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A new firefly genus from South America, with seven new species, a new combination, and notes on the phylogeny of Lampyrinae: Lucidotini (Coleoptera: Lampyridae)

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Background. Lucidotini is a diverse tribe of lampyrine fireflies present throughout the New World, Europe, and Asia. Most of the over 30 genera have overlapping diagnoses, largely due to a lack of revisionary and phylogenetic studies. Widespread convergence in sensory morphology, traditionally used in genus-level diagnoses, further compounds the taxonomic issues surrounding the Lucidotini. Recent work has cast light on the value of terminalia and genitalic traits for Lucidotini taxonomy and called for a more thorough screening of morphological characters. Of special interest are basal outgrowths of the phallus (i.e. ventrobasal processes) – currently only known in *Alychnus* Kirsch and *Photinus* Laporte –, that can be quite informative at the species level, but its variation within Lucidotini remains poorly studied. Most Lucidotini species remain only superficially described, while internal characters – including those of terminalia and genitalia– which could inform species identification and phylogenetic relatedness, remain unknown. Upon studying eight Lucidotini species superficially looking like *Photinus* and *Photinoides* McDermott –all of which bearing long ventrobasal processes–, we raised the hypothesis that they belonged to a genus yet to be recognized. **Methods.** Here, we analyzed 97 morphological characters of 32 lampyrid species spanning 17 of 30 Lucidotini genera under Bayesian Inference. **Results.** We found evidence for the recognition and description of *Saguassu* **gen. nov.** to include seven new species (*Saguassu acutum* **sp. nov.,** *Saguassu grossii* **sp. nov.,** *Saguassu manauara* **sp. nov.,** *Saguassu rebellum* **sp nov.,** *Saguassu roura* **sp. nov.,** *Saguassu serratum* **sp. nov.** and *Saguassu sinuosum* **sp. nov.**), in addition to *Photinus dissidens* Olivier (transferred herein, thus generating *Saguassu dissidens* **comb. nov.**), for which we also designate a lectotype and two paralectotypes).

This previously neglected lineage of Lucidotini spans 4 South American biomes: Amazon, Atlantic Rainforest, Cerrado, and Pampa. Interestingly, *Saguassu* species span a gradient of morphologies related to signaling: from *Lampyris*-style ventrally bulging eyes, tiny antennae and no lanterns; intermediate eyes and antennae, with complete lanterns as in *Photinus*; to small eyes and long antennae and small lanterns as in many *Lucidota* Laporte. *Saguassu* **gen. nov.** was consistently found closely related to the three other Lucidotini taxa with ventrobasal processes (i.e. *Alychnus*, *Photinoides*, and *Photinus*. We provide an occurrence map of and a dichotomous key to *Saguassu* species, thoroughly compare this genus with co-occurring Lucidotini genera, and suggest steps towards a revision of the Lucidotini tribe.

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Abstract

Background. Lucidotini is a diverse tribe of lampyrine fireflies present throughout the New World, Europe, and Asia. Most of the over 30 genera have overlapping diagnoses, largely due to a lack of revisionary and phylogenetic studies. Widespread convergence in sensory morphology, traditionally used in genus-level diagnoses, further compounds the taxonomic issues surrounding the Lucidotini. Recent work has cast light on the value of terminalia and genitalic traits for Lucidotini taxonomy and called for a more thorough screening of morphological characters. Of special interest are basal outgrowths of the phallus (i.e. ventrobasal processes) – currently only known in *Alychnus* Kirsch and *Photinus* Laporte –, that can be quite informative at the species level, but its variation within Lucidotini remains poorly studied. Most Lucidotini species remain only superficially described, while internal characters – including those of terminalia and genitalia – which could inform species identification and phylogenetic relatedness, remain unknown. Upon studying eight Lucidotini species superficially looking like *Photinus* and *Photinoides* McDermott – all of which bearing long ventrobasal processes –, we raised the hypothesis that they belonged to a genus yet to be recognized.

Methods. Here, we analyzed 97 morphological characters of 32 lampyrid species spanning 17 of 30 Lucidotini genera under Bayesian Inference.
Results. We found evidence for the recognition and description of *Saguassu* **gen. nov.** to include seven new species (*Saguassu acutum* **sp. nov.,** *Saguassu grossii* **sp. nov.,** *Saguassu manauara* **sp. nov.,** *Saguassu rebellum* **sp nov.,** *Saguassu roura* **sp. nov.,** *Saguassu serratum* **sp. nov.** and *Saguassu sinuosum* **sp. nov.**), in addition to *Photinus dissidens* Olivier (transferred herein, thus generating *Saguassu dissidens* **comb. nov.**), for which we also designate a lectotype and two paralectotypes). This previously neglected lineage of Lucidotini spans 4 South American biomes: Amazon, Atlantic Rainforest, Cerrado, and Pampa. Interestingly, *Saguassu* species span a gradient of morphologies related to signaling: from *Lampyris*-style ventrally bulging eyes, tiny antennae and no lanterns; intermediate eyes and antennae, with complete lanterns as in *Photinus*; to small eyes and long antennae and small lanterns as in many *Lucidota* Laporte. *Saguassu* **gen. nov.** was consistently found closely related to the three other Lucidotini taxa with ventrobasal processes (i.e. *Alychnus*, *Photinoides*, and *Photinus*. We provide an occurrence map of and a dichotomous key to *Saguassu* species, thoroughly compare this genus with co-occurring Lucidotini genera, and suggest steps towards a revision of the Lucidotini tribe.

Introduction

Lucidotini Lacordaire 1857 – a senior synonym of Photinini LeConte, 1881 (see Bouchard et al., 2011) overlooked in some recent works – is one of the largest firefly lineages, with over 820 species and 33 genera (Ladino-Peñuela et al., 2022; Roza et al., 2022; see also the lampyridae.world catalog [assessed on 04/Nov/2024]), i.e. a third of Lampyridae at large. It is unique among Lampyrinae Rafinesque, 1815 tribes in its adult morphology by the long, overlapping and often robust adult mandibles (typically reduced in other lampyrine groups) and dorsally placed abdominal spiracles (usually ventrally placed in the other Lampyrinae except Cratomorphini Olivier, 1911) (but see Silveira et al., 2019). Current genus-level diagnoses of Lucidotini genera are largely overlapping and rely on few external, homoplastic characters, which has led to taxonomic confusion. Recent research focusing on Neotropical fireflies has led to an accumulation of new species and genera of Lucidotini (Silveira & Mermudes, 2014; Silveira et al., 2016; Zaragoza-Caballero & Navarrete-Heredia, 2014; Zaragoza-Caballero, 2015; Zaragoza-Caballero, 2017; Zaragoza-Caballero et al., 2018; Campello-Gonçalves et al., 2019; Zaragoza-Caballero et al., 2020; Gutiérrez-Carranza et al, 2023a; Gutiérrez-Carranza et al, 2023b; Zaragoza-Caballero et al., 2023a, Gutiérrez-Carranza & Zaragoza-Caballero, 2024), sometimes supported by phylogenetic analyses (Silveira et al., 2021; Vaz et al., 2020; Roza et al., 2022; Silveira et al., 2022; Zaragoza-Caballero et al., 2023b) and taxonomic revisions (Ladino-Peñuela et al., 2022; Zeballos et al., 2022). However, the genus-level taxonomy of Lucidotini remains unstable.

The value of genitalic characters has long been recognized in firefly taxonomy, across levels (e.g. Gorham, 1884; Green, 1956; McDermott, 1962), but only more recently they were included in phylogenetic analysis (e.g. Jeng, 2008). For example, genitalic traits supported the resurrection of *Alychnus* Kirsch, 1865 (Ladino-Peñuela et al., 2022), the description of *Costalampys* Silveira, Roza, Vaz & Mermudes, 2021 and *Zoiudo* Roza, Mermudes, and Silveira 2022, and several new combinations (e.g. Silveira et al., 2021; Vaz et al., 2020; Zeballos et al., 2022), thus helping to stabilize Lucidotini taxonomy. Likewise, genitalic traits also supported the synonymization of *Macrolampis* Motschulsky, 1853 and *Ellychnia* Motschulsky, 1853 with *Photinus* Laporte, 1833 (Zaragoza-Caballero et al., 2020). This synonymization was based on the shared presence of basal processes of the dorsal plate of the phallus (therein referred to as dorsal excrescences [*sic*], but see Ladino-Peñuela et al., 2022 for a discussion; we from now on call it ventrobasal processes), but also by the findings of DNA-based or integrative phylogenies that found *Ellychnia* Motschulsky, 1853 nested with *Photinus* (Stanger-Hall et al., 2007; Stanger-Hall et al., 2015; Martin et al., 2017; Martin et al., 2019).

The current state of Lucidotini genera calls for a more comprehensive and thorough comparative study to consolidate their diagnoses and stabilize their taxonomy to facilitate identification. For example, ventrobasal processes are also present in *Alychnus*, but this genus can be easily distinguished from *Photinus* by the number of tibial spurs on each leg: zero on the proleg (versus one in *Photinus*) and one on meso- and metalegs (versus two on *Photinus*) (Ladino-Peñuela et al., 2022). While searching for Lucidotini specimens with similar leg traits across collections, we identified eight species with *Alychnus*-like tibial spurs but otherwise very disparate external morphologies (Fig. 1). Nevertheless, all of them share unique genitalic traits, while sharing a pair of ventrobasal processes on the dorsal plate with *Photinus*. Here, we included these eight species in a phylogenetic analysis to explore their relationship to other Lucidotini taxa and test the hypothesis that they form a monophyletic group not nested in *Photinus*.

Materials & Methods

Morphology and Terminology

Specimens were obtained from the following institutions:

BYU – USA, Utah, Provo, Brigham Young University, Monte L. Bean Life Science Museum (M. Whiting & S. Bybee).

CERPE – Brazil, Pernambuco, Recife, Coleção Entomológica da Universidade Federal Rural de Pernambuco (P. Grossi)

DZUP – Brazil, Paraná, Curitiba, Universidade Federal do Paraná, Departamento de Zoologia, Museu de Entomologia Pe. Jesus Santiago Moure (C. Ribeiro-Costa & N. Ganho).

FSCA – USA, Florida, Gainesville, Division of Plant Industry, Florida State Collection of Arthropods (P. Skelley & K. Schnepp).

IFML – Argentina, Tucumán, San Miguel de Tucumán, Instituto Fundación Miguel Lillo (C. Perez).

INPA – Brazil, Amazonas, Manaus, Instituto Nacional de Pesquisas da Amazônia, Coleção Sistemática da Entomologia (C. Vasconcellos da Fonseca).

MNHN – France, Paris, Muséum National d'Histoire Naturelle (A. Taghavian).
MPEG – Brazil, Pará, Belém, Museu Paraense Emilio Goeldi (O. Tobias).
MUSM –Peru, Lima, Universidad Nacional Mayor de San Marcos, Museo de Historia Natural (L. Figueiroa).
MSNG – Italy, Genova, Museo Civico di Storia Naturale "Giacomo Doria" (M. Tavano).
MZUF – Italy, Firenze, Museo di Storia Naturale ("La Specola") (L. Bartolozzi).
NCSU – USA, North Carolina, Raleigh, North Carolina State University Insect Collection (G. Powell & B. Blinn).
NHMUK – United Kingdom, London, the Natural History Museum [formerly British Museum (Natural History)] (Max Barclay & Michael Geiser).
UGCA – USA, Georgia, Athens, University of Georgia Collection of Arthropods (J. McHugh).
USNM– USA, Washington D.C., Smithsonian National Museum of Natural History (M. Branham).
WCCA – USA, North Carolina, Cullowhee, Western Carolina University Collection of Arthropods (L. Silveira).

Where dissections were permitted by the curators, one or more whole specimens were relaxed in warm water, then placed in 10% KOH, fully dissected ~~after 24h~~, and imaged under a stereomicroscope. Stacked images were prepared using Leica Application Suite X, and plates were assembled in Adobe Photoshop 2023. For the MPEG specimens (*S. sinuosum* **sp. nov.** and *S. serratum* **sp. nov.** – see below), only the abdomen was dissected. Terminology follows Roza et al. (2022). For the material examined, we transcribed the labels verbatim, and eventually added comments between brackets.

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Phylogenetic analysis

Our matrix expanded on the morphological characters listed in recent works of our group (Zeballos et al., 2022; Roza et al., 2022). Our taxon sampling was chosen to maximize the morphological and taxonomic diversity of Lucidotini, with an emphasis on taxa superficially similar to the eight focal species (examined material other than the eighth focal species can be found in Supplemental Material S1). Character coding followed the logical basis of Sereno (2007). The matrix was constructed in Mesquite v3.2 (Maddison & Maddison, 2022). The character matrix is provided as a nexus file in Supplemental Material S2, and a list of characters and states is provided in S3.

We ran phylogenetic analyses based Bayesian inference (BI) using MrBayes 3.2.7a (Huelsenbeck & Ronquist, 2001) (available at The CIPRES Science Gateway V. 3.3 (https://www.phylo.org/portal2/login!input.action, accessed on 13 September 2022; Miller et al., 2012). A model selection ran with ModelFinder in IQTREEE2 selected the MKV model with equal state frequencies, 4 gamma categories, and correction for ascertainment bias (i.e., MK+FQ+ASC+G4) (Lewis, 2001; Kalyaanamoorthy et al., 2017; Minh et al., 2020) (Supplemental File S4) as the best model of evolution. We ran 10×10^6 generations, saving trees every 2000 generations and discarding the first 25% as burn-in, and checked for convergence using Tracer v1.6 (Rambaut et al., 2018) (MrBayes input file can be found in Supplemental File 5). Character evolution was optimized on the resulting majority consensus tree using WinClada (Nixon, 2002).

Trees were read in FigTree version 1.4.4 (obtained at https://github.com/rambaut/figtree/releases; accessed on 2 January 2021) and edited in Adobe Photoshop 2023.

Distribution map

We built an occurrence map in R for the focal species of this work based on specimen collection labels. We colored the map by Neotropical dominions *sensu* Morrone (2014), based on the shapefile given in Morrone et al. (2022). The following packages were used for the generation of the map: “sf” (Pebesma, 2018), “dplyr” (Wickham, 2023), and “ggplot2” (Wickham, 2016).

Results

Phylogenetic analysis

Bayesian inference (BI) majority consensus (Fig. 2; Supplemental File 6) recovered *Saguassu* **gen. nov.** as monophyletic with high support (PP=97). This lineage is supported by 1 uncontroverted and 3 controverted (i.e. homoplastic) synapomorphies (Fig. 3): phallus, dorsal plate, basal 1/2 with dorsoventral depth at least 1/6 deeper than paramere (97:1, not homoplastic); phallus, endosac with clefted opening (86:2, homoplastic); paramere with subapical ventral spike elongate (90:1, homoplastic); and paramere with basal lobe absent (96:0, homoplastic). *Saguassu* **gen. nov.** was recovered with moderate support (PP=83, Fig. 2) as sister to a clade (PP=89) formed by *Alychnus* (*Photinoides* + *Photinus*). This relationship is supported by 2 uncontroverted and 4 controverted synapomorphies (Fig. 3): phallobase, sagittal line extending throughout the phallobase (57:0, homoplastic); phallobase, apical margin slightly emarginate (58:0, homoplastic); phallus, dorsal plate with basal protuberances (63:1, not homoplastic); phallus, endosac slightly shorter than phallus (84:2, not homoplastic); paramere, base laterally (coplanar) orientated in relation to phallus (91:1, homoplastic); and paramere, apex evenly curved inwards in lateral view (93: 2, homoplastic).

This larger clade was recovered, with low support (PP=70), as sister to *Ybytyramoan* Silveira and Mermudes, 2014 + *Zoiudo* (a strongly supported clade; PP=96), a relationship supported by 2 uncontroverted and 3 controverted synapomorphies (Fig. 3): sternum VII with lantern (33:1, not homoplastic); sternum VIII, posterior margin almost straight (36:0, homoplastic); phallus, dorsal plate as long as the parameres (69:2, homoplastic); phallus, dorsal plate slightly curved ventrally in lateral view (74:2, not homoplastic); and phallus with ventral plate rudimentary (83:2, homoplastic). The clades neighboring this most inclusive node are mostly weakly supported or polytomic (Fig. 2), except for the following relatively more inclusive nodes: (i) *Pyropyga* Motschulsky, 1852 (*Haplocauda* Silveira, Lima, Da Fonseca & McHugh, 2021 + *Scissicauda* McDermott, 1964) (PP=100); and (ii) *Luciuranus* Silveira, Khattar & Mermudes, 2016 (*Lucidota atra* (Olivier, 1790) (*Phosphaenus* Laporte, 1833 + *Phosphaenopterus* Schaufuss, 1870) (PP=81). These findings are discussed below (see Discussion).

Taxonomy
Lampyrinae Rafinesque, 1815
Lucidotini Lacordaire, 1957
Photinina LeConte, 1881

***Saguassu* gen. nov. Viana, Roza, Vaz, and Silveira**

(Figs. 1, 4–11)

Type-species: *Saguassu grossii* **sp. nov.** Viana, Roza, Vaz, and Silveira; by original designation.

Diagnosis (based on males): Antenna filiform, compressed (slightly serrate only in *S. rebellum* **sp. nov.** Fig. 4X). Mandible stout and almost right-angled. Pronotum with disc strongly convex, anterior margin rounded, anterior expansion very long (at least 2/3 as long as disc), lateral expansions narrow (~1/3 as wide as disc). Protibia without spurs. Meso and meta tibia with one spur. Sternum VIII ~~nearly a~~ 1/5 shorter than VII. Pygidium as wide as long, lacking posterolateral corners. Parameres completely separated in dorsal view, often bearing subapical membranous appendages. Phallus with dorsal plate of apically clefted, arms contiguous; ventral plate present, rudimentary; ventrobasal processes elongate and apically convergent, variably ornate apically.

Etymology. Saguassu is a singular gender neutral in the nominative case. Saguassu (saguaçú) comes from the Tupi-Grarani origin (Brazilian Indian languages), meaning “those with big eyes” (Barbosa, 1951). This name refers to the huge male eyes observed in species of this genus.

Immature stages. Unknown.

Distribution. South America East of the Andes, from Northern Amazon to Southern Atlantic Forest and Pampas, including the Cerrado (Fig. 12).

Biology. Field records and roughly documented flash patterns are available for *Saguassu acutum* **sp. nov.** and *S. grossi* **sp. nov.** (see below). Both species are nocturnal (active after dusk).

Remarks. *Saguassu* **gen. nov.** is overall similar to several Lucidotini: Photinina taxa (remarkably *Photinus*, *Ybytyramoan*, and *Zoiudo*) due to the presence of well-developed lanterns and eyes, and filiform antennae. These taxa cannot be easily distinguished from each other based on external characters alone due to broad variation within *Photinus*.

S. grossii **sp. nov.** is particularly similar to *Photinus*, due to its complete lanterns. However, *Saguassu* **gen. nov.** can be easily distinguished from these three genera by the very distinctive phallic dorsal plate, which is basally swollen leading to complete separation of the parameres in dorsal view. These are connected by a bridge in *Photinus*, *Ybytyramoan*, and *Zoiudo*. The presence of ventrobasal processes on the dorsal plate is shared between *Photinus* and *Saguassu* **gen. nov.**, and separates these two from *Ybytyramoan* and *Zoiudo*. Finally, *Saguassu* **gen. nov.** can be distinguished from *Photinus* by the elongate, apically oriented ventrobasal processes (growing outwards, globose, vestigial, or absent in *Photinus* [see for example Zaragoza-Caballero et al., 2023]).

In contrast, *S. rebellum* **sp. nov.** is most similar to *Lucidota*, due to the presence of small eyes and lanterns, but long serrate antennae. The question of the poor definition of *Lucidota* Laporte, 1833 has been addressed by multiple recent works (e.g. Vaz et al., 2020; Zeballos et al., 2022; note also that *Lucidota* has been consistently recovered as polyphyletic in recent phylogenetic analyses, including both morphological, molecular, and integrative phylogenetic analyses [e.g. Martin et al., 2017]). Comparing *S. rebellum* **sp. nov.** to the type of *Lucidota*, *L. banoni* Laporte, 1833, striking similarities on external morphologies arise, including the prothorax shape and color, tibial spur formula (0-1-1), rounded lanterns on sterna VI and VII, and emarginate posterior margin of sternum VIII. However, the aedeagal morphology is radically different: the dorsal plate is basally produced, and much longer than the phallobase, the ventral base is rudimentary, and the parameres are co-planar with the phallus and dorsally separated by the phallus in *S. rebellum* **sp. nov.** (whereas the dorsal plate is nearly flat and shorter than phallobase, the ventral plate is very well developed and basally widened, and the parameres are dorsal to the phallus and connected by a bridge in *L. banoni*).

Saguassu dissidens **comb. nov.** is incredibly similar to, and partly sympatric with, *Photinus cylindrus* (Olivier, 1905). Both species have really large eyes accommodated by the prothorax with anterior bulgings of the hypomeron, very short, cylindrical antennae, an anterior margin of the disc strongly curved, and moderately dehiscent elytra. However, *S. dissidens* **comb. nov.** can be distinguished from *Photinus cylindrus* by the absence of lanterns, tibial formula (0-1-1), and aedeagal morphology (dorsal plate basally produced and separating the parameres, and much longer than the phallobase, ventrobasal processes falciform and apically sharp) of the former (lanterns present and complete on sterna VI and VII, tibial formula *Photinus*-like [1-2-2], and aedeagal morphology *Photinus*-like [dorsal plate basally connected to the parameres by a thin bridge, shorter than the phallobase, ventrobasal processes short, projecting outwards and apically blunt in *Photinus cylindrus*).

The remaining four species (*Saguassu manauara* **sp. nov.,** *S. sinuosum* **sp. nov.**, *S. acutum* **sp. nov.,** and *S. serratum* **sp. nov.**) are superficially similar to *Photinoides mystrionophorus* McDermott, 1963 due to the intermediate-sized eyes and antennae, curved anterior margin of pronotal disc, well developed lanterns on sterna VI and VII, and sternum VII barely covering the anterior margins of VIII, versus broadly covering sternum VIII in most *Photinus*). However, these *Saguassu* species can be distinguished from *Photinoides mystrionophorus* based on the pronotal morphology (anterior expansion slightly longer than disc in *Saguassu* **gen. nov.** versus slightly shorter in *Photinoides*) tibia spur formula (0-1-1, versus 1-2-2 in *Photinoides*), in addition to aedegal morphology.

Checklist of *Saguassu* **gen. nov.** species:

– *Saguassu acutum* **sp. nov**
– *Saguassu dissidens* (Olivier, 1894) **comb. nov.**
– *Saguassu grossii* **sp. nov.**
– *Saguassu manauara* **sp. nov.**
– *Saguassu rebellum* **sp nov.**
– *Saguassu roura* **sp. nov.**
– *Saguassu serratum* **sp. nov.**
– *Saguassu sinuosum* **sp. nov.**

Key to *Saguassu* gen. nov. species based on males

1 – Antennae short (~1× as long as greater head width)(Fig. 1P), elytron moderately dehiscent; eyes ventrally approximate, distance between eyes narrower than submentum greatest width (Fig. 4Ee); lanterns absent (Fig. 1P)……………. *Saguassu dissidens* (Olivier, 1894) **comb. nov.**
1' – Antennae moderately long to long (~2 or 3× as long as greater head width)(eg. Fig. 1F, L, N), elytron not or just mildly dehiscent; distance between eyes at least 2× wider than submentum greater width; lanterns present on sternum VI and VII 2

2 – Antennae long (~3× as long as greater head width) (Fig. 1L); vertex plane; pronotum lateral margins divergent posteriorly (Fig. 5P-Q); sternum VII with an quadrangular, lantern, with posterior margin emarginate and covering the longitudinal medial third and up to two thirds of

the sternum length; sternum VI and VII with faint lanterns, lacking a reflector layer (Fig. 1L)…………………………………..……………… *Saguassu rebellum* **sp. nov.**
2’ – Antennae moderately long (~2× as long as greater head width); vertex concave; sides of pronotum rounded (eg. Fig. 5A, F, U); lanterns nearly or completely covering sterna VI and VII ……………………..... 3

3 – Elytron dark brown with a pale yellow spot at anterior half (Fig. 1M); lanterns covering the whole of sternal area; dorsal plate shorter than parameres, ventrobasal process with a basal projection; paramere with a basal, inward-facing spike (Fig. 10U–Y) ………………………..... *Saguassu grossii* **sp. nov.**
3’ – Elytral disc brown, lateral expansion pale yellow; lanterns not reaching outer margins; dorsal plate longer than parameres, ventrobasal process without a basal projection; parameres without a subapical spike ………………………………………………………………………... 4

4 – Dorsal plate distinctly globose at basal 1/3 (abruptly curved in lateral view), with a dorsolateral keel at basal third …………………………………………5

4’ – Dorsal plate less globose at basal 1/3 (more evenly tapered towards apex), without a dorsolateral keel at basal third …………………………………………6

5 – Parameres without a subapical membranous appendage, almost reaching apex of dorsal plate, ventrobasal process apically serrate.……………………………….… *Saguassu serratum* **sp. nov.**
5’ – Parameres with a subapical membranous appendage, a 1/5 shorter than dorsal plate, ventrobasal process apically acute and not serrate (Fig. 10K–M) ....*Saguassu roura* **sp. nov.**

6 – Tibia evenly brown; ventrobasal process wider apically, apically sinuose, without a subapical spike.… *Saguassu sinuosum* **sp. nov.**
6’ – Basal 1/5 of tibia testaceous, then progressively more dark-brown towards apex; ventrobasal process apically acute, with a subapical spike 7

7 – Anterior margin of labrum strongly emarginate; dorsal plate base narrow (as wide as phallobase at midlength), ventrobasal process almost as long as core paramere; ventral plate diamond-shaped (Fig. 10A–E)………. *Saguassu acutum* **sp. nov.**
7’ – Anterior margin of labrum straight. Dorsal plate base wide (a 1/5 wider than phallobase at midlength), ventrobasal process ~1/3 shorter than core paramere; ventral plate subcircular (Fig. 10F–J)……. *Saguassu manauara* **sp. nov.**

Saguassu acutum **sp. nov. Viana, Roza, Vaz, and Silveira**

(Figs. 1A–B; 4A–F; 5A–E; 7A,G; 9A–D; 10A–E)

Diagnostic description. Antennal sockets separated by less than half of socket width. Antennae moderately long (~2× as long as greater head width), antennomere III lateral margins subparallel, almost as long as IV length. Vertex concave. Eyes ventrally moderately approximate, distance between eyes around three times submentum greatest width. Labrum with anterior margin strongly emarginate. Pronotum lateral margins rounded. Elytron subparallel, brown with an inner and an outer pale-yellow stripes throughout its length. Legs with coxae and tibia yellowish brown, femur and tarsus brown. Sternum VI and VII with lanterns covering almost the whole sternal area, not reaching outer margins. Sternum VIII with emarginate posterior margin. Sternum IX with feebly emarginate posterior margin. Pygidium with anterior margin emarginate, lateral margins convergent and rounded acuminate apex. Syntergite with anterior margin slightly emarginate, subparallel lateral margins up to two thirds of its length. Dorsal plate distinctively longer than parameres, without apical membranous projection, as wide as phallobase at midlength, slightly globose at basal third, without a dorsolateral keel at basal third. Ventrobasal process almost as long as core paramere, without basal projection and with apex acute with two spikes. Ventral plate diamond-shaped. Parameres with a subapical membranous appendage, without medioventral projection.

Etymology. Acutum is the Latin word for sharp, and it refers to the apex of the ventrobasal processes of the male aedeagus in this species. The name is in the nominative neutral singular case.

Biology. Males were seen by G. Powell in Peru, Madre de Dios, Finca Las Piedras, in January 2022. Males produce very long (2-3 seconds) green flashes followed by a dark phase of 5-8 seconds. The glow seemed to be overly faint for their size.

Material examined. HOLOTYPE. PERU: Madre de Dios, Finca Las Piedras, BYU-PE-2022 (-12.2255, -69.1147), 16/01/2022, SM Bybee & GS Powell col., ♂ (MUSM).
33 PARATYPES: Madre de Dios, Finca Las Piedras, BYU-PE-2022 (-12.2255, -69.1147), 16/01/2022, SM Bybee & GS Powell col., 20♂ (BYU), idem 9♂ (USNM). Idem, Concession Bilca, -12.2248, -68.9699, 14/01/2022, SM Bybee & GS Powell col, 2♂ (NCSU). Idem, 2♂ (UGCA)

Saguassu manauara sp. nov. Viana, Roza, Vaz, and Silveira

(Figs. 1G–H; 4G–L; 5F–J; 7B,H; 9E–H; 10U–Y)

Diagnostic description. Antennal sockets separated by less than half of socket width. Antennae moderately long (~2× as long as greater head width), antennomere III lateral margins subparallel, almost as long as IV length. Vertex concave. Eyes ventrally moderately approximate, distance between ~~eyes~~ around three times submentum greatest width. Labrum with anterior margin straight. Pronotum lateral margins rounded. Elytron subparallel, brown with an inner and an outer pale-yellow stripes throughout its length, evanescence on elytral apex. Legs with coxae and tibia yellowish brown, femur and tarsus brown. Sternum VI and VII with lanterns covering almost the whole sternal area, not reaching outer margins. Sternum VIII with emarginate posterior margin. Sternum IX with feebly emarginate posterior margin. Pygidium with anterior margin emarginate, lateral margins convergent and acuminate apex. Syntergite with anterior margin deeply emarginate, subparallel lateral margins up to two thirds of its length. Dorsal plate as long as parameres, without apical membranous projection, one fifth wider than phallobase at midlength, slightly globose at basal third, without a dorsolateral keel at basal third. Ventrobasal process as long as two thirds of core paramere, without basal projection and with apex acute with two spikes. Ventral plate subcircular. Parameres with a subapical membranous appendage, without medioventral projection.

Etymology. Manauara is the gentilic word for “born in Manaus” in Portuguese, the main language spoken in Brazil. Name in apposition.

Material examined. HOLOTYPE: Brasil, AM, Manaus, Reserva Ducke, Malaise 5, Plot B, III/1995, 1 ♂ (BMNH).
15 PARATYPES: Brasil, AM, Manaus, Reserva Ducke, Malaise 2, Plot A, III/1995, 2♂, MGV Barbosa col.. Idem, Malaise 2, Plot B, III/1995, 1♂, MGV Barbosa col. (MNRJ). Idem, Malaise 3, Plot B, III/1995, 2♂, MGV Barbosa col. (INPA). Idem, Malaise 5, Plot A, III/1995, 2♂, MGV Barbosa col. (MPEG). Idem, Malaise 4, Plot A, II/1995, 1♂, MGV Barbosa col. (BMNH). Idem, Malaise 4, Plot A, III/1995, 1♂, MGV Barbosa col. (BMNH). Idem, Malaise 4, Plot A, I/1996, 2♂, MGV Barbosa col. (MZSP). Idem, Malaise 4, Plot B, III/1995, 3♂, MGV Barbosa col.. Idem, MGV Barbosa col. (BMNH). Idem, no date, MGV Barbosa col., 1♂ (BMNH).

Saguassu dissidens (Olivier, 1894) comb. nov.

(Figs. 1O–P; 4Ee–Jj; 5Z–Dd; 7F,L; 9Cc–Ff; 10Jj–Nn)

= *Photinus dissidens* Olivier, 1894
= *Heterophotinus dissidens* (Olivier, 1894)

Diagnostic description. Antennal sockets separated by almost the entire socket width. Antennae short (~1x as long as greater head width), antennomere III lateral margins subparallel, slightly longer than IV. Vertex slightly concave. Eyes ventrally approximate, distance between eyes narrower than submentum greatest width. Labrum with anterior margin straight. Pronotum lateral margins subparallel. Elytron moderately dehiscent, brown without any stripe or spot. Legs with coxae and tibia yellowish brown, femur and tarsus brown. Sternum VI and VII without lanterns. Sternum VIII with emarginate posterior margin. Sternum IX with truncate posterior margin. Pygidium with anterior margin emarginate, lateral margins convergent and almost straight apex. Syntergite with anterior margin slightly emarginate, subparallel lateral margins up to two thirds of its length. Dorsal plate shorter than parameres, with apical membranous projection, as wide as phallobase at midlength, distinctly globose at basal third, without a dorsolateral keel at basal third. Ventrobasal process as long as half of core paramere, without basal projection and with apex acute with one spike. Ventral plate absent. Parameres without a subapical membranous appendage, without medioventral projection.

Material examined. LECTOTYPE (designated herein). Banda Orienta[l] [URUGUAY] // *Heterophotinus dissidens*, Ern. Oliv., 1 ♂ (MNHN). **3 PARALECTOTYPES.** Banda Oriental, 2 ♂, 1 ♀ (MNHN).

Additional material examined. URUGUAY: Banda Oriental [Montevideo?], 1 ♂, 1 ♀ (MNHN). Banda Oriental [Montevideo?] 1 ♂ (MNHN). Idem, Cornell U. lot 631, Sub 248, 1 ♂ (CUIC). Uruguay, 1 ♀ (MNHN). ARGENTINA: Corrientes, I/1972, 3 ♂ (WCU). Sunchales, (Córdoba) [sic, currently Santa Fé], XI.1898, F. Silvestri, 1 ♂ (MSNG).

Remarks. Olivier (1894) described the species from both males and a female. We infer that four specimens in Olivier's collection at MNHN are syntypes because they have the same label data ("Banda Oriental"). In addition, the author gave a range (10-12mm) of male sizes, implying that he saw more than one male specimen. Even though this species was described as a *Photinus*, Olivier (1894) proceeded to say that it would constitute a section that he would call *Heterophotinus* Olivier, 1894, consistent with the label on the specimen designated here as lectotype.

Saguassu dissidens (Olivier, 1894) **comb. nov.** is similar to a few Lucidotini species from Southern South America with large eyes, short cylindrical antennae, elytra, convex pronotum, and dehiscent elytra, including *Photinus cylindra* (Olivier, 1905) and *Heterophotinus porrectus* Olivier, 1908. However, it can be distinguished from these by the tibial spur formula (0-1-1 vs 1-2-2 in *P. cylindra* and *H. porrectus*) and the absence of lanterns (in *P. cylindra* and *H. porrectus*).

Saguassu rebellum sp. nov. Viana, Roza, Vaz, and Silveira

(Figs. 1K–L; 4S–X; 5P–T; 7D,J; 9U–X; 10Z–Dd)

Diagnostic description. Antennal sockets separated by almost the entire socket width. Antennae long (~3× as long as greater head width), antennomere III lateral margins apically divergent, two thirds of IV length. Vertex plane. Eyes ventrally separated, distance between eyes around five times submentum greatest width. Labrum with anterior margin emarginate. Pronotum lateral margins divergent posteriorly. Elytron subparallel, brown with an inner and an outer pale-yellow stripes throughout its length. Legs with coxae and tibia yellowish brown, femur and tarsus brown. Sternum VI without lantern, VII with a roughly quadrangular lantern, with posterior margin emarginate and covering the longitudinal medial third and up to two thirds of the sternum length. Sternum VIII with emarginate posterior margin. Sternum IX with emarginate posterior margin. Pygidium with anterior margin emarginate, lateral margins convergent and truncated apex. Syntergite with anterior margin slightly emarginate, subparallel lateral margins up to half of its length. Dorsal plate slightly longer than parameres, without apical membranous projection, as wide as phallobase at midlength, distinctly globose at basal half, without a dorsolateral keel at basal third. Ventrobasal process as long as half of core paramere length, without basal projection and with apex acute with a single spike. Ventral plate absent. Parameres with a subapical membranous appendage, without medioventral projection.

Etymology. Rebellum is a Latin word for rebel, in the nominative singular, gender neutral form. The name refers to the unusual morphology of this species among its congenerics.

Material examined. HOLOTYPE: Brasil, MG, Chapada dos Guimarães, PI. 1, 12-18.X.2013, Malaise trap, G. Melo col., ♂ (DZUP).
2 PARATYPES: Brasil, MG, Chapada dos Guimarães, PI. 1, 12-18.X.2013, Malaise trap, G. Melo col., 2♂ (DZUP).

***Saguassu roura* sp. nov. Viana, Roza, Vaz, and Silveira**

(Figs. 1I–J; 4M–R; 5K–M; 7C,I; 9Q–T; 10U–Y)

Diagnostic description. Antennal sockets separated by less than half of socket width. Antennae moderately long (~2× as long as greater head width), antennomere III lateral margins subparallel, almost as long as IV length. Vertex concave. Eyes ventrally moderately approximate, distance between eyes around three times submentum greatest width. Labrum with anterior margin strongly emarginate. Pronotum lateral margins rounded. Elytron subparallel, brown with an inner and an outer pale-yellow stripes throughout its length, evanescence in the apex. Legs with coxae and tibia yellowish brown, femur and tarsus brown. Sternum VI and VII with lanterns covering almost the whole sternal area, not reaching outer margins. Sternum VIII with straight posterior margin. Sternum IX with distinctly emarginate posterior margin. Pygidium with anterior margin straight, lateral margins convergent and rounded acuminate apex. Syntergite with anterior margin distinctly emarginate, subparallel lateral margins up to two thirds of its length. Dorsal plate slightly longer than parameres, without apical membranous projection, as wide as phallobase at midlength, distinctly globose at basal third, with a dorsolateral keel at basal third. Ventrobasal process as long as two thirds of core paramere, without basal projection and with apex acute with two spikes. Ventral plate diamond-shaped. Parameres with a subapical membranous appendage, without medioventral projection.

Etymology. Roura is a commune in French Guyana and the type locality of this new species. Name in apposition.

Material examined. HOLOTYPE. FRENCH GUIANA: 30 km SE Roura on Kaw Rd., 11-ii-2010, N04º33.882', W052º12.404', J.E.Eger, coll., at night, 323m, ♂ (FSCA).
4 PARATYPES. FRENCH GUIANA: 21 km SE Roura on Kaw Rd., 12-ii-2010, N04º36.115', W052º15.972', J.E.Eger, coll., MV Light, voucher code PIE150, 1 ♂ (NCSU). Amazone Nature lodge, 30 km SE Roura on Kaw Rd., 5-19-ii-2010, N04º33.570', W052º12.433', J.E.Eger, coll., UV light trap, 300m, 1 ♂ (MZSP). idem, 1 ♂ (USNM). FRENCH GUIANA: 21 km SE Roura on Kaw Rd., 6-7-ii-2010, N04º36.115', W052º15.972', J.E.Eger, coll., MV Light, voucher code PIE150, 1 ♂ (FSCA).

Saguassu grossii sp. nov. Viana, Roza, Vaz, and Silveira

(Figs. 1M–N; 4Y–Dd; 5U–Y; 7E,K; 8A–L; 9Cc–Ff; 10Ee–Ii; 11A–I)

Diagnostic description. Antennal sockets separated by around half of the socket width. Antennae moderately long (~2× as long as greater head width), antennomere III lateral margins subparallel, almost as long as IV length. Vertex concave. Eyes ventrally separated, distance between eyes around five times submentum greatest width. Labrum with anterior margin emarginate. Pronotum lateral margins rounded. Elytron subparallel, dark brown with a pale yellow spot at anterior half, of variable length but usually from suture to two thirds of elytron width. Legs with coxae and tibia yellowish brown, femur and tarsus brown. Sternum VI and VII with lanterns covering the whole sternal area. Sternum VIII with tridentate posterior margin. Sternum IX with emarginate posterior margin. Pygidium with anterior margin emarginate, lateral margins rounded and rounded apex. Syntergite with anterior margin distinctly emarginate, subparallel lateral margins up to half of its length. Dorsal plate shorter than parameres, with apical membranous projection, one fifth thinner than phallobase at midlength, distinctly globose at basal two thirds, without a dorsolateral keel at basal third. Ventrobasal process as long as one third of core paramere length, with basal projection and with apex acute with a single spike. Ventral plate absent. Parameres without a subapical membranous appendage, with an inner medioventral tooth-like projection.

Etymology. The epithet is in honor of the former naturalist and professor Paschoal Grossi, who is, up to now, the only collector of this species. Name in the genitive masculine case

Biology. P. Grossi (pers. comm.) reported seeing them swarming deep into the woods on several occasions, males were flashing (and definitely not emitting long glows), but Grossi could not determine the exact flash pattern.

Material examined. HOLOTYPE: Brasil, PE, Paulista, Aldeia Granja do Delegado, Km 14, -7.919426°S, -35.019929°W, 128 m, 04-16.III.2022, Ponto Mata, Malaise trap, Grossi & Galdino col., ♂ (CERPE).

238 PARATYPES. Brasil, PE, Paulista, Aldeia Granja do Delegado, Km 14, -7.919426°S, -35.019929°W, 128 m, 04-16.III.2022, Ponto Mata, Malaise trap, Grossi & Galdino col., 5♂, (MZSP); idem, 17.II-04.III.2022, Ponto Mata, Malaise trap, Grossi & Galdino col., 33♂ (DZRJ); idem, 04-18.III.2022, Ponto Riacho, Malaise trap, Grossi, Costa & Galdino col., 4♂ (INPA); Brasil, PE, Paulista, Aldeia Granja do Delegado, 15-30.III.2022, Malaise trap, Grossi & Galdino col., 16♂ (MNRJ); Brasil, PE, Paulista, Aldeia Granja do Delegado, 15-30.III.2022, Ponto Mata, Malaise trap, Grossi & Galdino col., 2♂ (MPEG); Brasil, PE, Paulista, Aldeia Granja do Delegado, 15-30.III.2022, Ponto Riacho, Malaise trap, Grossi & Galdino col., 16♂ (DZUP); Brasil, PE, Paulista, Aldeia Granja do Delegado, 15-30.III.2022, Malaise trap, Grossi & Galdino col., 15♂ (DZRJ); Brasil, PE, Paulista, Aldeia Granja do Delegado, 30.III-11.IV.2022, Ponto Mata, Malaise trap, Grossi & Costa col., 19♂ (1 completely dissected), 1♀ (abdomen dissected) (DZRJ); Brasil, PE, Paulista, Aldeia Granja do Delegado, 30.III-11.IV.2022, Ponto Riacho, Malaise trap, Grossi & Costa col., 4♂ (DZRJ); Brasil, PE, Paulista, Aldeia Granja do Delegado, 11-28.IV.2022, Ponto Riacho, Malaise trap, Grossi & Costa col., 2♂ (DZRJ); Brasil, PE, Paulista, Aldeia Granja do Delegado, 11-28.IV.2022, Ponto Mata, Malaise trap, Grossi & Costa col., 22♂, 1♀ (DZRJ); Brasil, PE, Paulista, 28.IV-10.V.2022, Ponto Mata, Malaise trap, Grossi & Costa col., 15♂ (DZRJ); Brasil, PE, Paulista, Aldeia Granja do Delegado, 28.IV-10.V.2022, Ponto Riacho, Malaise trap, Grossi & Costa col., 6♂ (DZRJ). Idem, 04-16.III.2022, Malaise trap, 40♂ (CERPE); idem, 17.ii-04.iii.2022, Malaise trap, Costa, Galdino & Grossi col., 37♂ (CERPE).

***Saguassu sinuosum* sp. nov. Viana, Roza, Vaz, and Silveira**

(Figs. 1C–D; 9E–H; 10F–J)

Diagnostic description. Antennal sockets separated by less than half of socket width. Antennae moderately long (~2× as long as greater head width), antennomere III lateral margins subparallel, almost as long as IV length. Vertex concave. Eyes ventrally moderately approximate, distance between eyes around three times submentum greatest width. Labrum with anterior margin straight. Pronotum lateral margins rounded. Elytron subparallel, brown with an inner and an outer pale-yellow stripes throughout its length. Legs evenly brown. Sternum VI and VII with lanterns covering almost the whole sternal area, not reaching outer margins. Sternum VIII with sinuouse posterior margin. Sternum IX with rounded posterior margin. Pygidium with anterior margin emarginate, lateral margins convergent and rounded apex. Syntergite with anterior margin distinctly emarginate, subparallel lateral margins up to half of its length. Dorsal plate as long as parameres, without apical membranous projection, as wide as phallobase at midlength, slightly globose at basal third, without a dorsolateral keel at basal third. Ventrobasal process as long as half of core paramere, without basal projection and with sinuous apex, without spikes. Ventral plate diamond-shaped. Parameres with a subapical membranous appendage, without medial projection.

Etymology. The epithet refers to the sinuose shape of the apex of the ventrobasal process in this species. Name in the nominative neutral form.

Material examined. HOLOTYPE. Brasil, Pará, Melgaço, Caxiuanã-Grade, PPBio [Programa de Pesquisa em Biodiversidade], 22.III.2006, Silva S. S. & J. Dias, Malaise trap, ♂, (MPEG). **23 PARATYPES:** 5 specimens with same labels**,** 3♂, 1♀, 1 of indeterminate sex [lacking abdomen]) (MPEG); idem, 2♂ (MZSP); Brasil, Pará, Melgaço, Caxiuanã-Grade PPBio, 27.III.2006, Silva S. S. & J. Dias, Malaise trap, 1♂, (MPEG); Brasil, Pará, Melgaço, Caxiuanã - ECFPn, 23.III.1998, O. Oliveira & J. Pena col, S. Malaise trap, 1♂, 1♀ (MNRJ); Brasil, Pará, Melgaço, Caxiuanã - ECFPn, 28.III.1998, O. Oliveira & J. Pena col, S. Malaise, 1♂, 1♀ (MPEG); Brasil, Pará, Barcarena, Capoeira, 20 a 23.I.1984, Armadilha suspensa, 2m.a.s.l., 1♂ (MPEG); Brasil, Pará, Barcarena, 22.I.1984, Tadaieswky V. 1♂ (MPEG); Brasil, Pará, Belém, Icoraci, 19.XII.1961, J. & B. Bechyné, 7♂, 1♀ (MPEG); Brasil, Pará, Belém, Mocambo, 10.I.1978, Mata terra firme, Armadilha Malaise trap, 1♂ (MPEG).

Saguassu serratum **sp. nov. Viana, Roza, Vaz, and Silveira**

(Figs. 1E–F; 6A–C; 9I–L; 10K–O)

Diagnostic description. Antennal sockets separated by less than half of socket width. Antennae moderately long (~2x as long as greater head width), antennomere III lateral margins subparallel, almost as long as IV length. Vertex concave. Eyes ventrally moderately approximate, distance between eyes around three times submentum greatest width. Labrum with anterior margin emarginate. Pronotum lateral margins rounded. Elytron subparallel, brown with an inner and an outer pale-yellow stripes throughout its length. Legs with coxae and tibia yellowish brown, femur and tarsus brown. Sternum VI and VII with lanterns covering almost the whole sternal area, not reaching outer margins. Sternum VIII with emarginate posterior margin. Sternum IX with truncate posterior margin. Pygidium with anterior margin emarginate, lateral margins convergent and rounded apex. Syntergite with anterior margin slightly emarginate, subparallel lateral margins up to a third of its length. Dorsal plate as long as parameres, without apical membranous projection, as wide as phallobase at midlength, distinctly globose at basal third, with a dorsolateral keel at basal third. Ventrobasal process as long as half of core paramere, without basal projection and with serrate apex with an inconspicuous spike. Ventral plate diamond-shaped. Parameres without a subapical membranous appendage, without medial projection.

Etymology. The epithet refers to the serrate shape of the apex of the ventrobasal process in this species. Name in the nominative neutral form.

Material examined. HOLOTYPE. Brasil, Pará, Serra Norte, 15 a 18.II.1985, Armadilha Malaise, ♂ (MPEG). **PARATYPE.** Brasil, Pará, Serra Norte, 15 a 18.II.1985, Armadilha Malaise, ♂ (MPEG).

Discussion

Our results warranted the description of a new genus of Lucidotini: Photinina fireflies, based on a Bayesian phylogenetic analysis of 32 taxa and 97 characters. Our finds bear implications for the biology and taxonomy of Lucidotini fireflies, as discussed below.

Sensory morphology and lantern diversity within Saguassu ***gen. nov.*** *mirrors, at a smaller scale, the range seen for the family at large.*

Fireflies have evolved using a combination of visual and olfactory cues for mate finding and selection (Stanger-Hall et al., 2018; Powell et al. 2022; Jakubec & Novak, 2024). Visual cues include both continuous glows and rhythmic flashes (see Faust, 2017 for an excellent overview of bioluminescence in North American species). A few main "mating syndromes" result from the differential role each signal (light – flashes and glows; and pheromones) plays. Where males follow female glows, they usually have ventrally bulging eyes, and short filiform antennae (Stanger-Hall et al., 2018). In such systems, males may (e.g. *Phausis* LeConte, 1851, *Lamprohiza* Motschulsky, 1853, *Diaphanes* Motschulsky, 1853) or may not (*Lampyris* Geoffroy, 1762, *Pelania* Mulsant, 1860, *Pleotomodes* Green, 1948) have lanterns; when present, the lanterns never occupy the whole sterna. Where males and females use flashes to communicate, males have intermediate-sized eyes, and well developed lanterns that occupy the whole sterna VI and VII, which may be longer than preceding sterna. In contrast, when only pheromones are available, males have long and more elaborate (serrate, flabellate) antennae, smaller eyes, and, if present, rudimentary lanterns (e.g. *Costalampys*, *Lucidota banoni*).

Saguassu **gen. nov.** is an interesting case in which closely related species have widely different sensor and lantern morphology (Fig. 1). The spectrum of diversity seen on those structures mirrors that seen for the family at large (except for antennal lamellae, unknown in *Saguassu* **gen. nov.**). It is, to our knowledge, the firefly genus with the broadest variation in these external structures. In contrast, the aedeagal morphology is remarkably stable, comparatively.

Saguassu grossii **sp. nov.** is a textbook example of a "flasher" morphology, whereas *S. dissidens* **comb. nov.** has a "glower" morphology – the latter is indeed the first South American species with "Lampyris-like" morphology (enlarged eyes, short antennae, and no lanterns). Meanwhile, sensor and lantern morphology in *S. rebellum* **sp. nov.** matches those seen in many diurnal Lucidotini, and the remaining four species look like an intermediate between "flashers" and "glowers". Consistent with that observation, *S. acutum* **sp. nov.** males have been seen producing very long and faint flashes, which could be seen as an intermediate between short, very bright flashes and more or less continuous glows. However, given the long dark phases and the faint light it produces, it could also be seen as a pathway to a loss of light, as in many males of glowing species (e.g. *Lampyris*). Yet, the direction of eye growth is mainly ventral in *S. dissidens* **comb. nov.**, as in many other lampyrid “glowers”, in contrast to the more or less globular or elliptical (evenly bulging dorsally and ventrally) eyes of the flashers.

Other cases of closely related species with widely different sensory and lantern morphology – all in Lampyrinae – include species in *Photinus* (see Stanger-Hall et al., 2007, Zaragoza-Caballero et al., 2023), *Dilychnia* Motschulsky, 1853 (Vaz et al., 2020), *Diaphanes* (Li & Liang, 2007), and *Pyrocoelia* Gorham, 1880 (Jeng et al., 1999; Zhu et al., 2022). “Dark” (i.e. lanternless) *Photinus* species were found indeed nested with (Stanger-Hall et al., 2007 [including “*Ellychnia*” species, but also *Photinus cookii* Green, 1956 and *Photinus indictus* LeConte, 1881]) or very close to (Zaragoza-Caballero et al., 2023) flashing species of *Photinus*, which ultimately led to a redefinition of this genus by Zaragoza-Caballero et al. (2023). *Dilychnia* is another genus with species with greater eyes, smaller filiform antennae, and complete lanterns (e.g. *D. dumasi* Vaz, Mermudes, Paiva & Silveira, 2020, *D. propinqua* [Olivier, 1909], *D. cavicollis* Olivier, 1912), but also species with longer serrate antennae, intermediate-sized eyes, and rudimentary lanterns (e.g. *D. disparilis* Olivier, 1911, *D. guttula* [Fabricius, 1801], *D. ruficollis* Motschulsky, 1854) (Vaz et al., 2020).

A wide variation in sensory and lantern morphology is also seen in both *Diaphanes* and *Pyrocoelia*. For example, *Diaphanes pectinealis* Li and Liang, 2007 males have flabellate antennae and intermediate-sized eyes, unlike all other *Diaphanes*, which have enlarged eyes and filiform antennae. Despite important similarities between *D. pectinealis* and diurnal *Pyrocoelia* species, the former was confirmed as a *Diaphanes* by molecular phylogenetics and morphology (Li et al., 2006; Li & Liang, 2007; Zhu et al., 2022; but see Martin et al., 2019). The overlap between diagnostic sensory traits between *Diaphanes* and *Pyrocoelia* led Li and Liang (2007) to call for updated diagnoses of these genera. Likewise, *Pyrocoelia* species feature a broad range of variation in sensor and antennal morphology, including completely dark species with long, elaborate antennae, small eyes, and species with well developed lanterns, enlarged eyes and comparatively smaller, simpler antennae (see, for example, Jeng et al., 1999). The close relationship of species with such disparate external morphologies, independently confirmed by molecular phylogenies (e.g. Suzuki, 1997; Zhu et al., 2022), also suggests that other traits be used at the genus-level taxonomy of the Lampyrinae.

Given the wide variation in sensor morphology in *Saguassu* **gen. nov.**, our study echoes these claims for updated diagnoses of Lucidotini taxa, and suggests that diversification in mating signals and sensor morphology played a key role in the diversification of this lineage.

Steps towards a revision of the Lucidotini genera and subtribes

Our study corroborates the value of traits not traditionally used in lampyrid taxonomy for reconstructing evolutionary relationships of Lucidotini. It also reiterates the unsuitability of traditionally used traits in genus-level diagnoses, such as overall sensor and lantern traits (e.g. whether the antenna is serrate, flabellate or filiform; or the presence/absence or size of lanterns). For example, many *Saguassu* **gen. nov.** and *Photinus* species are incredibly similar based on traditional characters, and yet both lineages show parallel variations on these. Nevertheless, they can be easily separated by the tibial formula (0-1-1 and 1-2-2, respectively), or aedegal morphology (phallobase longer than dorsal plate, dorsal plate basally produced, and parameres completely separated in *Saguassu* **gen. nov.**; phallobase shorter than dorsal plate, dorsal plate not basally produced and connected to parameres by a thin bridge in *Photinus*). We note that many of the most useful traits require dissections, and future genus-level diagnoses of Lucidotini taxa may be dominated by such traits, given the overall lability of traditionally used external characters. Below, we discuss character variation in Lucidotini, with an emphasis on taxa most similar to *Saguassu* **gen. nov.**.

Saguassu **gen. nov.** is one of four valid genera bearing ventrobasal processes, along with *Alychnus*, *Photinus*, and *Photinoides*. Two junior synonyms of *Photinus*, *Ellychnia* and *Macrolampis*, were synonymized based on the shared presence of ventrobasal processes (Zaragoza-Caballero et al., 2020), which was later supported by phylogenetic analyses (Zaragoza-Caballero et al., 2023). Several *Photinus* species exist which do not have such processes (e.g., genus *Paraphotinus* Zaragoza, 1995, synonymized with *Photinus* in Zaragoza-Caballero et al., 2023), supposedly due to a secondary loss. However, the presence of these processes in closely related but reciprocally monophyletic (i.e., *Saguassu* **gen. nov.**) or neighboring taxa (i.e., *Alychnus* and *Photinoides*), that also happen to be morphologically very distinctive, calls for future studies with denser taxon and character sampling to revisit the condition of *Ellychnia* and *Macrolampis*. We believe that splitting (i.e., pulling monophyletic taxa out of) *Photinus* and providing authoritative species-level keys and illustrated atlases is sorely needed to facilitate identification of Lucidotini taxa. However, the shared presence of ventrobasal processes, in combination with other traits, may be used in the future to improve the diagnoses of higher-level taxa in Lucidotini.

Lucidotini has 4 subtribes: Photinina LeConte, 1881, Lucidotina Lacordaire 1857, Dadophorina Olivier, 1907, and Phosphaenina McDermott, 1964. In addition, there are several genera currently placed as "*incertae sedis*". While revising the subtribal classification of Lucidotini goes beyond the scope of this work, the amount of phylogenetic information recently accumulated yielded important information that we summarize below in hopes of fostering future revisionary work on this tribe.

Three groups within Lucidotini have started to emerge in phylogenetic analyses, both based on morphology and DNA. We will refer to them as "*Photinus* lineage", "*Scissicauda* lineage", and "*Phosphaenus* lineage" (note that these could serve as a basis for a revised Photinina and Phosphaenina in the future). Defining traits of these lineages are mostly based on features that require dissection (e.g. terminalic, genitalic, or otherwise cryptic [e.g. submentum]). These three lineages are consistent with and the most recent DNA-based phylogenetic analysis (Martin et al., 2019) and have also been recovered in most recent phylogenetic analyses based on morphology (Roza et al., 2022; Zeballos et al., 2022). We refrain from taking nomenclatural acts until a more comprehensive and thorough study of Lucidotini taxa is undertaken.

"*Photinus* lineage" as defined here include those taxa with submentum anteriorly membranous and usually rounded or straight, pygidium as wide as long or wider, posterior corners barely visible or absent; syntergite evenly sclerotized, and aedeagi with a dorsal plate entire and variably clefted, bearing ventrobasal processes, struts absent (not seen through phallobase), ventral plate rudimentary or absent, and paramere tips distinctly membranous and/or bearing subapical membranous appendages. The parameres are co-planar to the phallus, but never broadly fused at the base; instead, they are connected by a thin bridge. "*Photinus* lineage" include *Alychnus*, *Photinoides*, *Photinus*, and *Saguassu* **gen. nov.**.

The "*Scissicauda* lineage" include those taxa with submentum well sclerotized and notched anteriorly, pygidium usually longer than wide, sometimes as wide as long in some *Pyropyga*, posterior corners barely visible or absent, syntergite medially longitudinally split forming two plates, and aedeagi with a dorsal plate entire and variably clefted, without ventrobasal processes, struts absent (not seen through phallobase), ventral plate usually well-developed (except in *Haplocauda*), and parameres evenly sclerotized. The parameres are co-planar and broadly fused to the dorsal plate at the base. The "*Scissicauda* lineage" includes *Haplocauda*, *Scissicauda*, *Pyractonema* Solier, 1849, and *Pyropyga*. See Zeballos et al (2022) for a more detailed account on this lineage. Illustrations and descriptions of *Heterophotinus*, *Robopus* Motschulsky, 1853, and *Rufolychnia* Kazantsev, 2007 suggest they may also belong here (see Kazantsev & Zaitsev, 2008; Silveira pers. ob.).

Lastly, the "*Phosphaenus* lineage" includes those taxa with submentum anteriorly membranous, pygidium usually as wide as long but longer than wide in some *Luciuranus*, posterior corners well developed but absent in some *Luciuranus*, syntergite evenly sclerotized, and aedeagi with a dorsal plate longitudinally split forming two stylets or bars, often with a membranous endossac, without ventrobasal processes, struts present and with a unique joint, and parameres evenly sclerotized. The parameres are dorsal to the dorsal plate, and connate to this unique joint. "*Phosphaenus* lineage" includes *Phosphaenus*, *Phosphaenopterus*, and *Luciuranus*, in addition to a few *Lucidota* species that are very different from the type, *L. banoni*, such as *L. atra* and *L. punctata* (LeConte, 1852). Illustrations and descriptions (e.g. Kawashima, 2021) suggest that *Lucidina* Gorham, 1883 may also belong to this lineage.

Together, these observations highlight the value of thorough comparative studies in search of new traits, and the need for updated revisions of higher taxa in Lucidotini.

Conclusions

Our work includes the description of seven new species of Lucidotini fireflies. Our phylogenetic analysis supported the description of *Saguassu* **gen. nov.**, the transfer of a former *Photinus* species, *S. dissidens* **comb. nov.**, and the polyphyly of *Lucidota*. In addition, our work contributes to a revision of the higher-level taxonomy of the Lucidotini by providing a thorough comparison of the closely allied Photinina, and by pointing out key traits supporting a few inclusive nodes in the Lucidotini phylogeny.

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Figure 1

Diversity of *Saguassu* gen. nov.

This illustration highlights the diversity in sensor morphology (eyes and antennae) and lantern structures, as observed in the habitus, with dorsal views (A, C, E, G, I, K, M, O) and ventral views (B, D, F, H, J, L, N, P). A–B: *S. acutum* **sp. nov.**. C–D: *S. sinuosum* **sp. nov.**. E–F: *S. serratum* **sp. nov.**. G–H: *S. manauara* **sp. nov.**. I–J: *S. roura* **sp. nov.**. K–L: *S. rebellum* **sp. nov.**. M–N: *S. grossii* **sp. nov.**. O–P: *S. dissidens* (Olivier, 1894) **comb. nov.**. Scale bar: 1mm.

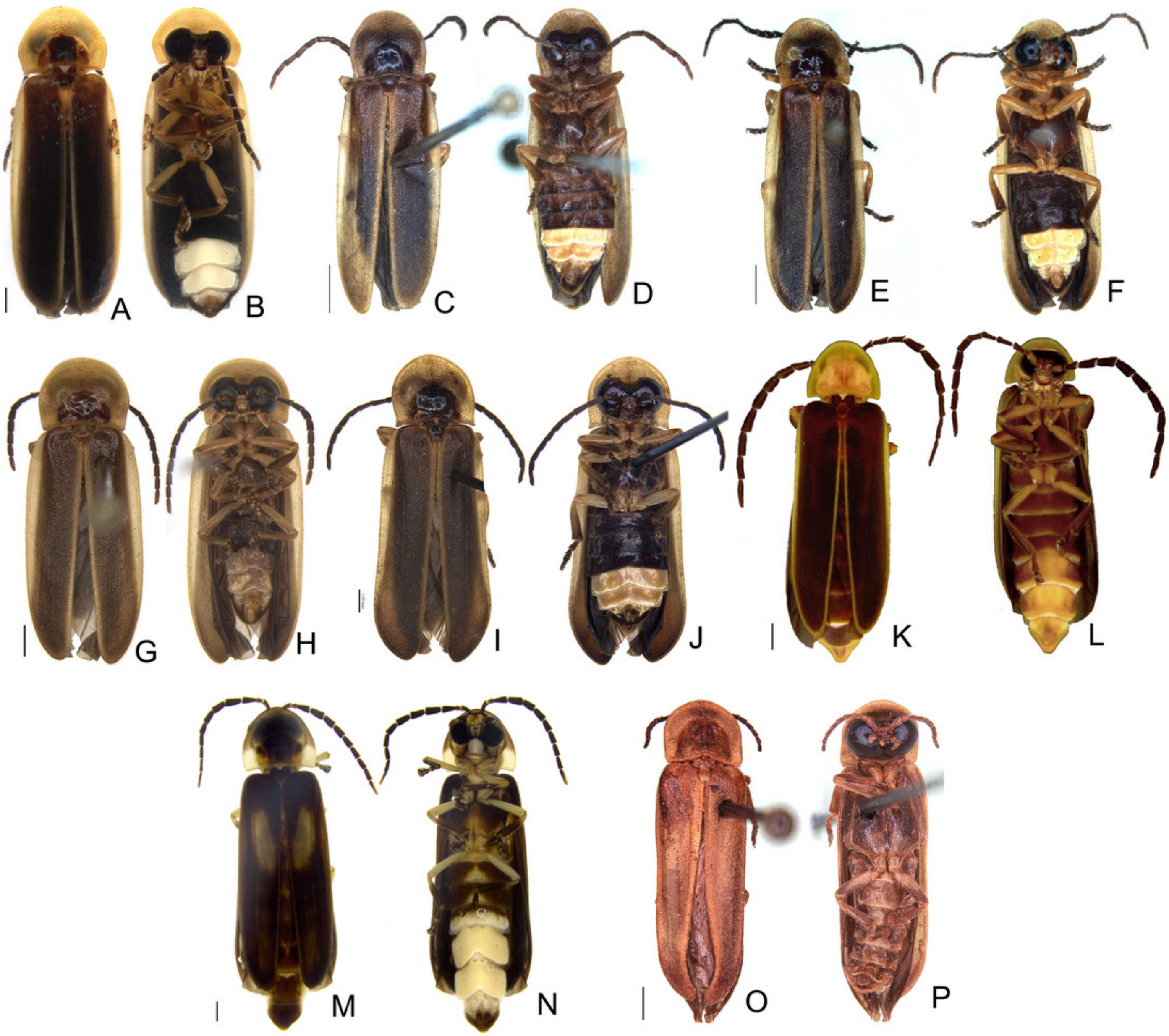
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Figure 2

Majority consensus of a Bayesian inference (see Material & Methods for more details) of 32 species and 97 traits.

The resulting phylogenetic tree found strong support for a monophyletic *Saguassu* **gen. nov.** upon the transfer of *Photinus dissidens* Olivier, 1894. *Saguassu* **gen. nov.** was found closer to other taxa bearing ventrobasal processes (i.e. *Alychnus*, *Photinus*, and *Photinoides*), forming the "*Photinus*" lineage discussed in this paper.

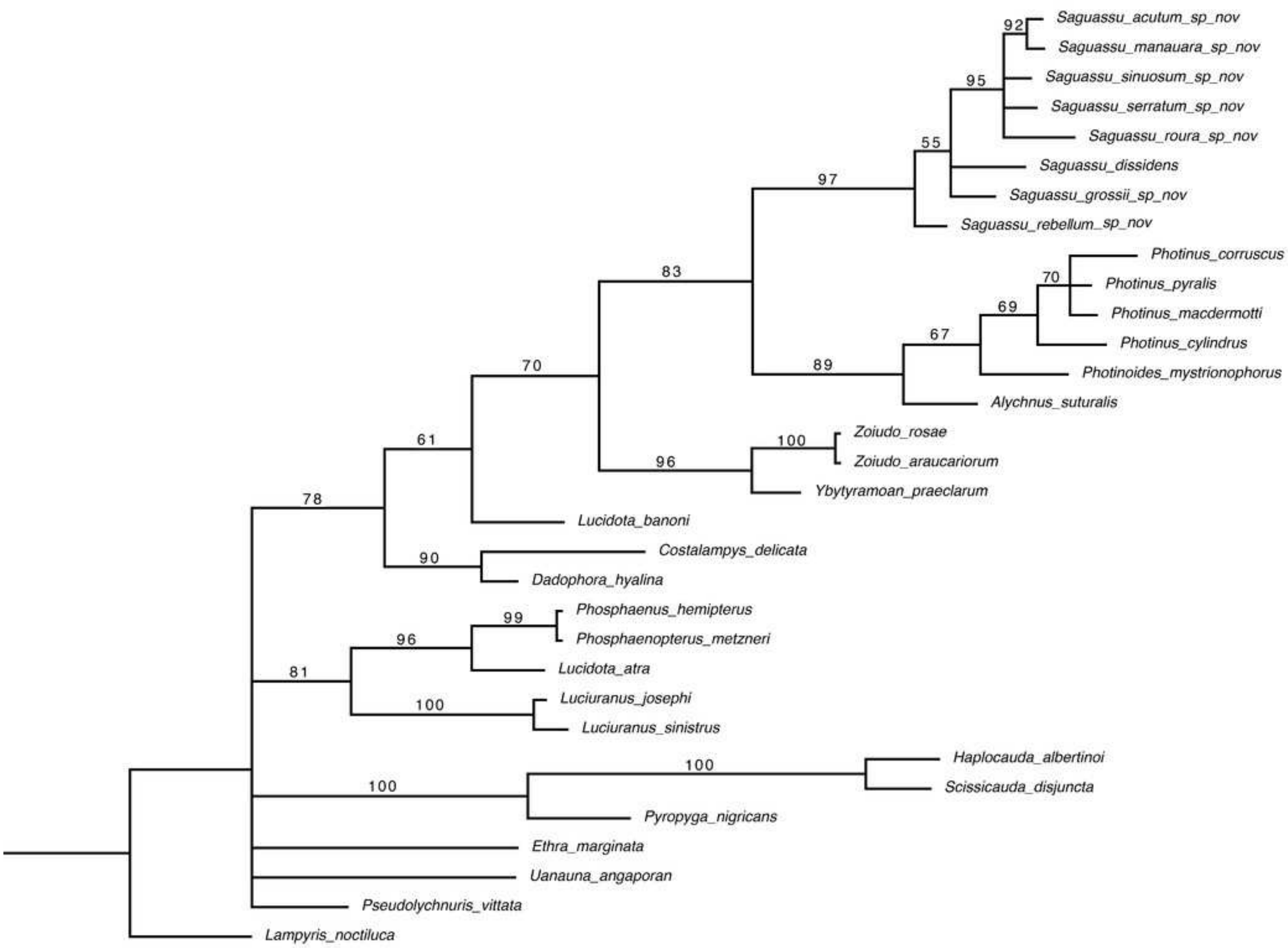

Figure 3

Maximum parsimony optimization of unambiguous character state changes plotted on the majority rule Bayesian consensus tree.

Black and white squares represent uncontroverted and controverted (i.e. homoplastic) synapomorphies, respectively.

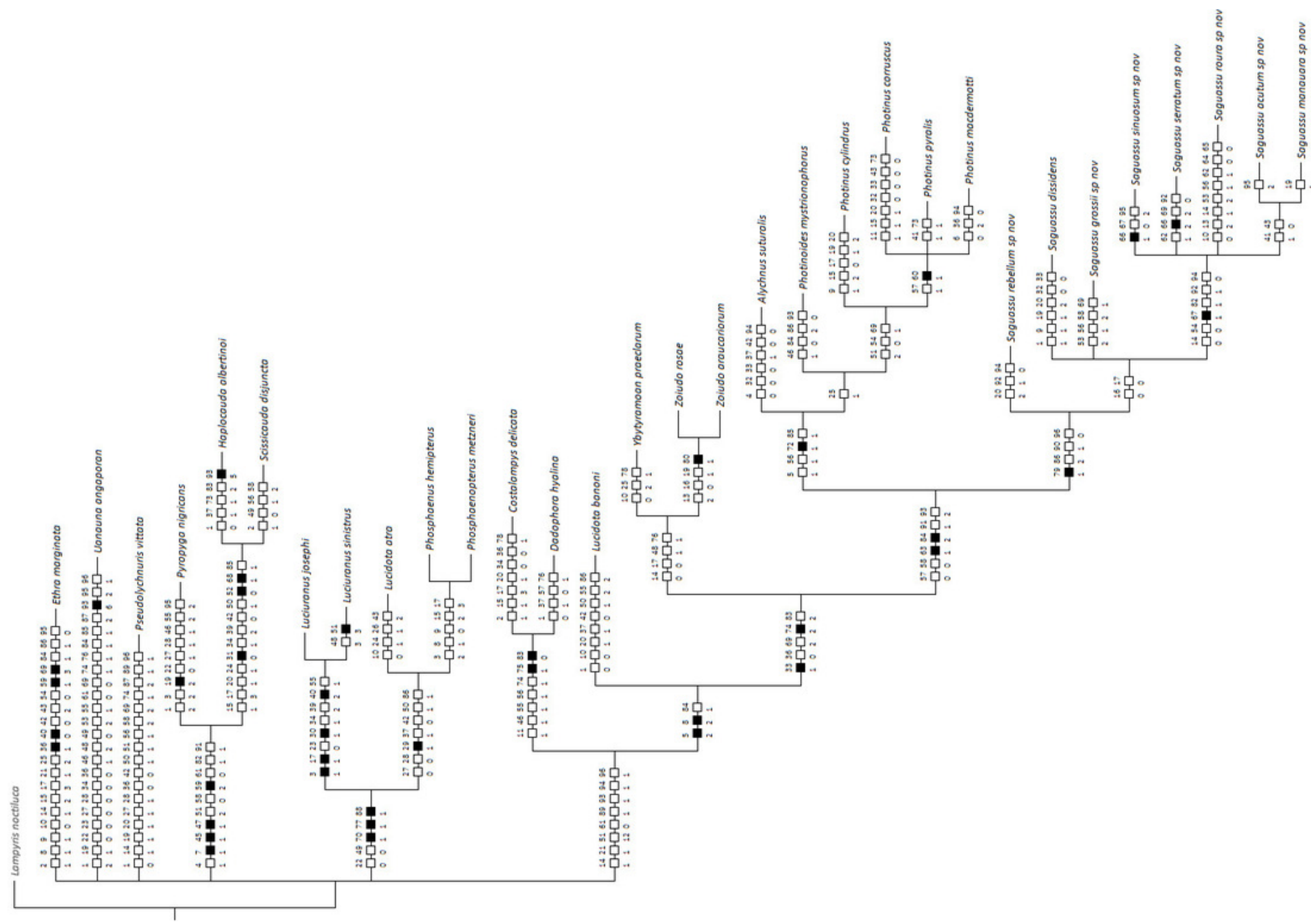

Figure 4

Diversity of head morphologies in *Saguassu* gen. nov..

A–F: *S. acutum* **sp. nov.**. G–L: *S. manauara* **sp. nov.**. M–R: *S. roura* **sp. nov.**. S–X: *S. rebellum* **sp. nov.**. Y–Dd: *S. grossii* **sp. nov.**. Ee–Jj: *S. dissidens* (Olivier, 1894) **comb. nov.**. Head, dorsal (A, G, M, S, Y, Ee), ventral (B, H, N, T, Z, Ff), frontal (C, I, O, U, Aa, Gg), lateral (D, J, P, V, Bb, Hh), occipital (E, K, Q, W, Cc, Ii) views. Left antenna, frontal (F, L, R, X, Dd, Jj) view. Scale bars: A–F, G–L, M–R, S–X, Y–Dd, Ee–Jj: 0.5mm.

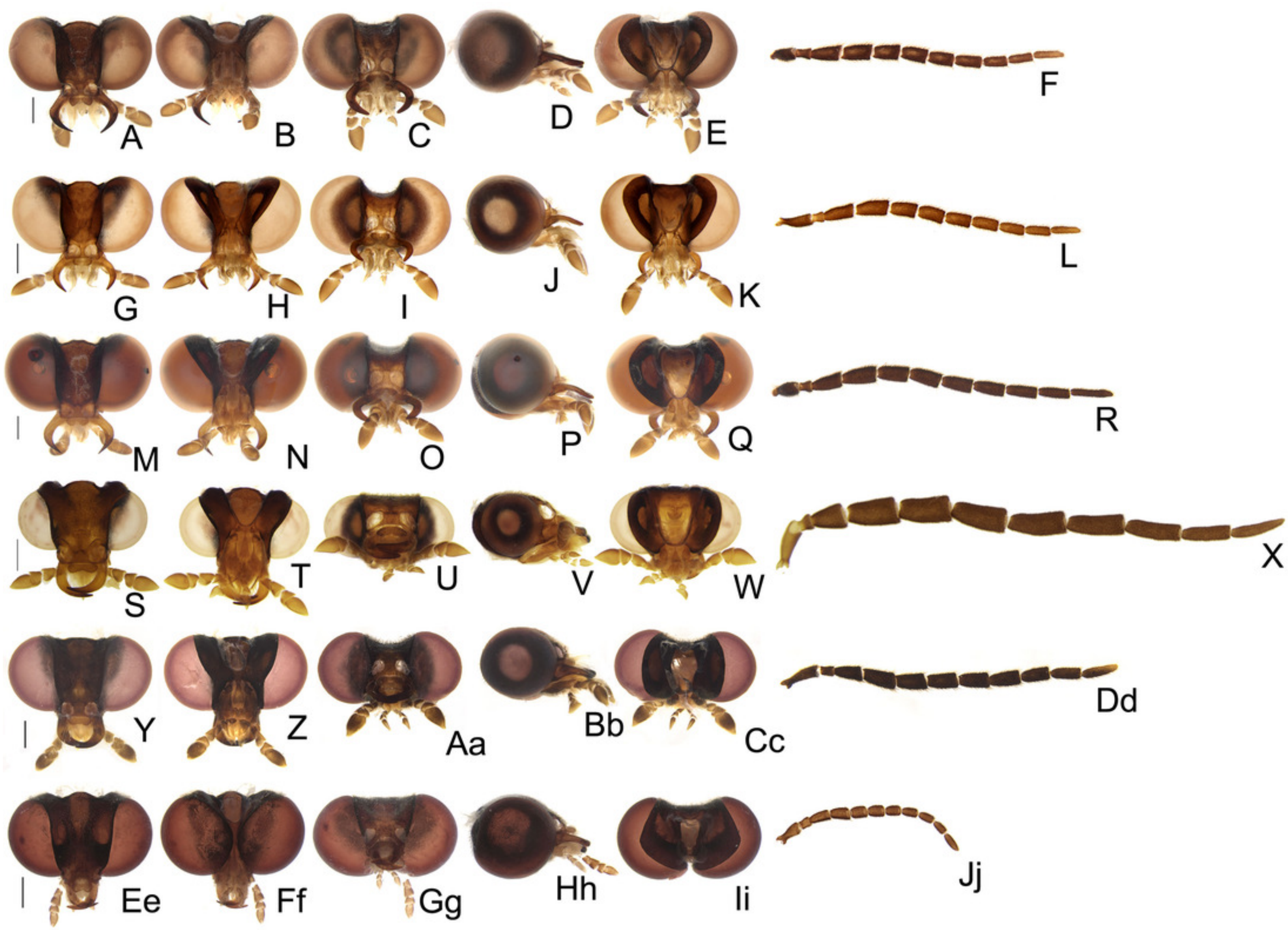

Figure 5

Diversity of prothoracic morphologies in *Saguassu* gen. nov..

A–E: *S. acutum* **sp. nov.**. F–J: *S. manauara* **sp. nov.**. K–M: *S. roura* **sp. nov.**. P–T: *S. rebellum* **sp. nov.**. U–Y: *S. grossii* **sp. nov.**. Z–Dd: *S. dissidens* (Olivier, 1894) **comb. nov.**. Prothorax, dorsal (A, F, K, P, U, Z); ventral (G, G, L, Q, V, Aa), lateral (C, H, M, R, W, Bb), D) frontal (D, I, N, S, X, Cc); E) posterior views (E, J, O, T, Y, Dd). Scale bars: A–F, F–J, K–O, P–T, U–Y, Z–Dd: 0.5mm.

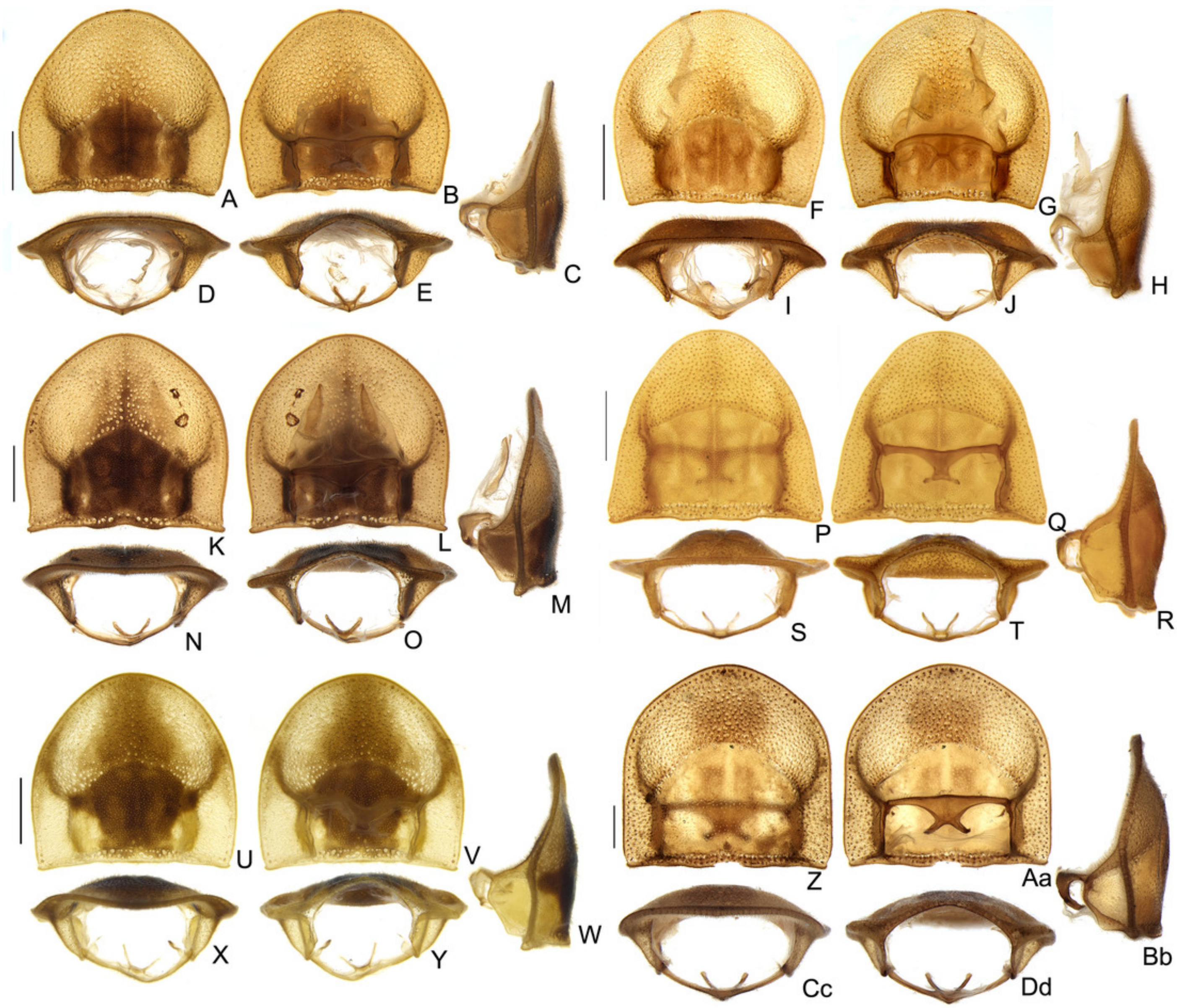
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Figure 6

Head and thoracic morphology of *Saguassu serratum* sp. nov. (A–C) and *S. marajoara* sp. nov. (D–F).

Ventral (A and D), lateral (B and E), and dorsal views. Scale bars: A–B and D–E: 1 mm; C and F: 1 mm.

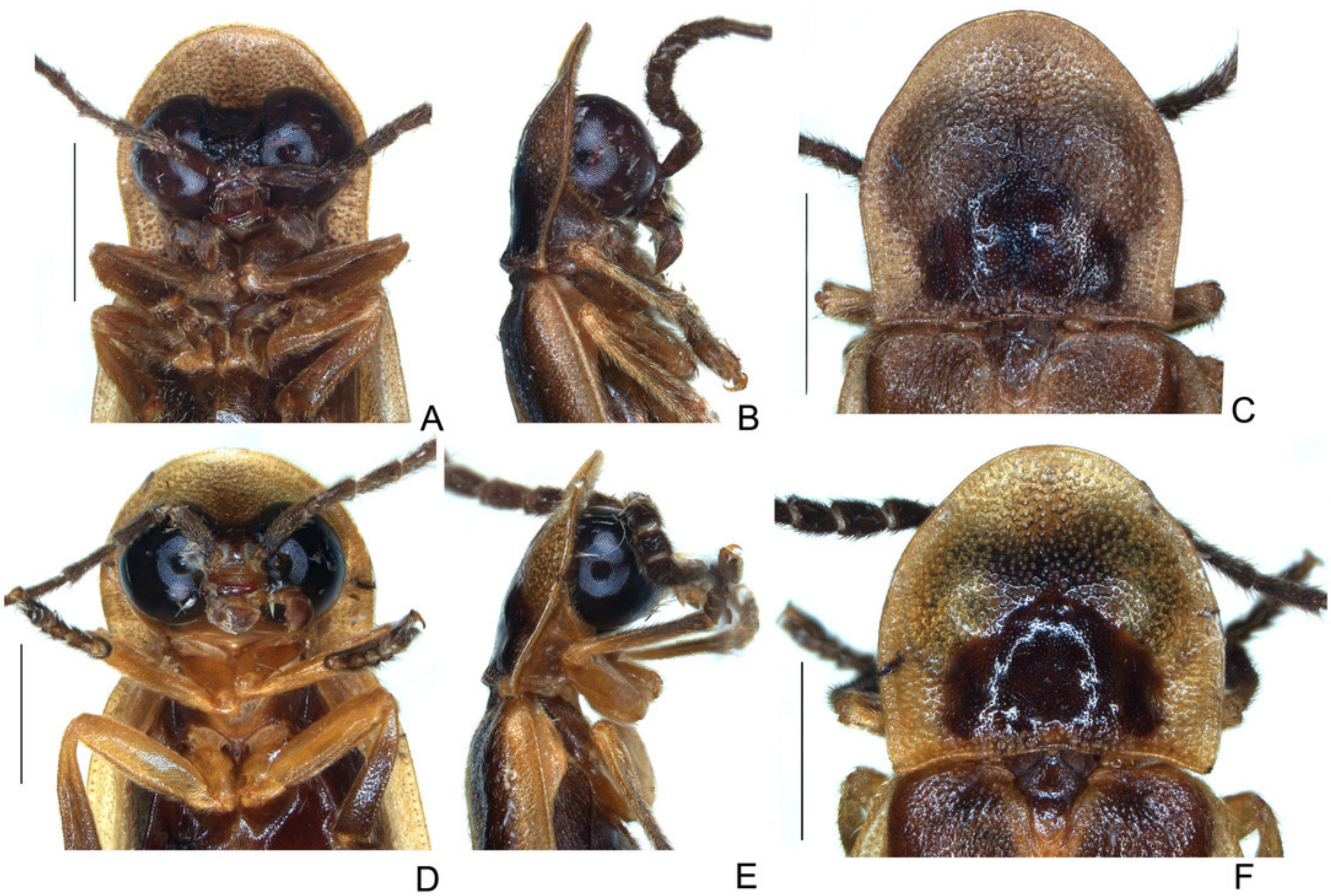

Figure 7

Diversity of elytron and wing morphologies in *Saguassu* gen. nov. *S. grossii* sp. nov..

A–E: left elytra, dorsal view. G–L, left wings, dorsal view. A and G: *S. acutum* **sp. nov.**. B and H: *S. manauara* **sp. nov.**. C and I: *S. roura* **sp. nov.**. D and J: *S. rebellum* **sp. nov.**. E and K: *S. grossii* **sp. nov.**. F and L: *S. dissidens* (Olivier, 1894) **comb. nov.**. Scale bars: 1 mm.

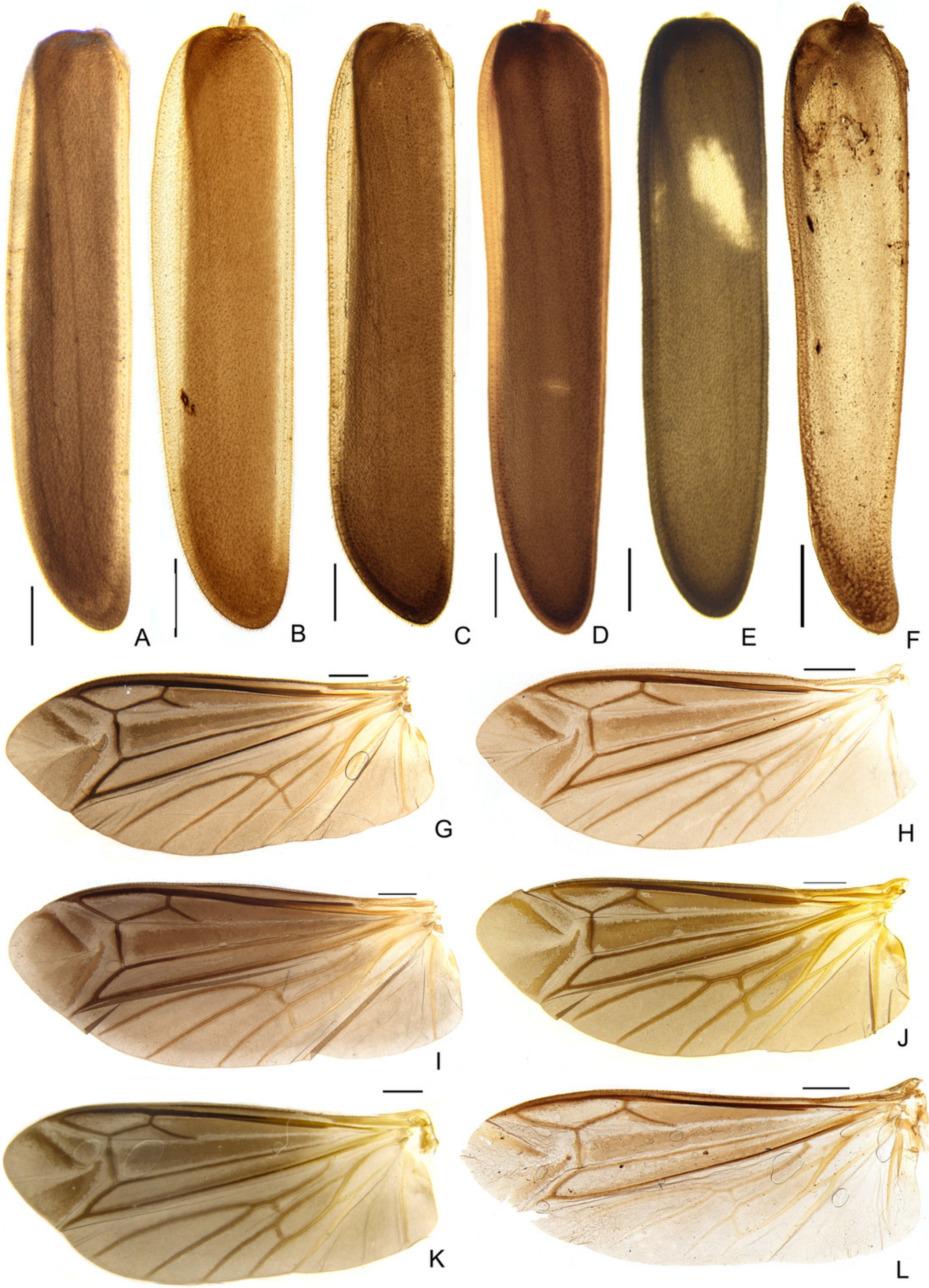
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Figure 8

Thoracic morphology of male *Saguassu grossii* sp. nov..

A) mesonotum, dorsal view. Alinotum, B) anterior and C) dorsal views. D–F: Pterothoracic in D) ventral, E) lateral, and F) ventral views. G–I are pro, meso and hindlegs, respectively. J–L are pro, meso and hindlegs, respectively. Black arrowheads show tibial spurs. Scale bars: A–F 2 mm; G–I and J–L 1 mm.

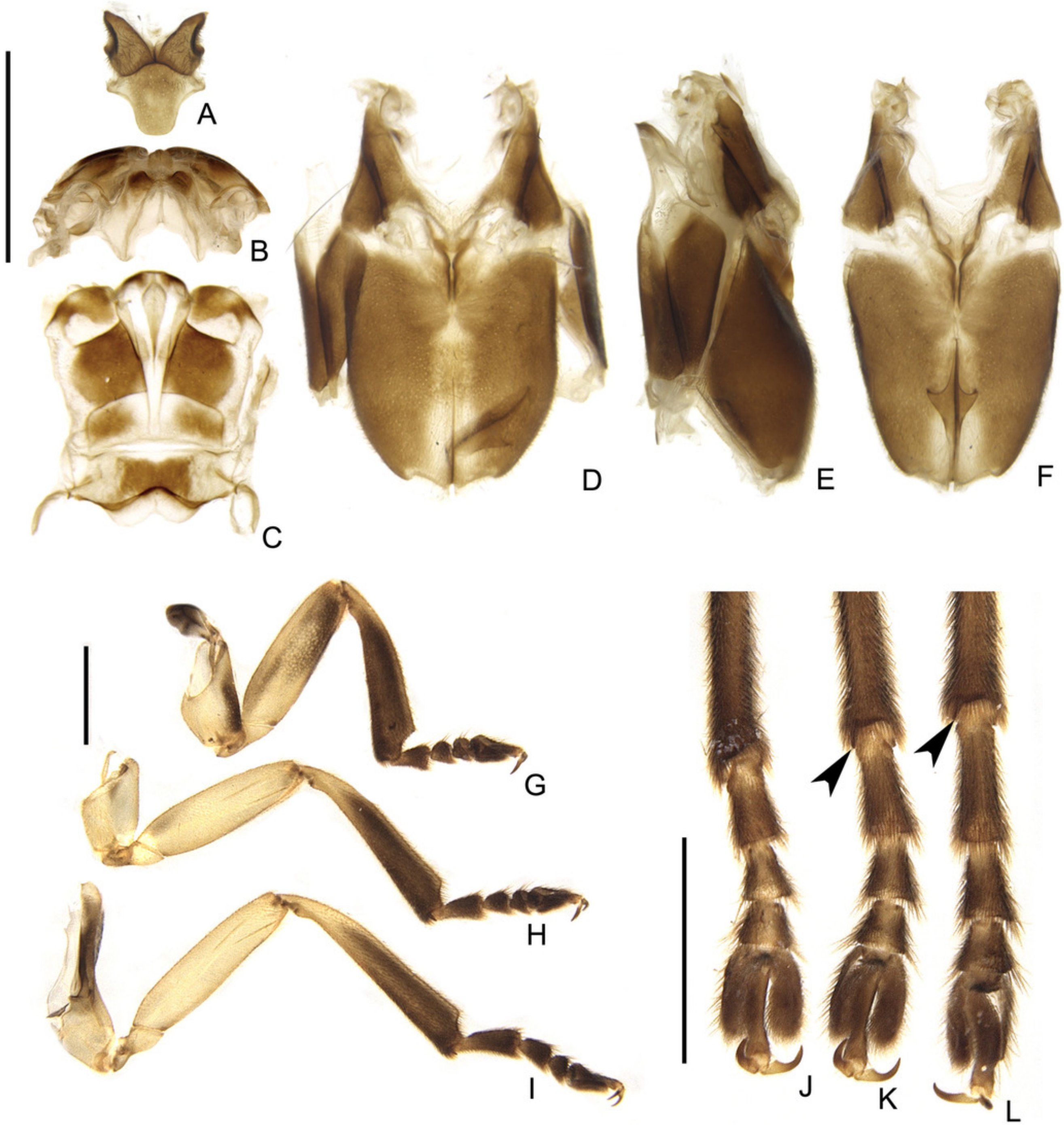
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Figure 9

Diversity of terminalia in *Saguassu* gen. nov..

A–D: *S. acutum* **sp. nov.**, E–H: *S. sinuosum* **sp. nov.,** I–L: *S. serratum* **sp. nov.**. M–P: *S. manauara* **sp. nov.**. Q–T: *S. roura* **sp. nov.**. U–X: *S. rebellum* **sp. nov.**. Y–Bb: *S. grossii* **sp. nov.**. Cc–Ff: *S. dissidens* (Olivier, 1894) **comb. nov.**. Pygidium, dorsal view (A, E, I, M, Q, U, Y, Cc). Sternum VIII, ventral view (B, F, J, N, R, V, Z, Dd). Aedeagal sheath, syntergite, dorsal view (C, G, K, O, S, W, Aa, Ee), sternum IX, ventral view (D, H, L, P, T, K, Bb, Ff). Scale bar: 0.5 mm.

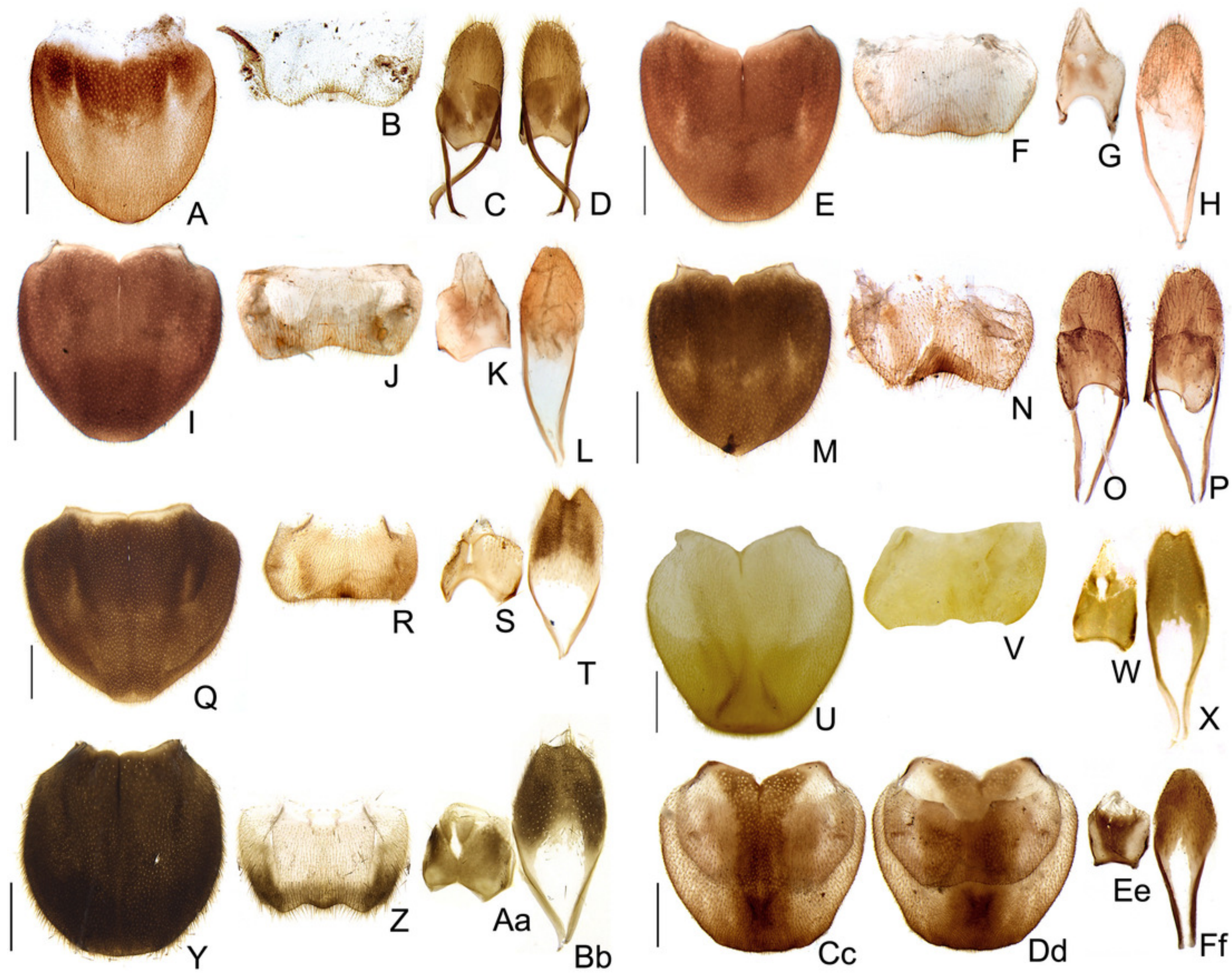
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Figure 10

Aedeagal diversity in *Saguassu* gen. nov..

A–E: *S. acutum* **sp. nov.**. F–J: *S. sinuosum* **sp. nov.**. K–O: *S. serratum* **sp. nov.**. P–T: *S. manauara* **sp. nov.**. U–Y: *S. roura* **sp. nov.**. Z–Dd: *S. rebellum* **sp. nov.**. Ee–Ii: *S. grossi* **sp. nov.**. Jj–Nn: *S. dissidens* (Olivier, 1894) **comb. nov.**. Aedeagus dorsal (A, F, K, P, U, Z, Ee, Jj), dorso-lateral (B, G, L, Q, V, Aa, Ff, Kk), lateral (C, H, M, R, W, Bb, Gg, Ll), latero-ventral (D, I, N, S, X, Cc, Hh, Mm); ventral views (E, J, O, T, Y, Dd, Ii, Nn). Scale bar: 0.5 mm.

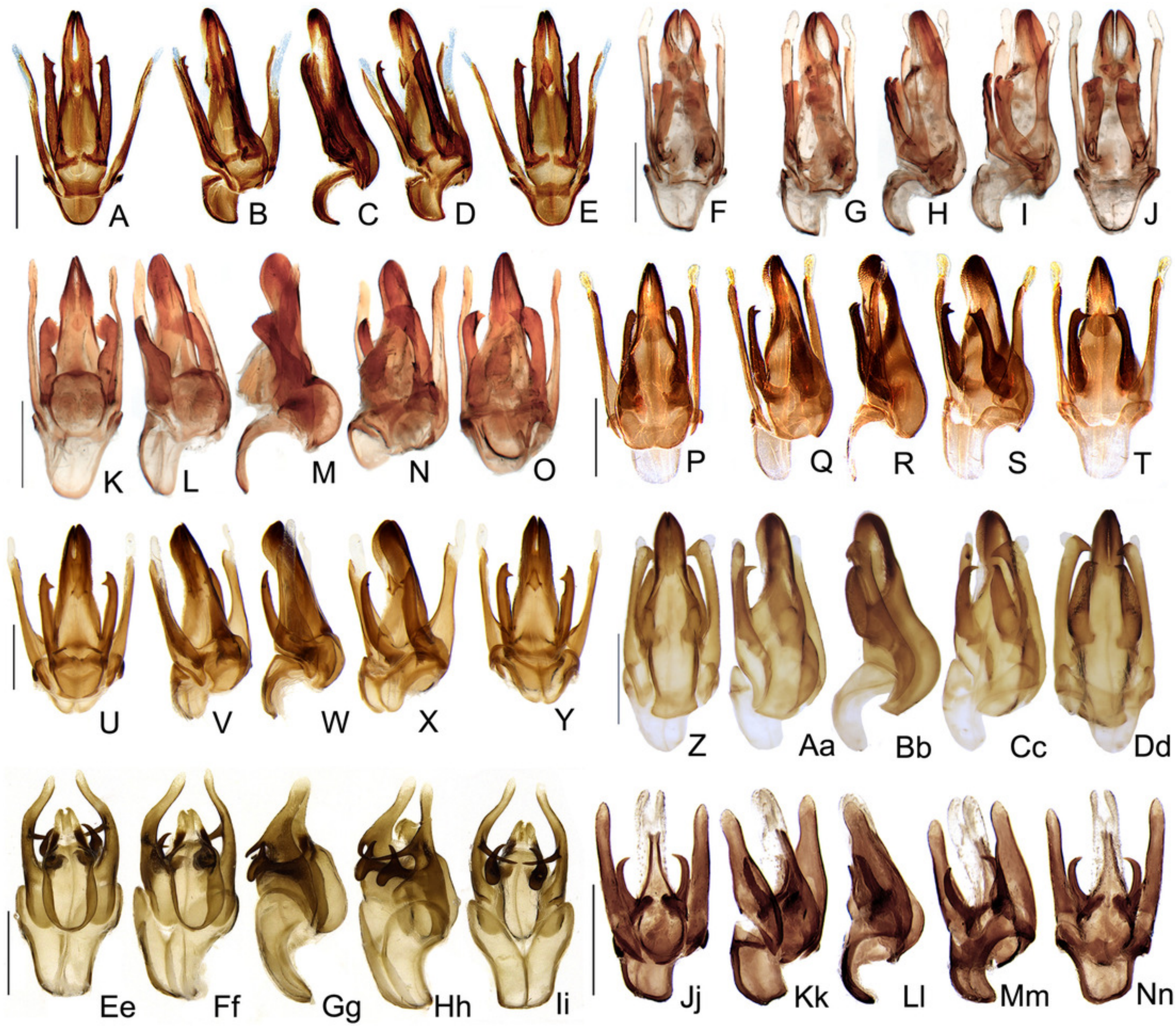
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Figure 11

Morphology of *Saguassu grossii* sp. nov. female.

Habitus: A) dorsal, B) ventral view. C) Abdominal tergites (left) and ventrites (right). D) Pygidium, dorsal view. E) Sternum VIII, ventral view. Genitalia: dorsal (F and H), and ventral (G and I) views. Scale bar: A–C: 2 mm; D–E: 1 mm; F–I: 0.5 mm.

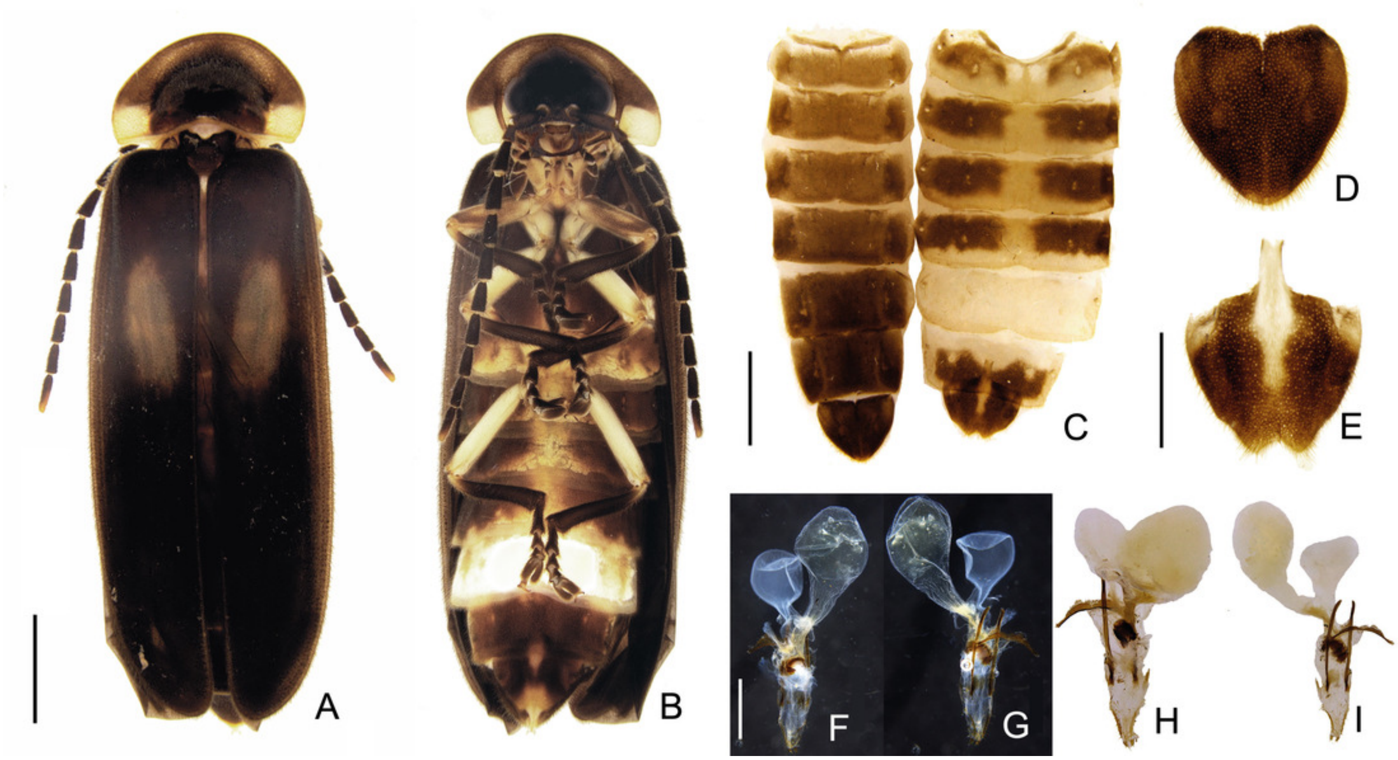

Figure 12

Geographic distribution map of *Saguassu* gen. nov.

Species of *Saguassu* **gen. nov.** are found in all Neotropical dominions completely enclosed in South America. This new genus is more diverse in the Amazonian dominions (Boreal Brazilian, South Brazilian, South-eastern Amazonian), and all its species are allopatric.