Systematics of the butterfly genus *Cissia* Doubleday, 1848 (Lepidoptera: Nymphalidae: Satyrinae) using an integrative approach

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**Abstract.** The genus *Cissia* Doubleday, 1848 is revised and its monophyly is tested using Maximum Likelihood analysis based on three genes (COI, GAPDH and RpS5). A new taxonomic arrangement is proposed based on molecular and morphological evidence, and *Cissia* now comprises six species, *C. penelope* (Fabricius, 1775), *C. pompilia* (C. Felder & R. Felder, 1867), *C. proba* (Weymer, 1911), *C. eous* (Butler, 1867) *comb.n.*, *C. phronius* (Godart, [1824]) *comb.n.* and *C. rubricata* (W.H. Edwards, 1871) *comb.n.*, distributed from the Southern US to Argentina. The remaining species previously treated in *Cissia* are here cited as "*Cissia*" until they can be removed to undescribed genera in upcoming papers. *Euptychia moneta* Weymer, 1911, *E. austera* Butler, 1867 and *Paryphthimoides kiliani* Anken, 1999 are new synonyms of *Cissia penelope*, *C. pompilia* and *C. eous*, respectively. Neotypes of *Euptychia moneta*, *Satyrus phronius* and *Neonympha rubricata* are designated, as well as the lectotypes of *Neonympha pompilia*, *N. thelete* Snellen, 1887, *Euptychia usitata* Butler, 1867, *E. pieria* Butler, 1867, *E. ergione f. proba* Weymer, 1911 and *E. eous*. The results confirm that is possible to distinguish most of the species of *Cissia* based on both morphological and molecular data, although *C. rubricata* shows some differences in the male genitalia compared to its sibling species.

**Key words.** Euptychiina, *Megisto*, molecular phylogeny, morphology, *Paryphthimoides*, seasonal polyphenism, taxonomy, *Yphthimoides*.

1. Introduction

Euptychiina is a subtribe of the diverse butterfly subfamily Satyrinae, which has been the focus of significant research in the last couple of decades, from both phylogenetic and biogeographic perspectives (Murray & Prowel 2005; Peña et al. 2006, 2010; Marín et al. 2017) to descriptions of new genera and species (e.g. Barbosa et al. 2015, 2016; Bensmehab 2015; Cong & Grishin 2014; Costa et al. 2016; Fratello et al. 2015; Freitas 2003; Freitas & Peña 2006; Freitas et al. 2013, 2015, 2016a; Huertas et al. 2016; Nakahara et al. 2015a,b, 2016a,b, 2017; Neil et al. 2014, 2015; Seraphim et al. 2013; Siewert et al. 2013; Zacca et al. 2013, 2017). A broader collaborative effort to revise the systematics of the subtribe has been underway since 2013, involving some 30 researchers from around the world, and resulting in approximately 40 papers published on this subtribe (see details in http://www.flmnh.ufl.edu/museum-voices/euptychiina/).

One of the oldest genera in the subtribe, *Cissia* Doubleday, 1848, has been shown to be polyphyletic in both
molecular and morphological phylogenies (Murray & Prowell 2005; Peña et al. 2006; Marin et al. 2017). Prior to the present study, Cissia comprised 17 species restricted to the Neotropical region (Lamas 2004; Brévignon 2005; Benmesbah 2015): C. cleophas (Godman & Salvin, 1889), C. confusa (Staudinger, 1887), C. joyceae Singer, DeVries & Ehrlich, 1983, C. labe (Butler, 1870), C. leshia (Staudinger, 1886), C. moneta (Weymer, 1911), C. myncea (Cramer, 1780), C. palladia (Butler, 1867), C. penelope (Fabricius, 1775) (and its synonym Papilio clarissa Fabricius, 1780, the type species of the genus), C. pompilia (C. Felder & R. Felder, 1867), C. proba (Weymer, 1911), C. pseudoconfusa Singer, DeVries & Ehrlich, 1983, C. similis (Butler, 1867), C. terrestris (Butler, 1867), C. thermis (Butler, 1867), C. maripa Brévignon, 2005 and C. touloulou Benmesbah, 2015. The yellowish patch in the submarginai region of the ventral forewing surface is a character that has presumably been widely used to group these species within Cissia, although there is variation in size, intensity and position of the patch among the species within the genus. Nevertheless, a number of other Euptychina species show a similar patch, such as Inbio hilara (C. Felder & R. Felder, 1867), Euptychia neblina Warren & Nakahara, 2015, Magneuptychia agnata (Schaus, 1913) and Magneuptychia drymo (Schaus, 1913). In museum collections it is not unusual to find specimens of these genera with each other, reflecting the current confusion surrounding their taxonomy.

Given the polyphyly of Cissia in existing phylogenies and the appearance of what was thought to be a diagnostic character in other genera, the limits of the genus clearly need revision. Furthermore, the taxonomy of Cissia species remains poorly understood and several species are phenotypically similar to other euptychine butterflies. The present study provides a taxonomic revision of the genus based on an integrative approach using molecular and morphological data.

2. Material and methods

We examined over 3500 specimens, including the types, from the following collections (acronyms as used in the text): AN – Andrew Neild collection, London, United Kingdom; BM – Booth Museum, Brighton, United Kingdom; CMNH – Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, United States; DD – Diego R. Dolibaina collection, Paraná, Brazil; DZUP – Coleção Entomológica Pe. Jesus de Santiago Mouré, Universidade Federal do Paraná, Paraná, Brazil; FD – Fernando M.S. Dias collection, Paraná, Brazil; IML – Instituto Miguel Lillo, Tucumán, Argentina; IOC – Instituto Oswaldo Cruz, Rio de Janeiro, Brazil; MB – Mohamed Benmesbah collection, Toulouse, France; MNHN – Muséum national d’Histoire naturelle, Paris, France; MTD – Senckenberg Museum für Tierkunde, Dresden, Germany; MZUJ – Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Krakow, Poland; NHMUK – Natural History Museum, London, United Kingdom; RA – Ralf H. Anken collection, Germany; RMNH – Rijksmuseum voor Natuurlijke Historie, Leiden, Netherlands; USNM – Smithsonian National Museum of Natural History, Washington, D.C., United States; ZMHB – Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; ZMUC – Natural History Museum of Denmark, Copenhagen, Denmark; ZSM – Zoologische Staatssammlung München, Munich, Germany; ZUEC – Museo de Zoología da Universidade Estadual de Campinas, São Paulo, Brazil.

Photographs of Neotropical butterfly type specimens taken by Gerardo Lamas and available in Warren et al. (2017) were consulted, especially for those relevant names and recognized species of Cissia.

Nomenclature used herein follows Lamas (2004) and subsequent works (Brévignon 2005; Benmesbah 2015). In the present study, we opted to refer as “Cissia” those species herein removed from the genus, but that will be transferred to undescribed genera in upcoming papers (Zacca et al. in prep.). The following abbreviations are used throughout the text: FW – forewing; HW – hindwing; DW – dorsal wings; VW – ventral wings; DFW – dorsal forewing; VFW – ventral forewing; DHW – dorsal hindwing; VHWW – ventral hindwing; HT – holotype; AT – allotype. In the section “Type material”, the labels are separated from one another by transverse bars.

We attempted to review all publications including members of Cissia, although given the broad distribution and abundance of several species, some publications will inevitably have been missed. This is particularly true for the North American literature relating to Cissia rubricata, since that species has already been the subject of a modern taxonomic revision (see Miller 1976).

Distribution maps were produced using the free software QGIS (QGIS Development Team 2016). Geographical data were obtained from label data in collections and the literature, including available information on host plants and immature stages.

2.1. Morphological study

Male and female specimens studied had their abdomen detached and soaked in a heated test tube with 10% potassium hydroxide solution (KOH) for about five minutes to facilitate the dissection of the genitalia. Dissected specimens are marked with an asterisk after the voucher number in the “Examined material” section. Images of genitalia were obtained in Leica LAS 3D view and LAS montage version 4.7 with the aid of a video camera Leica DFC 500 attached to a stereoscopic microscope Leica MZ16. Illustrations were prepared with the aid of a camera lucida attached to a stereoscopic microscope and subsequently vectorised by using the software GIMP version 2.8.10 (GIMP Team 2016).

Male and female genitalia terminology follow mostly Klots (1970), but the term “gnathos” is applied sensu
Table 1. Species of Euptychiina with sampling site data, code, and GenBank accession numbers from specimens used for phylogenetic analysis.

<table>
<thead>
<tr>
<th>Taxa</th>
<th>Locality</th>
<th>Code</th>
<th>COI</th>
<th>GAPDH</th>
<th>RPS5</th>
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PIERCE (1909), “futlura superior” and “futlura inferior” sensu PETERSEN (1904), “combination of ventral arm of tegumen and dorsal arm of saccus” sensu AUSTIN and MIELKE (2008). The intromittent male organ in butterflies is usually referred to as “aedeagus”, but here we use the term “phal1us”, since Agathiphagidae are the only Lepidoptera species to in the text as “complete” or “incomplete”; an ocellus is called “umbra”, as proposed by FORBES (1941). The ocelli are referred to in the text as “complete” or “incomplete”; an ocellus is considered “complete” when it has all elements of the eyespot (ocellar ring, ocellar spot and pupil), while it is “incomplete” when any of these elements are missing.

2.2. DNA sampling and analysis

Phylogenetic relationships and genetic distances among species of Cissia and appropriate outgroups were estimated to verify the monophyly of the redefined genus and assess the status of taxa.

Genomic DNA was extracted from one to two legs of adults using the DNeasy Blood & Tissue Kit with standard protocol (QIAGEN, Dusseldorf, Germany) or the Omniprep kit (G-Biosciences). DNA was stored in TE buffer at –20°C. We amplified the 658 bp barcode region of the mitochondrial gene COI as well as two clear genes GAPDH and RPS5, which have been shown to be useful in phylogenetic studies (Wahlberg & Wheat 2008). Primers and PCR reaction conditions followed NAKAHARA et al. (2015, 2017) and SILVA-BRANDÃO et al. (2005). All sequences were aligned using MAFFT v. 7 (Katoh & Stanley 2013) with sequences obtained previously and available on GenBank (see Table 1). The final matrix comprised 67 specimens and 2,772 bp. Based on previous molecular phylogenies (Pena et al. 2006, 2010) and on our unpublished data from additional euptychiine species, we chose sixteen species as outgroups, and Euphydia westwoodi Butler, 1867 to root the phylogenetic tree.

The data were divided into codon positions, and substitution models (see Electronic Supplement 2) and partitioning scheme were inferred using ModelFinder and on our unpublished data from additional euptychiine species, we chose sixteen species as outgroups, and Euphydia westwoodi Butler, 1867 to root the phylogenetic tree.

The data were divided into codon positions, and substitution models (see Electronic Supplement 2) and partitioning scheme were inferred using ModelFinder in IQ-TREE 1.5.4 NGUYEN et al. (2015). This was followed by 250 likelihood searches and 2000 nonparametric bootstrap replicates, also in IQ-TREE. Bayesian analysis was also performed for the combined data set under the model jumping (nst=–mixed), using the program MrBayes 3.2 (RONQUIST et al. 2012) on the CIPRES Science Gateway (MILLER et al. 2010). The matrix was divided in three partitions associated with the genes. As analysis of combined data by Bayesian methods permits partition-specific substitution models and parameters, all substitution model parameters (gamma shape, character state frequencies, substitution rates of GTR model) were allowed to vary across partitions (= genes). Four simultaneous chains were run for 10×106 generations for two runs, sampling trees every 1,000 cycles. The first 10 percent trees were discarded as fixed “burn in”. Considering the similarities between the results found in ML tree (Fig. 1) and Bayesian tree (see Electronic Supplement 3), we choose the ML tree to show and discuss our results.

Genetic distances (see Tables 2, 3) among species of Cissia were determined by using the Kimura-2-parameters substitution model (KIMURA 1980) in the program MEGA v. 6.0 (TAMURA et al. 2013).

### Table 1 continued.

<table>
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<th>Taxa</th>
<th>Locality</th>
<th>Code</th>
<th>COI</th>
<th>GAPDH</th>
<th>RPS5</th>
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3. Results

3.1. Molecular phylogeny and genetic distances

Maximum Likelihood (ML) analysis indicates that *C. penelope* (whose synonym *Papilio clarissa* is the type species for the genus) forms a clade with two species previously placed in the genus *Paryphthimoides* (*C. eous* comb.n. and *C. phronius* comb.n.), which were sister to one another (Fig. 1), with all of these relationships strongly supported (bootstrap support [bs] = 100). Although some differences in the male genitalia are observed (see discussion in “Taxonomy” section), *C. rubricata* (formerly placed in *Megisto*) is placed as sister to *C. penelope* + (*C. eous* + *C. phronius*), also with high support (bs = 98). This clade is sister (bs=89) to one containing the sister species *C. pompilia* and *C. proba* (bs=100) (Fig. 1).


Interspecific genetic distances among the six species that form a clade with *C. penelope* range from 6.4% to 15.5% (Table 2). Historically, *C. eous* and *C. phronius* have been confused with each other in several collections, but their genetic distances range from 6.0% to 6.6% (Table 3) supporting their status as distinct species (in addition to the morphological evidence discussed under Taxonomy section). Conversely, intraspecific genetic distances are highest among the individuals of *C. penelope* (3.5%), intermediate in individuals of *C. eous* (0.2%–1.7%) and lowest (0 – 0.2%) among the individuals of *C. phronius* (Table 3).

3.2. Taxonomy

*Cissia* Doubleday, 1848


**Diagnosis.** Species of *Cissia* are characterized by the following set of characters: (1) glabrous eyes, (2) bipupillated ocelli in Cu1–Cu3 in DHW, (3) silvery ocelli in M1–M3 and M1-Cu1 in VHW, (4) submarginal and marginal lines crenulated in VFW and VHW, (5) uncus arched downwards (Fig. 4A), (6) gnathos hook-like and short (except in *C. rubricata* that is sinuous and developed), (7)
phallus with anterior region bottle-shaped and posterior region with apex dorsally bifid (Fig. 4D,E), (8) absence of vesical cornuti in phallus, (9) lamella antevaginalis laterally expanded and orbicular or obovate in ventral view (Fig. 5A,B), (10) ductus bursae membranous and paired signa at corpus bursae.

**History of classification.** *Cissia* Doubleday, 1848 was described without any diagnosis, including only its type species *Cissia clarissa* (Cramer, 1782). *Papilio crantor* Fabricius, 1791 was included doubtfully in *Cissia* by Doubleday, being ineligible to be the type species of the genus under Article 67(h) of the ICZN. *laMas* (2004) treated this species as a junior synonym of "*C. myncea*" (Cramer, 1780). *godart* ([1824]) considered *Papilio clarissa* as a junior synonym of *Papilio penelope* Fabricius, 1775, which was also followed by *sCudder* (1875). *dyar* ([1903]) treated in *Cissia* the Nearctic species *Papilio cymela* Cramer, 1777 (replacement name for *P. eurytus* Fabricius, 1775), *Neonympha rubricata*, *N. mitchelli* French, 1889 and *P. sosybius* Fabricius, 1793; the first two species were placed by *lamas* (2004) in Megisto Hübner, [1819], and the last in *Hernympychia* Forster, 1964. *Barnes & Lindsey* (1922) suggested that the name *Megisto* should replace *Cissia*, based on the *sCudder’s* (1875) inclusion of *P. penelope* Fabricius, 1775 and *P. eurytus* Fabricius, 1775, the type species of *Megisto*, in *Cissia*. However, molecular data show that the type of *Megisto* is not closely related to true *Cissia* species ([Peña et al. 2006, 2010], as redefined in the present study.

The first systematic arrangement to include some species of *Cissia* was proposed by *Butler* (1867a), who placed them in “Division 1” of *Euptychia* Hübner, 1818 characterized by “Alae supra fuscae, rarissime albo violaceove variae; posticae plerumque ocello subanali distincto: subtus pallidiores, ocellis forma regularibus, plerumque distinctis, lineis duabus mediae, interna antecarum raro obsoleta”. In this category, *Butler* included *Papilio myncea* Cramer, 1780, *Euptychia palladia* Butler, 1867, *Euptychia terrestris* Butler, 1867, *Euptychia themis* Butler, 1867, *Euptychia similis* Butler, 1867, *Papilio clarissa* Cramer, 1780, *Euptychia usitata* Butler, 1867 and *Euptychia pieria* Butler, 1867. *Lamas* (2004) followed *godart* ([1824]) and *sCudder* (1875) in treating *P. clarissa* as a junior synonym of *C. penelope*, while *E. usitata* and *E. pieria* were placed as synonyms of *C. pompilia* (C. Felder & R. Felder, 1867).

In his “Catalogue of Diurnal Lepidoptera of the family Satyridae”, *Butler* (1868) erected the “Section

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**Fig. 1.** Phylogeny of the genus *Cissia* based on the Maximum Likelihood analysis of combined COI, GAPDH and RpS5 gene sequences. Bootstrap values < 75 not shown.
Megisto”, a category without diagnostic characters, and included 102 species, 10 of which were treated by Lamas (2004) in Cissia, including E. clarissa, E. crantor (Fabricius, 1793), E. myncea, E. palladia, E. pieria, E. pom-pilia, E. similis, E. terrestris, E. themis and E. usitata. Butler (1877) proposed the “Euptychia ocypete species group” to contain 31 species that he considered allied to each other by their wing phenotypes. Among them, eight
species placed in *Cissia* by Lamas (2004), were included: *E. labe* Butler, 1870, *E. myncea*, *E. palladia*, *E. ter-
restrial*, *E. penelope*, *E. themis*, *E. usitata*, *E. undina* Butler, 1870.

Mostly based on slight characters of the wing coloration and venation, Godman & Salvin (1879–1901) di-
vided the genus *Euptychia* in eight groups, named from “a” to “h”. “Group d” was characterized by the “wings
of male opaque brown, of female paler, the markings of the underside sometimes showing faintly above; upper
discocellular of primaries very short, directed outwards, middle discocellular strongly convex” (p. 78) and com-
prised by 17 species, including *E. labe*, *E. pieria*, *E. terrestrial* and *E. similis*; of which the first three former
were allocated in “subgroup a”, defined by the “first subcostal branch emitted before the end, the second
at the end of the cell” (p. 78), while *E. similis* belonged to “subgroup b”, characterized by the “first subcostal branch of prima-
ries emitted before the end of the cell, the second beyond it” (p. 81).

In his introduction to the genus *Euptychia*, Weymer
(1911) explained his decision to treat within that genus
all of the species that other authors had placed in *Cissia*
and *Neonympha*: “The American authors place the seven
species occurring there in the genera *Neonympha* Hübner
and *Cissia* Doubleday. But as these species have exactly
similar allies in Mexico and in tropical Central and South
America, I follow Butler and Godman & Salvin in ref-
erring them all to *Euptychia*. Still in this same work,
Weymer proposed the “oecytpe group” comprising 36
species, some of them not cited in Butler (1877), with-
out any explanation. However, Weymer treated all of the
*Cissia* species previously cited by Butler, and made
some recommendations about their taxonomic status, as
follows: 1) *E. pieria*, *E. pompilia* and *E. thelete* (Snellen,
1887) were treated as forms of *E. usitata*, 2) *E. themis*
and *E. undina* as forms of *E. similis*, and 3) *E. pytheus*
Möschler, 1883 as a form of *E. penelope*.

Forster (1964) described the genera *Argyreuptychia*
and *Vareuptychia* to a number of species placed by Lamas
(2004) in *Cissia*. The genus *Argyreuptychia* comprised 10
species, of which seven were placed in *Cissia* by Lamas
(2004) (*A. penelope*, *A. proba*, *A. labe*, *A. palladia*, *A. py-
theus*, *A. moneta* Weymer, 1911 and *A. lesbia* Staudinger,
[1886]), and stated that the genus was characterized by its “small size when compared to *Megenuptychia* Forster,
1964 and *Magneuptychia* Forster, 1964, silvery eyespots
in M2–M3, and M3–Cu1 on ventral hindwings, slender uncus,
and short and narrow aedeagus [= phallus]” (For-
ster 1964: 123). In contrast, *Vareuptychia*, containing
*V. similis* and *V. usitata*, was erected based on “dif-
ferences in the male genitalia structures when compared to the
closely related genus *Argyreuptychia* and the com-
pletely different pattern and coloration of the wing un-
derside, with straighter bands” (Forster 1964: 125).

Although Forster (1964) did not provide a detailed
description of the male genitalia, when comparing his il-
lustrations of *V. similis* and *V. usitata* (p. 125, figs. 145,
146), the only character that is shared by both species is
the presence of cornutal patches on the phallus. The dif-
fferences in wing pattern mentioned by Forster are likely
the median and/or submedian line(s) on the underside of
the wings, which are straighter in the species he placed in
*Vareuptychia*. It is known (Féritas 2004; Peña & Lamas
2005; Barbosa et al. 2015) that the limits of most of the
genera proposed by Forster are very wide and based on
vaguely defined features that also can be found in other
Euptychini genera, with no clear distinguishing diag-
nostic characters.

However, two important points must be considered
here: 1) by studying only Bolivian specimens, Forster ig-
nored the existence of *Cissia* Doubleday, 1848, a genus
with the same type species that he had chosen for
*Argyreuptychia*, and 2) the close relationship between
*Argyreuptychia* and *Vareuptychia*. The first point was noted
by Miller (1968) who placed *Argyreuptychia* as an ob-
jective synonym of *Cissia*, later followed by Singer et
al. (1983) and Lamas (2004). When describing the diag-
nostic characters of *Euptychini* (= *Euptychia*), Miller
(1968) stated that *Cissia* species are characterized by
having a spiny midtibia, while in the remaining genera of
the tribe the spines are slight or lacking (p. 91).

Singer et al. (1983) provided the first taxonomic re-
view of *Cissia* and proposed the most recent systematic
arrangement of this genus. Considering only species from
Costa Rica and Trinidad, the authors concluded that *Cis-
sia* species do not show clear characters in wings pattern
and male genitalia that enable them to be distinguished
from other genera (Singer et al. 1983: 106). In that study,
*Cissia* was mainly defined based on morphological fea-
tures of immatures, which led the authors to subdivid-
the genus into four subgroups: 1) “labe subgroup” – com-
prising *C. labe*, *C. palladia* and *C. penelope*; 2) “confusa
subgroup” – *C. myncea*, *C. confusa* and *C. pseudocon-
fusa*; 3) “gomezi subgroup” – only *C. gomezi* Singer,
DeVries & Ehrlich, 1983; and 4) “subgroup incertis” – C. drymo Schaus, 1913, C. agnata Schaus, 1913 and C. joyceae Singer, DeVries & Ehrlich, 1983. However, even after this study, some authors opted to treat Cissia as a catch-all genus (see DeVries 1987) including a number of what we now know to be unrelated.


described in \textit{Cissia} after Lamas’ publication, namely \textit{C. maripa} Brévignon, 2005 and \textit{C. touloulou} Benmesbah, 2015, and no formal taxonomic alteration has been made until the present paper.

\textbf{Taxonomy.} The genus \textit{Cissia} is redefined here to include six species: \textit{C. penelope}, \textit{C. pompilia}, \textit{C. proba}, \textit{C. eous comb.n.}, \textit{C. phronius comb.n.} and \textit{C. rubricata comb.n.}. Based on molecular data, the genus is a member of the ‘\textit{Megisto clade}’ as defined by Piña et al. (2010), whereas morphological data failed to recover \textit{Cissia} within this clade, but placed it as a nearby branch (Marín et al. 2017). The \textit{Megisto} clade contains genera which are typically most diverse in more temperate regions of the Americas, and our data suggest that the genus is sister to a clade comprising the genera \textit{Carminda}, \textit{Graphita}, \textit{Stegosatyrus}, \textit{Megisto}, \textit{Paleonympha} and several former \textit{Cissia} species which will need to be placed into other genera. In addition to our molecular results, several morphological features support the new taxonomic arrangement of \textit{Cissia}, including the the absence of setae on the eyes, wing pattern characters and venation, as well as the genitalia morphology. Singer et al. (1983) stated that the wings and male genitalia did not provide clear characters to delimit \textit{Cissia}, but the genus as redefined here does show a consilience of such characters that facilitate its recognition. Genitalic morphology remains one of the most useful tools in the delimitation of genera and species of Euptychiina (e.g.: Siewert 2013; Zacca et al. 2013, 2014, 2016; Freitas et al. 2015, 2016a; Nahakara et al. 2015), in combination with molecular data that support systematic evolutionary hypotheses.

The remaining species previously treated in \textit{Cissia} (Lamas 2004; Brévignon 2005; Benmesbah 2015) include: “C.” confusa, “C.” labe, “C.” leshia, “C.” mynacea, “C.” palladia, “C.” pseudoconfusa, “C.” similis, “C.” terres-tris, “C.” themis, “C.” maripa, “C.” cleophas, “C.” joyceae, and “C.” touloulou. Although the last three of these species have no DNA sequence data are yet available, we are confident (based on morphological evidence) that these are not closely related to the six species we treat
here in our redefined concept of *Cissia*. Some of them will shortly be moved into a redefined Parryphthimoides Forster, 1964 (Zacca et al. in prep.), while the most appropriate generic classification for the remainder is under study, with new genera being needed to accommodate at least some species (Zacca et al. in prep.). Since the ICZN requires that valid species names be binomens, we leave these species for the moment as “*Cissia*” until they can be moved into suitable genera, with the understanding that our use of the generic name *Cissia* throughout the remainder of the paper refers to the six species that will ultimately remain within the genus as newly defined here.

**Synonymic checklist of *Cissia* species**

(- indicates a synonym)

**Cissia** Doubleday, 1848

*Argyreuptchis* Forster, 1964

*Cissia* penelope (Fabricius, 1775)
- *Papilio clarissa* Cramer, 1775: 74; – *Euptychia* moneta* (Weymer, 1911) syn.n.
- *Neonympha* thelete (Snellen, 1887)
- *Euptychia* usitata* pieria* (Butler, 1867)
- *Euptychia* moneta* (Weymer, 1911) syn.n.
- *Papilio clarissa* (Fabricius, 1775)

**Cissia rubricata** (Weymer, 1911)
- *Euptychia* usitata* pieria* (Butler, 1867)
- *Cissia* penelope* (Weymer, 1911) syn.n.
- *Papilio clarissa* (Fabricius, 1775)

**Cissia penelope** (Fabricius, 1775)
(Figs. 2A – D, 3A,B, 4A – E, 5A,B, 8)


*Satyurus penelope*; *Godart* [1823]: 489.

*Neonympha clarissa*; *HERRICH-SCHÄFFER* 1864: 59.


*Argyreuptchis penelope*; *Forster* 1964: 123. – *Lewis* 1973: pl. 54, fig. 2.


**Cissia penelope** (Fabricius, 1775)

**Diagnosis.** *Cissia penelope* has a distinctive feature of the wing pattern that makes its identification easy when compared to all other Euptychina species: the presence of dark brown scattered dots on the ventral wings in the

**Key to species of *Cissia***

1. DFW and DHW with orange patches ................................................................. *C. rubricata* (Fig. 2U – X)
2. DFW and DHW totally brown ................................................................. 2
3. VW with well-marked dark brown scattered dots at the submarginal region (Fig. 2A); VHW with one developed incomplete silvery ocellus in Rs-M<sub>1</sub> (Fig. 2B) .................................................. *C. penelope* (Fig. 2A – D)
4. VW without dark brown scattered dots (or, if present, just a few and faded); VHW with one complete silvery ocellus in Rs-M<sub>1</sub> (or, if incomplete, is always small) ................................................................. 3
5. VW with submedian and median lines straight ......... 4
6. VW with submedian and median lines crenulated .... 5
7. VW without umbra (or, if present it is almost the same colour as the ground colour); VW with a narrow median line ............ *C. pompilia* (Fig. 2E – H)
8. VW with umbra darker than the ground colour; VW with a wide median line (approximately 1 mm) ...... ................................................................. *C. proba* (Fig. 2I – L)
submarginal region between R₇-Cu₀ on VFW and Rs-Cu₀ on the VHW. Additionally, the VHW has three silvery incomplete ocelli, each one in Rs-M₁, M₂-M₃, and M₃-Cu₁. The VHW submarginal and marginal lines are irregular and thin, widening between 1A+2A and the tornus.

**Male genitalia** (Fig. 5A–E). Tegumen slightly flattened, laterally subtriangular; uncus arched downward, about 2× length of tegumen, covered by small setae, smoothly dilated at median region in dorsal view, apex laterally curved downwards and dorsally truncated; gnathos hook-like, wide at base and tapering at apex, ½–⅔ × length of uncus; combination of ventral arm of tegumen and dorsal arm of saccus slightly sinuous; appendix angularis short; anterior projection of saccus developed, cylindrical, and almost same length as gnathos; furtura inferior present; furtura superior absent; valva sub-rectangular covered by long hair-like setae lateroventrally, and short setae at inner side, costa developed and sub-square; dorsal margin slightly projected at median region, ventral margin slightly projected at median region, apex wide and serrated; phallus straight, shorter than valva, cylindrical, anterior region bottle-shaped, posterior region about 2× longer than anterior region, with bifid apex in dorsal view, distal opening ventral and longer than proximal opening.

**Female genitalia** (Fig. 4A,B). 8⁰ tergite rectangular; papilla analis somewhat triangular and covered by long hair-like setae at distal region, apophysis posterior short; lamella antevaginalis fused to lamella postvaginalis with one spiral located at upper margin of lateral expansions of lamella antevaginalis; lamella postvaginalis obovate in ventral view; ductus bursae membranous; corpus bursae about same length as ductus bursae, with paired signa dorsally.

**Variation.** In general, males are smaller (FW length: 17–20 mm) than females (FW length: 18–22 mm), with a straight FW outer margin (rounded in females). The subapical ocellus on the DFW is larger in females than in males, and the VFW yellowish-ochre patch is larger in females. **Weymer** (1911) suggested that the absence of the silvery pupal at the apical ocellus on VFW could be used to distinguish males and females, but this feature can be present or absent in both sexes. The width of the median and submedian lines on ventral wings is intraspecifically variable. The median line on the VHW can be strongly concave in Cu₀-1A+2A, close to the inner margin. Sometimes, the three silvery incomplete ocelli located in R₇-M₁, M₂-M₃ and M₃-Cu₀ on VFW are faded, although it can be possible to see these elements by moving the specimens against the light. Ocelli ring coloration varies from pale-ochre to golden or orange. Some structures of the male genitalia can show intraspecific variation, such as the degree of concavity at the superior region of the gnathos, the anterior portion of saccus varying between straight and smoothly curved upwards, and the anterior region of the phallus being straight or slightly curved downward.

**Distribution.** This species occurs in Central and South America in Guatemala, Costa Rica, Colombia, Ecuador, Peru, Bolivia, Venezuela, Guyana, Suriname, French Guiana and Brazil, plus the islands of Curacao and Trinidad, mainly in association with Amazon and Atlantic forests, but being also found in dry forests in Central America and southwestern Brazil (Fig. 8). **Cissia penelope** is common and widely distributed in the cis-Andean region, with only one record (Garwood & Jaramillo 2016) in the valley drained by the river Cauca, between the Andean Cordilleras Occidental and Central in Colombia. It is found from sea level to about 2000 m. Regarding phenotypically similar species, C. penelope is sympatric in (1) Colombia with C. pompilia and C. proba; (2) Venezuela – C. pompilia; (3) Ecuador, Peru, Bolivia and Brazil – C. proba. It is syntopic with C. proba in Meta and Putumayo (Colombia), Napo and Orellana (Ecuador), Amazonas, Acre, Maranhão, Mato Grosso and Rondônia (Brazil), Junin, Loreto and Madre de Dios (Peru), and Santa Cruz (Bolivia). Although **Cock** (2013: 83) mentioned that specimens supposedly collected by Ralph du Boulay Evans in Trinidad could be mislabelled (e.g.: male specimen at NHM UK – voucher number BMNH(E) 1421881) and might have come from western Venezuela or Curacao, we found additional specimens of C. penelope from Trinidad collected by other naturalists, such as F. Birch, T.T. Dyer and A. Hall, as well as being included in publications (Kaye 1921; Barcant 1970; Singer et al. 1983; Singer & Ehrlich 1993), which confirm its occurrence on that island.

**Biological and phenology.** In general, C. penelope is found at the forest edge and in nearby open areas such as grassland or pasture, avoiding deep shade in forests (Singer et al. 1983), and it has been considered an indicator of disturbed areas (Singer & Ehrlich 1993; Brown & Hutchings 1997; Wood & Gillman 1998; Ramos 2000; Lande et al. 2003). It is multivoltine and flies year round. Adults are attracted by rotting fruits and other decaying material, and are consequently often captured in bait traps (Mielke & Casagrande 1992; Brown & Hutchings 1997; Casagrande et al. 2012).

**Host plants and immature stages.** Larvae of **Cissia penelope** have been recorded feeding on *Cyperus L.* and *Seleria B.* (Poales: Cyperaceae), and some species of Poaceae, such as *Ichnanthus pallens* (Sw.), *Lasiacis sloanei* (Griseb.), *Panicum pilosum* Sw., *P. polygonatum* Schrad., *Paspalum conjugatum* P.J. Bergius, *Pasp. decumbens* Sw., *Setaria paniculifera* (Steud.), and *Tripsacum* sp. (Singer et al. 1983; Ackery 1988; Beccaloni et al. 2008). The only information on the immature stages is found in Singer et al. (1983).

**Type material, neotypes designation and taxonomic history.** **Fabricius** (1775) described this species based on an unstated number of specimens from an imprecise locality in America, collected by Drury. Singer et al. (1983) designated the neotype of *Papilio penelope* Fabricius, 1775 (Fig. 58) in the ZMUC, with the following labels: /penelope ex. Am: Ma: Schmid", ex Sehested & Tender Collection [handwritten]/ Mus. Leh. e T. L. [handwritten]/ NEOTYPE *Papilio penelope* Fabricius,
Papilio clarissa Cramer, 1782 was described based on an unstated number of specimens from Surinam, collected by Stoll. Godart ([1823]) noted that P. clarissa is a junior synonym of P. penelope, and it treated in Satyras Latreille, 1810. The neotype female of Papilio clarissa Cramer, 1782 (fig. 59) is in the NHMUK and also designated in Singer et al. (1983) with the following labels: /N° 110. CLARISSA. Cr[amer]. IV. 293. D. E. [handwritten] Linnepl. Surin[ane]. [handwritten]/ FELDER COLL[ECTIO]N./ Rothschild Bequest B. M. 1939-1/ NEOTYPE/ Papilio clarissa Cramer NEOTYPE det. R. I. Vane-Wright 1983/.

Euptychia moneta Weymer, 1911 was described and figured based on an unstated number of specimens from Cayenne, French Guiana (Weymer 1911: 200, pl. 47b). Syntypes of E. moneta have not been found after an exhaustive search in the ZMHU, ZSM, MTDO or NHMUK collections, which house the majority of the type material of Weymer (Nekrutenko 2001; Pyrcz 2006). Among the Weymer types deposited at the ZSM, one specimen was found identified as E. moneta from "San Ramon[sic] [Junín]," Peru, but it was collected in 1956 by F. König, 45 years after the original description of this species. Several of Weymer's types went missing during World War II and neotype designations are needed for many names to permit their unambiguous identification and clarify their taxonomic status, such as E. moneta. Herein, the neotype of Euptychia moneta is designated, which agrees completely with the original illustration provided by Weymer; this neotype has the following labels: /Cayenne [French Guiana]/ Ex Oberthür Coll. Brit. Mus. 1927 – 3/ BMNH(E) #786267/; and two others will be added later: /Neotypus Neotypus Euptychia moneta Weymer, 1911. T. Zacca & B. Huertas, det. 2016/. NHMUK.

Furthermore, E. moneta is placed as a new synonym of C. penelope, since no other similar looking specimens of E. moneta have been found in French Guiana or surrounding countries, even though researches have been conducting extensive field works in these areas (A. Neild and M. Bennesbah pers. comm.), and no inventories have yet documented this species (e.g.: Brévignon 2005; Brévignon & Bennesbah 2012). We therefore regard the specimen used to represent E. moneta by Weymer, and the neotype designated here, as aberrant forms of C. penelope, as already suggested in Brévignon (2008: 71).

Remarks. Forster (1964) erected the genus Argyreuptychia to include E. penelope and six additional species, based on morphological characters of the male genitalia and some wings features, such as the silvery marked ocelli on the VHW. However, Argyreuptychia is a subjective junior synonym of Cissia Doubleday, 1848 since the types of the two genera are currently regarded as being synonymous (see discussion in "History of classification").

Examined material. See Electronic Supplement 1.

Cissia pomplia (C. Felder & R. Felder, 1867)

(Figs. 2E–H, 4F–J, 5C,D, 6A–D, 7A,B, 9)


Euptychia australa Butler, 1867a: 464, pl. 39, fig. 4; holotype: [Colombia] Bogotá; NHMUK (examined). syn.n.

Neonympha thelete Snellen, 1887: 18, pl. 1, fig. 3; lectotype: [Netherlands] Curacao; RMNH (examined).


Euptychia usitata thelete; Weymer 1911: 201

Vareuptychia usitata; Forster 1964: 125, fig. 146 (male genitalia).


Vareuptychia pieria; Llorente-Bousquets et al. 1986: 24.

Cissia usitata pieria; Ragooso & Llorente-Bousquets 1991: 132.

Cissia usitata; Meerman & Boissima 1993: 42.


Vareuptychia usitata pieria; POZO et al. 2003: 516.

Yphthimoides austera; LAMAS 2004: 224.

Diagnosis. Compared to all other species of Cissia, C. pomplia most closely resembles C. proba in its wing shape and element pattern, but it can be distinguished from this species by its paler ground color on both ventral wings surfaces and the narrower submedian and median lines.

Male genitalia (Fig. 4F–J). Tegumen slightly flattened in dorsal view, laterally subtriangular; uncus arched downwards, about 2 × length of tegumen, covered by small setae, not dilated at median region, apex curved downwards and truncated in dorsal view; gnathos hook-like, half length of uncus; combination of ventral arm of tegumen and dorsal arm of saccus straight; appendix angularis short and curved downwards; anterior projection of saccus developed, cylindrical, and longer than gnathos; fultura superior absent; fultura inferior present; valva sub-rectangular covered by long hair-like setae latero-ventrally, with short setae at inner side, costa developed and rectangular, dorsal and ventral margins slightly
projected at median region, apex pointed and serrated; phallus straight, almost same length of valva, cylindrical, anterior region bottle-shaped, posterior region about 2 × longer than anterior region with bifid apex in dorsal view, distal opening ventral and longer than proximal opening.

**Female genitalia** (Fig. 5C,D). 8th tergite rectangular; papilla analis somewhat triangular and covered by long hair-like setae at distal region, apophysis posterior absent; lamella antevaginalis fused to lamella postvaginalis with one spiracle located at upper margin of its lateral expansions; lamella postvaginalis orbicular in ventral view; ductus bursae membranous; corpus bursae 0.5–1.0 × length of ductus bursae, with a short paired signa dorsally.

**Variation.** Females are mostly larger (FW length: 20–22 mm) than males (FW length: 17–21 mm) and have a small subapical ocellus in M₄-M₅ on DFW. Females of *C. pompilia* sometimes have small ocelli in R₄₊₅-M₁, M₁-M₂, and M₁-Cu₁ on DFW and others similar in M₁-M₂, M₂-M₃, M₁-Cu₁, and Cu₁-1ₐ₊₂A on the DHW. If males have one ocellus in M₁-M₂ on DFW, it is never larger than that in females. A few specimens collected during the wet seasons showed extremely well-developed ocelli on VW (Fig. 6A). Some structures of the male genitalia can be variable, such as the shape of the tegumen varying on VW (Fig. 6A). Some structures of the male genitalia can be variable, such as the shape of the tegumen varying on VW (Fig. 6A).

**Distribution.** This species is widely distributed throughout Central America to South America, where it is restricted to western Colombia, Venezuela and Ecuador (Fig. 9). *Cissia pompilia* (Fig. 7A,B) is found in both rain and dry forests, especially along forest edges, and has also been documented in second-growth vegetation, riparian forests and pastures (DeVries et al. 1997; López & McNeely 2009). *Cissia pompilia* occurs up to altitude of 1600 m (Goldman & Salvin 1901: 80; DeVries 1987; specimen labels), The species is sympatric with *C. Felder & R. Felder, 1867*. Antioquia (Colombia) (Jarajillo & Garwood 2016a).

**Biology and phenology.** This species occurs throughout the year, although Pozo et al. (2008) recorded its highest abundance peak in October and its lowest abundance in January, May and June, in the Calakmul region, Campeche, Mexico. In Honduras, *C. pompilia* has been documented only in the rainy season, between May and September (Miller et al. 2012). Individuals have also been captured by bait traps in Honduras (Meeran & Boomsma 1993).

**Host plants and immature stages.** Recorded larval host plants include species of *Elaeis* Gaertn. (Chloridoideae, Poaceae) (DeVries 1987; Ackery 1988; Santín 2004; Beccaloni et al. 2008). The only information on the immature stages is found in DeVries (1987) and Janzen & Hallwachs (2009).

**Type material, lectotypes designation and taxonomic history.** *Neonympha pompilia* C. Felder & R. Felder, 1867 was described based on an un stated number of specimens from Colombia (Bogotá) and Mexico, collected by [Alexander] Lindig and [Auguste] Sallé, respectively. Four male syntypes of *N. pompilia* were found at NHMUK, two from Bogotá and two from Mexico. To fix the identity of the name, herein is designated the lectotype of this taxon; this specimen has the following labels: /TYPE/ Bogotá, Lindig, type/ Neon[syn.] pompilia Feld[er] = Euptychia pieria Butler (1866)/ Type of *N. pompilia* Feld[er] = *E. pieria* Butl[er] comp[ared]. w[iith], type 10.XII.12, NDR [Norman D. Riley]/ Rothschild Bequest B.M. 1939-1/ BMNH(E)#1267129/; and two other labels will be added later: /Lectotypus/ Lectotypus *Neonympha pompilia* C. Felder & R. Felder, 1867. T. Zacca & B. Huertas det. 2016/. NHMUK. The other three syntypes are here designated as paralectotypes and will be labelled accordingly.

*Euptychia usitata* Butler, 1867 was described based on an unstated number of specimens from Venezuela and Guatemala. Goldman & Salvin (1901: 80) stated that the identity of this Venezuelan form (*E. usitata*) of *E. pieria* need further consideration, as they did not have sufficient specimens to solve this puzzle. Only one female syntype was found at the NHMUK that agrees with the original description and illustration. To fix the identity of the name, this female syntype is designated herein as the lectotype of this taxon; this specimen has the following labels: /TYPE/ Euptychia usitata Butler Monograph/ by/ B. M. TYPE No. Rh. 3299, Euptychia usitata Butl[er]/ Venezuela/ Venezuela Pur[chased]. from Dyson 47-9/; and two other labels will be added later: /Lectotypus/ Lectotypus *Euptychia usitata* Butler, 1867. T. Zacca & B. Huertas det. 2016/. NHMUK.

*Euptychia pieria* Butler, 1867 was described based on an unstated number of specimens from Honduras. Only one male syntype was found at the NHMUK that agrees with the original description and illustration. To fix the identity of the name, this male syntype is designated herein as the lectotype of this taxon; this specimen has the following labels: /TYPE/ Euptychia pieria Butler Monograph/ by/ B. M. TYPE No. Rh. 3199, *Euptychia pieria* Butl[er]/ Honduras/ Honduras Pur[chased]. from Dyson 45-123/; and two other labels will be added later: /Lectotypus/ Lectotypus *Euptychia pieria* Butler, 1867. T. Zacca & B. Huertas det. 2016/. NHMUK.

*Euptychia austera* Butler, 1867 was described based on a single female [holotype] from Bogotá, Colombia. Currently this species is placed in *Yphthimoides* Forster, 1964 (Lamas 2004) and it is only known from the holotype deposited at NHMUK. No additional specimens have been found in several collections examined for the present study or in recent butterfly inventories performed in Colombia (e.g.: Donegan & Huertas 2005; Monte ro et al. 2009; Caldero-Mejia et al. 2013; Rodriguez & Miller 2013; Marin et al. 2014). The holotype specimen has the median and submedian bands fused into a single broad band on both wings, and similar blurring and fusion of the submarginal lines, strongly suggestive of a type of aberration that is observed rarely in other species. These observations, together with the otherwise similar morphology between the holotype of *E. austera* and specimens of *C. pompilia*, led us to place the former as synonym of the latter (syn.n.).
Neonympha thelete Snellen, 1887 was described based on two syntypes from Curaçao Islands [Netherlands]. Snellen provided a very precise illustration of this species that undoubtedly agrees with *N. pompilia*, and *N. thelete* was correctly synonymized by Lamas (2004). The Snellen collection is currently housed at the Naturalis Biodiversity Center, Leiden, Netherlands (RMNH). Only one syntype was found there; the second syntype is probably missing (E.G. Miracle pers. comm.). Although this syntype has a lectotype label affixed by G. Lamas in 1995, it was never published. This syntype is designated herein as the lectotype of this taxon to fix the identity of the name; this specimen has the following labels: /Curaçao [Netherlands] R. P. Janson/ Neonympha thelete Snell. nov. sp./ Lectotype ©Neonympha thelete Snellen, 1887, G. Lamas des[ignated]. 1995; and two other labels will be added later: /Lectotypus/ Lectotypus Neonympha thelete Snellen, 1887. T. Zaecca det. 2016/. RMNH.

**Remarks.** Determining the correct date of publication Butler’s “Monograph on the genus *Euptychia*” is important in a series of decisions related to the priority of euphentine names. According to Duncan (1937), the work was read in 1866 during the meeting of the Zoological Society of London. The proceedings of this meeting were divided into three issues, and Butler’s paper appeared in the third issue (pp. 377–645) published in April 1867, and therefore the correct year of publication is 1867 and not 1866. The correct month should be April without any specific date since this was never stated, and the default date therefore becomes April 30, the last day of the month. Lamas (1996), following Higgins (1963), clarified that the correct date of publication of C. Felder & R. Felder’s (1867) work was 25 April 1867, just five days before Butler’s publication. Godman (1901: 564) was therefore incorrect when he stated that *E. pieria* had priority over *N. pompilia*.

Butler (1867a) described *E. usitata* with two variations, one from Venezuela and the second from Guatemala. The former had a large ocellus in M3-Cu1 on DHW, and the latter had a rufous median line on DW. In the same work, Butler also described *E. pieria* from Honduras. Interestingly, Butler considered *E. pieria* closely related to *E. similis* (to be transferred to another genus – Zacca et al. in prep.), and not to *E. usitata*. Three years later, Butler (1870) published a work entitled “On new and recently described species of diurnal Lepidoptera” reporting his own mistake when considering *E. pieria* and *E. usitata* as distinct species, and treated *E. pieria* as a simple variety of *E. usitata* (Butler 1870: 252). Weymer (1911: 201) considered *E. pieria*, *E. pompilia* and *E. thelete* as forms of *E. usitata*.

The descriptions and illustrations of *N. pompilia*, *E. usitata* and *E. pieria* agree in many aspects; Lamas ([1997a]) came to the same conclusion, and synonymized *E. pieria* and *E. usitata* with *N. pompilia*. The types of these names differ only by their size, the expression of the ocelli, and the coloration of the ventral lines. After examining a large series of specimens from localities in Central and South America (see “Examined material” section), it is apparent that *C. pompilia* exhibits seasonal polymorphism, which could account for taxonomic disagreements over the years. For example, despite the absence of date on the labels of syntypes of *E. usitata* from Polochic Valley (Guatemala), the two specimens have a very characteristic phenotype of the dry season, with ocelli less apparent, and weak and rufous lines on the wings underside, similar to other specimens collected between January and April (dry season) in Mexico and Nicaragua (Fig. 6D). One specimen from Panama in the NHMUK (Fig. 6C), collected in July, displays a large ocellus and well-marked dark brown lines on the underside of the wings, similar to other specimens collected in the wet season.

Forster (1964: 125, fig. 146) illustrated the male genitalia of this species (considered by him as *Vareuptychia usitata*), but the cornuti were probably erroneously illustrated in the phallus. In all specimens of *C. pompilia* here examined, there are no cornuti, and all other structural features agree with Forster’s illustration. The absence of cornuti is one of the most important features of all species now allocated in *Cissia*.

Snellen (1887) considered *N. thelete* to be phenotypically similar to *E. liturata* Butler, 1867, but the wing elements of these two species are completely different, as are the structures of male and female genitalia. Recently, *E. liturata* was proposed as junior synonym of *Praefaunula armilla* (Zacca et al. 2017 – see also illustrations of the genitalia for comparison).

*Cissia pompilia* was not included in the taxonomic review of *Cissia* by Singer et al. (1983).

**Examined material.** See Electronic Supplement 1.

**Cissia proba** (Weymer, 1911)
(Figs. 21–L, 4K–O, 5E,F, 7C, 10)

*Euptychia erigone f. proba* Weymer, 1911: 203, pl. 47d, fig. 5; syntypes: Peru. Lectotype male herein designated: Peru, MTD (examined).
**Fig. 7.** Individuals in situ: A,B – *Cissia pompilia*, male (Colombia); C – *Cissia proba*, male (Junín, Peru). — Photos A,B: Juan Guillermo Jaramillo; C: David Geale.

**Euptychia mariameliae** Hayward, 1957: 109; holotype: Bolivia, Santa Cruz; IML.

**Argyreuptychia proba**; Forster 1964: 124; syn.: mariameliae.


**Cissia terrestris** [misidentification]; Willmott et al. 2011: 2, fig. 16.

**Diagnosis.** *Cissia proba* is distinguished from its congeners by the (1) remarkable grayish-brown ground colour on VW, (2) differentiated scales that gives the VW a “velvety texture”, (3) presence of a strong umbra on both VW surfaces, and (4) creamy band between the median and submarginal bands on both VW. *Cissia proba* might be confused with *Cissia terrestris* and *Iphthimoides maepius*, being differentiated from the former by the VHW submarginal line being rounded and crenulated between M₂–M₃ (pointed and crenulated in *E. terrestris*), and from the latter by the presence of 3 rounded ocelli on VHW (5 rounded ocelli in *Y. maepius*).

**Male genitalia** (Fig. 4K–O). Tegumen flattened, laterally subtriangular; uncus arched downward, about 1.5 × length of tegumen, covered by small setae, not dilated at median region in dorsal view, apex laterally curved downwards and truncated in dorsal view; gnathos hook-like, ⅓–⅔ length of uncus; combination of ventral arm of tegumen and dorsal arm of saccus slightly sinuous; appendix angularis short; anterior projection of saccus developed, cylindrical, and almost same length as gnathos; fultura superior absent; fultura inferior present; valva sub-rectangular covered by long hair-like setae lateroventrally, and short ones at inner side, costa developed and rectangular, dorsal margin straight at median region, ventral margin slightly projected at median region, apex pointed and serrated; phallus straight, longer than valva, cylindrical, anterior region bottle-shaped, posterior region about two times longer than anterior region with bifid apex in dorsal view, distal opening ventral and longer than proximal opening.

**Female genitalia** (Fig. 5E,F). 8th tergite rectangular; papilla analis somewhat oblong and covered by long hair-like setae in distal region, apophysis posterior short; lamella antevagnalis fused to lamella postvagnalis with one spiracle located at upper margin of its lateral expansions; lamella postvagnalis orbicular in ventral view and extremely well-developed; ductus bursae membranous; corpus bursae 1.5 × length of ductus bursae, with paired signa dorsally.

**Variation.** Sexual dimorphism related to the wingspan is not evident in *C. proba*. Females can be easily distinguished from males by having a subapical, well-developed ocellus in M₁–M₃ on DFW. The dorsal ground colour of the wings varies from brown to dark brown, being lighter in some old specimens in collections. The same occurs with the creamy band between the median and submarginal bands on both VW, which can be faded in old specimens. Additionally, the length of the anterior projection of the saccus can be short (the same length of the gnathos) or long (almost the same length of the uncus), but it is always large and cylindrical.

**Distribution.** This species has a trans-Andean distribution, occurring from Colombia to Bolivia, and to northern and midwest Brazil (Fig. 10), in altitudes not higher than 1450 m. *Cissia proba* is found almost exclusively in the Amazon rainforest, but there are some records from xerophytic vegetation in Bolivia and northern-midwestern Brazil. *Cissia proba* is sympatric with phenotypically similar species in (1) Colombia and Ecuador with *C. penelope* and *pompilia* (in the former country), (2) Peru, Bolivia and Brazil with *C. penelope*, being syntopic with the latter in Morona-Santiago, Pastaza, Sucumbios, Zamora-Chinchipe, Napo and Orellana (Ecuador), Loreto and Madre de Dios (Peru), Buenavista, Santa Cruz de la Sierra (Bolivia), and all those Brazilian states previously cited.

**Biology and phenology.** *Cissia proba* is multivoltine and flies throughout the year (Fig. 7C). Adults are attracted by rotting fruits and other decaying material, and consequently frequently captured in bait traps (AVLF pers. obs.). The species is common in disturbed areas and secondary growth near forest.

**Host plants and immature stages.** Unknown.

**Type material, lectotype designation and taxonomic history.** *Euptychia erigone* *E. proba* Weymer, 1911 was described based on an unstated number of specimens from Peru, and two syntypes were found deposited in the MTD. These syntypes are tagged with unpublished lectotype and paralectotype labels. To fix the identity
of the name, one of the syntypes is designated herein as the lectotype of this taxon; this specimen has the following labels: /proba/ Weym. [handwritten]/ Hillapani [Hillapani Viejo, Cuzco] Peru [handwritten]/ Lectotype Euptychia erigone f. proba Weymer by G. Lamas ‘91/ Stauding[er], & Bang-Haas Dresden. Ankauf 1961/ Staatl. Museum für Tierkunde Dresden/ GART specimen ‘91/ Stauding[er]. & Bang-Haas Dresden. Ankauf 1961/
Remarks. Cissia eous [misidentification]: Argyreuptychia; Paryphthimoides eous ♂ [Illapani Viejo, Cuzco] Peru [handwritten]/ Lectotype proba of the name, one of the syntypes is designated herein sic [Butler, 1867a: 477, pl. 39, fig. 15; syntypes: Euptychia eoüs laMas et al. (1983), but it was correctly transferred to Bolivia. The description of this species agrees with based on a single female [holotype] from Santa Cruz, Bolivia. The description of this species agrees with Euptychia erigone f. proba Weymer, 1911, and FORSTER (1964) correctly treated E. mariameliae as a junior synonym of the latter species.

Examed material. See Electronic Supplement 1.

Cissia eous (Butler, 1867) comb.n. (Figs. 2M–P, 4P–T, 5G,H, 11)

Euptychia eous [sic] Butler, 1867a: 477, pl. 39, fig. 15; syntypes: Brazil, Pará. Lectotype male herein designated: Brazil, Rio de Janeiro; NHMUK (examined); incorrect original spelling (ICZN 1999, Art. 32.5.2). – Butler 1868: 24.


Paryphthimoides bahleri Anken, 1994: 348, figs. 1 (male). 2 (male genitalia); holotype: Brazil, Mato Grosso do Sul, Navirai, Bar ranco do Rio Amambai; RA. syn.n.

Paryphthimoides kiliani Anken, 1999: 108–110, figs. 1–8 (male, female, genitalia); holotype: Brazil, Minas Gerais, Ponte; RA.

Diagnosis. Cissia eous is distinguished from its congener by the (1) DHW with a well-developed, rounded ocellus in C1–Cu, and circled by a well-marked golden ring, (2) VHW with dark brown, ochre and crenulated submedian, median, submarginal and marginal lines, (3) in general, the median line on VHW is pronounced inwards between C1, and the inner margin, and (4) the space between the marginal line and the outer margin is pale yellow ochre on VHW. The dorsal wing phenotype of C. eous is similar to C. proba, with no subapical ocellus on DFW, but C. eous can be differentiated from C. proba by the ocellus on DHW occupying half the space between C1–Cu, and the inner margin on VHW, and by having males with the wings totally brown (while these have a grey-brown aspect in C. phronius comb.n.)

Male genitalia (Fig. 4P–T). Tegumen slightly flattened, laterally subtriangular; uncus arched downward, about 1.5 × length of tegumen, covered by small setae, smoothly dilated at median region, apex curved downwards and truncated in dorsal view; gnathos hook-like (but not too accentuated as in C. pompilia and C. proba), half length of uncus; combination of ventral arm of tegumen and dorsal arm of saccus sinuus; appendix angularis short and curved downwards; anterior projection of saccus developed, cylindrical, longer than gnathos; fultura inferior present; fultura superior absent; valva sub-rectangular covered by long hair-like setae latero-ventrally, and short setae at inner side, costa developed and rectangular, dorsal and ventral margins slightly projected at median region, apex wide and serrated; phallus straight, about same length as valva, cylindrical, anterior region bottlenecked, posterior region about 2 × longer than anterior region with bifid apex in dorsal view, distal opening ventral and longer than proximal opening.

Female genitalia (Fig. 5G,H, 8th tergite rectangular; papilla analis somewhat triangular and covered by long hair-like setae at distal region, apophysis posterior short; lamella antevaginalis fused to lamella postvaginalis with one spiracle located at upper margin of lateral expansions of lamella antevaginalis; lamella postvaginalis orbicular in ventral view; ductus bursae membranous; corpus bursae about same length as ductus bursae, with paired signa latero-ventrally.

Variation. Females are normally larger (FW length: 18–21 mm) than males (FW length: 15–19 mm), and the distance between the median and submarginal lines is wider on the VFW. The number of ocelli on the VFW varies from three to four. The number of pupils in the first, third and fourth ocelli on the VHW can also vary from one to two. The size of the ocelli on the VHW is another variable feature, but even if the second and the fifth ocelli are reduced, the ochre-circled ring and the pupil(s) are always evident, which easily distinguishes C. eous from C. phronius. Seasonal polymorphism is also observed in C. eous (as also reported in Anken 1999), with the ocelli extremely reduced and ventral dark lines paler in the dry season.
Distribution. This species is restricted to South America, occurring in Brazil, Uruguay, Paraguay and Argentina (Fig. 11), and it has been found in several vegetational formations, such as riparian forests, open woods and second-growth forests, to anthropogenic areas (BIEZANKO et al. 1960a; BROWN & MIELKE 1967; ANKEN 1994; PAZ et al. 2013). It is mainly found in lowland areas, but can sometimes be found in mountainside forests (D.R. Dolibaina pers. comm.), at altitudes below 1100 m. In Brazil, *C. eous* is widely distributed in the northern, mid-west and southern regions, with only one old record from Manaus, Amazonas (AURIVILLIUS 1929) that is regarded

as erroneous. *Cissia eous* is sympatric with *C. penelope*, *C. proba* and *C. phronius* in midwestern Brazil, and only with *C. phronius* in all other places where it occurs as mentioned above, where both can also be found flying together.

**Biology and phenology.** *Cissia eous* is commonly found in moist and shady places of several different vegetal formations, including secondary forests and forest edges in coastal Brazil. Adults are attracted to fermented fruits and other decaying materials (Biezanko et al. 1960a; AVLFL pers. obs.), being commonly collected in bait traps (Garcia-Salik et al. 2014). It is multivoltine and flies throughout the year.

**Host plants and immature stages.** Larvae of *Cissia eous* have been recorded feeding on *Poa* L. species (Hayward 1969; Ackery 1988), more specifically in *Poa annua* L. (Biezanko et al. 1957), and also in *Digitaria sanguinalis* (L.) and *Stenotaphrum secundatum* (Walt.) (Biezanko et al. 1960a; Silva et al. 1968).

**Type material, lectotype designation and taxonomic history.** *Euptychia eous* Butler, 1867 was described based on an unstated number of specimens from Pará, Brazil. After exhaustive searches at the NHMUK collection, no syntypes from this type locality were found. Nevertheless, two specimens from Rio de Janeiro, Brazil were found at NHMUK, and they have the typical bluish identification labels of Butler. One of these specimens was chosen as the lectotype of *Euptychia eous* to fix the identity of the name; this specimen has the following labels: /Type/ Rio de Janeiro/ Rio/ E. eous Butler. Monograp[...] B. M. Type No. Rh 3210 /Euptychia eous\* /Butler/ /BMNH(E)/ 1267063; /and two other labels will be added later: /Lectotypus/ Lectotypus *Euptychia eous* Butler, 1867. T. Zacca & B. Huertas det. 2016/. NHMUK.

**Remarks.** According to William T.M. Forbes (in letter – Biezanko et al. 1960a), *Euptychia eous* differs from *E. pollys* in having two larger and darker ocelli (at M1–M2 and Cu1–Cu2). Forbes also regarded *Euptychia punctata* Weymer, 1911 as an extreme form of *E. eous*. However, Freitas et al. (2016) recently demonstrated that *E. punctata* is a valid species, currently placed in *Sepona* & Barbosa, 2016. Comparing *S. punctata* and *E. eous* there are clear differences between these species, such as the smaller size in *C. eous* (16–19 mm), ocelli generally bipupillated (always with only one pupil in *S. punctata*), short gnathos (longer in *S. punctata*) and the narrow and arched downward uncus (straight and wide in *S. punctata*). Weymer (1911) treated *Euptychia zeredatha* Butler, 1869 as a form of *E. eous*, stating that the former species was distinguished from the latter by the small and punctiform ocelli on the ventral surface. Interestingly, Biezanko et al. (1960b) found that *E. eous* and its *E. zeredatha* form were syntopic, being also very common in Rio Grande do Sul, Brazil. *Cissia eous comb.n.* and *E. zeredatha* are distinguished by the less dense scales (giving a translucide aspect) on the wings of the latter (Biezanko et al. 1960b) and by all the ocelli on the underside being very small and punctiform (Weymer 1911). Lamas (2004) raised *Paryphthimoides zeredatha* to species, and considered *P. bahneri* to be its synonym. However, morphological evidence supports *P. zeredatha* as a synonym of *Paryphthimoides pollys* (Zacca et al. in prep.). *Paryphthimoides bahneri* Anken, 1994 was described based on only one specimen [holotype] from Navirai, Mato Grosso do Sul, Brazil. According to Anken (1994), this species is characterized by its reduced wings markings, DHW with two small ocelli in Cu1–Cu2 and Cu2–1A+2A, apex of the valva serrated and cornutal patch located on the vesica. It has been observed that the two former characters are strongly variable among individuals of *C. eous*. The illustration of the genitalia provided by Anken shows strong similarities between his new species and *C. eous*. Although Anken described *P. bahneri* as having a cornutal patch, his illustration is not accurate concerning this structure, especially considering that the cornuti are generally located on the vesica in all *Euptychiina* genera that have this feature. Also, while Anken’s text affirms that the diagnostic character of the phallus of *P. bahneri* is the location of the cornutal patch, in the illustration of the phallus there is an arrow indicating the posterior region of phallus as a diagnostic feature. This arrow could also be interpreted as indicating the “cornuti” to which he refers, or indicating that the posterior region is bifid, which it most likely is. If the latter option is considered, the genitalia are clearly the same as in *C. eous*, for which reason we synonymize *P. bahneri* with *C. eous*, and not with *C. phronius* as suggested by Lamas (2004). In fact, *C. eous*, *C. phronius* and *P. pollys* are phenotypically similar to each other concerning their wing pattern, but their genitalia help reliably identify them.

**Anken** (1999) stated that *P. kiliani* differs from *P. eous* by having less crenulated lines on both ventral wings. Two male paratypes showed a distinct phenotype that Anken treated as a variation of *P. kiliani*. One of these paratypes is illustrated (p. 111, figs. 5, 6), and it is clearly a species of *Hermeuptychia*. One might suspect that Anken very probably choose to compare with the “true” *P. eous*, the genitalia of one of those misidentified paratypes. But curiously, the genitalia of the holotype illustrated in his work (Fig. 7) agrees in all aspects with *C. eous*, and does not support that explanation for Anken’s misinterpretation. As it was not possible to access the types of *P. kiliani*, there is no other option than basing the present taxonomic decision on the Anken’s paper and well-illustrated male holotype. *Paryphthimoides kiliani* was considered a synonym of *P. eous* by Lamas (2004).

**Examined material.** See Electronic Supplement 1.

**Cissia phronius** (Godart, [1824]) comb.n. (Figs. 2Q–T, 4U–Y, 5I, J, 12)

*Satyrus phronius* Godart, [1824]: 466, 496; holotype: Brazil. Neotype here designated: Brazil, Paraná, São José dos Pinhais; DZUP.

*Neonympha phronius*; *Westwood 1851*, in *Dubbeday* 376.


Diagnosis. Compared to all other species of Cissia, C. phronius closely resembles C. eous, from which it can be distinguished by its (1) angular hindwing shape with the outer margin being produced distally at Cu1, (2) males with greasy wings and less dense scales that are partly translucent, and (3) ventral ocelli extremely reduced (sometimes the only elements seen are the silvery pupils).

Male genitalia (Figs. 5U–Y). Tegumen flattened in dorsal view, laterally subtriangular; uncus arched downward, about 1.5 × length of tegumen, covered by small setae, smoothly dilated at median region in dorsal view, apex laterally curved downwards and truncated in dorsal view; gnathos hook-like, half length of uncus; combination of ventral arm of tegumen and dorsal arm of saccus sinuous, appendix angularis short and curved downwards; anterior or projection of saccus developed, cylindrical, with same length of gnathos; fultura superior absent; fultura inferior present; valva sub-rectangular covered by long hair-like setae latero-ventrally, and short ones at inner side, costa developed and rectangular, dorsal margin straight at median region, ventral margin projected at median region, apex wide and serrated; phallos straight, about same length as valva, cylindrical, anterior region bottle-shaped, posterior region about 2 × longer than anterior region with bifid apex in dorsal view, distal opening ventral and longer than proximal opening.

Female genitalia (Figs. 5L,J). 8th tergit rectangular; papilla analis somewhat triangular and covered by long hair-like setae at distal region, apophysis posterior short; lamella antevaginalis fused to lamella postvaginalis, with spiracle located at upper margin of its lateral expansions; lamella postvaginalis orbicular and projected distally at median region; ductus bursae membranous; corpus bursae about ½ smaller than ductus bursae, with paired signa ventrally.

Variation. Males are mostly smaller (14–18 mm) than females (18–21 mm) and their wings are greasy. Intraspecific variation can be noticed in the width of the apex of the valva, which can vary from wide to narrow, similar to the apex of C. proba.

Distribution. This species is restricted to South America, specifically Brazil, Uruguay, Paraguay and Argentina (Fig. 12). Cissia phronius is found in open grasslands, riparian forests, forest edge, and even anthropogenic areas (BROWN & MIELKE 1967; EBERT 1969; MOTTA 2002; MORAIS et al. 2007; BUSTOS 2008; PEIXOTO & BENSON 2008; PINHEIRO et al. 2008; NÚÑEZ-BUSTOS 2010; RITTER et al. 2011; ROSA et al. 2011; BELLAEVER et al. 2012; SILVA et al. 2012; CAPORALE et al. 2015); also in native forests and reforested areas of Araucaria, in mixed ombrophilous forest in Rio Grande do Sul, Brazil (ISERHARD et al. 2010; SANTOS et al. 2011). In Brazil, C. phronius is widely distributed from Goiás to Rio Grande do Sul, in altitudes up to 1500 m, but it is most common in elevations up to 800 m (D.R. Dolibaina pers. comm.). It is sympatric and syntopic with C. eous in a few localities, and sympatric with C. penelope only in Goiás.

Biology, phenoology and behaviour. Males of C. phronius are territorialist and defend their areas by chasing off conspecific rivals (PEIXOTO & BENSON 2008). According to PEIXOTO & BENSON (2009), the increase in the temperature during the dry and wet seasons is directly related to the increase of abundance of C. phronius in field. Cissia phronius is multivoltine and flies year round, and similarly to several other euptychines, this species flies close to the ground. Adults are attracted by rotted fruits and other decaying material, and consequently are often captured in bait traps (PAZ et al. 2014; SPANIOL & MORAIS 2015; AVLF pers. obs.), being one of the most abundant species of Euptychina in inventories (DESSUY & MORAIS 2007; TIIHELE et al. 2014).

Host plants and immature stages. Larvae of Cissia phronius have been recorded feeding on species of Poaceae, such as Poa annua L., Digitaria sanguinalis L., Paspalum distichum L., P. notatum Flüggé and Stenotaphrum secundatum Kuntze (NÚÑEZ-BUSTOS 2010). The only information on immature stages is that the eggs are rounded and yellow (NÚÑEZ-BUSTOS 2010).

Type material, neotype designation and taxonomic history. Satyrus phronius Godart, [1824] was described based on only one specimen [holotype] which had only the wings sent from a non-specific locality in Brazil. The description of this species species (as is the case with many other Euptychina species described by J.B. Godart) is very broad, not precisely defining S. phronius. The only character mentioned by Godart that permits discrimination between S. phronius and the phenotypically similar C. eous is the ventral ocelli not surrounded by yellowish ring, with the last two extreme ringed with black. The other characters mentioned by Godart, such as the 1) DW with the outer area darker, 2) VW yellowish, 3) three transversal dark brown waved lines, 4) outer line convoluted (crenulated) also fit with the description of E. eous. The VFW with a single white pupil, cited by Godart, is an intraspecifically variable feature in this species.
Considering that the wings [holotype] used to describe Satyrus phronius has neither been found at the Muséum national d’Histoire naturelle, Paris, France (O.H.H. Mielke, R. Rougeri, pers. comm.), nor at the NHMUK, a neotype of Satyrus phronius is designated herein; this specimen has the following labels: /Neotypus/ 19.II.1979, S[ão] José dos Pinhais, PR [Paraná], [Brazil], 850 m, Mielke leg/ DZ 28.625/ Neotypus Satyrus phronius Godart, [1824]. T. Zacca det. 2016/. DZUP.

**Examined material.** See Electronic Supplement 1.

**Cissia rubricata** (W.H. Edwards, 1871) comb.n. (Figs. 2U – X, 4Z – AD, 5K, 13)


**Diagnosis.** *Cissia rubricata* comb.n. is easily distinguished from its congeners by the reddish patches on both DFW and VWH.

**Remarks.** *Euptychia rubricata* was described based on at least three specimens, a male and two females, collected by G.W. Belfrage in Waco, Texas, USA (EDWARDS 1871). In his catalogue on the types of Satyrinae butterflies described by E.W. Edwards, M. BROWN (1964) did several nomenclatural acts, including the designation of the neotype of *E. rubricata* based on a male specimen from the original type-locality, currently deposited at the CMNH (for further information see M. Brown 1964: 334, 335). According to MILLER (1976), this species contains five subspecies, *C. rubricata rubricata* comb.n., *C. rubricata smithorum* (Wind, 1946) comb.n., *C. rubricata cheneyorum* (Chermock, 1949) comb.n., *C. rubricata anabaelae* (Miller, 1976) comb.n. and *C. rubricata pseudocoellesophes* (Miller, 1976) comb.n., distributed from southern USA to Honduras (Miller 1976; LOTT & NAHERHAUS 2017) (Fig. 13). A detailed comparative study of the morphology of the subspecies of *C. rubricata*, and information on their respective distribution and phenology, is found in MILLER (1976), but illustration of female genitalia is given herein for the first time (Fig. 5K). Although EDWARDS (1871) indicated that this species was closely related to *Pharneuptychia phares* (Godart, [1824]), based on the similarities of the wing elements pattern, molecular evidence presented herein strongly supports its inclusion in *Cissia* as redefined here.

**Examined material.** See Electronic Supplement 1.

4. Discussion

Both molecular and morphological phylogenies of Euptychiina (MURRAY & PROWELL 2005; PEÑA et al. 2010; MARIN et al. 2017) have shown *Cissia* as defined by previous authors to be a polyphyletic genus. Sampling six species of *Cissia* (*C. penelope*, *C. confusa*, *C. mynnea*, *C. similis*, *C. terrestris* and an unidentified species), MURRAY & PROWELL (2005) showed that *C. penelope* was not related to the other five species then included in the genus, but was more closely related to the genera Megisto, Cyllopsis R. Felder, 1869 and Paramacera Butler, 1868 (all of them with species occurring in the Nearctic region), or even the Neotropical Ypthimoides Forster, 1964. The results obtained by PEÑA et al. (2010) placed *C. phronius* as the sister of *C. penelope*, and both as sister of *C. proba*. This clade, also including Megisto and Paleonympha Butler, 1871, constitutes one of the first branches in the Euptychiina tree. The results obtained by MARIN et al. (2017) also indicate *C. penelope* as sister of *C. pompilia*, and that this clade is closely related to Megisto and Paleonympha. The molecular phylogenetic analysis performed in the present study mostly corroborates the results found in the previous studies. Our results (Fig. 1) show that *Cissia* is more closely related to a clade composed of species of Carminda Dias, 1998, Ypthimoides, Graphita Nakahara, MARIN & BARBOSA, 2016, Stegosatyrus Zacca, MIELKE & PYRCZ, 2013, and a new genus that will be described to contain some of the species removed from *Cissia* (ZACCA et al. in prep.).

Although the genus Atlanteuptychia Freitas, BARBOSA & MIELKE, 2013 seems morphologically similar to *Cissia*, sharing glabrous eyes and a short, hooked gnathos in the male genitalia (see FREITAS et al. 2013: 664, fig. 7), molecular evidence shows that these genera are distantly related (Fig. 1), with Atlanteuptychia more closely related to Paramacera and Cyllopsis, as already indicated by NAKAHARA et al. (2015). Conversely, *C. rubricata* is the only species of *Cissia* that does not have this short and hooked gnathos, with genitalia that are more similar to those found in some species of Magneuptychia Forster 1964 or Paryphthimoides Forster, 1964. According to DNA sequence data, gnathos morphology does not reflect the evolutionary history of extant species of *Cissia*.

Among all the species of *Cissia*, *C. pompilia* stands out by its remarkable seasonal polyphenism that historically has led to the description of three names for the same species. This species occurs in dry, forested regions in Central and South America, with a severe to absolute dry season for most part of the year, and rains falling sporadically. Seasonal polyphenism in satyrine butterflies has been documented in some Brazilian, African and Australian species (BRAKEFIELD & LARSEN 1984; BRAKEFIELD 1987; ROSKAM & BRAKEFIELD 1999; FREITAS 2007; FREITAS et al. 2010; ZACCA et al. 2014). This phenomenon seems related to temperature variation during the wet/dry seasons experienced by the larvae prior to pupation (BRAKEFIELD & REITZMA 1991; BRAKEFIELD & FRANKINO 2009; SIMPSON et al. 2012). In Euptychiina, it seems to directly affect the coloration and size of the wing elements, but their shape and location are not affected by the environmental factors (NIJHOUT 1991).
A detailed review of the immature stages is beyond of the scope of the present study, but it is worth noting that recent studies have indicated that the occurrence of four larval instars formerly considered to be exclusively found in *Cissia* (as suggested by Singer et al. 1983), is also present in other phylogenetically distant euptychine genera (Wahlberg et al. 2009; Peña et al. 2010; Marin et al. 2017), such as *Posttaygetis* Forster, 1964 (Murray 2003), *Taygetis* Hübner, [1819] (Murray 2001; Freitas 2017), *Forsterinia* Gray, 1973 (Freitas & Peña 2006), *Hermeuptychia* Forster, 1964 (Cosmo et al. 2014) and *Pareuptychia* Forster, 1964 (Freitas et al. 2016b,c). The number of larval instars does not seem to be a reliable feature to exclusively define the genera of Euptychiina, especially considering that some of them, such as *Taydeolis* Freitas, 2003, *Magpaneuptychia* and *Moneuptychia* Forster, 1964 may have five larval instars (Freitas 2003, 2007; Kaminski & Freitas 2008; Freitas et al. 2015). On the other hand, morphological characters related to egg, body colour, size and shape of the cephalic horns or scoli of the larvae, and pupae, seems to be more informative at the interspecific level. Future studies should focus on providing detailed comparative morphological studies of the immature stages of *Cissia*, *Magpaneuptychia* and *Paryphthimoides* to verify if the number of larval instars is congruent for each genus or if it is a variable character.

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