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A new species of planthopper from Costa Rica in the genus *Herpis* (Hemiptera: Derbidae) from palms in the cloud forest

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Abstract

Recent survey efforts in Costa Rica have documented many new species of planthoppers, primarily in the families Derbidae and Cixiidae, on palms. Recently, a specimen was collected sweeping palms in the Los Angeles cloud forest in Costa Rica and was identified as belonging to the genus *Herpis* (Derbidae). It was subsequently determined to represent a previously undescribed species. Herein, the new species, *Herpis circumsoros* Bahder & Bartlett **sp. n.** is described with supplemental molecular data for the cytochrome *c* oxidase subunit I (COI) gene and 18S rRNA gene to support placement of the new species in the genus *Herpis*.

Key words: biodiversity, DNA barcoding, survey, taxonomy, phylogenetics

Resumen

Estudios recientes en palmeras de Costa Rica han descubierto numerosas especies nuevas de chicharritas, principalmente en las familias Derbidae y Cixiidae. Recientemente, un espécimen que fue colectado mediante el uso de red entomológica en el bosque nuboso de Los Ángeles fue identificado como perteneciente al género *Herpis* (Derbidae). Posteriormente, se determinó que era una especie que no había sido descrita. En este documento, se describe la nueva especie *Herpis circumsoros* Bahder & Bartlett **sp. n.** y se suplementan datos moleculares para el gen de la subunidad I (COI) del citocromo c oxidasa y el gen 18S ARNr para respaldar la ubicación de la nueva especie bajo el género *Herpis*.

Palabras clave: biodiversidad, códigos de barras de ADN, encuesta, taxonomía, filogenia

Introduction

The genus *Herpis* Stål (type species *Herpis fuscovittata* Stål from Brazil; Stål 1862, Muir 1924, McAtee 1924, Metcalf 1945a) is a moderate-sized group of derbid planthoppers in the tribe Cenchreini of subfamily Derbinae. The Cenchreini are 'cixiid-like' derbids, with tectiform wings and the pronotal paradiscal regions forming foliate, cup-like fossae that partly circumscribe the antennae. Among New World cenchreine genera, *Herpis* is recognized as being moderately robust, approximately 4-8 mm (with wings), with broad frons (not concave) bearing parallel lateral margins, and a well-

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defined median carina, which is diagnostic for the genus. The most similar genera of New World Cenchreini appear to be *Oropuna* Fennah and perhaps *Omolicna* Fennah, but neither of these genera has a median carina on the frons.

As currently defined, *Herpis* includes 16 species (Bourgoin 2022), including 10 Neotropical and five Indomalayan (viz. Philippines, India, and Borneo; Muir 1917, Metcalf 1945a, Bourgoin 2022). The genus-level placement of these Indomalayan taxa requires review, but our current project is focused on New World species. Recently, *H. soros* Bahder & Bartlett was described and 3 congeners were illustrated (*H. metcalfi, H. albida, and H. fuscovittata;* Bahder *et al.* 2021a).

Recent surveys in the Caribbean focusing on planthoppers associated with palms has yielded a *Herpis* species near *H. soros* but is distinct based on morphological and molecular evidence. Herein a novel species of *Herpis* collected from palms in cloud forest habitat in Costa Rica is described, including COI and 18S sequence data, and an updated phylogeny of the Cenchreini based on available sequence data.

Materials and methods

Locality and Specimen Collection. Individuals of the novel taxon were collected by sweep netting trailside palms, aspirated, and immediately transferred to 95% ethanol. Specimens were collected (permit no. SINAC-ACTo-GASPPNI-016-2018) at Hotel Villa Blanca, Alajuela Province, Costa Rica (10.431269, -84.005961), and exported under permit number DGVS-256-2018 to 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 the Florida State Collection of Arthropods (FSCA) in Gainesville, FL, U.S.A. Label data were recorded for type specimens with label data quoted verbatim using "/" to indicate a line break and "//" to indicate a new label and with supplemental information given in brackets. For non-type specimens, label data were rewritten to maintain consistency in pattern, beginning with country, state, or province, followed by more specific locality data, collection date, collector, and lastly the number, sex, and specimen depository given in parentheses.

Morphological terminology and identification. Morphological terminology generally follows that of Bartlett *et al.* (2014), except for forewing venation following Bourgoin *et al.* (2015) and with male terminalia nomenclature modified after Bourgoin (1988) and Bourgoin & Huang (1990).

Dissections and DNA Extraction. The terminalia that were dissected also served as the source of tissue for DNA extraction. The terminal end of the abdomens was removed and placed directly into a solution of tissue lysis buffer (buffer ATL) and proteinase K (180 μ l ATL and 20 μ 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 μ l of buffer ATL and 200 μ l of buffer AL from the same kit and placed at 95°C for 24 hours to remove fat, wax, and residual tissue.

PCR Parameters, Sequence Data, and Analysis. To obtain COI sequence data, the DNA template from specimens was amplified using the primers TY-J-1460 (5'- TACAATTTATCGCCTAAACTTCAGCC -3') (Simon et al. 1994) and HCO2198 (5'-TCAGGGTGACCAAAAAAATCA-3') (Folmer et al. 1994). To obtain 18S sequence data, the forward primer 18S Fulfwd1 (5'- GGATAACTGTGGTAATTCTAG -3') (Urban & Cryan 2007) and reverse primer 18SR (5'-GTCCGAAGACCTCACTAAA-3') (Bahder et al. 2019) were used. PCR reactions contained 5x GoTaq Flexi Buffer, 25 mM MgCl₂, 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_0 to a final volume of 25 μ L. Thermal cycling conditions for COI 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 40°C, 1 min 30 sec extension at 72°C, followed by a 5 min extension at 72°C. 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 55°C, 2 min extension at 72°C, followed by a 5 min extension at 72°C. PCR products of the appropriate size were purified using the Exo-SAP-ITTM PCR Product Cleanup Reagent (ThermoFisher Scientific, Waltham, Massachusetts, USA). Purified PCR product was quantified using a NanoDropLite spectrophotometer (ThermoFisher Scientific, Waltham, Massachusetts, USA) and 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 ClustalW as part of the package MEGA7 (Kumar et al. 2016). A matrix of pairwise differences using the number of differences among COI and 18S

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. A Maximum Likelihood tree was generated using the Bootstrap method at 1,000 replicates based on the Tamura-Nei model for concatenated COI and 18S data to yield a consensus tree.

Taxon sampling. For both the COI and 18S loci, DNA sequence data was used from *Herpis soros* Bahder & Bartlett, eight species of *Omolicna* Fennah, four species of *Agoo* Bahder & Bartlett, four species of *Tico* Bahder & Bartlett, two species of *Anchimothon* Fennah, *Cenchrea dorsalis* Westwood, *Oropuna halo* Bahder & Bartlett, and *Neocenchrea heidemanni* (Ball) to generate a consensus tree with *Anotia firebugia* used as an outgroup (Otiocerini) to root the tree (Table 1).

	GenBank A	Accession No.
Species	COI	18S
Agoo beani	MT413388	MT415403
Agoo dahliana	MN496467	MH472754
Agoo luzdenia	MT085818	MN999709
Agoo xavieri	MK443068	MK443073
Anchimothon dubia	MN496470	MN474755
Anchimothon myriei	ON231398	ON230027
Anotia firebugia	MT084365	MT945942
Cenchrea dorsalis	MT413387	MN472756
Herpis soros	MT085817	MT415406
Neocenchrea heidemanni	MN496473	MT415406
Omolicna brunnea	MK443070	MK443071
Omolicna cubana	MT413386	MT415404
Omolicna joi	KF472312	MN472753
Omolicna latens	MN496472	MN472757
Omolicna mariajoseae	MT422534	MT424915
Omolicna puertana	MN496468	MN472751
Omolicna tarco	MT422533	MT424914
Omolicna triata	MK443069	MK443072
Oropuna halo	MZ836006	MZ828126
Tico emmettcarri	MT085816	MT526036
Tico pseudosoroius	MT997938	MT526037
Tico sierra	MT085817	MT415406
Tico villablanca	ON797450	ON783969

TABLE 1. Taxa used for constructing phylogeny based on the COI and 18S genes and performing pairwise comparisons.

Systematics

Family Derbidae Spinola 1839

Subfamily Derbinae Spinola 1839

Tribe Cenchreini Muir 1913

Genus Herpis Stål 1862

Type species *Herpis fuscovittata* Stål, 1862, by subsequent designation of Muir 1924: 16 (see also McAtee 1924: 175). *Syntames* Fowler, 1905 (Type species *Syntames delicatus* Fowler 1905, by monotypy). Synonym with *Herpis* according to Muir 1924: 16; Caldwell 1944: 99; O'Brien 1987: 383; treated as valid by Metcalf 1938: 324; 1945a: 101; 1945b: 125.
Synonymy of *Syntames* with *Herpis* confirmed in Bahder *et al.* (2021a).

Amended Diagnosis (Modified from Bahder *et al* 2021a). Relatively large, and robust cenchreines, measuring approximately 5-8 mm in length, including wings. Wings held tectiform in repose, distinctly exceeding abdomen. Vertex broad, trapezoidal, just broader than long, nearly flat to weakly concave, transverse carinae present at fastigium. Pits present along lateral carinae of vertex and frons, varying in distinctness, appearing to be in 2+ rows. Frons (frontal view) broad, flat or nearly so (not concave), lateral margins parallel, medium carina of frons evident, frontoclypeal margin straight. Clypeus elongate-triangular, approximately in the same plane as frons, median carina present. Genae without subantennal processes. Antennae short, pedicle spheroid, about as long as wide. Lateral ocelli obscure or absent.

Pronotum narrow, anterior convex, posterior concave, broadening laterally, in lateral view declinate anteriorly; paranotal region foliate, forming large foveae posterior to the antennae (a tribal feature). Mesonotum tricarinate, carinae approximately reaching posterior margin, scutellum contiguous with scutum (i.e., not separated by groove). Lateral teeth absent on tibiae.

Terminalia bilaterally symmetrical. Pygofer in lateral view narrow, irregular in outline; in ventral view, median process of pygofer present (longer than wide, apically conical). Gonostyli elongate, broad, bearing dorsal projection in proximal half, and (in ventral view) usually with a medial (ental) process near midlength. Aedeagal shaft with processes apically and near midlength; flagellum complex, with elongate retrorse processes. Anal tube elongate in lateral view (but usually shorter than gonostyli), distally expanded; in dorsal view appearing spatulate with caudal margin strongly bifid.

Herpis circumsoros Bahder & Bartlett sp. n.

(Figures 2–6)

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



FIGURE 1. Habitat and locality of Herpis circumsoros sp. n.

Diagnosis. Body pallid, wings marked with oblique fascia, and three fuscous patches at base of wing. Terminalia bilaterally symmetrical. Medioventral process of pygofer longer than wide, approximately triangular, apex acute. Gonostyli in lateral irregularly spatulate, apex medially inflected with sclerotized point, bearing an angular process

on oblique margin; in ventral view with large median hook just before midlength aedeagus bearing 6 pairs of processes plus a 5-parted endosoma; the aedeagal processes A1 & A2 are mildly serpentine and much shorter than processes A3 & A4 (Fig. 6, compared with *H. soros* in remarks below). Anal tube in lateral view elongate, distally enlarged with ventral margin concave; in dorsal view abruptly expanded just before anal column into pair of stout processes.

Description. *Color.* General body color predominantly white washed with yellowish (to tan) markings (Fig. 2), anterior region of the head dull orange, pronotum dull orange, mesonotum with dull orange distad of lateral carinae, white mesad of lateral carinae (forming median vitta), median carina dull orange (Fig. 3). Forewing transparent with fuscous oblique fascia extending from apex of RA proximad to Pcu with three fuscous patches in proximal portion of forewing (one at the base of the postcostal cell, one proximal between veins CuP and Pcu, and one proximal between Pcu and A1). Veins pale yellow distally, darker basally with apical vein washed with red from RA to clavus plus apices of MP and CuA. Abdominal tergites yellow-orange.

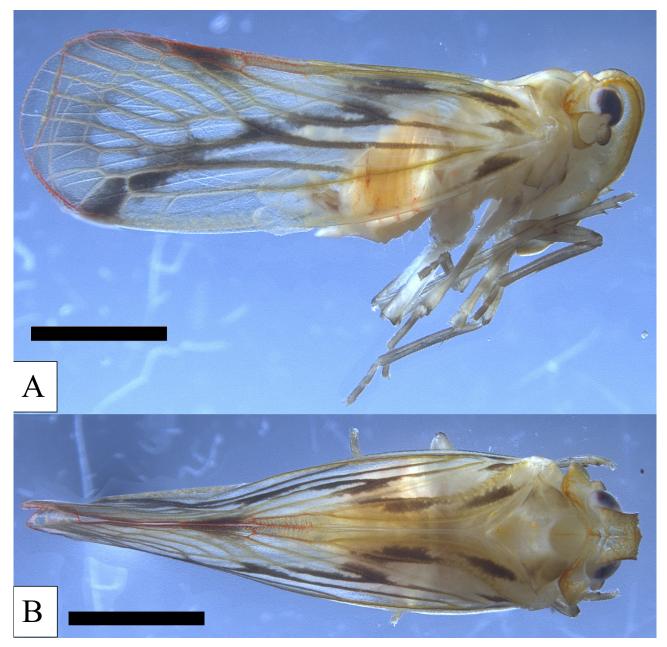


FIGURE 2. Male adult habitus, Herpis circumsoros sp. n. (A) lateral view; (B) dorsal view.

Structure. Body length male (with wings) 4.00 mm (n=1), female 4.15 (n=1) (Table 2). <u>Head</u>. Vertex broad, trapezoidal, wider than long, widest basally, narrowed distally, median carina distinct, apex bearing weakly concave transverse carina, posterior margin angulate, lateral margins bearing 2+ rows of pits of variable, continuing to

lateral margins of frons (Fig. 3A) although diminished in size (Fig. 3B); vertex weakly medially depressed in frontal view. Frons broad, lateral margins parallel and keeled; median carina distinct with dorsal portion convex forming projection near fastigium (evident from both frontal and dorsal views). Frontoclypeal suture straight, clypeus elongately triangular with distinct median keel. In lateral view, head evenly rounded from vertex, across fastigium, to face (Fig. 3C). Antennae short (greatly overtopped by foliate paradiscal region of pronotum in frontal view, Fig. 3B), scape very small, pedicle spheroid, about as wide as tall, with many placoid sensillae (roughly evenly dispersed), particularly on anterior margin. Lateral ocelli obsolete. Rostrum exceeding hind coxae, terminal segment short, about as long as wide.

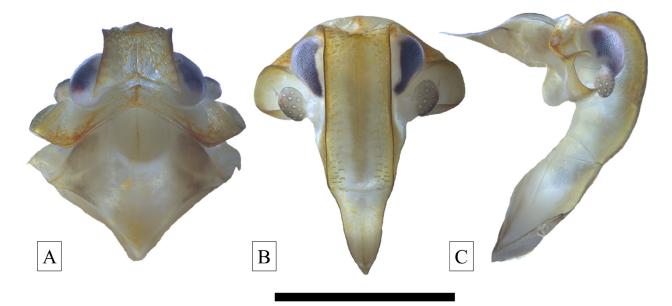


FIGURE 3. Adult *Herpis circumsoros* **sp. n.** (A) head, pronotum, mesonotum dorsal view; (B) head and pronotum frontal view; (C) head, pronotum, and mesonotum lateral view; scale = 1 mm.

Character	Male (<i>n</i> =1)	Female (<i>n</i> =1)	
Body length with wings	4.00	4.21	
Body length without wings	2.91	2.95	
Forewing length	3.33	3.36	
Vertex length	0.21	0.23	
Vertex width—basal	0.41	0.42	
Vertex width—distal	0.31	0.33	
Pronotum length-midline	0.10	0.12	
Mesonotum length-midline	0.66	0.68	
Mesonotum width	0.83	0.85	
Frons length	0.74	0.76	
Frons width—dorsal	0.31	0.33	
Frons width—frontoclypeal	0.31	0.33	
Clypeus length	0.27	0.28	

TABLE 2. Biometric data for Herpis circumsoros sp. n. (in mm)

<u>Thorax</u>. Pronotum narrow in dorsal view (about half length of vertex midlength), anterior margin moderately convex, posterior margin deeply concave, median carina distinct with disc depressed in lateral compartments; in lateral view with posterior margin foliately raised (anteriorly declinate); paranotal region expanded and greatly foliate forming fossae behind antennae (Fig. 3C), from frontal view expanded paradiscal region subquadrate, greatly exceeding antennae (Fig. 3B). Mesonotum at midline longer than vertex and pronotum combined; obscurely tricarinate, lateral carinae subparallel; median carina distinct on scutum, weaker on scutellum; notum weakly

inflected between scutum and scutellum. Tibiae lacking lateral spines; spinulation of hind leg 6–6–7. Forewing (Fig. 4) with apex of clavus near wing midlength, fork of CuA just basad of Sc+RA and RP fork (cell C1 longer than cell C5), both in proximal half of wing; vein MP combined with Sc+R forming short stem from basal cell; wing branching pattern RA 2-branched, RP 2-branched, MP 6-branched, CuA 2-branched CuA understood as fused and apex of C5 and subsequently forked); MP region of wing with 6 closed cells (C4-C3aa inclusive), wing cell C5 closed before wing margin, Pcu+A1 joining CuP before the composite vein reaches wing margin.



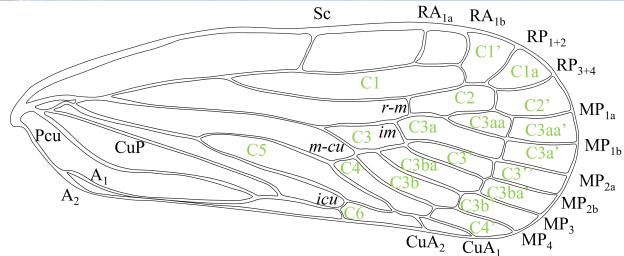


FIGURE 4. Male *Herpis circumsoros* sp. n. forewing venation; black = vein, green = cell, italics = crossvein.

<u>Terminalia</u>. Pygofer narrow (in lateral view), irregular in shape, narrowest subdorsally, widest ventrally, with irregularly sinuate anterior and posterior margins (Fig. 5A); in ventral view, medioventral process longer than wide, subtriangular at apex, lateral margins curved (Fig. 5B). Gonostyli in lateral view irregularly spatulate, narrowest near base, becoming abruptly wider with complex angular processes on incline of dorsal margin, distal margin broadly rounded (Fig. 5A), with dorsal apical margin medially curved (to sharply acuminate apex, visible from dorsal and ventral views, Figs. 5B, 5C); dorsal angular processes highly complex from dorsal view (Fig. 5C), rounded lobe with sclerotized tooth arising from base, second, larger lobe with constriction, forming circular apex angled mesad; in ventral view, gonostyli wide at base, abruptly constricting to sinuate medioventral margin bearing large, medial falcate processes before midlength (Fig. 5B). Aedeagus bilaterally symmetrical, in lateral view shaft upcurved bearing complex series of 6 pairs of processes, along shaft and at apex plus complex endosoma with 3 pairs of processes (Fig. 6); shaft with pair of elongate processes on both left and right margins (A1–A4) arising from lateral aspect before midlength on common base, proximal processes A3 and A4 more robust, longer than A1 and A2, curved slightly dorsad, directed posteriorly (Figs. 6A & 6B); shaft with two pair of subapical processes

(A5-A8), proximal pair (A7 & A8) retrorse and very elongate, extending almost to base of aedeagus, distal pair (A5 & A6) short and caudally directed processes; two pair of apical retrorse processes (A9-A12), both pair of moderate length, approximately 1/3 length of A5 & A6; processes A9 & A10 slightly downcurved; endosoma complex with 2 pairs of processes plus a single median process (E5); one dorsal pair (E1 & E2), arising at dorsal midline, curved medially, slender, extending to about midpoint of aedeagus; a second pair (E3 & E4) consisting of stout, elongate serrate lobes (E3 & E4);, extending to aedeagal base, serrate at apex and along dorsal margin; single median process (E5, visible from lateral view), stout, upcurved and apically round located beneath large serrate lobes (E3, E4) and half their length. Anal tube elongate in lateral view (approximately 2/3 length of gonostyli), distally expanded and inflected ventrad, narrowed to a sharp point; in dorsal view spatulate with caudal margin strongly bifid. Paraproct short and conical.

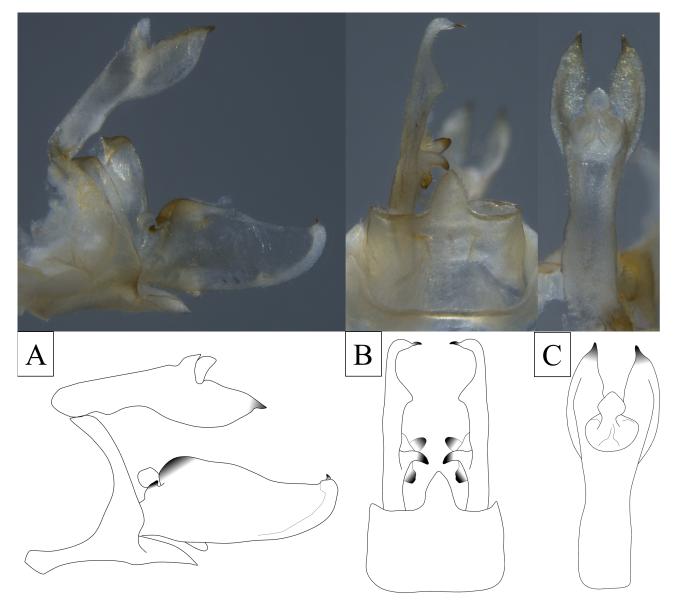


FIGURE 5. Male terminalia, Herpis circumsoros sp. n. (A) lateral view; (B) ventral view; (C) dorsal view.

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

Distribution. Costa Rica (Alajuela Province).

Etymology. The specific epithet refers to similarities in *habitus* between this species and *H. soros*; the name is derived from the Latin term *circum* (around) appended to the specific epithet '*soros*'.

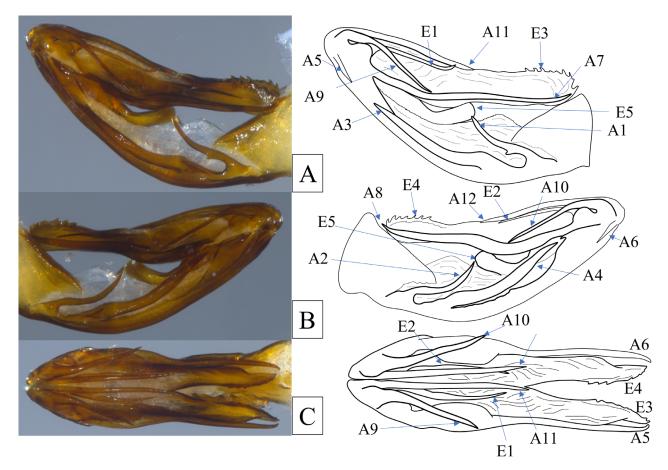


FIGURE 6. Aedeagus of Herpis circumsoros sp. n. (A) right lateral view; (B) left lateral view; (C) dorsal view.

Material examined. Holotype male, "Costa Rica, Alajuela Pr. / Hotel Villa Blanca / 21-VI-2019 / Coll.: B.W. Bahder / sweeping palm seedlings // Holotype / *Herpis circumsoros*" (FLREC). Paratypes, same as holotype (5 males, 5 females, 5 females, FLREC and FSCA).

Sequence Data. For the COI gene, a 705 bp product was generated (GenBank Accession No. OQ108307) and for the 18S genes, a 1,438 bp product was generated (GenBank Accession No. OQ108366). The phylogenetic analysis based on COI and 18S data show strong bootstrap support (99 and 100 respectively) for *Herpis circumsoros* **sp. n.** resolving adjacent to *H. soros* (Fig. 7). This relationship is also reflected in the consensus tree with strong bootstrap support (100) (Fig. 7C). In this phylogenetic analysis, *Herpis* is sister to *Oropuna*, the same relationship that was found in Bahder *et al.* (2021b).

Based on the pairwise comparison conducted using the 18S gene, *H. circumsoros* **sp. n.** differed by 2.9% from *H. soros*, whereas, it differed from other genera by an average of 8.8% (\pm 0.4) (Table 2). Of the taxa analyzed that had multiple species represented, the average variation within genera (intrageneric) was 1.7% (\pm 0.5) while the average variability among genera (intergeneric) was 7.3% (\pm 0.2). The level of variability between *H. circumsoros* **sp. n.** and *H. soros* is consistent with the expected intrageneric variability among available Cenchreini and the variability observed for both 18S and COI are consistent with interspecific levels of variability observed for respective genera, supporting the placement of *H. circumsoros* **sp. n.** in the genus *Herpis* and establishing it as distinct from *H. soros*.

Remarks. The new species placement in *Herpis* is strongly supported based on morphological characters. External diagnostic features for the genus include relatively large and stout (among New World Cenchreini), frons broad and parallel-sided, bearing a median carina, frontoclypeal margin straight; vertex broad (nearly flat from frontal view). Among species of *Herpis* so far examined (*H. metcalfi, H. albida, H. soros,* and *H. fuscovittata*), they are all relatively pale in coloration. Genus-level features for the terminalia include broad, elongate parameres, each bearing a dorsal process and, in ventral view, a median hook; the aedeagus with a complex array of processes on

the shaft and associated with the endosoma; and the anal tube elongate and, in dorsal view, apically bifid. These features appear to be consistent among the new species and terminalia figured by O'Brien 1987 (fig. 23 *H. delicata,* and fig. 17, *H. metcalfi*).

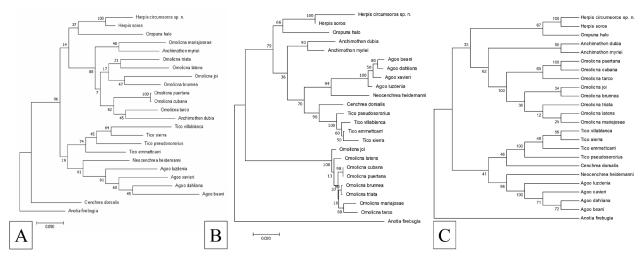


FIGURE 7. Maximum Likelihood trees (1,000 replicates) demonstrating relationship of *Herpis circumsoros* **sp. n.** relative to other Cenchreini planthoppers available with *Anotia firebugia* (Otiocerini) as an outgroup; (A) COI, (B)18S and (C) consensus tree based on concatenated COI and 18S sequence data, scale bar = percent nucleotide difference.

Herpis circumsoros sp. n. is similar to Herpis soros, and are superficially very similar. Differences between these species include the forewings with three basal black spots in *H. circumsoros* (two in *H. soros*), and the length of the MP₁ vein between the r-m crossvein and the MP₁ fork is longer circumsoros sp. n. (and the im-crossvein is shorter); differences in the terminalia include the aedeagal processes of the shaft are shorter and appressed to the shaft in H. circumsoros sp. n. (vs. elongate, falciform and diverging from the shaft in *H. soros*); also, the pair of processes A3 & A4 are much more elongate in H. circumsoros sp. n. Another difference appears to be that the distal portion of the anal tube is more elongated in *H. soros* than in *H. circumsoros* sp. n. In ventral view, the gonostyli are much narrower in *H. circumsoros* sp. n. than in *H. soros*, most notably distal to the hooked process on the inner margins. These relatively small differences in morphology are supported by molecular data from both the COI (99) and 18S (100) genes and is further reflected in the consensus phylogeny (100). Furthermore, the difference among species in the same genus for 18S. Of the other genera and species analyzed, the intrageneric variability is around 1%. This trend is particularly fascinating due to the morphological similarity between the two species of *Herpis* whereas all other species analyzed are far more distinct from each other yet have a smaller difference for the 18S gene.

Discussion

Herpis circumsoros **sp. n.** is the 11th described *Herpis* species from the new world, and the third species reported from Costa Rica (along with *H. albida* (Metcalf) and *H. soros*).

The discovery of a novel species of planthopper in the genus *Herpis* and the generation of sequence data for a previously understudied group from a phylogenetic perspective significantly enhances our understanding of the diversity of the Cenchreini and the overall evolutionary relationships among the New World cenchreine genera. Currently, no other genus within this tribe is as easily distinguished based on external morphological characteristics. Based on the samples analyzed, it appears the monophyly of *Herpis* is supported, however representatives of described taxa are still needed to definitively establish this.

This group of species within *Herpis* (those with a diagonal fuscous stripe on the wing; *H. delicata*, *H. metcalfi*, *H. soros*, and *H. circumsoros* **sp. n.**) is fascinating and highlights the need to revisit museum collections of specimens with this trait to determine if other, undescribed taxa exist that were erroneously identified as either *H. delicata* or *H. metcalfi*.

right=s	rigni-standard error, light blue cells-intergeneric variability, orange	0		· · · · · · · · · · · · · · · · · · ·														
		-	2	3	4	5	6	7	~	6	10	=	12	13	14	15	16	17
-	Herpis_circumsoros_spn.		0.005 0.008		0.008	0.008	0.007	0.007	0.008	0.008	0.008	0.008	0.008	0.008	0.008	0.007	0.008	0.010
2	Herpis_soros	0.029		0.007 0.007	0.007	0.007	0.005	0.006	0.007	0.006	0.007	0.008	0.008	0.007	0.007	0.006	0.006	0.009
З	Tico_sierra	0.080 0.054	0.054		0.003	0.003	0.006	0.006	0.007	0.007	0.007	0.008	0.008	0.008	0.006	0.006	0.005	0.010
4	Tico_emmettcarri	0.080	0.053	0.009		0.002	0.006	0.006	0.007	0.007	0.007	0.008	0.008	0.008	0.006	0.006	0.005	0.010
5	Tico_pseudosororius	0.080	0.053	0.013	0.008		0.006	0.006	0.007	0.007	0.007	0.008	0.008	0.008	0.007	0.006	0.005	0.010
9	Anchimothon_myriei	0.068	0.042	0.053	0.049	0.050		0.004	0.006	0.006	0.007	0.007	0.007	0.007	0.006	0.006	0.006	0.009
7	Anchimothon_dubia	0.078	0.052	0.054	0.050	0.052	0.026		0.007	0.007	0.007	0.008	0.007	0.007	0.006	0.006	0.005	0.009
8	Agoo_xavieri	0.087	0.060	0.059	0.057	0.059	0.065	0.074		0.003	0.002	0.008	0.008	0.008	0.006	0.007	0.007	0.009
6	Agoo_dahliana	0.088	0.061	0.061	0.058	0.060	0.064	0.073	0.010		0.003	0.008	0.008	0.008	0.006	0.007	0.007	0.009
10	Agoo_luzdenia	0.086	0.059	0.057	0.055	0.057	0.065	0.070	0.008	0.011		0.008	0.008	0.008	0.006	0.007	0.007	0.009
11	Omolicna_cubana	0.113	0.090	0.097	0.097	0.097	0.079	0.085	0.096	0.097	0.098		0.003	0.002	0.008	0.008	0.007	0.010
12	Omolicna_joi	0.112	0.089	0.098	0.099	0.097	0.081	0.088	0.095	0.096	0.097	0.009		0.003	0.008	0.008	0.007	0.010
13	Omolicna_triata	0.113	0.090	0.098	0.098	0.096	0.080	0.089	0.096	0.096	0.097	0.007	0.008		0.008	0.007	0.007	0.010
14	Neocenchrea_heidemanni	0.093	0.065	0.062	0.058	0.061	0.064	0.054	0.053	0.052	0.049	0.095	0.097	0.097		0.007	0.006	0.009
15	Oropuna_halo	0.073	0.046	0.057	0.057	0.057	0.057	0.060	0.073	0.071	0.073	0.097	0.096	0.097	0.073		0.006	0.009
16	Cenchrea_dorsalis	0.079	0.051	0.030	0.028	0.030	0.049	0.044	0.062	0.059	0.060	0.094	0.098	0.097	0.047	0.054		0.009
17	Anotia_firebugia	0.147	0.128	0.144	0.142	0.141	0.134	0.130	0.136	0.136	0.135	0.145	0.144	0.146	0.136	0.128	0.134	

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