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Phylogenetic analysis of the Oriental genera of Orthopagini Emeljanov, 1983 (Hemiptera: Fulgoromorpha: Dictyopharidae: Dictyopharinae), with a systematic revision of the genus *Centromeria* Stål, 1870

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A phylogenetic analysis is conducted for all 15 of the Oriental genera of Orthopagini (OGO), and representatives in Arjunini, Dictyopharini, and Hastini, so as to investigate the monophyly and phylogenetic relationships of the OGO. Although the length, thickness, and curvature of the cephalic process vary dramatically in different taxa of Orthopagini, most OGO make up a good monophylum if *Emeljanovina* Xing & Chen, 2013, is excluded. The revised OGO include 14 genera and can be divided into four unambiguous clades: *Medeusa*, *Dictyopharina*, *Orthopagus*, and *Dictyotenguna*. On the basis of the results of the above analysis, the phylogenetic analysis for all species of *Centromeria* Stål, 1870 is presented based on 48 adult characters. The revised *Centromeria* is monophyletic and can be separated into two unambiguous lineages: the *speilinea* clade and the *longipennis* clade. With the combination of the phylogeny and the updated geographical distribution, a Sundaland origin and a historically widespread distribution in Southeast Asia are suggested for *Centromeria*. Eight new *Centromeria* species, one new genus, and four new combinations are presented. Two synonymized *Centromeria* species are resurrected and two new specific synonyms are recognized. Diagnoses and descriptions, along with structural illustrations of male genitalia, are provided for all new species and four previously described species, excepting *Centromeria inspinata* Haupt, 1917. Keys to the OGO and to the species of *Centromeria* are provided.

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ADDITIONAL KEYWORDS: biogeography – cladistics – new genus – new species – taxonomy.

INTRODUCTION

The dictyopharid planthopper tribe Orthopagini (Dictyopharidae: Dictyopharinae) was first recognized by Emeljanov (1983) as a tribal taxon based on the type genus *Orthopagus* Uhler, 1896 and six other genera from the Oriental and Afrotropical regions. Emeljanov (1983) also erected seven other tribes to accommodate some genera originally placed in Dictyopharini, the only tribe left in Dictyopharinae after Dichopterini, including Cladodipterina and Dichopterina, was transferred into Fulgoridae (Emeljanov, 1979, 2011a). Nevertheless, a large number of genera remained unplaced in a tribe until an improved tribal classification was suggested by Emeljanov (2011b). A total of 19 genera were included in Orthopagini (Emeljanov, 2011b).

Emeljanov (2011b) defined Orthopagini based on the following combination of characters: wings fully developed, membranous; forewings projecting far beyond apex of abdomen (except four brachypterous genera: *Ellipoma* Emeljanov, 2008; *Fernandea* Melichar, 1912; *Macronaso* Synave, 1960; and *Nesolyncides* Fennah, 1858); veins cariniform; clavus closed; ScR and M originating from one point of basal cell or

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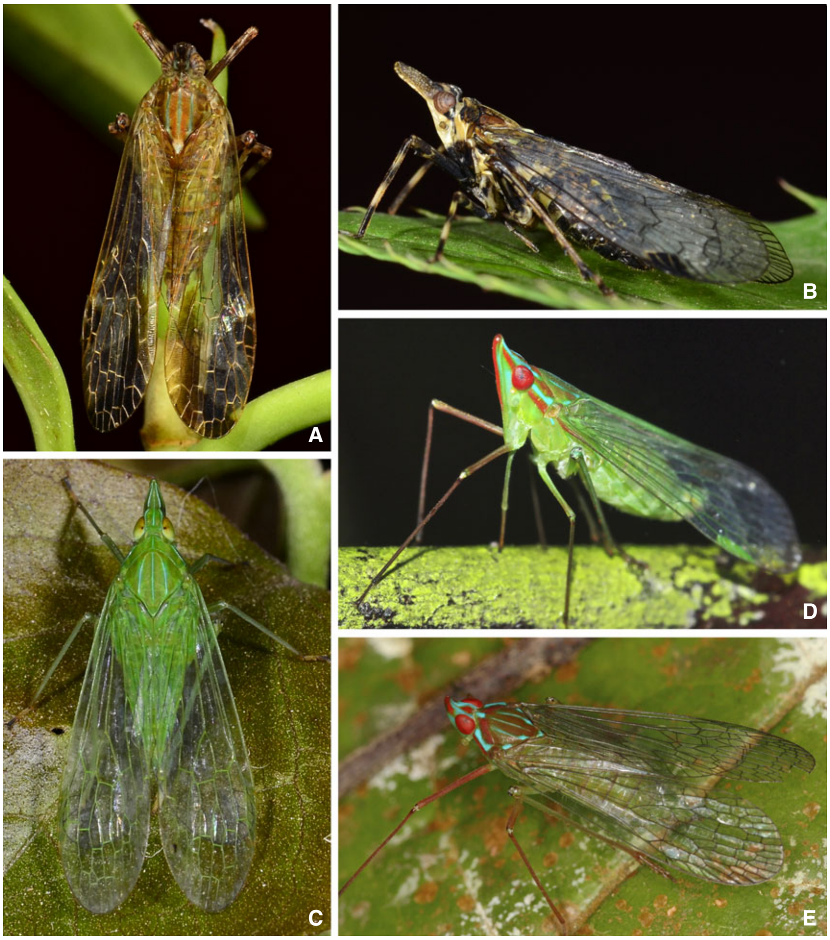

Figure 1. A, *Orthopagus* sp.; B, *Saigona fuscoclypeata*; C, *Tenguna medogensis*; (A–C) photographed by Z.-S. Song. D, ***Centromeria triangulata* sp. nov.**, photographed by Paul Bertner. E, *Centromeria speilinea*, photographed by Petr Kočárek.

closely to each other, without common stem; no carina separating apical and basal parts of lateral areas of metope; eyes separated from pronotum by callus postocularis; lower vesicles of theca without spicula; fore femora usually with ledge or tooth at posterior margin before apex; and apices of first and second segments of fore and middle tarsi with no more than two acutellae, surface covered with simple setae.

Orthopagini currently comprises 23 genera (including a new genus *Dictyomeria* gen. nov., described here), mainly distributed in the Old World tropics and subtropics, including sub-Saharan Africa, India, Sri Lanka, southern China, Indochina, Malay Peninsula, the Greater Sunda Islands, the Philippines, the Moluccas, northern Australia, and so on. Among them, 15 genera are mainly distributed in the Oriental region, with *Orthopagus* and *Saigona* Matsumura, 1910, extending into the eastern Palaearctic region, six genera are found in the Afrotropical region, and only one genus (*Ellipoma*) is restricted to northern Australia. In most central and western Palaearctic regions and the whole New World, there are no extant Orthopagini. One fossil genus *Alicodoxa* Emeljanov & Shcherbakov, 2011; found in Rovno and Baltic amber, is based on the nymphs of the genus (Emeljanov & Shcherbakov, 2011). There has been no systematic tribal-level review for the world Orthopagini, and the monophyly and phylogenetic relationships among the genera have never been tested cladistically.

In recent years, a continuing series of works emphasizing generic taxonomic revisions for the Oriental genera of Orthopagini (OGO) were published by the first author and his collaborators (Liang & Song, 2006; Song & Liang, 2006a, b, 2007, 2011a, 2012a, b; Song, Deckert & Liang, 2012; Song, Webb & Liang, 2014; Z.-S. Song, J. Deckert & A.P. Liang, unpubl. data). Among these publications, ten genera were studied, including three new genera *Truncatomeria* Song & Liang, 2011a;

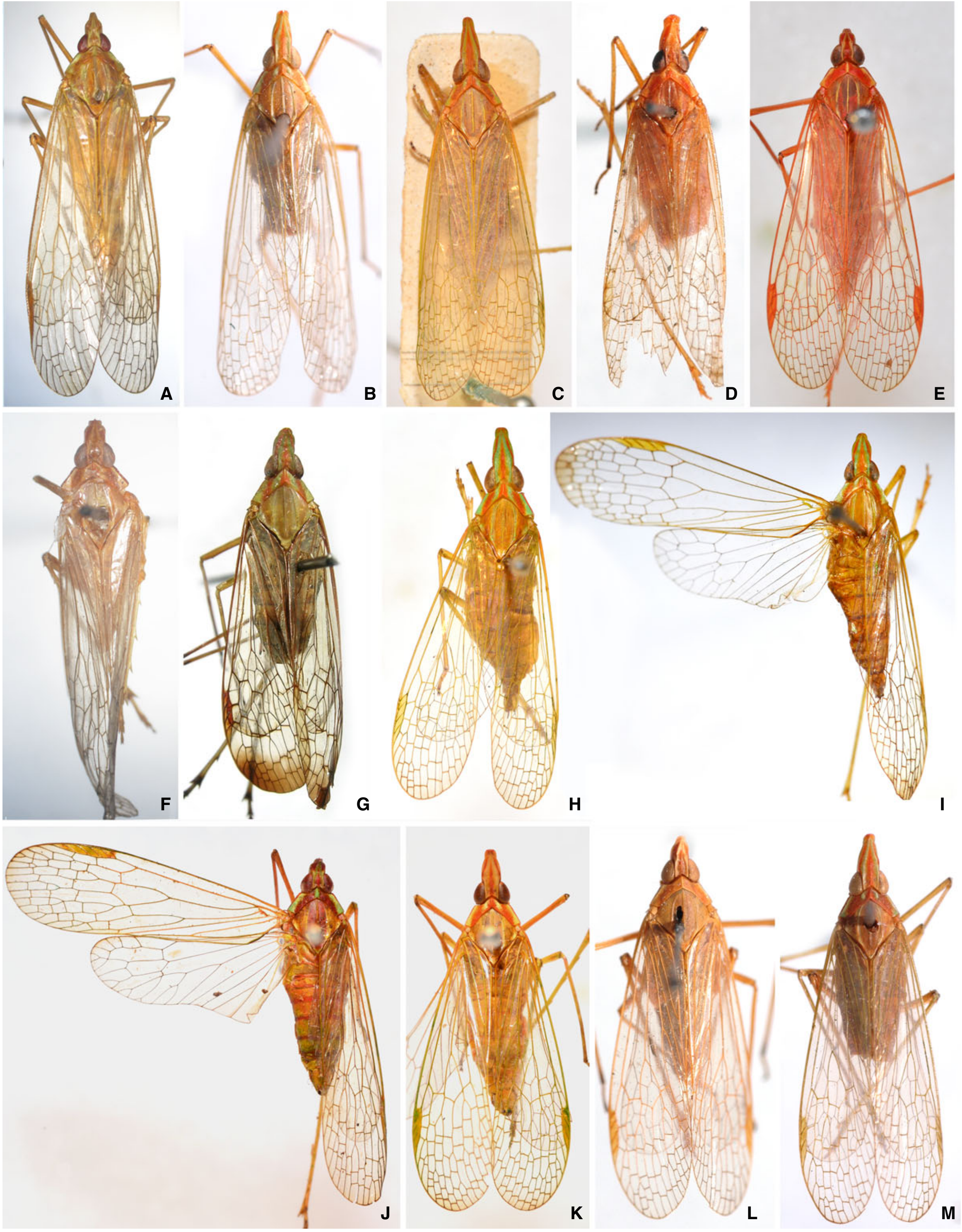

Figure 2. *Centromeria* species: A, ***Centromeria curva* sp. nov.**, holotype, male; B, ***Centromeria cuspidata* sp. nov.**, holotype, male; C, ***Centromeria deckerti* sp. nov.**, holotype, male; D, ***Centromeria inflata* sp. nov.**, holotype, male; E, *Centromeria inspinata*, female; F, *Centromeria longipennis*, male; G, ***Centromeria maculata* sp. nov.**, holotype, male; H, ***Centromeria melichari* sp. nov.**, holotype, male; I, *Centromeria nigroapicata*, male; J, *Centromeria speilinea*, male; K, ***Centromeria spinosa* sp. nov.**, holotype, male; L, *Centromeria surgens*, male; M, ***Centromeria triangulata* sp. nov.**, holotype, male.

Figure 3. Type species of Oriental genera of Orthopagini included in the phylogenetic analysis: A, *Dictyomeria simulata*; B, *Dictyopharina viridissima*; C, *Dictyotenguna choui*; D, *Indomiasa distanti*; E, *Leprota melichari*; F, *Medeusa speicarina*; G, *Metaurus reticulatus*; H, *Miasa smaragdilinea*; I, *Orthopagus lunulifer*; J, *Protolepta turbata*; K, *Saigona ussuriensis*; L, *Tenguna watanabei*; M, *Truncatomeria viridistigma*.

Dictyotenguna Song & Liang, 2012b; and *Indomasia* Song *et al.*, 2014. A phylogenetic analysis based on the morphological characters of adults was conducted to reconstruct the species-level phylogenetic relationships of *Miasa* Distant, 1906; and *Indomiasa* (Song *et al.*, 2014).

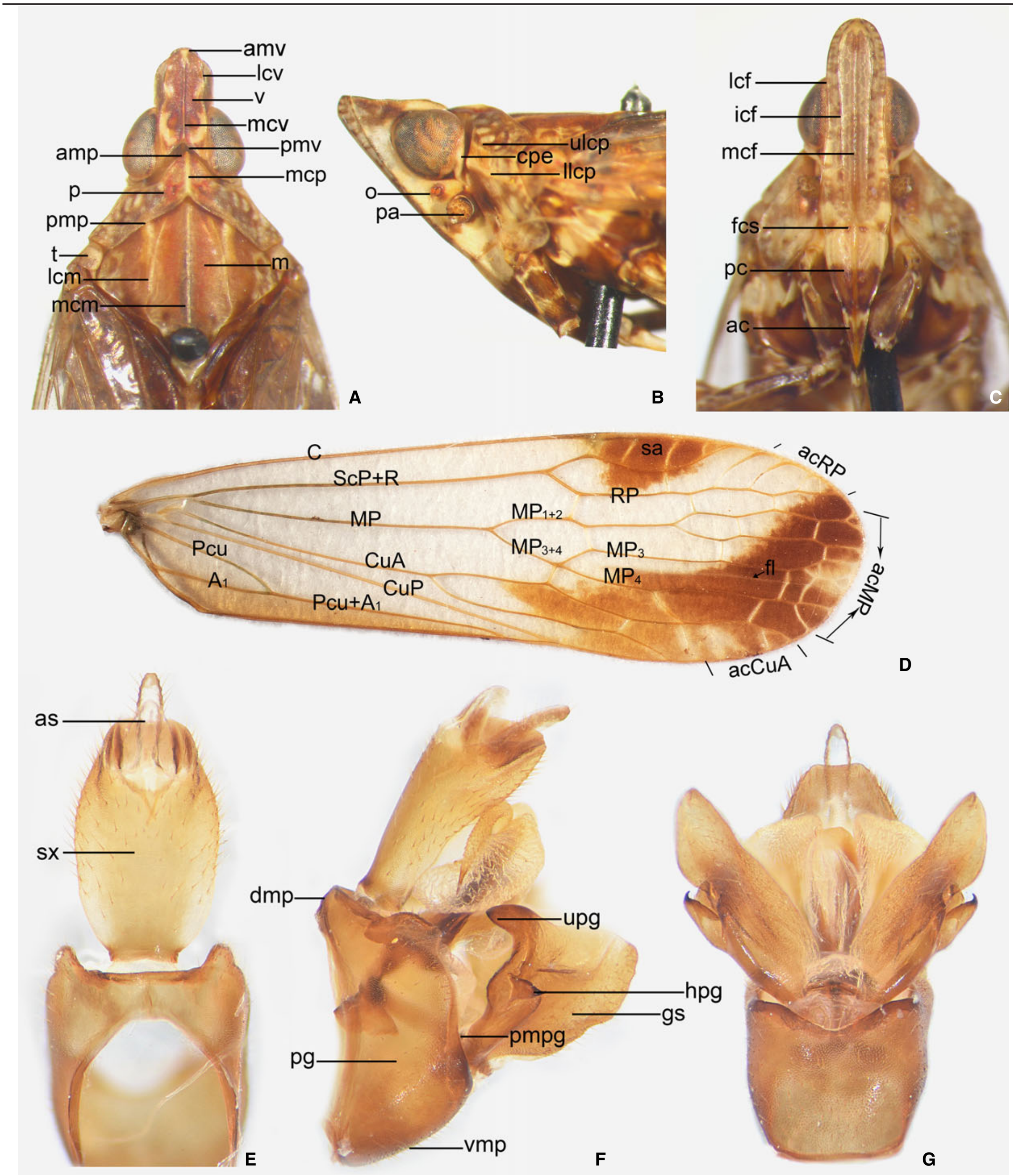

Figure 4. *Orthopagus lunulifer*: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head and pronotum, ventral view; D, tegmen; E, male pygofer and segment X, dorsal view; F, male genitalia, lateral view; G, male pygofer and gonostyles, ventral view. Abbreviations: ac, anteclypeus; acCuA, apical cells of CuA; acMP, apical cells of MP; acRP, apical cells of RP; amp, anterior margin of pronotum; amv, anterior margin of vertex; as, anal style; cpe, callus postocularis of eyes; dmp, dorsal margin of pygofer in profile; fcs, frontoclypeal suture; fl, folding line; gs, gonostyle; hpg, hook-like process of gonostyle; icf, intermediate carina of frons; lcf, lateral carina of frons; lcm, lateral carina of mesonotum; lcv, lateral carina of vertex; llcp, lower lateral carina of pronotum; m, mesonotum; mcf, median carina of frons; mcm, median carina of mesonotum; mcp, median carina of pronotum; mcv, median carina of vertex; o, ocellus; p, pronotum; pa, pedicel of antenna; pc, postclypeus; pg, pygofer; pmp, posterior margin of pronotum; pmpg, posterior margin of pygofer; pmv, posterior margin of vertex; sa, stigmal area; sx, segment X; t, tegula; ulcp, upper lateral carina of pronotum; upg, upper process of gonostyle; v, vertex; vmp, ventral margin of pygofer in profile.

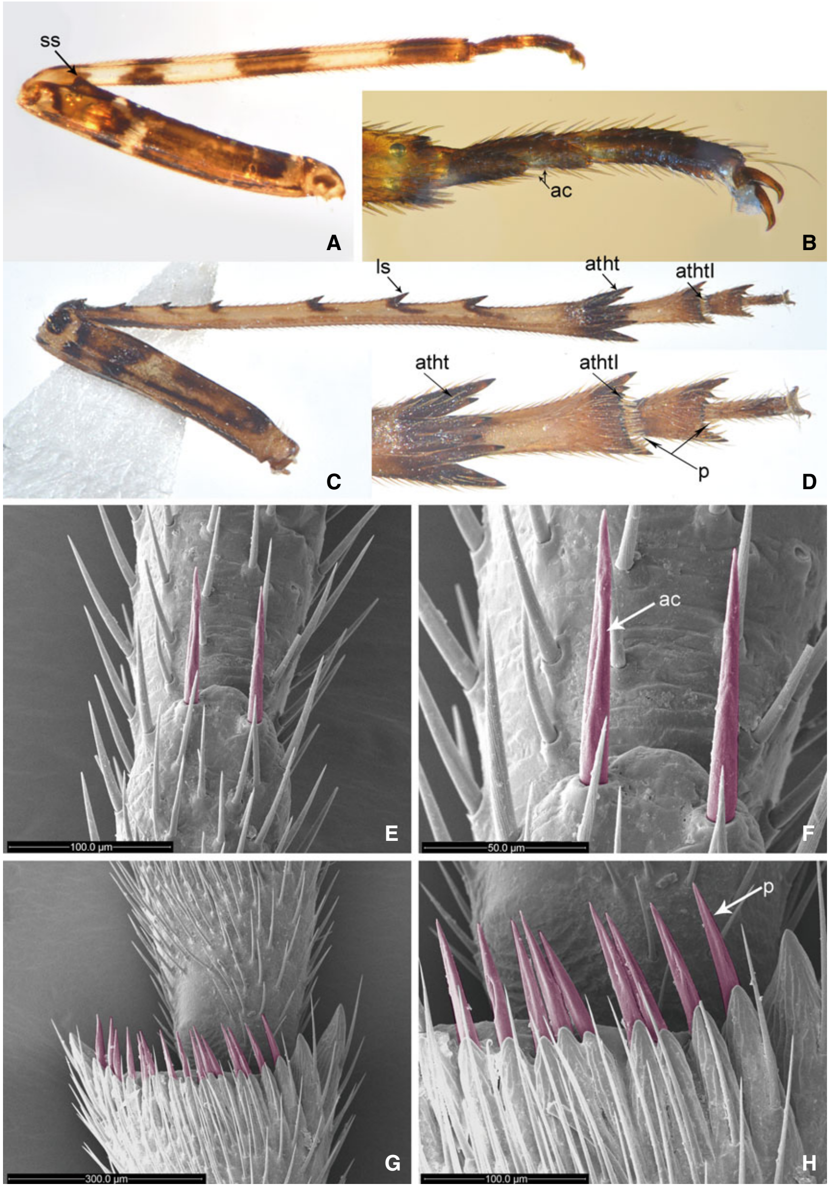

Figure 5. *Orthopagus lunulifer*: A, B, foreleg; C, D, hindleg; E, F, acutellae of fore tarsomeres I; G, H, apical teeth with platellae of hind tarsomeres I. Abbreviations: ac, acutellae; atht, apical teeth of hind tibiae; athtI, apical teeth of hind tarsomeres I; ls, lateral spine of hind tibiae; p, platellae; ss, subapical spine of fore femora.

Herein, we first undertake a phylogenetic analysis for all 15 of the OGO, and representatives in Arjunini, Dictyopharini, and Hastini, so as to investigate the phylogenetic relationships of the OGO using 116 morphological characters of adults. In addition, on the basis of the results of this analysis, another phylogenetic analysis for all species of *Centromeria* Stål, 1870 based on 48 adult characters is implemented to discuss the species-level phylogenetic relationships of *Centromeria*. These studies are preliminary, but are a substantial step towards reconstructing the systematics of the Orthopagini worldwide, and may provide important information on the phylogeny of the Dictyopharidae.

In the taxonomic part of this study, Orthopagini is redefined, a key to Oriental genera is provided, and the genus *Centromeria* is revised systematically. This genus was established by Stål (1870) based on *Dictyophora* [*sic*] *longipennis* Walker, 1851 (the type species) from the Philippines and *Dictyophora* [*sic*] *speilinea* Walker, 1857 from Borneo, Malaysia. Distant (1906) treated four *Centromeria* species, includ-

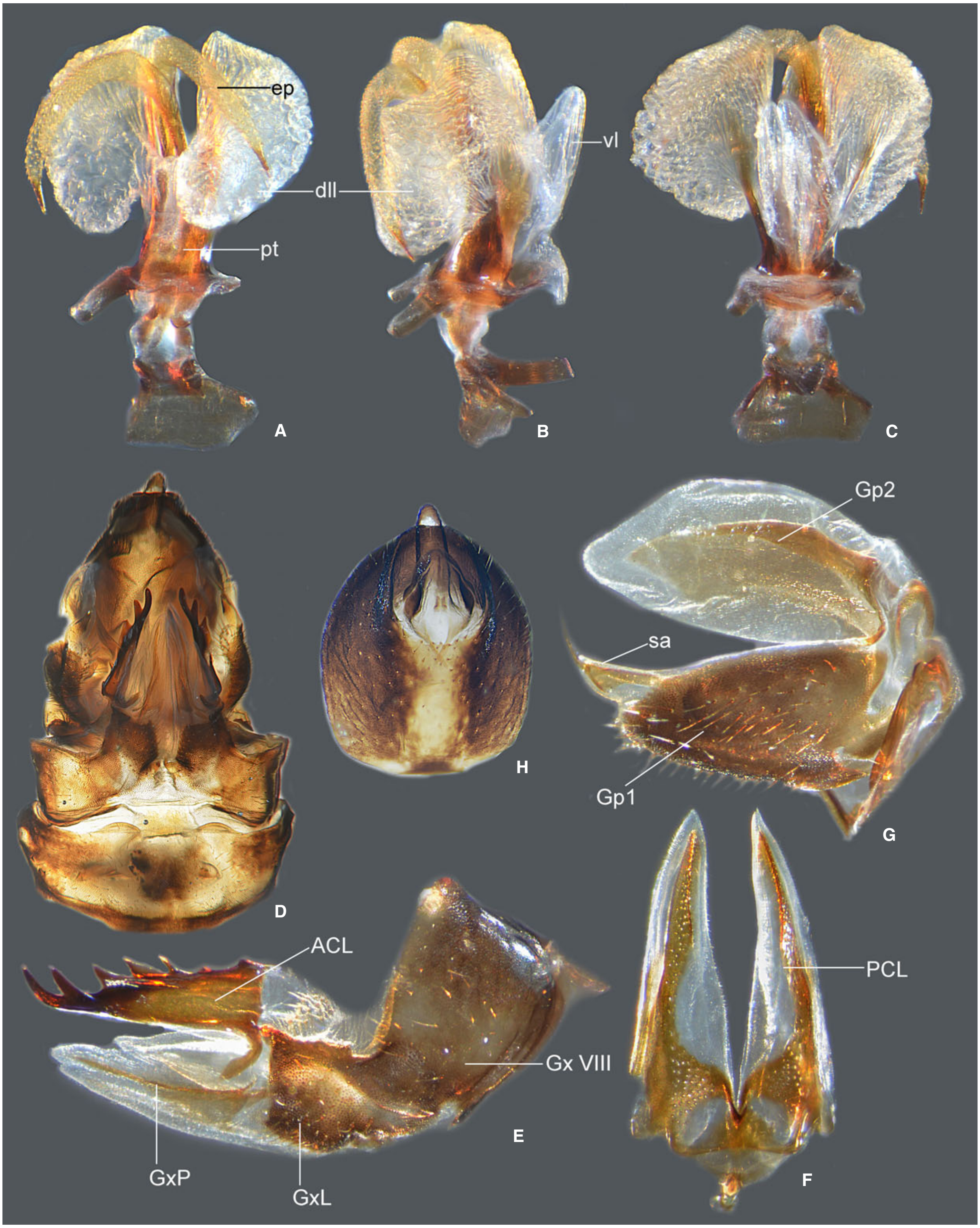

Figure 6. *Orthopagus lunulifer*: A, aedeagus, dorsal view; B, aedeagus, lateral view; C, aedeagus, ventral view; D, female genitalia; E, gonapophysis VIII, dorsolateral view; F, gonapophysis IX, ventral view; G, gonoplacs, ventrolateral view; H, female segment X, dorsal view. Abbreviations: ACL, anterior connective lamina of gonapophysis VIII; dll, dorsolateral lobe of phallotheca; ep, endosomal processes; Gp1 and Gp2, gonoplacs 1 and 2; GxL, gonocoxae VIII with endogonocoxal lobe; GxP, gonocoxae VIII with endogonocoxal process; Gx VIII, gonocoxae VIII; PCL, posterior connective lamina of gonapophysis IX; pt, phallotheca; sa, sensory appendage of Gp1; vl, ventral lobe of phallotheca.

ing two new species from India and a previously described species from Ceylon and Melichar (1912), redescribed this genus, and proposed three junior synonyms for *Centromeria longipennis* (Walker, 1851) and one junior synonym for *Centromeria speilinea* (Walker, 1857) (in error). A sixth species was added by Haupt (1917) from Sulawesi, Indonesia. The remaining two *Centromeria* species were erected by Kato (1932, 1933), but one, *Centromeria formosana* Kato, 1933, was synonymized with *Tenguna watanabei* Matsumura, 1910, by Matsumura (1940), and the other, *Centromeria manchurica* Kato, 1932, was synonymized with *Dictyophora* [*sic*] *koreana* Matsumura, 1915, by Song & Liang (2008). Recently, Song & Liang (2011a) transferred *Centromeria viridistigma* (Kirby, 1891) from *Centromeria* to a new genus *Truncatomeria* by a comparison between the types of *C. viridistigma* and *C. longipennis*.

Centromeria was initially placed in the Dictyopharini of Dictyopharinae (Melichar, 1912), but was later moved into Orthopagini (Emeljanov, 1983), and was regarded to be more closely related to *Truncatomeria*, *Tenguna* Matsumura, 1910, and *Dictyotenguna* (Song & Liang, 2007, 2011a, 2012b), although it is also exteriorly similar to *Medeusa* Emeljanov, 2011b, and *Emeljanovina* (= *Glochina* Emeljanov, 2011b) (Emeljanov, 2011b; Xing & Chen, 2013).

Based on an examination of most *Centromeria* types and a critical review of the literature, *Centromeria* is here revised to include 13 species in the present paper. Eight new species are established: *Centromeria curva* sp. nov., *Centromeria cuspidata* sp. nov., *Centromeria deckerti* sp. nov., *Centromeria inflata* sp. nov., *Centromeria maculata* sp. nov., *Centromeria melichari* sp. nov., *Centromeria spinosa* sp. nov., and *Centromeria triangulata* sp. nov. In addition, *Dictyophara nigroapicata* Lethierry, 1888 and *Dictyophora* [*sic*] *surgens* Walker, 1870 are resurrected from synonymy with *C. longipennis* and are transferred to *Centromeria*. Two new specific synonyms are proposed: *Centromeria speilinea* = *Centromeria bicolorata* Bierman, 1910 syn. nov. and *Centromeria surgens* (Walker, 1870) stat. rev., comb. nov. = *Fulgora nereides* Kirkaldy, 1913 syn. nov. A new genus *Dictyomeria* gen. nov. is described for *Centromeria simulata* Distant, 1906 and *Centromeria cephalica* Distant, 1906 is moved into *Paradictyopharina* Song & Liang, 2011a.

MATERIAL AND METHODS

SPECIMENS

The specimens studied in the course of this work are deposited in the following institutions, the names of which are abbreviated in the text as follows: AMNH, American Museum of Natural History, New York, USA; BMNH, Natural History Museum, London, UK; BPBM, Bernice P. Bishop Museum, Honolulu, HI, USA; HNHM, Hungarian Natural History Museum, Budapest, Hungary; HU, Laboratory of Systematic Entomology, Hokkaido University, Sapporo, Japan; IZCAS, Institute of Zoology, Chinese Academy of Sciences, Beijing, China; MFNB, Museum für Naturkunde der Humboldt Universität, Berlin, Germany; MIZPAS, Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, Poland; MMBC, Moravian Museum, Brno, Czech Republic; MNHN, Muséum National d'Histoire Naturelle, Paris, France; MZLU, Museum of Zoology, Lund University, Lund, Sweden; NCB, Naturalis Netherlands Centre for Biodiversity Naturalis, Leiden, the Netherlands; NCSU, Department of Entomology Insect Collection, North Carolina State University, Raleigh, NC, USA; NHMD, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; NHRS, Naturhistoriska riksmuseet, Stockholm, Sweden; NMPC, Department of Entomology, National Museum, Prague, Czech Republic; QM, Queensland Museum, South Brisbane BC, Queensland, Australia; SDEI, Senckenberg Deutsches Entomologisches Institut, Müncheberg, Germany; SNSD, Senckenberg Naturhistorische Sammlungen Dresden, Dresden, Germany; and USNM, National Museum of Natural History, Washington, DC, USA.

TERMINOLOGY AND TECHNIQUES

The morphological terminology used in this study follows Song *et al.* (2014) for most characters, Bourgoin *et al.* (2015) for the venation of tegmina (the forewings), and Bourgoin (1993) for the female genitalia.

The posterior abdomina of the specimens used for dissection were cleared in 10% KOH at room temperature (18–25 °C) for ~6–12 h, rinsed in distilled H_2O, and then transferred to 10% glycerol for examination. Observations, measurements, and photography were conducted under a Zeiss Discovery V12 compound stereomicroscope equipped with a Nikon D7000 digital camera in IZCAS or under a Leica Z16 APO A macroscope equipped with a Leica DFC495 microscope camera and Leica APPLICATION SUITE 3.7.0 in MFNB. The final images were compiled from multiple photographs using CombineZM image-stacking software, and were improved with Adobe PHOTOSHOP CS5. The morphological characters were also observed with a Zeiss Stemi SV II optical stereomicroscope and illustrated with the aid of a camera lucida attached to the microscope.

The following abbreviations are used in the text: ACL, gonapophyses VIII with anterior connective lamina; BL, body length (from apex of cephalic process to tip of tegmina); Gl, gonospiculum; Gp, gonoplacs; GxP, gonocoxae VIII with endogonocoxal process; HL, head length (from apex of cephalic process to posterior margin of eyes); HW, head width (including eyes); PCL, gonapophyses IX with posterior connective lamina; and TL, tegmen length.

Taxon sampling

The taxon sampling (Table A1) for the phylogenetic analysis of Orthopagini comprised just 34 species representing all of the 15 genera, mainly distributed in the Oriental region (not involving the Afrotropical and Australian regions), and nine species representing the three tribes of Arjunini, Dictyopharini, and Hastini, which are closely related to Orthopagini (Song *et al.*, 2016). The monophyly of most OGO is considered reliable based on recently published and continuing work of the first author and his collaborators (Liang & Song, 2006; Song & Liang, 2012a, b, 2006a, b, 2007, 2008, 2011a, b, 2012a, b; Song, Deckert & Liang, 2012; Song *et al.*, 2014; Z.-S. Song, unpubl. data; Z.-S. Song, J. Deckert & A.P. Liang, unpubl. data). Therefore, the in–group did not include all species of each genus except *Centromeria*. Three Aluntiini species were chosen as the out-group taxa, as this tribe is considered to be the sister group to all other Dictyopharidae (Song *et al.*, 2016). The taxa in this phylogenetic analysis are all distributed in the Old World, whereas the remaining tribes of Dictyopharinae mostly restricted to the New World were not involved in this study.

In the analysis of *Centromeria*, all 13 species are included (Table A1). *Dictyotenguna choui* Song & Liang, 2012b, and *Truncatomeria viridistigma* (Kirby, 1891) are selected as the out-group taxa based on the results of the phylogenetic analysis of the OGO.

Characters

The data matrix for the phylogenetic analysis of the OGO (Table A3) comprised 116 morphological characters (Table A2) from the coloration, head, thorax, and male and female genitalia of adults. Tables A4 and A5 represent the list of 48 adult morphological characters, their states, and the character matrix, respectively, used for the phylogenetic analysis of *Centromeria*. All characters were equally weighted, and all character states were treated as unordered. The character states were scored as dashes (–) if not applicable and as questions marks (?) if ambiguous or unexamined.

Cladistic analysis

The cladistic analysis was conducted with WinClada 1.00.08 (Nixon, 1999, 2002) implemented in NONA 2.0 (Goloboff, 2000). Phylogenetic relationships were reconstructed with a heuristic analysis by searching for the most parsimonious (MP) trees with 1000 maximum trees retained, 1000 replications, and ten starting trees per replication. Branch support values were calculated as standard bootstrap values and Bremer support. The bootstrap value was used as a support measure and calculated in NONA for the hypothesized clades, with 1000 replications. The Bremer support was calculated in TNT 1.1 (Goloboffa, Farris & Nixon, 2008) and obtained by tree bisection and reconnection (TBR) swapping on the most parsimonious trees and setting 'suboptimal' to 50.

RESULTS

Phylogenetic analysis of Oriental genera of Orthopagini

The analysis of the data set resulted in four equally long MP trees with tree lengths of 380 steps, consistency index (CI) of 0.39, and retention index (RI) of 0.75. A strict consensus of four trees collapsed four nodes and had a length of 384 steps, which is presented in Fig. 7 with the more robust bootstrap/Bremer support values mapped onto it.

Our results show that the Australian Arjunini (node 1 in Fig. 7) makes up a good monophylum with 100% bootstrap value and a Bremer support of 10; however, the monophyly of Hastini genera is not recognized. The topology of the strict consensus tree just supports the monophyly of Dictyopharini and Oriental Orthopagini (node 2), but *Emeljanovina* was grouped with Dictyopharini genera (node 3), indicating its placement in that tribe.

Node 4 supports the monophyly of the remaining OGO, which can be separated into four clades: *Medeusa*, *Dictyopharina*, *Orthopagus*, and *Dictyotenguna*. Among them, the *Medeusa* clade (node 5) includes two genera *Medeusa* and *Leprota* Melichar, 1912, strongly supported by 78% bootstrap value and a Bremer support of 6; *Dictyopharina* Melichar, 1903, is the only taxon in the *Dictyopharina* clade (node 6), whereas the *Orthopagus* clade (node 7) includes the following four genera: *Protolepta* Melichar, 1912, *Saigona*, *Dictyomeria* gen. nov., and *Orthopagus*. Node 7 (the *Dictyotenguna* clade) as a monophyletic lineage contains the remaining taxa of Oriental Orthopagini (*Dictyotenguna*, *Tenguna*, *Metaurus* Stal, 1866, *Indomiasa*, *Miasa*, *Truncatomeria*, and *Centromeria*).

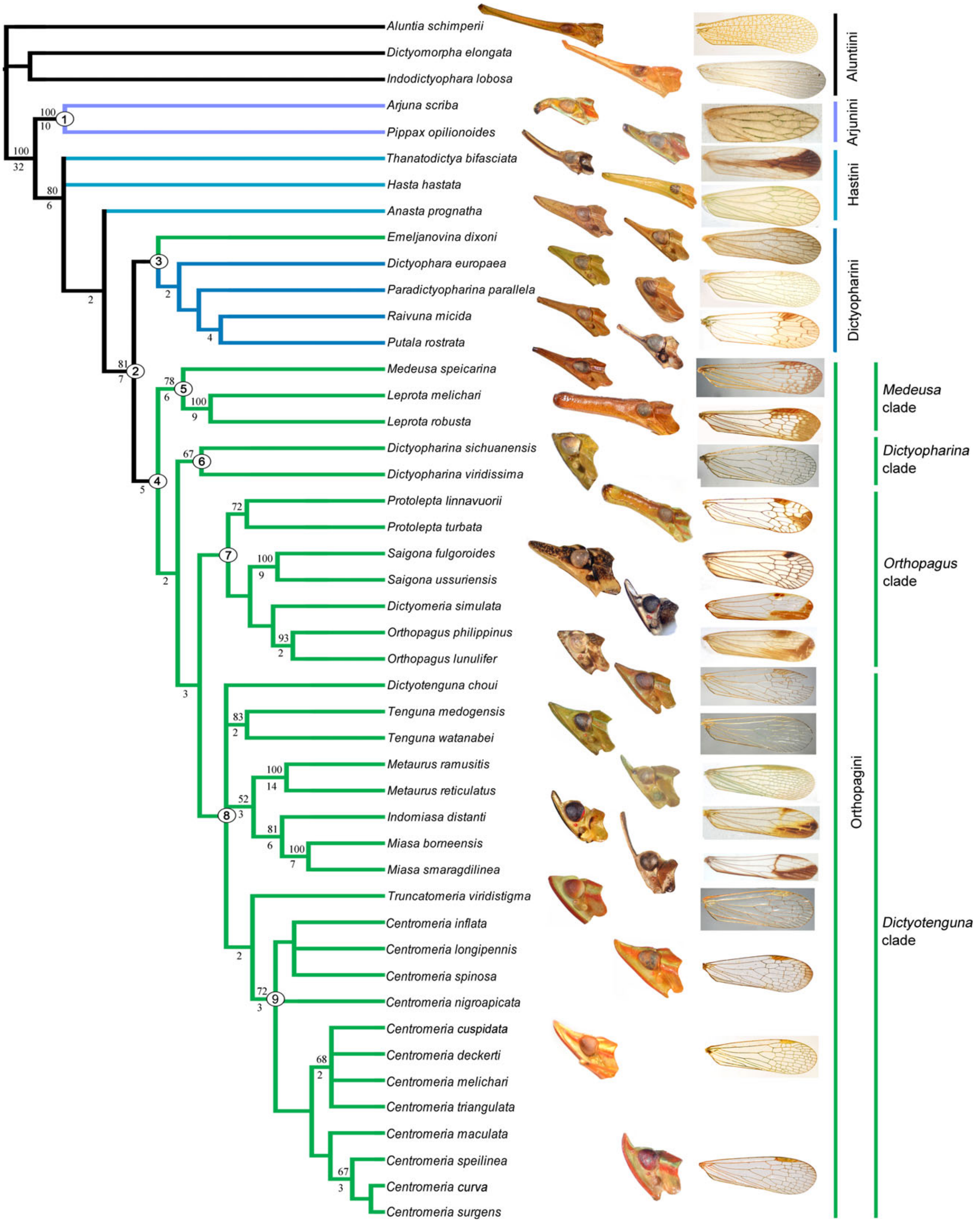

Figure 7. Phylogenetic reconstruction of Oriental Orthopagini: the strict consensus tree with clade number (on nodes); bootstrap value (above branch), for which values < 50% are not shown; and Bremer support (> 1, below branch). The head and pronotum (lateral view) and tegmen are mapped onto the tree.

PHYLOGENETIC ANALYSIS OF *CENTROMERIA*

In the phylogenetic analysis of *Centromeria*, the equal-weights parsimony analysis yielded two MP trees with a length of 89 steps, a consistency index of 0.60, and a retention index of 0.66, the strict consensus of which is shown in Figure 10. *Centromeria* can be divided into two distinct lineages: the *speilinea* clade (node 2 in Fig. 10), composed of *C. speilinea*, *C. surgens*, *C. curva* sp. nov., and *Centromeria inspinata* Haupt, 1917; and the *longipennis* clade (node 3), comprising *C. nigroapicata*, *C. maculata* sp. nov., *C. longipennis*, *C. inflata* sp. nov., *C. spinosa* sp. nov., *C. melichari* sp. nov., *C. triangulata* sp. nov., *C. cuspidata* sp. nov., and *C. deckerti* sp. nov.

DISCUSSION

ARJUNINI (NODE 1 IN FIG. 7) + HASTINI

The tribe Arjunini (*Arjuna* Muir, 1934 + *Pippax* Emeljanov, 2008) was newly established by Song *et al.* (2016), which also forms a good monophylum in this study, supported by 11 unambiguous characters, including five unique synapomorphies: character 34, state 1 (34–1; Fig. 8), 53–1, 54–2, 57–1, and 75–1. The homologue of the female genitalia strongly support Arjunini as a sister clade of the representatives of Hastini, Dictyopharini, and Orthopagini (Song *et al.*, 2016). This group appears to be closer phylogenetically to Hastini, with both restricted to the Australian region. Morphologically, ScP + R and MP veins of the tegmina, with a long common stem, and the consistency of the female genitalia support the close relatedness of the two tribes (Song & Liang, 2013; Song *et al.*, 2016).

The monophyly of Hastini, however, is not supported in the present analysis. There are eight genera (subgenera) within Hastini disjunctively distributed in the Australian and Neotropical regions (Emeljanov, 2011b). Only three Australian genera, *Anasta*, *Hasta*, and *Thanatodictya*, are involved in the phylogenetic analysis, and they fail to make up a monophylum, even though the diagnostic features suggested by Emeljanov (2011b) implied that this group should be monophyletic. A robust comparison with Neotropical Hastini is needed for a better understanding of the monophyly and phylogenetic relationships of this group.

DICTYOPHARINI + ORTHOPAGINI (NODE 2 IN FIG. 7)

Dictyopharini should be a sister group of Orthopagini, a conclusion consistent with the phylogenetic analysis of the tribe Aluntiini and its related taxa (Song *et al.*, 2016). Both tribes are distributed in the Old World and share similar tegmina and female genitalia, which are regarded as important to differentiate different Dictyopharinae tribes (Emeljanov, 1983, 2011b). They are supported by the following synapomorphic characters: tegmina with a folding line between MP_3 and MP_4 (59–1); basal teeth of ACL of gonapophyses VIII not prolonged (99–0); gonoplacs with apical margin of Gp1 more or less pointed (108–1); and gonoplacs with sensory appendage (110–1).

EMELJANOVINA + DICTYOPHARINI (NODE 3 IN FIG. 7)

Dictyopharini, including *Dictyophara* Germar, 1833 (the type genus of Dictyopharidae) and 28 other genera widely distributed in the Old World (Emeljanov, 2011b), represents the typical dictyopharid group. *Paradictyopharina* would also be included in this group, despite a superficial similiarity to the Orthopagini genus *Dictyopharina* (Song & Liang, 2011b). The monophyly and phylogenetic relationships of Dictyopharini have never before been studied by a cladistic analysis.

Dictyopharini is closely related to Orthopagini, as it shares considerable synapomorphies with the latter, especially in female genitalic structure. Emeljanov (2011b) proposed that four diagnostic features separate Dictyopharini from Orthopagini, as follows: the lower vesicles of the theca with spicula (89–1 in the present analysis); the fore femur without ledge or tooth at the posterior margin, but the margin of apex sometimes serrate (77–1); the lower surfaces of fore and middle tarsi entirely covered with acutellae (79–1); and the paranota of pronotum sometimes with pectoral carina (45–1). The last diagnostic feature is not a synapomorphy in all Dictyopharini genera, e.g. the pectoral carina is absent in *Pulata* Melichar, 1903 (Song & Liang, 2011b). The tribe has moderate to long spines on the apical lobes of the phallobase, which can occur on the dorsal lobes as well as on the ventral ones (89–1), whereas in Orthopagini there are very short small spines on the apical lobes, a characteristic that can be used to distinguish different species at the species level.

In our analysis, *Emeljanovina* falls into Dictyopharini in our strict consensus tree, sharing two synapomorphies (79–1 and 89–1) with representatives of Dictyopharini. This genus should be moved into Dictyopharini.

ORIENTAL ORTHOPAGINI (NODE 4 IN FIG. 7)

Excluding *Emeljanovina*, Oriental Orthopagini is a monophyletic group supported by six distinct characters: the apex of vertex broadly convex (21–2); the

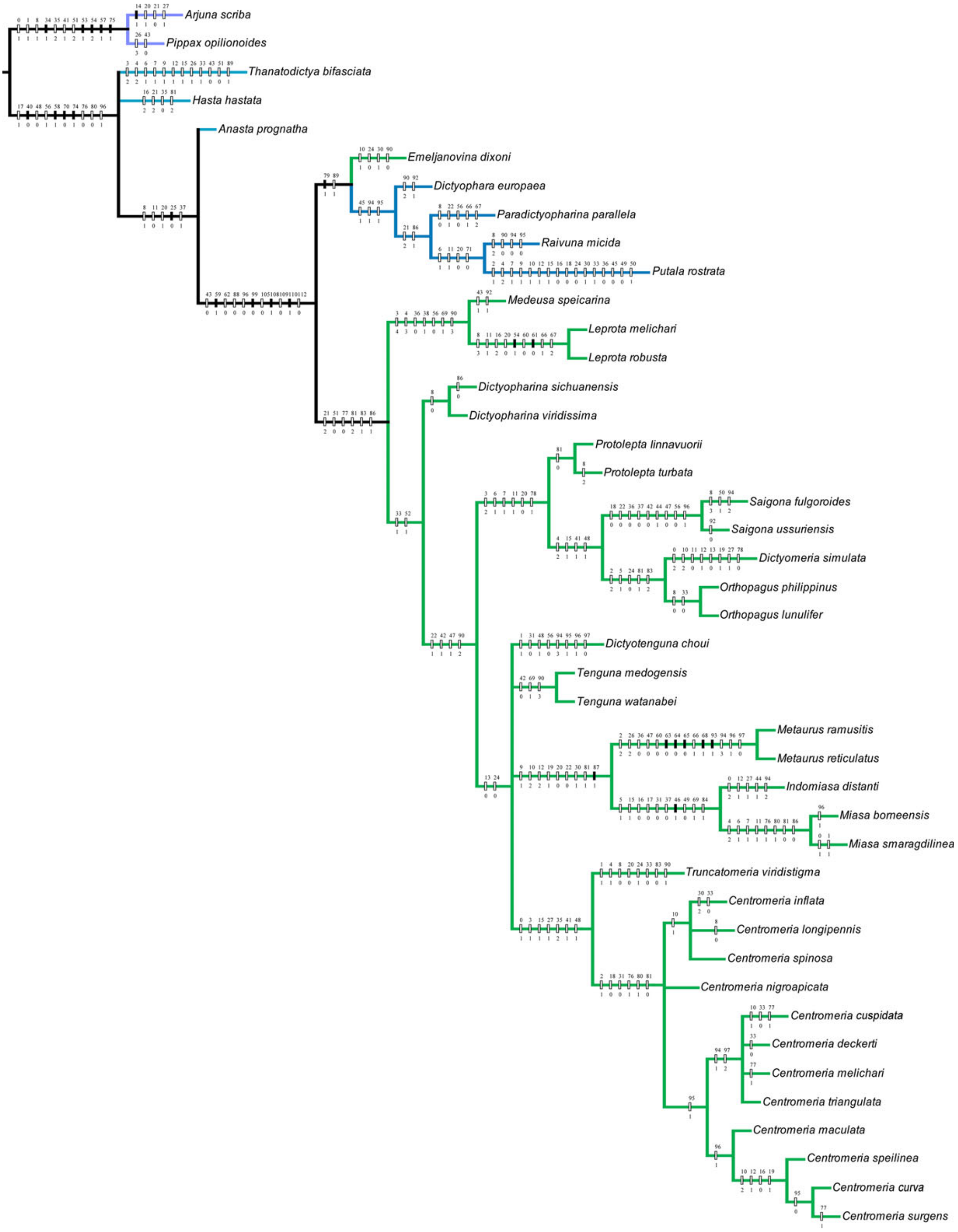

Figure 8. Srict consensus tree of phylogeny of Oriental Orthopagini, showing unambiguous characters supporting each clade (character number above and state number below) based on unambiguous optimization. Non-homoplastic characters with consistency index 1 are shown as filled rectangles, and homoplastic characters are shown as empty rectangles.

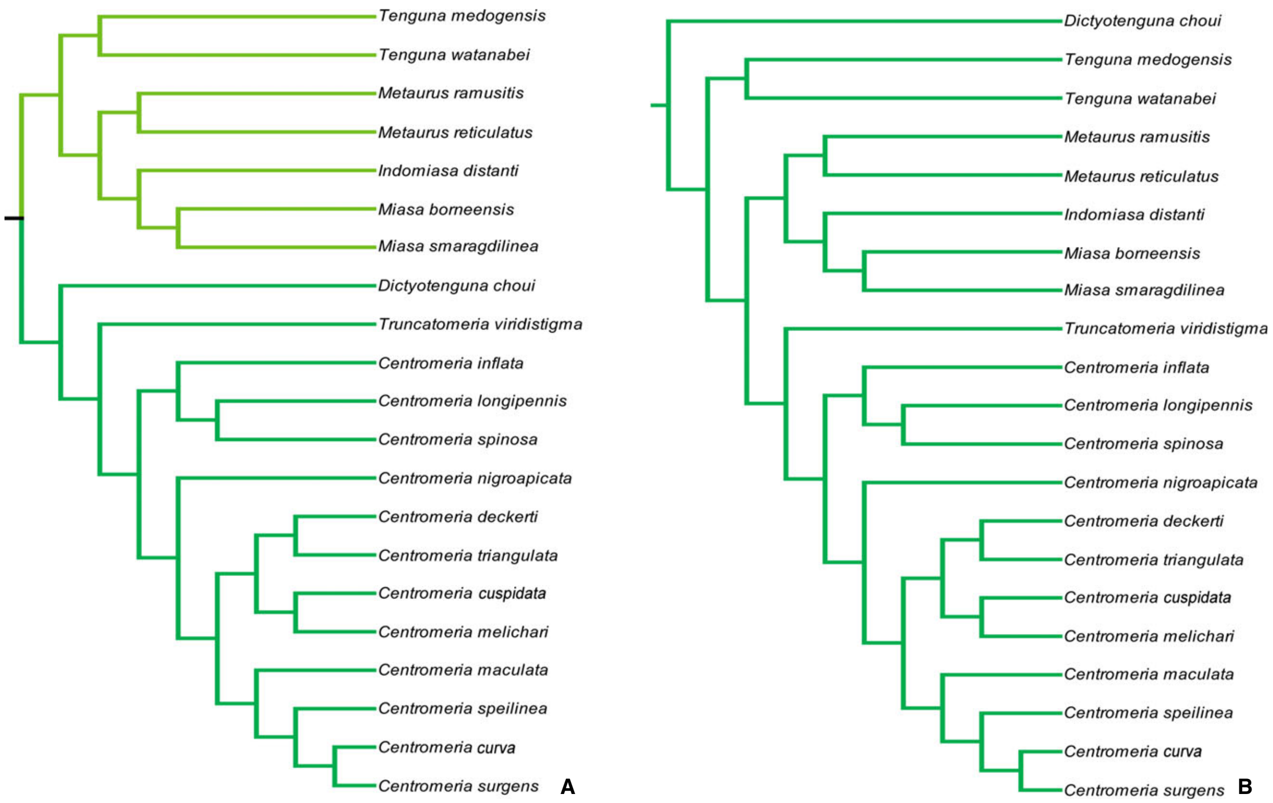

Figure 9. Reference trees selected from the four maximum-parsimony (MP) trees showing two phylogenetic relationships of the *Dictyotenguna* clade within Oriental Orthopagini.

lateral carinae of the mesonotum gradually incurved anteriorly (50–0); the ventral area of the fore femora with a subapical spine (77–0); the number of apical teeth of the hind tibiae (81–2); the number of apical teeth of the hind tarsomeres I (83–1); and the posterior margin of pygofer with process (86–1). Four unambiguous clades in Oriental Orthopagini are admitted in the light of the current phylogenetic analysis: *Medeusa*, *Dictyopharina*, *Orthopagus*, and *Dictyotenguna*.

In this group, the length, thickness, and curvature of the cephalic process vary dramatically in different genera: from very short (no longer than longitudinal diameter of eyes, 8–0) in *Orthopagus* (Figs 1A, 3I, 4A) to very elongate (much longer than pronotum and mesonotum combined, 8–3) in *Leprota* species (Fig. 3E); from very robust and inflated apically (12–0) in *Leprota* and *Protolepta* (Fig. 3J) to constricted to an extremely slender process (12–2) in *Miasa* species (Fig. 3H); and from unbent or slightly curved upwards (10–0) in *Medeusa* (Fig. 3G), *Protolepta*, and *Saigona* (Fig. 3K) to strongly curved upwards (10–2) in *Dictyomeria* (Fig. 3A), *Indomiasa* (Fig. 3D), and *Miasa*. Like its closely related sister group Fulgoridae, the head is remarkably plastic not only in Orthopagini, even across closely related lineages, such as the *Orthopagus* clade, but also in Dictyopharidae. Urban & Cryan (2009) suggested that the ancestors of Dictyopharidae and Fulgoridae had an elongate cephalic process, but it was lost and independently gained many times in the fulgorid lineages. Our phylogenetic analysis supports this hypothesis, although these multiple losses of the elongate cephalic process across dictyopharid evolution are weakly explained on the basis of our limited data.

Unfortunately, the absence of Afrotropical and Australian Orthopagini taxa, with a lack of research material, impedes our understanding of the phylogenetic relationships of genera within Orthopagini worldwide. The phylogeny of worldwide Orthopagini might change with the addition of more taxa in other zoogeographical regions. These generic relationships will also continue to be refined as more undescribed Orthopagini taxa are discovered, particularly in the Afrotropical region where there appears to be the greatest diversity of Dictyopharidae. The present phylogeny of Oriental Orthopagini is an attempt to provide not only the updated diagnostic characters for each Oriental Orthopagini genus, but also to set a basis for implementing a phylogenetic analysis for all *Centromeria* species. A future test, or

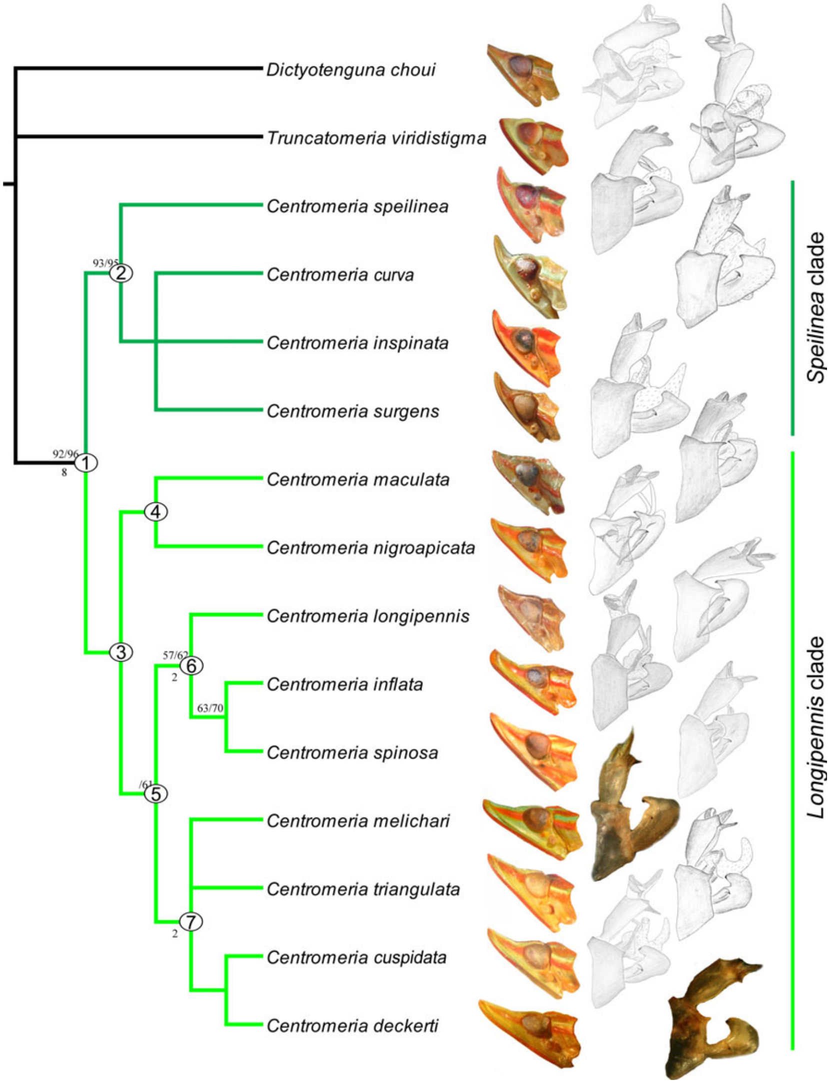

Figure 10. Phylogenetic reconstruction of *Centromeria*: strict consensus tree with clade number (on nodes), bootstrap value (above branch; values < 50% not shown), and Bremer support (> 1, below branch). The head and pronotum (lateral view) and male genitalia are mapped onto the tree.

confirmation, of the present phylogenetic inferences is expected to be developed, and will be improved by more material, allowing a more accurate understanding of the phylogenetic relationships of world Orthopagini.

MEDEUSA CLADE (NODE 5 IN FIG. 7)

The *Medeusa* clade, including two genera *Medeusa* and *Leprota* from the Malay Peninsula and the Greater Sundas, is a sister group of the remaining OGO. The following synapomorphies support this node: pronotum and mesonotum testaceous (3–4 and 4–3); rostrum with basal segment distinctly longer than distal segment (36–0); tegminal veins with setae (56–0); tegmina with nodal line (69–1); and aedeagus with endosomal processes very long, nearly as long or even longer than the phallobase with lobes (90–3).

Medeusa (Fig. 3F) was erected by Emeljanov based on *Dictyophora* [*sic*] *speicarina* Walker, 1857; from Borneo and *Dictyophara sumatrana* Lallemand, 1931, from Sumatra (Emeljanov, 2011b). It is far from *Centromeria* and closely related to *Leprota* in our analysis, but can be separated from *Leprota* by the cephalic process in front of eyes converging forwards (11–0), the median carina of the vertex nearly complete (18–1), the lateral carinae of the vertex in front of eyes gradually converging forwards (20–1), and the intermediate carinae of the pronotum complete (43–1). In addition, the fore femora have a small and acute spine on the ventral subapical area (78–0) in our specimens examined from Borneo and the Malay Peninsula, unlike those described by Emeljanov (2011b).

Leprota (Fig. 3E) was established based on a species from Sumatra misidentified as *Dictyophara fulgoroides* Walker, 1858 by Melichar (1912). Fennah (1963) corrected Melichar's misidentification and redesignated the type species as *Leprota melichari* Fennah, 1963. Song *et al.* (2012) revised this genus and added a second species, *Leprota robusta* Song, Deckert & Liang, 2012, from northern Borneo.

Dictyopharina clade (node 6 in Fig. 7)

This clade just includes a single genus *Dictyopharina* (Fig. 3B), supported by an unambiguous character: the cephalic process in front of eyes very short, no longer than longitudinal diameter of eyes (8–0). Song & Liang (2006a, b) described four new Dictyopharina species from southern China, Malaysia, and the Philippines, and Zheng & Chen (2012) added the seventh species from China. Emeljanov (2011b) proposed *Tropidophara* Bierman, 1910 as a junior synonym of the genus, bringing the total number of species recorded to nine. According to our view, however, *Dictyopharina dubiata* (Bierman, 1910), *Dictyopharina longicephala* Song & Liang, 2006b, and *Dictyopharina javana* (Lethierry, 1888) could turn out to be conspecific if the relevant types were examined.

Orthopagus clade (node 7 in Fig. 7)

This node contains four genera: *Protolepta*, *Saigona*, *Orthopagus*, and *Dictyomeria*. They are united by the following synapomorphies: pronotum with median carina whitish (3–2); legs and abdominal segments III–VI dark brown, with whitish spots or stripes (6–1 and 7–1); cephalic process in front of eyes nearly parallel (11–1); lateral carinae of the vertex subparallel (20–0); and fore femora with a large and blunt subapical spine (78–1).

Protolepta (Fig. 3J) was a monotypic taxon established for *Protolepta turbata* Melichar, 1912 from Sulawesi. The second species from Sulawesi was described (Z.-S. Song, J. Deckert & A.P. Liang, unpubl. data) and added to the present phylogenetic analysis.

Saigona (Figs 1B, 3K) includes 13 species mainly restricted to East Asia (Liang & Song, 2006; Zheng, Yang & Chen, 2014). The type species *Saigona ussuriensis* (Lethierry, 1878) was found in the Far Eastern region of Russia, which is the northernmost record for Orthopagini. Few biological data are currently available for *Saigona*, but its species seem well adapted to the cooler climates of high elevation (< 1500 m a.s.l.) in the Oriental subtropical region, based on our collecting data (Z.–S. Song, unpubl. data).

Orthopagus (Figs 1A, 3I) is the most widely distributed taxon within Orthopagini from the whole Oriental region to the eastern Palaearctic region. It contains five species, but some of them are seen as problematic and in need of detailed and full revision (Z.–S. Song, unpubl. data).

Dictyomeria, containing a single species (*Dictyomeria simulata* comb. nov.) transferred from *Centromeria* in this paper, shares the following unambiguous characters with *Orthopagus*: preocular field of the cephalic process with spots (2–2); tegmina with a sublunate streak on apical region (5–1); apical median carina between anterior margins of the vertex and intermediate carinae of the frons absent (24–0); hind tibiae with seven apical teeth (81–1); and hind tarsomeres I with over 14 apical teeth (83–2).

Dictyotenguna clade (node 8 in Fig. 7)

The *Dictyotenguna* clade, as a monophyletic lineage, contains the remaining taxa of Oriental Orthopagini. Synapomorphies supporting this node include: cephalic process with an oblique carina on the lateral surface in front of eyes (13–0); and a sharp apical median carina between the anterior margins of the vertex and the intermediate carinae of the frons (24–0). The relationships within the clade are not clear, however, because of two alternative topologies of MP trees (Fig. 9). One of them includes two distinct lineages – the *Tenguna* group and the *Dictyotenguna* group (Fig. 9A) – and the other forms a series of successive sister taxa to *Centromeria* (Fig. 9B).

Tenguna (Figs 1C, 3L) was established in 1910 based on a single species, *Tenguna watanabei* Matsumura, 1910, from Taiwan. It remained monotypic until Song & Liang (2007) added the second species *Tenguna medogensis* Song & Liang, 2007, from south-western Tibet, representing the first record of Dictyopharidae in Tibet.

Metaurus (Fig. 3G) is a very unique genus within Orthopagini. The anterior margin of the tegmina of *Metaurus* species is distinctly expanded into a broad, sclerotized costal area between costal vein and anterior margin (60–0). The similar character in *Leprota* has the expanded costal area only obvious in front of the stigmal area, unlike in *Metaurus*. In the tribe Aluntiini, the geuns *Dendrophora* Melichar, 1903 shares not only the same expanded costal area with *Metaurus*, but also some other features of the tegmina. For instance, the tegmina with MP bifurcating into MP_{1+2} and MP_{3+4} anterior to CuA near the basal one-third of corium (63–0 and 65–0), and then MP_{3+4}

bifurcating further into MP_3 and MP_4, anterior to the middle of corium (64–0), so that the MP vein is branched in succession to dozens of accessory veins on the apical two-thirds of corium. Besides that, there are numerous netted transverse veins among ScP+R, MP, and CuA on the apical two-thirds of the corium. These characters, shared by both *Dendrophora* and *Metaurus* species, were considered as plesiomorphic traits existing either in Aluntiini of Dictyopharidae or in many Fulgoridae, including *Zanna* Kirkaldy, 1902 (Z.–S. Song, unpubl. data). *Zanna* might be a sister group to all other dictypharid taxa (Urban & Cryan, 2009) or belong to a separate family Dichopteridae (Emeljanov, 2011b). In addition, the aedeagus of *Metaurus* species possessing a pair of branched endosomal processes is very rare within Dictyopharinae. Hence Song & Liang (2012a) suggested that *Metaurus* might even represent a new tribe in Dictyopharinae; however, this genus always fell into Orthopagini in the analyses of phylogenetic relationships based on morphological data for *Miasa* (Song *et al.*, 2014), Aluntiini (Song *et al.*, 2016), and Oriental Orthopagini in the present paper. Therefore, the above characters of *Metaurus*, suggesting a new tribal category, might be a reversal to the plesiomorphic condition within Dictyopharidae. To resolve this problem, more robustly selected Dictyopharidae taxa need to be added to the morphology-based phylogenetic analysis, and a molecular phylogenetic analysis is also worth considering.

Indomiasa (Fig. 3D) and *Miasa* (Fig. 3H), revised recently by Song *et al.* (2014), form a good monophylum on the basis of morphology-based phylogenetic analysis. They are closely related to *Metaurus*, which is also supported by the present study.

Dictyotenguna (Fig. 3C) is a well-defined genus including two species: *D. choui* (the type species) and *Dictyotenguna angusta* Zheng & Chen, 2014. This taxon can be regarded as the sister group of *Truncatomeria* and *Centromeria* in two alternative topologies of MP trees (Fig. 9A, B), so it is used for the out-group taxon in the phylogenetic analysis of *Centromeria*.

Truncatomeria is regarded as a closely related sister of *Centromeria* (node 9 in Fig. 7), which is defined by the following synapomorphies: frons with median carina broadly purplish red or reddish ochraceous (0–1); pronotum reddish ochraceous between carinae (3–1); posterior plane of the vertex elevated in relation to pronotum (15–1); frons with median carina robust and strongly convex (27–1); rostrum very long, with apex extending or even surpassing the apex of the hind femora (35–2); median carina of the pronotum strongly ridged (41–1); and posterior margin of the pronotum more or less angularly concave (no more than 120°) (48–1). The strict consensus tree failed to resolve the *Centromeria* phylogeny, however, as some definite species-level characters were not included in the phylogenetic analysis of OGO.

PHYLOGENY OF *CENTROMERIA*

The revised *Centromeria* (node 1 in Fig. 10) is a good monophylum in the species-level phylogeny after excluding *C. cephalica* and *C. simulata*. It is defined by the following nine synapomorphies: frons with area between intermediate carinae and median carina virescent or ochraceous (2–0 in Fig. 11); preocular field of cephalic process with a long strip from the front of eyes to the apex (3–1); median carina of the vertex distinct at base (15–0); apex of the vertex nearly acuminate (17–0); frons with apical area of intermediate carinae distinctly wide in relation to lateral carinae (20–1); fore femora, and hind femora and tibiae, slender and elongate (26–1 and 28–1); hind tibiae with six apical teeth (30–0); and aedeagus with endosomal processes curved in middle (40–1).

The monophyly of the *speilinea* clade (node 2) is supported by three synapomorphic characters: cephalic process in front of eyes relatively slender (12–1); vertex with basal width distinctly narrower than transverse diameter of eyes (14–0); and vertex with lateral carinae in front of eyes abruptly and strongly constricted (16–1). It is also supported by two homoplasies: the cephalic process in front of eyes strongly curved upwards (11–2); and aedeagus with one pair of dorsolateral apical lobes (42–1). Within the *speilinea* clade, the relationships among four species are undetermined, seemingly implying that there were two dispersal events in different directions during the diversification of this clade.

The *longipennis* lineage (node 3) is grouped based on the synapomorphy of the median carina of the pronotum purplish red or reddish ochraceous (4–1). Within this clade, *C. nigroapicata* is closely related to *C. maculata* sp. nov. by the tegmina with fuscous maculae on apical region (9–1), and the gonostyles with upper process acute (35–0). The two species (node 4) grouping together are considered a sister group of the remaining *Centromeria* species (node 5) from the Philippines. Node 6 is defined by four common characters: cephalic process in front of eyes moderately curved upwards (no more than 30°) (11–1); pygofer in lateral view with ventral margin 1.5–2.5 times as wide as dorsal margin (30–0); pygofer with posterior process relatively slim and obtuse (31–0 and 33–1); whereas node 7 forms a well-supported monophyletic group based on the following synapomorphies: pygofer with posterior process short (32–0); segment X in dorsal view truncate and projecting an angle on each side (44–1); segment X with ventral apical margin projecting a central triangular process (47–2).

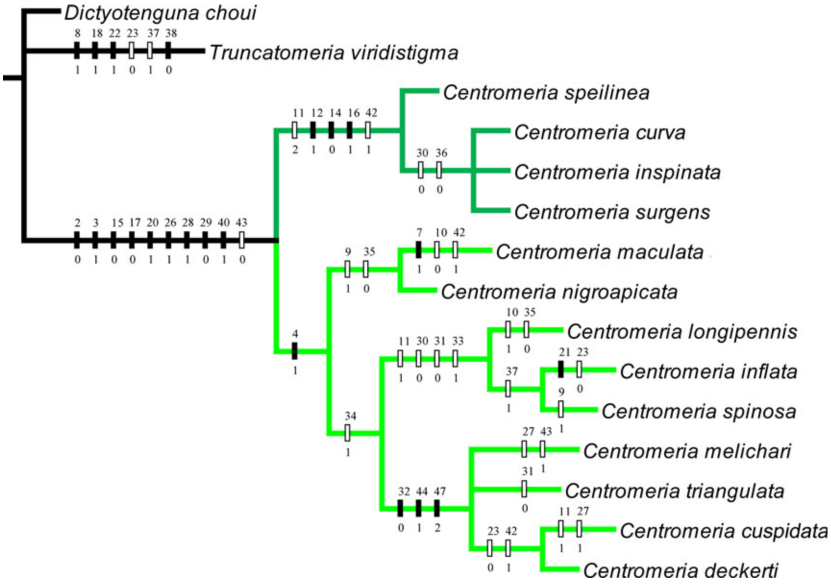

Figure 11. Strict consensus tree of phylogeny of *Centromeria*, showing unambiguous characters supporting each clade (character number above and state number below) based on unambiguous optimization. Non-homoplastic characters with consistency index 1 are shown as filled rectangles, and homoplastic characters are shown as empty rectangles.

DISTRIBUTION PATTERNS OF *CENTROMERIA*

The updated geographical distribution of *Centromeria* becomes narrower in the present study than was previously thought. The distribution range excludes South Asia and just includes the Indo-Chinese and Indo-Malayan subregions of the Oriental region and Wallacea (Fig. 12). The previous records from southern India (Nilgiri Hills) and north-eastern India (Assam) refer to *C. cephalica* and *C. simulata*, which are excluded from *Centromeria*.

Two distinct *Centromeria* lineages, obtained from our phylogenetic analysis, represent two distribution tracks from north to south-east and from west to east, respectively (Fig. 12). Within the *speilinea* lineage, *C. curva* sp. nov. is endemic in southern Yunnan, China, which would be temporally considered as the northernmost record of the genus. *Centromeria speilinea* is widespread in Southeast Asia from Burma via Thailand, Malaysia (the Malay Peninsula, north-western Borneo) to Indonesia (Sumatra, Java). *Centromeria surgens* is scattered in the Lesser Sundas and the Moluccas in Wallacea, and *C. inspinata* is only recorded in north-eastern Sulawesi. The clade follows a 'southern Yunnan – Indochina – Malay Peninsula – Greater Sundas – Lesser Sundas – Moluccas' distribution pattern.

Among the *longipennis* clade, only *C. triangulata* sp. nov. has a rather wide range in north-eastern Borneo, Malaysia, and Mindanao, the Philippines. The other species are local endemics that are respectively restricted to narrow regions. *Centromeria nigroapicata* occurrs in Nias and northern Sumatra, Indonesia; *C. maculata* sp. nov. is found in north-eastern Borneo, Malaysia; and the remaining species (*C. cuspidata* sp. nov., *C. deckerti* sp. nov., *C. melichari* sp. nov., *C. inflata* sp. nov., *C. spinosa* sp. nov., and *C. longipennis*) are endemic in the Philippine Islands. The second clade adheres to a 'northern Sumatra – northern Borneo – Philippines' distribution track, from west to east.

ORIGIN AND DIVERSIFICATION OF *CENTROMERIA*

The distribution patterns displayed by *Centromeria* are largely concordant with its phylogenetic relationship revealed by the present study, revealing the origin and diversification of this genus. *Centromeria* should originate somewhere in the Indo-Australian Archipelago (IAA), most likely Sundaland (the Malay Peninsula, Sumatra, Java, and Borneo). The IAA, also known as Malesia or the Malay Archipelago, is the most geographically complex tropical region on Earth, where it has a diverse and highly endemic biota (Lohman *et al.*, 2011). Sundaland is further considered as one of the eight hottest hotspots of global biodiversity (Myers *et al.*, 2000). There has been a high level of endemism in Sundaland fauna and flora, including masses of endemic dictyopharid species, such as the genera *Miasa*, *Leprota*, and *Metaurus* within Orthopagini, suggesting that this region could be a centre of speciation and diversification of Orthopagini (Song & Liang, 2012a; Song *et al.*, 2012, 2014).

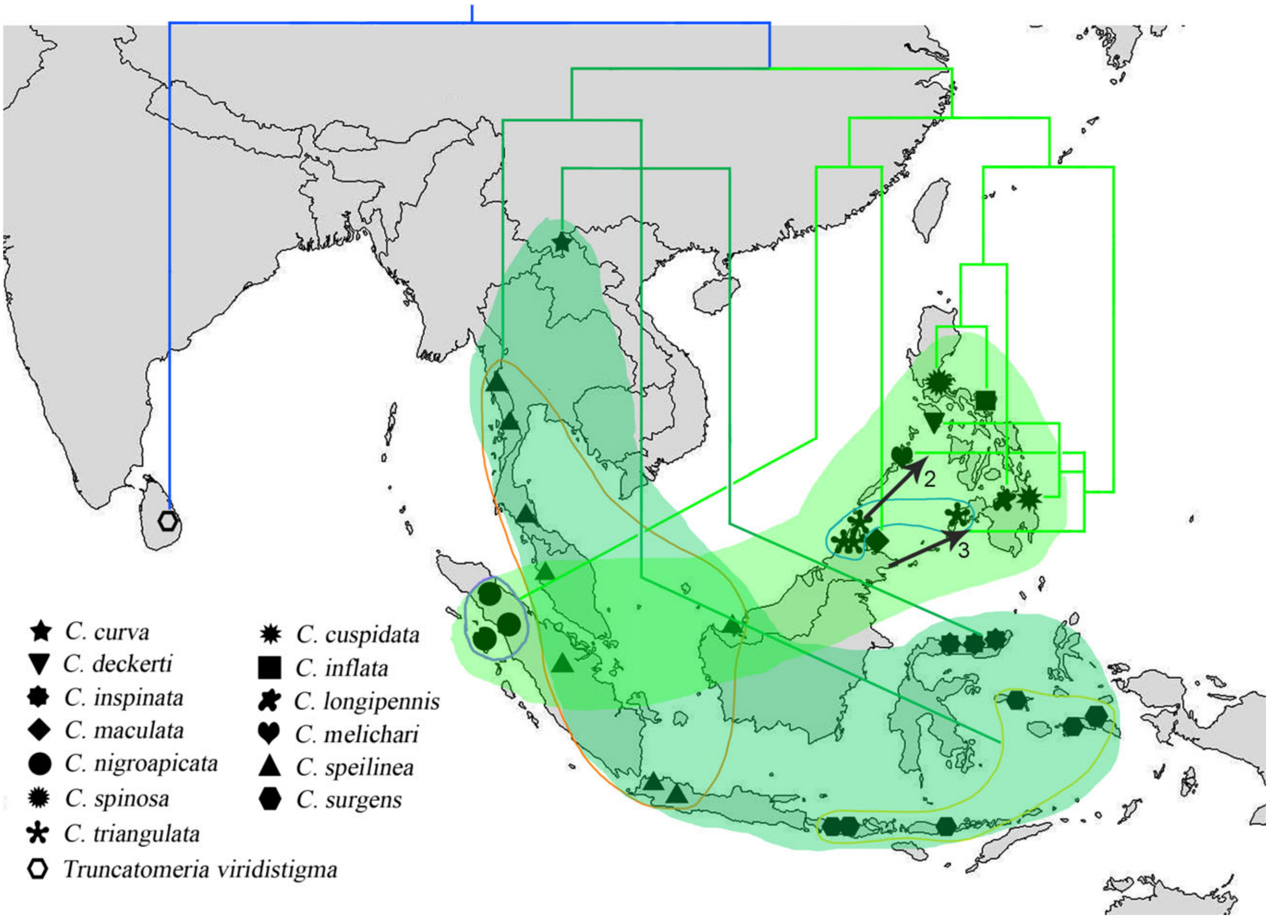

Figure 12. Geographical distribution of two *Centromeria* lineages mapped onto the phylogenetic tree, showing two distribution tracks.

As fossil and molecular data have not been gathered, it is difficult to estimate the separation time of two *Centromeria* clades. Some geographical events that occurred in the IAA are likely to be associated with the biogeographical patterns exhibited by *Centromeria*. For example, *C. surgens* was separated from *C. speilinea* within the *speilinea* clade by dispersal from Java to the Lesser Sundas and the Moluccas, which might have happened after the formation of both archipelagos, no earlier than the Pliocene. In the Late Miocene to Pliocene, Lombok and Sumbawa became significant volcanic centres for the last few million years, and were elevated above sea level in the relatively recent past (Hall, 2002), whereas Timor and Seram emerged in the past 2 million years from depths of several kilometers to elevations of more than 3 km (Lohman *et al.*, 2011). Most of Wallacea has been populated by plants and animals since 5 Mya (Hall, 2001), and hence the divergence between *C. surgens* and *C. speilinea* might have occured in the Pleistocene, or even later than that.

Similarly, the Philippine *Centromeria* fauna in the *longipennis* lineage had its origin in Borneo in light of our phylogenetic analysis. Thus the ancestors of ((*C. longipennis* + (*C. inflata* sp. nov. + *C. spinosa* sp. nov.)) + (*C. triangulata* sp. nov. + *C. melichari* sp. nov. + (*C. cuspidata* sp. nov. + *C. deckerti* sp. nov.))) colonizing the Philippines from north-eastern Borneo should be considered as a dispersal event also. The Philippine Islands, as well as the Lesser Sundas, lie adjacent to the continental Sunda Shelf, yet most of them, with the exception of Palawan and Mindoro, have never been directly attached to the Eurasian landmass. The isolation of the Philippines allowed it to develop its unique fauna and flora, thus explaining its high level of endemism, although its formation history was very complex (Hall, 2002, 2012). In the Pleistocene, many submerged lands in the IAA, defined by the 120–m bathymetric line, could have been exposed during the most recent glaciations (Heaney, 1986). The falling sea level caused many adjacent islands to temporarily merge into a single large island, which contributed signifi-

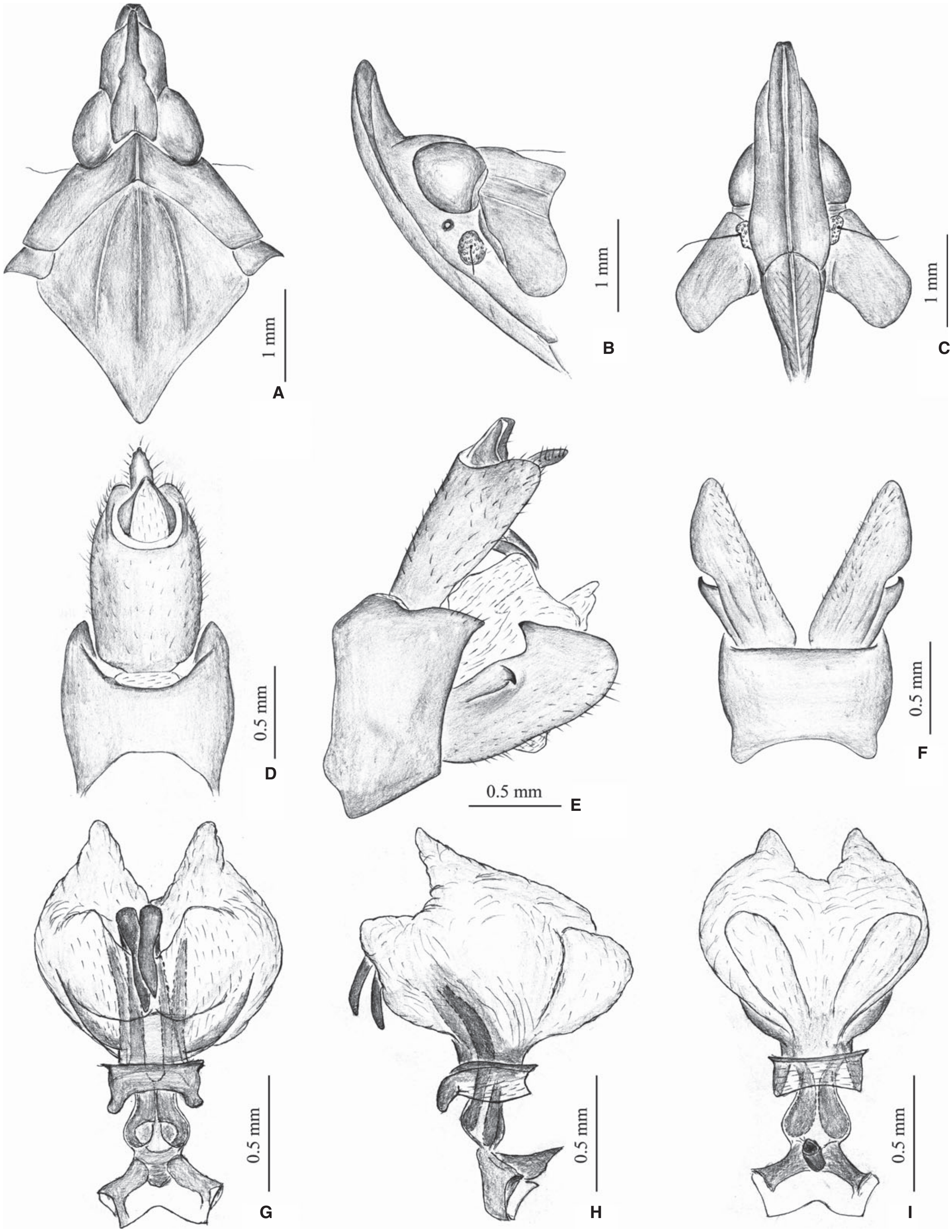

Figure 13. *Centromeria curva* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head and pronotum, ventral view; D, male pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

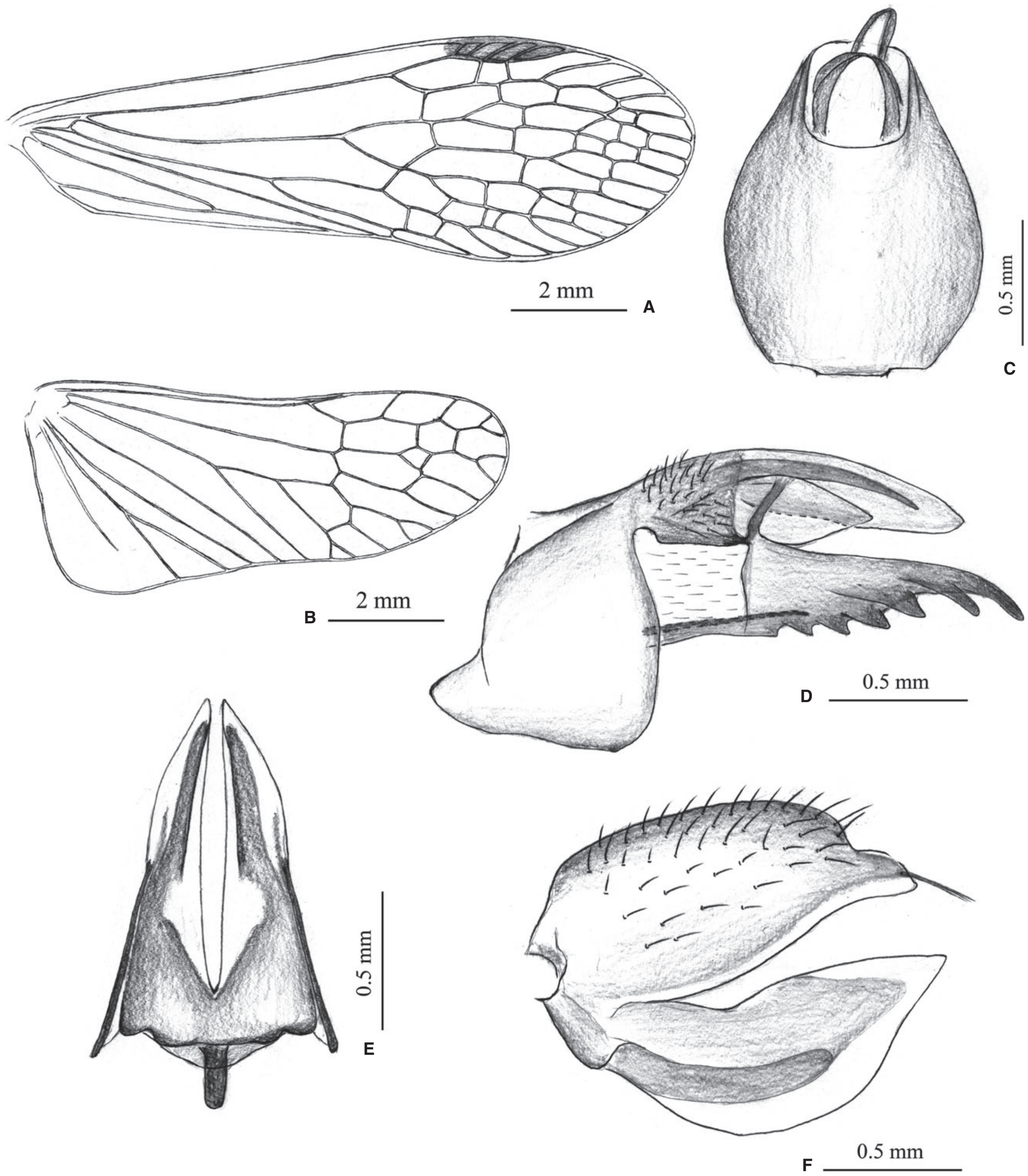

Figure 14. *Centromeria curva* sp. nov.: A, tegmen; B, hindwing; C, female segment X, dorsal view; D, gonapophysis VIII, dorsolateral view; E, gonapophysis IX, ventral view; F, gonoplacs, ventrolateral view.

cantly to terrestrial dispersal between islands that are currently separated (Lohman *et al.*, 2011). These changes could provide many chances to make the ancestors of Philippine *Centromeria* disperse to the Philippine Islands, although the dictyopharid species are not supposed to possess the ability of long-distance dispersal. In addition, the historical dispersal of *Centromeria* species to adjacent islands might also

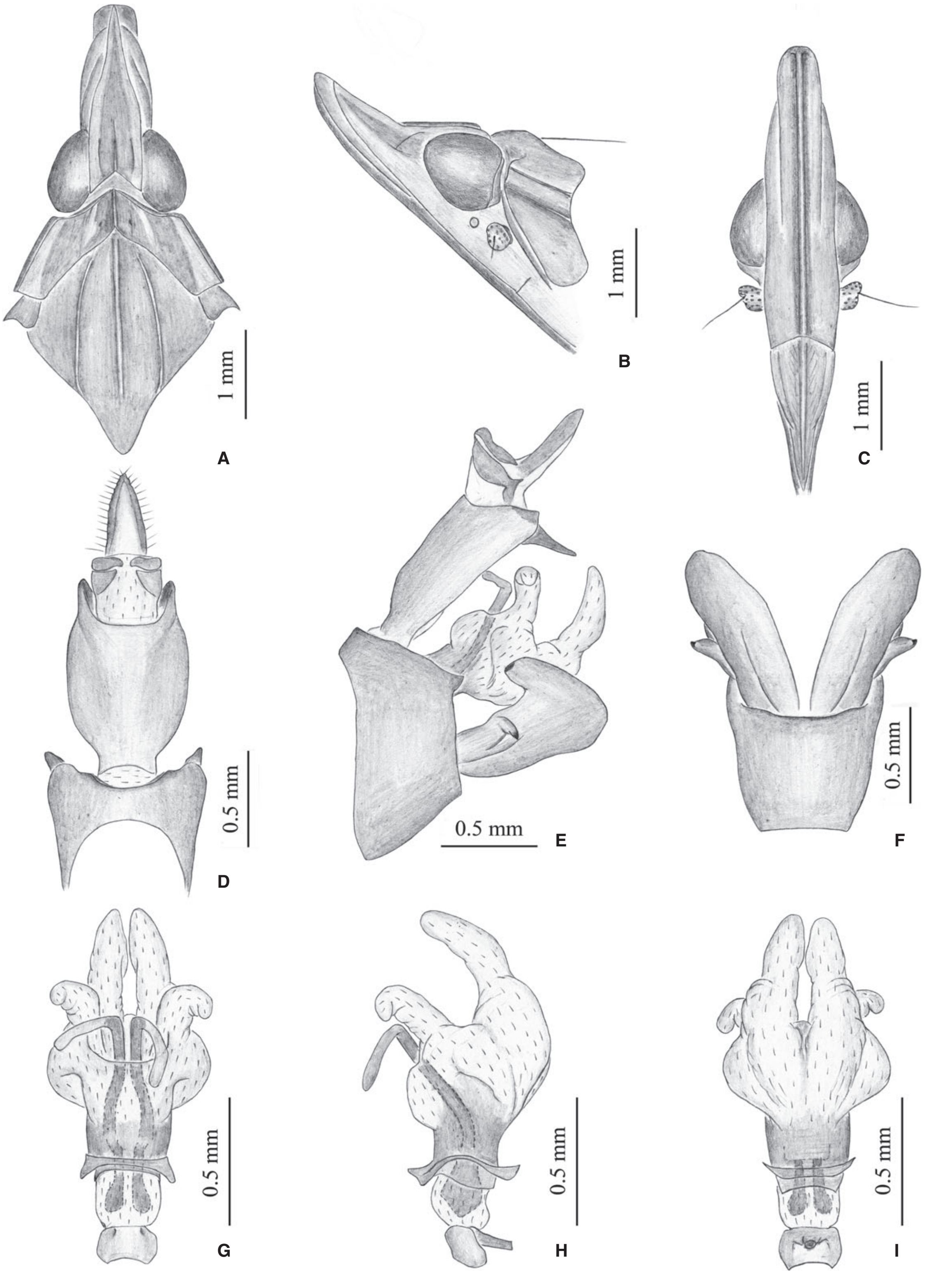

Figure 15. *Centromeria cuspidata* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

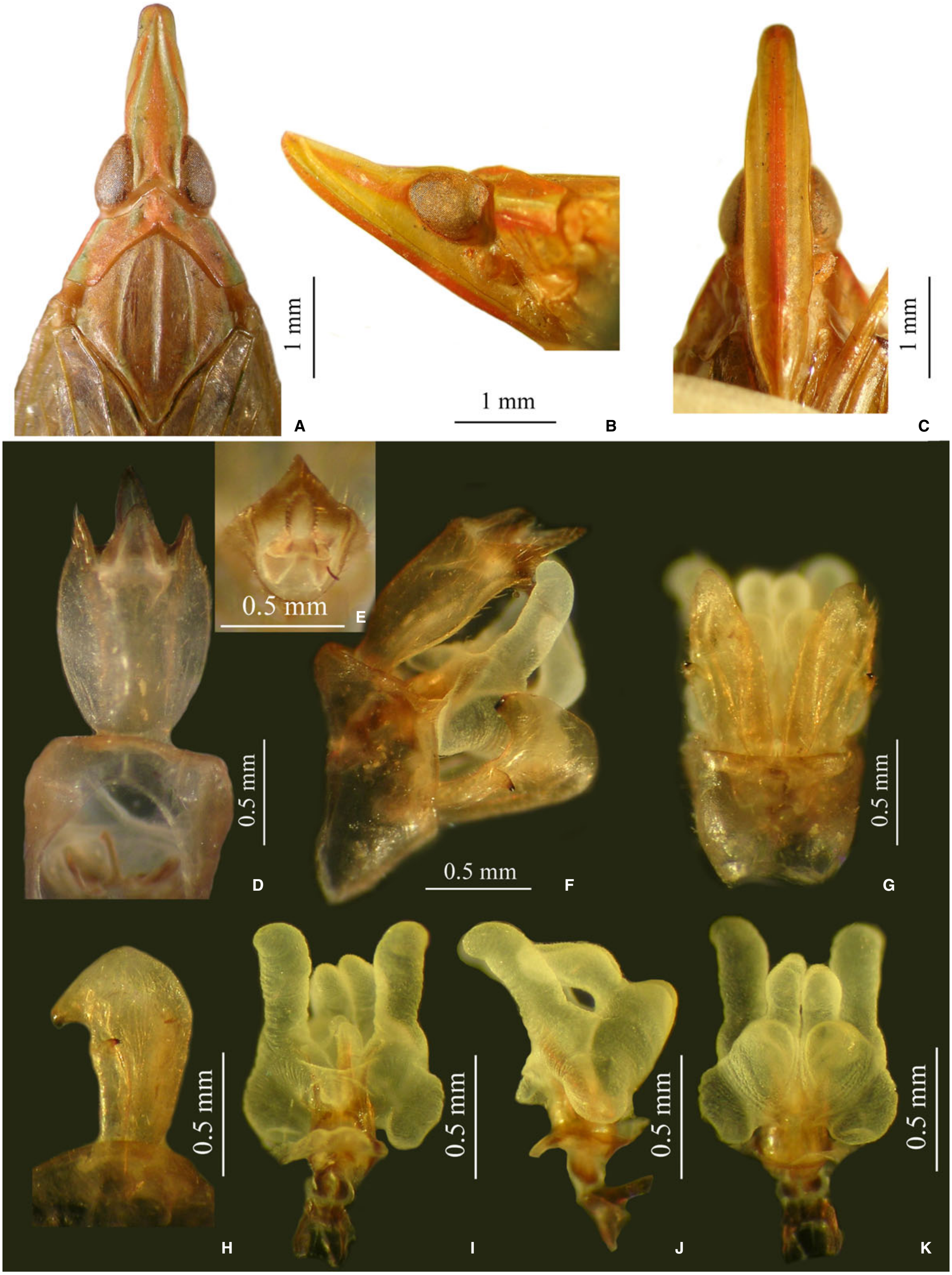

Figure 16. *Centromeria deckerti* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male pygofer and segment X, dorsal view; E, segment X, caudal view, showing apical ventral margin projecting a triangular process; F, male genitalia, lateral view; G, male pygofer and gonostyles, ventral view; H, gonostyle; I, aedeagus, dorsal view; J, aedeagus, lateral view; K, aedeagus, ventral view.

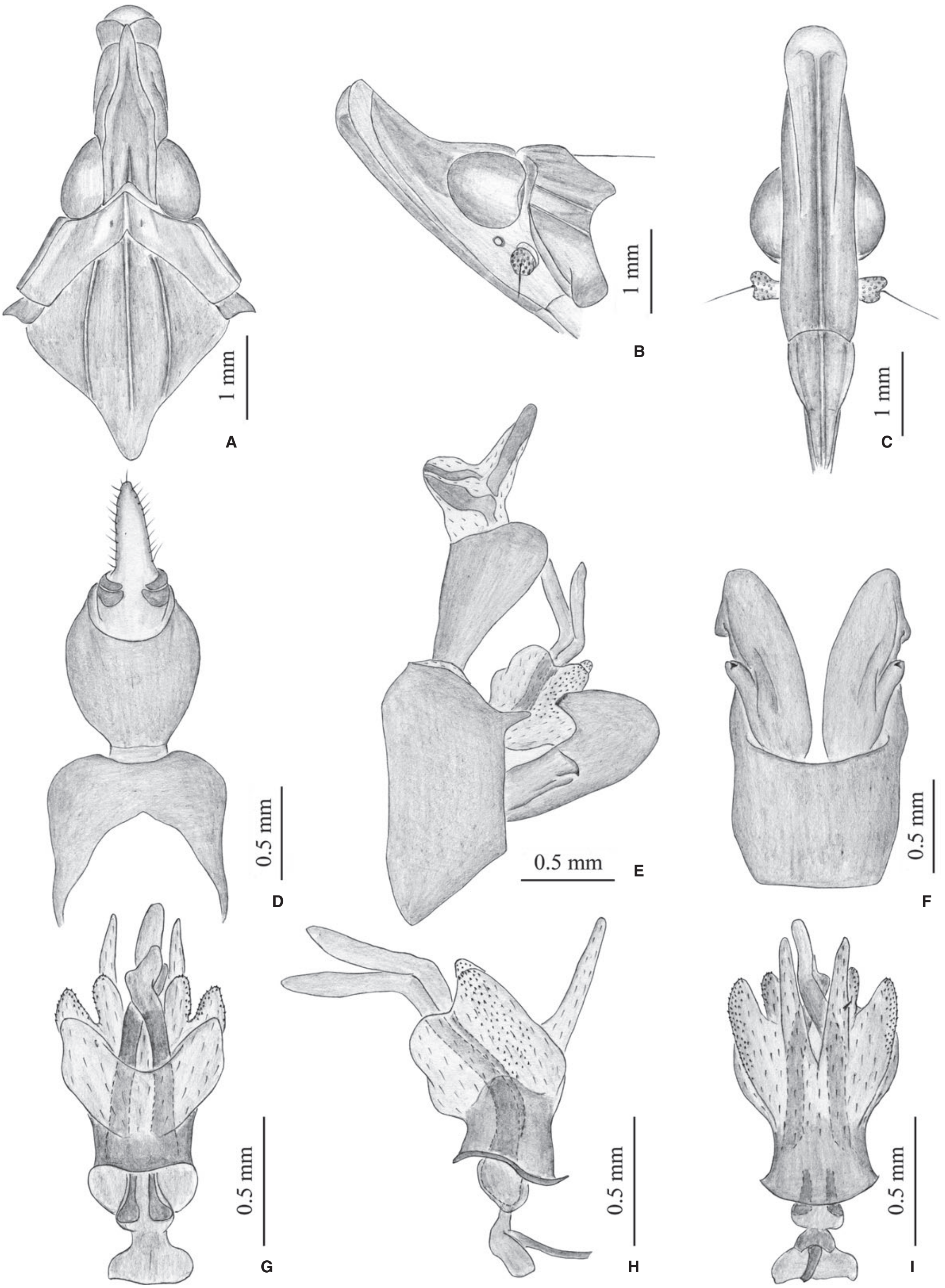

Figure 17. *Centromeria inflata* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

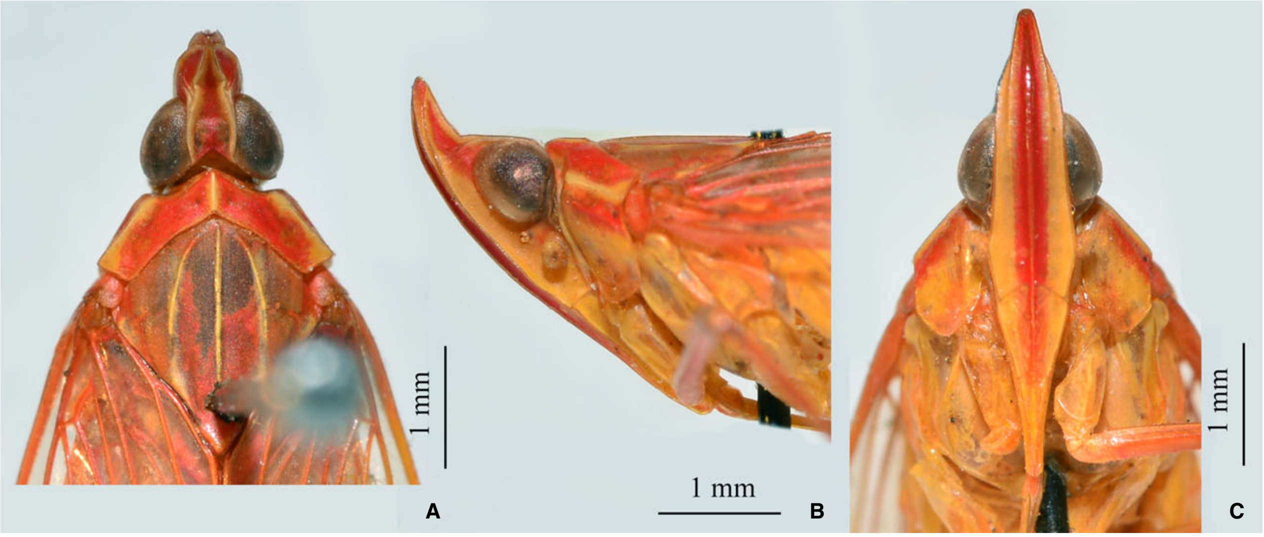

Figure 18. *Centromeria inspinata*: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view.

have been promoted by drifting floating vegetation of host plants along oceanic currents, resulting in the passive transport of adults, nymphs, and/or eggs inserted in the tissues of host plants, like the Philippine treehoppers (Su *et al.*, 2014), or by wind-assisted migration, as has been observed in the migratory planthoppers (Anderson *et al.*, 2010).

There are two colonization routes that might explain the origin of the Philippine fauna and flora by disperdal from Borneo to the Philippines: crossing either the Palawan (route 2) or the Sulu (route 3) archipelagos (Dickerson, 1928; Jones & Kennedy, 2008: fig. 1). In the *longipennis* lineage, *C. triangulata* sp. nov. is distributed in both north-eastern Borneo and north-western Mindanao, but is not found in Palawan, and *C. cuspidata* sp. nov. is recorded in Mindanao, whereas its sister groups, *C. melichari* sp. nov. and *C. deckerti* sp. nov., are restricted to Palawan and Mindoro, respectively. These distribution patterns implied that the colonization and diversification of this Philippine group probably occurred from north-eastern Borneo, either via the Sulu Islands to Mindanao, and then north to Luzon, or via Palawan to Mindoro, and then north to Luzon, approximating routes 2 and 3 of the four colonization routes to the Philippines (Fig. 12; Dickerson, 1928; Jones & Kennedy, 2008).

As most Philippine *Centromeria* (*C. cuspidata* sp. nov., *C. deckerti* sp. nov., *C. melichari* sp. nov., *C. inflata* sp. nov., *C. spinosa* sp. nov., and *C. longipennis*) are insular species on individual Philippine islands, vicariance also played a significant role in the course of speciation of Philippine *Centromeria* after their ancestrors dispersed into the Philippines. In the interglacial periods the glaciers melted, thereby disconnecting these islands. The distribution area of some *Centromeria* species and their ancestors was easily disrupted into disjunct distribution patterns, which in turn might have resulted in speciation events. For instance, divergences of (*C. inflata* sp. nov. + *C. spinosa* sp. nov.) from *C. longipennis*, and (*C. cuspidata* sp. nov. + *C. deckerti* sp. nov.) from *C. triangulata* sp. nov., could be driven by vicariance.

In summary, the origin and diversification centre of the genus is possibly located in Sundaland. The common ancestor of *Centromeria* possibly evolved later than ancestors of other Orthopagini genera when Sundaland was a conjunctive landmass. Some diversification events were likely to occur in the last few million years when those oceanic islands in Southeast Asia, such as the Lesser Sundas, the Moluccas, and the Philippines, were present or connected with Sundaland. Dispersal and vicariance both played a role in the evolutionary history of *Centromeria*, yet dispersal seemed more important in the initial phase. Similar cases include the cicada subtribe Cosmopsaltriina that dispersed initially from Southeast Asia to the West Pacific Islands (Duffels & Turner, 2002), the cixiid planthopper tribe Bennini in Southeast Asia (Hoch, 2013), and the origin and diversification of the leafhopper genus *Exitianus* Ball, 1929, distributed worldwide (Zahniser & Dietrich, 2015).

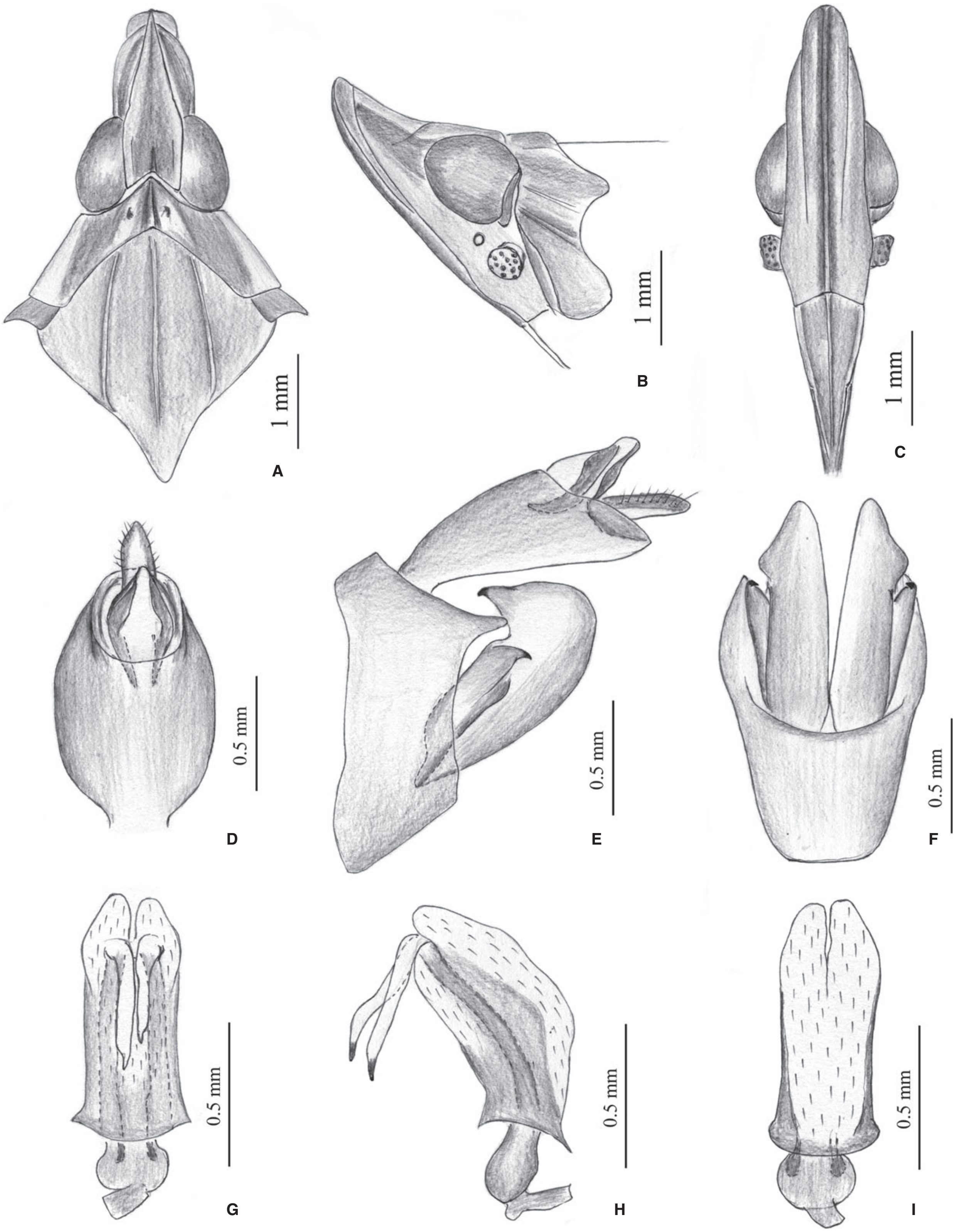

Figure 19. *Centromeria longipennis*: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

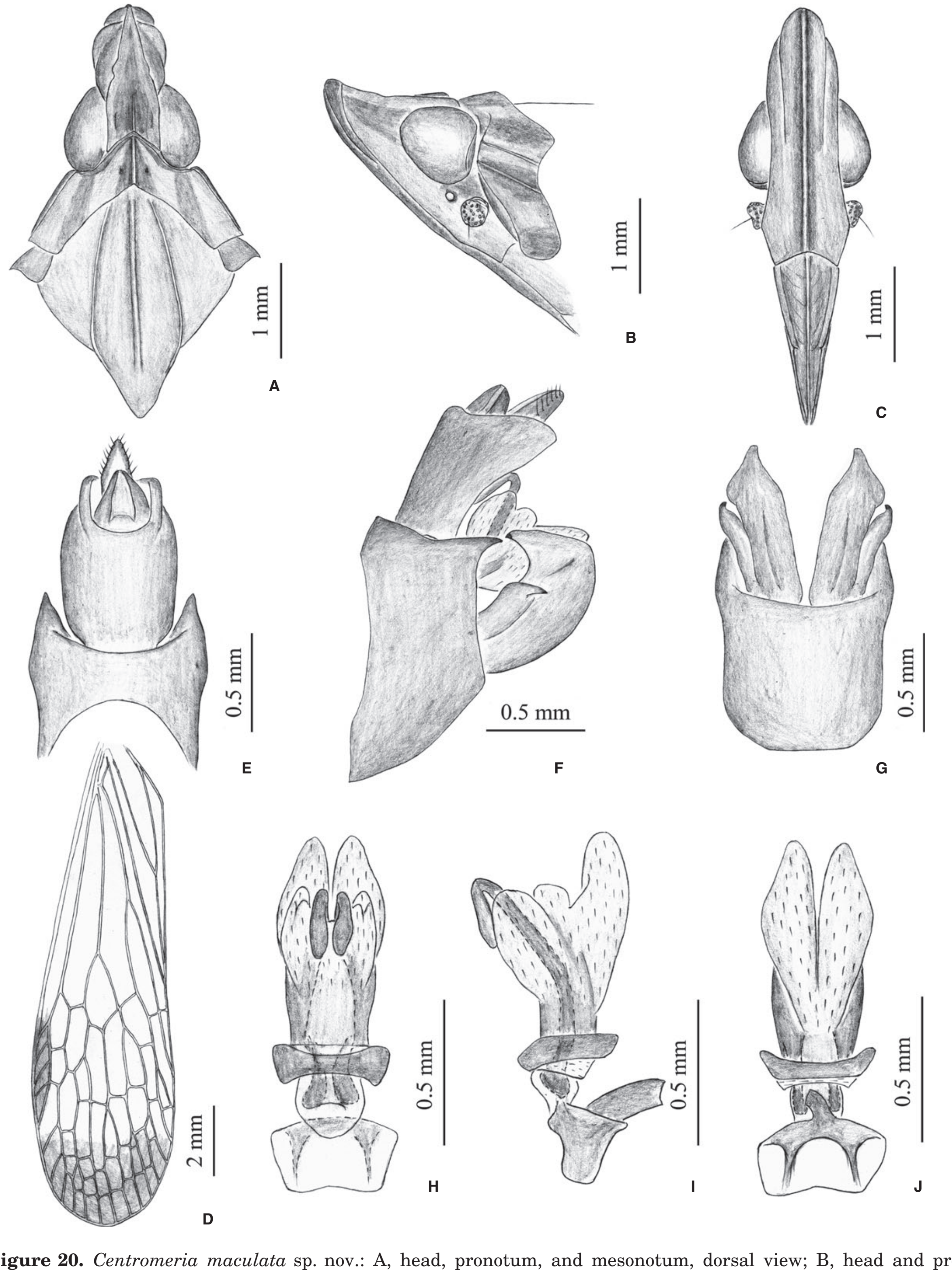

Figure 20. *Centromeria maculata* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, tegmen; E, male pygofer and segment X, dorsal view; F, male genitalia, lateral view; G, male pygofer and gonostyles, ventral view; H, aedeagus, dorsal view; I, aedeagus, lateral view; J, aedeagus, ventral view.

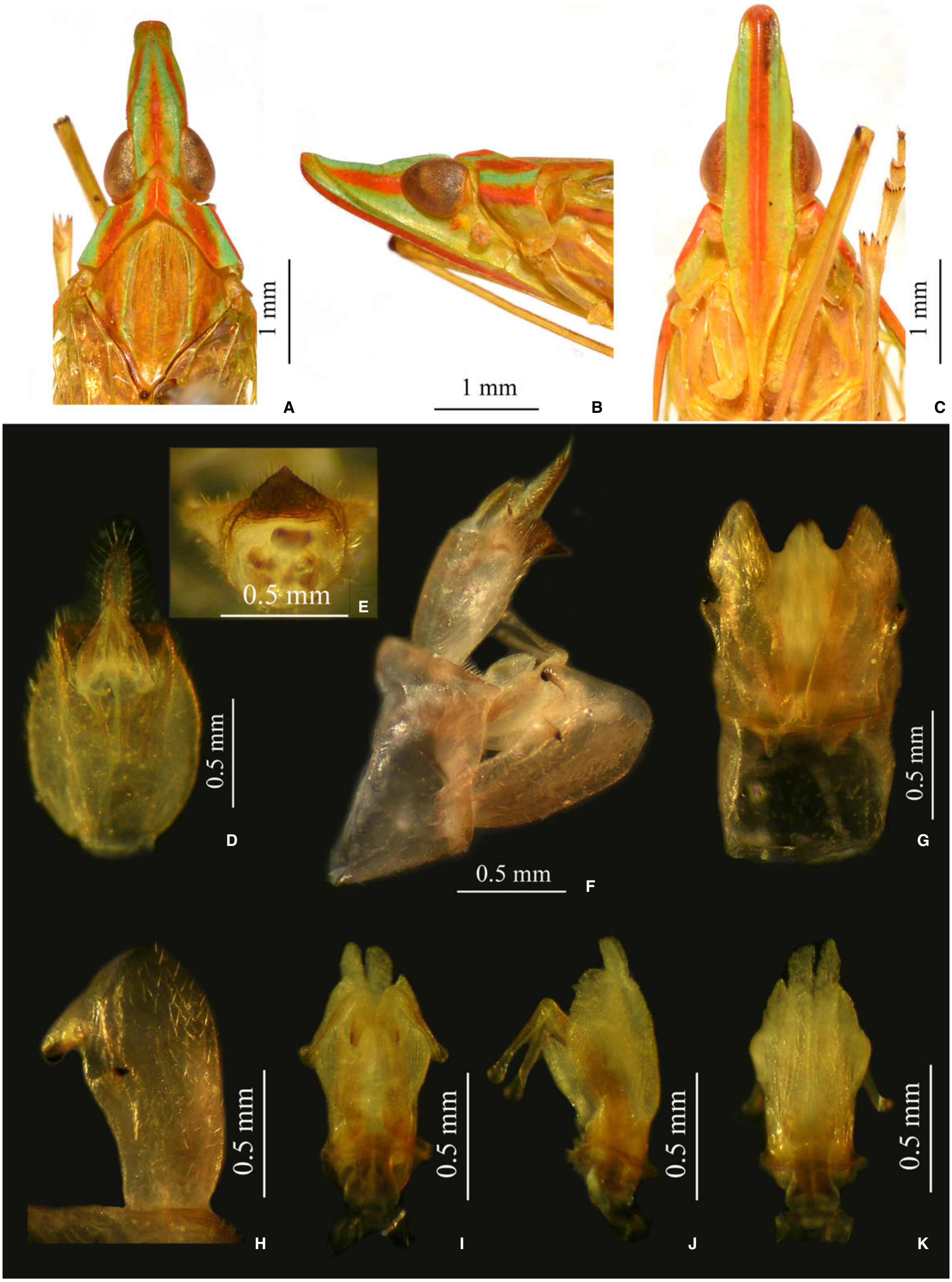

Figure 21. *Centromeria melichari* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male segment X, dorsal view; E, segment X, caudal view, showing apical ventral margin projecting a triangular process; F, male genitalia, lateral view; G, male pygofer and gonostyles, ventral view; H, gonostyle; I, aedeagus, dorsal view; J, aedeagus, lateral view; K, aedeagus, ventral view.

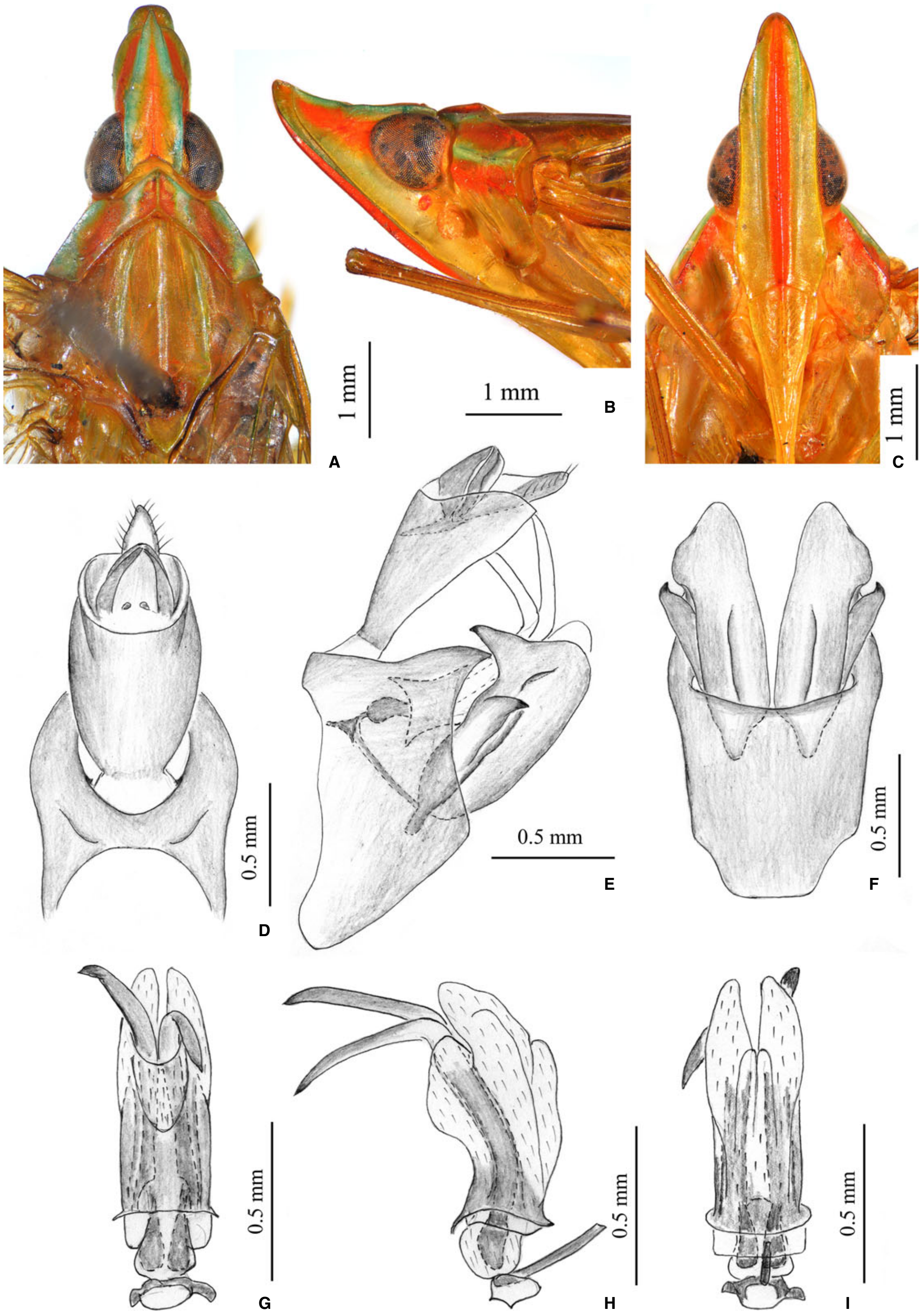

Figure 22. *Centromeria nigroapicata*: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

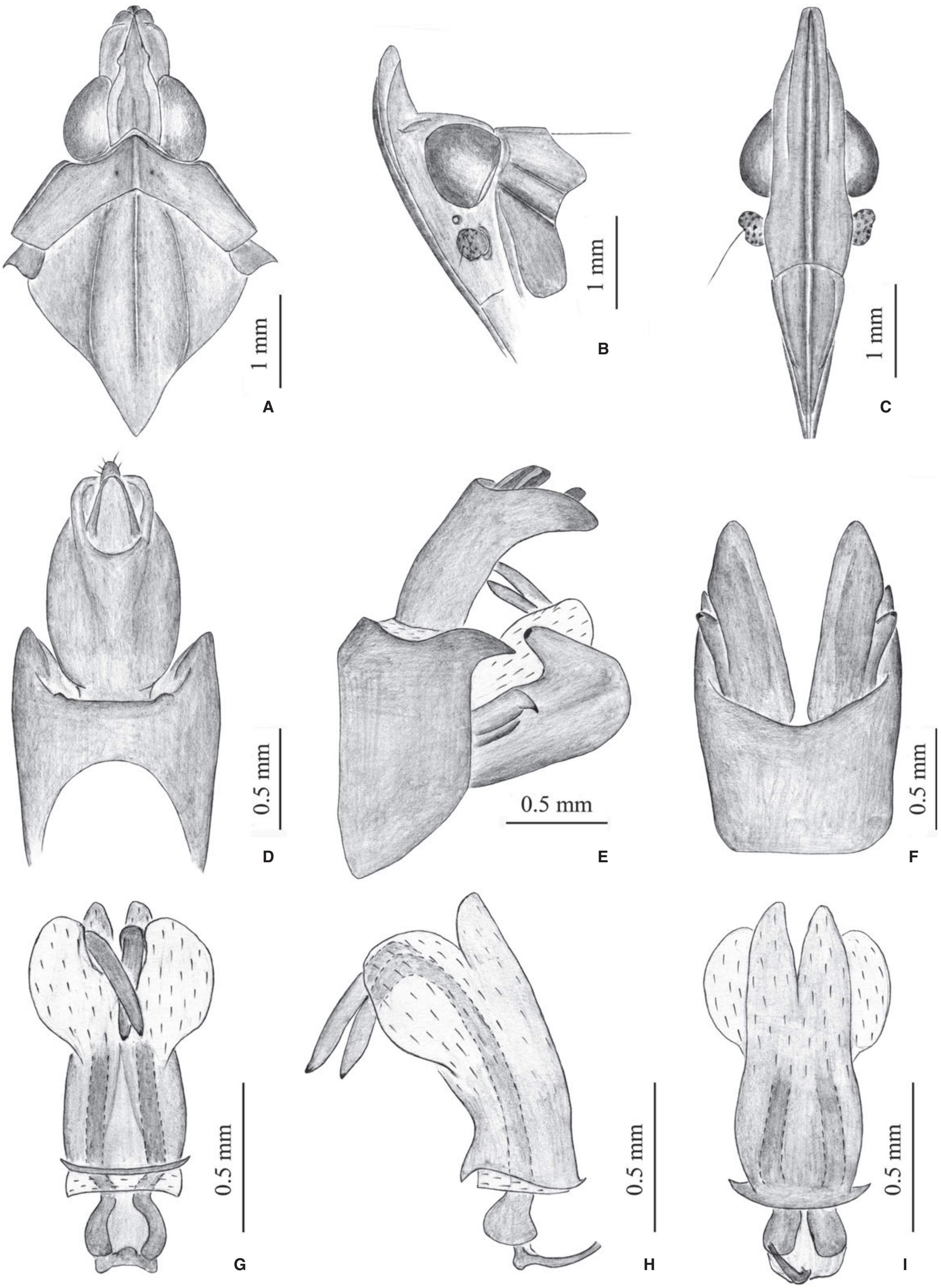

Figure 23. *Centromeria speilinea*: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

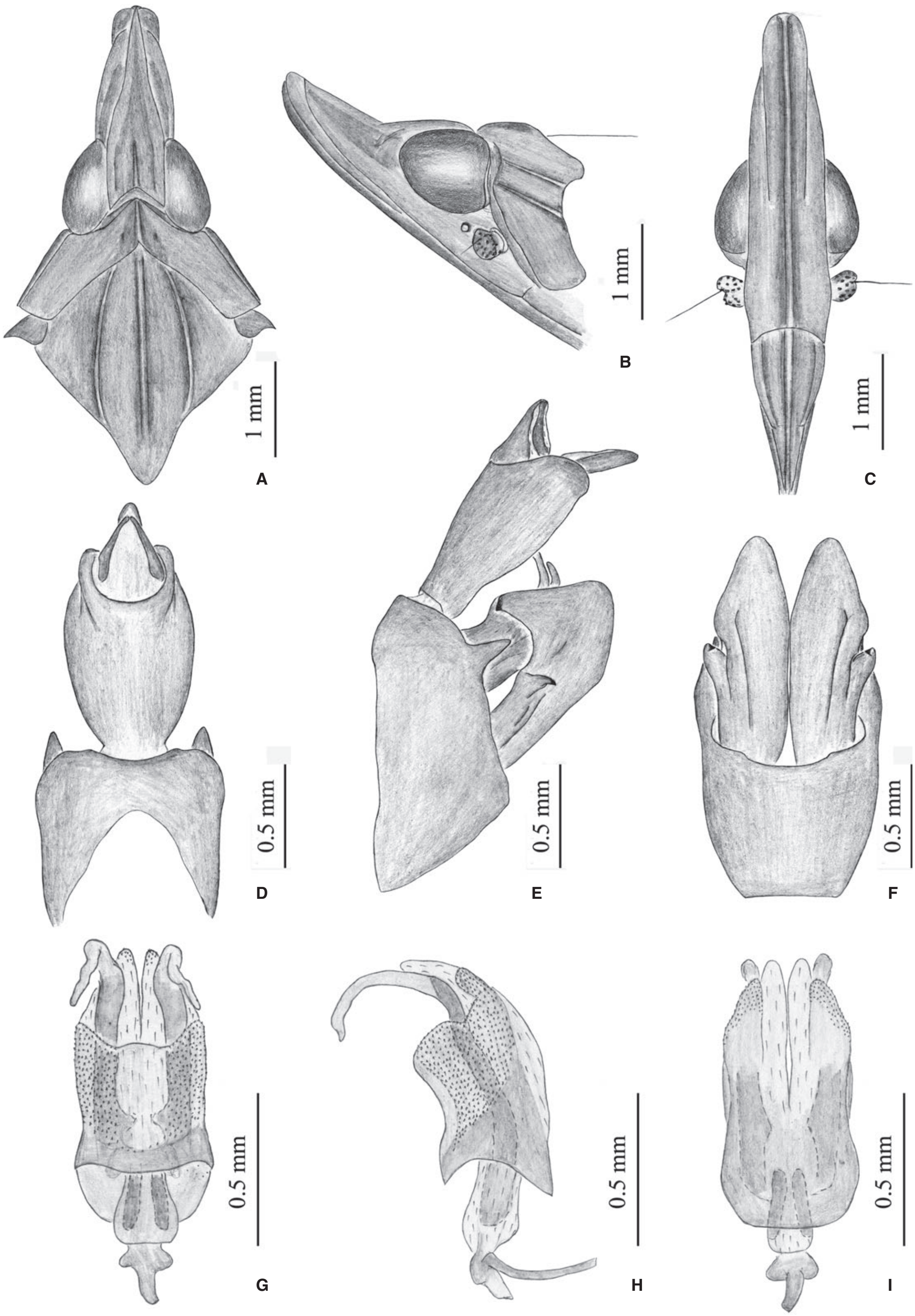

Figure 24. *Centromeria spinosa* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

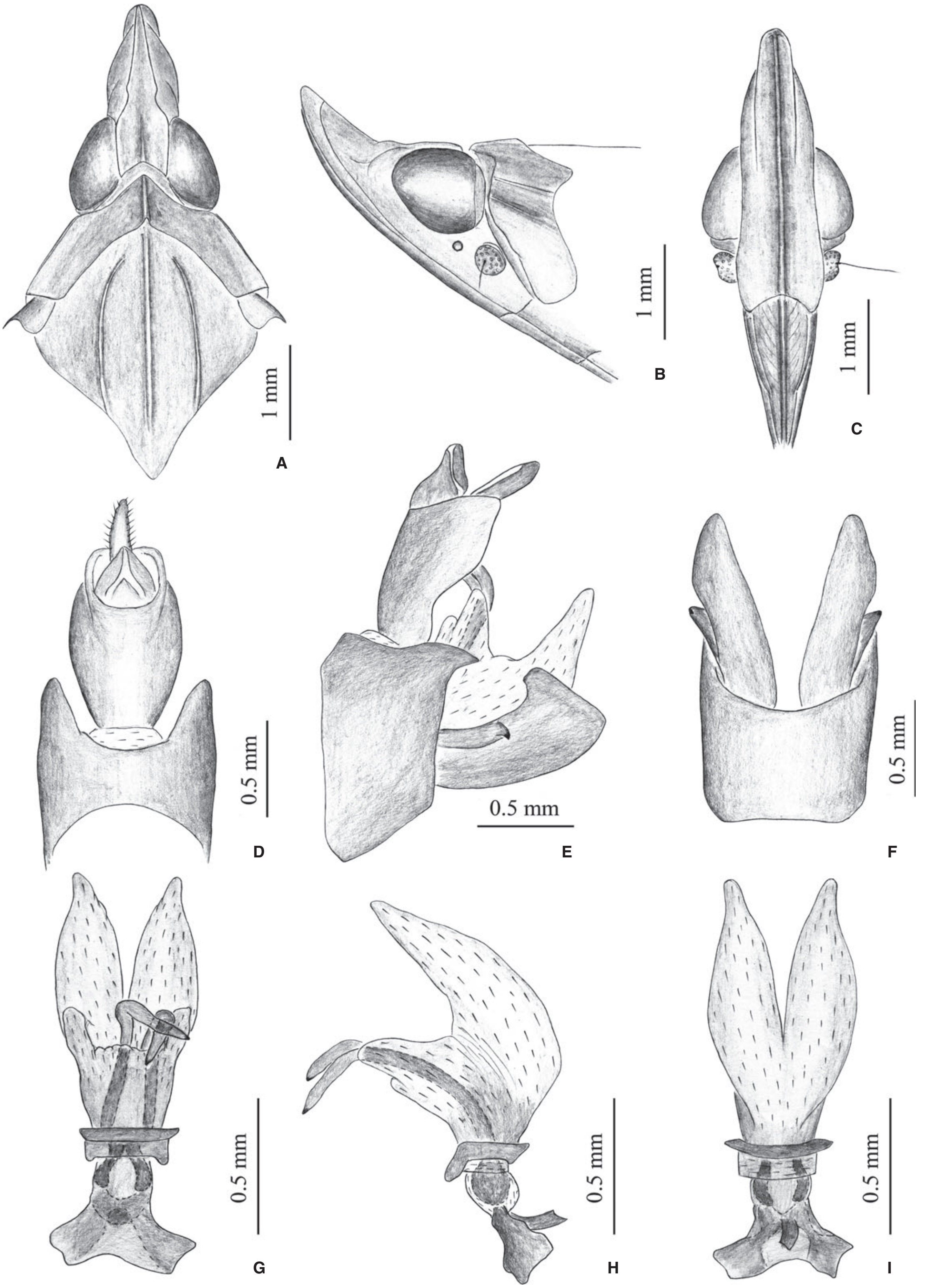

Figure 25. *Centromeria surgens*: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, male pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, male pygofer and gonostyles, ventral view; G, aedeagus, dorsal view; H, aedeagus, lateral view; I, aedeagus, ventral view.

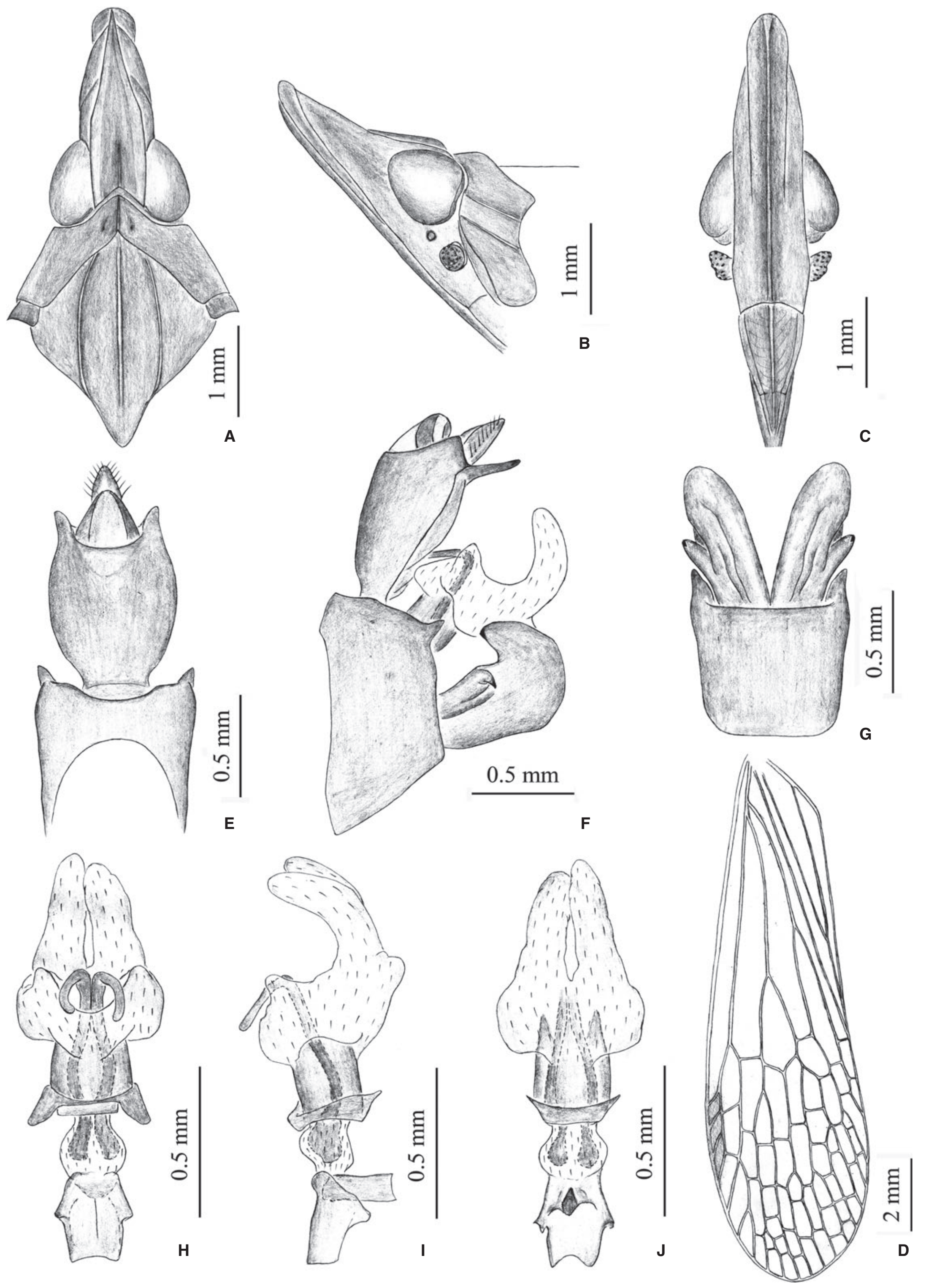

Figure 26. *Centromeria triangulata* sp. nov.: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, tegmen; E, male pygofer and segment X, dorsal view; F, male genitalia, lateral view; G, male pygofer and gonostyles, ventral view; H, aedeagus, dorsal view; I, aedeagus, lateral view; J, aedeagus, ventral view.

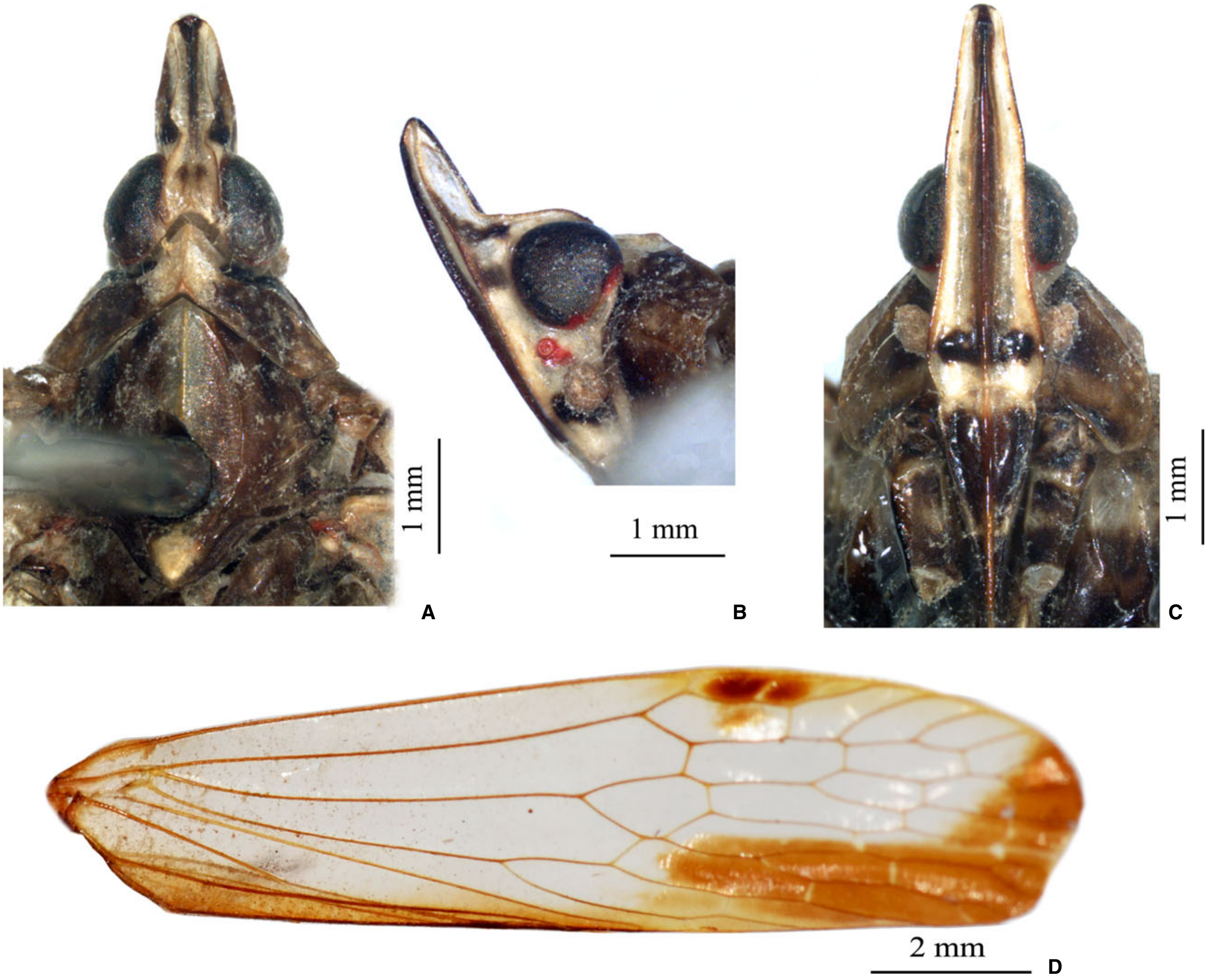

Figure 27. *Dictyomeira simulata*: A, head, pronotum, and mesonotum, dorsal view; B, head and pronotum, lateral view; C, head, ventral view; D, tegmen.

TAXONOMY

ORTHOPAGINI EMELJANOV, 1983

Orthopagini Emeljanov, 1983: 306, 2011b: 1124; Song *et al.*, 2014: 140.

Type genus. Orthopagus Uhler, 1896; by original designation.

Diagnosis (for macropterous taxa only). The tribe can be distinguished by the following combination of characters: cephalic process with length, thickness, curvature, and general shape diverse and various; pronotum with paranotal lobes without carina; mesonotum tricarinate, with lateral carinae gradually incurved and generally convergent; tegmina macropterous, with one folding line between MP_3 and MP_4, ScP+R and MP originating from basal cell without common stem or with a very short common stem; stigmal area present; clavus closed, claval suture extending to posterior margin; anal area of hindwings developed, with secondary fold; fore femora usually with a spine on ventral subapical area, fore and middle tarsomeres I and II usually with two acutellae; aedeagus with apical lobes of phallobase spineless or with very short small spines; and female gonapophyses VIII with ACL with more than five teeth from base to tip, varying in size and shape, gonoplacs with a sensory appendage of Gp1, without the third additional lobes.

Diversity and distribution. The tribe Orthopagini contains 22 genera mainly distributed in the Old World tropics and subtropics, including Sub-Saharan Africa, India, Sri Lanka, southern China, Indochina, Malay Peninsula, the Greater Sundas, the Lesser Sundas, the Philippines, the Moluccas, and northern

Australia. In the Palaearctic region, only the fossil *Alicodoxa* nymphs were found in Rovno and Baltic amber, and some *Orthopagus* and *Saigona* species spread to the eastern Palaearctic region.

Remarks. A total of 14 extant Orthopagini genera in the Oriental region are recognized and reviewed cladistically in this study, whereas the other seven Afrotropical and Australian taxa are not involved in this study because of the lack of research material. Within Orthopagini, four brachypterous genera distributed in the Australian and Afrotropical regions, *Ellipoma*, *Fernandea*, *Macronaso*, and *Nesolyncides*, should be revised further, especially focusing on the male and female genitalia structures, before they are added in the phylogenetic analysis of the world Orthopagini.

A key to the genera of Oriental Orthopagini is modified from our previous study (Song *et al.*, 2014).

KEY TO THE GENERA OF ORIENTAL ORTHOPAGINI

1. Cephalic process in front of eyes distinctly elongate, as long as or much longer than length of mesonotum (Fig. 3E, F, H, J, K)…2
– Cephalic process in front of eyes short, much shorter than length of mesonotum (Figs 1A, C–E, 2, 3A–D, G, I, L, M)…6
2. Cephalic process in front of eyes abruptly strongly constricted, forming a very slender linear process (Fig. 3H)…*Miasa* Distant, 1906
– Cephalic process in front of eyes not constricted and distinctly robust…3
3. Fore femora flattened and dilated, with a large blunt spine near apex…*Saigona* Matsumura, 1910
– Fore femora not flattened and dilated, with a small acute spine near apex…4
4. Cephalic process truncated cone shaped (Fig. 3F); vertex with lateral carinae converging forwards…*Medeusa* Emeljanov, 2011b
– Cephalic process cylindrical (Fig. 3E, J); vertex with lateral carinae subparallel…5
5. Tegmina with numerous netted transverse veins on apical one-fifth area; hind tibiae with eight apical teeth…*Leprota* Melichar, 1912;
– Tegmina with fewer transverse veins on apical one-fifth area; hind tibiae with six apical teeth…*Protolepta* Melichar, 1912
6. Tegmina with MP first bifurcating into MP_{1+2} and MP_{3+4} near basal one-third; numerous netted transverse veins among ScP+R, MP, and CuA on apical two-thirds (Fig. 3G)… *Metaurus* Stal, 1866
– Tegmina with MP first bifurcating into MP_{1+2} and MP_{3+4} near or posterior to middle; fewer transverse veins on apical two-thirds…7
7. Tegmina with a large sublunate fuscous streak on posterior margin of apical area…8
– Tegmina without sublunate fuscous streak on posterior margin of apical area…10
8. Cephalic process in front of eyes unbent; fore femora flattened and dilated, with a large blunt spine near apex (Fig. 5A)…*Orthopagus* Uhler, 1896
– Cephalic process in front of eyes strongly curved upwards; fore femora not flattened and dilated, with a small acute spine near apex…9
9. Pronotum with anterolateral angles rounded, two lateral carinae too obscure to be visible (Fig. 3D)…*Indomiasa* Song *et al.*, 2014
– Pronotum with anterolateral angles angulated, two lateral carinae distinct and complete (Fig. 27A–C)…*Dictyomeria* gen. nov.
10. Hind tibiae with six apical teeth…*Centromeria* Stål, 1870
– Hind tibiae with eight apical teeth…11
11. Frons with median carina robust and strongly produced…*Truncatomeria* Song & Liang, 2011a
– Frons with median carina moderately ridged…12
12. Apex of vertex between lateral carinae acuminate (Fig. 1C)…*Tenguna* Matsumura, 1910
– Apex of vertex between lateral carinae more or less truncate (Fig. 3B, C)…13
13. Male segment X with apical lateral margins strongly projecting posteriorly…*Dictyotenguna* Song & Liang, 2012b
– Male segment X with apical lateral margins not projecting…*Dictyopharina* Melichar, 1903

CENTROMERIA STÅL, 1870

Centromeria Stål, 1870: 745; Distant, 1906: 250; Melichar, 1912: 41; Metcalf, 1946: 36.

Type species. Dictyophora [*sic*] *longipennis* Walker, 1851; by original designation.

Diagnosis. The genus may be distinguished by the following combination of characters: cephalic process in front of eyes moderately to strongly curved upwards; vertex with lateral carinae moderately or abruptly constricted, and moderately or strongly upturned in front of eyes, then gradually convergent anteriorly, and acuminate at apex; frons with median carina robust and strongly convex, intermediate carinae extending to middle of eyes; rostrum very long, extending beyond apex of hind femora; pronotum with median carina sharp and complete, intermediate carinae indistinct; legs very slender and elongate; fore femora not flattened and dilated, with a minute spine near apex or spine absent; hind tibiae with six apical teeth; aedeagus with paired membranous inflated apical lobes covered with numerous minute spines or without spines.

Description. General colour virescent in fresh specimens and greenish ochraceous in dried ones, marked with bluish green and purplish red or reddish ochraceous on head and thorax (Fig. 1D, E). Vertex with lateral carinae, genae beneath eyes and frons pale green or bluish green, basal disc of vertex, preocular field, and broad median carina of frons reddish ochraceous. Pronotum reddish ochraceous, upper lateral margins and median carina pale green or bluish green in *speilinea* clade, or intermediate carinae pale green or bluish green but median carina reddish ochraceous in *longipennis* clade. Tegmina and hindwings hyaline, venation fuscous brown, stigmal area virescent to ochraceous. Thorax ventrally pale green. Legs testaceous, tip of femora black; tarsi piceous. Abdomen above and beneath virescent or greenish ochraceous.

Head (Fig. 1D, E) produced in a moderately long and slightly slender cephalic process. Cephalic process (Figs 13A–C, 16A–C) in front of eyes moderately to strongly curved upwards, gradually narrowed towards apex. Vertex (Figs 13A, 16A) broadest at base, posterior plane elevated above pronotum; lateral carinae ridged and subparallel at base, moderately or abruptly constricted, and moderately or strongly upturned in front of eyes, then gradually convergent anteriorly, and acuminate at apex; posterior margin ridged and angularly concave at about 100°; median carina only distinct on bulge at base. Frons (Figs 13C, 16C) elongate, apical portion with intermediate carinae distinctly expanded outwards at apex, and produced anteriorly and upwards in ventral and lateral views (Figs 13B, C, 16B, C), so its apical portion of frons distinctly visible in dorsal view (Figs 13A, 16A); lateral carinae ridged, nearly parallel and slightly expanded outwards below antennae; median carina robust and strongly convex; intermediate carinae slightly converging posteriorly and approaching middle of eyes, not to frontoclypeal suture. Postclypeus and anteclypeus (Figs 13C, 16C) strongly convex at middle, with distinct median carina. Rostrum very long, surpassing apex of hind femora; basal segment distinctly longer than distal segment. Genae beyond the eyes moderately or strongly arched outwards, thence converging acuminately, so area of the obliquely lying genae clearly visible in dorsal view (Figs 13A, 16A). Compound eye oval and large. Ocelli relatively large, reddish. Antenna with very small scape; pedicel large and subglobose, with more than 50 distinct sensory plaque organs distributed over entire surface; flagellum long, setuliform.

Pronotum (Figs 13A, 16A) distinctly shorter than mesonotum medially, narrow anteriorly, broad posteriorly; anterior margin centrally angularly convex, lateral marginal areas straight and sloping with two long longitudinal carinae on each side between eyes and tegulae, posterior margin angularly concave at about 110°; median carina sharp and high, with a lateral pit on each side, intermediate carinae absent or slightly present at base. Mesonotum (Figs 13A, 16A) tricarinate, lateral carinae incurved anteriorly towards median carina. Tegmina (Figs 14A, 20D) hyaline, much longer than tail of abdomen, with ratio of length to width about 3 : 1; veins without setae; MP bifurcating into MP_{1+2} and MP_{3+4} near middle, and posterior to CuA; number of apical cells between RP and CuA, 14–16; stigmal area elongate, with between three and five cells. Legs elongate and slender, fore and middle femora distinctly elongate, hind tibiae more than twice as long as hind femora; fore femora not flattened and dilated, with a minute spine near apex or spine absent; hind tibiae with between five and eight lateral spines and six apical teeth; hind tarsomeres I with between eight and 13 apical teeth and tarsomeres II with between eight and 12 apical teeth.

Male genitalia with pygofer in lateral view distinctly wider ventrally than dorsally, posterior margin with a process, directed posteriorly (Fig. 13E); in dorsal view dorsal margin slightly excavated to accommodate segment X, dorsolateral margins angularly produced posteriorly (Fig. 13D). Gonostyles (Fig. 13E) symmetrical, base narrow, expanded towards apex, broadest subapically; upper margin with a dorsally directed, black-tipped process at apex, and outer upper edge with a ventrally directed, hook-like process near middle. Aedeagus with one pair of long endosomal processes extended from phallotheca; phallobase membranous and inflated apically, with paired lobes covered with numerous minute spines or without spines (Fig. 13G–I). Segment X in dorsal view large and broad, apical dorsal margin deeply excavated to accommodate anal style (Fig. 13D); anal style distinctly elongate and large.

Female genitalia identical to other Orthopagini genera. Gonocoxae VIII (Fig. 14D) 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 (first valvulae) with anterior connective lamina (ACL) large and sclerotized, with seven teeth of varying size and shape in lateral view (Fig. 14D). Gonapophyses IX (second valvulae) with posterior connective lamina triangular, symmetrical in ventral view (Fig. 14E), fused with the intergonocoxal plate (iGxp) at base; iGxp extended cephalad into genital cavity, forming wall of gonospiculum. Gonoplacs (third valvulae) with two lobes homologous, fused basally; lateral lobe (Gp1) large and moderately sclerotized, four long setae at apex; the posterior lobe (Gp2) membranous, containing long sclerotized plate (Fig. 14F). Segment X large and broad, broadest in middle, gradually narrowed towards apex in dorsal view (Fig. 14C).

Biology. In common with most planthopper groups, very few biological data are currently available for the species of *Centromeria*. Our collecting data show that adults of *C. curva* sp. nov. were collected from *Ardisia arborescens* (Wall.) (Myrsinaceae) which is a subshrub growing in warm temperate to tropical regions in south-western China.

Diversity and distribution. Centromeria is composed of 13 species widely distributed in the Indo-Chinese and Indo-Malayan subregions of the Oriental region and the Wallacea.

Remarks. Based on an examination of female types, *C. cephalica* is moved into *Paradictyopharina* (Dictyopharidini) and *C. simulata* is proposed as the type species for new genus *Dictyomeria* (see below).

KEY TO THE SPECIES OF *CENTROMERIA* STÅL, 1870

1. Cephalic process in front of eyes strongly upturned and ascending at no less than 45° (Figs 13B, 18B, 23B, 25B); median carina of pronotum pale green…2
– Cephalic process in front of eyes moderately upturned and ascending at no more than 30° (Figs 15–17B, 19–22B, 24B, 26B); median carina of pronotum reddish…5
2. Cephalic process in front of eyes as long as length from anterior margins of eyes to posterior margin of vertex (Fig. 18B, 23B)…3
– Cephalic process in front of eyes longer than length from anterior margins of eyes to posterior margin of vertex (Figs 13B, 25B)…4
3. Fore femora with a minute spine near apex; Malaysia (the Malay Peninsula, Borneo), Burma, Indonesia (Sumatra, Java), Thailand…*Centromeria speilinea* (Walker, 1857)
– Fore femora without spine near apex; Indonesia (N. Sulawesi)…*Centromeria inspinata* Haupt, 1917
4. Phallobase with one pair of ventral lobes elongate and V–shaped; Indonesia (Lombok, Flores, Amboina, Ceram, Sula Islands)…*Centromeria surgens* (Walker, 1870).
– Phallobase with two pairs of ventral lobes relatively short and small; China (Yunnan)… *Centromeria curva* sp. nov.
5. Phallobase with very short small spines (Figs 17H, 24H)…6
– Phallobase without spines…7
6. Frons with apex distinctly inflated and bulbous in ventral view (Fig. 17C) and clearly visible in dorsal view (Fig. 17A); the Philippines… *Centromeria inflata* sp. nov.
– Frons not inflated and bulbous at apex; the Philippines (Luzon)…*Centromeria spinosa* sp. nov.
7. Tegmina with a fuscous macula on apical region (Fig. 20D)…8
– Tegmina without fascia or macula…9
8. Cephalic process in front of eyes little longer than length from anterior margins of eyes to posterior margin of vertex; segment X in lateral view (Fig. 22E) with basal ventral margins not projecting; Indonesia (Nias, Sumatra)…*Centromeria nigroapicata* (Lethierry, 1888) comb. nov.
– Cephalic process in front of eyes as long as length from anterior margins of eyes to posterior margin of vertex; segment X in lateral view (Fig. 20E) with basal ventral margins projecting ventrally; Malaysia (Borneo)…*Centromeria maculata* sp. nov.
9. Segment X with posterior margin not projecting; the Philippines…*Centromeria longipennis* (Walker, 1851)
– Segment X with posterior margin projecting in a long triangular process (Figs 16E, 21E)…10
10. Phallobase with a pair of lateral lobes long and thumb-like, directed laterally (Fig. 15I)…11
– Phallobase without a pair of lateral lobes (Fig. 26I)…12
11. Phallobase with lateral lobes distinctly longer (Fig. 16J) and a pair of additional lateral lobes directed anteriorly (Fig. 16K); the Philippines (Mindoro)…*Centromeria deckerti* sp. nov.
– Phallobase with lateral lobes relatively shorter (Fig. 15I), without additional lobes; the Philippines (Mindanao)…*Centromeria cuspidata* sp. nov.
12. Endosomal processes of aedeagus with apex distinctly inflated and bulbous (Fig. 22J); phallobase with a pair of dorsal apical lobes; the Philippines (N. Palawan)…*Centromeria melichari* sp. nov.
– Endosomal processes of aedeagus with apex not inflated and bulbous (Fig. 26I); phallobase without dorsal lobes; the Philippines (Mindanao), Malaysia (Borneo)…*Centromeria triangulata* sp. nov.

CENTROMERIA CURVA SP. NOV.
FIGS 2A, 13A–I, 14A–F

Type specimens. Holotype: ♂, China, Yunnan, Xishuangbanna, Menglun, 800 m a.s.l., 10.ix.2004, Z.S. Song (IZCAS).

Paratypes: China, 3♂♂, 1♀, same data as holotype; 1♀, Yunnan, Yiwubanna [Xishuangbanna], Menglun, 650 m a.s.l., 28.vii.1959, Z.F. Li; 1♂, Yunnan, Xishuangbanna, Mengla, Mangzhuang, 2.viii.2004, Z.Z. Yang (all in IZCAS).

Etymology. This new species name is derived from the Latin '*curvus*', referring to its strongly upwardly curved head process.

Diagnosis. This species is very similar to *C. speilinea* in the *speilinea* clade, but can be separated from the latter by the longer cephalic process and the male genitalia, especially the different aedeagus. It may be distinguished from *C. surgens* by the phallobase with two pairs of ventral lobes.

Description. BL, ♂ 15.2–15.6 mm, ♀ 16.7–17.0 mm; HL, ♂ 1.6–1.7 mm, ♀ 1.7–1.8 mm; HW, ♂ 1.2–1.3 mm, ♀ 1.3–1.4 mm; TL, ♂ 12.3–12.5 mm, ♀ 13.6–13.9 mm.

Cephalic process in front of eyes strongly upturned and ascending at about 60°; in lateral view slightly longer than length from anterior margins of eyes to posterior margin of vertex (Fig. 13B). Vertex relatively narrow, posterior margin narrower than transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 2.8 : 1 (Fig. 13A); lateral carinae abruptly constricted and strongly upturned in front of eyes (Fig. 13A). Tegmina and hindwings as Fig. 10A, B. Fore femora with a minute spine near apex; hind tibiae with six or seven lateral spines; hind tarsomeres I with 12 or 13 apical teeth and tarsomeres II with 11 or 12 apical teeth.

Male genitalia with pygofer in lateral view large and broad, with ratio of ventral to dorsal width about 2.0 : 1; posterior process near dorsal margin elongate, robust, and curved, apex acute (Fig. 13E). Gonostyles (Fig. 13E) more or less expanded towards apex, broadest subapically, apex bluntly rounded; upper process relatively short, acute apically. Aedeagus (Fig. 13G–I) large and robust, endosomal processes extended posteriorly and curved dorsoanteriorly, apex obtuse (Fig. 13G); phallobase membranous and strongly inflated, with one pair of apical lobes short and acute, directed dorsally on ventrolateral part, and one pair of additional lobes small and rounded on ventral base (Fig. 13H, I). Segment X in lateral view large and elongate, basal ventral margin projecting ventrally (Fig. 13E), in dorsal view with ratio of length to width near middle about 1.7 : 1 (Fig. 13D).

Distribution. China (Yunnan).

CENTROMERIA CUSPIDATA SP. NOV.

FIGS 2B, 15A–I

Type specimens. Holotype: ♂, Philippines, Mindanao, Agusan, S. Francisco 10 km. SE, 12.xi.1959, L.W. Quate (BPBM).

Etymology. This new species name is derived from the Latin '*cuspis*', referring to its acuminate cephalic process.

Diagnosis. The new species is similar to *C. deckerti* sp. nov. in the *longipennis* clade, but can be distinguished from the latter by the phallobase with lateral lobes relatively shorter, without additional lobes. It may be separated from *C. triangulata* sp. nov. by the phallobase with lateral lobes much longer.

Description. BL, ♂ 18.2 mm; HL, 2.6 mm; HW, 1.7 mm; TL, 13.0 mm.

Cephalic process in lateral view relatively elongate, distinctly longer than length from anterior margins of eyes to posterior margin of vertex; moderately upturned and ascending at about 20° (Fig. 15B). Vertex relatively broad, posterior margin nearly as wide as transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 3.5 : 1 (Fig. 15A); lateral carinae moderately constricted and moderately upturned in front of eyes (Fig. 15A). Fore femora practically without discernible spine at apex; hind tibiae with seven lateral spines; hind tarsomeres I with nine or ten apical teeth and tarsomeres II with 11 or 12 apical teeth.

Male genitalia with pygofer in lateral view broad and high, with ratio of ventral to dorsal width about 3.4 : 1; posterior process near middle short and small, but stout and slightly curved, acute apically (Fig. 15E). Gonostyles (Fig. 15E) relatively small, more or less expanded towards apex, broadest subapically, apex bluntly rounded; upper process large and stout, obtuse apically. Aedeagus (Fig. 6G–I) moderately large, endosomal processes extended posteriorly and curved dorsoanteriorly (Fig. 15G); phallobase sclerotized and pigmented at base, membranous and inflated apically, with one pair of lateral lobes long and thumb-like, directed laterally, and one pair of ventral lobes longer and thumb-like, directed posteriorly. Segment X in dorsal view large and elongate, projecting an angle on each side; apical ventral margin projecting at a long triangular process (Fig. 15E), with ratio of length to width near middle about 1.6 : 1 (Fig. 15D).

Distribution. Philippines (Mindanao).

CENTROMERIA DECKERTI SP. NOV.

FIGS 2C, 16A–K

Type specimens. Holotype: ♂, [Philippines], Mindoro, Subaan (Matang) (SNSD).

Paratypes: [Philippines], 2♀♀, same as holotype (SNSD).

Etymology. The new species is named after Dr Jürgen Deckert, curator of the collection Hemimetabola at the Museum für Naturkunde, Berlin, in recognition of his kindest help and support for the first author when he visited MFNB in 2014.

Diagnosis. This species may be distinguished from *C. cuspidataa* sp. nov. by the phallobase with lateral lobes distinctly longer and a pair of additional lateral lobes directed anteriorly.

Description. BL, ♂ 17.4 mm, ♀ 16.7–17.0 mm; HL, ♂ 2.9 mm, ♀ 1.7–1.8 mm; HW, ♂ 1.2 mm, ♀ 1.3–1.4 mm; TL, ♂ 12.8 mm, ♀ 13.6–13.9 mm.

Cephalic process in lateral view elongate, distinctly longer than length from anterior margins of eyes to posterior margin of vertex; slightly upturned and ascending at about 10° (Fig. 16B). Vertex relatively broad, posterior margin nearly as wide as transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 3.6 : 1 (Fig. 16A); lateral carinae moderately constricted and moderately curved upwards in front of eyes (Fig. 16A). Fore femora with a minute spine near apex; hind tibiae with seven lateral spines; hind tarsomeres I with 12 or 13 apical teeth and tarsomeres II with 11 or 12 apical teeth.

Male genitalia with pygofer in lateral view broad and high, with ratio of ventral to dorsal width about 3.4 : 1; posterior process near middle short and small, acute apically (Fig. 16F). Gonostyles (Fig. 16F, H) relatively small, apex bluntly rounded; upper process large and stout, obtuse apically. Aedeagus (Fig. 16I–K) large, endosomal processes extended posteriorly and curved dorsoanteriorly (Fig. 16G); phallobase sclerotized and pigmented at base, membranous and inflated apically, with one pair of lateral lobes long and thumb-like, directed laterally, pair of ventral lobes slender and thumb-like, directed posteriorly, and pair of additional lateral lobes short and robust, directed anteriorly (Fig. 16I). Segment X in dorsal view large, projecting at an angle on each side; apical ventral margin projecting a triangular process (Fig. 16E), with ratio of length to width near middle about 1.5 : 1 (Fig. 16D).

Distribution. Philippines (Mindoro).

***CENTROMERIA INFLATA* SP. NOV.**

FIGS 2D, 17A–I

Type specimens. Holotype: ♂, Philippines, Camarines Sur, Mount Isarog, 500–1200 m a.s.l., 27.iv.1963, H.M. Torrevillas (BPBM).

Paratype: Philippines, 1♂, Camarines Sur, Mount Iriga, 500–600 m a.s.l., 1.iv.1962, H.M. Torrevillas (BPBM).

Etymology. This new species name is derived from the Latin '*inflatus*', referring to its distinctly apically inflated and bulbous frons.

Diagnosis. This species can be distinguished from other known *Centromeria* species by its cephalic process being inflated and bulbous apically.

Description. BL, ♂ 17.8–18.6 mm; HL, 2.7–2.9 mm; HW, 1.8–1.9 mm; TL, 13.4–14.0 mm.

Cephalic process in lateral view elongate, distinctly longer than length from anterior margins of eyes to posterior margin of vertex; moderately upturned and ascending at about 30° (Fig. 17B); apex not narrowed in front of eyes (Fig. 17A) and differing from other *Centromeria* species because of apex of frons inflated (Fig. 17C). Vertex relatively broad, posterior margin nearly as wide as transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 3.3 : 1 (Fig. 17A); lateral carinae moderately constricted and moderately upturned in front of eyes (Fig. 17A). Frons (Fig. 17C) with apex distinctly inflated and bulbous, clearly visible in dorsal view (Fig. 17A). Fore femora with a distinct minute spine near apex; hind tibiae with seven or eight lateral spines; hind tarsomeres I with ten apical teeth and tarsomeres II with between ten and 12 apical teeth.

Male genitalia with pygofer in lateral view broad and high, with ratio of ventral to dorsal width about 2.0 : 1; posterior margin with a small, narrow, and straight process near middle, apex obtuse (Fig. 17E). Gonostyles (Fig. 17E) with upper process large and stout, slightly acute apically. Aedeagus (Fig. 17G–I) moderately large, with one pair of long and stout endosomal processes extended posteriorly and curved dorsally (Fig. 17H); phallobase sclerotized and pigmented at base, membranous and inflated apically, with two pairs of ventrolateral lobes covered with numerous small and short spines (Fig. 17H, I), and one pair of ventral lobes narrow and long, directed posteriorly, without spines (Fig. 17I). Segment X in dorsal view large and broad, nearly rounded, with ratio of length to width near middle about 1.3 : 1 (Fig. 17D).

Distribution. Philippines (Camarines Sur).

CENTROMERIA INSPINATA HAUPT, 1917

FIGS 2E, 18A–C

Centromeria inspinata Haupt, 1917: 307; Metcalf, 1946: 37.

Material examined. Indonesia, 1♀, Celebes [Sulawesi], Paleleh, 15.xii.1930, G. Heinrich; 1♀, Celebes [Sulawesi], Ile-ile, 500–800 m a.s.l., Anf. xii.1930, G. Heinrich (MFNB).

Distribution. Indonesia (Sulawesi).

Remarks. This species was described by Haupt (1917) based on two female specimens from Minahassa, Celebes. We could not examine its types and identified it in the present samples based on similar external morphology and locality. The species is very similar to *C. speilinea*, but can be distinguished from the latter by the fore femora without spine near apex (Haupt, 1917).

CENTROMERIA LONGIPENNIS (WALKER, 1851)
FIGS 2F, 19A–I

Dictyophora [*sic*] *longipennis* Walker, 1851: 316. Holotype: ♂, Philippines (BMNH) (examined).

Centromeria longipennis (Walker): Stål, 1870: 745; Melichar, 1912: 43; Metcalf, 1946: 37.

Dictyophora [*sic*] *surgens* Walker, 1870: 101. Holotype: ♀, Indonesia (Amboina) (BMNH) (examined). Synonymized by Melichar, 1912: 43. (Error)

Dictyophara nigroapicata Lethierry, 1888: 467. Holotype: ♂, Indonesia (Nias) (MNHN) (examined). Synonymized by Melichar, 1912: 43. (Error)

Centromeria bicolorata Bierman, 1910: 14. Holotype ♂, Indonesia (Java) (NCB Naturalis) (examined). Synonymized by Melichar, 1912: 43. (Error)

Redescription. BL, ♂ 15.8 mm; HL, 2.1 mm; HW, 1.5 mm; TL, 12.3 mm.

Male genitalia with pygofer in lateral view narrow and high, with ratio of ventral to dorsal width about 2.4 : 1; posterior process near middle elongate, slender, and straight, obtuse apically (Fig. 19E). Gonostyles (Fig. 19E) relatively large, upper process elongate, acute apically. Aedeagus (Fig. 19G–I) small, endosomal processes extended posteriorly and curved dorsoanteriorly, apical one-third membranous, acute apically (Fig. 19H); phallobase sclerotized and pigmented at lateral sides, membranous and moderately inflated dorsally and ventrally, with one pair of ventral lobes short and small, without spines (Fig. 19H, I). Segment X in dorsal view large and elongate, with ratio of length to width near middle about 1.6 : 1 (Fig. 19D).

Type material examined. Holotype ♂ of *Dictyophora longipennis* Walker, 1851, [Philippines], Phil Isla, Type, Dictyophora longipennis (BMNH).

Other material examined. Philippines, 1♂, P.I., Misamis Or., Mount Empagatao, 1050–1200 m a.s.l., Rain forest, 19–30.iv.1961, H. Torrevillas (BPBM).

Distribution. Philippines (northern Mindanao).

Remarks. The locality for this species was given only as ‘Philippine Islands’ by Walker (1851). Melichar (1912) listed it also from Indonesia (Nias, Sumatra, and Amboina), but our results show that *C. longipennis* redescribed by Melichar (1912) was a misidentification. This species is similar to *C. nigroapicata*, but can be separated from the latter by the tegmina without fuscous spot on the apical region and the posterior process of the pygofer slender and straight, obtuse apically.

CENTROMERIA MACULATA SP. NOV.
FIGS 2G, 20A–J

Type specimens. Holotype: ♂, Malaysia, Borneo (Brit. N.), Sandakan Bay (SW), Sapagaya Lumber, Camp, 2–20 m a.s.l., 5.xi.1957, J.L. Gressitt (BPBM).

Etymology. This new species name is derived from the Latin ‘*maculatus*’, referring to its tegmina with a large fuscous spot at apex.

Diagnosis. The new species is similar to *C. nigroapicata*, but can be distinguished from the latter by the shorter cephalic process and the differences of male genitalia and segment X.

Description. BL, ♂ 14.6 mm; HL, ♂ 1.9 mm; HW, ♂ 1.6 mm; TL, ♂ 11.6 mm.

Cephalic process in lateral view distinctly short, as long as length from anterior margins of eyes to posterior margin of vertex; more or less upturned in front of eyes and ascending at no more than 10° (Fig. 20B). Vertex relatively broad, posterior margin nearly as wide as transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 2.7 : 1 (Fig. 20A); lateral carinae moderately constricted and moderately curved upwards in front of eyes (Fig. 20A). Tegmina as Fig. 20D, with a large fuscous macula at apical one-fifth. Fore femora with a minute spine near apex; hind tibiae with six lateral spines; hind tarsomeres I with nine apical teeth and tarsomeres II with nine apical teeth.

Male genitalia with pygofer in lateral view broad and high, with ratio of ventral to dorsal width about 3.8 : 1; posterior process near subapex elongate, slender, and curved, acute apically (Fig. 20F). Gonostyles (Fig. 20F) with upper process large and stout, acute apically. Aedeagus (Fig. 10H–J) moderately large, endosomal processes bent anteriorly (Fig. 20I); phallobase sclerotized and pigmented at base, membranous and inflated apically, with one pair of ventrolateral lobes small, with a pair of ventral lobes large and long, directed posteriorly, without spines (Fig. 20I, J). Segment X large and stout, in lateral view basal and apical ventral margins projecting ventrally (Fig. 20F), in dorsal view with ratio of length to width near middle about 1.2 : 1 (Fig. 20E).

Distribution. Malaysia (northern Borneo).

CENTROMERIA MELICHARI SP. NOV.
FIGS 2H, 21A–K

Type specimens. Holotype: ♂, [Philippines], N. Palawan, Binaluan, xi–xii.1913, G. Boettcher (MMBC).

Paratype: 1♀, same as holotype (MMBC).

Etymology. The new species is named after Dr Leopold Melichar, excellent entomologist and expert in Hemiptera, who revised the world Dictyopharidae in 1912.

Diagnosis. The new species is similar to *C. triangulata* sp. nov., but can be distinguished from the latter by the endosomal processes of aedeagus with apex distinctly inflated and bulbous, and the phallobase with a pair of dorsal apical lobes.

Description. BL, ♂ 14.6 mm; HL, ♂ 1.9 mm; HW, ♂ 1.6 mm; TL, ♂ 11.6 mm.

Cephalic process in lateral view elongate, distinctly longer than length from anterior margins of eyes to posterior margin of vertex; slightly upturned and ascending at about 10° (Fig. 21B). Vertex relatively broad, posterior margin nearly as wide as transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 3.4 : 1 (Fig. 21A); lateral carinae moderately constricted and moderately upturned in front of eyes (Fig. 21A). Fore femora practically without a discernible spine at apex; hind tibiae with seven lateral spines; hind tarsomeres I with nine or ten apical teeth and tarsomeres II with 11 or 12 apical teeth.

Male genitalia with pygofer in lateral view broad and high, with ratio of ventral to dorsal width about 3.7 : 1; posterior process near middle short and small, acute apically (Fig. 21E). Gonostyles (Fig. 21E) relatively small, upper process large and stout, obtuse apically. Aedeagus (Fig. 6G–I) relatively small, endosomal processes extended posteriorly and curved dorsoanteriorly, apex distinctly inflated and bulbous (Fig. 21G); phallobase sclerotized and pigmented at base, membranous and inflated apically, with one pair of small dorsal lobes between endosomal processes, and a pair of ventral lobes slender and thumb-like, directed posteriorly (Fig. 21I). Segment X large, projecting at an angle on each side; apical ventral margin projecting a triangular process (Fig. 21E), in dorsal view with ratio of length to width near middle about 1.3 : 1 (Fig. 21D).

Distribution. Philippines (N. Palawan).

CENTROMERIA NIGROAPICATA (LETHIERRY, 1888) STAT. REV., COMB. NOV.

FIGS 2I, 22A–I

Dictyophara nigroapicata Lethierry, 1888: 467. Holotype: ♂, Indonesia (Nias) (MNHN) (examined). Synonymized under *Centromeria longipennis* (Walker) by Melichar, 1912: 43, and here resurrected.

Redescription. BL, ♂ 15.6–15.7 mm, ♀ 17.1–17.4 mm; HL, ♂ 2.0–2.1 mm, ♀ 2.2–2.3 mm; HW, ♂ 1.4–1.5 mm, ♀ 1.1.7–1.8 mm; TL, ♂ 11.8–12.1 mm, ♀ 13.2–13.3 mm.

Male genitalia with pygofer large and broad, ventrally distinctly wider than dorsally (about 5.3 : 1); posterior process near dorsal margin elongate, robust and curved, apex acute in lateral view (Fig. 22E). Gonostyles relatively large, more or less expanded toward apex, broadest subapically in lateral view (Fig. 22E), apex rounded; upper process elongate, acute apically. Aedeagus (Fig. 22G–I) small, with a pair of long endosomal processes extended posteriorly and curved dorsoanteriorly (Fig. 22H); phallobase sclerotized and pigmented at lateral sides, membranous and moderately inflated dorsally and ventrally, with a pair of ventral lobes short and small, and a pair of additional smaller lobes on ventral base, without spines (Fig. 22H, I). Segment X large and elongate, with ratio of length to width near middle about 1.7 : 1 in dorsal view (Fig. 22D).

Type material examined. Holotype ♂ of *Dictyophara nigroapicata* Lethierry, 1888 (Museun Paris MNHN (EH) 22987), [Indonesia], Is. Nias, Hili Zabobo, Agosto, 1886, Modigliani; Type, [Lethierry's handwriting] *Dictyophara nigroapicata* Leth.; *Centromeria* [handwriting] (MNHN).

Other material examined. [Indonesia], 1♂1♀ (MIZ 313224, 313225), Soekaranda, i.1894, Dohrn; *Centromeria longipennis* Walk. [handwriting]; Mus. Zool. Polonicum, Warszawa, 12/45; 1♂ (MIZ 313228), 2♀♀ (MIZ 313226, 313227), Sumatra, Soekaranda, Dohrn; *Centromeria longipennis* Walk. [Schmidt's handwriting], ♀ (♂), Edm. Schmidt, determ. 1915; Mus. Zool. Polonicum, Warszawa, 12/45 (all in MIZPAS); 1♀, Sumatra, Excell. V. Studt G.; *Centromeria longipennis* Walk. (MFNB); 1♀, West Sumatra prov., Kerinci Seblat N.P., 24 km NE Tapan, 2°05′S 101°15′E, 400–550 m a.s.l., Muara Sako to E env, 4–18.iii.2003, L. Dembicky (MMBC); 1♀, Sumatra, Bandar Baroe, Mjöberg (NHRS).

Distribution. Indonesia (Nias, northern Sumatra).

Remarks. Centromeria nigroapicata comb. nov. was described from Nias, Indonesia (Lethierry, 1888). The redescription of *C. longipennis* by Melichar (1912) was based on non-type specimens from Indonesia, including Nias, originally deposited in the Stettin Museum. After examining the types of *C. longipennis* and *C. nigroapicata*, we propose that *C. longipennis* redescribed in 1912 is a misidentification for *C. nigroapicata*, and that the latter should be resurrected as a valid species. The species can be easily distinguished from *C. longipennis* by the large fuscous spot on the apical region of the tegmina.

CENTROMERIA SPEILINEA (WALKER, 1857)

FIGS 2J, 23A–I

Dictyophora [*sic*] *speilinea* Walker, 1857: 84. Holotype: ♀, Malaysia (Borneo) (BMNH) (examined).

Centromeria speilinea (Walker): Stål, 1870: 745; Distant, 1906: 250; Fig. 110; Melichar, 1912: 42; Metcalf, 1946: 37.

Dictyophara psittacina Gerstaecker, 1895: 28. Synonymized by Melichar, 1912: 214.

Centromeria bicolorata Bierman, 1910: 14;. Holotype ♂, Indonesia (Java) (NCB Naturalis) (examined). Synonymized with *Centromeria longipennis* (Walker, 1851) by Melichar, 1912: 43 (error). New synonymy.

Redescription. BL, ♂ 16.1 mm, ♀ 15.0 mm; HL, ♂ 1.6–1.7 mm, ♀ 1.5 mm; HW, ♂ 1.5–1.6 mm, ♀ 1.5 mm; TL, ♂ 13.3 mm, ♀ 12.4 mm.

Male genitalia with pygofer in lateral view large and broad, with ratio of ventral to dorsal width about 3 : 1; posterior margin with a large horn-like process near subapex, acute apically (Fig. 23E). Gonostyles (Fig. 23E) with upper process large and elongate, obtuse apically. Aedeagus (Fig. 23G–I) relatively small, endosomal processes long and stout, diecteded dorsally (Fig. 23H); phallobase sclerotized and pigmented at base, membranous and inflated apically, with one pair of dorsolateral lobes large and rounded, and with one pair of ventral lobes short and small, tapered towards apex, directed posteriorly. Segment X large and broad, in lateral view basal and apical ventral margins projecting ventrally (Fig. 23E), in dorsal view with ratio of length to width near middle, about 1.6 : 1 (Fig. 23D).

Type material examined. Holotype ♀ of *Dictyophora* [*sic*] *speilinea* Walker, 1857; [Malaysia], Sar., Borneo, Type, Dictyophora speilinea (BMNH). Holotype ♂ of *Centromeria bicolorata* Bierman, 1910 (RMNH.INS.721708), [Indonesia], Java, Batavia, 1885, ♂, Type, [Bierman's handwriting] *Centromeria bicolorata* Bierm. 1908, Det. Bierman (Museum Leiden) (NCB Naturalis).

Other material examined. Malaysia, 1♂, Borneo, Sarawak, Gunong Matang, Second forest, 120 m a.s.l., Sweeping, 14.ix.1958, T.C. Maa (BPBM); 1♀, Borneo, Lelang, xii.[18]81, Grabowsky, [handwriting] *Centromeria speilinea* Walk. (MFNB); 5♀♀, Malacca, Perak (NHRS). Thailand, 1♂, S. Banna, Nakhon, 108 m a.s.l., 5–10.v.1958, T.C. Maa (BPBM). [Indonesia], 1♀, Java, Wijnkoopsbay, ii.1989, M.E. Walsh (MZLU); 2♂♂, 9♀♀, Sumatra, Soekaranda, H. Dohrn; [Nast's handwriting] *Centromeria speilinea* (Walk.), J. Nast det. 1957; Mus. Zool. Polonicum, Warszawa, 12/45 (MIZPAS).

Distribution. Malaysia (the Malay Peninsula, Borneo), Burma (Tenasserim, Myitta), Indonesia (Sumatra, Java), Singapore, Thailand.

Remarks. This species was originally described from Singapore (Walker, 1857), and the locality was later changed to 'Borneo' (Walker, 1588). It can be separated from *C. surgens* by the shorter head process and the phallobase with pair of dorsolateral lobes large and rounded and pair of ventral lobes short and small.

***CENTROMERIA SPINOSA* SP. NOV.**
FIGS 2K, 24A–I

Type specimens. Holotype: ♂, Philippines, Philippines Islands, Mount Makiling, 17.iii.1960, T.C. Maa (BPBM).

Paratypes: Philippines, 2♀♀, Mount Makiling, Luzon, Baker; *Centromeria longipennis* [Melichar's handwriting], Melichar det. (MMBC); 1♀, 7155, Luzon, Jagor. (MFNB); 1♀, Manilla, Tharey (NHRS); 2♀♀, Ins. Philipp., Semper (NHRS).

Etymology. This new species name is derived from the Latin '*spinosus*', referring to its phallobase covered with numerous small short spines.

Diagnosis. The new species is very similar to *C. cuspidata* sp. nov., but can be separated from the latter by very short small spines on the phallobase.

Description. BL, ♂ 16.7 mm, ♀ 16.3–17.5 mm; HL, ♂ 2.5 mm, ♀ 2.4–2.5 mm; HW, ♂ 1.7 mm, ♀ 1.6–1.7 mm; TL, ♂ 13.6 mm, ♀ 13.1–13.9 mm.

General colour and external morphology very similar to *C. cuspidata* sp. nov. Vertex in dorsal view with ratio of length to width between eyes about 3.4 : 1 (Fig. 24A). Fore femora missing; hind tibiae with seven lateral spines; hind tarsomeres I with nine or ten apical teeth and tarsomeres II with 11 or 12 apical teeth.

Male genitalia with pygofer in lateral view broad and high, distinctly wider ventrally than dorsally (about 2.5 : 1); posterior margin with a small, narrow, and straight process near middle, apex obtuse (Fig. 24E). Gonostyles (Fig. 24E) relatively large, upper process large and elongate, subacute apically. Aedeagus (Fig. 24G–I) relatively small, endosomal processes extended posteriorly and curved dorsally, apical one-third membranous and tortuous (Fig. 24G); phallobase sclerotized and pigmented at base, membranous apically, covered with numerous minute spines on lateral surfaces; ventral apical area with two pairs of lobes; outer lobes short and small, covered with numerous small spines; inner lobes a little longer and large, only covered with small spines at apex (Fig. 24H, I). Segment X large and elongate, in dorsal view with ratio of length to width near middle about 1.6 : 1 (Fig. 24D).

Distribution. Philippines (Luzon).

***CENTROMERIA SURGENS* (WALKER, 1870)**
STAT. REV., COMB. NOV. FIGS 2L, 25A–I

Dictyophora [*sic*] *surgens* Walker, 1870: 101. Holotype ♀, Indonesia (Amboina) (BMNH) (examined). Synonymized under *Centromeria longipennis* (Walker) by Melichar, 1912: 43, and here resurrected.

Fulgora nereides Kirkaldy, 1913: 14. Holotype ♂, Indonesia (Ceram) (BPBM) (not examined). New synonymy.

Dictyophara nereides (Kirkaldy): Muir, 1923: 239, pl. V, fig. 18.

Redescription. BL, ♂ 16.1–16.5 mm, ♀ 16.3 mm; HL, ♂ 2.0–2.2 mm, ♀ 1.9 mm; HW, ♂ 1.7 mm, ♀ 1.6 mm; TL, ♂ 12.8–13.0 mm, ♀ 13.1 mm.

Male genitalia with pygofer in lateral view large and broad, distinctly wider ventrally than dorsally (about 2.2 : 1); posterior margin with a large horn-like process near subapex, acute apically (Fig. 25E). Gonostyles (Fig. 25E) with upper process relatively short, truncate apically. Aedeagus (Fig. 25G–I) large and robust, endosomal processes long and stout, directeded dorsally; phallobase membranous and strongly inflated, with one pair of lateral lobes short, directed dorsally and with pair of ventral lobes distinctly large and elongate, tapered towards apex (Fig. 25H, I). Segment X large and broad, in lateral view ventral margins projecting ventrally in base and distinctly concave near middle (Fig. 25E); in dorsal view ratio of length to width near middle about 1.7 : 1 (Fig. 25D).

Type material examined. Holotype ♀ of *Dictyophora* [*sic*] *surgens* Walker, 1870. [Indonesia], Amboina, 67.66., Wallace, type, surgens (BMNH). Paratype ♂ of *Fulgora nereides* Kirkaldy, 1913. [Indonesia], Piroe, Ceram, i.1909, F. Muir; ♂, Paratype, Fulgora nereides Kirkaldy, 1913 (BPBM).

Other material examined. Indonesia: 1♂, Ambon I., Waai, 23.i.1965, A.M.R. Wegner; 1♂, Ambon I., Waai, v.1967, A.M.R. Wegner (both in BPBM); 1♂, Sunda, Lombok, 26.iii.1927 (Sunda Exp. Rensch); *Centromeria cephalica* Dist. [Synave's handwriting], H. Synave det., 1972; 1♀, O. Lombok, Selong, 21.v.1927 (Sunda Exp. Rensch); *Centromeria speilinea* Walk. [Synave's handwriting], H. Synave det., 1972 (both in MFNB); 1♂, O. Soembawa, 24-25.v.1927 (Dompoe); 1940–2; *Centromeria cephalica* Dist. [Handwriting] (SNSD).

Distribution. Indonesia (Lombok, Flores, Amboina, Ceram, Sula Islands).

Remarks. This species was described from Amboina, Indonesia (Walker, 1870), and synonymized wrongly under *C. longipennis* by Melichar (1912). We here resurrect *Dictyophora* [*sic*] *surgens* as a valid species and move it to *Centromeria*. *Fulgora nereides* Kirkaldy, 1913 was described from Amboina and Borneo. A male specimen from Ceram, near Amboina, is labelled as 'paratype' of *F. nereides*, which was examined in the present study, suggesting that *F. nereides* is a junior synonym of *C. surgens*. The species is similar to *C. speilinea*, but can be distinguished from the latter by the phallobase with pair of ventral lobes distinctly large and elongate.

CENTROMERIA TRIANGULATA SP. NOV.

FIGS 2M, 26A–J

Type specimens. Holotype: ♂, Philippines, G[Z] amloanga, Mindanao, Cp.8, 10.xii.1921, F.X. Williams (BPBM).

Paratypes: Malaysia, 1♂, British N. Borneo, Keningan[u], 12–17.i.1959, T.C. Maa; 1♂, North Borneo, Tenompok, Mount Kinabalu, 6.ii.1959, T.C. Maa (both in BPBM); 1♀ (MIZ 313229), Nord-Borneo, Waterstradt; *Centromeria longipennis* Walk. [Schmidt's handwriting], ♀, Edm. Schmidt, determ. 1915; Mus. Zool. Polonicum, Warszawa, 12/45 (MIZPAS).

Etymology. This new species name is derived from the Latin '*triangulus*', referring to segment X with a long triangular process at apical ventral margin.

Diagnosis. The new species is very similar to *C. cuspidata* sp. nov., but can be separated from the latter by the apical margin of ventral lobes of the pronotum virescent, and the phallobase without pair of lateral lobes.

Description. BL, ♂ 15.8–16.9 mm, ♀ 17.8 mm; HL, ♂ 2.2–2.6 mm, ♀ 2.7 mm; HW, ♂ 1.5–1.7 mm, ♀ 1.7 mm; TL, ♂ 11.8–12.6 mm, ♀ 13.9 mm.

Cephalic process in lateral view relatively elongate, distinctly longer than length from anterior margins of eyes to posterior margin of vertex; moderately upturned and ascending at about 20° in front of eyes (Fig. 26B). Vertex relatively broad, posterior margin nearly as wide as transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 3.4 : 1 (Fig. 26A). Pronotum (Fig. 26A) with intermediate carinae slightly present in base. Fore femora with a minute spine at apex; hind tibiae with seven lateral spines; hind tarsomeres I with eight or nine apical teeth and tarsomeres II with between eight and ten apical teeth.

Male genitalia with pygofer in lateral view broad and high, distinctly wider ventrally than dorsally (about 3 : 1); posterior margin with a short small process near middle, acute apically (Fig. 26E). Gonostyles (Fig. 26E) relatively small, upper process large and stout, subacute apically. Aedeagus (Fig. 26G–I) moderately large, endosomal processes extended posteriorly and curved dorsoanteriorly; phallobase sclerotized and pigmented at base, membranous and inflated apically, with one pair of lateral lobes distinctly short and small, slightly projecting posteriorly, and pair of ventral lobes elongate and thumb-like, directed posteriorly, without spines (Fig. 26H, I). Segment X large and elongate, apical ventral margin projecting a long triangular black process, in dorsal view with ratio of length to width near middle about 1.4 : 1 (Fig. 26D).

Distribution. Philippines (Mindanao), Malaysia (north-eastern Borneo).

DICTYOMERIA GEN. NOV

Type species. Centromeira simulata Distant, 1906, by present designation and monotypy.

Etymology. The new generic name is a combination of '*Dictyo*- plus the suffix '*meria*'. The gender is feminine.

Diagnosis. This new genus can be distinguished by the following combination of characters: cephalic process in front of eyes strongly upturned, gradually convergent anteriorly, more or less truncate apically; vertex with median carina distinct at base, absent in middle, and high and sharp from anterior margin of eyes to apex, lateral carinae in front of eyes more or less parallel anteriorly, truncate apically; frons with median carina robust and strongly convex, intermediate carinae extending anterior margin of eyes; pronotum with median carina sharp and complete, intermediate carinae absent; tegmina with a large sublunate streak on apical region; legs moderately elongate, fore femora not flattened and dilated, with a small spine near apex; hind tibiae with seven apical teeth.

Description. Head (Fig. 27A–C) produced in a moderate and slightly slender cephalic process. Cephalic process (Fig. 27A–C) in front of eyes strongly upturned, gradually convergent anteriorly, more or less truncate apically. Vertex (Fig. 27A) broadest at base, posterior plane elevated above pronotum; lateral carinae high and sharp, slightly convergent at base, abruptly constricted in front of eyes, strongly upturned and nearly parallel anteriorly; anterior margin broadly and angulately convex; posterior margin ridged and angularly concave at about 90°; median carina distinct at base, absent in middle, high and sharp towards apex. Frons (Fig. 27C) with lateral carinae ridged, gradually diverging posteriorly and slightly expanded outwards below antennae; posterior margin concave; median carina robust and strongly convex, intermediate carinae extending to anterior margin of eyes, not to frontoclypeal suture. Postclypeus and anteclypeus (Fig. 27C) strongly convex at middle, with distinct median carina. Rostrum short, extending base of hind femora; basal segment distinctly longer than distal segment. Compound eyes oval and large. Ocelli relatively large, reddish. Antennae with very small scape; pedicel large and subglobose, with more than 50 distinct sensory plaque organs distributed over entire surface; flagellum long, setuliform.

Pronotum (Fig. 27A) distinctly shorter than mesonotum medially, narrow anteriorly, broad posteriorly; anterior margin centrally angularly convex, lateral marginal areas straight and sloping, with two long longitudinal carinae on each side between eyes and tegulae, posterior margin angularly concave at about 110°; median carina sharp and high, with a big lateral pit on each side, intermediate carinae absent. Mesonotum (Fig. 27A) tricarinate, lateral carinae incurved anteriorly towards median carina. Tegmina (Fig. 27D) hyaline, with a large sublunate streak on apical region; slender and elongate, more or less parallel anteroposteriorly, somewhat truncate apically, with ratio of length to width about 4 : 1; veins without setae; MP bifurcating MP_{1+2} and MP_{3+4} near middle and posterior to CuA; transverse veins scarce, with 11 or 12 apical cells between RP and CuA; stigmal area elongate, with two cells. Legs relatively short, fore and middle femora moderately elongate, hind tibiae about 1.5 times as long as hind femora; fore femora not flattened and dilated, with a minute spine near apex; hind tibiae with seven lateral spines and seven apical spines; hind tarsomeres I and II both with between 16 and 20 apical teeth.

Male unknown and female genitalia identical to other Orthopagini genera.

Diversity and distribution. The new genus is monotypic and only found in north-eastern India.

Remarks. The new genus can be easily distinguished from *Centromeria* by: vertex with median carina high and sharp from anterior margin of the eyes to the apex; lateral carinae in front of eyes more or less parallel anteriorly, truncate apically; tegmina with a large sublunate streak on apical region; legs distinctly short; and hind tibiae with seven apical teeth. *Dictyomeria* gen. nov. is more closely related to *Orthopagus* in our phylogenetic analysis, but can be separated from the latter by the cephalic process in front of eyes strongly upturned and the frons with median carina robust and strongly convex. It is also externally similar to *Indomiasa*, but may be distinguished from the latter by the pronotum with anterolateral angles angulated, and two lateral carinae between eyes and tegulae distinct and complete, and legs relatively short and stout.

DICTYOMEIRA SIMULATA (DISTANT, 1906)
COMB. NOV.
FIGS 3A, 27A–D

Centromeira simulata Distant, 1906: 252; Melichar, 1912: 43; Metcalf, 1946: 37. Holotype ♀, India (Assam) (BMNH) (examined).

Redescription. Body length (from apex of cephalic process to tip of abdomen), ♀ 10.8 mm; length of head, ♀ 1.7 mm; width of head (including eyes), ♀ 1.5 mm; length of forewings, ♀ 13.2 mm.

For general colour, see the description by Distant (1906: 252). Cephalic process in lateral view strongly upturned and ascending at about 60°, a little longer than length from anterior margins of eyes to posterior margin of vertex (Fig. 27B). Vertex relatively narrow, posterior margin as broad as transverse diameter of eyes; in dorsal view ratio of length to width between eyes about 3.4 : 1 (Fig. 27A).

Male unknown.

Type material examined. Holotype ♀ of *Centromeira simulata* Distant, 1906. [India], Margh, Assam, Atkinson, 92–6, type, Centromeria simulata Distant (BMNH).

Distribution. North-eastern India (Assam).

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APPENDIX 1

Table A1. Material for the phylogenetic analyses of Oriental Orthopagini and *Centromeria*

Higher category	Genus	Species	Distribution
Aluntiini	*Aluntia*	*schimperii*	Afrotropical region (excluding Madagascar)
	Dictyomorpha	*elongata*	Papua New Guinea, Indonesia
	Indodictyophara	*lobosa*	Southern India
	Arjuna	*scriba*	Papua New Guinea
	Pippax	*opilionoides*	Papua New Guinea
Dictyopharini	*Dictyophara*	*europaea*	Palaearctic region
	Paradictyopharina	*parallela*	Southern India
	Putala	*rostrata*	Sri Lanka, southern India
	Raivuna	*micida*	Vietnam, southern China
Hastini	*Anasta*	*prognatha*	Australia, Papua New Guinea
	Hasta	*hastata*	Australia
	Thanatodictya	*bifasciata*	Australia
Orthopagini	*Centromeria*	***curva* sp. nov.***	South-western China
		cuspidata* sp. nov.	The Philippines (Mindanao)
		deckerti* sp. nov.	The Philippines (Mindoro)
		inflata* sp. nov.	The Philippines (Camarines Sur)
		*inspinata**	Indonesia (Sulawesi)
		*longipennis**	The Philippines (Mindanao)
		maculata* sp. nov.	Malaysia (Borneo)
		melichari* sp. nov.	The Philippines (Palawan)
		*nigroapicata**	Indonesia (Nias, Sumatra)
		*speilinea**	Malaysia (Borneo), Singapore, Thailand
		spinosa* sp. nov.	The Philippines (Luzon)
		*surgens**	Indonesia (Amboina, Ceram, Flores, Lombok, Sula)
		triangulata* sp. nov.	Malaysia (Borneo), Philippines (Mindanao)
	***Dictyomeria* gen. nov.**	*simulata*	India (Assam)
	Dictyopharina	*sichuanensis*	China (Sichuan)
		viridissima	Southern India
	Dictyotenguna	*choui**	China (Fujian, Guangxi)
	Emeljanovina	*dixoni*	India (Bombay)
	Indomiasa	*distanti*	Southern India
	Leprota	*melichari*	Indonesia (Sumatra), Malaysia (Borneo)
		robusta	Malaysia (Borneo)
	Medeusa	*speicarina*	Malaysia (Borneo)
	Metaurus	*ramusitis*	China (Yunnan)
		reticulatus	Cambodia, Laos
	Miasa	*borneensis*	Malaysia (Borneo)
		smaragdilinea	Indonesia (Sumatra, Java, Sipora, Siberut, North Pagi), Malaysia (the Malay Peninsula), Singapore
	Orthopagus	*lunulifer*	Japan, Korea, China, India, Sri Lanka, Southeast Asia
		philippinus	The Philippines
	Protolepta	*linnavuorii*	Indonesia (Sulawesi)
		turbata	Indonesia (Sulawesi)
	Saigona	*fulgoroides*	China
		ussuriensis	Russia (Far Eastern region), Japan, Korea, China
	Tenguna	*medogensis*	China (Tibet)
		watanabei	China
	Truncatomeria	*viridistigma**	Sri Lanka

*Material also used for the phylogenetic analysis of *Centromeria*.
Bold letters in are names of new taxa (scientific names).

Table A2. List of characters used in the phylogenetic analysis of Oriental Orthopagini

Coloration
0. Frons, median carina: 0, virescent or ochraceous (Fig. 4C); 1, purplish red or reddish ochraceous (Fig. 16C); 2, dark brown.
1. Frons, areas between intermediate carinae and median carina: 0, virescent or ochraceous (Fig. 16C); 1, reddish ochraceous or orange.
2. Cephalic process, preocular field (lateral area in front of eyes): 0, without strip or spot; 1, with a long strip from front of eyes to apex (Fig. 16B); 2, with large spots (Fig. 4B).
3. Pronotum, general colour: 0, virescent or ochraceous (Fig. 3B); 1, reddish ochraceous between carinae (Fig. 16A); 2, dark brown (Fig. 3K); 3, whitish; 4, testaceous (Fig. 3E).
4. Mesonotum, general colour: 0, virescent or ochraceous (Fig. 3B); 1, reddish ochraceous between carinae (Fig. 3M); 2, dark brown; 3, testaceous.
5. Tegmina, sublunate streak on apical region: 0, absent; 1, present (Fig. 4D).
6. Legs: 0, almost uniformly virescent; 1, brown with whitish stripe or spots.
7. Abdominal segments III–VI: 0, pale green without spots or stripes; 1, dark brown with whitish spots or stripes.

Head
8. Cephalic process in front of eyes, length from anterior margin of eyes to apex: 0, no longer than longitudinal diameter of eyes (Fig. 3B); 1, less than 2.5 times as long as longitudinal diameter of eyes (Fig. 3C); 2, as long as or a little longer than pronotum and mesonotum combined (Fig. 3F); 3, much longer than pronotum and mesonotum combined (Fig. 3E).
9. Cephalic process in front of eyes: 0, compressed dorsoventrally; 1, compressed laterally; 2, not distinctly compressed.
10. Cephalic process in front of eyes: 0, unbent or slightly curved upwards (ascending at no more than 10°); 1, moderately curved upwards (no more than 30°); 2, strongly curved upwards (distinctly more than 30°); 3, curved downwards.
11. Cephalic process in front of eyes in ventral view: 0, convergent (Fig. 3L); 1, nearly parallel (Fig. 3E).
12. Cephalic process in front of eyes: 0, robust (Fig. 3E); 1, distinctly slender (Fig. 3D); 2, constricted to an extremely slender process (Fig. 3H).
13. Cephalic process with an oblique carina in lateral surface in front of eyes: 0, present; 1, absent.
14. Vertex with a secondary carina bifurcated from subapex of lateral carinae: 0, absent; 1, present.
15. Vertex, posterior surface in relation to pronotum: 0, in the same plane; 1, in an elevated plane.
16. Vertex, base width in relation to transverse diameter of eyes: 0, distinctly narrower (Fig. 3D); 1, nearly equal or wider (Fig. 3C); 2, distinctly wider (more than 1.5 times, Fig. 3E).
17. Vertex, median carina: 0, absent; 1, present.
18. Vertex, median carina: 0, distinct in base; 1, nearly complete.
19. Vertex, lateral carinae in front of eyes: 0, not distinctly constricted (Fig. 3F); 1, abruptly and strongly constricted (Fig. 3G).
20. Vertex, lateral carinae in front of eyes: 0, subparallel (Fig. 3J); 1, gradually converging forwards (Fig. 3L).
21. Vertex, apex: 0, nearly acuminate (Fig. 1C); 1, angularly convex (no more than 100°); 2, broadly convex.
22. Vertex, posterior margin: 0, broadly concave; 1, angularly concave (no more than 100°, Fig. 16A).
23. Vertex, posterior margin in relation to posterior margin of eyes: 0, not surpassing; 1, slightly surpassing.
24. A sharp apical median carina between anterior margins of vertex and intermediate carinae of frons: 0, absent; 1, present.
25. Frons, apex between lateral carinae and intermediate carinae: 0, without carina; 1, with weak transverse carinae.
26. Frons, median carina: 0, complete; 1, mostly absent in middle; 2, absent in apical area; 3, only present below the eyes.
27. Frons, median carina: 0, ridged (Fig. 4C); 1, robust and strongly convex (Fig. 16C); 2, strongly elevated and blade-like, at least at apex and base.
28. Frons, anterior margin of intermediate carinae in relation to apex of vertex: 0, distinctly surpassing; 1, not surpassing.
29. Frons, apical area of intermediate carinae in relation to lateral carinae: 0, narrower; 1, wider.
30. Frons, intermediate carinae: 0, subparallel; 1, gradually divergent posteriorly and subparallel; 2, gradually convergent posteriorly.
31. Frons, intermediate carinae approaching: 0, anterior margin or middle of eyes (Fig. 16C); 1, frontoclypeal suture (Fig. 4C).
32. Frons, intermediate carinae: 0, ridged; 1, distinctly elevated and blade-like.

Table A2. *Continued*

33. Frons, lateral carinae below the antennae: 0, nearly straight; 1, convex.
34. Clypeus, apex: 0, distinctly surpassing apex of fore coxae; 1, extending apex of middle coxae.
35. Rostrum, apex: 0, not extending base of hind femora; 1, extending base of hind femora; 2, extending even surpassing apex of hind femora.
36. Rostrum, basal segment relative to distal segment: 0, distinctly longer (no less than 1.5 times as long as distal segment); 1, nearly equal or slightly longer.
37. Compound eyes, callus postocularis: 0, forming a triangular process projecting posteriorly; 1, forming a transverse process, more or less truncate posteriorly (Fig. 4B).
38. Compound eyes, shape: 0, nearly rounded; 1, long oval.
39. Antennal pedicel, shape: 0, globose; 1, elongate.

Thorax

40. Pronotum, length: 0, shorter than half of mesonotum; 1, longer than half of mesonotum.
41. Pronotum, median carina: 0, ridged; 1, strongly ridged.
42. Pronotum, intermediate carinae: 0, present; 1, absent.
43. Pronotum, intermediate carinae: 0, distinct in basal third to half present; 1, nearly complete.
44. Pronotum, two longitudinal carinae between eyes and tegulae: 0, complete (Fig. 4B); 1, incomplete.
45. Pronotum, paranotal lobes with an oblique carina: 0, absent; 1, present.
46. Pronotum, anterolateral angles: 0, angulated; 1, rounded.
47. Pronotum, anterior central margin: 0, arcuately convex; 1, angularly convex (Fig. 4A).
48. Pronotum, posterior margin: 0, broadly arcuately concave; 1, more or less angularly concave (no more than 120°, Fig. 4A).
49. Mesonotum: 0, distinctly arched; 1, slightly arched or nearly flat.
50. Mesonotum, median carina: 0, present; 1, absent.
51. Mesonotum, lateral carinae: 0, gradually incurved anteriorly (Fig. 4A); 1, nearly straight; 2, nearly straight and abruptly incurved apically.
52. Mesonotum, lateral carinae: 0, parallel; 1, convergent (Fig. 4A).
53. Tegmina: 0, macropterous; 1, brachypterous.
54. Tegmina, apical margin: 0, rounded (Fig. 4D); 1, somewhat truncate; 2, somewhat pointed.
55. Tegmina, unexpanded status: 0, overlapping each other; 1, not overlapping.
56. Tegmina, veins with setae: 0, present; 1, absent.
57. Tegmina, veins: 0, with short setae; 1, with long setae.
58. Tegmina, folding line: 0, absent; 1, 1 (Fig. 4D).
59. Tegmina, position of folding line: 0, between MP$_{1+2}$ and MP$_{3+4}$; 1, between MP$_3$ and MP$_4$ (Fig. 4D).
60. Tegmina, costal area: 0, expanded; 1, not expanded.
61. Tegmina, costal cell: 0, narrow (nearly half of width between ScP + R and MP); 1, normal (nearly as wide as width between ScP + R and MP); 2, wide (wider than width between ScP + R and MP).
62. Tegmina, ScP + R and MP originating from basal cell: 0, without stem or with a very short common stem (Fig. 4D); 1, with a distinctly long common stem.
63. Tegmina, MP bifurcating into MP$_{1+2}$ and MP$_{3+4}$: 0, in basal one-third; 1, near or posterior to middle (Fig. 4D).
64. Tegmina, MP$_{3+4}$ bifurcating into MP$_3$ and MP$_4$: 0, in basal half; 1, in posterior half (Fig. 4D).
65. Tegmina, bifurcation of MP relative to CuA: 0, MP distinctly bifurcated anterior to CuA; 1, MP distinctly bifurcated posterior to CuA (Fig. 4D); 2, nearly abreast (just little anterior to or posterior to).
66. Tegmina, number of apical cells of RP: 0, between one and three (Fig. 4D); 1, four or more.
67. Tegmina, number of apical cells of MP: 0, between four and six; 1, between seven and nine (Fig. 4D); 2, ten or more.
68. Tegmina, number of apical cells of CuA: 0, between one and three (Fig. 4D); 1, four or more.
69. Tegmina, nodal line: 0, absent (Fig. 4D); 1, present.
70. Tegmina, stigmal area: 0, present (Fig. 4D); 1, absent.
71. Tegmina, shape of stigmal area: 0, quadrangular (Fig. 4D); 1, elongate.
72. Tegmina, suboblique veins between costal margin and ScP + R: 0, present; 1, absent.
73. Tegmina, claval suture: 0, extending to posterior margin (Fig. 4D); 1, not extending to posterior margin.
74. Hindwings, secondary fold on anal area: 0, absent; 1, present.
75. Hindwings, anal area: 0, developed; 1, reduced.
76. Fore femora: 0, normal; 1, slender and elongate; 2, flattened and dilated (Fig. 5A).
77. Fore femora, a subapical spine on ventral area: 0, present (Fig. 5A); 1, absent.

Table A2. *Continued*

78. Fore femora, subapical spine: 0, small and acute; 1, large and blunt (Fig. 5A).
79. Fore and middle tarsomeres I and II, acutellae: 0, no more than two (Fig. 5E, F) (Fig.); 1, many more than two.
80. Hind femora and tibiae: 0, normal; 1, distinctly elongate.
81. Hind tibiae, number of apical teeth: 0, six; 1, seven (Fig. 5D); 2, eight.
82. Hind tarsomeres I and II, apical teeth: 0, with platellae (Fig. 5G, H); 1, with long setae.
83. Hind tarsomeres I, number of apical teeth: 0, between five and seven; 1, between eight and 13; 2, 14 or more (Fig. 5G).

Abdomen

84. Pregenital segments: 0, not distinctly elongate; 1, elongate.

Male abdomen

85. Pygofer (lateral view), length: 0, more than twice ventral width (Fig. 4F); 1, less than twice ventral width.
86. Pygofer (lateral view), posterior margin with process: 0, absent; 1, present.
87. Pygofer, posterior process: 0, one; 1, two.
88. Gonostyles, upper process: 0, not distinctly compressed; 1, compressed dorsoventrally.
89. Aedeagus, moderate to long spines on apical lobes of phallobase: 0, absent (Fig. 6A); 1, present.
90. Aedeagus, endosomal processes: 0, very short and invisible; 1, short, just visible from phallotheca; 2, moderately long, distinctly shorter than phallobase with lobes; 3, longer, nearly as long as or even longer than phallobase with lobes.
91. Aedeagus, endosomal processes with small spines: 0, absent; 1, present (Fig. 6A).
92. Aedeagus, endosomal processes: 0, nearly straight; 1, curved in middle (Fig. 6A).
93. Aedeagus, endosomal processes: 0, not forked (Fig. 6A); 1, forked.
94. Segment X, shape (dorsal view): 0, nearly oval; 1, truncate (projecting an angle on each side); 2, distinctly elongate; 3, irregular.
95. Segment X (lateral view), ventral margins in apex: 0, not projecting; 1, projecting ventrally.
96. Segment X (lateral view), ventral margins in base: 0, not projecting; 1, projecting ventrally.
97. Segment X, ventral apical margin: 0, distinctly concave; 1, more or less concave or convex; 2, projecting a central triangular process (Fig. 16E).

Female abdomen

98. Gonapophyses VIII, teeth of ACL: 0, only at the tip; 1, from base to tip (Fig. 6E).
99. Gonapophyses VIII, basal teeth of ACL: 0, not prolonged (Fig. 6E); 1, transversally prolonged and strongly ridged, forming two apices in some taxa.
100. Gonapophyses VIII, teeth of ACL: 0, very small; 1, large (Fig. 6E).
101. Gonapophyses VIII, teeth of ACL: 0, almost equal in size; 1, varying in size and shape (Fig. 6E).
102. Gonapophyses VIII, number of teeth of ACL: 0, between two and five; 1, five or more (Fig. 6E).
103. Gonapophyses VIII, an additional membranous process of ACL: 0, absent; 1, present.
104. Gonocoxae VIII, number of GxP: 0, one; 1, two (Fig. 6E).
105. Gonapophyses IX, apex of PCL: 0, not or weakly bifurcated (Fig. 6F); 1, distinctly bifurcated.
106. Gonapophyses IX, posterior fibula (Fp) extending to gonospiculum (Gl): 0, present; 1, absent (Fig. 6F).
107. Gonoplacs, the third additional lobes (Gp3): 0, absent; 1, present.
108. Gonoplacs, apical margin of Gp1: 0, truncate; 1, more or less pointed (Fig. 6G).
109. Gonoplacs, filmy edging of Gp1: 0, absent; 1, present.
110. Gonoplacs, sensory appendage of Gp1 (lower lobes): 0, absent; 1, present (Fig. 6G).
111. Gonoplacs, sensory field with numerous tiny setae at apex of Gp1: 0, absent (Fig. 6G); 1, present.
112. Gonoplacs, spinous setae on apical margin of Gp1: 0, absent; 1, present.
113. Gonoplacs, Gp2 (posterior lobes): 0, slender; 1, distinctly wider (Fig. 6G).
114. Segment X, shape: 0, nearly rounded (Fig. 6G); 1, distinctly elongate.
115. Segment X, setae sitting on high papilliform digitate socles on ventral surface: 0, absent; 1, present.

Table A3. Morphological character matrix used in the phylogenetic analysis of Oriental Orthopagini

	0000000000	1111111111	2222222222	3333333333
Taxa	0123456789	0123456789	0123456789	0123456789
Aluntia schimperii	0000000030	01000010–0	0111111001	2010011011
Dictyomorpha elongata	0000000030	01000010–0	0111110201	2010011011
Indodictyophara lobosa	0000000030	0100001100	0111110201	2010011011
Arjuna scriba	1100000012	31011010–0	1000110110	0000121000
Pippax opilionoides	1100000012	11010010–0	0100113010	0100121000
Dictyophara europaea	0100000012	0001001110	1100100010	0100011100
Paradictyopharina parallela	0000000002	0001001110	1210100010	0100011100
Putala rostrata	0113201111	1111010100	0200000010	1101010100
Raivuna micida	0101001022	0101001110	0200100010	0100011100
Anasta prognatha	0000000012	0001001100	1100100010	0100011100
Hasta hastata	0000000032	0101002100	0200110010	0100001000
Thanatodictya bifasciata	0002201131	1111011100	0110111010	0111011000
Centromeria curva sp. nov.	1011000012	2010010101	1010000111	0001021100
Centromeria cuspidata sp. nov.	1011000012	1000011100	1010000111	0000021100
Centromeria deckerti sp. nov.	1011000012	0000011100	1010000111	0000021100
Centromeria inflata sp. nov.	1011000012	1000011100	1010000111	2000021100
Centromeria longipennis	1011000002	1000011100	1010000111	0001021100
Centromeria maculata sp. nov.	1011100002	0000011100	1010000111	0001021100
Centromeria melichari sp. nov.	1011000012	0000011100	1010000111	0001021100
Centromeria nigroapicata	1011000012	0000011100	1010000111	0001021100
Centromeria speilinea	1011000002	2010010101	1010000111	0001021100
Centromeria spinosa sp. nov.	1011000012	1000011100	1010000111	0001021100
Centromeria surgens	1011000012	2010010101	1010000111	0001021100
Centromeria triangulata sp. nov.	1011000012	0000011100	1010000111	0001021100
Dictyomeria simulata	2022211112	2010011111	0210000110	1001011100
Dictyopharina sichuanensis	0000000002	0001001110	1200100010	2101011100
Dictyopharina viridissima	0000000002	0001001110	1200100010	2101011100
Dictyotenguna choui	0100000012	0000001110	1210000010	0001011100
Emeljanovina dixoni	0010000012	1001001100	1100000010	1100011100
Indomiasa distanti	2000010001	20100100–1	0000000110	1001011000
Leprota melichari	0004000032	0101002100	0200100010	0100010110
Leprota robusta	0004000032	0101002100	0200100010	0100010110
Medeusa speicarina	0004300012	0001001110	1200100010	0100010110
Metaurus ramusitis	0020000011	2020001101	0000002011	1101020100
Metaurus reticulatus	0020000011	2020001101	0000002011	1101020100
Miasa borneensis	0000211121	21200100–1	0000000011	1001021000
Miasa smaragdilinea	1100211121	21200100–1	0000000011	1001021000
Orthopagus philippinus	0022211102	0101011110	0210000010	2100011100
Orthopagus lunulifer	0022211102	0101011110	0210000010	2100011100
Protolepta linnavuorii	0002001112	0101001110	0210100010	2101011100
Protolepta turbata	0002001122	0101001110	0210100010	2101011100
Saigona fulgoroides	0002201132	0101011100	0200100010	0001010000
Saigona ussuriensis	0002201112	0101011100	0200100010	0001010000
Tenguna medogensis	0000000012	0000001110	1010000011	0101011100
Tenguna watanabei	0000000012	0000001110	1010000011	0101011100
Truncatomeria viridistigma	1101100002	0000011110	0210100110	0100021100

	4444444444	5555555555	6666666666	7777777777
Taxa	0123456789	0123456789	0123456789	0123456789
Aluntia schimperii	1001000011	010000000–	1201120100	1–010011–0
Dictyomorpha elongata	1001000011	010000000–	1201110000	1–010011–0

Table A3. *Continued*

Taxa	4444444444 0123456789	5555555555 0123456789	6666666666 0123456789	7777777777 0123456789
Indodictyophara lobosa	1001000011	010000000–	1201110000	1–010011–0
Arjuna scriba	1101000011	021121010–	1111110000	1–100111–0
Pippax opilionoides	1100000011	021121010–	1111110000	1–100111–0
Dictyophara europaea	0000010001	0100011–11	1101110100	01101001–1
Paradictyopharina parallela	001—10001	0100010011	1101111200	01101001–1
Putala rostrata	001–000000	1100011–11	1101110100	00101001–1
Raivuna micida	001–010001	0100011–11	1101110100	00101001–1
Anasta prognatha	0001000001	0100011–10	1111110000	01101001–0
Hasta hastata	0001000001	0100011–10	1111110100	01101001–0
Thanatodictya bifasciata	0000000001	0010011–10	1111110000	01101001–0
Centromeria curva sp. nov.	011–000111	0010011–11	1101110100	0110101000
Centromeria cuspidata sp. nov.	011–000111	0010011–11	1101110100	01101011–0
Centromeria deckerti sp. nov.	011–000111	0010011–11	1101110100	0110101000
Centromeria inflata sp. nov.	011–000111	0010011–11	1101110100	0110101000
Centromeria longipennis	011–000111	0010011–11	1101110100	0110101000
Centromeria maculata sp. nov.	011–000111	0010011–11	1101110100	0110101000
Centromeria melichari sp. nov.	011–000111	0010011–11	1101110100	01101011–0
Centromeria nigroapicata	011–000111	0010011–11	1101110100	0110101000
Centromeria speilinea	011–000111	0010011–11	1101110100	0110101000
Centromeria spinosa sp. nov.	011–000111	0010011–11	1101110100	0110101??0
Centromeria surgens	011–000111	0010011–11	1101110100	01101011–0
Centromeria triangulata sp. nov.	011–000111	0010011–11	1101110100	0110101000
Dictyomeria simulata	011–000111	0010011–11	1101110100	0110100000
Dictyopharina sichuanensis	0000000001	0010011–11	1101110100	0110100000
Dictyopharina viridissima	0000000001	0010011–11	1101110100	0110100000
Dictyotenguna choui	001–000111	0010010011	1101110100	0110100000
Emeljanovina dixoni	001–000001	0100011–11	1101110100	01101001–1
Indomiasa distanti	001–101100	0010011–11	1101110100	0110100000
Leprota melichari	0000000001	0000110011	0001111201	0110100000
Leprota robusta	0000000001	0000110011	0001111201	0110100000
Medeusa speicarina	0001000001	0000010011	1101110101	0110100000
Metaurus ramusitis	001–000001	0010010011	0100001210	0110100010
Metaurus reticulatus	001–000001	0010010011	0100001210	0110100010
Miasa borneensis	001–001100	0010010011	1101110001	0110101010
Miasa smaragdilinea	001–001100	0010010011	1101110001	0110101010
Orthopagus philippinus	011–000111	0010011–11	1101110100	0110102010
Orthopagus lunulifer	011–000111	0010011–11	1101110100	0110102010
Protolepta linnavuorii	001–000101	0010011–11	1101110100	0010100010
Protolepta turbata	001–000101	0010011–11	1101110100	0010100010
Saigona fulgoroides	0100100011	1010010011	1101110100	0010102010
Saigona ussuriensis	0100100011	0010010011	1101110100	0010102010
Tenguna medogensis	0000000101	0010011–11	1101110101	0110100000
Tenguna watanabei	0000000101	0010011–11	1101110101	0110100000
Truncatomeria viridistigma	011–000111	0010011–11	1101110100	0110100000

Taxa	8888888888 0123456789	9999999999 0123456789	1111111111 0000000000 0123456789	111111 111111 012345
Aluntia schimperii	1110110–00	301020010–	0000000100	010010
Dictyomorpha elongata	1110111000	301020010–	0000000100	010010
Indodictyophara lobosa	1110111000	301020010–	0000000100	010010

Table A3. *Continued*

			1111111111	111111
	8888888888	9999999999	0000000000	111111
Taxa	0123456789	0123456789	0123456789	012345
Arjuna scriba	1101000–10	2000000111	1110111001	001100
Pippax opilionoides	1101000–10	2000000111	1110111001	001100
Dictyophara europaea	0102000–01	2010110110	1110101010	100100
Paradictyopharina parallela	0102001001	1000110110	1110101010	100100
Putala rostrata	0102001001	1000110110	1110101010	100100
Raivuna micida	0102001001	0000000110	1110101010	100100
Anasta prognatha	0102000–10	1000001111	1111111001	001101
Hasta hastate	0202000–10	2000001111	1111111001	001101
Thanatodictya bifasciata	0102000–11	1000001111	1110111001	001100
Centromeria curva sp. nov.	1001001000	2010001110	1110101010	100100
Centromeria cuspidata sp. nov.	1001001000	2010110210	1110101010	100100
Centromeria deckerti sp. nov.	1001001000	2010110210	1110101010	100100
Centromeria inflata sp. nov.	1001001000	2010000110	1110101010	100100
Centromeria longipennis	1001001000	2010000110	1110101010	100100
Centromeria maculata sp. nov.	1001001000	2010011110	1110101010	100100
Centromeria melichari sp. nov.	1001001000	2010110210	1110101010	100100
Centromeria nigroapicata	1001001000	2010000110	1110101010	100100
Centromeria speilinea	1001001000	2010011110	1110101010	100100
Centromeria spinosa sp. nov.	1001001000	2010000110	1110101010	100100
Centromeria surgens	1001001000	2010001110	1110101010	100100
Centromeria triangulata sp. nov.	1001001000	2010110210	1110101010	100100
Dictyomeria simulata	01020?????	????????10	1110101010	100100
Dictyopharina sichuanensis	0201000–00	1000000110	1110101010	100100
Dictyopharina viridissima	0201001000	1000000110	1110101010	100100
Dictyotenguna choui	0201001000	2000311010	1110101010	100100
Emeljanovina dixoni	0102000–01	0000000110	1110101010	100100
Indomiasa distanti	0102101100	20102101??	??????????	??????
Leprota melichari	0201001000	3000000110	1110101010	100100
Leprota robusta	0201001000	3000000110	1110101010	100100
Medeusa speicarina	0201001000	30100001??	??????????	??????
Metaurus ramusitis	0102001100	2001311010	1110101010	100100
Metaurus reticulatus	0102001100	2001311010	1110101010	100100
Miasa borneensis	1001100–00	2010001110	1110101010	100100
Miasa smaragdilinea	1001100–00	2010000110	1110101010	100100
Orthopagus philippinus	0102000–00	3110000110	1110101010	100100
Orthopagus lunulifer	0102000–00	3110000110	1110101010	100100
Protolepta linnavuorii	0001001000	20100001??	??????????	??????
Protolepta turbata	0001001000	20100001??	??????????	??????
Saigona fulgoroides	0201001000	2010201110	1110101010	100100
Saigona ussuriensis	0201001000	2000001110	1110101010	100100
Tenguna medogensis	0201001000	3010000110	1110101010	100100
Tenguna watanabei	0201001000	3010000110	1110101010	100100
Truncatomeria viridistigma	0200001000	1000000110	1110101010	100100

Table A4. List of characters used in the phylogenetic analysis of *Centromeria*

Coloration

0. Vertex, central surface: 0, virescent or ochraceous; 1, purplish red or reddish ochraceous.
1. Frons, median carina: 0, virescent or ochraceous; 1, purplish red or reddish ochraceous.
2. Frons, areas between intermediate carinae and median carina: 0, virescent or ochraceous; 1, reddish ochraceous or orange.
3. Cephalic process, preocular field (lateral area in front of eyes): 0, without strip or spot; 1, with a long strip from front of eyes to apex.
4. Pronotum, median carina: 0, virescent or green; 1, purplish red or reddish ochraceous.
5. Pronotum, area of intermediate carinae: 0, virescent or green; 1, purplish red or reddish ochraceous.
6. Pronotum, general colour: 0, virescent or ochraceous; 1, reddish ochraceous between carinae.
7. Pronotum, apical margin of paranotal lobes: 0, virescent or green; 1, purplish red or reddish ochraceous.
8. Mesonotum, general colour: 0, virescent or ochraceous; 1, reddish ochraceous between carinae.
9. Tegmina, fuscous maculae on apical region: 0, absent; 1, present.

Head

10. Cephalic process in front of eyes, length from anterior margin of eyes to apex relative to length from anterior margins of eyes to posterior margin of vertex: 0, shorter (Fig. 23B); 1, nearly equal (Fig. 19B); 2, longer (Fig. 17B).
11. Cephalic process in front of eyes: 0, unbent or slightly curved upwards (ascending at no more than 15°, Fig. 16B); 1, moderately curved upwards (no more than 30°, Fig. 24B); 2, strongly curved upwards (distinctly more than 30°, Fig. 13B).
12. Cephalic process in front of eyes: 0, robust (Fig. 13A); 1, relatively slender (Fig. 15A).
13. Vertex, posterior surface in relation to pronotum: 0, in the same plane; 1, in an elevated plane.
14. Vertex, base width in relation to transverse diameter of eyes: 0, distinctly narrower (Fig. 13A); 1, nearly equal or wider (Fig. 15A).
15. Vertex, median carina: 0, distinct in base; 1, nearly complete.
16. Vertex, lateral carinae in front of eyes: 0, not distinctly constricted (Fig. 15A); 1, abruptly and strongly constricted (Fig. 13A).
17. Vertex, apex: 0, nearly acuminate; 1, broadly convex.
18. Frons, a sharp apical median carina between anterior margin of vertex and intermediate carinae of frons: 0, absent; 1, present.
19. Frons, median carina: 0, ridged; 1, robust and strongly convex.
20. Frons, apical area of intermediate carinae in relation to lateral carinae: 0, narrower; 1, wider (Fig. 17A).
21. Frons, intermediate carinae: 0, subparallel; 1, gradually convergent posteriorly (Fig. 17A).
22. Frons, intermediate carinae approaching: 0, anterior margin or middle of eyes; 1, frontoclypeal suture.
23. Frons, lateral carinae below the antennae: 0, nearly straight (Fig. 15C); 1, convex (Fig. 13C).
24. Rostrum, apex: 0, extending to base of hind femora; 1, extending to and even surpassing apex of hind femora.

Thorax

25. Tegmina, veins with setae: 0, present; 1, absent.
26. Fore femora: 0, normal; 1, slender and elongate.
27. Fore femora, ventral subapical area with a spine: 0, present; 1, absent.
28. Hind femora and tibiae: 0, normal; 1, distinctly elongate.
29. Hind tibiae, number of apical teeth: 0, six; 1, eight.

Male abdomen

30. Pygofer (lateral view), length of ventral margin in relation to dorsal one: 0, 1.5–2.5 times (Fig. 13E); 1, > 2.5 times (Fig. 15E).
31. Pygofer, posterior process: 0, slim (Fig. 17E); 1, stout (Fig. 13E).
32. Pygofer, posterior process: 0, short (Fig. 15E); 1, elongate (Fig. 13E).
33. Pygofer, posterior process: 0, acute (Fig. 13E); 1, obtuse (Fig. 17E).
34. Pygofer, posterior process: 0, curved (Fig. 23E); 1, not curved (Fig. 24E).
35. Gonostyles, upper process: 0, acute (Fig. 22E); 1, obtuse (Fig. 23E).
36. Gonostyles, upper process: 0, not elongate (Fig. 13E); 1, elongate (Fig. 24E).
37. Aedeagus, very short small spines on apical lobes of phallobase: 0, absent; 1, present (Fig. 24G–H).
38. Aedeagus, endosomal processes: 0, short, just visible from phallotheca; 1, long, distinctly visible from phallobase.
39. Aedeagus, apex of endosomal processes: 0, acute (Fig. 22H); 1, obtuse (Fig. 21J).
40. Aedeagus, endosomal processes: 0, nearly straight; 1, curved in middle.
41. Aedeagus, number of ventral apical lobes: 0, one pair; 1, two pairs; 2, three pairs.

Table A4. *Continued*

42. Aedeagus, number of dorsolateral apical lobes: 0, absent; 1, one pair.
43. Aedeagus, number of dorsal apical lobes: 0, absent; 1, one pair.
44. Segment X, shape (dorsal view): 0, nearly oval (Fig. 17D); 1, truncate (projecting an angle on each side, Fig. 26E); 2, irregular.
45. Segment X in lateral view, ventral margins of apex: 0, not projecting; 1, projecting ventrally (Fig. 23E).
46. Segment X in lateral view, ventral margins of base: 0, not projecting; 1, projecting ventrally (Fig. 23E).
47. Segment X, ventral apical margin: 0, distinctly concave; 1, more or less concave or convex; 2, projecting in a central triangular process (Fig. 15E).

Table A5. Morphological character matrix used in the phylogenetic analysis of *Centromeria*

	0000000000	1111111111	2222222222	3333333333	44444444
Taxa	0123456789	0123456789	0123456789	0123456789	01234567
Dictyotenguna choui	0010000000	1000110100	0001000001	1111100010	01012110
Centromeria curva sp. nov.	1101011000	2211001001	1001111010	0110010010	11100011
Centromeria cuspidata sp. nov.	1101101000	2101100001	1000111110	1100111011	10101102
Centromeria deckerti sp. nov.	1101101000	2001100001	1000111010	1100111011	11101102
Centromeria inflata sp. nov.	1101101000	2101100001	1100111010	0011111111	12000001
Centromeria inspinata	1101011000	1211001001	1001111110	??????????	????????
Centromeria longipennis	1101101000	1101100001	1001111010	0011101010	10000001
Centromeria maculata sp. nov.	1101101101	0001100001	1001111010	1110001011	11100111
Centromeria melichari sp. nov.	1101101000	2001100001	1001111110	1100111011	11011102
Centromeria nigroapicata	1101101001	2001100001	1001111010	1110001010	11000001
Centromeria speilinea	1101011000	1211001001	1001111010	1110011010	10100111
Centromeria spinosa sp. nov.	1101101001	2101100001	1001111?10	0011111111	11000001
Centromeria surgens	1101011000	2211001001	1001111110	0110010010	10100011
Centromeria triangulata sp. nov.	1101101000	2001100001	1001111010	1000111011	10001102
Tenguna watanabei	1110011010	0001110111	0010110001	1110011101	00010001