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ANIMAL SCIENCE

Description of *Uniphylus* gen. nov., a new genus of Carcharodini (Lepidoptera, Hesperiidae, Pyrginae) for *Staphylus evemerus* Godman & Salvin, 1896

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Abstract: *Staphylus evemerus* Godman & Salvin, 1896 is a species with a unique set of morphological characters within Carcharodini. Also, mitochondrial cytochrome oxidase subunit 1 (COI) sequences analysis demonstrated a large genetic distance with other related genera of the tribe. Therefore, this paper aims to describe a new genus for this species, which is named as *Uniphylus* **gen. nov.** Besides the morphological redescription of the male of *Uniphylus evemerus* (Godman & Salvin, 1896) **new comb.,** the description of the female is provided for the first time, as well as an updated distributional map with all records known so far for this species.

Key words: Skipper, Neotropical, Costa Rica, Panama, cytochrome oxidase subunit 1.

INTRODUCTION

Carcharodini is a tribe of Pyrginae (Hesperiidae, Lepidoptera) that includes approximately 300 species distributed in 35 genera, four of which are present in the Old World (*Carcharodus* Hübner, [1819], *Spialia* Swinhoe, 1912, *Gomalia* Moore, 1879 and *Muschampia* Tutt, 1906), while the others occur in the New World regions (Warren et al. 2009, Cong et al. 2019, Li et al. 2019, Zhang et al. 2020a). Carcharodini is a sister-group of Pyrgini, with the divergence time occurring in the Eocene around 42 Mya, together with the other two tribes of Pyrginae, Achlyodini and Erynnini (Li et al. 2019). Though the monophyly of Carcharodini is strongly recovered in molecular analysis performed in above cited studies, no morphological synapomorphy has been recognized so far. Despite this, Warren et al. (2009) partially characterized the males of Carcharodini to possess an asymmetrical pattern in the genitalia morphology, known as "*Nisoniades*-type" valva (*sensu* Evans 1953). Most of the female genitalia of Carcharodini, as it is for many other groups of Lepidoptera, are not described. However, Siewert et al. (2016) illustrated and described the female genitalia of *Sophista* as asymmetrical as well. Concerning the immature stages, Carcharodini larval foodplants include a variety of dicots, although *Cyclosemia herennius* (Stoll, 1782) is the only New World Carcharodini known to feed on monocots (Warren et al. 2009).

Although skippers are historically less studied than other butterfly families, this scenario is currently changing, with numerous studies taxonomically redefining subfamilies, tribes, genera, and subgenera with the use of molecular tools, most of them including genome sequencing (Cong et al. 2019, Li et al. 2019, Zhang et al. 2019a, b, 2020a, b, 2022a). Moreover, some of these studies suggest that different molecular analyses can produce good hypotheses regarding generic taxonomical levels (Cong et al. 2019, Zhang et al. 2022a). For example, some of the new genera recently proposed for Carcharodini, such as *Clytius* Grishin, 2019 (type species: *Pholisora clytius* Godman and Salvin, [1897]), *Incisus* Grishin, 2019 (type species: *Antigonus incisus* Mabille, 1878), *Perus* Grishin, 2019 (type species: *Pholisora cordillerae* Lindsey, 1925), and *Viuria* Grishin, 2019 (type species: *Pellicia licisca* Plötz, 1882), have been recovered in four different molecular approaches: nuclear genome, z chromosome, mitochondrial genome, and COI barcode (Cong et al. 2019). Also, when the morphological characters are evaluated, especially those of the male genitalia, these new taxa demonstrate good morphological diagnostic characters.

Staphylus Godman & Salvin, 1896 (type species: *Helias ascalaphus* Staudinger, 1876) is one of the richest genera of Carcharodini, with 47 species. A related genus is *Bolla* Mabille, 1903 (type species: *Bolla pullata* Mabille, 1903, currently a junior subjective synonym of *Bolla imbras* (Godman and Salvin, [1896]), comprising 29 species (Mielke 2005, Cong et al. 2019, Zhang et al. 2022a, b, Lemes et al. 2023). Together, these two genera of small brown Carcharodini represent very challenging groups, as their accurate identifications are usually possible only after dissecting and analyzing their genitalia (Lemes et al. 2021, 2023). Another close genus is *Pholisora* Scudder, 1872 (type species: *P. catullus* (Fabricius, 1793)), currently with only four valid species (Mielke 2005, Warren et al. 2023), although historically *Pholisora* has included several species of the above cited genera (Mielke 2005).

When studying some Carcharodini species, it was noted that the Central American species *Staphylus evemerus* Godman & Salvin, 1896 is morphologically distinct from other species of *Staphylus* Godman & Salvin, 1896, with larger wings, forewings with inner margin concave and a unique male and female genitalia pattern. The morphological combination of characters of *S. evemerus* also does not fit into any of the known Carcharodini genera. To test a generic taxonomical hypothesis for *S. evemerus*, COI-sequences of this species and 20 other of *Staphylus* were obtained. A large genetic distance was observed between *S. evemerus* and other *Staphylus*, corroborating the recognition of a new genus. Therefore, the aim of this paper is to describe a new Carcharodini genus to include *S. evemerus*, and to provide additional taxonomical notes on this species.

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MATERIALS AND METHODS

The material used in this study is from the following public and private collections: DZUP - Coleção Entomológica Pe. Jesus de Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil; MGCL - McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, United States; NHMUK - The Natural History Museum, London, United Kingdom; OM - Olaf Hermann Hendrik Mielke collection, Curitiba, Paraná, Brazil. Eight specimens of *Uniphylus evemerus* **new comb.** were found in these institutions.

For the molecular analysis, two legs (meso and metathoracic from the same side) from 22 skippers of the internal group and related Carcharodini genera (Table I) were detached and sent to the Canadian Center for DNA Barcoding (CCDB) for DNA extraction, amplification, and sequencing of the mitochondrial cytochrome

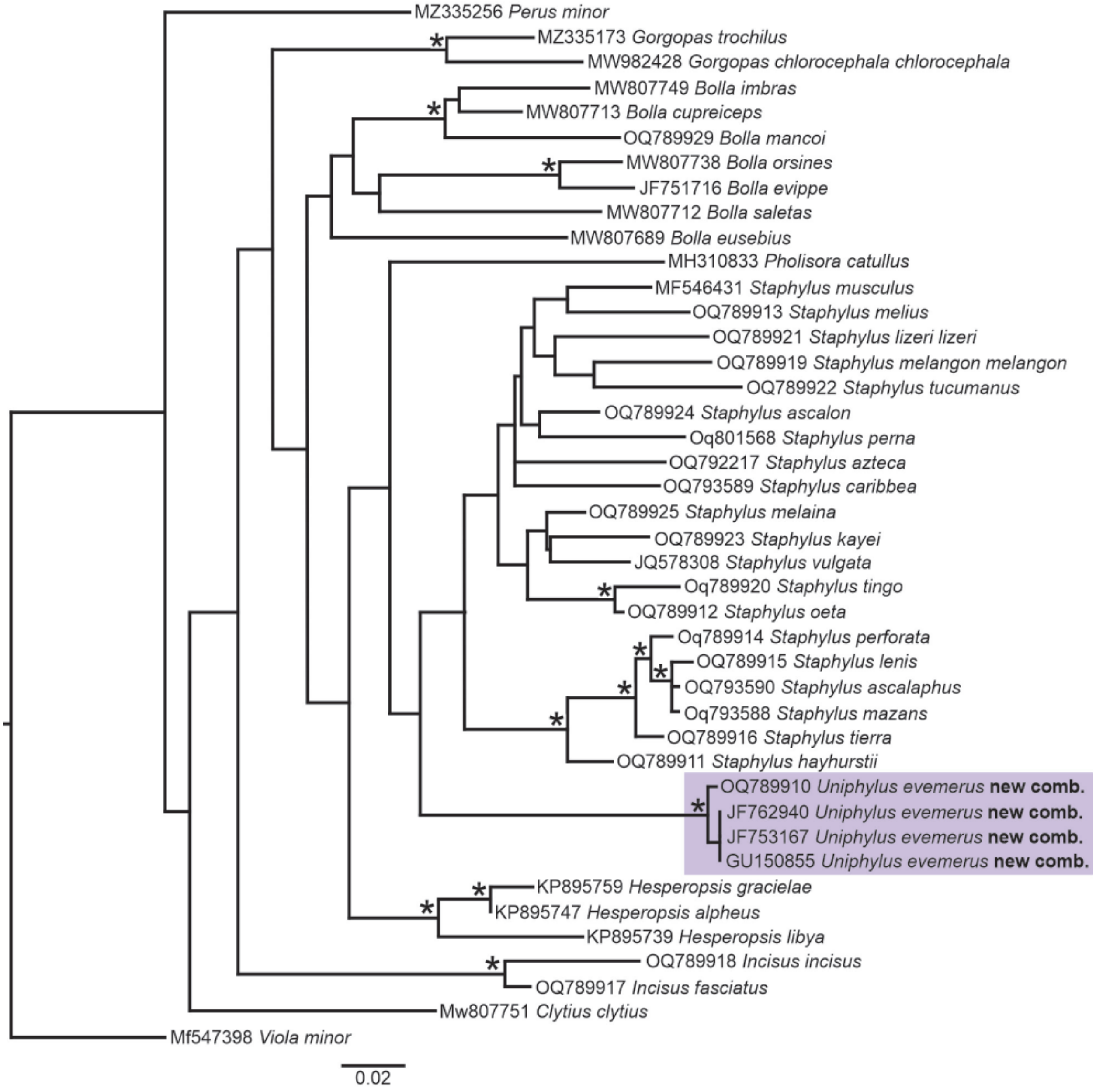

Figure 1. Relationship among *Uniphylus evemerus* (Godman & Salvin, 1896) new comb. and other genera of Carcharodini based on DNA barcode sequences obtained by Maximum likelihood inferred with IQTREE. Support values were considered sufficient when SH-aLRT ≥ 80 and UFBoot ≥ 95 at the same time ("*" represents sufficient support values).

oxidase subunit 1 (COI) using standardized methods (Hebert et al. 2003). The obtained sequences were included in GenBank with accession numbers available in table I. These specimens were identified through analysis of their genitalia and comparison with original descriptions and other important taxonomical studies, such as Evans (1953) and Steinhauser (1989). COI sequences available in GenBank (NCBI 2020) of other Carcharodini species were also included in the analysis (Janzen et al. 2011, Pratt et al. 2015, Lavinia et al. 2017, Pfeiler 2018, Attiná et al. 2021, Earl et al. 2021, Santos et al. 2022). The

Table I. Sequences of mitochondrial cytochrome oxidase subunit 1 (COI) used in this study. The depositary collections of the specimens used in this study and their respective accession numbers in GenBank are cited. Sequences of *Uniphylus evemerus* **new. comb.** bold highlighted.

GenBank accession numbers	Specimen identification	Locality	Reference	Collection - Voucher
MW807713	*Bolla cupreiceps*	Bolivia, La Paz	Earl et al. 2021	
MW807689	*Bolla eusebius*	Guatemala, Sacatepequez	Earl et al. 2021	
JF751716	*Bolla evippe*	Costa Rica, Guanacaste	Janzen et al. 2011	
MW807749	*Bolla imbras*	Mexico, Veracruz	Earl et al. 2021	
OQ789929	*Bolla mancoi*	Brazil, Acre	This study	DZ 45.685
MW807738	*Bolla orsines*	Guatemala, Sacatepequez	Earl et al. 2021	
MW807712	*Bolla saletas*	Guatemala, Sololá	Earl et al. 2021	
MW807751	*Clytius clytius*	Mexico, Veracruz	Earl et al. 2021	
GU150855	***Uniphylus evemerus* new comb.**	**Costa Rica, Guanacaste**	**Janzen et al. 2011**	
JF762940	***Uniphylus evemerus* new comb.**	**Costa Rica, Guanacaste**	**Janzen et al. 2011**	
JF753167	***Uniphylus evemerus* new comb.**	**Costa Rica, Guanacaste**	**Janzen et al. 2011**	
OQ789910	***Uniphylus evemerus* new comb.**	**Costa Rica, Alajuela**	**This study**	**MGCL - MGCL 1092142**
MW982428	*Gorgopas c. chlorocephala*	Peru, Cusco	Santos et al. 2022	
MZ335173	*Gorgopas trochilus*	Argentina, Jujuy	Attiná et al. 2021	
KP895747	*Hesperopsis alpheus*	United States, California	Pratt et al. 2015	
KP895759	*Hesperopsis gracielae*	United States, Nevada	Pratt et al. 2015	
KP895739	*Hesperopsis libya*	United States, California	Pratt et al. 2015	
OQ789917	*Incisus fasciatus*	Brazil, Paraná	This study	DZUP - DZ 46.510
OQ789918	*Incisus incisus*	Brazil, Paraná	This study	DZUP - DZ 44.241
MZ335256	*Perus minor*	Argentina, Salta	Attiná et al. 2021	
MH310833	*Pholisora catullus*	Mexico, Sonora	Pfeiler 2018	
OQ793590	*Staphylus ascalaphus*	Panama, Colón	This study	MGCL - MGCL 1112099
OQ789924	*Staphylus ascalon*	Brazil, Minas Gerais	This study	DZUP - DZ 44.775
OQ792217	*Staphylus azteca*	Panama, Panama	This study	MGCL - MGCL 1106913
OQ793589	*Staphylus caribbea*	Costa Rica, Limón	This study	MGCL - MGCL 1106974
OQ789911	*Staphylus hayhurstii*	United States, Oklahoma	This study	MGCL - MGCL 1112057
OQ789923	*Staphylus kayei*	Colombia, Meta	This study	DZUP - DZ 45.386
OQ789915	*Staphylus lenis*	Guatemala, Petén	This study	MGCL - MGCL 1092227
OQ789921	*Staphylus l. lizeri*	Colombia, Meta	This study	DZUP - DZ 45.296
OQ793588	*Staphylus mazans*	Mexico, Tampa	This study	MGCL - MGCL 1083984

Table I. Continuation.

OQ789925	*Staphylus melaina*	Bolivia, Santa Cruz	This study	OM - OM 56.023
OQ789919	*Staphylus m. melangon*	Brazil, Minas Gerais	This study	DZUP - DZ 46.563
OQ789913	*Staphylus melius*	Argentina, Salta	This study	MGCL - MGCL 1112054
MF546431	*Staphylus musculus*	Argentina, Entre Rios	Lavinia et al. 2017	
OQ789912	*Staphylus oeta*	Argentina, Jujuy	This study	MGCL - MGCL 1106794
OQ789914	*Staphylus perforata*	Bolivia, La Paz	This study	MGCL - MGCL 1092207
OQ801568	*Staphylus perna*	Brazil, Pernambuco	This study	DZUP - DZ 46.901
OQ789916	*Staphylus tierra*	Mexico, Jalisco	This study	MGCL - MGCL 1083879
OQ789920	*Staphylus tingo*	Peru, San Martin	This study	OM - OM 79.311
OQ789922	*Staphylus tucumanus*	Paraguay, Presidente Hayes	This study	OM - OM 36.162
JQ578308	*Staphylus vulgata*	Costa Rica, Guanacaste	Janzen et al. 2011	
MF547398	*Viola minor*	Argentina: Buenos Ayres	Lavinia et al. 2017	

chosen species for the analysis were selected based on the recent phylogenetic hypothesis for Carcharodini (Cong et al. 2019 and Zhang et al. 2022a). For this analysis, a total of 42 specimens from 39 species belonging to ten Carcharodini genera were used (Table I).

The molecular alignment for COI sequences was performed using the software Muscle in MEGA7 (Kumar et al. 2016). The pairwise genetic distances (%) was also calculated in MEGA7, and the frequency distribution of genetic divergence was plotted using pairwise values. The optimal model of nucleotide evolution was selected by ModelFinder (Kalyaanamoorthy et al. 2017) using the AICc criterion, resulting in GTR+F+I+G4. Maximum likelihood analysis was conducted using the software IQ-Tree (Nguyen et al. 2015) implemented in the PhyloSuit (Zhang et al. 2020c). For the Maximum Likelihood analysis, the ultra-fast bootstrap approximation method - UFBoot (5,000 bootstrap repetitions) was used (Minh et al. 2013), together with the SH-aLRT test (1,000 repetitions) (Guindon et al. 2010). The tree obtained was visualized and initially edited in the software FigTree v.1.4.3 (Rambaut 2006-2009), and later in the software Inkscape 1.0.1 (Harrington et al. 2004-2005). The tree was rooted at *Viola minor* (Hayward, 1933). Nodes were considered supported when both SH-aLRT ≥ 80 and UFBoot ≥ 95.

Abdomens of the studied specimens were detached and soaked in a heated 10% potassium hydroxide solution (KOH) for 5-10 minutes, and posteriorly dissected for the study of the genitalia. Dissected genitalia were stored in vials with glycerin, labeled accordingly, and photographed using a photo stacking process associated with a Leica® Application Suite Version 4.12.0 stereomicroscope. In the "examined material" section, the symbol "*" indicates that the genitalia of the specimens were dissected and analyzed. The general terminology follows Evans (1953), and the genitalia morphology follows Carneiro et al. (2013). The following abbreviations were used throughout the paper: DW (dorsal wing), FW (forewing), DFW (dorsal forewing), VFW (ventral forewing), HW (hindwing), DHW (dorsal hindwing), and VHW (ventral hindwing).

A taxonomical catalogue including all publications that mention the species is provided, following Mielke (2005). The full references cited in the catalogue are available in Lamas (2023). A distributional map was produced with SimpleMappr (Shorthouse 2010) from the label data of the specimens analyzed and literature records, consulting the geographic coordinates of the specific locality on Google Earth. In the cases where no specific locality was given, coordinates from the central region of the state were used.

RESULTS

Molecular data

A Maximum Likelihood analysis using the mitochondrial gene COI supported the monophyly of *Uniphylus* **gen. nov.** (ultrafast bootstrap support [ubs] = 100; SH-aLRT support = 100) (Fig. 1). The *Uniphylus* **gen. nov.** clade is sister to *Staphylus*, and these two forms a clade with *Pholisora* (Fig. 1).

Interspecific genetic distance ranged from 9% to 14% (Supplementary Material - Table SI, Fig. 2); the genetic distance between *Uniphylus* **gen. nov.** and *Staphylus* was 10.9%, and between *Uniphylus* **gen. nov.** and *Pholisora* was 11%. Based on the sequences of the mitochondrial gene COI, in conjunct with the morphological differences, these results support the description of new genus to include *Staphylus evemerus*.

Taxonomy

Uniphylus Lemes, Siewert, Mielke, Casagrande & Warren gen. nov.

ZooBank Life Science Identifier (LSID) - urn:lsid:zoobank.org:act:9E54C0B9-AFD7-4221-BA2F-C86DA45FF90D

(Figs. 1-8)

Type species (Fig. 3)

Staphylus evemerus Godman & Salvin, 1896.

Diagnosis

Uniphylus **gen. nov.** is readily distinguished from other genera of Carcharodini due to the following combination of characters (Figs. 3, 4, 5a-b, 6a-d, 7a-c, 8a-h): costal fold present on the male FW; FW inner margin concave; ampulla

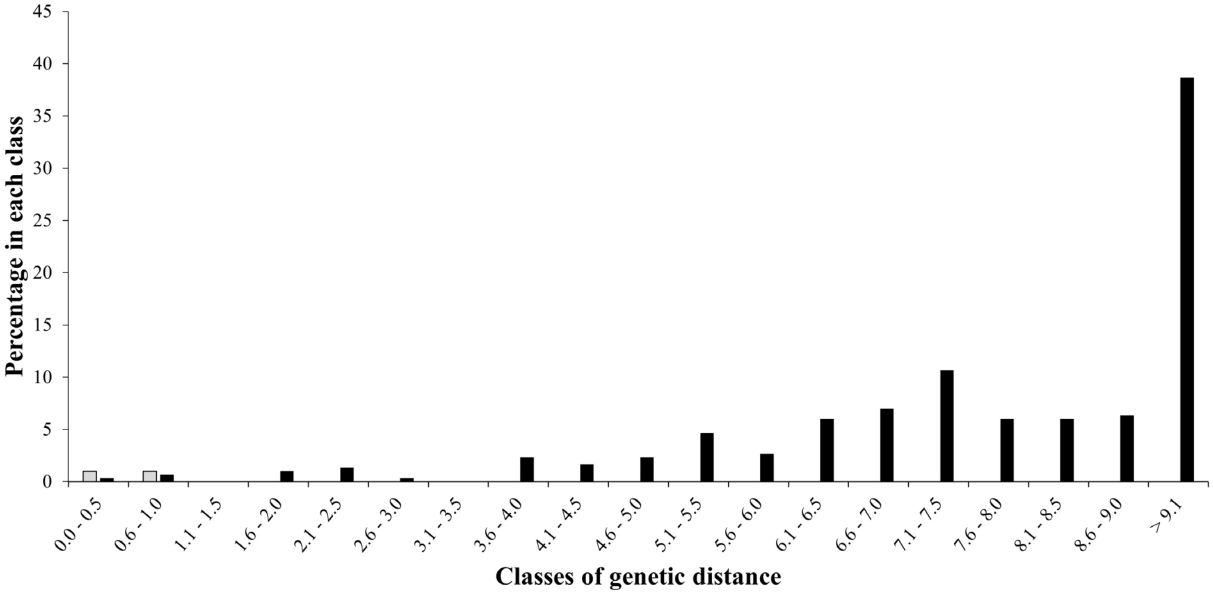

Figure 2. Frequency distribution of pairwise individual genetic distances within (*gray*) and between (*black*) the species of *Pholisora*, *Staphylus* and *Uniphylus* gen. nov.

very narrow, with upper margin concave; harpe about five times longer than wide, as a finger-like structure, with base surpassing the upper margin of ampulla, as a narrow conical process curved outwardly; tergum VIII with an anterior apophysis; lamella antevaginalis as a very sclerotized plate, quadrate in ventral view, with an excavation in the middle of the distal margin, and other larger excavation in the proximal margin in the region where presumably is the ostium bursae; lamella postvaginalis developed as narrow plate, with distal margin and proximal margin nearly straight, bearing microtrichia.

Male description (Figs. 3a-b, d, 4a-b, 5, 6, 8g-h)**.** ***Head:*** Brown with yellow scales dorsally; labial palpus pale-yellow ventrally, except the third segment which is brown. Antenna brown, ventrally with small yellow dots at the joints at the side. Nudum with 11 segments. ***Thorax:*** Brown with scarce yellow scales dorsally; brown with white hair-like scales ventrally. Legs brown with yellow scales and white hairs. ***FW length:*** Ranging between 1.3 cm and 1.5 cm (n = 4). ***FW shape:*** Outer margin rounded. Inner margin concave. ***DFW:*** Brown. Two transversal bands with paler pattern in the discal and postdiscal areas. Presence of costal fold. Absence of white dots in the subapical area. Presence of some sparse pale scales. Fringes brown. ***VFW:*** Brown with marginal and postdiscal areas clearer. Fringe brown. ***HW length:*** Ranging between 0.9 cm and 1.1 cm (n = 4). ***HW shape:*** Outer margin slightly undulated. ***DHW:*** Brown with sparse pale scales. Two transversal bands with paler pattern in the discal and postdiscal areas. Fringe as at DFW. ***VHW:*** Brown. Presence of sparse pale scales,

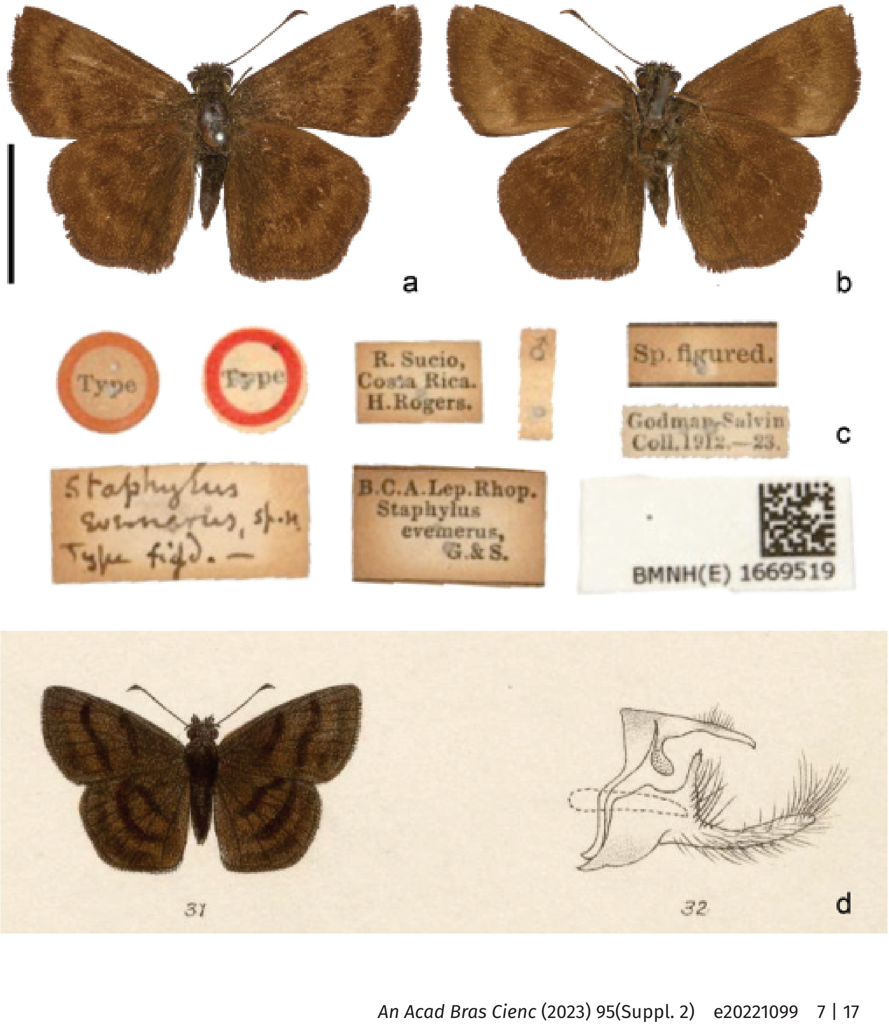

Figure 3. **Lectotype of *Staphylus evemerus* Godman & Salvin, 1896 deposited in the NHMUK in dorsal (a) and ventral (b) views, and its labels (c). Illustrations of the dorsal view of the adult and the male genitalia (d) of *Staphylus evemerus* available in Godman & Salvin (1896, volume B, Tab. 89). Scale bar = 1 cm.**

predominantly on the internal margin. Fringe brown. ***Abdomen*****:** Brown with scarce yellow scales dorsally and ventrally. ***Genitalia:*** Tegumen slightly longer than wide, with one central constricted region, proximal portion rounded at the proximal margin and larger than the distal margin. Ventral arms of the tegumen narrow and fused with dorsal projection of saccus, assuming that the boundaries between these structures are located at the angle between them. Saccus triangular, short, rounded proximally. Uncus conical-shaped, enlarged at the base, and ventrally with a large concavity that becomes a longitudinal opening towards the narrower apex, bearing some short hair-like scales dorsally. Gnathos developed as two short, sclerotized plates bearing fine microtrichia, fused ventrally by a thinner region bearing microtrichia. Valva longer than wide; sacculus slightly longer than wide, rectangle-shaped, as a fold into the valva; harpe about five times longer than wide, except at the base where it surpasses the dorsal margin of ampulla as a narrow conical process curved outwardly; the distal part of the harpe as a finger-like structure slightly curved upwardly, with upper margin subtly indented; ampulla very narrow, with upper margin concave; costa very thin following the general shape of the valve. Sacculus, harpe, and ampulla bear thin setae throughout their extensions, internally and externally. Aedeagus cylindrical, short, about half the length of valva; without spines and vesica without cornuti. Fultura superior absent. Fultura inferior developed, thin, crescent moon-shaped in anterior view.

Female description (Figs. 4c-d, 7)**.** ***FW length.*** 1.5 cm (n = 1). ***HW length.*** 1.1 cm (n = 1). ***Genitalia.*** Tergum VIII quadrate with anterior apophysis; papilla analis somewhat quadrate, covered by setae and posterior apophysis slightly curved, longer than the length of papilla analis. Lamella antevaginalis as a very sclerotized plate, quadrate in ventral view, with an excavation in the middle of the distal margin, and another larger excavation in the proximal margin in the region where presumably is the ostium bursae. Presence of a slender membranous area separating the lamella antevaginalis from the

Figure 4. ***Uniphylus evemerus*** **(Godman & Salvin, 1896) new comb. in dorsal and ventral views: a-b. Male (Costa Rica, San José, MGCL 1043687). c-d. Female (Panama, Chiriqui, Boquete, San Ramon, OM 46.830). Scale bar = 1 cm.**

lamella postvaginalis. Lamella postvaginalis as a narrow plate, with the distal margin and proximal margin nearly straight, bearing microtrichia. Ductus bursae membranous, about three times longer than corpus bursae. Corpus bursae rounded, membranous, about ¼ the length of ductus bursae.

Comments

The wing venation of *Uniphylus evemerus* **new comb.** is very similar to that of *Staphylus hayhurstii* (W. H. Edwards, 1870), *S. ceos* (W. H. Edwards, 1882) and *Pholisora catullus* (Fabricius, 1793), (Lindsey 1921, Fig. 13j, k, l). The concave inner margin of the FW of *Uniphylus evemerus* **new comb.** is similar with *I. incisus* (Mabille, 1878) (Fig. 8e). Despite that, the male genitalia are completely different between these two species (Fig. 8f). While males of *Incisus* species have a broader valva, *U. evemerus* **new comb.** has a narrow valva.

The valva of the male genitalia is probably the most remarkable difference between *U. evemerus* **new comb.**, and the other genera. While *U. evemerus* **new comb.** has a harpe developed as a finger-like structure, providing a unique aspect to the genitalia, in the other genera the valva is rectangular or ovoid (Fig. 8b, d, f, h). Regarding to the female genitalia, *U. evemerus* is the only Carcharodini species known to possess a developed anterior apophysis in the tergum VIII (Fig. 7b).

Etymology

The name *Uniphylus* is derived from two words: *unicus*, from the Latin for "only", an allusion to the unique morphology found in the type species of the genus, especially on the male genitalia morphology; and *phylus* from *Staphylus*, where the type species was included thus far. It is a noun in the genitive singular. The gender is masculine.

Uniphylus evemerus (Godman & Salvin, 1896), new combination

(Figs. 1-8)

Staphylus evemerus Godman & Salvin, 1896. **Biol. Centr.-Amer., Lep.-Rhop. 2**, p. 436; **3**, pl. 89, figs 31 (male d), 32 (male gen.); specimens, Caché, Rio Sucio, Irazu, Costa Rica, Rogers leg.; collection Godman & Salvin.- Draudt 1923, ***in*** Seitz. **Gross-Schmett. Erde 5**, p. 906, pl. 176g (d).- Evans 1953. **Cat. Amer. Hesp. 3**, p. 96, pl. 38 (male gen.).- Bridges 1983. **Lep. Hesp. 1**, p. 41; **2**,

Figure 5. Head in dorsal (a) and ventral (b) views of a male of *Uniphylus evemerus* (Godman & Salvin, 1896) new comb. (Panama, Chiriqui, Alto Lino, DZ 45.615).

p. 34.- DeVries, 1983, ***in*** Janzen. **Costa Rican Nat. Hist**., p. 676.- Bridges, 1988. **Cat. Hesp. 1**, p. 65; **2**, p. 57.- Bridges, 1994. **Cat. Fam.-Group, Gen.-Group, Sp. Group Nam. Hesp. (Lep.) World 8**, p. 78; **9**, p. 64.- O. Mielke 2004. Hesperioidea, p. 55, ***in*** Lamas (Ed.). **Checklist: Part 4A, Hesperioidea-Papilionoidea**, ***in*** Heppner (Ed.). **Atlas Neotrop. Lep. 5A**; ***syn***.: *evermerus*.- O. Mielke, 2005. **Cat. Amer. Hesperioidea 3**, p. 725; ***syn***.: *evermerus*.- Anderson, 2007. **Bull. Allyn Mus. 146**: 8.- Janzen et al. 2011. **PLoS ONE 6**(8) (e19874): Suppl. Fig. S1, Table SI, Table SII.- Garwood & Lehman 2013. **Butt. C. Amer. 3, Hesp**., p. 108, figs (d).- Fernández-Triana et al. 2014. **Zookeys 383**: 55, 141; parasitism.- Garwood ***et al***. 2021 (online). **Marip. de Colombia 1**, p. 258.

Bolla evemerus; Mabille, 1903, ***in*** Wytsman. **Gen. Ins. 17**, p. 72.

Pholisora evermerus [***sic***]; Shepard, 1935. **Lep. Cat. 69**, p. 345.

(no genus) *evemerus*; Beattie, 1976. **Rhop. Direct**., p. 142.

Taxonomic history. Godman & Salvin (1896) described *Staphylus evemerus*. The species was transferred by Mabille (1903) to *Bolla* Mabille, 1903, and after Shepard (1935) transferred it to *Pholisora* Scudder, 1872. Evans (1953) returned the species to *Staphylus*, and other authors followed this decision, mentioning the species in taxonomic comments, faunistic studies, and catalogs.

Type. *Staphylus evemerus* Godman & Salvin, 1896 was described based on an unspecified number of specimens from Caché, Rio Sucio, Irazu (Costa Rica), collected by H. Rogers, and deposited in the Godman & Salvin's collection. A male specimen was found in the NHMUK (Fig. 3a-c) with the following labels: / Type/ Type [H 736 written on the label back]/ R. Sucio, Costa Rica. H. Rogers / ♂/ Sp. figured./ *Staphylus evemerus*, sp. n. Type fig.-/ B.C.A.Lep.Rhop. *Staphylus evemerus*, G. & S./ Godman-Salvin Coll. 1912.-23./ BMNH(E) 1669519/. To stabilize the identity of this species, this male specimen is hereby designated lectotype of *Staphylus evemerus* and the following labels will be attached: / Lectotypus/ Lectotypus *Staphylus evemerus* Godman & Salvin, 1896; Lemes, Siewert, Mielke, Casagrande & Warren des. 2022/. These labels will be sent to the curator for the collection.

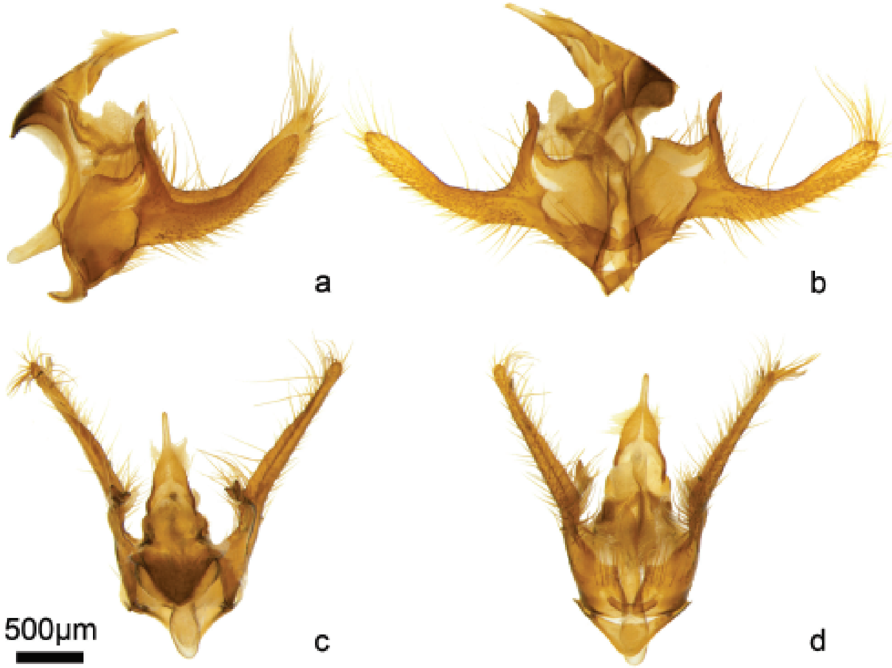

Figure 6. Male genitalia of *Uniphylus evemerus* (Godman & Salvin, 1896) new comb. in lateral **(a)**, internal **(b)**, dorsal **(c)** and ventral **(d)** views (Panama, Chiriqui, Boquete, San Ramon, OM 46.936).

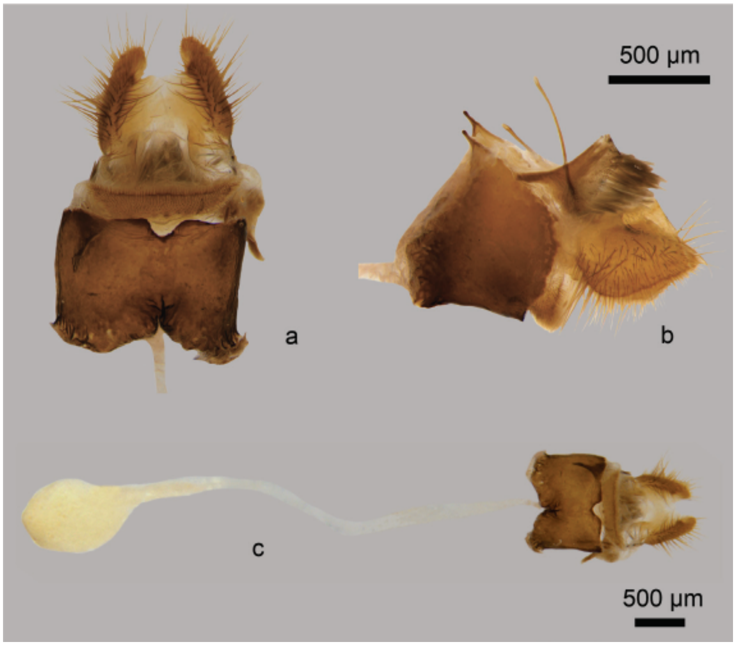

Figure 7. Female genitalia *Uniphylus evemerus* (Godman & Salvin, 1896) **new comb.** Sterigma in ventral **(a)**, and lateral views **(b)**, and general ventral view **(c)** (Panama, Chiriqui, Boquete, San Ramon, OM 46.830).

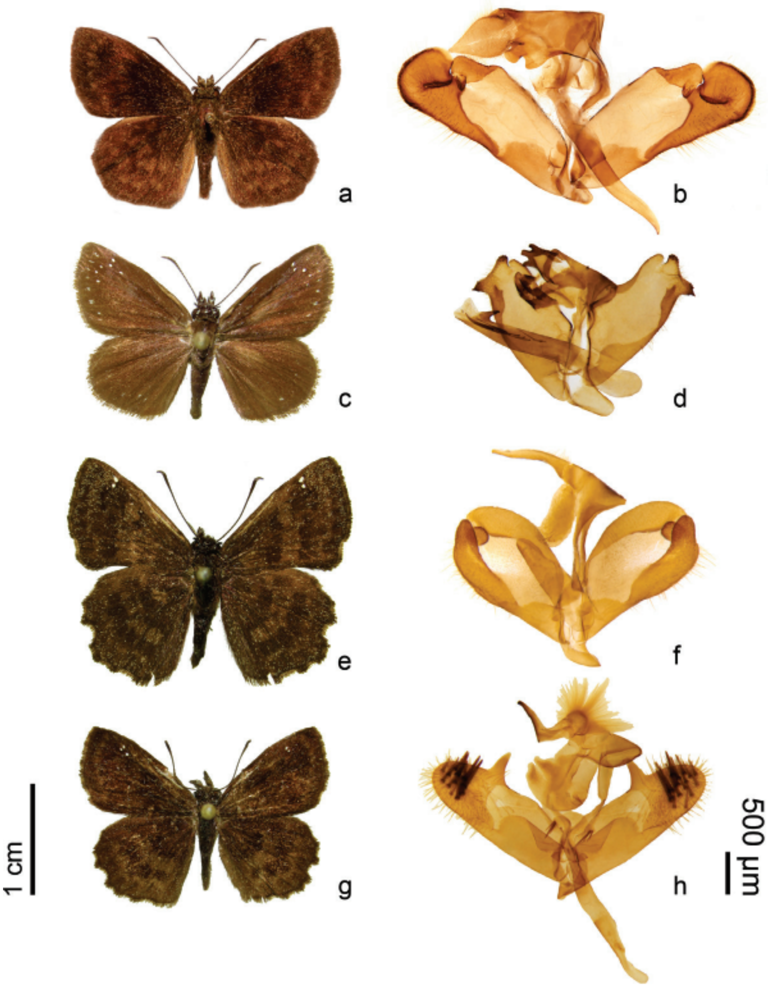

Figure 8. Type species of some Carcharodini genera in dorsal views and male genitalia in internal view. **(a-b)** *Bolla imbras* (Godman & Salvin, 1896), **(a)** El Salvador, Santa Tecla, 19.VIII.1972 (MGCL); **(b)** Guatemala, Retalhuleu Province, NN Nuevo San Carlos, 22.XII.2002, Ulrich Reber *leg.*, MGCL 1112131 (MGCL). **(c-d)** *Pholisora catullus* (Fabricius, 1793), **(c)** United States, Missouri, Jackson County, Blue Springs, 12.VIII.1967, Richard Heitzman *leg.*, DZ 58.624 (DZUP); **(d)** United States, New Mexico, Carlsbad, 3.VIII.1976, no colector, DZ 58.625 (DZUP). **(e-f)** *Incisus incisus* (Mabille, 1878), **(e)** Brazil, São Paulo, Campos do Jordão, 8-12.II.1982, Mielke & Casagrande *leg.*, DZ 46.504 (DZUP); **(f)** Brazil, Santa Catarina, Joinville, 28.X.1967, Mielke & Miers *leg.*, DZ 46.353 (DZUP). **(g-h)** *Staphylus ascalaphus* (Staudinger, 1876), **(g)** Guatemala, Zacapa, La Unión, 3.X.1981, Welling *leg.*, DZ 45.176 (DZUP); **(h)** Mexico, Chiapas, San Jerónimo, 17.VII.1978, Welling *leg.*, OM 44.713 (OM).

Diagnosis and description

Same as the diagnosis and description of the genus.

Biology

Janzen & Hallwachs (2009) provide photos of a parasitized immature in the last instar (Fig. 9a-c). The larva has a length of 28 mm., a green semi-hyaline body, and black head. *Uniphylus evemerus* **new comb.** larvae are host of the gregarious wasp *Apanteles duniagarciae* Fernández-Triana, 2014 (Hymenoptera, Braconidae, Microgastrinae) in the Area de Conservación Guanacaste, Costa Rica (Fernández-Triana et al. 2014). In the above-cited area, Janzen and Hallwachs have reared 86 wild-caught caterpillars, eight of them were parasitized by *A. duniagarcia,* apparently the unique parasitoid of the species (D.H. Janzen, personal communication).

Host plants

Pleuropetalum sprucei (Hook.fil.) Standl. (Amaranthaceae) (Janzen & Hallwachs 2009).

Distribution (Fig. 10)

Uniphylus evemerus (Godman & Salvin, 1896) **new comb.** is recorded from the following localities in Central America: Costa Rica – Alajuela and San José; and Panama – Chiriqui.

Temporal distribution

Uniphylus evemerus (Godman & Salvin, 1896) **new comb.** has been recorded in the following months: February, June, July, and December.

Etymology

Godman & Salvin (1896) did not provide an etymology for the name *evemerus*.

Examined material

COSTA RICA: ***Alajuela*** **– Socorro de la Virgen**, 13.II.1988, 1♂, D. L. Lindsley *leg*., D. L. Lindsley colln. - MGCL Accession #2008-20, DNA Voucher JRAL-COI-11 José R. A. Lemes, MGCL 1092142 (MGCL); 14.II.1988, 1♂, D. L. Lindsley *leg*., D. L. Lindsley colln. - MGCL Accession #2008-20 (MGCL). ***Cartago*** **- Irazu** Rio Sucio, no data, ♂, H. Rogers *leg*., BMNH(E) 1669519, lectotype, (NHMUK). ***San José*** **– No specific locality**, Km 117, 26.XII.1984, 2♂, G. T. Austin *leg*., G. T. Austin colln. - MGCL Acc. 2004-5, MGCL 1043687, MGCL 1043693* (MGCL).

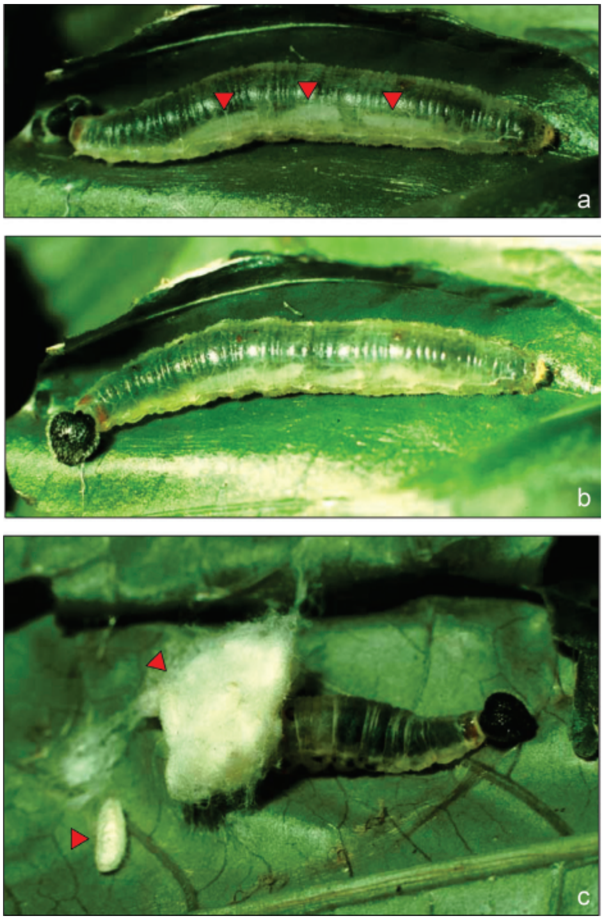

Figure 9. Larva of the same individual of *Uniphylus evemerus* (Godman & Salvin, 1896) **new comb.** in the last instar (a, b, c). Note the presence of the parasitoid larvae of the microgastrine braconid *Apanteles duniagarciae* Fernández-Triana, 2014 visible through the sides of the caterpillar (see arrows in figure a). Also, note the cocoons of the parasitoid larvae that have emerged from the caterpillar (see arrows in figure c). Costa Rica, Guanacaste Province, Area de Conservacion Guanacaste, 27.VI.1997, Ruth Franco *leg*., voucher 97-SRNP-1457, Area de Conservacion Guanacaste Collection. Photos by Ruth Franco.

PANAMA: ***Chiriqui* - Alto Lino**, 900 m, 23.VI.1965, 1♂, Small *leg*., DZ 45.615* (DZUP). **Boquete**, San Ramon, 1500-1650 m, 20, 24.VII.1997, 1♂, Mielke & Casagrande *leg*., OM 46.936* (OM); Finca Lerida, Alto Quiel, 1900-2200 m, 21, 23, 25.VII.1997, 1 ♀, Mielke & Casagrande *leg*., OM 46.830* (OM).

DISCUSSION

Many genera of brown skippers, such as the Carcharodini, have been historically neglected in systematics studies. This is probably due to their lack of charismatic features that are found in other families of butterflies. It is not uncommon that taxonomic studies of Hesperiidae result in the description of new species and the reallocation of known species into different genera (e.g. Cong et al. 2019, Medeiros et al. 2019, 2020, Siewert et al. 2016, 2020, Zhang et al. 2022a, Lemes et al. 2023).

The use of genome analysis is revolutionizing the systematic studies of Hesperiidae (Cong et al. 2019, Zhang et al. 2022a, b). Ideally, sampling many loci for many taxa would be the best solution, however, this practice is still unsustainable for most research laboratories due to the expensive costs of the protocols (Talavera et al. 2021). Despite this, COI analyses are corroborating phylogenomic findings (Cong et al. 2019), showing utility in recovering higher level relationships.

The COI-tree presented here demonstrated that *U. evemerus* **new comb.** forms a sister-group with *Staphylus*, and these two genera a larger clade including *Pholisora* (Fig. 1). However, it is important to emphasize that the inclusion of more species and more genes can change the relationships among clades. For example, *Staphylus*, with the new combination of *S. evemerus* (Godman & Salvin, 1896) in *Uniphylus*, includes now 47 species (Mielke 2005, Cong et al. 2019, Zhang et al. 2022a, b, Lemes et al. 2023), of which only 22 had their COI sequences analyzed in this study. Also, the inclusion of sequences of more species would likely increase the support values for the inner nodes on the COI-tree (Fig. 1).

In fact, the nuclear genome of Carcharodini suggests that *Staphylus* is a sister group with *Hesperopsis*, and *Bolla* is a sister group with

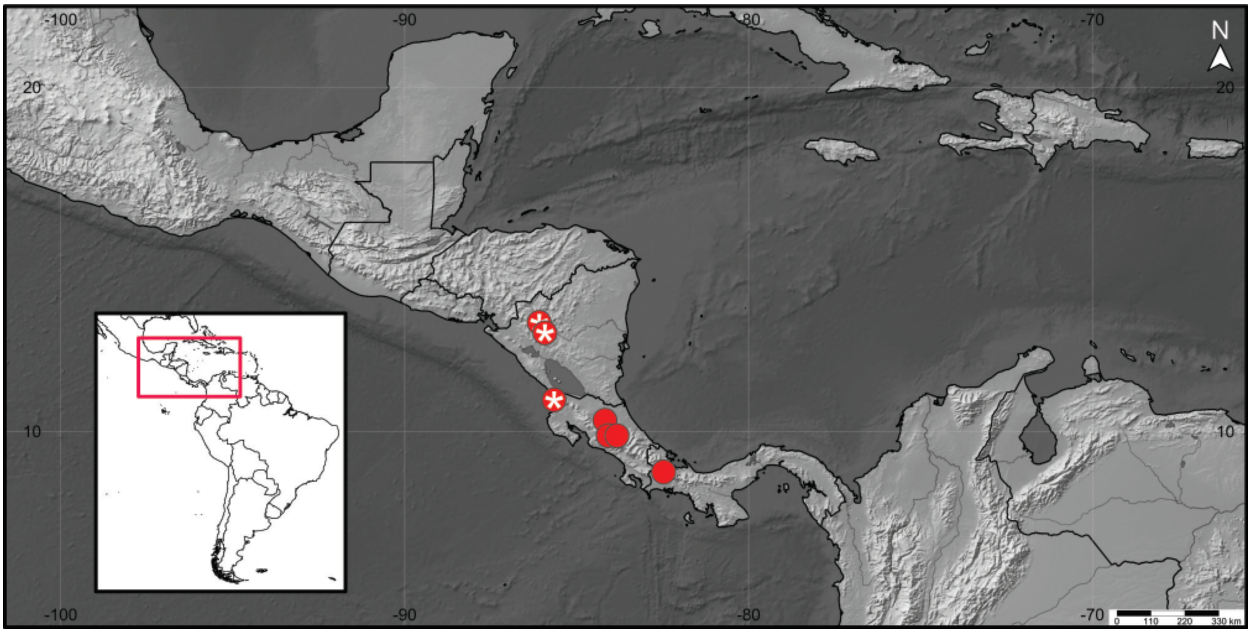

Figure 10. **Distributional map of *Uniphylus evemerus* (Godman & Salvin, 1896) new comb. The symbol "*" indicates literature records.**

Pholisora (Cong et al. 2019). The COI-tree of these same authors, on the other hand, suggests that *Staphylus* together with *Hesperopsis* forms a clade sister group with *Bolla*, which is recovered as paraphyletic, inside a larger clade including *Pholisora*. Therefore, the use of an integrative approach, using as much taxonomical tools as possible, is fundamental to understand the systematics of challenge groups, such as the "brown Carcharodini". Herein, it has been demonstrated that through molecular and morphology analysis, *Uniphylus* **gen. nov.** is supported as a strong taxonomic hypothesis.

The genetic distance of COI of *U. evemerus* **new comb.** compared to other Carcharodini genera is similar with the distance among genera in the tribe, ranging from 9% to 14% (Table SI). According to Cong et al. (2019), the genetic distance between clades of Hesperiidae genera is typically more than 10% in the COI.

Uniphylus evemerus (Godman & Salvin, 1896) **new comb.** has a unique combination of morphological characters that separates it from other genera. Godman & Salvin (1896) highlighted the distinctiveness of the male genitalia when compared to other *Staphylus* species, although these authors considered the species outwardly similar. Despite this, the strongest similarity between the wings of *U. evemerus* **new. comb.** with other *Staphylus* species is the brown ground color, present in most of the other genera of Carcharodini.

The concave inner margin of the FW of *Uniphylus evemerus* **new comb.** is morphologically closer to the FW of *Incisus* species, particularly *I. incisus* (Mabille, 1878) (Fig. 8e). In fact, Evans (1953, pages 95-96) had put these two species as closer species in his taxonomical key. However, the male and female genitalia pattern of *U. evemerus* **new comb.** is different than those of *Incisus* species (Lemes et al. in prep.). While males of *Incisus* species have a broader valva, *U. evemerus* **new comb.** has a narrow valva. In fact, *U. evemerus* **new comb.** has a unique genitalia pattern within Carcharodini. The very short aedeagus without spines or cornuti is another important characteristic. Although some studies recovered the male genitalia of some Carcharodini species as the "*Nisoniades*-type" valva (see Evans 1953, Warren et al. 2009, Siewert et al. 2016), this is not the case in any species of *Bolla, Pholisora, Staphylus* and *Incisus*, as well as it is not present in *U. evemerus* **new comb.** (Fig. 8b, d, f, h, j).

For the females, the lamella postvaginalis as a narrow plate and the lamella antivaginalis as a very sclerotized quadrate plate with an excavation in the middle of the distal margin, represent very different characteristics when compared to the same genitalia structures in other *Staphylus*, *Incisus,* and *Bolla* species (Mielke 1975, 1980, Steinhauser 1989, 1991, Steinhauser & Austin 1993, Austin 1997, Austin & Warren 2002, Lemes et al. in prep.). The presence of an anterior apophysis of *U. evemerus* **new comb.** is until now unknown from other females of Carcharodini.

Uniphylus **gen. nov.** is so far a monotypic genus, but the study of other genera of Carcharodini is encouraged, as this practice may reveal more species to be included in the genus. It is possible that the low number of specimens found in the visited collections is related to the drab wings ground color and the small size of Carcharodini species, which may be less interesting among Lepidoptera collectors, as suggested by Zacca et al. (2020). Fortunately, this Pyrginae tribe has recently received more attention by researchers, and other studies are currently in preparation to better elucidate their taxonomic diversity (Lemes et al. in prep.).

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SUPLEMENTARY MATERIAL

Table SI.

How to cite

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JRAL was responsible for the conceptualization and analysis of all data; the manuscript was written in consultation with RRS, OHHM, MMC and ADW, and all authors contributed to the design of the final version of the manuscript.