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Systematic revision of Aluntiini Emeljanov, 1979 (Hemiptera: Fulgoromorpha: Dictyopharidae: Dictyopharinae): reclassification, phylogenetic analysis, and biogeography

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The dictyopharid planthopper tribe Aluntiini s.l. is revised and reclassified into two tribes: Aluntiini s.s. and Arjunini Song & Szwedo trib. nov. The tribe Aluntiini s.s. includes five genera: Aluntia Stål, 1866; Dendrophora Melichar, 1903 stat. rev.; Dictyomorpha Melichar, 1912; Indodictyophara Liang & Song, 2012; and Madagascaritia Song & Liang gen. nov. The new tribe Arjunini comprises two genera – Arjuna Muir, 1934 and Pippax Emeljanov, 2008 – both moved from Aluntiini s.l. Four new species – Aluntia longicephalica Song & Szwedo sp. nov., Madagascaritia angusta Song & Liang sp. nov., Arjuna maai Song & Wang sp. nov., and Arjuna muiri Song & Wang sp. nov. – are described. A morphologically based phylogenetic analysis is undertaken for Aluntiini, Arjunini, and the representatives of Dictyopharini, Hastini, Orthopagini, and the fossil Worskaitini within Dictyopharinae, all distributed in the Old World. A matrix of 129 characters of the habitus, coloration, head, thorax, and male and female genitalia of the adults was used for the cladistic analysis. The phylogenetic results show that Aluntiini s.l. as placed in Dictyopharidae is well supported, but it is distinctly paraphyletic and should be separated into two unambiguous tribes. A palaeotropical distribution pattern displayed by Aluntiini is suggested. The origin and diversification of Aluntiini are discussed preliminarily.

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ADDITIONAL KEYWORDS: **Arjunini trib. nov**. – cladistics – new genus – new species – new tribe – taxonomy.

INTRODUCTION

Dictyopharidae are the sixth largest family of Fulgoromorpha, containing more than 740 described species in 166 genera (Bartlett, O'Brien & Wilson, 2014; Song, Webb & Liang, 2014; Bourgoin, 2015). The species of the family are widely distributed in all biogeographic regions, especially in tropical and subtropical regions such as South America, the Oriental Region,

and the East Indies (Metcalf, 1946). Most dictyopharids are macropterous; however, a considerable number of species are brachypterous, such as Orgeriinae, Capenini, and Rancodini, associated with adaptation to the more xeric and cooler environments in arid and semi-arid regions. Members of the group are predominantly monocot feeders, and a few species are major agricultural pests on grasses (Wilson & O'Brien, 1987; Wilson *et al.*, 1994).

Most previous studies have shown that this family is the sister clade of the lanternfly family Fulgoridae, according to hypotheses of Fulgoromorpha phylogeny

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based on both morphological characters and DNA sequence data, although such analyses in general have included very few representatives of Dictyopharidae (Asche, 1987; Emeljanov, 1990; Yeh, Yang & Hui, 2005; Urban & Cryan, 2007; Song & Liang, 2013a). Morphologically, the Dictyopharidae–Fulgoridae lineage shares distinctive expandable male genitalia, one of the most important synapomorphies in both families. Like fulgorids, many dictyopharid species have an elongate head process, but this trait is not unique and is present in many other planthopper families (O'Brien, 2002; Urban & Cryan, 2009).

Dictyopharidae currently include 18 tribes in two subfamilies, Dictyopharinae and Orgeriinae, with most tribes erected by Emeljanov (1969, 1983, 1997, 2008, 2011b, 2014). The subfamily Orgeriinae, as a distinct lineage within Dictyopharidae, comprise four tribes (Colobocini, Almanini, Orgeriini, and Ranissini) restricted to the arid regions of the Holarctic region (Emelianov et al., 2005). The phylogenetic relationships and evolution of Orgeriinae were proposed by Emeljanov (1980) and Emeljanov et al. (2005). Distributed worldwide, Dictyopharinae comprise 12 extant tribes (Aluntiini, Capenini, Cleotychini, Dictyopharini, Hastini, Lappidini, Nersiini, Orthopagini, Phylloscelini, Rancodini, Scoloptini, and Taosini) and two fossil tribes (Netutelini and Worskaitini) (Melichar, 1912; Muir, 1923; Metcalf, 1946; Emeljanov, 1983, 1997, 2008, 2011b, 2014; Szwedo, 2008). No phylogenetic hypothesis has been published for the subfamily.

As in many other groups of Fulgoromorpha, quite a number of genera and suprageneric taxa of Dictyopharidae lack standard revisionary studies, and their monophyly has never been tested cladistically (Liang & Song, 2012). Emeljanov's classification of the tribes in Dictyopharidae provides a basic hypothesis for constructing a higher-level Dictyopharidae phylogeny with an explicit cladistic analysis in the future.

The tribe Aluntiini Emeljanov s.l. was initially recognized as the monotypic subfamily Aluntiinae and placed in Fulgoridae by Emeljanov (1979), based on the genus Aluntia previously belonging to the tribe Dictyopharini. Emeljanov (1979) suggested that six of 18 morphological characters for distinguishing the differences between Fulgoridae and Dictyopharidae support Aluntiinae belonging to Fulgoridae. Emeljanov (1979), however, also noted that the taxon still reserved some plesiomorphic features in the common ancestor of Fulgoridae and Dictyopharidae, perhaps closer to Dictyopharidae, and a further detailed study based on a mass of materials was required because only one species, Aluntia hova Nast, 1949, was examined, but the male and female genitalia were not analysed.

Emeljanov (2008) subsequently downgraded Aluntiinae into a tribe, viz. Aluntiini, and moved it back to the subfamily Dictyopharinae of Dictyopharidae after re-

evaluating those characteristics supporting the ascription of Aluntiinae to Fulgoridae. Simultaneously, three genera including submacropterous Arjuna Muir, 1934 and Pippax Emeljanov, 2008, which are both very different from Aluntia, were transferred to Aluntiini (Emeljanov, 2008). Nast (1949) noted that Aluntia contained diverse morphology and a disjunct distribution, implying that it is not a natural taxon, but he did not classify it further. Liang & Song (2012) revised the Austro-Oriental genus Dictyomorpha and described a related genus, Indodictyophara, from southern India. Aluntiini currently comprise five genera, namely, Aluntia, Arjuna, Dictyomorpha, Indodictyophara, and Pippax (Emeljanov, 2011b; Liang & Song, 2012).

As small but little-studied groups, both the genus *Aluntia* and the tribe Aluntiini appear to be non-monophyletic morphologically. The purposes of the present study are as follows: (1) to revise and reclassify this tribe; (2) to verify that the reclassified taxa are correct, through a morphologically based phylogenetic analysis; (3) to analyse their phylogenetic relationships and biogeographical distribution patterns; and (4) to discuss the taxonomic status of the reclassified taxa of Aluntiini within Dictyopharidae.

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; CAS, California Academy of Sciences, San Francisco, CA, USA; HNHM, Hungarian Natural History Museum, Budapest, Hungary; 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; MZLU, Museum of Zoology, Lund University, Lund, Sweden; NCSU, Department of Entomology Insect Collection, North Carolina State University, Raleigh, NC, USA; NHMD, Natural History Museum of Denmark, University of Copenhagen, Copenhagen, Denmark; NMPC, Department of Entomology, National Museum, Prague, Czech Republic; NRM, Swedish Museum of Natural History, Stockholm, Sweden; 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 general morphology, Bourgoin & Huang (1990) for male genitalia, and Bourgoin (1993) for female genitalia.

The posterior abdomens of the specimens used for dissection were cleared in 10% KOH at room temperature for ~6–12 h, rinsed in distilled H₂O, and then transferred to 10% glycerol for examination. Observations, measurements, and photography were conducted under a Zeiss Discovery V12 stereomicroscope equipped with a Nikon D7000 digital camera in IZCAS, or a Leica Z16 APO A stereomicroscope equipped with a Leica DFC495 microscope camera and Leica APPLI-CATION SUITE 3.7.0 in MFNB. The final images were compiled from multiple photographs using CombineZM image-stacking software and improved with Adobe PHOTOSHOP CS5. The morphological characters were also observed with a Zeiss Stemi SV II stereomicroscope and illustrated with the aid of a camera lucida attached to the microscope.

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

TAXON SAMPLING

A cladistic analysis of the morphological characters of adults was conducted, including 18 species of seven genera within Aluntiini s.l. Because there is no phylogenetic hypothesis linking Aluntiini s.l. with other dictyopharid tribes, we also included representatives of Dictyopharini, Hastini, Orthopagini, and the fossil amber Worskaitini within Dictyopharinae to test the monophyly of Aluntiini s.l. (Table A1). These non-Aluntiini representatives have a similar distribution pattern in the Old World, whereas the remaining tribes of Dictyopharinae are mostly restricted to the New World, except the brachypterous tribes Capenini and Cleotychini. The tested species are mostly the type material examined or revised by the first author and/or his collaborators (Liang & Song, 2006, 2012; Song & Liang, 2006a,b, 2007, 2008a,b, 2011a,b, 2012a,b: 2013b; Szwedo, 2008; Song, Bourgoin & Liang, 2011; Song, Deckert & Liang, 2012; Song et al., 2014).

Three fulgorid species – Zanna chinensis (Distant, 1893) (Zanninae, Fulgoridae), Dichoptera similis Schumacher, 1915 (Dichopterinae, Fulgoridae), and

Dorysarthrus sumakowi Oshanin, 1908 (Dorysarthrinae, Fulgoridae) – were chosen as out-group taxa to test the taxonomic status of Aluntiini s.l. within Dictyopharidae. Zanna was considered the least advanced in Fulgoridae (Emeljanov, 1979; Emeljanov & Shcherbakov, 2011). In the phylogenetic investigation of Fulgoridae based on molecular data, this genus was excluded from Fulgoridae and more closely allied with Dictyopharidae, even possibly within Dictyopharidae (Urban & Cryan, 2009). Dichoptera and Dorysarthrus originally belonged to Dictyopharidae, and were later transferred, along with Aluntiini, to the family Fulgoridae (Emeljanov, 1979).

CHARACTER ANALYSIS

The data matrix (Table A3) comprises 129 morphological characters from the habitus, coloration, head, thorax, and male and female genitalia of adults (Table A2). Bias towards any particular body part was avoided as much as possible. All characters were equally weighted, and all character states were treated as unordered. In the case of characters for which more than one state was observed for a given taxon, all of the states were considered (polymorphic). The character states were scored as dashes (–) if not applicable and as question marks (?) if ambiguous or unexamined.

The cladistic analysis was conducted with WinClada 1.00.08 (Nixon, 1999, 2002) and implemented in NONA 2.0 (Goloboff, 2000). Phylogenetic relationships were reconstructed with a heuristic analysis by searching for the most parsimonious (MP) trees with 100 maximum trees, 1000 replications, and ten starting trees per replication. The characters were selected to map the homoplasy/homology in the homoplasy setting dialogue, with any extra steps to make it homoplasious. The bootstrap values (Felsenstein, 1985) were used as support measures and calculated in NONA for the hypothesized clades with 1000 replications. The Bremer support was calculated in TNT 1.1 (Goloboff, Farris & Nixon, 2008) and obtained by tree bisection and reconnection (TBR) swapping on the mostparsimonious trees and setting 'suboptimal' to 50.

TAXONOMY

ALUNTIINI EMELJANOV, 1979 S.S.

Aluntiinae Emeljanov, 1979 (Fulgoridae): 10.

Aluntiini Emeljanov: Emeljanov 2008: 306; Emeljanov 2011b: 1124.

Type genus Aluntia Stål, 1866.

Diagnosis

The tribe can be distinguished by the following combination of characters: vertex with posterior margin

slightly surpassing posterior margin of eyes; antennal pedicel elongate; pronotum narrow and elongate, longer than half of mesonotum, disc flat and tricarinate; tegmina macropterous, without fold, apical one-third broadening inward and overlapping distally at rest; Sc+R and M originating from basal cell without distinct common stem; stigmal area absent; clavus open, claval suture not extending to posterior margin; hindwings without secondary fold in the anal area; fore femora spineless, hind tibiae with seven apical teeth, apical teeth of hind tarsomeres I and II with long setae; and female genitalia with ACL of gonapophysis VIII with two or three small, almost same-sized, teeth at apex, Gp1 of gonoplacs with sensory field with numerous tiny setae, without sensory appendage, and gonoplacs with third additional lobe (Gp3).

Diversity and distribution

Aluntiini s.s. comprises five genera and 14 species all found in the Old World tropics. Perhaps many more species are undescribed.

ALUNTIA STÅL, 1866

Aluntia Stål, 1866: 160; Distant 1906: 237; Melichar 1912: 30; Schmidt 1915: 350; Metcalf 1946: 45; Emeljanov 1979: 10.

Dendrophora Melichar, 1903: 21. Type species: Dendrophora ramosa Melichar, 1903; by original designation. Synonymized by Distant 1906: 237, and resurrected below.

Type species

Fulgora schimperii Guérin-Méneville, 1849, by original designation.

Diagnosis

The genus may be distinguished by the following combination of characters: from with intermediate carinae strongly elevated, median carina incomplete, distinctly elevated at apex and base, absent in middle; tegmina

with dendroid veins among longitudinal veins; Sc+R bifurcating into Sc+RA and RP beyond middle; M and CuA branched before Sc+R near middle; apical area covered with relatively fewer transverse veins; costal cell distinctly broad, with dendroid secondary veins from basal one-third or halfway to apex; aedeagus with a pair of slender, elongate, and sclerotized endosomal processes.

Redescription of adults

General colour ochraceous in dead specimens (probably viridescent or stramineous green in life).

Head (Figs 3A–C, 4A–C) distinctly elongate, 1.6– 2.0 times longer than pronotum and mesonotum combined. Cephalic process (Figs 3B, 4B) moderately compressed dorsoventrally from base to apex. Vertex (Figs 3A, 4A) without median carina, only median furrowed suture visible; lateral carinae distinctly ridged, broadly sulcate, nearly parallel, except slightly sinuate before eyes; apical margin angulately convex at ~90°, posterior margin arcuately concave. Frons (Figs 3C, 4C) with lateral carinae narrow and elongate; intermediate carinae strongly elevated, converging posteriorly and extending before eyes, not to frontoclypeal suture; apical margin angulately convex, distinctly expanding and projecting forwards, visible in dorsal view (Figs 3A, 4A); median carina incomplete, distinctly elevated at apex and base, absent in middle. Postclypeus and anteclypeus convex medially, with distinct median carina. Rostrum extending to base of hind femora, basal segment slightly longer than distal segment. Antennae (Figs 3B, 4B) strongly shifted backwards and curved anteriorly; pedicel with ~40 distinct sensory plaque organs distributed over entire surface.

Pronotum (Figs 3A, 4A) with anterior margin centrally arched, lateral marginal areas straight and sloping, posterior margin angulately concave at ~100°; disc flat and tricarinate, median and intermediate carinae distinct and complete, with a lateral pit at side of median carina; lower lateral carinae between eyes

and tegulae visible in dorsal view. Tegmina (Fig. 2A, B) transparent and elongate, 2.8–3.3 times as long as broad; apex rounded; basal two-thirds with dendroid nodose secondary veins sparsely or densely interspersed among longitudinal veins; M and CuA branched before Sc+R near middle; M branching into accessory veins successively three or four times; apical area covered with relatively fewer transverse veins and 15 or 16 apical cells; costal cell between costal margin and Sc+R distinctly broad.

Legs very elongate and slender, hind tibiae with four or five black-tipped lateral spines (the extreme basal spine very small and obscure); hind tarsomeres I and II with five or six and six or seven black-tipped apical teeth, respectively.

Male genitalia with pygofer in lateral view distinctly wider ventrally than dorsally (Figs 3E, 4E); dorsal margin excavated to accommodate segment X, dorsolateral margins slightly produced posteriorly in dorsal view (Figs 3D, 4G). Gonostyles (Fig. 4F) symmetrical; base narrow, expanded towards middle, and then gradually narrowed towards apex; apex rounded bluntly and projecting backwards; upper margin with a long process directed dorsally near middle, apically obtuse; outer upper edge with a long ventrally directed, hook-like process near sub-middle. Aedeagus (Figs 3G-I, 4H-J) with a pair of slender and elongate endosomal processes extended from phallotheca; pigmented and sclerotized dorsally, membranous ventrally, moderately inflated, abruptly curved in middle, and gradually narrowed to acute; phallobase sclerotized and pigmented at base and laterally, the remainder membranous. Segment X (Figs 3D, 4G) narrow and elongate, base narrow, gradually expanded towards apex. Anal styles very short and small.

Female genitalia (Fig. 5A, B) with gonocoxae VIII with GxP membranous and flattened, in which a slender sclerotized plate is visible, apex with numerous setae dorsally (Fig. 5C). Gonopophyses VIII with ACL moderately sclerotized with two small apical teeth and numerous setae dorsally (Fig. 5D). Gonopophyses IX (Fig. 5E) with PCL mostly membranous, apex with numerous setae; posterior fibula (Fp) extending to gonospiculum (Gl). Gonoplacs (Fig. 5F, G) with three processes: the two posterior lobes (Gp1 and Gp2) homologous and fused basally; Gp1 large and moderately sclerotized, with a sensory field with numerous tiny setae at apex (Fig. 5D, E); the third process (Gp3) very small and membranous (Fig. 5G). Segment X in dorsal view relatively short and broad, with ratio of length to width at subapex ~2.0 : 1.0 (Fig. 5H).

Description of fifth-instar nymphs

The general habitus of the fifth-instar nymphs is very similar to that of adults, but the wings are undeveloped and the body is covered with numerous sensory pits.

Head (Fig. 6A-C) very elongate, distinctly broad and robust apically; cephalic process somewhat compressed laterally, distinctly upturned at apex. Vertex (Fig. 6A) with lateral carinae strongly ridged, median carina absent, replaced by median furrowed suture. Frons (Fig. 6C) with 45-50 sensory pits between lateral and intermediate carinae, mostly distributed in apical area; intermediate carinae prominent, extending to frontoclypeal suture, area between intermediate carinae broad and flat before eyes, narrowed and deeply grooved from eyes to frontoclypeal suture, median carina absent. Postclypeus and anteclypeus convex medially, with median carina indistinct. Rostrum moderately long, extending to hind coxae. Compound eyes prominent, ocelli absent. Antennae with pedicel cylindrical, possessing ~40 distinct sensory plaque organs distributed over entire surface.

Pronotum (Fig. 6A) distinctly narrow, produced anteriorly, posterior margin angulately concave; disc with 14–16 sensory pits between median carina and upper lateral carinae, and five pits between upper and lower lateral carinae. Mesonotum (Fig. 6D) with five or six pits outside lateral carinae. Metanotum (Fig. 6D) with six or seven pits outside lateral carinae. Tegmen pads (Fig. 6D) each with five or six pits arranged in longitudinal line on disc. Legs similar to adults, very elongate and slender.

Abdomen (Fig. 6D) nine-segmented, elongate, and slightly flat dorsoventrally. Tergites I-VIII with distinct median carina; tergites IV-VI with four, seven, and four pits between lateral carinae and median carina, nine, eight, and zero pits between lateral margin and lateral carinae, respectively; tergites VI–VIII each with a pair of very large wax-secreting plates that occupy almost whole tergite (Fig. 6E); wax plates on tergite VI transversely elongate and narrower than those on tergites VII and VIII, those on tergite VII very broad and transversely elongate, and those on tergite VIII largest and longitudinally elongate; surface of wax plates covered with numerous fine cuticular structures for moulding wax, with the wax gland pores and longitudinal linear areas separating wax gland pores (Liang & Song, 2012).

Diversity and distribution

The revised genus is composed of two species restricted to the Afrotropical region, excluding Madagascar.

Remarks

Aluntia originally included four known species: Aluntia borneensis Schmidt, 1915 (Malaysia), Aluntia hova Nast, 1949 (Madagascar), Aluntia ramosa (Melichar, 1903) (Sri Lanka), and Aluntia schimperii (Guérin-Méneville, 1849) (type species, Afrotropical region). Nast (1949) noted the morphological disparity and disjunct geographic distribution within Aluntia, but he still 'decided

KEY TO SPECIES OF ALUNTIA STÅL

to consider provisionally all the above-mentioned species as belonging to the genus *Aluntia* Stål until more material is obtainable (Nast, 1949: 125). We examined more *Aluntia* material involving most historical types and found two new species. Our results support the division of this unnatural taxon into three monophyletic groups: *Aluntia*, *Dendrophora*, and *Madagascaritia* gen. nov.

The revised *Aluntia* can be distinguished from *Dendrophora* and *Madagascaritia* by the frons with the median carina distinctly elevated at apex and base, and absent in the middle, the tegmina with Sc+R vein bifurcating into Sc+RA and RP veins beyond the middle, and M and CuA veins branched before Sc+R in the middle.

ALUNTIA LONGICEPHALICA SONG & SZWEDO SP. NOV. (FIGS 1A, 2A, 3A–I)

Description

General colour ochraceous, with a large pale black spot at apex of head; ♂, BL 17.8 mm, HL 5.7 mm, HW 1.3 mm, TL 10.5 mm.

Head (Fig. 3A–C) much longer, nearly two times longer than pronotum and mesonotum combined. Tegmina (Fig. 2A) distinctly narrow and elongate, nearly 3.3 times as long as broad; basal two-thirds with nodose veins sparsely interspersed among longitudinal veins.

Male genitalia with pygofer broad, with ratio of ventral to dorsal width ~2.1: 1.0 in lateral view; posterior margin more or less projecting near upper middle (Fig. 3E). Gonostyles with upper process long, directed dorsally, and obtuse apically (Fig. 3E). Aedeagus with endosomal processes curved dorsally in middle, apical part turned ventrolaterally; in dorsal view, inflated dorsal lobe of phallobase with long slender process, directed anteriorly, acute apically (Fig. 3I); in ventral view with two lamellar processes ventrally (Fig. 3G). Segment X in dorsal view with ratio of length to width at apex of ~2.5: 1.0 (Fig. 3D).

Material examined

Holotype of, Cameroon: Kamerun, Conradt, 8 (MMBC).

Etymology

The new species is named for its extremely elongate cephalic process.

Distribution

Cameroon.

Remarks

The new species can be easily separated from *A. schimperii* by the longer cephalic process and the elongate and slender tegmina with fewer nodose veins.

ALUNTIA SCHIMPERII (GUÉRIN-MÉNEVILLE, 1849) (FIGS 1B, 2B, 4A–J, 5A–H)

Fulgora schimperii Guérin-Méneville, 1849: 343, pl. 6, fig. 7a–c.

Aluntia schimperii (Guérin-Méneville): Stål 1866: 160; Distant 1907: 189, pl. XIX, fig. 5a, b; Melichar 1912: 30, pl. II, figs 20, 21; Metcalf 1946: 46.

Aselgeia longiceps Melichar, 1905: 28. Synonymized by Melichar 1912: 62.

Redescription

BL, \circlearrowleft 16.8–18.5 mm, \circlearrowleft 17.5–18.7 mm; HL, \circlearrowleft 5.2–6.0 mm, \circlearrowleft 5.5–5.7 mm; HW, \circlearrowleft 1.2 mm, \circlearrowleft 1.3 mm; TL, \circlearrowleft 10.2–10.8 mm, \circlearrowleft 10.2–11.0 mm.

Head (Fig. 4A–C) relatively short, nearly 1.6–1.7 times longer than pronotum and mesonotum combined. Tegmina (Fig. 2B) distinctly broader, nearly 2.8 times as long as broad; basal two-thirds with nodose veins densely interspersed among longitudinal veins.

Male genitalia similar to *A. longicephalica* sp. nov., in lateral view pygofer with ratio of ventral to dorsal width ~2.4:1.0 (Fig. 4E). Gonostyles with upper process more or less directed inwards and apically obtuse (Fig. 4E). Aedeagus with endosomal processes curved laterally in middle, apical part turned ventrolaterally; in dorsal view phallobase stout, dorsal lobe with longer and slender process (Fig. 4J), and in ventral view two lamellar processes ventrally (Fig. 4H). Segment X in dorsal view with ratio of length to width at apex of ~2.5:1.0 (Fig. 4G).

Female genitalia (Fig. 5A-H) as in generic description.

Type material examined

Holotype ♀ of Aselgeia longiceps Melichar, 1905, [Tanzania]: O. Afr., Kiboteni, 12.VI.1904; Aselgeia Walk.; longiceps [Melichar's handwriting], Melichar det.; Typ. Exempl. Dr. L Melichar; Aluntia schimperii Guer. [Melichar's handwriting]; Holotypus (red label); ♀,

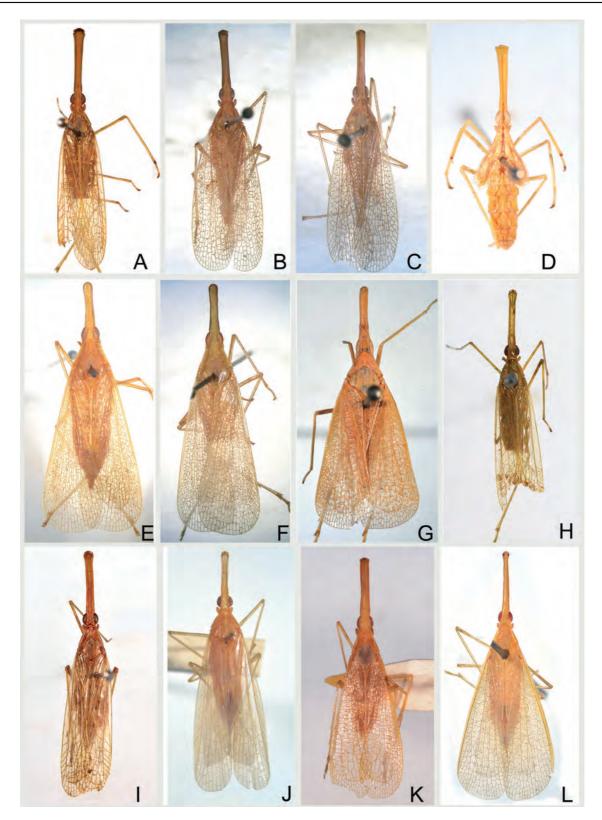


Figure 1. A, Aluntia longicephalica sp. nov., male; B, Aluntia schimperii, male; C, Aluntia schimperii, female; D, Aluntia sp. indet., fifth-instar nymph; E, Dendrophora borneensis, male; F, Dendrophora borneensis, female; G, Dendrophora ramosa, male; H, Dictyomorpha hectica, male; I, same, female; J, Indodictyophara lobosa, female; K, Madagascaritia angusta sp. nov., male; L, Madagascaritia hova, female.

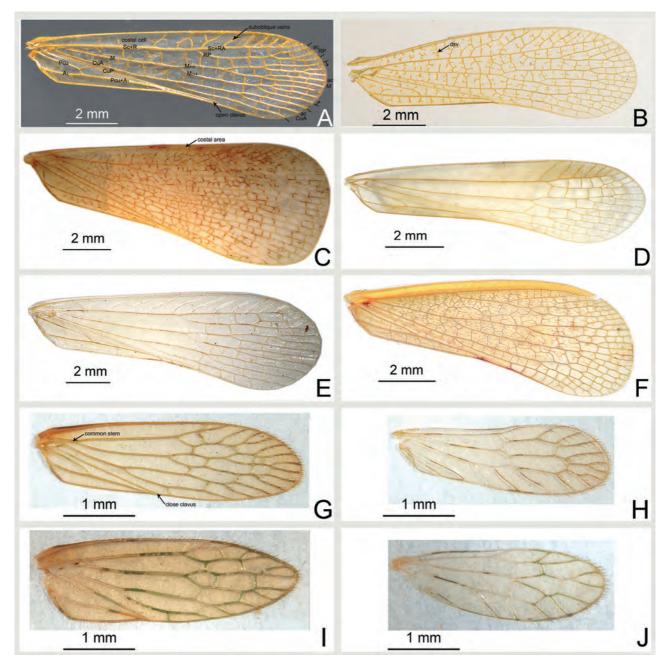


Figure 2. Tegmina (A–F, G, I) and hindwings (H, J) of Aluntiini and Arjunini trib. nov. A, *Aluntia longicephalica* sp. nov.; B, *Aluntia schimperii*; C, *Dendrophora borneensis*; D, *Dictyomorpha moluccana*; E, *Indodictyophara lobosa*; F, *Madagascaritia hova*; G, H, *Arjuna scriba*; I, J, *Pippax opilionoides*. Abbreviations: ac, apical cell; dsv, dendroid secondary veins.

Aselgeia longiceps Melichar, det. Melichar 1905 [Lauterer's handwriting] P. Lauterer det. 1991 (MMBC).

Other material examined

Cameroon: 10° , Makak, 1949–50, 6–13.XII., 29, J.B.–S., J.D., *Aluntia schimperii* Gu-Mén, det. R.G. Fennah; 1° , Disp. 1949–50, 21.XII., 63, J.B.–S., J.D. (both in

BMNH); $1\circlearrowleft$ (NHRS-GULI 000009214), Camerun, Valdau (NRM); $1\circlearrowleft$, Kamerun, Conradt; Melichar det.; $1\circlearrowleft$, N. Camerun, Johann Albrechtshöhe; coll. Breddin; Aluntia schimperii Guer.; Melichar det. (both in SDEI); $1\circlearrowleft$, Kamerun, Conradt; Aluntia Stål (Dendrophora Mel.) schimperii Guer. (Melichar's handwriting (MMBC); $1\circlearrowleft$, N. Kamerun, Johann Albrechtshöhe, L. Conradt S; $1\circlearrowleft$, Neu-Kamerun, No. 507–15, Tessmann S.G.; Aluntia

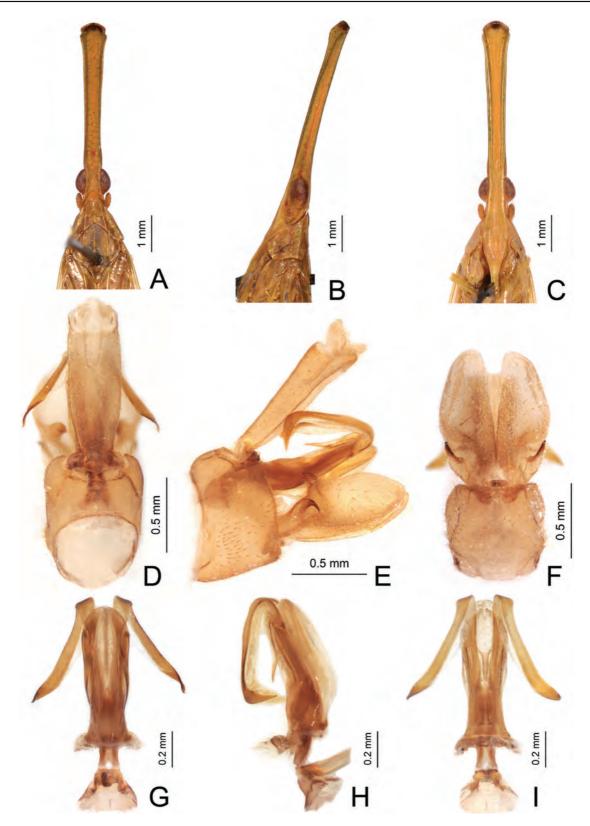


Figure 3. Aluntia longicephalica sp. nov. A, head, pronotum and mesonotum, dorsal view; B, head, lateral view; C, head, ventral view; D, pygofer and segment X, dorsal view; E, male genitalia, lateral view; F, pygofer and gonostyles, ventral view; G, aedeagus, ventral view; H, aedeagus, lateral view; I, aedeagus, dorsal view.

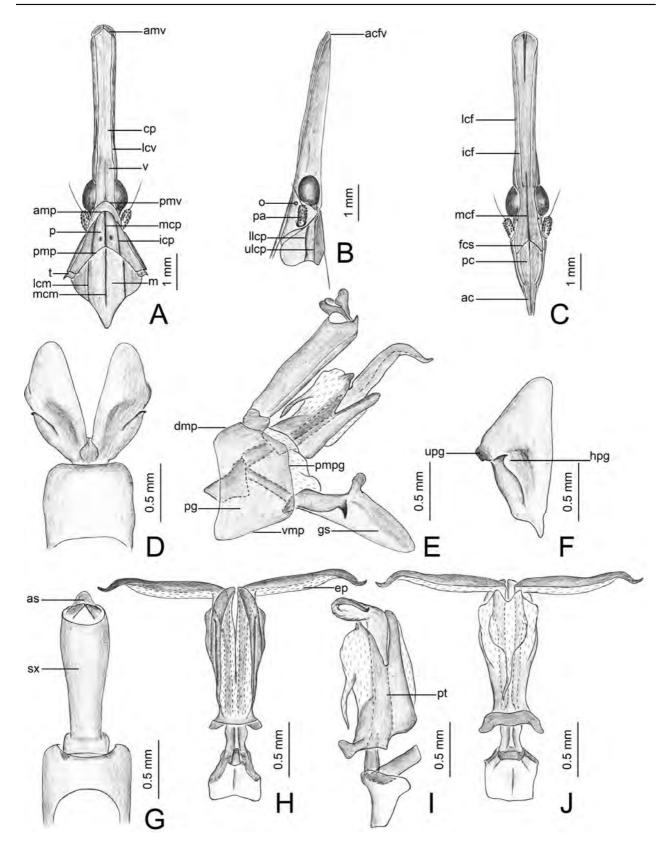


Figure 4. Aluntia schimperii. A, head, pronotum, and mesonotum, dorsal view; B, head, lateral view; C, head, ventral view; D, pygofer and gonostyles, ventral view; E, male genitalia, lateral view; F, gonostyles, lateral view; G, pygofer and segment X, dorsal view; H, aedeagus, ventral view; I, aedeagus, lateral view; J, aedeagus, dorsal view. Abbreviations: ac, anteclypeus; acfv, apical carina between anterior margins of frons and vertex; amp, anterior margin of pronotum; amv, anterior margin of vertex; as, anal style; cp, cephalic process; dmp, dorsal margin of pygofer in profile; ep, endosomal processes; fcs, frontoclypeal suture; gs, gonostyle; hpg, hook-like process of gonostyle; icf, intermediate carina of frons; icp, intermediate carina of pronotum; 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; 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; pt, phallotheca; sx, segment X (anal tube); t, tegula; ulcp, upper lateral carina of pronotum; upg, upper process of gonostyle; v, vertex; vmp, ventral margin of pygofer in profile.

schimperii Guer. [Synave's handwriting], H. Synave det., 1972 (both in MFNB).

Equatorial Guinea: 1♀, Span Guinea, Nkolentangan, 7.XI–8.V, G. Peβmann S.G. (MFNB).

Togo: 1♀, Misahöhe, Mitte V.1894, E. Saumann (MFNB).

Distribution

Ethiopia, Cameroon, Equatorial Guinea, Kenya, South Africa, Congo, West Africa, and East Africa.

ALUNTIA SP. INDET. (FIG. 6A–E)

Material examined

Cameroon: one nymph (NHRS-GULI 000009241), Kamerun, Mungo, Mukonje Fram (NRM).

Distribution Cameroon.

Remarks

It is difficult to decide to which species this nymph specimen belongs because *A. schimperii* is widely distributed in the Afrotropical region (Metcalf, 1946).

DENDROPHORA MELICHAR, 1903 STAT. REV.

Dendrophora Melichar, 1903: 21.

Synonymized under *Aselgeia* Walker, 1851 by Melichar 1905: 281.

Synonymized under *Aluntia* Stål, 1866 by Distant 1906: 237 and here resurrected.

Type species

Dendrophora ramosa Melichar, 1903; by original designation.

Diagnosis

The genus can be separated from other Aluntiini genera by the following combination of characters: from with intermediate carinae weakly ridged, median carina incomplete, absent in middle; tegmina somewhat truncate apically, with numerous dendroid nodose veins; Sc+R and M branched before CuA at basal one-third; apical area densely covered with transverse veins; costal cell distinctly broad, with dendroid nodose veins in entire area; and aedeagus with a pair of slender, elongate, sclerotized endosomal processes.

Redescription

Body distinctly large and robust. General colour ochraceous in dead specimens (probably viridescent or stramineous green in life).

Head (Figs 7A–C, 9A–C) as long as or a little longer than pronotum and mesonotum combined. Cephalic process (Figs 7B, 9B) more or less compressed dorsoventrally. Vertex (Figs 7A, 9A) with median carina absent, only median furrowed suture visible between eyes; lateral carinae ridged, nearly parallel, relatively broad and flat towards apex; anterior margin angulately convex at ~90°, posterior margin indistinct, sloped down into the pronotum. Frons (Figs 7C, 9C) with intermediate carinae converging posteriorly and extending before compound eyes; median carina incomplete, distinct at apex and base, absent in middle. Rostrum, eyes, ocelli, and antennae similar to *Aluntia*.

Pronotum and mesonotum (Figs 7C, 9C) similar to *Aluntia*, but mesonotum with lateral carinae more or less curved outwards. Tegmina (Fig. 2C) transparent, large, and broad, nearly 2.4–2.5 times as long as broad; apex somewhat truncate; anterior margin distinctly expanded into broad sclerotized costal area; basal two-thirds to four-fifths with dendroid veins densely interspersed among longitudinal veins; Sc+R and M branched before CuA at basal one-third; M_{3+4} bifurcating M_3 and M_4 not beyond the middle; Sc+R, M, and CuA branching into accessory veins successively four times; apical area densely covered with transverse veins, with 21–25 apical cells; costal cell distinctly broad, with numerous dendroid veins in entire area. Legs similar to *Aluntia*.

Male genitalia with pygofer similar to *Aluntia*, in lateral view posterior margin more or less projecting near upper middle (Figs 7E, 9E), in dorsal view

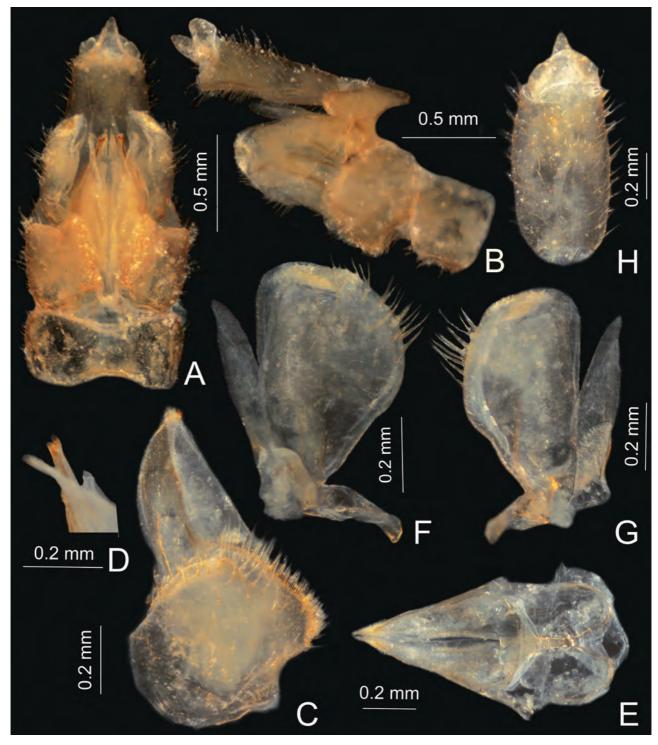


Figure 5. Aluntia schimperii. A, female genitalia, ventral view; B, female genitalia, lateral view; C, gonopophysis VIII, dorsolateral view; D, teeth of anterior connective lamina (ACL) of gonopophyses VIII; E, gonopophysis IX, ventral view; F, gonoplacs, lateral view; G, gonoplacs, dorsolateral view; H, female segment X, dorsal view.

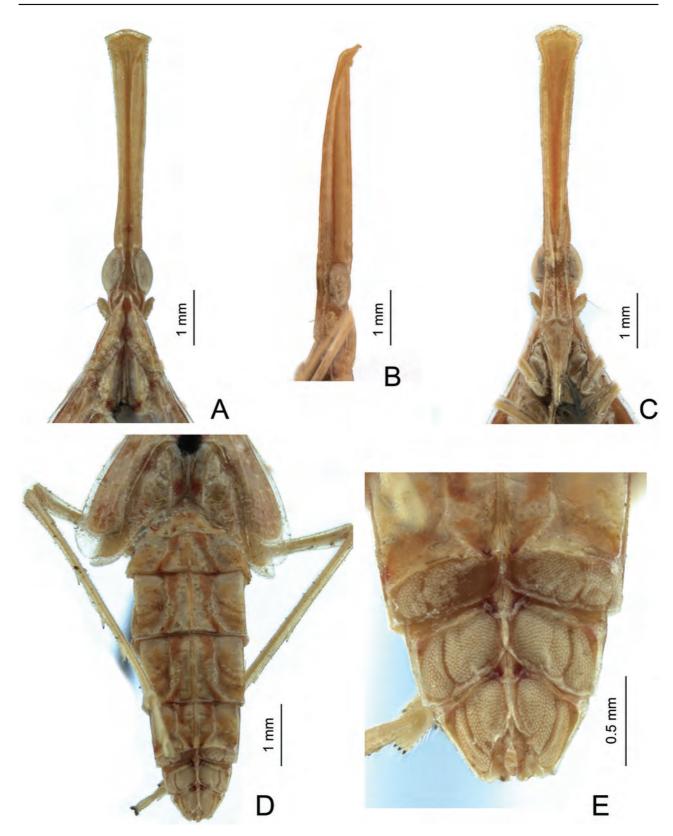


Figure 6. Fifth-instar nymph of *Aluntia* sp. A, head and pronotum, dorsal view; B, head, lateral view; C, head, ventral view; D, thorax and abdomen, dorsal view; E, abdominal tergites VI–VIII, dorsal view showing wax plates.

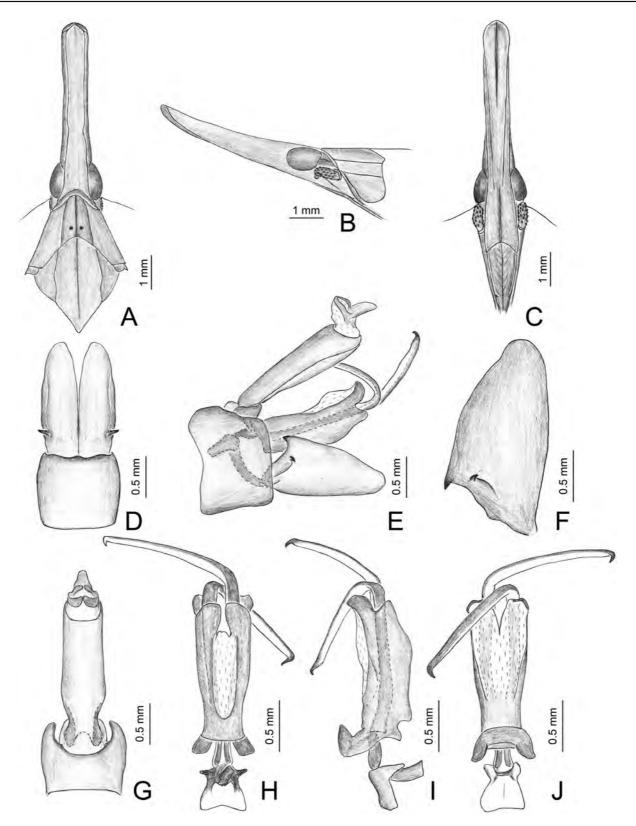


Figure 7. Dendrophora borneensis. A, head, pronotum, and mesonotum, dorsal view; B, head, lateral view; C, head, ventral view; D, pygofer and gonostyles, ventral view; E, male genitalia, lateral view; F, gonostyles, lateral view; G, pygofer and segment X, dorsal view; H, aedeagus, ventral view; I, aedeagus, lateral view; J, aedeagus, dorsal view.

KEY TO SPECIES OF DENDROPHORA MELICHAR

- 1. Gonostyles with upper process acute (Fig. 7F); segment X narrow and elongate (Fig. 7G)......
- Gonostyles with upper process large, broad, and blunt (Fig. 9F); segment X oval, large, and broad in dorsal view

dorsolateral margins slightly produced posteriorly (Figs 7G, 9G). Gonostyles similar to Aluntia. Aedeagus (Figs 7H–J, 9H–J) with a pair of slender and elongate endosomal processes extended from phallotheca: pigmented and sclerotized ventrally, abruptly curved in middle, apex hook-like and acute; phallobase sclerotized and pigmented at base and laterally, the remainder membranous, without inflated lobe; apex produced in two lamellar processes dorsally and ventrally, respectively.

Female genitalia similar to Aluntia, but gonopophyses VIII with ACL with three small apical teeth.

Diversity and distribution

This Oriental genus comprises two species found in Sri Lanka, Indonesia, and Malaysia.

Remarks

Dendrophora was established by Melichar to contain a single species, D. ramosa, from Sri Lanka (Melichar, 1903). Melichar (1905) synonymized this genus with the Afrotropical genus Aselgeia and Distant (1906) synonymized it with another Afrotropical genus Aluntia. In our analysis, the species Aluntia borneensis and Aluntia ramosa represent an independent genus; therefore, here, we resurrect *Dendrophora* from synonymy with Aluntia. As these two species were included in Metcalf's (1946) catalogue of world Dictyopharidae, they have not been mentioned. We herein describe and illustrate for the first time their male and female genitalia.

The genus differs from Aluntia in the following characters: the apex of the tegmina truncate, M vein distinctly bifurcated before CuA, and M₃₊₄ bifurcating M₃ and M₄ not beyond the middle.

DENDROPHORA BORNEENSIS (SCHMIDT, 1915) **COMB. NOV.** (FIGS 1E, F, 2C, 7A–J, 8A–E)

Aluntia borneensis Schmidt, 1915: 350; Metcalf 1946: 46.

Redescription

BL, \bigcirc 22.2 mm, \bigcirc 21.7 mm; HL, \bigcirc 5.5 mm, \bigcirc 5.2 mm; HW, \circlearrowleft 1.5 mm, \circlearrowleft 1.5–1.7 mm; TL, \circlearrowleft 13.4 mm, \circlearrowleft 12.9– 14.7 mm.

Head (Fig. 7A-C) as long as or a little longer than pronotum and mesonotum combined. Tegmina (Fig. 2C) nearly 2.5 times as long as broad; basal two-thirds with dendroid veins dense.

Male genitalia with pygofer, with ratio of ventral to dorsal width ~2.0:1.0, posterior margin more or less projecting near upper middle in lateral view (Fig. 7E). Gonostyles with apex bluntly rounded and distinctly projecting backwards; in lateral view upper margin with a small acute process directed anteriorly near middle (Fig. 7F). Aedeagus with endosomal processes abruptly curved dorsolaterally in middle, and crossing each other; phallobase with apex produced in two lamellar processes dorsally and ventrally, respectively; dorsal pair elongate and large (Fig. 7H–J). Segment X in dorsal view narrow and elongate, base widest, slightly narrowed towards apex, with ratio of length to width at base ~2.7:1.0 (Fig. 7G). Female genitalia (Fig. 8A– E) as described in generic description.

Type material examined

Holotype ♀ (MIZ 313168), [Malaysia]: Baram, Oct. 17, 1910; Type [red label]; Aluntia borneensis Schmidt, 1915 [Schmidt's handwriting], Q, Edm. Schmidt, determ. 1916; 253 [white label] (Mus. Zool. Polonicum, Warszawa, 12/45; MIZPAS).

Other material examined

Malaysia: 107, North Borneo (SE), Forest Camp, 19 km, N. of Kalabakan, 30.X.1962, K.J. Kuncheria; 107, Penang, 22–26.XII.1958, L.W. Quate; 1, PEN, SE Pahang, Rompin Mining Co., Railway Track, 32-37 km, Petoh, 24.I.1961, T.C. Maa (all in BPBM).

Indonesia: 1 nymph (MIZ 313205), Soekaranda, I.1894, Dohrn; Doryphorina stali Mel [Schmidt's handwriting], Edm. Schmidt, determ. 1915 (Mus. Zool. Polonicum, Warszawa, 12/45; MIZPAS).

Distribution

Indonesia (Sumatra) and Malaysia (Malay Peninsula, northern Borneo).

DENDROPHORA RAMOSA MELICHAR, 1903 STAT. REV. (FIGS 1G, 9A–J)

Dendrophora ramosa Melichar, 1903: 22, pl. I, fig. 5.

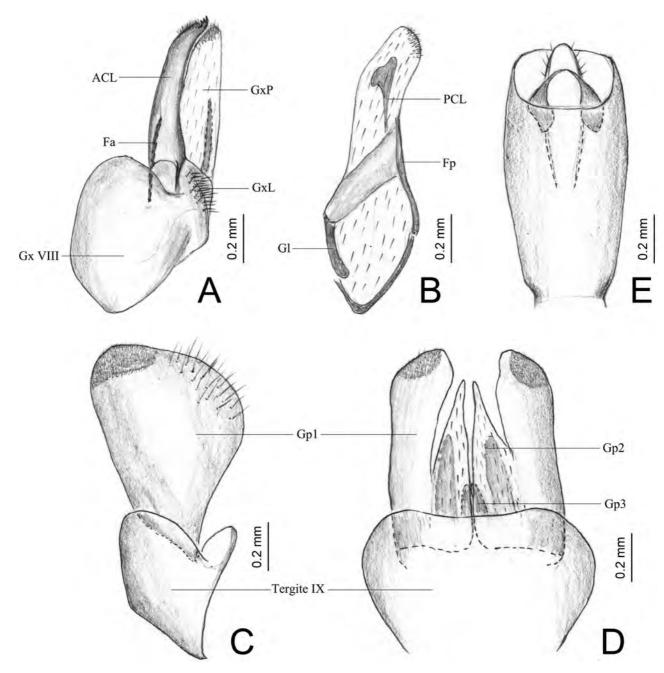


Figure 8. Dendrophora borneensis. A, segment X of female, dorsal view; B, gonopophysis VIII, dorsolateral view; C, gonopophysis IX, lateral view; D, gonoplacs, lateral view; E, gonoplacs, dorsal view. Abbreviations: ACL, anterior connective lamina; Fa, anterior fibula; Fp, posterior fibula; Gl, gonospiculum; Gp1, gonoplac 1; Gp2, gonoplac 2; Gp3, gonoplac 3; Gx VIII, gonocoxae VIII; GxL, endogonocoxal lobe; GxP, endogonocoxal process; PCL, posterior connective lamina.

Aluntia ramosa (Melichar): Distant 1906: 241, fig. 105; Melichar 1912: 63; Metcalf 1946: 46.

Redescription

BL, of 14.8–16.6 mm; HL, of 4.5–4.9 mm; HW, of 1.1–1.2 mm; TL, of 9.4–10.5 mm.

Head (Fig. 9A–C) elongate, 1.2–1.3 times as long as pronotum and mesonotum combined. Tegmina nearly 2.4 times as long as broad; basal four-fifths with dendroid veins dense.

Male genitalia with pygofer with ratio of ventral to dorsal width ~2.0: 1.0 in lateral view, posterior margin

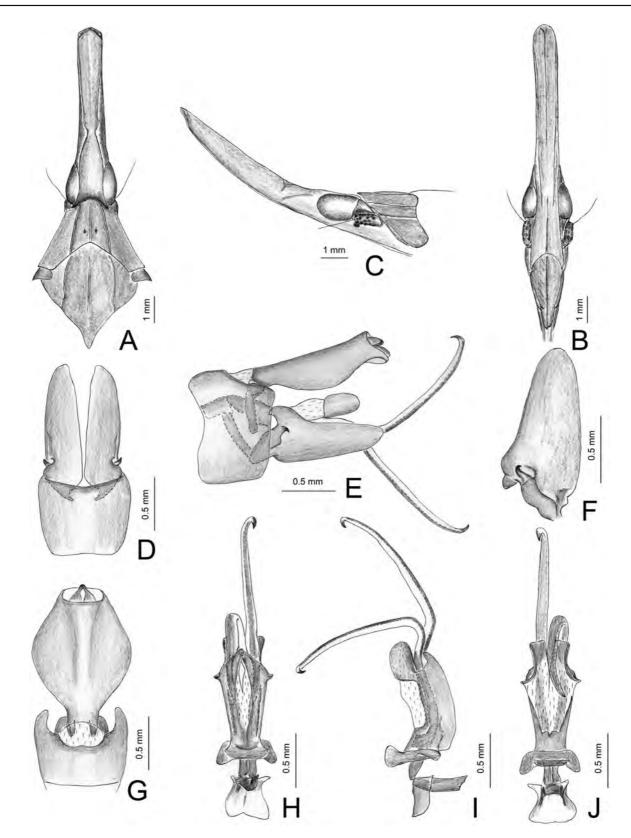


Figure 9. Dendrophora ramosa. A, head, pronotum, and mesonotum, dorsal view; B, head, lateral view; C, head, ventral view; D, pygofer and gonostyles, ventral view; E, male genitalia, lateral view; F, gonostyles, lateral view; G, pygofer and segment X, dorsal view; H, aedeagus, ventral view; I, aedeagus, lateral view; J, aedeagus, dorsal view.

distinctly projecting near upper middle (Fig. 9E). Gonostyles with apex bluntly rounded and strongly projecting backward; in lateral view upper margin with a large, broad, and blunt process near middle, directed anteriorly (Fig. 9F). Aedeagus with endosomal processes abruptly curved dorsolaterally in middle; phallobase with apex produced in two lamellar processes dorsally and ventrally, respectively: dorsal pair elongate and large (Fig. 9H–J). Segment X in dorsal view oval, large, and broad, with ratio of length to width in middle ~1.3: 1.0 (Fig. 9G).

Type material examined

Syntype of, [Sri Lanka]: 2–86; 239; romosa [Melichar's handwriting], det. Melichar; Aselgeia = Dendrophora [Melichar's handwriting]; Aluntia romosa [Melichar's handwriting]; Collection Dr. Melichar; Dendrophora ramosa sp.n. L. Melichar, 1903 [Lauterer's handwriting], P. Lauterer det. 1991 (MMBC).

Other material examined

[Sri Lanka]: 10°, Ceylon, E. Prov., Kuchchavell, 20 miles NW Trincomalee, 9–10.II.1962, Loc. 60., Semi desert; 10°, Ceylon, E. Prov., Madura Oya, 15 miles NNW Bibile, 13.III.1962, Loc. 138., Swept on veg, by stream (both in MZLU, Lund University Ceylon Expedition 1962, Brinck-Andersson-Cederholm).

Distribution Sri Lanka.

Remarks

Distant (1906) listed that *D. ramosa* was recorded from the Malay Peninsula, but his description probably represented a *D. borneensis*. Nast (1949) suggested that the record from the Malay Peninsula was wrong.

DICTYOMORPHA MELICHAR, 1912

Dictyomorpha Melichar, 1912: 103; Metcalf 1946: 81; Emeljanov 2008: 372; Emeljanov 2011b: 1144; Liang & Song 2012: 404.

Amboina Kirkaldy, 1913: 16; Metcalf 1946: 86. Type species: Amboina moluccana Kirkaldy, 1913; by original designation. Synonymized by Emeljanov 2011b: 1144.

Type species

Dictyomorpha elongata Melichar, 1912; by original designation.

Diagnosis

The genus may be distinguished by the following combination of characters: cephalic process distinctly compressed dorsoventrally, flat and narrowing from base to apex; frons with intermediate carinae strongly elevated, median carina complete, strongly elevated at

apex, and slightly keeled in middle; tegmina distinctly elongate, without dendroid secondary veins; Cu branched before Sc+R and M; costal cell with suboblique veins on apical one-third; male pygofer with an obtuse posterior process; and aedeagus with a pair of elongate, large, strongly inflated, and membranous endosomal processes.

Diversity and distribution

Dictyomorpha includes seven species and exhibits an Austro-Oriental distribution.

Remarks

This genus was recently revised by Liang & Song (2012). Six species, except for *Dictyomorpha hectica* Haupt, 1926, were described and illustrated, along with fifth-instar nymph and wax glands of parts of *Dictyomorpha* species.

DICTYOMORPHA HECTICA HAUPT, 1926 (Figs 1H, I, 10A–I)

Dictyomorpha hectica Haupt, 1926: 431; Metcalf 1946: 81, Liang & Song 2012: 412, figs 4, 13.

Redescription

Body relatively small. General colour ochraceous in dead specimens (probably viridescent or stramineous green in life). BL, \circlearrowleft 16.9 mm, \circlearrowleft 18.6 mm; HL, \circlearrowleft 5.4 mm, \circlearrowleft 5.7 mm; HW, \circlearrowleft 1.1 mm, \circlearrowleft 1.2 mm; TL, \circlearrowleft 10.5 mm, \circlearrowleft 12.3 mm.

Cephalic process (Fig. 10A–C) 1.9 times as long as pronotum and mesonotum combined. Vertex (Fig. 10A) with median carina distinct only at extreme apical part and basal one-fifth, rest of carina indistinct and sometimes slightly sutured. Frons (Fig. 10C) with intermediate carinae strongly elevated and blade-like, converging at eye level; median carina complete. Tegmina elongate and slender, nearly 3.5 times as long as broad; costal cell with between six and eight suboblique veins.

Male genitalia with pygofer relatively large and broad, with ratio of ventral to dorsal width ~1.4:1.0, in lateral view posterior margin distinctly produced posteriorly near middle, with posteriorly produced part obtuse apically (Fig. 10E); in dorsal view dorsal margin excavated to accommodate segment X, dorsolateral margins strongly produced posteriorly (Fig. 10F). Gonostyles symmetrical; base narrow, expanded towards middle, then gradually narrowed towards apex; apex bluntly rounded; upper process large and blunt, directed dorsally (Fig. 10E). Aedeagus (Fig. 10G–I) with endosomal processes extended from phallotheca: in lateral view apical half membranous and inflated, turned dorsoposteriorly; relatively short, small, and slender, apex acute; phallobase relatively narrow and elongate, phallobase

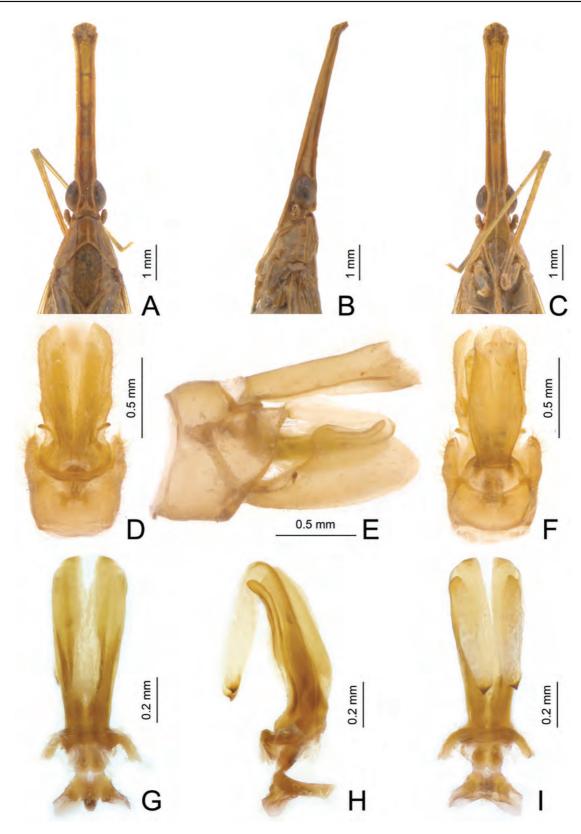


Figure 10. Dictyomorpha hectica. A, head, pronotum, and mesonotum, dorsal view; B, head, lateral view; C, head, ventral view; D, pygofer and gonostyles, ventral view; E, male genitalia, lateral view; F, pygofer and segment X, dorsal view; G, aedeagus, ventral view; H, aedeagus, lateral view; I, aedeagus, dorsal view.

with two membranous lobes ventrally. Segment X in dorsal view with ratio of length to width in middle $\sim 2.1:1.0$ (Fig. 10F).

Type material examined

Paratype \c , [Philippines]: Mt. Banahao, Luzon, IV.1923, $Dictyomorpha\ hectica\$ Hpt. [Haupt's handwriting], Paratypoid [red label], \c , $Dictyomorpha\ hectica\$ Haupt, 1926, des. R. Remane 2003 (SNSD).

Other material examined

[Philippines]: 10°, Mt. Banahao, P.I., Baker; *Dictyomorpha elongata* Mel. [Melichar's handwriting], det. Melichar; Cotypus [red label]; Collection Dr. Melichar; *Dictyomorpha elongata* Melichar, 1903, 0°, Melichar det. 1912 [Lauterer's handwriting] (MMBC); 1 nymph, Los Banos, P.I., IX.1915 (BPBM).

Distribution

Philippines (Luzon, Los Banos).

Remarks

Liang & Song (2012) did not examine the type and other adult material of *D. hectica* except for a nymph from Los Banos, Luzon, Philippines, which is adjacent to the type locality. One male specimen from Mt. Banahao, Philippines, deposited in MMBC was determined as *D. elongata* by Melichar and designated as a co-type of *D. elongata* by Lauterer. In fact, Mt. Banahao was not recorded in Melichar's dictyopharid monograph (Melichar, 1912: 104); hence, the designation for *D. elongata* is rejected here. We redescribe this species and add the description of male genitalia for the first time.

INDODICTYOPHARA LIANG & SONG, 2012 Indodictyophara Liang & Song, 2012: 418.

Type species

Indodictyophara lobosa Liang & Song, 2012; by original designation.

Diagnosis

The genus can be separated from other Aluntiini genera by the following combination of characters: cephalic process nearly 1.3 times as long as pronotum and mesonotum combined; vertex with median carina only visible basally; frons with lateral and median carinae strongly ridged and blade-like; tegmina without dendroid secondary veins; ten suboblique veins on costal cell from basal one-third to apex; and aedeagus with a pair of spinous, sclerotized, black-tipped, and not inflated endosomal processes.

Diversity and distribution

Indodictyophara is a monotypic genus known only from southern India.

MADAGASCARITIA SONG & LIANG GEN. NOV.

Type species

Madagascaritia angusta Song & Liang sp. nov., by present designation.

Diagnosis

This new genus can be separated from other Aluntiini genera by the following combination of characters: cephalic process with dorsal surface very narrow and compressed laterally before the eyes, so it becomes nearly triangular in cross section; frons with intermediate carinae strongly elevated, median carina incomplete or complete but obscure in middle; tegmina with costal cell distinctly narrow, coriaceous, opaque, and bright yellow, with suboblique veins (although observed with difficulty because of sclerotic surface), without dendroid secondary veins; basal three-quarters with dendroid nodose secondary veins densely interspersed among longitudinal veins; Sc+R, M, and CuA first branching nearly abreast.

Description

General colour ochraceous in dead specimens (probably viridescent or stramineous green in life).

Head (Fig. 11A-C) distinctly elongate, 1.5-1.8 times as long as pronotum and mesonotum combined. Cephalic process with dorsal surface very narrow and compressed laterally before the eyes in dorsal view (Fig. 11A), so it becomes nearly triangular in cross section. Vertex (Fig. 11A) with median carina absent, only median furrowed suture visible; lateral carinae strongly ridged, convergent anteriorly between eyes, slightly sinuate in front of eyes, and then narrowed and nearly subparallel towards apex, but apex acuate; posterior margin weakly ridged, arcuately concave. Frons (Fig. 11C) with lateral carinae narrow and elongate; intermediate carinae strongly elevated, converging posteriorly and extending before eyes; median carina incomplete, or complete but obscure in middle. Clypeus, rostrum, eyes, ocelli, and antennae similar to Aluntia.

Pronotum and mesonotum (Fig. 11A) similar to *Aluntia*. Tegmina (Fig. 2F) elongate and broad, translucent, and dull whitish, nearly 2.5 times as long as broad; costal cell very narrow, mostly coriaceous, opaque, and bright yellow in colour, with suboblique veins (although observed with difficulty because of sclerotic surface), without dendroid secondary veins; apex rounded; basal two-thirds with dendroid nodose

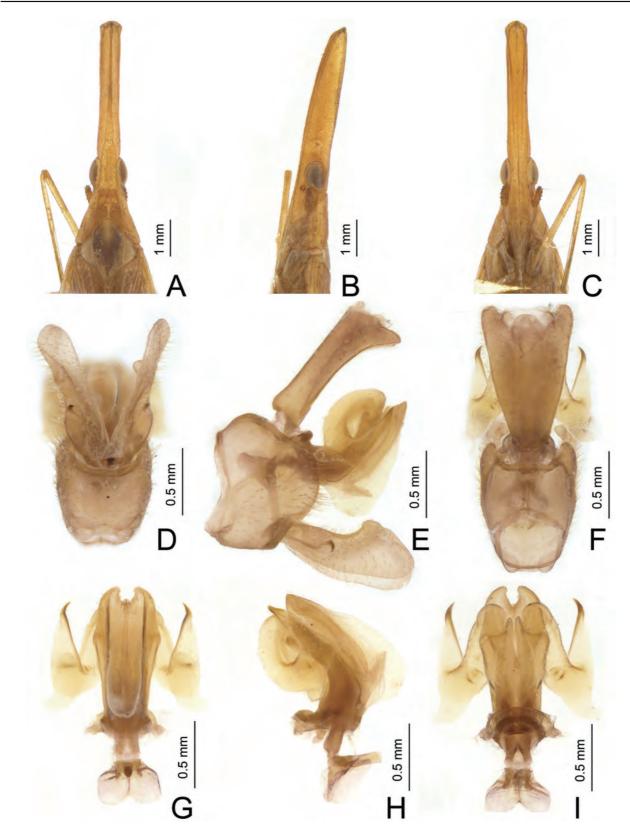


Figure 11. *Madagascaritia angusta* sp. nov. A, head, pronotum, and mesonotum, dorsal view; B, head, lateral view; C, head, ventral view; D, pygofer and gonostyles, ventral view; E, male genitalia, lateral view; F, pygofer and segment X, dorsal view; G, aedeagus, ventral view; H, aedeagus, lateral view; I, aedeagus, dorsal view.

KEY TO SPECIES OF MADAGASCARITIA GEN. NOV.

- Apex of cephalic process with brownish black spots above and beneath (Fig. 12A); cephalic process relatively elongate and slender, nearly 1.8 times as long as pronotum and mesonotum combined......

secondary veins dense; Sc+R, M, and CuA branching nearly abreast at basal one-third, and M branching into accessory veins successively three to four times; apical area densely covered with transverse veins, with 16–25 apical cells. Legs similar to *Aluntia*.

For male genitalia see *Madagascaritia angusta* sp. nov. and female genitalia see *Madagascaritia hova* comb. nov.

Etymology

The new genus name is a combination of 'Madagascar' plus the suffix 'itia', to indicate that it comes from Madagascar. The gender is feminine.

Diversity and distribution

Madagascaritia contains two species both restricted to Madagascar.

Remarks

Based on examining *Aluntia* material and other Aluntiini such as *Dictyomorpha* and *Indodictyophara*, we elevate *A. hova* and a new species to generic status.

The new genus can be distinguished from *Aluntia* and *Dendrophora* by the cephalic process with dorsal surface very narrow and compressed laterally before the eyes; the frons with median carina complete, strongly elevated; and the tegmina with costal cell very narrow, coriaceous, opaque, and bright yellow in colour. The last character appears to be an autapomorphy of *Madagascaritia* that supports the monophyly of the genus.

MADAGASCARITIA ANGUSTA SONG & LIANG SP. NOV. (FIGS 1K, 11A-I)

Description

General colour similar to M. hova, but without brownish black spots above and beneath apical head (Fig. 11A); BL, \circlearrowleft 15.2 mm; HL, \circlearrowleft 4.7 mm; HW, \circlearrowleft 1.1 mm; TL, \circlearrowleft 9.9 mm.

Head (Fig. 11A–C) relatively short and broad, nearly 1.6 times as long as pronotum and mesonotum combined. Vertex (Fig. 11) with lateral carinae very narrow before eyes (much narrower than $M.\ hova$) and nearly subparallel towards apex. Frons (Fig. 11C) with median carina incomplete, distinct at apex and base, absent in upper middle. Tegmina with costal cell coriaceous

and bright yellow at basal two-thirds; Sc+R, M, and CuA branching into accessory veins successively three times; apical margin with 16–18 apical cells.

Male genitalia with pygofer large and broad, with ratio of ventral to dorsal width ~1.4:1.0, posterior margin distinctly projecting in lateral view (Fig. 11E); in dorsal view dorsal margin excavated to accommodate segment X, dorsolateral margins distinctly produced posteriorly (Fig. 11F). Gonostyles symmetrical; base narrow, expanded towards middle, then gradually narrowed towards apex; apex bluntly rounded; upper process large, broad, and blunt near middle, directed inwards in lateral view (Fig. 11F). Aedeagus (Fig. 11G–I) with endosomal processes extended from phallotheca: membranous, inflated, and abruptly incurved anteriorly, and then bent posteriorly in middle, with a small process directed anteriorly there, apex sclerotized and acute; phallobase with membranous lobe dorsally and ventrally, respectively; ventral lobe much larger than dorsal lobe. Segment X elongate, broad, and inverted trapezoidal, in dorsal view with ratio of length to width at apex ~1.6:1.0 (Fig. 11F), basal ventral margins projecting ventrally in ventral view (Fig. 11E).

Female unknown.

Material examined

Holotype O, Madagascar: Environs de Rogez (NMPC).

Etymology

The new species is named for its extremely narrow vertex.

Distribution

Madagascar.

Remarks

The new species is similar to *M. hova*, but can be distinguished from *M. hova* by the shorter and broader cephalic process, the narrower vertex, and the brownish black spots above and beneath apex of cephalic process absent in *M. angusta* sp. nov.

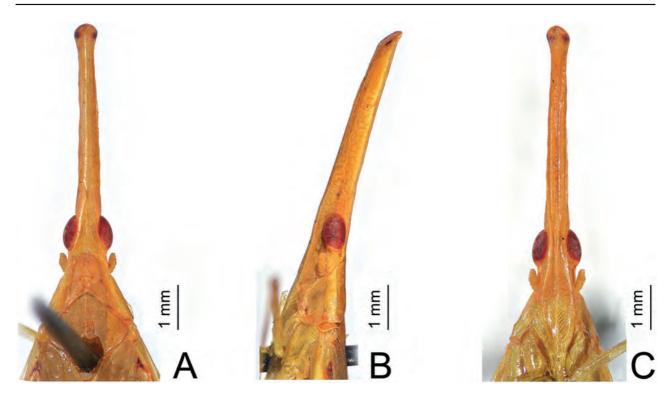


Figure 12. Madagascaritia hova. A, head, pronotum, and mesonotum, dorsal view; B, head, lateral view; C, head, ventral view.

MADAGASCARITIA HOVA (NAST, 1949) COMB. NOV. (FIGS 1L, 2F, 12A–C)

Aluntia hova Nast, 1949: 121, figs 1–3; Emeljanov, 1979: 10.

Redescription

Apex of head with a pair of irregular bronwnish black spots visible from above and beneath (Fig. 12A, B); BL, \bigcirc 18.9 mm; HL, \bigcirc 5.6 mm; HW, \bigcirc 1.2 mm; TL, \bigcirc 11.1 mm.

Head nearly 1.8 times as long as pronotum and mesonotum combined (Fig. 12A). Tegmina (Fig. 2F) with Sc+R, M, and CuA branching into accessory veins successively four times; apical margin with 24 cells.

Female genitalia similar to *Aluntia*. Segment X relatively broad, base narrow, gradually expanded towards apex, with ratio of length to width at apex $\sim 1.8:1.0$. Male unknown.

Type material examined

Holotype $\[\bigcirc \]$ (MIZ 313167), Madagascar: Périnet, 8.I.1938; B. Kreczmer & A. Fiedler leg.; Type [red label]; *Aluntia hova* sp. nov. $\[\bigcirc \]$, J. Nast, det. 1949 [Nast's handwriting] (Mus. Zool. Polonicum, Warszawa, 12/45; MIZPAS).

Distribution Madagascar.

ARJUNINI SONG & SZWEDO TRIB. NOV.

Type genus Arjuna Muir, 1934.

Diagnosis

This new tribe can be distinguished by the following combination of characters: clypeus distinctly elongate, extending to apex of middle coxae; rostrum distinctly elongate, beyond apex of hind femora; tegmina submacropterous and transparent, apical one-third not overlapping, apex somewhat pointed; corium without fold; veins with long setae, Sc+R and M veins on tegmina with a long common stem; claval suture extending to posterior margin; hindwings with anal area reduced, only a very small portion folded inwards, secondary fold absent; ACL of gonapophysis VIII with seven large teeth of varying sizes and shapes from base to apex; basal four teeth with base transversally prolonged and strongly ridged; and Gp1 of gonoplacs with filmy edging, without sensory appendage.

Diversity and distribution

Arjunini includes eight species in two genera restricted to the southern Sunda Islands and New Guinea only (Fig. 25). This group may be distributed widely in Wallacea, New Guinea, and the western Pacific, which

KEY TO GENERA OF ARJUNINI TRIB. NOV.

- Cephalic process before eyes curved upwards; vertex without secondary carinae...........Pippax Emeljanov, 2008

are recognized as several areas of endemism in the Australian Region (Duffels & Turner, 2002). It is also thought to exist in the northern Australian mainland, although it has not yet been found there.

ARJUNA MUIR, 1934

Arjuna Muir, 1934: 583; Metcalf 1946: 90; Emeljanov 2008: 311; Emeljanov 2011: 1124.

Type species

Arjuna dohertyi Muir, 1934; by original designation.

Diagnosis

The genus can be distinguished by the following combination of characters: cephalic process curved downwards before eyes; vertex with a secondary longitudinal carina bifurcating from subapex of lateral carinae; frons with lateral carinae well developed from clypeus, but obscure and gradually disappearing anterad to eyes, only a pale trace extending forwards; intermediate carinae extending before eyes; median carina complete, robust, and strongly convex; and aedeagus with a pair of ventrolateral lobes twining around endosomal processes.

Redescription

Head (Fig. 14A-I) moderately elongate, as long as or slightly longer than pronotum and mesonotum combined, and curved downwards before eyes. Vertex (Fig. 14A, D, G) with lateral carinae distinctly thickened, gradually widened from base, widest before eyes, gradually narrowed towards subapex, then abruptly converging to apex; surface between lateral carinae more or less convex, median carina absent, a transverse depression present at widest area; apex acute; posterior margin weakly ridged, arcuately concave. Apex of cephalic process with sharp secondary longitudinal carina bifurcating from subapex of lateral carinae of vertex, extending to the dorsal branch of lateral carinae of frons forming areolets (lanceolate cells in Emeljanov, 2008: 311), then joining to apex of intermediate carinae of frons (Fig. 14J, K). Frons (Fig. 14C, F, I) widest below antennae, slightly constricted between eyes and narrowed forwards; lateral carinae well developed from clypeus, but obscure and gradually disappearing anterad to eyes, only a pale trace extending forwards (Fig. 14B, J); a weak carina crossed areolets, sometimes too weak to be visible (Emeljanov, 2008); intermediate carinae converging posteriorly and extending before eyes; median carina complete, robust, and strongly convex. An apical median longitudinal carina between anterior margins of frons and vertex very sharp and convex (Fig. 14K). Eyes nearly rounded, callus postocularis reduced, forming a triangular process projecting posteriorly. Antennae shifted backwards, pedicel globose, with ~40 distinct sensory plaque organs distributed over the entire surface.

Pronotum (Fig. 14A, D, G) relatively large, longer than half of mesonotum; anterior margin centrally arcuately convex, lateral marginal areas straight and sloping, with two lateral carinae on each side; upper carinae narrower than the lower carinae, so in dorsal view the lower carinae are distinctly visible (Fig. 14A, D, G); posterior margin broadly angularly concave; disc flat and tricarinate, median and intermediate carinae sharp and high, with a lateral pit on each side. Mesonotum (Fig. 14A, D, G) transversely broad, short, flat, and tricarinate; lateral carinae weakly tortuous and abruptly incurved apically, slightly converging forwards. Tegmina (Fig. 2G) nearly three times as long as broad; apical area with transverse veins sparse. Legs elongate and slender, fore and middle femora and tibiae distinctly elongate, hind tibiae more than twice as long as hind femora; fore and middle femora slightly thickened at apex, without spine; hind tibiae with four lateral spines and seven apical teeth; hind tarsomeres I and II with between eight and 13 apical teeth, respectively.

Male genitalia with pygofer distinctly narrow and elongate, more than twice ventral width, distinctly wider ventrally than dorsally, in lateral view posterior margin more or less projecting near upper middle (Figs 15B, 16B, 17B). Gonostyles symmetrical; base narrow, expanded towards middle, then gradually narrowed towards apex; apex bluntly rounded and projecting backwards; upper process elongate, obtuse, and compressed dorsoventrally (Figs 16E, 17E). Aedeagus (Figs 15A, D, E, 16A, F, G, 17A, F, G) with a pair of slender and moderately long endosomal processes extended from phallotheca: pigmented, sclerotized, nearly straight, and obtuse apically; phallobase sclerotized and pigmented at base, with inflated membranous apical lobes, without spines; dorsal lobe directed posteriorly and two ventrolateral lobes twining around endosomal processes, directed laterally. Segment X in dorsal view long, oval, dorsal margin deeply excavated to accommodate anal style, with ratio of length to width at base

KEY TO SPECIES OF ARJUNA MUIR, 1934

 \sim 1.7:1.0 (Figs 15C, 16C, 17C). Anal style short and small, not extending beyond the apical ventral margin of segment X.

Female genitalia (Fig. 18A, B) with gonocoxae VIII (Fig. 18C) with two membranous and flattened GxPs covered with small setae: Gxp1 large and elongate, with a long sclerotized plate in it; Gxp2 smaller, without sclerotized plate. Gonopophyses VIII in lateral view (Fig. 18C) with ACL large and sclerotized, with seven teeth of varying sizes and shapes from base to apex (Fig. 18D); basal four teeth with base transversally prolonged and strongly ridged (Fig. 18D). Gonopophyses IX (Fig. 18E) with PCL distinctly bifurcating apically; inner processes membranous covered with small setae, outer processes sclerotized and strongly ridged from middle to apex, acute apically. Gonoplacs (Fig. 18F) with two lobes: Gp1 large and broad, moderately sclerotized, and truncate apically, with filmy edging but spinous setae absent; Gp2 small and membranous, in which a long sclerotized plate is visible. Segment X (Fig. 18G) relatively small and oval, dorsal margin deeply excavated to accommodate anal style.

Diversity and distribution

Four *Arjuna* species including two new species in this paper are distributed in Indonesia and Papua New Guinea.

Remarks

Emeljanov (2008) suggested that several important diagnostic characters were omitted or described wrongly by Muir (1934) in his first description for *Arjuna*; hence, we redescribe and illustrate this genus.

ARJUNA MAAI SONG & WANG **SP. NOV.** (FIGS 13A, 14A–C, 15A–E)

Description

BL, \circlearrowleft 7.7–7.8 mm; HL, \circlearrowleft 1.8–1.9 mm; HW, \circlearrowleft 1.0 mm; TL, \circlearrowleft 5.2–5.4 mm.

Vertex with lateral carinae, genae beneath eyes and frons yellowish; most disc of vertex, areas of genae before eyes, and broad median carina of frons reddish ochraceous. Eyes reddish brown. Pronotum reddish ochraceous; intermediate carinae, broad upper lateral margins, and lower margin of paranota pale yellow; basal part of humeral area including lower lateral carina and paranotal lobe reddish. Mesonotum pale reddish ochraceous. Thorax ventrally yellowish ochraceous. Legs brown; fore and middle femora with dark stripes on ventral and anterior surfaces, narrow area between stripes yellowish; tibiae and tarsi dark brown. Abdomen above and beneath reddish ochraceous.

Head (Fig. 14A–C) about 1.3 times as long as pronotum and mesonotum combined, and slightly curved downwards in front of eyes. Vertex (Fig. 14A) with lateral carinae distinctly widened before eyes, length from anterior margin of eyes to apex 1.8 times as long as longitudinal length of eyes; surface between lateral carinae distinctly convex. Pronotum with intermediate carinae nearly complete, but not extending to the posterior margin of pronotum.

Male genitalia with aedeagus (Fig. 15A, D, E) with dorsal lobe large and robust, directed dorsoposteriorly; ventrolateral lobes very elongate, twisted two and a half times. Segment X in dorsal view with ratio of length to width at base ~1.7: 1.0 (Fig. 15C).

Material examined

Holotype ♂, [Indonesia]: NEW GUINEA: NETH.: Hollanda Area, W. Sentani, Cyclops Mts., 150–250 m, 19.VI.1959, T.C. Maa (BPBM). Paratypes: [Indonesia]: 1♂ (head missing), same as holotype; 1♂ (damaged specimen), NEW GUINEA: NETH.: Ifar, 300–250 m, 22.VI.1959, T.C. Maa (both in BPBM).

Etymology

The new species is named after the collector of the type material, Dr Tsing-Chao Maa, an outstanding Chinese entomologist from Bernice P. Bishop Museum, Honolulu, USA.

Distribution

Indonesia (Jayapura).

Remarks

Arjuna maai sp. nov. is similar to *A. dohertyi* but can be distinguished from *A. dohertyi* by the general reddish

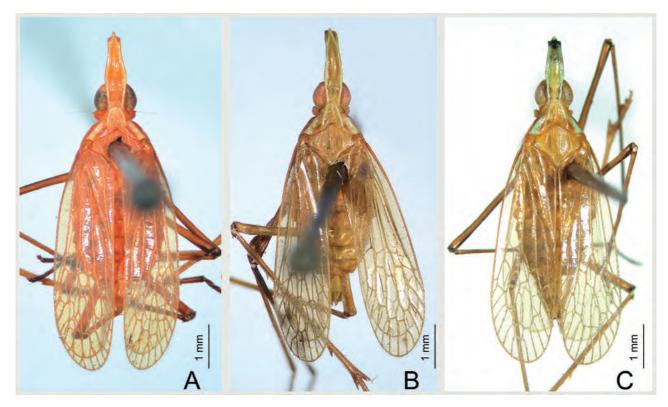


Figure 13. A, Arjuna maai sp. nov., male; B, Arjuna muiri sp. nov., male; C, Arjuna scriba, male.

ochraceous colour, the longer cephalic process, and the intermediate carniae of the pronotum not extending to the posterior margin. Muir (1934) described A. dohertyi based on a male specimen from Java that should be considered as the holotype and also stated that one female paratypic specimen from Humboldt Bay, New Guinea, was redder than that from Java. This female A. dohertyi from Humboldt Bay might be conspecific with A. maai sp. nov. collected in the Cyclops Mountains, very close to Humboldt Bay.

ARJUNA MUIRI SONG & WANG SP. NOV. (FIGS 13B, 14D-F, 16A-G)

Description

BL, \circlearrowleft 7.9 mm; HL, \circlearrowleft 1.9 mm; HW, \circlearrowleft 0.9 mm; TL, \circlearrowleft 5.2 mm.

Vertex with lateral carinae, genae beneath eyes and frons pale green, surface of vertex ochraceous, areas of genae before eyes and broad median carina of frons reddish. Eyes reddish brown. Pronotum ochraceous, intermediate carinae, broad upper lateral margins, and lower margin of paranota greenish, basal part of humeral area including lower lateral carina and paranotal lobe reddish. Mesonotum pale ochraceous. Legs same as *maai*. Abdomen above and beneath ochraceous.

Head (Fig. 14D–F) relatively elongate, about 1.4 times as long as pronotum and mesonotum combined, and distinctly curved downwards before eyes. Vertex (Fig. 14D) with lateral carinae more or less widened before eyes, length from anterior margin of eyes to apex twice as long as longitudinal length of eyes; surface between lateral carinae slightly convex; apex distinctly elongate and pointed. Pronotum with intermediate carinae complete, almost extending to posterior margin of pronotum.

Aedeagus (Fig. 16A, F, G) with dorsal lobe large, directed dorsally; ventrolateral lobes elongate, twisted twice.

Material examined

Holotype ♂, [Indonesia]: NEW GUINEA: NETH.: Vogelkop: Manokwari, 75 m, 11.VIII.1959, D.E. Hardy (BPBM).

Etymology

The new species is named after the hemipterist Dr Frederick Muir, an outstanding entomologist and the author of the genus *Arjuna*.

Distribution

Indonesia (West Papua).

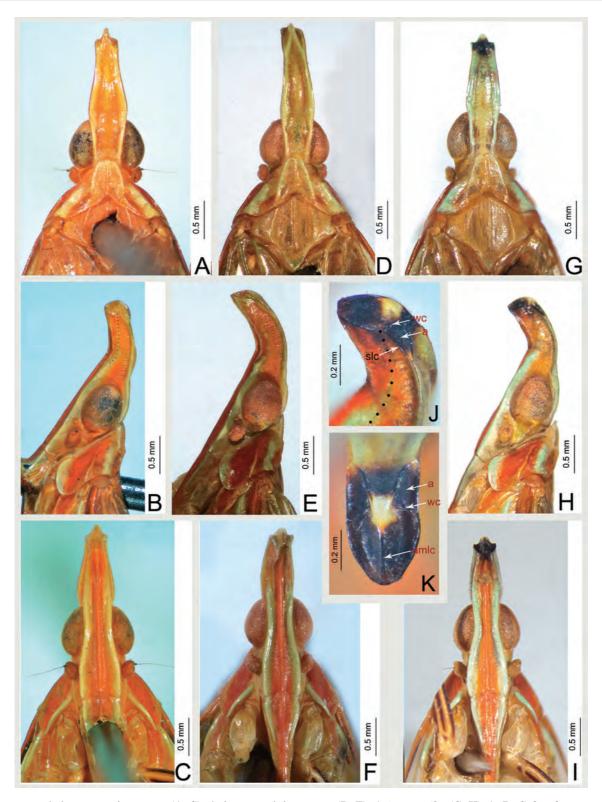


Figure 14. Arjuna maai sp. nov. (A–C), Arjuna muiri sp. nov. (D–F), Arjuna scriba (G–K). A, D, G, head, pronotum, and mesonotum, dorsal view; B, E, H, head, lateral view; C, F, I, head, ventral view; J, apex of head, lateral view; K, apex of head, anterodorsal view. Abbreviations: a, areolet; amlc, apical median longitudinal carina between anterior margins of frons and vertex; slc, secondary longitudinal carina bifurcating from subapex of lateral carinae of vertex; wc, weak carina crossed areolet. Dotted line shows a pale trace of lateral carinae of frons extending anteriorly.

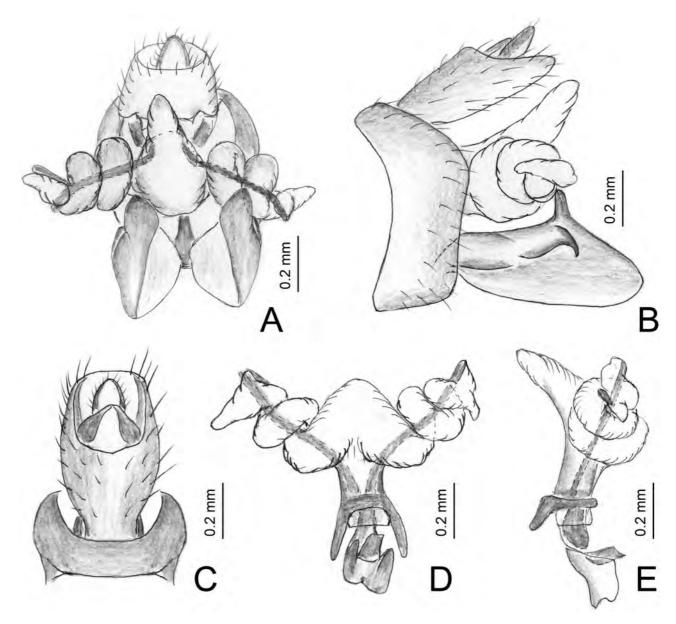


Figure 15. *Arjuna maai* **sp. nov.** A, male genitalia, caudal view; B, male genitalia, lateral view; C, pygofer and segment X, dorsal view; D, aedeagus, ventral view; E, aedeagus, lateral view.

Remarks

The new species can be distinguished from the other *Arjuna* species by the longest cephalic process, distinctly curved downwards before eyes.

 $\begin{array}{c} \textit{Arjuna scriba} \text{ Emeljanov, 2008 (Figs 2G, H, 13C,} \\ 14\text{G-K, 17A-G, 18A-G)} \end{array}$

Arjuna scriba Emeljanov, 2008: 311.

Redescription

BL, \circlearrowleft 7.5–8.1 mm, \circlearrowleft 9.5 mm; HL, 1.7–1.8 mm, \circlearrowleft 2.0 mm; HW, \circlearrowleft 0.9–1.0 mm, \circlearrowleft 1.0 mm; TL, \circlearrowleft 5.0–5.4 mm, \circlearrowleft 6.7 mm.

Male genitalia with aedeagus (Fig. 17A, F, G) with dorsal lobe large and robust, directed dorsoposteriorly; ventrolateral lobes moderately elongate, twisted one and a half times.

Female genitalia (Fig. 18A-G) as in generic description.

Material examined

Papua New Guinea: 2♂♂, Madang Province, Nobonob Hill, 7 km NW Madang (5°10′ S, 145°45′ E), 11.II.1987, N.D. Penny (CAS); 1♂, NEW GUINEA, NE Angoram, 10 m, 15.VIII.1978, J. L. Gressitt (BPBM). [Indonesia]: 1♂, WEST NEW GUINEA, Nabire, S. Geelvink Bay,

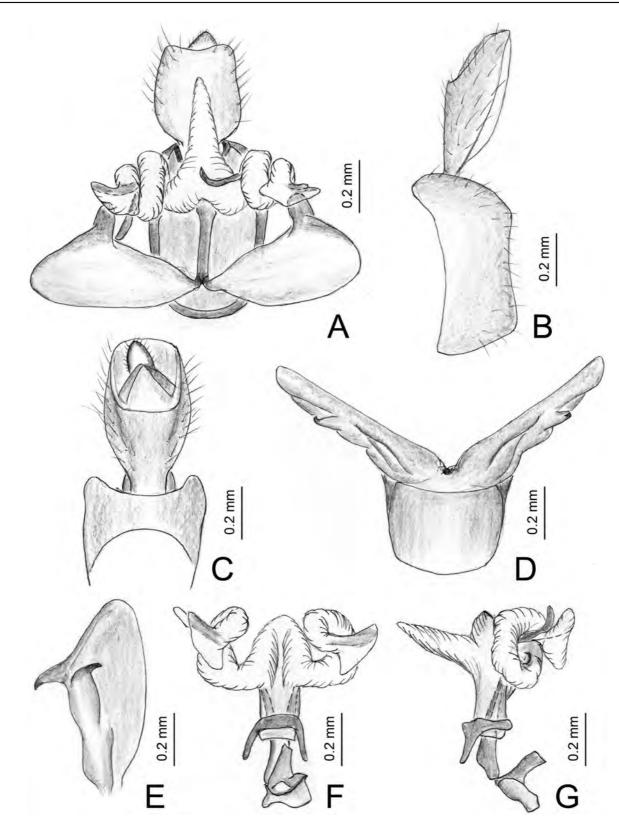


Figure 16. Arjuna muiri sp. nov. A, male genitalia, caudal view; B, pygofer and segment X, lateral view; C, pygofer and segment X, dorsal view; D, pygofer and gonostyles, ventral view; E, gonostyle, lateral view; F, aedeagus, ventral view; G, aedeagus, lateral view.

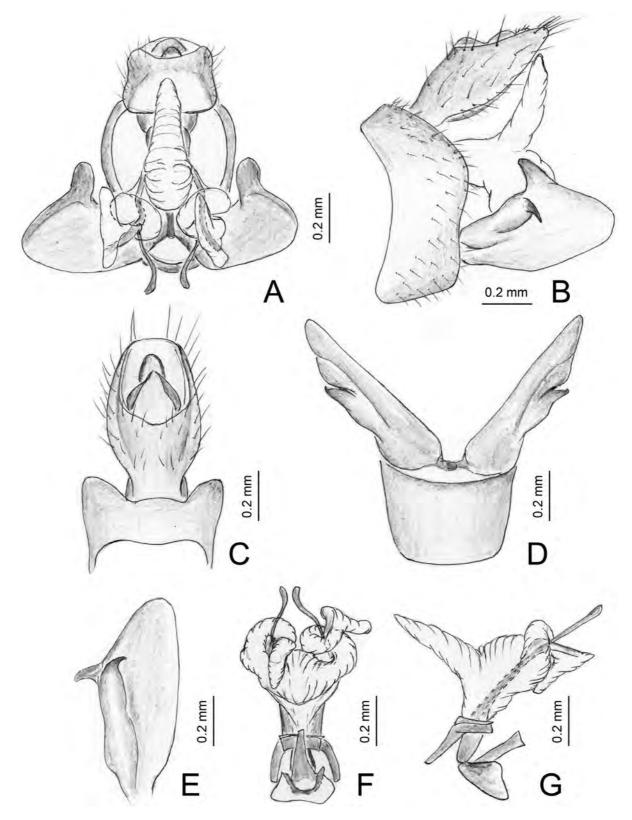


Figure 17. Arjuna scriba. A, male genitalia, caudal view; B, male genitalia, lateral view; C, pygofer and segment X, dorsal view; D, pygofer and gonostyles, ventral view; E, gonostyle, lateral view; F, aedeagus, ventral view; G, aedeagus, lateral view.

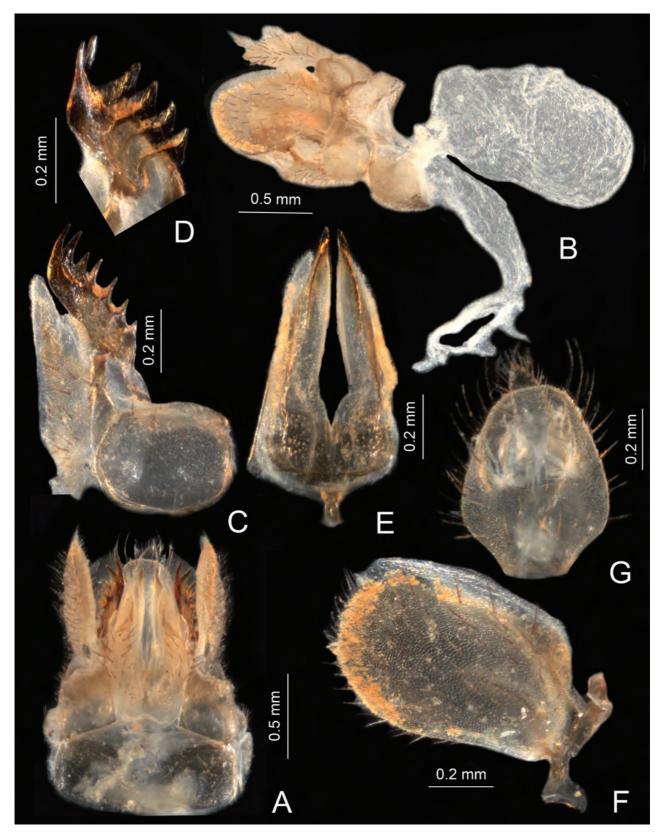


Figure 18. Arjuna scriba. A, female genitalia, ventral view; B, female genitalia, lateral view; C, gonopophysis VIII, dorsolateral view; D, teeth of ACL; E, gonopophysis IX, ventral view; F, gonoplacs, lateral view; G, female segment X, dorsal view.

1-20 m, Malaise Trap, 22.IV.1966, J. L. Gressitt (BPBM); 1 \bigcirc , D.N. Guinea, Mäanderberg, 10-20.VIII.1913, S. G. Mürgers (Kais. Augustafl. Exp., MFNB).

Distribution

Indonesia (New Guinea), Papua New Guinea.

PIPPAX EMELJANOV, 2008

Pippax Emeljanov, 2008: 307; Emeljanov 2011b: 1124.

Type species

Pippax opilionoides Emeljanov, 2008; by original designation.

Diagnosis

The genus can be distinguished from *Arjuna* by the following combination of characters: vertex with lateral carinae abruptly incurved before eyes and narrowed into half as wide, parallel forwards, then distinctly widened at subapex, angularly convex at apex; frons with intermediate carinae strongly ridged, nearly parallel and extending below antennae; median carina almost absent, only poorly marked below antennae.

Diversity and distribution

Pippax was erected by Emeljanov (2008) based on four new species: Pippax alboruber, Pippax bulbinaso, Pippax opilionoides, and Pippax vanstallei from Papua New Guinea.

Remarks

Emeljanov (2008) provided a key to the species of the genus. We here provide a first description of the male and female genitalia of *P. opilionoides*.

PIPPAX OPILIONOIDES EMELJANOV, 2008 (FIGS 19A-E, 20A-D, 21A-F)

Pippax opilionoides Emeljanov, 2008: 309, figs 30, 31, 33–35.

Redescription

BL, \circlearrowleft 5.8–6.5 mm, \circlearrowleft 6.6 mm; HL, \circlearrowleft 1.5–1.7 mm, \circlearrowleft 1.7 mm; HW, \circlearrowleft 0.8–0.9 mm, \circlearrowleft 0.9 mm; TL, \circlearrowleft 3.8–4.1 mm, \circlearrowleft 4.1 mm.

Male genitalia with pygofer distinctly narrow and elongate, more than twice ventral width, distinctly wider ventrally than dorsally (~3.0:1.0), posterior margin more or less projecting near upper middle in lateral view (Fig. 20B). Gonostyles (Fig. 20C) symmetrical; base narrow, expanded towards middle, then gradually narrowed towards apex; in lateral view apex bluntly rounded and projecting backwards; upper process elongate, obtuse, and compressed dorsoventrally (Fig. 20D). Aedeagus (Fig. 21A, B) with a pair of slender and mod-

erately long endosomal processes extended from phallotheca: pigmented, sclerotized, nearly straight, and obtuse apically; phallobase sclerotized and pigmented at base and laterally, the remainder membranous, without spines; dorsal area with a large and elongate lobe, acute apically, and directed dorsally; ventrolateral area with two narrow and elongate lobes, directed posteriorly. Segment X in dorsal view oval, with ratio of length to width at base $\sim 1.2:1.0$ (Fig. 20A). Anal style elongate, beyond the apical ventral margin of segment X.

Female genitalia (Fig. 21C-F) similar to Arjuna.

Material examined

Papua New Guinea: 1♂, 1♀, Madang Province, Bundi (5°45′S, 145°15′E), 10–12.III.1987, N.D. Penny; 1♂, So. Side Mt. Missim, 1000 m, 24.II.1978, E.I. Schlinger (all in CAS); 1♂, Wau, Morobe Distr., Mt. Missim, 1800 m, Malaise Trap, 22.IV.1966, Gressitt & Wilkes (BPBM).

Distribution

Papua New Guinea (Morobe and Madang).

PHYLOGENETIC RESULTS

The analysis of the data set (Table A3) resulted in nine equally long MP trees with a tree length of 403 steps, consistency index (CI) = 0.41, and retention index (RI) = 0.76, implemented by NONA. A strict consensus of nine MP trees collapsed three nodes and had a length of 408 steps, presented in Figure 22, with more robust bootstrap and Bremer support values mapped onto it.

According to the results of the phylogenetic analysis, the monophyly of the in-group (clade 1 in Fig. 22) is well defined by ten characters in the strict consensus tree (Fig. 23), which is strongly supported by the 88% bootstrap value and Bremer support of 6. Among the ten characters supporting clade 1, five are unambiguous synapomorphies: apex of clypeus distinctly beyond apex of fore coxae (character 29, state 1: 29-1); tegmina without a claval transverse vein between CuP and Pcu (57–1); fore coxae relatively short, not extending to apex of clypeus (77-1); arolium developed (88-1); and segment X with ventral apical margin not distinctly concave (128-0). This clade is further defined by five unambiguous changes in characters: 31-1, 42–0, 43–2, 44–1, and 62–1. The in-group clade can be divided into two distinct monophyletic lineages (clades 2 and 9).

Clade 2 includes most genera of Aluntiini s.l. ((Aluntia + (Madagascaritia + Dendrophora)) + (Indodictyophara + Dictyomorpha)). This clade is strongly supported by ten unique synapomorphies: posterior margin of vertex slightly beyond posterior margin of

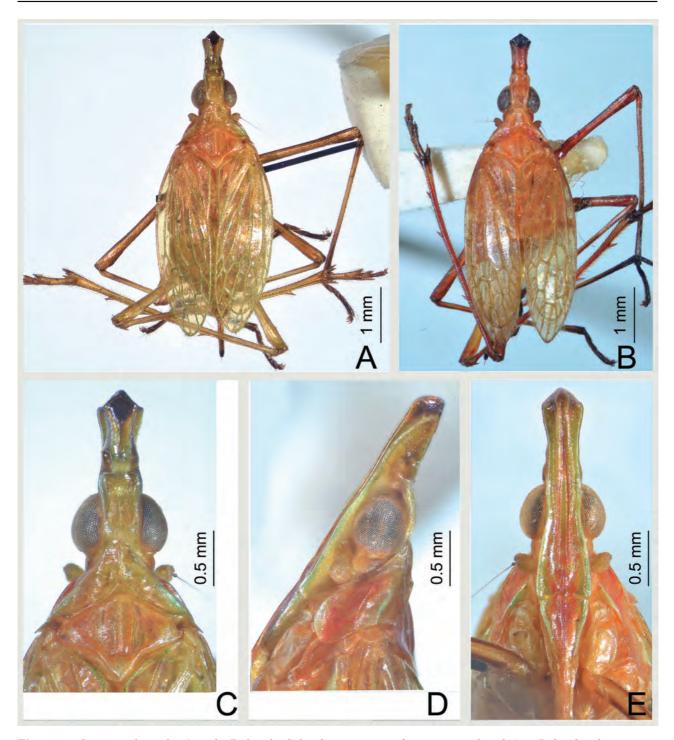


Figure 19. Pippax opilionoides. A, male; B, female; C, head, pronotum, and mesonotum, dorsal view; D, head and pronotum, lateral view; E, head and pronotum, ventral view.

compound eyes (19–1), compound eyes elongate oval (34–1), pedicel elongate (35–1), tegmina with suboblique veins in costal cell (69–0), pregenital segments elongate (89–1), pygofer distinctly wide in lateral view (90–1), teeth of ACL in gonapophysis VIII very small

(112–0), gonocoxae VIII with one GxP (116–0), gonapophysis IX with posterior fibula extending to gonospiculum (119–0), and gonoplacs with Gp3 (120–1). There are also nine additional changes in characters to support this clade: 3–0, 9–0, 25–3, 26–0, 37–1, 96–1,

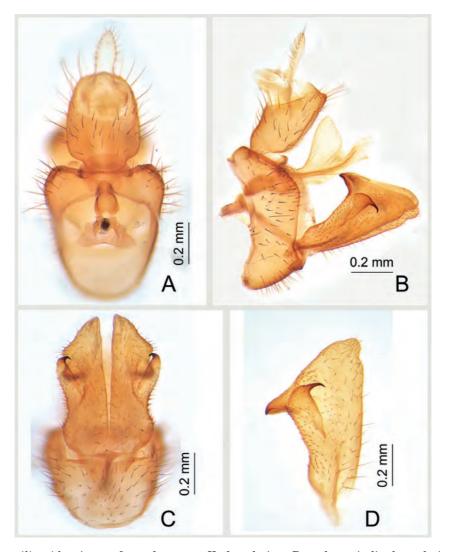


Figure 20. Pippax opilionoides. A, pygofer and segment X, dorsal view; B, male genitalia, lateral view; C, pygofer and gonostyles, ventral view; D, gonostyle, lateral view.

99–2, 104–1, and 122–0. This clade is strongly supported by 100% bootstrap value and Bremer support of 16, and separated into two distinct groups (clades 3 and 7).

Clade 3 (*Aluntia* + (*Madagascaritia* + *Dendrophora*)) is supported by four unambiguous character changes: frons with median carina absent in the middle (24–1); tegmina with branching of M relative to CuA nearly abreast (62–2); tegmina with dendroid secondary veins among longitudinal veins (72–1); and apical half of endosomal processes distinctly inflated (101–1). *Aluntia* (clade 4) is defined by two changes in characters: 25–1 and 97–1. Clades 5 and 6 are closely related and share seven common characters: posterior margin of vertex weakly ridged (18–0); an apical carina between anterior margins of frons and vertex (20–0); median carina of pronotum weakly ridged (37–0); tegmina with costal area expanded (54–0); M bifurcating M₁₊₂ and M₃₊₄ sur-

passing basal one-third of tegmina (60-0), between four and six apical cells of RP in tegmina (63-1), and more than four apical cells of CuA in tegmina (65-1). Madagascaritia (clade 5) is supported by three unambiguous character changes (5-2, 16-0, and 55-0) and one unique synapomorphic character (tegmina with costal cell coriaceous, 55-1). Dendrophora (clade 6), as a sister group of Madagascaritia, is defined by six homoplasious characters: 25-0, 46-0, 49-1, 61-0, 62-0, and 96-0.

Clade 7 (*Indodictyophara* + *Dictyomorpha*) is defined by two homoplasious characters: 91–1 and 100–0. *Dictyomorpha* (clade 8), as a sister group of *Indodictyophara*, is supported by one synapomorphy (suboblique veins at apical one-third of costal cell in tegmina, 70–0) and one homoplasious character (101–2).

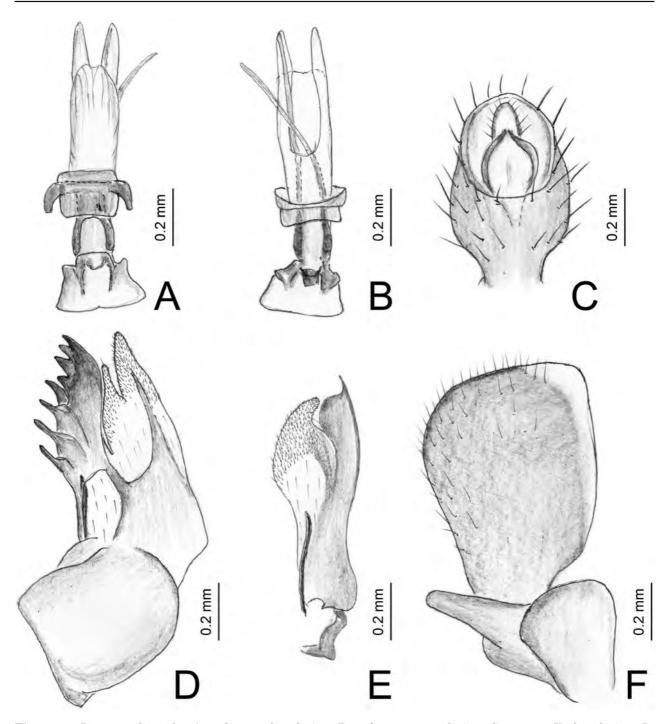


Figure 21. Pippax opilionoides. A, aedeagus, dorsal view; B, aedeagus, ventral view; C, segment X, dorsal view; D, gonopophysis VIII, dorsolateral view; E, gonopophysis IX, lateral view; D, gonoplacs, lateral view.

Clade 9 comprises the remainders of Aluntiini s.l. (*Pippax + Arjuna*) and all representatives of the tribes Dictyopharini, Hastini, Orthopagini, and Worskaitini. This clade is supported by six unique synapomorphies: fore and middle tarsomeres I and II with acutellae (82–1); hind tarsomeres I and II, apical

teeth with platellae (85–1); teeth of ACL in gonapophysis VIII arranged from base to tip (110–1); teeth of ACL varying in size and shape (113–1); number of teeth of ACL more than five (114–1); and Gp2 of gonoplacs distinctly wide (126–1). It is also supported by two unambiguous changes in characters: tegmina

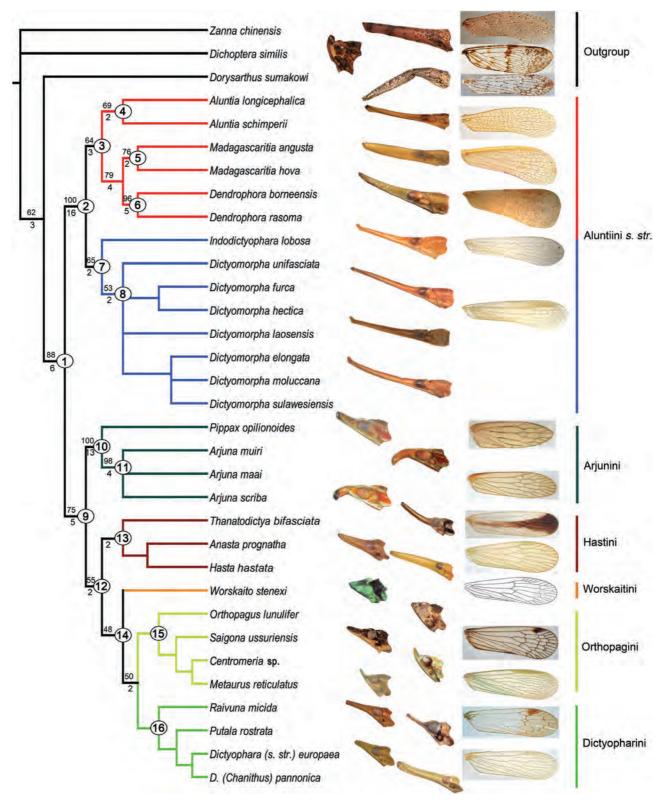


Figure 22. Strict consensus of the most parsimonious trees with clade number (on nodes), bootstrap value (above branch), of which the values of less than 50% are not shown, and Bremer support (>1, below branch). The head and pronotum (lateral view) and tegmen are mapped on the tree.

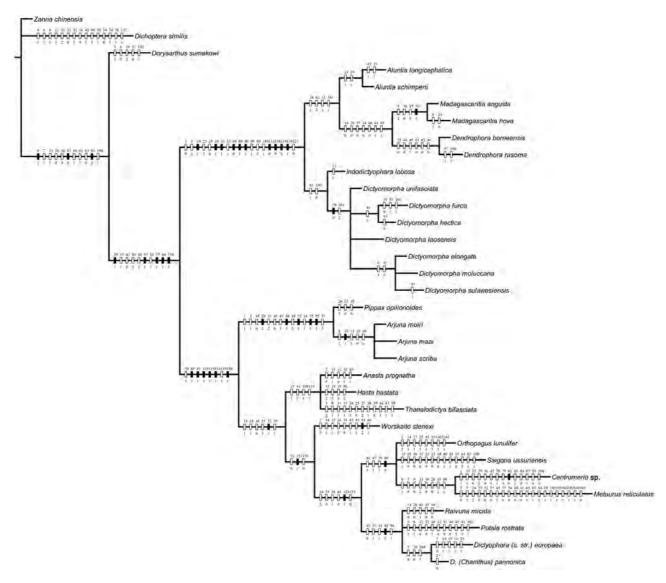


Figure 23. Strict consensus tree showing unambiguous characters supporting each clade (character number above and state number below). Homoplasious characters are shown as empty ellipses, and synapomorphies are shown as filled ellipses.

not overlapping when unexpanded status (50–1) and spinous setae on apical margin of Gp1 in gonoplacs (125–1).

The new tribe Arjunini (clade 10) is strongly supported by the 100% bootstrap value and Bremer support of 13, and is defined by 14 unambiguous characters, including five unique synapomorphies: apex of clypeus extending to apex of middle coxae (29–2); submacropterous tegmina (48–1); veins of tegmina with long setae (52–1); anal area of hindwings reduced (75–1); and upper process of gonostyles compressed dorsoventrally (95–1). The remaining nine homoplasious characters are as follows: 1–1, 2–1, 18–0, 31–2,

46–0, 47–1, 49–2, 74–1, and 97–1. Clade 11, the sister group of *Pippax*, is strongly supported by one synapomorphic character (vertex with a secondary longitudinal carina bifurcating from subapex of lateral carinae, 10–1), and is further defined by four homoplasious characters: 6–2, 15–1, 16–0, and 26–0. This clade achieved a 98% bootstrap value and Bremer support of 4.

Clade 12 consists of the representatives of the tribes Hastini, Worskaitini, Orthopagini, and Dictyopharini, and is supported by six unambiguous character changes, including one unique synapomorphy (53–1). The position of the fossil amber Worskaitini is closely related

to Orthopagini and Dictyopharini, and the monophyly of each tribe is generally supported (clades 13, 15, and 16).

DISCUSSION

PLACEMENT AND RECLASSIFICATION OF ALUNTIINI S.L.

The inclusion of Aluntiini s.l. in Dictyopharidae has received strong characteristic support in our phylogenetic analysis. Aluntiini had been considered as the most primitive branch on the evolutionary tree of Fugoridae suggested by Emeljanov (1979). After more representatives of the genera Dictyomorpha, Arjuna, and Pippax were examined, this group was moved back to Dictyopharidae (Emeljanov, 2008). Emeljanov (2008) proposed that the lack of a transverse vein on the clavus of the tegmina was one typical character for Dictyopharidae, whereas all of the original dictyopharid groups with a claval transverse vein between CuP and Pcu should be transferred to Fulgoridae (Emeljanov, 1979, 2011a). The dendroid nodose veins of Aluntia are secondary and different from those in Fulgoridae with a primary claval transverse vein (Emeljanov, 2008). Our phylogenetic analysis agrees with Emeljanov's taxonomic change in that Aluntiini s.l. should be placed in Dictyopharidae rather than in Fulgoridae.

The monophyly of Aluntiini s.l., however, is not recognized in our study. Emeljanov (2008) proposed that for Aluntiini s.l., the 'particular characters of the tribe are the eyes shifted from the pronotum (from neck), absence of postocular swellings, and presence of additional carinae before the apex of head which separates small apical areas of the outer lobes from their basal parts' (Emeljanov, 2008: 306-307). These characters, however, should not be treated as the autapomorphies of Aluntiini s.l. because they are often present in the other tribes of Dictyopharinae. For example, the presence of additional carinae on the apex between lateral carinae and intermediate carinae of frons (21-1) and the absence of postocular swellings (33–0) also occur in *Thanatodictya* of Hastini. In a key to the tribes of the subfamily Dictyopharinae provided by Emeljanov (2011b), Aluntiini s.l. was also clearly separated into two lineages.

Our analysis shows that Aluntiini s.l. is distinctly paraphyletic and can be reclassified into two unambiguous tribes with very high support values. Aluntiini s.s. ((Aluntia + (Madagascaritia + Dendrophora)) + (Indodictyophara + Dictyomorpha), clade 2 in Fig. 22) is definitely monophyletic, with 19 diagnostic characteristics that support it as a good monophylum. In addition, two distinct characters of the fifth-instar nymphs (the largest wax-secreting plates

and the presence of the longitudinal linear areas separating wax gland pores on the wax-secreting plates) are likely to be two autapomorphies of Aluntiini s.s., also supporting its monophyly. Among Aluntiini s.s., the unnatural genus Aluntia s.l. is reclassified into three monophyletic groups — Aluntia, Madagascaritia, and Dendrophora — with a large number of morphological characters supporting their monophylies.

The new tribe Arjunini (*Pippax + Arjuna*, clade 10 in Fig. 22) forms another different lineage of Aluntiini *s.l.* Eight unambiguous morphological characters, especially the homologue of the female genitalia, strongly support this group as a sister clade of the representatives of Dictyopharini, Hastini, Orthopagini, and Worskaitini. In addition, 14 unambiguous characters strongly define the monophyly of Arjunini and support it as a new tribe within Dictyopharinae. In the phylogeny within Dictyopharinae, Arjunini appears to be closer phylogenetically to Hastini, and both are restricted to the Australian region. Morphologically, Sc+R and M veins of tegmina with a long common stem and the consistency of the female genitalia support the close relatedness of the two tribes.

TAXONOMIC STATUS OF ALUNTIINI S.S. WITHIN DICTYOPHARIDAE

As reported by Emeljanov (1979), Aluntiini s.s. shares many common features with Zanna chinensis (Zanninae), Dichoptera similis (Dichopterinae), and/ or Dorysarthrus sumakowi (Dorysarthrinae), including: claval suture of the tegmina not extending to the posterior margin (71–1); hindwings without a secondary fold in the anal area (76-0); between two and four small teeth of ACL in gonapophysis VIII only at the tip, and almost the same size (110-0, 112-0, 113-0, and 114–0); and sensory field with numerous tiny setae at apex of Gp1 in gonoplacs (124-1). These characters should be plesiomorphies occurring in Aluntiini as well as partially occurring in Zanninae, Dichopterinae, Dorysarthrinae, and other fulgorid groups, but they seldom exist in other Dictyopharidae. These symplesiomorphic characters show that the status of Aluntiini is likely to be in a transitional position between Dictyopharidae and Fulgoridae, but much more inclined towards Dictyopharidae, indicating that this taxon could be considered as the most primitive branch and 'living fossils' of Dictyopharidae.

Actually, the results of the present analysis suggest that Aluntiini could be elevated to a status of a separate dictyopharid subfamily if Zanninae, Dichopterinae, and Dorysarthrinae were assigned to Fulgoridae; however, until more comprehensive sampling (representatives of more tribes) and data (morphological and/or molecular) are used in phylogenetic analyses of

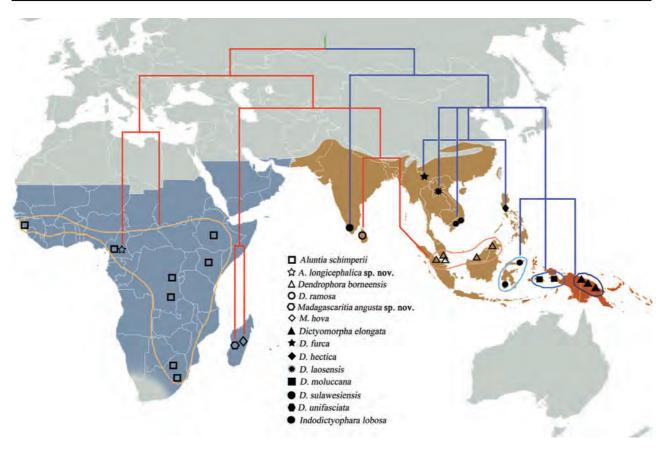


Figure 24. Geographic distribution of the species of Aluntiini showing a palaeotropical distribution pattern.

Dictyopharidae, we suggest Aluntiini to be a tribe of Dictyopharinae in the present study.

DISTRIBUTION PATTERNS OF ALUNTIINI S.S.

Aluntiini s.s. is widely distributed in the Old World tropics, including sub-Saharan Africa, Madagascar, southern India, Sri Lanka, Mainland Southeast Asia, the Greater Sunda Islands, the Philippines, the Moluccas, and New Guinea (Fig. 24). Except for Dictyomorpha, all of the genera are oligotypic. Aluntia schimperii is widespread in sub-Saharan Africa, but A. longicephalica sp. nov. is found only in Cameroon. Madagascaritia is endemic to Madagascar. Two Dendrophora species are restricted to Sri Lanka, Indonesia, and Malaysia. These genera form an unambiguous clade of Aluntiini sharing one synapomorphy: tegmina with dendroid secondary veins among longitudinal veins.

Dictyomorpha is widespread in the Austro-Oriental region, including south-western China, Laos, Vietnam, the Philippines, Sulawesi, the Moluccas, and New Guinea. No species of the genus has been recorded on the Malay Peninsula, Sumatra, Java, or Borneo, which

are considered to be one of the hottest hot spots of global biodiversity (Myers et al., 2000). More new species and potential distribution areas are expected to be found in this genus. There is no record of any *Dictyomorpha* species from India, but a closely related genus, *Indodictyophara*, was discovered in southern India. Both genera constitute another clade of Aluntiini.

The distribution patterns of Aluntiini s.s. fall in line with many groups of Dictyopharinae, Aphrophoridae (Cercopoidea), Zanna, and perhaps additional Auchenorrhyncha groups, following the 'Afrotropical Region – Oriental Region – western Pacific' track (Liang, 1998; Z.-S. Song, unpubl. data). This biogeographic distribution is almost entirely consistent with the Palaeotropical Kingdom in the phytogeographical regions (Takhtajan, 1986), and can also be referred to as the African–Asian disjunctions.

The African–Asian disjunctions displayed by Aluntiini are common in the palaeotropical plant taxa in phytogeography (Zhou *et al.*, 2012). Differing from zoogeography, the Palaeotropical Kingdom is a floristic region comprising the tropical areas of Africa, Asia, and Oceania, excluding Australia and New Zealand (Takhtajan, 1986), which is roughly equivalent to a union of the Afrotropical, Oriental, and northern

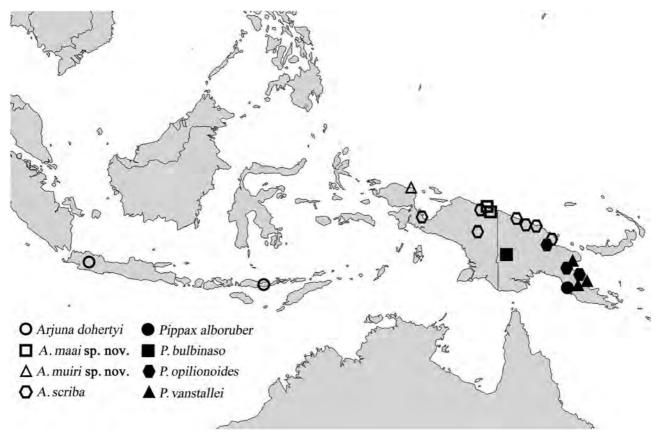


Figure 25. Geographic distribution of the species of Arjunini trib. nov.

Australian regions, excluding Australia and New Zealand, in zoogeographic regions recognized by Wallace (1876), based mainly on the distributions of world vertebrates. As typical phytophagous insects, planthopper distributions should be associated more with colonization and diversification of their host plants than with animals. Therefore, a palaeotropical distribution pattern derived from plant geography is suggested not only for Aluntiini but also for other planthopper groups, such as Orthopagini and Zanna. Furthermore, a novel global division of insect biogeographic regions, especially for phytophagous insects, based on phytogeographic kingdoms, may be expected to be updated and even replace traditional zoogeographic regions in insect biogeography if more phytophagous insect groups could be tested by combining data on the distributions and phylogenetic relationships, such as the update of Wallace's zoogeographic regions of the world (Holt et al., 2012).

ORIGIN AND DIVERSIFICATION OF ALUNTIINI S.S.

All fossils of Dictyopharidae were found hitherto in the Northern Hemisphere, especially in Eurasia (Szwedo, Bourgoin & Lefebvre, 2004; Szwedo, 2008). The oldest known fossil Dictyopharidae, Netutela annunciator Emeljanov, 1983, representing an extinct tribe Netutelini within Dictyopharinae, was recorded in the Upper Cretaceous, Santonian deposits of the Taimyr Peninsula, from approximately 85 Mya (Emeljanov, 1983; Szwedo, 2008). Unfortunately, only the tegmina and a small part of the hindwing remain largely intact in the type specimen, and the remaining features are unavailable; thus, this species was excluded in our cladistic analysis. In Netutelini, the stigmal area presented in the tegmina is similar to that of most extant dictyophrid taxa, but absent in Aluntiini, Arjunini, and Zanna, implying that Netutelini may not be the ancestor of Dictyopharidae, and that the family should have a longer evolutionary history. Song & Liang (2013a) estimated that the divergence between Dictyopharidae and Fulgoridae occurred in the early Cretaceous, c. 123 Mya, based on a preliminary molecular phylogeny of Fulgoroidea.

Another fossil tribe Worskaitini, *Worskaito stenexi* Szwedo, 2008, which was well-preserved in the Eocene Baltic amber c. 37–47 Mya (Weitschat & Wichard, 2010), was added to the present phylogenetic analysis. Our results infer that Worskaitini shares more synapomorphies with the extant dictyopharid taxa, Orthopagini and Dictyopharini, implying that

Worskaitini should be more advanced than Aluntiini in the dictyopharid evolutionary tree; therefore, this tribe has a limited contribution to the discovery of the origin and diversification of Aluntiini, except to testify that Aluntiini had a more ancient evolutionary history.

Although fossils might theoretically become available for study, a great majority of species were not perpetuated as fossils, particularly the more numerous tropical species (Gressitt, 1974). Biogeography is also widely accepted to provide valuable information for reconstructing a meaningful evolutionary history. Our phylogenetic analysis of this tribe shows that a sister relationship between two clades of Aluntiini might occur in the Indian subcontinent. The early divergent branches of the Aluntia group (clade 3 in Fig. 22) are restricted to Africa, and the later branches are found from Madagascar to Sri Lanka to south-east Asia, suggesting a probable origin in Africa, and subsequent colonization of South Asia and then Southeast Asia. The Indodictyophara group (clade 7 in Fig. 22) most likely originated in southern India and diversified in the Austro-Oriental region.

In the Palaeotropical Kingdom, many angiosperms were considered to have an African origin with diverse 'out-of-Africa' scenarios (Zhou et al., 2012). Aluntiini is small but widespread in the palaeotropical region, and could be associated with the origin and diversification of their host plants. Unfortunately, we have no knowledge of the host plants of Aluntiini and cannot discuss evolutionary patterns in biogeography and the host plant association of Aluntiini. There have been several alternative hypotheses for explaining the 'outof-Africa' scenario in the palaeotropical taxa, involving different dispersal mechanisms at different times through different geographical routes. Among them, 'rafting' of taxa on the Indian tectonic plate is one of four explanations that were most widely accepted for the terrestrial lineages (Zhou et al., 2012).

As discussed above, if Aluntiini were the most primitive lineage and 'living fossils' of Dictyopharidae, which appear to be more ancient than Worskaitini, and even Netutelini, it might have originated in the early Cretaceous when the continental block of Madagascar and India broke away from Africa and began moving southeast (Sanmartín & Ronquist, 2004). Therefore, the origin and diversification of Aluntiini is likely to follow the hypothesis that 'rafting' and collision of fauna and flora on the Indian plate enabled the unidirectional migration of African taxa into Asia. The Cretaceous breakup of Gondwana was an important mechanism in the evolution of this ancient taxon in Dictyopharidae. Some geotectonic scenarios occurring in Gondwana may be associated with the biogeographic pattern exhibited by Aluntiini. For example, the diversification of two distinct clades within Aluntiini most likely occurred in the Indian subcontinent when it drifted northwards after separating from the Gondwanan landmass. Liang (1998) assumed that the collision of the Indian subcontinent with southern Eurasia brought many Gondwanan elements of the cercopoid and fulgorid faunas to Eurasia based on his study of the cladistic biogeography of Cercopoidea and Fulgoroidea.

A similar origin and diversification is also likely to have occurred in another 'living fossil', Zanninae, for which the distribution pattern is quite consistent with that of Aluntiini. As the sister clade of Dictyopharidae, Fulgoridae may have a Gondwana origin in their two alternative biogeographic hypotheses based on the molecular data (Urban & Cryan, 2009), implying that Zanna + Dictyopharidae + Fulgoridae share a common ancestor in the Gondwanan landmass.

CONCLUSION

Here we present a morphologically based phylogenetic analysis for all Aluntiini s.l. genera and the representatives of extant Dictyopharini, Hastini, Orthopagini, and the fossil Worskaitini within the Old World Dictyopharinae. The results of our phylogenetic analysis support the following assertions: (1) the placement of Aluntiini s.l. placed within Dictyopharidae has strong support; (2) Aluntiini s.l. is distinctly paraphyletic and can be separated into two unambiguous tribes, Aluntiini s.s. and Arjunini; (3) beyond only an independent tribe, Aluntiini s.s. may even reach a new subfamilial status in Dictyopharidae; (4) the genus Aluntia s.l. can be divided into three monophyletic genera, namely, Aluntia s.s., Madagascaritia, and Dendrophora; and (5) Arjunini, the second lineage of Aluntiini s.l., is erected as a new tribe in Dictyopharinae.

A palaeotropical distribution pattern derived from phytogeography for Aluntiini is suggested. Based on the distribution and phylogenetic relationships of Aluntiini, the origin and diversification of Aluntiini are discussed preliminarily. The biogeographic scenario to explain the distribution of extant Aluntiini is provisional and subject to being evaluated in greater detail by the addition of more taxa to the data set.

Furthermore, the monophylies of Dictyopharini, Hastini, Orthopagini, and Worskaitini in Dictyopharinae are tentatively supported as well, although more taxa are expected to be added in future analyses. The present phylogenetic study is a preliminary cladistic analysis of the morphological characteristics in Dictyopharinae. We could not include other tribes of the worldwide subfamily in our analysis; therefore, a more rigorous study with broader representation of the subfamily is required in the near future (Z.-S. Song, unpubl.).

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APPENDIX

Table A1. Materials for the phylogenetic analysis

Higher category	Genus	Species in analysis	Species distribution		
Fulgoridae					
Zanninae	Zanna	chinensis	China (Yunnan)		
Dichopterinae	Dichoptera	similis	China (Yunnan), Thailand, Vietnam		
Dorysarthrinae	Dorysarthus	sumakowi	Iran		
Dictyopharidae					
Dictyopharinae					
Aluntiini	$Aluntia\ s.s.$	longicephalica sp. nov.	Cameroon		
		schimperii	Afrotropical region (excluding Madagascar)		
	Dendrophora	borneensis	Malaysia		
		ramosa	Sri Lanka		
	Dictyomorpha	elongata	Papua New Guinea, Indonesia		
		furca	China (Yunnan)		
		hectica	Philippines		
		laosensis	Laos		
		moluccana	Indonesia		
		sulawesiensis	Indonesia		
		unifasciata	Vietnam		
	Indodicty ophara	lobosa	India		
	Madagascaritia angusta sp. nov. Madagasc		Madagascar		
		hova	Madagascar		
Arjunini	Arjuna	maai sp. nov.	Indonesia (Jayapura)		
		muiri sp. nov.	Indonesia (West Papua)		
		scriba	Papua New Guinea		
	Pippax	opilionoides	Papua New Guinea		
Dictyopharini	$Dictyophara\ s.s.$	europaea	Palaearctic region		
	D. (Chanithus)	pannonica	Palaearctic region		
	Raivuna	micida	Vietnam, southern China		
	Putala	rostrata	Sri Lanka, southern India		
Hastini	Anasta	prognatha	Australia, Papua New Guinea		
	Hasta	hastata	Australia		
	Than atodic ty a	bifasciata	Australia		
Orthopagini	Centromeria	sp.	China (Yunnan)		
	Metaurus	reticulatus	Cambodia, Laos		
	Orthopagus	lunulifer	Japan, Korea, China, Southeast Asia		
	Saigona	ussuriensis	Russia (Far Eastern region), Japan, Korea, China		
Worskaitini	Worskaito	stenexi	Baltic region		

Table A2. List of characters used in the phylogenetic analysis

Habitus

0. Habitus (body length including tegmina): 0, large-sized, >25 mm; 1, small to medium-sized, usually 10–20 mm.

Coloration

- 1. Frons, media carina: 0, viridescent or green; 1, broadly purplish red or reddish ochraceous; 2, pale brown.
- 2. Frons, areas between intermediate carinae and media carina: 0, viridescent; 1, reddish ochraceous; 2, pale brown, sometimes with fuscous spots.
- 3. Pronotum and mesonotum, general colour: 0, nearly viridescent (ochraceous in dried specimens; 1, variably coloured, usually with reddish ochraceous stripes or fuscous spots.

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Table A2. Continued

Head

- 4. Cephalic process before eyes, length: 0, short, no more than longitudinal diameter of eyes; 1, moderately elongate, no longer than pronotum and mesonotum combined; 2, very elongate, distinctly longer than pronotum and mesonotum combined (Fig. 1).
- 5. Cephalic process before eyes: 0, compressed dorsoventrally (Fig. 4B); 1, strongly compressed dorsoventrally (Fig. 10B); 2, compressed laterally (Fig. 11A); 3, not distinctly compressed.
- Cephalic process before eyes: 0, unbent or slightly curved upwards (Fig. 4B); 1, distinctly curved upwards; 2, curved downwards (Fig. 13B).
- 7. Cephalic process before eyes: 0, convergent; 1, nearly parallel (Fig. 4A).
- 8. Cephalic process before eyes: 0, robust (Fig. 4A); 1, distinctly slender; 2, constricted to an extremely slender process.
- 9. Cephalic process with a longitudinal carina in lateral surface before eyes: 0, present; 1, absent.
- 10. Vertex with a secondary carina bifurcating from subapex of lateral carinae: 0, absent; 1, present (Fig. 14J).
- 11. Vertex, posterior surface in relation to pronotum: 0, in the same plane; 1, in an elevated plane.
- 12. Vertex, base width in relation to transverse diameter of eyes: 0, distinctly narrower; 1, nearly equal or wider; 2, distinctly wider (more than twice).
- 13. Median carina of vertex: 0, absent; 1, present.
- 14. Vertex, median carina: 0, only distinct in base and (or) apex; 1, nearly complete (at least two-thirds).
- 15. Vertex, lateral carinae before eyes: 0, subparallel; 1, gradually convergent forwards; 2, abruptly constricted and convergent forwards.
- 16. Vertx, apex: 0, acuminate; 1, angulately convex (no more than 100°, Fig. 4A); 2, broadly angulately convex.
- 17. Vertex, posterior margin: 0, broadly concave; 1, angularly concave (no more than 100°, Fig. 4A); 2, nearly straight.
- 18. Vertex, posterior margin: 0, weakly ridged; 1, distinctly ridged.
- 19. Vertex, posterior margin in relation to posterior margin of eyes: 0, not surpassing; 1, slightly surpassing (Fig. 4A).
- 20. A sharp apical carina between anterior margins of frons and vertex: 0, absent; 1, present (Fig. 4B).
- 21. Frons, apex between lateral carinae and intermediate carinae: 0, without carina; 1, with weak transverse carinae.
- 22. Frons, anterior margin in relation to apex of vertex: 0, distinctly surpassing; 1, not surpassing.
- 23. Frons, median carina: 0, present; 1, absent.
- 24. Frons, median carina: 0, complete; 1, absent in the middle (Fig. 4C); 2, absent in apical part; 3, only present under the eyes.
- 25. Frons, median carina: 0, weakly ridged; 1, distinctly ridged; 2, robust and strongly convex; 3, strongly elevated and blade-like (at least at apex and base).
- 26. Frons, intermediate carinae approaching: 0, anterior margin or middle of eyes (Fig. 4C); 1, frontoclypeal suture.
- 27. Frons, intermediate carinae: 0, weakly ridged; 1, distinctly ridged; 2, strongly elevated and blade-like.
- 28. Frons, lateral carinae below the antennae: 0, nearly straight; 1, distinctly convex.
- 29. Clypeus, apex: 0, not extending to apex of fore coxae; 1, distinctly surpassing apex of fore coxae; 2, extending to apex of middle coxae.
- 30. Clypeus, apex somewhat projecting above labrum: 0, present; 1, absent.
- 31. Rostrum, apex: 0, extending to base of middle femora; 1, extending to base of hind femora; 2, extending or surpassing apex of hind femora.
- 32. Rostrum, basal segment relative to distal one: 0, distinctly longer (no less than 1.5 times as long as distal one); 1, slightly longer or nearly equal.
- 33. Compound eyes, callus postocularis: 0, forming a triangular process projecting posteriorly (Fig. 4B); 1, forming a transverse process, more or less truncate posteriorly.
- 34. Compound eyes, shape: 0, nearly rounded; 1, elongate oval (Fig. 4B).
- 35. Antennal pedicel, shape: 0, globose; 1, elongate (Fig. 4B).

Thorax

- 36. Pronotum, length: 0, shorter than half of mesonotum; 1, longer than half of mesonotum (Fig. 4A).
- 37. Pronotum, median carina: 0, weakly ridged; 1, distinctly ridged; 2, strongly ridged.
- 38. Pronotum, intermediate carinae: 0, present; 1, absent.
- 39. Pronotum, intermediate carinae: 0, distinct in basal third to half present; 1, nearly complete (Fig. 4A).
- 40. Pronotum, two longitudinal carinae between eyes and tegulae: 0, complete (Fig. 4B); 1, incomplete.
- 41. Pronotum, paranotal lobes with a short carina: 0, absent; 1, present.
- 42. Pronotum, anterior central margin: 0, arcuately convex (Fig. 4A); 1, angularly convex; 2, nearly straight.

Table A2. Continued

Thorax

- 43. Pronotum, posterior margin: 0, nearly straight; 1, arcuately concave; 2, angularly concave (Fig. 4A).
- 44. Mesonotum: 0, distinctly arched; 1, slightly arched or nearly flat.
- 45. Mesonotum, median carina: 0, present; 1, absent.
- 46. Mesonotum, lateral carinae: 0, weakly tortuous and abruptly incurved apically; 1, gradually incurved; 2, nearly straight (Fig. 4A).
- 47. Mesonotum, lateral carinae: 0, parallel (Fig. 4A); 1, convergent.
- 48. Tegmina: 0, macropterous (Fig. 2A); 1, submacropterous (Fig. 2G).
- 49. Tegmina, apical margin: 0, rounded (Fig. 2A); 1, somewhat truncate (Fig. 2C); 2, somewhat pointed (Fig. 2G).
- 50. Tegmina, unexpanded status: 0, overlapping each other; 1, not overlapping.
- 51. Tegmina, veins with setae: 0, present; 1, absent.
- 52. Tegmina, veins: 0, with short setae; 1, with long setae.
- 53. Tegmina, number of folds: 0, zero; 1, one; 2, two; 3, more than five.
- 54. Tegmina, costal area: 0, expanded; 1, not expanded.
- 55. Tegmina, costal cell (space of between costal margin and Sc+R): 0, distinctly narrow (Fig. 2F); 1, normal (Fig. 2G); 2, distinctly wide (Fig. 2B).
- 56. Tegmina, costal cell: 0, membranous (Fig. 2A); 1, coriaceous (Fig. 2F).
- 57. Tegmina with claval transverse vein (at least one) between CuP and Pcu: 0, present; 1, absent.
- 58. Tegmina, Sc+R and M originating from basal cell: 0, without stem or with a very short common stem (Fig. 2A); 1, with a distinctly long common stem (Fig. 2G).
- 59. Tegmina, Sc+R bifurcating into Sc+RA and RP veins: 0, near basal one-third (Fig. 2C); 1, beyond middle (Fig. 2A).
- 60. Tegmina, M bifurcating into M_{1+2} and M_{3+4} : 0, near basal one-third (Fig. 2C); 1, near or beyond middle (Fig. 2A).
- 61. Tegmina, M₃₊₄ bifurcating into M₃ and M₄: 0, near middle (Fig. 2C); 1, distinctly beyond middle (Fig. 2A).
- 62. Tegmina, bifurcation of M relative to CuA: 0, M distinctly bifurcated before CuA (Fig. 2C); 1, M distinctly bifurcated beyond CuA (Fig. 2E); 2, nearly abreast (just little before or beyond) (Fig. 2A).
- 63. Tegmina, number of apical cells of RP: 0, 1–3; 1, 4–6; 2, \geq 7.
- 64. Tegmina, number of apical cells of M: 0, 3–5 (Fig. 7A); 1, 6–8 (Fig. 7A); 2, 9–11; 3, \geq 12.
- 65. Tegmina, number of apical cells of CuA: 0, 1–3; 1, \geq 4.
- 66. Tegmina, nodal line: 0, absent; 1, present.
- 67. Tegmina, stigmal area: 0, present; 1, absent (Fig. 2A).
- 68. Tegmina, shape of stigmal area: 0, quadrangular; 1, elongate.
- 69. Tegmina, suboblique veins in costal cell: 0, present (Fig. 2A); 1, absent.
- 70. Tegmina, suboblique veins in costal cell: 0, at apical one-third (Fig. 2D); 1, from basal one-third or one-half to apex (Fig. 2E).
- 71. Tegmina, claval suture extending to posterior margin: 0, extending (Fig. 2G); 1, not extending (Fig. 2A).
- 72. Tegmina, dendroid secondary veins among longitudinal veins: 0, absent (Fig. 2D); 1, present (Fig. 2B).
- 73. Hindwings, apical and hind areas with many transverse veins: 0, present; 1, absent.
- 74. Hindwings, unexpanded status: 0, overlapping each other; 1, not overlapping.
- 75. Hindwings: 0, anal area developed; 1, anal area reduced (Fig. 2H).
- 76. Hindwings, secondary fold in the anal area: 0, absent; 1, present.
- 77. Fore coxae: 0, long, beyond apex of clypeus; 1, relatively short, not extending to apex of clypeus.
- 78. Fore femora, length: 0, normal; 1, slender and elongate.
- 79. Fore femora, length: 0, normal; 1, flattened and dilated.
- 80. Fore femora, ventral subapical part with a spine; 0, present; 1, absent.
- 81. Fore femora, subapical spine: 0, minute; 1, large and blunt.
- 82. Fore and middle tarsomeres I and II, acutellae: 0, absent; 1, 2; 2, \geq 4.
- 83. Hind femora and tibiae: 0, normal; 1, distinctly elongate.
- 84. Hind tibiae, number of apical teeth: 0, 6; 1, 7; 2, 8.
- 85. Hind tarsomeres I and II, apical teeth: 0, without setae; 1, with platellae; 2, with long setae.
- 86. Hind tarsomeres I and II, special chaetotaxy on ventral surface: 0, absent; 1, present.
- 87. Hind tarsomeres I and II, number of apical teeth: 0, 5–7; 1, 8–13; 2, 14–20.
- 88. Arolium: 0, not developed; 1, developed.

Table A2. Continued

Abdomen

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

Male abdomen

- 90. Pygofer (lateral view), length: 0, > twice ventral width; 1, < twice ventral width (Fig. 2E).
- 91. Pygofer, posterior margin with a process: 0, absent; 1, present.
- 92. Pygofer, posterior process: 0, small; 1, robust.
- 93. Pygofer, posterior process: 0, acute; 1, obtuse.
- 94. Gonostyles, upper process: 0, present; 1, absent.
- 95. Gonostyles, upper process: 0, not distinctly compressed; 1, compressed dorsoventrally.
- 96. Gonostyles, upper process: 0, acute (Fig. 7F); 1, obtuse (Fig. 2F).
- 97. Gonostyles, upper process: 0, not elongate; 1, elongate.
- 98. Aedeagus, apical membranous lobes of phallobase: 0, without spine or with very short small spines; 1, with moderate to long spines.
- 99. Aedeagus, endosomal processes: 0, very short and invisible; 1, moderately long, no longer or little longer than apical lobes (Fig. 15D); 2, much longer (Fig. 2H).
- 100. Aedeagus, endosomal processes (apical part from extended from phallotheca excluding apex): 0, nearly membranous and translucent (Fig. 10H); 1, sclerotized and pigmented (at least partly, Figure 2H).
- 101. Aedeagus, apical half of endosomal processes: 0, not distinctly inflated; 1, distinctly inflated (Fig. 2H); 2, strongly inflated (Fig. 10H).
- 102. Aedeagus, endosomal processes with small spines: 0, absent; 1, present.
- 103. Aedeagus, apex of endosomal processes: 0, acute; 1, obtuse.
- 104. Aedeagus, endosomal processes: 0, nearly straight; 1, curved in middle.
- 105. Aedeagus, endosomal processes: 0, not forked; 1, forked.
- 106. Segment X, shape (dorsal view): 0, oval; 1, truncate; 2, distinctly elongate (Fig. 2G); 3, irregular.
- 107. Segment X (lateral view), ventral margins in apex: 0, not projecting; 1, projecting ventrally.
- 108. Segment X (lateral view), ventral margins in base: 0, not projecting; 1, projecting ventrally.
- 109. Segment X, ventral apical margin: 0, distinctly concave; 1, more or less concave or convex.

Female abdomen

- 110. Gonapophysis VIII, teeth of anterior connective lamina: 0, only at the tip (Fig. 8A); 1, from base to tip (Fig. 21D).
- 111. Gonapophysis VIII, basal teeth of anterior connective lamina: 0, not prolonged (Fig. 8A); 1, transversally prolonged and strongly ridged, maybe forming two apices (Fig. 21D).
- 112. Gonapophysis VIII, teeth of anterior connective lamina: 0, very small (Fig. 8A); 1, large (Fig. 21D).
- 113. Gonapophysis VIII, teeth of anterior connective lamina: 0, almost same-sized (Fig. 8A); 1, varying sizes and shapes (Fig. 21D).
- 114. Gonapophysis VIII, number of teeth of anterior connective lamina: 0, 2–5 (Fig. 8A); 1, >5 (Fig. 21D).
- 115. Gonapophysis VIII, an additional mambranous process of anterior connective lamina: 0, absent; 1, present.
- 116. Gonocoxae VIII, number of GxP: 0, 1; 1, 2 (Fig. 2D).
- 117. Gonapophysis IX, apex of posterior connective lamina: 0, not or weakly bifurcating; 1, distinctly bifurcating (Fig. 2E).
- 118. Gonapophysis IX, tiny setae on apex of posterior connective lamina: 0, absent; 1, present.
- 119. Gonapophysis IX, posterior fibula (Fp) extending to gonospiculum (Gl): 0, present (Fig. 8B); 1, absent.
- 120. Gonoplacs, the third additional lobes (Gp3): 0, absent; 1, present (Fig. 8D).
- 121. Gonoplacs, apical margin of Gp1: 0, truncate (Fig. 8C); 1, more or less pointed.
- 122. Gonoplacs, filmy edging of Gp1: 0, absent; 1, present.
- 123. Gonoplacs, sensory appendage of Gp1 (lower lobes): 0, absent; 1, present.
- 124. Gonoplacs, sensory field with numerous tiny setae at apex of Gp1: 0, absent; 1, present.
- 125. Gonoplacs, spinous setae on apical margin of Gp1: 0, absent; 1, present.
- 126. Gonoplacs, Gp2 (posterior lobes): 0, slender; 1, distinctly wider.
- 127. Segment X, shape: 0, nearly rounded; 1, truncate; 2, distinctly elongate; 3, heart-shaped.
- 128. Segment X, ventral apical margin: 0, distinctly concave; 1, more or less concave or convex.

Table A3. Morphological character matrix for the phylogenetic analysis

	0000000000	1111111111	222222222	3333333333
Taxa	0123456789	0123456789	0123456789	0123456789
Zanna chinensis	0221230000	0020-11210	1001—1010	0010001-1-
Dichoptera similis	0001031011	0110-21010	1000021110	120100021-
Dorysarthus sumakowi	1-01222101	0010-02210	1111—1200	0010001001
Aluntia longicephalica sp. nov.	1000200100	0010-01111	1100110101	1110111101
Aluntia schimperii	1000200100	0010-01111	1100110201	1110111101
Dendrophora borneensis	1000200100	0010-01001	0100100101	1110111001
Dendrophora ramosa	1000200100	0010-01001	0100100101	1110111001
Dictyomorpha elongata	1000210101	0010-01111	1100030201	1110111101
Dictyomorpha furca	1000210100	0010-01111	1100030201	1110111001
Dictyomorpha hectica	1000210100	0010-01111	1100030201	1110111101
Dictyomorpha laosensis	1000210100	0010-01111	1100030201	1110111101
Dictyomorpha moluccana	1000210101	0010-01111	1100030201	1110111101
Dictyomorpha sulawesiensis	1000210101	0010-01111	1100030201	1110111101
Dictyomorpha unifasciata	1000210100	0010-01111	1100030201	1110111101
Indodictyophara lobosa	1000210100	0011001111	1100030201	1110111101
Madagascaritia angusta sp. nov.	1000220100	0010-00001	0100130201	1110111101
Madagascaritia hova	1000220110	0010-00001	0100030201	1110111001
Arjuna maai sp. nov.	1111132101	1010-10000	1110020102	1210001201
Arjuna muiri sp. nov.	1111132101	1010-10000	1110020102	1210001201
Arjuna scriba	1111132101	1010-10000	1110020102	1210001201
Pippax opilionoides	1111130101	0010-01000	1110320102	1210001200
Dictyophara (s.str.) europaea	1000130001	0011111010	0010011101	1111000100
D. (Chanithus) pannonica	1000230101	0011002010	0010001001	1111000101
Raivuna micida	1011230101	0011002010	1010001001	1111000101
Putala rostrata	1011120111	0101002010	001000101	110100011
Anasta prognatha	1000130001	0011011010	10100111101	1111000101
Hasta hastata	1000130001	0021002010	1110011101	101000101
Thanatodictya bifasciata	1000220101	0111001110	1110111111	1110000101
Centromeria sp.	1101031010	0011020110	0000020111	121100021-
Metaurus reticulatus	1000121020	0011020110	0010201011	120100021-
Orthopagus lunulifer	1021030101	0111102110	0010201011	111100021-
Saigona ussuriensis	1001130101	0111102110	1010000011	11000021
Worskaito stenexi	100?130101	0111111010	1010000011	101?000201
worskuito sienexi				
m.	444444444	555555555	666666666	777777777
Taxa	0123456789	0123456789	0123456789	0123456789
Zanna chinensis	102001—00	0003120000	00023101-1	-110000000
Dichoptera similis	0010000001	1003000001	0002311011	-101101000
Dorysarthus sumakowi	0020012000	0000100001	1101101011	-001000000
Aluntia longicephalica sp. nov.	0002112000	01-0120101	11201001-0	1111000110
Aluntia schimperii	0002102000	0000120101	11201001-0	1111000110
Dendrophora borneensis	0002100001	0000020100	00012101-0	1111000110
Dendrophora ramosa	0002100001	0000020100	00012101-0	1111000110
Dictyomorpha elongata	0002102000	0000120101	11100001-0	0101000110
Dictyomorpha furca	0002112000	0000120101	11100001-0	0101000110
Dictyomorpha hectica	0002112000	0000120101	11100001-0	0101000110
Dictyomorpha laosensis	0002102000	0000120101	11100001-0	0101000110
Dictyomorpha moluccana	0002102000	0000120101	11100001-0	0101000110
Dictyomorpha sulawesiensis	0002102000	0000120101	11100001-0	0101000110
Dictyomorpha unifasciata	0002102000	0000120101	11100001-0	0101000110
	0002102000	0000120101	11100001-0	1101000110
lnaoaictvophara lobosa				
Indodictyophara lobosa Madagascaritia angusta sp. nov.	0002102000	0000001101	01210101-0	1111000110
Inaoaictyophara totosa Madagascaritia angusta sp. nov. Madagascaritia hova	$0002102000 \\ 0002102000$	0000001101 0000001100	01210101-0 01212101-0	1111000110 1111000110

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Table A3. Continued

Тотто	44444444 012345678			6666666666	777777777 0123456789
Taxa	012345678	9 01234	56789	0123456789	0123456788
Arjuna muiri sp. nov.	000210011	2 10101	10111	11100001-1	-001110110
Arjuna scriba	000210011	2 10101	10111	11100001-1	-001110110
Pippax opilionoides	000210011	2 10101	10111	11100001-1	-001110110
Dictyophara (s.str.) europaea	010110200	0 11-111	.0101	1110100001	-001001100
D. (Chanithus) pannonica	010110200	0 11-111	.0101	1110100001	-001001100
Raivuna micida	010110200	0 11-111	.0101	1110110001	-001001100
Putala rostrata	000101200	0 11-111	.0101	1110100001	-001001100
Anasta prognatha	000110200	0 11-111	11-1110111		-001001100
Hasta hastata	000110200	0 11-111	.0111	1110100011	-001001100
Thanatodictya bifasciata	0001101100	0 11-111	.0111	1110000011	-001001100
Centromeria sp.	001210110	0 11-111	.0101	1110100011	-001001110
Metaurus reticulatus	000110110	0 10010	10101	0001210011	-001001101
Orthopagus lunulifer	001210110			1110100001	-001001101
Saigona ussuriensis	1002111100	1002111100 10011		1110100001	-001001101
Worskaito stenexi	0?12112000	0 11-211	.0101	1110101011	-00100?100
			1111111111		1111111111
	888888888	999999999	0000000000		22222222
Taxa	0123456789	0123456789	0123456789	0123456789	012345678
Zanna chinensis	1-00201100	00—1—00	0001003000	0-10011011	00101003-
Dichoptera similis	1-00000000	00-000001	0000001101	0-10001011	001011010
Dorysarthus sumakowi	1-00120000	00-101	1011001100	0-10011011	001000010
Aluntia longicephalica sp. nov.	1-01120011	10-001102	1100102001	0-00000010	100010021
Aluntia schimperii	1-01120011	10-001102	1100102001	0-00000010	100010021
Dendrophora borneensis	1-01120011	10-000002	1100102001	0-00000010	100010021
Dendrophora ramosa	1-01120011	10-000102	1100100001	0-00000010	100010021
Dictyomorpha elongata	1-01120011	1101001002	0200102001	0-00000010	100010021
Dictyomorpha furca	1-01120111	1111001002	0200112001	0-0000010	100010021
Dictyomorpha hectica	1-01120011	1110001002	0200102001	0-0000010	100010021
Dictyomorpha laosensis	1-01120011	1111001002	0200102001		100010021
Dictyomorpha moluccana	1-01120011	1101001002	0200102001	0-0000010	100010021
Dictyomorpha sulawesiensis	1-01120011	1101001102	0200102001		100010021
Dictyomorpha unifasciata	1-01120011	1111001002	0200102001		100010021
Indodictyophara lobosa	1-01120011	1111001002	0000102001		100010021
Madagascaritia angusta sp. nov.	1-01120011	10-001002	0200112101		100010021
Madagascaritia hova	1-01120011	?????????	?????????1		100010021
Arjuna maai sp. nov.	1-11110110	00-010101	1001000001		001001101
Arjuna muiri sp. nov.	1-11110110	00-010101	1001000001		001001101
Arjuna scriba	1-11110110	00-010101	1001000001		001001101
Pippax opilionoides	1-11110110	00-010101	1001000001		001001101
Dictyophara (s.str.) europaea	1-20110210	00-000011	0000101101		010100101
D. (Chanithus) pannonica	1-20110210	00-000011	0000101101		010100101
Raivuna micida	1-20110010	00-000010	-000000001		010100101
Putala rostrata	1-20110210	0110000011	0001001101		010100101
Anasta prognatha	1-10110210	00-000001	1000000011		001001101
Hasta hastata Thanatadiatus hifacciata	1-10210210	?????????	??????????		001001101
Thanatodictya bifasciata	1-10110210	00-000011	1000000011 0000100001		001001101
Centromeria sp. Mataurus reticulatus	$\begin{array}{c} 0011010110 \\ 0110110210 \end{array}$	0110000001 0101000001	010-013110	1011101001	010100101 010100101
Metaurus reticulatus Orthopagus lunulifer	0110110210	00-000101	010-013110		010100101
Saigona ussuriensis	0110110210	0101000101	000000001		010100101
Worskaito stenexi	1-10110010	??????????	??????????	?????????	?10001?01
	1-10110010				,10001:01