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A new species of planthopper in the genus *Shellenius* (Hemiptera: Fulgoroidea: Derbidae) from palms in Costa Rica

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Abstract

The genus *Shellenius* is a small taxon of planthoppers in the family Derbidae (Otiocerinae: Otiocerini) found in the eastern United States and Mesoamerica. A new species of *Shellenius* associated with palms is herein described from Costa Rica. Molecular data for the barcoding region cytochrome *c* oxidase subunit I (COI) and 18S rRNA gene is provided to produce a preliminary phylogenetic tree for related taxa and support placement of the novel taxon in *Shellenius*. A review of Fowler type material suggests that *Otiocerus interruptus* Fowler is a *Shellenius* species and is here transferred to that genus as *Shellenius interruptus* **new combination.**

Key words: taxonomy, phylogeny, biodiversity, systematics, survey, Otiocerini

Resumen

El género Shellenius es un taxón pequeño de chicharritas de la familia Derbidae (Otiocerinae: Otiocerini) que se encuentra en el este de los Estados Unidos y Mesoamérica. Se describe aquí una especie nueva de *Shellenius* asociada con palmas en Costa Rica. Se proporcionan datos moleculares para el gen de la subunidad I (COI) del citocromo c oxidasa de la región del código de barras y el gen 18S ARNr para producir un árbol filogenético preliminar para taxones relacionados y apoyar la colocación del nuevo taxón en *Shellenius*. Una revisión del material tipo Fowler sugiere que *Otiocerus interruptus* Fowler es un especie de *Shellenius* y aquí se transfiere a ese género como una nueva combinación de *Shellenius interruptus*.

Palabras clave: taxonomía, filogenia, biodiversidad, sistemática, encuesta, Otiocerini

Introduction

The genus *Shellenius* Ball, 1928 is a small taxon of planthoppers in the family Derbidae (Otiocerinae: Otiocerini) that is currently comprised of five species (see below) two from the USA and three from Mesoamerica. The derbid subfamily Otiocerinae are generally elongated, fragile forms with the wings projecting well beyond the body (more than 2.5x longer than broad), with the head strongly compressed (bearing sensory pits along margins), the clavus usually open (the Pcu+A1 does not reach the claval margin, instead merges with CuP), and the jugal region of the hind wings bear a stridulatory plate with a concave external margin (Fennah 1952, Emeljanov 1996). Compared with other tribes of Otiocerinae in the New World (viz. Patarini, Sikaianini), the Otiocerini have a strongly projected head.

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The New World Otiocerini is currently comprised of 11 genera (Bourgoin 2023). *Shellenius* is among a small number of New World Otiocerini with a large antennal appendage, a feature shared with the similar genera *Apache* Kirkaldy, 1901, *Otiocerus* Kirby, 1821 (Bartlett *et al.* 2011, 2014), and evidently also *Kubilaya* Koçak & Kemal, 2010 (see Fennah 1952, fig. 37A and Fennah 1945, figs 39, 40 as *Iquitosa* Fennah, 1945) and *Labicerus* Erichson, 1848 (part of the description [p. 615, translated], reads "…for the third [!] segment of the antennae is divided into two branches, the inner branch twice as long as the outer…"). *Kubilaya* is a South American form whose wings are held broadly tent-like (against the body in *Apache*, *Otiocerus,* and *Shellenius*) and has an irregular costal margin (see Fennah 1945 fig. 41). *Labicerus* (from Guyana) is unknown to us, but the description suggests it to be a pale spotted species. In *Shellenius* the projected head is rounded, whereas in *Otiocerus* the dorsum is flattened with an obtusely angular demarcation at the apex and *Apache* has the dorsum of the head sinuate (and the dorsal margin of the wings angled upward). See Muir 1918a,b; Fennah 1952, and Emeljanov 1996 for keys to higher groupings and Metcalf 1938, Bartlett *et al.* 2014 for keys to American genera.

Shellenius species are infrequently collected and poorly represented in most institutional collections. Their biology is assumed to be similar to *Otiocerus* and *Apache* (viz. nymphs subterranean, or in dead logs, feeding on fungal hyphae, presumably with a single generation per year, overwintering as late instar nymphs or adults (Wilson 1982, Bartlett *et al.* 2014, Gossner & Damken 2018). Adults of *Shellenius ballii* (McAtee, 1923) and *S. schellenbergii* (Kirby, 1821) are reported from the end of May to early November (based on 56 records from iDigBio, https://www.idigbio.org/) and are presumed to have a single generation a year.

Recent survey work in Costa Rica studying planthopper diversity on palms has resulted in the discovery of a large number of undescribed Derbidae and Cixiidae. So far, the only species in the Otiocerini described in this work, *Anotia firebugia* Bahder & Bartlett, was discovered on coconut palm (*Cocos nucifera* L.) (Barrantes *et. al*. 2020). Subsequently, a new *Shellenius* was found while sweeping palm seedlings along the side of trails at La Selva Biological Station. Herein, the novel taxon is described and presented with novel molecular data for the cytochrome *c* oxidase subunit I (COI) gene and 18S rRNA gene.

Materials and methods

Locality and specimen collection. Individuals of the novel taxon were swept from palm seedlings along trails and were immediately transferred to 95% ethanol. Specimens were collected (permit no. SINAC-ACTo-GASPPNI-016-2018) at La Selva Biological Station from 20-V-2018 to 22-V-2018, Heredia province, Costa Rica (10.431269, -84.005961), and exported under permit number DGVS-256-2018 to the U.S.A. under permit number P526-170201-001. All specimens collected were measured, photographed, and dissected using a Leica M205 C stereoscope. Images of specimens and all features photographed were generated using the LAS Core Software v4.12. Voucher specimens, including primary types of the new species, are deposited at the University of Florida—Fort Lauderdale Research and Education Center (FLREC) in Davie, FL, U.S.A and the Florida State Collection of Arthropods (FSCA) in Gainesville, FL, U.S.A. The new species was compared with images of the primary types of *Otiocerus* species (from the Natural History Museum, London; BMNH) described by Fowler (1900). Specimen label data for the Fowler species is quoted verbatim, with each line break indicated by "/" and each label separated by "//" with added notes in square brackets. Verifiable distribution records from iNaturalist (https://www.inaturalist.org) and Bugguide (https://bugguide.net/) were noted in addition to published records in the species checklist.

Morphological terminology and identification. Morphological terminology generally follows that of Bartlett *et al.* (2014), except forewing venation following Bourgoin *et al.* (2015) and with male terminalia nomenclature modified after Bourgoin (1988) and Bourgoin & Huang (1990). New taxa are intended to be attributed to Bahder & Bartlett.

Dissections and DNA extraction. The male terminalia that was dissected for morphological examination also served as the source of tissue for DNA extraction. The terminal end of the abdomens was removed and placed directly into a solution of tissue lysis buffer (buffer ATL) and proteinase K (180 µl ATL and 20 µl proteinase K) from the DNeasy® Blood and Tissue Kit (Qiagen). The abdomen was left to lyse for 24 hours at 56°C. Following lysis, eluate was transferred to a new 1.5 ml microcentrifuge tube and DNA extraction proceeded as per the manufacturer's instructions. The terminalia were then immersed in 200 µl of buffer ATL and 200 µl of buffer AL from the same kit and placed at 95°C for 24 hours to remove fat, wax, and residual tissue. The cleared genitalia were then used for morphological characterization and photography.

PCR Parameters, Sequence Data, and Analysis. Primers to amplify COI and 18S loci are presented in Table 1. PCR reactions contained 5x GoTaq Flexi Buffer, 25 mM $MgCl_2$, 10 mM dNTP's, 10 mM of each primer, 10% PVP-40, and 2.5U GoTaq Flexi DNA Polymerase, 2 µl DNA template, and sterile dH_20 to a final volume of 25 µL. Thermal cycling conditions were as follows: 2 min initial denaturation at 95°C, followed by 35 cycles of 30-sec denaturation at 95°C, 30-sec annealing, extension at 72°C, followed by a 5 min extension at 72°C. Annealing temperatures and extension times for corresponding primers/loci are presented in Table 1. PCR product was run on a 2% agarose gel stained with GelRed (Biotium) amplicons of the appropriate size and were purified using the Exo-SAP-IT™ PCR Product Cleanup Reagent (ThermoFisher Scientific, Waltham, Massachusetts, USA). The purified PCR product was quantified using a NanoDropLite spectrophotometer (ThermoFisher Scientific, Waltham, Massachusetts, USA) and sent for sequencing at Eurofins Scientific (Louisville, KY, USA). Contiguous files were assembled using DNA Baser (Version 4.36) (Heracle BioSoft SRL, Pitesti, Romania), and aligned using Clustal*W* as part of the package MEGA7 (Kumar *et al.* 2016). Maximum Likelihood trees were generated using the Bootstrap method at 1,000 replicates based on the Tamura-Nei model for both the COI and 18S loci separately as well as one based on concatenated data forming a consensus tree between COI and 18S with MEGA7 (Kumar *et al.* 2016).

TABLE 1. Primers used to amplify loci used for assessment of *Shellenius serratus* **sp. n.** and corresponding annealing temperatures and extension times.

Primer Name	Gene	Sequence (5'→3')	Annealing	Extension	Reference
LCO1490	COI	GGTCAACAAATCATAAAGATATTG	40˚C	1 min. 30 sec.	Folmer *et*
HCO2198		TCAGGGTGACCAAAAAAATCA			*al.* 1994
18SACDN_F1	18S	AGAGGGAGCCTGAGAAACG	60˚C	1 min. 45 sec.	This study
18SACDN_R1		GGGCAGGGACGTAATCAAC			

Taxon sampling. For molecular in-group comparisons, specimens of *S. ballii* and *S. schellenbergii* were used. Other Otiocerinae (Otiocerini) taxa used to construct phylogenies included *Anotia firebugia* Bahder & Bartlett. In addition, *Patara vanduzei* Ball (Otiocerinae: Patarini), *Mula resonans* Ball (Otiocerinae: Sikaianini), and *Agoo xavieri* Bahder & Bartlett (Derbinae: Cenchreini) were included to root the Otiocerini analyzed in this study. All GenBank accession numbers for taxa analyzed are included in Table 2.

TABLE 2. Representative Otiocerinae used for morphological and molecular comparisons with *Agoo xavieri* as subfamily outgroup (Derbinae).

	Locus	
Species	COI	18S
Agoo xavieri	MK443068	MK443073
Anotia firebugia	MT084365	MT945942
Mula resonans	OQ473376	OQ519977
Patara vanduzei	OQ473377	OQ519977
Shellenius ballii	OQ473378	OQ519976
Shellenius schellenbergii	OQ473379	OQ519975
Shellenius serratus **sp. n.**	OQ473380	OQ519974

Systematics

Family Derbidae Spinola 1839

Subfamily Otiocerinae Muir 1917

Tribe Otiocerini Muir 1917

Genus *Shellenius* Ball, 1928

Type species: *Otiocerus ballii* McAtee 1923 by original designation

Species composition

Shellenius ballii (McAtee 1923) (Fig. 8)—USA: FL, IL, LA, MD, MS, OH, TN; CAN: ON (Bartlett *et al.* 2014), also AL, MO, NC, NH, SC; CAN: QC (iNaturalist).
S. gracilior (Fowler 1900) (Fig. 13C)—Guatemala (Fowler, 1900, Metcalf 1945).
S. griseus (Fowler 1900) (Fig. 13B)—Mexico (Guerrero) (Fowler, 1900, Metcalf 1945).
S. interruptus (Fowler 1900), **new combination** (Fig. 13D)—Guatemala (Fowler, 1900, Metcalf 1945).
S. montanus (Fowler 1900) (Fig. 13A)—Mexico (Guerrero), Panama (Fowler, 1900, Metcalf 1945).
S. schellenbergii (Kirby 1821) (Fig. 9)—USA: AZ, FL, GA, IL, LA, MO, MS, NJ, NY, OH (Bartlett *et al.* 2014); also AL, MA, MD, NC, TN, WV (iNaturalist, Bugguide).
Shellenius serratus **sp. n.** (Fig. 2)—Costa Rica

Amended diagnosis. Elongate, fragile forms, wings greatly exceeding body (in life held parallel to body in repose), approximately 8–14 mm in length (including wings). Head strongly projecting and greatly compressed, in dorsal view narrower than pronotum, vertex narrowly elongate-triangular, narrowing anteriorly; medially strongly concave (median carina absent), lateral margins elevated, pustulate; posterior margin concave in lateral view, head projecting about 2.5–3.0x width of eye, dorsal margin weakly sinuate, apex smoothly rounding (not angled, viz. *Otiocerus*, *Apache*). Antennae directed anteriorly in repose, with scape short, pedicel elongate (~2/3 to subequal distal head margin), palpiform (appearing to bear rings of small projections) bearing prominent elongate sinuate appendage appearing to arise ventrally from the base of the pedicel, curved forward, subequal in length of antennae; apex of pedicel bearing bristle-like flagellum with bulbous base. Compound eyes prominent, ocelli obscure or absent. Pronotum in dorsal view very short at midline, posterior margin deeply concave, lateral (paradiscal) small, not foliately expanded. Wings exceeding abdomen by nearly length of body, hindwings about ¾ length of forewing.

Forewing more than 3x longer than wide (at widest point), without evident pustules or setae on veins (except along costal margin). Forewing venation with composite vein Sc+R+M (from leading margin of basal cell) with M branched from R+Sc in basal fourth of wing (proximad of fusion of Pcu+A1 in clavus), and RP forked from Sc+RA nearly at midlength. CuA branched and anastomosed to form closed C5 cell (i.e., procubital cell of Emeljanov 1996); fused vein Pcu+A combining with CuP and CuA before extending to wing margin as composite vein (beyond wing midlength) forming an open clavus.

Male terminalia. Terminalia weakly bilaterally asymmetrical. Pygofer in lateral view narrow (straplike) and irregular in form, expanded ventrally; medioventral lobe present, varied in shape. Gonostyli elongate, cupped, apex medially pointed; in ventral view, medial margins bearing large projections near midlength. Aedeagal shaft tubular, distally upcurved, bearing varied subapical, apical, and retrorse processes including a large membranous endosoma. Anal tube elongate, roughly equal to gonostyli in length, in lateral view roughly quadrate (to weakly triangular) with ventrolateral apex weakly produced; in dorsal view elongate quadrate.

Etymology. According to Dmitriev (2020), *Shellenius* was named in honor of Johann Rudolph Schellenberg (1740–1806), as *Shellen–* + *–ius* (noun suffix); *Shellenius* is to be treated as masculine.

Remarks. The genus *Shellenius* was erected for species "[r]esembling *Otiocerus* in general form and structure but with the elytra extremely long and narrow before the roundingly expanded apex. The head is horizontal, extremely long and thin, the upper and lower margins almost straight, the apex rounding (Ball 1928: 197). Ball (1928) provided a key to genera for North America members of the '*Otiocerus* group' (*Shellenius*, *Otiocerus*, *Apache*) and specified *O. ballii* as the type and included in the genus *schellenbergii*, *gracilior*, *griseus*, and *montanus*. Ball noted that the head of *interruptus* was not described or figured. Images of the type material of *Otiocerus interruptus* (Fig. 13D) exhibit a head structure that appears consistent with *Shellenius*, although the apex is broken, and so that species is here transferred to that genus. Fowler (1900) indicated that he examined only a single specimen from Cerro Zunil, Guatemala, and so this specimen appears to be a holotype by monotypy (viz. ICZN 1999, article 73.1.2).

Critical synonymy.
Shellenius interruptus (Fowler, 1900) **new combination**
= *Otiocerus interruptus* Fowler, 1900: 75 (original description).

Shellenius serratus Bahder & Bartlett sp. n.

(Figures 2–6)

Type locality. Costa Rica, Heredia, La Selva Biological Station.

Diagnosis. Body and forewings mainly yellow with red wash on portions of head, red patches near anterio-lateral margin of mesonotum, and a diagonal red line (bifurcating at apex) for near entire length of forewing. Head broad (relative to other members of genus) with serrations along dorsal margin and subapical transverse carina resulting in a subapical inflection of the head. Male pygofer with triangular medioapical process (with a thin flange on ental side, giving the process a doubled appearance from lateral view). Aedeagus with diagonal row of 4 large teeth ventrally near apex, plus 2 short and 2 long apical processes; endosoma with large irregular membranous portion with two large processes.

Description. *Color*. Body yellow with legs more pallid, vertex and dorsal half of frons washed with red, in lateral view red color present in dorsal half of genae with ventral margin of red patch strongly sinuate (Fig. 2); in dorsal view, disc of vertex with blackish patch between eyes. Mesonotum with two red patches near anterio-lateral margins. Forewings translucent basally, yellow distally (and along costal margin), with red stripe extending lengthwise from base to forewing apex, bifurcating near distal apex of cell C2 (Fig. 4).

Structure. Body length (including wings) males: 11.1 mm (n = 1) and females: 13.4 mm (n=2) (Table 3). Head. In lateral view (Fig. 3A), head broad and strongly projecting anteriorly (about 2.5x width of eye, widest head height about equal to head projection beyond eye); dorsal margin straight (between eye and fastigium) with minute serrulations along length; at apex slightly inflected dorsad with transverse carina, anterior margin rounded, ventral margin weakly convex; lateral portion of head marked with two obscure carina: one extending anteriorly over top of eye, slightly declining then inclining to end in lateral carina of vertex near apex; a second carina from lateral extreme of transverse carina extending posteriorly at weak diagonal, becoming obsolete well before eye. In dorsal view, strongly compressed, vertex widest at base, constricting distally (disc of vertex obsolete near midlength), posterior margin slightly concave, anterior margin linear, frons visible beyond transverse carina from dorsal view (Fig. 3B). Eyes large, laterally projecting, in lateral view rounded with large posterior emargination; ocelli apparently absent. Antennae with long sinuate process, nearly as long as antennae.

TABLE 3. Biometric data for *Shellenius serratus* **sp. n.** (in mm)

Character	Male (n=1)	Female (n=2)
Body length with wings	10.00	10.26
Body length without wings	5.84	6.01
Forewing length	7.19	7.22
Vertex length	0.79	0.83
Vertex width—basal	0.25	0.25
Vertex width—distal	0.03	0.03
Pronotum length—midline	0.03	0.03
Mesonotum length—midline	0.58	0.59
Mesonotum width	0.43	0.44
Frons length	0.40	0.40
Frons width—dorsal	0.03	0.03
Frons width—frontoclypeal	0.04	0.04
Clypeus length	0.41	0.41

Thorax. Pronotum in dorsal view very short at midline, anterior margin convex, posterior margin strongly and deeply invaginated making a nearly quadrate concavity (Fig. 3B), in lateral view pronotum weakly declining

anteriorly, paradiscal region relatively small, cupped, extending to lower level of eye. Mesonotum in dorsal view with single carina at midline, approximately as wide as long, in lateral view, slightly arched (scutellum not clearly separated from scutum; Fig. 3A). Hind leg lacking lateral spines on tibia; spinulation formula: 5-3-2. Forewing slender very elongate, length males: 7.64 mm; females: 8.01 mm, spatulate, widest subapically, apex irregularly rounded; CuA anastomosing to form closed C5 (procubital) cell; clavus open, composite vein Pcu+A1 joined with CuP and CuA before extending to wing margin; branching pattern RA 2-branched, RP 3-branched, MP 7-branched, CuA 2-branched.

FIGURE 1. Habitat and locality of *Shellenius serratus* **sp. n.**

FIGURE 2. Adult habitus of male *Shellenius serratus* **sp. n.**; (A) lateral view and (B) dorsal view.

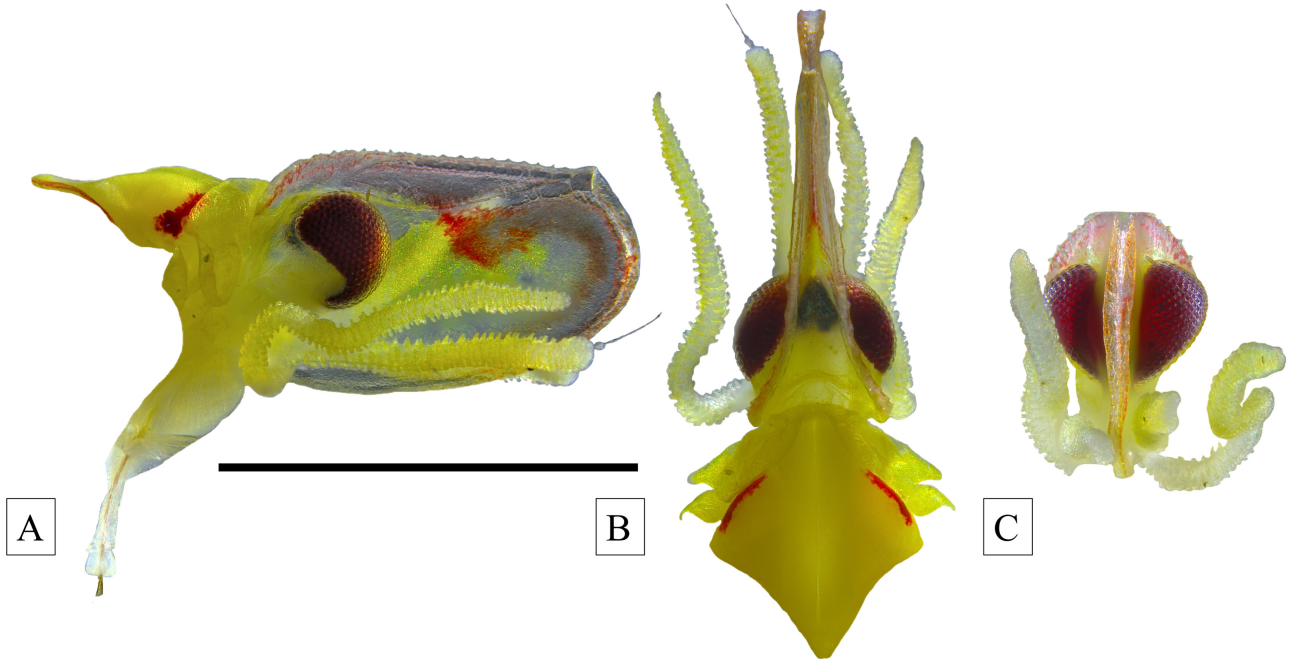

FIGURE 3. Adult *Shellenius serratus* **sp. n.**; (A) head, pronotum, mesonotum lateral view, (B) head, pronotum, and mesonotum dorsal view and (C) head frontal view; scale = 1 mm.

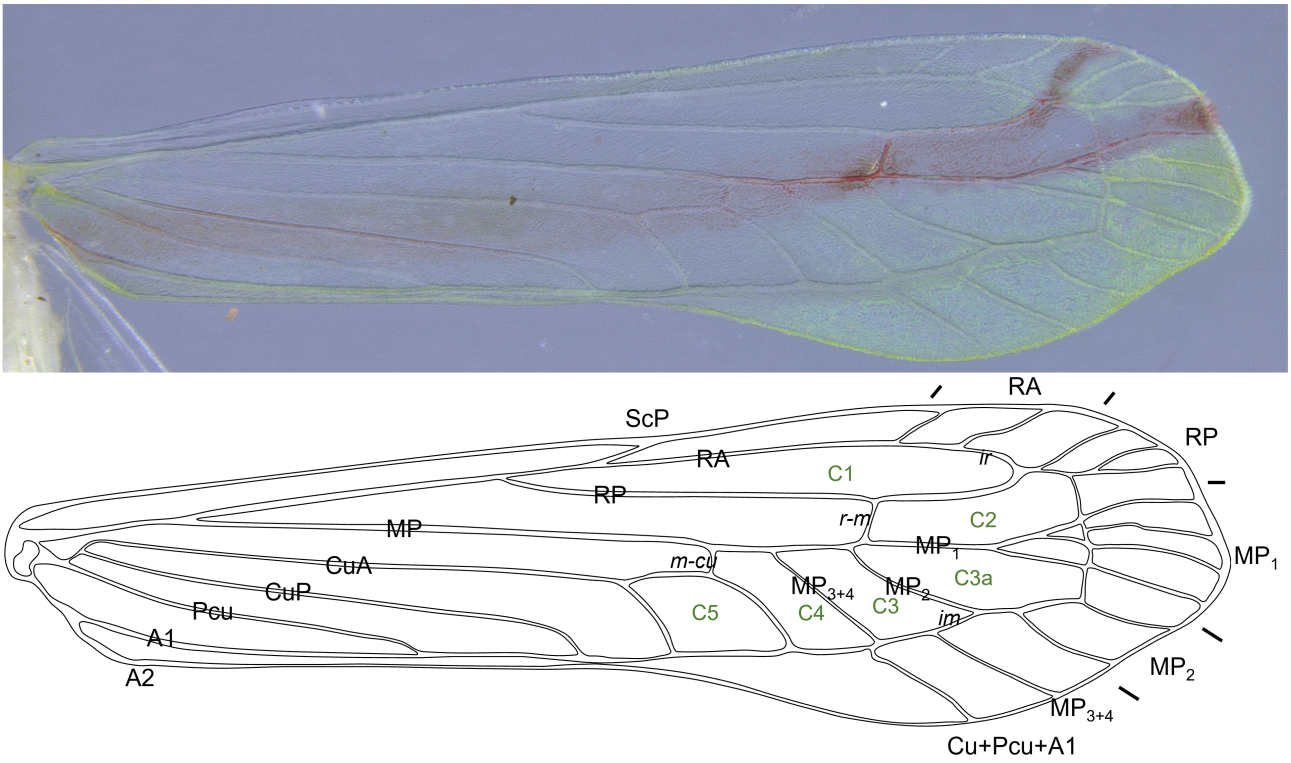

FIGURE 4. Male *Shellenius serratus* **sp. n.** forewing venation; black = vein, green = cell, italics = crossvein.

Terminalia. Pygofer in lateral view narrow, irregular in form; widest at ventral margin, narrowest dorsally, irregularly sinuate on anterior and posterior margin, posterior margin forms truncated process with slight invagination just below dorsal margin (Fig. 5A); in ventral view, medioventral process present, broadly triangular, base wide, nearly reaching lateral margins, bi-layered with inner process slight larger than external process (Fig. 5B). Gonostyli in lateral view elongate, scoop-like, somewhat upcurved, nearly uniform in width across length (slightly constricted at base), dorsal and ventral margins irregularly sinuate, apex rounded, curved dorsad (Fig. 5A). In ventral view, gonostyli narrow basally, expanding greatly at midpoint with inner margins forming beak-like processes, curving slightly cephalad, narrowing distally near apex then expanding to rounded apices bearing subapical processes on inner margin, angled cephalad with sclerotized, hooked apices, curving caudad (Fig. 5B). Aedeagus cylindrical, distally upcurved, bearing bilaterally asymmetrical processes (Figs. 6 & 7), including a pair of short, robust apical processes (Fig. 7, A1 & A2) curved dorsad; right lateral side with one robust process (A3) angled cephalad, reaching approximately 1/3 point of aedeagus; left lateral side with three robust processes (Fig. 7B, A4, A5, and A6) arising subapically, approximately equal in length, dorsal most process (A4), nearly straight, angled slightly dorsad, middle process (A5) with dorsal margin sinuate, curved dorsad, ventral most process (A6) with dorsal and ventral margins sinuate, generally angled cephalad with apex curving dorsad. Four small processes in a row on right ventral margin (Fig. 7D, A7–A10), basal process (A7) anvil-shaped, next process (A8) curved spine angled caudad, A9 similar to A8, and A10 similar to A8 and A9 but reduced in size. Endosoma complex with two large sclerotized processes, the first (Fig. 7B, E1) arising on right lateral side, long, nearly reaching base of aedeagal shaft, extending along dorsal margin and second process (E2) arising on left lateral side, similar in shape to E2, slightly shorts, extending along lateral margin. Anal segment elongate (subequal in length to gonostyli), in lateral view weakly expanding distally, irregularly sinuate on dorsal and ventral margins, apex narrowed greatly and curved ventrad (Fig. 5A).

Plant associations. Unknown palms (Arecaceae).

Distribution. Heredia Province, Costa Rica.

Etymology. The specific name is given in reference to the serrated appearance of the dorsal part of the head in lateral view and ventral margin of the aedeagus. The specific name is derived from the Latin word *serratus* (toothed like a saw), with the masculine (*–us*) ending to match the gender of *Shellenius*.

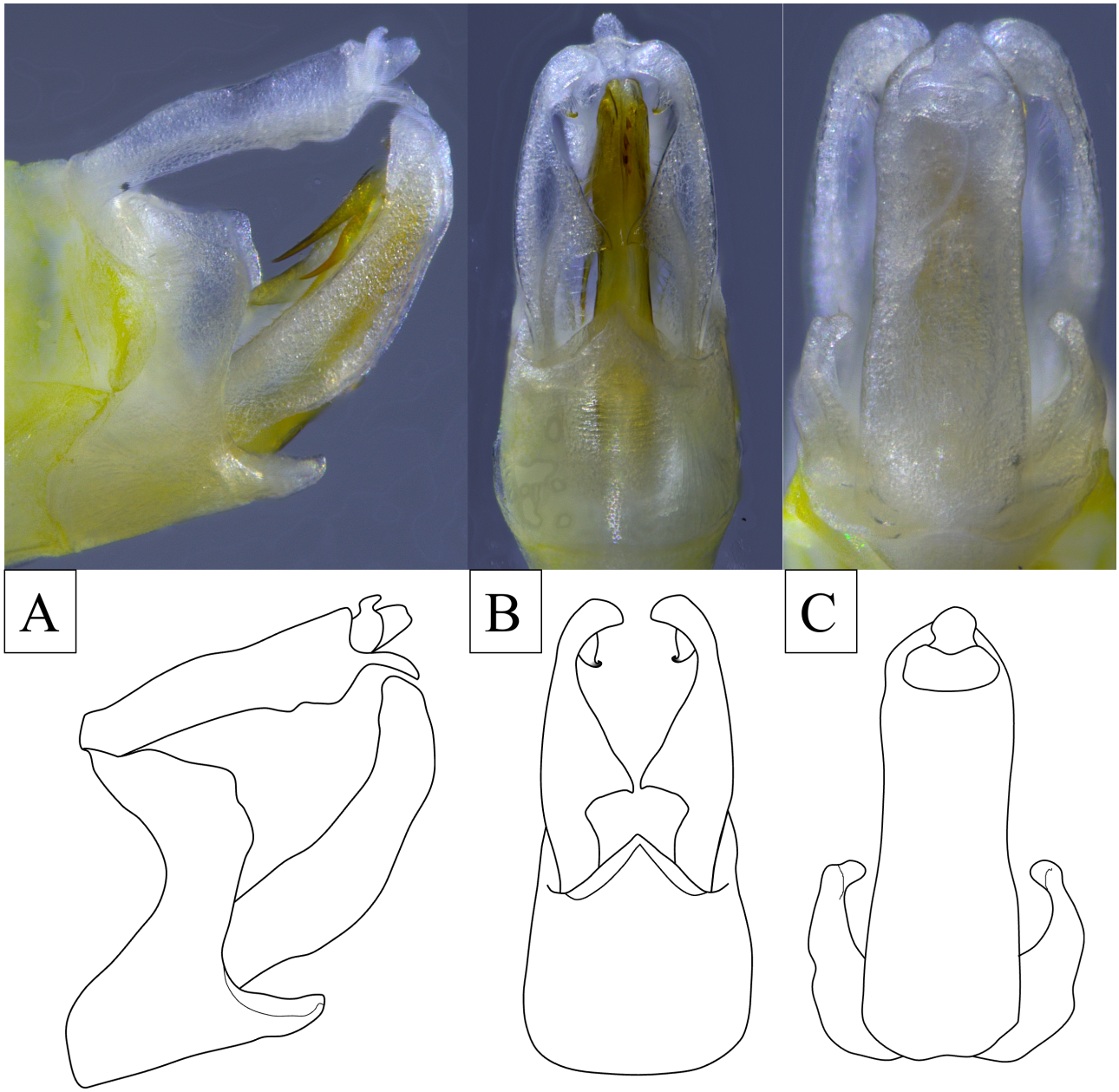

FIGURE 5. Male *Shellenius serratus* **sp. n.** terminalia; (A) lateral view, (B) ventral view, and (C) dorsal view.

Material examined. Holotype male, "Costa Rica, Heredia Pr. / La Selva Biological Station / 12.V.2018, sweeping palms / Coll.: B.W.Bahder // Holotype / *Shellenius serratus* ♂ /" (FLREC); Paratypes, 2 females, same as holotype (FLREC).

Sequence data. For the COI locus, sequences for *Shellenius serratus* **sp. n.** (712 bp), *S. schellenbergii* (684 bp), *S. ballii* (712 bp), *Patara vanduzei* (714 bp), and *Mula resonans* (599 bp) were generated (Table 2). For the 18S locus, sequences for *Shellenius serratus* **sp. n.** (1,632 bp), *S. schellenbergii* (1,626 bp), *S. ballii* (1,633 bp), *Patara vanduzei* (1,297 bp), and *Mula resonans* (1,062 bp) were generated (Table 2). The Maximum Likelihood phylogeny generated for COI demonstrates weak bootstrap support (<50) for all branches in the tree (Fig. 12) whereas most branches in the phylogeny generated based on 18S showed strong bootstrap support (>95) except for the relationship of *Shellenius* to *Patara*, which was moderate to weak (61) (Fig. 12). Additionally, *Shellenius serratus* **sp. n.** resolved adjacent to *S. ballii* (the type species of *Shellenius*) with strong bootstrap support (95) with the genus also being strongly supported (98) based on 18S for the taxa analyzed (Fig. 12). The consensus tree generated from concatenated COI and 18S sequences data showed strong bootstrap support (98) for *Shellenius* and moderate bootstrap support (72) for placement of *Shellenius serratus* **sp. n.** adjacent to *S. ballii* (Fig. 12).

FIGURE 6. Aedeagus of *Shellenius serratus* **sp. n.**; (A) right lateral view, (B) left lateral view, (C) dorsal view, and (D) ventral view.

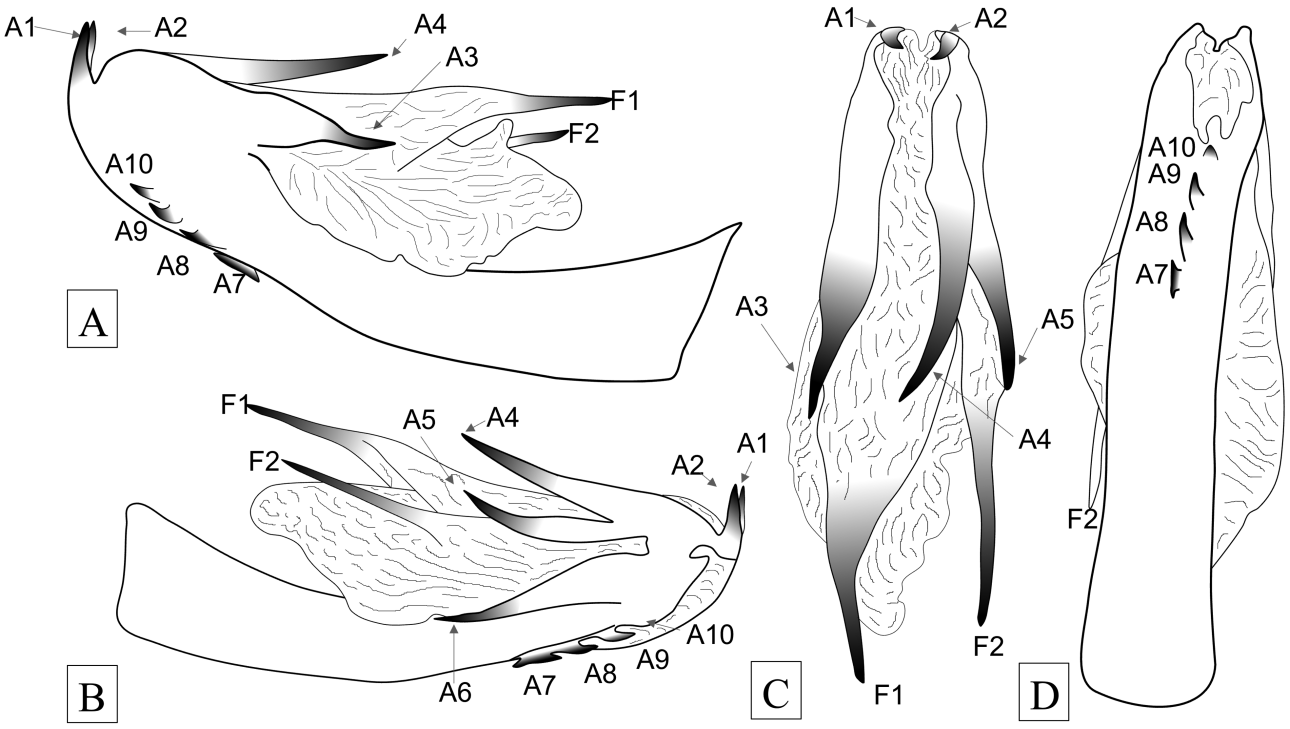

FIGURE 7. Line art of aedeagus of *Shellenius serratus* **sp. n.**; (A) right lateral view, (B) left lateral view, (C) dorsal view, and (D) ventral view.

Remarks. The novel taxon, while resolving with other species of *Shellenius* based on available sequence data and displaying morphological similarities to other members of *Shellenius*, appears unique among congeners. The head characteristics of *Shellenius serratus* **sp. n.** seem closest to *Shellenius*, however, the relatively straight vertex

(in lateral view) with the apical inflection is very similar to *Otiocerus* (from which *Shellenius* was segregated by Ball 1928). The diagnostic differences among the genera *Shellenius*, *Otiocerus*, and *Apache* have historically relied on the shape of the head (e.g., Bartlett *et al.* 2011, 2014). The monophyly of the New World genera of Otiocerini has not yet been verified using molecular tools. Also, the male terminalia, the usual source of definitive species diagnostics, has not been described for most species of *Otiocerus* and *Shellenius* (the two *Apache* species were described by Wilkey 1963). However, Hendrix & Bartlett (in press) illustrate the terminalia of three species of *Otiocerus*. The aedeagus of each of the 3 *Otiocerus* species illustrated in Hendrix & Bartlett (in press) includes 7 processes (1 elongate process on the shaft, 2 apical processes, and 4 subapical retrorse processes) with carrying details, but no conspicuous membranous endosoma.

At present, male terminalia has not been described for any *Shellenius* species outside of the new species and *S. ballii* in this work. Species diagnostics are based mostly on differences in color patterns and the shape of the head. Among species of *Shellenius*, *S. serratus* **sp. n.** is most similar to taxa with a relatively short and broad head (viz. *S. schellenbergii* [Fig. 9] and S. *griseus* [Fig. 13B]), but among these species *S. serratus* **sp. n.** is unique is possessing the apical inflection near the dorsal apex of the head, and appears to be the only species in the genus with red spots on the anterior margin of the mesonotum. *Shellenius serratus* **sp. n.** also lacks the longitudinal black marking found on the head of *S. griseus*, and *S. schellenbergii* is more extensively washed with red on the head and forewings.

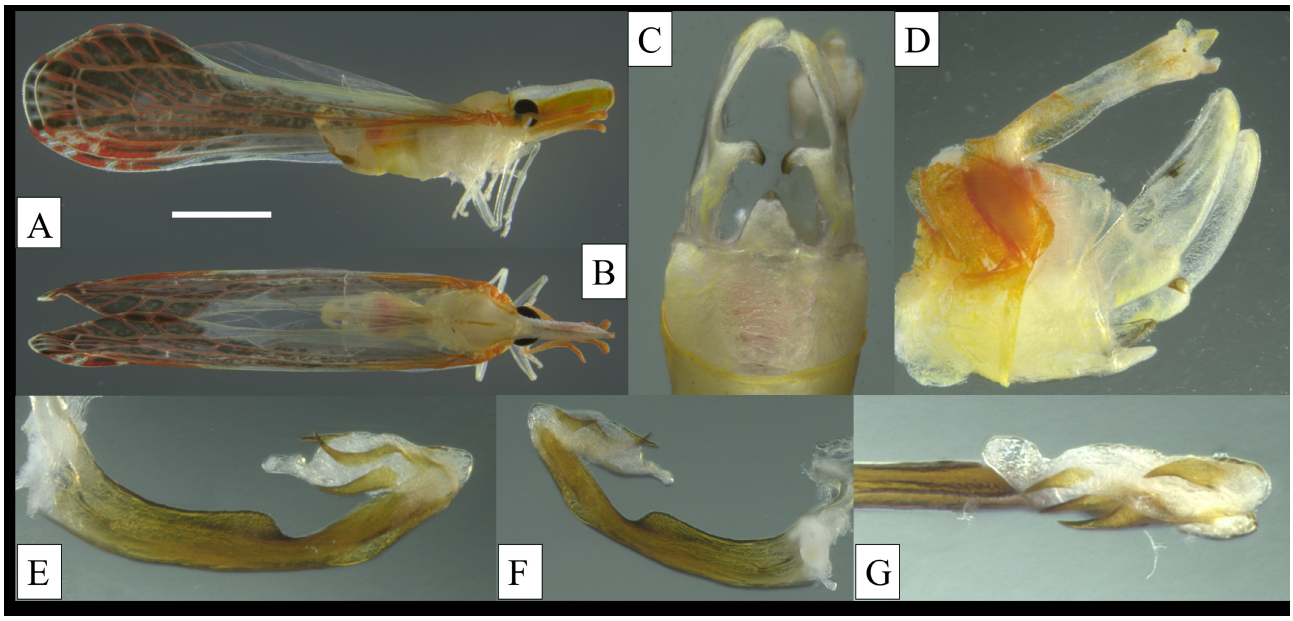

FIGURE 8. Adult male of *Shellenius ballii*; (A) habitus lateral view, (B) habitus dorsal view, (C) terminalia in ventral view, (D) terminalia in lateral view, (E) aedeagus left lateral view, (F) aedeagus right lateral view and (G) aedeagus dorsal view; scale = 1 mm.

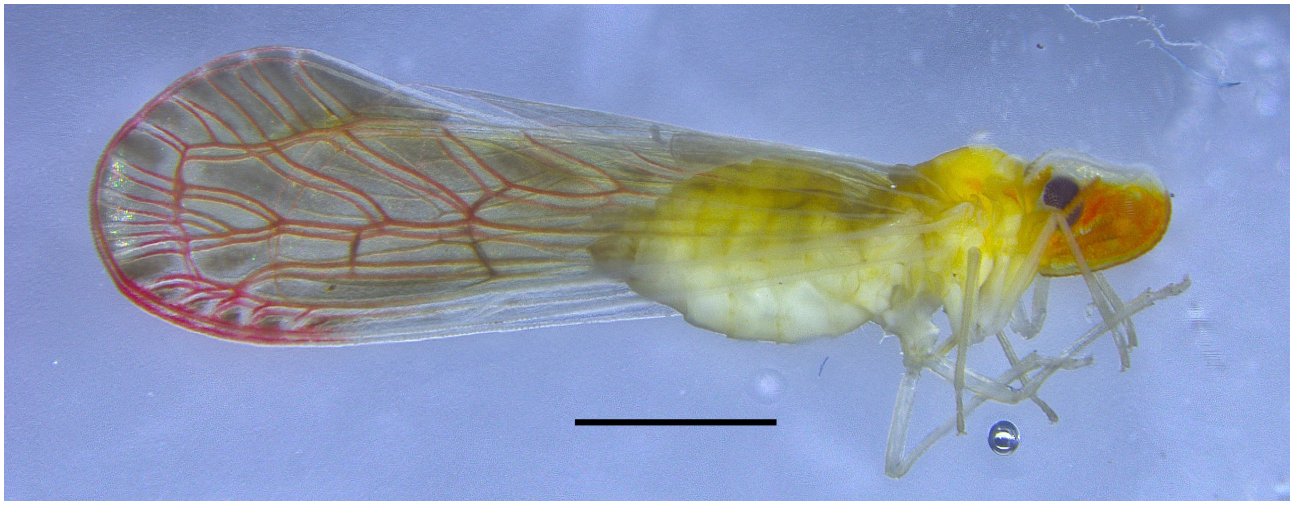

FIGURE 9. Lateral habitus of an adult female *Shellenius schellenbergii*; scale = 1 mm.

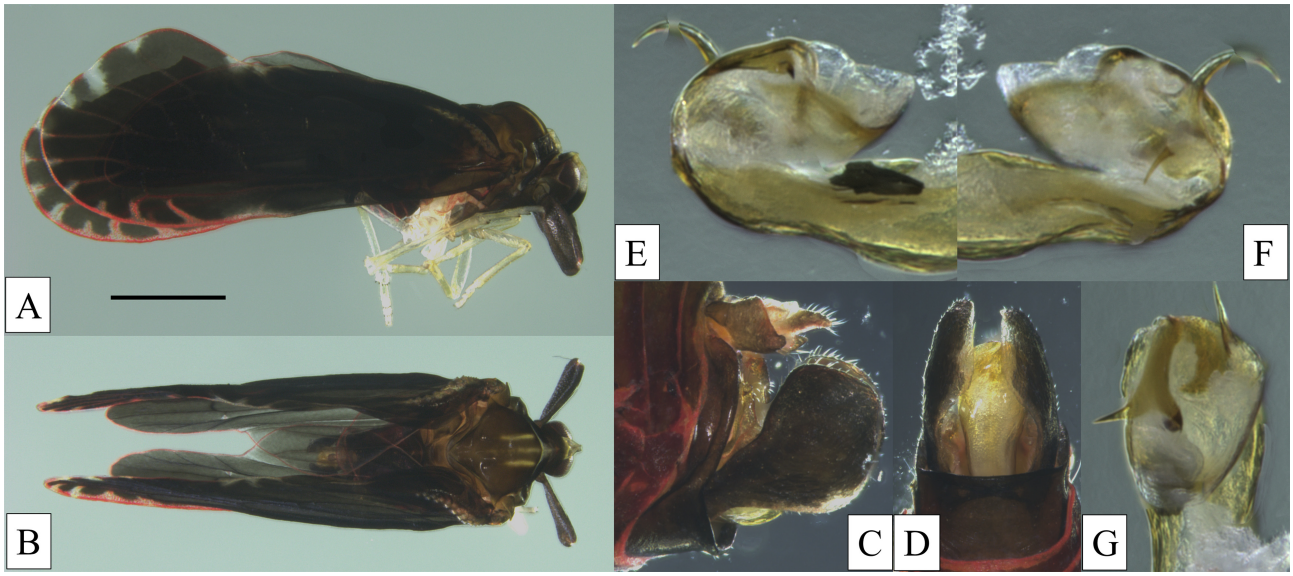

FIGURE 10. Adult male of *Patara vanduzei*; (A) habitus lateral view, (B) habitus dorsal view, (C) terminalia lateral view, (D) terminalia ventral view, (E) aedeagus right lateral view, (F) aedeagus left lateral view and (G) aedeagus dorsal view; scale = 1 mm.

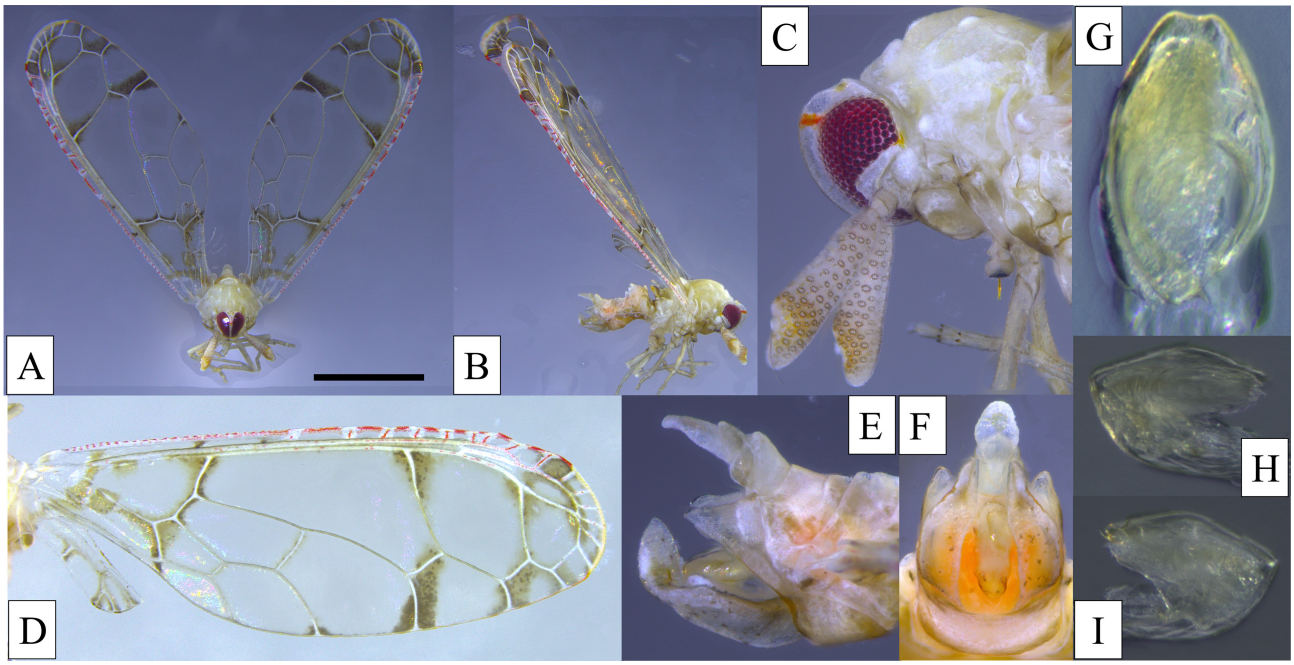

FIGURE 11. Adult male of *Mula resonans*; (A) habitus frontal view, (B) habitus lateral view, (C) head lateral view, (D) forewing, (E) terminalia lateral view, (F) terminalia ventral view (G) aedeagus dorsal view, (H) aedeagus right lateral view and (I) aedeagus left lateral view; scale = 1 mm.

Other material examined.

Otiocerus montanus Fowler, 1900. (Fig. 13A; BMNH, male syntype) "B.C.A. Homopt.I. / Otiocerus / montanus, / Fowl. // V. de Chiriqui, / 25–4000 ft. / Champion. // O. montanus Fowler [handwritten] // syn-/ type [round label, blue border] // ♂ // NHMUK 013589084 [2d barcode label]".

Otiocerus venustus Fowler, 1900. (BMNH, syntype, gender not specified, abdomen missing) "B.C.A. Homopt. I. / Otiocerus / venustus, / Fowl. // Chiacaman, / Vera Paz. / Champion. // Sp. figured. // Otiocerus / venustus Fowler / type [handwritten] // Type [round label, red border] // syn-/ type [round label, blue border] // NHMUK 013589088 [2d barcode label]"; (BMHH, syntype, gender not specified, apparently female) "B.C.A. Homopt. I. / Otiocerus / venustus, / Fowl. // V. de Chiriqui, / 2–3000 ft. / Champion. // Sp. figured. // O. venustus Fowler

[handwritten] // syn-/ type [round label, blue border] // NHMUK 013589087 [2d barcode label]".

Otiocerus griseus Fowler, 1900 (Fig. 13B; BMNH, syntype, female) "B.C.A. Homopt.I. / Otiocerus / griseus, / Fowl. // Xucumanatlan / Guerrero, / 7000 ft / July. H.H. Smith. // Sp. figured. // Otiocerus / griseus Fowler / type [handwritten] // Type [round label, red border] // syn-/ type [round label, blue border] // NHMUK 013589085 [2d barcode label]"

Otiocerus gracilior Fowler, 1900 (Fig. 13C; BMNH, syntype, female) "B.C.A. Homopt.I. / Otiocerus / gracilior, / Fowl. // Cerro Zunil / 4–5000 ft. / Champion. // Sp. figured. // Otiocerus / gracilior Fowler / type [handwritten] // Type [round label, red border] // ♀ // syn-/ type [round label, blue border] // NHMUK 013589086 [2d barcode label]"

Otiocerus interruptus Fowler, 1900 (Fig 13D; BMNH, syntype, male) "B.C.A. Homopt.I. / Otiocerus / interruptus, / Fowl. // Cerro Zunil / 4–5000 ft. / Champion. // Otiocerus / interruptus Fowler / type [handwritten] // Type [round label, red border] // ♂ // syn-/ type [round label, blue border] // NHMUK 013589089 [2d barcode label]"

Otiocerus breviceps Fowler, 1900 (BMNH, syntype, male) "B.C.A. Homopt.I. / Otiocerus / breviceps, / Fowl. // V. de Chiriqui, / 25–4000 ft. / Champion. // Otiocerus / breviceps Fowler / type [handwritten] // Type [round label, red border] // ♂ // syn-/ type [round label, blue border] // NHMUK 013589092 [2d barcode label]"

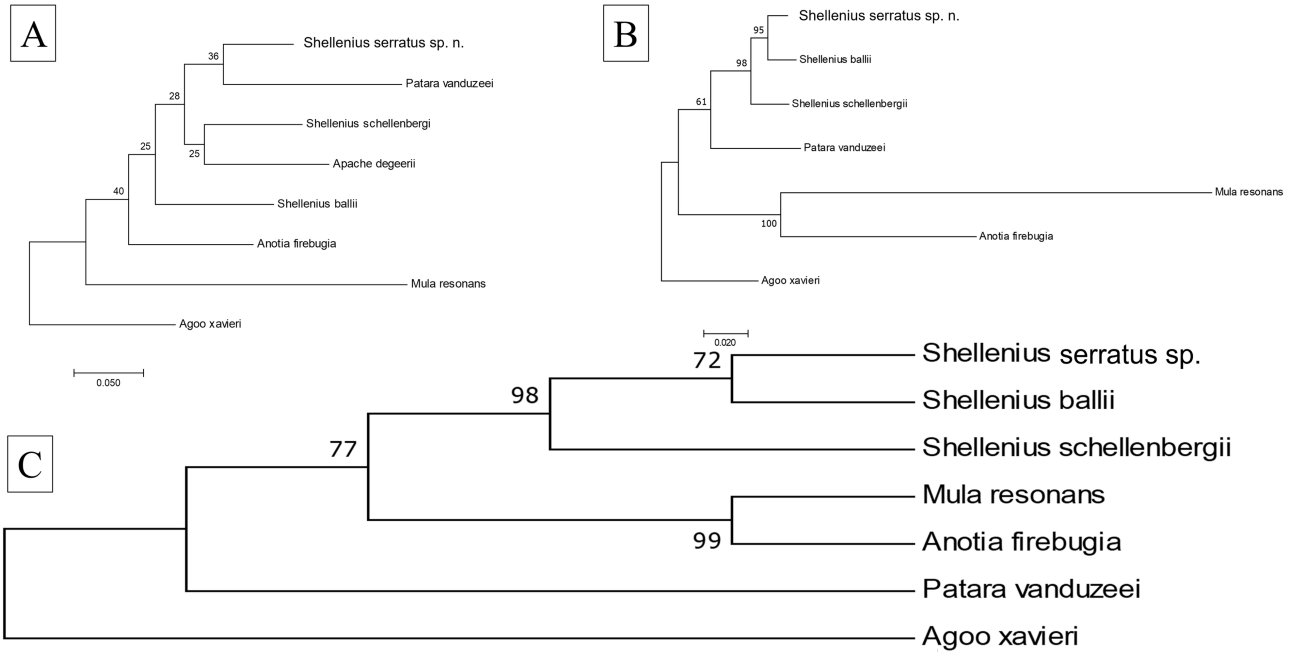

FIGURE 12. Maximum Likelihood trees (1,000 replicates) demonstrating the relationship of *Shellenius serratus* **sp. n.** relative to other available species of *Shellenius*; (A) COI, (B)18S and (C) consensus tree based on concatenated COI and 18S sequence data, scale bar = percent nucleotide difference.

Discussion

The similarity of the terminalia of *Shellenius serratus* **sp. n.** and *S. ballii,* including the similar arrangement of aedeagal processes and the presence of a distinct membranous endosoma, and the results of the molecular analysis all suggest that the new species is best placed in *Shellenius*. However, the molecular resources for New World Otiocerini are sparse, and the definitive morphological diagnostic features of the male terminalia are not described for many of the component species. Genus concepts and monophyly remain untested using quantitative phylogenetics, and so it is unclear whether current New World otiocerine genus concepts would survive detailed skeptical scrutiny, but it seems prudent to accept the genera as currently understood until additional data (morphological and molecular) are available to test current ideas.

The discovery of *Shellenius serratus* **sp. n.** on palms in Costa Rica further highlights the close association of Derbidae with the Arecaceae. While the majority of recent discoveries from planthopper survey efforts from palms

in Costa Rica are of Cenchreini, *Shellenius serratus* **sp. n.** represents the second otiocerine derbid from palms. The first was *Anotia firebugia* (Barrantes *et al.* 2020) found associated with coconut palm in northern Costa Rica. While *A. firebugia* was found along a roadside/disturbed habitat, *Shellenius serratus* **sp. n.** was found in primary growth, tropical lowland rainforest, and as such, is likely not to have as an extensive range. The New World Otiocerini is not a large/speciose group, however, continued survey efforts are critical because they will likely yield many new taxa in the tribe, drastically increasing the documented diversity of the group similar to the trend seen with the Cenchreini.

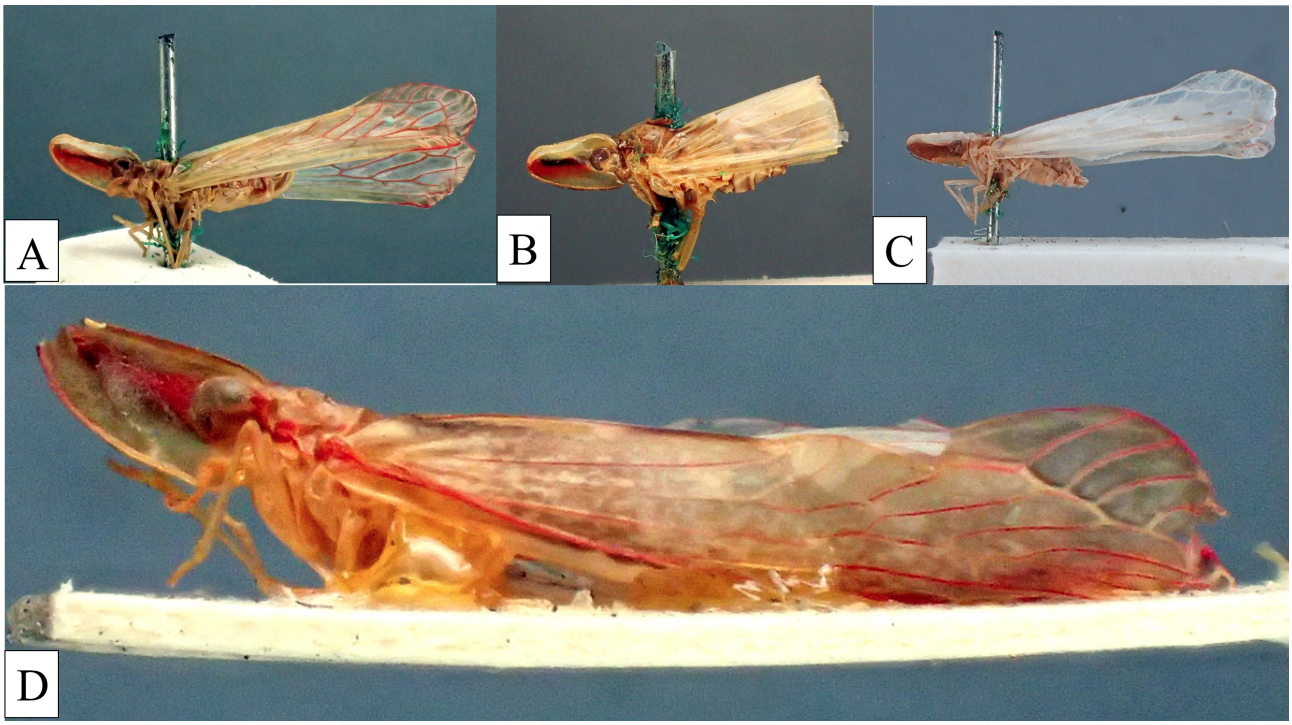

FIGURE 13. Lateral views of type material of Fowler *Otiocerus* species from BMNH now placed in *Shellenius*; (A) *Shellenius montanus*, (B) *Shellenius griseus*, (C) *Shellenius gracilior*, and (D) *Shellenius interruptus,* new comb.

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