





http://doi.org/10.11646/zootaxa.5057.1.8 http://zoobank.org/urn:lsid:zoobank.org:pub:A1CC26A3-6B1A-4253-B095-003459F2D78C

Bitara gen. nov. of Tropiduchidae (Hemiptera: Fulgoromorpha) east of Wallace line

ADAM STROIŃSKI1 & JACEK SZWEDO2,*

¹Museum and Institute of Zoology, Polish Academy of Sciences, 64, Wilcza St, PL00-679 Warszawa, Poland. ■ adam@miiz.waw.pl; ● https://orcid.org/0000-0003-0876-9263 ²Laboratory of Evolutionary Entomology and Museum of Amber Inclusions, Department of Invertebrate Zoology and Parasitology, Faculty of Biology, University of Gdańsk, 59, Wita Stwosza St., PL80-308 Gdańsk, Poland. * Corresponding author: ■ jacek.szwedo@biol.ug.edu.pl; ● https://orcid.org/0000-0002-2796-9538

Abstract

A new genus and species of the tropiduchid planthopper of the tribe Tropiduchini is described as *Bitara augusta* gen. et sp. nov. from Madang Province, Papua New Guinea. It is the 18th species of Tropiduchini and the 9th genus known east of the Wallace line. It is another taxon with characteristic asymmetric genitalia within this tribe.

Key words: Tropiduchini, *Bitara augusta* gen. et sp. nov., taxonomy, new genus, new species, terminalia asymmetry, Papua New Guinea

Introduction

Planthoppers of the family Tropiduchidae Stål, 1866 (Hemiptera, Fulgoromorpha, Fulgoroidea) has attracted more attention recently both because of the description of new extant representatives, the revision of several tribes, the discovery of several key fossil taxa (Bourgoin 2021), and also because the family taxonomic concept has been substantially modified. The subfamily Tropiduchinae Stål, 1866 comprises the majority of tribes, of which Tropiduchini Stål, 1866 comprises 26 genera and 121 species known so far (Bourgoin 2021). Wang et al. (2017) investigated the systematics and zoogeography of the tribe and reported it as a monophyletic group (Wang *et al.* 2017). Representatives of the tribe Tropiduchini reported from New Guinea, East of Wallace line, comprises 17 species distributed in 8 genera before this report.

Material and methods

The nomenclature of the fore wing (tegmen) follows the interpretation proposed by Bourgoin *et al.* (2015) and Stroiński (2020). Antennal structures are named following Stroiński *et al.* (2011). The terminology of the genitalia follows Bourgoin (1988) and Bourgoin & Huang (1990) for the male and Bourgoin (1993) for the female.

To reveal genitalic structures the whole abdomen of the specimen examined was cut off and cleared for 30 min in a warm (50°C) 10% potassium hydroxide (KOH) solution with a few drops of black chlorazol (CAS No. 1937-37-7) for staining the ectodermic genital structures, based on the method introduced by Carayon (1969). Dissections and cleaning of the genital structures were carried out in distilled water. Final observations were made in glycerol using an Olympus SZH10 and SZX10 stereomicroscopes. The photographs of the habitus and internal structures were taken using a stereomicroscope Leica MZ 16 with IC3D camera. Final images were adjusted using Helicon 5.0 software and Adobe Photoshop (version 7.0). The SEM photographs of uncoated specimens were taken in the Laboratory of Scanning Microscopy, MIZ PAS (Warsaw), using a scanning electron microscope HITACHI S-3400N under low vacuum conditions.

Measurements and abbreviations. Measurements were taken with an ocular micrometer. The following measurements, ratios and their abbreviations were used in this study:

Total length—measured (in dorsal view) from head apex to tegmina apex;

A/B—width of vertex measured at anterior margin / length of vertex measured at midline;

C/E—width of frons at upper margin / length of frons at midline;

D/E—maximum width of frons / length of frons at midline;

F/B—length of pronotum at midline / length of the vertex at midline;

G/F—length of mesonotum / length of pronotum at midline;

G/B+F—length of mesonotum / cumulative length of vertex and pronotum at midline;

G/H—length of mesonotum at midline / width of mesonotum between lateral angles;

I/J—length of tegmen measured from the base to the apical margin in median portion / width of tegmen measured at the widest part.

The material studied is deposited in the following collections: MNHU—Museum für Naturkunde, Humboldt Universität, Berlin; MIZ—Museum and Institute of Zoology, Polish Academy of Sciences, Warsaw.

Systematics

Family Tropiduchidae Stål, 1866

Subfamily Tropiduchinae Stål, 1866

Tribe Tropiduchini Stål, 1866

Bitara gen. nov.

Type species. *Bitara augusta* sp. nov.; by present designation and monotypy.

Diagnosis. Similar to Oechalinella Wang, 2017 in Wang et al. 2017, in general appearance. Differ in shape of the head, at lateral margin as long as wide, with anterior margin arcuate (nearly three times as long as wide, with anterior margin acutely angulate in Oechalinella); pronotum with median carina not reaching anterior margin (median carina reaching anterior margin in Oechalinella); male pygofer, medially fused gonostyli and aedeagus asymmetrical, male pygofer with posterodorsal elongate process on right side, left side without process (in Oechalinella male pygofer with posterior margin sinuate, with short lobate semicircular expansion on posterodorsal margin in right side, lobate subquadrate expansion in posterodorsal margin in left side); dorsal margin not excavate at level of anal tube base (dorsal margin distinctly excavate to accommodate base of anal tube in Oechalinella); aedeagal complex straight caudad (aedeagal complex curved in Oechalinella); genital styles tips of dorsal projections teeth-like, directed mediad (margin of dorsal projections smooth and not curved median in Oechalinella); female pregnital sternite narrow, posterior margin medially deeply concave, with median sclerotised process; anal tube distinctly shorter than gonoplac, tubular; gonoplac unilobate, with row of distinct teeth on posterior margin; bases of gonapophysis lobate, smooth.

Description. Head including compound eyes narrower than pronotum. Vertex chevron-like in dorsal view, with lateral margins as long as wide, anterior margin arcuate. Frons twice as long as broad in middle, roughly quadrate except abruptly narrowing in ventral forth; lateral margins of frons thickened, carinate, median carina simple. Frontoclypeal suture widely angulate. Clypeus with median longitudinal eminence. Pronotum with anterior margin produced anteriad between compound eyes, with median carina not reaching anterior margin, disc of pronotum not elevated. Mesonotum tricarinate, longer than broad, at same plane as vertex and pronotum, flat, with carinae connected at base, lateral carinae reaching posterior margin. Tegmen hyperpterous long and narrow, membranous, without granulation, with three defined lines formed by veins and veinlets: nodal, first and second postnodal lines. Male pygofer, medially fused gonostyli and aedeagus asymmetrical. Female pregenital sternite narrow, posterior margin medially deeply concave, with median sclerotised process. Anal tube distinctly shorter than gonoplac, tubular. Gonoplac unilobate, with row of distinct teeth on posterior margin. Bases of gonapophyses VIII asymmetrical.

Etymology. Generic name is derived from the name of the Sepik language Bitara (Berinomo), spoken in East Sepik Province, Papua-New Guinea, in the area where the specimens were collected. Gender: feminine.

Bitara augusta sp. nov.

(Figs 1-46)

Diagnosis. Tegmen with cells C1 and C3 of similar length, terminal MP_2 single. Metatibia with 3 lateral spines (including genual one) and row of 6 apical teeth (4+2) forming irregular line without diastema. Process of right lobe of pygofer, arcuately curved, tapering caudad. Spines of endosoma of different sizes; one oriented caudad, ventral one oriented cephalad; dorsal one the shortest, oriented dorsocephalad.

Description. *Measurements*: Total length 1.03–1.16 cm. Head. Vertex: proportion A/B = 1.64-1.81. Frons: proportion C/E = 0.42-0.45; proportion D/E = 0.53-0.58. Thorax. Pronotum: proportion F/B = 0.64-0.68. Mesonotum: proportion G/F+B = 2.22-2.40, proportion G/F = 5.45-5.90, proportion G/H = 1.09-1.18. Tegmina: proportion I/J = 2.41-2.64.



FIGURES 1–5. *Bitara augusta* **gen. et sp. nov.**, paratype, female. (1) habitus, lateral view; (2) same, dorsal view; (3) anterior part of body, dorsal view; (4) head, frontal view; (anterior part of body, lateral view.



FIGURES 6–11. *Bitara augusta* **gen. et sp. nov.**, paratype, female, SEM micrographs. (6–7) anterior part of body: (6) dorsal view, (7) lateral view; (80) head, frontal view; (9) upper part of frons, frontal view; (10 median carina of frons, frontal view; (11) lateral part of head and pronotum, lateral view.

Coloration (Figs 1–5). General colour ochraceous, speckled with lighter and darker irregular markings. Anterior and lateral margins of vertex mahogany-red; disc of vertex lighter straw-coloured. Frons ochraceous, with lighter speckles, median carina coloured as background, lateral carinations mahogany-brown. Postclypeus and anteclypeus ochraceous. Anterolateral and posterior margin of pronotum mahogany-reddish, disc of pronotum straw-coloured. Mesonotum with lateral carinae mahogany-reddish, disc light straw-coloured, lateral margins ochraceous, speckled. Tegulae ochraceous. Tegmen transparent, membranous, venation ochraceous. Legs uniformly coloured, ochraceous.

Head (Figs 1–13). Head with compound eyes narrower than pronotum. Vertex anteriorly projected, much wider than long, chevron-like in dorsal view, anterior margin angulately rounded, posterior margin deeply arcuately incised, lateral margins slightly diverging posteriad, all margins elevated, median carina almost reaching anterior margin; disc of vertex flat. Frons twice as long as broad in middle, roughly quadrate except abruptly narrowing in ventral fourth; lateral margins of frons thickened, carinate, median carina simple. Frontoclypeal suture broadly angulate. Clypeus with median longitudinal eminence. Rostrum reaching hind coxae bases; apical segment longer than broad, shorter than subapical segment. Callus small, posteriad of compound eye (Fig. 5). Ocelli small, below midpoint on compound eye. Antenna with scape very short, pedicel elongated, cylindrical (about as long as wide), with plate organs present on leading surface, tip of pedicel and ventral surface, trichoid sensilla type 1 and type 2 present: plate organs of crenelated type surrounded by a ring of elevated spines, higher than sensorial crests of the plate organ of pedicel.



FIGURES 12–17. *Bitara augusta* gen. et sp. nov., paratype, female, SEM micrographs. (12) Antennal, lateral view; (13) antennal plate organs; (14–17) tegmen: (14) apical part, (15) basal part, (16) end of clavus and CuA veins, (17) end of costal membrane and ScRA veins.



FIGURES 18–23. *Bitara augusta* **gen. et sp. nov.**, holotype, male, SEM micrographs. (18), abdomen, left side, lateral view; (19) terminalia, left side, lateral view; (20) abdomen, right side, lateral view; (21) terminalia, right side lateral view; (22) abdomen, ventral view; (23) genital capsule, ventral view.

Thorax (Figs 1–7, 11, 14–17). Pronotum short, approximately crescent-shaped in dorsal view; anterior margin roundly produced anteriad between compound eyes; tricarinate, disc not elevated, delimited by lateral carinae, lateral carinae distinctly elevated, median one not so, not reaching anterior margin; posterior margin carinate; sideways T-shaped lateral carina between eye and tegula (base toward tegula).

Mesonotum longer than broad, on same plane as vertex and pronotum, flat; conspicuously tricarinate, lateral carinae anteriorly curved to reach median carina, posteriorly parallel, reaching posterior margin; median carina approximately reaching mesoscutellar suture. Mesoscutellar suture straight; posterior margin of mesoscutellum acute. Tegula not carinate.

Procoxa shorter than profemur, subquadrate, with margins slightly carinate, smooth. Profemur slightly shorter than protibia, subquadrate in cross-section with rows of setae along. Protibia subquadrate in cross-section; short decumbent setae along margins. Protarsus shorter than half of protibia length, basiprotarsomere scaphoid, apical protarsomere longer than combined length of basiprotarsomere and midprotarsomere.



FIGURES 24–29. *Bitara augusta* gen. et sp. nov., holotype, male. (24–25) terminalia: (24) left side, (25) right side; (26–27) gonostyli: (26) left side, lateral view, (27) dorsal view; (28–29) phallic complex: (28) lateral view, (29) apical part, ventral view.

Mesocoxa slightly shorter than mesofemur, subquadrate, with margins smooth. Mesofemur subquadrate in crosssection, shorter than mesotibia, short, decumbent setae along margins. Mesotibia subquadrate in cross-section, with rows of setae along, slightly longer than protibia; Mesotarsus shorter than half of mesotibia length, basimesotarsomere scaphoid, apical mesotarsomere longer than combined length of basiprotarsomere and midprotarsomere. Metacoxa with coxal process widely triangular, very wide at base, spinose at apex. Metatibia distinctly longer than metafemur, not widened apically, with 3 lateral spines and row of 6 apical teeth (4+2) forming irregular line, without diastema: both lateral teeth same size; 4 internal spines different - two lateral internal teeth same size and same as lateral teeth; pair of middle teeth same size and distinctly shorter than others. Basimetatarsomere about as long as cumulative length of mid- and apical metatarsomeres, with apical row of 6 teeth; all teeth almost same size (see also Wang *et al.* 2017 Fig. 7F).



FIGURES 30–35. *Bitara augusta* **gen. et sp. nov.**, holotype (male) and paratype (female), SEM micrographs. (30–31) male. (30) abdomen, dorsal view; (31) terminalia, dorsal view. (32–35) female. (32) terminalia, lateral view; (33) end of gonoplac, dorsal view; (34) abdomen, dorsal view; (35) terminalia, dorsal view.



FIGURES 36–39. Bitara augusta gen. et sp. nov., paratype, female, SEM micrographs. (36–39) terminalia, ventral view.

Wings as in *Oechalinella* (for veins and cells nomenclature see Wang *et al.* 2017, Figs. 3E, 4D). Tegmen hyperpterous, long and narrow, membranous, without granulation, with three defined transverse lines formed by veins and veinlets (proximal to distal): nodal, first and second postnodal lines. Costal area present, narrower than costal cell, nearly reaching the level of tip of clavus, with sparse cross veins. Costal cell extending beyond midlength the length of tegmen and without transverse veinlets. Stems ScP+R and MP leaving basal cell with a short common stalk; stem ScP+R forked basad of tegmen midlength; branch ScP+RA separated from RP before nodal line. ScP+RA₁ forked before at nodal line, slightly basad of apex of costal area; first fork of RP distinctly apicad of nodal line, at level of first postnodal line. Stem MP forking first at level of nodal line; stalk MP₃₊₄; MP₁₊₂ forked at level of first postnodal line; stalk MP₃₊₄ forked at level of nodal line. Stem CuA forked basad of ScP+R fork, proximad of tegmen midlength, distad of claval veins junction. Postnodal and subapical row of cells of similar length. Clavus closed (*i.e.*, with CuP reaching margin and claval veins reaching margin), with apical tip acute, basad of end of costal area; claval veins Pcu and A₁ fused basad of half of CuP. Posterocubital cell, postcubital cell and anal cell without transverse veinlets.

Hind wings 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. Stem ScP+R forked at level of wing coupling apparatus (see Wang *et al.* 2017, Figs 4E & 5D), at level of CuA₁ branching; branch ScP+RA with single or two terminals, reaching margin well basad of apex of wing; branch RP with three terminals reaching margin at apical angle of wing. Stem MP not forked before *rp-mp* and *mp-cua* veinlets, three terminals MP₁, MP₂ and MP₃₊₄ reaching margin forked well apicad. Stem CuA forked slightly basad of stem ScP+R forking, branch CuA₁ forked again basad of *mp-cua* veinlet; terminals CuA_{1a}, CuA_{1b} and CuA₂ forked apically, reaching margin with five-six terminals. Stem CuP single. Stem Pcu distinctly curved before apex, fused for a distance with branching of A₁, A₂ single. Stems CuA and CuP connected more distad. Veinlets *rp-mp* slightly apicad of *mp-cua* at about same level, apicad of CuA₂ forking, *cua-cup* more basal, apicad of CuA forking.



FIGURES 40–46. *Bitara augusta* **gen. et sp. nov.**, paratype, female. (40) pregenital sternite (right side), flattened; (41) anal tube, dorsal view; (gonoplac, lateral view; (43–44) gonapophysis VIII and endogonocoxal process, lateral view: (43) left, (44) right; (45–46) gonapophysis IX and gonospiculum bridge: (45) dorsal view, (46) lateral view.

Male terminalia (Figs 18–29). Pygofer asymmetrical, roughly triangular in lateral view, upper margin declivous, lower margin straight; with posterodorsal elongate process on right side, left side without process; dorsal margin not excavate at level of anal tube base; ventral margin deeply, arcuately excavate. Gonostyli asymmetrical, medially fused into a plate, convex medially in ventral plane, in lateral view left gonostylus elongate, with subapical triangular process, dorsal edge with an oblique hook-like process at about half of gonostylus length, directed cephalad; in lateral view right gonostylus subtriangular, caudodorsal margin arcuate, dorsal margin without hook. Phallic complex straight caudad; periandrium tubular, short, membranous, endosoma bulbous, spiniferous, with three asymmetric distinct spines. Anal tube elongate, tubular, reaching almost to apex of gonostyli; with ventrocaudal, triangular expansion, epiproct and paraproct of similar size.

Female terminalia (Figs 30–46). Pregenital sternite narrow, posterior margin medially deeply concave, with median sclerotised process; anal tube distinctly shorter than gonoplac, tubular; gonoplac unilobate, with row of distinct teeth on posterior margin; bases of gonapophyses VIII asymmetrical—left gonapophysis base lobate, with hook-like process; right base of gonapophysis lobate, smooth; gonapophysis VIII with teeth on apical portion

of dorsal margin, ventral margin arcuate, with three apical teeth; endogonocoxal process sabre-like, as long as gonapophysis VIII.

Type material. Holotype, male: [D.N. Guinea 150. / Standlager a. Aprilfluss / 183, 12.-14.IX.1912 / Kais. Augustafl. Exp. / Bürgers S.G.] (MNHU). Paratypes, 2 males, 1 female: [D.N. Guinea 150. / Standlager a. Aprilfluss / 183, 12.-14.IX.1912 / Kais. Augustafl. Exp. / Bürgers S.G.]—male (MNHU); [D.N. Guinea / Regenberg 550 m / 8.-15.V.13 / Kais. Augustafl. Exp. / Bürgers S.G.], [331 / 9.X.13.]—male (MIZ); [D. N. Guinea / Standlager b. Malu / 12.–13.III.1912 / Dr. Bürgers S.G.]—female (MNHU).

Distribution. New Guinea, Papua New Guinea, Madang Province.

Discussion

With the finding here of *Bitara* gen. nov., the key to the genera of Tropiduchini (Wang *et al.* 2017) should be modified by replacing couplets 9 as follows:

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) 9a
Pronotum with median carina reaching anterior margin; male pygofer with short lobate semicircular expansion on posterodorsal margin in right side, lobate subquadrate expansion in posterodorsal margin in left side *Oechalinella* Wang, 2017
Pronotum with median carina not reaching anterior margin; male pygofer with posterodorsal elongate process on right side, left

Bitara gen. nov. is another planthopper of the tribe Tropiduchini reported from New Guinea, east of Wallace line. From the island of New Guinea, 17 species in 8 genera had been known before this report (Wang *et al.* 2017, Bourgoin 2021). After the inclusion of *Bitara augusta* gen. et sp. nov. to of New Guinean Tropiduchidae, 13 species (of 18) and 7 genera (of 9) represent the tribe Tropiduchini. These species are mainly inhabiting the ecoregion of Northern New Guinea lowland rain and freshwater swamp forests (Cámara-Leret *et al.* 2019). The Wallace line—a hypothetical boundary that separates the highly distinctive faunas of the Asian and Australian biogeographic regions and passes between the islands of Bali and Lombok in Indonesia, between Borneo and Sulawesi, and between the Philippines and the Moluccas, was first noted by Wallace (1860, 1863) and got its name by Huxley (1868). The Wallace line and area of Wallacea were recently discussed by Ali & Heaney (2021), re-analyzed and discussed, *e.g.* by Beron (2015) regarding arachnids, White *et al.* (2020) regarding birds and mammals. Such analyses are lacking for planthoppers; in respect of Tropiduchini, we can say only that currently 18 species distributed in 9 genera (including *Bitara augusta* gen. et sp. nov. is known east of Wallace line, while west of Wallace line 21 species of 7 genera were reported (Wang *et al.* 2017, Bourgoin 2021). Only 2 species were reported from both sides of Wallace line.

According to Wang *et al.* (2017) monophyly of Tropiduchini is supported based on seven synapomorphies: (1) the posterior margin of the vertex reaching nearly to anterior margin of eyes; (2) the anteriorly produced pronotum reaching the anterior margin of the eyes; (3) the asymmetrical pygofer; (4) the asymmetrical gonostyli; (5) periandrium surrounding a base of aedeagus; (6) endsomal processes membranous; (7) at least one median processes on the ventrocaudad margin of the gonostylus. All these features are observable in *Bitara* gen. nov. placing this genus clearly in Tropiduchini.

Left–right genital asymmetry is a recurring phenomenon in insect morphology, and recent studies have highlighted its potential impact on our understanding of fundamental evolutionary processes like the evolution of development and the selection for morphological novelties caused by behavioural changes. Current data suggest that in insect taxa it has arisen multiple times independently (Huber *et al.* 2007, Huber 2010), but male asymmetries tend to evolve first, and female asymmetries evolve later, if at all. In Heteroptera, for example, taxa with female genital asymmetries are always nested within larger taxa in which male genital asymmetry exists, but rarely vice versa (Larsén 1938). According to Huber *et al.* (2007) and Huber (2010) the evolution of left-right asymmetric genitalia in insects is assumed as evolved in response to changes in mating behaviour. These changes could result from so-called 'behavioural drive' (Huey *et al.* 2003, Acurio *et al.* 2019), where contact with new environmental factors, can initiate evolutionary shifts in morphology, physiology or ecology. On the other hand, according to results of Eberle *et al.* (2015) in *Schizonycha* chafer beetles (Coleoptera: Scarabaeidae: Schizonychini) there is no

significant correlation of asymmetric genitalia and an increase in the rate of genital shape divergence. The situation seems to be even more complex and underlines the highly complex mechanisms by which male genital morphology might be under sexual selection (Hosken & Stockley 2004, Simmons 2014, Simmons *et al.* 2009). Interpretation of the observed evolutionary patterns in morphology depends on detailed knowledge on copulation, courtship, speciation mechanisms and infraspecific variation of the internal copulation organs, but this data is yet lacking for most of the Tropiduchidae.

Acknowledgements

We would like to thank Dr. Jürgen Deckert for the privilege of studying material from the entomological collection of Museum für Naturkunde (Berlin, Germany) and Dr. Charles R. Bartlett (University of Delaware, U.S.A.) for comments on earlier version of manuscript.

References

- Acurio, A.E., Rhebergen, F.T., Paulus, S., Courtier-Orgogozo, V. & Lang, M. (2019) Repeated evolution of asymmetric genitalia and right-sided mating behavior in the *Drosophila nannoptera* species group. *BMC Evolutionary Biology*, 19 (109), 1–14. https://doi.org/10.1186/s12862-019-1434-z
- Ali, J.R. & Heaney, L.R. (2021) Wallace's line, Wallacea, and associated divides and areas: history of a tortuous tangle of ideas and labels. *Biological Reviews*, 96, 922–942. https://doi.org/10.1111/brv.12683
- Beron, P. (2015) The Arachnogeography and the "lines" (of Wallace, Lydekker, Weber). *Historia naturalis bulgarica*, 22, 5–30.
- Bourgoin, T. (1988) A new interpretation of the homologies of the Hemiptera male genitalia, illustrated by the Tettigometridae (Hemiptera, Fulgoromorpha). In: Vidano, C. & Arzone, A. (Eds.), 6th Auchenorrhyncha Meeting, Turin, Italy, 7–11 September 1987. Consiglio Nazionale delle Ricerche-Special Project IPRA, Turin, pp. 113–120.
- Bourgoin, T. (1993) Female genitalia in Hemiptera Fulgoromorpha morphological and phylogenetic data. *Annales de la Société entomologique de France*, 29 (3), 225–244.
- Bourgoin, T. (2021) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8. Updated 17 July 2021. Available from: http://hemiptera-databases.org/flow/ (accessed 6 October 2021)
- 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*, Nouvelle Série, 26 (4), 555–564.
- Bourgoin, T., Wang, R.-R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroiński, A., Yap, S. & Szwedo, J. (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. https://doi.org/10.1007/s00435-014-0243-6
- Cámara-Leret, R., Raes, N., Roehrdanz, P., De Fretes, Y., Heatubun, C. D., Roeble, L., Schuiteman, A., van Welzen, P. C. & Hannah, L. (2019) Climate change threatens New Guinea's biocultural heritage. *Science Advances*, 5 (11), eaaz1455, 1–8. https://doi.org/10.1126/sciadv.aaz1455
- Carayon, J. (1969) Emploi du noir chlorazol en anatomie microscopique des insectes. *Annales de la Société entomologique de France*, Nouvelle Série, 5, 179–193.
- Eberle, J., Walbaum, W., Warnock, R.C.M., Fabrizi, S. & Ahrens, D. (2015) Asymmetry in genitalia does not increase the rate of their evolution. *Molecular Phylogenetics and Evolution*, 93, 180–187. https://doi.org/10.1016/j.ympey.2015.08.005
- Hosken, D.J. & Stockley, P., (2004) Sexual selection and genital evolution. *Trends in Ecology and Evolution*, 19 (2), 87–93. https://doi.org/10.1016/j.tree.2003.11.012
- Huber, B.A. (2010) Mating positions and the evolution of asymmetric insect genitalia. *Genetica*, 138 (1), 19–25. https://doi.org/10.1007/s10709-008-9339-6
- Huber, B.A., Sinclair, B.J. & Schmitt, M. (2007) The evolution of asymmetric genitalia in spiders and insects. *Biological Review*, 82 (4), 647–698.
 - https://doi.org/10.1111/j.1469-185X.2007.00029.x
- Huey, R.B., Hertz, P.E. & Sinervo, B. (2003) Behavioral drive versus behavioral inertia in evolution: a null model approach. *The American Naturalist*, 161, 357–366.

https://doi.org/10.1086/346135

Huxley, T.H. (1868) On the classification and distribution of the Alectoromorphae and Heteromorphae. *Proceedings of the Zoological Society of London*, 1868, 294–319.

- Larsén, O. (1938) Untersuchungen über den Geschlechtsapparat der aquatilen Wanzen. *Opuscula Entomologica*, Supplement, 1, 1–388.
- Simmons, L.W. (2014) Sexual selection and genital evolution. *Austral Entomology*, 53 (1), 1–17. https://doi.org/10.1111/aen.12053
- Simmons, L.W., House, C.M., Hunt, J. & García-González, F. (2009) Evolutionary response to sexual selection in male genital morphology. *Current Biology*, 19 (17), 1442–1446. https://doi.org/10.1016/j.cub.2009.06.056
- Stroiński, A. (2020) *Hagneia kallea* gen. and sp. nov. (Hemiptera: Fulgoromorpha: Ricaniidae) from North Vietnam. *Zootaxa*, 4861 (2), 241–256.
 - https://doi.org/10.11646/zootaxa.4861.2.5
- Wallace, A.R. (1860) On the zoological geography of the Malay archipelago. *Journal of the Proceedings of the Linnean Society of London. Zoology*, 4 (16), 172–184.
 - https://doi.org/10.1111/j.1096-3642.1860.tb00090.x
- Wallace, A.R. (1863) On the physical geography of the Malay archipelago. *The Journal of the Royal Geographical Society of London*, 33, 217–234.
 - https://doi.org/10.2307/1798448
- Wang, R.R., Li, X.L., Szwedo, J., Stroiński, A., Liang, A.P. & Bourgoin, T. (2017) 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. *Systematic Entomology*, 42 (2), 359–378. https://doi.org/10.1111/syen.12219
- White, A.E., Day, K.K., Stephens, M. & Price, T.D. (2020) Dispersal syndromes drive the formation of biogeographical regions, illustrated by the case of Wallace's Line. *Global Ecology and Biogeography*, 30, 685–696. https://doi.org/10.1111/geb.13250