

Research article

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Taxonomic revision of the *Lycocerus hanatanii* species group (Coleoptera, Cantharidae), with the description of new species from Taiwan

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Abstract. The *Lycocerus hanatanii* species group is revised, with the addition of seven taxa: *L. araticollis* (Fairmaire, 1897), *L. nigripennis* (Pic, 1938), *L. griseopubens* (Pic, 1928), *L. yitingi* Hsiao & Okushima sp. nov., *L. aurantiacus* Hsiao & Okushima sp. nov., *L. evangelium* Hsiao & Okushima sp. nov. and *L. kintaroi* Hsiao & Okushima sp. nov. Supplementary descriptions of the males of *L. araticollis* and *L. griseopubens* are provided. *Lycocerus nigripennis* (Pic, 1938) and *L. pictus* (Wittmer, 1983) are redescribed in detail. Each species is provided with photos or illustrations of genitalia of both sexes and abdominal ventrite VII of the female if available. Distribution maps and a key to the species of the *L. hanatanii* species group are presented. In addition, the monophyly of the *L. hanatanii* species group is supported based on a morphological phylogenetic analysis.

Keywords. Soldier beetles, taxonomy, new taxa, classification, Asia.

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Introduction

The genus *Lycocerus* Gorham, 1889 is a highly species-rich taxon in Asia, with more than 300 species and distributed in the Oriental and eastern Palaearctic regions (Kazantsev & Brancucci 2007). Okushima (2005) revised the Japanese fauna of *Lycocerus* and proposed 9 species groups with 23 subgroups based

on morphological characters, including external morphology and the genital organs of both sexes. Okushima & Brancucci (2008) and Yang *et al.* (2014) proposed two more species groups based on species from Laos, Vietnam and China. All of the Japanese species and several species from China, Taiwan, India and the Indo-China Peninsula were included in these defined species groups (Okushima 2005, 2007a, 2007b; Okushima & Brancucci 2008; Yang & Yang 2011; Okushima & Yang 2013; Yang *et al.* 2014; Hsiao & Okushima 2015). However, there has been no systematic study to examine the monophyly of each species group or to clarify their relationship using a phylogenetic analysis.

The *Lycocerus hanatanii* species group is characterized by the following combination of characters: small-sized body; small and not very prominent eyes; knife-shaped and slender apical maxillary palpomere; filiform antennae, not exceeding half of elytral length, without groove; subquadrate pronotum; both sexes with simple tarsal claws; laterophyses of aedeagus very short, barely visible or invisible in lateral view; long spermathecal duct; spermatheca provided with a spiral tube. So far only three species, *L. hanatanii* (Okushima, 1996), *L. ueharaensis* (Okushima, 1996) and *L. pictus* (Wittmer, 1983), have been included (Okushima 2005).

In this study, we aim to revise the fauna of this species group, with the addition of three new members, *L. araticollis* (Fairmaire, 1897), *L. nigripennis* (Pic, 1938) and *L. griseopubens* (Pic, 1928), and the description of four new taxa, *L. yitingi* Hsiao & Okushima sp. nov., *L. aurantiacus* Hsiao & Okushima sp. nov., *L. evangelium* Hsiao & Okushima sp. nov., and *L. kintaroi* Hsiao & Okushima sp. nov. We also use a morphology-based phylogenetic approach to support our classification and confirm the monophyly of the *L. hanatanii* species group.

Materials and methods

The materials examined in this paper are deposited in the following institutions and personal collection:

BMNH	=	Natural History Museum, London, UK
CAS	=	California Academy of Sciences, San Francisco, USA
CBM	=	Natural History Museum and Institute, Chiba, Japan
EUMJ	=	Ehime University Museum, Matsuyama, Japan
KURA	=	Kurashiki Museum of Natural History, Kurashiki, Japan
MNHN	=	Muséum national d'Histoire naturelle, Paris, France
NHMB	=	Naturhistorisches Museum Basel, Switzerland
NMNS	=	National Museum of Natural Science, Taichung, Taiwan
SDEI	=	Senckenberg, Deutsches Entomologisches Institut, Müncheberg, Germany
TARI	=	Taiwan Agricultural Research Institute, Wufeng, Taichung, Taiwan
YHC	=	Y. Hsiao's private collection

The terminology used in the descriptions and the methods employed follow those of Okushima (2005) and Hsiao (2015), but Double Stain (BioQuip, USA) was used for the staining of female genitalia. The distribution map was prepared using the SimpleMappr program (Shorthouse 2010), based on the label data of examined material in this study. Some old names or supplementary information on localities are updated in square brackets [] if necessary. The type specimen data are quoted verbatim: [p] indicates that the following data are printed and [h] that they are handwritten. A double backslash (//) is used to separate data from different labels and a single one (/) to separate data from different lines on the same label. Abbreviations:

ex	=	specimen/s
ag	=	accessory gland
di	=	diverticulum

dp = dorsal plate
 is = inner sac
 lp = laterophyses
 sd = spermathecal duct
 sp = spermatheca
 te = tegmen
 va = vagina
 vp = ventral process

Following Okushima (2005), Kasantsev (1999) and our observations, 29 adult morphological characters and 1 geographical character were used for the phylogenetic analysis as follows:

- 01 Body size: (0) small (5–7mm); (1) medium (8–10mm); (2) large (> 10mm).
- 02 Body form judged on the ratio of the length to the width at the widest part of the conjoint elytra: (0) stout (about 2.2); (1) middle (about 2.5–3.0); slender (mainly greater than 3.0).
- 03 Antennal length in males: (0) exceeding ½ elytral length; (1) extending to ½ elytral length.
- 04 Antennal length in females: (0) extending to ½ of elytral length; (1) barely exceeding the humeri, but not extending to ½ of elytral length.
- 05 Form of antennae: (0) filiform; (1) serrate.
- 06 Grooves on male antennal segments: (0) absent; (1) present.
- 07 Shape of terminal maxillary palpomere: (0) stout (Fig. 1A); (1) subtriangular (Fig. 1B); (2) slender (Fig. 1C).
- 08 Size of eyes: (0) large and prominent (Fig. 1D); (1) small and not very prominent (Fig. 1E).
- 09 Vertex: (0) flat and glabrous; (1) faintly hollowed and distinctly punctate.
- 10 Form of pronotum: (0) trapezoid (Fig. 1F); (1) subquadrate (Fig. 1G); (2) flattened and rectangular (Fig. 1H).
- 11 Greatest width of pronotum in male: (0) wider than head; (1) nearly as wide as head; (2) narrower than head.
- 12 Angular convexity on pronotum: (0) distinct (Fig. 1G); (1) indistinct.
- 13 Form of elytra: (0) subparallel at the sides; (1) apically expanded; (2) moderately narrowed apically; (3) strongly narrowed apically.
- 14 Costae on elytra: (0) distinct; (1) hardly recognizable.
- 15 Size of legs: (0) stout (Fig. 1I); (1) slender (Fig. 1J).
- 16 Form of male claws: (0) all claws simple; (1) each outer claw of fore and middle legs with tooth.
- 17 Form of female claws: (0) all claws simple; (1) each outer claw of fore and middle legs with tooth.
- 18 Dorsal plate of each paramere of aedeagus: (0) fused or nearly fused; (1) separated.
- 19 Inner surface of dorsal plate of aedeagus: (0) modified, with processes; (1) simple.
- 20 Laterophyses of aedeagus: (0) nearly fused; (1) widely separated on both sides of median lobe.
- 21 Laterophyses of aedeagus: (0) long, distinctly visible in lateral view; (1) short, barely visible or invisible in lateral view.
- 22 Apical part of median lobe of aedeagus: (0) widened apically; (1) strongly narrowed apically; (2) moderately narrowed apically.
- 23 Apical part of vagina: (0) broad; (1) extended apically as a thick duct.
- 24 Shape of diverticulum: (0) short, thick and rod-shaped; (1) long and thin; (2) short and thin.
- 25 Spermathecal duct: (0) absent; (1) present.
- 26 If spermathecal duct present, length of spermathecal duct: (0) short; (1) long.
- 27 Shape of spermatheca: (0) short, sac-shaped; (1) long and thin, provided with spiral tube(s).
- 28 If spermatheca long and thin: (0) provided with a spiral tube; (1) provided with two spiral tubes.
- 29 Shape of accessory gland: (0) simple (thin, filiform); (1) modified (abruptly expanded).
- 30 Distribution: (0) continental; (1) insular.

Table 1. Data matrix.

Taxa	<i>Themus nobilis nobilis</i>	<i>Lycocerus maculicollis</i>	<i>L. suturellus suturellus</i>	<i>L. vitellinus</i>	<i>L. purpureus</i>	<i>L. adusticollis</i>	<i>L. yamatensis</i>	<i>L. aegrotus</i>	<i>L. watanabei</i>	<i>L. michiaki</i>	<i>L. sichuanus</i>	<i>L. rhagonychiformis</i>	<i>L. hanatanii</i>	<i>L. ueharaensis</i>	<i>L. pictus</i>	<i>L. yitingi</i> sp. nov.	<i>L. araticollis</i>	<i>L. nigripennis</i>	<i>L. evangelium</i> sp. nov.	<i>L. griseopubens</i>	<i>L. aurantiacus</i> sp. nov.	<i>L. kintaroi</i> sp. nov.
01	2	2	2	1	0	1	1	1	2	1	1	0	0	0	0	0	0	0	0	0	0	0
02	0	0	1	1	0	1	1	1	2	2	2	1	1	1	1	1	1	1	1	1	1	1
03	1	0	0	0	1	0	0	0	0	0	0	0	1	1	1	1	1	0	1	?	0	1
04	1	1	0	0	1	0	0	0	0	0	0	0	1	1	1	1	?	1	1	1	1	?
05	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
06	1	0	1	1	0	1	1	1	0	1	1	0	0	0	0	0	0	0	0	?	0	0
07	0	1	1	2	0	1	2	1	1	1	1	1	2	2	2	2	2	2	2	2	2	2
08	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1	1
09	0	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
10	2	0	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1
11	0	0	1	1	1	2	2	1	1	1	2	2	1	1	1	1	1	1	1	1	1	1
12	1	1	1	1	1	1	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0	0
13	2	1	0	0	0	0	0	0	0	3	0	0	0	0	0	0	0	0	0	0	0	0
14	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
15	1	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
16	0	0	0	1	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
17	0	1	1	1	1	0	1	1	0	1	1	0	0	0	0	0	?	0	0	0	0	?
18	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
19	0	0	1	1	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	1	1	1
20	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
21	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	1	1	1	1	1	1	1
22	0	2	2	2	2	2	2	2	2	2	2	1	1	1	1	1	?	1	1	1	1	1
23	0	0	1	0	0	0	0	1	0	0	0	1	1	1	1	1	?	1	1	?	1	?
24	0	1	1	1	1	2	1	1	1	2	1	1	1	1	1	1	?	1	1	?	1	?
25	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1	?
26	-	0	0	0	0	0	0	1	1	0	0	1	1	1	1	1	?	1	1	?	1	?
27	0	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	?	1	1	?	1	?
28	-	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	?	0	0	?	0	?
29	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	?	0	0	?	0	?
30	0	0	1	1	0	1	1	1	1	0	0	1	1	1	1	1	0	1	1	0	1	1

The ingroup taxa include 3 *Lycocerus* species previously attributed to the *L. hanatanii* Group in Okushima (2005) and 6 species we herein attribute to this species group, *L. rhagonychiformis* (Wittmer, 1983) and one representative species of each defined species group, including *L. maculicollis* (Hope, 1831), *L. suturellus suturellus* (Motschulsky, 1860), *L. vitellinus* (Kiesenwetter, 1874), *L. purpureus* Kazantsev, 2007, *L. adusticollis* (Kiesenwetter, 1874), *L. yamatensis* Okushima, 2005, *L. watanabei*

(Ishida & M. Satô, 1993), *L. aegrotus* (Kiesenwetter, 1874), *L. michiakii* Okushima & Brancucci, 2008 and *L. sichuanus* Y. Yang & X. Yang, 2014. The outgroup taxon is *Themus (Themus) nobilis nobilis* (Gorham, 1889). The data matrix (Table 1) was coded and edited with WinClada ver. 10.00.08 (Nixon 2002). Inapplicable data were coded as “-” and missing data were coded with “?”. Most characters were based on our own observations. The data matrix was analyzed using NONA ver. 2.0 (Goloboff 1999) from WinClada. All characters were run equally weighted and not additive. The commands of heuristic analysis, ‘hold 10000’, ‘hold/20’, ‘mult*50’ and ‘mult*max*’ were used to search for the most parsimonious tree(s). In the resultant trees, the unsupported nodes were hard collapsed and only the best trees were kept in WinClada. The characters and character states on the tree were optimized using unambiguous character changes in WinClada.

Results

Phylogenetic analysis of the L. hanatanii species group

The heuristic analysis resulted in 10 most parsimonious trees (L 63; CI 61; RI 80) and their strict consensus tree (L 72; CI 54; RI 72) is used in the discussion (Fig. 9). The monophyly of the *L. hanatanii* species group is supported by several synapomorphies: relatively short antennae, slender apical maxillary palpomere and very short laterophyses of the aedeagus. *Lycocerus rhagonychiformis* (Wittmer, 1983) is presented as the sister group of the *L. hanatanii* species group, which shows high morphological similarity to it. However, the relationships between the clade *L. hanatanii* Group + *L. rhagonychiformis* and the other species groups are presented as an unresolved bush. Hence, the phylogenetic position of this clade remains unknown.

Taxonomy

Key to the species of the *L. hanatanii* species group

1. Coloration: mostly yellowish or blackish, with wide yellowish stripe on head, pronotum and elytra, respectively 2
 - Coloration: mostly blackish; pronotum completely black or fringed with yellowish margins or orange to yellowish brown, with black marking in middle; elytra completely black, or with small and slender yellowish brown stripes on humeri 5
2. Head black, with frons yellowish; pronotum yellowish brown, with a large black marking in middle; aedeagus: dorsal plate of each paramere nearly touching on inner margin (Fig. 1K) 3
 - Head dark yellow, with a black marking on the vertex; pronotum dark yellow, with a longitudinal black marking in middle, elytra completely pale yellow or fuscous, with pale yellow longitudinal stripe on each elytron; aedeagus: dorsal plate of each paramere concave on inner margin (Fig. 1L) 4
3. Aedeagus: ventral process expanded apically, curved inwards; dorsal plate with a rounded apex; laterophyse acute and barely visible in lateral view *L. hanatanii* (Okushima, 1996)
 - Aedeagus: ventral process almost straight and slightly curved inwards; dorsal plate with a pointed apex; laterophyse stout and invisible in lateral view *L. ueharaensis* (Okushima, 1996)
4. Elytra completely pale yellow; aedeagus: laterophyse with pointed apex (Fig. 3B) *L. pictus* (Wittmer, 1983)
 - Elytra fuscous, with wide pale yellow longitudinal stripe on each elytron; aedeagus: laterophyse with truncated apex (Fig. 3E) *L. yitingi* Hsiao & Okushima sp. nov.
5. Aedeagus: dorsal plate of each paramere nearly touching on inner margin (Fig. 1K) 6
 - Aedeagus: dorsal plate of each paramere concave on inner margin (Fig. 1L) 9

6. Pronotum completely black; aedeagus: apical margin of dorsal plate truncated (Fig. 4B) *L. araticollis* (Fairmaire, 1897)
 – Pronotum completely black or orange, with a black marking in middle; aedeagus: apical margin of dorsal plate rounded (Fig. 4C, G, J) 7
7. Coloration of pronotum varying from completely black or orange, with a black marking in middle; aedeagus: dorsal plate longer than ventral process *L. nigripennis* (Pic, 1938)
 – Coloration of pronotum uniform, orange, with a black marking in middle; aedeagus: dorsal plate nearly as long as ventral process 8
8. Surface of body lusterless; aedeagus: ventral process moderately expanded apically, curved inwards *L. griseopubens* (Pic, 1928)
 – Surface of body semilustrous; aedeagus: ventral process strongly expanded apically, slightly curved inwards *L. aurantiacus* Hsiao & Okushima sp. nov.
9. Body and legs nearly black; aedeagus: apex of laterophyse more slender and acute (Fig. 5B) *L. evangelium* Hsiao & Okushima sp. nov.
 – Pronotum black, fringed with yellowish margins; aedeagus: apex of laterophyse far from apical margin of dorsal plate in lateral view (Fig. 5E) *L. kintaroi* Hsiao & Okushima sp. nov.

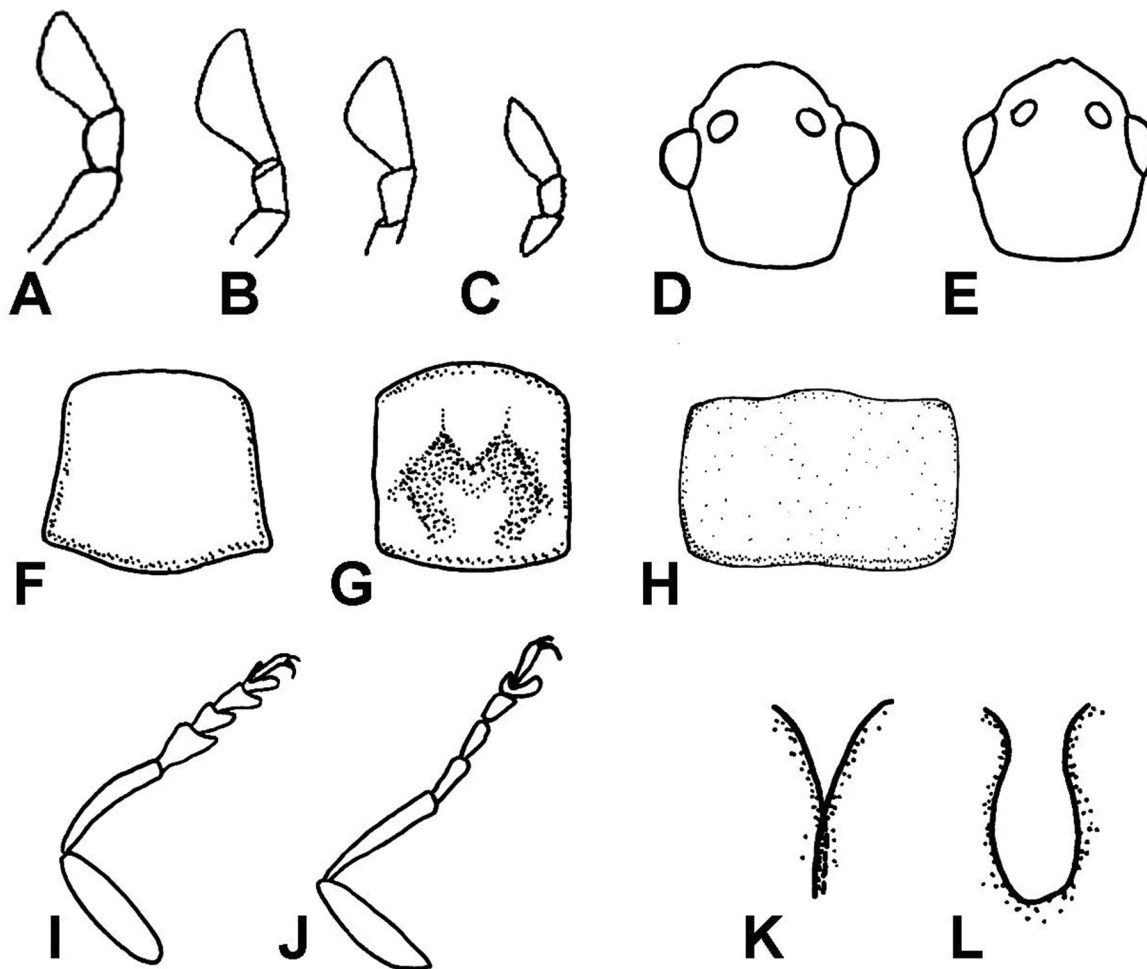


Fig. 1. Morphological characters used for the phylogenetic analysis and key. A–C. Terminal maxillary palpomere. D–E. Eyes. F–H. Pronotum. I–J. Leg. K–L. Inner margin of dorsal plate of aedeagus.

Class Hexapoda Blainville, 1816
Order Coleoptera Linnaeus, 1758
Superfamily Elateroidea Leach, 1815
Family Cantharidae Imhoff, 1856

Genus *Lycocerus* Gorham, 1889

Lycocerus hanatanii Group

Lycocerus hanatanii (Okushima, 1996)

Athemellus hanatanii Okushima, 1996: 118, figs 6–10.

Athemus (*Athemellus*) *hanatanii* – Takahashi 1998: 43.

Lycocerus hanatanii – Okushima 2005: 242, figs 11r, 13u, 15r, 60, 131, 174. — Kazantsev & Brancucci 2007: 250.

Material examined

Holotype

JAPAN: ♂, Mt. Omoto-dake, Ishigaki-jima Is., Ryukyus, 1 Mar. 1990, Y. Okushima leg. (KURA).

Other material

JAPAN: 1 ♂, 1 ♀, Omoto-dake, Ishigaki-jima, Okinawa, Ryukyu, 9 Mar. 1999, T. Kurihara leg. (KURA); 1 ♂, 1 ♀, same locality, 12 Mar. 2002, T. Kurihara leg. (KURA); 15 ♂♂, 7 ♀♀, same locality, 21 Feb. 2003, T. Nakata leg. (13 ♂♂, 5 ♀♀ in KURA; 2 ♂♂, 2 ♀♀ in YHC); 2 ♂♂, Aira-gawa, Iriomote-jima, Okinawa, Ryukyu, 14 Mar. 1999, T. Kurihara leg. (KURA).

Description

See Okushima (1996, 2005).

Distribution

Japan (Okinawa: Iriomote Island and Ishigaki Island).

Lycocerus ueharaensis (Okushima, 1996)

Athemellus ueharaensis Okushima, 1996: 121, figs 11–14.

Athemus (*Athemellus*) *ueharaensis* – Takahashi 1998: 43.

Lycocerus ueharaensis – Okushima 2005: 245, figs 61, 132, 175. — Kazantsev & Brancucci 2007: 254.

Material examined

Holotype

JAPAN: ♂, Mt. Uehara-yama, Iriomote-jima Is., Ryukyus, 11 Mar. 1995, Y. Okushima leg. (KURA).

Other material

JAPAN: 1 ♂, Nakasuji, Ishigaki-jima, Okinawa, Ryukyu, 6 Mar. 1999, T. Kurihara leg. (KURA); 10 ♂♂, Yanbare, Ishigaki-jima, Okinawa, Ryukyu, 3 Feb. 2003, T. Nakata leg. (8 ♂♂ in KURA; 2 ♂♂ in YHC).

Description

See Okushima (1996, 2005).

Distribution

Japan (Okinawa: Iriomote Island and Ishigaki Island).

Lycocerus pictus (Wittmer, 1983)

Figs 2A–B, 3A–C, 6A–B, 7

Athemellus pictus Wittmer, 1983: 170.

Lycocerus pictus – Okushima 2005: 242. — Okushima 2008: 282, fig. 26. — Kazantsev & Brancucci 2007: 253. — Satô *et al.* 2015: 51.

Diagnosis

This species resembles *L. yitingi* Hsiao & Okushima sp. nov.; the differential diagnosis is given in Table 2.

Material examined

Holotype

TAIWAN: ♂, Nan shan chi, Nantou Hsien, 9–11 Mar. 1980, T. Shimomura leg. (NHMB).

Paratypes

TAIWAN: 10 ex, same data as for holotype (NHMB).

Other material

TAIWAN: 15 ♂♂, 7 ♀♀, Nanshanchi, Nantou, 27 Mar. 1981, H. Yoshimoto leg. (KURA); 1 ♀, Hsileng, Taouan, 26 Apr. 1982, N. Obayashi leg. (KURA); 13 ♂♂, 5 ♀♀, Nanshanchi, Nantou, 13 Apr. 1985, Y. Kusakabe leg. (KURA); 1 ♀, Kukuan, Taichung, 11–12 May 1986, C.-S. Lin leg. (NMNS); 4 ♂♂, 3 ♀♀, Nanshanchi, Nantou, 5 Apr. 1988, C. Lou leg. (KURA); 1 ♂, Baling, Taoyuan, 5 Apr. 1991, Y. Okushima leg. (KURA); 1 ♀, Shitzutou, Nantou, 9 Apr. 1991, Y. Okushima leg. (KURA); 28 ♂♂, 37 ♀♀, Nanshanchi, Nantou, 10 Apr. 1991, Y. Okushima leg. (KURA); 1 ♂, 3 ♀♀, Kukuan, Taichung, 11 Apr. 1991, Y. Okushima leg. (KURA); 1 ♀, Shitzutou, Nantou, 12 Apr. 1991, Y. Okushima leg. (KURA); 1 ♂, Nanshanchi, Nantou, 12 Apr. 1991, K. La leg. (KURA); 4 ♂♂, 10 ♀♀, Nanshanchi, Nantou, 3 Apr. 1993, K. Okajima & T. Nonaka leg. (KURA); 4 ♂♂, Nanshanchi, Nantou, 6 Apr. 1993, T. Nonaka leg. (KURA); 3 ♀♀, Wushe, Nantou, 28–29 Apr. 1993, C.-S. Lin & W.-T. Yang leg. (NMNS); 4 ♂♂, 14 ♀♀, Lushan Hot Spring, Nantou, 24 Apr. 1994, T. Kishimoto leg. (KURA); 1 ♂, Gauvaw [=Luofu], 380 m, Taovuan, 25 Apr. 1996, L.-J. Wang leg. (KURA); 4 ♂♂, 3 ♀♀, Nanshanchi, Nantou, 21 Mar. 1998, F. Hayashi leg. (KURA); 3 ♂♂, Chunyang, Nantou, 12 Mar.–9 Apr. 2002, C.-S. Lin & W.-T. Yang leg. (NMNS); 1 ♂, 1 ♀, Nanshanchi, Nantou, 1 Apr. 2012, Y.-T. Wang leg. (YHC); 1 ♀, Puli, Nantou, Apr. 2014, C.-H. Wu leg. (YHC); 2 ♂♂, Chungyang, Nantou, 4 May 2014, Y. Hsiao leg. (YHC); 1 ♀, Simashuan Forest Trail, 500m, Miaoli, Y. Hsiao leg. (YHC).

Redescription

Coloration

Eyes black. Head dark yellow, with black marking on vertex. Antennae dark yellow or black, with first two or three segments and basal parts of remaining segments dark yellow. Pronotum dark yellow, with black marking in medio-longitudinal part. Elytra completely pale yellow or slightly dark in narrow suture. Legs dark yellow, with apical parts of femora, tibiae and tarsi blackish. Prosternum dark yellow, mesoventrites, metaventrites and abdomen black, with margin of abdominal ventrites and entire abdominal ventrite VII yellowish brown. Body closely covered with fine yellowish pubescence; anterior margin of clypeus fringed with pale bristles; antennae, elytra and legs with some yellowish bristles intermingled with primary pubescence.

Male (Fig. 2A)

HEAD. Nearly as long as wide; vertex faintly hollowed, depressed along apical margin of clypeus and in lateral areas before eyes; surface densely and finely punctate and semilustrous; anterior margin of clypeus

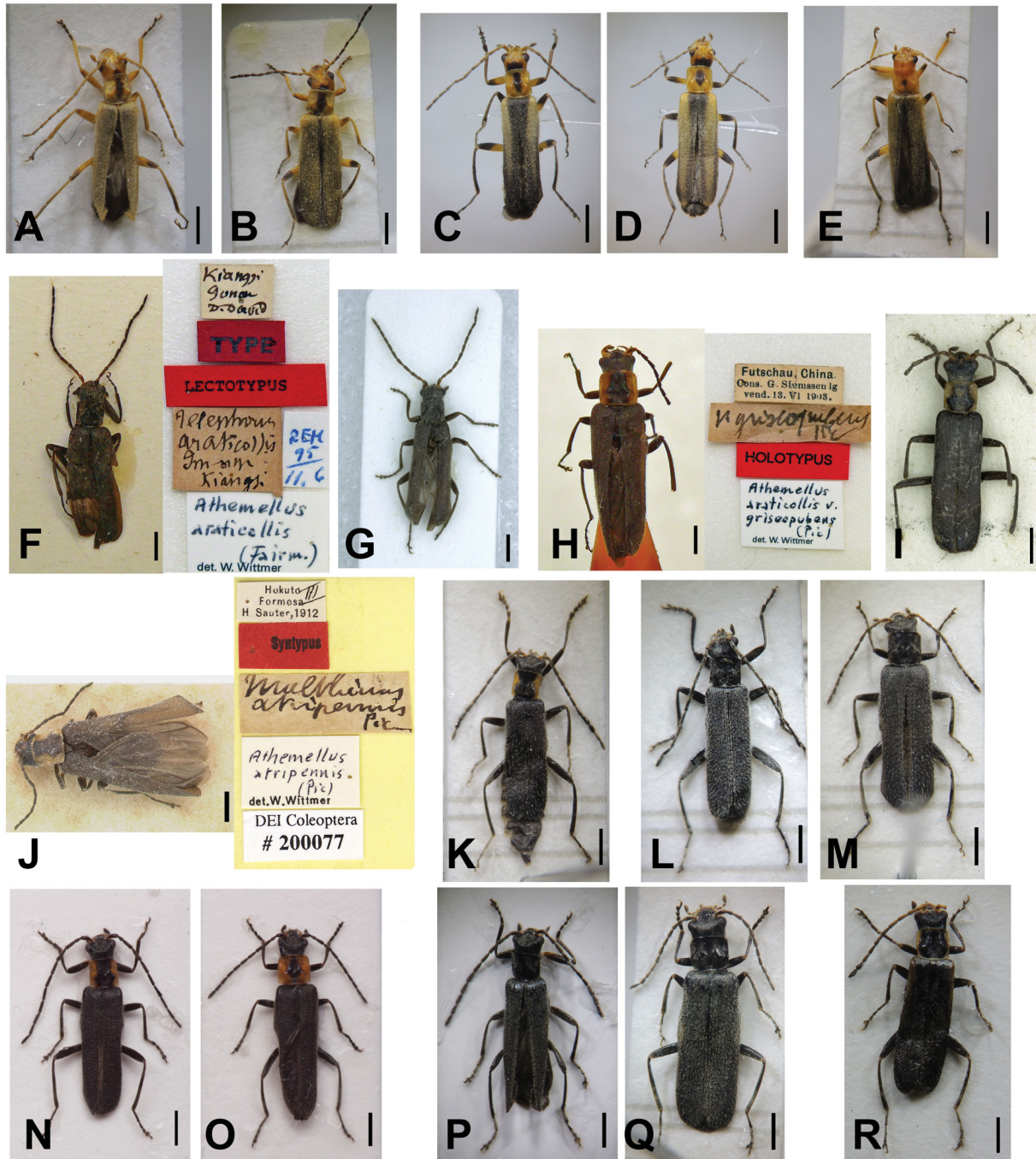


Fig. 2. Habitus, dorsal view. A–B. *Lycocerus pictus* (Wittmer, 1983). C–E. *L. yitingi* Hsiao & Okushima sp. nov. F–G. *L. araticollis* (Fairmaire, 1897). H–I. *L. griseopubens* (Pic, 1928). J–M. *L. nigripennis* (Pic, 1938). N–O. *L. aurantiacus* Hsiao & Okushima sp. nov. P–Q. *L. evangelium* Hsiao & Okushima sp. nov. R. *L. kintaroi* Hsiao & Okushima sp. nov. C, F, H, J, N, P, R. Name-bearing types. D, O, Q. Paratypes. A–B, E, G, I, K–M. Non-type specimens. A, C, F–G, I, K–L, N, P, R. Male. B, D–E, H, J, M, O, Q. Female. Scale bars: 1.0 mm.

arcuate and faintly indented in middle; eyes not so large, globular and slightly prominent, ratio of eye diameter to interocular space 1:4.4; terminal labial palpomeres rounded ax-shaped; terminal maxillary palpomeres rounded ax-shaped; antennae filiform, extending to elytral midlength; antennomere I clavate, II short and a little expanded apically, III to XI subcylindrical, all antennomeres without groove, ratio of antennomere lengths: 13:10:13:15:16:16:14:14:13.5:13:14.

PRONOTUM. Subquadrate, slightly narrower than head, nearly as long as wide; anterior and posterior margins moderately arcuate; lateral margins feebly sinuate, slightly diverging posteriorly; anterior angles rounded; posterior angles obtuse; dorsum convex in postero-lateral and hollowed in antero-lateral areas; medio-longitudinal groove distinct in posterior half; surface smooth and semilustrous. Scutellum triangular, with rounded apex.

ELYTRA. Conjointly about 1.4 times as wide as pronotum, about 3.0 times as long as wide, sides subparallel; surface densely and finely punctate and without luster.

LEGS. Moderately slender; femora mostly straight; tibiae mostly straight, with basal part feebly arcuate; claws simple.

AEDEAGUS (Fig. 3A–C). Ventral process expanded apically, apex curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere as long as ventral process, stout and subtruncated, slightly narrowed apically, apical margin with some hairs on it, concave on inner margin. Laterophyse very short, with pointed apex, invisible in lateral view. Inner sac swollen apically, somewhat shorter than tegmen.

Body length 4.00–5.50 mm; width 1.00–1.50 mm.

Female (Fig. 2B)

Similar to male. Body wider than in male. Eyes somewhat smaller than in male, ratio of eye diameter to interocular space 1:4.9. Antennae distinctly shorter than in male, barely exceeding humeri, ratio of antennomere lengths: 13.5:10:13:15:15:14:14:14:13:12:14.

PRONOTUM. Nearly as wide as head, about 1.10 times as long as wide. Elytra conjointly about 1.5 times as wide as pronotum, about 2.6 times as long as wide. Claws simple. Abdominal ventrite VII widely emarginate on each side of terminal margin, forming subtriangular lateral lobes, median lobe moderately developed and triangularly concave in middle, median lobe indistinct in some specimens (Fig. 6A).

FEMALE GENITALIA (Fig. 6B). Vagina broad and rounded, abruptly extended apically as a long and thick duct; diverticulum and spermathecal duct arising from apex of long duct of vagina; diverticulum moderately thin and spiral; spermathecal duct shorter than diverticulum; spermatheca provided with thin spiral tube, tube longer than diverticulum; accessory gland thin, shorter than spermatheca.

Body length 5.00–6.00 mm; width 1.50–1.75 mm.

Remarks

Individuals of this species were observed visiting flowers of Lauraceae during the day.

Distribution (Fig. 7)

Taiwan (endemic).

Table 2. Diagnostic characters of *Lycocerus pictus* (Wittmer, 1983) and *L. yitingi* Hsiao & Okushima sp. nov.

	<i>L. pictus</i>	<i>L. yitingi</i> sp. nov.
Coloration	Elytra almost pale yellow, and smaller black parts on the vertex and legs	Elytra with large fuscous area, and larger black parts on the vertex and legs
Aedeagus	Ventral process thicker, laterophyse with pointed apex, apical margin of dorsal plate subtruncated	Ventral process thinner, laterophyse truncated apically, apical margin of dorsal plate rounded
Abdominal ventrite VII of female	Mostly yellowish brown and median lobe less protuberant	Mostly fuscous and median lobe more protuberant
Female genitalia	Vagina broader and rounded, spermathecal duct and accessory gland longer	Vagina stouter, spermathecal duct and accessory gland shorter

Lycocerus yitingi Hsiao & Okushima sp. nov.

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Figs 2C–E, 3D–F, 6C–D, 7

Diagnosis

This species resembles *L. pictus*; the differential diagnosis is given in Table 2.

Etymology

The specific epithet is dedicated to one of its collectors, Mr. Yi-Ting Chung (Pingtung, Taiwan).

Material examined**Holotype**

TAIWAN: ♂, Dahanshan, 1000m, Pingtung, 26 Feb. 2013, Y.-T. Chung leg. (NMNS).

Paratypes

TAIWAN: 3 ♂♂, 4 ♀♀, same data as for holotype (2 ♂♂, 2 ♀♀ in NMNS; 1 ♂, 2 ♀♀ in YHC); 1 ♀, Chufengkou, Manchou, Pintung, 15 Jan. 1998, C.-S. Lin leg. (NMNS); 2 ♂♂, 3 ♀♀, Chun Jin [=Chunrih], 950–1000m, Ping Tung Co., 21 Mar. 2000, C.-L. Li leg. (KURA).

Other material

TAIWAN: 1 ♂, 1 ♀, Chihpen-spa, Peinan Hsiang, Taitung, 5 Apr. 2004, T. Tsuru leg. (KURA); 1 ♀, Roshan Waterfall, Fuli, Hualien, 16 Feb. 2014, W.-J. Huang leg. (YHC); 2 ♀♀, Majia, Pingtung, 12 Mar. 2014, Y.-T. Chung leg. (YHC).

Description**Coloration**

Eyes black. Head dark yellow, with black marking on vertex. Antennae brownish yellow. Pronotum dark yellow, with black marking in medio-longitudinal part. Elytra fuscous, with wide, pale yellow longitudinal stripe on each elytron. Legs black, with costae, trochanters and basal parts of femora dark yellow; tibiae with dark yellow tinge. Prosternum dark yellow, mesoventrites, metaventrites and abdomen black, with margin of abdominal ventrites pale yellow. Body closely covered with fine

yellowish pubescence; anterior margin of clypeus fringed with pale bristles; antennae, elytra and legs with some yellowish bristles intermingled with primary pubescence.

Male (Fig. 2C)

HEAD. Nearly as long as wide; vertex faintly hollowed, depressed along apical margin of clypeus and in lateral areas before eyes; surface densely and finely punctate and semilustrous; anterior margin of clypeus

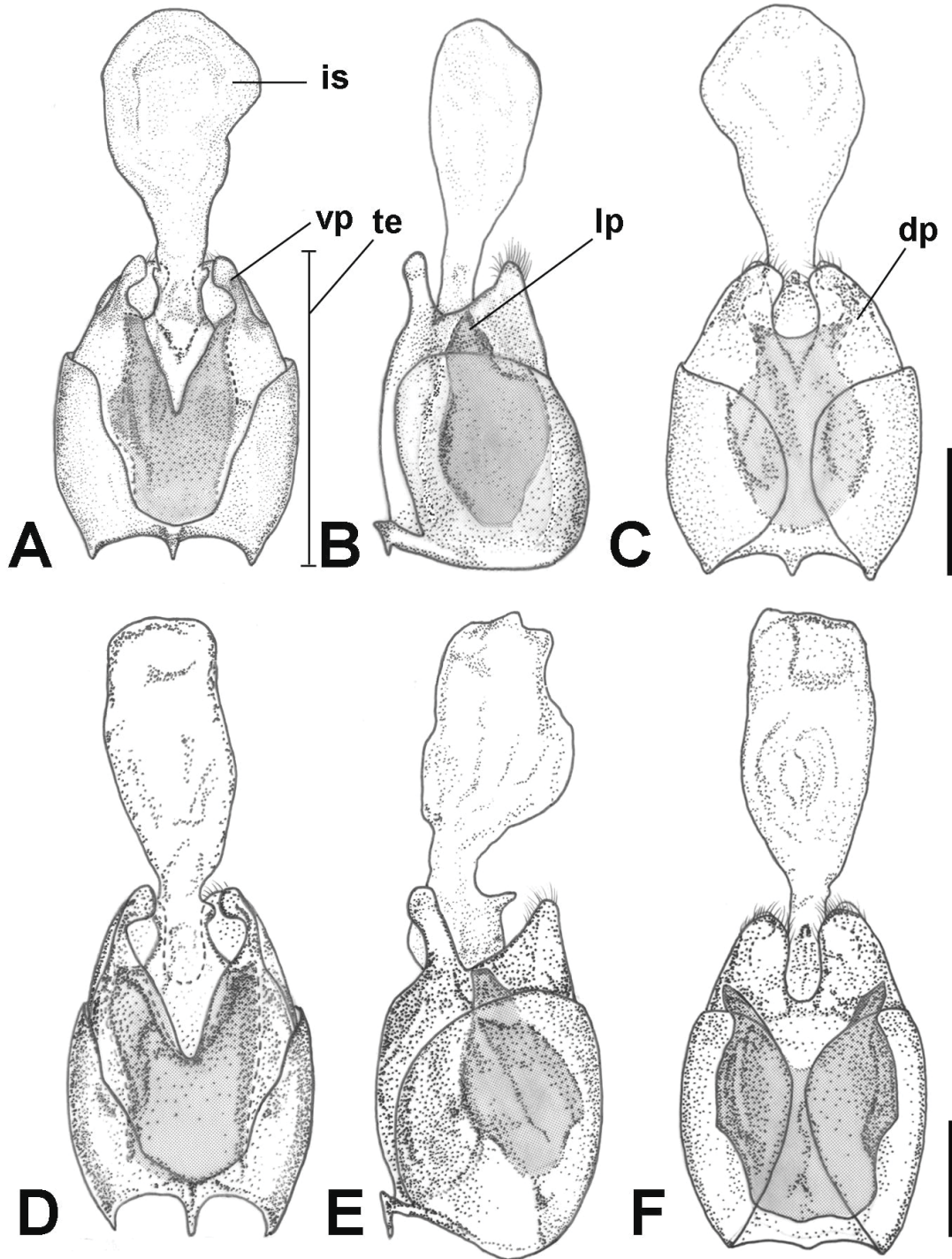


Fig. 3. Aedeagus. **A–C.** *Lycocerus pictus* (Wittmer, 1983). **D–F.** *L. yitingi* Hsiao & Okushima sp. nov. **A, D.** Ventral view. **B, E.** Lateral view. **C, F.** Dorsal view. Scale bars: 0.5 mm.

arcuate and faintly indented in middle; eyes not so large, globular and slightly prominent, ratio of eye diameter to interocular space 1:4.6; terminal labial palpomeres rounded ax-shaped; terminal maxillary palpomeres rounded ax-shaped; antennae filiform, extending to elytral midlength; antennomere I clavate, II short and a little expanded apicad, III to XI subcylindrical, all antennomeres without groove, ratio of antennomere lengths: 11 : 10 : 12 : 16 : 16 : 16 : 15 : 15 : 14 : 13 : 14.

PRONOTUM. Subquadrate, about 0.90 times as wide as head, about 1.10 times as long as wide; anterior and posterior margins moderately arcuate; lateral margins feebly sinuate, slightly diverging posteriorly; anterior angles rounded; posterior angles obtuse; dorsum convex in postero-lateral and hollowed in antero-lateral areas; medio-longitudinal groove distinct in posterior half; surface smooth and semilustrous. Scutellum triangular with rounded apex.

ELYTRA. Conjointly about 1.5 times as wide as pronotum, about 3.1 times as long as wide, sides subparallel; surface covered with minute grains and without luster.

LEGS. Moderately slender; femora mostly straight; tibiae mostly straight, with basal part feebly arcuate; claws simple.

AEDEAGUS (Fig. 3D–F). Ventral process expanded apically, apex curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere as long as ventral process, stout, apical margin rounded, with some hairs on it, concave on inner margin. Laterophyse very short and truncated apically, invisible in lateral view. Inner sac swollen, lengthened behind, and somewhat shorter than tegmen.

Body length 4.95–6.70 mm (holotype: 5.00 mm); width 1.00–1.70 mm (1.00 mm).

Female (Fig. 2D)

Similar to male. Body wider than in male. Eyes somewhat smaller than in male, ratio of eye diameter to interocular space 1:5.1. Antennae distinctly shorter than in male, barely exceeding humeri, ratio of antennomere lengths: 11 : 10 : 11 : 13 : 13 : 13 : 12 : 12 : 11 : 10 : 12.

PRONOTUM. Nearly as wide as head, slightly longer than width. Elytra conjointly about 1.5 times as wide as pronotum, about 2.9 times as long as wide. Claws simple. Abdominal ventrite VII widely emarginate on each side of terminal margin, forming subtriangular lateral lobes, median lobe moderately developed and triangularly concave in middle (Fig. 6C).

FEMALE GENITALIA (Fig. 6D). Vagina stout and abruptly extended apically as a long and thick duct; diverticulum and spermathecal duct arising from apex of long duct of vagina; diverticulum moderately thin and spiral; spermathecal duct shorter than diverticulum; spermatheca provided with a thin spiral tube, tube longer than diverticulum; accessory gland thin, shorter than spermatheca.

Body length 6.00–7.50 mm; width 1.30–1.80 mm.

Remarks

Several examined specimens listed as other material were different from the type by having the head, antennae, thorax, basal half of the femora and tibiae orange yellow; the black markings on the vertex, pronotum and legs smaller or indistinct; elytra mostly dark yellow, with suture and lateral sides narrowly black (Fig. 2E), but display no distinct differences compared to the type specimens on the structure of the aedeagus. Because insufficient materials were available and distinct diagnostic characters were not discovered, we herein prefer to regard these specimens as representing a color variation of *L. yitingi* sp. nov. rather than giving it a new taxonomic status. Nevertheless, we choose not to place these

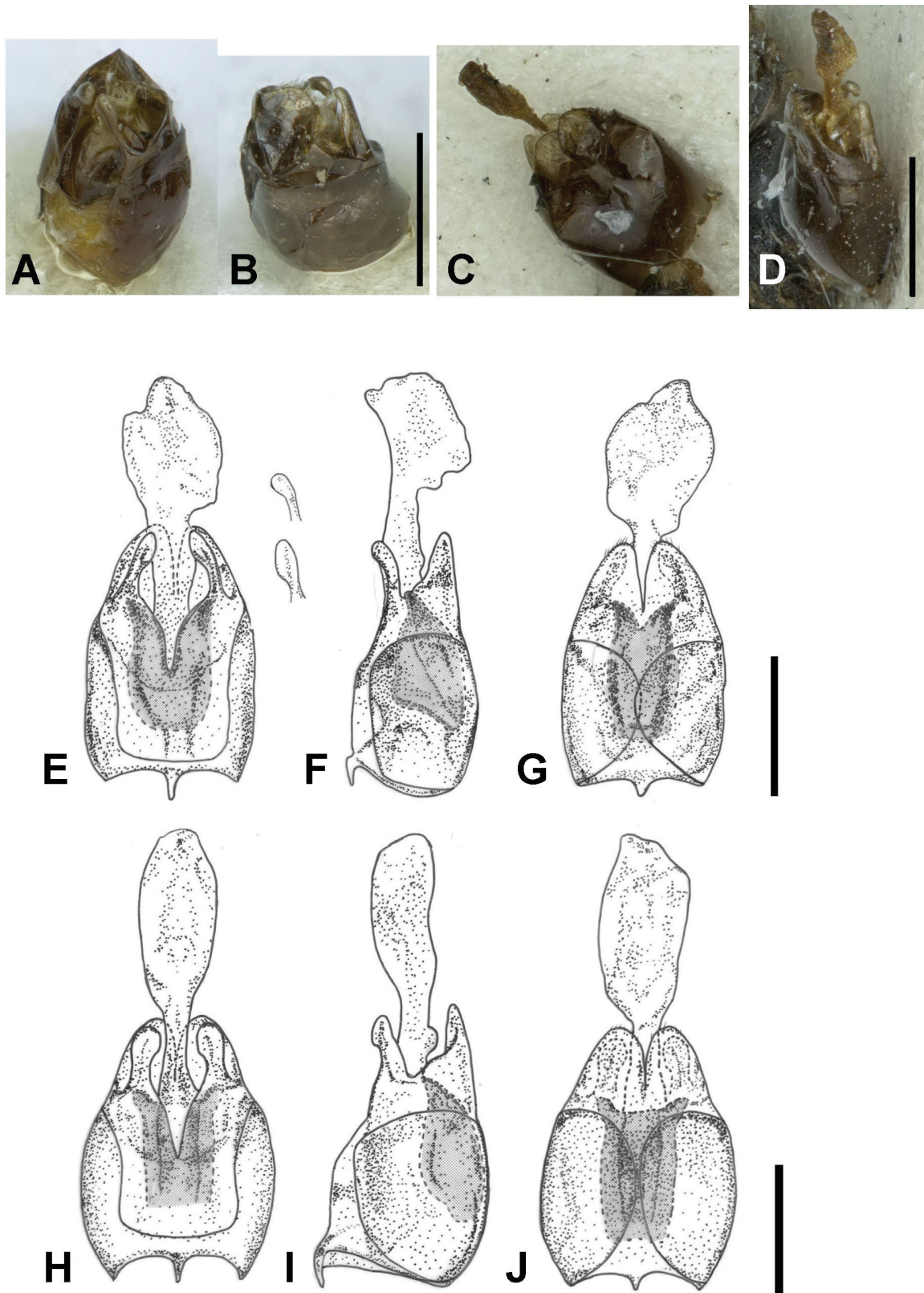


Fig. 4. Aedeagus. **A–B.** *Lycocerus araticollis* (Fairmaire, 1897). **C–D.** *L. griseopubens* (Pic, 1928). **E–G.** *L. nigripennis* (Pic, 1938). **H–J.** *L. aurantiacus* Hsiao & Okushima sp. nov. **A.** Ventrolateral view. **B.** Dorsolateral view. **E, H.** Ventral view. **D, F, I.** Lateral view. **C, G, J.** Dorsal view. Scale bars: 0.5 mm.

specimens among the paratypes because they will possibly be confirmed as a new taxon in the future after more material is examined.

Distribution (Fig. 7)

Taiwan (endemic).

Lycocerus araticollis (Fairmaire, 1897)

Figs 2F–G, 4A–B

Telephorus araticollis Fairmaire, 1897: 216.

Cantharis araticollis – Delkeskamp 1977: 62. — Kazantsev & Brancucci 2007: 239.

Lycocerus araticollis – Okushima 2007b: 257, fig. 1.

Diagnosis

This species resembles the nearly black forms of *L. nigripennis* and *L. evangelium* Hsiao & Okushima sp. nov.; the differential diagnosis is given in Table 3.

Material examined

Lectotype

CHINA: ♂ (MNHN): [h] Kiangsi [=Jiangxi] / Gonon / D. David // [p] TYPE // [p] LECTOTYPUS // [h] *Telephorus / araticollis / Fairm / Kiangsi [=Jiangxi] // [h] REM / 95 / 11.6 // [h] *Athemellus / araticollis / (Fairm.) / [p] det. W. Wittmer.**

Other material

CHINA: 1 ♂, Taichow, 19 Apr. 1935, collector unknown (NHMB).

Note

The locality of the additional material possibly referred to Taizhou, but there are two localities in China named Taizhou in Zhejiang and Jiangsu, respectively.

Description

See Okushima (2007b).

Supplementary description

AEDEAGUS (Fig. 4A–B). Ventral process expanded and rounded apically, apex curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere somewhat longer than ventral process, protuberant, apical margin truncated, with some hairs on it. Laterophyse very short and slender, with pointed apex, barely visible in lateral view.

Remarks

This species should be attributed to *L. hanatanii* species group because its morphological characteristics match the definition of this species group, in agreement with the cladogram (Fig. 9), although the female genitalia have not been examined.

Distribution

China (Jiangxi Province).

Lycocerus griseopubens (Pic, 1928)

Figs 2H–I, 4C–D

Malthinus atripennis var. *griseopubens* Pic, 1928: 55.

Malthinus nigripennis var. *griseopubens* – Delkeskamp 1977: 354.

Lycocerus atripennis – Kazantsev 2007: 48. — Kazantsev & Brancucci 2007: 249.

Lycocerus griseopubens – Okushima 2007b: 259, figs 2, 6.

Diagnosis

This species resembles the yellowish brown pronotum forms of *L. nigripennis* and *L. aurantiacus* Hsiao & Okushima sp. nov.; the differential diagnosis is given in Table 3.

Material examined

Holotype

CHINA: ♀ (MNHN): [p] Futschau [=Fuzhou], China / Cos. G. Siemssen lg / vend. 13. VI 1903. // [h] var. *griseopubens* / Pic // [p] HOLOTYPUS // [h] *Athemellus / araticollis / griseopubens* / (Pic) / [p] det. W. Wittmer.

Other material

CHINA: 1 ♂, 1 ♀, Fiuchou [=Fuzhou], Fujian, date and collector unknown (NHMB).

Description

See Okushima (2007b).

Supplementary description

Male (Fig. 2I)

Similar to female (= holotype). Body narrower than in female. Eyes somewhat larger than in female, ratio of eye diameter to interocular space 1:4.5. Antennomeres IV to VII longer than in female, VIII to XI unavailable, ratio of antennomere lengths: 15:10:12:15:15:15:12:-:-:-:-.

PRONOTUM. About 0.95 times as wide as head, nearly as long as wide. Elytra conjointly about 1.6 times as wide as pronotum, about 2.8 times as long as wide. Legs moderately slender; femora mostly straight; tibiae mostly straight, with basal part feebly arcuate; claws simple.

AEDEAGUS (Fig. 4C–D). Ventral process moderately expanded and rounded apically, apex curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere as long as ventral process, broad, apical margin rounded, with some hairs on it. Laterophyse very short, invisible in lateral view. Inner sac swollen, shorter than tegmen.

Remarks

This species should be attributed to the *L. hanatanii* species group as its morphological characteristics match the definition of this species group, in agreement with the cladogram (Fig. 9); however, the female genitalia remain unexamined.

Distribution

China (Fujian Province).

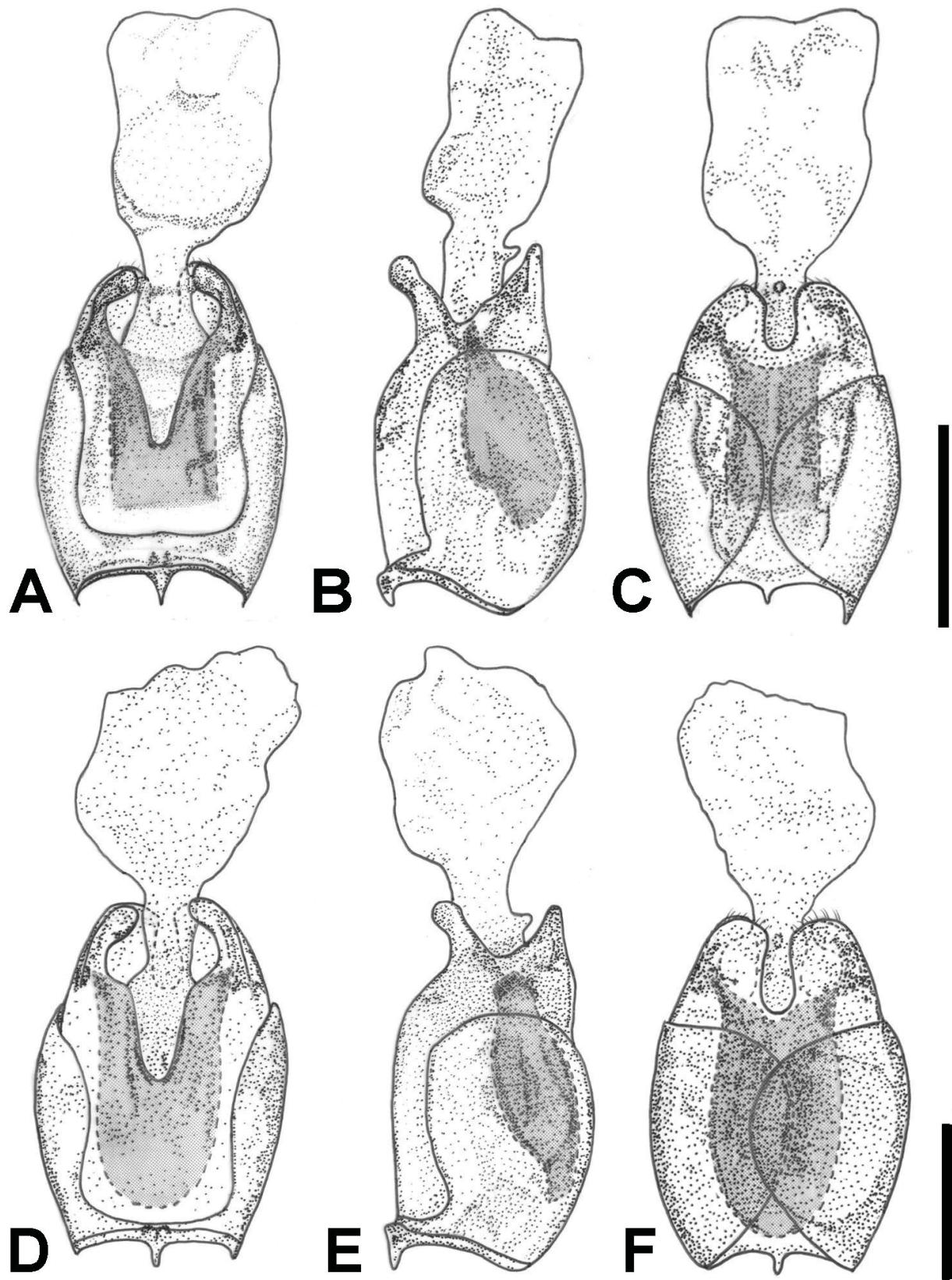


Fig. 5. Aedeagus. **A–C.** *Lycocerus evangelium* Hsiao & Okushima sp. nov. **D–F.** *L. kintaroi* Hsiao & Okushima sp. nov. **A, D.** Ventral view. **B, E.** Lateral view. **C, F.** Dorsal view. Scale bars: 0.5 mm.

Table 3. Diagnostic characters of *L. nigripennis* (Pic, 1938) and similar species.

	<i>L. araticollis</i>	<i>L. griseopubens</i>	<i>L. nigripennis</i>	<i>L. aurantiacus</i> sp. nov.	<i>L. evangelium</i> sp. nov.
Antennomeres in males	Shorter	Shorter	More elongated	More elongated	Shorter
Coloration of pronotum	Black	Orange, with a black marking in middle	Black or orange to yellowish brown, with a black marking in middle	Orange, with a black marking in middle	Black
Surface of elytra	Lusterless	Lusterless	Semilustrous	Semilustrous	Moderately lustrous
Convexity on the pronotum	Less angular	Less angular	Angular	Angular	Angular
Pubescence on the elytra	Slightly sparser	Slightly sparser	Slightly sparser	Slightly sparser	Slightly denser
Ventral process of aedeagus	Moderate and expanded apically, the apex curved inwards	Moderate and expanded apically, the apex curved inwards	Moderate and expanded apically, the apex curved inwards	Thick and strongly expanded apically, the apex slightly curved inwards	Moderate and expanded apically, the apex curved inwards
Dorsal plate of aedeagus	Protuberant, somewhat longer than ventral process, the apical margin truncated	Broad, as long as ventral process, the apical margin rounded	Protuberant and narrowed apically, somewhat longer than ventral process, the apical margin rounded	Protuberant and narrowed apically, slightly longer than ventral process, the apical margin rounded	Broad, as long as ventral process, the apical margin rounded, and concave on inner margin

Lycocerus nigripennis (Pic, 1938)

Figs 2J–M, 4E–G, 6E–F, 8

Malthinus atripennis Pic, 1922: 30.*Malthinus nigripennis* Pic, 1938: 121 [new name for *Malthinus atripennis* Pic, 1922].*Podabrinus taihokuensis* Wittmer, 1954: 276.*Athemellus taihokuensis* – Wittmer 1972: 126, fig. 1.*Athemellus atripennis* – Wittmer 1983: 168.*Lycocerus atripennis* – Kazantsev & Brancucci 2007: 249.*Lycocerus nigripennis* – Okushima 2007b: 260; 2008: 282, fig. 25. — Satô *et al.* 2015: 51.**Diagnosis**

The nearly black form of this species resembles *L. araticollis* and *L. evangelium* Hsiao & Okushima sp. nov., and the yellowish brown pronotum form resembles *L. griseopubens* and *L. aurantiacus* Hsiao & Okushima sp. nov.; the differential diagnosis is given in Table 3.

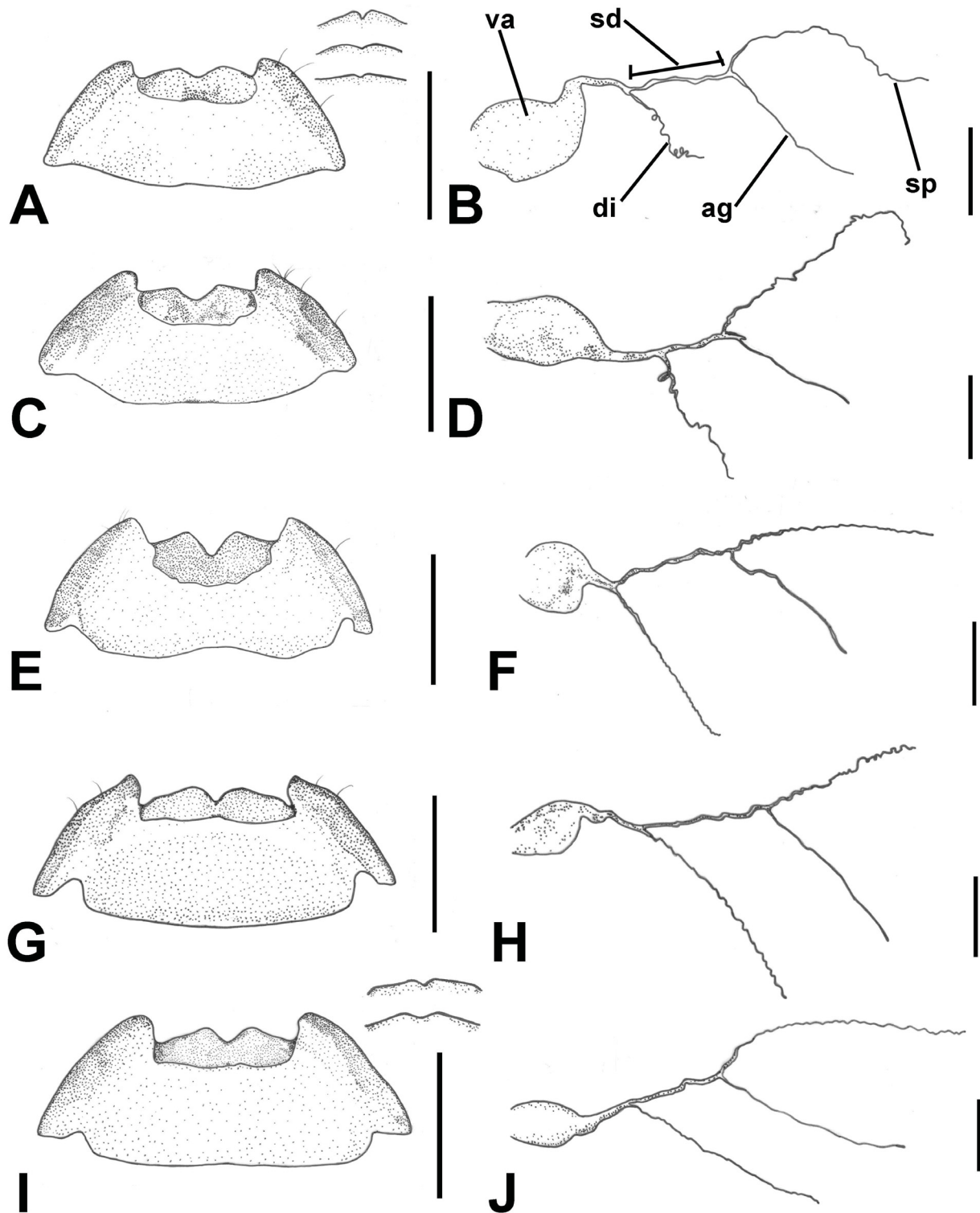


Fig. 6. A–B. *Lycocerus pictus* (Wittmer, 1983). C–D. *L. yitingi* Hsiao & Okushima sp. nov. E–F. *L. nigripennis* (Pic, 1938). G–H. *L. aurantiacus* Hsiao & Okushima sp. nov. I–J. *L. evangelium* Hsiao & Okushima sp. nov. A, C, E, G, I. Abdominal ventrite VII of female. B, D, F, H, J. Female genitalia, lateral view. Scale bars: A, C, E, G, I = 1.0 mm; B, D, F, H, J = 0.5 mm.

Material examined

Syntype of *Malthinus atripennis* Pic, 1922

TAIWAN: ♀ (SDEI): [p] Hokuto / [h] III / [p] Formosa / H. Sauter, 1912 // [p] Syntypus // [h] *Malthinus atripennis* / Pic // [h] *Athemellus atripennis* / (Pic) / [p] det. W. Wittmer // [p] DEI Coleoptera / # 200077. [Note: This female syntype of *M. atripennis* is possibly the female holotype which Wittmer (1983) referred to.]

Holotype of *Podabrinus taihokuensis* Wittmer, 1954

TAIWAN: ♂ (CAS): [p] Taihoku / Formosa / [h] III-27-32 // [p] L. Gressitt / Collection // [p] L. Gressitt Collector // [h] Holotypus // [h] *Podabrinus taihokuensis* / Wittmer / [p] det. W. Wittmer // [p] California Academy of Sciences / Type No. [h] 7787.

Paratype of *Podabrinus taihokuensis* Wittmer, 1954

TAIWAN: ♂ (NHMB): [h] *A. taihokuensis* / (Wittmer) / [p] det. W. Wittmer // [h] *P. taihokuensis* / Wittmer / [p] det. W. Wittmer // [h] *Athemellus atripennis* / (Pic) / [p] det. W. Wittmer // [p] Paratypus // [p] Taihoku / Formosa / [h] III-27-32 // [h] 37 // [p] L. Gressitt / Collection // [p] Naturhistorisches / Museum Basel / Coll. W. Wittmer // [p] CANTHARIDAE / CANTH00003105.

Other material

TAIWAN: 2 ♂♂, Junhua, Taoyuan, 11 Mar. 1972, B.-S. Chang leg. (NMNS); 1 ♀, Bajie [=Baigi], Taoyuan, 11 Mar. 1972, B.-S. Chang leg. (NMNS); 1 ♀, Hsileng, Taoyuan Hsien, 2 Apr. 1982, N. Ohbayashi leg. (EUMJ); 2 ♂♂, Lushan spa, Nantou Hsien, 2 May 1982, N. Ohbayashi leg. (KURA); 1 ♀, Fukukoo, Toen-ken [=Taoyuan], 28 Jan. 1983, K. Baba leg. (EUMJ); 1 ♂, Tam Shui, N Taiwan, 20 Feb. 1987, K. Baba leg. (EUMJ); 1 ♂, Sun Moon Lake, 1000 m, M Taiwan, 14 Mar. 1989, K. Baba leg. (EUMJ); 2 ♂♂, 1 ♀, Mu-Tsar, Taipei, 9 Feb. 1991, C.-L. Li leg. (KURA); 1 ♀, Baling, Taoyuan Hsien, 5–8 Apr. 1991, T. Kishimoto leg. (KURA); 1 ♂, 2 ♀♀, Nanshanchi, Nantou Hsien, 10 Apr. 1991, Y. Okushima leg. (KURA); 1 ♀, Fuhsing, Taoyuan, 30 Mar. 1992, I.-S. Hsu leg. (NMNS); 1 ♂, 1 ♀, Wanjung, Hualien, 2 Feb. 1992, C.-Y. Lee leg. (NMNS); 2 ♂♂, 3 ♀♀, Yangmingshan, Taipei, 27 Mar. 1993, T. Nonaka leg. (KURA); 2 ♀♀, Lushan spa, Nantou Hsien, 24 Apr. 1994, T. Kishimoto leg. (KURA); 1 ♀, Chikou, 350m, Taoyuan Hsien, 25 Apr. 1996, L.-J. Wang leg. (KURA); 1 ♂, 1 ♀, Fushan, 21 Mar. 1998, M. Satô leg. (KURA); 7 ♀♀, Paling, Taoyuan, 31 Mar. 1998, M. Satô leg. (KURA); 1 ♂, Lushan, Nantou, 2 Apr. 1998, F. Hayashi leg. (KURA); 4 ♂♂, 2 ♀♀, Gauvaw [=Luofu], 380 m, Taovuan, 25 Apr. 1998, L.-J. Wang leg. (KURA); 2 ♂♂, Chunyang, Jenai, Nantou, 8–10 Mar. 1999, C.-S. Lin leg. (NMNS); 12 ♂♂, 6 ♀♀, Hushichun, Yuanshan, Ilan Hsien, 4–16 Mar. 1999, T. Mizusawa leg. (KURA); 7 ♂♂, 1 ♀, Yuanshan, Ilan Hsien, 23 Mar. 2000, T. Mizusawa leg. (KURA); 11 ♂♂, 13 ♀♀, Yuanshan, Ilan Hsien, 23–25 Mar. 2000, T. Mizusawa leg. (KURA); 1 ♂, Foshan, Sanxia, Taipei, 27 Apr. 2009, S.-H. Chang leg. (YHC); 1 ♀, Baishihu, Neihu, Taipei, 14 Feb. 2013, L. Huang leg. (YHC); 5 ♂♂, 2 ♀♀, Neikouli, Neihu, Taipei, 23 Feb. 2014, L. Huang leg. (YHC); 3 ♂♂, 1 ♀, Shuanchiyen, Taipei, 7 Mar. 2014, L. Huang leg. (YHC); 1 ♀, Fuchushan, Taipei, 25 Mar. 2014, C.-J. Li leg. (YHC); 1 ♀, Baehengonlu [=Northern Cross Island Highway], 9 Apr. 2014, L. Huang leg. (YHC); 1 ♀, Fushan, Taipei, 24 May 2014, L. Huang leg. (YHC); 1 ♂, Fuchushan, Taipei, 27 Feb. 2015, T. Hsieh leg. (YHC); 1 ♀, Huangdidian, Shuding, Taipei, 28 Feb. 2015, L. Huang leg. (YHC); 4 ♂♂, 6 ♀♀, Kantoushan, Tainan, 28 Feb. 2015, W.-C. Liao leg. (YHC); 3 ♂♂, 4 ♀♀, Xankonchuan, Danshui, Taipei, Y.-J. Lu leg. (YHC); 1 ♀, Shanming, Taoyuan, 14 Mar. 2015, Y. Hsiao leg. (YHC).

Redescription

Coloration

Eyes black. Head black, but brown in frons. Antennae black, with yellow tinge in the first two segments. Mandibles yellowish brown. Pronotum yellowish brown to orange, with a black marking in medio-longitudinal part. Elytra black. Legs black, with coxae more or less yellowish brown. Prosternum

yellowish brown; mesoventrites, metaventrites and abdomen black. Body closely covered with pale pubescence; anterior margin of clypeus, antennae, elytra and legs fringed with pale bristles.

Male (Fig. 2K–L)

HEAD. Nearly as long as wide; vertex faintly hollowed, depressed along apical margin of clypeus and in lateral areas before eyes; surface densely and finely punctate and semilustrous; anterior margin of

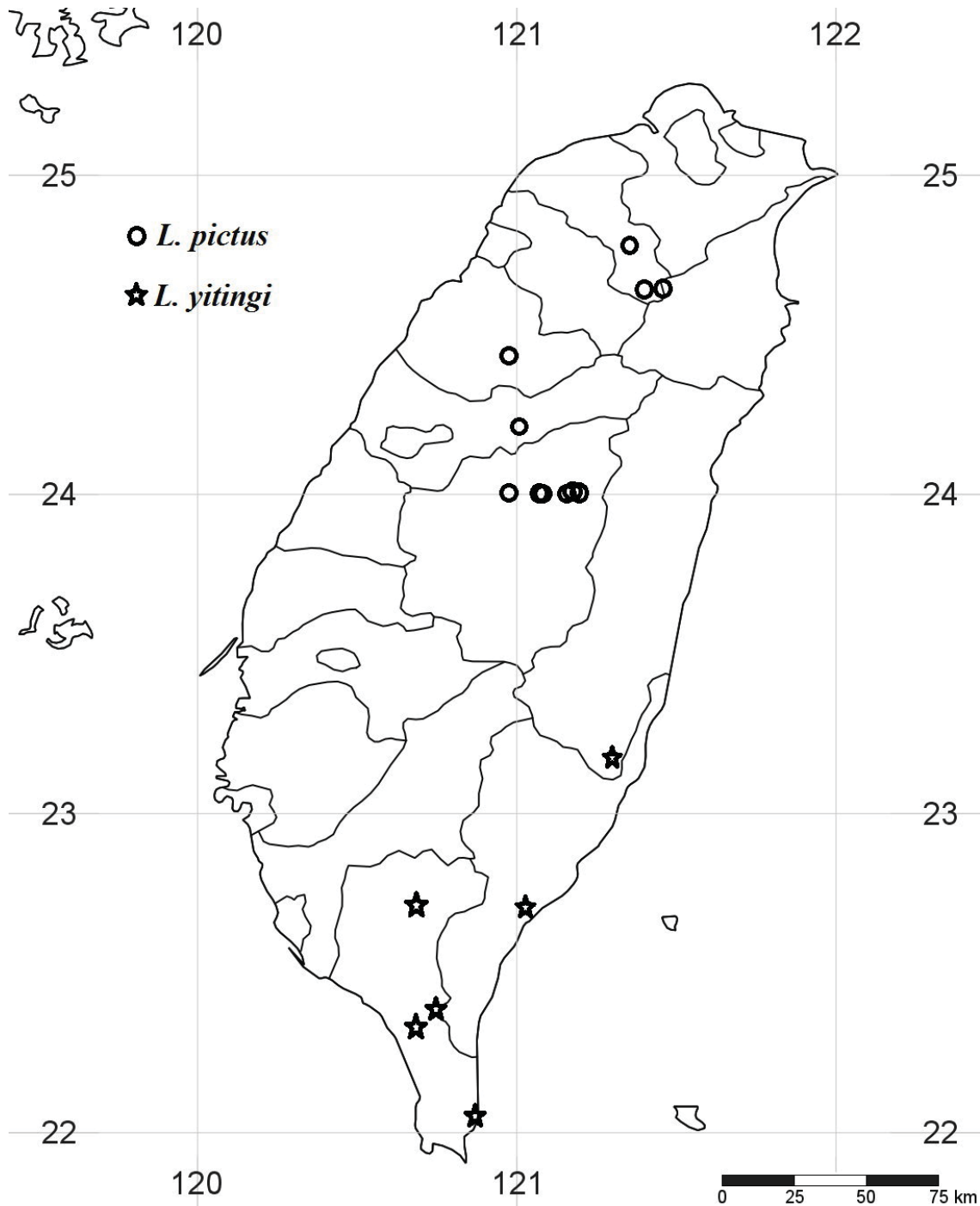


Fig. 7. Distribution map of *Lycocerus pictus* (Wittmer, 1983) and *L. yitingi* Hsiao & Okushima sp. nov. from Taiwan.

clypeus arcuate and faintly indented in middle; eyes not so large, globular and slightly prominent, ratio of eye diameter to interocular space 1:4.0; terminal labial palpomeres rounded ax-shaped; terminal maxillary palpomeres rounded ax-shaped; antennae filiform, somewhat exceeding elytral midlength; antennomere I clavate, II short and a little expanded apicad, III to XI subcylindrical, all antennomeres without groove, ratio of antennomere lengths: 15:10:14.5:17.5:17.5:17.5:17:16:15.5:15:16.5.

PRONOTUM. Subquadrate, about 0.90 times as wide as head, slightly longer than width; anterior and posterior margins moderately arcuate; lateral margins feebly sinuate, slightly diverging posteriorly; anterior angles rounded; posterior angles obtuse; dorsum convex in postero-lateral and hollowed in antero-lateral areas; medio-longitudinal groove distinct in posterior half; surface smooth and semilustrous. Scutellum triangular, with rounded apex.

ELYTRA. Conjointly about 1.6 times as wide as pronotum, about 2.9 times as long as wide, sides subparallel; surface densely and finely punctate and semilustrous.

LEGS. Moderately slender; femora mostly straight; tibiae mostly straight, with basal part feebly arcuate; claws simple.

AEDEAGUS (Fig. 4E–G). Ventral process expanded apically, apex strongly or moderately expanded, apex curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere somewhat longer than ventral process, protuberant and narrowed apically, apical margin rounded, with some hairs on it. Laterophyse very short, with rounded apex, barely visible in lateral view. Inner sac swollen, lengthened behind, and shorter than tegmen.

Body length 4.80–6.70 mm; width 1.15–2.30 mm.

Female (Fig. 2J, M)

Similar to male. Body wider than in male. Eyes somewhat smaller than in male, ratio of eye diameter to interocular space 1:4.8. Antennae distinctly shorter than in male, barely exceeding humeri, ratio of antennomere lengths: 12:10:11.5:12.5:12:13:12:11.5:11:10:12.

PRONOTUM. Nearly as wide as head, nearly as long as wide. Elytra conjointly about 1.6 times as wide as pronotum, about 3.1 times as long as wide. Abdominal ventrite VII widely emarginate on each side of terminal margin, forming subtriangular lateral lobes, median lobe considerably developed and triangularly concave in middle (Fig. 6E).

FEMALE GENITALIA (Fig. 6F). Vagina rounded, abruptly extended apically as a long and thick duct; diverticulum and spermathecal duct arising from apex of long duct of vagina; diverticulum moderately thin and spiral, longer than spermathecal duct; spermatheca provided with thin spiral tube, tube nearly as long as diverticulum; accessory gland thin, shorter than spermatheca.

Body length 6.10–7.00 mm; width 1.30–1.80 mm.

Variation

Body nearly black, including pronotum.

Remarks

This species is widely distributed in low-altitude forest in Taiwan and appears mainly in the spring according to the label data. It was observed visiting flowers of *Machilus thunbergii* Siebold & Zucc. (Lauraceae) during the day. Additionally, during our study of the collections of different institutions and the survey of the first author's personal field trip, the nearly black pronotum form was found to be typical

of this species, although all of the type specimens including those of *Malthinus atripennis* Pic, 1922 and *Podabrinus taihokuensis* Wittmer, 1954 represent the yellowish fringed pronotum form.

Distribution (Fig. 8)

Taiwan (endemic).

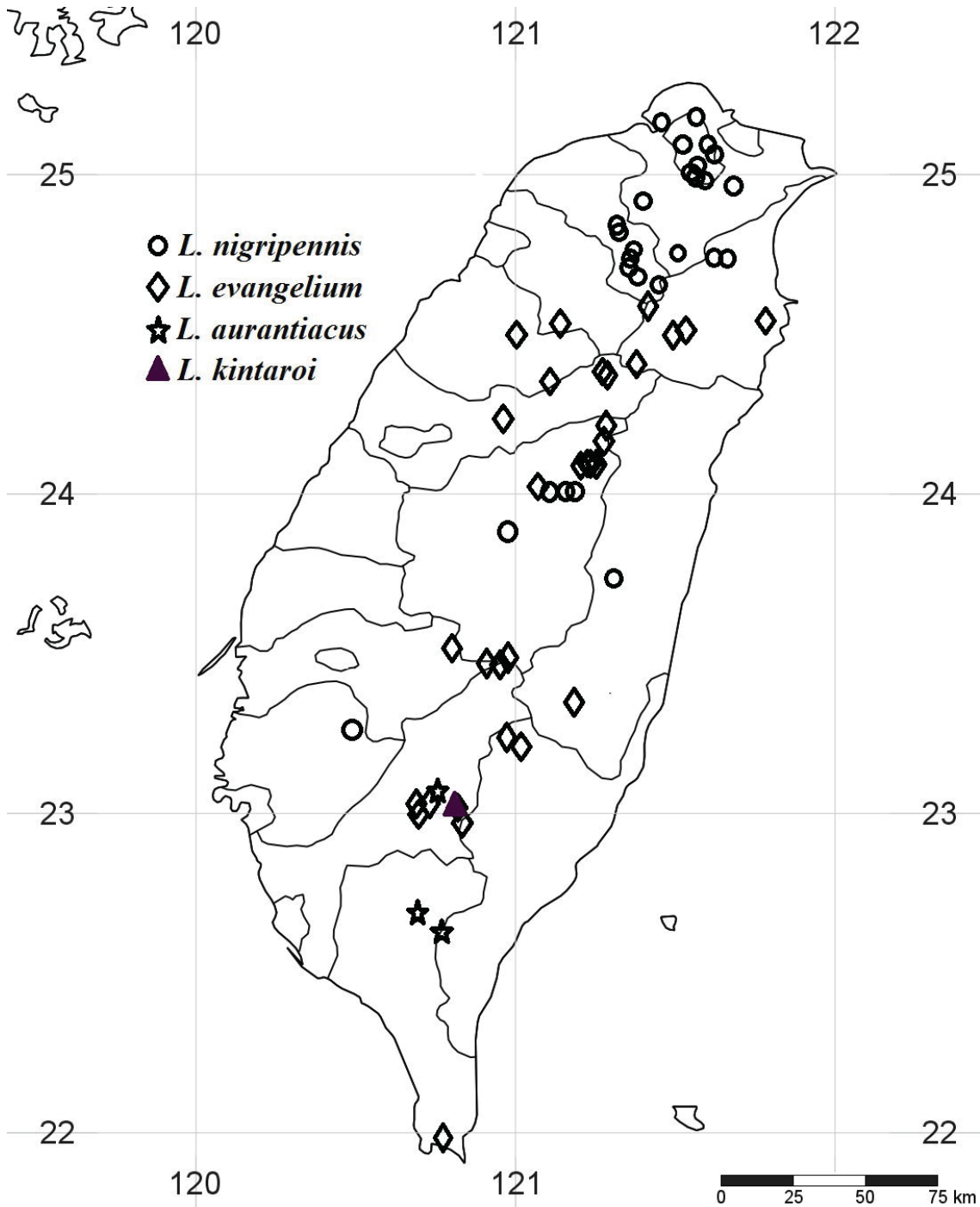


Fig. 8. Distribution map of *L. nigripennis* (Pic, 1938), *L. evangelium* Hsiao & Okushima sp. nov., *L. aurantiacus* Hsiao & Okushima sp. nov. and *L. kintaroi* Hsiao & Okushima sp. nov. from Taiwan.

Lycocerus aurantiacus Hsiao & Okushima sp. nov.

urn:lsid:zoobank.org:act:1CD64F32-4749-48C6-80CF-C8981514E12B

Figs 2N–O, 4H–J, 6G–H, 8

Diagnosis

This species resembles *L. griseopubens* and the yellowish brown pronotum form of *L. nigripennis*; the differential diagnosis is given in Table 3.

Etymology

The specific epithet is derived from the Latin *aurantiacus* (“orange”), referring to its orange fringed pronotum.

Type material

Holotype

TAIWAN: ♂, Majia Township, 900 m, Pingtung, 12 Mar. 2014, Y.-T. Chung leg. (NMNS).

Paratypes

TAIWAN: 9 ♂♂, 9 ♀♀, same data as for holotype (5 ♂♂, 5 ♀♀ in NMNS; 2 ♂♂, 2 ♀♀ in TARI; 2 ♂♂, 2 ♀♀ in YHC); 1 ♂, 1 ♀, Tengchih, Taoyuan, Kaohsiung Hsien, 29 Mar.–1 Apr. 2001, S. Nagashima leg. (KURA); 1 ♀, Baedawushan [=North Dawushan], Pingtung, 2 Apr. 2013, R.-H. Liou leg. (YHC); 2 ♂♂, Tienchih, Kaohsiung, 8 Mar. 2014, W.-C. Liao leg. (1 ♂ in NMNS; 1 ♂ in YHC).

Description

Coloration

Eyes and head black. Antennae black, with yellow tinge at base of first segment. Mandibles yellowish brown. Pronotum orange, with black marking in medio-longitudinal part. Elytra black. Legs black. Pro-, meso- and metasterna, as well as abdomen black, with margins of abdominal ventrites yellowish brown. Body closely covered with pale pubescence; anterior margin of clypeus, antennae, elytra and legs fringed with pale bristles.

Male (Fig. 2N)

HEAD. Nearly as long as wide; vertex faintly hollowed, depressed along apical margin of clypeus and in lateral areas before eyes; surface densely and finely punctate and semilustrous; anterior margin of clypeus arcuate and faintly indented in middle; eyes not so large, globular and slightly prominent, ratio of eye diameter to interocular space 1:5.3; terminal labial palpomeres rounded ax-shaped; terminal maxillary palpomeres rounded ax-shaped; antennae filiform, barely exceeding elytral midlength; antennomere I clavate, II short and a little expanded apicad, III to XI subcylindrical, all antennomeres without groove, ratio of antennomere lengths: 16:10:18:21:21:20:20:20:19:17:19.

PRONOTUM. Subquadrate, about 0.90 times as wide as head, slightly longer than width; anterior and posterior margins moderately arcuate; lateral margins feebly sinuate, slightly diverging posteriorly; anterior angles rounded; posterior angles obtuse; dorsum convex in postero-lateral and hollowed in antero-lateral areas; medio-longitudinal groove distinct in posterior half; surface smooth and semilustrous. Scutellum triangular with rounded apex.

ELYTRA. Conjointly about 1.5 times as wide as pronotum, about 3.0 times as long as wide, sides subparallel; surface densely and finely punctate and semilustrous.

LEGS. Moderately slender; femora mostly straight; tibiae mostly straight, with basal part feebly arcuate; claws simple.

AEDEAGUS (Fig. 4H–J). Ventral process thick, strongly expanded and rounded apically, apex moderately curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere slightly longer than ventral process, protuberant and narrowed apically, apical margin rounded, with some hairs on it. Laterophyse very short, with pointed apex, invisible in lateral view. Inner sac swollen, lengthened behind, somewhat shorter than tegmen.

Body length 5.00–6.00 mm (holotype: 5.60 mm); width 0.80–1.30 mm (1.10 mm).

Female (Fig. 2O)

Similar to male. Body wider than in male. Eyes somewhat smaller than in male, ratio of eye diameter to interocular space 1:5.4. Antennae distinctly shorter than in male, barely exceeding humeri, ratio of antennomere lengths: 14.5:10:13.5:15:15:14:14:13:13:12:15.

PRONOTUM. Slightly wider than head, slightly shorter than width. Elytra conjointly about 1.4 times as wide as pronotum, about 2.8 times as long as wide. Claws simple. Abdominal ventrite VII widely emarginate on each side of terminal margin, forming subtriangular lateral lobes, median lobe moderately developed and triangularly concave in middle (Fig. 6G).

FEMALE GENITALIA (Fig. 6H). Vagina stout, abruptly extended apically as long and thick duct; diverticulum and spermathecal duct arising from apex of long duct of vagina; diverticulum moderately thin and spiral; spermathecal duct considerably shorter than diverticulum; spermatheca provided with thin spiral tube, tube shorter than diverticulum; accessory gland thin, shorter than spermatheca.

Body length 5.50–6.50 mm; width 1.20–1.50 mm.

Remarks

This species is distributed in the southern area of Taiwan at about 1000 m altitude according to the label data. It was observed being attracted by light at night.

Distribution (Fig. 8)

Taiwan (endemic).

Lycocerus evangelium Hsiao & Okushima sp. nov.

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Figs 2P–Q, 5A–C, 6I–J, 8

Diagnosis

This species resembles *L. araticollis* and the nearly black form of *L. nigripennis*; the differential diagnosis is given in Table 3.

Etymology

The specific epithet is derived from the Latin *evangelium* (“good news”), referring to fact that its discovery was good news for the team; the specific name is also in memory of the anime “Neon Genesis Evangelion”, which is one of the greatest animes in Japanese history and had a strong impact on Japanese popular culture.

Material examined

Holotype

TAIWAN: ♂, Meifeng, Nantou, 26 Apr. 2015, Y. Hsiao leg (NMNS).

Paratypes

TAIWAN: 1 ♂, 2 ♀♀, same data as for holotype (NMNS); 10 ♂♂, 2 ♀♀, Tsuifeng, Nantou Hsien, 18 Jun. 1989, M. Satô leg. (2 ♂♂, 1 ♀ in EUMJ; 8 ♂♂, 1 ♀ in KURA); 1 ♂, 2 ♀♀, Tsuifeng, Nantou Hsien, 24 Jun. 1989, M. Satô leg. (KURA); 1 ♂, 3 ♀♀, Yuanfeng, Nantou Hsien, 24 Jun. 1989, M. Owada leg. (KURA); 5 ♂♂, 3 ♀♀, Hohuanshan, Nantou Hsien, 25 Jun. 1989, M. Satô leg. (1 ♂, 1 ♀ in EUMJ; 4 ♂♂, 2 ♀♀ in KURA); 1 ♂, Piluchi, Nantou Hsien, 26 Jun. 1989, M. Satô leg. (KURA); 3 ♂♂, 1 ♀, Anmashan, 2600 m, Taichung Hsien, 29 Jul. 1997, B. Tanaka leg. (KURA); 2 ♀♀, Dalu Forest Trail, Hsinchu, 21 Jun. 2008, L.-P. Hsu leg. (NMNS); 1 ♂, 1 ♀, Sungkang, Natou, 31 Mar. 2012, Y.-T. Wang leg. (YHC); 1 ♀, Liyuan, Haiduan, Taitung, 19 Apr. 2014, W.-J. Huang (NMNS); 5 ♀♀, Jianchin Historical Trail, Ilan, 1900 m, 26 Apr. 2014, Y. Hsiao leg. (3 ♀♀ in TARI; 2 ♀♀ in YHC); 2 ♀♀, Walami Trail, 23.344679° N, 121.201454° E, 862 m, Huangma, Zhuoxi County, Hualian, 28 Feb. 2015, Y.-M. Weng leg. (YHC); 2 ♂♂, 1 ♀, Dabaishan, Ilan, 14 Apr. 2015, L. Huang leg. (TARI); 1 ♀, Chiarouhu, Ilan, 25 Apr. 2015, F.-C. Hsu leg. (NMNS).

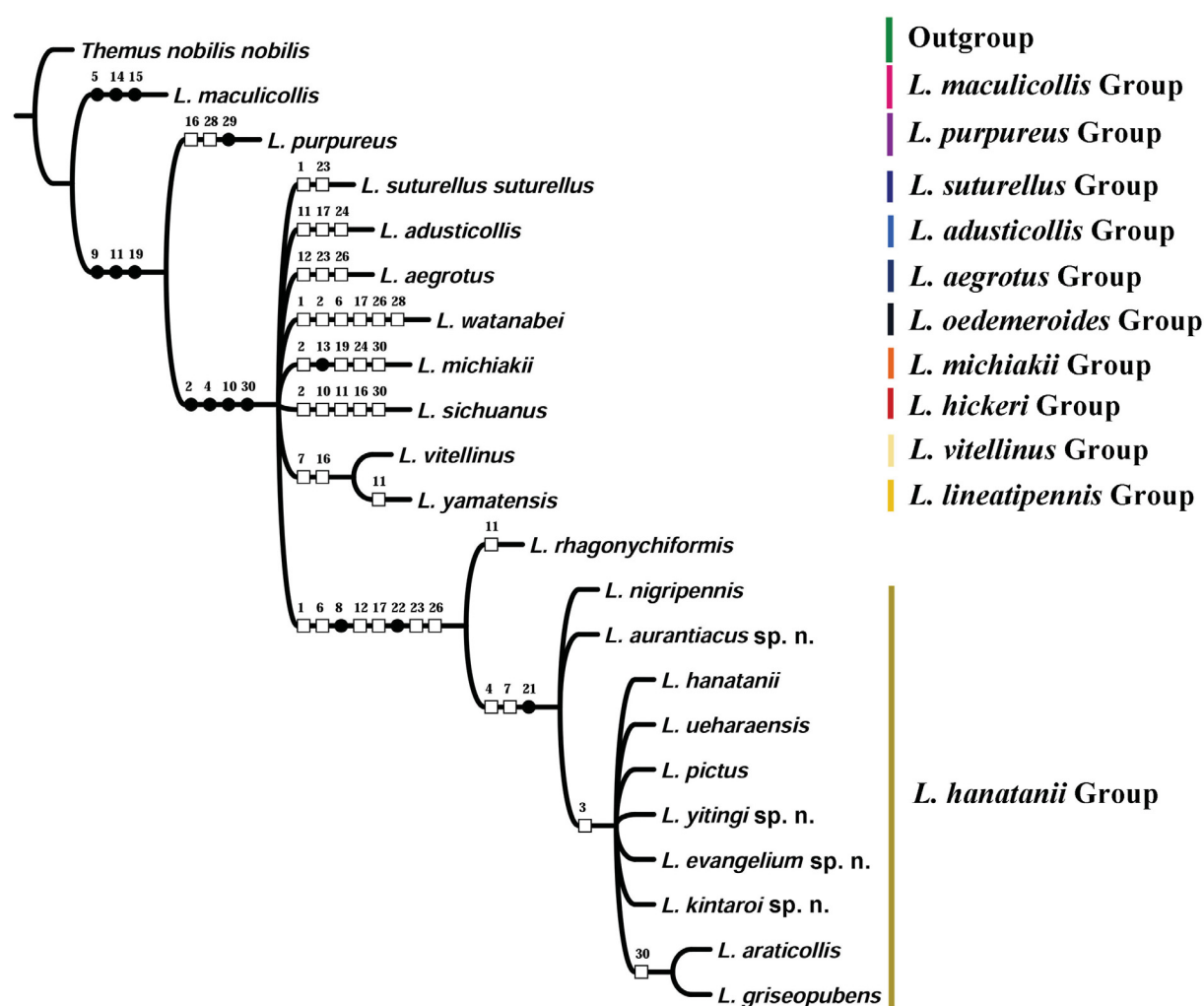


Fig. 9. Phylogenetic reconstruction of the *Lycocerus hanatanii* species group. Strict consensus tree with characters mapped on branches using unambiguous character changes in WinClada. Tree length = 72; Consistency Index = 54; Retention Index = 72.

Other material

TAIWAN: 1 ♀, Alishan, Chiayi Hsien, 17 May 1968, Y. Watanabe leg. (KURA); 2 ♀♀, Mt. Yushan, Nantou Hsien, 20 May 1968, Y. Watanabe leg. (KURA); 1 ♂, 3 ♀♀, Mt. Alishan, 27 Jul. 1970, M. Chujo leg. (1 ♂ in NHMB; 3 ♀♀ in KURA); 1 ♂, Mt. Alishan, 28 Jul. 1970, M. Chujo leg. (NHMB); 9 ♂♂, 2 ♀♀, Meifeng, Nantou Hsien, 15 Jun. 1976, T. Matsumoto leg. (KURA); 2 ♀♀, Sungkang-Meifeng, Nantou Hsien, 2 May 1977, W. Suzuki leg. (KURA); 1 ♂, 1 ♀, Tsuifen, Nantou Hsien, 4 May 1979, S. Tsuyuki leg. (KURA); 1 ♂, Nanfanshan, Kaoshun [=Kaohsiung], 28 Apr. 1981, S. Tsuyuki leg. (KURA); 1 ♂, Lake Yenyanfu, Ilan Hsien, 29 Apr. 1982, N. Ohbayashi leg. (KURA); 1 ♀, Kengting Park, Pingtung Hsien, 4 May 1982, N. Ohbayashi leg. (KURA); 1 ♀, Shyk Shan, near Liu Kui, S Taiwan, 12 Jun. 1986, K. Baba leg. (KURA); 2 ♂♂, 1 ♀, Shyk Shan, near Liu Kui, S Taiwan, 28 Jun. 1986, K. Baba leg. (KURA); 4 ♀♀, Shi Nan Shan, near Liu Kui, S Taiwan, 23 Jul. 1986, K. Baba leg. (KURA); 2 ♂♂, 1 ♀, Thu Yun Shan, near Liu Kui, S Taiwan, 28 Jun. 1986, K. Baba leg. (KURA); 1 ♂, 2 ♀♀, Hohuanshan, Nan Tow Hsien, M Taiwan, 6 Aug. 1986, K. Baba leg. (KURA); 1 ♀, Twolin, Ilan Hsien, 29 Apr. 1987, N. Ohbayashi leg. (KURA); 2 ♂♂, Meifeng, 2150 m, M Taiwan, 15 Mar. 1989, K. Baba leg. (KURA); 6 ♂♂, 2 ♀♀, 1 ex, Yuanfeng, Nantou Hsien, 24 Jun. 1989, M. Owada leg. (KURA); 17 ♂♂, 2 ♀♀, 369 Cottage, Hsueshantungfeng, Taichung Hsien, 30 Jun. 1989, M. Satô leg. (KURA); 8 ♂♂, 9 ♀♀, 369 Cottage, Hsueshantungfeng, Taichung Hsien, 2 Jul. 1989, M. Satô leg. (2 ♂♂, 2 ♀♀ in EUMJ; 6 ♂♂, 7 ♀♀ in KURA); 1 ♂, Patungkuan, Hsini, Nantou, 20–22 Jun. 1990, J.-T. Yang (NMNS); 1 ♀, 230 Forest trail, Anmashan, Taichung, 3 May 1990, C.-C. Chiang (NMNS); 1 ♂, Yu-shan West peak, Chiayi, 15 May 1991, C.-C. Chiang (NMNS); 1 ♀, Mt. Anmashan, Taichung, 2 May 1991, A. Shinohara leg. (KURA); 1 ♂, Chung-hsueh Shan (Erh-san-ling Lin-tao [=230 Forest trail]), 2450–2500 m, Tai-an Hsiang, Miao-li Hsien, 24 May 1991, A. Saito leg. (CBM); 1 ♂, An-ma Shan, 2160–2300 m, Ho-p'ing, T'aichung Hsien, 25 May 1991, K.-F. Shih leg. (CBM); 2 ♂♂, Chia-li Shan, 2600–2850 m, Tai-an Hsiang, Miao-li Hsien, 27 May 1991, A. Saito leg. (CBM); 1 ♀, Sungkang, Nantou Hsien, 1 Jul. 1995, C. Lou leg. (KURA); 2 ♂♂, 1 ♀, Guandoushan, Nantou Hsien, 15 Apr. 1996, C. Lou leg. (KURA); 1 ♂, Tatachia, Nantou, 5 May 1998, M.-M. Yang & S.-Y. Yang (NMNS); 1 ♂, Tengchih, 1400 m, Taoyuan, Kaohsiung Hsien, 24 Mar. 2002, B. Tanaka leg. (KURA); 11 ♂♂, 7 ♀♀, 369 Cottage, 3100 m, Hoping, Taichung, 7 Jun. 2008, W.-T. Yang leg. (NMNS); 1 ♂, 1 ♀, Yakou Country Inn, 23°16.063' N, 120°58.419' E, 2582 m, Taitung County, 11 Aug. 2008, H. Mendel & MVL Barclay leg. (BMNH).

Description**Coloration**

Body and legs nearly black. Antennae dark brown to black. Mandibles yellowish brown. Body closely covered with pale pubescence; anterior margin of clypeus, antennae, elytra and legs fringed with pale bristles.

Male (Fig. 2P)

HEAD. Nearly as long as wide; vertex faintly hollowed, depressed along apical margin of clypeus and in lateral areas before eyes; surface densely and finely punctate and semilustrous; anterior margin of clypeus arcuate and faintly indented in middle; eyes not so large, globular and slightly prominent, ratio of eye diameter to interocular space 1:5.3; terminal labial palpomeres rounded ax-shaped; terminal maxillary palpomeres rounded ax-shaped; antennae filiform, extending to elytral midlength; antennomere I clavate, II short and a little expanded apicad, III to XI subcylindrical, all antennomeres without groove, ratio of antennomere lengths: 16:10:15.5:20.5:20.5:20.5:20.5:20:20:18.5:23.

PRONOTUM. Subquadrate, about 0.90 times as wide as head, nearly as long as wide; anterior and posterior margins moderately arcuate; lateral margins feebly arcuate; anterior angles rounded; posterior angles obtuse; dorsum convex in postero-lateral and hollowed in antero-lateral areas; medio-longitudinal groove distinct in posterior half; surface smooth and semilustrous. Scutellum triangular with rounded apex.

ELYTRA. Conjointly about 1.6 times as wide as pronotum, about 2.6 times as long as wide, sides subparallel; surface densely and finely punctate and moderately lustrous.

LEGS. Moderately slender; femora mostly straight; tibiae mostly straight, with basal part feebly arcuate; claws simple.

AEDEAGUS (Fig. 5A–C). Ventral process expanded and rounded apically, apex curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere as long as ventral process, broad and slightly narrowed apically, apical margin rounded, with some hairs on it, concave on inner margin. Laterophyse very short, with truncated apex, invisible in lateral view. Inner sac swollen, lengthened behind, and somewhat shorter than tegmen.

Body length 4.50–5.75 mm (holotype: 5.50 mm); width 0.80–1.25 mm (1.25).

Female (Fig. 2Q)

Similar to male. Body wider than in male. Eyes smaller than in male, ratio of eye diameter to interocular space 1:6.4. Antennae distinctly shorter than in male, barely exceeding humeri, ratio of antennomere lengths: 13 : 10 : 14 : 16 : 15 : 16 : 14 : 16 : 14 : 13 : 16.5.

PRONOTUM. About 0.95 times as wide as head, about 0.95 times as long as wide. Elytra conjointly about 1.6 times as wide as pronotum, about 2.6 times as long as wide. Claws simple. Abdominal ventrite VII widely emarginate on each side of terminal margin, forming subtriangular lateral lobes, median lobe indistinct in some specimens (Fig. 6I).

FEMALE GENITALIA (Fig. 6J). Vagina stout and rounded, abruptly extended apically as long and thick duct; diverticulum and spermathecal duct arising from apex of long duct of vagina; diverticulum moderately thin and spiral, longer than spermathecal duct; spermatheca provided with thin spiral tube, tube slightly longer than diverticulum; accessory gland thin, shorter than spermatheca.

Body length 4.75–6.50 mm; width 1.50–2.25 mm.

Variation

Lateral sides of pronotum somewhat converging or diverging posteriorly; body lusterless.

Remarks

This species is widely distributed in the Central Mountain Range at mid to high altitude except one specimen collected from the Kenting Park, which is at low altitude. It appears mainly from spring to summer according to label data.

Distribution (Fig. 8)

Taiwan (endemic).

Lycocerus kintaroi Hsiao & Okushima sp. nov.

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Figs 2R, 5D–F, 8

Diagnosis

This species can easily be distinguished from other members of this species group by the black pronotum, with yellowish fringed margins; black elytra, with very slender yellowish stripe on each humeral side; aedeagus with dorsal plate broad and subtruncated; apex of laterophyse far from apical margin of dorsal plate in lateral view.

Etymology

The specific epithet is dedicated to its collector, the late Dr. Kintaro Baba who was one of the great Japanese entomologists.

Type material**Holotype**

TAIWAN: ♂, Shi Nan Shan, near Liu Kui, S Taiwan, 5 May 1986, K. Baba leg. (NMNS).

Paratype

TAIWAN: 1 ♂, same data as for holotype (EUMJ).

Description**Coloration**

Eyes and head black. Antennae dark brown to black. Mandibles yellowish brown. Pronotum black, fringed with yellowish margins. Elytra black, with very slender yellowish stripe on each humeral side. Legs black. Pro-, meso- and metasterna, as well as abdomen blackish brown, with margins of abdominal ventrites yellowish brown. Body closely covered with pale pubescence; anterior margin of clypeus, antennae, elytra and legs fringed with pale bristles.

Male (Fig. 2R)

HEAD. Nearly as long as wide; vertex faintly hollowed, depressed along apical margin of clypeus and in lateral areas before eyes; surface densely and finely punctate and lustrous; anterior margin of clypeus arcuate and faintly indented in middle; eyes not so large, globular and slightly prominent, ratio of eye diameter to interocular space 1:5.0; terminal labial palpomeres rounded ax-shaped; terminal maxillary palpomeres rounded ax-shaped; antennae filiform, extending to elytral midlength; antennomere I clavate, II short and a little expanded apicad, III to XI subcylindrical, all antennomeres without groove, ratio of antennomere lengths: 16:10:13.5:15.5:15.5:15:14.5:15:14:13:14.5.

PRONOTUM. Subquadrate, slightly narrower than head, about 0.95 times as long as wide; anterior and posterior margins moderately arcuate; lateral margins feebly sinuate; anterior angles rounded; posterior angles obtuse; dorsum convex in postero-lateral and hollowed in antero-lateral areas; medio-longitudinal groove distinct in posterior half; surface smooth and lustrous. Scutellum triangular, with rounded apex.

ELYTRA. Conjointly about 1.3 times as wide as pronotum, about 2.5 times as long as wide, sides sub-parallel; surface densely and finely punctate and lustrous.

LEGS. Moderately slender; femora mostly straight; tibiae mostly straight, with basal part feebly arcuate; claws simple.

AEDEAGUS (Fig. 5D–F). Ventral process moderately expanded and rounded apically, apex curved inwards, basal part broad and extending inwards onto ventral side; dorsal plate of each paramere as long as ventral process, broad and subtruncated, apical margin with some hairs on it, concave on inner margin. Laterophyse very short with obtuse apex, invisible in lateral view. Inner sac swollen, lengthened behind, somewhat shorter than tegmen.

Body length 5.50–6.00 mm (holotype: 5.50 mm); width 1.50–1.70 mm (1.50 mm).

Female

Unknown.

Remarks

The right antenna of the holotype is missing.

Distribution (Fig. 8)

Taiwan (endemic).

Discussion

Members of the *Lycocerus hanatanii* species group have a uniform appearance, with only minor, but diagnostic differences in the structure of genitalia, which implies that these species possibly went through a relatively young history of speciation, resulting in morphological divergences that are indistinct. Due to a lack of recognized synapomorphies in the phylogenetic analysis, the relationship between other species groups and this species group as well as that among the members of *L. hanatanii* species group are not well-resolved. A molecular approach could solve the problem of insufficient synapomorphic characters and give higher resolution to the relationship within this species group and its phylogenetic position in *Lycocerus*.

In view of the greater species diversity, it seems that Taiwan is the center of origin of the *L. hanatanii* species group. However, in point of the origin of islands, Taiwan is a continental island, which is generally believed to have a biota related to the mainland of Eurasia (Creer *et al.* 2001; Jang-Liaw *et*

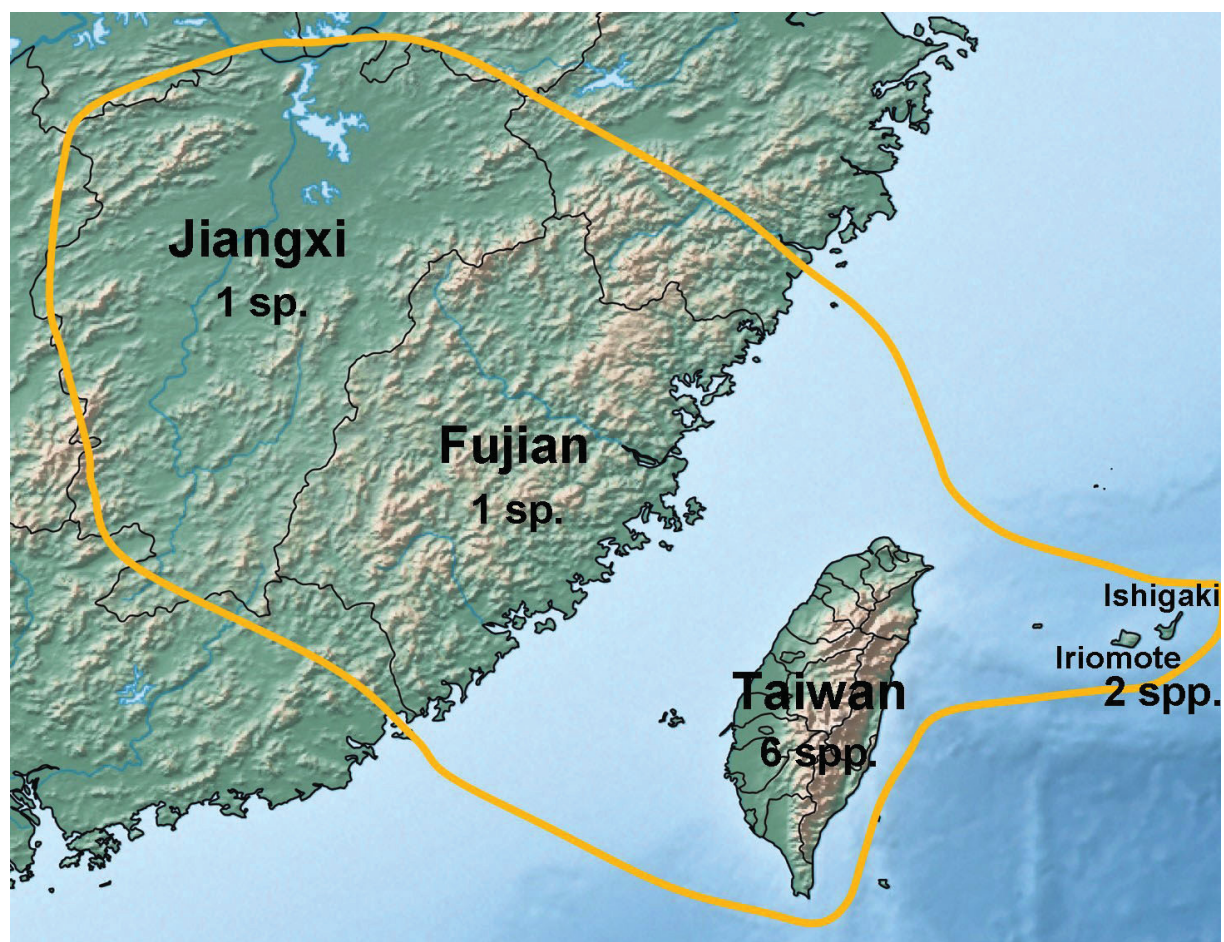


Fig. 10. Range map of the *Lycocerus hanatanii* species group and the number of species in each geographic region.

al. 2008; Huang & Lin 2011; Tsai *et al.* 2014). Furthermore, the taxonomy of the cantharids of China has not been studied completely yet, and it is possible that more members of this species group will be discovered and the present conjecture will be challenged or invalidated. On the other hand, according to known distribution information, this species group exhibits a China–Taiwan–Southern Ryukyus distribution pattern (Fig. 10). The speciation process of this species group, especially insular species such as *L. hanatanii* and *L. ueharaensis*, is possibly associated with the paleogeographic history of the East China Sea and the islands of eastern Asia during the Pleistocene glaciation, as in the case of the grass lizards (Lin *et al.* 2002). Sea level changed during this period and resulted in the appearance of a larger continental land area to provide animals the opportunity to migrate from continent to islands, then some populations were isolated when sea levels rose again, and speciation occurred. Further studies of historical biogeography are needed and will give insight into the evolutionary history of this species group.

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