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"The *Hermeuptychia* Papers"

"Los papeles de *Hermeuptychia*"

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ABSTRACT

Investigations on the nomenclature of the American butterfly genus *Hermeuptychia* Forster, 1964 (Lepidoptera: Nymphalidae, Satyrinae) yielded the reinstatement of three species, the proposal of four new combinations, and the recognition of eight new synonymies; mainly through the study and scrutiny of information published in scientific papers, books, and web pages; but also by the examination of its diversity represented in biological collections. The novel taxonomic arrangement proposed for this genus is as follows: *Hermeuptychia acmenis* (Hübner, 1823), **comb. nov.** (= *H. hermybius* Grishin, 2014, **syn. nov.**), *Hermeuptychia atalanta* (Butler, 1867), *Hermeuptychia camerta* (Cramer, 1780), **sp. restit.**, **comb. nov.**, *Hermeuptychia canthe* (Hübner, [1811]), **sp. restit.**, **comb. nov.** (= *Neonympha pimpla* C. Felder & R. Felder, 1862, **syn. nov.** = *Euptychia maimoune* Butler, 1870, **syn. nov.** = *Euptychia nana* Möschler, 1877, **syn. nov.**), *Hermeuptychia cautheus* (Godart, [1824]), **sp. restit.**, **comb. nov.** (= *Hermeuptychia intricata* Grishin, 2014, **syn. nov.**), *Hermeuptychia cucullina* (Weymer, 1911), *Hermeuptychia gisella* (Hayward, 1957) (= *Hermeuptychia hermes* var. *hermesina* Forster, 1964, **syn. nov.** = *Hermeuptychia clara* Nakahara, Tan, Lamas & Willmott, 2016, **syn. nov.**), *Hermeuptychia harmonia* (Butler, 1867) (= *Euptychia calixta* Butler, 1877 = *Hermeuptychia callixta* Forster, 1964, **syn. nov.**), *Hermeuptychia hermes* (Fabricius, 1775) (= *Hermeuptychia hermes isabella* Anken, 1994), *Hermeuptychia lupita* (Reakirt, [1867]) and *Hermeuptychia sosybius* (Fabricius, 1793) (= *Hermeuptychia hermes kappeli* Anken, 1993).

Keywords: America, integrative taxonomy, Lepidoptera, nomenclature, Nymphalidae, Satyrinae.

RESUMEN

Investigaciones en la nomenclatura del género de mariposas americanas *Hermeuptychia* Forster, 1964 (Lepidoptera: Nymphalidae, Satyrinae), principalmente mediante el estudio y escrutinio de información publicada en artículos, páginas web y libros científicos, pero también en el examen de su diversidad representada en colecciones biológicas, arrojó la restitución de tres especies, la propuesta de cuatro nuevas combinaciones y el reconocimiento de ocho nuevas sinonimias. El nuevo arreglo taxonómico propuesto para este género es el siguiente: *Hermeuptychia acmenis* (Hübner, 1823), **comb. nov.** (= *H. hermybius* Grishin, 2014, **syn. nov.**), *Hermeuptychia atalanta* (Butler, 1867), *Hermeuptychia camerta* (Cramer, 1780), **sp. restit.**, **comb. nov.**, *Hermeuptychia canthe* (Hübner, [1811]), **sp. restit.**, **comb. nov.** (= *Neonympha pimpla* C. Felder & R. Felder, 1862, **syn. nov.** = *Euptychia maimoune* Butler, 1870, **syn. nov.** = *Euptychia nana* Möschler, 1877, **syn. nov.**), *Hermeuptychia cautheus* (Godart, [1824]), **sp. restit.**, **comb. nov.** (= *Hermeuptychia intricata* Grishin, 2014, **syn. nov.**), *Hermeuptychia cucullina* (Weymer, 1911), *Hermeuptychia gisella* (Hayward, 1957) (= *Hermeuptychia hermes* var. *hermesina* Forster, 1964, **syn. nov.** = *Hermeuptychia clara* Nakahara, Tan, Lamas & Willmott, 2016, **syn. nov.**), *Hermeuptychia harmonia* (Butler, 1867) (= *Euptychia calixta* Butler, 1877 = *Hermeuptychia callixta* Forster, 1964, **syn. nov.**),

Hermeuptychia hermes (Fabricius, 1775) (= *Hermeuptychia hermes isabella* Anken, 1994), *Hermeuptychia lupita* (Reakirt, [1867]) y *Hermeuptychia sosybius* (Fabricius, 1793) (= *Hermeuptychia hermes kappeli* Anken, 1993).

Palabras clave: América, Lepidoptera, nomenclatura, Nymphalidae, Satyrinae, taxonomía integradora.

INTRODUCTION

The genus *Hermeuptychia* Forster, 1964 (Lepidoptera: Nymphalidae, Satyrinae) is only found in the American continent, at tropical and subtropical latitudes, and from sea level to around 2,500 m, in the equatorial Andes. It comprises a group of small-sized species of brown butterflies, characterized by possessing few external characteristics that determine their interspecific differences: basically, the dorsal surface of their wings is entirely fuscous and of limited usefulness for specific discrimination; the ventral basic pattern for all its taxa, which is developed over a brown background, is characterized by two darker discal lines (uniform or variably undulate) running more or less parallel to the outer margins, which are also delineated by fine submarginal and marginal lines. Darker marks develop over the veins that close the discal cell. They possess ocelli (usually black, ringed with ochraceous color, with a single silver white pupil) in the postdiscal region. There are six ocelli on the hindwing – exceptionally five in some individuals –, and a variable number on the forewing, from none to five. The male genital armature, which has been reasonably well studied has a dome-like tegumen, a lanceolate uncus, and well-developed brachia (subunci) that may reach the length of the uncus but are usually shorter. The saccus is digitiform and well-developed, and the valvae distinctively elongated, with the distal half thinner than the basal. The aedeagus is relatively thick and straight, devoid of particularities of taxonomic interest. Their female genitalia, known for two or three species, have so far been set aside as a very informative source of characters for comparative morphology.

The taxonomy of the species included in this genus goes as far back as J. C. Fabricius, who described the first known species from Brazil in 1775, *Papilio hermes*, the type of the genus erected by W. Forster almost two hundred years later. Species belonging to *Hermeuptychia* have a rich taxonomic history, as it will be seen in this work. Their names have been historically combined within genera like *Papilio* Linnaeus, 1758, *Satyrus* Latreille, 1810, *Oreas* Hübner, [1807], *Euptychia* Hübner, 1818, *Neonympha*, Hübner, 1818, *Megisto* Hübner, [1819], *Cissia* Doubleday, 1848 and *Yphthimoides* Forster, 1964. Most species were described between the 18th and 19th centuries, but a few were discovered later, mainly in the 20th century, with two highly advertised cases in 2014 ([Anonymous] 2014; Rick 2014) and the most recent in 2016. The genus has attracted considerable attention of molecular systematists during the last ten years, and several interesting and sometimes lengthy papers have been produced as a result of their comparative studies. This increasing interest has been also supplemented by initiatives in comparative morphology, biology and ecology (Seraphim *et al.* 2014, Cong & Grishin 2014, Cosmo *et al*. 2014, Warren *et al*. 2014a, 2014b, Anken *et al*. 2015, Tan & Lucky 2016, Nakahara *et al.* 2016 and Austin 2018).

This work considered the relevant information available in the literature about the butterflies of the genus *Hermeuptychia*, critically emphasizing the evaluation of the taxonomic hypotheses put forward in publications that have appeared during the last 30 years. I call these publications "The *Hermeuptychia* papers".

This is not yet a taxonomic revision, which will surely involve much more comparative, morphological, molecular, ethological, and biogeographical work. This is just an exhaustive exercise in nomenclature that any alpha-taxonomist should do before attempting a revisionary study or even the description of new species.

Our resulting taxonomic hypotheses are substantially different from what have been traditionally accepted. They bring some questions about how integral is the so called "integrative taxonomy", and about its failure in recognizing the fundamental role of nomenclature and biogeography to biological systematics.

MATERIAL AND METHODS

Two phases of research were accomplished in parallel; the examination, dissection, and comparison of butterfly specimens preserved in entomological collections (mainly public natural history museums, but also to a lesser degree, private collections), and the critical and careful reading of the content of numerous scientific papers, books, and web pages. Comparative, logical, and coherent criteria were conceived to aim an objective taxonomic arrangement. It was a work of comparative zoology. When the synonymies were built in regard to the species treated in this work, special attention was paid to the original descriptions and re-descriptions, the different phylogenetic hypotheses in which they are included, and the congruence of the latter with basic notion of biogeography.

Many illustrations of *Hermeuptychia* butterflies have been published, including photographs of most type specimens known, the habitus of all species (described and undescribed), and male genital structures. Both drawings and photographs are from a wide variety of localities and habitats of the American continent. Good quality data on the immature stages of at least three species are available, as well as data on hostplants, behavior, and ecology. The amount of data is overwhelming. The preparation of this notes has taken nearly ten years, and a supplement with the examined material will be timely published. Opinions on authority, typification, priority, synonymy, and homonymy followed the provisions of the International Code of Zoological Nomenclature (ICZN 1999).

Abbreviations: comb. nov.: new combination; *et al*.: *et alii* (and others); GLAHM: Hunterian Museum and Art Gallery, University of Glasgow, Glasgow, UK; IML: Museo de Ciencias Naturales de la Fundación Miguel Lillo, Tucumán, Argentina; *in litt*.: *in litteris*; MS: manuscript; NHMUK: The Natural History Museum, London, UK; *nom. nov.*: *nomen novum*, new name; *nom. nud.*: *nomen nudum*, name not available; *op. cit.*: *opere citato*, work cited; sp. restit.: species restored or reinstated; syn. nov.: new synonym; TL: Type Locality; USNM: United States National Museum, Smithsonian Institution, Washington, D. C., USA; ZMHB: Museum für Naturkunde Berlin (Zoological Collections), Germany.

RESULTS

Nomenclature and synonymy of the species belonging to Hermeuptychia

The names *hermes* Fabricius and *sosybius* Fabricius have long been erroneously applied to other *Hermeuptychia* species (and to other taxa belonging to different genera) in a significant number of papers and popular books. The synonymic citations for these two taxa in this article are not exhaustive.

Hermeuptychia Forster, 1964: 87-91.

Type species: *Papilio hermes* Fabricius, 1775; by original designation (Forster, 1964: 87).

Hermeuptychia Forster; Miller, 1968: 93, 168; 1976: 1; Miller & Brown, 1981: 191, 241; Viloria, 1990: xx, 88; Anken, 1993: 418; 1994: 283, 1995a: 8; 1995b: 237, 238; Poole & Lewis, 1996: 621, 904; Opler & Warren, 2002: 42; Lamas, 2003: 69; 2004: 220; Piñas Rubio, 2004: 3; Murray & Prowell, 2004: 74, 77, 78; Brown, Jr. *et al*., 2007: 478; Koçak & Kemal, 2007: 121; 2015: 54; Pelham, 2008: 404, 492, 627; Pulido & Andrade, 2009: 520, 551; Marín *et al*., 2009: 237, 239 tabl. 2 (part), 241, 242; 2011: 6, 8, 10; 2012: 209, 212 fig. 1C (tRNA structure), 213 fig. 2 (comparative sequence alignment), 214 fig. 3 (trees) part; Peña *et al*., 2010: 249, 252, 254; Matos-Maraví *et al*., 2013: 55, 64; Seraphim *et al*., 2014: 39, 40, 43, 45, 46; Cong & Grishin, 2014: 43, 44, 45, 46, 47, 51, 52, 54, 55, 56, 57, 58, 60, 61, 65, 66, 67, 68, 72, 73, 76, 78, 79, 80, 81, 86, 87, 88; Cosmo *et al*., 2014: 82, 86; Warren *et al*., 2014a: 83, 85; 2014b: 45, 46, 47, 48, 50; Anken *et al*., 2015: 157, 158; Nakahara *et al*., 2016: 77, 78, 80; Marín *et al*., 2017: 768, 769, 774, 775, 781; 2019: 91, 98; Austin, 2018: 311; Espeland *et al*., 2019: 116, 120, 121, 122; Benmesbah *et al*., [2021]: 19, 28.

Hermeuptychia acmenis (Hübner, 1823), **comb. nov.**

[*Megisto acmenis* Hübner, [1819]: 54], *nom. nud.*

Megisto acmenis Hübner, 1823: pl. [41], figs. 233 (male dorsal), 234 (male ventral). [TL: "Baltimore"].

Neonympha acmenis (Hübner); Westwood, 1851: 375; Morris, 1860: 10; Weidemeyer, 1864: 527; Herrich-Schäffer, 1865: 70; Mombert, 1869: 562.

Euptychia acmenis (Hübner); Butler, 1867: 476-477; 1868: 24; 1877a: 119; Gerhard, 1878: 2; Kirby, 1871: 50; 1880: 296; Staudinger, 1887: 227, pl. 81 [row 3] (misidentification of *Godartiana byses* (Godart)); Mabilde, 1896: 97 (misidentification); Eimer & Fickert, 1897: 314; Sanders, 1904: 366 (misidentification); Weymer, 1911: 206, t. 51b [2]; Gaede, 1931: 437; D'Abrera, 1988: 778 fig. [row 4] male ventral.

Megisto acmenis (Hübner); Scudder, 1875: 244; Möschler, 1876: 35; Barnes & Lindsey, 1922: 90.

[*Hermeuptychia hermes* (Fabricius); D'Abrera, 1988: 777 fig. [row 1, fig. 3] male verso (misidentification)].

Yphthimoides acmenis (Hübner); Lamas, 2004: 223.

[*Hermeuptychia sosybius* (Fabricius); Glassberg, 2007: 139 [row 2, fig. 3]; 2012: 257 [fig. Hidalgo Co., TX] (misidentifications)].

Yphthymoides [*sic*] *acmenis* (Hübner); Teston & Corseuil, 2008: 47 (misidentification).

Hermeuptychia hermybius Grishin, 2014: 44, 49, 50, 68-81, 83 figs 48–59, 60b, e, h, k, 61b, 62a–m, 64q–z, 67 (distribution map) part, 70, 75 fig 63 (morphometry, in part), 76 fig. 65, 78 fig. 66 (cladogram) part, 83 fig, 70 (life cycle), 84, 85, 86, 87, 88, **syn. nov.** [TL: "E of Brownsville, Texas, USA"].

Hermeuptychia hermybius Grishin; Nakahara *et al*., 2016: 83; See *et al*., 2018: 51; Marín *et al*., 2019: 91.

Megisto acmenis is a small satyrine butterfly species that was originally illustrated by Hübner, who depicted it with reasonable detail in dorsal and ventral views (1823: pl. [41], figs. 233, 234). Its type locality is "Baltimore", presumably in what corresponds to the great city of the state of Maryland, founded in 1729 on the Patapsco River, near its mouth in the Chesapeake Bay (United States of America). For a long time, it has been an ignored, neglected, or omitted taxon, because historically no other records of a similar insect have been known, and because most of the authors questioned its geographical origin from very early on. Despite many efforts, it has not been possible to relocate the biological material studied by Hübner to illustrate this species. Hemming (1937) and Calhoun (2018) mentioned that at least part of the butterflies available to Hübner to produce his original illustrations were later kept in the form of wings pasted in scrapbook-like volumes (or possibly as lepidochromes?), whose whereabouts is currently unknown.

Butler (1868: 24) pointed out that William Henry Edwards (*in litt*.) referred to this species as inhabitant of the "southern states". In this way Butler, relying on Edwards' authority, seemed to admit that it is reliably a North American species. However, Scudder (1875: 244) denounced the opposite: "this butterfly in unknown to American lepidopterists, as it seems very doubtful whether it can be considered American, more particularly as three [*sic*] other Satyrids given by Hübner in this same work [referring to the "*Zütrage zur Sammlung exotischer Schmettlinge*"] under the names of *Symphaedra*, *Alcandra*, *Mycalesis*, *Otrea* and *Yphthima* [*sic*], *Philomela* (all said by him to come *aus Georgien in Florida*) have since been discovered to be East Indian species." However, this assertion is arguable, as Hübner had already identified and named this taxon as early as 1819, because the name appeared printed in that year in the "*Verzeichniss bekannter Schmettlinge* [*sic*]" (therefore, at that moment a *nomen nudum*). It would be interesting to investigate whether the taxa referred to by Scudder have also been known already earlier than 1823.

Hübner's figures of *Megisto acmenis* are sufficiently clear and unequivocal, so that they qualify as iconotypical representation of the species. The International Code of Zoological Nomenclature, allows for the designation of one of these figures as the lectotype (ICZN 1999: 82, Art. 74.4), and although I interpret the illustration of the underside habitus (Hübner, 1823: pl. [41], figs. 234) as such, there is no intention in this work to allocate a type for this taxon.

After extensive comparative studies with numerous species of Satyrinae from all continents, I consider that according to size, wing shape, and coloration pattern; *Megisto acmenis* evidently represents a species of *Hermeuptychia* Forster, 1964, whose uniqueness and rarity consists of it being devoid of ocelli. D'Abrera (1988: 778 fig. [Row 4] male ventral) presented the photographic image of what in his opinion is the only authenticated specimen (without abdomen) of "*Euptychia acmenis*" in the collections of the NHMUK. His illustration represents an insect that compares favorably with the iconotypic image of Hübner. I examined this specimen in June 2016 (its detached abdomen is kept in a gelatin capsule). It appears to represent a species of *Hermeuptychia* by the detection of a few features in the wing pattern, such as the system of lines or bands, the small dark dash on the veins that distally close the discal cells and the punctual vestiges of the ocellar system. D'Abrera's identification appears correct, but it was taken from an old identity label in the drawer, and it must be attributed to the work of a former curator of the collections in London. This specimen is labeled with an elongated piece of paper which is folded several times. It bears the faint shadow of a handwritten line with fountain pen ink, which is illegible.

The abundance of *Hermeuptychia* butterflies in wild populations may be usually medium to high (DeVries 1987, Viloria 1990, Peixoto & Benson 2009, Warren *et al*. 2014a), so it is also its individual frequency (pers. obs. in Venezuela, 1988-2019). For this reason, it seems unusual that over almost two centuries since its discovery, *Hermeuptychia acmenis* Hübner **comb. nov.**, is not adequately represented in collections, at least in the form that Hübner examined it. This suggests that we might be facing a true case of ecological rarity.

In some common species of the genus *Hermeuptychia*, the size and conformation of the ocelli usually vary markedly among individuals of the same population. However, in entomological collections it is appreciated that a small proportion of individuals of a species can be represented by extreme variations in the number and size of ocelli that are expressed on the ventral side of their wings. Complete ocellar reduction or suppression appears to be very rare; that is, infrequent. However, it does indeed occur, and particularly in some individuals recently recognized through the extensive comparative studies of Cong & Grishin (2014). It is unknown whether this particularity has to do with the proportion of alleles within populations or it is a phenomenon linked to seasonality, as it occurs in well-studied cases in African satyrids, mainly mycalesines and melanitines (Brakefield & Larsen 1984, Braby 1995, Dongmo *et al*. 2018).

The three cryptic taxa detected and discriminated by Cong & Grishin in their exhaustive work on the genus *Hermeuptychia* in the United States of America (*op. cit.*), have genetically and unobjectionable specific statuses. One such species shows a very large morphological variation in the degree of expression of its ocelli and of the band system of the ventral surface of the wings. In its most extreme forms, the maximum reduction is evident (Cong & Grishin, 2014: 70, figs. 53, 55) or the suppression of bands and ocelli (https://www.butterfliesofamerica.com/L/hermeuptychia_hermybius_types3.htm), in the manner of the two credited illustrations of *Hermeuptychia acmenis* (Hübner) **comb. nov.**, of which I have already spoken. No other *Hermeuptychia* appears to express that kind of extreme morphotype. Therefore, I propose the consideration of *Hermeuptychia hermybius* Grishin as a junior synonym (**syn. nov.**) of *H. acmenis* (Hübner) **comb. nov.**, as the latter is the oldest available name.

As for the authenticity of the locality "Baltimore" recorded by Hübner, the case requires further consideration. References are found to at least 23 North American historical localities – some now missing – in the states of Alabama, California, Colorado, Delaware, Georgia, Indiana, Iowa, Kansas (2), Kentucky (2), Maryland, Michigan, New York, North Carolina (2), Ohio (3), Tennessee and Vermont (USA), New Brunswick and Ontario (Canada) (https://roadsidethoughts.com/ga/baltimore-xx-wilkes-profile.htm). A good proportion of such sites do not qualify as a possible place of origin of any species of *Hermeuptychia*, because they are found in latitudes outside the biogeographic distribution of this genus, others are place names applied to villages or hamlets founded after the publication of Hübner's work.

Personally, I am inclined to think that the locality provided by this author is inaccurate and perhaps it refers (as seems to happen in many historical cases of doubtful or mistaken provenance records of plants and animals, particularly in dates before 1850) to a simple error originated by the supplier, to the reference of the place where the sample was acquired or the port where it was shipped to Europe. The geographic records provided by Cong & Grishin correspond only to the southeast of the state of Texas, along the current border with Mexico. Little is known about its real distribution, both in the USA and in Mexico. It is worth pointing out that in 1823 and before, Texas was still part of the Mexican territory. There is an unfortunate information gap regarding travelers and naturalists who explored the northern region of Mexico in the two decades prior to 1819-1823, the years of the publications of Hübner's name and illustration of *Megisto acmenis* (Silva 1944, Mayer 1961, Glantz 1982, Morales 1986). Both Hemming (1937) and Calhoun (2018) claim that the origin of much of Hübner's North American material is unknown.

Hermeuptychia atalanta (Butler, 1867)

Euptychia atalanta Butler, 1867: 474-475, pl. 39, fig. 12. [TL: "Venezuela"].

Euptychia atalanta Butler; Butler, 1868: 24; 1877a: 119; Kirby, 1871: 50; Weymer & Maassen, 1890: 17, 74 (misidentifications); Weymer 1911: 207, pl. 48a [3] (mistakenly as a synonym of *Euptychia fallax* (C. Felder & R. Felder)); Riley & Gabriel, 1924: 9 (types 1 male, 1 female); Gaede, 1931: 449 (last one as a synonym of *Euptychia hermes* (Fabricius)); Hayward, 1958b: 236 (as a synonym of *Euptychia hermes* (Fabricius)).

Euptychia fallax (C. Felder & R. Felder) var. *atalanta* Butler; Butler, 1870b: 251.

[*Euptychia hermes* (Fabricius); Longstaff, 1912: 54; 255, 264, 306, 307, 309, 310, 313, 320, 323, 329, 578-579 (misidentifications in part)].

[*Euptychia hermes fallax* (C. Felder & R. Felder); Beebe, 1951: 9 (misidentification)].

Hermeuptychia atalanta (Butler); Lamas, 2004: 220; Seraphim *et al.*, 2014: 42 fig. 1 (cladogram) part, 45, 46, 47, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: TO02, morphogroup 11; Cong & Grishin, 2014: 51, 78 fig. 66 (cladogram) part; Cosmo *et al.,* 2014: 82-86, figs. 1A (egg), B (1st instar), C (2nd instar), D (3rd instar), E (4th instar), F (prepupa), G-I (pupa), J (adult male, dorsal), K (adult male, ventral), fig. 2 (morphological details egg, larvae), fig. 3 (chaetotaxy 1st instar); Anken *et al*., 2015: 157, 159; Nakahara *et al*., 2016: 81, 83, 84 (all except Lamas, misidentifications of *Hermeuptychia hermes* (Fabricius)); Marín *et al*., 2019: 91; Ríos-Málaver *et al.*, [2021]: 85, 99.

Two syntypes of *Euptychia atalanta* Butler, 1867 (male and female) are recorded in the NHMUK by Riley & Gabriel (1924). They were collected by David Dyson in the surroundings of Caracas in 1846. Photographs of the male syntype taken by G. Lamas and N. V. Grishin are available online (Warren *et al*. 2012): [Ven / Venezuela pur. from Dyson 46-75/ B.M. Type No Rh 3228, *Euptychia atalanta* ♂ Butl. / Syntype, (examined)].

Forster (1964) did not take this taxon into account in his monograph. It was also missed by D'Abrera (1988). Lamas (2004) correctly transferred this species to the genus *Hermeuptychia* Forster.

Specimens figured by Seraphim *et al.* (2014, suppl. material, figs. S3 [male genitalia], S4 [underside habitus]: TO02, morphogroup 11) under this name belong to *Hermeuptychia hermes* (Fabricius). This error is reflected in the entire content of their work; where the type species of the genus, *H. hermes*, the most common species found in southeastern Brazil, is misidentified as *H. atalanta*.

Cosmo *et al.* (2014) also misidentified typical individuals of *H. hermes* – whose type specimens come from southeastern Brazil –, described and illustrated their life cycle under the erroneous name of *Hermeuptychia atalanta* (Butler). This notorious mistake has been repeated in the works of Anken *et al.* (2015) and Nakahara *et al.* (2016).

Seraphim *et al.* (2014: 46) considered that "*H. atalanta* is highly widespread". It is in fact one of the several middle elevation satyrine butterfly species, endemic to the mountains of the Cordillera de La Costa, in northern Venezuela (Ríos-Málaver *et al.* [2021]). Therefore, it is probably the most geographically confined taxon of the genus. It does not occur in the neighboring Venezuelan Andes or the Serranía del Turimiquire.

Longstaff (1912) alleged that individuals of *H. atalanta* taken in the vicinity of Caracas represented a dry season form (with reduced ocelli) of the same species he captured in Panamá, Trinidad and Tobago (probably mainly *H. canthe* (Hübner) **sp. restit.**, **comb. nov.** See below). As most authors, Longstaff misidentified three different taxa under the name of *Euptychia hermes*.

Hermeuptychia camerta (Cramer, 1780), **sp. restit.**, **comb. nov.**

Pap.[*ilio*] *Nymph.*[*alis*] *Gemm.*[*ata*] *camerta* Cramer, 1780: 10, pl. 313, fig. F. [TL: "Surinamsche", "Surinamе"].

Papilio camertus [*sic*] Cramer; Herbst, 1796: 91, pl. 195, fig. 8; Godart, [1824]: 495 (as a synonym of *Satyrus sosybius* (Fabricius)); Weidemeyer, 1864: 527; Strecker, 1878: 149; Skinner, 1898: 33 (last three as a synonym of *Neonympha sosybius* (Fabricius)).

Satyrus camerta (Cramer); Ménétriés, 1829: 191 (misidentification of *H. hermes* (F.)); Verloren, 1837: 111, 203 (as asynonym of *S. sosibius* [*sic*] (Fabricius)).

Papilio camerta Cramer; Hübner, [1819]: 54 (as a synonym of *Megisto euridice* [*sic*] Linnaeus); Godart, [1824]: 495 (as a synonym of *Satyrus sosybius* (Fabricius)); Doubleday, [1845]: 137 (as a synonym of *Euptychia sosybius* (Fabricius), misidentifications, in part); Lamas, 2004: 220; Pelham, 2008: 404, 616 (last two as a synonym of *Hermeuptychia hermes* (Fabricius)).

Neonympha camerta (Cramer); Westwood, 1851: 375; Herrich-Schäffer, 1865: 70; Prittwitz, 1865: 310-311 (misidentification of *H. hermes* (Fabricius)); Strecker, 1878: 149 (as a synonym of *Neonympha sosybius* (Fabricius)).

Euptychia camerta (Cramer); Butler, 1867: 462-463; 1868: 16; 1877: 119; Kirby, 1871: 48; Butler & Druce, 1874: 335; Druce, 1876: 213; Godman & Salvin, 1880a: xxxii, 74, 80, 86-87, 88, pl. 8, figs. 6, 7 (males); 1880b: 122; Staudinger, 1887: 226, 324, 333, t. 81 (male identified as *E. hermes* (F.)) (misidentifications in both cases); Shannon, 1898: 356; Bayern, 1901: 266; 1908: 312 (all misidentifications); Godman, 1901: 656 (erroneously as a synonym of *E. hermes* (Fabricius), *E. sosybius* (Fabricius), *E. fallax* (C. Felder & R. Felder) and *E. maimoune* (Butler)); Sanders, 1904: 366-367 (in part misidentifications of *H. hermes* (Fabricius) and *H. canthe* (Hübner) **sp. restit.**, **comb. nov.**); Clark, 1905: 9; Longstaff, 1908: 54, 1912: 255, 578 (both mistakenly as a synonym of *E. hermes* (F.)); Weymer, 1911: 207; Dyar, 1913: 635 (in part misidentifications of *H. canthe* (Hübner) **sp. restit.**, **comb. nov.**, and *H. gisella* (Hayward)); 1914: 143 (misidentification); Herrera, 1923: 133 (misidentification); Davis, 1928: 59 (misidentification); Gaede, 1931: 441-442; D'Abrera, 1988: 777 (the latter as a synonym of *E. hermes* (Fabricius)).

[*Euptychia atalanta* Butler var.; Butler, 1867: 475 [Pará] (misidentification)].

[*Euptychia hermes* (Fabricius); Kaye, 1904: 180; Longstaff, 1912: 54; 255, 264, 306, 307, 309, 310, 313, 320, 323, 329, 578-579 (misidentifications in part)].

Megisto camerta (Cramer); Barnes & Lindsey, 1922: 90 (as a synonym of *Megisto euridice* [*sic*] (Linnaeus).

[*Hermeuptychia hermes* (Fabricius); Seraphim *et al.*, 2014: 39, 40, 41, 42 fig. 1 (cladogram) part, 45, 46 (misidentification in part), suppl. material: figs. S3 (male genitalia), S4 (underside habitus): PA04, morphogroup 10 (misidentification)].

Cramer (1780: 10, pl. 313, fig. F) illustrated this taxon from a Surinamese specimen, which has not been located.

Hermeuptychia camerta (Cramer, 1780) **sp. restit.**, **comb. nov.**, is a very distinctive but uncommon species that is found flying in sympatry with the much more common *H. canthe* (Hübner, [1811]) **sp. restit.**, **comb. nov.**, in the lowlands of the Guiana Shield (but the latter has a wider distribution, both latitudinally and altitudinally). The first one is recognized by the uniform small size of its hindwing ventral ocelli, smaller than those of the type spe-

cies of the genus, *H. hermes* (which apparently does not occur in northern South America).

The phenotype of the specimen illustrated by Seraphim *et al.* (2014: suppl. material, figs. S3 [male genitalia], S4 [underside habitus]: PA04, morphogroup 10), and especially the male genitalia, with a remarkably long saccus, are features determined as characteristic of *H. camerta* (Cramer) **sp. restit.**, **comb. nov.** In this case the specimen illustrated comes from the state of Pará. I have dissected and examined specimens with similar genitalia, from southeastern Venezuela (Viloria: *Los Satyrinae de Venezuela*, in prep.) and French Guiana. The habitus of the specimens with these peculiar male genitalia fits well Cramer's published illustration of his *Papilio camerta*, even though it is markedly stylized.

This taxon is found to be partly sympatric with *H. canthe* **sp. restit.**, **comb. nov.**, but *H. camerta* **sp. restit.**, **comb. nov.**, is apparently less frequent.

It is probable that Longstaff's mention of one "dry season" specimen of "*E. hermes*" from Trinidad among several other "wet season" specimens (Longstaff 1912: 579), represents the only insular record known for this taxon. The satyrine butterfly fauna of Trinidad & Tobago (Cock 2014, 2017) is representative — but less diverse — of what is known for the Guiana Shield lowlands.

Hermeuptychia canthe (Hübner, [1811]), **sp. restit.**, **comb. nov.**

Oreas Strigata canthe Hübner, [1811]: pl. [87]: male [figs.] 1, 2; female [figs.] 3, 4, *nom. nov.* [TL: ?Surinam].

Oread. strig. canthe Hübner, [1819]: 54 (as a synonym of *Megisto euridice* [*sic*] (Linnaeus), erroneous.

Euptychia canthe (Hübner); Westwood, 1851: 373; Butler, 1867: 474; 1868: 23; [1870]a: 13; 1870b: 251; Weymer, 1911: 207; Gaede, 1931: 449 (the last six as a synonym of *Euptychia hermes* (F.)).

Neonympha pimpla C. Felder & R. Felder, 1862: 177, **syn. nov.** [TL: Rio Negro].

Neonympha canthe (Hübner); Herrich-Schäffer, 1865: 70.

[*Neonympha nana* Herrich-Schäffer, 1865: 70], *nom. nud.*, **syn. nov.**

Neonympha pimpla C. Felder & R. Felder; Herrich-Schäffer, 1865: 70; Kirby, 1871: 49 (as a synonym of *Euptychia renata* (Cramer [*sic*]) var.); Hayward, 1958b: 236 (as a synonym of *E. hermes* (Fabricius)).

Euptychia pimpla (C. Felder & R. Felder); Butler, 1867: 470; 1868: 20; 1877a: 119; Weymer, 1911: 208; Gaede, 1931: 449.

[*Euptychia fallax* C. Felder & R. Felder, var.; Butler, 1867: 474 [Venezuela] (misidentification)].

Oreas (strigata) canthe (Hübner); Butler, 1867: 475; 1868: 23; Burmeister, 1878: 210 (all as a synonym of *Papilio hermes* Fabricius); McDunnough, 1938: 11, 190 (as a synonym of *Megisto hermes* (Fabricius)); Hayward, 1958b: 236 (as a synonym of *Euptychia hermes* (Fabricius)); Poole & Lewis, 1996: 962; Lamas, 2004: 220; Koçak & Kemal, 2007: 959; 2015: 1463; Pelham, 2008: 404, 616 (all as a synonym of *Hermeuptychia hermes* (Fabricius)).

Euptychia maimoune Butler, 1870b: 251, pl. 1, fig. 4., **syn. nov.** [TL: Pebas, E. Peru].

Euptychia maimoune Butler; Kirby, 1871: 643; Distant, 1876: xiii; Butler, 1877a: 119; Weymer, 1911: 207; Riley & Gabriel, 1924: 34 (type male); Gaede, 1931: 454; Hayward, 1951: 229; 1958b: 236 (as a synonym of *E. hermes* (Fabricius)); Lamas, 1969: 283; D'Abrera, 1988: 789.

[*Euptychia camerta* (Cramer); Butler & Druce, 1874: 335; Druce, 1876: 213; Godman & Salvin, 1880a: xxxii, 74, 80, 86-87, 88, pl. 8, figs. 6, 7 (males); 1880b: 122; Godman, 1901: 656; Sanders, 1904: 366-367; Clark, 1905: 9; Dyar, 1913: 635 (all, in part misidentifications)].

Euptychia nana Möschler, 1877: 323-324, **syn. nov.** [TL: "dem innern Surinams"].

Euptychia nana Möschler; Kirby, 1877: 843; Butler, 1877a: 128; Weymer, 1911: 207; Gaede, 1931: 449; Hayward, 1951: 229; 1958b: 236 (as a synonym of *H. hermes* (Fabricius)); Forster, 1964: 88; Lamas, 2004: 220; Pelham, 2008: 404 (all, except Kirby, as a synonym of *E. hermes* (Fabricius)).

[*Euptychia hermes* (Fabricius); Kaye, 1904: 180 (misidentification, in part); DeVries, 1983: 722-723, fig. (misidentification, at least in part)].

[*Euptychia sosybius* (Fabricius); Kaye, 1904: 180 (misidentification)].

[*Hermeuptychia hermes* (Fabricius); Forster, 1964: 88, fig. 60 (male genitalia), 89-90; Barcant, 1970: 143, 160, pl. 13, [fig.] 13; Viloria, 1990: xx, xxvii, 88-94, 271, figs. 44 (male dorsal), 45 (male ventral), 46 (male genitalia); Garwood & Lehman, 2011: 274 [figs.]; Gernaat *et al.*, 2012: 242, 243, pl. 38, figs. 7 & 8 (all misidentifications)].

Hermeuptychia pimpla (C. Felder & R. Felder); Forster, 1964: 88, fig. 62 (male genitalia); Lamas, 2004: 220; Seraphim *et al.*, 2009: 331; 2014: 42 fig. 1 (cladogram) part, 44, 45, 46, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: [uncoded], morphogroup 02 (misidentification of *Hermeuptychia*

harmonia (Butler)); Peña *et al*., 2010: 247, 250 fig. 2 (phylogenetic tree) part, 251 fig. 3 (cladogram) part, 253 fig. 4 (divergence time) part (misidentification); Cong & Grishin, 2014: 51, 78 fig. 66 (cladogram) part (misidentification); Nakahara *et al*., 2016: 81 fig. 4 (phylogenetic tree) part, 83, 84 (misidentification); Marín *et al*., 2019: 91 (misidentification).

Oreas canthe Hübner; Miller & Brown, 1981: 191, 241 (as a possible synonym of *H. hermes* (Fabricius)).

[*Cissia hermes* (Fabricius); DeVries, 1987: 258, 276, 277, 298, pl. 41, fig. 3 (misidentification)].

['*Euptichia*' [*sic*] *hermes* (Fabricius); Convey, 1990: 169 (misidentification)].

Hermeuptychia maimoune (Butler); Lamas, 2004: 220; Seraphim *et al.*, 2014: 42 fig. 1 (cladogram) part, 45, 46, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: CO04, morphogroup 08 and TO01, morphogroup 09; Cong & Grishin, 2014: 51, 66, 78 fig. 66 (cladogram) part, 86; Nahakara *et al*., 2016: 81 fig. 4 (phylogenetic tree) part, 83, 84; Marín *et al*., 2019: 91.

Hübner [1811] illustrated male and female (both dorsal and ventral) of what he might have thought to be good examples of the Fabrician *P. canthus* (described from "America boreali", 1775). The latter was a name preoccupied by a distinct and different Linnean taxon, also from North America (Linnaeus 1767). Thus, due to the similarity of their names, it is reasonable to interpret Hübner's proposal of *Oreas Strigata canthe* as a *nomen novum* to replace the Fabrician junior homonym of the Linnean species. The taxonomic history of *Papilio canthus* Fabricius has been well investigated and described by Cardé *et al*. (1970). The taxon does exist, and it has an aspect very similar to Hübner's *O. S. canthe*, but obviously its first name is invalid and unavailable (see below, under next species).

However, Hübner's attempt to replace the aforementioned Fabricius' homonym, cannot be accepted because the provenance of the specimens used by Hübner for his illustrations was later found to be South America, and therefore they represent a different taxon.

In a detailed study of Jacob Hübner's published works and manuscripts, Hemming (1937) reproduced an incomplete list of localities of the species figured by that author in his *Sammlung exotischer schmetterlinge*, taken from Hübner MS. 35, in the library of the Royal Entomological Society of London. Among those, there is a record of "? Surinam" for "*Papilio nymphalis canthe*" (Hemming, 1937, vol. 1: 122; vol. 2: 424; Pelham, 2008: 404). Hübner's illustrations do indeed represent one male and one female of the most common species of *Hermeuptychia* found not only in Surinam, but also in the entire adjacent Guyana Shield region and beyond, in a considerable extension of the Amazon basin, to the lowlands of northern Venezuela including Margarita island, Trinidad & Tobago and perhaps northeastern Colombia.

This taxon differs from *P. camerta* Cramer **sp. restit.**, **comb. nov.**, by the presence of ventral forewing subapical ocelli (visible in Hübner's fine and trustworthy figures, but see below under *H. sosybius*), and much more developed ocelli on the hindwing underside. In a second mention of this taxon as *Oreas canthe*, Hübner ([1819]: 514), introduces another bit of taxonomic noise not only by repeating the confusion of the Fabrician species with *Megisto euridice* [*sic*] (Linnaeus, 1763a) and *Papilio canthus* Linnaeus, 1767, but also mistakenly adding *Papilio camerta* Cramer, 1780 to the synonymic list; the distinctive South American taxon already discussed above. However, unlike Fabricius and Herbst, who had confusions regarding the identity of other satyrine taxa, Hübner recognized *Papilio argante* Cramer as a valid, separate species.

There is one male (?) specimen, allegedly a syntype of *Neonympha pimpla* C. Felder & R. Felder, 1862, **syn. nov.**, in NHMUK, lacking its head and abdomen [Rio Negro / Felder colln. / Rothschild Bequest B. M. 1939-1 (examined), photographs in Warren *et al*. 2012]. I do not recognize it as a possible type of *N. pimpla*, as its appearance does not entirely fit the original description of this taxon, which seems to depict instead the phenotype of *H. canthe*, a true lowland Guianan-Amazonian species. The male genitalia illustrated by Forster (1964: 89, fig. 62) is erroneous.

Seraphim *et al.* (2014, suppl. material) misidentified *Hermeuptychia harmonia* (Butler) as *H. pimpla* (C. & R. Felder) (figs. S3 [male genitalia], S4 [underside habitus]: [uncoded, San Antonio, Colombia], morphogroup 02).

Euptychia nana Möschler (1877) **syn. nov.**, was described from a small sized single male specimen that is not in good condition. It was collected in the inner land of Surinam and represents *Hermeuptychia canthe* (Hübner, [1811]) **sp. restit.**, **comb. nov.** Forster (1964: 88) erroneously synonymized *E. nana* with *H. hermes* claiming to have had its type in front of him. The referred specimen, a lectotype designated by L. D. Miller in 1989, is in the ZMHB (examined). It bears a typical Forster's label stating "Präparat Nr. 154 Zool. Staatssammlung München"; however, judging from the prevalence of its entire abdomen it seems that Forster never dissected its genitalia. The explanation of this confusion can be deducted from the observation of Forster's figure of the male genitalia of *H. hermes*, which is wrong (Forster, 1964: 88, fig. 60). The representation of the genital structures of true *Her-*

meuptychia canthe **sp. restit., comb. nov.**, is comparable to what I have dissected and examined from northwestern and southeastern Venezuela, Trinidad and French Guiana (illustrated in Viloria 1990: 90 fig. 46, under the wrong name of *H. hermes*). *Euptychia maimoune* Butler (1870b: 251, pl. 1, fig. 4) **syn. nov.**, described apparently from a single male specimen (Riley & Gabriel 1924, Warren *et al*. 2012), taken at the Amazonian locality of Pebas in Peru (NHMUK, examined), also represents the same taxon.

Illustrations of male underside habitus and genitalia under the name of *Hermeuptychia maimoune* (Butler) **syn. nov.**, in Seraphim *et al.* (2014, suppl. material, figs. S3, S4: CO04, morphogroup 08, but not TO01, morphogroup 09 [08 *sic*!], which represents *H. hermes*) are in our view correct, but they had to be referred to its prior name, *Hermeuptychia canthe* **sp. restit., comb. nov.**

Hermeuptychia cautheus (Godart, [1824]), **sp. restit., comb. nov.**

Papilio canthus Fabricius, 1775: 486, *nom. praeoc.* (*nec Papilio canthus* Linnaeus, 1767; TL: America Septentrionali). [TL: America boreali].

Papilio canthus Fabricius; Fabricius, 1781: 64; 1787: 31; 1793: 157; 1796: 120; Gmelin, [1790]: 2285 (in part misidentification of *Papilio canthus* Linnaeus, *Papilio eurydice* Linnaeus and *Papilio argante* Cramer); Harris, 1862: 306.

Papilio canthus Cramer [*sic*]; Jones, 1785 [vol. VI]: pl. 38 (misidentification of *Papilio argante* Cramer, 1779).

Papilio canthus Linnaeus [*sic*]; Herbst, 1796: 70, pl. 192, figs. 5, 6 (misidentification of *Papilio argante* Cramer, 1779); Hübner, [1819]: 54 (in part) (as a synonym of *Megisto euridice* [*sic*] (Linnaeus), erroneous); Butler, 1867: 503 (in part).

Satyrus cautheus Godart, [1824]: 465, *nom. nov.*

Satyrus cantheus [*sic*] Godart, [1824]: 493-494.

Satyrus canthus (Fabricius); Verloren, 1837: 83 (as a synonym of *Papilio argante* Cramer).

Neonympha canthus (Linnaeus) [*sic*]; Westwood, 1851: 375; Morris, 1860: 10 (both in part misidentifications).

Neonympha cantheus [*sic*] (Fabricius [*sic*]); Morris, 1860: 10 (misidentification in part); Weidemeyer, 1864: 527; Herrich-Schäffer, 1865: 69; Mombert, 1869: 562.

Papilio (*D. F.*) *canthus* (part.) Fabricius; Butler, [1870] a: 13 (as a synonym of *P. argante* Cramer).

E.?[uptychia] canthus (Linnaeus [*sic*]); Kirby, 1871: 55 (misidentification in part).

Satyrus cantheus [*sic*] Godart; Scudder, 1875: 243 (as a synonym of *Papilio eurydice* Linnaeus).

Satyrus canthus (Linnaeus [*sic*]); Kirby, 1877: 704 (misidentification in part).

Euptychia canthus (Linnaeus [*sic*]); Kirby, 1880: 296 (misidentification in part).

Megisto canthus (Fabricius); Barnes & Lindsey, 1922: 90 (as a synonym of *Megisto euridice* [*sic*] (Linnaeus) and also as a synonym of *Megisto camerta* (Cramer)).

Hermeuptychia intricata Grishin, 2014: 43, 50, 51, 61-68 figs. 23-31, figs. 32-35, 40-43, 62n, 68 part, 72 figs. 60c, f, i, l, 73 fig. 61a, 76 figs. 64i-p, 77 fig. 65 part, 78 fig. 66 (cladogram) part, 79, 80 fig. 67 (distribution map) part, 81 fig. 68 part, 84, 85, 86, 87, 88., **syn. nov.** [TL: Brazos Bend State Park, Texas, USA].

Hermeuptychia intricata Grishin; Warren *et al.,* 2014a: 83, 84 fig. 1a (habitus dorsal, lacking androconia), c (habitus ventral), e (habitus dorsal), g (habitus ventral), j (male genitalia), l (female genitalia), n (distribution map) part, 85; 2014b: 44, 45 figs. 1a (habitus dorsal), c (habitus ventral), e (holotype dorsal), g (holotype ventral), I (paratype dorsal, in part); 46 figs. 2 b, d, f, h (wing scales), 47 figs. 3, l-n, 48 figs. 4 c-l, u –x, 49 fig. 5 (distribution map), 50, 51; Tan & Lucky, 2016: 3-4, figs. 6 (comparative wing characters), 7 (male genitalia compared); Austin, 2018: 307-313, fig. 1 (partial life cycle), fig. 2 (last larval instar), fig. 3 (habitat); Nakahara *et al*., 2016: 83; Marín *et al*., 2019: 91.

The synonymy of the homonym *Papilio canthus* Linnaeus, 1767, a different and distinct taxon, now considered a junior synonym of *Satyrodes eurydice* (Linnaeus, 1763a) (Nymphalidae: Satyrinae, Elymniini) is not included here. An explanation for that case and an introduction to the case of *Hermeuptychia cautheus* (Godart, [1824]) **sp. restit., comb. nov.**, needs the recapitulation of a fragment of the work of Cardé *et al*. (1970) about *S. eurydice* (pp. 74, notes by the present author inserted in square brackets):

> "*Taxonomic History*: the *Euptychia* names. – The taxonomy of *L.*[*ethe*] *e.*[*urydice*] e*urydice* is complicated by confusion with *Yphthimoides* (= *Euptychia*) *argulus* (Godart) [currently, *Emeryus argulus* (Godart)]. This problem was not noted by dos Passos, and it is reviewed here.
>
> Fabricius (1775) reworked the description of *canthus*, adding "immaculatis" to the upperside diagnosis and altering various details. The "immaculatis" may have been inferred from the lack of reference to spots in the

earlier descriptions, but it seems more likely that Fabricius was working from some other insect he confused with the Linnean one. In 1779 Cramer described and figured a species from Surinam as *Papilio argante*. This name is a junior homonym of *Papilio argante* Fabricius 1775 (now *Phoebis argante*, Pieridae). Fabricius synonymized *argante* Cramer to *canthus* (Fabricius, 1781), improperly emending it to *arganthe* in synonymy. (*Arganthe* is not available as a replacement name because it was proposed in synonymy). He repeated this usage in 1787 and 1793. His own descriptions of "*canthus*" do not fit Cramer's figure well.

Godart (1821 [*sic*]) recognized that three species were included in the Fabrician concept "*canthus*" and attempted to end the confusion by redescribing the true *canthus* (translating Linnaeus), and naming two new entities, *argulus* and *cantheus* [*sic*]. Godart's *argulus* is a replacement name for the preoccupied *argante* and is the oldest valid name of this taxon. *Cantheus* [*sic*] is a renaming o the entity Fabricius first thought was *canthus*, theretofore without a valid name. The identity of this animal cannot be determined if, as appears, Fabrician specimens o "*canthus*" do not exist."

pp. 76 (notes by the present author inserted in square brackets):

"*Cantheus* [*sic*], which is the unknown animal Fabricius confounded with *canthus* and then with *argante*, usually appears in the synonymy of *eurydice* = *canthus*, but its only proper claim there is its mistaken use in synonymy by Morris (1860). We have removed *cantheus* Godart from the synonymies of the other entities and regard it as a *nomen dubium*, presumably a species of *Euptychia sens. lat.* Its synonymy is:

‡ *Papilio canthus* (*nec* Linnaeus 1767): Fabricius 1775 (*partim*), Syst. Ent.: 486; 1781, Spec. Ins. 2: 64; 1787, Mant. Ins. 2: 31; 1793, Ent. Syst. 3(1): 157.

Satyrus cantheus [*sic*] Godart 1821, Encyl. Meth. 9: 465, 493; type locality "l'Amerique septentrionale"; type not investigated, probably never existed.

Godart's description of *cantheus* erroneously cites Fabricius, "Species Insectorum" or "Mantissa Insectorum". The name is misspelled "*cautheus*" in the heading on page 465."

These extraordinary observations, written about fifty years ago, remain fundamentally valid, but a few facts need to be corrected or added:

1. It is true that Fabricius (1781) wrongly listed *Papilio eurydice* Linnaeus (1767) and *Papilio arganthe* [*sic*] Cramer (1779) as synonyms of his *P. canthus*. However, he later suppressed this idea in *Mantissa insectorvm, tom. II* (Fabricius, 1787: 31). Some contemporary authors not only ignored this significant change of criterion, but they introduced further confusion to the case. For instance, Herbst (1796) applied the name *P. canthus* Linnaeus without making any distinction from its junior homonym *P. canthus* Fabricius (1775). His illustrations of *P. canthus* (Herbst, 1796: pl. 192, figs. 5, 6) seem to be copied from the previously published illustrations of *Papilio argante* (Cramer, 1779: pl. 204), a very different, larger satyrine butterfly described from Surinam, whose name, as explained by Cardé *et al.* (1970), was preoccupied and subsequently replaced by *Satyrus argulus* Godart ([1824]). Zacca *et al.* (2020) designated a neotype for Godart's taxon and proposed it as the type species of the genus *Emeryus* Zacca, Casagrande & Mielke, 2020. Members of *Emeryus* are also superficially distinct from any *Hermeuptychia* species by having a larger size, and five, bipupillated ocelli on the hindwing underside (not six, monopupillated, as in *Hermeuptychia*). In his text, Herbst (*op cit.*, pp. 70), refers again to the synonymy between *Papilio eurydice* Linneaus, 1763a (prioritary, currently *Satyrodes eurydice* (L.)) and its replacement name *P. canthus* Linnaeus, 1767 (invalid, and not the Fabrician *P. canthus*), and erroneously repeated *Papilio arganthe* [*sic*] Cramer as another synonym.
2. In 2016, during a consultation with Jeanne Robinson, curator of the historical material of Lepidoptera at the Hunterian Museum in Glasgow (GLAHM), the present author detected a male individual of a species of *Hermeuptychia* associated to a cabinet label with the manuscript legend "Pap. Canthus / Fabr. pag 64 N° 288", current reference number of the specimen 127581. Its habitus represents reasonably well the physical description published by Fabricius (1775, 1781, 1787, 1793) for this species. It is known that Fabricius was heavily involved with the curation of the insect collection of Dr William Hunter during several of his visits to London, particularly between 1780 and 1787 (Fabricius 1784, Hope 1845, Armitage 1958, Tuxen 1967, Vane-Wright 2007, Hancock 2015): "I knew it [Hunter's collection] very well because I laid it out myself and contributed to its gradual increase in size" (Hancock 2015: 158, translating the fifth letter of Fabricius' *Briefe* of 1784). Thus, the cabinet labels of the Hunterian collection document directly the taxonomic identifications by Johann Christian Fabricius, the only autho-

rity in the case of his *Papilio canthus*. Fabricius used his own work *Species insectorum* (1781) as a source catalogue in his lengthy process of identification and curation. Thus, each specimen identified by him was cross-referenced by the page and species name in that work. The current labels in the Hunterian cabinets were handwritten by Matthew Baillie, Hunter's nephew and inheritor, whose style corresponds with the same handwriting of the Trustees' manuscript catalogue signed off in 1785 (Hancock 2015). Because of its clear provenance and documented association with Fabricius, this *Hermeuptychia* specimen qualifies at least as a Neotype of *Papilio canthus* Fabricius, 1775 (Viloria & Robinson, MS), which by that recognition is no longer a *nomen dubium*.

3. *P. canthus* Fabricius, 1775, not a *nomen dubium*, however is unavailable by homonymy (with *P. canthus* Linnaeus, 1767). Therefore, the species to which it corresponds should adopt the next available name, proposed by Godart ([1824]). Most authors, if not all – including Cardé *et al*. (1970) –, have wrongly recorded the name *Satyrus cantheus* Godart, assuming that the appearance of the printed word "*cautheus*" in page 465 of Godart's work must be taken just as a misspelling of "*cantheus*" (page 493). The appearance of the first spelling is not a mere heading as stated by Cardé *et al*. (1970: 76), because it is immediately followed by Godart's short diagnosis of the Fabrician taxon: "Ailes entières, d'un brun-noirâtre et sans taches en dessus: dessous des inférieures avec six jeux. Fab."

   It should instead be objectively taken as the first use of the replacement name, even if it was a printing error appearing 28 pages prior to a different spelling of the name applied to the same entity followed by a more extense description (several cases like this are known among the Lepidoptera, for instance within the Nymphalidae Satyrinae, *Paramacera* Butler, which should have been *Paramecera*, or *Praefaunala* Forster, the true first spelling of *Praefaunula* of the auctorum). In any case, a provision of the ICZN, called the Principle of the First Reviser (ICZN 1999: 30, Art. 24.2) allows the present author to make this decision.

4. The putative type specimen of *Papilio canthus* Fabricius referred above, is a male of a species of *Hermeuptychia* that bears the distinctive external features of a taxon recently detected in North America. It was named *Hermeuptychia intricata* Grishin, 2014, **syn. nov.** The Fabrician/Hunterian specimen has been identified as such by the apparent absence of an androconial patch on the forewing recto, a diagnostic feature, characteristic of its sibiline and sympatric *H. sosybius* (Fabricius), but also by the presence of other less stable characteristics extensively studied by the experts (Cong & Grishin 2014, Warren *et al.* 2014a, 2014b, Tan & Lucky 2016, Austin 2018).

Hermeuptychia cucullina (Weymer, 1911)

[*Euptychia cucullina* Staudinger, *in litt.*], *nom. nud.*

Euptychia calixta Butler f. *cucullina* Weymer, 1911: 209, pl. 48 c, fig. [3]. [TL: wrongly stated by Weymer as Choco, Colombia; it is in fact Chaco (La Paz), 2-3000 m, Bolivia].

Euptychia calixta Butler var. *cucullina* Weymer; Gaede, 1931: 441 (as a synonym of *Euptychia calixta* Butler); Hayward, 1958c: 64, 65, fig. 13 (male genitalia).

Hermeuptychia cucullina (Weymer); Forster, 1964: 88, 89, fig. 65 (male genitalia), 91, pl. 30, figs. 8 (male recto), 9 (male verso); Anken, 1994: 283, 286, 288 (misidentification); 1995a: 8, 9, 11 figs. 1 (habitus dorsal), 2 (habitus ventral) (misidentification); 1995b: 237-239, figs. 1 (habitus dorsal), 2 (habitus ventral) (misidentifications of another taxon); Lamas, 2003: 69, 145, lám. 25, fig. 273; 2004: 220; Piñas Rubio, 2004: 6, 29, figs. 211, 212 (misidentification of *H. gisella* (Hayward)); Gottsberger & Silberbaur-Gottsberger, 2006: 75; Seraphim *et al*., 2014: 39, 42 fig. 1 (cladogram) part, 44, 45, 46, 47, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: PE03, morphogroup 05 (misidentification in part)]; Cong & Grishin, 2014: 44, 45, 51, 52, 78 fig. 66 (cladogram) part, 85, 86; Nakahara *et al*., 2016: 81 fig. 4 (phylogenetic tree) part, 84; Marín *et al*., 2019: 91.

Euptychia 'hermesina' Staudinger, *nom. nud.*; D'Abrera, 1988: 777 figs. [row 2] male recto & verso, Anken, 1994: 286 (misidentifications).

Euptychia cucullina Weymer; D'Abrera, 1988: 777 fig. [row 2] male verso (misidentification of *H. gisella* (Hayward)); Anken, 1994: 286; 1995a: 9; 1995b: 237; Fagua, 1999: 358 (misidentifications).

Hermeuptychia cuculina [*sic*] (Weymer); Peña *et al*., 2010: 247, 250 fig. 2 (phylogenetic tree) part, 251 fig. 3 (cladogram) part, 253 fig. 4 (divergence time) part.

Hermeuptychia pompilia Marín *et al*., 2011: 7 fig. 3 (misidentification), *nom. nud.*

Described from at least two male specimens collected in 1893-1894 by one of the Garlepp brothers (Gustav and

Otto), in Chaco, at 2,000-3,000 m, [Yungas de] La Paz, Bolivia. They are deposited at ZMHB. One of them designated lectotype by G. Lamas in 1994. The other individual is very peculiar, as it has only five ocelli (instead of six) on its hindwing verso (examined). Photographs of these specimens taken by Lamas and Grishin are available at Warren *et al*. (2012).

Male genitalia correctly illustrated by Forster (1964: 89, fig. 65).

Seraphim *et al.* (2014, suppl. material) correctly identified *Hermeuptychia cucullina* (Weymer) from Peru (figs. S3 [male genitalia], S4 [underside habitus]: PE03, morphogroup 05).

Hermeuptychia gisella (Hayward, 1957)

Euptychia gisella Hayward, 1957: 112-113, 119, fig. 2. [TL: Yungas del Palmar, 2000 m, Bolivia].

[*Euptychia camerta* (Cramer); Dyar, 1913: 635 (misidentification in part)].

Hermeuptychia gisella (Hayward); Forster, 1964: 88, fig. 61 (male genitalia), 90; pl. 30, figs. 5 (male recto), 6 (male verso); Anken, 1994: 286; 1995a: 9; 1995b: 237, 238 (in part, misidentifications); Lamas, 1997: 217; T. Racheli & L. Racheli, 2001: 326; Matos-Maraví *et al.*, 2013: 60 fig. 3A (divergence times) part, 61 fig. 4 (ancestral areas of distribution) (misidentification); Seraphim *et al.*, 2014: 42 fig. 1 (cladogram) part, 45, 47, supplementary material: figs. S3 [male genitalia], S4 [underside habitus] [MT13 -morphogroup 06] (misidentification); Cong & Grishin, 2014: 44, 45, 51, 52, 78 fig. 66 (cladogram) part, 85, 86 (misidentification); Nakahara *et al*., 2016: 81 fig. 4 (phylogenetic tree) part, 83, 84 (misidentification); Marín *et al*., 2019: 91.

Hermeuptychia hermes var. *hermesina* Forster, 1964: 90 (mistakenly as a synonym of *H. hermes* (Fabricius)), **syn. nov.** [TL: Chaco, Yungas de La Paz, 2-3000 m, Bolivia].

Hermeuptychia hermes f. *hermesina* (Staudinger), *in litt*.; Forster, 1964: 90 (mistakenly as a synonym of *H. hermes* (Fabricius)); Lamas, 2004: 220 (as a synonym of *H. hermes* (Fabricius)).

[*Euptychia cucullina* Weymer; D'Abrera, 1988: 777 fig. [row 2] male verso (misidentification)].

Euptychia gisella Hayward; D'Abrera, 1988: 789; Lamas, 2004: 220 (as a synonym of *Hermeuptychia cucullina* (Weymer)).

Euptychia hermesina (Forster); Anken, 1994: 288.

Euptychia hermes hermesina (Forster); Anken, 1994: 288.

Hermeuptychia hermes hermesina Forster; Anken, 1994: 290; 1995a: 9; 1995b: 237, 238 (in part, misidentification); Pelham, 2008: 404 (as a synonym of *H. hermes* (Fabricius)).

Hermeuptychia [n. sp.] Lamas, MS; Lamas, 2004: 220 [# 138].

[*Hermeuptychia cucullina* (Weymer); Piñas Rubio, 2004: 6, 29, figs. 211, 212 (misidentification)].

Hermeuptychia clara Nakahara, Tan, Lamas & Willmott, 2016: 77, 78, 79 figs. 1A, B (male, dorsal and ventral), C, D (female, dorsal and ventral), 80 figs. 2A (male wing venation), B, C (male and female palpi), D (male foreleg), E (female foreleg), 3A, B, C (male genitalia), D, E, F (female genitalia), 81 fig. 4 (phylogenetic tree) part, 82 figs. 5 (map, locality records), 6 (habitat & habitus), **syn. nov.** [TL: Quimi-Cóndor Mirador rd., Zamora-Chinchipe, 1000 m, Ecuador].

Hermeuptychia clara Nakahara, Tan, Lamas & Willmott; Marín *et al*., 2019: 91.

Most of the type specimens of the satyrine butterfly species described by Hayward from Bolivia in 1957 are missing (Benmesbah *et al*. [2021]: 51-52). However, the holotype of *Euptychia gisella* is in IML (Tucumán, Argentina). Photographs by G. Lamas are available at Warren *et al.* (2012).

Hayward (1957) presented a very gross drawing of the male genitalia of the holotype of *E. gisella*. It was probably executed without the aid of a camera lucida (as it appears to be the case for his many illustrations of butterfly genitalia). In this case, both the saccus and the aedeagus appear to be partly cut or lost.

Male genitalia of this species illustrated by Forster (1964: 88, fig. 61) have a very similar aspect of those of *Hermeuptychia clara* Nakahara, Tan, Lamas & Willmott **syn. nov.** (Nakahara *et al.* 2016: 80, figs. 3 A-C). However, they are difficult to compare with the caricaturesque, inaccurate drawings of Hayward. Forster (1964) seems to have correctly identified individuals of *H. gisella* (Hayward) (pl. 30, figs. 5 [dorsal] and 6 [ventral]) from Yungas del Palmar, its type locality. As the preceding species *H. cucullina* (Weymer), *H. gisella* (Hayward) is a montane to upper montane (1,000-2,000 m), Andean species, distributed along the eastern slopes of the main Andes from southern Colombia to Bolivia, with some morphological variation along the latitude gradient. *Hermeuptychia gisella* is not documented by Nakahara *et al*. (2016).

Illustrations of a Brazilian individual MT13 -morphogroup 06- in Seraphim *et al.* (2014, supplementary material, figs. S3 [male genitalia], S4 [underside habitus]) do

not represent *H. gisella* (Hayward). Biogeographically, it is predictable that this Andean taxon does not occur in Brazil.

Hermeuptychia harmonia (Butler, 1867)

Euptychia harmonia Butler, 1867: 478, pl. 39, fig. 17. [TL: Quito, Ecuador].

[*Euptychia harmonia* Butler, var.; Butler, 1867: 478 (Ecuador)].

Euptychia harmonia Butler; Butler, 1868: 24; 1870b: 251; 1877a: 120; Kirby, 1871: 50; Godman & Salvin, 1880a: 88; Dognin, 1891: 93; Weymer, 1911: 209, t. 48 b fig. [6]; Riley & Gabriel, 1924: 23 (type female); Gaede, 1931: 448; Lewis, 1973: 58, fig. 9; D'Abrera, 1988: 777 (in text); Manara, 1994: 23 (misidentification of *Optimandes eugenia* (C. Felder & R. Felder)).

Euptychia calixta Butler, 1877a: 125, pl. 12, fig. 8. [TL: Bogotá, Colombia] [synonymy established by Lamas, 2004: 220].

Euptychia calixta Butler; Kirby, 1877: 843; Weymer, 1911: 209, t. 48 c fig. [2]; Gaede, 1931: 441; Beebe, 1951: 9 (misidentification of *Optimandes eugenia* (C. Felder & R. Felder)); DeVries, 1986: 332; D'Abrera, 1988: 777 figs. [row 3] male recto & verso; Kochalka *et al*., 1996: 212; Tobar *et al*., 2002: 400; García- Pérez *et al*., 2007: 648.

Euptychia cucullixta Weymer, 1911: 209, 1082, *nom. nud.* [synonymy established by Lamas, 2004: 220].

Euptychia cuculixta Staudinger, *in litt*.; Gaede, 1931: 441 [synonymy established].

Hermeuptychia harmonia (Butler); Forster, 1964: 89, fig. 66 (male genitalia); Anken, 1994: 286; T. Racheli & L. Racheli, 2001: 325; Lamas, 2004: 220; Murray & Prowell, 2004: 69, 72 fig. 1 (phylogram) part, 73 fig. 2 (phylogenetic tree) part, 75 fig. 3 (phylogenetic tree) part, 76 fig. 4 (phylogeny) part; Emery *et al*., 2006: 90 (misidentification); Chacón & Montero, 2007: lám. 129 [row 3, left, male ventral] (misidentification); Beccaloni *et al*., 2008: 334; Pulido & Andrade, 2009: 541, 551; Seraphim *et al.*, 2009: 331; 2014: 42 fig. 1 (cladogram) part, 45, 46, 47, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: CO36, morphogroup 03; Peña *et al*., 2010: 247, 250 fig. 2 (phylogenetic tree) part, 251 fig. 3 (cladogram) part, 253 fig. 4 (divergence time) part; Garwood & Lehman, 2011: 274 [figs.]; Pulido & Parrales, 2011: 198; Marín *et al*., 2014: 204; Cong & Grishin, 2014: 51, 78 fig. 66 (cladogram), part; Nakahara *et al*., 2016: 81 fig. 4 (phylogenetic tree) part, 83, 84; Hanson & Nishida, 2016: 253 fig.; Marín *et al*., 2017: 776 fig. 64 (male genitalia), 777 fig. 7D (wing venation), 778 fig. 8 (cladogram); 2019: 91; Glassberg, 2018: 162 fig.

Hermeuptychia calixta Butler; Forster, 1964: 89, fig. 67 (male genitalia [of type specimen]); Anken, 1994: 286; Lamas, 1997: 217; T. Racheli & L. Racheli, 2001: 326.

Hermeuptychia callixta [*sic*] Butler; Forster, 1964: 89, **syn. nov.**

Cissia calixta (Butler); DeVries, 1987: 276-277, 298, pl. 41, fig. 2; Chacón, 1988: 72; Van den Berghe *et al*., 1995: 39; Vega, 2004: 123.

Euptychia harmonica [*sic*] Butler; D'Abrera, 1988: 777 figs. [row 4] male recto & verso; T. Racheli & L. Racheli, 2001: 325 (as a synonym).

[*Hermeuptychia pimpla* (C. Felder & R. Felder); Seraphim *et al*., 2014: 42 fig. 1 (cladogram) part, 44, 45, 46, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: [uncoded], morphogroup 02 (misidentification)].

Riley & Gabriel (1924) indicated the existence of one female type specimen of *Euptychia harmonia* Butler in the NHMUK [Quito coll. By M. Bourcier 50 -111 / BM Type No. Rh 3231 *Euptychia harmonia* ♀ Butler / Type (examined)]. The lectotype ♂ of *Euptychia calixta* Butler, designated by L. D. Miller in 1989, is in the ZMHB [Bogota Nolcken / Origin / *E. calixta* Butler type / Ex collect. Staudinger (examined)]. Both are represented in photographs taken by G. Lamas and N. V. Grishin in Warren *et al.* (2012).

Male genitalia of *H. harmonia* by Forster (1964: 89, fig. 66) appear correct. Male genitalia of the type of *H. calixta* (Forster's Präparat Nr. 155 Zool. Staatssammlung München, label pinned with the lectotype) are also illustrated by Forster (1964: 89, fig. 67).

Seraphim *et al.* (2014, suppl. material) correctly identified *H. harmonia* (Butler) (figs. S3 [male genitalia], S4 [underside habitus]: CO36, morphogroup 03).

This is a montane to upper montane taxon, distributed in the Northern Andes (Ecuador, Colombia, western Venezuela) and apparently also in part of the mountains of Central America (Panama, Costa Rica, Nicaragua). It shows a perceptible degree of physical variability across its range of distribution.

Hermeuptychia hermes (Fabricius, 1775)

P.[*apilio*] *D.*[*anaus*] *F.*[*estivus*] *hermes* Fabricius, 1775: 487; Jones, 1785 [vol. V]: pl. 52. [TL: "Brasilia"].

Papilio hermes Fabricius; Fabricius, 1787: 32, 1793: 158; 1796: 123; Gmelin, [1790]: 2285 (in part misidentification of *Papilio antonoe* Cramer); Erichson, [1849]: 600 (as a synonym of *Euptychia libye* (Linnaeus), as figured by Herbst, 1796); Herbst, 1796: 68-69, pl. 192, fig. 4 (misidentification of *Papilio antonoe* Cramer, 1775); Riley & Gabriel, 1924: 24 (type, male); Cong & Grishin, 2014: 54; Nakahara *et al*., 2016: 77.

Euptychia hermessa Hübner, [1819]: 508, *nom. nov.* (in part misidentification of *Papilio antonoe* Cramer, 1775); Lamas, 2004: 220; Pelham, 2008: 404, 627 (both as synonyms).

Satyrus hermes (Fabricius); Godart, [1824]: 463, 487-488; Verloren, 1837: 36, 203 (as a synonym of *Satyrus antonoë* [*sic*] (Cramer)).

[*Satyrus camerta* (Cramer); Ménétriés, 1829: 191 (misidentification)].

Neonympha hermes (Fabricius); Doubleday, [1845]: 138; Westwood, 1851: 375; Herrich-Schäffer, 1865: 70 (the latter as a synonym of *Papilio antonoe* Cramer, 1775).

Euptychia hermes (Fabricius); Erichson, [1849]: 600 (probably misidentifications of *H. camerta* (Cramer) **sp. restit.**, **comb. nov.**, or *H. canthe* (Hübner) **sp. restit.**, **comb. nov.**); Butler, 1867: 475; 1868: 23; [1870]a: 13, 297; 1870b: 251; 1877a: 119; 1877b: 112 (misidentification); Kirby, 1871: 50; 1880: 296; Butler & Druce, 1874; 336 (misidentification); Möschler, 1877: 323; Butler, 1877a: 125, 128; Burmeister, 1878: 210-211; Weymer & Maassen, 1890: 99 (misidentification); Sharpe 1890: 569 (misidentification); Dognin, 1891: 33 (misidentification); Weymer, 1895: 323; 1911: 207, t. 48 a figs. [4, 5] (misidentification); Kaye, 1904: 180 (misidentification of *H. camerta* (Cramer) **sp. restit.**, **comb. nov.** and *H. canthe* Hübner **sp. restit.**, **comb. nov.**); Longstaff, 1908: 54; 255, 264, 306, 307, 309, 310, 313, 320, 323, 329, 578-579 (misidentifications of *H. camerta* (Cramer) **sp. restit.**, **comb. nov.**, *H. canthe* Hübner **sp. restit.**, **comb. nov.** and *H. atalanta* (Butler)); Aurivillius, 1929: 158 (misidentification); Ribeiro, 1931: 40 (misidentification); Travassos-Filho & Carrera, 1946: 197; Bryk, 1952: 60, 61; Hayward, 1958a: 168 (redescription); 1958b: 231 fig. 30 (male genitalia), 236-237, lám. 4, fig. 139; 1960: 77; Biezanko, 1960: 2; Emmel, 1970: 153-164, fig. 1 (ocellar pattern) (misidentification); DeVries, 1983: 722-723; 1986: 331 (misidentifications); D'Abrera, 1988: 777 fig. [row 1, figs. 1, 2, 3] [1] male recto (possible misidentification of *H. sosybius* (Fabricius), [2] male verso (misidentification of *H. sosybius* (Fabricius), [3] male verso (misidentification of *H. acmenis* (Hübner) **comb. nov.**); Álvarez *et al.*, 2005: 27-30, fig. 3 (last three, misidentifications).

Eupt.[*ychia*] ? *hermes* (Fabricius); Westwood, 1851: 374.

[*Neonympha sosybius* (Fabricius); Capronnier, 1874: 30; 1881: 103 (misidentifications)].

[*Neonympha camerta* (Cramer); Prittwitz, 1865: 310-311 (misidentification)].

[*Euptychia fallax* (C. Felder & R. Felder); Mabilde, 1896: 98 (misidentification)].

Megisto hermes (Fabricius); McDunnough, 1938: 11, 216 (misidentification).

Hermeuptychia hermes (Fabricius); Forster, 1964: 88, fig. 60 (male genitalia), 89-90 (misidentification); Barcant, 1970: 143, 160, pl. 13, [fig.] 13 misidentifications of *H. canthe* (Hübner) **sp. restit.**, **comb. nov.**); Biezanko *et al*., 1974: 112; Miller & Brown, 1981: 191, 241; Whittaker, 1983: 109 (misidentification); Brown, 1992: 152; Anken, 1994: 283, 284, 286, 287, 288, 289, 291; 1995a: 9; 1995b: 237, 238; Poole & Lewis, 1996: 962, 1010; Fagua, 1999: 358 (misidentification); Maes, 1999: 21 (misidentification); Kaminski *et al*., 2001: 196; Schantz *et al*., 2001: 214; T. Racheli & L. Racheli, 2001: 325 (misidentification); Opler & Warren, 2002: 42; Tobar *et al*., 2002: 397 (misidentification); Romanowski *et al*., 2003: 4; Iserhard & Romanowski, 2004: 653; Lamas, 2004: 220; Murray & Prowell, 2004: 69, 72 fig. 1 (phylogram) part, 73 fig. 2 (phylogenetic tree) part, 75 fig. 3 (phylogenetic tree) part, 76 fig. 4 (phylogeny) part; Piñas Rubio, 2004: 6, 29, figs. 213, 214 (misidentification); Emery *et al*., 2006: 90; Marchiori & Romanowski, 2006a: 447, 450; 2006b: 1031, 1032; Brown, Jr. *et al*., 2007: 473, 478 (misidentification); Dessuy & de Morais, 2007: 113; Koçak & Kemal, 2007: 959; 2015: 1463 (in part misidentifications); Chacón & Montero, 2007: lám. 129 [row 3, right, male ventral] (misidentification); García-Pérez *et al*., 2007: 648, 651 (misidentification); Teston & Corseuil, 2008: 47; Beccaloni *et al*., 2008: 334 (in part misidentifications); Pelham, 2008: 404, 492, 627 (misidentification); Peixoto & Benson, 2009: 1, 2, 5, 6, 9, 11; Pulido & Andrade, 2009: 541, 551 (misidentification); Marín *et al*., 2009: 242 (misidentification); Seraphim *et al.*, 2009: 331; 2014: 39, 40, 41, 42 fig. 1 (cladogram) part, 45, 46 (misidentification in part), suppl. material, figs. S3 [male genitalia], S4 [underside habitus]: PA04, morphogroup 10 (all misidentifications of

Hermeuptychia camerta (Cramer) **sp. restit., comb. nov.**); Peña *et al*., 2010: 247, 250 fig. 2 (phylogenetic tree) part, 251 fig. 3 (cladogram) part, 253 fig. 4 (divergence time) part (misidentification); 2011: 69, 80 fig. 6 (cronogram) part; Garwood & Lehman, 2011: 274 [figs.]; Prado *et al*., 2011: 3, 4, 5 [ECO01, ECO02, ECO03], figs. E1 (probably *H. acmenis* (Hübner) **comb. nov.**), E2, E3 (misidentifications); Gernaat *et al.*, 2012: 242, 243, pl. 38, figs. 7 & 8; Córdoba-Alfaro, [2012]: 123 (misidentification); Cock, 2014: 11; 2017: 24 (misidentifications); Cong & Grishin, 2014: 43, 44, 51, 52, 54, 66, 73, 78 fig. 66 (cladogram) part, 85, 86, 87; Anken *et al*., 2015: 157, 159 (misidentification); Tan & Lucky, 2016: 1; Nakahara *et al*., 2016: 81 fig. 4 (phylogenetic tree) part, 83, 84 (misidentification in part); Marín *et al*., 2017: 778 fig. 8 (cladogram); 2019: 91.

Cissia hermes (Fabricius); DeVries, 1987: 258, 276, 277, 298, pl. 41, fig. 3 (misidentification); Singer & Ehrlich, 1993: 249, 250, 251 fig. 1 (part), 252, 253, 254 (misidentification).

'*Euptichia*' [*sic*] *hermes* (Fabricius); Convey, 1990: 169 (misidentifications *H. camerta* (Cramer) **sp. restit., comb. nov.** and *H. canthe* (Hübner) **sp. restit., comb. nov.**)]).

Hermeuptychia hermes isabella Anken, 1994: 283, 284, 287 figs. 3 a (habitus dorsal), b (habitus ventral), 288 fig. 4 (male genitalia), 289-290. [TL:"Barranca do Rio Amambai, Navirai, Mato Grosso do Sul, Brasil"].

Hermeuptychia (= *Cissia*) *hermes* (Fabricius); Van den Berghe *et al*., 1995: 39.

Hermeuptychia hermes isabella Anken; Anken, 1995a: 9; 1995b: 237, 238; Lamas, 2004: 220 (synonymy established); Pelham, 2008: 404, 629; Anken *et al.*, 2015: 157, 158 figs. 3 (holotype dorsal), 4 (holotype ventral), 159 (last as a synonym of *H. atalanta* (C. Felder & R. Felder)).

Hermeuptychia hermes (Fabricius); Anken, 1995b: 238.

[*Hermeuptychia atalanta* (C. Felder & R. Felder); Seraphim *et al.*, 2014: 42 fig. 1 (cladogram) part, 45, 46, 47, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: TO02, morphogroup 11; Cong & Grishin, 2014: 51, 78 fig. 66 (cladogram) part; Cosmo *et al.,* 2014: 82-86, figs. 1A (egg), B (1st instar), C (2nd instar), D (3rd instar), E (4th instar), F (prepupa), G-I (pupa), J (adult male, dorsal), K (adult male, ventral), fig. 2 (morphological details egg, larvae), fig. 3 (chaetotaxy 1st instar); Anken *et al*., 2015: 157, 159; Nakahara *et al*., 2016: 81, 83, 84 (misidentifications)].

H.[*ermeuptychia*] *isabella* Anken; Anken *et al*., 2015: 158, figs. 3 (holotype dorsal), 4 (holotype ventral) (as a synonym of *H. atalanta* (C. Felder & R. Felder).

Hermeuptychia atalanta isabella Anken; Anken *et al*., 2015: 157, 159.

For this species Fabricius (1775: 487) stated a "habitat in Brasilia". According to Miller & Brown (1981: 241) this provenance almost certainly corresponds to a locality of the Rio de Janeiro area in southeastern Brazil. Specimens were probably collected by Sir Joseph Banks in 1768 as the naturalist of the *Endeavour*, during the first of James Cook's circumnavigations. The specimens Fabricius first examined during his second visit to London in 1772 were cited as from "Mus. Banks". Jones' illustration of 1785 is also referred as to "Sr Jos^{ph} Banks". Butler ([1870]a: 13) indicates the presence of one type specimen in the Banksian collection (then already deposited in the British Museum), as well as referred by Riley & Gabriel (1924: 24, 1♂). This putative syntype currently in the NHMUK [BM Type No Rh 5036, *Papilio hermes* Fab. / Type / Syntype; cabinet label: *Papilio hermes* Fab. *Entomol.* p. 487 n. 194 (examined); photos in Warren *et al*. (2012)] lacks one of its hindwings (right). Another possible syntype is in GLAHM, which could have come from Joseph Banks through a contemporary exchange with William Hunter. It is known from several sources that J. C. Fabricius promoted the exchange of duplicate specimens between different collections, especially in London (Hancock 2015). The Glasgow specimen is associated to a Baillie's cabinet label: *Pap. hermes* Fabr. pag 64 No 292; current reference number of the specimen 127582. It lacks its left forewing (Viloria & Robinson, MS).

Herbst (1796: 68-69), Hübner ([1819]: 508) and Godart ([1824]: 487) erroneously synonymized this taxon and *Papilio antonoe* Cramer, 1775 (currently *Megeuptychia antonoe* (Cr.)). They are widely separated entities. The synonymic history of *Hermeuptychia hermes* (Fabricius) is very rich in misidentifications.

Genitalia figured in Forster (1964: 88, fig. 60) is incorrect. It represents the genitalia of. *H. canthe* (Hübner) **sp. restit., comb. nov.**

Anken (1994: fig. 4) illustrated the holotype male genitalia of *H. hermes isabella* (a synonym of *H. hermes*). Its general aspect is reminiscent in shape of that of *H. gisella* (Hayward) illustrated by Forster (1964: 88, fig. 61).

Male habitus and genitalia illustrated in Seraphim *et al.* (2014, suppl. material, figs. S3 [male genitalia], S4 [underside habitus]: PA04, morphogroup 10, from Carajás, Pará)

do not appear to represent true *H. hermes* (F). The saccus of the genital armature photographed is unusually long, like in typical specimens of *H. camerta* (Cramer) **sp. restit.**, **comb. nov.**, from Surinam, Guyane Française, Guyana and southern Venezuela. On the other hand, specimens TO01, morphogrop 09 (it reads 08 [*sic*]) and TO02, morphogroup 11, agree much better with *H. hermes* (not *H. maimoune* (Butler) and *H. atalanta* (Butler), respectively, as wrongly indicated for each case).

The life cycle of *Hermeuptychia hermes* was described by Cosmo *et al.* (2014), under the erroneous identity of *H. atalanta* (a montane species, endemic to the Venezuelan Cordillera de La Costa).

Hermeuptychia lupita (Reakirt, [1867])

Neonympha lupita Reakirt, [1867]: 331 (female) [TL: Orizaba, Veracruz, Mexico].

Neonympha lupita Reakirt; Gerstaecker, 1867: 367; 1869: 63; Hayward, 1951: 229 (as a synonym of *E. hermes* (Fabricius)); Lamas, 2004: 223; Llorente-Bousquets *et al.*, 2006: 975.

Euptychia lupita (Reakirt); Butler, 1868: 39; 1877a: 123; D'Abrera, 1988: 789.

Zischkaia lupita (Reakirt); Llorente-Bousquets *et al.*, 2006: 975.

Hermeuptychia lupita (Reakirt); Marín *et al*., 2019: 91.

The female type specimen of Reakirt's *Neonympha lupita* has not been found, despite several searches and inquiries in different museums of the United States of America. This is probably the largest species of the genus (and not the one represented as such in Warren *et al*. 2012). Only three male specimens of *bona fide H. lupita* are known to the present author. They were obtained in 2015 at middle elevations in the mountains of the Sierra Madre del Sur, Oaxaca, Mexico (Llorente-Bousquets *et al*., in prep.).

Hermeuptychia sosybius (Fabricius, 1793)

Papilio sosybius Fabricius, 1793: 219 [Jon. fig. pict. 6. tab. 52. fig. 2.] [TL: ?].

Papilio sosybius Fabricius; Fabricius, 1796: 128; Herbst, 1796: 148 [cites Jones' illustrations]; Hayward, 1958b: 236 (as a synonym of *E. hermes* (Fabricius)); Cong & Grishin, 2014: 43, 52, 54, 56 [lectotype designation of Jones' illustrations], 58 [neotype designation], 60. [TL: Savannah, Georgia, USA].

Satyrus sosybius (Fabricius); Godart, [1824]: 465, 495; Ménétriés, 1829: 191 (mistakenly as a synonym of *Satyrus camerta* (Cramer), but also a misidentification of *H. hermes* (F.)); Boisduval & Le Conte, [1835]: pl. 63, figs. 1-4 (early stages).

Satyrus sosibius [*sic*] (Fabricius); Verloren, 1837: 111, 203.

Neonympha sosybius (Fabricius); Doubleday, [1845]: 137 (misidentifications, in part); Westwood, 1851: 375; Morris, 1860: 10; Weidemeyer, 1864: 527; Herrich-Schäffer, 1865: 70; Prittwitz, 1865: 311 (misidentification); Boisduval, 1870: 63; Capronnier, 1874: 30; 1881: 103 (misidentifications of *H. hermes* (Fabricius)); Edwards, 1877: 229-231(early stages); 1883: 68, 69; 1884: 288; Strecker, 1878: 149; Chambers, 1879: 73; French, 1886: 67, 240-242 (life cycle); Skinner, 1898: 33, xiii; Holland, 1898: 204, pl. 25, fig. 5 (male); Denton, 1900: viii, 220-221, figs. (male upper and underside), 360; Sharpe, 1914: 35; Brimley, 1921: 77; Clark, 1932: viii, 244, 331, 335, pl. 56 fig. 7 (male dorsal), 8 (male ventral).

Euptychia sosybius (Fabricius); Butler, 1867: 474; 1868: 22; [1870]a: 13, 302; 1877a: 119; Edwards, 1872: 24; Kirby, 1871: 49; 1880: 296; Gerhard, 1878: 2; Gosse, 1880: 202 (misidentification); Kaye, 1904: 180 (last one misidentification of *H. canthe* (Hübner) **sp. restit.**, **comb. nov.**); A. H. Clark & L. F. Clark, 1951: 8, 12, 38, 232, 238, pl. 3 fig. i (male ventral); Comstock & Vázquez, 1961: 379.

Euptychia hermes (Fabricius) var. *sosybius* Fabricius; Butler, 1870b: 251.

Cissia sosybius (Fabricius); Scudder, 1875: 245; 1889, vol. I: xxi; vol. III: 1786-1788 (imago and immature stages); Möschler, 1876: 35; Dyar, 1903: 32; Grossbeck, 1917: 19.

Euptychia sasybius [*sic*] (Fabricius); Aurivillius, 1929: 158 (wrongly as a synonym of *E. hermes* (Fabricius)).

Megisto hermes sosybius (Fabricius); Richards, 1931: 244.

Megisto hermes (Fabricius) f. *sosybius* (Fabricius); McDunnough, 1938: 11, 259 (erroneously as a synonym of *Megisto hermes* (Fabricius).

Hermeuptychia sosybius (Fabricius)*;* Forster, 1964: 88, 89, fig. 64 [male genitalia]; Miller & Brown, 1981: 191; Anken, 1994: 286; Poole & Lewis, 1996: 1095; Calhoun, 1997: 47; Opler & Warren, 2002: 42; Lamas, 2004: 220; Murray & Prowell, 2004: 69, 72 fig. 1 (phylogram) part, 73 fig. 2 (phylogenetic tree) part, 75 fig. 3 (phylogenetic tree) part, 76 fig. 4 (phylogeny) part; Glassberg, 2007: 139 [row 2, fig. 3] (misidentification of *H. acmenis* (Hübner) **comb. nov.**; 2012: 257 [figs.] (misidentifications of *H. cautheus* (Godart) **sp. restit.**, **comb. nov.** [Suffolk Co, VA] and *H. acmenis* (Hübner) **comb. nov.** [Hi-

dalgo, Co, TX]); 2018: 162 fig. (misidentification); Koçak & Kemal, 2007: 959; 2015: 1463; Pelham, 2008: 404, 492, 646; Seraphim *et al.*, 2014: 42 fig. 1 (cladogram) part, 45, 46, suppl. material: figs. S3 [male genitalia], S4 [underside habitus]: EUA03, morphogroup 04; Cong & Grishin, 2014: 43, 44, 45, 46, 48, 49, 50, 51, 52, 53 figs. 1-9, 54, 55, 56, 57, 58, 59 figs. 10-21, 60, 61, 63, 64 figs. 36-39, 44-47, 66, 67, 68, 69, 72 figs, 60a, d, g, j, 73 fig. 61c, 74 figs. 62o-z2, 75 fig. 63 (morphometry, in part), 76 figs. 64a-h, 77 fig. 65, 78 fig. 66 (cladogram) part, 79, 80 fig. 67 (distribution map) part, 81 fig. 68 part, 82 fig. 69 (life cycle), 83, 85, 86, 87, 88 [neotype designated. TL: Savannah, Georgia, USA]; Warren *et al.,* 2014a: 83, 84 fig. 1b (habitus dorsal, with androconia), d (habitus ventral), f (habitus dorsal), h (habitus ventral), k (male genitalia), m (female genitalia), n (distribution map) part, 85; 2014b: 44, 45 figs. 1 b (habitus dorsal), d (habitus ventral), f (neotype dorsal androconia), h (neotype ventral), j (androconia), 46 figs. 2 a, c, e, g (wing scales), 47 figs. 3 a-h, 48 figs. 4 a-b, m-t, 49, 50; Anken *et al*., 2015: 157, 158; Tan & Lucky, 2016: 1-5, figs. 1 (female habitus), 2 (ocellar pattern), 3 (distribution map), 4 (egg and first instar larva), 5 (early stages), 6 (comparative wing characters), 7 (genitalia compared), 8 (pair in copula); Nakahara *et al*., 2016: 83, 84; Marín *et al*., 2017: 778 fig. 8 (cladogram); 2019: 91; Austin, 2018: 307-313, fig. 2 (last larval instar), fig. 4 (imagos); See *et al*., 2018: 51.

[*Hermeuptychia hermes* (Fabricius); D'Abrera, 1988: 777 figs. [row 1, fig. 1] male recto with androconia (possible misidentification)], [row 1, fig. 2] male verso (misidentification)].

Hermeuptychia hermes kappeli Anken, 1993: 418-419, figs. 2a (male holotype dorsal), 2b (male holotype ventral). [TL: Lake Okeechopee, Fla., USA].

Hermeuptychia hermes kappeli Anken; Anken, 1994: 288; Calhoun, 1997: 47 [synonymy established]; Lamas, 2004: 220; Pelham, 2008: 404, 630; Cong & Grishin, 2014: 46, 51, 59 figs. 12 (holotype dorsal), 13 (holotype ventral), 60, 61; Anken *et al.,* 2015: 157, 158, figs. 1 (holotype dorsal), 2 (holotype ventral); Tan & Lucky, 2016: 2 (all as a synonym of *H. sosybius* (Fabricius)).

Hermeuptychia hermes sosybius (Fabricius); Whittaker, 1983: 109 fig. 2 (capture numbers) (misidentification); Raguso & Llorente, 1997: 286 (misidentification?).

Hermeuptychia sosybius kappeli Anken; Cong & Grishin, 2014: 44.

H.[*ermeuptychia*] *kappeli* Anken; Anken *et al.,* 2015: 158, figs. 1 (holotype dorsal), 2 (holotype ventral) (as a synonym of *H. sosybius* (Fabricius).

In the original description of *Papilio sosybius*, Fabricius (1793: 219) indicated that the specimens he examined were from the collection of Dru Drury (London). He also referred to illustrations of this taxon by William Jones in his "*Icones*" ("Jon. fig. pict. 6. tab. 52. fig. 2"). Two figures fully identified with the name *sosybius*, representing upper and underside of this butterfly species do appear in manuscript volume V of Jones, with the explicit indication of being in the collection of Dru Drury (Jones, 1785 [vol. V]: pl. 52) (available at: http://www.jonesicones.com/. The referred illustrations were reproduced by Cong & Grishin, 2014: 53, figs. 1-3). An account of the search for surviving Drury's specimens of this species in the Macleay Museum at Sydney, Australia, is given by the latter authors.

Fabricius did not designate a locality of provenance for this taxon, and its alleged North American origin has been taken for granted since a very early date. Many authors have largely associated the name *sosybius* to a common species found in great part of the southern United States. On this assumption, and following a series of reasonable criteria, Cong & Grishin (2014) established a type locality (Savannah, Georgia, USA) while designating a neotype for *P. sosybius* (deposited in the USNM). But in the same work, presumably under the rules of Article 74.4 of the International Code of Zoological Nomenclature (ICZN 1999: 82) they also designated a lectotype [!] for the same taxon (Jones' watercolor painting examined and referred to by Fabricius). Here, there is a blatant contradiction (Articles 74 and 75 of the Code), as there cannot be two types for the same taxon. Only one can be the bearer of the name.

On the other hand, there are several clues that could point out to a South American origin for the true *Papilio sosybius* (Viloria & Robinson, MS), in which case the only possibility of identity for the insect described by Fabricius (and illustrated by Jones) as such, is what has been here denominated *Hermeuptychia canthe* (Hübner) **sp. restit.**, **comb. nov.** Should a definite proof of such an undesirable situation emerge, a supported case for the protection of the name *sosybius* for the North American butterfly species traditionally called so, must be referred to the International Commission of Zoological Nomenclature.

According to the current situation, figure 64 in Forster (1964: 89) is correct for North American *H. sosybius*. Seraphim *et al.* (2014, suppl. material) correctly identified *Hermeuptychia sosybius* (F.) as well (figs. S3 [male genitalia], S4 [underside habitus]: EUA03, morphogroup 04).

Edwards (1877), French (1886) and Scudder (1889) described the early stages of this species in such a detail that it is possible to separate certain of its characters from those of *H. acmenis* **comb. nov.** (particularly their pupae). Cong & Grishin (2014) also described and superbly illustrated the life cycle of *H. sosybius* and *H. hermybius* **syn. nov.**, but they failed to even cite the foundational works of those pioneers.

CONCLUSIONS

The current investigations on the nomenclature of the American genus *Hermeuptychia* Forster (Lepidoptera, Nymphalidae, Satyrinae), mainly through the study and scrutiny of information published in scientific documents, but also by the examination of its diversity in biological collections, yielded the reinstatement of three species, the proposal of four new combinations and the recognition of eight new synonymies. The novel taxonomic arrangement proposed for this genus is as follows: *Hermeuptychia acmenis* (Hübner, 1823), **comb. nov.** (= *H. hermybius* Grishin, 2014, **syn. nov.**), *Hermeuptychia atalanta* (Butler, 1867), *Hermeuptychia camerta* (Cramer, 1780), **sp. restit.**, **comb. nov.**, *Hermeuptychia canthe* (Hübner, [1811]), **sp. restit.**, **comb. nov.** (= *Neonympha pimpla* C. Felder & R. Felder, 1862, **syn. nov.** = *Euptychia maimoune* Butler, 1870, **syn. nov**. = *Euptychia nana* Möschler, 1877, **syn. nov.**), *Hermeuptychia cautheus* (Godart, [1824]), **sp. restit.**, **comb. nov.** (= *Hermeuptychia intricata* Grishin, 2014, **syn. nov.**), *Hermeuptychia cucullina* (Weymer, 1911), *Hermeuptychia gisella* (Hayward, 1957) (= *Hermeuptychia hermes* var. *hermesina* Forster, 1964, **syn. nov.** = *Hermeuptychia clara* Nakahara, Tan, Lamas & Willmott, 2016, **syn. nov.**), *Hermeuptychia harmonia* (Butler, 1867) (= *Euptychia calixta* Butler, 1877 = *Hermeuptychia callixta* Forster, 1964, **syn. nov.**), *Hermeuptychia hermes* (Fabricius, 1775) (= *Hermeuptychia hermes isabella* Anken, 1994), *Hermeuptychia lupita* (Reakirt, [1867]), *Hermeuptychia sosybius* (Fabricius, 1793) (= *Hermeuptychia hermes kappeli* Anken, 1993).

Any other species historically classified within *Hermeuptychia* are not considered members of this genus by the present author.

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Nota bene: This article was already fully corrected and integrated to the other parts of this journal at the time when the following paper was published on line (March 10th, 2021). I consider that the results presented by its authors are congruent with the systematic arrangement herein proposed, although our nomenclatural approaches are different:

Tan, D., A. Parus, M. Dumbar, M. Espeland & K. R. Willmott. 2021. Cytochrome *c* oxidase subunit I barcode species delineation methods imply critically underestimated diversity in 'common' *Hermeuptychia* butterflies (Lepidoptera: Nymphalidae: Satyrinae). *Zoological Journal of the Linnean Society.* Zlab007 https://doi.org/10.1093/zoolinnean/zlab007