Testing Tropiduchini Stål 1866 (Hemiptera: Tropiduchidae) monophyly, a young inter-tropical taxon of mainly insular species: taxonomy, distribution patterns and phylogeny, with the description of a new genus from Papua New Guinea

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Abstract. A morphological phylogenetic analysis of the tribe Tropiduchini (Hemiptera: Tropiduchidae) is provided for 21 genera among the 26 recognized, including the new genus *Oechalinella* Wang **gen.n.**, with a new species *Oechalinella bifasciata* Wang **sp.n.** Monophyly of the tribe is well supported by synapomorphies derived from the male genitalia. The strict consensus supports two subclades: ((*Montrouzierana* + *Thymbra*) + *Thaumantia*[+]) as sister to the clade (*Leptovanua* + (*Vanua* + *Varma*[+]) + *Daradacella*[+]). In the first subclade, the clade (*Montrouzierana* + *Thymbra*), distributed in New Caledonia and Papua New Guinea, is well supported by three synapomorphies based on the tegmina, while the *Thaumantia*[+] group is characterized by the conformation of the anal tube and male gonostyli, and distributed from Malesia to Papuasia and in Central Africa. The second subclade is largely distributed from China to Malesia, Papuasia, Southwestern and the Northwestern Pacific islands. The position of the genus *Leptovanua* remains uncertain. The *Varma*[+] clade is recovered in all analyses. Implied weighting analysis placed the *Varma*[+] lineage as sister to all other genera forming a new group (*Leptovanua*[+] + ((*Montrouzierana* + *Thymbra*) + *Thaumantia*[+])). Fennah's definition of Tropiduchini is reviewed according to the phylogenetic results and an identification key to all genera is provided with a referenced synopsis of their distribution. Globally, Tropiduchini exhibits an inter-tropical latitudinal distribution and a paradoxical bimodal longitudinal distribution pattern in continental Africa, South-east Asia and the Pacific islands. Distribution data concern nearly 80% of insular taxa. The phylogenetical results suggest that: (i) the tribe originates from continental China; (ii) it evolved mainly from Papuasia by stepping-stone colonization events, promoting subsequent insular speciation; and (iii) its evolution has mainly been directed by dispersion versus vicariance.

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Introduction

Tropiduchidae is a relatively small planthopper family of about 179 genera and 641 species (Bourgoin, 2016), which is part of the Fulgoromorpha in the order Hemiptera. They have adapted to various habitats, from rainforest to macchia and semi-desert biotopes, feeding on diverse herbaceous monocots, ferns and woody dicotyledon plants. Some species, such as the dubas bug, *Ommatissus binotatus* Fieber, can cause devastating damage to major agricultural and economic crops worldwide, and even vector various plant pathogens such as phytoplasmas, viruses and other prokaryote-like organisms (Fennah, 1982; Wilson & O'Brien, 1987; Wilson *et al.*, 1994; O'Brien, 2002; Wilson, 2005). Extant tropiduchids are mainly distributed in tropical areas, with several species extending to temperate zones, and fossils from the Eocene warmer climates are known from more northern parts in the Palaearctic and Nearctic realms (Bourgoin, 2016).

Fennah (1982) provided the most recent higher classification of Tropiduchidae, following pioneering work by Melichar (1914) and Muir (1923). Removing Hiracini Melichar, 1914 from the Tropiduchidae, he defined 15 tribes (three of them divided into subtribes) based on a combination of morphological characters (Fennah, 1982) that appeared later to be variable and not always homologous (Asche & Wilson, 1989). Some 20 years later, two extinct and fossil tribes were added to the family: Jantaritambiini Szwedo, 2000 from the Eocene Baltic amber and Emilianini Shcherbakov, 2006 from the Eocene of Green River, Colorado. In 2007, Gnezdilov transferred the subtribe Gaetuliina Fennah, 1978 and the tribe Trienopini Fennah, 1954 into Tropiduchidae from Nogodinidae Melichar, 1898 and Issidae Spinola, 1839, respectively (Gnezdilov, 2007). In 2013, he grouped all Fennah's tribes plus a new Madagascarian monotypic tribe, Chrysopuchini Gnezdilov, 2013, into the subfamily Tropiduchinae Stål, 1866 (Gnezdilov, 2013). He established also the new subfamily Elicinae Melichar, 1915, with two tribes, Elicini Melichar, 1915 (former, Gaetulini Fennah, 1978) and Parathisciini Gnezdilov, 2013. He added two new, recently described fossil taxa to the Elicinae – Austrini Szwedo and Stroiński, 2010 and Patollini Szwedo & Stroiński, 2013 – both from the Eocene Baltic amber (Gnezdilov, 2014). Still more recently one more additional new Neotropical tribe was established for the New World genus *Buca* Walker, 1858 (Gnezdilov *et al.*, 2016), previously placed as Tropiduchidae *incertae sedis* (Gnezdilov, 2013, 2014). All these taxonomic transfers and additional information were precisely listed in Gnezdilov *et al.* (2016), which also provides the current classification of this family.

All these taxonomic changes in the classification of the family during the last 10 years have resulted in about one-third of the tropiduchid genera being transferred from or to other planthopper families and in ten new tribes being recognized. However, a formal phylogenetic analysis to evaluate and confirm these numerous taxonomic changes is still lacking (Wang *et al.*, 2012a). Moreover, the discoveries of new fossils and new extant taxa and the transfer of numerous other taxa previously placed in different planthoppers families have made the family-level definition of Tropiduchidae quite ambiguous, challenging its monophyly, but also impeding further phylogenetic analysis of planthoppers and particularly taxa closely related to tropiduchids (Wang *et al.*, 2012a,b, 2013a,b; Gnezdilov *et al.*, 2015; Gnezdilov & Bourgoin, 2015).

To address these problems, morphological and taxonomic data on the family were reviewed in a series of publications by the co-authors of this paper in various Tropiduchidae tribes: Cixiopsini (Wang *et al.*, 2013b, 2014b), Tambiniini (Wang *et al.*, 2014a), Paricanini (Stroiński *et al.*, 2015), Elicini (Gnezdilov & Bourgoin, 2015; Wang *et al.*, 2015), Bucini (Gnezdilov *et al.*, 2016), Tropiduchini (Wang *et al.*, 2013a, 2014a), and several other papers are in preparation. Moreover, a clear definition of the tribe Tropiduchini Stål, 1866 that contains the type genus of the family is also a necessary step towards a better understanding of the family-level concept of Tropiduchidae. Including the new taxa described here, this tribe currently comprises 26 genera representing 131 species and subspecies (Bourgoin, 2016). Accordingly, the objectives of the present paper are:

1 to deliver a comprehensive systematic revision of the Tropiduchini at the generic level with a key to all genera of the tribe, including a new genus representing a new species, which is described;
2 to deliver a morphological phylogenetic analysis of the Tropiduchini genera (inferred from adult morphological characters); and
3 to briefly address the distribution and biogeographical patterns observed in light of the phylogeny established for the tribe.

Material and methods

Taxonomic study

Scanning electron microscopy photographs of uncoated specimens were taken in the Laboratory of Scanning Microscopy, Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw, through a Hitachi S-34Q scanning microscope (Japan) under low-vacuum conditions. Dry-mounted specimens were used to document the characters in the key, and to describe and illustrate the new taxa. External morphology was observed under a stereoscopic microscope and measurements were done with an ocular micrometer. To examine male and female genitalia, abdomens were removed and macerated in 10% KOH overnight. Dissections and cleaning of genitalic structures were performed in distilled water. After being transferred to distilled water, the genitalia were stained with methylrosanilinium chloride (solution including methyl violet, ethanol and purified water) to highlight the internal thin and transparent membranous parts (Wang *et al.*, 2009). Observations and drawings were made in glycerine under a compound microscope. Photographs of the habitus were taken with a Nikon Coolpix 5400 digital camera (Japan) or a Leica DFC 295 digital camera (Germany) associated with a Leica Z16 APO microscope (Germany). Digital images were imported into Adobe PHOTOSHOP

CS4 for labelling and plate composition. Line figures were drawn with a camera lucida mounted on a Zeiss Stemi SV-11 stereomicroscope (Germany) or an Olympus BX41 compound microscope (Japan).

Morphological terminology follows Bourgoin & Huang (1990) and Bourgoin (1997), respectively, for male and female genitalia. Venation interpretation and terminology were adapted from Bourgoin *et al.* (2015) for both the forewing and hindwing. Distribution and specimen data were first assembled from Metcalf (1954), and then completed, updated and synthesized in FLOW (Bourgoin, 2016). The holotype of the new species described in the following is deposited at the California Academy of Sciences, U.S.A.

The specimens examined in the present study belongs to the following institutions:

BPBM, Bernice P. Bishop Museum, Honolulu, Hawaii, U.S.A.
CAS, California Academy of Sciences, Entomology, San Francisco, U.S.A.
INHS, Illinois Natural History Survey, Illinois, Champaign, U.S.A.
HU, Laboratory of Systematic Entomology, Hokkaido University, Sapporo, Japan.
IZCAS, Chinese Academy of Sciences, Beijing, China.
MIZ, Museum and Institute of Zoology PAS, Warszawa, Poland.
MMBC, Moravian Museum, Brno, Czech Republic.
MNHN, Museum National d'Histoire Naturelle, Paris.
NHM, Natural History Museum, London, U.K.
NHMW, Naturhistorisches Museum, Wien, Austria.
RBINS, Royal Belgian Institute of Natural Sciences, Brussels, Belgium.
USMB, Upper Silesian Museum in Bytom, Poland.
ZMUC, Zoological Museum, University of Copenhagen, Denmark.

Distribution pattern

The EDIT MAP REST services (v1.1) as provided by FLOW (Bourgoin, 2016) were used to generate distribution maps according to the global standard codes of the International Working Group on the Taxonomic Databases for Plant Sciences (TDWG) (Brummitt, 2001). The division into realms and regions follow the recent proposal of Holt *et al.* (2013). All published data for Tropiduchini species have been checked to infer global distribution patterns of the Tropiduchini and subclades, and their collection data are listed in Appendix S3 in Supporting Information at level 4 accuracy according to the global TDWG global standard (Brummitt, 2001). This level corresponds to the 'basic recording units' within the level 3 'botanical country units' used to record plant distributions worldwide. This internationally recognized standard allows botanical data to be compared and exchanged between scientific institutions without loss of information due to incompatible geographical boundaries. Because plants are essential to

planthoppers, this system was adopted to record planthopper distribution in FLOW (Bourgoin, 2016) and is also used in this study.

Phylogenetic analysis

In all, 27 species representing 27 genera were selected for phylogenetic analysis, including 21 ingroup and six outgroup taxa, 21 of which were Tropiduchini. Six other tropiduchid tribes were selected as outgroup taxa for the cladistic analysis in order to root the cladogram and for the assessment of in-group homologies. The corresponding genera were chosen to include representatives of major species-rich taxa and type species were preferentially selected when possible: *Chasmacephala pluvialis* Fennah, 1946 (Chasmacephalini), *Epora subtilis* Walker, 1857 (Eporini), *Paricana dilatipennis* Walker, 1857 (Paricanini), *Remosa cultellator* (Walker, 1858) (Remosini), *Tambinia macula* Wang & Liang, 2011 (Tambiini). A fossil taxa, *Jantaritambia serafini*† Szwedo, 2000 (Jantaritambiini), was also selected. In Tropiduchini, the monotypic genera *Leptotambinia* Kato, 1931, *Nesotemora* Fennah, 1956, *Oligaethus* Jacobi, 1928 and *Peltodictya* Kirkaldy, 1906, and *Ficarasa* Walker, 1857 that includes two species, for which we were unable to examine specimens and for which information in the literature was insufficiently detailed, were not included in the analysis.

A total of 68 characters (64 binary, four multi-state) were included in the phylogenetic analysis, including 12 characters from the head capsule, 26 from the thorax (20 from the tegmen), and 30 from the genitalia (three from the pygofer, seven from the anal tube, eight from the periandrium, 10 from gonostyle and two from aedeagus) (Appendix S1 in Supporting Information). The full data matrix was compiled using MESQUITE V. 2.74 (Maddison & Maddison, 2010), and is provided in Appendix S2, Supporting Information. Characters that were not applicable were scored as dashes (−) and as questions marks (?) if ambiguous or missing. Data were analysed using TNT version 1.1, 2005 (Goloboff *et al.*, 2003). Multi-state characters were treated as unordered, and both unweighted and implied weighting analyses ($k = 3$) (Goloboff, 1993) were conducted under the parsimony criterion. Heuristic searches that use tree−bisection−reconnection (TBR) branch swapping under 'traditional search' (TS) was run with the following parameters: general RAM of 1000 Mb, maximum tree of 10 000, one random addition sequence, with 10 trees saved per replicate; branches were collapsed if the maximum branch length was 0. 'New technology search' (NTS) was also applied and performed using five replications as a starting point for each hit, finding minimum length trees ten times, multiplying trees by fusing after hitting the best score and saving one tree per replicate; these trees were reanalysed by TS using 'trees from RAM' to find all the results. Character optimization and mapping were conduct with WIN-CLADA V. 1.00.08 (Nixon, 1999).

Bremer support was calculated using TNT (Goloboff *et al.*, 2003) on both the unweighted and the weighted data. Weighted B0remer support was calculated and rescaled to 'match' unweighted support (Bremer, 1994). Suboptimal trees were

searched for five steps longer than the optimal trees and Bremer support was calculated from 100 000 retained trees (increasing the number of retained trees to 100 000 had no effect on support values). In the text, we name clades following the format suggested by De Souza Amorim (1982): taxa A+ = A+ ((B + C)) or (A + B) + ((C+ (D+ (…))).

Results

Taxonomy

While sorting and identifying Tropiduchidae in the materials from the CAS, we found one undescribed taxon collected from Papua New Guinea with very distinct forewing venation, which could not be placed in any known genus, most of them presented in Figs 1–2 for quicker comparison. It is described here.

Family Tropiduchidae Stål.
Subfamily Tropiduchinae Stål.
Tribe Tropiduchini Stål.

Oechalinella Wang gen.n.
Figs 3–8; http://zoobank.org/urn:lsid.zoobank.org:act:/E226135E-02EB-4EB0-B0A1-A9BDFDA11F5C

Type species. Oechalinella bifasciata Wang **sp.n.**; designated here.

Diagnosis. Similar to *Oechalina* Melichar, 1914 in external appearance, but tegmen venation (Figs 3E, 4D, 5C) with regular distal postnodal line of transverse veinlets (irregular in *Oechalina*); costal area with less numerous veinlets, about 10 (more than 12 in *Oechalina*); stem ScP+R forked basad of junction of claval veins and apicad of CuA forking (basad of junction of claval veins and CuA forking in *Oechalina*); claval veins Pcu and A_1 fused basad of middle of clavus length (apicad in *Oechalina*). Metatibio-tarsal formula 3-6/6/2. Anal tube (Figs 4F, H–I, 5H–I) without apical part curved ventrally (elongate and bent ventrally in *Oechalina*). Pygofer, medially fused gonostyli and aedeagus asymmetrical. Dorsolateral angles of pygofer (Fig. 4F) broadly produced (not produced in *Oechalina*) and left gonostylus (Figs 4H, 5I) relatively long and narrow in left view (relatively short and broad in *Oechalina*).

Known distribution. Papua New Guinea (Madang Province).

Description. Medium-sized tropiduchid (10.6 mm), hyperpterous (Bourgoin *et al.*, 2015), body uniformly coloured with distinctly contrasting pattern (Fig. 5A, B).

Head (Figs 3A, 4A, 5A, E, 6A) with compound eyes narrower than pronotum. Vertex nearly triangular in dorsal view, twice as long as broad at base, distinctly bent upwards at apex; lateral margins ridged, converging anteriad to apex; median carina simple, not reaching anterior margin. Frons (Figs 3C, 4C, 5G, 6C–E, 7A) more than twice as long as broad in middle; lateral margins of frons carinate, median carina simple. Frontoclypeal

suture arcuate. Clypeus with median longitudinal eminence. Rostrum reaching hind coxae bases; apical segment longer than broad, shorter than subapical segment. Postocular eminence (Figs 5F, 6B) distinct, posteriad of compound eye. Ocelli (Figs 4B, 5F, 6B) vestigial. Antenna (Figs 4B, C, 5B, F, 6B–F, 7A–D) with pedicel club-like, covered with microsetae to its base, flagellum emerging from a depression in the tip of pedicel, clover-leaf-like type placodea sensilla.

Pronotum (Figs 3A, 4A, B, 5A, B, E, F, 6A, B) tricarinate, disc of pronotum elevated, delimited by lateral carinae, lateral carinae distinctly elevated, median one not so; posterior margin of pronotum carinate; one lateral carina between eye and tegula.

Mesonotum (Figs 4A, B, 5A, B, E, F, 6A, B) longer than broad, disc elevated above disc of pronotum, flat. Mesoscutellar suture (Figs 4A, 5A, E) arcuate; posterior margin of mesoscutellum angulate. Tegula (Figs 4A, B, 5A, B, E, F, 6A–D) carinate.

Hind coxa (Figs 3D, 7E, F) with coxal process widely triangular, very wide at base, spinose at apex. Hind tibia with three lateral spines and six apical teeth. Metabasitarsomere with six apical teeth. Metamidtarsomere with two lateral spines (Fig. 7F).

Tegmen hyperpterous (Figs 3E, 4D, 5A–C, 8A–F) long and narrow, membranous, without granulation, with three defined lines formed by veins and veinlets: nodal, first and second postnodal lines (Fig. 3E). Costal area (Figs 3E, 4D, 5A–C, 8A, F) present, narrower than costal cell, nearly reaching the level of tip of clavus, with sparse cross veins. Costal cell extending beyond half the length of tegmen and without transverse veinlets. Stems ScP+R and MP (Fig. 3E) leaving basal cell with a short common stalk; stem ScP+R forked basad of tegmen midlength and well basad of nodal line; branch ScP+RA separated from RP before nodal line (Fig. 3E). Stem MP forking first at level of nodal line; MP_1, MP_2, MP_3 and MP_4 each forking again after second postnodal line. Characteristic hyperpterous series of nine closed postnodal cells. Stem CuA forked basad of ScP+R forking, basad of half of tegmen length, apicad of claval veins junction.

Hindwings (Figs 4E, 5D) with stems ScP+R, M and CuA, fused at base, stem ScP+R emerging at very base, common portion of stems M and CuA short; branch ScP+RA single; branch RP with three terminals. Stem M forked well apicad, with three terminals. Stem CuA forked basad of stem ScP+R forking, then forked again, reaching margin with six terminals. Stem CuP single, reaching margin in a short distance of last terminal of CuA.

Male genitalia (Figs 4F–J, 5H–J) asymmetrical, gonostyli (Figs 4H–J, 5I, J) fused medially, concave medially in ventral aspect. Male anal tube (Figs 4F, H, I, 5H–J) elongate, epiproct and paraprocts placed in apical third of anal tube length, apical portion of anal tube not curved ventrally.

Etymology. The new genus name is a combination of the similar-looking genus *Oechalina* with the diminutive suffix '*ella*'. Gender: feminine.

Remarks. Oechalinella belongs to the tribe Tropiduchini according to the generic characters provided by Fennah (1982),
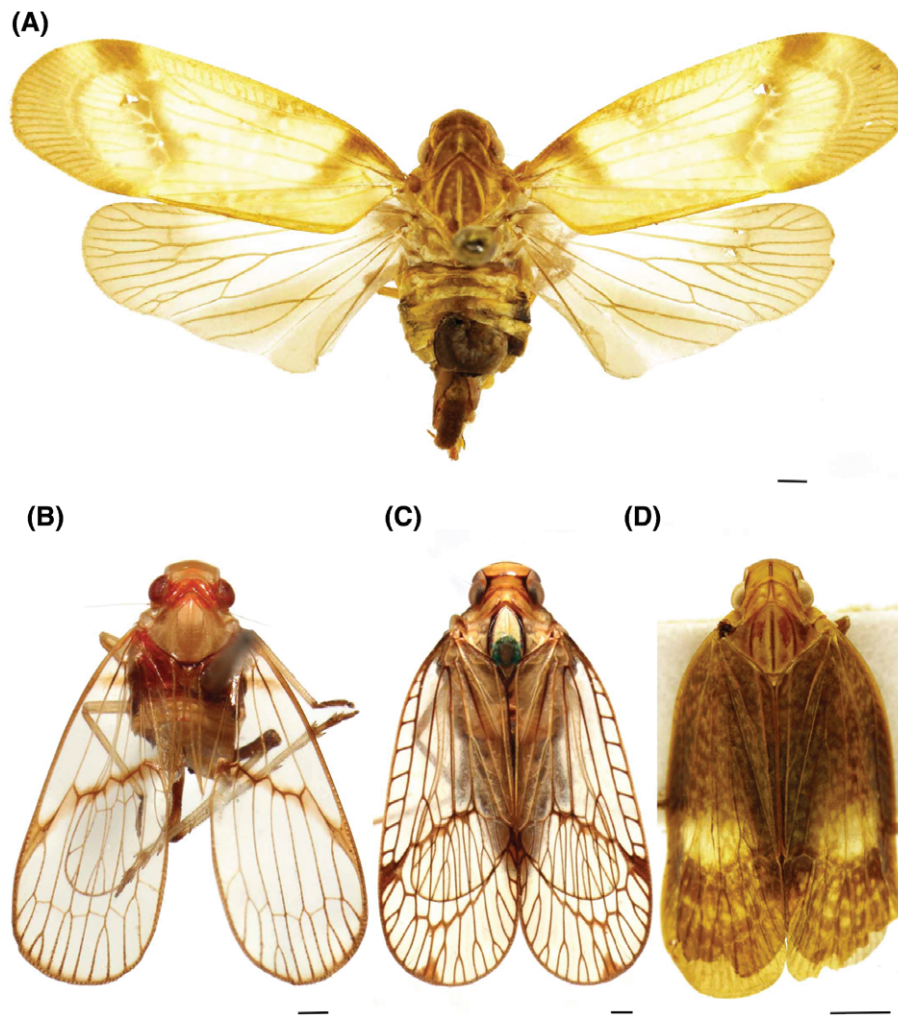
Fig. 1. Dorsal habitus of key taxa in Tropiduchini. (A) *Tropiduchus* sp. [Museum National d'Histoire Naturelle (MNHN)]; (B), *Pseudoparicana analoga* Wang & Malenovský, 2013 [*Holotype*, California Academy of Sciences (CAS)]; (C) *Lavora similis* Wang, 2013 [*Holotype*; Natural History Museum (NHM)]; (D) *Haliartus centralis* (Gerstaecker, 1895) (MNHN). Scale bars: A–C, 1 mm; D, 2 mm.

i.e. frons unicarinate, antennal pedicel with microsetae extending to base, apical segment of rostrum not broader than long, post-tibia with three spines laterally, tegmen with costal area with transverse veinlets present, branch ScRA$_1$ emitted before the nodal line, gonostyles asymmetrical and fused.

Oechalinella bifasciata Wang sp.n.
Figs 3–8; http://zoobank.org/urn:lsid.zoobank.org:act:/4A5B8 628-8083-4337-9625-AC3695F963E6

Diagnosis. Large species uniformly straw-coloured but carinae of vertex, pronotum and mesonotum suffused with orange and two reddish stripes on vertex. Hyperpterous species: cell C1 prenodal and shorter than C5 prenodal ; first transverse row of six postnodal closed cells ; second transverse row of nine closed postnodal cells ; 21–22 open apical cells about as long as postnodal ones.

Description. Size: Male. Total length (from apex of vertex to tip of forewings): 10.63 mm; body length (from apex of vertex to tip of anal tube): 7.38 mm; forewing length: 8.17 mm.

Coloration. General colour uniformly straw-coloured (Fig. 5A, B). Vertex (Fig. 5A, E) with lateral margins, all carinae of pronotum and mesonotum, and posterior areas of disc in pronotum all suffused with orange.

Head and thorax: Head (Figs 4A, 5A, E, 6A) long and narrow, produced in front of eyes approximately for three times length of compound eye. Vertex (see generic description) (Figs 2A, 3A, 4A, B, 5A, B, E, F, 6A, B) about 1.5× as long at midline as broad at the widest point, about 4× as long as pronotum at midline; lateral margins ridged, diverging from base to near level of anterior border of compound eyes, then converging to a bluntly pointed apex; median carina simple (see generic description), posterior margin deeply excavated, margins slightly ridged; both median and lateral carinae raised, disc of vertex flat, depressed.
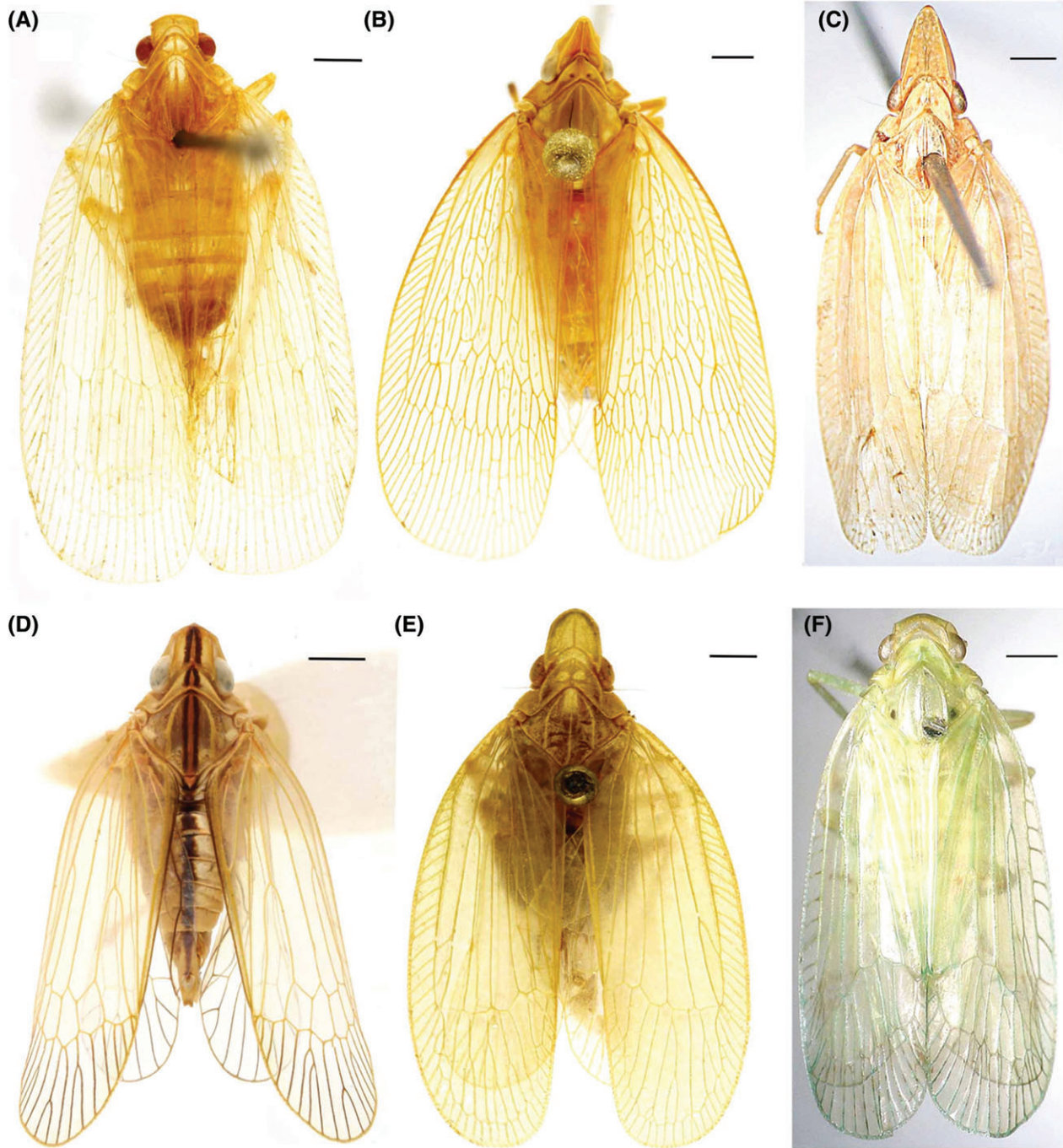
Fig. 2. Dorsal habitus of key taxa in Tropiduchini. (A) *Thymbra latipennis* Melichar, 1914 [Royal Belgian Institute of Natural Sciences, Brussels (RBINS)]; (B) *Thaumantia buhleri* Lallemand & Synave, 1953 (RBINS); (C) *Montrouzierana oxycephala* (Montrouzier, 1861) [Museum National d'Histoire Naturelle (MNHN)]; (D) *Daradax* sp. (MNHN); (E) *Varma bimaculata* Wang & Liang, 2008 (*Holotype*, Chinese Academy of Sciences); (F) *Scenoma glabrio* Fennah, 1969 (MNHN). Scale bars: A–F, 1 mm.

Frons (Figs 4C, 5G, 6C–E, 7A) 2.5× as long in middle as broad, lateral margins carinate, sinuous, diverging from apex, concave at level of compound eyes, then diverging further to reach their widest point near the antennal sockets, then converging to frontoclypeal suture. Median portion of disc of frons slightly elevated, this eminence with delicate transversely wrinkled sculpture; median carina percurrent. Frontoclypeal suture (Figs 3C, 4C, 5G; 6C–E, 7A) obtusely angled. Clypeus (see generic description) angulate at line prolonging lateral margins of frons. Rostrum (Figs 5G, 6E): see generic description.
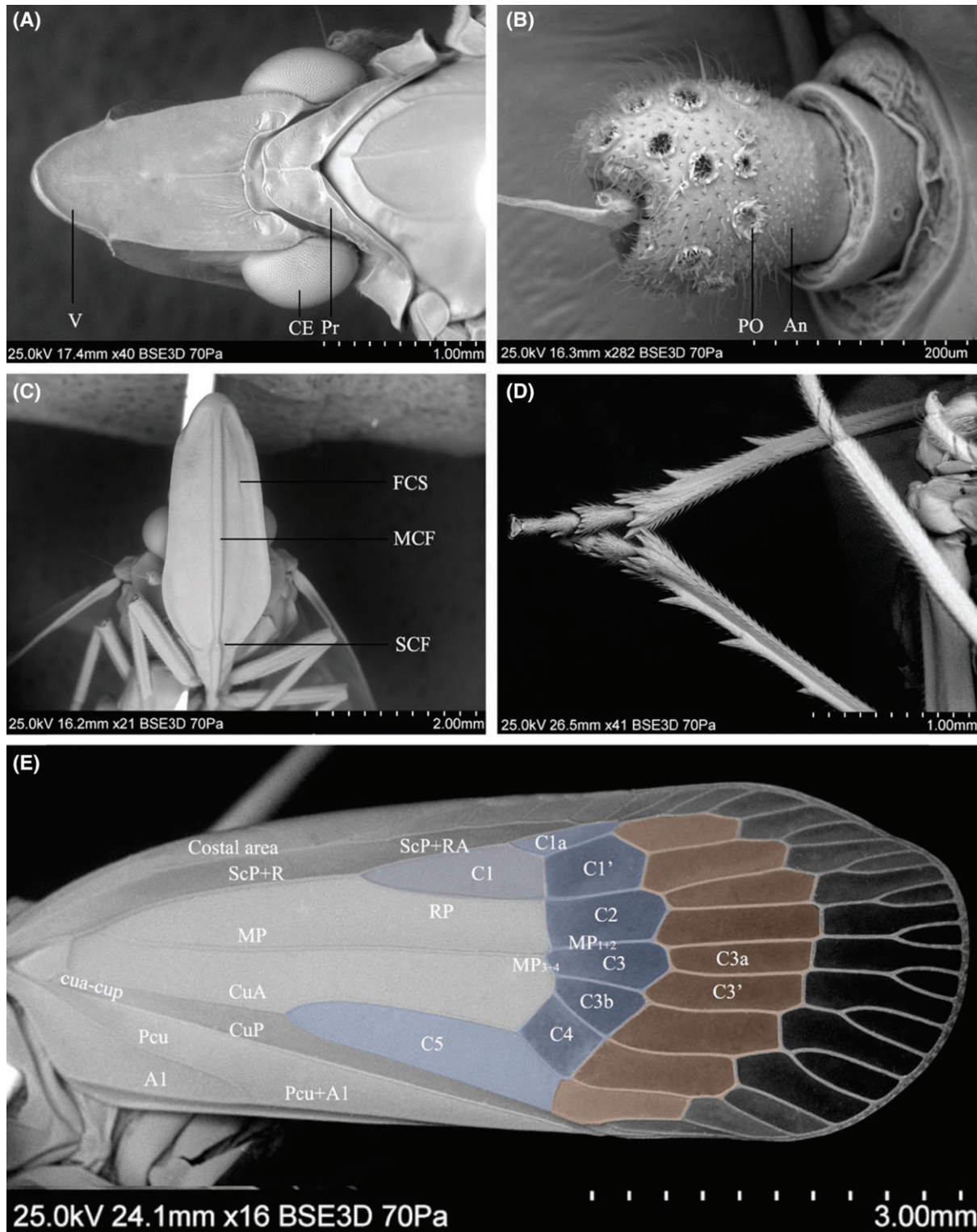
Fig. 3. *Oechalinella bifasciata* Wang **sp.n.** (*Holotype*, California Academy of Sciences). (A) Head, compound eyes and pronotum dorsal view; (B) antenna and plate organ; (C) frons; (D) leg; (E) tegmina, showing the first postnodal line between blue and red cells and the second postnodal line at the apex of red cells. A, anal vein; An, antenna; C, cell; CE, compound eyes; CuA, cubital anterior; CuP, cubitus posterior; FCS, frontoclypeal suture; MCF, median carina of frons; MP, media posterior; Pcu, postcubitus; PO, plate organ; Pr, pronotum; R, radius; RP, radial posterior; SCF, subcarina of frons; ScP, subcostal posterior; v, vertex.
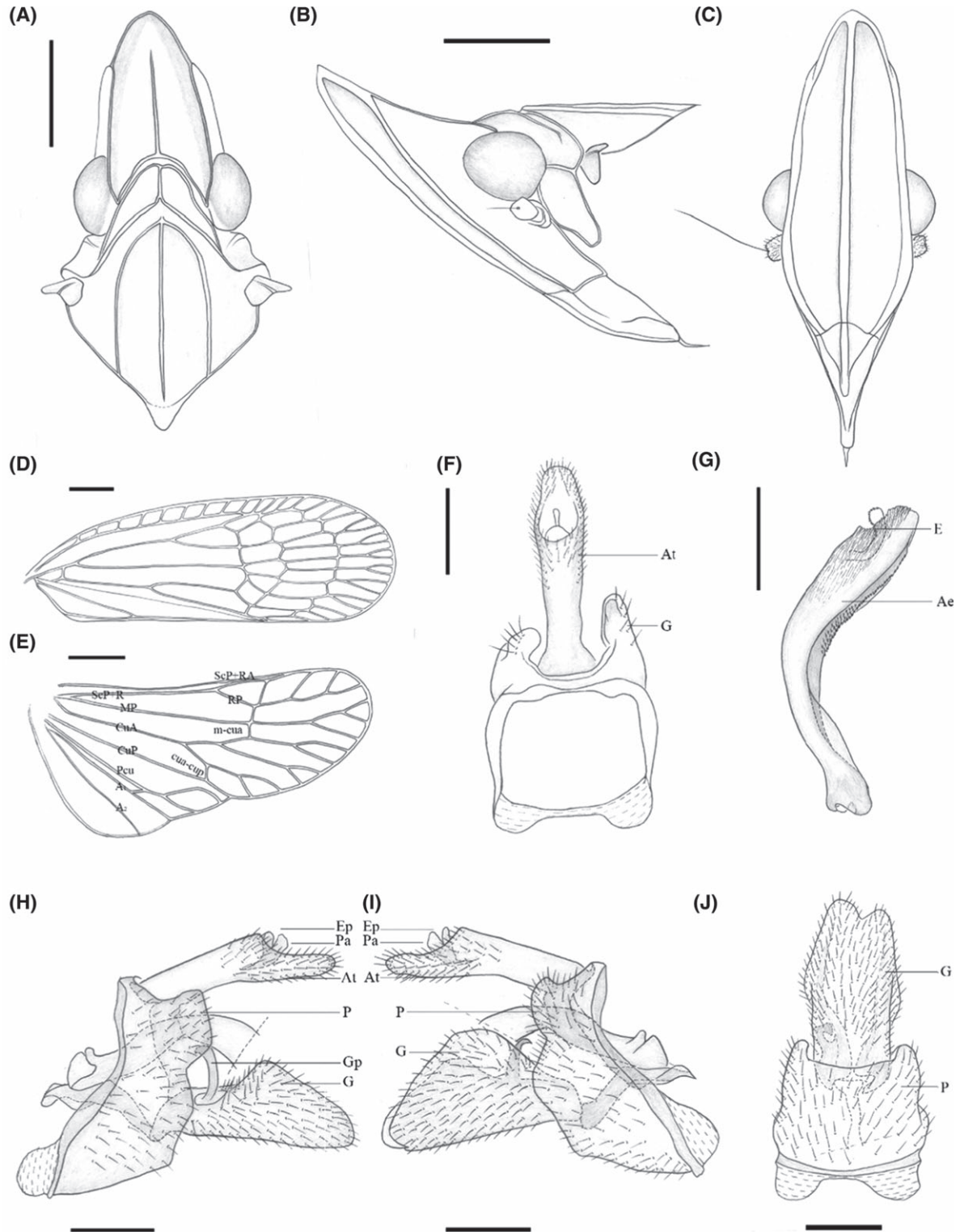
Fig. 4. *Oechalinella bifasciata* Wang **sp.n.** (*Holotype*, California Academy of Sciences). (A) Head, pronotum and mesonotum, dorsal view; (B) head, pronotum and mesonotum, lateral view; (C) head, oblique ventral view; (D) right forewing; (E) right hindwing; (F) anal tube and pygofer, dorsal view; (G) aedeagus, right lateral view; (H) male genitalia, left view; (I) male genitalia, right view; (J) male genitalia, ventral view. A, anal vein; Ae, aedeagus; CuA, cubital anterior; CuP, cubitus posterior; E, endosome; Ep, epiproct; Pa, paraprocts; Pcu, postcubitus; G, gonostyli; Gp, gonostyli process; MP, media posterior; P, pygofer; R, radius; RP, radial posterior; ScP, subcostal posterior. Scale bars: A–E, 1 mm; F–J, 0.5 mm.
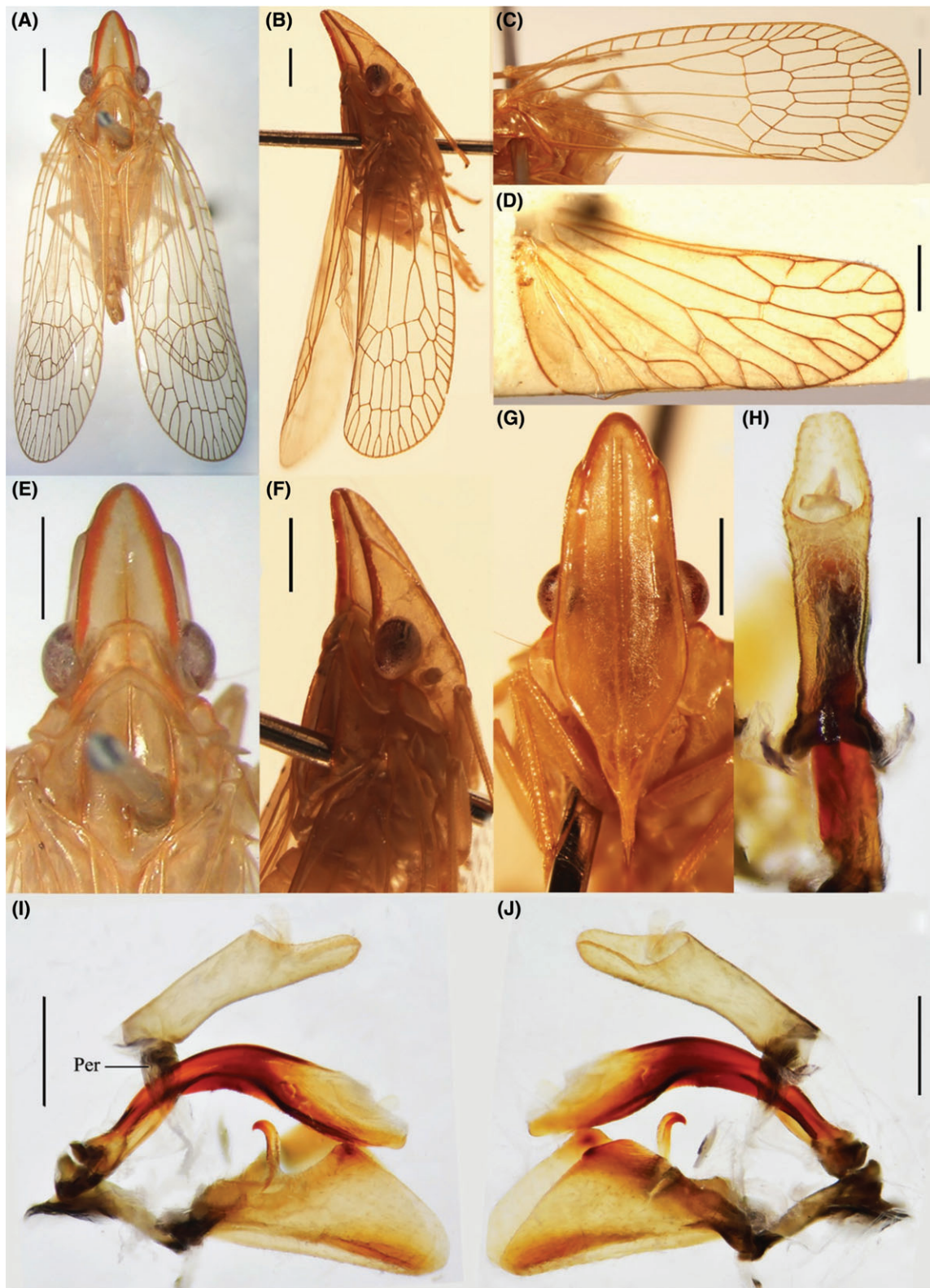
Fig. 5. *Oechalinella bifasciata* Wang **sp.n.** (A) Dorsal habitus; (B) lateral habitus; (C) right forewing; (D) right hindwing; (E) head, pronotum and mesonotum, dorsal view; (F) head, pronotum and mesonotum, lateral view; (G) head, oblique ventral view; (H) anal tube, dorsal view; (I) male genitalia without pygofer, left view; (J) male genitalia, anal tube and gonostyli, right view. Per, periandrium; Scale bars: A–G, 1 mm; H–J, 0.5 mm.
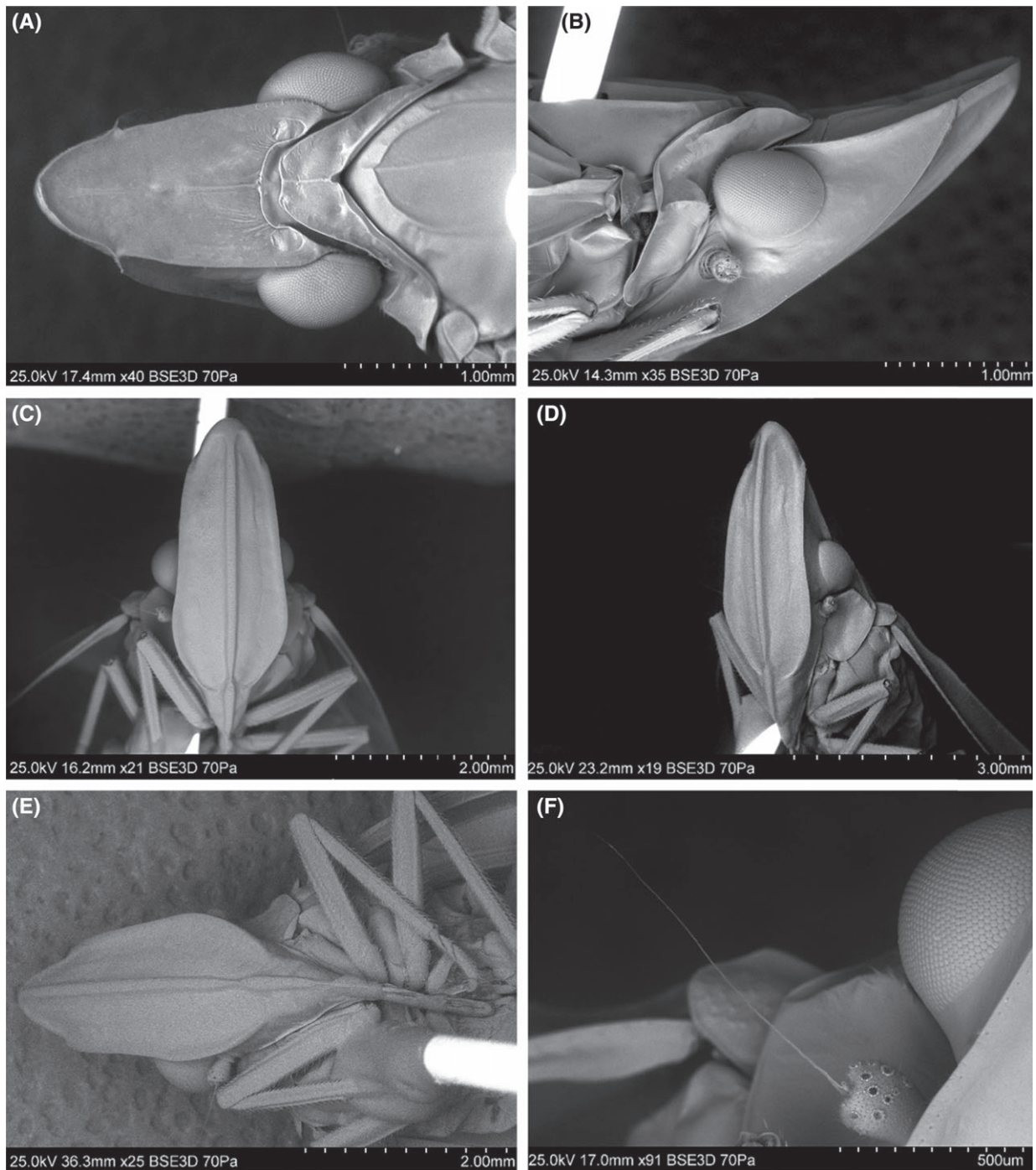
Fig. 6. *Oechalinella bifasciata* Wang **sp.n.** (*Holotype*, California Academy of Sciences). (A) Head and pronotum, dorsal view; (B) head and pronotum, lateral view; (C) head, oblique ventral view; (D) head, oblique ventral and 3/4 left view; (E) head, ventral view; (F) right antenna, lateral view.

Compound eyes (Figs 4A–C, 5A, B, E–G, 6A–F, 7A) oval, postocular eminence distinct, posteriad of compound eye. Lateral ocelli: see generic description (Figs 5F, 6B). Antennal socket (Figs 4B–C, 5B, F, 6B–F, 7A–D) with margin elevated, in lower portion carinately extending downwards. Antenna (see generic description) (Figs 4B, 5B, F, 6B, F, 7B–D) with scape short,

ring-like, pedicel club-like bearing less than 20 clover-leaf like placodea sensilla.

Combined length of pronotum and mesonotum about 1.8× as long as vertex at midline. Pronotum (see generic description) (Figs 3A, 4A, B, 5A, B, E, F, 6A, B) at midline about 1/6 of length of mesonotum at midline; lateral carinae (see
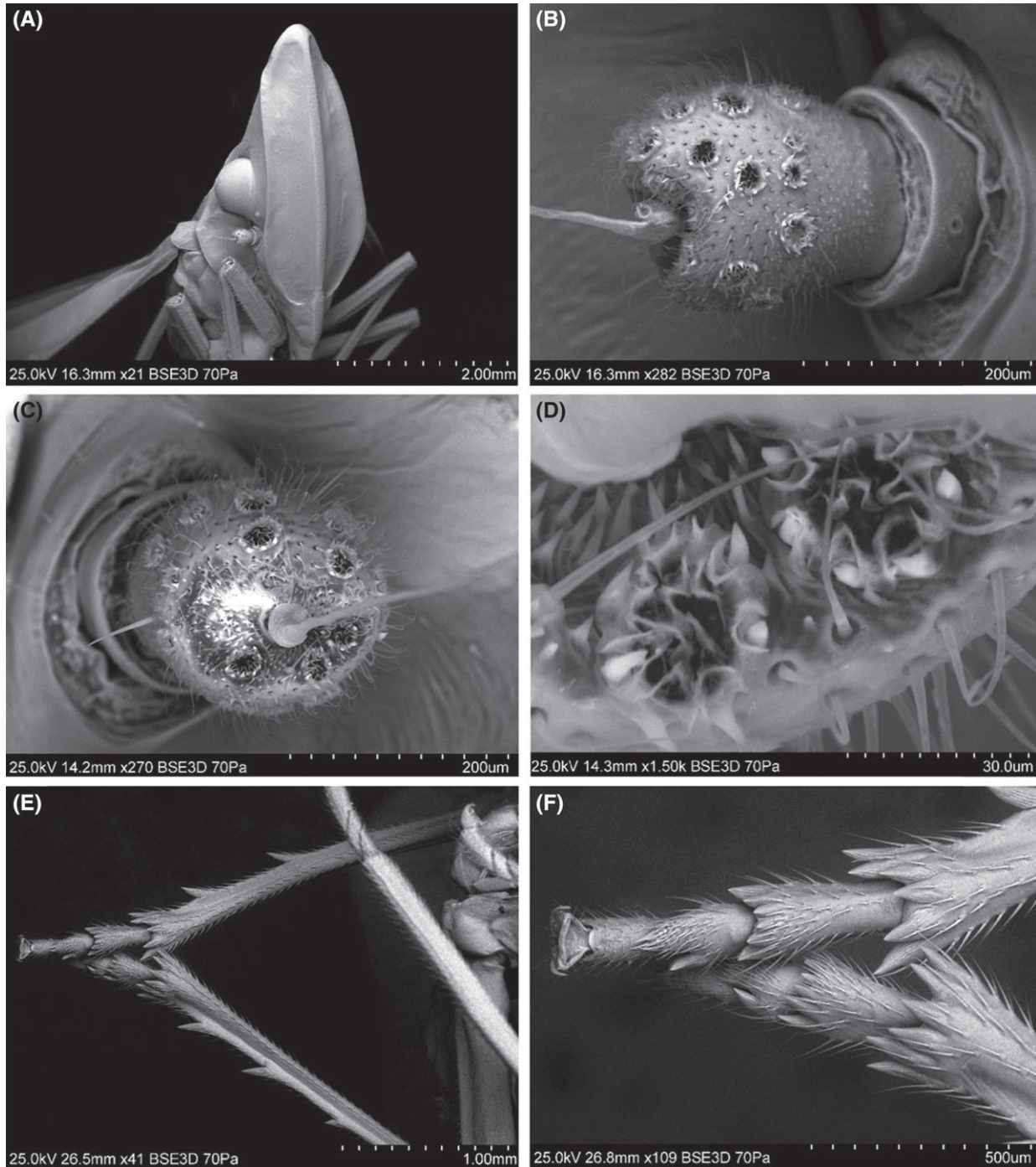
Fig. 7. *Oechalinella bifasciata* Wang **sp.n.** (*Holotype*, California Academy of Sciences). (A) Head, three-quarter right and oblique ventral view; (B) antenna, ventral view; (C) antenna, dorsal view; (D) plate organs, lateral view; (E) hind legs; (F) apical part of hind legs.

generic description); disc deeply depressed between median and lateral carinae; posterior margin (see generic description) deeply angulately excavated (Fig. 6B, F).

Mesonotum (see generic description) (Figs 4A, B, 5A, B, E, F, 6A, B) delimited by lateral carinae; tricarinate, lateral carinae parallel to median one at posterior two-thirds, reaching margin

of mesonotum, arcuately converging anteriorly, fused to median carina. Mesoscutellar suture: see generic description. Tegula (Figs 4A, B, 5A, B, E, F, 6A–D) carinate on the dorsal position.

Tegmina (Figs 3A, 4D, 5A–C, 8A–F). Costal area (Figs 3A, 4D, 5A, C, 8A, B, E) well developed, narrower than costal cell, but wider than half of costal cell width, with apex nearly
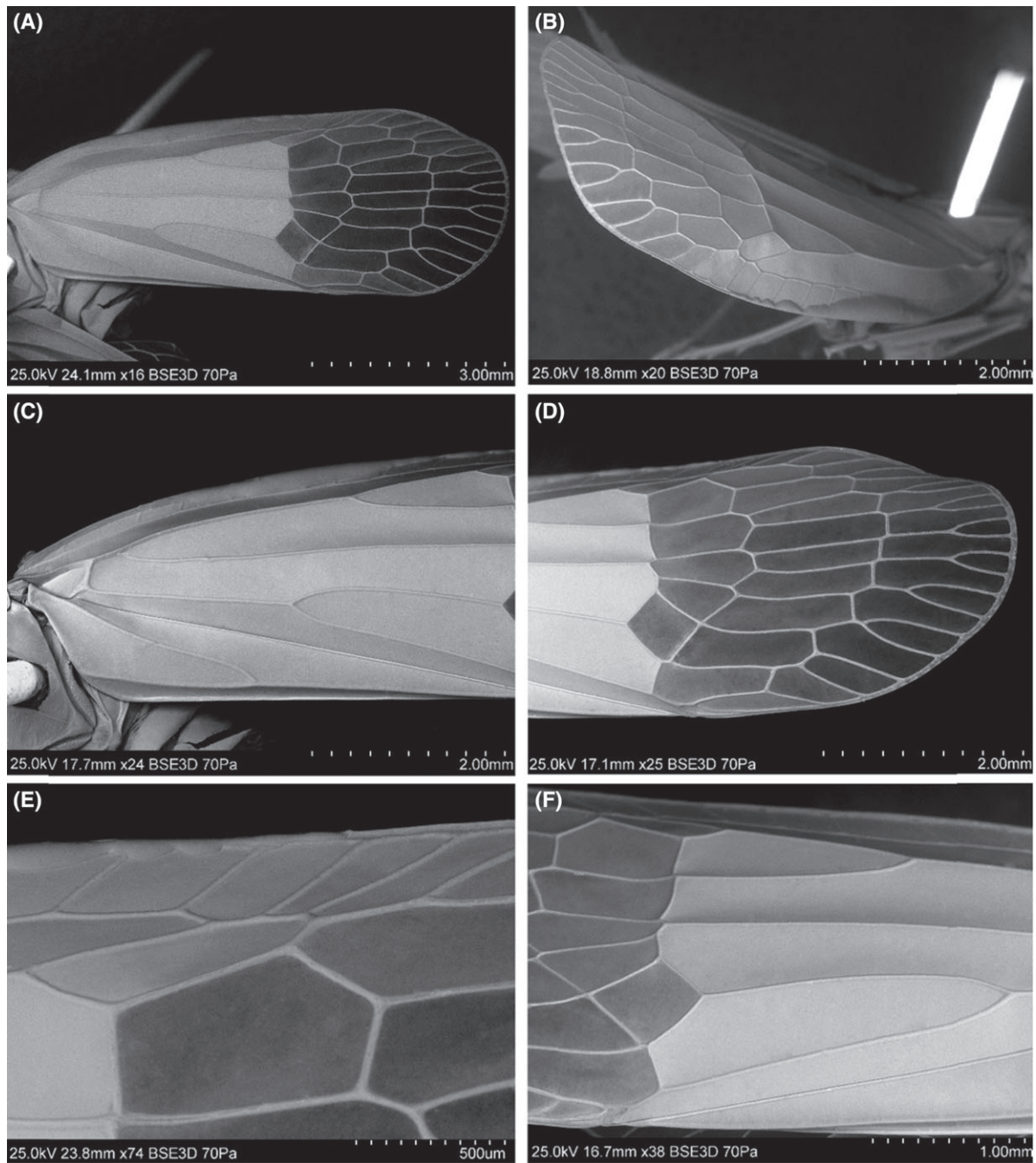
Fig. 8. *Oechalinella bifasciata* Wang **sp.n.** (*Holotype*, California Academy of Sciences). (A)–(F) Right forewing.

reaching the level of tip of clavus, with nine cross-veins. Costal cell: see generic description (Figs 4D, 5B, C, 8A–C). Branch RA (Fig. 3E) forked at subapical line, reaching margin with five terminals; branch RP (Fig. 3E) forked at subapical line, then apicad of apical line, reaching margin with four terminals. Branch MP (Fig. 3E) with eight terminals, forked first at level of nodal line, branch MP_{1+2} forked at level of subapical line, terminal MP_1 forked apicad of transverse apical line; terminal MP_2 forked apicad of transverse apical line; branch MP_{3+4}

forked at nodal line, terminals MP_3 and MP_4 forked apicad of transverse apical line. Branch CuA_1 forked at level of apical line, branch CuA_2 forked apicad of nodal line, with two or three terminals, arcuately convex, very close to, but distinct from, postclaval margin; CuA_{2a} arcuately concave (Fig. 3E). Clavus with apex exceeding two-thirds of tegmen length, claval veins Pcu and A_1 joined basad of half of clavus length. Nodal veinlets *ir* and *r-m* straight, nodal veinlet *m-cua* oblique, nodal veinlet *icu* present. Additional subapical line formed by the section of
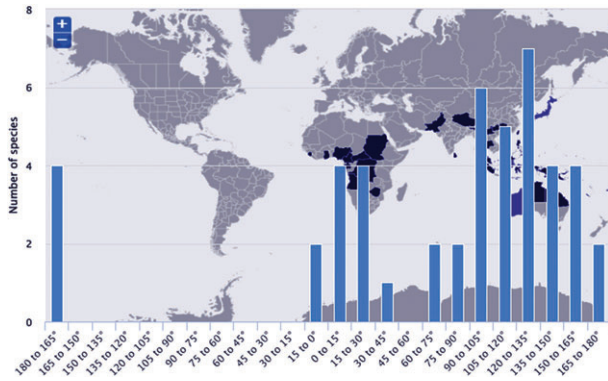
Fig. 9. Longitudinal profile of the global distribution pattern of Tropiduchini according to the International Working Group on the Taxonomic Databases for Plant Sciences (TDWG) global standard, level 4 accuracy (according to FLOW in Bourgoin, 2016).

RA, subapical *ir* veinlet, section of RP, subapical *r-m* veinlet, section of MP_{1+2} and MP_2, subapical *im* veinlet, section of MP_3, subapical *im* veinlet, and subapical *m-cua* veinlet. Apical line arcuate. Cell C1 prenodal, shorter than C5, also prenodal; first transverse row formed by six postnodal closed cells: C1a, C1′, C2, C3, C3b, C4 (Fig. 3E). Second transverse row of nine postnodal cells closed; 21–22 open apical cells about as long as postnodal ones (Fig. 3E).

Hindwings (Figs 4E, 5D) hyaline, elongate, slightly shorter than tegmen, with costal cell widened at base, with anal lobe wide. Stems ScP+R, MP and CuA, fused at base (see generic description). Stem ScP+R forked at level of wing coupling apparatus, at level of second CuA branching; branch ScP+RA single, reaching margin basad of apex of wing; branch RP with three terminals reaching margin at apical angle of wing. Stem M not forked before *r-m* and *m-cua* veinlets, three terminals reaching margin forked well apicad. Stem CuA (see generic description), branch CuA_1 forked again basad of *m-cua* veinlet; terminals CuA_{1a}, CuA_{1b} and CuA_2 forked apically, reaching margin with six terminals. Stem CuP single (see generic description). Stem Pcu distinctly curved before apex, fused for a distance with branching of A_1, A_2 single. Stems CuA and CuP connected more distad. Veinlets *ir*, *r-m* and *m-cua* at about same level, at level of branch CuA_2 forking.

Hind tibia (Figs 3D, 7E, F) with three lateral spines, the first one basad of half of tibia length; and six apical teeth; tarsi with metabasitarsus the longest, bearing six apical teeth; shorter than combined length of mid- and apical tarsomeres. Metatibio-tarsal formula 3-6/6/2.

Male terminalia: Pygofer asymmetrical (Fig. 4F, H–J), in lateral view short and high, forming irregular rectangle, wider ventrally than dorsally; dorsolateral angles of pygofer broadly produced posteriorly in left side view, posterior margin of right pygofer lobe sinuate, dorsolateral angles produced dorso-mesad, dorsal margin deeply excavated to accommodate anal tube. Anal tube (Figs 4F, H, I, 5H–J) elongate, not surpassing apex of aedeagus, distinctly projected caudad, apical margin distinctly concave in dorsal view; epiproct and paraprocts short (Figs 4F,

H, I, 5H–J), not reaching the ventral margin of anal tube in dorsal view.

Gonostyli (Figs 4H–J, 5I, J) asymmetrical, medially fused into a plate, concave medially in ventral aspect, curved on its medial axis; 2.34× as long as broad in left lateral view; left gonostylus (Figs 4H, 5I) forming irregular triangle, dorsal edge with an oblique hook-like process at basal quarter of left side directed dorsally and curved cephaloventrad; right gonostylus (Figs 4I, 5J) forming irregular triangle, relatively large and broad.

Periandrium (Figs 4H–I, 5I–J) reduced and very short, ring-like, nearly indistinct, dorsally connected by a short membranous area bearing the tectiductus with ventrobasal margin of anal tube, fused by a membrane with pygofer laterally and ventrally, surrounding aedeagus basally. Aedeagus (Figs 4G, 5I–J) asymmetrical, elongate, sinuate and tubular, basal part directed anterodorsally, then curved and directed ventrally; shaft of aedeagus with many micro-teeth along the ventral side; endosoma (Figs 4G, 5I–J) with one process, denticulate along the whole margins, subapically in dorsal side.

Female not known.

Type material. Holotype, ♂, PAPUA NEW GUINEA: Madang Province, Baiteta (12 km NW Alexishafen) 5°00′S 145°45′E, 9 November 1987, collected in Malaise trap, M. Wasbauer leg. Collection of the California Academy of Sciences, San Francisco, California, U.S.A. Deposited in CAS.

Etymology. This new species is named for the presence of two reddish stripes on lateral carinae of vertex (Fig. 5A, E). The Latin *fasciatus* meaning 'striped, banded'.

Host plant: unknown.

Tropiduchini taxa and identification key to Tropiduchini genera of the world

With the new taxa herein described, the Tropiduchini includes 162 taxa: 26 genera (1.1% of the Fulgoromorpha), seven of which are monotypic (28% of the genera in the tribe), 120 species and 16 subspecies (1% of the Fulgoromorpha) (Bourgoin, 2016). The following key allows identification of all genera classified in the tribe. For ease of use, no genital characters were included and key taxa are illustrated.

Key to Tropiduchini genera

1. Tegmina with costal area more than half of width of costal cell and traversed by veinlets 2
−. Tegmina with costal area less than half of width of costal cell and without distinct veinlets 24
2. Vertex distinctly longer than pronotum and mesonotum combined 3
−. Vertex not longer than pronotum and mesonotum combined 4
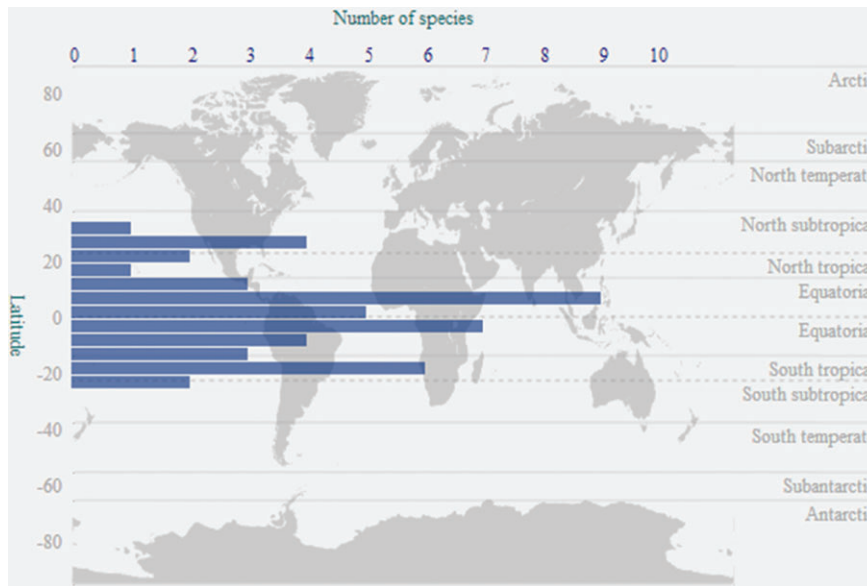
Fig. 10. Global latitudinal profile of Tropiduchini species according to the International Working Group on the Taxonomic Databases for Plant Sciences (TDWG) global standard, level 4 accuracy (according to FLOW in Bourgoin, 2016).

3. Frons with a pair of supplementary carinae distally between median carina and lateral margins . . . . *Rhinodictya* Kirkady, 1906
−. Frons with only median carina on disc. . . . . *Peggioga* Kirkady, 1905
4. Frons with a pair of supplementary carinae or transversely wrinkled sculpture between median carina and lateral margins 5
−. Frons without supplementary carinae between median carina and lateral margins 11
5. Vertex with a pair of facets, or small areas bounded by carinae lateroapically . . . . *Vanua* Kirkady, 1906
−. Vertex without such lateroapical facets 6
6. Vertex not longer than broad 7
−. Vertex longer than broad 8
7. Stem Sc+R fork basad of union of claval veins . . . . *Leptovanua* Melichar, 1914
−. Stem Sc+R fork distad of union of claval veins (Fig. 1C) . . . . *Lavora* Muir, 1931
8. Tegmina with two postnodal lines 9
−. Tegmina with only one postnodal line 10
9. Stem Sc+R fork basad of union of claval veins; distal postnodal line of tranverse veinlet irregular . . . . *Oechalina* Melichar, 1914
−. Stem Sc+R fork distad of union of claval veins; distal postnodal apical line of transverse veinlets regular (Fig. 5A) . . . . *Oechalinella* Wang **gen.n.**
10. Vertex rounded anteriorly (Fig. 2B) . . . . *Thaumantia* Melichar, 1914
−. Vertex conical . . . . *Macrovanua* Fennah, 1950
11. Tegmina with stems Sc+R forking near base, C1 closed before the nodal line, corium with veinlets 12

−. Tegmina with stems Sc+R not forking near base, C1 closed at the nodal line, corium without veinlets 14
12. Vertex conical in dorsal view 13
−. Vertex apically truncated in dorsal view (Fig. 2C) . . . . *Thymbra* Melichar, 1914
13. Tegmina with irregular and blind veins and veinlets (Fig. 2C) . . . . *Montrouzierana* Signoret, 1861
−. Tegmina without blind veins or veinlets (Fig. 2B) . . . . *Oligaethus* Melichar, 1914
14. Vertex longer than broad 15
−. Vertex not longer than broad 18
15. Tegmina with apical cells much shorter than subapical cells 16
−. Tegmina with apical cells not shorter than subapical cells 17
16. Pronotum with a single median carina; claval veins uniting at middle of clavus (Fig. 2D) . . . . *Daradax* Walker, 1857
−. Pronotum medially bicarinated, claval veins uniting close to the apex of clavus . . . . *Daradacella* Fennah, 1949
17. Stem Sc+R fork distad of union of claval veins . . . . *Swezeyaria* Metcalf, 1946
−. Stem Sc+R fork basad of union of claval veins (Fig. 2F) . . . . *Scenoma* Fennah, 1969
18. Terminal ScRA1 forked from RA branch distinctly basad of nodal line level 19
−. Terminal ScRA1 forked from RA branch close to the nodal line level 20
19. Stem Sc+R fork basad of union of claval veins; costal area with about 11 transverse veinlets; distance from apical margin to apical transverse line of cross veins 1.5× that from apical transverse veins to nodal line . . . . . . *Peltodictya* Kirkaldy, 1906
−. Stem Sc+R fork distad of union of claval veins; costal area with about 20 transverse veinlets; distance from apical margin to
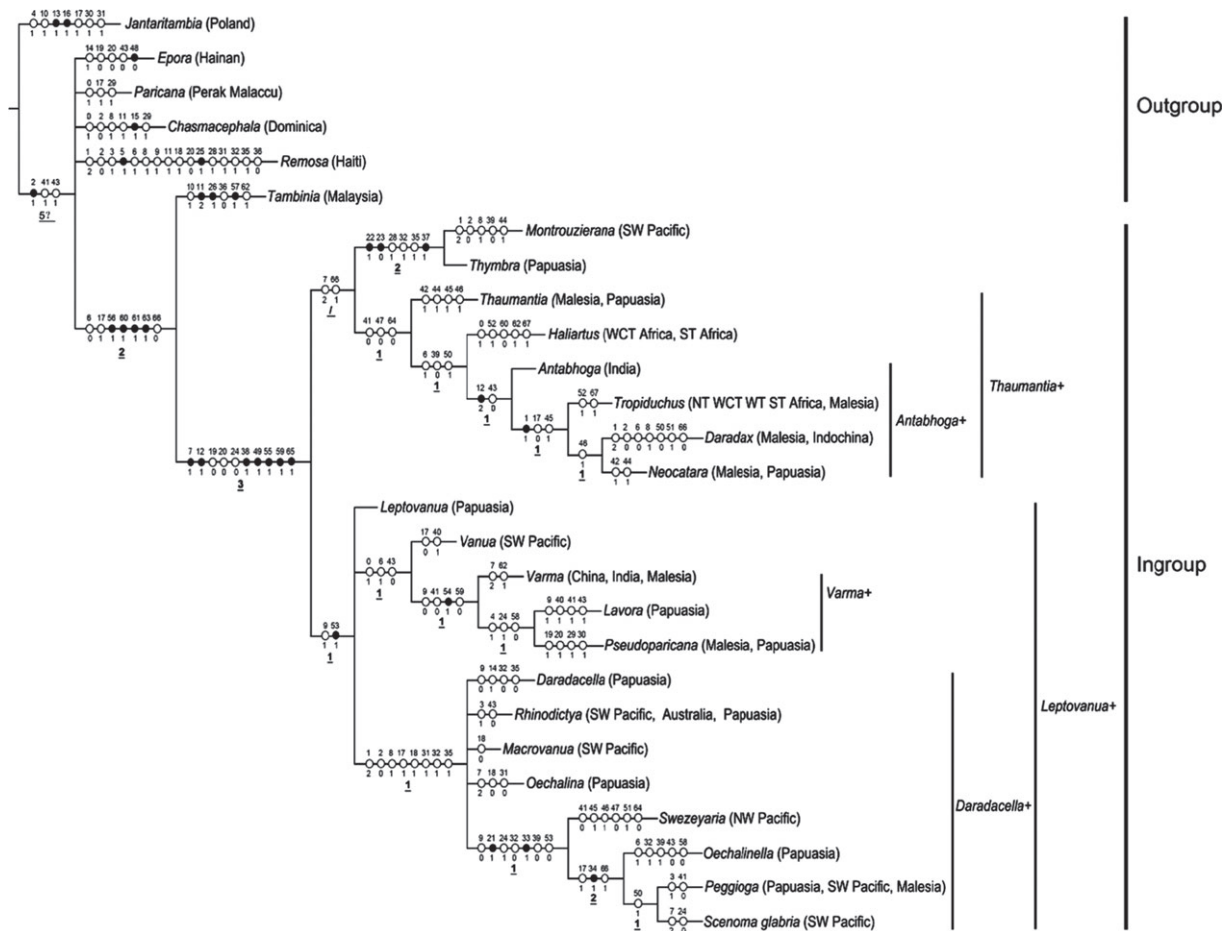
Fig. 11. The strict consensus tree (176 steps, consistency index = 40, retention index = 61, ten most-parsimonious trees). Numbers above the circles refer to characters and those below refer to character states. Black and white circles represent synapomorphies and homoplasious character states, respectively. Underlined numbers below the branches are Bremer support values, and one collapsed branch is marked with a solidus (/). Distribution abbreviations according to the International Working Group on the Taxonomic Databases for Plant Sciences (TDWG), level 2: NT, Northeast Tropical; ST, South Tropical; SW, South West; WCT, West Central Tropical; WT, West Tropical.

apical transverse line less than 1.5× that from apical transverse veins to nodal line . . . . *Ficarasa* Walker, 1857
20. Stem Sc+R forked at, or basad of, middle of corium 21
−. Stem Sc+R forked distad of middle of corium (Fig. 1D) . . .
. . . . *Haliartus* Melichar, 1914
21. Tegmina with nodal line oblique . . . .
. . . . *Neocatara* Distant, 1910
−. Tegmina with nodal line transverse, not oblique 22
22. Vertex short, rounded anteriorly 23
−. Vertex quadrate or pentagonal (Fig. 1A) . . . .
. . . . *Tropiduchus* Stål, 1854
23. Tegmina with apical cells much shorter than subapical cells . . . . *Antabhoga* Distant, 1912
−. Tegmina with apical cells not shorter than subapical cells (Fig. 2E) . . . . *Varma* Kirkalsy, 1906
24. Vertex more than 2× longer than wide . . . .
. . . . *Leptotambinia* Kato, 1931
−. Vertex shorter, rounded anteriorly 25

25. Claval veins uniting basad of middle of clavus, apical cells shorter than subapical cells (Fig. 1B) . . . .
. . . . *Pseudoparicana* Melichar, 1914
−. Claval veins uniting distad of middle of clavus, apical cells longer than subapical cells . . . . *Nesotemora* Fennah, 1956

Tropiduchini distribution

Appendix S3, Supporting Information, provides the currently known distribution of Tropiduchini for each species according to the literature. Globally, the tribe exhibits a bimodal longitudinal distribution (Figs 9, 10) with Oriental genera restricted to the Pacific islands and Southeast Asia, absent from India but known from Sri Lanka and with African genera distributed in central West Africa up to the southern part of Sudan for its northeast part. They are absent from the Arabian Peninsula and East Africa. According to the new zoogeographic regions of the world system (Holt *et al.*, 2013), Tropiduchini
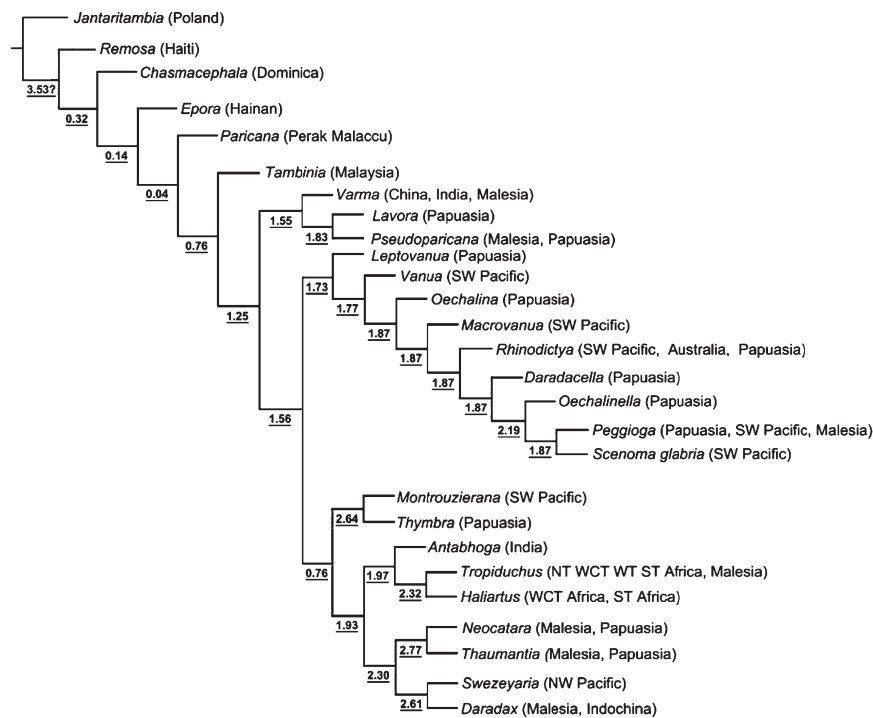
Fig. 12. Implied weight ($k = 3$, 169 steps) cladogram of Tropiduchini genera using 'new technology' search. Numbers are Bremer support values. Distribution abbreviations according to the International Working Group on the Taxonomic Databases for Plant Sciences (TDWG), level 2: NT, Northeast Tropical; ST, South Tropical; SW, South West; WCT, West Central Tropical; WT, West Tropical.

are therefore present in the Sino-Japanese (South China, Japan), Oriental (Indo-Malayan), Australian (north east), Afrotropical (Guineo-Congolian) and Oceanian (Papua-Melanesian) realms. They are absent from the Nearctic, Panamanian, Neotropical, Palearctic, Madagascan and Saharo-Arabian realms. According to their latitudinal profile (Figs 9, 10) Tropiduchini is essentially an inter-tropical taxa between the north subtropical and, more particularly, the south tropical bioclimatic zones (Bourgoin, 2016).

Phylogeny

'Traditional search' and NTS searches found the same results with ten most parsimonious trees resulting from the analyses (length = 166 steps; consistency index, CI = 42; retention index, RI = 65). The resulting strict consensus tree (length = 176 steps; CI = 40; RI = 61) and the Bremer support are shown in Fig. 11. Implied weighting search provided one tree of 170 steps (TS) and one of 169 steps (NTS, IE) with the Bremer support presented in Fig. 12.

Tropiduchini is always well supported as a monophyletic group based on seven synapomorphies (Fig. 11): the posterior margin of the vertex (K7) and the anteriorly produced pronotum (K12) reaching the anterior margin of the eyes, the asymmetrical pygofer (K38) and gonostyli (K55), periandrium surrounding a shorter (K49) and membranous aedeagus (K65), and at least one median processes on the ventrocaudad margin of the gonostylus

(K58). The consensus tree of the ten most parsimonious trees allows identification of a deep split within the Tropiduchini, with the ((*Montrouzierana* + *Thymbra*) + *Thaumantia*[+]) group on one side and the (*Leptovanua*, (*Vanua* + *Varma*[+]) and *Daradacella*[+]) group on the other side. In this latter clade, *Leptovanua* is 50% nested with the (*Vanua* + *Varma*[+]) group or 50% sister to all other genera of this lineage. In the strict consensus tree, the *Daradacella*[+] group shows a basal polytomy of four genera (*Daradacella*, *Rhinodictya*, *Macrovanua*, *Oechalina*) plus the *Swezeyaria*[+] clade. This polytomy reflects only two equal grouping schemas among the ten most parsimonious trees: (*Daradacella* + (*Rhinodictya*[+] + *Swezeyaria*[+])) or (*Oechalina* + (*Macrovanua* + (*Rhinodictya* + (*Daradacella* + *Swezeyaria*[+])))).

The ((*Montrouzierana* + *Thymbra*) + *Thaumantia*[+]) group is always recovered based on two synapomorphies: the margin of the posterior vertex surpassing the anterior eye margin (K7) and a regular periandrium (K66). The (*Montrouzierana* + *Thymbra*) clade is well supported by at least three synapomorphies: a late ScP+R stem forking (K22), an antenodal separation of RA1 from stem ScP+RA (K23) and the presence of an irregular bacillum-like blister and/or blind veinlets on the tegmen (K37). The *Thaumantia*[+] group is also always recovered with three homoplastic synapomorphies: the anal tube with a proximal paraproct (K41) and a ventral acute prolongation (K47), and male gonostyli with asymmetrical apical lobes (K64).

The (*Leptovanua*, *Vanua* + *Varma*[+], *Daradacella*[+]) second group is supported by one synapomorphy, the presence of a

periandrium apical process directed cephalad (K53). Within the clade, (*Vanua* + *Varma*⁺) and *Daradacella*⁺ clades are supported by a series of three and eight homoplastic synapomorphies, respectively. The *Varma*⁺ clade is always recovered in all analyses and supported by at least one synapomorphy: the trumpet-shaped apex of the periandrium (K54).

In the tree obtained with the implied weighting analysis (Fig. 12), the ((*Montrouzierana* + *Thymbra*) + *Antabhoga*⁺) group (= the Indian genus *Antabhoga* sister to the two African taxa (*Tropiduchus* + *Haliartus*), all sister to the other Oriental genera of the clade, represents only an internal rearrangement of ((*Montrouzierana* + *Thymbra*) + *Thaumantia*⁺) (Fig. 11). The sister-group relationship of (*Neocatara* + *Thaumantia*) and (*Swezeyaria* + *Daradax*) is therefore suggested (Fig. 12). From the second group recognized in the consensus tree, the *Varma*⁺ lineage separates from all genera as sister to a new group (*Leptovanua*⁺ + ((*Montrouzierana* + *Thymbra*) + *Thaumantia*⁺)) (Fig. 12).

Discussion

Tropiduchini definition and monophyly status

The tribe Tropiduchini was defined by Fennah (1982: 639) with the following characteristics: 'Frons unicarinate, sometimes broadly so and sometimes with supplementary incomplete oblique carinae in distal half. Antenna II with microsetae extending to base. Apical segment of rostrum not broader than long. Post-tibia with three spines laterally. Posterior margin of mesoscutellum angulate. Tegmen macropterous, rarely coeliopterous; a costal area with oblique cross-veins usually present; Sc usually emitting an oblique vein to C before nodal line, but if not, subapical segment of rostrum more than 3 times as long as apical segment, or Cu, not forked before nodal line, and cell Cu1a in membrane long and tranversed by only a single cross-vein. Genital styles asymmetrical, fused together at least in basal half and with an obliquely ascending process on one side. First valvula of ovipositor with two teeth at most on ventral margin, and at least four teeth on dorsal margin. Third valvula with teeth at apex and 5–11 teeth on ventral margin'. However, none of these characters appears to be autapomorphic and the recognition of taxa belonging to the tribe relies on a combination of several of them, not always the same according to the genera. While the fusion of gonostyli is known to occur in other taxa (e.g. Tettigometridae, Eurybrachidae or Issidae, for instance), it is probable that it is primarily this particular fusion of the asymmetrical gonostyli, unique in the family, that led Fennah (1982) to group all these taxa around the type genus of the family *Tropiduchus*, and that he defined the tribe according to the taxa bearing this character. However, this grouping lacks any other character to support it. Moreover, three different types of phallic complexes are observed among the Tropiduchini genera. The first is represented by the Afrotropical genera *Tropiduchus* and *Haliartus* with an enlarged phallic complex, armed with additional processes and lobes and distinctly asymmetrical. The second is characteristic of some genera from the Papua–Melanesian realm

(i.e. *Oechalinella* **gen.n.**) with a tubular phallic complex, distinctly sclerotized, without distinct additional processes or lobes at the basal part but with the membranous apex (endosoma) bearing spines. The third is present in the remaining genera, with a simple structure, expanded at the apical part, bearing several processes or extra-lobes. The absence of any phylogenetic support and non-significant autapomorphy raised therefore the question of the monophyletic status of this tribe.

Surprisingly, our phylogenetic analysis shows that monophyly of the tribe is always recovered and supported by several male genitalic characters (and this, despite the three different morphological types of male genitalia recognized before), even if most of the other morphological characters proposed by Fennah (1982) are not supported by the present analysis. Within these already mentioned synapomorphic characters (see Results), the asymmetrical pygofer (K38) and gonostyli (K55) are probably the most significant (autapomorphies for Tropiduchidae-Tropiduchini). The two median processes on the gonostylus ventrocaudad margin (K59) form another apomorphic character, except for the *Varma*⁺ clade, which is depicted as the probable older lineage of the tribe. Several previous hypotheses and taxonomic changes are confirmed, such as that Peggionini are a synonym of Tropiduchini (Fennah, 1982), transfer of the enigmatic genus *Pseudoparicana* from Paricanini to Tropiduchidini (Fennah, 1982; Wang *et al.*, 2013b), separation of *Remosa* into the Remosini (Fennah, 1982), and the sister-relationship hypothesis between *Montrouzierana* and *Thymbra* (Wang *et al.*, 2014a).

It is most probable that even when more tropiduchid taxa are added to address the monophyly of the 24 tribes of Tropiduchidae currently recognized, the Tropiduchini will be kept as a monophyletic unit. Interestingly the genus *Tambinia*, the type genus of the Tambiniiini formerly believed to form a separate subfamily Tambiniinae (Muir, 1923), is also placed in a sister-group position to the Tropiduchini. Together they share four synapomorphies comprising the gonostyli, which are fused (K56:1) without tooth-like process on their dorsal margin (K61, K63) and with a long hook-like process (K60) present on the left gonostylus margin. Although part of the outgroup taxa, it is interesting to note that our representatives of Fennah's (1982) tribes, Remosini, Chasmacephalini and Eporini, which according to Melichar (1914) were placed in his tribe Tropiduchini, appear to be less closely related to Tropiduchini than *Tambinia* in our analysis.

Distribution patterns and biogeographical data

According to current data in the literature, Tropiduchidae appears to be a intertropical taxon, only distributed on the sides of the southern Palaearctic (Eurasia) and southern Nearctic (North America) realms due to some invasive or pest species, or by marginal speciation events (Bourgoin, 2016). They are also present in Australia. These few Australian taxa, mostly monotypic, were not included in the analysis and we can only hypothesise (to be tested later) that they dispersed from Southeast Asia, where the higher diversity of species is observed.

Our review of the distribution of the taxa shows that Tropiduchini form an inter-tropical taxon, absent from the New World but well represented in the Oriental, Chinese, Papua–Melanesian, Australian and Oceanian realms. Two genera extend their distribution to the Afrotropical realm, *Haliartus* and *Tropiduchus*, and five have been recorded from Australia. Accordingly, the Tropiduchini exhibit a paradoxical bimodal distribution, disjointed, with no representatives known between 30° and 60° of longitude east to Greenwich, only present in the western and central Afrotropical areas and in the Southeast Asia and Pacific islands area.

However, a more precise analysis of these records reveals a remarkable characteristic of Tropichinini taxa: genera and species are represented by 73.1 and 77.5%, respectively, of taxa inhabiting islands. If the three monospecific Australian genera, *Oligethus*, *Peltodictya* and, *Rhinodictya*, are excluded (hypothesizing that they result from dispersion events from adjacent insular areas), these figures rise to 84.6 and 78.9%. Only three to four genera are continental taxa: the only two and notable African genera *Tropiduchus* (17 species out of 22 in total) and *Haliartus* (two species) and the Asiatic one *Varma* (5 species). The fourth one concerns the monospecific genus *Antabhoga* originally described from Laccadive Island (Distant, 1912). However, this continental occurrence is doubtful and, according to the drawings provided, this taxon in Pakistan belongs very probably to a still undescribed *Varma* species. We consider all other genera as originally insular taxa, including the two genera that include isolated species with a continental distribution: *Ficarasa* (two species), with one collected species in Australia, and *Daradax* (six species) with two species collected from Thailand and Malaysian Peninsula. The genus *Thaumantia* (seven species) was wrongly reported by Metcalf (1954: 30) as collected from Australia because of Muir (1927: 13), who qualified erroneously *T. straminea* as an Australian taxa. The mostly central African genus *Tropiduchus* needs a careful revision as, surprisingly, five species also occur in Indonesia and the Philippine islands.

In reference to the phylogeny of the tribe as provided by the strict consensus tree, the (*Leptovanua* + (*Vanua* + *Varma*+) + *Daradacella*) group forms a rather widely distributed clade ranging from continental China and India to Malesia, Papuasia and the southwest Pacific. Its sister group ((*Montrouzierana* + *Thymbra*) + *Thaumantia*+) is still more widely and incoherently distributed, extending from Papuasia and the southwest Pacific to Thailand, Malesia (Borneo, Malaya, Philippines, Sumatera), India (Laccadive Islands) and western and central Africa. Accordingly and optimizing the distribution on the phylogeny, the most parsimonious scenario would anchor Tropiduchini in Papuasia.

However, and besides a formal biogeographic analysis outside the scope of this paper, the phylogeny provided by the implied weighting analysis seems to suggest the base for a more coherent scenario making the hypothesis that Tropiduchini probably evolved from continental China (*Varma*+). Progressively the group evolved eastern to Papuasia with a succession of genera established along the Pacific islands and reaching Australia as shown by the *Leptovanua*+ group. Within the second group, the

Thaumantia+ group lineage followed the same scenario, establishing genera in Papuasia and Malesia, while a lineage dispersed west, crossing the Wallace line. In this second clade, an Afrotropical lineage evolved with *Haliartus* restricted to the west side of the Guineo-Congolian realm, with only two species and *Tropiduchus* largely distributed with 22 Afrotropical (particularly the Guineo-Congolian realm) but also five Southeast Asian species.

The insular status of most of the taxa and the possible origin of most clades in Papuasia, and therefore no older than 20 million years (Lohman *et al.*, 2011), indicate a probable recent age of most of the Tropiduchini lineages, even if the origin of tribe might be older were a continental origin scenario to be considered. It also suggests that the whole tribe evolved by stepping-stone colonization events that promoted subsequent local insular speciation events and that dispersion versus vicariance has mainly directed the evolution of the tribe.

To further test these hypotheses, a careful taxonomic revision of the species is first needed to confirm their generic status (at least in the genera *Tropiduchus*, *Varma*, *Thaumantia*, *Antahoga*) and their distribution. The phylogenetic analysis will have to be strengthened by including the few missing Tropiduchini genera that were not available for this study, as well as Tambinini genera, the probable sister group of Tropiduchini, in order to test the basal dichotomy of the clade depicted by the implied weighting analysis, and then completing and testing the analysis with a molecular approach.

Supporting Information

Additional Supporting Information may be found in the online version of this article under the DOI reference: 10.1111/syen.12219

Appendix S1. Morphological characters.
Appendix S2. Morphological data matrix.
Appendix S3. The full distribution of Tropiduchini for each species.

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References

Asche, M. & Wilson, M.R. (1989) The palm-feeding planthopper genus *Ommatissus* (Homoptera: Fulgoroidea: Tropiduchidae). *Systematic Entomology*, **14**, 127–147.

Bourgoin, T. (1997) The Meenoplidae (Hemiptera, Fulgoromorpha) of New Caledonia, with a revision of the genus *Eponisia* Matsumura, 1914, and new morphological data on forewing venation and wax plate areas. *Memoires du Museum National d'Histoire Naturelle*, **171**, 197–249.

Bourgoin, T. (2016) *FLOW (Fulgoromorpha Lists on the Web): A World Knowledge Base Dedicated to Fulgoromorpha, Version 8*, updated 4 January 2016. [WWW document]. URL http://www.hemiptera-databases.org/flow/ [accessed on October 2016].

Bourgoin, T. & Huang, J. (1990) Morphologie comparée des genitalia mâles des Trypetimorphini et remarques phylogénétiques (Hemiptera: Fulgoromorpha: Tropiduchidae). *Annales de la Société Entomologique de France*, **26**, 555–564.

Bourgoin, T., Wang, R.R., Asche, M. *et al.* (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology*, **134**, 63–77.

Bremer, K. (1994) Branch support and tree stability. *Cladistics*, **10**, 295–304.

Brummitt, R.K. (2001) *Plant Taxonomic Database Standards No. 2*, 2, August 2001. Published by Biodiversity Information Standards, Modified 8 May 2007. TDWG Standard: http://www.tdwg.org/standards/109/ edn.

De Souza Amorim, D. (1982) Classificaçao por sequenciaçao: uma proposta para a denominaçao dos ramos retardados. *Revista Brasileira de Zoologia*, **1**, 1–9.

Distant, W.L. (1912) XVI. – Descriptions of new genera and species of Oriental Homoptera. *Annals and Magazine of Natural History*, **9**, 181–194.

Fennah, R.G. (1982) A tribal classification of the Tropiduchidae (Homoptera: Fulgoroidea), with the description of a new species on tea in Malaysia. *Bulletin of Entomological Research*, **72**, 631–643.

Gnezdilov, V.M. (2007) On the systematic positions of the Bladinini Kirkaldy, Tonginae Kirkaldy, and Trienopinae Fennah (Homoptera, Fulgoroidea). *Zoosystematica Rossica*, **15**, 293–297.

Gnezdilov, V.M. (2013) Contribution to the taxonomy of the family Tropiduchidae Stål (Hemiptera, Fulgoroidea) with description of two new tribes from Afrotropical Region. *Deutsche Entomologische Zeitschrift*, **60**, 179–191.

Gnezdilov, V.M. (2014) Modern classification and distribution of the family Issidae Spinola (Homoptera, Auchenorrhyncha: Fulgoroidea). *Entomological Review*, **94**, 687–697.

Gnezdilov, V.M. & Bourgoin, T. (2015) New genera and new species of the tribe Elicini (Hemiptera: Fulgoroidea: Tropiduchidae) with key to Tropiduchid genera known from Madagascar. *Annales Zoologici*, **65**, 599–618.

Gnezdilov, V.M., Bourgoin, T., Mozaffarian, F. & Manzari, S. (2015) Difficulties in building a molecular phylogeny of the issidoid planthopper lineages (Insecta: Hemiptera: Fulgoroidea). *Proceedings 1th Iranian International Congress of Entomology*. Tehran, pp. 38–47.

Gnezdilov, V.M., Bartlett, C. & Bourgoin, T. (2016) A new tribe of Tropiduchidae (Hemiptera, Fulgoroidea) with revision of the genus *Buca* Walker and description of asymmetric hind leg spinulation. *Florida Entomologist*, **99**, 406–416.

Goloboff, P. (1993) Estimating character weights during tree search. *Cladistics*, **9**, 83–91.

Goloboff, P., Farris, S. & Nixon, K. (2003) *T.N.T.: Tree Analysis Using New Technology. Version 1.1*. Program and documentation available from the authors. [WWW document]. URL http://www.zmuc.dk/public/phylogeny [accessed on February 2014].

Holt, B., Lessard, J., Borregaard, M. *et al.* (2013) An update of Wallace's zoogeographic regions of the world. *Science*, **339**, 74–78.

Lohman, D.J., Bruyn, M., Page, T. *et al.* (2011) Biogeography of the Indo-Australian archipelago. *Annual Review of Ecology, Evolution, and Systematics*, **42**, 205–226.

Maddison, W.P. & Maddison, D.R. (2010) *Mesquite: A Modular System for Evolutionary Analysis. Version 2.73*. [WWW document]. URL http://mesquiteproject.org. [accessed on February 2014].

Melichar, L. (1914) Monographie der Tropiduchinen (Homoptera). *Verhandlungen des Naturforschenden Vereines in Brünn*, **53**, 1–145.

Metcalf, Z.P. (1954) *General Catalogue of the Homoptera*, Fascicule IV. North Carolina State College, Raleigh, North Carolina.

Muir, F. (1923) On the classification of the Fulgoroidea (Homoptera). *Proceedings of the Hawaiian Entomological Society*, **5**, 205–247.

Muir, F. (1927) Hemiptera. Fulgoroidea. *Insects of Somoa and other Samoan Terrestrial Arthropoda*, Vol. **1**, (ed. by British Museum (Natural History), Department of Entomology), pp. 1–27. British Museum, London.

Nixon, K.C. (1999) *Winclada, Version 1.00.08*. Published by the Author, Ithaca, New York. [WWW document]. URL http://www.cladistics.com [accessed on February 2014].

O'Brien, L.B. (2002) The wild wonderful world of Fulgoromorpha. *Zikaden-Leafhoppers, Planthoppers and Cicadas (Insecta: Hemiptera: Auchenorrhyncha)* (ed. by W. Holzinger), pp. 83–102. Oberösterreichisches Landesmuseum, Linz.

Stroiński, A., Wang, R.R., Bourgoin, T., Liang, A.P. & Szwedo, J. (2015) Review of the Paricanini (Hemiptera: Fulgoromorpha: Tropiduchidae). *Annales Zoologici*, **65**, 579–597.

Wang, R., Liang, A. & Webb, M.D. (2009) A new tropiduchid planthopper genus and species from China with descriptions of *in copula* genitalic structures (Hemiptera: Fulgoromorpha). *Systematic Entomology*, **34**, 434–442.

Wang, R.R., Stroiński, A., Szwedo, J. & Bourgoin, T. (2012a) What are really Tropiduchidae? What tell us the tegmina venation patterns. *Sixth European Hemiptera Congress*. Blagoevgrad, p. 110.

Wang, R.R., Wan, X.Y., Liang, A.P. & Bourgoin, T. (2012b) Ultrastructure of sensory equipments on the heads of *Kallitaxila* granulata (Stål) (Hemiptera: Fulgoromorpha: Tropiduchidae). *Microscopy Research and Technique*, **75**, 1659–1665.

Wang, R.R., Malenovský, I., Liang, A.P. & Bourgoin, T. (2013a) Revision of *Pseudoparicana* (Hemiptera: Fulgoromorpha: Tropiduchidae) with description of a new species. *European Journal of Entomology*, **110**, 365–377.

Wang, R.R., Wan, X.Y., Liang, A.P. & Bourgoin, T. (2013b) A SEM study of antennal and maxillary sensilla in *Zema gressitti* Fennah (Hemiptera: Fulgoromorpha: Tropiduchidae). *Micron*, **44**, 261–267.

Wang, R.R., Stroinski, A., Szwedo, J., Bourgoin, T. & Liang, A.P. (2014a) Recent dispersal and diet relaxation might explain the monotypic and endemic genus *Montrouzierana* Signoret, 1861 in New Caledonia (Hemiptera: Fulgoromorpha: Tropiduchidae). *Annales Zoologici*, **64**, 693–708.

Wang, R.R., Wan, X.Y. & Liang, A.P. (2014b) Fine structure of sensory apparatus on the head of *Cixiopsis punctatus*. *Journal of Insect Science*, **14**, 99.

Wang, M.L., Stroiński, A., Bourgoin, T. & Zhang, Y.L. (2015) A new Asian genus of the tribe Elicini (Hemiptera: Fulgoromorpha:

Tropiduchidae) with two new species from Vietnam. *Zootaxa*, **4018**, 563–572.

Wilson, S.W. (2005) Keys to the families of Fulgoromorpha with emphasis on planthoppers of potential economic importance in the southeastern United States (Hemiptera: Auchenorrhyncha). *Florida Entomologist*, **88**, 464–481.

Wilson, S.W. & O'Brien, L.B. (1987) A survey of planthopper pests of economically important plants (Homoptera: Fulgoroidea). *Proceedings of the 2nd International Workshop on Leafhoppers and Planthoppers of Economic Importance*. Brigham Young University, Provo, 28th July–1st August 1986 (ed. by M.R. Wilson and L.R. Nault), pp. 343–360. CAB International Institute of Entomology, London.

Wilson, S.W., Mitter, C., Denno, R.F. & Wilson, M.R. (1994) Evolutionary patterns of host plant use by delphacid planthoppers and their relatives. *Planthoppers: Their Ecology and Management* (ed. by R.F. Denno and T.J. Perfect), pp. 7–113. Chapman & Hall, New York, New York.