

New satyrine butterflies from the Venezuelan Andes (Lepidoptera: Nymphalidae)

Ángel L. Viloría¹, José R. Ferrer-Paris², Jesús Camacho³
and Mauro Costa⁴

¹ Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC),
Apartado Postal 20632, Caracas 1020-A, Venezuela. aviloría@ivic.gob.ve

² Centro de Estudios Botánicos y Agroforestales, Instituto Venezolano de
Investigaciones Científicas (IVIC), Av. 8, c. 79-80, Maracaibo, Venezuela.
jferrer@ivic.gob.ve

³ Museo de Artrópodos, Facultad de Agronomía, Universidad del Zulia
(MALUZ), Apartado 526, Maracaibo 4011, Zulia, Venezuela.
jcamacho@fa.luz.edu.ve

⁴ Res. Las Cumbres, Av. Las Acacias, La Florida, Caracas 1010A, D. C., Venezuela.
mauro13x50@gmail.com

Abstract

Members of the speciose subtribe Pronophilina (Nymphalidae: Satyrinae) are Neotropical butterflies predominantly found in cloud forests. A few species live exclusively in open habitats above the tree line: paramo and puna biomes. This habit requires special adaptation to particular physical and climatic conditions of the orcal zone in the tropics. At least ten species of the endemic genus *Redonda* Adams and Bernard inhabit the paramos of the Venezuelan Andes. We herein describe seven of them: *R. castellana* Viloría and Camacho, **n. sp.**, *R. centenaria* Viloría and Camacho, **n. sp.**, *R. chiquinquirana* Ferrer-Paris, **n. sp.**, *R. frailejona* Ferrer-Paris and Costa, **n. sp.**, *R. lathraia* Viloría and Camacho, **n.sp.**, *R. leukasmena* Viloría and Camacho, **n. sp.**, and *R. lossadana* Ferrer-Paris,

n. sp., and rank *Redonda empetrus bolivari* Adams and Bernard to full specific status.

Keywords: Andes, biogeography, *Diaphanos*, paramo, Quaternary, *Redonda*, *Steromapedaliodes*.

Nuevas mariposas satíridas de los Andes Venezolanos (Lepidoptera: Nymphalidae)

Resumen

Los miembros de la riquísima subtribu Pronophilina (Nymphalidae: Satyrinae) son mariposas neotropicales que se encuentran predominantemente en bosques nublados. Pocas especies viven exclusivamente en ambientes abiertos, por encima de la ceja de montaña: biomas de páramo y puna. Este hábito demanda adaptación especial a condiciones físicas y climáticas particulares de la zona orear tropical. Al menos diez especies del género endémico *Redonda* Adams y Bernard habitan los páramos de los Andes de Venezuela. Describimos aquí siete de ellas: *R. castellana* Viloria y Camacho, **n. sp.**, *R. centenaria* Viloria y Camacho, **n. sp.**, *R. chiquinquirana* Ferrer-Paris, **n. sp.**, *R. frailejona* Ferrer-Paris y Costa, **n. sp.**, *R. lathraia* Viloria y Camacho, **n.sp.**, *R. leukasmena* Viloria y Camacho, **n. sp.**, *R. lossadana* Ferrer-Paris, **n. sp.**, y elevamos *Redonda empetrus bolivari* Adams and Bernard a estatus específico.

Palabras clave: Andes, biogeografía, Cuaternario, *Diaphanos*, páramo, *Redonda*, *Steromapedaliodes*.

INTRODUCTION

In his monograph on the genus *Pedaliodes* Butler, Thieme (1905) described the Venezuelan species *Pedaliodes empetrus* (pp. 95, 98-99, tbl. 1, fig. 7), based on a single specimen allegedly collected in the "Schneebergen von Merida" [snowy mountains of Merida]. He however seemed to have doubts in placing it amongst other north Andean representatives of the group. Pointing out its bigger size, slightly different habitus, lighter colour, hindwings elongated as compared to typical *Pedaliodes*, unique spatulate antennae and long labial palpi, Thieme appropriately compared the underside

wing pattern of his '*P.* *empetrus*' with that of '*P.* *albonotata*' Godman, another endemic species of the Venezuelan Andes, and possibly a closely related taxon. Forster (1964) successfully split *Pedaliodes* into several new genera, placing *P. albonotata* under *Steromapedaliodes*, but neglecting *P. empetrus*, apparently because he had no access to the type material (one single male, originally in Thieme's collection, which has not been located – see below). Huber's study of 1973 revealed that the biotope occupied by *empetrus* is the open, windswept paramo above 3200 m (oreal biome), but failed in arbitrarily assigning the species to the genus *Punapedaliodes* Forster. Any way, Huber, not being a butterfly taxonomist, perhaps based its combination exclusively on the external appearance of the specimens he caught, which is reminiscent of certain high elevation genera from the Equatorial and southern Andes (*Altopedaliodes* Forster, *Punapedaliodes*, *Argyrophorus* Blanchard). Later, in 1975 and 1977, Adams and Bernard (1981) researched the butterflies of the central Cordillera de Mérida, and obtained a new, good series, of this "unusual" butterfly species. They studied the morphological structure of the male genitalia, wing venation and pattern, and some ecological features of '*Pedaliodes*' *empetrus*, finding enough synapomorphies to justify the diagnosis of the genus *Redonda*, to include Thieme's taxon and another subspecific one they described from the southwestern portion of the central Mérida range. We herein consider the latter as a separate species, *Redonda bolivari* Adams and Bernard, **stat. nov.**, based on morphological features, but also on biogeographical inferences.

In the 1990s and the beginning of the following decade, during a series of butterfly surveys conducted by the authors and collaborators in the oréal biomes of the Venezuelan Andes ("páramos", in Spanish), several undescribed forms of *Redonda* were discovered inhabiting separate allopatric paramo units, and contiguous parapatric altitudinal zones. One species from the western Cordillera de Mérida, *Redonda bordoni* Vilorio and Pycrz, was already described in Vilorio *et al.* (2003), who at that time suggested its female might be the first known case of brachyptery in butterflies. More ecological and distribution data of each member, so far detected, of the genus *Redonda* have also been gathered along the last 25 years. Extensive collecting by several people allowed for improving the understanding of their geographical distributions (see Pycrz 2010a, 2010b).

Distribution studies and biogeographic analyses of this genus will be published separately.

Seven new species of *Redonda* are described in this work, and brief information on their geographic distribution, behaviour and affinities is presented and discussed for them and for the three taxa previously known.

MATERIALS AND METHODS

Butterflies were collected by conventional methods (hand nets) in several sectors of the Andes of Venezuela, between 1991 and 1995, 1999 and 2000, and 2001-2015. Observations on the ecology of the butterflies and other field notes were taken *in situ*, during the course of sampling activities.

The following is a list of localities (from Northeast to Southwest, with dates and names of collectors) from where type specimens for this study were obtained:

- *Páramo de Los Nepes*, 2450-2850 m, Serranía del Cendé, Trujillo-Lara States borderline [Dinira National Park]: 12.viii.1991, Ángel L. Viloria, Jesús Camacho, Rosanna Calchi; ii.2000, Á. L. Viloria, José Rafael Ferrer-Paris.
- *Páramo de Las Rosas*, 2800-3100 m, Serranía del Cendé, Trujillo-Lara States borderline [Dinira National Park]: 20.viii.1991, Jesús Camacho; 12/16.i.1994, Á. L. Viloria, J. Camacho, R. Calchi; iii-1994, Á. L. Viloria, J. Camacho, Mauricio García, Carlos Fernández; 8-viii-1995, M. García.
- *Páramo del Cendé*, 3100 m, Serranía del Cendé, Trujillo-Lara States borderline [Dinira National Park]: iii.1994, Á. L. Viloria, J. Camacho, M. García, C. Fernández; 8.viii.1995, M. García.
- *Páramo de Jabón*, 3000 m, Serranía del Cendé, Trujillo-Lara States borderline [Dinira National Park]: 25.xii.1989, CEUM [Centro Excursionista de la Facultad de Agronomía, Universidad Central de Venezuela, Maracay].
- *Páramo de La Cristalina*, 2800 m, north of Niquitao Massif, Trujillo State: 14.v. 1986; 14.vi. 1986, John Edwin Lattke.

- *Páramo de Las Moras*, 3000 m, north of Niquitao Massif, Trujillo State: 19/20.ii.2007, Mauro Costa.
- *Páramo de Ortiz*, 2850-3100 m, upper Río Castán, north of the Niquitao Massif, Trujillo State: 12.ix.1991, Á. L. Viloria, Rosanna Calchi, Edwin Moscó; 7.i.1992, Á. L. Viloria, J. Camacho; 16.viii.2003, Á. L. Viloria, Mariana Alarcón, Wilmer Rojas, Giovanni Fagua, Mónica Higuera.
- *Páramo de Cabimbú*, 2850-2950 m, Serranía de Niquitao (Niquitao Massif), Trujillo State: 11-ix-1991; Á. L. Viloria, R. Calchi.
- *Teta de Niquitao* (base), 3325 m, Serranía de Niquitao (Niquitao Massif), Trujillo State: 23.ii.2000, Á. L. Viloria, J. Camacho, J. R. Ferrer-Paris, Freddy García.
- *Páramo de Tuñame*, 3100-3200 m, between Tuñame and Las Mesitas, south of the Niquitao Massif, Trujillo State (borderline with Mérida State): 10.ix.1991, Á. L. Viloria, R. Calchi; 15.viii.2003, Á. L. Viloria, Tomasz W. Pyrcz, Mariana Alarcón, Wilmer Rojas, Giovanni Fagua, Mónica Higuera; 16.ii.2010, M. Costa.
- *Páramo de Santo Domingo*, 3000-3300 m (including Hotel Los Frailes and Laguna Victoria), Serranía de Santo Domingo, on the road between Santo Domingo and Apartaderos, Mérida State [P. N. Sierra Nevada, in part]: 5.ix.1971, Herbert Huber; 26.ix.1997, Andrew F. N. Neild; 12.iv.2004; 31.iii.2012, M. Costa; 25.iii.2015, Cecilia Lozano, Leandro Morán.
- *Páramo de Mucubají*, 3400-3600, upper Serranía de Santo Domingo (including Laguna de Mucubají and Laguna Negra), Mérida State [P. N. Sierra Nevada]: 28.iii.1992; 20.iv.1992, T.W. Pyrcz; 25.i.2000, 7 and 16.ii.2000, 13 and 20-21.iii.2000, J. R. Ferrer-Paris; 1.i.2002, J. R. Ferrer-Paris, Bertha Condori; 14.ix.2004, J. R. Ferrer-Paris, M. Alarcón; 25.iii.2015, J. R. Ferrer-Paris, Leinny González.
- *Páramo de La Culata*, 3300-3400 m, upper Río Mucujún (including Valle del Muerto), Serranía de La Culata, N of Mérida city, Mérida State [P. N. La Culata]: 30.i.2000, J. R. Ferrer-Paris, Á. L. Viloria; 15.ii.2000, J. R. Ferrer-Paris; ii.2008, Pierre Boyer.
- *Páramo de Los Conejos*, 3400-4300 m, upper Río Albarregas (including Pico Campanario, 4300 m), Serranía de La Culata,

- NW of Mérida City, Mérida State [P. N. La Culata]: 10.ix.1938, Tracey; 29.viii.1971, H. Huber; 20.vi.1975; 15.viii.1977, Michael J. Adams, George I. Bernard; 31.viii.2001, J. Camacho.
- *Laguna Verde-Laguna del Suero*, 4000 m, above La Mucuy, SE of Mérida City, Sierra Nevada de Mérida, Mérida State [P. N. Sierra Nevada]: 12.ii.1985, CEUM.
 - *Loma Redonda*, 3900-4000 m, S of Mérida City, Sierra Nevada de Mérida, Mérida State [P. N. Sierra Nevada]: 21.iv.1975, M. J. Adams, G. I. Bernard; 8.ii.2007, T. W. Pyrcz.
 - *Páramo La Negra*, 3200 m, southwestern Cordillera de Mérida, Mérida State [P. N. Juan Peñaloza]: 30.ix.1951, P. Fenjues; 14.i.1982, Carlos Bordón.
 - *Páramo El Batallón*, 3000-3800 m, southwestern Cordillera de Mérida, Mérida-Táchira States borderline (including Sumusica, Laguna El Cenegón, Laguna Grande, Pico El Pulpito) [P. N. Juan Peñaloza]: 26/28-ii-1994, Á. L. Viloria, J. Camacho, M. García; 16-xii-1994, M. García; 12/14-i-1995, J. Camacho, M. García; 2/4.iii.1996, J. Camacho, M. García, Janusz Wojtusiak, T. W. Pyrcz; 12-13.ii.2000, Á. L. Viloria, J. Camacho, M. García, J. R. Ferrer-Paris; 2.iv.2000, J. R. Ferrer-Paris.

We set, labelled and examined the butterflies, dissected their wings and genitalia, and made ink drawings by means of standard methods, using different kinds of WILD and Leica stereomicroscopes and adapted cameras lucidas. Photographs were obtained with a Canon Camera EOS Rebel 3Ti, with a 100 mm macro lens, using ring flash lights and several other kind of artificial illumination like fixwed fluorescent and led ring and conventional reflector lamps, in the laboratories of the Departament of Biology, Faculty of Sciences and the Faculty of Agronomy of the University of Zulia in Maracaibo, and the Centre of Ecology of the Venezuelan Institute for Scientific Research, Altos de Pipe. Types and other specimens examined are deposited in the following private and public (institutional) collections (abbreviations cited in text):

AFN: Collection of Andrew Neild, London, England; **BMNH**: The Natural History Museum, London, England; **IVIC**: Instituto Venezolano de Investigaciones Científicas –Centro de Estudios Botánicos y Agroforestales, Maracaibo, Venezuela; **JFLC**: Collection of Jean-François LeCrom, Bogotá, Colombia; **MALUZ**:

Museo de Artrópodos, Facultad de Agronomía, La Universidad del Zulia, Maracaibo, Venezuela; **MC**: Collection of Mauro Costa, Caracas, Venezuela; **MIZA**: Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela; **MPUJ**: Museo Javeriano de Historia Natural Lorenzo Uribe, S.J., Pontificia Universidad Javeriana, Bogotá, Colombia; **MUSM**: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú; **MZUJ**: Muzeum Zoologiczne Instytutu Zoologii Uniwersytetu Jagiellńskiego, Kraków, Poland; **ZMHU**: Zoologisches Museum Humboldt Universität, Berlin, Germany; **ZSBS**: Zoologische Staatssammlung München, Germany.

Comparative morphological examinations of preserved butterflies and their structures, and their descriptions, were performed at several stages in the Museo de Biología de La Universidad del Zulia, Maracaibo, Venezuela (MBLUZ: 1991-1995, 1999-2000, 2014), MALUZ (1991-1995, 2012, 2014), BMNH (1995-1998, 2001, 2003, 2011), MZUJ (1997), ZSBS (1997), the Universität Bayreuth, Germany (1999-2000), and most recently in the Centro de Estudios Botánicos y Agroforestales (Maracaibo, 2011-2015) and the Centro de Ecología (Altos de Pipe, 2000-2015), IVIC.

We present our results as taxonomic hypotheses based on comparative morphology and biogeography, coupled with the interpretation of phylogenetic essays already published for some members of the genus *Redonda*. Our recognition of the specific status of each butterfly taxa described or treated in this study follows the intuition of such hierarchy through cumulative evidence: observation and homological comparison of colour pattern of wings and palpi, as well as morphological features of different structures of the male genitalic armature. Our previous experience in the systematics of satyrine butterflies indicates that closely related species among the *Pronophilina* may show subtle but constant morphological differences with respect to the characters evaluated, although there is some degree of individual variation, that sometimes is validated by bionomic information derived from field observations. We have also followed intuitive interpretation of the discrete distribution of the taxa (both in altitude and latitude) in the Venezuelan Andes, in agreement with the evolutionary model of speciation of Michael J. Adams (1977, 1985), which one of the authors of this contribution tested through the methods of cladistics and found to be accept-

able, coherent, suitable and reliable as a working hypothesis (Viloria 1998). Adams' model allows for rational explanations of the diversity and distribution in allopatry, parapatry and sympatry of the different species of *Redonda* in the Venezuelan Andes.

The ten taxa herein studied are all considered fully developed species, unable to hybridize among them in natural conditions. Some very similar, apparently closely related species, inhabit discrete allopatric and parapatric areas of paramo that are geographically very close to each other (for instance, in the páramos of Trujillo state), and some others that are otherwise morphologically different, can live in contiguous elevation zones (for instance, in the páramo El Batallón, Mérida-Táchira states), and are therefore parapatric or even partly sympatric in some very narrow ecological bands of contact. At least one case of wind drift recorded in this study indicates that there may be certain degree of accidental sympatry among species that are in a strict sense, endemic to separate, disjunct geographic ranges. All of this sum up to evidence that peculiarities of geographic distribution within this genus support on one side the assumption that our taxa are species on their own right and not geographic races (subspecies), and on the other, that their evolutionary development may have been mediated not only by historical geographic isolation of their high altitude habitats but also by ecological factors intrinsic to each species, most of which remain unknown.

RESULTS

Genus *Redonda* Adams and Bernard, 1981

[*Pedaliodes* Butler; Thieme, 1905: 95, 98-99 (in part)]

[*Punapedaliodes* Forster; Huber, 1973: 195 (misidentification)]

Redonda Adams and Bernard, 1981: 367-368.

Redonda Adams and Bernard; Adams, 1985: 38; d'Abrera 1988: 871; Viloria, 1990: 218, 219; 1993: 69; 1994: 180, 184, 185; 1997: 15; 1998: 7, 14, 24, 37, 77, 78, 91, 95, 97, 99, 108, 124, 126, 182, 318-320, 409, 414, 415, 427, 445, 464, 467 (tbl. 1), 476 (fig. 1, distribution); 2000: 266, 269, 271; 2002: 178 (tbl. V), 190; 2005: 450; 2007: 1, 2, 9; Viloria et al., 1993: 226-227; Pyrcz, 1999: 354; 2004a: 289, 295, 296; 2004b: 570, 616; 2007a: 40, 41; 2007b: 17-19; 2008: 126; 2010a: 12, 13 (fig. 17, antennal clubs), 38, 45 (fig. 35, females venation), 55, 69, 87 (fig. 82, cladogram), 88, 91, 109, 113, 116, 126, 171, 180 (fig. 131, wing area), 181 (figs. 132, dimorphism; 134, habitats), 183, 184 (fig. 136, distribution map), 185 (fig. 137, potential distribu-

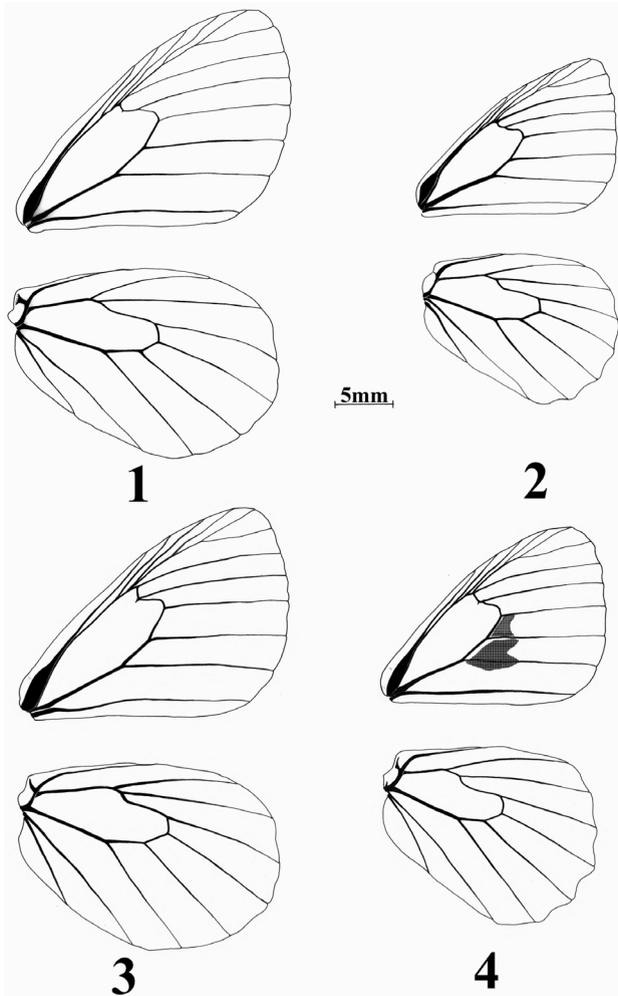
tion), 186, 207 (putative hostplants), 214; 2010b: 265, 266 (fig. 1), 267, 268 (fig. 2, distribution), 270 (fig. 4, habitats), 271 (fig. 5), 272, 273; Ferrer-Paris, 2000: i-xiii, 1, 6, 8, 9, 10, 12, 13, 15, 17, 19, 20, 27 (fig. 3.1), 28, 30, 32, 36, 38, 39 (fig. 3.6), 40 (tbl. 3.5), 47, 48 (fig. 3.11), 49, 50 (tbl. 3.9), 51 (fig. 3.13), 52, 63, 66, 67, 68, 69, 70, 78 (fig. A.5), 81, 89 (tbl. C.5), 94-96 (tbl. C.9); Viloría and Pyrcz, 2001: 1, 2, 5, 6, 12, 15, 17; Ferrer-Paris and Viloría, 2002: 138-139; [2004]: 626, 627, 628 (fig. 1, cladogram), 629, 630 (fig. 3, wing area), 631; Viloría *et al.*, 2003: 21, 22 (figs. 1, 2), 23 (fig. 3), e-appendices: [6]; 2007: [23], [24]; Lamas *et al.*, 2004: 215; Orellana, 2004: 5-54; Bálint and Wojtusiak, 2006: 283; Shou *et al.*, 2006: 105; Silva Dias, 2006: 21; Pyrcz *et al.*, 2009: 508, 525; 2014: suppl. material: [2 (tbl. S1)]; Pyrcz and Viloría, 2007: 46, 47 (tbl. 3); Posso Duque *et al.*, 2010: [185]

[“*Pedaliodes*” Butler; Descimon, 1986: 510]

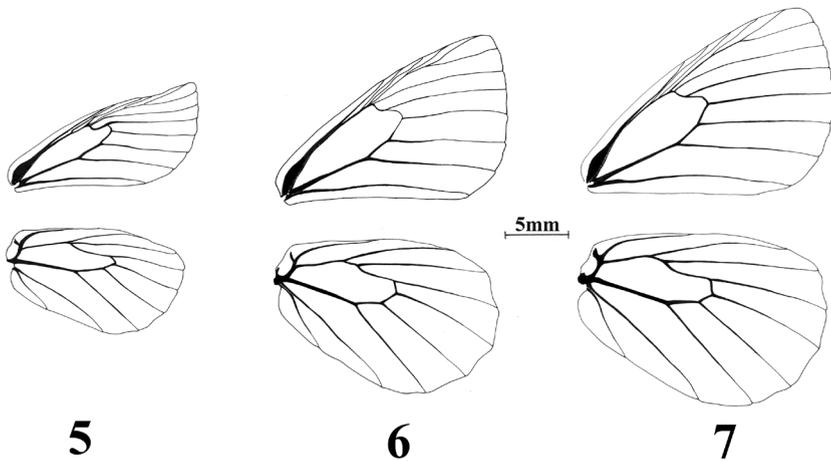
Redononda [sic]; Pyrcz and Fratello, 2005: 211.

Type species: *Pedaliodes empetrus* Thieme, 1905, by original designation.

Revised diagnosis. Butterflies of medium size, some females rather smaller than males; colour pattern could be sexually dimorphic as well; females strongly sedentary (except for that of *R. leukasmena*, **n. sp.**, which is almost as active in flying like males). Antenna to two-fifths costa. Antennal club heavily spatulated and concave. Eyes densely hairy. Palpi twice as long as head; first segment one-quarter the length of the second; third segment three-quarters the length of the first. Forewing subtriangular; hindwing suboval, longer than in *Pedaliodes* Butler, outer margins rounded and regular, sometimes slightly scalloped in hindwing (wings generally much narrower in dimorphic females). Androconial patches absent. Ocellar elements present in postdiscal area of both wings (either dorsally or ventrally, or both), but simplified as white spots, which are sometimes elongated and highly distorted (fusiform, v-shaped, or in the form of a fleur-de-lys); ventral wing pattern highly cryptical for grass or sandy habitats, sometimes stereomorphic in the sense of Schwanwitsch (1938); upperside wing pattern with conspicuous marks (grey or white) developed in discal area at different degrees. Venation (Fig. 1): Forewing Sc, R1 and R2 all independent, R3, R4, R5 originated from common root at distal third of wing; R3 half nearer to root of R4 than to discal cell, no r-m1, but M1 emerging from R3-5 (totally independent in *Steromapedaliodes* Forster (Fig. 2), *Dangond* Adams and Bernard (Fig. 3) and *Paramo* Adams and Bernard (Fig. 4)) m1-m2 curves inwards, vestigial veinlet (only in males) entering discal cell in the middle of m1-m2 (closer to root



Figs. 1-4. Male wing venation of the type species of four oreal pronophiline butterfly genera endemic to the Northernmost Andes and the Sierra Nevada de Santa Marta; **1.** *Redonda empetrus* (Thieme, 1905), Venezuela, Cordillera de Mérida, Río Albarregas, N of Merida, 3400 m (wing prep. ALV27-1997, in BMNH); **2.** *Steromapedaliodes albonotata* (Godman, 1905), Venezuela, Cordillera de Mérida, Río Albarregas, N of Merida, 3400 m (wing prep. ALV07-1997, in BMNH); **3.** *Dangond dangondi* Adams and Bernard, 1979, Venezuela, Sierra de Perijá, S slope of Cerro Avi6n, 3450 m (wing prep. ALV11-1997, in BMNH); **4.** *Paramo oculata* (Krüger, 1924), Colombia, Sierra Nevada de Santa Marta, Cambirumeina, 3950 m –dark areas represent androconial patches (wing prep. ALV12-1997, in BMNH).



Figs. 5-7. Female wing venation, and comparative shape and size proportions of selected species of *Redonda* Adams and Bernard; 5. *R. bordoni* Vilorio and Pyrcz, 2003 (paratype, wing prep. ALVSN0-1997, in MALUZ); 6. *R. centenaria* Vilorio and Camacho, **n. sp.** (paratype, wing prep. ALVSN1-1997, in MALUZ); 7. *R. leukasmena* Vilorio and Camacho, **n. sp.** (paratype, wing prep. ALVSN2-1997, in MALUZ).

of M2 in *Paramo*, right at base of M2 in *Dangond*, absent in *Steromapedaliodes*); hindwing humeral vein moderately developed, broadened at extreme (unlike *Paramo* and *Dangond*, where it is not broadened, and *Steromapedaliodes*, where it is vestigial); root of Cu1 closer to that of M3 than that of Cu2; root of M3 halfway between those of Cu1 and M2; A2 and A3 independent, m1-m2 long (twice as long as cu1-cu2; shorter in *Steromapedaliodes*, *Paramo* and *Dangond*) and moderately curved inwards; discal cell about half the length of the hindwing. Male genitalia: tegumen bubble-domed, and well differentiated from uncus; uncus strong and slightly hooked, as long as tegumen; gnathi absent or vestigial; saccus short and globular; aedeagus generally straight, or slightly contorted, relatively short (as long as tegumen + uncus, or slightly longer in *R. bolivari* Adams and Bernard, **n. stat.**), never totally symmetrical; valvae broad, subtriangular, simple, moderately hairy and devoid of ornamentation.

Comments. *Redonda* comprises a group of, so far ten, high elevation-specialized satyrine butterflies species. A genus endemic to the easternmost branch of the northern Andes, in Venezuela. Most of its species are distributed discretely in separate, archipelago-like,

high elevation paramo units (above 2700 m) of the Cordillera de Mérida, northwest of the Táchira Depression. It has been mentioned as a putative example of rapid radiation in small isolated areas under extreme environmental conditions (see Viloria 1998, Ferrer-Paris 2000, Viloria *et al.* 2003, Ferrer-Paris and Viloria 2004, Pyrcz 2010a, 2010b).

SPECIES ACCOUNT

Redonda bolivari Adams and Bernard, 1981, **n. stat.**

Figs. 8, 9, 10, 11, 12, 13 (males), 46, 47 (male genitalia)

Redonda empetrus bolivari Adams and Bernard, 1981: 368-369, fig. 28; d'Abbrera, 1988: 871, fig. (identification erroneously given in caption as *Diaphanos huberi* Adams and Bernard); Viloria, 1998: 319 (in part misidentification of *R. empetrus*); 2000: 269, 270 (last, misidentification of *R. empetrus*); 2002: 190; 2005: 459; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution [in part misidentification of *R. empetrus*]), 36, 37 (fig. 3.5), 91-92 (tbl. C.7); Viloria *et al.*, 2003: 22 (fig. 1c, male), 23 (fig. 3); Ferrer-Paris and Viloria, [2004]: 629 (tbl. 1), 630 (fig. 3); Lamas *et al.*, 2004: 215; Pyrcz, 2007b: 18, 19; 2010a: 87 (fig. 82, cladogram), 180 (fig. 131, wing area), 181 (fig. 134B, habitat), 184 (fig. 136, distribution), 244; 2010b: 266 (fig. 1J male), 267, 268 (fig. 2, distribution), 270 (fig 4C, habitat), 272.

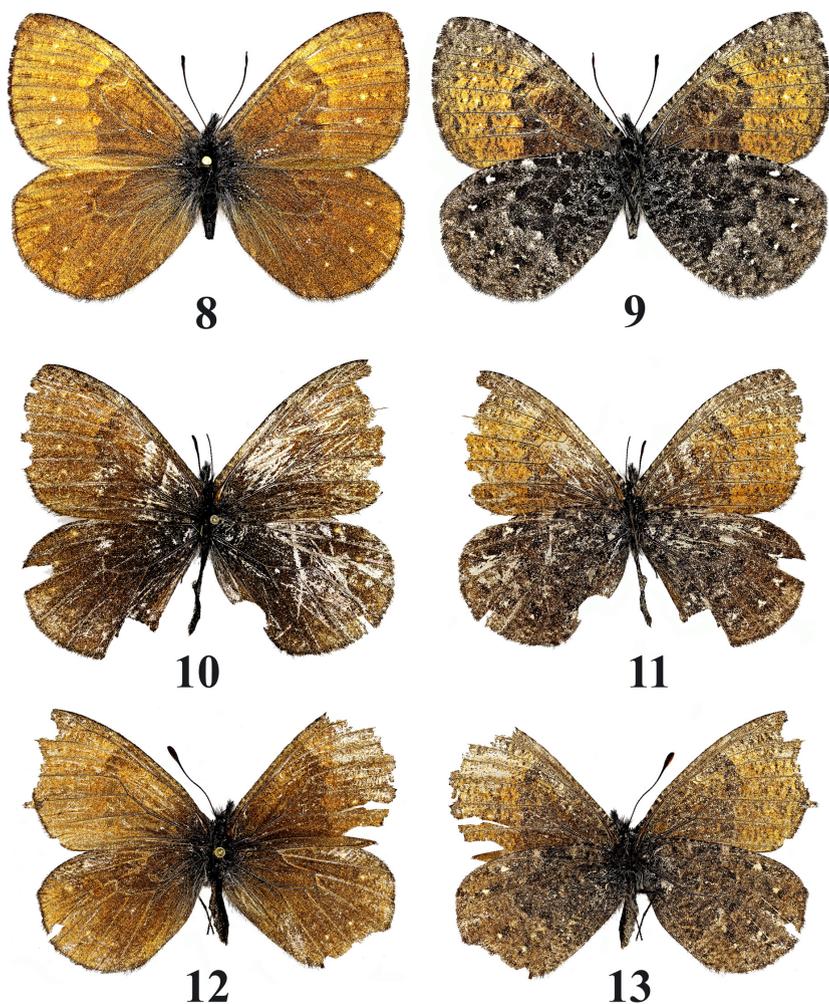
[*Redonda bordoni* Viloria and Pyrcz, 2003: 21-24, e-appendix A: pp. [1-2] (misidentification, in part)].

Type locality: 4000 m, [paramo of] Loma Redonda, Cordillera de Mérida [northern slopes of the Sierra Nevada de Mérida, and south of the city of Mérida, Mérida State], Venezuela. Established by Adams and Bernard (1981).

Comments. Our recognition of *Redonda bolivari* as a species in its own right obeys to several sources of evidence. It is the only species of the genus known to have an aedeagus longer (average 1.3 times) than the combined length of its tegumen + uncus. None of the other species of *Redonda* reach 1.0 in the aedeagus/tegumen +uncus ratio. Additionally, the aedeagus of *R. bolivari* is more robust and straight than in any other species so far recognized within the genus (notably shorter and thinner, and more asymmetrical in *R. empetrus*). Its saccus is also more robust than that of *R. empetrus*, and definitely the longer within the genus; the valvae are more oblong than in *R. empetrus*. All individuals of this species which we have examined are steadily large in wingspan (unlike *R. empetrus*).

The wings of *Redonda bolivari* are basally broader and with a more rounded profile than those of *R. empetrus*. Males of *R. bolivari* (like in *R. bordoni* Viloría and Pycz and *R. leukasmena* Viloría and Camacho, **n. sp.**, which are quite distinctive in wing pattern) have no scalloping on the hindwing margins. These three species have coincidentally the largest and fastest males. The dark colour of *R. bolivari*, as well as its notably reduced ocellar elements are stable characters (along a broad geographic distribution). Its upperside tends to lack one of the diagnostic characters established by Thieme (1905) for *R. empetrus*: a well defined dark discal stripe on the forewing. Morphological variation among males cannot be well ascertained due to the few specimens known, but some individuals have a more marked distinction between the basal (darker) and the distal half (lighter) of the forewing on both sides. Females have not yet been discovered, as they are inconspicuous and probably, much smaller than males, flightless, and brachypterous, as in some other species of the genus.

The natural area of distribution of *Redonda bolivari* is the Sierra Nevada de Mérida (south of the city of Mérida), a mountain range that contains the highest elevations of Venezuela (reaching nearly 5000 m elevation). All Sierra Nevada records come from the uppermost level of the paramo between 3900 and 4000 m, around the highest prominences, the peaks Humboldt and Bonpland (Laguna Verde-Laguna Suero) and the peaks Bolívar and Espejo (Loma Redonda). However, the paramo biome of this area is extensive and continuous from an unknown ecological limit near the Mucubajá area (Sierra de Santo Domingo, northeast of Mérida) to the Los Nevados area, right to the south of Mérida. It might well reach the paramos of Acequias and San Pedro, as well as those ones in the region of the Pueblos del Sur. This supposition is based on the eventual finding of two aged, badly worn-out and isolated male individuals of *Redonda bolivari* (Figs. 10-13, 47) in the páramo del Batallón (3200-3400 m) in February 1994 (together with 24 males and 2 females of *R. bordoni*, and 2 males of *R. lathraia* Viloría and Camacho, **n. sp.**). This region is orographically and ecologically separated from the paramos of the Sierra Nevada de Mérida by *ca.* 60 km of distance across territories whose maximum elevations are too low for developing paramo biome. El Batallón is the natural habitat of two endemic, possibly allopatric taxa, *Redonda bordoni* and *R. lathraia*, **n. sp.**, and the two butterflies above referred, cer-



Figs. 8-13. Males of *Redonda bolivari* Adams and Bernard, 1981, **n. stat.**;
8. Loma Redonda, Sierra Nevada de Mérida (upperside); **9.** *Ibid.* (underside); **10.** Worn-out specimen (1) from Páramo del Batallón (upperside); **11.** *Ibid.* (underside); **12.** Worn-out specimen (2) from Páramo del Batallón, **13.** *Ibid.* (underside).

tainly endemic to the Sierra Nevada de Mérida, may have reached this area by action of the strong, trade winds of the dry season, that notably affect the west of Venezuela between December and March. This fact raises interesting questions about the possibility of even-



14



15

Figs. 14-15. Adults of *Redonda bordoni* Vilorio and Pyrcz, 2003; **14**. Male holotype (Páramo del Batallón), left upperside, right underside; **15**. Female paratype (same locality), left upperside, right underside.

tual hybridization or successful gene exchange between the taxa involved in accidental meetings of local populations with windswept, flying, foreign males relocated by force in areas where only females of other species inhabit. However, we believe that gene flow, if any, must be extremely small. We are inclined to think that mechanisms of partner recognition may be different for each species, thus, precluding the possibility of interspecific mating, even when statistically plausible.

Material examined. VENEZUELA: 1 male, Estado Mérida, Parque Nacional Sierra Nevada, Laguna Verde-Laguna Suero, 4000 m, 12.ii.1985, CEUM *leg.* (in MIZA); 1 male, Estado Mérida, Sierra Nevada de Mérida, Loma Redonda, 3900 m, 08.ii.2007 (genit. prep. ALV550-15) (in MC); 2 males, Estado Táchira, Páramo El Batallón, entre Laguna El Cenegón y Laguna Grande, 3200-3400 m; 28.ii.1994; Á. Vilorio, M. García and J. Camacho *leg.* (1 genit. prep. ALV544-15)

(in MALUZ. These unusual records are commented upon above); 1 male, Estado Mérida, S. of Mérida, Loma Redonda, 4000 m, 21.iv.1975, M. J. Adams, AB2, *holotype* of *Redonda empetrus bolivari* Adams and Bernard (in BMNH).

Redonda bordoni Viloria and Pycrz, 2003

Figs. 5 (female wing venation), 14 (male), 15 (female), 48 (male genitalia)

[*Redonda bordoni* Viloria and Pycrz, MS, *nom. nud.*; Viloria, 1998: 319; Ferrer-Paris, 2000: 96 (tbl. C.9)]

[*Redonda* sp. nov. 1; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution), 29 (tbl. 3.1), 36, 37 (fig. 3.5), 38, 40, 41 (tbl. 3.6), 69, 91 (tbl. C.7); Viloria, 2000: 269; Ferrer-Paris and Viloria, [2004]: 628 (fig.1); 629 (tbl. 1), 630 (fig. 3), 631]

Redonda bordoni Viloria and Pycrz, in Viloria et al., 2003: 21-23 (figs. 1a, male, female, 2, 3, 4), e-appendices: [1], [4 (fig. 5, female)], [5 (fig. 6 a male genitalia, b female genitalia, c female wing venation)] (in part misidentifications of *R. bolivari* and *R. lathraia*, **n. sp.**); [Anonymous], 2003: 24; Blackman, 2003: 26; Williams, 2003: R467; Lamas et al., 2004: 215; Viloria, 2005: 459; 2008: 278; Bálint and Wojtusiak, 2006: 288; Pycrz, 2007a: 40, 41; 2007b: 17, 18, 19; 2010a: 36 (fig. 17C, antennal club), 45 (fig. 35C, female venation), 87 (fig. 82, cladogram), 111, 179, 180 (fig. 131, wing area), 181 (figs. 132A, male; B, female, 133A, pair in copula), 182, 183, 184 (fig. 136, distribution), 244; 2010b: 265, 266 (figs. 1K male, 1L female, 267, 268 (fig. 2), 269 (figs. 3A, B, C females), 271 (fig. 5B pair in copula), 272, 273; ³abno, 2007: 104; Hazel and Butler, 2008: 33; Ferrer-Paris et al., [in press]

Type locality: between Laguna El Cenegón and Laguna Grande, Páramo El Batallón, Estado Táchira, Venezuela, 3200-3400 m, by original designation.

Comments. Among individuals of the type series of *Redonda bordoni* there were actually four males which represent two additional species (one partly sympatric). They were misidentified by Viloria and Pycrz (in Viloria et al. 2003). These four specimens were collected, together with 24 males and two females of *R. bordoni*, in an extense area of paramo in the neighbourhood of Laguna El Cenegón (3100-3250 m) by Á. L. Viloria, J. Camacho and M. García on 27 february 1994. Two dark individuals, very much worn-out by age and the action of wind are here unequivocally identified as belonging to *Redonda bolivari*, **n. stat.** (see above for implications of this discovery). The remaining two, formerly believed to be also a melanic male form of *R. bordoni*, are herein recognized as belonging to a new specific entity, *Redonda lathraia* Viloria and Camacho, **n. sp.**, and thus, correspondingly justified.

In the year 2000 we observed males of *R. bordoni* in the area of Sumusica (Táchira state), flying at 7 m/s wind speed and temperatures under 10° C and with similar wind conditions but only at 2° C in the region of El Cenegón. Their flight was erratical and low, stopping sometimes on the vegetation with wings open and oriented to the sun. Seldom, they were found resting motionless in the shadowy side of some leaves. In some places, male individuals have been found on flowers, especially those of *Berberis* sp. (Berberidaceae) and of ground herbs like *Gnaphalium* (Asteraceae). However, we have never seen them feeding on the flowers of *Espeletia* (unlike *R. castellana*, **n. sp.**, and *R. centenaria*, **n. sp.**, from the paramos of Trujillo).

One satyrine larva was discovered on *Orthosanthus chimboracensis* (Kunth) Baker (Iridaceae), in the paramo of Sumusica, and it was probably of *Redonda bordoni*: head capsule 4.10 mm wide, 4.02 mm high; colour: brown with some dark pigmentation on the sides, no dorsolateral horns. Body pale brown with black marks on both sides of segments 4-9, body length when caught: 35.20 mm; *ca.* 0.5 mm longer after a week in captivity. With a pair of tail appendices, 0.08 mm long, not specially coloured. It was fed in captivity on *O. chimboracensis* and bamboo leaves. It became inactive after two weeks and apparently entered the praepupa stadium, but we were unable to continue its rearing.

Material examined. VENEZUELA: 1 male, Estado Táchira, Páramo El Batallón, entre Laguna El Cenegón y Laguna Grande, 3200-3400 m; 28.ii.1994; Á. Viloría, M. García and J. Camacho *leg.*, holotype of *Redonda bordoni* Viloría and Pycrz; 23 males (3 in MUSM, 3 in JFLC), 2 females, same data (1 wing prep. ALVSN0-1997); 19 males (2 in MZUJ, 2 in BMNH), Estado Táchira, Páramo El Batallón, entre la Antena CANTV y la Laguna El Cenegón, 3100-3250 m; 27.ii.1994; Á. Viloría, M. García and J. Camacho *leg.*; 4 males, Estado Táchira, Municipio Jaúregui, Callejón del Cenegón, 16.xii.1994; M. García *leg.*; 6 males, 1 female, Estado Táchira, Parque Nacional Juan Peñaloza, Páramo El Rosal, 3000 m, 12/14.i.1995; J. Camacho and M. García *leg.*; 10 males, Estado Táchira, Páramo El Batallón, Entre El Cenegón y Laguna Grande, 3000-3400 m, 05.iii.1996, J. Camacho, M. García, T. Pycrz, J. Wojtusiak *leg.*, *paratypes* of *R. bordoni* Viloría and Pycrz (all in MALUZ, except where indicated); 1 male, Estado Táchira, Páramo de La Negra, 30.ix.1951, P. Fenjues *leg.*; 1 male, Estado Mérida, Páramo de La Negra, 3200 m., 14.i.1982, C. Bordón *leg.*, *paratypes* of *R. bordoni* Viloría and Pycrz (in MIZA); 51 males, 1 female, Estado Táchira, Páramo El Batallón, Vía El Púlpito, 3500-3800 m, 02/04.iii.1996, T. Pycrz, J. Wojtusiak, J. Camacho, M. García *leg.*; 5 males, Estado Táchira, Páramo El Batallón, Vía El Cenegón,

04.iii.1996, T. Pyrcz, J. Wojtusiak, J. Camacho, M. García *leg.*, paratypes of *R. bordoni* Viloria and Pyrcz (in MZUJ).

Redonda castellana Viloria and Camacho, **n. sp.**

Figs. 16, 17 (male), 18, 19 (female), 49 (male genitalia)

Synonymy, description, type material, distribution, comments, and etymology, below.

Type locality: Venezuela: E[sta]do. Trujillo, Páramo de Ortiz, 3170 m, 9° 14' 5.7 N, 70° 23' 39.2 W. Herein established.

Redonda centenaria Viloria and Camacho, **n. sp.**

Figs. 6 (female wing venation), 20, 21 (male), 22, 23 (female), 50 (male genitalia)

Synonymy, description, type material, distribution, comments, and etymology, below.

Type locality: Venezuela: Estado Trujillo, Páramo de Cabimbú, 2900 m. Herein established.

Redonda chiquinquirana Ferrer-Paris, **n. sp.**

Figs. 24, 25 (male), 26 (female), 51 (male genitalia)

Synonymy, description, type material, distribution, comments, and etymology, below.

Type locality: Venezuela: Estado Mérida, [Páramo de] Mucubají, 3600 m. Herein established.

Redonda empetrus (Thieme, 1905)

Figs. 1 (male wing venation), 27, 28, 29, 30, 31, 32 (males), 52, 53, 54 (male genitalia)

Pedaliodes empetrus Thieme, 1905: 95, 98-99, pl. 1, fig. 7; Thieme; Weymer, 1912: 258, pl. 54, row e; Gaede, 1931: 489; Adams and Bernard, 1979: 99; Descimon, 1986: 506, 518; Viloria and Pyrcz, 2001: 3.

Punapedaliodes [*Pedaliodes*] *empetrus* (Thieme); Huber, 1973: 195.

Redonda empetrus empetrus (Thieme): Adams and Bernard, 1981: 368 (in part misidentification of *R. chiquinquirana*, **n. sp.**, female description of this taxon), figs. 13 (male genitalia), 27 (female of *R. chiquinquirana*, **n. sp.**); Adams, 1983: 474; 1984: 93; d'Abbrera, 1988: 871 (in part misidentification of *R. chiquinquirana*, **n. sp.**); 2001: 186, 341, pl. 141, fig. 17; Pyrcz, 1995: 523; 2007b: 17, 18; 2010a: 87

(fig. 82, cladogram), 184 (fig. 136, distribution), 244; 2010b: 266 (fig. 1I male), 267, 268 (fig. 2, distribution); Viloría, 1998: 10, 11, 13, 141, 142, 144, 146 (tbl. 1), 147 (tbl. 2), 150 (fig. 23, male), 158 (fig. 72, wing venation), 170 (fig. 125, male genitalia), 320 (last, in part misidentification of other taxa, but fig. 23 correct); 2000: 269, 270; 2002: 190; 2005: 459; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution [in part misidentifications of *R. bolivari* and *R. chiquinquirana* n. sp.]), 29 (tbl. 3.1), 36, 37 (fig. 3.5), 38, 41 (tbl. 3.6), 91-92 (tbl. C.7); Viloría and Pyrcz, 2001: 12, 13; Viloría *et al.*, 2003: 22 (fig. 1(b) male); Ferrer-Paris and Viloría, [2004]: 627, 628 (fig. 1), 629 (tbl. 1), Lamas *et al.*, 2004: 215.

Redonda empetrus (Thieme); Viloría, 1990: 223; 1998: 126, 176-181 (figs. 151-157, cladograms), 343, 474 (tbl. 8); 2003: 247, 248 (figs. 1, 2, cladograms); Díaz *et al.*, 1997: 284, 811; Ferrer-Paris, 2000: x, 17, 30, 31 (fig. 3.2), 32 (fig. 3.3), 33, 34 (tbl. 3.2), 35 (tbl. 3.3), 36 (fig. 3.4), 40, 41, 42 (tbl. 3.7), 43 (fig. 3.7), 44 (fig. 3.8), 45 (fig. 3.9), 46 (fig. 3.10), 47 (tbl. 3.8), 66, 69, 78 (fig. A.5, eggs and larvae, fig. A.6), 84 (tbl. C.1), 85-86 (tbl. C.2), 87 (tbl. C.3), 88 (tbl. C.4), 96 (tbl. C.9); Orellana, 2004: 5-57, 5-63, 5-69, 5-70, 5-1; Shou *et al.*, 2006: 105; Viloría *et al.*, 2007: [23]; Pyrcz, 2007a: 40, 41; 2010a: 46, 82, 134, 182, 183; 2010b: 265, 267, 272, 273; Peña, 2009: 102 (figs. 2, cladogram), 103 (fig. 3, cladogram), 105 (fig. 5, cladogram), 107 (fig. 8, cladogram), 111; Bolaños-Martínez *et al.*, 2010: 89; Padrón Martínez, 2010: 19 (fig. 2-1, cladograms A, B), 26 (tbl. 2-1), 84; Peña *et al.*, 2011: 70 (tbl. 1), 80 (fig. 6, cladogram).

[*Redonda empetrus bolivari* Adams and Bernard; Viloría, 1998: 319; 2000: 270; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution) (misidentifications, at least in part)].

Redonda empetrus georgei Pyrcz and Viloría, *nom. nud.*; Pyrcz, 2007b: 18, 19; 2010a: 181 (figs. 132C, male; D, female; 133, female), 182, 184 (fig. 136, distribution), 244; 2010b: 272. *Redonda emperatus* [sic] (Thieme); Peña, 2009: 104 (fig. 4, cladogram).

Redonda empetrus ssp. 1; Pyrcz, 2010b: 266 (Figs. 1A male, 1B female), 267, 268 (fig. 2, distribution), 270 (fig. 4D, habitat), 271 (figs. 5C, female, 5D, pair in copula).

Type locality: Herein restricted to the páramos of the upper Albarregas river (páramo de Los Conejos, pico Campanario, 3100-4300 m), westernmost extreme of the Serranía de La Culata, north of the city of Mérida, Mérida State, Venezuela.

Original description, translated into English from Thieme (1905), by Á.L.V. (diagnostic characters in bold letters):

“*Ped. Empetrus* n. sp. mine (Tbl. 1, Fig. 7)

A form of *Pedaliodes* between *albonotata* Godm. and *albomaculata* Weymer, bigger than both, posterior [wing] prolonged, elongated (as in *albomaculata*). Fringe of wings all pale white between veins, anterior entire, posterior barely scalloped. Antennal club thickened, claviform, palps longer than usual, without a scaled area.

Above diluted yellow instead of brown, not quite unicolor, but brownish stripe, bent, **outerly sharp**, internally diffuse, anterior proximal part [of the wing] separated from the distal part. Also rotten-gray spot in the forewing median cell, crossed by transverse veins of discal cell. Also posterior discal veins rake-like and greyish. Anterior points (or spots) greater, six submarginal covertly white, five posteriorly.

Underside anterior saturate brown, discal stripe the same as above, **but rather thin and sharp**, submarginal points (spots) the same, as above. Posterior not brown, but fuscus, all clouded, injected of irregular spots of “dirty dog”. Five transverse submarginal signs covertly white, **like figures of the fleur-de-lys**, which, that between veins U R and O R, apart from the shape almost the same as in *Pedaliodes albonotata* Godm.

Bigger than the others in the group. Conspicuous by the pale, wood-tone upperside, which gets blurred by patch bands and some dirty stains. It recalls *albopunctata* Weymer due to the extended, oblong hindwing, and *albonotata* Godm. (with which it shares a common locality) by the underside submarginal design of the hindwing.

The absence of the recurrent vein from the angle of the M D C duly belongs to *Pedaliodes*, but the palps are exceptionally long, the club thickened as a lobe, a case not known to me in any other *Pedaliodes*.*)

*Related to the South American species of *Oeneis* (*Argyrophorus* Blanch.) and recalls *Argyrophorus Lamna* mine (Berl. Ent. Zeitschr. Vol. XLIX 1904 p. 160), in characters and design of the underside.”

A male in my collection from the snowy mountains of Merida.

Comments. The extraordinary monograph on the genus *Pedaliodes*, published by Otto Thieme in 1905 appears to basically be the result of Thieme’s overtaking of the work started by Otto Staudinger, the prominent German entomologist and insect dealer, who died in October 1900. It is evident that the aforementioned research paper took several years of study of the material deposited in three German and British collections, namely, Thieme’s own collection, Staudinger collection (transferred in 1907 to the Humboldt University Zoological Museum–Berlin), and the Walter Lionel

Rothschild collection at Tring, England (later on, bequeathed to the British Museum (Natural History), now the Natural History Museum of London). A significant proportion of the new *Pedaliodes* species described by Thieme had been, at least in part, previously identified as such by Staudinger. Thieme not only may have had access to the Staudinger butterfly collection, but also to his unpublished taxonomic notes. Along his monograph, Thieme duly mentioned Staudinger's manuscript names several times, and sometimes he even applied those names to his new species. This is not the case for '*Pedaliodes*' *empetrus*, whose description was based on just one male specimen, preserved in the private collection of Thieme (black and white photographic image of its upperside illustrated in Thieme's plate 1, figure 7). This individual might have come to Thieme's possession via some insect dealer based in Berlin; most probably, Ernst A. Böttcher, and it seems unlikely that Staudinger had ever known of this taxon. The type specimen of '*P.*' *empetrus* allegedly came from the snowy mountains of Mérida, but Mérida (1600-1800 m) was, and still is, a small city that lies in the river Chama valley, between two, parallel, very high mountain chains that were both 'snowy' in that time, the second more than the first: the northern Serranía de La Culata (with 54 peaks above 4300 m, maximum elevation at Pico Piedras Blancas, 4737 m) and the southern Sierra Nevada (with 14 peaks above 4300 m, maximum elevation at Pico Bolívar, 5010 m). A detached portion of the latter, the Sierra de Santo Domingo, contains the other two peaks in Venezuela that reach above 4300 m (maximum elevation at Pico Mucuñuque, 4660 m) (Silva León 2001).

These geographic considerations are relevant because part of Thieme's type material of *Pedaliodes sensu lato* (a dozen taxa), including his only individual of '*P.*' *empetrus*, is currently lost or has not yet been located. Rumors spread about the disappearance or loss of his collections after WWII, but a note published in a German magazine, the second half of the last century (Gerardo Lamas, pers. comm.), indicates that his collection, or part of it, was purchased by Kurt Beuthan after Thieme's death (in 1907). Beuthan was apparently an amateur entomologist established in Weissenfels, where he was, at some point, the Director of the local historical museum. Beuthan's entomological collection –or the largest part of it– was auctioned in 1963. The whereabouts of this potentially very valuable collection

is unknown. In May 2003, two of the authors (Á.L.V. and J.R.F.-P.) visited the Heimat-Naturgarten in Weissenfels, where there still exist 20+ entomological drawers containing butterflies, moths and other insects of the Kurt Beuthan collection. However, there are no neotropical butterflies among them. Consequently, we have been forced to consider unavailable for this study the type specimen of *Pedaliodes empetrus* Thieme.

In the high mountains around Mérida we recognize four species of *Redonda*, all of them show certain degree of morphological variability and are externally rather similar to each other. They all live in paramo environments characterized by open grasslands with rosettes of *Espeletia* and/or related genera, that develop as a biome generally around 3000 m and above, just below the periglacial zone. However, only some male individuals from the Serranía de La Culata match well the diagnostic characters highlighted in the translation of the original description above. The best examples of large imagos with the characteristic shape of lily flowers (fleur-de-lys) in the submarginal ocellar elements of the hindwing underside come from the upper Albarregas river (páramo de Los Conejos and surroundings of the Pico Campanario). Additionally, the recto of those specimens show the closest similarity to the upperside of the type illustrated by Thieme, especially the shape and size of the submarginal white dots of the hindwing. Male individuals of the easternmost population in La Culata (upper Mucujún river) are very variable in size (FWL: 25-30 mm) and colour pattern. For instance, the series we have collected and/or examined from the upper Mucujún river, represents a range of various degrees of grey dusted over the upperside of the forewing cell, and show great variation in length and shape of the white ocellar elements of the submarginal area of the hindwing underside (Fig. 27-32). Nevertheless, there are specimens in the Mucujún population that are indistinguishable from those from the Albarregas, and have, for example, a well developed “fleur-de-lys pattern”. We have not been able to detect the diagnostic features selected from Thieme’s original description of ‘*P.*’ *empetrus*, either in the Sierra Nevada individuals of *Redonda* (*R. bolivari*) or in those from the Sierra de Santo Domingo (altitudinal parapatics *R. frailejona*, **n. sp.** and *R. chiquinquirana*, **n. sp.**). Therefore, we interpret the identity of *Redonda empetrus* as applicable to those individuals of *Redonda* from the Serranía de La Culata, but restrict its type

locality to the area where its phenotype appears to be more stable, the upper Albarregas river.

We believe the type specimen of '*P. empetrus*' was obtained by Salomón Briceño Gabaldón at the end of the XIX Century or beginnings of the XX in the Serranía de La Culata, region of the Páramo de Los Conejos. He was the only active, local butterfly collector and dealer in the Andes of Venezuela during the time that the first paramo endemic satyrine butterflies reached Europe and were consequently described: '*Oxeoschistus opalinus*' (Staudinger, 1897) [Lectotype from Mérida, Bricenno [sic], in ZMHU, examined], '*Pedaliodes albonotata*' (Godman, 1905) [Lectotype from Mérida, Venezuela, Ex Staudinger, in BMNH, examined]. His collecting localities in the Andes around Mérida (La Culata, La Pedregosa, Quintero, etc.) were all located north of the Chama river. There is no evidence that he, or any other entomologist before 1905, had collected butterflies in the highest elevations of the Sierra Nevada de Mérida or in the Sierra de Santo Domingo, which are south or southeast of the city, and were far more inaccessible than the Serranía de La Culata (see Vilorio and Pycrz 2001: 2-3).

Male specimens of *R. empetrus* from the region of the Páramo de Los Conejos (upper Albarregas river) westernmost portion of the Serranía de La Culata, are in average larger (29-30 mm in FWL, mean 29.5 mm) than those from the upper Mucujún river (25-29.5 mm in FWL, mean 27.06 mm).

Adams and Bernard (1981: 368) obtained specimens of *Redonda* from the Mucubají lagoon area (Serranía de Santo Domingo). From this material, they described under the name of *R. empetrus* the female of *R. chiquinquirana*, **n. sp.** (*op. cit.*, fig. 27). One specimen located in the Adams and Bernard collection, which one of us (Á.L.V.) have examined at the BMNH, is unlabelled. It certainly comes from the Mucubají area (Serranía de Santo Domingo) as it fits the phenotype of females collected later on in Mucubají (illustrations in Vilorio *et al.* 2003: fig. 1B, and Pycrz 2010b: fig. 1D; both also misidentified). Females of putative *Redonda empetrus* from the upper Mucujún river population have been illustrated by Pycrz under a different nominal identity (2010a: 181, figs. 132D, 133; 2010b: 266, fig. 1B, 271, figs. 5C, D). They are different from *R. chiquinquirana*, **n. sp.** Photographic illustrations show that their antennae are approximately

the same length as those of their corresponding males, reaching only half length of the costa (vs. 2/3 in males). Thus, females are about 3/4 the size of males. Their wing upperside is metallic yellowish, almost golden, and their underside is cryptic and similar in general pattern to the males, but lighter and with reduced ocellar elements. The few female specimens known did not come from the restricted type locality herein established by us. They are all in foreign private collections and were not available for this study. Thus, the female of *Redonda empetrus* remains formally undescribed.

Some bionomic notes of this species have been presented by Adams and Bernard (1981). In wild conditions they behave more or less similar to other species belonging to its genus. We observed small groups of males of *R. empetrus* in the upper Mucujún river very active under extreme climatic conditions; some were seen at 8 o'clock in the morning, as the first sun rays penetrated the valley of the river at around 3400 m elevation (refugio Casa de Piedra, on the way from La Culata to Pico Pan de Azúcar) as the thermometer in the shading side of the valley marked -3° C.

Material examined. VENEZUELA: 1 male, [Edo.] Mérida, Sierra [de] La Culata, Páramo [de] Los Conejos, Laguna [de] Los Conejos, 8° 41' 51" N, 71° 12' 01" W, 3950 m, 31.viii.2001, J. Camacho *leg.* (genit. prep. ALV553-15) (in MALUZ); 1 male, Estado Mérida, N de Mérida, Río Albarregas, 3400 m, 20.vi.1975, M. J. Adams and G. I. Bernard *leg.* (in MIZA); 2 males, Venezuela, Edo. Mérida, [Serranía de La Culata] P. N. La Culata, Valle del Muerto (páramo) [upper río Mucujún], 08° 44' N, 71° 11' W, alt. 3350 m, 15.ii.2000, 11:00-12:00, J. R. Ferrer-Paris *leg.*; 4 males, same locality, 3325 m, 30.i.2000, 12:00-12:30 (in IVIC); 1 male, Venezuela, Edo. Mérida, Serranía de La Culata, alto río Mucujún, 3400 m, 01.ii.2008, P. Boyer *leg.* (genit. prep. ALV551-15); 1 male, Venezuela, Edo. Mérida, La Culata, 3300, 21.ii.2008, [P. Boyer *leg.*] (genit. prep. ALV549-15) (in MC); 1 male, Est. Mérida, Campanario, 13500 ft, 10.ix.1938, J. H. Tracey *leg.*, Brit. Mus. 1939-114, 2 males, Cordillera de Mérida, N of Mérida, Río Albarregas, 3400 m, 15.viii.1977, M.J. Adams and G. I. Bernard *leg.*, AB2 (1 genit prep. ALV088-96, wing prep. ALV27-97); 1 male, same data, 3600 m (in BMNH); 1 male, Edo. Mérida, Tal des Río Albarregas, 2100 m [*sic*], 29.viii.1971, H. Huber *leg.* (in ZSBS).

***Redonda frailejona* Ferrer-Paris and Costa, n. sp.**

Figs. 33, 34 (male), 35, 36 (female), 37 (dimorphism), 55 (male genitalia)

Synonymy, description, type material, distribution, comments, and etymology, below.

Type locality: Venezuela, Edo. Mérida, Sto. Domingo – Apartaderos, 3000 m. Herein established.

Redonda lathraia Viloría and Camacho, **n. sp.**

Figs. 38, 39 (male), 56 (male genitalia)

Synonymy, description, type material, distribution, comments, and etymology, below.

Type locality: Venezuela: [Estado] Táchira, P[á]ra]mo El Batallón, entre Laguna El Cenegón – Laguna Grande, 3200-3400 m. Herein established.

Redonda leukasmena Viloría and Camacho, **n. sp.**

Figs. 7 (female wing venation), 40, 41 (male), 42, 43 (female), 57 (male genitalia)

Synonymy, description, type material, distribution, comments, and etymology, below.

Type locality: Venezuela, Estado Lara, Municipio Morán, Páramo de La Rosa [*sic*], 3000 m. Herein established.

Redonda lossadana Ferrer-Paris, **n. sp.**

Figs. 44, 45 (male), 58 (male genitalia)

Synonymy, description, type material, distribution, comments, and etymology, below.

Type locality: Venezuela, [Edo.] Trujillo, Páramo de Tuñame, vía Las Mesitas, 3100 m. Herein established.

DESCRIPTIONS

Redonda castellana Viloría and Camacho, **new species**

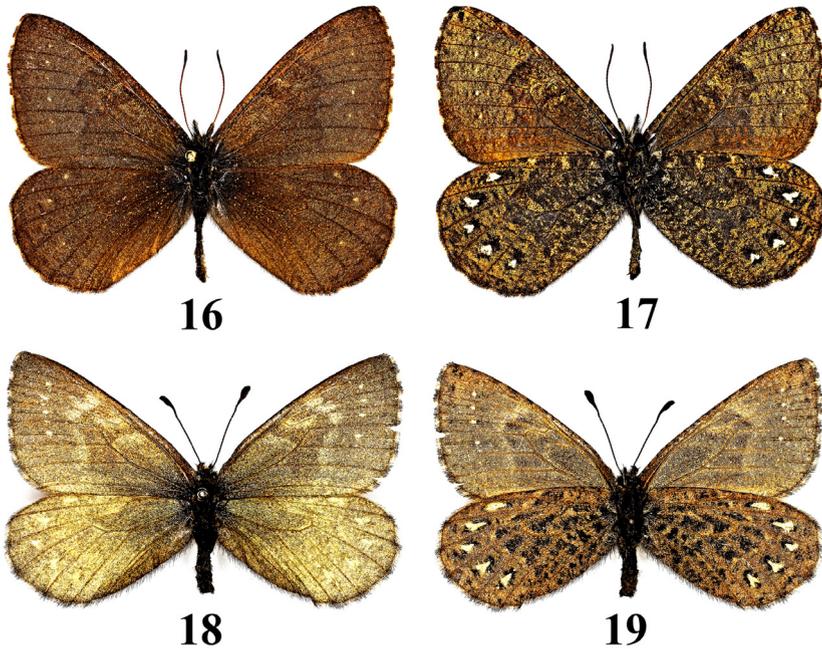
Figs. 16, 17 (male), 18, 19 (female), 49 (male genitalia)

urn:lsid:zoobank.org:act:971ED3B8-355D-4B8F-B718-3BC7EC48591B

[*Redonda empetrus* ssp. nov. 1; Viloría, 2000: 270 (misidentification) (in part)].

[*Redonda empetrus* n. ssp.; Viloría and Pycrz, 2001: 12 (misidentification) (in part)].

[*Redonda empetrus* ssp. nov.; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution), 29 (tbl. 3.1), 36, 37 (fig. 3.5), 38, 69, 91-92 (tbl. C.7); Viloría *et al.*, 2003: 23 (fig. 3, wing



Figs. 16-19. Adults of *Redonda castellana* Viloria and Camacho, n. sp.; **16.** Male holotype (Páramo de Ortiz), upperside; **17.** *Ibid.*, underside; **18.** Female paratype (Páramo de Las Moras), upperside; **19.** *Ibid.*, underside.

area); Ferrer-Paris and Viloria, [2004]: 629 (tbl. 1), 630 (fig. 3) (misidentification) (in part)].

[*Redonda empetrus* c] [n. ssp.] Viloria and Pyrcz, MS]; Lamas *et al.*, 2004: 215 (misidentification) (in part)].

[*Redonda empetrus* ssp.; Viloria, 2005: 459 (misidentification) (in part)].

[*Redonda empetrus millenaria*] *nom. nud.*; Pyrcz, 2007b: 18 (misidentification in part).

[*Redonda empetrus centenaria* Viloria and Pyrcz] *nom. nud.*; Viloria, 1998: 320; Pyrcz, 2010a: 36 (fig. 17A, antennal club), 100 (fig. 86F, male), 180 (fig. 131, wing area), 182 (fig. 135, polymorphism), 184, 184 (fig. 136, distribution), 244 (misidentifications in part)].

[*Redonda empetrus* ssp. 4; Pyrcz, 2010b: 268 (fig. 2, distribution) (misidentification) (in part)].

Male. Forewing length: 22.5-29 mm; mean: 26.87; n = 167. Eyes very hairy, dark coffee brown, almost black. Palpi twice the length of head, whitish in basal segment; silvery white scales all

along, sparsely, setae predominantly black, inserted with ochraceous. Antennae to two fifths of costa. Body moderately hairy, upperside black, underside similar in thorax, but shiny brown on abdomen. Forewing triangular (outer margin notably more straight, less convex than similar species *R. centenaria*, **n. sp.**, its closest allopatric); upperside uniform dark brown with ochraceous scales finely and scarcely dusted all over, more densely along costa and over the forewing discal cell and on its distal extreme; basal and discal areas darker, but not very distinctly defined, a series of five to six minute postdiscal yellowish dots (more or less marked in different individuals), from cell R5 to Cu2, fringes with alternate yellowish between veins. Hindwing oval, only slightly scalloped, upperside as in forewing but without a darker discal area; a series of three to five postdiscal yellowish dots (from R5 to Cu1). Forewing underside reddish brown ground colour, more towards posterior portion of discal area; outer half of the wing and distal quarter of discal cell densely scaled with ocher, also along costa, but inserted with coffee brown; coffee brown spotted alternate along costa and outer margin (fringe), and limiting both sides of discal area, especially in anterior half. Hindwing underside brown, with dense dark coffee scaling mostly on its basal half; discretely mottled on its distal half; postdiscal-submarginal series of five to six conspicuous white-to-yellowish, triangular to >-shaped, spots (R5 to Cu1 or Cu2); anterior in general larger and variably more elongated than posterior, all more or less surrounded by dark coffee brown. Genitalia illustrated in figure 49; characterized by a very short and very wide saccus (the shortest and widest of all species so far known in the genus); uncus stylized (more than in *R. centenaria*, **n. sp.**), subunci absent, and valva less deep in lateral view than that of *R. centenaria*, **n. sp.**

Female. Forewing length: 21-27; mean: 22.83 mm; n = 32. Palpi covered by scales creamy brown, setae shorter than in male, light creamy brown and black. Smaller and slender than male (and smaller and slender in average, and lighter in colour, than females of *R. centenaria*, **n. sp.**). Differs from male in having narrower wings, but forewing still notably triangular (as compared to females of *R. centenaria*, **n. sp.**, its closest species both morphologically and geographically). Upperside golden brown, darker in forewing and basal third of hindwing (including discal cell); forewing lighter areas along discal-postdiscal border, the distal extreme and the middle of

the discal cell; dots as in males. Forewing underside similar to upperside, reddish ochraceous scales along veins, mottled with coffee brown along costa and on submargin in anterior half and apex of wing. Hindwing underside reddish ochraceous background; mottled with dark coffee brown on basal two thirds of wing and less in the submargin; series of five triangular-to >-shaped yellowish spots very conspicuous (R5 to Cu1), more or less surrounded by dark coffee brown. All fringes yellowish between veins.

Holotype. Male, Venezuela: Estado Trujillo, Páramo de Ortiz, 3170 m, 9° 14' 5.7 N, 70° 23' 39.3 W, 16.viii.2003, Á. L. Viloria, M. Alarcón, W. Rojas *leg.* (in MALUZ).

Paratypes. 57 males (4 MUSM, 2 MC), 15 females (4 MUSM, 1 MC), same data as holotype; 15 males (2 in MZUJ), 4 females (1 in MZUJ), Venezuela: Estado Trujillo, Páramo de Ortiz, 2850-3100 m; 12.ix.1991; Á. L. Viloria and E. Moscó *leg.*; 30 males (1 in BMNH), 4 females, same locality, 3100 m; 7.i.1992; J. Camacho and Á. L. Viloria *leg.*; (in MALUZ); 37 males, 7 females, same locality and date as holotype, G. Fagua, M. Higuera *leg.* (in PUJB); 3 males, Venezuela: Estado Trujillo, Vía Boconó-Páramo La Cristalina, 2400-2800 m, 14.vi.1986, J. E. Lattke *leg.*; 1 male, Venezuela: Estado Trujillo, Páramo La Cristalina, 2800 m, 14.v.1986, J. E. Lattke *leg.* (in MIZA); 1 male, Venezuela: Estado Trujillo, Páramo Las Moras, 3000 m, 19.ii.2007, M. Costa *leg.*; 22 males, 2 females, same locality and collector, 20.ii.2007 (in MC).

Distribution. 2800-3170 m. Paramo region between Trujillo and Boconó, divide of the basins of rivers Castán and Burate, NE of the Teta de Niquitao. This region comprises the paramos La Cristalina, Las Moras, El Atajo, Ortiz, Los Pozos, El Corazón and Filo La Ovejera. It is just orographically separated from Cabimbú and La Teta de Niquitao by a small disjunction W of the Páramo El Corazón.

Comments. A few *Swallichloa* clumps were found patchily distributed only in the Páramo de Ortiz, mainly along creeks. The butterflies did not appear to be associated with bamboos, but with grasses. During a visit to the Páramo de Ortiz in the dry season, we found aggregations of males of *R. centenaria* "puddling" at midday and in the early afternoon in humid parts of the soil along a dirt road, where they were protected from direct sunshine by the shade

of the neighbouring hills. In such spots they were easy to collect. Thirteen (out of fifteen) females captured in 2003, laid numerous eggs free of glue (2 to 47 each, totaling 156), during handling. Eggs are spherical, light green and shiny. Attempts to rear larvae from such eggs in laboratory conditions have always been unsuccessful.

This butterfly co-exists with *Diaphanos curvignathos* Viloría and *Steromapedaliodes albonotata* (Godman) (Satyrinae), *Colias dimera* Doubleday, *Catasticta chrysolopha spectrum* Reissinger (Pieridae), *Hylephila* sp. (Hesperiidae), and several species of high altitude Lycaenidae.

Etymology. We respectfully dedicate the name of this new species of butterfly, *Redonda castellana*, **n. sp.**, to our friend, Dr. Rafael Ramón Castellanos; diplomat, academician and historian, and a prolific writer who, with more than 70 published books, has contributed much to literature and history of Venezuela, and to the promotion of the Andean regional history and identity. He is a native of Santa Ana de Trujillo (b. 1931), a village located not far from the area of distribution of *R. castellana*, **n. sp.** Well known to Venezuelan intellectuals, readers, and bibliophiles, Rafael Ramón Castellanos has owned and managed the “Gran Pulpería del Libro Venezolano” in Caracas for many years, one of the largest and most important book shops (new, second hand and antiquarian) of Latin America.

***Redonda centenaria* Viloría and Camacho, new species**

Figs. 6 (female wing venation), 20, 21 (male), 22, 23 (female), 50 (male genitalia)

urn:lsid:zoobank.org:act:53550B6B-35EC-4E71-9943-E7D6604FAFC8

[*Redonda empetrus* ssp. nov. 1; Viloría, 2000: 270 (misidentification) (in part)].

[*Redonda empetrus* n. ssp.; Viloría and Pyrcz, 2001: 12 (misidentification) (in part)].

[*Redonda empetrus* ssp. nov.; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution), 29 (tbl. 3.1), 36, 37 (fig. 3.5), 38, 69, 91-92 (tbl. C.7); Viloría *et al.*, 2003: 22 (fig. 1d, male, female), 23 (fig. 3, wing area); Ferrer-Paris and Viloría, [2004]: 629 (tbl. 1), 630 (fig. 3) (misidentification) (in part)].

[*Redonda empetrus* c) [n. ssp.] Viloría and Pyrcz, MS]; Lamas *et al.*, 2004: 215 (misidentification) (in part)]

[*Redonda empetrus* ssp.; Viloría, 2005: 459 (misidentification) (in part)].

[*Redonda empetrus millenaria*] *nom. nud.*; Pyrcz, 2007b: 18.

[*Redonda empetrus centenaria* Viloria and Pyrcz] *nom. nud.*; Viloria, 1998: 320; Pyrcz, 2010a: 36 (fig. 17A, antennal club), 100 (fig. 86F, male), 180 (fig. 131, wing area), 182 (fig. 135, polymorphism), 184, 184 (fig. 136, distribution), 244 (misidentifications in part)].

[*Redonda camachoi* Viloria and Pyrcz, *nom. nud.*; Pyrcz, 2010a: 45 (fig. 35B, female venation) (misidentification)]

[*Redonda empetrus* ssp. 4; Pyrcz, 2010b: 268 (fig. 2, distribution) (misidentification) (in part)]

[*Redonda empetrus* ssp. 5; Pyrcz, 2010b: 266 (figs. 1G, male, 1H, female), 267, 268 (fig. 2, distribution), 270 (fig. 4B, habitat) (misidentification) (in part)]

Male. Forewing length: 25-30 mm; mean: 26.75 mm; n = 11. Eyes hairy, black. Palpi twice as long as head; silver white at base, coffee brown all along, with dusting of white scales, mixed setae black, coffee and cream, more or less in the same proportion. Antennae reaching two fifths of costa. Body dark brown, light brown on abdomen underside. Forewing subtriangular, with outer margin notably convex (different from that of *R. castellana*, **n. sp.**, which is more straight, and from that of *R. lossadana*, **n. sp.**, which is slightly truncated towards apex). Upperside ground colour dark brown, rather uniform on both wings; anterior half of discal area of forewing diffusely bordered with lighter brown, white over transverse veins closing the outer extreme of the discal cell, some light brown dusting along forewing subcostal region, and very subtle on basal half of both wings; forewing series of four to five postdiscal-submarginal white dots (from R5 to M3 or Cu1); forewing fringes with white dots between veins; hindwing series of submarginal white dots usually reduced to two or three (on M1 and M3, sometimes on M2). Hindwing more crenulated than those of *R. castellana*, **n. sp.**, and *R. lossadana*, **n. sp.** Forewing underside ground colour reddish brown, mottled with dark brown all over (more towards edges and base); white speckling over distal half of the wing and along costal and apical areas, as well as in the middle of discal cell, series of white dots as on upperside, but dots larger (wider). Hindwing underside ground colour dark brown, heavily mottled and speckled with white, and light brown all over, white mottling more intense on both sides of discal area; series of five submarginal white >-shaped spots, from R5 to Cu1; those on R5 and M1 twice as long as the other three. Genitalia illustrated in figure 50; subunci vestigial.

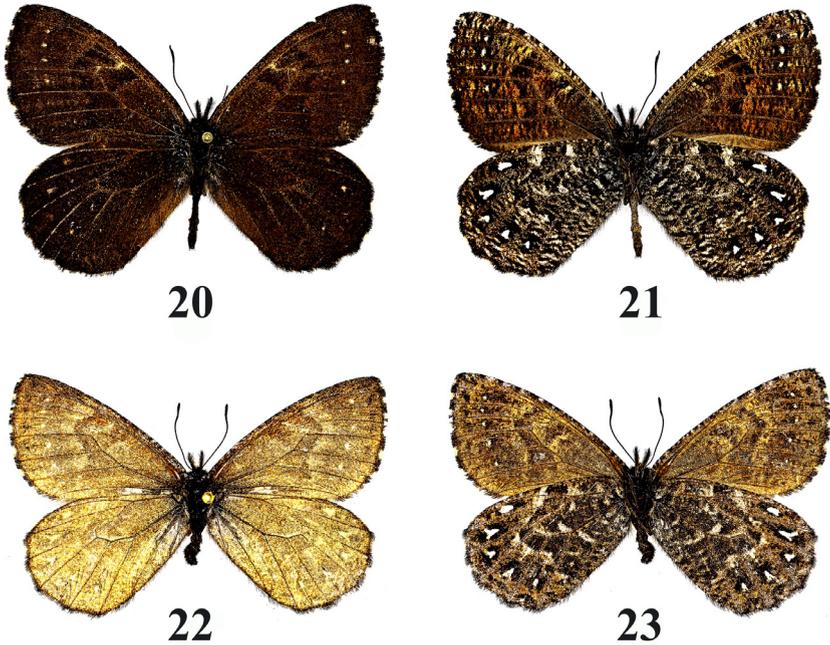
Female. Forewing length: 24-26 mm; mean = 25 mm; n = 2. Smaller and slightly slender than male, but larger and darker than females of *R. castellana*, **n. sp.** Palpi all covered with silvery white scales, setae predominantly light brown, alternate with black. Wings upperside golden brown, slightly darker forewing; all fringes dark brown with white between veins. Forewing postdiscal area lighter, forewing series of dots as in males, but relatively larger and less distinct; hindwing series of dorsal dots >-shaped as on underside. Underside pattern in general very similar to male, but ground colour lighter, especially on the outer third of wings, mottling and speckling more moderate; forewing submarginal white dots smaller.

Holotype. Male, Venezuela: Estado Trujillo, Páramo de Cabimbú, 2900 m; 11-ix-1991; Á. L. Vilorio and R. Calchi *leg.* (genit. prep. ALV548-15) (in MALUZ).

Paratypes. 9 males, 2 females (1 wing prep. ALVSN1-1997), same data as holotype (in MALUZ); 1 male, Venezuela, Edo. Trujillo, región de Niquitao, M.-N, Teta de Niquitao N 09° 07', W 10° 24', alt. 3325 m (páramo), 23.ii.2000, 10:30-12:00, J. R. Ferrer-Paris *leg.* (in IVIC).

Distribution: 2900-3325 m. *Redonda centenaria*, **n. sp.**, appears to be restricted to the páramo surroundings of the Teta de Niquitao (whose NW portion is called páramo de Cabimbú). This is a relatively isolated high altitude unit in the state of Trujillo (Briceño-Valero 1920; highest elevation in La Teta, 4006 m), just separated from a northern portion of paramo biome where another, externally similar species occur (*R. castellana*, **n. sp.**). The latter paramo unit divides the valleys of the cities of Trujillo and Boconó (see distribution of *R. castellana*, **n. sp.**). Most of the páramos of the Niquitao region, have a single, long, wet season (*ca.* April-August), which is probably due to the influence of the climatic conditions of the Llanos, south of the Andes (Monasterio and Reyes 1980). The local vegetation is characterized by the predominance of *Espeletia* and other asteraceous rosettes and bunch grasses (Vareschi 1970, Cuatrecasas 1979).

Comments. *Redonda centenaria*, **n. sp.**, is a common insect throughout the year. Both males and females fly actively during sunny periods. Females can be distinguished by their slightly smaller size, lighter upperside coloration, and relative weakness in flight.



Figs. 20-23. Adults of *Redonda centenaria* Viloria and Camacho, n. sp.; 20. Male holotype (Páramo de Cabimbú), upperside; 21. *Ibid.*, underside; 22. Female paratype (same locality), upperside; 23. *Ibid.*, underside.

Usually they seem unable to sustain a long flight, which is undertaken in “steps”, and very close to the grasses, most commonly following the direction of the wind. Resting females are very difficult to see because of their cryptic underside pattern, but they can be observed dropping suddenly into the grass after a short flight. Then, they take another flight-step in the same way. When collected, females released many spherical eggs from the moment of capture and throughout several hours whilst kept alive in paper envelopes. All the eggs were also free of cement.

Etymology. La Universidad del Zulia (Maracaibo, Venezuela), began academic activities on September 11th 1891, under the principalship of the notable lawyer Dr. Francisco Ochoa, first Rector. This new species of *Redonda* was first noticed by Á.L.V. in the Páramo de Cabimbú, one hundred years later, on September 11th 1991. We name it *R. centenaria* in celebration of the centennial of our *Alma Mater*. We also want to record our gratitude for the unique

opportunity we (A.L.V. and J.C.) have had to develop our professional careers in this institution.

***Redonda chiquinquirana* Ferrer-Paris, new species**

Figs. 24, 25 (male), 26 (female), 51 (male genitalia)

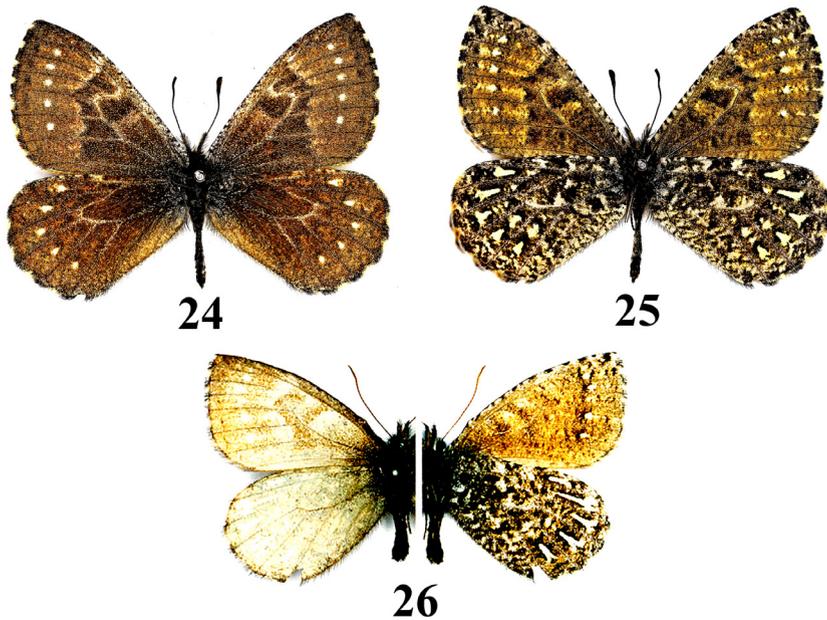
urn:lsid:zoobank.org:act:F56B4A32-2F3E-430E-9E53-C38A22EF1EE0

[*Redonda empetrus empetrus* (Thieme); Adams and Bernard, 1981: 363 (fig. 27, female), 368 (description of female); d'Abbrera, 1988: 871; Viloría, 1998: 320; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution); Viloría *et al.*, 2003: 21-23 (figs. 1(b), [female], 2, 3); Ferrer-Paris and Viloría, [2004]: 630 (fig. 3) (misidentifications, at least in part)]

Redonda empetrus miki Pyrcz and Viloría, *nom. nud.*; Pyrcz, 2007b: 18; 2010a: 180 (fig. 131, wing area), 182, 184 (fig. 136, distribution), 244.

[*Redonda empetrus* ssp. 2; Pyrcz, 2010b: 266 (figs. 1C male, 1D female), 266, 268 (fig. 2) (misidentification)]

Male. Forewing length: 20.5-26 mm; mean = 24.76 mm, n = 23. Eyes hairy, black. Palpi twice the length of head, white at basal segment, remaining segments black, with sparse white scales, black



Figs. 24-26. Adults of *Redonda chiquinquirana* Ferrer-Paris, n. sp.; 24. Male holotype (Páramo de Mucubaji), upperside; 25. *Ibid.*, underside; 26. Female paratype (vía Laguna Negra), left upperside, right underside.

and cream setae alternatively inserted more or less in the same proportion. Antennae to two fifths of costa. Body black, only brown laterally on abdomen. Forewing subtriangular, outer margin convex, tornus rounded. Hindwing oval and distally elongated as in *R. empetrus*, but base wider than the latter, outer margin scalloped. Dorsal ground colour of wings brown (darker than in *R. empetrus*, but lighter than in *R. bolivari*, *R. castellana*, **n. sp.**, *R. centenaria*, **n. sp.**, and *R. lossadana*, **n. sp.**), slightly darker on basal half. Veins on basal half of wings covered with whitish scales, very notable on those closing discal cell. Forewing discal area limited by diffuse white on both sides, more distinctly in forehalf, white speckling along two thirds of costal area, distinct white between veins along fringe, submarginal series of five to six circular dots, as large as those of *R. empetrus*, and in general twice to three times the diameter of most dark species from Trujillo (*i. e.*, *R. castellana*, **n. sp.**, and *R. centenaria*, **n. sp.**) and Mérida (*i. e.*, *R. bolivari* and *R. lossadana*, **n. sp.**), in cells R3 (minute or missing), R5 to Cu1; forewing marginal area darker. Hindwing upperside postdiscal-submarginal series of five white, subtriangular dots, from R5 to Cu1, those in R5 and M1 double the length of the others. Genitalia in figure 51. It has a very tiny, vestigial subunci attached to tegumen, valvae with distinctive shape, as they are triangular with a sharp tip, a feature only shared with *Redonda lossadana*, **n. sp.**

Female. Forewing length: 18-20.5 mm, n = unknown (Adams and Bernard, 1981: 368); 1 female in MALUZ: 19 mm. It has already been described and illustrated by Adams and Bernard (1981: 363, 368), although they have misidentified it as *R. empetrus*. An example is illustrated in figure 26.

Holotype. Male, Venezuela, Edo. Mérida, [Páramo de] Mucubají, 3600 m, 11.x.2010, M. Costa *leg.* (in MIZA).

Paratypes. 2 males, same data as holotype (1 genit. prep. ALV554-15) (in MC); 1 male, Venezuela, Edo. Mérida, P. N. Sierra Nevada, Valle del Mucubají (páramo), 08° 45' N, 70° 49' W, alt. 3400 m, 25.i.2000, 11:30-12:30, J. R. Ferrer-Paris *leg.*, 3 males, same locality, 01.i.2002, 11:00-12:00, J. R. Ferrer-Paris, B. Condori *leg.*; 3 males, same locality, 14.ix.2004, 8:40-8:55, J. R. Ferrer-Paris, M. Alarcón *leg.*; 11 males, Venezuela, Edo. Mérida, P. N. Sierra Nevada, Quebrada de Mucubají, 2ª morrena de retroceso, 25.iii.2015,

9:00-9:45, J. R. Ferrer-Paris, L. González *leg.* (in IVIC); 1 male, Venezuela, Estado Mérida, Parque Nacional Sierra Nevada, Laguna Negra, 3550 m, 28.iii.1992, T. Pyrcz *leg.*; 1 male, 1 female, Estado Mérida, Parque Nacional Sierra Nevada, vía Laguna Negra, 3600 m, 20.iv.1992, T. Pyrcz *leg.* (in MALUZ); 1 female [no data] [M. J. Adams and G. I. Bernard, AB1] (in BMNH); 1 male, Venezuela, Edo. Mérida, Zw Laguna Grande und Laguna Negra, 3450 m, 12.ix.1971, H. Huber *leg.* (in ZSBS).

Distribution. 3400-3600 m. *Redonda chiquinquirana*, **n. sp.**, is known from the upper paramos of the Serranía de Santo Domingo, SE of Sierra Nevada de Mérida. It has been observed and captured in the surroundings of the Laguna de Mucubají, Laguna Negra and Laguna Grande. It is altitudinally parapatric with *R. frailejona*, **n. sp.**, which is found in a lower level of these paramos (see below, under that species).

Comments. The flight activity of males of this species seems to be restricted to short periods of the day, and also limited by apparently constant good weather, as it is the case of most species of the genus. Four females (not available for this taxonomic study) were captured, at different days, in Mucubají during a period of ecological studies pursued in 2000. All were sampled from the ground vegetation, where they were resting or basking with open wings. Two of them tried to scape from the net by flying 2 to 3 m, before hiding again inside the very abundant bunches of grass. Some of the females kept in captivity laid several individual, loose eggs. They were spherical, green to yellowish green when fresh, 1.01 ± 0.03 mm in diameter and 0.31 ± 0.03 mg in weight ($N = 7$). Some of them became more yellowish or brown after 1 to 2 weeks but did not hatch. Two larvae of *Redonda chiquinquirana*, **n. sp.**, were found at Mucubají, feeding on *Calamagrostis* sp. and *Agrostis trichodes* (Kunth) Roem. and Schult., both Poaceae. These larvae were resting in the centre of grass bunches. They were kept alive in laboratory boxes and observed resting between the leaves of grass and paper sheets during the day. They were active, feeding at night.

Synoptical description of the larvae: Head capsule 3.30 and 3.33 mm wide, 2.99 and 3.01 mm high respectively. Colour: dark brown with black lines on both sides and the front, no dorsolateral horns. Body dark brown with black stripes on both sides and on

the dorsum, body length when caught: 27,70 mm and 28,30 mm, respectively, both with a pair of tail appendices, 0.1 mm long, not especially coloured.

Etymology. J.R.F.-P. first noticed the occurrence of this new taxon in the Laguna de Mucubají region in 2000, when pursuing field work for his Biology Diplom Thesis on the ecology of the butterflies of the genus *Redonda*. He names it *R. chiquinquirana* after his father, Dr. José Chiquinquirá Ferrer González –“Chinco” Ferrer–, a petroleum engineer, Emeritus Professor of the Faculty of Engineering of La Universidad del Zulia, Venezuela, of which he was its 20th Rector (1984-1988). *Chiquinquirana* is a derivation of the second name of Professor Ferrer, applied to this butterfly species as a token of love and gratitude for his continuous and steady support along the author’s (J.R.F.-P.) life and professional career.

***Redonda frailejona* Ferrer-Paris and Costa, new species**

Figs. 33, 34 (male), 35, 36 (female), 37 (dimorphism), 55 (male genitalia)

urn:lsid:zoobank.org:act:B5DA0BB7-5774-45C1-A3B2-ACC7E2F01917

Male. Forewing length: 24-29.5 mm; mean: 26.04 mm; n = 12. Eyes hairy, black. Palpi twice as long as head, white at base, remaining part with scattered white scales ventrally; black setae predominant over some inserted creamy brown ones. Antennae reaching two fifths of costa. Body black, except for abdomen underside which is brown. Forewing subtriangular, outer margin almost straight. Hindwing oval, elongated beyond the outer borders of forewing, outer edge crenate. Upperside ground colour brownish, notably darker on basal half, especially hindwing; fringes dark, white between veins. Forewing upperside: distal half more or less discretely separated of darker basal half by a sinuous division, dusting of whitish scales along the outer part of this sinuous line, and along subcostal area; light, whitish dusting above distal extreme and center of discal cell; submarginal series of five to six large circular white dots with diffuse borders on cells R4 (tiny, sometimes absent) to Cu1, regularly aligned; costa dark brown. Hindwing upperside with a series of four submarginal >-shaped white dots, from M1 to Cu1, those in M1 and M2 larger and more distinctly shaped; a similar dot in cell R5, but discal in relation to the position of the others. Forewing underside ground colour ochraceous brown, mottled with dark brown on

basal half, more distinctly at base and at the border of discal area, distal half speckled with brown, fine dusting of dark brown and white towards subapical and apical region; white dots as above, but less distinct and less rounded; all veins dark in distal half of wing. Hindwing underside ground colour coffee brown, dusted all over with white, more densely in the outer half of wing, anal area, and costa at inner border of discal region; white dots more distinctly >-shaped, and more or less surrounded by coffee brown, their positions as above; white specks beside each dot, discal to them. Genitalia illustrated in figure 55; vestigial subunci attached to tegumen, saccus tubular, in the shape of a barrel, aedeagus straight in dorsal view.

Female. Forewing length: 13; n = 1. Much smaller and lighter than male. It is so small, and their wings are so narrow, that it has the aspect of a micromoth. Brachypterous and flightless. Palpi twice as long as head, devoid of scales (naked), setae shiny golden at basal third, black in remaining two-thirds of its length. Antennae reaching two thirds of costa. Body black. Forewing slender, narrower than hindwing, spatulate, slightly wider in distal half, outer margin convex, costa convex, but almost parallel to anal margin, veins much closer to each other than in males; hindwing slender and narrow, but broader than forewing, spatulate, outer margin rounded, not scalloped. Fringes with tufts of long scales at the end of the veins. Upperside ground colour golden white, base of wings, forewing costa (and basal half of costal region), and hindwing anal region very dark brown, almost black. Hindwing bearing a lightly marked series of five >-shaped, submarginal white spots (R5 to Cu1), M3 and Cu1 larger than the others. Forewing underside ground colour yellow; all mottled with dark chocolate brown, especially along coastal border, centre of postdiscal area, discal area, and base; series of five tiny, postdiscal, white dots. Hindwing underside groundcolour coffee brown, speckled and mottled with white, especially on basal and distal thirds, discal area darker; series of six submarginal white dots from R5 to Cu2, those in M1, M2, M3 and Cu1 larger and with characteristic >-shape, all more or less surrounded by dark coffee brown.

Holotype. Male, Venezuela, Edo. Mérida, Sto. Domingo – Apartaderos, 3000 m, 31.iii.2012, M. Costa *leg.* (in MIZA).



27



28



29



30

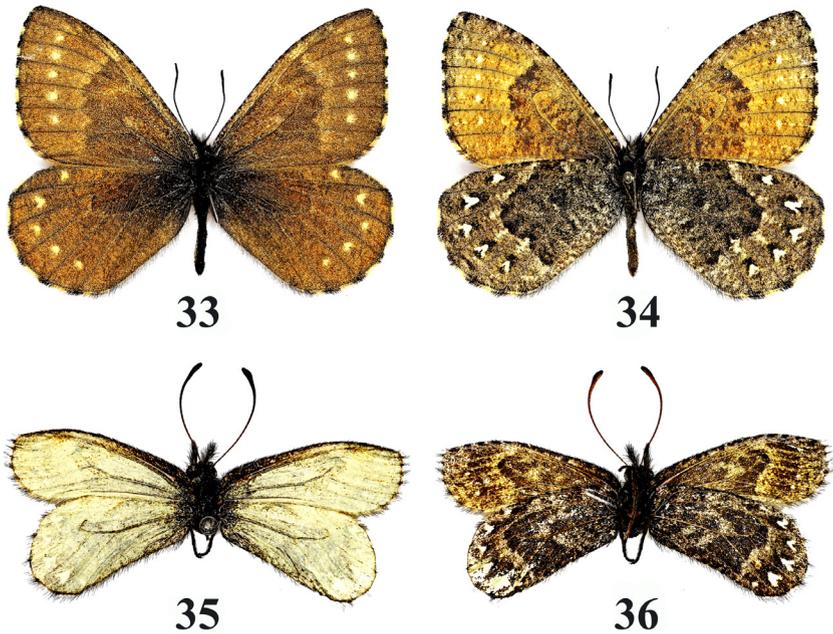


31



32

Figs. 27-32. Morphological (size and wing pattern) variability among adult males of *Redonda empetrus* (Thieme, 1905) from the Serranía de La Culata (SC); **27**. Large individual (FWL: 30 mm) with typical wing colour pattern as described and illustrated by Thieme, from the páramo de Los Conejos, upper río Albarregas, SE-SC, upperside; **28**. *Ibid.*, underside; **29**. Darker, large size form (FWL: 29.5 mm), with reduced hindwing postdiscal ocellar elements, from the upper río Mucujún, NW-SC, upperside; **30**. *Ibid.*, underside; **31**. Smaller individual (FWL: 25 mm) with more marked bluish grey on the upperside of FW discal cell, from the upper río Mucujún, NW-SC, same locality as 29-30; **32**. *Ibid.*, underside.



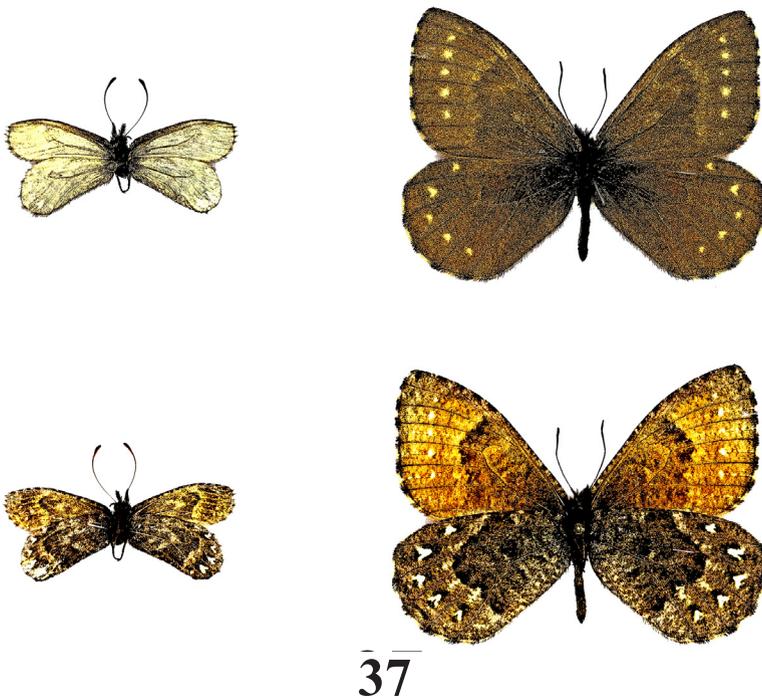
Figs. 33-36. Adults of *Redonda frailejona* Ferrer-Paris and Costa, *n. sp.*; 33. Male holotype (Santo Domingo - Apartaderos, 3000 m), upperside; 34. *Ibid.*, underside; 35. Female paratype (Hotel Los Frailes), upperside; 36. *Ibid.*, underside.

Paratypes. 1 male, Venezuela, Edo. Mérida, valle de Santo Domingo, cerca Hotel Los Frailes, 3000 m, 31.iii.2012, M. Costa *leg.* (genit. prep. ALV552-15); 4 males, Venezuela, Edo. Mérida, Los Frailes, 3100 m, 12.iv.2004, M. Costa; 1 female, same data, 3050 m (in MC); 1 male, Venezuela, Edo. Mérida, Hotel Los Frailes, 3000 m, 25.iii.2015, 10:30-11:35, C. Lozano *leg.*; 5 males, Venezuela, Edo. Mérida, Laguna Victoria, 3000-3050 m, C. Lozano, L. Morán *leg.* (in IVIC); 7 males, Venezuela, Mérida, Apartaderos-Sto. Domingo, km 12.5, ca. 3100-3300 m, 26.ix.1997, A. Neild (in AFN) [not measured]; 19 males, Edo. Mérida, oberes Domingo tal, 3070 m, 5.ix.1971, H. Huber; 2 males, same data, 3050 m [not measured] (in ZSBS).

Distribution. 3000-3300 m. Known only from a reduced sector of the Serranía de Santo Domingo (southern slopes). It is the lower, altitudinally parapatric species of *Redonda chiquinquirana*, *n. sp.*, which flies in an upper level of those paramos.

Comments. There is very little bionomic information available of this species, apart from what is known of its behaviour. Males are strong flyers and the solitary female known in not capable of flight. They represent the most outstanding case of sexual dimorphism within the genus *Redonda* (Fig. 37).

Etymology. *Frailejona*, is a feminine derivation of “frailejón”, the vernacular name applied in Venezuela, Colombia and Ecuador to numerous species of asteraceous plants of the genus *Espeletia* (and some related genera) which grow exclusively in the paramo, and are characteristic elements of its vegetation adapted to high altitude North Andean environments. They have long, wooly, succulent leaves that grow in a rosette-like pattern. Their flowers are bright yellow, and are very attractive to the paramo butterflies and other pollinator insects. “Frailejón” is possibly an archaic Castillian



37

Fig. 37. Proportional images, showing the most marked sexual dimorphism among representatives of the genus *Redonda*: *R. frailejona* Ferrer-Paris and Costa, **n. sp.** (left: female paratype, right: male holotype).

word equivalent to the most modern “fraile” (friar). The application of this name to *Espeletia* plants may have derived from the appearance of some columnar forms, that grow as tall as a person, looking like static friars in the misty landscape of the paramo. Most specimens known of *R. frailejona*, **n. sp.**, were observed and captured in the surrounding of the Hotel Los Frailes (The Friars), a well known touristic destination on the road between Santo Domingo and the Mucubají Lagoon (Mérida state), established in an emblematic colonial building that once was the dwelling for some hermits, friars of a religious, Catholic Order. Thus, the name is both related to the frailejón plants and to the Hotel Los Frailes.

***Redonda lathraia* Viloría and Camacho, new species**

Figs. 38, 39 (male), 56 (male genitalia)

urn:lsid:zoobank.org:act:F5C1ABEA-20EC-448A-A473-2EEC06B92D22

[*Redonda bordoni* Viloría and Pyrcz, 2003: 21-24, e-appendix A: pp. [1-2] (misidentification, in part)].

[*Redonda kenke* Pyrcz and Viloría] *nom. nud.*; Pyrcz, 2007a: 40; 2007b: 17, 18, 19.

[*Redonda veilloni* Pyrcz and Viloría] *nom. nud.*; Pyrcz, 2010a: 36 (fig. 17B, antennal club), 181 (fig. 132E, male; F, female), 182, 184 (fig. 136, distribution), 244.

[*Redonda* n. sp. Pyrcz and Viloría]; Pyrcz, 2010b: 265.

[*Redonda* sp.]; Pyrcz, 2010b: 266 (figs. 1M, male, 1N, female), 267, 268 (fig. 2, distribution).

Male. Forewing length: 27-28 mm; mean: 27.5; n = 2. Eyes hairy, black. Palpi twice as long as head, brown, without scales,



Figs. 38-39. Adult male holotype of *Redonda lathraia* Viloría and Camacho, **n. sp.** (Páramo del Batallón); **38.** Upperside; **39.** Underside.

setae dark brown and creamy brown alternate, some silvery setae on ventral surface of basal segment. Antennae reaching two fifths of costa. Body dark brown above, ventrally brown. Forewing triangular, apex acute, outer margin slightly convex. Hindwing oval not exceeding the extent of forewing (unlike *R. bordoni*, *R. empetrus* and *R. frailejona*, **n. sp.**), outer margin slightly scalloped. Upperside ground colour chestnut, finely dusted with brown scales all over, a bit more dense above the distal extremity of forewing discal cell; fringes dark chocolate brown; vestigial submarginal white dots on forewing (only in paratype). Underside colour brown, finely dusted with ochraceous yellow, more on anterior half of forewing. Apex and anterior half of marginal region of forewing dusted with chocolate brown; same colour softly speckled on the limit of discal and postdiscal regions; a series of five submarginal white dots, small and slightly oval, from cell R5 to Cu1. Hindwing underside with chocolate brown along outer margin, a submarginal undulated, fine line of the same colour, running parallel to margin; basal half to two-thirds of hindwing heavily dusted of whitish, especially near veins and along cell Cu2, which are dark brown; dark chocolate brown mottled inside discal cell, also running parallel to both sides of whitish line in cell Cu2, and forming >-shaped discal lines pointing basad in cells that also bear submarginal fusiform cream-white stripe-dots: R5, M1, M2, M3, Cu1. Genitalia illustrated in figure 56. Uncus stout, not well differentiated from tegumen, valvae with rounded tip, covered with very short setae, aedeagus relatively small.

Female. Unavailable for this study. Illustrated by Pycrz 2010a (pp.181, fig. 132F) and 2010b (pp. 266, fig. 1N). The aforementioned figures show that female is slightly smaller and lighter in colour than male, but generally similar in colour pattern.

Holotype. Male, Venezuela: [Estado] Táchira, P[á]ra]mo El Batallón, entre Laguna El Cenegón – Laguna Grande, 3200-3400 m; 28.ii.1994, Á. L. Viloria, M. García and J. Camacho *leg.* (in MALUZ) [previously misidentified as *Redonda bordoni* Viloria and Pycrz, and designated as paratype of that species].

Paratype. 1 male, same data as holotype (genit. prep. ALV546-15) (in MALUZ) [previously misidentified as *Redonda bordoni*, and designated as paratype of that species].

Distribution. 3200-3400 m. Apparently, an endemic to the lower level of the open páramos of the La Negra-El Batallón range (southwestern Cordillera de Mérida), where it is possibly an altitudinal parapatric, and certainly, partly sympatric with *Redonda bordoni* (3000-3800 m). Most of the area shared by these two endemic taxa is protected by a National Park (Parque Nacional Juan Peñaloza). The paramos occupied by *R. bordoni* and *R. lathraia* seem to be pristine in a large extension, especially towards the eastern El Batallón region (in Táchira State), which is wetter than the Páramo de La Negra (in Mérida State), but we noticed some agricultural activities and cattle grazing entering the boundary zone of the National Park in the páramo. This is increasingly depauperating the original paramo biome in the region of the Pico El Púlpito (near Sumusica).

Vegetation in the Páramo El Batallón is dominated by a dense cover of grasses such as *Cortaderia* spp. and *Calamagrostis* spp. (Poaceae) (“pajonal and pastizal paramero”, *sensu* Bono 1996). The “frail-ejones” (*Ruilopezia jahonii* (Standl.), *R. atropurpurea* (A. C. Smith), Asteraceae) are outstanding floristic elements all over this páramo, and rosettes of these plants are profusely scattered from the very humid intermontane valleys (where glacial lagoons often occur) to dry and rocky cliffs on the higher peaks. Nearly 20 lagoons have been recorded in the Park, but there are many other small ones or even swampy areas that seem to be remnants of recent glacial pools. The vegetation is noticeably more diverse in the narrow humid valleys, especially around lagoons or flooded areas, where bamboos (*Swal-lenochloa angustifolia* (Soderstrom and Calderón), *S. spencei* (Ernst), Poaceae) occasionally occur. There is also a high number of flowering plants in these places (see Vareschi 1970 and Bono 1996).

Comments. We found *Redonda lathraia* occasionally entering open grassland areas above the treeline, between 3200-3400. However, according to Pyrcz (2010b: 265) it is parapatric to *R. bordoni*, occupying a lower elevation level of the paramo. Perhaps, its true elevation preference may not be much higher than 3100 m. Higher up, there is a total dominance of *R. bordoni* (up to Pico El Púlpito, *ca.* 3950 m). We found only two males among very abundant individuals of *R. bordoni*, during the dry season, in February 1994. Even at that time this páramo was apparently more windy, humid and cloudy than the neighbouring ones of the Cordillera de Mérida. The behaviour of males of both species is very similar. They are fast-

flying insects that drift with the wind, but are also capable of flying strongly against it. Like all species of *Redonda*, and especially their males, this one avoid attacks by stalling in flight, thus allowing the wind to change their flight vector very suddenly.

Etymology. Two males of this butterfly species had been collected in the páramo del Batallón in 1994. They were misidentified as dark representatives of *Redonda bordoni* (Viloria et al. 2003), and so, erroneously included among its type series. As a result of such a confusion we decided to name this taxon with the epithet *lathraia*, derived from *λαθραίος*, the greek adjective for clandestine, smuggled, or surreptitious.

***Redonda leukasmena* Viloria and Camacho, new species**

Figs. 7 (female wing venation), 40, 41 (male), 42, 43 (female), 57 (male genitalia)

urn:lsid:zoobank.org:act:41B76B14-BD5C-4885-B795-159917FD309B

[*Redonda* sp. nov. 2]; Viloria, 2000: 270; Ferrer-Paris, 2000: 27 (fig. 3.1, distribution), 29 (tbl. 3.1), 36, 37 (fig. 3.5), 38, 69, 91-92 (tbl. C.7); Ferrer-Paris and Viloria, [2004]: 628 (fig. 1), 629 (tbl. 1), 630 (fig. 3).

[*Redonda* n. sp.]; Viloria and Pyrcz, 2001: 15.

[*Redonda* sp. nov.]; Viloria et al., 2003: 22 (fig. 1e, male, female), 23 (fig. 3, wing area).

[*Redonda* [n. sp.] Viloria and Pyrcz, MS]; Lamas et al., 2004: 215.

[*Redonda* sp.]; Viloria, 2005: 459.

[*Redonda camachoi* Viloria and Pyrcz] *nom. nud.*; Viloria, 1998: 319; Ferrer-Paris, 2000: 96 (tbl. C.9); Pyrcz, 2007a: 40, 41; 2007b: 17, 18, 19; 2010a: 38 (fig. 22D), 45 (fig. 35A, female venation), 87 (fig. 82, cladogram), 111, 180 (fig. 131, wing area), 181 (figs. 132G, male; H, female; 134A, hábitat), 182,183, 184 (fig. 136, distribution), 244; 2010b: 265, 266 (figs. 1O, male, 1P, female), 267, 268 (fig. 2, distribution), 270 (fig. 4A, habitat), 273.

Male. Forewing length: 28-33 mm; mean: 30.13 mm; n = 27. Eyes hairy, reddish brown, tiny black hairs. Palpi twice as long as head, dark coffee brown, devoid of scales, with long black setae, some sparse bright brown setae on dorsum. Antennae two fifths length of costa, 37-38 segments; shaft orange-brown, with some sparse hairs and light brown scales; club broadened and concave (but less so than *R. bordoni*), keel running along the concavity of the club. Body dark coffee brown, with exception of ventral surface of abdomen, which is light creamy-brown; ventral surface of body very hairy (less so than *R. bordoni*). Forewing triangular, tornus obtuse;

hindwing oval, outer margin very slightly scalloped. Groundcolour of dorsal surface of wings dark coffee brown, darker on discal area of both wings; basal third of wings with greenish sheen; forewing slightly hairy at base, showing sparse white scales along costal margin, and much more distinct on outer margin, between veins; polygonal subdiscal silvery white patch within discal cell, distal edge of which straight and well defined at second third of cell, basal edge rather diffuse, following vein Cu2; hindwing lacking additional markings except darker postdiscal line and some white scales flanking margin in cells M1 and M3. Ground colour of forewing ventral surface chocolate brown, becoming coffee brown towards costal margin and apex; speckling of dark coffee brown over entire surface of wing, denser in apical region and discal area, which appears well limited at its edges; white scales dusted along costal margin and apical region; two postdiscal white dots (one basal, the other distal, separated by *ca.* 2 mm) in R5; another dot in M2, parallel to that distal in R5; all of them irregularly surrounded by dark brown. Groundcolour of hindwing ventral surface chocolate brown, entirely speckled by black, notably denser on basal half of wing and in submarginal region of each cell; series of five postdiscal creamy-yellow >-shaped spots, in cells R5 to Cu1, all pointing basad and surrounded by irregular "shadows" of dark coffee-brown; heavy dusting of white scales on inner and outer edges of discal area, as well as on distal margin and around veins; distal margin flanked with white between the extremities of veins. Genitalia illustrated in figure 57, shows a long and very stout uncus, lack of subunci; valvae broad, with rounded tips, saccus wide but small.

Female. Forewing length: 26.5-29 mm; mean: 27.87 mm; n = 4. It differs from male by its slightly smaller size and narrower wings. More pointed forewing apex and tornus. Antennae 42 segments. Palpi devoid of scales (only very few ventral white scales at base), brown, setae brown and coffee brown, less abundant than in male. Dorsal surface of wings less dark and brownish, forewing showing postdiscal series of 4-5 ochraceous, minute dots, in cells R5 to Cu1 (sometimes missing in M2). Groundcolour of forewing ventral surface brown, light brown at apex; postdiscal series of five white dots in cells R5 to Cu1. Groundcolour of hindwing ventral surface not chocolate, but pale brown, which gives higher colour contrast to general design.

Holotype. Male, Venezuela: Estado Lara, Municipio Morán, Páramo de La Rosa [*sic*], 3000 m, 20-viii-1991, J. Camacho *leg.* (in MALUZ).

Paratypes. 6 males, 2 females (1 wing prep. ALVSN2-1997), Venezuela: Estado Lara, Parque Nacional Dinira, Páramo La Rosa [*sic*], 2800 m; 16-i-1994; Á. [L.] Viloria and J. Camacho *leg.*; 18 males (1 in BMNH, 1 in MZUJ), 2 females, Estado Lara, Parque Nacional Dinira, Páramo Cendé, 3100 m; 8-viii-1995, M. García *leg.* (in MALUZ); 2 males, Estados Lara-Trujillo, Páramo El Jabón, 3000 m, 25-xii-1989, CEUM *leg.* (in MIZA).

Distribution. 3000-3100 m. High and humid paramos of the Cendé Region, easternmost extreme of the Venezuelan Andes, between the States of Trujillo and Lara. This geographic unit includes the highlands or paramos of Agua de Obispos, Las Rosas, Jabón, Guache, Naríz, Los Nepes, Cendé, and El Vigía, among others (Briceño-Valero 1920). Monasterio (1980) has defined the main vegetation there as "rosetal de *Espeletia jabonensis*" (Asteraceae) because of the remarkable dominance of this endemic plant, but *R. leukasmena* is better associated with the equally common "pastizal de *Swallenochloa-E. jabonensis*" (Poaceae-Asteraceae). These páramos are highly influenced by the atmospheric conditions of the Lake Maracaibo basin, which results in two highly pronounced wet seasons (Monasterio and Reyes 1980). Most of the paramo area is protected within the Dinira National Park.

Comments. This species has never been found abundant. Males and females show similar behaviour, and it is almost impossible to sex individuals in flight, because they share similar wing patterns and size. Both sexes fly energetically, 1-2 m above the thick bambusoid grasses (mainly *Swallenochloa angustifolia* (Soderstrom and Calderón) and *Rhipidocladum geminatum* (McClure) (Poaceae), Viloria 1994) that grow in the Cendé paramos. We failed to find *R. leukasmena* in the dry, low Páramo de Los Nepes (2400-2850 m), where bamboos seem to be partly replaced by tussock grasses such as *Agrostis* and *Calamagrostis* (Poaceae). The first female collected laid one egg immediately upon capture. It was spherical and pale green, with no evidence of any adhesive on its surface.

Like most butterflies found at very high elevations in the northern Andes, *R. leukasmena* only flies in sunshine and is very hard

to see on the wing in either cloudy or foggy conditions. Then, the adults tend to hide in the bamboo grasses, preferring the most inaccessible basal stems, where they are also thought to spend the night. Nothing is known about its biology. However, from observations of the biotopes occupied by the adults, we infer that their larvae feed on bamboos throughout the paramo. *Diaphanos fuscus* Viloría and *Steromapedaliodes schuberti* Viloría and Pycrz are two more satyrines of the paramos of the Cendé region. *S. schuberti* shows a similar wing pattern and behaviour, which may suggest a possible mimetic relationship with *Redonda leukasmena*, but they have not been found flying together (see comments in Viloría and Pycrz 2001).

Etymology. *Redonda leukasmena* owes its specific name to the conspicuous white patches on the dorsal surface of its forewings, which look like bleached portions of the very dark background. Therefore, we designate this new species with the greek word *λευκασμένα*, which literally means bleached.

***Redonda lossadana* Ferrer-Paris, new species**

Figs. 44, 45 (male), 58 (male genitalia)

urn:lsid:zoobank.org:act:23E43E42-CA82-4FC3-A37B-2EB9677F684B

[*Redonda empetrus* ssp. nov. 1; Viloría, 2000: 270 (in part misidentification of *R. centenaria centenaria*, n. sp.)]

Redonda empetrus decenia Pycrz and Viloría, *nom. nud.*; Pycrz, 2010a: 83 (fig. 79A), 182, 184 (fig. 136, distribution), 244.

[*Redonda empetrus* ssp. 3; Pycrz, 2010b: 266 (figs. 1E male, 1F female), 268 (fig. 2), 270 (fig. 5A male) (misidentification)]

Male. Forewing length: 24-28 mm; mean: 25.87 mm; n = 4. Eyes hairy, dark coffee brown. Palpi twice the length of costa, white, dusted with black laterally, setae coffee brown and light brown alternate more or less in equal proportion. Antennae reaching two fifths of costa. Body dorsally dark brown, ventrally dusted with white scales, abdomen brown. Forewing subtriangular, apex acute, outer margin convex. Hindwing oval, about same extent of forewing, outer margin softly scalloped. Upperside ground colour dark brown, finely dusted with ochraceous scales. Forewing discal area darker (less ochraceous scales), but also limited on both sides by more dense light dusting, whitish scaling above veins closing distal extremity of discal cell; a series of tiny, almost vestigial, white, sub-marginal dots, from R5 to Cu1; fringes dark, white between veins.



40



41



42

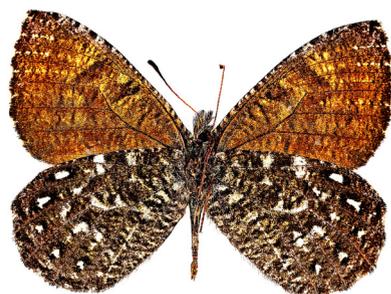


43

Figs. 40-43. Adults of *Redonda leukasmena* Viloria and Camacho, *n. sp.* (Páramo de Las Rosas); 40. Male holotype, upperside; 41. *Ibid.*, underside; 42. Female paratype, upperside; 43. *Ibid.*, underside.



44



45

Figs. 44-45. Adult male holotype of *Redonda lossadana* Ferrer-Paris, *n. sp.* (Páramo de Tuñame); 44. Upperside; 45. Underside.

Hindwing unicoloured; white marginal dots in cell R5 (diffuse), M1, M3 (diffuse). Forewing underside ground colour hazelnut, generally speckled with chocolate brown, more densely at both sides of discal area; yellow scales dusted irregularly all over, mottled along costal margin and in subapical region, just beyond the limit of discal dark area; dense yellow and dark brown dusting inside discal cell; tiny submarginal white dots as above, but continued with a series of linear dots towards the outer edge of wing. Hindwing underside ground colour brown, heavily mottled with dark coffee brown and white; a series of white elongated dots (sometimes >-shaped), submarginal, from R5 to Cu2, those in R5 and M1 twice the length of the others, all surrounded by dark brown; white mottling especially heavy on discal area, which has a lichenous aspect; a white, fine line along the middle of cell Cu2; marginal area darker. Genitalia as illustrated in figure 58, valvae with sharp tips.

Female. Unavailable for this study. Illustrated by Pyrcz (2010b: 266, fig. 1F). Similar in general appearance to the female of *R. castellana*, **n. sp.**, but slightly smaller and with broader and less pointed forewing.

Holotype. Male, Venezuela, [Edo.] Trujillo, Páramo de Tuñame, vía Las Mesitas, 3100 m, 10.ix.1991, Á. L. Vilorio, R. Calchi leg. (in MALUZ).

Paratypes. 2 males, same data as holotype (2 genit. prep. ALV545-15, ALV547-15) (in MALUZ); 1 male, Venezuela, Estado Trujillo, Páramo de Tuñame, 3200 m, 16.ii.2010, M. Costa leg. (in MC)

Distribution. 3200 m. Restricted to the paramo area of Tuñame and Guirigay (border of Trujillo and Mérida states), SW of the Niquitao massif.

Comments. This butterfly has been found scarce, and was collected by two of the authors (Á. L. V. and M. C.) only once each (September 1991 and February 2010, respectively). It was not found in the same places during a visit to the area in August 2003.

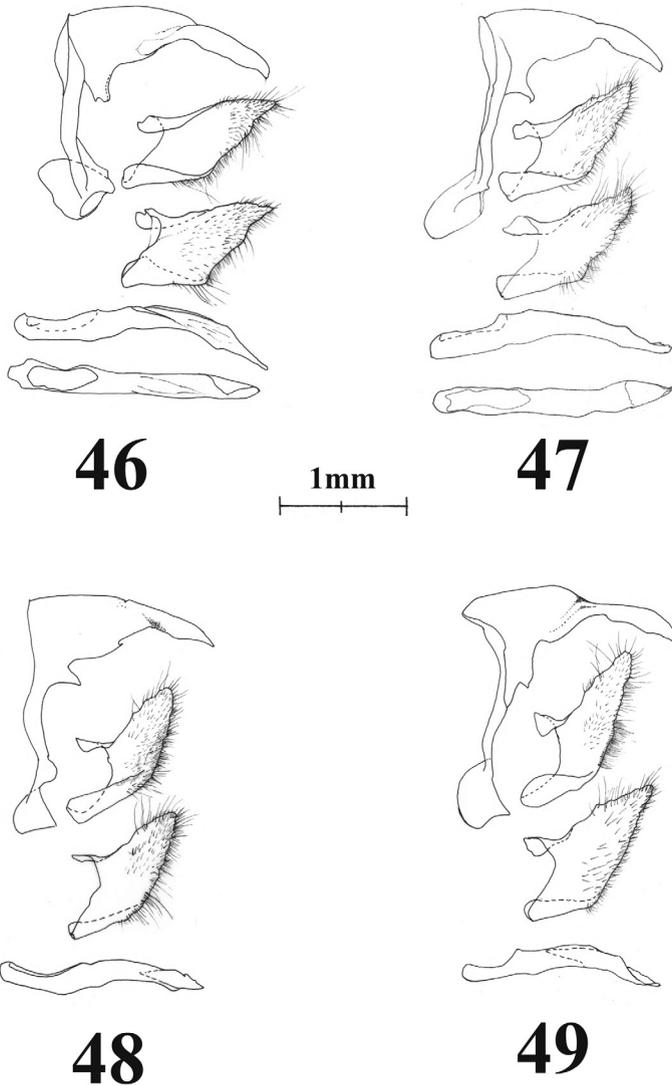
Etymology. The University of Zulia in Maracaibo operated as a novel institution between 1891 and 1904, the year that Cipriano Castro, President of Venezuela decreed its closure on the ground of certain academic and administrative recommendations of Eduardo Blanco, Ministry of Public Instruction. It was formally re-

opened only in August 1946 under the national administration of a Revolutionary Joint of Government. Dr. Jesús Enrique Lossada (1892-1948) was appointed as the new Rector of the university. Lossada was a professional lawyer and educator from Maracaibo. He was in fact, a polymath, who apart from have taken several government responsibilities, played music, wrote narrative, poems and theatrical plays, among others heterodox activities. His role in the reinstatement, consolidation and development of the university, was a renowned example of academicism, austerity and honesty. He is well remembered as a scholar; a respectable figure, who led a group of colleagues and disciples to establish a modern university. His untimely death came not long after he was removed from the rectorship. The name *lossadana* is a posthumous homage to this most noble man, Jesús Enrique Lossada.

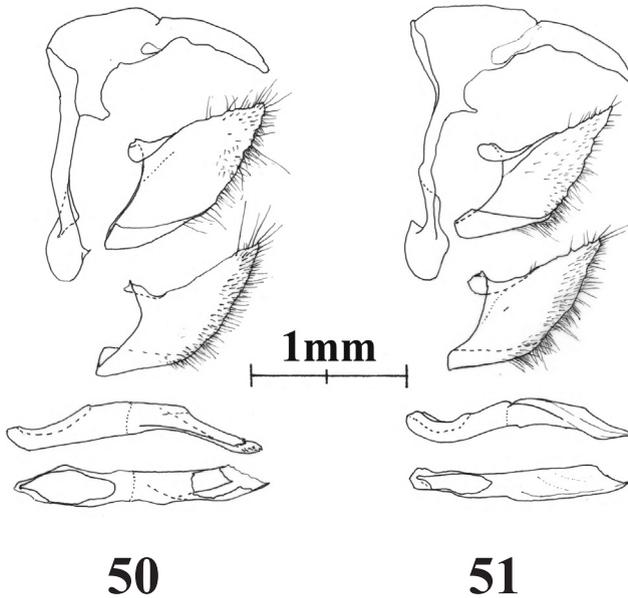
CONSIDERATIONS ON THE POSSIBLE ORIGINS OF REDONDA AND CONCLUSIONS

Preliminary phylogenetic hypotheses suggest that the genus *Redonda* is monophyletic (Viloria, 1997, 1998, 2003, 2007, Ferrer-Paris 2000, Viloria *et al.*, 2003, 2007, Ferrer-Paris and Viloria 2004, Pycz 2007a, 2007b, 2010a, 2010b, Posso Duque *et al.* 2010). Results of any robust cladistic analysis of its species should be correlated with vicariant events in which the current páramo units sequentially fragmented, and alternatively connected, during the cycles of the Mérida Glaciation (geologically documented for each range in Schubert 1970, 1972, 1974, 1975, 1982, Schubert and Valastro 1974, and Schubert and Vivas 1993).

The glaciers in the Venezuelan Andes, and the consequent elevation of the páramo biome, may have retreated gradually and simultaneously at the end of the Mérida Glaciation (Salgado-Labouriau *et al.* 1988, Schubert and Vivas 1993). It is plausible therefore that, the narrower the geographic connection of the current páramo units during the glacial maximum, the sooner a disjunction would occur as glacial conditions ended. If so, we can predict a most recent sequential splitting of the páramo units: (Cendé (Batallón-La Negra (Niquitao + Mérida + La Culata))). Any attempt to unveil the phylogenetic history of *Redonda* needs to take the evidence for these events into account.

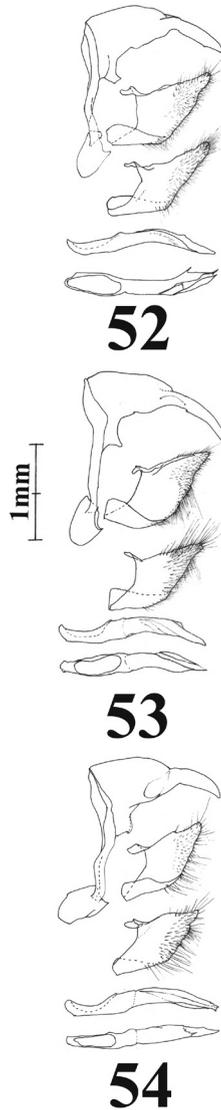


Figs. 46-49. Lateral views of the male genitalia of three species of *Redonda*. Valvae and aedeagus have been detached from natural positions. Valvae: upper, inner side; lower, outer side. Aedeagus: upper, lateral view; lower, dorsal view; **46.** *R. bolivari* Adams and Bernard, **n. stat.**, Loma Redonda; **47.** Same species, Páramo del Batallón; **48.** *R. bordoni* Viloría and Pýrcz, Páramo del Batallón (paratype); **49.** *R. castellana* Viloría and Camacho, **n. sp.**, Páramo de Ortiz (paratype).

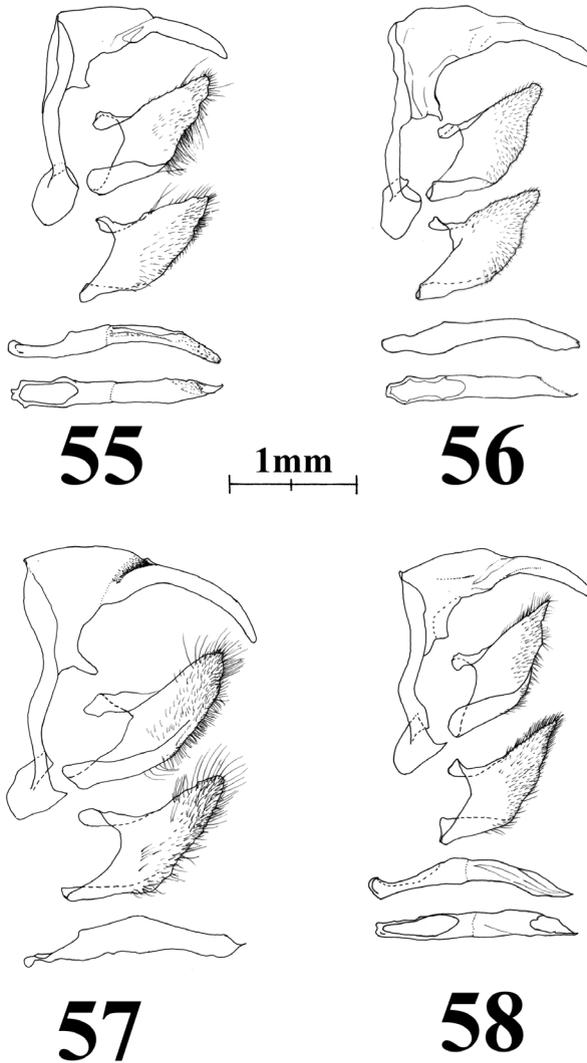


Figs. 50-51. Lateral views of the male genitalia of two species of *Redonda*. Valvae and aedeagus have been detached from natural positions. Valvae: upper, inner side; lower, outer side. Aedeagus: upper, lateral view; lower, dorsal view; **50.** *R. centenaria* Viloria and Camacho, **n. sp.**, Páramo de Cabimbú (holotype); **51.** *R. chiquinquirana* Ferrer-Paris, **n. sp.**, Páramo de Mucubají (paratype).

The problem of the origins of the high montane representatives of the satyrine subtribe Pronophilina has been raised in previous works (*i. e.*, Brown 1942, Adams 1977, 1985, Adams and Bernard 1981, Descimon 1986, Shapiro 1992, Viloria 1998, 2007, Pycz 2010a, 2010b). Adams and Bernard (1981) considered that the oreal genera *Dangond* and *Redonda* were relics “which have their origins in an early south-temperate pronophilina fauna”. More recent morphological investigations (Viloria 1998, 2003, 2007) and DNA phylogenies (Peña 2009, Peña *et al.* 2011) have shown that the majority of genera of the Satyrinae in the austral region of South America might not belong to the same group of Pronophilina than those of the Tropical Andes. There have not been comparative studies on the tribe to determine what can be a “relic” or an “early” genus, but from field observations on the flight behaviour of the butterflies in question, we hypothesize that dispersal within these pronophilines



Figs. 52-54. Lateral views of the male genitalia of *Redonda empetrus* (Thieme). Valvae and aedeagus have been detached from natural positions. Valvae: upper, inner side; lower, outer side. Aedeagus: upper, lateral view; lower, dorsal view; **52**. Typical individual from the Páramo de Los Conejos (type locality, herein established); **53**. Large, dark form individual from the upper Río Mucujún; **54**. Small, grey-marked individual from same locality and date.



Figs. 55-58. Lateral views of the male genitalia of four species of *Redonda*. Valvae and aedeagus have been detached from natural positions. Valvae: upper, inner side; lower, outer side. Aedeagus: upper, lateral view; lower, dorsal view; 55. *R. frailejona* Ferrer-Paris and Costa, **n. sp.**, Páramo de Santo Domingo (paratype); 56. *R. lathraia* Viloria and Camacho, **n. sp.**, Páramo del Batallón (paratype); 57. *R. leukasmena* Viloria and Camacho, **n. sp.**, Páramo de Las Rosas (paratype); 58. *R. lossadana* Ferrer-Paris, **n. sp.**, Páramo de Tuñame (paratype).

must be exceedingly slow. Pronophiline butterflies were most probably lowland forest dwellers in the past, and continuous forests in large portions of the South American continent may have favoured a wide distribution. However, extant genera show very localised distribution patterns, which also suggests local origins and local speciation processes that can be better understood by correlation of phylogenies with the geological history of each area. As the open habitats of the high Andes are certainly one of the most recently established biomes in South America, we consider a local, relatively recent origin for their faunas far more likely than dispersal of an ancient fauna, and thus explain the occurrence of highly specialised pronophiline butterflies in the oréal zone of the northernmost extremity of the Andes.

This assertion is reinforced by considering also the results of Vuilleumier and Ewert (1978) and Vuilleumier (1981), who found very little evidence for an austral origin of the high Andean birds in Venezuela. The conclusion is also consistent with the ideas of Kroonenberg, Bakker and van der Wiel (1990), who suggested that the recent origin of the Colombian and Venezuelan high Andes leaves no temporal or spatial possibility for austral-antarctic biotic colonization, as had been previously conceived. Additionally, the mountains considered in this study have always been separate from the Colombian Eastern Cordillera (the only link with the main Andean chain) by a major orographical barrier, the so called "Táchira Depression"* (Vuilleumier 1984). To explain this scenario, it is necessary to review the local geological history.

Vigorous mountain uplift to the páramo zones above 3000 m in the non-volcanic, extreme northern end of the Andes (Sierra Nevada de Santa Marta, Sierra de Perijá, Cordillera de Mérida, Seranía del Tamá and Sierra Nevada del Cocuy) occurred less than 6 million years ago, in the Late Miocene, long after the establishment of high elevation regions in the rest of the Andean chain south of the Santander Massif (Kroonenberg *et al.* 1990). An open

* A geographical depression is defined as a portion of land lying below the sea level. Although largely accepted in Venezuelan toponymy, the term "Táchira depression" should not strictly be used in this case, because it refers to the wide and low intermontane valley of the rivers Uribante and Táchira.

type of vegetation (preparamo) is thought to have occurred locally on hilltops before the northern Andes rose to its present level (van der Hammen and Cleef, 1986). The formation of preparamo areas would have been more influenced by local edaphic and climatical conditions (like the savannahs of the Pantepui), than altitudinal alone, but the theoretical possibility of an early open vegetation at increasingly higher elevations during the Late Tertiary uplift should be considered (“embryonic paramillos” *sensu* van der Hammen and Cleef). The possible precursor of the paramo vegetation may have been present in such open areas and developed from floristic elements of these “paramillos” in the Early Pliocene, when the tree line was about 2500 m. The upper forest-páramo belts started to change position when more land was available for the establishment of true paramo vegetation, and subsequently with the climatic fluctuations of the Quaternary.

Since there are no true pronophiline butterflies inhabiting open Andean vegetation habitats at low or middle elevations (they occur only in the cloud forests where their foodplant *Chusquea* is abundant and diverse; see Clark 1995), we assume that the few existing pronophiline butterflies of the paramos (and montane savannah) are exceptions within the tribe. These taxa may have a relatively recent origin, more or less contemporary with the new high altitude habitats to which they are exclusively adapted. Therefore, the north Andean species belonging to endemic genera of the high elevations *Paramo*, *Dangond*, *Redonda*, and *Steromapedaliodes* are here considered very recently evolved animals whose precursors conquered the protoparamo from the upper cloud forests, most probably at the end of the Miocene. Other satyrine genera inhabiting the high paramos of the northern Andes (*Diaphanos* Adams and Bernard, *Idioneurula* Strand, and *Sabatoga* Staudinger) are morphologically, ethologically and ecologically different from what we consider true pronophilines, and their must be set apart.

By the time the Cordillera de Mérida had reached its present elevation, the genus *Redonda* could already have been differentiated from the cloud forest fauna. The former occurrence of a continuous paramo along the different units of the Cordillera de Mérida (north-east of the “Táchira Depression”, from El Batallón to the Cendé) suggests that a single species of *Redonda* inhabited the páramo at least during the first fragmentation to form the current units dur-

ing the last Quaternary glacial period (dated 11,100 years ago; Rull 1996). Thus, the ten species of *Redonda* are probably geographic vicariants, forming a cohesive monophyletic clade.

ACKNOWLEDGEMENTS

This long term research has been undertaken with support of the División de Investigación and the Decanato de la Facultad Experimental de Ciencias, La Universidad del Zulia, as well as from MALUZ through the efforts of M. Quirós. Financial support in different stages came from Fundayacucho, CONICIT (Venezuela), British Council, BMNH, King's College London, The Linnean Society (UK); Funding from IVIC was instrumental between 2000 and 2015. Thanks to those who contributed in field work and research, M. Alarcón, T. R. Barros, P. Boyer, R. Calchi, V. Carrizo, B. Condori Ramos, E. Contreras, L. Morán, M. Duarte, G. Fagua, F. García, M. García, L. González, M. González, M. Higuera, N. León (†), C. Lozano, J. Moscó (†), E. Moscó, P. Mora, N. Pérez, A.Y. Sánchez-Mercado, J. Suárez, R. Piña, T. W. Pyrcz, W. Rojas, J. Wojtusiak (†), L. Zambrano; and the officers of INPARQUES in Lara, Mérida, and Táchira for providing us with permits for scientific research in National Parks. H. Suárez (IVIC) took the photographs of the type specimens and set the plates that illustrate this work. Our gratitude to those who gave support during our work in public and private collections and other institutions; AFN: Andrew Neild; BMNH: P. R. Ackery, B. and L. d'Abreu, J. Harvey, B. Huertas; G. Martin; L. Mitchell, J. Reynolds, J. T. Tennent; R. I. Vane-Wright; IVIC: R. Chiussi, X. Jayaro, M. Losada, A. Mata, J. Mavarez, R. Miller, J. Nassar, D. Posso-Duque, B. Quiroz, C. Ríos-Málaver, G. Rodríguez (†), J. P. Rodríguez, W. Rojas, A. Ruiz, C. Schubert (†), H. Suárez, Y. Velásquez, E. Wagner; JFLC: J.-F. LeCrom and C. LeCrom; MALUZ: R. Carvajal, D. Chirinos, I. Dorado, F. Geraud, E. Inciarte, M. Quirós, E. Rubio, MBLUZ: R. J. Acosta (†), V. H. Gutiérrez, A. Hernández-Casanova, J. Moscó (†); MIZA: Q. Arias, C. Bordón (†), A. Chacón, J. Clavijo, J. De Marmels, M. Gaiani, E. Guerrero, L. J. Joly, L. D. Otero, F. Romero; MPUJ: G. Fagua, M. Higuera; MUSM: J. Grados, G. Lamas; MZUJ: T. W. Pyrcz, J. Wojtusiak (†), ZMHU: W. Mey, M. Nuss, ZSBS: U. Buschbaum; A. Hausmann; Heimatnaturgarten Weissenfels: U. Radestock. A num-

ber of friends assisted and offered hospitality and support during academic and field trips; Families Dáger, Jaimez and Otero (Mérida), Family Duque (La Grita), Family Mora (Trujillo), A. Jasiński (Warsaw), T.W. and J. Pyrcz, R. Laskowski, J. Weiner, J. Wojtusiak (†) (Kraków), Mr. and Mssrs W. Neukirchen (Berlin), C. Häuser (Stuttgart), G. W. and J. Beccaloni, A.F.N. and A. Neild, B. Huertas and T. Donovan, J. and P. Banks (London). The work of M. J. Adams and G. I. Bernard was a source of inspiration; we thank them for their friendship and encouraging during Á.L.V. studies in the UK. Long time ago, G. W. Beccaloni, I. Kitching, D. C. Lees, K. Sattler, M. Scoble, C. Vardy, and R. I. Vane-Wright (BMNH), B. G. Gardiner (Linnean Society) and K. Fiedler (Universität Bayreuth) reviewed and edited several parts of earlier versions of this manuscript. T. R. Barros, G. Rivas, and an anonymous reviewer made useful commentaries and suggestions to improve the organization and edition of the definitive article.

BIBLIOGRAPHY

- Adams, M. J. 1977. Trapped in a Colombian Sierra. *Geographical Magazine* 49: 250–254.
- Adams, M. J. 1983. Andean brown butterflies. Pp. 473–476. In: Wells, S.M., R. M. Pyle and N. M. Collins (eds.): *The IUCN Red Data Book*. Gland, IUCN.
- 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* 1985 (suppl. 1): 33–49.
- Adams, M. J. and G. I. Bernard. 1979. Pronophiline butterflies (Satyridae) of the Serranía de Valledupar, Colombia-Venezuela border. *Systematic Entomology* 4: 95–118.
- Adams, M. J. and G. I. Bernard. 1981. Pronophiline butterflies (Satyridae) of the Cordillera de Mérida, Venezuela. *Zoological Journal of the Linnean Society* 71: 343–372.
- [Anonymous]. 2003. In brief. New species of wood nymph found. Flutter-free lifestyles. *New Scientist* 2397: 24.

- Bálint, Z. and J. Wojtusiak. 2006. Notes on the genus *Podanotum* with description of a new species (Lepidoptera: Lycaenidae: Eumaeini). *Genus. International Journal of Invertebrate Taxonomy* 17(2): 283–289.
- Beccaloni, G. W., Á. L. Vilorio, S. K. Hall and G. S. Robinson. 2008. *Catalogue of the hostplants of the Neotropical butterflies. Catálogo de las plantas huésped de las mariposas neotropicales*. m3m: Monografías 3er Milenio, volumen 8. Zaragoza: Sociedad Entomológica Aragonesa (SEA)/ Red Iberoamericana de Biogeografía y Entomología Sistemática (RIBES)/ Ciencia y Tecnología para el Desarrollo (CYTED) / Natural History Museum, London (NHM) / Instituto Venezolano de Investigaciones Científicas (IVIC), 536 pp.
- Blackman, S. 2003. Flutterless butterfly. *BBC Wildlife Magazine* (London) 21(8): 26.
- Bolaños-Martínez, I. A. and G. Zambrano-González. 2010. Análisis morfológico de *Dangond dangondi* Adams and Bernard, 1979 (Lepidoptera: Nymphalidae). In: *Creando un clima para el cambio. La biodiversidad, servicios para la humanidad. III Congreso Colombiano de Zoología. Resúmenes del congreso*. Medellín, 21-26 November 2010. Bogotá: Asociación Colombiana de Zoología, pp. 89 [abstract].
- Bono, G. 1996. *Flora y vegetación del Estado Táchira, Venezuela*. Torino: Museo Regionale di Scienze Naturali, 952 pp. [93 pls.] + [1] map.
- Briceño-Valero, A. 1920. *Geografía del Estado Trujillo*. Caracas: Tipografía Cultura Venezolana, 139 pp. + [iii].
- Brown, F. M. 1942. Animals above timberline. Colorado and Ecuador. *Colorado College Publication Studies Series* 33: 1–29.
- Clark, L. G. 1995. Diversity and distribution of the Andean woody bamboos (Poaceae: Bambuseae). Pp. 501–512. In: Churchill, S. P., H. Balslev, E. Forero and J. L. Luteyn (eds.): *Biodiversity and conservation of Neotropical montane forests*. New York: The New York Botanical Garden.
- Cuatrecasas, J. 1979. Comparación fitogeográfica de páramos entre varias cordilleras. Pp. 89–99. In: Salgado-Labouriau, M. L. (ed.): *El medio ambiente páramo*. Caracas: Centro de Estudios Avanzados IVIC.
- d'Abrera, B. 1988. *Butterflies of the Neotropical region. Part V. Nymphalidae (Conc.) and Satyridae*. Victoria, Black Rock: Hill House, [viii] + pp. 679–877.
- d'Abrera, B. 2001. *The concise atlas of butterflies of the world*. Melbourne / London: Hill House, 353 pp. + [i].

- Davies, H. and C. A. Butler. 2008. *Do butterflies bite?. Fascinating answers to questions about butterflies and moths*. New Brunswick, NJ: Rutgers University Press, 240 pp.
- Descimon, H. 1986. Origins of lepidopteran faunas in the high tropical Andes. Pp. 500–532. *In*: Vuilleumier, F. and M. Monasterio (eds.): *High altitude tropical biogeography*. New York: Oxford University Press.
- Díaz, A., J. Péfaur and P. Durant. 1997. Ecology of South American paramos with emphasis on the fauna of the Venezuelan paramos. Pp. 263–310. *In*: Wiegolaski, F. E. (ed.): *Ecosystems of the world 3. Polar and alpine tundra*. Amsterdam: Elsevier Science, B.V.
- Ferrer-Paris, J. R. 2000. *The genus Redonda (Lepidoptera: Satyrinae): a model to study adaptation and distribution in the páramos of Venezuela. Der Genus Redonda (Lepidoptera: Satyrinae): Fallstudie über Anpassung und Verbreitung in den Páramos von Venezuela*. Bayreuth: Universität Bayreuth, [ii] + xiii + 111 pp. [Dipl. Biol. thesis].
- Ferrer-Paris, J. R., A. Cardozo-Urdaneta and Á. L. Viloria. [in press]. Mariposa braquíptera de Bordón. *Redonda bordoni* Viloria y Pyrcz, 2003. Insecta, Lepidoptera, Nymphalidae. *In*: Rodríguez, J. P. and F. Rojas-Suárez (eds.): *Libro rojo de la fauna venezolana*. [4th ed.]. Caracas: Provita.
- Ferrer-Paris, J. R. and Á. L. Viloria. 2002. Mariposas altiandinas (Lepidoptera: Nymphalidae, Satyrinae) y la conservación de los páramos en Venezuela. *Resúmenes. Congreso Mundial de Páramos. Estrategias para la conservación y sostenibilidad de sus bienes y servicios ambientales*. Paipa, Colombia, [13-18 May 2002]: Conservación Internacional Colombia, pp. 138-139 [abstract].
- Ferrer-Paris, J. R. and Á. L. Vitoria [sic]. [2004]. Mariposas altiandinas (Lepidoptera: Nymphalidae, Satyrinae) y la conservación de los páramos en Venezuela. Pp. 626–633. *In*: Jaramillo, C. A., C. Castaño Uribe, F. Arjona Hincapié, J. V. Rodríguez and C. L. Durán (eds.): *Congreso Mundial de Páramos. Memorias Tomo I*. Bogotá: Conservación Internacional Colombia.
- Forster, W. 1964. Beiträge zur Kenntnis der Insektenfauna Boliviens, XIX. Lepidoptera III. Satyridae. *Veröffentlichungen der Zoologische Staatssammlung München* 8: 51–188.
- Gaede, M. 1931. Satyridae. II. *In*: Strand, E. (ed.): *Lepidopterorum catalogus* 29(46): 321–544.
- Godman, F. Du C. 1905. Description of some new species of Satyridae from South America. *Transactions of the Entomological Society of London* 1905(1): 185–190, pl. 10.

- Huber, H. 1973. Die Walder in den Anden von Merida (Venezuela) und ihre Tagfalter. *Mitteilungen der Pollichia* 20: 164–201.
- Kroonenberg, S. B., J. G. M. Bakker and A. M. van der Wiel. 1990. Late Cenozoic uplift and paleogeography of the Colombian Andes: constraints on the development of high-andean biota. *Geologie en Mijnbouw* 69: 279–290.
- Łabno, R. 2007. Studenci pisza. Z kraju, gdzie lato trwa wiecznie. *Alma Mater. Miesiecznik Uniwersytetu Jagiellońskiego* (Krakow) 98:104–107.
- Lamas, G., . L. Vilorio and T. W. Pyrcz. 2004. 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*. Vol. 4. Gainesville, Fl.: Association for Tropical Lepidoptera / Scientific Publishers.
- Monasterio, M. 1980. Las formaciones vegetales de los paramos de Venezuela. Pp. 93–158. *In*: Monasterio M. (ed.): *Estudios ecologicos en los paramos andinos*. Merida: Ediciones de la Universidad de Los Andes.
- Monasterio M. and S. Reyes. 1980. Diversidad ambiental y variacion de la vegetacion en los paramos de los Andes venezolanos. Pp. 47–91. *In*: Monasterio, M. (ed.): *Estudios ecologicos en los paramos andinos*. Merida: Ediciones de la Universidad de Los Andes.
- Orellana B., A. M. 2004. Mariposas de los paramos de la Sierra Nevada y Sierra de La Culata (Cordillera de Merida, Venezuela). Pp. 57–71. *In*: Andressen, R. and M. Monasterio (eds.): *Memorias del IV Simposio Internacional de Desarrollo Sustentable en Los Andes. La estrategia andina para el siglo XXI*. Merida, Venezuela: Asociacion de Montanas Andinas.
- Padron Martinez, P. S. 2010. *Systematics and biogeography of high altitude Tropical Andean satyrines (Lepidoptera, Nymphalidae, Satyrinae)*. Gainesville, Fl: University of Florida, 98 pp. [MSc thesis].
- Pena, C. A. 2009. *Evolutionary history of the butterfly subfamily Satyrinae (Nymphalidae)*. Stockholm: Department of Zoology, Stockholm University, 146 pp. [Doctoral Dissertation].
- Pena, C. A., S. Nylin and N. Wahlberg. 2011. The radiation of the Satyrini butterflies (Nymphalidae: Satyrinae): a challenge for phylogenetic methods. *Zoological Journal of the Linnean Society* 161: 64–87.
- Posso-Duque, D., J. Mavarez and . L. Vilorio. 2010. Sistematica molecular de los generos de mariposas *Redonda* y *Steromapedaliodes* (Lepidoptera: Nymphalidae) endemicos del paramo venezolano. *In*: *I Congreso Venezolano de Diversidad Biologica*. Maracay, 5-8 May 2010. Caracas: Ministerio del Poder Popular para el Ambiente / Ministerio

del Poder Popular para Ciencia, Tecnología e Industrias Intermedias, pp. [185] [abstract].

- Pyrz, T. W. 1995. A new genus, *Tamania*, and a new species, *Tamania jacquelineae*, from the Tama Range, Venezuela Colombia border, and some thoughts on the diagnosis of the tribe Pronophilini (Nymphalidae: Satyrinae). *Lambillionea* 95: 519–525.
- Pyrz, T. W. 1999. The E. Krüger collection of pronophiline butterflies. Part II: genera *Manerebia* to *Theimeia* [sic] (Lepidoptera: Nymphalidae: Satyrinae). *Lambillionea* 99: 351–376.
- Pyrz, T. W. 2004a. New oreal pedalioidine butterflies from Ecuador and Colombia (Nymphalidae: Satyrinae: Pronophilini). *Boletín científico. Museo de Historia natural. Universidad de Caldas* (Manizales) 8: 287–301.
- Pyrz, T. W. 2004b. Pronophiline butterflies of the highlands of Chachapoyas in northern Peru: faunal survey, diversity and distribution patterns (Lepidoptera, Nymphalidae, Satyrinae). *Genus* 15(4): 455–622.
- Pyrz, T. W. 2007a. Ewolucja motyli z rodzaju *Redonda* (Lepidoptera, Nymphalidae) ze szczególnym uwzględnieniem przystosowań do wysokogórskich warunków środowiskowych Andów. *Polskie Badania Środowiska Przyrodniczo-kulturowego w Ameryce Łacińskiej* [28-30 maja 2007]. Kraków: Instytut Botaniki im W. Szafera Polska Akademia Nauk, pp. 40–41.
- Pyrz, T. W. 2007b. Ewolucja motyli z rodzaju *Redonda* (Lepidoptera, Nymphalidae) ze szczególnym uwzględnieniem przystosowań do wysokogórskich warunków środowiskowych Andów. *Ogólnopolski Kongres Zoologiczny, Zmienność, Adaptacja, Ewolucja* [12-16 września 2007]: Olsztyn: Polskie Towarzystwo Zoologiczne, Uniwersytet Warmińsko-Mazurski, 2007, pp. 17–19.
- Pyrz, T. W. 2008. Description of a new pronophiline butterfly from the Venezuelan Cordillera de Mérida previously known as *Pedaliodes feratilis* form *luteocosta* Adams and Bernard with data on its altitudinal distribution (Lepidoptera: Nymphalidae: Satyrinae). *Genus* 19(1): 125–134.
- Pyrz, T. W. 2010a. *Wybrane zagadnienia z taksonomii, zoogeografii i ewolucji faun górskich na przykładzie grupy modelowej motyli z plemienia Pronophilini (Nymphalidae)*. Olsztyn: Wydawnictwo Mantis, 245 pp. + [i]; [1] leaf errata.
- Pyrz, T. W. 2010b. Evolution of butterflies of the genus *Redonda* (Lepidoptera, Nymphalidae, Satyrinae), and their adaptation to the high Andean environment. Pp. 265-273. *In: Mirek, Z., A. Flakus, A. Krz-*

- anowska, A. Paulo and J. Wojtusiak (eds.): *The Nature and Culture of Latin America. Review of Polish Studies*. Kraków: Szafer Institute of Botany, Polish Academy of Sciences.
- Pyrz, T. W., K. L. Casner and J. Wojtusiak. 2009. Polytypic species of pronophiline butterflies in the subpáramo and páramo of the Venezuelan Cordillera de Mérida I: Distribution patterns and affinities of *Lymanopoda marianna* Staudinger based on morphological and molecular data (Lepidoptera: Nymphalidae: Satyrinae). *Genus* 20(3): 507–532.
- Pyrz, T. W. and S. 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.
- Pyrz, T. W. and Á. L. Vilorio. 2007. Erebiine and pronophiline butterflies of the Serranía del Tamá, Venezuela-Colombia border (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera* 15(1-2): 18–52.
- Pyrz, T. W., K. Willmott, R. Garlacz, P. Boyer and Y. Gareca. 2014. The latitudinal gradient and spatial covariance in species richness of tropical Lepidoptera in the Andes. *Insect Conservation and Diversity* 7: 355–364 + [5] pp. suppl. material.
- Rull, V. 1996. Late Pleistocene and Holocene climates of Venezuela. *Quaternary International* 31: 85–94.
- Salgado-Labouriau, M. L., V. Rull, C. Schubert and S. Valastro, Jr. 1988. The establishment of vegetation after late Pleistocene deglaciation in the Paramo de Miranda, Venezuelan Andes. *Review of Paleobotany and Palynology* 55: 5–17.
- Schubert, C. 1970. Glaciation of the Sierra de Santo Domingo, Venezuelan Andes. *Quaternaria* 13: 225–246.
- Schubert, C. 1972. Cronología glacial tardía y evidencias neotectónicas en los Andes venezolanos nororientales. *Acta Científica Venezolana* 23 (Supl. 3): 89–94.
- Schubert, C. 1974. Late Pleistocene Mérida glaciation, Venezuelan Andes. *Boreas* 3: 147–152.
- Schubert, C. 1975. Glaciation and periglacial morphology in the north-western Venezuelan Andes. *Eiszeitalter und Gegenwart* 26: 196–211.
- Schubert, C. 1982. Geología glacial del Páramo El Batallón, Estado Táchira, Venezuela. *Acta Científica Venezolana* 33: 66–71.

- Schubert, C. and S. Valastro, Jr. 1974. Late Pleistocene glaciation of Páramo de La Culata, north-central Venezuelan Andes. *Geologische Rundschau* 63: 516–538.
- Schubert, C. and L. Vivas. 1993. *El Cuaternario de la Cordillera de Mérida, Andes venezolanos*. Mérida: Universidad de Los Andes / Fundación Polar, 345 pp. + [iii].
- Schwanwitsch, B. N. 1928. Studies upon the wing-pattern of *Pierella* and related genera of South American satyridan butterflies. *Zeitschrift für Morphologie und Ökologie der Tiere (A)*, 10: 433–532, pls. 10–14.
- Schwanwitsch, B. N. 1938. On the stereoeffect of cryptic colour-patterns in Lepidoptera. *Comptes Rendus (Doklady) de l'Académie des Sciences de l'URSS*, 21(4): 179–182.
- Shapiro, A. M. 1992. Why are there so few butterflies in the high Andes?. *Journal of Research on the Lepidoptera* 31: 35–56.
- Shou, J.; I. Chou and L. Yufei. 2006. *Systematic butterfly names of the world*. Xian: Shaanxi Science and Technology Press, 4 + 6 + 20 + 450 pp., 32 pls.
- Silva Dias, F. M. 2006. *Chave pictórica para as famílias e subfamílias de Hesperioidea e Papilionoidea (Lepidoptera) Neotropicais, exceto subfamílias de Nymphalidae*. Curitiba: Universidade Federal do Paraná, viii + 37 pp.
- Silva León, G. A. 2001. Los picos más altos del estado Mérida-Venezuela. *Revista Geográfica Venezolana (Mérida)* 42(1): 73–97.
- Staudinger, O. 1897. Neue südamerikanische Tagfalter. *Deutsche Entomologische Zeitschrift "Iris"*, 10(1): 123–151, pls. 5–8.
- Thieme, O. 1905. Monographie der Gattung *Pedaliodes* Butl. (Lepidoptera. Rhopalocera. Satyridae). *Berliner Entomologische Zeitschrift* 50: 43–141, pls. 1–3.
- Van der Hammen T. and A. M. Cleef. 1986. Development of the high Andean Páramo Flora and Vegetation. Pp. 153–201. In: Vuilleumier F. and M. Monasterio (eds.): *High altitude tropical biogeography*. New York: Oxford University Press.
- Vareschi, V. 1970. *Flora de los páramos de Venezuela*. Mérida, Universidad de Los Andes, 429 pp. + [i].
- Viloria, Á. L. 1990. *Taxonomía y distribución de los Satyridae (Lepidoptera: Rhopalocera) en la Sierra de Perijá, frontera colombo-venezolana*. Maracaibo: La Universidad del Zulia, Facultad Experimental de Ciencias, xxxviii + 296 pp. [Lic. Biol. thesis]
- Viloria, Á. L. 1993. Los géneros *Diaphanos* y *Redonda* (Lepidoptera: Satyridae) como indicadores de centros de endemismo en los altos Andes venezolanos. *VI Jornadas Científicas de la Facultad Experimental de Cien-*

- cias de La Universidad del Zulia*. Maracaibo, 13 al 16 de julio de 1993, pp. 69 [abstract].
- Viloria, Á. L. 1994. High Andean Pronophilini from Venezuela: Two new species of *Diaphanos* (Nymphalidae: Satyrinae). *Journal of the Lepidopterists' Society* 48: 180–189.
- Viloria, Á. L. 1997. Phylogeny and biogeography of the high Andean genus *Redonda* (Lepidoptera: Nymphalidae, Satyrinae). *Division of Life Sciences Research Day, Friday April 25th 1997*. London: King's College London, University of London, pp. 15 [abstract].
- Viloria, Á. L. 1998. *Studies on the systematics and biogeography of some montane satyrid butterflies (Lepidoptera)*. London: The University of London (King's College London) / The Natural History Museum, 493 pp. [Dr Phil thesis].
- 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 and 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. 2002. Limitaciones que ofrecen distintas interpretaciones taxonómicas y biogeográficas al inventario de lepidópteros hiperdiversos de las montañas neotropicales y a sus posibles aplicaciones. Pp. 173–190. *In: Costa C., S. A. Vanin, J. M. Lobo and A. Melic (eds.): Proyecto de Red Iberoamericana de Biogeografía y Entomología Sistemática PrIBES 2002*. m3m-Monografías Tercer Milenio, vol. 2. Zaragoza: Sociedad Entomológica Aragonesa, CYTED.
- Viloria, Á. L. 2003. Historical biogeography and the origins of the satyrine butterflies of the Tropical Andes (Insecta: Lepidoptera, Rhopalocera). Pp. 247–261. *In: Morrone, J. J. and J. Llorente-Bousquets (eds.): Una perspectiva latinoamericana de la biogeografía*. México, D. F.: Las Prensas de Ciencias, Facultad de Ciencias, UNAM.
- Viloria, Á. L. 2005. Las mariposas (Lepidoptera: Papilionoidea) y la regionalización biogeográfica de Venezuela. Pp. 441–459. *In: Llorente Bousquets, J. E. and J. J. Morrone (eds.): Regionalización biogeográfica en Iberoamérica y tópicos afines. Primeras Jornadas Biogeográficas de la Red Iberoamericana de Biogeografía y Entomología Sistemática (RIBES XIII-CYTED)*. México, D. F.: Las Prensas de Ciencias, Facultad de Ciencias, UNAM.
- 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. 2008. Mariposa braquíptera de Bordón. *Redonda bordoni* Viloria and Pyrcz 2003. Pp. 278. In: Rodríguez, J. P. and F. Rojas-Suárez (eds.): *Libro rojo de la fauna venezolana*. [3rd ed.]. Caracas: Pro-vita y Shell de Venezuela.
- Viloria, Á. L. and T. W. Pyrcz. 2001. Revalidación y revisión de *Steromapedaliodes* Forster, con descripción de dos especies nuevas (Lepidoptera: Nymphalidae, Satyrinae). *Anartia* 15: 1–22.
- Viloria, Á. L., T. W. Pyrcz and J. Camacho. 1993. Sistemática de los Satyridae de media y alta montaña (Pronophilini) y la determinación de regiones de endemismo en el territorio venezolano. *V Congreso Latinoamericano y XIII Venezolano de Entomología*. Porlamar (Venezuela), 4-8 July 1993, pp. 226-227 [abstract].
- Viloria, Á. L., T. W. Pyrcz and J. R. Ferrer-Paris. 2007. Systematics, biogeography and ecology of *Redonda* Adams and Bernard (Satyrinae: Pronophilina). *II ELEN, Encuentro de Lepidopterología Neotropical*. Ciudad de Panamá, Panamá, [29 April-3 May 2007], pp. [23-24] [abstract].
- Viloria, Á. L., T. W. Pyrcz, J. Wojtusiak, J. R. Ferrer-Paris, G. W. Becaloni, K. Sattler and D. C. Lees. 2003. A brachypterous butterfly?. *Proceedings of the Royal Society of London, B, (Suppl.), Biology Letters* 270(s1): 21–24 + [9] pp. [e-appendices].
- Vuilleumier, F. 1981. The origin of high Andean birds. *Natural History* 90: 50-57.
- Vuilleumier, F. 1984. Zoogeography of Andean birds: two major barriers; and speciation and taxonomy of the *Diglossa carbonaria* superspecies. *National Geographic Society Research Report* 16: 713–731.
- Vuilleumier, F. and D. N. Ewert. 1978. The distribution of birds in Venezuelan páramos. *Bulletin of the American Museum of Natural History* 162: 47–90.
- Weymer, G. 1912. 4 Familie: Satyridae. Pp. 173–283. In: Seitz, A. (ed.): *Die Gross-Schmetterlinge der Erde, 2; Exotische Fauna*, 5. Stuttgart: A Kernen.
- Williams, N. 2003. All of a flutter. *Current Biology* 13(12): R467.