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## Why so scarce? Dictyopharidae from Madagascar (Hemiptera: Fulgoromorpha)

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### Abstract

A new genus and species of Dictyopharidae from Madagascar—*Tupala occulta* **gen. et sp. nov.** is described and illustrated. It is the third known dictyopharid and the second representing tribe Dictyopharini. Two other taxa with taxonomic problems ascribed to Dictyopharidae are discussed. The question of paucity of Dictyopharidae of Madagascar is raised and several possible explanations are presented.

**Key words:** new genus, new species, Dictyopharini, Madagascar, faunistics, biogeography

### Introduction

Dictyopharidae Spinola, 1839 is a moderately large family of planthoppers (Hemiptera: Fulgoroidea) with 167 genera and 739 species recorded (Bourgoin 2015). It comprises medium-sized insects gathered in two subfamilies: Dictyopharinae Spinola, 1839—generally macropterous and larger (10–26 mm long), usually with anteriorly prolonged head; and Orgeriinae Fieber, 1872—brachypterous (flightless) and smaller (up to 10 mm), with thickened short tegmen and rounded body. The Dictyopharinae is of worldwide distribution (Melichar 1912; Metcalf 1946; Emeljanov 1983; Bourgoin 2015), while Orgeriinae, being a distinct lineage, is mainly characterized by morphological reduction and adaptation to arid conditions and distributed in the Holarctic (Emeljanov 1969, 1980, 2006, 2007; Emeljanov *et al.* 2005; Bartlett *et al.* 2014).

Analyses of the phylogenetic relationships among the higher taxa of the family as a whole are lacking (Donovall & Bartlett 2005), however some indications were proposed. The classification and relationships within Dictyopharinae are still poorly known, whereas those within Orgeriinae are well supported by morphological (Emeljanov 1980), cytogenetic (Kuznetsova 1985; Kuznetsova *et al.* 2009), and preliminary molecular (Emeljanov *et al.* 2005) data.

Members of Dictyopharinae are dorsoventrally compressed, with head narrower than pronotum, often greatly produced in front of compound eyes, tegmina membranous, venation regular with a number of cross veins, costal area with numerous cross veins, aedeagal complex semi-sclerotized, with membranous and sclerotized apical processes. The Dictyopharinae are usually collected from herbs, grass, and shrubs, but little is known about their life habits. Majority of them feed on the phloem of woody or herbaceous plants (Wilson *et al.* 1994). Dictyopharinae are primarily distributed in arid, semiarid, and tropical zones worldwide.

The subfamily Dictyopharinae is subdivided into 12 tribes: two extinct—Netutelini Emeljanov, 1983 and Worskaitini Szwedo, 2008, and 10 recent ones—Aluntiini Emeljanov, 1979, Capenini Emeljanov, 1969, Cladodipterini Metcalf, 1938, Cleotychini Emeljanov, 1997, Dictyopharini Spinola, 1839, Hastini Emeljanov, 1983, Nersiini Emeljanov, 1983, Orthopagini Emeljanov, 1983, Phylloscelini Emeljanov, 1983 and Scoloptini Emeljanov, 1983 (Emeljanov 1969, 1983, 1997, 2007, 2008; Szwedo 2008; Kuznetsova *et al.* 2009).

Subfamily Orgeriinae comprises four tribes (Emeljanov 2004, 2007, 2008; Emeljanov *et al.* 2005; Szwedo 2008; Kuznetsova *et al.* 2009): Almanini Kusnetzov, 1936, Colobocini Emeljanov, 1969, Orgeriini Fieber, 1872 and Ranissini Emeljanov, 1969.

The number of units of the families Dictyopharidae and their presumed sister group—family Fulgoridae were moved from one family to another (Emeljanov 1979, 2004, 2008, 2013; Kuznetsova *et al.* 2009). Therefore the content of these families and status of some units recognized is still far from final understanding. Dictyopharidae + Fulgoridae lineage is believed to be the oldest of extant planthoppers groups with long-legged, adult-like nymphs (Shcherbakov & Popov 2002; Emeljanov & Shcherbakov 2005).

The fauna of Madagascar Dictyopharidae is extremely poor (Fig. 55), with only *Aluntia hova* Nast, 1949 (Aluntini) and *Zaputala bourgoini* Emeljanov, 2008 (Dictyopharini; Figs 51–54). Status of *Mahanorona cowani* Distant, 1909 remains unclear, as this taxon was transferred to Issidae by Jacobi (1917), then moved back to Dictyopharidae by Fennah (1967). Next problematic taxon is *Dictyophara unicolor* Signoret, 1860, originally described from Madagascar. Data about its placement from Madagascar and adjacent islands (Signoret 1860, Schmidt 1915, Jacobi 1917) are correct. The *Dictyophara unicolor* var. *ochracea* Lallemand, 1950, described from Mt. d'Ambre (North Madagascar) needs to be revised. The other data about presence of *Dictyophara unicolor* Signoret, 1860 in Algeria (Lethierry 1889) and Palestine (Bodenheimer 1937) result from nomenclatorial and misinterpretations of usage and identity of species described under the name *Dictyophara unicolor* Signoret var. *vittata* Puton, 1892, which needs to be a subject of separate taxonomic studies (work in progress).

## Material and methods

**Material.** The studied material comes from the entomological collections of the Royal Belgian Institute of Natural Sciences (RIScNB), Brussels, Belgium and Muséum national d'Histoire naturelle (MNHN), Paris, France.

**Preparations and illustration.** The abdomens of the specimens examined were cut off and cleared for 30 min in a warm (50°C) 10% KOH solution with a few drops of black chlorazol (CAS No. 1937-37-7) for dyeing the ectodermic genital structures on the method introduced by Carayon (1969) and Bourgoïn (1993). Dissections and cleaning of the genital structures were carried out in distilled water. Final observations were made in glycerol using a Olympus stereoscopic (SZH10). The photographs were taken using a stereoscopic microscope Leica MZ 16 with IC3D camera; final images were created using the Helicon 5.0 software and Adobe Photoshop. The scanning electron micrographs of uncoated specimens were taken in the Laboratory of Scanning Microscopy, MIZ PAS (Warsaw), using a scanning microscope HITACHI S-3400N under low-vacuum conditions.

**Measurements and abbreviations.** Proportions and measurements taken are listed with the abbreviations used in this study: Total length, measured (in dorsal view) from the apex of head to the apex of tegmina; A/B, width of vertex measured at the posterior margin/length of vertex 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 in mid-line/length of 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 base to the apical margin in median portion/width of tegmen measured from the apex of clavus to the anterior margin.

The nomenclature of the male genitalia follows Bourgoïn and Huang (1990). Venation nomenclature follows the interpretation proposed by Bourgoïn *et al.* (2015).

## Systematics

### Family Dictyopharidae Spinola, 1839

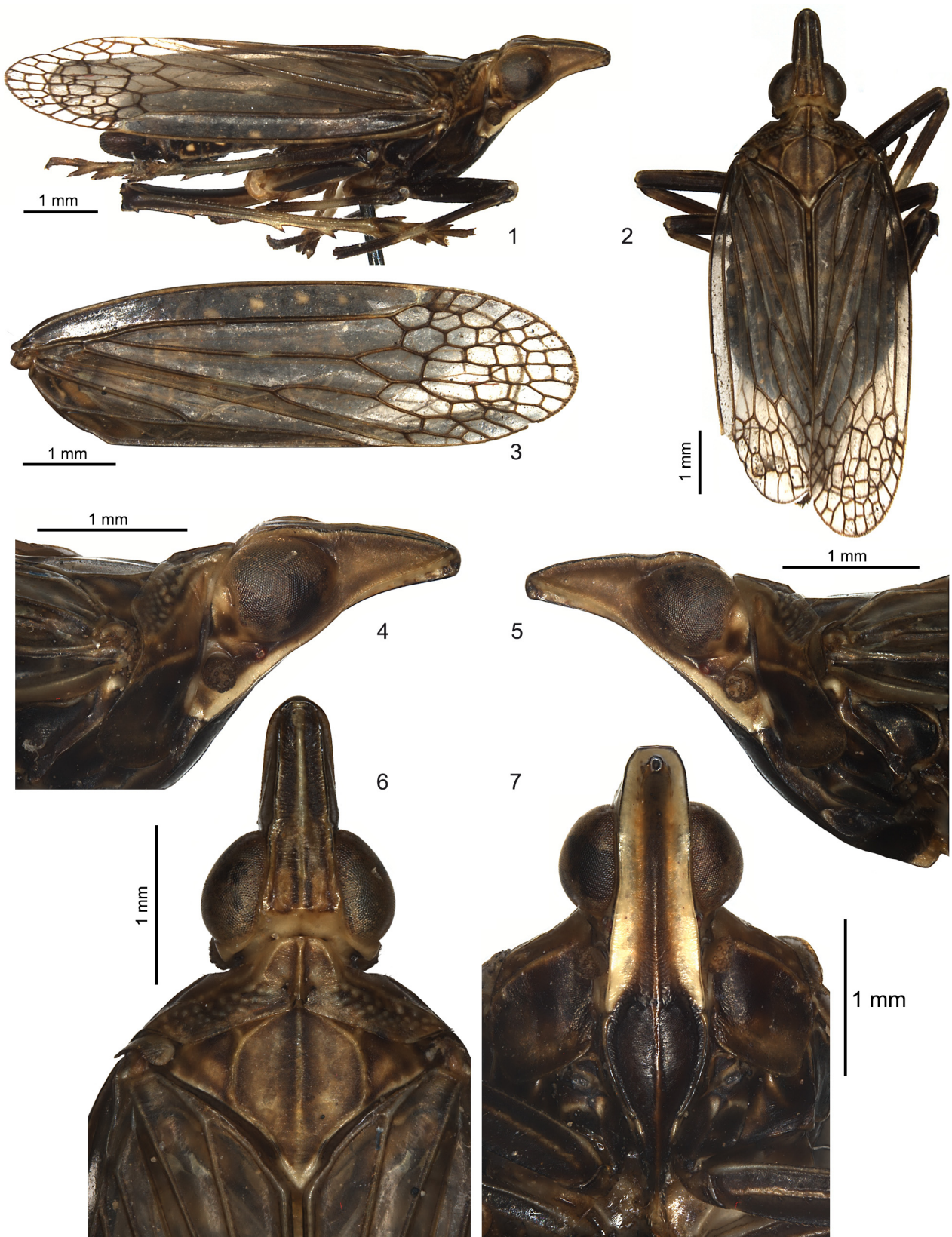
### Subfamily Dictyopharinae Spinola, 1839

### Tribe Dictyopharini Spinola, 1839

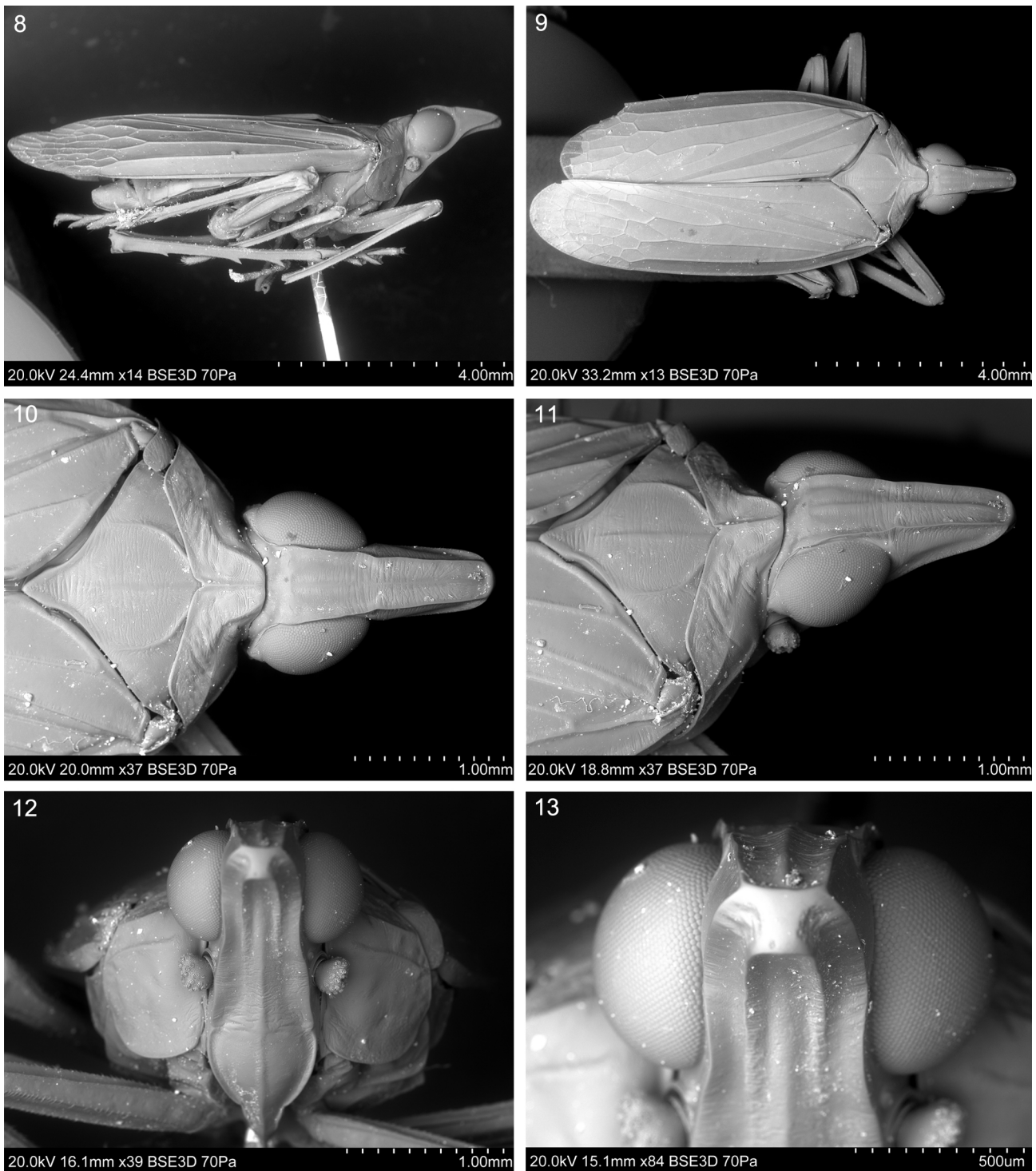
#### *Tupala* gen. nov.

(Figs 1–50, 55)

**Type species.** *Tupala occulta* sp. nov., here designated.



**FIGURES 1–7.** *Tupala occulta* gen. et sp. nov., holotype, male. (1) habitus, lateral view; (2) same, dorsal view; (3) right tegmen, dorsal view; (4–7) anterior part of body: (4) right side, lateral view, (5) left side, lateral view, (6) dorsal view, (7) frontal view.



**FIGURES 8–13.** *Tupala occulta* gen. et sp. nov., holotype, male. (8) habitus, lateral view; (9) same, dorsal view; (10–12) anterior part of body: (10) dorsal view, (11) dorso-lateral view, (12) frontal view; (13) upper part of head capsule.

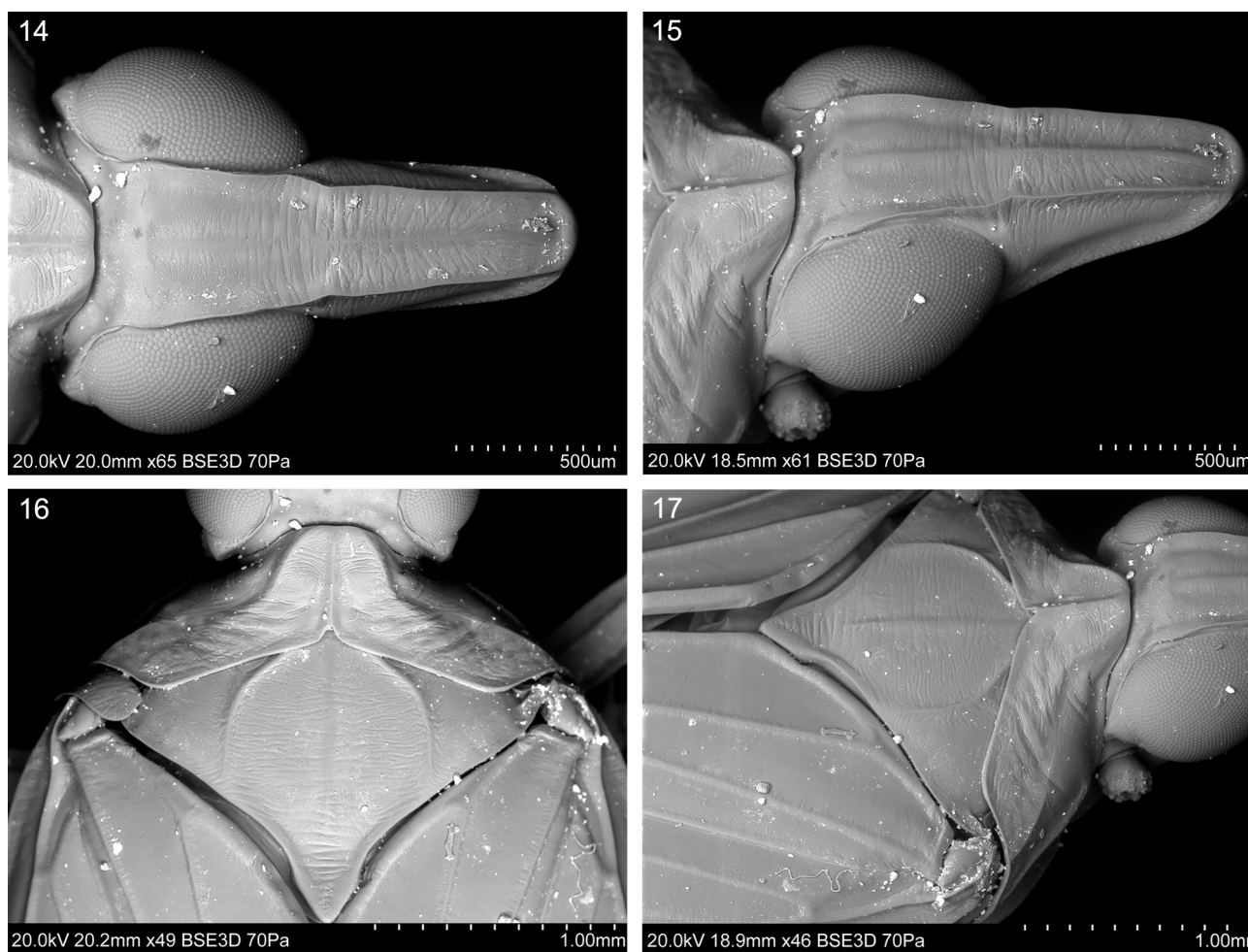
**Etymology.** Generic name is an anagram of dictyopharid generic name *Putala*. Gender: feminine.

**Diagnosis.** Differs from *Zaputala* (Figs 51–54) by: presence of longitudinal carina of vertex (absent in *Zaputala*); tricarinate pronotum (single carina in *Zaputala*); frons with median carina (absent in *Zaputala*); different organization of head capsule extension. Lateral portions of pronotum with obsolete granulation (lateral portions of pronotum smooth in *Zaputala*).

**Description.** Head with compound eyes distinctly narrower than pronotum. Vertex longer than wide at base, tapering apicad; anterior margin arcuate, lateral margins with shallow incision at about half of their length,

posterior margin shallowly convex, indistinct; lateral margins carinate, anterior margin thickened, callose; disc of vertex flat, with faint longitudinal carina. Posterior margin of vertex at posterior  $\frac{1}{3}$  of compound eyes length.

Frons longer than wide at frontoclypeal suture, with lateral margins carinate, merely sigmoid, diverging towards frontoclypeal suture, with breaking point above the level of antennae base, then more distinctly diverging, lateral carinae reaching to half of frons length, in upper portion, forming obtuse extension, convex in upper portion towards margin with vertex, concave in lower portion towards disc of frons, median carina reaching frontoclypeal suture; disc of frons concave laterad, with median convexity at lower  $\frac{1}{3}$  of its length. Frontoclypeal suture straight, not distinct. Postclypeus with distinct lateral carinae and median carina, disc of clypeus convex, anteclypeus distinguishable, convex, with lateral and median carinae. Compound eyes with small posteroventral callus. Lateral ocelli present. Antennal fovea deep, emarginated; scapus short, pedicel bulbiform, with sensory plates in upper portion distributed in apical half, and sensory plates of lower hemisphere distributed in basal and apical parts; trichoid sensilla type I present. Rostrum with apical segment almost as long as subapical one, apex of rostrum reaching to metacoxae.

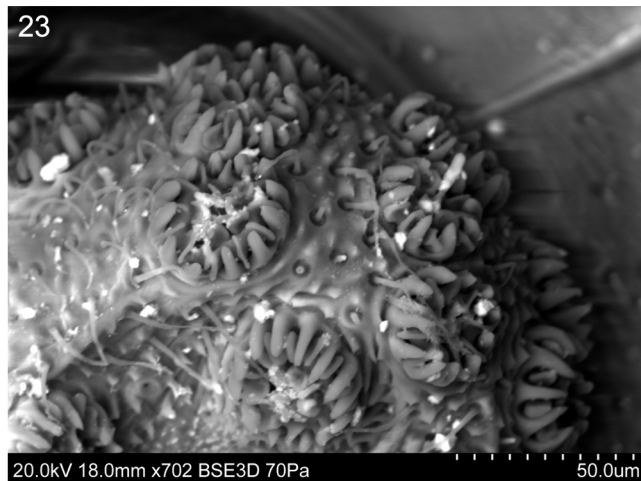
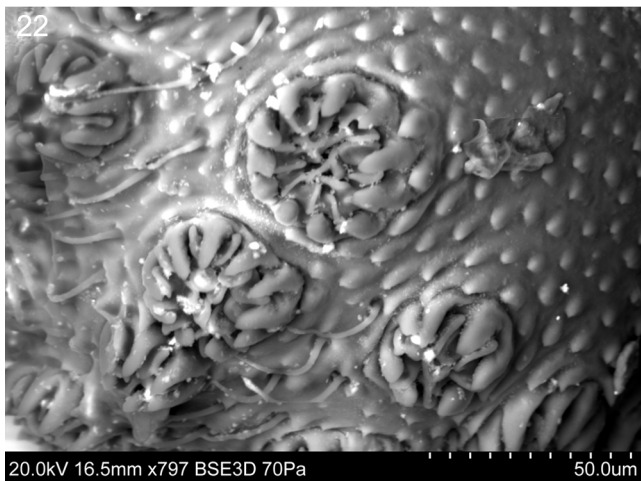
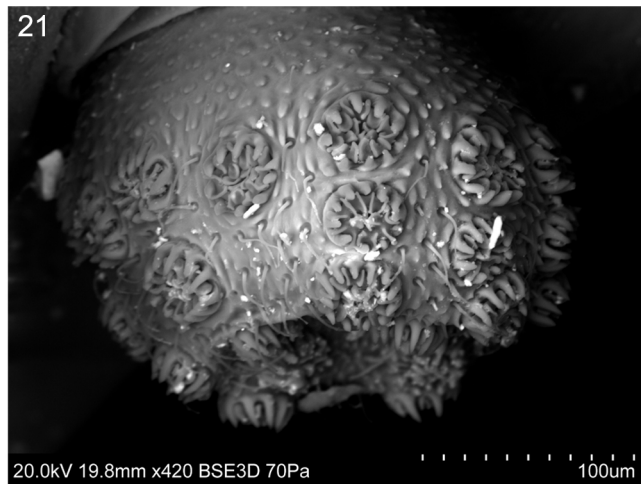
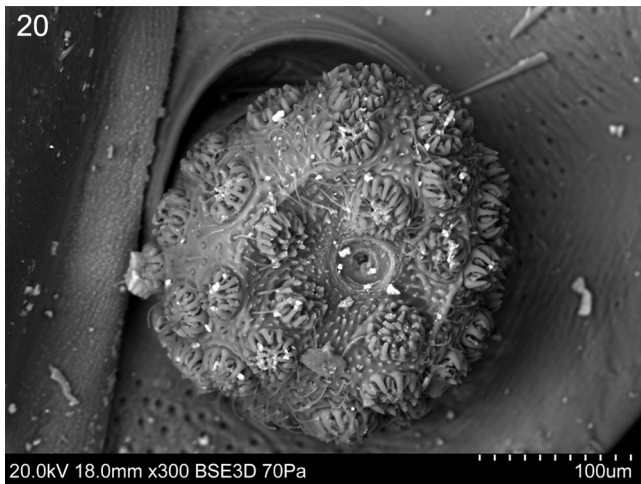
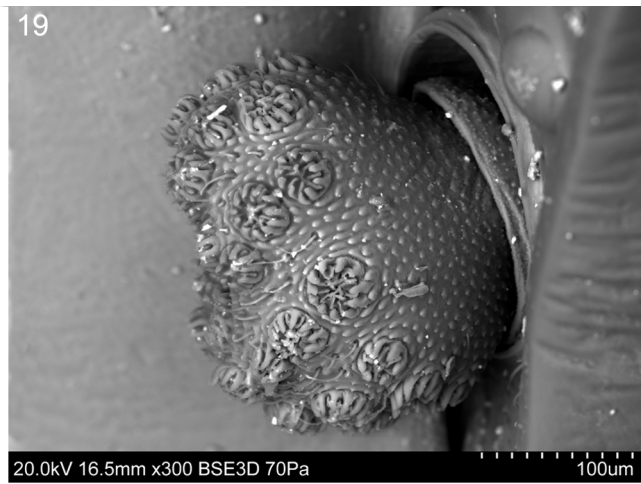
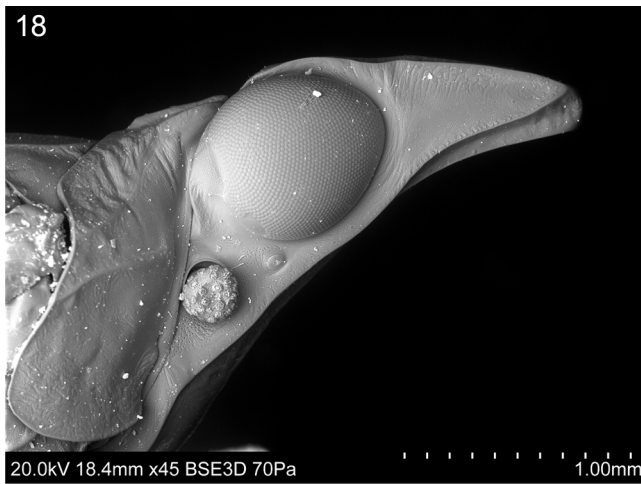


**FIGURES 14–17.** *Tupala occulta* gen. et sp. nov., holotype, male. (14–15) vertex: (14) dorsal view, (15) dorsolateral view; (16–17) pronotum and mesonotum: (16) dorsal view; (17) dorsolateral view.

Pronotum heptagonal, with disc slightly elevated, delimited by straight anterior margin, incomplete anterolateral carinae, strongly diverging posteriad, not reaching to posterior margin, with distinct median carina, posterior margin of pronotum widely triangularly incised, with small but distinct triangular incision at terminus of median carina; lateral portions of pronotum descending lateroposteriad, with oblique postocular carina, reaching posterior margin, and lateral carina reaching posterior margin.

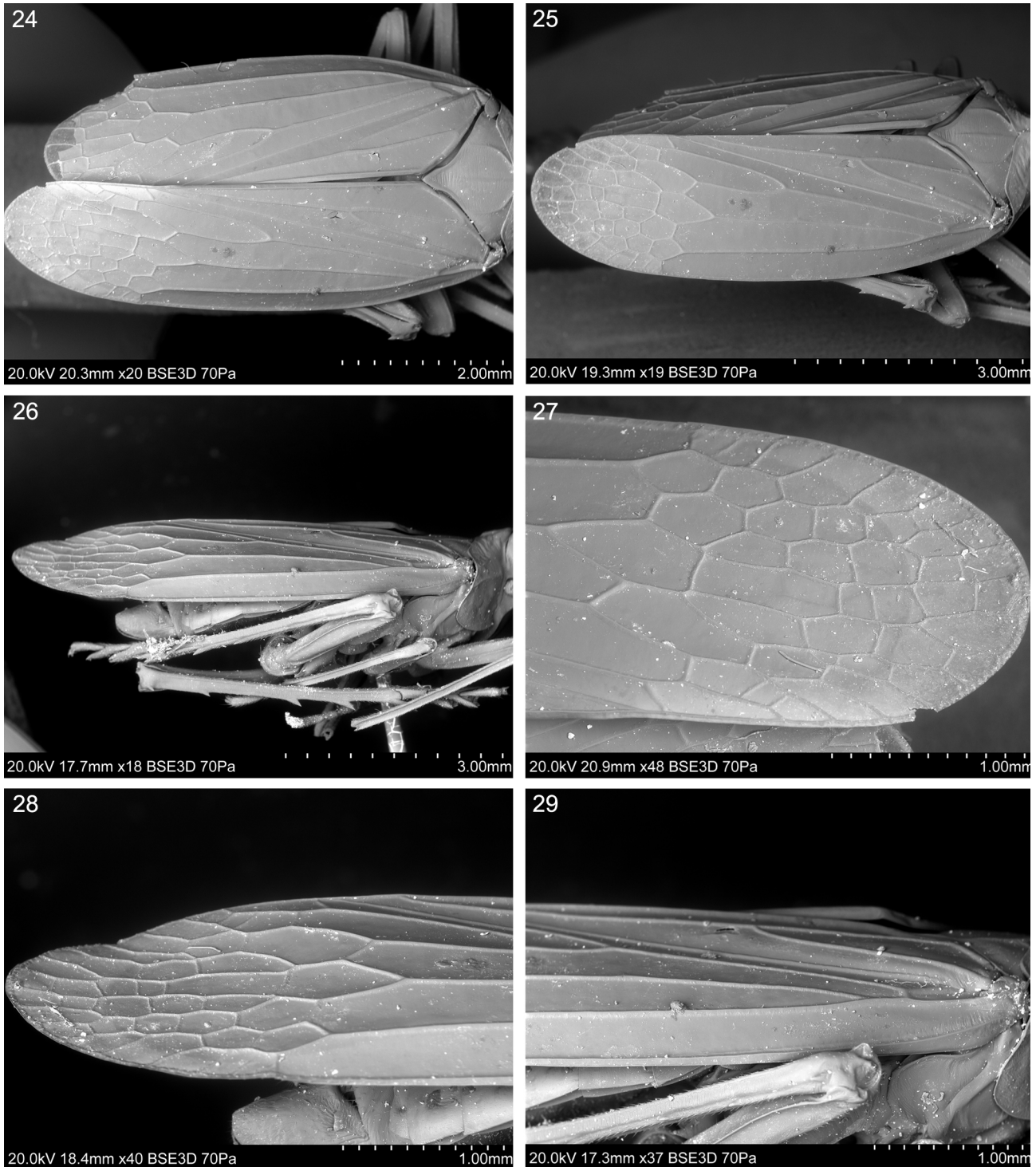
Tegulae large, without carinae.

Mesonotum wider than long in mid line, with distinct median carina, reaching to level of scutellum and lateral carinae reaching posterior margin, delimiting flattened disc, lateral margins descending.



**FIGURES 18–23.** *Tupala occulta* gen. et sp. nov., holotype, male. (18) anterior part of body, lateral view; (19–23) antenna and antennal plate organs.

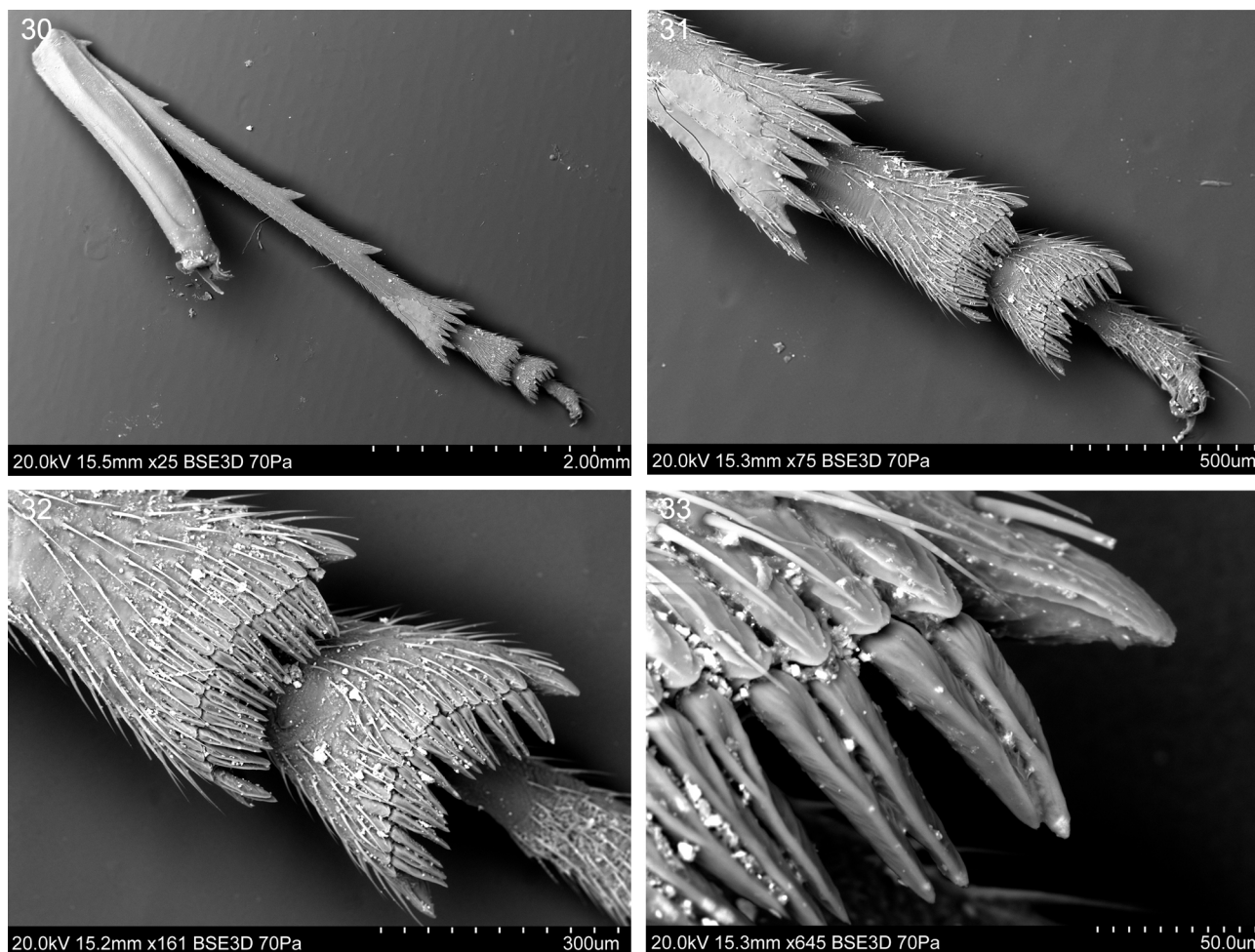
Tegmen membranous, macropterous, with venation distinct; apex of clavus exceeding  $\frac{2}{3}$  of tegmen length. Costal margin arcuate, veins of costal complex fused, anteroapical angle wide, apex rounded, apical point at level of middle of tegmen width, posteroapical angle wide, tornus long. Basal cell narrow, elongate, stems ScP+R and M leaving basal cell with a short common stalk, about half as long as basal cell; stem ScP+R long, slightly curved, subparallel to costal margin, forked posteriad of stems M and CuA forkings, merely basad of level of claval apex, branch ScP+RA reaching margin with three terminals, terminal ScP+RA<sub>1</sub> reaching margin apicad of claval apex; branch RP forked apicad of RA, terminus at margin, reaching margin with two terminals. Stem M merely sigmoid, forked slightly basad of claval apex, basad of stem ScP+R forking, branch M<sub>1+2</sub> forked slightly apicad of branch



**FIGURES 24–29.** *Tupala occulta* gen. et sp. nov., holotype, male, tegmen. (24) dorsal view; (25) dorsolateral view; (26) lateral view; (27) apical part, dorsal view; (28) apical part, lateral view; (29) basal part, lateral view.

$M_{3+4}$  forking, then  $M_1$  forked again on membrane, forking of branch  $M_{3+4}$  slightly apicad of claval apex, then branches  $M_3$  and  $M_4$  forked again on membrane, then stem  $M$  reaching margin with 7 terminals. Stem  $CuA$  straight, long, forked apicad of claval veins junction, branch  $CuA_1$  forked subapically on membrane, branch  $CuA_2$  single. Claval veins  $Pcu$  and  $A_1$  fused before half of claval suture ( $CuP$ ) length. Veinlet *peccacp-scr*a delimiting anterior margin of ‘stigmal area’ placed slightly apicad of transverse veinlet *Ir-m*, apicad of claval apex, callose at costal margin. Nodal veinlet *Ir-m* at level claval apex; nodal veinlet *Im-cu* slightly oblique, basad of *Ir-m*; veinlet *icu* oblique, reaching margin of tornus apicad of claval apex. Costal cell without transverse veinlets. Membrane with

net of transverse veinlets delimiting polygonal cells. ‘Stigmal area’ wide, dissected by ScP+RA<sub>1</sub> and RA<sub>2</sub> terminals. Cell C1 pentagonal, slightly longer than wide; cell C3 elongately pentagonal, longer than wide, about twice as long as C1; cell C5 lanceolate, tapering posteriad, more than twice as long as cell C3.



**FIGURES 30–33.** *Tupala occulta* gen. et sp. nov., holotype, male, hind leg. (30) hind leg, ventral view; (31) apex of tibia and tarsomere; (32–33) tibia.

Legs long, slender, tibiae not flattened. Profemur longer than mesofemur. Metatibia longer than metafemur, with four lateral spines and 8 apical teeth arranged in a row. Metabasitarsomere about as long as cumulative length of mid and apical metatarsomeres; Basimetatarsomere with row of apical teeth; subconical lateral ones and row of 22 dorsoventrally flattened and elongated teeth with subapical needle-shaped platellae, laterally compressed, with dorsal fuller in median portion. Midmetatarsomere with row of apical teeth, subconical lateral ones, and row of 18 dorsoventrally flattened and elongated teeth with subapical needle-shaped platellae, laterally compressed, with dorsal fuller in median portion. Apical metatarsomere about as long as preceding one; tarsal claws distinct, arolium wide.

Male terminalia: pygofer laterally compressed, distinctly higher than long in lateral view, posterior margin smooth, with posterodorsal portion declining posteriad. Anal tube distinctly shorter than gonostyles, tubular, with short, triangular, posteroventral projections; anus placed apically. Gonostyles symmetrical, not fused; base narrow, expanded towards middle, then mildly tapering towards apex; dorsobasal margin straight, dorsoapical margin straight, apical portion bluntly rounded, ventral margin widely arcuate; upper margin with dorsal process in the middle, acutely tapering basad, hook-like process near sub-middle in lateral view, closer to dorsobasal margin.

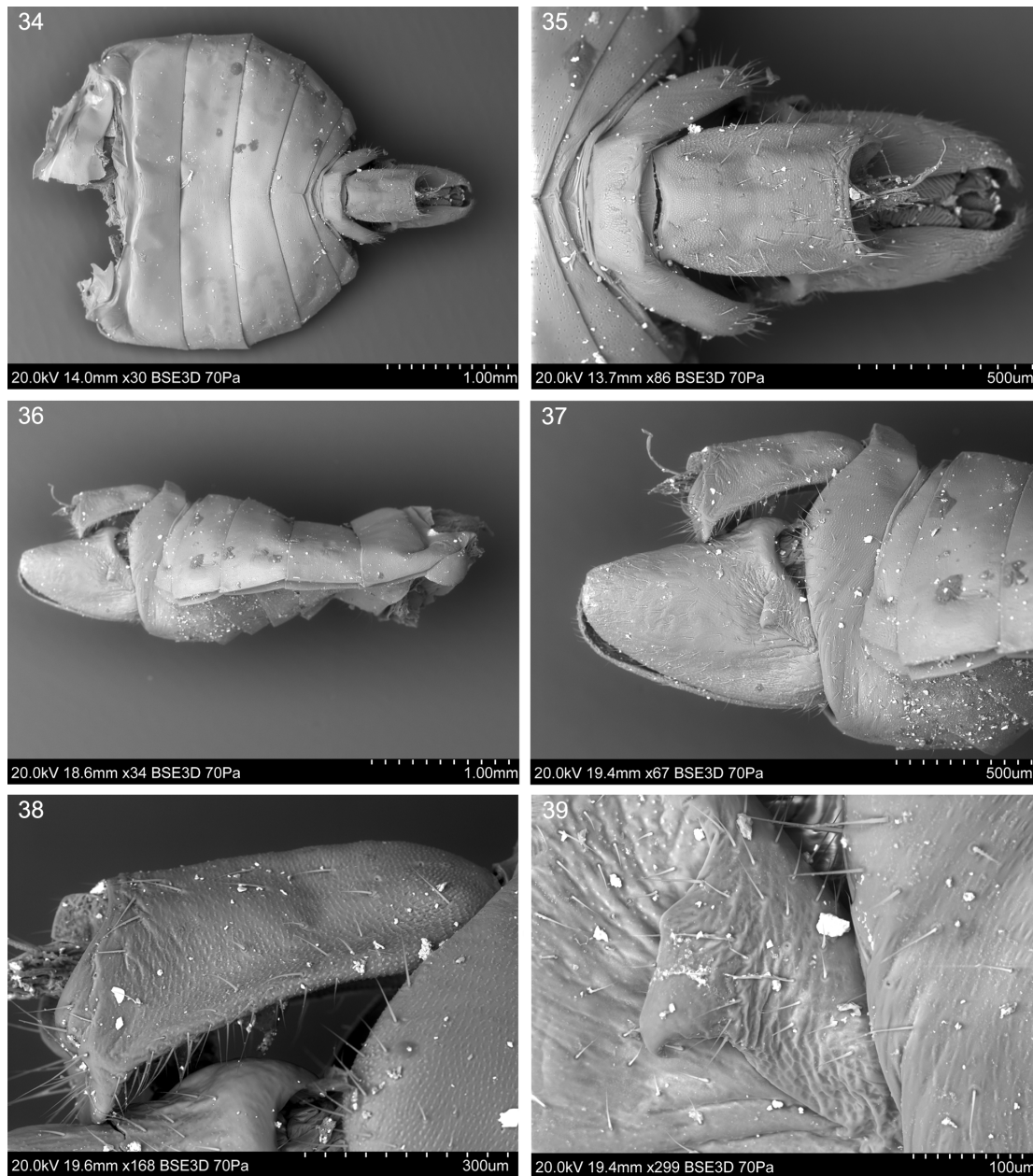
Phallic complex almost symmetrical, with periandrium composed of two dorsolateral membranous sacs, with ventroapical sclerotized hemicircular lobes and sclerotized, double spine-like processes present in laterobasal portion, dorsal spine distinctly bigger than ventral one; apical part of dorsal periandrium with two elongate, tapered, sclerotized processes. Aedeagus membranous sac-like, distinctly longer than periandrium, with double



row of longitudinal pine-like processes, increasing in size from aedeagus base and posterodorsal portion covered with spiniferous microsculpture.

Female unknown.

**Distribution.** Madagascar, Antsiranana Province, Sava Region (Fig. 55).



**FIGURES 34–39.** *Tupala occulta* gen. et sp. nov., holotype, male. (34) abdomen, dorsal view; (35) anal tube, dorsal view; abdomen, lateral view; (37) male terminalia, lateral view; (38) anal tube, lateral view; (39) hook-line process on gonostylus, lateral view.

***Tupala occulta* sp. nov.**

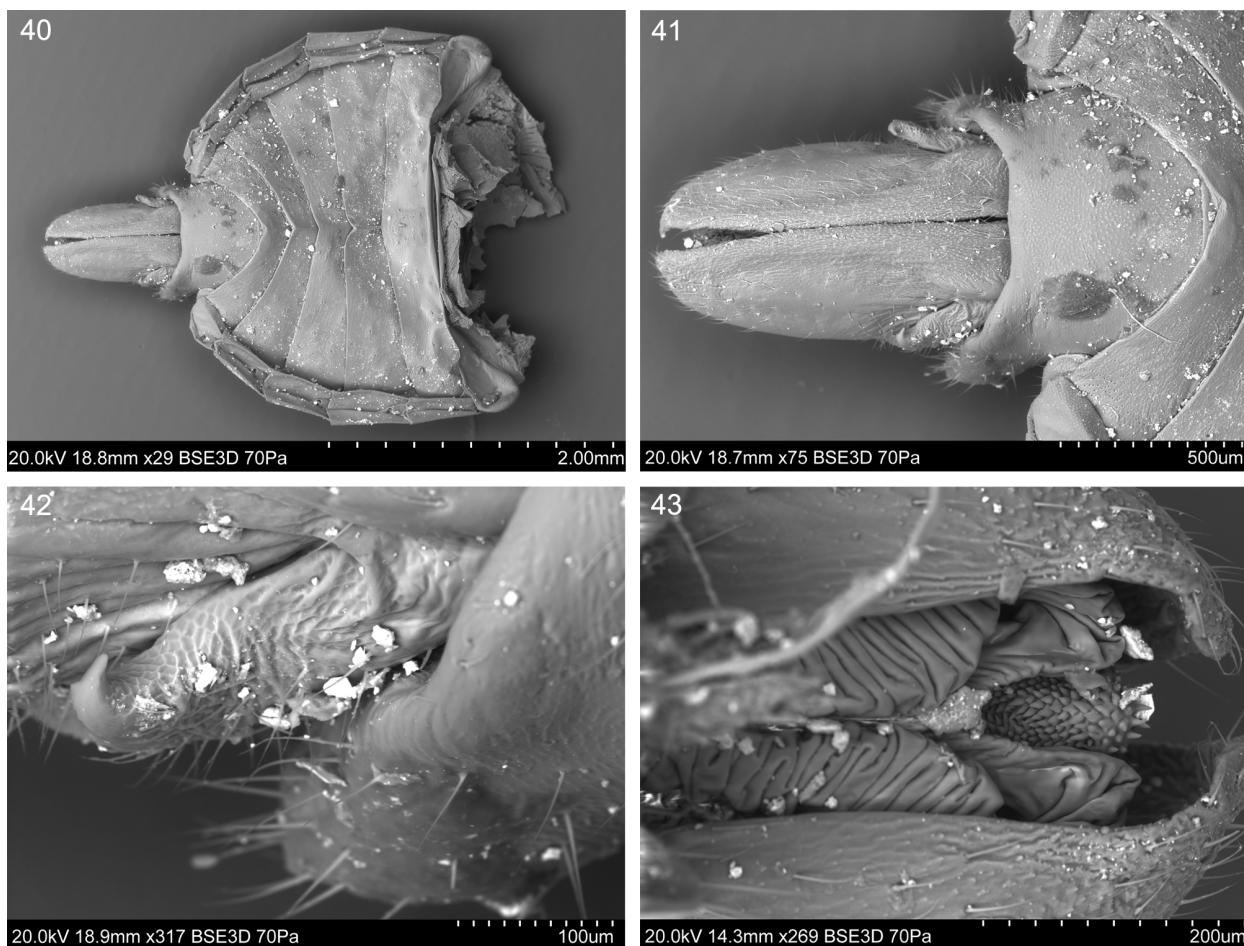
(Figs 1–50, 55)

**Etymology.** Specific epithet is derived from Latin ‘*occultus*’, meaning figuratively secret and refers to unclear provenance of the taxon (see Discussion).

**Diagnosis.** Face with lateral portions of frons yellowish; clypeus black. Tegmen with cell C1 shorter than cell C3; cell C5 more than twice as long as cell C3.

**Description.** General coloration dark brown. Lateral portion of frons yellowish, median streak brown; clypeus black. Lateral portion of head brownish, anterior portion of gena yellowish anteriorly; lora dark brown. Posterior margin of scutellum yellowish. Wings transparent, with brownish veins, indistinct lighter spots in median portion. Legs dark brown; metatibia brownish at base, yellowish toward apex. Ventral side of abdomen brown, dorsal side with pattern of spots and streaks. Anal tube brown, with lighter median band and yellowish apical margin. Genital styles brownish.

Total length 0.74–0.86 mm.



**FIGURES 40–43.** *Tupala occulta* gen. et sp. nov., holotype, male. (40) abdomen, dorsal view; (41) male terminalia, ventral view; (42) hook-line process on gonostylus, ventral view, (43) apex of aedeagus, dorsal view.

**Head.** Vertex: proportion A/B = 0.37–0.47, Frons: proportion C/E = 0.15–0.16, proportion D/E = 0.38–0.40.

**Thorax.** Pronotum: proportion F/B = 0.30–0.33; Mesonotum: proportion G/F = 2.82–2.85, proportion G/B+F = 0.55–0.70, proportion G/H = 0.68–0.70. Tegmina: proportion I/J = 2.95–3.11.

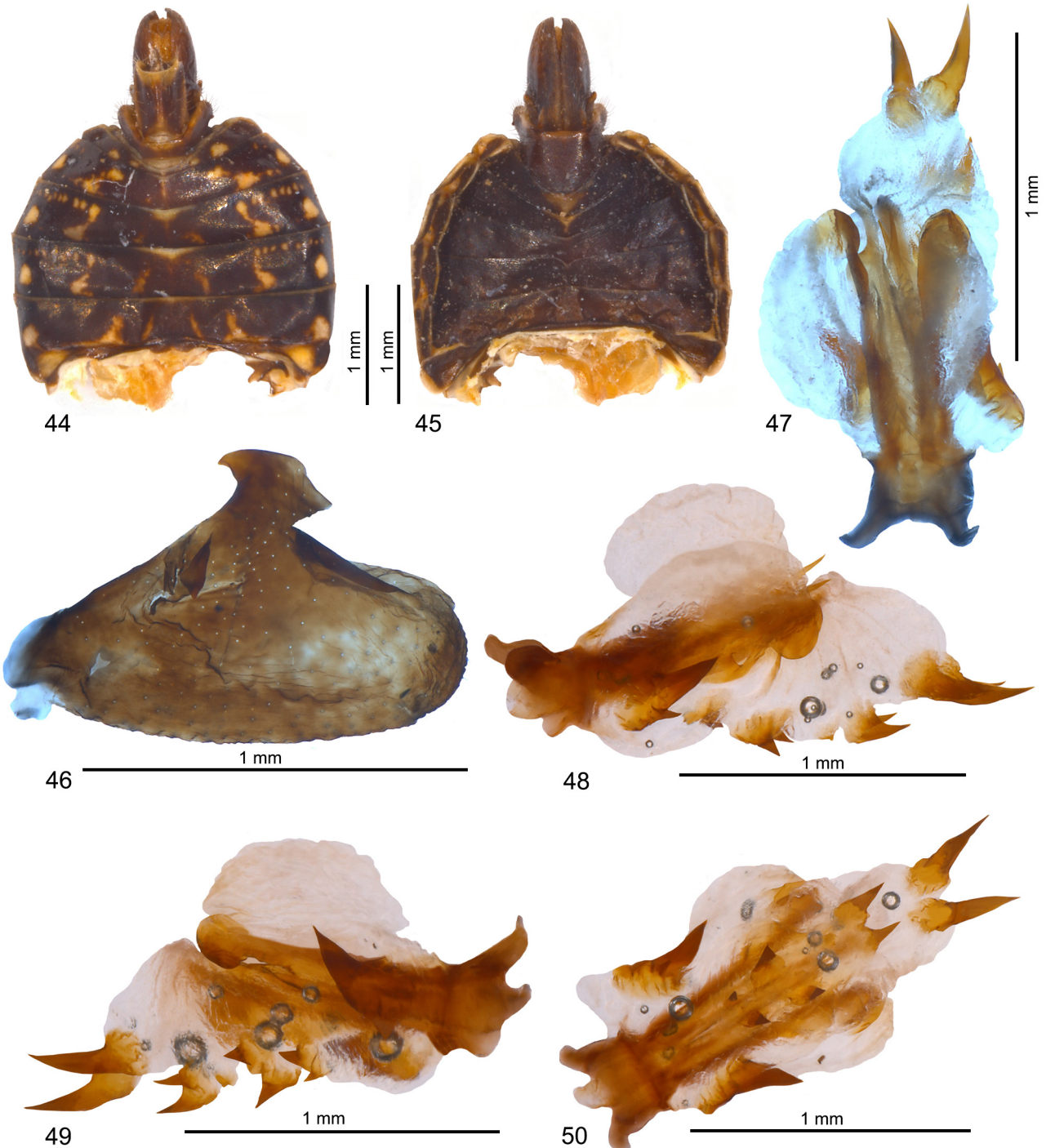
**Type locality and occurrence.** Madagascar, Antsiranana Province, Sava Region, Maroantsetra (Fig. 55).

**Type material.** Holotype male and 2 male paratypes, all labeled: [Coll. R.I.Sc.N.B. / Madagascar / Maroantsetra II-1919 / Ex. Coll. Le Moul]. Specimens deposited in Royal Belgian Institute of Natural Sciences, Brussels, Belgium.

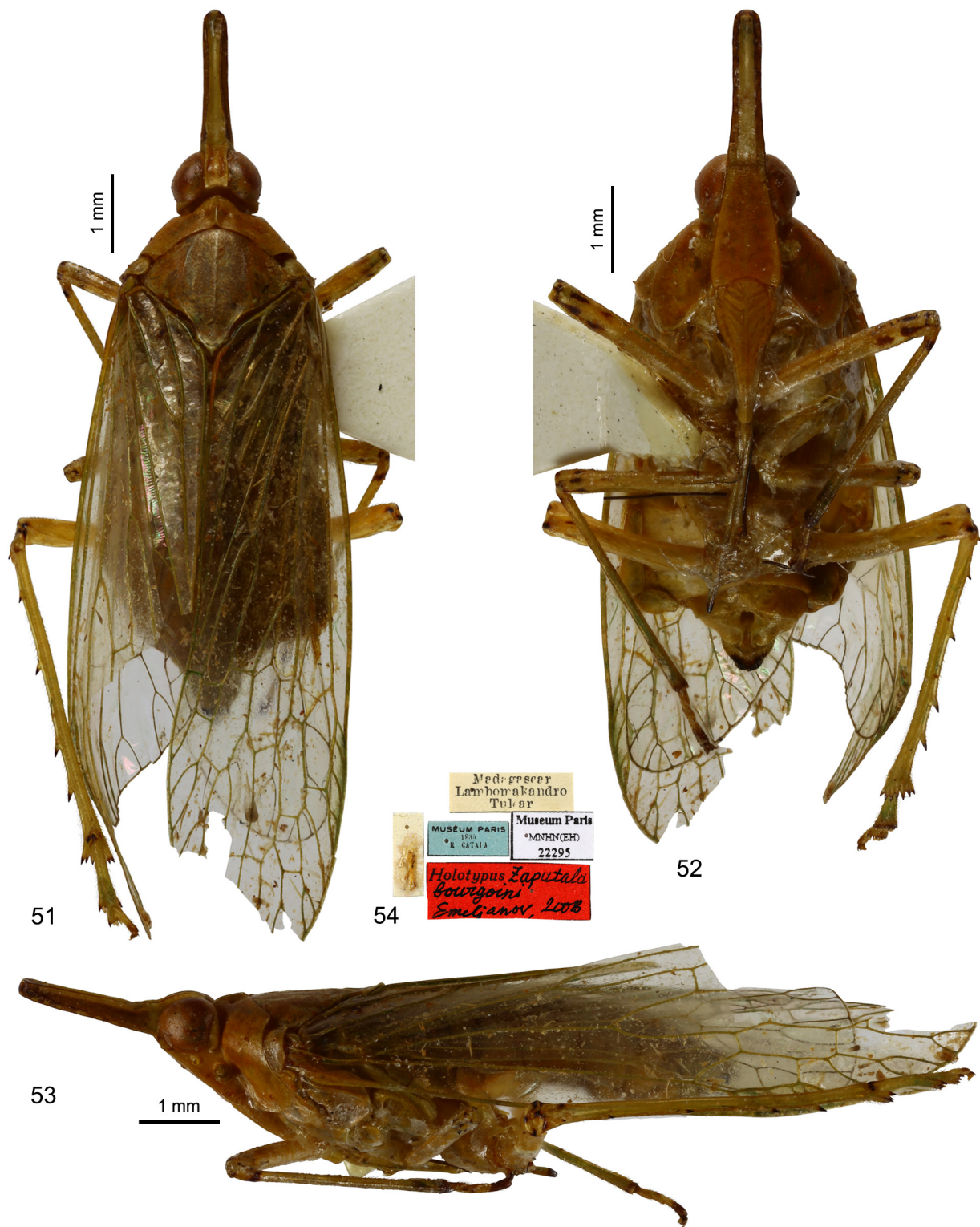
## Discussion

The described above taxon and its position as a new genus and species is causing some suspicions. It is taxon externally looking exactly as *Sicoris gayi* (Spinola, 1852) from Chile (*vide* Donovall 2008: Fig. 34). The specimens under our study comes from the collection of Eugène Le Moul (1882–1967), French naturalist and entomologist specialised in butterflies; hunter, businessman and collector. We have some doubts, that mislabeling of these

specimens probably occurred, as Le Moutt collected a lot in Southern America and received the material from other collectors as well. Alas, original description of Spinola (1852) gave no clear external and internal (genital structures) details enabling resolution of this question, prior to re-examination and preparation of the type material and/or other specimens coming from type locality. Second possibility is, that the specimens under scope of this study were incidental introduced from South America. Third explanation, the less probable in our opinion is that we have to deal with externally twin species, differing only by internal (sexual) structures, but see above. Anyhoo, the identity of *Tupala occulta* with *Sicoris gayi* (Spinola, 1852) calls for urgent studies.



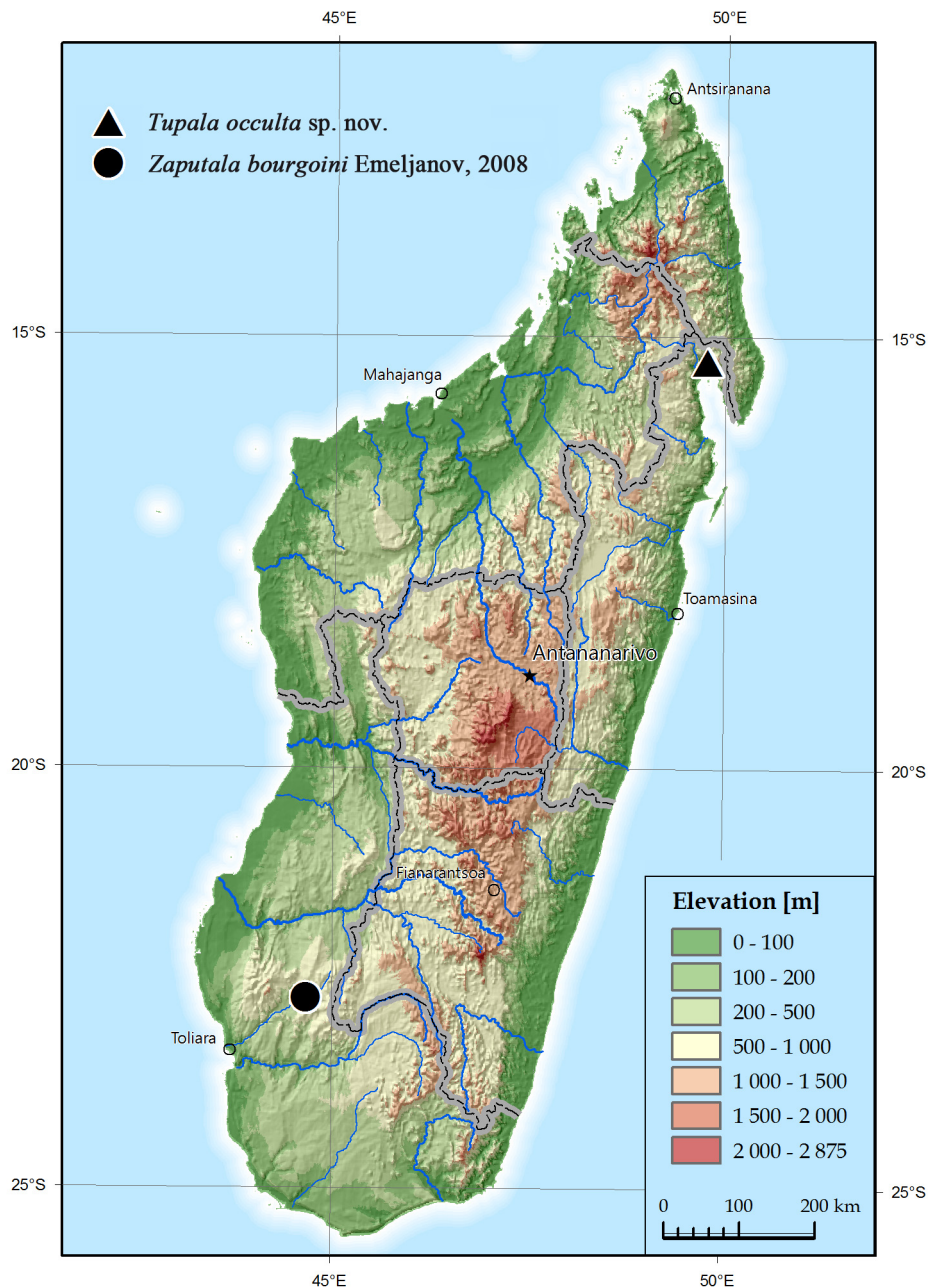
**FIGURES 44–50.** *Tupala occulta* gen. et sp. nov., holotype, male. (44–45) abdomen: (44) dorsal view, (45) ventral view; (46) gonostyles, lateral view; (47–50) aedeagus: (47) dorsal view, (48) lateral view, (49) ventrolateral view, (50) ventral view.



**FIGURES 51–54.** *Zaputala bourgoini* Emeljanov, 2008, holotype, female. (51) habitus, dorsal view; (52) same, ventral view; same, lateral view; (54) labels. Photo: Laurent Fauvre (MNHN, Paris).

The distribution of Dictyopharidae in continental Sub-Saharan Africa, Madagascar and adjacent areas is extremely uneven. Continental Sub-Saharan Africa hosts 104 known species of Dictyopharidae. These species are segregated between several tribes: Aluntini, Capenini, Orthopagini, Nersiini, Hastini, and majority of 80 known species is placed within Dictyopharini. Contrary, the Dictyopharidae of Madagascar are extremely scarce—*Aluntia hova* Nast, 1949 (Aluntini) and *Zaputala bourgoini* Emeljanov, 2008 (Dictyopharini) were known so far. The placement of *Mahanorona cowani* Distant, 1906 in Dictyopharidae remains not yet resolved. Also *Dictyophara*

*unicolor* Signoret, 1860 needs further taxonomic attention (work in progress). The Mascarenes houses no Dictyopharidae [sic!]. On the opposite side of the Indian Ocean, the Dictyopharidae of Oriental Asia are quite numerous. For the moment 95 species are counted, divided between tribes: Aluntini, Dictyopharini, Hastini, Nersini and Orthopagini, and with majority of species segregated between Orthopagini (50 species) and Dictyopharini (25 species).



**FIGURE 55.** Dictyopharini of Madagascar, distribution map.

Then, the reasons for extremely low diversity of Dictyopharidae in Madagascar claims for attention. Could it be the result of bias in collecting? We believe the answer should be rather negative. There were several expeditions and collectors exploring the fauna of Madagascar, specimens collected on the island are deposited in various institutions, so the Dictyopharidae should be present as well as other groups. Maybe biological properties of Dictyopharidae or their ecological interactions with environment could limit their presence in Madagascar? This question seems to be composed—we do not know much about the ecological requirements of the particular taxa. However, the family is widespread in high range of habitats, from dry to wet, from cool to tropical. It could be

assumed that the potential of the Dictyopharidae to be established in various types of habitats is high. Maybe the paucity of Dictyopharidae could be the result of competition with other group? This question remains open—no data are available to put hypotheses on such interactions. Continuing the question of ecological factors limiting Dictyopharidae diversity in Madagascar—maybe absence of suitable host plants could lay behind this scarcity? Dictyopharidae are reported as feeding on a variety of plants, with most species associated with dicotyledons, and are most often reported as monophagous (Wilson *et al.* 1994). But, dicotyledons is paraphyletic assemblage (APG III 2009; Stevens 2015), and all data available should be re-checked and re-considered. As hypothesized by Attié (2008) and already exemplified by Flatidae in Madagascar and Socotra (Stroiński & Świerczewski 2013, Świerczewski *et al.* 2014) and Ricaniidae in the Seychelles archipelago (Stroiński 2013), planthoppers, after reaching the island, present high adaptation potential for a host-plant diet, sufficiently large to overcome the high specificity of the botanical endemics and resulting in speciation. The linkage of the relaxation/inhibition of some ancestral constraints on feeding behavior, with the dispersion event, seems to be functional mechanism in the islands (Wang *et al.* 2014). Is paucity of Dictyopharidae in Madagascar result of young arrival of the group to the island with too short time for adaptation for more specific host plants? More precise data and further field studies will be necessary to answer this question.

Last but not least—the geological and biogeographical history of Madagascar. The island is result of the late Jurassic to upper Cretaceous fragmentation of Gondwana, during which Madagascar separated from Africa 183–158 Ma, from India 96–65 Ma and from Antarctica 130 Ma, with land bridges to this continent and thus connections to South America via Antarctica probably persisting until 90–80 Ma (Geiger *et al.* 2004; Noonan & Chippindale 2006; Ali & Aitchison 2008). The zoogeographical peculiarities of Madagascan fauna were widely deliberated (Lourenço 1996, Lourenço & Goodman 2000, Yoder & Nowak 2006, Agnarsson & Kuntner 2012). The current consensus is that combination of Cretaceous vicariance and Cenozoic dispersal shaped biogeographic history of Madagascar. The overseas dispersal of African founder individuals during the Cenozoic, from 65.5 million years ago (Ma) to the present (Yoder & Nowak 2006) is widely accepted opinion on the origins of many endemic lineages of the island. Radiations of these Malagasy lineages resulted in a wealth of endemic species, many of which are also a present a pattern of microendemism to small ranges within the landmass, leading to high spatial species turnover, as in many other tropical regions (Vences *et al.* 2009). The paucity of Dictyopharidae in Madagascar cannot be at the moment explained from the distributional data on these insects from continental Africa and oriental part of Asia, raising new questions and new research fields to explore.

Madagascar faces ongoing ecological devastation in the form of increased deforestation, mining and indiscriminate pesticide usage, resulting in massive erosion and environment degradation, which is rapidly decreasing viable habitats across the island. Due to this ecological degradation several species have likely already gone extinct. These circumstances create urgency in the scientific community to document the remaining biodiversity of the island, and to increase conservation efforts to maintain the few undisturbed natural areas of this biological hotspot.

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## References

- Agnarsson, I. & Kuntner, M. (2012) The generation of a biodiversity hotspot: Biogeography and phylogeography of the Western Indian Ocean islands. *In*: Anamthawat-Jónsson, K. (Ed.), *Current Topics in Phylogenetics and Phylogeography of Terrestrial and Aquatic Systems*. InTech Open, Rijeka/Shanghai, pp. 33–82.
- Ali, J.R. & Aitchison, J.C. (2008) Gondwana to Asia: plate tectonics, paleogeography and the biological connectivity of the Indian subcontinent from the Middle Jurassic through latest Eocene (166–35 Ma). *Earth Sciences Review*, 88, 145–166. <http://dx.doi.org/10.1016/j.earscirev.2008.01.007>

- APG III (2009) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. This paper was compiled by Bremer, B., Bremer, K., Chase, M.W., Fay, M.F., Reveal, J.L., Soltis, D.E., Soltis, P.S. & Stevens, P.F., who were equally responsible and listed here in alphabetical order only, with contributions from Anderberg, A.A., Moore, M.J., Olmstead, R.G., Rudall, P.J., Sytsma, K.J., Tank, D.C., Wurdack, K., Xiang, J.Q.-Y. & Y Zmarzly, S. (in alphabetical order). *Botanical Journal of the Linnean Society*, 161, 105–121.
- Attié, M., Bourgoïn, T., Veslot, J. & Soulier-Perkins, A. (2008) Patterns of trophic relationships between planthoppers (Hemiptera: Fulgoromorpha) and their host plants on the Mascarene Islands. *Journal of Natural History*, 42 (23), 1591–1638.  
<http://dx.doi.org/10.1080/00222930802106963>
- Bartlett, C.R., O'Brien, L.B. & Wilson, S.W. (2014) A review of the planthoppers (Hemiptera: Fulgoroidea) of the United States. *Memoirs of the American Entomological Society*, 50, 1–287.
- Bodenheimer, F.S. (1937) Prodrômus faunae Palaestinae: essai sur les éléments zoogéographiques et historiques du sud-ouest du sous-regne paléarctique. *Mémoires présentés à l'Institut d'Égypte*, 33, 1–286.
- Bourgoïn, 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, 555–564.
- Bourgoïn, T. (1993) Female genitalia in Hemiptera Fulgoromorpha, morphological and phylogenetic data. *Annales de la Société Entomologique de France, Nouvelle Série*, 29, 225–244.
- Bourgoïn, T. (2015) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8, updated 3 September 2015. Available from: <http://hemiptera-databases.org/flow/> (accessed 3 September 2015)
- Bourgoïn, T., Wang, R.R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroiński, A., Yap, S. & Szwedlo, J. (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns of planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology*, 134 (1), 63–77.  
<http://dx.doi.org/10.1007/s00435-014-0243-6>
- Carayon, J. (1969) Emploi du noir chlorazol en anatomie microscopique des insectes. *Annales de la Société Entomologique de France, Nouvelle Série*, 5, 179–193.
- Donovall, L.R. (2008) A generic revision of the New World Dictyopharinae (Hemiptera: Dictyopharidae). Masters Thesis. University of Delaware, Newark, Delaware, x+401 pp.
- Donovall, L.R. & Bartlett, C.R. (2005) The phylogenetic relationships among the higher taxa of the Dictyopharidae (Hemiptera: Fulgoroidea). *Abstracts of the 12<sup>th</sup> International Auchenorrhyncha Congress and the 5<sup>th</sup> International Workshop on Leafhoppers and Planthoppers of Economic Importance, University of California, Berkeley, California, USA, 8–12 August 2005, Posters P-20.*
- Emeljanov, A.F. & Shcherbakov, D.E. (2005) Planthoppers: from the Permian to Cenozoic. *Programme and Abstracts 3<sup>rd</sup> International Congress of Palaeoentomology with 2<sup>nd</sup> International Meeting on Palaeoarthropodology and 2<sup>nd</sup> World Congress on Amber and its Inclusions, 7<sup>th</sup>–11<sup>th</sup> February 2005, Pretoria, South Africa, 17–18.*
- Emeljanov, A.F. (1969) Reklassifikatsia nosatok podsemeïstva Orgeriinae palearkticheskoï fauny (Homoptera, Dictyopharidae). *Entomologicheskoe Obozrenie*, 48 (2), 324–339. [in Russian] Published in English as: Yemel'yanov, A. F. (1969) Reclassification of Palearctic planthoppers of the subfamily Orgeriinae (Homoptera, Dictyopharidae).—*Entomological Review*, 48 (2), 189–198.
- Emeljanov, A.F. (1979) Problema razgranicheniya semeïstv Fulgoridae i Dictyopharidae (Homoptera, Auchenorrhyncha). [To the problem of division of the families Fulgoridae and Dictyopharidae (Homoptera, Auchenorrhyncha)]. *Trudy Zoologicheskogo Instituta Akademii Nauk SSSR*, 82, 3–22. [in Russian]
- Emeljanov, A.F. (1980) Filogeniya i evolyutsiya nosatok podsemeïstva Orgeriinae (Homoptera, Dictyopharidae). [Phylogeny and evolution of subfamily Orgeriinae (Homoptera, Dictyopharidae)]. *Doklad na tridtsat' vtorom ezhegodnom chtenii pamyatii N.A. Kholodkovskogo, 10 aprelya 1979 g.*, 32, 3–96. [in Russian]
- Emeljanov, A.F. (1983) Nosatka iz mela Taïmyra (Insecta, Homoptera). *Paleontologicheskii Zhurnal*, 3, 79–85. Published in English as: Yemel'yanov, A.F. (1984) Dictyopharidae from the Cretaceous deposits on the Taymyr Peninsula (Insecta, Homoptera). *Paleontological Journal*, 17 (3), 77–82.
- Emeljanov, A.F. (1997) A new genus and species of the Dictyopharidae from Australia belonging to a new tribe (Homoptera, Cicadina). *Zoosystematica Rossica*, 6 (1/2), 77–82.
- Emeljanov, A.F. (2004) A new genus and tribe of Strongylodematinae (Homoptera: Fulgoridae). *Zoosystematica Rossica*, 13 (1), 52.
- Emeljanov, A.F. (2006) Taxonomic changes in American Orgeriinae (Homoptera: Dictyopharidae). *Zoosystematica Rossica*, 15 (1), 73–76.
- Emeljanov, A.F. (2007) Sostav i puti formirovaniya fauny osnovnykh zoogeograficheskikh oblastei (tsarstv) v semeïstve Dictyopharidae (Homoptera, Fulgoroidea). *Problemy i perspektivy obshchei entomologii. Tezisy dokladov 13 s'ezda Russkogo entomologicheskogo obshchestva, Krasnodar, 9–15 sentyabrya 2007* (Structure and ways of formation of faunae of the main zoogeographical regions (kingdoms) in the family Dictyopharidae (Homoptera, Fulgoroidea). *Problems and Perspectives of General Entomology. Abstract XIII<sup>th</sup> Congress of Russian Entomological Society, Krasnodar, September 9–15, 2007*), 103–104. [in Russian]
- Emeljanov, A.F. (2008) Novye rody i vidy sem. Dictyopharidae (Homoptera) s zamechaniyami o sistematike podsem.

- Dictyopharinae. *Entomologicheskoe Obozrenie*, 87 (2), 360–396. [in Russian, published in English as: Emeljanov, A.F. (2008) New genera and species of the family Dictyopharidae (Homoptera), with notes on the systematics of the subfamily Dictyopharinae. *Entomological Review*, 88 (3), 296–328.]  
<http://dx.doi.org/10.1134/S0013873808030056>
- Emeljanov, A.F. (2011) Utochnennoe delenie podsem. Dictyopharinae na triby i opisaniya novykh rodov i vidov (Homoptera, Dictyopharidae). *Entomologicheskoe Obozrenie*, 90 (2), 299–328. [in Russian, published in English as: Emeljanov, A.F. (2011) Improved tribal delimitation of the subfamily Dictyopharinae and description of new genera and new species (Homoptera, Fulgoroidea, Dictyopharidae). *Entomological Review*, 91 (9), 1122–1145.]  
<http://dx.doi.org/10.1134/S0013873811090053>
- Emeljanov, A.F. (2013) Novyĭ vid roda *Pibrocha* Kirkaldy (Homoptera, Fulgoridae) i zamechaniya o sisteme podsem. Dichopterinae s opisaniem novoĭ triby. *Entomologicheskoe Obozrenie*, 92 (1), 123–129 [in Russian, published in English as Emeljanov, A.F. (2013) A new species of the genus *Pibrocha* Kirkaldy (Homoptera, Fulgoridae) with notes on the systematics of the subfamily Dichopterinae and with description of a new tribe. *Entomological Review*, 93 (6), 775–780.]  
<http://dx.doi.org/10.1134/S0013873813060092>
- Emeljanov, A.F., Kuznetsova, V.G., Nokkala, C. & Nokkala, S. (2005) Phylogeny and evolution of the subfamily Orgeriinae (Homoptera, Dictyopharidae). *Abstracts of the 12<sup>th</sup> International Auchenorrhyncha Congress and the 5<sup>th</sup> International Workshop on Leafhoppers and Planthoppers of Economic Importance. University of California, Berkeley, California, USA, 8–12 August 2005, Symposia S15–S16.*
- Fennah, R.G. (1967) New and little known Fulgoroidea from South Africa (Homoptera). *Annals of Natal Museum*, 18 (3), 655–714.
- Geiger, M., Clark, D.N. & Mette, W. (2004) Reappraisal of the timing of the breakup of Gondwana based on sedimentological and seismic evidence from the Morondava Basin, Madagascar. *Journal of African Earth Sciences*, 38 (4), 363–381.  
<http://dx.doi.org/10.1016/j.jafrearsci.2004.02.003>
- Jacobi, A. (1917) Die Zikadenfauna Madagascars und der Comoren. In: *Reise in Ostafrika in den Jahren 1903-1905 mit Mitteln der Hermann und Elise geb. Heckmann Wentzel-Stiftung ausgeführt von Professor Dr. Alfred Voeltzkow*, Wissenschaftliche Ergebnisse Band 3, Systematische Arbeiten, pp. 519–552.
- Kuznetsova, V.G. (1985) Filogeneticheskiĭ analiz khromosomnoĭ izmenchivosti i kariosystematika tsikadovykh sem. Dictyopharidae (Homoptera, Auchenorrhyncha). [Phylogenetic analysis of chromosome variability and karyosystematics of Cicadina of the family Dictyopharidae (Homoptera, Auchenorrhyncha).] *Entomologicheskoe Obozrenie*, 65 (3), 539–553. [in Russian]
- Kuznetsova, V.G., Maryńska-Nadachowska, A. & Emeljanov, A.F. (2009) A contribution to the karyosystematics of the planthopper families Dictyopharidae and Fulgoridae (Hemiptera: Auchenorrhyncha). *European Journal of Entomology*, 106 (2), 159–170.  
<http://dx.doi.org/10.14411/eje.2009.019>
- Lallemand, V. (1950) Contribution à l'étude des Homoptères de Madagascar. *Mémoire de l'Institut Scientifique de Madagascar*, 4A, 83–95.
- Lethierry, L.F. (1889) Contributions à la faune Algérienne. Liste des Hémiptères recueillis par M. Desbrochers des Loges et description des espèces nouvelles. *Revue d'Entomologie*, 8, 310–318.
- Lourenço, W.R. & Goodman, S.M. (Eds.) (2000) *Diversité et endémisme à Madagascar*. Mémoires de la Société de Biogéographie, Paris, vi + 379 pp.
- Lourenço, W.R. (Ed.) (1996) *Biogéographie de Madagascar*. ORSTOM, Paris, x + 588 pp.
- Melichar, L. (1912) Monographie der Dictyophorinen (Homoptera). *Abhandlungen der K. K. Zoologisch-botanischen Gesellschaft in Wien*, 7 (1), 1–221.
- Metcalf, Z.P. (1946) Part 8. Dictyopharidae. *General Catalogue of the Homoptera. Fascicule IV*, Smith College, Northampton, Mass, pp. 1–246.
- Noonan, B.P. & Chippindale, B.T. (2006) Vicariant origin of Malagasy reptiles supports Late Cretaceous Antarctic land bridge. *American Naturalist*, 168 (6), 730–741.  
<http://dx.doi.org/10.1086/509052>
- Puton, A. (1892) Hémiptères nouveaux ou peu connus et notes diverses. *Revue d'Entomologie*, 11, 24–31.
- Schmidt, E. (1915) Die Dictyopharinen des Stettiner Museums. (Hemiptera-Homoptera). *Entomologische Zeitung, Stettin*, 76, 345–358.
- Shcherbakov, D.E. & Popov, Yu A. (2002) Superorder Cimicidea Laichartang, 1781 Order Hemiptera Linné, 1758. The bugs, cicadas, plantlice, scale insects, etc. In: Rasnitsyn, A.P. & Quicke, D.L.J. (Eds.), *History of Insects*. Kluwer Academic Publishers, Dordrecht, pp. 143–157
- Signoret, V. (1860) Faune des hémiptères de Madagascar. 1<sup>ère</sup> partie. Homoptères. *Annales de la Société Entomologique de France*, Series 3, 8, 177–206.
- Spinola, M. (1852) Tribu IV. Hipocefalocera. *Gay's Historia fisica y politica de Chile*, 7, 238–305.
- Stevens, P.F. (2015) Angiosperm Phylogeny Website. Version 12, July 2012 [and more or less continuously updated since]. Page last updated: 29 August 2015. Available from: <http://www.mobot.org/MOBOT/research/APweb/> (accessed 4 September 2015)
- Stroiński, A. (2013) A new extraordinary genus of Ricaniidae from the Seychelles (Hemiptera: Fulgoromorpha). *Annales*



*Zoologici*, 63 (1), 57–69.

<http://dx.doi.org/10.3161/000345413X666101>

Stroiński, A. & Świerczewski, D. (2013) *Peyrierasus* gen. nov.—a new genus of Flatidae (Hemiptera: Fulgoromorpha) from southeastern Madagascar. *Annales Zoologici*, 63 (2), 251–262.

<http://dx.doi.org/10.3161/000345413X669559>

Świerczewski, D., Malenovsky, I. & Stroiński A. (2014) *Kirkamflata*, a new planthopper genus from Socotra Island (Hemiptera: Fulgoromorpha: Flatidae). *Annales Zoologici*, 64 (3), 517–534.

<http://dx.doi.org/10.3161/000345414X684830>

Szwedo, J. (2008) A new tribe of Dictyopharidae planthoppers from Eocene Baltic amber (Hemiptera: Fulgoromorpha: Fulgoroidae), with a brief review of the fossil record of the family. *Palaeodiversity*, 1, 75–85.

Vences, M., Wollenberg, K.C., Vieites, D.R. & Lees, D.C. (2009). Madagascar as a model region of species diversification. *Trends in Ecology and Evolution*, 24 (8), 456–465.

<http://dx.doi.org/10.1016/j.tree.2009.03.011>

Wang, R.R., Stroiński, A., Szwedo, J., Bourgoin, T. & Liang, A.P. (2014) Recent dispersal and diet relaxation might explain the monotypic and endemic genus *Montrouzierana* Signoret, 1861 in New Caledonia (Hemiptera: Fulgoromorpha: Tropiduchidae). *Annales Zoologici*, 64 (4), 693–708.

<http://dx.doi.org/10.3161/000345414X685974>

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

Yoder, A.D. & Nowak, M.D. (2006) Has vicariance or dispersal been the predominant biogeographic force in Madagascar? Only time will tell. *Annual Review of Ecology Evolution and Systematics*, 37, 405–431.

<http://dx.doi.org/10.1146/annurev.ecolsys.37.091305.110239>