

Taxonomic review of the planthopper genus *Orthopagus* (Hemiptera, Fulgoromorpha, Dictyopharidae), with descriptions of two new species

Zhi-Shun Song^{1,2}, Igor Malenovský³, Jian-Qin Chen¹, Jürgen Deckert⁴, Ai-Ping Liang^{5,6}

¹ Jiangsu Key Laboratory of Biofunctional Molecules, School of Life Sciences, Chemistry & Chemical Engineering, Jiangsu Second Normal University, Nanjing 210013, China

² Southeast Asia Biodiversity Research Institute, Chinese Academy of Sciences, Yezin, Nay Pyi Taw 05282, Myanmar

³ Department of Botany and Zoology, Faculty of Science, Masaryk University, Kotlářská 2, 611 37 Brno, Czech Republic

⁴ Museum für Naturkunde, Leibniz Institute for Research on Evolution and Biodiversity Science, Invalidenstrasse 43, Berlin 10115, Germany

⁵ Key Laboratory of Zoological Systematics and Evolution, Institute of Zoology, Chinese Academy of Sciences, Beijing 100101, China

⁶ College of Life Sciences, University of Chinese Academy of Sciences, Beijing 100049, China

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Corresponding authors: Igor Malenovský (malenovsky@sci.muni.cz); Ai-Ping Liang (liangap@ioz.ac.cn)

Abstract

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The Oriental and eastern Palearctic planthopper genus *Orthopagus* Uhler, 1897 (Hemiptera, Fulgoromorpha, Dictyopharidae, Dictyopharinae, Orthopagini) is revised. Six species are included: *O. bartletti* Song, Malenovský & Deckert, **sp. n.** (described from India), *O. exoletus* (Melichar, 1903), **comb. n., stat. rev.** (material studied from India and Sri Lanka), *O. hainanensis* Song, Chen & Liang, **sp. n.** (described from China: Hainan island), *O. lunulifer* Uhler, 1897 (the type species of the genus; confirmed from Japan, China, Vietnam, Laos, India, and Nepal), *O. philippinus* Melichar, 1914 (Philippines), and *O. splendens* (Germar, 1830) (confirmed from China, Vietnam, Thailand, India, Malaysia, and Indonesia). *Orthopagus helios* Melichar, 1912 is newly synonymized with *O. lunulifer*. Lectotypes are designated for *O. helios*, *O. helios* var. *diffusus* Melichar, 1912, *O. elegans* Melichar, 1912, and *O. philippinus*. *Dictyophara indiana* Walker, 1851 is considered a nomen dubium. All species are redescribed, including habitus photographs and detailed illustrations of the male genitalia. Female genitalia are described for the genus for the first time. A key for identification of the species of *Orthopagus* and a distribution map are given.

Introduction

The family Dictyopharidae is one of twenty currently recognized extant families of planthoppers (Hemiptera, Fulgoromorpha) (Bourgoin 2018). With more than 720 species in 155 extant and extinct genera, this family is currently divided into two subfamilies Dictyopharinae Spinola, 1839 and Orgeriinae Fieber, 1872 (Muir 1923, Metcalf 1946, Song et al. 2016c, 2018). The dictyopharid species are widely distributed in all biogeographic regions, being most numerous in tropical and subtropical zones, e.g. in South America, the Oriental region and the East Indies (Metcalf 1946, Bourgoin 2018). Both adults

and nymphs of Dictyopharidae are phytophagous and suck phloem sap from above-ground portions of plants. Their associations with host-plants are generally poorly known. Most species are probably dicot feeders, perhaps often with narrow trophic niches (monophagous), but there are also polyphagous and monocot-feeding taxa (Wilson et al. 1994, Krstić et al. 2016). A few species are economically important agricultural pests, e.g. on rice, sugarcane and cranberry (Wilson and O'Brien 1987), with the potential of acquiring and spreading phytoplasma pathogens (Krstić et al. 2016).

The larger nominotypic subfamily Dictyopharinae is further divided in twelve extant tribes (Song et al. 2018).

One of them is Orthopagini first recognized by Emeljanov (1983) based on the type genus *Orthopagus* Uhler, 1897 and six other genera, and later extended to include a total of 23 genera (Emeljanov 2011, Song et al. 2014, 2016d). The Orthopagini taxa are mainly distributed in the Old World tropics and subtropics, including sub-Saharan Africa, India, Sri Lanka, southern China, Indochina, Malaya, the Greater Sunda Islands, the Philippines, the Moluccas, and northern Australia (Song et al. 2016d, Bourgoin 2018). A few species of *Orthopagus* and *Saigona* Matsuura, 1910 extend into the eastern Palaearctic region (Liang and Song 2006). Recently, most Orthopagini genera have been revised (Liang and Song 2006, Song and Liang 2006a, b, 2007, 2011, 2012a, b, Song et al. 2012, 2014, 2016a, b, d, 2017). The monophyly of the tribe was tested and phylogenetic relationships among most genera were analysed by Song et al. (2014, 2016d, 2018). Morphological characters support Orthopagini as a sister-group to Dictyopharini (Song et al. 2016b, d, 2018).

The genus *Orthopagus* has been known to include five valid species distributed in the Oriental and eastern Palaearctic regions (Bourgoin 2018). Its complicated nomenclatorial and taxonomic history can be summarised as follows. The type species, *Orthopagus lunulifer* Uhler, 1897 was described from Japan. *Orthopagus* is congeneric with *Anagnia* erected earlier by Stål (1861) for *Flata splendens* Germar, 1830 from Java, which Stål considered a senior synonym of *Dictyophara indiana* Walker, 1851 described from India, but *Anagnia* had been preoccupied by Walker (1854) for a genus of moths in the Erebidae (Lepidoptera). Melichar (1903) described *Udugama* based on *Udugama exoleta* Melichar, 1903 from Sri Lanka. Kirkaldy (1904) proposed a new generic name *Kareol* Kirkaldy to replace *Anagnia* Stål (nec Walker). *Kareol* was later synonymized with *Udugama* by Distant (1906), and the latter was synonymized with *Orthopagus* by Oshanin (1908). Distant (1906) also proposed that the species names *U. exoleta* and *F. splendens* were synonyms. Melichar (1912) redescribed *Orthopagus* and added two species names based on specimens from Taiwan, China, *O. elegans* Melichar, 1912 and *O. helios* Melichar, 1912. *Udugama fletcheri* Kirkaldy, 1908 also listed by Melichar (1912) in *Orthopagus* is currently considered a junior synonym of *Truncatomeria viridistigma* (Kirby, 1891) (see Song and Liang 2011). The last species described so far and still placed in *Orthopagus* was *O. philippinus* Melichar, 1914 from Luzon, the Philippines (Melichar 1914).

Based on examination of most *Orthopagus* types and a critical review of the literature, *Orthopagus* is here revised. We redescribe all previously known taxa and add two new species, *O. bartletti* Song, Malenovský & Deckert, sp. n. from India and *O. hainanensis* Song, Chen & Liang, sp. n. from China. We provide an identification key and photographic illustrations for each species, showing also the structures of the male and female genitalia, described and illustrated in detail.

Material and methods

The specimens studied in the course of this work are deposited in the following institutions, which are subsequently referred to by their acronyms: **BMNH**, Natural History Museum, London, UK; **BPBM**, Bernice Pahau Bishop Museum, Honolulu, Hawaii, USA; **HNHM**, Magyar Természeti-Tudományi Múzeum (Hungarian Natural History Museum), Budapest, Hungary; **IZCAS**, Institute of Zoology, Chinese Academy of Sciences, Beijing, China; **JSSNU**, Jiangsu Second Normal University, Nanjing, China; **LBOB**, personal collection of Lois B. O'Brien, Tucson, Arizona, USA; **MFNB**, Museum für Naturkunde, Berlin, Germany; **MMBC**, Moravské zemské muzeum (Moravian Museum), Brno, Czech Republic; **MZPW**, Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland; **SDEI**, Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; **SNSD**, Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany; **UDCC**, Department of Entomology and Wildlife Ecology Collection, University of Delaware, Newark, Delaware, USA; and **USNM**, National Museum of Natural History, Smithsonian Institution, Washington D. C., USA.

The post-abdomina of the specimens used for dissections were cleared in 10% KOH at room temperature for ca. 6–12 hours, rinsed and examined in distilled H₂O and then transferred to 10% glycerol and enclosed in microvials to be preserved with the specimens. Observations were conducted under a stereomicroscope, measurements and photography under Zeiss Discovery V12 or Leica M205 C stereomicroscopes equipped with a Nikon D7000 digital camera in IZCAS. Some final images were compiled from multiple photographs using CombineZM image stacking software and improved with the Adobe Photoshop CS5 software.

The morphological terminology and measurements used in this study follow Song et al. (2016c, d, 2018) for most characters, Bourgoin (1993) for the female genitalia, and Bourgoin et al. (2015) for the forewing.

Results

Orthopagus Uhler, 1897

Anagnia Stål, 1861: 149. Type species: *Flata splendens* Germar, 1830; by original designation and monotypy. Preoccupied by *Anagnia* Walker, 1854: 446 (Lepidoptera: Erebidae).

Orthopagus Uhler, 1897: 278; Melichar 1912: 57. Type species: *Orthopagus lunulifer* Uhler, 1897; by original designation and monotypy. *Udugama* Melichar, 1903: 27; Distant 1906: 249. Type species: *Udugama exoleta* Melichar, 1903; by original designation and monotypy. Synonymized with *Orthopagus* by Oshanin 1908: 444.

Kareol Kirkaldy, 1904: 279. Replacement name for *Anagnia* Stål. Synonymized with *Udugama* by Distant 1906: 249.

Diagnosis. *Orthopagus* can be distinguished from other genera in the Orthopagini by the following combination of characters: cephalic process short, truncated in front in dorsal view; vertex with lateral carinae strongly ridged and sub-parallel in basal half, slightly constricted at an-

terior margin of eyes, median carina sharp and complete; frons with intermediate carinae approaching frontoclypeal suture, median carina complete; pronotum with intermediate carinae distinct in basal half; mesonotum with lateral carinae curving anteriorly towards median carina; forewings with a wide sublunate streak on distal half of wing, transverse veins sparse, pterostigmal area with 2–4 cells; fore femora flattened and dilated, with a large and blunt spine near apex; hind tibiae with seven apical teeth; phallobase with inflated membranous paired lobes, with or without numerous small superficial spines.

Description. Adult. General colour of body brownish ochraceous to dark brown marbled, with pale green and reddish ochraceous streaks on dorsum (Figs 1A–B, 2A–L). Females distinctly darker than males. Head pale ochraceous with dark brown markings on vertex and frons the extent of which varies among species. Clypeus pale ochraceous basally, with two small dark spots at frontoclypeal suture on each side of median carina, apical half dark brown. Pronotum brownish ochraceous to dark brown, median carina and spots on lateral marginal areas and paranotal lobes pale ochraceous. Mesonotum dark brown, median and lateral carinae, and lateral marginal areas flavescent or greenish. Forewing veins light ochraceous, membrane hyaline to translucent with three dark brown markings: (i) a large sublunate streak extending along the posterior–apical margin from basal portion of areola postica across apical portions of cells of the medial area to the apex of RP vein; (ii) triangular patch on pterostigma, extending also into radial area (C1 cell) and rarely more mesiad as a dark streak along nodal line; (iii) streak along postclaval wing margin filling out whole inner claval cell (Figs 2A–L, 3A–F). Hind wing veins ochraceous, membrane clear, with a more or less developed dark brown marking along the apical portion of CuA₁ vein. Legs pale to dark brown: femora dull ochraceous to fuscous, banded and marked with ivory white; fore and mid tibiae yellowish green to ochraceous with two dark brown transverse bands medially; hind tibiae yellowish green (pale ochraceous in old dry-mounted specimens), with base and apex including lateral and apical spines fuscous; fore and mid tarsi fuscous, hind tarsi ochraceous. Abdomen dorsally and ventrally ochraceous to dark brown, with dark brown or pale ochraceous spots and stripes of various sizes and shape.

Head (Figs 4A–C, 5A–C, 6A–C, 8A–C, 9A–C, 10A–C) usually produced in a short and stout cephalic process. Vertex (Figs 4A, 5A, 6A, 8A, 9A, 10A) moderately broad, basal width slightly greater than transverse diameter of eyes in dorsal view, posterior plane elevated above pronotum; lateral carinae strongly ridged, foliaceous, and sub-parallel in basal half, slightly constricted at anterior margin of eyes, broadly convex at apex; posterior margin ridged, concave, forming angle of 80–90°; median carina sharp and complete. Frons (Figs 4C, 5C, 6C, 8C, 9C, 10C) with lateral carinae ridged, nearly parallel, slightly expanded outward below antennae; intermediate carinae slightly converging posteriorly and approaching frontoclypeal suture; median carina distinct and complete; basal margin of frons projecting anteriorly of apex

of vertex. Postclypeus and anteclypeus (Figs 4C, 5C, 6C, 8C, 9C, 10C) convex medially, with distinct median carina. Rostrum long, surpassing base of hind femora; basal segment nearly equal to distal one. Compound eyes large and globose. Ocelli relatively large, reddish. Antennae with very small scape; pedicel large and subglobular, with more than 50 distinct sensory plaque organs distributed over entire surface; flagellum long, setuliform.

Pronotum (Figs 4A, 5A, 6A, 8A, 9A, 10A) distinctly shorter than mesonotum at midline, anterior margin angularly convex medially, lateral marginal areas straight and sloping down with two long longitudinal carinae on each side, posterior margin concave, forming obtuse angle (100–120°); intermediate carinae distinct in basal half, strongly diverging laterad; median carina sharp and elevated, with a large lateral pit on each side. Mesonotum (Figs 4A, 5A, 6A, 8A, 9A, 10A) tricarinate on disc, lateral carinae converging anteriorly towards median carina. Forewings (Fig. 3A–F) hyaline, ratio of length to width about 3:1; venation with sparse transverse veins; MP bifurcating MP₁₊₂ and MP₃₊₄ near middle and beyond CuA; number of apical cells between R and CuA equal to 14; Pcu and A₁ veins fused into a long Pcu+A₁ vein at apical 1/5 in clavus; pterostigmal area clear, with 2–4 cells. Legs moderately long; fore femora flattened and dilated, with a large and blunt spine near apex; hind tibiae with 5–7 (mostly six) lateral spines and seven apical teeth; hind tarsomeres I with 18–20 and tarsomeres II with 12–14 apical teeth, respectively.

Male genitalia. Pygofer (Figs 4D–F, 5D–F, 6D–F, 8D–F, 9D–F, 10D–F) in lateral view distinctly wider ventrally than dorsally, dorsal margin slightly excavated to accommodate segment X, dorso-posterior margins angular, produced into a distinct lobe which is short and broad or larger and tooth-like. Gonostyles (Figs 4E–F, 5E–F, 6E–F, 8E–F, 9G, 10E–F) symmetrical, with narrow base, expanded toward apex, broadest at apical fourth; dorsal margin with a claw-like, apically sclerotised process directed dorsad, outer dorsal edge with a spiny hook-like sclerotised process near middle directed ventrad. Aedeagus (Figs 4G–I, 5G–I, 6G–I, 8G–I, 9H–J, 10G–I) with one pair of elongate endosomal processes extended from phallobase posteriorly and strongly curved dorso-anteriorly or laterad; these processes are membranous, acute apically and smooth or bearing numerous minute spines over their entire surface; phallobase sclerotised and pigmented basally, membranous and inflated apically, with paired lobes. Segment X (Figs 4D–E, 5D–E, 6D–E, 8D–E, 9D–E, 10D–E) large, in dorsal view with apex deeply excavated to accommodate anal style; anal style elongate and large.

Female genitalia. Gonocoxae VIII (Fig. 7D) with two membranous and flattened endogonocoxal processes (Gxp) on endogonocoxal lobe: Gxp1 large and elongate, with a long sclerotized plate in it; Gxp2 smaller and shorter. Gonapophyses VIII (Fig. 7D) with anterior connective lamina large and sclerotized, with seven teeth of varying sizes and shapes. Gonapophyses IX (Fig. 7E–F) with posterior connective lamina triangular, symmetrical, fused with intergonocoxal plate at base; intergonocoxal



Figure 1. (A) *Orthopagus lumulifer* Uhler, female, Henan, China; (B) *Orthopagus splendens* (Germar), male, Yunnan, China. Photographed by Z.-S. Song.

plate extended cephalad into genital cavity, forming wall of gonospiculum. Gonoplasts (Fig. 7G) with two lobes homologous; lateral lobe large and moderately sclerotized, with long setae at apex; the posterior lobe membranous, containing long sclerotized plate. Segment X (Fig. 7A) large and broad in dorsal view, apex deeply excavated to accommodate anal style; anal style large and elongate. Female ectodermal genital ducts ditrysian. Bursa copulatrix (Fig. 7A–C) superficially membranous, regularly gridded, without sclerotized ornamentations. A pair of large digitiform glands (Fig. 7B) branched at anterior extremity of the anterior vagina on each side of the spermatheca. Spermatheca (Fig. 7B) divided clearly into five parts: orificium receptaculi, ductus receptaculi, diverticulum ductus, pars intermedialis, and glandula apicalis.

Fifth instar nymph. See Yang and Yeh (1994) for a detailed description.

Diversity and distribution. *Orthopagus* is revised here to include six valid species (see below). The species of the genus are widely distributed in the Oriental and eastern Palearctic regions from India in the southwest to Japan in the northeast (Fig. 11).

Nomenclatorial remark on *Dictyophara indiana* Walker, 1851. The identity of one more available species name

belonging to *Orthopagus* could not be sufficiently cleared during this study: *Dictyophara* [sic] *indiana* Walker, 1851: 310 described from India (without more precise locality data). This name was synonymized under *Anagnia splendens* (Germar) (now *Orthopagus splendens*) by Stål (1861): 149. However, this synonymy is considered doubtful here because the original description of *D. indiana* lacks diagnostic information and illustrations which would enable recognition of its species identity and the single available type specimen of *D. indiana* (deposited in BMNH) could not be directly examined during this study due to its very poor condition which did not allow its sending out for a loan. Based on a photograph kindly provided by M. D. Webb (BMNH), the type specimen belongs to an *Orthopagus* species but it lacks the abdomen and its head has been partly damaged. As the details of the male genitalia and the coloration and proportions of the head, i.e. the characters which are missing or damaged in the type, are the most reliable diagnostic morphological characters of *Orthopagus* species, it is not certain that even a direct examination of the type would help to solve the identity of *D. indiana*. Therefore, it is proposed here to treat *Dictyophara indiana* as a nomen dubium. Currently, four *Orthopagus* species are known from the Indian subcontinent: *O. bartletti* sp. n., *O. exoletus*, *O. lumulifer* and *O. splendens*, of which *O. exoletus* is the most widespread (Fig. 11).

Key to the species of *Orthopagus*

- 1 Forewings with a dull brownish streak along nodal line connecting pterostigmal area and distal sublunate streak (Fig. 3A); head very short, hardly produced in front of eyes, in lateral view, broadly rounded (Fig. 4A–B); male pygofer, in lateral view, with dorso-posterior margin on each side produced into a large, broadly truncate, biangular lobe (Fig. 4E); lobes of phallobase muricate apically (Fig. 4G–I) *O. bartletti* Song, Malenovský & Deckert, sp. n.
- Forewings without a brownish streak along nodal line (Fig. 3B–F); head longer, distinctly produced in front of eyes (Figs 5A–B, 6A–B, 8A–B, 9A–B, 10A–B); male pygofer, in lateral view, with dorso-posterior margin on each side produced either into a large but narrow, simply tooth-like lobe (Figs 5E, 9E, 10E) or into a broadly truncate but short and blunt lobe (Figs 6E, 8E); lobes of phallobase smooth apically (Figs 5G, 6G, 8G, 9H, 10G)..... 2
- 2 Male pygofer, in lateral view, with dorso-posterior margin produced into a large and narrow tooth-like lobe (Figs 5E, 9E, 10E) 3
- Male pygofer, in lateral view, with dorso-posterior margin produced into a short and broad lobe (Figs 6E, 8E)..... 5
- 3 Vertex ivory white to pale ochraceous, with 3–4 pairs of small dark brown markings (Fig. 5A); aedeagus with endosomal processes lacking minute superficial spines; phallobase with three pairs of membranous lobes, of which dorsal lobes thumb-like, directed dorso-laterad (Fig. 5G–I) *O. exoletus* (Melichar, 1903)
- Vertex largely dark brown from base to apex (Figs 9A, 10A); aedeagus with endosomal processes covered with numerous minute spines; phallobase with two pairs of membranous lobes, of which dorsolateral lobes relatively large, bladder-like (Figs 9H–J, 10G–I)..... 4
- 4 Head, in lateral view, distinctly inflated and bulbous apically (Fig. 9B); frons with a large roundish dark brown spot at base (Fig. 9C); aedeagus with endosomal processes relatively slender, weakly curved dorso-laterad (Fig. 9H–I)..... *O. philippinus* Melichar, 1914
- Head, in lateral view, not inflated, narrow apically (Fig. 10B); frons light, without roundish dark brown spot at base (Fig. 10C); aedeagus with endosomal processes relatively robust, strongly curved cephalad (Fig. 10G–H)..... *O. splendens* (Germar, 1830)
- 5 Vertex light ochraceous, with a pair of small dark brown patches on each side of midline in basal third (Fig. 6A); transition of vertex to frons, in lateral view, broadly rounded (Fig. 6B); male segment X elongate in dorsal view, with ratio of length to width near middle 1.9–2.0 (Fig. 6D)..... *O. hainanensis* Song, Chen & Liang, sp. n.
- Vertex nearly dark brown from base to apex (Fig. 8A); transition of vertex to frons, in lateral view, almost angular (Fig. 8B); male segment X relatively short and broad in dorsal view, with ratio of length to width near middle 1.2–1.3 (Fig. 8D)..... *O. lunulifer* Uhler, 1897

Species descriptions (character states shared with the generic description are not repeated)

***Orthopagus bartletti* Song, Malenovský & Deckert, sp. n.**

<http://zoobank.org/7CA90D40-0E5F-47CF-B85B-04321A516EED>

Figs 2A–B, 3A, 4A–I

Type material. Holotype male, **INDIA:** Karnataka: Shimoga district, Someshwari Wildlife Sanctuary, 10 km W Agumbe, 13°28'24"N; 75°00'40" E, alt. 372 ft, early successional, wet evergreen forest, 22.ix.2005, C. R. Bartlett leg. (UDCC).

Diagnosis. *Orthopagus bartletti* sp. n. can be separated from all other *Orthopagus* species by the very short head, hardly produced in front of eyes; the forewings with a brownish streak along nodal line connecting the pterostigmal area with the distal sublunate streak; the dorso-posterior margin of the male pygofer with a large and broad process forming two distinct angles; the robust male segment X; and the lobes of the phallobase muricate apically.

Description. Measurements (1 male). Body length (from apex of head to tip of forewings): 11.5 mm; head length (from apex of cephalic process to base of eyes): 1.2 mm; head width (including eyes): 1.5 mm; forewing length: 9.6 mm.

Coloration (Fig. 2A–B). General colour brownish ochraceous marked with dark brown on dorsum. Head greenish ochraceous, vertex with basal corners, a pair of round patches in basal third, and apical diamond-shaped spot dark brown (Fig. 4A); frons with median area between intermediate carinae extensively dark brown anteriorly and with series of small pale fuscous spots along intermediate and lateral carinae and narrow ivory white band basally (Fig. 4C). Clypeus ivory white, with two small spots at base and apex dark brown. Compound eyes fuscous with posterior margin ochraceous; ocelli purplish-red. Pronotum brownish ochraceous, median carina, apical marginal areas of ventral lobes, and posterior lateral angles ivory white. Mesonotum brownish ochraceous (Fig. 4A). Forewings hyaline, veins ochraceous, pterostigmal area, a streak along nodal line, and a wide sublunate streak on distal third dull ochraceous; posterior (claval) margin broadly faintly brown (Fig. 3A). Hind wings hyaline, veins and an apical spot dull ochraceous. Legs pale brown; fore femora subapically and hind tibiae at base and apex (including lateral and apical spines) blackish. Abdomen dorsally and ventrally brownish ochraceous.

Structure. Head (Fig. 4A–C) very short, cephalic process practically absent. Vertex (Fig. 4A) with ratio of length at midline to width between eyes 1.4. Frons with base slightly inflated anteriorly in dorsal view (Fig. 4A),



Figure 2. Habitus of *Orthopagus* species. (A, B) *O. bartletti* sp. n., male, holotype, Karnataka, India; (C, D) *O. exoletus* (Melichar), male and female, Sri Lanka; (E, F) *O. hainanensis* sp. n., male and female, paratypes, Hainan, China; (G, H) *O. lunulifer* Uhler, male and female, China; (I, J) *O. philippinus* Melichar, male and female, Philippines; (K, L) *O. splendens* (Germar), male and female, China.

with transition to vertex broadly rounded in lateral view (Fig. 4B); in ventral view, frons with ratio of length at midline to maximum width 2.2; median carina more or less obscure at base (Fig. 4C).

Male genitalia. Pygofer, in lateral view, with dorso-posterior margin forming a large, broad, biangular lobe (Fig. 4E); in ventral view (Fig. 4F) much longer than in dorsal view (Fig. 4D) with ratio of ventral to dorsal

width about 3.4. Gonostyles (Fig. 4E, F) elongate, relatively narrow in basal half, with strongly sinuate dorsal margin medially. Aedeagus (Fig. 4G–I) with endosomal processes relatively short and robust, without distinct minute superficial spines, and directed laterad; phallobase with a pair of large, elongate, thumb-like ventral lobes, curved dorso-posteriad and muricate apically (Fig. 4G–H); and a pair of shorter lateral lobes, directed posteriad (Fig. 4H). Segment X, in lateral view, relatively short and robust, with ventral margin gradually widening from base to broadly truncate apex (Fig. 4E); in dorsal view broad, broadest medially, with ratio of length to maximum width 1.1 (Fig. 4D).

Female genitalia unknown.

Etymology. The new species is named after Dr. Charles R. Bartlett, collector of the type specimen and curator of the insect collection at the Department of Entomology and Wildlife Ecology, University of Delaware, USA, in recognition of his kindest help and support to the first author when he visited UDCC in 2017. The species name is to be treated as a noun in genitive case.

Distribution. So far only known from southwestern India (Fig. 11).

***Orthopagus exoletus* (Melichar, 1903), comb. n., stat. rev.**

Figs 2C–D, 3B, 5A–I

Udugama exoleta Melichar, 1903: 28, Pl. I, figs 7, 7a–b. Syntypes: 5 females, Moruwale, Sri Lanka (not examined). Synonymized under *Udugama splendens* (Germar, 1830) by Distant 1906: 249. *Udugama exoleta*: Kirkaldy 1908: 14.

Material examined. **INDIA:** 2 females, [no state indicated], 1934–394, T. R. Bell leg. (BMNH); West Bengal: 1 female, Calcutta [= Kolkata], 3.x.1907 (coll. Distant, BMNH); Maharashtra: 1 male, Sindhudurg district, roadside on ridge 2 km W Amboli, 15°58'04"N, 73°59'23"E, alt. 2394 ft, pasture and successional, moist deciduous forest, 28.ix.2005, C. R. Bartlett leg. (UDCC); 1 male, Pune district, 5 km E Mulshi Lake near Tamini village, 18°26'37"N, 73°25'46"E, alt. 2047 ft, deciduous forest and open areas, 2.x.2005, C. R. Bartlett (UDCC); Goa: 2 females, Sanguem district, near Bhagwan Mahaveer Sanctuary 100 m E Molem, 15°22'43"N, 74°13'52"E, alt. 342 ft, moist deciduous forest, 24–25.ix.2005, C. R. Bartlett leg. (UDCC); Kerala: 2 males, Malabar, Nadungayam [forest near Nilambur], 200 ft, 16.–22.ix.1938 (BMNH); 1 female, Parambikulam, alt. 1700–3200 ft, 16.–24.ix.1914, F. H. Gravely leg. (coll. Distant, BMNH); 2 females, Tenmalai [= Thenmala], 12.–15.v.1937 (BMNH); Tamil Nadu: 1 female, Nilgiri Hills, 11 km SE Kotagiri, Kunchappanai, 11°24'N 76°56'E, alt. 1100 ± 100 m, 3.–15.v.2002, L. Dembický leg. (MMBC). **SRI LANKA:** North Western Province: 1 female, Puttalam district, Puttalam, “12.” [= ?1912] (coll. Melichar, MMBC); North Central Province: 1 male, Anuradnapura district, Wilpattu National Wild-

life Park, Hunuwilagama, Wildlife Soc. Bungalow, 200 ft, 10–19.iii.1970, D. Davis & B. Rowe leg. (USNM); Central Province: 1 female, Kandy district, Talwatte, 29.xi.1995, M. Schaffer leg. (BMNH); Samaragamuwa: 1 male, Ratnapura district, Uggalkaltota, Irrigation Bungalow, alt. 350 ft, 31.i–8.ii.1970, D. Davis & B. Rowe leg. (USNM).

Redescription. Measurements (2 males, 8 females). Body length (from apex of head to tip of forewings): male 11.1 mm, female 12.3–14.7 mm; head length (from apex of cephalic process to base of eyes): male 1.28–1.30 mm, female 1.28–1.40 mm; head width (including eyes): male 1.40–1.45 mm, female 1.48–1.60 mm; forewing length: male 9.0–9.4 mm, female 10.2–12.2 mm.

Coloration. General coloration as in generic description (Fig. 2A). Vertex predominantly light ochraceous, with 3–4 pairs of small dark brown markings: an elongate patch on each side of midline apically, a small spot at each lateral keel medially, a roundish spot on each side of midline at basal third, and a small spot in each postero-lateral corner (Fig. 5A). Frons light ochraceous with small dark brown spots along intermediate and lateral carinae, frons base slightly infuscated (Fig. 5C). Forewing membrane pattern as in Fig. 3B. Hind wing membrane with a relatively narrow dark brown streak along the apical portion of CuA₁ vein, extending along hind wing apical margin in some specimens.

Structure. Head with cephalic process very short, not inflated (Figs 5A–C). Vertex (Fig. 5A) with ratio of length at midline to width between eyes 1.2–1.5. Transition of vertex to frons narrowly rounded in lateral view (Fig. 5B). Frons relatively broad, with ratio of length at midline to maximum width 2.3–2.7.

Male genitalia. Pygofer, in lateral view, with dorso-posterior margin produced into a relatively large but narrow, tooth-like, apically obtuse process (Fig. 5E); in ventral view (Fig. 5F) much longer than in dorsal view (Fig. 5D) with ratio of ventral to dorsal width about 2.6. Gonostyles (Fig. 5E) large and broad medially, with dorsal margin weakly sinuate medially. Aedeagus (Fig. 5G–I) relatively small and slender, endosomal processes curved laterad and slightly ventro- or dorsoanteriorad, membranous, without distinct minute superficial spines; phallobase with three pairs of relatively small (not conspicuously inflated) membranous lobes: a pair of elongate lateral lobes with their apices gradually convergent and tapering posteriad (Fig. 5H–I), a pair of elongate thumb-like ventral lobes, directed ventroposteriad (Fig. 5H), and a pair of small thumb-like dorsal lobes, directed dorsolaterad (Fig. 5G). Segment X, in lateral view, elongate, basal half narrow, gradually widening to apex beyond middle (Fig. 5E); in dorsal view, widest medially, with ratio of length to maximum width 1.1 (Fig. 5D).

Female genitalia as in generic description.

Distribution. India (southwestern part and West Bengal), Sri Lanka (Fig. 11).

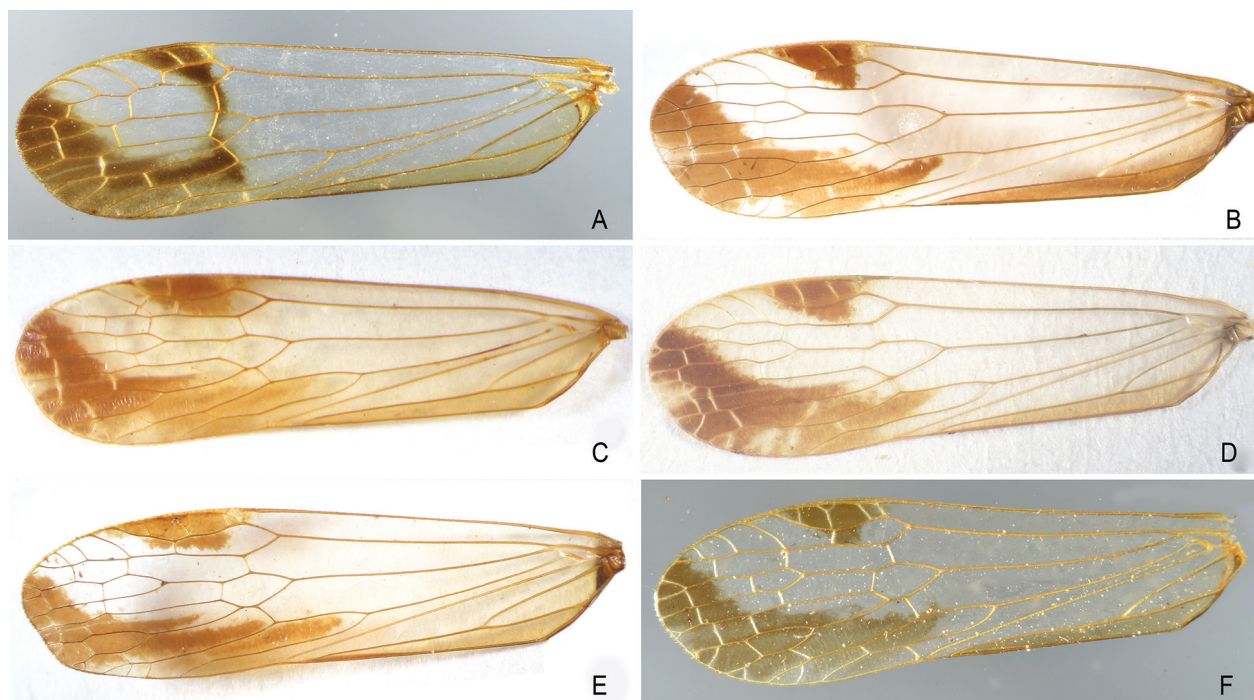


Figure 3. Forewing of *Orthopagus* species. (A) *O. bartletti* sp. n.; (B) *O. exoletus* (Melichar); (C) *O. hainanensis* sp. n.; (D) *O. lunulifer* Uhler; (E) *O. philippinus* Melichar; (F) *O. splendens* (Germar).

Remarks. *Udugama exoleta* was described from Sri Lanka as the type species of *Udugama* (Melichar 1903). Distant (1906) synonymized this species name with *Udugama splendens* described from Java, Indonesia. However, Kirkaldy (1908), probably based on comparisons of figures in Melichar (1903) and Distant (1906), commented that *U. exoleta* was “very different” from *U. splendens* in having a much longer face. Nevertheless, the synonymy of *U. exoleta* with *U. splendens* was accepted by Melichar (1912), and later included in Metcalf’s (1946) catalogue of world Dictyopharidae.

Based on our critical review of the published information and examination of *Orthopagus* material from Sri Lanka which agrees with the original description of *U. exoleta*, we propose here to resurrect *Orthopagus exoletus* comb. n. from the synonymy with *O. splendens* and to restore it as a valid species. *Orthopagus exoletus* can be distinguished from *O. splendens* by the coloration of the vertex and the structure of the male genitalia, particularly the structure of the endosomal processes of aedeagus, lobes of the phallobase and the shape of the segment X. The relative length of frons mentioned by Kirkaldy (1908) is probably not a relevant diagnostic character because the length of the head in *Orthopagus* species varies within a certain range.

According to Melichar (1903), *U. exoleta* was described based on five female specimens from “Moruwale”, deposited in the collection of the museum in Colombo, Sri Lanka. This material was not available to our study. Nevertheless, we have studied one female from Sri Lanka, “Puttalam” preserved in Melichar’s personal collection in MMBC. Even though this specimen bears original identification la-

bel handwritten by Melichar as “*Udugama*” and “*exoleta* det. Melichar” and a dark red label “Typus” originally also attached to the specimen by Melichar, it probably cannot be considered as a syntype because it differs in its locality and deposition from the information published in the original description and probably it was also collected later than the original species description had been published. Melichar did not use type labels in the modern sense. He had rather adopted the practice of placing a ‘type’ label on one or more specimens of the most taxa (even on species previously described by other authors and identified by Melichar), specimens presumably which he himself used for comparison (Young & Soós 1964, Wilson & Malenovský 2007).

***Orthopagus hainanensis* Song, Chen & Liang, sp. n.**

<http://zoobank.org/3809F64E-8BDD-47F3-83B8-97FEAB5692C4>

Figs 2E–F, 3C, 6A–I, 7A–G

Type material. Holotype male, **CHINA:** Hainan: Baoting, 80 m, 21.vii.1960, S. F. Li leg. (IZCAS).

Paratypes. **CHINA:** Hainan: 6 males, 24 females, Baoting, 80 m, 23., 24. and 27.vii.1960, S. F. Li, X. Z. Zhang & C. Q. Li leg.; 11 males, 15 females, Tongshi, 340 m, 23., 24. and 25.vi., 31.vii., 1., 4. and 6.viii.1960, S. F. Li, X. Z. Zhang & C. Q. Li leg.; 1 male, 1 female, Yinggen, 200 m, 4.v. and 5.vii.1960, S. F. Li leg.; 1 female, Shuiman, 640 m, 25.v.1960, C. Q. Li leg.; 2 males, Wanning, 10 m, 12., 13.iv.1960, S. F. Li & C. Q. Li leg.; 3 females, Qiongzong, 15–17.vii.1960, X. Z. Zhang & C. Q. Li leg.; 2 males, 3 females, Kwangtung, 3., 4. and 5.iv., 13. and 26.viii.1934, C. Ho leg. (all IZ-

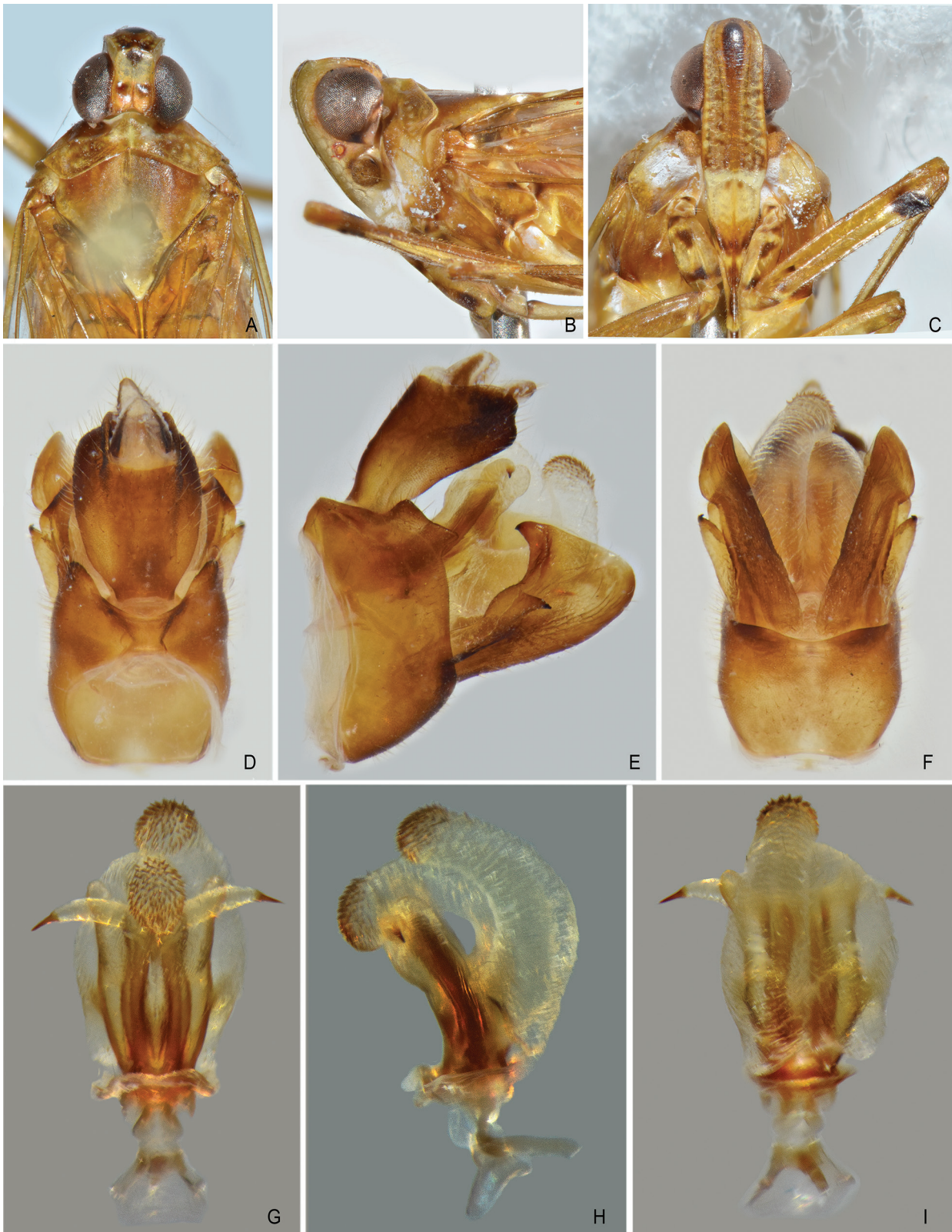


Figure 4. *Orthopagus bartletti* sp. n. (A) Head, pronotum and mesonotum, dorsal view. (B) Head and pronotum, lateral view. (C) Head and pronotum, ventral view. (D) Male segment X and pygofer, dorsal view. (E) Male pygofer, gonostyles, and segment X, lateral view. (F) Male pygofer and gonostyles, ventral view. (G) Aedeagus, dorsal view. (H) Aedeagus, lateral view. (I) Aedeagus, ventral view.

CAS); 1 male, Mangrin, 9.vi.1904; 1 female, Mon Boi, 29.v.1904 (both BMNH).

Diagnosis. *Orthopagus hainanensis* sp. n. is similar to *O. lunulifer* in most characters, but can be differentiated from

the latter by the ivory white to pale ochraceous vertex with a pair of dark brown spots on each side of midline in basal third (in *O. lunulifer*, the vertex is nearly dark brown from base to apex) and the male segment X being elongate in dorsal view, with ratio of length to width near middle 1.9–2.0 (in *O. lunulifer*, the male segment X is shorter and wider in dorsal view, with ratio of length to width near middle 1.2–1.3). *Orthopagus hainanensis* sp. n. is also similar to *O. exoletus* in the predominantly light vertex but it differs from the latter by a slightly longer head, the male pygofer with dorso-posterior margin produced into a broad and short lobe in lateral view (the pygofer bears a larger tooth-like process dorso-posteriorly in *O. exoletus*) and the aedeagus with two pairs of larger (more strongly inflated) dorsolateral membranous lobes and endosomal processes covered with minute spines (indistinct in *O. exoletus*).

Description. Measurements (5 males, 10 females). Body length (from apex of head to tip of forewings): male 11.7–12.9 mm, female 13.1–14.6 mm; head length (from apex of cephalic process to base of eyes): male 1.4–1.5 mm, female 1.5–1.6 mm; head width (including eyes): male 1.6–1.7 mm, female 1.6–1.7 mm; forewing length: male 9.3–10.3 mm, female 10.6–11.8 mm.

Coloration. General coloration as in generic description (Fig. 2E–F). Head ivory white to pale ochraceous, vertex with basal corners castaneous, a pair of large fuscous patches on each side of midline at basal third, and pale fuscous apical diamond-shaped spot (Fig. 6A); frons pale with series of small pale fuscous spots along intermediate and lateral carinae, base without distinct dark spot (Fig. 6C). Forewing pattern as in Fig. 3C. Hind wing membrane with a relatively narrow dark brown streak along the apical portion of CuA_1 vein, extending along hind wing apical margin.

Structure. Cephalic process (Fig. 6A–C) relatively elongate. Vertex (Fig. 6A) with ratio of length at midline to width between eyes 1.65–1.75. Transition of vertex to frons narrowly rounded in lateral view (Fig. 6B). Frons (Fig. 6C) relatively narrow, with ratio of length at midline to maximum width 2.7–2.9.

Male genitalia. Pygofer in lateral view (Fig. 6E) with dorso-posterior margin produced into a broad and relatively short blunt lobe; in ventral view (Fig. 6F) much longer than in dorsal view (Fig. 6D) with ratio of ventral to dorsal length about 4.2. Gonostyles (Fig. 6E–F) large, broad medially, with dorsal margin weakly sinuate. Aedeagus (Fig. 6G–I) with endosomal processes covered with minute spines, extended posteriad and strongly curved dorso-anteriad; phallobase with one pair of large, strongly inflated dorsolateral lobes, their apices gradually convergent and tapering posteriad (Fig. 6G–I), and one pair of small, thumb-like ventral lobes (Fig. 6I). Segment X relatively narrow and elongate, in lateral view, narrow basally, widening beyond middle, apex subacute (Fig. 6E), in dorsal view, widest medially, with ratio of length to width 1.9–2.0 (Fig. 6D).

Female genitalia as in generic description (Fig. 7A–G).

Etymology. The new species is named for its occurrence in Hainan Island, China. The specific epithet *hainanensis* is to be treated as a latinized adjective in nominative singular.

Distribution. So far only known from Hainan Island, China.

Orthopagus lunulifer Uhler, 1897

Figs 1A, 2G,H, 3D, 8A–I

Orthopagus lunulifer Uhler, 1897: 279. Lectotype (designated by Liang 1996: 47): male, Gifu, Japan (USNM, examined).

Orthopagus splendens: Matsumura 1905a: 61, Pl. 21, fig. 14; Matsumura 1905b: 19; nec Germar 1830: 48.

Orthopagus helios Melichar, 1912: 60. Lectotype (here designated): female, Ku Sia, Taiwan, China (MMBC, examined). **Syn. n.**

Orthopagus helios var. *diffusus* Melichar, 1912: 61. Lectotype (here designated), female, Taihanroku, Taiwan, China (HNHM, examined). Synonymized under *Orthopagus helios* Melichar by Schumacher (1915): 130.

Orthopagus elegans Melichar, 1912: 61. Lectotype (here designated), female, Taihanroku, Taiwan, China (MMBC, examined). Synonymized under *Orthopagus helios* Melichar by Schumacher 1915: 130.

Orthopagus lunulifer: Melichar 1912: 60; Liang 1996: 47, fig. 4; Song et al. 2016d: 36–39, figs 3I, 4A–G, 5A–H, 6A–F; Song et al. 2018: figs 5A–B, D–G, 6A–C.

Type material examined. *Orthopagus lunulifer*: Lectotype, male, (1) 25,18,0., Gifu, male; (2) Type, No. 3123, U.S.N.M. [red label]; (3) Cotype No. U.S.N.M. [red label] (USNM). Paralectotypes: 1 male, (1) 25,18,0., Gifu, male; (2) Type, No. 3123, U.S.N.M. [red label]; (3) Cotype No. U.S.N.M. [red label]; 1 male, 1 female, (1) 25,8,0., Gifu; (2) Type, No. 3123, U.S.N.M. [red label]; (3) Cotype No. U.S.N.M. [red label]; 1 female, (1) 20,4,27., Gifu; (2) Type, No. 3123, U.S.N.M. [red label]; (3) Cotype No. U.S.N.M. [red label]; (4) *Orthopagus lunulifer* Uhler [Uhler's handwriting]; (5) 1164 [Uhler's handwriting] (all USNM).

Orthopagus helios: Lectotype (here designated), female, (1) Formosa, Ku Sia [handwriting, yellow label]; (2) *helios* Mel. [Melichar's handwriting], det. Melichar; (3) Typus [dark red label]; (4) Transcriptio, *Orthopagus helios* sp.n. female [P. Lauterer's handwriting], L. Melichar det 1912; (5) Collectio Dr. L. Melichar, Moravské museum Brno; (6) Syn-typus [red label]; (7) Invent. č. 4947/Ent., Mor. muzeum, Brno; (8) Lectotypus female, *Orthopagus helios* Melichar, 1912, designated by Z. S. Song & I. Malenovský, 2018 [newly added red label] (MMBC). Paralectotypes, 2 females, (1) Formosa, Ku Sia [handwriting, yellow label]; (2) Paralectotypus female, *Orthopagus helios* Melichar, 1912, designated by Z. S. Song & I. Malenovský, 2018 [newly added red label] (SNSD).

Orthopagus helios var. *diffusus*: Lectotype (here designated), male, (1) Formosa, Sauter; (2) Taihanroku, 908.; (3) v. *diffusus* M. [handwriting, underlined with red], det. Melichar; (4) typus [label with red frame]; (5) Hung. Nat. Hist. Museum Budapest, coll. Hemiptera [yel-

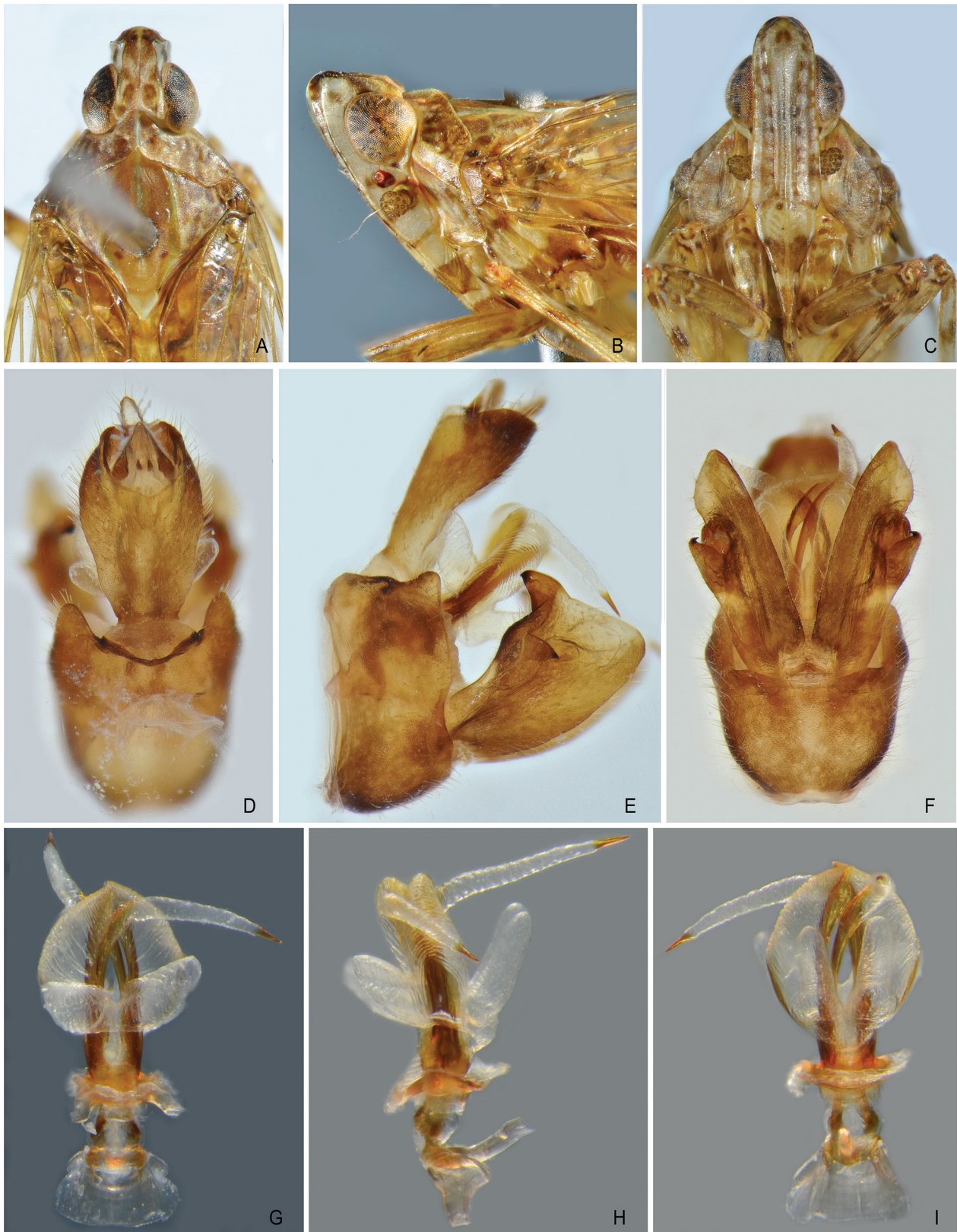


Figure 5. *Orthopagus exoletus* (Melichar). (A) Head, pronotum and mesonotum, dorsal view. (B) Head and pronotum, lateral view. (C) Head and pronotum, ventral view. (D) Male segment X and pygofer, dorsal view. (E) Male pygofer, gonostyles, and segment X, lateral view. (F) Male pygofer and gonostyles, ventral view. (G) Aedeagus, dorsal view. (H) Aedeagus, lateral view. (I) Aedeagus, ventral view.

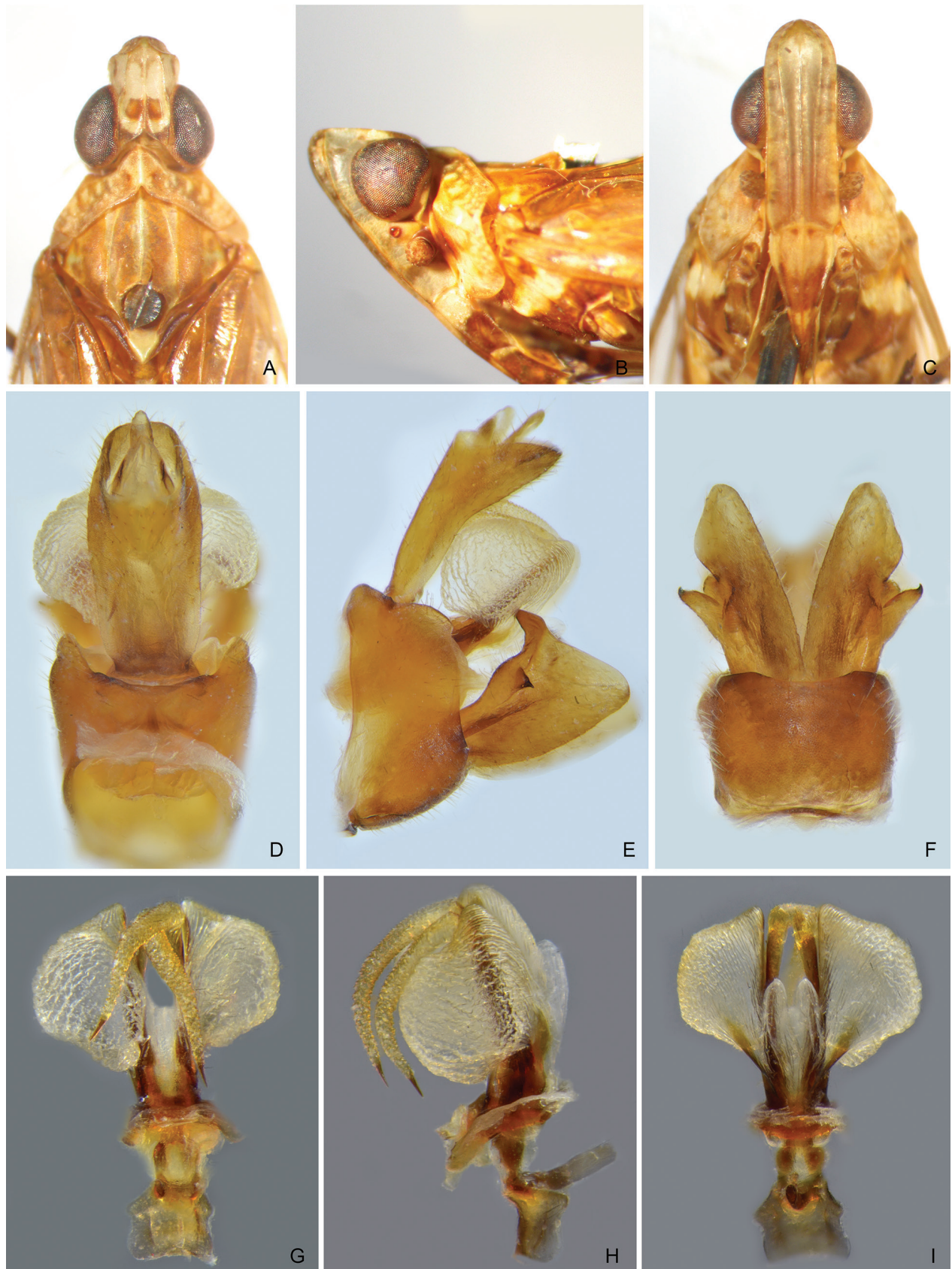


Figure 6. *Orthopagus hainanensis* sp. n. (A) Head, pronotum and mesonotum, dorsal view. (B) Head and pronotum, lateral view. (C) Head and pronotum, ventral view. (D) Male segment X and pygofer, dorsal view. (E) Male pygofer, gonostyles, and segment X, lateral view. (F) Male pygofer and gonostyles, ventral view. (G) Aedeagus, dorsal view. (H) Aedeagus, lateral view. (I) Aedeagus, ventral view.



Figure 7. *Orthopagus hainanensis* sp. n. (A) Female terminalia and ectodermal genital ducts, dorsal view. (B) Female terminalia and ectodermal genital ducts, lateral view. (C) Female terminalia and ectodermal genital ducts, ventral view. (D) Gonapophysis VIII, dorsolateral view. (E) Gonapophysis IX, ventral view. (F) Gonapophysis IX, lateral view. (G) Gonoplasts, lateral view.

low label] (6) Lectotypus male, *Orthopagus helios* var. *diffusus* Melichar, 1912, designated by I. Malenovský in Song et al., 2018 [newly added red label] (HNHM). Paralectotype, male, (1) Formosa, Sauter; (2) Kosempo, 908.; (3) v. *diffusus* M. [handwriting, underlined with red], det. Melichar; (4) typus [label with red frame and a hindwing glued to it]; (5) Hung. Nat. Hist. Museum Budapest, coll. Hemiptera [yellow label] (6) Paralectotypus

male, *Orthopagus helios* var. *diffusus* Melichar, 1912, designated by I. Malenovský in Song et al., 2018 [newly added red label] (HNHM, abdomen detached and glued to a separate label attached to the same pin).

Orthopagus elegans: Lectotype (here designated), female, (1) Formosa, Sauter; (2) Taihanroku, 908.; (3) elegantulus [Melichar’s handwriting], det. Melichar; (4) Typus [dark red label]; (5) Collectio Dr. L. Melichar,

Moravské museum Brno; (6) *Orthopagus* female *elegans* sp. n. female, L. Melichar det. 1912 [Lauterer's handwriting], P. Lauterer's det. 1991; (7) Syn-typus [red label]; (8) Invent. č. 4948/Ent., Mor. muzeum, Brno; (9) Lectotypus female, *Orthopagus elegans* Melichar, 1912, designated by Z. S. Song & I. Malenovský, 2018 [newly added red label] (MMBC). Paralectotype, female, (1) Formosa, Sauter; (2) Taihanroku, 908.; (3) *elegans* M. [handwriting, underlined with red], det. Melichar; (4) typus [label with red frame]; (5) Hung. Nat. Hist. Museum Budapest, coll. Hemiptera [yellow label] (6) Paralectotypus female, *Orthopagus elegans* Melichar, 1912, designated by I. Malenovský in Song et al., 2018 [newly added red label] (HNHM).

Other material examined. **JAPAN:** Honshu island: 1 female, Tokyo, Matsumura leg. (IZCAS); 1 male, Kamakura, ix.1913, F. Muir leg. (BPBM); 1 female, Mie prefecture, Matagari lke, 24.x.1989, C. W. O'Brien & L. B. O'Brien leg. (LBOB). **CHINA:** Beijing municipality: 1 female, Peiping; 9 males, 15 females, Peiping, 9., 10. and 21.vii.1938, 4., 13., 15. and 28.viii.1938, 11., 16., 19., and 24.ix.1938, T. P. Chang leg.; 1 male, 1 female, Juyongguan, 250–280 m, 3. and 6.viii.1961, S. Y. Wang & X. Z. Zhang leg.; 1 male, 1 female, Zhongguancun, 4.ix.1962, S. Y. Wang leg.; 3 males, 2 females, Shisanling, 12.ix.1962, R. Z. Xie leg. (all IZCAS); 2 males, 2 females, Changping, 8.vii.2007, Z. S. Song leg. (JSSNU); Tianjin municipality: Jixian, 4.ix.1988, K. H. Zhang leg. (IZCAS); Shandong province: 2 males, 1 female, Tsingtao [Musée Heude]; 1 male, Laoshan, 800 m [Musée Heude] (all IZCAS); Henan province: 1 male, 1 female, Henan, 8.viii.2013, D. J. Zhang (JSSNU); Anhui province: 2 males, Huang Mountain, 6.viii.1936 (IZCAS); Shanghai municipality: 1 male, 1 female, 27.vii.1932, O. Piel leg. [Musée Heude] (IZCAS); Zhejiang province: 18 males, 10 females, T'ienmo Shan, 22–28.viii.1936; 2 females, Hangzhou, 24. and 25.viii.1942; 8 males, 8 females, Chusan, 7., 8., 10., 18., 20., 28. and 29.viii.1931, O. Piel leg. [Musée Heude] (all IZCAS); 1♀, Fujian province: 1 female, Jiayang, Chengguan, 90–120 m, 12.viii.1960, Y. R. Zhang leg.; 1 male, 1 female, Chongan, Xingcun, Sangang, 740 m, 12. and 20.viii.1960, Y. Zuo & C. L. Ma leg.; 1 male, 2 females, Jiangle, Longqishan, 500–700 m, 12., 13. and 19.viii.1991, S. M. Song leg. (all IZCAS); Hunan province: 1 female, Hoeng-Shan, 900 m, 1933, H. Höne leg. (MFNB); Guizhou province: 1 female, Libo, 21.viii.2000, F. M. Shi leg. (IZCAS); Sichuan province: 5 males, 3 females, Emei Mountain, Baoguosi, 550–750 m, 7., 9., 10. and 14.ix.1957, F. X. Zhu & Z. Y. Wang leg. (IZCAS); Tibet (Xizang) autonomous region: 1 female, Chayu, Xiachayu, 1900 m, 21.viii.2005, Z. S. Song leg. (IZCAS); Guangxi autonomous region: 4 males, 5 females, Guilin, Yanshan, 2., 7. and 23.viii.1952, 20., 22. and 24.vii.1953; 2 females, Pingxiang, 12. and 16.vi.1976, B. L. Zhang leg.; 5 males, 5 females, Nandan, Luofu, 350 m, 27.vii.2006, J. Liu leg. (all IZCAS); 2 males, 2 females, Guangnan, Bamei, Shiw. Taoyuan, 24°18'51"N, 105°02'08"E, 811 m, 12.viii.2012, D. Rédei leg.; 2 males, same but 24°19'08"N,

105°02'57"E, 891 m; 1 male 1 female, same but 24°19'11"N, 105°01'49"E, 834 m, 13.viii.2012 (all HNHM); Yunnan province: 1 male, 5 females, Hekou, 80 m, 5. and 7.vi.1956, K. R. Huang leg.; 3 females, Hekou, Nanxi, 200 m, 8. and 12.vi.1956, K. R. Huang leg.; 1 male, 1 female, Pingbian, 1400 m, 15.vi.1956, K. R. Huang leg. (all IZCAS); Taiwan: 1 male, Tainan, Formosa, vi.1912, H. Sauter, *Orthopagus helios* Mel. F. Schumacher det. [Schumacher's handwriting] (SDEI); 2 males, 1 female, Taihanroku, vii. and 10.xi, H. Sauter leg. (MFNB); 1 male, 1 female, same data (MZPW); 5 males, 2 females, Taihanroku, 1908, Sauter leg. (HNHM); 1 male, 1 female, Hoozan, 10.vii. and 10.ix., H. Sauter leg. (MFNB); 1 female, Kotobuki, 11.vi.1935, (IZCAS); 2 females, Tainan county, ca. 350 m, 2–3 km S Kwanzuling, bamboo, shrub, 26–28.vi.1980, D. R. Davis leg. (USNM); 1 female, Chi Pen, 10.vi.1997, B. Herczig & L. Ronkay leg. (HNHM). **VIETNAM:** 1 female, "Indo China", R. V. de Salvaza leg. (BMNH); 1 female, Chapa [= Sa Pa], v.–vi.1916, R. V. de Salvaza leg. (BMNH); 2 males, 1 female, Hoa Binh, vii.1939, A. de Cooma leg.; 5 males, 2 females Hoa Binh; 1 male, 1 female, Hoa Binh, Thanh-ha district, 12. and 13.vi.1966, R. Bielawski & B. Pisarski leg.; 2 males, 1 female, Hanoi, 24.vi.1959, B. Pisarski & J. Prószyński leg.; 4 males, 2 females Ninh Binh, Cuc Phuong, 5., 7. and 8.vi.1966, R. Bielawski & B. Pisarski leg.; 1 female, Nghe An district, Phu Quy, 17.vi.1959, B. Pisarski & J. Prószyński leg. (all MZPW); 1 female, Cuc Phuong, 400 m, at light, 17.x.1986, Vársárhelyi leg. (HNHM). **LAOS:** 1 male, Borikhane Prov., Pakkading, 31.vii.1965, native collector leg. (BPBM). **INDIA:** Assam: 2 males, Chabua, 10.x.1943, D. E. Hardy leg. (USNM); 1 female, Tocklai, light trap, ix.1983, 943/6, C.I.E.A. 15663 (BMNH). **NEPAL:** 1 male, Chitwan National Park, Island Jungle reserve, 29–30.x.1995, L. Peregovits leg. (HNHM).

Redescription. Measurements (10 males, 9 females). Body length (from apex of head to tip of forewings): male 11.7–13.4 mm, female 13.0–14.9 mm; head length (from apex of cephalic process to base of eyes): male 1.33–1.50 mm, female 1.50–1.65 mm; head width (including eyes): male 1.30–1.60 mm, female 1.48–1.75 mm; forewing length: male 9.4–10.8 mm, female 10.2–11.9 mm.

Coloration. General coloration as in generic description (Figs 1A, 2G–H). Vertex dark brown with five light ochraceous streaks: along median carina in anterior third (in some specimens, the whole median carina is light), along each lateral carina subapically and along each lateral carina basally, the latter streaks being sickle-shaped and curved to median carina at the base (Fig. 8A). Frons light ochraceous with small dark brown spots along intermediate and lateral carinae, frons base slightly infuscated (Fig. 8C). Forewing membrane pattern as in Fig. 3D. Hind wing membrane with a dark brown streak along the apical portion of CuA₁ vein, extending along hind wing apical margin.

Structure. Head with cephalic process moderately long, not inflated (Figs 8A–C). Vertex (Fig. 8A) with ratio of length at midline to width between eyes 1.6–2.0. Transition of vertex to frons relatively sharp, almost angular

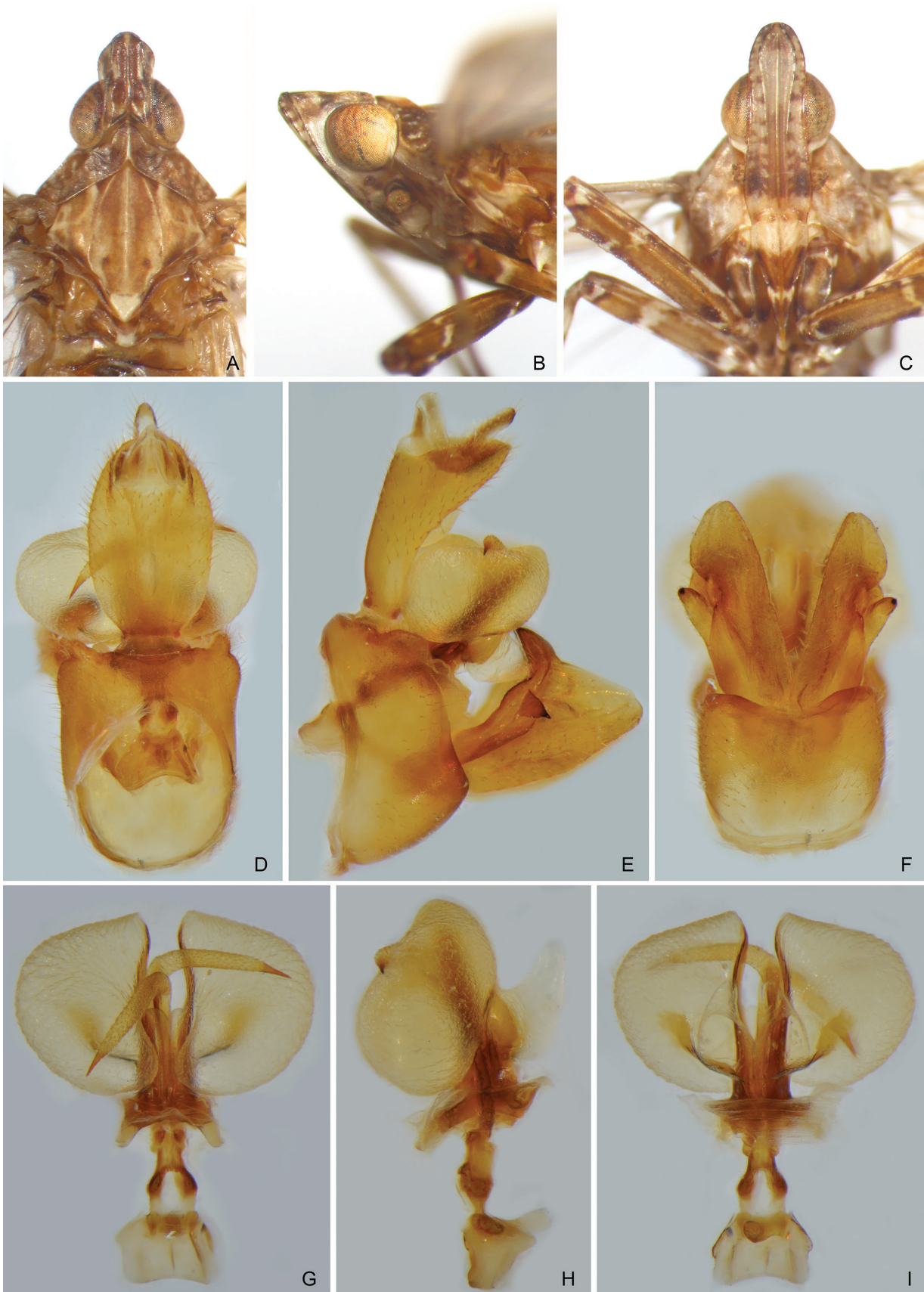


Figure 8. *Orthopagus lunulifer* Uhler. (A) Head, pronotum and mesonotum, dorsal view. (B) Head and pronotum, lateral view. (C) Head and pronotum, ventral view. (D) Male segment X and pygofer, dorsal view. (E) Male pygofer, gonostyles, and segment X, lateral view. (F) Male pygofer and gonostyles, ventral view. (G) Aedeagus, dorsal view. (H) Aedeagus, lateral view. (I) Aedeagus, ventral view.

in lateral view (Fig. 8B). Frons relatively narrow, with ratio of length at midline to maximum width 2.6–3.0.

Male genitalia. Pygofer, in lateral view (Fig. 8E), with dorso-posterior margin produced into a short and broad lobe; in ventral view (Fig. 8F) much longer than in dorsal view (Fig. 8D) with ratio of ventral to dorsal length about 4.0. Gonostyles (Fig. 8E–F) large, broad medially, with dorsal margin weakly sinuate. Aedeagus (Fig. 8G–I) with endosomal processes extended posteriad and strongly curved dorso-anteriad, relatively short, their apices not reaching the base of phallobase; phallobase with one pair of large, strongly inflated dorsolateral lobes (Fig. 8H), their apices blunt, and one pair of small, thumb-like ventral lobes, directed posteriad (Fig. 8I). Segment X, in lateral view, narrow basally, widening to apex beyond middle, apex subacute (Fig. 8E); in dorsal view, relatively short and broad in dorsal view, widest medially, with ratio of length to maximum width 1.2–1.3 (Fig. 8D).

Female genitalia as in generic description.

Distribution. Widely distributed in tropical, subtropical and temperate eastern Asia (Japan, China, Korea, Vietnam, Laos, northeastern India and Nepal).

Ecology and economic importance. Adult *O. lunulifer* was reported as a minor pest of leaves of *Morus alba* L. (Pu and Mao 2012) and *Camellia oleifera* Abel in southeastern China (Zhao et al. 2013). Matsumura (1910) listed "*Anagnia splendens*" among pests of sugarcane in Taiwan; this record perhaps also refers to *O. lunulifer*.

Remarks. Erroneously according to Metcalf (1946), Matsumura (1905a, b) considered *O. lunulifer* to be a junior synonym of *Anagnia splendens* (Germar). As he probably studied material from Japan, the description and illustration of "*Anagnia splendens*" in Matsumura (1905a) probably refer to *O. lunulifer* (i.e., the only *Orthopagus* species currently confirmed from Japan). The same is probable for the records and a figure of "*Anagnia splendens*" from Okinawa and Taiwan published in Matsumura (1905b and 1910, respectively).

Melichar (1912) differentiated *O. elegans*, *O. helios* and *O. lunulifer* based on slight differences in the transparency of the forewing membrane, extent of the dark brown apical band on the forewing and the shape of frons. Based on a study of material from Taiwan, Schumacher (1915) suggested that *Orthopagus helios* and *O. elegans* described by Melichar (1912) belong to the same species. However, his synonymisation of *O. helios* var. *diffusus* Melichar and *O. elegans* Melichar under *O. helios* Melichar was not widely accepted (Metcalf 1946). We have examined the corresponding type specimens and additional specimens from the same series collected by H. Sauter in Taiwan and currently deposited in HNHM, MFNB, MMBC, SDEI, and SNSD, and confirm here Schumacher's conclusion. Simultaneously, we suggest that *O. helios* should be treated as a junior synonym of *O. lunulifer* because we consider the differences among

these taxa listed by Melichar (1912) to represent intraspecific variation. We designate here the lectotypes for *O. elegans*, *O. helios* and *O. helios* var. *diffusus* to stabilize the nomenclature according to Article 74 of ICZN (1999).

Liang (1996) designated the lectotype for *O. lunulifer*, and provided a left lateral view of male genitalia for this species. Detailed illustrations of the male and female genitalia (but no detailed description) were also provided for *O. lunulifer* by Song et al. (2016d, 2018).

The single male specimen examined from Nepal (Chitwan National Park) is identical in external characters to specimens of *O. lunulifer* from Japan, China, Taiwan and Vietnam. However, it differs in the shape of the lobe on the dorso-posterior margin of the pygofer which is smaller (shorter and simply angular) than in the rest of *O. lunulifer* males studied. The phallobase of this specimen could not be sufficiently compared as its membranous lobes failed to inflate during the preparation. More specimens and data are needed to confirm the identification.

Orthopagus philippinus Melichar, 1914

Figs 2I–J, 3E, 9A–J

Orthopagus philippinus Melichar, 1914: 173, Pl. I, figs 1, 2. Lectotype (here designated) male, Los Baños, Philippines (MMBC, examined).

Type material examined. Lectotype male (here designated), (1) Los Baños, P.I. Baker; (2) 1311; (3) *philippinus* [Melichar's handwriting] det. Melichar; (4) Collectio Dr. L. Melichar, Moravské museum Brno; (5) *Orthopagus* male *philippinus* sp.n., L. Melichar, 1914 [Lauterer's handwriting], P. Lauterer det. 1991; (6) Syn-typus [red label]; (7) Invent. č. 4954/Ent., Mor. muzeum, Brno; (8) Lectotypus male, *Orthopagus philippinus* Melichar, 1914, designated by Z. S. Song & I. Malenovský, 2018 [newly added red label] (MMBC).

Paralectotypes, 4 females, same locality labels as holotype but Inv. nos 4949–4951, 4953; 1 female, Mt. Makiling, Luzon, Baker (MMBC, Inv. no. 4952, all paralectotypes bearing the following label: Paralectotypus female, *Orthopagus philippinus* Melichar, 1914, designated by Z. S. Song & I. Malenovský, 2018).

Other material examined. PHILIPPINES: Luzon island: 1 male, Mt. Makiling, Baker leg. (USNM); 1 male, Los Baños, 11.xii.1913, D. T. Fullaway leg. (BPBM); 1 male, Los Baños, i.1913, P. Ledyard leg. (LBOB); 2 males, Mt. Montalban, Rizal, Wa-wa Dam, 150–200 m, 6. and 17.iii.1965, H. M. Torre Villas leg. (BPBM); 1 male, 4 females, Manila, G. Boettcher leg. (MMBC); 1 male, 2 females, "B. M. 1925-491", E. M. Ledyard leg.; 1 female, "Acc. No. 6625, Lot, Bu. of Sci., P. I., 1908-228", C. S. Banks leg.; 1 male, "Acc. No. 5364, Lot, Govt. Lab. Coll., 1908-228", C. S. Banks leg. (all BMNH).

Redescription. Measurements (4 males, 9 females). Body length (from apex of head to tip of forewings): male 10.6–11.4 mm, female 12.9–13.9 mm; head length (from



Figure 9. *Orthopagus philippinus* Melichar. (A) Head, pronotum and mesonotum, dorsal view. (B) Head and pronotum, lateral view. (C) Head and pronotum, ventral view. (D) Male segment X and pygofer, dorsal view. (E) Male pygofer, gonostyles, and segment X, lateral view. (F) Male pygofer and gonostyles, caudal view. (G) Gonostyle; (H) Aedeagus, dorsal view. (I) Aedeagus, lateral view. (J) Aedeagus, ventral view.

apex of cephalic process to base of eyes): male 1.25–1.33 mm, female 1.35–1.45 mm; head width (including eyes): male 1.30–1.43 mm, female 1.50–1.60 mm; forewing length: male 8.5–9.1 mm, female 10.3–11.4 mm.

Coloration. General coloration as in generic description (Figs 2I–J). Vertex predominantly dark brown, lateral margins with a pale ochraceous S-shaped streak in posterior three quarters (Fig. 9A). Frons light ochraceous with small dark brown spots along intermediate and lateral carinae and a large roundish dark brown spot at base (Fig. 9C). Forewing membrane pattern as in Fig. 3E. Hind wing membrane with a narrow dark brown infuscation along the apical portion of CuA₁ vein, not extending along hind wing apical margin.

Structure. Head with cephalic process moderately elongate (Figs 9A–B). Vertex (Fig. 9A) with ratio of length at midline to width between eyes 1.6–1.8. Transition of vertex to frons blunt, broadly rounded in lateral view, cephalic process thus appearing inflated and bulbous apically (Fig. 9B). Frons relatively narrow, with ratio of length at midline to maximum width 2.7–3.1.

Male genitalia. Pygofer, in lateral view, with dorso-posterior margin produced into a relatively large but narrow, tooth-like, apically obtuse process (Fig. 9E); in ventral view (Fig. 9F) much longer than in dorsal view (Fig. 9D) with ratio of ventral to dorsal width about 2.5. Gonostyles (Fig. 9G) large, broad medially, with dorsal margin weakly sinuate. Aedeagus (Fig. 9H–J) with endosomal processes covered with minute superficial spines, extended posteriad and strongly curved laterad and dorso-anteriad but not reaching the base of phallobase; phallobase with one pair of large, strongly inflated dorsolateral lobes, their apex convergent and tapering posteriad (Fig. 9I), and one pair of smaller, thumb-like ventral lobes, directed ventro-posteriad (Fig. 9I–J). Segment X, in lateral view, relatively narrow basally, widening to apex beyond middle, apex blunt (Fig. 9E); in dorsal view, relatively large and broad, widest in apical third, ratio of length to maximum width 1.0–1.1 (Fig. 9D).

Female genitalia as in generic description.

Distribution. So far only known from the Luzon island, Philippines.

Remarks. *Orthopagus philippinus* can be easily recognized from other species of the genus by the shape of the head and the presence of a relatively large roundish dark spot at base of frons which is present in all specimens studied.

Melichar (1914) indicated that he described this species based on five (male and female) specimens from “Luzon, Los Baños, Mt. Maquiling (C. F. Baker)”. Six specimens (1 male, 5 females) preserved in Melichar personal collection in MMBC and labelled as either from Los Baños or Mt. Makiling and collected by Baker are considered here as the original syntypes. The male specimen is designated here as the lectotype for *O. philippinus* to stabilize the nomenclature according to Article 74 of ICZN (1999).

Orthopagus splendens (Germar, 1830)

Figs 1B, 2K–L, 3F, 10A–I

Flata splendens Germar, 1830: 48. Syntype(s) (number of specimens and sex unknown), Java, Indonesia (not examined).

Pseudophana splendens: Westwood 1839: 151.

Dictyophora [sic] *splendens*: Walker 1851: 310.

Anagnia splendens: Stål 1861: 149.

Udugama splendens: Distant 1906: 249.

Udugama flavocarinata Bierman, 1907: 161; Bierman (1908): 151, Pl. 3, fig. 1. Syntypes 2 males, 1 female, Semarang, Java, Indonesia (not examined). Synonymized under *Orthopagus splendens* (Germar) by Melichar 1912: 59.

Orthopagus splendens: Oshanin 1908: 444; Melichar 1912: 59; Yang and Yeh 1994: 108, 116, figs 71, 76.

Orthopagus splendens var. *tibialis* Kirkaldy in Kirkaldy & Muir, 1913: 12. Syntypes (number of specimens and sex unknown), Macao, China (not examined).

Material examined. CHINA: Hainan island: 1 male, Hainan, 5.v.1934, C. Ho leg.; 2 females, Shuiman, 640 m, 25.v.1960, C. Q. Li leg.; 2 males, 5 females, Tongshi, 340 m, 23. and 25.vi.1960, C. Q. Li leg.; 1 female, Yinggen, 200 m, 6.vii.1960, S. F. Li leg.; Yunnan province: 1 male, 1 female, Hekou, 80 m, 7.vi.1956, K. R. Huang leg.; 3 females, Hekou, Xioananyi, 200 m, 8.vi.1956, K. R. Huang leg.; 1 male, Gaoligong Mountain, 1000 m, 20.viii.1958, C. L. Li leg.; 1 male, Malipo, 20.vii.1958; 1 female, Xishuangbanna, Menga, 1050 m, 18.ix.1957, F. J. Pu leg.; 1 male, 1 female, Xishuangbanna, Menglun, 600 m, 9.ix.1993, H. L. Xu & L. L. Yang leg.; 1 male, Xishuangbanna, Menglun, 10.ix.1993, X. Y. Cheng leg. (all IZCAS). **VIETNAM:** 1 female, Lao Kay, 31.v.1960, at light, K. Galewski leg. (MZPW); 1 male, 1 female, Ninh Binh, Cuo-phuong, 5., 7, and 8.vi.1966, R. Bielawski & B. Pisarski leg. (MZPW); 2 males, 22 km S of Nha Trang, 20–26.xi.1960, C. M. Yoshimoto leg. (BPBM); 1 male, DaiLanh, N of Nha Trang, 30.xi.–5.xii.1960, C. M. Yoshimoto leg. (BPBM). **THAILAND:** Trang province: 1 male, Khaophappa Khaochang, 200–400 m, 3.i.1964, G. A. Samuelson leg. (BPBM). **INDIA:** Assam: 1 female, Mazbat near Mangaldai, 11–15.x.1910 (coll. Distant, BMNH). **MALAYSIA:** Penang: 1 male, Island of Penang, Baker leg. (USNM). **INDONESIA:** Java: 1 male, Java (West), Djasinga, 5.i.1966, J. Stusak (BPBM); 1 female, Samarang, iv.1909, E. Jacobson; 1 female, same but vi.1909 (both coll. Melichar, MMBC); 1 female, Wied. in CW. Java, GW [handwriting] (coll. Zool. Mus. Leipzig Übernahme 1971, SNSD); 1 male, Java [handwriting] (MFNB).

Redescription. Measurements (3 males, 11 females). Body length (from apex of head to tip of forewings): male 10.3–11.8 mm, female 12.7–13.6 mm; head length (from apex of cephalic process to base of eyes): male 1.28–1.36 mm, female 1.35–1.48 mm; head width (including eyes): male 1.30–1.49 mm, female 1.50–1.59 mm; forewing length: male 8.5–9.1 mm, female 10.4–11.3 mm.

Coloration. General coloration as in generic description (Figs 1B, 2K–L). Vertex predominantly dark brown, lateral margins with a pale greenish or ochraceous S-shaped streak in posterior three quarters, median ca-



Figure 10. *Orthopagus splendens* (Germar). (A) Head, pronotum and mesonotum, dorsal view. (B) Head and pronotum, lateral view. (C) Head and pronotum, ventral view. (D) Male segment X and pygofer, dorsal view. (E) Male pygofer, gonostyles, and segment X, lateral view. (F) Male pygofer and gonostyles, ventral view. (G) Aedeagus, dorsal view. (H) Aedeagus, lateral view. (I) Aedeagus, ventral view.

rina anteriorly light in some specimens (Figs 1B, 10A). Frons light ochraceous with small dark brown spots along intermediate and lateral carinae and indistinct infuscation at base (Fig. 10C). Forewing membrane pattern as in Fig. 3F. Hind wing membrane with a narrow dark brown infuscation along the apical portion of CuA_1 vein, extending into a narrow infuscation along hind wing apical margin.

Structure. Head with cephalic process relatively short (Fig. 10A–B). Vertex (Fig. 10A) with ratio of length at midline to width between eyes 1.5–1.6. Transition of vertex to frons narrowly rounded in lateral view, cephalic process not inflated apically (Fig. 10B). Frons relatively narrow, with ratio of length at midline to maximum width 2.8–3.1.

Male genitalia. Pygofer, in lateral view, similar to *O. philippinus*, with dorso-posterior margin with a large and relatively narrow, tooth-like, apically obtuse process (Fig. 10E); pygofer with ratio of ventral to dorsal width about 2.6 (Fig. 10D, F). Gonostyles (Fig. 10E) large, broad medially, with dorsal margin weakly sinuate. Aedeagus (Fig. 10G–I) with endosomal processes very long, extended posteriad and strongly curved dorso-anteriad, reaching the base of phallobase; phallobase with one pair of relatively small, inflated dorsolateral lobes, their apex elongate, thumb-like, directed posteriad (Fig. 10H), and one pair of relatively large ventral lobes, convergent and tapering posteriad (Fig. 10H–I). Segment X, in lateral view, narrow basally, widening to apex beyond middle (Fig. 10E); in dorsal view, elongate, widest at apical third, ratio of length to maximum width 1.5–1.6 (Fig. 10D).

Female genitalia as in generic description.

Distribution. Confirmed records are from Indonesia (Java), West Malaysia, Vietnam, Thailand, southern China (Hainan, Yunnan) and north-eastern India (Assam). Based on the description and illustrations in Yang and Yeh (1994), *O. splendens* probably also occurs in Taiwan (see also Tsaur 2005). Published records from the Philippines (Luzon; Stål 1861, Distant 1906) probably refer to *O. philippinus*, while the records from Sri Lanka (Melichar 1903, 1912; Distant 1906) concern *O. exoletus* and the ones from Japan (Matsumura 1905a, b, 1910) refer to *O. lunulifer*. Records from western India (Stål 1861), Myanmar (Distant 1906), Singapore, and Indonesia: Sumatra (Bierman 1908) still need to be checked.

Remarks. *Flata splendens* was described by Germar (1830) from Java, and was designated as the type species of *Anagnia* by Stål (1861). *Udugama flavocarinata* Bierman, 1907 from Java was considered as a junior synonym of *O. splendens* by Melichar (1912). *Orthopagus splendens* var. *tibialis* Kirkaldy was differentiated from the typical form by having “the fore and middle tibiae distinctly bi- or tri-angulate with brownish” (Kirkaldy and Muir 1913). However, this pattern is typical for all *Orthopagus* species.

The synonymy of *Dictyophara indiana* Walker, 1851 with *Orthopagus splendens* proposed by Stål (1861) is considered doubtful (see above).

Orthopagus splendens has been frequently confused in literature and museum collections with other species of the genus. It can be differentiated from them by the combination of the following characters: a relatively small body size, a moderately short head, an extensive dark pattern on vertex, the pygofer with dorso-posterior margin bearing a relatively large but narrow, simply tooth-like process, the endosomal processes of the aedeagus relatively long and robust, covered with minute superficial spines and phalotheca bearing two pairs of membranous lobes.

Discussion and conclusions

The six currently recognised species of *Orthopagus* are very similar in external morphology and female genitalia and also the differences in the male genitalia between some pairs of species are subtle. This is probably the reason for the relatively complicated synonymy and frequent misidentifications by previous authors. The individual species can be recognised mainly by the differences in extent of the dark pattern on the vertex and frons, the size and shape of the cephalic process, the extent of the dark brown infuscation on the hind wing, the shape of the male pygofer, the structure of the aedeagus (the length of the endosomal processes and the shape and size of the membranous lobes of the phallobase), and the shape of the male segment X.

Three species, *Orthopagus bartletti* sp. n., *O. hainanensis* sp. n., and *O. philippinus*, have, as far as known, very restricted distributions, being endemic to south-western India and the islands of Hainan (China) and Luzon (Philippines), respectively. The distribution of *O. exoletus* is, as far as known, restricted to the Indian subcontinent (southern India, West Bengal and Sri Lanka). *Orthopagus lunulifer* is widespread in the tropical, subtropical and temperate eastern Asia from Nepal and northeastern India in the southwest to Korea and Japan in the northeast, while the distribution of *O. splendens* is probably restricted to the tropical zone slightly more south. The areas of distribution of the latter two species, however, overlap in northeastern India (Assam), northern Vietnam, and southern China (Yunnan, Hainan and Taiwan) (Fig. 11). *Orthopagus splendens* is also sympatric with *O. hainanensis* in the Hainan island, and *O. exoletus* is sympatric with *O. bartletti* in southwestern India. More data, e.g. from molecular markers, are needed to infer a phylogeny of *Orthopagus* and propose some evolutionary scenario which would also help to explain these distributions and mechanisms of speciation involved. More studies are also needed to understand the ecology and economic importance of *Orthopagus* species since the currently available data are scarce and insufficient (Matsumura 1910, Pu and Mao 2012, Zhao et al. 2013).

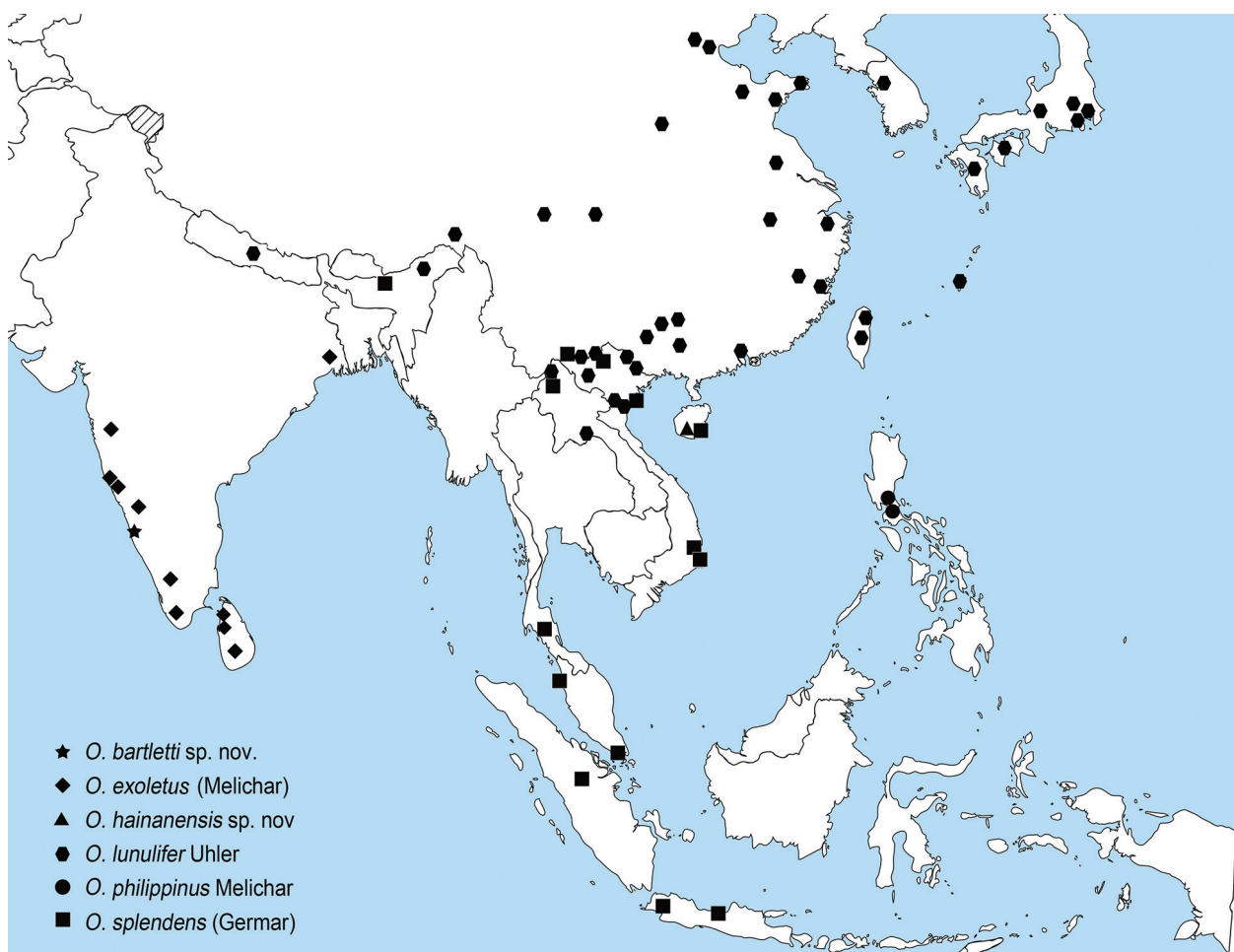


Figure 11. Geographical distribution of the *Orthopagus* species.

According to the phylogenetic hypothesis by Song et al. (2016d, 2018), *Orthopagus* is most closely related to the monotypic genus *Dictyomeria* Song, Webb & Liang, 2016, represented by *D. simulata* (Distant, 1906) from India which has been known only from the female holotype so far (Song et al. 2016d). Both genera share a similar forewing shape, venation and dark brown pattern on the forewing membrane. *Orthopagus* can be distinguished from *Dictyomeria* by the following characters: short and nearly straight head (in contrast, the cephalic process in *Dictyomeria* is strongly upturned in front of eyes); frons with median carina ridged and intermediate carinae approaching frontoclypeal suture (with median carina robust and strongly convex and intermediate carinae extending to anterior margin of eyes in *Dictyomeria*); pronotum with intermediate carinae distinct in basal half (indistinct in *Dictyomeria*); fore femora flattened and dilated, with a large and blunt spine near apex (fore femora not flattened and dilated, with a small spine in *Dictyomeria*).

Orthopagus is also similar, e.g. in the head morphology, to another monotypic genus *Truncatomeria* Song & Liang, 2011, established for *T. viridistigma* (Kirby, 1891) (= *Udugama fletcheri* Kirkaldy, 1908) from Sri Lanka. *Orthopagus* can be distinguished from *Truncatomeria* by the following characters: frons with median carina mod-

erately ridged (very strongly produced in *Truncatomeria*); fore femora flattened and dilated, with a large blunt spine near apex (slender with a short small spine near apex in *Truncatomeria*); the hind tibiae with seven black-tipped apical spines (eight spines in *Truncatomeria*); the forewing relatively shorter, broader and with membrane bearing well-developed dark brown markings (clear in *Truncatomeria*); and the long, apically pointed endosomal processes of the aedeagus (short and apically obtuse in *Truncatomeria*; see Song and Liang 2011). The similarity in the head shape between the two genera might be a symplesiomorphy or a convergence; according to Song et al. (2016d, 2018), *Truncatomeria* is more closely related to *Centromeria* Stål, 1870 and a few other genera.

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