns (page 7), dorsal aspect of female (page 11) and male (pages 38, 45), SEMs of anterior head (page 62) and a species overview (in Japanese, page 109). Jeng *et al.* (2003) keyed aquatic Taiwanese and Japanese Luciolinae males.

Systematics of Luciola Laporte, 1833 – quo vadis?

Luciola s. str.

Ballantyne and colleagues identified very early on that the grouping of 276 species under *Luciola* in McDermott (1966) was at best arbitrary, and morphological phylogenetic analyses (see Ballantyne *et al.* 2019 for a review) identified within McDermott's *Luciola* many new genera, many including species which were transferred from what McDermott had placed under *Luciola*. It became clear that '*Luciola*' was a heterogeneous assemblage of species and that it was necessary to be able to define what constituted *Luciola* s. str.

This was achieved by comparison of morphological features of the type species *Luciola italica* with the other species. Fu *et al.* (2010) first identified two species, *Luciola italica* and the Japanese species *Luciola parvula* Kiesenwetter, 1874 as *Luciola* s. str., and Fu *et al.* (2012a) an additional species but without further definition. Ballantyne *et al.* (2013) first formally addressed and redescribed *Luciola* s. str. Subsequently Ballantyne *et al.* (2015: fig. 1; 2016: figs 1–2; 2019: fig. s1), and Jusoh *et al.* (2021: 1) further refined the concept and composition of *Luciola* s. str.

Our exhaustive literature reviews and taxonomic revisions reveal two possible options to resolve *Luciola* taxonomy insofar as it relates to a definition of *Luciola* s. str. Such a definition is essential to our argument (and the status of *Hotaria*) as well as the resolution of a position for *Luciola cruciata* and *L. owadai*. Here we follow Jusoh *et al.* (2021: 8, fig. 3).

The options are:

1. Subsume all three current members of *Luciola* subgenus *Hotaria* Yuasa, 1937 (*unmunsana*, *papariensis* and *tsushimana*) into one genus, i.e., *Luciola* s. str. (Jusoh *et al.* 2021: fig. 3 Clade G), and retain the remaining five species in *Luciola* s. str. *Luciola* s. str. thus comprises the 7 species from

Jusoh *et al.* (2021: fig. 3) including the type species *L. italica*, and is clearly distinct from the clade E which includes *L. cruciata*/*owadai* and species of *Aquatica*.

2. Subsume all current members of *Luciola* subgenus *Hotaria* into one genus, i.e., *Luciola* s. str. (Jusoh *et al.* 2021: Clade G) which subsequently restricts *Luciola* s. str. to four species within the same clade as *Luciola italica* (Clade G Part II), and erect a new genus to accommodate *Luciola pallidipes* + *niah* Jusoh, 2019 (Clade G Part I)

Option 2 while extreme, may indicate a future path, but is untenable at present without evidence to support the split between *niah/pallidipes* and *Luciola* s. str., the extensive and presently uninvestigated '*Luciola*' of Africa (about 100 species are assigned to *Luciola* in McDermott 1966), and species of '*Luciola*' in Europe such as *L. lusitanica* Charpentier, 1825, *L. italica*, and *L. mingrelica* Motschulsky, 1854. There is no present agreement on just which populations comprise the aforementioned three species.

Option 1 permits a wider definition of *Luciola* s. str., where all the species in Jusoh's Clade G are assigned, and is supported by morphological considerations (including males females and larvae). This definition of *Luciola* s. str. will accommodate possible future directions as well as existing problems, while still defining a narrow group of species forming a clade with the type species.

Neither of these options address specifically what course of action should be taken with three of the four species of '*Hotaria*' which the analysis indicates may well be the same species, distinct from *L. parvula*. However, as each option recommends that *Hotaria* be subsumed under *Luciola* s. str. (as already undertaken by Kawashima *et al*. 2003) we advise this recommendation (Supp. file 1: 3).

All comments above relating to suggested placements of species still listed as *Luciola* sp. relate specifically to the wide, and defined study area of Ballantyne *et al.* (2019: 5) in SE Asia and the Australopacific area.

The remaining *Luciola*

The situation with regard to the remaining species still standing under *Luciola* by McDermott (1966) can also be addressed. Ballantyne *et al.* (2019) addressed *Luciola* s. str. from 17 species, including the type species *L. italica*. However, they did not regard their treatment of all the species listed by McDermott (1966) under *Luciola* as finished. Clearly they did not attempt to address the *Luciola* of Africa (ca 100 species), nor the *Luciola* of Europe. Their specified area of coverage extended from India in the west through Asia (excluding Russia), the Philippines to the Australopacific region (see listing in Ballantyne *et al.* 2019: 5), where in the Australopacific region the firefly fauna is exclusively Luciolinae.

In attempting to address the range of species, Ballantyne *et al.* (2019) were confronted with many of the problems we have outlined here. Two solutions were proposed specifically for the remaining species still standing under *Luciola*, occurring in the study area as defined above:

1. Species incertae sedis. Thirty-five species of '*Luciola*' were assigned to species incertae sedis (Ballantyne *et al.* 2019: 151, table 28). While each species was individually addressed, each had certain attributes which the authors felt would preclude any further attempt to conclusively identify them. These included absence of types, poor condition of types (if represented at all what body parts that remained were not useful in diagnosis), and types that were females. This sex is presently of little use in what is still a male based Luciolinae taxonomy.

2. *Luciola* s. lat. The second solution addressed the remaining species from the defined study area still assigned to *Luciola* in McDermott (1966). Although a 'heterogeneous assemblage of species' (Ballantyne *et al.* 2019: 102), they were considered sufficiently distinctive (usually in colour, and in

many cases because of the existence of a type specimen in some sort of condition that might permit re-examination), that the very real possibility existed for future assignment of males and elucidation of generic affinities. All are in MNHN. Of the thirty-three species listed in Ballantyne *et al.* (2019: 103–104, table 18) seven have female types but distinctive colouration, 18 have male types in various condition, and types were not found for 11.

It was anticipated that a visit to the MNHN in Paris and work on the collection would eventuate, as this museum will no longer loan types. However Covid intruded, as did the very real financial situation the retired senior author finds herself in, that further precludes any possibilities of additional investigation in the immediate future.

Discussion

We have achieved our stated aims:

1. A new genus *Nipponoluciola* is described for two species which are transferred from *Luciola*. *Nipponoluciola cruciata* gen. et comb. nov. is the new generic name for the Genji-botaru. *Nipponoluciola owadai* gen. et comb. nov. is the new generic name for the Kumejima-botaru.

2. A neotype is designated for *Luciola cruciata*.

3. We address and define *Luciola* s. str., and include a list of species.

4. Additionally, we address the remaining species still listed under *Luciola* in McDermott (1966) which occur in a defined study area, and confirm the suggestions for placements for many of them in Ballantyne *et al.* (2019).

However, we encountered many problems along the way. It appeared that the only justifiable way to interpret the information in front of us was to rely on what could be substantiated, and to ignore suppositions and suggestions that could not. In so doing there has been no recourse to any type material so we are unable to confirm many of the identifications in the old literature.

Taxonomy is governed by a strict set of rules. These rules should apply equally to those doing morphological taxonomy as well as to molecular biologists. For insects these are encompassed in the International Code of Zoological Nomenclature (ICZN).

There are many situations taxonomists find themselves in where the ICZN rules may not be of much help. Here we faced the possibility of misidentifications among specimens examined, loss of holotypes (all too common an occurrence among soft bodied fireflies), and mislabelling. We dealt with original descriptions which are often hopelessly inadequate, and which may consist of a single line. Translation from the original French or Latin is now made much easier with translation services on the Web, but sometimes the precise meaning of the words is clouded by the passage of years.

We were unable to find type material of *Luciola cruciata* and have only located three syntypes of *Luciola picticollis*.

More often than not the 19th and early 20th century taxonomists generously distributed specimens (and thus potential syntypes) all over Europe. Museums and curators nowadays cannot always be sure of the 'provenance' of their specimens, and may attribute holotype status to single specimens when they are not. In fact, trying to determine if a specimen is indeed a unique holotype is often in itself an exercise in futility. The holotype itself may be so old and discoloured that it conveys little, and if the museum

regulations do not permit dissection, (understandable with fragile types), then we have to find other ways to identify our specimens.

Larval morphology requires a consistent approach especially as preliminary indications are that all Lampyridae larvae conform to a certain pattern especially with regard to their ventral surfaces (Riley *et al.* 2021). Here our descriptions attempt to address this situation.

Taxonomic endeavours require the support of museum staff, but this aspect is now poorly funded worldwide. Some museums can provide lists of types and even pictures. Others not so well endowed may require a visit. For antipodeans, visits to European museums where most of the Lampyridae types are housed, (a consequence of the early European influence in these countries), are exorbitantly expensive. Now Covid just increases the difficulty. Restrictive loaning practices, although sometimes understandable, may further inhibit investigation.

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References

Ballantyne L.A. & Lambkin C.L. 2009. Systematics of Indo-Pacific fireflies with a redefinition of Australasian *Atyphella* Olliff, Madagascan *Photuroluciola* Pic, and description of seven new genera from the Luciolinae (Coleoptera: Lampyridae). *Zootaxa* 1997 (1): 1–188.
https://doi.org/10.11646/zootaxa.1997.1.1

Ballantyne L.A. & Lambkin C.L. 2013. Systematics and phylogenetics of Indo-Pacific Luciolinae fireflies (Coleoptera: Lampyridae) and the description of new genera. *Zootaxa* 3653 (1): 1–162.
https://doi.org/10.11646/zootaxa.3653.1.1

Ballantyne L.A. & McLean M.R. 1970. Revisional studies of the firefly genus *Pteroptyx* (Coleoptera: Lampyridae: Luciolinae: Luciolini). *Transactions of the American Entomological Society* 96 (2): 223–305.

Ballantyne L.A. & Menayah R. 2002. A description of larvae and redescription of adults of the firefly *Pteroptyx valida* Olivier in Selangor, Malaysia (Coleoptera: Lampyridae: Luciolinae), with notes on Luciolinae larvae. *Raffles Bulletin of Zoology* 50 (1): 101–109.

Ballantyne L.A., Fu X.H., Shih C.H., Cheng C.Y. & Yiu V. 2011. *Pteroptyx maipo* Ballantyne, a new species of bent-winged firefly (Coleoptera: Lampyridae) from Hong Kong, and its relevance to firefly biology and conservation. *Zootaxa* 2931 (1): 8–34. https://doi.org/10.11646/zootaxa.2931.1.2

Ballantyne L.A., Fu X-H., Lambkin C., Jeng M-L., Faust L., Wijekoon W.M.C.D., Li D-Q. & Zhu T.F. 2013. Studies on South-east Asian fireflies: *Abscondita*, a new genus with details of life history, flashing patterns and behaviour of *Abs. chinensis* (L.) and *Abs. terminalis* (Olivier) (Coleoptera: Lampyridae: Luciolinae). *Zootaxa* 3721 (1): 1–48. https://doi.org/10.11646/zootaxa.3721.1.1

Ballantyne L.A., Lambkin C.L., Boontop Y. & Jusoh W.F.A. 2015. Revisional studies on the Luciolinae fireflies of Asia (Coleoptera: Lampyridae): 1. The genus *Pyrophane*s Olivier with two new species. 2. Four new species of *Pteroptyx* Olivier and 3. A new genus *Inflata* Boontop, with redescription of *Luciola indica* (Motsch.) as *Inflata indica* comb. nov. *Zootaxa* 3959 (1): 1–84. https://doi.org/10.11646/zootaxa.3959.1.1

Ballantyne L.A., Lambkin C.L., Luan X., Boontop Y., Nak-Eiam S., Pimpasalee S., Silalom S. & Thancharoen A. 2016. Further studies on south eastern Asian Luciolinae: 1. *Sclerotia* Ballantyne, a new genus of fireflies with back swimming larvae 2. *Triangulara* Pimpasalee, a new genus from Thailand (Coleoptera: Lampyridae). *Zootaxa* 4170 (2): 201–249. https://doi.org/10.11646/zootaxa.4170.2.1

Ballantyne L.A., Lambkin C.L., Ho J-Z., Jusoh W.F.A., Nada B., Nak-eiam S., Thancharoen A., Wattanachaiyingcharoen W. & Yiu V. 2019. Luciolinae of S. E. Asia and the Australopacific region: a revisionary checklist (Coleoptera: Lampyridae) including description of three new genera and 13 new species. *Zootaxa* 4687 (1): 1–174. https://doi.org/10.11646/zootaxa.4687.1.1

Bertrand H.P.I. 1972. Lampyridae. *In*: Bertrand H.P.I. (ed.) *Larves et Nymphes des Coléoptères aquatiques du Globe: avec Tableaux de Détermination des Genres*: 598–603. Impr. F. Paillart, Abbeville.

Bertrand H.P.I. 1973. Part XI: larvae and pupae of water beetles collected from the island of Ceylon. *Bulletin of the Fisheries Research Station*, *Sri Lanka (Ceylon)* 24 (1 & 2): 95–112.

Blair K.G. 1927. An aquatic Lampyrid larva from S. Celebes. *Transactions of the Entomological Society of London* 75 (1): 43–45. https://doi.org/10.1111/j.1365-2311.1927.tb00056.x

Branham M.A. & Wenzel J.W. 2003. The origin of photic behavior and the evolution of sexual communication in fireflies (Coleoptera: Lampyridae). *Cladistics* 19 (1): 1–22. https://doi.org/10.1111/j.1096-0031.2003.tb00404.x

Choi Y.S., Bae J.S., Lee K.S., Kim S.R., Kim I., Kim J.G., Kim K.Y., Kim S.E., Suzuki H., Lee S.M., Sohn H.D. & Jin B.R. 2003. Genomic structure of the luciferase gene and phylogenetic analysis in the *Hotaria*-group fireflies. *Comparative Biochemistry and Physiology B Biochemistry & Molecular Biology* 134B (2): 199–214. https://doi.org/10.1016/s1096-4959(02)00249-x

Fu X.H. & Ballantyne L.A. 2009. Larval respiration system and evolution in aquatic fireflies (Coleoptera: Lampyridae: Luciolinae). *In*: Meyer-Rochow V.B. (ed.) *Bioluminescence in Focus – A Collection of Illuminating Essays*: 243–253. Research Signpost, Kerala.

Fu X.H., Meyer-Rochow V.B., Tyler J., Suzuki H. & De Cock R. 2009. Structure and function of the eversible organs of several genera of larval firefly (Coleoptera: Lampyridae). *Chemoecology* 19: 155–168. https://doi.org/10.1007/s00049-009-0016-8

Fu X.H., Ballantyne L.A. & Lambkin C.L. 2010. *Aquatica* gen. nov. from mainland China with a description of *Aquatica wuhana* sp. nov. (Coleoptera: Lampyridae: Luciolinae). *Zootaxa* 2530 (1): 1–18. https://doi.org/10.11646/zootaxa.2530.1.1

Fu X.H., Ballantyne L.A. & Lambkin C.L. 2012a. *Emeia* gen. nov., a new genus of Luciolinae fireflies from China (Coleoptera: Lampyridae) with an unusual trilobite-like larva, and a redescription of the genus *Curtos* Motschulsky. *Zootaxa* 3403 (1): 1–53. https://doi.org/10.11646/zootaxa.3403.1.1

Fu X.H., Ballantyne L.A. & Lambkin C.L. 2012b. The external larval morphology of aquatic and terrestrial Luciolinae fireflies (Coleoptera: Lampyridae). *Zootaxa* 3405 (1): 1–34. https://doi.org/10.11646/zootaxa.3405.1.1

Geisthardt M. & Satô M. 2007. Lampyridae. *In*: Löbl I. & Smetana A. (eds) *Catalogue of Palaearctic Coleoptera, Vol. 4*: 225–234. Apollo Books, Stenstrup, Denmark.

Gorham H.S. 1880. VIII. Materials for a revision of the Lampyridae. *The Transactions of the Entomological Society of London* 1880: 83–112. https://doi.org/10.1111/j.1365-2311.1880.tb02023.x

Gorham H.S. 1883. Revision of the genera and species of Malacoderm Coleoptera of the Japanese fauna. *The Transactions of the Entomological Society of London* 1883: 393–411. https://doi.org/10.1111/j.1365-2311.1883.tb02955.x

Han T., Kim S-H., Yoon H.J., Park I.G. & Park H. 2019. Evolutionary history of species of the firefly subgenus *Hotaria* (Coleoptera, Lampyridae, Luciolinae, *Luciola*) inferred from DNA barcoding data. *Contributions to Zoology* 2019: 1–19. https://doi.org/10.1163/18759866-20191420

Hara S. 1962. Larvae of *Luciola cruciata* and *L. lateralis* (Coleoptera). *Kontyû* 30 (4): 230–235. [In Japanese with English title.]

Harold E. 1877. Beiträge zur Käferfauna von Japan (Zweites Stuck). *Deutsche Entomologische Zeitschrift* 21: 337–367. https://doi.org/10.1002/mmnd.4800210220

Hasama B. 1942a. Über die Biolumineszenz der *Luciola lateralis* im zytologischen Bild sowie im Potentialbild ihres Leuchtorgans. *Cytologia* 12: 366–377. https://doi.org/10.1508/cytologia.12.366

Hasama B. 1942b. Über die Biolumineszenz der Larve von *Luciola cruciata* sowie von *Pyrocoelia rufa* im Aktionsstrombild und im histologischen Bild ihres Leuchtorgans. *Cytologia* 12: 378–388. https://doi.org/10.1508/cytologia.12.378

Hasama B. 1943. Lebensgeschichte der *Luciola cruciata* und der *Luciola lateralis*. *Annotationes Zoologicae Japonenses* 22 (1): 23–47.

Hasama B. 1944. Entwicklung des imaginalen Leuchtorgans der *Luciola cruciata* in histologischer sowie bioelektrischer Hinsicht. *Cytologia* 13 (2): 155–161. https://doi.org/10.1508/cytologia.13.155

Heyden L. v. 1879. Die coleopterologishce Ausbeute des Prof. Dr. Rein in Japan 1874–1875. *Deutsche entomologische Zeitschrift* 23: 321–365. https://doi.org/10.1002/mmnd.48018790221

Holthuis L.B. 1993. The three Dutch authors of Von Siebold's Fauna Japonica, with some notes on the artists. *In*: Yamaguchi T. (ed.) *Ph. F. von Siebold and Natural History of Japan: Crustacea*: 689–708. The Carcinological Society of Japan, Tokyo.

Hu J. & Fu X. 2018. The complete mitochondrial genome of the firefly, *Abscondita anceyi* (Olivier) (Coleoptera: Lampyridae). *Mitochondrial DNA B Resources* 3 (1): 442–443. https://doi.org/10.1080/23802359.2018.1456373

ICZN (International Commission on Zoological Nomenclature) 1999. *International Code of Zoological Nomenclature. Fourth edition*. International Trust for Zoological Nomenclature, London. Available from https://www.iczn.org/the-code/the-code-online/ [accessed 15 Nov. 2022].

Iguchi Y. 2001. Seasonal variation in the adult body size of the Genji-firefly *Luciola cruciata* (Coleoptera: Lampyridae). *Entomological Review of Japan* 56 (1): 35–38.

Iguchi Y. 2009a. The ecological impact of an introduced population on a native population in the firefly *Luciola cruciata* (Coleoptera: Lampyridae). *Biodiversity and Conservation* 18: 2119–2126. https://doi.org/10.1007/s10531-009-9576-8

Iguchi Y. 2009b. Genji firefly import problem. *Journal of the National Firefly Research Association* 42: 35–38. [In Japanese.]

Iguchi Y. 2010. Temperature-dependent geographic variation in the flashes of the firefly *Luciola cruciata* (Coleoptera: Lampyridae). *Journal of Natural History* 44 (13–14): 861–867. https://doi.org/10.1080/00222930903528206

Jeng M.-L., Lai J. & Yang P.-S. 2003. Lampyridae: a synopsis of aquatic fireflies with description of a new species. *In*: Jäch M.A. & Ji L. (eds) *Water Beetles of China* Vol. 3: 539–562. Zoologisch-Botanische Gesellschaft in Österreich und Wiener Coleopterologenverein, Vienna, Austria.

Jusoh W.F.A., Ballantyne L.A., Lambkin C.L., Hashim N.R. & Wahlberg N. 2018. The firefly genus *Pteroptyx* Olivier revisited (Coleoptera: Lampyridae: Luciolinae). *Zootaxa* 4456 (1): 1–71. https://doi.org/10.11646/zootaxa.4456.1.1

Jusoh W.F.A., Ballantyne L., Chan S.H., Wong T.W., Yeo D. & Nada B. 2021. Molecular systematics of the firefly genus *Luciola* (Coleoptera: Lampyridae: Luciolinae) with the description of a new species from Singapore. *Animals* 2021 11: 687. https://doi.org/10.3390/ani11030687

Kanda S. 1933. Hotaru no kenkyu (1) Genji-botaru no seikatushi (Study of firefly (1) Life history of Genji firefly). *Kontyû, Tokyo* 7 (5–6): 219–239. [In Japanese.]

Kanda S. 1935. *Hotaru* (The Fireflies). Association of Luminous Organisms of Japan, Tokyo, Japan. [In Japanese.]

Kato D., Suzuki H., Tsuruta A., Maeda J., Hayashi Y., Arima K., Ito Y. & Nagano Y. 2020. Evaluation of the population structure and phylogeography of the Japanese Genji firefly, *Luciola cruciata*, at the nuclear DNA level using RAD-Seq analysis. *Scientific Reports* 2020 (10): 1533. https://doi.org/10.1038/s41598-020-58324-9

Kawano K. 2013. *Studies on Mating Behavior of Luciola cruciata Motschulsky (Coleoptera: Lampyridae)*. Personal Publication Yamaguchi. [In Japanese with English abstract.]

Kawashima I. 2018. External characters of the naturalized species, *Pyropyga alticola* Green, 1961 (Coleoptera: Lampyridae: Lampyrinae: Photinini) settled in the Kantô plain, central Honshû, Japan. *Japanese Journal of Systematic Entomology* 24 (1): 67–72.

Kawashima I. 2019. Larval morphology of *Luciola parvula* Kiesenwetter (Coleoptera, Lampyridae, Luciolinae) from Kyushu, Japan. *Japanese Journal of Systematic Entomology* 25 (2): 237–244.

Kawashima I. 2021. A new species of the genus *Lucidina* Gorham (Coleoptera, Lampyridae, Lampyrinae) from Yaku-shima Is., Ôsumi Isls., Japan. *Japanese Journal of Systematic Entomology* 27 (1): 131–137.

Kawashima I., Suzuki H. & Satô M. 2003. A check-list of Japanese fireflies (Coleoptera, Lampyridae and Rhagophthalmidae). *Japanese Journal of Systematic Entomology* 9 (2): 241–261.

Kawashima I., Satou F. & Satô M. 2005. The lampyrid Genus *Drilaster* (Coleoptera, Lampyridae, Ototretinae) from the Ryukyu Archipelago, southwest Japan. *Japanese Journal of Systematic Entomology* 11 (2): 225–262.

Kazantsev S.V. & Nikitsky N.B. 2008. Types of fireflies (Coleoptera, Lampyridae) in the Motschulsky collection at the Zoological Museum of Moscow Lomonosov University. *Bulletin de la Société des Naturalistes de Moscou* 113 (5): 23–30.

Kiesenwetter E.A.H. v. 1874. Die Malacodermen Japans nach dem Ergebnisse der Sammlungen des Herrn G. Lewis während der Jahre 1869–1871. *Berliner entomologische Zeitschrift* 18: 241–288.

Kim J.G., Choi Y.S., Kim K.Y., Bae J.S., Kim I., Sohn H.D. & Jin B.R. 2004. Genomic structure and phylogenetic analysis of the luciferase gene of the firefly, *Luciola lateralis* (Coleoptera: Lampyridae). *European Journal of Entomology* 101 (1): 1–11.

Kishida K. 1936. Family Cantharidae, Insects of Jehol (VI) – Order Coleoptera (I). *Report of the First Scientific Expedition Manchoukuo* V (X) Art. No. 46: 1–21, pls 1–11. [In Japanese and English.]

Kuribayashi S. 1979. *Genji-botaru (Luciola cruciata)*. Nature Books, Tokyo. [In Japanese with English explanation.]

Lacordaire J.T. 1857. Tribu II. Lampyrides. *In*: Lacordaire J.T. (ed.) *Histoire Naturelle des Insectes. Genera des Coléoptères ou Exposé Méthodique et Critique de tous les Genres Proposés jusqu'ici dans cet Ordre d'Insectes. Volume 4*: 304–341. Librairie encyclopédique de Roret, Paris. https://doi.org/10.5962/bhl.title.8864

Lawrence J.F. & Ślipiński A. (2013) *Australian Beetles. Volume I: Morphology, Classification and Keys.* CSIRO Publishing Collingwood Victoria. https://doi.org/10.1071/9780643097292

Lewis G. 1879. *A Catalogue of Coleoptera from the Japanese Archipelago*. Taylor and Francis, London, UK.

Maeda J., Kato D., Arima K., Ito Y., Toyoda A. & Noguchi H. 2017. The complete mitogenome and phylogenetic analysis of Japanese firefly 'Genji Botaru' *Luciola cruciata* (Coleoptera: Lampyridae). *Mitochondrial DNA Part B* 2 (2): 522–523. https://doi.org/10.1080/23802359.2017.1365641

Matsumura S. 1918. *Nihon no Hotaru* (The fireflies of Japan). *Kyôiku-Gahô* 6 (3): 82–89. [In Japanese.]

Matsumura S. 1928. II. Hotaru (Chapter II The fireflies). *In*: Matsumura S. (ed.) *Omoshiroki Chûkai no Kyôzai* (Interesting Insects for Educational Materials). Tokyo-dô Publishing Company, Tokyo. [In Japanese.]

McDermott F.A. 1962. Illustrations of the aedeagi of the Lampyridae (Coleoptera). *The Coleopterists Bulletin* 16 (1): 21–27.

McDermott F.A. 1966. Lampyridae. *In*: Steel W.O. (ed.) *Coleopterorum Catalogus Supplementa*, Pars 9: 1–149. Uitgeverij Dr. W. Junk, The Hague.

Minami K. 1961. *Hotaru no Kenkyu* (A study of fireflies). Ohta-shoten, Hikone. [In Japanese.]

Miyashita M. 2011. Effects of LED lighting on the oviposition of firefly, *Luciola cruciata* and *Luciola lateralis*. *Journal of Japan Society of Civil Engineers Ser G (Environmental Research)* 67 (1): 21–29. [In Japanese with English abstract.] https://doi.org/10.2208/jscejer.67.21

Moriya S., Yamanichi T. & Nagaghoshi N. 2009. Sex ratios in the Japanese firefly, *Luciola cruciata* (Coleoptera: Lampyridae) at emergence. *Japanese Journal of Limnology* 69 (3): 255–258. https://doi.org/10.3739/rikusui.69.255

Motschulsky V. 1854. Lampyrides. *Études Entomologiques* 3: 47–62.
Available from https://www.biodiversitylibrary.org/page/51901305 [accessed 16 Nov. 2022].

Motschulsky V. 1866. Catalogue des insectes reçus du Japon. *Bulletin de la Société impériale des naturalistes de Moscou* 39 (1): 163–200.
Available from https://www.biodiversitylibrary.org/page/44324258 [accessed 16 Nov. 2022].

Nada B., Ballantyne L.A. & Jusoh W.F.A. 2021. Description of the larva of a firefly species, *Pygoluciola dunguna* Nada (Coleoptera: Lampyridae). *Zootaxa* 4920 (1): 528–542.
https://doi.org/10.11646/zootaxa.4920.4.4

Nakane T. 1960. Lampyridae. *In*: Nakane T. & The Japan Coleopterological Society (eds) *Coloured Illustrations of the Insects of Japan*. *Coleoptera*: 118−119, pl. 36. Kinki Coleopterological Society, Hoikusha Publishing, Tokyo. [In Japanese.]

Nakane T. 1968. Hotaru no bunrui (Classification of lampyrid beetles). *The Nature and Insects* 3 (6): 3–6. [In Japanese.]

Nakane T. 1970. On the cantharoid Coleoptera found in the islands of Tsushima (Insecta). *Memoirs of the National Science Museum, Tokyo* 3: 287–288. [In Japanese with English summary.]

Nakane T. 1983. *In*: *Hotaru no Kansatsu to Shiiku* (Observation and Breeding of Fireflies): 81–113. New Science Co.

Nakane T. 1987. Notes on some little-known beetles (Coleoptera) in Japan. *Kita-Kyûshû no Konchû*, *Fukuoka* 34 (3): 171–176. [In Japanese with English title and descriptions.]

Nakane T., Ohbayashi K., Nomura S. & Kurosawa Y. 1959. *Iconographia Insectorum Japonicorum Colore Naturali Edita. Vol. II (Coleoptera). Lampyridae*: 169–170, pl. 85. Hokuryu-kan Publishing Co., Tokyo. [In Japanese with Latin title.]

Oba Y., Mori N., Yoshida M. & Inouye S. 2010. Identification and characterisation of a Luciferase isotope in the Japanese firefly, *Luciola cruciata*, involving in the dim glow of firefly eggs. *Biochemistry* 49: 10788–10795. https://doi.org/10.1021/bi1016342

Oba Y., Branham M.A. & Fukatsu T. 2011. The terrestrial bioluminescent animals of Japan. *Zoological Science* 28 (11): 771–789. https://doi.org/10.2108/zsj.28.771

Oba Y., Furuhashi M., Bessho M., Sagawa S., Ikeya H. & Inouye S. 2013. Bioluminescence of firefly pupa: involvement of a luciferase isotope in the dim glow of pupae and eggs in the Japanese firefly, *Luciola lateralis*. *Photochemical and Photobiological Sciences* 12: 854–863.
https://doi.org/10.1039/c3pp25363e

Ohba N. 1978. Morphology and behavior of the Lampyridae (Coleoptera, Insecta). *Science Report of the Yokosuka City Museum* 25: 15–28, pls 2–3. [In Japanese with English abstract.]

Ohba N. 1983. Studies on the communication system of Japanese fireflies. *Science Report of the Yokosuka City Museum* 30: 1–62, pls 1–6.

Ohba N. 1984. Synchronous flashing in the Japanese firefly, *Luciola cruciata* (Coleoptera: Lampyridae). *Science Report of the Yokosuka City Museum* 32: 23–32, pl. 8.

Ohba N. 1988. *Genjibotaru* (Genji firefly). Bun-ichi Publishing Co. Ltd., Tokyo. [In Japanese.]

Ohba N. 1996. Ecological study of the firefly, *Luciola owadai* and conservation of its habitat. *The Nature and Insects* 31 (6): 17–21. [In Japanese.]

Ohba N. 2001. Geographical variation, morphology and flash pattern of the firefly, *Luciola cruciata* (Coleoptera: Lampyridae). *Science Report of the Yokosuka City Museum* 48: 45–89. [In Japanese with English abstract.]

Ohba N. 2004a. Flash communication systems of Japanese fireflies. *Integrative Comparative Biology* 44: 225–233. https://doi.org/10.1093/icb/44.3.225

Ohba N. (ed.) 2004b. *Hotaru Tenmetsu no Fushigi, Chikyû no Kiseki (Mystery of Fireflies)*. Yokosuka City Museum, Yokosuka. [In Japanese with English title.]

Ohba N. 2005. Lampyridae, Rhagophthalmidae. *In*: Ishiwata S. *et al.* (eds) *Insect Larvae of Japan*: 237–243. Gakken, Tokyo. [In Japanese.]

Ohba N. 2012. The restoration and maintenance of firefly habitats in Japan – case studies from Yokosuka City. *Lampyrid* 2: 13–23.

Ohba N., Azuma S., Nishiyama K., Goto Y., Suzuki H., Sato Y. & Kawashima I. 1994. Morphology, life history and behaviour of the firefly *Luciola owadai* (Coleoptera: Lampyridae). *Science Report of the Yokosuka City Museum* 42: 13–26. [In Japanese with English abstract.]

Ohba S-y., Numata K. & Kawano K. 2020. Variation in flash speed of Japanese firefly, *Luciola cruciata* (Coleoptera: Lampyridae), identifies distinct southern "quick-flash" population on Goto Islands, Japan. *Entomological Science* 23 (2): 117–230. https://doi.org/10.1111/ens.12403

Okada Y.K. 1928. Two Japanese aquatic glowworms. *Transactions of the Royal Entomological Society of London* 76 (1): 101–108. https://doi.org/10.1111/j.1365-2311.1928.tb01193.x

Okada Y.K. 1931. Honpôsan Hotaru-rui Gakumei no Kousatsu (Notes on the scientific names of the Japanese fireflies). *Zoological Magazine Tokyo* 43: 130–149. [In Japanese.]

Okamoto H. 1924. The insect fauna of Quelpart island (Saishu-to). *Bulletin of the Agricultural Experiment Station, Government-General of Chosen* 1 (2): IV + 47–233, pls VII–X.

Olivier E. 1902a. Catalogue des espèces de *Luciola* et genres voisins décrits jusqu'à ce jour. *Revue Scientifique du Bourbonnais et du Centre de la France* 15: 69–88.

Olivier E. 1902b. Coléoptères Lampyrides receueillis aux environs de Tokio (Japon) par M. le Dr Harmand. *Bulletin du Muséum d'histoire naturelle* 8 (2): 188–190.
Available from https://www.biodiversitylibrary.org/page/42896473 [accessed 17 Nov. 2022].

Olivier E. 1907. Coleoptera. Fam. Lampyridae. *In*: Wytsman P.A. (ed.) *Genera Insectorum* 54: 1–74, pls 1–3. Verteneuil & Desmet, Bruxelles.
Available from https://www.biodiversitylibrary.org/page/33991802 [accessed 17 Nov. 2022].

Olivier E. 1910. Lampyridae. *In*: Schenkling S. (ed.) *Coleopterorum Catalogus* pars 9: 1–68. W. Junk, Berlin, Germany. https://doi.org/10.1007/978-94-011-9697-0_1

Riley W.B., Rosa S.P. & da Silviera L.F.L. 2021. A comprehensive review and call for studies on firefly larvae. *PeerJ* 9: e12121. https://doi.org/10.7717/peerj.12121

Satô M. 1974. Luminous insects. *In*: *Konchû no Sekai (The World of Insects)*: 130–137. Hoikusha Publishing Co., Ltd., Osaka. [In Japanese.]

Satô M. 1978. Lampyrid-beetles of Japan. *The Insectarium, Tokyo* 15: 168–173. [In Japanese.]

Satô M. 1985. Lampyridae. *In*: Kurosawa Y., Hisamatsu S. & Sasaji H. (eds) *Colored Illustrations of the Coleoptera of Japan* Vol. III: 121–124, pl. 20. Hoikusha Publishing Co., Ltd., Osaka, Japan. [In Japanese.]

Satô M. 1989. *A Check List of Japanese Insects. I. Lampyridae*: 351–353. Kyushu University, Fukuoka. [In Japanese with English title.]

Satô M. & Kimura M. 1994. Discovery of a new firefly of the genus *Luciola* (Coleoptera, Lampyridae) from Kume-jima of the Ryukyu islands. *Elytra*, *Tokyo* 22 (1): 159–162.

Sawada Y. 2000. A List of Japanese Insect Collection by P. F. von Siebold and H. Burger preserved in Nationaal Natuurhistorisch Museum, Leiden, The Netherlands Part 2. Coleoptera. *Bulletin Kitakyushu Museum Natural History* 19: 77–104

Suzuki H. 1997. Molecular phylogenetic studies of Japanese fireflies and their mating systems (Coleoptera: Cantharoidea). *Tokyo Metropolitan University Bulletin of Natural History* 3: 1–53.

Suzuki H. 2001. Studies on biological diversity of firefly in Japan. *International Journal of Industrial Entomology* 2 (2): 91–105.

Suzuki H., Sato Y., Fujiyama S. & Ohba N. 1996a. Allozymic differentiation between two ecological types of flashing behavior in the Japanese firefly, *Luciola cruciata*. *Japanese Journal of Entomology* 64 (3): 682–691.

Suzuki H., Sato Y., Fujiyama S. & Ohba N.1996b. Biochemical systematics of Japanese fireflies of the subfamily Luciolinae and their flash communication systems. *Biochemical Genetics* 34 (5/6): 191–200. https://doi.org/10.1007/BF02407019

Suzuki H., Sato Y. & Ohba N. 2002. Gene diversity and geographic differentiation in mitochondrial DNA of the Genji firefly, *Luciola cruciata* (Coleoptera: Lampyridae). *Molecular Phylogenetics and Evolution* 22 (2): 193–205. https://doi.org/10.1006/mpev.2001.1046

Suzuki H., Sato Y., Ohba N., Bae J-S., Jin B-R., Sohn H-D. & Kim S-E. 2004. Phylogeographic analysis of the firefly, *Luciola lateralis*, in Japan and Korea based on mitochondrial cytochrome oxidase II gene sequences (Coleoptera: Lampyridae). *Biochemical Genetics* 42 (9/10): 287–300. https://doi.org/10.1023/B:BIGI.0000039805.75118.8f

Takada K. 2011. Beetle in our culture – A mini review of cultural entomology of lampyrid beetles. *Sayabane New Series*, *Tokyo* 2: 25–31.

Takada T. 2012. Commentary on the "Beetle Queen Conquers Tokyo (Kabuto Tokyo in Japanese)", a movie exploring the mystery of the Japanese fascination with insects, from the aspect of cultural entomology. *Elytra*, *Tokyo* New Series 2 (1): 127–129.

Takakura Y. 1977. Cantharoidea of Fukuoka Prefecture (Coleoptera). *Biologia Fukuokana* 17: 6–13. [In Japanese with English title.]

Takeda M., Amano T., Katoh K. & Higuchi H. 2006. The habitat requirement of the Genji-firefly *Luciola cruciata* (Coleoptera: Lampyridae), a representative endemic species of Japanese rural landscapes. *Biodiversity and Conservation* 15: 177–189. https://doi.org/10.1007/s10531-004-6903-y

Tamura M., Yokoyama J., Ohba N. & Kawata M. 2005. Geographic differences in flash intervals and pre-mating isolation between populations of the Genji firefly *Luciola cruciata*. *Ecological Entomology* 30: 241–245. https://doi.org/10.1111/j.0307-6946.2005.00683.x

Thapa V.K. 2000. *An Inventory of Nepal's Insects*. Vol. III. IUCN Nepal, Kathmandu.

Thunberg C. P. 1784. *Dissertatio entomologica novas insectorum species, sistens, cujus partem qvartam, cons. exper. facult. med. Upsal., publice ventilandam exhibent praeses Carol. P. Thunberg, et respondens Carolus P. Engström. Stipendiarius regius Uplandus. In audit. gust. maj. D. XXXI Maji anno MDCCLXXXIV. Horis solitis. Pars 4*: 69–84. Johan. Edman, Upsaliae [Uppsala]. [In Latin.] https://doi.org/10.5962/bhl.title.12285

Tojo K., Sekine K., Takenaka M., Isaka Y., Komaki S., Suzuki T. & Schoville S.D. 2017. Species diversity of insects in Japan: their origins and diversification processes. *Entomological Science* 20: 357–381. https://doi.org/10.1111/ens.12261

Tomita M. 2006. Regional comparison of environmental factors influencing distribution of genji-firefly *Luciola cruciata*. *Journal of the Japanese Institute of Landscape Architecture (Japan)* 65 (5): 557–560. [In Japanese with English abstract.] https://doi.org/10.5632/jila.69.557

Toussaint E.F.A. & Balke M. 2016. Historical biogeography of *Polyura* butterflies in the oriental Paleotropics: trans-archipelagic routes and South Pacific island hopping. *Journal of Biogeography* 43: 1560–1572. https://doi.org/10.1111/jbi.12741

Trice E., Tyler J. & Day J.C. 2004. Description of pleural defensive organs in three species of firefly larvae (Coleoptera, Lampyridae). *Zootaxa* 768: 1–11. https://doi.org/10.11646/zootaxa.768.1.1

Watasé S. 1902. *Hotaru no Hanashi* (The story of fireflies). Kaiseikan Publishing, Tokyo. [In Japanese.]

Yuasa H. 1937. Description of a new genus of the family Lampyridae (Coleoptera). *Kontyû, Tokyo* 11 (1–2): 107–109.

Yuma M. 1981. The body size variations of the climbing larvae of the firefly, *Luciola cruciata* (Coleoptera; Lampyridae). *Japanese Journal of Ecology* 31 (1): 57–66.

Yuma M. 1984. Egg size and viability of the firefly, *Luciola cruciata* (Coleoptera, Lampyridae). *Kontyû, Tokyo* 52 (4): 615–629.

Yuma M. 1986. Growth and size variations in the larvae of *Luciola cruciata* (Coleoptera: Lampyridae) in relation to the egg size. *Physiology and Ecology Japan* 23: 45–78.

Yuma M. 2001. Effects of illuminance and tree coverage on the density of adult Genji-firefly, *Luciola cruciata* (Coleoptera). *Ecology and Civil Engineering* 4 (1): 59–63. https://doi.org/10.3825/ece.4.59 [In Japanese with English abstract.]

Yuma M. 2007. Effect of rainfall on the long-term population dynamics of the aquatic firefly *Luciola cruciata*. *Entomological Science* 10 (3): 237–244. https://doi.org/10.1111/j.1479-8298.2007.00219.x

Yuma M. & Hori M. 1981. Gregarious oviposition of *Luciola cruciata* Motschulsky (Coleoptera: Lampyridae). *Physiology and Ecology Japan* 18: 93–112.

Yuma M. & Hori M. 1990. Seasonal and age-related changes in the behaviour of the Genji firefly, *Luciola cruciata* (Coleoptera, Lampyridae). *Japanese Journal of Entomology* 58 (4): 863–870.

Yuma M. & Ono K. 1985. Seasonal changes and population estimate of the adult firefly, *Luciola cruciata* (Coleoptera: Lampyridae), along the Biwako Canal, Kyoto City. *Science Report of the Yokosuka City Museum* 33: 1–11. [In Japanese with English abstract.]

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Supplementary material

Supp. file 1. Supplementary information. https://doi.org/10.5852/ejt.2022.855.2023.8323

1. Mtgenome analyses of the Luciolinae Lacordaire, 1857 (addressing *Luciola cruciata* Motschulsky, 1854 and *L. owadai* Satô & Kimura, 1994).

2. List of species of *Luciola* s. str.

3. List of Japanese Luciolinae Lacordaire, 1857.

4. The identity of *Luciola lateralis* Motschulsky, 1860.