

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. erigone* 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, *Ypthimoides*.

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; BENMESBAH 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; NEILD 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; MARÍN et al. 2017). Prior to the present study, *Cissia* comprised 17 species restricted to the Neotropical region (LAMAS 2004; BRÉVIGNON 2005; BENMESBAH 2015): *C. cleophes* (Godman & Salvin, 1889), *C. confusa* (Staudinger, 1887), *C. joyceae* Singer, DeVries & Ehrlich, 1983, *C. labe* (Butler, 1870), *C. lesbia* (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. themis* (Butler, 1867), *C. maripa* Brévignon, 2005 and *C. touloulou* Benmesbah, 2015. The yellowish patch in the submarginal 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 Euptychiina 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 euptychiine 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 Moure, 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 Jagiellonskiego, 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; **ZMHU** – Museum für Naturkunde der Humboldt-Universität, Berlin, Germany; **ZMUC** – Natural History Museum of Denmark, Copenhagen, Denmark; **ZSM** – Zoologische Staatssammlung München, Munich, Germany; **ZUEC** – Museu de Zoologia 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; **VHW** – 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.

Taxa	Locality	Code	COI	GAPDH	RPS5
<i>Cissia eous</i>	Brazil, São Paulo, Jundiá, Serra do Japi	BLU573	MG209743	—	—
<i>Cissia eous</i>	Brazil, Bahia, Reserva de Una	BLU667	MG209748	—	—
<i>Cissia eous</i>	Brazil, São Paulo, Picinguaba, Casa da Farinha	BLU658	MG209744	—	—
<i>Cissia eous</i>	Brazil, Bahia, Vitória da Conquista	BLU664	MG209747	—	—
<i>Cissia eous</i>	Brazil, São Paulo, Cebimar, São Sebastião	BLU618	KU340893	—	—
<i>Cissia eous</i>	Brazil, Bahia, Reserva de Una	BLU660	MG209745	—	—
<i>Cissia eous</i>	Brazil, Minas Gerais, Serra do Cipó, Santana do Riacho	BLU621	KU340896	—	—
<i>Cissia eous</i>	Brazil, São Paulo, Campinas, Unicamp, Mata da Zoologia	YPH0104	KU340856	KU340901	KU340934
<i>Cissia eous</i>	Brazil, Bahia, Reserva de Una	BLU661	MG209746	—	—
<i>Cissia eous</i>	Brazil, Paraná, Foz do Iguaçu	BLU619	KU340894	—	—
<i>Cissia eous</i>	Brazil, Paraná, Foz do Iguaçu	BLU620	KU340895	—	—
<i>Cissia eous</i>	Brazil, Rio Grande do Sul, Alegrete	YPH0422	KU340872	KU340920	KU340955
<i>Cissia phronius</i>	Brazil, São Paulo, Ribeirão Grande, Trilha do Capinzal	BLU378	KU340890	—	—
<i>Cissia phronius</i>	Brazil, São Paulo, Ribeirão Grande, Trilha do Capinzal	BLU380	KU340892	—	—
<i>Cissia phronius</i>	Brazil, São Paulo, Atibaia	NW126-7	DQ338807	GU205973	GU206034
<i>Cissia phronius</i>	Brazil, São Paulo, Ribeirão Grande, Trilha do Capinzal	BLU379	KU340891	—	—
<i>Cissia penelope</i>	Peru, Junin, La Solitaria-Quebrada Siete Jeringas	CP07-58	GU205833	GU205945	GU206005
<i>Cissia penelope</i>	Ecuador, Napo	DNA99-028	AY508530	—	—
<i>Cissia rubricata chenevorum</i>	USA, Arizona, Southwestern Research Station, Portal	LEP-19315	MG209757	MG546314	MG546327
<i>Cissia proba</i>	Ecuador, Zamora-Chinchi, E of Zumba, km 2.6 El Pite-Río Mayo rd.	KW-140622-01	MG209751	MG546309	MG546319
<i>Cissia proba</i>	Peru, Madre de Dios, Tambopata Research Center	CP01-30	GQ864751	GQ864945	GQ865416
<i>Cissia pompilia</i>	Costa Rica, Area de Conservacion Guanacaste, Sector San Cristobal, Estacion San Gerardo	07-SRNP-100013	JQ573901	—	—
<i>Cissia pompilia</i>	Mexico, Yucatan, Valladolid, carretera a Xocen	MAL-02577	GU659737	—	—
<i>Carminda paeon</i>	Brazil, São Paulo	B-17-41	DQ338801	—	—
<i>Carminda paeon</i>	Brazil, São Paulo, Ribeirão das Pedras	NW126-11	GQ864792	GQ865004	GQ865473
<i>Carminda paeon</i>	Brazil, São Paulo, Jundiá, Serra do Japi	BLU324	MG209740	—	—
<i>Carminda paeon</i>	Brazil, São Paulo, Jundiá, Serra do Japi	BLU325	MG209741	—	—
<i>Carminda paeon</i>	Brazil, São Paulo, Jundiá, Serra do Japi	BLU326	MG209742	—	—
<i>Carminda paeon</i>	Brazil, Paraná, Foz do Iguaçu, Trilha Poço Preto	YPH0357	MG209761	MG546318	MG546323
<i>Carminda umuarama</i>	Brazil, Minas Gerais, Pq. Itatiaia, Itamonte	YPH0437	KU340873	KU340921	KU340956
<i>Carminda umuarama</i>	Brazil, Espírito Santo, Caparaó	YPH0459	KU340874	KU340922	KU340957
" <i>Cissia</i> " <i>labe</i> (= sp. Janzen13)	Costa Rica, Area de Conservacion Guanacaste, Sector Pitilla, Sendero Nacho	11-SRNP-30733	JQ526864	—	—
" <i>Cissia</i> " <i>labe</i>	Ecuador, Carchi, Lita, ridge east of Río Baboso	KW-140721-04	MG209753	MG546311	MG546325
" <i>Cissia</i> " <i>palladia</i>	Brazil, São Paulo, Campinas, Unicamp	MGCL-LOAN-191	MG209759	MG546316	MG546328
<i>Carminda griseldis</i>	Brazil, Mato Grosso, Extrema	NW127-17	GU205853	GU205965	GU206025
<i>Carminda griseldis</i>	Brazil, São Paulo, Alto do Capivari, Campos do Jordão	YPH0394	KU340869	KU340917	KU340952
<i>Carminda griseldis</i>	Brazil, Espírito Santo, Caparaó	YPH0462	KU340875	KU340923	KU340958
<i>Yphthimoides pacta</i>	Brazil, Mato Grosso, Diamantino	MGCL-LOAN-355	MG209760	MG546317	MG546322
<i>Graphita griphe</i>	Colombia, Cali, San Antonio	YPH0361	KU340866	KU340915	KU340948
<i>Graphita griphe</i>	Colombia, Cali, San Antonio	YPH0362	KU340867	—	KU340949
<i>Stegosatyryus ocelloides</i>	Brazil, Minas Gerais, Serra do Cipó	YPH0527	KU340879	—	KU340966
<i>Stegosatyryus ocelloides</i>	Brazil, Minas Gerais, Serra do Cipó	YPH0543	KU340883	KU340928	KU340970
<i>Stegosatyryus ocelloides</i>	Brazil, Minas Gerais, Serra do Cipó	YPH0530	KU340880	KU340925	KU340967
<i>Stegosatyryus periphias</i>	Argentina, Buenos Aires Province, Ituzaingó	LEP-18718	MG209756	MG546313	MG546326
<i>Megisto cymela</i>	USA, Rhode Island, Valley Falls	CP21-04	GQ357208	GQ357439	GQ357569
<i>Paleonympha opalina</i>	Taiwan, Pingtung County, Hsiaokuehu, Wutai Shiang	EW25-21	DQ338880	GQ865010	GQ865479
" <i>Cissia</i> " <i>myncea</i>	Peru, Madre de Dios	DNA99-009	AY508556	—	—
" <i>Cissia</i> " <i>myncea</i>	Brazil, São Paulo, Ubatuba, Picinguaba	NW108-6	DQ338581	GQ357427	GQ357556
" <i>Cissia</i> " <i>myncea</i>	Peru, Madre de Dios, Tambopata Research Center	CP01-58	GU205832	GU205944	GU206004
" <i>Cissia</i> " <i>confusa</i>	Costa Rica, Area de Conservacion Guanacaste, Sector Pitilla, Sendero Tierra Blanca	11-SRNP-30020 (DHJ02)	JQ526869	—	—
" <i>Cissia</i> " <i>confusa</i>		DNA99-082	AY508533	—	—
<i>Magneuptychia agnata</i>	Ecuador, Esmeraldas, km 42 San Lorenzo-Lita rd., Finca Cypris	LEP-15103	MG209755	MG546312	MG546321
<i>Magneuptychia libye</i>	Ecuador, Zamora-Chinchi, km 6 Los Encuentros-El Pangú	LEP-14777	MG209754	MF192728	MG546320
" <i>Cissia</i> " <i>similis</i>	Costa Rica, Area de Conservacion Guanacaste, Sector Horizontes, Laguna Bejuco	07-SRNP-14171	JQ538434	—	—

Table 1 continued.

Taxa	Locality	Code	COI	GAPDH	RPS5
<i>Cissia similis</i>		DNA97-014	AY508529	—	—
<i>Hermeuptychia hermes</i> (= sp. Janzen04)	Costa Rica, Area de Conservacion Guanacaste, Sector Mundo Nuevo, Quebrada Tibio Perla	07-SRNP-55888	JQ535699	—	—
<i>Cissia terrestris</i>	Panama, Isla Barro Colorado	YB-BCI2873	HM406607	—	—
<i>Cissia pseudoconfusa</i>	Mexico, Quintana Roo, Ejido X-maben: camino a Noh-cancab	MAL-02559	HQ990161	—	—
<i>Cissia pseudoconfusa</i>	Panama, Isla Barro Colorado	YB-BCI11849	HM416553	—	—
<i>Amphidecta calliomma</i>	Peru, Madre de Dios, Los Amigos Biological Station	LEP-19579	MG209758	MG546315	MG546329
<i>Atlanteuptychia ernestina</i>	Brazil, São Paulo, Jundiá, Serra do Japi	EE002	MG209750	MG546308	—
<i>Atlanteuptychia ernestina</i>	Brazil, São Paulo, Serra do Japi	YPH0191	KP994863	KU340904	KU340937
<i>Atlanteuptychia ernestina</i>	Brazil, São Paulo, Jundiá, Serra do Japi	EE001	MG209749	MG546307	—
<i>Paramacera xicaque</i>	Brazil, Distrito Federal, Magdalena Contreras, Cañada de los Dinamos	CP15-08	GQ357210	GQ357442	GQ357571
<i>Cyllopsis pertepida</i>	Mexico, Guanajuato. Mpio. San Felipe/Leon 8 km NE El Zuaco	NW165-3	GQ357204	GQ357428	GQ357557
<i>Euptychia westwoodi</i>	Ecuador, Esmeraldas, km 17 San Lorenzo-Ibarra rd., San Francisco ridge	KW-140718-03	MG209752	MG546310	MG546324

PIERCE (1909), “fultura superior” and “fultura 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 as “aedeagus”, but here we use the term “phallus”, since Agathiphagidae are the only Lepidoptera with a true aedeagus (see KRISTENSEN 1979, 2003). The nomenclature of the wing venation mostly follows COMSTOCK & NEEDHAM (1898–99) and COMSTOCK (1918), and for broad regions of the wing we follow NEILD (1996). The extra band located at the submarginal region on both ventral wings between the median and submarginal lines is called “umbra”, as proposed by SCHWANWITSCH (1924), and followed 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, Düsseldorf, 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 the nuclear genes GAPDH and RPS5, which have been shown to be useful in phylogenetic studies (WAHLBERG & WHEAT 2008). Primers and PCR reaction conditions follows NAKAHARA et al. (2015, 2017) and SILVA-BRANDÃO et al. (2005). All sequences were aligned using MAFFT v. 7 (KATO & 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 (PEÑA et al. 2006, 2010)

Table 2. Mean genetic distances among the species of *Cissia*.

	1	2	3	4	5
1 <i>Cissia rubricata</i>					
2 <i>Cissia proba</i>	13.4				
3 <i>Cissia pompilia</i>	11.7	7.0			
4 <i>Cissia penelope</i>	13.6	14.8	15.5		
5 <i>Cissia phronius</i>	12.0	11.4	13.0	10.3	
6 <i>Cissia eous</i>	10.3	9.3	8.0	11.0	6.4

and on our unpublished data from additional euptychiine species, we chose sixteen species as outgroups, and *Euptychia 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 10×10^6 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 3. Pairwise genetic distances among the species of *Cissia*.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	
1 <i>Cissia rubricata</i> LEP19315																						
2 <i>Cissia proba</i> CP01-30	13.4																					
3 <i>Cissia pompilia</i> 07-SRNP-100013	11.1	6.3																				
4 <i>Cissia pompilia</i> MAL-02577	12.3	7.7	1.2																			
5 <i>Cissia penelope</i> DNA99-028	12.9	14.9	14.9	15.8																		
6 <i>Cissia penelope</i> CP07-58	14.4	14.6	15.2	16.1	3.5																	
7 <i>Cissia phronius</i> NW126-7	12.0	11.4	12.3	13.8	10.1	10.6																
8 <i>Cissia phronius</i> BLU378	12.0	11.4	12.3	13.8	10.1	10.6	0.0															
9 <i>Cissia phronius</i> BLU379	12.0	11.4	12.3	13.8	10.1	10.6	0.0	0.0														
10 <i>Cissia phronius</i> BLU380	12.0	11.4	12.3	13.8	10.1	10.6	0.0	0.0	0.0													
11 <i>Cissia eous</i> YPH-0422	10.3	9.8	7.3	8.7	11.4	11.2	6.9	6.9	6.9	6.9												
12 <i>Cissia eous</i> BLU619	10.3	9.8	7.3	8.7	11.1	10.9	6.6	6.6	6.6	6.6	0.2											
13 <i>Cissia eous</i> BLU620	10.3	9.8	7.3	8.7	11.1	10.9	6.6	6.6	6.6	6.6	0.2	0.0										
14 <i>Cissia eous</i> BLU573	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7									
15 <i>Cissia eous</i> BLU618	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7	0.0								
16 <i>Cissia eous</i> BLU621	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7	0.0	0.0							
17 <i>Cissia eous</i> BLU658	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7	0.0	0.0	0.0						
18 <i>Cissia eous</i> BLU660	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7	0.0	0.0	0.0	0.0					
19 <i>Cissia eous</i> BLU661	10.0	8.9	7.6	8.9	10.9	10.6	6.0	6.0	6.0	6.0	1.7	2.0	2.0	0.2	0.2	0.2	0.2	0.2				
20 <i>Cissia eous</i> BLU664	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.2		
21 <i>Cissia eous</i> BLU667	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	
22 <i>Cissia eous</i> YPH-0104	10.3	9.2	7.3	8.7	11.1	10.9	6.3	6.3	6.3	6.3	1.5	1.7	1.7	0.0	0.0	0.0	0.0	0.0	0.0	0.2	0.0	0.0

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).

Ten of the remaining 13 species formerly placed in *Cissia* (LAMAS 2004; BRÉVIGON 2005; BENMESBAH 2015) are scattered more distantly across the Euptychiina phylogeny (see Fig. 1 – collapsed clades labelled as “Taxa removed from *Cissia*” and “*Magneuptychia* + taxa removed from *Cissia*”), including “*Cissia*” *confusa* (Staudinger, 1887), “*C.*” *labe* (Butler, 1870), “*C.*” *lesbia* (Staudinger, [1886]), “*C.*” *myncea* (Cramer, 1780), “*C.*” *palladia* (Butler, 1867), “*C.*” *pseudoconfusa* Singer, DeVries & Ehrlich, 1983, “*C.*” *similis* (Butler, 1867), “*C.*” *terrestris* (Butler, 1867), “*C.*” *themis* (Butler, 1867) and “*C.*” *maripa* Brévignon, 2005. Three former *Cissia* species, “*C.*” *cleophes* (Godman & Salvin, 1889), “*C.*” *joyceae* Singer, DeVries & Ehrlich, 1983 and “*C.*” *touloulou* Benmesbah, 2015 have yet to be included in our molecular dataset (M.

Espeland unpubl. data), although genitalic morphology is clearly distinct from all members of the redefined *Cissia*.

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

Cissia Doubleday, 1848: 33; type-species *Papilio clarissa* Cramer, 1775, by monotypy; a synonym of *Papilio penelope* Fabricius, 1775. – HEMMING 1967: 116. – MILLER 1968: 92; **syn.** *Argyreuptychia*. – SINGER et al. 1983: 101. – LAMAS 2004: 218; **syn.:** *Vareuptychia*. – PEÑA et al. 2006: 31.

Argyreuptychia Forster, 1964: 123; type-species *Papilio penelope* Fabricius, 1775, by original designation.

Diagnosis. Species of *Cissia* are characterized by the following set of characters: (1) glabrous eyes, (2) bipupillated ocellus in Cu₁-Cu₂ in DHW, (3) silvery ocelli in M₂-M₃ and M₃-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)

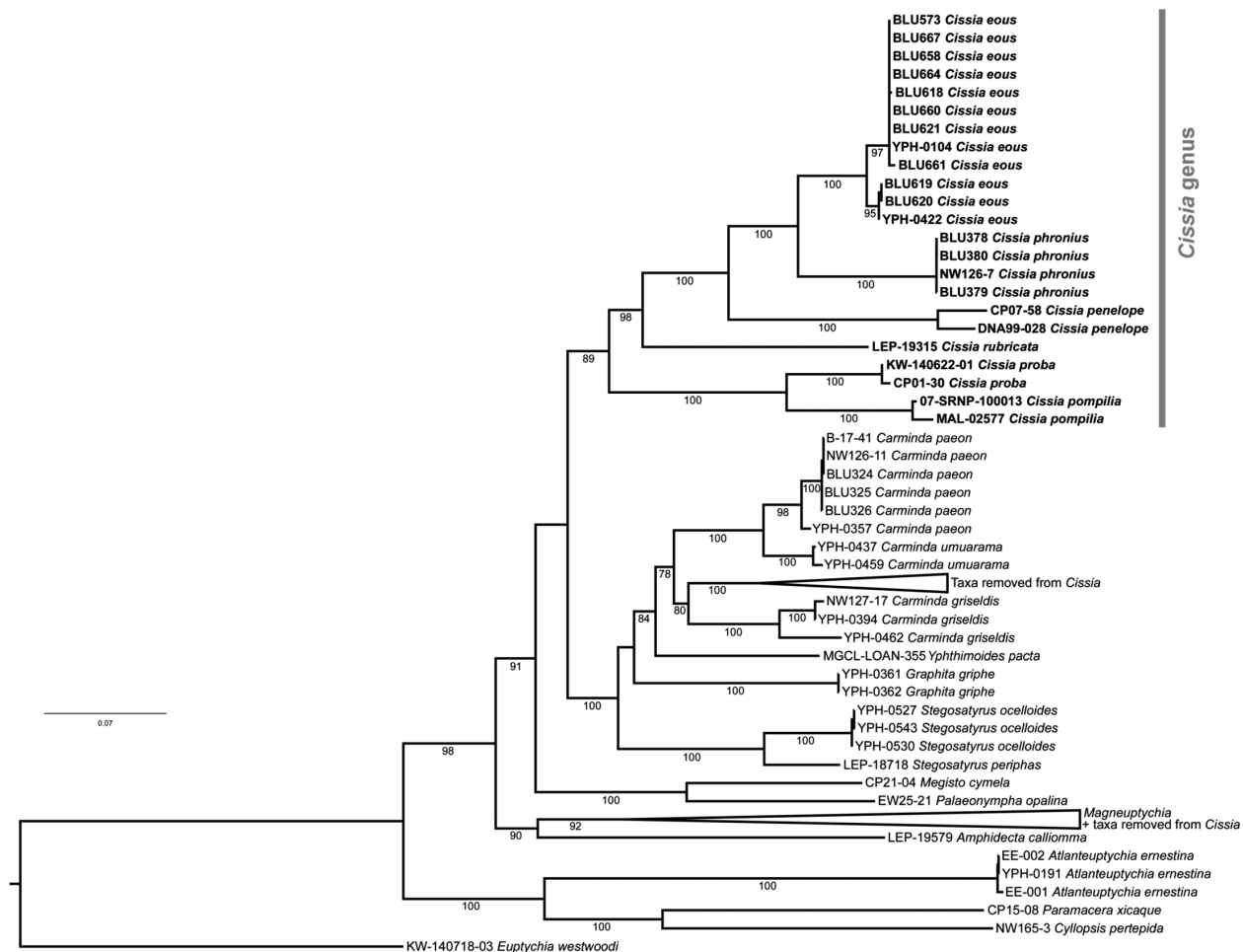


Fig. 1. Phylogeny of the genus *Cissia* based on the Maximum Likelihood analysis of combined COI, GAPDH and RpS5 gene sequences. Bootstrap values < 75 not shown.

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 *Hermeuptychia* 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 medii, interna anticarum 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



Fig. 2. Species of *Cissia*. **A–D:** *C. penelope*: **A** – Male, dorsal; **B** – Male, ventral; **C** – Female, dorsal; **D** – Female, ventral. **E–H:** *C. pompilia*: **E** – Male, dorsal; **F** – Male, ventral; **G** – Female, dorsal; **H** – Female, ventral. **I–L:** *C. proba*: **I** – Male, dorsal; **J** – Male, ventral; **K** – Female, dorsal; **L** – Female, ventral. **M–P:** *C. eous*: **M** – Male, dorsal; **N** – Male, ventral; **O** – Female, dorsal; **P** – Female, ventral. **Q–T:** *C. phronius*: **Q** – Neotype male, dorsal; **R** – Neotype male, ventral; **S** – Female, dorsal; **T** – Female, ventral. **U–X:** *C. rubricata rubricata*: **U** – Male, dorsal; **V** – Male, ventral; **W** – Female, dorsal; **X** – Female, ventral. — Arrows indicate diagnostic characters of the wing patterns to the species (see text). Scale = 1 cm.

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. terrestris*, *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) divided 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 comprised by 17 species, including *E. labe*, *E. pieria*, *E. terrestris* 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 primaries 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 referring them all to *Euptychia*”. Still in this same work, Weymer proposed the “*ocypete* group” comprising 36 species, some of them not cited in BUTLER (1877), without 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. pytheus*, *A. moneta* Weymer, 1911 and *A. lesbia* Staudinger, [1886]), and stated that the genus was characterized by its “small size when compared to *Megeuptychia* Forster, 1964 and *Magneuptychia* Forster, 1964, silvery eyespots in M_2 - M_3 and M_3 - Cu_1 on ventral hindwings, slender uncus, and short and narrow aedeagus [= phallus]” (FORSTER 1964: 123). In contrast, *Vareuptychia*, containing *V. similis* and *V. usitata*, was erected based on “differences in the male genitalia structures when compared to the closely related genus *Argyreuptychia* and the completely different pattern and coloration of the wing underside, with straighter bands” (FORSTER 1964: 125).

Although FORSTER (1964) did not provide a detailed description of the male genitalia, when comparing his illustrations of *V. similis* and *V. usitata* (p. 125, figs. 145, 146), the only character that is shared by both species is

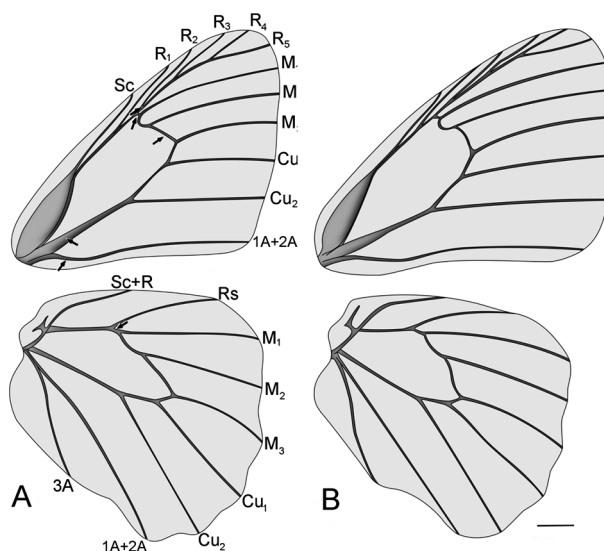


Fig. 3. Wing venation of *Cissia penelope*. **A** – Male; **B** – Female. — **Abbreviations:** Sc – subcostal vein; R – radial vein; Rs – sector radial vein; M – median vein; Cu – cubital vein; A – anal vein. — Scale = 1 cm.

the presence of cornutal patches on the phallus. The differences 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 (FREITAS 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 Euptychiina genera, with no clear distinguishing diagnostic characters.

However, two important points must be considered here: 1) by studying only Bolivian specimens, Forster ignored 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 objective synonym of *Cissia*, later followed by SINGER et al. (1983) and LAMAS (2004). When describing the diagnostic characters of Euptychiini (= Euptychiina), 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 review of *Cissia* and proposed the most recent systematic arrangement of this genus. Considering only species from Costa Rica and Trinidad, the authors concluded that *Cissia* 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 features of immatures, which led the authors to subdivided the genus into four subgroups: 1) “*labe* subgroup” – comprising *C. labe*, *C. palladia* and *C. penelope*; 2) “*confusa* subgroup” – *C. myncea*, *C. confusa* and *C. pseudoconfusa*; 3) “*gomezi* subgroup” – only *C. gomezi* Singer,

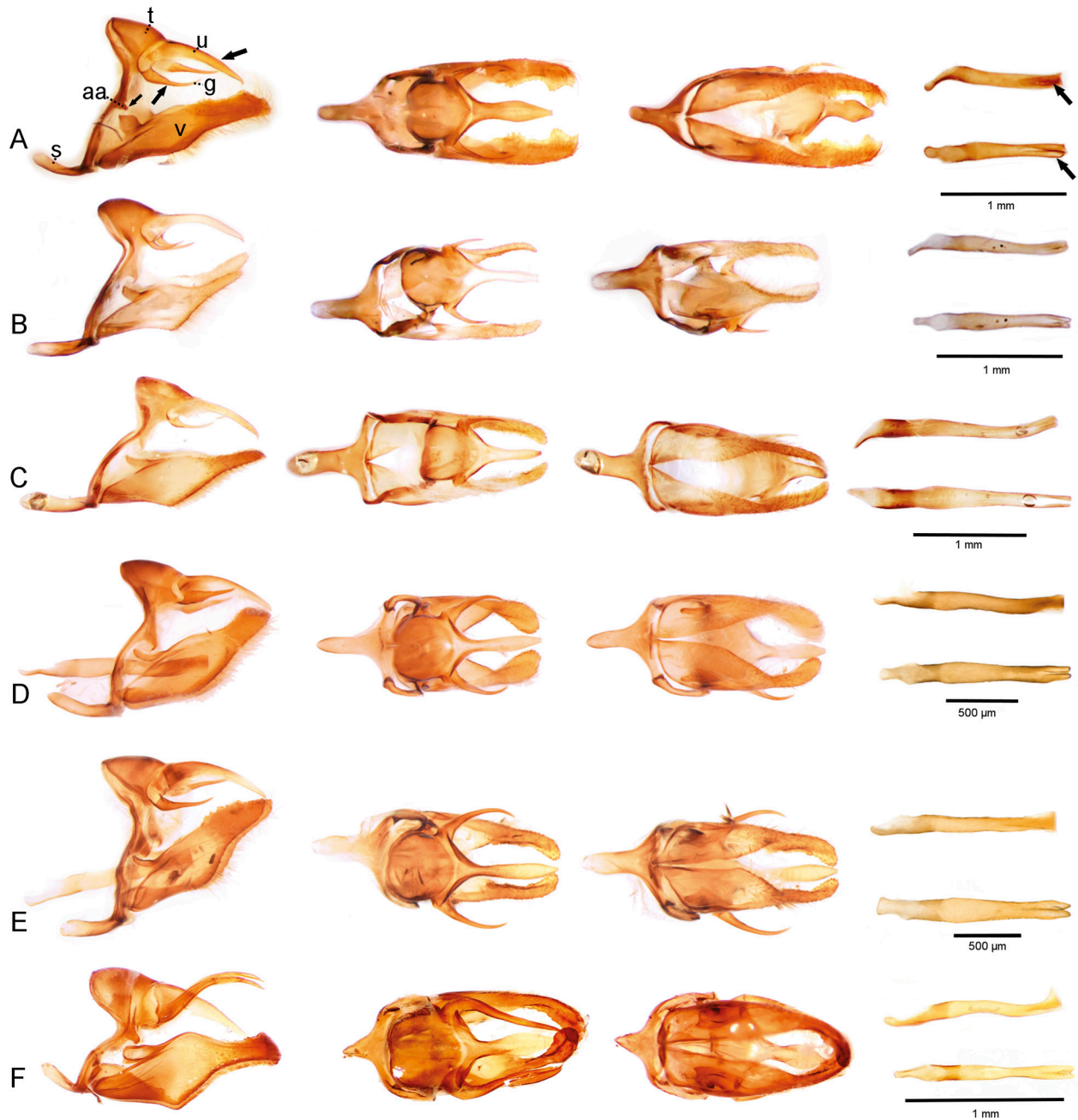


Fig. 4. Male genitalia of species of *Cissia*. **A:** *C. penelope* (from left to right): lateral, dorsal, ventral, phallus lateral, phallus dorsal. **B:** *C. pompilia*: lateral, dorsal, ventral, phallus lateral, phallus dorsal. **C:** *C. proba*: lateral, dorsal, ventral, phallus lateral, phallus dorsal. **D:** *C. eous*: lateral, dorsal, ventral, phallus lateral, phallus dorsal. **E:** *C. phronius*: lateral, dorsal, ventral, phallus lateral, phallus dorsal. **F:** *C. rubricata*: lateral, dorsal, ventral, phallus lateral, phallus dorsal. — **Abbreviations:** t – tegumen; u – uncus; g – gnathos; aa – appendix angularis; s – saccus; v – valvae. — Arrows indicate diagnostic characters to the genus (see text).

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.

D’ABRERA (1988) placed most species of Euptychiina in the genus *Euptychia*, including some species placed in *Cissia* by LAMAS (2004), such as: *E. cleophes*, *E. palladia*, *E. labe*, *E. confusa*, *E. myncea*, *E. terrestris*, *E. lesbia*, *E. penelope*, *E. usitata* and *E. similis*. LAMAS

(2004) followed MILLER’S (1968) and SINGER et al.’s (1983) concept of *Cissia*, but also included eight more species: *C. cleophes*, *C. lesbia*, *C. moneta*, *C. pompilia*, *C. proba*, *C. similis*, *C. terrestris* and *C. themis*. In addition, LAMAS (2004) transferred *C. agnata*, *C. drymo* and *C. gomezii* to *Magneuptychia* Forster, 1964, and treated *Cissia ucumariensis* Andrade, 1991 as a junior synonym of *Euptychoides griphe* (C. Felder & R. Felder, 1867) (= *Graphita griphe*). This classification of LAMAS (2004) is the one currently used, with *Cissia* comprising 15 species. Two Amazonian species from French Guiana were

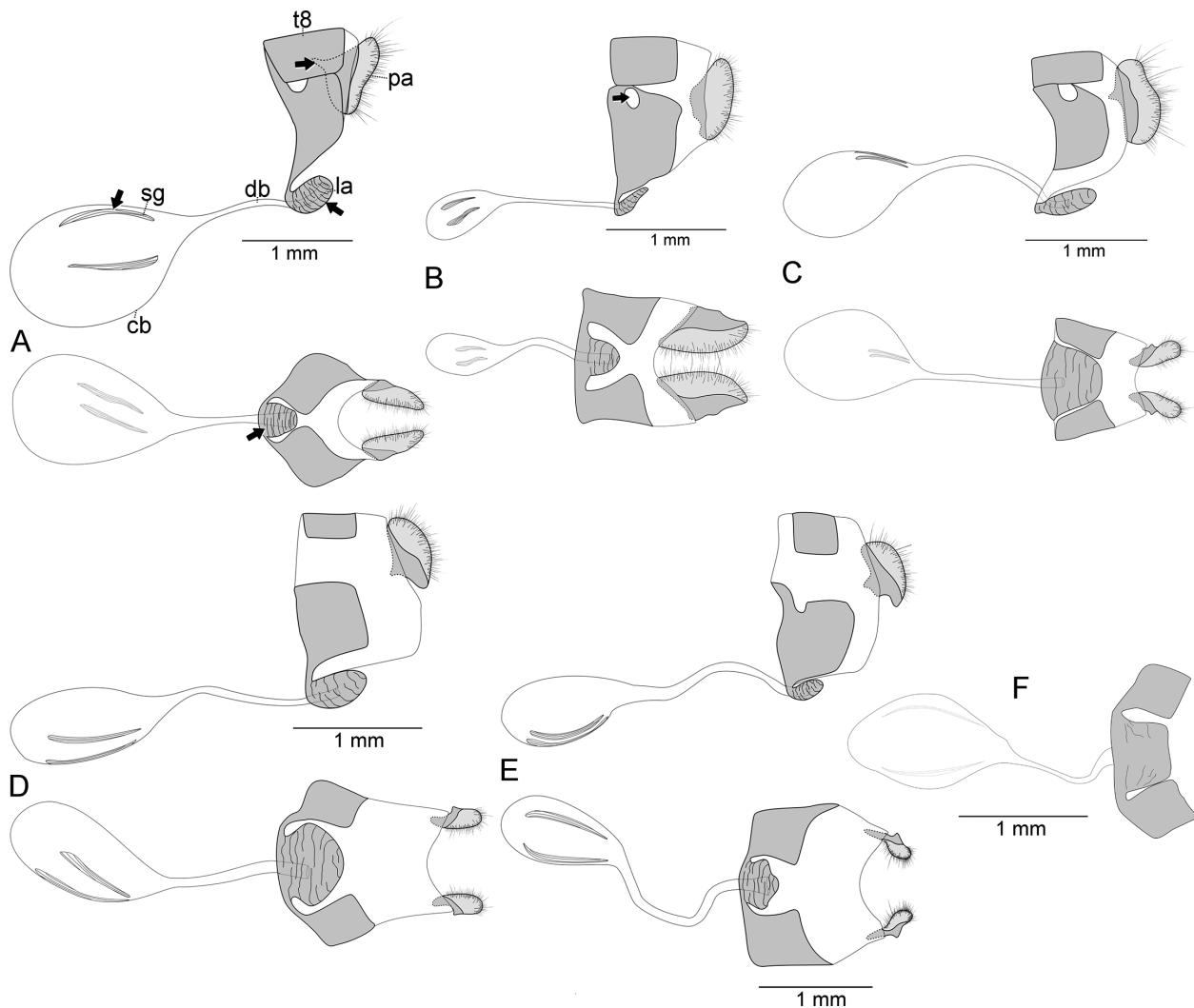


Fig. 5. Female genitalia of species of *Cissia*. **A:** *C. penelope*: lateral (above), ventral (below). **B:** *C. pompilia*: lateral (above), ventral (below). **C:** *C. proba*: lateral (above), ventral (below). **D:** *C. eous*: lateral (above), ventral (below). **E:** *C. phronius*: lateral (left), ventral (right). **F:** *C. rubricata*: ventral. — **Abbreviations:** t8 – 8th tergum; pa – papilla analis; la – lamellae antevaginalis; db – ductus bursae; cb – corpus bursae; sg – signa. — Arrows indicate diagnostic characters to the genus (see text).

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

Taxonomy. The genus *Cissia* is redefined here to include six species: *C. penelope*, *C. pompilia*, *C. proba*, *C. eous* **comb.n.**, *C. phronius* **comb.n.** and *C. rubricata* **comb.n.**. Based on molecular data, the genus is a member of the 'Megisto clade' as defined by PEÑA et al. (2010), whereas morphological data failed to recover *Cissia* within this clade, but placed it as a nearby branch (MARÍN et al. 2017). The *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 *Carminda*, *Graphita*, *Stegosatyrus*, *Megisto*, *Paleonympha* and several former *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 *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 *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 *Cissia* (LAMAS 2004; BRÉVIGNON 2005; BENMESBAH 2015) include: "*C.*" *confusa*, "*C.*" *labe*, "*C.*" *lesbia*, "*C.*" *myncea*, "*C.*" *palladia*, "*C.*" *pseudoconfusa*, "*C.*" *similis*, "*C.*" *terrestris*, "*C.*" *themis*, "*C.*" *maripa*, "*C.*" *cleophes*, "*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 *Paryphthimoides* 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 binomials, 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

Argyreuptychia Forster, 1964

Cissia penelope (Fabricius, 1775)

- *Papilio clarissa* Cramer, 1782

- *Euptychia moneta* Weymer, 1911 **syn.n.**

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

- *Euptychia usitata* Butler, 1867

- *Euptychia usitata pieria* Butler, 1867

- *Euptychia austera* Butler, 1867 **syn.n.**

- *Euptychia usitata pompilia* C. Felder & R. Felder, 1867

- *Neonympha thelete* Snellen, 1887

- *Euptychia usitata thelete* Weymer, 1911

Cissia proba (Weymer, 1911)

Cissia eous (Butler, 1867) **comb.n.**

- *Paryphthimoides bahneri* Anken, 1994 **syn.n.**

- *Paryphthimoides kiliani* Anken, 1999 **syn.n.**

Cissia phronius (Godart, [1824]) **comb.n.**

Cissia rubricata (W.H. Edwards, 1871) **comb.n.**

Cissia rubricata rubricata (W.H. Edwards, 1871) **comb.n.**

Cissia rubricata smithorum (Wind, 1946) **comb.n.**

Cissia rubricata cheneyorum (R. Chermock, 1949) **comb.n.**

Cissia rubricata anabelae (L. Miller, 1976) **comb.n.**

Cissia rubricata pseudocleophes (L. Miller, 1976) **comb.n.**

Key to species of *Cissia*

- 1 DFW and DHW with orange patches *C. rubricata* (Fig. 2U–X)
- 1' DFW and DHW totally brown 2
- 2 VW with well-marked dark brown scattered dots at the submarginal region (Fig. 2A); VHW with one developed incomplete silvery ocellus in Rs-M₁ (Fig. 2B) *C. penelope* (Fig. 2A–D)
- 2' VW without dark brown scattered dots (or, if present, just a few and faded); VHW with one complete silvery ocellus in Rs-M₁ (or, if incomplete, is always small) 3
- 3 VW with submedian and median lines straight 4
- 3' VW with submedian and median lines crenulated ... 5
- 4 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)
- 4' VW with umbra darker than the ground colour; VW with a wide median line (approximately 1 mm) *C. proba* (Fig. 2I–L)

- 5 DHW with developed and well-marked ocellus at Cu₁-Cu₂ (Fig. 2M); VHW with outer margin crenulated along its entire length; VHW with developed ocelli at M₁-M₂ and Cu₁-Cu₂ (in general, with a well-marked ochre ocellar ring) *C. eous* (Fig. 2M–P)
- 5' DHW with reduced or absent ocellus at Cu₁-Cu₂; VHW with outer margin slightly crenulated and pronounced at Cu₁; VHW with reduced ocelli (in general, noticed only by the silvery pupils and the pale ocellar ring) *C. phronius* (Fig. 2Q–T)

Cissia penelope (Fabricius, 1775)

(Figs. 2A–D, 3A,B, 4A–E, 5A,B, 8)

Papilio penelope Fabricius, 1775: 493; syntype: America. – FABRICIUS 1793: 96. – SINGER et al. 1983: 110, fig. 4D; neotype: America (photograph examined); ZMUC. – MILLER 1968: 93. – ZIMSEN 1964: 515.

Papilio clarissa Cramer, 1782: pl. 293, figs. D, E; syntype: Suriname. – SINGER et al. 1983: 110; neotype: Suriname; NHMUK (examined); **syn. P. penelope**. – MILLER 1968: 92. – LAMAS 2004: 218.

Euptychia clarissa; HÜBNER [1819]: 54. – WESTWOOD 1851 *in* DOUBLEDAY: 373. – BUTLER 1867a: 462. – BUTLER 1868: 16.

Satyrus penelope; GODART [1823]: 489.

Cissia clarissa; DOUBLEDAY 1848: 33.

Neonympha clarissa; HERRICH-SCHÄFFER 1864: 59.

Euptychia penelope; KIRBY 1871: 48. – MÖSCHLER 1877: 323. – BUTLER 1877: 118. – KIRBY 1879: 134. – SHARPE 1890: 568. – KAYE 1904: 179. – WEYMER 1911: 200, pl. 47b. – AURIVILLIUS 1929: 158. – GAEDE 1931: 459. – BARCANT 1970: 143, 161, pl. 13, fig. 10 (male). – WESLEY & EMMEL 1975: 24, 30. – D'ABRERA 1988: 772 (male). – EMMEL & AUSTIN 1990: 10. – VARGAS-ZAPATA et al. 2011: 51.

Argyreuptychia penelope; FORSTER 1964: 123. – LEWIS 1973: pl. 54, fig. 2.

Cissia penelope; MILLER 1968: 123. – SINGER et al. 1983: 110. – ACKERY 1988: 114, table 9. – MIELKE & CASAGRANDE 1992: 181. – SINGER & EHRLICH 1993: 252. – LAMAS 1994a: 165. – BROWN & HUTCHINGS 1997: 106. – LAMAS [1997b]: 65. – MIELKE & CASAGRANDE 1998: 468. – WOOD & GILLMAN 1998: 609, 613. – T. RACHELI & L. RACHELI 1998: 111. – DEVRIES & WALLA 1999: 347. – RAMOS 2000: 40. – T. RACHELI & L. RACHELI 2001: 213. – BROWN & FREITAS 2002: pl. 15. – LAMAS 2003: appendix 3, 203. – LANDE et al. 2003: 153. – LAMAS 2004: 218. – MURRAY & PROWELL 2005: 69. – BROWN et al. 2007 (appendix): 10. – PINHEIRO & EMERY 2007: 72. – BECCALONI et al. 2008: 329. – BRÉVIGNON 2008: 72. – KAMINSKI & FREITAS 2008: 171. – BARLOW et al. 2009: 174. – MARIN & URIBE 2009: 25. – MARIN et al. 2009: 242. – MIELKE et al. 2010: 289. – PEÑA et al. 2010: 246. – SALAZAR et al. 2011: 166. – WILLMOTT et al. 2011: 2, fig. 15 (male). – CASAGRANDE et al. 2012: 25. – MONTERO & ORTIZ 2013: 58. – COCK 2014: 11. – GARWOOD 2014: 24, figs. 253, 254. – GARWOOD 2015: 57, figs. 727–729. – GARWOOD & JARAMILLO 2016: 107, figs. 1219–1222.

Euptychia moneta Weymer, 1911: 200, pl. 47b; neotype herein designated: [French Guiana] Cayenne; NHMUK; **syn.n.** – GAEDE 1931: 455.

Euptychia maepius [misidentification]; LEWIS 1973: pl. 58, fig. 10. *Cissia moneta*; LAMAS 2004: 218.

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

submarginal region between R_5 - Cu_2 on VFW and Rs - Cu_2 on the VHW. Additionally, the VHW has three silvery incomplete ocelli, each one in Rs - M_1 , M_2 - M_3 and M_3 - Cu_1 . 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 $2 \times$ 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, $\frac{1}{2}$ – $\frac{2}{3} \times$ 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 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 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 $2 \times$ longer than anterior region, with bifid apex in dorsal view, distal opening ventral and longer than proximal opening.

Female genitalia (Fig. 4A,B). 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 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 pupil 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 Cu_2 -1A+2A, close to the inner margin. Sometimes, the three silvery incomplete ocelli located in R_5 - M_1 , M_2 - M_3 and M_3 - Cu_1 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, Surinam, French Guiana and Brazil, plus the islands of Curaçao and Trinidad, mainly in association with Amazon and Atlantic forests, but being also found in dry forests in Central America and midwestern 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), Junín, 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 NHMUK – voucher number BMNH(E) 1421881) and might have come from western Venezuela or Curaçao, 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.

Biology 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 around. 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 & Tonder Collection [handwritten]/ Mus. Leh. e T. L. [handwritten]/ NEOTYPE *Papilio penelope* Fabricius,

1775, Singer et al., 1983: 110 [red label]/ photographed [handwritten] R. I. Vane-Wright. 197/8/.

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 treated it in *Satyrus* 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]/ Linnep. Surin[ame]. [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, MTD 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 Ramons [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. Benmesbah pers. comm.), and no inventories have yet documented this species (e.g.: BRÉVIGNON 2005; BRÉVIGNON & BENMESBAH 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 pompilia (C. Felder & R. Felder, 1867)

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

Neonympha pompilia C. Felder & R. Felder, [25.IV].1867: 479; syntypes: [Colombia] Bogotá and Mexico. Lectotype herein designated: [Colombia] Bogotá; NHMUK (examined).

Euptychia usitata Butler, [30.IV].1867a: 463, pl. 39, fig. 2; syntypes: Venezuela and Guatemala. Lectotype herein designated: Venezuela; NHMUK (examined). – BUTLER 1868: 17. – KIRBY 1871: 48. – BUTLER & DRUCE 1874: 336. – KIRBY 1879: 132. – WEYMER 1890: 35. – WEYMER 1911: 201, pl. 47e. – DEVRIES 1987: 272, pl. 48, figs. 22, 23 (male) [misidentification]. – D’ABRERA 1988: 773 (female). – SANTINI 2004: 1056.

Euptychia pieria Butler, 1867a: 463, pl. 39, fig. 3; syntype: Honduras. Lectotype male here designated: Honduras; NHMUK (examined). – BUTLER 1868: 17. – BUTLER 1870: 252. – KIRBY 1871: 48. – BUTLER & DRUCE 1874: 336. – GODMAN & SALVIN 1880: 79–80. – WEYMER 1890: 9. – GODMAN 1901 in GODMAN & SALVIN: 654.

Euptychia austera 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] Curaçao; RMNH (examined).

Euptychia usitata pieria; BUTLER 1870: 252. – WEYMER 1911: 201.

Euptychia usitata pompilia; WEYMER 1911: 201, pl. 47e.

Euptychia usitata thelete; WEYMER 1911: 201

Vareuptychia usitata; FORSTER 1964: 125, fig. 146 (male genitalia). – ACKERY 1988: 115, table 9. – LEWIS 1973: 65, fig. 9. – AUSTIN et al. 1996: 33.

Vareuptychia pieria; LLORENTE-BOUSQUETS et al. 1986: 24.

Cissia usitata pieria; RAGUSO & LLORENTE-BOUSQUETS 1991: 132.

Cissia usitata; MEERMAN & BOOMSMA 1993: 42.

Cissia pompilia; LUIS-MARTÍNEZ et al. 1995: 119. – LAMAS 1996: 53. – LAMAS 2003: appendix 3, 203. – LAMAS 2004: 218; **syn.**: *usitata*, *thelete*. – LUIS-MARTÍNEZ et al. 2004: 349. – BECCALONI et al. 2008: 329. – POZO et al. 2008: 415. – LÓPEZ 2009: 28. – MARÍN & URIBE 2009: 25. – MARÍN et al. 2009: 237. – BALAM & LEÓN 2010: 531. – LUIS-MARTÍNEZ et al. 2011: 23. – MARÍN et al. 2012: 209. – MILLER et al. 2012: 58. – GARWOOD 2014: 58, figs. 742–746. – GARWOOD 2015: 38, figs. 448–453. – GARWOOD & JARAMILO 2016a: 107, figs. 1223–1228. – GARWOOD & JARAMILO 2016b: 103, figs. 1155–1160. – LUIS-MARTÍNEZ et al. 2016: 214.

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

Ypthimoides austera; LAMAS 2004: 224.

Diagnosis. Compared to all other species of *Cissia*, *C. pompilia* 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 M₁-M₂ on DFW. Females of *C. pompilia* sometimes have small ocelli in R₄₊₅-M₁, M₂-M₃ and M₃-Cu₁ on DFW and others similar in M₁-M₂, M₂-M₃, M₃-Cu₁ and Cu₂-1A+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 extremelly well-developed ocelli on VW (Fig. 6A). Some structures of the male genitalia can be variable, such as the shape of the tegumen varying from flattened to slightly convex in lateral view, and the length of the anterior projection of the saccus.

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 & MCNEELLY 2009). *Cissia pompilia* occurs up to altitude of 1600 m (GODMAN & SALVIN 1901: 80; DEVRIES 1987; specimen labels). The species is sympatric with *C. penelope* in Colombia and Venezuela, and syntopic in Titiribí, Antioquia (Colombia) (JARAMILLO & 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 (MEERMAN & BOOMSMA 1993).

Host plants and immature stages. Recorded larval host plants include species of *Eleusine* Gaertn. (Chloridoideae, Poaceae) (DEVRIES 1987; ACKERY 1988; SANTIN 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 unstated 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.[ympha] pompilia* Feld/ = *Euptychia pieria* Butler (1866)/ Type of *N. pompilia* Feld[er] = *E. pieria* Butl[er]. comp[ared]. w[ith]. 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. GODMAN & 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 Monog[raphy]./ 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 name; this specimen has the following labels: /TYPE/ *Euptychia pieria* Butler Monog[raphy]./ B. M. TYPE No. Rh. 3199, *Euptychia pieria* ♂ Butl[er]./ Honduras/ Honduras Pur[chased]. from Dyson 45-123/; and two others 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 *Ypthimoides* 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; MONTERO et al. 2009; CALERO-MEJÍA et al. 2013; RODRÍGUEZ & MILLER 2013; MARÍN 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.**).

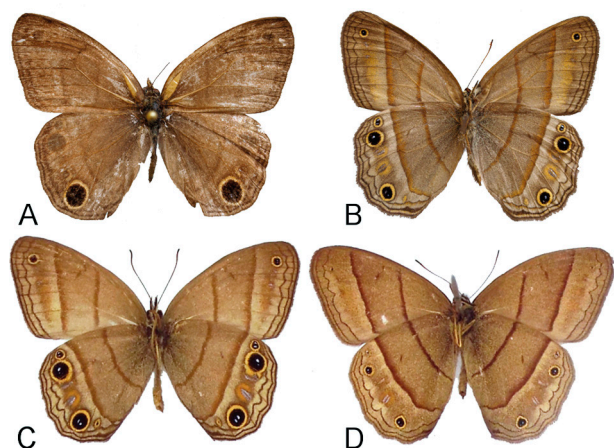


Fig. 6. Seasonal polyphenism in *Cissia pompilia*: **A,B**: Costa Rica, Puntarenas, Osa, collected in February: male: **A** – dorsal, **B** – ventral; **C**: Panama, collected in July (wet season): male; **D**: Mexico, collected in January (dry season): male. — © Trustees of the Natural History Museum, London.

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. Zacca 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 euptychiine 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 M_3 - Cu_1 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 *Praefaula 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. 2I–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 (Junin, 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 proba; LAMAS 1991: 10. – LAMAS 1994: 165. – DEVRIES et al. 1997: 355. – LAMAS [1997b]: 65. – BROWN & FREITAS, 2002: pl. 15. – LAMAS 2004: 218; **syn.**: *mariameliae*. – MARIN & URIBE 2009: 25. – WAHLBERG et al. 2009: table 1s (suppl.). – MIELKE et al. 2010: 290. – PEÑA et al. 2010: 246. – PIÑAS-RUBIO 2010: 31, figs. 233–238. – CHECA et al. 2013: 486.

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 *Ypthimoides maepius*, being differentiated from the former by the VHW submarginal line being rounded and crenulated between M_1 - Cu_2 (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, $\frac{2}{3}$ – $\frac{1}{2}$ 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 latero-ventrally, 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 antevaginalis fused to lamella postvaginalis with

one spiracle located at upper margin of its lateral expansions; lamella postvaginalis 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 M_1 - M_2 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-Chinchipec, 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* f. *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 [Illapani 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 ID: 02428 Exemplar + Etiketten/; and two others labels will be added later: /Lectotypus/ Lectotypus *Euptychia erigone* f. *proba* Weymer, 1911. T. Zacca det. 2016/. The lectotype photo is also available in WARREN et al. (2017). *Euptychia mariameliae* Hayward, 1957 was described 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.

Remarks. According to WEYMER (1911), the Peruvian *E. erigone* f. *proba* is distinguished from *E. erigone* (currently in *Yphthimoides* Forster, 1964) by a few characters of the VHW, such as the silvery incomplete ocelli in M_2 - M_3 and M_3 - Cu_1 , and the wide submedian and median lines. *Euptychia erigone* f. *proba* was raised to species by FORSTER (1964), who transferred it to his new genus *Argyreuptychia*. This species was not treated in SINGER et al. (1983), but it was correctly transferred to *Cissia* by LAMAS (1991).

Examined 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.

Euptychia eous; KIRBY 1871: 580. – WEYMER 1911: 208, pl. 48a. – AURIVILLIUS 1929: 157. – GAEDE 1931: 445. – KÖHLER 1935: 213. – BIEZANKO et al. 1957: 117. – BIEZANKO 1960a: 3. – BIEZANKO 1960b: 2. – BIEZANKO et al. 1962: 93. – BIEZANKO et al. 1966: 33. – D'ABRERA 1988: 774 (male). – ISERHARD & ROMANOWSKI 2004: 652.

Paryphthimoides eous; FORSTER 1964: 107, fig. 109 (male genitalia). – BROWN & MIELKE 1967: 91. – BIEZANKO et al. 1974: 112. – KRÜGER & SILVA 2003: 40. – LAMAS 2004: 221; **syn.**: *kiliani*. – BAR et al. 2008: 336. – NÚÑEZ-BUSTOS 2008: 82. – PAZ et al. 2008: 145. – TESTON & CORSEUIL 2008: 47. – BENTANCUR-VIGLIONE 2009: 35. – NÚÑEZ-BUSTOS 2009: 75. – DOLIBAINA et al. 2011: 349. – NÚÑEZ-BUSTOS et al. 2011: 40. – MIELKE et al. [2012]: 301. – GIACOMET et al. 2012: 118. – SILVA et al. 2013: 90. – PAZ et al. 2013: 420. – GARCIA-SALIK et al. 2014: 279. – THIELE et al. 2014: 7.

Paryphthimoides phronius [misidentification]; BROWN 1992: 152, 153, fig. 5. – FREITAS & BROWN 2004: 365. – FRANCINI et al. 2011: 65.

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

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

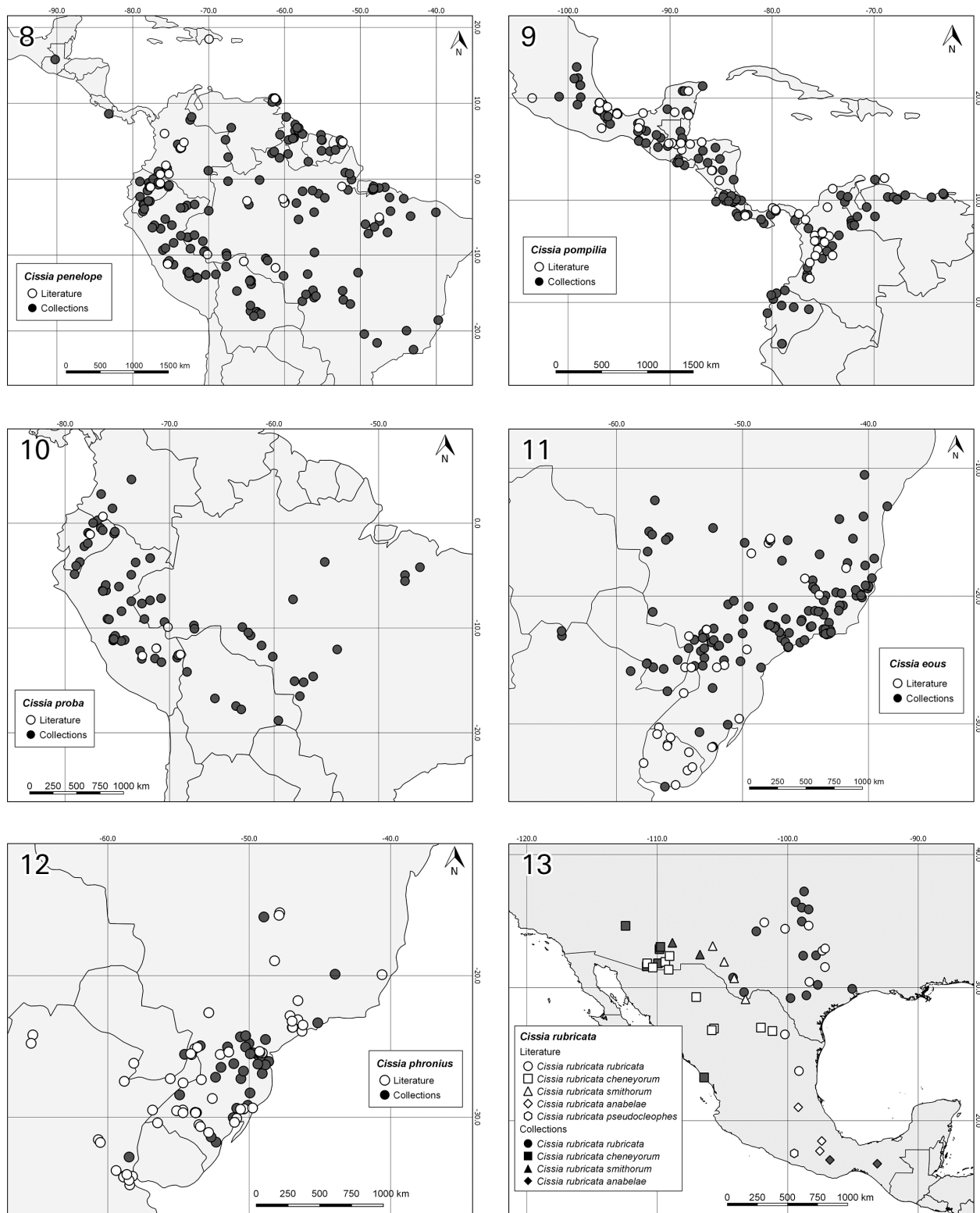
Diagnosis. *Cissia eous* is distinguished from its congeners by the (1) DHW with a well-developed, rounded

ocellus in Cu_1 - Cu_2 , 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 Cu_2 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 Cu_1 - Cu_2 (while this ocellus occupies the entire space in *C. proba*). *Cissia eous* is readily distinguished from *C. phronius* **comb.n.** by the median line being shifted inwards between Cu_2 and the inner margin on VHW, and by having males with the wings totally brown (while these have a greasy-brown aspect in *C. phronius* **comb.n.**)

Male genitalia (Fig. 4P–T). Tegumen slightly flattened, laterally subtriangular; uncus arched downward, about $1.5 \times$ 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 sinuous; 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 bottle-shaped, posterior region about $2 \times$ 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 polyphenism 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.



Figs. 8–13. Geographical distribution of *Cissia* species. 8: *C. penelope*. 9: *C. pompilia*. 10: *C. proba*. 11: *C. eous*. 12: *C. phronius*. 13: *C. rubricata* and its subspecies.

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; AVLF 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/ *Euptychia eous* Butler. Monog[raph]./ B. M. Type No. Rh 3210 *Euptychia eous* ♂Butl[er]./ 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. poltys* 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* Freitas & 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 be-

ing 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 poltys* (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. poltys* 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* DOUBLEDAY: 376.

Euptychia phronius; BUTLER 1867a: 470. – WEYMER 1911: 206, pl. 48. – BIEZANKO et al. 1960a: 5. – BIEZANKO et al. 1962: 94. – EBERT 1969: 47. – D'ABRERA 1988: 774.

Paryphthimoides phronius; FORSTER 1964: 107. – BROWN & MIELKE 1967: 92. – MIELKE 1994: 772. – BROWN & FREITAS 2000: 104. – MOTTA 2002: 157. – UEHARA-PRADO et al. 2004: 14. – EMERY et al. 2006: 90. – MACHIORI & ROMANOWSKI 2006a: 447. – MACHIORI & ROMANOWSKI 2006b: 1032. – PINHEIRO & EMERY 2006: 12. – DESSUY & MORAIS 2007: 113. – MORAIS et al. 2007: 42. – PINHEIRO & EMERY 2007: 72. – NÚÑEZ-BUSTOS 2008: 82. – GIOVENARDI et al. 2008: 603. – PAZ et al. 2008: 145. – PEIXOTO & BENSON 2008: 1069. – PINHEIRO et al. 2008: 142. – TESTON & CORSEUIL 2008: 47. – BETANCUR-VIGLIONE 2009: 35. – NÚÑEZ-BUSTOS 2009: 75. – PEIXOTO & BENSON 2009: 1–14. – GRAZIA et al. 2010: 187. – ISERHARD et al. 2010: 312. – NÚÑEZ-BUSTOS 2010: 120. – PEÑA et al. 2010: 248. – SILVA et al. 2010: 10. – BONFANTTI et al. 2011: 250. – DOLIBAINA et al. 2011: 349. – NÚÑEZ-BUSTOS et al. 2011: 40. – PEDROTTI et al. 2011: 387. – RITTER 2011: 5. – ROSA et al. 2011: 3. – SANTOS et al. 2011: 272. – BELLAVER et al. 2012: 185. – GIACOMET et al. 2012: 118. – SILVA et al. 2012: 295. – UEHARA-PRADO & RIBEIRO 2012: 174. – MACHIORI et al. 2013: 7. – PAZ et al. 2013: 420. – GARCÍA-SALIK et al. 2014: 279. – PAZ et al. 2014: 413. – THIELE et al. 2014: 7. – CAPORALE et al. 2015: 5. – SPANIOL & MORAIS 2015: 39. – GRACIOTIM & MORAES 2016: 120.

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 Cu_1 , (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 $1.5 \times$ 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 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; phallus straight, about same length as valva, cylindrical, anterior region bottle-shaped, posterior region about $2 \times$ longer than anterior region with bifid apex in dorsal view, distal opening ventral and longer than proximal opening.

Female genitalia (Figs. 5I,J). 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 spiracle located at upper margin of its lateral expansions; lamella postvaginalis orbicular and projected distally at median region; ductus bursae membranous; corpus bursae about $\frac{1}{3}$ 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. In-

traspecific 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 antropogenic 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; BELLAVER 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, phenology 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 euptychiines, this species flies close to the ground. Adults are attracted by rotting 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 Euptychiina in inventories (DESSUY & MORAES 2007; THIELE 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* Flügge 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. *Satyrys 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 (as is the case with many other Euptychiina 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.III.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)

Euptychia rubricata W.H. Edwards, 1871: 212. Neotype designated by F. Brown, 1964: Waco, Texas; CMNH. – M. BROWN 1964: 334, fig. 2.

Megisto rubricata; MILLER 1976: 9, figs. 21–25.

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 anabelae* (Miller, 1976) **comb.n.** and *C. rubricata pseudocleophes* (Miller, 1976) **comb.n.**, distributed from southern USA to Honduras (MILLER 1976; LOTTIS & NABERHAUS 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;

MARÍN 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. myncea*, *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 MARÍN 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, Marín & 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 *Parypthimoides* 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 & REITSMA 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 euptychiine genera (WAHLBERG et al. 2009; PEÑA et al. 2010; MARÍN et al. 2017), such as *Posttaygetis* Forster, 1964 (MURRAY 2003), *Taygetis* Hübner, [1819] (MURRAY 2001; FREITAS 2017), *Forsterinaria* 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 *Taydebis* Freitas, 2003, *Magneuptychia* 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*, *Magneuptychia* 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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File 1: [zacca&al-cissiasatyridae-asp2018-electronicssupplement-1.doc](#) — List of examined material.

File 2: [zacca&al-cissiasatyridae-asp2018-electronicssupplement-2.nex](#) — Partition and substitutions models.

File 3: [zacca&al-cissiasatyridae-asp2018-electronicssupplement-3.tif](#) — Phylogeny of the genus *Cissia* based on Bayesian Inference of combined COI, GAPDH and RpS5 gene sequences.