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A new species of *Oecleus* (Hemiptera: Auchenorrhyncha: Fulgoromorpha: Cixiidae) from the Osa Peninsula in Costa Rica

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Abstract

Recent palm survey work in Costa Rica focusing on planthoppers has resulted in the discovery of several new taxa, primarily in Cixiidae and Derbidae. In addition to sampling palms directly, light trapping has been utilized to collect a broader range of planthoppers that may not be found on palms. During a light trapping event at the Cotinga Biological station on the Osa peninsula in Costa Rica, a cixiid was collected and subsequently determined to be an unidentified species in the genus *Oecleus* Stål. Herein, the novel taxon, *Oecleus urru* **sp. n.**, is described. Supplemental molecular data for the barcoding region (5' half) of the cytochrome *c* oxidase subunit I (COI) gene, 18S rRNA gene, and histone 3 (H3) gene is provided to support the placement of the novel taxon in the genus *Oecleus*.

Key words: new species, Oecleini, phylogeny, taxonomy, planthopper

Resumen

El reciente trabajo de investigación en palmeras de Costa Rica para la búsqueda e identificación de chicharritas ha resultado en el descubrimiento de varios taxones nuevos, principalmente en las familias Cixiidae y Derbidae. Además de tomar muestras directas de las palmeras, se utilizaron trampas de luz para recolectar una variedad más amplia de chicharritas que podrían no encontrarse en las palmeras. Durante un evento de captura mediante trampa de luz en la Estación Biológica Cotinga en la península de Osa en Costa Rica, se recolectó un cixíido y posteriormente se determinó que era una especie no identificada del género *Oecleus* Stål. En este documento se describe el nuevo taxón, *Oecleus urru* **sp. n.** Además, se proporcionan datos moleculares complementarios para la región del código de barras (extremo 5 ') del gen de la subunidad I del citocromo *c* oxidasa (COI), el gen 18S del ARNr y el gen de la histona 3 (H3) para respaldar la ubicación del nuevo taxón dentro del género *Oecleus*.

Palabras clave: especie nueva, Oecleini, filogenia, taxonomía, chicharrita

Introduction

The genus *Oecleus* Stål, 1862 is a New World taxon in the family Cixiidae Spinola, 1839 (Cixiinae, Oecleini), comprised of 67 species (Myrie *et al*. 2019, Barrantes *et al.* 2022, Bourgoin 2023). the greatest diversity of *Oecleus* species is in the southwestern United States and conterminous Mesoamerica (south to El Salvador) (Caldwell 1944, Kramer 1977, Bartlett *et al*., 2014, 2018; Myrie *et al*. 2019).

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Recent work on the genus (Bartlett *et al*. 2018, Myrie *et al*. 2019, Barrantes *et al*. 2022) has focused on tropical *Oecleus* associated with palms, including the first *Oecleus* species recorded from Brazil (Bartlett *et al.* 2018) and Costa Rica (Barrantes *et al.* 2022). The recently described species, *O. mackaspringi* Bahder & Bartlett 2019 was discovered while seeking to assess potential vectors in plots of coconut palms affected by lethal yellowing (LY) in Jamaica (Myrie *et al*. 2019).

Oecleus is the type genus of the tribe Oecleini Muir, 1922. The Oecleini are small cixiids, diagnosed by the absence of lateral teeth on the hind tibiae and the common stem of the longitudinal veins Sc, R, and M on the forewing forming a long common stalk from the basal cell (Muir 1922, Emeljanov 2007, Barrantes *et al.* 2022). Most New World genera of Oecleini possess a narrow, elongate vertex. *Oecleus* is distinctive with a very narrow, trough-like vertex, with the head somewhat forward-projecting, and (usually) five carinae on the mesonotum (Although Caldwell 1944: 175 noted that the intermediate carinae are weak, and the appearance of 5 prominent carinae is the result of color contrast rather than bas relief). The Oecleini includes *Haplaxius crudus* (Van Duzee, 1907), the vector of the LY phytoplasma in Florida (Howard & Thomas 1980, Mou *et al*. 2020a, b) and putative vector elsewhere in the Caribbean Basin (Dzido *et al*. 2020). Due to the previously presumed close phylogenetic relationship of *Oecleus* to *Haplaxius* Fowler, 1907, any species found on palms are of interest as a potential phytoplasma vector.

The phylogenetic relationships among species of *Oecleus* have not yet been investigated in any detail, but external morphological variation suggests that the genus may be heterogeneous. Among genera of Oecleini, preliminary findings suggest that *Oecleus* form a clade sister to the remaining genera of Oecleini in the corresponding analyses (viz. *Haplaxius* Fowler, *Myxia* Bahder & Bartlett, 2019 and *Nymphocixia* Van Duzee 1923; Barrantes *et al*. 2022). As new species of *Oecleus* are discovered and the material becomes available for other groups, these relationships can be further explored.

Herein we describe a new species of *Oecleus* from palm-related survey work on the Osa Peninsula of Costa Rica. We present COI, 18S, and H3 sequence data for the new species and provide phylogenetic analyses for the individual and combined genes for the new species, other available *Oecleus* species, and available New World oecleine genera to test the genus-level placement of the new species and provide a preliminary indication of the relationship among the New World genera of Oecleini

Materials and methods

Locality and specimen collection. Specimens were collected sweeping long grasses in an abandoned pasture at the Cotinga Biological Research Station, Costa Rica, Puntarenas province (8.621825,-83.478819). Specimens were aspirated from the sweep net and transferred directly to 95% ethanol. 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, are stored at the University of Florida – Fort Lauderdale Research and Education Center (FLREC) in Davie, and the Florida State Collection of Arthropods (FSCA) in Gainesville, FL, U.S.A.

Distributional data for the genus were extracted from data downloads from iNaturalist (https://www.inaturalist.org/) and the Tri-Trophic Thematic Collection Network (http://tcn.amnh.org/).

Morphological terminology. Morphological terminology generally follows Kramer (1977) except with male terminalia nomenclature updated after Bourgoin (1988) and Bourgoin & Huang (1990) and forewing venation following Bourgoin *et al*. (2015). New taxa are to be attributed to Bahder and Bartlett.

Dissections and DNA extraction. The terminalia that were dissected 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, the 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 and sequence data. To obtain COI, 18S, and H3 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_20 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 denaturation 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). 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 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, 18S, and H3 loci as well as the consensus tree with concatenated data for COI, 18S and H3 data. A matrix of pairwise differences using the number of differences among 18S for a subset of taxa within each genus was calculated with MEGA7 (Kumar *et al.* 2016). The bootstrap method was used for variance estimation at 1,000 replicates and using the p-distance model.

TABLE 1. Primers, annealing temperatures and extension times used in this study.

Locus	Primer	Direction	Sequence (5'→3')	Annealing	Extension	Reference
COI	COI_D1_F	Forward	GGAACWATAAGAAGWATAATYATYCG	40˚C	1 min. 30	Humphries
	C1-J-2195RC	Reverse	ACTTCTGGATGACCAAAAAATCAA		sec.	*et al.* 2021
18S	18SF	Forward	ACTGTCGATGGTAGGTTCTG	50˚C	2 min.	Bahder *et*
	18SR	Reverse	GTCCGAAGACCTCACTAAA			*al.* 2019
H3	H3F	Forward	CAGACGGCBMGKAARTCSACC	55˚C	30 sec.	Echavarria
	H3R	Reverse	GTKACHCKCTTRGCGTGRAT			*et al.* 2021

TABLE 2. Molecular taxon sampling and GenBank accession numbers.

		GenBank Accession No.			
Taxon	Locality	COI	18S	H3	Collection
Haplaxius crudus	Costa Rica	MT080284	MT002393	MZ274037	FLREC
Haplaxius dougwalshi	Costa Rica	MT080284	MT002395	MZ297815	FLREC
Haplaxius lunatus	Florida, U.S.A.	OM264285	OM258692	OM262388	FLREC
Haplaxius skarphion	Costa Rica	MT900603	MT892907	MZ274039	FLREC
Haplaxius pocococo	Costa Rica	MW086873	MW086509	OM262387	FLREC
Haplaxius pictifrons	Delaware, U.S.A.	MT946292	MN200098	MZ274038	FLREC
Myxia belinda	Costa Rica	MT900605	MN200095	MZ274041	FLREC
Myxia delta	Costa Rica	MT900602	MT892907	MZ274042	FLREC
Myxia hernandezi	Costa Rica	MZ234085	MZ262449	MZ274043	FLREC
Myxia baynardi	Costa Rica	MT900604	MT892909	MZ274040	FLREC
Nymphocixia unipunctata	Florida, U.S.A.	OM264284	OM258690	OM262389	FLREC
Nymphocixia caribbea	Jamaica	MT080286	MT002394	MZ274044	FLREC
Oecleus borealis	Florida, U.S.A.	OM264286	OM258691	OM262390	FLREC
Oecleus dormido	Costa Rica	OM264283	OM258693	OM262392	FLREC
Oecleus mackaspringi	Jamaica	MN488999	MN422261	MZ274045	FLREC
Melanoliarus chuliotus	Florida, U.S.A.	OM264287	OM258689	OM262392	FLREC

Taxon sampling. For molecular comparisons, *O. borealis* Van Duzee, 1912 *O. dormido* Bahder & Bartlett, 2022and *O. mackaspringi* were used to represent *Oecleus* (ingroup); other Oecleini (outgroup relative to *Oecelus*) were *Haplaxius cotinga* Bahder & Bartlett, 2022 *H. crudus*, *H. dougwalshi* Bahder & Bartlett, 2022, *H. skarphion* (Kramer, 1979), *H. pocococo* Bahder & Bartlett, 2021 *H. pictifrons* (Stål, 1862), *H. lunatus* (Van Duzee, 1909), *Myxia belinda* Bahder & Bartlett, 2019 *M. delta* (Kramer, 1979), *M. hernandezi* Bahder & Bartlett, 2021, *Myxia*

baynardi Bahder & Bartlett, 2021, *Nymphocixia unipunctata* Van Duzee, 1923, and *Nymphocixia caribbea* (Fennah, 1971). The outgroup for Oecleini was *Melanoliarus chuliotus* (Ball, 1934) (Cixiinae, Pentastirini Emeljanov, 1971). GenBank Accession numbers for all included taxa are provided in Table 2.

Systematics

Family Cixiidae Spinola, 1839

Subfamily Cixiinae Spinola, 1839

Tribe Oecleini Muir, 1922

Genus *Oecleus* Stål, 1862

Type species: *Oecleus seminiger* Stål, 1862: 306.

Diagnostic features. (Modified after Kramer 1977 and Barrantes *et al*. 2022) Small to midsize (3.3–8.5 mm; usually 3.5–6.0); head and eyes narrower than pronotum in dorsal view. Head appearing rounded to slightly projected from lateral view. Vertex narrow, trough-like and parallel-sided, distal margin with transverse carina, sides carinate and raised; proximally narrowed and distally produced beyond eyes for a variable distance. In lateral view, apex of head acutely or obtusely angled, eyes large, emarginate near antennae, lateral ocelli present just under each eye (just anterior to antennae) and median ocellus near midline above frontoclypeal suture. In frontal view, frons elongately ovate, lateral margins arched (widest below eye) and narrowing towards vertex, carina on midline of frons present (sometimes obsolete). Clypeus triangular to subtriangular (median carina present). Antennae originating from a large socket, scape small, collar-like, pedicel globular with sensoria, flagellum beadlike basally and filamentous distally. Pronotum short with irregular ridges, narrowest on midline, indented on posterior margin, carinate on posterior and lateral margins. Mesonotum longer at midline than vertex and pronotum combined, flattened, usually with five longitudinal carinae; intermediate carinae sometimes reduced to pigmented lines. Hind tibiae lacking lateral spines. Forewings transparent, rarely with patterns, veins usually dotted with pustules, often bearing setae; composite vein ScP+R+MP elongate from basal cell. Pygofer broadly triangular in lateral view (narrowed dorsally, broadly enlarged ventrally); in ventral view bearing medioventral lobe (often situated on quadrangular plate). Gonostyli simple (usually with large median dentation subapically). Aedeagus with shaft straight (or nearly so), usually bearing 1–3 processes (1–2 subapical), endosoma retrorse, membranous, usually bearing 1–3 processes. Anal tube large and elongate, varied in form.

Oecleus urru Bahder & Bartlett sp. n.

(Figures 1–5)

Type locality. Cotinga Biological Station, Puntarenas Province, Costa Rica.

Diagnosis. Moderate-sized (~6 mm) species with a golden-brown coloration and five carinae on the mesonotum and head slightly projecting beyond the eyes. Male terminalia with elongate pygofer bearing a broad, rounded medioventral process, apically concave. Aedeagal shaft without processes or lobes near base or midlength, bearing 2 subapical processes (right process much longer than left, exceeding half-length of shaft), endosoma with 2 processes, both less than half length of shaft (proximal process short and straight, distal exceeding endosomal apex). Anal tube, in lateral view much broadened distally, ventrally convex, distally forming large, quadrangular lobes.

Description. *Color*. General body color in males pale yellow with fuscous wash, darkly infuscated in concavities (Fig. 1). Frons and genae dark brown (carinae pale), clypeus dark brown below antennae, otherwise paler; ocelli reddish. Carinae of mesonotum stramineous, region between lateral carinae strongly infuscate (carinae pale).

FIGURE 1. Adult male habitus of *Oecleus urru* **sp. n.**; (A) lateral view and (B) dorsal view, scale = 1 mm**.**

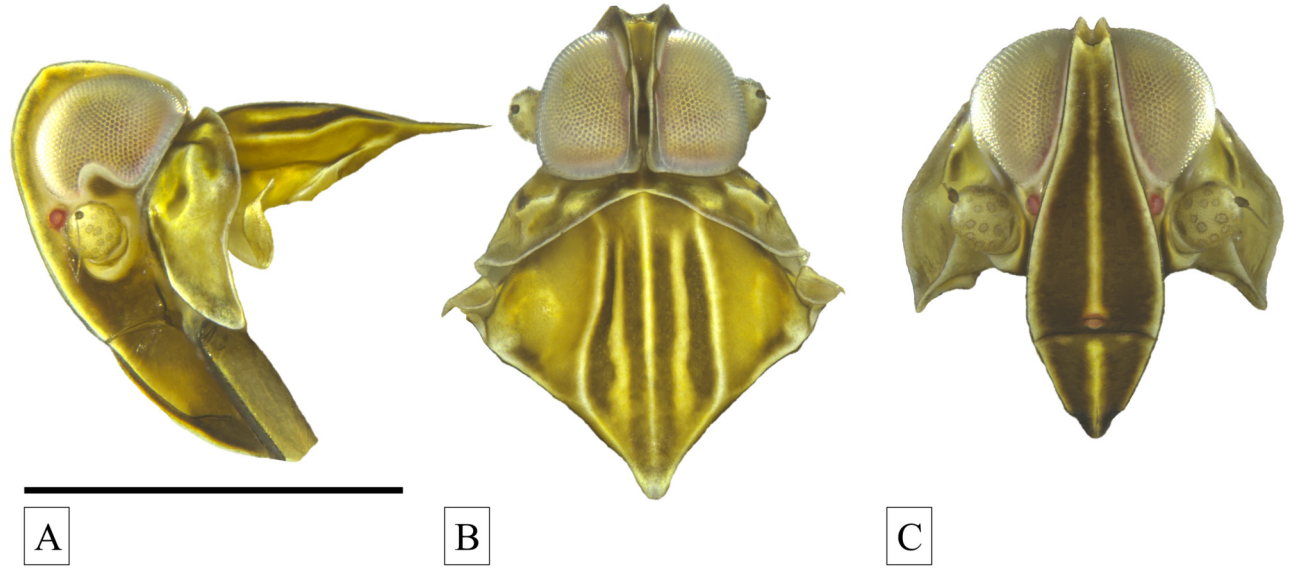

FIGURE 2. Adult *Oecleus urru* **sp. n.** (A) head and pronotum lateral view, (B) head, pronotum, and mesonotum dorsal view, and (C) head, pronotum, and mesonotum frontal view; scale = 1 mm.

Structure. Body length males (n = 4): 6.02–6.05 mm with wings; 4.22–4.25 mm without wings (Table 3). Head. Anterior margin (lateral view, Fig. 2A) of head rounded (with slight keel on fastigium corresponding to transverse carina), weakly projected in front of eyes, vertex and face (below fastigium) weakly convex. Vertex very narrow (dorsal view, Figs 2B, median carina absent), trough-like, broadest at fastigium, narrowed posteriorly, lateral keels foliate, nearly in contact at posterior margin, apex with transverse carinae. Frons in frontal view (Fig. 3A) elongately oval, foliately keeled on lateral margins, median carina distinct, becoming obsolete near fastigium, dorsal margin "U-shaped", lateral margins sinuate, narrowest between eyes, distinctly expanding to level of antennae, widest just above frontoclypeal suture; median ocellus distinct just above frontoclypeal suture; frontoclypeal suture approximately straight (angled slightly ventrad at lateral margins), clypeus triangular with distinct median carina. Antennae bulbous with scape ring-like and very short (Figs. 2A, C), pedicle rounded (as wide as tall) bearing many sensory plaques, flagellum elongate, bristle-like with bulbous base. Lateral ocelli distinct below compound eye, anterior to antennae.

TABLE 3. Biometric data for *Oecleus urru* **sp. n.** (in mm).

	Male (n=4)		Female (n=3)	
Character	Range	Average ± SE	Range	Average±SE
Body length, with wings	6.02–6.05	6.04±0.01	9.09–9.11	9.10±0.02
Body length, no wings	4.22–4.25	4.24±0.01	7.88–7.90	7.90±0.01
Forewing length	4.94–4.94	4.94±0.00	8.21–8.21	8.21±0.00
Vertex length	0.55–0.55	0.55±0.00	0.62–0.62	0.62±0.00
Vertex width, basal margin	0.15–0.15	0.15±0.00	0.17–0.17	0.17±0.00
Vertex width, distal margin	0.19–0.19	0.19±0.00	0.21–0.21	0.21±0.00
Pronotum length, midline	0.15–0.16	0.16±0.01	0.17–0.17	0.17±0.00
Mesonotum length, midline	1.04–1.05	1.04±0.01	1.11–1.11	1.11±0.00
Mesonotum width	1.09–1.10	1.10±0.01	1.18–1.18	1.18±0.00
Frons width, dorsal margin	0.14–0.14	0.14±0.00	0.16–0.16	0.16±0.00
Frons width, clypeal suture	0.36–0.36	0.36±0.36	0.39–0.39	0.39±0.00
Frons width, widest	0.47–0.47	0.47±0.00	0.50–0.50	0.50±0.00
Frons width, narrowest	0.14–0.14	0.14±0.00	0.16–0.16	0.16±0.00
Frons length, midline	0.84–0.84	0.84±0.84	0.87–0.87	0.87±0.87
Clypeus length	0.22–0.22	0.22±0.00	0.26–0.26	0.26±0.00

Thorax. Pronotum short in dorsal view (Fig 2B), anterior margin hidden by head posterior margin concave; disc with median carina nearly obsolete, laterally flanked with serpentine oblique carinae, lateral margins with carinae between tegula and eye; in lateral view (Fig. 2A), paradiscal region broad forming rough parallelogram between ventral margin and lateral carina. Mesonotum longer at midlength than vertex plus pronotum combined (Fig. 2B), disc bearing five carinae, lateral and intermediate carinae subparallel, slightly serpentine.

Wings transparent (Fig. 3), inconspicuous setae-bearing nodes along veins, forewings with a distinct stigma. Forewings elongate-oval, with leading and trailing sides approximately parallel-sided (leading margin arched); apex of clavus exceeding forewing midlength, Pcu+A1 fused before claval midlength, composite vein reaching wing margin well before CuP, combined vein stem ScP+R+MP forming long stem from basal cell, fork of MP from ScP+R at level with fusion of Pcu+A1; fork of RP from ScP+RA near wing midlength; CuA forked close to claval margin distal. Branching pattern RA2 two-branched, RP 3-branched, MP 5-branched of anterior trifid Type (Le Cesne *et al.*, 2021); CuA 2-branched, distally anastamosed after nodal line forming the characterical oecleininian diamond C5 cell (='procubital cell', Emeljanov 1996]); crossveins ir, r-m, im, m-cu and icu present, the later very short joining distal extremity of CuP.

Terminalia. Terminalia approximately bilaterally symmetrical. Pygofer in lateral view broad (Fig. 4A), narrowest at dorsal margin, greatly expanded ventrally, ventral margin irregularly sinuate, with invagination just before medioventral process, posterior margin convex, anterior margin concave, irregularly sinuate. In ventral view (Fig 4B), medioventral process rounded with invagination at apex, slightly wider than long, attached to a trapezoidal

base bearing lateral ridges, appearing “crown-like”. Gonostyli in lateral view (Fig 4A) slender, expanded in distal half, dorsal margin bearing two small triangular projections near apex, apex rounded, ventral margin with 1 small rounded projection near apex; in ventral view (Fig. 4B), margins subparallel, curving mesad, forming subtriangular apices, inner margins with bifurcated hooked process curving subapically. Aedeagus slender (Fig. 5), shaft lacking processes or lobes except two slender subapical retrorse processes (A1 & A2) on lateral margins, right lateral process (A2) elongate, reaching just past midpoint, slightly curved distad and ventrad, left lateral process (A1) approximately half the length of A2, curved distad and ventrad. Endosoma with two processes (E1 & E2); E1 proximad, arising on left lateral margin, directed dorsad, short, not reaching base of second process (E2), E2 more distad, arising subapically on left lateroventral margin, elongate and directed dorsoventrad, nearly reaching base of aedeagus, endosoma helical, completing one rotation around axis from base to apex (Fig. 5). Anal tube in lateral view (Fig. 4A) greatly enlarged distally and strongly downcurved (forming pair of quadrangular lateral flanges), basis narrow; in dorsal view (Fig. 4C), obovate, narrowed distally; paraproct elongate lingulate.

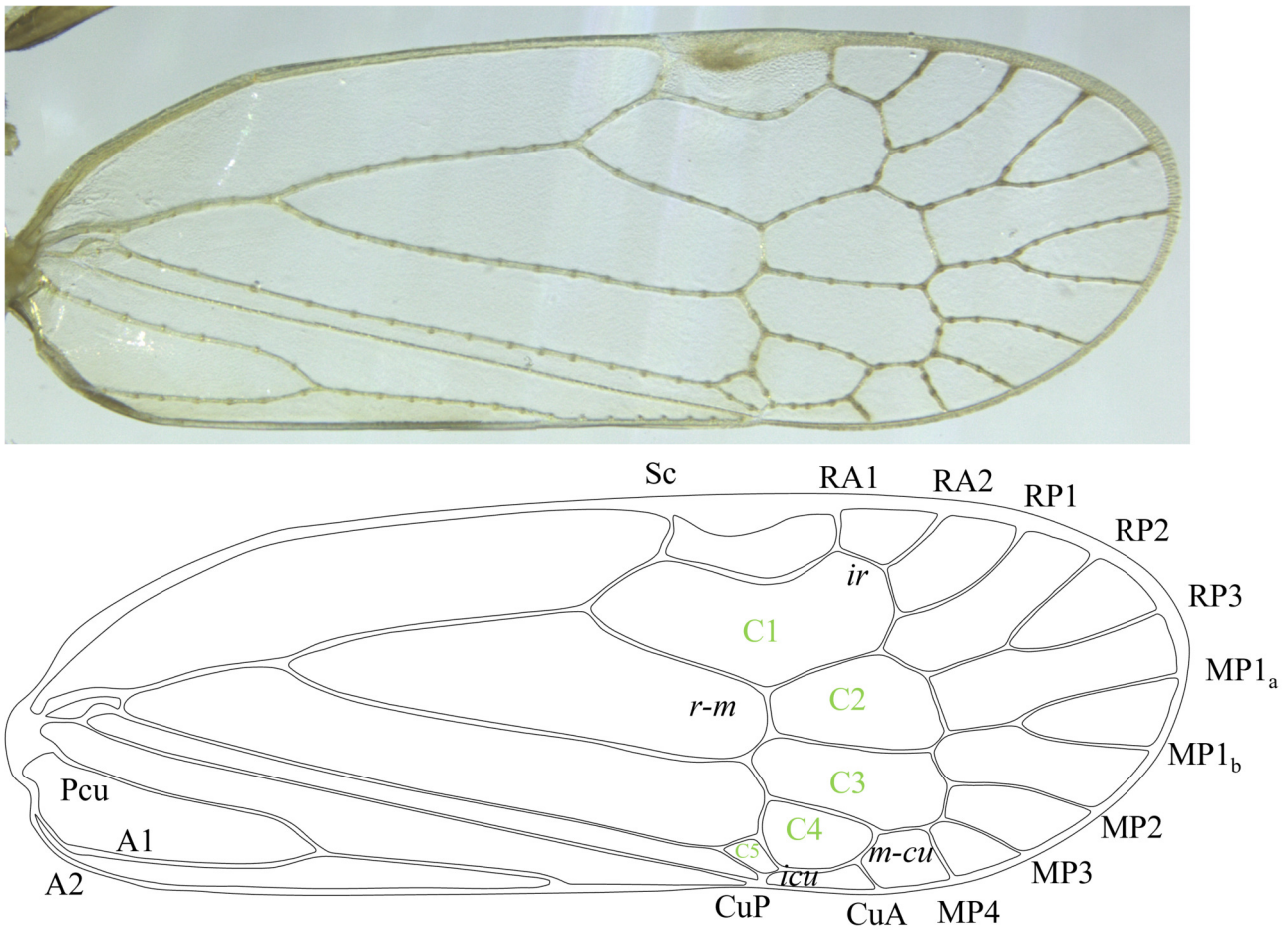

FIGURE 3. Forewing venation of *Oecleus urru* **sp. n.**; black = vein, italics = crossvein, green = cell; nomenclature following Bourgoin *et al.* 2015,.

Plant associations. Unknown; collected sweeping edge habitat, predominantly grasses.

Distribution. Cotinga Biological Station, Puntarenas Province, Costa Rica (8.621825,-83.478819).

Etymology. The specific epithet is a reference to the aedeagus in a left lateral view resembling the head of the urru from the film “The Dark Crystal”.

Material examined. Holotype male “Costa Rica, Puntarenas Pr. / Cotinga Biological Station / 16.VII.2021 / Coll.: B.W.Bahder // Holotype / *Oecleus urru* ♂” (FLREC); Paratypes 1 male, 3 females, same data as holotype (FSCA).

Sequence data. For the COI locus, a 700 bp product was generated (GenBank Accession No. OQ749902), for the 18S locus, a 1,399 bp product was generated (GenBank Accession No. OQ745735), and for the H3 locus, a 344 bp product was generated (GenBank Accession No. OQ744000). Based on the phylogenetic analyses of the COI, 18S, and H3 loci and the consensus analysis (Fig. 6), *Oecleus urru* **sp. n.** resolves adjacent to *O. dormido* (Fig. 6D).

Based on the consensus tree, *Oecleus* (assessing the three taxa available here) is monophyletic with strong bootstrap support (99). This is also seen in the 18S phylogeny (91 bootstrap support) (Fig. 6B). Based solely on COI or H3, *Oecleus* is not monophyletic (Fig. 6A & 6C). Despite this, *Oecleus urru* **sp. n.** resolves adjacent to *O. dormido* for COI, 18S, H3, and in the consensus tree with strong bootstrap support, respectively 97, 91, 99, and 99.

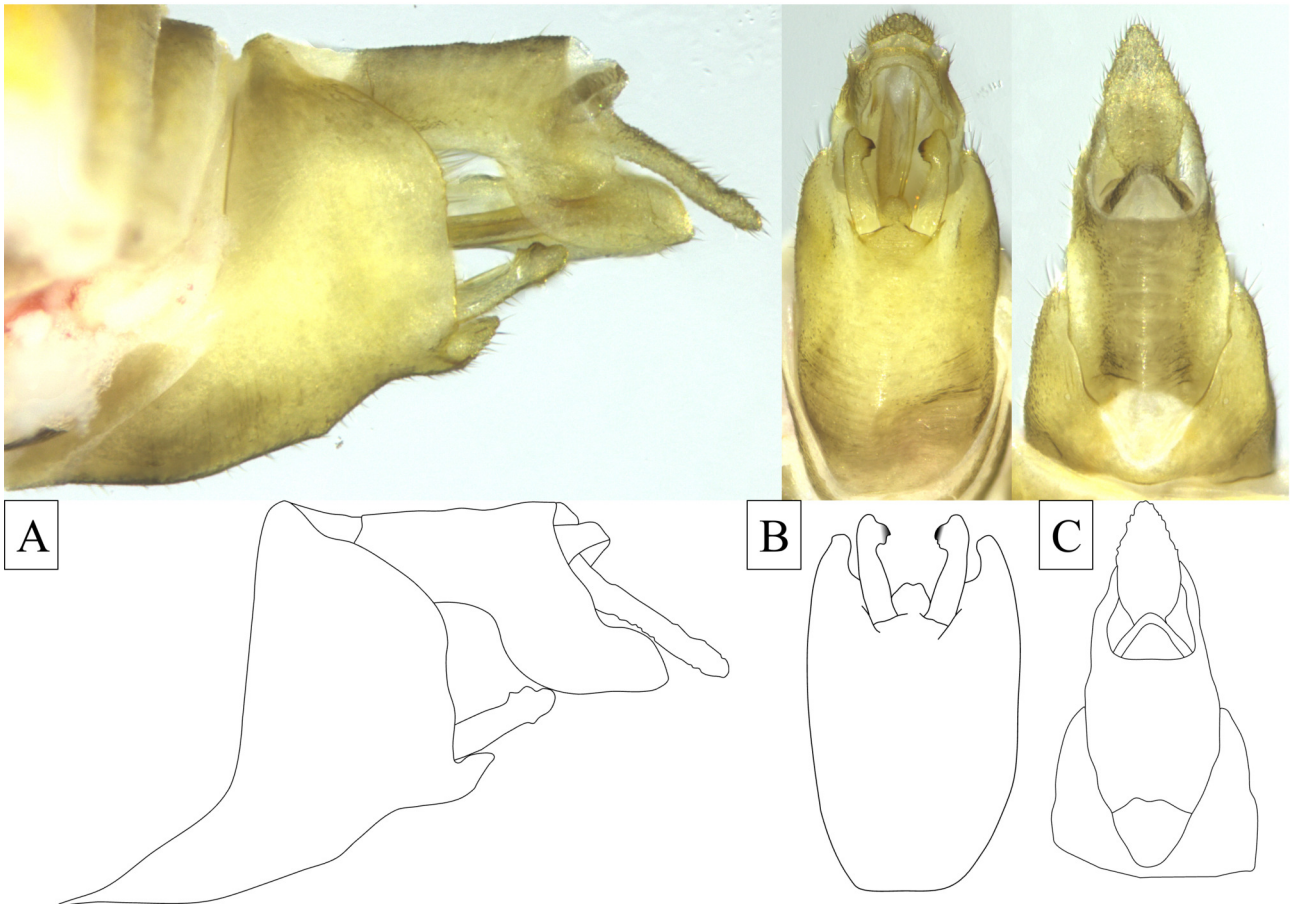

FIGURE 4. Male *Oecleus urru* **sp. n.** terminalia; (A) lateral view, (B) ventral view, and (C) dorsal view.

Based on the pairwise comparison of the 18S gene for taxa assessed, the average variability within genus is 0.3% (±0.1), 0.6% (±0.3), 0.5% (±0.1), and 0.8% for *Oecleus*, *Myxia*, *Haplaxius*, and *Nymphocixia* respectively (Table 4), while the variability among genera is an average of 2.1% (±0.04). *Oecleus urru* **sp. n.** differs from *O. borealis* and *O. mackaspringi* by 0.1% and 0.5%, respectively. However, *Oecleus urru* **sp. n.** is 100% identical to *O. dormido* at the 18S locus. For the COI gene, *Oecleus urru* **sp. n.** differs from *O. dormido* by 8.2% and approximately 14% compared to *O. borealis* and *O. mackaspringi* (Table 5). For the H3 gene, *Oecleus urru* **sp. n.** differs by 0.6% to *O. dormido* and 7.2% and 12.5% to *O. borealis* and *O. mackspringi*, respectively (Table 6).

Remarks *Oecleus urru* **sp. n.** is placed in *Oecleus* based on both morphological (lacking spines on hind tibia, trough-like vertex, head slightly projecting, and five longitudinal carinae on mesonotum) and molecular features based on analysis of three independent loci.

Most species of *Oecleus* are treated (described or redescribed) in Kramer (1977) for forms north of Mexico and Caldwell (1944) for Mesoamerican forms. Caldwell (1944) does not provide a key but does illustrate terminalia. *Oecleus urru* **sp. n.** can be separated from the 13 illustrated forms by the shape of the medioventral lobe (most of the forms illustrated by Caldwell, 1944, have elongated, not rounded, medioventral lobes) along with the shape of the anal tube; and from the two species *O. seminiger* Stål, 1862. *O. apicatus* Caldwell 1944) by Caldwell's descriptions (and for *O. seminiger* the illustration in Fowler, 1904).

Using the key in Kramer (1977), the new species keys most readily to couplet 24, a choice between *O. chrisjohni* Kramer 1977 (from southcentral US) and *O. lineatus* Ball, 1902 (from southwestern US). The main diagnostic features used in the key include the aedeagus shaft with 2 subapical processes (right process much longer than left, exceeding half-length of shaft), aedeagal shaft without lobes or projections at midlength or base, endosoma with 2

processes, both less than half length of shaft (proximal process short and straight), anal tube much broadened distally, medioventral lobe of pygofer rounded with apex indented. *O. urru* **sp. n.** most strongly resembles *O. lineatus* in structure, but differs most obviously in the shape of the medioventral lobe (more broadly rounded with an apical concavity in *O. urru* **sp. n.**), the lengths of both aedeagal (right about twice length of left in *O. urru* **sp. n.,** subequal in length in *O. lineatus*) and endosomal (proximal much shorter than distal in *O. urru* **sp. n**., proximal marginally shorter than distal in *O. lineatus*) processes, and the anal tube more greatly enlarged and projecting in *O. urru* **sp. n.**).

Oecleus species not treated in Caldwell 1944 and Kramer 1977 are described in O'Brien (1982), Emeljanov (2007), Bartlett *et al*. (2018), and Barrantes *et al*. (2022), but none of these species are closely similar to *O. urru* **sp. n.**

While the level of variability between *Oecleus urru* **sp. n.** and *O. dormido* for COI is lower than that observed with other species, it is still within an acceptable level of interspecific variation (i.e. *H. pocococo* and *H. dougwalshi* differ by 10.2% according to Barrantes *et al.* (2021)). The variability between the two species for H3 shows a substantially smaller difference (0.6%) when other species differ by approximately 7%. Finally, the observation that 18S was identical between *Oecleus urru* **sp. n.** and *O. dormido* is interesting. Under most circumstances, there is some measurable level of variability in 18S among species in the same genus but recently it was shown that distinct species can have identical 18S sequences (Myrie *et al*. 2023) and has also been shown that sister taxa can have extremely limited variation in 18S sequences, as in the case of *H. dougwalshi* and *H. pocococo* (Barrantes *et al.* 2021).

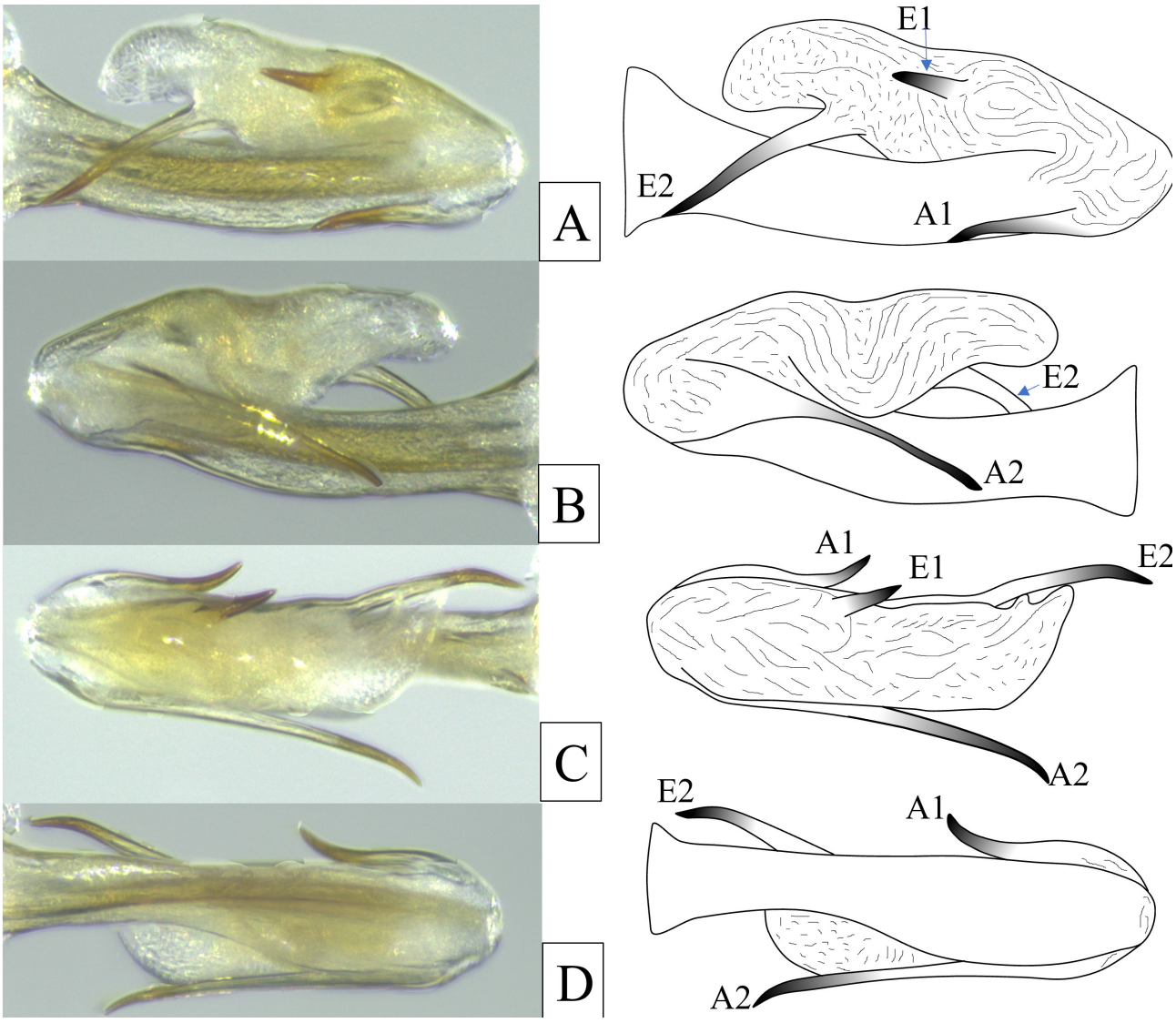

FIGURE 5. Aedeagus of *Oecleus urru* **sp. n.;** (A) left lateral view, (B) right lateral view, (C) dorsal view and (D) ventral view; A = aedeagal process, E = endosomal process.

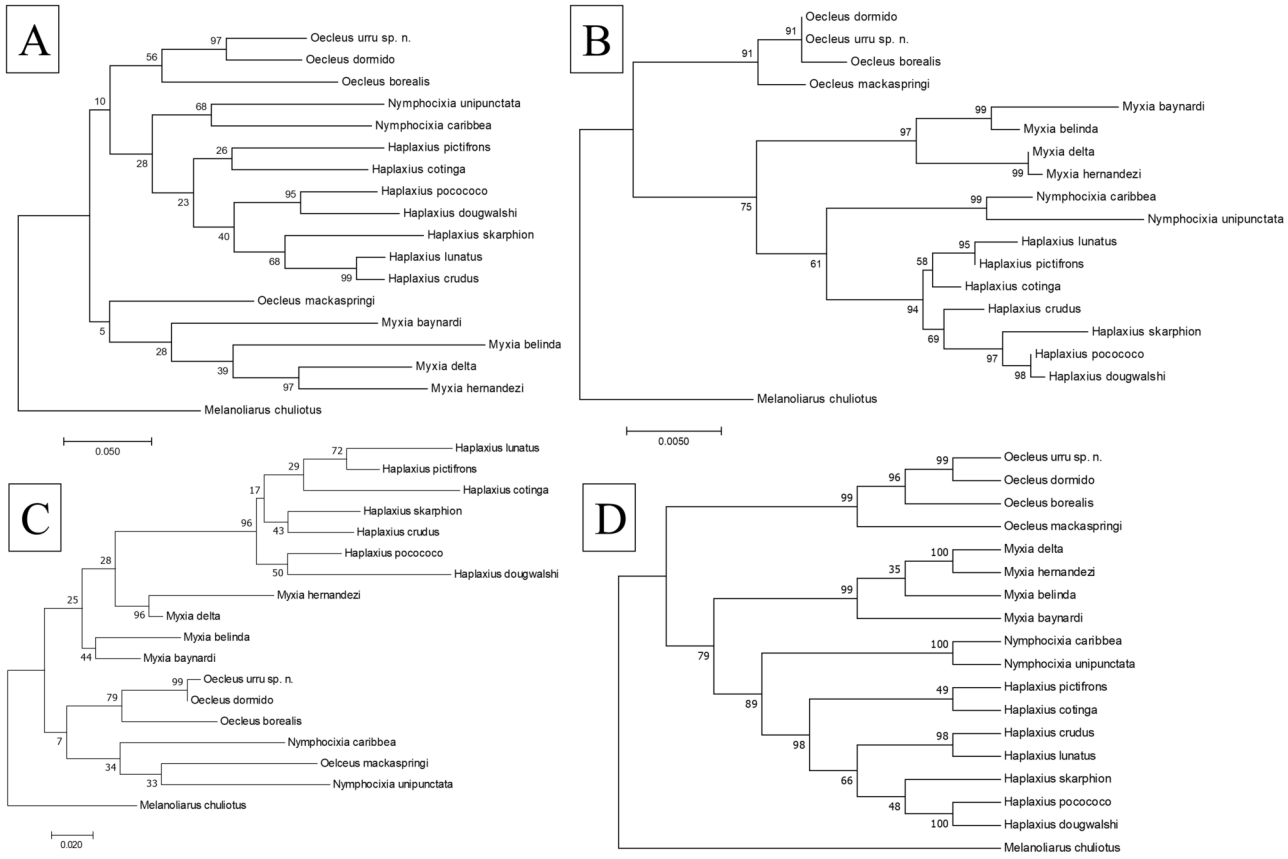

FIGURE 6. Maximum likelihood phylogenetic tree based on 1,000 replicates: (A) COI gene, (B) 18S rRNA gene, (C) H3 gene, and (D) consensus tree of concatenated COI, 18S, and H3 sequences.

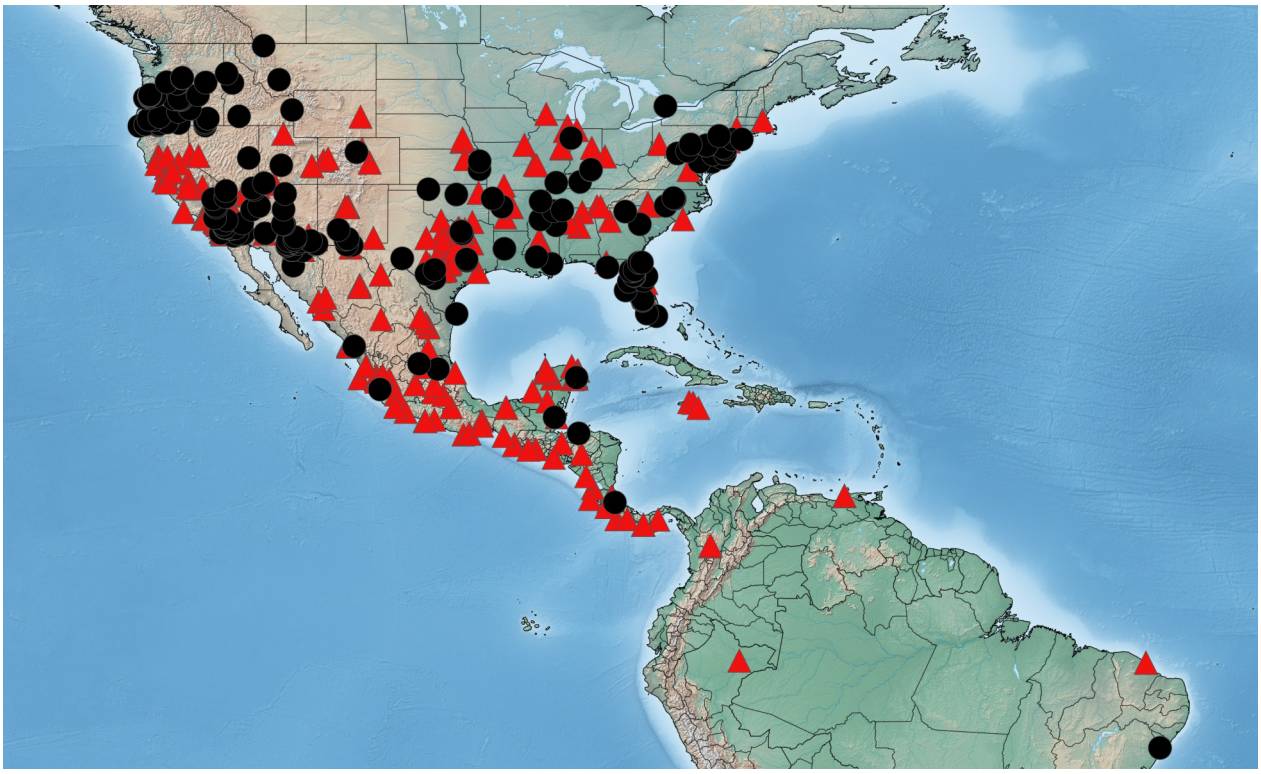

FIGURE 7. Distribution of *Oecleus*; data from Tri-Trophic Thematic Collection Network (black circles, 529 specimens) and iNaturalist (red triangles, 546 records).

TABLE 4. Pairwise comparison based on the 18S rRNA locus to demonstrate intra (orange) and inter (blue) generic variability by percent nucleotide difference (bottom left) and standard error (top right).

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	*Oecleus urru* **sp. n.**		0.000	0.001	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.003
2	*Oecleus dormido*	0.000		0.001	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.003
3	*Oecleus borealis*	0.001	0.001		0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.003
4	*Oecleus mackaspringi*	0.004	0.004	0.006		0.003	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004
5	*Haplaxius cotinga*	0.018	0.018	0.019	0.016		0.002	0.002	0.004	0.003	0.004	0.003	0.004	0.004
6	*Haplaxius pocococo*	0.023	0.023	0.025	0.022	0.007		0.002	0.004	0.004	0.004	0.004	0.004	0.004
7	*Haplaxius crudus*	0.019	0.019	0.021	0.019	0.004	0.005		0.004	0.003	0.003	0.003	0.004	0.004
8	*Nymphocixia unipunctata*	0.025	0.025	0.027	0.025	0.018	0.023	0.020		0.002	0.004	0.004	0.004	0.005
9	*Nymphocixia caribbea*	0.022	0.022	0.024	0.021	0.013	0.016	0.013	0.009		0.004	0.004	0.004	0.005
10	*Myxia hernandezi*	0.022	0.022	0.023	0.023	0.018	0.020	0.018	0.025	0.020		0.001	0.003	0.004
11	*Myxia delta*	0.022	0.022	0.024	0.022	0.017	0.019	0.017	0.025	0.019	0.001		0.003	0.004
12	*Myxia belinda*	0.022	0.022	0.023	0.022	0.019	0.023	0.019	0.025	0.021	0.008	0.008		0.004
13	*Melanoliarus chuliotus*	0.016	0.016	0.017	0.018	0.022	0.025	0.023	0.028	0.025	0.023	0.023	0.022	

TABLE 5. Pairwise comparison based on the COI locus to demonstrate intra (orange) and inter (blue) generic variability by percent nucleotide difference (bottom left) and standard error (top right).

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	*Oecleus urru* **sp. n.**		0.011	0.014	0.015	0.014	0.015	0.015	0.016	0.015	0.016	0.015	0.016	0.016
2	*Oecleus dormido*	0.082		0.014	0.014	0.015	0.015	0.015	0.016	0.015	0.016	0.015	0.016	0.016
3	*Oecleus borealis*	0.146	0.146		0.015	0.015	0.015	0.016	0.017	0.015	0.017	0.017	0.017	0.018
4	*Oecleus mackaspringi*	0.148	0.141	0.159		0.016	0.014	0.015	0.016	0.015	0.015	0.016	0.016	0.016
5	*Haplaxius cotinga*	0.159	0.166	0.164	0.188		0.015	0.014	0.016	0.015	0.017	0.017	0.015	0.016
6	*Haplaxius pocococo*	0.161	0.161	0.166	0.168	0.153		0.014	0.016	0.015	0.015	0.015	0.016	0.017
7	*Haplaxius crudus*	0.155	0.168	0.186	0.181	0.139	0.139		0.015	0.015	0.016	0.017	0.017	0.016
8	*Nymphocixia unipunctata*	0.172	0.177	0.201	0.197	0.164	0.190	0.175		0.015	0.017	0.016	0.017	0.017
9	*Nymphocixia caribbea*	0.184	0.177	0.181	0.190	0.161	0.168	0.175	0.164		0.016	0.016	0.016	0.016
10	*Myxia hernandezi*	0.197	0.190	0.206	0.177	0.221	0.193	0.192	0.223	0.204		0.013	0.016	0.017
11	*Myxia delta*	0.179	0.177	0.206	0.192	0.208	0.190	0.193	0.197	0.203	0.120		0.016	0.018
12	*Myxia belinda*	0.208	0.206	0.204	0.199	0.177	0.192	0.206	0.232	0.212	0.186	0.192		0.018
13	*Melanoliarus chuliotus*	0.182	0.188	0.219	0.182	0.190	0.210	0.195	0.195	0.208	0.223	0.203	0.219	

TABLE 6. Pairwise comparison based on the H3 locus to demonstrate intra (orange) and inter (blue) generic variability by percent nucleotide difference (bottom left) and standard error (top right).

		1	2	3	4	5	6	7	8	9	10	11	12	13
1	*Oecleus urru* **sp. n.**		0.004	0.013	0.017	0.019	0.018	0.019	0.019	0.019	0.019	0.017	0.016	0.017
2	Oecleus dormido	0.006		0.014	0.017	0.019	0.018	0.019	0.019	0.019	0.019	0.016	0.016	0.017
3	*Oecleus borealis*	0.072	0.072		0.018	0.020	0.018	0.020	0.020	0.017	0.019	0.017	0.017	0.016
4	*Oecleus mackaspringi*	0.125	0.125	0.134		0.021	0.020	0.020	0.019	0.018	0.021	0.019	0.018	0.019
5	*Haplaxius cotinga*	0.143	0.143	0.162	0.184		0.015	0.016	0.019	0.020	0.020	0.017	0.019	0.020
6	Haplaxius pocococo	0.121	0.125	0.134	0.159	0.103		0.014	0.018	0.019	0.019	0.016	0.018	0.019
7	*Haplaxius crudus*	0.134	0.137	0.150	0.165	0.100	0.081		0.019	0.020	0.020	0.017	0.019	0.020
8	*Nymphocixia unipunctata*	0.134	0.131	0.162	0.140	0.146	0.137	0.159		0.019	0.020	0.017	0.018	0.019
9	*Nymphocixia caribbea*	0.143	0.140	0.125	0.134	0.168	0.140	0.162	0.140		0.019	0.018	0.017	0.018
10	Myxia hernandezi	0.159	0.156	0.156	0.178	0.159	0.143	0.153	0.162	0.137		0.014	0.018	0.020
11	*Myxia delta*	0.109	0.106	0.109	0.143	0.121	0.103	0.115	0.115	0.118	0.062		0.014	0.017
12	*Myxia belinda*	0.103	0.100	0.106	0.131	0.137	0.121	0.128	0.134	0.106	0.109	0.072		0.016
13	*Melanoliarus chuliotus*	0.121	0.118	0.112	0.143	0.162	0.140	0.159	0.146	0.137	0.156	0.121	0.115	

Discussion

The genus *Oecleus*, as currently comprised, is most diverse in the southwest US (about 40 species) and Mexico (24 species, including some also in the US), and is reported contiguously to El Salvador (i.e., reported from Guatemala and El Salvador), but sparsely elsewhere except Haiti, Jamaica, and Brazil (Sergipe) (Caldwell 1944, Kramer 1977, O'Brien 1982, Emeljanov 2007, Bartlett *et al*. 2014, 2018; Myrie *et al*. 2019, Bourgoin 2023). However, it appears that this paucity records represents a lack of survey effort together with the taxonomic diagnostic challenges and the relatively small and cryptic nature of the genus, as available data (Figure 7) suggests that the genus is distributed throughout North and Mesoamerica and into northern South America. The association of *Oecleus* (and other oecleines) with palms (Bartlett *et al*. 2018, Myrie *et al.* 2019) and the possibility that oecleines may vector phytoplasmas suggests that this group is an important target for further studies of systematics and vector ecology.

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