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**Taxonomic notes on *Euptychia modesta* Butler, 1867,
Neonympha alcinoe C. Felder & R. Felder, 1867
and *Euptychia pamela* Hayward, 1957
(Lepidoptera: Nymphalidae: Satyrinae), with descriptions
of three new genera, five new species and two new subspecies
from Central and South America**

Notas taxonómicas sobre *Euptychia modesta* Butler, 1867,
Neonympha alcinoe C. Felder & R. Felder, 1867 y *Euptychia pamela* Hayward, 1957
(Lepidoptera: Nymphalidae: Satyrinae), con descripciones de tres géneros nuevos,
cinco especies y dos subespecies nuevas de Centroamérica y Suramérica

Mohamed Benmesbah¹, Ángel L. Viloría^{2,3} & Jérôme Murienne⁴

¹28T avenue des Pyrénées 31880 La Salvetat-Saint-Gilles, Francia.

²Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), Apartado Postal 20632, Caracas 1020-A, Venezuela.

³Simon Bolivar Professor, Centre of Latin American Studies, University of Cambridge, Alison Richard Building, 7 West Road, Cambridge CB3 9DT, Reino Unido.

⁴Laboratoire Évolution & Diversité Biologique (UMR5174) - Université de Toulouse Midi-Pyrénées, CNRS, IRD, UPS - 118, route de Narbonne, Bât. 4R1, F-31062 Toulouse Cedex 9, Francia.

Correspondence: M. Benmesbah: modjojojo66@hotmail.com

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ABSTRACT

The identity, status and taxonomic position of seven species of Neotropical satyrine butterflies are discussed and defined: *Euptychia modesta* Butler, 1867, *Euptychia nebulosa* Butler, 1867, *Neonympha alcinoe* C. Felder & R. Felder, 1867, *Euptychia mimas* Godman, 1905, *Euptychia mimula* Hayward, 1954, *Euptychia pamela* Hayward, 1957 and *Cissia gomezi* Singer, DeVries & Ehrlich, 1983. These taxa lately remained in genera such as *Cissia* Doubleday, 1848, *Magneuptychia* Forster, 1964 and *Ypthimoides* Forster, 1964. Based on the particular combination of selected morphological characters and comparative DNA analysis of these and other evidently related species, three new genera (with seven new combinations), five new species and two new subspecies are proposed, diagnosed and described: *Modestia* Viloría & Benmesbah, **gen. nov.**, with four taxa, *M. modesta* (Butler, 1867), **comb. nov.**, *M. gomezi* (Singer, DeVries & Ehrlich, 1983), **comb. nov.**, *M. remypignoux* Benmesbah & Viloría, **sp. nov.** and *M. remypignoux shueyi* Benmesbah & Viloría, **ssp. nov.**; *Malaveria* Viloría & Benmesbah, **gen. nov.**, with nine taxa, *M. alcinoe* (C. Felder & R. Felder, 1867), **comb. nov.**, *M. nebulosa* (Butler, 1867), **comb. nov.**, *M. mimas* (Godman, 1905), **comb. nov.**, *M. ballofi* Benmesbah & Viloría, **sp. nov.**, *M. rodriguezii* Benmesbah & Viloría, **sp. nov.**, *M. rodriguezii risaralda* Benmesbah & Viloría, **ssp. nov.**, *M. bottoi* Benmesbah & Viloría, **sp. nov.**, *M. duponti* Benmesbah & Murienne, **sp. nov.** and *M. mimula* (Hayward, 1954), **comb. nov.**; and *Koutalina* Viloría & Murienne, **gen. nov.**, for a single known species, *K. pamela* (Hayward, 1957), **comb. nov.** Lectotypes of *Euptychia modesta*, *Neonympha alcinoe* and *Neonympha sylvina* C. Felder & R. Felder, 1867, are designated. Variability

in morphology and aspect of the male genitalia is discussed, as well as number of pupils in ocelli and the occasional presence of supernumerary anal ocellus on ventral hindwing.

Key words: Argentina, Belize, Bolivia, *Cissia*, Colombia, Costa Rica, DNA, Ecuador, Euptychiina, French Guiana, *Magneuptychia*, Panama, Paraguay, Peru, Venezuela, *Ypthimoides*.

RESUMEN

Se discuten y definen la identidad, el estatus y la posición taxonómica de siete especies de mariposas satirinas neotropicales: *Euptychia modesta* Butler, 1867, *Euptychia nebulosa* Butler, 1867, *Neonympha alcinoe* C. Felder & R. Felder, 1867, *Euptychia mimas* Godman, 1905, *Euptychia mimula* Hayward, 1954, *Euptychia pamela* Hayward, 1957 y *Cissia gomezi* Singer, DeVries & Ehrlich, 1983. Estos taxones permanecían últimamente en géneros tales como *Cissia* Doubleday, 1848, *Magneuptychia* Forster, 1964 e *Ypthimoides* Forster, 1964. Con base en la combinación particular de caracteres morfológicos selectos y el análisis comparativo de ADN de éstas y otras especies evidentemente relacionadas, se proponen, diagnostican y describen tres nuevos géneros (con siete combinaciones nuevas), cinco nuevas especies y dos nuevas subespecies: *Modestia* Viloría & Benmesbah, **gen. nov.**, con cuatro taxones, *M. modesta* (Butler, 1867), **comb. nov.**, *M. gomezi* (Singer, DeVries & Ehrlich, 1983), **comb. nov.**, *M. remypignoux* Benmesbah & Viloría, **sp. nov.** y *M. remypignoux shueyi*, Benmesbah & Viloría, **ssp. nov.**; *Malaveria* Viloría & Benmesbah, **gen. nov.**, con nueve taxones, *M. alcinoe* (C. Felder & R. Felder, 1867), **comb. nov.**, *M. nebulosa* (Butler, 1867), **comb. nov.**, *M. mimas* (Godman, 1905), **comb. nov.**, *M. ballofi* Benmesbah & Viloría, **sp. nov.**, *M. rodriguezi* Benmesbah & Viloría, **sp. nov.**, *M. rodriguezi risaralda* Benmesbah & Viloría, **ssp. nov.**, *M. bottoi* Benmesbah & Viloría, **sp. nov.**, *M. duponti* Benmesbah & Murienne, **sp. nov.** y *M. mimula* (Hayward, 1954), **comb. nov.**; y *Koutalina* Viloría & Murienne, **gen. nov.**, para una sola especie conocida, *K. pamela* (Hayward, 1957), **comb. nov.** Se designan los lectotipos de *Euptychia modesta*, *Neonympha alcinoe* y *Neonympha sylvina* C. Felder & R. Felder, 1867. Se discute la variabilidad en la morfología y el aspecto del genital masculino, así como el número de pupilas en los ocelos y la presencia ocasional de un ocelo anal supernumerario en la cara ventral del ala posterior.

Palabras clave: ADN, Argentina, Belize, Bolivia, *Cissia*, Colombia, Costa Rica, Ecuador, Euptychiina, Guyana Francesa, *Magneuptychia*, Panamá, Paraguay, Perú, Venezuela, *Ypthimoides*.

INTRODUCTION

Neotropical nymphalid butterflies of the subfamily Satyrinae have been the subject of fast growing interest during the past two decades. A look over published work on their systematics during the last three years accounts for an exceptional example of fruitful developments: more than 30 papers, of which about half are revisionary (Barbosa *et al.* 2018, Benmesbah *et al.* 2018, Henao-Bañol & Meneses [2018], Matos-Maraví *et al.* 2019, Nakahara *et al.* 2018a, 2018b, 2019a, 2019b, 2019c, 2020, Pyrcz & Nuñez 2018, Pyrcz *et al.* 2018a, 2018b, 2018c, 2019a, 2019b, 2020, Willmott *et al.* 2018, 2019, Zacca *et al.* 2018, 2020a, 2020b, 2020c, Andrade *et al.* 2019, Brévignon *et al.* 2019, Costa *et al.* 2019, 2020, Espeland *et al.* 2019, Freitas *et al.* 2018, 2019, Henao-Bañol 2019, Nakahara & Gallardo 2019, Orellana *et al.* 2019, Ríos Málaver 2019, Viloría & Luis Martínez 2019).

Based on morphological characters, Costa *et al.* (2016) re-defined the genus *Magneuptychia* Forster, 1964 and restricted it to three species: *Magneuptychia libye* (Linnaeus, 1767), type of the genus by original designation, *M. libyoides* (Butler, 1866) and *M. lethra* (Möschler, 1883). Later

on, a number of studies in comparative morphology, but also others combining traditional approaches with molecular cladistics at different degrees, have resulted in the progressive resolution of the evident polyphyly of *Magneuptychia sensu lato* (Benmesbah *et al.* 2018, Andrade *et al.* 2019, Nakahara *et al.* 2020). The taxonomy of several of the remaining species within this genus (as presented by Forster 1964 and later Lamas 2004) is still in need of redefinition. Several efforts are being currently addressed to this worthy task.

The aim of this paper is to provide additional information and propose a new taxonomical arrangement to contribute to a more coherent taxonomic reorganization of some butterfly taxa formerly allocated in this complex genus.

The discovery in French Guiana of a new species, previously misidentified as *Magneuptychia modesta* (Butler, 1867) (Brévignon 2008, Brévignon & Benmesbah 2012) prompted us to examine similar looking taxa classified for over 50 years within *Magneuptychia sensu lato*. Our comparative studies, based on morphological character and molecular analyses, revealed the compared set of species to belong to two distinct entities, which are herein described

as new genera: *Modestia* Viloría & Benmesbah, **gen. nov.** and *Malaveria* Viloría & Benmesbah, **gen. nov.** These two genera appear to be close to each other and exhibit some external similarities, which has led to confusion in the past identifications of the species involved.

We discuss the occasional presence of an additional anal ocellus on VHW, the relative importance of the number of pupils on VHW ocelli, the intra- and inter-specific variability in male genitalia and the limits of the DNA analysis. In addition to the new taxa described here, we found that several cryptic species have still to be described. Due to very close habitus and genitalic morphology, scarcity of comparative material as well as accurate collecting data, we were able to describe with sufficient confidence only the taxa for which we had the appropriate information.

We designate the Lectotypes for *Euptychia modesta* Butler, 1867 (Fig. 12a), *Neonympha sylvina* C. Felder & R. Felder, 1867 (Fig. 12b) and *Neonympha alcinoe* C. Felder & R. Felder, 1867 (Fig. 12c) in order to fix their identity and provide the stability necessary for our nomenclatural acts.

Applying similar criteria and using the same methods, we also investigated the identity of *Euptychia pamela* Hayward, 1957. The resulting evidence allowed us to recognize and restore its full specific status, and to justify its separation from any known genera of the Satyrinae. We therefore describe the new genus *Koutalina* Viloría & Muriene, **gen. nov.**, to include this species.

MATERIAL AND METHODS

Specimens from the following public and private collections (acronyms used throughout the text) were examined for comparative morphological study and to compile distribution data:

- AN: Andrew Neild collection, Saint Albans, United Kingdom.
- DT: David Trembath collection, Dorking, United Kingdom.
- DZUP: Entomological Collection Padre Jesus Santiago Moure, Curitiba, Paraná, Brazil.
- ICRM: Indiana Cristóbal Ríos Málaver collection, Manizales, Colombia.
- IVIC: Instituto Venezolano de Investigaciones Científicas, Centro de Ecología, reference collection, Venezuela.
- JMD: John MacDonald collection, Starkville, Mississippi, United States of America.
- JS: John Shuey collection, Indiana, United States of America.
- LCB: Lalita and Christian Brévignon collection, Matoury, French Guiana.
- MB: Mohamed Benmesbah collection, La Salvetat-Saint-Gilles, France.
- MBLUZ: Museo de Biología de La Universidad del Zulia, Maracaibo, Venezuela.
- MIZA: Museo del Instituto de Zoología Agrícola, Universidad Central de Venezuela, Maracay, Venezuela.
- MNHN: Muséum National d'Histoire Naturelle, Paris, France.
- NHMUK: Natural History Museum, London, United Kingdom.
- ZUEC: Museu de Zoologia da Universidade Estadual de Campinas, São Paulo, Brazil.

The following abbreviations are used throughout the text: DFW—dorsal forewing; DHW—dorsal hindwing; FW—Forewing, FWL—Forewing length, HW—Hindwing, TL—Type locality, VFW—ventral forewing; VHW—ventral hindwing. “*” indicates specimens from which genitalia have been dissected for study.

A list of the specimens selected for DNA analysis is given.

For morphological examination, the specimens studied had their abdomen removed and soaked in a test tube containing a heated 10% potassium hydroxide (KOH) or caustic soda (NaOH) solution before dissection of their genitalia. Male and female genitalia preserved in glycerol were contained in microvials and each one attached to their respective specimen with corresponding label data. Genitalia were dissected and examined when material was available but in some cases (lack of material, type specimens) this was not possible. Wing venation preparations were performed by dislocating forewing and hindwing from the body; to remove scales, wings were soaked in a 90° alcohol solution for 30 seconds, rinsed with water and then soaked in a caustic soda solution (NaOH, 10%) for one minute; after being rinsed again and dried, wings were mounted on glass slides; references to specimens were attached to each corresponding slide. In most cases only a single specimen per species was prepared and analyzed. Wing venation preparation was not possible for two species (*M. bottoi* **sp. nov.** and *M. gomezi* **comb. nov.**) because only unique specimen were available. Venation was compared between the genera based on their respective type species: *Magneuptychia*: type species *Papilio libye* Linnaeus, 1767; *Emeryus* Zacca, Casagrande & Mielke in Zacca *et al.* (2020a): type species *Satyrus argulus* Godart, [1824]; *Paryphthimoides* Forster, 1964: type species *Neonympha poltys* Prittwitz, 1865; *Cissia* Doubleday, 1848: type species *Papilio clarissa* Cramer, 1775 = *Papilio penelope* Fabricius, 1775. Imago habitus, genitalia and wing venation photos were taken with a Canon Powershot G7X reflex digital camera. Illustrations were edited using the

software GIMP v.2.8 (GIMP team 2016). Specimens were examined by at least one of the authors directly or via photographs, with the agreement of the photographer and the institution authorities where the specimens are housed.

Due to the complexity found in the morphological variation of the butterfly taxa studied, the type series, when possible, has been restricted to a small and coherent biogeographical area, although other specimens were available. For the same reasons, only data from specimens which were identified with good confidence were included in distribution maps and additional data, undetermined specimens were listed under “sp”. We attempted to review all major publications where relevant taxonomic names were cited since the year of their descriptions, with the caveat that some inevitably have been unintentionally missed. The original descriptions of *Papilio argante* Cramer, 1779, *Satyrus argulus* Godart, [1824], *Satyrus grimon* Godart, [1824], *Neonympha alcinoe* C. Felder & R. Felder, 1867, *Neonympha numeria* C. Felder & R. Felder, 1867, *Neonympha numilia* C. Felder & R. Felder, 1867, *Neonympha sylvina* C. Felder & R. Felder 1867, *Euptychia huebneri* Butler, 1867, *Euptychia modesta* Butler, 1867, *Euptychia nebulosa* Butler, 1867, *Neonympha melobosis* Capronnier, 1874, *Euptychia ambigua* Butler, 1876, *Euptychia benedicta* Butler, 1877, *Euptychia mimas* Godman, 1905, *Euptychia mimula* Hayward, 1954, *Euptychia pamela* Hayward, 1957 and *Cissia gomezi* Singer, DeVries & Ehrlich, 1983, were consulted and translated into French and English. Images of the type specimens of all the above mentioned species were examined except for *E. pamela*, *P. argante*, *N. melobosis* and *S. grimon*, whose types have not been located yet or are supposed to be lost. The taxonomic classification follows Lamas (2004) and the descriptive terminology of the wings and genitalia follows Klots (1970), Neild (1996), Kristensen (2003), Peña & Lamas (2005) and Benmesbah *et al.* (2018) with a few modifications (Figs. 1, 2, 4a).

Because of the very similar habitus exhibited by each species treated in this work, we have chosen to describe here their general aspect, to avoid unnecessarily long descriptions and repetition of common elements. Only some particular relevant characters are given under the account of each species.

Male (Figs. 00, 000): *Head*: brown; front and vertex white mixed with brown; eyes hairy and dark brown; antennae light brown with white scales at base on each flagellomere; antennal club dark with tip light brown; labial palpi with elongated white scales medially, and mixed dark brown and white scales laterally. In one species *Koutalina pamela* (Butler) **comb. nov.** front and vertex brown; eyes glabrous, dark brown; antennal club dark; labial palpi with

elongated white scales medially, and short white scales laterally on either sides of a central row of longer dark brown scales. *Thorax*: dark covered with blond setae with greenish-blue reflection; tegulae light brown mixed with reddish and greenish iridescent scales; prothoracic legs whitish; meso- and metathoracic legs light brown, coxae and femora setose. *Abdomen*: dark covered by blond to brown setae with a greenish-ginger reflection. FWL: 0-00 mm, average 0.00 mm (x specimens); FW subtriangular, costal margin convex, apex rounded, outer margin straight, inner margin slightly concave, cubital and radial veins swollen at their base. DFW: ground color brown or greyish brown almost uniform; VFW: ground color brown or greyish brown; submedian and median lines more or less parallel, straight, perpendicular to inner margin running from radius to 2A, median line passing outside the cell and submedian through the middle of the cell, crossing Cu2 origin; submarginal band dark brown, little marked, barely visible, straight from costa to 2A, parallel to precedent lines; one small black ocellus circled by a yellowish /brownish ring in M1-M2 with one or two small white pupils, two others reduced and much less defined, if not vestigial or invisible, in M2-M3 and M3-Cu2; submarginal line thicker, scalloped, running from radius to inner margin, pointing distally in R5 to 2A; marginal line straight, thin, parallel and close to outer margin. DHW: ground color same as DFW; outer margin slightly scalloped; marginal and submarginal lines observable through translucent surface, thin marginal area outside marginal line lighter at tornus; one species *K. pamela* **comb. nov.**, with black ocelli surrounded by yellow ring with 2 tiny white pupils, more or less well defined, in Cu1-Cu2 and Cu2-2A. VHW: ground color same as VFW; one small basal line very close to base, almost non visible; submedian and median lines perpendicular to costa, median line passing through the distal extremity of the cell, and submedian line through the middle of the cell, both lines running from costa to inner margin; a thin dark line almost non visible, very close and parallel to inner margin, joins submedian, median, submarginal and marginal lines; submarginal line thicker, from costa to inner margin, scalloped, composed by more or less straight or curved adjacent segments, basally convex from M1-M2 to Cu2-2A; marginal dark line thin parallel to outer margin from costa to tornus, one species *K. pamela* **comb. nov.**, with marginal line clearly wider between anal part of Cu2-2A and tornus; submarginal area with five ocelli, one in each space between Rs and Cu2, of variable size, usually black circled with yellowish/brownish ring and centered by one or two white pupils, ocellus in M1-M2 well defined with one or two pupils, ocellus in Cu1-Cu2 well defined with two white pupils, ocelli in M2-M3 and M3-Cu1

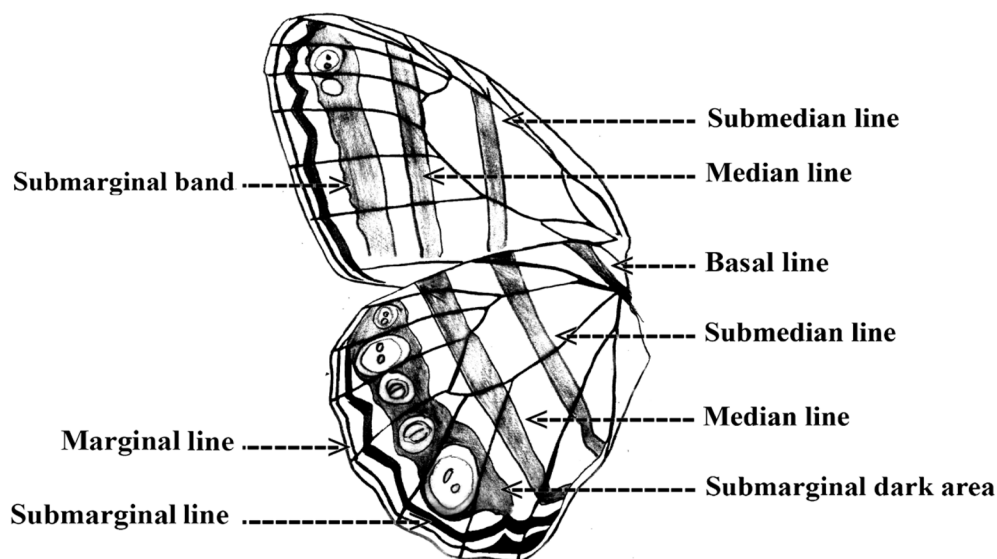


Figure 1. Terminology of wing pattern elements.

more or less well defined, ocellus in M2-M3 usually ovoid slightly displaced basally compared to the others, ocellus in Rs-M1 usually much smaller than precedents, usually well defined, centered by one or two white pupils, all these ocelli surrounded by a thin submarginal dark area; one species *K. pamela* **comb. nov.**, with a sixth ocellus with two pupils in Cu2-2A.

Female (Figs. 00, 000) – FWL: 0-00 mm, average 0.00 mm (x specimens). Usually similar to male, but differs from that by upper side darker or lighter, and global shape of FW more rounded and less elongated with outer margin shorter, giving a more crenulated aspect to HW in some species.

Male genitalia were positioned in a standardized way to best allow comparison. The angle of view in which they are studied and illustrated has an important influence over their perceived aspect (see discussion). For the entire male genitalic structure, it is shown the upper and lateral view (one valva removed); external, inner and upper view for valvae; upper and lateral view for aedeagi. For each species, when possible, several specimens were dissected to evaluate intraspecific morphological stability and variability; the number of specimens dissected are indicated in the examined material section and marked by an asterisk “*”. We focused mainly on the shape of valvae and aedeagi, which seem, from our experience, to reveal the most informative and discriminating characters. In case of infraspecific variation, we choose to illustrate a specimen that was representative of the majority of the specimens studied. Comments on variability of the male genitalia are also discussed (see discussion).

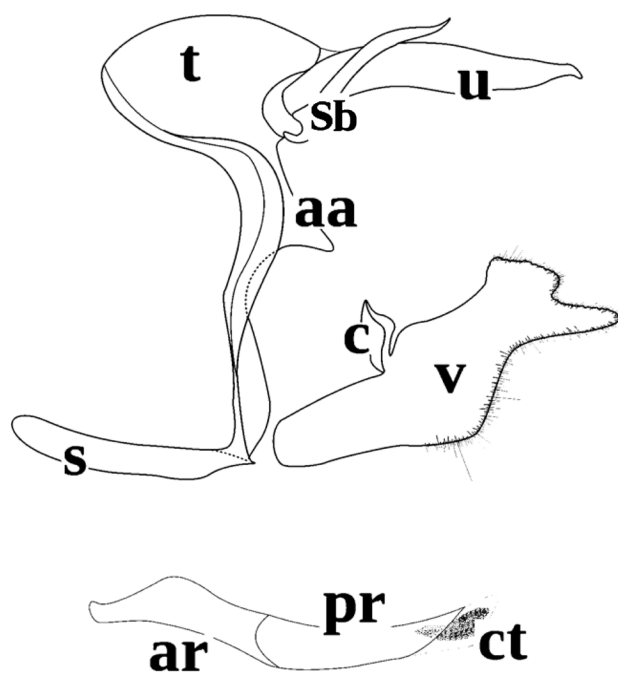


Figure 2. Terminology of male genitalia elements: lateral view and aedeagus: aa: appendix angularis; ar: anterior region of aedeagus; c: costa; ct: cornuti; Sb: subuncus; pr: posterior region of aedeagus; s: saccus; t: tegumen; u: uncus; v: valva.

Female genitalia are also illustrated, but due to few available material at our disposition, not all species could be studied and few specimens were dissected.

DNA extraction was performed using a Chelex protocol (Casquet *et al.* 2012) as in Benmesbah *et al.* (2019). We chose to amplify a short fragment of the 16S mitochondrial rRNA using the Ins16S_1 primer pair (Clarke *et al.*

2014): Ins16S_1-F: TRRGACGAGAAGACCCTATA; Ins16S_1-R: TCTTAATCCAACATCGAGGTC. Despite being originally developed for metabarcoding studies, this fragment has been shown to provide good resolution at the species level in several insect groups (Kocher *et al.* 2017a, 2017b, Talaga *et al.* 2017). Because of its small size (*ca.* 220 bp), it allows to provide good amplification results even from degraded material. Amplification and sequencing was performed on 101 specimens following Kocher *et al.* 2017a, 2017b, of which 84 specimens were represented in Table 1 to avoid unnecessary and non-significant redundancy of the same sequence. Sequences were aligned using Muscle (Edgar 2004) and a Maximum Likelihood analysis was performed in Raxml-ng with a JC substitution model (Jukes & Cantor 1969) as inferred by Modeltest-ng (Darriba *et al.* 2020) and a midpoint rooting.

RESULTS

Modestia Viloria & Benmesbah, **gen. nov.**

(Figs. 3a-3d)

<http://zoobank.org/urn:lsid:zoobank.org:act:3D9F6817-3BF0-48F4-9E65-1695D697AB44>

Type species: *Euptychia modesta* Butler, 1867a; herein designated.

Diagnosis (Figs. 3, 4, 5)

Superficially similar to members of the genera *Emeryus*, *Malaveria* Viloria & Benmesbah, **gen. nov.**, *Koutalina* Viloria & Murienne, **gen. nov.** and *Paryphthimoides* (*sensu* Zacca *et al.* 2020c). It differs from the latter in its larger size and in the number of VHW ocelli: five in *Modestia* Viloria & Benmesbah, **gen. nov.**, six in *Paryphthimoides* as in *Koutalina* **gen. nov.** The ocellar pattern of *Modestia* **gen. nov.**, is characterized by a subapical VFW ocellus in M1-M2 invariably monopupillate (two pupils in *Malaveria* **gen. nov.** and *Koutalina* **gen. nov.**, two vestigial in *Emeryus*). Ventral HW with five ocelli, the ones in Rs-M1 and M1-M2 with single white pupil (five ocelli in *Emeryus* and *Malaveria* **gen. nov.**, six in *Koutalina* **gen. nov.**, but in all these cases with double pupils, see discussion). The upper surface of both wings is brown, uniform, devoid of ocelli (similar in *Magneuptychia* and *Malaveria* **gen. nov.**, but different in *Ypthimoides* Forster, 1964, *Paryphthimoides*, *Emeryus* and *Koutalina* **gen. nov.**, in which there is always at least one or two anal HW ocelli). Forewing venation is most similar to *Emeryus*, especially regarding the origin of R2, proximal and close to the separation of R and M1, but *Modestia* **gen. nov.**, differs by m1-m2 less curved and m2-m3 more curved than in *Emeryus*. *Modestia* **gen.**

nov., differs from *Magneuptychia*, *Paryphthimoides*, *Cissia* and *Koutalina* **gen. nov.**, also by the more curved m2-m3 (straight in all these genera). Hindwing venation, although superficially similar with all the following genera, differs in the significantly higher ratio between discal length/M3 length in *Modestia* **gen. nov.**, when compared to *Magneuptychia*, *Emeryus*, *Paryphthimoides*, *Cissia*, *Malaveria* **gen. nov.** and *Koutalina* **gen. nov.** (Figs. 3, 4, 5). Additional differences with *Malaveria* **gen. nov.**, are discussed under the latter. Male genitalia in the species of *Modestia* **gen. nov.**, bear simple, not ornamented, moderately elongated valvae, with an internal bulge at its distal part, less robust at distal half than those of *Paryphthimoides*, not digitiform like in *Malaveria* **gen. nov.**, or not distally broadened like in *Emeryus* or *Koutalina* **gen. nov.**

DNA analysis shows a difference ratio between the respective type species of the following genera in comparison to *Modestia* **gen. nov.**, of: 5.9% for *Magneuptychia*, 14.4% for *Cissia* (*sensu stricto*), 10% for *Malaveria* **gen. nov.**, and 10.9% for *Koutalina* **gen. nov.**, which are coherent with generic distances (Tables 1 and 2).

Description (Figs. 3a-3d)

Butterflies of medium size (FWL: 19-23mm), without sexual dimorphism. Wings dorsally brown, devoid of ocelli. Ventrally ground color brown with two darker stripes or bands, crossing both wings more or less in parallel, one through the middle of the discal cell (submedian), the other one median; two dark brown lines, one indented, submarginal, the other marginal, smooth, parallel to outer margin and not wider at tornus. Ventral ocelli, when not vestigial, all black, with white pupils, iris yellow, circled with brown. FW with a subapical M1-M2 ocellus with one pupil, depending on the species there may appear other similar ocelli in M2-M3 and M3-Cu1. Females tend to develop more ventral FW ocelli. HW with five ocelli, Rs-M1 and M1-M2 with single pupil, M2-M3, M3-Cu1 and Cu1-Cu2 with double pupils (but sometimes pupils in M2-M3 and M3-Cu1 either fused, vestigial or not developed). FW venation: Sc markedly swollen at basal third, ending at three fifths of costa, R1 emerging at fourth fifth of discal cell, R2 and R3-R5 emerging close to each other, but clearly separated, R3 emerging half the length of distance between the root of R3-R5 and the bifurcation of R4 and R5; rs-m1 very short and straight, a sixth of the length of m1-m2 (which is convex towards base), m2-m3 slightly curved, twice the length of m1-m2, about same length of m3-cu1; cu1-cu2 straight, twice as long as m3-cu1, Cu2-A2 notably swollen at basal half, A2 independent; HW venation: Humeral present; Sc + R1 ending at first third of costa, Rs emerging nearly at half

Table 1. Phylogenetic tree representing genetic distances and relationships among butterfly species of the satyrine genera *Modestia* gen. nov., *Malaveria* gen. nov., and *Koutalina* gen. nov. together with representatives of four additional genera of the Neotropical Euptychiina.

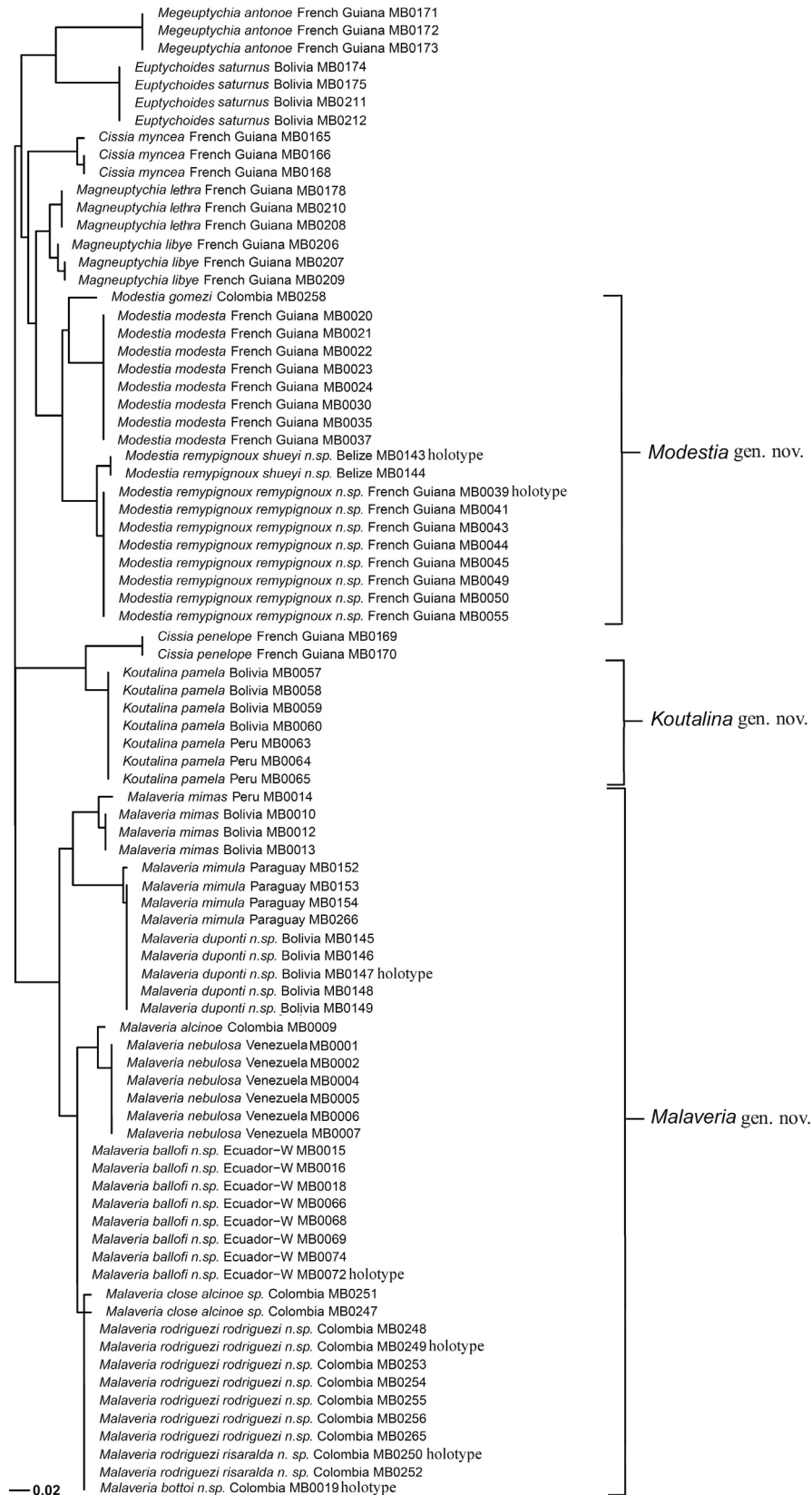


Table 2. Representation of the percentage of genetic similarity between the different satyrine taxa sampled for this study. These results were obtained from the analysis of a short fragment of 218-220 base pairs (16S marker) of mitochondrial rDNA.

	<i>M. antonoe</i>	<i>E. saturnus</i>	<i>K. pamela</i>	<i>C. penelope</i>	<i>M. duponti</i>	<i>M. mimula</i>	<i>M. minima</i>	<i>M. bottoi</i>	<i>M. r. rodriquez</i>	<i>M. r. risaralda</i>	<i>M. ballofi</i>	<i>M. nebulosa</i>	<i>M. alcinoe</i>	<i>C. myncea</i>	<i>M. libye</i>	<i>M. modesta</i>	<i>M. gomezi</i>	<i>M. r. remyi</i>	<i>M. r. shueyi</i>
<i>M. antonoe</i>	88.7	83.9	83.0	86.1	86.1	86.9	87.8	87.8	87.8	87.8	88.2	88.2	88.2	85.3	87.4	86.5	86.0	85.1	86.0
<i>E. saturnus</i>	88.7	87.3	86.9	86.8	86.8	88.6	89.5	89.5	89.5	89.5	87.7	87.7	87.7	89.1	90.9	90.4	90.4	88.6	88.6
<i>K. pamela</i>	87.3	87.3	92.8	88.3	88.3	89.1	88.7	88.7	88.7	88.7	89.1	89.1	88.6	87.4	91.0	89.1	88.7	88.7	88.7
<i>C. penelope</i>	83.0	86.9	92.8	84.8	84.8	84.7	85.6	85.6	85.6	85.6	86.0	86.4	86.4	85.7	86.5	85.6	85.1	84.2	84.2
<i>M. duponti</i>	86.1	86.8	88.3	84.8	100.0	94.1	94.1	94.1	94.1	94.1	94.5	93.2	92.7	87.8	91.0	90.9	91.8	90.9	91.8
<i>M. mimula</i>	86.1	86.8	88.3	84.8	100.0	94.1	94.1	94.1	94.1	94.1	94.5	93.2	92.7	87.8	91.0	90.9	91.8	90.9	91.8
<i>M. minas</i>	86.9	88.6	89.1	84.7	94.1	95.4	95.4	95.4	95.4	95.4	95.9	94.1	93.6	90.0	91.4	90.0	90.9	90.4	91.3
<i>M. bottoi</i>	87.8	89.5	88.7	85.6	94.1	94.1	100.0	100.0	100.0	99.5	96.8	97.3	97.3	91.0	92.3	90.9	91.8	90.4	91.3
<i>M. r. rodriquez</i>	87.8	89.5	88.7	85.6	94.1	95.4	100.0	100.0	100.0	99.5	96.8	97.3	97.3	91.0	92.3	90.9	91.8	90.4	91.3
<i>M. r. risaralda</i>	87.8	89.5	88.7	85.6	94.1	95.4	100.0	100.0	100.0	99.5	96.8	97.3	97.3	91.0	92.3	90.9	91.8	90.4	91.3
<i>M. ballofi</i>	87.8	90.0	89.1	86.0	94.5	95.9	99.5	99.5	99.5	99.5	97.3	97.3	97.7	91.4	92.7	91.3	92.2	90.9	91.8
<i>M. nebulosa</i>	88.2	87.7	89.1	86.4	93.2	93.2	94.1	96.8	96.8	96.8	97.3	97.3	98.6	90.5	90.9	90.0	90.4	89.0	90.0
<i>M. alcinoe</i>	88.2	87.7	89.1	86.4	93.2	93.2	94.1	96.8	96.8	96.8	97.3	97.3	98.6	90.0	90.5	89.5	90.0	88.6	89.5
<i>C. myncea</i>	85.3	89.1	87.4	85.7	87.8	87.8	90.0	91.0	91.0	91.0	91.4	90.5	90.0	93.7	93.7	91.4	91.0	91.0	90.5
<i>M. libye</i>	87.4	90.9	91.0	86.5	91.0	91.4	92.3	92.3	92.3	92.7	90.9	90.5	90.5	93.7	94.1	94.1	94.1	94.5	93.2
<i>M. modesta</i>	86.5	90.4	89.1	85.6	90.9	90.0	90.9	90.9	90.9	91.3	90.0	89.5	89.5	91.4	94.1	95.9	94.5	94.5	94.1
<i>M. gomezi</i>	86.0	90.4	88.7	85.1	91.8	90.9	91.8	91.8	91.8	92.2	90.4	90.0	90.0	91.0	94.1	95.9	95.4	95.4	95.9
<i>M. r. remyi</i>	85.1	88.6	88.7	84.2	90.9	90.9	90.4	90.4	90.4	90.9	89.0	88.6	88.6	91.0	94.5	94.5	95.4	95.4	98.6
<i>M. r. shueyi</i>	86.0	88.6	88.7	84.2	91.8	91.3	91.3	91.3	91.3	91.8	90.0	89.5	89.5	90.5	93.2	94.1	95.9	95.9	98.6

length of discal cell and ending at apex; m1-m2 slightly convex towards base, m2-m3 three times the length of rs-m1, and twice the length of m1-m2. Male genitalia characterized by a short globular tegumen, long lanceolate uncus, twice the length of the tegumen, subunci thin, two thirds the length of uncus, vinculum dorsally strong, ventrally thin, attached to a stylized, long saccus (as long as the brachia of the subunci), valvae elongated, gradually thinner towards distal extremity, with a non-conspicuous ampullar protuberance, with tiny ornamentations, as long as tegumen plus uncus and presenting an internal bulge at its distal extremity; aedeagus thin and at least as long as valva (Figs. 13j-k, 14i-j, 15j-k, 16h-i), straight or slightly curved upwards.

Derivatio nominis

Modestia is a feminine noun that means modesty, which is the quality of being modest or humble. The name is also intended to produce a euphonic combination with the name of the type species of the genus, *Euptychia modesta* Butler, 1867a.

Modestia **gen. nov.**, is basically a genus embracing species of lowland Neotropical forests.

Species belonging to Modestia Viloría & Benmesbah, gen. nov.:

Modestia gomezi (Singer, DeVries & Ehrlich, 1983), **comb. nov.**

Cissia gomezi Singer, DeVries & Ehrlich, 1983: 114, figs. 2C, 3C [TL: Costa Rica]; DeVries, 1987: 274, pl. 48 figs. 32, 33, 35c; Matamoros & Seal, 1994: 9, 17, 44, 70; Maes, 1995: 26, 27; Pelz, 1997: 41; Núñez Miño 2004: 29, Fratello, 2007: 1-5; Wiemers & Fiedler, 2008: 290; Albert *et al.*, 2010: 68; Costa *et al.*, 2016: 199; See *et al.*, 2018: 52; Zacca *et al.*, 2018: 356, 357.

Euptychia gomezi (Singer, DeVries & Ehrlich, 1983); D'Abbrera, 1988: 789.

Magneuptychia gomezi (Singer, DeVries & Ehrlich, 1983); Lamas, 2004: 220; Wiemers & Fiedler, 2008: 290; Marín & Uribe, 2009: 28, 29; Albert *et al.*, 2010: 68; Garwood & Lehman, 2011: 273 [row 3, figs.]; See *et al.*, 2018: 52.

"*M. gomezi* (Singer, DeVries & Ehrlich, 1983); Costa *et al.*, 2016: 204.

Modestia modesta (Butler, 1867a), **comb. nov.**

Euptychia modesta Butler, 1867a: 473 [TL: Brazil (Pará)]; Butler, 1867b: pl. 12, fig. 12; Butler, 1868: 21; Kirby, 1871: 49; Weymer, 1911: 206; Hall, 1939: 33; D'Abbrera, 1988: 776 [row 2, figs.].

[*Euptychia gracilis* Weymer 1911: D'Abrera, 1988: 780 [row 6, fig. male] (misidentification)].

Euptychia ambigua Butler var. *modesta* Butler; Gaele, 1931: 438.

Yphtimoides modesta (Butler, 1867a); Forster, 1964: 102, fig. 99 (male genitalia).

[*Cissia alcinoe* (C. Felder & R. Felder, 1867); DeVries, 1987: 276, pl. 41 fig. 1; Singer & Ehrlich, 1993: 51 (misidentifications)]

Magneuptychia modesta (Butler, 1867a); Lamas, 2004: 220; Cock, 2014: 11; Nakahara *et al.*, 2015: 143; Sambhu & Nankishore, 2018: 119.

[*Magneuptychia alcinoe* (C. Felder & R. Felder, 1867); Chacón & Montero 2007: pl. 174; Garwood & Lehman, 2011: 274 [row 2, fig.] (misidentifications)]

[*Megeuptychia antonoe* (Cramer, 1775); Garwood & Lehman, 2011: 275 [row 4, fig.] (misidentification)]

Modestia remypignoux remypignoux Benmesbah & Viloría, **sp. nov.** [TL: French Guiana]

[*Euptychia modesta* Butler, 1867a var.]; Butler, 1867a: 473; 1868: 21.

[*Euptychia nebulosa* Butler, 1867a; Godman & Salvin, 1880: 86, pl. 8, fig. 10 (misidentification)]

Modestia remypignoux shueyi Benmesbah & Viloría **ssp. nov.** [TL: Belize]

Malaveria* Viloría & Benmesbah, **gen. nov.*

(Figs. 3e-3h)

<http://zoobank.org/urn:lsid:zoobank.org:act:40D0F5BB-5728-42EB-B7BF-2704D0BEC845>

Type species: *Euptychia nebulosa* Butler, 1867a; herein designated.

Diagnosis (Figs. 3, 4, 5)

Malaveria gen. nov., is most similar in size and appearance to *Modestia gen. nov.*, which has been diagnosed above; their differences can be summarized as follows: 1. FW venation in *Malaveria gen. nov.* is characterized by a tiny basally-pointing recurrent vein on discocellular m1-m2, present in all the species treated here as belonging to *Malaveria gen. nov.* (absent in *Modestia gen. nov.*); 2. VHW ocelli in M1-M2 and Rs-M1 are bipupillate in all known species of *Malaveria gen. nov.*, instead of monopupillate in *Modestia gen. nov.* (see discussion); 3. dorsal edge of the valvae in male genitalia presenting a marked bulge in *Malaveria gen. nov.* (straight in *Modestia gen. nov.*); 4. distal extremity of the valvae digitiform and hooked in *Malaveria gen. nov.*, instead of relatively wider and gradually pointed in *Modestia gen. nov.*; 5. presence

of a small and well differentiated internal horn emerging more basally in the valvae of the species of *Malaveria gen. nov.*, instead of a bulge at the distal part of the valvae (*Modestia gen. nov.*); 6. aedeagus in *Malaveria gen. nov.*, equally long (as much as valvae) but relatively thicker and more straight than in *Modestia*,

DNA analysis shows different percentages of divergence between the respective type species of the following genera in comparison to *Malaveria gen. nov.*: 9.1% for *Magneuptychia*, 13.6% for *Cissia (sensu stricto)*, 10% for *Modestia gen. nov.*, and 10.9% for *Koutalina gen. nov.*, which are coherent with generic distances (Tables 1 and 2).

Description

Butterflies of medium size (FWL: 19-26mm). Wings dorsally brown except for two darker marginal lines, more visible on HW. Ventrally ground color brown with two darker reddish lines, crossing both wings more or less in parallel, one submedian, the other one discal, they can be straight, moderately or strongly undulated, depending on the species; two dark brown lines, one thicker, indented, submarginal, meeting the discal one near the anal margin of HW, the other thinner, marginal, smooth, parallel to outer margin. Ventral ocelli, when not vestigial, all black, with white pupils, iris yellow, circled with brown. FW with a subapical M1-M2 ocellus with two tiny pupils. HW with five ocelli or ocellar vestigia, in Rs to Cu2, all when apparent, with double pupils (but sometimes pupils in Rs fused in one). FW venation: Sc broadly swollen at basal third, thinning abruptly, ending at half costa; R1 emerging at distal fifth of discal cell, R2-R5 emerging at distal tip of discal cell, R2 and R3-R5 branching about 2 millimeters further towards the apex, R3 and R4 separating equidistantly, at first and second third of their root, respectively, R5 ending at apex; r2-5-m1 very short and straight, a sixth of the length of m1-m2, which is convex towards base with a tiny recurrent vein at angle, inside discal cell; m2-m3 slightly concave towards base, twice the length of m1-m2, about same length of m3-cu1; cu1-cu2 one and a half times as long as m3-cu1; Cu2-A2 moderately inflated at basal two fifths; A2 independent. HW venation: Humeral present, but short and simple; Sc thin, ending at basal third of costa; Rs and M1 branching separately but close to each other at half length of discal cell; m1-m2 slightly curved towards the cell; M2 emerging equidistantly from roots of M1 and M3; cu1-cu2 2 times the length of m3-cu1; A2 and A3 independent. Male genitalia: tegumen globular, long, lanceolate uncus, almost twice the length of the tegumen, subunci thin, as long as uncus, usually pointing

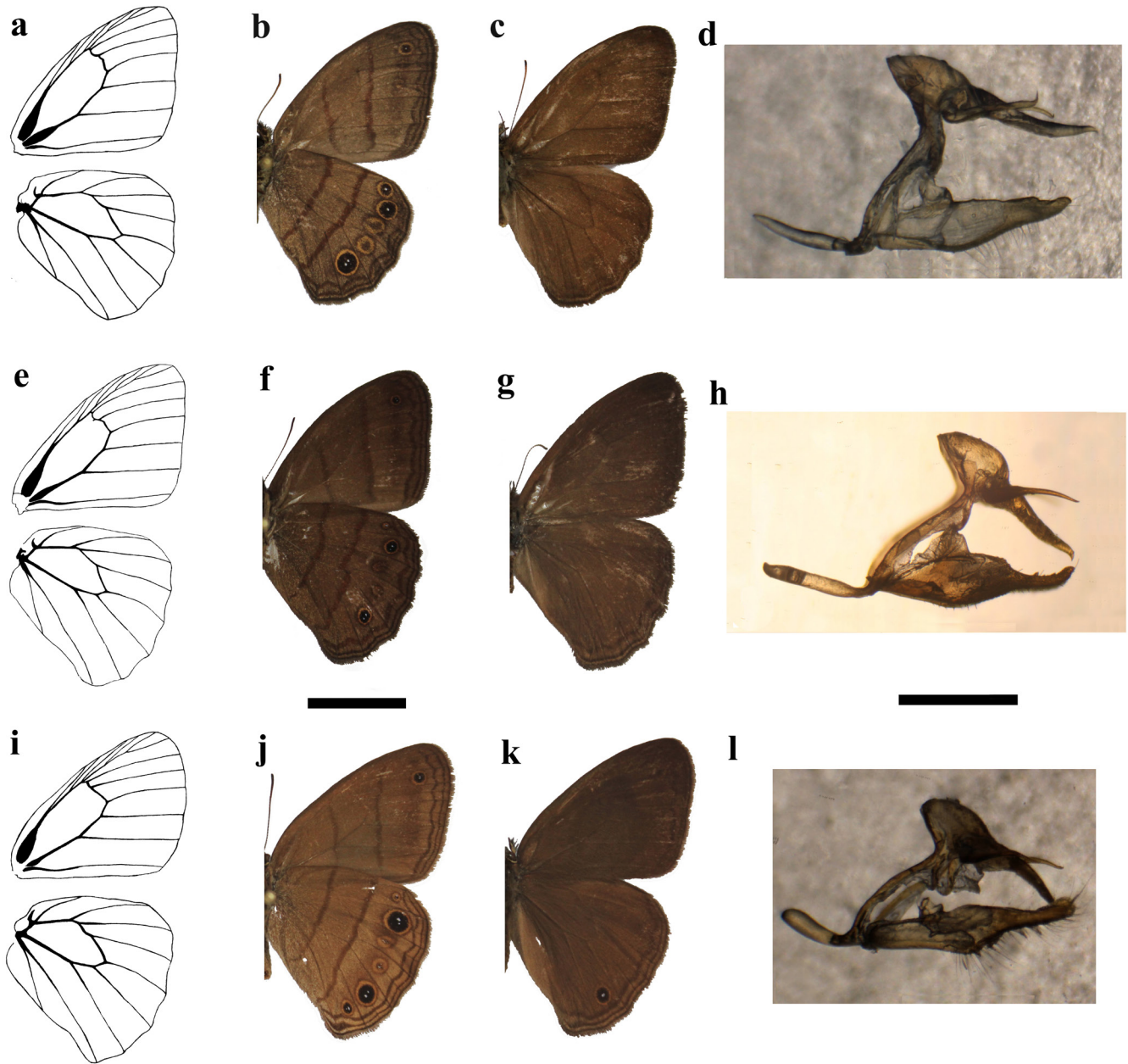


Figure 3. New genera, male wing venation, habitus and genitalia. a. *Modestia* gen. nov., venation; b. Habitus ventral; c. Habitus dorsal; d. Male genitalia lateral view; e. *Malaveria* gen. nov., venation; f. Habitus ventral; g. Habitus dorsal; h. Male genitalia lateral view; i. *Koutalina* gen. nov., venation; j. Habitus ventral; k. Habitus dorsal; l. Male genitalia lateral view. (Scale habitus: 1 cm; scale genitalia: 1 mm).

upwards; vinculum strong and relatively thick, attached to a relatively long, tubular saccus (slightly shorter than uncus), valvae robust at basal half, laterally quadrangular, with a very broad base (half the lateral length of vinculum), abruptly thinner towards distal half, which becomes a digitiform extremity, at whose base emerges internally a distinctive horn-like protuberance; aedeagus regular and at least as long as valva, broader at base, straight or just slightly sinuous.

Derivatio nominis

Malaveria is a feminine Latinization of the Spanish family name Málaver. It is dedicated to our friend and colleague Indiana Cristóbal Ríos Málaver, a talented young scientist in Neotropical lepidopterology and an expert in the butterflies of Colombia, his native country. Cristo – as he is known among lepidopterists – is certainly the person who best knows the biology of the type species of this genus, *Euptychia nebulosa* Butler, 1867a, an endemic of the

Cordillera de la Costa in Venezuela, where Cristo developed butterfly studies for his MSc thesis.

All species of *Malaveria* **gen. nov.**, are basically denizens of middle elevation montane forests in Tropical America.

Species belonging to Malaveria Viloría & Benmesbah, gen. nov.:

Malaveria alcinoe (C. Felder & R. Felder, 1867), **comb. nov.**

Neonympha alcinoë C. Felder & R. Felder, 1867: 477 [TL: Colombia (Bogotá), herein restricted].

Euptychia alcinoë (C. Felder & R. Felder, 1867); Butler, 1868: 25; Kirby, 1871: 51; Weymer, 1911: 209, pl. 48 row c.

Euptychia benedicta Butler, 1877: 124, pl. 12, fig. 14 [TL: Ecuador]; Kirby, 1877: 843; Weymer, 1911: 206-207; D'Abbrera, 1988: 778 [row 1, figs.]; Lamas, 2004: 220 (as a synonym of *Magneuptychia alcinoe* (C. Felder & R. Felder, 1867))

Euptychia ambigua (Butler, 1867a) var. *benedicta* Butler, 1877; Gaede, 1931: 437-438.

Euptychia alcinoe (C. Felder & R. Felder, 1867); Gaede, 1931: 437; D'Abbrera, 1988: 777 [row 8, figs.].

Ypthimoides benedicta (Butler, 1877); Forster, 1964: 101 fig. 94 (male genitalia, probably erroneous), 104.

Cissia alcinoe (C. Felder & R. Felder, 1867); DeVries, 1987: 276, pl. 41 fig. 1 (probably misidentification of *Modestia remypignoux shueyi* **ssp. nov.**); Singer & Ehrlich, 1993: 251 (misidentification of *Modestia modesta* (Butler, 1867a), **comb. nov.**, from Costa Rica and Trinidad, respectively)

Magneuptychia alcinoe (C. Felder & R. Felder, 1867); Lamas, 2004: 220; Chacón & Montero 2007: pl. 174; Garwood & Lehman, 2011: 274 [row 2, fig.] (last two misidentifications of *Modestia modesta* (Butler, 1867a), **comb. nov.**, from Costa Rica); Beccaloni *et al.*, 2008: 335; Nakahara *et al.*, 2015: 136, 137-139 fig. 1d (male syntype), 142, 144, 145.

Malaveria ballofi Benmesbah & Viloría, **sp. nov.** [TL: Ecuador (Pichincha)]

Malaveria bottoi Benmesbah & Viloría, **sp. nov.** [TL: Colombia (Cundinamarca)]

Malaveria duponti Benmesbah & Murienne, **sp. nov.** [TL: Bolivia (La Paz)]

[*Ypthimoides nebulosa* (Butler, 1867a); Forster, 1964: 104 fig. 105 (male genitalia), 106 (misidentification)]

Malaveria mimas (Godman, 1905), **comb. nov.**

Euptychia mimas Godman, 1905: 187, pl. 10, fig. 6 (male) [TL: Bolivia (Coroico)]; Weymer, 1911: 2010, t. 48 d; Gaede 1931: 454; D'Abbrera, 1988: 777 [row 7, figs.]

Ypthimoides mimas (Godman, 1905); Forster, 1964: 101 fig. 96 (male genitalia), 102, 105.

Magneuptychia mimas (Godman, 1905); Lamas, 2004: 220; Nakahara *et al.*, 2015: 136, 137, 139 fig. 1e (male syntype), 142.

Malaveria mimula (Hayward, 1954), **comb. nov.**

Euptychia mimula Hayward, 1954: 16-17, fig. 1 (male genitalia) [TL: Bolivia (Chulumani)]; D'Abbrera, 1988: 789.

Ypthimoides mimula (Hayward); Forster, 1964: 102, 105; Lamas, 2004: 223.

Malaveria nebulosa (Butler, 1867a), **comb. nov.**

Euptychia nebulosa Butler, 1867a: 474 [TL: Venezuela (Cordillera de la Costa)]; 1867b: pl. 12, fig. 2; 1868: 26; Kirby, 1871: 50; Godman & Salvin, 1880: 86, pl. 8, fig. 10 (misidentification of *Modestia remypignoux* **sp. nov.**, from Panama); Hall, 1939: 236 (misidentification of *Modestia remypignoux* **sp. nov.**, from Guyana); D'Abbrera, 1988: 776 [row 3, figs. male] (misidentification of *Malaveria mimula* **comb. nov.**).

Ypthimoides nebulosa (Butler, 1867a); Forster, 1964: 104 fig. 105 (male genitalia), 106 (misidentification of *Malaveria duponti* **sp. nov.**, from Bolivia); Brown & Mielke, 1967: 91 (misidentification of 'Parypthimoides' *grimon* (Godart, [1824]) from Brazil).

Magneuptychia nebulosa (Butler, 1867a); Lamas, 2004: 220; Nakahara *et al.* 2015: 135-147 figs. 2a (head), 2b, c (male genitalia), 2d, e, f (female genitalia), 3 (distribution map), 4 (habitus).

Malaveria rodriguezii rodriguezii Benmesbah & Viloría, **sp. nov.** [TL: Colombia (Antioquia)]

Malaveria rodriguezii risaralda Benmesbah & Viloría, **ssp. nov.** [TL: Colombia (Risaralda)]

Koutalina Viloría & Murienne, **gen. nov.**
(Figs. 3i-3l)

<http://zoobank.org/urn:lsid:zoobank.org:act:610B37EC-1C54-4073-81DB-80DF1CAC95EF>

Type species: *Euptychia pamela* Hayward, 1957; herein designated.

Diagnosis (Figs. 3, 4, 5, 29)

Koutalina **gen. nov.**, differs from all other genera of the Euptychiina by the presence in males of a large dark patch

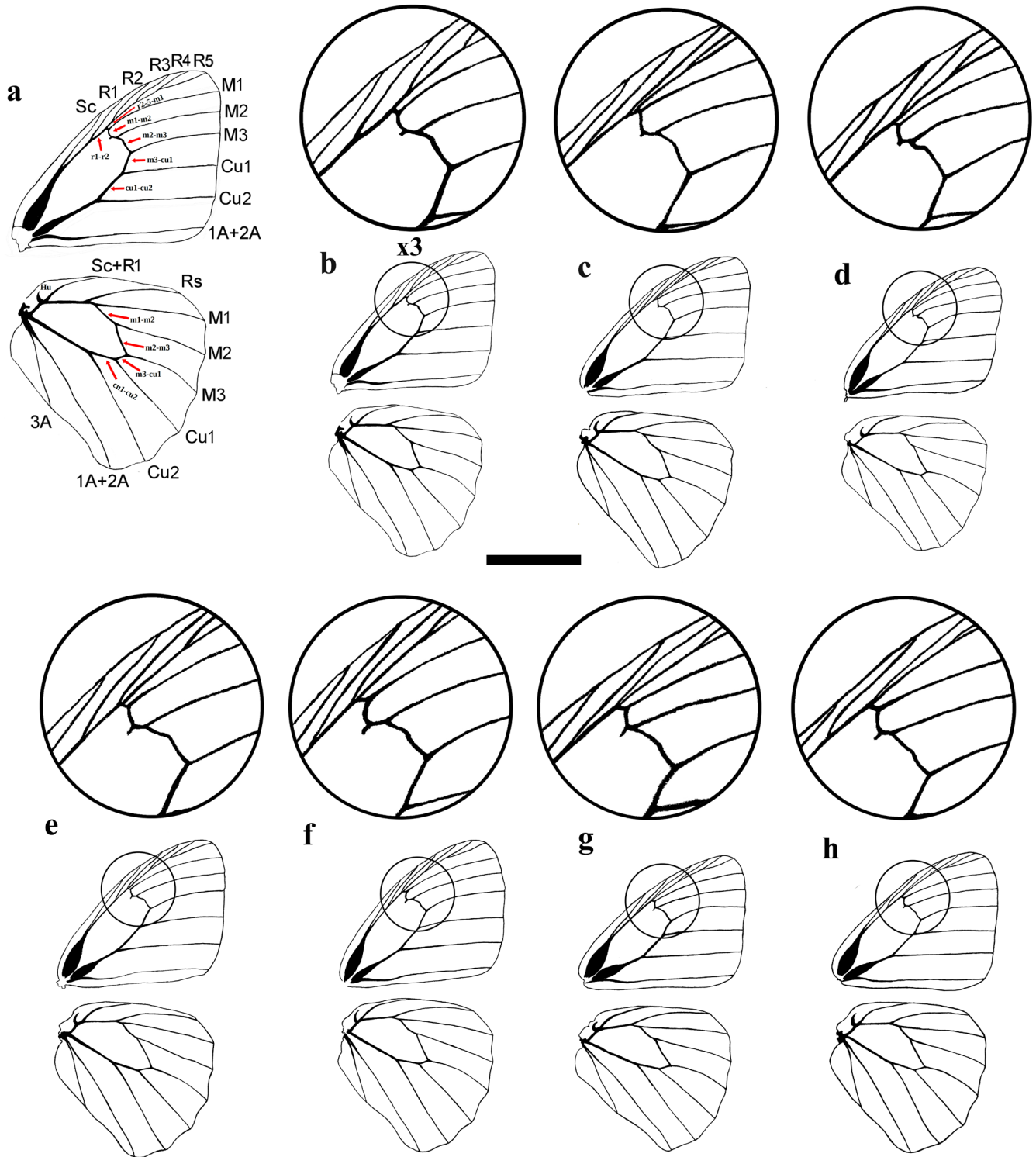


Figure 4. Species of *Malaveria* gen. nov., male wing venation with focus on forewing cell (x3). a. Venation terminology; b. *M. nebulosa* comb. nov.; c. *M. mimas* comb. nov.; d. *M. alcinoe* comb. nov.; e. *M. ballofi* sp. nov.; f. *M. rodriguezii* sp. nov.; g. *M. mimula*; h. *M. duponti* sp. nov. (Scale: 1 cm).

of modified scales on DFW probably representing androconia (see under *Koutalina pamela* **comb. nov.**). Furthermore *Koutalina* **gen. nov.**, differs from *Modestia* **gen. nov.**, and *Malaveria* **gen. nov.**, by the following major features: 1. *Koutalina* **gen. nov.**, presents a sixth supplementary ocellus on VHW, near the tornus, which is absent in *Modestia* **gen. nov.** and *Malaveria* **gen. nov.**; 2. on DHW *Koutalina* **gen. nov.** has a bipupillate ocellus in Cu1-Cu2, which is missing in *Modestia* **gen. nov.** and *Malaveria* **gen. nov.**; 3. VHW marginal line broadens at tornus in *Koutalina* **gen. nov.**, which does not occur in *Modestia* **gen. nov.** nor *Malaveria* **gen. nov.**; 4. singular spatulate aspect of the distal extremity of the valvae in *Koutalina* **gen. nov.**, very distinctive and different from those of *Paryphthimoides* and *Emeryus*. Even if *Koutalina* **gen. nov.**, bears six VHW ocelli, it differs from *Magneuptychia* in the position of the sixth ocellus (Cu2-2A in *Koutalina* **gen. nov.**, 1A-2A-3A in *Magneuptychia*) and also in wing venation and male genitalic morphology. *Koutalina* **gen. nov.**, phenotypically differs from *Euptychoides* Forster, 1964 in ocellus Cu1-Cu2 on VHW, which bears a single pupil in the latter (with the notable exception of *E. pseudosaturnus*

Forster, 1964). Furthermore, typical *Euptychoides* species have only five VHW ocelli and have a serrate process in the valvae of male genitalia; these characters are not found in *Koutalina* **gen. nov.** Species of the genus *Optimandes* Marín, Nakahara & Willmott, 2019, which might show a superficial similarity to *Koutalina pamela* (Hayward, 1957), **comb. nov.**, have only five ocelli on VHW, and those are all monopupillate. The same kind of singled-pupil ocelli are found in all species of *Hermeuptychia* Forster, 1964, whose largest species, such as *H. harmonia* (Butler, 1867a), resemble the habitus of *Koutalina* **gen. nov.**

DNA analysis shows different divergence ratios between the respective type species of the following genera in comparison to *Koutalina* **gen. nov.**, of: 9% for *Magneuptychia*, 7.2% for *Cissia* (*sensu stricto*), 10.9% for *Malaveria* **gen. nov.** and 12.7% for *Euptychoides*, which are coherent with generic distances (Tables 1 and 2).

Description (Figs. 3i-3l)

Butterflies of medium size (FWL: 19-23mm). Wings dorsally brown with a large dark patch of modified scales on FW, presenting a bipupillate ocellus in Cu1-Cu2 and

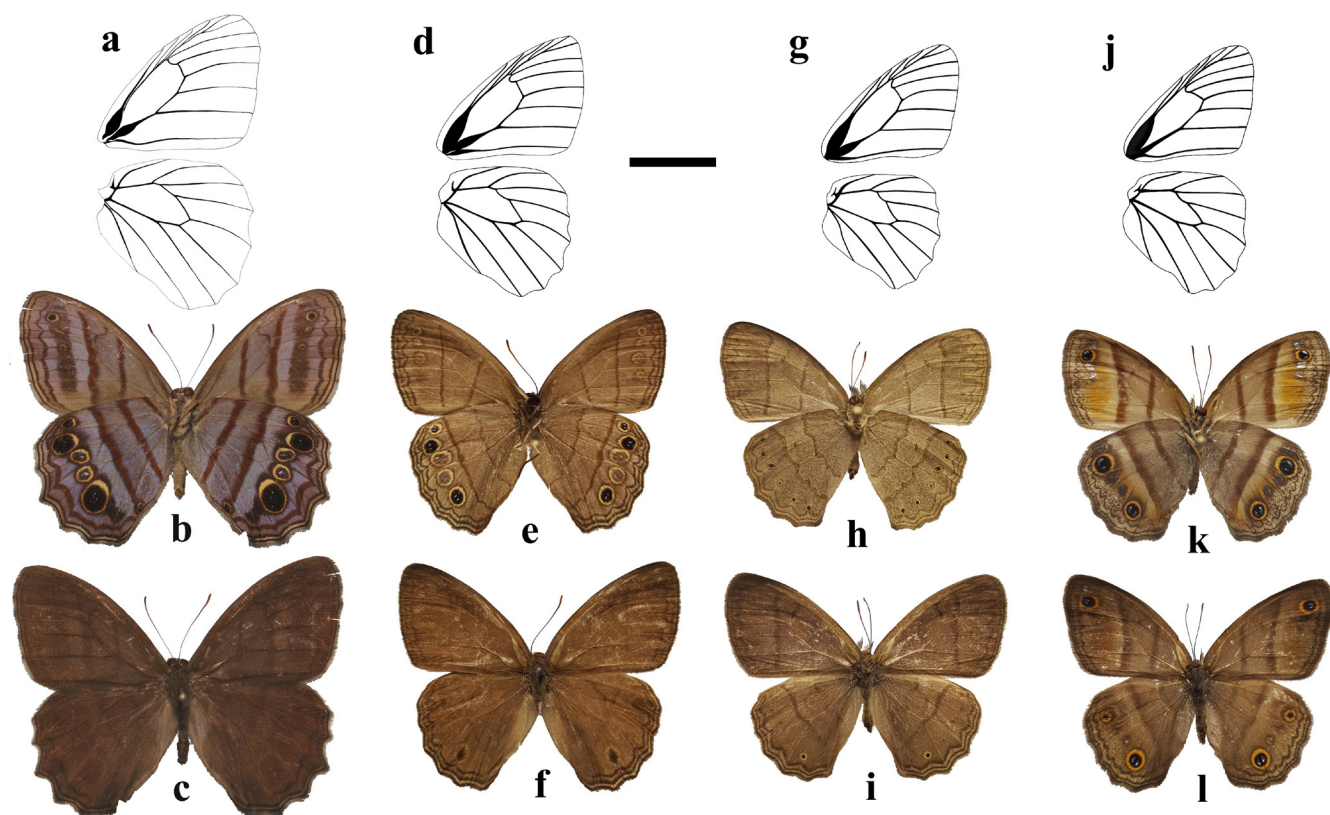


Figure 5. Comparative venation and habitus of male imagos of the type species of similar genera: a. *Magneuptychia* venation (type species *M. libye*); b. Male ventral; c. Dorsal; d. *Emeryus* venation (type species *E. argulus*); e. Male ventral; f. Dorsal; g. *Paryphthimoides* venation (type species *P. poltys*); h. Female ventral; i. Dorsal; j. *Cissia* venation (type species *C. penelope*); k. Male ventral; l. Dorsal. (Scale: 1 cm).

occasionally an additional one much smaller in Cu2-1A+2A; two darker marginal lines more visible on HW. Ventrally ground color brown (lighter) with two darker grossly straight lines crossing both wings more or less in parallel, one submedian, the other median; two dark brown lines, one irregularly undulated, submarginal, meeting the median line near the anal margin of HW, the other thinner, marginal, parallel to outer margin, notably broadening in tornus. Ventral ocelli, when not vestigial, all black, with double white pupils, iris ochreous yellow, finely circled with brown. FW with a subapical ocellus in M1-M2 with two tiny pupils. HW with six ocelli from Rs to 1A+2A, all with double pupils (but sometimes pupils barely visible in M2 and M3). FW venation: Sc broadly swollen at basal third of the cell, ending approximately at half costa; R1 emerging at distal sixth of discal cell, R2 and R3-R5 branching at distal tip of discal cell, R3 emerging half way between the end of discal cell and the final branching of R4 and R5; r2-5-m1 very short and straight, m1-m2 and m2-m3 notably straight; m2-m3 four times as long as m1-m2, and m1-m2 twice as long as r2-5-m1; m3-cu1 and cu1-cu2 straight, all giving the cell a quadrangular aspect; cu1-cu2 twice as long as m3-cu1, and about same length as m2-m3; Cu2-A2 only slightly swollen at base; 1A+2A independent. HW venation: Humeral present, thick and well developed but simple; Sc thin, ending at basal third of costa; Rs and M1 branching separately; m1-m2 curved towards the cell; M2 emerging closer to M1 than to M3; cu1-cu2 twice the length of m3-cu1; 1A+2A and A3 independent but running together at base. Male genitalia: tegumen globular, uncus lanceolate, broad, about same length of tegumen, subunci thin, not reaching the length of uncus; vinculum stylized and sigmoidal in lateral view, saccus tubular, thick, as long as tegumen, valvae strong but elongated, equally thick at base and basal half, slightly thinner towards distal half, which ends in a spatulate extremity, reminiscent of the shape of a wooden kitchen spoon; aedeagus thin, as long as valva, slightly curved upwards.

Derivatio nominis

Koutalina is a Latinized feminine diminutive for *koutáli* (κουτάλι), the Greek word for spoon. This name is proposed for this new genus of butterflies because male individuals of its only known species, *K. pamela* (Hayward, 1957), **comb. nov.**, bear a distinctive genitalia, whose valvae have a spoon-shaped tip.

Koutalina gen. nov., is so far represented by a single known species that inhabits medium elevations in the Andes of Bolivia and Peru.

Species belonging to Koutalina Viloria & Murienne, gen. nov.:

Koutalina pamela (Hayward, 1957), **comb. nov.**

Euptychia pamela Hayward, 1957: 113-115, 119 fig. 3 (male genitalia).

Euptychia pamela Hayward; Forster, 1964: 105 (erroneously as a synonym of *Ypthimoides benedicta* (Butler, 1877)); Lamas, 2004: 220 (erroneously as a synonym of *Magneuptychia alcinoe* (C. Felder & R. Felder, 1867)).

Euptychia ? sp.; D'Abbrera, 1988: 777 [row 6, fig.] (misidentification).

DISCUSSION

Extended comparison between *Modestia gen. nov.* and *Malaveria gen. nov.*: Ocellar pattern and male genitalia

Number of pupils in VHW ocelli (Figs. 6-9)

Ocellus M1-M2

On VHW the number of pupils in ocelli M1-M2 and Rs-M1 can be subject to some apparent variation. In *Modestia gen. nov.*, pupils are well defined, formed by several white/silver scales, placed in the center of the ocellus (Fig. 6a). In *Malaveria gen. nov.*, the two pupils in M1-M2 are formed typically by fewer silver scales, both disposed on a line passing through the center of the ocellus and parallel to the median line. The more anterior pupil is usually larger than the posterior one (Figs. 6b-6d), which can be represented by at least one or two scales. Ocellus in Rs-M1 seems to be too small to always allow expression of the pupils, it is probably a bipupillate ocellus but the silver scales can either represent clearly two different small pupils, be fused in one big pupil or simply not be present. It is more or less the same for ocelli M2-M3 and M3-Cu1, which are of almost the same small size as the latter in both genera, and its pupils are only well and constantly expressed in *M. r. remypignoux sp. nov.* The examination of specimens belonging to *Malaveria gen. nov.* and *Modestia gen. nov.*, shows that, when silver scales are present, these two ocelli are usually bipupillate. In *Modestia gen. nov.* (19 *Modestia modesta comb. nov.* and 19 *M. r. remypignoux sp. nov.*, examined), ocelli M1-M2 and Rs-M1 are always well defined and monopupillate. None of the specimens examined showed two pupils. In *Malaveria gen. nov.* (15 *Malaveria ballofi sp. nov.*, 1 *Malaveria bottoi sp. nov.*, 5 *Malaveria mimas comb. nov.* and 7 *Malaveria nebulosa comb. nov.* examined), ocellus M1-M2 shows generally

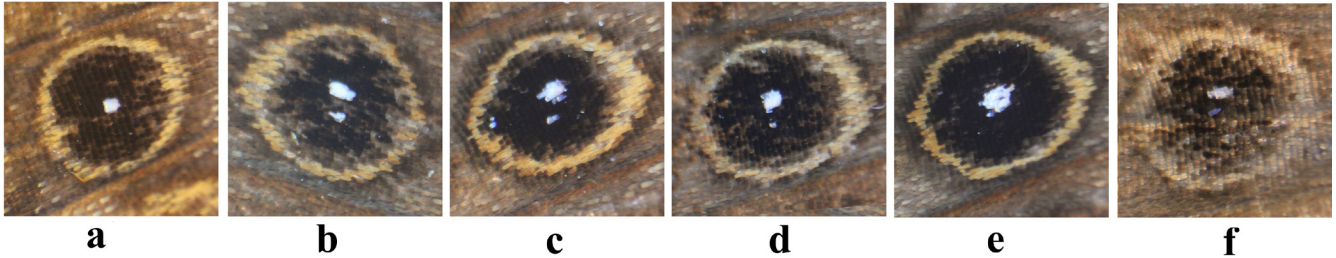


Figure 6. Detail of ocellus M1-M2 on VHW: a. *Modestia modesta* comb. nov. (MB-0023); b. *Malaveria ballofi* sp. nov. (MB-0070); c. *M. ballofi* sp. nov. (MB-0076); d. *M. ballofi* sp. nov. (MB-0074); e. *M. ballofi* sp. nov. (MB-0257); f. *M. ballofi* sp. nov. (MB-0016).

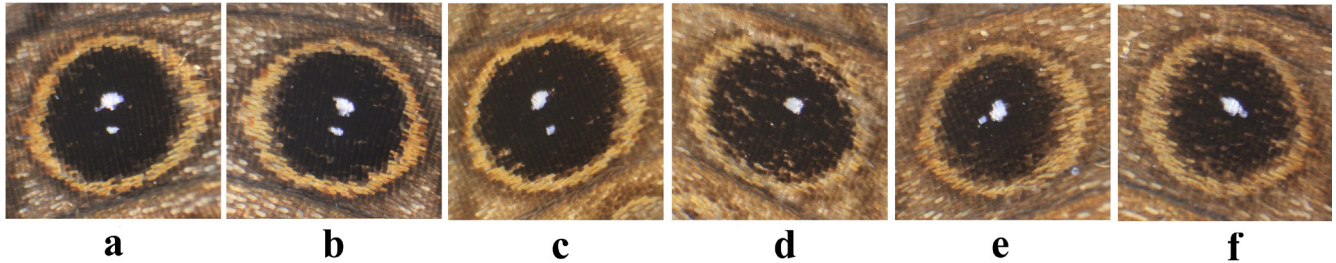


Figure 7. Detail of ocellus M1-M2 on VHW, fusion of the two pupils: a-b. *Malaveria mimas* comb. nov. (MB-0014) left and right HW; c-d. *M. mimas* comb. nov. (MB-0012) left and right HW; e-f. *M. mimas* comb. nov. (MB-0010) left and right HW.

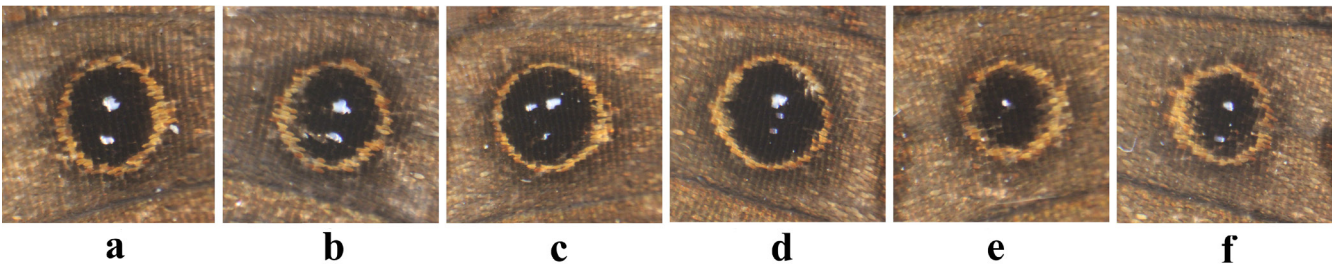


Figure 8. Detail of ocellus M1-M2 on VHW, no expression or reduction of one of the two pupils: a-b. *Malaveria nebulosa* comb. nov. (MB-0004) left and right HW; c-d. *M. nebulosa* comb. nov. (MB-0007) left and right HW; e-f. *M. nebulosa* comb. nov. (MB-0003) left and right HW.

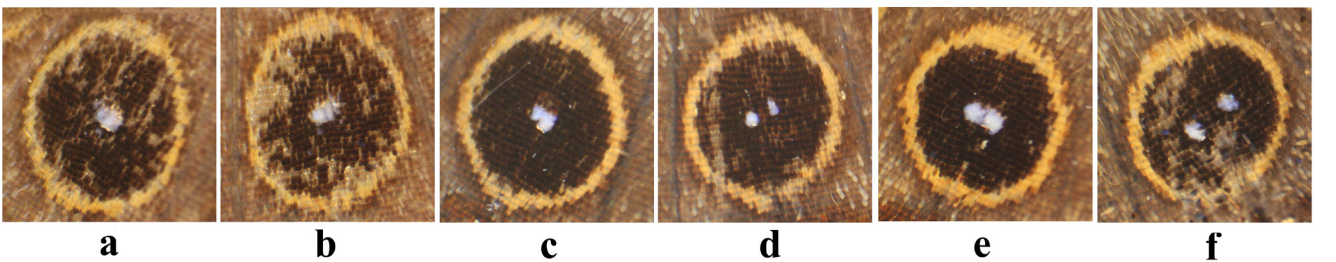


Figure 9. Detail of ocellus Cu1-Cu2 on VHW, fusion of the two pupils: a-b. *Modestia modesta* comb. nov. (MB-0022) left and right HW; c-d. *M. modesta* comb. nov. (MB-0023) left and right HW; e-f. *M. modesta* comb. nov. (MB-0030) left and right HW.

two silver pupils but only one in some specimens. The study with stereoscopic microscope has shown that the apparent single pupil is in fact not a variation but an artefact due to several factors:

- Fusion of the two pupils, which appear larger than a central unique average pupil. For example, in *M. mimas* comb. nov.: 1. Figs. 7a-7b. normal bipupillate ocelli;

- 2. Figs. 7c-7d. in the same specimen a transitional variation with a bipupillate ocellus on one wing and a fusion of the two pupils on the other; 3. Figs. 7e-7f. variation where the two pupils are almost completely fused on both wings. Another example in *M. ballofi* sp. nov., where the two pupils have fused together in a large central unique pupil (Fig. 6c).

- No expression, or loss of scales of one of the pupils (usually the smallest one), the apparent pupil is then not in the center (usually in the more anterior position). For example, in *M. nebulosa* **comb. nov.**: Figs. 8a-8b: normal bipupillate ocelli; Figs. 8c-8d: transitional variation with one of the two pupils only represented by a single scale (note, in this particular specimen a few scales aberrantly located, look like forming a third pupil); Figs. 8e-8f: in the same specimen one ocellus still has two pupils composed by a few scales, while the other ocellus presents a single, eccentric, tiny pupil, due to the non-expression of the second pupil; Fig. 6f: apparent loss of the smallest pupil due to the worn condition of the specimen.

Ocellus Cu1-Cu2

Contrastingly in both genera, the number of pupils (two) in ocellus Cu1-Cu2 is very stable. Only one specimen (over 66 examined) showed an apparent unique pupil (Figs. 9a-9b.). The mechanism involved is probably the same as explained above: fusion of the two pupils like in Figs. 9c-9f. It is worth noting that the only syntype of *Neonympha sylvina* C. Felder & R. Felder, 1867, we are aware of (Fig. 12b.) presents a single pupil in ocellus Cu1-Cu2 on both VHWs (see discussion in description of *M. r. remypignoux* **sp. nov.**).

It appears from our analysis that the number of pupils in ocelli M1-M2 and Cu1-Cu2 is a primary character that easily differentiates phenotypically these two genera. The “apparent” single pupil is an artifact of the mechanisms above mentioned. In most cases, it can be unmasked through careful examination. Based on our experience, we recognize the number of ocelli, their composition and the number of pupils as good elements to establish morphological homologies to support taxonomic arrangements at generic level in the Satyrinae. This hypothesis should be tested with other butterfly groups and compared with male genitalia morphology and DNA analysis to explore if they are consistent to support new taxonomic arrangements.

Variation in distal extremity of the valvae (Figs. 10)

Generally, most satyrine species are distinguishable from their congeners by the morphology of their male genitalia (Nakahara *et al.* 2015). Other groups of butterflies have shown male genitalia morphology not to be discriminating between closely related species (*e. g.*, the genus *Adelpha* Hübner, 1819; see Willmott 2003). A preliminary study of Nakahara *et al.* (2015) pointed out that male genitalia in *M. nebulosa* **comb. nov.** and *M. alcinoe* **comb. nov.**, were very close and subject to some variation. In this study the examination of more than 60 male genitalia belonging to *Modestia* **gen. nov.** and *Malaveria* **gen.**

nov., showed that intraspecific variation is much more important than previously estimated. The range of variation overlaps within species respectively belonging to each genus and causes some confusion. The distal extremity of the valvae seems to be the potentially most diagnostic part of the genitalia at the specific level. Unfortunately, it is subject to a wide range of variation regarding the presence, location and development of the inner spiny process and the membranous part of the valva, some specimens exhibiting different distal shapes for each valvae (Figs. 10a-10l.). Nevertheless, although for some species we did not manage to detect specific genitalia characters that differentiate them from others, we have been able to discern the basal genitalia pattern for each species. Our conclusions were limited by the number of specimens available for dissection for each taxon. Genitalia morphology variation and basal genitalia pattern will be discussed under each taxon.

Another crucial point is the use of a standardized method to reliably compare male genitalia morphology. The angle of view is of foremost importance, as even a little variation of a few degrees can result in a completely different appreciation of the valva morphology. A tri-dimensional comparison is essential to appreciate subtle morphological differences. Illustrations of two-dimensional photographs to represent genitalia are seriously limited as a source of information. We do insist on the fact that, when studying closely related species, differences in male genitalia between two or more species must be confirmed by the dissection of several specimens, and if possible, examination and comparison by the same technician.

Inner margin supernumerary ocellus on VHW (Figs. 11)

The inner margin ocellus on VHW is a diagnostic character for the genus *Magneptychia* (*sensu* Costa *et al.*, 2016), which comprises at least 3 species: *M. libye* (Linnaeus, 1767), *M. libyoidea* (Butler, 1866) and *M. lethra* (Möschler, 1883). During our analyses, we found some individuals expressing this ocellus in species that normally do not exhibit it. Here we illustrate some examples from different genera: ‘*Magneptychia*’ *tricolor* (Hewitson, 1850), *Megisto cymela* (Cramer, 1777), *Modestia remypignoux* **sp. nov.** and *Euptychia marceli* Brévignon, 2005 (Figs. 11a-11d, 11g-11h). By way of contrast, we have also illustrated a male specimen of *Magneptychia libye* from Tobago, in which this ocellus is absent when it should normally be present (Figs. 11e-11f). The taxon *Euptychia benedicta* described by Butler (1877) is apparently based on a single female specimen from Ecuador, which was appropriately illustrated in its original description and deposited in the NHMUK (Fig. 12d.). This specimen is similar to the lectotype of *Neonympha alcinoe* C. Felder & R. Felder, 1867

(see under this species) but presents an additional ocellus on the inner margin of VHW. Although we did not find another similar specimen which exhibit this additional ocellus, we think that it represents no more than a variation (see discussion in *M. alcinoe* **comb. nov.**) as it can occasionally occur in the above mentioned species. The presence of this ocellus, almost totally neglected in previous

comparative studies of butterfly wing patterns, probably represents an ancestral trait still present in *Magneptychia* and some other species of the Neotropical Satyrinae, like *Euptychia attenboroughi* Neild, Nakahara, Fratello & Le Crom, 2015, *E. sophiae* Zacca, Nakahara, Dolibaina & Dias, *Vanima lesbia* (Staudinger, 1886) and *V. palladia* (Butler, 1867), among others.

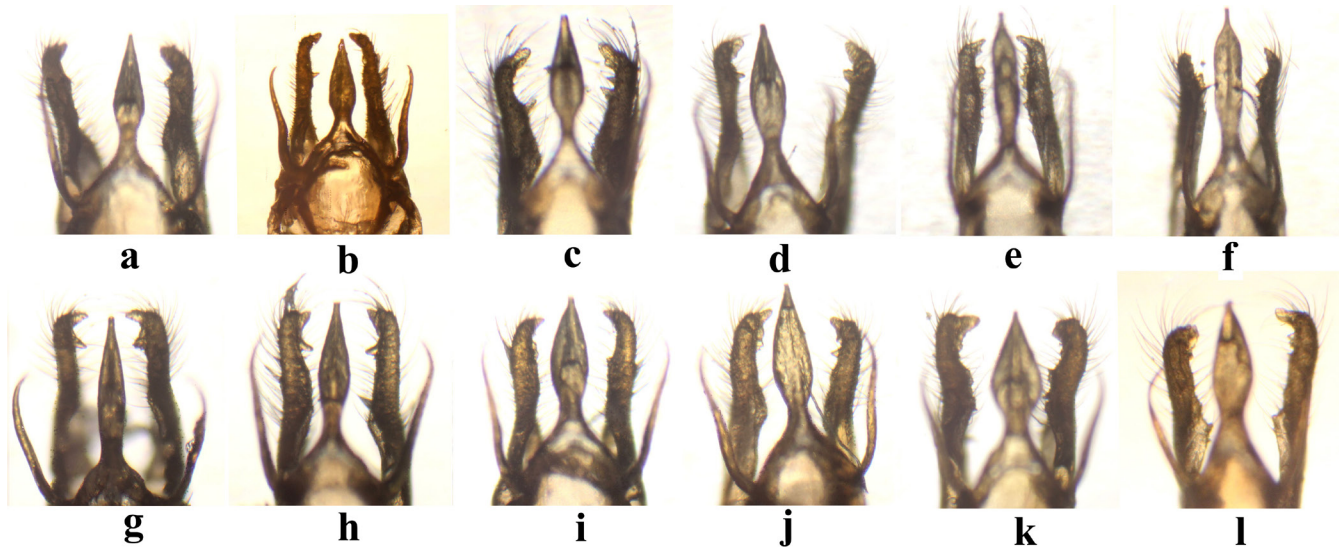


Figure 10. Male genitalia dorsal view showing intraspecific variation and variability within the same specimen. a. *Malaveria nebulosa* **comb. nov.** (MB-0004); b. *M. nebulosa* **comb. nov.** (MB-006); c. *Malaveria rodriguezii risaralda* **ssp. nov.** (MB-013); d. *Malaveria* sp. (MB-014); e. *Modestia remypignoux* **sp. nov.** (MB-0039); f. *Modestia remypignoux shueyi* **ssp. nov.** (MB-0213); g. *Malaveria mimas* **comb. nov.** (MB-0010); h. *M. mimas* **comb. nov.** (MB-0014); i. *Malaveria ballofi* **sp. nov.** (MB-0072); j. *M. ballofi* **sp. nov.** (MB-0073); k. *Malaveria duponti* **sp. nov.** (MB-0145); l. *M. duponti* **sp. nov.** (MB-0146).

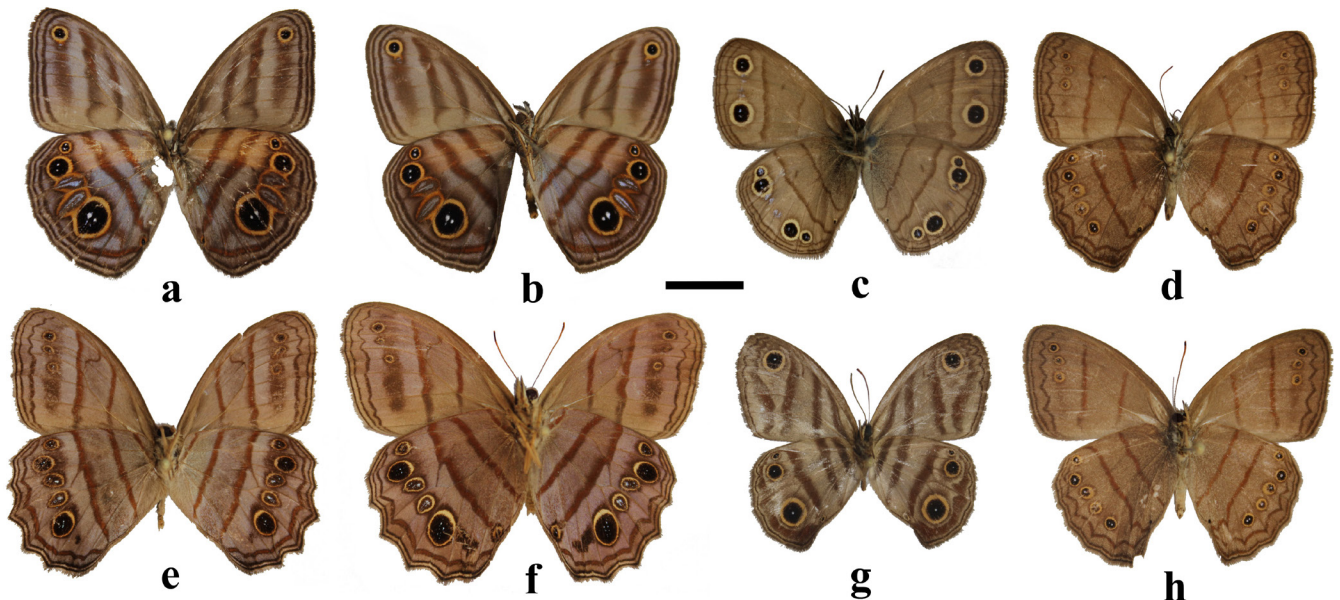


Figure 11. Additional inner margin ocellus on VHW in some species of Euptychiina. a. “*Magneptychia*” *tricolor*; b. “*M.*” *tricolor*; c. *Megisto cymela*; d. *Modestia remypignoux* **sp. nov.**; e. *Magneptychia libye*; f. *M. libye*; g. *Euptychia marceli*; h. *Modestia remypignoux* **sp. nov.** (Scale: 1 cm).

DNA analysis and results (Tables 1-3).

General comparison for Modestia gen. nov., *Malaveria gen. nov.* and *Koutalina gen. nov.*

We obtained 16S sequences for 101 specimens (of which only 17 were excluded in the following tables to avoid space-consuming repetitions of the same sequences), with a fragment size ranging from 218 to 220 base pairs. The final alignment comprised 231 sites among which 71.43% were invariant. The marker (16S) shows expected patterns of genetic distances, with intra-specific distances typically above 97% divergence (*i.e.*, *M. r. shueyi* **ssp. nov.** / *M. r. remypignoux* **sp. nov.** at 98.6% similarity). Genetic similarity among closely related species is below 97% for *M. gomezi* **comb. nov.** / *M. modesta* **comb. nov.** (95.9%), *M. modesta* **comb. nov.** / *M. r. remypignoux* **sp. nov.** (94.1%), *M. mimas* **comb. nov.** / *M. duponti* **sp. nov.** (94.1%). In the same fashion, comparison of inter-generic distances shows even lower similarity for *Cissia* (*sensu stricto*) / *Koutalina gen. nov.* (92.8%), *Malaveria gen. nov.* / *Koutalina gen. nov.* (89.1%), *Modestia gen. nov.* / *Magneuptychia* (93.2%) and *Megeuptychia* Forster, 1964 / *Euptychoides* (88.7%). However, there are also a few instances in the genus *Malaveria gen. nov.*, where the 16S fragment could not discriminate between closely related species. Indeed, *M. mimula* **comb. nov.**, and *M. duponti* **sp. nov.**, as well as *M. r. rodriguezii* **sp. nov.**, and *M. bottoi* **sp. nov.**, show exactly the same sequence. In addition, the cluster *M. ballofi* **sp. nov.**, *M. r. rodriguezii* **sp. nov.** / *M. bottoi* **sp. nov.**, despite showing few differences, present a very high genetic similarity of 99.5%. While a phenomenon of introgression is possible, the lack of resolution of the 16S marker is most probably related to the relatively small size of the fragment.

SPECIES ACCOUNT

Modestia Viloria & Benmesbah, **gen. nov.**

Modestia modesta (Butler, 1867), **comb. nov.**
(Figs. 3a-3d, 12a, 13a-13m)

Type material: Butler described *Euptychia modesta* based on an unspecified number of specimens from Pará (eastern Amazonian Brazil) in the Bates collection, and provided an illustration. A male syntype in good condition, which agrees with the original description, is hosted in the NHMUK (Fig. 12a). To fix the identity of this taxon, to stabilize its taxonomy and to avoid any further confusion in this group of very similar species, we designate this syntype as the **LECTOTYPE** of *Euptychia modesta*: / Type H.T./Syntype/♂/Type of Species./ Godman-Salvin

Coll. 1904.--1./*Euptychia modesta*, Butl./♂ *Pará modesta* *Butler type* / Para, L. Amazons. H. W. Bates. / B. M. TYPE N°. Rh 3222 *Euptychia modesta*, ♂ *Butl.*/BMNH(E) #986581/(examined) [NHMUK].

Material examined: 6 males (6 dissected), 13 females (5 dissected). FRENCH GUIANA (6 males, 13 females): Grand-Santi: 16.V.2012 1 female (MB-0036*); Mitaraka: 01.III.2015 1 female (MB-0026*); Mont Itoupé: 28.XI.2014 1 male (MB-0024*); 27.XI.2014 1 female (MB-0027); 30.XI.2014 1 female (MB-0030); 02.XII.2014 1 female (MB-0035); Papaïchton: 23.VII.2012 2 males (MB-0023*, MB-0025*); 23.VII.2012 1 female (MB-0029); Saint-Jean du Maroni: 02.VII.2015 1 female (MB-0038*); Saint-Laurent du Maroni: 10.I.2012 1 female (MB-0031*); Saül: 12.IX.2013 1 male (MB-0020*); 03.IX.2011 1 male (MB-0021*); 30.IX.2012 1 male (MB-0022*); 12.IX.2013 1 female (MB-0028); 11.IX.2013 1 female (MB-0032*); 07.VIII.2012 1 female (MB-0034); 11.IX.2013 1 female (MB-0033); 07.X.2011 1 female (MB-0037) [MB].

Redescription: Male (Figs. 13a-13b)– FWL: 21-22 mm (6 specimens), average 21.5 mm; DFW: ground color brown, almost uniform; VFW: ground color brown; submedian and median lines thin, dark brown, slightly ferruginous; submarginal band dark brown, discreet; one small black ocellus at the apex in M1-M2 with one tiny white pupil, two others reduced and almost invisible in M2-M3 and M3-Cu1; submarginal line thinner, scalloped, pointing distally in R5 to 2A; marginal line straight, thin, parallel and close to outer margin. DHW: ground color uniform, same as DFW; outer margin slightly scalloped; thin marginal area outside marginal line more clear near tornus. VHW: ground color same as VFW; submedian and median lines of same width and color as in VFW, slightly irregular, joining anal margin without making a curve; submarginal line scalloped, composed by curved adjacent segments, basally convex from M1 to 2A; marginal dark line thin, parallel to outer margin from costa to tornus; five ocelli surrounded with discreet dark brown in submarginal area, one in each space between Rs and Cu2, ocelli in Rs-M1, M1-M2 and Cu1-Cu2 rounded, well defined, black circled with yellow ring, ocellus in Cu1- Cu2 larger, with two white pupils, ocelli in Rs-M1 and M1-M2 smaller with one white pupil, ocelli in M2-M3 and M3-Cu1 less defined, lacking black central area and pupils.

Female (Figs. 13c-13d) – FWL: 20-22 mm (12 specimens), average 20,8 mm. Similar to male, but differs by underside color lighter and greyish, ocelli in M2-M3 and M3-Cu1 on VFW and VHW well defined, each with two white pupils.

Table 3. Data of the specimens of several satyrine taxa selected and sampled for 16S mitochondrial rDNA sequencing in this study (genera *Cissia*, *Euptychoides*, *Magneptychia*, *Megeptychia*, *Modestia* *gen. nov.*, *Malaveria* *gen. nov.* and *Koutalina* *gen. nov.*). Individual codes generated for each voucher specimen in first column, GenBank accession codes in fourth column.

Code	Genus	species	Code	16s	Sex	Country	Locality	Collector
MB-0001	<i>Malaveria</i>	<i>nebulosa</i>	SUB8712959	MW366404	F	Venezuela	Miranda, El Jarillo, Municipio Guaicaipuro, Quebrada Honda	C.R. Malaver
MB-0002	<i>Malaveria</i>	<i>nebulosa</i>	SUB8712959	MW366405	M	Venezuela	Miranda, El Jarillo, Municipio Guaicaipuro, Quebrada Honda	C.R. Malaver
MB-0004	<i>Malaveria</i>	<i>nebulosa</i>	SUB8712959	MW366406	M	Venezuela	Miranda, El Jarillo, Municipio Guaicaipuro, Quebrada Honda	C.R. Malaver
MB-0005	<i>Malaveria</i>	<i>nebulosa</i>	SUB8712959	MW366407	F	Venezuela	Miranda, El Jarillo, Municipio Guaicaipuro, Quebrada Honda	C.R. Malaver
MB-0006	<i>Malaveria</i>	<i>nebulosa</i>	SUB8712959	MW366408	M	Venezuela	Miranda, El Jarillo, Municipio Guaicaipuro, Quebrada Honda	C.R. Malaver
MB-0007	<i>Malaveria</i>	<i>nebulosa</i>	SUB8712959	MW366409	M	Venezuela	Miranda, El Jarillo, Municipio Guaicaipuro, Quebrada Honda	C.R. Malaver
MB-0009	<i>Malaveria</i>	<i>alcinoe</i>	SUB8712959	MW366410	F	Colombia	Cundinamarca, Colegio, 430m	C.R. Malaver
MB-0010	<i>Malaveria</i>	<i>mimas</i>	SUB8712959	MW366411	M	Bolivia	Caranavi	P. Botto
MB-0012	<i>Malaveria</i>	<i>mimas</i>	SUB8712959	MW366412	M	Bolivia	Caranavi	
MB-0013	<i>Malaveria</i>	<i>mimas</i>	SUB8712959	MW366413	M	Bolivia	Caranavi	
MB-0014	<i>Malaveria</i>	<i>mimas</i>	SUB8712959	MW366414	M	Peru	Cusco, carretera Manu, 1900-2900m	C. Faynel
MB-0015	<i>Malaveria</i>	<i>ballofi</i>	SUB8712959	MW366415	M	Ecuador-W	Pichincha, Nanegalito	R. Aldaz
MB-0016	<i>Malaveria</i>	<i>ballofi</i>	SUB8712959	MW366416	M	Ecuador-W	Pichincha, Nanegalito	R. Aldaz
MB-0018	<i>Malaveria</i>	<i>ballofi</i>	SUB8712959	MW366418	M	Ecuador-W	Pichincha, Nanegalito	R. Aldaz
MB-0019	<i>Malaveria</i>	<i>battoi</i>	SUB8712959	MW366419	M	Colombia	Cundinamarca, Colegio, 430m	P. Botto
MB-0020	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366420	M	French Guiana	Saul, Gros Arbres	M. Benmesbah
MB-0021	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366421	M	French Guiana	Saul, Boeuf-Mort	M. Benmesbah
MB-0022	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366422	M	French Guiana	Saul	M. Benmesbah
MB-0023	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366423	M	French Guiana	Papaichton	M. Benmesbah
MB-0024	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366424	M	French Guiana	Itoupe	M. Benmesbah
MB-0030	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366425	F	French Guiana	Itoupe, forêt bambou, 550-750m	M. Benmesbah
MB-0035	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366426	F	French Guiana	Itoupe, forêt bambou, 550-750m	M. Benmesbah
MB-0037	<i>Modestia</i>	<i>modesta</i>	SUB8712959	MW366427	F	French Guiana	Saul, vers Galbao	M. Benmesbah
MB-0039	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366428	M	French Guiana	Antecume-Pata	M. Benmesbah
MB-0041	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366429	M	French Guiana	Kaw, Degrad Escolle	M. Benmesbah
MB-0043	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366431	M	French Guiana	Saint-Laurent-du-Maroni	M. Benmesbah
MB-0044	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366432	M	French Guiana	Saint-Laurent-du-Maroni, route Apatou	M. Benmesbah
MB-0045	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366433	M	French Guiana	Talwen, Maroni	M. Benmesbah
MB-0049	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366437	F	French Guiana	Matti	M. Benmesbah
MB-0050	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366438	F	French Guiana	Antecume-Pata	M. Benmesbah
MB-0055	<i>Modestia</i>	<i>r. remypignoux</i>	SUB8712959	MW366443	F	French Guiana	Grand-Santi	M. Benmesbah
MB-0057	<i>Koutalina</i>	<i>pamela</i>	SUB8712959	MW366445	M	Bolivia	La Paz, Caranavi, 800-1500m	M. Benmesbah
MB-0058	<i>Koutalina</i>	<i>pamela</i>	SUB8712959	MW366446	M	Bolivia	La Paz, Caranavi, 800-1500m	M. Benmesbah
MB-0059	<i>Koutalina</i>	<i>pamela</i>	SUB8712959	MW366447	M	Bolivia	La Paz, Caranavi, 800-1500m	M. Benmesbah
MB-0060	<i>Koutalina</i>	<i>pamela</i>	SUB8712959	MW366448	M	Bolivia	La Paz, Caranavi, 800-1500m	M. Benmesbah
MB-0063	<i>Koutalina</i>	<i>pamela</i>	SUB8712959	MW366449	M	Peru	Cusco, carretera Manu, 1900-2900m	C. Faynel
MB-0064	<i>Koutalina</i>	<i>pamela</i>	SUB8712959	MW366450	M	Peru	Junin, Mina Pichita, 2100m	A. Vitoria & M. Suarez
MB-0065	<i>Koutalina</i>	<i>pamela</i>	SUB8712959	MW366451	M	Peru	Junin, Mina Pichita, 2100m	A. Vitoria & M. Suarez
MB-0066	<i>Malaveria</i>	<i>ballofi</i>	SUB8712959	MW366452	M	Ecuador-W	Pichincha, Nanegalito	R. Aldaz
MB-0068	<i>Malaveria</i>	<i>ballofi</i>	SUB8712959	MW366454	M	Ecuador-W	Carchi, Baboso, 800m	R. Aldaz

Table 3. (*Continuation*)

MB-0069	<i>Malaveria balliofi</i>	SUB8712959	MW366455	M	Ecuador-W	Carchi, Baboso, 800m	Sept. 2016	R. Aldaz
MB-0072	<i>Malaveria balliofi</i>	SUB8712959	MW366458	M	Ecuador-W	Pichincha, Nanegalito	2016	R. Aldaz
MB-0074	<i>Malaveria balliofi</i>	SUB8712959	MW366460	M	Ecuador-W	Pichincha, Nanegalito	2016	R. Aldaz
MB-0143	<i>Modestia r. shueyi</i>	SUB8712959	MW366463	M	Belize	Cayo Dist, Baldy Beacon, 750m	23.IX.2016	J. Shuey/P. Labus
MB-0144	<i>Modestia r. shueyi</i>	SUB8712959	MW366464	M	Belize	Cayo Dist, Baldy Beacon, 750m	23.IX.2016	J. Shuey/P. Labus
MB-0145	<i>Malaveria duponti</i>	SUB8712959	MW366465	M	Bolivia	Caranavi		
MB-0146	<i>Malaveria duponti</i>	SUB8712959	MW366466	M	Bolivia	Caranavi		
MB-0147	<i>Malaveria duponti</i>	SUB8712959	MW366467	M	Bolivia	Caranavi		
MB-0148	<i>Malaveria duponti</i>	SUB8712959	MW366468	M	Bolivia	Caranavi		
MB-0149	<i>Malaveria duponti</i>	SUB8712959	MW366469	F	Bolivia	Caranavi		
MB-0152	<i>Malaveria mimula</i>	SUB8712959	MW366470	M	Paraguay	PARAGUARY, Sapucaí	08.IX.2014	M. Benmesbah
MB-0153	<i>Malaveria mimula</i>	SUB8712959	MW366471	M	Paraguay	PARAGUARI, Cerro Achay, 4km y 7km de la ruta	05.IX.2014	M. Benmesbah
MB-0154	<i>Malaveria mimula</i>	SUB8712959	MW366472	M	Paraguay	PARAGUARI, Cerro Achay, 4km de la ruta	04.IX.2014	M. Benmesbah
MB-0165	<i>Cissia myncea</i>	SUB8712959	MW366473	M	French Guiana	Maripasoula, vers Wacapou, Filet	18.IX.2013	M. Benmesbah
MB-0166	<i>Cissia myncea</i>	SUB8712959	MW366474	M	French Guiana	Mitaraka, camp de base	01.III.2015	M. Benmesbah
MB-0168	<i>Cissia myncea</i>	SUB8712959	MW366475	M	French Guiana	Maripasoula, vers Wacapou, Filet	18.IX.2013	M. Benmesbah
MB-0169	<i>Cissia penelope</i>	SUB8712959	MW366476	M	French Guiana	Kaw, Degrad Escolle, Filet	16.XI.2011	M. Benmesbah
MB-0170	<i>Cissia penelope</i>	SUB8712959	MW366477	F	French Guiana	Mitaraka, sommet en cloche	15.II.2015	M. Benmesbah
MB-0171	<i>Megneuptychia antonoe</i>	SUB8712959	MW366478	M	French Guiana	Cacao, Banane	Sept. 2011	M. Benmesbah
MB-0172	<i>Megneuptychia antonoe</i>	SUB8712959	MW366479	M	French Guiana	Cacao, Banane	Sept. 2011	M. Benmesbah
MB-0173	<i>Megneuptychia antonoe</i>	SUB8712959	MW366480	M	French Guiana	Cacao, Banane	Sept. 2011	M. Benmesbah
MB-0174	<i>Euptychoides saturnus</i>	SUB8712959	MW366481	M	Bolivia	Caranavi		
MB-0175	<i>Euptychoides saturnus</i>	SUB8712959	MW366482	M	Bolivia	Caranavi		
MB-0178	<i>Magneuptychia lethra</i>	SUB8712959	MW366483	M	French Guiana	Mitaraka, savane roche	28.II.2015	M. Benmesbah
MB-0206	<i>Magneuptychia libye</i>	SUB8712959	MW366484	M	French Guiana	Cayenne, Bourda	2011	M. Benmesbah
MB-0207	<i>Magneuptychia libye</i>	SUB8712959	MW366485	M	French Guiana	Cayenne, Bourda	2011	M. Benmesbah
MB-0208	<i>Magneuptychia lethra</i>	SUB8712959	MW366486	F	French Guiana	Saul, vers Galbao	07.X.2011	M. Benmesbah
MB-0209	<i>Magneuptychia libye</i>	SUB8712959	MW366487	F	French Guiana	Montsinery, Crique Couleuvre	21.X.2011	M. Benmesbah
MB-0210	<i>Magneuptychia lethra</i>	SUB8712959	MW366488	F	French Guiana	Maripasoula, Talwen	15.III.2012	M. Benmesbah
MB-0211	<i>Euptychoides saturnus</i>	SUB8712959	MW366489	M	Bolivia	Caranavi		
MB-0212	<i>Euptychoides saturnus</i>	SUB8712959	MW366490	M	Bolivia	Caranavi		
MB-0247	<i>Malaveria sp.</i>	SUB8712959	MW366491	M	Colombia	Cesar, San Alberto, 300m	14.VI.2017	G. Rodriguez
MB-0248	<i>Malaveria r. rodriguezi</i>	SUB8712959	MW366492	M	Colombia	Antioquia, Amaga, 1700m	17.VII.2003	G. Rodriguez
MB-0249	<i>Malaveria r. rodriguezi</i>	SUB8712959	MW366493	M	Colombia	Antioquia, Frontino, 2000m	22.IV.2007	G. Rodriguez
MB-0250	<i>Malaveria r. risaralda</i>	SUB8712959	MW366494	M	Colombia	Risaralda, Pueblo Rico, 1400m	20.VII.2005	G. Rodriguez
MB-0251	<i>Malaveria sp.</i>	SUB8712959	MW366495	M	Colombia	Santander, Via Mesa-Santos, 1500m	22.XII.2007	G. Rodriguez
MB-0252	<i>Malaveria r. risaralda</i>	SUB8712959	MW366496	M	Colombia	Risaralda, Pueblo Rico, 1400m	20.VII.2005	G. Rodriguez
MB-0253	<i>Malaveria r. rodriguezi</i>	SUB8712959	MW366497	M	Colombia	Antioquia, Frontino, 1900m	22.IV.2000	G. Rodriguez
MB-0254	<i>Malaveria r. rodriguezi</i>	SUB8712959	MW366498	M	Colombia	Antioquia, Guarne, 2000m	20.XI.2003	G. Rodriguez
MB-0255	<i>Malaveria r. rodriguezi</i>	SUB8712959	MW366499	M	Colombia	Antioquia, La Mansa-Ciudad Bolívar, 2400m	25.I.2004	G. Rodriguez
MB-0256	<i>Malaveria r. rodriguezi</i>	SUB8712959	MW366500	M	Colombia	Tolima, Prado, 700m	Sept. 2003	G. Rodriguez
MB-0258	<i>Modestia gomezi</i>	SUB8712959	MW366502	M	Colombia	Antioquia, Porce, 800m	27.VIII.2017	G. Rodriguez
MB-0265	<i>Malaveria r. rodriguezi</i>	SUB8712959	MW366503	M	Colombia	Antioquia, Porce, 1000m	09.VIII.2003	G. Rodriguez
MB-0266	<i>Malaveria mimula</i>	SUB8712959	MW366504	F	Paraguay	PARAGUARY, Sapucaí	08.IX.2014	M. Benmesbah

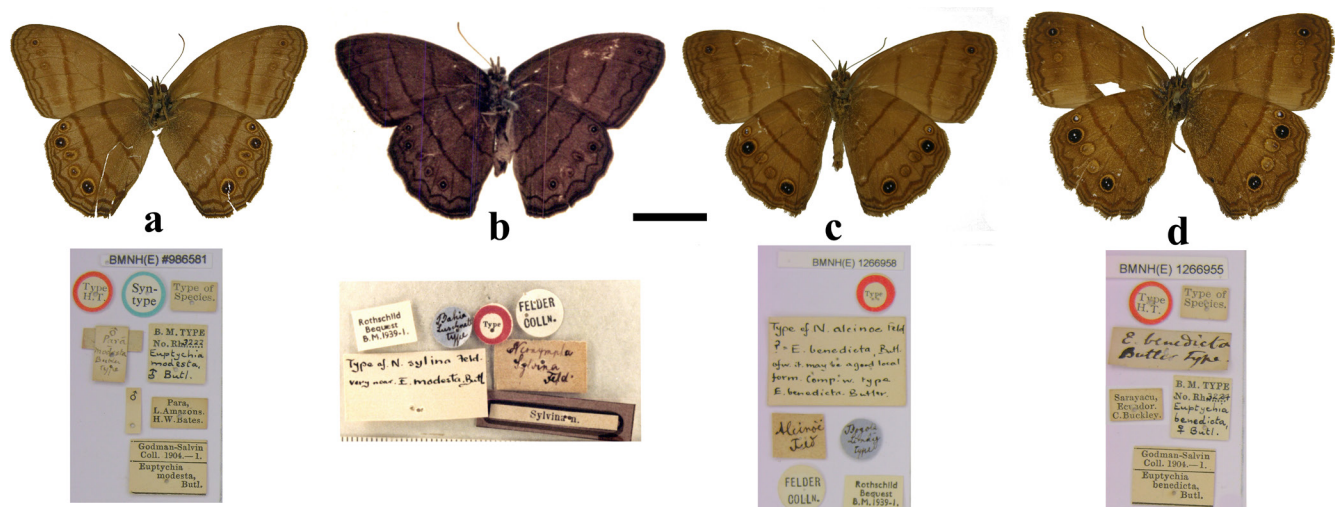


Figure 12. Historical type specimens with corresponding labels. a. Lectotype of *Euptychia modesta* Butler, 1867; b. Lectotype of *Neonympha sylvina* C. Felder & R. Felder, 1867; c. Lectotype of *Neonympha alcinoe* C. Felder & R. Felder, 1867; d. Syntype of *Euptychia benedicta* Butler, 1877. (Scale: 1 cm; labels not presented to scale).

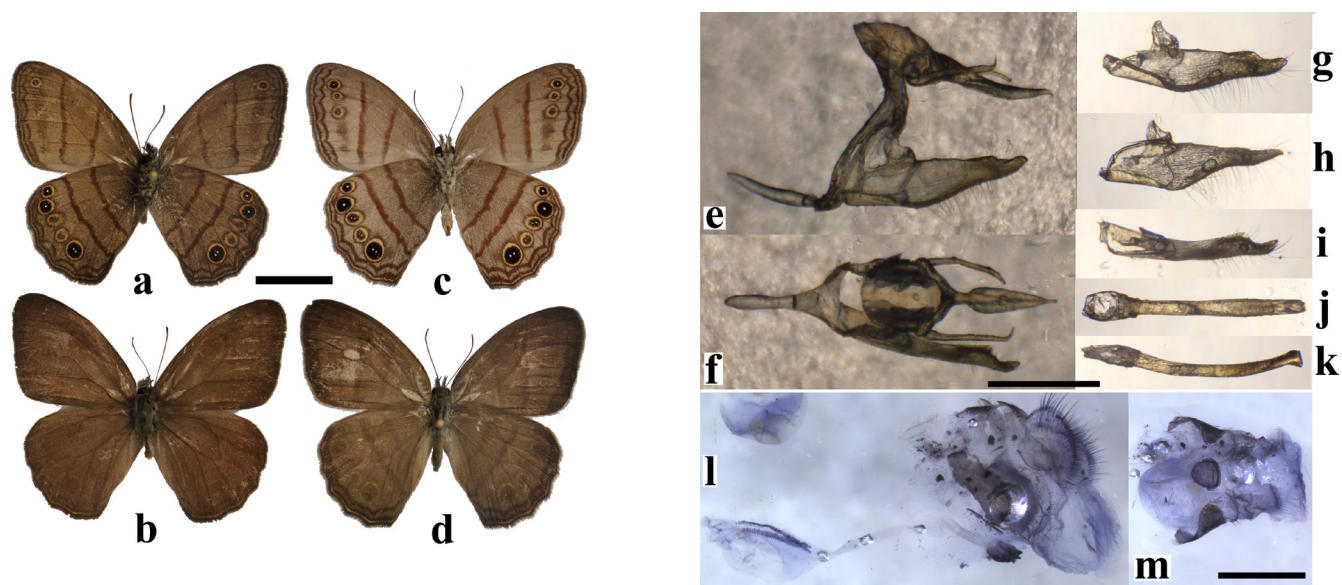


Figure 13. *Modestia modesta* comb. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. *idem* dorsal; e. Male genitalia lateral view (one valva removed); f. *idem* dorsal view; g. Valva lateral inner view; h. *idem* lateral outer view; i. *idem* dorsal view; j. Aedeagus dorsal view; k. *idem* lateral view; l. Female genitalia lateral view; m. *idem* ventral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

Male genitalia (6 dissected) (Figs. 13e-13k): characterized by the shape of the valvae, which are long and gradually pointed distally. In lateral view the valvae have a particular ampullar ridge (dorsal) with a moderate notch, just before their tip. This is not seen in other species of the genus. Uncus lanceolate, twice as long as tegumen; saccus digitiform, same length as subunci; aedeagus long, about same length as tegumen + uncus.

Female genitalia (5 dissected) (Figs. 13l-13m): external sclerites of the 8th abdominal segment (ventral) very

similar to those of *M. remypignoux* sp. nov.; papillae anales prominent and setose, bursa copulatrix bearing two parallel signa, almost as long as the corpus bursae.

Variation: there is slight variation on VHW in the size of the ocelli and the distance between submarginal and marginal lines, but no consistent difference has been noticed.

Diagnosis: *M. modesta* comb. nov., differs from *M. gomezi* comb. nov. (Fig. 14a-14c) by: 1. less marked median and post median lines on the underside, which are brown

and heavily marked in *M. gomezi* **comb. nov.**; 2. shape of the ocelli in M2-M3 and M3-Cu1 on VHW, in which the yellow ring almost invade the entire ocelli in *M. gomezi* **comb. nov.**, the brown center being reduced to only a dash; 3. distal extremity of the valvae sharper and presenting an obvious inner protrusion in *M. modesta* **comb. nov.** (Figs. 13g-13i), while it is more spatulate and with a much less developed inner protrusion in *M. gomezi* **comb. nov.** (Figs. 14f-14h). Differences with *M. remypignoux* **sp. nov.**, are treated under that species.

Habitat and behavior: *M. modesta* **comb. nov.**, has been captured several times in French Guiana and is probably more widespread. One of the syntypes is from the Lower Amazon in Pará state of Brazil. The species seems to fly all year round. It has been encountered as well in primary forest (Mitaraka Mounts), secondary forest (Saint-Jean-du-Maroni), close to cassava plantations (Païchton) or close to human habitation (Saül). At Saül, the specimens collected were flying in the late morning at the edge of the trail, together with *Cissia penelope* (Fabricius, 1775) and species of *Hermeuptychia*. Its flight is characteristic for members of the Euptychiina: shy, in the shade of the understory, flying for several meters before resting again, wings closed, at the edge of the trail. Distinction between *M. modesta* **comb. nov.** and *Hermeuptychia* sp. was very difficult on the wing and only systematic collecting allowed the capture of a few specimens of *M. modesta* **comb. nov.** It has also been observed during the middle morning (between 9:30 and 10:30am) at the edges of a wide bamboo field on the slopes of Mount Itoupé at around 630m. Several specimens were observed over several days revealing the same behavior. The butterfly had a nervous flight at the summit of the bamboos (2 to 3m high) and rested on leaves for a few seconds to a few minutes before flying. The specimens appeared when the angled sunlight lit up this part of the bamboo field, and then stopped flying when sunshine became strong. One specimen was collected at the summit of the same mount (second highest summit in French Guiana at 750m) in late evening, close to the ground when it had been obviously disturbed. The species has thus been collected in French Guiana from 0 to 750m. Nevertheless, it has been rarely encountered and there are few specimens in recent French Guianan collections. While reporting several species of the Euptychiina hilltopping in the same site in Saül (French Guiana), neither *M. modesta* **comb. nov.**, nor *M. remypignoux* **sp. nov.**, have been observed among them. They were captured a few hundred meters from this hilltop (Benmesbah *et al.* 2018).

Discussion: the specimens which we identified as *M. modesta* **comb. nov.**, from French Guiana completely

agree with the original description and are similar to the lectotype of this species. Distance between French Guiana and Pará state (Brazil) is not excessive and the two regions, being biogeographically continuous, share various species of Satyrinae (*e. g.*, several *Euptychia*, *Pareuptychia* Forster, 1964, *Emeryus*, *Cissia*). Butler also mentions in its description a variety of *E. modesta* without naming it, with “smaller ocelli on ventral surface” from Cameta (also a locality in Pará) in the Bates collection. This latter variety could refer to *M. remypignoux* **sp. nov.**, which is sympatric with *modesta* in French Guiana and flies also in close Pará state. There are two records from the Orinoco Delta in Venezuela (A. Neild, pers. comm.), and we examined some other specimens very similar to *M. modesta* from Venezuela, Brazil, Peru, Colombia, Panama and Belize. There is some variation in the ventral color, size of the ocelli on VHW, shape, distance to margin and width of the submarginal line on VHW. Unfortunately, we did not have this material to hand to compare specimens directly and appreciate the subtle differences that could occur. Two males (1 from Panama and 1 from Belize) did not show consistent differences in the male genitalia when compared with those from French Guiana. There are probably other similar, cryptic species, such as *M. remypignoux* **sp. nov.**, herein described. The study of different populations of this widely distributed complex is beyond the scope of this work and would require larger number of samples, accurate locality data, numerous dissections and DNA comparative studies.

Modestia gomezi (Singer, DeVries & Ehrlich, 1983),
comb. nov.
(Figs. 14a-14j)

Type material: HOLOTYPE male: /Holotype/Costa Rica/Rothschild Bequest, B.M. 1939-1/*Cissia gomezi* det. P. J. DeVries/BMNH(E) #806407/; PARATYPES (all from Costa Rica): 2 males, same data as holotype; 1 female, Parque Nacional Corcovado, Osa Peninsula, Sirena, ex. larva 24 Sept. 1980 [NHMUK] (examined).

Redescription: Male (Figs. 14a-14b): FWL: 21-22 mm (2 specimens), average 21.5 mm. DFW: background brown uniform. VFW: ground color light brown; submedian and median lines thick, color ferruginous brown; submarginal band dark brown, well defined from costa to 2A-Cu2; only one small black ocellus circled by a yellowish ring in the apex in M1-M2 with one small white pupil; submarginal line dark brown thinner, scalloped, running from radius to inner margin, pointing distally in M1 to 2A; marginal line straight, thinner, parallel and close to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observ-

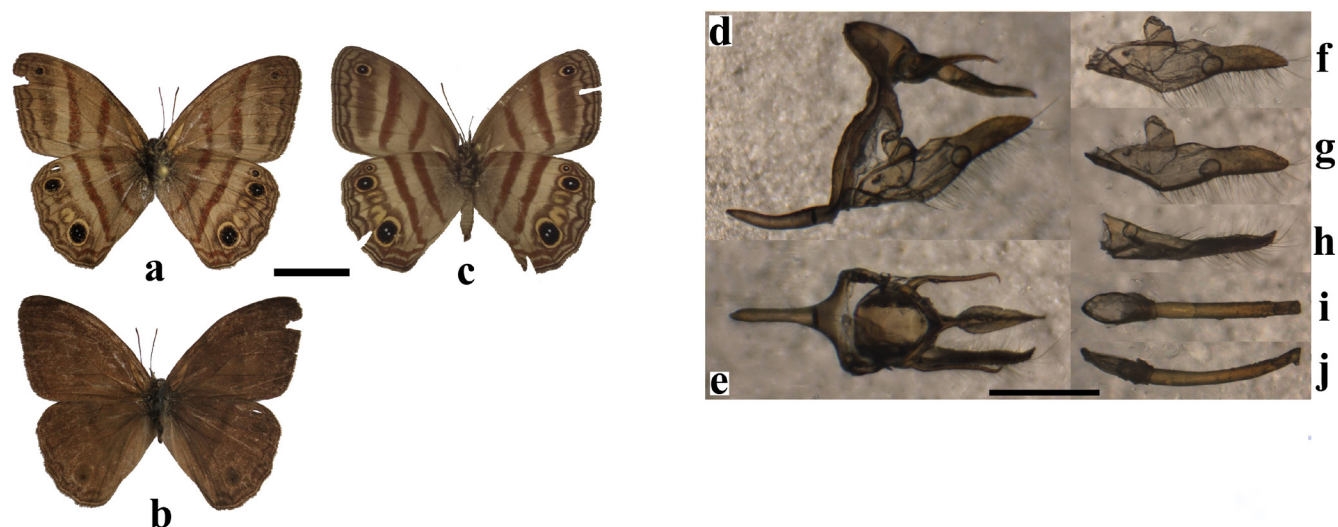


Figure 14. *Modestia gomezi* comb. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. Male genitalia lateral view; e. *idem* dorsal view; f. Valva lateral inner view; g. *idem* lateral outer view; h. *idem* dorsal view; i. Aedeagus dorsal view; j. *idem* lateral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

able through translucent wing; thin marginal area outside marginal line lighter near tornus; ocellus Cu1-Cu2 barely visible. VHW: ground color same as VFW; median and submedian lines thick, ferruginous brown; median line joining anal margin with a marked angulation; submarginal line thinner, scalloped, basally convex from M1-M2 to Cu2-2A; marginal dark line thin, parallel to outer margin from costa to tornus, thicker in Cu2-2A; submarginal area with five ocelli, one in each space between Rs and Cu2, which external counter touching adjacent veins, ocellus in Cu1-Cu2 larger, well defined with two tiny white pupils, ocellus in M1-M2 smaller and ocellus in M2-M3 even smaller, well defined, centered by one white pupil, ocelli in M2-M3 and M3-Cu1 less defined, lacking black central area and white pupils; all ocelli surrounded by irregular thin brown area.

Female (Fig. 14c) – FWL: 22 mm (1 specimen). Similar to male on ventral surface (dorsal surface not examined).

Male genitalia (1 dissected) (Fig. 14d-14j): chitinized structures of the genitalia show the characteristic features for the genus: globular and short tegumen, long lanceolate uncus, subunci straight, stylized, as long as the digitiform saccus. Valvae in this species are characterized by a continuous ampullar (dorsal) ridge, convex, with tiny irregular denticles; aedeagus slightly curved upwards.

Female genitalia: not examined.

Variation: the specimens examined showed only slight variation in wing pattern.

Diagnosis: *M. gomezi* comb. nov., differs from all other members of *Modestia* gen. nov., by having: 1. the wid-

est ocelli on VHW; 2. the widest submedian and median lines on underside; 3. almost no membrane on the distal extremity of the valvae of male genitalia which is more spatulate than in *M. modesta* comb. nov. and *M. remypignoux* sp. nov.

Hostplant: reported by DeVries (1986) as a grass (Poaceae). Early stages described by Singer *et al.* (1983).

Habitat and behavior: we have not observed this species in nature. Museum records show that it ranges from Costa Rica to Colombia through Panama.

Discussion: Singer *et al.* (1983) defined the “*Cissia confusa*-species group” mainly on the basis of early instar morphology and divided it into 4 subgroups. They assigned *M. gomezi* comb. nov., to one of these subgroups, of which it was the only representative. They pointed out the differences observed with respect to other species of the “*Cissia confusa*-species group”: larval head, pupae shape, and adult hindwing ocelli in Rs-M1 and M1-M2 with only one pupil each. As discussed above, ocellar pattern is in our view diagnostic at generic level. These differences support our decision to remove *gomezi* from that species-group and transfer it to *Modestia* gen. nov. Furthermore, DNA comparative analysis shows that *M. gomezi* is evidently closer to *M. modesta* comb. nov. (95.9% similarity), than to ‘*Cissia*’ *myncea* (91.4% similarity) (Tables 1 and 2).

Material examined: 3 males (1 dissected), 2 females: COLOMBIA (1 male): Antioquia: Porce 800m, 27.VIII.2017 1 male (MB-0258*) [MB]; PANAMA (1 male, 1 female): Zona del Canal: Cocolí, 06.IV.1987 1 male (photograph) and 28.XII.1986 1 female (photograph) [JMD]; COSTA RICA (1 male, 1 female): 1 male

(holotype) no precise locality (photograph) [NHMUK];
1 female Parque Corcovado-Sirena (photograph).

Modestia remypignoux Benmesbah & Viloria, sp. nov.

(Figs. 15a-15m)

<http://zoobank.org/urn:lsid:zoobank.org:act:DC4CBBA5-0DA9-4DB7-8682-315391AAFBAD>

Type material: HOLOTYPE male (Figs. 15a-15b): / French Guiana, Maripasoula, Antecume Pata, 13.III.2012/ Holotype of *Modestia remypignoux remypignoux* Benmesbah & Viloria, 2020/MB-0039*/ [MB]; PARATYPES: 9 males (4 dissected), 13 females (3 dissected) (all from FRENCH GUIANA): Kaw: Dégrad Escolle, 14.XI.2011 1 male (MB-0041*) [MB] and 1 female (MB-0047*) [MB]; Kaw pk 8 17.IX.2010 1 female (MB-0053*) [MB]; Grand Santi: 16.V.2012 1 female (MB-0055*) [MB]; 18.V.2012 1 female (MB-0355) [MB]; Kourou: Montagne des Pères 22.VI.2012 1 male (MB-0042) [MB]; 31.I.2013 1 male (MB-0040*) [MNHN]; Macouria: Matiti 18.VIII.2012 2 females (MB-0049) [MB], (MB-0054) [MIZA]; Maripasoula: Antecume Pata 13.III.2012 2 females (MB-0048*, MB-0050) [MB]; Talwen 15.III.2012 1 male (MB-0045*) [MB]; Matoury: Rochambeau 20.XII.2008 1 male [LCB]; 29.VIII.2009 1 female [LCB]; Rémire: Dégrad des Cannes 06.XI.1988 2 males [LCB]; Saint-Laurent-du-Maroni: 07.VI.1992 1 male [LCB]; 24.X.2011 1 female (MB-0051) [AN]; 19.I.2012 1 male (MB-0044) [MIZA], 1 female (MB-0052) [IVIC]; Ouanary II.2019

1 female (MB-0371) [MB]; Sinnamary: pk 17 D21 1 female 06.IX.2009 [LCB].

Description: Male (Figs. 15a-15b): FWL: Holotype 21 mm, 21–23 mm (7 specimens), average 21.9 mm. DFW: background light brown uniform. VFW: ground color light greyish brown; submedian and median lines thin, ferruginous brown, median line curved outwards, and basally concave in Cu2-2A; submarginal band thin, dark brown, discreet; submarginal area with three small ocelli, one black, circled by a yellowish ring in the apex in M1-M2, with one small white pupils, two others even smaller, less defined in M2-M3 and M3-Cu1; submarginal line thinner, dark brown, scalloped, pointing distally in R5 to 2A; marginal line straight, of same width, parallel and close to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; median and submedian lines thin, ferruginous brown, discreetly irregular; median line joining anal margin making a double angulation; submarginal line thinner, scalloped, pointing distally in M1 to 2A; marginal dark line thin, parallel to outer margin from costa to torus, thicker in Cu2-2A; submarginal area with five small ocelli almost of same size, one in each space between Rs and Cu2, ocellus in Cu1- Cu2 slightly bigger, well defined, with two tiny white pupils, ocelli in M2-M3 and M3-Cu1 with one or two apparent pupils, ocelli in Rs-M1 and M1-M2 centered by one white pupil; thin brown area surrounding all ocelli.

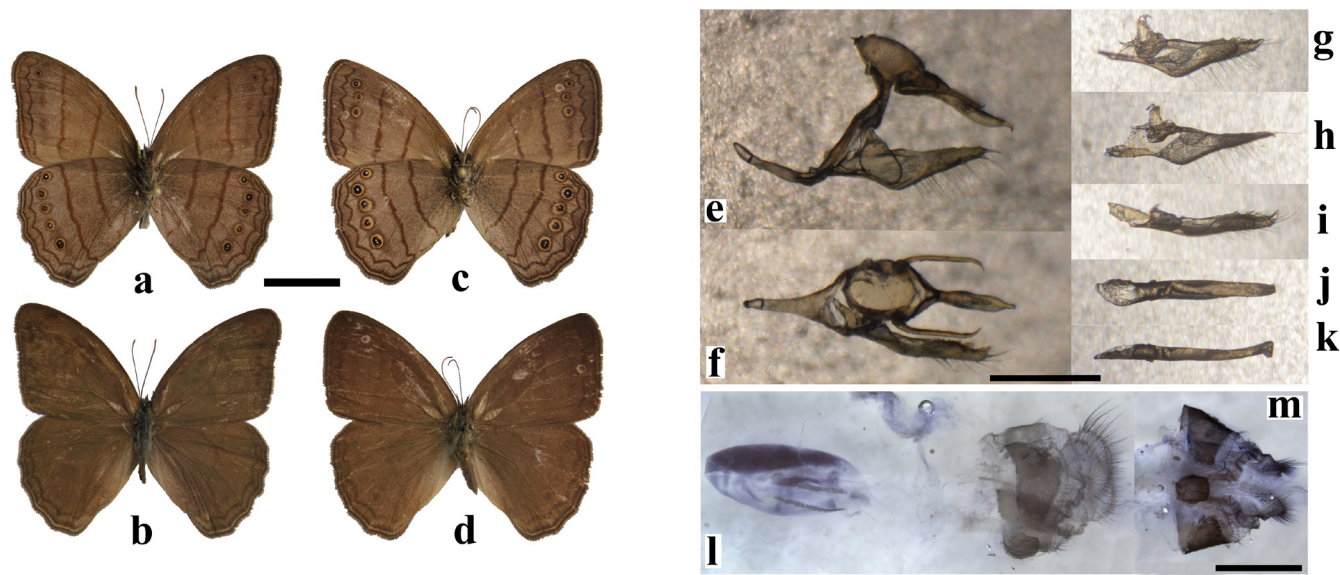


Figure 15. *Modestia remypignoux remypignoux* sp. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. *idem* dorsal; e. Male genitalia lateral view; f. *idem* dorsal view; g. Valva lateral inner view; h. *idem* lateral outer view; i. *idem* dorsal view; j. Aedeagus dorsal view; k. *idem* lateral view; l. Female genitalia lateral view; m. *idem* ventral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

Female (Figs. 15c-15d) – FWL: 19–22 mm (8 specimens), average 20,1 mm. Similar to male but differs from it by the more rounded shape, underside slightly lighter and greyish, ocelli on ventral side a little bit wider.

Male genitalia (5 dissected) (Figs. 15e-15k): very similar to that of the preceding two species, but uncus rectangular and regular, saccus is not as digitiform (more conical); the valvae closer in shape to those of *M. modesta* **comb. nov.**, but with an indented ampullar ridge and lacking the notch. Aedeagus straight and shorter.

Female genitalia (3 dissected) (Figs. 15l-15m): similar to that of *M. modesta* **comb. nov.**

Diagnosis: *M. remypignoux* **sp. nov.**, can be differentiated from *M. modesta* **comb. nov.**, by the following characters: 1. ocelli on VHW almost of equal size and smaller than in *M. modesta* **comb. nov.**; 2. submarginal line more distant from marginal line on VFW and VHW than in *M. modesta* **comb. nov.**; 3. median line on VHW making a double angulation when joining the anal margin, whereas it is almost straight in *M. modesta* **comb. nov.**; 4. uncus rectangular and regular instead of tapered in *M. modesta* **comb. nov.**; 5. distal extremity of the valvae more regular, with less membrane than in *M. modesta* **comb. nov.** *M. remypignoux* **sp. nov.**, is differentiated from *M. remypignoux shueyi* **ssp. nov.**, under this taxon. For differences with *M. gomezi* **comb. nov.**, see under that species.

Etymology: we name this species in honor of our friend Doctor Rémy Pignoux, French physician and naturalist in love with nature in general and birds in particular, who has been living in French Guiana for decades, still providing constant devoted care to the populations of the Maroni river and instilling great ethical values to his young doctoral students. *Modestia remypignoux* is a masculine noun in apposition.

Hostplant: unknown to us.

Habitat and behavior: *M. remypignoux* **sp. nov.**, was observed on several occasions in French Guiana. Its behavior is typical of the Euptychiina (see under *M. modesta* **comb. nov.**). The species is widespread all over the country and present in different types of habitat, from primary to secondary forest, near human habitation and patches of low forest within savannah. *M. remypignoux* **sp. nov.**, is described from French Guiana, but it is likely to be more widespread in similar habitats in the Amazonian region.

Discussion: *M. remypignoux* **sp. nov.**, is sympatric with *M. modesta* **comb. nov.**, in French Guiana. This species has been collected before and was known to local entomologists. Brévignon (2008) who provided important knowledge on the French Guianan butterfly fauna identified this species as *Magneuptychia modesta* and provided a picture of the male and its genitalia. At that time Brévignon (pers.

comm.) considered the specimens of *M. remypignoux* **sp. nov.**, to agree with the syntype of *Euptychia modesta*, of which he examined photographs. He studied a single female of *M. modesta* **comb. nov.**, in the collection of Père Barbotin captured in Saül in September 1961, but did not notice the difference with *M. remypignoux* **sp. nov.** In fact, true *M. modesta* **comb. nov.**, is much more rarely encountered than *M. remypignoux* **sp. nov.**, in French Guiana, and larger series of this species were only very recently collected there, which allowed clearly separation of these two species. In a more recent work, *M. modesta* **comb. nov.**, was erroneously identified by Brévignon & Benmesbah (2012) as *Magneuptychia alcinoe*.

Apart from *M. modesta* **comb. nov.**, the species superficially closer to *M. remypignoux* **sp. nov.**, is *Neonympha sylvina* C. Felder & R. Felder, 1867, which was dubiously placed in the genus *Paryphthimoides* (Lamas 2004). Following the original description, it was described from at least two specimens (a male and a female) from Bahia (Brazil), and no illustration was provided by the authors. A single syntype (probably a male) is known, hosted in the NHMUK (Fig. 12b). Because of the possible presence of at least 2 syntypes and the close habitus shared by different taxa in this group, for the purpose of nomenclatural stability, we fix here the identity of *Neonympha sylvina* and designate as LECTOTYPE of this taxon the specimen with the following labels (Fig. 12b): /*Neonympha sylvina* Feld./Bahia Luschnatt type/FELDER COLLⁿ/Type/Type of *N. sylvina* Feld, very near *E. modesta*. Butl/*Sylvina* n./Rothschild Bequest B.M.1939-1/ [NHMUK]. We did not have access to this specimen to perform dissections. To date we are not aware of the existence of another syntype. In the original description the male presents ventral surface ocelli with one pupil, and this corresponds with the syntype which presents a unique pupil in ocellus Cu1-Cu2 on VHW. On the other hand, the female description mentions a trace on DHW (presumably in the tornus) of a bipupillate ocellus, which should correspond to a VHW ocellus in Cu1-Cu2 with two pupils. As discussed above the number of pupils appears to be a discriminating supraspecific character not just in *Modestia* **gen. nov.** and *Malaveria* **gen. nov.**, but also in other genera of the Euptychiina. Plausible morphogenic mechanisms leading some specimens to present a single pupilled VHW ocellus in Cu1-Cu2 are also discussed above (Figs. 9a-9f). Actually, some specimens (of both sexes) of *N. sylvina* from northeastern and mid-western Brazil presenting single pupils have been found at DZUP and ZUEC collections. These specimens agree with the lectotype of *N. sylvina* (T. Zacca pers. comm.). Although it is possible that the lectotype of *N. sylvina* represents an aberrant individual (*i.e.*, with sin-

gle pupil in the Cu1-Cu2 VHW ocellus), it is more likely to be a valid species, probably belonging to a different genus. A deeper study of this taxon (Zacca *et al.* in prep.) should confirm this hypothesis.

Notwithstanding, the examination of the lectotype of *N. sylvina* and three additional specimens (2 males and 1 female, courtesy of T. Zacca) shows at least three additional differences compared with *M. remypignoux* sp. nov.: 1. ocelli in M3-Cu1 and Cu1-Cu2 on VHW are much less defined in *N. sylvina* than in *M. remypignoux* sp. nov.; 2. ocellus in M3-Cu1 is more ovoid in *N. sylvina* than in *M. remypignoux* sp. nov.; 3. median line on VFW is straight in Cu2-2A in *N. sylvina* and neither curved outwards nor basally concave as in *M. remypignoux* sp. nov. Finally, *N. sylvina* is described from Bahia, which is more than 2,500 km from French Guiana, and both territories represent two different areas of endemism for butterflies, comprising various different species of the subtribe Euptychiina (for instance, *Euptychia atlantica* Nakahara & Freitas [in Nakahara *et al.* 2017], *Godartiana amadoi* Paluch, Zacca & Freitas [in Zacca *et al.* 2016], for the Bahia region; T. Zacca pers. comm.). Based on what precedes we treat *M. remypignoux* sp. nov., as a different taxon from *N. sylvina*.

We examined several similar specimens from various locations in Brazil, Peru and Ecuador. We noticed some consistent differences, although subtle, in wing pattern and genitalia. The study of these specimens is beyond the scope of this paper and the only other taxon we describe here is a subspecies of *M. remypignoux* sp. nov., from Central America. More comprehensive morphological studies and molecular analyses are likely to reveal several cryptic species (Zacca *et al.* in prep.).

Modestia remypignoux shueyi Benmesbah & Viloria,
sp. nov.

(Figs. 16a-16i)

<http://zoobank.org/urn:lsid:zoobank.org:act:99ACCD73-0E4E-4FA9-B3F1-33FE91C4C7DC>

Type material: HOLOTYPE male (Figs. 16a-16b): / Belize, Cayo Dist., Baldy Beacon- 3,5km SSW - 1F5231 logging road in pine/oak, 750m, 23.IX.2016, J. Shuey - P. Labus, coll./Holotype of *Modestia remypignoux shueyi* Benmesbah & Viloria, 2020/MB-0143/ [MB]; PARATYPES (8 males, all from Belize): same data 1 male (MB-0144) [MB] and 4 males [JS]; same data 700m, 24.IX.2016 1 male [JS]; same data 750m, 24.IX.2016 2 males [JS].

Material examined (not included in the type series): 6 males (3 dissected).- PANAMA: Colón: Cerro Santa Rita, 225m, 08.I.1987 1 male (MB-0216*) [MB] and

1 male (photograph) [JMD]; 245m, 18.II.2014 1 male (MB-0213); Cocle: El Valle, 600m, 22.VIII.2015 1 male (photograph) [JMD]; 800-850m, 02.IV.1987 1 male (MB-0214*) [MB]; Gatun, West Creek trail, 30.XII.1985 1 male (MB-0215*) [MB].

Description: Male (Figs. 16a-16b): FWL: Holotype 22 mm, 21–22 mm (2 specimens), average 21.5 mm. Male similar to *M. remypignoux* sp. nov., but differs in having a darker ground color on both sides and ocelli M2-M3 and M3-Cu1 on VHW less defined, lacking the black central area and the pupils.

Female: not examined.

Male genitalia (5 dissected) (Figs. 16c-16i): similar to *M. remypignoux* sp. nov., in the 2 specimens examined.

Female genitalia: not examined.

Variation: there is slight variation in the size of the ocelli on VHW in the specimens examined.

Diagnosis: subspecies *shueyi* is very similar to the nominal subspecies, nevertheless it differs from it by the darker ground color and the less defined ocelli on VHW in M2-M3 (which is elongated) and M3-Cu1 (well defined black ocelli centered by white pupil in *M. r. remypignoux* sp. nov.). For differences with *M. modesta* comb. nov., see under *M. r. remypignoux* sp. nov. For differences with *M. gomezi* comb. nov., see under that species.

Etymology: dedicated to John Shuey, a North-American entomologist who is passionately keen on the Hesperriidae and butterfly fauna of Belize. He collected all the specimens of the type series. The Latinized subspecies name *shueyi* is a masculine noun in the genitive case.

Host plant: unknown.

Habitat and behavior: comments regarding habitat and behavior are directly quoted from J. Shuey who collected all the specimens of the type series. "The locality is located at ~ 16° 58' 37" x 88° 46' 34" and is a narrow ridgeline that descends from approximately 900m altitude to 600m. In totality, this ridgeline supports a complex ecotonal habitat, transitioning from short-statured, open grassland at 900m to pine dominated forest on eastern facing ridge lines and steep slopes. Immediately downslope, riparian broadleaf shrubs line the adjacent stream bottoms and adjacent slopes. A dirt logging road follows the ridgeline southward, ultimately descending into broadleaf rainforest in the Sibun River Valley 4km to the south. At the type locality, the ridge line is very narrow and supports pine woodlands with riparian scrub immediately downslope along stream bottoms. This species is very localized in Belize, and known only from the type locality. Even here, they were found at only two places along the trail in two days collecting, and were common at only one of the sites. Only males were observed, flying very rapidly upslope

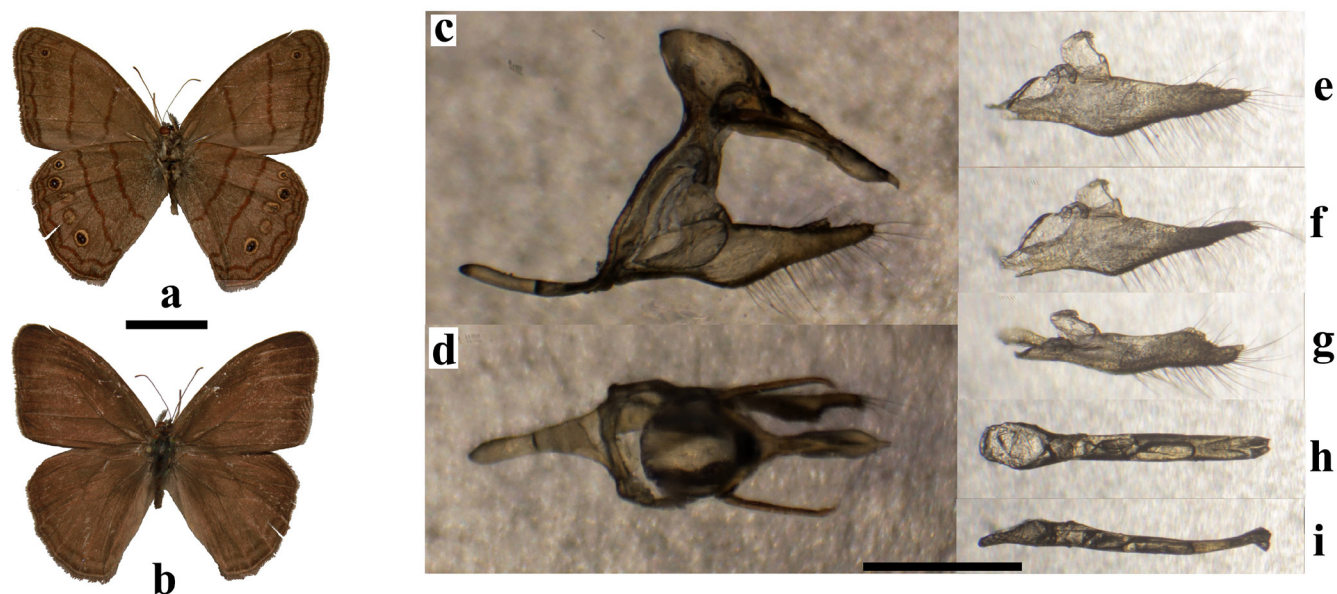


Figure 16. *Modestia remypignoux shueyi* ssp. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Male genitalia lateral view (one valva removed); d. *idem* dorsal view; e. Valva lateral inner view; f. *idem* lateral outer view; g. *idem* dorsal view; h. Aedeagus dorsal view; i. *idem* lateral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

through dense vegetation, and then briefly along the ridge-line before descending back downslope. They appeared to be “hill topping” in search of mates and they were not observed resting on any vegetation. Because of their rapid flight and because they fly through, not around, dense vegetation, specimens were difficult to capture. However, they generally followed set paths along the road edge that allowed a few individuals to be netted while in flight.”

We have records from Belize and Panama suggesting this subspecies probably ranges through a great part of Central America.

Discussion: the characters that differentiate the two subspecies are stable in the specimens we examined (16 specimens of *shueyi* ssp. nov. and 22 of ssp. *remypignoux* sp. nov.). Although the study of male genitalia did not evidence differences, DNA comparative analysis showed the two specimens from Belize to slightly group apart from those of *M. r. remypignoux* sp. nov. with 98.6% similarity (Tables 1-2). This is likely to agree with a subspecific genetical distance. Finally, important geographical distance separate these two taxa belonging to two different areas of endemism for butterflies. For these reasons we treat this population as a subspecies of *M. remypignoux* sp. nov. Specimens from Belize represent the westernmost sample we could examine. Six other specimens from Panama (3 dissected) similar to *shueyi* ssp. nov., were also identified as this subspecies. We did not include them in the type series because of the distance separating them from the type locality. As it was said for the nominal subspecies,

we examined various specimens from Brazil, Peru and Ecuador that probably represent undescribed new taxa.

Malaveria Viloría & Benmesbah, gen. nov.

Malaveria nebulosa (Butler, 1867), comb. nov.
(Figs. 17a-17l)

Type material: LECTOTYPE male: /Venezuela/Venezuela Pur. from Dyson 47-9/[NHMUK] (examined).

Material examined: 92 males (8 dissected), 46 females (2 dissected).- VENEZUELA, Miranda: Altos de Pipe, IVIC 1,650m 22.VI.2012 1 male (MB-0338*); 18.IX.2013 2 males (MB-0336*, MB-0341*); 19.IX.2013 1 male (MB-0333*); 25.X.2017 1 male (MB-0339) and 21.V.2012 1 female (MB-0337); 22.VI.2012 1 female (MB-0332); 31.X.2012 1 female (MB-0331); Guaicai-puro, El Jarillo, Quebrada Honda 1,300m, 23.VII.2013 2 males (MB-0002, MB-0006*); 1,700m, 23.VII.2013 1 male (MB-0003); 05.VIII.2013 1 male (MB-0004*); 1,200m 12.VIII.2013 1 male (MB-0334*); 26.VIII.2013 1 male (MB-0007*) and 05.III.2013 3 females (MB-0335, MB-0340, MB-0342); 06.III.2013 2 females (MB-0001*, MB-0005*)[MB]; Altos de Pipe, IVIC 1,650m 30.VI.2011 2 females; 30.VII.2011 1 female; 22.VI.2012 2 males, 2 females; 29.VI.2012 1 male, 2 females; 30.VI.2012 1 female; 30.VII.2012 2 males, 1 female; 31.VII.2012 1 male; 23.VIII.2012 1 male; 24.VIII.2012 3 males, 5 females; 25.VIII.2012 1 male; 31.VIII.2012 1 male;

11.IX.2012 1 male; 16.IX.2012 2 males; 17.IX.2012 3 males; 29.IX.2012 2 males, 1 female; 15.X.2012 1 male; 17.X.2012 1 male; 19.XI.2012 1 male; 21.XI.2012 3 males; 22.XI.2012 2 males; 23.XI.2012 5 males, 2 females; 24.XI.2012 2 males; 6.XII.2012 2 males; 7.XII.2012 1 male; 8.XII.2012 1 male; 15.I.2013 1 male, 1 female; 16.I.2013 1 male, 1 female; 17.I.2013 2 males; 9.II.2013 2 males; 10.II.2013 2 males; 16.II.2013 1 male, 2 females; 17.II.2013 2 males; 17.IV.2013 2 males; Guaicaipuro, El Jarillo, Quebrada Honda 1,300m, 6.VIII.2013 18 males, 4 females; 3.IV.2013 2 males, 1 female; 30.V.2013 3 males; 22.VII.2013 4 males, 3 females; 23.VII.2013 3 females; 26.VIII.2013 2 females; 14.IX.2013 1 male; 15.IX.2013 1 male; 30.X.2013 4 females; 31.X.2013 1 female [IVIC].

Redescription: Male (Figs. 17a-17b): FWL: 20-22 mm (11 specimens), average 21 mm. DFW: background dark brown uniform. VFW: ground color dark brown; submedian and median lines thin, color darker ferruginous brown, median line curved outwards in Cu2-2A, submedian line slightly wavy; submarginal area with one small black ocellus in the apex, circled by a yellowish ring in M1-M2 with two tiny white pupils; submarginal line of same width than median line, more scalloped at the apex, pointing distally in R5 to 2A; marginal dark line thin and straight, parallel and close to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; median and submedian lines of same width and color as on VFW, submedian line a little irregular, median line more irregular, curved to the base when

passing through the cell, making a slight angulation when joining anal margin; submarginal line of same width and color, scalloped, composed by straight adjacent segments, pointing distally in M1 to 2A; marginal dark line thin, scalloped, parallel to outer margin from costa to tornus; submarginal area with five ocelli, one in each space between Rs and Cu2, ocelli in M1-M2 and Cu1-Cu2 larger, of same size, black circled by a yellowish ring, each with two small white pupils, ocelli in M2-M3 and M3-Cu1 smaller, without black in the center, less defined, ocellus in Rs-M1 very small.

Female (Figs. 17c-17d) – FWL: 19-21 mm (8 specimens), average 20,4 mm. Similar to male but differs from it by the more rounded shape, both sides slightly lighter.

Male genitalia (8 dissected) (Figs. 17e-17k): the entire structure robust; tegumen globular, well differentiated from uncus, which is one and a half times longer than tegumen, lanceolate, but shorter than in the species of *Modestia gen. nov.*; subunci about same length as tegumen, slightly sinuous in upper view; saccus tubular, broad at base in the joint with vinculum; valvae well developed, elongated, ending in a digitiform extreme, slightly hooked, with a prominent horn-like process at tip and another one half way the narrowing of the valva, both pointing inwards; aedeagus as long as valva, as thick as saccus.

Female genitalia (2 dissected) (Fig. 17l): externally similar to that of the species of *Modestia gen. nov.*, papillae anales well developed, setose; corpus bursae bearing two very well developed signa along three quarters of its length.

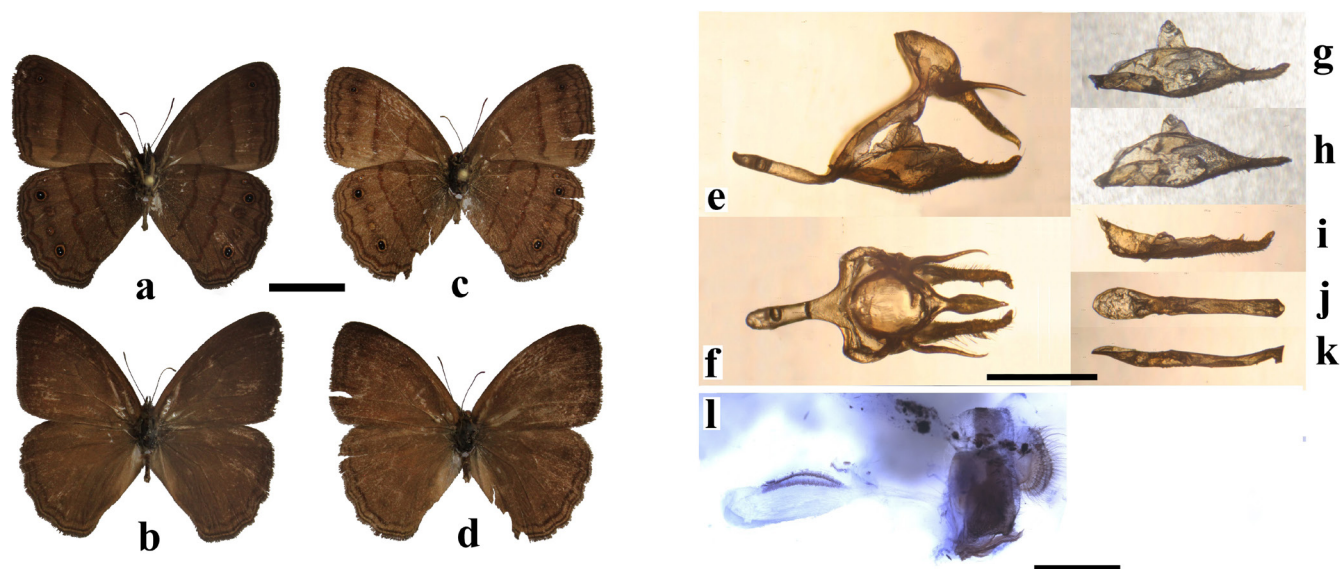


Figure 17. *Malaveria nebulosa* comb. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. *idem* dorsal; e. Male genitalia lateral view (one valva removed); f. *idem* dorsal view; g. Valva lateral inner view; h. *idem* lateral outer view; i. *idem* dorsal view; j. Aedeagus dorsal view; k. *idem* lateral view; l. Female genitalia lateral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

Variation: all specimens examined show very stable wing pattern.

Diagnosis: *M. nebulosa* **comb. nov.**, differs from the other species treated here (except *M. duponti* **sp. nov.**, for which character one is different) by: 1. darker ground color; 2. tiny ocelli on VHW; 3. markedly irregular wavy median line on VHW, typically curved basally when passing through the discal cell; 4. distal extremity of the valvae thin without membranous extension, presence of a spiny proximal inner projection on the distal portion of the valvae. For differences with *M. duponti* **sp. nov.**, see under this species.

Hostplant: unknown.

Habitat and behavior: similar to other euptychiines of the same size (see *M. modesta* **comb. nov.**). This species is restricted to the Cordillera de la Costa in northern Venezuela.

Discussion: Nakahara *et al.* (2015) discuss the taxonomic status of *M. nebulosa* **comb. nov.**, and although they compared it to different species then identified under *Magneuptychia alcinoe*, we agree with their ideas. They treated *Magneuptychia nebulosa* as a *bona fide* species, comparing it with the assumed variable *M. alcinoe* and *M. mimas*, and they designated the lectotype for this species. In fact, as this study shows, several different species have been considered as *M. alcinoe* (see under *Malaveria alcinoe* **comb. nov.**) and represent a complex group of different species. All specimens examined of *M. nebulosa* **comb. nov.**, showed a remarkably stable habitus with almost no variation. Being an endemic to the Cordillera de la Costa in northern Venezuela, it is geographically isolated from other species of *Malaveria* **gen. nov.** (Nakahara *et al.* 2015), and is the only representative of this genus in this area (Viloria pers. obs.). The closest record of a member of the “*alcinoe*-complex” is in Lara state in the northern part of the Cordillera de Mérida, and corresponds to *M. alcinoe* **comb. nov.**, where *M. nebulosa* **comb. nov.**, has not been recorded. Furthermore, in our DNA comparative analysis, the 6 specimens of *M. nebulosa* **comb. nov.**, clearly grouped apart from the other species of the genus. The wavy median line and the tiny ocelli on VHW of *M. nebulosa* **comb. nov.**, are reminiscent of the geographically distant *M. duponti* **sp. nov.** (see under this taxon), but the 2 taxa seem not to be so close, as their molecular divergence is 6.8%. In fact, the similar shape of the distal extremity of the valva and the closer similarity ratio in the molecular fragment analyzed (98.6%) support the hypothesis that *nebulosa* and *alcinoe* are closer to each other than to the remaining species of the “*alcinoe*-complex”. Finally the FW venation of *M. nebulosa* **comb. nov.**, presents a particular character also shared by *M. alcinoe* **comb. nov.**, and not

encountered in the other species of *Malaveria* **gen. nov.**: the origin of R2 is distal to the bifurcation between r2-5-m1 and r1-r2 (Fig. 4).

Malaveria mimas (Godman, 1905), **comb. nov.**
(Figs. 18a-18i)

Type material: SYNTYPE Male: /Type H.T./♂/Type of Species./Coroico. 6500ft., Bolivia. Garlepp./B.M. TYPE No. Rh3225. *Euptychia mimas*, Godm./B.M.(N.H) Rhopalocera Slide No. 16843./T.G.H. 1953. 16./Godman-Salvin Coll. 1904.-1. *Euptychia mimas*, Godm./BMNH(E) #983007/ [NHMUK] (examined).

Material examined: 6 males (6 genitalia dissected*).- BOLIVIA (4 males): La Paz: Caranavi 4 males (MB-0010*, MB-0011*, MB-0012*, MB-0013*) [MB].- PERU (2 males): Cusco: Cusco, carretera Manu 800-2900m, October 2015 1 male (MB-0014*) [MB]; 2000-3000m, 1908 1 male (MB-12*) [MNHN].

Redescription: Male (Figs. 18a-18b): FWL: 22-25 mm (6 specimens), average 23.5 mm. DFW: background brown uniform. VFW: ground color brown, lighter than upperside; submedian and median lines very thin, darker brown, curved outwards in Cu2-2A; submarginal band dark brown, discreet; submarginal area with one small black ocellus in the apex in M1-M2, circled by a brownish ring with two tiny white pupils; submarginal line of same width as median line, more scalloped at the apex and flattened from M3 to 2A, pointing distally in M2 and M3; marginal dark line thinner and regular, parallel and close to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; median and submedian lines of same width and color as VFW, submedian line making an angulation when joining the anal margin, median line regular joining anal margin without making angulation; submarginal line of same width and color, scalloped, composed by straight adjacent segments, pointing distally from M1 to 2A; marginal dark line thinner, discreetly scalloped, parallel to outer margin from costa to tornus; submarginal area with five ocelli, one in each space between Rs and Cu2, ocelli in M1-M2 and Cu1-Cu2 of same size, well defined, black, circled by a brownish ring, each with two small white pupils, ocelli in M2-M3 and M3-Cu1 of almost same size, less defined without black in the center, ocellus in Rs-M1 very small.

Female: not examined.

Male genitalia (6 dissected) (Figs. 18c-18i): Similar to that of *M. nebulosa* **comb. nov.**, but base of saccus more robust; strong narrowing of the valva in its middle part on lateral view; inner horn-like processes of the valvae more

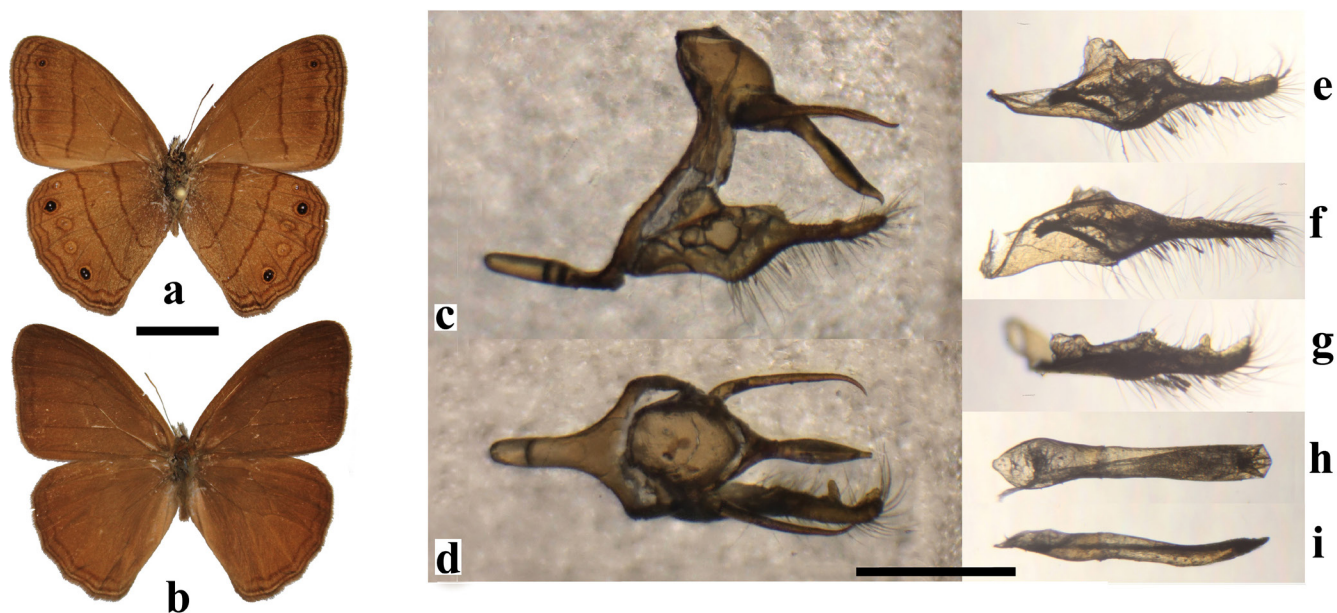


Figure 18. *Malaveria mimas* comb. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Male genitalia lateral view (one valva removed); d. *idem* dorsal view; e. Valva lateral inner view; f. *idem* lateral outer view; g. *idem* dorsal view; h. Aedeagus dorsal view; i. *idem* lateral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

developed and prominent; aedeagus thicker and slightly sinuous in lateral view.

Female genitalia: not examined.

Variation: the 6 specimens examined did not show significant variation in wing pattern. Differences in coloration are discussed below.

Diagnosis: *M. mimas* comb. nov., differs from all the other species treated here by: 1. background brown color lighter, almost coppered in specimens from Bolivia (darker and greyish in specimens from Peru); 2. thinner and more delicate elements of the underside pattern (bigger and wider in most other species); 3. submarginal line on VHW and VFW more flattened and less scalloped (more irregular and scalloped in others); 4. submedian line on VHW angled when joining anal margin (straight in all others); 5. aedeagus short and stocky (proportionally longer and thinner in others); 6. strong narrowing of the valva in its middle part on lateral view giving a markedly angled aspect to its dorsal edge.

Hostplant: unknown.

Habitat and behavior: we did not observe *M. mimas* comb. nov., in the field but its behavior is presumably similar to that of its congeners. Our records range from northern Bolivia to southern Peru.

Discussion: *Euptychia mimas* was described by Godman in 1905 on the basis of 3 specimens from Coroico, La Paz, Bolivia, collected either by Otto or most probably Gustav Garlepp at 6,500 ft. (1,980m). An illustration is

given in the original description and a syntype is hosted in the NHMUK. The type locality is 20 km from where our recent specimens come from, in Bolivia. They fully correspond with the original description. The discriminating characters in the habitus listed above that differentiate *M. mimas* comb. nov., from other species of *Malaveria* gen. nov, are clearly evident in the original illustration and in the syntype. Nakahara *et al.* (2015) discussed the possible conspecificity of *M. mimas* with *M. alcinoe*. In this work we have been able to distinguish between what those authors considered to be variations of *M. alcinoe* comb. nov., and stable wing patterns that we have assigned to different species (see below). We treat here *M. mimas* comb. nov., as a *bona fide* species based on the differences in habitus (see diagnosis), the differences in male genitalia (mainly the aedeagus), wing venation (see under *M. alcinoe* comb. nov.) and DNA sequence analyses in which the specimens identified as *M. mimas* (3 from Bolivia and 1 from Peru) clearly stand apart from other species of the “*alcinoe*-complex”. From the latter point of view, the closest representative of the “*alcinoe*-complex” is *M. ballofi* sp. nov., sharing 95.9% similarity, whereas in *M. alcinoe* comb. nov., this is only 93.3%. Furthermore, *M. mimas* comb. nov., seems to be restricted to Bolivia and southern Peru, at least. We are not aware of the presence of *M. alcinoe* comb. nov., or close similar species in southern Peru or in Bolivia. The ranges of the “*alcinoe*-complex” and *M. mimas* comb. nov., seem not to overlap, but the study of more material

from these areas is needed to confirm this hypothesis. We examined two specimens from Peru. Both are from Cuzco, one recently collected (2015), the other, much older (collected in 1908). The former differs from the specimens we examined from Bolivia by its clearly darker coloration, while the latter shows similar coloration. Godman in his description mentioned the ground color (probably of the upperside) as dark-brown and the underside paler. The illustration seems to present a darker specimen than the series we examined from Bolivia and the syntype hosted in the NHMUK. It is likely that these differences in coloration are simply related to the age of the specimens and do not represent a strong diagnostic character to differentiate populations within the species.

Malaveria alcinoe (C. Felder & R. Felder, 1867),
comb. nov.
 (Figs. 19a-19m)

Type material: *Neonympha alcinoe* C. Felder & R. Felder: LECTOTYPE male (Fig. 12c): /Type/FELDER COLL^N./*Alcinoë* Feld./Rothschild Bequest B.M. 1939-1./Type of *N. alcinoe* Feld? = *E. benedicta*, Butl. of w. it. may be a good local form. Comp. w. type *E. benedicta* Butler./BMNH(E)1266958/[NHMUK] (examined); *Euptychia benedicta* Butler: SYNTYPE female (Fig. 12d): /Type H.T./Type of Species./*E. benedicta* Butler type./B.M. TYPE No. Rh3227. *Euptychia benedicta*, ♀ Butl./Sarayacu, Ecuador. C. Buckley./Godman-Salvin Coll. 1904-1. *Euptychia benedicta*, Butl./BMNH(E)1266955/[NHMUK] (examined).

Material examined: *M. alcinoe* **comb. nov.**: 4 males (1 dissected) and 4 females (1 dissected).- VENEZUELA (2 males, 3 females): Barinas: Barinitas, La Chimenea, La Soledad, 1450m, 24.X.2008 1 male (photograph) [DT]; Táchira: Siberia 1000m, 26/28.X.2008 1 female (photograph) [DT]; Lara: Parque Nacional Yacambú, 13km South Sanare, 15-21.I.1979 1 male (MB-0008*) [MALUZ]; Trujillo: El Boquerón, West of Alto de Escuque 1050-1100m, 17.X.1999 1 female (photograph) [AN]; El Paramito, 7-11km South-West of Escuque 1550-1600m, 18.X.1999 1 female (photograph) [AN].- COLOMBIA (1 male, 1 female): Cundinamarca: Bogota 1 male (BMNH(E) 1205423) [NHMUK]; Colegio 430m, 15.VII.1975 1 female (MB-0009*) [MB].- ECUADOR (1 male): Morona-Santiago: Parque Nacional Sangay, San Isidro 1 male (photograph) (web site : www.sangay.eu). *Malaveria* sp.: 22 males (4 dissected), 1 female.- COLOMBIA (15 males): Cundinamarca: Santa Fé de Bogota 1850 1 male (MB-14*) [MNHN]; Caldas: Samaná, Florencia 1581m, 21.II.2020 1 male (photo-

graph) [ICRM]; Cesar: San Alberto 300m, 14.VI.2017 1 male (MB-0247*) [MB]; Santander: El Hato, Serranía de los Yariguíes 2100m, 25-28.XI.2019 10 males (photograph) [ICRM]; La Mesa-Santos 1500m, 28.XII.2007 1 male (MB-0251*); *No precise locality*: 1 male (MB-11*) [MNHN].- ECUADOR (6 males): Pastaza: Canelos 1 male (BMNH(E) 1205364) [NHMUK]; Morona-Santiago: Parque Nacional Sangay 3 males (photograph) (web site: www.sangay.eu); Tungurahua: Rio Machay 1700m, 04-05.VII.1993 1 male (photograph) [MGCL]; Zamora-Chinchipec: Zamora 3000-4000ft 1 male (BMNH(E) 1025422) [NHMUK].- PERU (1 male, 1 female): Madre de Dios: Parque Manu, Pakitza, 1 male 400m, 06.X.1990 (photograph), 1 female 340m, 04.X.1991 (photograph).

Redescription: Male – (Figs. 19a-19b): FWL: 21-22 mm (3 specimens), average 21.3 mm. DFW: ground color brown uniform. VFW: ground color as upperside; submedian and median lines thin, darker brown, median line slightly curved outwards in Cu2-2A; submarginal area with one small ocellus, black circled by a yellowish ring in the apex in M1-M2 with two tiny white pupils, two other ocelli faded in M2-M3 and M3-Cu1; submarginal line of same width as median line, scalloped from radius to 2A, running from radius to inner margin, pointing distally in M1 to Cu2; marginal dark line thinner and straight, parallel to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; median and submedian lines regular, of same width and color as on VFW, submedian line joining anal margin without making angulation, median line making a curved angulation when joining the anal margin; submarginal line of same color and width, scalloped composed with almost straight adjacent segments, pointing distally from M1 to Cu2; marginal dark line thin, parallel to outer margin from costa to tornus; submarginal area with five ocelli, one in each space between Rs and Cu2, ocelli in M1-M2 and Cu1-Cu2 of same size, rounded, bigger, black, circled by a yellowish ring, with two small white pupils, ocelli in M2-M3 and M3-Cu1 smaller and less defined, without black in the center, with two white pupils, ocellus in Rs-M1 very small, black with two white pupils.

Female – (Figs. 19c-19d): FWL: 20-22 mm (4 specimens), average 21 mm. Similar to male, differs by its more rounded shape. The specimen illustrated presents a more wavy median line and a lighter underside coloration.

Male genitalia (1 dissected) (Figs. 19e-19k): similar to that of *M. mimas* **comb. nov.**, but valvae clearly broader (in lateral view) at basal half, consequently, distal half (digitiform) more differentiated, horn-like inner processes

similar in proportional size to those of *M. nebulosa* **comb. nov.**; aedeagus relatively robust, but notably broad and flat at basal extremity.

Female genitalia (1 dissected) (Figs. 19l-19m): setae of the papillae anales longer than in previous species of *Malaveria* **gen. nov.**; corpus bursae apparently longer than in *M. nebulosa* **comb. nov.**, signa running parallel to each other, reaching only three fifths of the length of the corpus.

Variation: there is slight variation in the size of ocellus Cu1-Cu2 that seems to be slightly wider in the northern part of the range, especially in females.

Hostplant: unknown.

Habitat and behavior: we did not observe *M. alcinoe*, **comb. nov.**, in natural conditions, but its behavior is presumably typical of other similar representatives of the Euptychiina, see *M. modesta*, **comb. nov.** For range distribution see under “Discussion”.

Diagnosis (Figs. 20a-20l): *M. alcinoe* **comb. nov.**, is, together with *M. nebulosa* **comb. nov.**, the smallest species in *Malaveria* **gen. nov.** They differ from *M. bottoi* **sp. nov.**, by: 1. more rounded shape of HW external margin in *M. bottoi* **sp. nov.**; 2. smaller ocelli on VHW that are all of almost same size in *M. bottoi*; 3. more sinuous median line on VHW in *M. bottoi* **sp. nov.**; 4. more flattened submarginal line on VFW and VHW in *M. bottoi* **sp. nov.**

M. alcinoe **comb. nov.** differs from *M. rodriguezii* **sp. nov.** by: 1. smaller ocelli on VHW in *M. rodriguezii* **sp. nov.**; 2. more sinuous median line on VFW and VHW in *M. rodriguezii* **sp. nov.**; 3. the median line on VHW joins the anal margin more straightly and in contact with the submarginal line in *M. rodriguezii* **sp. nov.**

M. alcinoe **comb. nov.** differs from *M. ballofi* **sp. nov.** by: 1. its smaller size (average FWL: 21.3 mm for *M. alcinoe* **comb. nov.** vs. 24.3 mm for *M. ballofi* **sp. nov.**); 2. the dark brown color in fresh specimens of *M. ballofi* **sp. nov.**; 3. proportionally smaller ocelli on VHW in *M. ballofi* **sp. nov.**; 4. the median line on VFW and VHW more sinuous in *M. ballofi* **sp. nov.**; 5. the median line joining the anal margin with a distinct angulation in *M. ballofi* **sp. nov.**, whereas it is curved in *M. alcinoe* **comb. nov.** For differences with *M. nebulosa* **comb. nov.**, and *M. mimas* **comb. nov.**, see under those respective taxa.

Discussion: the taxonomic problem set by the “*alcinoe*-complex” is difficult to solve. Based on differences in the habitus of the imago, DNA analysis results, wing venation and biogeographical inference, we describe here three new species belonging to this group of butterflies with very similar habitus. We hope this comparative study will help clarify the situation and encourage other entomologists to investigate deeper the issue of species limits within this group.

During this study we found that several different taxa have been treated under *alcinoe*, some even belonging to different genera. For example, DeVries (1987) reported *alcinoe* from Costa Rica flying up to 600m and described the imago as presenting double pupilled ocelli on VHW, but the specimen illustrated (pl. 41, fig. 1) presents a unique pupil in ocellus M1-M2, characteristic of *Modestia* **gen. nov.** (in this case, probably *M. r. shueyi* **ssp. nov.**). Lamas (2004) put *E. benedicta* and *E. pamela* in synonymy with *Magneuptychia alcinoe*. We show here that *pamela* is clearly different and belongs to another entity, *Koutalina* **gen. nov.** Later, Brévignon & Benmesbah (2012) erroneously identified true *M. modesta* **comb. nov.**, as *Magneuptychia alcinoe*, which is not present in French Guiana. And more recently, Nakahara *et al.* (2015) considered *M. alcinoe* to be variable regarding the number of pupils in ocellus M1-M2 on VHW, possibly misidentifying specimens belonging to *Modestia* **gen. nov.**, as *M. alcinoe*. This character is very diagnostic at the generic level, as we discuss it here. *Malaveria alcinoe* **comb. nov.**, has been thought to be a widespread and variable species. In fact, based on the data we have, members of the “*alcinoe*-complex” are predominantly inhabitants of semi-montane areas, from 700 to 2,300m elevation. A few records from lower altitudes do exist but are all from the Andean foothills (for example *M. ballofi* **sp. nov.**). These species seem to all be restricted to the Andean slopes from Peru to its northern prolongation in Colombia (Cordilleras Oriental, Central and Occidental) and Venezuela (Cordillera de Mérida). We obtained little data from Peru and Venezuela. It seems replaced in the south by *M. mimas* **comb. nov.**, from southern Peru (Cuzco) and Bolivia, and in the north by *M. nebulosa* **comb. nov.**, in the Venezuelan Cordillera de la Costa. Samples from the Sierra de Perijá and the Sierra Nevada de Santa Marta have not been studied in detail in this work. To date this species-group has not been recorded in the Pantepui region of Venezuela (M. Costa pers. comm.), nor in Brazil or the Guianas.

Colombia is the key region where most of the taxa involved occurs, and a more detailed study has begun to take place (Le Crom *et al.*, in prep.). The difficulty to identify and understand the relationships between them are due to several problems: 1. complexity of the topography, some areas being isolated from each other by high mountains, whereas others are separated by lower elevations that allow butterflies dispersion (such as in the northernmost tips of the Cordilleras Oriental, Central and Occidental) (Fig. 21); 2. intraspecific variability of the habitus: sometimes difficult to assess and sort out pertinent diagnostic characters, larger series of specimens with precise locality data are needed and they are currently not easily available;

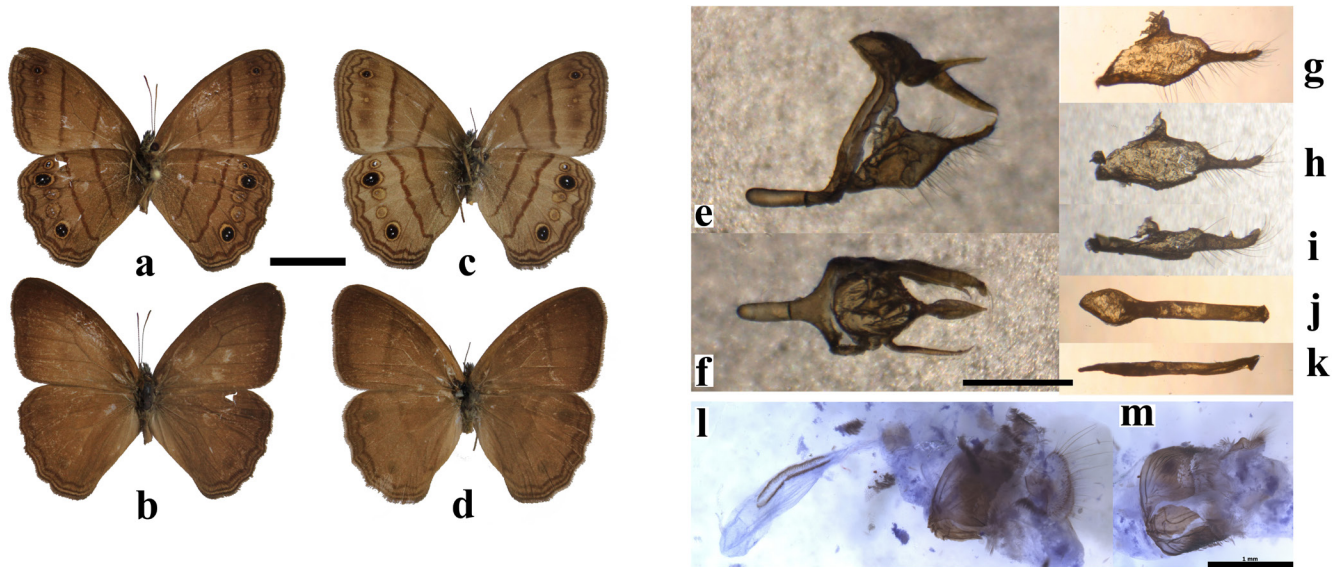


Figure 19. *Malaveria alcinoe* comb. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. *idem* dorsal; e. Male genitalia lateral view (one valva removed); f. *idem* dorsal view; g. Valva lateral inner view; h. *idem* lateral outer view; i. *idem* dorsal view; j. Aedeagus dorsal view; k. *idem* lateral view; l. Female genitalia lateral view; m. *idem* ventral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

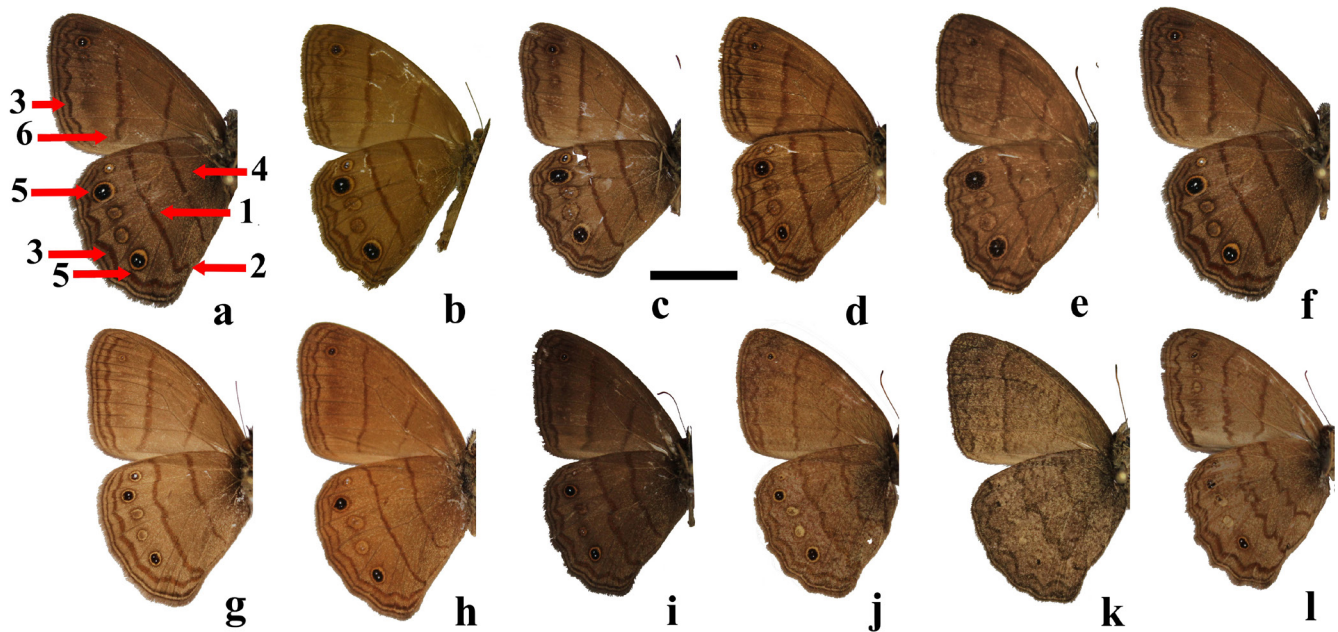


Figure 20. Species of *Malaveria* gen. nov. and related taxon '*Paryphthimoides*' *grimon*, underside pattern. a. Taxonomically diagnostic elements of the underside pattern (number references in main text); b. *M. alcinoe* comb. nov. (Lectotype); c. *M. alcinoe* comb. nov. (Venezuela); d. *M. rodriguezi rodriguezi* sp. nov. (Colombia); e. *M. rodriguezi risaralda* ssp. nov. (Colombia); f. *M. ballofi* sp. nov. (Ecuador); g. *M. bottoi* sp. nov. (Colombia); h. *M. mimas* comb. nov. (Bolivia); i. *M. nebulosa* comb. nov. (Venezuela); j. *M. duponti* sp. nov. (Bolivia); k. *M. mimula* comb. nov. (Paraguay); l. '*P.*' *grimon* (Brazil). (Scale imago: 1 cm).

3. overlapping of distribution ranges (Fig. 21): more than one taxon can be found at the same place which seemingly complicates the assessment of the discriminative value of some habitus characters (as on the eastern slopes of the Andes in Ecuador and the western slopes of the Cordillera Ori-

ental in Colombia); 4. poor discriminative value at specific level of male genitalia structures; 5. few museum specimens available from Colombia with phenotype matching that of the type specimens of *N. alcinoe* and *E. benedicta* (see under *M. alcinoe* comb. nov.); 6. probable lack of power of

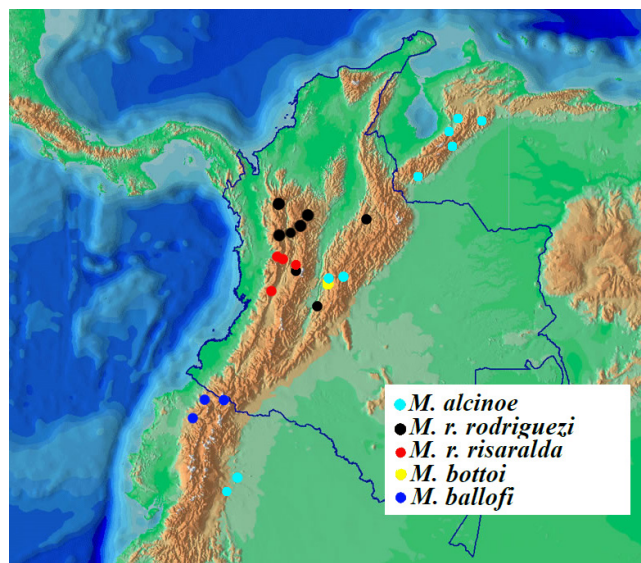


Figure 21. Map of distribution of species and subspecies of the *Malaveria* “alcinoe-complex”.

the DNA analysis in this study, due to the size of molecular fragments used from Colombian samples. We examined 40 specimens directly or in photographs, and dissected 13 males from different locations very likely to represent several new taxa. Nevertheless, because of what precedes, we feel more prudent treating this subject in a more comprehensive study in the future (Le Crom *et al.* in prep.) and describe here only two distinctive new species *M. rodriguezii* sp. nov. (two subspecies) and *M. bottoi* sp. nov., from Colombia. In Ecuador we identified a third distinctive species West of the Andes, *M. ballofi* sp. nov., described herein. We examined other specimens from the eastern slopes of the Andes that belong to at least two different taxa (one being probably new). The northernmost record identified as *M. alcinoe* comb. nov., is from the northeastern slopes of the Cordillera de Mérida in the Parque Nacional Yacambú (Lara state); the southernmost record is from the eastern slopes of the Andes in Madre de Dios, Peru, and it likely represents another undescribed species. For the same reasons above mentioned we do not treat these taxa here.

We studied 82 specimens belonging to the “alcinoe-complex”, 7 from Venezuela, 33 from Ecuador, 40 from different parts of Colombia and 2 from Peru. Among them 46 were examined directly and the other 36 studied on high quality photographs. Some of the characters that could have initially appeared as phenotypic variations were revealed to be sufficiently repetitive and stable. Their occurrence was also coherent with biogeographical distribution and discriminating DNA analysis results. Wing venation study was performed on a limited number of

specimens (1 or 2) and provided interesting characters at specific level that need more investigation.

Twenty five male genitalia have been dissected and compared. We focused on the shape of the distal extremity of the valvae, which was expected to be diagnostic at specific level. The only specimen of *M. alcinoe* comb. nov. from Venezuela (Figs. 18a-18b) we could dissect showed a valva more similar to that of *M. nebulosa* comb. nov., than to those of other species of the “alcinoe-complex”, characterized by the presence of a proximal spiny inner projection and the absence of membrane in the distal part of the valva (Figs. 18e-18k). Nevertheless, the examination of this single specimen is to be interpreted with caution. Indeed, we found that all the genitalia examined were very similar and the range of variability could not provide sufficient arguments by itself to distinguish all the species.

We performed DNA analysis using the ADN 16S fragment of 218-220 base pairs (Table 1). The specimens sampled were from north-western Ecuador (16 specimens), western (4 specimens) and eastern (1 specimens) slopes of the Cordillera Occidental, eastern (3 specimens) slopes of the Cordillera Central and western slopes (3 specimens) of the Cordillera Oriental of Colombia (Table 2). The DNA analysis for the Venezuelan male of *M. alcinoe* comb. nov., failed but the corresponding female from Cundinamarca (Figs. 18c-18d) surprisingly revealed to be more related to *M. nebulosa* comb. nov., than to *M. rodriguezii* sp. nov., *M. bottoi* sp. nov. and *M. ballofi* sp. nov. This unexpected result and the similarity in the male genitalic valvae suggest that *M. alcinoe* comb. nov. could be rather closer to *M. nebulosa* comb. nov., than to the other species of the “alcinoe-complex”. The results showed that *M. ballofi* sp. nov., from western Ecuador, although slightly different, grouped apart, arguing for its specific status. Two specimens from Cesar and Santander (Colombia) differed by a few basis from the main group. Their habitus is a little distinct and potentially they represent different taxa that need a deeper study. All the other specimens did not show differences in the DNA fragment analyzed and corresponded to *M. rodriguezii* sp. nov. (two subspecies) and *M. bottoi* sp. nov.

Finally, although performed on a limited number of specimens, the wing venation study highlighted an interesting and potentially specifically discriminating character: the origin of R2 on the FW. In *M. nebulosa* comb. nov., and *M. alcinoe* comb. nov., the latter is distal to the bifurcation between r2-5-m1 and r1-r2, whereas it is proximal to it in *M. mimas* comb. nov. and *M. rodriguezii* sp. nov. In *M. ballofi* sp. nov., *M. mimula* comb. nov., and *M. duponti* sp. nov., R2, r2-5-m1 and r1-r2 share the same origin (Figs. 4a-4h).

The similarity in habitus, genitalia and genetic distance suggests the “alcinoe-complex” is composed of sev-

eral very close sister species. Based on the examination of these specimens and our experience in taxonomy of the Satyrinae, we retained the following habitus morphological characters for being useful to separate the different taxa (Fig. 20a-20l). Some of these are strong and clearly discriminating at the specific level: they represent differences in the structure pattern itself (A), while others are weaker and affect qualitatively the pattern without modifying its structure and composition (B):

- (1) shape of the median line on VHW: straight, sinuous or irregular (A).
- (2) junction between median line and anal margin on VHW: straight, slightly angled or strongly angled (A).
- (3) shape of the submarginal line on the underside: flattened or more scalloped (A), thin or wide (B).
- (4) background color (A and B).
- (5) proportion between ocelli in Cu1-Cu2 and M1-M2 on VHW: same size, wider or ratio inverted (B).
- (6) shape of the median line in Cu2-2A on VFW in some species (A).
- average size of the specimens (A and B).
- size of the ocelli on VHW: small, medium, or large (B).

Using these characters associated with biogeographical patterns of distribution and, in some cases genitalia morphology, venation study, and DNA similarity (genetic distances), we identified 3 new taxa belonging to the “*alcinoe*-complex”. These taxa are described as new species because the differences observed are sufficient to justify this treatment. A more complete morphological study gathering series of samples from various localities and a DNA analysis using longer segments of nucleotide chains and different genes will probably improve the taxonomic discrimination within this group.

Cajetan and Rudolf Felder described *Neonympha alcinoe* in 1867 based on an unspecified number of specimens from Nova Granada: Bogotá and Venezuela [*sic*]. A syntype male from Bogotá is hosted in the NHMUK (Fig. 12c). Another male specimen in the NHMUK is possibly a syntype from Venezuela, but we could only examine its underside. Furthermore, the original description of *alcinoe* mentions both sexes. It is thus plausible that the type series comprises at least 3 specimens (2 males and 1 female). A female syntype remains unknown to us. Because of the various similar taxa involved in the “*alcinoe*-complex”, the possible inclusion of more than one taxon under Felder’s description and for nomenclature stability purposes, it is necessary to fix the identity of this taxon. Therefore, we designate the specimen with the following labels as the LECTOTYPE of *Neonympha alcinoe* C. Felder & R. Felder, 1867 (Fig. 12c): /Type/FELDER COLL^N./ *Alcinoë* Feld/Rothschild Bequest B.M. 1939-1./Type of *N. alcinoe* Feld? = *E. benedicta*, Butl. of w. it. may be

a good local form. Comp. w. type *E. benedicta*. Butler./ BMNH(E)1266958/[NHMUK] (examined).

The habitus of the lectotype is characterized on VHW by: 1. regular median line, 2. median line making a slight angulation when reaching the anal margin at a short distance from the submarginal line, 3. ocelli of almost the same size in M1-M2 and Cu1-Cu2, 4. submarginal line scalloped, composed by almost straight adjacent segments, 5. relatively small size (FWL: 21 mm). We found 4 males closely matching this habitus: 1 from Bogotá (NHMUK), 1 from Sangay National Reserve in the eastern Andes of Ecuador (illustrated on the website www.sangay.eu) and 2 from the Cordillera de Mérida (from Barinas and Lara states) in Venezuela. We examined 3 additional corresponding females from the Cordillera de Mérida (from Táchira and Trujillo states, Venezuela) very similar to the female from Cundinamarca (Figs. 18c-18d). We identified all these specimens as true *alcinoe*. Unfortunately, we only had direct access to 2 of these specimens (the male from Lara state and the female from Cundinamarca) for dissections and DNA analysis.

The potential syntype from Venezuela differs notably from the lectotype on VHW by having the ocellus in M1-M2 bigger than that in Cu1-Cu2 and by the much smaller ocelli in M2-M3 and M3-Cu1. We encountered a single specimen hosted in the MNHN, labelled “Colombia”, presenting a similar habitus. The latter specimen is very old, and for this reason the locality “Colombia” is vague and could have applied to some part of Venezuela, or even Ecuador. We believe this particular phenotype is likely to represent an extreme variation of the true *alcinoe* pattern or possibly a different taxon whose distribution area is unknown. Ocellus in Cu1-Cu2 seems to be slightly wider in the northern part of the distribution of *M. alcinoe*, especially in females.

Butler described *Euptychia benedicta* from an unspecified number of specimens from Sarayacu, Ecuador, and illustrated the species. A female syntype is hosted in the NHMUK (Fig. 12d). This specimen corresponds exactly to Butler’s description and illustration. It has a particular character indicated in its description: the sixth anal ocellus on VHW. This is very likely to represent an aberrant character whose presence is rarely encountered (see discussion above). It is likely that Butler based his description on this unique specimen. The location Sarayacu is in Pastaza Province in the Amazonian lowlands of Ecuador, east of the Andes at around 400 m altitude. A few reliable records from specimens belonging to the “*alcinoe*-complex” exist from the lowlands and thus, this altitude record may be or may be not plausible. One of the labels mentions “C. Buckley” who was certainly its collector. Clarence Buckley, was a successful British natural history collector in the

Andes of Colombia, Ecuador and Bolivia (1868-1878), and a notable supplier of butterfly specimens to William Chapman Hewitson in England. He collected extensively in localities on the eastern slopes of the Ecuadorian Andes (Vane-Wright 1991). We then assume the syntype of *E. benedicta* came indeed from the Sarayacu region, a locality also recorded in mammals and birds obtained by Buckley. The particular characters of *alcinoe*, already mentioned, are apparently shared by *benedicta* and we agree with Lamas (2004) in temporarily considering *benedicta* as a junior synonym of *alcinoe*. Specimens collected by A. Neild (pers. comm.) on the eastern slopes of the Andes of Ecuador have a distinctive golden look to the ventral brown, and probably represent a different, new taxon.

The type locality of *alcinoe*, “Bogotá”, is far from being precise and could represent various localities in Colombia. The exact distribution range of true *alcinoe* remains uncertain (Fig. 21), and further collecting in the area of Bogotá and the surrounding lower mountains is needed. All the specimens we identified as true *alcinoe* are from the eastern slopes of the Andes in Ecuador to the northern tip of the Cordillera de Mérida in Venezuela, where the lower mountains probably allow the species to flow on both slopes. The only specimen located outside this area is the Colombian female from Cundinamarca (again a large department mostly covering part of the Cordillera Oriental, including Bogotá) on which some doubts remains about the precise collecting locality. Nevertheless, given the absence of other specimens matching the lectotype in the material examined elsewhere in Colombia, this record requires confirmation. We hypothesize *M. alcinoe* **comb. nov.**, to be restricted to eastern slopes of the Andes of Ecuador, the Cordillera Oriental in Colombia and the Cordillera de Mérida in Venezuela.

Although *M. alcinoe* **comb. nov.**, is likely to be the only representative of the “*alcinoe*-complex” in the Cordillera de Mérida, it is probably sympatric with some related taxa in Colombia and Ecuador. Comprehensive sampling along the eastern slopes of the Andes and the regions surrounding Bogotá might confirm this hypothesis.

Additional specimens examined that did not match the species herein described are listed under *Malaveria* sp., and will be studied separately (Le Crom *et al.* in prep.).

***Malaveria ballofi* Benmesbah & Viloria, sp. nov.**

(Figs. 22a-22m)

<http://zoobank.org/urn:lsid:zoobank.org:act:44958377-2D0A-4DD7-A107-1A802A967D08>

Type material: HOLOTYPE male (Figs. 22a-22b): /ECUADOR, Pichincha, Nanegalito, 2016/Holotype male

of *Malaveria ballofi* Benmesbah & Viloria, 2020/Raúl Aldaz collector/MB-0072*/[MB]. PARATYPES (all from ECUADOR): 26 males (11 dissected), 5 females (2 dissected): 1 female (MB-0075*) and 9 males same data as Holotype (MB-0017*, MB-0066, MB-0067, MB-0071, MB-0070*, MB-0074*, MB-0076*, MB-0257*) [MB, except 0067 in IVIC], (MB-0073*) [MIZA]; Imbabura, Parambas 3500ft, 1913 2 females (MB-06, MB-07*) [MNHN]; and 2 males (MB-08*, MB-09*) [MNHN]; February 1897 2 males [NHMUK]; March 1897 2 males [NHMUK]; 20.III.1897 1 male [NHMUK]; 20.III.1897 1 female [NHMUK]; Pichincha, Nanegalito, October 2015 1 male (MB-0015*) [MIZA]; 16.X.2015 2 males (MB-0016*, MB-0018), 1 female (MB-0370) [MB]; Carchi, Rio Baboso 800m, IX.2016 2 males (MB-0068*, MB-0069); Carchi, El Carmelo, VIII.2017 4 males (MB-0365) [AN], (MB-0366, MB-0367, MB-0368) [MB].

Description: Male (Figs. 22a-22b): FWL: Holotype 25 mm, 23-26 mm (15 specimens), average 24.3 mm. DFW: ground color dark brown uniform. VFW: ground color as upperside; submedian and median lines thin, brown slightly ferruginous, median line curved outwards in Cu2-2A; submarginal area with three small ocelli, one black circled by a yellowish ring in the apex, in M1-M2, with two tiny white pupils, two others faded in M2-M3 and M3-Cu1; submarginal line same width as median line, scalloped from radius to 2A, pointing distally in M1 to Cu2; marginal dark line thinner and regular, parallel to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; median and submedian line slightly irregular, of same width and color as on VFW, submedian line joining anal margin without making angulation, median line making a marked angulation when joining the anal margin; submarginal line of same color but slightly wider, scalloped, composed by almost straight adjacent segments, pointing distally from M1 to Cu2; marginal dark line thin, parallel to outer margin from costa to torus; submarginal area with five ocelli, one in each space between Rs and Cu2, ocelli in M1-M2 and Cu1-Cu2 rounded, bigger, of almost same size, black, circled by a yellowish ring, each with two small white pupils, ocelli in M2-M3 and M3-Cu1 smaller and less defined, without black in the center, ocellus in Rs-M1 very small.

Female (Figs. 22c-22d) – FWL: 22-23 mm (3 specimens), average 22,7 mm. Similar to male, but differing by the more clear coloration, and the faded ocelli on underside more marked.

Male genitalia (11 dissected) (Figs. 22e-22k): general structure similar to previous species herein described; the valvae being more elongated and stylized than those of

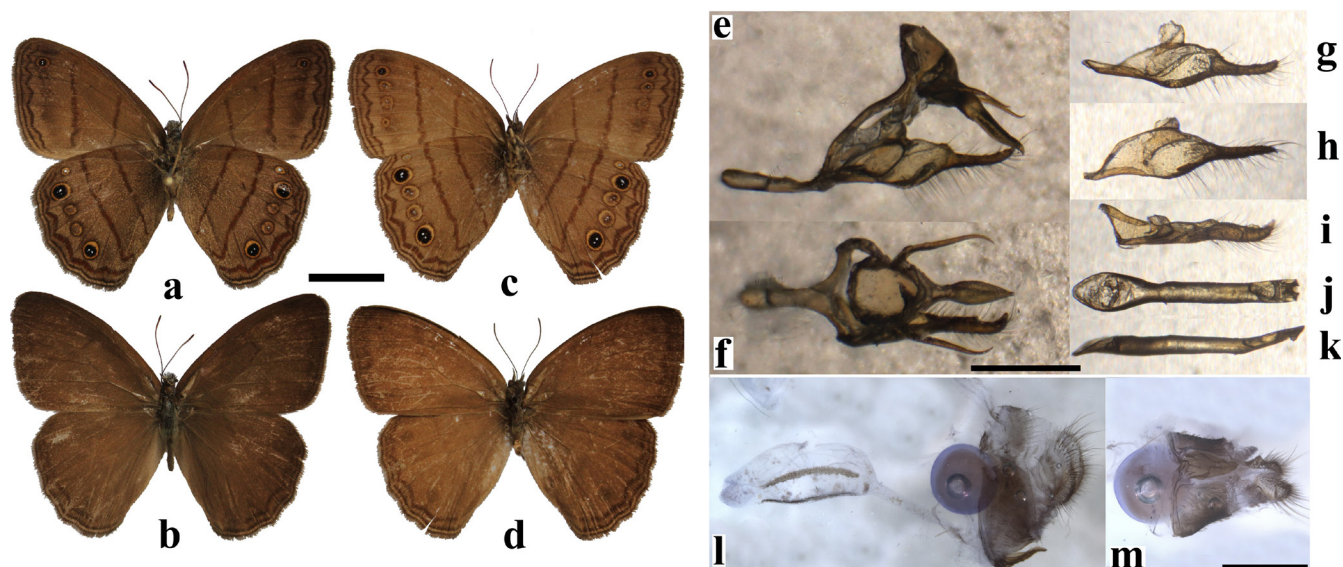


Figure 22. *Malaveria ballofi* sp. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. *idem* dorsal; e. Male genitalia lateral view (one valva removed); f. *idem* dorsal view; g. Valva lateral inner view; h. *idem* lateral outer view; i. *idem* dorsal view; j. Aedeagus dorsal view; k. *idem* lateral view; l. Female genitalia lateral view; m. *idem* ventral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

M. nebulosa comb. nov., *M. mimas* comb. nov., and *M. alcinoe* comb. nov., horn-like inner processes less evident; base of aedeagus broad as in *alcinoe*.

Female genitalia (2 dissected) (Figs. 22l-22m): no significant variation found when compared to the female genitalia of *M. nebulosa* comb. nov., the type species of this genus. Perhaps fine dissections of membranous structures would allow for detecting differences in less evident structures like the spermatheca (and the lagenae) and the different ducti.

Variability: all specimens examined are very similar to each other, and show a slight variability in the shape of the VHW median line, which is usually a little more wavy than in the holotype.

Diagnosis: *M. ballofi* sp. nov., is the larger species of the “*alcinoe*-complex”. It differs from *M. alcinoe* comb. nov., *M. bottoi* sp. nov. and *M. rodriguezii* sp. nov., by: 1. its larger size (FWL average 24.3 mm for *M. ballofi* sp. nov., 21.0 mm for *M. alcinoe* comb. nov., 22.0 mm for *M. bottoi* sp. nov., 22.9 mm for *M. rodriguezii rodriguezii* sp. nov., 23.0 mm for *M. rodriguezii risaralda* ssp. nov.); 2. the marked angle made by the median line when reaching the anal margin on VHW; 3. median line markedly curved outwards in Cu2-2A on VFW as a dome concave to the base. Moreover, it differs from *M. alcinoe* comb. nov., by the more wavy median line on VHW, the presence of membranes and the absence of the inner spiny projection on the distal part of the valvae; from *M. bottoi* sp. nov., by the darker ground color and the more angular submarginal lines on underside.

Etymology: dedicated to our friend Daniel Ballof, a French entomologist who is passionately keen on Neotropical and African butterflies, in gratitude for his generosity and hospitality. He has travelled to various countries, but especially French Guiana, where he lived for years and contributed greatly to the better knowledge of its butterfly fauna. The species name *ballofi* is a Latinized masculine noun in the genitive case.

Hostplant: unknown.

Habitat and behavior: we did not observe *M. ballofi* sp. nov., in the field, but its behavior is presumably typical of that of other members of *Malaveria* gen. nov. See also *Modestia modesta* comb. nov. This species seems to be restricted to the western slopes of the Andes in Ecuador, part of the Chocó area of endemism (Fig. 21). We have no information on collecting records in southwestern Colombia (departments of Cauca and Nariño), where it could also occur. There are records from sea level up to 1,400m.

Discussion: *M. ballofi* sp. nov. is geographically isolated from the other members of the “*alcinoe*-complex”. Several endemic species and subspecies of butterflies have been recently described from northwestern Ecuador (Benmesbah *et al.* 2019). The 32 specimens examined showed little variation in the habitus, which is clearly different from the other species of *Malaveria* gen. nov. In our DNA study, the specimens analyzed clearly grouped apart from the other species of the “*alcinoe*-complex” (except *M. rodriguezii* sp. nov. and *M. bottoi* sp. nov.) with significant difference: 5.5% for *M. duponti* sp. nov. and *M. mimula* comb. nov., 4.1% with *M. mimas* comb. nov., 2.7% with

M. nebulosa **comb. nov.** and 2.3% with *M. alcinoe* **comb. nov.** (Tables 1 and 2). The difference observed with *M. rodriguezi* **sp. nov.** and *M. bottoi* **sp. nov.**, is low (Table 2) and probably due to a lack of power of the DNA test used here (see above). On the other hand, wing venation structure on FW is most similar to *M. duponti* **sp. nov.** and *M. mimula* **comb. nov.**, in which R2, r2-5-m1 and r1-r2 roots share the same origin at the distal edge of the cell, differing in this from *M. rodriguezi* **sp. nov.**, in which the origin of R2 is proximal to the separation between r2-5-m1 and r1-r2 (Figs. 4a-4h). The specimens dissected (12 males) showed certain homogeneity in the shape of the distal extremity of the valvae. Conversely to *M. nebulosa* **comb. nov.** and *M. alcinoe* **comb. nov.**, small irregular membranes are present at the distal tip of the valvae and the inner spiny projection is usually absent, or if present, it is very small and more distally located. All these elements argue for its specific status and its closer proximity within *Malaveria* **gen. nov.**, to *M. rodriguezi* **sp. nov.** and *M. bottoi* **sp. nov.**

Malaveria rodriguezi Benmesbah & Viloria, **sp. nov.**
(Figs. 23a-23i)

<http://zoobank.org/urn:lsid:zoobank.org:act:AF9CCEA0-B91D-414C-94E9-853E38BA8318>

Type material: HOLOTYPE (Figs. 23a-23b) male: / COLOMBIA, Antioquia, Frontino 2000m, 22.IV.2007/ Holotype of *Malaveria rodriguezi* Benmesbah & Viloria, 2020/Gabriel Rodríguez leg./MB-0249*/ [MB]. PARATYPES (all from COLOMBIA): 5 males: 1 male Antioquia, Amagá 1700m, 17.08.2003 (MB-0248) [MNHN]; 1 male Antioquia, Frontino 1900m, 22.IV.2000 (MB-0253) [MB]; 1 male Antioquia, Guarne 2000m, 20.XI.2003 (MB-0254*) [MB]; 1 male Antioquia, La Mansa, Ciudad Bolívar 2400m, 25.01.2004 (MB-0255*) [MB]; 1 male Antioquia, Porce 1000m, 09.08.2003 (MB-0265*) [MB].

Additional material: 8 specimens (1 male dissected) not included in the type series:

COLOMBIA (8 specimens): Caldas: Manizales, Barrio Los Nogales 1950m, 03-10.IX.2019 6 specimens (photograph) [ICRM]; Santander: El Hato, Serranía de los Yariguíes 2100m, 25-28.XI.2019 1 male (photograph) [ICRM]; Tolima: Prado 700m, September 2003 1 male (MB-0256*).

Description: Male (Figs. 23a-23b): FWL: Holotype 22 mm, 22-24 mm (7 specimens), average 22.9 mm. DFW: ground color brown uniform. VFW: ground color same as DFW; submedian and median lines thin, brown slightly ferruginous, submedian line straight, median line curved inside near the costa and outwards in Cu2-

2A; submarginal area with one small ocellus, black with two tiny pupils circled by a brownish ring in the apex in M1-M2; submarginal line of almost same width as median line darker, scalloped from radius to 2A, pointing distally in M1 to 2A; marginal dark line thinner and regular, parallel to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; median and submedian lines slightly irregular, of same width and color as on VFW, joining anal margin without making angulation, median line joining the anal margin at the origin of the submarginal line; submarginal line of same color but slightly wider, scalloped, pointing distally from M1 to 2A; marginal dark line thin parallel to outer margin from costa to tornus; submarginal area with five ocelli, one in each space between Rs and Cu2, ocellus in M1-M2 the biggest, black circled by a yellowish ring with two small white pupils, ocellus in Cu1-Cu2 similar, more ovoid and slightly smaller, ocelli in M2-M3 and M3-Cu1 smaller and less defined without black in the center, ocellus in Rs-M1 the smallest bipupillate without black in the center.

Female: not examined.

Male genitalia (5 dissected) (Fig. 23c-23i): general structure similar to other species of the genus. Shape of the valvae very similar to those of *M. ballofi* **sp. nov.**, but horn-like inner processes more developed; aedeagus larger than valva and more robust than in the species previously studied.

Female genitalia: not examined.

Variation: the specimens from the type series present little variation, mainly in the median line on VHW that can be a little more wavy than in the holotype. Size of the ocelli on VHW seems to vary slightly, being wider in specimens from the south (the holotype presenting the smallest ones).

Diagnosis (Figs. 20a-20l): *M. rodriguezi* **sp. nov.**, differs from *M. alcinoe* **comb. nov.** and *M. ballofi* **sp. nov.**, by the median line on VHW joining the anal margin at the origin of the submarginal line without making a pronounced angle; in the two latter species the median line joins the anal margin at a distance from the origin of the submarginal line and forms a greater angle in *M. ballofi* **sp. nov.** and *M. alcinoe* **comb. nov.** (a little less in the latter than the former). *M. rodriguezi* **sp. nov.**, differs from *M. bottoi* **sp. nov.** by: 1. its darker background color; 2. straighter median line on VHW; 3. wider ocelli on the underside and 4. submarginal line more angular on VHW and VFW (flattened in *M. bottoi* **sp. nov.**). Male genitalia morphology does not differ evidently from the other species of *Malaveria* **gen. nov.**

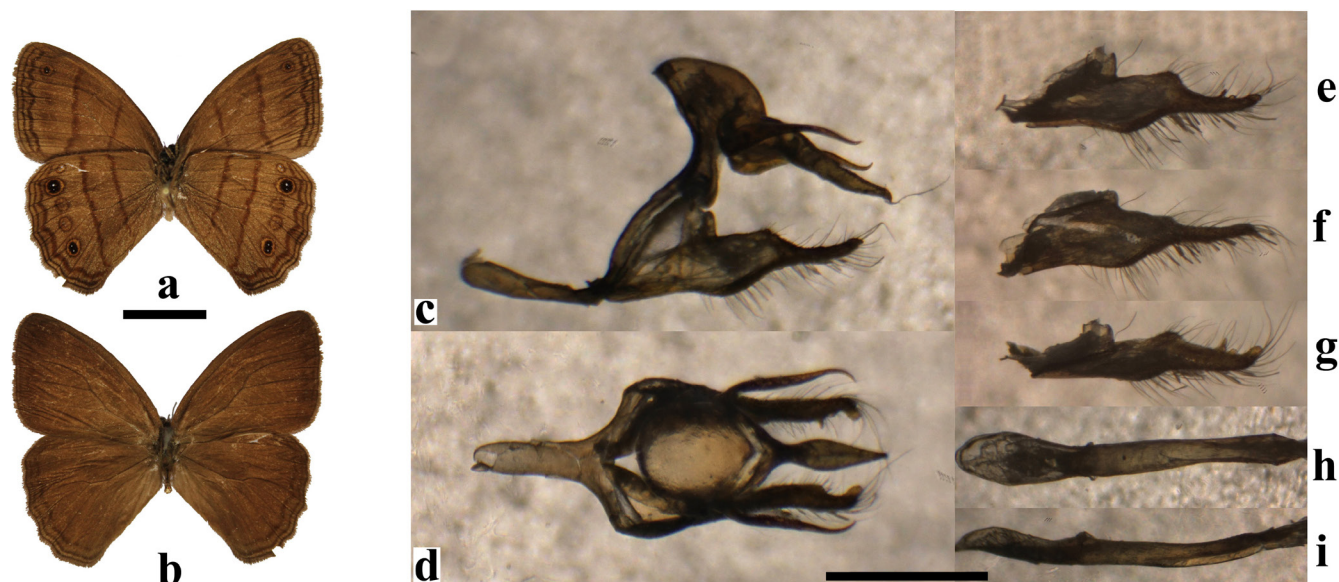


Figure 23. *Malaveria rodriguezii rodriguezii* sp. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Male genitalia lateral view (one valva removed); d. *idem* dorsal view; e. Valva lateral inner view; f. *idem* lateral outer view; g. *idem* dorsal view; h. Aedeagus dorsal view; i. *idem* lateral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

Etymology: dedicated to Gabriel Rodríguez, a Colombian geologist and entomologist studying the butterfly fauna of his country, who collected the type series and kindly shared this study material with us. The name *rodriguezii* is a Latinized masculine noun in the genitive case.

Hostplant: unknown.

Habitat and behavior: we did not observe *M. rodriguezii* sp. nov., in natural conditions. As in the previous case, we can only presume that its behavior is similar to other species of *Malaveria* gen. nov. This species seems to be distributed at least through the three Cordilleras in the northern half of Colombia, with the exception of the eastern slopes of the Cordillera Oriental (Fig. 21). Recorded from 700 to 2,400m.

Discussion: although similar in appearance to the other species of the “*alcinoe*-complex”, *M. rodriguezii* sp. nov. shows particular characters arguing for its specific status: 1. the most evident is the shape of the median line on VHW when joining the anal margin (Figs. 20a-20l); 2. the DNA analysis performed here shows important similarity with *M. bottoi* sp. nov. (100%) and *M. ballofi* sp. nov. (99.5%), from which *M. rodriguezii* sp. nov., is, nevertheless, clearly differentiated by the previous morphological criteria, pointing out the probable lack of power of the DNA technique used here. On the other hand specimens of *M. rodriguezii* sp. nov., grouped apart from *M. mimas* comb. nov., *M. nebulosa* comb. nov. and *M. alcinoe* comb. nov. (Table 1), and showed respectively significant difference: (4.6%), (3.2%) and (2.7%) (Table 2); 3. FW wing

venation presents the particularity (shared also with *M. mimas* comb. nov.) that R2 origin is proximal to the bifurcation between r2-5-m1 and r1-r2 (distal in *M. nebulosa* comb. nov. and *M. alcinoe* comb. nov., and emerging from the same root in *M. ballofi* sp. nov.) (Figs. 4a-4h).

The description of *M. rodriguezii* sp. nov., is based on a series of 6 similar specimens from different localities in Antioquia sharing stable characters. We also examine specimens directly and photographs of specimens we also identified as *M. rodriguezii* sp. nov., from Caldas, Santander and Tolima departments in Colombia. *M. rodriguezii* sp. nov., has a large distribution within Colombia, except the eastern slopes of the Cordillera Oriental, where *M. alcinoe* comb. nov., is present. The wide altitudinal range from where it is recorded may explain its ability for dispersion over natural barriers as mountains and valleys. Southern specimens from the “*alcinoe*-complex” from Risaralda, Caldas and Valle del Cauca showed some differences with typical individuals of *M. rodriguezii* sp. nov., and are described below tentatively as a different subspecies.

Malaveria rodriguezii risaralda Benmesbah & Vioria,
ssp. nov.
(Figs. 24a-24i)

<http://zoobank.org/urn:lsid:zoobank.org:act:39FBA58D-DF90-458A-B0BA-A450C040D1B9>

Type material: HOLOTYPE male (Figs. 24a-24b): /COLOMBIA, Risaralda, Pueblo Rico 1400m, 20.VII.2005/

Holotype of *Malaveria rodriguezi risaralda* Benmesbah & Viloria, 2020/Gabriel Rodríguez leg./MB-0250*/ [MB]. PARATYPES: COLOMBIA: Risaralda: 1 males Pueblo Rico 1400m, 20.VII.2005 (MB-0252*) [MB]; Valle del Cauca: 1 male 1902 (MB-13*) [MNHN].

Additional material: 4 specimens not included in the type series: COLOMBIA: Caldas: Anserma, Ecoparque los Tucanes 1907m, 16-19.II.2019 3 males (photograph) [ICRM]; Manizales, Quebrada El Águila 1750m, 04.II.2019 (photograph) 1 male [ICRM].

Description: Male (Figs. 24a-24b): FWL: Holotype 23 mm, 22–24 mm (7 specimens), average 22,9 mm. DFW: ground color brown uniform. VFW: ground color same as upperside; submedian and median lines thin, brown slightly ferruginous, median line curved inside near the costa and outwards in Cu2-2A; submarginal area with three small ocelli, one black, circled by a brownish ring in the apex in M1-M2, two others faded in M2-M3 and M3-Cu1, almost not visible; submarginal line of same width as median line, scalloped from radius to 2A, pointing distally in M1 to 2A; marginal dark line thinner and regular, parallel to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; median and submedian lines broken and irregular, of same width and color as on VFW, median line making a slight angulation when joining the anal margin at the origin of the submarginal line; submarginal line of same color but slightly wider, scalloped, composed by straight adjacent segments,

pointing distally from M1 to 2A; marginal dark line thin, parallel to outer margin from costa to tornus; submarginal area with five ocelli, one in each space between Rs and Cu2, ocellus in M1-M2 the biggest oval with long axis directed to the base, black, circled by a yellowish ring with two small white pupils, ocellus in Cu1-Cu2 similar but slightly smaller, ocelli in M2-M3 and M3-Cu1 even smaller and less defined without black in the center, ocellus in Rs-M1 the smallest with little black in the center and two small white pupils.

Female: not examined.

Male genitalia (3 dissected) (Fig. 24c-24i): there is certain variation between the general aspect of the genital structures of this subspecies and those of the nominotypical one; however, it seems to be within the extremes of individual variation of the specimens examined. The structure illustrated shows a sacculus narrower at base and valvae with more prominent processes. The aedeagus looks relatively thicker than that of *M. rodriguezi rodriguezi* sp. nov.

Female genitalia: not examined.

Variation: the shape of the median line on VHW can be more or less wavy. The two specimens from Risaralda (holotype and one paratype) present a markedly wavy median line.

Diagnosis: *M. rodriguezi risaralda* ssp. nov., differs from the nominate subspecies on VHW by: 1. larger ocelli, especially in M1-M2 and Cu1-Cu2; 2. ocellus in M1-M2 a little elongated with its long axis pointing towards the base (rounded in the nominate) and 3. ocellus in M1-

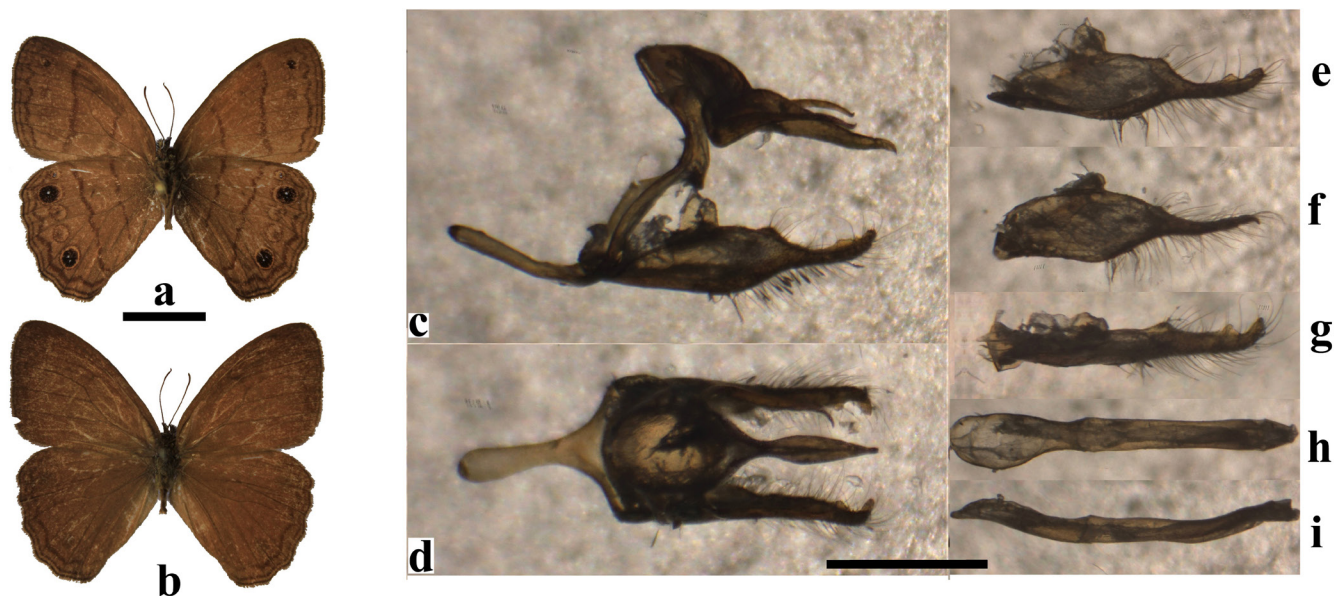


Figure 24. *Malaveria rodriguezi risaralda* ssp. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Male genitalia lateral view (one valva removed); d. *idem* dorsal view; e. Valva lateral inner view; f. *idem* lateral outer view; g. *idem* dorsal view; h. Aedeagus dorsal view; i. *idem* lateral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

M2 only slightly bigger than ocellus in Cu1-Cu2 (notably bigger in the nominate subspecies).

Etymology: in allusion to the type locality, Risaralda department in Colombia. “*risaralda*” is a feminine noun in apposition.

Hostplant: unknown.

Habitat and behavior: we did not observe this subspecies in the field. The records are located on both slopes of the Cordillera Occidental in the departments of Risaralda, Caldas and Valle del Cauca in Colombia (Fig. 21). Recorded from 1,400 to 1,907m.

Discussion: subspecies *risaralda* shares the same diagnostic characters that differentiate *M. r. rodriguezii* sp. nov., from *M. alcinoe* comb. nov., *M. ballofi* sp. nov., and *M. bottoi* sp. nov. (see under nominate). This subspecies ranges south and west from the area of distribution of the nominate subspecies (Fig. 21). All the records we have (7 males) are from the western (Pueblo Rico, Risaralda) and the eastern (Anserma y Quebrada el Aguila, Caldas) slopes of the Cordillera Occidental. These localities are very close geographically (20 km) and separated by mountains between 2,000m and 2,800m high. The continuity of the mountains probably allows butterflies of this species to flow between them. The specimen labelled Valle del Cauca could have originated from either side. The study of male genitalia, with 5 specimens of the nominate and 3 specimens from *M. r. risaralda* ssp. nov., dissected, did not show significant differences. The DNA analysis performed here with 7 specimens of the nominate and 2 specimens of *M. r. risaralda* ssp. nov., did not show difference on the analyzed fragment. Furthermore, we found a few specimens from Manizales, Caldas, with larger ocelli on VHW and 1 from Anserma with smaller ocelli than usual on VHW, that are probably intermediate between the 2 subspecies. For these reasons we treat here *risaralda* as a subspecies of *M. rodriguezii* sp. nov.

***Malaveria bottoi* Benmesbah & Vilorio, sp. nov.**

(Figs. 25a-25i)

<http://zoobank.org/urn:lsid:zoobank.org:act:122E610E-9A01-4D95-A4F5-4FD1F2D729C9>

Type material: HOLOTYPE male: COLOMBIA: Cundinamarca, Colegio 430m/Holotype male of *Malaveria bottoi* Benmesbah & Vilorio, 2020/Patrick Botto leg./MB-0019*/ [MB].

Description: Male (Figs. 25a-25b): FWL: 22 mm (1 specimen). DFW: ground color brown uniform. VFW: ground color brown lighter than DFW; submedian and median lines thin, brown slightly ferruginous, submedian line straight, median line curved outwards in Cu2-2A;

submarginal area with one faded, very small ocellus in the apex in M1-M2; submarginal line of same width and color as median line, discreetly scalloped from radius to 2A, pointing distally in M1 to 2A; marginal dark line thinner and regular, parallel to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; submedian and median lines irregular and wavy, of same width and color as on VFW, submedian line joining anal margin without making angulation, median line joining the anal margin making a slight angulation at the origin of the submarginal line; submarginal line of same color and width, flattened and discreetly scalloped, pointing distally from M1 to 2A; marginal dark line thin parallel to outer margin from costa to tornus; submarginal area with five ocelli of almost same size, one in each space between Rs and Cu2, ocelli in M1-M2 and Cu1-Cu2 black, circled by a yellowish ring with two small white pupils, ocelli in M2-M3 and M3-Cu1 less defined, without black in the center, ocellus in Rs-M1 with a single and wide white pupil.

Female: not examined.

Male genitalia (1 dissected) (Figs. 25c-25i): a single individual dissected shows genitalic structures closer in appearance to *M. rodriguezii* sp. nov., than to its allegedly sympatric (or altitudinal parapatric) *M. alcinoe* comb. nov.

Female genitalia: not examined (unknown).

Diagnosis: *M. bottoi* sp. nov., differs from all the other species of *Malaveria* gen. nov., by: 1. submarginal line on VHW and VFW flattened and subtly scalloped, and much more removed from the marginal line than in other species (except *M. mimas* comb. nov.); 2. markedly wavy VHW median line, especially near the costa; 3. more rounded outer margin on hindwing (except *M. mimas* comb. nov.), and 4. lighter brown underside. For differences with *M. mimas* comb. nov., see under the latter.

Etymology: in honor of our friend Doctor Patrick Botto, a French physician and entomologist who is an enthusiast student of Neotropical butterflies and in particular satyrines of the tribe Haeterini. He collected the holotype of this species and kindly allowed us to study it. The Latinized species name *bottoi* is treated as a masculine noun in the genitive case.

Hostplant: unknown.

Habitat and behavior: we did not observe *M. bottoi* sp. nov., in its natural habitat. Following indications from the collector, the holotype was captured in a locality called Colegio (430 m) in Cundinamarca. It possibly corresponds to Mesitas del Colegio, 630 m, in the Bogotá river valley (A. Neild pers. comm.) (Fig. 21). This locality is considerably lower than those in which *M. alcinoe* comb. nov., has been recorded. We think these apparently different species

might fly in parapatry, at different altitude levels. We have no other record for this species.

Discussion: the description of *M. bottoi* sp. nov., is based on a unique male specimen. This specimen presents several particular characters that clearly differentiate it from the other species of *Malaveria* gen. nov. (see diagnosis). The combination of these characters makes improbable that this specimen represents an aberration or a particular form of *M. alcinoe* comb. nov., or related species. Unsurprisingly, the male genitalia are similar to the other species of the “*alcinoe*-complex” and the analyzed fragment of DNA in our molecular study did not show significant differences with *M. rodriguezii* sp. nov. (0%) and *M. ballofi* sp. nov. (0.5%) (see above). Wing venation has not been examined because we were not able to dissect the single specimen available.

Malaveria mimula (Hayward, 1954), **comb. nov.**
(Figs. 26a-26m)

Type material: HOLOTYPE male: /Misiones, San Ignacio, 1937 D.149/Holotipo/*Euptychia mimula* Hayw. Holotipo ♂ K. J. Hayward det./Holotipo/Prep. Gen SAT.159 K. J. Hayward det./1079 K. J. Hayward det./ [in Museo de Ciencias Naturales de la Fundación Miguel Lillo, Tucumán, Argentina] (photograph examined).

Additional material examined: 11 males (2 dissected) and 2 females (1 dissected). PARAGUAY (11 males, 2 females): Cordillera: Compañía Naranjo, Barrio San José, 03.IX.2014 3 males (MB-0349, MB-0350, MB-0351); Guaira: Colonia Independencia, 07.IX.2014 1 male (MB-0155); Kaaguasú: 20 km South Repatriacion, 07.IX.2014 1 male (MB-0352); Paraguari: Cerro Acahay, 05.IX.2014 4 males (MB-0153*, MB-0154, MB-0353, MB-0354); La Colmena, Kaatymi, 08.IX.2014 1 male (MB-0156); Sapucaí, 08.IX.2014 1 male (MB-0152*); 08.IX.2014 2 females (MB-0266, MB-0343*) [MB].

Redescription: Male (Figs. 26a-26b): FWL: 20–23 mm (11 specimens); average 22 mm. DFW: ground color brown uniform. VFW: ground color brown lighter than DFW, almost greyish, picked with creamy light scales except on anal margin, giving a smoky aspect to the pattern elements; submedian and median lines thin, dark brown, submedian line slightly curved outside in Cu2-2A, median line curved inside near the costa and straight up to 2A; submarginal area with one faded very small black ocellus in the apex in M1-M2; submarginal line of same width and color as median line, markedly scalloped from radius to 2A, pointing distally in M1 to 2A; marginal dark line thinner and regular, parallel to outer margin. DHW: ground color same as DFW; marginal and submarginal

lines observable by transparency. VHW: ground color same as VFW; submedian and median lines of same width and color as on VFW, markedly irregular and broken, median line joining the anal margin at the origin of the submarginal line; submarginal line of same color and width, markedly scalloped, pointing distally from M1 to 2A; marginal dark line thin parallel to outer margin from costa to tornus; submarginal area with five very small ocelli, one in each space between Rs and Cu2, ocelli in M1-M2 and Cu1-Cu2 black, circled by a yellowish ring, with two very small white pupils, ocelli in M2-M3 and M3-Cu1 almost non visible represented by a creamy oval dash, ocellus in Rs-M1 the smallest, represented by a black dash.

Female (Figs. 26c-26d): FWL: 19-21 mm (2 specimens); average 20 mm. Similar to male, differing by its rounder global shape and lighter color on the underside.

Male genitalia (2 dissected) (Figs. 26e-26k): the general armature in characteristic of the genus *Malaveria* gen. nov. The uncus is lanceolate but relatively less stylized (shorter and broader); the shape of the valvae is distinctive in the basal half, where it has a dorsal sinusoidal ridge, the digitiform distal half more ornamented with processes; aedeagus relatively chubby.

Female genitalia (2 dissected) (Figs. 26l-26m): we can only distinguish that the corpus bursae is seemingly less elongated than in other species of the genus, the signa are thick, almost as long as the corpus, running parallel to each other.

Variation: specimens examined from Paraguay did not show significant variation among them.

Diagnosis: *M. mimula* comb. nov., differs from all the other species of *Malaveria* gen. nov., by: 1. smoky aspect of the underside pattern (except *M. duponti* sp. nov.); 2. markedly irregular and broken median line on VHW; 3. very small ocelli on underside and 4. markedly scalloped and broken submarginal line on underside. For differences with *M. duponti* sp. nov., see under that species.

Hostplant: unknown.

Habitat and behavior: *M. mimula* comb. nov., has been observed by one of the authors (MB) in Paraguay. It was a common species in the region of Asunción, being collected at various sites. It was mostly encountered in secondary growth forest in more or less open areas. The behavior was typical of other common species of satyrine butterflies of the subtribe Euptychiina (see under *M. modesta* comb. nov.). The species is distributed in Paraguay, Southeastern Bolivia, Argentina and Southeastern Brazil.

Discussion: *Euptychia mimula* was described by Hayward in 1954 from two male individuals, one (holotype) from San Ignacio, Misiones, Argentina; the other (paratype) from Santa Cruz, Bolivia. The holotype is illustrated

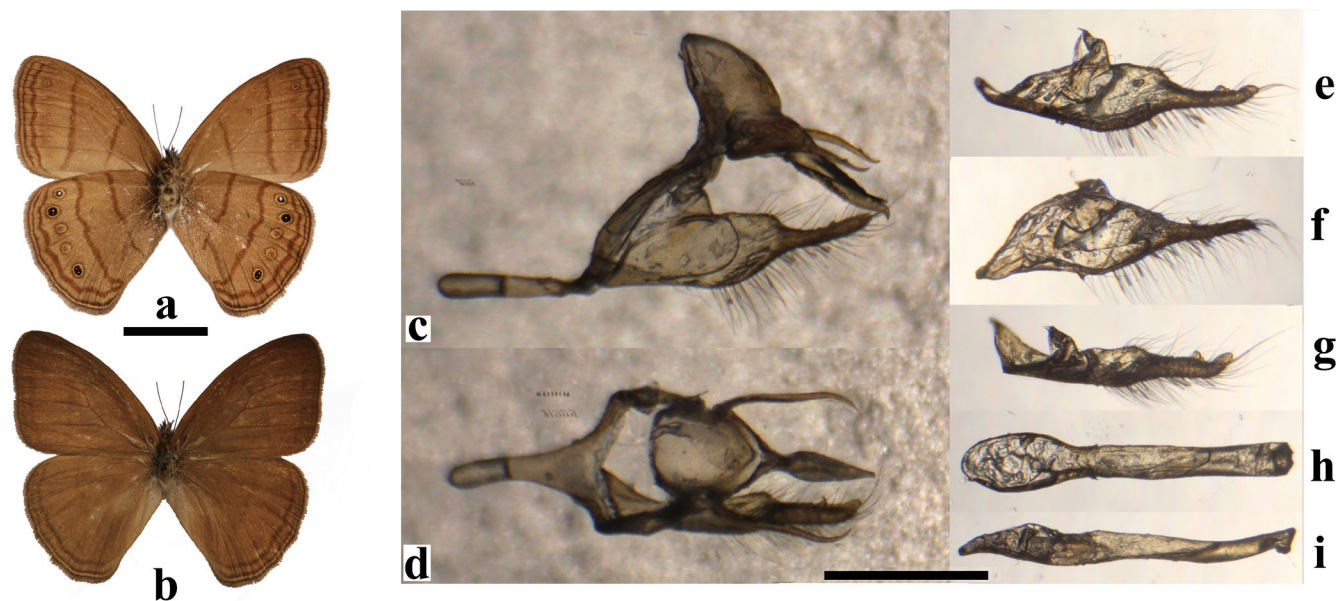


Figure 25. *Malaveria bottoi* sp. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Male genitalia lateral view (one valva removed); d. *idem* dorsal view; e. Valva lateral inner view, f. *idem* lateral outer view; g. *idem* dorsal view; h. Aedeagus dorsal view; i. *idem* lateral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

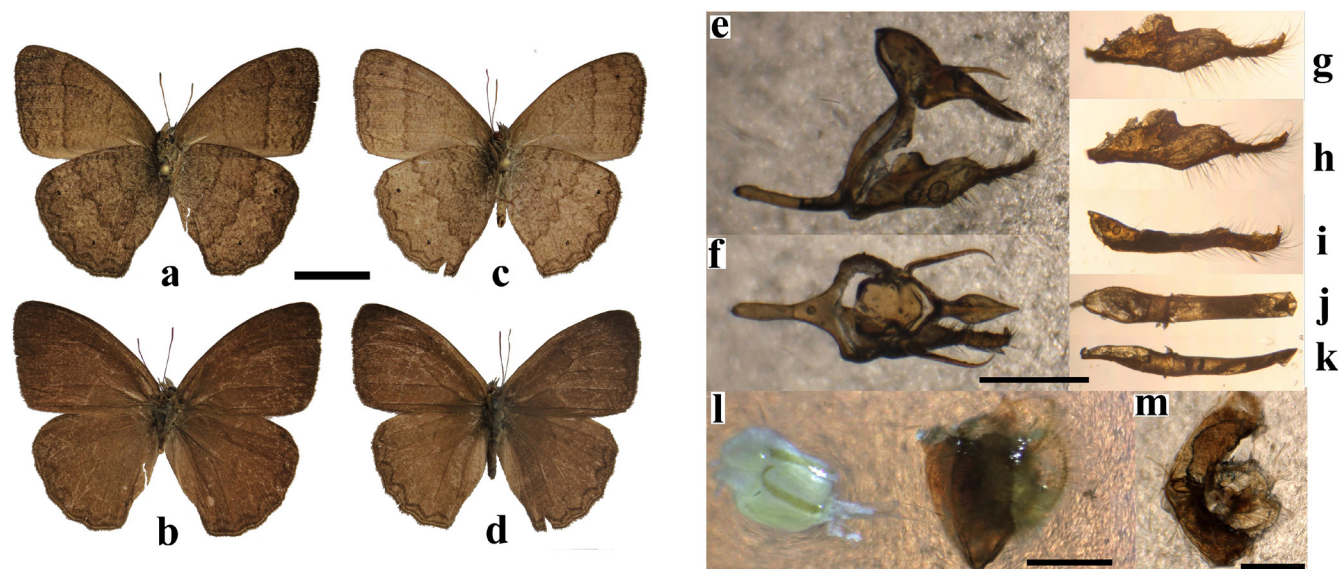


Figure 26. *Malaveria mimula* comb. nov., imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. *idem* dorsal; e. Male genitalia lateral view (one valva removed); f. *idem* dorsal view; g. Valva lateral inner view; h. *idem* lateral external view; i. *idem* dorsal view; j. Aedeagus dorsal view; k. *idem* lateral view; l. Female genitalia lateral view; m. *idem* ventral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

on the BOA website (http://www.butterfliesofamerica.com/L/t/Yphthimoides_mimula_a.htm), and agrees very well with the specimens we examined and dissected from Paraguay. Despite the apparently modified pattern of the underside with the smoky aspect, the markedly irregular submedian and median lines, the markedly broken submarginal line and the very small ocelli, we found that this species shares most of the characteristics defining *Malaveria*

gen. nov. Furthermore, the male genitalia are very similar to those of the other species of *Malaveria gen. nov.* Our study found that *M. mimula comb. nov.*, and *M. duponti sp. nov.*, share the same sequence in the DNA fragment analyzed (see discussion under DNA results section, Table 2) and the same venation (Figs. 4g-4h). *Malaveria mimula comb. nov.*, represents the sister of the Andean species of *Malaveria gen. nov.* These arguments confirm

the new taxonomic arrangement adopted here by transferring *mimula* to *Malaveria* **gen. nov.**

Malaveria duponti Benmesbah & Murienne, **sp. nov.**

(Figs. 27a-27m)

<http://zoobank.org/urn:lsid:zoobank.org:act:4BE287E2-28C0-4C95-AC3C-D22F053D02D0>

Type material: HOLOTYPE male (Figs. 27a-27b): /BOLIVIA: Caranavi/Holotype male of *Malaveria duponti* Benmesbah & Murienne, 2020/Daniel Dupont leg./MB-0147*/ [MB]. PARATYPES: 3 males: same data as Holotype (MB-0145*, MB-0146*) [MB], (MB-0148*) [MNHN]; 1 female: same data as Holotype (MB-0149*) [MB].

Description: Male (Figs. 27a-27b): FWL: Holotype 22 mm, 22–22 mm (4 specimens); average 22 mm. DFW: ground color brown uniform. VFW: ground color brown, lighter than DFW; submedian and median lines slightly irregular, thin, brown, slightly ferruginous, submedian line curved outside in Cu2-2A, median line curved inside near the costa and straight up to 2A; submarginal area with a small black ocellus circled by a yellowish ring with two tiny white pupils in the apex in M1-M2; submarginal line of same width and color than median line, scalloped from radius to 2A, pointing distally in Rs to Cu2; marginal line thinner and regular, parallel and closer to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing. VHW: ground color same as VFW; submedian and me-

dian lines very irregular and broken of same width and color as on VFW, median line joining the anal margin at the origin of the submarginal line; submarginal line of same color and width, scalloped, pointing distally from M1 to 2A; marginal dark line thin, parallel to outer margin from costa to tornus; submarginal area with five ocelli, one in each space between Rs and Cu2, ocelli in M1-M2 and Cu1-Cu2 rounded, black, circled by a yellowish ring with two very small white pupils, ocelli in M2-M3 and M3-Cu1 of same size as the precedents, yellowish without black or pupils in the center, ocellus in Rs-M1 the smallest, represented by a black dash circled with a yellowish ring.

Female (Figs. 27c-27d): FWL: 22 mm (1 specimen). Similar to male, the only female examined differs by the lighter under and upperside ground color.

Male genitalia (4 dissected) (Figs. 27e-27k): the general aspect of the genital structure of this distinctive species matches all features described for *Malaveria* **gen. nov.** The tegumen is globular; the uncus lanceolate and proportionally similar to that of the type species of the genus; the saccus is more stylized (thinner); the valvae have an angled corner on the dorsal ridge, at the end of its basal half, just before the constriction in which the digitiform extremity is formed, the distal horn-like inner process of the valva is particularly well developed; the aedeagus is roughly the same length as the valva, and is moderately robust, broader at its base.

Female genitalia (1 dissected) (Figs. 27l-27m): very well developed papillae anales, setose; ostium bursae lo-

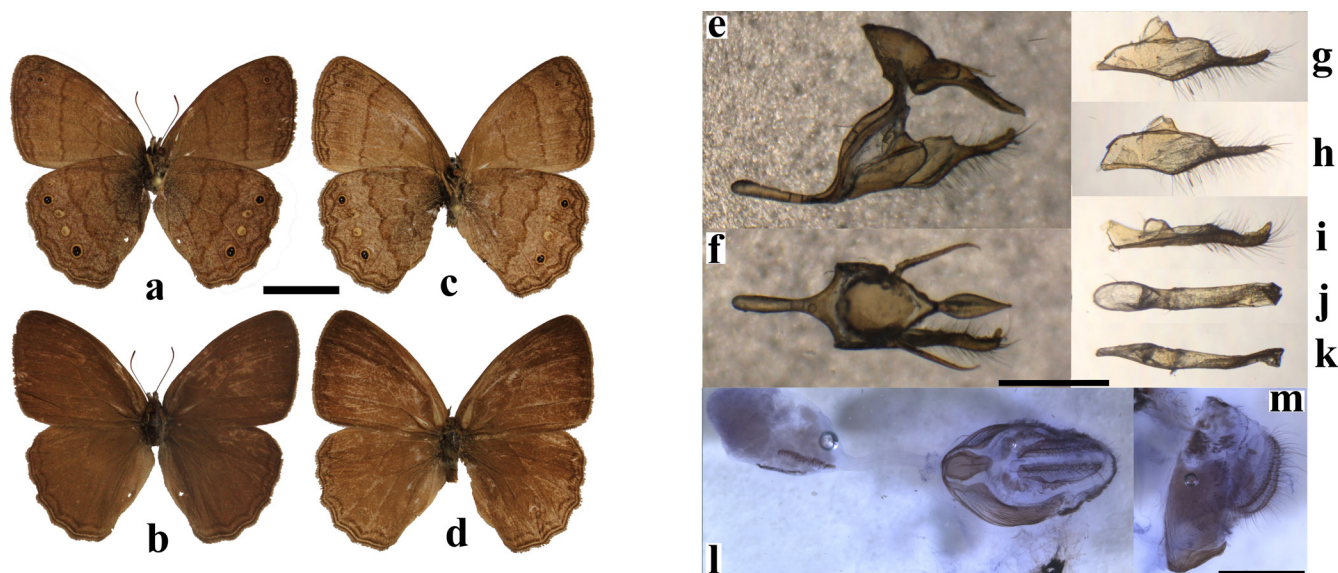


Figure 27. *Malaveria duponti* **sp. nov.**, imagos and genitalia. a. Male ventral; b. *idem* dorsal; c. Female ventral; d. *idem* dorsal; e. Male genitalia lateral view (one valva removed); f. *idem* dorsal view; g. Valva lateral inner view; h. *idem* lateral outer view; i. *idem* dorsal view; j. Aedeagus dorsal view; k. *idem* lateral view; l. Female genitalia lateral view; m. *idem* ventral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

cated immediately below; ductus as long as the corpus bursae, in which there are two longitudinal, parallel signa, running from its base to the middle of its length.

Variation: all the specimens examined did not show significant variations.

Diagnosis: *M. duponti* sp. nov., differs from all the other members of *Malaveria* gen. nov. (except *M. mimula* comb. nov.), by the markedly irregular and angled submedian and median lines on VHW. In this aspect it is reminiscent of *M. nebulosa* comb. nov., in which these two lines are less irregular and more wavy (Fig. 20). Furthermore the distal extremity of the valvae is different: 1. membranes present in *M. duponti* sp. nov. (absent in *M. nebulosa* comb. nov.), and 2. proximal spiny inner projection present in *M. nebulosa* comb. nov., is absent in *M. duponti* sp. nov. DNA analysis showed specimens of *M. nebulosa* and *M. duponti* sp. nov., to clearly group separately within *Malaveria* gen. nov. (Table 1), and their difference is 6.8% (Table 2). *M. duponti* sp. nov., is very close to *M. mimula* comb. nov., but differs by: 1. the ground color of the underside (brown in *M. duponti* sp. nov., greyish in *M. mimula* comb. nov.); 2. the more clearly defined pattern of the underside in *M. duponti* sp. nov.; 3. the bigger ocelli in *M. duponti* sp. nov. The latter is also apparently close to '*Yphthimoides*' *grimon* (Godart, [1824]) with which it shares the markedly irregular and angled submedian, median and submarginal lines (Fig. 20l). A careful examination shows the median line drawing is not exactly the same and differs subtly from each other. Furthermore, the male genitalia (4 specimens of *M. duponti* sp. nov., and 2 of '*Y.*' *grimon* dissected) are distinct: 1. upperside of the uncus markedly convex upward in '*Y.*' *grimon* (flattened and straight in *M. duponti* sp. nov.); 2. distal part of the valvae much shorter in '*Y.*' *grimon* and 3. dorsal part of the valvae much more angular in '*Y.*' *grimon*.

Etymology: dedicated to honor our friend Daniel Dupont, a French entomologist and collector, who provided many interesting butterfly samples for study from South America, including the type series of this species. The name *duponti* is a Latinized masculine noun in the genitive case.

Hostplant: unknown.

Habitat and behavior: we did not observe this species in the field. All the specimens we could examine are from Caranavi, Bolivia. They were included in a mixed sample of papered Satyrinae collected from that region. No information for elevation data was provided, but it is presumably up to 800m as most of the other species were collected within that range.

Discussion: the examination of male genitalia (4 males dissected) did not show significant interspecific differ-

ences; as discussed before, male genitalia are very similar among different species in this genus and are not always diagnostic at specific level. Molecular analysis showed specimens of *M. duponti* sp. nov., and *M. mimula* comb. nov., to have the same nucleotide sequence in the DNA fragment analyzed; as discussed above, we think this is due to the lack of discriminating power of the method used here as it occurred with *M. modesta* comb. nov. and *M. remypignoux* sp. nov., and with *M. rodriguezii* sp. nov. and *M. bottoi* sp. nov. Given the differences in habitus and the distance separating the two species, we treat here *M. duponti* sp. nov., as a species in its own right. *M. duponti* sp. nov. and *M. mimula* comb. nov., are probably sister taxa inhabiting in two different biogeographical areas, the Andean foothill for the former and the Chaco and adjacent lowlands of Bolivia, Paraguay, Argentina and Brazil (and perhaps Uruguay) for the latter. Further collecting in Bolivia and a more comprehensive DNA comparative study could provide a better understanding of the relationships between these 2 taxa and other species of the "*alcinoe*-complex". Although similar in appearance to *M. duponti* sp. nov., '*Yphthimoides*' *grimon* shows different male genitalia characters that could be specific of a distinct species group.

Koutalina Vilorio & Muriene, gen. nov.

Koutalina pamela (Hayward, 1957), comb. nov.
(Figs. 28a-28o)

Type material: not located. Hayward (1957) designated a male holotype (genitalia preparation No. MSS 26) that was deposited at the Instituto de Historia Natural "Sánchez Labrador" in San Miguel de Buenos Aires, Argentina (an ephemeral institution that lasted just a few years mainly due to the tragic death of its founder – Father Albino J. Bridarolli – in 1949). According to Williner (1938, 1950), SEA (1950) and Asúa (2019), the Bridarolli collection of the mentioned institute was kept in the Colegio Máximo de San José. Bachmann (2003) indicates that in 1983 the founders of the Instituto de Entomología de Salta (INESALT) in Rosario de Lerma, received a minimal part of that entomological collection. The other part (which is the largest) was first transferred to the Colegio del Salvador in Buenos Aires, where it was properly cared for, but finally donated and transferred to the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), on February 25, 2003. Some samples remain at the Colegio del Salvador for educational purposes (Bachmann 2003). Barbosa *et al.* (2018) also failed to locate in the MACN collection a type specimen of another Boliv-

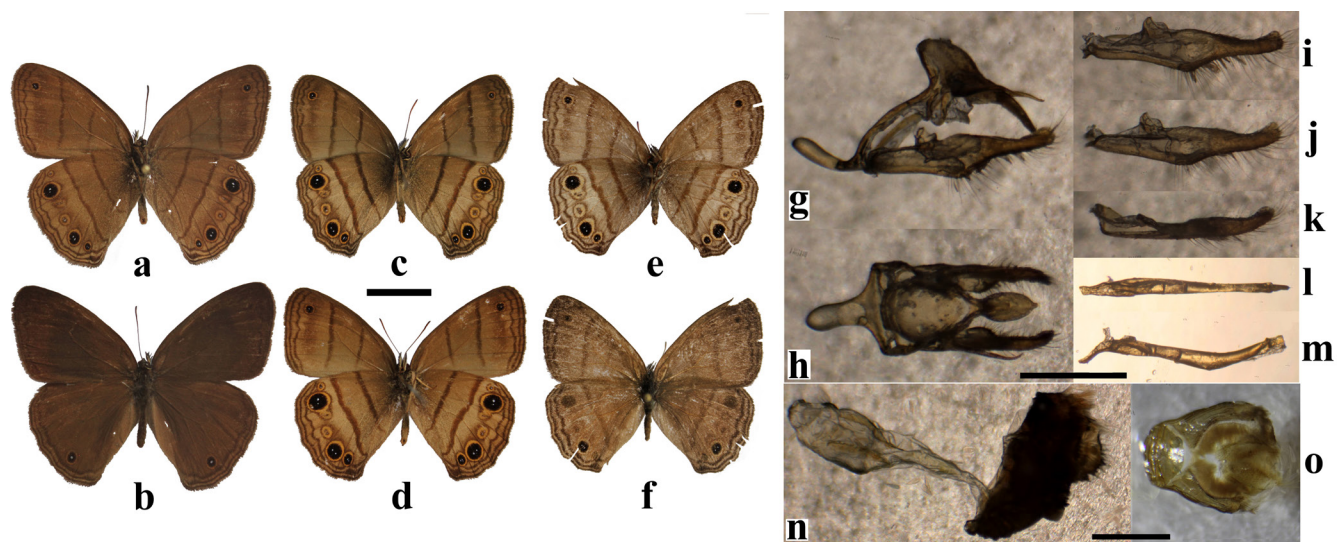


Figure 28. *Koutalina pamela* comb. nov., imagos and genitalia. a. Male from Bolivia ventral; b. *idem* dorsal; c. Male from Peru ventral; d. Male from Bolivia ventral; e. Female from Peru ventral; f. *idem* dorsal; g. Male genitalia lateral view (one valva removed); h. *idem* dorsal view; i. Valva lateral inner view; j. *idem* lateral outer view; k. *idem* dorsal view; l. Aedeagus dorsal view; m. *idem* lateral view; n. Female genitalia lateral view; o. *idem* ventral view. (Scale imago: 1 cm; scale genitalia: 1 mm).

ian satyrine species described by Hayward, *Euptychia patricia*. Ellenrieder (2009) does not mention any type of Lepidoptera in the collections of the Museo de Ciencias Naturales de Salta.

Material examined: 15 males (4 dissected), 1 female (1 dissected): - BOLIVIA (9 males): La Paz: Caranavi 800-1500m, January 2013 6 males (MB-0057, MB-0058, MB-0059*, MB-0060, MB-0061, MB-0062*) [MB], Yungas de la Paz 1000m, 1913 2 males (MB-03, MB-04) [MNHN]; No precise location: 1902 1 male (MB-01) [MNHN].- PERU (6 males, 1 female): Cusco: Carretera Manu 1 male (MB-0063*), Quincemil 26km Southwest 1580m, 28-30.VI.2019 2 males (MB-0347, MB-0348) [MB] and 1 female (MB-0346*) [MB]; Junín: Mina Pichita 2100m, 12.IX.2001 2 males (MB-0064, MB-0065*) [MB]; Pasco: Huacabamba, Cerro del Pasco, 1913 1 male (MB-02) [MNHN].

Redescription: Male (Figs. 28a-28d): FWL: 19-23 mm, average 20.7 mm (15 specimens). DFW: ground color dark-brown; large darker and rectangular androconial patch in the middle of the forewing (Figs. 29a-29d). VFW: ground color brown lighter than DFW, discreetly coppered; submedian and median lines slightly irregular, thin, dark-brown, median line running outside between Cu2 and 2A; submarginal area with a small black ocellus in the apex in M1-M2, circled by a yellowish ring, with two tiny white pupils; submarginal line of same color, slightly thinner than median line, scalloped from radius to 2A, pointing distally in Rs to Cu2; marginal line thinner

and regular, parallel to outer margin. DHW: ground color same as DFW; marginal and submarginal lines observable through translucent wing; ocellus in Cu1-Cu2 black circled with yellowish ring, with two tiny white pupils in the center; marginal line broadened at tornus; areas between submarginal line and outer margin lighter. VHW: ground color same as VFW; submedian and median lines slightly irregular, of same width and color as on VFW, median line making a smooth curve before joining the anal margin at the origin of the submarginal line; submarginal line slightly thinner, of same color, scalloped, pointing distally from M1 to 2A, making a double sinuosity towards the base in M2-M3, and flat in Cu1-Cu2; marginal dark line thinner, parallel to outer margin, broadened at tornus; submarginal area with six ocelli, all with two tiny white pupils, circled by a yellowish ring and surrounded by a discreet dark brown area, one in each space between Rs to 2A, ocellus in M1-M2 bigger, rounded and black, touching M1 and M2, ocellus in Cu1-Cu2 similar, slightly smaller, ocelli in M2-M3 oval and M3-Cu1 rounded, both yellowish without black in the center, ocellus in Rs-M1 the smallest, anal ocellus in Cu2-2A black, same size as that one in M3-Cu1.

Female (Figs. 28e-28f): FWL: 20 mm (1 specimen). Similar to male but differs by much lighter upper and underside and by the absence of androconial patch on DFW.

Male genitalia (4 dissected) (Figs. 28g-28m): as in the generic description above.

Female genitalia (1 dissected) (Figs. 28n-28o): ventral sclerite of the 8th abdominal segment much broader than

in the representatives of *Modestia* **gen. nov.**, and *Malaveria* **gen. nov.** Papillae anales proportionally smaller than in *Malaveria* **gen. nov.**; bursa copulatrix with two distinctive signa, running parallel to each other throughout basal half of the corpus, but notably separated, perhaps twice as much as in the species of *Malaveria* **gen. nov.**, ductus as long as the corpus bursae.

Variation (Figs. 28a-28d): the 16 specimens (15 males and 1 female) from Bolivia and Peru showed variation in the average size, specimens from Peru being smaller with a more rounded wing shape: average FWL 21.2 mm from Bolivia (9 specimens), 19.8 mm from Peru (6 specimens). In general specimens from Peru seem to have a more greyish underside and ocelli, median and submedian band wider on VHW than specimens from Bolivia (see discussion). Only 1 female was examined and it is from Peru. On DHW, ocellus in Cu1-Cu2 appears with two distinct pupils or with a single fused wider pupil in the same fashion as it has been discussed above for species belonging in *Modestia* **gen. nov.**, and *Malaveria* **gen. nov.** The tiny ocellus in Cu2-2A is present in half of the specimens (none from Caranavi).

Diagnosis: *Koutalina pamela* **comb. nov.**, is easily differentiated from all other genera currently included in the Euptychiina by the presence of 6 ocelli on VHW, all bipupillate and a large androconial patch (Figs. 29a-29d) on DFW in males.

Hostplant: unknown.

Habitat and behavior: Á. L. Viloría observed and collected *K. pamela* **comb. nov.**, in the locality of Mina Pichita (2,100m), Junín, Peru. This butterfly was found flying fast and erratically in slightly disturbed, dry, low cloud forest. Short periods of the butterfly resting on the leaves of the shrubs at clearings under sunshine allowed their

capture, but in general, individuals escaped by skipping and fast flying upwards. All the specimens we examined are from the eastern slopes of the Andes from las yungas (Bolivia) to Pasco (Central Peru). Records are from 800m to 2,100m.

Discussion: *E. pamela* was described by Hayward in 1957 apparently based on a single specimen from Chulumani, South Yungas, Bolivia. A meticulous description is given and the male genitalia are illustrated. Hayward mentions two ocelli on the DHW tornus (see Fig. 29a). We found this character to be inconstant, half of the specimens showing only the biggest ocellus in Cu1-Cu2. Although the androconial patches are not clearly mentioned, Hayward noticed that the ground color of the DFW was dark brown (almost black), and the distal third of the wing lighter. Hayward finished his description considering *E. pamela* to be close to *E. phineus* Butler, 1867, a junior synonym of *Optimandes eugenia eugenia* (C. Felder & R. Felder, 1867), the type species of the clearly different genus *Optimandes* Marín, Nakahara & Willmott, 2019 (in Willmott *et al.* 2019). *Optimandes eugenia* differs from it in many aspects: 1. a single pupil in all the ocelli of the VHW; 2. absence of androconial patch on DFW and 3. different morphology of their male genitalia. To date the holotype of *E. pamela* has not been found but it is probably preserved in a minor Argentinian collection (see above). Lamas (2004) treated *E. pamela* as a synonym of *N. alcinoe*, which it is clearly not. D'Abbrera represented two males or *K. pamela* **comb. nov.**, as "*Euptychia* sp. ?" (p. 777) from Peru and Bolivia in the NHMUK, just between *E. phineus* and *E. mimas*, *E. alcinoe* and *E. benedicta*.

This species possesses very particular characters. They enabled us to erect and describe the new genus *Koutalina* **gen. nov.**, of which it is the only known representative.

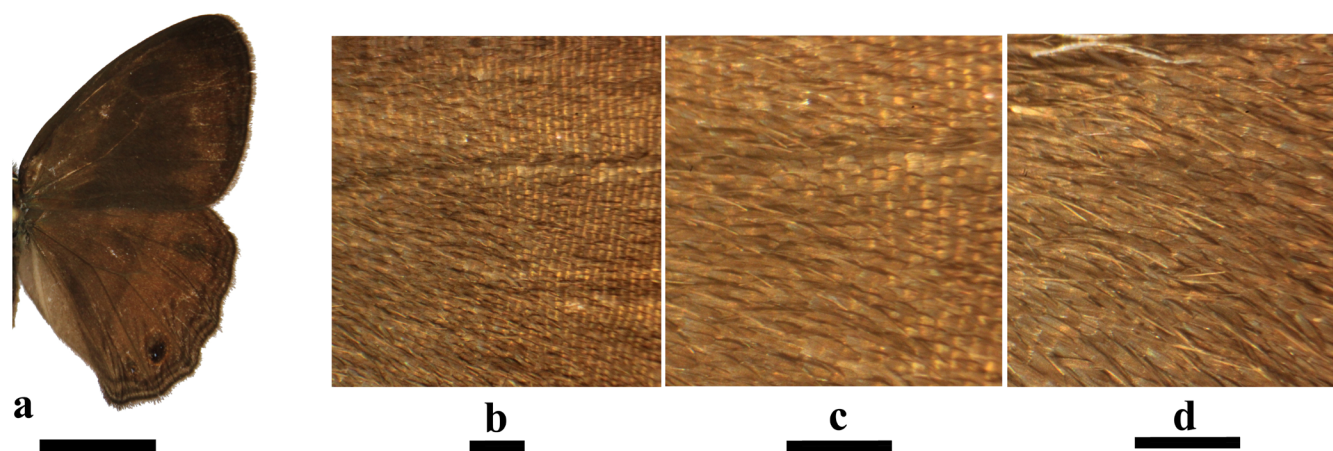


Figure 29. *Koutalina pamela* **comb. nov.** DFW androconial patch. a. Male dorsal; b-d. Details of DFW scaling. (Scale image: 1 cm; scale detail DFW: 1 mm).

The original description by Hayward (1957) mentions 4 characters particular to *K. pamela* **comb. nov.**: 1. presence of two ocelli in the tornus on DHW (it varies, some specimens have only one); 2. lighter area outside the median line on VHW; 3. wide VHW ocellus in M1-M2 linked with oval ocellus in M2-M3 which seems compressed by the former; 4. VHW ocellus in M3-Cu1 oval, with long axis parallel to external margin. These characters are present in two specimens from Bolivia (Fig. 28d) labelled “Yungas de la Paz, 1000m” collected in 1913. After a careful study of the original description and the original illustration of the male genitalia, we have no doubt Hayward based its description on a similar specimen, and the name “*pamela*” applies to the taxon represented here by one of these specimens. They come from a locality 60 km south of Caranavi, in the same region of Las Yungas. These two specimens seem to represent an intermediate habitus between the populations from Caranavi (Bolivia) and Peru. For the moment, we prefer treating them as the same taxon.

In general what we identified as *pamela* is represented by specimens that seem to show some variation in their habitus (see “Variation”), and schematically two different phenotypes can be distinguished. Five of the 6 males from Caranavi (Bolivia) showed (Figs. 28a-28b): 1. larger size; 2. homogenous light brown coloration on the underside; 3. relatively small ocelli on VHW; 4. thin median and post median lines on VHW. The specimens from south and central Peru differed as follows (Figs. 28c, 28e-28f): 1. smaller; 2. with a greyish VHW; 3. bigger ocelli on VHW and 4. wider median and submedian lines on VHW. Furthermore, none of the 6 specimens from Caranavi have an ocellus on DHW in Cu2-2A, whereas 5 of the 6 specimens from Peru do present it. We did not find differences in male genitalia (2 specimens from Caranavi and 2 from Peru dissected), nor in DNA analysis (4 specimens from Caranavi and 3 specimens from Peru). Two specimens from the Yungas (Fig. 28d.), 1 from Caranavi (Bolivia), and 2 others from Cusco and Pasco (Peru), had intermediate habitus.

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APPENDIX.

DATA OF SPECIMENS ILLUSTRATED

Figure 3:

- 3a. *Modestia modesta* **comb. nov.**, male: French Guiana, Saül, 12.IX.2013 (MB-0021) (MB).
- 3b-3c. *Modestia modesta* **comb. nov.**, male: French Guiana, Saül, 12.IX.2013 (MB-0020) (MB).
- 3d. *Modestia modesta* **comb. nov.**, male: French Guiana, Saül, 30.IX.2012 (MB-0022) (MB).
- 3e. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda, El Jarillo, Guaicaipuro, Quebrada Honda 1300m, 23.VII.2013 (MB-0002) (MB).
- 3f-3h. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda, El Jarillo, Guaicaipuro, Quebrada Honda 1300m, 23.VII.2013 (MB-0006) (MB).
- 3i., 3l. *Koutalina pamela* **comb. nov.**, male: Bolivia, La Paz, Caranavi 800-1500m, I.2013 (MB-0059) (MB).
- 3j-3k. *Koutalina pamela* **comb. nov.**, male: Bolivia, La Paz, Caranavi 800-1500m, I.2013 (MB-0060) (MB).

Figure 4:

- 4b. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda, El Jarillo, Guaicaipuro, Quebrada Honda 1300m, 23.VII.2013 (MB-0002) (MB).
- 4c. *Malaveria mimas* **comb. nov.**, male: Bolivia, La Paz, Caranavi (MB-0013) (MB).
- 4d. *Malaveria alcinoe* **comb. nov.**, male: Venezuela, Lara, Parque Nacional Yacambú, 13km South Sanare, 15-21.I.1979 (MB-0008) (IVIC).
- 4e. *Malaveria ballofi* **sp. nov.**, male: Ecuador, Pichincha, Nanegalito, 16.X.2015 (MB-0071) (MB).
- 4f. *Malaveria rodriguezi* **sp. nov.**, male: Colombia, Antioquia, Frontino 1900m, 22.IV.2000 (MB-0253) (MB).
- 4g. *Malaveria mimula* **comb. nov.**, male: Paraguay, Cordillera, Compañía Naranjo, Barrio San José, 03.IX.2014 (MB-0349) (MB).
- 4h. *Malaveria duponti* **sp. nov.**, male: Bolivia, Caranavi (MB-0145) (MB).

Figure 5:

- 5a. *Magneptychia libye* male: Venezuela, Cordillera de la Costa, wing prep. ALV0004-14 (ALV).
- 5b-5c. *Magneptychia libye* male: French Guiana.
- 5d. based on *Emeryus argulus* male venation in Zacca *et al.* (2020, Fig. 3a).
- 5e-5f. *Emeryus argulus magnum* Zacca, Casagrande & Mielke, 2020, male: French Guiana,

- 5g. based on *Paryphthimoides poltys* male venation in Zacca *et al.* (2020, Fig. 68).
- 5h-5i. *Paryphthimoides poltys* female: Paraguay,
- 5j. based on *Cissia penelope* male venation in Zacca *et al.* (2018, Fig. 3A).
- 5k-5l. *Cissia penelope* male: French Guiana, Saül, Boeufmort, 03.IX.2011 (MB-0021) (MB).

Figure 6:

- 6a. *Modestia modesta* **comb. nov.**, male: French Guiana, Papaichton, 23.VII.2012 (MB-0023) (MB).
- 6b. *Malaveria ballofi* **sp. nov.**, male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0070) (MB).
- 6c. *Malaveria ballofi* **sp. nov.**, male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0076) (MB).
- 6d. *Malaveria ballofi* **sp. nov.**, male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0074) (MB).
- 6e. *Malaveria ballofi* **sp. nov.**, male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0257) (MB).
- 6f. *Malaveria ballofi* **sp. nov.**, male: Ecuador, Pichincha, Nanegalito, 16.X.2015 (MB-0016) (MB).

Figure 7:

- 7a-b. *Malaveria mimas* **comb. nov.**, male: Peru, Cusco, Cusco, carretera Manu 800-2900m, October 2015 1 male (MB-0014) (MB).
- 7c-d. *Malaveria mimas* **comb. nov.**, male: Bolivia, La Paz, Caranavi (MB-0012) (MB).
- 7e-f. *Malaveria mimas* **comb. nov.**, male: Bolivia, La Paz, Caranavi (MB-0010) (MB).

Figure 8:

- 8a-b. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda: El Jarillo, Guaicaipuro, Quebrada Honda 1700m, 05.VIII.2013 (MB-0004) (MB).
- 8c-d. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda: El Jarillo, Guaicaipuro, Quebrada Honda 1200m, 26.VIII.2013 (MB-0007) (MB).
- 8e-f. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda: El Jarillo, Guaicaipuro, Quebrada Honda 1700m, 23.VII.2013 (MB-0003) (MB).

Figure 9:

- 9a-b. *Modestia modesta* **comb. nov.**, male: French Guiana, Saül, 30.IX.2012 (MB-0022) (MB).
- 9c-d. *Modestia modesta* **comb. nov.**, male: French Guiana, Papaichton, 23.VII.2012 (MB-0023) (MB).
- 9e-f. *Modestia modesta* **comb. nov.**, female: French Guiana, Itoupé, 30.XI.2014 (MB-0030) (MB).

Figure 10:

- 10a. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda, El Jarillo, Guaicaipuro, Quebrada Honda 1300m, 05.VIII.2013 (MB-0004) (MB).
- 10b. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda: El Jarillo, Guaicaipuro, Quebrada Honda 1300m, 23.VII.2013 (MB-0006) (MB).
- 10c. *Malaveria rodriguezii risaralda* **ssp. nov.**, male: Colombia, Valle del Cauca, 1902 (MB-013) (MNHN).
- 10d. *Malaveria* sp. male: Colombia, Bogotá, Santa Fé de Bogotá 1850m (MB-014) (MNHN).
- 10e. *Modestia remypignoux* **sp. nov.**, Holotype male: French Guiana, Maripasoula, Antecume Pata, 13.III.2012 (MB-0039) (MB).
- 10f. *Modestia remypignoux shueyi* **ssp. nov.**, male: Panamá, Colón, Santa Rita 245m, 18.II.2014 (MB-0213) (MB).
- 10g. *Malaveria mimas* **comb. nov.**, male: Bolivia, La Paz: Caranavi (MB-0010) (MB).
- 10h. *Malaveria mimas* **comb. nov.**, male: Peru, Cusco, carretera Manu 800-2900m, October 2015 (MB-0014) (MB).
- 10i. *Malaveria ballofi* **sp. nov.**, Holotype male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0072) (MB).
- 10j. *Malaveria ballofi* **sp. nov.**, male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0073) (MB).
- 10k. *Malaveria duponti* **sp. nov.**, male: Bolivia, Caranavi (MB-0145) (MB).
- 10l. *Malaveria duponti* **sp. nov.**, male: Bolivia, Caranavi (MB-0146) (MB).

Figure 11:

- 11a. '*Magneuptychia*' *tricolor* male: Peru, Loreto, September 2013 (MB).
- 11b. '*Magneuptychia*' *tricolor* male: Peru, Loreto, September 2013 (MB).
- 11c. *Megisto cymela* male: USA, Ohio, Muskingum County, Zanesville, 03.VI.1978 (MB).
- 11d. *Modestia remypignoux* **sp. nov.**, female: French Guiana, Maripasoula, Antecume Pata, 13.III.2012 (MB-0050) (MB).
- 11e. *Magneuptychia libye* male: Tobago, January 2009 (MB).
- 11f. *Magneuptychia libye* female: French Guiana, Saint-Laurent-du-Maroni, 24.X.2011 (MB).
- 11g. *Euptychia marceli* male: French Guiana, Saül, 05.X.2011 (MB).
- 11h. *Modestia remypignoux* **sp. nov.**, female: French Guiana, Saint-Laurent-du-Maroni, 24.X.2011 (MB-0051) (MB).

Figure 12:

- 12a. Lectotype of *Euptychia modesta*: /Type H.T./Syn-type/♂/Type of Species./ Godman-Salvin Coll. 1904.-1./*Euptychia modesta*, Butl./♂ *Pará modesta* Butler type / Para, L. Amazons. H. W. Bates. / B. M. TYPE N°. Rh 3222 *Euptychia modesta*, ♂ Butl./BMNH(E) #986581 (NHMUK).
- 12b. Lectotype of *Neonympha sylvina*: /*Neonympha sylvina* Feld./Bahia Luschnatt type/FELDER COLLⁿ/Type/Type of *N. sylvina* Feld, very near *E. modesta*. Butl./*Sylvina* n./Rothschild Bequest B.M.1939-1/ (NHMUK).
- 12c. Lectotype of *Neonympha alcinoe*: Type/FELDER COLLⁿ./*Alcinoë* Feld./Rothschild Bequest B.M. 1939-1./Type of *N. alcinoe* Feld? = *E. benedicta*, Butl. of w. it. may be a good local form. Comp. w. type *E. benedicta* Butler./BMNH(E)1266958/(NHMUK).
- 12d. Syntype of *Euptychia benedicta*: /Type H.T./Type of Species./*E. benedicta* Butler type./B.M. TYPE No. Rh3227. *Euptychia benedicta*, ♀ Butl./Sarayacu, Ecuador. C. Buckley./Godman-Salvin Coll. 1904.-1. *Euptychia benedicta*, Butl./BMNH(E)1266955/(NHMUK).

Figure 13:

- 13a-13b. *Modestia modesta* **comb. nov.**, male: French Guiana, Saül, 12.IX.2013 (MB-0020) (MB).
- 13c-13k. *Modestia modesta* **comb. nov.**, male: French Guiana, Saül, 30.IX.2012 (MB-0022) (MB).
- 13c-13d, 13l-13m: *Modestia modesta* **comb. nov.**, female: French Guiana, Mitaraka, 01.III.2015 (MB-0026) (MB).

Figure 14:

- 14a-14b, 14d-14j. *Modestia gomezi* **comb. nov.**, male: Colombia, Antioquia, Porce 800m, 27.VIII.2017 (MB-0258) (MB).
- 14c. *Modestia gomezi* **comb. nov.**, female: Panamá, Zona del Canal, Cocoli, 28.XII.1986 (JMD).

Figure 15:

- 15a-15b, 15e-15k. *Modestia remypignoux* **sp. nov.**, Holotype male: French Guiana, Maripasoula, Antecume Pata, 13.III.2012 (MB-0039) (MB).
- 15c-15d. *Modestia remypignoux* **sp. nov.**, paratype female: French Guiana, Macouria, Matiti, 18.VIII.2012 (MB-0049) (MB).
- 15l-15m. *Modestia remypignoux* **sp. nov.**, paratype female: French Guiana, Kaw, Dégrad Escolle, 14.XI.2011 (MB-0047) (MB).

Figure 16:

- 16a-16i. *Modestia remypignoux shueyi* **ssp. nov.**, Belize. Holotype male: Belize, Cayo Dist., Baldy Beacon 3,5km SSW - 1F5231 logging road in pine/oak, 750m, 23.IX.2016 (MB-0143) (MB).

Figure 17:

- 17a-17b, 17e-17k. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda, El Jarillo, Guaicaipuro, Quebrada Honda 1300m, 23.VII.2013 (MB-0006) (MB).
- 17c-17d, 17l. *Malaveria nebulosa* **comb. nov.**, female: Venezuela, Miranda, El Jarillo, Guaicaipuro, Quebrada Honda 1200m, 06.III.2013 (MB-0005) (MB).

Figure 18:

- 18a-18i. *Malaveria mimas* **comb. nov.**, male: Bolivia, La Paz, Caranavi (MB-0012) (MB).

Figure 19:

- 19a-19b, 19e-19k. *Malaveria alcinoe* **comb. nov.**, male: Venezuela, Lara, Parque Nacional Yacambú, 13km South Sanare, 15-21.I.1979 (MB-0008) (IVIC).
- 19c-19d, 19l-19m. *Malaveria alcinoe* **comb. nov.**, female: Colombia, Cundinamarca, Colegio 430m, 15.VII.1975 (MB-0009) (MB).

Figure 20:

- 20b. *Malaveria alcinoe* **comb. nov.**, Lectotype male: / Type/FELDER COLL^N./*Alcinoë* Feld./Rothschild Bequest B.M. 1939-1./Type of *N. alcinoe* Feld? = *E. benedicta*, Butl. of w. it. may be a good local form. Comp. w. type *E. benedicta* Butler./BMNH(E)1266958 (NH-MUK).
- 20c. *Malaveria alcinoe* **comb. nov.**, male: Venezuela, Lara, Parque Nacional Yacambú, 13km South Sanare, 15-21.I.1979 (MB-0008) (IVIC).
- 20d. *Malaveria rodriguezi rodriguezi* **sp. nov.**, Holotype male: Colombia, Antioquia, Frontino 2000m, 22.IV.2007 (MB-0249) (MB).
- 20e. *Malaveria rodriguezi risaralda* **ssp. nov.**, Holotype male: Colombia, Risaralda, Pueblo Rico 1400m, 20.VII.2005 (MB-0250) (MB).
- 20f. *Malaveria ballofi* **sp. nov.**, Holotype male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0072) (MB).
- 20g. *Malaveria bottoi* **sp. nov.**, Holotype male: Colombia: Cundinamarca, Colegio 430m (MB-0019) (MB).
- 20h. *Malaveria mimas* **comb. nov.**, male: Bolivia, La Paz, Caranavi (MB-0012) (MB).

- 20i. *Malaveria nebulosa* **comb. nov.**, male: Venezuela, Miranda, El Jarillo, Guaicaipuro, Quebrada Honda 1300m, 23.VII.2013 (MB-0006) (MB).
- 20j. *Malaveria duponti* **sp. nov.**, Holotype male: Bolivia, Caranavi (MB-0147) (MB).
- 20k. *Malaveria mimula* **comb. nov.**, male: Paraguay, Paraguari, Sapucaí, 08.IX.2014 (MB-0152) (MB).
- 20m. '*Paryphthimoides*.' *grimon* male: Brazil (MB-05) (MNHN).

Figure 22:

- 22a-22b, 22e-22k. *Malaveria ballofi* **sp. nov.**, Holotype male: Ecuador, Pichincha, Nanegalito, 2016 (MB-0072) (MB).
- 22c-22d, 22l-22m. *Malaveria ballofi* **sp. nov.**, Paratype female: Ecuador, Imbabura, Parambas 3500ft, 1913 (MB-06) (MNHN).

Figure 23:

- 18a-18i. *Malaveria rodriguezi rodriguezi* **sp. nov.**, Holotype male: Colombia, Antioquia, Frontino 2000m, 22.IV.2007 (MB-0249) (MB).

Figure 24:

- 24a-24i. *Malaveria rodriguezi risaralda* **ssp. nov.**, Holotype male: Colombia, Risaralda, Pueblo Rico 1400m, 20.VII.2005 (MB-0250) (MB).

Figure 25:

- 25a-25i. *Malaveria bottoi* **sp. nov.**, Holotype male: Colombia: Cundinamarca, Colegio 430m (MB-0019) (MB).

Figure 26:

- 26a-26b, 26e-26k. *Malaveria mimula* **comb. nov.**, male: Paraguay, Paraguari, Sapucaí, 08.IX.2014 (MB-0152) (MB).
- 26c-26d, 26l-26m. *Malaveria mimula* **comb. nov.**, female: Paraguay, Paraguari, Sapucaí, 08.IX.2014 (MB-0343) (MB).

Figure 27:

- 27a-27b, 27e-27k. *Malaveria duponti* **sp. nov.**, Holotype male: Bolivia, Caranavi (MB-0147) (MB).
- 27c-27d, 27l-27m. *Malaveria duponti* **sp. nov.**, Paratype female: Bolivia, Caranavi (MB-0147) (MB).

Figure 28:

- 28a-28b. *Koutalina pamela* **comb. nov.**, male: Bolivia, La Paz, Caranavi 800-1500m, January 2013 (MB-0060) (MB).

- 28c. *Koutalina pamela* **comb. nov.**, male: Peru, Cusco, Quincemil 26km SouthWest 1580m, 28-30.VI.2019 (MB-0348) (MB).
- 28d. *Koutalina pamela* **comb. nov.**, male: Bolivia, La Paz, Yungas de la Paz 1000m, 1913 (MB-03) (MNHN).
- 28g-28m. *Koutalina pamela* **comb. nov.**, male: Bolivia, La Paz, Caranavi 800-1500m, January 2013 (MB-0059) (MB).
- 28e-28f, 28n-28o. *Koutalina pamela* **comb. nov.**, female: Peru, Cusco, Quincemil 26km SouthWest 1580m, 28-30.VI.2019 (MB-0346) (MB).