

Makaya gen. nov. (Hemiptera: Fulgoromorpha: Flatidae) from dry forests in western Madagascar

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Abstract: A new monospecific genus of flatid planthoppers (Hemiptera: Fulgoromorpha: Flatidae), *Makaya* gen. nov., is described for *Makaya voluntary* sp. nov. (type species) from the island of Madagascar. Habitus, male and female external and internal genital structures of the new species are illustrated and compared with related taxa. *Makaya voluntary* is endemic to Madagascar where it is currently known from different types of dry forests in the western part of the island.

Key words: Afrotropical, Fulgoroidea, systematics, taxonomy, new species

Introduction

Within the planthoppers Fulgoromorpha Evans, 1946, the Flatidae are the fourth largest family of the suborder. With 297 genera and 1445 species, they respectively represent 11,9% and 10,4% of the known taxa in planthoppers (Bourgoin 2021). Although the family is widely distributed, it is mostly diverse in all regions of the tropics and far less diverse in the Holarctic (Bartlett *et al.* 2018). As planthoppers, Flatidae are obligatory phytophagous taxa, mostly oligophagous and sap sucking on a great variety of Eudicots plants predominantly Fabiales (17,3%), Lamiales (12%), Caryophyllales (10,7%) and Rosales (6,7%) (Bourgoin 2021). The diagnostic characters of the family include numerous crossveins paralleling the distal margin of the tegmina defining a series of marginal cells in its apical and leading portion and with wax-bearing pustules in its claval region that often coat their wings with a dusting of wax. Nymphs often exhibit long and floccose whitish wax filaments.

The family is divided into two easily distinguishable subfamilies: Flatinae Spinola,

1839 and Flatoidinae Melichar, 1901. In Madagascar, Flatidae are represented by 22 genera with 53 species of Flatinae, and by 11 genera with 41 species for Flatoidinae. Within Flatinae, Madagascan Selizini Distant, 1906, are represented by six genera and nine species, mostly associated with dry habitats in the western part of the island. The review of all these taxa can be found in the recent paper of Świerczewski & Stroiński (2021). An additional monospecific new genus, *Makaya* gen. nov., is described here for *Makaya voluntary* sp. nov. (type species), which is associated with dry forests of western Madagascar.

Material and Methods

Material: The type specimens are deposited in the following collections:

CAS – California Academy of Sciences, Department of Entomology, San Francisco (USA)

MNHN – Muséum national d'Histoire naturelle, Paris (France)

MIZ – Museum and Institute of Zoology PAS, Warsaw (Poland).

Label information of all specimens examined is in square brackets and provided *verbatim* with each line separated by a slash (/).

Preparations and illustrations: CAS specimens were originally preserved in 70% ethanol, and were subsequently dried and pinned; MNHN specimens were originally collected dried and were subsequently pinned. The abdomens of the examined specimens were removed and cleared for 30 minutes in warm (50°C) 10% KOH solution with a few drops of chlorazol black (CAS No. 1937-37-7) for staining the ectodermic structures based on the method introduced by Carayon (1969) and adapted by Bourgoïn (1993). Dissections and cleaning of genital structures were performed in distilled water. Final observations and drawings of genital structures were done in glycerol using a camera lucida attached to a light microscope. The SEM photographs of dry, uncoated specimens were taken in the Laboratory of Scanning Microscopy, Museum and Institute of Zoology, Polish Academy of Sciences (Warsaw), using a scanning electron microscope HITACHI S-3400N under low vacuum conditions.

Descriptions of external characters of head, thorax and abdomen were based on SEM photographs, whereas descriptions of male and female terminalia were based on macerated and stained structures.

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

Total length – length of specimen from anterior margin of head to tegmina apex (in dorsal view);

A/B = width of vertex at anterior 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 at midline / length of vertex at midline;

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

G/B+F = length of mesonotum at midline / 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 from the base to the apical margin in median portion / width of tegmen measured from the apex of clavus to the anterior margin;

I/K = length of tegmen from the base to the apical margin in median portion / width of tegmen at the widest part.

Terminology: The nomenclature of the forewing (tegmen) veins follows the interpretation proposed by Bourgoïn *et al.* (2015). Antennal structures are named in accordance with Stroiński *et al.* (2011). The terminology of the genitalia follows Bourgoïn (1988) updated in Bourgoïn & Huang (1990) for the male, and Bourgoïn (1993) for the female. The metatibiotarsal formula LT-T/Mt1/Mt2 provides the number of teeth on the side of the metatibia LT- on the apex of metatibia T, eventually distributed in two groups of internal Ti and external Te teeth, separated with a diastema (Ti-Te) / on the apex of the first metatarsomere Mt1 / on the apex of the second metatarsomere Mt2 (Luo *et al.* 2021).

Systematics

Class Insecta Linnaeus, 1758

Order Hemiptera Linnaeus, 1758

Suborder Fulgoromorpha Evans, 1946

Superfamily Fulgoroidea Latreille, 1810

Family Flatidae Spinola, 1839

Subfamily Flatinae Spinola, 1839

Tribe Selizini Distant, 1906

Makaya gen. nov.

(Figs 1–7)

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Type species. *Makaya voluntary* sp. nov., here designated.

Diagnostic characters. The new genus differs from other Selizini genera by the following characters:

1) wings subrectangular (wings strongly constricted apically in *Stenocyarda* Fennah, 1965);

2) frons without median carina, mesonotum without gibbosities (frons with Y-shaped median carina, mesonotum with four gibbosities in *Urana* Melichar, 1902);

3) dorsal part of periandrium bilobate (dorsal part of periandrium trilobate in *Kelyflata* Świerczewski & Stroiński, 2019 and unilobate in *Selizitapia* Świerczewski & Stroiński, 2021);

4) processes of aedeagus located apically (processes of aedeagus located subapically in *Lembakaria* Świerczewski & Stroiński, 2019);

5) lateral split of periandrium exceeding $\frac{1}{3}$ of its length (lateral split of periandrium reaching $\frac{1}{3}$ of its length in *Peyrierasus* Stroiński & Świerczewski, 2013).

Description. Head with compound eyes, in dorsal view, slightly narrower than thorax. Vertex transverse, without carinae; anterior and posterior margins at the same level, carinate, anterior margin slightly elevated medially, posterior margin linear, widened medially; lateral margins carinate and parallel (Figs 1B, D, F, 2 A–E).

Frons convex, widest at its lower third in frontal view; lateral margins carinate, sinuate and strongly elevated, without incisions; upper margin weakly concave medially; disc of frons without carinae, with two lateral ridges and one transverse ridge; lateral ridges sinuate, widening downwards, transverse ridge straight, connected with lateral ridges in upper part of frons; central area of disc

concave; frontoclypeal suture strongly arcuate (Fig. 2A–E).

Clypeus smooth, convex, without carinae (Fig. 2C). Rostrum with apical segment shorter than subapical one, apex reaching hind coxae level. Compound eyes oval, with narrow callus at posterior margin. Lateral ocelli present (Fig. 3A–B). Antennae placed very close to medio-ventral margin of eyes; scapus small, ring-like, with single seta; pedicel shorter than diameter of eye but distinctly longer than scapus, bulbous, functional area at the top, on dorsal and ventral surface with trichoid sensilla type 1, antennal plate organs present on apical concavity and basally delimiting lateral margins of dorsal functional surface (Fig. 3A–F).

Thorax. Pronotum, in dorsal view, distinctly shorter than mesonotum at midline: anterior margin strongly arcuate with median portion almost straight, lateral parts elevated; posterior margin concave medially, distinctly higher than anterior margin; disc of pronotum without carinae and lateral impressions but with shallow median groove; postocular eminences conical (Figs 1B, D, F; 2 A–E).

Mesonotum with scutellum widely deltoid, almost as long as wide, anterior part slightly humped, posterior part flattened, scutellum with elevated apex; disc of mesonotum with median shallow groove almost reaching scutellum and lateral carinae; lateral carinae incomplete, parallel, well-visible in posterior part, connected with posterior margin (Figs 1B, D, F; 2 A, C, F).

Vertex, disc of pronotum and disc of mesonotum in ascending, stepwise planes (Figs 1 A, C, E; 3 A; 4 A).

Tegmina longer than wide, subrectangular, with distinct venation and bulla; scarce, irregularly placed transverse veinlets mainly in apical part; nodal line weak and irregular, subapical line more regular; costal margin sinuate, costal and sutural angle rounded, apical margin slightly rounded, postclaval sutural margin convex. Costal area with dense transverse veinlets, ending at the level of tip

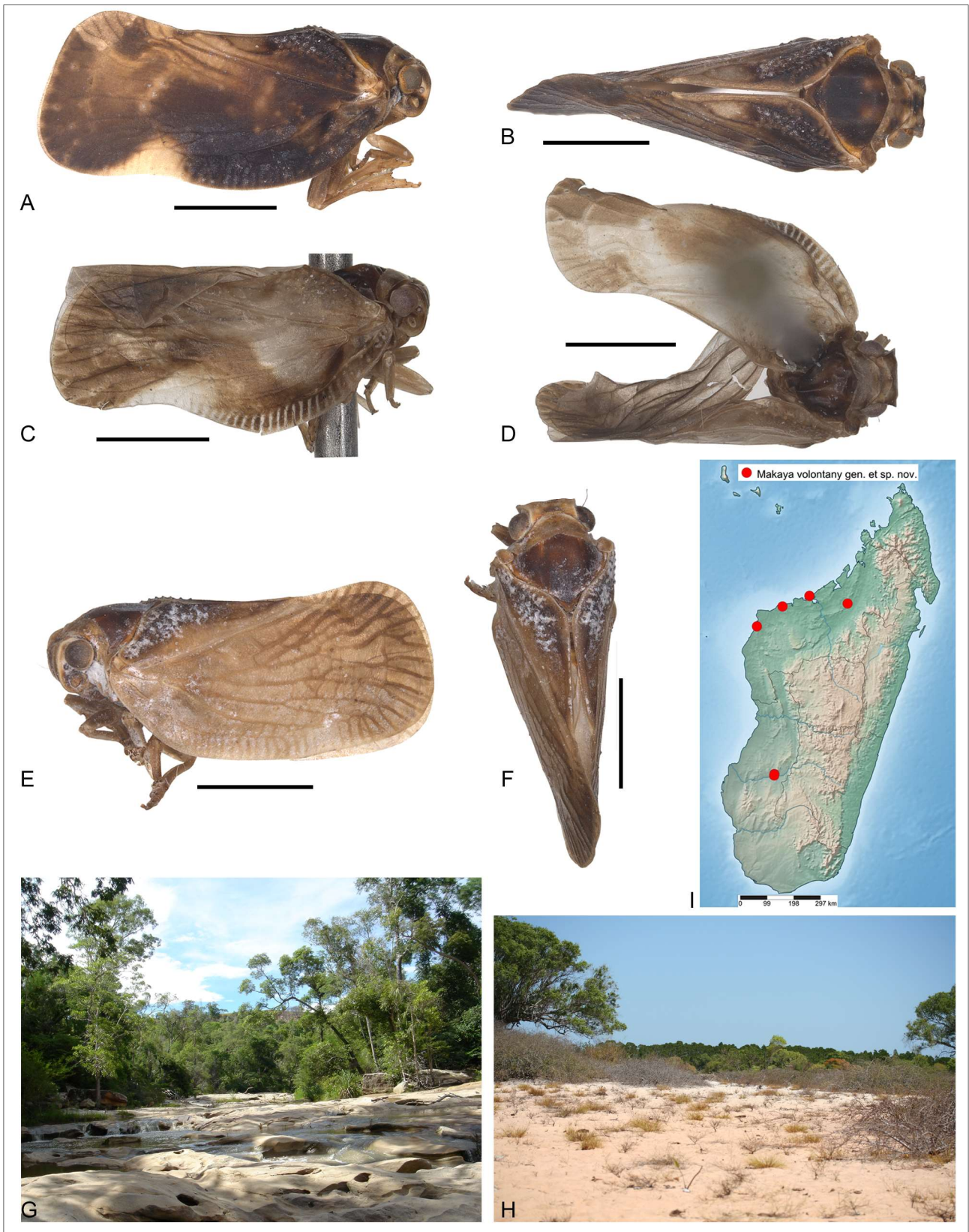


Fig. 1. *Makaya voluntany* gen. et sp. nov.: A, B) Holotype (locality 6), habitus – lateral and dorsal view; C, D) paratype (locality 1), habitus – lateral and dorsal view; E, F) paratype (locality 3), habitus – lateral and dorsal view; G) environment of locus typicus (locality 6) – the Makay massif (massif du Makay), photo by D. Ouvrard; H) environment of locality 3 – region of Antrema, photo by D. Ouvrard; I) distribution map (localities 2 and 3 as one dot). Scale bar = 1.5 mm.

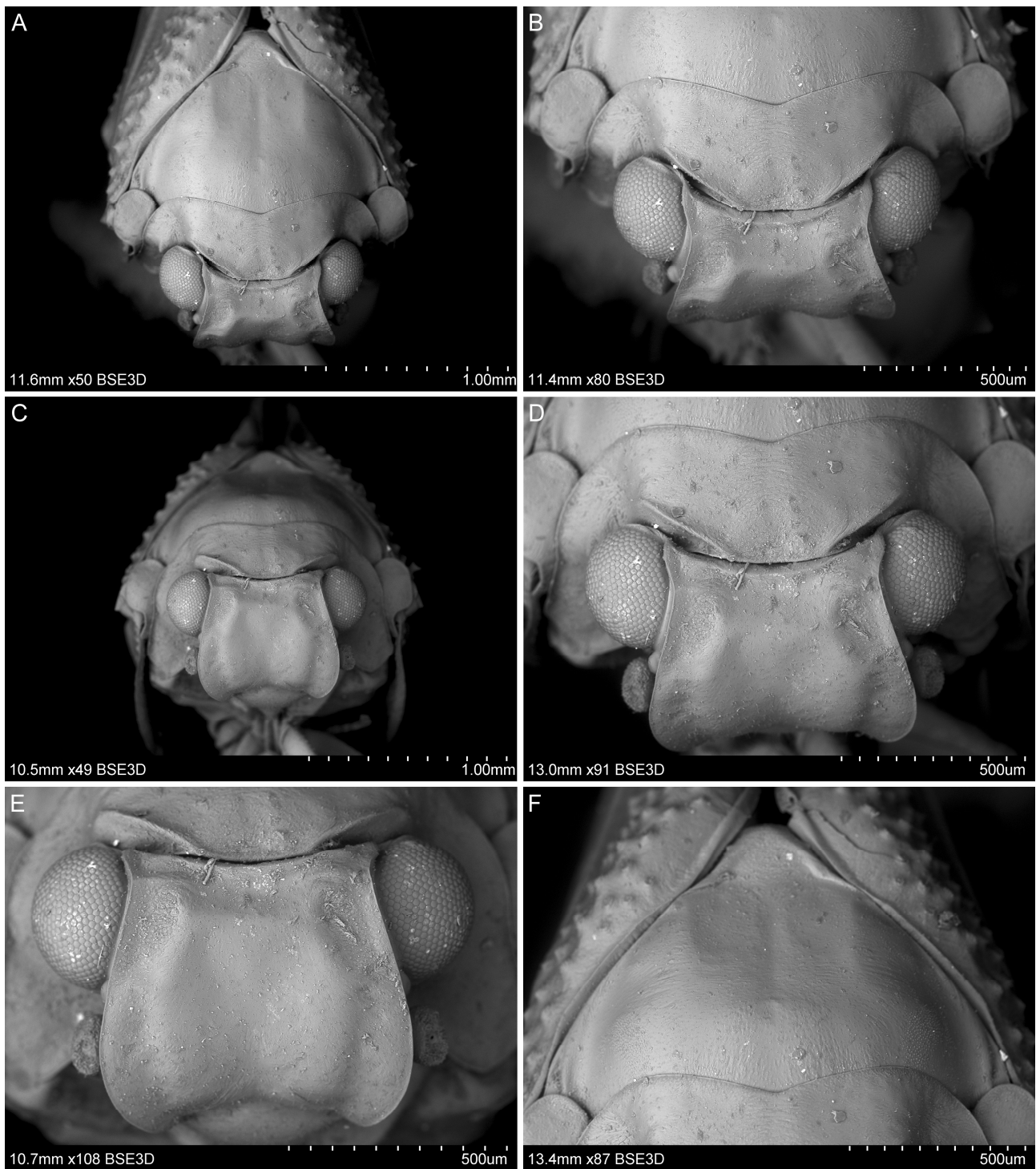


Fig. 2. *Makaya voluntany* gen. et sp. nov., holotype, SEM photographs: A) anterior part of body, dorsal view; B) head and pronotum, dorsal view; C) anterior part of body, frontal view; D) upper part of head and pronotum, fronto-dorsal view; E) head, frontal view; F) mesonotum, dorsal view.

of clavus. Costal cell about the same width as costal area (at the level of bulla), tapering apicad. Basal cell long and narrow (Figs 4A–B).

Tegmen with longitudinal veins ScP+RA and RP arising as short common stem, diverging just before bulla: ScP+RA vein crossing the top

of bulla, RP vein passing near the base of bulla; RP fork placed distinctly before ScP+RA fork but after MP and CuA forks; MP vein placed much closer to ScP+RA and RP stem than to CuA vein; MP and CuA forks about the level of the end of claval wax glands plate;

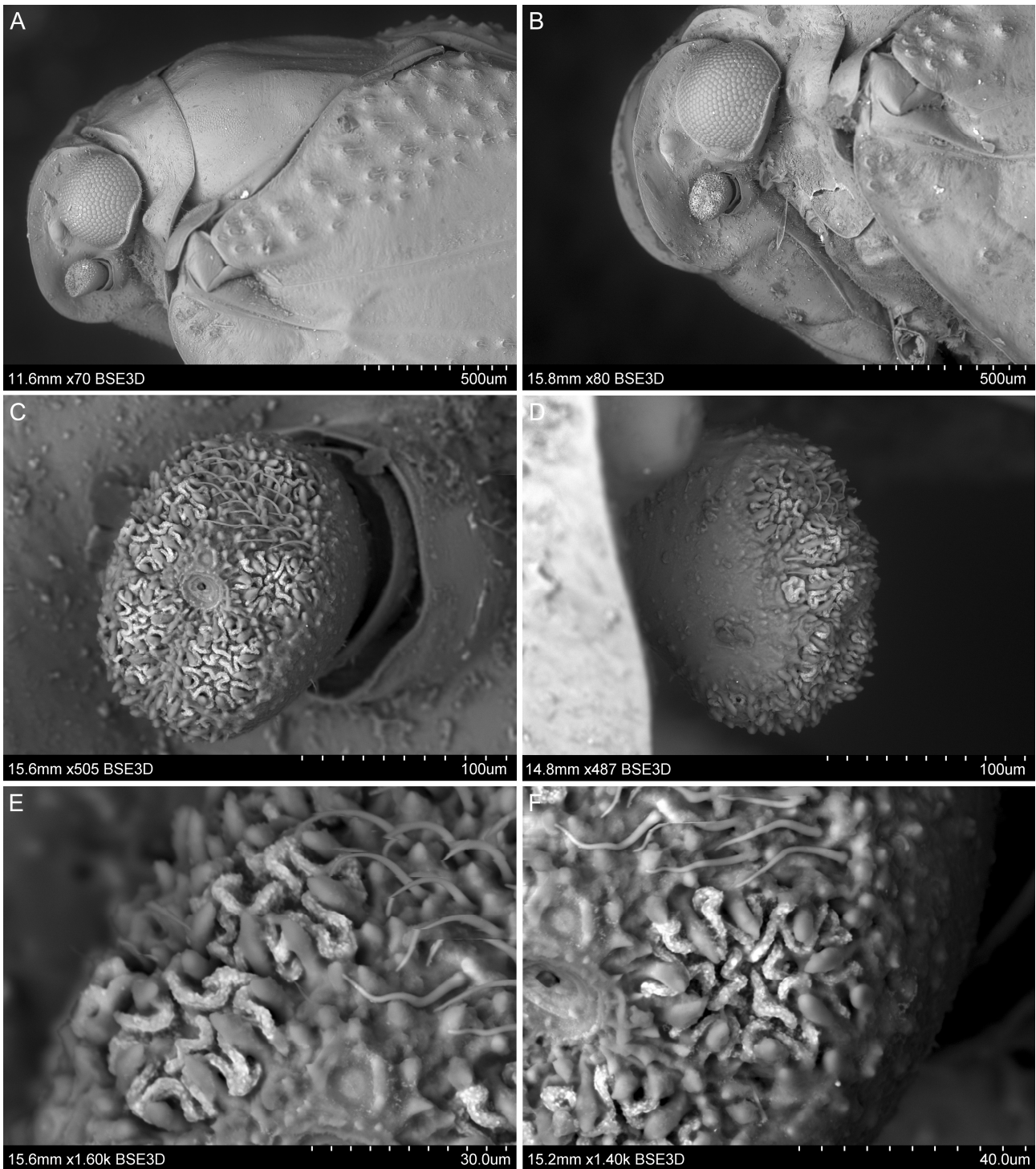


Fig. 3. *Makaya voluntany* gen. et sp. nov., holotype, SEM photographs: A) anterior part of body, lateral view; B) same, latero-ventral view; C) antenna, fronto-dorsal view; D) same, dorso-lateral view; E, F) antenna surface.

CuA first fork distinctly before RP fork and slightly before MP fork; all first forks placed in the basal part of tegmen. Veins distally delimited by nodal line flattened and wrinkled. Sensory and wax glands plates concentrated on costal area, near bulla (between ScP+RA and MP), on clavus (between basal parts of Pcu and A₁ and

between A₁ and A₂), with a few scattered on the whole tegmen (Figs 4A–F). Clavus terminating at the level of the end of costal area; Pcu and A₁ veins joined distinctly after CuP vein midlength, before clavus apex; A₁ and A₂ slightly elevated before the end of sensory glands plates area; clavus with or without single transverse veinlet after Pcu-A₁

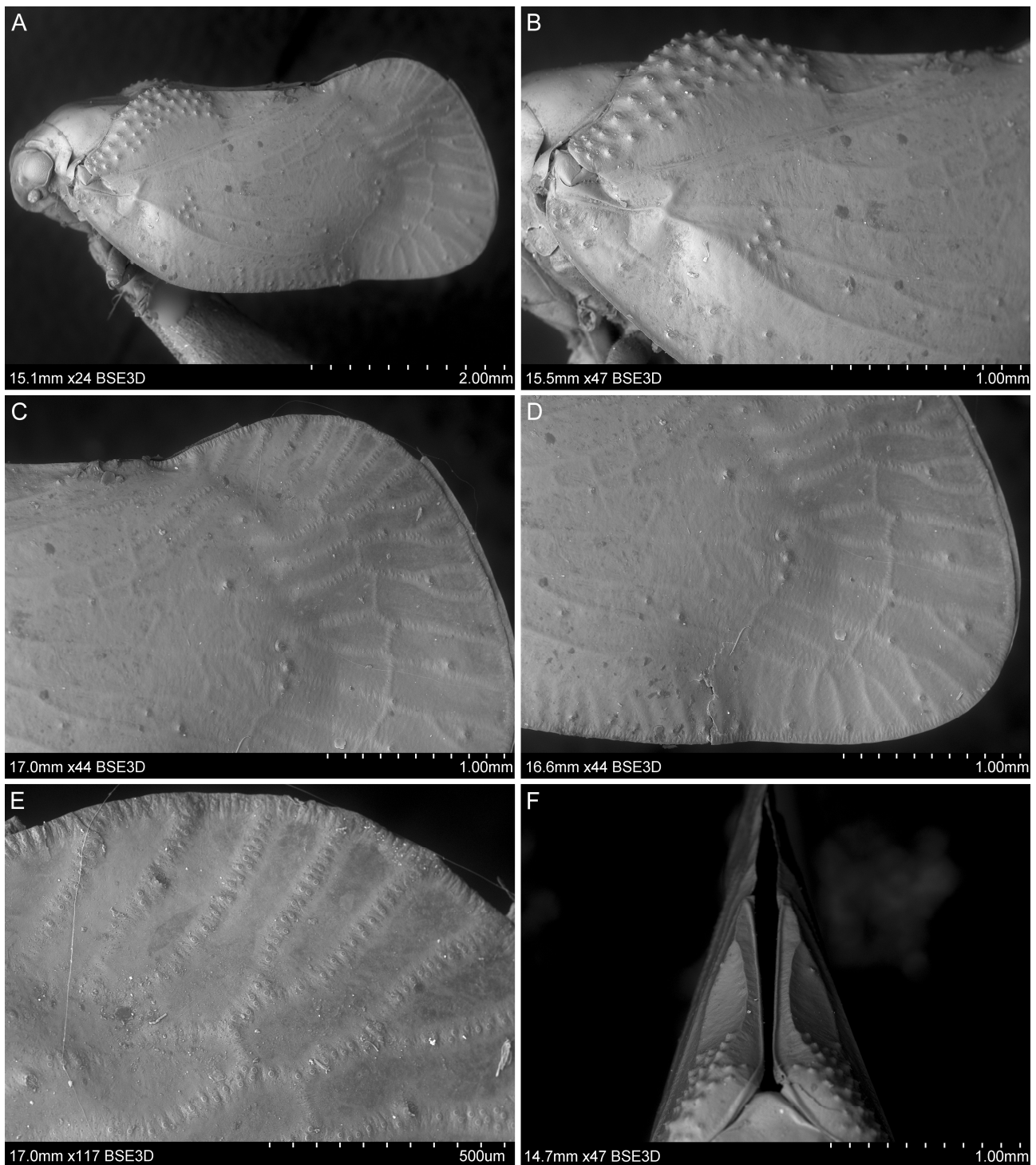


Fig. 4. *Makaya voluntany* gen. et sp. nov., holotype, tegmen, SEM photographs: A) general view; B) basal part; C, D, E) apical part; F) clavus.

connection (Figs 4A, B, F).

Metatibiae distinctly longer than metafemora, triangular in cross section with two lateral spines and a row of five apical spines without diastema – first lateral spine placed subapically, second lateral spine placed a bit after midlength; basitarsomere of

metatarsus a bit longer than cumulative length of second and apical tarsomeres, with apical teeth lined as row – 2 external teeth the same length as the 4 internal ones, that bear a single, distinct seta; second segment of tarsomere with lateral teeth and median pad with setae; median pad with setae extending

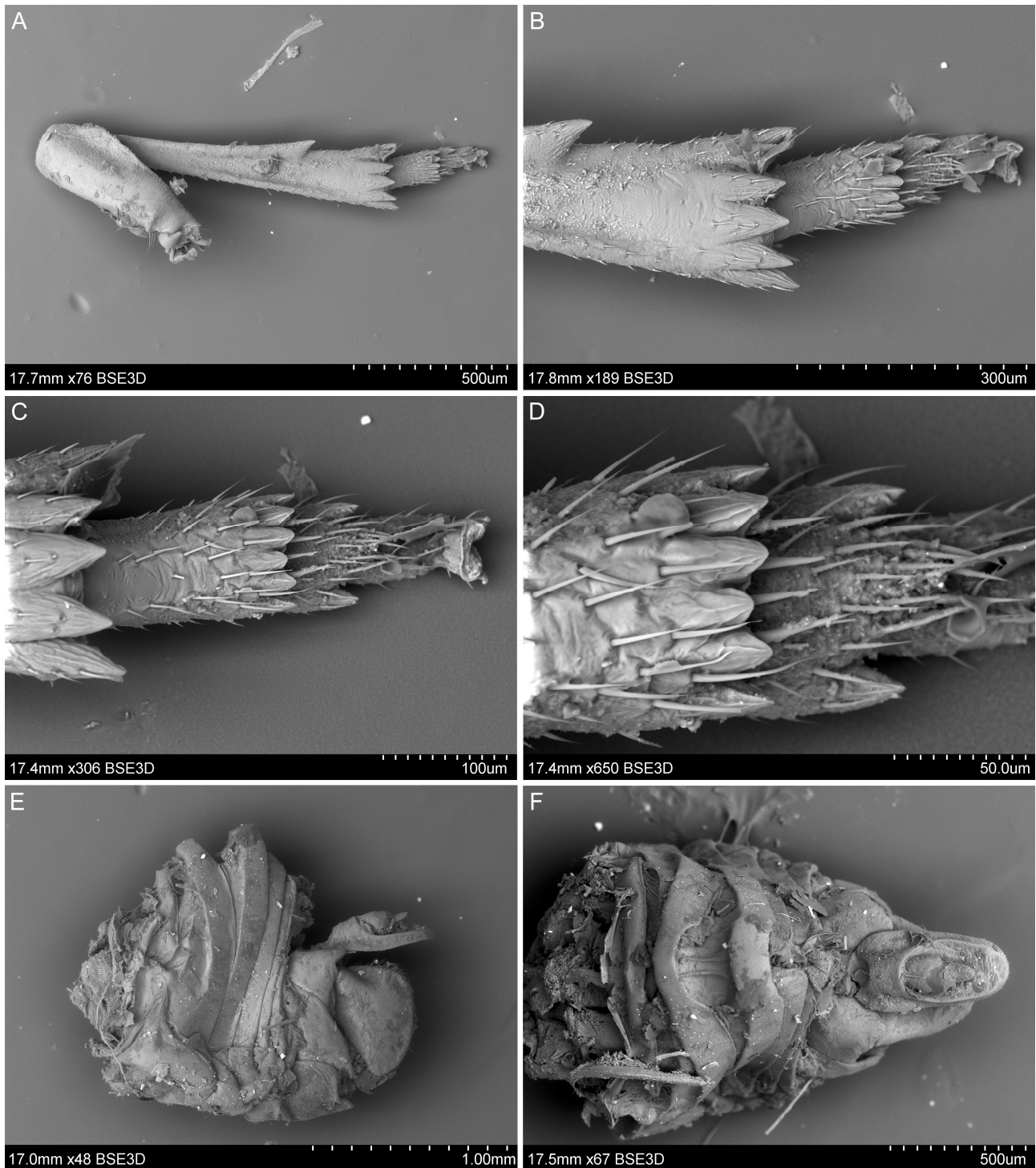


Fig. 5. *Makaya voluntany* gen. et sp. nov., female, SEM photographs: A) hind leg; B) apical part of metatibia and metatarsus; C, D) metatarsus; E) abdomen, lateral view; F) same, dorsal view.

lateral teeth. Metatibiotarsal formula: 2-(5)/(6)/2 (Figs 5 A-D).

Male terminalia. Anal tube, in lateral view, elongate, with breaking point before anal opening, tapering apicad; anal opening placed distinctly after midlength (Fig. 7A); in dorsal view, ensiform (Fig. 7B). Pygofer, in lateral

view, with dorsal part distinctly narrower than ventral part; anterior margin shallowly concave, posterior margin convex with breaking point in lower part. Genital style distinctly protruded posteriorly, bearing short, hook-like, strongly sclerotized capitulum (Fig. 7A).

Phallic complex. Periandrium, in lateral view, about as long as aedeagus; lateral split reaching about midlength (Fig. 7C). Dorsal part of periandrium, in dorsal view, a bit longer than ventral part, apically with two narrow lobes connected with membrane; in lateral view, subapically with single appendage possessing two well sclerotized arms; proximal part of dorsal periandrium with narrow lobe covering completely second arm (Fig. 7C). Ventral part of periandrium, in lateral view, apically with hook-like tip (Fig. 7C); in ventral view with two wide lobes located on both lateral margins (Fig. 7D). Aedeagus, in lateral view, long, slightly arcuate, orientated dorsad; apically with long dorsal process orientated apicad (Fig. 7E); in ventral view, bipartite, symmetrical, with deep median split surpassing midlength (Fig. 7F).

Female terminalia. Pregenital sternite massive, without median narrowing; two sclerotisations, medially subparallel, oblique, placed on ventral side of sternite (Figs 6 C, D; 7G). Anal tube, in lateral view, distinctly surpassing gonoplac, anal opening placed distinctly before midlength (Figs 5E; 6A); in dorsal view, oval; anal opening placed distinctly before midlength (Figs 5F; 6B). Gonoplac unilobate, rounded posteriorly, orientated ventrad, covering gonapophysis VIII; posterior margin with one row of large, sharp, densely aligned teeth; teeth of both gonoplacs fitting together in a zip-like manner (Figs 6E, F; 7 H). Gonapophysis VIII widely triangular, flattened, slightly oblique in respect to longitudinal body axis; endogonocoxal process as long as gonapophysis, wide, tapering apicad, with spiniferous microsculpture (Fig. 7I). Gonospiculum as in Fig. 7 K, J. Bursa copulatrix with single pouch, reniform, cells with sclerotized central areas (Fig. 7L). Spermatheca well developed; *ductus receptaculi* longer than *diverticulum ductus*, both parts smooth (Fig. 7M).

Diversity and distribution. The genus is monospecific and contains a single species from Madagascar (Fig 1I).

Etymology. The generic name refers to the *locus typicus* of the type species – Makay massif located in the center-west of Madagascar. Gender feminine.

***Makaya volontany* sp. nov.**

(Figs 1–7)

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Diagnostic characters. The only known species in the genus.

Description. Total length 4.2–4.9 mm.

Head. Vertex: A/B = 5.25–5.75. Frons: C/E = 0.87–1.09; D/E = 1.09–1.30.

Thorax. Pronotum: F/B = 2.50; Mesonotum: G/F = 3.50–4.00; G/B+F = 2.50–2.86; G/H = 0.80–0.92; Tegmen: I/J = 2.19–2.38; I/K = 2.10–2.21.

Male terminalia. Anal tube, in lateral view, with ventral margin sinuate (Fig. 7A); in dorsal view with rounded apex (Fig. 7B). Genital style with ventral and dorsal margins subparallel, almost straight, postero-ventral angle widely rounded; capitulum placed distinctly before postero-ventral angle (Fig. 7A). Appendage of dorsal periandrium with first arm short, stout, oriented postero-ventrad and second arm long, arcuate, sharp, oriented anteriad (Fig. 7C). Dorsal process of aedeagus with short acute, strongly sclerotized tip and denticulate ventral margin (Fig. 7E).

Female terminalia. Pregenital sternite with anterior margin almost straight, posterior margin distinctly convex, with tip placed before the level of lateral lobes (Fig. 7G).

Anal tube, in lateral view, tapering apicad, with ventral margin almost straight (Fig. 5E, 6A).

Membranous part of gonoplac narrow, placed alongside ventral margin (Fig. 7H). Gonapophysis VIII with subapical 6 massive teeth at dorsal margin (Fig. 7I). *Ductus receptaculi* widening apically, *diverticulum*

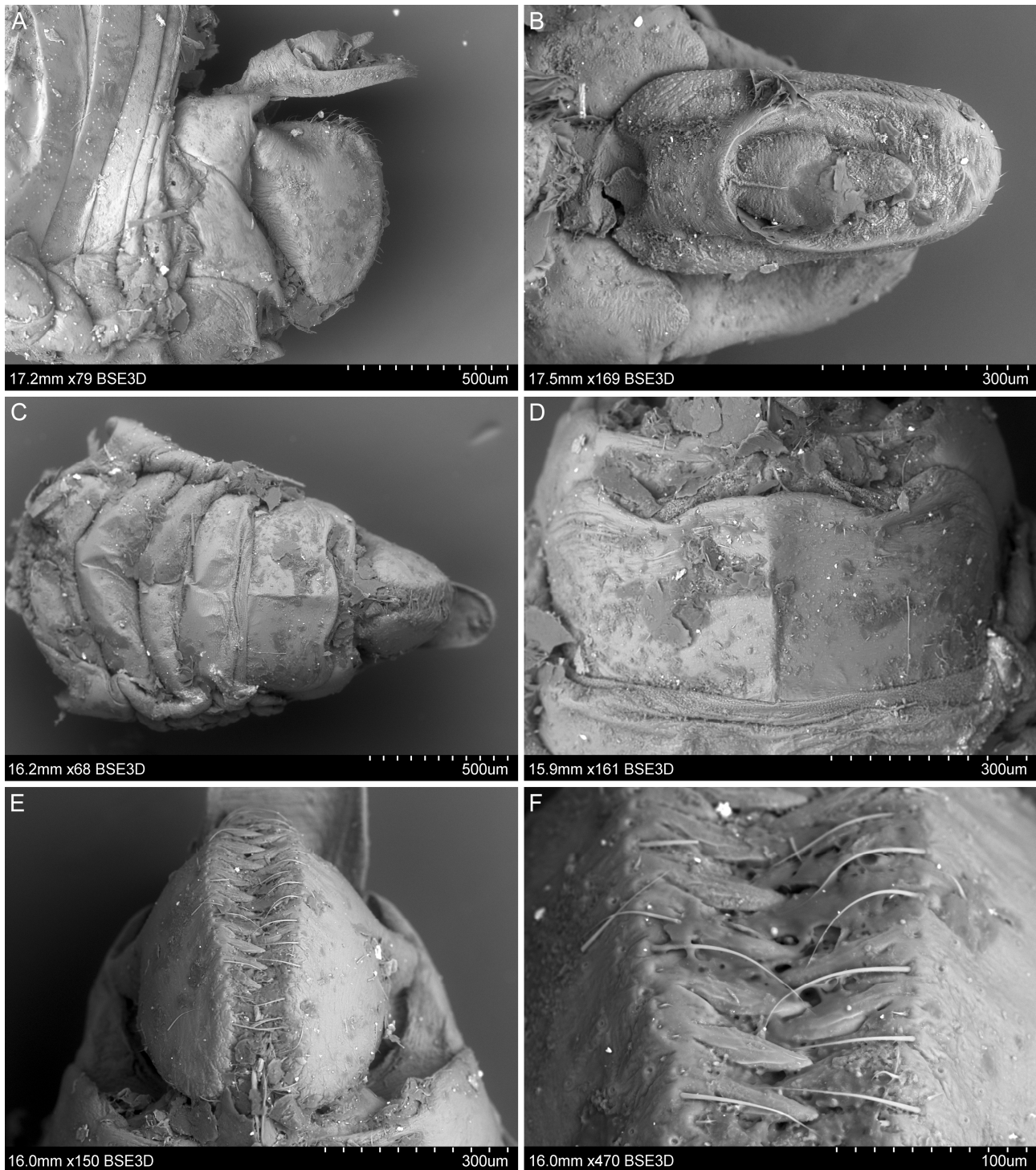


Fig. 6. *Makaya voluntany* gen. et sp. nov., female, SEM photographs: A) terminalia, lateral view; B) same, dorsal view; C) same; ventral view; D) pregenital sternite; E) gonoplace, fronto-ventral view; F) gonoplace teeth.

ductus divided into two parts: first part widening apically, second part tubuliform with apical bulba (Fig. 7M).

Coloration. There are two color forms of the species:

color form 1: localities 1, 4, 5 (Fig. 1C–D) and 6 (Fig. 1A–B). General coloration from

light to dark brown; head: vertex with lateral discolorations, clypeus and rostrum yellowish; thorax: disc of pronotum yellowish with median dark brown band, anterior part of mesonotum with two lighter dots; tegmen – basal cell yellowish; anterior part of basal half of tegmen almost black; end of costal area

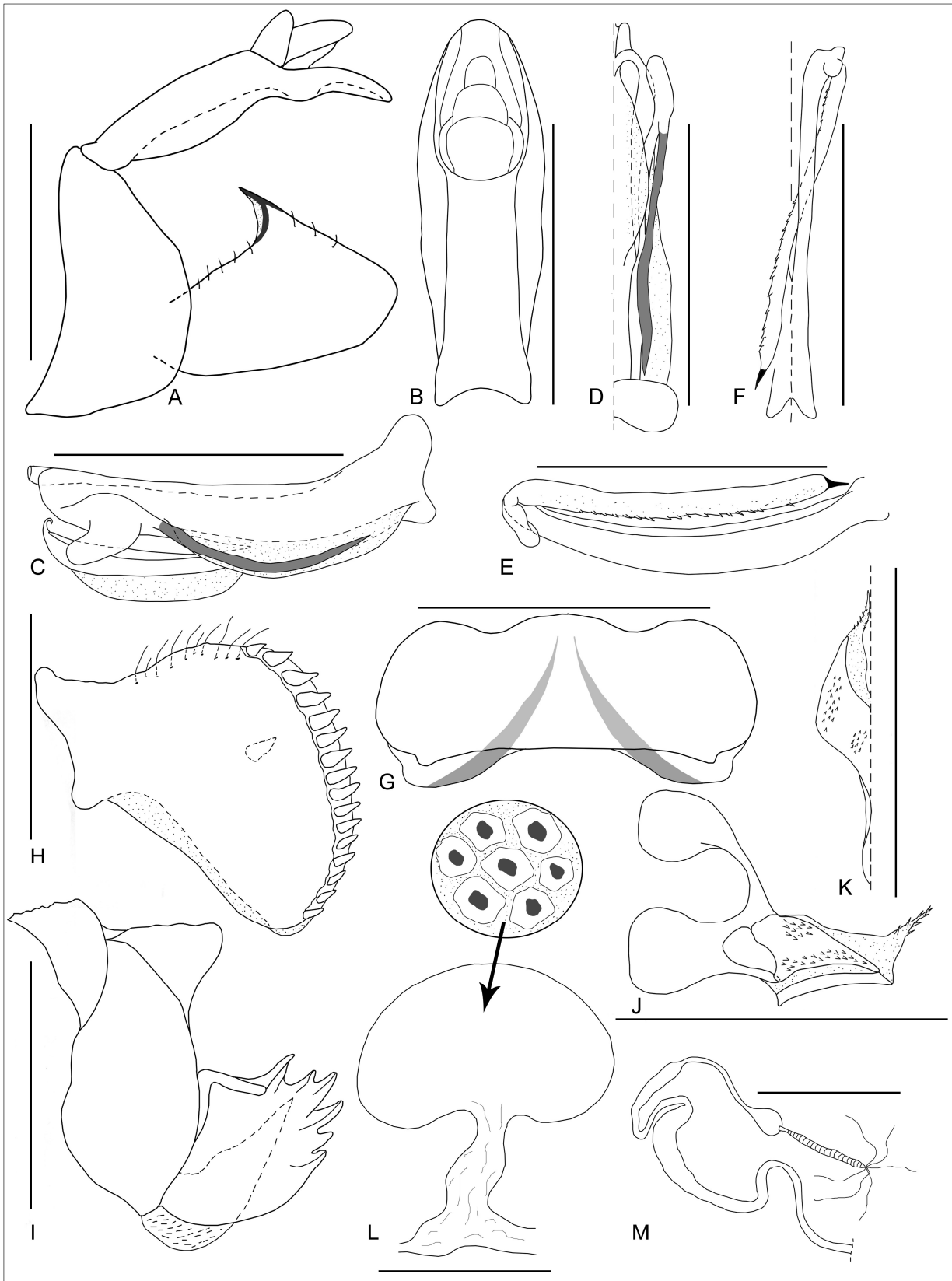


Fig. 7. *Makaya voluntany* gen. et sp. nov., A-F male, G-M female, line drawings: A) terminalia, lateral view; B) anal tube, dorsal view; C) periandrium, lateral view; D) same, ventral view (one half shown in the figure); E) aedeagus, lateral view; F) same, ventral view (one half shown in the figure); G) pregenital sternite, flattened, ventral view; H) gonoplac, lateral view; I) gonapophysis VIII, lateral view; J) gonapophyses IX and gonospiculum bridge, lateral view; K) same, dorsal view (one half shown in the figure); L) bursa copulatrix with cells, lateral view; M) spermatheca. Scale bars = 0.5 mm.

with large, triangular, whitish patch; basal half of clavus almost black, apical half yellowish. Remark: specimens from localities 1, 4 and 5 have the same color pattern as those from locality 6 but were originally preserved in 70% ethanol and are consequently lighter.

color form 2: localities 2, 3 (Fig. 1E–F). General coloration stramineous; head: disc of vertex, disc of frons, clypeus and rostrum brownish; thorax: mesonotum dark brown; tegmen – main longitudinal veins, especially in the apical part, brown; end of costal area with large, triangular, whitish patch, posterior part of clavus dark brown; teeth of metatibiae, basi- and metatarsomeres with black tips; abdomen: male and female anal tube brownish, pregenital sternite brownish.

Distribution and habitat. Madagascar; so far only known from six localities in the center-west and north-western part of the island (Fig. 1 G–I).

Type material examined. Holotype, ♂: [Madagascar/ Province de Toliara/ massif du Makay, 153 m/ 21°40'27.6" E 44°59'45.3"S], [MUSEUM PARIS/ forêt sèche Ambalamanga/ 19-I-2011/ A. Soulier-Perkins rec.], [Museum Paris/MNHN(EH)/ 22167] – (MNHN).

Paratypes (22♂♂, 26♀♀). **Locality 1** – [MADAGASCAR: Mahajanga/ Forêt Ambohimanga, 26.1 km/ 314° Mampikony, elev 250 m/ 13 December, 2004], [15°57'46"S 047°26'17"E/ California Acad. of Sciences/ coll. B.L.Fisher, malaise trap/ tropical dry forest BLF11670] – (1♂, CAS). **Locality 2** – [MUSEUM PARIS/ MADAGASCAR 2005/ Bourgoin, Ouvrard/ Attié, Soulier-Perkins], [09-12/ XI/ 2005/ région Mahajanga/ Antrema, 15 m, P.L./ 15°42.686'S 46°10.515'E] – (3♂♂ 3♀♀, MNHN). **Locality 3** – [MUSEUM PARIS/ MADAGASCAR 2005/ Bourgoin, Ouvrard/ Attié, Soulier-Perkins], [11/ XI/ 2005/ région Mahajanga/ Antrema, forêt, 54 m/ 15°42.444'S 46°10.184'E] – (7♂♂ 7♀♀, MNHN); [12/ XI/ 2005/ 54 m/ région Mahajanga/ Antrema, forêt, légumineus/ 15°42.444'S 46°10.184'E] – (7♂♂ 8♀♀, MNHN, 1♂ 1♀ MIZ). **Locality 4** –

[MADAGASCAR: Majunga/ Province, Anjaabo,/ 3 km N Baly village/ 26 Sept - 4 Oct 2007], [16° 3.54' S, 45° 16.45' E/ Calif Acad of Sciences/ coll: M.Irwin, R.Harin'Hala/ malaise, stabilised dunes/ elev 24 ft MG-39B-02] – (1♂, CAS) ; [22 Oct - 1 Nov 2007], [MG-39B-05] – (1♀, CAS). **Locality 5** – [MADAGASCAR: Majunga/ Prov. Besalampy District/ Marofototra palm forest/ 17 km W of Besalampy/ 12-19 November 2007], [16°43.30' S 44°25.42' E/ Calif. Acad. of Sciences/ coll: M.Irwin, R.Harin'Hala/ palm trees on sand el 35 ft/ malaise/ MG-42B-08] – (1♀, CAS); [9-16 June 2008], [MG-42B-24] – (1♂, CAS); [6-13 October 2008], [MG-42B-41] – (1♂, MIZ); [14-21 July 2008], [MG-42B-29] – (1♀, CAS); [26 May-2 June 2008], [MG-42B-22] – (1♀, CAS); [1-8 October 2007], [MG-42B-02] – (1♀, CAS); [9-16 June 2008], [dry wash in forest/ elev 170 ft, MG-42A-24] – (1♀, MIZ). **Locality 6** – [Madagascar/ Province de Toliara/ massif du Makay, 203 m/ 21°37'41.6"E 45°00'13.7"S], [MUSEUM PARIS/ forêt sèche 'humide'/ 23-I-2011/ D. Ouvrard rec.], [Museum Paris/ MNHN(EH)/ 22290] – (1♀, MNHN)

Etymology. The specific name comes from the Malagasy word "volontany", which means "brown" and refers to the coloration of the species.

Discussion

As elsewhere, differentiated alternative mechanisms may have played an important role in the development of local endemism in Madagascar, such as isolation due to rivers and watersheds, environmental gradients or post-speciation range shifts (Pearson & Raxworthy 2009). Moreover, the long isolation of the island (about 90 million years) from all other land masses (Storey *et al.* 1995) has favored the development of rich supra-specific endemic lineages. Indeed, the ecosystems of Madagascar have long been recognized not only for its globally significant diversity but also for its exceptionally high

levels of endemism for many terrestrial clades (Myers *et al.* 2000). The biodiversity of Malagasy entomofauna and in particular that of Hemiptera Fulgoromorpha, is a perfect example of these high levels of endemism and with many new endemic species discovered each year (Stroiński *et al.* 2011, Junkiert *et al.* 2021, Stroiński 2021).

Most Madagascar Selizini genera described so far are encountered mainly in two types of forests, namely the western dry forests and the southwestern dry spiny forest-thickets and are all endemic to the island. The high diversity and endemism of Madagascar Selizini (including descriptions in progress of additional genera) might be explained by the hypothesis proposed by Wells (2003) in which, after Madagascar and India separated some 88 Ma, the island located within the 30 degree latitude subtropical arid belt and likely experienced a generally dry climate. Probably, the arid to seasonally dry biomes were therefore dominant in the Late Cretaceous and through the Paleocene. The island's northern drift in the Eocene resulted in constricting the range of the arid spiny bush biome to the west, south and southwest, favouring new speciation events and modelling the current distribution of endemism patterns associated with dry biotopes.

Accordingly, all populations of *Makaya voluntany* distributed within the dry forest ecoregion (*sensu* Vieilledent *et al.* 2018), were divided into a north-western group and an isolated more southern one in Makay, with diversified colour forms as already observed in other Madagascar taxa such as the sub-brachypterous Ricaniidae, e.g. in the species *Globularica diversicolorata* Stroiński, Gnezdilov & Bourgoïn, 2011. In the case of the populations occurring along the north-western coast (Melaky center of endemism *sensu* Wilmé *et al.* 2012), the current narrow range can result from the contraction of a once wider distribution. During the dry phases of the paleoclimate oscillations, sea

level was below the current level. For instance, it was at ca. 130 m below that of present-day during the last glacial maximum, some 20,000 years ago (Mercier & Wilmé 2013, Lourenço & Wilmé 2016). The newly described species might have had a wider distribution over the today submerged continental plateau, resulting in a narrow coastal range nowadays.

The more enigmatic southern population is located within the spectacular Makay massif, located north of the Mangoky River in the Atsimo-Andrefana region, approximately 100 km inland from Madagascar's western coast. It is dissected by a dense network of narrow and deep canyons with steep and up to 400 m high cliff walls, where permanent, temporary or groundwater flow. The rocks are represented by sandstones and conglomerates of Late Triassic origin. Referring to the vegetation of the area, the smaller canyons harbour deep lakes or swamps that are characterized by special vegetation dominated by *Pandanus*, palms and ferns. The less humid slopes and mountain saddles have extensions of either western dry or sub-humid forests. Remoteness and the difficulty in accessing Makay's interior results in very poor knowledge of the flora (Allorge *et al.* 2015) and fauna (Dolch *et al.* 2011, Lourenço & Wilmé 2015, Belluardo *et al.* 2021) of the region.

A possible explanation of such disjoint distribution of the populations (center-west *versus* north-western) can result from the recent anthropological deforestation. Western dry forest today covers an area of 31 800 km² and has been reduced since the 1970s by almost 40% (Moat & Smith 2007). This forest type is diverse and forms impenetrable thickets as well as bushland and low scrub. Environmental degradation of this vegetation results from its important socio-economic role, providing building materials, firewood, medicinal plants, grazing habitat for cattle, to mention these few. These

hypotheses proposed to explain the patterns of distribution of *Seliziini* in Madagascar and of *Makaya* in particular, would have to be confirmed in the future in reference to a phylogenetic framework.

Unfortunately, dry forests in Madagascar, with an estimated area similar to the humid forests, are far less protected (27% versus 48%) and research on sustainable management of dry forest is likely the biggest gap to date, taking into account a steadily growing human population and a constantly growing need for more arable land, constituting a pressure on the remaining forests (Waeber *et al.* 2015). Undoubtedly, environmental research should be based on a holistic approach, not only producing new knowledge but also providing scientifically based tools to carefully weigh the protection of the natural resources versus the investments and needs of the local populations, which still lives following traditional norms and rules.

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