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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

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Abstract

Myxia belinda **gen. et sp. nov.** is established for a new taxon of Cixiidae in the tribe Oecleini collected from palms in Costa Rica. The new taxon was discovered while surveying palms for potential phytoplasma vectors. Placement in a new genus is supported by a 1,383 bp sequence of 18S that differs by 2.77% from *Haplaxius*, 5.20% from *Myndus taffini*, and 2.80% from *Nymphomyndus caribbea*. Intrageneric variation for 18S was found to be approximately 0.5% to 0.6% within *Haplaxius*. Generic level differences within the Oecleini for COI ranged from 15% to 17% with the novel taxon differing by about 16% from other genera. The new genus is most similar in appearance to *Haplaxius* but possesses striking sexual dimorphism, and the aedeagus is only partially surrounded by the phallobase (versus entirely enveloped in *Haplaxius*). The discovery of a novel taxon of cixiid on palms that is similar to *Haplaxius* is important because of the role that *Haplaxius crudus* plays in phytoplasma transmission in palm agro- and natural ecosystems.

Key words: Fulgoromorpha, Cixiidae, Oecleini, *Haplaxius,* Palms

Resumen

La especie *Myxia belinda* **gen. et sp. nov.** se establece para un nuevo taxón de Cixiidae en la tribu Oecleini la cual fue colectada en palmeras en Costa Rica. El nuevo taxón fue descubierto durante un estudio en el que se buscan posibles vectores de fitoplasma en palmeras. La colocación de esta especie en un nuevo género está respaldado por un valor de 1.383 pb en la secuencia del 18S que difiere en un 2.77% de *Haplaxius*, 5.20% de *Myndus taffini* y 2.80% de *Nymphomyndus caribbea*. Se encontró que la variación intragenérica para 18S era de aproximadamente 0.5% a 0.6% en *Haplaxius*. Generic level differences within the Oecleini for COI ranged from 15% to 17% with the novel taxon differing by about 16% from other genera. El nuevo género es más similar en apariencia a *Haplaxius,* pero posee un notable dimorfismo sexual y el aedeagus está rodeado solamente de manera parcial por la falobase (en lugar de estar completamente envuelto como en el caso de *Haplaxius*). El descubrimiento de un nuevo taxón de Cixido en las palmeras, el cual es similar a *Haplaxius,* es importante debido al rol que desempeña *Haplaxius crudus* en la transmisión del fitoplasma en los ecosistemas agrícolas y naturales de las palmeras.

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Palabras clave: Fulgoromorpha, Cixiidae, Oecleini, *Haplaxius*, Palmeras

Introduction

The planthopper genus *Haplaxius* Fowler, 1904 (Cixiidae: Cixiinae: Oecleini), currently consists of 64 species with 34 species north of Mexico and 30 additional species in the Neotropics (Holzinger *et al*. 2002, Bartlett *et al*. 2014, Bourgoin 2019). The genus *Haplaxius* is currently defined as lacking preapical spines on the hind tibiae (a tribal feature), tegulae evident, median carina present on the frons, vertex lacking carina on midline and between anterior portion of the eyes, and longitudinal midlength of mesonotum about twice as long (or less) as the longitudinal midlength of the vertex (Bartlett *et al*. 2014).

Historically, *Haplaxius* had been subsumed under *Myndus* Stål 1862, by Kramer (1979), but was restored by Emeljanov (1989), a placement subsequently affirmed by Holzinger *et al*. (2002). Emeljanov (1989) distinguished the two genera by *Mydnus* possessing a denticle at the distal end of the fore coxae, lacking in *Haplaxius*, and by *Myndus* having a lateral pronotal carina that terminates in the middle of the lower lateral pronotal margin, where this carina in *Haplaxius* extends to lateral corner. Additionally, *Myndus* has an Old World distribution whereas *Haplaxius* is only found in the New World. The genus *Myndus* is currently comprised of 83 species (Bourgoin 2019), although Holzinger *et al*. (2002) indicated that many Old World *Myndus* may be better placed in *Colvanalia* Muir, 1925. Holzinger *et al*. (2002) did not elaborate and no subsequent work considered this point. Kramer (1979) stated that his treatment of New World *Myndus* (i.e., *Haplaxius*) was broad and highlighted distinct variations in the terminalia, especially the aedeagus and that there could be various genera erected from within *Haplaxius* to reflect these variations. Significantly, there has been very little quantitative phylogenetic investigations in the Cixiidae (viz. Ceotto & Bourgoin 2008, Ceotto *et al* 2008), and the monophyly of these genera has never been tested.

The genus *Paramyndus* Fennah, 1945 (type species *Paramyndus cocois* Fennah, 1945, a junior synonym of *Haplaxius crudus*) was synonymized with *Haplaxius* by Caldwell, 1946. *Paramyndus* has not been considered valid since (viz. Kramer 1979, Holzinger *et al*. 2002); however, *Paramyndus* might be restored as a valid genus should *Haplaxius* be broken into smaller genus-groups.

One species, *Haplaxius crudus*—an important vector of palm phytoplasmas (see below) –is present in both the United States and throughout the Caribbean, Mesoamerica, and into northern South America (Kramer 1979, Bartlett *et al*. 2014, Silva *et al*. 2019). *Haplaxius* is an economically important taxon because *H. crudus* is the putative vector of the lethal yellowing (LY) phytoplasma (16SrIV-A) (Howard & Thomas 1980, Howard *et al*. 1983) and is a candidate as a vector of lethal bronzing disease (LBD), caused by the 16SrIV-D phytoplasma (Halbert *et al*. 2014) discovered in Florida in 2006 (Harrison *et al*. 2008). *Haplaxius crudus* is likely the most abundant and widespread species in the genus. In the United States, it is documented in Florida (Howard 1980), Texas (Meyerdirk & Hart 1982) and recently Mississippi (Hill *et al*. 2018). In the Caribbean, it is reported from the Cayman Islands, Cuba, Dominican Republic, Jamaica, Puerto Rico, Trinidad and Tobago and also the Bahamas; from Mesoamerica it is known from Mexico, Belize, Honduras, Costa Rica, Panama; and from South America is reported from Colombia, Venezuela and recently Brazil (Kramer 1979, Bartlett *et al*. 2014, Silva *et al*. 2019). Currently, *H. crudus* is the only known cixiid to transmit palm-infecting phytoplasmas; however, the data presented by Howard & Thomas (1980) and Howard *et al*. (1983) is not conclusive. The lack of transmission research and logistical issues with conducting research on this group of phytoplasmas in palms makes elucidating the evolutionary relationship between the pathogens and their associated vectors difficult, but in most other plant pathosystems, multiple species are capable of transmitting a given pathogen. If this trend is reflected in the palm phytoplasma pathosystem, then other species of *Haplaxius* or other cixiids that feed on palms are likely competent vectors of the 16SrIV phytoplasmas. Because of the potential for related species of *Haplaxius* to contribute to phytoplasma-caused disease spread, gaining a better understanding of the cixiids associated with palms in the Neotropics is an important preliminary step for monitoring programs. In addition to *H. crudus* being a vector of LY, the planthopper *Myndus taffini* Bonfils, 1982 is a vector of the lethal virus *Coconut foliar decay virus* (CFDV) in the Vanuatu archipelago, located in the South Pacific Ocean (Julia 1985, Wefels *et al*. 2015). While this virus is not known from the New World, the potential for undescribed strains and species of viruses associated with palm feeding cixiids belonging to the *Haplaxius-Myndus* group is intriguing.

Because of a poor understanding of host preferences for *Haplaxius* species, and a limited understanding of planthopper diversity on palms in the Neotropics, a survey was recently initiated to evaluate declining palms and their associated auchenorrhynchan fauna in order to identify the causal pathogens and potential vectors. In addition, palms in natural habitats were included in the survey for collecting planthoppers to evaluate what species were unique to disturbed habitat, which species were unique to natural habitat, and which species were present in both. This research was initiated in Costa Rica due to high levels of documented biodiversity (insect, plant, and microorganism) in the region, along with reasonably good infrastructure and safe working conditions. Thus far, Bahder *et al*. (2019) documented a new species of derbid planthopper in the genus *Omolicna* Fennah on coconut palm (*Cocos nucifera* L.) as well as two new country records for *O. brunnea* (McAtee) and *O. triata* (Caldwell). While *Omolicna* is not a known group of phytoplasma vectors, phytoplasmas have been isolated from derbids in the genus *Cedusa* Fowler in Jamaica (Brown *et al*. 2006).

In this manuscript, a new genus and species of cixiid planthopper is described from palms in the Reserva Privada el Silencio de Los Angeles, Alajuela Province, Costa Rica. The newly described genus and species displays a remarkable degree of sexual dimorphism and it possesses morphological traits of *Haplaxius senso stricto* and features of *Myndus senso stricto*. Molecular evidence was used to ensure proper association of males and females and to support generic placement of the new species.

Materials and methods

Locality and Specimen Collection. Specimens were collected in the Reserva Privada el Silencio de Los Angeles, Hotel Villa Blanca, Alajeula, Costa Rica (permit no. SINAC-ACTo-GASPPNI-016-2018) from May 14, 2018 to May 18, 2018 by aspirating directly from palm fronds. Specimens were exported under permit number DGVS-256-2018 and imported into the U.S.A. under permit number P526-170201-001. All specimens collected were measured, photographed and dissected using a Leica M205 C stereoscope. Images of specimens and all features photographed were generated using the LAS Core Software v4.12. Voucher specimens, including primary types, are stored at the University of Florida—Fort Lauderdale Research and Education Center (FLREC) in Davie, FL, U.S.A and Florida State Collection of Arthropods (FSCA).

Morphological terminology. Morphological terminology generally follows Kramer (1979) except with male terminalia nomenclature updated after Bourgoin (1988) and Bourgoin & Huang (1990). New taxa are to be attributed to Bahder and Bartlett.

Dissections and DNA Extraction. The male terminalia that were dissected also served as the source of tissue for DNA extraction. The terminal end of the abdomens with genitalia were 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 terminalia were 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 genitalia 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 terminalia were then used for morphological characterization and photography.

PCR Parameters and Sequence Data. Primers used for the amplification of 18S were those presented by Bahder *et al*. (2019). PCR reactions contained 5x GoTaq Flexi Buffer, 25 mM $MgCl_2$, 10 mM dNTP's, 10 mM of each primer, 10% PVP-40, and 2.5U GoTaq Flexi DNA Polymerase, 2 µl DNA template, and sterile dH_20 to a final volume of 25 µL. Thermal cycling conditions for 18S were as follows: 2 min initial denaturation at 95°C, followed by 35 cycles of 30 sec denaturation at 95°C, 30 sec annealing at 60°C, 2 min 30 sec extension at 72°C, followed by a 5 min extension at 72°C. All products were run on a 1.5% agarose gel stained with 1% GelRed (Biotium, Fremont, California, USA). PCR products of the appropriate size were purified using the Exo-SAP-IT™ PCR Product Clean-up Reagent (ThermoFisher Scientific, Waltham, Massachusetts, USA). PCR products were cloned using the TOPO® TA Cloning® Kit into vector pCR™2.1-TOPO® (Invitrogen) per the manufacturers protocol. The cloning constructs were transformed into TOPO One Shot® Chemically Competent E. coli cells and plated on LB plates containing 50 µg/mL Kanamycin. Plates were incubated overnight at 37°C and transformed colonies were chosen for colony PCR using the universal M13 primers to verify that they contained the correct insert. Clones with the insert of the correct size were incubated on a shaker overnight in 20 mL LB broth with 50 µg/mL Kanamycin. Plasmids were extracted using a QIAprep Spin Miniprep Kit (Qiagen) per the manufacturer's protocol. Plasmid concentrations were quan-

tified using a NanoDropLite Spectrophotometer (ThermoFisher Scientific, Waltham). Purified PCR product and plasmids sent for sequencing at Eurofins Scientific (Louisville, KY, USA). Contiguous files were assembled using DNA Baser (Version 4.36) (Heracle BioSoft SRL, Pitesti, Romania), aligned using MEGA7 (Kumar *et al.* 2016).

DNA Sequence Analysis. Sequence data for the 18S loci were downloaded for 26 different species of cixiid, represented by three subfamilies, eight tribes, and 21 genera (Table 1) in order to establish what constituted generic level distances with 18S. Sequence data for the corresponding region of COI amplified for the novel taxon was available for six different species (Table 1) and were used as outgroups in the data analysis. Also, an undetermined species of *Oecleus* from Costa Rica and *Haplaxius crudus* were used to generate additional COI data to from generic comparisons within the Oecleini. Using MEGA7, a matrix of genetic distance was generated using proportional distance (p-distance), bootstrapped using 1,000 samples and analyzed using the Maximum Composite Likelihood model. Sequence data was also used to generate a phylogenetic tree using the Maximum Likelihood method in MEGA7 based on the Tamura-Nei model and 1,000 bootstrap sample. Both analyses were completed for both 18S and COI.

TABLE 1.

Species	Subfamily	Tribe	18S Accession	COI Accession
Oecleus sp.	Cixiinae	Oecleini	DQ532512.1	N/A
Oecleus perpictus	Cixiinae	Oecleini	JQ982515.1	N/A
Haplaxius crudus	Cixiinae	Oecleini	HM017261.1	N/A
Haplaxius deleter	Cixiinae	Oecleini	EU183552.1	N/A
Haplaxius pictifrons	Cixiinae	Oecleini	MN200098.1	N/A
Nymphomyndus caribbea	Cixiinae	Oecleini	EU183561.1	N/A
Myndus taffini	Cixiinae	Oecleini	EU183560.1	N/A
Cubana sp.	Cixiinae	Pintaliini	EU183551.1	N/A
Pintalia alta	Cixiinae	Pintaliini	AY744804.1	N/A
Pintalia vibex	Cixiinae	Pintaliini	JQ982513.1	N/A
Mnemosyne sp.	Cixiinae	Mnemosynini	EU183556.1	N/A
Andes simplex	Cixiinae	Andini	EU183568.1	N/A
Typhlobrixia namorokensis	Cixiinae	Brixiini	KT602431.1	N/A
Betacixius sp.	Cixiinae	Semonini	JX556744.1	N/A
Cixius sp.	Cixiinae	Cixiini	JQ982514.1	N/A
Hyalesthes luteipes	Cixiinae	Pentastirini	N/A	GU553003.1
Hyalesthes obsoletus	Cixiinae	Pentastirini	N/A	GU553000.1
Hyalesthes scotti	Cixiinae	Pentastirini	EU183565.1	FN428805.1
Oliarus slossonae	Cixiinae	Pentastirini	DQ532510.1	N/A
Olarius hesperinus	Cixiinae	Pentastirini	EU15215.1	N/A
Oliarus hamatus	Cixiinae	Pentastirini	EU183562.1	N/A
Ozoliarus sp.	Cixiinae	Pentastirini	EU183563.1	N/A
Melanoliarus humilis	Cixiinae	Pentastirini	EU183559.1	N/A
Melanoliarus vicarious	Cixiinae	Pentastirini	EU183550.1	N/A
Oecleopsis sinicus	Cixiinae	Pentastirini	JX556766.1	N/A
Reptalus quinquecostatus	Cixiinae	Pentastirini	EU183564.1	JF319661.1
Borysthenes sp.	Borystheninae	N/A	EU183557.1	N/A
Bothriocera eborea	Bothriocerinae	N/A	DQ532511.1	N/A

Results

Sequence Data and Analysis. For both the male and female of the new species, 1,383 bps of the 18S gene were generated (Accession No. MN200096 and MN200095, respectively). The pairwise comparison revealed that the male and female were 100% identical (Table 2), confirming the association of males and females and the strong sexual dimorphism of the new species.

TABLE 2. Pairwise comparison using Maximum Composite Likelihood method based on the 18S gene for various cixiid species (bottom) and standard error (top); blue cells=intratribal, orange cells=intrageneric, yellow cells=intertribal, green cells=intersubfamilial.

		1	2	3	4	5	6	7	8	9	10	11	12	13	14
1	Myxia_belinda_female		0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
2	Myxia_belinda_male	0.0		0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
3	Oecleus_sp.	2.7	2.7		0.00	0.00	0.00	0.00	0.00	0.01	0.00	0.01	0.00	0.01	0.01
4	Oecleus_perpictus	3.1	3.1	0.8		0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
5	Haplaxius_crudus	2.7	2.7	2.3	2.8		0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01
6	Haplaxius_deleter	2.9	2.9	2.2	2.6	0.8		0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01
7	Haplaxius_pictifrons	2.9	2.9	2.2	2.6	0.7	1.0		0.00	0.01	0.01	0.01	0.01	0.01	0.01
8	Nymphomyndus_caribbea	2.8	2.8	2.5	3.3	1.9	2.2	2.1		0.01	0.01	0.01	0.01	0.01	0.01
9	Myndus_taffini	5.6	5.6	4.2	4.3	5.1	4.8	4.8	5.3		0.01	0.01	0.01	0.01	0.01
10	Cubana_sp.	3.6	3.6	2.4	2.4	2.8	2.8	2.8	3.2	4.9		0.00	0.00	0.01	0.00
11	Pintalia_alta	3.6	3.6	2.4	2.3	3.0	3.1	2.9	3.4	4.9	1.0		0.00	0.01	0.01
12	Pintalia_vibex	3.5	3.5	2.6	3.2	3.0	3.2	3.0	3.4	5.4	1.2	1.5		0.01	0.01
13	Mnemosyne_sp.	4.3	4.3	3.2	3.4	4.3	4.3	4.2	5.0	5.8	3.4	3.2	3.6		0.01
14	Andes_simplex	4.5	4.5	3.1	3.6	3.5	3.2	3.3	4.0	5.8	2.5	2.9	2.8	4.3	
15	Typhlobrixia_namorokensis	3.6	3.6	2.9	3.0	3.1	3.3	2.9	3.5	6.0	1.8	2.0	2.0	3.7	3.1
16	Betacixius_sp.	4.6	4.6	4.4	4.4	4.7	5.0	4.7	5.2	6.1	3.9	4.0	4.4	4.9	5.3
17	Cixius_sp.	3.1	3.1	0.7	2.0	2.7	2.6	2.6	3.3	4.3	2.5	2.4	3.1	3.4	3.8
18	Hyalesthes_scotti	3.1	3.1	2.8	2.8	2.9	3.1	2.7	3.2	5.4	2.1	2.1	2.3	3.4	3.1
19	Oliarus_slossonae	3.6	3.6	2.5	2.4	3.4	3.6	3.2	3.8	5.2	1.5	1.5	2.2	3.6	3.6
20	Olarius_hesperinus	3.4	3.4	2.5	2.3	3.3	3.5	3.1	3.8	5.4	1.6	1.5	2.2	3.5	3.5
21	Oliarus_hamatus	3.6	3.6	2.9	2.7	3.3	3.3	3.1	3.8	5.5	1.6	1.8	2.0	3.4	3.2
22	Ozoliarus_sp.	3.4	3.4	2.7	2.5	3.5	3.5	3.3	3.9	5.4	1.6	1.7	2.2	3.5	3.5
23	Melanoliarus_humilis	3.6	3.6	2.9	2.9	3.5	3.5	3.3	3.9	5.2	1.8	1.9	2.3	3.8	3.6
24	Melanoliarus_vicarius	2.8	2.8	2.9	3.2	2.2	2.4	2.4	1.0	5.2	2.8	3.2	3.0	4.8	3.7
25	Oecleopsis_sinicus	6.4	6.4	5.4	5.3	6.4	6.5	6.3	6.7	7.0	5.0	5.0	5.5	6.3	5.9
26	Reptalus_quinquecostatus	3.5	3.5	2.6	2.5	3.2	3.2	3.0	3.7	5.4	1.9	2.2	2.4	3.8	3.7
27	Borysthenes_sp.	3.8	3.8	2.5	2.6	3.7	3.3	3.4	3.5	5.4	1.5	1.6	2.3	4.0	3.0
28	Bothriocera_eborea	6.2	6.2	5.1	5.5	5.4	5.5	5.4	5.5	6.9	5.9	5.9	6.2	5.9	6.9

.....continued on the next page

TABLE 2. (Continued)

		15	16	17	18	19	20	21	22	23	24	25	26	27	28
1	Myxia_belinda_female	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
2	Myxia_belinda_male	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
3	Oecleus_sp.	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
4	Oecleus_perpictus	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
5	Haplaxius_crudus	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
6	Haplaxius_deleter	0.01	0.01	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
7	Haplaxius_pictifrons	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
8	Nymphomyndus_caribbea	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.00	0.01	0.01	0.01	0.01
9	Myndus_taffini	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
10	Cubana_sp.	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01
11	Pintalia_alta	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01
12	Pintalia_vibex	0.00	0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01
13	Mnemosyne_sp.	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
14	Andes_simplex	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
15	Typhlobrixia_namorokensis		0.01	0.01	0.00	0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.01	0.01	0.01
16	Betacixius_sp.	3.9		0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
17	Cixius_sp.	3.0	4.4		0.01	0.00	0.00	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
18	Hyalesthes_scotti	2.4	3.3	2.8		0.00	0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.01	0.01
19	Oliarus_slossonae	2.3	3.3	2.3	1.3		0.00	0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01
20	Olarius_hesperinus	2.1	3.2	2.2	1.0	1.0		0.00	0.00	0.00	0.01	0.01	0.00	0.00	0.01
21	Oliarus_hamatus	2.1	3.3	2.6	0.7	0.8	1.0		0.00	0.00	0.01	0.01	0.00	0.01	0.01
22	Ozoliarus_sp.	2.3	3.2	2.5	1.0	0.7	0.3	1.0		0.00	0.01	0.01	0.00	0.01	0.01
23	Melanoliarus_humilis	2.6	3.4	2.7	1.3	0.9	1.0	0.8	1.0		0.01	0.01	0.00	0.01	0.01
24	Melanoliarus_vicarius	3.3	5.0	3.2	2.7	3.2	3.1	2.9	3.1	3.1		0.01	0.01	0.01	0.01
25	Oecleopsis_sinicus	5.3	3.6	5.3	5.4	5.3	5.1	5.2	5.3	5.3	6.4		0.01	0.01	0.01
26	Reptalus_quinquecostatus	2.6	3.4	2.4	1.5	1.3	1.0	1.0	0.9	1.1	2.9	5.6		0.01	0.01
27	Borysthenes_sp.	2.8	4.6	2.7	2.9	2.5	2.4	2.5	2.5	2.6	3.3	5.8	2.5		0.01
28	Bothriocera_eborea	6.3	7.0	5.6	6.2	6.4	6.2	6.4	6.4	6.5	5.8	7.0	6.4	6.1	

With respect to other similar genera in the Oecleini, the 1,383 bp sequence of 18S from the new taxon differs by an average of 2.77% from *Haplaxius*, 5.20% from *Myndus taffini*, and 2.80% from *Nymphomyndus caribbea* (Table 2). For *Haplaxius*, there is an average of 0.57% variation among species. *Myndus taffini* differs from the *Haplaxius* species by an average of 4.8%. *Nymphomyndus carribea* differs from the species analyzed in *Haplaxius* by an average of 2.0% and differs from *Myndus taffini* by 5.1%. In addition to support from the pairwise comparison, phylogenetic analysis showed this new taxon as a distinct lineage relative to both *Haplaxius* and *Myndus* (Fig. 1A). Furthermore, the average variation among available genera for other tribes was 1.1% (Pintaliini) and 2.5% (Pentastrini). The range of variation among genera in the Penastirini was 0.3% to 6.4% (Table 2) while the range in Pintaliini was 1.0% to 1.2% (Table 2). *Bothriocera erobea* (Bothriocerinae) differed by an average of 5.9%, ranging from 5.1% to 7.0% variance for 18S (Table 2). The *Borysthenes* specimens varied by an average of 4.9% with a range of 1.5% to 6.1% variance for 18S (Table 2). Among different genera between tribes, there was an average of 4.4% difference and a range of 0.7% to 6.7% difference for 18S (Table 2).

For the COI data generated from the novel taxon, it showed to be about 16% to 17% different from the available data belonging to other Oeclein genera (Table 3), where it was about 18% to 19% different compared to genera in the Pentastirini (Table 3). The difference between two established genera, *Haplaxius* and *Oecleus* was shown to be 15.3% in this instance with the novel taxon varying from both these genera by 1% to 2% more (Table 3). Furthermore, the generic level difference in the Pentastirini was lower than that measured for the novel taxon relative to *Haplaxius* and *Oecleus* (Table 3). For COI, the novel taxon resolved into a distinct lineage relative to two other Oeclein genera (*Haplaxius* and *Oecleus*) with strong bootstrap support (99) (Figure 1B). While the bootstrap support for the 18S marker was weak, it still yielded a distinct clade which was replicated with a more phylogenetically useful marker, COI, with much higher bootstrap support, providing further evidence.

TABLE 3. Pairwise comparison using Maximum Composite Likelihood method based on the COI gene for various cixiid species (bottom) and standard error (top); blue cells=intratribal, orange cells=intrageneric, yellow cells=intertribal.

		1	2	3	4	5	6	7
1	Myxia_belinda		0.013	0.014	0.014	0.014	0.015	0.014
2	Haplaxius_crudus	16.3		0.014	0.015	0.014	0.015	0.014
3	Oecleus_sp.	16.9	15.2		0.015	0.014	0.015	0.014
4	Hyalesthes_luteipes	18.2	18.2	19.7		0.012	0.009	0.013
5	Hyalesthes_obsoletus	17.7	17.3	17.9	11.7		0.012	0.012
6	Hyalesthes_scotti	17.9	17.4	19.1	6.5	11.9		0.013
7	Reptalus_quadricinctus	18.6	17.5	17.0	14.5	13.0	14.3	

Systematics

Family Cixiidae Spinola, 1839

Subfamily Cixiinae Spinola, 1839

Tribe Oecleini Muir, 1922

Myxia gen. n.

Type species. *Myxia belinda* **sp. n.** by monotypy and current designation.

Diagnosis. *Myxia* **gen. n.** possesses lateral pronotal carinae terminating on the ventral margin of the prothorax, a character shared with *Myndus* but lacks the denticle of the forecoxae (Fig. 2), a feature shared with *Haplaxius*. Tegulae evident and tibiae of hind legs lack spines (tribal feature of Oecleini). The genus *Myxia* **gen. n.** can be diagnosed from *Haplaxius* and *Myndus* by the overall form of the gonostyli. In *Myxia* **gen. n.**, the gonostyli appear distally bifid, possessing a dorsal process near the terminus of each gonostylus in lateral view pointing dorsad and in ventral view, and a lateral tooth on the inner margin with an acute apex. In addition, medioventral process of pygofer is subtriangular. Phallobase separated from aedeagus.

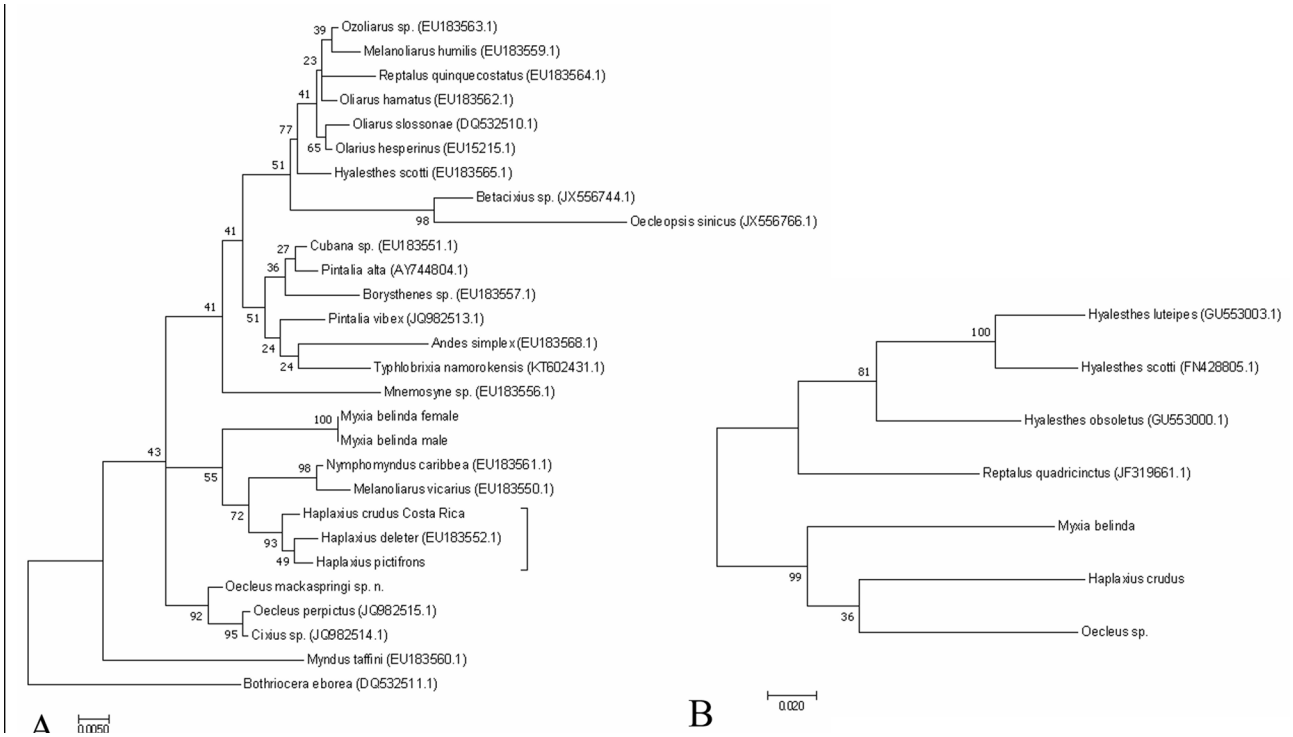

FIGURE 1. Maximum Likelihood phylogenetic tree based on 18S sequence data (A) and COI sequence data (B). Branch support was assessed using 1,000 bootstrap replicates.

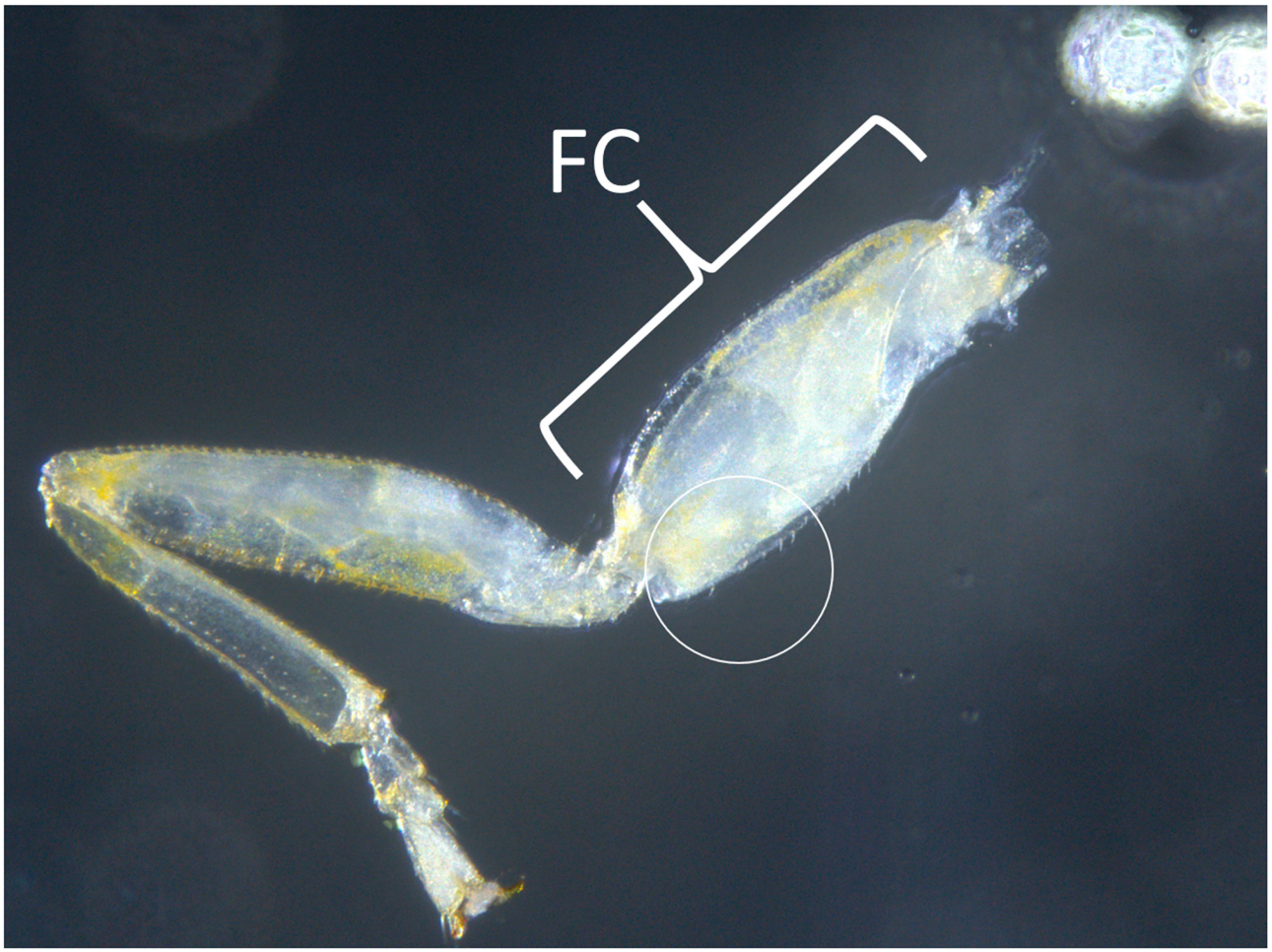

FIGURE 2. Front leg of adult male *Myxia* **gen. n.** *belinda* **sp. n.** demonstrating lack of denticle on forecoxa (FC), location where denticle is present in *Myndus* in white circle.

Description (Figures 4–9). Head much narrower than pronotum, weakly projecting in front of eyes. Vertex much wider than long, approximately quadrate, lateral margins foliate, disk concave, median carina weak posteriorly, obsolete anteriorly. Fastigium rounded, frons approximately triangular, widening to frontoclypeal suture, median carinae present. Clypeus inversely triangular, narrowed to labrum. Pronotum very narrow, tricarinate, carinae reaching posterior margin; paradiscal region nearly exceeding antennae. Mesonotum broad and longer than vertex+pronotum, tricarinate; scutum and scutellum distinctly separated by inflection. Tegulae evident, without carinae. Coxae of front leg without ventral denticles. Fore femora lacking denticle. Tibiae of hind legs lacking spines. Wings transparent, macropterous, well-exceeding apex of abdomen. Abdomen weakly compressed. Pygofer in lateral view roughly triangular, widest ventrally; ventral margin of pygofer opening bearing elongate subtriangular projection. Gonostyli elongate, distally bearing apical and subapical tooth (at least in type species), giving a broadly bifid appearance. Anal tube broad, distally enlarged, relatively short (*sensu* Kramer 1979); anal column elongate. Aedeagus simple bearing small apical flagellum, phallobase surrounding aedeagal base and projecting caudally to subtend aedeagus, bearing multiple elongate projections.

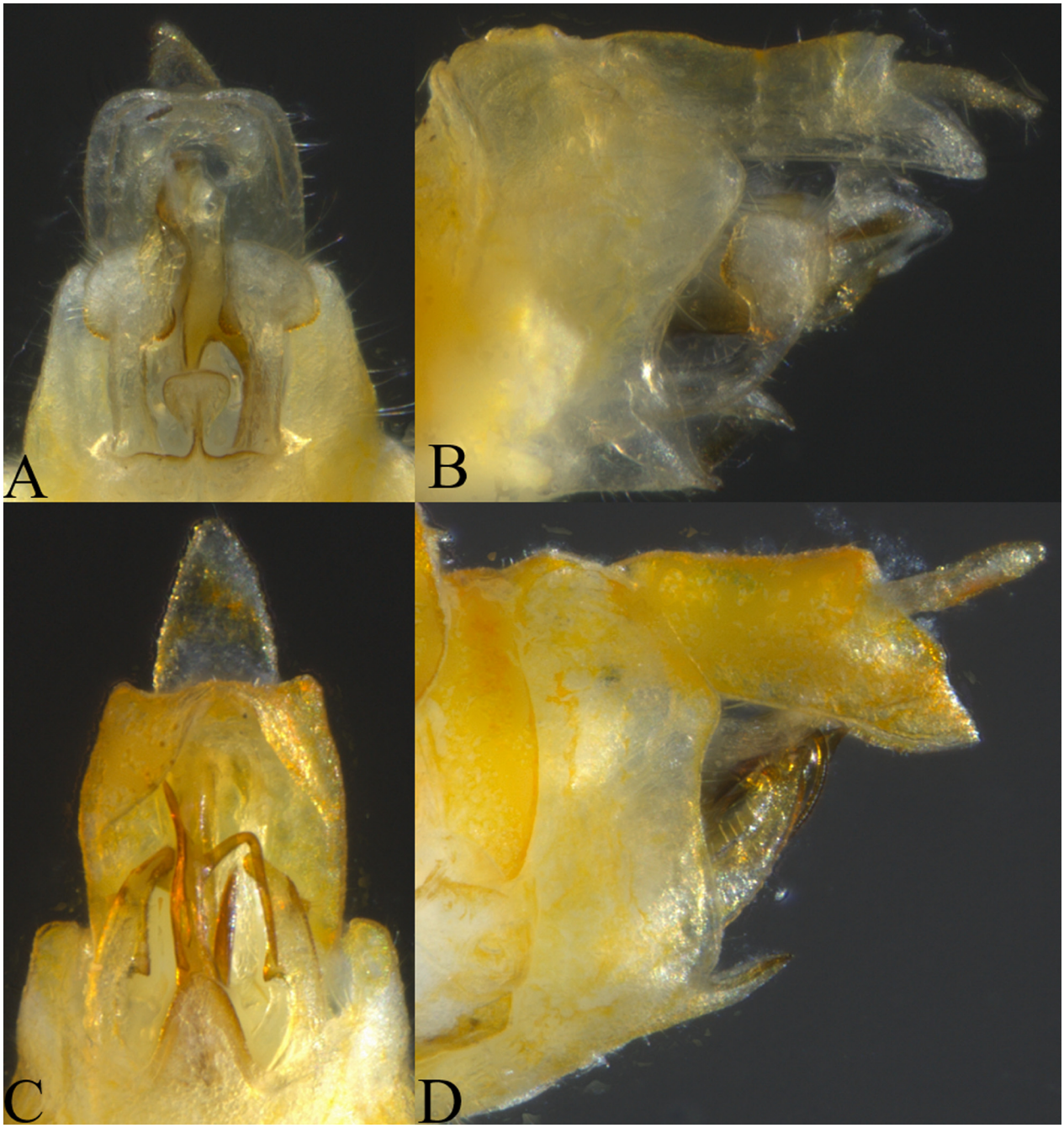

FIGURE 3. Terminalia of *Haplaxius crudus* in ventral view (A) and lateral view (B) terminalia of *Myxia* **gen. n.** *belinda* **sp. n.** in ventral view (C) and lateral view (D).

Remarks. In the field, the specimen was tentatively identified as *Haplaxius* due to overall similarity in structure and general habit. More careful morphological examination seemed to confirm generic placement. The general form and behavior of this taxon appeared to coincide with *Haplaxius*. While differences in terminalia set this species apart from other *Haplaxius*, it was molecular characterization that made it apparent that observed differences merited genus level designation.

A difference that appears to set *Myxia* n. g. apart from *Haplaxius*, is that in *Myxia*, the phallus consists of the phallobase that surrounds the base of the aedeagus and projects beneath to subtend it, whereas in *Haplaxius*, the phallobase envelopes the aedeagus forming a phallotheca. The variation in degree to which the phallobase surrounds the aedeagus in *Myxia* cannot be discerned from the single species described here, but this character appears to be an important difference among the genera.

The form of the gonostyli also appears different among the genera. The general form of gonostyli in *Haplaxius senso stricto* is that of a larger, globular apex in ventral view and in lateral view, the rounded apex is generally visible but usually angled upward. However, many *Haplaxius* deviate from this morphological type. The illustrations of the type species *H. laevis* Fowler, 1904 (Kramer 1979, figs. 159–162), terminalia exhibit a rounded terminus of the gonostyli in both ventral and lateral views. *Haplaxius crudus* have the same general form of the gonostyli and aedeagus as *H. laevis* and provided a useful comparison (Fig. 3). The structure of the terminalia of *H. crudus* appears to be comparable to that of *H. laevis* and serves as a useful morphological template for comparison. Caldwell (1946) also considered *H. crudus* (as *Paramyndus cocois*) similar enough based on general body structure to *H. laevis* to place them in the same genus, suggesting that there were other species that appeared more distinct from *H. laevis* than *H. crudus*. It had previously been suggested that *Haplaxius* (as *Myndus*) "...could be subdivided into a series of genera or subgenera; these divisions would be based primarily upon structural features or variations in the pattern of the male genitalia, especially the aedeagus." Kramer (1979: 302). This represents the first genus-group to be erected associated with *Haplaxius* based on molecular data and morphology. One other species of *Haplaxius*, *H. delta*, according to Kramer (1977) possesses a similar form for both the gonostyli (bifurcated with dorsal process angled dorsad) and medioventral process (subtriangular). Also, the aedeagus is simple with hooked flagellum and phallobase bearing large processes according to Kramer (1979; Fig. 175–179). Based on the overall similarity of the terminalia to the novel taxon we propose *H. delta* be moved to the novel taxon, bringing the species number for *Myxia* **gen. n.** to two species.

Etymology. The generic name is an arbitrary amalgamation of *Haplaxius* and *Myndus* suggestive of the similarities of *Myxia* to both genera. The genus name is feminine in gender.

Myxia belinda sp. n.

(Figures 4–9)

Type locality. Costa Rica, Alajuela, Reserva Privada el Silencio de Los Angeles, Hotel Villa Blanca.

Diagnosis. A remarkable species displaying a significant degree of sexual dimorphism with males yellow and females orange and black. Forewing pterostigma conspicuous. The medioventral process of the pygofer is subtriangular. The gonostyli (dorsal view) bear anterior facing hooks arising approximately midlength. Aedeagus simple, apex hooked right bearing flagellum. Phallobase ventrally projecting, subtending aedeagus, and bearing four stout elongate projections.

Description. *Color*. General body color (males): bright, yellow, legs paler (Fig. 4A, B). Wings transparent, veins yellow. General body color (females) bright orange (Fig. 4C, D). Lateral carinae of head and abdominal tergites black. Wings transparent, veins orange.

Structure. Body length males (n=15): 5.98–6.04 mm with wings and 3.99–4.02 mm without wings; females (n=8): 6.39–6.42 mm with wings and 4.11–4.13 mm without wings. Head. Head in lateral view obtusely rounded, more evident in female than male (Fig. 5C, F). Vertex broadest basally, weakly narrowing distally; posterior margin medially notched, anterior margin truncate (Fig. 5B, E). Median carina of vertex present near posterior margin, becoming obsolete distally near eyes. Transverse apical carina present at fastigium. Vertex length males: 0.25–0.27 mm; females: 0.36–0.38 mm. Vertex width at hind margin males: 0.52–0.54 mm; females 0.51–0.53 mm. Vertex width at distal margin males: 0.22–0.24 mm; females: 0.23–0.25 mm. Frons roughly triangular, narrowest between eyes then broadening nearly to frontoclypeal suture, then abruptly narrowing; clypeus an inverse triangle, lateral margin profile continuous with frons (Fig 5C, F); frontoclypeal suture slightly concave. Median carina present

on frons, 1/3 obsolete (Fig. 5). Frons width (dorsal), males: 0.22–0.23 mm; females: 0.22–0.23 mm; frons width (widest part) males: 0.57–0.59 mm; females: 0.62–0.63 mm. Frons width (frontoclypeal suture) males: 0.43–0.44 mm; females: 0.45–0.46 mm. Frons length (midline) males: 0.75–0.76 mm; females: 0.80–0.81 mm. Frons length (lateral margin) males: 0.85–0.86 mm; females: 0.87–0.88 mm. Clypeus length, males: 0.71–0.72 mm; females: 0.78–0.79 mm. Lateral ocelli conspicuous, below leading margin of compound eye, anterior to antennae; median ocellus obscure, near frontoclypeal suture. Antennal pedicle very short, scape bulbous bearing irregularly arranged rhinia, flagellum elongate, bristlelike.

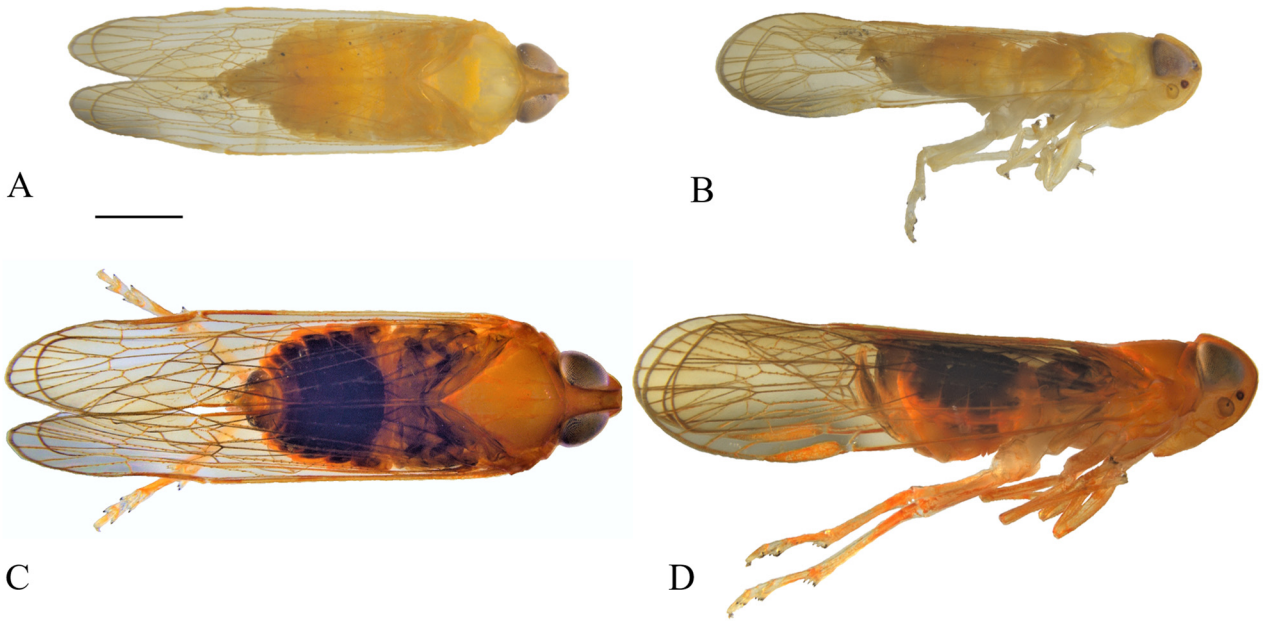

FIGURE 4. Adult habitus *Myxia* **gen. n.** *belinda* **sp. n.**; **(**A) body dorsal view male, (B) body lateral view male, (C) body dorsal view female, and (D) body lateral view female, scale = 1mm.

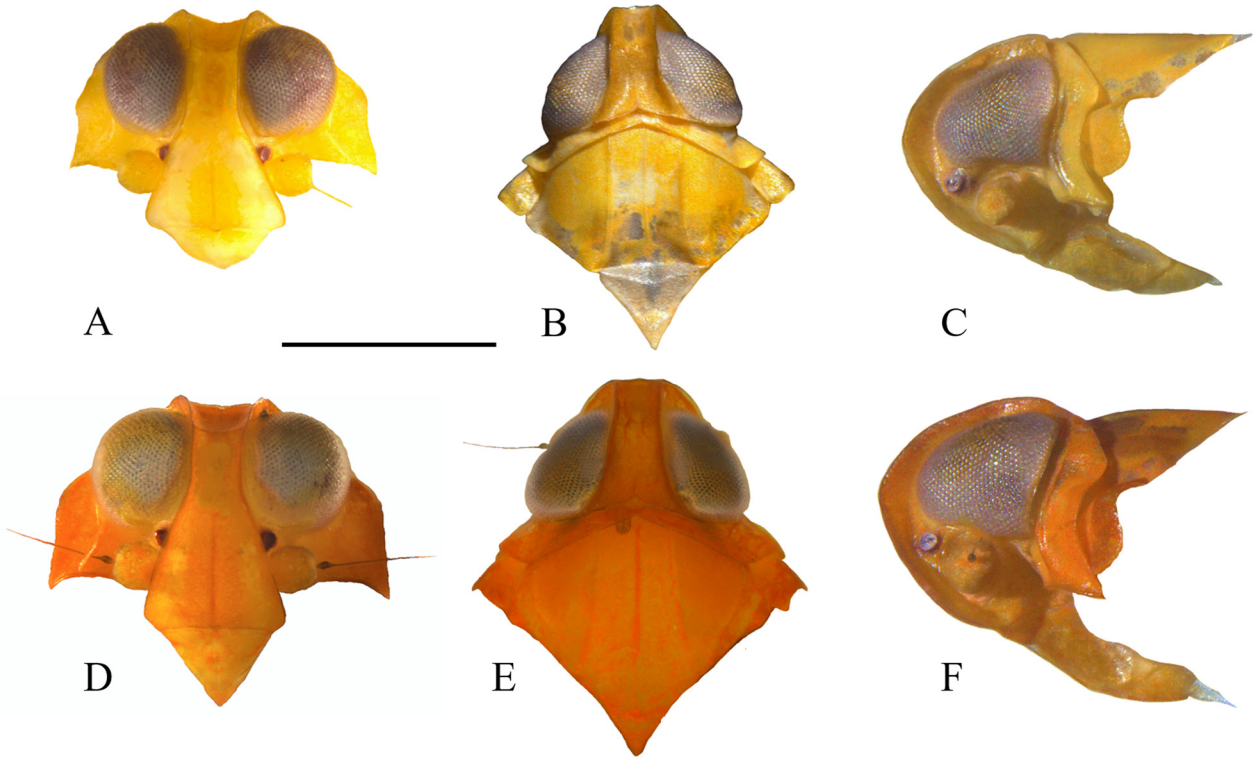

FIGURE 5. Adult *Myxia* **gen. n.** *belinda* **sp. n.**; (A) male head frontal view, (B) male head, pronotum, mesonotum dorsal view, (C) male head, pronotum, mesonotum lateral view, (D) female head frontal view, (E) female head, pronotum, mesonotum dorsal view, (F) female head, pronotum, mesonotum lateral view, scale = 1mm.

Thorax. Pronotum very short, anteriorly convex, conforming hind margin of head; posteriorly broadly acute (Fig. 5B, F); median carina present, lateral pronotal carinae arising near midlength of eye, arched laterally to ventral margin. Paradiscal fields of pronotum (lateral view) foliate, extending ventrad to antennae. Pronotum length at midline males: 7.0–0.08 mm; females: 0.09–0.10 mm. Pronotal carinae terminating on the ventral margin. Mesonotum level with dorsal margin of head in lateral view (Fig. 5C, F) with three subparallel longitudinal carinae (lateral reaching hind margin, median reaching scutellum, Fig. 5B, E). Mesonotum length at midline males: 1.16–1.18 mm; females: 1.22–1.24 mm. Mesonotum width males: 1.19–1.20 mm; females: 1.23–1.24 mm.

Forewing (Fig. 6) with conspicuous pterostigma, wing margin entirely enclosed by sclerotized vein; veins punctate with setal bases. CuA fork much distal from ScP+R fork ('inner marginal' cell—cell C5—much shorter than 'outer marginal' cell—cell C1). Branching pattern: ScP 1 branched, RA 1 branched, RP 3 branched, MP 4 branched, CuA 2 branched; CuA and CuP distally merged. Pcu and A1 meeting proximad of ScP+R fork, combined Pcu+A1 reaching wing margin proximad of claval apex. Wings well exceeding abdomen, forewing length males: 5.00–5.02 mm; females: 5.45–5.46 mm.

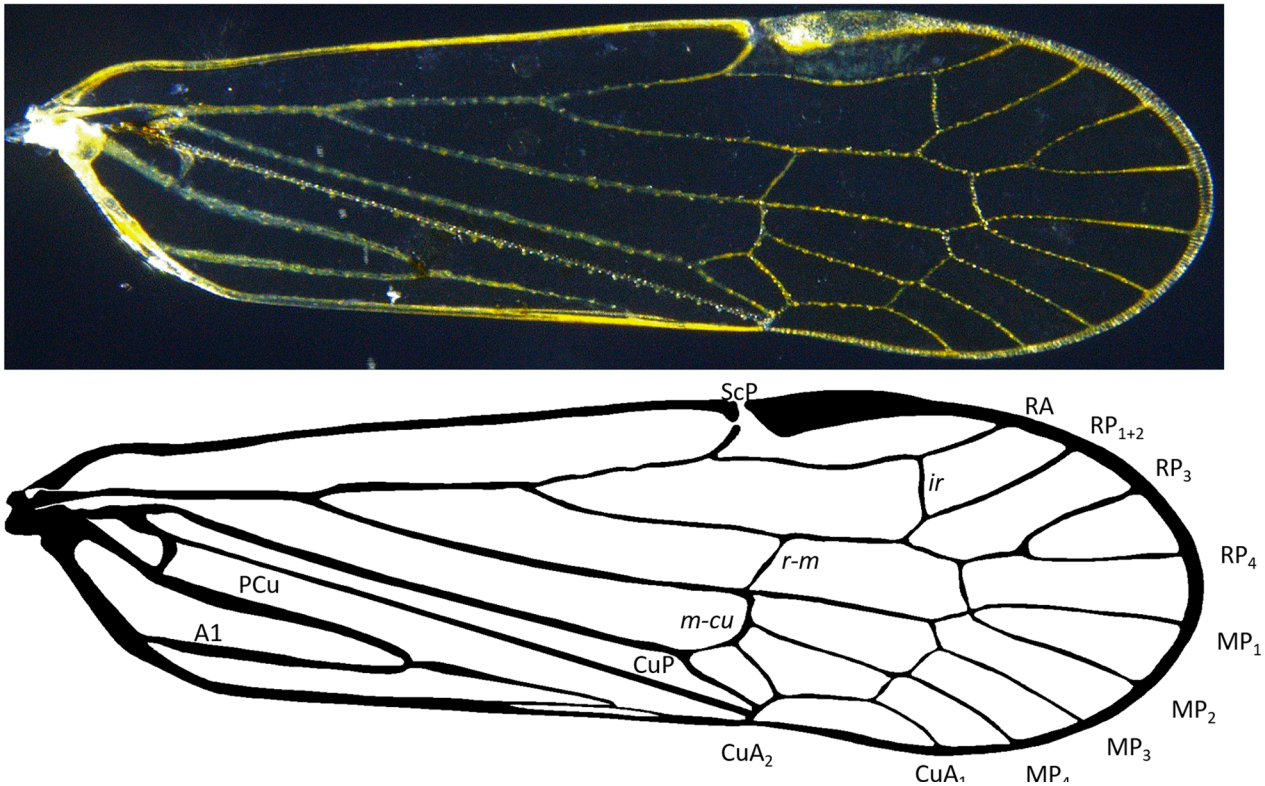

FIGURE 6. Forewing venation of *Myxia* **gen. n.** *belinda* **sp. n.**

Male Terminalia. Pygofer in lateral view robust, widest ventrally, narrowed dorsad, anterior and caudal margins sinuate (Fig. 7A). Pygofer opening with ventral median process that, in ventral view, is subtriangular, widest at base, attenuating distally to rounded apex (Fig. 7B). Gonostyli proximally diverging, distally converging; widest in ventral view near midlength at rounded dorsomedial projection, distally narrowed, terminating in a pair of rounded knobs (Fig. 7). Anal tube in lateral view robust, irregular in shape, broadening distad (stout and short in the sense of Kramer, 1979; Fig. 7), ventral margin at diagonal, weakly concave; in caudal view, ventral margin asymmetrically notched. Anal column elongate. Aedeagus simple, shaft without processes, distally blunt, apex curved rightward with fine, elongate subapical dorsal projection. Phallobase surrounding aedeagal base, projecting caudally beneath aedeagus; subtending portion bearing 4 projections (Fig. 8A-C): one elongate ventral (anteriorly projecting), two elongate on right side (one proximad, projecting caudally, one midlength, strongly retrorsely arched), one short left side (projecting lateral), plus pointed apex.

Female Terminalia. Gonoplac oblong, mildly crescent shaped reach ventral margin of segment 10 (Fig. 9A & C). Segment 10 wider than long in dorsal view (Fig. 9B) and widest on ventral margin in lateral view with dorsal margin approximately 2/3 width of ventral margin (Fig. 9C). Gonapophyses slightly sclerotized basally and heavily sclerotized in distal 2/3 (Fig. 9D); bulbous in basal third; irregularly sinuate on inner and outer margins (Fig. 9D)

Plant associations. Palm (*Geonoma* sp.), Arecaceae.

Distribution. Costa Rica (Alajuela).

Etymology. The specific name is given in honor of the lead author's mother, Belinda Miller Bahder. The specific name is feminine.

Material examined. Holotype male "Costa Rica, Alajeula / Los Angeles Cloud Forest / Brian W. Bahder / 15 May 2018 / aspirated from *Geonoma* sp. palm// Holotype/*Myxia*/*belinda*" (FSCA); Paratypes, Los Angeles Cloud Forest [15 May 2018] (14 males, 8 females, FLREC).

Remarks. The most notable feature of this species is the brilliant orange coloration of the adult female and while sexual dimorphism is known in *Haplaxius*, especially the commonly studied *H. crudus*, the difference observed in the new taxon appears more extreme than other described species in *Haplaxius*.

In form, *Haplaxius delta* (Kramer) has a similar medioventral process on the pygofer. Also, in ventral view, the gonostyli of *H. delta* are very similar with the difference being that the lateral teeth in *H. delta* do not hook towards the anterior, which is seen in *Myxia belinda* **sp. n.** In lateral view, the gonostyli still differ only slightly with the dorsal process in *H. delta* being a rounded hook rather than a simple rounded end as is in *Myxia belinda* **sp. n.** There is a noticeable difference in the anal tube where the terminus in *H. delta* is distinctly down curved whereas this is not seen in *Myxia belinda* **sp. n.** Additionally, the aedeagus in *H. delta* is significantly different with no spines arising on the basal half and the spines present situated on the left side, not the right as in *Myxia belinda* **sp. n.** The aedeagus in *H. delta* has a rather robust and blunt terminus and does not terminate in an acute, upward facing hook as seen in *Myxia belinda* **sp. n.** Based on the terminalia, *H. delta* is closest to the novel taxon but differs significantly in the aedeagus. Furthermore, both females and males are known from *H. delta* and the color scheme from *H. delta* is that both males and females are yellow as well as being substantially smaller.

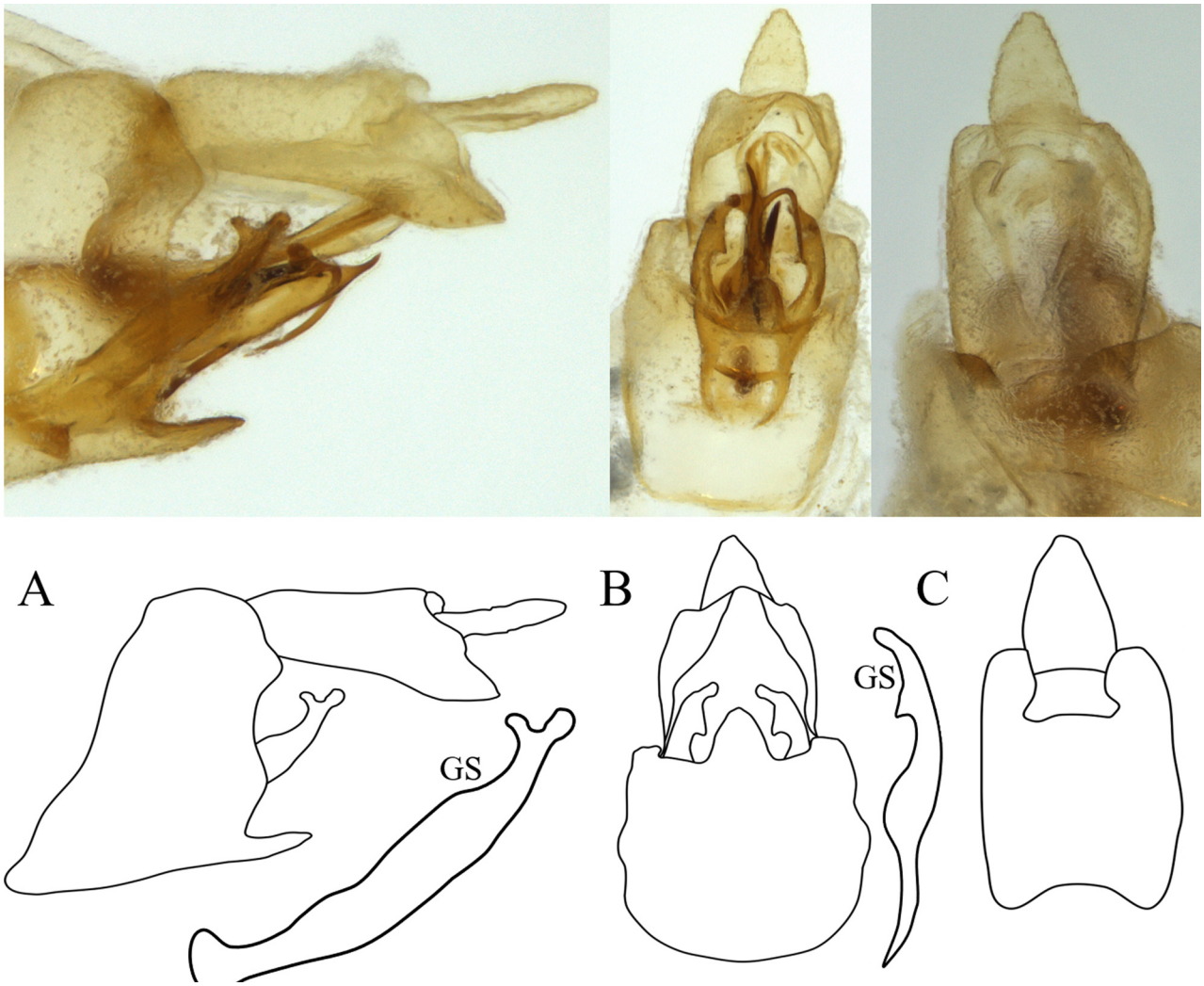

FIGURE 7. Male terminalia of *Myxia* **gen. n.** *belinda* **sp. n.**; (A) lateral view, (B) ventral view, and (C) dorsal view.

This species is unique in that is also possesses features of *Myndus*, pronotal carinae terminating on the ventral margin and not the lateral margin, but also lack the denticle of the forecoxae (Fig. 6), a feature of *Haplaxius*. This combination further supports its establishment as a novel genus as well as species.

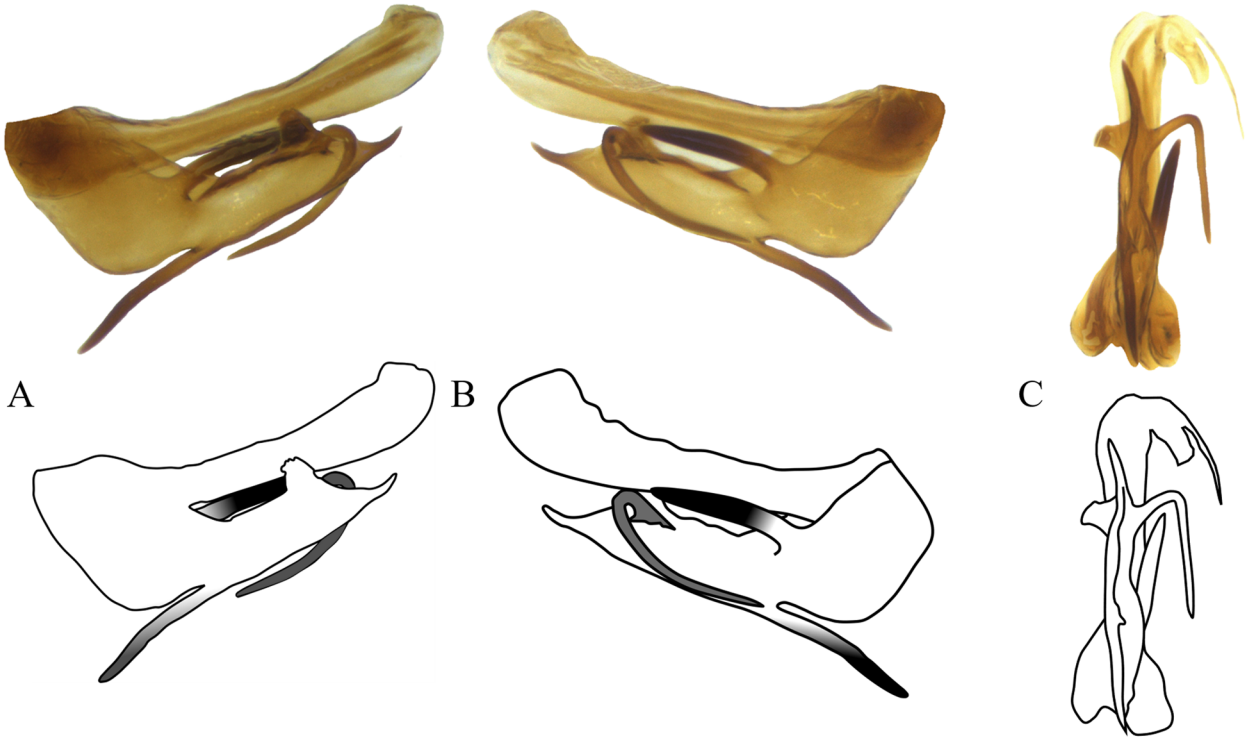

FIGURE 8. Aedeagus of adult male *Myxia* **gen. n.** *belinda* **sp. n.**; (A) right lateral view, (B) left lateral view, and C. ventral view.

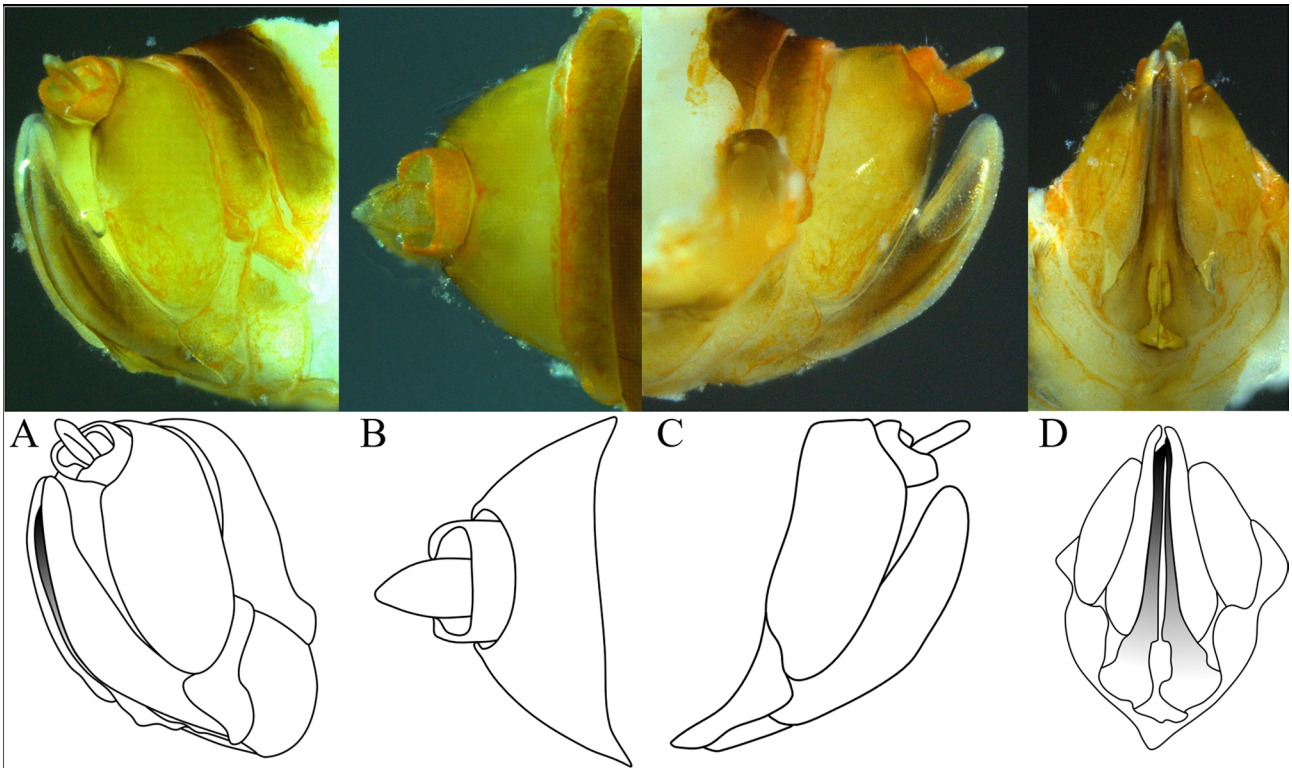

FIGURE 9. Female terminalia of *Myxia* **gen. n.** *belinda* **sp. n.**; (A) lateral view, (B) ventral view, and (C) dorsal view.

Discussion

This new taxon was found in the context of a survey of potential phytoplasma vectors on coconut and other palms. While no palms exhibited symptoms that the novel taxon was collected from, the possibility of novel strains of phytoplasma existing in isolated/unexplored habitat exists. Since the characterization of LY, other subgroups of the 16SrIV phytoplasmas have been discovered in regions without a documented history of palm lethal decline, such as the 16SrIV-B from Coyol palms in Honduras (Roca *et al*. 2007) and the 16SrIV-E phytoplasma from coconut palms in the Dominican Republic (Martinez *et al*. 2008). The evolutionary relationship between the 16SrIV phytoplasmas and cixiids is poorly understood due the lack of data on competent vectors outside the 16SrIV-A phytoplasma regarding *Haplaxius crudus*. This in part is due to the difficulty in conducting transmission studies with these phytoplasmas. Various plant pathogens are known to be transmitted by a multitude of closely related taxa. For example, the Chrysanthemum yellows (CY) phytoplasma has been transmitted by at least three different species of leafhoppers, all in different genera (Bosco *et al*. 1997) and *grapevine leafroll associated virus-3* has been transmitted by over 10 species of insect in both the Pseudococcidae and Coccidae (Bahder *et al*. 2013). Because of the flexibility observed in other systems with regard to vector-pathogen relationships, it is not unreasonable to assume that *Haplaxius crudus* could transmit other subgroups of the 16SrIV phytoplasmas or that other species of *Haplaxius* and even closely related genera could also transmit any of the 16SrIV phytoplasmas, both known and unknown strains.

While the molecular evidence so far available is limited, it seems to suggest that *Haplaxius* (*sensu* Holzinger *et al*. 2002) may not be monophyletic, as was alluded to in Kramer's (1979) revision, based on molecular data from Ceotto *et al*. (2008) and data generated in this study. Molecular evidence would be highly instructive in segregating *Haplaxius* into smaller genus-groups, as well as better establishing genus divisions—aside from geographic—between *Myndus, Colvanalia* and *Haplaxius* (or *Haplaxius* segregates), and investigating the relationships between plant associations—especially palm feeding—among taxonomic lineages. It is certain that further taxonomic investigations will reveal a variety of groups within these genera that merit genus level classification.

Because of the role that *Haplaxius crudus* plays in the epidemiology of palm-infecting phytoplasma diseases and that *Myndus taffini* plays in the epidemiology of CFDaV, that these two genera, as currently defined need revision and a more stringent look at the currently defined taxa. This is apparent from the significant differences observed in the sequence data generated in this study but also due to the factor that vector-pathogen relationships are due to a long, coevolutionary history (Purcell 1982) and by having a clear understanding of the taxonomy and phylogeny of group, a more comprehensive understanding of the group in terms of potential for phytoplasma and virus spread can be attained.

Future efforts need to focus on attaining as many representatives of the genus *Haplaxius* as possible, specifically representing distinct morphological groups based on terminalia. Supplemented with appropriate molecular analyses, this will allow for a more appropriate classification system for this taxon. Due to the economic importance of this group, having a clear understanding of the taxonomy and phylogeny is essential.

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