Article

A new species of *Oecleus* (Hemiptera: Auchenorrhyncha: Fulgoroidea: Cixiidae) from the Caribbean coast of Costa Rica and a reassessment of the generic status of *Nymphomyndus*

EDWIN A. BARRANTES BARRANTES[1], MARCO A. ZUMBADO ECHAVARRIA[2],
CHARLES R. BARTLETT[3], ERICKA E. HELMICK[4] & BRIAN W. BAHDER[5*]

[1]*Universidad of Costa Rica—Sede San Ramón, Departmento de Ciencias Naturales, de la Iglesia el Tremedal 400 mts al Oeste carretera hacia San Pedro, San Ramón, Alajuela, Costa Rica.*
✉ *edwin.barrantes@ucr.ac.cr; edwbarrantes@gmail.com;* ⓘ *https://orcid.org/0000-0001-9565-2105*

[2]*Universidad of Costa Rica—Sede San Ramón, Departmento de Ciencias Naturales, de la Iglesia el Tremedal 400 mts al Oeste carretera hacia San Pedro, San Ramón, Alajuela, Costa Rica.*
✉ *marco.zumbado@ucr.ac.cr; nassua75@gmail.com;* ⓘ *https://orcid.org/0000-0002-2591-7662*

[3]*University of Delaware, Department of Entomology and Wildlife Ecology, 250 Townsend Hall, Newark, DE 19716-2160, USA.*
✉ *bartlett@udel.edu;* ⓘ *https://orcid.org/0000-0001-9428-7337*

[4]*University of Florida, Department of Entomology and Nematology—Fort Lauderdale Research and Education Center; 3205 College Ave., Davie, FL 33314-7719, USA.*
✉ *ehelmick@ufl.edu;* ⓘ *https://orcid.org/0000-0002-5153-0891*

[5]*University of Florida, Department of Entomology and Nematology—Fort Lauderdale Research and Education Center; 3205 College Ave., Davie, FL 33314-7719, USA.*
✉ *bbahder@ufl.edu;* ⓘ *https://orcid.org/0000-0002-1118-4832*

Abstract

A new species of cixiid planthopper in the genus *Oecleus* Stål is described from Tortuguero, Limón Province, Costa Rica. This is the first *Oecleus* species reported from Costa Rica. The new species, *Oecleus dormido* **sp. n.,** was collected sweeping grassy edge habitat near the Caribbean coast. Sequence data for COI, 18S, and H3 was generated for phylogenetic comparison of the new species with other available *Oecleus* species and New World Oecleini to test genus-level placement and provide a preliminary examination of the phylogenetic relationships among New World genera of Oecleini. The results indicate that *Oecleus*, *Haplaxius* and *Myxia* are monophyletic, at least among the included taxa, the genera (*Myxia*+((*Nymphocixia*+*Nymphomyndus*)+*Haplaxius*)) may form a clade apart from *Oecleus*. The monobasic genera *Nymphocixia*+*Nymphomyndus* are closely allied, with a difference of 0.98% for 18S, compared to an average of 2.2% among other included oecleine genera. In view of the limited morphological and molecular differences between these genera, we propose *Nymphomyndus* as a junior synonym of *Nymphocixia*.

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

Resumen

Se describe una especie nueva de chicharrita de la familia Cixididae, perteneciente al género *Oecleus Stål* encontrada en Tortuguero, provincia de Limón, Costa Rica. Esta es la primera especie de *Oecleus* reportada para Costa Rica. La nueva especie, *Oecleus dormido* **sp. n**., se recolectó en un hábitat de césped al margen de la carretera localizado en la costa Caribeña. Se generaron datos de secuencia para COI, 18S y H3 para la comparación filogenética de la nueva especie con otras especies disponibles de *Oecleus* y Oecleini del Nuevo Mundo, así como para corroborar la identificación a nivel de género y proporcionar una evaluación preliminar de las relaciones filogenéticas entre los géneros de Oecleini del Nuevo Mundo. Los resultados indican que *Oecleus*, *Haplaxius* y *Myxia* son monofiléticos, al menos entre los taxones incluidos, y los géneros (*Myxia*+((*Nymphocixia*+*Nymphomyndus*)+*Haplaxius*)) pueden formar un clado aparte de *Oecleus*. Los géneros monobásicos *Nymphocixia*+*Nymphomyndu*s están estrechamente relacionados, con una diferencia del 0,98% para 18S, en comparación con un promedio de 2,2% entre otros géneros oecleine incluidos. En vista de las limitadas diferencias morfológicas y moleculares entre estos géneros, proponemos *Nymphomyndu*s como sinónimo junior de *Nymphocixia*.

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

Introduction

The genus *Oecleus* Stål, 1862 is a large taxon in the family Cixiidae, currently comprised of 66 species (Myrie *et al.* 2019, Bourgoin 2022). The greatest diversity of *Oecleus* species are found in southwestern United States and conterminous Mesoamerica (south to El Salvador), but the genus as a whole occurs from southern Canada to South America, including the Greater Antilles (Caldwell 1944, Kramer 1977, Bartlett *et al.*, 2014, 2018; Myrie *et al.* 2019). *Oecleus* has not been reported from Costa Rica in the literature but has been reported on the iNaturalist citizen science forum.

Oecleus is the type genus of the tribe Oecleini, including 25 genera of which nine are New World. The Oecleini are relatively small cixiids, most readily diagnosed by the absence of lateral teeth on the hind tibiae and the common stem of the longitudinal veins ScP, R, and MP forming a long common stalk from the basal cell in the forewing (so that only two veins appear to arise from the basal cell) (Muir 1922, Emeljanov 2007). Aside from the monobasic genera *Notolathrus* Remes Lenicov, 1992 and *Proclytus* Emeljanov, 2007, New World Oecleini has a narrow and elongate vertex. *Oecleus* is distinctive with a very narrow, trough-like vertex, head somewhat forward-projecting, and (usually) five carinae on the mesonotum. The genera *Rhamphixius* Fowler, 1904 and *Antillixius* Myers, 1928 share with *Oecleus* a tough-like vertex, but both of these genera have elongate heads and tricarinate mesonota (Fowler 1904, Myers 1928). *Antillixius* resembles *Oecleus* in most respects, differing in the length of the head projection. The phylogenetic relationship between these genera deserves closer scrutiny, and *Oecleus* as currently comprised is diverse in form and may be heterogeneous. As yet, there are no phylogenetic hypotheses tested among the genera of the tribe Oecleini.

The recently described species, *Oecleus mackaspringi* Bahder & Bartlett, 2019 was discovered during palm survey work in Jamaica seeking to assess potential vectors in plots of coconut palms affected by lethal yellowing (LY) (Myrie *et al.* 2019). Additional species collected during these survey efforts in Jamaica and Florida, U.S.A. include *Nymphomyndus caribbea* (Fennah 1971), *Nymphocixia unipunctata* Van Duzee, 1923, *Haplaxius lunatus* (Van Duzee, 1909), *Oecleus borealis* Van Duzee, 1912, and *Melanoliarus chuliotus* (Ball, 1934) (B.W. Bahder, *unpublished data*). *Nymphomyndus caribbea* was collected from coconut palms in Jamaica in October of 2018. *Nymphocixia unipunctata* was collected on sticky traps placed in palms at the Montgomery Botanical Collection (Miami-Dade County, Florida), however, these individuals are likely from nearby mangroves. Specimens of *Haplaxius lunatus*, *Oecleus borealis*, and *Melanoliarus chuliotus* were all collected from saw palmetto (*Serenoa repens* (W. Bartram) Small). Additionally, *O. sergipenis* Bartlett, Dos Passos, Gonçalves da Silva, Diniz & Dollet 2018 was described from survey work on coconut palms in Brazil (Bartlett *et al.* 2018). 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 close phylogenetic relationship of *Oecleus* to *Haplaxius* Fowler, 1904, any species found on palms are of interest as a potential phytoplasma vector.

Herein we describe a new species of *Oecleus* from palm-related survey work on the Caribbean coast 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 near the runway of the airstrip in Tortuguero, Costa Rica, Limón province (10.565922, -83.513517) (Fig. 1). 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.

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.

FIGURE 1. Habitat and locality of *Oecleus dormido* **sp. n.**

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, 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_2O 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 manufacturers' 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), 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 and 18S data. A matrix of pairwise differences using 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 sec.	Humphries *et al.* 2021
	C1-J-2195RC	Reverse	ACTTCTGGATGACCAAAAAATCAA			
18S	18SF	Forward	ACTGTCGATGGTAGGTTCTG	50°C	2 min.	Bahder *et al.* 2019
	18SR	Reverse	GTCCGAAGACCTCACTAAA			
H3	H3F	Forward	CAGACGGCBMGKAARTCSACC	55°C	30 sec.	Echavarria *et al.* 2021a
	H3R	Reverse	GTKACHCKCTTRGCGTGRAT			

Taxon sampling. For molecular comparisons, *O. borealis* Van Duzee and *O. mackaspringi* Bahder & Bartlett were used to represent *Oecleus*; other ingroup Oecleini were *Haplaxius crudus* (Van Duzee), *H. dougwalshi* Bahder & Bartlett 2020, *H. skarphion* (Kramer) 1979, *H. pocococo* Bahder & Bartlett 2021, *H. pictifrons* (Stål) 1862, *H. lunatus* (Van Duzee), *Myxia belinda* Bahder & Bartlett 2019, *M. delta* (Kramer) 1979, *M. hernandezi* Bahder & Bartlett 2021, *Myxia baynardi* Bahder & Bartlett 2021, *Nymphocixia unipunctata* Van Duzee, and *Nymphomyndus caribbea* (Fennah). The outgroup was *Melanoliarus chuliotus* (Ball) (Cixiinae, Pentastirini). GenBank Accession numbers for all included taxa are provided in Table 2.

TABLE 2. Molecular taxon sampling and GenBank accession numbers

Taxon	Locality	GenBank Accession No.			Collection
		COI	18S	H3	
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 mackaspringi	Jamaica	MN488999	MN422261	MZ274045	FLREC
Melanoliarus chuliotus	Florida, U.S.A.	OM264287	OM258689	OM262392	FLREC

Systematics

Family Cixiidae Spinola, 1839

Subfamily Cixiinae Spinola, 1839

Tribe Oecleini Muir, 1922

Genus *Oecleus* Stål, 1862

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

Diagnosis. (Modified after Kramer 1977) Small to midsize (3.3–8.5 mm; mostly 3.5–6.0); large eyes and head narrower than pronotum in dorsal view. Head appearing rounded to slightly projected from lateral view. Vertex narrow,

trough-like and parallel-sided, distally 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 emarginate, ocellus present under each eye and near midline above frontoclypeal suture. In frontal view, frons elongate, 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; carinae flanking midline (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 dormido Bahder & Bartlett sp. n.
(Figures 2–6)

Type locality. Tortuguero, Limón Province, Costa Rica

Diagnosis. Moderate sized (~6 mm) species with five carinae on the mesonotum and head slightly projecting beyond the eyes with a golden-brown coloration. Forewing vein CuA forked close to claval margin, anastomosing to form a small closed C5 ('procubital cell'). Male terminalia with elongate pygofer bearing a broad, rounded medioventral process situated between a pair of upturned rounded lobes, endosoma strongly contorted, forming distinct helix, with two processes (one exceeding endosomal apex), aedeagus with two long, slender processes and endosoma with two long, slender processes (in ventral view, right process nearly straight, much longer than left). Anal tube, in lateral view convex ventrally forming large, quadrangular lobes.

Description. *Color*. General body color in males pale orange-brown, darkly infuscated in concavities (Fig. 2). Frons and genae dark brown, clypeus dark brown below antennae, otherwise paler; lateral ocelli reddish. Metanotum with carinae of mesonotum stramineous, region between lateral and intermediate carinae strongly infuscate. *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 in transverse carina), head weakly projected in front of eyes, vertex and face (below fastigium) weakly convex. Vertex very narrow (Figs 2B, 3C, median carina absent), broadest at fastigium, narrowed posteriorly, lateral keels foliate, nearly in contact at posterior margin. Frons in frontal view (Fig. 3A) foliately keeled on lateral margins, median carina distinct, becoming obsolete near fastigium, dorsal margin "V-shaped", lateral margins sinuate, narrowest between eyes, distinctly expanding at level of antennae, widest just above frontoclypeal suture; median ocellus distinct just above frontoclypeal suture; frontoclypeal suture approximately straight, clypeus triangular with distinct median carina. Antennae bulbous with scape ring-like and very short (Figs. 3A, B), 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 antenna.

Thorax. Pronotum short in dorsal view (Fig 2B, 3C), anterior margin hidden by head, posterior margin concave; disc with median carina near obsolete laterally flanked with serpentine oblique carinae, lateral margins with carinae between tegula and eye; in lateral view (Fig. 3B), paradiscal region broad forming rough parallelogram between ventral margin and lateral carina. Mesonotum longer at midlength then vertex plus pronotum combined (Fig. 3C), disc bearing five carinae, lateral and intermediate carinae subparallel, slightly sinuate.

Wings transparent (Fig. 4), inconspicuous setae-bearing pustules along veins, forewings with a distinct stigma. Forewings elongate with leading and trailing sides approximately parallel-sided (leading margin weakly arched); apex of clavus past forewing midlength, Pcu+A1 fused before midlength of clavus (at about 1/4 forewing length), 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+A$_1$; fork of RP from ScP+RA near wing midlength; CuA forked close to claval margin distal. Branching pattern: RA 1-branched, RP 4-branched, MP 5-branched; CuA

2-branched (distally anastamosed in CuA$_1$+CuA$_2$ forming small closed 'procubital cell' [i.e., Emeljanov 1996]); crossveins ir, r-m, im, m-cu and icu present (Fig. 4).

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

Character	Male		Female	
	Range	Average ± SE	Range	Average±SE
Body length, with wings	6.03–6.05	6.04±0.01	9.10–9.21	9.19±0.02
Body length, no wings	4.23–4.25	4.24±0.01	7.89–7.90	7.90±0.01
Forewing length	4.95–4.95	4.95±0.00	8.23–8.23	8.23±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

FIGURE 2. Adult male habitus of *Oecleus dormido* **sp. n.**; (A) lateral view and (B) dorsal view, scale = 1 mm**.**
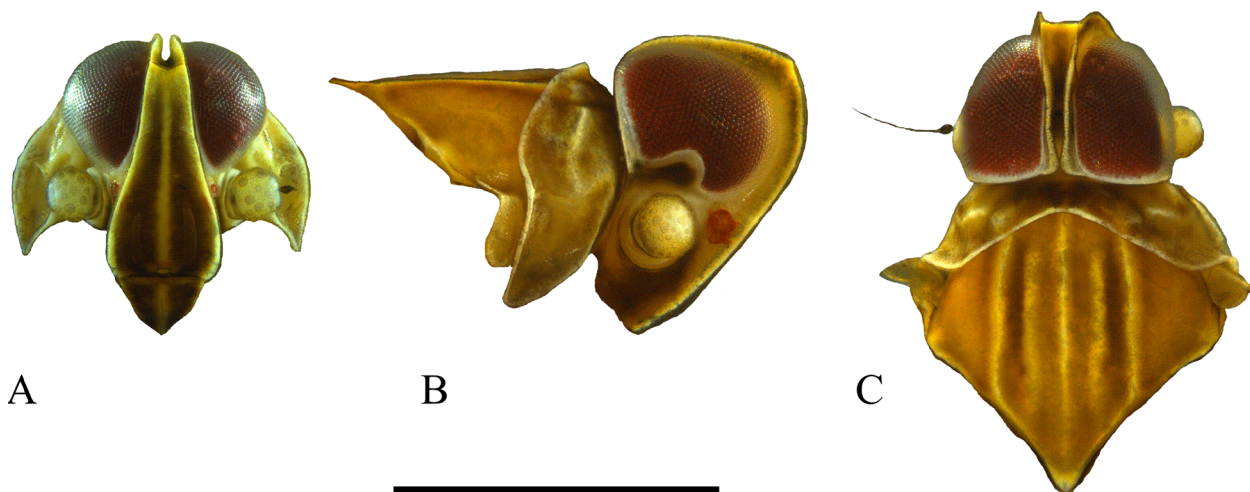
FIGURE 3. Adult *Oecleus dormido* **sp. n.** (A) head and pronotum frontal view, (B) head, pronotum, and mesonotum lateral view, and (C) head, pronotum, and mesonotum dorsal view; scale = 1 mm.
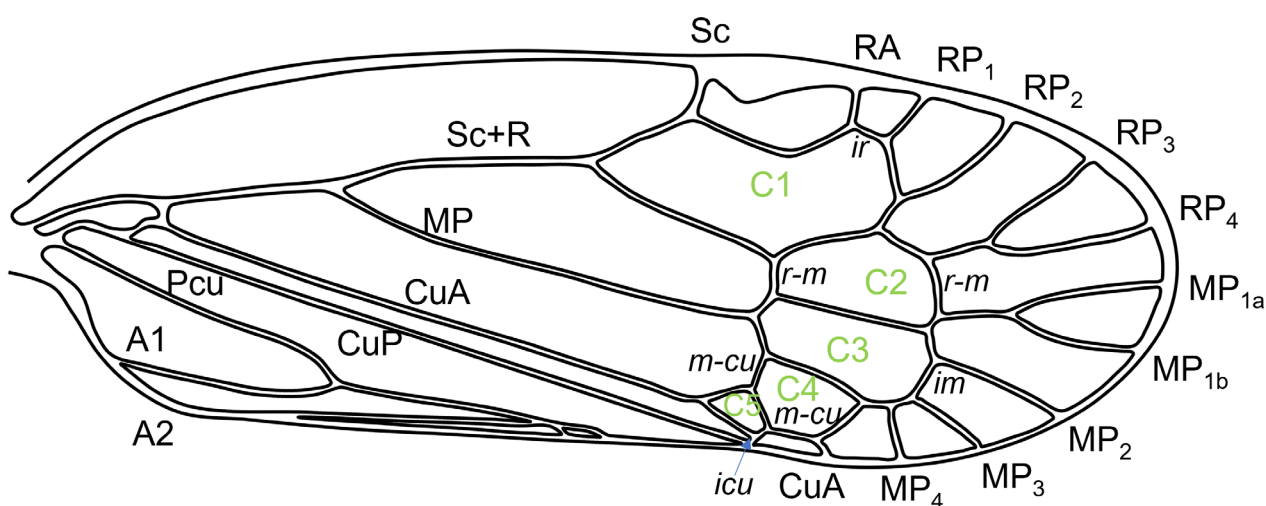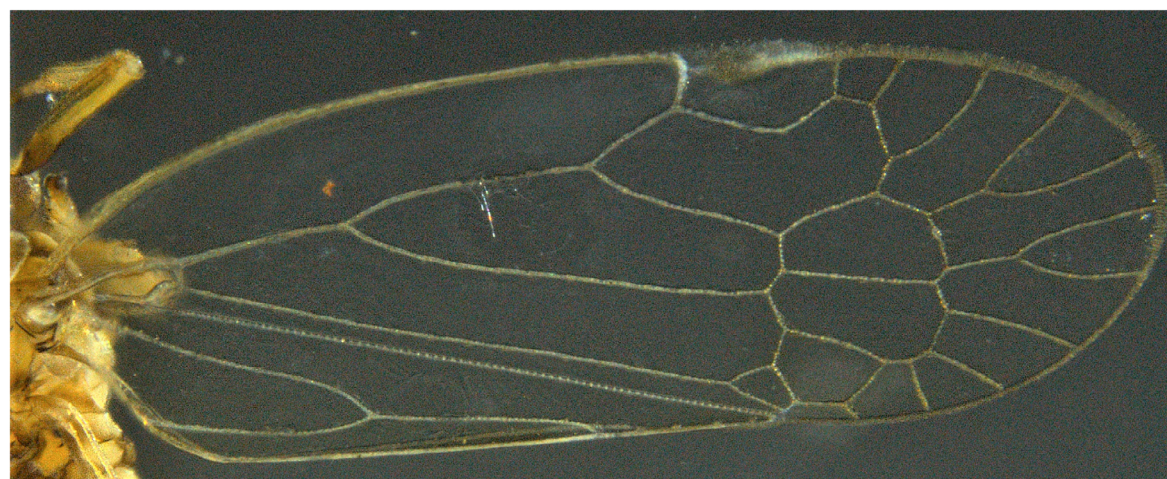

FIGURE 4. Forewing venation of *Oecleus dormido* **sp. n.**; black = vein, italics = crossvein, green = cell.

Terminalia. Terminalia approximately bilaterally symmetrical. Pygofer in lateral view broad (Fig. 5A), narrowest and roundly projected at dorsal margin, greatly expanded ventrally, ventral margin irregularly sinuate, with strong invagination just prior to medioventral process, posterior margin convex, anterior margin concave, irregularly sinuate. In ventral view (Fig 5B), medioventral process rounded, slightly longer than wide, attached to a trapezoidal base bearing lateral rounded lobes, appearing "crown-like". Gonostyli in lateral view (Fig 5A) slender, expanded in

distal half, dorsal margin bearing triangular projection, apex rounded; in ventral view (Fig. 5B), margins subparallel, curving mesad, forming subtriangular apices, inner margins hooked subapically, curving basad. Aedeagus slender (Fig. 6), two slender subapical retrorse processes (A1 & A2) on lateral margins, right lateral process (A1) elongate, nearly reaching base, slightly curved distad, left lateral process (A2) approximately half the length of A1, curved distad. Endosoma complex, with two large processes (E1 & E2); E1 arising on dorsal margin, angled dorsad, nearly reaching apex of flagellum, E2 arising subapically on left lateral margin, curved ventrad, nearly reaching base of aedeagus, flagellum strongly helical, completing 1.75 rotations around axis from base to apex (Fig. 6D). Anal segment in lateral view (Fig. 5A) expanded distally and strongly downcurved (forming pair of quadrangular lateral flanges), basis narrow. In dorsal view (Fig. 5C), tear-drop shaped, narrowed distally; paraproct lingulate.
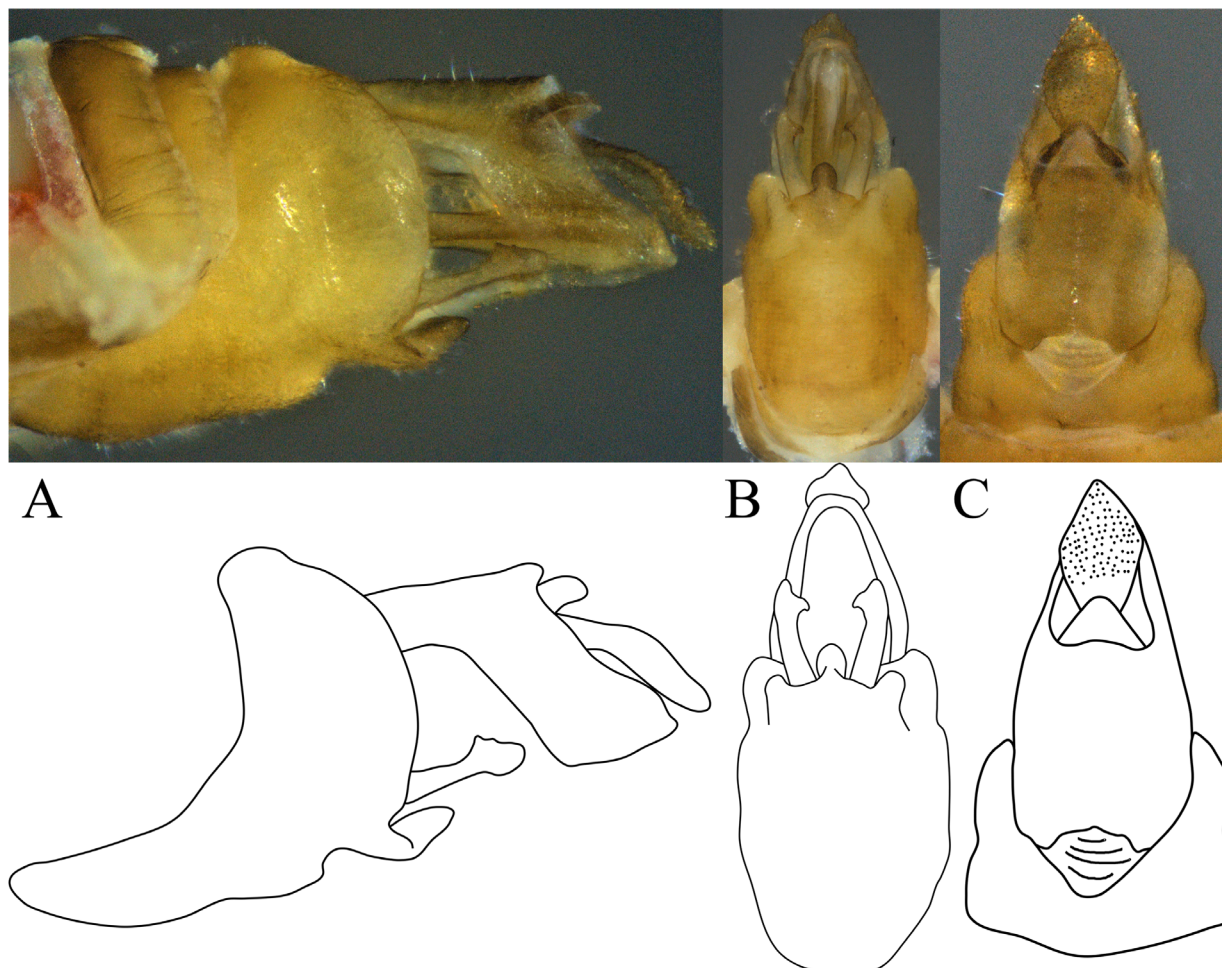

FIGURE 5. Male *Oecleus dormido* **sp. n.** terminalia; (A) lateral view, (B) ventral view, and (C) dorsal view.

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

Distribution. Tortuguero, Limón Province, Costa Rica.

Etymology. The specific epithet is the Spanish slang for sleepy.

Material examined. Holotype male "Costa Rica, Limón Pr. / Tortuguero / 13.V.2018 / Coll.: M.A. Echavarria // Holotype / *Oecleus dormido* ♂" (FLREC); Paratypes 2 males, 2 females, same data as holotype (FSCA).

Sequence data. For the COI locus, a 545 bp product was generated (GenBank Accession No. OM264283), for the 18S locus, a 1,349 bp product was generated (GenBank Accession No. OM258693), and for the H3 locus, a 280 bp product was generated (GenBank Accession No. OM262392). Based on the phylogenetic analyses of the COI, 18S, and H3 loci and the consensus analysis (Fig. 7D), *Oecleus dormido* **sp. n.** resolves adjacent to *O. borealis* (Fig. 8). Based on the consensus tree, *Oecleus* (assessing the three taxa available here) is monophyletic with strong bootstrap support (95). This is also seen in the 18S phylogeny (94 bootstrap support) (Fig. 7B). There is weak bootstrap support for this based on H3 (18, Fig. 7C) and *Oecleus* is not monophyletic based on COI (Fig. 7A). In all analyses except for H3 (which is based on 280 bp), the genera *Nymphomyndus* and *Nymphocixia* are sister groups. The strong phylogenetic bootstrap support (99) for these two genera as a clade.
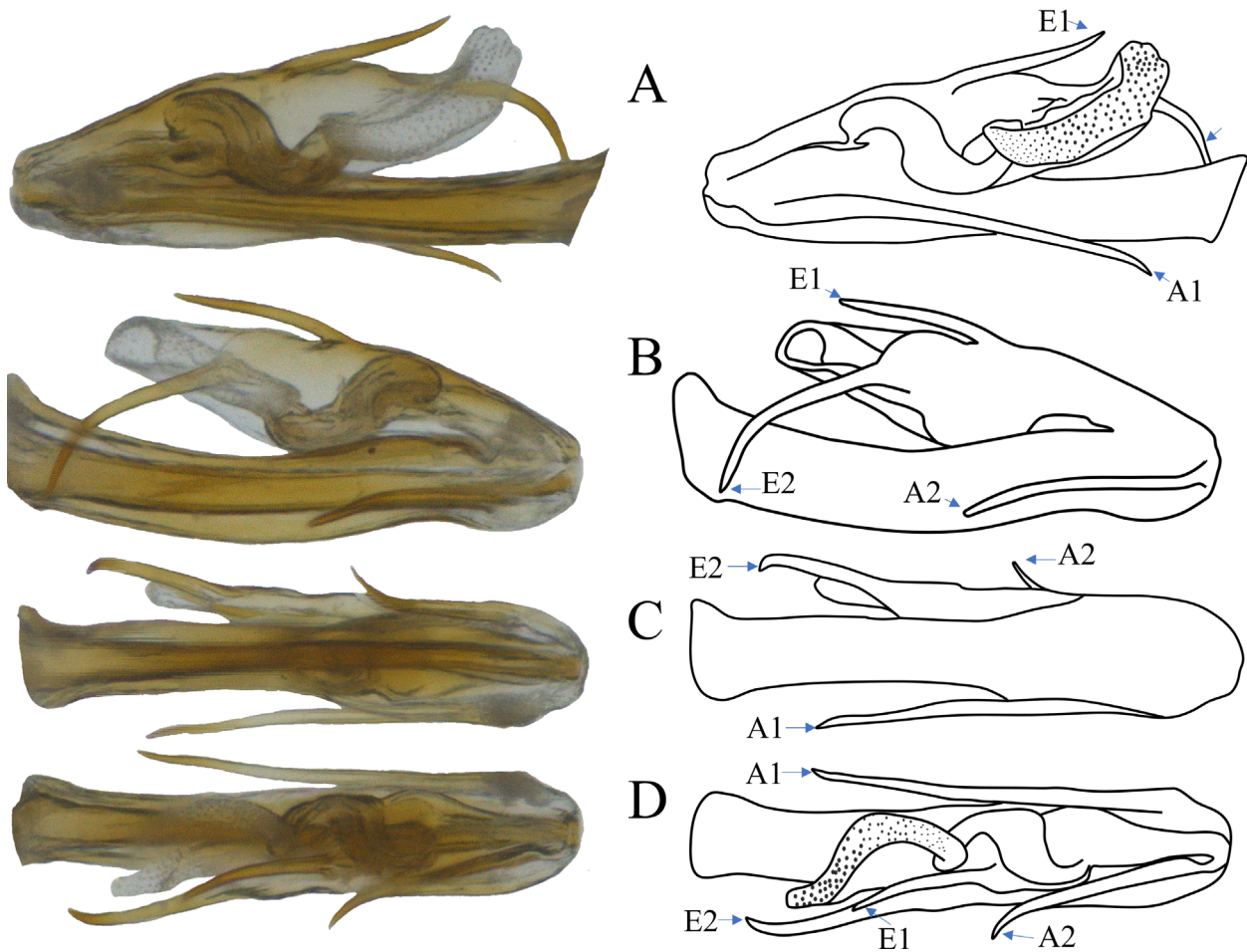
FIGURE 6. Aedeagus of *Oecleus dormido* **sp. n.**; (A) left lateral view, (B) right lateral view, (C) ventral view, and (D) dorsal view.

Based on the pairwise comparison of the 18S gene for taxa assessed, the average variability within genus is 0.4% (±0.1), 0.6% (±0.3), 0.7% (±0.2) for *Oecleus*, *Myxia*, and *Haplaxius* respectively (Table 4), while the variability among genera is an average of 2.2% (±0.04). *Oecleus dormido* **sp. n.** differs from *O. borealis* and *O. mackaspringi* by 0.2% and 0.5%, respectively. The difference between *Nymphomyndus and Nymphocixia* is 0.98% at the 18S locus

Remarks *Oecleus dormido* **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 (see below).

In Kramer's (1977) key to US species (treating 40 species north of Mexico), *Oecleus dormido* **sp. n.** appears to trace to couplet 28–29 (viz. *O. jenniferae* Kramer, *O. excavatus* Ball, *O. palton* Kramer) based on the following features used in the key: aedeagal shaft with 2 processes (shaft without acute projection near midlength or base), aedeagal shaft without expansion on dorsal margin, anal tube not triangular (anal tube in lateral view ventrally strongly convex and lobed); endosoma with 2 processes (proximal process [E1] not strongly recurved [viz. couplet 16] or minute [viz. couplet 26]), right aedeagal process [A1] in lateral view more than half length of shaft, not strongly bowed and protruding beyond flagellum. Of these species *Oecleus dormido* **sp. n.** has terminalia most similar to *O. jenniferae* but has only one (not both) flagellar processes shorter than the flagellum, and the shape of the medioventral process of the pygofer is different (rounded, slightly longer than wide in *O. dormido* **sp. n.**, versus ovately produced from subtriangular base, Kramer 1977, fig. 91). *Oecleus dormido* **sp. n.** differs from both *O. excavatus* and *O. palton* in having one of the endosomal processes shorter than the endosoma (vs. both longer) and the shape of the medioventral process (more elongate in both *O. excavatus* and *O. palton*), and also the shape of the anal tube (see Kramer 1977, figs 85–87 and 94–96). *Oecleus dormido* **sp. n.** appears unique among its congeners by have a strongly helical endosoma.

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
1	*Oecleus dormido* **sp. n.**		0.001	0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.003
2	*Oecleus borealis*	0.002		0.002	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.003
3	*Oecleus mackaspringi*	0.005	0.006		0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004	0.004
4	*Myxia belinda*	0.022	0.023	0.023		0.003	0.003	0.004	0.004	0.004	0.004	0.004	0.004
5	*Myxia delta*	0.024	0.026	0.024	0.009		0.001	0.004	0.004	0.004	0.004	0.004	0.004
6	*Myxia hernandezi*	0.023	0.025	0.025	0.009	0.001		0.004	0.004	0.004	0.004	0.004	0.004
7	*Haplaxius pocococo*	0.023	0.025	0.022	0.023	0.021	0.022		0.003	0.002	0.004	0.004	0.004
8	*Haplaxius lunatus*	0.021	0.023	0.020	0.023	0.023	0.023	0.011		0.002	0.004	0.004	0.004
9	*Haplaxius crudus*	0.020	0.021	0.019	0.020	0.019	0.020	0.005	0.008		0.003	0.004	0.004
10	*Nymphocixia caribbea*	0.023	0.024	0.021	0.022	0.021	0.022	0.017	0.017	0.014		0.003	0.004
11	*Nymphocixia unipunctata*	0.025	0.026	0.024	0.026	0.027	0.027	0.023	0.020	0.020	0.010		0.004
12	*Melanoliarus chuliotus*	0.016	0.017	0.018	0.022	0.025	0.025	0.026	0.023	0.023	0.026	0.028	

Aside from species treated in Kramer (1977), 18 species of *Oecleus* were described or redescribed (with terminalia illustrated) by Caldwell (1944), O'Brien (1982), Emeljanov (2007), Bartlett *et al.* (2018), and Myrie *et al.* (2019) all of which differ from *Oecleus dormido* **sp. n.** based on male terminalia (especially the shape of the anal tube and the medioventral pygofer process). Of the remaining eight species, seven from Mexico are treated by Fowler (1904, table 10, figs. 3–13) and differ from the new species in coloration and or shape of the head (although Kramer 1977: 379–380 notes that *Oecleus decens* Stål is an 'unrecognizable species' based on 'one female from an unspecified locality in Mexico'), and finally, *Oecleus monilipennis* Van Duzee (from 'Ceralbo Island', now Isla Jacques Cousteau, in the Gulf of California) as described by Van Duzee (1923: 190–191) as close to *Oecleus fulvidorsum* Ball (see Kramer 1977, figs 28–30), except with a 'subtriangular' medioventral process of the pygofer and the anal tube 'scarcely surpassing' the gonostyli. From these observations, we conclude that that *Oecleus dormido* **sp. n.** is an undescribed species.
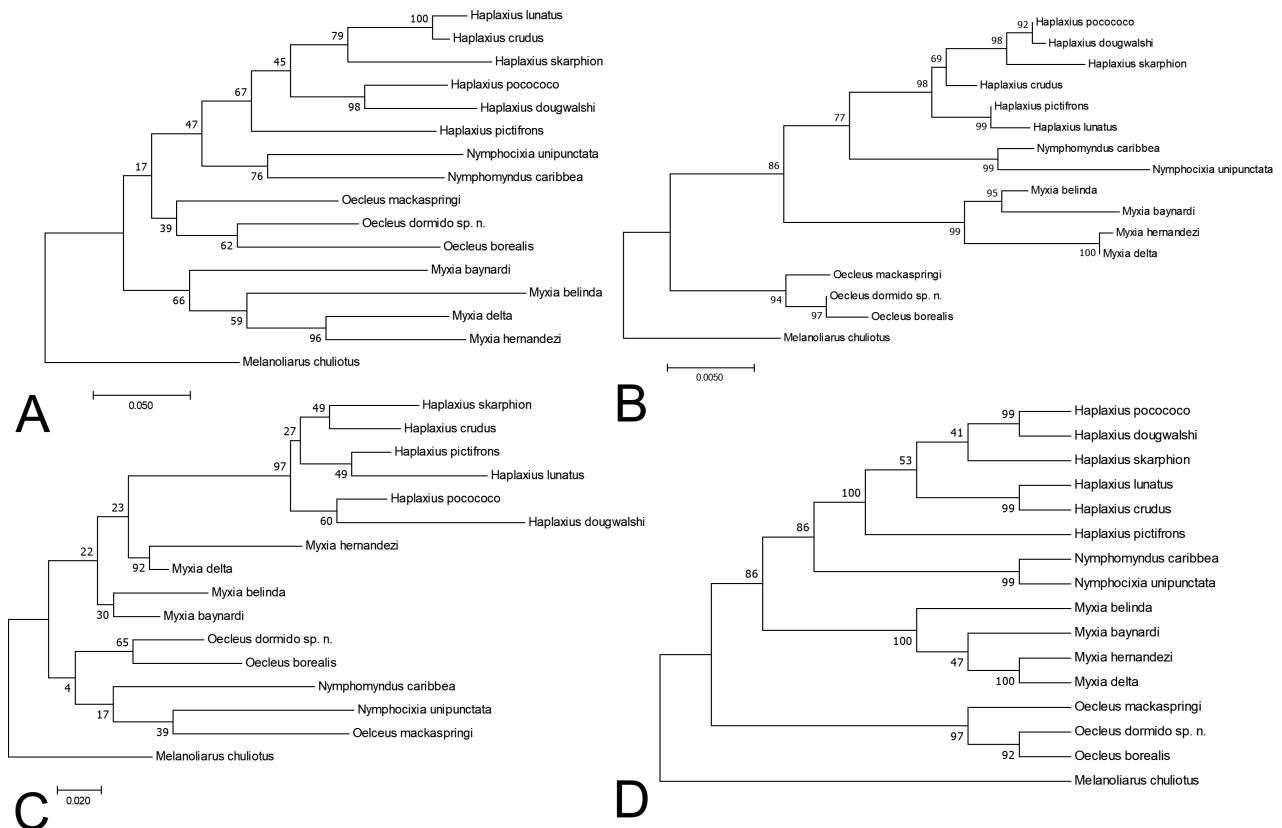

FIGURE 7. Maximum likelihood phylogenetic tree based on 1,000 replicates: (A) COI gene, (B) 18S rRNA gene, (C) H3 gene, and (D) consensus tree of concatenated COI, 18S, and H3 sequences.

Phylogenetic analyses

While bootstrap support and phylogenies for COI and H3 were not robust along the tree backbone, they exhibited similar patterns. The phylogenetic hypotheses appear strongest for 18S among individual genes, which is reflected in the consensus tree. All of these analyses suggest that the new species is sister to *O. borealis* (Fig. 8) among the included taxa, supporting placement of the new species in *Oecleus*.

In the combined analysis, the genera with multiple species represented (viz. *Oecleus*, *Haplaxius*, *Myxia*) appear to be monophyletic. Within the Oecleini, a clade is formed by (*Myxia*+((*Nymphocixia*+*Nymphomyndus*)+*Haplaxius*) with moderate to high bootstrap support (86), with *Oecleus* in a separate clade with strong bootstrap support for this separation (97), sister to the outgroup *Melanoliarus chuliotus* (Fig. 9). This same set of relationships are seen in the 18S gene phylogeny with comparable statistical support (86 and 94 respectively), but not in the H3 or COI phylogenies.

The relationship of *H. lunatus* (Fig. 10) to *H. crudus* is interesting. While normal levels of variability were ob-

served for 18S and H3 between *H. lunatus* and other congeners, the percent different COI between *H. lunatus* and *H. crudus* was low (2.6%). Normally for COI, the level of variability among species in *Haplaxius* is approximately 15% with 2.6% being intraspecific variability (Humphries *et al.* 2021). While 2.6% is much lower than is expected, the sequence generated from *H. lunatus* does not match any known haplotype of *H. crudus* in Florida. The data from 18S and H3 combined with morphological data make it evident that these are distinct species, but all phylogenies show these species to be closely related.
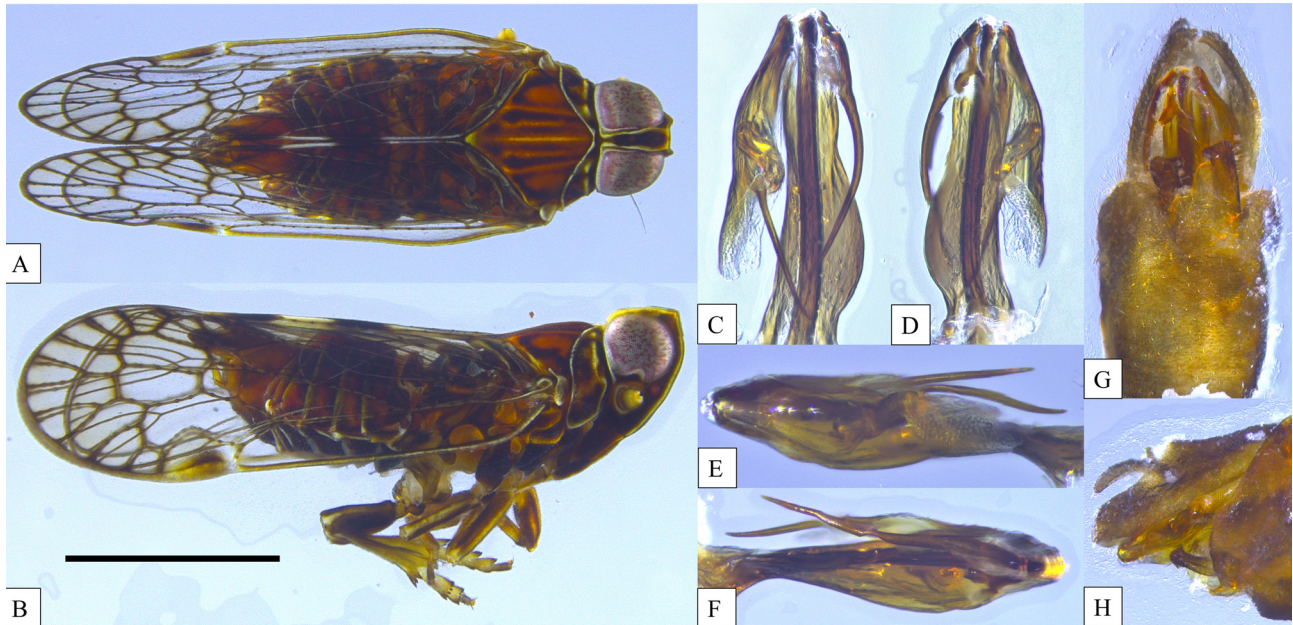
FIGURE 8. Adult male of *Oecleus borealis*; (A) dorsal view, (B) lateral view, (C) dorsal view of aedeagus, (D) ventral view of aedeagus, (E) right lateral view of aedeagus, (F) left lateral view of aedeagus, (G) ventral view of terminalia, and (H) lateral view of terminalia; scale = 1 mm.
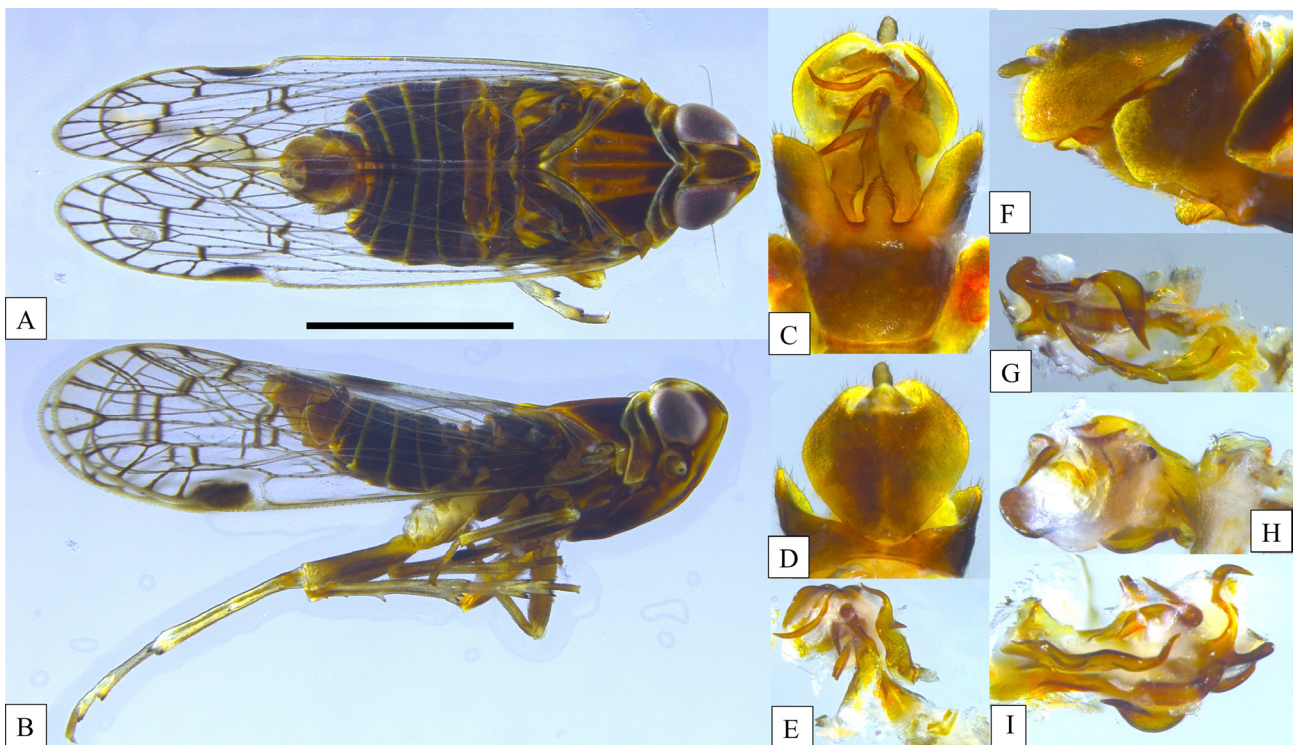

FIGURE 9. Adult male of *Melanoliarus chuliotus*; (A) dorsal view, (B) lateral view, (C) ventral view of terminalia, (D) dorsal view of terminalia, (E) ventral view of aedeagus, (F) lateral view of terminalia, (G) left lateral view of aedeagus, (H) right lateral view of aedeagus, and (I) dorsal view of aedeagus; scale = 1 mm.

The placement of *Oecleus* was closer to *Melanoliarus chuliotus* than to other Oecleini in unrooted trees. While more taxa from other subfamilies and tribes as well as more members of *Oecleus* are needed, these preliminary findings suggest that Oecleini as currently understood may not be monophyletic. Within the Oecleini, *Oecleus* appears quite distinct relative to all other genera examined (*Haplaxius*, *Myxia*, *Nymphocixia*, and *Nymphomyndus*) which indeed form distinct clades. As more taxa are described or become available, a significant revision of the tribal structure in Cixiidae is needed but is beyond the scope of the current work.
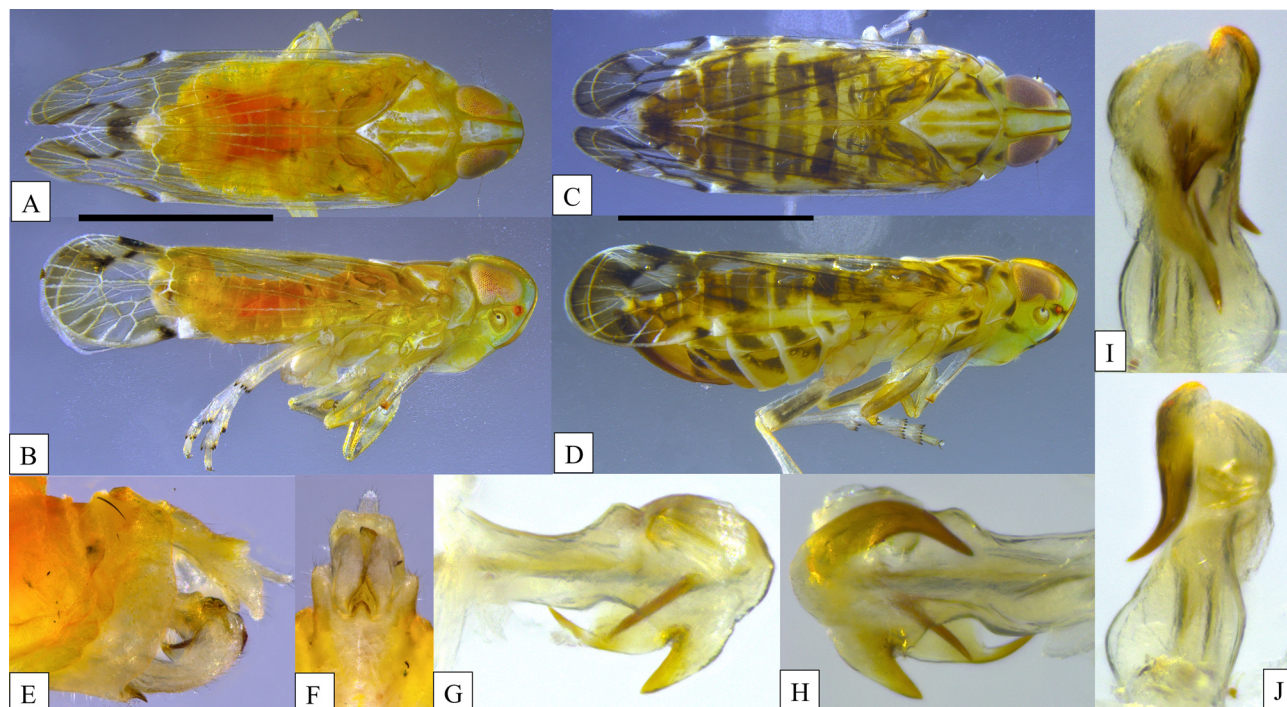

FIGURE 10. Adult *Haplaxius lunatus*; (A) dorsal view of adult male, (B) lateral view of adult male, (C) dorsal view of adult female, (D) lateral view of adult female, (E) lateral view of terminalia, (F) ventral view of terminalia, (G) left lateral view of aedeagus, (H) right lateral view of aedeagus, (I) ventral view of aedeagus, and (J) dorsal view of aedeagus; scale = 1 mm.

Status of *Nymphocixia* and *Nymphomyndus*

Nymphocixia unipunctata (Fig. 11) was described from Mexico (Isla Espíritu Santo, Gulf of California; Van Duzee 1923) with the genus established to accommodate the species due to characteristics of the head compared to *Oecleus* (greatly elevated lateral carinae of vertex with vertex hiding the pronotum). *Nymphomyndus caribbea* (Fig. 12) was originally described as *Nymphocixia* (Fennah 1971), however, Emeljanov (2007) established *Nymphomyndus* for *N. caribbea* based on differences in the head. Emeljanov (2007) discussed *Nymphocixia* in comparison with his new genus *Nymphomyndus* (and the monobasic genus *Nesomyndus* Jacobi from Madagascar), but provided little for diagnostic comparisons among genera. The key diagnostic differences between the genera appear to be that in *Nymphomyndus* the lateral margins of the vertex (dorsal view) are anteriorly converging (parallel in *Nymphocixia*), the posterior margin of the vertex does not entirely overlap the pronotum (posterior margin of vertex overlapping in *Nymphocixia*) and in lateral view, anterior profile of head "almost straight in distal three-quarters" (quoting Emeljanov (2007: 292) from Fennah (1971: 313)) (versus smoothly rounding in *Nymphocixia*) (Fig. 13).

The level of variability between *Nymphocixia* and *Nymphomyndus* for 18S is significantly less than what was observed among other genera, indicating that the separation into these two genera was not warranted. Because the features listed by (Van Duzee as indicative of *Nymphocixia* are present in *Nymphomyndus caribbea*, lack of strong characters to merit the establishment of *Nymphomyndus* as a distinct genus, and strong molecular support that *Nymphocixia* and *Nymphomyndus* are closely related, we here synonymize *Nymphomyndus* under *Nymphocixia*, with the composition of *Nymphocixia* as follows.
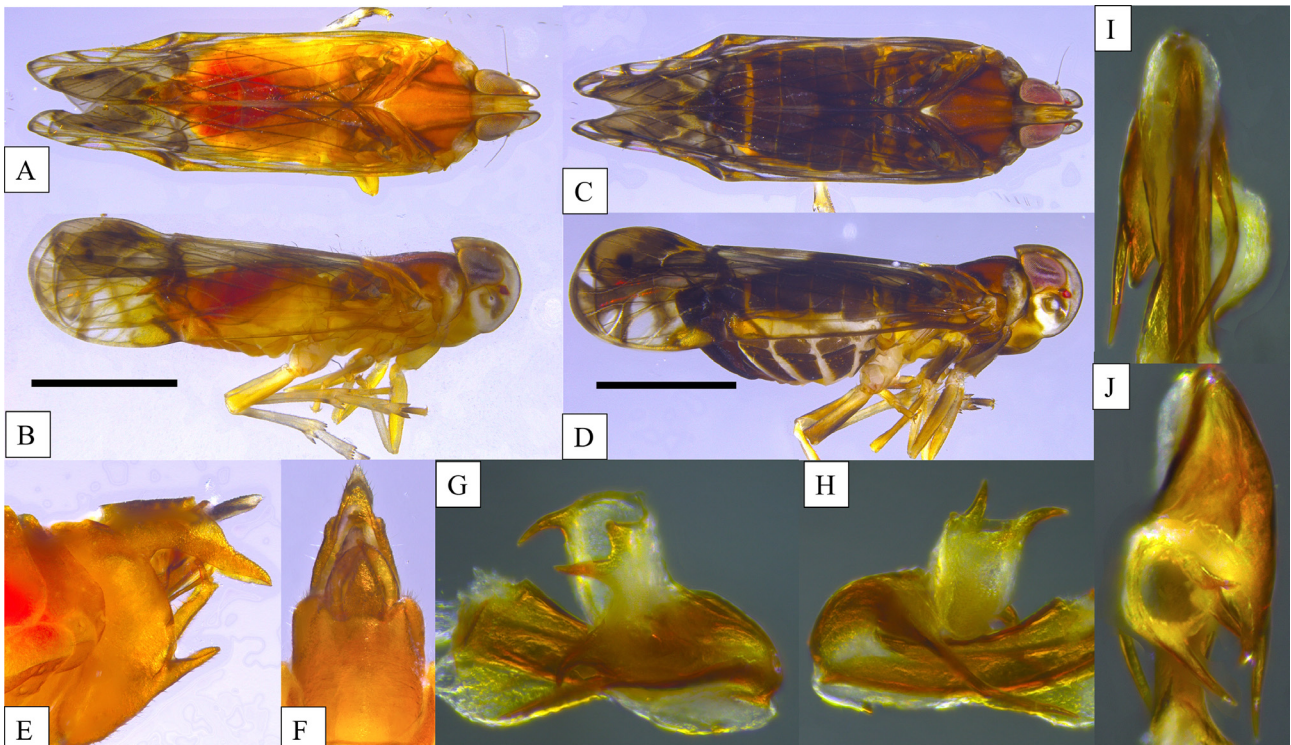
FIGURE 11. Adult *Nymphocixia unipunctata*; (A) dorsal view of adult male, (B) lateral view of adult male, (C) dorsal view of adult female, (D) lateral view of adult female, (E) lateral view of terminalia, (F) ventral view of terminalia, (G) left lateral view of aedeagus, (H) right lateral view of aedeagus, (I) ventral view of aedeagus, and (J) dorsal view of aedeagus; scale = 1 mm.
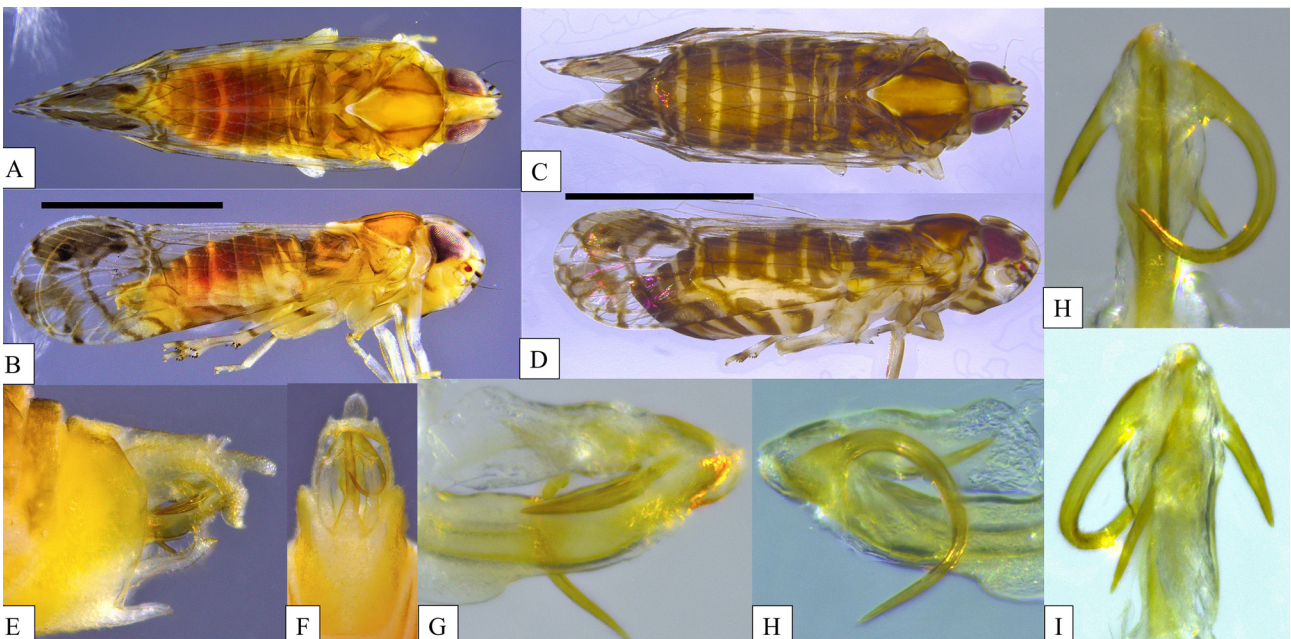

FIGURE 12. Adult *Nymphocixia caribbea*; (A) dorsal view of adult male, (B) lateral view of adult male, (C) dorsal view of adult female, (D) lateral view of adult female, (E) lateral view of terminalia, (F) ventral view of terminalia, (G) left lateral view of aedeagus, (H) right lateral view of aedeagus, (I) ventral view of aedeagus, and (J) dorsal view of aedeagus; scale = 1 mm.
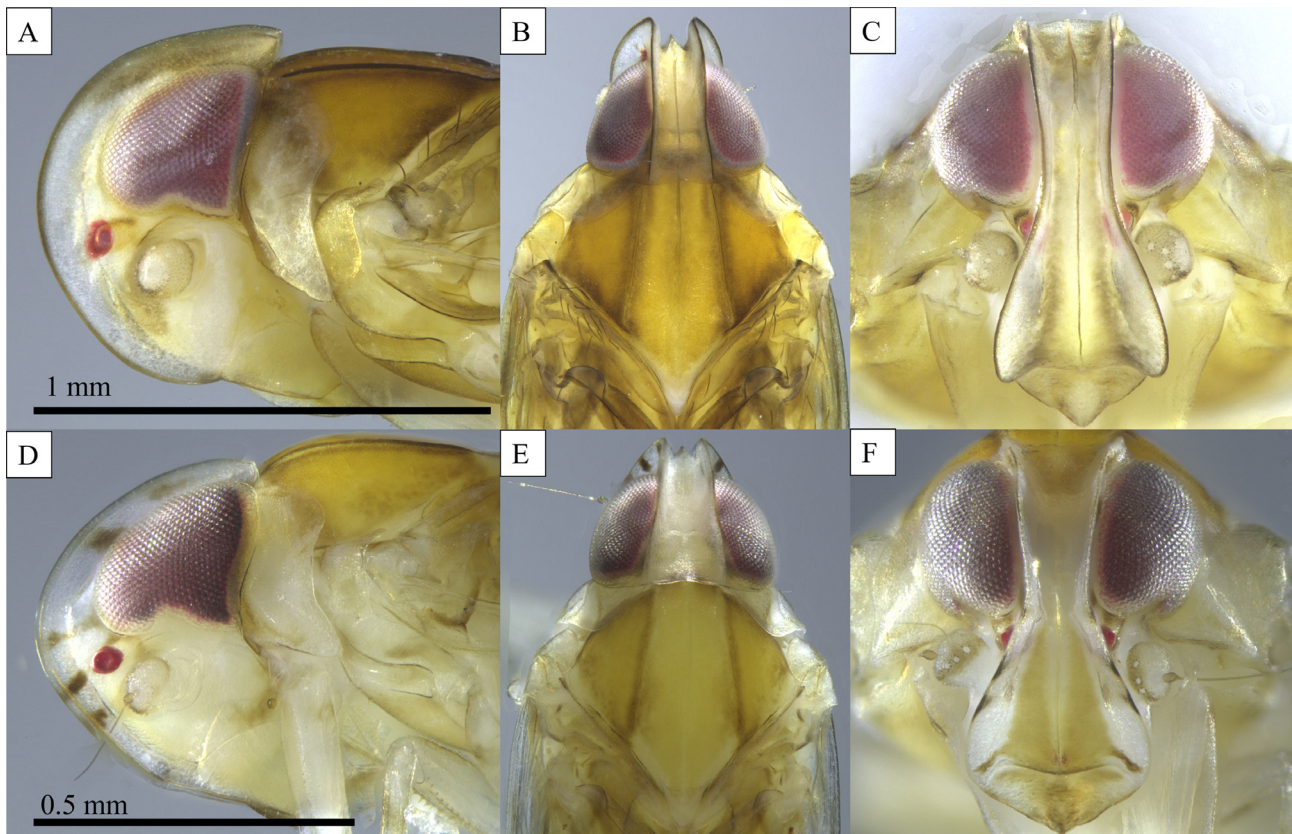
FIGURE 13. Adult *Nymphocixia unipunctata*; (A) lateral view of head, (B) dorsal view of head and (C) frontal view of head; Adult *Nymphocixia caribbea*; (D) lateral view of head, (E) dorsal view of head and (F) frontal view of head.

Genus *Nymphocixia* Van Duzee

Nymphocixia Van Duzee, 1923: 189 (type species *Nymphocixia unipunctata* Van Duzee 1923:189, by monotypy.)
    = *Nymphomyndus* Emeljanov, 2007, **new syn**. (type species *Nymphocixia caribbea* Fennah, 1971, by original designation and monotypy).

Included taxa

Nymphocixia unipunctata Van Duzee, 1923 (type locality Isla Espíritu Santo, Mexico, holotype male, California Academy of Sciences, missing from point)
= *Nymphocixia vanduzeei* Muir, 1930, syn. by Kramer 1983: 45 (type locality Cartagena, Colombia, holotype male Zoological Museum Hamburg).
= *Nymphocixia vanduzeei floridensis* Caldwell, 1944 syn. by Kramer 1983: 45 (type locality Cortes Beach, Manatee County, Florida, Holotype female Ohio State University).

Distribution: Belize, Colombia, Costa Rica, Galapagos, Mexico (Isla Espíritu Santo, Nayarit), Nicaragua, Panama, USA (Florida, South Carolina) (Muir 1930, Caldwell 1944, Fennah 1967, 1971, Kramer 1983, Bartlett *et al.* 2014).

Nymphocixia unipunctata galapagensis Fennah, 1967: 58 (type locality Galapagos Archipelago, Fernandina Island, Punta Espinosa, holotype male, California Academy of Sciences)
= *Nymphocixia vanduzeei galapagensis* Fennah, 1967, original combination.
= *Nymphocixia unipunctata galapagensis* Fennah, 1967, combination by implication Kramer, 1983: 45.

Distribution: Galapagos Archipelago (Fennah 1967)

Nymphocixia caribbea Fennah, 1971: 313 (type locality Cayman Islands, Grand Cayman; holotype male British Museum Natural History).

= *Nymphomyndus caribbea* (Fennah, 1971), comb. by Emeljanov (2007: 292).
= *Nymphocixia caribbea* Fennah, 1971, restored combination.

Distribution: Cayman Islands (Fennah 1971), Jamaica

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 not Belize, Honduras and points south 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 2022). Based on this study (also Bartlett *et al.* 2018 and iNaturalist records) it appears that the lack of *Oecleus* records in southern Mesoamerica may represent lack of survey effort together with the taxonomic diagnostic challenges and the relatively small and cryptic nature of the genus. However, the association of *Oecleus* with palms (Bartlett *et al.* 2019, Myrie *et al* 2019) and the possibility that it may be a phytoplasma vector suggests that *Oecleus* may be an important topic for further study, and such study will find additional undescribed species, especially in Mesoamerica. The monophyly of the genus *Oecleus* as currently comprised has been assumed, but is untested. Some species of *Oecleus* stray from the usual form, such as the large species *Oecleus snowi* Ball, and some with more elongate heads (e.g., *Oecleus sergipensis*). Also, the type species, *Oecleus seminiger*, has the basal half of the forewings fuscous (see Fowler 1904, tab. 10, fig 3), whereas most members of the genus have entirely clear forewings. These observations collectively suggest that the monophyly and composition of *Oecleus* deserve closer assessment.

Sequence data for *Oecleus borealis* and *Oecleus dormido* **sp. n.** are useful for beginning to construct phylogenies that will lead to testing of the monophyly of the group. However, as sequence data becomes available for other species of described *Oecleus* and new taxa are discovered, it is likely that new genera will be segregated out of *Oecleus*. Recently this was done with another large genus, *Haplaxius*, where novel species were collected and determined to represent a new genus, *Myxia* (Bahder *et al.* 2019) and subsequently a species from *Haplaxius*, *H. delta*, was transferred to *Myxia* based on molecular and morphological support (Echavarria *et al.* 2021a, b). Finally, understanding the taxonomy and phylogeny for *Oecleus* due to the recent discovery of *O. mackaspringi* on coconut palms (Myrie *et al.* 2019) in Jamaica and its close association with lethal yellowing (LY) spread is important for understanding the vector relationship between Oecleini and palm-infecting phytoplasmas.

The phylogenetic relationships among the genera of Oecleini deserve further assessment. The preliminary phylogenetic analyses presented here among the New World genera of Oecleini suggest a relationship of (*Myx*ia+*Nymp hocixia*+*Haplaxius*), with these genera standing apart from *Oecleus*. Additional taxon sampling and data are needed to determine whether Oecleini, as currently comprised, is monophyletic. Our analyses do suggest that *Nymphomyndus* is too closely allied with *Nymphocixia* to merit standing as an independent genus.

Acknowledgements

References

Bahder, B.W., Bartlett, C.R., Barrantes, E.A.B., Echavarria, M.A.Z., Humphries, A.R., Helmick, E.E., Goss, E.M. & Ascunce, M.S. (2019) A new genus and species of cixiid planthopper (Hemiptera: Auchenorrhyncha: Fulgoroidea) from the Reserva Privada el Silencio de Los Angeles Cloud Forest in Costa Rica. *Zootaxa*, 4701 (1), 65–81.

https://doi.org/10.11646/zootaxa.4701.1.5

Bartlett, C.R., O'Brien, L.B. & Wilson, S.W. (2014) A review of the planthoppers (Hemiptera: Fulgoroidea) of the United States. *Memoirs of the American Entomological Society*, 50, 1–287.

Bartlett, C.R., Dos Passos, E.M., Da Silva, F.G., Diniz, L.E.C. & Dollet, M. (2018) A new species of *Oecleus* Stål (Hemiptera: Fulgoroidea: Cixiidae) from coconut in Brazil. *Zootaxa*, 4472 (2), 358–364.
https://doi.org/10.11646/zootaxa.4472.2.8

Bourgoin, T. (1988) A new interpretation of the homologies of the Hemiptera male genitalia illustrated by the Tettigometridae (Hemiptera, Fulgoromorpha). *In*: Vidano, C. & Arzone, A. (Eds.), *Proceedings of the 6th Auchenorrhyncha Meeting, Turin, Italy, 7–11 September 1987*. Consiglio Nazionale delle Ricerche, IPRA, Rome, pp. 113–120.

Bourgoin, T. (2022) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8. Available from: http://www.hemiptera-databases.org/flow/ (accessed 3 January 2022)

Bourgoin, T., Wang, R.R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroinski, A., Yap, S. & Szwedo, J. (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology*, 134 (1), 63–77.
https://doi.org/10.1007/s00435-014-0243-6

Bourgoin, T. & Huang, J. (1990) Morphologie comparée des genitalia mâles des Trypetimorphini et remarques phylogénétiques (Hemiptera: Fulgoromorpha: Tropiduchidae). *Annales de la Société Entomologique de France*, Nouvelle Serie, 26, 555–564.
https://doi.org/10.1002/jmor.1052070205

Caldwell, J.S. (1944) Notes on *Oecleus* Stål (Homoptera: Cixiidae). *Entomological News*, 8, 174–176 + 198–202

Dzido, J.L., Sánchez, R., Dollet, M. Julia, J.F., Narvaez, M., Fabre, S. & Oropeza, C. (2020) *Haplaxius crudus* (Hemiptera: Cixiidae) transmits the lethal yellowing phytoplasmas, 16SrIV, to *Pritchardia pacifica* Seem. & H. Wendl (Arecaceae) in Yucatan, Mexico. *Neotropical Entomology*, 49, 795–805.
https://doi.org/10.1007/s13744-020-00799-2

Echavarria, M.A.Z., Barrantes, E.A.B., Bartlett, C.R., Helmick, E.E. & Bahder, B.W. (2021a) A new species of *Myxia* (Hemiptera: Auchenorrhyncha: Cixiidae) collected on palms from the Reserva Privada el Silencio de Los Angeles Cloud Forest in Costa Rica. *Zootaxa*, 5027 (3), 417–428.
https://doi.org/10.11646/zootaxa.5027.3.7

Echavarria, M.A.Z., Barrantes, E.A.B., Bartlett, C.R. Helmick, E.E. & Bahder, B.W. (2021b) A new species of planthopper in the genus *Myxia* (Hemiptera: Auchenorrhyncha: Cixiidae) from the Reserva Privada el Silencio de Los Angeles Cloud Forest in Costa Rica. *Zootaxa*, 4915 (3), 351–363.
https://doi.org/10.11646/zootaxa.4915.3.4

Emeljanov, A.F. (2007) New and little known taxa of the family Cixiidae (Homoptera, Fulgoroidea). *Entomological Review*, 87, 287–308. [English translation from *Entomologicheskoe Obozrenie*, 86 (1), 107–131 (2007, in Russian)]
https://doi.org/10.1134/S0013873807030062

Fennah, R.G. (1967) Fulgoroidea from the Galápagos Archipelago. *Proceedings of the California Academy of Sciences*, 35. 53–102.

Fennah, R.G. (1971) Fulgoroidea from the Cayman Islands and adjacent areas. *Journal of Natural History*, 5, 299–342.

Fowler, W.W. (1904) Order Rhynchota. Suborder Hemiptera-Homoptera. (Continued). *Biologia Centrali-Americana; contributions to the knowledge of the fauna and flora of Mexico and Central America*, 1, 85–124.

Howard, F.W. & Thomas, D.L. (1980) Transmission of palm lethal decline to *Veitchia merrillii* by a planthopper *Myndus crudus*. *Journal of Economic Entomology*, 73 (5), 715–717.
https://doi.org/10.1093/jee/73.5.715

Humphries, A.R., Ascunce, M.S., Goss, E.M., Helmick, E.E., Bartlett, C.R, Myrie, W., Barrantes, E.A.B., Zumbado, M.A.Z., Bustillo, A.E. & Bahder, B.W. (2021) Genetic variability of *Haplaxius crudus* based on the 5' region of the cytochrome *c* oxidase subunit I gene shed light on the epidemiology of palm lethal decline phytoplasmas. *Phytofrontiers*, 1 (3), 127–134.
https://doi.org/10.1094/PHYTOFR-12-20-0048-R

Kramer, J.P. (1977) Taxonomic study of the planthopper genus *Oecleus* in the United States (Homoptera: Fulgoroidea: Cixiidae). *Transactions of the American Entomological Society*, 103 (2), 379–449.

Kramer, J.P. (1983) Taxonomic study of the planthopper family Cixiidae in the United States (Homoptera: Fulgoroidea). *Transactions of the American Entomological Society*, 109, 1–57.

Kumar, S., Stecher, G. & Tamura, K. (2016) MEGA7: Molecular Evolutionary Genetics Analysis version 7.0 for bigger datasets. *Molecular Biology and Evolution*, 33, 1870–1874.
https://doi.org/10.1093/molbev/msw054

Mou, D.F., Humphries, A.R., Soto, N., Helmick, E.E., Ascunce, M.S., Goss E.M. & Bahder, B.W. (2020a) A survey of Auchenorrhynchan insects for identification of potential vectors of the 16SrIV-D phytoplasma in Florida. *Florida Entomologist*, 103 (3), 344–352.
https://doi.org/10.1653/024.103.0306

Mou, D.F., Lee, C.C., Hahn, P.G., Soto, N., Humphries, A.R., Helmick, E.E. & Bahder, B.W. (2020b) Effects of lethal bronzing disease, palm height, and temperature on abundance and monitoring of *Haplaxius crudus*. *Insects*, 11 (Article 748), 1–12.

https://doi.org/10.3390/insects11110748

Muir, F.A.G. (1922) New Malayan Cixiidae (Homoptera). *Philippine Journal of Science*, 20, 111–119.

Muir, F.A.G. (1930). Three new species of American Cixiidae (Fulgoroidea, Homoptera). *Pan-Pacific Entomologist*, 7 (1), 12–14.

Myers, J.G. (1928) Notes on Cuban fulgoroid Homoptera. *In*: *Studies on Cuban insects. Vol. 1.* Harvard biological laboratory and botanical garden in Cuba, Cambridge, Massachusetts, pp. 11–31.

Myrie, W., Helmick, E.E., Bartlett, C.R., Bertaccini, A. & Bahder, B.W. (2019) A new species of planthopper belonging to the genus *Oecleus* Stål, 1862 (Hemiptera: Fulgoroidea: Cixiidae) from coconut palm (*Cocos nucifera* L) in Jamaica. *Zootaxa,* 4712 (1), 127–137.
https://doi.org/10.11646/zootaxa.4712.1.9

O'Brien, L.B. (1982) Two new species of *Oecleus* from Texas and Arizona (Homoptera: Fulgoroidea: Cixiidae). *Southwestern Entomologist*, 7 (4), 252–254.

Remes Lenicov, A.M.M. (1992) Fulgoroideos sudamericanos. 1. Un nuevo genero y especie de Cixiidae cavernicola de la Patagonia (Insecta: Homoptera). *Neotropica, La Plata*, 38 (100), 155–160.

Spinola, M. (1839) Essai sur les Folgorelles, sous-tribu des Cicadaires, ordre des Rhyngotes. *Annales de la Société Entomologique de France*, 8, 133–337.

Stål, C. (1862) Novae vel minus cognitae Homopterorum formae et species. *Berliner Entomologische Zeitschrift*, 6, 303–315.

Van Duzee, E.P. (1923) Expedition of the California Academy of Sciences to the Gulf of California in 1921—The Hemiptera (True Bugs, etc.). *Proceedings of the California Academy of Sciences*, Series 4, 12, 123–200.