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Generic reassignments of satyrine butterflies from Colombia and Venezuela (Lepidoptera: Nymphalidae)

Reasignaciones genéricas de mariposas satírinas de Colombia y Venezuela (Lepidoptera: Nymphalidae)

M. Gonzalo Andrade-C.[1], Ángel L. Viloria[2], Efraín R. Henao-Bañol[1,4] & Jean-François Le Crom[3]

[1]*Instituto de Ciencias Naturales - ICN, Universidad Nacional de Colombia, Bogotá, Colombia.*

[2]*Centro de Ecología, Instituto Venezolano de Investigaciones Científicas (IVIC), km 11 carretera Panamericana, Altos de Pipe, Edo. Miranda, Venezuela.*

[3]*Calle 45 N° 9-42, ofic. 202, Edif. Carlec, Bogotá, Colombia.*

[4]*Instituto Amazónico de Investigaciones Científicas SINCHI. Calle 20, No. 5-44, Bogotá, D. C., Colombia*

Correspondencia: M. G. Andrade-C.: mgandradec@unal.edu.co

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ABSTRACT

Four genera of butterflies belonging to the Nymphalidae: Satyrinae are erected, diagnosized, described and discussed in order to reassign ten species recently classified within the genus *Magneuptychia* Forster, several of which occur in Colombia and Venezuela: ***Nubila*** Viloria, Andrade & Henao, **gen. nov.** (to include *Euptychia gera* Hewitson, *E. metagera* Butler, *E. moderata* Weymer, *E. nortia* Hewitson, *E. purusana* Aurivillius and *E. segesta* Weymer), ***Macrocissia*** Viloria, Le Crom & Andrade, **gen. nov.** (including *Neonympha iris* C. Felder & R. Felder and *Euptychia inani* Staudinger), ***Colombeia*** Viloria, Andrade & Le Crom, **gen. nov.** (including *Euptychia mycalesis* Röber) and ***Omacha*** Andrade, Viloria, Henao & Le Crom, **gen. nov.** (including *Magneuptychia pax* Huertas, Lamas, Fagua & Willmott). Additionally, *Euptychia tiessa* Hewitson is transfered to the genus *Satyrotaygetis* Forster, which is revised. Eleven new combinations are established, one new synonym is proposed and two species are reinstated.

Keywords: *Cissia, Colombeia* **gen. nov.**, *Euptychia, Huberonympha, Macrocissia* **gen. nov.**, *Magneuptychia, Neonympha, Nubila* **gen. nov.**, *Omacha* **gen. nov.**, *Satyrotaygetis, Splendeuptychia, Stevenaria.*

RESUMEN

Se erigen, diagnostican, describen y discuten cuatro géneros de mariposas pertenecientes a las Nymphalidae, Satyrinae, con el fin de reubicar diez especies recientemente clasificadas dentro del género *Magneuptychia* Forster, varias de las cuales se encuentran en Colombia y Venezuela: ***Nubila*** Viloria, Andrade & Henao, **gen. nov.** (para incluir *Euptychia gera* Hewitson, *E. metagera* Butler, *E. moderata* Weymer, *E. nortia* Hewitson, *E. purusana* Aurivillius y *E. segesta* Weymer), ***Macrocissia*** Viloria, Le Crom & Andrade, **gen. nov.** (incluyendo *Neonympha iris* C. Felder & R. Felder y *Euptychia inani* Staudinger), ***Colombeia*** Viloria, Andrade & Le Crom, **gen. nov.** (incluyendo *Euptychia mycalesis* Röber) y ***Omacha*** Andrade, Viloria, Henao & Le Crom, **gen. nov.** (incluyendo *Magneuptychia pax* Huertas, Lamas, Fagua & Willmott). Adicionalmente se transfiere *Euptychia tiessa* Hewitson al género *Satyrotaygetis* Forster, el cual se revisa. Se establecen once nuevas combinaciones, se propone un nuevo sinónimo y se restituyen dos especies.

Palabras clave: *Cissia, Colombeia* **gen. nov.**, *Euptychia, Huberonympha, Macrocissia* **gen. nov.**, *Magneuptychia, Neonympha, Nubila* **gen. nov.**, *Omacha* **gen. nov.**, *Satyrotaygetis, Splendeuptychia, Stevenaria.*

INTRODUCTION

The apparent polyphyletic and paraphyletic natures of the genus *Magneuptychia*, as loosely diagnosized by Forster (1964), has been pointed out by Murray & Prowell (2005: 72), Marín (2011: 13, 84); Marín *et al.* (2011: 9, 10; 2017: 768, 774, 781, 182) and Costa *et al*. (2016: 200). The latter authors discussed this historical case in some detail and designated a Neotype for *Papilio libye* Linnaeus, the type species of *Magneuptychia* Forster. This nomenclatural act, followed by a comparative study of morphology and the consideration of genetic evidence available through phylogenies recently published by molecular scientists, allowed for the establishment of the boundaries of the genus based on morphological singularities of its type species and the application of basic logic. Thus, Costa *et al*. (2016) recognized only three nominal species within the genus: *M. libye*, *M. libyoidea* Butler and *M. lethra* Möschler (plus one yet to be described), and explicitly excluded 36 taxa from *Magneuptychia*. Notwithstanding the foregoing, recent work by a number of experts has deliberately chosen to disdain such taxonomic proposal (Huertas *et al*. 2016, Marín *et al.* 2017, Zacca *et al.* 2017), even if their results may appear contradictory with their approaches.

In inventorying and classifying the satyrine butterfly fauna of our countries, Colombia and Venezuela, we have dealt with the generic allocation of a number of species formerly assigned to *Magneuptychia.* In this article we erect, diagnosize, describe and discuss four genera belonging to the Nymphalidae, Satyrinae, in which we reassign ten species: ***Nubila*** Viloria, Andrade & Henao, **gen. nov.** (for *Euptychia gera* Hewitson, *E. metagera* Butler, *E. moderata* Weymer, *E. nortia* Hewitson, *E. purusana* Aurivillius and *E. segesta* Weymer), ***Macrocissia*** Viloria, Le Crom & Andrade, **gen. nov.** (for *Neonympha iris* C. Felder & R. Felder and *Euptychia inani* Staudinger), ***Colombeia*** Viloria, Andrade & Le Crom, **gen. nov.** (for *Euptychia mycalesis* Röber) and ***Omacha*** Andrade, Viloria, Henao & Le Crom, **gen. nov.** (for *Magneuptychia pax* Huertas, Lamas, Fagua & Willmott). Additionally, we transfer *Euptychia tiessa* Hewitson to the genus *Satyrotaygetis* Forster, which is revised.

MATERIALS AND METHODS

Apart from collateral biological evidence gathered from published sources and considered in the discussion of this article to support our systematic hypotheses, this study is solely based upon the common practices of comparative morphology: observation, recognition and interpretation of homologies. The resulting taxonomy constructed with the information thus generated obeys logical inference of set theory. We classify in the same category one or more species that share similar and equivalent morphological traits. Each group of species embraced by the four entities herein treated as new genera share common distinctive phenotypic characters in wing venation and wing visual pattern, as well as in the shape and proportions of certain major structures of the male genitalia. The sharing of those morphological traits appears sufficiently informative for our purposes and makes cohesive each of the proposed species groups. Therefore, their taxonomy coherent and plausible, but by no means exempt of further test by appropriate modern genetic techniques.

In this work we recognize fourteen species and allocate them in five genera. In the past, those species had been described as, or arbitrarily ascribed, to *Euptychia* Hübner (1818), *Splendeuptychia* Forster (1964) and/or *Magneuptychia* Forster (1964).

Members of *Euptychia*, as defined in modern taxonomy exhibit some, possibly unique, morphological characters (Singer *et al*. 1983, Murray 2001, Viloria 2007, Neild *et al.* 2014), that are entirely absent in our four new genera.

In part for this reason, morphological diagnoses for the new genera established in this paper are almost entirely based on comparisons with *Splendeuptychia* and *Magneuptychia*. In few cases we exceptionally invoke characters distinctive for the genera *Cissia* Doubleday (1848), *Satyrotaygetis* Forster (1964), *Huberonympha* Viloria & Costa (in Costa *et al.* 2016) and *Stevenaria* Viloria *et al.* (in Costa *et al*. 2016). However, elementary structures of the wing pattern characteristic for all ten genera are abstracted in comparative Table 1. In our opinion other satyrine butterfly genera known in the American continent bear not enough resemblance to the taxa herein treated and they have not been taken into consideration.

Nomenclatural acts in this work follow the provisions of the latest edition of the International Code of Zoological Nomenclature (ICZN 1999).

Technical procedures

Morphological examinations were performed on dry museum specimens kept in standard entomological cabinets. As indicated for each case, they are in the custody of individuals or institutions mentioned in the abbreviations section, below. When necessary for study, a limited number of samples were dissected, chemically treated according to the purpose by following well known protocols, and their structures cleaned under magnification with appropriate microdissecting tools by standard methods and preserved either in liquid (ethanol/glycerin for genitalia) or in fixing media (euparal in glass slides for diaphanized wings). Most of this entomological material had been collected by some

of the authors in multiple expeditions to several natural regions of Colombia and Venezuela. In those cases the butterflies were set, labeled, dissected and generally studied and photographed locally by each author. When necessary we have used magnifying optic devices and various sources of artificial illumination, like several brands and models of stereomicroscopes (Leica, Wild, Olympus) with coupled cameras, both lucid and photographic, for producing precision drawings and colour pictures, respectively. Manual 35 mm digital photographic cameras have also been used to record all specimens examined and their data labels.

Abbreviations

comb. nov.: *combinatio nova*; **e. g.**: *exempli gratia*; **FWL**: Forewing length; **gen. nov.**: *genus novo*; **gen. rev.**: genus revised; **ICN**: Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Bogotá D.C., Colombia; **i. e.**: *id est*; **IVIC**: Instituto Venezolano de Investigaciones Científicas, Centro de Ecología, Altos de Pipe, Venezuela; **JFLC**: Collection of Jean-François Le Crom, Bogotá, Colombia; **MALUZ**: Museo de Artrópodos, Facultad de Agronomía, La Universidad del Zulia, Maracaibo, Venezuela; **MC**: Collection of Mauro Costa, Caracas, Venezuela; **MHNUC**: Museo de Historia Natural, Universidad de Caldas, Manizales, Colombia; **MIZA**: Museo del Instituto de Zoología Agrícola, Facultad de Agronomía, Universidad Central de Venezuela, Maracay, Venezuela; **NHMUK**: The Natural History Museum, London, United Kingdom, **MNKB**: Museum für Naturkunde, Berlin, Germany, **SMTD**: Staatssammlung Museum für Tierkunde, Dresden, Sajonia, Germany; **ZSM**: Zoologisches Staatssammlung München, Munich, Germany; **sp. restit.**: *speciebus restituit*; **syn. nov.**: *synonymum novo*; **TL**: Type locality.

RESULTS

Nubila Viloria, Andrade & Henao, **gen. nov.**

(Figs. 1, 2, 10, 11, 12)

http://zoobank.org/urn:lsid:zoobank.org:act:5C8ACA7D-8F2D-4FEB-BC57-984013C375C5

Type species: *Euptychia gera* Hewitson, 1850; herein designated.

Diagnosis

Butterflies of small to medium size (FWL: 17.5-23 mm), superficially comparable in size and general aspect to those of *Splendeuptychia* Forster *sensu stricto**. However, it differs from the latter by having two well defined forewing underside central bands in postbasal and discal positions (faint and thin, postbasal and postdiscal in *Splendeuptychia*, the latter much more divergent towards the tornus). Hindwing ocellus prominent on Cu1, with two pupillae in *Nubila*, only one in *Splendeuptychia*. Differs from *Magneuptychia* Forster *sensu stricto*** by having a smaller size and by lacking the sixth ocellus on the anal margin on the hindwing underside. Forewing vein R2 emerges very close to the root of R3+R4+R5 at the anterior distal extremity of the discal cell (similarly in *Cissia* Doubleday, *Colombeia*, **gen. nov.** and *Macrocissia*, **gen. nov.**); in *Magneuptychia*, *Satyrotaygetis* Forster, *Stevenaria* Viloria *et al.* and *Huberonympha* Viloria & Costa, R2 emerges well before the end of the discal cell, closer to the root of R1; Sc ends at two fifths of the length of the Costa, as in *Stevenaria* (but approximately at the middle point of the Costa in *Cissia*, *Magneuptychia*, *Satyrotaygetis*, *Huberonympha*, *Colombeia*, **gen. nov.** and *Macrocissia*, **gen. nov.**). Forewing crossvein m1-m2, forming a distinct angle that points basad, from this angle emerges a short, but distinct recurrent veinlet, into the discal cell. Both angle and veinlet missing in *Cissia, Magneuptychia* and *Huberonympha*, but present in *Satyrotaygetis*, *Stevenaria*, *Colombeia*, **gen. nov.** and *Macrocissia*, **gen. nov.** (see below). Male genitalia with saccus slender, about same length as uncus (similarly to *Satyrotaygetis*, which exhibits more robust saccus and uncus; slightly shorter than uncus in *Macrocissia*, **gen. nov.**, notably shorter than uncus in *Cissia*, *Magneuptychia*, *Splendeuptychia, Huberonympha* and *Omacha*, **gen. nov.**; much longer than uncus in *Stevenaria*); valvae simply subtriangular (similar to *Splendeuptychia* and *Huberonympha*, but not quite as elongated as in *Magneuptychia*; not subrectangular as in *Cissia*, not hooked as in *Stevenaria*, not spine-tipped as in *Satyrotaygetis*, *Colombeia*, **gen. nov.** and *Macrocissia*, **gen. nov.**, not tricuspid at the tip as in *Omacha*, **gen. nov.**); aedeagus shorter than uncus, a character not shared with any of the nine genera herein compared with.

Description

Antennae relatively short, reaching to one third of the costa. *Forewings* subtriangular, apex and tornus rounded, *hindwings* suboval, outer margin slightly sinuous. *Venation* (Figs. 1, 2): forewing subcosta notably swollen at

* It is our criterion that only its type species, *Euptychia ashna* Hewitson (1869), and *Euptychia ambra* Weymer (1911), strictly qualify to belong to *Splendeuptychia* Forster. Other species allocated in that genus by several authors, as arranged in Warren *et al.* (2012b) are in need of generic reassignment.

** As re-defined by Costa *et al.* (2016).

basal half, gradually diminishing until third quarter its length, ending at two fifths of costa; R1 independently emerging at distal quarter of discal cell, ending within third fifth of the costa; R2 independent, emerging much closer to root of R3-R5 than to R1; root of R3, R4 and R5 emerging from anterior extremity of discal cell; R5 ending at apex; R3 and R4 ending more or less equidistant from the end of R2 and R5; M1, M2, M3, Cu1 and Cu2 all independent, emerging from the discal cell; crossvein m1-m2 forming a distinct angle pointing basad; a short but distinct recurrent veinlet emerging from its angle inside the discal cell; m2-m3 longer than m1-m2, slightly curved distad; root of Cubitals notably swollen at basal half, closing the cell at base with the swollen basal portion of Sc; A2 not inflated, independent, slightly sinuous at basal third; discal cell about half of wing length. Hindwing humeral present, but short and diffuse; all principal veins independent; Sc + R1 emerging at base of cell, ending at two thirds of costa; Rs ending at apex; A2 and A3 independent but their basal portions running together for about one fifth of A3, then diverging; m3-cu1 nearly half length of m1-m2, m2-m3 and cu1-cu2 about one and a half the length of m1-m2; discal cell about three fifths of wing length. *Ocellar pattern* as described in Table 1. *Male genitalia* (Figs. 10-12): tegumen dome-like, relatively small (shorter than uncus); base of uncus lanceolate, clearly distinguished from tegument; subunci well formed, almost as long as uncus, robust at base; vinculum stylized but strong; appendices angulares regularly developed but not very conspicuous; saccus flattened dorsoventrally, laterally slender, tubular, slightly curved upwards, shorter than uncus; valvae subtriangular, externally covered by short setae, only finely irregular along the dorsal edge between the ampulla and the cucullus; aedeagus shorter than uncus, thickset.

Derivatio nominis

As an adjective *Nubila* means "clear" in Latin, but it also means "clouds" as a substantive. Both meanings evoke visual reminiscences of the white colour pattern of the males of *Euptychia gera* Hewitson, its sexually dimorphic, type species. Among its known congeners, appropriately defined here by other relations of homology, males of *E. metagera* Butler are the only representatives in the group to share a comparable whitish aspect.

Species belonging to Nubila

Nubila gera (Hewitson, 1850), **comb. nov.**

[*Euptychia gera* Hewitson, MS, pl. 63, fig. 4 (female)], *nomen nudum*

Euptychia gera Hewitson, 1850: 439-440 [female] [TL: Amazon]

Neonympha gera (Hewitson); Herrich-Schäffer, 1865: 70.

Euptychia gera Hewitson; Westwood, 1850: pl. 63, fig. 4, 1851: 373; Butler, 1867a: 494; 1868: 35; 1877: 121; Kirby, 1871: 54; 1879: 134; Weymer, 1911: 215; Gaede 1931: 447; Lamas, 1969: 346; Lewis, 1973, 1987: 233, pl.58, fig. 2 (male); d'Abrera, 1988: 770, 771, row [8] figs. [1] (male dorsal), [2] (male [sic] dorsal)(misidentification of *E. metagera* Butler, female), row [9] figs. [1] (female dorsal), [2] (male ventral), 874; 2001: 183, pl. 137, fig. 17 (male); Overal & da Silva, 2002: 532; Shou *et al*., 2006: 84.

Euptychia hiemalis Butler, 1867a: 494 [male]. [TL: Amazons]

Euptychia hiemalis Butler; Butler, 1867b: 109, pl. 12, fig. 4; 1868: 35; 1877: 121; Kirby, 1871: 54; Druce, 1876: 213; Weymer, 1911: 215; Aurivillius, 1929: 158; Gaede, 1931: 451; d'Abrera, 1988: 789, 874.

Euptychia metaleuca distingüenda Bryk, 1953: 58-59 [female] [TL: Manaos, sv. Amaz.] (synonymy established by Lamas, 2004: 220)

[*Magneuptychia gera* (Hewitson); Forster, 1964: 126, 127 fig. 153 (male genitalia) (misidentification)]

Splendeuptychia distinguenda (Bryk); Forster, 1964: 130.

Magneuptychia gera (Hewitson); Brown, 1991: 376; T. & L: Racheli, 2001: 329; Brévignon, 2008: 73, 82, 84, 93, pl. 4, figs. 39a, 39b (male genitalia), 39c; Pascal *et al*., 2015: 108. 111 fig. F (male); Huertas *et al.*, 2016: 7.

Magneuptychia gera gera (Hewitson); Lamas, 2004: 220; Rodríguez & Miller, 2013: 210.

M.[*agneuptychia*] *gera* (Hewitson); Costa *et al.*, 2016: 199.

[¿?] *gera* Hewitson; Costa *et al*., 2016: 204.

[¿?] *hiemalis* Butler; Costa *et al*., 2016: 204.

Nubila metagera (Butler, 1867), **comb. nov.**

Euptychia metagera Butler, 1867a: 494 [male]. [TL: Ega, U. Amazons]

Euptychia metagera Butler; Butler, 1867b: 109, pl. 11, fig. 4; 1868: 35; 1877: 121; Kirby, 1871: 54; Weymer, 1911: 215; Gaede, 1931: 454; d'Abrera, 1988: 770, 771, figs. [1] (male syntype, dorsal), [2] (male ventral), 875.

Euptychia nortia abrahami Bryk, 1953: 63 [female] [TL: Tarocuá, Sv. Amaz.] (synonymy established by Lamas, 2004: 220); Costa *et al.*, 2016: 199 (as a synonym)

Splendeuptychia abrahami (Bryk); Forster, 1964: 130.
[*Euptychia gera* Butler; d'Abrera, 1988: 771, row [9], fig. 2 (female dorsal misidentification)]
Magneuptychia metagera (Butler); Lamas, 2004: 220; Rodríguez & Miller, 2013: 210.
E.[*uptychia*] *metagera* (Butler); Costa *et al.*, 2016: 199.
[¿?] *metagera* Butler; Costa *et al*., 2016: 204.

Nubila moderata (Weymer, 1911), **comb. nov.**
Euptychia nortia Hewitson f. *moderata* Weymer, 1911: 214, pl. 48 row g. [female] [TL: Mapiri, Bolivia]
Euptychia moderata Weymer; Aurivillius, 1929: 158; Lamas, 1969: 346.
Euptychia nortia Hewitson ab. *moderata* Weymer; Gaede, 1931: 457.
Splendeuptychia moderata (Weymer); Forster, 1964: 130 [type examined].
[*Euptychia nortia* Hewitson; d'Abrera, 1988: 771, row [1], fig. [5] (female dorsal) (misidentification)]
M.[*agneuptychia*] *moderata moderata* (Weymer); Lamas *et al.,* 1991: 10.
M.[*agneuptychia*] *moderata* (Weymer); Robbins *et al*., 1996: 231.
Magneuptychia moderata (Weymer); Lamas, 2003: 203; 2004: 220; Murray & Prowell, 2005: 69,72, 73, 75, 76; Peña *et al*., 2010: 247, 250 fig. 2, 251 fig. 3, 253 fig. 4.
E.[*uptychia*] *moderata* Weymer; Costa *et al.*, 2016: 199.
[¿?] *moderata* Weymer; Costa *et al*., 2016: 204.

Nubila nortia (Hewitson, 1862), **comb. nov.**
Euptychia nortia Hewitson, 1862: pl. [44], n. 2, fig. 2 [male] [TL: Amazon]
Neonympha nortia (Hewitson); Herrich-Schäffer, 1865: 70.
Euptychia nortia Hewitson; Butler, 1867a: 494; 1868: 35; 1877: 121; Kirby, 1871: 54; 1879: 134; Staudinger, 1886: tfl. 80; 1887: 225; Weeks, 1905: 29; Weymer, 1911: 214, pl. 49, row a; Gaede, 1931: 457; d'Abrera, 1988: 770, 771, row [1], figs. [3] (male dorsal), [4] (female dorsal, erroneously identified as male), [5](female dorsal, misidentification of *E. moderata* Weymer), row [2], figs. [4] (male ventral), [5] (female ventral, misidentified as male), 876; Shou *et al*., 2006: 85.
Euptychia nortia Hewitson f. *nobilis* Weymer, 1911: 214, pl. 49 row a, **syn. nov.** [female] [TL: Tabatinga, Amazon, Brazil]
E.[*uptychia*] *nortia* Hewitson; Aurivillius, 1929: 158.
Euptychia nortia Hewitson ab. *nobilis* Weymer; Gaede, 1931: 457.
Magneuptychia nortia (Hewitson); Forster, 1964: 126, 127 fig. 152 (male genitalia), 130; Lewis, 1973, 1987: 233, 234, pl. 60, fig. 3 (female, *nec* male); Costa *et al.*, 2016: 199.
Splendeuptychia nobilis (Weymer); Forster, 1964: 130.
Magneuptychia gera nobilis (Weymer); Lamas, 2004: 220.
Magneuptychia gera nortia (Weymer); Lamas, 2004: 220.
E.[*uptychia*] *nobilis* Weymer; Costa *et al.*, 2016: 199.
[¿?] *nobilis* Weymer; Costa *et al.*, 2016: 204.
[¿?] *nortia* Hewitson; Costa *et al.*, 2016: 204.

Nubila purusana (Aurivillius, 1929), **comb. nov.**
Euptychia purusana Aurivillius, 1929: 158, fig. 1 [male]. [TL: Rio Purus, Amazon]
Euptychia purusama [*sic*] Aurivillius, 1929: 158.
Euptychia purusana Aurivillius; Gaede, 1931: 462.
[*Euptychia* ? *segesta* Weymer; d'Abrera, 1988: 771, row [3], fig. [2] (male ventral, misidentification)]
S.[*plendeuptychia*] *purusana* (Aurivillius); Lamas *et al*., 1991: 10; Robbins *et al.*, 1996: 232.
Splendeuptychia purusana (Aurivillius); Lamas, 2004: 222; Brévignon, 2008: 80, 82, 84, 94, pl. 6, figs. 65a, 65b (male genitalia), 65c; Peña *et al*., 2010: 247, 250 fig. 2, 251 fig. 3, 253 fig. 4.; Brévignon & Benmesbah, 2012: 52 (Brévignon 2008 and the last probably misidentifications of an undescribed taxon).

Nubila segesta (Weymer, 1911), **comb. nov.**
Euptychia segesta Weymer, 1911: 214-215, pl. 51, row b [male] [TL: Gramal near Muzo, Colombia]
Euptychia segesta Weymer; Apolinar, 1928: 14; Gaede, 1931: 464; d'Abrera, 2001: 183, pl. 137, fig. 18 (male); Shou *et al*., 2006: 85.
Euptychia ? *segesta* Weymer; d'Abrera, 1988: 770, 771, row [3], figs. [2] (male ventral) (misidentification of *E. purusana* Aurivillius), [3] (male ventral), 877.
M.[*agneuptychia*] *segesta* (Weymer); Robbins *et al.*, 1996: 231.
Magneuptychia segesta (Weymer); Lamas, 2004: 220.
E.[*uptychia*] *segesta* Weymer; Costa *et al*., 2016: 199.
[¿?] *segesta* Weymer; Costa *et al.*, 2016: 204.

Weymer's treatment of the species herein assigned to *Nubila*, **gen. nov.**, is partly misleading. He did not illustrate any sex of either *Euptychia gera* (= *E. hiemalis*) nor *E. metagera* (= *E. nortia abrahami*). In the first case, he correctly identified the female, whose pattern description corresponds well with that of the female syntype of *Euptychia gera* at the NHMUK (examined), but wrongly

described the male of *Euptychia metagera* (syntype examined, NHMUK) under the name of *E. gera* Hewitson. On the other hand, his description of *E. hiemalis* appears correct, but he did not notice that it is in fact the strongly dimorphic male of *E. gera*. The latter name has 17 years precedence over the first. The description of *E. metagera* given by Weymer also matches well the taxon described originally by Butler under that name. We believe that Weymer also made a mistake in describing a female for *Euptychia nortia* Hewitson that does not correspond to that species (p. 214). Its illustrations (pl. 49 row a) appear much closer to *E. purusana* Aurivillius, but might represent an undescribed taxon from French Guyana, whose male is identified and illustrated as *Splendeuptychia purusana* (Aurivillius) by Brévignon (2008: 80, 84, pl. 6, figs. 65a, b, c). Weymer may have referred to the female he illustrated when mentioning Cayenne as a locality for *E. nortia*. We do not know of any reliable record of *nortia* for the Guyana region. The female of *Nubila nortia*, **comb. nov.**, corresponds to what is described by Weymer as form *nobilis*, **syn. nov.** (1911: 214, pl. 49, row a). It is also appropriately illustrated by Lewis (1973, 1987: pl. 60, fig. 3) and in the photograph by K. Garwood of one specimen from the surroundings of Cacaulandia (Rancho Grande) in the state of Rondonia, Brazil (under *Magneuptychia gera nortia* in Warren *et al.* 2012).

The male genitalia illustrated by Forster (1964: 127, fig. 153; herein reproduced in our Fig. 11) for "*Magneuptychia*" *gera* does not correspond to this taxon, although it appears to represent another species of *Nubila,* **gen. nov.** We herein illustrate both male genitalia (Fig. 10) and wing venation (Fig. 1) for this species, the type of the genus.

Material examined

Nubila gera: **BRAZIL**: 1 female, Amazon, Hew. Coll. 79-69, B. M. Type No. Rh. 3187, *Euptychia gera* Hew., Type [Syntype], 1 male, Amazons, coll. By Wallace, 51-119, B. M. Type No. Rh. 3186, *Euptychia hiemalis* Butl., Type [Syntype] (NHMUK); **COLOMBIA: Amazonas**: 2 males, La Pedrera, Río Apaporis, 165 m, 9.xi. 1994, leg. G. Andrade-C., GAC 6678, 6680, ICN-MHN-L 12634, 12635; **Caquetá**: 1 female, Araracuara, Río Mesay, Puerto Abeja, 450 m, 27.i.1998, leg. M. Porras, MP 171, ICN-MHN-L 24465; 2 males, 1 female, 13.i.1998, leg. M. Porras, MP 26, 20, 30, ICN-MHN-L 223724, 11311, 24466, Gen. 1978; 2 females, San Vicente del Caguán, Caño Ima, 4.viii.1992, leg. J. Langley, ICN-MHN-L 12040, 12039; 2 females, San Vicente del Caguán, Caño Ima, 4.viii.1992, leg. J. Langley, ICN-MHN-L 12039, 12040; 1 female, San Vicente del Caguán, Mamachi, 21.vi.1992, leg. L. Langley, ICN-MHN-L 9047; **Guainía**: 1 male, 1 female, Inirida, La Ceiba, 3,6329720 N, -67,8894720 W, 103 m, 21.iii.1998, leg. A. Gabanzo, ICN-MHN-L 23723, 35990 (ICN); **Guaviare**: 2 females, Calamar, Río Tunia, 1.490833 N, -72.876111 W, 240 m, 17.ii.2017, leg. E. Henao, EH 95, 219, ICN-MHN-L 18928, 18929 (ICN); 1 male San José de Guaviare, i.[19]92, leg. J. Urbina?; 1 male, same data, xi. [19]91; 1 male, same data, ix.[19]92; 2 males [1 Genit. JFL 603] (JFLC); **Vaupés**: 1 male, Taraira, Estación Caparú, 2.ix.[19]93+, leg. J. Pinzón (JFLC); 1 female, Cararu, La Libertad, 300 m., 5.ix. 1993, leg. G. Fagua, ICN-MHN-L 12340; 1 male, Pacoa, Quebrada Jotabeya, Comunidad Jotabeya -0,6147220 S, -70,1897777 W, 328 m., 27.iii.2009, leg. L. González, ICN-MHN-L 25082; 1 female, Pacoa, Rio Apaporis, comunidad de Jirijirimo, -0,4400000 S., -70,9607770 W., 360 m., 21.iii.2009, leg. L. González, ICN-MHN-L25079; 1 female, same data, 19.iii.2009 ICN-MHN-L 25080; 1 female, same data, 21.iii.2009, ICN-MHN-L 25081; 1 female, same data, 27.iii.2009, ICN-MHN-L 25108; 1 male, Pacoa, Quebrada Jotabeya, Comunidad Buenos Aires -00°01'21,3" S, -71°00'09,4" W, 181 m., 21.ii.2018, leg. E. Henao; 1 male, Soratama – Río Apaporis, 250 m, iii.1952, leg. L. Richter, ICN-MHN-L 18881; 1 male Serrania de Chiribiquete bajo el Tepui, 24.viii.1994, leg. J. Langley, ICN-MHN-L 18889; **VENEZUELA**: 1 male, Amazonas, Morganito, 21.vii.2012, col. Mattei [Wing prep. ALV014-17 (fig. 1)]; 1 female, same locality, 6.xi.2014 [Genit. prep. ALV-566-17]; 1 female, same locality, 11.x.2015; 3 males [1 Genit. prep. ALV-521-14 (fig. 10)], Amazonas, Mcpio. Guainía, camino Yavita-Maroa, 2° 55'16" N, 67° 26'25" W, 300 m, 29-31.viii. 1996, cols. J. Camacho, A. Heenan (MALUZ); 2 males, 1 female, Amazonas, Raudal del Danto, 5°02'39" N; 67°33'40"W, 100 m, 19.xii.2016, M. Costa (IVIC). ***Nubila metagera***: **BRAZIL**: 1 male, Ega, U. Amazons, H. W. Bates, Godman-Salvin coll. 1904-1, *Euptychia metagera* Btl., B. M. Type No. Rh. 3188, Type [Syntype] (NHMUK); **COLOMBIA**: **Amazonas**: 1 female, La Pedrera, 1 Kilómetro arriba trocha centro Providencia, 205 m, 16.xi.1994, leg. G. Andrade-C. GAC 6770, ICN-MHN-L 12871; **Caquetá**: 2 males, San Vicente del Caguán, Morichal Caño Rico, forest path, leg. J Langley ICN-MHN-L 9045, 9046 [Wing prep. ALV052-17 (fig. 2), Genit. prep. ALV568-17]; **Vaupés**: 1 male, Caparu, camino a mina "La Libertad", 290 m, 29.viii.1993, leg. G. Fagua, G10-0175, ICN-MHN-L 12329; 1 female, Pacoa, Río Apaporís, Comunidad de Jirijirimo, -0,4400000 S, -70,960777 W, 350 m, 19.iii.2009, leg. González-M., L. A. leg. ICN-MHN-L 23083 (ICN); 1 female, Serranía de Chiribiquete, camino hacia el Tepui, leg. J. Langley, 31.vii.1994, ICN-MHN-L 18888; 1 female, Serranía de Chiribiquete, camino hacia el Tepui, leg. J. Langley,

7.viii.1994, ICN-MHN-L 18880; 1 female, Serranía de Chiribiquete, camino hacia el Tepui, 7.viii.1994, ICN -MHN-L 18873; 1 female, Taraira, Estación Caparú, 2 sem. 93+, leg., J. Pinzón [Genit. JFL 612] (JFLC); **VENEZUELA**: **Amazonas:** 1 male, Morganito, 11.x.2015, Col. Mattei (IVIC). ***Nubila moderata***: **BOLIVIA**: 1 male, Mapiri, Collection v. Rosen, Cotypus Nr. *Euptychia moderata* Weym., Zoologische Staatssammlung München (ZSBS). ***Nubila nortia***: **BRAZIL**: **Amazon**: 1 male, Hewitson Coll. 79-69, *Euptychia nortia* Hew. 2, B. M. Type No. 3185, *Euptychia nortia* Hew., Type [Syntype] (NHMUK); 1 female, Brasilia, sept., Taperjos Präparat Nr. SA 108 Zoolog. Staatssmmlung München; 1 male Brasilia, sept., Rio Madeird, Manicore Jr., Amazonas Coll. Fassl in Coll Arp.; 1 male, Brasilia, sept., Tapajos viii. 20. Leg. Jr. Bug, Präparat Nr. SA 142 Zoolog. Staatssmmlun München; 1 male, Brasilia, sept. Tapajos, Amazonas, Coll. Fassl in Coll. Arp.; 1 male, Amazonas, Coll. Fassl in Coll, Arp., Präparat Nr. SA 109 Zoolog. Staatsammlung München (fig. 12, reproduced from Forster 1964) (ZSM); ***Nubila purusana***: no specimens examined. ***Nubila segesta***: **COLOMBIA**: **Caldas**: 1 female, Manzanares, 19.xii.1992, leg. J. Salazar [Genit. JFL 618] (JFLC); 1 female, La Victoria, 1946, leg. E. Schmidt-Mumm, MHN-UC 303 (ICN); **Tolima**: 1 male, Lérida, vereda el Bledo, Finca El Bledo, 4, 8946100 N, -74,9696600 W, 9.viii.2009, leg. L. Ospina, 293 m, ICN-MHN-L 32239.

Macrocissia Viloria, Le Crom & Andrade, **gen. nov.**
(Figs. 3, 4, 13, 14, 15)

http://zoobank.org/urn:lsid:zoobank.org:act:879ECA3B-C455-478E-AF80-1AB2FF9B7B7B

Type species: *Neonympha iris* C. Felder & R. Felder, 1867; herein designated.

Diagnosis

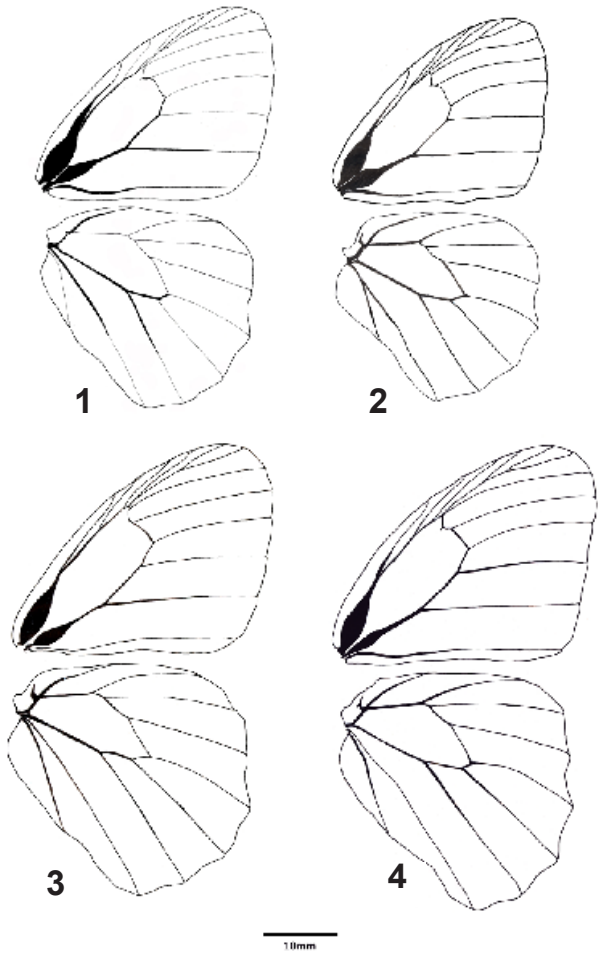
Butterflies of medium size (FWL: 22-23 mm) with aspect comparable to that of the members of *Magneuptychia sensu stricto*, *Satyrotaygetis* and *Colombeia*, **gen. nov.** Differs from *Magneuptychia* in that the females may exhibit dorsal ocellar elements on the hindwing, which however can be seen also in *Satyrotaygetis* and *Colombeia*, **gen. nov.** *Macrocissia*, **gen. nov.**, has a single, forewing underside monopupillated ocellus (M1), like in *Satyrotaygetis*; it is bipupillated in *Magneuptychia* and *Colombeia*, **gen. nov.** Hindwing underside ocellar pattern widely differs from that of *Satyrotaygetis* in having ocelli R5, M1, M2 and M3 with two pupillae (monopupillated in *Satyrotaygetis*); Cu1 may have only one pupilla. Differs from *Magneuptychia* in lacking the sixth microocellus over the anal margin. Hindwing dorsum of male *Macrocissia* exhibits darker androconial scales, notably in *M. iris* (C. Felder & R. Felder), **comb. nov.**, inner margin less excavated that in *Magneuptychia*, *Huberonympha* and *Colombeia*, **gen. nov.** Wing venation fundamentally differs from that of *Magneuptychia* by the presence of a vestigial recurrent vein into the discal cell, emerging from m1-m2 (similar to that in *Satyrotaygetis* and *Colombeia*, **gen. nov.**, but less pronounced than in *Nubila*, **gen. nov.**). Male genitalia of *Macrocissia* bears distinctive valvae, with a hook-like distal process and a finely serrate cucullus. Similar characters are observable in species of *Satyrotaygetis*, where the cucullar and distal processes are however, separated by a constriction or diastema. A few other Neotropical species of satyrine butteflies with a similar shape in their valvae have been classified in the genera *Pareuptychia* Forster and *Splendeuptychia*, but their wing shape, size and patterns are not comparable to the species of *Macrocissia*, **gen. nov.**

Description

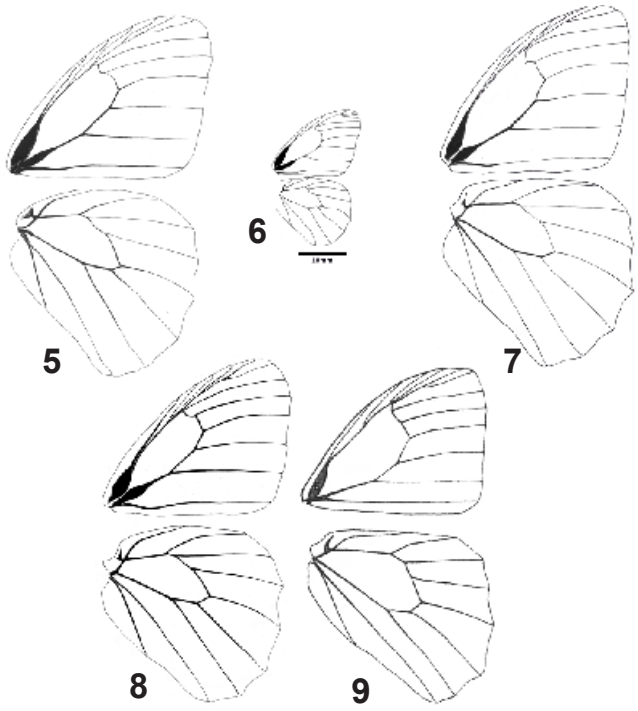
Antennae reaching to two fifths the length of the costa, shaft thin, club not conspicuous and gradually formed. *Wings*: forewing subtriangular, apex notably rounded, outer margin slightly convex, tornus moderately rounded. Hindwing suboval, outer margin softly scalloped, anal margin slightly excavated near the tornus. *Venation* (Figs. 3, 4): forewing as in *Magneuptychia*, except for the presence of a short, primordial recurrent vein in m1-m2, and for the emergence of R1 closer to the base, at the beginning of the distal quarter of discal cell; roots of R5 and M1 closer to each other in *Macrocissia*, **gen. nov.** *Male genitalia* (Figs. 13-15): origin of uncus more or less continuous with tegumen (unlike *Magneuptychia*); tegumen same length as uncus; gnathos well developed, emerging from both basal sides of the tegumen, almost reaching the tip of the uncus; vinculum robust, especially towards the pedunculus; saccus tubular in lateral view, about the same length of gnathos; valvae subtriangular and elongated, reaching the tip of uncus, cucullus finely serrate with a distal hook-like distal spine pointing upwards; aedeagus robust, laterally thicker than saccus, slightly curved upwards, about three quarters of the length of tegumen plus uncus.

Derivatio nominis

The undersides of the species we herein place within this genus are in external aspect reminiscent of *Papilio clarissa* Cramer (a junior synonym of *Papilio penelope* Fabricius), the type species of the genus *Cissia* Doubleday. However, they are considerably larger in wingspan. Therefore we name this new genus, *Macrocissia*, which literally means "long *Cissia*", it is a feminine term compound by and adjective and a noun, and its etymological roots are

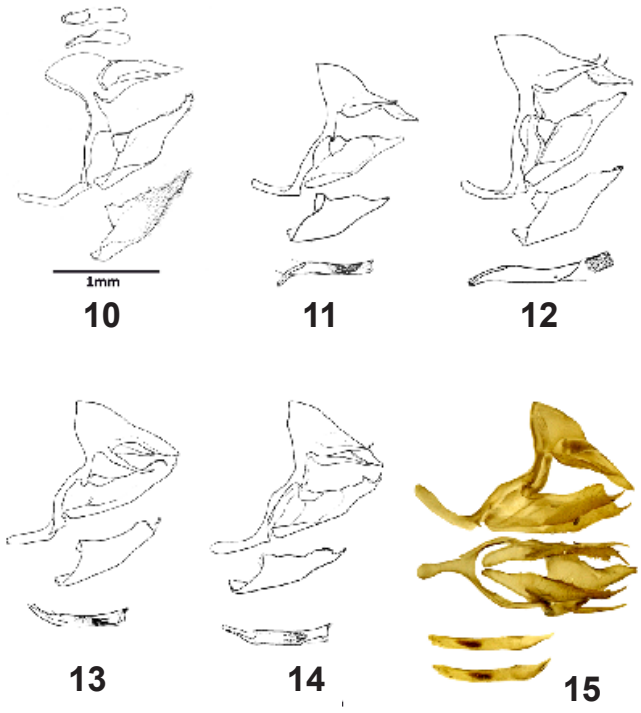


Figures. 1-4. Wing venation of four species representative of two new genera of Neotropical satyrine butterflies (males). **1**. *Nubila gera* (Hewitson), **comb. nov.**, type species of the genus *Nubila*, **gen. nov.**; **2**. *Nubila metagera* (Butler), **comb. nov.**; **3**. *Macrocissia iris* (C. Felder & R. Felder), **comb. nov.**, type species of the genus *Macrocissia*, **gen. nov.**; **4**. *Macrocissia inani* (Staudinger), **comb. nov.**



Figures. 5-9. Wing venation of five species representative of four genera (two new) of Neotropical satyrine butterflies (males). **5**. *Colombeia mycalesis* (Röber), **comb. nov.**, type species of the genus *Colombeia*, **gen. nov.**; **6**. *Omacha pax* (Huertas, Lamas, Fagua & Willmott), **comb. nov.**, type species of the genus *Omacha*, **gen. nov.**; **7**. *Satyrotaygetis tiessa* (Hewitson), **comb. nov.**; **8**. *Magneuptychia libye* (Linnaeus), type species of the genus *Magneuptychia* Forster; **9**. *Satyrotaygetis satyrina* (H. W. Bates), type species of the genus *Satyrotaygetis* Forster.

Figures. 10-15. Lateral (and in last case ventral as well) views of the male genitalia structures of five species representative of two new genera of Neotropical satyrine butterflies. In lateral view drawings, left valve and aedeagus have been detached from armature for better visualization. **10**. *Nubila gera* (Hewitson), **comb. nov.**, type species of the genus *Nubila*, **gen. nov.**; **11**. *Nubila* sp. [probably new, after Forster, 1964; not *Magneuptychia gera* (Hew.) as originally indicated]; **12**. *Nubila nortia* (Hewitson), **comb. nov.** [after Forster, 1964]; **13**. *Macrocissia iris* (C. Felder & R. Felder), **comb. nov.**, type species of the genus *Macrocissia*, **gen. nov.** [after Forster's *Magneuptychia ayaya* (= *M. iris*)], 1964; **14**. *Macrocissia inani* (Staudinger), **comb. nov.**, type specimen as illustrated by Forster, 1964 under *Magneuptychia juani* [*sic*]; **15**. *Macrocissia inani* (Staudinger), **comb. nov.**, upper lateral view, lower ventral view; detached aedeagus pointing to the left.



entirely Greek (*μάκρος*: long; *Κισσία*: a region of the ancient Persian Empire).

Species belonging to Macrocissia

Macrocissia inani (Staudinger, [1886]), **comb. nov.**

Euptychia inani Staudinger, [1886]: tfl. 80. [TL: Rio S. Juan, Columb.]

Euptychia juani [*sic*] Staudinger, 1887: 226; Weymer, 1911: 214, pl. 49, row a; Gaede, 1931: 451; d'Abrera, 1988: 764, 765, row [2], figs. [1] (male dorsal), [2] (male ventral), 875; Shou *et al*., 2006: 84.

E.[*uptychia*] *juani* [*sic*]; Staudinger; Schaus, 1913: 342.

Magneuptychia juani [*sic*] (Staudinger); Forster, 1964: 126, fig. 150 (male genitalia, type); T. & L. Racheli, 2001: 329; Palacios & Constantino, 2006: 266; Costa *et al*., 2016: 199.

[*Euptychia*] *inani* Staudinger; T. & L. Racheli, 2001: 329.

Magneuptychia inani (Staudinger); Lamas, 2004: 220; Marín, 2011: 48 fig. 45, 56, 60, 65, 69, 71.

[¿?] *inani* Staudinger; Costa *et al*., 2016: 204.

Macrocissia iris (C. Felder & R. Felder, 1867), **comb. nov.**

Neonympha iris C. Felder & R. Felder, 1867: 483-484. [TL: Bogota]

Euptychia ayaya Butler, 1867a: 492-493, pl. 40, fig. 11. [TL: Tapajos, Amazons]

Euptychia ayaya Butler; Butler, 1868: 34; 1877: 122; Kirby, 1871: 54; Holdich & Hinks, 1918: 234; Gaede, 1931: 440; d'Abrera, 1988: 785, row [5], fig. [1] (male dorsal), [2] (male ventral), 873; Lamas, [1997]: 53 (synonymic priority established); 2004: 220 (as a synonym); T. & L. Racheli, 2001: 329 (as a synonym); d'Abrera, 2001: 183, pl. 135, figs. 34 male dorsal, 35 male ventral; Brévignon, 2008: 74 (as a synonym); Shou *et al*., 2006: 83.

Euptychia iris (C. Felder & R. Felder); Butler, 1868: 34, 1877: 122; Kirby, 1871: 54; Weymer, 1911: 221 (synonymy with *E. agaya* [*sic*] Butler established); Gaede, 1931: 440 (as a synonym).

Euptychia agaya [*sic*] Butler; Weymer, 1911: 221, pl. 49, row g; Chai, 1990: 56.

Euptychia agaya [*sic*] Butler f. *azulina* Ribeiro, 1931: 34. [TL: Jamary, Rondonia, Brasil]

Euptychia agaya [*sic*] *azulina* Ribeiro; Ribeiro, 1931: 40; May, 1933: 125 (synonymy established).

Magneuptychia ayaya (Butler); Forster, 1964: 126, 127 fig. 151 (male genitalia); Lamas, 1981: 29; Costa *et al*., 2016: 199 (last one as a synonym of *Neonympha iris* C. & R. Felder).

Euptychia agava [*sic*] Butler f. *azulina* Ribeiro; Mielke & Casagrande, 1987: 22, 23, fig. 8.

M.[*agneuptychia*] *ayaya* (Butler); Lamas *et al*., 1991: 10.

M.[*agneuptychia*] *iris* (C. Felder & R. Felder); Robbins *et al*., 1996: 231.

Magneuptychia iris (C. Felder & R. Felder); Lamas, [1997]: 53; 2004: 220; T. & L. Racheli, 2001: 329; Brévignon, 2008: 74, 82, 84, 93, pl. 4, figs. 43a, 43b (male genitalia), 43c.

Chloreuptychia ayaya (Butler); Piñas, 2004: 35, figs. 279, 280.

Chloreuptychia agaya [*sic*] (Butler); Lewis, 1973, 1987: 233, pl. 55, fig. 17 (male); Shou *et al*., 2006: 82.

M.[*agneuptychia*] *iris* (C. Felder & R. Felder); Costa *et al*., 2016: 199.

[¿?] *iris* C. Felder & R. Felder; Costa *et al*., 2016: 204.

Judging by the similitudes of the structure of the valvae of the male genitalia, and the homologies of most elements of the wing pattern, the genus *Macrocissia*, **nov.**, is close to *Satyrotaygetis* Forster and to *Colombeia*, **gen. nov.**

Material examined

Macrocissia inani: **COLOMBIA**: 1 male, Rio S. Juan, Columb. [*sic*] Jr., ex collect. Staudinger, Origin., Eigentum Mus. Berlin, Präparat No. 149 Zoolog. Staatssammlung München (fig. 14, reproduced from Forster, 1964) [Lectotype Miller 1989]; 1 female Rio S. Juan, Columb. Jr., Origin., genitalia vial M-9093, [Paralectotype Miller, 1989] (ZMHB); **Chocó**: 1 male, Guadalupe, 50 m, leg. J. Umaña; 2 males, Tado, 20.iii.[19]90, leg. J. Salazar [Genit. JFL 606, (fig. 15)]; 1 female, Bahia Solano, 1.i.[19]97, leg. J. F. Le Crom (JFLC); **Risaralda**: 1 female Santa Cecilia, 650 m., x.1952, leg., J. Vélez, MHN-UC 13 (MHNUC). **ECUADOR**: **Esmeraldas**: Esmeraldas, 3 females, 600 m, vii.1959, leg. L. Richter, ICN-MHN-L 2707, 2706 [Wing prep. ALV050-17 (fig. 4)]; **Santo Domingo**: 3 males, Santo Domingo de los Colorados, 600 m, viii.1958, leg. L. Richter, ICN-MHN-L 2705, 5980, 28525 [Genit. prep. ALV571-17], 3050; 1 female, same data, xi.1959, leg. L. Richter, ICN-MHN-L 2708; 1 male, Santo Domingo, Santo Domingo de los Colorados, 500 m, iv.1959, leg. L. Richter, ICN-MHN-L 5980; 1 male, Pichincha, Sant[o] Domingo de los Colorados, 650 m, 25.10.1956, leg. J. Foerster (ZSM). ***Macrocissia iris***: **COLOMBIA**: [**Cundinamarca**]: 1 male, Bogotá, Lindig, Type, *iris*, Felder Colln., Rothschild Bequest B. M. 1939-1 [Syntype of

Neonympha iris C. Felder & R. Felder, label with note by N. D. Riley: "Type of *N. iris* Feld. = *E. ayaya* Butl. Comp. w. type xii.1912 NDR."]; 1 male, Tapajos, Amazons, H. W. Bates, B. M. Type No. 3264, *Euptychia ayaya* [male] Butl., Godman-Salvin Coll. 1904-1, *Euptychia ayaya* Butl. Type, H. T. [Holotype of *Euptychia ayaya* Butler, label with note by N. D. Riley: "Agrees with type of *N. iris* Feld. Brand perhaps rather bigger in this specimen, NDR."] (NHMUK); 1 male, Butler Rio Guayabero, Macarena Sur, 300 m., 15.1.1959, leg. D. Trapp, label with note Abdomen gekilobt Haerelberm; 1 male Amazonas, Coll Fassl in Coll, Arp., Präparat Nr. SA 136 Zoolog. Staatssmmlung München (fig. 13, reproduced from Forster, 1964) (ZSM), **Caquetá**: 1 female, San Vicente del Caguán, Caño Grande, 500 m, 17.viii.1992, leg. J. Langley, ICN-MHN-L 12043; 1 male, San Vicente del Caguán, Las Vegas, Pato Bajo, 500 m, 17.ix.1995, leg., G. Andrade-C., GAC 8037, ICN-MHN-L 24468 [Wing prep. ALV055-17 (fig. 3), Genit. prep. ALV572-17)]; 2 males, same data, 12.ix.1995, leg, G. Andrade-C., GAC, ICN-MHN-L 14292, 37143; **Guaviare**: 1 male, San José del Guaviare, i.[19]92, leg. J. Urbina; 1 male, same data, ix.[19]92 (Genit. JFL 607)(JFLC); **Meta**: 1 male, San Juan de Arama, Serranía de la Macarena, 650 m, leg. L. Richter, ICN-MHN-L 37178; **Vaupés**: 1 female, Pacoa, Rió Apaporís, comunidad de Jirijirimo, 0.400000 N, -70.9607770 W; 360 m, 20.iii.2009, leg. L. González, ICN-MHN-L 25390; 1 female, Soratama, Río Apaporís, i.1952, no more data, leg. L. Richter, ICN-MHN-L 6143; 4 females, mer. Umbria. SMD, (STMD-D); **ECUADOR**: 1 male, Ecuador, leg. Velástegui (JFLC). **SURINAM** [?]: 3 male, SMD, (STMD-D).

Colombeia Viloria, Andrade & Le Crom, **gen. nov.**
(Figs. 5, 16)

http://zoobank.org/urn:lsid:zoobank.org:act:D2E62DCC-F456-4792-BC22-86BDA0801F29

Type species: *Euptychia mycalesis* Röber, 1927; herein designated.

Diagnosis

Butterflies of medium size (FWL: 28-30 mm), superficially comparable in size and aspect to the species belonging to *Magneuptychia*, *Megeuptychia* Forster and *Satyrotaygetis*. However, it is distinguished from these genera by the moderate but evident excavation of the anal margin near the tornus; never as soft as in *Megeuptychia*, notably larger, or as marked as in *Erichthodes* Forster, which is smaller, but like in *Huberonympha*, from which it differs externally by never having sinuous or irregular underside dark bands. Butterflies belonging to *Colombeia*, **gen. nov.**, bear double white pupillae on each complete ocellus of its underside (one pupilla in *Satyrotaygetis*, a combination of one and two or just one in *Megeuptychia*), not unlike *Magneuptychia*, which however is diagnosized by the presence of a seventh micro-ocellus, at discal level on the anal margin. This ocellus is entirely absent in *Colombeia*, **gen. nov.**, which is also characterized by the long diameter of its hindwing underside ocelli on cells M1 and Cu1 (round, never oval as in *Magneuptychia*). The latter especially conspicuous. *Magneuptychia* and *Omacha*, **gen. nov.**, both lack a recurrent veinlet emerging from m1-m2 in the forewing discal cell, a character common to *Satyrotaygetis*, *Colombeia*, **gen. nov.**, *Nubila*, **gen. nov.** and *Macrocissia*, **gen. nov.** The last two genera, as well as *Omacha*, **gen. nov.**, have characteristic elongated silver ocellar elements on hindwing underside cells M2 and M3. These features are missing in *Colombeia*. Due to the shape of the valvae, and the tegument-uncus configuration *Colombeia*, **gen. nov.**, shows affinities in male genitalia to *Magneuptychia*. They however differ in wing pattern homologies as mentioned above.

Description

Antennae simple, reaching two fifths of the costa, club formed gradually and not conspicuous. *Forewings* subtriangular, outer margin slightly excavated, apex and tornus moderately round. *Hindwings* suboval, outer margin crenulate, anal margin moderately excavated near tornus. *Venation* (fig. 5): Forewing subcosta notably inflated at basal third, root of cubitals moderately swollen at basal half; both converging at base to close the discal cell; A2 independent but closely attached to root of cubitals at base, slightly inflated in its first fifth of its length. Sc ending nearly at half length of costa; R1 emerging at the beginning of last distal quarter of discal cell, ending at limit of discal area; R2 independent emerging near tip of discal cell just before the root of R3+R4+R5; R3 emerging equidistantly between extremity of cell and bifurcation of R4 and R5; R5 ending at apex; M1 to Cu2 all independent and running more or less parallel to the outer margin of wing; m1-m2 slightly curved inwards to cell; short recurrent veinlet emerging from curvature, closer to root of M2; m2-m3 slightly curved outwards the cell. Hindwing Hu present, short, thick and diffused toward wing base; Sc ending at middle costa; RS ending at apex; all veins independent; A2 and A3 running closely together for the basal quarter of the second; m1-m2 just slightly concave; m2-m3 just slightly convex; m3-cu1 about half-length of m1-m2 and a quarter length of m2-m3. *Ocellar pattern* as presented in Table 1. *Male genitalia* (Fig. 16): Tegumen globular, origin of uncus differentiated from tegumen as in

Magneuptychia, but subunci emerging from the lower base of uncus, not as broad at the base as in *Magneuptychia*. Saccus as long as uncus, more conical and longer than that of *Magneuptychia*. Valvae subtriangular and elongated, reaching the same length as uncus, laterally less broad than those of *Magneuptychia*, but presenting the same kind of tiny processes at their distal third; never with serrate or spiny distal processes (like those in *Macrocissia*, **gen. nov.** or *Satyrotaygetis*). Aedeagus robust but more stylized than in *Magneuptychia*, lacking spiny areas.

Derivatio nominis

Colombeia is a word composed in Greek by the polymath, cosmopolitan military leader and revolutionary Francisco de Miranda (Caracas, 1750-Cádiz, 1816), precursor of the independence of Venezuela and Spanish America. It was intended to mean "the papers related to Colombia", a name he gave to his monumental personal archives (63 volumes of documents, preserved in Caracas, Venezuela. http://www.franciscodemiranda.org/colombeia/), but it probably has no precise translation. Paraphrasing the Aristotelian *Politeia*, the name *Colombeia* derives from the notion of the "Great Independent State of Colombia" (*Colombia* is a latinization itself for the Columbian Continent, honouring Christophorus Columbus). It was a utopian geopolitical project conceived by Miranda as early as 1798, as a single republic from the Mississippi to Cabo de Hornos. Simón Bolívar borrowed the name to establish Colombia (1819), a more modest Republic that, by 1822, embraced the current territories of Venezuela, Colombia, Panamá and Ecuador. Its dissolution began in 1830. *Colombeia mycalesis* Röber, **comb. nov.**, is a distinctive butterfly species, so far the only member of its genus. Its distribution is restricted to the Western portion (biogeographical Chocó) of the current Republics of Colombia and Ecuador (and possibly the adjacent Pacific slopes of Panamá). We think *Colombeia*, feminine substantive, is an appropriate name for a genus endemic to that region, and a tribute to Miranda.

Species belonging to Colombeia

Colombeia mycalesis (Röber, 1927), **comb. nov.**

Euptychia mycalesis Röber, 1927: 281. [TL: West-Columbien, 500 meter]

Euptychia mycalesis Röber; Gaede, 1931: 456; d'Abrera, 1988: 764, 765 row [1], figs. [1] (male syntype ventral), [2] (female dorsal), 875; 2001: 183, pl. 137, fig. 7 (male); Lamas, 2001: 32; Shou *et al*., 2006: 85.

Magneuptychia mycalesis (Röber); Lamas, 2001: 32; 2004: 220; T. & L. Racheli, 2001: 329; Piñas, 2004: 34, figs. 267, 268; Palacios & Constantino, 2006: 266; Checa, 2008: 34 figs. (male ventral, dorsal).

E.[*uptychia*] *mycalesis* Röber; Costa et al., 2016: 199.

[¿?] *mycalesis* Röber; Costa *et al.*, 2016: 204.

Material examined

Colombeia mycalesis: **COLOMBIA**: 1 male, West-Columbien, 500 meter, März-Juni, *mycalesis* Type Röb [male], Brit. Mus. 1928-508, Type [Syntype](NHMUK); **Chocó**: 1 female, Río San Juan, 100 m, febrero 2009, leg. J. Urbina [Genit. JFL 617]; 1 male, Rio St. Juan, Columb. Jr., Eupt. spec. 2, [genitalia vial 9091 Lee D. Miller]; 1 female, Rio St. Juan. Columb. Jr. [genitalia vial 9092 Lee D. Miller]; **Valle del Cauca**: 1 male, Bajo Calima, 300 m [Genit. JFL1859 (fig. 16)]; 1 female, same data (JFLC); **ECUADOR**: 1 male, Santo Domingo, Santo Domingo de los Colorados, octubre 1959, ICN-MHN-L 28527 [Wing prep. ALV054-17 (fig. 5), Genit. prep. ALV550-17].

Omacha Andrade, Viloria, Henao & Le Crom, **gen. nov.**
(Figs. 6, 17)

http://zoobank.org/urn:lsid:zoobank.org:act:AC65B91F-7D82-40C7-93E9-DEED5D435F47

Type species: *Magneuptychia pax* Huertas, Lamas, Fagua & Willmott, 2016; herein designated.

Diagnosis

Because of the superficial appearance, ocelli and bands on the underside, *Omacha* Andrade, Viloria, Henao & Le Crom, **gen. nov.**, is comparable with other Neotropical genera as *Magneuptychia* Forster, *Cissia* Doubleday, *Huberonympha* Viloria & Costa, *Stevenaria* Viloria, Costa, Neild & Nakahara and *Nubila* Viloria & Andrade, **gen. nov.** Its type species herein designated is *Magneuptychia pax* Huertas, Lamas, Fagua & Willmott (in Huertas *et al.* 2016). However, the new entity differs homologically from all the genera mentioned in several characters of the wing size, pattern, venation and male genitalia. The presence of a series of five, well developed, monopupillated ocellar elements from R5 to Cu1 on the hindwing verso, a character found also in the members of *Nubila*, which however have different venation and male genitalic structure, is diagnostic for *Omacha* (see above).

Comparisons for the following description refer to *Magneuptychia* and *Cissia sensu stricto*, as considered by Costa *et al.* (2016)

Description

Butterflies of small to medium size (average FWL, male: *ca*. 21mm; female: *ca*. 20.5 mm). *Antennae* reaching two thirds of the costa, club formed gradually. Eyes

prominent and setose. Palpi setose, twice as long as head, cream white in general, with white setae on the outer sides and dark brown ones in the inner, first segment subrectangular in lateral view, second one cylindric, almost twice as long as first, third segment small and pointed. *Forewings* subtriangular, corners rounded, margins smooth; hindwings oblong, external margin slightly undulated. No androconial scales detectable. Ocellar elements well developed only in the hindwing: characteristically represented by a series of five contiguous elements, with single pupils, in cells R5 to Cu1; those in R5, M1 and Cu1 are black ocelli fully developed; cells M2 and M2 bear ocellar elements lacking dense black around the pupils, but pupillar elements large and silvery (never elongate as in *Nubila*). Well developed ocellus in Cu1 above. *Venation* (Fig. 6): forewing Subcosta, R1 and root of Cubitals swollen at base; Subcosta ending circa half length of the costa; R1 emerging at distal quarter of discal cell, ending within the beginning of distal third of the costa; R2 ending at costal limit of apex (at the end of fourth fifth of the costa in *Magneuptychia*, *Huberonympha*, *Cissia* and *Stevenaria*); R3 ending at tip of apex (before apex in *Magneuptychia*, *Huberonympha*, *Cissia* and *Stevenaria*); R4 and R5 ending at outer margin limit of apex (R4 before apex and R5 at apical tip in *Magneuptychia*, *Huberonympha*, *Cissia* and *Stevenaria*); M1 emerging independently from Rs, like in *Huberonympha* and *Stevenaria*, but both roots not as close as in *Magneuptychia*, and much less distant from each other than in *Cissia*; root of A2 not swollen, emerging independently and separate from discal cell (unlike other genera considered here for comparisons); m1-m2 strongly curved basally, resembling the case of *Stevenaria*, but without a recurrent veinlet towards the interior of the cell; m2-m3 sinuous. Hindwing Humeral well developed, reaching the coastal margin at the distal end of the first quarter of the coastal length, emerging together with Sc + R1 and Rs; A3 emerging from first sixth of A2 (unlike *Magneuptychia*, *Huberonympha*, *Cissia* and *Stevenaria*, in which it rises independently from the wing base); rs-m1 shorter than in *Magneuptychia*, *Huberonympha*, *Cissia* and *Stevenaria*; m1-m2 long and strongly curved inwards the cell, contrasting with *Magneuptychia*, in which this vein is straight (and only slightly curved in *Huberonympha*, *Cissia* and *Stevenaria*). *Male genitalia* (Fig. 17): Male genital armature stylized; tegumen dome-like, relatively small; uncus straight, lanceolate, one and half times longer than tegumen; subunci thick at base, emerging laterally in divergent angle, below the base of uncus, curving upwards and ending above the latter, more or less at the same height of tegumen; aedeagus stylized, as long as tegumen + uncus; saccus long and tubular in lateral and superior view; valvae elongate, characterized by a diagnostic, unique tricuspid tip.

Derivatio nominis

Omacha is the aboriginal name for the largest of all the species of river dolphins of South America, *Inia geoffrensis* de Blainville, but it is also the name of a prize winning non-government environmental organization (Fundación Omacha) established in Colombia in 1993 for the purposes of developing research and conservation projects in the Amazonia. We dedicate the name of this new genus of Amazonian butterflies to this successful institution and to its President, our friend and colleague Dr. Fernando Trujillo for his devoted labour to conservation biology in Colombia and other countries of South America.

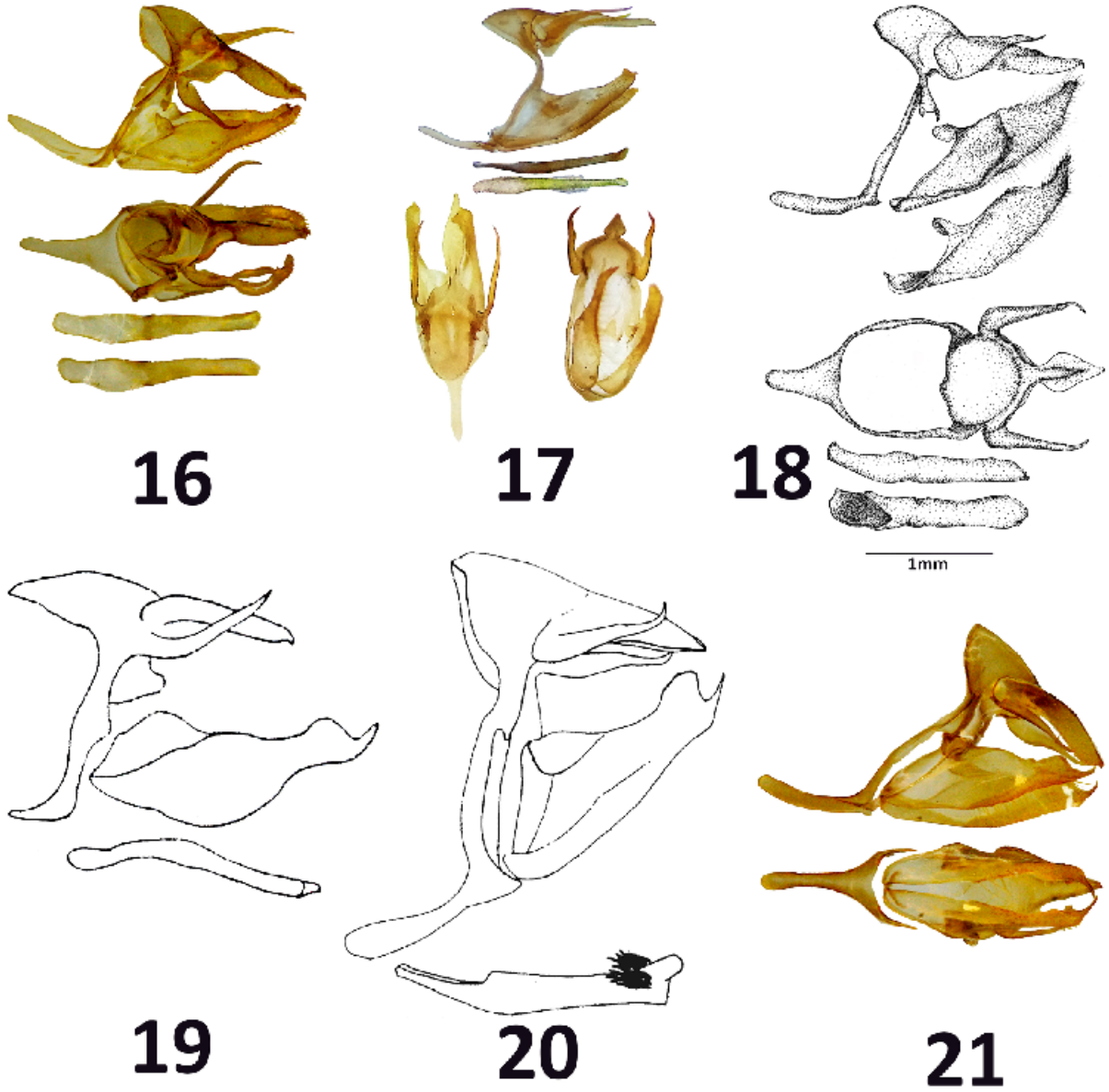
Species belonging to Omacha

Omacha pax (Huertas, Lamas, Fagua & Willmott, 2016), **comb. nov.**

['*Euptychia*'? sp.: d'Abrera, 1988: 786-787, row [7], figs. [1] (male dorsal), [2] (female ventral)]
[*Magneuptychia* sp. n. 1; Lamas *et al.*, [1997]: 65]
[*Magneuptychia* [n. sp.]; Lamas, 2004: 220 (no. 1416)]
[*Magneuptychia* sp. 3; Piñas, 2004: 34, figs. 271-272]
Magneuptychia pax Huertas, Lamas, Fagua & Willmott, 2016: 6-10, figs. 1A (male), 1B (female), 2A-D (male abdomen & genitalia), 2E-G (female abdomen & genitalia), H-I (larval head capsule), 3 (distribution & habitat). [TL: [Colombia, Putumayo], n[ea]r. Villa Garzón, Los Naranjos [1°34'13"N, 75°43'W]]

Material examined

Omacha pax: **COLOMBIA**: **Amazonas**: 1 male, Puerto Nariño, ix.[19]94+, leg. F. Montero (JFLC); 1 female, Leticia, Caño Yaguarcaca, 150 m, 3.xii.1982, leg. J. Salazar, MHN-UC (MHNUC); 1 male, Puerto Nariño, Camino San Martín de Amacayacu, 105 m, -3,7761111 S, -70,3444444 W, 1.iv.2015, leg. G. Andrade-C., GAC 11988 ICN-MHN-L 34065 (ICN); **Caquetá**: 1 male, San Vicente del Caguán, Río Yarí, Puerto Mosco, 217 m, 1,0849166 N., -74,2861111 W, 13.iii.2017, leg. E. Henao, EH 293, ICN-MHN-L 37152; 1 male, same data, 1,1218611 N, -74,2918889 W, 15.iii.2017, leg. E. Henao, EH 319, ICN-MHN-L 37151; 1 male, same data, 185 m, 0,1218333 N,-74,0932777 W, 20.iii.2017, leg. E. Henao, EH 521, ICN-MHN-L 31449 [Wing prep. (Fig. 6), Gen. No. 1649 (Fig. 17)]; 1 female, same data, 420 m, 27.vii.1995, leg. G. Fagua, ICN-MHN-L 31449 (ICN).



Figs. 16-21. Lateral (and in some cases dorsal and/or ventral) views of the male genitalia structures of six species representative of four genera (two new) of Neotropical satyrine butterflies. In lateral view drawings, left valve and aedeagus have been detached from armature for better visualization. **16**. *Colombeia mycalesis* (Röber), **comb. nov.**, type species of the genus *Colombeia*, **gen. nov.**; **17**. *Omacha pax* (Huertas, Lamas, Fagua & Willmott), **comb. nov.**, type species of the genus *Omacha*, **gen. nov.**; **18**. *Magneuptychia libye* (Linnaeus), type species of the genus *Magneuptychia* Forster (after Costa *et al.* 2016); **19**. *Satyrotaygetis incerta* (Butler & Druce) (example from Costa Rica, after Hayward, [1964]. Not *Euptychia satyrina* (H. W. Bates) as originally indicated); **20**. *Satyrotaygetis gigas* (Butler) (after Forster, 1964); **21**. *Satyrotaygetis tiessa* (Hewitson), **comb. nov.**; upper lateral view, lower ventral view; aedeagus missing.

Taxonomic position of Euptychia tiessa *Hewitson, 1869* (Figs. 7, 21)

Molecular studies by Murray & Prowell (2005: 77) and Marín *et al*. (2017: 15) detected and drew the attention to the apparent genetic closeness of *Magneuptychia tiessa* (Hewitson) and *Satyrotaygetis satyrina* (Bates) as shown by their resulting phylogenetic trees (sister species). Wing pattern of the members of *Satyrotaygetis* Forster is characterized by monopupillated ocelli unlike any other taxon treated in this work (see Table 1). This singularity is combined with a distinctly serrate cucullus, a hooked distal process of the valva, and a thick aedeagus (see corresponding correct figures of the male genitalia of *S. incerta* in Hayward, [1964]: 513, fig. 101, and *S. gigas* in Forster, 1964: 75, fig. 35; herein reproduced as Figs. 19 and 20, respectively). *E. tiessa* not only shares these external (habitus in Warren *et al*. 2012a) and internal (male genitalia in fig. 21, this work) characters, but also shows the typical venation (fig. 7) of other members of *Satyrotaygetis* (e. g., *S. satyrina*, type of the genus, as illustrated by Forster, 1964: 75, fig. 34; herein reproduced in Fig. 9). Genitalia and venation are both very different from those of the type species of *Magneuptychia*, *Papilio libye* Linnaeus (see figs. 8 venation, 18 male genitalia). This cumulative evidence allows for confidently transfer *E. tiessa* to *Satyrotaygetis.*

Satyrotaygetis Forster, 1964, **gen. rev.**

Satyrotaygetis Forster, 1964: 73; Miller, 1968: 94; Lamas, 2004: 222; Costa *et al*., 2016: 200.

Type species: *Taygetis satyrina* H. W. Bates, 1865; by original designation (Forster, 1964: 73).

Species belonging to Satyrotaygetis

Satyrotaygetis gigas (Butler, 1867a), **sp. restit.**

Euptychia gigas Butler, 1867a: 486, pl. 40, fig. 7 [TL: México]

Euptychia gigas Butler; Butler, 1868: 30; 1877: 120; Kirby, 1871: 52; Hayward, [1964]: 514; Lamas, 2004: 222 (last two as as synonym of *S. satyrina* (H. W. Bates))

Euptychia satyrina (H. W. Bates) f. *gigas* Butler; Weymer, 1911: 212, pl. 48, row e.

Euptychia satyrina (H. W. Bates) var. *gigas* Butler; Gaede, 1931: 464.

Satyrotaygetis gigas (Butler); Forster, 1964: 73, 75 fig. 35 (male genitalia), t. 29 fig. 7; Raguso & Llorente, 1997: 287.

Cissia gigas (Butler); DeVries, 1987: 275, pl. 48, fig. 6 (male), 7 (female); Shou *et al*., 2006: 82.

[*Euptychia satyrina* H. W. Bates; d'Abrera, 1988: 781, row [5] (male ventral, pale form) (misidentification)]

[*Satyrotaygetis satyrina* (H. W. Bates); Chacón & Montero, 2007: pls. 177 figs. (two males verso, one is a misidentification); Garwood & Lehman, 2011: Garwood & Lehman, 2011: 280 figs. (five figures misidentifications, from Guatemala and Honduras); Marín, 2011: 49 fig. 71, 56, 59, 66, 69, 71 (misidentification)]

Satyrotaygetis incerta (Butler & Druce, 1872), **sp. restit.**

Taygetis incerta Butler & Druce, 1872: 98. [TL: Costa Rica]

Taygetis incerta Butler & Druce; Butler, 1873: 149, pl. 53, fig. 1; Butler & Druce, 1874: 335; Kirby, 1877: 711; Godman & Salvin, 1880: 85; Lamas, 2004: 222 (last two as a synonym of *S. satyrina* (H. W. Bates))

Euptychia satyrina (H. W. Bates) f. *incerta* (Butler & Druce); Weymer, 1911: 212.

Euptychia satyrina (H. W. Bates) var. *incerta* (Butler & Druce); Gaede, 1931: 464.

[*Euptychia satyrina* (H. W. Bates); Hayward, [1964]: 513 fig. 101, 514 (misidentification)]

Satyrotaygetis incerta (Butler & Druce); Forster, 1964: 73, t. 29, fig. 5.

[*Cissia satyrina* (W. H. Bates); DeVries, 1987: 275, pl. 48, figs. 8 (male), 9 (male) (misidentification)]

[*Euptychia satyrina* H. W. Bates; d'Abrera, 1988: 781, row [4], fig. [2] (male dorsal, pale form) (misidentification)]

[*Satyrotaygetis satyrina* (H. W. Bates); Beccaloni *et al.* 2008: 343 (misidentification)]

Satyrotaygetis satyrina (H. W. Bates, 1865)

Taygetis satyrina H. W. Bates, 1865: 179. [TL: Guatemala]

Taygetis satyrina H. W. Bates; Butler, 1868: 13; Kirby, 1871: 110; Butler & Druce, 1874: 335; Marín, 2011: 63.

Euptychia satyrina (H. W. Bates); Butler, 1877: 120; Godman & Salvin, 1880: 84, pl. 8, fig. 23; Godman, 1901: 653 (misidentifications in part); Weymer, 1911: 212, pl. 48, row e; Gaede, 1931: 464; Hayward, [1964]: 513 fig. 1001 (male genitalia), 514 [misidentification of *S. incerta* (Butler & Druce)]; d'Abrera, 1988: 781, row [4], figs. [1] (male dorsal, dark form), [2] (male dorsal, pale form, misidentification of *T. incerta* Butler & Druce), row [5] (male

ventral, pale form, misidentification of *E. gigas* Butler), 789, 877.

Satyrotaygetis satyrina (H. W. Bates); Forster, 1964: 73, 75 fig. 34 (venation), t. 29, fig. 6; Lamas, 2004: 222; Murray & Prowell, 2005: 70, 72, 73, 75, 76, 77; Chacón & Montero, 2007: pls. 177 figs. (male verso, one is a misidentification of *S. gigas* Btlr.), 178 fig. (pupa); Glassberg, 2007: 140, row [2], fig. [2]; Peña *et al*., 2010: 248, 250 fig. 2, 251 fig. 3, 253 fig. 4; Garwood & Lehman, 2011: 280 figs. (only one specimen correct [western Chiriqui, Panama]; five misidentifications of *S. gigas* (Butler)[Guatemala and Honduras])

[*Cissia satyrina* (W. H. Bates); DeVries, 1987: 275, pl. 48, figs. 8 (male), 9 (male) (misidentification of *S. incerta* (Butler & Druce))]

Cissia satyrina (W. H. Bates); Shou *et al*., 2006: 83.

[*Satyrotaygetis satyrina* (H. W. Bates); Beccaloni *et al.*, 2008: 343 (misidentification of *S. incerta* (Butler & Druce), Marín, 2011: 49 fig. 71, 56, 59, 66, 69, 71 (misidentification of *S. gigas* (Butler))]

Satyrotaygetis tiessa (Hewitson, 1869), **comb. nov.**

Euptychia tiessa Hewitson, 1869: 37. [TL: Ecuador]

Euptychia tiessa Hewitson; Butler, 1870: 48, pl. 18, fig. 4; 1877: 120; Kirby, 1871: 643; 1879: 135; Butler & Druce, 1874: 336; Godman & Salvin, 1880: 84; Weymer, 1911: 212; Gaede, 1931: 466; d'Abrera, 1988: 764, 765, row [4], figs. [1] (male dorsal), [2] (female ventral), row [5], fig. [1] (male ventral), 877.

Cissia tiessa (Hewitson); DeVries, 1987: 275, pl. 48, fig. 10 (male); T. & L. Racheli, 2001: 329; Shou *et al*., 2006: 83.

Magneuptychia tiessa (Hewitson); Lamas, 2004: 220; Piñas, 2004: 34, figs. 263, 264; Murray & Prowell, 2005: 69, 72, 73, 75, 76, 77; Valencia-Martínez *et al.*, 2005: 167, pl. 33 fig. 3 [misidentification of *Magneuptychia libye* (Linnaeus)]; Chacón & Montero, 2007: pl. 175 fig. (male verso); Orozco *et al.*, 2009: 37; Salinas *et al*., 2009: 436; Garwood & Lehman, 2011: 273, figs. (female and male), 80, fig.; Vargas & Salazar, 2014: 273.

E.[*uptychia*] *tiessa* Hewitson; Costa *et al*., 2016: 199.

[*¿?*] *tiessa* Hewitson; Costa *et al*., 2016: 204.

Material examined

Satyrotaygetis gigas: **MEXICO**: 1 female, Oajaco [*sic*], pur. From Hartwegg 44-13, Mexico, Type, B. M. Type No. Rh 3245, *Euptychia gigas* [female] Butler [Syntype] (NHMUK); **HONDURAS:** 1 male, SMD (STMD-D). ***Satyrotaygetis incerta***: **COSTA RICA**: 1 male, Costa Rica, Van Patten, Druce Coll. *Taygetis incerta* Butl. & Dr. Type. Godman-Salvin Coll. 1904-1, B. C. A. Lep. Rhop. *Euptychia satyrina* Bates, B. M. Type No. Rh. 3246, *Euptychia incerta* [male] Butl. & Dr. *T. incerta* Butl. Type. Type H. T. [Holotype] (NHMUK); **PANAMA**: 1 male SMD (SMTD-D); 2 female, SMD, (SMTD-D). ***Satyrotaygetis satyrina***: **GUATEMALA**: 1 male, Centr. Valleys, Guatemala, F. D. G. & O. S. Type, Sp. figured, Godman-Salvin Coll. 1904-1, B. C. A. Lep. Rhop. *Euptychia satyrina* Bates, B. M. Type No. Rh. 3244, *Euptychia satyrina* [male] Bates, Type, H. T. [Holotype] (NHMUK). ***Satyrotaygetis tiessa***: **COLOMBIA**: **Chocó**: 1 male, El Tabor, Chocó, 1500 m, 10.v.[19]90, leg. J. Salazar; 1 male, same data, 1800 m; 1 male, San José del Palmar, 1800 m, viii.[19]94, leg. D. Acosta; Cauca: 1 male, Tambito, 1000 m, 23.iii.[19]96, leg. T. Pyrcz (Genit. JFL 619 [fig. 21]) (JFLC); **Risaralda**: 1 male, Pueblo Rico, 1650 m, xi.[19]93, leg. F. Montero (JFLC); 1 male, Mistrato, Alto de Pisones, 1725 m, 3.vi.1992, leg. G. Andrade-C., GAC 3461, ICN-MHN-L 8983; 1 male, same data, 1740 m, 4.vi.1992, leg. G. Andrade-C., GAC 3463, ICN.MHN-L 8985 [Wing prep. ALV053-17 (fig. 7), Genit. prep. ALV569-17]; 3 females, Mistrato, San Antonio del Chami, camino al alto de Pisones, 1500, 17.iv.1993, leg., G. Andrade-C., GAC 4609, 4615, 4606, Gen. No. 1977, ICN-MHN-L 28535, 11295, 28538; 1 male, Santa Cecilia, x.1982, leg. J. Vélez, MHN-UC 12 (MHNUC); **Valle del Cauca**: 1 male, 1 female, Queremal, km 55, 1200 m, 10. iv. [19]90, leg. J. Salazar (JFLC); 1 male, Queremal, Kilómetro 55, 278 m, 20.xii.1984, leg. J. Salazar, MHN-UC 278 (MHNUC); 1 male, Dagua, Columb occ. 95 Kalbr, SMD Museum Berlin. **ECUADOR**: 1 male, Ecuador, Hewitson Coll. 79-69, *Euptychia tiessa* Hew. 2., B. M. Type No. Rh. 3150, *Euptychia tiessa* [male] Hew., Type [Syntype] (NHMUK); **Esmeraldas**: 2 males, Esmeraldas, 500 m, viii.1959, leg. L. Richter, ICN-MHN-L 2698, 5929; 2 females, same data, vii.1959, leg. L. Richter, ICN-MHN-L 2709, 2703.

DeVries (1987: 275) provided some information on the natural history of *S. tiessa*. Individuals referred as to *S. satyrina* from Costa Rica are certainly representatives of *S. incerta* (Butler & Druce), **sp. restit.** To our knowledge, *S. satyrina*, described from Guatemala, is distributed only in this country and the southern part of Mexico.

Nota bene: as a complement to the study of *Magneuptychia* included in Costa *et al.* (2016) we present here three cases of misidentification of *Magneuptychia lethra* (Möschler) as *Magneuptychia libye* (Linnaeus) (figs. 8 wing venation, 16 male genitalia), type species of its genus: Barcant, 1970: pl. 13, fig. 17; Lewis, 1973: pl. 60, fig. 2 [same

error in edition of 1987]; Urich, 1978: 12, figs., 13 [error pointed out by Cock (2014: 12), but the latter used the name *M. newtoni* (Hall), a junior synonym of *M. lethra*].

CONCLUSIONS

A number of independent phylogenetic studies based on the comparative analyses of DNA sequences, both mitochondrial (COI, Cyt b and ND1) and nuclear (EF-1α, wingless, GAPDH y RpS5), have revealed paraphyly and polyphyly among many of the taxa conveniently accommodated under *Magneuptychia* Forster by most authors (Murray 2001, Murray & Prowell 2005, Peña *et al.* 2006, 2010, 2011; Marín *et al.* 2009, 2011, 2012, 2017; Marín 2011). For instance, Murray (2001) and Murray & Prowell (2005) included in their analysis six species of "*Magneuptychia*" and none formed monophyletic groups with any other (Murray, 2001: 360; Murray & Prowell, 2005:72). In all variants of their cladograms "*Magneuptychia*" *moderata* appeared, well supported, as the closest taxon to *Splendeuptychia ashna* (type species of the genus). There was also strong support for the closest genetic distance between *M. tiessa* and *S. satyrina* (Murray 2001: 282, fig. 4.2; Murray & Prowell 2005: 77). Peña *et al*. (2010: 247, 250 fig. 2, 251 fig. 3, 253 fig. 4) got *Satyrotaygetis satyrina* notably separated (and nested among other genera) from any "*Magneuptychia*" included in their analyses, and "*Magneuptychia*" *moderata* and "*Splendeuptychia*" *purusana* closely associated as sister taxa in the last branch of every cladogram (Figs. 2, 3, 4). This collection of evidence is congruent with the taxonomic hypotheses herein proposed for *Nubila*, **gen. nov.**, and *Satyrotaygetis,* **gen. rev.** Not only it is not in conflict with our generic arrangement, but in fact it appears to support it.

According to our morphological observations *Nubila*, **gen. nov.**, should be considered one sister genus to *Splendeuptychia*, and quite apart from *Magneuptychia*.

Based on a morphology study in which a considerable number of characters were coded, Marín (2011) generated a cladogram in which "*Magneuptychia*" *inani* emerged very distant (sister to the *Pareuptychia* clade, pp. 56) from *Magneuptychia libye* (type species of the genus, derived in an unnamed group close to the *Megisto* clade), and at least once very close to *Satyrotaygetis satyrina* (pp. 59). On the other hand Murray (2001) studied, described and compared some morphological characters of the early stages of *M. libye* (later published by Kaminsky & Freitas, in 2008) and "*Magneuptychia*" *ayaya* (a junior synonym of *Macrocissia iris*, **comb. nov.**). She found considerable differences between the two taxa. These cases account for additional elements to justify the erection of *Macrocissia*, **gen. nov.** It is morphologic and genetically distinct, but comparable and very close to the genus *Satyrotaygetis* (see Marín *et al.* 2017).

Colombeia, **gen. nov.** and *Omacha*, **gen. nov**. are rather peculiar, so far monospecific genera, whose relationships with other equivalent species groups of the Satyrinae cannot yet be established. Probably *Colombeia*, **gen. nov.** is truly related to *Magneuptychia*.

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Table 1. Descriptive comparison of the ocellar elements of the underside wing patterns of ten genera of Neotropical satyrine butterflies.

Genus	Upperside		Underside	
	Forewing	Hindwing	Forewing	Hindwing
Magneuptychia	Lacks ocelli	Lacks ocelli	Ocelli not well developed, except for subapical, bipupillated	Ocellar series: R5-Cu1+A2 (obsolete), generally bipupillated but sometimes fused as one
Huberonympha	Lacks ocelli	Only females with blind, subanal ocellus	With single subapical ocellus, bipupillated. Other vestigial on M1	Ocellar series: R5-Cu1, all five bipupillated (white)
Cissia	With one subapical ocellus, bipupillated	With subanal ocellus, bipupillated	With single subapical (M1) ocellus, bipupillated	Ocellar series: R5-Cu1. R5, M2 and M3 only double spots (pupillae and spots all silver)
Stevenaria	Lacks ocelli	With subapical dark spot (M1) and a very diffuse dark vertigial spot on Cu1	With vestigial ocelli	Ocellar series: R5-Cu1. R5, M2 and M3 without black; all five bipupillated (R5, M2, M3 silver; M1 Cu1 white)
Satyrotaygetis	Only females with diffuse ocellar dark mark (subapical)	With submarginal ocellar element on Cu1 (monopupillated), vestigial or smaller in males. Better developed in females	Subapical ocellus on M1; vestigial ocelli may variably appear on R5, M2 and M3. Monopupillated	Ocelli prominent on R5, M1 and notably Cu1. Absent, vestigial or poorly developed (females) on M2 and M3. All monopupillated (white)
Colombeia	Only females with subapical dark mark (M1), and one dark vestigial on M3	Females with subanal blind ocellus (Cu1), with diffuse yellow ring; males only dark spot, smaller	Ocellar series M1-M3 (Cu1 in females). All bipupillated (white); M1 prominent, subapical: M2 fused to M1	Ocellar series R5-M1, M3-Cu1 (M2 generally missing in males, vestigial in females). M3 and Cu1 fused. All bipupillated (white)
Macrocissia	Lacks ocelli	May exhibit dark ocellar element (Cu1), specially females	Subapical monopupillated ocellus (M1)	Ocellar series R5-Cu1. R5 and M1bipupillated; Cu1 either with one or two pupillae, always exceeding limits of cell; M2 and M3 with double pupilla, elongated, silvery; lacking black
Nubila	Lacks ocelli	May exhibit two diffuse dark ocellar spots (M1, Cu1)	Lacks ocellar elements	Ocellar series R5-Cu2. R5, M1, Cu1 and Cu2 fully ocellated (one pupil, white), M3,M3 lacking black, elongated, double pupillae, silver
Omacha	Lacks ocelli	Single, monopupillated ocellus (Cu1)	With vestigial subapical ocelli	Ocellar series R5-Cu1 complete. All ocelli monopupillated
Splendeuptychia	Lacks ocelli	Exhibit one diffuse dark ocellar spot on Cu1. Sometimes one even less distinct on M1	Lacks ocellar elements	Ocellar series R5-Cu1 complete. R5 and M1 monopupillated, M2 to Cu1 bipupillated. Obsolescent or vestigial ocellar mark on Cu2