

LAMPYRIDAE:
A synopsis of aquatic fireflies
with description of a new species
(Coleoptera)

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Abstract

A synopsis of the Lampyridae (Coleoptera) hitherto reported to be aquatic is given. The authors could confirm aquatic larval stages for five out of the fifteen reported cases: *Luciola cruciata* MOTSCHULSKY (Japan), *L. ficta* OLIVIER (China, incl. Taiwan), *L. lateralis* MOTSCHULSKY (Japan, Korea, China and Russia), *L. ovoidai* SATO & KIMURA (Japan) and *L. substriata* Gorham (= *L. formosana* PIC syn.n.) (Taiwan, Myanmar and India). A sixth species, *L. hydrophila* sp.n. (Taiwan), is described. The larvae of all but *L. substriata* have lateral tracheal gills on abdominal segments 1-8; *L. substriata* has a metapneustic larval stage with a pair of functional spiracles on the eighth abdominal segment. It is suggested that the aquatic habits in *Luciola* LAPORTE have evolved at least twice. The species with facultatively aquatic larvae are summarized also. A lectotype is designated for *L. ficta*.

Key words: Coleoptera, Lampyridae, *Luciola*, aquatic, new species.

Introduction

Lampyridae, or fireflies, belong to the superfamily Cantharoidea (sensu CROWSON 1972) or Elateroidea (sensu LAWRENCE & NEWTON 1995). Over 90 genera and about 1900 species in eight subfamilies have been described (MCDERMOTT 1966), however, the taxonomy of the family group definitely needs a thorough revision (NAKANE 1991).

Knowledge of the lampyrid fauna of Mainland China is very incomplete and based largely on works published between 1880 and 1920. WU (1937) listed 56 species from China and Mongolia; no further review or revision has been published since then. According to MCDERMOTT (1966) and miscellaneous recent publications, about 100 species were recorded from China although a much higher diversity is to be expected.

The Lampyridae of Taiwan were well studied by European and Japanese naturalists before World War II, and by Taiwanese researchers in the last decade. More than 50 species are known (LAI et al. 1998, JENG et al. 1998a, b, 1999a, b, c, 2000, 2001, 2002).

Ecologically, lampyrid larvae can be divided into three major groups: terrestrial, aquatic and facultatively aquatic (or semiaquatic). Aquatic larvae live under water and have obvious morphological adaptations for aquatic life. Facultatively aquatic larvae usually live in riparian habitats and regularly enter water in search of prey or in order to escape predators; they do not have obvious morphological adaptations to aquatic life (JÄCH 1998).

Most species of Lampyridae are terrestrial in their larval stage, yet a few species were reported to be associated more or less closely with aquatic habitats. Li Zi-Qing, a Chinese poet of the Tang dynasty, composed a poem (Shui Ying Fu) about aquatic fireflies in the eighth century.

ANNANDALE (1900) was the first to report on an aquatic firefly larva (from the Malay Peninsula), but failed to identify the species. Later, another aquatic species (from India) was identified as *Luciola vespertina* FABRICIUS by the same author (ANNANDALE 1906). BLAIR (1927) described and depicted an aquatic firefly larva from Celebes [Sulawesi] and inferred it was *Pyrophanes similis* OLIVIER. OKADA (1928) identified two Japanese species as aquatic, *Luciola cruciata* MOTSCHULSKY and *Luciola lateralis* MOTSCHULSKY, and KANDA (1935) depicted the life history of these two Japanese species. IMMS (1933) found a firefly larva, probably belonging to *Luciola* LAPORTE, in a hot spring from East Africa, but he was not sure if it really was aquatic. BERTRAND (1965, 1972, 1973) mentioned several aquatic larvae of different species from Africa, incl. Madagascar, but none were identified to species or even genus. Aquatic lampyrid larvae (probably belonging to the genus *Luciola*) were collected abundantly from mountain streams of Sri Lanka by JÄCH (1982, 1984) and STARMÜHLNER (1993); their abundance often was found to be positively correlated with water snails of the genus *Paludomus*; a brief morphological description was provided by BERTRAND (1973). OHBA (1981, 1983) studied an aquatic species from Taiwan and demonstrated that its female is able to attract and to copulate with *L. lateralis* from Japan. Later he briefly reviewed the aquatic fireflies of the world, emphasizing on the bionomics of the Japanese species (OHBA 1988b). LLOYD & WING (1989) inferred that the larvae of *Luciola japonica* (THUNBERG) from Thailand were aquatic since the adults are always associated with still waters. In 1994, a new species of aquatic firefly, *Luciola owadai* SATŌ & KIMURA, was described from the Ryukyu Archipelago and its bionomics were studied by OHBA et al. (1994). CHANG (1994) managed to mass rear the aquatic *Luciola ficta* OLIVIER from Taiwan, but misidentified the species as *Luciola ovalis* HOPE. HO (1997) and HO & JIANG (1997) reported on *Luciola ficta* and an undescribed congeneric species from Taiwan. Recently, HO et al. (1998) identified another aquatic species, *Luciola substriata* GORHAM, from Taiwan and briefly described its immature stages. OHBA (2001) and OHBA et al. (2001) analyzed the morphological and bioluminescent variations among different geographic populations of *L. cruciata* and *L. lateralis*, respectively.

Among the cases reported above, only five species from Japan and Taiwan are identified specifically and their aquatic habits confirmed; the remaining cases are either uncertain in species identity or just inferred to be aquatic. Herein we provide a review of these five species and describe a new species from Taiwan.

Methods and abbreviations

Specimens were examined with a Nikon SMZ-10 stereoscopic microscope. Measurements were made by illustrating the body outline with the aid of a camera lucida. Body length (BL) is the sum of pronotal (PL) and elytral length (EL); body width (BW) means twice the width of the broadest width of one elytron (EW = BW). "T" and "V" represent tergite and abdominal ventrite (visible sternum) respectively; aedeagal sheath is composed of T9 + 10 (= TS, tergite of aedeagal sheath) and 9th abdominal sternite (S9) (see BALLANTYNE 1987). Male genitalia, aedeagal sheath, maxillary and labial palpi were examined and illustrated with an Olympus BH-50 transmitted light microscope with a drawing tube. Male genitalia were soaked in 30% KOH solution for 2-3 days before being examined.

CAIEU College of Agriculture, Ehime University, Matsuyama, Japan (N. Ohbayashi)

MNIIN Muséum national d'Histoire naturelle, Paris, France (J. Menier)

NMNS National Museum of Natural Science, Taichung, Taiwan (M.-L. Chan)

NMW Naturhistorisches Museum Wien, Austria (M.A. Jäch)

NTU Department of Entomology, National Taiwan University, Taipei, Taiwan (S.-F. Hsiao)

TARI Department of Applied Zoology, Taiwan Agricultural Research Institute, Taichung, Taiwan (S.-C. Shi)

YCM Yokosuka City Museum, Yokosuka, Japan (N. Ohba)

Key to the adults of aquatic fireflies from Taiwan and Japan

- 1 Coloration yellowish orange; luminous organ on V6 of male V-shaped (Fig.12); male with pair of hooked sclerites between T8 and TS (Fig.14); India, Myanmar, Taiwan .. *Luciola substriata*
- Coloration not yellowish orange; luminous organ on V6 of male not V-shaped (Fig. 7); male without sclerite between T8 and TS..... 2
- 2 Scutellum black; pronotum reddish pink 3
- Scutellum dark yellow or yellowish brown; pronotum pale yellow or orange yellow 4
- 3 Body size large (BL: 10.5 - 18.6 mm); pronotum with cross-like marking¹ along median sulcus; male genitalia with median lobe moderately stout, and parameres not hooked apically (Fig. 33); Japan *Luciola cruciata*
- Body size smaller (BL: 6.5 - 10.5 mm); pronotum with longitudinally broad band along median sulcus; male genitalia with median lobe very stout, and parameres hooked apically (Fig. 37); Japan, Korea, China, Russia *Luciola lateralis*
- 4 Elytral suture and lateral margins yellowish brown; body length: 7.5 - 10.0 mm; Taiwan, China..... *Luciola ficta*
- Elytra without yellowish brown margins; body length: 10 - 16 mm 5
- 5 Elytra with carinae more or less distinct; T8 of male broadly rounded apically (Fig. 22); aedeagal sheath stout (Fig. 28); Japan *Luciola owadai*
- Elytra with carinae obsolete; T8 of male slightly sinuate laterally at apex (Fig. 23); aedeagal sheath elongate (Fig. 31); Taiwan..... *Luciola hydrophila* sp.n.

Key to mature larvae of aquatic fireflies from Taiwan and Japan

- 1 Lateral margins of abdominal segments 1-8 with tracheal gills..... 2
- Abdominal segments without tracheal gills but with pair of functional spiracles on lateroapical area of 8th segment *Luciola substriata*
- 2 Dorsal sclerites from mesothorax to abdominal segment 8 widely separated 3
- Dorsal sclerites from mesothorax to abdominal segment 8 separated narrowly by suture..... *Luciola ficta*
- 3 Pronotal sclerite dark brown, with four pale yellow markings in four corners; tracheal gills of abdominal segments 2-8 long and with apices acute 4
- Pronotal sclerite unicoloured dark brown; tracheal gills of abdominal segments 2-8 short and obtuse apically *Luciola hydrophila* sp.n.
- 4 Pronotum subrectangular, with broad stripe on disc.....*Luciola lateralis*
- Pronotum oblong, with boldly crossed or diamond-shaped markings on disc..... 5
- 5 Pronotum with boldly crossed marking on disc; legs black with white rings near joints..... *Luciola owadai*
- Pronotum with diamond-shaped marking on disc; legs yellowish or reddish brown..... *Luciola cruciata*

Luciola cruciata MOTSCHULSKY

Luciola cruciata MOTSCHULSKY 1854: 53. – MOTSCHULSKY 1866: 167 (name list). – OLIVIER 1907: 51 (check list). OKADA 1931: 134 (synonymy). – McDERMOTT 1966: 102 (check list). – OHBA 1988b: 9 (ecology), 1989: 2 (ecological variation). – SUZUKI 1997: 24 (allozyme analysis). – OHBA 2001: 45 (flash pattern, morphological variation).

¹ Some populations do not have pronotal markings (OHBA 2001).

Luciola picticollis KIESENWETTER 1874: 262. – HAROLD 1877: 357 (syn.). – OKADA 1931: 133 (review). – MCDERMOTT 1966: 111 (check list).

Luciola vitticollis KIESENWETTER 1874: 261. – OLIVIER 1902a: 77, 1902b: 189 (variety of *L. cruciata*), 1907: 51 (var.). – OKADA 1931: 146 (syn. of *L. lateralis*). – MCDERMOTT 1966: 102 (syn. of *L. cruciata*, check list).

TYPE LOCALITY: Japan (mistaken as Java in the original description).

TYPE MATERIAL: Not examined. According to OKADA (1931), at least some of the syntypes are preserved in MNHN.

MATERIAL EXAMINED:

J A P A N: 11 exs., Japan: Ehime Pref., Matsuyama, 6.VI.1966, Y. Hori leg.; 1 ex., Nagasaki Pref., Tsushima Is., Mt. Ohboshi, 5.-9.VII.1983, H. Makihara leg.; 2 exs., Gifu Pref., Seki, 7.VI.1952, K. Ohbayashi leg.; 2 exs., Mie Pref., Toba, Gochi-dani, 12.VI.1966, M. Satô leg.; 1 ex., Ooita Pref., Yamagamachi, 16.VI.1966, K. Iwao leg.; 2 exs., Niigata Pref., N-Echigo, Kurokawa, 29.VI.1964, K. Baba leg.

DIAGNOSIS: BL: 10.5 - 16.5 mm (male), 15.0 - 18.6 mm (female); BW: 3.0 - 5.0 mm (male), 5.0 - 6.0 mm (female). Coloration black, pronotum reddish pink with longitudinal cross marking along central sulcus; venter dark brown, V5-6 pale yellow in male; V5 pale yellow, V6 reddish pink and V7 dark yellow to dark brown in female. Labial palpi (Fig. 1) with three to five teeth on inner margins of apical segments in male. Pronotum broadest at base; basal angles with apices acute and protruding posterolaterally. Elytra elongate, clytral carinae more or less distinct. V6 of male (Fig. 7) significantly protruding at central apex, with luminous organ occupying almost entire segment; V6 of female (Fig. 15) nearly truncate apically. T8 of male (Fig. 21) subquadrate, with apex arched.

Aedeagal sheath (Fig. 27) about 2.1 mm long, oblong; apex of TS with a small round projection centrally; S9 asymmetric, tilted left in apical 1/2; apical 1/2 broad and thumb-like. Male genitalia (Fig. 33) about 1.7 - 1.9 mm long, very similar to those of the following species, except parameres less broad and basal piece notched apically.

Externally the species is similar to *L. owadai* and *L. hydrophila*. It can be distinguished easily from both by its reddish pink pronotum, distinctive cross markings on pronotum, black scutellum, reddish pink abdominal ventrite 6 of female and so on, though some populations in Japan lack pronotal markings. *Luciola cruciata* also resembles *L. kagiana* MATSUMURA from Taiwan in coloration and body size, but differs from the latter by the conspicuously projecting apex of V6 of the male, which is broadly rounded in *L. kagiana*.

REMARKS: *Luciola vitticollis* KIESENWETTER has been associated wrongly with *L. cruciata* for a long time. In the original description, KIESENWETTER (1874) very likely reversed the body sizes of *L. vitticollis* and *L. picticollis*. HAROLD (1877) recognized the mistake and synonymized *L. picticollis* with *L. cruciata*. However, GORHAM (1880) wrongly stated that HAROLD (1877) synonymized both *L. picticollis* and *L. vitticollis* with *L. cruciata*, then maintained that all three species are valid. OLIVIER (1902a, b, 1907) adopted Gorham's misinterpretation and listed *L. picticollis* as a valid species with *L. cruciata* sensu HAROLD (1877) as a synonym. In addition he regarded *L. vitticollis* as a variety of *L. cruciata*. After examining the type material of all four species, OKADA (1931) verified that *L. cruciata* and *L. lateralis* were valid species while *L. picticollis* and *L. vitticollis* were synonyms of the former two species, respectively. Unfortunately, Okada's report was overlooked by MCDERMOTT (1966) who adopted Olivier's treatment. As a consequence, the distributions of *L. cruciata* and *L. lateralis* are identical and *L. picticollis* is cited as a valid name in McDermott's catalogue. In fact, *L. cruciata* is probably limited to Japan while *L. lateralis* is distributed more widely.

DISTRIBUTION and PHENOLOGY: This species is endemic to Japan (Honshu, Shikoku, and Kyushu). The only record from Korea was not confirmed (OHBA 1988a, b). Adults occur from early May to early July.

BIONOMICS: The ecology of the species is reported in detail by OHBA (1988a, b, 1989). It is a running water dweller; the larvae live in various kinds of environment such as small ditches, creeks and rivers with mud or pebble substrates. Six to seven instars have been observed in the larval stage and the generation time is 1 - 2 years. The populations from western and eastern Japan are differentiated in flash pattern, phenology and behavior. In western Japan, males fly gregariously and glow synchronously after sunset; females begin to fly with luminescence from midnight to about 3:00 a.m. and then oviposit in groups until dawn; those from eastern Japan usually stop flying before midnight and then stay on vegetation with luminescence until dawn. Females from western Japan usually aggregate to oviposit but those from eastern Japan usually oviposit solitarily. The number of eggs ranges from 500 - 1000. Intermediate flash patterns were observed in a hybrid zone between the western and eastern Japanese populations (OHBA 2001).

Luciola owadai SATÔ & KIMURA

Luciola owadai SATÔ & KIMURA 1994: 160. - OHBA et al. 1994: 13 (life cycle, larval morphology and behavior).

TYPE LOCALITY: Shirasegawa, Kumejima, Ryukyu, Japan.

TYPE MATERIAL: **Holotype** ♂ (NSMT): not examined. **Paratypes:** 2 ♂♂, 2 ♀♀: "Shirasegawa, Kume-jima, 27-IV-1993, M. Kimura / PARATYPE *Luciola owadai* M. Satô et Kimura, 1994, DET. M. SATÔ 1994" (NTU).

ADDITIONAL MATERIAL EXAMINED:

J A P A N: 3 ♂♂, 3 ♀♀, "SHIRASEGAWA, Kumejima Is., Okinawa Pref., 26. Apr. 1994, Coll. N. Ohba / Yokosuka City Museum, Insect Collection" (YCM).

DIAGNOSIS: BL: 12.5. - 15.0 mm (male), 14.5 - 16.0 mm (female), BW: 4.5 - 5.0 mm (male), 5.0 - 5.5 mm (female). Body form elongate. Coloration black, with prothorax, scutellum and mesoventrite dark yellow; venter dark brown to black, V5 and V6 of male pale yellow; V5 of female pale yellow and V6-7 dark brown. Labial palpi (Fig. 2) with three to five teeth on inner margins of apical segments. Pronotum subparallel or broadest at base; basal angles somewhat acute and conspicuously projecting posterolaterally. Elytra elongate, subparallel, with four more or less distinct carinae. V5-6 almost entirely occupied by luminous organs, V6 of male (Fig. 8) with central apex distinctly projecting; V6 of female (Fig. 16) with apex emarginate at middle. T8 of male (Fig. 22) broadly rounded apically.

Aedeagal sheath (Fig. 28) about 2.3 mm long, oblong; TS sinuate laterally and significantly roundly protruding at apex; S9 tilted left in apical 1/2, broad and thumb-like. Male genitalia (Fig. 34) almost identical to those of *L. cruciata*.

DIFFERENTIAL DIAGNOSIS: Though the larval morphology, male genitalia and 16S r-DNA partial sequence (OHBA et al. 1994, SUZUKI 1997) of the species are very similar to those of *L. cruciata*, they differ in lighting behavior, ecology and geographical distributions. Allozyme analyses also show that they are well separated on species level (SUZUKI 1997). No zone of hybridization has been reported. The existence of premating isolation between these two species is highly possible.

DISTRIBUTION and PHENOLOGY: Known only from Japan (Ryukyu: Kume-jima). Adults appear from April to June (OHBA et al. 1994).

BIONOMICS: The ecology of the species was reported in detail by OHBA et al. (1994). The larval stage has six instars and lives in small creeks with cobble and pebble benthos. Mature larvae enter diapause or quiescence from October to February and stay beneath the bottom of the stream, but young larvae continue feeding during this time. Adults emerge approximately synchronously in April for seasonal mating. Male adults fly in groups and glow synchronously from after sunset to about 4:30 a.m. Eventually, copulated females begin to fly and glow continuously, and then gather on mossy rocks near water to lay eggs. All adults cease activity before dawn.

Luciola hydrophila n.sp.

TYPE LOCALITY: Wulai, Taipei, Taiwan.

TYPE SERIES: **Holotype** ♂ (NMNS): "Taiwan: Taipei County, Wulai, Shinshien, 26.IV.1997, J. Lai leg.". **Paratypes** (NMW, NTU, CAEU, YCM): 5 exs. with same data as holotype; 1 ex., same locality, 16.III.1996, L.-J. Wang leg.; 2 exs, same locality, 11.V.1998, M.-L. Jeng leg.; 3 exs., Taipei County, Fushan, 3.V.1996, M.-F. Chen leg.; 2 exs., Taipei County, Jingshan, 4.IV.1996, M.-F. Chen leg.; 2 exs., Taipei County: Matsao, 30.IV.1996, M.-F. Chen leg.; 1 ex., Taipei City: Shihlin, 9.VI.1997, M.-L. Jeng leg.; 2 exs., Taipei City: Mujia, 24.V.1996, C.-F. Lee leg.; 2 exs., Taipei City, Mujia, 26.VI.1998, M.-L. Jeng leg.; 2 exs., Hsinchu County, Dashanbei, 9.V.1998, M.-L. Jeng leg.; 1 ex., Hsinchu County, Chingchen, 3.IV.1996, M.-F. Chen leg.; 2 exs., Taichung County: Guguan, 3.IV.1997, M.-L. Jeng leg.

DESCRIPTION: Adult: BL: 11 - 14 mm (male), 11 - 15 mm (female); BW: 4 - 5 mm (both sexes).

Body form elongate, subparallel, strongly convex, closely covered with superficial golden pubescence. Coloration black; prothorax and scutellum pale yellow; elytral suture brown; meso- and metaventricle dark yellow to brown, somewhat darker in central disc; ventral basal 3/4 of all femora dark yellow; V1-4 brown to black; V5 waxy white, basal 1/2 of V6 waxy white and apical 1/2 dark yellow in male but entirely dark yellow on V6-7 in female.

Eyes of male larger than those of female. Vertex weakly concave between eyes in male but flat in female. Labial palpi (Fig. 3) with three teeth on inner margin of apical segments in male.

Pronotum about 1.6 - 1.7 times broader than long, with disk strongly convex, coarsely and densely punctate; apical margin arched; lateral margins nearly straight, broadest at base; hind angle subrectangular, inconspicuously protruding, with apex obtuse; basal margin trisinate, broadly sinuate just in front of scutellum. Disk with shallow broad longitudinal median impression.

Elytra elongate and subparallel; surface densely punctate and pubescent, punctuation similar to that of pronotum; elytral costa obsolete. EL/EW= 2.2 - 2.4, EL/PL= 4.3 - 4.7

Metaventricle strongly convex. V1-4 with surface leathery, superficially punctate and densely pubescent; V6 of male (Fig. 11) with luminous organ in basal 1/2, and broadly protruding apically; V6 of female almost straight (Fig. 17). T8 of male slightly sinuate laterally (Fig. 23).

Aedeagal sheath (Fig. 31) about 3.1 mm long, elongate oblong; TS with two small round projections at apex; S9 elongate, asymmetric, tilted right apically, with two projections laterally in apical 1/3. Male genitalia (Fig. 35) about 1.5 mm long. Median lobe flat laterally but slender dorsally in apical 1/4, gradually widening toward apical 1/2 and thence subparallel to base which bears lateral foldings. Paramere broad, well sclerotized dorsally but membranous at venter; inner margin of venter with slender fold from apex to base; few long setae appear in apical 1/3 of ventral margin. Basal piece well sclerotized at margins, and broadly rounded at apex.

DIFFERENTIAL DIAGNOSIS: This species is closely related to *Luciola owadai* SATŌ & KIMURA, from which it differs in the obsolete elytral carinae, slightly sinuate lateral margins of T8 of male, elongate aedeagal sheath, broader parameres and broadly round apex of basal piece of male genitalia. Pic misidentified some specimens deposited in the MNHN as *Luciola clara* OLIVIER, which can be separated by the broadly round apex of V6, which is entirely occupied by a luminous organ in the male.

MATURE LARVAE: (Fig. 39) About 19 - 21 mm long and 5 - 6 mm wide; general appearance very similar to that of *L. owadai* (see OHBA et al. 1994: Fig. 5). Pronotum unicolor in the former but with four pale markings in the latter; gills of *L. hydrophila* shorter and more obtuse at apices than those of *L. owadai*; basal row of pygopods composed of two retractable filaments in *L. hydrophila* but four in *L. owadai*.

ETYMOLOGY: The specific name refers to the aquatic habit of the species.

DISTRIBUTION and PHENOLOGY: This species is known only from Taiwan. It can be found throughout the island up to 1000 m above sea level, and it is more abundant in northern and central areas. Adults occur mainly from late March to early July, and the life cycle is probably univoltine.

BIONOMICS: The ecology of the species was reported briefly by HO (1997) and HO & JIANG (1997). The larvae usually live in ditches or small creeks with shallow and clear water, fast current and cobble benthos. The major prey are water snails, e.g., *Semisulcospira libertina* (GOULD) and *Thiara tuberculata* (MÜLLER) (HO & JIANG 1997). At Matsao we have observed more than 50 adults staying near a small, well-concealed artificial waterfall (a vertical section of an irrigation ditch) and searching for mates among riparian plants. Adults emit green-yellow light and males can be attracted by an artificial light source.

Luciola ficta OLIVIER

Luciola ficta OLIVIER 1909: 249 (orig. descr., China: Guizhou). - PIC 1911:188 (Taiwan). - McDERMOTT 1966: 104 (check list). - HO & JIANG 1997: 42 (ecology & morphology).

Luciola ovalis HOPE: MATSUMURA 1918: 84 (misidentification). - CHIANG 1994: 1 (misidentification, life cycle and mass reproduction).

TYPE LOCALITY: Pin-fa (Ping-Ba), Anshun Co., Guizhou, China.

TYPE MATERIAL: **Lectotype** ♀ (by present designation, MNHN, in a box labelled "Oberthur's Cantharidae's *Diaphanes* / *Luciola* / *Lampyris*"): "*Luciola ficta* / Lectotype, *Luciola ficta* Olivier, J. LAI & M.L. JENG des.". The lectotype designation is made to support stability of the nomenclature. **Paralectotypes:** 2 ♀ without labels were pinned beside the lectotype. Three males were cited in the original description, but no male syntype was found in the MNHN.

ADDITIONAL MATERIAL EXAMINED:

C H I N A: FUJIAN: 2 exs., "Fookien" [= Fujian] (MNHN); HONG KONG: 2 exs., "Hong Kong" (MNHN); TAIWAN: More than 150 specimens from many localities.

DIAGNOSIS: BL: 7.0 - 11.0 mm (male), 8.0 - 11.0 mm (female); BW: 3.0 - 4.0 mm (both sexes). Body form elongate-oval. Coloration black, with pronotum and scutellum pale to orange yellow; elytra fringed with yellowish brown margins; all femora and base of tibiae yellowish brown; venter yellowish brown except V1-4 dark brown to black; V5 and basal 1/2 of V6 of male pale yellow, apical 1/2 of V6 yellowish brown; V5 of female pale yellow, V6-7 yellowish brown. Labial palpus (Fig. 4) with three teeth on inner margins of apical segments in male. Pronotum subparallel; basal angles subrectangular, but prominent. Elytra elongately oval, carinae obsolete. V6 of male (Fig. 9) roundly protruding, weakly sinuate at sides; V6 of female (Fig. 19) with apex almost truncate, V7 broadly rounded apically; T8 of male (Fig. 24) shell-like.

Aedeagal sheath (Fig. 29) about 1.9 - 2.0 mm, oblong; TS with apex roundly projecting centrally; S9 tilted right in apical 1/2, with a sclerotized arm at left side from basal 1/4 to apical 1/4. Male genitalia (Fig. 36) about 1.6 - 1.8 mm long, elongate and subparallel. Median lobe slender, subparallel from basal 2/5 to apex. Paramere elongate, well sclerotized dorsally but poorly ventrally, with a tuft of setae at inner margins of apical 1/4. Basal piece comparatively short, about 2/5 length of paramere, broadly rounded apically.

DISCUSSION: The species was misidentified as *Luciola ovalis* by MATSUMURA (1918, 1928) and the result was adopted by CHIANG (1994). In fact, these two species are different in several aspects such as coloration, body form, luminous organ and so on.

This species is closely related to *Luciola lateralis*. The pronotum of *L. lateralis* is reddish pink and with a black marking, while that of *L. ficta* is yellowish orange; male genitalia of *L. lateralis*

possess a pair of hooks near the apices of the parameres from ventral view, while those of *L. ficta* are not conspicuously hooked.

We examined a specimen labelled *L. limbalis* FAIRMAIRE (MNHN) which was identified by Fairmaire himself, and which agrees well with *L. ficta*. It is possible that *L. ficta* is a junior synonym of *L. limbalis* since they are found in adjacent areas (Jiangxi vs. Guizhou, Fujian and Hong Kong). Unfortunately, we did not find the holotype of *L. limbalis*.

DISTRIBUTION and PHENOLOGY: The species is now known from SE China (Guizhou, Fujian, Hong Kong) and Taiwan. The adults can be found throughout the year, but are more abundant in April and August in Taiwan.

BIONOMICS: In contrast to the preceding three species, *L. ficta* is a typical still water dweller. Paddies are the most common habitats in Taiwan. Male adults fly and search for mates around the fields and females usually stay on the ground or in weeds. Individual females lay about 100 eggs on average on moist soil or riparian vegetation (CHANG 1994). Larvae prefer waters with muddy benthos and probably pass arid periods by burrowing deeply in mud. They prey on small aquatic invertebrates or eat newly dead carrion. The life cycle takes about 120 days in laboratory rearings and there are six larval instars (CHANG 1994). Adults emit green-yellow light.

Luciola lateralis MOTSCHULSKY

Luciola lateralis MOTSCHULSKY 1860: 144. – OLIVIER 1902a: 82 (check list). – OLIVIER 1907: 53 (check list). – MCDERMOTT 1966: 108 (check list). – OHTA 1986: 6 (ecology). – OHTA 1988b: 12 (ecology).

Luciola vitticollis KIESENWETTER 1874: 261. – GORHAM 1883: 409 (name list). – OLIVIER 1902a: 77, 1902b: 189 (variety of *L. cruciata*). – OKADA 1931: 146 (syn. of *L. lateralis*). – MCDERMOTT 1966: 102 (syn. of *L. cruciata*).

TYPE LOCALITY: Daourie, E Siberia, Russia.

TYPE MATERIAL: Not examined. According to OKADA (1931), some syntypes are deposited in MNHN.

MATERIAL EXAMINED:

J A P A N: 6 exs., Ehime Pref., Matsuyama, 5.VI.1966, K. Iwao leg.; 2 exs., Nagasaki Pref., Tsushima Is., Mt. Ariake, 16.VI.1960, M. Satô leg.; 2 exs., Aichi Pref., Shinano-cho, V-VI.1964, M. Satô leg.; 3 exs., Gifu Pref., Terakawado, VIII.1969, Y. Arita leg.; 3 exs., Gifu Pref., Seki, 7.VI.1952, K. Ohbayashi leg.; Niigata Pref., Kooridono, Ojima, 29.VII.1972, K. Yamagishi leg.

DIAGNOSIS: BL: 6.5 - 9.5 mm (male), 7.5 - 10.5 mm (female); BW: 2.3 - 3.3 mm (male), 2.5 - 3.5 mm (female). Body form elongate oval. Coloration black, pronotum reddish pink with longitudinal broad band along median sulcus from apex to base; venter dark brown, male with V5 and basal 1/3 of V6 pale yellow, and rest of V6 yellowish to dark brown; female with V5 pale yellow, basal 4/5 of V6 reddish pink, rest of V6 and V7 dark brown. Labial palpus (Fig. 5) with three to four teeth on inner margin of apical segment. Pronotum broadest at base or subparallel-sided; basal angles subrectangular, not prominently protruding. Elytra elongate oval, with carinae more or less conspicuous. V6 of male (Fig. 10) with luminous organ in basal 1/3, broadly roundly protruding apically; V6 of female (Fig. 18) slightly emarginate at apex, V7 broadly rounded. T8 of male (Fig. 25) subquadrate, slightly arched apically.

Aedeagal sheath (Fig. 30) about 2.3 mm long, oblong; TS roundly protruding apically; S9 asymmetric, tilted left, becoming a broad arm from apical 1/3 to apex. Male genitalia (Fig. 37) about 1.5 - 1.7 mm long. Median lobe broad except apical 1/8 more slender. Parameres asymmetric, right paramere a little longer than left one, with hook on inner margin near apex of each paramere. Basal piece short, about 1/4 as long as paramere, and notched apically.

This species is similar to *L. cruciata* in coloration and to *L. ficta* in many characters. It can be separated from *L. cruciata* by its smaller size, elongate-oval body form, pronotal markings,

shape of luminous organs, and hooked apices of parameres of male genitalia. From *L. ficta* it differs in possessing a reddish pink pronotum and in the V6 of the female, black scutellum, metaventrite and femora, and stout median lobe and conspicuous apical hooks on the parameres of the male genitalia.

REMARKS: MCDERMOTT (1966) listed *Luciola vitticollis* as a synonym of *L. cruciata*. In fact, it is a synonym of *L. lateralis*.

DISTRIBUTION and PHENOLOGY: Japan (Hokkaido, Honshu, Shikoku and Kyushu), NE China, Korea and Russia (E Siberia and Kurile Islands) (OHBA 1986). Adults appear from April to November, and are most abundant June to August.

BIONOMICS: The ecology and behavior of this species were studied by OHBA (1986, 1988b). Ecologically, this species is very similar to *L. ficta* in many aspects. Larvae overwinter as third or fourth instars and burrow in benthic soils or conceal in stubble in paddies. They become active again in next spring (MITSUISHI 1996). Male adults can be attracted easily by simulated artificial lights (OHBA 1986), and can copulate with females of *L. ficta* (OHBA 1981, 1983, 1986).

Luciola substriata GORHAM

Luciola substriata GORHAM 1880: 100. – GORHAM 1895: 305. – OLIVIER 1902a: 86 (check list), 1907: 54 (check list), 1913: 271 (Taiwan). – OKADA 1928: 137 (Taiwan). – MIWA 1931: 102 (Taiwan). – MCDERMOTT 1966: 113 (check list). – HO et al. 1998: 47 (aquatic habit).

Luciola formosana PIC 1916: 9 (= syn.n.).

TYPE LOCALITY: Bombay, India (wrongly cited as "Rangoon" by OLIVIER 1902a, 1895, 1907).

TYPE MATERIAL: We examined a possible type specimen of *L. substriata* in MNHN (Gorham collection). It is deposited in a box which contains most of the firefly species described by GORHAM (1880). However, except an identification label, no other label was found attached to the specimen. We examined the holotype ♂ of *Luciola formosana* labelled "Formose / *formosana* Pic / 50 / type / *Luciola* Olivier vid / TYPE" (MNHN). It is undoubtedly conspecific with *L. substriata*, although its tibiae are dark brown rather than sandy yellow.

ADDITIONAL MATERIAL EXAMINED:

C H I N A: TAIWAN: 1 ex., Taipei Co., Wulai, 26.VII.1993, S.-C. Yang leg.; 2 exs., Miaoli Co., Tongshao, 3.V.1980, N. Ohba leg.; 1 ex., Miaoli Co., Shitan, 2.IV.1988, J.-C. Yeh leg.; 2 exs., Pingtung Co., Kenting, 8.VII.1996, M.-F. Chen leg., 1 ex., Taitung Co.: Chipen, 12.VI.1970, Y. Hori leg.; 7 exs., Jinmen Co: Chonglin, V.1998, J. Lai leg.; 1 ex., "Kankau (Koshun), Formosa, H. Sauter, VII.1912" (MNHN); 2 exs., "Formose / *Luciola substriata* Gorch." (MNHN).

M Y A N M A R: 3 exs., "Rangoon / *Luciola substriata* Gorham" (MNHN).

Two specimens labelled "Taipei, V / *Luciola japonica* Thumb. Det. T. Shiraki" (TARI) have dark yellow tibiae which differ from those of the other specimens from Taiwan. The specimens were apparently mislabelled and possibly part of the "Shiraki Collection", which was brought back from the Natural History Museum of London in 1913.

DIAGNOSIS: BL: 9.5 - 10.5 mm (male), 10.5 - 11.5 mm (female); BW: 3.5 - 3.8 mm (male), 4.0 - 4.2 mm (female). Body form elongately-oval. Coloration yellowish orange, epicranium, eyes, antennae, palpi of mouth parts, all tibiae and tarsi, elytral apex, and V4 or V3-4 dark brown to black; elytral suture and margins light yellow; luminous organs waxy white with weak yellowish green luster. Vertex of both sexes flat. Labial palpi (Fig. 6) each with three teeth on inner margin of apical segment in male. Pronotum broadest at basal 1/2 or base; basal angles prominently projecting posterolaterally, with apices obtuse. Elytra with punctate-striae more or less distinct. V6 of male (Fig. 12, 13) subtriangular, with V-shaped luminous organ at apical 1/2; V6 of female (Fig. 20) broadly emarginate apically. T8 of male (Fig. 26) arched at apex, slightly notched at middle, and with two prolonged arms in basolateral margins. Intersegmental membrane between T8 and TS well sclerotized and hooked (Fig. 14).

Aedeagal sheath (Fig. 32) about 3.0 mm long, elongate oblong; TS with an oval projection at apex; S9 elongate, asymmetric in apical 1/2, with two angles at apex. Male genitalia (Fig. 38) about 1.2 mm long, short and stout. Median lobe robust, gradually widening from base to a broadly rounded apex. Parameres broad, slightly shorter than median lobe, well sclerotized dorsally but membranous ventrally, with a row of hairs in apical 1/2 ventrally. Basal piece semi-circularly ringed, about half length of male genitalia.

This species is closely related to *Luciola brahmina* BOURGEOIS from "Indo-China", *Luciola cingulata* OLIVIER from Ceylon and *Luciola flavida* HOPE from southern China. All of these species have a V-shaped luminous organ on V6 of male. *L. brahmina* is pale yellow in coloration; the head of *L. cingulata* is dark yellow; and the male luminous organ of *L. flavida* is more slender on V6 and with a short projection at the apex. *Luciola japonica* is another similar species which differs in possessing pale grayish brown coloration.

Mature larvae: about 20 mm long, 3 mm wide. Body form very slender, subparallel; cuticle hard. Coloration brown, median suture of dorsum, all femora and basal 2/3 of tibiae and all sutures of venter yellowish brown; luminous organs pale yellow. Pronotum elongate, subtrapezoid; mesonotum to abdominal T5 subrectangular, about similar in size, then gradually diminishing toward T8, and abruptly narrowed in T9; mesonotum to abdominal T8 each with pair of ridges parallel to median suture, and with four projections apically; T9 oblong and small. Procoxal cavity closed. Meso- and metapleuron (Fig. 40) composed of two parts. Abdominal segments 1-8 with pleura, weakly ridged medially; abdominal spiracles 1-7 located on dorsal edges of pleura; pleurite 8 (Fig. 41) partially fused with tergite 8 at apices, where they bear functional spiracles; sternum 8 with pair of luminous organs in apical 1/2; pleuron of segment 9 weakly sclerotized; segment 10 very small, suboval; pygopods composed of at least 4 retractable filaments in two rows.

DISTRIBUTION and PHENOLOGY: Taiwan, Myanmar and India. In Taiwan, the species is distributed widely around the island up to about 500 m a.s.l. Adults appear from April to December, but become scarce after September.

BIONOMICS: The species was first reported to be aquatic by HO et al. (1998) who found larvae in marshes along rivers in southern Taiwan. Paddies are another kind of habitat preferred by this species (Y.-S. Chang, pers. comm.). Females lay eggs on submerged parts of vegetation or fallen leaves. It takes about 140-150 days to reach adulthood under laboratory conditions; seven instars were observed. The first instar can remain submerged in water for a long time without coming to the surface, implying that the larvae may exchange oxygen through the cuticle. The second instar is metapneustic and breathes via functional spiracles on abdominal pleurite 8. The fifth instar leaves the water intermittently (HO et al. 1998). Unlike the other aquatic species, larvae of this species are not benthos dwelling. They usually crawl or stay on floating substrates and aquatic vegetation, or float upside down under the surface film if no suitable substrates are available. They spend most of the time under water even while searching for prey and molting (Y.-S. Chang, pers. comm.). Water snails like *Stenothyra formosana* PILSBRY & HIRASE, *Gyrallus spirillus* (GOULD) are known prey of the larvae. No evidence of cooperation is found between two or more larvae in attacking snails. Mature larvae build earthen cocoons before pupating (HO et al. 1998). The larvae glow weakly and intermittently.

DISCUSSION: The distinctive male genital segments indicate that *L. substriata* is a peculiar species. The intersegmental membrane between T8 and TS of males is well sclerotized and hooked, and the well sclerotized S8 lies between S7 (= V6) and S9. Both characters are not known from any of the known subgenera of *Luciola*. Though the V6 of the male is somewhat similar to that of the subgenus *Pygoluciola* WITTMER, the male genitalia and T8 are very different (see BALLANTYNE 1968, Figs. 110, 139). Other species, such as *L. brahmina*, *L.*

cingulata, *L. flavida* and *L. japonica* are very similar to *L. substriata* in having V-shaped male lantern and substriated elytra. Probably these species represent a distinctive lineage in the genus *Luciola*. However, it is better to avoid any taxonomic change in the group as long as the genus *Luciola* is not revised thoroughly (see BALLANTYNE & LAMBKIN 2001).

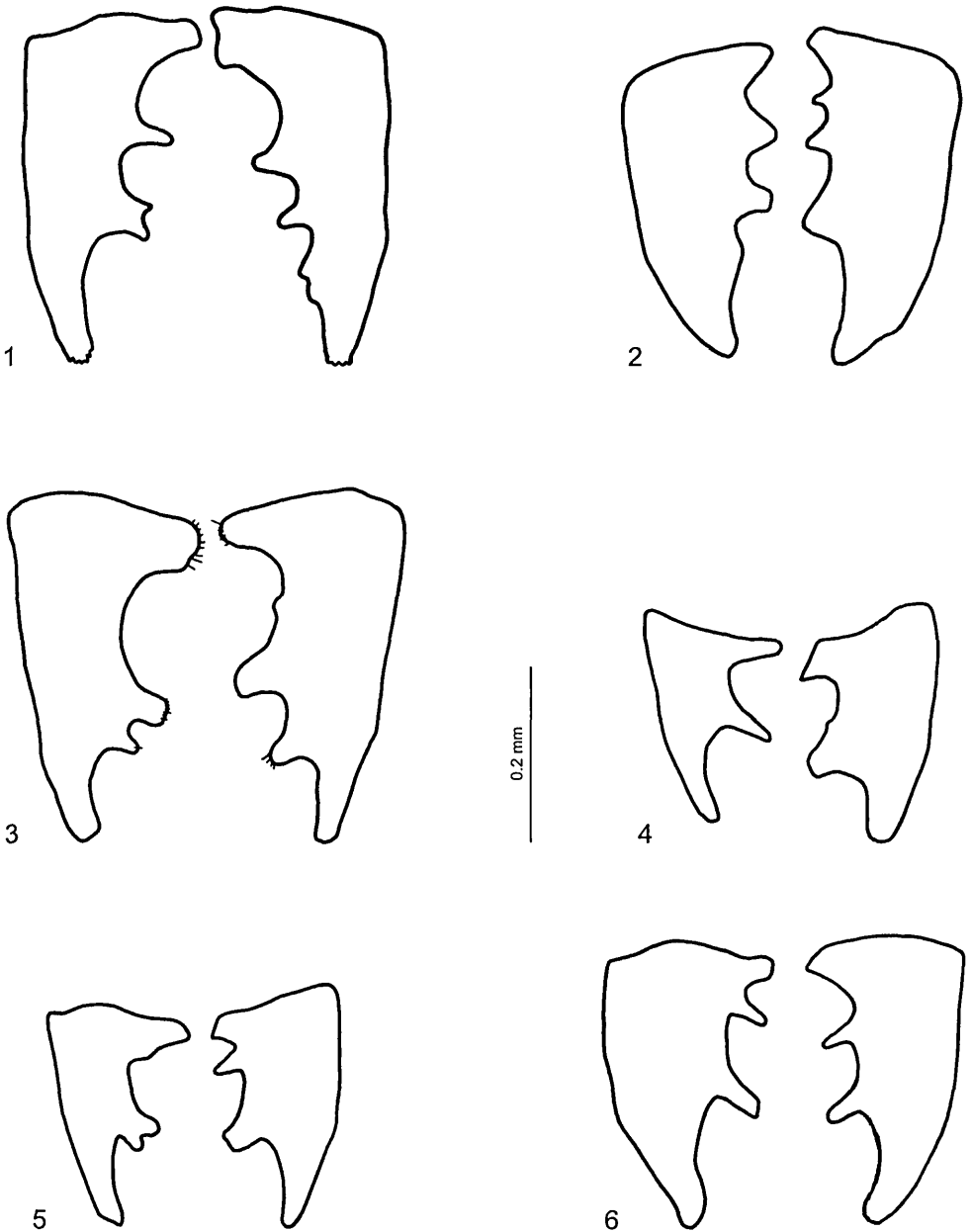
Discussion

Among the known species of aquatic fireflies, *L. substriata* is distinctive ecologically and morphologically. The first instar of *L. substriata* is able to breathe under water by means of its soft cuticle, while instars 2 - 4 are metapneustic, and the fifth instar is finally facultatively aquatic (HO et al. 1998). Young larvae have many lateral setae reminiscent of many terrestrial *Luciola* larvae, but the general morphology changes significantly with the second instar. They become elongate, resemble fallen leaves, and lose their lateral setae. Mature larvae develop very short wing pads and die if they are kept in water (T.-R. Chen, pers. comm.). The resemblance of the young larvae of *L. substriata* to those of terrestrial species suggests that the species has a terrestrial origin. The aquatic habit of *L. substriata* thus may have evolved independently from those species which possess tracheal gills. Furthermore, it seems obvious, that the aquatic habits of lucioline genera have evolved independently (see BLAIR 1927, and BERTRAND 1965, 1972, 1973).

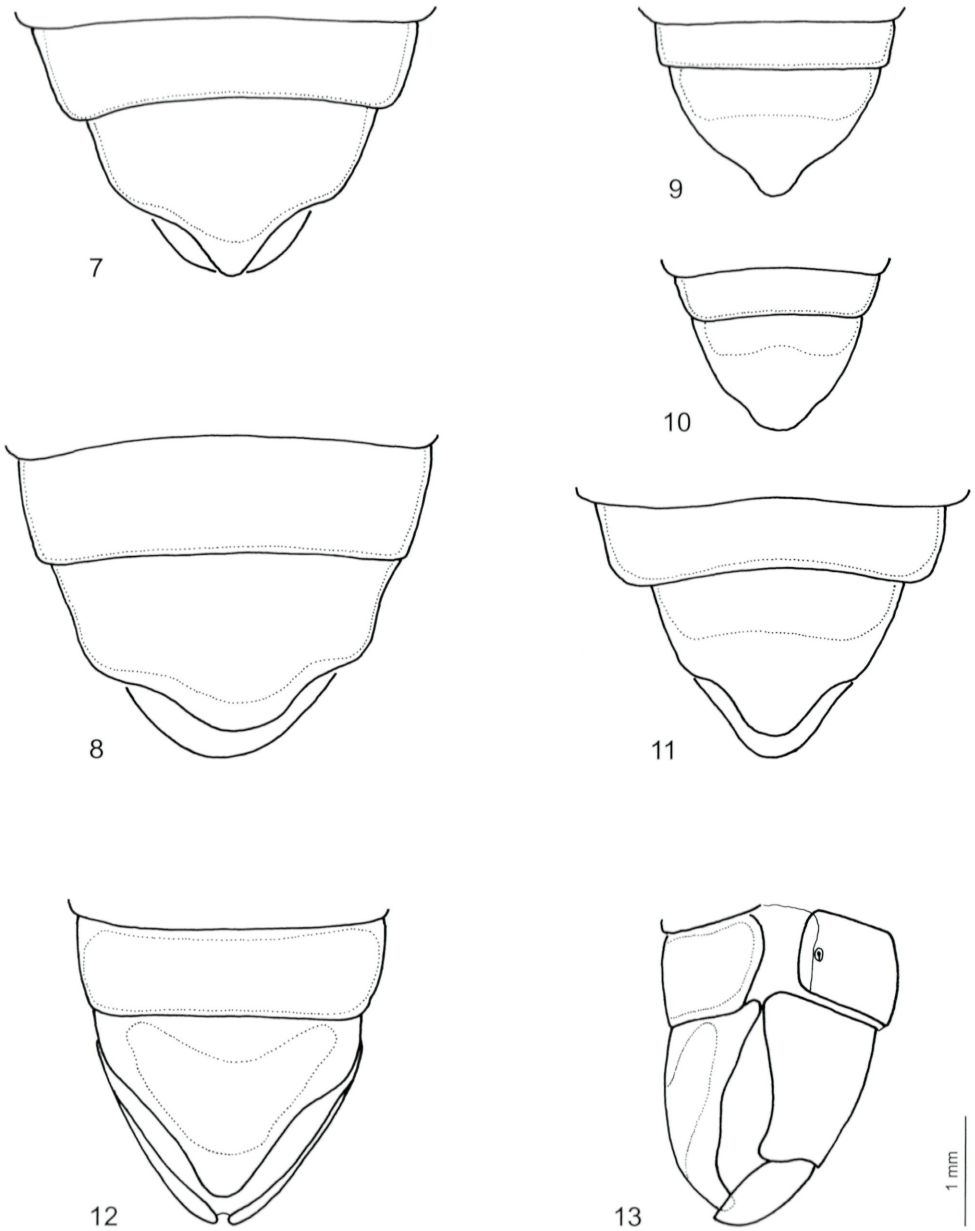
The aquatic larva described by ANNADALE (1900) from southern Thailand is very likely conspecific with *L. substriata* or a related species. Just as *L. substriata* they lack tracheal gills, they are able to walk upside down beneath the water surface and live in vegetation rich stagnant water. Furthermore, *L. japonica*, a species closely related to *L. substriata* and inferred to be aquatic by LLOYD & WING (1984), also is very likely to be confirmed as such.

On the other hand, *L. cruciata*, *L. hydrophila*, *L. lateralis*, *L. ficta* and *L. owadai* could be a monophyletic group featuring synapomorphic tracheal gills and projecting spiracles on the gills. A phylogenetic analysis based on 16S r-DNA sequence supported the monophyly of Japanese aquatic species (SUZUKI 1997).

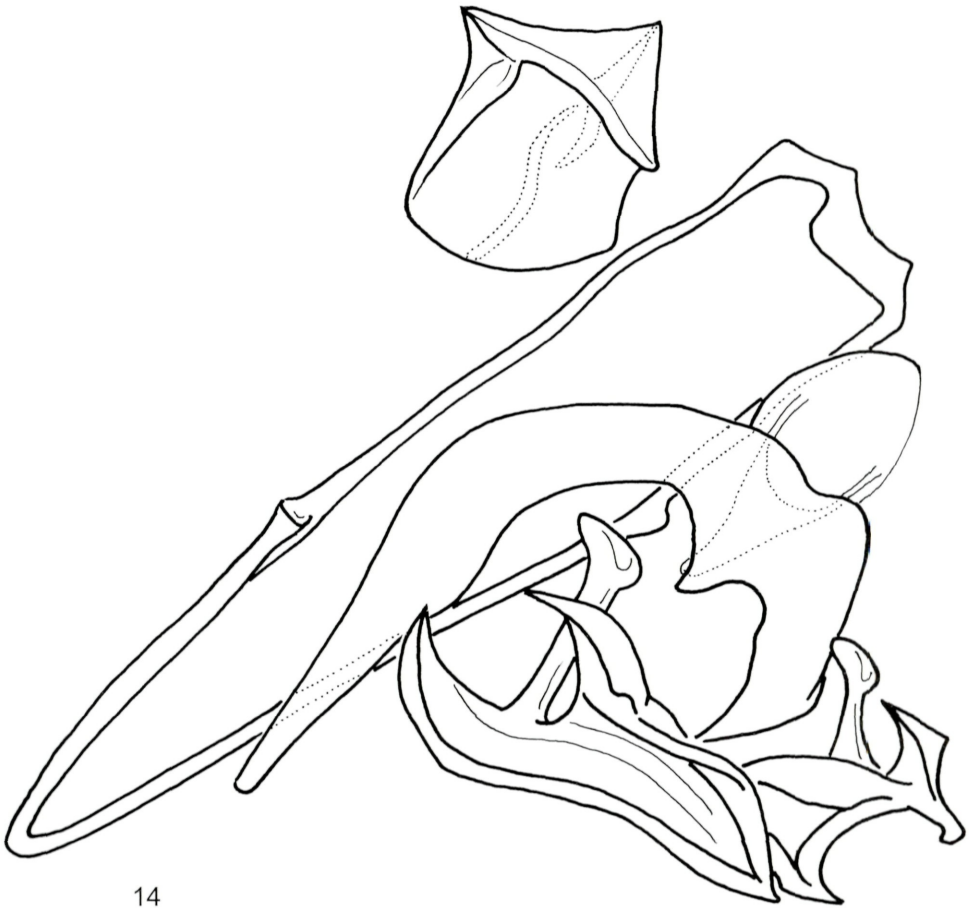
Besides truly aquatic species, some other fireflies were reported to be facultatively aquatic. They live near hygropetric habitats, creeks, swamps, spray zones and so on. MCDERMOTT (1953) found some larvae of an unknown species living in marine littoral areas in Jamaica. Larvae of *Atyphella aphrogeneia* (BALLANTYNE) were reported from the coral reefs in the spray zone in Papua New Guinea, and were found preying on sea snails (BUCK & BUCK 1970, LLOYD 1973, BALLANTYNE & BUCK 1979, BALLANTYNE & LAMBKIN 2001). The larvae of the North American *Pyraetomena lucifera* MELSHEIMER usually live in marshes and crawl on emergent parts of aquatic vegetation. They hunt freshwater snails under water but eat them above the water surface (BUSCHMAN 1984). Similar habits were found in *Pristolytus* species from Japan and Taiwan (OHBA & GOTO 1991, HO & JONG 1997, JENG et al. 2002). Typically, larvae of *P. kanoi* NAKANE from Taiwan live in hygropetric habitats which are well canopied and have thin water films on ambient rocks. No obvious structural adaptation to aquatic life could be found in the larval stages of facultatively aquatic species.



Figs. 1 - 6: Apical segment of male labial palpi: 1) *Luciola cruciata* (Honshu); 2) *L. owadai*, paratype; 3) *L. hydrophila*, paratype; 4) *L. ficta* (Taiwan); 5) *L. lateralis*, (Honshu); 6) *L. substriata* (Taiwan).

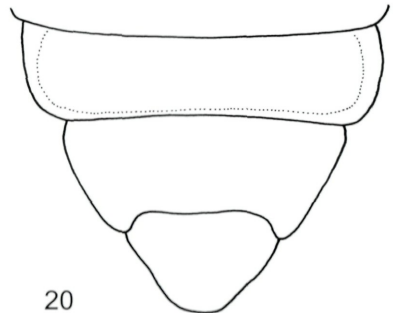
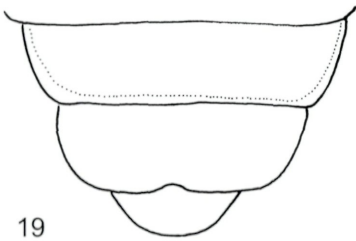
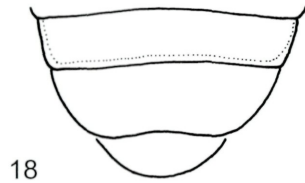
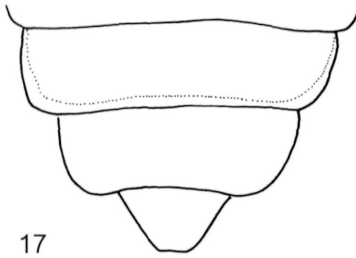
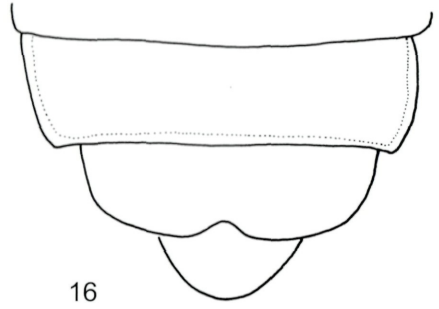
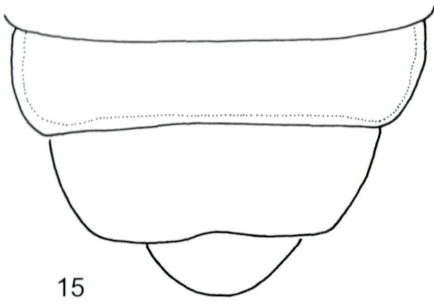


Figs. 7 - 13: Male abdominal ventrites 5-6: 7) *Luciola cruciata* (Honshu); 8) *L. owadai*, paratype; 9) *L. ficta* (Taiwan); 10) *L. lateralis* (Honshu); 11) *L. hydrophila*, paratype; 12) *L. substriata* (Taiwan); 13) same, lateral aspect. Dotted areas indicating luminous organs.

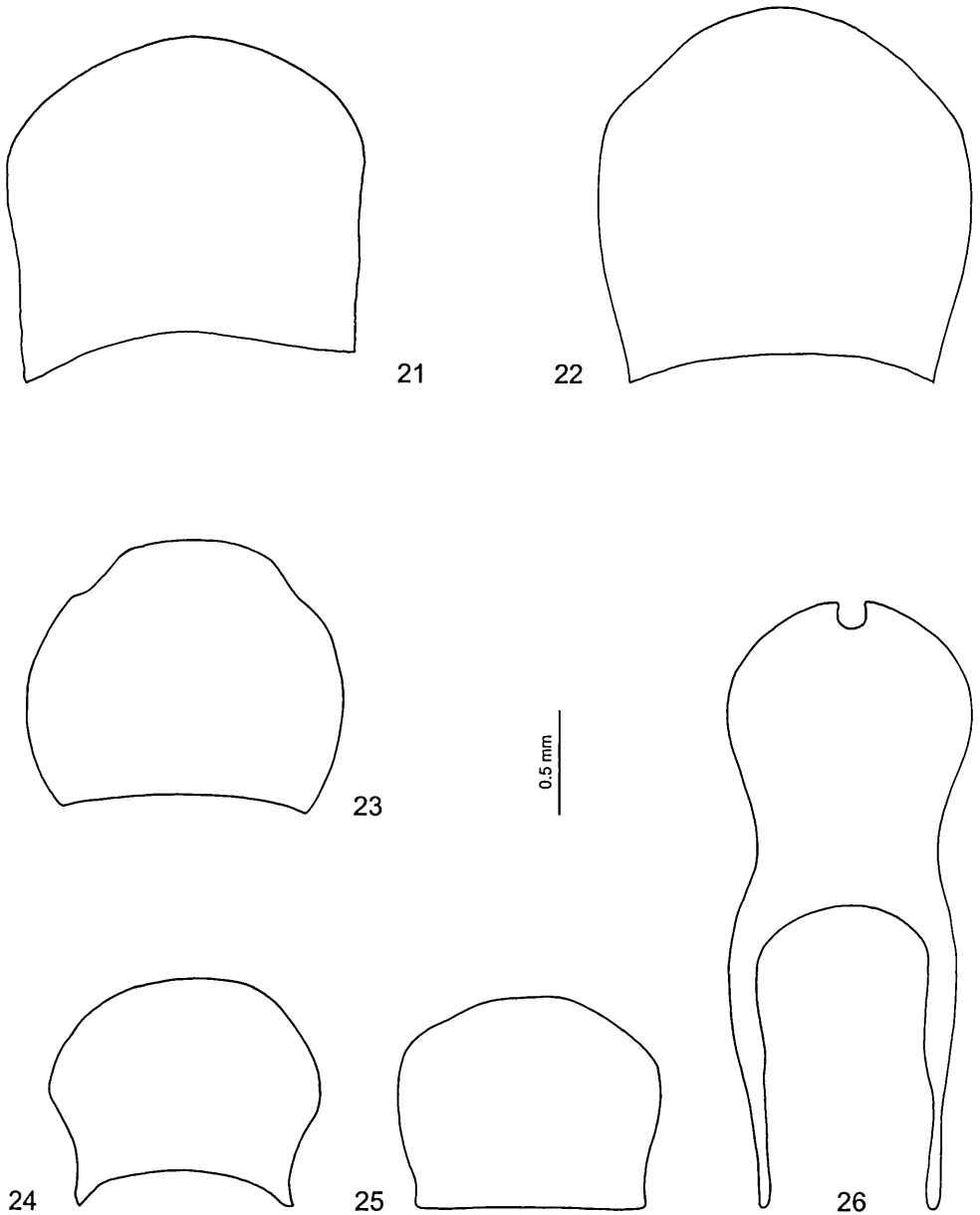


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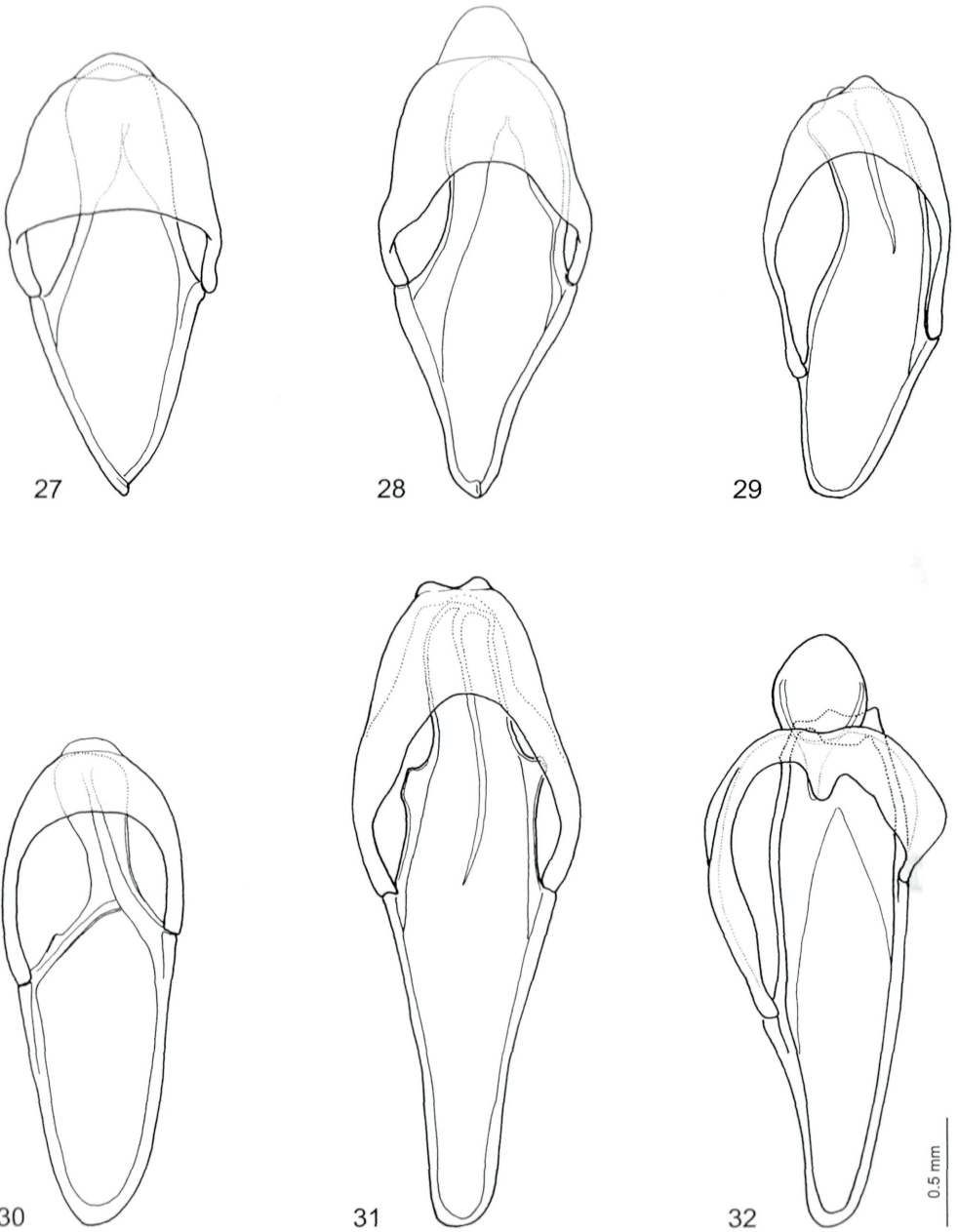
Fig. 14: Anatomy of male genital segments of *Luciola substriata*. From top: dorsal sclerites between abdominal tergite 8 and tergite of aedeagal sheath; tergite of aedeagal sheath; sternite of aedeagal sheath; ventral sclerite between abdominal ventrite 6 and aedeagal sheath.



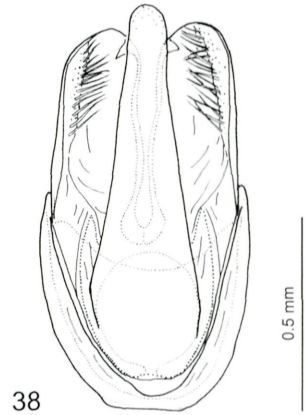
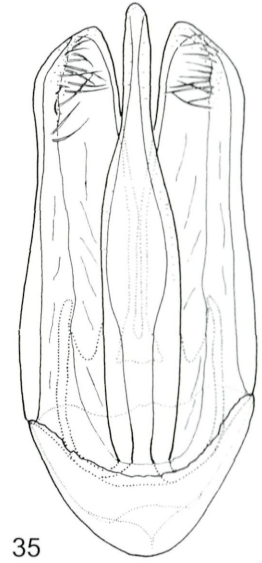
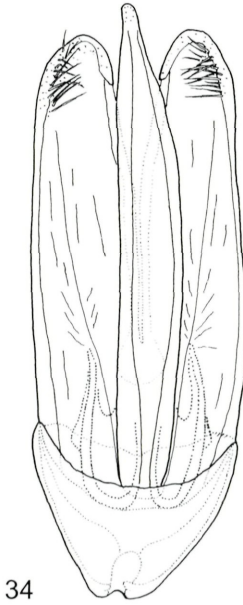
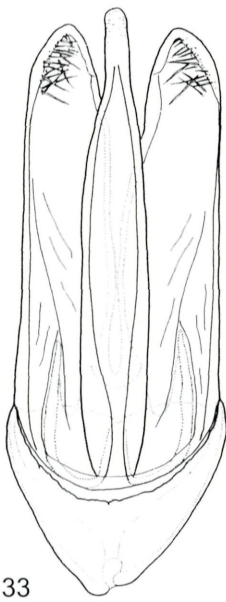
Figs. 15 - 20: Female abdominal ventrites 5-7: 15) *Luciola cruciata* (Honshu); 16) *L. owadai*, paratype; 17) *L. hydrophila*, paratype; 18) *L. lateralis* (Honshu); 19) *L. ficta* (Taiwan); 20) *L. substriata* (Taiwan). Dotted areas indicating luminous organs.



Figs. 21 - 26: Male abdominal tergite 8, pubescence omitted: 21) *Luciola cruciata* (Honshu); 22) *L. owadai*, paratype; 23) *L. hydrophila*, paratype; 24) *L. ficta* (Taiwan); 25) *L. lateralis* (Honshu); 26) *L. substriata* (Taiwan).



Figs. 27 - 32: Male aedeagal sheath: 27) *Luciola cruciata* (Honshu); 28) *L. owadai*, paratype; 29) *L. ficta* (Taiwan); 30) *L. lateralis* (Honshu); 31) *L. hydrophila*, paratype; 32) *L. substriata* (Taiwan), dorsal aspect.

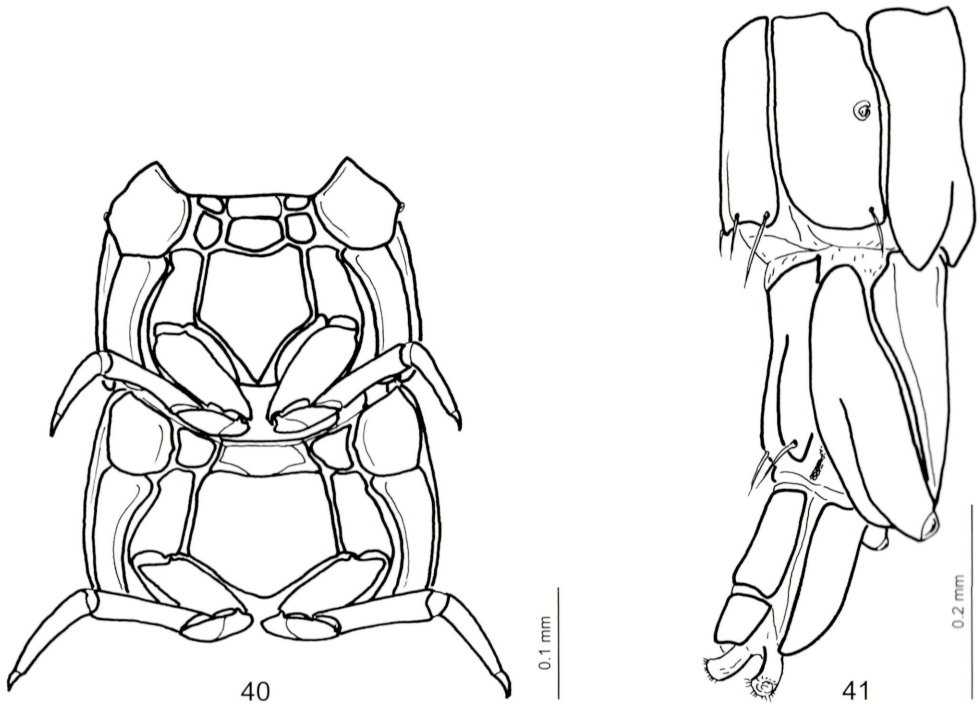


0.5 mm

Figs. 33 - 38: Male genitalia: 33) *Luciola cruciata* (E. Honshu); 34) *L. owadai*, paratype; 35) *L. hydrophila*, paratype; 36) *L. ficta* (Taiwan); 37) *L. lateralis* (Honshu); 38) *L. substriata* (Taiwan), ventral aspect.



Fig. 39: Habitus of mature larva of *Luciola hydrophila*.



Figs. 40 - 41: Mature larva of *Luciola substriata*: 40) venter of meso- and metathorax; 41) abdominal segments 7-10, lateral view.

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