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A new species of *Euptychia* Hübner, 1818 (Lepidoptera: Nymphalidae: Satyrinae: Satyrini) from Mount Roraima, Guyana

SHINICHI NAKAHARA^{1,4}, STEVEN A. FRATELLO² & DONALD J. HARVEY³

¹McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA. E-mail: snakahara@ufl.edu

²11 First St, W. Islip, NY 11795, USA. E-mail: sfratell@suffolk.lib.ny.us

³Department of Entomology, Smithsonian Institution, Washington, D.C. 20560-0127, USA. E-mail: harveyd@si.edu ⁴Corresponding author

Abstract

A new nymphalid species in the subtribe Euptychiana, *Euptychia roraima* Nakahara, Fratello & Harvey **n. sp.**, is described from Mount Roraima, Guyana. Both internal and external morphology of *E. roraima* are compared against several *Euptychia* species and the relationship between *E. roraima* and congeners is briefly discussed. A strong case is put forth for further and extensive exploration of the Pantepui region concerning its poorly known butterfly fauna.

Key words: Euptychiina, genitalia, Guianas, Neotropical, Pantepui, Satyrinae

Introduction

The Pantepui is a large region of mountainous tablelands located predominantly in southeastern Venezuela, but also extending into northwestern Guyana and northern Brazil (Braun *et al.* 2003). Mayr & Phelps (1955) first used this term 'Pantepui' and subsequently defined the region as "the sandstone tabletop mountains in the Venezuelan Territorio Amazonas and Estado Bolívar and in the adjacent border regions of Brazil and Guyana" (Mayr & Phelps 1967), their research pertaining to the region's avifauna. The actual area defined by the term 'Pantepui' varies by authors (e.g. Müller 1973; Steyermark 1982) in respect to faunistic, floristic and topographic features. Despite these variable definitions, it is widely accepted that the Pantepui represents a biogeographical region that harbors numerous endemic taxa and is one of the least explored and known areas on earth. As proposed by Neild (1996, 2008), the Pantepui is plausibly considered to form a biogeographic region for butterflies, which is supported by the discoveries of endemic butterfly taxa (e.g. *Stalachtis halloweeni* Hall, 2006 (Riodinidae); *Eretris agata* Pyrcz, 2005 (Nymphalidae); *Forsterinaria hannieri* Zubek & Pyrcz, 2011(Nymphalidae)) inhabiting the cloud forest and scrub of the tepuis' slopes and plateaus. It is important to note that there will be a series of publications regarding the butterfly fauna of this region, the first two parts very recently published (Costa *et al.* 2014a, 2014b).

Mount Roraima (2810m) is situated in the Pantepui region, at the juncture of Venezuela, Guyana and Brazil. It is one of the table mountains called 'tepuis' composed of sandstone layers, which are the remnants of an ancient erosional earth process (Berry *et al.* 1995; Braun *et al.* 2003). A large section of the Guyana Pantepui (the easternmost section of the Pantepui) are known as the Pacaraima (or Pakaraima) Mountains, and Mt. Roraima represents the tallest peak of this range (Braun *et al.* 2003) and one of the loftiest tepuis, only surpassed by Brazil's Pico da Neblina (2994m) and its satellite peak. Compared to the remoteness of most of these tepuis, Mt. Roraima is moderately easy to access on the Venezuelan side, and it is the first tepui to have been explored (McDiarmid & Donnelly 2005). Subsequent to this first expedition, many discoveries of Pantepui endemic taxa have been made during the numerous scientific expeditions to Mt. Roraima.

The purpose of this paper is to describe and name a new species of *Euptychia* from the Pantepui, *Euptychia* being a speciose genus in the subtribe Euptychian, a poorly known clade of Satyrinae (Nymphalidae) (Marin *et al.*

2011). Basic information regarding the genus *Euptychia* can be found in the introduction of our recently published new species description of *Euptychia alacristata* Neild, Nakahara & Fratello, 2014, a taxon predominantly from the Amazon Basin (Neild *et al.* 2014). The latter is the first paper in a series in which we and a number of colleagues intend to describe new *Euptychia* species from the Guiana Shield and Amazon Basin.

This present new Euptychia was discovered during a Smithsonian ornithology expedition to Mt. Roraima in March-April 2001. The second author had asked his friend and previous expeditions partner Romeo Williams, a Guyanese national, to undertake limited collecting to further knowledge of the little known butterfly fauna of Guyana's remote montane hinterlands, while he was involved with a expedition to Guyana's Iwokrama Mountains. Romeo, with collecting help from Wiltshire Hinds, a Guyanese national university student, and Chris Milensky, a Smithsonian ornithologist, collected a limited number of specimens, well less than 100. This small catch resulted in exciting discoveries: a unique undescribed *Euptychia*, which we describe in this paper, a male and female of an undescribed pronophiline satyrine (subsequently named Oxeoschistus romeo Pyrcz & Fratello, 2005), the first record of this genus from the Pantepui, and a female Brevianta Johnson, Kruse & Kroenlein, 1997 (Lycaenidae) hairstreak that may represent a new taxon and also the first record of this genus from the Pantepui (Fratello 2004; Pyrcz & Fratello 2005). Disappointing to the second author, and no doubt also to the expedition members, is that this ornithology expedition reached no higher than approximately 1675m on the Guyanan side of Roraima; at least one earlier biological expedition to the same area had reached over 2450m elevation, exploring upper montane cloud forest with its different biota. This earlier expedition also included limited butterfly collecting which produced some exciting finds: a couple of undetermined pronophiline specimens and a few undetermined acraeine specimens, which are in the University of Guyana collection.

Methods

External morphology and internal morphology were studied using the naked eye and a binocular microscope. Dissections were made using standard techniques (see Neild *et al.* 2014). Forewing length was measured from the base to the apex of the wing using a ruler divided into 1-millimeter increments. All these examinations, photographs, dissections and measurements of the single holotype were performed at the USNM. Taxonomic nomenclature for genital and abdominal structures largely conforms to Klots (1956), taxonomic nomenclature for wing venation follows the Comstock-Needham system described by Miller (1970), and elements of wing pattern follow those of Peña & Lamas (2005) and wing areas follow Neild (1996). The following collection acronyms are used throughout this paper:

NHM The Natural History Museum, London, UKUSNM National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA

Euptychia roraima Nakahara, Fratello & Harvey, new species

(Figs. 1–3)

Euptychia sp.; Fratello, 2004: 125, figs. 7-8

Description. MALE: Holotype forewing length 16 mm.

Wing shape. Forewing nearly triangular but with costa convex, inner margin almost straight, outer margin almost straight (very slightly concave), with a distinctive, sharply angled apex, tornus approximately right-angled; hindwing subtriangular, costa slightly convex, outer margin convex, rounded tornus, anal margin incised basal to tornus.

Wing venation. Forewing recurrent vein present in discal cell.

Dorsal surface. Ground colour dark brown on inner two thirds of forewing and inner half of hindwing, lighter brown and moderately translucent distal to dark brown inner wing areas and along costa and subcosta of both wings and also anal margin and anal interspaces of hindwing; fringe greyish brown.

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FIGURE 1. Holotype male of *Euptychia roraima* from Mount Roraima, Guyana; left, dorsum, right, venter. Scale bar = 10 mm.



FIGURE 2. Body morphology of *E. roraima*. A. head (lateral view). B. head (front view). C. legs. D. antennae (dorsal view). E. antennae (ventral view).

Ventral surface. Forewing ground colour greyish brown, distal one-third slightly paler; a narrow, dark brown band extends basally along the inflation (swollen vein) from radial vein to wing base; regular, narrow and dark brown discal band extends from radial vein, crossing discal cell in a slightly outward diagonal direction, fading away before touching vein 2A, slightly inward diagonal direction below cubital vein; postdiscal band almost parallel, same color, but broader than discal band, extends from radial vein and traverses towards the inner margin until reaching vein 2A, and roughly delimiting the paler distal region; sinuate submarginal band, extends from apex to tornus, in a slightly inward direction below vein M3, gradually broadens towards vein Cu2 and slightly narrower after this vein and also very slightly angled back towards the outer margin; undulating marginal band, extends from the apex towards the tornus, undulating until vein Cu1 and then straight and narrowing towards the inner margin at the tornus after this vein; fringe brownish; ocellus in cell M1, wider than the interspace and spilling over vein M1 and M2, ringed in yellow with one centered white pupil in black area; **hindwing** ground color almost



FIGURE 3. Male genitalia of holotype of *E. roraima*. A. dorsal view. B. lateral view. Scale bar = 1 mm. (Photo courtesy Karie Darrow, USNM).

same as that of forewing, distal one-third slightly paler; dark brown regular band extends from the costal margin to inner margin, near the base of hindwing; discal band almost same color, same width as that of forewing band, traverses from costal margin towards inner margin, very slightly curved distally, near the inner margin sharply angled basally; postdiscal band almost same color, mostly same width as that of fore- wing band, extends from costal margin towards the inner margin, bent outwardly posterior to vein M2, parallel to discal band after vein M3,

narrower and curving distally below 1A, joining the submarginal band near the anal margin, roughly delimiting the paler distal region; irregular submarginal band, slightly paler than basal three bands, traverses from apex along submargin towards the tornus, broadens and rounded M-shaped in each of cells M3 and M2, fused to post discal band in cell 2A and ScR1; wavy marginal band, much thinner and same color as submarginal band, traverses along the distal margin from the apex towards tornus; rufous hints at the tornus; fringe greyish brown; three submarginal ocelli, the smallest of all, in cell ScRs, encircled by a yellow ring surrounded by dark brown ring, with one centered white pupil in the black area; larger ocellus in cell M1, tornally spilling over vein M2, encircled by a yellow ring sur rounded by dark brown ring, with one centered white pupil in the black area in cell Cu1, apically and tornally spilling over vein Cu1 and Cu2 respectively.

Head. (Figs. 2A–B, 2D–E) Eyes dark brown and densely hairy; palpi prominent, approximately 2 times head height, cream-colored, densely pilose ventrally with long brown hairs (see Figs. 2A–B for detail); antennae orange-brown, approximately half of the length of costa from base to apex (see Figs. 2D–E for detail).

Thorax. (Fig. 2C) Dark brown and hairy (see Figs. 2C for detail).

Abdomen. Dark brown and hairy, dorsally and laterally, grayish and hairy ventrally.

Genitalia. (Fig. 3) (1 specimen prepared: vial #2013-06 (USNM)) Tegumen shaped somewhat like a parallelogram in lateral view, anterior dorsal margin concave, ventral margin concave, shaped like a trapezium in dorsal view, a short conspicuous posterior projection of the tegumen above the uncus, one-third length of uncus; uncus anteriorly hairy, rather narrow and short, posterior tapered and hooked in lateral view, evenly broad in dorsal view; gnathos extending ventrally from the posterior ventral margin of tegumen, triangular in lateral view; vinculum fused to anterior ventral margin of tegumen and medially divided; appendices angulares present; saccus short and broad in lateral view, anteroventrally a continuation of the vinculum; valvae sparsely hairy, positioned at approximately a 45 degree angle to the horizontal; valva distal one-third narrow and tapered, apex slightly rounded; basal two-thirds rather oval, ventral margin convex when compared to the dorsal margin, slightly narrowing posteriorly in lateral view, hooked right-angled inwards forming a boot-shape in dorsal view; aedeagus tubular, in dorsal view straight and with broadening anterior portion which opens anterodorsally, in lateral view posterior half of aedeagus narrower, curved upwards, broadening anteriorly, approximately the length of the saccus plus tegumen, with cornuti absent.

FEMALE: Unknown.

Holotype. ♂, Guyana: N. slope Mt. Roraima, 1st Camp 800m, 5°17'N 60°45'W, 12.lll–16.IV.2001, W. Hinds & R. Williams leg. This holotype is deposited in the USNM (USNM ENT 00275158).

Etymology. This specific epithet is derived from the Pemón Indian word, in regard to the great tepui massif where the first and only known specimen was found. This female noun is used here in apposition to the genus name.

Distribution. (Fig. 5) Euptychia roraima is known to date only from the type locality low on the northern slope of Mt. Roraima in northwestern Guyana. This site lies within the Pantepui region which has been described briefly in the introduction. The elevation (800m) at which E. roraima was collected, with no known lowland records, implies that it could be a premontane species (see Neild 1996, for explanation of premontane and montane). If true, this species could also be found in other areas of the Mt. Roraima massif; where there are existing tracts of premontane forest on all aspects of Mt. Roraima (see Google Earth). Given that there has been both a rather limited collecting effort and publication record from a small total part of this great tepui massif: the Guyanan side, the Brazilian aspect, the Gran Sabana approach on the extensive Venezuelan portion, and the summit plateau (e.g. Bell 1932; Huntington 1933; Viloria & Pyrcz 1994, 1999), we assume there remain vast areas of premontane forest on the various aspects that have never been explored for butterflies (A. Neild, pers. comm.). However, most premontane species would probably not be restricted to a single tepui massif, but have wider distributions in the Pantepui, as noted in many endemic species from this biogeographic region (e.g. Greta clavijoi Neild, 2008 (Ithomiinae), Antirrhea ulei (Strand, 1912) (Morphinae), Catasticta duida Brown, 1932 (Pieridae); see Costa et al. 2014a). Though there are a small number of butterflies from other groups that have thus far been found on only a single tepui: Pagyris renelichyi Neild, 2008 (Ithomiinae), Memphis viloriae Pyrcz & Neild, 1996 (Charaxinae), Perisama tepuiensis Attal & De Marmels, 2012 (Biblidinae) and others (A. Neild, pers. comm.), the few known Rhopalocera possibly considered endemic to a single tepui massif are upper premontane and montane pronophiline Satyrinae whose lower elevation limits are substantially higher than the elevation at which E. roraima was collected (e.g. Viloria 1995; Viloria *et al.* 1999). However, for any butterfly species to be considered truly endemic to a single tepui massif, this would need to be proven through extensive collecting on all tepuis, entailing numerous expeditions to individual tepuis in different seasons and on various aspects of the tepuis. As for the probability that *E. roraima* is a more widespread Guianan and Amazonian lowland species that ranges into premontane forest in the Pantepui, this is a possibility we cannot certainly exclude; however, a fairly extensive collecting history in these regions to this date, with no known lowland records as previously mentioned, seems to indicate otherwise (A. Neild, pers. comm.; Neild, 1996, 2008; pers. obs. based on 500+ days collecting by SF and museum collection examination).

Behavior and habitat. Nothing is known concerning the behavior of this species. The single individual was captured by people dedicated solely to collect some butterflies in a remote, little studied region. Even though the photos of Mt. Roraima (Figs. 4–5) were taken at elevations above the capture site (800m) of *E. roraima*, they are indicative of this species' habitat and there is some evidence to assume this species could also be found at these higher elevations. As noted above, extensive collecting in both the Guyanan and Venezuelan lowlands with no records of this taxon, suggests that it is a premontane Pantepui endemic. Even though it is presumed to be so, there is a possibility that this species will be found at elevations lower than 800m in the Pantepui. For example, the second author has recorded a small number of species, that though considered premontane species, were captured at much lower elevations at Kaieteur Falls and Gorge in the easternmost area of Guyana's Pacaraima Mountains: the charaxine *Memphis montesino* Pyrcz, 1995 (250m) and the riodinids *Napaea fratelloi* Hall & Harvey, 2005 (400m), and *Mesosemia phace* Godman, 1903 and *Hyphilaria anthias* (Hewitson, 1874), both taken as low as 100m (Fratello 2012). It is interesting to note that another undescribed *Euptychia* species collected in the Venezuelan Pantepui at approximately 1000m and above, is known from a single NHM specimen from the lower elevations of Kaieteur (A. Neild and M. Costa, pers. comm.).

Diagnosis. *Euptychia roraima* can be separated from other members of the genus by its combination of triangular forewing shape resulting from an especially acute apex and sharply angled tornus; dark coloration, both dorsally and ventrally; thin ventral median and postmedian bands, and a prominent ventral wavy marginal band.



FIGURE 4. NE slope of Mt. Roraima taken from a clearing at approx. 1300m.



FIGURE 5. NE slope of Mt. Roraima taken from approx. 1450m.



FIGURE 6. Map showing the type locality for Euptychia roraima (black square) (Map data: ©2013 Google, MapLink).

Discussion

Based on phenotypic aspects, the second author assumed that this species is a member of *Euptychia* in a previous paper (Fratello 2004). In addition to this external analysis, dissection results of male genitalia revealed that the prominent projection of the tegumen over the uncus is present in the male genitalia. This conspicuous projection is thought to be a diagnostic character for *Euptychia* (Freitas *et al.* 2012; Neild *et al.* 2014), and this combination of facts has influenced our decision to place this species in the genus *Euptychia*. In addition, the presence of the forewing recurrent vein reinforces this placement, as this is considered to be a shared character for known *Euptychia* species (Freitas *et al.* 2012; pers. obs.).

Unexpectedly, genitalic dissection revealed E. roraima possesses male genitalia very similar to two undescribed species of Euptychia known so far only from the Guianas, that are in the process of being described (Fratello et al. MS); its male genitalia are less similar to the predominantly Guianan E. marceli Brévignon, 2005. These three species have phenotypes more similar to each other and dissimilar to *E. roraima*: more rounded wings, a distinctive ventral hindwing ocelli pattern (most pronounced in E. marceli and the other two species' males), a much larger tornal ocellus compared to the large apical ocellus, this tornal ocellus also having a wider yellow ring compared to the yellow ring of the apical ocellus (in cell M1). In E. roraima both the tornal and large apical ventral hindwing ocelli and their yellow rings are much more similar in dimensions. Also noteworthy is that one of the new Guianan Euptychia species mentioned above is very dark both dorsally and ventrally, even more so than E. roraima, making it the darkest of known Euptychia species. As noted above, these probable Guianan endemic undescribed species are most similar in genitalia to the presumed Guianan endemic, E. roraima. This is because all these species share a distally narrow and tapered, and basally oval valva. It is interesting to note that these three species share a relatively small gnathos, a structure present in the type species of the genus Euptychia, E. mollina Hübner, 1818, but absent in many species currently placed in Euptychia (Forster 1964; Neild et al. 2014; pers. obs.). Note that E. marceli somewhat resembles these species in respect of the overall valvae shape, but differs significantly since this species does not possess a gnathos. However, considering the variation of the size and shape of gnathi in the genus *Euptychia* or its complete absence, it is necessary to investigate this structure further in order to use this as a diagnostic character to classify these euptychiine butterflies. Coupling genitalic similarity and probable endemicity to the Guianan region, the authors deduce that the closest known congeners of E. roraima are possibly these two undescribed Guianan Euptychia species. The first author is currently working to revise the genus Euptychia based on both morphological and molecular data, which should elucidate the relationships of these various taxa.

Euptychia roraima is described based solely on the male holotype, as we hope to encourage the discovery of the female, additional specimens, new locality records, and other biological information concerning this unique species. Given the fact that we were not able to find any additional specimens of this taxon in public and private collections, we decided to describe this species based on a single specimen in order to increase the probability of obtaining the above information. The fact that almost nothing is known about this taxon is most probably more due to the inaccessibility of its habitat rather than its natural rarity, and will justify our decision to describe this species based on a single specimen. There are several other discoveries regarding the Lepidopteran fauna of the Pantepui that have been published recently (e.g. Pyrcz *et al.* 2013). However, our knowledge of the butterflies of the remote Guyanan Pantepui remains very limited, despite the specimens collecting by the second author at Kaieteur, some extensive collecting by the second author and partners on Mt. Ayanganna and Mt. Wokomong, and some rather limited prior collecting on Mt. Roraima, at Kaieteur and a few other areas. It is our hope that prior lepidopterists' impressive efforts to explore the Venezuelan Pantepui, and this article and previous ones dealing with Guyana's Pantepui butterflies (e.g. Fratello 2004; Fratello 2012), will inspire further exploration and a deeper ecological and biogeographic knowledge of the Rhopalocera of this incredible region.

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Pantepui and Andean *Euptychia* species; this additional information added context to the one known specimen of *E. roraima* and accounted for a better article. We are grateful to Andrew Neild for reading and making comment on our manuscript. Karie Darrow (USNM, USA) took the excellent genitalia photos. The first author acknowledges support from the National Science Foundation, Grant No. DEB-1256742. The second author thanks the following people for the specimen of *E. roraima* and other butterflies collected on the Smithsonian Mt. Roraima ornithology expedition: expedition leader Dr. Mike Braun (USNM, USA) allowed butterfly collecting on this Smithsonian Division of Birds expedition; Museum Specialist Chris Milensky (USNM, USA), and predominantly University of Guyana student Wiltshire Hinds (Guyana) and Guyanese national expedition guide/worker Romeo Williams (Guyana) undertook the collecting effort; Chris Milensky assiduously made sure specimens and data were brought back to the Smithsonian Lepidoptera collection. Chris Milensky also generously allowed his photos of Mt. Roraima to be used on this and the second author's previous article. Finally, we thank Rayner Núñez Agulia (Cuba) and an anonymous reviewer for their helpful comments on the manuscript.

Literature cited

- Bell, E.L. (1932) Hesperiidae (Lepidoptera, Rhopalocera) of the Roraima and Duida expeditions, with descriptions of new species. *American Museum Novitates*, 555, 1–16.
- Berry, P.E., Holst, B.K. & Yatskievych, K. (1995) *In:* Berry, P.E., Holst, B.K. & Yatskievych, K. (Eds.), *Flora of the Venezuelan Guayana, Vol. 1. Introduction.* Missouri Botanical Garden and Timber Press, St. Louis, 393 pp.
- Braun, M.J., Robbins, M.B., Milensky, C.M., O'Shea, B.J., Barber, B.M., Hinds, W. & Prince, W.S. (2003) New birds for Guyana from Mts. Roraima and Ayanganna. *Bulletin of the British Ornithologists' Club*, 123, 24–32.
- Costa, M., Viloria, A.L., Huber, O., Attal, S. & Orellana, A. (2014a) Lepidoptera del Pantepui. Parte I: Endemismo y caracterización biogeográfica. *Entomotropica*, 28 (3), 193–216. [December 2013]
- Costa, M., Viloria, A.L., Attal, S. & Orellana, A. (2014b) Lepidoptera del Pantepui. Parte II: Descripción de nuevos Nymphalidae (Papilionoidea). *Bulletin de la Société entomologique de France*, 119 (1), 39–52.
- Forster, R. (1964) Beiträge zur Kenntnis der Insektenfauna Boliviens XIX. Lepidoptera III. Satyridae. Veröffentlichungen der zoologischen Staatssammlung München, 8, 511–88.
- Fratello, S.A. (2004) New species from Mt. Roraima. News of the Lepidopterists' Society, 46 (4), 122–125.
- Fratello, S.A. (2012) *Memphis montesino* Pyrcz collected in Guyana, S. America & notes concerning a few Riodinids from the same habitat. *News of the Lepidopterists' Society*, 54 (2), 46–47.
- Freitas, A.V.L., Wahlberg, N., Matos-Maravi, P.F., Marín, M.A. & Mielke, O.H.M. (2012) Euptychia boulleti (Le Cerf) n. comb. (Lepidoptera: Nymphalidae: Satyrinae), a rare and endangered butterfly from Southeastern Brazil. Neotropical Entomology, 41 (6), 461–467.

http://dx.doi.org/10.1007/s13744-012-0073-5

- Huntington, E.L. (1933) Erycinidae and Lycaenidae (Lepidoptera, Rhopalocera) from the regions of Mt. Roraima and Mt. Duida. *American Museum Novitates*, 611, 1–5.
- Klots, A.B. (1956) Lepidoptera. In: Tuxen, S.L. (Ed.), Taxonomists's Glossary of Genitalia in Insects. Copenhagen, Munksgaard, Copenhagen, pp. 97-111.
- McDiarmid, R.W. & Donnelly, M.A. (2005) The herpetofauna of the Guayana Highlands: amphibians and reptiles of the Lost World. *In*: Donnelly, M.A., Crother, B.I., Guyer, C.W., Marvalee, H. & White, M.E. (Ed.), *Ecology and evolution in the tropics: a herpetological perspective*. University of Chicago Press, USA, pp. 461–560. [584pp]
- 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. *Neotropical Entomology*, 40 (1), 1–13.

http://dx.doi.org/10.1590/S1519-566X2011000100001

- Mayr, E. & Phelps, W.H. Jr. (1955) The origin of the bird fauna of South Venezuelan Highlands. *Bulletin of the American Museum of Natural History*, 136 (5), 269–328.
- Mayr, E. & Phelps, W.H. Jr. (1967) The origin of the bird fauna of the south Venezuelan highlands. *Bulletin of the American Museum of Natural History*, 136, 273–327.
- Miller, L.D. (1970) Nomenclature of wing veins and cells. Journal of Research on the Lepidoptera, 8 (2), 37-48.
- Müller, P. (1973) The dispersal centres of terrestrial vertebrates in the Neotropical realm. *Biogeographica*, 2, 1–244.
- Neild, A.F.E. (1996) The Butterflies of Venezuela. Part 1: Nymphalidae I (Limenitidinae, Apaturinae, Charaxinae). A comprehensive guide to the identification of adult Nymphalidae, Papilionidae, and Pieridae. Meridian Publications, Greenwich, 144 pp.
- Neild, A.F.E. (2008) The Butterflies of Venezuela. Part 2: Nymphalidae II (Acraeinae, Libytheinae, Nymphalinae, Ithomiinae, Morphinae). A comprehensive guide to the identification of adult Nymphalidae, Papilionidae, and Pieridae. Meridian Publications, London, 276 pp.
- Neild, A.F.E., Nakahara, S., Fratello, S.A. & Harvey, D.J. (2014) A new species of Euptychia Hübner, 1818 (Nymphalidae:

Satyrinae: Satyrini) from the Amazon basin and the Guianas. Tropical Lepidoptera Research, 24 (1), 4-9.

- Peña, C. & Lamas, G. (2005) Revision of the butterfly genus *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae, Satyrinae). *Revista Peruana de Biología*, 12, 5–48.
- Pulido, H.W., Andrade, M.G., Peña, C. & Lamas, G. (2011) Two new taxa of *Euptychia* Hübner, 1818 (Lepidoptera: Nymphalidae: Satyrinae) from the Andes of Colombia and Peru. *Zootaxa*, 2906, 43–51.
- Pyrcz, T.W. & Fratello, S. (2005) Cloud Forest butterfly fauna of the Pantepui poor or poorly known? Description of new species and records of new genera of Pronophilina: *Eretris agata* and *Oxeoschistus romeo* (Nymphalidae, Satyrinae). *Journal of the Lepidopterists' Society*, 59 (4), 200–211.
- Pyrcz, T.W., Stachowicz, I. & Garlacz, R. (2013) A new Andean element in the lepidopterous fauna of the Guiana Shield: the day-flying genus Erateina Doubleday, with the description of two new species from Roraima, Tramen and Auyán Tepui (Geometridae: Larentiinae). *Genus*, 24 (3–4), 291–301.
- Steyermark, J.A. (1982) Relationships of Some Venezuelan Forest Refuges with Lowland Tropical Floras. Pp. 182–221. In: Prance, G.T. (Ed.), Biological diversification in the tropics. Columbia University Press, New York, 714 pp.
- Viloria, A.L. (1995) Description of a new species of *Pedaloides* (Lepidoptera: Satyridae: Pronophilini) from the Cerro de la Neblina, Venezuela. *Atalanta*, 25 (3–4), 525–529.
- Viloria, A.L. & Pyrcz, T.W. (1994) A new genus *Protopedaliodes* and a new species *Protopedaliodes kukenani* from the Pantepui, Venezuela (Lepidoptera, Nymphalidae, Satyrinae). *Lambillionea*, 94 (3), 345–352.
- Viloria, A.L. & Pyrcz, T.W. (1999) New pronophiline butterflies from the Venezuelan Tepuyes (Nymphalidae: Satyrinae). Journal of the Lepidopterists' Society, 53 (3), 90–98.