



## A new species of planthopper in the genus *Melanoliarus* (Hemiptera: Auchenorrhyncha: Fulgoroidea: Cixiidae) from coconut palms (*Cocos nucifera*) in Trinidad

WAYNE MYRIE<sup>1</sup>, ALBADA BEEKHAM<sup>2</sup>, AMEL BAKSH<sup>3</sup>, JULIA PARRIS<sup>4</sup>, FAYAZ SHAH<sup>5</sup>, CHARLES R. BARTLETT<sup>6</sup>, ERICKA E. HELMICK<sup>7</sup>, SOLOMON HENDRIX<sup>8</sup> & BRIAN W. BAHDER<sup>9\*</sup>

<sup>1</sup>Coconut Industry Board, 18 Waterloo Road, Kingston 10, Jamaica W. I. [✉ cocomax@cwjamaica.com](mailto:cocomax@cwjamaica.com)

<sup>2</sup>Ministry of Agriculture, Land and Fisheries, Research Division, Caroni North Bank Road, Centeno, Trinidad and Tobago, W.I.

[✉ ABeekham@fp.gov.tt](mailto:ABeekham@fp.gov.tt)

<sup>3</sup>Ministry of Agriculture, Land and Fisheries, Research Division, Caroni North Bank Road, Centeno, Trinidad and Tobago, W.I.

[✉ Amel.Baksh@gov.tt](mailto:Amel.Baksh@gov.tt)

<sup>4</sup>Ministry of Agriculture, Land and Fisheries, Research Division, Caroni North Bank Road, Centeno, Trinidad and Tobago, W.I.

[✉ Jparris@gov.tt](mailto:Jparris@gov.tt)

<sup>5</sup>Caribbean Agricultural Research and Development Institute, Frederic Hardy Building, U.W.I., St. Augustine Campus, Trinidad and Tobago. [✉ FShah@cardi.org](mailto:FShah@cardi.org)

<sup>6</sup>University of Delaware, Department of Entomology and Wildlife Ecology, 250 Townsend Hall, Newark, DE 19716-2160, USA.

[✉ Bartlett@udel.edu](mailto:Bartlett@udel.edu); [✉ bartlett@udel.edu](mailto:bartlett@udel.edu); <https://orcid.org/0000-0001-9428-7337>

<sup>7</sup>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](mailto:ehelmick@ufl.edu); <https://orcid.org/0000-0002-5153-0891>

<sup>8</sup>University of Delaware, Department of Entomology and Wildlife Ecology, 250 Townsend Hall, Newark, DE 19716-2160, USA.

[✉ solvhent@udel.edu](mailto:solvhent@udel.edu)

<sup>9</sup>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](mailto:bbahder@ufl.edu); <https://orcid.org/0000-0002-1118-4832>

\*Corresponding author. [✉ bbahder@ufl.edu](mailto:bbahder@ufl.edu)

### Abstract

During a survey in Trinidad and Grenada for putative vectors of palm lethal decline phytoplasmas, three species of planthopper in the genus *Melanoliarus* (Hemiptera, Cixiidae) were collected. *Melanoliarus maidis* was collected from coconut palms in Grenada, *M. kindli* was collected from grasses in a coconut plot in Trinidad and a new species of *Melanoliarus* was collected from coconut palms in Trinidad. Herein the novel taxon is described with supplementary molecular data for the cytochrome *c* oxidase subunit I (COI) gene, 18S rRNA gene, and histone 3 (H3) gene to support placement in the genus *Melanoliarus* in the strict sense.

**Key words:** Caribbean, biodiversity, taxonomy, phylogenetics, Cixiinae, Pentastirini

### Resumen

Durante un muestreo de vectores potenciales de fitoplasmas causantes del declive letal en palmeras en Trinidad y Granada, se recolectaron tres especies de chicharritas del género *Melanoliarus* (Hemiptera, Cixiidae). La especie *Melanoliarus maidis* fue colectada en cocoteros en Granada, *M. kindli* fue colectada en césped en una parcela de cocoteros en Trinidad y una nueva especie de *Melanoliarus* fue colectada en cocoteros en Trinidad. En este documento, el nuevo taxón se describe con datos moleculares complementarios para el gen de la subunidad I del citocromo *c* oxidasa (COI), el gen del ARNr 18S y el gen de la histona 3 (H3) para respaldar su ubicación en el género *Melanoliarus* en sensu stricto.

**Palabras clave:** Caribe, biodiversidad, taxonomía, filogenética, Cixiinae, Pentastirini

## Introduction

Recent survey work for putative vectors of palm lethal decline phytoplasmas in Florida, U.S.A., and throughout the Caribbean basin has resulted in the discovery of many new planthopper species. In June of 2022, an expedition to assess the occurrence of lethal yellowing (LY) and its confirmed vector (Howard & Thomas 1980), *Haplaxius crudus* (Van Duzee 1907), was undertaken on the islands of Trinidad and Grenada. During this expedition, various planthoppers were collected from coconut palms (*Cocos nucifera* L.) and tentatively identified as belonging to *Melanoliarius*. Subsequently, two species were identified (*M. kindli* (Bourgoin, Wilson & Couturier, 1998) from Trinidad and *M. maidis* Fennah, 1945 from Grenada) and one species from Trinidad was determined to represent a new species.

The genus *Melanoliarius* Fennah, 1945a, is a large taxon of planthopper in the family Cixiidae (Cixiinae: Pentastirini). *Melanoliarius s.s.* was described as a subgenus of *Oliarius* Stål, 1862, for two Caribbean species, and is now comprised of four species: *M. maidis*, type species, *M. acicus* (Caldwell, 1947), *M. complectus* (Ball, 1902), and *M. viequensis* (Caldwell, 1951) (Fennah 1945a, Caldwell & Martorell 1951, Mead & Kramer 1982). However, in a review of the world fauna of Cixiidae Holzinger *et al.* (2002) treated all New World *Oliarius* as belonging to the genus *Melanoliarius* and in so doing moved approximately 79 additional species into the genus by implication, although a few of these have since been placed in *Pentastiridius* Kirschbaum, 1868 or *Reptalus* Emeljanov, 1971 (Emeljanov 2001). If *Melanoliarius* is understood as all New World Pentastirini formerly in *Oliarius* (excluding those moved elsewhere by Emeljanov 2001), the genus consists of 48 species north of Mexico (e.g., Mead & Kramer 1982, Bartlett *et al.* 2014), plus an additional 31 species from the Caribbean, Mesoamerica, and South America collectively (Metcalf 1936, 1945; Ball 1937, Caldwell 1938, 1947a,b; Fennah 1945b, 1967, Caldwell & Martorell 1951, Mead & Kramer 1982, Bourgoin *et al.* 1998, Campodonico, 2018). While the majority of currently described taxa are known from North America, there are likely many undiscovered taxa in the Neotropics.

The tribe Pentastirini includes all the New World genera of Cixiinae with a 5-keeled mesonotum, except that this feature is shared with a few Oecleini and the Mnemosynini. The Oecleini lack lateral spines on the hind tibia, which are always present in Pentastirini. The tribal features of the Mnemosynini, consisting of five fossil genera and *Mnemosyne* Stål, 1866, were discussed in detail by Szwedo (2004). *Mnemosyne* is easily recognized as a large-bodied genus (mostly 8–15 mm, Van Stalle, 1987), with forewing bearing rows of setae in the apical cells between the veins; but also differs from *Melanoliarius* in that the aedeagus is connected to the anal tube (as opposed to the pygofer in Pentastirini), and the  $MP_{3+4}$  forks well before the  $MP_{1+2}$  (reversed in Pentastirini) (Emeljanov, 2002, Szwedo 2004, Le Cesne *et al.*, 2022).

In the New World, the Pentastirini consists of six genera (*Cyclopoliarus* Fennah, 1945a, *Melanoliarius*, *Nivcentia* Holzinger, 2004, *Oliaronus* Ball, 1934, *Pentastiridius*, and *Reptalus*). All species north of Mexico were treated by Mead and Kramer (1982) and Kramer (1983) with keys to the genera North of Mexico in Bartlett *et al.* (2014). Keys to the genera of the Caribbean are in Fennah (1945a). *Melanoliarius s.l.* (*sensu* Holzinger *et al.* 2002) appears to be a heterogeneous grouping and the diagnostic features separating it from *Reptalus* and *Nivcentia* are inadequately elucidated.

*Melanoliarius* in the strict sense is recognized as being small pentastirines (~3–4 mm), having 2–3 lateral spines on hind tibiae (the spine closest to the femur may be obsolete), hind leg spinulation 6-7-7 (apical spinules on the tarsomeres small and uniform, on the tibia, the lateral spine largest, others uniform in a diagonal row), and the anal tube slightly asymmetric bearing a spine at the ventral apex (*viz.* Mead & Kramer 1982, figs. 288–289). Mead & Kramer (1982: 395) noted that in the subgenus *Melanoliarius*, the “basal ring of the periandrium [phallobase] that gives rise to two or three short processes ventrally and laterally”.

Herein, the new species of *Melanoliarius* is described along with accompanying molecular data for the 18S rRNA gene, cytochrome *c* oxidase subunit I (COI) gene, and histone 3 (H3) gene to support placement relative to congeners. Molecular data for these three loci are also provided for *M. kindli* and *M. maidis*.

## Materials and methods

**Locality and specimen collection.** Specimens of *Melanoliarius* were collected at two sites in Trinidad and one site in Grenada (Fig. 1). All specimens were collected by sweeping accessible coconut fronds, aspirating, and then

transferring them to 95% ethanol for transport. The habitat where specimens were collected was agricultural coconut production plots/edge habitat (Fig. 1). All specimens were collected by permission of property owners and imported under permit P526P-20-00214. Specimens deposited in the University of Florida, Department of Entomology and Nematology—Fort Lauderdale Research and Education Center, Davie, FL (FLREC). Other reference species examined from the following collections: North Carolina State University, Raleigh, NC (NCSU); University of Delaware Insect Reference Collection, Newark, DE (UDCC), and the Smithsonian, National Museum of Natural History, Washington, DE (USNM).



**FIGURE 1.** Habitat and locality of *Melanoliarus castro* sp. n.

**Morphological terminology.** Morphological terminology generally follows Mead & Kramer (1982) 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 was 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  $\mu$ l ATL and 20  $\mu$ l 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  $\mu$ l of buffer ATL and 200  $\mu$ l 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 was 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). For COI, the primers used amplify the 5' half of the COI gene, representing the barcode region of COI. PCR reactions contained 5x GoTaq Flexi Buffer, 25 mM MgCl<sub>2</sub>, 10 mM dNTP's, 10 mM of each primer, 10% PVP-40, and 2.5U GoTaq Flexi DNA Polymerase, 2  $\mu$ l DNA template, and sterile dH<sub>2</sub>O to a final volume of 25  $\mu$ L. 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). 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 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 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 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 sec.	Humphries <i>et al.</i> 2021
	C1-J-2195RC	Reverse	ACTTCTGGATGACCAAAAAATCAA			
18S	18SF	Forward	ACTGTCGATGGTAGGTTCTG	50°C	2 min.	Bahder <i>et al.</i> 2019
	18SR	Reverse	GTCCGAAGACCTCACTAAA			
H3	H3F	Forward	CAGACGGCBMGKAARTCSACC	55°C	30 sec.	Echavarria <i>et al.</i> 2021
	H3R	Reverse	GTKACHCKCTTRGCGTGRAT			

**Taxon sampling.** For molecular comparisons, available members of *Melanoliarius* were sequenced (Table 2), including *M. maidis* and *M. kindli* collected in the same expedition as the new taxon, plus *M. placitus* (Van Duzee, 1912; from Delaware, USA), and *M. chuliotus* (Ball 1934; from Florida). Oecleini served as an outgroup to polarize these data, including *Haplaxius crudus* Van Duzee 1907, *Nymphocixia unipunctata* Van Duzee, 1923, *Oecleus dormido* Bahder & Bartlett, 2022 and *Myxia belinda* Bahder & Bartlett, 2019.

**TABLE 2.** Molecular taxon sampling and GenBank accession numbers

Taxon	Locality	GenBank Accession No.			Collection
		COI	18S	H3	
<i>Haplaxius crudus</i>	Costa Rica	MT080284	MT002393	MZ274037	FLREC
<i>Myxia belinda</i>	Costa Rica	MT900605	MN200095	MZ274041	FLREC
<i>Nymphocixia caribbea</i>	Jamaica	MT080286	MT002394	MZ274044	FLREC
<i>Oecleus dormido</i>	Costa Rica	OM264283	OM258693	OM262392	FLREC
<i>Melanoliaurs castro sp. n.</i>	Trinidad	OP871033	OP889237	OP896205	FLREC
<i>Melanoliarius chuliotus</i>	Florida, U.S.A.	OM264287	OM258689	OM262391	FLREC
<i>Melanoliarius kindli</i>	Trinidad	OP871034	OP889234	OP896206	FLREC
<i>Melanoliaurs maidis</i>	Grenada	OP871035	OP889235	OP896207	FLREC
<i>Melanoliarius placitus</i>	Delaware, U.S.A.	OP871036	OP889236	OP896208	FLREC

## Systematics

### Family Cixiidae Spinola, 1839

#### Subfamily Cixiinae Spinola, 1839

#### Tribe Pentastrini Emeljanov, 1971

## Genus *Melanoliarius* Fennah, 1945a

Type species: *Melanoliarius maidis* Stål, 1862: 306.

**Amended description** (modified after Mead & Kramer 1982). Small to medium planthoppers (~3–8 mm in total length) generally dark (brown to black) in coloration. Head narrower than prothorax, angularly emarginate posteriorly, truncate or weakly concave anteriorly. Vertex concave, weakly projecting in front of eyes, length at midline usually longer than width at posterior margin and a little less than length of eyes in dorsal view; with or without a median carina extending forward from the base; lateral carinae diverging posteriorly; sublateral carina usually joined subapically just before a frontal transverse carina at apex; the sublateral and frontal carinae usually joined (sometimes feebly) by two longitudinal carinae, the four carinae thus forming two lateral foveae and a small central quadrate compartment or pit (Mead & Kramer 1982, fig. 7). Face (frontal view) with the frons and clypeus together broadest at about the midlength of face, together broadly elliptical; frontoclypeal suture arched dorsally (angular in *Melanoliarius* s.s., but quadrate in others), median carina (usually conspicuous but may be obscure) extending from apex of anteclypeus to dorsum of frons where a fork occurs, creating a small areolet between the transverse carina and the arms of the fork of the median carina. Median ocellus present at juncture of frons and postclypeus, lateral ocelli below anterior margin of eyes. Antennae short, scale ring-like, pedicel ovoid bearing many sensory plaques, flagellum long, bristle-like with bulbous base. Rostrum varies in length from definitely not attaining caudal margin of posterior trochanters to surpassing trochanters by length of terminal segment.

Thorax with pronotum short (and tricarinate, lateral carinae curving laterally to follow profile of eye becoming obsolete or continuing onto paradiscal region); transverse carinae on lateral margin of pronotum near tegulae; posteriorly deeply and angularly emarginate in median area, curving laterally; anterior margin truncate. Mesonotum with five carinae (intermediate pair sometimes weak), tegulae conspicuous. Tegmina at rest longer than the abdomen, weakly spatulate (leading and trailing margins weakly diverging, approximately straight to claval apex), broadly rounded at the apex, veins ScP + R branching from MP at apex of basal cell, fork of MP<sub>1+2</sub> well proximad of fork of MP<sub>3+4</sub>; veins setose (lacking conspicuous setae on membrane), usually with 10 to 12 apical cells (between proximal fork of RA and icu) and 5 or 6 anteapical cells (viz. C1–C5, with or without C3a). Hind tibiae with 2–3 (usually 3) lateral spines, apical spinulation usually 6-7-7 with the spinules of the tarsomeres fine and uniform; apical spinulation of hind tibiae with row of five spines followed by a gap then the sixth spine (in *Melanoliarius* s.s.), without diastema, or 3+3, platellae (e.g., Löcker *et al.* 2006, fig. 1, Löcker 2020, fig. 7E) usually absent.

Male terminalia with broad pygofer, varied in shape, often irregularly triangular, broadest ventrally; lateral margins of pygofer opening often produced in various ways, medioventral lobe of pygofer present, greatly varied in shape; pygofer sometimes bilaterally asymmetrical. Aedeagal complex with phallobase well developed and greatly varied, usually bearing several processes, phallobase articulated dorsally with the pygofer, with weak, membranous attachment to anal tube (anal segment attached and articulated with dorsal bridge of pygofer); aedeagus conspicuous within phallobase, bearing apical endophallus (= flagellum of Mead & Kramer 1982), often having several processes, endophallus directed variously left (in ventral view). Gonostyli often asymmetrical, independently movable, usually irregularly spatulate, often broadly expanded distally, and bearing a thumb-like median process. Anal tube varied, narrow and flaplike to broad and hoodlike, often (from dorsal view) broadly oval and slightly asymmetrical, from lateral view, appearing elongate triangular, distally expanded; *Melanoliarius* s.s. with anal tube bearing single, asymmetrical apicoventral process (absent elsewhere).

**Diagnosis.** Members of the Pentastrini can generally be separated from other New World tribes by bearing 5 carinae on the mesonotum, the posterior margin of the vertex angularly incised, and hind tibiae with 2–3 lateral teeth. The genera of Pentastrini in the New World remain incompletely elucidated, especially since the reallocation of species formerly placed in a cosmopolitan *Oliarius* into a more broadly construed *Melanoliarius*, and the subsequent partitioning out of a few species into *Reptalus* and *Pentastiridius* (Emeljanov 1978, 2001, Holzinger *et al.* 2002). In the New World *Pentastiridius* (with 2 species in eastern North America) may be diagnosed by the presence of more than 10 apical teeth of the first and second hind tarsomeres (7 in *Melanoliarius*). *Oliaronus* (1 species, southwestern US) has the middle region of the forewing costa thickened and setaceous (Kramer 1983) but also bears about 15 apical cells in the forewing (vs 10–12 in *Melanoliarius*). *Cyclopoliarus* species (8 taxa, Caribbean and Neotropical) are large (generally 7 mm or larger), with a long rostrum (“subapical joint attaining hind trochanters”, Fennah 1945a: 135), and the anal tube is asymmetrical bearing a short terminal projection (Fennah 1945a, plate XI, fig.

24). *Nivcentia* species (4 species, Caribbean), are medium-sized (less than 6 mm) and were contrasted against *Melanoliarius* s.s. by Fennah (1945a: 135, as *Vincentia* Uhler, 1895), as lacking the “deflexed median point” of the anal tube and having the “apex of rostrum surpassing hind trochanters” (vs. “scarcely attaining hind trochanters” in *Melanoliarius* s.s.), but these features are inadequate to diagnose *Nivcentia* against *Melanoliarius* s.l., without also taking geography into account. *Reptalus* (3 new world species in the subgenus *Pererepa* Emeljanov, 2020, mostly in the pacific region of the US and Canada) has never been directly contrasted with *Melanoliarius*. Concerning *Nivcentia* and *Reptalus*, we feel that they are likely valid genera, but *Melanoliarius* s.l. as currently comprised is too broadly construed and needs review to construct smaller, diagnosable clades.

***Melanoliarius (Melanoliarius) castro* Bahder & Bartlett sp. n.**

(Figures 2–6)

**Type locality.** Felicity, Chaguanas, Trinidad.

**Diagnosis.** Moderate-sized (~5 mm) species, ventral apex of male anal tube narrowed into elongate ventral spine (i.e. *Melanoliarius* s.s.). Aedeagal complex short and robust, without corkscrew-shaped process (viz. *M. acicus*), in ventral view, bearing ventrally directed process (Fig. 7B, A1) at the end of the aedeagus and 2 processes at the end of the endophallus, a short ventrally directed process and a more elongate dorsal process (Fig. 7B, A2 & A3).



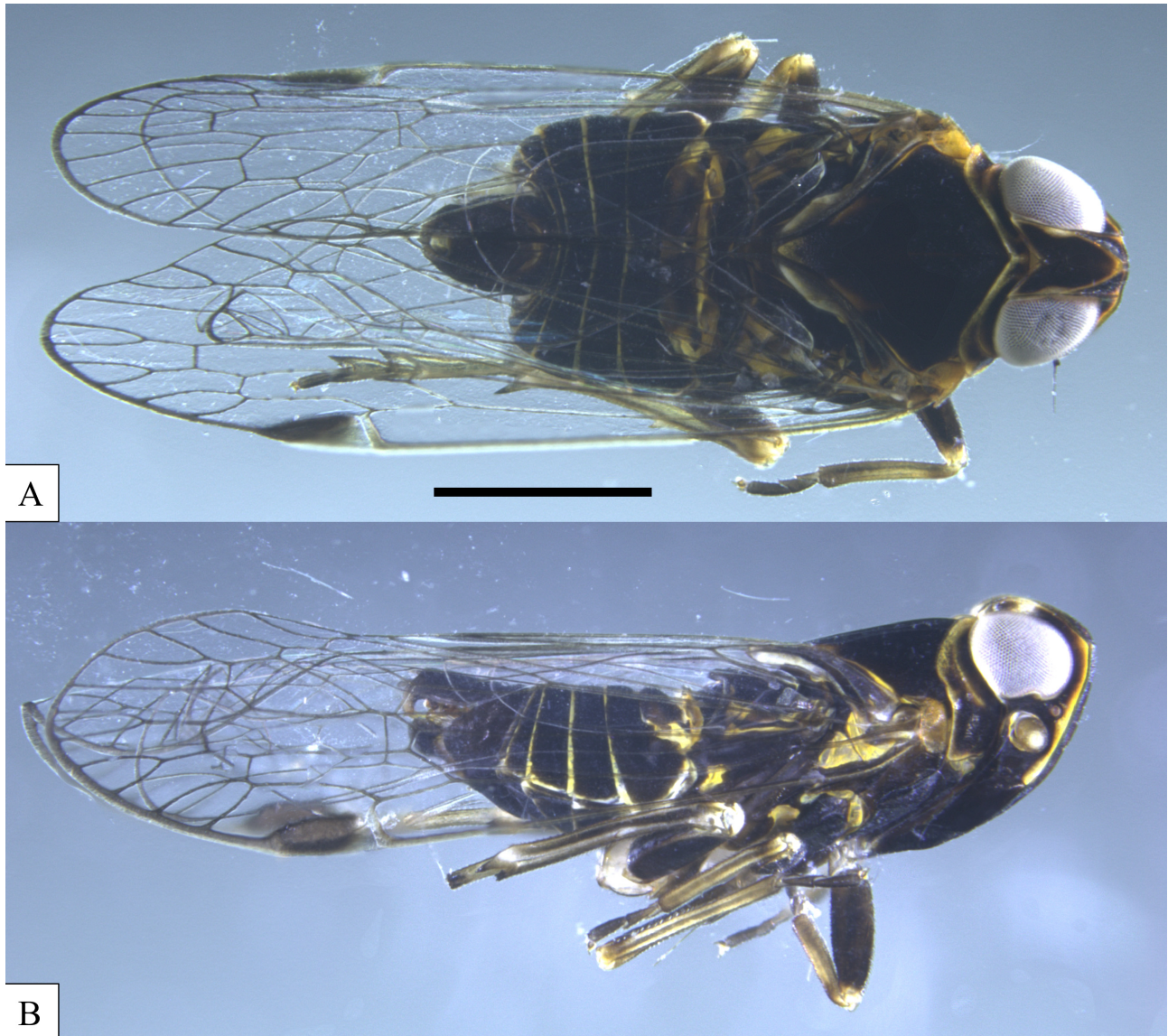
**FIGURE 2.** *In vivo* adult *Melanoliarius castro* sp. n. on coconut palm.

**Description.** *Color.* General body color black. Carinae and margins of head and thorax golden yellow, posterior margins of abdominal tergites golden yellow, legs fuscous, darker basally, wings transparent, veins fuscous.

*Structure.* Body weakly compressed, length (including wings, Table 3), males: 4.61–4.64 mm ( $n = 8$ ), females 4.83–4.91 mm ( $n = 8$ ).

*Head.* Head (dorsal view) narrower than pronotum (Fig. 4A), weakly projected in front of eyes; anterior margin concave, posterior margin angularly incised. Vertex strongly concave (Fig. 4C), lateral carinae subparallel (weakly expanded posteriorly), median carina present posteriorly, obsolete anteriorly; sublateral carinae arched to join subapically on vertex before distinct apical transverse carinae at fastigium (forming a pair of broadly triangular fovea on vertex between lateral, sublateral and apical transverse carinae), sublateral carina jointed to apical transverse carina by two longitudinal carinae forming an elongate median quadrangular compartment (approximately 3X longer than wide, Fig. 4A, 4C). In frontal view, vertex strongly concave (Fig. 4C), frons and clypeus collectively ovate in shape, frons narrowest dorsally, expanding about to level of median ocellus, then constricting ventrally (Fig. 4C); median carinae distinct from postclypeus to fastigium, forked just before transverse carina at fastigium with areolet appearing contiguous with quadrangular median compartment of vertex. Frontoclypeal suture angulately incised

into frons. In lateral view (Fig. 4B), generally rounded, vertex declining to slightly angulate fastigium, face weakly convex. Median ocellus present just above apex of frontoclypeal suture, lateral ocelli distinct below anterior margin of eye (Figs. 4B, 4C). Eyes elongate oval with small ventral emargination above antennae. Antennae short, scape ringlike, pedicel cylindrical, about as tall as wide, bearing numerous sensory plaques.

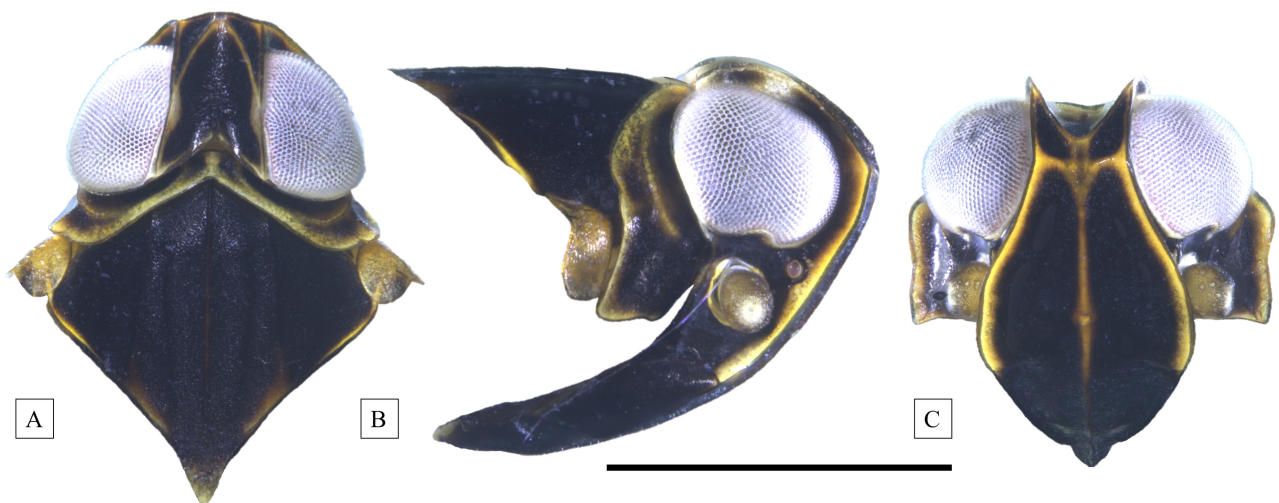


**FIGURE 3.** *Habitus* adult male *Melanoliarus castro* sp. n. in dorsal view (A) and lateral view (B).

Thorax. Pronotum in dorsal view very short (Fig. 4A), anterior margin convex, posterior margin broadly angulately incised, tricarinate, lateral carinae arched laterally following contour of eyes onto paradiscal region, becoming obsolete at ventral margin of eye (in lateral view, fig. 4B); pronotum (lateral view) with weakly diagonal carinae on lateral margins from level of tegula toward eye (Figs. 4A, B); paradiscal region (Fig. 4B) reaching below tegulae, distal margin broad, weakly concave. Mesonotum approximately as wide as long (longer than vertex and pronotum combined at midline), bearing five carinae present, median carina reaching posterior margin, lateral carinae straight, diverging posteriorly, intermediate carinae sinuate (Fig. 4A). Forewing weakly spatulate (Fig. 5), leading and trailing margin subparallel to apex of clavus, slightly expanded distally; fork of MP from SCP+R at apex of basal cell; claval apex near wing midlength, composite vein Pcu+A1 reaching wing margin well before claval apex; fork of CuA (forming C5 cell) well proximad of fork ScP+RA from RP (forming C1 cell); 5 subapical cells (i.e., cells C1–C5, cell C3a absent), 11 apical cells between RA<sub>1</sub> and icu; branching sequence MA 2-branched, MP 3-branched; MP 4-branched, CuA 2-branched.

**TABLE 3.** Biometric data for *Melanoliarus castro* sp. n. (in mm).

Character	Male		Female	
	Range	Average ± SE	Range	Average±SE
Body length, with wings	4.61–4.64	4.62±0.1	4.83–4.91	4.88±0.3
Body length, no wings	3.39–3.42	3.4±0.1	3.72–3.76	3.74±0.2
Forewing length	3.80–3.81	3.80±0.1	4.01–4.03	4.02±0.1
Vertex length	0.37–0.37	0.37±0.0	0.39–0.39	0.39±0.0
Vertex width, basal margin	0.39–0.39	0.39±0.0	0.40–0.40	0.40±0.0
Vertex width, distal margin	0.20–0.20	0.20±0.0	0.21–0.21	0.21±0.0
Pronotum length, midline	0.08–0.08	0.08±0.0	0.08–0.08	0.08±0.0
Mesonotum length, midline	1.03–1.03	1.03±0.0	1.04–1.04	1.04±0.0
Mesonotum width	1.01–1.01	1.01±0.0	1.01–1.01	1.01±0.0
Frons width, dorsal margin	0.24–0.24	0.24±0.0	0.25–0.25	0.25±0.0
Frons width, clypeal suture	0.55–0.55	0.55±0.0	0.55–0.55	0.55±0.0
Frons width, widest	0.63–0.63	0.63±0.0	0.63–0.63	0.63±0.0
Frons width, narrowest	0.24–0.24	0.24±0.0	0.25–0.25	0.25±0.0
Frons length, midline	0.43–0.43	0.43±0.0	0.43–0.43	0.43±0.0
Clypeus length	0.67–0.67	0.67±0.0	0.68–0.68	0.68±0.0

**FIGURE 4.** Adult male *Melanoliarus castro* sp. n. head, prothorax, and mesonotum in dorsal view (A), lateral view (B), and head and prothorax in frontal view (C).

**Terminalia.** Pygofer in lateral view broad and irregular in shape, anterior and posterior margins irregularly sinuate, narrowest dorsally, expanding widest point near midlength, constricting ventrally (Fig. 6A); lateral margins of pygofer opening bearing broad apical truncate lobes; in ventral view, medioventral process of pygofer taller than wide at base, with subtriangular apex and parallel lateral margins; medioventral process greatly exceeded by lateral projections of pygofer (Fig. 6C). Gonostyli in lateral view with apex strongly upcurved distally, apex subquadrate with slight median concavity, ventral margin strongly sinuate, forming distinct node basally (Fig. 6B), inner median margin bearing sclerotized spine (G1) (Fig. 6B); gonostyli in ventral view with lateral margins irregularly sinuate, strongly curving laterad at apex (Fig. 6B). Aedeagal complex short and stout with sclerotized aedeagus entirely subsumed within membranous phallosome (Fig. 7), with short, stout apical endophallus (angled left in ventral view, Fig. 7B), aedeagal complex bearing various processes indicated as A1–A7 for simplicity; process A1 arising dorsally at aedeagal complex apex on right side (ventral view, Fig. 7B), angled cephalad, curving ventrad, A2 and A3 arising at apex of endophallus (Fig. 7A on right, Fig. 7B on left), A2 on left lateral side, curving dorsad, A3 arising at same location as A2, strongly sinuate, apex angled ventrad; A4 arising on ventral surface, angled ventrad;



processes A5–A7 are short processes from base of endophallus (as noted by Mead & Kramer 1982: 395), A5 arising on ventral margin, angled caudad, A6 and A7 arising on left lateral and right lateral margins, respectively, angled laterad. Anal tube in dorsal view (fig 6D) ovoid (weakly bilaterally asymmetrical), in lateral view with apex narrowed into elongate ventral spine (Fig. 6A, B); paraproct tubular, just exceeding apex of anal tube.

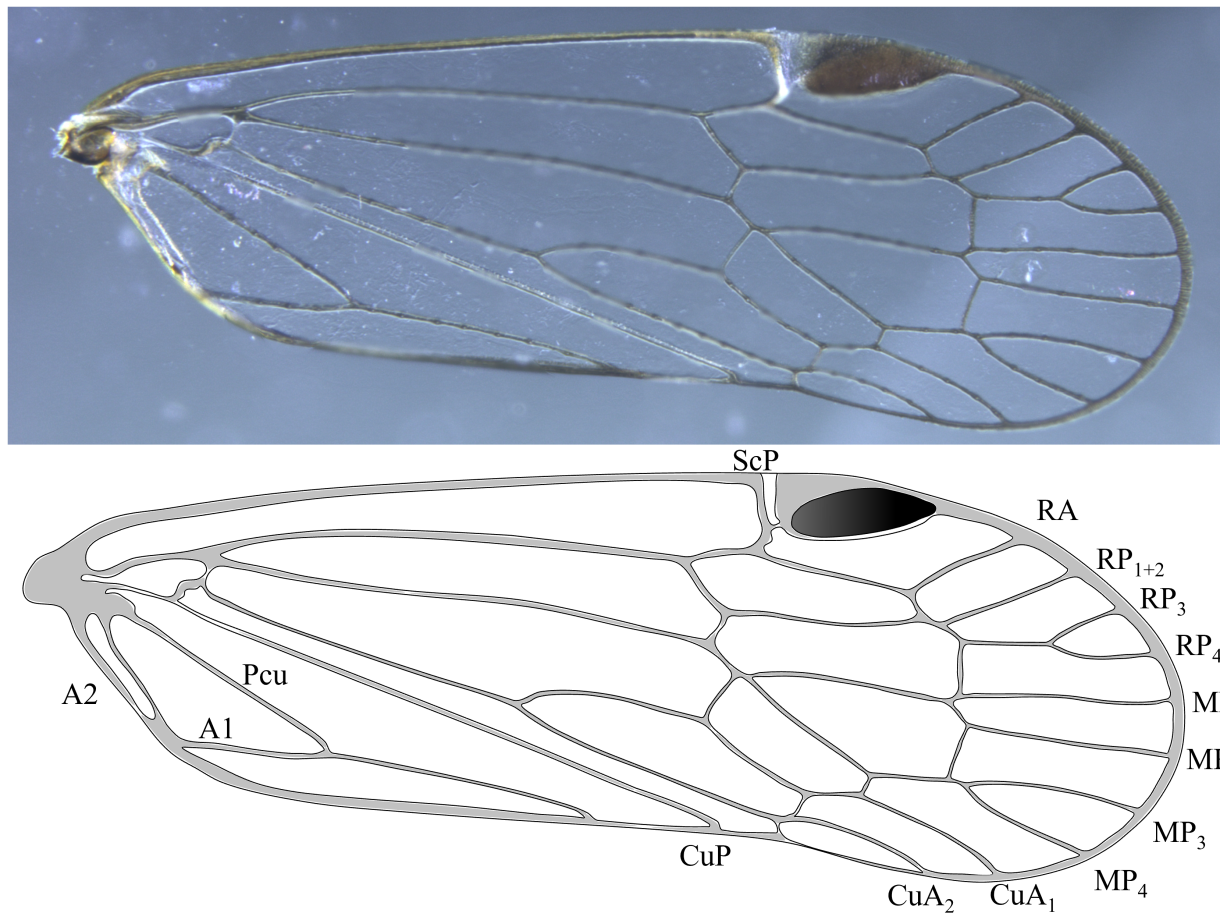


FIGURE 5. Adult male *Melanoliarus castro* sp. n. forewing.

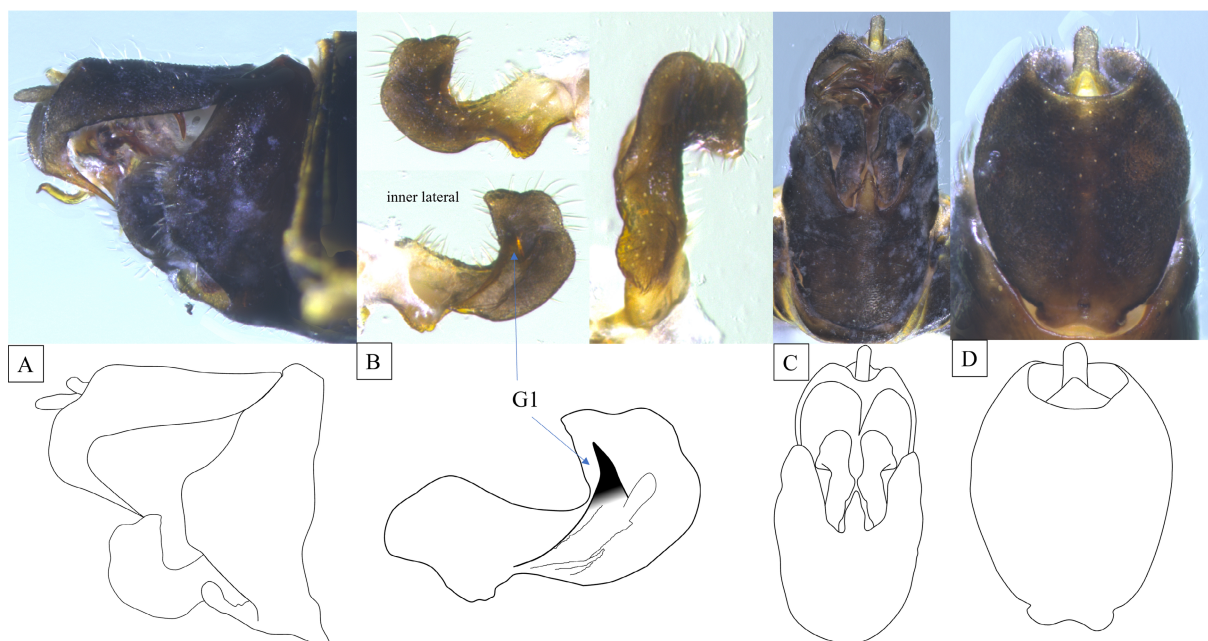
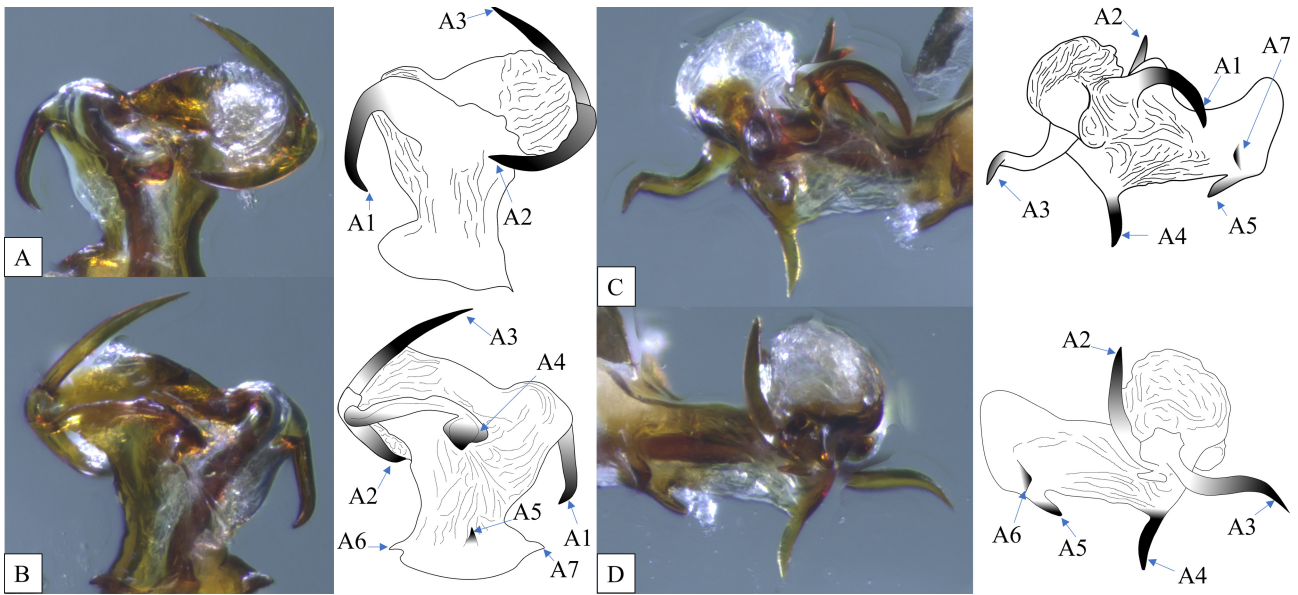
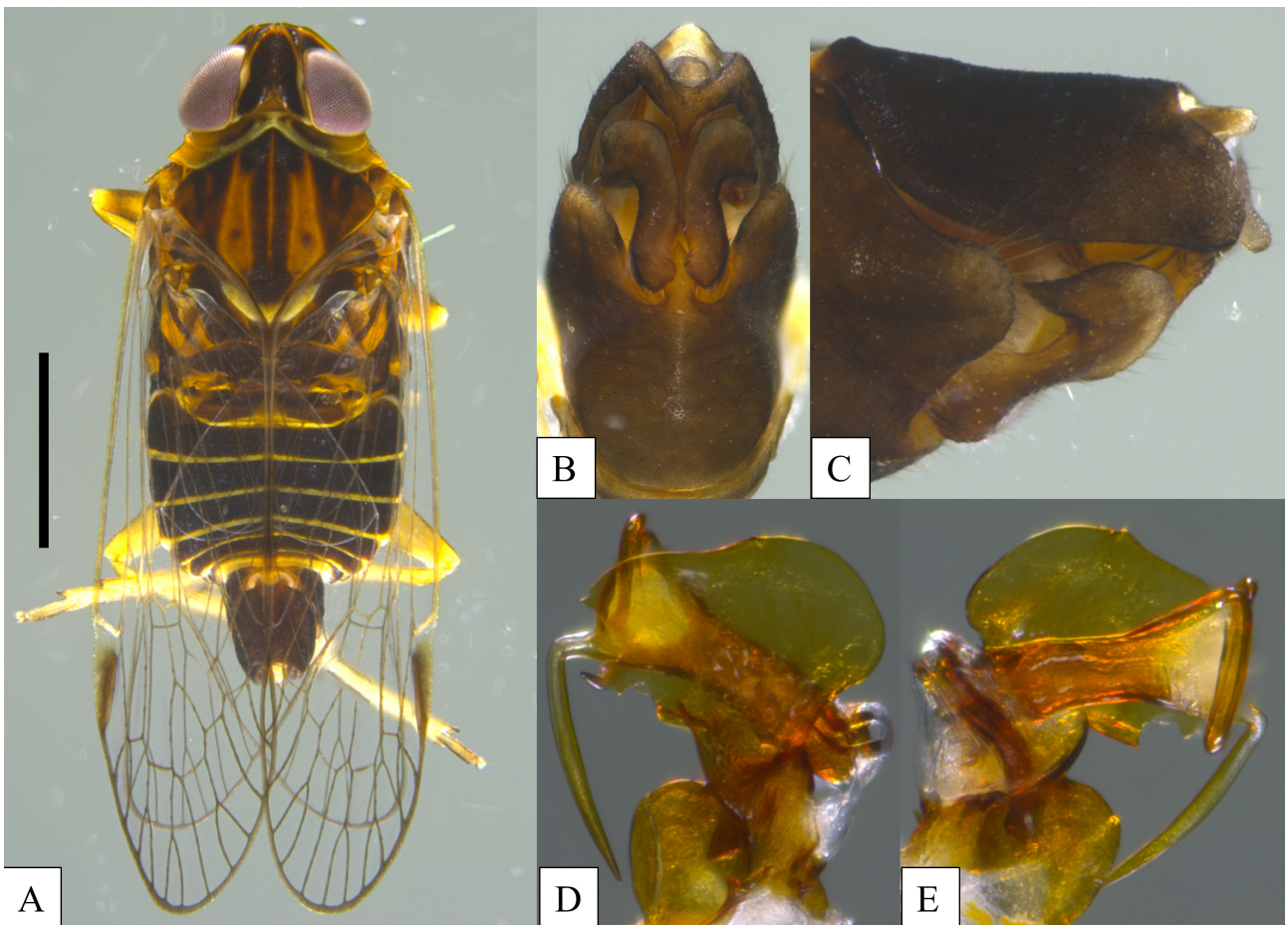


FIGURE 6. Adult male *Melanoliarus castro* sp. n. genitalia; (A) right lateral view. (B) gonostylus (line art from inner lateral view), (C) ventral view, and (D) anal tube, dorsal view.



**FIGURE 7.** *Melanoliarius castro* sp. n. aedeagal complex (aedeagus and phallobase); (A) dorsal view, (B) ventral view (C) right lateral view, and (D) left lateral view.



**FIGURE 8.** Adult male *Melanoliarius maidis*; (A) habitus dorsal view, (B) genitalia ventral view, (C) genitalia left lateral view, (D) aedeagus dorsal view, and (E) aedeagus ventral view.

**Plant associations.** Coconut palm (*Cocos nucifera*), undetermined grasses (Poaceae), and undetermined sedges (Cyperaceae).

**Distribution.** Felicity, Chaguanas Municipality and Sangre Grande Region, Trinidad.

**Etymology.** The specific name is in honor of Mr. William Castro, who helped coordinate the expedition to Trinidad.

**Material examined.** Holotype male “Felicity, Chaguanas Munic. / Trinidad and Tobago / 13.V.2018 / Coll.: B.W. Bahder // Holotype / *Melanoliarius castro* ♂” (FLREC); Paratypes 1 male, 2 females, same data as holotype (FSCA).

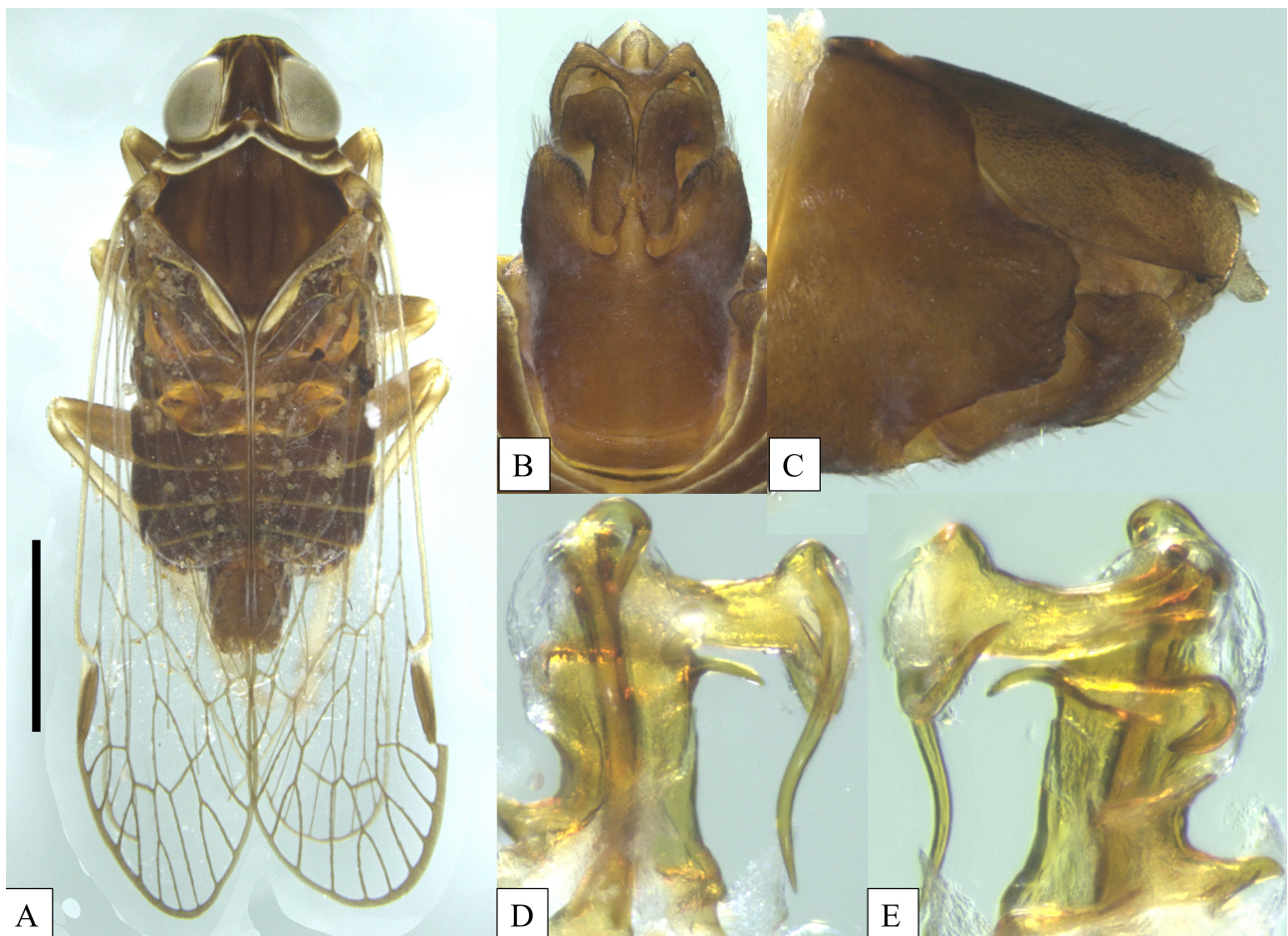
**Other material examined.**

*Melanoliarius (Melanoliarius) maidis*. St Lucia, East Wind Inn, 4 mi. N. Castries, 5 Aug. 1986, C.W. & L.B. O’Brien (1 female, UDCC); same except 7 Aug. 1986 (1 male, UDCC). *Other material examined.* Grenada (unknown location).

*Melanoliarius (Melanoliarius) complectus*. Lectotype “Pt. Au Pr. / Hayti feb // TYPE // Allotype / O. / Complectus / E. D. Ball [red paper] // Cotype No / USNM / Oliarius complectus / Ball / Det. F. W. Mead 1982 // ‘Allotype’ / Allolectotype / Oliarius / complectus / Ball // UDCC\_TCN 00101648 [2D barcode label]” (type designation by Mead & Kramer 1982: 487). *Other material examined.* Puerto Rico, Cerro Maravillas, Villalba, 3 Nov. 1952, J. A. Ramos (1 male, NCSU); Vieques Island, 23 Oct. 1947, J.S. Caldwell (1 male, USNM); Haiti, Ouest Dept., Kenscoff, 23 June 1938, J. A. Ramos (1 male, NCSU).

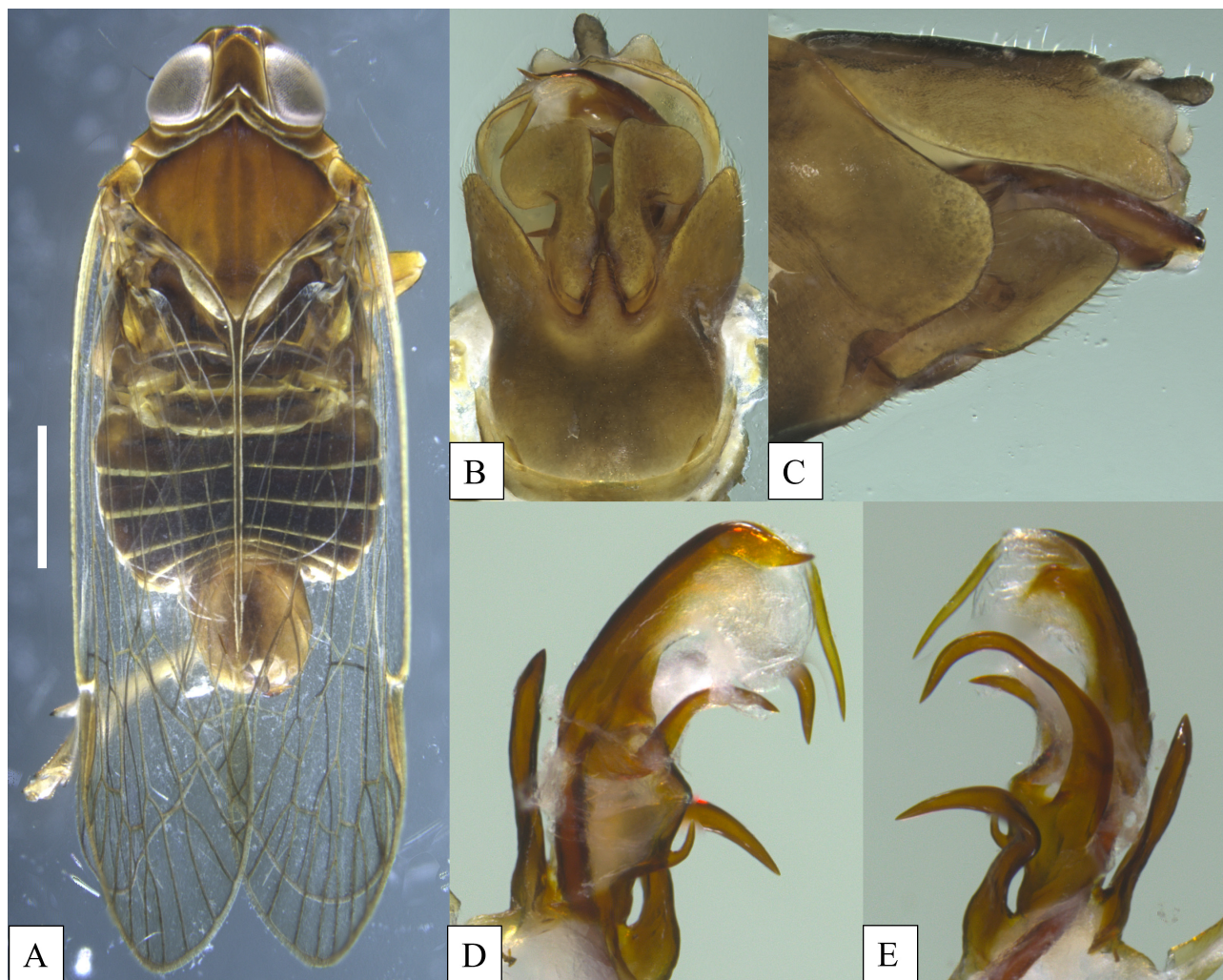
*Melanoliarius (Melanoliarius) complectus*. USA, Texas, Hidalgo Co., Pharr Import Lot near bridge, (25.ix)–(5.x).2016, J.M. Leavengood jr., D. McCoy, A. Cisneros & A. Garza (Malaise, 1 male, UDCC); same except (31.viii)–(6.ix)-2016, J.M. Leavengood jr., D. McCoy & A. Garza (Malaise, 1 male, 1 female; UDCC). *Other material examined.* Jamaica, Portland Parish, Spring Garden field site, 4-X-2019, B.W.Bahder (sweeping grasses, 7 males, 9 females, FLREC).

*Melanoliarius kindli*. Trinidad, Sangre Grande, Nariva, 2-VI-2022, B.W.Bahder (sweeping grasses, 3 males, 6 females, FLREC).



**FIGURE 9.** Adult male *Melanoliarius complectus*; (A) habitus dorsal view, (B) genitalia ventral view, (C) genitalia left lateral view, (D) aedeagus dorsal view, and (E) aedeagus ventral view.

**Sequence Data.** For *Melanoliarius castro* sp. n., a 584 bp product was generated for the five prime (barcode) region of COI, a 1,607 bp product was generated for the 18S gene, and a 334 bp product for the H3 gene). For *M. kindli* (Fig. 10), a 624 bp product for COI was generated, a 1,624 bp for 18S was generated, and a 344 bp product for H3 was generated. Finally, for *M. maidis*, a 584 bp product was generated for COI, a 1,620 bp product was generated for 18S and a 334 bp product was generated for H3. Based on the 18S gene, there is strong bootstrap support (100) for *Melanoliarius* as a monophyletic clade and strong bootstrap support (90) for *M. castro* sp. n. resolving adjacent to *M. maidis* (Fig. 10A). While *M. castro* sp. n. resolves adjacent to other species of *Melanoliarius* based on COI (Fig. 10B), the bootstrap support is low (39); however, the tree based on H3 show strong bootstrap support for *Melanoliarius* (91) and also shows strong bootstrap support for the placement of the *M. castro* sp. n. adjacent to *M. kindli* (84) (Fig. 10C). The consensus tree based on COI, 18S, and H3 also showed strong bootstrap support (81) for placement of *M. castro* sp. n. adjacent to *M. maidis*, and very strong support (99) for the monophyly of *Melanoliarius* based on the species analyzed.



**FIGURE 10.** Adult male *Melanoliarius kindli*; (A) habitus dorsal view, (B) genitalia ventral view, (C) genitalia right lateral view, (D) aedeagus dorsal view, and (E) aedeagus ventral view.

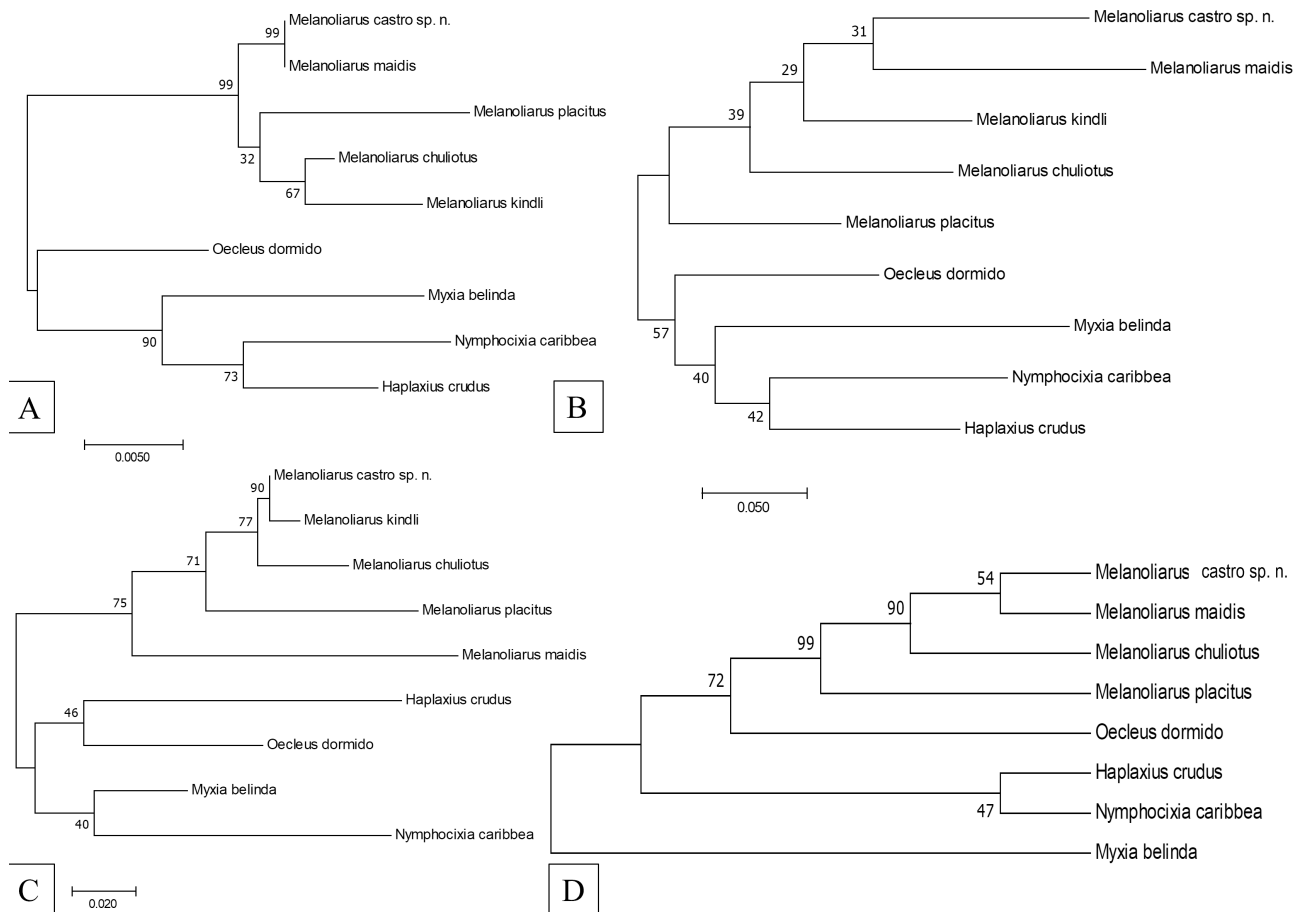
The multiple pairwise comparisons based on the 18S gene showed *Melanoliarius castro* sp. n. differed on average by 0.4% ( $\pm 0.2$ ) from the other members of *Melanoliarius* analyzed and 2.3% ( $\pm 0.1$ ) different from members of other genera (Table 4). For the region sequenced, *M. castro* sp. n. was identical (100% nucleotide identity) to *M. maidis*. The multiple pairwise comparisons based on the COI gene showed that *Melanoliarius castro* sp. n. differed on average by 18.2% ( $\pm 0.5$ ) from other members of *Melanoliarius* and 20.6% different ( $\pm 0.6$ ) from other genera analyzed (Table 5). Based on the region analyzed, *M. castro* sp. n. was most similar to *M. kindli*, differing by 17.1%, whereas it differed by 19.3% to *M. maidis* (Table 5).

**TABLE 4.** Pairwise comparison based on the 18S 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	14
1 Melanoliarus_castro_sp._n.		0.0000	0.0021	0.0012	0.0023	0.0038	0.0035	0.0036	0.0040	0.0040	0.0038	0.0043	0.0040	0.0040
2 Melanoliarus_maidis	0.0000		0.0021	0.0012	0.0023	0.0038	0.0035	0.0036	0.0040	0.0040	0.0038	0.0043	0.0040	0.0040
3 Melanoliarus_kindli	0.0067	0.0067		0.0023	0.0031	0.0043	0.0041	0.0042	0.0043	0.0043	0.0043	0.0044	0.0042	0.0041
4 Melanoliarus_chuliotus	0.0022	0.0022	0.0075		0.0026	0.0037	0.0034	0.0035	0.0041	0.0041	0.0037	0.0042	0.0041	0.0041
5 Melanoliarus_placitus	0.0075	0.0075	0.0142	0.0097		0.0044	0.0043	0.0044	0.0044	0.0044	0.0041	0.0047	0.0045	0.0045
6 Oecleus_mackaspringi	0.0194	0.0194	0.0246	0.0179	0.0269		0.0017	0.0019	0.0043	0.0042	0.0040	0.0041	0.0040	0.0039
7 Oecleus_dormido	0.0172	0.0172	0.0224	0.0157	0.0246	0.0045		0.0010	0.0041	0.0042	0.0040	0.0042	0.0040	0.0040
8 Oecleus_borealis	0.0187	0.0187	0.0239	0.0172	0.0261	0.0060	0.0015		0.0042	0.0043	0.0040	0.0043	0.0041	0.0041
9 Myxia_hernandezi	0.0232	0.0232	0.0254	0.0232	0.0284	0.0239	0.0224	0.0239		0.0008	0.0025	0.0040	0.0037	0.0037
10 Myxia_delta	0.0232	0.0232	0.0254	0.0232	0.0284	0.0232	0.0232	0.0246	0.0007		0.0025	0.0039	0.0036	0.0035
11 Myxia_belinda	0.0232	0.0232	0.0254	0.0217	0.0276	0.0232	0.0224	0.0239	0.0082	0.0082		0.0040	0.0039	0.0039
12 Haplaxius_skarpion	0.0291	0.0291	0.0329	0.0276	0.0351	0.0239	0.0254	0.0269	0.0232	0.0224	0.0261		0.0019	0.0021
13 Haplaxius_pocococo	0.0254	0.0254	0.0291	0.0254	0.0306	0.0217	0.0232	0.0246	0.0209	0.0202	0.0239	0.0052		0.0007
14 Haplaxius_dougwalshi	0.0246	0.0246	0.0284	0.0246	0.0299	0.0209	0.0224	0.0239	0.0202	0.0194	0.0232	0.0060	0.0007	

**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	14
1 Melanoliarus_castro_sp_n.		0.016	0.015	0.016	0.016	0.017	0.016	0.015	0.017	0.016	0.016	0.016	0.017	0.016
2 Melanoliarus_maidis	0.193		0.016	0.016	0.016	0.016	0.016	0.016	0.017	0.016	0.017	0.015	0.017	0.016
3 Melanoliarus_kindli	0.171	0.180		0.015	0.015	0.015	0.015	0.015	0.016	0.016	0.016	0.016	0.015	0.016
4 Melanoliarus_placitus	0.180	0.203	0.154		0.015	0.015	0.016	0.015	0.017	0.015	0.016	0.015	0.016	0.017
5 Melanoliarus_chuliotus	0.182	0.217	0.165	0.171		0.015	0.017	0.017	0.016	0.015	0.016	0.016	0.016	0.018
6 Haplaxius_crudus	0.221	0.201	0.191	0.173	0.197		0.014	0.014	0.016	0.016	0.016	0.015	0.016	0.016
7 Haplaxius_dougwalshi	0.191	0.201	0.178	0.184	0.199	0.125		0.012	0.016	0.016	0.017	0.015	0.016	0.016
8 Haplaxius_pocococo	0.193	0.206	0.190	0.167	0.210	0.139	0.091		0.016	0.016	0.017	0.015	0.015	0.015
9 Myxia_belinda	0.243	0.238	0.203	0.216	0.217	0.206	0.197	0.193		0.016	0.016	0.017	0.017	0.016
10 Myxia_delta	0.216	0.214	0.195	0.169	0.197	0.190	0.191	0.188	0.191		0.013	0.015	0.016	0.016
11 Myxia_hernandezi	0.204	0.216	0.191	0.186	0.217	0.188	0.193	0.188	0.182	0.119		0.017	0.016	0.016
12 Oecleus_dormido	0.191	0.184	0.193	0.162	0.190	0.171	0.175	0.162	0.206	0.173	0.186		0.015	0.014
113 Oecleus_mackaspringi	0.191	0.197	0.169	0.173	0.182	0.182	0.164	0.167	0.197	0.186	0.171	0.141		0.015
14 Oecleus_borealis	0.199	0.201	0.190	0.191	0.221	0.190	0.169	0.167	0.204	0.203	0.203	0.149	0.160	



**FIGURE 11.** Maximum likelihood phylogenetic tree based on 1,000 replicates: A) 18S rRNA gene, B) COI gene, C) H3 gene and D) consensus tree of concatenated COI, 18S, and H3 sequences; scale bar = percent nucleotide difference.

**Remarks.** *Melanoliarius castro sp. n.* is a new species of *Melanoliarius* in the strict sense. The new species would key into couplet 31 in Mead & Kramer, 1982, but it differs from both *M. complectus* and *M. viequensis* in details of aedeagal structure. Like other *Melanoliarius s.s.*, the aedeagus from ventral view has a left-directed endophallus, but it is much shorter than either of these species and lacks the elongate ventrally-directed process. This placement is supported by strong molecular support observed in the consensus tree. The fact that the region for 18S analyzed is identical between *M. castro sp. n.* and *M. maidis* is interesting, especially because the level of variability between these species for COI is normal species-level differences, and among the taxa analyzed for *Melanoliarius*, is the most different. In other genera, closely related (perhaps sister taxa) species display significantly reduced levels of variation for 18S. For example, the difference between *Haplaxius pocococo* Bahder & Bartlett and *H. dougwalshi* Bahder & Bartlett is 0.07% and the difference between *Myxia delta* (Kramer) and *Myxia hernandezi* Bahder & Bartlett is also 0.07% (Echavarría *et al.* 2022). While having the specimen of *M. castro sp. n.* match *M. maidis* for 18S was unexpected, the normal levels of variability for COI and the distinct differences in the genitalia establish *M. castro sp. n.* as a distinct species from *M. maidis*. However, the identity of the 18S region analyzed also indicates that these two species are very closely related.

## Discussion

The genus *Melanoliarius s.l.* requires review, with reference to the other genera of New World Pentastirini, to define smaller, diagnosable clades. *Melanoliarius s.s.* appears diagnosable on morphological grounds, including placement of *M. castro sp. n.* sister to *M. maidis* based on combined data from COI, 18S, and H3 data. Mead & Kramer (1982) discussed ‘species-groups’ for species north of Mexico—but see also groups in Fennah (1967) for Galapagos and Bourgoïn *et al.* (1998) for South American taxa—which may prove to be a good starting point for new generic concepts.

While the documentation of a new species of cixiid planthopper on palms in the Caribbean is not unique due to findings from recent survey efforts in the region, *Melanoliarus castro* sp. n. does represent the first taxon described that is not in the tribe Oecleini as it is currently comprised. Interestingly, this species appeared to fill a similar niche as *Haplaxius crudus*, in that adults were found on palm foliage near disturbed edge habitat. However, the full biology and life history of this species remain to be determined.

This species was found during a survey in Trinidad to scout for the presence of lethal yellowing (LY) in coconut palms as well as for the vector, *H. crudus*. While LY was not observed in the sites visited, *H. crudus* was found at two sites in north-central Trinidad. Despite finding *H. crudus*, only a total of five specimens were collected during this survey, indicating that the current population appears low. A larger survey effort over greater areas and multiple years is necessary to fully understand the population dynamics of *H. crudus*, and ultimately the risk of LY to the island, but preliminary survey observations showed the population appears low, and thus low risk of LY at the current time.

## Acknowledgements

We thank Bob Blinn, Lew Deitz (both retired, NCSU), Stuart McKamey (USNM) for loans of specimens of *Melanoliarus* s.s., including the type specimen of *M. complectus*. We thank Luz Bahder for translating the abstract into Spanish.

## References

- Bahder, B.W., Bartlett, C.R., Barrantes, E.A.B., Echavarría, 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>
- Ball, E.D. (1902) Some new North American Fulgoridae. *Canadian Entomologist*, 34, 147–157.  
<https://doi.org/10.4039/Ent34147-6>
- Ball, E.D. (1934) The genus *Oliarus* and its allies in North America (Homoptera: Fulgoridae). *Journal of the Washington Academy of Sciences*, 24, 268–276.
- Ball, E.D. (1937) Some New Fulgoridae from the Western United States. *Bulletin of the Brooklyn Entomological Society*, 32 (5), 171–183.
- 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.
- 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, September 7–11, 1987*. Consiglio Nazionale delle Ricerche, IPRA, Rome, pp. 113–120.
- Bourgoin, T., Wang, R.R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroinski, A., Yap, S. & Szwed, 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>
- Bourgoin, T., Wilson, M.R. & Couturier, G. (1998) Description of two new species of South American *Oliarus* Stål (Homoptera: Fulgoromorpha: Cixiidae), including a rice-associated species from Peru. *Proceedings of the Entomological Society of Washington*, 100 (1), 108–113.
- Caldwell, J.S. (1938) New Texan Fulgoridae (Homoptera). *Ohio Journal of Science*, 38, 304–306.
- Caldwell, J.S. (1947a) New species of *Oliarus* Stål from southwestern United States and Mexico (Homoptera: Cixiidae). *Pan-Pacific Entomologist*, 23 (4), 145–151.
- Caldwell, J.S. (1947b). New Fulgoroidea from North America (Homoptera). *Ohio Journal of Science*, 47, 76–78
- Caldwell, J.S. & Martorell, L.F. (1951 [dated 1950]) Review of the Auchenorrhynchos [sic] Homoptera of Puerto Rico. Part II. The Fulgoroidea except Kinnaridae. *Journal of Agriculture of the University of Puerto Rico*, 34 (2), 133–269.  
<https://doi.org/10.46429/jaupr.v34i2.12835>
- Campodonico, J.F. (2018) Nueva especie de *Melanoliarus* Fennah (Hemiptera Cixiidae) del extremo norte de Chile. *Revista Chilena de Entomología*, 44 (1), 23–28.



- Echavarría, M.A.Z., Barrantes, E.A.B., Bartlett, C.R., Helmick, E.E. & Bahder, B.W. (2021) 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>
- Echavarría, M.A.Z., Barrantes, E.A.B., Bartlett, C.R., Helmick, E.E., Kunz, G. & Bahder, B.W. (2022) A new species of planthopper in the genus *Haplaxius* from Osa Peninsula in Costa Rica (Hemiptera: Fulgoroidea: Cixiidae). *Zootaxa*, 5209 (2), 257–269.  
<https://doi.org/10.11646/zootaxa.5209.2.6>
- Emeljanov, A.F. (1971) New genera of leafhoppers of the families Cixiidae and Issidae (Homoptera, Auchenorrhyncha) in the USSR. *Entomologicheskoe Obozrenie*, 50, 619–627.
- Emeljanov, A.F. (1978) New genera and species of leafhoppers (Homoptera, Auchenorrhyncha) from the USSR and Mongolia. *Entomologicheskoe Obozrenie*, 57 (2), 316–332.
- Emeljanov, A.F. (2001) The generic position of some Nearctic Pentastirini (Homoptera: Fulgoroidea: Cixiidae). *Zoosystematica Rossica*, 9 (1), 122–122.
- Emeljanov, A.F. (2002) Contribution to classification and phylogeny of the family Cixiidae (Hemiptera, Fulgoromorpha). *Denisia*, 4, 103–112.
- Emeljanov, A.F. (2020) Nomenclatorial changes in the family Cixiidae (Homoptera, Auchenorrhyncha, Fulgoroidea), with fixation of type species of the genus *Reptalus* Emeljanov, 1971 and description of a new subgenus. *Zootaxa*, 4780 (1), 197–200.  
<https://doi.org/10.11646/zootaxa.4780.1.11>
- Fennah, R.G. (1945a) The Cixiini of the lesser Antilles (Homoptera: Fulgoroidea). *Proceedings of the Biological Society of Washington*, 58, 133–146.
- Fennah, R.G. (1945b) The Fulgoroidea, or lanternflies, of Trinidad and adjacent parts of South America. *Proceedings of the United States National Museum*, 95, 411–520.  
<https://doi.org/10.5479/si.00963801.95-3184.411>
- Fennah, R.G. (1967) Fulgoroidea from the Galápagos Archipelago. *Proceedings of the California Academy of Sciences*, 35, 53–102.
- 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.
- Holzinger, W.E. (2004) A new replacement name for *Vincentia* Uhler, 1895 (non Castelnau, 1872) (Insecta: Hemiptera: Cixiidae). *Revue Suisse de Zoologie*, 111 (4), 951–952.  
<https://doi.org/10.5962/bhl.part.80280>
- Holzinger, W.E., Emeljanov, A.F. & Kammerlander, I. (2002) The family Cixiidae Spinola, 1839 (Hemiptera: Fulgoromorpha)—a review. *Denisia*, 4, 113–138
- 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>
- Kirschbaum, C.L. (1868) Die Cicadinen der gegend von Wiesbaden und Frankfurt A. M. nebst einer anzahl neuer oder Schwer zu unterscheidender Arten aus anderen Gegenden Europa's Tabellarisch Beschrieben. *Jahrbücher des Vereins für Naturkunde im Herzogthum Nassau*, 21, 1–202.
- 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>
- Le Cesne, M., Bourgoin, T., Hoch, H., Yang, L. & Zhang, Y. (2022) *Coframalaxius bletteryi* gen. et sp. nov. from subterranean habitat in Southern France (Hemiptera, Fulgoromorpha, Cixiidae, Oecleini). *Subterranean Biology*, 43, 145–168.  
<https://doi.org/10.3897/subtbiol.43.85804>
- Löcker, B. (2020) Revision of *Leades* Jacobi with the description of a new genus, *Yamirrina* gen. nov., and notes on the absence of *Iolania* Kirkaldy from Australia (Hemiptera: Auchenorrhyncha: Fulgoromorpha: Cixiidae: Cixiini). *Journal of Insect Biodiversity*, 18 (1), 17–49.  
<https://doi.org/10.12976/jib/2020.18.1.2>
- Löcker, B., Fletcher, M.J., Larivière, M.C. & Gurr, G.M. (2006) The Australian Pentastirini (Hemiptera: Fulgoromorpha: Cixiidae). *Zootaxa*, 1290 (1), 1–138.  
<https://doi.org/10.11646/zootaxa.1290.1.1>
- Mead, F.W. & Kramer, J.P. (1982) Taxonomic study of the planthopper genus *Oliarus* in the United States (Homoptera:

- Fulgoroidea: Cixiidae). *Transactions of the American Entomological Society*, 107, 381–569.
- Metcalf, Z.P. (1936) *General Catalogue of the Homoptera. Fascicle IV Fulgoroidea. Part 2 Cixiidae*. Smith College, Northhampton, Massachusetts, 269 pp.
- Metcalf, Z.P. (1945) Fulgoroidea (Homoptera) of Kartabo, Bartica District, British Guiana. *Zoologica [Scientific contributions of the New York Zoological Society]*, 30 (3), 125–143.  
<https://doi.org/10.5962/p.210851>
- Spinola, M. (1839) Essai sur les Folgorelles, sous-tribu des Cicadaïres, 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.  
<https://doi.org/10.1002/mmnd.47918620303>
- Stål, C. (1866) Hemiptera Homoptera Latr. *Hemiptera Africana*, 4, 1–276.
- Szwedo, J. (2004) *Autrimpus sambiorum* gen. and sp. nov. from eocene baltic amber and notes on Mnemosynini stat. nov. (Hemiptera: Fulgoroidea: Cixiidae). *Annales Zoologici*, 54 (3), 567–578.
- Uhler, P.R. (1895) An enumeration of the Hemiptera-Homoptera of the Island of St. Vincent, W. I. *Proceedings of the Zoological Society of London*, 1895, 55–84.
- Van Duzee, E.P. (1907) Notes on Jamaican Hemiptera: A report on a collection of Hemiptera made on the Island of Jamaica in the spring of 1906. *Bulletin of the Buffalo Society of Natural Sciences*, 8 (5), 3–79.
- Van Duzee, E.P. (1912) Hemipterological gleanings. *Bulletin of the Buffalo Society of Natural Sciences*, 10, 477–512.
- 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.
- Van Stalle, J. (1987) A revision of the Neotropical species of the genus *Mnemosyne* Stål, 1866 (Homoptera, Cixiidae). *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique*, 57, 121–139.