

Taxonomy, phylogeny and distribution of the genus *Steromapedaliodes sensu novo* in the Cordillera de Mérida, Venezuela (Lepidoptera: Nymphalidae: Satyrinae: Satyrini)

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Abstract

We revise the taxonomy and phylogeny of the genera *Steromapedaliodes* Forster, 1964 and *Redonda* Adams & Bernard, 1981, both subparamo and paramo endemics of the Cordillera de Mérida (Venezuela). *Redonda* is hereby synonymized with *Steromapedaliodes*, a decision supported by a comparative study evidencing several synapomorphies of both genera in external characters and genitalia, and the lack of salient synapomorphies specific to each genus in morphological, biogeographical and ecological traits. Also, *Steromapedaliodes mavarezi* sp.n. presents several intermediate characters in relation to the species traditionally assigned to *Redonda* and *Steromapedaliodes*. Furthermore, a molecular phylogenetic analysis with the use of one nuclear and three mitochondrial markers shows no support for reciprocal monophyly between *Redonda* and *Steromapedaliodes* but provides strong support for the monophyly of *Steromapedaliodes sensu novo*, with low levels of genetic divergence among species. Two new species of *Steromapedaliodes* are described, *S. kahlua* sp.n. and *S. mavarezi* sp.n. We describe five new subspecies of *S. albonotata* (Godman, 1905), two of *S. albarregas* (Adams & Bernard, 1981), and the females of *S. empetrus empetrus* (Thieme, 1905) comb.n. and *S. lathraia* Viloría & Camacho, 2015 comb.n. Several new status and synonymies are also established. Accordingly, *Steromapedaliodes* contains nine species, including four that are highly polytypic. Adult *Steromapedaliodes* share several striking morphological and genital similarities with another north Andean paramo genus, *Dangond* Adams & Bernard, 1979 from the Sierra de Perijá. However, our phylogenetic analysis shows that the two are not sister taxa and that they originated in separate clades of the speciose *Pedaliodes* complex. This shows that convergence in butterflies affects not only external morphology traits directly correlated with habitat selection but also genitalia. *Steromapedaliodes* has undergone an adaptive radiation in geographically isolated paramos resulting in unusual morphological and behavioural characters such as brachyptery and flightlessness of the females of *S. bordoni* Viloría & Pyrcz, 2003 comb.n. and *S. empetrus* (Thieme, 1905) comb.n., a unique adaptation among the world's butterflies.

Key words

Adaptive radiation, Andes, convergence, endemism, species description, generic revision, paramo, *Steromapedaliodes*, *Redonda*.

1. Introduction

Montane forests cover most of the areas in the Northern Andes, but the altitudinal belt above 3000 m corresponds to a tundra-like or grasslands ecosystem known as *paramo* (hereafter paramo, SALGADO-LABOURIAU et al. 1988). This ecosystem is therefore found between the continuous tree line and the snow line and is characterised by a very high proportion of giant rosette plants, alongside shrubs and grasses (LUTEYN 1999). Paramo habitats are very young, because although the Northern Andes started to rise in the late Oligocene, they were ridges and small mountains smaller than 700 m in elevation by mid-Miocene, attained 30–40% of their modern elevation by 5.3 Mya early-Pliocene) and reached present-day heights through a rapid final uplift by 2.7 Mya (late-Pliocene) (VAN DER HAMMEN et al. 1973; VAN DER HAMMEN & CLEEF 1986; VAN DER HAMMEN 1989; KROONENBERG et al. 1990; ANDRIESEN et al. 1992; HELMENS & VAN DER HAMMEN 1994; GREGORY-WODZICKI 2000; HOOGHIEMSTRA et al. 2006). Besides, paramos are also very fragmented; structured as many small “islands” of cold grassland habitats surrounded by a “sea” of warm forest. This geological and ecological set-up has had a profound impact on the biodiversity of the paramo ecosystem, making it the one with the highest diversity and the highest proportion of plant endemics among the world’s high-altitude habitats. For instance, paramos are home to no less than 20 endemic plant genera and an unknown but large number of endemic monophyletic groups within other taxa (LUTEYN 1999; SKLENÁŘ et al. 2011).

In Venezuela, most paramos are found in the high-elevation areas of the Cordillera de Mérida, which is a fairly isolated branch of the Northern Andes (Fig. 1A). Here too, evolution has favoured the rise and further diversification of several endemic or quasi-endemic taxa such as a monophyletic clade of ~ 60 spp. in the subtribe Espeletiinae (Asteraceae) (Pouchon et al. unpubl. data), and seemingly monophyletic groups within *Pentacalia* (Asteraceae) (LAPP 2014), *Hinterhubera* (Asteraceae) (KARAMAN 2006), *Valeriana* (Valerianaceae) (XENA DE ENRECH 1993) and many others. In animals, a few groups include endemic genera in the Cordillera de Mérida, such as the mouse genus *Aepeomys* and its two described species (VOSS et al. 2002) and the grasshopper genus *Meridacris*, also with two species (ROBERTS 1937). However, the largest number of endemic animal genera in the Cordillera de Mérida occurs in the Lepidoptera, particularly among the better-studied butterflies (Papilionoidea; NEILD 1996, 2008; PYRCZ et al. 2010), and most notably among the montane subtribe Pronophilina (Nymphalidae, Satyrinae), for which at least four genera endemic to this range have been described: *Cheimas* Weymer, 1912 (1 sp.), *Diaphanos* Adams & Bernard, 1981 (3 spp.), *Steromapedaliodes* (sensu Viloria & Pyrcz, 2001) (2 spp., but see below) and *Redonda* Adams & Bernard, 1981 (10 spp., but see below), all of them restricted to the forest-paramo ecotone and paramo grassland. This is

outstanding in comparison to other isolated mountainous massifs of northern South America or Central America, which harbour one endemic butterfly genus at most: *Paramo* Adams & Bernard, 1977 (1 sp.) in the Sierra Nevada de Santa Marta (other two genera originally described as endemic by ADAMS & BERNARD (1977) were subsequently synonymized or found to be more widely distributed), *Dangond* (1 sp.) in the Sierra de Perijá and *Drucina* Butler, 1872 (2 spp.) in Panama/Costa Rica (Sierra de Talamanca and Meseta Central) and southern Mexico.

It must however be acknowledged that further progresses in the understanding of the biogeography and evolution of endemic taxa from the Cordillera de Mérida, and the Pronophilina in particular, have been hampered by a lack of studies on their phylogenetic relationships and taxonomy. Only one molecular phylogenetic analysis including samples of the genera discussed herein has been conducted so far, and it was designed more to depict the high level phylogeny of the subfamily Satyrinae rather than to establish relationships among genera (PEÑA et al. 2011). In consequence, the phylogenetic relationships of the endemic Pronophilina from the Cordillera de Mérida remain largely unstudied, which also contributes in some degree to the taxonomic ambiguity associated with some of these taxa. For instance, the highly distinctive *Diaphanos*, with three described species, appears distantly related to *Lymanopoda* Westwood, [1851] (PEÑA et al. 2011), but its position within the Pronophilina remains a matter of controversy (PYRCZ 2010a). On the other hand, the phylogenetic affinities of the monobasic genus *Cheimas* are even more dubious, as the analysis of PEÑA et al. (2011) indicates that it is only loosely related to *Corades* Hewitson, 1849, within a highly polytomic clade that also includes the genera *Pronophila* Doubleday, [1849] and *Lasiophila* C. Felder & R. Felder, 1859 among others. However, as for *Diaphanos*, the generic status of *Cheimas* remains unquestioned given its characteristic external morphology (ADAMS & BERNARD 1981).

The phylogenetic affinities of the two remaining endemic genera from the Cordillera de Mérida, *Steromapedaliodes* (sensu Viloria & Pyrcz) and *Redonda*, are particularly interesting because these are the two most speciose taxa and *Redonda* includes the only known examples of brachyptery and loss of the ability to fly among the world’s butterflies (Rhopalocera) (VILORIA et al. 2003; PYRCZ 2010a,b). However, although the positions of both taxa within the speciose (> 300 spp.) *Pedaliodes* Butler, 1867 complex, to which they belong, have been subject to some discussion in the past (ADAMS & BERNARD 1981), their phylogenetic relationships have not been rigorously explored. The validity of the two genera as separate entities has not been challenged despite that they appear to be closely related sister taxa (PEÑA et al. 2011). This is surprising when we consider the lack of good synapomorphic characters specific to each genus together with the existence of good synapomorphic characters linking both of them into a single group. Thus, *Steromapedaliodes* (sensu Viloria & Pyrcz) and *Redonda* share highly similar ecological requirements in terms of habitat used, male

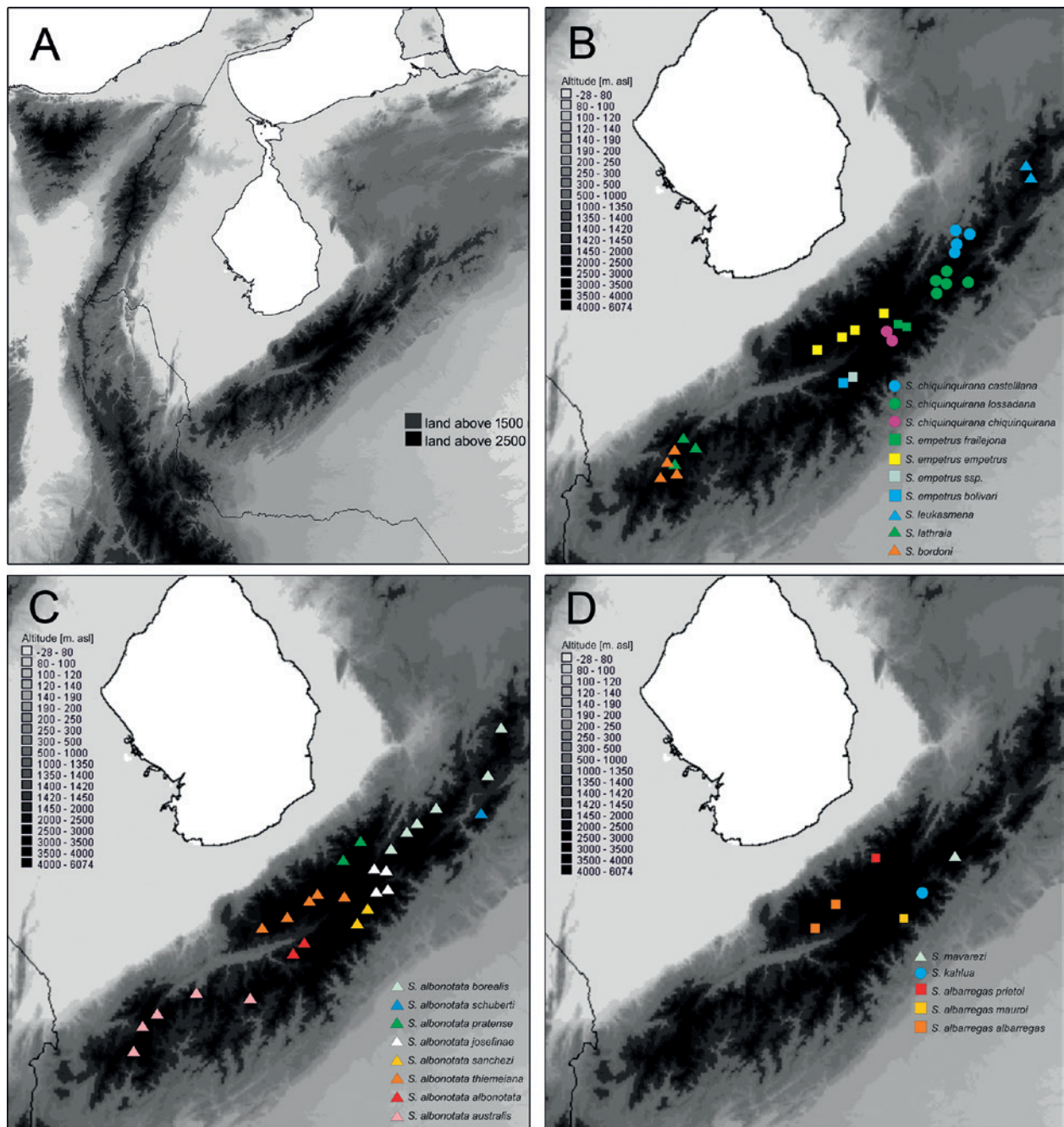


Fig. 1. Maps. **A:** Schematic representation of the land area above 1500 m and above 2500 m (dark grey) in the Northern Andes of Colombia and Venezuela. **B:** Sampling sites of *Steromapedaliodes chiquinquirana* (3 spp.), *S. empetrus* (4 spp.), *S. leukasmena*, *S. lathraia* and *S. bordoni*. **C:** Sampling sites of *Steromapedaliodes albonotata* (8 spp.). **D:** Sampling sites of *Steromapedaliodes mavarezi*, *S. kahlua* and *S. albarregas* (3 spp.).

genitalia and most notably colour patterns, particularly on the hindwing venter, in particular the configuration of median, postdiscal and submarginal lines and eyespots, parts of the so-called nymphalid groundplan (Nijhout 1991), considered as a valuable character for phylogenetic relationship among the Pronophilina (Pyrz et al. 2008). This combination of ecological and morphological features is exclusive to *Steromapedaliodes* and *Redonda* among the speciose *Pedaliodes* complex. *Redonda* does show some characteristics that at first glance make it look different from *Steromapedaliodes* (*sensu* Viloria & Pyrcz), notably the major reduction or absence

of the subuncus in the male genitalia and a tendency for larger males than females. Yet the systematic value of such traits has never been evaluated properly and there are good reasons to raise doubts about them. For example, reduced or absent subunci are also found in the genus *Dangond* and in *Panyapedaliodes stellata* Pyrcz, 2004 (Pyrz 2004). Both taxa are most probably phylogenetically distant from *Redonda*, but they share with it a life in the paramo, suggesting that these characters of male genitalia are relatively plastic and able to evolve repeatedly in response to the extreme conditions of high elevation habitats. In regards to the relative size of males

and females, there are considerable differences among species within both *Steromapedaliodes* (*sensu* Viloria & Pyrcz) and *Redonda*, as it seems also to be the case in other genera of Pronophilina such as *Dangond*, *Paramo* and *Punapedaliodes* Forster, 1964 (ADAMS & BERNARD 1977, 1979; PYRCZ 2004, 2007a,b; VILORIA 2007).

This study is mainly focused on investigating the phylogenetic relationship between *Steromapedaliodes* (*sensu* Viloria & Pyrcz) and *Redonda*. Two main scenarios are tested: **i)** *Steromapedaliodes* (*sensu* Viloria & Pyrcz) and *Redonda* form two well-defined and reciprocally monophyletic groups, in which case their lack of respectively synapomorphic characters is somehow a reflect of a slower rate of morphological evolution; **ii)** *Steromapedaliodes* (*sensu* Viloria & Pyrcz) and *Redonda* do not form reciprocally monophyletic groups, in agreement with the lack of morphological synapomorphies and in which case the two genera should be unified into a single one, *Steromapedaliodes sensu novo*. In addition, we explore the phylogenetic relationships of both taxa with other Neotropical Satyrinae, in particular other groups found in oreol habitats such as some lineages in the *Pedaliodes* complex from the Cordillera de Mérida and *Dangond* from the Sierra de Perijá.

The assessment of these scenarios and relationships will certainly provide another example of the utility of molecular phylogenies in disentangling of the complex patterns of butterfly systematics associated with pre-cladistic nomenclature (WAHLBERG et al. 2005; PEÑA et al. 2006). For *Steromapedaliodes* (*sensu* Viloria & Pyrcz) and *Redonda*, the abandonment of traditional taxonomic usages could be a necessary consequence of an advanced knowledge about their mutual relationship and evolutionary history. In any case, the result will be an updated lexicon of generic, specific and sub-specific names that will facilitate a more effective communication among researchers and enthusiasts of Neotropical butterflies.

2. Materials and methods

2.1. Taxa studied

The genus *Steromapedaliodes* was raised by FORSTER (1964) for a single species found in the Venezuelan Andes, *Pedaliodes albonotata* Godman, 1905, mostly based on male genitalia. ADAMS & BERNARD (1981) rejected this action, placed *albonotata* in another genus, *Altopedaliodes* Forster, 1964 and described another apparently closely related species, *Altopedaliodes albarregas* Adams & Bernard, 1981. VILORIA & PYRCZ (2001) demonstrated that the abdomen studied by Forster was glued to the thorax and that it belonged to a species of the genus *Manerebia* Staudinger, 1987. They sustained however the validity of *Steromapedaliodes* and described two new taxa at the specific level, *S. schuberti* Viloria & Pyrcz, 2001 and *S. sanchezi* Viloria & Pyrcz, 2001.

The genus *Redonda* was erected by ADAMS & BERNARD (1981) for a single species, originally described as *Pedaliodes empetrus* by THIEME (1905), based on male genitalia, wing pattern, and some ecological features. They additionally described one new subspecies, *R. empetrus bolivari* Adams & Bernard, 1981. A second species, *R. bordoni* Viloria & Pyrcz, 2003 was also described (VILORIA et al. 2003). Recent field studies show that the genus is much more diverse, and brought to light the existence of complex biogeographic patterns within the Cordillera de Mérida (PYRCZ 2010a; VILORIA et al. 2015).

The genus *Dangond* was described as monobasic for the monotypic species *Dangond dangondi* Adams & Bernard, 1979 (ADAMS & BERNARD 1979). Its taxonomy and phylogeny have not been studied since.

2.2. Study area

Butterflies in the genera *Steromapedaliodes* (*sensu* Viloria & Pyrcz) and *Redonda* are distributed along the Cordillera de Mérida in Venezuela, which is a north-eastern extension of the Andes (Fig. 1A). It runs south-west–north-east between the Colombian Eastern Andean branch (Cordillera Oriental) and the Venezuelan coastal range, but it is separated from them by the Táchira depression and the Lara depression, respectively. The Cordillera de Mérida is indeed composed by two ranges of peaks; the Sierra de la Culata to the north and the Sierra Nevada de Mérida to the south, which includes the highest peak in Venezuela, Pico Bolívar (4981 m). Tributaries of the Orinoco River drain its south-eastern slopes, while the streams that drain the north-western slopes empty into Lake Maracaibo. *Dangond dangondi* is found in the Sierra de Perijá, which is a mountain range that represents a northward extension of the Colombian Eastern Andean branch (Cordillera Oriental), between Colombia and Venezuela, and ending in the Guajira Desert. It is separated from the Cordillera Oriental by the Catatumbo river in the Maracaibo basin. The highest point is Cerro Pintado (3660 m), followed by Cerro de Las Tetras (3630 m) and Cerro Irapa (3540 m). The mountains of the Cordillera de Mérida and the Sierra de Perijá are separated from the Colombian Eastern Cordillera by a major orographical and biogeographical barrier, the so-called “Táchira Depression” (PYRCZ & VILORIA 2007).

2.3. Field work

Field work was carried out by TP, PB and JM throughout the Cordillera de Mérida from 1991–2015, and by TP in the Sierra de Perijá in 2012. The list of sampled localities is given in Table 1. Collecting was conducted on each locality with standard entomological nets. Van-Someren Rydon baited traps were used only to a limited degree as they have proved to be inefficient. They only sporadically attract adult butterflies in paramo grassland, contrary

to cloud forests (PYRCZ et al. 2009). Field observations of adult behaviour were carried out in all the sampled localities with an emphasis on diurnal activity pattern, mate locating strategies and feeding behaviour. Specimens intended for molecular analyses were preserved in absolute ethanol or kept dry in glassine envelopes.

2.4. Morphological data

The following abbreviations were used in the text: **FW**, forewing; **HW**, hindwing; **D**, dorsum; **V**, venter. Further abbreviations are given in the legends of Figs. 4 (wing venation), 12 (male genitalia), and 16 (female genitalia). The morphological characters used in analysis include: wing venation and colour pattern, microstructure of antennae, eyes, labial palpi and tegulae as well as male and female genitalia. Wing slides were made by removing scales in warm 10% KOH solution. Genital preparations were done using standard procedures, by soaking in warm 10% KOH solution for 10 min. Scales and internal organs were cleaned out in distilled water. Female genital organs were stained with chlorazole black. Genital organs were examined and measured, alongside other morphological microstructures, under an Olympus SZX9 stereomicroscope equipped with a Nikon Digital sight Ds-Fi1 camera. Male and female genital preparations are preserved in glycerol vials and pinned under the specimens. Genital morphology follows mostly KLOTS (1970) and RAZOWSKI (1996). We chose to use the term “subuncus” instead of “gnathos” mostly, because subuncus (plural: subunci) was used extensively by ADAMS & BERNARD (1977, 1979, 1981) in their revisional papers to designate this structure, and by all subsequent authors dealing with Pronophilina taxonomy. Several taxonomists dealing with neotropical Satyrinae, especially with Euptychiina, prefer the term gnathos (FREITAS et al. 2013; NEILD et al. 2014). There is some controversy whether the two structures are homologous (KLOTS 1970), although this uncertainty does not seem apply to Pronophilina and Euptychiina.

Adults were photographed with an Olympus E-500 digital camera equipped with 50 mm macro lens. Colour plates were composed using Adobe PhotoShop version 9, and their quality was enhanced by CombineZ software.

A total of over 400 adult specimens of the genera *Stenomapedaliodes* (*sensu* Viloría & Pyrcz), *Redonda* and *Dangond dangondi* were examined (listed under each taxon). Type and other specimens deposited in the following institutional and private collections were examined (acronyms are cited in the text): **AME**: Allyn Museum of Entomology, Sarasota, USA; **BMNH**: The Natural History Museum (formerly British Museum of Natural History), London, United Kingdom; **JFLC**: collection of Jean Francois Le Crom, Bogota, Colombia; **MALUZ**: Museo de Artrópodos, Facultad de Agronomía, La Universidad del Zulia, Maracaibo, Venezuela; **MHN-UN**: Museo de Historia Natural, Facultad de Ciencias, Universidad Nacional, Bogotá, Colombia; **MIZA**: Museo del Instituto de

Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela; **AFN**: collection of Andrew F. Neild, London, UK; **CEP-MZUJ**: Centrum Edukacji Przyrodniczej (formerly Muzeum Zoologiczne) Uniwersytetu Jagiellońskiego; **ZSM**: Zoologische Staatssammlung München, Germany; **PBF**: collection of Pierre Boyer, Le Puy Sainte Réparate, France; **MCC**: collection of Mauro Costa, Caracas, Venezuela; **TWP**: collection of Tomasz W. Pyrcz, Warsaw, Poland (incorporated into MZUJ).

2.5. Molecular data and analyses

DNA was obtained from dry or ethanol preserved specimens listed in Tables 1 and 2 using QIAGEN's DNeasy kit and following the manufacturer's protocol. In general DNA was extracted from two legs of each specimen but in the case of poor yields, the whole body was used for the extraction. Both mitochondrial and nuclear regions were sequenced in this study using PCR primers described in Electronic Supplement Table S1.

Mitochondrial. Sequences from three mitochondrial regions were amplified: *Cytochrome Oxidase I* gene (*COI*), tRNA-Leu and *Cytochrome Oxidase II* gene (*COII*). PCR reactions were performed in a 25 µl reaction volume with 5–100 ng of DNA template, 0.5 µM of each primer, 0.2 mM of each dNTP, 1 U of GoTaq DNA polymerase (Promega), 1X GoTaq DNA polymerase buffer and 1.5 mM MgCl₂. The PCR cycling profile comprised an initial denaturation at 95°C for 5 min followed by 40 cycles of 95°C for 30 s, 50°C for 30 s, 72°C for 1 min, and a final extension period of 72°C for 10 min.

Nuclear. Sequences of the *Glyceraldehyde-3-Phosphate Dehydrogenase* gene (*GAPDH*) were amplified using primers HybFrigga and HybBurre (Electronic Supplement Table S1). PCR reactions were performed as above, but with an annealing temperature of 55°C.

All amplifications were performed in a PTC-100 Thermal Cycler (MJ Research Inc.) or in an Eppendorf Mastercycler ep thermal cycler (Perkin-Elmer Corp.). The PCR products were purified with the MagneSil Green sequencing clean-up reagent (Promega) and sequenced using ABI Big-Dye v3.1 terminator chemistry on an ABI 3130 DNA Sequencer (Applied Biosystems) following the manufacturer's protocols.

Chromatograms were edited and base calls checked using GeneMapper v4.1 (Applied Biosystems). We searched for reading frame errors and unexpected stop codons by translating the nucleotide sequences to peptides using Mega5 (TAMURA et al. 2011). Sequences were aligned with Clustal W (THOMPSON et al. 1994) under default settings, and then manually adjusted. The alignment included also GenBank sequences of some taxa within the *Pedaliodes* complex (*Pedaliodes*, *Altapedaliodes*, *Punapedaliodes* and *Panyapedaliodes* Forster, 1964) and of several genera within the Pronophilina used as out-group taxa (*Manerebia*, *Lymanopoda*, *Ianussiusa* Pyrcz & Viloría, 2004, *Pronophila* Doubleday, [1849] and

Table 1. A list of the localities, altitudes, coordinates and GenBank accession numbers for *Steromapedaliodes sensu novo* and outgroup taxa (*Dangond dangondi*, *Pedaliodes plotina*, *Diaphanos fuscus* and *Tamania jacquelineae*) sequenced in this study. Accession numbers: left column: *COI-COI*, right column: *GAPDH*.

Species	Locality	Altitude (m)	Longitude	Latitude	Accession Numbers	
<i>S. leukasmena</i>	Páramo de Las Rosas	3000–3200	70°07'07"	09°34'36"	KF157845	KR476346
<i>S. chiquinquirana chiquinquirana</i>	Laguna de Mucubají	3550–3650	70°48'46"	08°47'19"	KF157848	KR476348
<i>S. chiquinquirana castellana</i>	Páramo de Cabimbú	2850–2950	70°27'26"	09°10'34"	KF157846	KR476347
<i>S. chiquinquirana lossadana</i>	Teta de Niquitao	3200–3250	70°27'46"	09°25'37"	KF157847	KR476349
<i>S. empetrus empetrus</i>	La Culata	3100–3300	71°02'40"	08°45'59"	KF157850	KR476340
<i>S. empetrus bolivari</i>	Loma Redonda	3850–4000	71°04'38"	08°32'52"	KF157843	KR476339
<i>S. empetrus frailejona</i>	Los Frailes	2850–3100	70°46'37"	08°48'45"	KF157849	KR476338
<i>S. bordoni</i>	above Las Antenas	3250–3500	71°54'18"	08°07'44"	KF157844	KR476344
<i>S. lathraia</i>	Mesa Alta	2700–2800	71°52'45"	08°09'29"	KF157851	KR476341
<i>S. albarregas albarregas</i>	Qda. La Boba	3200–3250	71°16'36"	08°37'41"	KF157857	KR476355
<i>S. albonotata schuberti</i>	Páramo Guaramacal	3100–3150	70°11'05"	09°14'18"	KF157853	KR476352
<i>S. albonotata pratense</i>	El Potrero	2900–2950	70°53'15"	08°59'59"	KF157856	KR476353
<i>S. albonotata borealis</i>	Páramo Cendé	3000–3050	70°07'24"	09°39'40"	KF157852	KR476351
<i>S. albonotata josefinae</i>	Los Frailes	2900–2950	70°45'53"	08°49'09"	KF157854	KR476354
<i>S. mavarezi</i>	Páramo de Guirigay	2800–3000	70°25'41"	09°03'10"	KY851302	KY851303
<i>Dangond dangondi</i>	Casa de Vidrio	3200–3250	72°54'01"	10°27'36"	KF157859, KF157860	KR476356, KR476357
<i>Pedaliodes plotina plotina</i>	Colonia Tovar	1900–1950	67°16'53"	10°24'56"	KF157858	KR476358
<i>Diaphanos fuscus</i>	Páramo Cendé	3100–3150	70°07'09"	09°34'33"	KF157861	KR476336
<i>Tamania jacquelineae</i>	Betania	2350–2400	72°25'39"	07°27'54"	KF157862	KR476337

Table 2. Pronophilina outgroup taxa extracted from GenBank. Accession numbers: left column: *COI*, right column: *GAPDH*.

Outgroup taxa GenBank	Locality	Accession numbers	
<i>Pedaliodes ewelina</i>	Laguna Uspacocha, 3668 m, Peru	DQ338856	EU528407
<i>Pedaliodes ampayana</i>	Laguna Angascocha, 3270 m, Peru	GQ357239	GQ357489
<i>Punapedaliodes flavopunctata</i>	Cerro de Pasco, 4318 m, Peru	DQ338861	GQ357493
<i>Pedaliodes phrasiclea</i>	Quebrada 7 Jeringas, 1700 m, Peru	GQ357238	GQ357488
<i>Panyapedaliodes drymaea</i>	Laguna Angascocha, 3270 m, Peru	DQ338855	GQ357486
<i>Altopedaliodes</i> sp.	Cerro de Pasco, 4318 m, Peru	GQ357223	GQ357464
<i>Lymanopoda rana</i>	Pampa Hermosa, 1300 m, Peru	DQ338853	GQ357479
<i>Manerebia lisa</i>	Quebrada Malambo, 2600 m, Peru	GQ357233	GQ357480
<i>Ianusiusa maso</i>	Runtun, 2600 m, Ecuador	GQ861947	GQ861918
<i>Eteona tisiphone</i>	Extrema, 1000 m, Brazil	DQ338849	GQ357473
<i>Pronophila thelebe</i>	Quebrada 7 Jeringas, 1700 m, Peru	DQ338859	EU528410

Eteona Doubleday, 1848) (accession numbers given in Table 1). In this study, we cannot designate the closest relative to the *Steromapedaliodes sensu nov.* taxon, therefore we use a series of genera belonging to the subtribe Pronophilina. To investigate potential conflict between the partitions of the mitochondrial and nuclear datasets, we performed a test of Congruence Among Distance Matrices (i.e. CADM, CAMPBELL et al. 2011) as implemented in the R-package *ape* (PARADIS et al. 2004) and using pairwise distances calculated with the Maximum Composite Likelihood model (MCL, TAMURA et al. 2004) in Mega5. Bayesian phylogenetic analyses of the mitochondrial, nuclear and mitochondrial + nuclear datasets were performed using MrBayes 3.2 (RONQUIST et al. 2012), applying the most appropriate substitution model for each region as estimated with the Bayesian Information Criterion (BIC) implemented in Mega5 (TAMURA et al. 2011). Four Markov chains were run simultane-

ously, each one was started from a random tree and run for one million generations, sampling a tree every 100 generations. All sample points prior to reaching stationarity (~1000 trees) were discarded as burn-in samples. Data remaining after burn-in (9000 trees) were used to generate a majority rule consensus tree, with branch supports calculated as the proportion of trees that contained the clade and representing the posterior probability of the existence of that clade given the data and model of evolution (HUELSENBECK & RONQUIST 2001). Probabilities > 0.95 were arbitrarily considered indicative of significant support. Maximum likelihood (ML) analyses were also performed in Mega5 (TAMURA et al. 2011), with alignments partitioned by region (mitochondrial, nuclear and mitochondrial + nuclear), assigning a separate model of nucleotide substitution to each partition. Statistical support was calculated from 100 nonparametric bootstrap replicates under the same partitioning scheme.

3. Results

3.1. Genus-level comparative morphology

The most striking result of the comparative morphological analysis of the adults of *Steromapedaliodes* (*sensu* Viloría & Pyrcz) and *Redonda* is the absence of synapomorphies of either genus for any of the morphologic features analysed.

Body size. In both groups the females are marginally, noticeably or considerably smaller than males (Figs. 5–11). However this feature is not necessarily phylogenetically informative since this pattern is seen in several other paramo taxa in the *Pedaliodes* complex, including the genera *Dangond* (Fig. 7A,B), *Paramo*, and *Punapedaliodes*, probably related to the adaptation to paramo conditions, as discussed by PYRCZ (2010b). Males of the species until now associated with *Redonda* are generally larger than the males of *Steromapedaliodes* (*sensu* Viloría & Pyrcz), but with some overlap. For example, larger males of some subspecies of *S. albonotata* are similar in size to males of some smaller species of *Redonda*. Moreover, the males, and particularly the females of one of the new species of *Steromapedaliodes* described in this study (see description 4 below), are larger than the males of any other species known so far in both genera.

Wing patterns. There is one striking character present in all the species of *Steromapedaliodes* (*sensu* Viloría & Pyrcz) and *Redonda*: ocellar elements in postdiscal area of both wings (either dorsally, or ventrally, or both), but simplified as white, sometimes highly distorted spots, v-shaped and elongated (fusiform) (Figs. 5–11). This feature is very diagnostic, unique to these two taxa (absent in *Dangond*, Fig. 10A,B), and is therefore a strong synapomorphy within the *Pedaliodes* complex. On the other hand, there is a FWD white discal patch in most taxa of *Steromapedaliodes*, except for two new species described herein, one of which has an entirely brown dorsum (see description 3 below) and the other has instead a white patch in the discal cell of the hindwing (see description 4 below). The latter represents a unique feature not only for this group of species but also for the entire *Pedaliodes* complex. Other similarities in the colour patterns between *Steromapedaliodes* (*sensu* Viloría & Pyrcz) and *Redonda* consist in the elaborate markings of the HWV imitating grass, sandy habitat or lichens.

Genitalia. Male genitalia in *Steromapedaliodes* (*sensu* Viloría & Pyrcz), *Redonda* and *Dangond* present several common characters, particularly a stout, slightly hooked uncus, and a small, globular saccus (Figs. 12–15). The aedeagus is straight or slightly arched, but rather short (compared to other species of *Pedaliodes* complex), without the apical crest or lateral serration present in most species of *Pedaliodes* complex. The valvae are subtriangular have a smooth dorsal surface without any trace of dorsal

or apical processes, again, a feature characteristic to most species of the *Pedaliodes* complex (e.g. Fig. 15E: *Panyapedaliodes panyasis* (Hewitson, 1862), Fig. 15F: *Pedaliodes plotina* (Hewitson, 1862)). The only apparent difference is the presence of subunci (gnathos) in *S. albonotata* and *S. albarregas*, compared to absent or strongly reduced subunci in *Redonda*. Subunci are also reduced in *Dangond* (Fig. 13F), with the difference that in this genus, there is a stout base of subunci and a wide breach between it and the base of uncus, whereas subunci in *Redonda*, when present, are short tips adhering to ventral surface of uncus. The presence or absence of subunci in male genitalia of the species of *Pedaliodes* complex was strongly emphasized by ADAMS & BERNARD (1977, 1979, 1981), as one of the key diagnostic characters at the genus level. It is a fact that subunci are present in the overwhelming majority of > 300 species of the *Pedaliodes* complex, with the exceptions mentioned just above. However, PYRCZ (2004) described a species from northern Peru with no subunci, *Panyapedaliodes stellata*, and questioned the phyletic validity of this character. Interestingly, that species is also a paramo denizen, which suggests that the atrophy of subunci may have some adaptive role to oreol grassland habitats. Also, as we will see below, the absence of subunci in both *Dangond* and *Redonda* brings no phyletic value, since the two groups are very distantly related.

Female genitalia in *Steromapedaliodes* (*sensu* Viloría & Pyrcz), *Redonda* and *Dangond* (Fig. 19D: *Dangond dangondi*), contrary to other genera of the *Pedaliodes* complex (Fig. 19E: *Panyapedaliodes drymaea* (Hewitson 1858), Fig. 19F: *Pedaliodes plotina*), show no signa on bursa copulatrix. However, this is again hardly a phylogenetically informative character, but most likely a plastic adaptation to life in oreol habitats. In some species of *Altopedaliodes* signa are also lacking or are extremely reduced, as is also the case in another paramo-puna genus, *Punapedaliodes*. Ductus bursae is somewhat longer in *Steromapedaliodes* (*sensu* Viloría & Pyrcz) than in the other two genera, but in all three ductus bursae is weakly sclerotized compared to other taxa in the *Pedaliodes* complex, including *Pedaliodes*, and to an even more degree compared to *Panyapedaliodes*, *Corderopedaliodes* Forster, 1964, *Praepedaliodes* Forster, 1964 and also *Punapedaliodes*, being the latter a paramo-puna genus with a wide, slat-like strongly sclerotized lamella. Furthermore, in all the species of *Steromapedaliodes* (*sensu* Viloría & Pyrcz) and *Redonda*, lamella postvaginalis forms a wide shield covering the antrum, much narrower and less prominent than in *Dangond*. This character appears to be quite variable among different species of *Pedaliodes* and other species of the *Pedaliodes* complex, although some phylogenetically informative characters can be found in the shape of lamellas, for example in *Praepedaliodes* (Pyrcz et al. in press).

3.2. Molecular phylogeny

The mitochondrial dataset consisted of 2226 aligned nucleotides (*COI*: 1507 bp, tRNA–Leu: 67 bp, *COII*:

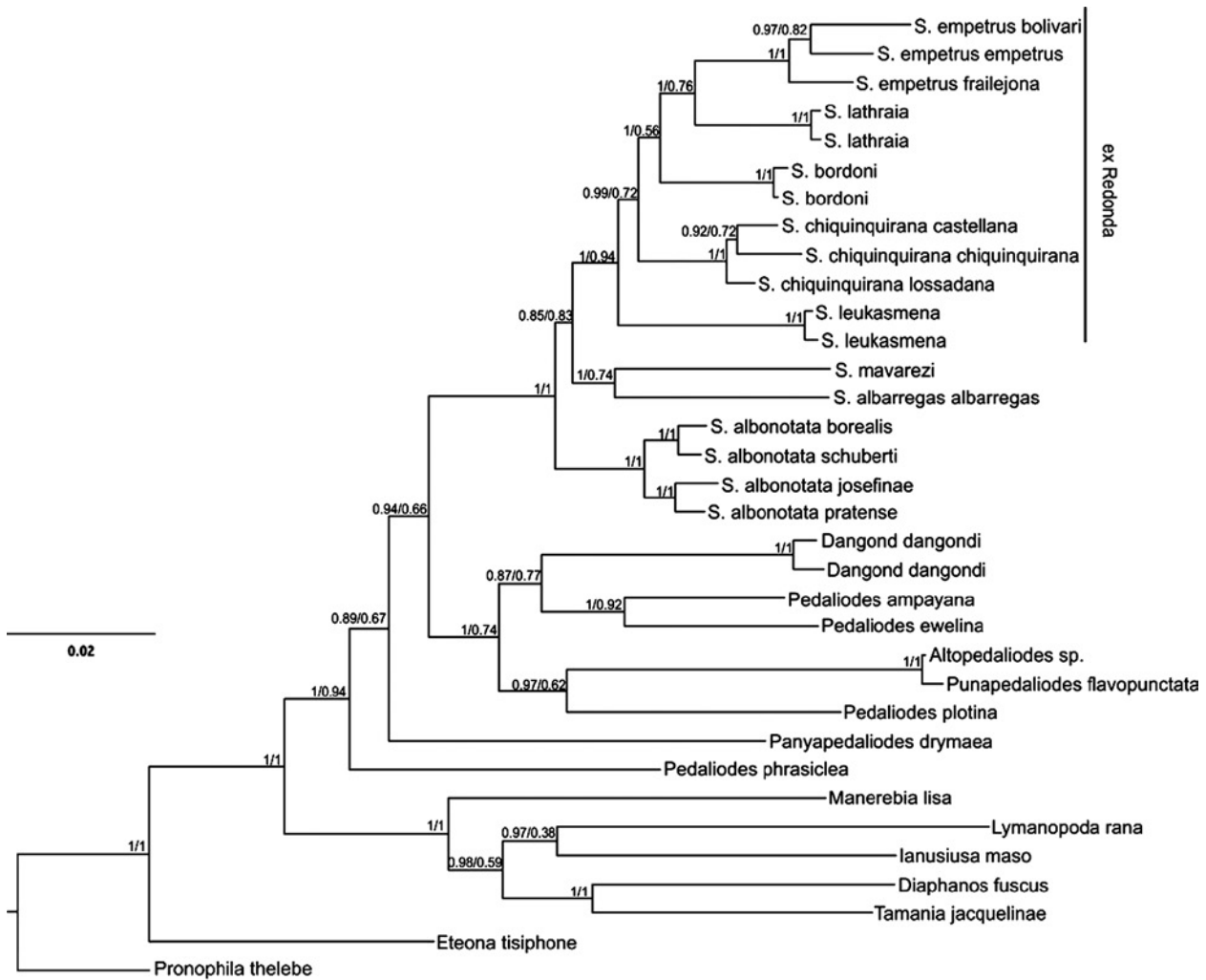


Fig. 2. Molecular phylogenetic hypothesis of the genus *Steromapedaliodes* sensu novo and some high-altitude tropical Pronophilina genera. Combined mtDNA (*COI*, *tRNA-Leu* and *COII*) and nuclear (*GAPDH*) data set. Values at the left of the slash (/) represent posterior probabilities from the Bayesian analyses, while values at the right of the slash (/) represent bootstrap values (0 to 1 scale) from the maximum likelihood analysis.

652 bp), of which 600 (26.95%) were variable and 453 (20.35%) were phylogenetically informative (excluding outgroup taxa). Maximum likelihood and Bayesian analyses resulted in almost identical tree topologies under the selected model of sequence evolution, GTR+G+I. The nuclear dataset consisted of 710 aligned nucleotide sequences of the *GAPDH* gene, of which 128 (18.03%) were variable and 172 (10.14%) were phylogenetically informative (excluding outgroup taxa). Again, maximum likelihood and Bayesian analyses resulted in almost the same tree topology under the selected model of sequence evolution, GTR+G+I. The mitochondrial and nuclear datasets were found to be congruent based on the CADM test ($p=0.18$) and a simultaneous phylogenetic analysis using both markers was therefore performed. As before, maximum likelihood and Bayesian analyses of the combined mitochondrial + nuclear dataset resulted in basically the same tree topology, which was very similar to the phylogenetic trees obtained with single DNA regions and particularly with mitochondrial data, although some differences are observed (see below). In all the analyses, re-

gardless of the partition and phylogenetic approach used, *Steromapedaliodes* (*sensu* Viloría & Pyrcz) and *Redonda* form a clade, with bootstrap and posterior probability values equal to 1 (Figs. 2, 3). The Bayesian and likelihood analyses of the combined mitochondrial + nuclear dataset indicate that *S. albonotata* is the sister group of the remaining taxa, with the newly described species (description 4 below) being associated with *S. albarregas*. In all the analyses, *Redonda* appears to be nested within *Steromapedaliodes* (*sensu* Viloría & Pyrcz), sometimes with quite high statistical support (posterior probability > 0.85). For instance, the combined analysis indicates that *Redonda* forms a clade with *S. albarregas* and one of the newly described species of *Steromapedaliodes* (see description 4 below).

Interestingly, two species previously associated with the genus *Redonda*, *R. empetrus* and *R. chiquinquirana* Ferrer-Paris, 2015, are extremely similar morphologically, yet they are never found in sympatry although sometimes they can be found flying in localities geographically close. The molecular phylogenetic analysis indicates

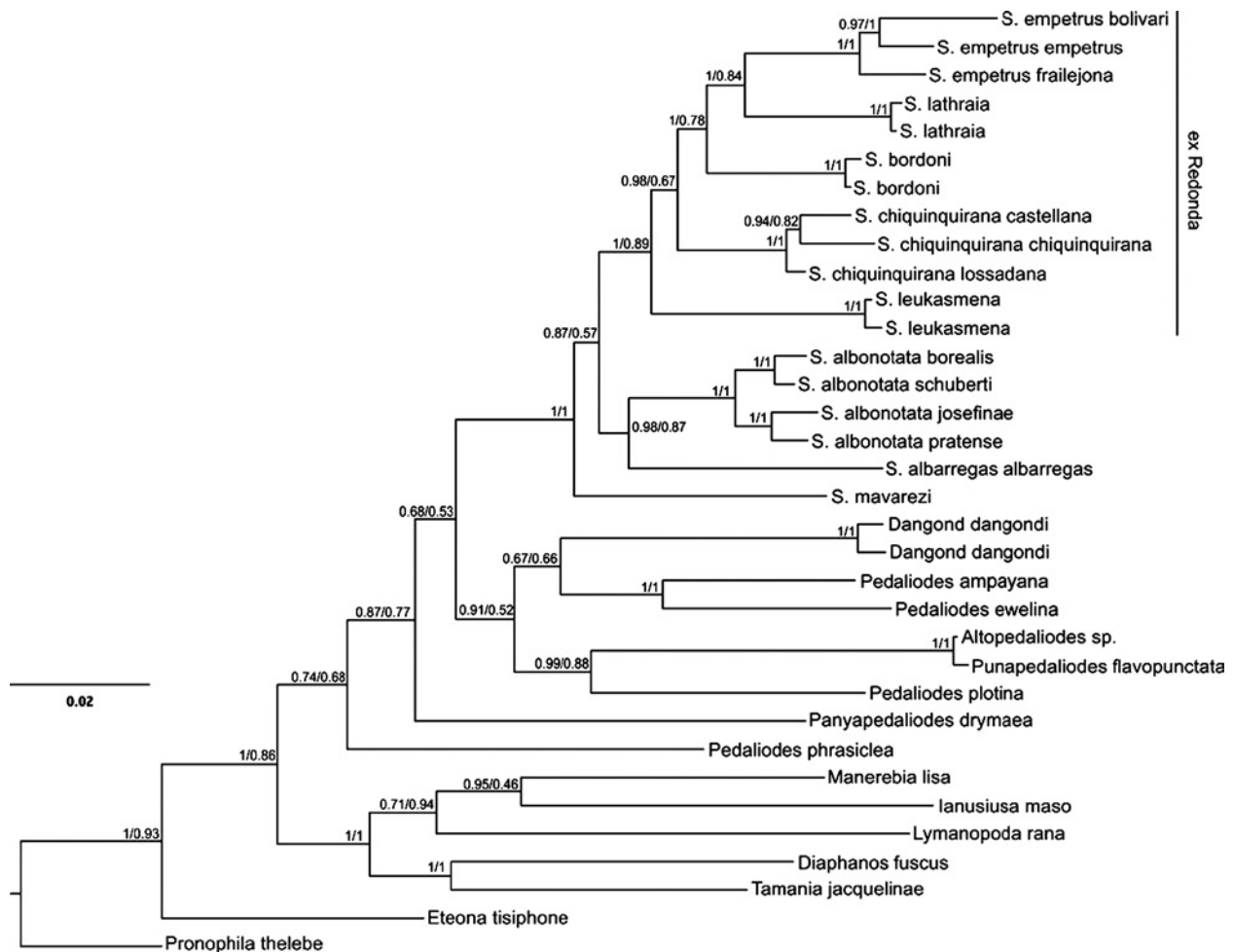


Fig. 3. Molecular phylogenetic hypothesis based exclusively on the mtDNA data, otherwise as specified for Fig. 2.

that they are genetically quite distant, which suggests that their morphological similarities are not the result of a recent common ancestry but probably a convergence somehow due to the adaptations to the same ecological conditions.

In all analyses the clade *Steromapedaliodes* (*sensu* Viloría & Pýrcz) + *Redonda* appears nested within the *Pedaliodes* complex, although more closely related to a clade comprising some *Pedaliodes* (*P. plotina*, *P. ampayana* Lamas, Viloría & Pýrcz, 2008, *P. ewelina* Pýrcz, 2008), *Dangond* and some genera belonging to *Pedaliodes* complex (e.g. *Altopedaliodes*, *Punapedaliodes*). Further taxonomic/systematic work will be necessary in order to establish with precision the phylogenetic relationships of the clade *Steromapedaliodes* (including *Redonda*) within the large *Pedaliodes* complex.

In summary, the high phylogenetic resolution provided by the analyses of mitochondrial and nuclear DNA markers, altogether with the morphological analyses described above, suggest that there is no valid reason to maintain *Steromapedaliodes* (*sensu* Viloría & Pýrcz) and *Redonda* as two separate genera. We therefore propose formally to synonymize *Redonda* **syn.n.** as a subjective junior synonym of *Steromapedaliodes*. Thus, *Steromapedaliodes sensu novo* represents a monophyletic clade composed by

two species previously associated with *Steromapedaliodes* (*sensu* Viloría & Pýrcz), five species previously associated with *Redonda* and two species described below.

3.3. Systematic overview

Steromapedaliodes Forster, 1964, *sensu novo*

[*Steropoda* Staudinger, *in litt.*] *nomen nudum*.

[*Steropoda* Thieme, 1905: 95, 141 (as a synonym of *Pedaliodes* Butler)] *nomen nudum*, Synonymy established by VILORÍA & PÝRCZ 2001].

Steromapedaliodes Forster, 1964: 148; MILLER 1968: 117; HUBER 1973: 195, 199; ADAMS & BERNARD 1977: 273; 1981: 348 (the latter as a synonym of *Altopedaliodes*); LAMAS [1997]: 49 (as a synonym of *Altopedaliodes*); VILORÍA & PÝRCZ 2001: 7; LAMAS et al. 2004: 215.

[*Altopedaliodes* Forster; ADAMS & BERNARD 1981: 348; ADAMS 1986: 246; DESCIMON 1986: 506; VILORÍA & PÝRCZ 1994: 347; LAMAS [1997]: 49–50 (in part)].

[*Redonda* Adams & Bernard, 1981: 367–368, **syn.n.**; ADAMS 1983: 474; 1984: 93; ADAMS 1985: 38; D'ABRERA 1988: 871; VILORÍA 1994: 180, 184, 185; 2000: 266, 269, 271; PÝRCZ 1999: 354; VILORÍA & PÝRCZ 2001: 1–2, 5–6, 12, 15, 17; VILORÍA et al. 2003: 21–23; PÝRCZ 2010a: 36, 38, 45, 179–186, 244; 2010b: 265–273.]

[*Punapedaliodes* Forster; HUBER 1973: 195.]

[“*Pedaliodes*” Butler; DESCIMON 1986: 510.]

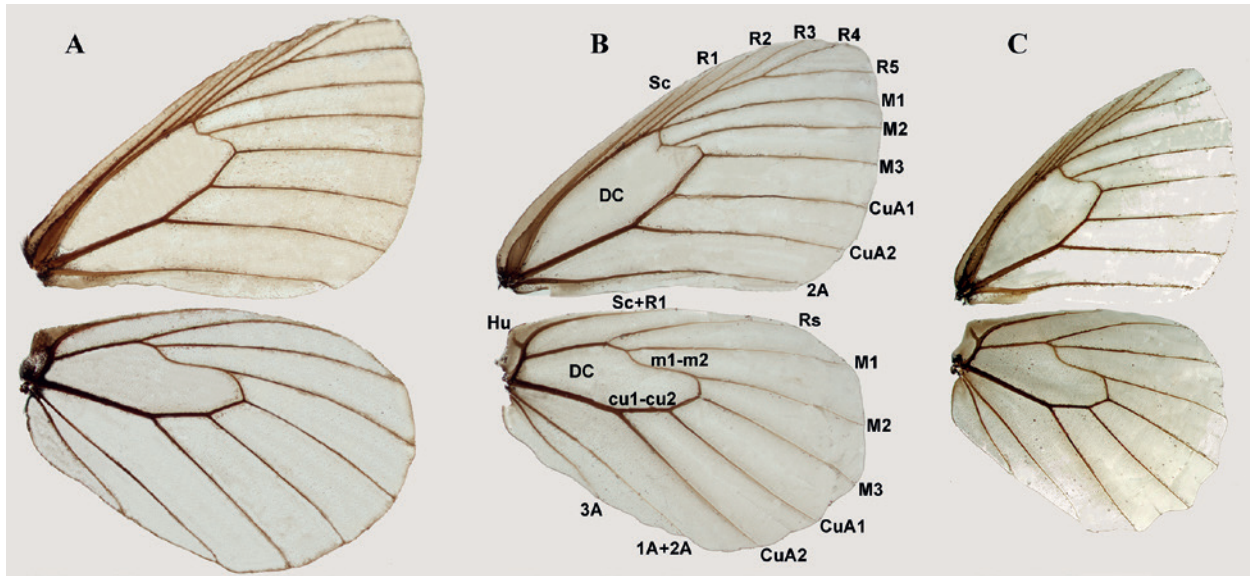


Fig. 4. Examples of wing venation of *Steromapedaliodes sensu novo*. **A:** *Steromapedaliodes bordoni*, Páramo del Batallón. **B:** *Steromapedaliodes chiquinquirana castellana*, Páramo de Las Moras. **C:** *Steromapedaliodes albonotata schuberti*, Boconó – La Vega. — **Abbreviations:** Sc Subcostal; R Radial; M Median; CuA Cubital; A Anal; H Humeral; DC Discal cell.

Type species: *Pedaliodes albonotata* Godman, 1905 (by original designation).

Generic diagnosis. Adults: Sexual dimorphism variable, slight and expressed only in a slightly smaller size of the females, to extreme, with very small, brachypterous females. Antenna: reaching $\frac{2}{3}$ of FW costa, mostly naked, except for some basal flagellomeres, club variable between species, between flattened and $2 \times$ than shaft to spoon like and three times thicker. Venation (Fig. 4: FW characterized by Sc, R1 and R2 independent, R3, R4 and R5 originating from a common root near or at base of m1–m2; R3 $\frac{1}{2}$ – $\frac{2}{3}$ the distance from discal cell to R4; R3–5 and M1 originating from the same root or marginally separated; m1–2 and m2–m3 slightly incurved basally; root of M2 emerging half way between root of M1 and M3, very slightly closer to M2; a vestigial discal veinlet occasionally present in some species (*S. chiquinquirana* (Ferrer-Paris) comb.n., *S. empetrus* (Thieme) comb.n.) but generally absent. HW venation with humeral vein present; root of M1 much closer to Rs than to M2; m1–m2 bent basally; m1–m2 2 – $2.5 \times$ as long as cu1–cu2; 1A2 and 1A3 independent. No androconial scales on the FW upperside. Wings colour patterns predominantly of variable shades of brown, with some discrete patterns of yellowish submarginal dots on the upperside, and white patches in forewing discal cell present in most species; a diagnostic row of hindwing underside submarginal milky white or snow white dots shaped as arrow-heads pointing basally, the latter character being, in our opinion, the strongest qualitative synapomorphy of the genus. Male genitalia: saccus globular and small; aedeagus straight or slightly arched with no apical crest or lateral serration; valvae subtriangular with a smooth dorsal surface without any trace of dorsal or apical processes. Female genitalia: no signa; ductus

bursae weakly sclerotized; postvaginal lamella wide, slat-like and strongly sclerotized, forming a wide shield covering the antrum. **Preimaginal stages** have not been entirely investigated for any extant species of this genus.

(1a) *Steromapedaliodes albonotata albonotata* (Godman), stat.rev.

(Figs. 5A,B, 12A, 17F)

[*Steropoda diplogramma* Staudinger, in litt.] *nomen nudum*.

[*Pedaliodes diplogramma* Thieme, 1905: 96 (synonymy given); GAEDE 1931: 488; FORSTER 1964: 148; LAMAS et al. 2004: 215 (all as synonym of *P. albonotata*)] *nomem nudum*.

Pedaliodes albonotata Godman, 1905: 189, pl. 10, fig. 11; THIEME 1905: 95, 96–97; WEYMER 1912: 257, pl. 54, row d; RILEY & GABRIEL 1924: 6; GAEDE 1931: 488, d'ABRERA 1988: 856, fig.; LAMAS [1997]: 49.

Steromapedaliodes albonotata (Godman); FORSTER 1964: 148, fig. 172 (male genitalia, erroneous); HUBER 1973: 195; VILORIA & PYRCZ 2001: 10; LAMAS et al. 2004: 215.

Altopedaliodes albonotata (Godman); ADAMS & BERNARD 1981: 345, 348; ADAMS 1983: 474; 1984: 93; 1987: 38, fig. 4; VILORIA 1994: 187.

Material examined. Lectotype, ♂, of *Pedaliodes albonotata* Godman [designated by VILORIA & PYRCZ 2001: 11], VENEZUELA: Mérida, Ex Staudinger, G–S, BMNH type No. Rh. 3991; 1 ♂: same data; 5 ♂ and 2 ♀: Mérida, Bricenno [sic] ZMHB; 1 ♂: Cordillera de Mérida, S. of Mérida, La Aguada, 3500 m, 07.viii.1977, M.J. Adams & G.I. Bernard, AB2; 3 ♂: same data, 10.viii.1977; 4 ♂: Cordillera de Mérida, S. of Mérida, SE of La Aguada, 3450 m, 20.viii.1977, M.J. Adams & G.I. Bernard, AB2; 1 ♂: Cordillera de Mérida, S of Mérida, Above La Aguada, 3550–3650 m, 10.viii.1977, M.J. Adams & G.I. Bernard, AB2; 1 ♂: same data, 3500 m BMNH; 2 ♂ and 1 ♀: Venezuela, Edo. Mérida, P. N. Sierra Nevada, La Aguada, 3400–3450 m, 01.ii.2007, T. Pyrcz leg. (male: prep. genit. 08/18.07.2013 J. Lorenc-Brudecka, female: prep. genit. 318/12.01.2016 J. Lorenc-Brudecka), MZUJ.

Type locality: Mérida, Venezuela.

Redescription. MALE (Fig. 5A): **Head:** Eyes glabrous, lustrous, chocolate brown with irregular seal brown patches, covered with long and dense black hair. Labial palpi $2 \times$ length of head, covered mostly with blackish brown hairy scales, except for some basal sandy yellow ventral hair, ventrally three times longer than dorsally, and adorned with some sparse snow-white scales. Frons with a tuft of long blackish brown hair. Antennae slender, composed of 33 flagellomeres, russet brown, mostly naked except for some snow white and grey scales on basal and sub-clubbal segments; club $2 \times$ wider than shaft, flattened dorso-ventrally, composed of 10 flagellomeres, ventrally lighter, orange brown. **Thorax:** black, dorsally covered with blackish brown and navy blue scales on metathorax, and sparse golden brown hair, denser on patagia; ventrally covered with dense brown, grey and sandy yellow hair; mid and hind legs russet brown, femorae mostly naked except for a crest of brown and grey hair, tibiae and tarsi densely covered with steely grey hair, numerous ventral spines on tarsi. **Wings:** FW (19–20 mm) with a subacute apex, slightly convex distal margin and gently bent at tornus; fringes dark grey at vein ends and snow white in between. FWD uniform dark chocolate brown, except for sparse snow white scales along costa and in apical area, a snow white elongated mid discal patch, and two snow white submarginal dots in M1–M2 and CuA1–CuA2. FWV uniform chocolate brown, lustrous, a shade lighter than on the upperside, with snow white scaling denser than on the upperside along costa and in apical area, and along distal margin to M3; discal cell white patch not apparent; a row of submarginal snow white minute dots from R5–M1 to CuA1–CuA2, somewhat more prominent in M1–M2. HW oval with a slightly undulated distal margin; fringes longer than on the FW, mostly dark grey, white scales in intravenal spaces, scarcer than on the FW. HWD uniform dark chocolate brown, covered with hairy scales in median half and along anal margin. HWV ground colour blackish brown and bistre brown with a heavy and regular overcast of snow white scales, with a few concentrations producing a more definite pattern, a short mid-costal streak, and a row of submarginal dots, two arrow-head like in Rs–M1 and, a much longer one in M1–M2, and three half-moon shaped in M2–M3, M3–CuA1 and CuA1–CuA2. **Abdomen:** dorsally and laterally covered with black, and basal segments, lustrous navy blue scales and dense, golden brown hair, ventrally with densely packed up scales of different colours, brown, grey and sandy yellow, and sparser hair. **Male genitalia** (Fig. 12A): Uncus aligned to tegumen shoulder, approximately the same length, slightly arched, and with a blunt tip; subunci $\frac{2}{3}$ the length of uncus, slender and compressed laterally; pedunculus short, subacute; vinculum s-shaped; saccus wide but shallow; valvae the length of tegumen+half uncus, elongated and slender, with a delicately irrorated dorsal surface and a subacute tip; aedeagus tubular, slightly arched, not contorted, with the proximal opening half the entire end, and an acute tip, without any crest or lateral teeth. **FEMALE** (Fig.

5B): Sexual dimorphism slight, lighter brown, especially on ventral surface, HWV duller, with sparser snow white pattern restricted to the costal streak and submarginal dots, with a noticeable median darker brown band. **Female genitalia** (Fig. 17F): As illustrated.

Remarks. GODMAN (1905), in the original description of *Pedaliodes albonotata*, referred to four males, two labelled Mérida in his collection (acquired from Staudinger) and two in the BMNH (one labelled La Culata and one La Pedregosa). Accordingly, VILORIA & PYRCZ (2001: figs. 1, 2) designated the Lectotype from Godman's collection. However, their treatment of *S. albonotata* was somewhat simplistic. They considered that the species is monotypic, and that the differences presented by several populations of *S. albonotata* from central and southern Cordillera de Mérida are negligible. They also failed to point out a detail that reveals crucial for the identification of the nominotypical subspecies. In fact, only the nominotypical subspecies of *S. albonotata* has conspicuous FWD white submarginal spots. The nominotypical subspecies of *S. albonotata*, as far as currently known, is restricted to the northern (El Chama) slopes of the Sierra Nevada, where it was collected along the La Mucuy – Laguna Verde and La Aguada – Loma Redonda trails. (Fig. 1C)

(1b) *Steromapedaliodes albonotata thiemeiana* Pyrcz, repl. name

(Figs. 7G,H, 12B, 17B)

Pedaliodes albonotata ab. *privigna* Thieme, 1905: 96–97.

Altopedaliodes albonotata ab. *privigna* (Thieme); GAEDE 1931: 488; ADAMS & BERNARD 1981: 348 (as synonym of *Altopedaliodes albonotata*).

Steromapedaliodes albonotata ab. *privigna* Thieme; VILORIA & PYRCZ 2001: 10; LAMAS et al. 2004: 215 (as synonym of *Steromapedaliodes albonotata*).

Material examined. Paralectotype, ♂, of *Pedaliodes albonotata* Godman, VENEZUELA: Pedregosa; **Paralectotype**, ♂, of *Pedaliodes albonotata* Godman: Culata, CB; 1 ♂: Quintero, [S.] Briceño, RB; 1 ♂: Quintero, 14.iv.1898, [S.] Briceño, RB; 1 ♂: Quintero, 04.v.1898, [S.] Briceño, RB; 1 ♂: no data, RB; 3 ♂ and 1 ♀: Mérida, Ex Grose Smith, 1910, JB; BMNH; 1 ♂: E. Mérida, Campo Ella [sic] Dist., Páramo de Conejos, 13000 ft., 09.ix.1938, J. Hanbury Tracey, Brit. Mus. 1939–117; 1 ♂ and 1 ♀: E. Mérida, Páramo Campanario, 13500 ft., 18.ix.1938, J. Hanbury Tracey, Brit. Mus. 1939–117; 1 ♂: Cordillera de Mérida, N. of Mérida, Río Albarregas, 3300 m, 14.viii.1977, M.J. Adams & G.I. Bernard, AB2; 10 ♂: same data, 3400 m, 15.viii.1977; 1 ♂: same data, 2650 m; 1 ♂: same data, 3650 m; 2 ♀: same data, 3450 m. BMNH; 1 ♂: Venezuela, x.23 von Dr. Lück, Ex Coll. Fruhstorfer, Collection v. Rosen, Präparat Nr. SA 439, ZSM; 1 ♂: Edo. Mérida, Laguna Negra, 3480 m, 12.ix.1971, H. Huber, ZSBS; 7 ♂ and 1 ♀: Edo. Mérida, Parque Nacional La Culata, Alto Mucujún, 3400–3500 m, 17.iv.1996, T. Pyrcz leg. (male: prep. genit. 03/18.07.2013 J. Lorenc-Brudecka); 5 ♂: same data but 2900–2950 m; 1 ♂: same data but 2950–3050 m; 5 ♂: same data but 3350–3400 m, 25.XII.1991; 1 ♂: same data but 29.XII.1991; 5 ♂: same data 3000–3050 m, 01.iv.1992, T. Pyrcz leg. (1 prep. genit. 01/18.07.2013 J. Lorenc-Brudecka); 12 ♂ and 2 ♀: same data but 3200–3250 m, 03.iv.1992; 1 ♂: Edo. Mérida, Parque Nacional La Culata, Mucujún, 01.iv.1992, T.

Pyrcz leg.; 2 ♂: Edo. Mérida, locality?; 1 ♂: Edo. Mérida, Parque Nacional La Culata, Monte Zerpa, 2200–3000 m, 20.ii.1996, T. Pyrcz leg.; 1 ♂: same data but 2950–3000 m, 31.v.1992; 1 ♂: same data but 31.v.1991, prep. genit. 1010/18 T. Pyrcz; 1 ♂: same data but 3250–3300 m, 13.ii.1996, J. Wojtusiak leg.; 1 ♂: Edo. Mérida, Parque Nacional La Culata, Alto Mucujún, 3400–3500 m, 06.ii.2007, T. Pyrcz leg.; 7 ♂: same data but 01.ii.2008; 1 ♂: Mérida, Quebrada Achotón, 3200, 09.i.1992, T. Pyrcz; 5 ♂ and 2 ♀: Edo. Mérida, Parque Nacional La Culata, Sector Monterrey, 3000–3050 m, 06.iv.2006, T. Pyrcz leg.; 1 ♂: Edo. Mérida, Parque Nacional La Culata, Jaji – Las Gonzales, Qda. La Boba, 3200–3250 m, 18.vii.2006, T. Pyrcz leg.; MZUJ; 5 ♂ and 2 ♀: Edo. Mérida, La Culata, “Cabaña de los Curas”, sector Monterrey, 3100–3150 m; 06.iv.2006, P. Boyer leg.; 8 ♂ and 1 ♀: Edo. Mérida, La Culata, 3000–3200 m, 3.iv.2006, P. Boyer leg., PBF.

Type locality: Mérida, Venezuela.

Diagnosis. **MALE** (Fig. 7G): This subspecies differs from the nominate *S. albonotata* in several aspects. First of all, its FWD discal cell white patch, although quite variable in size, is always wider, approximately the width and shape of *S. albonotata australis* ssp.n., whose patch has a characteristic steely sheen. In most examined individuals there are two, whitish FWD submarginal dots but they are invariably very small or obsolete, compared to conspicuous dots in *S. albonotata albonotata*. Importantly, the HWV is dull, and snow-white scaling is sparse, compared to the nominate subspecies or indeed to *S. albonotata australis* ssp.n. restricted to one or two costal streak and the submarginal dots, with the two arrowhead shaped much shorter and thinner. **Male genitalia** (Fig. 12B): Do not differ from the nominate subspecies except for the straight uncus. **FEMALE** (Fig. 7H): It is approximately the size of the male, typically slightly lighter coloured on the upperside and paler on the underside, especially on the FWV which has a rusty sheen, with a sandy yellow suffusion on the HWV, however not as prominent as in some other subspecies, in this respect similar to *S. albonotata borealis* ssp.n. **Female genitalia** (Fig. 17B): As illustrated.

Etymology. This subspecies is dedicated to the eminent German Lepidopterist Otto Thieme, author of excellent systematic monographs of the Pronophilina.

Remarks. In the original description of *S. albonotata* GODMAN (1905) noticed that the specimens from la Culata and La Pedregosa have very small, or obsolete two submarginal (white) spots on the FWD compared to the type specimens. THIEME (1905) called these subsequently as an aberration *privigna*. ADAMS & BERNARD (1981) obviously misunderstood the description of *privigna*, as they stated that this aberration corresponds to the individuals in which two white postdiscal spots on the forewing show through on the underside[!]. VILORIA & PYRCZ (2001) in their treatment of *Steromapedaliodes* (*sensu* Viloria & Pyrcz) did not deal with the name *privigna* and simply quoted its reference. None of the consulted authors had associated the expression of the white spots with any particular population. It is however evident from extensive

sampling throughout the range of *S. albonotata*, that the individuals whose white spots are faint or absent, corresponding with the diagnosis of *privigna*, represent a geographic form. Nevertheless, the name *privigna* was clearly created as an infrasubspecific epithet (ICZN article 45.6.2). For this reason, a new name is proposed. *S. albonotata thiemeiana* occurs on the SE Chama valley slopes of the Sierra de La Culata (La Pedregosa, Monte Zerpa, La Culata, Mucujún, Qda. Achotón) and locally in the watershed of Chama (Mucubají) (Fig. 1C).

(1c) *Steromapedaliodes albonotata australis* Pyrcz & Boyer, ssp.n.

(Figs. 5C–H, 12C, 17C,D)

Material examined. **Holotype**, ♂, VENEZUELA: Edo. Mérida / Táchira border, El Batallón, Mesa Alta, 2900–2950 m, 03.xii.2005, T. Pyrcz leg., MZUJ, to be deposited in MIZA; **Paratypes** (126 ♂ and 21 ♀): 14 ♂ and 2 ♀: Edo. Mérida, San José, Páramo de San José, 3000–3050 m, 05.xii.2007, T. Pyrcz leg. (1 male genit. 15/09.03.2006 T. Pyrcz); 1 ♂: same locality but 2800–2850 m, 11.ii.2007, T. Pyrcz leg.; 14 ♂: same data but 12.ii.2007; 6 ♂ and 6 ♀: same locality but 2950–3000 m, 20.ii.2008, T. Pyrcz leg. (prep. genit. 09/18.07.2012 J. Lorenc-Brudecka); 5 ♂: same locality but 2900–2950 m, 28.ii.2010; 21 ♂ and 3 ♀: Edo. Mérida, Tovar – Guaraque, Las Antenas, 2550–2600 m, 04.XII.2005, T. Pyrcz leg. (1 prep. genit. 02/18.07.2013 J. Lorenc-Brudecka); 16 ♂ and 1 ♀: Edo. Mérida / Táchira border, El Batallón, Mesa Alta, 2900–2950 m, 03.XII.2005, T. Pyrcz leg. (1 prep. genit. 04/18.07.2013 J. Lorenc-Brudecka); 4 ♂: Edo. Táchira, Páramo El Batallón, Antena – Cenegón, 3300–3350 m, 01.ii.2008, T. Pyrcz leg.; 3 ♂ and 1 ♀: Edo. Táchira, Páramo El Batallón, vía El Pulpito, 3500–3800 m, 03.iii.1996, T. Pyrcz; 4 ♂: Edo. Táchira, Páramo El Rosal, 2950–3050 m, 01–02.iii.1996, T. Pyrcz (1 prep. genit. 08/18.07.2013 J. Lorenc-Brudecka); 10 ♂ and 1 ♀: same locality but 3000–3050 m, 01.xii.2005; 1 ♂: Edo. Mérida, locality? MZUJ; 7 ♂ and 1 ♀: Edo. Mérida, San José vers Mucutuy km11, 3000, 5.xii.2005, P. Boyer leg.; 2 ♀: Edo. Mérida, Páramo de San José, 3100 m, 20.ii.2008, P. Boyer leg.; 7 ♂ and 1 ♀: Edo. Mérida, Mesa Alta, La Grita-Pregonero km3 3–5, bifurcation Pregonero vers Bailadores km 5–6, 2850 m, 29.xi.2005, P. Boyer leg.; 1 ♂: Edo. Mérida, Mesa Alta, Bailadores-Pregonero km 33,5, 5,5 km après la jonction de la Grita, 2750 m, 02.xii.2005, P. Boyer leg.; 8 ♂ and 1 ♀: Edo. Táchira, Páramo El Rosal, La Grita vers San José de Bolívar km 22, 3350 m, 01.xii.2005, P. Boyer leg.; 1 ♀: Edo. Táchira, Antenas, vía a Cenegón, Páramo El Batallón, 3200–3300 m, 19.ii.2008, P. Boyer leg.; 9 ♂ and 1 ♀: Edo. Mérida, Las Antenas, Tovar vers Guaraque km 22, 04.xii.2005, P. Boyer leg., PBF.

Type locality: Mesa Alta, El Batallón, Estado Táchira – Estado Mérida border, Venezuela.

Diagnosis. **MALE** (Fig. 5C,E,G): This subspecies is slightly smaller (FW length: 18–20 mm) than most other subspecies, probably except for the nominate and *S. albonotata borealis* ssp.n., although the infrasubspecific variation is appreciable, with the smallest individuals of all reported from the Páramo de Guaraque. The FWD discal cell white patch is also rather variable across the subspecies range and within populations, but it is larger than in the nominate and also from *S. albonotata thiemeiana*, in some individuals marginally entering the base of CuA1–CuA2 and CuA2–1A1B. It has a character-

istic steely sheen not apparent in any other subspecies. In most individuals there are two vestigial submarginal white dots on the FWD, but in some a third one shows in M3–CuA1. The HWV is more brightly patterned than in *S. albonotata thiemeiana*, with more whitish scaling, and comparable to the nominate, but the arrowhead submarginal spots are larger than in the latter subspecies, except for space M1–M2. **Male genitalia** (Fig. 12C): Do not differ noticeably from the nominate subspecies. **FEMALE** (Fig. 5D,F,H): Slightly smaller than the male, duller and slightly lighter brown on the upperside, lighter brown on the FWV and considerably lighter with a sandy yellow suffusion on the HWV. **Female genitalia** (Fig. 17C,D): As illustrated.

Etymology. The epithet of this subspecies refers to its southerly distribution relative to other populations of *S. albonotata*.

Remarks. *S. albonotata australis* ssp.n. has a wider range than any other subspecies and is probably also the most variable across its range. However, there are some morphological and genetic traits that allow its identification. It is usually very common wherever it occurs. It flies in humid lower paramo, and in some areas it occurs at much lower elevation than any other subspecies. In the Páramo de Guaraque area it can be found down to 2450 m, which is also due to the fact that the timberline is locally situated at a lower elevation than elsewhere in the Cordillera de Mérida (Fig. 1C).

(1d) *Steromapedaliodes albonotata sanchezi* Viloría & Pyrcz, stat.n.

(Figs. 6C, 12D)

Steromapedaliodes sanchezi Viloría & Pyrcz, 2001: 12, 13, figs. 5, 6, 11; LAMAS et al. 2004: 215.

Material examined. VENEZUELA: 1 ♂: Estado Mérida, Parque Nacional Sierra Nevada, Páramo del Tisure, 3300–3700 m, 28/29. xii.1994, J. Camacho & M. García (**Holotype** of *Steromapedaliodes sanchezi* Viloría & Pyrcz); 14 ♂: same data as the holotype (**Paratypes** of *S. sanchezi* Viloría & Pyrcz) MALUZ; 18 ♂ and 1 ♀: Venezuela, Estado Barinas, Parque Nacional Sierra Nevada, Los Morritos, 3000–3050 m, 06.i.2006, M. Costa leg. (1 prep. genit. 15/18.07.2013 J. Lorenc-Brudecka); 1 ♂: same data but 04.i.2006 (prep. genit. 07/05.2006 T. Pyrcz); 2 ♂: same data but 17.ii.2010, T. Pyrcz leg. (1 prep. genit. 12/18.07.2013 J. Lorenc-Brudecka) MZUJ; 1 ♂ and 1 ♀: Edo. Barinas, Los Morritos, 3000 m, 06.i.2006, M. Costa leg., PBF.

Type locality: Páramo El Tisure, Parque Nacional Sierra Nevada, Estado Mérida, Venezuela.

Diagnosis. **MALE** (Fig. 6C): This subspecies can be recognized immediately from any other, except for *S. albonotata pratense* ssp.n., by the very large FWD snow white discal cell patch which penetrates into the base of CuA1–CuA2, and extends widely into CuA2–1A/1B as far as vein 1A/1B and basally nearly to wing base. In

this respect this subspecies is almost identical to the next, *S. albonotata pratense* ssp.n. However, in *S. albonotata sanchezi* ssp.n. the presence of some chestnut and sandy yellow scales and denser hair give it a lighter appearance than in *S. albonotata pratense* ssp.n. There are no FWD submarginal white dots, or they are vestigial, whereas in *S. albonotata pratense* ssp.n. there is usually a small CuA1–CuA2 white dot. Another difference between the two subspecies is the lighter chocolate brown colour of the FWV in *S. albonotata sanchezi* ssp.n. compared to blackish brown in *S. albonotata pratense* ssp.n. **Male genitalia** (Fig. 12D): Do not differ noticeably from the nominate subspecies except for the more prominently arched aedeagus and the slightly lifted uncus tip. **FEMALE:** Not examined.

Remarks. This taxon was described as a separate species. Morphological differences between *S. albonotata sanchezi* ssp.n. and the nominotypical *S. albonotata* affect mostly the significantly larger wingspan in *S. a. sanchezi* ssp.n., and its considerably larger size of the FWD post-basal white patch. Male genitalia of *S. a. sanchezi* ssp.n. and *S. a. albonotata* are, however, almost indistinguishable. Considered the lack of sympatry, slight morphological differences and molecular phylogeny evidence, the two are considered here as subspecies of the same species. *S. albonotata sanchezi* ssp.n. is found on the eastern, Llanos slopes of the Sierra Nevada. It has been found only in a geographically restricted area in the north of the Sierra Nevada and southern extreme of the Serranía de Santo Domingo, however it is most probably much wider widespread to the south where, however, the Sierra Nevada eastern slopes have no trail access (Fig. 1C).

(1e) *Steromapedaliodes albonotata pratense* Pyrcz & Boyer, ssp.n.

(Figs. 6A,B,D, 12E, 16B)

Material examined. **Holotype.** ♂, VENEZUELA: Edo. Mérida, El Aguila–Piñango, Sector Potrero Km 26, 2900–2950 m, 09.iv.2006, T. Pyrcz leg. (to be deposited in MIZA), (prep. genit. 03/30.05.2006 T. Pyrcz); **Paratypes** (17 ♂, 5 ♀): VENEZUELA: Edo. Mérida, El Aguila–Piñango, Sector Potrero Km 26, 2900–2950 m, 09.iv.2006, T. Pyrcz leg., (1 prep. genit.: 03/30.05.2006 T. Pyrcz); (19 ♂, 4 ♀): same locality but 3100–3150 m, 04.iv.2006, (2 prep. genit.: 14/18.08.2013 J. Lorenc-Brudecka, 18/18.07.2013 J. Lorenc-Brudecka); 1 ♂: same locality but 08.iv.2006; (2 ♂), same locality but 3300–3350 m, 03.ii.2008; (5 ♂, 1 ♀), no data (1 prep. genit. 02/12.10.2011 J. Lorenc-Brudecka); 1 ♀: Edo. Trujillo, Timotes–Piñango, Alto de Tafayes, 2650–2700 m, 26.ii.2006, M. Costa leg., MZUJ; (10 ♂, 8 ♀): Edo. Mérida, vía El Aguila–Piñango km 26, Potrero, 3200–3300 m, 08.iv.2006, P. Boyer leg.; 1 ♂: Edo. Mérida, col de la route de Tafayes à Piñango 3100 m, 30.vii.2009 P. Boyer leg.; 1 ♂: Edo. Mérida, Potrero, route de Piñango, 3200 m, 30.vii.2009, P. Boyer leg., PBF.

Type locality: Sector El Potrero, vía Pico Aguila–Piñango, Estado Mérida, Venezuela.

Diagnosis. **MALE** (Fig. 6A,B): This subspecies can be recognized immediately from any other, except for

S. albonotata sanchezi ssp.n., by the large size (FW length 23–25 mm), and a very large FWD snow white discal cell patch which penetrates into the base of CuA1–CuA2, and extends widely into CuA2–1A/1B as far as vein 1A/1B and basally nearly to wing base. However, in *S. albonotata pratense* ssp.n. the HWD is darker and less hairy than in *S. albonotata sanchezi* ssp.n. There is usually one FWD vestigial submarginal white dot in CuA1–CuA2. FWV is blackish brown, darker than the chocolate brown of *S. albonotata sanchezi* ssp.n. HWV ground colour is almost black and snow white pattern is prominent, with a heavy white scale suffusion over the entire wing surface, a mid-costal streak generally longer than in the nominate, extending as far as vein M1, similarly in this respect to *S. albonotata sanchezi* ssp.n. All the submarginal dots are arrow-head shaped but the largest of all, the one in M1–M2, is slightly longer than in the nominate subspecies, also similar to *S. albonotata sanchezi* ssp.n. and considerably larger and longer than in *S. albonotata thiemeiana*. **Male genitalia** (Fig. 12E): Not differing from the nominate subspecies except for the slightly lifted uncus tip. **FEMALE** (Fig. 6D): Smaller than the male; wings colour pattern paler and duller dorsally and ventrally; HWV submarginal arrowhead white dots considerably smaller and shorter. **Female genitalia** (Fig. 16B): Papillae anales membranous in apical half, gently rounded in lateral view, covered with short, delicate and rather dense hair, sclerotized in basal half, with developed, apophyses posteriors short; sternite viii, in lateral view, as sclerotized as the basal part of papillae anales, without spiracle; viii fused with tergum viii in lateral view; postvaginal lamella sclerotized, wide, entirely covering the antrum; ductus bursae narrow, membranous, ½ the length of bursa, gradually opening into an oval bursa copulatrix, without signa; ductus seminalis connecting to bursa near the opening of ductus.

Etymology. This subspecies epithet is derived from the type locality, El Potrero, meaning meadow, thus *pratense* in Latin.

Remarks. This is a puzzling subspecies. It is apparently most closely related to *S. albonotata sanchezi* ssp.n. as indicated by both morphological and molecular data. However, the two are widely separated geographically by the high central part of the range, as they occur on the opposite slopes of the Cordillera. In between, another quite distinctive subspecies is found, *S. albonotata josefinae* ssp.n. Considered the above, it seems plausible that they differentiated in the process of allopatric divergence through extinction in the central part of the range, nowadays extremely dry but apparently connected by an ecological corridor during a warmer and more humid phase. For the time being, *S. albonotata pratense* ssp.n. is known only from the type locality situated in NW, Lago de Maracaibo slopes of the Sierra de La Culata, however it is most probable that its distribution extends southwards where there are very few access trails to the subparamo (Fig. 1C). *S. albonotata pratense* ssp.n. has been found

only flying in humid meadows within the forest paramo ecotone at 2900–3150 m approximately. Male genitalia differ marginally from the nominate subspecies, as in *S. a. sanchezi* ssp.n. the uncus tip is slightly more lifted, and valvae are even narrower than in other subspecies.

(1f) *Steromapedaliodes albonotata josefinae* Pyrcz & Boyer, ssp.n.

(Figs. 7C–F, 12F, 17E)

Material examined. **Holotype**, ♂, VENEZUELA: Edo. Mérida, El Baho, El Hatico, 3000–3050 m, 19.XI.2005, T. Pyrcz leg. (currently in MZUJ, to be deposited in MIZA); **Paratypes** (69 ♂ and 12 ♀): 6 ♂ and 1 ♀: Edo. Mérida, Mucubají – Los Frailes, Qda. Km 4, 3200–3250 m, 22.xi.2005, T. Pyrcz leg.; 3 ♂: same locality but 3400–3450 m, 02.ii.2008; 4 ♂: Edo. Mérida, Mucubají – Santo Domingo, Los Frailes, 3000–3050 m, 08.vii.2006, T. Pyrcz leg. (1 prep. genit. 16/18.07.2013 J. Lorenc-Brudecka); 2 ♂: same data but 31.vii.2009; 1 ♂: Parque Nacional Sierra Nevada, Mucubají, 3500–3550 m, 28.iii.1992, T. Pyrcz leg., prep. genit. 11/18.07.2013 J. Lorenc-Brudecka; 1 ♂ and 1 ♀: Edo. Mérida, El Baho, El Hatico, 3000–3050 m, 19.xi.2005, T. Pyrcz leg.; 6 ♂: same data but 21.xi.2005; 3 ♂: same data but 24.xi.2005; 1 ♂: same data but 14.xi.2005; 4 ♂: Edo. Mérida, El Baho, via paramo, 3050–3150 m, 26.xi.2005, T. Pyrcz leg.; 1 ♂ and 1 ♀: Edo. Mérida, El Baho, La Ciénaga, 2900 m, 26.xi.2005, T. Pyrcz leg.; 2 ♂: Edo. Mérida, Parque Nacional Sierra Nevada, El Baho, 3000–3050 m, 28.i.2008, T. Pyrcz leg.; 5 ♂ and 2 ♀: Edo. Mérida, Pueblo Llano – Tuñame, Qda. Ranchería, 3000–3050 m, 27.xi.2005, T. Pyrcz leg., (1 female genit. 330/19.01.2016 J. Lorenc-Brudecka); 2 ♂: Edo. Trujillo, Tuñame – Esnujaque, La Morita, 2900–2950 m, 16.ii.2010, T. Pyrcz leg.; 1 ♂: Edo. Trujillo, Timotes SE, Antenas, 2850–2900 m, 29.vii.2009, T. Pyrcz leg.; 1 ♂: no data; 2 ♂: Edo. Mérida, Laguna Negra, 28.iii.1992, T. Pyrcz leg., MZUJ; 5 ♂ and 1 ♀: Edo. Mérida, Oberes Santo Domingo-tal, 2800 m, 21.iii.1971, H. Huber; 1 ♂ and 1 female, same data, 3050 m, 05.ix.1971, (**paratypes** of *S. sanchezi* Viloria & Pyrcz) ZSM; 1 ♂ and 1 ♀: Mérida, km 12.5, Apartaderos–Santo Domingo, ca. 3100–3200 m, 26.ix.1997, A. Neild [AFN]; 2 ♂: Edo. Mérida, El Baho, Santo Domingo vers Apartaderos km 4, 3300 m, 24.xi.2005, P. Boyer leg.; 4 ♂ and 3 ♀: Edo. Mérida, El Baho, Santo Domingo vers Apartaderos km 4, 2850–3100 m, 21.xi.2005, P. Boyer leg.; 2 ♂ and 2 ♀: Edo. Mérida, El Baho, Santo Domingo vers Apartaderos km 4, 2850–3100 m, 26.xi.2005, P. Boyer leg.; 1 ♂: Edo. Mérida, El Baho, Santo Domingo vers Apartaderos km 4, 2800–3000, 19.xi.2005, P. Boyer leg.; 5 ♂ and 1 ♀: Mérida, Ranchería vers Niquitao km7, (route Pueblo Llano–Niquitao), 3050 m, 27.xi.2005, Pierre Boyer leg.; 1 ♂: same data but 23.xi.2005; 1 ♂: Mérida, SE de Timotes, près de la route de Pueblo Llano, 2700–2800 m, 29.vii.2009, Pierre Boyer leg.; 6 ♂ 1 ♀: Edo. Mérida, Mucubají vers Los Frailes km 4, 3400 m, 22.xi.2005, P. Boyer leg.; 1 ♂: same locality but 3200 m, 02.iv.2006; 1 ♂: Edo. Mérida, Los Frailes, Santo Domingo vers Apartaderos km 10, 2900–3000 m, 19.iv.2006, P. Boyer leg., PBF.

Type locality: Estado Mérida, Santo Domingo Valley, El Baho.

Diagnosis. **MALE** (Fig. 7C,E): This is a large subspecies (FW length: 20–22.5 mm), about the same size as *S. albonotata sanchezi* ssp.n., *S. a. pratense* ssp.n. and *S. a. schuberti*., considerably larger than the nominate, *S. a. thiemeiana* and *S. a. australis* ssp.n. Its FWD discal cell snow white patch is smaller than in *S. a. sanchezi* ssp.n. and *S. a. pratense* ssp.n., does not extend into wing base and penetrates only marginally into base of cells

CuA1–CuA2 and CuA2–1A/1B, which is still more than *S. a. schuberti*, which has an even smaller white patch, narrower, rectangular rather than square, and never extending, not even marginally into bases of the two cells. Some individuals present a tiny white submarginal dot in cell CuA1–CuA2. FWV is blackish brown, similar to *S. a. pratense* ssp.n. and *S. a. schuberti*, but darker than the chocolate brown of *S. a. sanchezi* ssp.n. HWV, although quite variable, is generally less speckled with white scales, mid–costal streak extends to vein M2, and the white arrow-head shaped submarginal dots are considerably smaller and shorter than in the above mentioned two subspecies. **Male genitalia** (Fig. 12F): similar to the nominate subspecies except for the straight uncus, as in *S. a. sanchezi* ssp.n., and a longer, gently s-shaped aedeagus, valvae are slightly longer than in other subspecies, nearly approaching the length of tegumen+uncus. **FEMALE** (Fig. 7D,F): Slightly smaller than the male, FW and HWD ground colour lighter brown; FWV slightly lighter brown and duller; HWV with a sandy yellow overcast and a noticeable darker brown median band. **Female genitalia** (Fig. 17E): As illustrated.

Etymology. This subspecies is called after Josefina Balzam, a Venezuelan citizen of Polish origin, the owner of the area of El Baho where it was discovered, in recognition for her help during the carrying out of this research.

Remarks. This subspecies is geographically squeezed within the west-east oriented *S. a. pratense* ssp.n. and *S. a. sanchezi* ssp.n. on the one hand, and north-south oriented *S. a. thiemeiana* and *S. a. borealis* ssp.n. on the other. It is also morphologically intermediate between the four as far as its wing size and the diagnostic FWD discal cell snow patch size and shape are concerned. It seems to be limited to the small geographical region comprised within the Santo Domingo valley (Fig. 1C). This is a similar distribution pattern as for the sympatric *Lymanopoda marianna valentinae* Pyrcz, 2009 (PYRCZ et al. 2009). *S. a. josefinae* ssp.n. occurs in humid gullies amidst bamboo clumps but also in open, and drier paramo dominated by *Espeletia*.

(1g) *Steromapedaliodes albonotata schuberti* Viloría & Pyrcz, stat.n.

(Figs. 7A,B, 13A, 17A, 21C)

Steromapedaliodes schuberti Viloría & Pyrcz, 2001: 13–14, figs. 7, 8, 12; LAMAS et al. 2004: 215.

Material examined. Holotype, ♂, of *Steromapedaliodes schuberti* Viloría & Pyrcz, VENEZUELA: Trujillo, Parque Nacional Guaramacal, vía Boconó–Guaramacal, 1500–2700 m, 29.viii.1991, J. De Marmels; 2 ♂: same data, **Paratypes** of *S. schuberti* Viloría & Pyrcz MIZA; 9 ♂ and 3 ♀: Estado Trujillo, Parque Nacional Guaramacal, Páramo del Guaramacal, 2800–3100 m, 24.viii.1995, J. Camacho & M. García; 7 ♂ and 1 ♀: Estado Lara, Parque Nacional Dinira, Páramo del Cendé, 3100 m, 08.viii.1996, M. García, **Paratypes** of *S. schuberti* Viloría & Pyrcz; 1 ♂: Páramo de Ortiz,

2850–3100 m, Estado Trujillo, 12.xi.1991, A. Viloría & E. Moscó, MALUZ; 17 ♂: Trujillo, Parque Nacional Guaramacal, Boconó La Vega, 2900–2950 m, 15.ii.2007, T. Pyrcz leg.; 11 ♂ and 1 ♀: same data but 16.ii.2007; 2 ♂ and 1 ♀: Parque Nacional Guaramacal, vía Las Antenas, 3000–3050 m, 08.xii.2005, T. Pyrcz leg.; 16 ♂ and 2 ♀: Parque Nacional Guaramacal, Paso–Las Antenas, 2900–2950 m, 26.iv.2007, T. Pyrcz leg. (2 prep. genit. 05/18.07.2013 J. Lorenc-Brudecka, 07/18.07.2013 J. Lorenc-Brudecka); 1 ♀: Parque Nacional Guaramacal, vía La Vega de Guaramacal, 2800–2850 m, 22.xii.2004, M. Costa leg., MZUJ; 5 ♂ and 3 ♀: Edo. Trujillo, Massif du Guaramacal, Las Antenas, 2700–2800 m, 26.vii.2009, P. Boyer leg.; 2 ♂ males, 1 ♀: Edo. Trujillo, Boconó vers Guaramacal, Les Antennes, 2850 m, 08.xii.2005, P. Boyer leg.; 1 ♂: Edo. Trujillo, route Boconó vers La Vega, Guaramacal, 2700 m, 17.ii.2007, T. Pyrcz leg., PBF.

Type locality: Vía Boconó–Guaramacal, Parque Nacional Guaramacal, Estado Trujillo, Venezuela.

Diagnosis. MALE (Fig. 7A): This subspecies is larger (FW length: 19.5–22 mm) than the nominate or *S. a. thiemeiana* but marginally smaller than *S. a. pratense* ssp.n. and *S. a. josefinae* ssp.n. The FWD discal cell snow-white patch is generally marginally smaller than in *S. a. josefinae* ssp.n., rectangular, compact and usually with sharp edges, unlike the latter subspecies whose basal edge is often blurry. It never presents any trace of FWD submarginal white dots, contrary to more southerly subspecies. FWV is blackish brown with white scaling restricted to costal and apical area. HWV ground colour is very dark, nearly black, and densely speckled with white scales, similarly to *S. a. pratense* ssp.n. but its arrowhead shaped white patch in M1–M2 is consistently shorter. **Male genitalia** (Fig. 13A): Slightly different from the nominate subspecies in the wider and stouter subunci and wider valvae, not narrowing gradually but tapering at a blunt tip. **FEMALE** (Fig. 7B): Approximately the size of the male, very slightly lighter on the upperside and duller, without the olive sheen typical of the male; FWV duller with more prominent yellowish scaling in apical area; HWV with a heavy sandy yellow overcast, and smaller arrow-head submarginal whitish dots. **Female genitalia** (Fig. 17A): As illustrated.

Remarks. This taxon was originally described as a species, as was *S. a. sanchezi* ssp.n. However, it is not morphologically distinct enough to deserve a separate status. Also, it clearly forms an internal clade of *S. albonotata*.

(1h) *Steromapedaliodes albonotata borealis* Pyrcz & Boyer, ssp.n.

(Figs. 6E–H, 13B, 16A)

Material examined. Holotype, ♂, VENEZUELA: Edo. Trujillo, Parque Nacional Dinira, Páramo Jabón (South), 3100–3150 m, 07.ii.2008, T. Pyrcz leg. (in MZUJ, to be deposited in MIZA); **Paratypes** (57 ♂ and 3 ♀): 4 ♂ and 1 ♀: same data as the Holotype; 31 ♂: Edo. Trujillo, Boconó – Burbusay, Cabimbu de San Miguel, 2900–2950 m, 19.ii.2007, T. Pyrcz leg.; 4 ♂: Edo. Trujillo, Páramo Las Moras, 2950–3050 m, 21.ii.2007, T. Pyrcz leg. (1 prep. genit. 13/18.07.2013 J. Lorenc-Brudecka); 2 ♂ and 1 ♀: Edo. Trujillo, vía Páramo Ortiz, Qda. Ortiz, 2900–2950 m, 05.ii.2008, T. Pyrcz

leg. (1 prep. genit. 17/18.07.2013 J. Lorenc-Brudecka); 3 ♂: Edo. Trujillo, Parque Nacional Dinira, Páramo Cendé, 3000–3050 m, 13.ii.2010, T. Pyrcz leg., MZUJ; 4 ♂: Edo. Trujillo, Páramo de Ortiz, 2900 m, 05.ii.2008, P. Boyer leg.; 2 ♂: Edo. Trujillo, Cabimbu de San Miguel, nord de Boconó, 3000 m, 19.ii.2007, T. Pyrcz leg.; 5 ♂ and 1 ♀: Edo. Trujillo, Páramo de Jabón, NE de Carache, Masif du Cendé, 3100, 07.ii.2008, P. Boyer leg., PBF.

Type locality: Páramo de Las Rosas, Parque Nacional Dinira, Estado Trujillo, Venezuela.

Diagnosis. MALE (Fig. 6E,G): *S. albonotata borealis* ssp.n. is smaller (FW length: than the subspecies found directly southwards, and similar in size to *S. a. thiemeiana*. The FWD discal cell snow-white patch is slightly smaller than in *S. a. schuberti*. As with the latter subspecies, there is no trace of any FWD submarginal white dots. FWV is blackish brown with rather prominent whitish speckling along costa and in apical area, slightly more prominent than in *S. a. schuberti*. HWV ground colour is blackish brown dusted densely with white scales. Submarginal white dots are less conspicuous than in *S. a. schuberti* and in some individuals, especially in the more northerly populations, barely noticeable, the arrow-head shaped M1–M2 spot is generally smaller and shorter than in *S. a. schuberti*. **Male genitalia** (Fig. 13B): differing little from the nominate subspecies, but even less so from *S. a. schuberti* with which it shares similarly shaped valvae, not narrowing apically as in other subspecies, and rather stout subunci. Aedeagus is slender and nearly straight. **FEMALE** (Fig. 6F,H): Slightly lighter and duller on both the upper and underside; sandy overcast on the HWV less prominent than in other subspecies, in some individuals not apparent, arrow-head submarginal dots larger and longer than in the male, especially in the subapical area. **Female genitalia** (Fig. 16A): As illustrated.

Etymology. The subspecific name of this taxon refers to its northerly distribution compared to other geographical races of *S. albonotata*.

Remarks. This is the northernmost subspecies of *S. albonotata* distributed between the Niquitao massif and the Páramo de Cendé (Fig. 1C). It is found at similar elevations as other subspecies and occurs in a mosaic of forest and paramo and in the lower paramo, occasionally sympatrically with local populations of other *Steromapedaliodes sensu novo*. Its morphology and molecular data indicate it is most closely related to *S. a. schuberti*, an endemic subspecies found only in the Guaramacal Massif.

(2a) *Steromapedaliodes albarregas albarregas*
(Adams & Bernard)

(Figs. 8A,B, 13C, 16C)

Altopedaliodes albarregas Adams & Bernard, 1981: 345, 347–348, figs. 1 (male genitalia), 14, 15.

Altopedaliodes albarregas Adams & Bernard; ADAMS 1983: 474; 1986: 303; 1987: 38, fig. 4.

Pedaliodes albarregas (Adams & Bernard); D'ABRERA 1988: 864.

Steromapedaliodes albarregas (Adams & Bernard); VILORIA & PYRCZ 2001: 9–10; LAMAS et al. 2004: 215.

Material examined. Holotype, ♂, of *Altopedaliodes albarregas* Adams & Bernard, VENEZUELA: Estado Mérida, Cordillera de Mérida, Río Albarregas, 3150 m, 16.viii.1977, M.J. Adams, AB2; 2 ♂: same data; M.J. Adams & G.I. Bernard, AB2; 1 ♀: same locality, 3300 m, 14.viii.1977; 5 ♂: same locality, 3100–3150 m, 13.viii.1977; 1 ♀: same locality, 3000, 19.vi.1975; 1 ♂: same locality, 3200, 17.vi.1975; 1 ♂: same locality, 3200, 20.vi.1975; 1 ♂: same locality, 3200 m, 21.vi.1975; 1 ♂: same locality, 3100, 15.viii.1977; 1 ♂: Estado Mérida, Cordillera de Mérida, La Aguada + La Montaña, 2500 m, 03.viii.1977 [locality erroneous?], AB2, **Paratypes** of *A. albarregas* A. & B. BMNH; 2 ♂ and 2 ♀: Edo. Mérida, Páramo de los Conejos, Las Gonzales, Quebrada de la Boba, 3150 m, 19.ii.2010, T. Pyrcz leg., PBF; 13 ♂ and 1 ♀: Edo. Mérida, La Culata – Jají, Qda. De La Boba, 3200–3250 m, 18–19.ii.2010, T. Pyrcz leg. (5 ♂ prep. genit.: 08/21.09.2010 T. Pyrcz, 20/18.07.2013 J. Lorenc-Brudecka, 04/27.04.2013 J. Lorenc-Brudecka, 19/18.07.2013 J. Lorenc-Brudecka, 01/18.07.2013 J. Lorenc-Brudecka) MZUJ.

Type locality: Cordillera de Mérida, upper Río Albarregas valley.

Redescription. MALE (Fig. 8A): **Head:** glabrous, chocolate brown with dark brown irregular patches, covered with dense black hair; collar golden yellow; labial palpi 2 × length of head covered with longer blackish brown and shorter golden yellow hair, ventrally three times longer than dorsally; frons with a tuft of long, grey and brown hair. Antennae slender, reaching $\frac{2}{3}$ the length of costa, composed of 33 flagellomeres, club 2 × width of shaft, formed gradually, compressed dorso-ventrally, blackish brown dorsally, golden brown ventrally, mostly naked, except for some sparse white scales on basal segments. **Thorax:** black, dorsally covered with golden brown hair, thicker on patagia, ventrally covered with dense brown, grey and sandy yellow hair; mid and hind legs brown, femorae covered with brown hair, tibiae and tarsi densely covered with grey and brown, and sparse milky white scales, numerous ventral spines on tarsi. **Wings:** FW (21–22 mm) triangular with a subacute apex, straight distal margin and tornus at a straight angle. Fringes mostly snow white and black at vein ends. FWD black brown, except for some sparse white scales along costal margin and a snow white oblique mid discal cell band of some 2 mm width throughout, extending from Sc to just beyond vein CuA2. FWV blackish brown, glossy, slightly lighter than on the upperside turning dark chocolate brown distally; white scaling along costa; snow white oblique mid discal cell shaped as on the upperside; a straight row of five, half-moon shaped, milky white, small submarginal dots from R4–R5 to M3–CuA1, the largest of which in R5–M1. HW oval sharply angles at apex and tornus with a slightly undulated distal margin. Fringes white and black at vein ends. HWD uniform blackish brown, basal $\frac{2}{3}$ hairy. HWV ground colour blackish brown and chocolate brown with rather sparse dusting of silver scales slightly denser only in median area where forming a mid-costal streak and anal wedge; a row of five arrow-head shaped,

milky white submarginal dots, the largest of which in Rs–M1. **Abdomen:** dorsally and laterally covered with black, and basal segments, lustrous navy blue scales and dense, golden brown hair, ventrally with densely packed up scales of different colours, brown, grey and sandy yellow, and sparser hair. **Male genitalia** (Fig. 13C): Tegumen dorsum gently arched; uncus $\frac{3}{4}$ the length of tegumen shoulder, slender, nearly straight with gently down curved blunt tip; subunci $\frac{2}{5}$ the length of uncus, massive at base, narrowing to a sharp tip, compressed laterally; pedunculus little developed, blunt; vinculum gently s-shaped; saccus flattened dorso-ventrally, shallow; valvae the length of tegumen + half uncus, massive at base, then gradually narrowing to a blunt tip, with a delicately irrorated dorsal surface; aedeagus tubular, slightly arched, not contorted, with the proximal opening half the entire end, and an acute tip, without any crest or lateral teeth. **FEMALE** (Fig. 8B): Lighter brown on both the upper and underside, with more prominent sandy yellow speckling on the underside, especially on FWV subapical area and on the HW; arrow-head submarginal milky white dots more prominent. **Female genitalia** (Fig. 16C): Papillae anales membranous in apical half, flattened in lateral view, covered with short, delicate and rather dense hair, sclerotized in basal half, with developed, short apophyses posteriores; sternite viii, in lateral view, as sclerotized as the basal part of papillae anales, without spiracle; viii fused with tergum viii in lateral view; postvaginal lamella sclerotized, massive, strongly sclerotized, entirely covering the antrum; ductus bursae wide, membranous, the length of bursa, suddenly opening into a rounded bursa copulatrix, without signa; ductus seminalis connecting in the middle of ductus bursae.

Remarks. This species was described based on a series of individuals found in the uppermost valley of the river Albarregas in Sierra de La Culata. For many years it was known only from the type locality until its rediscovery in the southern extremity of the same La Culata range. As pointed out correctly by ADAMS & BERNARD (1981), *S. albarregas* and *S. albonotata* are separated ecologically. Even though they may occur locally in the same area, in the uppermost cloud forest at the paramo border, *S. albonotata* keeps close to the ground level, flying above marshy meadows, whereas *S. albarregas* flies in the canopy. *S. albarregas* is also a much more energetic flier, and actively patrols along apparently well-established pathways. In the Quebrada la Boba *S. albarregas* was found to be quite common in February of 2010, and it appears that the species is highly seasonal.

(2b) *Steromapedaliodes albarregas mauroi* Pycrz, ssp.n.

(Fig. 8E)

Material examined. *Holotype*, ♂, VENEZUELA: Edo. Barinas, Parque Nacional Sierra Nevada, Los Morritos, 3000 m, 06.i.2006, M. Costa leg. (in MCC, to be deposited in MIZA).

Type locality: Venezuela, Cordillera de Mérida, Los Morritos.

Diagnosis. **MALE** (Fig. 8E): This subspecies differs from the nominate in a similar way as *S. albarregas prietoi* ssp.n. that is in the wider, approximately 3 mm wide FW mid discal cell snow white band, which however does not enter cell CuA1 + CuA2. As in *S. a. prietoi* there is a whitish FW postdiscal streak. There are four fully developed moon shaped milky white spots from R4–R5 to M2–M3 and two tiny dots in M3–CuA1 and CuA1–CuA2. This subspecies differs from *S. albarregas prietoi* ssp.n. most of all in the more prominent ventral white dusting, on the FWV apical area, and especially on the HWV where white scales densely cover the entire wing surface. Also, the arrowhead shaped submarginal spots are considerably larger than in *S. a. prietoi* and milky white, similarly to the nominate subspecies. **Male genitalia:** Not examined. **FEMALE:** Not known.

Etymology. This subspecies is dedicated to its discoverer, an amateur lepidopterist from Caracas, Mauro Costa, in recognition for his support to the first author over several years of research visits in Venezuela.

Remarks. This subspecies is known only from the type locality, the valley of the Río Gavidia, one of the tributaries of Apure, on the eastern slopes of the Sierra Nevada (Fig. 1D). It is the same locality as for *S. albonotata pratense* ssp.n., which is locally sympatric, but contrary to *S. albarregas* occurs also at higher elevations in the open paramo as far as the Páramo de Tisure. In morphological terms it is intermediate between the nominate found on the southern slopes of the Sierra de La Culata and *S. albarregas prietoi* ssp.n. detected on the north-western slopes of the range.

(2c) *Steromapedaliodes albarregas prietoi* Pycrz, ssp.n.

(Figs. 8C,D, 13D, 16D)

Material examined. *Holotype*, ♂, VENEZUELA: Edo. Mérida, via Piñango, Sector El Potrero, 3200 m, 08.iv.2006, M. Costa leg. (in MCC to be deposited in MIZA); *Paratypes* (1 ♂ and 1 ♀): 1 ♂: Edo. Mérida, El Aguila – Piñango, Sector Potrero (Km 26), 2900–2950 m, 09.iv.2006, T. Pycrz leg. (male: prep. genit. 09/21.09.2010 A. Zubek, female: prep. genit. 332/19.01.2016 J. Lorenc-Brudecka), MZUJ.

Type locality: Sector El Potrero, Piñango Road, NW slopes of the Sierra de La Culata, Estado Mérida, Venezuela.

Diagnosis. **MALE** (Fig. 8C): FW length 21 mm. This subspecies differs immediately from the nominate by the consistently wider FW oblique snow white band, some 3 mm wide, not penetrating into CuA2–1A/1B, in one of the examined individuals with an irregular outer edge, occasionally penetrating deeper into base of cell

CuA1–CuA2. There is a diffused FW whitish postdiscal streak extending from Sc to M1 on the upperside, and to M2 on the underside. FWV submarginal dots are smaller and not moon shaped, white instead of milky white. Also on the HWV submarginal arrowhead shaped dots are white not milky white, and slightly more compact. **Male genitalia** (Fig. 13D): Differing marginally from the nominate subspecies, in the slightly shorter tegumen, noticeably longer saccus and slightly shorter valvae. **FEMALE** (Fig. 8D): FW length: 23 mm. Sexual dimorphism little marked, female a shade lighter on the upperside, and considerably lighter on the HWV with a heavy sandy yellow suffusion, especially in the postdiscal area; arrow head white spots slightly lighter, especially the three towards apex. **Female genitalia** (Fig. 16D): Differing from the nominate subspecies only in the longer and narrower ductus bursa, however given that these two are weakly sclerotized the apparent differences may be an artefact of dissection and photography technique.

Etymology. This subspecies is dedicated to the Colombian lepidopterist specializing in the taxonomy and ecology of Lycaenidae, Carlos Prieto, in recognition for his numerous valuable contributions to the knowledge of Andean butterflies, and support to the first author during field work in Colombia.

Remarks. *S. albarregas prietoi* ssp.n. is known so far only from the type locality. It is morphologically more related to *S. albarregas mauroi* ssp.n. from the opposite slopes of the Cordillera than to the nominate subspecies found southwards in the Sierra de La Culata.

(3) *Steromapedaliodes kahlua* Pyrcz & Boyer, sp.n.

(Figs. 8F, 16E)

Material examined. *Holotype*, ♀, VENEZUELA: Edo. Mérida, El Baho – via Páramo, La Ciénaga, 2900–2950 m, 26.xi.2005, T. Pyrcz leg. (prep. genit. 03/12.10.2011 J. Lorenc-Brudecka) (in MZUJ, to be deposited in MIZA).

Type locality: El Baho – via páramo, La Ciénaga, Edo. Mérida, Venezuela.

Diagnosis. This species is recognized immediately from *S. albarregas* and *S. albonotata* by the fact that the FW is entirely blackish-brown lacking any white patch in the FW or HW discal area, it is also smaller than most taxa in the *Steromapedaliodes sensu novo*.

Description. **FEMALE** (Fig. 8F): **Head:** Eyes glabrous, lustrous, chestnut brown, covered with long and dense black hair. Labial palpi 2 × the length of head, covered with black, grey and sandy yellow hairy scales, ventrally three times longer than dorsally. Crest composed of greyish hair and basal golden green scales. Antennae slender, dorsally chestnut, ventrally orange, covered with sparse black scales, club two time wider than shaft, widening gradually, flattened dorso-ventrally, composed of 10 flag-

ellomeres. **Thorax:** black, dorsally covered with sparse black scales on metathorax, and sparse golden brown hair, somewhat denser on patagia; ventrally also mostly naked, with some sparse brown, grey and sandy yellow hair, chiefly on legs base; mid and hind legs brown, lustrous, femorae covered with rather sparse brown and grey hair, tibiae and tarsi more densely covered with grey and sandy yellow hair. **Wings:** FW (length: 23 mm) roughly triangular, with a subacute apex, slightly convex distal margin and gently bent at tornus; fringes short, dark grey, intermittently dirty white in the interveins. FWD uniform dark brown. FWV almost uniform brown, pale, lighter than on the upperside, especially towards outer margin and apex, with sparse sandy yellow scaling in subapical area and along costa, and a short sinuate blackish line in submarginal area extending from costa to vein M2; a series of five minute yellowish submarginal dots. HW rounded with a slightly undulated distal margin; fringes short except for vein ends, mostly dark grey. HWD uniform dark brown, same shade as on the FW. HWV ground colour brown, with a narrow light brown postbasal band, and wide blackish brown median band; postdiscal area light brown suffused with whitish scales especially towards apical area; a sinuate submarginal line defining a dark brown marginal area; and a row of five minute milky white spots, three of which, towards apex, short arrow-headed, slightly larger than the remaining. **Abdomen:** dorsally and laterally black, covered with black, and laterally with grey, and ventrally with densely packed up scales of different colours, brown, sandy yellow and predominantly grey. **Female genitalia** (Fig. 16E): Papillae anales membranous in apical half, flattened in lateral view, covered with short, delicate and rather dense hair, slightly sclerotized in basal half, with developed, short apophyses posteriores; sternite viii, in lateral view without spiracle, fused with tergum; postvaginal lamella sclerotized, massive, strongly sclerotized but smooth, as a wide pocket entirely covering the antrum; ductus bursae wide, membranous, half the length of bursa, suddenly opening into a rounded bursa copulatrix, without signa; ductus seminalis connecting in the middle of ductus bursae. **MALE:** Hitherto unknown.

Etymology. This specific epithet is an allusion to the alcoholic beverage of Caribbean origin, *kahlua*, which is characterized by brownish colour, similar to this species colour patterns, and incidentally is dedicated to author's brown furred cat, Kahlua who frequently accompanied the first author while setting butterflies.

Remarks. This species is described based on a single female collected in the forest paramo ecotone above El Baho (Fig. 1D). Despite numerous attempts no further individuals were obtained. Nonetheless, the collected individual is attributed with confidence a separate specific status considered its distinctive morphological characters. In particular, its wing shape, and the ventral colour pattern is not attributable to either *S. albarregas* or *S. albonotata*. The latter species is sympatric with *S. kahlua*

sp.n., the former has a wide geographical distribution in the Cordillera de Mérida, and is immediately recognized from other related congeners by the more acute FW apex. *S. kahlua* sp.n. is either extremely localized, which can be the case with some representatives of *Steromapedaliodes*, or/and highly seasonal as is *S. albarregas*.

(4) *Steromapedaliodes mavarezi* Pycrz sp.n.

(Figs. 8G,H, 13E, 16F)

Material examined. *Holotype*, ♂, VENEZUELA: Edo. Barinas, Páramo de Guirigay, 2800–3000 m, 01.xi.2015, J. Mavárez leg. (prep. genit. 315/11.01.2016 J. Lorenc-Brudecka) (in MZUJ, to be deposited in MIZA); *Paratype*, 1 ♀: same data, (prep. genit. 316/11.01.2016 J. Lorenc-Brudecka), MZUJ.

Type locality: Páramo de Guirigay, Cordillera de Mérida, Venezuela.

Diagnosis. Immediately recognized from other congeners by its larger size, expressed in the wider wings, and the white discal patch on the hindwing dorsum.

Description. **MALE** (Fig. 8G): **Head:** Eyes glabrous, lustrous, chestnut brown with irregular blackish brown patches, covered with long and dense black hair. Labial palpi $2 \times$ length of head, covered with black, grey and sandy yellow hairy scales, ventrally three times longer than dorsally, and adorned with snow-white scales near base. Frons with a tuft of long blackish brown and golden hair. Antennae slender, dorsally blackish brown, ventrally chestnut, naked; club slightly wider than shaft, widening gradually, flattened dorso-ventrally, composed of 11 flagellomeres, ventrally orange brown. **Thorax:** black, dorsally mostly naked, covered with sparse blackish brown and navy blue scales on metathorax, and sparse golden brown hair, somewhat denser on patagia; ventrally also mostly naked, with some sparse brown, grey and sandy yellow hair, chiefly on legs base; mid and hind legs brown, lustrous, femorae covered with rather sparse brown and grey hair, tibiae and tarsi more densely covered with grey and sandy yellow hair, numerous ventral spines on tarsi. **Wings:** FW (length: 30 mm) roughly triangular, with a subacute apex, slightly convex distal margin and gently bent at tornus; fringes short, dark grey, intermittently snow white towards apex. FWD lustrous, uniform black. FWV almost uniform blackish brown, pale, lighter than on the upperside, especially towards outer margin, with sparse snow white scaling in subapical area and along costa. HW rounded with a slightly undulated distal margin; fringes short, mostly dark grey and white. HWD blackish brown, lighter towards anal margin, with an olive sheen, with some sparse hairy scales in basal area; a large snow-white patch covering most of discal cell, except for its basal part. HWV ground colour blackish brown, a shade darker, wide median band; post-discal line edged distally with some lighter, dirty white scales concentrated into a faint band, sharply bent at vein

M1 producing a short mid-costal streak; and a row of five minute milky white submarginal arrow-headed dots, none of which is considerably larger than the remaining; a shade darker submarginal line. **Abdomen:** dorsally and laterally black, covered with black, and laterally with grey, and ventrally with densely packed up scales of different colours, brown, grey and, predominantly sandy yellow. **Male genitalia** (Fig. 13E): Tegumen dorsum gently arched; uncus the length of tegumen shoulder, slender, with a gently down curved blunt tip; subunci absent; pedunculus very short, blunt; vinculum gently s-shaped; saccus flattened dorso-ventrally, shallow; valvae the length of tegumen + half uncus, massive at base, then gradually narrowing to a blunt tip, with a delicately irrorated dorsal surface in apical $\frac{1}{3}$; aedeagus tubular, slightly arched, not contorted, with the proximal opening half the entire length, and an acute tip, without any crest or lateral teeth. **FEMALE** (Fig. 8H): Sexual dimorphism slight. Slightly smaller than the male (FW length 26 mm), and a shade lighter, especially on ventral surface. HWV duller, with a more prominently marked median darker brown band, arrow-headed dots slightly larger. **Female genitalia** (Fig. 16F): Papillae anales membranous in apical half, flattened in lateral view, covered with short, delicate and rather dense hair, slightly sclerotized in basal half, with developed, short apophyses posteriores; sternite viii, in lateral view, as sclerotized as the basal part of papillae anales, without spiracle; viii fused with tergum viii in lateral view; postvaginal lamella sclerotized, massive, strongly sclerotized but smooth, as a wide pocket entirely covering the antrum; ductus bursae wide, membranous, the length of bursa, suddenly opening into a rounded bursa copulatrix, without signa; ductus seminalis connecting in the middle of ductus bursae.

Etymology. This species is dedicated to Jesús Mavárez, eminent Venezuelan biologist, entomologist and geneticist who contributed significantly in the studies of neotropical butterflies and paramo plants.

Comments. This intriguing species is known so far only from a small area situated in the Páramo de Guirigay SW of the locality of Las Mesitas (Fig. 1D). It was spotted while flying low in a subparamo habitat constituted by a mixture of bunch grasses, rosette plants and cloud forest pockets. Its external morphology stands apart from any other species of *Steromapedaliodes sensu novo*. Its wing shape and the presence of the whitish patch in the HW discal area are strongly reminiscent of *Cheimas opalinus* (Staudinger, 1897), which occurs in the same habitat, and these species are possibly involved in a mimicry relationship (Pycrz in prep.). Male genitalia are very indicative of its phylogenetic position as they show intermediate characters of *Steromapedaliodes* (*sensu* Viloría & Pycrz), and in particular of *S. albarregas*, namely the shape of tegumen and uncus, but has atrophied subunci similarly to the species previously associated with the genus *Redonda*.

(5a) *Steromapedaliodes empetrus empetrus* Adams & Bernard, comb.n.

(Figs. 9A–C, 14C, 18B)

Pedaliodes empetrus Thieme, 1905: 95, 98–99, pl. 1, fig. 7.*Pedaliodes empetrus* Thieme; WEYMER 1912: 258, pl. 54, row e; GAEDE 1931: 489; ADAMS & BERNARD 1979: 99; DESCIMON 1986: 506, 518.*Punapedaliodes empetrus* (Thieme); HUBER 1973: 195.*Redonda empetrus empetrus* (Thieme); ADAMS & BERNARD 1981: 368, figs. 13, 27; ADAMS 1983: 474; 1984: 93; D'ABRERA 1988: 871 (misidentified); 2001: 186, 341, pl. 141, fig. 17 (misidentified); VILORIA 2000: 269, 270; VILORIA & PYRCZ 2001: 12, 13; VILORIA et al. 2003: 22 (misidentified); PYRCZ 2010a: 180–185; 2010a: 265–273.*Redonda empetrus* (Thieme); VILORIA et al. 2015: 112–118.[*Redonda empetrus georgei nomen nudum* Pyrcz, 2010a: 179–185, 244.][*Redonda empetrus* ssp.n.; Pyrcz, 2010b: 265–273.]

Material examined. VENEZUELA: 1 ♂: Edo. Mérida, La Culata, 3400 m, 26.vii.2010, J. Wojtusiak leg., MIZA; 2 ♂: Cordillera de Mérida, N. of Mérida, Río Albarregas, 3400 m, 15.viii.1977, M.J. Adams & G.I. Bernard, AB2; 1 ♂: same data, 3600 m; 1 ♂: Estado Mérida, N de Mérida, Río Albarregas, 3400 m, 20.vi.1975, M.J. Adams & G.I. Bernard; 1 ♂: Edo. Mérida, Tal des Río Albarregas, 2100 m, 29.vii.1971, H. Huber, ZSBS; 1 ♂: Estado Mérida, Parque Nacional La Culata, Mucujún, 3600–3700 m, 02.i.1992, T. Pyrcz leg., MALUZ; 5 ♂: (1 in MALUZ), same data, 11.iv.1992; 9 ♂: same data, 09.i.1992; 2 ♂: same data, 29.xii.1991; 3 ♂: same data, 09.ii.1996; 2 ♂: same data, 17.iv.1996, MZUJ; 24 ♂: P. N. La Culata, Alto Río Mucujún, 3400–3450 m, 01.ii.2008, T. Pyrcz leg., (prep. genit. 07/18.10.2011 J. Lorenc-Brudecka), TWP; 13 ♂: same locality but 3200–3250 m (incorrect altitude data), 03.iv.2006, TWP; 9 ♂ and 2 ♀: same data but 3400–3450 m, 06.ii.2007, T. Pyrcz (prep. genit. 02/21.11.2011 J. Lorenc-Brudecka), TWP; 15 ♂: Mérida, La Culata, 3000–3200 m, 3.iv.2006, P. Boyer leg., PBF; 12 ♂: Mérida, La Culata, 3400 m, 01.ii.2008, P. Boyer leg., PBF; 1 ♀: Mérida, La Culata, 3400 m, 21.ii.2008, P. Boyer leg., PBF.

Type locality: [“snow mountains of Merida”], Sierra de la Culata, Cordillera de Mérida, Venezuela.

Redescription. MALE (Fig. 9A,B): Head: Eyes chocolate brown with some black patches, lustrous, covered with dense, long, black hair; antennae $\frac{2}{3}$ the length of costa, orange brown, naked except for a few basal segments covered with white scales, shaft slender, club spatulate, made of 11 segments, with two lateral, ventral bristles, blackish brown; labial palpi two $2 \times$ length of head, covered with sandy yellow, brown and black hair, ventrally three times as long as dorsally, and with some snow white dorsal scales; frons with a tuft of long blackish hair. Thorax: dorsally black, mostly naked, except for some sparse velvet bluish-black scales, patagia and base of prothorax covered with long and dense golden brown hair, meso and metathorax only with sparse golden brown hair; ventrally black densely covered with tufts of brown chestnut hair; mid and hindlegs chestnut, femora and tibiae covered with sparse, brown hair, tarsi with grey and whitish scales. Abdomen: black, lustrous, covered with brown, russet and sandy yellow hair, dorsally sparse, ventrally dense, and additionally laterally with some whitish scales. Wings: FW (FW length: 23–30 mm, mean: 27.2

mm, n=69) apex subacute, outer margin slightly concave; fringes made of elongated scales, alternately medium brown and sandy yellow in the interveins. HW oval, outer margin gently undulated; fringes made of elongated scales, alternately chestnut and sandy yellow in the interveins. FWD covered with hair along inner margin, otherwise chestnut, liberally dusted with sandy yellow scales, denser towards distal edge of a faint, irregularly shaped postdiscal line which divides wing's surface into a slightly darker basal and lighter distal half; a row of five sandy yellow submarginal rounded spots, from R5–M1 to Cu1–Cu2, rather similar in size, occasionally a sixth, small spot in R3–R4; in some individual a faint lilac or pale white, roughly rectangular patch in outer $\frac{1}{3}$ of discal cell. HWD covered with long chestnut hair in basal and postbasal area, and along inner margin; blackish in basal area, otherwise chestnut, liberally dusted with sandy yellow scales, a row of five sandy yellow, oval or subtriangular submarginal spots, in Rs–M1 to Cu1–Cu2. FWV predominantly sandy yellow although quite variable and turning orange brown in some individuals, darker basally from postdiscal line where more heavily dusted with brown scales; a row of submarginal sandy yellow dots, noticeably smaller than on dorsum; subapical and apical area dusted with somewhat more prominent sandy yellow and milky white scales. HWV dark brown, sandy yellow and milky white, with a wide darker band between median and postdiscal lines, and extending from costal to inner margin; a row of five submarginal milky white triangular patches, from Rs–M1 to Cu1–Cu2, pointing basally, somewhat variable in size but invariably more prominent than on dorsum. **Male genitalia** (Fig. 14C): Very similar to the *S. empetrus frailejona*, and differing from other subspecies in the wide, blunt apex of the valvae. **FEMALE** (Fig. 9C): Much smaller than the male (FW length 16 mm, n=3) with slightly deformed wings, especially the folded FW outer half (antennae reaching half the length of costa); FWD and HWD almost uniform lustrous golden yellow, except for the barely visible row of tiny, whitish FWD subapical dots; outer margin brown; FWV and HWV colour pattern similar to that of the male. **Female genitalia** (Fig. 18B): Papillae anales gently rounded in lateral view, covered with long, rather sparse hair (some of them in ventral half transformed into thicker spines); lamella postvaginalis wide, with a single shallow concavity; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae short, approximately $\frac{1}{3}$ the length of bursa copulatrix, wide, tubular, without any sclerotized structures, gently opening into bursa copulatrix, with ductus seminalis originating at its middle; bursa copulatrix oval, without any visible signa.

Comments. The identification of the nominotypical subspecies of *S. empetrus* is crucial for the stability of the nomenclature in the light of the existence of several local populations of this species associated with separate subspecies. VILORIA et al. (2015) dedicated a lot of attention to this issue. They concluded that the types of Thieme

were collected in the La Culata range, and designated it as nominotypical *Redonda empetrus*. We are inclined to agree, tentatively with their decision although the ultimate recognition of the exact origin of the Thieme taxon is not rendered easy by the fact that the type specimen is missing, as is most of the Satyrinae type collection of Thieme (for details see VILORIA et al. 2015), and that the original illustration in THIEME (1905), a fairly good black and white photograph, shows the upperside of a male individual, whereas the original descriptive text is not accurate enough as to sort out definitely between the subspecies. Individual variation among the individuals of the La Culata population is admittedly impressive and affects the size, upperside and underside colour patterns. In our opinion, arguably the most important feature indicated by THIEME (1905) which would point out to the La Culata population is the presence of a, usually faint, silvery or silvery patch in the FWD discal cell, not apparent in the Mucubají, Los Frailes or Loma Redonda population individuals, which otherwise correspond closely to the upperside of the specimen illustrated by Thieme. It is not impossible that further sampling in the Cordillera de Mérida, and more precisely in the La Culata range, which has been very superficially and only locally sampled for paramo butterflies will reveal a population which even more closely matches the type of Thieme than the specimens examined from the upper valleys of Río Albarregas (collected by Adams & Bernard) or Río Mucujún. The non-designation of a neotype of *Pedaliodes empetrus* by VILORIA et al. (2015) was therefore a sound decision. Interestingly, ADAMS & BERNARD (1981) did not recognise the populations occurring in La Culata and Sierra Nevada as representing a separate subspecies and misidentified it with *S. empetrus bolivari*, which is found across the Chama. The two differ in size, upper and underside colours, although admittedly individual variation of *S. empetrus empetrus* is impressive.

Steromapedaliodes empetrus empetrus is found in the Sierra de La Culata, it has been evidenced from the upper valley of Río Albarregas in the south, to Pico El Aguila in the north (Fig. 1B). *S. empetrus empetrus* is known from several localities, however the best investigated, and also the most accessible is the one inhabiting the upper Río Mucujún valley just above the large moraine dominating the landscape of the La Culata valley. Contrary to *S. empetrus bolivari*, numerous individuals can be observed on the wing every year being most abundant in January and February. It could indicate that locally this subspecies takes only one year to achieve complete development. Although rather common, the Mucujún population never attains the level of abundance of *S. empetrus frailejona* in Los Frailes. Also, contrary to the latter subspecies it is rather widespread in the La Culata range and is not as sedentary. Wandering individuals of *S. empetrus empetrus* have been observed by TP far from boggy paramos in inhospitable high altitude desert in the Páramo de Piedras Blancas at 4300 m. Also, a single individual was seen by TP and PB north of the Pico El Aguila at 4200 m in a paramo dominated by tall *Coespeletia timotensis* in

an area that was previously visited several times without noticing the presence of *Steromapedaliodes*. Studies of the Mucujún daily activity pattern were made by FERRER-PARIS (2000). The first known female was collected by K. Casner. Another female was found by TP only minutes later, and the third a year later in the very same spot as the previous two. All the females were observed in the early morning at around 9.00. They were receptive, sunning on the leaves of *Espeletia* with wings wide open exposing a shining golden yellow upperside. An attempt of mating was observed, and whilst one male was engaged in copulation with the female, another male approached and stood up to the competition. Our observations strongly indicate that females of brachypterous *S. empetrus* are active in the sunny mornings. Despite dozens of visits to the site, no other female was observed later in the day.

(5b) *Steromapedaliodes empetrus bolivari* (Adams & Bernard, 1981), comb.n., stat. reinst.

(Figs. 10G,H, 14B)

Redonda empetrus bolivari Adams & Bernard, 1981: 368–369, fig. 28.

Redonda empetrus bolivari Adams & Bernard; VILORIA 2000: 269, 270; PYRCZ 2010a: 179–185, 244; 2010b: 265–273.

Redonda empetrus Adams & Bernard; D'ABRERA 1988: 871 (erroneous photograph caption, as *Diaphanos huberi*).

Redonda bolivari Adams & Bernard; VILORIA et al. 2015: 106.

Material examined. *Holotype*, ♂, VENEZUELA: Estado Mérida, S of Mérida, Loma; Redonda, 4000 m, 21.iv.1975, M.J. Adams leg., BMNH; 15 ♂: Estado Mérida, P. N. Sierra Nevada, below Loma Redonda, 3900–3950 m, 03.ii.2007, T. Pyrcz leg., (prep. genit. 04/18.10.2011 J. Lorenc-Brudecka), TWP; 12 ♂: same data but 08.ii.2007, TWP; 1 ♂, Loma Redonda, 3900 m, 08.ii.2007, Estado Mérida, Venezuela, T. Pyrcz leg., MCC.

Type locality: Loma Redonda, South of Mérida, Cordillera de Mérida, Venezuela.

Redescription. **MALE** (Fig. 10G,H): Differs from other subspecies in the larger size (FW length: 26–30 mm, mean: 28.12 mm, n=24), although some individuals of the nominate are equal in size to *S. empetrus bolivari*; FWD and HWD colour pattern is little contrasting compared to other subspecies; ground colour has a golden sheen; submarginal dots are tiny and faint. FWV ground colour is fairly variable but has a prominent golden or golden brown sheen, and is quite uniform, except for the darker basal half, submarginal spots are small and faint. HWV is also rather uniform, predominantly grey brown with a darker basal half and some whitish scales in distal half; submarginal dots are small, milky white triangles. **Male genitalia** (Fig. 14B): Differs from the nominate in the slightly shorter valvae with a more acute apex, and from both the nominate and *S. chiquinquirana* by the ¼ longer aedeagus. **FEMALE:** So far unknown.

Comments. This subspecies is distributed on the north-western slopes of the Sierra Nevada (Fig. 1B). Currently

known only from the type locality below Loma Redonda where it occurs at 3800–4000 m and the trail from La Mucuy to the Humboldt and Bompland glaciers. Its entire distribution is unknown and possibly extends over large portions of the Sierra Nevada including the south-eastern slopes, which are mostly inaccessible and have not been sampled for butterflies so far. Males are larger than other subspecies of *S. empetrus* except particularly large individuals of *S. empetrus empetrus*. They are very active fliers and behave in a way very reminiscent of *S. bordoni*. The female is still unknown and we suspect that it is brachypterous. *S. empetrus bolivari* flies at higher elevations than other subspecies, except some reports of *S. empetrus empetrus*.

(5c) *Steromapedaliodes empetrus frailejona* (Ferrer-Paris & Costa), comb.n., stat.n.

(Figs. 9D,E, 14A, 18A)

Redonda empetrus empetrus (Thieme); PYRCZ 2010a: 180–185, 2010a: 265–273 (misidentified).

Redonda frailejona Ferrer-Paris & Costa (in VILORIA et al. 2015): 118, 130, figs. 33–37 (adults), 55 (male genitalia).

Material examined. VENEZUELA: 7 ♂: Mérida, Apartaderos – Sto. Domingo, km 12.5, ca. 3100–3300 m, 26.ix.1997, A. Neild, AFN; 19 males: Edo. Mérida, oberes Domingo tal [upper valley of “River Santo” Domingo], 3070 m, 05.ix.1971, H. Huber; 2 ♂: same data, 3050 m, ZSBS; 17 ♂: Edo. Mérida, Mucubají – Santo Domingo, Los Frailes, 3000–3050 m, 08.vii.2006, T. Pyrcz leg. (prep. genit. 04/27.10.2014 J. Lorenc-Brudecka); 44 ♂: same data but 19.iv.2006; 3 ♂: same data but 12.iv.2004; 1 ♂: same data but 02.ii.2008; 2 ♂: same data but 31.vii.2009; 1 ♂: same data but 24.ii.2010, MZUJ; 39 ♂: Mérida, Los Frailes, Santo Domingo vers Apartaderos km 10, 2900–3000 m, 19.iv.2006, P. Boyer leg., PBF; 4 ♂: same data but 8.iv.2006, P. Boyer leg., PBF; 1 ♂: Mérida, Los Frailes, Santo Domingo vers Apartaderos, 2900 m, 31.vii.2009, P. Boyer leg., PBF; 1 ♂: Mérida, Apartaderos – Santo Domingo km 12.5, 3100–3200, 26.vii.1997, A. Neild leg., PBF; 1 ♀: Edo. Mérida, Los Frailes, 3050 m, 12.iv.2004 [collecting year probably erroneous, 2014?], M. Costa leg., (prep. genit. 05/04.10.2012, J. Lorenc-Brudecka), MCC.

Type locality: Santo Domingo – Apartaderos, Estado Mérida, Cordillera de Mérida, Venezuela.

Redescription. **MALE** (Fig. 9D): Differs from the nominate and *S. empetrus bolivari* in the smaller size (length: 24–28 mm, 24.72 mm, n=69); otherwise wings dorsal colour patterns are closely similar to the nominate subspecies, except that postdiscal yellow dots are usually larger, and on the HW rather triangular than oval, a feature which more obvious on the HWV; light milky white or lilac FWD discal patches sometimes apparent in the nominate subspecies are absent or nearly so; FWV is darker than in the nominate, orange brown instead of sandy yellow, but usually lighter than in *S. empetrus bolivari*. **Male genitalia** (Fig. 14A): Uncus stout, aligned with and approximately the length of dorsum of tegumen; subunci as very small tips adhered to base of uncus; pedunculus medium sized; saccus wide and shallow; valvae the length of tegumen + uncus, massive, gradually

narrowing towards a gently rounded apex, ventrally with a noticeable subapical notch, dorsally smooth; aedeagus the length of saccus + valve, slender and gently arched, terminated with a small bulbous membrane with tiny cornuti. **FEMALE** (Fig. 9E): The only known specimen is much smaller than the male (FW length: 12 mm) with narrow, deformed wings (antennae reaching half the length of costa); FWD and HWD almost uniform lustrous silver yellow, except brown costa and the barely visible row of tiny, whitish spearhead triangular subapical dots on the HW; outer margin brown; FWV and HWV colour pattern similar to that of the male except for the disproportionately large spearhead submarginal white spots. **Female genitalia** (Fig. 18A): Papillae anales gently rounded in lateral view, covered with long, rather sparse hair; lamella post-vaginalis wide, with a single shallow concavity; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae short, approximately $\frac{1}{3}$ the length of bursa copulatrix, tubular, without any sclerotized structures, gradually widening and gently opening into bursa copulatrix, with ductus seminalis originating at its middle; bursa copulatrix oval, without any visible signa.

Comments. It is worth pointing out that *S. empetrus frailejona* is known so far only from a very small area concentrated around a bog located above the main Mucubají – Santo Domingo road at 2850–3100 m (Fig. 1B). Despite extensive sampling carried out by TP and co-workers in apparently appropriate habitats at slightly higher elevations towards the Mucubají Pass or above the village of El Baho at different seasons of the year, no other population of *S. empetrus* was detected in the Santo Domingo valley. It is highly alarming and suggests that the Los Frailes bog may be effectively the only extant locality of this subspecies. *S. empetrus frailejona* occurs locally at high density at the peak of its flight season. Simultaneously up to 10 adults can be observed fluttering around above *Espeletia* spp. inflorescences. Occasionally individuals are seen crossing the asphalt road, overflying *Blechnum* ferns thickets, and entering the gardens and yards of the “Los Frailes” hotel facilities. Observations carried out by the first author during consecutive years from 2003–2010 in the Santo Domingo valley indicate that *S. empetrus frailejona* larvae take two years to achieve their development. In 2006 and 2008 high flight period took place in February–March whereas next year’s March only sporadic individuals were observed. It appears that the flight season of *S. empetrus frailejona* corresponds with the late blooming period of the local *Espeletia schultzei* (Asteraceae), the source of nectar for adults, which falls at the end of the rainy season and through most of the dry season from November to March.

(5d) *Steromapedaliodes empetrus* ssp.

Material examined. VENEZUELA, 1 ♂: Est. Mérida, Campanario, 13500 ft, 10.ix.1938, J. H. Tracey, BM 1939–114, BMNH; 1 ♂:

Estado Mérida, P. N. Sierra Nevada, Laguna Verde Laguna Suero, 4000 m, 12.ii.1985, CEUM leg., MIZA; 1 ♂: Venezuela, Ch. Blanchier, MHNG.

Comments. Three specimens of *S. empetrus* could not be attributed to any subspecies. They are left without suggesting any taxonomical status for one, collected in the Laguna Suero, is badly damaged, while the other has no exact collecting locality data. Nevertheless, they present some morphological characters that let us suppose they could represent yet another undescribed subspecies of *Steromapedaliodes empetrus*. This needs to be corroborated by more sampling.

(6a) *Steromapedaliodes chiquinquirana* (Ferrer-Paris), comb.n.

(Figs. 9F,G, 14D, 18C)

[*Redonda empetrus empetrus* Adams & Bernard; VILORIA et al. 2003: 22 (female misidentified).]

[*Redonda empetrus miki* nomen nudum Pyrcz, 2010a: 179–185, 244.]

[*Redonda empetrus* ssp.n.; Pyrcz, 2010b: 265–273.]

Redonda chiquinquirana Ferrer-Paris (in VILORIA et al. 2015): 112, 127–130, figs. 24–26 (adults), 51 (male genitalia).

Material examined. VENEZUELA: 1 ♂: Estado Mérida, Parque Nacional Sierra Nevada, Laguna Negra, 3550 m, 28.iii.1992, T. Pyrcz, MZUJ; 1 ♂ and 1 ♀: Estado Mérida, Parque Nacional Sierra Nevada, vía Laguna Negra, 3600 m, 20.iv.1992, T. Pyrcz (male: prep. genit. 02/18.10.2011 J. Lorenc-Brudecka; female: prep. genit. 04/07.11.2011 J. Lorenc-Brudecka), MALUZ; 8 ♂: Estado Mérida, Parque Nacional Sierra Nevada, Laguna de Mucubají, 3600 m, 05.x.1975, M. Rafiński; 1 ♂: same data, 01.ix.1988, R. Manrique; 9 ♂ and 2 ♀: same data, 20.iv.1992, T. Pyrcz, MZUJ; 1 ♂: Edo. Mérida, zw. Laguna Grande und Laguna Negra, 3450 m, 12.ix.1971, H. Huber, ZSBS; 1 ♀: no data [M.J. Adams & G.I. Bernard, AB1], BMNH; 1 ♂: Mérida, PN Sierra Nevada, Páramo de Mucubají, 3500–3600 m, 5.x.1975, J. Rafiński, PBF; 1 ♂: Mérida, Mucubají, vía a la Laguna Negra, 3400 m, 19.iv.2006, P. Boyer, PBF.

Type locality: Páramo de Mucubají, Serranía de Santo Domingo, Cordillera de Mérida, Venezuela.

Redescription. **MALE** (Fig. 9F): **Head:** Eyes chocolate brown and black, lustrous, covered with dense, long, brown and whitish hair; antennae $\frac{2}{5}$ the length of costa, orange brown, naked except for a few basal segments covered with white scales, shaft slender, club spatulate, made of 11 segments, with two lateral, ventral bristles; labial palpi $2 \times$ length of head, covered with sandy yellow and brown hair, ventrally three times as long as dorsally, and laterally with white; frons with a tuft of long sandy yellow hair. **Thorax:** dorsally black, base of prothorax covered with long and dense chestnut and sandy yellow hair, meso and metathorax only with sparse brown hair; ventrally black densely covered with tufts of brown and chestnut hair; mid and hindlegs femora covered with sandy yellow hair, tibiae and tarsi with brown and silvery scales. **Abdomen:** dorsally and laterally covered with black scales, ventrally with silvery scales and sandy yellow

low hair. **Wings:** FW length: 23–26 mm, mean: 24.8 mm, $n=19$; FWD ground colour varies between chestnut and olive brown, submarginal dots are generally richer yellow and fainter. HWD ground colour is similarly variable as on the FW, submarginal dots, although quite variable are generally elongated, instead of rounded, and richer yellow. FWV ground colour is richer yellow with a brown or golden shade, submarginal dots are fainter. HWV is conspicuously lighter due the presence of prominent sandy yellow scaling; submarginal dots are considerably elongated, and this is the most immediate diagnostic feature, which allows the identification of this compared to other subspecies. **Male genitalia** (Fig. 14D): Very similar to *S. empetrus* except for the slightly more acute apex of the valvae. **FEMALE** (Fig. 9G): Much smaller than the male (FW length 18.5–19 mm); FW and HWD light chestnut with a strong silvery overcast, in some individuals nearly all shinning silvery; FWD median half and apical area generally slightly darker with more prominent chestnut pattern; minute submarginal whitish barely noticeable on HWD, slightly more prominent on FWD; FWV and HWV similar to male, with characteristic HV submarginal elongated milky white streaks, even longer than in the male particularly in Rs–M1 and M1–M2; silver scaling on HW less prominent than in the male, in some specimens nearly absent. **Female genitalia** (Fig. 18C): Papillae anales gently rounded in lateral view, covered with long hair (some of them in ventral half transformed into thicker spines); lamella postvaginalis wide, with two shallow concavities; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae short, approximately $\frac{1}{3}$ the length of bursa copulatrix, wide, tubular, without any sclerotized structures, gently opening into bursa copulatrix, with ductus seminalis originating at its middle; bursa copulatrix oval, without any visible signa.

Remarks. *S. chiquinquirana chiquinquirana* differs from all the subspecies of *S. chiquinquirana* by the slightly smaller size; FWD submarginal dots are generally richer yellow and fainter; HWD submarginal dots, although quite variable, are generally elongated, instead of rounded, and richer yellow; FWV is richer yellow with a brown or golden shade, submarginal dots are fainter; HWV is conspicuously lighter due the presence of prominent sandy yellow scaling; submarginal dots are considerably elongated, and this is the most immediate diagnostic feature which allows the identification of this compared to other subspecies. ADAMS & BERNARD (1981) thought that the population found in the Mucubají area represents the nominate *S. empetrus* and failed to recognize it as new. There are seemingly two generations per year, the first emerging in January and the second in October. Males are strong fliers, perhaps as energetic as the other species. Females, which are much smaller than males as recorded previously by ADAMS & BERNARD (1981), are “very loath to fly even when disturbed, and after very short flights disappeared among low tussocks of grass”.

(6b) *Steromapedaliodes chiquinquirana lossadana* (Ferrer-Paris), comb.n., stat.n.

(Figs. 9H–J, 14E,F, 18E,F)

[*Redonda empetrus decennia nomen nudum* Pyrcz, 2010a: 179–185, 244.][*Redonda empetrus ssp.n.*; PYRCZ, 2010b: 265–273.]*Redonda lossadana* Ferrer-Paris (in VILORIA et al. 2015): 119, 141–144, figs. 44, 45 (adults), 58 (male genitalia), 141–144.*Redonda centenaria* Viloría & Camacho (in VILORIA et al. 2015): 112, 123–127, figs. 6 (female wing venation), 20–23 (adults), 50 (male genitalia), **syn.n.**

Material examined. VENEZUELA: 1 ♂: Edo. Mérida, Las Mesitas, Páramo Guirigay, 3100–3150 m, 27.vii.2009, T. Pyrcz leg., MZUJ; 15 ♂ and 3 ♀: Edo. Mérida, Las Mesitas, Páramo Guirigay, 3100–3150 m, 27.vii.2009, T. Pyrcz, TWP; 29 ♂ and 1 ♀: Edo. Mérida, Tuñame, Pueblo Llano crossroad, 3200–3250 m, 25.xi.2005, T. Pyrcz, TWP (male: prep. genit. 01/27.10.2014 J. Lorenc-Brudecka; female: prep. genit. 06/18.10.2011 J. Lorenc-Brudecka); 7 ♂: Edo. Mérida Las Mesitas, vía Teta de Niquitao, 3300–3400 m, 27.vii.2009, T. Pyrcz, TWP; 8 ♂ and 1 ♀: Edo. Trujillo, Páramo de Guirigay, 3000–3100 m, SE de Las Mesitas, 3000–3100 m, 27.vii.2009, P. Boyer, PBF; 12 ♂: Edo. Trujillo, Jonction Niquitao/pueblo Llano × Niquitao/Tuñame vers Pueblo Llano km5, 3150 m, 23.XI.2005, P. Boyer, PBF; 16 ♂: Edo. Trujillo, Jonction Niquitao/pueblo Llano × Niquitao/Tuñame vers Pueblo Llano km7, 3300 m, 25.XI.2005, P. Boyer, PBF; 20 ♂ and 1 ♀: Edo. Trujillo, Jonction Niquitao/pueblo Llano × Niquitao/Tuñame, 3150 m, 25.XI.2005, P. Boyer, PBF; 3 ♂ and 1 ♀: Edo. Trujillo, Las Mesitas vers Teta de Niquitao, 3200–3300 m, NW de las Mesitas, 27.vii.2009, P. Boyer, PBF.

Type locality: Páramo de Tuñame, Estado Trujillo, Cordillera de Mérida, Venezuela.

Redescription. MALE (Fig. 9H): Differs from the nominate subspecies in the considerably darker, chocolate brown FW and HWD; in a faint and diffused reddish brown postmedian band; smaller submarginal dots on FW and particularly on HW, where barely noticeable. FWV is suffused with reddish brown, a diagnostic character of this subspecies. HWV is blackish brown, darker than in the nominate and more contrasting due to the presence of white scales in basal, postbasal and postdiscal areas; submarginal triangular dots are larger than in *S. empetrus* but shorter than in the nominate *S. chiquinquirana*. Average size is similar to the nominate (FW length: 24–29 mm, mean: 26.2 mm, n=52). **Male genitalia** (Fig. 14E,F): Differs from the nominate and other subspecies in the slender valvae. **FEMALE** (Fig. 9I,J): Considerably smaller than the male (FW length: 21.5–22.5 mm, mean: 22 mm, n=3); FW and HWD light beige with a silvery sheen; FWD with a slightly darker brown median band and submarginal line; a row of 5 submarginal subapical yellow FW dots and HW spearhead shaped. FWV and HWD similar to the male but generally more contrasting due to prominent yellow dusting of FW, instead of reddish–yellow of the male, and heavier whitish speckling of HW. **Female genitalia** (Fig. 18E,F): very similar to nominate *S. chiquinquirana chiquinquirana*. Papillae anales gently rounded in lateral view, covered with long hair (some of them in ventral half transformed into thicker spines) and with short, strongly sclerotized apophyse

posteriores; lamella postvaginalis wide, with two shallow concavities; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae short, approximately $\frac{1}{3}$ the length of bursa copulatrix, and wide, slightly sclerotized, with ductus seminalis originating at its middle; bursa copulatrix large, oval, no signa.

Comments. This subspecies occurs in the Tuñame meseta area, on the southeastern slopes of Teta de Niquitao, and Guirigay massif (Fig. 1B). Habitats vary between dry, rocky slopes dominated by *rosetal* paramo communities of *Espeletia tenorae*, and bogs. At the peak of the flying season, this subspecies can be quite common and at least 5–10 individuals can be observed on the wing simultaneously. Monitoring is needed and the establishment of small but protected areas should be considered. Other species found in the bogs include *Diaphanos curvignathos* Viloría, 1994 and some endemic *Espeletia* (VILORIA 1994). *Redonda centenaria* described from the Teta de Niquitao (VILORIA & CAMACHO 2015) is considered here as the junior synonym of *S. chiquinquirana lossadana*. The types and the individuals collected by the authors of this article in the type locality of *centenaria* do not differ from *S. chiquinquirana lossadana*.

(6c) *Steromapedaliodes chiquinquirana castellana* (Viloría & Camacho), comb.n., stat.n.

(Figs. 11A–F, 15A, 18D, 21B)

[*Redonda empetrus ssp.n.* 1; VILORIA, 2000: 270; VILORIA & PYRCZ 2001: 12; VILORIA et al. 2003: 22; PYRCZ 2010b: 265–273.][*Redonda empetrus centenaria nomen nudum* Pyrcz, 2010a: 36, 179–185, 244.]*Redonda castellana* Viloría & Camacho (in VILORIA et al. 2015): 112, 119–123, figs. 16–19 (adults), 49 (male genitalia).

Material examined. VENEZUELA: 1 ♂: Estado Trujillo, Ortíz, Páramo Ortíz, 3100–3150 m, 05.ii.2008, T. Pyrcz (prep. genit. 03/27.10.2014 J. Lorenc-Brudecka), MZUJ; 1 ♂: Estado Trujillo, Páramo de Cabimbú, 2900 m; 11.ix.1991, A. Viloría & R. Calchi, MALUZ; 9 ♂ and 2 ♀: same data as holotype, MALUZ; 15 ♂ and 4 ♀: Estado Trujillo, Páramo de Ortíz, 2850–3100 m; 12.ix.1991, A. Viloría & E. Moscó leg., (2 ♂ and 1 ♀ in TWP); 30 ♂ and 4 ♀: same locality, 3100; 07.i.1992, J. Camacho & A. Viloría, MALUZ (1 ♂ in BMNH); 3 ♂: Estado Trujillo, Vía Boconó–Páramo La Cristalina, 2400–2800 m, 14.vi.1986, J.E. Lattke, MIZA; 1 ♂: Estado Trujillo, Páramo La Cristalina, 2800 m, 14.v.1986, J.E. Lattke, MIZA; 54 ♂ and 3 ♀: Estado Trujillo, Boconó–Trujillo, Páramo Las Moras, 2950–3050 m, 21.ii.2007, T. Pyrcz (prep. genit. 02/07.11.2011 J. Lorenc-Brudecka), TWP; 10 ♂ and 2 ♀: Trujillo, Páramo de Ortíz, 3100, 5.ii.2008, P. Boyer, PBF; 3 ♂: Trujillo, Route Ortíz vers Boconó, Páramo las Moras, 3000 m, 21.ii.2007, T. Pyrcz, PBF; 2 ♀: Páramo Las Moras, 3000 m, 20.ii.2007, M. Costa, MCC; 1 ♀: Páramo de Ortíz, 3170 m, 18.viii.2003, A. Viloría and M. Alaracón, MCC.

Type locality: Páramo de Ortíz, Estado Trujillo, Venezuela.

Redescription. MALE (Fig. 11A,C,E): FW (length: 25–31 mm; n=57; mean: 27.38 mm). Differs from the nominate and *S. chiquinquirana lossadana* in more elon-

gated wings, and somewhat more acute FW apex; also differs from the nominate in the darker brown FW and HWD, but most examined individuals are a shade lighter than *S. chiquinquirana lossadana*; also compared to *S. chiquinquirana lossadana*, dorsal colour pattern is more lustrous, and uniform, apart from a shade darker median band, and has no reddish brown postmedian suffusion; FW and HWD submarginal dots are as small and faint as in *S. chiquinquirana lossadana*. FWV ground colour is quite variable, but in most individuals dark chestnut, much darker than in the nominate, and considerably duller and less contrasting than in *S. chiquinquirana lossadana*, without the diagnostic reddish brown overcast covering the whole wing, instead distal part of the wing is lighter, sandy yellow occasionally with some orange shade; submarginal dots are small and faint, similar as in *S. chiquinquirana lossadana*. HWV ground colour is grey brown, dull and generally little contrasting; postdiscal darker line is always noticeable, in most individuals edged distally with some sandy yellow scaling; submarginal sandy yellow dots are the same size and shape as in *S. chiquinquirana lossadana*, and generally larger than in the nominate. **Male genitalia** (Fig. 15A): Differs from the nominate in the slightly shorter valvae terminated with an acute apex, similarly to *S. chiquinquirana lossadana* whose valvae are however slender and longer. **FEMALE** (Fig. 11B,D,F): Considerably smaller than the male (FW length: 21–26 mm; n=12; mean=22.50 mm), greatly variable, some being larger and more pigmented than others; in melanic specimens differences with *S. chiquinquirana chiquinquirana* are exaggerated, FWD ground colour ochraceous brown, with some areas creamy-yellow (for example, distal extremity of discal cell, and edges of discal region); postdiscal dots appear more discrete and small, in contrast to darkened groundcolour; HWD similar to typical subspecies but densely dusted with ochraceous brown, more thickly at base and margins; HWV both groundcolour and speckling darker; speckling much more dense (as in males); FW submarginal dots reduced, and some bluish-white scales on apex; hindwing with much thicker and more distinct dark-coffee speckling, which is heavier in basal half; white speckling in general denser than in typical subspecies; postdiscal arrow-head shaped white spots less elongated. **Female genitalia** (Fig. 18D): Very similar to the preceding subspecies. Papillae anales gently rounded in lateral view, covered with long hair (some of them in ventral half transformed into thicker spines); lamella postvaginalis wide, with two shallow concavities; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae short, approximately $\frac{1}{3}$ the length of bursa copulatrix, and wide, little sclerotized gently widening and opening into bursa copulatrix, with ductus seminalis originating at its middle; bursa copulatrix large, pear-like, without any visible signa.

Comments. This subspecies is restricted to the paramos of the Niquitao region in Trujillo State. It comprises the localities of La Cristalina, Cabimbú, and northern slopes

of La Teta de Niquitao (4006 m) (Fig. 1B). Most of these paramos, particularly those located in the Río Boconó basin, 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 & REYES 1980). Within its area of distribution, *S. chiquinquirana castellana* is an abundant insect throughout the year. Both males and females fly actively during sunny periods, but females can be distinguished by their smaller size, paler upperside coloration, and relative weakness in flight. 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, most females released many spherical eggs from the moment of capture and throughout several hours whilst kept alive in paper envelopes. Two females placed together in the same envelope produced 167 olivaceous green eggs in a few hours; a further four specimens produced 113 ova (some of them pale green to yellowish) and died with many eggs still within the abdomen. All the eggs were also free of cement.

The paramos in the Niquitao region differ from the areas inhabited by other subspecies in the heavy presence of *Chusquea* which constitutes a co-dominant element of orael plant communities alongside *Espeletia* rosettes, *Puya* bromeliads and bunch grasses (VARESCHI 1970; CUTRECASES 1979). A few *Swallenochloa* clumps are found patchily distributed only in the Páramo de Ortiz, mainly along creeks. This butterfly co-exists with *Diaphanos curvignathos* Viloría and *Steromapedaliodes albonotata borealis*, *Colias dimera* Doubleday, 1847, *Catasticta chrysolopha spectrum* Reissinger, 1972, *Hylephila* sp., *Rhamma* sp., *Podanotum andrewneildi* Bálint, 2001 and *Rhamma commodus* (C. Felder & R. Felder, 1865).

(7) *Steromapedaliodes leukasmena* (Viloría & Camacho), comb.n.

(Figs. 11G,H, 15B, 19C)

[*Redonda* sp.n. 2; VILORIA 2000: 270.]

[*Redonda* sp.n.; VILORIA & PYRCZ 2001: 15; VILORIA et al. 2003: 22].

[*Redonda camachoi nomen nudum*; PYRCZ, 2010a: 38, 45, 180–185, 244; PYRCZ 2010b: 265–273.]

Redonda leukasmena Viloría & Camacho (in VILORIA et al. 2015): 119, 138–141, figs. 7 (female wing venation), 40–43 (adults), 57 (male genitalia).

Material examined. VENEZUELA: 1 ♂: Estados Trujillo–Lara, P.N. Dinira, Páramo Jabón (south slopes), 3100–3150 m, 07.ii.2008, T. Pyrcz; 1 ♂: Estado Lara, Municipio Morán, Páramo de La Rosa [sic], 3000 m, 20.viii.1991, J. Camacho leg., MALUZ; 6 ♂ and 2 ♀: Estado Lara, Parque Nacional Dinira, Páramo La Rosa [sic], 2800; 16.i.1994; A. Viloría & J. Camacho; 18 ♂ (1 in BMNH, 1 in MZUJ) and 2 ♀: Estado Lara, Parque Nacional Dinira, Páramo Cendé, 3100 m; 08.viii.1995, M. García, MALUZ; 1 ♂: Estado Trujillo, P. N. Dinira, Pmo. Cende, 3100–3150 m, 07.ii.2008, T.

Pyrcz (male: prep. genit. 06/18.10.2011 J. Lorenc-Brudecka); 2 ♂: Estados Lara-Trujillo, Páramo El Jabón, 3000 m, 25.xii.1989, CEUM, MIZA; 10 ♂ and 2 ♀: Estados Trujillo-Lara border, P.N. Dinira, Páramo Jabón (south slopes), 3100–3150 m, 07.ii.2008, T. Pyrcz (female: prep. genit. 01/07.11.2011 J. Lorenc-Brudecka); 2 ♂: same locality but 3000–3050 m, 13.ii.2010, MZUJ; 8 ♂: Trujillo, Páramo de Jabón, NE de Carache, massif du Cendé, 3100 m, 07.ii.2008, P. Boyer, PBF.

Type locality: Páramo de La Rosa, Municipio Morán, Estado Lara, Cordillera de Mérida, Venezuela.

Redescription. **MALE** (Fig. 11G): **Head:** Eyes chocolate brown with black patches, lustrous, covered with dense, long, black hair; antennae 2/5 the length of costa, orange brown, naked except for a few basal segments covered with white scales, shaft slender, club 2 × as wide, elongated, composed of 10 segments, with a deep ventral cavity; labial palpi 2 × length of head, covered with sparse sandy yellow and brown hair, ventrally three times as long as dorsally, frons with a tuft of long blackish brown hair. **Thorax:** dorsally black, covered with black scales and russet hair; ventrally black densely covered with tufts of brown and russet hair; mid and hindlegs dark brown, with dense dark brown spines and silver scales somewhat dense on tarsi and tibiae. **Abdomen:** black, covered with brown scales sandy yellow hair on ventral side. **Wings:** FW (length: 27.5–30.5 mm, mean: 28.8 mm, n=13) apex subacute, outer margin slightly concave, tornus obtuse; fringes alternately dark brown and white in the interveins. HW oval, outer margin regular; fringes dark brown. FWD slightly hairy at base, lustrous dark brown, slightly darker in distal half of discal cell, with a large, polygonal subdiscal silvery white patch within discal cell, distal edge of which is straight and well defined at 2/3 of cell, basal edge rather diffuse, following vein Cu2, and a row of faint, sometimes not apparent, five sandy yellow submarginal rounded dots, from R5–M1 to Cu1–Cu2, basal 1/3 with greenish sheen. HWD covered with long chestnut hair in basal and postbasal area, and along inner margin; blackish in basal area, otherwise almost uniform lustrous dark brown. FWV chocolate brown, duller and becoming coffee brown towards costal margin and apex, lustrous and with a delicate chestnut sheen in basal half; a row of faint, submarginal sandy yellow dots; subapical, apical and marginal area speckled with dark coffee brown. HWV chocolate brown speckled with white scales somewhat denser along distal edge of median and postdiscal line, and black, notably dense on basal half of wing and in submarginal region of each cell; a row of five submarginal milky white roughly triangular patches, from Rs–M1 to Cu1–Cu2, pointing basally, all of them irregularly surrounded by dark brown; a faint submarginal darker blackish line. **Male genitalia** (Fig. 15B): Similar to *S. chiquinquirana* except for the considerably, 1/3 longer uncus, completely atrophied subunci and the longer and slender valvae, which resembles mostly that of *S. chiquinquirana lossadana*, but sharing with all the subspecies of *S. chiquinquirana* the characteristic ven-

tral notch; saccus wider than in *S. chiquinquirana* with singularly folded upwards sides. **FEMALE** (Fig. 11H): Smaller than the male (FW length: 25–28.5 mm; mean: 26.8 mm; n=5), with narrower wings, more pointed apex and tornus of FW; FW and HWD surface less dark and brownish, forewing showing postdiscal series of 4–5 ochraceous and minute dots, in cells R5 to Cu1 (sometimes missing in M2). FWV groundcolour surface brown, light brown at apex; submarginal series of five white dots in cells R5 to Cu1; HWV groundcolour not chocolate, but pale brown, which gives higher colour contrast in general design. **Female genitalia** (Fig. 19C): Papillae anales gently rounded in lateral view, covered with long, thin hair; lamella postvaginalis wide, with two shallow concavities; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae very short, approximately 1/5 the length of bursa copulatrix, strongly sclerotized laterally and compressed in the middle, then opening into a wide, tubular second section which opens into bursa copulatrix, with ductus seminalis originating at the compression of ductus bursae; bursa copulatrix large, rounded, without any visible signa.

Comments. This species differs from other species of *Steromapedaliodes*, and most particularly those hitherto associated with *Redonda*, in the dark, nearly black dorsal wing surface and a snow white FWD discal cell patch. Such a dorsal colour pattern is strongly reminiscent of *Steromapedaliodes albonotata*, however the much larger wingspan and rounded wings immediately allow its association with *S. chiquinquirana* and *S. empetrus*.

It occurs in high and humid paramos of the Cendé Region, north-easternmost extreme of the Venezuelan Andes, between the States of Trujillo and Lara (Fig. 1B). This geographic unit includes the highlands or paramos of Agua de Obispos, Las Rosas, Jabón, Guache, Nariz, Los Nepes, Cendé, and El Vigía. MONASTERIO (1980) has defined the main vegetation there as “rosetal de *Ruilopezia jaborensis*” (Asteraceae) because of the remarkable dominance of this endemic plant. But *S. leukasmene* is better associated with the equally common “*Swallenochloa–Ruilopezia jaborensis* grassland” (Poaceae-Asteraceae). These paramos are highly influenced by the atmospheric conditions of the Lake Maracaibo basin, which results in two highly pronounced wet seasons (MONASTERIO & REYES 1980).

This species has never been found abundant. The behaviour is similar in males and females, and as the wing patterns are almost identical, it is almost impossible to recognize the sex of flying individuals. They fly energetically, 1–2 m above the thick bambusoid grasses (mainly *Swallenochloa angustifolia* and *Rhipidocladum geminatum* (Poaceae), which grow in the Cendé paramos (VILORIA 1994; JUDZIEWICZ & RIINA 2005). We failed to find *S. leukasmene* in the dry, low Páramo de Los Nepes (2400–2850 m), where bamboos seem to be partially 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, *S. leukasmena* only flies in sunshine and is very hard to find 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. Interestingly, adults are active early in the morning on sunny days, at 9–11 AM, afterwards their activity nearly stops. This differs from *S. chiquinquirana castellana*, which can be seen on the wing even in the afternoon at 2–3 PM. Nothing is known about its biology. However, from observations of the biotopes occupied by the adults, we infer that the larvae feed on bamboos throughout the páramo. *Diaphanos fuscus* Viloría, 1994 and *Steromapedaliodes albonotata borealis* are two more satyrines of the páramo of the Cendé region (VILORIA 1994). *Steromapedaliodes albonotata borealis* shows a similar wing pattern and behaviour, which may suggest a possible mimetic relationship with *Steromapedaliodes leukasmena*, but they have not been found flying together (see comments in VILORIA & PYRCZ 2001).

(8) *Steromapedaliodes bordoni* (Viloría & Pyrcz), comb.n.

(Figs. 10C,D, 15C, 18A, 21A)

[*Redonda* sp.n. 1; VILORIA 2000: 269.]

Redonda bordoni Viloría & Pyrcz, 2003: 21–23 (in VILORIA et al. 2003).

Redonda bordoni Viloría & Pyrcz; PYRCZ 2010a: 36, 45, 179–185, 244; 2010b; PYRCZ 2010b: 265–273; VILORIA et al. 2015: 110–112, figs. 5 (female wing venation), 14–15 (adults), 48 (male genitalia).

Material examined. *Holotype*, ♂, VENEZUELA: Estado Táchira, Páramo El Batallón, entre Laguna El Cenegón y Laguna Grande, 3200–3400 m; 28.ii.1994, A. Viloría, M. García & J. Camacho, MIZA; 27 ♂ and 2 ♀: same data (3 ♂ in MHN, 3 ♂ JFLC); 19 ♂: Estado Táchira, Páramo El Batallón, entre la Antena CANTV y la Laguna El Cenegón, 3100–3250 m, 27.ii.1994, A. Viloría, M. García & J. Camacho, (2 in TWP, 2 in BMNH); 4 ♂: Estado Táchira, Municipio Jáuregui, Callejón del Cenegón, 16.xii.1994; M. García; 6 ♂ and 1 ♀: Estado Táchira, Parque Nacional Juan Peñaloza, Páramo El Rosal, 3000 m, 12–14.i.1995, J. Camacho & M. García; 10 ♂: Estado Táchira, Páramo El Batallón, entre El Cenegón y Laguna Grande, 3300–3400 m, 05.iii.1996, J. Camacho, M. García, T. Pyrcz and J. Wojtusiak, MALUZ; 1 ♂: Estado Táchira, Páramo de La Negra, 30.ix.1951, P. Fenjues; 1 ♂: same locality, 3200 m, 14.i.1982, C. Bordón, MIZA; 51 ♂ and 1 ♀: Estado Táchira, Páramo El Batallón, vía El Pulpito, 3500–3800 m, 02–04.iii.1996, T. Pyrcz, J. Wojtusiak, J. Camacho, M. García (female: prep. genit. 05/07.11.2011 J. Lorenc-Brudecka); 5 ♂: Estado Táchira, Páramo El Batallón, vía El Cenegón, 04.iii.1996, T. Pyrcz, J. Wojtusiak, J. Camacho and M. García, MZUJ (all *Paratypes*); 4 ♂: Estado Táchira, Páramo El Batallón, Páramo El Rosal, 3300–3350 m, 02.xii.2005, T. Pyrcz; 22 ♂: Estado Táchira, Páramo El Batallón, Antenas – Cenegón, 2900–2950 m, 01.ii.2008, T. Pyrcz, MZUJ; 1 ♂: same data but 3300 m, 19.ii.2008, (prep. genit. 01/07.10.2014 J. Lorenc-Brudecka); 20 ♂ and 1 ♀: Tachira, Antenas, vía a Cenegón, Páramo el Batallón, 3200–3300 m, 19.ii.2008, P. Boyer, PBF; 15 ♂: Tachira, Páramo el Rosal, La Grita vers San Jose de Bolívar km 22, 3150 m, 01.xii.2005, P. Boyer, PBF; 1 ♂: Tachira, vía El Pulpito, 3500–3800 m, 03.iii.1996, T. Pyrcz, PBF.

Type locality: Between Laguna El Cenegón and Laguna Grande, 3200–3400 m, Páramo El Batallón, Estado Táchira, Venezuela.

Redescription. *MALE* (Fig. 10C): Head: Eyes chocolate brown, lustrous, covered with dense, long, black hair; antennae 2/5 the length of costa, orange brown, naked except for a few basal segments covered with white scales, shaft slender, club spatulate, made of 11 segments, with two lateral, ventral bruises; labial palpi 2 × length of head, covered with sandy yellow and blackish hair, ventrally three times as long as dorsally, and with whitish scales laterally; frons with a tuft of long orange and chocolate brown hair. Thorax: dorsally black, base of prothorax covered with long and dense russet hair, meso and metathorax only with sparse brown hair; ventrally black densely covered with tufts of brown chestnut hair; mid and hindleg femora brown densely covered with sandy yellow hair, tibiae brown with a gorget of yellow hair and sparse whitish hair, tarsi medium brown with dense spines. Abdomen: black, lustrous, dorsally covered with black scales, laterally with sandy yellow and ventrally with whitish and brown scales and yellowish hair. Wings: FW (length: 25–32.5 mm, mean: 29.05 mm) apex subacute, outer margin slightly concave; fringes chestnut and whitish in the interveins. HW oval, smooth; fringes mostly whitish intermixed with some chestnut scales. FWD lustrous, chestnut, with fairly variable pattern of darker grey brown, in some specimens covering most of basal half and forming a zigzagging median line, in others faint and barely noticeable; a row of five sandy yellow submarginal dots, from R5–M1 to Cu1–Cu2, apparent in all the specimens. HWD covered with long chestnut hair in basal and postbasal area, and along inner margin; chestnut, lustrous, less patterned than FWV, in most specimens median half slightly darker, grey brown; submarginal yellow streak visible in most specimens in spaces Cu1–Cu2 and Cu2–1A, rarely in other spaces. FWV varying between light chestnut and sandy yellow, with a postmedian zigzagging grey brown line, and some darker dusting on the apex; a series of yellow submarginal dots as on the upperside. HWV ground colour chestnut with greyish sheen; dark brown areas forming well defined intravenal stripes in most individuals merging into a zigzagging postdiscal line; a series of five submarginal milky white streaks, from Rs–M1 to Cu1–Cu2, somewhat variable in size but extending over at least 3–6 mm. **Male genitalia** (Fig. 15C): Very similar to *S. chiquinquirana chiquinquirana* in most sclerites, uncus, aedeagus and saccus and especially in the massive valvae terminated bluntly, also closely resembling nominate *S. empetrus*, differing only in the subunci, which are small but fully developed not atrophied. **FEMALE** (Fig. 10D): Brachypterous and flightless, much smaller than the male. FW (length 21–22 mm, mean: 21.5 mm, n=5) and HW elongated, FW apex acute. FWD almost uniform lustrous silver, except for the row of tiny, whitish subapical elongated dots, and some brown basal, costal and apical dusting; HWD silver with some faint slightly

darker greyish areas in discal cell, along anal and outer margin; FWV and HWV colour pattern similar to that of the male but ground colour lighter, whitish. **Female genitalia** (Fig. 19A): Papillae anales gently rounded in lateral view, covered with long, thin hair; lamella postvaginalis wide, with two shallow concavities; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae short, approximately $\frac{1}{3}$ the length of bursa copulatrix, narrow, tubular, little sclerotized, approximately the same width throughout its length, with ductus seminalis originating in its middle; bursa copulatrix large, balloon-like, without any visible signa.

Comments. This species is restricted to the open paramo of the La Negra–El Batallón range (southwestern Cordillera de Mérida), which is now protected as a national park (Parque Nacional Juan Peñalosa) (Fig. 1B). *Steromapedaliodes bordoni* only inhabits open areas above the treeline, from 3000 m upwards (the highest altitude in the region is the Pico El Pulpito, about 3950 m). We found males very abundant during the dry season in February and March, but even at that time this paramo was apparently more windy, humid and cloudy than the neighbouring ones of the Cordillera de Mérida. Fast-flying, very active males exploited short periods of sunshine around midday to travel medium distances across the paramo, flying erratically over grasses. They drifted with the wind, but were also able to fly strongly against it. In that case (as in other paramo species, which usually fly in windswept places) the butterflies avoided attack (for instance, from collectors) by stalling in flight, thus allowing the wind to change their flight vector very suddenly. During a very foggy morning with occasional rain and strong wind some males were found resting in the centre of rosettes of *Ruilopezia* sp. (Asteraceae), in which they were difficult to disturb.

Females, with reduced and deformed wings, do not fly under natural conditions and spend most of their time resting on grasses, where they are effectively protected from predators by highly cryptic underside wing pattern (VILORIA et al. 2003). All females were collected directly from the ground and bunch grasses by hand, two of them were observed walking and jumping on the ground, and after exposure to strong sunshine for five or six minutes (for observation), one made a very weak ‘flight’ of about 3 m, probably the limit of its capabilities. An explanation for this very unusual behaviour was presented by VILORIA et al. (2003) and PYRCZ (2010b). One female violently expelled five mature eggs when captured, a reaction already recorded for other species of *Steromapedaliodes* and two species of the genus *Diaphanos*, which probably resulted from the stress caused by handling (VILORIA 1994). As the eggs are always free of any adhesive, it is obvious that these butterflies do not oviposit on a particular substrate but scatter the eggs over the continuous grassland. An unusual behaviour was observed by Mauro Costa in December 2007. Males of *S. bordoni* were seen when overflying a large puddle, and from time to time throwing themselves against the water, possibly engaging in

interactions with their reflection on the water surface. *S. bordoni* was never seen mud puddling or drinking water from the ground.

(9) *Steromapedaliodes lathraia* (Viloria & Camacho), comb.n.

(Figs. 10E,F, 15D, 19B)

[*Redonda casneri nomen nudum*; PYRCZ 2010a: 36, 180–185]
Redonda lathraia Viloria & Camacho (in VILORIA et al. 2015): 119, 135–138, figs. 38–39 (adults), 56 (male genitalia).

Material examined. VENEZUELA: 1 ♂, Estados Mérida/Táchira border, El Batallón, Mesa Alta, 2700–2800 m, 03.xii.2005, T. Pyrcz, (prep. genit. 02/07.10.2014 J. Lorenc-Brudecka); 32 ♂ and 1 ♀: Estados Mérida/Táchira border, El Batallón, Mesa Alta, 2700–2800 m, 03.XII.2005, T. Pyrcz, (female: prep. genit. 03/07.11.2011 J. Lorenc-Brudecka) TWP; 3 ♂: same data but 10.ii.2007, TWP; 17 ♂ and 2 ♀: Mérida, Mesa Alta, Bailadores vers Pregonero km 33,5, 5,5 km après jonction de la Grita, 02.XII.2005, P. Boyer leg., PBF.

Type locality: Entre Laguna El Cenegón and Laguna Grande, Páramo El Batallón, Estado Táchira, Cordillera de Mérida, Venezuela.

Redescription. **MALE** (Fig. 10E): **Head:** Eyes chocolate brown, lustrous, covered with dense, long, black hair; antennae $\frac{2}{5}$ the length of costa, orange brown, naked except for a few basal segments covered with white scales, shaft slender, club spatulate, composed of 11 segments, with two lateral, ventral bruises; labial palpi $2 \times$ length of head, covered with sparse sandy yellow and brown hair, ventrally three times as long as dorsally, frons with a tuft of long chocolate brown and chestnut hair. **Thorax:** dorsally black, base of prothorax covered with long and dense russet hair, meso and metathorax only with sparse brown hair; ventrally black densely covered with tufts of brown chestnut hair; mid and hindlegs chestnut, covered with grey brown and silver scales, denser on tarsi. **Abdomen:** black, lustrous, covered with grey brown scales, somewhat lighter ventrally. **Wings:** FW (length: 23–26.5 mm, mean: 24.83 mm, n=28) apex subacute, outer margin slightly concave; fringes chestnut except for some sandy yellow scales in the interveins. HW oval, outer margin gently undulated; fringes chestnut and sandy yellow in apical area. FWD lustrous, chestnut with a greyish sheen, a row of five sandy yellow submarginal minute dots, from R5–M1 to Cu1–Cu2, in some specimens not apparent. HWD covered with long chestnut hair in basal and postbasal area, and along inner margin; uniform chestnut, lustrous. FWV chestnut, slightly darker brown along costa and along outer margin; a row of five small submarginal sandy yellow elongated dots. HWV ground colour chestnut with darker brown areas forming diffused intravenal stripes and a series of lunular spots along outer margin; a series of five submarginal milky white patches, from Rs–M1 to Cu1–Cu2, pointing basally, somewhat variable in size but invariably forming elongated spearheads pointing basally extending over 2–5 mm. **Male genitalia** (Fig. 15D): Most closely resembling *S. bordoni*

in the shape of massive valvae terminated with a blunt apex, and *S. leuksamena* in the completely atrophied subunci fused with ventral surface of base of uncus, and the longer uncus than in any subspecies of *S. empetrus* or *S. bordoni*. **FEMALE** (Fig. 10F): Sexual dimorphism inconsiderable except for the slightly smaller size of the female (FW length 23 mm, n=3), somewhat lighter upperside, with a characteristic FW and HW golden sheen and particularly lighter underside due to a yellowish suffusion of FW and the presence of dense, fine milky white dusting especially in outer $\frac{1}{3}$. **Female genitalia** (Fig. 19B): Papillae anales gently rounded in lateral view, covered with long, thin hair; lamella postvaginalis wide, with two shallow concavities; lamella antevaginalis with a single, little prominent, blunt protrusion; ductus bursae short, approximately $\frac{1}{3}$ the length of bursa copulatrix, narrow, tubular, with a prominently corrugated and more noticeably sclerotized distal half, gently opening into bursa copulatrix, with ductus seminalis originating in its middle; bursa copulatrix small, roughly oval, without any visible signa.

Comments. This species differs from *S. bordoni* in the smaller size, more elongated FW, and the much darker, chestnut with a greyish sheen FW and HWD. In this respect it resembles closely *S. chiquinquirana lossadana* from which it however differs in the much elongated HWV submarginal milky white markings and the more acute FW apex.

Steromapedaliodes lathraia occurs in boggy paramo just above timberline overgrown with dwarf *Chusquea*, which is possibly its host plant, whereas *S. bordoni* inhabits high paramo grasslands devoid of *Chusquea*. Marginally however, for example along the Antenas–Cienagas trail, at some 3100–3200 m the two species are syntopic. This fact mislead previous authors who included several specimens of *S. bordoni* in the paratype series of this species, which they tentatively identified as an individual “grey” form of *S. bordoni*.

4. Discussion: evolution and systematics of *Steromapedaliodes sensu novo*

Our decision on considering *Redonda* as a subjective junior synonym of *Steromapedaliodes sensu novo* is supported by molecular and morphological evidence. Molecular analyses clearly show that although the species associated previously with *Redonda* form a clade, this group and *Steromapedaliodes sensu Vitoria & Pyrcz* never appear to be reciprocally monophyletic in our phylogenetic analyses. Indeed, *Redonda* is always nested within the genus *Steromapedaliodes sensu Vitoria & Pyrcz*, which makes the latter paraphyletic. Also, our point of view is strengthened by the discovery of a new species, *S. mavarezi*, whose genital characters appear in-

termediate between *Steromapedaliodes sensu Vitoria & Pyrcz* and *Redonda*, but being placed phylogenetically in a clade with *S. albarregas* and *Redonda*. From a cladistic perspective, the retention of *Redonda* as a separate entity would require the inclusion of *S. mavarezi* and *S. albarregas* within *Redonda*, and the restriction of the other species to *Steromapedaliodes*. However, such scheme would be in strong contradiction with the morphological results shown above. We opted for a simpler scheme, with only one supra-specific category and without negative effects on the catalogue of biodiversity as measured by the number of species.

The decision to consider a single genus, *Steromapedaliodes sensu novo*, is strongly supported by two results from the morphological analyses. On the one hand by the absence of any salient synapomorphies in adult morphology of the two genera previously considered (*ex Steromapedaliodes sensu Vitoria & Pyrcz* and *ex Redonda*), and on the other by the existence of synapomorphic characters of the genus *Steromapedaliodes sensu novo* in male and female genitalia and colour patterns. This agrees with the view that the comparative analysis of genital structures provides valuable data, and can be crucial in assessing phyletic affinities of taxa of butterflies in general (TURNER et al. 1961; LORKOVIĆ 1993; FREITAS & BROWN 2004), and those belonging to the subtribe Pronophilina in particular (VILORIA 2000; PYRCZ 2008; PYRCZ & VILORIA 2008; PYRCZ et al. 2010). In particular, the presence of the singular arrowhead HWV submarginal dots, unique among all the species of the speciose *Pedaliodes* complex, is considered here as a strong synapomorphy. Our results provide further support to the idea that colour patterns, particularly on the hindwing venter, are good characters to consider in the phylogenetic reconstruction of relationships among butterflies (PYRCZ et al. 2008).

Our results indicate that putative ecological differences between *ex Steromapedaliodes sensu Vitoria & Pyrcz* and *ex Redonda* pointed out in some previous papers do not stand (PYRCZ 2010a; VILORIA et al. 2015). In fact, although all the species previously associated with *ex Redonda* are paramo dwellers, this is by no means an exclusive feature, as several subspecies of *S. albonotata* are also found above timberline, living in association with the high-altitude tropical grassland characteristic of the paramo habitat. On the other hand, the habitat of *S. albarregas* is confined to dense uppermost forests, where it flies above canopy, and it does not occur in open grassland or even in forest-paramo patches, as do some populations of *S. albonotata* or *S. mavarezi*. We believe that *S. albarregas* could have retained several plesiomorphic and less specialised characters than other congeners, which can be related to its preferred habitat, typical of most Pronophilina and particularly of most *Pedaliodes*. Accordingly, *S. albarregas* females are only marginally smaller than the males and are vigorous fliers.

It seems however plausible that some ecological processes are at play in the divergence and further maintenance of species differences in *Steromapedaliodes sensu*

novo. Most species show rather restricted geographic distributions with almost no overlap with other taxa, indicating that mechanisms of allopatric or parapatric speciation must have played a role during the initial phases of divergence in the genus. Thus, *S. leukasmena* is distributed allopatrically in the north (Cendé massif), *S. empetrus*, *S. chiquinquirana* and *S. albarregas*, are distributed parapatrically in the main central ranges of the Cordillera de Mérida (Culata and Sierra Nevada massifs), and *S. bordoni* and *S. lathraia*, are distributed sympatrically but rarely syntopically in the southern paramos (Batallón and La Negra). Very little is known about the geographic distributions of *S. mavarezi* sp.n. (Guirigay massif) and *S. kahlua* sp.n. (Santo Domingo range), but both seem to be distributed parapatrically in regards to *S. chiquinquirana* and *S. albonotata*, respectively. There are only two exceptions to this pattern, the sympatry between *S. bordoni* and *S. lathraia* mentioned above, and *S. albonotata*, a species with a very large distribution covering almost entirely the Cordillera de Mérida and that has been found in sympatry with *S. albarregas* and *S. chiquinquirana* in the main central ranges and with *S. leukasmena* in the north (Cendé massif), but never in syntopy. Indeed, as mentioned above, *S. albonotata* is generally a ground-level flying species in the forest-paramo ecotone that seems to be ecologically separated from other locally sympatric species by microhabitat use: above the forest canopy at a 4–5 m flight-height (*S. albarregas*) and true paramo (*S. chiquinquirana* and *S. leukasmena*). The only known case of syntopy in *Steromapedaliodes sensu novo*, although rather marginal, is therefore found in *S. bordoni* and *S. lathraia*. Yet, again, these are two ecologically divergent species that also differ greatly in almost any other respect, including male genitalia and male wing colours, but most notably on female wing shape (*S. bordoni* are brachypterous, *S. lathraia* are normal-shaped and good flyers). No hybrid individual between *S. bordoni* and *S. lathraia* has ever been found, which provides support for the idea of a presumably strong isolation between these two species. Unfortunately, nothing is known about the reproductive biology of any species of *Steromapedaliodes sensu novo* so the relative importance of pre-zygotic mechanisms (i.e. ecological isolation) and post-zygotic mechanisms (i.e. hybrid sterility or inviability) for species isolation cannot be stated at this time.

In any case, the ensemble of genetic, ecologic and geographic data suggest that the divergence within *Steromapedaliodes sensu novo* in the Cordillera de Mérida occurred first parapatrically along a habitat axis, i.e. elfin forest forest canopy (*S. albarregas*) – forest-paramo ecotone (*S. mavarezi*, *S. albonotata*, *S. lathraia*, and perhaps *S. kahlua*) – grassland paramo (*S. bordoni*, *S. chiquinquirana*, *S. empetrus* and *S. leukasmena*), and then mostly allopatrically within similar habitat zones separated geographically. These findings provide additional support for what is emerging as a general model of butterfly diversification in the high-altitude habitats of the Andes. For example, in the genus *Lymanopoda* (Nymphalidae: Satyriinae: Pronophilina) the earlier divergences of lin-

eages are associated with large changes in altitudinal distribution while recent speciation events appear to be linked to geographic shifts within the same elevational band (ADAMS 1985; CASNER & PYRCZ 2010). Similar evolutionary patterns were considered for the genera *Theope* Doubleday, 1847, *Hypanartia* Hübner, 1921 (Nymphalidae: Nymphalinae), and *Eois* Hübner, 1818 (Geometridae: Larentiinae) (HALL & WILLMOTT 1996; WILLMOTT et al. 2001; STRUTZENBERGER & FIEDLER 2011). It is interesting to note that a similar scenario might also be at work in other taxa, such as the emblematic paramo endemic plants of the subfamily Espeletiinae (Asteraceae), in which divergence has produced genera specifically associated with habitat types/altitudinal limits, i.e. *Carramboa* and *Libanothamnus* in the forest-paramo ecotone, *Espeletia* and *Espeletiopsis* in the paramo proper and *Coespeletia* in the desertic superparamo (CUATRECASAS 2013).

The approach towards the species-level taxonomy of *ex Redonda* presented by VILORIA et al. (2015) reflects a “splitter” perspective, as all the subspecies of the polytypic *S. chiquinquirana* and *S. empetrus* are treated as specifically distinct. Such a position is not supported by our analysis of morphologic and genetic data. Putative morphological differences separating the various taxa, particularly in male genitalia, are weak and merely quantitative, referring to somewhat larger or longer sclerites such as uncus, subunci or valvae. Our comparative studies of genital organs show that individual variation in male genitalia is important, and there is extensive overlap in most characters, especially among the subspecies of *S. chiquinquirana*. Also, female genitalia were not studied by VILORIA et al. (2015). There is on the other hand evidence based on field observations suggesting that male individuals of *S. chiquinquirana* and *S. empetrus* are particularly active and have been seen several kilometres away from the nearest established populations, in inhospitable superparamo habitat such as in the Pico El Aguila or in the Páramo de Piedras Blancas at about 4300 m. We propose that *S. chiquinquirana*, *S. empetrus*, *S. albonotata* and *S. albarregas* are four species with significant polytypic variation. The remaining taxa, *S. bordoni*, *S. kahlua* sp.n., *S. lathraia*, *S. leukasmena* and *S. mavarezi* sp.n., are sufficiently distinctive from the genetic, morphologic and biogeographic standpoints so that their specific status is supported. Indeed, they all represent divergent phylogenetic lineages, show non-overlapping morphologies in regards to variation in wing size, shape, colours, and at a certain degree on genital traits, and generally exhibit disjunct geographic distributions.

Our study emphasizes the convenience and importance of analyses that combine different sources of information, particularly morphological and molecular, while assessing phylogenetic relationships. Morphological data, especially male and female genitalia, originally suggested the presence of as a highly polytypic species (*S. empetrus*, 6 ssp.) in the central part of the Cordillera de Mérida. However, molecular data favour the identification of two different and somehow distantly related

species (*S. empetrus*, 3 ssp., and *S. chiquinquirana*, 3 ssp.). Their distribution is locally adjacent in the Santo Domingo area without apparent overlapping. It seems therefore that life in the same or very similar habitats has led to the development of highly similar wing patterns in these two species. Convergence driven by adaptation appears therefore to be a common feature of *Steromapedaliodes sensu novo* butterflies. The newly described species, *S. mavarezi*, which bears striking resemblance to the syntopic *Cheimas opalinus* seems to be another evident example of this phenomenon.

As stated earlier, the somehow morphologically similar *Dangond* is not the sister taxon of *Steromapedaliodes sensu novo*, and they are in fact distantly related within the *Pedaliodes* complex. This suggests that the similarities between the two taxa are the product of some sort of morphological convergence probably associated with life in the high altitudes of the Cordillera de Mérida and Perijá, respectively. Our study indicates therefore that the evolutionary responses to similar extrinsic factors may induce morphological convergence not only affecting discrete colour pattern and other external characters, but also male and female genitalia. It is difficult at the moment to establish the origin or the processes behind such convergences for genitalia since there are no obvious ecological correlations between life in the paramo and, for example, the loss of subunci or signa. However, we notice that the members of *Steromapedaliodes sensu novo* and *Dangond* occupy habitats with no other congeners and therefore there are no chances of interspecific signal jamming in species recognition and courtship, which in turn may lead to the disappearing of some sexually related characters associated with species recognition. This may explain the presence of simple aedeagus in the males coupled with short ductus bursae in the females. On the other hand, the inefficiency of chemical communication in windswept open grassland may induce the disappearing of specialized androconial scales. In fact, several other paramo species of *Pedaliodes* complex associated with the genus *Altopedaliodes* also have short and straight aedeagus, and no specialized androconial scales in *Punapedaliodes* (PYRCZ & VILORIA 1999; VILORIA 2000), although they may occur syntopically with one or two congeners. However, this remark seems to apply to Satyrinae only, since within some members of paramo dwelling Lycaenidae, such as the genus *Penaincisalia* Johnson, 1990, scent organs are fully developed and differ between sympatric species (PRIETO 2008).

Certain important issues deserve further consideration, although some of them remain yet unsolved due to

insufficient data. First, the closest relative of the genus *Steromapedaliodes sensu novo* clade is still to be identified. Morphological data clearly point out that it should be a member of the *Pedaliodes* complex, but our molecular phylogenetic analysis failed to identify a clear relationship between the genus *Steromapedaliodes sensu novo* and any taxa in the set used as outgroup taxa, either of our own or from GenBank. It must be acknowledged however that taxa in the *Pedaliodes* complex with available mitochondrial and nuclear sequences in GenBank represent a very small fraction of this large group, both in terms of diversity (i.e. 25 taxa out of ~ 300) and geographic distribution (i.e. only Peruvian taxa although the group is distributed from Mexico to Argentina). The genus *Steromapedaliodes sensu novo* must therefore remain *incertae sedis* until a thorough phylogenetic analysis using a much larger taxonomic and geographic sampling within the *Pedaliodes* complex could be achieved.

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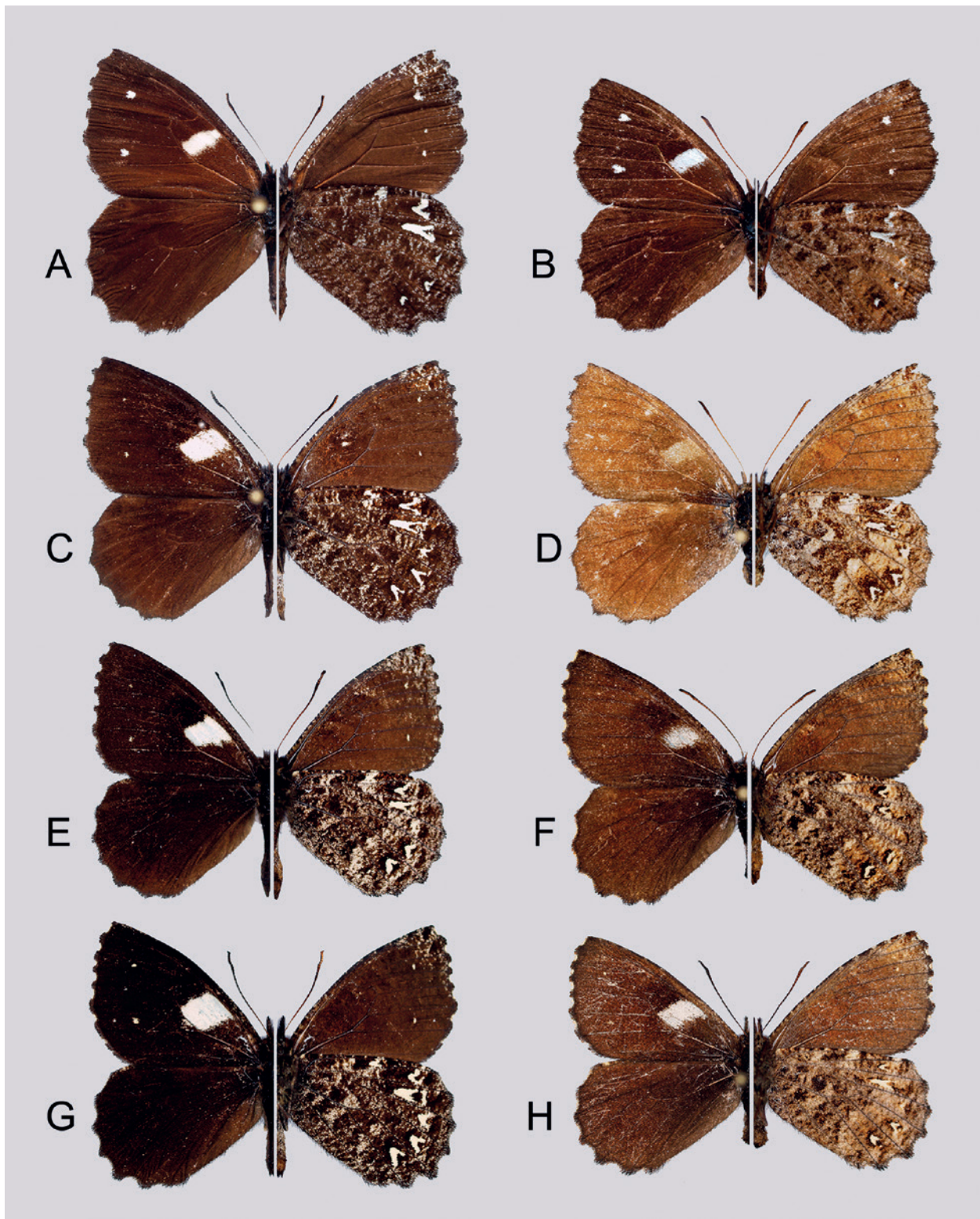


Fig. 5. Entire adults (left: dorsum; right: venter). **A:** *Steromapedaliodes albonotata albonotata* ♂, La Aguada. **B:** *S. albonotata albonotata* ♀, La Aguada. **C:** *S. albonotata australis* ♂, Páramo de San José. **D:** *S. albonotata australis* ♀, Páramo de San José. **E:** *S. albonotata australis* ♂, Mesa Alta. **F:** *S. albonotata australis* ♀, Mesa Alta. **G:** *S. albonotata australis* ♂, Páramo de Guaraque. **H:** *S. albonotata australis* ♀, Páramo de Guaraque.

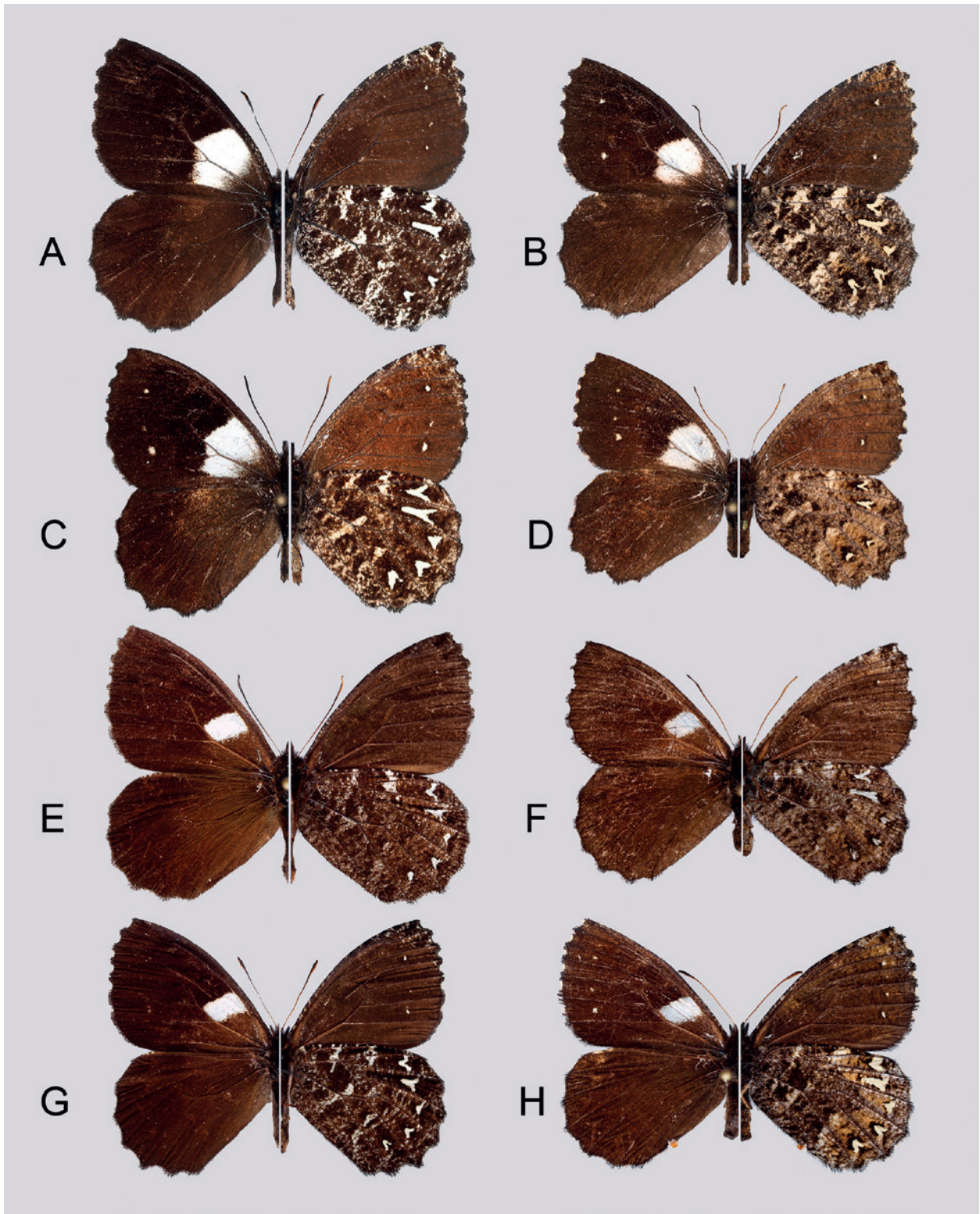


Fig. 6. Entire adults (left: dorsum; right: venter). **A:** *Steromapedaliodes albonotata pratense* ♂, El Potrero, Piñango. **B:** *S. albonotata pratense* ♂, El Potrero, Piñango. **C:** *S. albonotata sanchezi* ♂, Los Morritos. **D:** *S. albonotata pratense* ♀, El Potrero, Piñango. **E:** *S. albonotata borealis* ♂, Páramo de las Rosas. **F:** *S. albonotata borealis* ♀, Páramo de las Rosas. **G:** *S. albonotata borealis* ♂, Páramo de las Rosas. **H:** *S. albonotata borealis* ♀, Páramo de las Rosas.

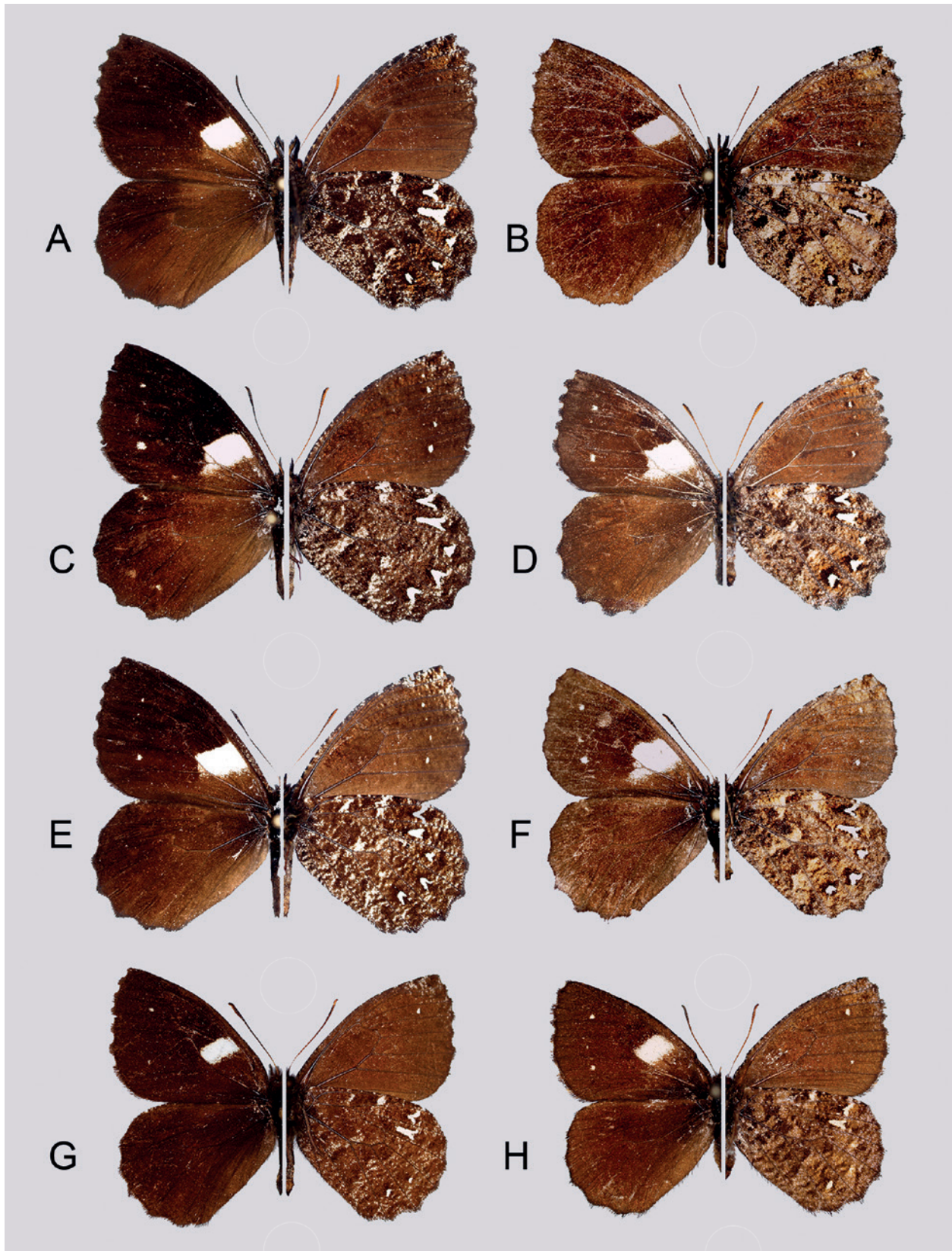


Fig. 7. Entire adults (left: dorsum; right: venter). **A:** *Steromapedaliodes albonotata schuberti* ♂, Páramo de Guaramacal. **B:** *S. albonotata schuberti* ♀, Páramo de Guaramacal. **C:** *S. albonotata josefinae* ♂, El Baho. **D:** *S. albonotata josefinae* ♀, El Baho. **E:** *S. albonotata josefinae* ♂, El Baho. **F:** *S. albonotata josefinae* ♀, El Baho. **G:** *S. albonotata thiemeiana* ♂, Páramo La Culata. **H:** *S. albonotata thiemeiana* ♀, Páramo La Culata.

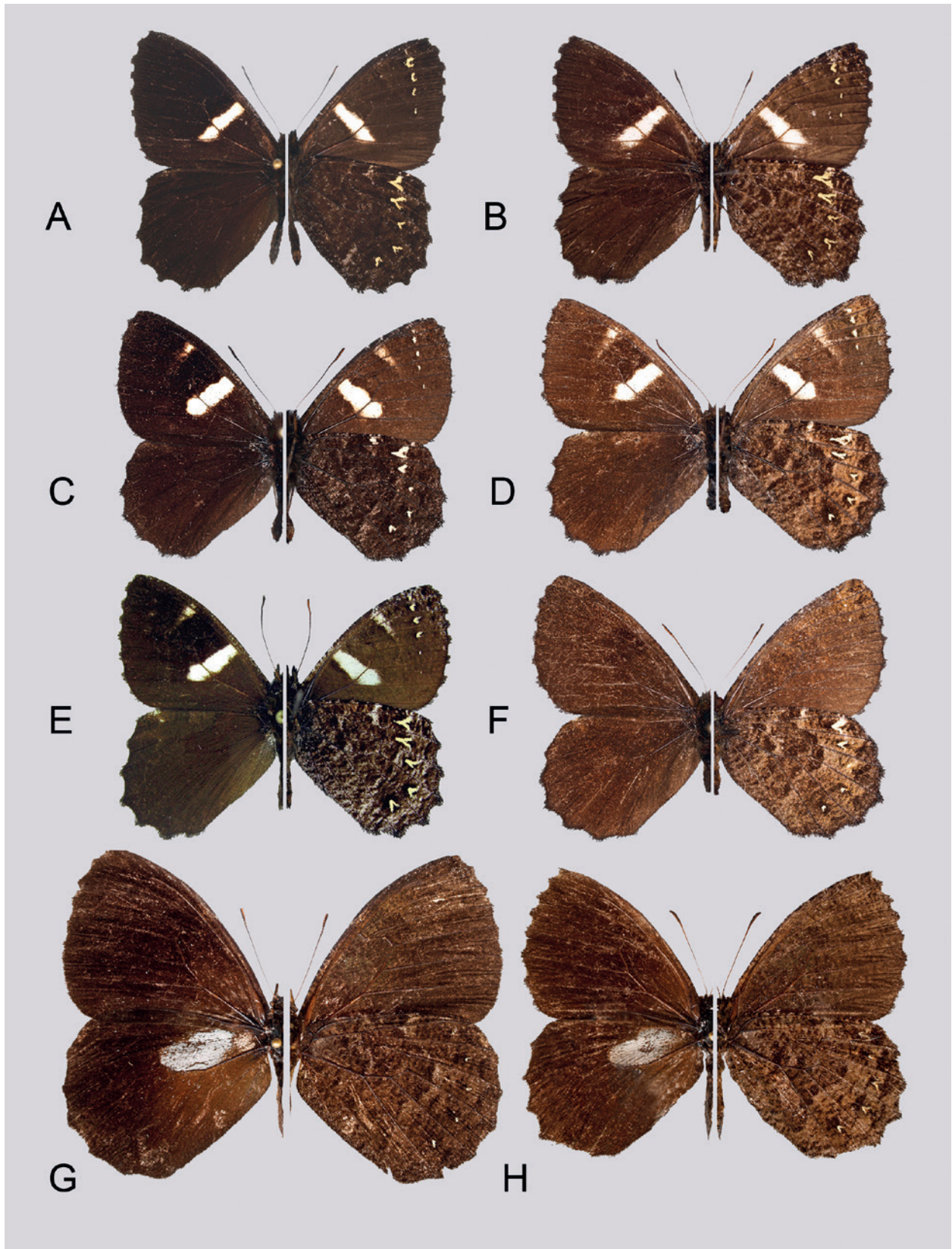


Fig. 8. Entire adults (left: dorsum; right: venter). **A:** *Steromapedaliodes albarregas albarregas* ♂, Quebrada de La Boba. **B:** *S. albarregas albarregas* ♀, Quebrada de La Boba. **C:** *S. albarregas prietoi* ♂, El Potrero, Piñango. **D:** *S. albarregas prietoi* ♀, El Potrero, Piñango. **E:** *S. albarregas mauroi* ♂, Los Morritos, Río Gavidia. **F:** *S. kahlua* ♀, El Baho, la Ciénaga. **G:** *S. mavarezi* ♂, Páramo de Guirigay. **H:** *S. mavarezi* ♀, Páramo de Guirigay.

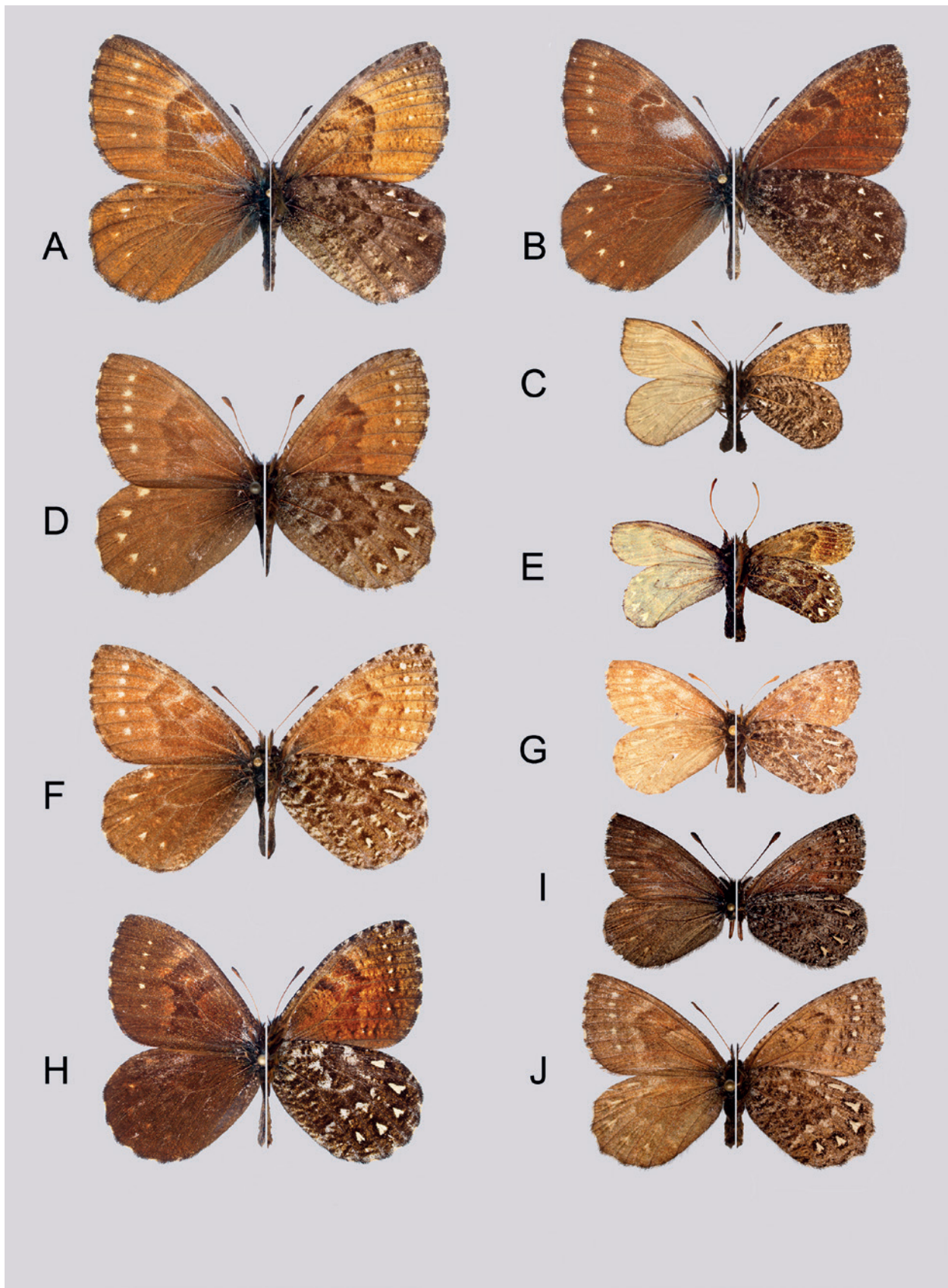


Fig. 9. Entire adults (left: dorsum; right: venter). **A:** *Steromapedaliodes empetrus empetrus* ♂, Páramo La Culata. **B:** *S. empetrus empetrus* ♂, Páramo de la Culata. **C:** *S. empetrus empetrus* ♀, Páramo La Culata. **D:** *S. empetrus frailejona* ♂, Los Frailes. **E:** *S. empetrus frailejona* ♀, Los Frailes. **F:** *S. chiquinquirana chiquinquirana* ♂, Laguna Mucubají. **G:** *S. chiquinquirana chiquinquirana* ♀, Laguna de Mucubají. **H:** *S. chiquinquirana lossadana* ♂, Páramo de Tuñame. **I:** *S. chiquinquirana lossadana* ♀, Páramo de Tuñame. **J:** *S. chiquinquirana lossadana* ♀, Páramo de Tuñame.

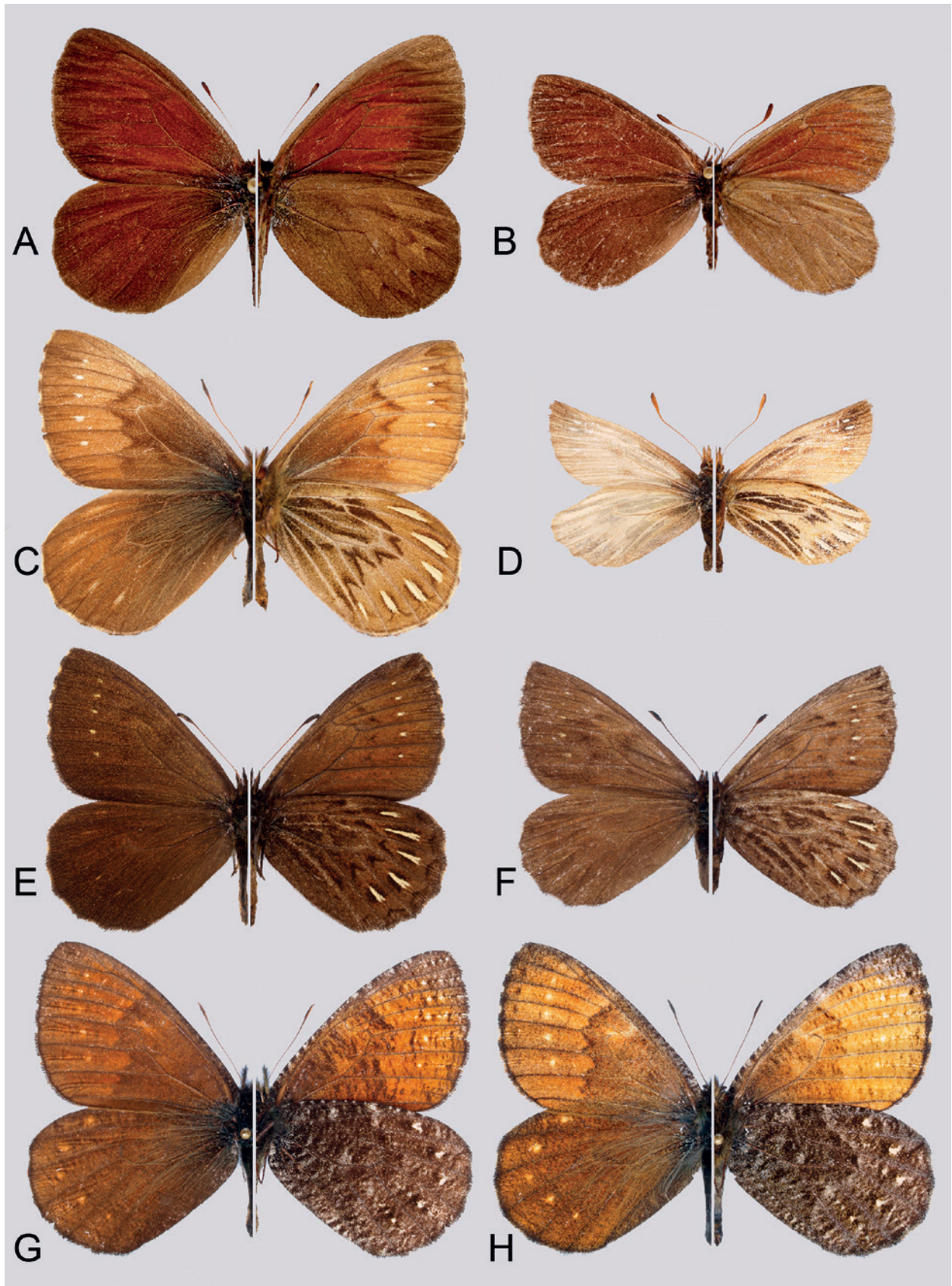


Fig. 10. Entire adults (left: dorsum; right: venter). **A:** *Dangond dangondi* ♂, Páramo el Avión. **B:** *Dangond dangondi* ♀, Páramo el Avión. **C:** *Steromapedaliodes bordoni* ♂, Páramo El Rosal. **D:** *S. bordoni* ♀, Páramo El Rosal. **E:** *S. lathraia* ♂, Mesa Alta. **F:** *S. lathraia* ♀, Mesa Alta. **G:** *S. empetrus bolivari* ♂, Loma Redonda. **H:** *S. empetrus bolivari* ♀, Loma Redonda.

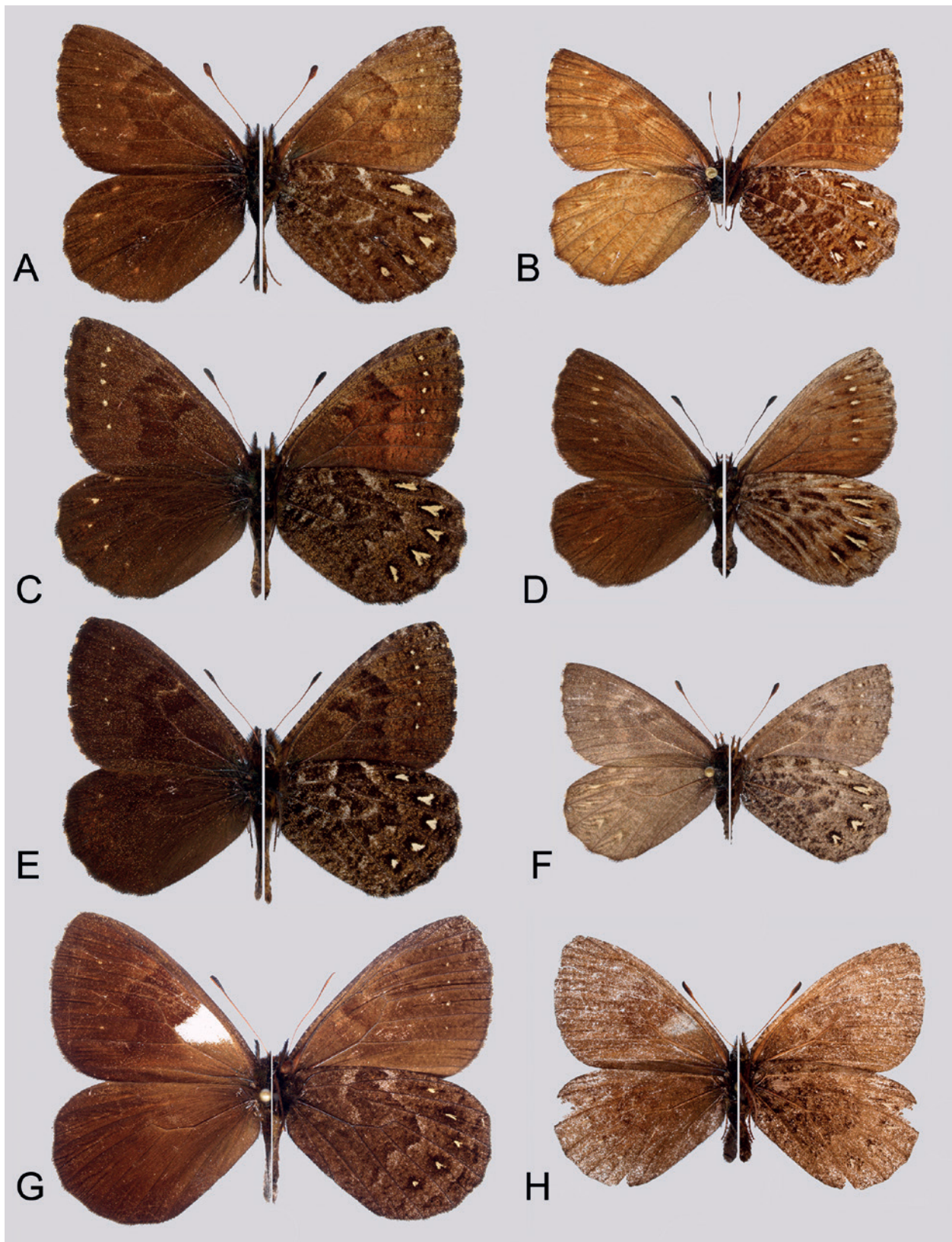


Fig. 11. Entire adults (left: dorsum; right: venter). **A:** *Steromapedaliodes chiquinquirana castellana* ♂, Páramo de Cabimbú. **B:** *S. chiquinquirana castellana* ♀, Páramo de Cabimbú. **C:** *S. chiquinquirana castellana* ♂, Páramo de Las Moras. **D:** *S. chiquinquirana castellana* ♀, Páramo de Las Moras. **E:** *S. chiquinquirana castellana* ♂, Páramo de Las Moras. **F:** *S. chiquinquirana castellana* ♀, Páramo de Las Moras. **G:** *S. leukasmena* ♂, Páramo de Las Rosas. **H:** *S. leukasmena* ♀, Páramo de Las Rosas.

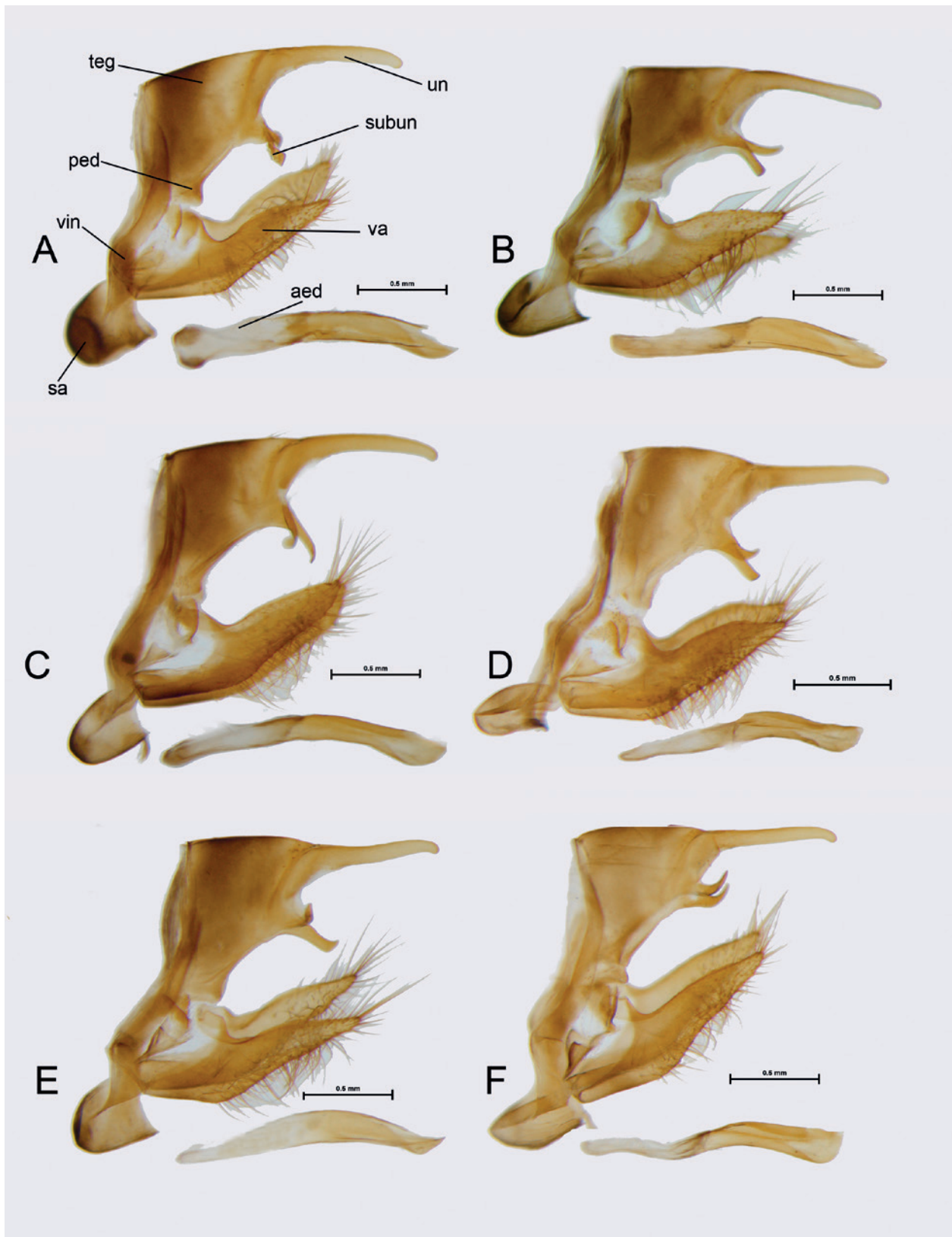


Fig. 12. Male genitalia (in lateral view, aedeagus removed from its natural position). **A:** *Steromapedaliodes albonotata albonotata*, La Aguada. **B:** *S. albonotata thiemeiana*, Páramo La Culata. **C:** *S. albonotata australis*, El Batallón, Mesa Alta. **D:** *S. albonotata sanchezi*, Los Morritos. **E:** *S. albonotata pratense*, El Potrero, Piñango. **F:** *S. albonotata josefinae*, El Baho. — **Abbreviations:** un uncus; subun subuncus; va valva; aed aedeagus; teg tegumen; ped pedunculus; vin vinculum; sa saccus.

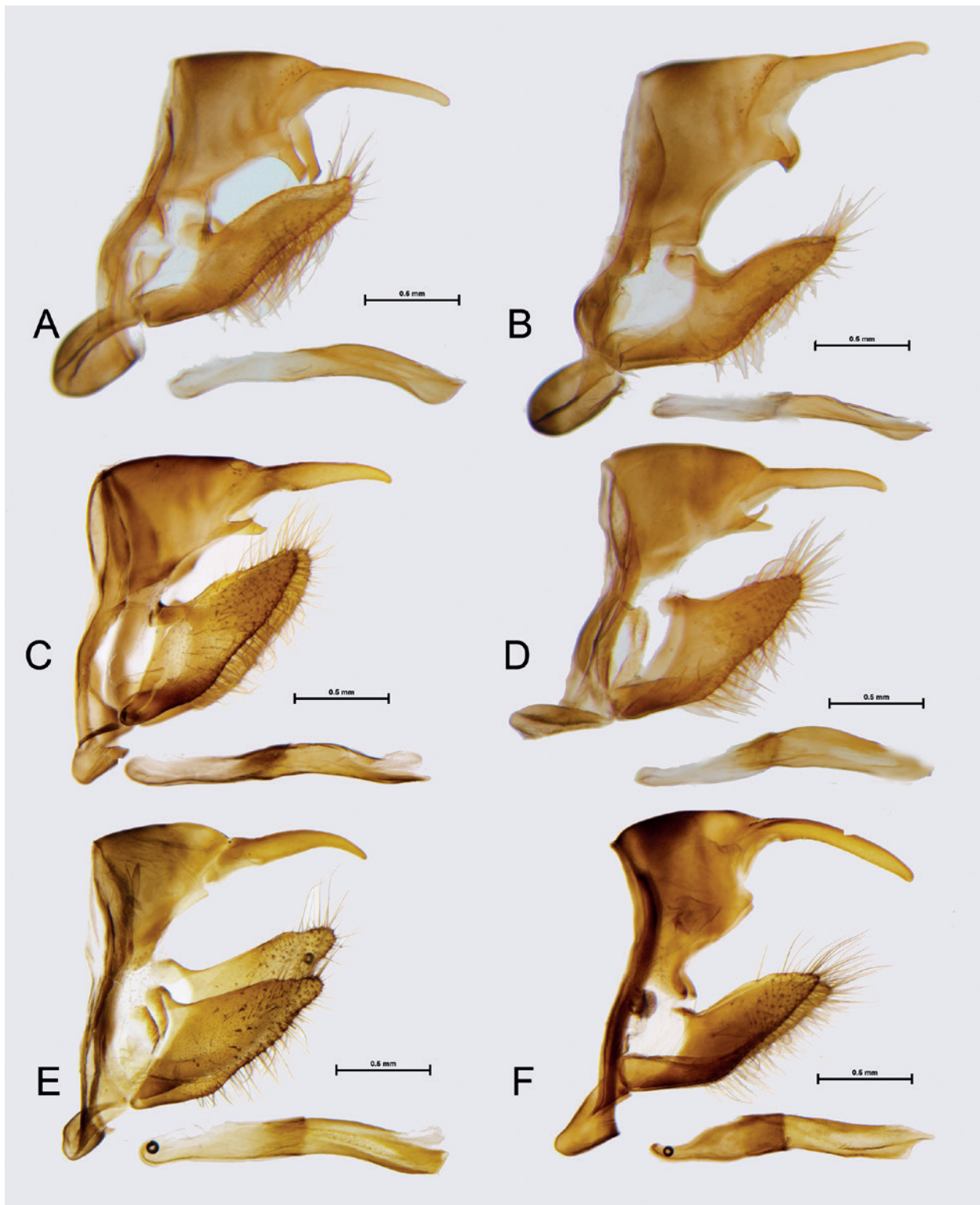


Fig. 13. Male genitalia (in lateral view, aedeagus removed from its natural position). **A:** *Steromapedaliodes albonotata schuberti*, Páramo de Guaramacal. **B:** *S. albonotata borealis*, Páramo de las Rosas. **C:** *S. albarregas albarregas*, Quebrada de La Boba. **D:** *S. albarregas prietoi*, El Potrero, Piñango. **E:** *S. mavarezi*, Páramo de Guirigay. **F:** *D. dangondi*, Sabana Rubia.

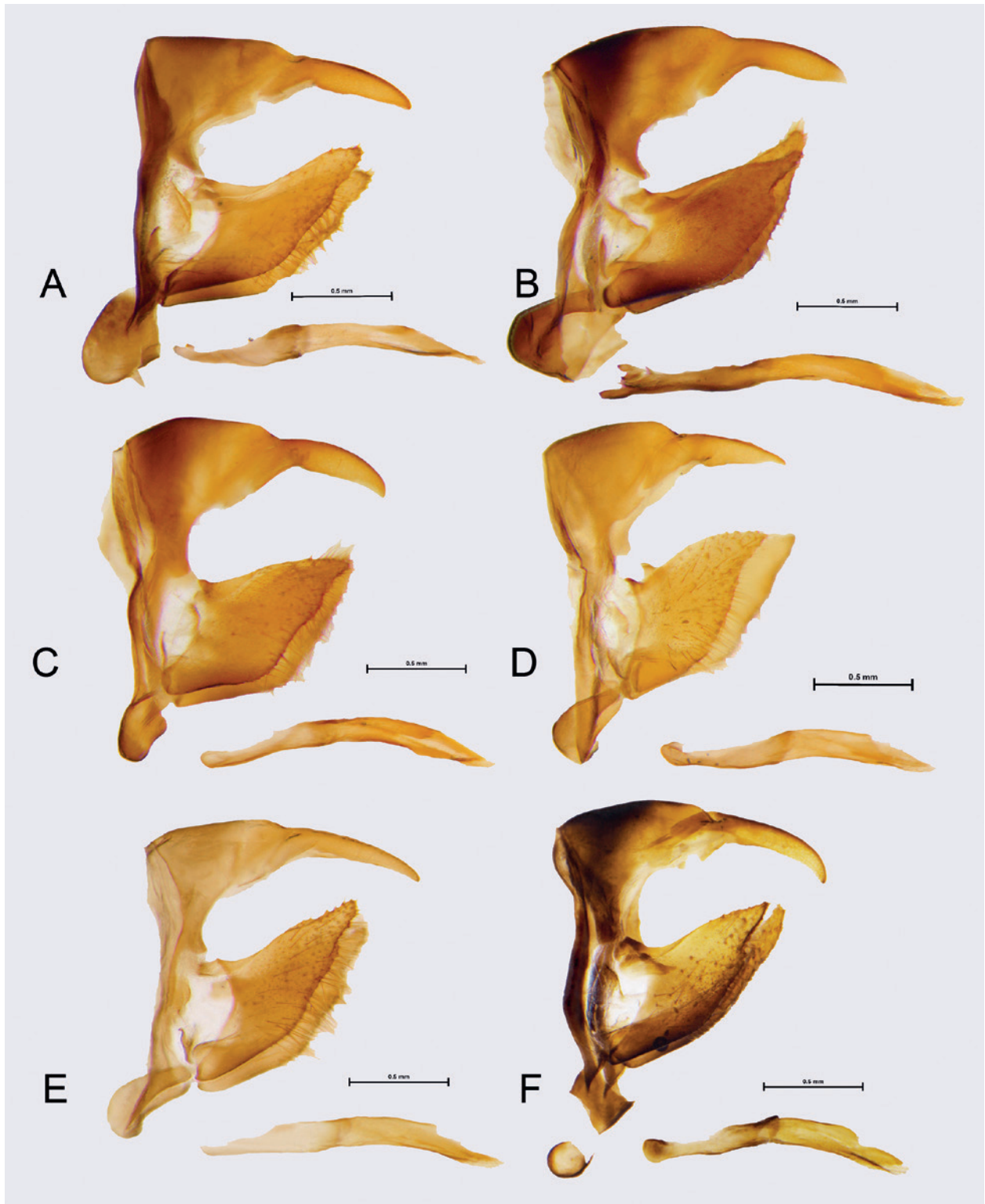


Fig. 14. Male genitalia (in lateral view, aedeagus removed from its natural position). **A:** *Steromapedaliodes empetrus frailejona*, Los Frailes. **B:** *S. empetrus bolivari*, Loma Redonda. **C:** *S. empetrus empetrus*, Páramo La Culata. **D:** *S. chiquinquirana chiquinquirana*, Laguna de Mucubají. **E:** *S. chiquinquirana lossadana*, Páramo de Tuñame. **F:** *S. chiquinquirana lossadana*, Páramo de Tuñame.

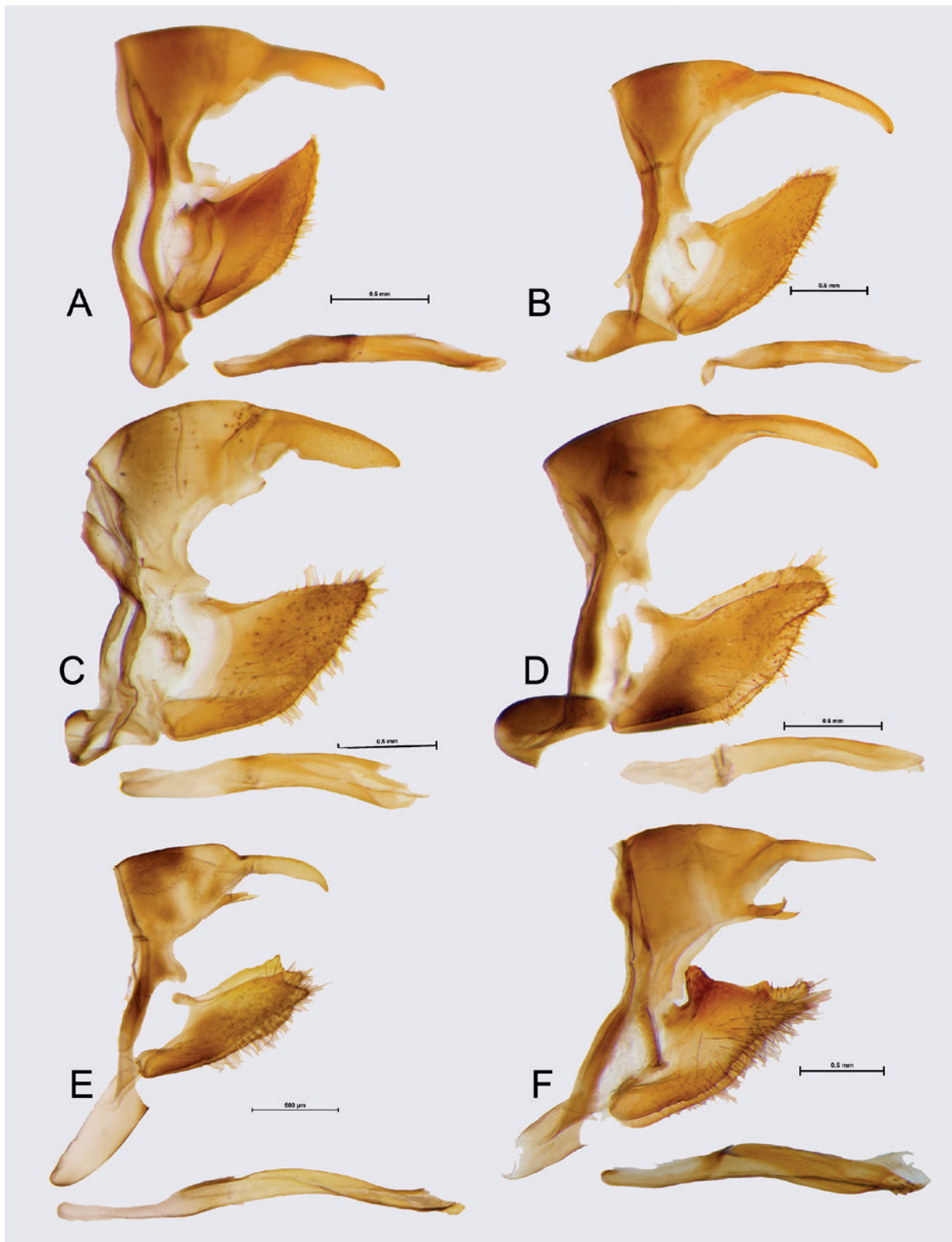


Fig. 15. Male genitalia (in lateral view, aedeagus removed from its natural position). **A:** *Steromapedaliodes chiquinquirana castellana*, Páramo Las Moras. **B:** *S. leukasmena*, Páramo de Las Rosas. **C:** *S. bordoni*, Páramo El Rosal. **D:** *S. lathraia*, Mesa Alta. **E:** *Panyapedaliodes panyasis*, Acjanaco–Pillcopata. **F:** *Pedaliodes plotina plotina*, Colonia Tovar.

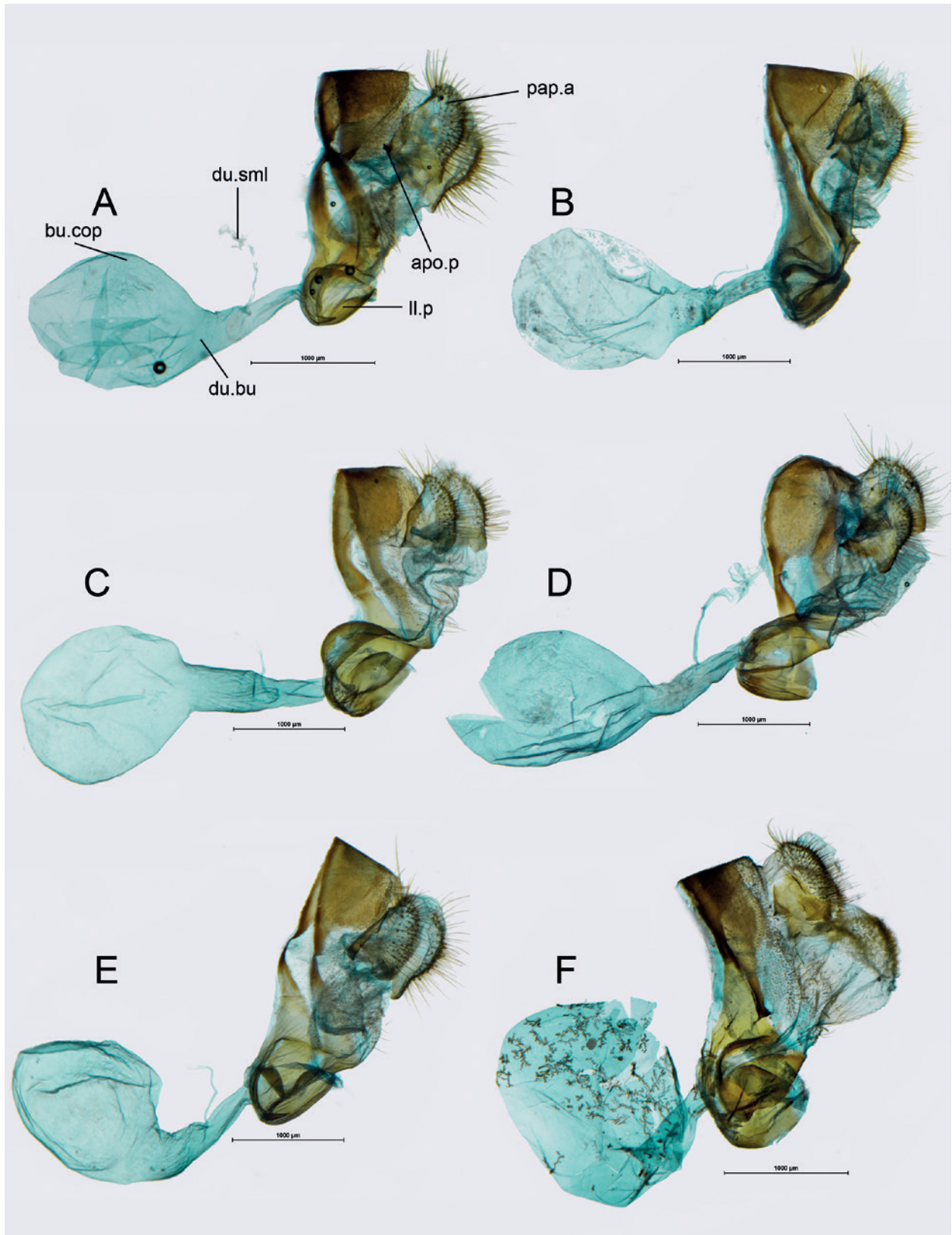


Fig. 16. Female genitalia (in lateral view). **A:** *Steromapedaliodes albonotata borealis*, Páramo de las Rosas. **B:** *S. albonotata pratense*, El Potrero, Piñango. **C:** *S. albarregas albarregas*, Quebrada de La Boba. **D:** *S. albarregas prietoi*, El Potrero, Piñango. **E:** *S. kahlua*, El Baho, la Ciénaga. **F:** *S. mavarezi*, Páramo de Guirigay. — **Abbreviations:** **pap.a** papillae anales; **apo.p** apophyses posteriores; **ll.p** postvaginal lamella; **du.bu** ductus bursae; **du.sml** ductus seminalis; **bu.cop** bursa copulatrix.

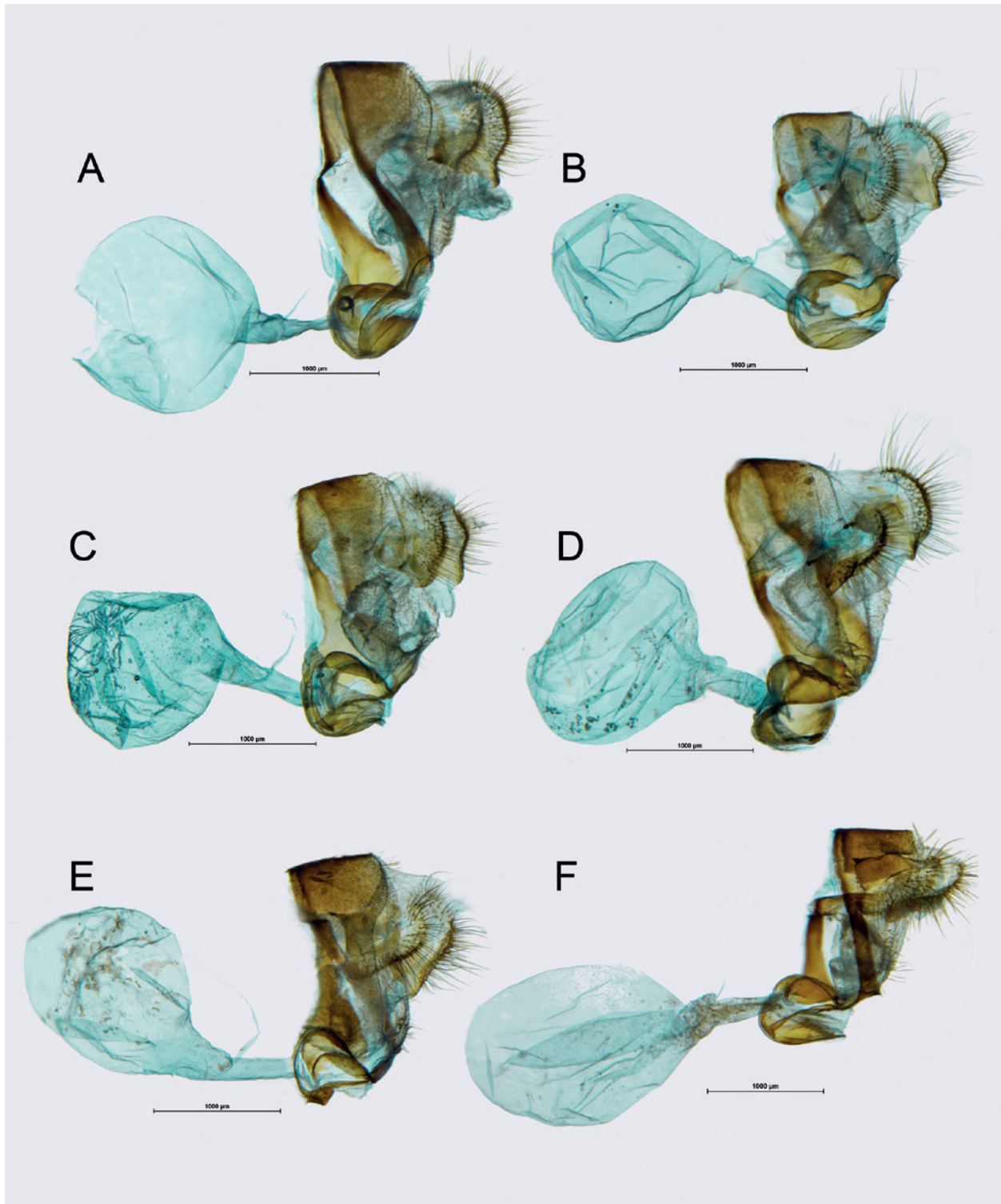


Fig. 17. Female genitalia (in lateral view). **A:** *Steromapedaliodes albonotata schuberti*, Páramo de Guaramacal. **B:** *S. albonotata thiemiana*, Páramo La Culata. **C:** *S. albonotata australis*, Páramo San Jose. **D:** *S. albonotata australis*, El Batallón, Mesa Alta. **E:** *S. albonotata josefinae*, El Baho. **F:** *S. albonotata albonotata*, La Aguada.

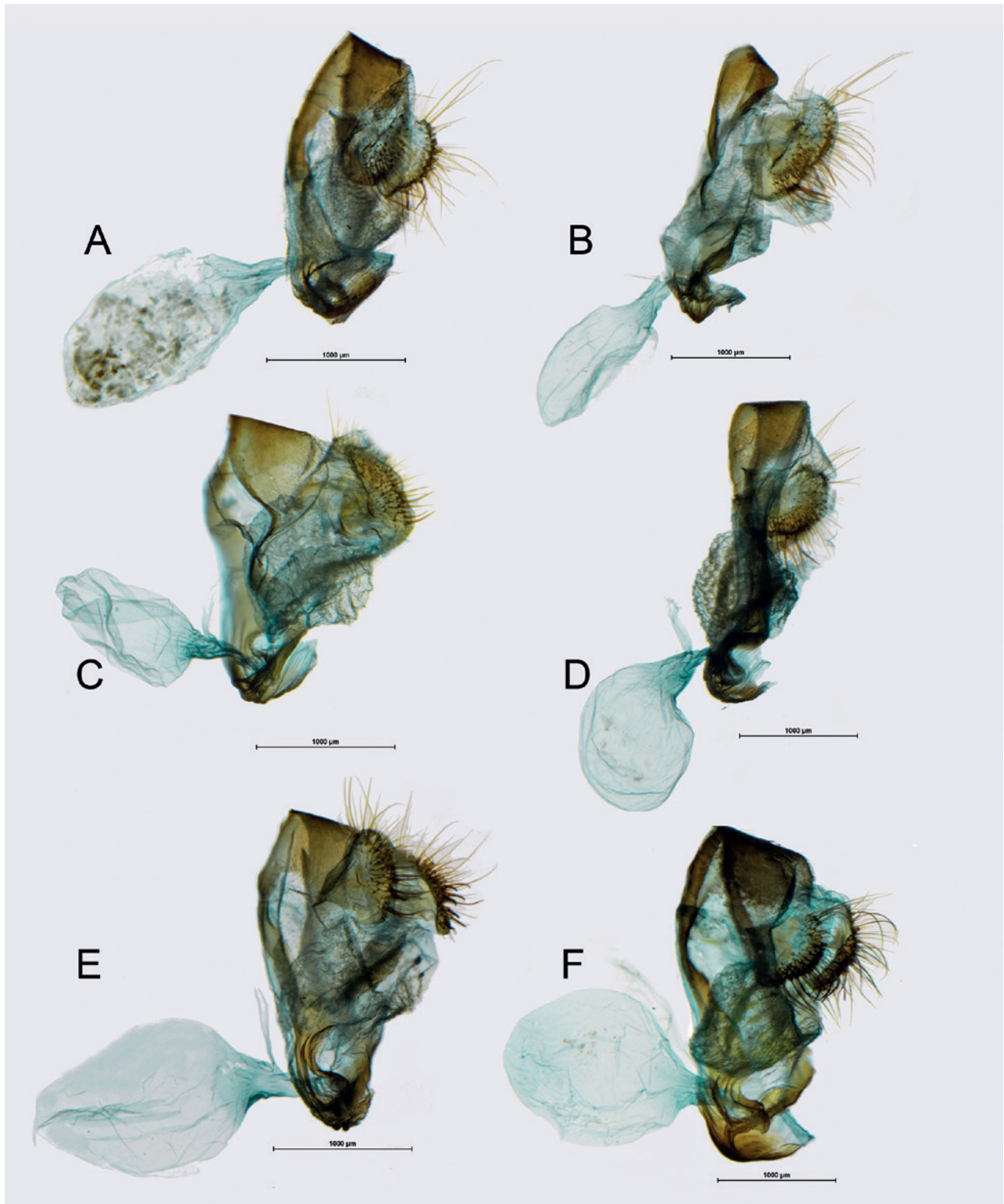


Fig. 18. Female genitalia (in lateral view). **A:** *Steromapedaliodes empetrus frailejona*, Los Frailes. **B:** *S. empetrus empetrus*, Páramo de la Culata. **C:** *S. chiquinquirana chiquinquirana*, Laguna de Mucubají. **D:** *S. chiquinquirana castellana*, Páramo Las Moras. **E:** *S. chiquinquirana lossadana*, Páramo de Tuñame. **F:** *S. chiquinquirana lossadana*, Páramo de Tuñame.

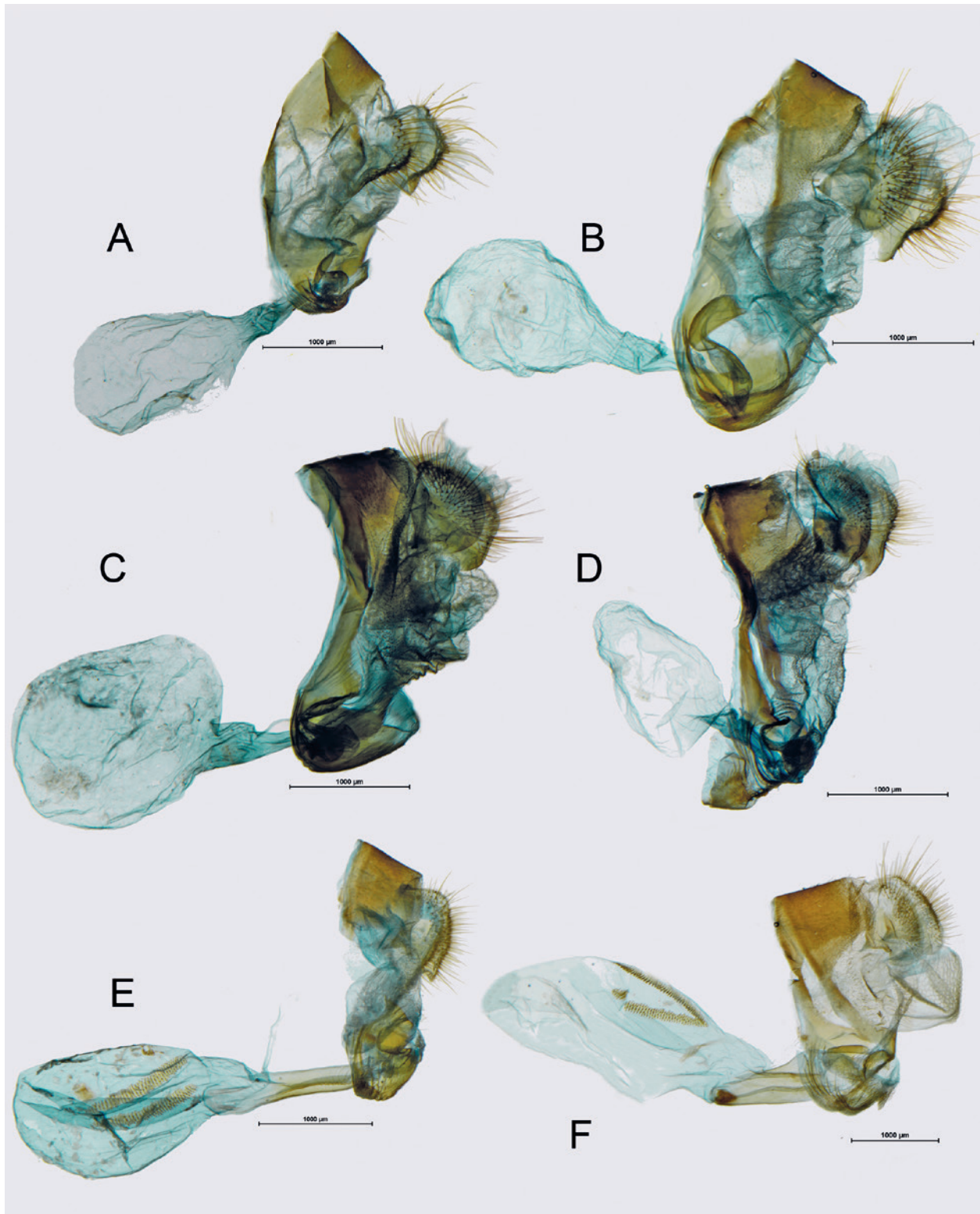


Fig. 19. Female genitalia (in lateral view). **A:** *Steromapedaliodes bordoni*, Páramo El Rosal. **B:** *S. lathraia*, Mesa Alta. **C:** *S. leukasmena*, Páramo de Las Rosas. **D:** *Dangond dangondi*, Sabana Rubia. **E:** *Panyapedaliodes drymaea*, Chachapoyas. **F:** *Pedaliodes plotina plotina*, Colonia Tovar.

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Electronic Supplement File

at <http://www.senckenberg.de/arthropod-systematics>

File 1: [pyrcz&al-nymphalidae-steromapedaliodes-asp2017-electronicsupplement.doc](#) – **Table S1.** Primers used to amplify mitochondrial and nuclear markers.

Zoobank registrations

at <http://zoobank.org>

- Present article:** <http://zoobank.org/urn:lsid:zoobank.org:pub:191503DF-9514-4E65-A19F-2DDFB4C545B9>
- Steromapedaliodes albonotata mauroi* Pyrcz, 2017:** <http://zoobank.org/urn:lsid:zoobank.org:act:4FE92377-165C-434A-9B55-730A271DA021>
- Steromapedaliodes albonotata prietoi* Pyrcz, 2017:** <http://zoobank.org/urn:lsid:zoobank.org:act:554E49C4-647E-415F-B3DC-D22D5AD8F801>
- Steromapedaliodes albonotata australis* Pyrcz & Boyer, 2017:** <http://zoobank.org/urn:lsid:zoobank.org:act:EA5A3B94-E145-4522-984A-A519ACAF8E1>
- Steromapedaliodes albonotata borealis* Pyrcz & Boyer, 2017:** <http://zoobank.org/urn:lsid:zoobank.org:act:182F7645-219D-4A4D-8E16-06B411A8936F>
- Steromapedaliodes albonotata josefinae* Pyrcz & Boyer, 2017:** <http://zoobank.org/urn:lsid:zoobank.org:act:4B2AE5D9-F96B-4272-9AB7-BC83376378D3>
- Steromapedaliodes albonotata pratense* Pyrcz & Boyer, 2017:** <http://zoobank.org/urn:lsid:zoobank.org:act:D2A7C3AC-E3DC-4073-A421-F3720AD6DB04>
- Steromapedaliodes albonotata thiemeiana* Pyrcz, 2017:** <http://zoobank.org/urn:lsid:zoobank.org:act:AC2C283A-B9CE-44A5-BB80-875E0D949799>

