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A new genus in the tribe Bothriocerini (Hemiptera: Auchenorrhyncha: Fulgoroidea: Cixiidae) from the cloud forests of Costa Rica, a key to genus, and an updated molecular phylogeny

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Abstract

A recent survey of planthoppers on palms (Arecaceae) in Costa Rica found a new genus of Cixiidae (Bothriocerini), described here as *Circumdara* **gen. nov.**, with two new species, *C. cidicera* **gen. et sp. nov.** and *C. nela* **gen. et sp. nov.**, from palms in the Los Angeles cloud forest. They are described with supplemental molecular data for the cytochrome *c* oxidase subunit I (COI), histone 3 (H3), 18S rRNA and D8–D10 expansion regions of 28S rRNA genes. The molecular data are analyzed to provide an updated phylogeny for the Bothriocerini relative to the Oecleini.

Key words: taxonomy, phylogenetics, biodiversity, survey, Cixiinae

Resumen

Durante un reciente trabajo de investigación en Costa Rica se ha descubierto y descrito un genero nuevo, *Circumdara* **gen. nov.** y dos especies nuevas, *C. cidicera* **gen. et sp. nov.** y *C. nela* **gen. et sp. nov.** en palmeras del bosque nuboso Los Angeles. En este documento, se describe los taxones nuevos y se proporcionan datos moleculares complementarios para la subunidad I (COI) el gen del citocromo *c* oxidasa, histona 3 (H3), el gen 18S ARNr y la región de expansión D8–D10 del gen 28S ARNr. Los datos moleculares se analizan para proporcionar una filogenia actualizada de los Bothriocerini en relación con los Oecleini.

Palabras clave: taxonomía, filogenética, biodiversidad, muestreo, Cixiinae

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Introduction

Planthoppers in the tribe Bothriocerini Muir, 1923 (Cixiidae, Cixiinae) are a unique group found in the New World, easily recognized by the large, ear-like cavity, anterior to the eyes, containing the antennae. Muir (1923) established the Bothriocerini, and subsequently (Muir 1925) specified that the tribe included five genera (*Bothriocera* Burmeister, *Borysthenes* Stål, *Kinnara* Distant, *Euryphlepsia* Muir, *Stenophlepsia* Muir). Subsequently, Metcalf (1938) treated the tribe as a subfamily (Bothriocerinae) consisting of *Bothriocera* and *Borysthenes.* The genus *Bothrioceretta* Caldwell was described as a segregate from *Bothriocera* (Caldwell 1950). Emeljanov (1989) removed *Borysthenes* to the Borysthenini. Finally, Szwedo (2002) and Szwedo *et al*. (2019) described four extinct genera in the Bothriocerini.

Extant Bothriocerini are recognized by having a broad head, strongly produced anterior to the eyes, with the antennae situated within a fossa anterior to the eyes defined by foliate carinae on the anterior margin of the head, an arrangement unique in the Cixiidae. The ocelli are conspicuous above the antennae near the anterodorsal margin of the eye. *Bothriobaltia* Szwedo, described from Baltic amber, has the antenna anterior to the eyes, but lacks the fossae formed by the carinae on the anterior margin of the head (Szwedo 2002). The remaining three extinct genera were described based on tegmina in late Eocene limestone compression fossils from the Isle of Wight (Szwedo *et al*. 2019). Currently, the tribe is represented by two extant genera.

The status of the Bothriocerini has recently been controversial, as Luo *et al.* (2021) considered Bothriocerini a tribe belonging to the oecleinian lineage. Subsequently, Le Cesne *et al*. (2022) asserted, based on morphological and molecular evidence, that the Bothriocerini were derived within the Oecleini, a result also found by the subsequent analyses of Luo *et al*. (2024).

Currently, the genus *Bothriocera* comprises 47 species (Bourgoin 2025, Barrantes *et al.* 2025), and *Bothrioceretta* four species (Caldwell 1950, Bourgoin 2025). While both genera have the large cavity at the front of the head with the antennae situated anterior to the eyes, *Bothrioceretta* is separated from *Bothriocera* by the shape of the medioventral process of the pygofer (elongate in *Bothrioceretta*, triangular in *Bothriocera*), the presence of a transverse carina posterior to the apical transverse carina (near vertex midlength in *Bothrioceretta*, absent, or possibly displaced to the posterior margin (Szwedo 2002), in *Bothriocera*), and the forewings broadly overlapping in *Bothrioceretta* (narrowly in *Bothriocera*).

During recent surveys to document planthopper diversity on palms in Costa Rica, a small pale bothriocerine was collected on trailside palms and a light trap. Further examination revealed two species representing a new genus. The taxa are herein described along with supplemental molecular data for the cytochrome *c* oxidase subunit I (COI) gene (both 5' and 3' regions), histone 3 (H3) gene, 18S rRNA gene, and the D8–D10 expansion regions of the 28S rRNA gene to examine the monophly of the genus relative to available taxa in the Bothriocerini and Oecleini.

Materials and methods

Locality and specimen collection. The specimens were collected by sweeping palms along trails and light trapping at Hotel Villa Blanca in Costa Rica (10.203231, -84.485094) (Fig. 1). Specimens were aspirated and then transferred directly to 95% ethanol, and exported to the U.S.A. The specimens were collected under project No. 836-C4-092 and exported under permit number CUSBSE-793-2025. The specimens collected were measured, photographed, and dissected using a Leica M205 C stereoscope and Leica DFC25 camera. For photography, specimens were placed in a petri dish with generic hand sanitizer and covered with a layer of 85% ethanol. Images of the specimens and all features photographed were generated using the LAS Core Software v4.12. Type material is deposited at the University of Florida—Fort Lauderdale Research and Education Center (FLREC) in Davie, FL, U.S.A. The locality map was generated using SimpleMappr (Shorthouse 2010).

Morphological terminology and identification. Morphological terminology generally follows Bartlett *et al.* (2014) except with male terminalia nomenclature updated after Bourgoin (1988) and Bourgoin & Huang (1990), and forewing venation following Bourgoin *et al*. (2015). Names for the carinae of the head are used inconsistently in Cixiidae (without established homology), and we will follow Hendrix & Bartlett (2025) in using topological names, with the anterior most carinae on the vertex termed the 'apical transverse carina', and the more proximal the 'subapical transverse carina'. New taxa are to be attributed to Bahder and Bartlett.

Dissections and DNA extraction. For the generation of COI, 18S and 28S data, the terminalia that were dissected for photography also served as the source of tissue for DNA extraction. The terminal end of the abdomens were 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 were left to lyse for 24 hours at 56°C. Following lysis, the eluate was transferred to a new 1.5 ml microcentrifuge tube and DNA extraction proceeded as per the manufacturer's instructions.

FIGURE 1. Habitat and locality of *Circumdara cidicera* **gen. et sp. nov.** and *Circumdara nela* **gen. et sp. nov.**; view from platform at entrance of main building of Hotel Villa Blanca.

PCR parameters, sequence data, and analysis. To obtain COI, H3, 18S and 28S sequence data, previously published primers were used in all PCR reactions (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$_2$0 to a final volume of 25 µL. Thermal cycling conditions for all loci involved were as follows: 2 min initial denaturation at 95°C, followed by 35 cycles of 30-sec denaturations at 95°C, 30-sec annealing, and extension at 72°C. Specific annealing temperatures and extension times for respective loci are presented in Table 1. Products were visualized on a 1.5% agarose gel stained with GelRed (Biotium). PCR products of the appropriate size were purified using the ExoSAP-IT™ Express PCR Product Cleanup Reagent per the manufacturer's protocol (ThermoFisher Scientific, Waltham, Massachusetts, USA). The purified PCR product was quantified using a NanoDrop Lite Spectrophotometer (ThermoFisher Scientific, Waltham, Massachusetts, USA) and sequenced using the SeqStudio Genetic Analyzer (Applied Biosystems). Contiguous files were assembled using DNA Baser (Version 4.36) (Heracle BioSoft SRL, Pitesti, Romania), and aligned using ClustalW as part of the package MEGA12 (Kumar *et al.* 2024). Maximum Likelihood (ML) analysis for phylogenies generated in IQ-TREE (Minh *et al*. 2020) using a concatenated matrix of COI (5' half and 3' half), H3, 18S rRNA and the D8–D10 expansion region of 28S rRNA. The matrix was partitioned (Chernomor *et al.* 2016) by marker and the best-fit partitioning scheme and model was selected according to the Bayesian information criterion (BIC) score in ModelFinder (Kalyaanamoorthy *et al.* 2017) implemented in IQ-TREE. Substitution models selected and applied for each partition of the combined data matrix to ML analysis were (1) 28SD8+28SD9D10+18S: TIM3e+I+G4 and (2) COI5+COI3: TIM2+F+R5 and (3) H3: GTR+F+I+G4. Clade support was calculated by 1,000 replicates of Shimodaira-Hasegawa approximate likelihood ratio test (SH-aLRT; Guindon *et al*. 2010, Hoang *et al*. 2018) in ML analysis. Reliable support values are SH-aLRT ≥80 and UFboot ≥95 (Guidon *et al*. 2010, Minh *et al*. 2013). The resulting tree was viewed and edited in FigTree v1.4.4.

TABLE 1. Primers used to amplify corresponding gene regions used to assess the placement of novel taxon and PCR parameters for each locus.

Locus	Primer	Direction	Sequence (5' →3')	Annealing	Extension	Reference
COI (5')	COI_D1_F	Forward	GGAACWATAAGAAGWATAATYATYCG	40°C	1 min. 30 sec.	Humphries *et al.* 2021
	C1-J-2195RC	Reverse	ACTTCTGGATGACCAAAAAATCAA			
COI (3')	C1-J-2195	Forward	TTGATTTTTTGGTCATCCAGAAGT	40°C	1 min. 30 sec.	Simon *et al.* 1994
	TL2-N-3014	Reverse	TCCAATGCACTAATCTGCCATATTA			
18S	18SF	Forward	GGATAACTGTGGTAATTCTAG	50°C	2 min.	Bahder *et al.* 2019
	18SR	Reverse	GTCCGAAGACCTCACTAAA			
H3	H3F2	Forward	GKAARTCSACCGGHGGHAARGC	55°C	30 sec.	Bahder *et al.* 2023 Echavarria *et al.* 2021
	H3R	Reverse	GTKACHCKCTTRGCGTGRAT			
28S (D8)	Lalt	Forward	CCTCGGACCTTGAAAATCC	55 °C	1 min. 30 sec.	Cryan *et al.* 2000
	Galt	Reverse	TGTCTCCTTACAGTGCCAGA			
28S (D9–D10)	V	Forward	GTAGCCAAATGCCTCGTCA	55 °C	1 min. 30 sec.	Cryan *et al.* 2000
	X	Reverse	CACAATGATAGGAAGAGCC			

Taxon sampling. For molecular comparisons, seven species of *Bothriocera* were included in the analysis (Supplementary Table 1). Non-Bothriocerini outgroup taxa from the Pintaliini, Oecleini, and Pentastirini were included to root the tree. Two species of Delphacidae were included to further polarize the tree and provide deeper support. GenBank accession numbers for all taxa are presented in Supplementary Table 1.

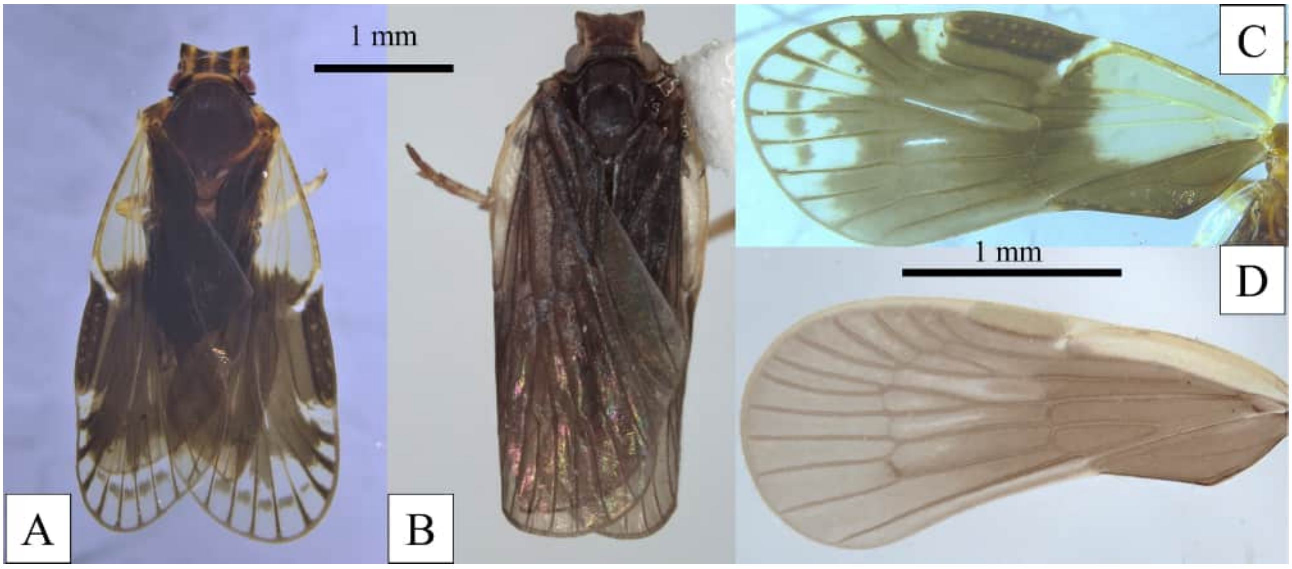

FIGURE 2. Dorsal habitus view of *Bothriocera basalis* (A) and *Bothrioceretta nigra* (B) and respective forewings (C & D).

Results

Systematics

Family Cixiidae Spinola, 1839

Subfamily Cixiinae Spinola, 1839

Tribe Bothriocerini Muir, 1923

Key to genera of extant Bothriocerini

1. Vertex with subapical transverse carina absent (or at posterior margin of vertex, Figs. 3A, 5A), forewings patterned or transparent (Figs. 2C, 6) , males with medioventral process of the pygofer relatively short (usually wider than long, Fig. 3B, 7B) 2

-. Vertex bearing subapical transverse carina between apical transverse carina and posterior margin of vertex (Fig. 3C), forewings deeply embrowned (Fig. 2D), males with medioventral process of the pygofer elongated (nearly 2x as long as greatest width, Fig. 3D). . . . . *Bothrioceretta* Caldwell

2. Forewings transparent with few markings (Fig. 6); aedeagus with shield-like structure arising at the aedeagal apex (Fig. 9B, AF) . . . . *Circumdara* **gen. nov.**

-. Forewings often extensively patterned (Fig. 2C); aedeagus without shield-like sclerite. . . . . *Bothriocera* Burmeister

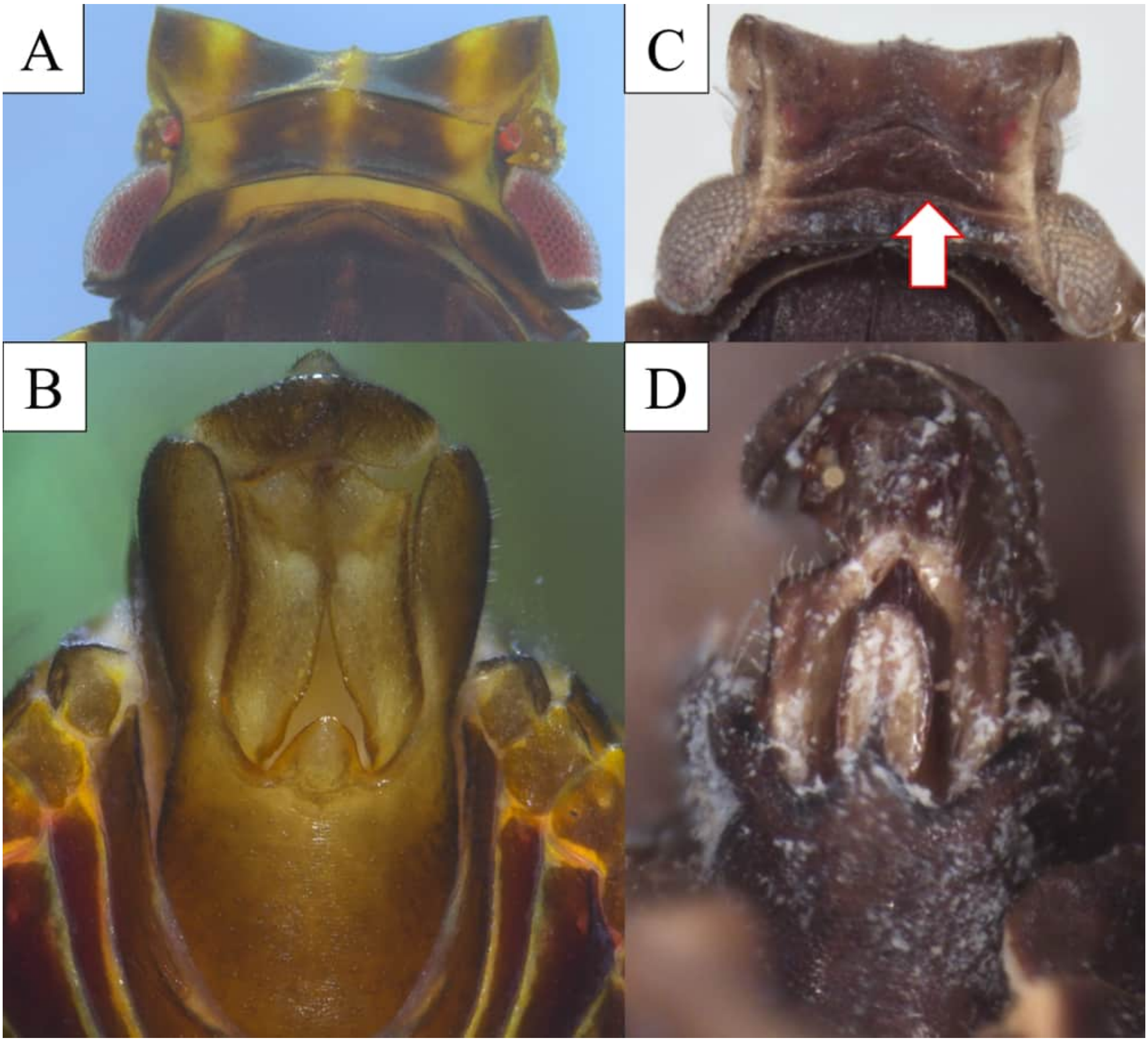

FIGURE 3. *Bothriocera basalis* dorsal view of head (A) and medioventral process of pygofer (B) and *Bothrioceretta nigra* dorsal view of head (C) and medioventral process of pygofer (D); arrow indicates transverse carina.

Circumdara Bahder & Bartlett gen. nov.

Diagnosis. Small to average-sized cixiids (4.6–4.8 mm). Head in dorsal view narrower than pronotum. Vertex broad and quadrate, greatest length (near anterior margin) wider than midlength, produced in front of eyes, anterior margin concave, posterior margin truncate. Vertex bearing apical transverse carinae (convexly arched) near level of antennae, meet anteriorly by median carina of frons; subapical transverse carinae absent on disc. Head in lateral view produced in front of antennae, lateral carinae of frons forming a c-shaped flange defining deep elongated antennal depression. Antennae anterior to eyes, short, scape hidden, flagellum apical and setaceous. Lateral ocelli above antennae at anteriordorsal margin of eyes. Eyes elongate-oval (long axis lateral), medially compressed at antennae. Genae bearing transverse carina, most distinct between ventral margin of eye and lateral carina of face. Head in facial view broad, with sides of frons and clypeus carinate, dorsolateral portions of frons expanded and auriculate, longitudinal midline of frons carinate on dorsal portion. Face bearing sublateral carina, dorsal margin curled medially, ventral margins meeting just below median ocellus, circumscribing a triangular central tablet. Frontal ocellus prominent. Frontoclypeal suture linear. Clypeus elongated, tricarinate, anterior margin of maxillary plate convex. Rostrum exceeding hindcoxae.

Pronotum medially very narrow, posterior margin broadly concave. Mesonotum tricarinate. Hind tibiae with six lateral spines, apical spinulation 5-6-6. Forewings weakly patterned, held broadly overlapped in repose; relatively short and broadly spatulate, dorsal margin broadly convex, ventral margin concave, apex broadly rounded; clavus short, apex in basal third, pterostigma proximad of midlength, veins ScP+R and MP separate at apex of basal cell, post cubital cell broad, branching pattern RA 2-branched, RP 3-branched, MP 5-branched, CuA 2-branched. Veins without setae-bearing pustules. Male terminalia with pygofer irregular in shape from lateral view, broadest medially, caudal margin broadly concave, medioventral process triangular, broader than tall. Aedeagus with straight shaft, subapically bearing large shield-like process along left lateral margin, and dextrally curled. Partly membranous endosoma with two large projections that encompass aedeagal shaft. Anal tube short, apices elongated and downcurved, paraproct short and conical.

Remarks. The new genus can be distinguished from *Bothrioceretta* because it lacks the subapical transverse carina on the vertex (or, as described by Szwedo, 2002, it is shifted to posterior margin, creating small areolets in the posterior angles), and the medioventral process of the pygofer is triangular (elongate in *Bothrioceretta*), similar to that of *Bothriocera*. The apices of the forewings in *Circumdara* **gen. nov.** overlap as seen in *Bothrioceretta*. Superficially, *Circumdara* **gen. nov.** resembles *Bothriocera*; however, there are two distinct features of the aedeagus that separate the two. *Circumdara* **gen. nov.** possesses a large, shield-like structure arising at the aedeagal apex that extends cephalad, nearly reaching the base (Figs. 8, 14) (absent in *Bothriocera*). Secondly, *Circumdara* **gen. nov.** possesses a unique endosoma that is split into two major regions (similar to *Bothriocera*); however, the novel taxon has the anterior region of the endosoma with two large, lateral projections that curve ventrally, completely encompassing the aedeagal shaft, a feature absent in *Bothriocera*.

In life, both species of *Circumdara* **gen. nov.** had waxy pruinosity (similar to iNaturalist observation 287025230), making specimens nearly white *in vivo*. In available specimens, the wing markings were intraspecifically similar, suggesting that forewing patterns may be a more reliable diagnostic character than appear to be in *Bothriocera*.

Other material examined

Bothriocera basalis. COSTA RICA: Puntarenas, La Tarde Ecolodge, Osa Peninsula, 16.VI.2021 (1 male, FLREC).

Bothrioceretta nigra. MEXICO: Michoacán, Hwy 15, 7 mi. E. Quiroga, 8,100 ft., 15 Aug. 1982, CW & L. O'Brien & G. Wibmer (1 male, UDCC); same, 31 mi. E. Morelia, 7750 ft, 15 Aug. 1982, CW & L. O'Brien & G. Wibmer (1 female, UDCC).

Circumdara cidicera Bahder & Bartlett gen. et sp. nov.

(Figures 4–9)

Type locality. Hotel Villa Blanca, Alajuela Province, Costa Rica (10.203231, -84.485094) (Fig. 1).

FIGURE 4. Habitus view of *Circumdara cidicera* **gen. et sp. nov.**: (A) dorsal view and (B) lateral view.

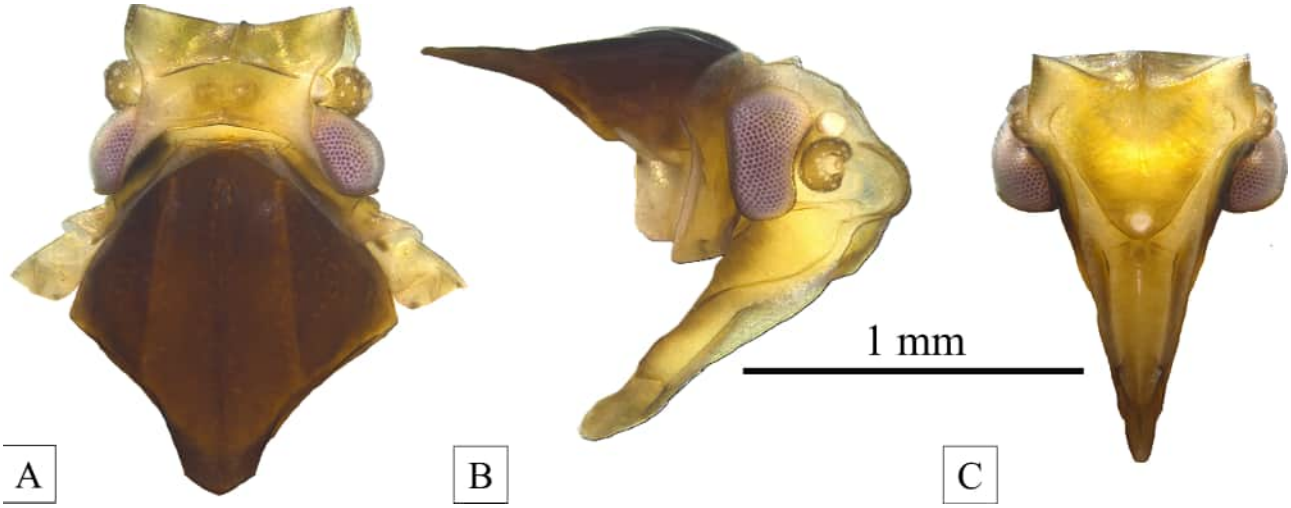

FIGURE 5. *Circumdara cidicera* **gen. et sp. nov.**: (A) dorsal view of head-pronotum-mesonotum, (B) lateral view of head-pronotum-mesonotum and (C) frontal view of head.

Diagnosis. Forewings transparent with three fuscous spots along nodal line (between $MP_{1.1}$ and *im*). Medioventral process of pygofer very broad at base, subtriangular, approximately 4X as wide as long at midpoint; endosoma with single row of serrated flanges on dorsal margin; aedeagal flange with apex blunt in dorsal view, bearing a flap-like process.

Description. *Color*. General body color medium brown (Fig. 4), lighter on mesonotum from median carina to lateral carinae; head, pronotum and legs almost testaceous (Fig. 5), forewings clear, slightly tinted yellow in basal half, three distinct spots at the *r-m* and two *im* crossveins, one fuscous patch at wing margin between the RP_{1+2} and RP_3 and fuscous patch along posterior margin of clavus (Fig. 6).

Structure. Body length with wings; male 4.6 mm, female 4.8 mm (Table 2). Head. In dorsal view (Fig. 5A), head broad, roughly quadrangular, wider anterior to eyes, width at widest point about 2.2X length at midline. Vertex with apical transverse carinae arched, extending transversely to join at midline just in front of eyes (bisecting head apex, joined anteriorly by extension of median carina of frons); subapical transverse carina absent (or along posterior margin), median carinae obsolete; disc depressed posterior to anterior transverse carinae (bearing a pit on either side of midline); anterior and posterior margins concave; in lateral view (Fig. 5B), profile irregularly sinuate, posterior margin of vertex raised, irregularly declinate anteriorly, anterior margin projecting in front of eyes, lateral margin of frons forming conspicuous c-shaped keels anterior to antenna defining deep elongated antennal depression. Antennae situated directly in front of eyes. Lateral ocelli conspicuous, dorsal to antennae at anterodorsal margin of eye. Eyes dumbbell-shaped (long axis verticle), narrowed at antennae. Transverse carina on gena below antenna between ventroanterior margin of eye to anterior margin of head. In frontal view (Fig. 5C), face broad, roughly triangular in shape, widest dorsally at auriculate expansion of head, constricting ventrad to frontoclypeal suture, median carina distinct to median ocellus. Distinct lateral carinae, meeting medially below antennae, forming u-shape. Frontoclypeal suture obscure, roughly transverse (a pair of lateral dark markings near lateral extensions of frontoclypeal sutures perhaps marking anterior tentorial pits). Eyes in lateral view roughly dumbbell-shaped. Antennae short, scape hidden, pedicel wider than tall, roughly C-shaped in lateral view, bearing irregularly placed sensory plaques, flagellum setaceous with bulbous base.

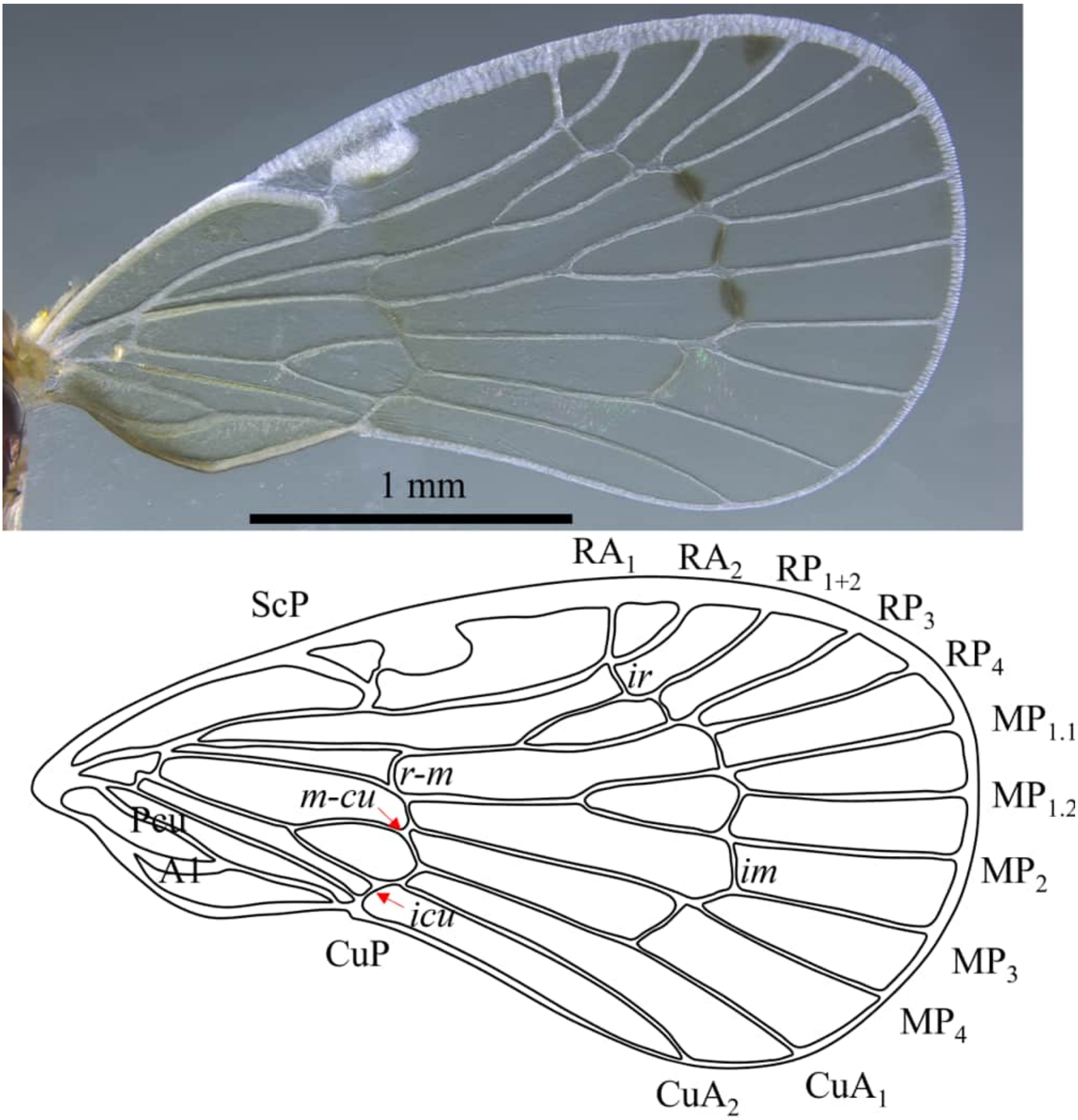

FIGURE 6. *Circumdara cidicera* **gen. et sp. nov.** forewing venation; italic text = crossvein, non-italic text = main vein, abbreviations follow Bourgoin *et al.* (2015).

Thorax. Pronotum in dorsal view very narrow, anterior margin linear, posterior margin deeply concave, apparently tricarinate (Fig. 5A). Mesonotum in dorsal view approximately as wide as long at midpoint, tricarinate, lateral carinae weekly diverging, all carinae appearing to reach posterior margin (Fig. 5A). Forewing broadly spatulate, narrow basally, expanding to approximately 2X the width in distal 2/3 after clavus; RA 2-branched, RP 3-branched, MP 5-branched, CuA 2-branched (Fig. 6). Hind tibiae lacking lateral spines. Spinulation of tibal apex and tarsomeres 5-6-6.

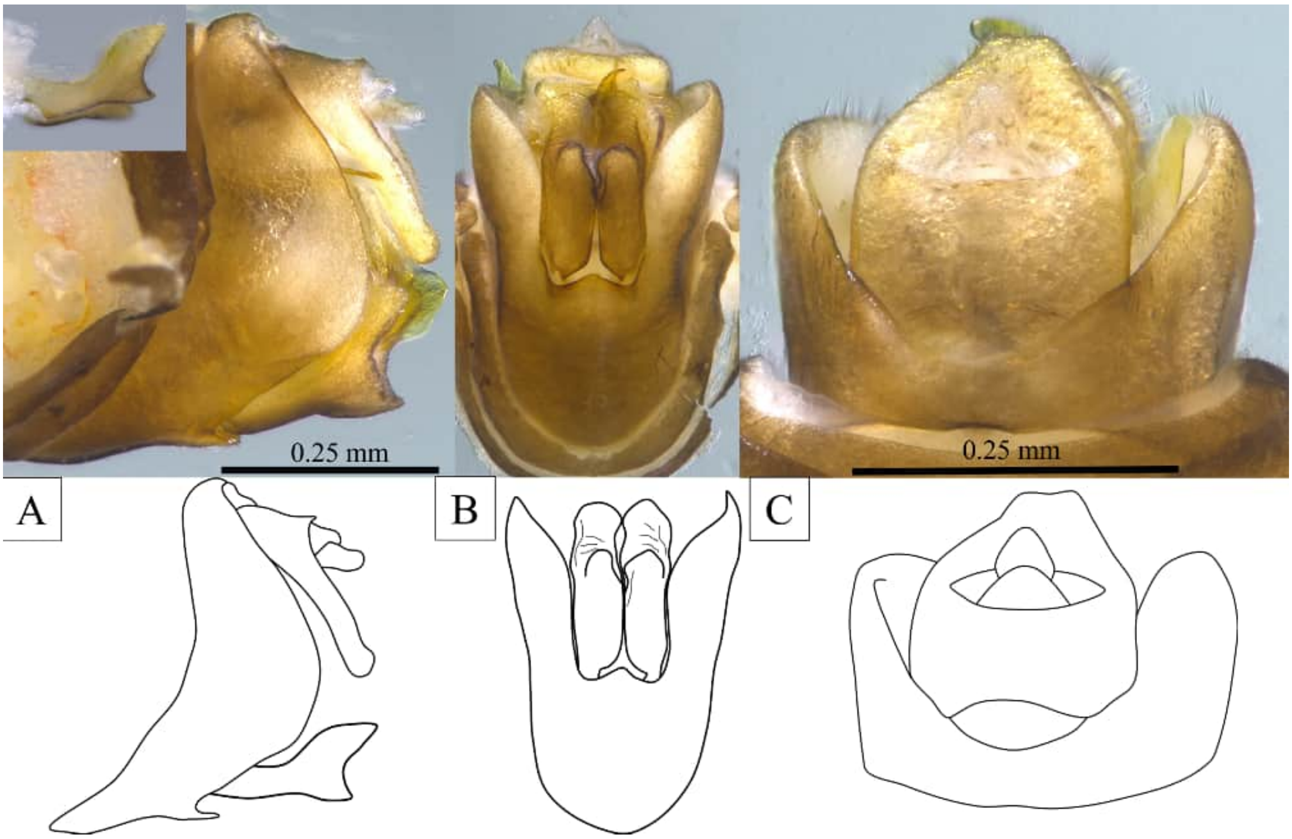

FIGURE 7. *Circumdara cidicera* **gen. et sp. nov.** male terminalia: (A) lateral view, (B) ventral view and (C) dorsal view.

TABLE 2. Biometric data for novel taxa described in this study**.**

	Circumdara cidicera **gen. et sp. nov.**				*Circumdara nela* **gen. et sp. nov.**			
	Male (*n*=3)		Female (*n*=3)		Male (*n* = 2)		Female (*n*=4)	
Character	Range	Average ± SE	Range	Average ± SE	Range	Average ± SE	Range	Average ± SE
Body length, with wings	4.6	4.6±0.0	4.8–4.9	4.8±0.1	4.6	4.6±0.0	4.8	4.8±0.0
Body length, no wings	2.2	2.2±0.0	2.4	2.4±0.0	2.2	2.2±0.0	2.4	2.4±0.0
Forewing length	3.3	3.3±0.0	3.5–3.7	3.5±0.1	3.3	3.3±0.0	3.5	3.5±0.0
Vertex length	0.2	0.2±0.0	0.2	0.2±0.0	0.2	0.2±0.0	0.2	0.2±0.0
Vertex width, basal margin	0.6	0.6±0.0	0.6	0.6±0.0	0.6	0.6±0.0	0.6	0.6±0.0
Vertex width, distal margin	0.5	0.5±0.0	0.5	0.5±0.0	0.5	0.5±0.0	0.5	0.5±0.0
Pronotum length, midline	0.03	0.03±0.0	0.03	0.03±0.0	0.03	0.03±0.0	0.03	0.03±0.0
Mesonotum length, midline	1.0	1.0±0.0	1.1	1.1±0.0	1.0	1.0±0.0	1.1	1.1±0.0
Mesonotum width	1.0	1.0±0.0	1.1	1.1±0.0	1.0	1.0±0.0	1.1	1.1±0.0
Frons width, dorsal margin	0.7	0.7±0.0	0.7	0.7±0.0	0.7	0.7±0.0	0.7	0.7±0.0
Frons width, clypeal suture	0.4	0.4±0.0	0.4	0.4±0.0	0.4	0.4±0.0	0.4	0.4±0.0
Frons width, widest	0.7	0.7±0.0	0.7	0.7±0.0	0.7	0.7±0.0	0.7	0.7±0.0
Frons width, narrowest	0.4	0.4±0.0	0.4	0.4±0.0	0.4	0.4±0.0	0.4	0.4±0.0
Frons length, midline	0.5	0.5±0.0	0.5	0.5±0.0	0.5	0.5±0.0	0.5	0.5±0.0
Clypeus length	0.5	0.5±0.0	0.5	0.5±0.0	0.5	0.5±0.0	0.5	0.5±0.0

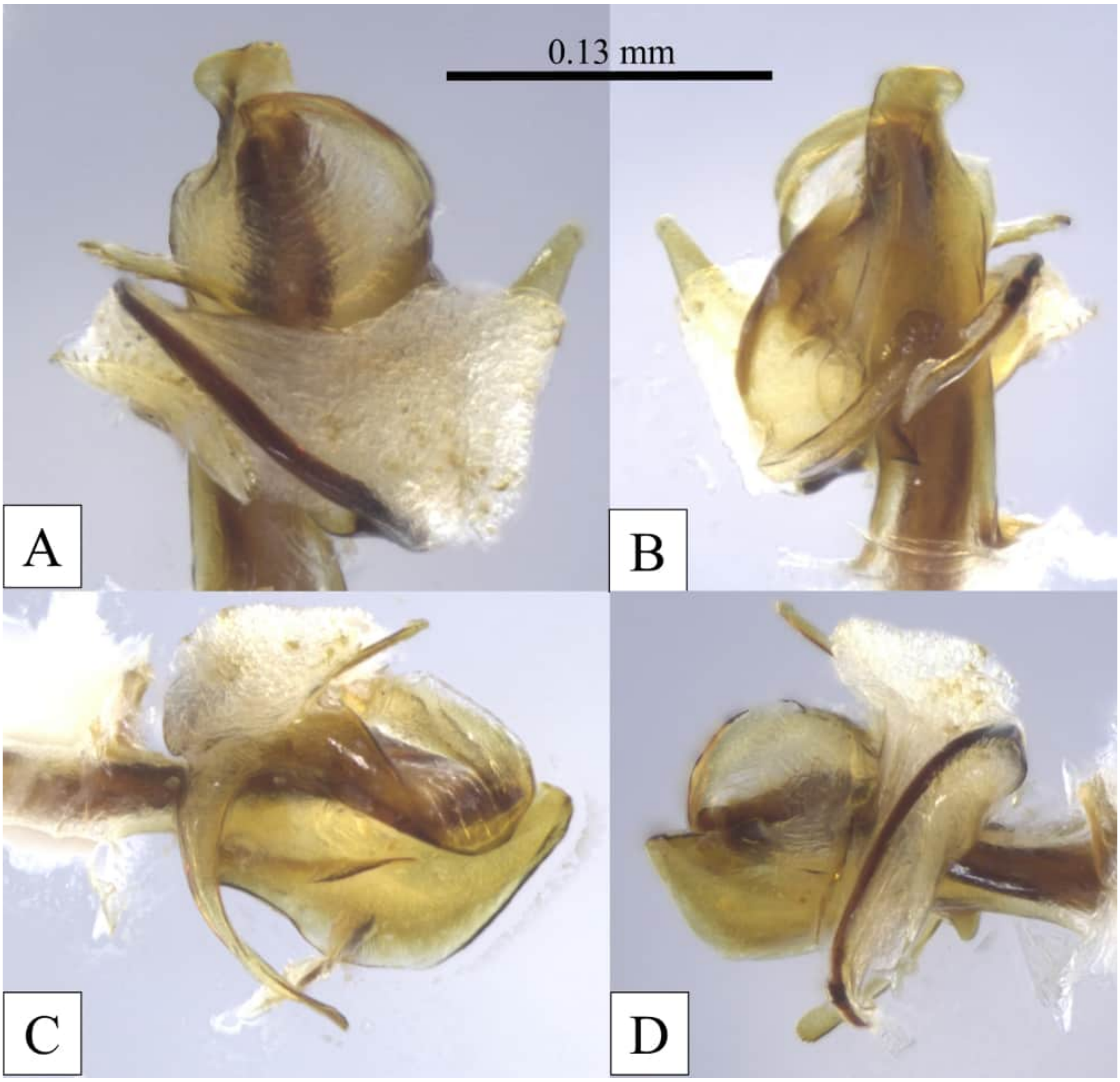

FIGURE 8. *Circumdara cidicera* **gen. et sp. nov.** aedeagus: (A) dorsal view, (B) ventral view, (C) left lateral view and (D) right lateral view.

Terminalia. Pygofer in lateral view narrow dorsally, expanded medially (widest just below midpoint), constricting to ventral margin, anterior margin concave, posterior margin convex (Fig. 7). In ventral view, medioventral process low subtriangular, broad at base, approximately 4X wider than long (Fig. 7). Gonostyli in lateral view stout and upcurved, concave on dorsal margin, pointed at apex, ventral margin with large subtriangular projection (Fig. 7); in ventral view closely approximated, irregularly sinuate on inner and outer margins, ventral projections appearing rounded, apices irregularly rounded (Fig. 7). Aedeagus complex (Figs. 8 & 9), bearing large, lateral flange (AF) with flap-like processes (AP) arising on left lateral side. Endosoma complex, dextrally helically curved, split into two distinct regions; the first region near aedeagal apex bears single, serrated process (E1, Fig. 9B), angled towards right lateral side with E1 curving ventrad. Second region of endosoma positioned on dorsal margin bearing three processes; E2 arising on left lateral margin, angled caudad and dorsad, E3 arising on left lateral side extending dorsally over aedeagal shaft, curving ventrally on right lateral side, terminating under aedeagal shaft, E4 arising on left lateral side (Fig. 9B), curved ventrally, rounded at apex, extending underneath aedeagal shaft, E3 and E4 apices cross below aedeagal shaft, completely encompassing the shaft. Anal tube in lateral view short, apices elongated, directed ventrad, apex rounded, approximately reaching gonostyli, dorsal margin slightly sinuate (Fig. 7A); in dorsal view, asymmetrical, apex skewed slightly to right lateral side, apex truncate (Fig. 7C).

Plant associations. Unidentified palm species (Arecaceae).

Distribution. Costa Rica, Alajuela Province.

Etymology. The specific name is given as an honorific of the Centro de Investigación sobre Diversidad Cultural y Estudios Regionales (CIDICER) whose support for this research was integral. The name is intended to be indeclinable.

Material examined. Holotype male "Costa Rica, Alajuela Pr. / Hotel Villa Blanca / 15.VII.2025 / sweeping palms / Coll.: B.W.Bahder // Holotype / *Circumdara cidicera* ♂" (FLREC). Paratypes (2 males, 3 females); 1 male same data as holotype, 1 male, 3 females collected on same date at light trap.

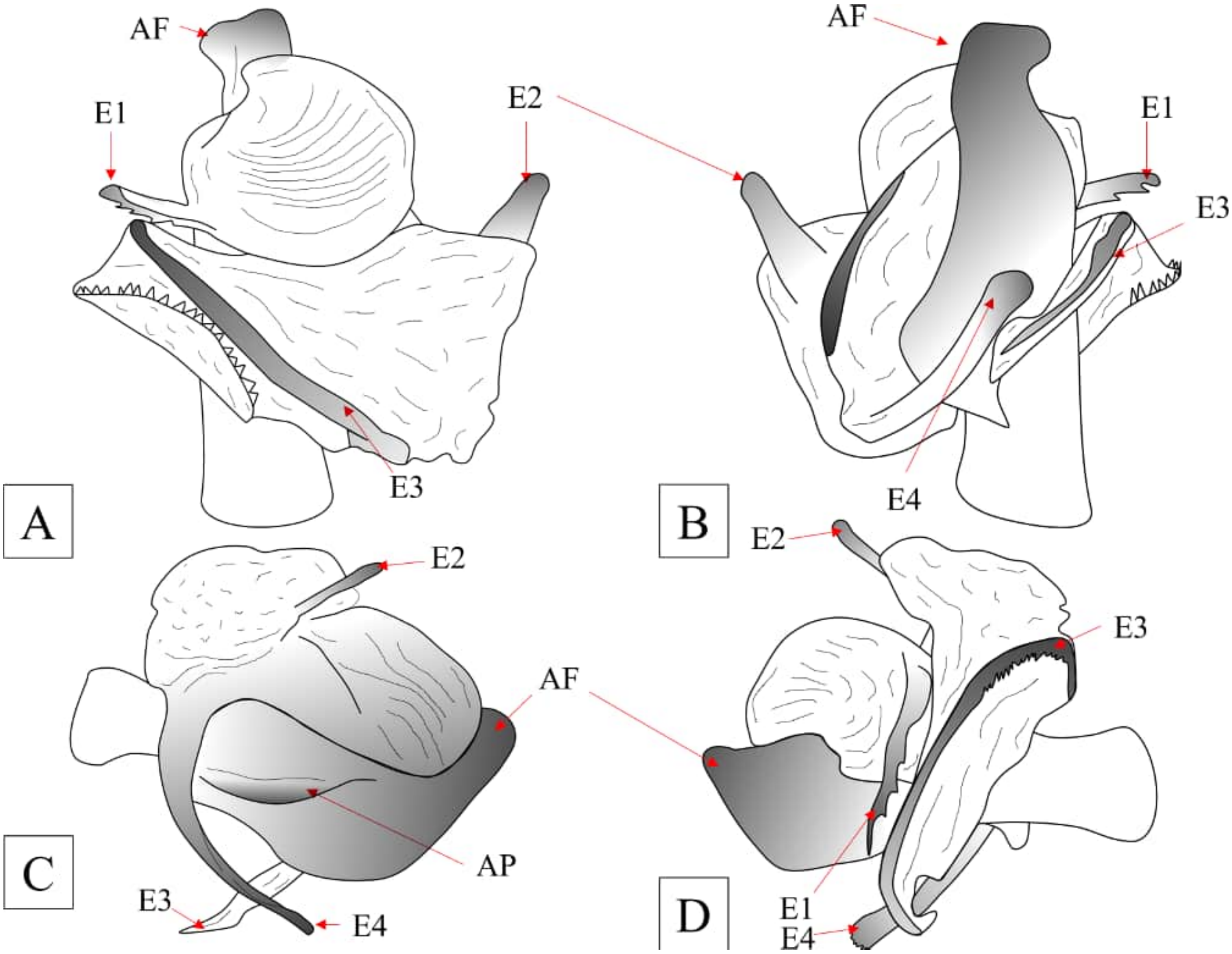

FIGURE 9. *Circumdara cidicera* **gen. et sp. nov.** aedeagus line art: (A) dorsal view, (B) ventral view, (C) left lateral view and (D) right lateral view.

Circumdara nela Bahder & Bartlett gen. et sp. nov.

(Figures 10–15)

Type locality. Hotel Villa Blanca, Alajuela Province, Costa Rica (10.203231, -84.485094) (Fig. 1).

Diagnosis. Forewings irregularly mottled with fuscous patches (mainly along nodal line and crossveins at level with *r-m*). Medioventral process of pygofer subtriangular, approximately as wide as long at midpoint. Aedeagal endosoma with two long rows of serrated flanges on dorsal margin; aedeagal flange with apex strongly pointed in dorsal view, bearing a process that is spinose on outer margin.

FIGURE 10. Habitus view of *Circumdara nela* **gen. et sp. nov.**: (A) dorsal view and (B) lateral view.

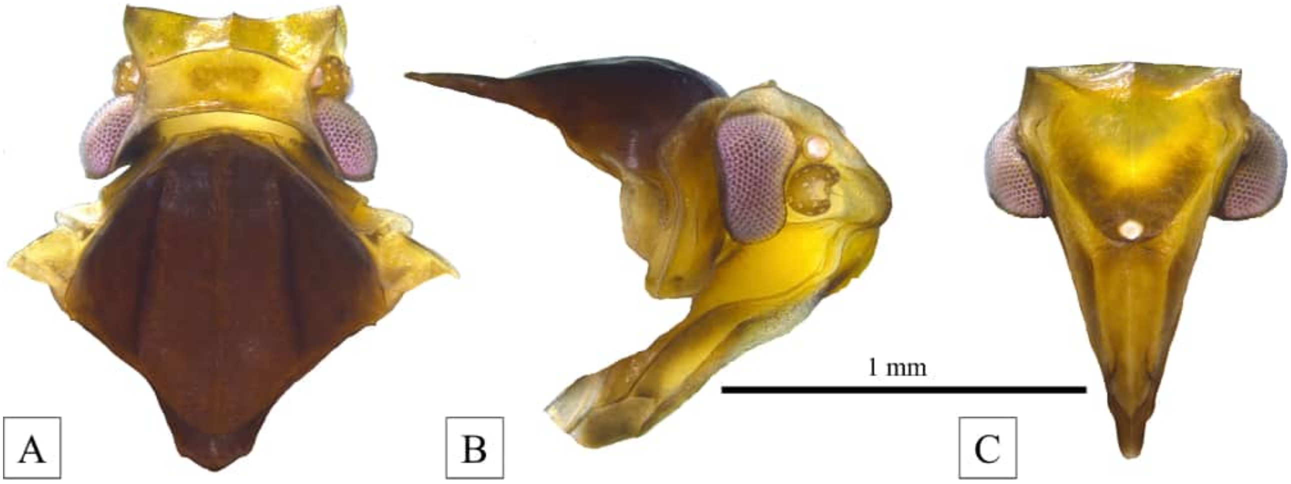

FIGURE 11. *Circumdara nela* **gen. et sp. nov.**: (A) head-pronotum-mesonotum dorsal view, (B) lateral view and (C) head frontal view.

Description. *Color*. General body color dark brown (Fig. 10), lighter on mesonotum from median carina to lateral carinae; head, pronotum and legs almost testaceous (Fig. 11); forewings clear, slightly tinted yellow in basal half, irregularly mottled with fuscous patches (Fig. 10).

Structure. Body length with wings; male 4.6 mm, female 4.8 mm (Table 3). Head. In dorsal view (Fig. 11A), head roughly quadrangular, wider anterior to eyes, width at widest point about 2.2X length at midline. Vertex with apical transverse carinae arched, extending transversely to join at midline just in front of eyes (bisecting head apex, joined anteriorly by extension of median carina of frons); subapical transverse carina absent (or along posterior margin); median carinae obsolete, disc depressed (bearing defined pit on either side of midline); anterior and posterior margins concave; in lateral view (Fig. 11B), profile irregularly sinuate, vertex posterior margin raised, irregularly declinate anteriorly, projecting in front of eyes, lateral margins of head forming deep elongated depression, antennae situated directly anterior to eyes, lateral ocelli dorsal to antennae at anterodorsal margin of eye, transverse carina on gena below antenna between ventroanterior margin of eye to anterior margin of head. In frontal view (Fig. 11C), face broad, roughly triangular in shape, frons widest dorsally at auriculate expansion of head, constricting ventrad to frontoclypeal suture, median carina distinct to median ocellus; distinct lateral carinae, meeting medially below antennae, forming a U-shaped tablet from level of ventral margin of eyes to beneath the median ocellus. Frontoclypeal suture obscure and roughly transverse (a pair of lateral dark markings near lateral extensions of frontoclypeal sutures perhaps marking anterior tentorial pits). Eyes in lateral view roughly dumbbell shaped (long axis vertical). Antennae short, scape hidden, pedicel wider than tall, roughly C-shaped in lateral view, bearing irregularly placed sensory plaques, flagellum setaceous with bulbous base.

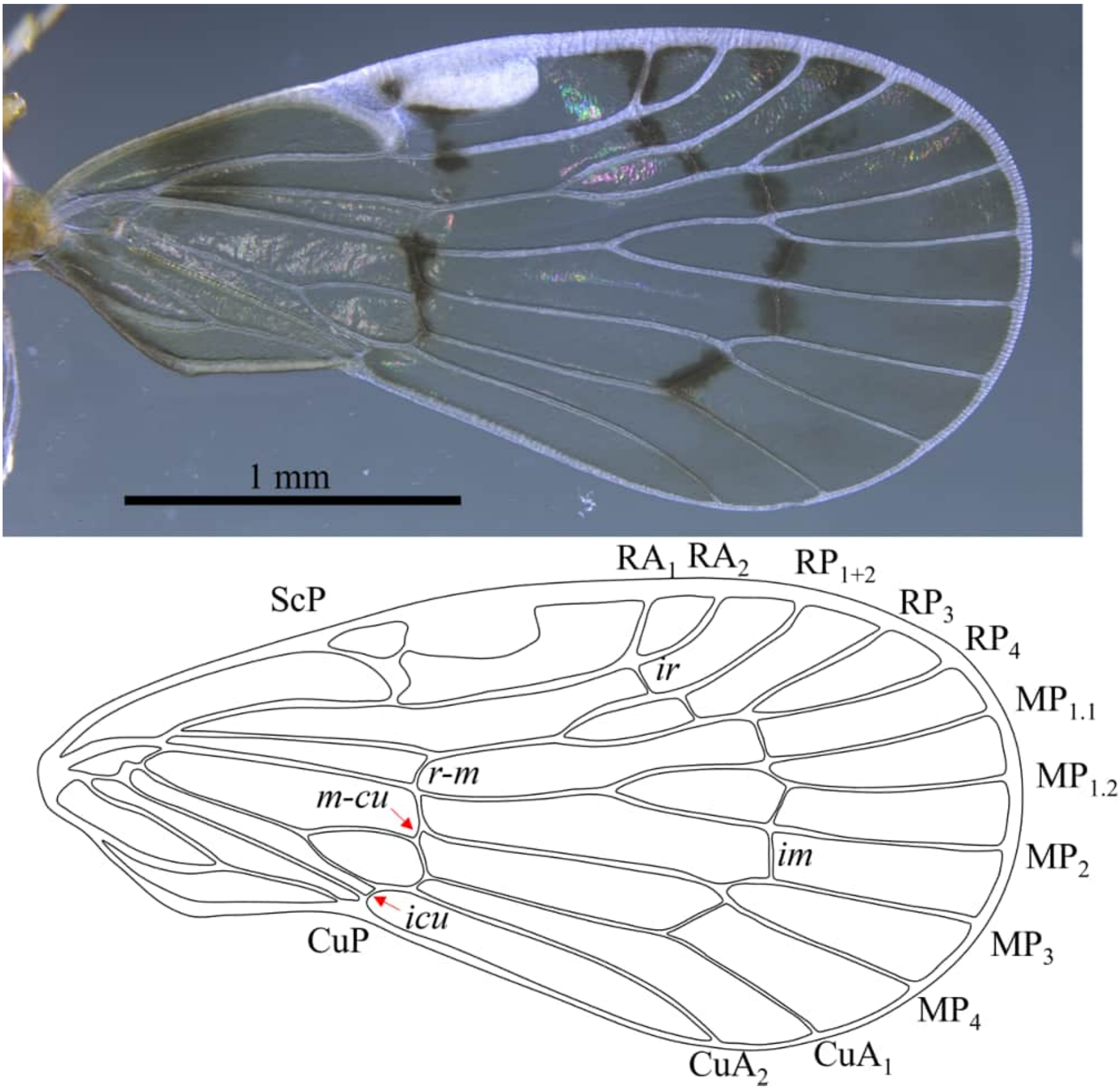

FIGURE 12. *Circumdara nela* **gen. et sp. nov.** forewing venation; italic text = crossvein, non-italic text = main vein, abbreviations follow Bourgoin *et al.* (2015)..

Thorax. Pronotum in dorsal view very short with anterior margin linear, posterior margin deeply concave, appearing tricarinate (Fig. 11A). Mesonotum in dorsal view approximately as wide as long at midpoint, tricarinate (Fig. 11A). Forewing spatulate, narrow basally, expanding to approximately 2X the width in distal 2/3 after clavus; RA 2-branched, RP 3-branches, MP 5-branched, CuA 2-branched (Fig. 12). Hind tibiae lacking lateral spines, apical spinulation of tibal apex and tarsomeres 5-6-6.

Terminalia. Pygofer in lateral view narrow dorsally, expanded ventrad (widest near midpoint), constricted ventrad except expanded on ventral margin; anterior margin concave, posterior margin irregularly sinuate (Fig. 13A); in ventral view, medioventral process subtriangular, approximately as wide as long at midpoint (Fig. 13B). Gonostyli in lateral view stout, angled dorsad, dorsal surface concave, apex rounded; subtriangular projection on ventral margin near midlength (Fig. 13A); in ventral view, gonostyli approximated, lateral margins subparallel, ventral projections arising medially, apices semitruncate (Fig. 13B). Aedeagus complex, shaft straight, tubular, apex bearing large, shield-like flange (AF, Figs. 14B, 15B), extending almost to aedeagal base on left lateral margin, in dorsal view (Figs. 14A, 15A), apex pointed, small process (AP) rising on outer lateral side near midpoint, angled dorsad. Endosoma helically twisted, split into two regions, posterior region curved dorsally over shaft to right lateral side, bearing one large, serrated process (E1); anterior region larger, bearing rounded process (E2) along dorsal margin on left lateral side and two additional lateral processes curving ventrad, surrounding aedeagal shaft, process arising on left lateral side (E3) curving dorsally initially over aedeagal shaft then ventrally and process on right lateral side (E4) immediately curving ventrally. Two rows of serrations along dorsal margin of anterior region (Figs. 14, 15). Anal tube in lateral view short, apices elongated, directed ventrad, apex pointed, approximately reaching gonostyli, dorsal margin slightly sinuate (Fig. 13A); in dorsal view, asymmetrical, apex skewed slightly to right lateral side, apex truncate (Fig. 13C).

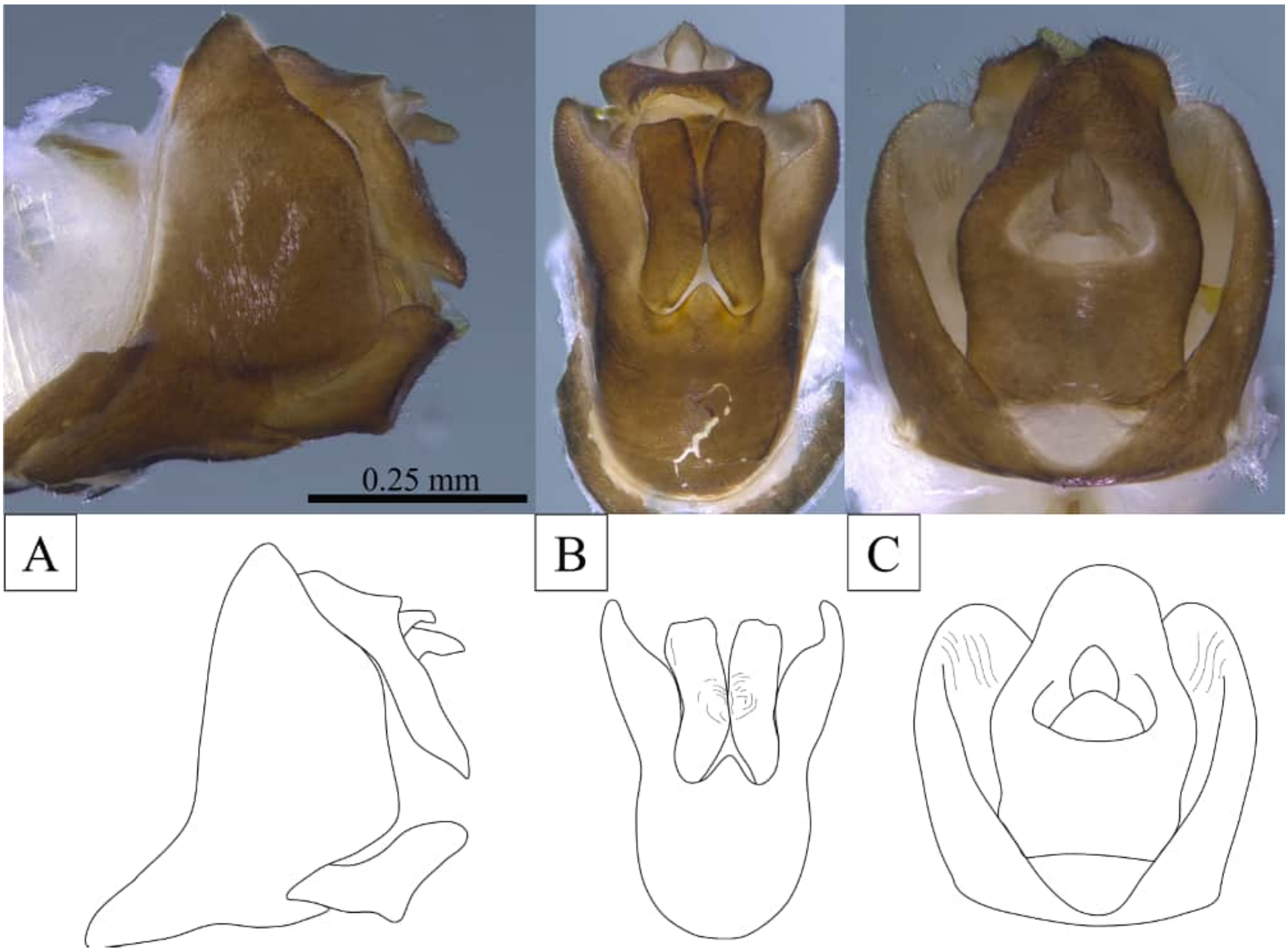

FIGURE 13. *Circumdara nela* **gen. et sp. nov.** male terminalia: (A) lateral view, (B) ventral view, and (C) dorsal view.

Plant associations. Multiple, unidentified immature palm species (Arecaceae).

Distribution. Alajuela Province, Costa Rica.

Etymology. The specific name is a nickname of Marienla Hidalgo Matamoros from CIDICER. It is named in recognition of her assistance in establishing this project. The name is intended to be indeclinable.

Material examined. Holotype male “Costa Rica, Alajuela Pr. / Hotel Villa Blanca / 15.VII.2025 / sweeping palms / Coll.: B.W.Bahder // Holotype / *Circumdara nela* ♂” (FLREC). Paratypes (1 male, 4 females); 1 male same data as holotype, 4 females collected on same date at light trap.

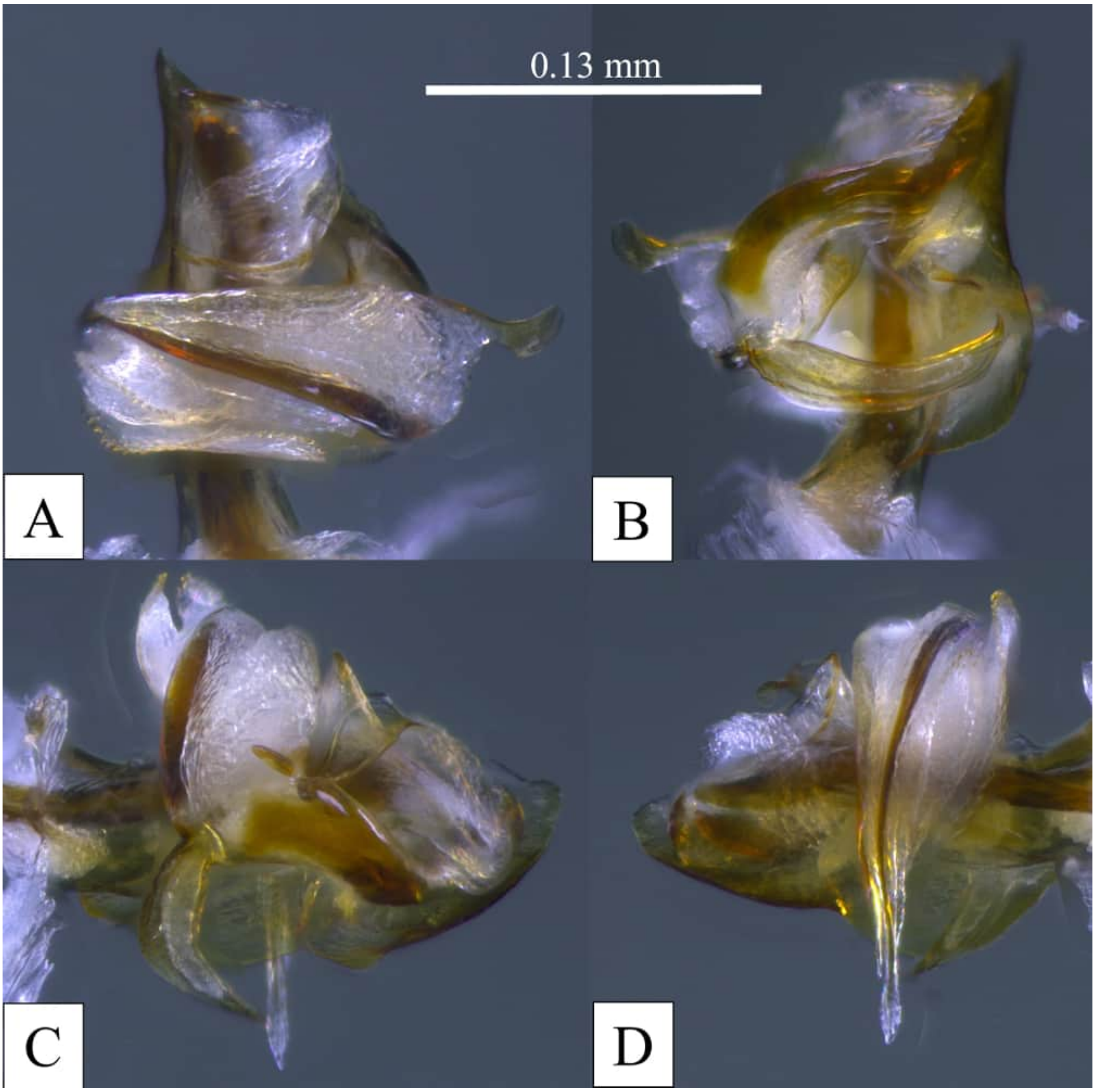

FIGURE 14. *Circumdara nela* **gen. et sp. nov.** aedeagus: (A) dorsal view, (B) ventral view, (C) left lateral view, and (D) right lateral view.

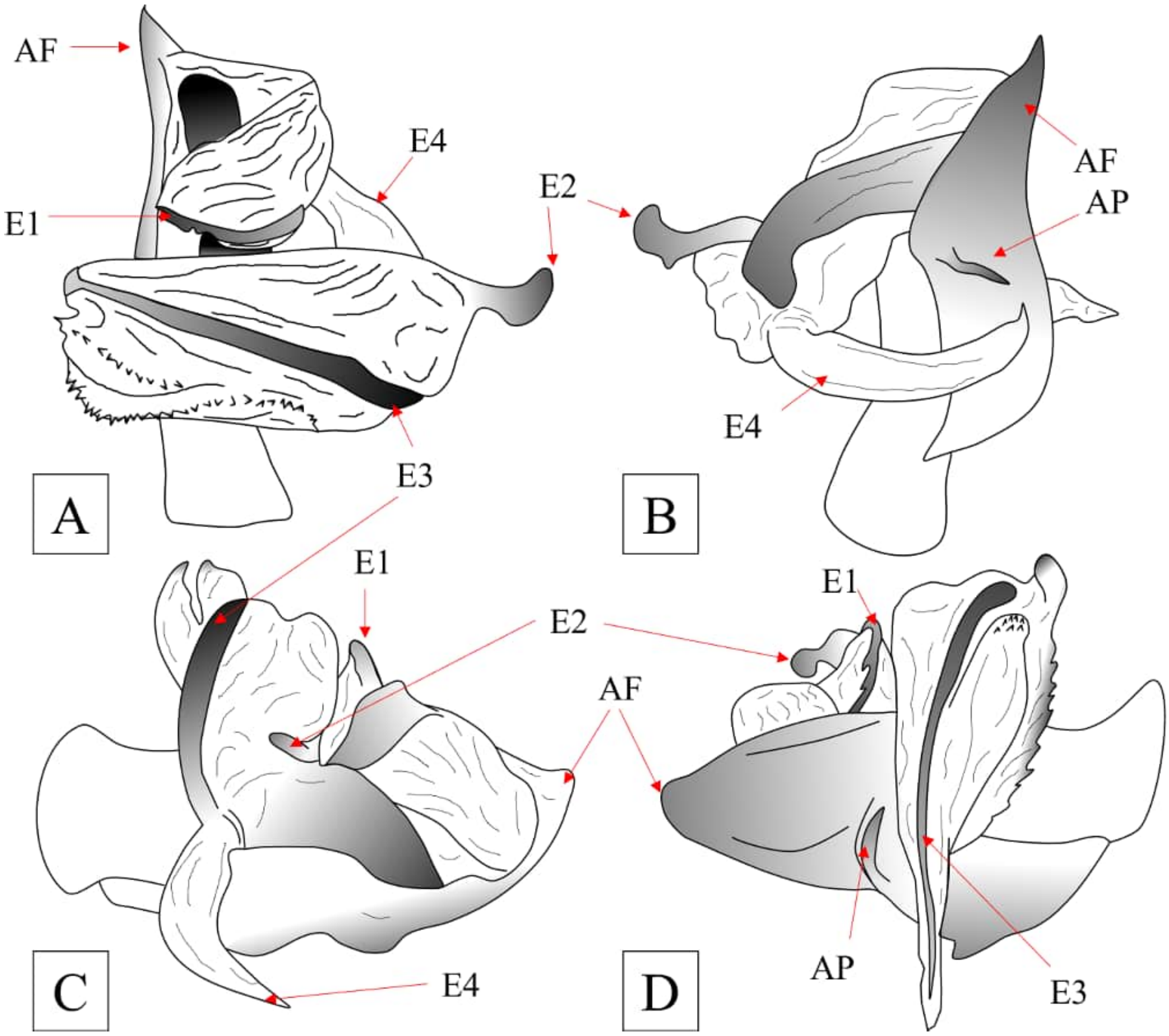

FIGURE 15. *Circumdara nela* **gen. et sp. nov.** aedeagus line art: (A) dorsal view, (B) ventral view, (C) left lateral view and (D) right lateral view; AF = aedeagal flange, AP = aedeagal process, E = endosoma.

Sequence Data and Molecular Analysis

For both of the novel taxa, molecular data was recovered for COI (5' and 3' regions), H3, 18S rRNA and 28S rRNA (D8–D10 expansion regions). Sequences obtained were 520, 633, 315, 1364, 738 and 768 base pairs (bp) long, respectively. Accession numbers for each loci used to generate phylogenies for each species are presented in Supplementary Table 1. The rooted tree (Fig. 16) generated for the molecular phylogeny had both *Bothriocera* and *Circumdara* **gen. nov.** arising adjacent to the Oecleini with strong support (99.6/96). Additionally, *Circumdara cidicera* **gen. et sp. nov.** and *Circumdara nela* **gen. et sp. nov.** resolved adjacent to each other as a clade within the Bothriocerini relative to *Bothriocera* with strong support (100/100).

Remarks. The clear morphological differences of *Circumdara* **gen. nov.** to both *Bothriocerettta* and *Bothriocera* and strong molecular support for the novel taxa resolving adjacent to each other in a clade distinct from *Bothriocera* support the establishment of a novel genus, despite not having *Bothrioceretta* available for molecular analysis.

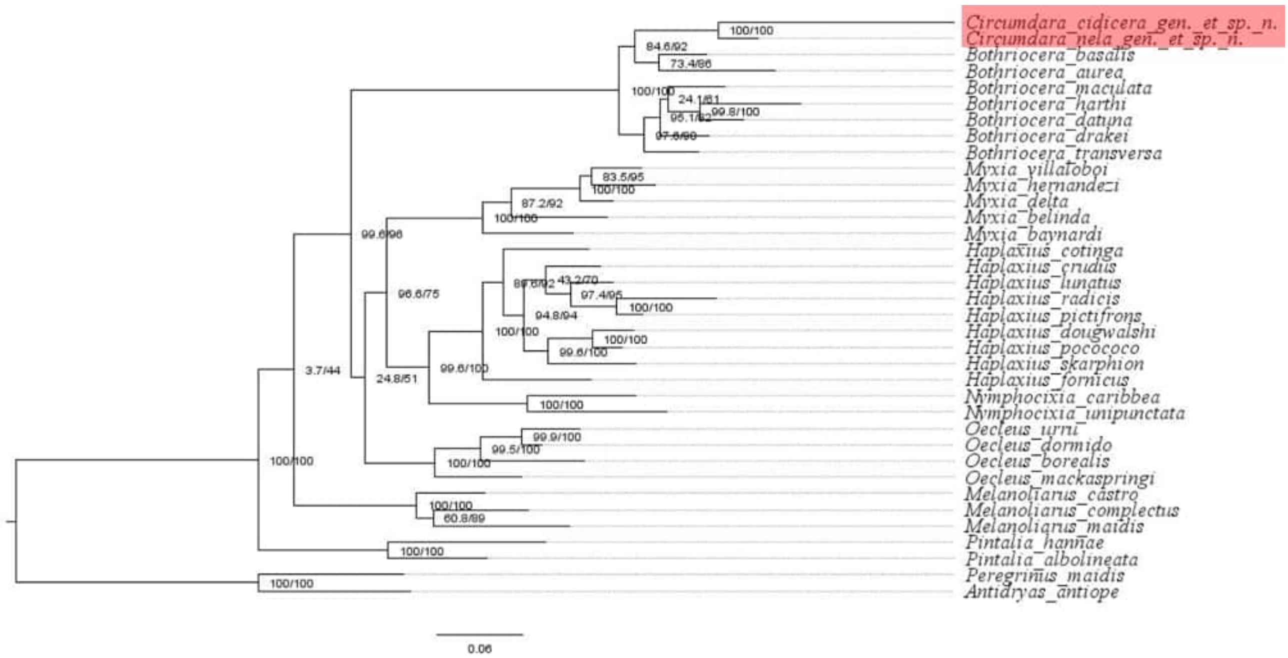

FIGURE 16. Bothriocerini rooted Maximum Likelihood phylogenetic tree (-ln L -32580.9862) based on concatenated data for all loci selected in this study; scale bar = percent nucleotide variability, solid branch line = percent nucleotide variance, broken branch line = aligned for visual display, novel taxa highlighted red, support values = SH-aLRT/UFboot.

Discussion

The discovery of a new genus and species within Bothriocerini is significant. First, this tribe consists of only two extant genera, *Bothrioceretta* with four species and *Bothriocera* with 47 (Bourgoin 2025, Barrantes *et al.* 2025). *Bothriocera* appears heterogeneous—partially indicated by the relationships between *B. aurea* and *B. basalis* with North American and Caribbean taxa—but it hasn't been studied sufficiently to warrant reclassification into different genera. Moreover, the type species (*Bothriocera tinealis* Burmeister, described from Bahia and Pará, Brazil, Burmeister (1835)) is poorly known and needs redescription (as was recently undertaken with *B. substigmatica* (Lethierry), Le Cesne *et al*. 2025) to define *Bothriocera sensu stricto* more clearly. Despite the ambiguous nature of *B. tinealis*, *B. basalis* (and this group in general) is similar based on wing patterns and terminalia structures and is clearly closer to *B. tinealis* than the new genus. Because of the clear morphological characters outlined above and the genetic distinction of the specimen of *B. basalis* used in this study, the novel taxa clearly can be distinguished at the generic level with *B. basalis* as a proxy for *Bothriocera* senso stricto.

Second, as new taxa become available for molecular analysis, the relationships within this group and to other cixiids will become clearer. According to Luo *et al*. (2024), the Bothriocerini belong to the oecleinian lineage, justifying their classification within the Cixiinae. However, our analysis with the new taxa implies that the Bothriocerini are not within the Oecleini and may deserve subfamily status. With greater taxon sampling from both the Bothriocerini and other tribes (both Old and New World), these relationships should be clarified, which will be a focus of future research.

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SUPPLEMENTARY TABLE 1. Molecular taxon sampling and GenBank accession numbers.

Species	Locus					
	COI (5’)	COI (3’)	18S	H3	28S (D8)	28S (D9–D10)
Circumdara cidicera **gen. et sp. nov.**	PX092720	PX092663	PX093633	PX096635	PX093634	PX093637
Circumdara nela **gen. et sp. nov.**	PX092719	PX092664	PX093632	PX096634	PX093635	PX093638
Bothriocera aurea Bahder & Bartlett	PQ492664	PQ492663	PQ492716	PQ505808	PQ492718	PQ492717
Bothriocera harthi Bahder & Bartlett	OR115602	PQ051105	OR120252	OR133714	PQ057111	OR116974
Bothriocera basalis Metcalf	OR115604	PQ051108	OR120254	OR133717	PQ057114	OR116975
Bothriocera datuna Kramer	OR115603	PQ051107	OR120253	OR133715	PQ057113	OR116979
Bothriocera drakei Metcalf	OR115605	PQ051106	OR120256	OR133716	PQ057112	OR116976
Bothriocera maculata Caldwell	OR115606	PQ051104	OR120255	OR133718	PQ057110	OR116978
Bothriocera transversa Caldwell	OR115607	PQ051103	OR120257	OR133719	PQ057109	OR116977
Haplaxius cotinga Bahder & Bartlett	ON763279	PQ051102	ON758370	ON755134	PQ057100	PP379292
Haplaxius crudus (Van Duzee)	MT080284	PQ051101	MT002393	MZ274037	PQ057108	OR116983
Haplaxius dougwalshi Bahder & Bartlett	MT080284	PQ051100	MT002395	MZ297815	PQ075107	PP379291
Haplaxius fornicus Bahder & Bartlett	OP160200	PQ051099	OP158203	OP179300	PQ057106	PP379290
Haplaxius lunatus (Van Duzee)	OM264285	PQ051098	OM258692	OM262388	PQ057105	PP379289
Haplaxius radicis (Osborn)	PP379550	PQ051095	PP379293	PP389033	PQ057102	PP370286
Haplaxius skarphion (Kramer)	MT900603	PQ051094	MT892907	MZ274039	PQ057101	PP382226
Haplaxius pocococo Bahder & Bartlett	MW086873	PQ051096	MW086509	OM262387	PQ057103	PP379287
Haplaxius pictifrons (Stål)	MT946292	PQ051097	MN200098	MZ274038	PQ057104	PP379288
Myxia belinda Bahder & Bartlett	MT900605	PQ056946	MN200095	MZ274041	PQ057092	OR116981
Myxia delta (Kramer)	MT900602	PQ056945	MT892907	MZ274042	PQ057091	PP379279
Myxia hernandezi Bahder & Bartlett	MZ234085	PQ056944	MZ262449	MZ274043	PQ057090	PP379278
Myxia baynardi Bahder & Bartlett	MT900604	PQ056947	MT892909	MZ274040	PQ057092	PP379280
Myxia villaloboi Bahder & Bartlett	PP379549	PQ056943	PP379294	PP389034	PQ057089	PP379277
Nymphocixia unipunctata Van Duzee	OM264284	PQ051086	OM258690	OM262389	PQ057087	OR116982
Nymphocixia caribbea Fennah	MT080286	PQ051087	MT002394	MZ274044	PQ057088	PP379276
Oecleus borealis Van Duzee	OM264286	PQ051081	OM258691	OM262390	PQ057083	PP379275
Oecleus dormido Bahder & Bartlett	OM264283	PQ051080	OM258693	OM262392	PQ057086	PP379274
Oecleus mackaspringi Bahder & Bartlett	MN488999	PQ051082	MN422261	MZ274045	PQ057085	OR116980
Oecleus urru Bahder & Bartlett	OQ749902	PQ051079	OQ745735	OQ744000	PQ057084	PP379273
Melanoliarus castro Bahder & Bartlett	OP871033	PQ051093	OP889237	OP896205	PQ057099	PP379285
Melanoliarus complectus (Ball)	PP379551	PQ051091	PP379295	PP389035	PQ057097	PP379283
Melanoliarus maidis Fennah	OP871035	PQ051089	OP889235	OP896207	PQ057095	OR116984