

<http://zoobank.org/urn:lsid:zoobank.org:pub:5902C23E-7DFB-4826-BDB8-953DAF32033B>

# A new subspecies of *Oxeoschistus puerta* (Westwood, 1851), from the Sierra de Perijá, western Venezuela (Lepidoptera: Nymphalidae: Satyrinae)

Una nueva subespecie de *Oxeoschistus puerta* (Westwood, 1851), de la  
 Sierra de Perijá, Venezuela occidental (Lepidoptera: Nymphalidae: Satyrinae)

Ángel L. Viloria<sup>1</sup> & Mauro Costa<sup>2</sup>

<sup>1</sup>Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), km 11 carretera Panamericana, Altos de Pipe, estado Miranda 1204, Venezuela.

<sup>2</sup>Residencias Las Cumbres, avenida Las Acacias, La Florida, Caracas 1050, Distrito Capital, Venezuela.

Correspondence: sebastianviloriacarrizo@gmail.com; aviloria@ivic.gob.ve

(Received: 02-11-2021 / Accepted: 15-02-2022 / On line: 30-09-2022)

## ABSTRACT

*Oxeoschistus puerta sabinoi* ssp. nov., a pronophiline butterfly (Lepidoptera: Nymphalidae: Satyrinae) from the montane and upper montane forests (1,100-1,900 m a.s.l.) of the Venezuelan slope of the Sierra de Perijá, Zulia state, Venezuela, is described, illustrated and compared with its close congeners. The taxon *O. puerta magnus* Pyrcz & Viloria, 2007, from the Serranía del Tamá, is revised and newly identified as *Oxeoschistus simplex magnus* comb. nov.

**Keywords:** Northern Andes, Lake Maracaibo basin, Pronophilina, Satyrini.

## RESUMEN

Se describe, ilustra y compara *Oxeoschistus puerta sabinoi* ssp. nov., una mariposa pronofilina (Lepidoptera: Nymphalidae: Satyrinae) procedente de los bosques montanos y altimontanos (1.100-1.900 m s.n.m.) de la vertiente venezolana de la Sierra de Perijá, estado Zulia, Venezuela. Se revisa el taxón *O. puerta magnus* Pyrcz & Viloria, 2007, de la Serranía del Tamá, y se reidentifica como *Oxeoschistus simplex magnus* comb. nov.

**Palabras clave:** Andes septentrionales, cuenca del Lago de Maracaibo, Pronophilina, Satyrini,

## INTRODUCTION

The Sierra de Perijá is a mountain range at the northernmost tip of the Andes. Its main ridge (maximum elevation ca. 3,670 m a.s.l.) divides the Magdalena River (Colombia) and the Lake Maracaibo (Venezuela) basins. So, it harbors slightly different biological elements on each slope, which according to Morrone *et al.* (2022), belong to the adjacent biogeographical Provinces of Magdalena and Guajira (Pacific Dominion), as well as higher elevation Andean elements, part of which are endemics and char-

acteristic to the Paramo Province of the South American transition zone.

The study of the butterfly fauna of the Perijá Mountains began in the late 19<sup>th</sup> Century (Godman & Salvin 1880). Viloria (1990b, 1997) compiled a number of bibliographic sources with references to a few entomological expeditions to this range and the adjacent lowlands. These works also included the citation of systematic revisions of some Neotropical butterfly genera with mention to species and subspecies from Perijá and papers with descriptions of several of its endemic taxa. Starting in the late 1970s,

interest in the butterflies of this region increased remarkably, and a number of taxonomic and faunistic studies have been accomplished to improve the knowledge of the regional Papilioidea, most notably the Nymphalidae (Adams 1977, 1984, 1985, Adams & Bernard 1979 [Colombian slope], Viloria 1989, 1990a, b, 1991a, b, c, 1992, 1994, 1995, 2000, 2005, [2006], Pineda 1991, Viloria *et al.* 1992, 2008, Neild 1996, 2008 [Venezuelan slope], Pulido, 2007, Pulido & Andrade 2007, 2008, 2010, Andrade 2008, Pulido *et al.* 2010, 2011 [Colombian slope]).

Among the nymphalid butterflies of the Sierra de Perijá, the members of the Satyrinae have been particularly well studied, especially the montane and high Andean members of the subtribe Pronophilina, whose inventory was first achieved by Adams & Bernard (1979), followed by Viloria (1990b) and Pulido & Andrade (2007, 2010). Only Viloria (*op. cit.*) detected and reported the presence of one species of *Oxeoschistus* Butler, 1867 in this mountain range.

The genus *Oxeoschistus* was erected by Butler (1867). He defined it by having forewings elongated and subfalcate with outer margin moderately wavy (minimally sinuous) and notably wavy in hindwings; labial palpi long and wavy. One diagnostic character was also the “forewing cell bifurcated at the apex”, that is to say, divided by the presence of a prominent recurrent vein entering the discal cell, being the “lower fork” greater and arched, with three angles, and the “upper fork” pointed and originating the five radial veins and M1 (Butler 1867: 267, [fig.] 2, but see Figure 3 of the present work). The type species of the genus, by original designation, is *Pronophila puerta* Westwood, 1851, a taxon endemic to the middle elevations of the Cordillera de la Costa in northern Venezuela.

Forty years later, the genus was revised by Thieme (1907) and more recently by Pyrcz *et al.* (2020) (in part). Judging from its morphological affinities – palpi, legs, wing pattern and venation, genitalic structure – (Reuter 1896, Miller 1968, Adams 1986, Viloria 2007, Pyrcz 2010), and genetic (molecular) relationships (Matz & Brower 2016), *Oxeoschistus* belongs in the tribe Satyrini Boisduval, 1833, subtribe Pronophilina Reuter, 1896, and should be placed close to its type genus, *Pronophila* Doubleday, 1849.

Modern taxonomy of the species of *Oxeoschistus* has been the subject of two arrangements (Lamas *et al.* 2004, Pyrcz 2000). However, its species have been catalogued or listed with synonymy by several authors since the 19<sup>th</sup> Century (Kirby 1871, Thieme 1907, Weymer 1911, Gaede 1931, D'Abraera 1988, Lamas *et al.* 2004, Pyrcz 2010, Pyrcz *et al.* 2020).

The most recently described taxa are from Peru (*O. puerta garleppi* Lamas 2003, *O. iphigenia* Pyrcz 2004), Venezuela (*O. romeo* Pyrcz & Fratello 2005, *O. puerta*

*magnus* Pyrcz & Viloria 2007), Colombia (*O. simplex triplex* Pyrcz & Salazar in Pyrcz & Rodríguez 2007), Costa Rica and Honduras (respectively, *O. tauropolis mitsuko* Pyrcz & Nakamura and *O. hilara lempira* Pyrcz in Pyrcz *et al.* 2020).

The species of *Oxeoschistus* known to Venezuela have been described, illustrated, reported or cited by Westwood (1851), Raymond (1982), Viloria (1990b), Fratello (2004), Pyrcz & Fratello (2005), Pyrcz & Viloria (2007), Viloria *et al.* (2010), Viloria & Costa (2019) and Orellana *et al.* (2019) (for a conclusive identification of the taxa present in Venezuela, see discussion). In this paper we describe a new subspecies of *Oxeoschistus puerta*, which corresponds with the taxon referred to by Viloria (1990b) as *Oxeoschistus* sp., and *Oxeoschistus puerta* ssp. nov. (Viloria 2000, Lamas *et al.* 2004).

## MATERIAL AND METHODS

The butterflies studied for this report were collected in the Sierra de Perijá, western Venezuela in three different occasions: December 1950, by Francisco Fernández Yépez, October 1989, by Ángel L. Viloria and April 2011, by Mauro Costa. It was first detected as a new taxon during the studies conducted by Viloria in 1988-1990 for his first degree thesis (Viloria 1990b). Thus, the specimens of the type series have been examined several times ever since. We have used standard techniques of observation and capturing the adult insects in the field (hand nets), ordinary methods of setting the specimens, pinned for dry preservation in entomological cabinets. The right wings of one male specimen were removed, diaphanized by immersion in diluted commercial bleach 1% for approximately 10 minutes, then profusely washed in distilled water, transferred subsequently to ethanol 70% for 15 minutes, and then to absolute ethanol. They were immediately fixed and permanently preserved in euparal between a large glass microscope slide (76 × 51 mm) and its cover (64 × 50 mm). One male abdomen was removed and soaked overnight in KOH 10% solution to digest and remove flesh and fat from the chitinous structures. Genitalic structures were mechanically removed, transferred to distilled water for 8 hh and cleaned with microdissecting tools under a stereoscopic microscope. After study, these microstructures were stored in plastic vials with a solution of 70% ethanol and 30% glycerine. Slides and vials have been externally labelled and catalogued. Both wing veins and genitalic structures were drawn with the aid of a camera lucida. Observing the specimens of the type series with and without magnification, and their dissected organs and structures, allowed for comparisons with other taxa (actual specimens

preserved, photographs and drawings), which eventually led to the diagnosis and description of the new taxon.

Our criteria to establish the classification of the new taxon were the stable differences of some features of its wing color and design patterns, as well as the lack of significant variation of its wing venation and male genitalia, when compared to typical *Oxeoschistus puerta puerta* (Westwood, 1851). However, we also took into account the geographic distribution of the several species and subspecies of *Oxeoschistus* to evaluate spatial patterns, both horizontal (latitudinal) and perpendicular (altitudinal) and consider the more plausible hypothesis to justify the new geographic race of *Oxeoschistus puerta* as a subspecies.

The following acronyms and abbreviations are used in this text: FW: Forewing; FWL: Forewing length; HW: Hindwing; MBLUZ: Museo de Biología de la Universidad del Zulia, Facultad Experimental de Ciencias, Maracaibo, Venezuela; MC: Mauro Costa collection, Cara-

cas, Venezuela; MIZA: Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay.

## RESULTS

### *Oxeoschistus puerta sabinoi* Viloria & Costa, ssp. nov.

(Figs. 1a, b, c, d, 3, 4)

<http://zoobank.org/urn:lsid:zoobank.org:act:4E01D3CF-5820-4F99-AE67-0B775AF9AAEB>

*Oxeoschistus* sp.; Viloria, 1990b: 244–246, 269, 270, 271, figs. 157 (male habitus, dorsal), 158 (male habitus, ventral), 159 (male genitalia) (MBLUZ-0557).

*Oxeoschistus puerta* ssp. nov. Viloria, MS; Viloria, 2000: 268.

*Oxeoschistus puerta* [n. ssp.] Viloria, MS; Lamas *et al.*, 2004: 211.

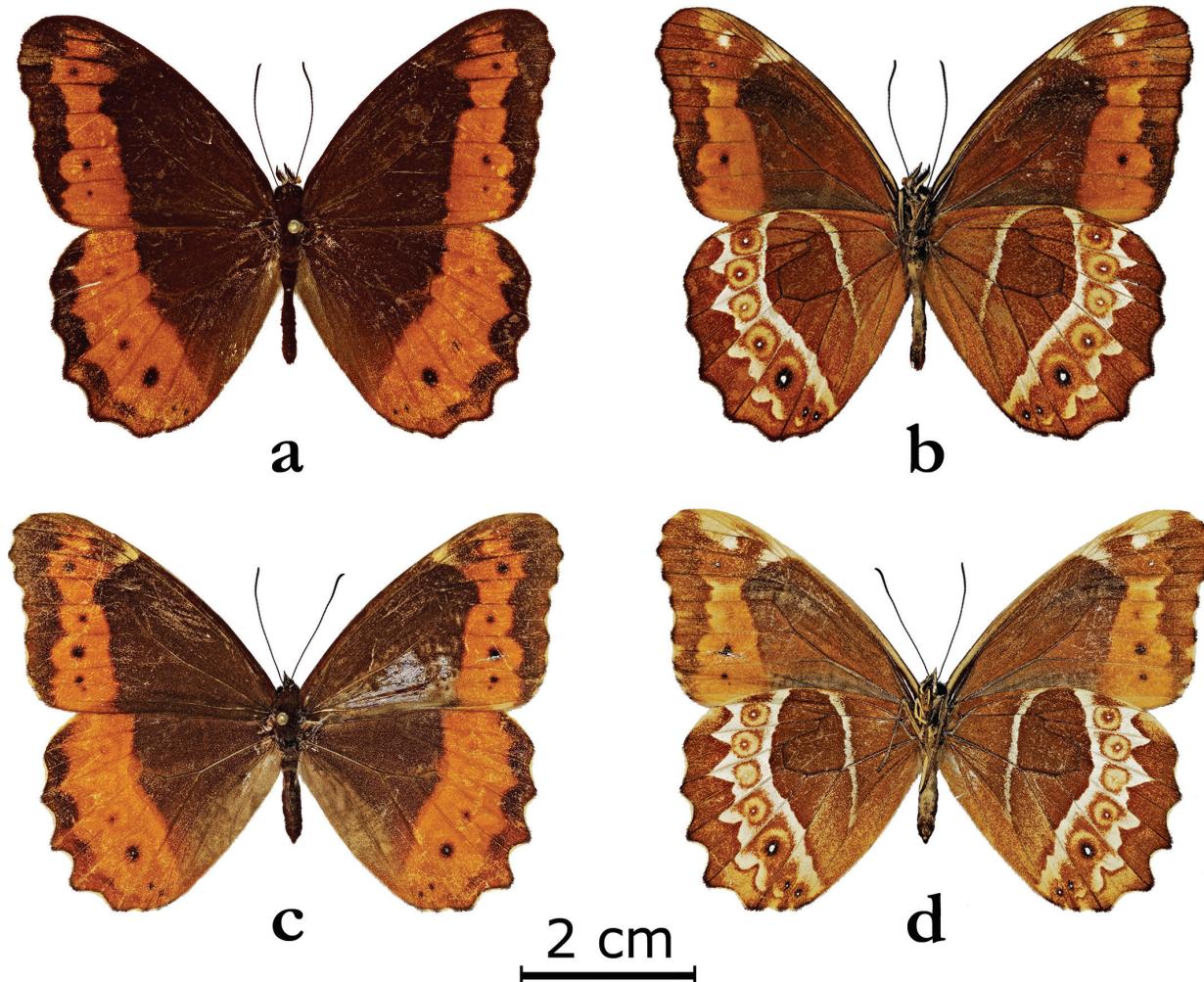


Figure 1. Habitus of *Oxeoschistus puerta sabinoi* ssp. nov. a. Holotype male, dorsal view; b. Same, ventral view; c. Allotype female, dorsal view; d. Same, ventral view.

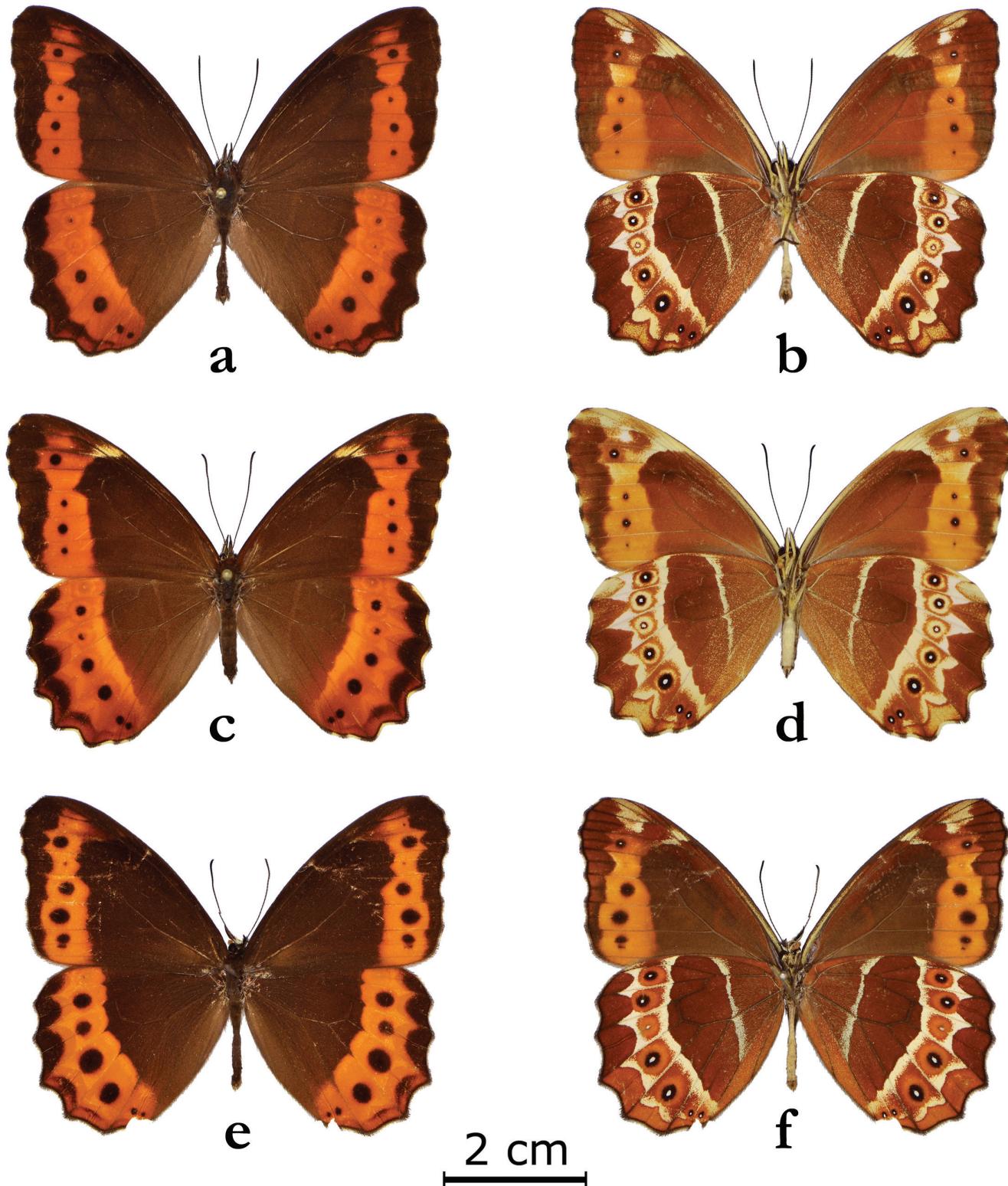


Figure 2. Habitus of two species of *Oxeoschistus* Butler from Venezuela. a. Male, dorsal view *O. puerta puerta* (Westwood); b. Same, ventral view; c. Female, dorsal view *O. puerta puerta*; d. Same, ventral view (individuals from Colonia Tovar, 1,650m, Aragua State, Venezuela); e. Male, dorsal view *O. simplex magnus* Pyrcz & Viloria, comb. nov.; f. Same, ventral view (individual from Matamula, 1,800m, Táchira State, Venezuela).

**Type material:** HOLOTYPE ♂, Ven.[ezuela], [Sierra de Perijá, 10° 19' 35" N, 72° 35' 27" W, 1,900 m, 06-IV-2011, [M. Costa] [MIZA]; ALLOTYPE ♀, same data as holotype; PARATYPES: 1 ♂, same data as holotype (wing prep. ALV062-19)[MC]; 1 ♂, [Venezuela, Sierra de Perijá], SM, Kunana, [10° 03' 08" N, 72° 47'48" W, 1,127 m], 30-XII-[19]50, Expedición La Salle [MIZA]; 1 ♂, Venezuela, Sierra de Perijá, SM, Kunana, [10° 03' 08" N, 72° 47'48" W, 1,127 m], 24-X-1989, Á. L. Viloria leg. (MBLUZ-0557, genit. prep. ALV-s/n) [MBLUZ].

**Diagnosis:** *Oxeoschistus puerta sabinoi* ssp. nov., from the Sierra de Perijá, differs from the typical subspecies *O. puerta puerta* (Westwood, 1851), from the Cordillera de la Costa of Venezuela, in the following characters: Male. FW upperside postdiscal dark brown dot on M3 absent; underside postdiscal brick-orange patch on M1 darker; postdiscal patch on M2 slightly wider on both sides, as well as that of M1; postdiscal patch on R5 basally longer; postdiscal patch on R3 more developed; FW underside ground color with more distinct borders, darker on the basal two thirds of the wing, as well as in submarginal and marginal areas. HW upperside postdiscal dark brown dots less distinct, especially on M3; a pair of minute dots on Cu2. HW underside ocelli in R5 and M1 brown instead of black, that on M3 black but reduced. Female. HW upperside lacking postdiscal brown dots on M1 and M2, that on M3 and a pair on Cu2 notably reduced; dot on Cu1 reduced, with a white pupil. HW underside postdiscal ocelli in R5, M1, M2 and M3 lacking black.

**Description:** Male (Figs. 1a, b, 3, 4). FWL: 34-35 mm (mean 34.5 mm). Body dorsally dark coffee, almost black, ventrally light brown, legs light brown. Antennae dark coffee, reaching two fifths of costa, club gradually formed. Palpi twice as long as head, dorsally and laterally cream-white, ventrally densely covered with long black scales. FW subtriangular, apex and tornus rounded, outer margin moderately scalloped, pronounced at distal end of vein M1. HW suboval, costal margin basally straight to two thirds of its length, outer margin markedly scalloped. FW upperside ground color coffee brown, postdiscal area occupied by a brick-orange band formed by contiguous patches (divided by crossing coffee brown veins); three postdiscal circular dark brown spots on M1, Cu1 and Cu2, respectively, Cu1 twice the diameter of the others. HW upperside ground color coffee brown; a wide brick-orange postdiscal-submarginal band; a suffusion of the same color on marginal area from vein M3 to tornus, finely bordered with dark coffee along outer margin; over the band one vestigial, very diffused dark spot on M1, another one more visible on M3, another one more distinct on Cu1, with tiny white pupil; two small

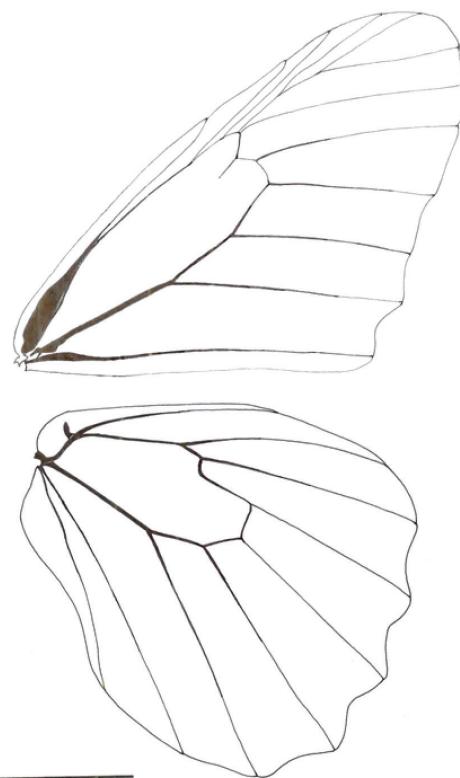


Figure 3. Wing venation of *Oxeoschistus puerta sabinoi* ssp. nov., male paratype (wing prep. ALV062-19, scale bar: 1 cm).

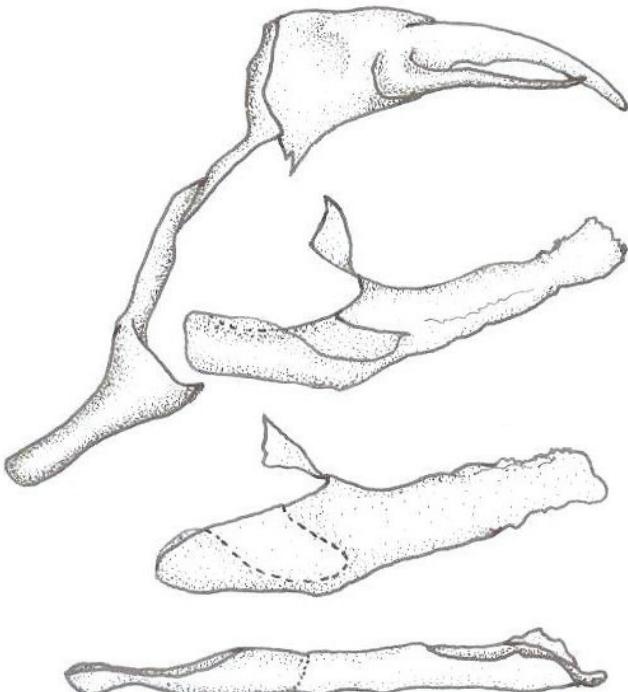


Figure 4. Male genitalia of *Oxeoschistus puerta sabinoi* ssp. nov. (Paratype, MBLUZ-0557, genit. prep. ALV-s/n, scale bar: 1 mm). Re-drawn from Viloria (1990b).

anal dark spots on cell Cu2. Basal two thirds of FW underside ground color hazelnut, chocolate brown towards anal margin, coffee brown towards anterior half of discal area, markedly over recurrent vein inside discal cell; costal line light ochraceous, more visible along two basal thirds; veins dark brown; brick-orange postdiscal band running only from vein M2 to tornus, progressively widening in that direction, twice as broad in tornus as in cell M2; two ocellar postdiscal dark brown dots on M1 (with tiny pupil) and Cu1, respectively; subapical white dot (2 mm diameter) on R5, contiguous to another one smaller in R4, just in branching of veins R4 and R5; distal to these dots an area of lighter pale brown that reaches the costa; a cream-white postdiscal wedge from costa to anterior base of cell M1. HW underside ground color hazelnut dusted with ochraceous brown on basal, anal and distal half of marginal areas; cream-white stripe, running from costa on limit of discal and postdiscal area, across the middle of discal cell, more or less straight to vein A2; on the costa it reaches the anterior extremity of the wide cream-white postdiscal band, which runs from apex to tornus; its inner margin more or less regular, slightly sigmoidal, concave from costal margin to vein M3 and slightly convex from there to tornus; its distal margin dentate, pointing distad on apex (vein Rs), veins M1 and M3; from M3 to Cu1 and Cu2 the shape of that margin is more or less scalloped but not regular; a series of seven round ocelli in the middle of the postdiscal band, four ocelli of similar size and aspect in cells R5, M1, M2 and M3, respectively, with dark hazelnut centers and white pupils (R5 and M3 with some black around pupils), widely surrounded by yellow-orange and finely circled with hazelnut; one larger ocellus with black center and larger pupil on Cu1; two small, twin, black ocelli on Cu2 (in tornus), the last three ocelli surrounded with a diffuse mixture of hazelnut and yellow-orange.

**Genitalia.** Tegumen flattened; uncus conical and slightly curved downwards, as long as tegumen, emerging at same level of the latter; subunci well developed, as long as uncus, but emerging laterally and just behind its base; vinculum strong but thin; saccus tubular, slightly shorter than subuncus; Valvae subrectangular in lateral view, 1.3 times the length of tegumen + uncus, distal extremity almost as deep as base, with some rugosity around its distal extremity, more prominent on ampulla. Aedeagus straight and robust, slightly thicker than saccus, and slightly longer than valvae.

In general the male genitalia of this subspecies does not differ significantly from that of *O. puerta puerta*.

**Female** (Figs. 1c, d). FWL: 36 mm. Similar to male but slightly larger and paler in coloration. FW upperside

with prominent postdiscal-subapical wedge on costal area (as on underside); postdiscal dark dots larger, one in cell M3.

**Etymology:** The name of this new taxon is dedicated to the memory of Sabino Romero Izarra (b. Sierra de Perijá, Venezuela, February 9, 1965), uatpú (chief) of the indigenous community of Chaktapa, in the Yasa river basin, southern Venezuelan slope of the Sierra de Perijá. In the present century, Sabino was so far the most outstanding defender in the struggle of the Yukpa ethnic group for the recovery of their original lands. He was murdered in Los Angeles del Tukuko on March 3, 2013.

**Habitat and behaviour:** The different species and subspecies of *Oxeoschistus* known in Venezuela (see discussion) have similar habits. They are insects associated with montane and upper montane forests, recorded between 1,000 and 2,000 m. However, only the first two known individuals of *O. puerta sabinoi* ssp. nov., come from a bamboo forest at around 1,100 m on the trail that connects the Yukpa populations of Ayajpaina and Kunana in the central sector of the Sierra de Perijá, on its Venezuelan slope. At this altitude the presence of the species is so rare that it could be considered occasional. However, we have noticed that although more frequently found above 1,500 m, they are always quite localized in dense forested sectors, with the presence of bamboo (*Guadua* spp. and *Chusquea* spp.), presumably their host plants. They seldom fly in clearings or open spaces. They do not fly if there is not enough sunlight entering the forest; their flight is erratic and can be remarkably fast when the animals are startled. That is why they are difficult to catch on the wing. They prefer to move between 1 and 3 meters from the ground.

Females and males of *Oxeoschistus* in the Tamá, Perijá, Cordillera de la Costa and Pantepui are attracted by fermented plantain baits, whose sugary fluids are among their favorite foods. In this way, once their presence is detected, it is easier to observe and capture them when feeding on these fruits (figs. 5–7).

Pyrucz *et al.* (2020) commented on behavioral trends, habitat and distribution of the species of *Oxeoschistus* (*s. l.*) in Central America.

## DISCUSSION

Adams (1986) pointed out the presence of distinctive yellow-orange rings (iris) in the ocelli of the hindwing underside of three north Andean taxa of this genus (*sensu stricto*). He also offered morphological criteria and biogeographic reasons to consider each of them a separate species: *O. puerta* (Westwood), *O. protogenia* (Hewitson, 1862) and *O. pervius* Thieme, 1907. We agree with this point of



Figure 5. Adult female *Oxeoschistus puerta puerta* (Westwood), resting on a palm leave. Near Colonia Tovar, 1,650 m, Aragua State, Cordillera de La Costa, northern Venezuela (photo M. Costa).



Figure 6. Adult female *Oxeoschistus puerta puerta* (Westwood) baited with rotten fruit (plantain). Neighbouring forest of the Colonia Tovar, 1,650 m, Aragua State, Cordillera de La Costa, northern Venezuela (photo M. Costa).



**Figure 7.** Three adult individuals of *Oxeoschistus romeo* Pyrcz & Fratello, an endemic to the Pantepui, feeding on rotting plantain. Sierra de Lema, 1,400 m, Bolívar State, southeastern Venezuela (photo M. Costa).

view. Our new taxon bears those yellow-orange rings and is morphologically (wing pattern, male genitalia) and biogeographically closer to typical *O. puerta* from the Cordillera de La Costa, therefore we comparatively consider *sabinoi* ssp. nov., a subspecies of *puerta*. Both *Oxeoschistus protogenia* and *O. simplex* Butler, 1868 fly parapatrically, the first below (800-1,000 m) the second one (1,800-2,350 m), in the Cordillera Oriental of Colombia. *Oxeoschistus simplex* belongs to a group of species that lacks the presence of the above mentioned yellow-orange rings. The taxon *magnus*, described by Pyrcz & Viloria (2007), clearly lacking the yellow-ringed ocelli, being but slightly different from typical *O. simplex*, and distributed in the barely disjunct northernmost extreme of the Cordillera Oriental (El Tamá), should be regarded as a subspecies of the latter taxon. We herein establish this new combination.

Thus, there are three different species of *Oxeoschistus* recorded in Venezuela, one with two subspecies:

*Oxeoschistus puerta puerta* (Westwood, 1851) (Figs. 4a, b, c, d, 5, 6). Type locality: Venezuela [Cordillera de La Costa].

*Oxeoschistus puerta sabinoi* Viloria & Costa, ssp. nov.

(Figs. 1a, b, c, d, 2, 3). Type locality: Venezuela, Sierra de Perijá, 10° 19' 35" N, 72° 35' 27" W, 1,900 m.

*Oxeoschistus simplex magnus* Pyrcz & Viloria, 2007, comb. nov. (Figs. 4e, f). Type locality: Venezuela, Táchira, Delicias, 1,000 m.

*Oxeoschistus romeo* Pyrcz & Fratello, 2005 (Fig. 7). Type locality: Guyana, N. slope of Mt. Roraima, 2<sup>nd</sup> Camp, 5° 16' N, 60° 44' W, 1,300 m.

#### ACKNOWLEDGEMENTS

We thank Tito R. Barros, Nelson Delgado (†), Leonel Lanier, Jesús Camacho, Tomasz W. Pyrcz, Florencio Bernal, Guillermo Morales, Rafael Carreño and Lusbi Portillo for their companionship and assistance during field activities associated with the discovery of the new subspecies herein described (1989 and 2011). Professors Francis Geraud, Magally Quiróz (†), Ramón Acosta (†) and José Moscó (†) (La Universidad del Zulia), helped the first author in many ways during the early days of surveying the satyrine butterflies of the Sierra de Perijá (1984-1993). Jürg De Marmels, Luis D. Otero, José A. Clavijo and Carlos Bordón (†) are warmly thanked for their hospitality and assistance at MIZA. Héctor Suárez (IVIC) took the photographs of the type material. The first drafts of this article were critically read by I. B. Petit, M. Quiróz, F. Geraud and Gilson Rivas. The latter, together with Neva Mora and María Eugenia Andara were responsible for the final editing of text and figures.

#### REFERENCES

- Adams, M. J. 1977. Trapped in a Colombian Sierra. *Geographical Magazine* 49(4): 250-254.
- Adams, M. J. 1984. Northern Andean butterflies - Search and research. *The Alpine Journal* 1984: 90-96.
- Adams, M. J. 1985. Speciation in the pronophiline butterflies (Satyridae) of the northern Andes. *Journal of Research on the Lepidoptera Supplement* 1: 33-49.
- Adams, M. J. 1986. Pronophiline butterflies (Satyridae) of the three Andean Cordilleras of Colombia. *Zoological Journal of the Linnean Society* 87(3): 235-320.
- Adams, M. J. & G. I. Bernard. 1979. Pronophiline butterflies (Satyridae) of the Serranía de Valledupar, Colombia-Venezuela border. *Systematic Entomology* 4(2): 95-118.
- Andrade, M. G. 2008. Descubierta nueva especie de mariposa. *El Tiempo* (Bogotá), 9 marzo 2008, pp. 14.
- Butler, A. G. 1867. Revision of the group of lepidopterous insects hitherto included in the genus *Pronophila* of Westwood. *Annals and Magazine of Natural History* (3)20(118): 266-268.

- D'Abraira, B. 1988. *Butterflies of the Neotropical Region. Part V. Nymphalidae (Conc.) & Satyridae*. Victoria, Black Rock: Hill House, [viii] + pp. 679–877.
- Fratello, S. A. 2004. New species from Mt. Roraima. *News of the Lepidopterists' Society* 46(4): 122–126.
- Gaede, M. 1931. Familia Satyridae. In: Strand, E. (ed.). *Lepidopterorum Catalogus* 43: 1–320; 46: 321–544; 48: 545–759.
- Godman, F. D. C. & O. Salvin. 1880. A list of diurnal Lepidoptera collected in the Sierra Nevada of Santa Marta, Colombia, and the vicinity. *Transactions of the Entomological Society of London* 1880(3): 119–132, pls. 3–4.
- Kirby, W. F. 1871. *A synonymic catalogue of diurnal Lepidoptera*. London: John van Voorst, vii + 690 pp.
- Lamas, G. 2003. *Las Mariposas de Machu Picchu. Guía ilustrada de las mariposas del Santuario Histórico Machu Picchu, Cuzco, Perú*. Lima: PROFONANPE, [vi] + 221 pp., 34 pls.
- Lamas, G., Á. L. Viloria & T. W. Pyrcz. 2004. Nymphalidae. Satyrinae. Tribe Satyrini. Subtribe Pronophilina. pp. 206–215. In: Lamas, G. (ed.): Checklist: Part 4A. Hesperioidea – Papilionoidea. In: Heppner, J. B. (ed.): *Atlas of Neotropical Lepidoptera. Volume 5A*. Gainesville: Association for Tropical Lepidoptera / Scientific Publishers.
- Matz, J. & A. V. Z. Brower. 2016. The south temperate Pronophilina (Lepidoptera: Nymphalidae: Satyrinae): a phylogenetic hypothesis, redescriptions and revisionary notes. *Zootaxa* 4125(1): 1–108.
- Miller, L. D. 1968. The higher classification, phylogeny and zoogeography of the Satyridae (Lepidoptera). *Memoirs of the American Entomological Society* 24: [6] + iii + 174 pp.
- 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*. Greenwich, London: Meridian Publications, 144 pp., 32 pls.
- 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*. Greenwich, London: Meridian Publications, 275 pp., 84 pls.
- Orellana, A. M., J. M. González & Á. L. Viloria. 2019. Adiciones, rectificaciones y actualizaciones a “Mariposas de Venezuela” por Théophile Raymond. VI Satyrinae (Insecta: Lepidoptera: Nymphalidae). *Anartia* 29: 54–67.
- Pineda, A. 1991. En la Sierra de Perijá la vida viaja en alas de mariposas. *Ciencias (Maracaibo)* 7(49): 15.
- Pulido-B., H. W. 2007. High altitudes [sic] butterflies (Lepidoptera: Rhopalocera) of the Serranía de Perijá, Colombia. *II ELEN, Encuentro de Lepidopterología Neotropical*. Ciudad de Panamá, Panamá, [29 April – 3 May 2007], pp. [14–15] [abstract].
- Pulido-B., H. W. & M. G. Andrade-C. 2007. Mariposas de las partes altas de la Serranía de Perijá. pp. 235–248. In: Rangel-Ch., J. O. (ed.): *Colombia, diversidad biótica V. La alta montaña de la Serranía de Perijá*. Bogotá: Universidad Nacional de Colombia, Instituto de Ciencias Naturales.
- Pulido-B., H. W. & M. G. Andrade-C. 2008. A new species of *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae: Satyrinae) from the Serranía del Perijá, Cesar, Colombia. *Caldasia* 30(1): 189–195.
- Pulido-B., H. W. & M. G. Andrade-C. 2010. Las mariposas de la Serranía de Perijá. pp. 509–559. In: Rangel-Ch., J. O. (ed.): *Colombia, diversidad biótica VIII. Media y baja montaña de la Serranía de Perijá*. Bogotá: Universidad Nacional de Colombia, Instituto de Ciencias Naturales.
- Pulido-B., H. W., M. G. Andrade-C. & J. Llorente-Bousquets. 2010. Taxonomía y distribución de *Nathalis* (Lepidoptera: Pieridae) en Colombia. *Revista de Biología Tropical (International Journal of Tropical Biology)* 58(1): 273–285.
- Pulido-B., H. W., M. G. Andrade-C., C. Peña & G. Lamas. 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. 2004. Pronophiline butterflies of the highlands of Chachapoyas in northern Peru: faunal survey, diversity and distribution patterns (Lepidoptera, Nymphalidae, Satyrinae). *Genus* 15(4): 455–622.
- Pyrcz, T. W. 2010. *Wybrane zagadnienia z taksonomii, zoogeografii i ewolucji faun górskich na przykładzie grupy modelowej motyli z plemienia Pronophilini (Nymphalidae)*. Olsztyn: Wydawnictwo Mantis, 245 pp. + [iii].
- Pyrcz, T. W. & S. A. Fratello. 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. & G. Rodríguez. 2007. Mariposas de la tribu Pronophilini en la Cordillera Occidental de los Andes de Colombia (Lepidoptera: Nymphalidae, Satyrinae). *Shilap* 35(140): 455–489.
- Pyrcz, T. W. & Á. L. Viloria. 2007. Erebiine and pronophiline butterflies of the Serranía del Tamá, Venezuela-Colombia border (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera* 15(1/2): 18–52.
- Pyrcz, T. W., A. Zubek, P. Boyer, I. Nakamura, B. Waclawik & K. Florkzyk. 2020. Revisional notes on the cloud forest butterfly genus *Oxeoschistus* Butler in Central America (Lepidoptera: Nymphalidae: Satyrinae). *Neotropical Entomology* 49(3): 392–411.
- Raymond, T. 1982. *Mariposas de Venezuela*. [1<sup>st</sup> ed.]. Caracas: Ediciones Corpoven / Armitano Editor, 277 pp. + [iii].
- Reuter, E. 1896. Über die Palpen der Rhopalocera. Ein Beitrag zur Erkenntnis der verwandtschaftlichen Beziehungen unter den Tagfaltern. *Acta Societatis Scientiarum Fennicae* 22(1): i–xvi + 577 pp. + [i], 6 pls.
- Thieme, O. 1907. Monographische bearbeitung der Gattungen *Lasiophila* Felder, *Daedalma* Hew., *Catargynnis* Röber, *Oxeoschistus* Butler, *Pronophila* Westwood, *Corades* Doubl. Hew. *Berliner Entomologische Zeitschrift* 51(2/3): 99–234, pls. 3–5.
- Viloria, Á. L. 1989. Estudio preliminar de la fauna de lepidópteros de Perijá, Estado Zulia. Parte I. Nymphalidae: Itho-

- miinae. *XI Congreso Venezolano de Entomología*. Maracaibo (Venezuela), July 5-8, 1989, pp. 54 [abstract].
- Viloria, Á. L. 1990a. Consideraciones sobre los niveles de endemismo en mariposas (Lepidoptera: Rhopalocera) de Perijá, frontera colombo-venezolana. *XI Congreso Latinoamericano de Zoología*. Cartagena (Colombia), April 1990, pp. 68 [abstract].
- Viloria, Á. L. 1990b. *Taxonomía y distribución de los Satyridae (Lepidoptera: Rhopalocera) en la Sierra de Perijá, frontera colombo-venezolana*. Maracaibo: Facultad Experimental de Ciencias, Universidad del Zulia, [ii] + xxxviii + 296 pp. + [ii] [thesis].
- Viloria, Á. L. 1991a. Catatumbo un centro de evolución, evidencia de una mayor amplitud en base a la distribución geográfica de algunos lepidópteros aposemáticos del oeste de Venezuela. p. 37. *V Jornadas Científicas de la Facultad Experimental de Ciencias de la Universidad del Zulia*. Maracaibo (Venezuela), June 26-28, 1991 [abstract].
- Viloria, Á. L. 1991b. Los páramos de Perijá. *Natura* (Caracas) 93: 25-29.
- Viloria, Á. L. 1991c. Estudio preliminar de la fauna de lepidópteros de Perijá, Colombia-Venezuela. Parte II. Satyridae. p. 215. *XII Congreso Venezolano de Entomología*. Mérida (Venezuela), July 1-4, 1991 [abstract].
- Viloria, Á. L. 1992. Taxonomía y distribución de los Satyridae (Lepidoptera: Rhopalocera) en la Sierra de Perijá, frontera colombo-venezolana. pp. 199-200. In: Vicerrectorado Académico (ed.). *Producción intelectual de LUZ, Facultad Experimental de Ciencias, años 1983-1991*. Maracaibo: Universidad del Zulia, Biblioteca Central "Gral. Rafael Urdaneta", Impresos Chirinos.
- Viloria, Á. L. 1994. Dos expediciones a los páramos de la Sierra de Perijá, frontera colombo-venezolana, 1989. *El Guácharo, Boletín de Divulgación Espeleológica* (Caracas) 35: 16-21.
- Viloria, Á. L. 1995. Informe general de la expedición a Cerro Pintao (Cerro Viruela), frontera colombo-venezolana. Marzo 1993. *El Guácharo, Boletín de Divulgación Espeleológica* (Caracas) 36: 61-64.
- Viloria, Á. L. 1997. *Fuentes para el estudio de la Sierra de Perijá*. Maracaibo: Universidad del Zulia, 176 pp.
- Viloria, Á. L. 2000. Estado actual del conocimiento taxonómico de las mariposas (Lepidoptera: Rhopalocera) de Venezuela. pp. 261-274. In: Martín-Piera, F., J. J. Morrone & A. Melic (eds.). *Hacia un Proyecto CYTED para el inventario y estimación de la diversidad entomológica en Ibero-américa: PRIBES-2000*. m3m-Monografías Tercer Milenio, vol. 1. Zaragoza: Sociedad Entomológica Aragonesa.
- Viloria, Á. L. 2005. Las mariposas (Lepidoptera: Papilionoidea) y la regionalización biogeográfica de Venezuela. pp. 441-459. In: Llorente Bousquets, J. E. & J. J. Morrone (eds.). *Regionalización biogeográfica en Iberoamérica y tópicos afines. Primeras Jornadas Biogeográficas de la Red Iberoamericana de Biogeografía y Entomología Sistemática (RIBES XII-I-CYTED)*. México, D. F.: Las Prensas de Ciencias, Facultad de Ciencias, UNAM.
- Viloria, Á. L. [2006]. Cuatro noticias zoológicas de interés bioespeleológico. *Boletín de la Sociedad Venezolana de Espeleología* 39: 83-87.
- Viloria, Á. L. 2007. The Pronophilina: synopsis of their biology and systematics (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera* 15(1-2): 1-17.
- Viloria, Á. L. & M. Costa. 2019. Endemic butterflies. pp. 193-222. In: Rull, V., T. Vegas-Vilarubia, O. Huber & C. Señaris (eds.). *Biodiversity of Pantepui: The pristine "Lost World" of the Neotropics*. Cambridge, Massachussets: Elsevier.
- Viloria, Á. L., F. Herrera & C. Galán. 1992. Resultados preliminares del estudio del material biológico colectado en Mesa Turik y cuenca del Río Socuy. *Boletín de la Sociedad Venezolana de Espeleología* 26: 7-9.
- Viloria, Á. L., T. W. Pyrcz & A. Orellana. 2010. A survey of the Neotropical montane butterflies of the subtribe Pronophilina (Lepidoptera, Nymphalidae) in the Venezuelan Cordillera de la Costa. *Zootaxa* 2622: 1-41.
- Viloria, Á. L., A. D. Warren & G. T. Austin. 2008. A spectacular new *Dalla Mabilie*, 1904 from Venezuela-Colombia (Hesperiidae: Heteropterinae). *Bulletin of the Allyn Museum* 156: 1-12.
- Westwood, J. O. 1851. pp. 327-466, pls. 59, 67-77. In: Doubleday, E.: *The genera of diurnal Lepidoptera: comprising their generic characters, a notice of their habits and transformations, and a catalogue of the species of each genus*, vol. 1. London: Longman, Brown, Green & Longmans.
- Weymer, G. 1911. 4. Familie: Satyridae. pp. 193-240, pls. 42-50. In: Seitz, A. (ed.). *Die Gross-Schmetterlinge der Erde*, 5. Stuttgart: A. Kernen.