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Before it is too late: description of a new genus and species of butterfly from a highly threatened Brazilian biome

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ABSTRACT

A new genus, *Nhambikuara* Freitas, Barbosa & Zacca **gen. nov.**, and species, *Nhambikuara cerradensis* Freitas, Barbosa & Zacca **sp. nov.**, of the highly diverse Neotropical butterfly subtribe Euptychiina are described. *Nhambikuara cerradensis* **sp. nov.** is the type species for the genus, and *Euptychia mima* Butler, 1867 is also transferred to the new genus, as *Nhambikuara mima* (Butler, 1867) **comb. nov.**, from the genus *Zischkaia* Forster, 1964. The taxonomy, phylogenetic relationships, geographic distribution and natural history of species of the genus are also discussed.

<http://zoobank.org/urn:lsid:zoobank.org:pub:41AD7568-3490-4F63-A019-32D5592A8C44>

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Introduction

Originally covering more than 2 million km², the cerrado (a Brazilian tropical savanna, see Goodland, 1971) is the second largest Brazilian biome, after Amazonia (Klink and Machado, 2005). About 15 years ago, Cavalcanti and Joly (2002) called attention to the fact that the conservation of the cerrado biome has been neglected, providing a list of priority areas for conservation together with recommendations for conservation strategies. However, very few of their recommendations have since been adopted, and accelerating destruction and conversion of the natural habitats into an agricultural landscape has resulted in the complete loss of almost half of the original cerrado vegetation, with only ca. of 20% of the remaining vegetation considered as undisturbed (Strassburg et al., 2017). This rampant process of destruction is putting at risk an exceptional number of species that are endemic to this important biodiversity hotspot (Myers et al., 2000).

As mentioned above, the cerrado savannas are extremely high in species richness and endemism of several groups of plants and

animals (Oliveira and Marquis, 2002). For Lepidoptera, in particular, and considering also subspecific taxa, some groups present levels of endemism as high as 40% or more, such as Ithomiini (Nymphalidae), myrmecophilous Riodinidae and Troidini swallowtails (Papilionidae) (Brown and Gifford, 2002). Additionally, Brown and Gifford (2002) predicted that some groups, such as grass feeding Satyrinae (Nymphalidae) and Hesperinae (Hesperiidae), should also show higher levels of endemism with additional taxonomic studies.

Notwithstanding the high levels of habitat degradation, several new endemic species of Satyrinae butterflies have been discovered in the cerrado in recent years, and while some of them have been described (Freitas, 2004; Freitas et al., 2010, 2015; Zacca et al., 2014; Barbosa et al., 2015; Kaminski et al., 2015), several are awaiting formal description. Among these, our research showed that a very distinctive undescribed species of Euptychiina (Nymphalidae: Satyrinae) could not be adequately accommodated in any described genus.

In the present paper a new genus, *Nhambikuara* Freitas, Barbosa & Zacca **gen. nov.**, is therefore described to house this new species endemic to the cerrado savannas, *Nhambikuara cerradensis* **sp. nov.** Freitas, Barbosa & Zacca. In addition, we transfer *Euptychia mima* Butler, 1867 from *Zischkaia* Forster, 1964, into *Nhambikuara* (**comb. nov.**).

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Material and methods

Material examined

A total of 150 specimens of *Nhambikuara cerradensis* **sp. nov.** and *Nhambikuara mima* **comb. nov.** were examined in the following institutions: **CLEIC** – Coleção do Laboratório de Ecologia e Interações de Insetos da Caatinga, Universidade Federal de Campina Grande, Patos, Paraíba, Brazil; **DD** – Diego Dolibaina collection, Curitiba, Paraná, Brazil; **DZUP** – Entomological Collection Padre Jesus Santiago Moure, Universidade Federal do Paraná, Curitiba, Paraná, Brazil; **MGCL** – McGuire Center for Lepidoptera, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; **MNHU** – Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität, Berlin, Germany; **MUSM** – Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **MZFS** – Entomological Collection Prof. Johann Becker, Universidade Estadual de Feira de Santana, Feira de Santana, Bahia, Brazil; **USNM** – National Museum of Natural History, Smithsonian Institution, Washington, DC, USA; **ZUEC** – Museu de Zoologia da Universidade Estadual de Campinas, Unicamp, Campinas, São Paulo, Brazil; **ZUEC-AVLF** – André V. L. Freitas Collection, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. Some strongly damaged specimens of *N. cerradensis* **sp. nov.** were not designated as paratypes and listed in the “Additional material examined” section.

Morphological study

The specimens studied had their abdomen detached and soaked in a heated test tube with 10% potassium hydroxide solution (KOH) for about 5 min in bain marie before dissection of the genitalia. Dissected specimens are marked with an asterisk (*) after the voucher number in the examined material section. The genitalia images were obtained in two different equipment, Leica LAS 3D view with the aid of a video camera Leica DFC 500 attached to a stereoscopic microscope Leica MZ16 using the software LAS montage version 4.7 and a Zeiss Discovery.V20 Stereomicroscope. Male and female genitalia terminologies are indicated in Fig. 2.

Wings were measured with a ruler and measures were taken from the insertion to the apex in the forewing and from the insertion to the tornus region in the hindwing. Nomenclature of venation used herein follows Comstock & Needham (1898–99) and Comstock (1918), and for broad regions of the wing we follow Neild (1996). The following abbreviations were used throughout the text: FW – forewing; HW – hindwing; DW – dorsal wings; VW – ventral wings; DFW – dorsal forewing; VFW – ventral forewing; DHW – dorsal hindwing; VHW – ventral hindwing. The geographical distribution of the species is based on label data and literature records. The taxonomic classification follows Lamas (2004) modified after Peña et al. (2006, 2010) and Wahlberg et al. (2009).

DNA sampling and analysis

Total DNA was extracted from two legs of adults using the DNeasy Blood & Tissue Kit protocol (QIAGEN, Düsseldorf, Germany). DNA was stored in TE buffer at –20 °C. The mitochondrial gene cytochrome c oxidase I (COI – 1498 bp) and the nuclear genes GAPDH (691 bp) and RpS5 (610 bp) for all specimens were amplified, purified and sequenced using standard techniques (see Barbosa et al., 2015; Silva-Brandão et al., 2005; Wahlberg and Wheat, 2008) and deposited at GenBank (Benson et al., 2013) (see Table 1 for account numbers). All sequences were analyzed with the program FinchTV v. 1.4.0 (Geospiza, PerkinElmer Inc., Waltham, MA), and posteriorly aligned manually with sequences obtained previously and available on GenBank by using BioEdit

v.7.2.4 (Hall, 2013). The final matrix comprised 30 specimens from species of eight genera (including eight specimens from the new genus *Nhambikuara* **gen. nov.** – see Table 1 for the sequence codes). The phylogenetic relationships of the new species were estimated using a maximum likelihood (ML) analysis. Analyses were run using RAXML (Stamatakis et al., 2008) with 1000 rapid bootstrap replicates on the CIPRES portal (Miller et al., 2010). The data were modeled according to the GTR+CAT model.

Genetic distances among the species of *Nhambikuara* **gen. nov.** and species of its sister-clade (Tables 2 and 3) were determined using the program MEGA v. 6.0 (Tamura et al., 2013) under Kimura-2-parameters (K2P) model of nucleotide substitution (Kimura, 1980).

Adult ecology

Adult ecology was studied through trap studies (see Freitas et al., 2014) in three sites in Minas Gerais State, and one in São Paulo State, Southeastern Brazil: 1) Área de Proteção Especial Manancial Cercadinho, Belo Horizonte, Minas Gerais, 900–1000 m, 19°58'S, 43°54'W, Oct/2006–Sep/2007 (see details in Silva et al., 2012); 2) Área de Proteção Ambiental Morro da Pedreira, Santana do Riacho, Minas Gerais, 900 m, 19°21'S, 43°36'W, Oct/2011–Jul/2013 (MVB, unpublished); 3) Parque Municipal das Mangabeiras, Belo Horizonte, Minas Gerais, 1100 m, 19°56'S, 43°54'W, Jan–Dec/2014 (ARMS, unpublished); 4) Cerrado da Graúna, Itirapina, São Paulo, 800 m, 22°15'S, 47°47'W, Nov/2009–Oct/2010 (AVLF, unpublished). Traps were hung 1.5 m above the ground and a standard mixture of mashed banana with sugar cane juice, fermented for at least 48 h, was used as attractant. The bait was placed inside the traps in plastic pots with a perforated cover. The traps were checked every 24 h, and the baits were replaced at each visit. All butterflies were collected.

Results

Taxonomy

Nhambikuara Freitas, Barbosa & Zacca, **gen. nov.**

Euptychia mima Butler, 1867: 500 [no illustration].

Zischkaia Forster, 1964 [in part.]

Zischkaia mima; Lamas 2004: 223. – Brévignon & Benmesbah, 2012: 46.

Ypthimoides sp.1; Silva et al., 2012: 295

Satyrinae sp.1; Freire Júnior & Diniz, 2015: 1214

Type-species: *Nhambikuara cerradensis* Freitas, Barbosa & Zacca, **sp. nov.**

Diagnosis. *Nhambikuara* **gen. nov.** differs from all other genera of Euptychiina by the following combination of characters: 1) VW with submedian, median, submarginal and marginal lines, 2) VHW with six ocelli between Rs and 2A, with variable number (1 or 2) of pupils; 3) appendices angulares reduced; 4) anterior projection of saccus developed; 5) apex of valva serrated; 6) aedeagus with paired cornutal patches; 7) female genitalia with lamella antevaginalis and postvaginalis fused forming a sclerotized sterigma; 8) ductus bursae with sclerotized plates variable in shape. Species of *Nhambikuara* are easily distinguished from *Zischkaia* species by the absence of androconial patches on dorsal wing surfaces in males, absence of the dorsal projection of tegumen in male genitalia and female genitalia with sterigma.

Etymology. The generic name is derived from that of the Nhambikuara, an ethnic group of Brazilian Native Americans inhabiting the cerrado and Amazon biomes (see Setz, 1983 for a detailed study of the Nhambikuaras). It should be treated as a noun in the nominative singular, be the gender of the noun masculine or feminine.

Table 1
Species of Euptychiina with code, sampling site data and GenBank accession numbers for sequenced genes. Species of *Nhambikuara* **gen. nov.** are in bold.

Species name	Code	Locality	COI	GAPDH	RpS5
<i>Oressinoma sorata</i>	CP06-89	Peru, Pasco, Oxapampa	GQ357209	GQ357440	GQ357570
<i>Yphthimoides eriphule</i>	YPH-0063	Brazil, São Paulo, Santa Rita do Passa Quatro	MF489977	MF489997	MF490010
<i>Yphthimoides mimula</i>	YPH-0348	Brazil, Paraná, Foz do Iguaçu	MF489981	MF490001	MF490014
<i>Yphthimoides maepius</i>	YPH-0466	Colombia, Amazonas, Leticia	MF489982	MF490002	MF490015
<i>Yphthimoides affinis</i>	YPH-0082	Brazil, São Paulo, Luís Antônio, Reserva Jataí	MF489978	MF489998	MF490011
<i>Paryphthimoides</i> sp.	YPH-0544	Brazil, Amazonas, Manaus	MF489983	MF490003	MF490016
<i>Paryphthimoides</i> sp.	NW167-6	Brazil, Mato Grosso do Sul, Três Lagoas	MF489989	MF490008	MF490022
<i>Paryphthimoides</i> sp.	YPH-0336	Brazil, Goiás, Pirenópolis	MF489980	MF490000	MF490013
<i>Paryphthimoides</i> sp.	YPH-0267	Brazil, Minas Gerais, Santana do Riacho	MF489979	MF489999	MF490012
<i>Erichthodes julia</i>	CP04-65	Peru, Junín, Quebrada Siete Jeringas	GU205834	GU205946	GU206006
<i>Erichthodes antonina</i>	YPH-0325	Brazil, Alagoas, Serra Grande	KU340864	KU340913	KU340946
<i>Erichthodes antonina</i>	CP02-24	Peru, Madre de Díos, Albergue Posada Amazonas	DQ338792	GQ357429	GQ357558
<i>Neonympha areolatus</i>	CP22-03	USA	GU205856	GU205967	GU206028
<i>Pareuptychia binocula</i>	CP02-42	Peru, Madre de Díos, Albergue Posada Amazonas	GU205858	GU205969	GU206030
<i>Pareuptychia ocirrhoe</i>	NW126-6	Brazil, São Paulo, Atibaia	GU205859	GU205970	GU206031
<i>Splendeuptychia toynei</i>	LEP-10657	Ecuador, Zamora-Chinchi, La Libertad, km 11.5 Los Encuentros-Zarza	MF489990	–	MF490023
<i>Splendeuptychia furina</i>	CP02-39	Peru, Madre de Díos, Albergue Posada Amazonas	GU205868	GU205982	GU206043
<i>Splendeuptychia doxes</i>	NW126-8	Brazil, São Paulo, Atibaia	GU205867	GU205981	GU206042
<i>Splendeuptychia doxes</i>	BC-DZWillmott-092	Brazil, Paraná, Campo Mourão, Parque Estadual Lago Azul	MF489991	–	MF490024
<i>Splendeuptychia doxes</i>	YPH-0172	Brazil, São Paulo, Jundiá, Serra do Japi	KR349478	KR349474	–
<i>Splendeuptychia doxes</i>	MGCL-LOAN-386	Brazil, São Paulo, Jundiá, Serra do Japi	MF489992	–	–
<i>Splendeuptychia latia</i>	MGCL-LOAN-500	Brazil, Bahia, Una, Reserva Biológica de Una	MF489996	–	–
<i>Nhambikuara mima</i>	MGCL-LOAN-550	Brazil, Rondônia, Porto Velho	MF489994	MF490009	MF490025
<i>Nhambikuara mima</i>	MGCL-LOAN-175	Brazil, Alagoas, Ibatiguara	MF489993	–	–
<i>Nhambikuara cerradensis</i>	MGCL-LOAN-134	Brazil, São Paulo, Itirapina	MF489995	–	–
<i>Nhambikuara cerradensis</i>	YPH-0572	Brazil, Minas Gerais, Santana do Riacho	MF489984	MF490004	MF490017
<i>Nhambikuara cerradensis</i>	YPH-0573	Brazil, Minas Gerais, Santana do Riacho	MF489985	MF490005	MF490018
<i>Nhambikuara cerradensis</i>	YPH-0574	Brazil, Minas Gerais, Santana do Riacho	MF489986	MF490006	MF490019
<i>Nhambikuara cerradensis</i>	YPH-0575	Brazil, Mato Grosso do Sul, Aquidauana	MF489987	–	MF490020
<i>Nhambikuara cerradensis</i>	YPH-0576	Brazil, Mato Grosso do Sul, Aquidauana	MF489988	MF490007	MF490021

***Nhambikuara cerradensis* Freitas, Barbosa & Zacca, sp. nov.**
(Figs. 1, 2, 5, 6)

Yphthimoides sp.1; Silva et al., 2012: 295

Satyrinae sp.1; Freire Júnior & Diniz, 2015: 1214

Type material. Holotype male deposited at ZUEC (Figs. 1A, 1B) with the following labels (separated by transverse bars): /Holotypus/Serra do Cipó, Santana do Riacho, Minas Gerais, Brasil, 08.III.2009, Kaminski L. A. leg./ZUEC LEP 10071/*Nhambikuara cerradensis* Freitas, Barbosa & Zacca det. 2018/

Allotype female deposited at ZUEC (Figs. 1C, 1D) with the following labels (separated by transverse bars): /Allotypus/Serra do

Cipó, Santana do Riacho, Minas Gerais, Brasil, 11.III.2009, Kaminski L. A. leg./ZUEC LEP 10073/*Nhambikuara cerradensis* Freitas, Barbosa & Zacca det. 2018/

Diagnosis. This species is characterized by the following combination of characters: 1) absence of ocelli in DW, 2) ochre wavy submedian, median, submarginal and marginal lines in VHW, 3) six small bipupilated ocelli in VHW between Rs and 2A, 4) valva with subtriangular developed costae and apex strongly serrated, 5) aedeagus with elongated paired cornutal patches and anterior region strongly curved upwards, 6) sterigma strongly sclerotized and developed, almost three times longer than wider, 7) ductus

Table 2Pairwise genetic distances among species of *Nhambikuara* and *Splendeptychia*. Species of *Nhambikuara* **gen. nov.** are in bold.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14
1. <i>Nhambikuara mima</i> MGCL-LOAN-175														
2. <i>Nhambikuara mima</i> MGCL-LOAN-550	1.2													
3. <i>Nhambikuara cerradensis</i> YPH-0572	4.6	5.4												
4. <i>Nhambikuara cerradensis</i> YPH-0573	4.6	5.4	0.0											
5. <i>Nhambikuara cerradensis</i> YPH-0574	4.6	5.4	0.0	0.0										
6. <i>Nhambikuara cerradensis</i> YPH-0575	4.6	5.0	1.2	1.2	1.2									
7. <i>Nhambikuara cerradensis</i> YPH-0576	4.6	5.0	1.2	1.2	1.2	0.0								
8. <i>Nhambikuara cerradensis</i> MGCL-LOAN-134	4.6	5.0	1.2	1.2	1.2	0.0	0.0							
9. <i>Splendeptychia furina</i> CP02-39	5.6	6.0	5.6	5.6	5.6	5.2	5.2	5.2						
10. <i>Splendeptychia toynei</i> LEP-10657	6.7	6.7	6.1	6.1	6.1	6.1	6.1	6.1	4.2					
11. <i>Splendeptychia doxes</i> MGCL-LOAN-386	5.4	6.3	5.8	5.8	5.8	6.7	6.7	6.7	5.0	5.0				
12. <i>Splendeptychia doxes</i> BC-DZWill-092	5.2	6.1	5.6	5.6	5.6	6.5	6.5	6.5	4.8	4.8	0.2			
13. <i>Splendeptychia doxes</i> NW126-8	5.4	6.3	5.8	5.8	5.8	6.7	6.7	6.7	5.0	5.0	0.4	0.2		
14. <i>Splendeptychia doxes</i> YPH-0172	5.2	6.1	5.6	5.6	5.6	6.5	6.5	6.5	4.8	4.8	0.2	0.0	0.2	
15. <i>Splendeptychia latia</i> MGCL-LOAN-500	5.6	6.0	6.7	6.7	6.7	5.8	5.8	5.8	4.4	5.0	2.0	1.8	2.0	1.8

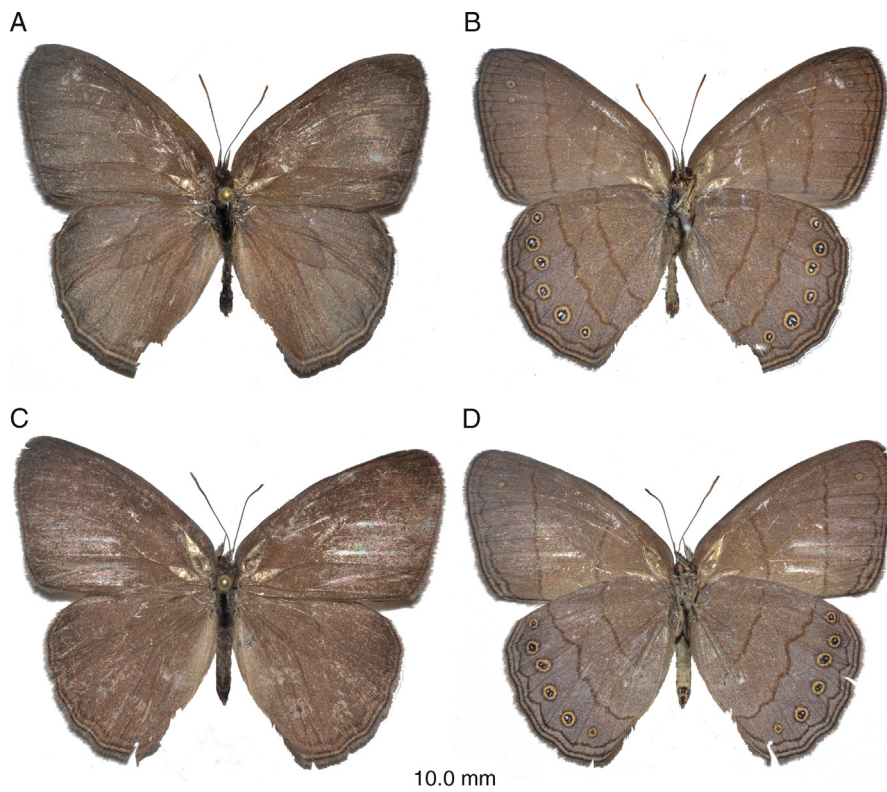
Table 3Mean genetic distances among species of *Nhambikuara* and *Splendeptychia*. Species of *Nhambikuara* **gen. nov.** are in bold.

	1	2	3	4	5
1. <i>Nhambikuara mima</i>					
2. <i>Nhambikuara cerradensis</i>	4.9				
3. <i>Splendeptychia furina</i>	5.8	5.4			
4. <i>Splendeptychia toynei</i>	6.7	6.1	4.2		
5. <i>Splendeptychia doxes</i>	5.7	6.1	4.9	4.9	
6. <i>Splendeptychia latia</i>	5.8	6.2	4.4	5.0	1.9

bursae membranous with a half-ring sclerotized plate and, 8) corpus bursae with dorsal paired signa. DNA sequence data suggest that its sister species is *Nhambikuara mima* **comb. nov.**, and the differences between these two species are discussed further below, under the account for *N. mima*.

Description. *Head:* dark brown, frons with mixed creamy and light brown scales; eyes chestnut brown, with sparsely localized

bristles; post-genal area creamy mixed with light brown scales; labial palpus curved upwards, dorsally short, creamy mixed with brown scales, laterally short, creamy scales, ventrally elongated with creamy mixed with light brown scales at first and second segment, short scales at third segment; antennae brown with apex dark brown, laterally with white scales in each side of the base of the flagellomeres. *Thorax:* dorsally brown, ventrally covered in long mixed creamy and brown scales; legs mixed with creamy and light brown scales. *Wings:* males FW: 17–19 mm ($n=7$), HW: 14–15 mm ($n=5$) (Holotype: FW: 19 mm; HW: 14 mm), females FW: 19–21 mm ($n=8$), HW: 15–16 mm ($n=6$) (Allotype: FW: 20 mm; HW: 15 mm). *DFW:* ground color brown, submarginal and marginal lines dark brown, marginal region light brown. *DHW:* similar to DFW. *VFW:* ground color light brown, four parallels brown ochre lines, submedian and median lines crossing from Radius to 1A+2A, and submarginal and marginal lines crossing from R₄ to inner margin; two small ocelli in M₁-M₂ and M₂-M₃ in submarginal

**Fig. 1.** *Nhambikuara cerradensis* **gen. et sp. nov.** A – holotype male, dorsal; B – holotype male, ventral; C – allotype female, dorsal; D – allotype female, ventral.

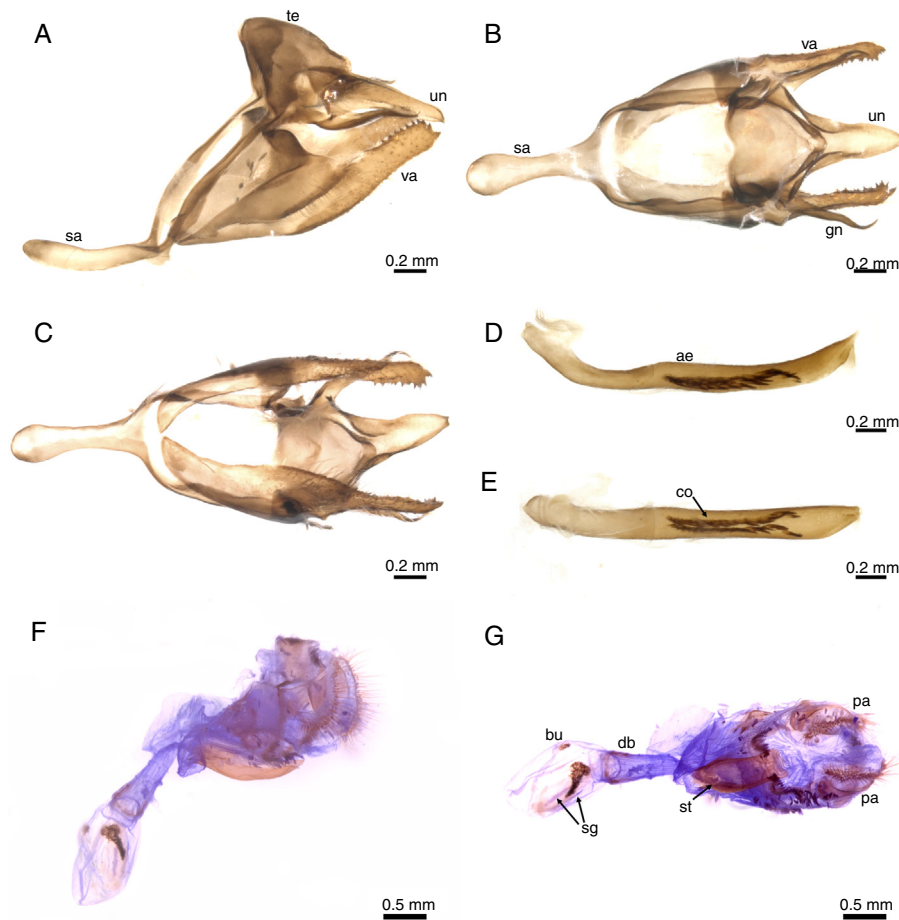


Fig. 2. *Nhambikuara cerradensis* gen. et sp. nov., male (YPH-0574) and female (DZ 33.900) genitalia. A – male lateral; B – male dorsal; C – male ventral; D – male aedeagus, lateral; E – male aedeagus, dorsal; F – female lateral; G – female ventral. Abbreviations: sa – saccus; te – tegumen; un – uncus; va – valva; gn – gnathos; ae – aedeagus; co – cornuti; bu – bursae coppulatrix; db – ductus bursae; pa – papilla anallis; st – sterigma; sg – signa.

region. VHW: ground color light brown, four parallels brown ochre lines crossing from costal margin to inner margin, median and submarginal lines irregular fused to each other at tornal area, a series of six ocelli at submarginal region in Rs-M₁, M₁-M₂, M₂-M₃, M₃-Cu₁, Cu₁-Cu₂, Cu₂-1A+2A, ocelli Rs-M₁ and Cu₂-1A+2A with only a silvery pupil, ocelli M₁-M₂ to CuA₁-CuA₂ bipupilated. **Abdomen:** dorsally brown, ventrally with mixed creamy and brown scales.

Male genitalia (Figs 2A–2E). Tegumen dorsally flattened, anterior margin concave at median region; gnathos 2/3 the length of uncus, sinuous and curved upwards; uncus straight, apex curved downwards, basal third as long as the median region; appendices angulares reduced; anterior projection of saccus almost two times longer than valva; fultura superior absent; fultura inferior sclerotized in U-shape; valva with a developed costae, dorso-apical region serrated, basal region narrow; aedeagus with anterior region strongly curved upwards, posterior region about 1 ½ length of anterior region, elongated paired cornutal patches.

Female genitalia (Figs 2F, 2G). 8th tergite half-sclerotized, not fused with the lateral expansions of lamella antevaginalis, spiracle absent; papilla analis developed, sub-squared, basal half strongly sclerotized, setae sparsely distributed at distal region, apophysis posterior reduced; lamella antevaginalis fused to lamella postvaginalis forming the sterigma which is strongly sclerotized and developed, almost three times longer than wider; ductus bursae membranous, as long as corpus bursae, sclerotized half-ring between ductus bursae and corpus bursae, paired signa dorsally.

Variation (Figs 1E, 1F). Seasonal variation seems to occur in this species, as has also been reported for many other species of Euptychiina from the Brazilian savanna (Freitas, 2007; Freitas et al., 2010; Siewert et al., 2013; Zacca et al., 2014). During the rainy season (October to March), the wing ventral ocelli are developed, filling in most of the intervenal spaces on the VHW, whereas these ocelli become strongly reduced in the dry season (April to September).

Distribution (Fig. 6). This species is mostly associated to open vegetation, especially the Brazilian cerrado (States of Maranhão, Ceará, Bahia, Goiás, Distrito Federal, Mato Grosso, Mato Grosso do Sul, Minas Gerais and São Paulo), a biome that presents a high richness of endemic species (Ratter et al., 1997; Brown and Gifford, 2002).

Natural history. This species is restricted to open savannic vegetations in the cerrado biome, montane rocky fields (known locally as “campos rupestres”), flying both in open vegetation and at the edges of the riparian forests along small streams. In the region of Belo Horizonte, Minas Gerais, 46 out of the 48 sampled individuals were captured in the cerrado area, and only two in the adjacent riparian forest. In a cerrado area in Brasília (central Brazil), 72 out of the 104 sampled individuals were captured in the cerrado area and 32 in the adjacent riparian forest (Freire Júnior, 2015). Adults have a low flight, usually not flying more than 1.5 m above the ground. The species is usually localized and although it has been throughout the year, typically no more than 10 individuals are seen in a single day. However, the species was found to be common in some sites, such as Santana do Riacho, Minas Gerais, where from 30 to nearly 60 individuals were captured with bait traps in single

months (MVB, unpublished; see also Freire Júnior, 2015 and Freire Júnior and Diniz, 2015). Males and females were observed feeding on animal feces and other decaying material and were easily attracted to traps baited with fermented fruits (AVLF, MVB and ARMS, pers. obs., Silva et al., 2012). The sex ratio was close to 1:1 in two bait trap studies, with females being more common in both studies: 1) in Santana do Riacho, a total of 81 females and 64 males were captured ($\chi^2 = 1.99$, $P = 0.18$, $DF = 1$); 2) in Itirapina, a total of 10 females and four males were captured ($\chi^2 = 2.57$, $P = 0.11$, $DF = 1$). Individuals were more active during the morning, and no territorial behavior has been reported (AVLF pers. obs.).

Etymology. The name of this species is formed by adding the suffix -ensis to the toponym “cerrado” to form an adjective which means “from the cerrado”, alluding to its strong association with the savannic Brazilian cerrado biome. As mentioned before, the cerrado is one of the most threatened phytophysiognomies in Brazil (Strassburg et al., 2017), suffering from high anthropic conversion rates every year, mostly to give place to extensive soybean and sugarcane plantations.

Paratypes. BRAZIL – Maranhão: **Feira Nova** – 26 km East, Fazenda Forquilha dos Brejos, 1 male, 13-16-IV-2011, Mielke & Casagrande leg., DZ 32.041 (DZUP); **Imperatriz** – 1 male, 9-VII-1974, Exc. Depto Zool., DZ 31.804 (DZUP). Ceará: **Viçosa do Ceará** – 3 km W, 750 m, 1 male, 28.V.2013, Dolibaina & Pessoa leg., DD 226* (DD). Bahia: **Catolés** – Abaíra, Chapada Diamantina, 1 male, 1.XI.2013, S. M. Kerpel & A. F. Junior leg., CLEIIC802 (CLEIC), 1 female, 2.XI.2013, S. M. Kerpel & A. F. Junior leg., CLEIIC803 (CLEIC), 1 male, 3.XI.2013, S. M. Kerpel & A. F. Junior leg., CLEIIC804 (CLEIC), 1 male, 31.X.2013, S. M. Kerpel & A. F. Junior leg., CLEIIC805 (CLEIC); **Morro do Chapéu** – Capão do Pinho, 1 male, 1 female, 22.VI.2009, T. Zacca leg., MZUEFS#5.0060, MZUEFS#5.0059 (MZFS); **Pindobaçu** – Cachoeira da Fumaça, 10°28'43"S 40°12'27.6"W, 1 male, XII.2009, T. Zacca leg., MZUEFS#46.805 (MZFS); **Senhor do Bonfim** – Serra da Maravilha, 1 male, 1 female, 20.VII.2009, T. Zacca leg., MZUEFS#45220, MZUEFS#45179 (MZFS). Distrito Federal: **Brasília** – 1000 m, 1 male, 8.IX.1969, H. Ebert leg., DZ 35.043 (DZUP), 4 females, 14.V.1969, ex-coll. H. Ebert, DZ 34.963, DZ 34.983, DZ 35.213, DZ 35.273 (DZUP), Parque do Gama, 1000 m, 1 male and 2 females, 17-VI-1972, Mielke & Brown leg., DZ 33.899*, DZ 35.113, DZ 35.073 (DZUP), 1 male, 4 females, 17.V.1969, ZUEC-LEP 10285, ZUEC-LEP 10286, ZUEC-LEP 10287, ZUEC-LEP 10288, ZUEC-LEP 10289 (ZUEC), 1 male, 20.VI.1972, K. S. Brown leg., ZUEC-LEP 10297 (ZUEC), Fazenda Água Limpa, 1 female, 11.VII.1976, K. S. Brown leg., ZUEC-LEP 10266 (ZUEC), Brasília Country Club, 1200 m, 1 female, 17.VI.1972, Mielke & Brown leg., DZ 35.173 (DZUP), 2 females, 19.VI.1972, DZ 35.183, DZ 35.193 (DZUP), 2 females, 18.VI.1972, K. S. Brown leg., ZUEC-LEP 10267, ZUEC-LEP 10269 (ZUEC); **Planaltina** – 15°35'5 47°42'W, 1000 m, 1 male, 4.XII.1982, Mielke & Becker leg., DZ 35.153 (DZUP). Goiás: 2 males, 31.VIII.1969, ex-coll. H. Ebert, DZ 34.953, DZ 35.243 (DZUP); **Goiânia** – 2 males and 1 female, 17.XII.1968, K. S. Brown leg., ZUEC-LEP 10282, ZUEC-LEP 10283, ZUEC-LEP 10284 (ZUEC); **Rio Quente** – Pousada do Rio Quente, 2 males, 12.II.1979, A. Raw leg., DZ 35.023, DZ 35.163 (DZUP); **Iporá** – 1 male, 21.VI.1972, K. S. Brown leg., ZUEC-LEP 10299 (ZUEC). Mato Grosso: **Diamantino** – Rio Arinos, Fazenda Diamantino, 300–400 m, 1 male (no abdomen), 5.V.1986, H. & H. D. Ebert leg., DZ 35.103 (DZUP), 1 female, 26.VIII.1978, Mielke & Furtado leg., DZ 35.013 (DZUP), 1 female, 5-IX-1996, E. Furtado leg., DZ 33.900* (DZUP), 1 male, 7-IX-1978, Mielke & Furtado leg., DZ 31.884 (DZUP); **São Vicente** – São José da Serra, 700 m, 1 male, 24.VI.1972, Mielke & Brown leg., DZ 35.093 (DZUP), 1 female, 24.VI.1972, K. S. Brown leg., ZUEC-LEP 10295 (ZUEC). Mato Grosso do Sul: **Aquidauana** – 20°25'59.23"S–55°39'30.28"W, 2 females, no date, (DNA Vouchers YPH-0575, YPH-0576), J. Lener leg., ZUEC-LEP 10013, ZUEC-LEP 10014 (ZUEC). Minas Gerais: **Belo Horizonte** – 4 males, 5 females, Área de Proteção Especial Manacial

Cercadinho, 2007, 19°58'18.4"S 43°54'30"W, Silva A.R.M. leg., ZUEC-LEP 10076, ZUEC-LEP 10078, ZUEC-LEP 10080, ZUEC-LEP 10084, ZUEC-LEP 10077, ZUEC-LEP 10079, ZUEC-LEP 10080, ZUEC-LEP 10081, ZUEC-LEP 10082 (ZUEC); **Letícia** – Córrego leitão, 19°06'38"S 44°32'14"W, 1 male, 15.VI.1972, K. S. Brown leg., ZUEC-LEP 10296 (ZUEC); **Paracatu** – 1 female, 13.V.1969, K. S. Brown leg., ZUEC-LEP 10274 (ZUEC), 1 male, 16.V.1969, ex-coll. H. Ebert, DZ 35.003 (DZUP); **Buritis** – 1 female and 1 (no abdomen), 23.XII.1968, ex-coll. H. Ebert, DZ 34.993, DZ 35.233 (DZUP), 8 males and 4 females, 23.XII.1968, K. S. Brown leg., ZUEC-LEP 10268, ZUEC-LEP 10270, ZUEC-LEP 10271, ZUEC-LEP 10272, ZUEC-LEP 10273, ZUEC-LEP 10275, ZUEC-LEP 10276, ZUEC-LEP 10277, ZUEC-LEP 10278, ZUEC-LEP 10279, ZUEC-LEP 10280, ZUEC-LEP 10281 (ZUEC), 1 male, 6.XI.1976, D. Gifford leg., DZ 35.033 (DZUP); **São Gonçalo do Rio Preto** – Parque Estadual do Rio Preto, 811 m, 1 male, 26.III.2015, I. Saraiva et al. leg. (ZUEC), 1 male, 27.V.2015 (PUC-MG), 1 male, 16.VII.2015 (ZUEC), 808 m, 2 males, 29.V.2015, I. Saraiva et al. leg. (PUC-MG), 899 m, 4 males, 16.VII.2015 (PUC-MG), 2 males, 18.VII.2015 (PUC-MG), 766 m, 3 males, 2 females, 19.VII.2015 (PUC-MG), 2 males, 19.IX.2015 (PUC-MG), 1 male, 20.IX.2015 (PUC-MG), 1 male, 28.V.2015 (PUC-MG), 1 male, 25.IX.2015 (PUC-MG), 1 male, 2 females, 23.II.2016 (PUC-MG), 1 male, 26.III.2016 (PUC-MG), 1 female, 19.IX.2016 (PUC-MG), 2 females, 25.XI.2016 (PUC-MG), 787 m, 1 male, 26.III.2016, I. Saraiva et al. leg. ZUEC-LEP 10016 (ZUEC), 899 m, 1 female, 16.VII.2015, I. Saraiva et al. leg. ZUEC-LEP 10017 (ZUEC), 801 m, 1 female, 28.VII.2016, Geanne leg., ZUEC-LEP 10571 (ZUEC), 904 m, 1 female, 29.VII.2016, Geanne leg., ZUEC-LEP 10572 (ZUEC), 914 m, 1 male, 27.VII.2016, Geanne leg., ZUEC-LEP 10573 (ZUEC), 752 m, 1 female, 27.VII.2016, Geanne leg., ZUEC-LEP 10574 (ZUEC), 882 m, 1 female, 27.VII.2016, Geanne leg., ZUEC-LEP 10575 (ZUEC); **São João del Rei** – Rio das Mortes, 800–1000 m, 1 (no abdomen), 16.IV.1955, H. Ebert leg., DZ 35.203 (DZUP); **Santana do Riacho** – Serra do Cipó, 1100 m, 1 male, 1 female, 7–10.V.2002, A. V. L. Freitas leg. (ZUEC-AVLF), APA Morro da Pedreira, 1 female, 14.IV.2012, 1 female, 24.X.2012, 1 male, 15.IV.2012, (DNA vouchers YPH-0572, YPH-0573, YPH-0574), M. Beirão leg., ZUEC-LEP 10010, ZUEC-LEP 10011*, ZUEC-LEP 10012* (ZUEC), 1 male, 08.III.2009, 1 male, 11.III.2009, Kaminski L.A. leg., ZUEC-LEP 10072, ZUEC-LEP 10074 (ZUEC); **Santa Barbara** – Serra do Caraça, 1300–1500 m, 1 male, 1–5-II-1985, Mielke & Casagrande leg., DZ 31806 (DZUP); **Lagoa Santa**: Serra do Cipó, 1000–1300 m, 1 female, 30-I-1985, Mielke & Casagrande leg., DZ 31.848 (DZUP); **Cardeal Mota** – Serra do Cipó, 19°21'S 43°36'W, 1 male, 07-XII-2005, Oliveira L. B. leg., ZUEC-LEP 10298 (ZUEC). São Paulo: **Campo Alegre** – Brotas, 750 m, 2 males, 1.V.1966, H. Ebert leg., DZ 35.223, DZ 35.263, 1 male, 21.V.1967, DZ 34.973 (DZUP); **Santa Rita do Passa Quatro** – Gleba Pé do Gigante, Parque Estadual da Vassungua, 21°37'36.52"S 47°37'34.57"W, 1 male, 1–3.V.2003, A.V.L. Freitas leg. (ZUEC-AVLF), 1 female, 1–3.V.2003, A.V.L. Freitas leg. (ZUEC), 1 female, IV.2003, A. V. L. Freitas leg., ZUEC-LEP 10265 (ZUEC), 1 female, IV.2003, (DNA Voucher YPH-0065), A.V.L. Freitas leg., ZUEC-LEP 10015 (ZUEC); **Itirapina** – Cerrado da Graúna, 1 female, 13.VIII.2010, D.G.M. Silva leg., (DNA voucher MGCL-LOAN-150) (ZUEC), 1 male, 31.VIII.2010, D.G.M. Silva leg., (DNA voucher MGCL-LOAN-134) (ZUEC).

Additional examined material. Minas Gerais: **Santana do Riacho** – Serra do Cipó, 1 female, 11.III.2009, Kaminski L.A. leg., ZUEC-LEP 10075 (ZUEC); **Belo Horizonte** – Área de Proteção Especial Manacial Cercadinho, 19°58'18.4"S 43°54'30"W, 2007, 1 male, 8 females, Silva A.R.M. leg., ZUEC-LEP 10087, ZUEC-LEP 10083, ZUEC-LEP 10085, ZUEC-LEP 10086, ZUEC-LEP 10088, ZUEC-LEP 10089, ZUEC-LEP 10090, ZUEC-LEP 10091, ZUEC-LEP 10092 (ZUEC).

Nhambikuara mima (Butler, 1867) comb. nov. (Figs. 3–6)
Euptychia mima Butler, 1867: 500 [no illustration].
Zischkaia mima; Lamas 2004: 223. – Brévignon & Benmesbah, 2012: 46.

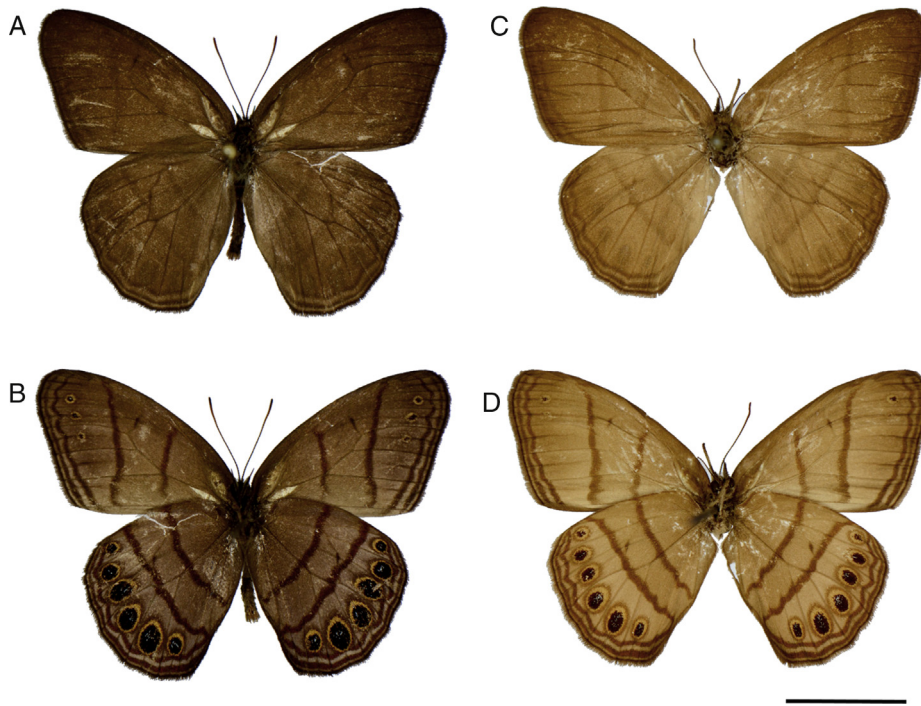


Fig. 3. *Nhambikuara mimia* **comb. nov.** A – male, dorsal (DZ 35.877); B – male, ventral; C – female, dorsal (DZ 34.823); D – female, ventral.

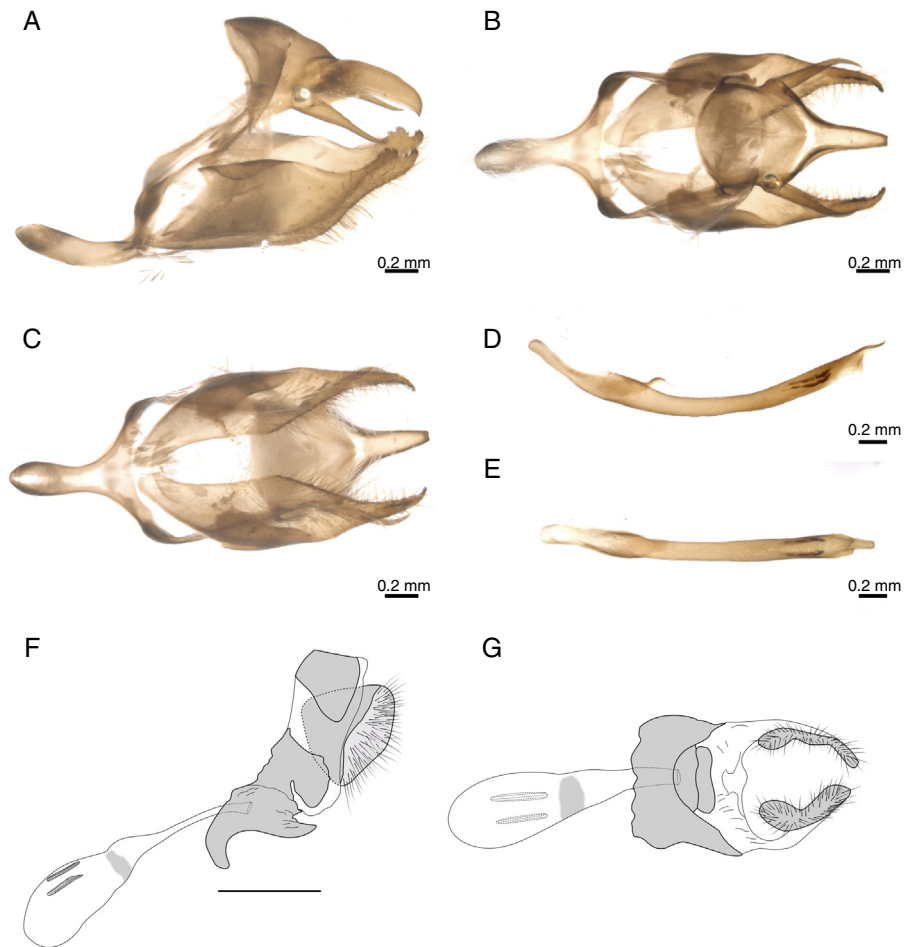


Fig. 4. *Nhambikuara mimia* **comb. nov.**, male (MGCL-LOAN-175) and female genitalia (FLMNH-MGCL-278955). A – lateral; B – dorsal; C – ventral; D – aedeagus, lateral; E – aedeagus, dorsal; F – female lateral; G – female ventral.

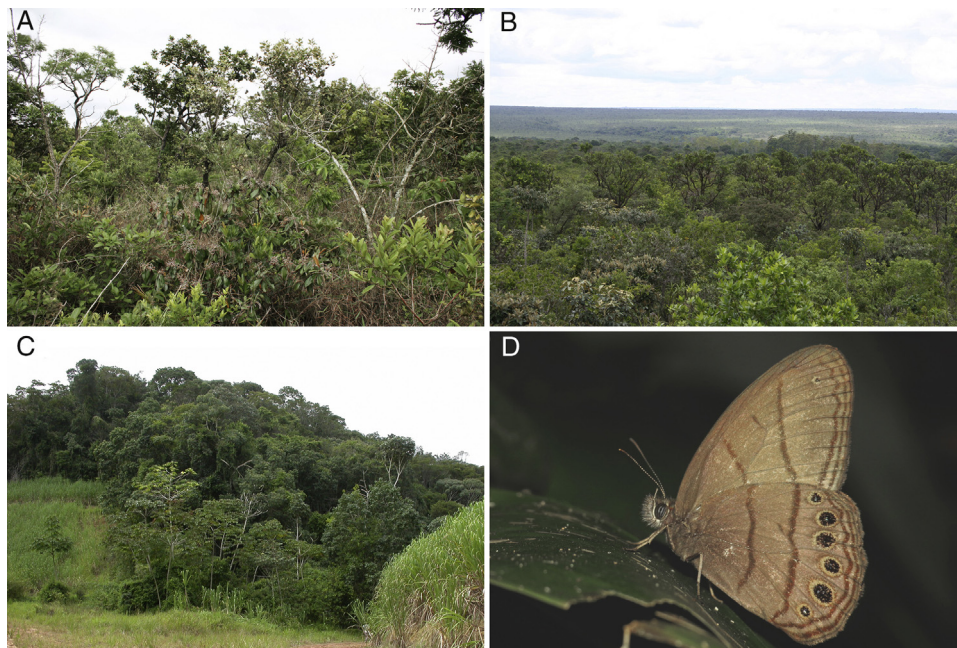


Fig. 5. Natural habitats of *Nhambikuara cerradensis* gen. et sp. nov. in the Cerrado: A – Itirapina, São Paulo; B – Brasília, Distrito Federal and *Nhambikuara mima* comb. nov.: C – Sirinhaém, Pernambuco; D – an individual in its natural habitat in Guiana, Surama, north Rupununi (Photo: David Geale).

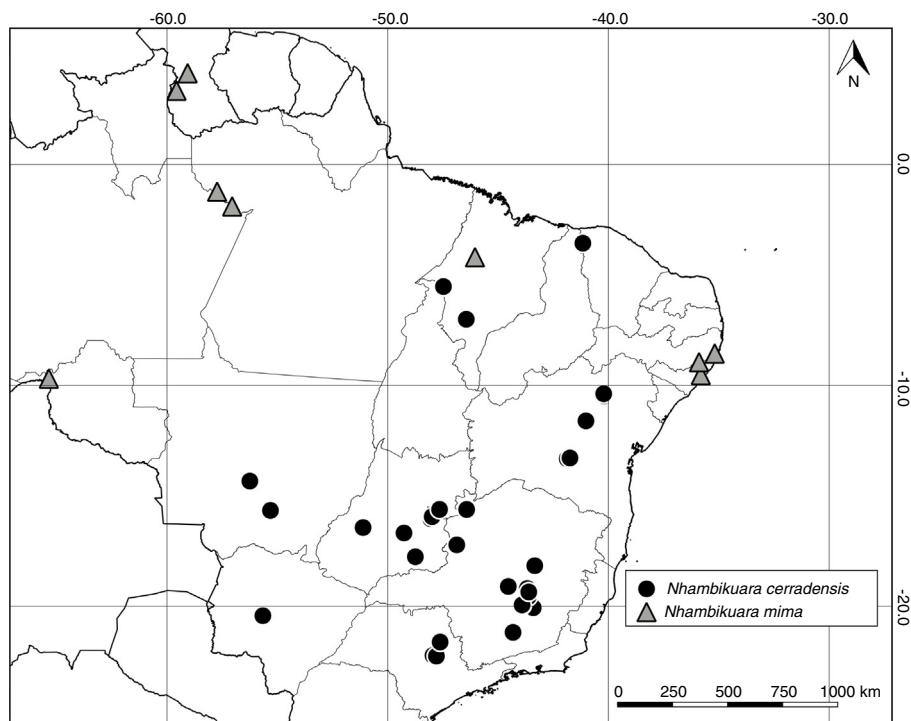


Fig. 6. Map showing the geographical distribution of *Nhambikuara cerradensis* gen. et sp. nov. (black circle) and *Nhambikuara mima* comb. nov. (black triangle).

Diagnosis. *Nhambikuara mima* comb. nov. (Fig. 3) differs from *Nhambikuara cerradensis* sp. nov. by the slightly more elongated ocelli in the VHW, wider lines on the VW, the male genitalia with a truncated uncus, about the same length as the gnathos, the apex of the valva with a developed dorsal serrated projection, the aedeagus with short paired cornuti, the female genitalia with a rectangular lamella antevaginalis, which is ventrally concave at median region in apical portion, the corpus bursae with a sclerotized half-ring at close to ductus region, and latero-ventrally short, paired signa.

Taxonomic comments. *Euptychia mima* Butler, 1867 was described based on an unstated number of specimens from Tapajós, Pará, Brazil. One of them is designated herein as the lectotype of *Euptychia mima* to fix the identity of the name; this specimen has the following labels: /Type H.T./*Euptychia mima* Butler. Monograph/B.M.TYPE No Rh 3250 *Euptychia mima* ♂ Butl[er]/Type of Species/Tapajos, Amazonas, H.W. Bates./Goldman-Salvin Coll. 1904 – 1. *Euptychia mima*, Butl[er]/*mima*; and two other labels will be added later: /Lectotypus/Lectotypus *Euptychia mima* Butler, 1867. A.V.L. Freitas, E.P.

Barbosa, T. Zacca, det. 2018/. Deposited at NHMUK. The last two labels will be sent to the curator later.

Butler (1867) treated this species in "Division VI" of *Euptychia*, characterized by the absence of ocelli on both DW and VFW, and six black and ovoid ocelli with silvery pupils in VHW. In this division were also included *Euptychia saundersii* Butler, 1867, *Euptychia fumata* Butler, 1867, *Euptychia pacarus* Butler, 1867 and *Euptychia insignis* Butler, 1867, species currently placed in *Zischkaia* Forster, 1964. When describing *Zischkaia*, Forster (1964) did not include *E. mima*, *E. pacarus* or *E. insignis*, but only *E. fumata* and *E. saundersii*. The current taxonomic classification for *Zischkaia* is that of Lamas (2004), who partially followed Butler's arrangement (except by treating *E. insignis* within an *Incertae sedis* group), but also included *E. mima* in the genus. An ongoing revision of *Zischkaia* (Nakahara et al., *in prep.*) shows that *E. mima* is not closely related to other *Zischkaia*, based on morphological and molecular evidence, reinforcing its removal from that genus.

Variation. Sexual dimorphism is not well marked, but, like virtually all euptychines, females are typically larger and paler than males and have more rounded wings. Intraspecific variation is also low, being restricted to the size of VHW ocelli and the irregularity of the VHW median line.

Male genitalia (Fig. 4). Tegumen dorsally flattened, anterior margin concave at median region; gnathos about the same length of uncus and curved upwards; uncus broad and straight, apex curved downwards, basal third wide; appendices angulares reduced; anterior projection of saccus 1/3 length of valva; fultura superior absent; fultura inferior sclerotized in U-shape; valva with a developed costae, dorso-apical region serrated with a small dorsal projection; aedeagus with anterior region curved upwards, posterior region about 2 times longer than anterior region, short paired cornutal patches.

Female genitalia. 8th tergite sclerotized, not fused with the lateral expansions of lamella antevaginalis, spiracle absent; papilla analis developed, sub-squared, basal half strongly sclerotized, setae sparsely at distal region, apophysis posterior absent; lamella antevaginalis fused to lamella postvaginalis forming the squared sterigma which is strongly sclerotized and developed; ductus bursae totally membranous, as long as corpus bursae, weakly sclerotized half-ring between ductus bursae and corpus bursae, paired signa dorsally.

Distribution (Fig. 6). *Nhambikuara mima comb. nov.* is present in the humid forests both in the Amazon region (including records from French Guiana – Brévignon and Benmesbah, 2012) and in northeastern Brazil (Alagoas and Pernambuco).

Examined material. 9 males and 7 females (4 specimens dissected). VENEZUELA – Bolívar: **Canaima**, [6°14'23"N, 62°51'8"W], 1 female, 10 Aug 1973, FLMNH-MGCL-278955* (MGCL). GUYANA – Takutu-Upper Essequibo: Kanuku Mts., Nappi Creek, 500–1000 m, 03°20.7'N 59°34.2'W, 1 female, 21.I–10.III.1999, Fratello S., Hanner R., Hendricks S. & Williams R. *leg.* (USNM), 1500–2700 m, 03°18.8'N 59°33.9'W, 1 female, 21.II–10.III.1999 (DNA voucher LEP-18705), Fratello S., Hanner R., Hendricks S. & Williams R. *leg.* (USNM). SURINAM – Brokopondo: **Bronsweg**, 2 males, 8 Mar 1971, FLMNH-MGCL-278952, FLMNH-MGCL-278953, (MGCL). FRENCH GUIANA – St-Laurent du Maroni: **Maroni River**, 1 male, FLMNH-MGCL-278954 (MGCL). BRAZIL – Amazonas: **Nhamundá** – Rio Nhamundá, Cuipiranga, 1°53'58"S 57°02'59"W, 1 male, 20–22.V.2008, Mielke & Casagrande *leg.*, DZ 35.877 (DZUP). Pará: **Faro** – Co[mpanhia]mi[neradora]sa[ntarém], 1 male, 24.VII.1973, K. S. Brown *leg.*, ZUEC-LEP 10264 (ZUEC). Rondônia: **Porto Velho** – Abunã, U[sina] H[idr]E[létrica] Jirau, 250 m, 1 female, 15.IX.2012, (DNA voucher MGCL-LOAN-550*), A.V.L. Freitas *leg.*, ZUEC-LEP 10107 (ZUEC). Maranhão: **Santa Luzia** – Santa Luzia-Açailândia, Fazenda Terrasse road, km 108, 1 male, 3.VIII.1974, Mielke *leg.*, DZ 35.878 (DZUP). Pernambuco: **Sirinhaém** – Matas da Usina Trapiche,

1 male, 14.VIII.2006, B-834/TPICH, (DNA voucher MGCL-LOAN-406), A.V.L. Freitas *leg.* (ZUEC-AVLF). Alagoas: **Rio Largo** – Utinga, 1 female, 16.VI.1949, ex-coll. A. Cardoso, DZ 34.823* (DZUP); **Ibateguara** – Serra Grande, 1 male, 16.XI.2012 (DNA voucher MGCL-LOAN-175*), D.H.A. Melo *leg.*, ZUEC-LEP 10106 (ZUEC). PERU – Huánuco: **Cordillera del Sira**, [9°25'S, 74°45'W], 800 m, 2 females, Sep 1987–Aug 1988, Exp. Universidad Vienna, MUSM-LEP-105652, MUSM-LEP-105653 (MUSM).

BOLIVIA – La Paz: **Zongo** [16°7'S, 68°2'W], 1 male, Garlepp *leg.* (MNHU).

Phylogenetic analyses and genetic distances

The ML analysis using molecular evidence from three genes (Fig. 7) is in agreement with morphological data and supports the close relationship of *Euptychia mima* with the new species here described, *N. cerradensis sp. nov.*, and we thus move it into the new genus as *N. mima comb. nov.* The ML consensus tree shows that *N. mima comb. nov.* is sister to *N. cerradensis sp. nov.*, although with low bootstrap value (BS=66), in the "Pareuptychia clade" (*sensu* Peña et al., 2010), and close to a clade containing several species currently placed in *Splendeuptychia*, with high bootstrap value (BS=100).

Intraspecific genetic distances ranged from 0% to 2.0% and inter-specific distances ranged from 4.2% to 6.7% (Fig. 8). The genetic distance between the two individuals of *N. mima comb. nov.* was 1.2% and the genetic distances among individuals of *N. cerradensis sp. nov.* ranged from 0% to 1.2% (see Table 2). The mean genetic distances among the species analyzed are shown in Table 3.

Discussion

The genus *Nhambikuara gen. nov.* contains two species that phenotypically resemble two other genera of Euptychiina, namely *Zischkaia* Forster, 1964 and *Paryphthimoides* Forster, 1964. However, both morphological and molecular evidence confirm that the two species are unrelated to both of the above genera.

Morphologically, species of *Nhambikuara gen. nov.* are different from species of *Zischkaia* by the absence of a dorsal and a latero-ventral projection of the tegumen, in addition to the absence of sclerotized plates in the ductus bursae of females. Compared to species of *Paryphthimoides*, species of *Nhambikuara gen. nov.* can be differentiated by the truncated uncus, valvae with well-developed costae, and well developed cornuti, in addition to the sterigma in female genitalia. Ongoing taxonomic revisions and phylogenies of *Zischkaia* (Nakahara et al., *in prep.*) and *Paryphthimoides* (Zacca et al., *in prep.*) have also reinforced the results presented herein.

Actually, species of *Nhambikuara gen. nov.* are part of the "Pareuptychia clade" (*sensu* Peña et al., 2010), and appear to be most closely related to several species of *Splendeuptychia* Forster, 1964 (see Fig. 7). In fact, *Nhambikuara gen. nov.* shares several morphological characters with *Splendeuptychia toynei* Willmott & J. Hall, 1995, *Splendeuptychia furina* (Hewitson, 1862), *Splendeuptychia latia* (Butler, 1867) and *Splendeuptychia doxes* (Godart, [1824]), such as the shape of uncus, well-developed anterior projection of saccus, paired and strong sclerotized cornutal patches in aedeagus, female genitalia with sterigma and ductus bursae with sclerotized plates variable in shape, reinforcing the potential close affinities of these taxa.

Based on previous morphological and molecular studies of the Euptychiina (Murray and Prowell, 2005; Peña et al., 2010; Huetas, 2011; Marín et al., 2011, 2017), the genus *Splendeuptychia* has been shown to be polyphyletic, with species spread in at least three different clades. In the present study, the four species above mentioned formed a clade sister to *Nhambikuara gen. nov.* (Fig. 7).

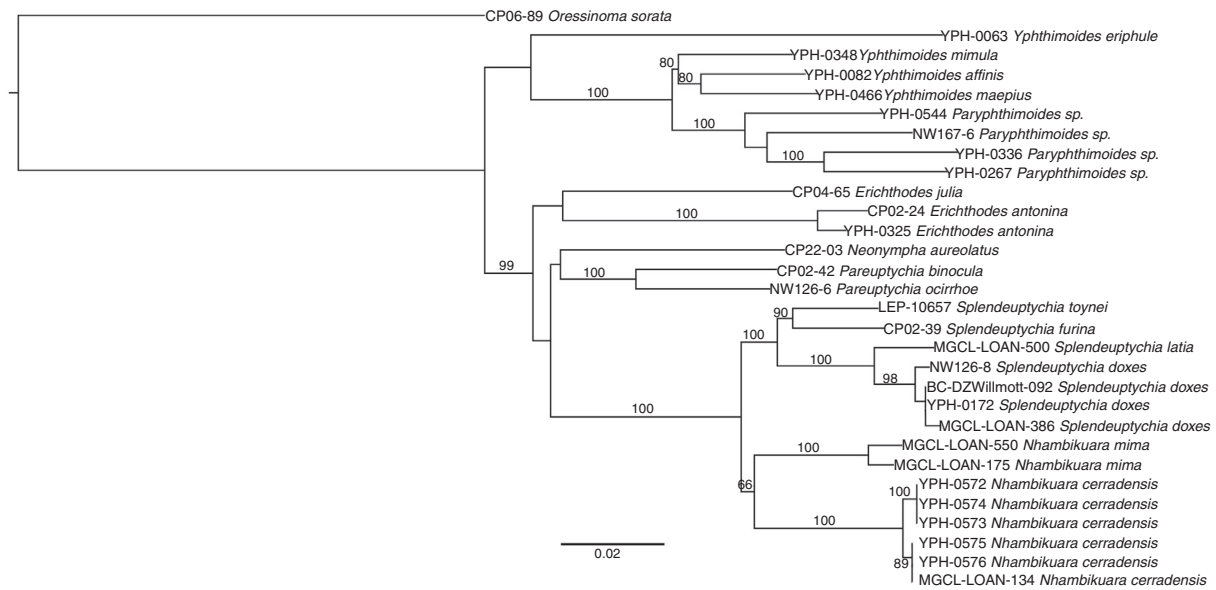


Fig. 7. Maximum likelihood consensus tree showing the phylogenetic relationships among species of *Nhabikuara* **gen. nov.** and exemplar species of *Splendeuptychia*. Numbers above branches are bootstrap values.

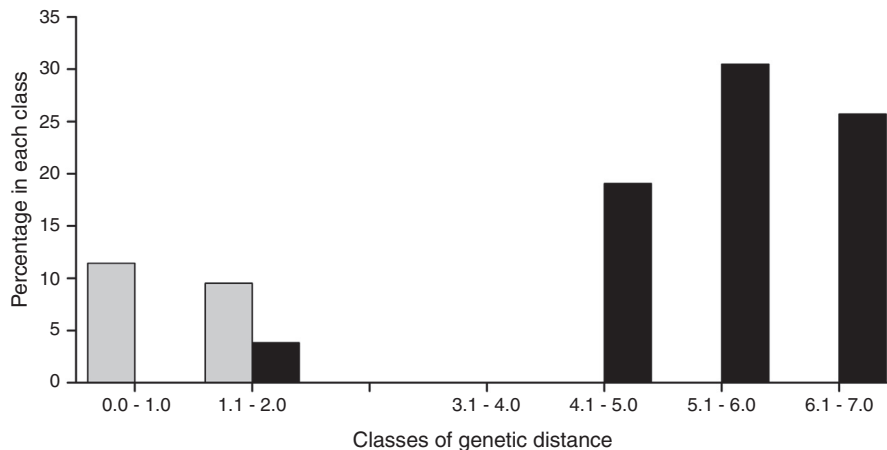


Fig. 8. Frequency distribution of pairwise individual genetic distances within (gray) and between (black) species of *Nhabikuara* **gen. nov.** and *Splendeuptychia* species. The black bar in the class 1.1–2.0 indicates an overlapping of *Splendeuptychia doxes* and *Splendeuptychia latia*.

Other species that are phenotypically similar and that could be part of this clade include *Splendeuptychia junonia* (Butler, 1867), *Splendeuptychia ackeryi* Huertas, Ríos & Le Crom, 2009 and *Splendeuptychia mercedes* Huertas, 2011 (Huertas et al., 2009; Huertas, 2011). More comprehensive morphological and molecular studies are needed to confidently resolve the generic classification of these other potentially closely related species currently treated in *Splendeuptychia*, and ongoing taxonomic revision of the genus *Splendeuptychia* should clarify the taxonomy (Huertas, *in prep.*). Here, we decided to proceed with the description of a new species and genus for a species that is distinctive, widespread, often sampled and whose description could contribute to focusing attention on the need to conserve the poorly studied and threatened Brazilian cerrado habitats. As with several other recent species descriptions in Euptychiina (e.g. Huertas et al., 2016; Zacca et al., 2017; Nakahara et al., 2017), where issues still remain to be resolved in terms of the generic classification, there is a real need for names for distinctive species to facilitate the higher-level phylogenetic research needed to ultimately resolve the subtribe's classification.

The present study is one more example of the complexity faced by researchers working on the taxonomy of Euptychiina. Hopefully,

recent collaborative efforts combining several research groups and many subprojects focusing on the systematics of Euptychiina (<http://www.flmnh.ufl.edu/museum-voices/euptychiina/>) will shed light on the relationships and diversity within this large Neotropical butterfly clade.

Conflicts of interest

The authors declare no conflicts of interest.

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References

- Barbosa, E.P., Silva, A.K., Paluch, M., Azeredo-Espin, A.M., Freitas, A.V.L., 2015. *Uncovering the hidden diversity of the Neotropical butterfly genus Ypthimoides Forster (Nymphalidae: Satyrinae): description of three new species based on morphological and molecular data.* *Org. Divers. Evol.* 15, 577–589.
- Benson, D.A., Cavanaugh, M., Clark, K., Karsch-Mizrachi, L., Lipman, D.J., Ostell, J., Sayers, E.W., 2013. *Genbank. Nucleic Acids Res* 41, D36–D42.
- Brévignon, C., Benmesbah, M., 2012. *Complément à l'inventaire des Satyrinae de Guyane (Lepidoptera: Nymphalidae).* In: Lacomme, D., Manil, L. (Eds.), *Lépidoptères de Guyane.* Tome 7. Nymphalidae. Association des Lépidoptéristes de France, Paris, pp. 36–52.
- Brown Jr., K.S., Gifford, D.R., 2002. *Lepidoptera in the Cerrado landscape and the conservation of vegetation, soil and topographical mosaics.* In: Oliveira, P.S., Marquis, R.J. (Eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna.* Columbia University Press, New York, pp. 201–222.
- Butler, A.G., 1867. *A monograph of the Genus Euptychia, a numerous race of butterflies belonging to the family Satyridae; with descriptions of sixty species new to science, and notes on their affinities.* *Proc. Zool. Soc.*, 465–504.
- Cavalcanti, R.B., Joly, C.A., 2002. *Biodiversity and conservation priorities in the Cerrado region.* In: Oliveira, P.S., Marquis, R.J. (Eds.), *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna.* Columbia University Press, New York, pp. 351–367.
- Comstock, J.H., 1918. *The Wings of Insects.* Comstock Publishing Company, New York, pp. 430.
- Comstock, J.H., Needham, J.G., 1898–1899. *The wings of insects.* *Am. Natural.* 32 (374), 81–89.
- Forster, W., 1964. *Beiträge zur Kenntnis der Insektenfauna Boliviens XIX. Lepidoptera III. Satyridae.* Veröffentlichungen der zoologischen Staatssammlung München 8, 51–188, pls. 27–35.
- Freire Júnior, G.B.F., Ph.D. Thesis 2015. *Dinâmica temporal e espacial da comunidade de borboletas frugívoras (Nymphalidae) do Cerrado.* Universidade Federal de Brasília, Brasília, DF, Brazil, xi + 133 pp.
- Freire Júnior, G.de B.F., Diniz, I.R., 2015. *Temporal dynamics of fruit-feeding butterflies (Lepidoptera: Nymphalidae) in two habitats in a seasonal Brazilian environment.* *Fla. Entomol.* 98 (4), 1207–1216.
- Freitas, A.V.L., 2004. *A new species of Ypthimoides (Nymphalidae Satyrinae) from southeastern Brazil.* *J. Lepid. Soc.* 58 (1), 7–12.
- Freitas, A.V.L., 2007. *A new species of Moneuptychia Forster (Lepidoptera: Satyrinae Euptychiina) from the highlands of southeastern Brazil.* *Neotrop. Entomol.* 36 (6), 919–925.
- Freitas, A.V.L., Emery, E.O., Mielke, O.H.H., 2010. *A new species of Moneuptychia Forster (Lepidoptera: Satyrinae Euptychiina) from central Brazil.* *Neotrop. Entomol.* 39 (1), 83–90.
- Freitas, A.V.L., Iserhard, C.A., Santos, J.P., Carreira, J.Y.O., Ribeiro, D.B., Melo, D.H.A., Rosa, A.H.B., Marini-Filho, O.J., Accacio, G.M., Uehara-Prado, M., 2014. *Studies with butterfly bait traps: an overview.* *Rev. Col. Entomol.* 40, 209–218.
- Freitas, A.V.L., Barbosa, E.P., Siewert, R.R., Mielke, O.H.H., Zacca, T., Azeredo-Espin, A.M.L., 2015. *Four new species of Moneuptychia (Lepidoptera: Satyrinae: Euptychiina) from Brazil.* *Zootaxa* 3981 (4), 521–541.
- Goodland, R., 1971. *A physiognomic analysis of the "cerrado" vegetation of central Brazil.* *J. Ecol.* 59, 411–419.
- Hall, T., 2013. *Biological sequence alignment editor software.* Ibis Biosciences 92008, Carlsbad, Available from <http://www.mbio.ncsu.edu/bioedit/bioedit.html#downloads>.
- Huertas, B., Ríos, M.C., Le Crom, J.F., 2009. *A new species of Splendeuptychia from the Magdalena Valley in Colombia (Lepidoptera: Nymphalidae: Satyrinae).* *Zootaxa* 2014, 51–58.
- Huertas, B., Lamas, G., Fagua, G., Mallet, J., Nakahara, S., Willmott, K.R., 2016. *A remarkable new butterfly species from western Amazonia (Lepidoptera: Nymphalidae: Satyrinae).* *Conserv. Colomb.* 24, 1–5.
- Huertas, B., 2011. *A new species of Satyrinae butterfly from Peru (Nymphalidae: Satyrini: Euptychiina).* *Zootaxa* 2802, 63–68.
- Kaminski, L.A., Dell'Erba, R., Barbosa, E.P., Freitas, A.V.L., 2015. *New distribution records and notes on the habitat of Magneuptychia flavofascia Zacca & Siewert, 2014 (Lepidoptera: Nymphalidae).* *Check List* 11 (4), article 1692.
- Kimura, M., 1980. *A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences.* *J. Mol. Evol.* 16, 111–120.
- Klink, C.A., Machado, R.B., 2005. *Conservation of the Brazilian Cerrado.* *Conserv. Biol.* 19, 707–713.
- Lamas, G., 2004. *Checklist: Part 4A. Hesperioidea-Papilionoidea.* In: Heppner, J.B. (Ed.), *Atlas of the Neotropical Lepidoptera*, vol. 5A. Association for Tropical Lepidoptera/Scientific Publishers, Gainesville.
- Marín, M.A., Peña, C., Freitas, A.V.L., Wahlberg, N., Uribe, S.I., 2011. *From the phylogeny of the satyrinae butterflies to the systematics of Euptychiina (Lepidoptera: Nymphalidae): history, progress and prospects.* *Neotrop. Entomol.* 40, 1–13.
- Marín, M.A., Peña, C., Uribe, S.I., Freitas, A.V.L., 2017. *Morphology agrees with molecular data: phylogenetic affinities of Euptychiina butterflies (Nymphalidae: Satyrinae).* *Syst. Entomol.*, <http://dx.doi.org/10.1111/syen.12245>, on-line first.
- Miller, M.A., Pfeiffer, W., Schwartz, T., 2010. *Creating the CIPRES Science Gateway for inference of large phylogenetic trees.* In: *Proceedings of the Gateway Computing Environments Workshop (GCE)*, 14 November 2010, New Orleans, LA, pp. 1–8.
- Murray, D.L., Prowell, D.P., 2005. *Molecular phylogenetics and evolutionary history of the neotropical satyrine subtribe Euptychiina (Nymphalidae: Satyrinae).* *Mol. Phylogenet. Evol.* 34, 67–80.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A.B., Kent, J., 2000. *Biodiversity hotspots for conservation priorities.* *Nature* 403, 853–858.
- Nakahara, S., Zacca, T., Huertas, B., Neild, A.F.E., Hall, J.P.W., Lamas, G., Holian, L.A., Espeland, M., Willmott, K.R., 2017. *Remarkable sexual dimorphism, rarity and cryptic species: a revision of the 'aegrota species group' of the Neotropical butterfly genus Caeruleuptychia Forster, 1964 with the description of three new species (Lepidoptera, Nymphalidae, Satyrinae).* *Insect Syst. Evol.*, 1–53.
- Neild, A.F.E., 1996. *The butterflies of Venezuela. Part 1: Nymphalidae I (Limenitidinae, Apaturinae, Charaxinae).* In: *A Comprehensive Guide to the Identification of Adult Nymphalidae, Papilionidae, and Pieridae.* Meridian Publications, Greenwich, 144 pp., 32 pls., 18 figs.
- Oliveira, P.S., Marquis, R.J., 2002. *The Cerrados of Brazil: Ecology and Natural History of a Neotropical Savanna.* Columbia University Press, New York, viii + 398 pp.
- Peña, C., Nylin, S., Freitas, A.V.L., Wahlberg, N., 2010. *Biogeographic history of the butterfly subtribe Euptychiina (Lepidoptera, Nymphalidae, Satyrinae).* *Zool. Scr.* 39, 243–258.
- Peña, C., Wahlberg, N., Weingartner, E., Kondandaramaiah, U., Nylin, S., Freitas, A.V.L., Brower, A.V.Z., 2006. *Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data.* *Mol. Phylogenet. Evol.* 40, 29–49.
- Ratter, J.A., Ribeiro, J.F., Bridgewater, S., 1997. *The Brazilian cerrado vegetation and threats to its biodiversity.* *Ann. Bot.* 80, 223–230.
- Setz, E.Z.F., Master Thesis 1983. *Ecologia alimentar em um grupo indígena: Comparação entre aldeias Nambiquara de floresta e de cerrado.* Universidade Estadual de Campinas, Campinas, São Paulo, xi + 209 pp.
- Siewert, R.R., Zacca, T., Dias, F.M.S., Freitas, A.V.L., Mielke, O.H.H., Casagrande, M.M., 2013. *The "Taygetis ypthima species group" (Lepidoptera, Nymphalidae, Satyrinae): taxonomy, variation and description of a new species.* *Zookeys* 356, 11–29.
- Silva, A.R.M., Castro, C.O., Mafia, P.O., Mendonça, M.O.C., Alves, T.C.C., Beirão, M.V., 2012. *Borboletas frugívoras (Lepidoptera: Nymphalidae) de uma área urbana (Área de Proteção Especial Manancial Cercadinho) em Belo Horizonte, Minas Gerais, Brasil.* *Biota Neotrop.* 12 (3), 293–297.
- Silva-Brandão, K.L., Freitas, A.V.L., Brower, A.V.Z., Solferini, V.N., 2005. *Phylogenetic relationships of the New World Troidini swallowtails (Lepidoptera: Papilionidae) based on COI, COII, and EF-1 alpha genes.* *Mol. Phylogenet. Evol.* 36, 468–483.
- Stamatakis, A., Hoover, P., Rougemont, J., 2008. *A rapid bootstrap algorithm for the RAxML web-servers.* *Syst. Biol.* 57, 758–771.
- Strassburg, B.B.N., Brooks, T., Feltran-Barbieri, R., Iribarrem, A., Crouzeilles, R., Loyola, R., Latawiec, A.E., Filho, F.J.B.O., Scaramuzza, C.A.M., Scarano, F.R., Soares-Filho, B., Balmford, A., 2017. *Moment of truth for the Cerrado hotspot.* *Nat. Ecol. Evol.* 99, <http://dx.doi.org/10.1038/s41559-017-0099>.
- Tamura, K., Stecher, G., Peterson, D., Filipiński, A., Kumar, S., 2013. *MEGA6: molecular evolutionary genetics analysis version 6.0.* *Mol. Biol. Evol.* 30, 2725–2729.
- Wahlberg, N., Wheat, C.W., 2008. *Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of Lepidoptera.* *Syst. Biol.* 57, 231–242.
- Wahlberg, N., Leneveu, J., Kondandaramaiah, U., Peña, C., Nylin, S., Freitas, A.V.L., Brower, A.V.Z., 2009. *Nymphalid butterflies diversify following near demise at the Cretaceous/Tertiary boundary.* *Proc. R. Soc. B* 276, 4295–4302.
- Zacca, T., Siewert, R.R., Mielke, O.H.H., Casagrande, M.M., 2014. *A new species of Magneuptychia Forster, 1964 (Lepidoptera: Nymphalidae: Satyrinae) from Brazilian Savanna.* *Zootaxa* 3795 (1), 71–78.
- Zacca, T., Casagrande, M.M., Mielke, O.H.H., Huertas, B., Neild, A.F.E., Benmesbah, M., 2017. *Description of a new species of Euptychiina (Lepidoptera: Nymphalidae: Satyrinae) from South America.* *Zootaxa* 4231, 442–450.