

Taxonomy

Systematic Revision of a New Butterfly Genus, *Cisandina* Nakahara & Espeland, n. gen., with Descriptions of Three New Taxa (Lepidoptera: Nymphalidae: Satyrinae)

Shinichi Nakahara,^{1,2,3,11} Maryzender Rodríguez-Melgarejo,^{2,4} Kaylin Kleckner,^{3,6} Thalia Corahua-Espinoza,^{5,6} Rafael Tejera,^{5,7} Marianne Espeland,⁸ Mirna M. Casagrande,⁹ Eduardo P. Barbosa,¹⁰ Joseph See,⁵ Geoffrey Gallice,^{1,5} Gerardo Lamas,² and Keith R. Willmott¹

¹McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA, ²Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú, ³Entomology and Nematology Department, University of Florida, Gainesville, FL 32611, USA, ⁴Laboratorio de Entomología, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, CCT CONICET, Mendoza), 5500 Mendoza, Argentina, ⁵Alliance for a Sustainable Amazon, Hanover, MD 21076, USA, ⁶Universidad Nacional Amazónica de Madre de Dios, Av. Jorge Chávez 1160, Puerto Maldonado, Madre de Dios 17000, Perú, ⁷Universidad Nacional de San Antonio Abad del Cuzco, Av. de La Cultura 773, Cuzco 08000, Perú, ⁸Leibniz Institute for the Analysis of Biodiversity Change, Zoological Research Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany, ⁹Laboratório de Estudos de Lepidoptera Neotropical, Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Paraná, Brazil, ¹⁰Departamento de Biologia Animal, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil, and ¹¹Corresponding author, e-mail: snakahara@ufl.edu

Subject Editor: Marko Mutanen

Received 18 July 2021; Editorial decision 25 October 2021

Abstract

We here establish a new genus in the nymphalid butterfly subtribe Euptychiina, *Cisandina* Nakahara & Espeland, n. gen. to harbor five species hitherto placed within two polyphyletic genera, namely *Magneuptychia* Forster, 1964 and *Euptychoides* Forster, 1964. We compiled data from over 350 specimens in 17 public and private collections, as well as DNA sequence data for all relevant species, to revise the species-level classification of this new genus. According to our multi-locus molecular phylogeny estimated with the maximum likelihood approach, *Cisandina lea* n. comb., *Cisandina philippa* n. comb. & reinst. stat., *Cisandina fida* n. comb., *Cisandina sanmarcos* n. comb., and *Cisandina trinitensis* n. comb. are proposed as new taxonomic combinations, since these species are distantly related to the type species of *Magneuptychia* and *Euptychoides* and cannot reasonably be accommodated in any other genus. Lectotypes are designated for *Papilio lea* Cramer, 1777, *Papilio junia* Cramer, 1780, *Euptychia philippa* Butler, 1867, and *Euptychia fida* Weymer, 1911. Two new species of *Cisandina* n. gen. are named and described herein, *C. esmeralda* Nakahara & Barbosa, n. sp. and *C. castanya* Lamas & Nakahara, n. sp., increasing the described species diversity of the genus to seven. The immature stages of *C. castanya* n. sp. and *C. philippa* n. comb. & reinst. stat. are documented along with their natural hostplants, representing the first two species of the genus with known life history information. We describe a new subspecies, *Cisandina fida directa* Nakahara & Willmott, n. ssp., based on a limited number of specimens from southern Ecuador and central Peru. We were unable to obtain genetic data for the nominate race of *C. fida* n. comb., and thus, this taxonomic hypothesis is currently based solely on phenotypic characters.

Resumen

Se establece un nuevo género de mariposas ninfálicas de la subtribu Euptychiina, *Cisandina* Nakahara & Espeland, n. gen. para albergar cinco especies previamente ubicadas dentro de dos géneros polifiléticos, *Magneuptychia* Forster, 1964 y *Euptychoides* Forster, 1964. Se recopiló datos de más de 350 especímenes de 17 colecciones públicas y privadas, así como datos de secuencias de ADN para todas las especies

relevantes y así poder revisar la clasificación a nivel de especie de este nuevo género. De acuerdo con nuestra filogenia molecular multilocus, estimada con el enfoque de máxima verosimilitud, se propone como nuevas combinaciones taxonómicas a *Cisandina lea* **n. comb.**, *Cisandina philippa* **n. comb. & reinst. stat.**, *Cisandina fida* **n. comb.**, *Cisandina sanmarcos* **n. comb.** y *Cisandina trinitensis* **n. comb.**, ya que estas especies se relacionan lejanamente con las especies tipo de *Magneuptychia* y *Euptychoides* y no pueden acomodarse razonablemente en ningún otro género. Se designa lectotipos para *Papilio lea* Cramer, 1777, *Papilio junia* Cramer, 1780, *Euptychia philippa* Butler, 1867 y, *Eupytchia fida* Weymer, 1911. Adicionalmente se nombra y describe aquí dos nuevas especies de *Cisandina* **n. gen.**, *C. esmeralda* Nakahara & Barbosa, **n. sp.** y *C. castanya* Lamas & Nakahara, **n. sp.**, aumentando la riqueza de especies descritas del género a siete. Los estadios inmaduros de *C. castanya* Lamas & Nakahara, **n. sp.** y *C. philippa* **n. comb. & reinst. stat.**, son documentados junto con su planta hospedante natural, aportando nueva información sobre el ciclo de vida del género. Además, describimos una nueva subespecie, *Cisandina fida directa* Nakahara & Willmott, **n. ssp.**, con base en un número limitado de especímenes del sur de Ecuador y del centro de Perú. No obtuvimos datos genéticos para la raza nominada de *C. fida* **n. comb.**, por lo que esta hipótesis taxonómica se establece únicamente con base en caracteres fenotípicos.

Resumo

Estabelecemos aqui um novo gênero na subtribe de borboletas ninfalídeas Euptychiina, *Cisandina* Nakahara & Espeland, **n. gen.** para abrigar cinco espécies até agora alocadas dentro de dois gêneros polifiléticos, *Magneuptychia* Forster 1964 e *Euptychoides* Forster 1964. Compilamos dados de mais de 350 espécimes em 17 coleções públicas e privadas, bem como dados de sequência de DNA para todas as espécies relevantes, para revisar a classificação a nível de espécie deste novo gênero. De acordo com nossa filogenia molecular multilocus estimada com a abordagem de máxima verossimilhança, são propostas como novas combinações taxonômicas: *Cisandina lea* **n. comb.**, *Cisandina philippa* **n. comb. & reinst. stat.**, *Cisandina fida* **n. comb.**, *Cisandina sanmarcos* **n. comb.** e *Cisandina trinitensis* **n. comb.**, uma vez que essas espécies estão distantemente relacionadas às espécies-tipo de *Magneuptychia* e *Euptychoides* e não podem ser razoavelmente acomodadas em qualquer outro gênero. Lectótipos são designados para *Papilio lea* Cramer 1777, *Papilio junia* Cramer 1780, *Euptychia philippa* Butler 1867 e *Eupytchia fida* Weymer 1911. Duas novas espécies de *Cisandina* **n. gen.** são nomeadas e descritas aqui, *C. esmeralda* Nakahara & Barbosa, **n. sp.** e *C. castanya* Lamas & Nakahara, **n. sp.**, resultando no aumento da diversidade de espécies do gênero para sete. Os estágios imaturos de *C. castanya* **n. sp.** e *C. philippa* **n. comb. & reinst. stat.**, são documentados junto com sua planta hospedeira natural, representando duas espécies com informações de história de vida conhecidas para o gênero. Descrevemos uma nova subespécie, *Cisandina fida directa* Nakahara & Willmott, **n. ssp.**, com base em um número limitado de espécimes do sul do Equador e centro do Peru. Não foi possível obter dados genéticos para a raça nominal de *C. fida* **n. comb.**, e, portanto, esta hipótese taxonômica é atualmente baseada apenas em caracteres fenotípicos.

Key words: Euptychiina, Lectotype, taxonomy, *Magneuptychia*, *Euptychoides*

The nymphalid genus *Magneuptychia* Forster, 1964 was erected by Forster (1964) to accommodate 15 species previously associated with *Euptychia* Hübner, 1818 (*sensu lato*), by designating *Papilio libye* Cramer, 1767 as the type species. Nevertheless, as indicated by Forster (1964: 125) in his description, this placement of species in *Magneuptychia* is ‘bis auf weiteres’ (i.e., for the time being), and the genus was established based on differences in wing span and pattern, as well as male genitalic characters in comparison with *Argyreuptychia* Forster, 1964 without any supporting phylogenetic hypotheses. Forster’s (1964) tentative classification of *Magneuptychia* was followed by subsequent authors such as Miller (1968) and was one of the most diverse genera with 29 described species recognized by Lamas (2004) in his comprehensive checklist of the satyrine subtribe Euptychiina. Subsequent molecular (Murray and Prowell 2005; Peña et al. 2010, Espeland et al. 2019) and morphological (Marín et al. 2017) phylogenetic studies, however, have shown *Magneuptychia* to be thoroughly polyphyletic. Costa et al. (2016) discussed the taxonomy of *Magneuptychia* and Andrade et al. (2019) proposed generic classifications for nine putative species previously placed in *Magneuptychia* by transferring

them into four new genera erected in that study, as well as one existing genus *Satyrotaygetis* Forster, 1964. However, taxonomic hypotheses in both of these two publications were based solely on comparative morphology without providing any supporting phylogenetic analysis. Following Nakahara et al. (2020a) and Zacca et al. (2021), a phylogenetic study is underway by SN and collaborators to classify taxa previously placed in *Magneuptychia* (*sensu* Lamas 2004). Meanwhile, during attempts to revise another polyphyletic euptychiine genus, *Euptychoides* Forster, 1964, Nakahara et al. (2016), and Willmott et al. (2019) described new genera, supported by phylogenetic analyses, for taxa unrelated to the type species of that genus, *Euptychia saturnus* Butler, 1867. This ongoing effort to unravel the systematics of *Euptychoides* is still underway by this study’s authors and colleagues.

This article, therefore, aimed to further clarify the systematics of both *Magneuptychia* and *Euptychoides*, with emphasis on a clade of seven species with similar ventral wing patterns and genitalia, that are distributed entirely east of the Andes. We here propose a new genus for this clade and review its species-level taxonomy, including providing descriptions of three new species-group names.

Materials and Methods

We conducted field work in Brazil, Ecuador, and Peru to study euptychiines and collect specimens for morphological and molecular analysis. Additionally, specimens in the following public and private collections were examined and the following collection abbreviations are used:

| | |
|---------|--|
| ASA: | Alliance for a Sustainable Amazon collection, Puerto Maldonado, Perú |
| BMB: | Booth Museum of Natural History, Brighton, UK |
| DEMU: | Debra Murray collection, USA |
| DZUP: | Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil |
| FLMNH: | McGuire Center for Lepidoptera and Biodiversity (MGCL), Florida Museum of Natural History, University of Florida, Gainesville, USA |
| INABIO: | Instituto Nacional de Biodiversidad, Quito, Ecuador (formerly MECN) |
| MACN: | Museo Argentino de Ciencias Naturales ‘Bernardino Rivadavia’, Buenos Aires, Argentina |
| MIPE: | Mike J. Perceval collection, Surrey, UK |
| MNHU: | Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität, Berlin, Germany |
| MOBE: | Mohamed Benmesbah collection, Toulouse, France |
| MUSM: | Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú |
| MZUJ: | Zoological Museum, Jagellonian University, Krakow, Poland |
| NHMUK: | Natural History Museum, London, UK (formerly BMNH) |
| RMNH: | Rijksmuseum van Natuurlijke Historie (currently Netherlands Centre for Biodiversity Naturalis), Leiden, Netherlands |
| SMT: | Senckenberg Museum für Tierkunde, Dresden, Germany |
| USNM: | National Museum of Natural History, Smithsonian Institution, Washington, DC, USA |
| ZSM: | Zoologische Staatssammlung München, Munich, Germany |
| ZUEC: | Museu de Zoologia da Universidade Estadual de Campinas ‘Adão José Cardoso’, Campinas, Brazil. |

Over 350 specimens examined in these collections were databased and georeferenced in accordance with Nakahara et al. (2019b). Label data for name-bearing types are written verbatim with labels separated by double-forward slashes.

We studied morphology using standard techniques, with abdomens and other appendages being soaked in hot (80°C) 10% KOH for 5–10 min. These appendages and genitalia were dissected and subsequently stored in glass tubes and/or small plastic vials filled with glycerine. The wing venation was visualized by clearing scales of the ventral surface using 70% ethanol. Morphological features were studied using a Leica MZ 16 stereomicroscope at magnifications up to 100×, and a Leica LED2500 (10–160×). Almost all the illustrations were made using a camera lucida attached to a Leica MZ 16 stereomicroscope, except that illustrations of head capsules of the immature stages were drawn in Adobe Illustrator under constant observation in the Leica LED2500 stereomicroscope. The study site and methods for the immature stages’ documentation largely follow Baine et al. (2019). The terminology associated with wings and genitalia follows Nakahara et al. (2018a, b), and the following

abbreviations are used: DFW: dorsal forewing; DHW: dorsal hindwing; VFW: ventral forewing; VHW: ventral hindwing.

We follow Nakahara et al. (2020b) for methods for DNA extractions, internal primer design, PCR, and Sanger sequencing for the first half of the mitochondrial gene *cytochrome oxidase I* (COI), commonly known as the ‘DNA barcode’ (*sensu* Hebert et al. 2003), as well as for three nuclear gene sequences: *elongation factor 1-alpha* (Ef1a), *glyceraldehyde-3-phosphate dehydrogenase* (GAPDH), and *ribosomal protein S5* (RpS5). These four genes were amplified for selected individuals of the ‘*Archeuptychia* clade’, coupled with four out-group individuals, and used to produce a phylogenetic hypothesis to support our taxonomic proposal. Information regarding sequences used in this study, including new DNA sequence data generated, is provided with GenBank voucher codes (Table 1). We performed a phylogenetic analysis with maximum likelihood as the optimality criterion on an alignment of these mitochondrial and nuclear gene sequences in IQ-TREE v2.0.5 (Minh et al. 2020). The data were partitioned into codon positions and best-fit substitution models individually derived through ModelFinder (Kalyaanamoorthy et al. 2017) were applied, with information provided in Table 2. In total, 20 independent analyses were conducted based on the above dataset, with branch support estimated through 2,000 replications of both ultrafast bootstrap (UFBoot) with the ‘-bnni’ option to reduce model violation, and Shimodaira-Hasegawa-like approximate likelihood ratio test (SH-aLRT). The run which gave the tree with the highest log-likelihood score for the above dataset was selected and the tree was rooted with *Godartiana byses* (Godart, [1824]). We also calculated infra- and interspecific genetic distances based on ‘DNA barcode’ data among *Cisandina* n. gen. taxa based on Kimura-2-parameter (Table 3).

Nomenclature

This article has been registered in ZooBank (www.zoobank.org), the official register of the International Commission on Zoological Nomenclature. The LSID (Life Science Identifier) number of the publication is: urn:lsid:zoobank.org:pub:ACFA7036-C10E-4370-BF43-D22288168F33

Results

Systematics

Our multi-locus maximum likelihood tree (Fig. 1; LnL = -11380.331) shows that *Papilio lea* Cramer, 1777 and *Euptychia philippa* Butler, 1867 (see our discussion below for the specific status of this taxon), two taxa hitherto placed in *Magneuptychia*, do not group closely with the type species of *Magneuptychia*, *Papilio libye* Linnaeus, 1767. This phylogenetic hypothesis also indicates that *Euptychoides sanmarcos* Nakahara & Lamas, 2018 and *Euptychia fida* Weymer, 1911, two species previously provisionally placed in *Euptychoides*, are strongly supported as sister to the clade including *Papilio lea* and *Euptychia philippa* (Fig. 1; SH-aLRT/UFBoot = 96.5/95). As discussed and demonstrated in a number of phylogenetic studies (e.g., Peña et al. 2010, Nakahara et al. 2016, Willmott et al. 2019), other species currently placed in *Euptychoides* are either in the so-called ‘*Pareuptychia* clade’ or ‘*Splendeuptychia* clade’, with the type species in the former clade. Finally, the recently described species *Magneuptychia trinitensis* Brévignon & Benmesbah, 2012 was moderately to strongly supported as sister to the clade containing the above-mentioned former *Magneuptychia* and *Euptychoides* species (Fig. 1; SH-aLRT/UFBoot = 91.9/92), which it also closely resembles in male genitalia and ventral wing pattern. Therefore, we herein describe a new genus

Table 1. GenBank Accession number information for DNA sequences used in this study

| Voucher code | Genus | Species | COI | Ef1a | RpS5 | GAPDH | Locality |
|--------------------|-----------------------|--------------------|----------|----------|----------|----------|--|
| BC-DZ Willmott-137 | <i>Cisandina</i> | <i>esmeralda</i> | MW008458 | MT999012 | N/A | MT998979 | Brazil: Paraná: Reservas Particulares do Patrimônio Natural (RPPN) Moreira Salles (−24.071, −53.033) |
| BC-DZ Willmott-138 | <i>Cisandina</i> | <i>lea</i> | MW018438 | N/A | N/A | N/A | Brazil: Amazonas: Foz do Rio Curuduri (−0.092, −63.287) |
| BC-DZ Willmott-139 | <i>Cisandina</i> | <i>castanya</i> | MW008460 | N/A | N/A | N/A | Brazil: Acre: Reserva Caruaba (−10.071, −67.619) |
| BC-DZ Willmott-250 | <i>Archeuptychia</i> | <i>cluena</i> | MW008469 | MT999007 | MT998995 | MT998984 | Brazil: Espírito Santo: Reserva Ecológica de Sooretama (−19.054, −40.142) |
| IN014 | <i>Erichthodes</i> | <i>arius</i> | MW008470 | N/A | N/A | N/A | Peru: Junín: 2.5 km N San Ramón, Genova (−11.091, −75.351) |
| KW-090113-21 | <i>Cepheuptychia</i> | <i>cephus</i> | MW008471 | N/A | MT998996 | MT998985 | Ecuador: Orellana: Boca del Río Añangu (−0.529, −76.395) |
| KW-140708-02 | <i>Chloreuptychia</i> | <i>chlorimene</i> | MW008474 | MT999008 | MT998997 | MT998986 | Ecuador: Orellana: Estación Científica Yasuní (−0.674, −76.397) |
| KW-15-025 | <i>Euptychoides</i> | <i>sannarcos</i> | MW008466 | MT999005 | MT998993 | MT998982 | Peru: Cuzco: Quebrada Quitacalzón (−13.022, −71.493) |
| KW-15-034 | <i>Pseudeuptychia</i> | <i>languida</i> | MW008473 | N/A | N/A | N/A | Peru: Cuzco: Quebrada Quitacalzón (−13.022, −71.493) |
| LCB353 | <i>Chloreuptychia</i> | <i>marica</i> | MW008475 | N/A | N/A | N/A | French Guiana: Cayenne: Nouragues Station (4.083, −52.683) |
| LCB356 | <i>Cisandina</i> | <i>trinitensis</i> | MW008463 | N/A | N/A | N/A | French Guiana: Not located: 'French Guiana' |
| LEP-08983 | <i>Cisandina</i> | <i>philippa</i> | MW008467 | N/A | MT998990 | N/A | Ecuador: Zamora-Chinchipe: La Libertad (−3.798, −78.607) |
| LEP-10517 | <i>Pseudeuptychia</i> | <i>languida</i> | MW008472 | N/A | N/A | N/A | Ecuador: Orellana: Reserva Biológica del Río Bigal, 'the Hooch' (−0.524, −77.419) |
| LEP-16705 | <i>Cisandina</i> | <i>fida</i> | MW008465 | MT999004 | MT998992 | MT998981 | Ecuador: Zamora-Chinchipe: Juyapa (−3.58, −78.951) |
| LEP-16939 | <i>Cisandina</i> | <i>philippa</i> | MW008468 | MT999006 | MT998994 | MT998983 | Ecuador: Morona-Santiago: Isla de las Conchas (−3.036, −77.975) |
| LEP-18697 | <i>Stevenaria</i> | <i>eriphae</i> | MW008477 | N/A | MT999001 | N/A | Guyana: Upper Takutu-Upper Essequibo: Kanuku Mountains (3.2, −59.567) |
| LEP-19580 | <i>Chloreuptychia</i> | <i>herseis</i> | MW008476 | MT999009 | MT998998 | MT998987 | Peru: Madre de Dios: Los Amigos Biological Station (−12.567, −70.093) |
| LEP-34359 | <i>Cisandina</i> | <i>lea</i> | MW008459 | N/A | N/A | N/A | French Guiana: St-Laurent du Maroni: Saül (3.855, −53.302) |
| LEP-58115 | <i>Cisandina</i> | <i>fida</i> | MW008464 | N/A | N/A | N/A | Peru: Ucayali: Previsto (−9.05, −73.633) |
| MB-1708-15 | <i>Cisandina</i> | <i>trinitensis</i> | MW008462 | N/A | N/A | N/A | French Guiana: Cayenne: Nouragues Station (4.083, −52.683) |
| LCB251 | <i>Cisandina</i> | <i>trinitensis</i> | MW008461 | MT999003 | MT998991 | MT998980 | French Guiana: St-Laurent du Maroni: Antecume-Pata, 'filet' (3.292, −54.069) |
| MGCL-LOAN-523 | <i>Godartiana</i> | <i>byes</i> | KU892533 | N/A | KU892535 | KU892534 | Brazil: Bahia: Reserva Biológica de Una (−15.173, −39.103) |
| LEP-14777 | <i>Magneuptychia</i> | <i>libye</i> | MG209754 | MF192722 | MG546320 | MF192728 | Ecuador: Zamora-Chinchipe: km 6 Los Encuentros-El Panguí (−3.731, −78.609) |
| NW149-9 | <i>Archeuptychia</i> | <i>cluena</i> | GQ864736 | GQ864830 | GQ865392 | GQ864926 | Brazil: São Paulo: Salesópolis |
| CP02-50 | <i>Chloreuptychia</i> | <i>marica</i> | GU20583 | GU205887 | GU206064 | GU20594 | Peru: Madre de Dios: Posada Amazonas (−12.801, −69.293) |
| DNA99-050 | <i>Chloreuptychia</i> | <i>rectilinea</i> | AY508528 | AY509055 | N/A | N/A | Ecuador: Napo: no specific locality |
| LEP-14945 | <i>Chloreuptychia</i> | <i>herseis</i> | | MT999010 | MT998999 | MT998988 | Suriname: Nickerie: Kabalebo Dam |
| KW-081111-49 | <i>Chloreuptychia</i> | <i>rectilinea</i> | | MT999011 | MT999000 | MT998989 | Ecuador: Orellana: Boca del Río Añangu (−0.529, −76.395) |
| LEP-34283 | <i>Cisandina</i> | <i>philippa</i> | MW018439 | N/A | N/A | N/A | Ecuador: Morona-Santiago: Santiago de Mendez (−3.036, −78.033) |
| LEP-10686 | <i>Cisandina</i> | <i>fida</i> | MW018440 | N/A | N/A | N/A | Ecuador: Zamora-Chinchipe: ridge E San Roque (−3.703, −78.593) |
| LEP-08986 | <i>Cisandina</i> | <i>philippa</i> | MW018441 | N/A | N/A | N/A | Ecuador: Zamora-Chinchipe: Centro Shuar Cháarip (−3.635, −78.558) |
| LEP-08984 | <i>Cisandina</i> | <i>philippa</i> | MW018442 | N/A | N/A | N/A | Ecuador: Zamora-Chinchipe: La Libertad (−3.798, −78.607) |
| KW-081111-38 | <i>Cisandina</i> | <i>philippa</i> | MW018443 | N/A | N/A | N/A | Ecuador: Orellana: Boca del Río Añangu (−0.529, −76.395) |

Table 2. Best-fit substitution models by partition derived from ModelFinder and applied in this study

| Codon position | Model |
|----------------|-----------|
| COI 1st | TIM2+F+G4 |
| COI 2nd | K3Pu+F+I |
| COI 3rd | TIM+F+G4 |
| EF1a 1st | FN+F |
| EF1a 2nd | F81+F+I |
| EF1a 3rd | TPM3+F+G4 |
| GAPDH 1st | F81+F+I |
| GAPDH 2nd | F81+F+I |
| GAPDH 3rd | TPM+F+G4 |
| RPS5 1st | TNe+I |
| RPS5 2nd | JC |
| RPS5 3rd | TIM2e+G4 |

to harbor all of these taxa, in addition to naming two new species and one new subspecies within the new genus.

Family Nymphalidae Rafinesque, 1815

Cisandina Nakahara & Espeland, New Genus

Type species: *Papilio lea* Cramer, 1777 – by present designation

Species Account:

Cisandina Nakahara & Espeland, n. gen.

Cisandina lea (Cramer, 1777) (*Papilio*), n. comb.

= *Papilio junia* Cramer, 1780

Cisandina esmeralda Nakahara & Barbosa, n. sp.

Cisandina philippa (Butler, 1867) (*Euptychia*), n. comb. & reinst. stat.

= *Euptychia batesii* f. *tersa* Weymer, 1911

Cisandina castanya Lamas & Nakahara, n. sp.

Cisandina fida fida (Weymer, 1911) (*Euptychia*), n. comb.

Cisandina fida directa Nakahara & Willmott, n. ssp.

Cisandina sanmarcos (Nakahara & Lamas, 2018) (*Euptychoides*), n. comb.

Cisandina trinitensis (Brévignon & Benmesbah, 2012) (*Magneuptychia*), n. comb.

Generic Relationships and Diagnosis:

Based on hybrid enrichment data, Espeland et al. (2019) found ‘*Magneuptychia lea philippa*’ as a member of strongly supported (UFBoot > 95; Posterior Probability [PP] > 0.95) ‘*Archeuptychia* clade’, sister to *Chloreuptychia herseis* (Godart, [1824]), although with weak support (UFBoot < 75; PP < 0.75). The ‘*Archeuptychia* clade’ is weakly supported (UFBoot < 75; PP < 0.75) as sister to the ‘*Splendeuptychia* clade’. Analyses conducted here (and in ongoing research, Espeland et al., unpublished data) including additional members of the ‘*Archeuptychia* clade’ recovered *Cisandina* n. gen. as a monophyletic group with moderate support (Fig. 1; SH-aLRT/UFBoot = 91.9/92), although its closest relatives were not strongly resolved. It is worth mentioning that the monophyly of *Cisandina* n. gen. is strongly supported (UFBoot > 95) in a molecular phylogeny generated to describe a new genus for its potential sister group, as mentioned below. Our analysis found the sister group to be *Ypthimoides eriphule* (Butler, 1867) + *Erichthodes arius* (Weymer, 1911), with other closely related taxa including *Chloreuptychia herseis*, *Chloreuptychia marica* (Weymer, 1911), *Pseudeuptychia*

Forster, 1964, and *Archeuptychia* Forster, 1964. Research is underway on the generic classification of these various clades.

Cisandina n. gen. is distinguished from other members of the ‘*Archeuptychia* clade’ by the configuration of the VHW submarginal ocelli, with each having only a single, central white pupil (except for the ocellus in cell M_2), and which are largest in cells Cu_1 and M_1 and reduced in size in adjacent cells but otherwise similar in form, with the ocellus in M_2 notably offset basally in comparison with the neighboring ocelli. *Erichthodes arius* and *A. cluena* (Drury, 1782) have VHW submarginal ocelli of similar shape and appearance, but they are roughly uniform in size throughout the wing, while remaining species have the ‘middle’ two ocelli (in cells M_2 and M_3) different in form (elongate, with stretched silvery or whitish pupils, or very much reduced) compared with the ocelli in the cells bounding them. All members of *Cisandina* n. gen., except for *C. trinitensis* n. comb., possess a sixth VHW ocellus in cell Cu_2 , whereas most other species in the ‘*Archeuptychia*’ clade lack this ocellus in cell Cu_2 . The male genitalia are relatively uniform and are distinguished from other ‘*Archeuptychia* clade’ members by having a valva that is broad basally then tapers sharply in the middle to form an elongate, narrow posterior projection (instead of gradually tapering throughout as in *E. arius* and *A. cluena*, or broad throughout as in *Pseudeuptychia* and *Chloreuptychia*). Furthermore, the reduced appendices angulares (more visible in posterior view and hardly visible in lateral view), rather broad base of brachia, sclerotized portion of manica extending from phallobase at its juncture with aedeagus (this character is also seen in *E. arius* and *Ypthimoides eriphule* (Butler, 1867)), and large antero-dorsal opening of phallus is apparently unique features within Euptychiina that are restricted to this genus. The genitalia, however, differ slightly among species in *Cisandina* n. gen. For example, the postero-dorsal process of the phallus (i.e. aedeagus) is shorter in *C. lea* n. comb., *C. philippa* n. comb. & reinst. stat., and the two new species (*C. castanya* n. sp. and *C. esmeralda* n. sp.), compared with *C. fida* n. comb. and *C. sanmarcos* n. comb. Furthermore, the lamella antevaginalis is more rectangular and smaller compared with the lateral plate of the eighth abdominal segment and the lateral margin of the lamella antevaginalis is not fused with this plate in *C. lea* n. comb., *C. philippa* n. comb. & reinst. stat., *C. castanya* n. sp., and *C. esmeralda* n. sp., whereas this structure is larger and more rounded with a concave posterior margin in ventral view in *C. fida* n. comb. and *C. sanmarcos* n. comb., and notably both sides of the lamella antevaginalis are fused with the lateral plate of the eighth abdominal segment in these two taxa. Despite the immature stages being known for only two species, the final instar larva of *C. philippa* n. comb. & reinst. stat. and *C. castanya* n. sp. both possess rounded, stubby, and blunt head scoli, transforming from the ‘antler-like’ bifurcating head scoli of the penultimate instar, whereas most other known last instar larva of euptychiines exhibit developed horn-like scoli throughout the last two instars or simply lack scoli, such as species in the genus *Hermeuptychia* Forster, 1964 (e.g., Cong & Grishin 2014).

Cisandina n. gen.

This description is intended to serve as a template description for taxa described herein, thus it accommodates both inter- and intra-specific characters without the need for a separate ‘variation’ section.

Male: Forewing length: 22–26 mm (mean: 23.8 mm; $n = 13$)

Head: Eyes brown with lightly colored hair-like setae, white scales at base; frons dark brownish to blackish, covered with greyish and whitish scales, as well as lightly colored elongate hair-like setae; first

Table 3. Genetic distances among *Cisandina* n. gen. taxa based on DNA 'barcodes'

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|--|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| 1. LEP-10686 Cisandina_fida_Ecuador_Zamorachinchi | | 0.0247 | 0.0004 | 0.0647 | 0.0674 | 0.0592 | 0.0794 | 0.0796 | 0.0794 | 0.0517 | 0.0519 | 0.064 | 0.0563 | 0.0529 | 0.0747 | 0.0516 | 0.0094 | 0.1257 | 0.1385 | 0.1059 |
| 2. LEP-58115 Cisandina_fida_Peru_Ucayali | 0.0247 | | 0.0246 | 0.0754 | 0.0782 | 0.0699 | 0.0902 | 0.0904 | 0.0902 | 0.0625 | 0.0626 | 0.0747 | 0.067 | 0.0636 | 0.0855 | 0.0623 | 0.0202 | 0.1365 | 0.1492 | 0.1167 |
| 3. LEP-16705 Cisandina_fida_Ecuador_Zamorachinchi | 0.0004 | 0.0246 | | 0.0646 | 0.0673 | 0.0591 | 0.0793 | 0.0795 | 0.0793 | 0.0516 | 0.0518 | 0.0639 | 0.0562 | 0.0528 | 0.0746 | 0.0515 | 0.0093 | 0.1256 | 0.1384 | 0.1058 |
| 4. BC-DZ 138 Cisandina lea_Brazil_Amazonas | 0.0647 | 0.0754 | 0.0646 | | 0.0084 | 0.0505 | 0.0501 | 0.0503 | 0.0501 | 0.0431 | 0.0432 | 0.0553 | 0.0476 | 0.0442 | 0.066 | 0.0429 | 0.0602 | 0.117 | 0.1298 | 0.0973 |
| 5. LEP-34359 Cisandina_Jea_French | 0.0674 | 0.0782 | 0.0673 | 0.0084 | | 0.0533 | 0.0528 | 0.053 | 0.0528 | 0.0458 | 0.0459 | 0.058 | 0.0503 | 0.047 | 0.0688 | 0.0457 | 0.063 | 0.1198 | 0.1325 | 0.1 |
| 6. BC-DZ 139 Cisandina_castanya_Brazil_Acre | 0.0592 | 0.0699 | 0.0591 | 0.0505 | 0.0533 | | 0.0652 | 0.0654 | 0.0652 | 0.0376 | 0.0377 | 0.0498 | 0.0421 | 0.0387 | 0.0605 | 0.0374 | 0.0547 | 0.1115 | 0.1243 | 0.0918 |
| 7. MF546153LEPIG190-11_Cisandina_Jea_Argentina_Misiones | 0.0794 | 0.0902 | 0.0793 | 0.0501 | 0.0528 | 0.0652 | | 0.0002 | 0 | 0.0578 | 0.0579 | 0.07 | 0.0623 | 0.0589 | 0.0807 | 0.0576 | 0.0749 | 0.1318 | 0.1445 | 0.112 |
| 8. BC-DZ 137 Cisandina_esmeralda_Brazil_Parana | 0.0796 | 0.0904 | 0.0795 | 0.0503 | 0.053 | 0.0654 | 0.0002 | | 0.0002 | 0.058 | 0.0581 | 0.0702 | 0.0625 | 0.0591 | 0.081 | 0.0579 | 0.0752 | 0.132 | 0.1447 | 0.1122 |
| 9. MF545572LEPIG013-11_Cisandina_Jea_Argentina_Misiones | 0.0794 | 0.0902 | 0.0793 | 0.0501 | 0.0528 | 0.0652 | 0 | 0.0002 | | 0.0578 | 0.0579 | 0.07 | 0.0623 | 0.0589 | 0.0807 | 0.0576 | 0.0749 | 0.1318 | 0.1445 | 0.112 |
| 10. LEP-08986 Cisandina_philippa_Ecuador_Zamora-Chinchi | 0.0517 | 0.0625 | 0.0516 | 0.0431 | 0.0458 | 0.0376 | 0.0578 | 0.058 | 0.0578 | | 0.0004 | 0.0125 | 0.0048 | 0.0014 | 0.0233 | 0.0001 | 0.0473 | 0.1041 | 0.1168 | 0.0843 |
| 11. LEP-08983 Cisandina_philippa_Ecuador_Zamora-Chinchi | 0.0519 | 0.0626 | 0.0518 | 0.0432 | 0.0459 | 0.0377 | 0.0579 | 0.0581 | 0.0579 | 0.0004 | | 0.0127 | 0.0049 | 0.0016 | 0.0234 | 0.0003 | 0.0474 | 0.1042 | 0.117 | 0.0845 |
| 12. LEP-34283 Cisandina_philippa_Ecuador_Morona-Santiago | 0.064 | 0.0747 | 0.0639 | 0.0553 | 0.058 | 0.0498 | 0.07 | 0.0702 | 0.07 | 0.0125 | 0.0127 | | 0.0171 | 0.0137 | 0.0355 | 0.0124 | 0.0595 | 0.1163 | 0.1291 | 0.0966 |
| 13. LEP-16939 Cisandina_philippa_Ecuador_Morona-Santiago | 0.0563 | 0.067 | 0.0562 | 0.0476 | 0.0503 | 0.0421 | 0.0623 | 0.0625 | 0.0623 | 0.0048 | 0.0049 | 0.0171 | | 0.006 | 0.0278 | 0.0047 | 0.0518 | 0.1086 | 0.1214 | 0.0889 |
| 14. KW-081111-38 Cisandina_philippa_Ecuador_Orellana | 0.0529 | 0.0636 | 0.0528 | 0.0442 | 0.047 | 0.0387 | 0.0589 | 0.0591 | 0.0589 | 0.0014 | 0.0016 | 0.0137 | 0.006 | | 0.0244 | 0.0013 | 0.0484 | 0.1052 | 0.118 | 0.0855 |
| 15. DNA99-022 Cisandina_philippa_MD_Peru | 0.0747 | 0.0855 | 0.0746 | 0.066 | 0.0688 | 0.0605 | 0.0807 | 0.081 | 0.0807 | 0.0233 | 0.0234 | 0.0355 | 0.0278 | 0.0244 | | 0.0231 | 0.0702 | 0.1271 | 0.1398 | 0.1073 |
| 16. LEP-08984 Cisandina_philippa_Ecuador_Zamora-Chinchi | 0.0516 | 0.0623 | 0.0515 | 0.0429 | 0.0457 | 0.0374 | 0.0576 | 0.0579 | 0.0576 | 0.0001 | 0.0003 | 0.0124 | 0.0047 | 0.0013 | 0.0231 | | 0.0471 | 0.1039 | 0.1167 | 0.0842 |
| 17. KW-15-025 Cisandina_sanmarcos_Peru_Cuzco | 0.0094 | 0.0202 | 0.0093 | 0.0602 | 0.063 | 0.0547 | 0.0749 | 0.0752 | 0.0749 | 0.0473 | 0.0474 | 0.0595 | 0.0518 | 0.0484 | 0.0702 | 0.0471 | | 0.1212 | 0.134 | 0.1015 |
| 18. LCB232 Cisandina_trinitensis_French_Guiana | 0.1257 | 0.1365 | 0.1256 | 0.117 | 0.1198 | 0.1115 | 0.1318 | 0.132 | 0.1318 | 0.1041 | 0.1042 | 0.1163 | 0.1086 | 0.1052 | 0.1271 | 0.1039 | 0.1212 | | | 0.0128 |

Table 3. Continued

| | 1 | 2 | 3 | 4 | 5 | 6 | 7 | 8 | 9 | 10 | 11 | 12 | 13 | 14 | 15 | 16 | 17 | 18 | 19 | 20 |
|--|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|--------|
| 19. MB-1708-15_Cisandina_ trinitensis_French_Guiana | 0.1385 | 0.1492 | 0.1384 | 0.1298 | 0.1325 | 0.1243 | 0.1445 | 0.1447 | 0.1445 | 0.1168 | 0.117 | 0.1291 | 0.1214 | 0.118 | 0.1398 | 0.1167 | 0.134 | 0.0128 | | 0.0326 |
| 20. LCB356_Cisandina_ trinitensis_French_Guiana | 0.1059 | 0.1167 | 0.1058 | 0.0973 | 0.1 | 0.0918 | 0.112 | 0.1122 | 0.112 | 0.0843 | 0.0845 | 0.0966 | 0.0889 | 0.0855 | 0.1073 | 0.0842 | 0.1015 | 0.0199 | 0.0326 | |

segment of labial palpi short, covered with white scales and white hair-like scales and black hair-like scales, second segment about twice as long as eye depth and covered with white scales and white hair-like scales laterally and dorsally, in addition to brownish elongated scales, ventrally adorned with brownish hair-like scales and whitish hair-like scales longer than segment width, third segment apparently roughly one-third of second segment in length (although this can be somewhat variable), and covered with brownish scales dorsally and ventrally, with white scales laterally; antennae approximately two-fifths of forewing length, with ca. 38–39 antennomeres ($n = 4$), scape rounded, about as twice as long as pedicel and wider, flagellomeres orangish, distal few flagellomeres appearing dark, covered with greyish scales with whitish scales visible on each side at base of each flagellomeres, these scales more apparent on basal flagellomeres, distal 12–13 flagellomeres composing club.

Thorax: Brownish, dorsally with greyish scales and scales with iridescent coloration, in addition to lightly colored long hair-like scales; laterally and ventrally brownish, scattered with greyish scales and some lightly colored scales, in addition to long hair-like scales; foreleg with whitish long hair-like scales and brownish long hair-like scales, femur, tibia and tarsus similar in length, tarsus not divided into subsegments; pterothoracic legs ventrally appearing lighter compared with more greyish or darker dorsal surface, tibia with two longitudinal rows of spines on ventral surface, as well as spines present laterally, tarsus with three longitudinal rows of spines ventrally until distal end of first tarsomer, number of rows increasing to four from distal end of first tarsomer onwards, pair of tibial spurs, equal in length, present at distal end of tibia.

Wing venation: Basal half of forewing subcostal vein swollen; base of cubitus swollen; forewing recurrent vein absent; discocellular vein m_1-m_2 (i.e., dcs) curved basally, m_2-m_3 (i.e., dcm) appearing rather straight; hindwing humeral vein present, exiting from origin of R_s and curving; origin of M_2 slightly towards M_1 than M_3 (Fig. 5).

Wing shape: Forewing variably sub-triangular, apex rounded, costal margin slightly convex, outer margin somewhat variable but almost straight, inner margin almost straight; hindwing rounded, appearing slightly elongate (apparent in *C. lea* n. comb. and *C. esmeralda* n. sp. due to their rather elongated forewing shape), apex angular, costal margin slightly convex, angled inwards at base, outer margin slightly undulating, inner margin slightly curved inwards near tornus, anal lobe convex, slightly rounded (Fig. 2).

Dorsal forewing: Ground color brownish, varying from being rather uniformly brownish to covered with iridescent to semi-iridescent scales (Fig. 2), submarginal and marginal bands occasionally visible as darker bands.

Dorsal hindwing: Ground color similar to forewing, varying from being rather uniformly brownish to covered with iridescent to semi-iridescent scales (Fig. 2); submarginal and marginal bands occasionally visible as darker bands.

Ventral forewing: Ground color variable, from greyish brown to more brownish, may or may not be covered variably with iridescent scales (Fig. 2); discal band extending from radial vein, crossing discal cell, often passing just basal of origin of Cu_2 , fading and terminating in cell Cu_2 ; concolorous postdiscal band extending from radial vein towards inner margin, terminating at 2A if not already faded in Cu_2 ,

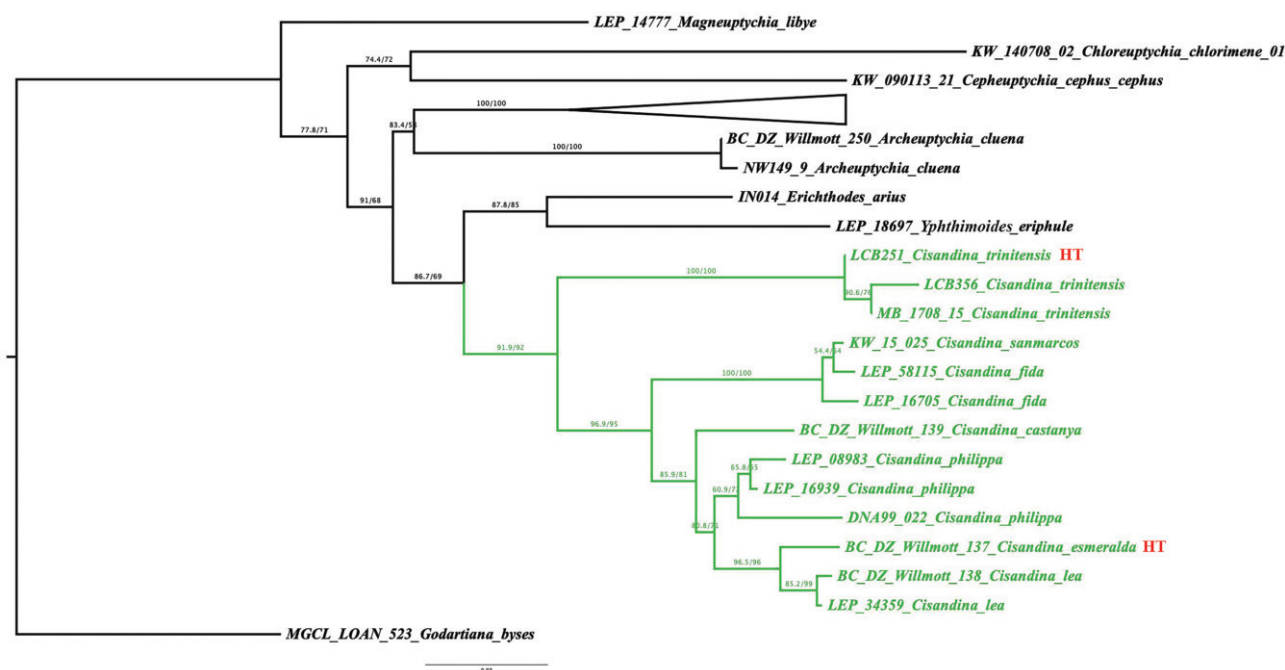


Fig. 1. Maximum likelihood tree (LnL = -11380.331) inferred in IQ-TREE v2.0.5, showing monophyly of *Cisandina* n. gen., as well as relationships of taxa within these genera. Numbers beside branches are SH-aLRT/UFBoot values. HT denotes holotype specimens.

more or less parallel to discal band albeit they may appear close to each other at posterior end; umbra appearing as undefined dark brownish shading extending from area near VFW ocellus (in cell M_1) to cell Cu_2 , if not terminating earlier; submarginal band, appearing darker compared with discal and postdiscal band, often narrower than previous two bands, extending from apex towards tornus, rather smooth although jaggedness can be somewhat variable, appearing more or less evenly broad perhaps except for anterior and posterior end; concolorous marginal band, not jagged, narrower than submarginal band, traversing along marginal area from apex to tornus; fringe greyish; small ocellus in cell M_1 , often possessing black central area and single white pupil with pale ring but may lack one or two of these elements, additional ocellus or ocelli may appear in cells R_s , M_2 , M_3 , and Cu_1 .

Ventral hindwing: Ground color range and variation similar to forewing, may or may not be covered variably with iridescent scales (Fig. 2); discal band, concolorous to that of VFW, similar in width or broader, extending from costa to inner margin, often passing origin of R_s , or just basal of origin of this vein; concolorous postdiscal band passing origin of M_2 and/or Cu_1 , otherwise near origin of these veins, similar in width or broader compared with previous band and appearing more or less parallel; submarginal band, concolorous to that of VFW, similar in width or broader, more jagged, extending from apex towards tornus, posterior end occasionally fused or terminating very close to postdiscal band near inner margin; concolorous marginal band, narrower than previous band and less sinuate, traversing along marginal area from apex to tornus; fringe greyish; six submarginal ocelli in cells R_s , M_1 , M_2 , M_3 , Cu_1 , and Cu_2 (ocellus in cell Cu_2 absent in *C. trinitensis* n. comb.), ocelli in cells M_1 and Cu_1 similar in size (as in *C. castanya* n. sp., *C. fida* n. comb., *C. sanmarcos* n. comb., and *C. esmeralda* n. sp.) or ocellus in Cu_1 may be larger (as in *C. trinitensis* n. comb., *C. lea* n. comb., and *C. philippa* n. comb. & reinst. stat.), both ocelli

often possessing black central area and single white pupil ringed in yellow, ocelli in cells R_s and Cu_2 smaller compared with previous two ocelli but general appearance is same, ocelli in cells M_2 and M_3 are similar in size and appearance to those in cells R_s and Cu_2 but lacking black area, ocellus in cell M_2 placed more basally compared with ocellus in cell M_3 .

Abdomen: Eighth tergite sclerotized in narrow anterior band and broader posterior patch; eighth sternite variable in appearance from rather narrow band to broader patch, as well as separated into two patches in some specimens (see below for further details).

Genitalia: Tegumen somewhat trapezoidal in lateral view (compared with more semi-circular and/or elongated tegumen in many other euptychiines) due to convexity of dorsal margin located posteriorly and anterior portion being rather straight, this convexity of dorsal margin variable as to its degree, ventral margin convex; uncus longer than tegumen in lateral view, setae visible at base and along ventral margin towards posterior end, uncus roughly straight in lateral view, appearing somewhat broad in lateral view towards base, middle section evenly broad in dorsal view, posteriorly terminating in slightly hooked point in lateral view, rather blunt in dorsal view; brachium broad at base, longer than uncus, tapering towards apex and terminating in pointed apical edge, dorsally projecting away from uncus with posterior portion curving back in; combination of ventral arms from tegumen and dorsal arms from saccus somewhat sinuate, roughly evenly broad; appendices angulares present, but not discernible in lateral view, visible as rectangular projection in posterior view (when valva removed); saccus appearance in lateral view varying from straight to curved, but generally length not exceeding uncus; juxta (i.e., fultura inferior) present as narrow stripe; valvae, distal half setose, basal two-thirds roughly rhomboidal in lateral view, apical process approximately one-third of valva although this ratio is variable (see below for further details), varying in

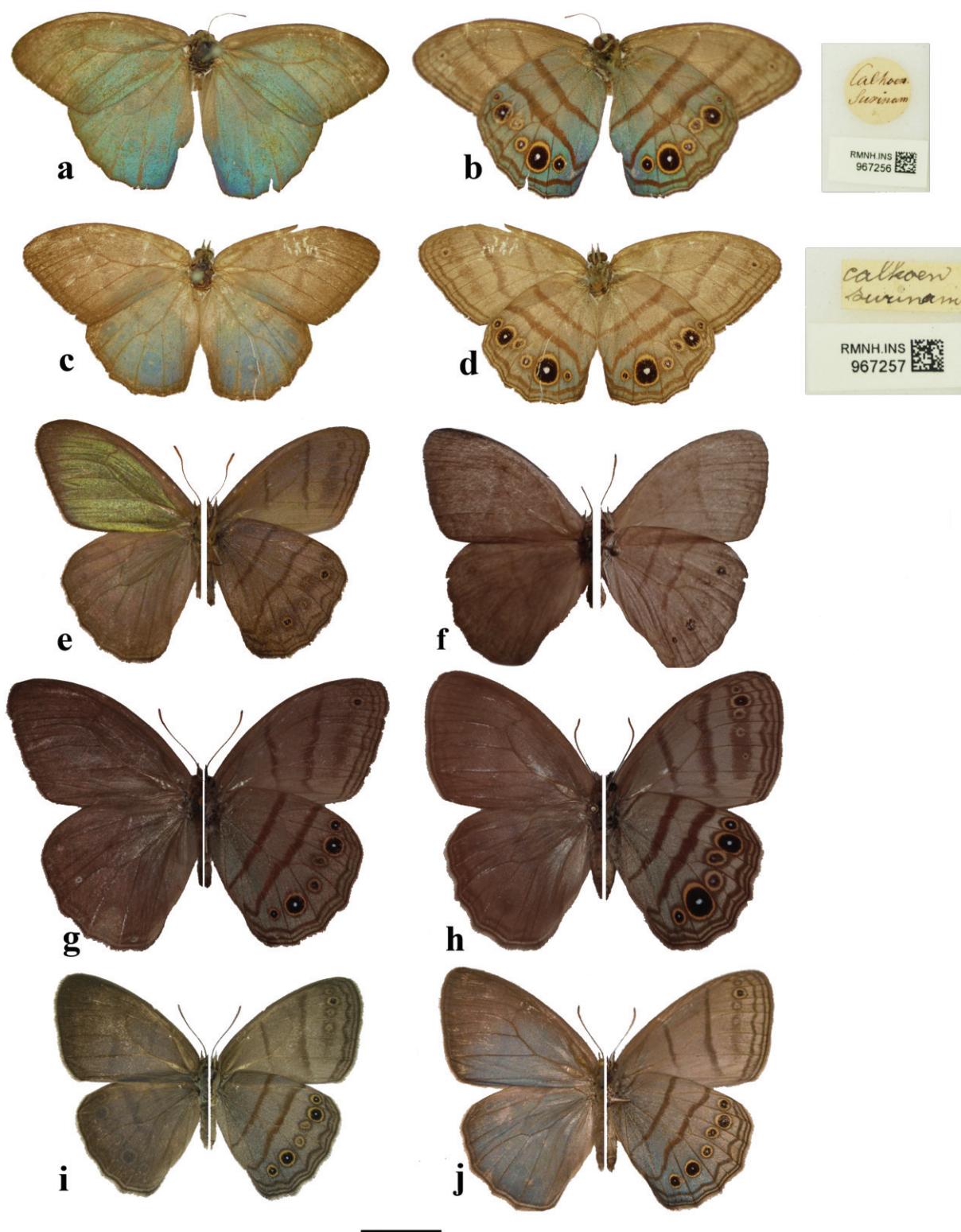


Fig. 2. *Cisandina* n. gen. adults, *C. lea* n. comb.: (a) male lectotype of *Papilio lea* in dorsal view; (b) male lectotype of *Papilio lea* in ventral view (associated labels to the right); (c) female lectotype of *Papilio junia* in dorsal view; (d) female lectotype of *Papilio junia* in ventral view (associated labels to the right); *C. esmeralda* n. sp., (e) male holotype in dorsal view (left), ventral view (right); (f) female paratype in dorsal view (left), ventral view (right) (BC-DZ-139); *C. philippa* n. comb. & reinst. stat.: (g) male individual in dorsal view (left), ventral view (right) (MUSM-LEP-103081); (h) female individual in dorsal view (left), ventral view (right) (MUSM-LEP-103092); *C. castanya* n. sp.: (i) male holotype in dorsal view (left), ventral view (right); (j) female paratype in dorsal view (left), ventral view (right); *C. fida fida* n. comb.: (k) male paralectotype in dorsal view (left), ventral view (right); (l) female lectotype in dorsal view (left), ventral view (right); *C. fida directa* n. ssp.: (m) male holotype in dorsal view (left), ventral view (right); (n) female paratype in dorsal view (left), ventral view (right) (DNA voucher LEP-14650, but sequence not obtained); *C. sanmarcos* n. comb.: (o) male holotype in dorsal view (left), ventral view (right); (p) female paratype in dorsal view (left), ventral view (right) (MUSM-LEP 103661); *C. trinitesis* n. comb.: (q) male holotype in dorsal view (left), ventral view (right); (r) female allotype in dorsal view (left), ventral view (right). Scale bar = 10 mm.

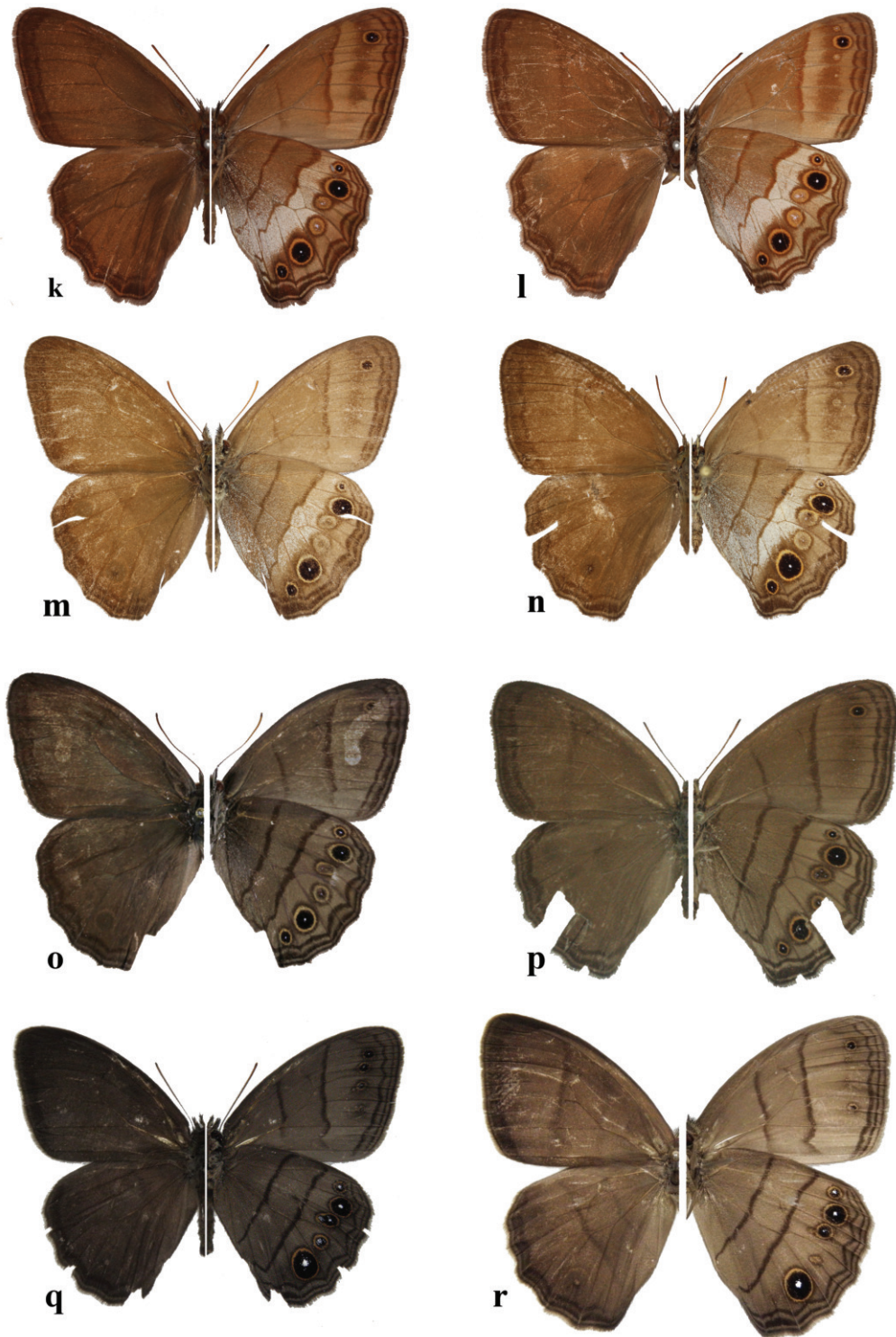


Fig. 2. Continued.

appearance from a narrow, curving process slightly tapering towards apex to a broader, straight process (see below for further details), y terminating in angular tip, dorsal margin just distal of costa curving interiorly forming a sharp projection visible in dorsal view in *C. lea* **n. comb.** but apparently absent in other species, costa appearing somewhat as 'fan-shaped' plate, dorsal margin curving inwards

and folded towards appendices angulares; phallus roughly straight, similar in length to valva in lateral in view, phallobase occupying about half of phallus, antero-dorsal opening large, sclerotized region from dorsal margin of phallobase projecting upwards and apparently forming part of manica at juncture of phallobase and aedeagus, manica covering approximately half of aedeagus, cornuti visible as

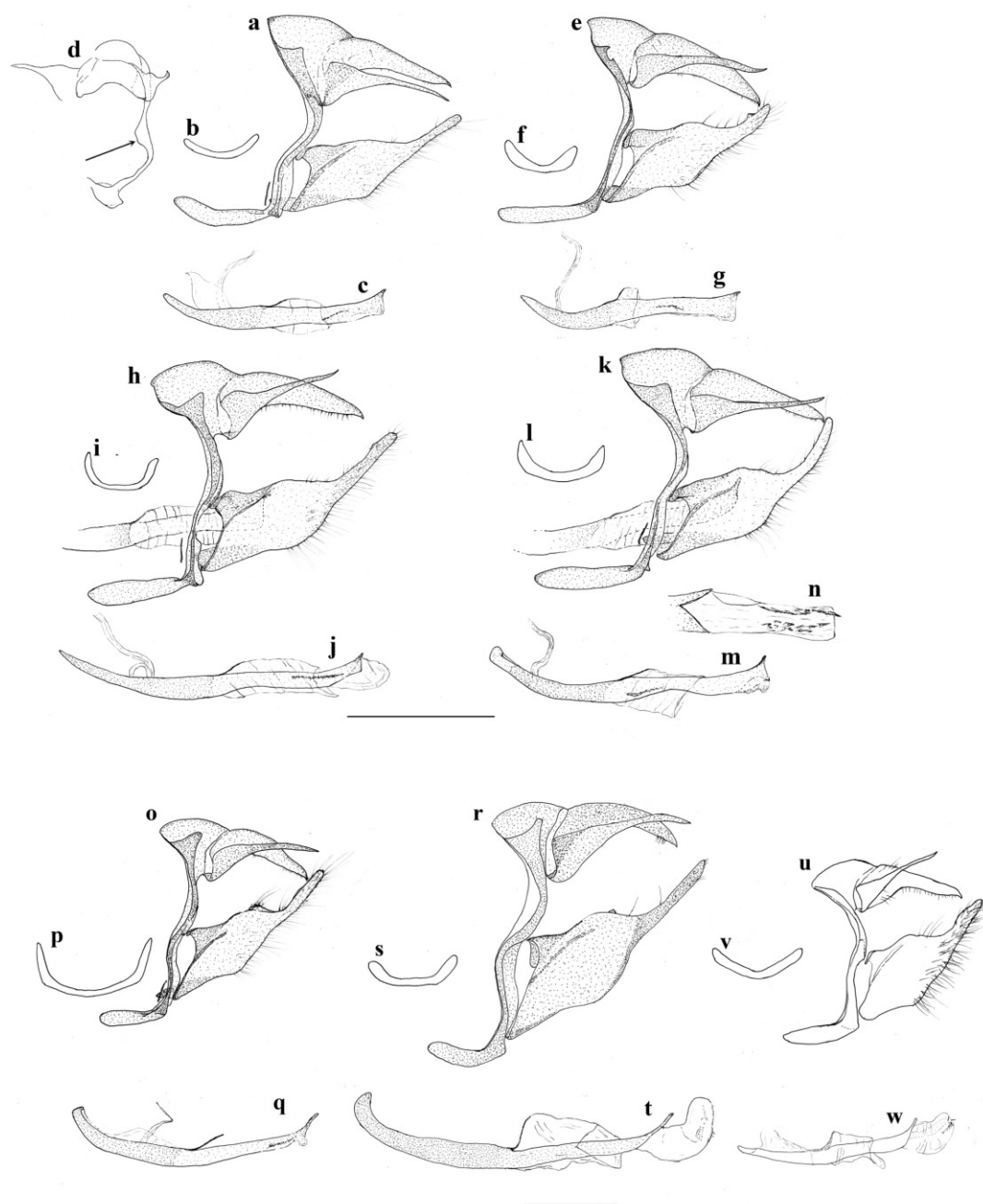


Fig. 3. *Cisandina* n. gen. male genitalia, *C. lea* n. comb.: (a) lateral view of genitalic capsule without phallus; (b) posterior view of juxta; (c) lateral view of phallus; (d) posterior view of genitalic capsule indicating the reduced appendices angulares ([a to c] based on dissection KW-14-18, [d] based on dissection SN-20-16); *C. esmeralda* n. sp.: (e) lateral view of genitalic capsule without phallus; (f) posterior view of juxta; (g) lateral view of phallus (e to g) based on dissection SN-20-14); *C. philippa* n. comb. & reinst. stat.: (h) lateral view of genitalic capsule with phallus; (i) posterior view of juxta; (j) lateral view of phallus ([h to j] based on dissection SN-20-34); *C. castanya* n. sp.: (k) lateral view of genitalic capsule without phallus; (l) posterior view of juxta; (m) lateral view of phallus; (n) vesica everted to visualize cornuti ([k to m] based on dissection SN-20-12, [n] based on SN-20-32); *C. fida* n. comb.: (o) lateral view of genitalic capsule without phallus; (p) posterior view of juxta; (q) lateral view of phallus ([o to q] based on dissection SN-20-40); *C. sanmarcos* n. comb.: (r) lateral view of genitalic capsule with phallus; (s) posterior view of juxta; (t) lateral view of phallus ([r to t] based on dissection SN-14-149); *C. trinitesis* n. comb.: (u) lateral view of genitalic capsule without phallus; (v) posterior view of juxta; (w) lateral view of phallus ([u to w] based on dissection SN-20-84). Scale bar = 1 mm. Drawings of *C. sanmarcos* n. comb. are reproduced from Nakahara et al. (2018a).

roughly two sclerotized narrow patches of vesica, vesica visible at posterior opening of aedeagus (Fig. 3).

Female: Forewing length: 21–27 mm (mean: 23.3 mm; $n = 10$)

Similar to male except as follows: Foretarsus divided into five tarsomeres; forewing somewhat rounded and broader (apparent in *C. lea* n. comb., *C. esmeralda* n. sp., *C. fida* n. comb., and *C. sanmarcos* n. comb. due to their rather elongated male forewing);

overall coloration lighter; iridescent purple-ish lilac reflection on DFW variable, from absent to covering about basal half of DFW; iridescent purple-ish lilac reflection on DHW similarly variable, from absent to covering entire surface of DFW; iridescent scales around VHW tornus often less intense.

Female genitalia and abdomen: Eighth tergite fully developed (as seventh tergite); papilla analis lacking posterior apophysis; lamella antevaginalis sclerotized, forming rounded to rectangular plate with wrinkled margin; sclerotized plate present at lateral side of eighth abdominal segment, anterior margin fused with lamella antevaginalis (lateral margin fused as well in *C. fida* n. comb. and *C. sammarcos* n. comb.), dorsal margin of this lateral sclerotized plate indented around spiracle; inter-segmental membrane of seventh and eighth abdominal segment pleated and expandable, elongated weakly sclerotized region present; ductus bursae membranous, ductus seminalis exits close to ostium bursae, ductus bursae somewhat inflated between origin of ductus seminalis and ostium bursae, corpus bursae ellipse in dorsal view, with two relatively short signa parallel to each other and apparently located laterally, bursa extending to juncture of third and fourth abdominal segment (Fig. 4).

Etymology: This generic name is based on the Spanish word ‘cisandina’, itself a compound word formed of the Latin preposition ‘cis’, meaning ‘on this side of’, and the Spanish adjective ‘andina’, meaning ‘Andean’, which is widely used to refer to the Neotropical region east of the Andes. The name refers to the fact that the species currently contained within this genus are found exclusively east of the Andean continental divide. The generic name should be regarded as a feminine noun in the nominative singular.

Distribution and natural history: *Cisandina* n. gen. is an entirely South American genus known exclusively from east of the Andes (Fig. 8). Specifically, members are known from the cloud forests of the eastern Andes, the lowland rainforest of the Amazon basin, the Guianas, Trinidad, and the Atlantic coastal forest of Brazil and northeastern Argentina. Despite this broad range, no more than two species ever occur in sympatry. All species seem to be uncommon to very rare and are typically found in undisturbed forest. Singer and Ehrlich (1993) reported the host plant of *Cisandina lea* n. comb. (under the name ‘*Cissia junia*’) as being an unidentified Gramineae (Poaceae) species according to their study in Trinidad, although this record is based on a plant accepted by the female in captivity in their oviposition trials. We here provide data on the immature stages of *C. philippa* n. comb. & reinst. stat. and *C. castanya* n. sp., including its natural host plant (Figs. 6 and 7), which constitute to date the only reliable immature stage data available for this genus.

***Cisandina lea* (Cramer, 1777), New Combination**

(Figs. 1, 2a–d, 3a–d, 4a and b, 5, 8)

Papilio lea Cramer, 1777: 87, pl. 151, figs. C, D. Lectotype, designated herein.

=*Papilio junia* Cramer, 1780: 9, pl. 292, figs. D, E. Lectotype, designated herein.

Satyrus lea: Godart [1824]: 464, 492.

Satyrus junia: Godart [1824]: 492.

Euptychia lea: Westwood 1851: 373, Butler 1868: 29, Kirby 1871: 52, Butler 1877: 121, Weymer 1911: 216, pl. 48, fig. f, Gaede 1931: 452, D’Abrera 1988: 768–769, figs.

Euptychia junia: Westwood 1851: 373, Butler 1868: 30, Kirby 1871: 52, Butler 1877: 121, Kirby 1879: 135, Forster 1964: 128, Lamas 2004: 220.

Magneuptychia lea: Forster 1964: 128, Lamas 2004: 220, Beccaloni et al. 2008: 335.

Euptichia [sic] *junia*: Geyer 1832: 12, pl. [109], figs. 627, 628.

Euptychia lea f. *junia*: Weymer 1911: 216.

Euptychia lea var. *junia*: Gaede 1931: 452.

Cissia junia: Singer and Ehrlich 1993: 251, fig. 1.

Systematic placement and diagnosis: Our phylogenetic hypothesis places *Cisandina lea* n. comb. as sister to *C. esmeralda* n. sp., with strong support (Fig. 1; SH-aLRT/UFBoot = 96.5/96). The infra-specific genetic divergence based on DNA barcodes between the two sequenced individuals of *C. lea* n. comb. from two localities (LEP-34359 from French Guiana; BC-DZ-138 from Amazonas, Brazil) was 0.84%, whereas interspecific divergences between *C. lea* n. comb. and three sampled specimens of *C. esmeralda* n. sp. range from 5.01 to 5.3%. These three individuals of *C. esmeralda* n. sp. are from two sites, including BC-DZ-137 (holotype) from Paraná, Brazil, and the other two specimens from Misiones, Argentina. The infraspecific genetic divergences among these three sequenced individuals of *C. esmeralda* n. sp. were 0.02%. See Table 3 for further information regarding genetic divergence among *Cisandina* n. gen. taxa. The male of *C. lea* n. comb. is readily distinguished from *C. esmeralda* n. sp. by its iridescent to semi-iridescent bluish flush covering the DFW and DHW, whereas the DFW and DHW discal cell and adjacent area is greenish in male *C. esmeralda* n. sp. The broader ventral bands and larger ventral submarginal ocelli of *C. lea* n. sp. can be used to distinguish both sexes of these two closely related species. The female of *C. lea* n. comb. is also distinguished from the female of *C. esmeralda* n. sp. by the presence of iridescent bluish lilac reflection on the DHW, whereas this reflection appears more purplish in the female of *C. esmeralda* n. sp., and the ventral bands and ocelli overall appear larger in *C. lea* n. sp. compared with its sister species.

Taxonomy: *Papilio lea* was described by Pieter Cramer, a Dutch merchant, in his *De Uitlandsche Kapellen* series (work completed by Caspar Stoll) based on an unspecified number of specimen(s) from ‘Berbices’, a then Dutch colony (i.e. Dutch Guiana) along Rio Berbice, an area now part of the Republic of Guyana. The original description only states ‘the blue color on both sides of the wings is shiny’. Nevertheless, Cramer provided illustrations of both wing surfaces of this taxon (pl. 151, figs. C, D), which can be used to narrow down the identity of *P. lea*. His drawings of this species clearly show the basal half of its DFW and all of the DHW being blue, although the anterior side of the DHW is not visible due to being covered by the forewing. The hindwing illustration shows six individual submarginal ocelli on the VHW in cells Rs, M₁, M₂, M₃, Cu₁, and Cu₂, with the ocellus in cell M₂ placed more basally compared with that in cell M₃, as well as a single ocellus present on the VFW. There is some bluish coloration visible on the DFW and DHW, especially along the ventral bands and around the VHW submarginal ocelli. The presence of six VHW ocelli excludes all Neotropical satyrine species with blue DFW and/or DHW, in genera such as *Caeruleuptychia* Forster, 1964, *Magneuptychia*, *Chloeuptychia* and *Amiga* Nakahara, Willmott, & Espeland 2019, as candidates for the species under description by Cramer, because all the species in those genera which possess bluish coloration only have five VHW ocelli, with the exception of a few species in *Caeruleuptychia*. *Caeruleuptychia twalela* Brévignon, 2005, *Cae. pilata* (Butler, 1867), and *Cae. scripta* Nakahara, Zacca,

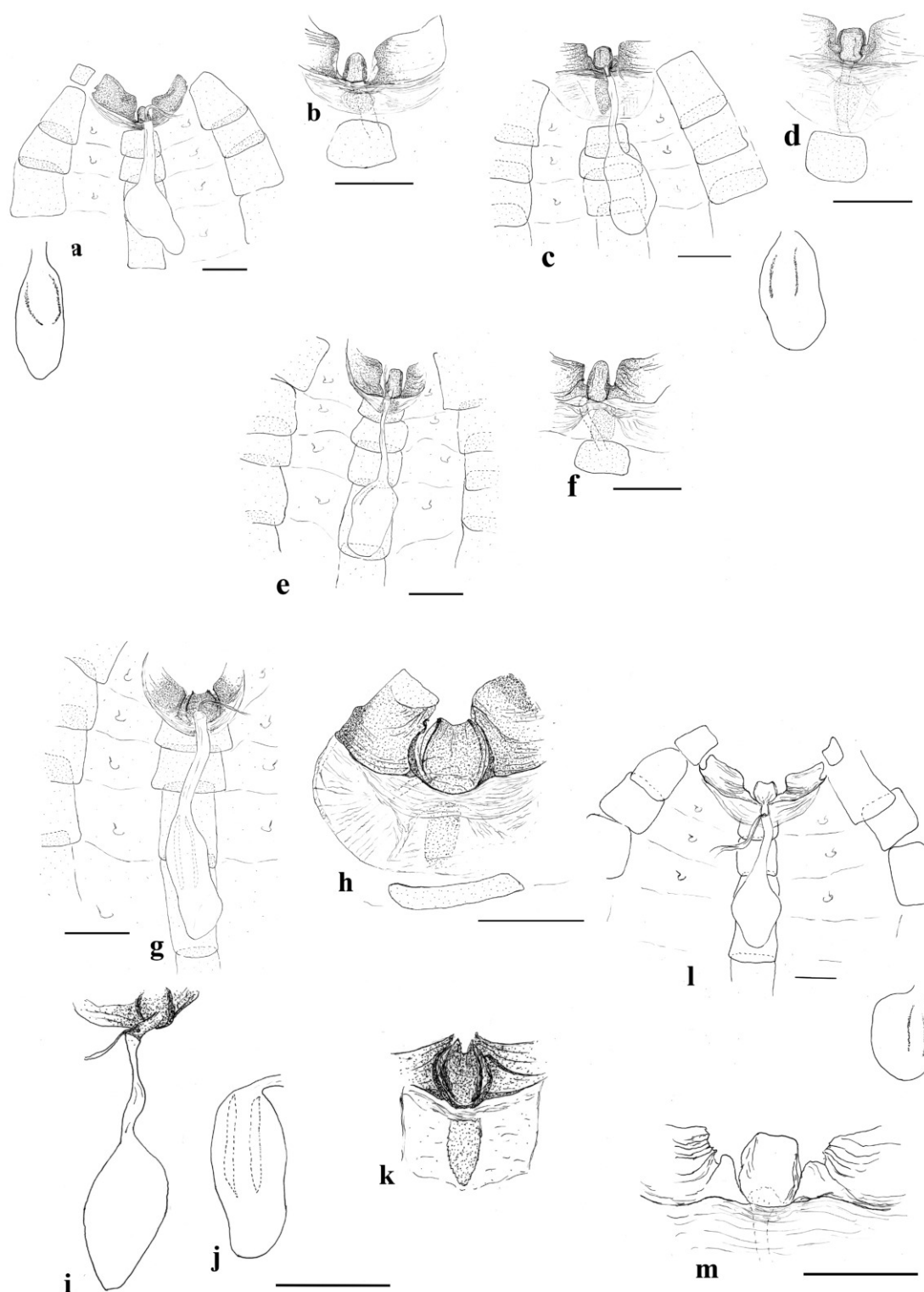


Fig. 4. *Cisandina* n. gen. female genitalia, *C. lea* n. comb.: (a) dorsal view of genitalia with intersegmental membrane of seventh and eighth abdominal segments folded; illustration showing arrangement of signa below (not to scale); (b) ventral view of lamella antevaginalis with intersegmental membrane of 7th and 8th abdominal segments expanded ([a and b] based on dissection SN-20-53); *C. philippa* n. comb. & reinst. stat.: (c) dorsal view of genitalia with intersegmental membrane of seventh and eighth abdominal segments expanded; illustration showing arrangement of signa to right (not to scale); (d) ventral view of lamella antevaginalis with intersegmental membrane of seventh and eighth abdominal segments expanded ([c and d] based on dissection SN-20-11); *C. castanya* n. sp.: (e) dorsal view of genitalia with intersegmental membrane of seventh and eighth abdominal segments folded; (f) ventral view of lamella antevaginalis with intersegmental membrane of seventh and eighth abdominal segments expanded ([e and f] based on dissection SN-20-13); *C. fida* n. comb.: (g) dorsal view of genitalia with intersegmental membrane of seventh and eighth abdominal segments folded; (h) ventral view of lamella antevaginalis with intersegmental membrane of 7th and 8th abdominal segments expanded ([g and h] based on dissection SN-15-180); *C. sanmarcos* n. comb.: (i) female genitalia

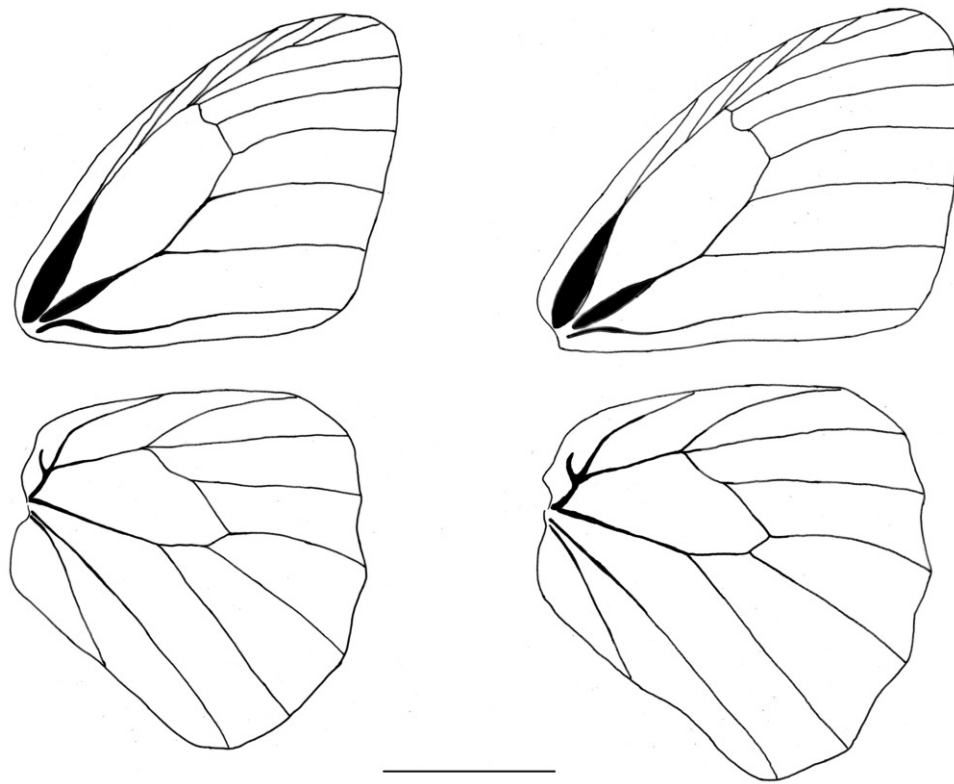


Fig. 5. *Cisandina lea* n. comb. wing venation, male to the left, female to the right. Scale bar = 10 mm.

& Huertas, 2017 are the only three *Caeruleptychia* species with bluish scales and six VHW ocelli, but the dorsal surface of *Cae. twalela* is entirely brown; the orangish rings of the VHW ocelli in cells M_1 and Cu_1 are skewed (i.e., not evenly broad) in *Cae. pilata* and *Cae. scripta*, whereas the rings of these ocelli are evenly broad in Cramer's illustration. Perhaps one of the most notable features in Cramer's drawing is the VHW ocellus in cell M_2 being placed more basally compared with that in cell M_3 , a distinctive feature of *Cisandina* n. gen. This character excludes the possibility of Cramer referring to virtually any other euptychiine species apart from those discussed herein. Those few exceptions include some species in *Moneuptychia* Forster, 1964 such as *M. vitellina* Freitas & Barbosa, 2015, which can easily be distinguished by the lack of bluish coloration on the wing surface. Thus, Cramer's *P. lea* represents either the female of *P. lea* as conceived herein, possibly *C. philippa* n. comb. & reinst. stat. (in which some females have bluish dorsal coloration), or one of the new species described and named in this study. However, it is very unlikely that Cramer's illustration represents *C. castanya* n. sp., *C. esmeralda* n. sp., or *C. philippa* n. comb. & reinst. stat., since none of these species are known from the Guianas.

Our attempt to locate syntype(s) of *P. lea* resulted in finding three candidate specimens in RMNH, two females each with a label indicating '[Johan] Calkoen' with the locality 'Surinam[e]' (RMNH. INS 967256 and 967257), and a male specimen with a round label indicating 'Verloren [van Themaat] Brasil' (RMNH.INS 967280). Two collections now housed at RMNH, namely Joan Raye Heer

van Breukelerwaard's and Johan Calkoen's collections, are both known to include Cramer types (de Jong 1982, Smit et al. 1986, Gernaat et al. 2012), and the former pair from 'Surinam[e]' are evidently from the latter collection. The latter male from the Verloren van Themaat collection can also be regarded as a Cramer type based on information from some existing literature on his collection (e.g., Roepke 1941). Verloren van Themaat purchased van Eyndhoven's collection that was believed to have been sold on 14 October 1861 (see Chainey 2005; Smit et al. 1986) which is another collection believed to have included Cramer specimens (Horn and Kahle 1935, Roepke 1941). Despite the fact that Verloren van Themaat's collection is supposed to have been destroyed due to an unfortunate battle when the collection was kept near Utrecht (Chainey 2005), we cannot exclude the possibility of some specimens ending up at Leiden where the RMNH is situated. Although lacking the abdomen, the female specimen (RMNH.INS 967257) does overall match Cramer's illustration of *P. lea*, with minor differences, such as bluish scales on the DFW being somewhat restricted to cells Cu_2 and 2A (not covering the basal half as in fig. C), but this is likely due to the color being faded over time. Nevertheless, its locality 'Surinam[e]' historically never included 'Berbice' (the type locality of *P. lea*), which was then referred to as Dutch Guiana, and thus, it is debatable whether this female represents a syntype of *P. lea* or not. Confusingly, Butler (1877: 121) listed 'Surinam[e]' as the type locality for *Euptychia lea* (= *P. lea*), without any apparent evidence as to whether this was a misinterpretation or not. The only clue as

without abdomen illustration; (j) illustration indicating location of signa on corpus bursae to left; (k) ventral view of lamella antevaginalis with intersegmental membrane of seventh and eighth abdominal segments expanded ([j and k] based on dissection SN-16-17); *C. trinitensis* n. comb.: (l) dorsal view of genitalia with intersegmental membrane of seventh and eighth abdominal segments folded; illustration showing arrangement of signa to right (not to scale); (m) ventral view of lamella antevaginalis with intersegmental membrane of 7th and 8th abdominal segments expanded ([l and m] based on dissection SN-20-85). Scale bar = 1 mm. Drawings of *C. sanmarcos* n. comb. are reproduced from Nakahara et al. (2018a).

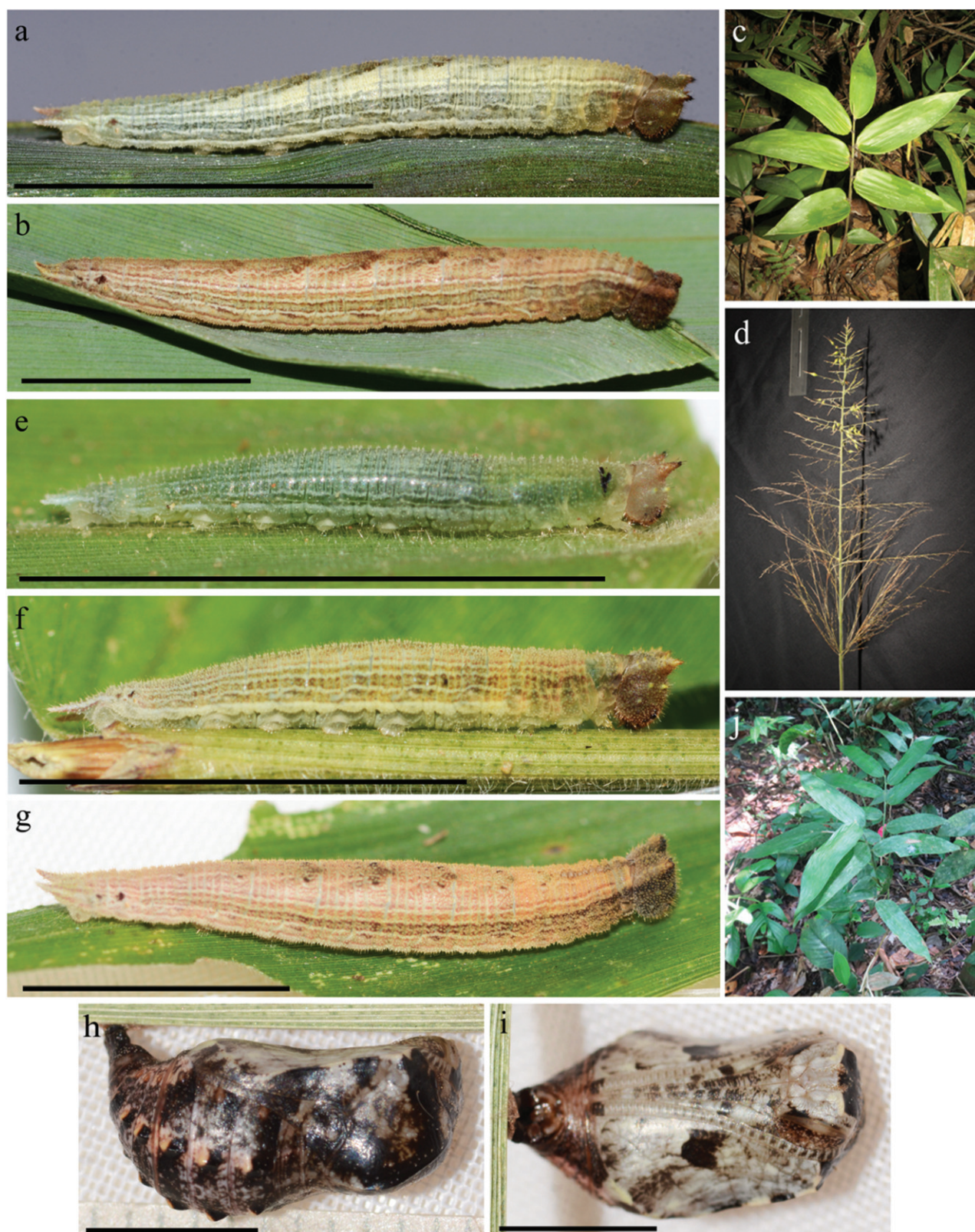


Fig. 6. *Cisandina* n. gen. immature stages, *C. philippa* n. comb. & reinst. stat. based on 2020-FLP-IMM-0336: (a) penultimate instar in dorso-lateral view; (b) last instar in dorso-lateral view; (c) host plant of *C. philippa* n. comb. & reinst. stat., *Taquara micrantha* (Poaceae) *in situ*; (d) inflorescence material of (c); *C. castanya* n. sp. based on 2020-FLP-IMM-0188: (e) second instar in lateral view; (f) third instar in lateral view; (g) fourth instar in lateral view; (h) pupa in lateral view; (i) pupa in ventral view; (j) host plant of *C. castanya* n. sp., *Olyra latifolia* (Poaceae) *in situ*. Scale bar = 1 mm for a, b, e-g; 5 mm for h, i.

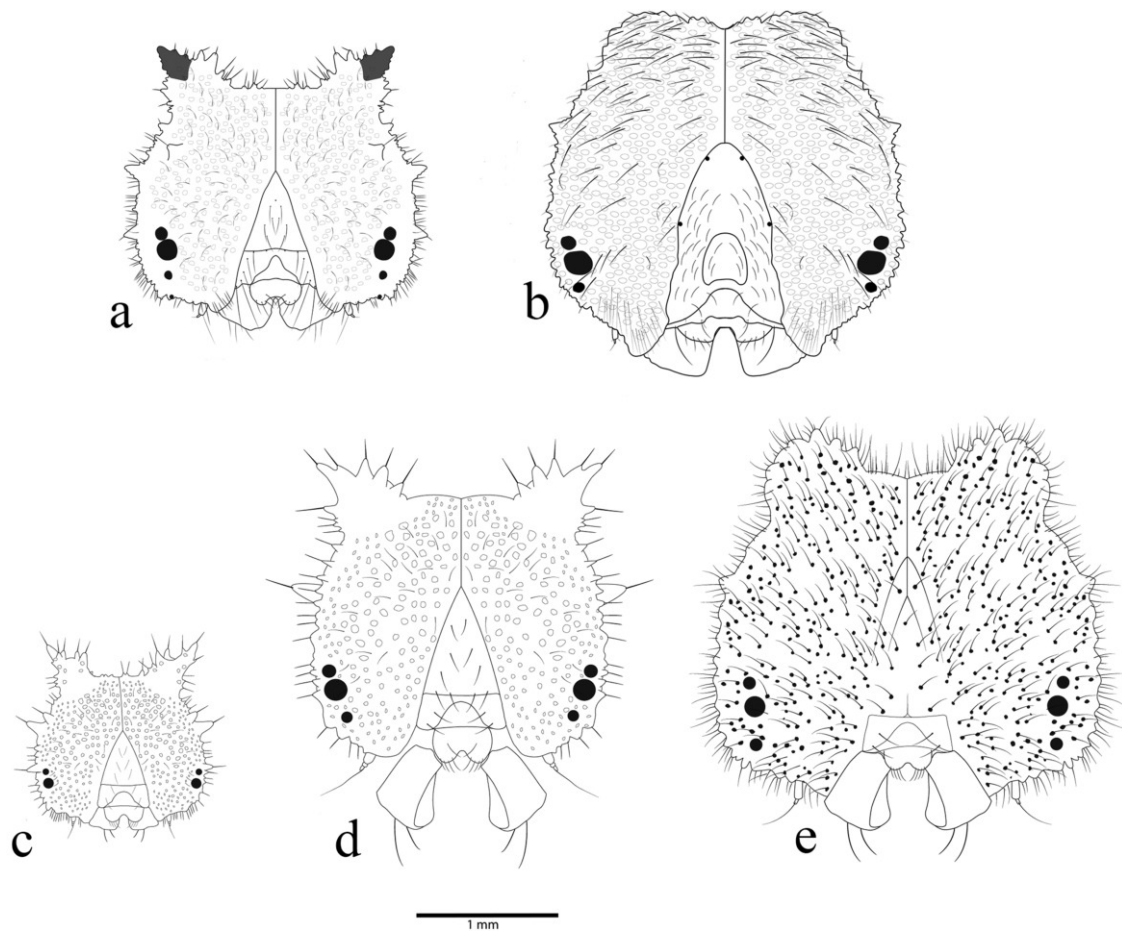


Fig. 7. *Cisandina philippa* n. comb. & reinst. stat. head capsule illustration based on 2020-FLP-IMM-0336: (a) penultimate instar in frontal view; (b) last instar in frontal view. *Cisandina castanya* n. sp. head capsule illustrations based on 2020-FLP-IMM-0188: (c) second instar in frontal view; (d) third instar in frontal view; (e) fourth (last) instar in frontal view. Scale bar = 1 mm.

to the whereabouts of the syntypes is contained in the last part of Cramer's description '[The specimen(s)] now rests in the previous collection', referring to the last part of the description of the immediately preceding taxon, 'Merope', described on the same page, 'She rests in the Cabinet (=collection) of the honorable gentleman A. Gevers'. As mentioned by Chainey (2005), this 'A. Gevers' most likely refers to Abraham Paulusz Gevers (1712–1780), then the Mayor of Rotterdam, who had a natural history collection which was auctioned in 1787. Despite having no evidence of acquisition, specimens from his collection were perhaps bought by Calkoen and ended up in the RMNH, thus there exist a possibility that the provenance of the aforementioned specimen from 'Surinam[e]' is the Gevers collection, but with a changed locality.

Three years later, Cramer described *Papilio junia*, a taxon now regarded as a junior subjective synonym of *Papilio lea* by Lamas (2004), again in his *De Uitlandsche Kapellen*. Like his description of *Papilio lea*, the number and sex of the examined specimen(s) used to describe *P. junia* cannot be unambiguously determined from the original description, except for the type locality being 'Surinam[e]'. Cramer's description is again terse, and his Dutch and French texts are accompanied with illustrations of both dorsal and ventral surfaces (pl. 292, figs. D, E). As stated in the text, the DFW and DHW are entirely bluish (described as 'cerulean satin-like shine' by Cramer), with his paintings reflecting a lighter blue color relative to the darker blue coloration of the dorsal wing

shown in his illustration of *P. lea*. The general wing pattern of the ventral surface is similar to that of his illustration of *P. lea*, with some minor differences such as a paler ground color, more elongated VHW submarginal ocelli, and bluish coloration on the VHW restricted to the inner margin. It must be noted that a number of painters were involved in producing copies of Cramer's work, and there is some evidence that inevitably some variability in markings and coloration resulted, in comparison with his original drawings (Chainey 2005). Thus, these subtle dissimilarities mentioned above may not actually reflect the differences observed by Cramer himself. However, it is worth noting the small incomplete ocelli in VFW cells M_2 and M_3 visible in the illustration of *P. junia*, which are especially apparent on the right wing, and which appear to be absent in his illustration of *P. lea*. The male specimen from the Verloren collection mentioned above (RMNH.INS 967280) does exhibit ocelli on the right VFW in cells M_2 and M_3 , in addition to having an extra ocellus above M_1 . The male specimen from the Calkoen collection also possesses a tiny smudge-like ocellus in the right VFW cell M_2 , although apparently the ocellus is absent in cell M_3 . Since its description, the taxonomic viewpoint of subsequent authors concerning *P. junia* has been variable, ranging between some regarding it as a valid species (e.g., Butler 1877, Forster 1964) and some considering it to be conspecific with *P. lea* (e.g., Weymer 1911, Lamas 2004). Despite this unstable taxonomic status, it is noteworthy that these names have rarely been applied

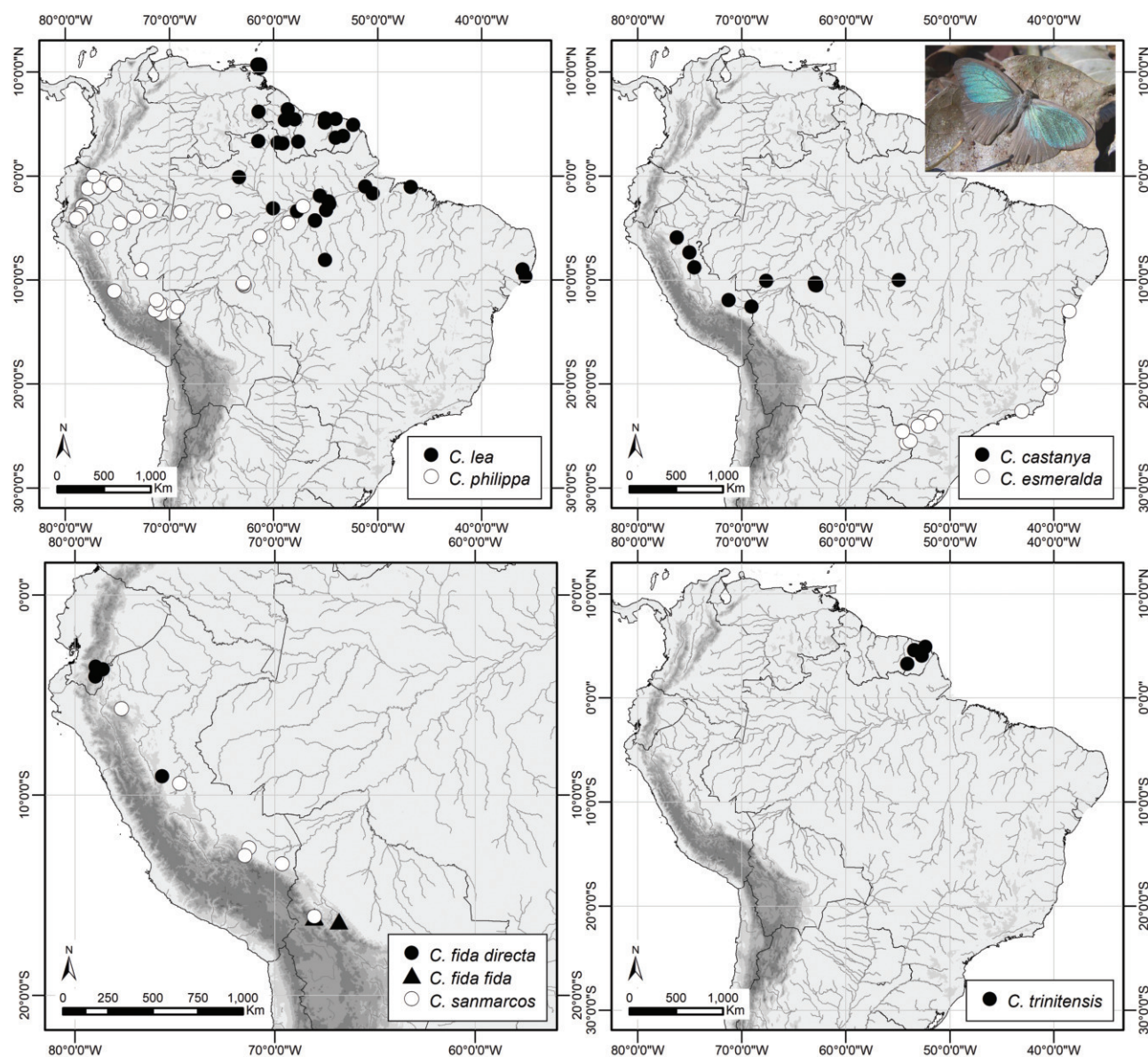


Fig. 8. Distribution map for *Cisandina* n. gen. taxa discussed herein.

to other euptychiine species in museum collections and/or scientific articles, with few exceptions (e.g., D'Abrera 1988), an unusual situation for a group where misidentification is extremely common. Specifically, the male specimen of this taxon, as painted by Cramer (pl. 292, figs. D, E), is distinctive and is less likely to be misidentified compared with the female which can be confused with species in the same genus such as *C. castanya* n. sp. Recently, Nakahara et al. (2019a) did not accept Calkoen specimens (also housed in the RMNH) as potential syntypes of *Papilio ebusa* Cramer 1780 because of the discrepancy in terms of the type locality indicated on the associated label. Unlike this previous case, the handwritten locality on the rounded label for RMNH.INS 967256 does match the type locality indicated in Cramer's description of *P. junia*, both being 'Surinam[e]'. Thus, there seems to be no reason to reject this male specimen as a syntype, and thus we here designate this male syntype as the lectotype for *P. junia* with the following labels separated by double-forward slashes (lectotype designation): //Calkoen Suriname// RMNH.INS 967256//. Accepting this male specimen as

a former syntype of *P. junia* reinforces the possibility of the aforementioned female specimen (RMNH.INS 967257) being a syntype of *P. lea* with an erroneous locality on the label. The fact that only a single female for a possible Cramer syntype was located at RMNH matches the fact that Cramer illustrated a female for *P. lea* and a male specimen for *P. junia*. Therefore, we designate this female from the Calkoen collection as the lectotype of *P. lea* with the following labels separated by double-forward slashes (lectotype designation): //Calkoen Suriname// RMNH.INS 967257//.

Distribution and natural history: *Cisandina lea* n. comb. is known from the Guianas, Trinidad, southern Venezuela, as well as the central and lower Amazon in Brazil, in addition to northeastern Brazil (Fig. 8).

Specimens examined (129 ♂, 80 ♀): **Brazil:** Alagoas: São José de Lage, Usina Serra Grande, [8°58'S, 36°3'W], 400–500 m, 1–3 Aug 2003, 1 ♀, (ZUEC); Maceió, [9°39'S, 35°46'W], (Cardoso, A.), 30

Apr 1945, 1 ♀, (DZUP); *Amazonas*: Barcelos, Rio Aracá, Foz do Rio Curuduri, [0°5'50"S, 63°17'22"W], (Mielke, O. H. H., Casagrande, M. M.), 15–19 Jun 2010, 1 ♀, (DZ 49.955, BC-DZ 138) (DZUP); Ega (= Tefé), [3°22'S, 64°42'W], (Bates, H. W.), 1 ♀ [BMNH(E)-1497637], (NHMUK); Manaus, [3°7'S, 60°2'W], (Hahnel, 1886, 1 ♀, (MNHU); Manicoré, [5°49'S, 61°17'W], (Le Moul, E.), 1 ♂ [FLMNH-MGCL-265701], (FLMNH); Maués, [3°22'S, 57°43'W], (Le Moul, E.), 1 ♂ [FLMNH-MGCL-265699], 1 ♀ [FLMNH-MGCL-265703], (FLMNH); Rio Negro, 50-km NW Manaus, (Schmidt, U.), 1–4 Nov 1993, 1 ♀ [FLMNH-MGCL-265705], [dissection, SN-20-31] (FLMNH); *Bahia*: [12°59'S, 38°31'W], 1 ♂ [BMNH(E)-1497632], (NHMUK); *Espírito Santo*: [20°20'S, 40°17'W], 1 ♂ [BMNH(E)-1497649], 1 ♂ [BMNH(E)-1497650], 1 ♂ [BMNH(E)-1497651], (NHMUK); *Pará*: [Rio] Tapajós, [4°16'8"S, 55°59'10"W], 25 m, (Bates, H. W.), 1 ♂ [BMNH(E)-1497630], (NHMUK); *Amazonas*, (Fassl, A. H.), (ZSM); Bragança, [1°3'S, 46°47'W], (Mathan, M. de), 1 ♀ [BMNH(E)-1497641], (NHMUK); Breves, [1°40'S, 50°28'W], 1 ♀ [BMNH(E)-525609], (NHMUK); hwy Cuiabá-Santarém, km 1666, [3°17'17"S, 54°56'22"W], -150, (Callaghan, C. J.), 28 Jul 1978, 1 ♂ [FLMNH-MGCL-265697], (FLMNH); hwy Cuiabá-Santarém, km 958, [8°3'S, 55°2'W], (Callaghan, C. J.), 30 Jul 1978, 1 ♀ [FLMNH-MGCL-265706] [dissection, SN-20-17], (FLMNH); Itaituba on Rio Tapajós, [4°16'8"S, 55°59'10"W], (Le Moul, E.), 1 ♂ [FLMNH-MGCL-265702], [dissection, SN-20-16] (FLMNH); Itaituba, [4°17'S, 55°59'W], (Mich.), 1890, 1 ♀ [dissection, Lee D. Miller 9136], (MNHU), 1893, 1 ♂ [dissection, Lee D. Miller 9135], (MNHU); Itaituba, Rio Tapajós, [4°16'8"S, 55°59'10"W], 25 m, (Lathy), May 1932, 1 ♂ [BMNH(E)-1670284], (NHMUK); Óbidos, [1°54'S, 55°31'W], (Le Moul, E.), 1 ♂ [FLMNH-MGCL-265700], (FLMNH); Pará, [1°0'S, 51°11'W], 1 ♂ [BMNH(E)-1497629], 1 ♀ [BMNH(E)-1497640], (NHMUK), (Bates, H. W.), 1 ♀ [BMNH(E)-1497638], (NHMUK), (Wallace), 1 ♀ [BMNH(E)-1497639], (NHMUK); Rio Tapajós, [4°16'8"S, 55°59'10"W], 25 m, (Klug, G. G.), Chainey 2005 Cramer ep 1931, 1 ♀ [BMNH(E)-1497729], (NHMUK); Rio Tapajós, Mujo, [2°41'S, 54°38'W], (Le Moul, E.), 1 ♂ [FLMNH-MGCL-265698], (FLMNH), Sep 1922, 1 ♀ [FLMNH-MGCL-265704], (FLMNH); Santarém, [2°26'S, 54°43'W], (Smith, H. H.), 1 ♂ [BMNH(E)-1497631], 1 ♀ [BMNH(E)-1497642], 1 ♀ [BMNH(E)-1497643], (NHMUK); *Roraima*: Alto Alegre, Ilha de Maracá, [3°21'41"N, 61°26'2"W], (Mielke, O. H. H., Casagrande, M. M.), 24–31 Aug 1987, 3 ♂ 1 ♀ (DZ 49.925, DZ 49.935 - BC-DZ Willmott 191, DZ 49.945, DZ 49.965, 23–28 Feb 1988, 2 ♀ (DZ 5371, DZ 49975) (DZUP); *Not located*: 'Brasília', 1 ♂ [BMNH(E)-1497635], (NHMUK); 'Brazil', 1 ♂ [BMNH(E)-1497633], 1 ♂ [BMNH(E)-1497634], 1 ♂ [BMNH(E)-1497636], 1 ♂ [BMNH(E)-1497652], 1 ♂ [BMNH(E)-1497653], 1 ♂ [BMNH(E)-1497654], 1 ♀ [BMNH(E)-1497647], 1 ♀ [BMNH(E)-1497648], (NHMUK); *not located*: 'Amazon', 1 ♂ [BMNH(E)-1497714], 1 ♂ [BMNH(E)-1497727], (NHMUK), (Bates, H. W.), 1 ♀ [BMNH(E)-1497730], (NHMUK) [Bates only collected in Brazil]. **French Guiana**: *Cayenne*: Cayenne, [4°56'N, 52°20'W], 1 ♂ [BMNH(E)-787669], (NHMUK); *Saint-Laurent-du-Maroni*: Bas Maroni, 1 ♂ [FLMNH-MGCL-265707; dissection, KW-14-018], (FLMNH); Maroni River, (Le Moul, E.), 1 ♀ [FLMNH-MGCL-265708], (FLMNH); Maroni river, Maripasoula, [3°41'N, 54°2'W], (Brévignon, C.), 14 May 1987, 1 ♂ [MUSM-LEP-103094], (MUSM); Saül, [3°51'30"N, 53°18'14"W], 200–450 m, (Nakahara, S.), 5 Aug 2014, 1 ♂ [FLMNH-MGCL-209436], 1 ♀ [FLMNH-MGCL-195747], (FLMNH); St. Laurent du Maroni, [5°30'N, 54°2'W], Jul-Sep 1915, 1 ♂ [BMNH(E)-1497720], (NHMUK), (Le Moul), Nov, 1 ♂ [BMNH(E)-1497721], (NHMUK);

Not located: 'French Guiana', (Bar, C.), 1 ♂ [BMNH(E)-1497722], 1 ♂ [BMNH(E)-1497723], (NHMUK). **Guyana**: *Cuyuni-Mazaruni*: Bartica, [6°24'N, 58°37'W], (Parish, H. S.), 1 ♂ [BMNH(E)-787654], 1 ♀ [BMNH(E)-787665], (NHMUK), (Parish, H.S.), 1 ♂ [BMNH-E-787654], 1 ♀ [BMNH-E-787665], (NHMUK); *East Berbice-Corentyne*: New River Triangle, Camp Jaguar, [3°18'23"N, 57°35'21"W], 152 m, (Steinhauser, S. R.), 13 Nov 1980, 1 ♀ [FLMNH-MGCL-265710], (FLMNH); *Upper Demerara-Berbice*: Berbice, [5°27'N, 57°57'W], 1 ♂ [BMNH(E)-787651], 1 ♂ [BMNH-E-787651], (NHMUK); *Upper Takutu-Upper Essequibo*: E. Kanuku Mountains, Two Hat Mountain, [3°8'48"N, 59°6'54"W], 244 m, (Fratello, S., et al), 17 Sep–2 Oct 2000, 1 ♂, (USNM); Essequibo River, (Büche, M.), Jul 1997, 1 ♂ [MUSM-LEP-103093], (MUSM); Essequibo River, Aunai, [5°22'N, 58°53'W], (Whitely, H.), 1 ♂ [BMNH(E)-787650], 1 ♂ [BMNH-E-787650], 1 ♀ [BMNH(E)-787664], 1 ♀ [BMNH-E-787664], (NHMUK); Kanuku Mountains, [3°12'N, 59°34'W], 152–305 m, (Fratello, S., Hanner, R., Hendricks, S., Williams, R.), 21 Feb–10 Mar 1999, 1 ♂, (USNM); Lethem, (Le Moul, E.), 8 Aug 1971, 1 ♀ [FLMNH-MGCL-265709], (FLMNH); *Not located*: 'Guyana', 1 ♂ [BMNH(E)-787652], 1 ♂ [BMNH-E-787652], 1 ♀ [BMNH(E)-1497716], 1 ♀ [BMNH-E-787669], (NHMUK), (Parish), 1 ♀ [BMNH-E-787667], (NHMUK), (Parish, H. S.), 1 ♀ [BMNH(E)-787667], (NHMUK), (Whitely), 1 ♀ [BMNH-E-787666], (NHMUK), (Whitely, H.), 1 ♀ [BMNH(E)-787666], (NHMUK); Demerara River, Akayma Fort, 1 ♀ [BMNH(E)-1497715], (NHMUK). **Suriname**: *Brokopondo*: Berg-en-Dal, [5°9'N, 55°4'W], (Ellacombe, C. W.), Apr 1892, 1 ♂ [BMNH(E)-787668], (NHMUK), (Ellacombe, C.W.), Apr 1892, 1 ♀ [BMNH-E-787668], (NHMUK); *Para*: Bersaba, [5°32'N, 55°3'W], (Michls.), 1898–1899, 1 ♂ [dissection, M-9137 Lee D. Miller], (MNHU); *Not located*: 'Surinam', 1 ♂ [BMNH(E)-1497718], 1 ♂ [BMNH(E)-1497719], 1 ♂ [BMNH(E)-787656], (NHMUK), (Fruhstorfer), May–Sep, 1 ♂ [BMNH-E-787656], (NHMUK); 'Surinam', (ZSM); 'interior Surinam', (Ellacombe, C. W.), Sept 1892, 1 ♂ [BMNH(E)-1497717], (NHMUK). **Trinidad**: *Couva-Tarabaquite-Talparo*: Caparo, [10°34'N, 61°16'W], (Birch, F.), 1 ♀ [BMNH-E-787662], (NHMUK); Narieva, Tabaquite, [10°23'N, 61°18'W], 1 ♂ [BMNH(E)-1497678], 1 ♂ [BMNH(E)-1497679], 1 ♀ [BMNH(E)-1497671], 1 ♀ [BMNH(E)-1497672], (NHMUK); *Diego Martin*: Fort George, [10°42'N, 61°32'W], Sept. 1891, 1 ♂ [BMNH(E)-1497660], 1 ♂ [BMNH(E)-1497661], 1 ♂ [BMNH(E)-1497662], 1 ♂ [BMNH(E)-1497663], 1 ♂ [BMNH(E)-1497664], 1 ♂ [BMNH(E)-1497665], 1 ♀ [BMNH(E)-1497666], 1 ♀ [BMNH(E)-1497667], (NHMUK); Mt. Catherine upper trail, (Preston, J. & F.), 27 Feb 1982, 1 ♀ [FLMNH-MGCL-265722], 1 ♀ [FLMNH-MGCL-265723], (FLMNH); *Port of Spain*: Port of Spain, [10°40'N, 61°31'W], (Jenkins, D. W.), 27 Jan 1977, 1 ♂ [FLMNH-MGCL-265715], (FLMNH), (Rosen, V.), 23 Oct, (ZSM); *Rio Claro-Mayaro*: 'Nariva', 06-05-1993, 1 ♂ [BMNH(E)-1670212; 'Swamp'], (NHMUK); *San Juan-Laventille*: Fondes Amandes Road, (Patterson, E. J.), 1 ♀ [FLMNH-MGCL-265724], (FLMNH); Hololo Mt., [10°41'29"N, 61°29'7"W], (Morrall, J.), 4 Oct 2012, 1 ♂, (MZUJ); Maraval, [10°43'N, 61°31'W], Jan '92, 1 ♂ [BMNH(E)-1497680], 1 ♂ [BMNH(E)-1497681], 1 ♀ [BMNH(E)-1497684], 1 ♀ [BMNH(E)-1497685], (NHMUK), (Hall, A.), Nov 1931–Feb 1932, 1 ♂, (BMB); St. Annes Valley, [10°41'N, 61°30'W], 1 ♂ [FLMNH-MGCL-265718], (FLMNH), 1 ♂ [BMNH(E)-787646], 1 ♂ [BMNH(E)-787647], 1 ♂ [BMNH(E)-787648], (NHMUK); St. Anns, [10°41'N, 61°30'W], 1 ♂ [BMNH-E-787646], 1 ♂ [BMNH-E-787647], 1 ♂ [BMNH-E-787648], (NHMUK), (Hall, A.), Nov–Dec 1931, 1 ♀, (BMB); *Tunapuna-Piarco*: 6 mi. N Arima, [10°42'12"N, 61°17'28"W], 300 m, (Pliske,

T. E.), 30 Jun 1962, 1 ♂ [FLMNH-MGCL-265720], (FLMNH); Arima Valley, [10°41'N, 61°17'30"W], 305–457 m, (Breedlove, D. E.), 14–19 Dec 1970, 1 ♀, (CAS); Tunapuna, [10°39'7"N, 61°23'17"W], 50 m, 1 ♂ [BMNH(E)-1497690], 1 ♀ [BMNH(E)-787660], 1 ♀ [BMNH(E)-787660], (NHMUK); *Not located*: 'Trinidad', [10°26'17"N, 61°15'12"W], 1 ♂ [BMNH(E)-1497704], 1 ♂ [BMNH(E)-1497705], 1 ♂ [BMNH(E)-1497707], 1 ♂ [BMNH(E)-1497708], 1 ♂ [BMNH(E)-1497709], 1 ♂ [BMNH(E)-1497710], 1 ♂ [BMNH(E)-1497711], 1 ♂ [BMNH(E)-1497712], 1 ♂ [BMNH(E)-787643], 1 ♂ [BMNH(E)-787655], 1 ♂ [BMNH(E)-787643], 1 ♂ [BMNH(E)-787644], 1 ♂ [BMNH(E)-787655], 1 ♀ [BMNH(E)-1497696], 1 ♀ [BMNH(E)-1497697], 1 ♀ [BMNH(E)-1497699], 1 ♀ [BMNH(E)-787657], 1 ♀ [BMNH(E)-787658], 1 ♀ [BMNH(E)-787657], 1 ♀ [BMNH(E)-787658], (NHMUK), (Feather), 1 ♂ [BMNH(E)-1497706], 1 ♀ [BMNH(E)-1497688], (NHMUK), (Fountaine, M.), Dec. 1911, 1 ♂ [BMNH(E)-1497693], 1 ♂ [BMNH(E)-1497694], 1 ♂ [BMNH(E)-1497695], 1 ♂ [BMNH(E)-1497702], 1 ♂ [BMNH(E)-1497703], 1 ♂ [BMNH(E)-787653], 1 ♀ [BMNH(E)-1497687], 1 ♀ [BMNH(E)-1497698], 1 ♀ [BMNH(E)-1497700], 1 ♀ [BMNH(E)-1497701], 1 ♀ [BMNH(E)-787661], 1 ♀ [BMNH(E)-787663], (NHMUK), Dec 1911, 1 ♂ [BMNH(E)-787653], 1 ♀ [BMNH(E)-787661], 1 ♀ [BMNH(E)-787663], (NHMUK), (Hall, A.), Jan 1936, 1 ♂, 1 ♂ [Booth Mus: Collection 00-5938], (BMB), Oct-Dec 1920, 1 ♂, (BMB), (Kaye, W. J.), May 1898, 1 ♂ [FLMNH-MGCL-265719], (FLMNH), May 1898, 1 ♂ [FLMNH-MGCL-265716], (FLMNH), (Neuburger), (ZSM); Arima Valley, vicinity Asa Wright Nature Centre vic, [10°43'3"N, 61°17'55"W], (Austin, G.T.), Feb 1993, 1 ♂ [FLMNH-MGCL-296554], [dissection, SN-20-30] (FLMNH), (Gomes, O.), Feb 1993, 1 ♀ [FLMNH-MGCL-298000], (FLMNH); Behind St. Benet's Hall, (Preston, J. & F.), 2 Jan 1982, 1 ♀ [FLMNH-MGCL-265721], (FLMNH); Caparo, (Birch, F.), 4th Aug., 1 ♀ [BMNH(E)-1497683], (NHMUK), 4th Sept. '04, 1 ♀ [BMNH(E)-787662], (NHMUK), (Klages, S.M.), Jan 1906, 1 ♂ [BMNH(E)-1497682], (NHMUK); Northern Mts., (Hall, A.), Dec 1938-Jan 1939, 1 ♀, (BMB); Port of Spain, (Rendall), II.97, 1 ♂ [BMNH(E)-1497691], 1 ♀ [BMNH(E)-1497686], (NHMUK); 'Saint George', (Ellacombe, C.W.), 1 ♂ [BMNH(E)-787645], 1 ♀ [BMNH(E)-787659], (NHMUK); Santa Margarita, (Preston, J. & F.), 13 Oct 1981, 1 ♂ [FLMNH-MGCL-265717], (FLMNH); St. George, (Ellacombe, G. W.), 1 ♂ [BMNH(E)-787645], 1 ♀ [BMNH(E)-787659], (NHMUK), Dec. 1891, 1 ♀ [BMNH(E)-1497668], 1 ♀ [BMNH(E)-1497669], 1 ♀ [BMNH(E)-1497760], (NHMUK), Oct. 1891, 1 ♂ [BMNH(E)-1497673], 1 ♂ [BMNH(E)-1497674], 1 ♂ [BMNH(E)-1497675], 1 ♂ [BMNH(E)-1497676], 1 ♂ [BMNH(E)-1497677], (NHMUK); Stanway Parris River, Feb 1921, 1 ♂ [BMNH(E)-1497692], (NHMUK); Symonds Valley, (Hall, A.), Apr 1930, 1 ♂, (BMB), Mar 1930, 1 ♀, (BMB). **Venezuela:** Amazonas: Samariapo, 120 m, (Lichy, R.), 7 Oct 1946, 1 ♀ [FLMNH-MGCL-265714], (FLMNH); Bolívar: 80 km S El Dorado, [6°11'8"N, 61°24'36"W], (Nation, J. L.), 26 Jun 1984, 1 ♂ [FLMNH-MGCL-265712], (FLMNH); *Not located*: 'Venezuela', 1 ♂ [BMNH(E)-1497659], 1 ♂ [BMNH(E)-1497713], (NHMUK); Pitotan, (Nation, J. L.), 9 Jun 1937, 1 ♂ [FLMNH-MGCL-265713], (FLMNH). **Country unknown:** no data, 1 ♀ [FLMNH-MGCL-265711], (FLMNH), 1 ♂ [BMNH(E)-1497655], 1 ♂ [BMNH(E)-1497656], 1 ♂ [BMNH(E)-1497724], 1 ♂ [BMNH(E)-1497725], 1 ♂ [BMNH(E)-1497726], 1 ♂ [BMNH(E)-787649], 1 ♂ [BMNH(E)-787649], 1 ♀ [BMNH(E)-1497728], (NHMUK), (Hall, A.), 18 Mar 1934, 1 ♀, (BMB). **Doubtful locality:** 'Cauca valley', 1 ♂ [BMNH(E)-1497657], (NHMUK). 'Haiti', 1 ♂ [BMNH(E)-1497731], 1 ♂ [BMNH(E)-1497732], (NHMUK).

Cisandina esmeralda Nakahara & Barbosa, New Species

(Figs. 1, 2e and f, 3e–g, 8)

Euptychia lea [misidentification]: D'Abrera 1988: 768–769, figs.

Systematic placement and diagnosis: As discussed under the immediately preceding taxon, *C. esmeralda* n. sp. is recovered as sister to *C. lea* n. comb. with a strong support (Fig. 1; SH-aLRT/UFBoot = 96.5/96). Our molecular phylogeny and DNA sequence divergence between these two species support its species-level status indicated by its distinctive male phenotype. Indeed, the iridescent greenish lilac scales possessed by the male of *C. esmeralda* n. sp. readily distinguish this species from the remainder of the genus and furthermore from all other known euptychiines. In addition, the more brownish ventral ground color, small ventral submarginal ocelli (smallest among all *Cisandina* n. gen. species), narrow and somewhat sinuate VHW postdiscal band, coupled with other narrow ventral bands (narrowest among all four similar-appearing *Cisandina* n. gen. species with iridescent scales) separate the male of this species from the other three *Cisandina* n. gen. species with iridescent scales discussed herein. The more elongate forewing is a character shared with the male of *C. lea* n. comb., but not with males of other taxa discussed herein. The female of *C. esmeralda* n. sp. is distinguished from the female specimens of *C. lea* n. comb. and *C. castanya* n. sp. by its lack of purple lilac scales on the dorsal surface thus the female of *C. esmeralda* n. sp. possesses a uniformly brown dorsal wing surface. *Cisandina philippa* n. comb. & reinst. stat. is similar in this respect because the female of *C. esmeralda* n. sp. is brown dorsally. Nevertheless, the narrower ventral bands and smaller ventral submarginal ocelli of *C. esmeralda* n. sp., as well as its smaller adult size, can be used to separate females of these two species. Furthermore, the outward-curving VFW postdiscal band of the female *C. esmeralda* n. sp. is rather distinctive. See also 'Remarks' below for further information regarding the identity of the female of this species.

Male (Fig. 2e): Forewing length 23 mm ($n = 1$).

Head: See head description for *Cisandina* n. gen. above.

Thorax: See thorax description for *Cisandina* n. gen. above.

Abdomen: See abdomen description for *Cisandina* n. gen. above, eighth sternite appearing as two separate, somewhat broader patches.

Wing venation: See wing venation description for *Cisandina* n. gen. above.

Wing shape: See wing shape description for *Cisandina* n. gen., notable features include forewing appearing elongate due to angle between forewing outer margin and inner margin being obtuse.

Dorsal forewing: Notable features include, ground color brownish, iridescent greenish lilac scales covering most of DFW except for area anterior of costal vein (Fig. 2e), apex and distal side of cells M_1 , M_2 , M_3 , Cu_1 , although this area revealing ground color narrows posteriorly; see also DFW description for *Cisandina* n. gen. above.

Dorsal hindwing: Notable features include, ground color similar to forewing, iridescent greenish lilac scales visible in discal cell and adjacent area just outside of this cell (Fig. 2e); see also DHW description for *Cisandina* n. gen. above.

Ventral forewing: Notable features include ventral bands narrow, discal band and postdiscal band parallel to each other and traversing straight from near costa towards inner margin but terminating in cell Cu₂, ocellus in cell M1 small somewhat insignificant with pupil apparently invisible (Fig. 2e); see also VFW description for *Cisandina* n. gen. above.

Ventral hindwing: Notable features include, iridescent scales absent, postdiscal band slightly sinuate, submarginal ocelli small, ocelli in cells M₁ and Cu₁ not reaching veins defining these cells, ocelli in cells Rs and Cu₂ smaller than previously mentioned two ocelli (Fig. 2e); see also VHW description for *Cisandina* n. gen. above.

Genitalia: Notable features include, dorsal margin of tegumen rather smoothly curved as well as anterior portion of ventral margin of tegumen appearing only slightly convex, rather straight saccus in lateral view, apical process of valva somewhat broad and straight, occupying about one-fourth of valva in length (Fig. 3e–g); see also male genitalia description for *Cisandina* n. gen. above.

Female (Fig. 2f): Forewing length 24 mm ($n = 1$).

Similar to male except as follows: Notable features include, iridescent greenish lilac scales absent on dorsal surface which appears uniformly brown, posterior end of VFW postdiscal band curving outwards (Fig. 2f); see also female wing shape and pattern description for *Cisandina* n. gen. above.

Female genitalia and abdomen: Not examined.

Type material: Holotype male, with the following labels separated by double-forward slashes: //BRASIL, PARANÁ, MOREIRA SALLES, RPPN MOREIRA SALLES, 24° 04' 25" S, 53° 02' 46" W, 7-X-2012 LABLEP LEG// BC-DZ Willmott 137// (DZUP).

Paratypes (13 ♂, 6 ♀): **Argentina:** Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Sección Yacui, [25°40'47"S, 54°10'12"W], 240 m, (Núñez Bustos, E., Kopuchian, C., Tubaro, P., Fortino, A.), 11 Apr 2011, 1 ♂, (MACN) (Lavinia et al. (2017)), 13 Apr 2011, 1 ♀, (MACN) (Lavinia et al. (2017)). **Brazil:** Bahia: [12°59'S, 38°31'W], 4 ♂, (MNHU); Espírito Santo: [20°20'S, 40°17'W], 1 ♂, (MNHU), 1 ♂, (MNHU); Leopoldina (= Santa Leopoldina?), [20°6'S, 40°32'W], (Michaelis), 1894, 1 ♂, (MNHU); Linhares, [19°23'S, 40°4'W], (Elias, P. C.), Feb 1972, 1 ♂ [FLMNH-MGCL-265692], (FLMNH); Rio de Janeiro: hwy km 27 Rio - Teresópolis, [6°51'57"S, 78°4'35"W], (Callaghan, C. J.), 9 Oct 1971, 1 ♂ [FLMNH-MGCL-265693], [dissection, SN-20-14] (FLMNH). **Paraná:** São Pedro do Ivaí, RPPN Barbacena, 300m, (Mielke, Dolibaina, Carneiro, Maia), 8 Oct 2010, 1 ♀ [DZ 29.315 – BC DZ Willmott 192] (DZUP); Londrina, Fazenda Santa Helena, 650m, (Moure, Mielke, Wedderhoff), 7 Dez 1975, 2 ♀ [DZ 29.317, DZ 52. 557] (DZUP); Jussara: Horto CMNP, (Moure, Mielke, Wedderhoff), 12 Dez 1975, 1 ♂ [DZ 52.559] (DZUP); Foz do Iguaçu, (Mielke & Casagrande), 6 Sep 1985, 1 ♀ [DZ 52.556]; Moreira Salles, RPPN Moreira Salles, (Lablep), 7 Oct 2012, 1 ♂ 1 ♀ [DZ 49.895, DZ 49.915] (DZUP). **Country unknown:** Not located: 'Surinam'-error, 1 ♂, (MNHU).

Other records (1 ♂, 7 ♀): **Brazil:** Bahia: Bahía, [12°59'S, 38°31'W], 2 ♀ (MNHU); Espírito Santo: Espírito Santo, [20°20'S, 40°17'W], 1 ♀ [BMNH(E)-1497645], 1 ♀ [BMNH(E)-1497646], (NHMUK); Leopoldina (= Santa Leopoldina?), [20°6'S, 40°32'W], 1 ♀, (MNHU),

(Michaelis); Linhares, [19°23'S, 40°4'W], (Elias, P. C.), Mar 1972, 1 ♀ [FLMNH-MGCL-265694] [dissection, SN-20-15], 1 ♀ [FLMNH-MGCL-265695], (FLMNH), May 1972, 1 ♀ [FLMNH-MGCL-265696], (FLMNH); **Paraguay:** Canindeyú: Armistício, [-24.57487, -54.53756], 28 Aug 2008, 1 ♂ (sight record, photographed by Ulf Drechsel; Fig. 8).

Etymology: This specific epithet is based on the Spanish and Portuguese noun 'esmeralda', meaning 'emerald', in reference to the male of this species possessing characteristic brilliant green scales on the DFW and part of the DHW. The name is a feminine noun in apposition.

Distribution and natural history: This species is known from eastern and southeastern Brazil and northeastern Argentina, as well as by a single sight record from Paraguay (Fig. 8).

Remarks: The barcoded female from Argentina (LEPIG190-11) is the only reliable female of *C. esmeralda* n. sp. to date. During the course of compiling specimens data for the present study, several females from southeastern Brazil (listed under 'Other records') were examined by the authors as potentially being conspecific with the male *C. esmeralda* n. sp. from the same area. Nevertheless, their phenotype is not consistent with the barcoded female mainly by virtue of them possessing a purple-ish sheen on the wing surface and the ventral ground color being greyish. We are not aware of any male specimen(s) corresponding to this female phenotype, and thus we decided to exclude these female individuals from the type series until further data becomes available to assess their identifiability.

Cisandina philippa (Butler, 1867), New Combination, Reinstated Status

(Figs. 1, 2g and h, 3h–j, 4c and d, 6a and b, 7a and b, 8)

Euptychia philippa Butler, 1867: 485. Lectotype, designated herein; Butler 1868: 30, Kirby 1871: 52, Butler 1877: 121; Weymer 1911: 216, Riley and Gabriel 1924: 46, D'Abrera 1988: 768–769, figs.

Euptychia lea f. *philippa*: Weymer 1911: 216.

Euptychia lea var. *philippa*: Gaede 1931: 452.

Euptychia batesii f. *tersa* Weymer 1911: 214, pl. 49, fig. a, Lamas 2004: 220. Lectotype, designated herein.

Magneuptychia lea philippa: Lamas 2004: 220.

Systematic placement and diagnosis: Our maximum likelihood approach found *Cisandina philippa* n. comb. & reinst. stat. as a sister taxon to *C. lea* n. comb. + *C. esmeralda* n. sp., with a weak to moderate support (Fig. 1; SH-aLRT/UFBoot = 80.8/71). The infra-specific genetic divergence among seven sequenced *C. philippa* n. comb. & reinst. stat. specimens varies from 0.04% to 3.55%, although this remarkably high maximum value (3.55%) is due to DNA99-022 (from Madre de Dios, Peru), which lacks data for the first approximately 250 nucleotides. The six Ecuadorian individuals, representing samples from Zamora-Chinchipe and Morona-Santiago provinces, exhibit a range of within-species COI divergence from 0.01 to 1.71% with a mean of 0.626%. Based on our COI data, genetic distance among these sampled *C. philippa* n. comb. & reinst. stat. individuals and four other closely related *Cisandina* n. gen. species sequenced for this study is a minimum of 3.74%, suggesting an existence of a 'barcoding gap'. See Table 3 for further

information regarding genetic divergence of *Cisandina* n. gen. taxa. The male of *C. philippa* n. comb. & reinst. stat. is readily distinguished from males of other species in the genus by its uniformly brown dorsal surface, whereas male specimens of other species exhibit either bluish or greenish iridescent scales on the dorsal surface. The female specimens of this species are also dorsally brown, which is also the case with *C. esmeralda* n. sp. but not two other species in the genus; see corresponding section of *C. esmeralda* n. sp. for further diagnostic characters to identify females.

Taxonomy: *Euptychia philippa* was described by Arthur Gardiner Butler in his monograph of *Euptychia* (*sensu lato*), where he introduced 60 new euptychiine butterflies to science. Like many other species described by Butler, information regarding the number of examined specimens and sex was not provided in the original description of *E. philippa*. His description of *E. philippa* was also not accompanied by any illustration of this taxon, but the identity of this species can be guessed from the Latin text and interpretation of a few other aspects of Butler's work. First, *E. philippa* was described in his 'Division II' of *Euptychia*, which is one of his seven subdivisions of *Euptychia* he erected in his monograph of the group. Butler (1867: 481) characterized this 'Division II' as 'wings variable above and below, of violet, blue and green'. Those species classified in this division, along with *E. philippa*, include *E. picea* Butler, 1867, *E. lysidice* (Cramer, 1777), *E. glaucina* Bates, 1865, *E. aegrota* Butler, 1867, *E. pilata* Butler, 1867, *E. brixiola* Butler, 1867, *E. brixius* (= *Satyrus brixus* Godart [1824]), *E. coelestis* Butler, 1867, *E. urania* Butler, 1867, *E. lea*, and *E. junia*. Despite some of these names not being considered valid today, Butler apparently grouped together species that possess iridescent wing coloration, judging from the phenotypes of the species listed by him. It is also worth noting that the two species immediately preceding *E. philippa* in Butler's monograph are *E. lea* and *E. junia*, two names considered as applying to the same species by Lamas (2004), a proposal followed by the present study, and which species proves to be a member of *Cisandina* n. gen. in our molecular phylogeny (Fig. 1). Furthermore, the description of *E. philippa* begins by stating '*alae supra fuscae*' which translates to 'wings above dark brown', and ends by noting its ventral similarity with *E. junia*, both statements that narrow down the candidates examined by Butler to female *C. esmeralda* n. sp. or what we regard here as *E. philippa*. If this assumption is correct, the possibility of Butler examining female *C. esmeralda* n. sp. can be excluded on the basis of the type locality of *E. philippa* being Ega [=Tefé] according to the original description, whereas *C. esmeralda* n. sp. is a taxon known from the Atlantic coastal forest of Brazil and Argentina. The syntype housed at the NHMUK is a male specimen with a uniformly brown dorsal surface as described by Butler and in accordance with characters and inferences discussed above. Like Butler, who considered the brown dorsal surface to be a character to justify *E. philippa* as a species-level taxon, some subsequent authors also followed this trend (e.g., D'Abrera 1988). On the other hand, other authors proposed an opposing taxonomic hypothesis, such as Weymer (1911), who regarded *E. philippa* to be a 'form' of *P. lea* from Ega (=Tefé). Following Weymer's (1911) proposal, in which the name was considered to be subspecific according to Article 45.6.4.1 of the ICZN (1999), Lamas (2004) also regarded this taxon as subspecific. Nevertheless, both genetic divergence based on COI and multi-locus maximum likelihood (see 'Systematic Placement and Diagnosis', Fig. 1 and Table 2 for further information) are in favor of species-level status for this taxon with its uniformly brown dorsal surface. To reflect this taxonomic change and to settle its

nomenclature as a senior subjective synonym of *Euptychia batesii* f. *tersa*, we here designate the aforementioned male syntype in the NHMUK as the lectotype of *E. philippa*, with the following labels separated by double-forward slashes, and reinstate its taxonomic status from subspecific to specific (**lectotype designation, reinstated status**): //B.M. TYPE No. Rh 3178 *Euptychia philippa*, ♂ Butl.//♂// Type of Species//Ega, U.Amazonas. H.W. Bates.// ♂ Ega *Philippa* Butl. Type// Type H. T.// Godman-Salvin Coll. 1904.-1. *Euptychia Philippa*, Butl.//.

Euptychia batesii f. *tersa* was described by Gustav Weymer in Seitz's *Macrolepidoptera of the World*. The original description did not specify the number of specimen(s) he examined nor the sex, in addition to not providing any information on its locality. Despite being unrelated to *Euptychia batesii* Butler, 1867 (currently regarded as a subspecies of *Magneutpychia harpyia* (C. Felder & R. Felder, 1867), according to Lamas (2004)), Weymer described this taxon as a form of *Euptychia batesii* and also compared it with a close relative of that species, *Euptychia analis* Godman, 1905. The original description noted that the VHW ocelli in cells M_2 and M_3 were formed of a circular ring with a central pupil, rather than being silver spots as in *Euptychia batesii* (= *Neonympha harpyia*) and *Euptychia analis*. Also, Weymer pointed out the presence/absence of the VHW ocellus in cell Cu_2 as his justification for erecting this new 'form'. Nevertheless, these phenotypes discussed by Weymer are often considered as informative characters at euptychiine species-level classification, and it is unclear why he considered *tersa* and *batesii* as conspecific. The illustration of the ventral surface associated with the original description (pl. 49, fig. a) does indeed show the phenotypic features described by Weymer, as well as the presence of the VFW ocellus in cell Cu_1 , which is apparently an unusual character for species discussed in this article. Lamas (2004) considered *Euptychia batesii* f. *tersa* as a junior subjective synonym of *E. philippa*. The female syntype, which is most likely the specimen on which Weymer based his illustration, given the presence of a VFW ocellus in cell Cu_1 , is housed at SMT and figured in Warren et al. (2017). We here designate this female specimen, with the following labels separated by double-forward slashes, as the lectotype of *E. batesii* f. *tersa* in order to settle its nomenclature, and follow Lamas (2004) in regarding this taxon as a junior subjective synonym of *E. philippa* (**lectotype designation**): //GART specimen ID: 02498 Exemplar + Etiketten dokumentiert specimen + label data documented 2003// LECTOTYPUS// LECTOTYPE ♀ *Euptychia batesii* f. *tersa* Weymer by G. Lamas '91// Stauding.& Bang-Haas Dresden, Ankauf 1961// Staatl. Museum für Tierkunde Dresden// *tersa* Weym.// Spec.// Original?//.

Distribution and natural history: This species is known from the western Amazon, from the Andean foothills from Ecuador to southern Peru, east to the central Amazon, with a possible small area of sympatry with *C. lea* n. comb. in Tefé and the vicinity of Manaus (Fig. 8). It is sympatric with *C. castanya* sp. n. from central to southern Peru and in western Brazil (Rondônia). In Ecuador, this species occurs in lowland rainforest up to 1,400 m, where it is uncommon. Males and females were encountered at similar frequency, in a variety of sites, mostly in undisturbed *terra firme* forest, but also in floodplain secondary forest with abundant *Guadua* (Poaceae) bamboo. Individuals were encountered flying at varying heights above the ground, from 1 to 4 m, in both shady understory and in light gaps and at forest edges. A penultimate instar caterpillar was found on species of herbaceous bamboo, *Taquara micrantha* (Kunth) L.L.C.O liveira & R.P.O liveira (Poaceae) at Finca Las Piedras, Madre de Dios, Peru, on 20 April 2021 (voucher: 2020-FLP-IMM-0336), and the immature stages are described below.

Specimens examined (39 ♂, 31 ♀): **Brazil:** Acre: Marechal Thaumaturgo, Foz do Rio Tejo, Reserva Extrativista Alto Juruá, estrada para o Rio Arara, (Brown, K. S., Freitas, A. V. L.), 16 Sep 1997, 1 ♂, (ZUEC); [Marechal Thaumaturgo, Boca do Rio Tejo, Reserva Extrativista Alto Juruá], 20–27 Aug 1997, 1 ♂ [‘BTEJO-REAJ-AC’], (ZUEC); Senador Guiomard, Reserva Catuaba, (Mielke & Casagrande), 31 Jan – 5 Feb – 2009, 1 ♂ 1 ♀ [DZ 52.562, DZ 52. 564] (DZUP); Amazonas: Borba, Rio Abacaxis, Comunidade Paxiúba, [4°28’48”S, 58°34’W], (Mielke, O. H. H., Casagrande, M. M.), 2–4 Jun 2008, 1 ♀, [DZ 52.563 – BC-DZ Willmott – 140] (DZUP); Ega (= Tefé), [3°22’S, 64°42’W], (Bates, H. W.), 1 ♂ [‘♂ Type of Species.’//Godman-Salvin Coll. 1904-1. *Euptychia philippa*, Butl.’//Ega, U. Amazons. H.W. Bates.’//♂ Ega Philippa Butl. Type’//Type H.T.’//B.M. TYPE No. Rh3178. *Euptychia philippa*. ♂ Butl.’], 1 ♂ [BMNH(E)-1266946; HT of *philippa*], 1 ♂ [BMNH(E)-1670283], 1 ♂ [BMNH(E)-1670295], 1 ♀ [BMNH(E)-1670287], 1 ♀ [BMNH(E)-1670288], (NHMUK); Igarapé Massauari, [2°54’17”S, 57°8’23”W], (Hahnel, P.), 1 ♂, (MNHU); Manicoré, [5°49’S, 61°17’W], (Hahnel, P.), 1887, 1 ♂, (MNHU); São Paulo de Olivença, [3°28’S, 68°57’W], (Mathan, M. de), 1 ♂ [BMNH(E)-1670280], 1 ♂ [BMNH(E)-1670281], 1 ♂ [BMNH(E)-1670282], 1 ♀ [BMNH(E)-1670211], (NHMUK), Jun–Jul 1883, 1 ♂ [BMNH(E)-1670275], 1 ♂ [BMNH(E)-1670276], 1 ♂ [BMNH(E)-1670277], 1 ♂ [BMNH(E)-1670278], 1 ♂ [BMNH(E)-1670279], 1 ♀ [BMNH(E)-1670285], 1 ♀ [BMNH(E)-1670286], (NHMUK), (Moss, A. M.), 1 ♀ [BMNH(E)-525170], (NHMUK); Tefé, [3°22’S, 64°44’W], (Hahnel, P.), 1 ♂ [dissection, 9076; ‘NEOTYPE ♂ *Euptychia batesii* f. *tersa* Weymer designated by Lee D. Miller 1989//Teffe (=Tefé)Hhl.’//Genitalia vial M-9076 ♂ Lee D. Miller’], (MNHU) [unpublished neotype designation]; *Rondonia*: 1 km N Cacaúlândia, [10°31’30”S, 62°48’W], 168 m, (Brock, J. P.), 28 Oct 1990, 1 ♂ [FLMNH-MGCL-265727], [dissection, SN-20-34] (FLMNH); 5 km S of Cacaúlândia on Linha C-10 at Rio Pardo off B-65, [10°23’15”S, 62°54’53”W], (Gomes, O.), 13 Mar 1984, 1 ♂ [FLMNH-MGCL-296552], (FLMNH), 29 Aug 1993, 1 ♀ [FLMNH-MGCL-265729; Station #15 forest], [dissection, SN-20-11] (FLMNH); Cacaúlândia, 7 km E B-65, Fazenda Rancho Grande, [10°17’58”S, 62°52’14”W], (Austin, G. T.), 19 Nov 1992, 1 ♂ [FLMNH-MGCL-265728], (FLMNH), (Bongiolo, G.), 14 Jun 1992, 1 ♂ [FLMNH-MGCL-265726; Station #3 forest], (FLMNH). **Ecuador:** *Morona-Santiago*: jct. Río Mayalico-Río Santiago, Isla de las Conchas, [3°2’10”S, 77°58’29”W], 250 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 8,10 Aug 2015, 1 ♂ [FLMNH-MGCL-217579], (FLMNH); hwy km 20 Méndez-Santiago rd., [2°47’6”S, 78°15’24”W], 850 m, (Perceval, M. J.), 14 Oct 1997, 1 ♀, (MIPE); km 30 Méndez-Limón rd., Río Yungantza, [2°52’13”S, 78°21’56”W], 650 m, (Hall, J. P. W.), 1–3 Mar 2017, 1 ♀ [FLMNH-MGCL-281450], (FLMNH); Santiago de Méndez, [3°2’11”S, 78°2’W], (Nakahara, S.), 16 Jun 2014, 1 ♀, (FLMNH); *Napo*: Río Napo, hwy Puerto Napo-Ahuano rd., Chichicorrumi, [1°4’11”S, 77°37’45”W], 450 m, (Willmott, K. R., Hall, J. P. W.), 2,9 Jul 1993, 1 ♀, (FLMNH); *Orellana*: Laguna Zancudococha, military trail, [0°35’16”S, 75°28’16”W], 220 m, (Aldaz, R.), 9–13 Jul 2017, 1 ♂ [FLMNH-MGCL-288722], (FLMNH); Río Aguarico, Zancudococha, [0°34’23”S, 75°26’13”W], 240 m, (Willmott, K.R., J.C.R., J.I.R., Aldaz, R.), 14 Jul 2017, 1 ♀, (INABIO); Río Napo, Boca del Río Añangu, [0°31’43”S, 76°23’41”W], 220–300 m, (Willmott, K. R.), 27 Oct 2005, 1 ♀ [FLMNH-MGCL-111516], (FLMNH); Shiripuno Lodge, Mirador trail, [1°4’50”S, 76°44’42”W], 350 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R.), 8,9,11 Aug 2018, 1 ♂, 1 ♀, (FLMNH); *Sucumbíos*: Cerro Lumbaquí Norte, [0°1’42”N, 77°19”W], 800–950 m, (Willmott, K. R., Hall, J. P.

W.), 21–23 Jul 1999, 1 ♂, (FLMNH); *Zamora-Chinchipe*: 3 km E El Panguí, Centro Shuar Cháarip, [3°38’6”S, 78°33’29”W], 800 m, (Willmott, K. R., Hall, J. P. W.), 4 Aug 2009, 1 ♀ [FLMNH-MGCL-145674], (FLMNH); km 11.5 Los Encuentros-Zarza, La Libertad, [3°47’54”S, 78°36’26”W], 1,250 m, (Willmott, K. R., Hall, J. P. W.), 6,8 Aug 2009, 1 ♂ [FLMNH-MGCL-145675], 1 ♂ [FLMNH-MGCL-145676], (FLMNH); Zamora, ridge to west, [4°4’30”S, 78°58’7”W], 1,400–1,450 m, (Willmott, K. R.), 20 May 2000, 1 ♂ [dissection, KW-14-008], (FLMNH). **Peru:** *Cuzco*: Pilcopata, Villa Carmen, [12°54’S, 71°24’W], 540 m, (Brock, J.), 31 Jan 2013, 1 ♀ [MUSM-LEP-103083], (MUSM); Quincemil, Quebrada Yanaorcco, [13°16’S, 70°47’W], 900 m, (Rodríguez, M.), Feb 2010, 1 ♀ [MUSM-LEP-103084], (MUSM); *Junín*: La Merced, [11°3’S, 75°19’W], 790–762 m, (Watkins & Tomlinson), May–Jun 1903, 1 ♀ [BMNH(E)-1670293], (NHMUK); *Loreto*: Castaña, [0°48’S, 75°14’W], 150 m, (Lamas, G.), 26 Oct 1993, 1 ♂ [MUSM-LEP-103079], (MUSM), 29 Oct 1993, 1 ♂ [MUSM-LEP-103080], (MUSM); Lower Río Ucayali, Río Pacaya, Aug–Sep 1912, 1 ♂ [BMNH(E)-1670291], (NHMUK); Pebas, [3°19’S, 71°51’W], 120 m, (Hahnel, P.), 1 ♀ [dissection, 9077], (MNHU), (Mathan, M. de), Dec 1879–Mar 1880, 1 ♂ [BMNH(E)-1670290], (NHMUK), Nov 1906, 1 ♂ [BMNH(E)-1497733], (NHMUK); Zona Reservada Allpahuayo-Mishana, [3°57’30”S, 73°25’30”W], 170 m, (Ramírez, J. J.), 8 Aug 2001, 1 ♀ [MUSM-LEP-103092], (MUSM); *Madre de Dios*: 30 km SW Puerto Maldonado, [12°36’S, 69°11’W], 200 m, (Anderson, J. J.), 18–23 Oct 1982, 1 ♀ [MUSM-LEP-103087], (MUSM); Boca Río La Torre, [12°50’S, 69°17’W], 300 m, (Lamas, G.), 12 Feb 1982, 1 ♂ [MUSM-LEP-103082], (MUSM), 26 Sep 1981, 1 ♀ [MUSM-LEP-103085], (MUSM), 27 Sep 1981, 1 ♀ [MUSM-LEP-103086], (MUSM); Parque Nacional del Manu, Pakitza, [11°55’48”S, 71°15’18”W], 400 m, (Lamas, G.), 13 Oct 1990, 1 ♀ [MUSM-LEP-103089], (MUSM), 18 Oct 1990, 1 ♂ [MUSM-LEP-103081], 1 ♀ [MUSM-LEP-103090], (MUSM), (Rowe, W.), 3 Nov 1990, 1 ♀ [MUSM-LEP-103088], (MUSM); Reserva Tambopata, La Colpa, [13°9’S, 69°37’W], 250 m, (Aibar, P.), 19 Oct 2000, 1 ♀ [MUSM-LEP-103091], (MUSM); *Puno*: Río Tambopata, [12°36’S, 69°11’W], 270 m, 15 Jul 1979, 1 ♂ [FLMNH-MGCL-265725], [dissection, SN-20-10] (FLMNH); *San Martín*: near Yurimaguas, ‘Chambireyacu’ [=Río Chambirayacu], [5°54’S, 76°14’W], 100 m, (Mathan, M. de), Jun–Aug 1885, 1 ♂ [BMNH(E)-1670292], (NHMUK); Moyobamba, [6°2’S, 76°58’W], 855 m, Jan–Jun 1887, 1 ♀ [BMNH(E)-1670294], (NHMUK). **Country unknown:** *Not located*: ‘Amaz[on] S’, 1 ♀ [BMNH(E)-1497644], (NHMUK); no data, 1 ♂, (MNHU), 1 ♂, (MNHU).

Other records: **Ecuador:** *Napo*: Tena-Puyo rd., El Capricho, [1°11’14”S, 77°49’53”W], 850 m, (Neild, A.), 20 Oct 2015, 1 ♂, (photograph live specimen) (Neild, A. F. E. (20 Oct 2015, sight record, by email with photo to KRW)); **Peru:** *Madre de Dios*: Madre de Dios, [12°16’S, 70°55’W] [ID based on DNA barcode], (DEMU) (Murray and Prowell (2005)).

Immature Stages (Figs. 6a and b; 7a and b):

Penultimate instar: Head capsule (Fig. 7a) dark olive, bearing pair of stubby but rather pointed somewhat ‘antler-like’ scoli on vertex, apex of scoli appearing darker; six stemmata present in lateral view, third stemma largest, first and sixth stemmata transparent thus somewhat insignificant, fifth semi-transparent; head capsule width c. 1.9 mm; scoli length c. 0.4 mm; body (Fig. 6a) appearing dark char- treuse, two jagged and somewhat undefined dorsal lines, with three

creamy-whitish dorsolateral to lateral lines, pair of short caudal filaments; body length *c.* 18 mm. Duration 13 d (*n* = 1).

Ultimate instar: Head capsule (Fig. 7b) dark brown, bearing pair of rounded, stubby and blunt scoli; six stemmata present in lateral view, third stemma largest, first and sixth stemmata transparent thus somewhat insignificant, fifth semi-transparent; labrum appearing reduced compared with previous instar; secondary setae increasing in number and length, head capsule overall rounder compared with immediately preceding instar; light area present in frontal view appearing as 'M-shaped' (not illustrated); head capsule width *c.* 2.5 mm; scoli length *c.* 0.2 mm; body (Fig. 6b) appearing flesh-coloured, two jagged and somewhat undefined dorsal lines, with three creamy-whitish dorsolateral to lateral lines, pair of short caudal filaments; body length *c.* 28 mm. Duration 13 d (*n* = 1).

Pupa: Not described or illustrated. Duration 16 d (*n* = 1).

***Cisandina castanya* Lamas & Nakahara, New Species**

(Figs. 1, 2i and j, 3k–n, 4e and f, 6e–i, 7c–e, 8)

Caeruleptychia sp. n. 2: Robbins, Lamas, Mielke, Harvey & Casagrande, 1996: 231.

Caeruleptychia n. sp. Lamas, MS: Lamas 2004: 218.

Systematic placement and diagnosis. The phylogenetic analysis placed *Cisandina castanya* n. sp. as sister to (*C. lea* n. comb. + *C. esmeralda* n. sp.) + *C. philippa* n. comb. & reinst. stat., although the support for this placement is moderate (Fig. 1; SH-aLRT/UFBoot = 85.9/81). The single barcoded individual of *C. castanya* n. sp. (DZ 52.561–BC-DZ-139, from Acre, Brazil) shows high genetic divergence, greater than 3.74% (ranging from 3.74 to 6.54%; mean 5.0283% (*n* = 12), see Table 3) compared with the three other *Cisandina* n. gen. species which form a clade to which it is supported as sister, reinforcing our taxonomic hypothesis. Males of *C. castanya* n. sp. are readily distinguishable from other species in the genus by their small forewing length, in addition to the presence of semi-iridescent bluish scales on the DFW and DHW. Females are distinguished from other species in the genus by possessing similar semi-iridescent bluish scales on the DFW and DHW, which extend from the inner margin of DFW and reach the discocellular vein, whereas the bluish scales on the DFW are more restricted to basal area in female *C. lea* n. comb. and absent in *C. philippa* n. comb. & reinst. stat. As explained under the immediately preceding taxon, *C. castanya* n. sp. is sympatric with *C. philippa* n. comb. & reinst. stat. and species-level diagnostic characters can be found in the immature stages as well, namely head scoli appearing more developed in *C. castanya* n. sp. (scoli/headcapsule width ratio = 0.14; scoli length *c.* 0.4 mm.) compared with *C. philippa* n. comb. & reinst. stat. (scoli/headcapsule width ratio=0.08; scoli length *c.* 0.2 mm.).

Male (Fig. 2i): Forewing length 22–23 mm (mean 22.3 mm; *n* = 3).

Head: See head description for *Cisandina* n. gen. above.

Thorax: See thorax description for *Cisandina* n. gen. above.

Abdomen: See abdomen description for *Cisandina* n. gen. above, eighth sternite rather narrow and appearing as two separated patches at anterior side.

Wing venation: See wing venation description for *Cisandina* n. gen. above.

Wing shape: See wing shape description for *Cisandina* n. gen. above, notable features include forewing appearing less elongate due to angle between forewing outer margin and inner margin being roughly right angle.

Dorsal forewing: Notable features include, ground color brownish, iridescent purple-ish lilac scales covering most of DFW except for area anterior of costal vein, apex and distal side of cells M_1 , M_2 , M_3 , Cu_1 , although this area revealing ground color narrows posteriorly (Fig. 2i); see also DFW description for *Cisandina* n. gen. above.

Dorsal hindwing: Notable features include, ground color similar to forewing, iridescent purplish lilac scales covering most of DHW except for area anterior of Rs and area posterior of 3A (Fig. 2i); see also DHW description for *Cisandina* n. gen. above.

Ventral forewing: Notable features include, ventral bands narrow, discal band and postdiscal band parallel to each other and traversing in slightly outward diagonal direction, ocellus in cell M_1 small and may appear insignificant with pupil being invisible, additional ocellus may be present in adjacent cells (Fig. 2i); see also VFW description for *Cisandina* n. gen. above.

Ventral hindwing: Notable features include, grey-ish blue scales covering areas in cells Cu_1 , Cu_2 and 2A, submarginal ocelli appearing small, ocelli in cells M_1 and Cu_1 not reaching or barely reaching veins defining these cells, small ocellus may be visible at posterior end of postdiscal band in some specimens (Fig. 2i); see also VHW description for *Cisandina* n. gen. above.

Genitalia: Notable features include, dorsal margin of tegumen rather smoothly curved as well as anterior portion of ventral margin of tegumen appearing 'bent' in lateral view, rather straight saccus in lateral view, apical process of valva narrow and curving (Fig. 3k–n); see also male genitalia description for *Cisandina* n. gen. above.

Female (Fig. 2j): Forewing length 21–22 mm (mean 21.7 mm, *n* = 3).

Similar to male except as follows: Notable features include, area of iridescent purplish lilac scales on DFW restricted to discal cell, basal part of cell M_3 , more than half of Cu_1 , most of cells Cu_2 and 2A (Fig. 2j); see also female wing shape and pattern description for *Cisandina* n. gen. above.

Female genitalia: Notable features include, lamella antevaginalis appearing as rectangular 'thumb-like' plate with wrinkled margin; signa short, occupying basal half of corpus bursae, length of corpus bursae similar to ductus bursae (Fig. 4e and f); see also male genitalia description for *Cisandina* n. gen. above.

Type material: Holotype male, with the following labels separated by double-forward slashes: //PERU, MD, Albergue Pantiacolla 400

m 12° 39'S, 71° 14'W 22.vi.2019 W. Dempwolff// SN-DNA19-48 (MUSM).

Paratypes (10 ♂, 22 ♀): **Brazil:** *Acre:* Senador Guimard, Reserva Catuaba, [9°37'S,68°18'W], (Mielke & Casagrande), 31 Jan–5 Feb 2009, 2 ♀ [DZ 52.561] (DZUP); *Mato Grosso:* hwy Cuiabá-Santarém, km 715, [9°58'54"S,54°54'20"W], 300 m, (Callaghan, C. J.), 14 Jul 1978, 1 ♂ [FLMNH-MGCL-265741], (FLMNH); *Rondonia:* Cacaulândia, 'Big Rock Trail', 3 km E of Fazenda Rancho Grande on Linha C-20, [10°17'47"S,62°50'27"W], (Austin, G. T.), 21 Sep 1992, 1 ♀ [FLMNH-MGCL-265743], (FLMNH); 12.5 km S of Cacaulândia, off B-65, Linha C-2.5, [10°27'16"S,62°53'59"W], (Austin, G. T.), 12 Nov 1990, 1 ♀ [FLMNH-MGCL-265736], (FLMNH); 9 Dec 1990, 1 ♂ [FLMNH-MGCL-265734], (FLMNH); 15 km S of Cacaulândia, off B-65, Linha C-0, [10°28'43"S,62°53'46"W], (Austin, G. T.), 22 Apr 1991, 1 ♀ [FLMNH-MGCL-265737], (FLMNH); 3 km N Cacaulândia, dry trail off B-65, [10°30'24"S,62°48'W], (Smith, J.), 23 Apr 1991, 1 ♀ [FLMNH-MGCL-296555], (FLMNH); Cacaulândia, vicinity of Fazenda Rancho Grande, [10°17'58"S,62°52'14"W], 180 m, (Austin, G. T.), 20 Oct 1989, 1 ♀ [FLMNH-MGCL-265739], (FLMNH); 29 Oct 1989, 1 ♂ [FLMNH-MGCL-265730] [dissection, SN-20-12] (FLMNH); 5 km S of Cacaulândia on Linha C-10 at Rio Pardo off B-65, [10°2'3'15"S,62°54'53"W], (Gomes, O.), 23 Apr 1993, 1 ♀ [FLMNH-MGCL-265738] [dissection, SN-20-13], (FLMNH); 23 Jun 1996, 1 ♀ [FLMNH-MGCL-265742], (FLMNH); 7 Aug 1994, 1 ♀ [FLMNH-MGCL-265744], (FLMNH); 8 Jun 1996, 1 ♀ [FLMNH-MGCL-296559], (FLMNH); Cacaulândia, 7 km E B-65, Fazenda Rancho Grande, [10°17'58"S,62°52'14"W], (Austin, G. T.), 16 Sep 1992, 1 ♀ [FLMNH-MGCL-265745] [dissection, SN-20-33], (FLMNH); 26 Nov 1991, 1 ♀ [FLMNH-MGCL-265735], (FLMNH); 29 Nov 1991, 1 ♀ [FLMNH-MGCL-265740], (FLMNH); (Austin, G.T.), 17 Jul 1995, 1 ♀ [FLMNH-MGCL-296557], (FLMNH); 22 Jul 1994, 1 ♂ [FLMNH-MGCL-296553] [dissection, SN-20-32], (FLMNH); 3 May 1995, 1 ♀ [FLMNH-MGCL-296558], (FLMNH); 5 May 1995, 1 ♀ [FLMNH-MGCL-296556], (FLMNH); (Brock, J. P.), 5 Nov 1989, 1 ♂ [FLMNH-MGCL-265733], (FLMNH); (Gomes, O.), 27 Jun 1989, 1 ♂ [FLMNH-MGCL-265731], (FLMNH); off B-65, Linha C-20 at Rio Pardo, [10°17'58"S,62°57'5"W], (Austin, G. T.), 18 Sep 1992, 1 ♂ [FLMNH-MGCL-265732], (FLMNH). **Peru:** *Huánuco:* Lower Ucayali, Río Pachitea, [8°46'S,74°32'W], 150 m, (Tessman, G.), 1 ♀, (MNHU); *Madre de Dios:* 15 km E Puerto Maldonado, [12°32'S,69°3'W], 200 m, (Medina, M.), 6 Feb 1990, 1 ♀ [MUSM-LEP-100320] [dissection, SN-16-20], (MUSM); Parque Nacional del Manu, Pakitzta, [11°55'48"S,71°15'18"W], 340 m, (Harvey, D. J.), 27 Apr 1991, 1 ♀ [MUSM-LEP-100319], (MUSM); (Mielke, O. H. H.), 3 Oct 1991, 1 ♂ [MUSM-LEP-100316], (MUSM); (Robbins, R. K.), 2 Oct 1991, 1 ♂ [MUSM-LEP-100317] [dissection, SN-16-36], (MUSM); Albergue Pantiacolla, [12°39'S,71°14'W], 400–450m, (Lamas, G.), 29 Oct 2016, 1 ♀, (MUSM); 400m, (Gibson, L.), 30 Oct 2018, [SN-DNA19-49], 1 ♂, (MUSM).

Other records: **Peru:** *Loreto:* Río Parapapura, Chambira, [5°54'S,76°14'W], 120 m, (Razzeto, O.), 1 ♂ [MUSM-LEP-100318], (MUSM); Río Ucayali, Contamana, [7°21'S,75°0'W], 135 m, (Büche, M.), Sep 1999, 1 ♂ [MUSM-LEP-100315], (MUSM).

Etymology: The specific epithet is derived from the Spanish word 'castaña' and the Portuguese word 'castanha', both meaning 'chestnut' in English and, in much of Peru, Bolivia, and Brazil, more specifically 'Brazil nut'; Brazil nuts are large, emergent trees

(*Bertholletia excelsa* Humb. & Bonpl. (Lecythidaceae)) that dominate the rainforest of the southwestern Amazon basin and whose distribution somewhat overlaps with that of this new butterfly species. These trees grow in abundance and characterize the landscape at Finca Las Piedras (Madre de Dios, Peru), where the immature stages of this new species were discovered. This species-group name is a feminine noun in apposition.

Distribution and natural history: This species is distributed in the southwestern Amazon basin, from central and southern Peru eastwards into Brazil (Mato Grosso) (Fig. 8). A second-instar caterpillar and the last instar was found on a herbaceous bamboo, *Olyra latifolia* L. (Poaceae) at Finca Las Piedras, Madre de Dios, Peru, on 20 June 2020 (voucher: 2020-FLP-IMM-0188) and on 14 March 2021 (voucher: 2021-FLP-IMM-0234), respectively, and the immature stages are described below. The instar number (second) for 2020-FLP-IMM-0188 was determined based on comparing its size and appearance with other euptychiine larval instars. The host plant with the caterpillar was located at an edge habitat of a *terra firme* forest dominated by Brazil nut trees, with high incidence of light in the understory, fostering the growth of understory grasses.

Remarks. The two male individuals from Loreto, Peru (MUSM-LEP-100315 and MUSM-LEP-100318) are classified as this taxon in MUSM. Nevertheless, these specimens possess some phenotypic characters not observed in other individuals examined for *C. castanya* n. sp. such as large ventral ocelli and presence of small ocellus at the VHW inner margin (at the posterior end of the VHW postdiscal band). Thus, we decided to exclude these individuals from the type series until further data becomes available to assess its identity.

Immature Stages (Figs. 6e–i, 7c–e):

Egg: Not Recorded.

First instar: Not Recorded.

Second instar: Head capsule (Fig. 7c) light brown, bearing pair of stubby but rather pointed, somewhat 'antler-like' scoli on vertex, apex of scoli appearing darker; six stemmata present in lateral view, third stemma largest, first and sixth stemmata transparent thus somewhat insignificant, fifth semi-transparent; head capsule width *c.* 1.4 mm; scoli length *c.* 0.4 mm; body (Fig. 6e) pale green, with creamy-whitish dorso-lateral lines and similar but narrower lateral lines, pair of short caudal filaments; body length *c.* 11 mm. Molted to third instar 6 d after collecting in the field (on June 26th 2020; *n* = 1).

Third instar: Head capsule (Fig. 7d) light brown, bearing pair of stubby but rather pointed, somewhat 'antler-like' scoli on vertex, apex of scoli appearing lighter; six stemmata present in lateral view, third stemma largest, first and sixth stemmata transparent thus somewhat insignificant, fifth semi-transparent; head capsule width *c.* 2.1 mm; scoli length *c.* 0.5 mm; body (Fig. 6f) appearing chartreuse, two jagged and somewhat undefined dorsal lines, with three creamy-whitish dorsolateral to lateral lines, pair of short caudal filaments; body length *c.* 14 mm. Duration 13 d (*n* = 1).

Fourth (ultimate) instar: Head capsule (Fig. 7e) dark brown, bearing pair of rounded, stubby and blunt scoli on vertex, scoli appearing lighter posteriorly; six stemmata present in lateral view,

third stemma largest, first and sixth stemmata transparent thus somewhat insignificant, fifth semi-transparent; labrum appearing reduced compared with previous instars; secondary setae increasing in number and posterior portion of head capsule broadens compared with immediately preceding instar; light area present in frontal view appearing as ‘M-shaped’ (not illustrated); head capsule width *c.* 2.8 mm; scoli length *c.* 0.4 mm; body flesh-colored, two jagged and somewhat indistinctive dorsal lines, with three creamy-whitish dorsolateral to lateral lines, pair of short caudal filaments; body length *c.* 24 mm. Duration 20 d (*n* = 1).

Pupa: Short and relatively smooth, with reduced ocular caps, overall appearing somewhat mottled, ventrally, including wing case, creamy white scattered with dark brown, dorsally appearing darker brownish except for rather pinkish two longitudinal rows of protuberances on abdomen and small areas of creamy-white elsewhere, cremaster short (Fig. 6h and i). Duration 13–15 d (*n* = 2).

Adult: Two males, eclosed on 13 August 2020 (2020-FLP-IMM-0188) and 5 April 2021 (2021-FLP-IMM-0234).

Cisandina fida (Weymer, 1911), New Combination

Cisandina fida fida (Weymer, 1911), New Combination

(Figs. 2k and l, 8)

Euptychia fida Weymer, 1911: 196, pl. 46, fig. f. Lectotype, designated herein.

Euptychia fida: Gaede 1931: 446.

Euptychoides fida: Forster 1964: 98, fig. 87; Lamas 2004: 219.

Systematic placement and diagnosis: According to our molecular data, *Cisandina fida* n. comb. is paraphyletic, although the sister relationship between Peruvian *C. fida* n. comb. (LEP-58115) and *C. sanmarcos* n. comb. (KW-15-025) is poorly supported (Fig. 1; SH-aLRT/UFBot=54.4/64). Discussion of this paraphyly is further developed in the ‘discussion’ section below. As mentioned in Nakahara et al. (2018a), these two species can be easily distinguished based on the following phenotypic characters: the nominate phenotype of *Cisandina fida* n. comb. has a jagged VHW postdiscal band (but see also diagnostic characters for the following taxon), whereas this band is rather straight in *C. sanmarcos* n. comb.; *C. fida* n. comb. possesses whitish coloration distal to the VHW postdiscal band, whereas this whitish coloration is absent in *C. sanmarcos* n. comb. and all other species discussed herein. Nakahara et al. (2018a) mentioned the length of VFW postdiscal band as a diagnostic character to distinguish these two species, but examination of additional Ecuadorian *C. fida* n. comb. revealed some individuals (e.g., FLMNH# 145742) in which the VFW postdiscal band terminates at 2A, as in *C. sanmarcos* n. comb.

Taxonomy: Gustav Weymer (1911) described *Euptychia fida* in his ‘Saturnus group’ of *Euptychia*, based on an unspecified number of individuals from [Río] Songo [sic] and ‘Corvico’ (=Coroico), both situated in La Paz, Bolivia. The original description compared *E. fida* with *E. vesta* Butler, 1867 (= *Graphita griphe* (C. Felder & R. Felder, 1867); see Nakahara et al. (2016) for further details regarding its synonymy and systematic placement), which is a distantly related taxon phenotypically resembling *E. fida*. However, as mentioned by Weymer (1911), male specimens of *E. fida* can easily be distinguished from *G. griphe*

by the absence of androconial scales (termed ‘raised scale-streak’ by Weymer) on the DFW. The illustration of *E. fida* associated with the description (on pl. 46, fig. f) and showing its dorsal surface clearly indicates the absence of DFW androconial scales, which are visible on the painting of *E. vesta* on the same plate. Another wing pattern character that is informative in terms of identifying these two taxa is the presence/absence of the DHW ocellus in cell Cu2, which is also vaguely discussed by Weymer. As reflected in the illustration provided by him, this DHW ocellus is present in *G. griphe* and absent in *E. fida*, regardless of the sex. Despite referring to some ventral wing pattern differences between these two species, Weymer only provided a drawing of the ventral surface for *E. vesta*, and not for *E. fida*. Given this information, four syntypes were located, three specimens at MNHU and a single male at ZSM, all from Songo [sic], Bolivia. We were unable to locate any syntype(s) from Coroico. Three syntypes in the MNHU were mentioned and discussed in Nakahara et al. (2018a) in association with the description of *Euptychoides sanmarcos*, although due to an unfortunate oversight, the specimen housed at ZSM was omitted. Nakahara et al. (2018a) noted wing pattern differences between Ecuadorian and Bolivian specimens, including the possibility of these two populations representing two species. All examined Ecuadorian specimens (all from Zamora-Chinipe; *n* = 5) possess a rather straight VHW postdiscal band, whereas this band is jagged in Bolivian specimens (*n* = 5, including three syntypes). The single known Peruvian specimen, a male from Ucayali [doubtful locality – see below], has a straight VHW postdiscal band, suggesting that this specimen represents the same taxon as those individuals from southern Ecuador. The COI sequence of this Peruvian specimen (LEP-58115) exhibits a genetic divergence of 2.46–7% compared with those two sequenced Ecuadorian specimens (LEP-16705 and LEP-10686). We also lack DNA data for Bolivian specimens, thus preventing further assessment based on molecular data and our judgement regarding taxonomic status of *E. fida* from southern Ecuador to central Peru must remain tentative. All known Bolivian specimens are phenotypically distinguishable from individuals collected in southern Ecuador and central Peru, suggesting that the latter population should be regarded as a distinct taxon, either as a species or subspecies. Apart from the lack of molecular data for Bolivian specimens, another piece of evidence needed to assess the taxonomic status for its neighboring northern population is material from other places in Peru. Without such data, it is impossible to determine whether the observed wing pattern differences are broadly clinal, or even potentially partially sympatric. We therefore follow Nakahara et al.’s (2019a) approach of generating a parsimonious hypothesis for a single species, namely by considering it of subspecific rank and waiting for further evidence until we can test this null hypothesis. Additionally, in order to settle the nomenclature of this species, we here designate a lectotype for *Euptychia fida* based on the dissected female (male identification on the label apparently erroneous) specimen from Río Songo housed at the MNHU with the following labels separated by double-forward slashes (lectotype designation): // Songo stgr/Salona stgr.// LECTOTYPE ♂ *Euptychia fida* Weymer designated by: Lee D. Miller 1989// Río Songo (1,200 m) Bolivia (Yungas) 1895–1896. Garlepp// genitalia vial M-9051 ♂ Lee D. Miller//. Despite having a lectotype label attached, L. D. Miller never published these designations as already noted by Nakahara et al. (2015).

Specimens examined (5 ♂, 1 ♀): **Bolivia:** La Paz: Río Zongo, [16°3’40”S, 68°1’2”W], 1,200 m, (Garlepp), 1895–1896, 1 ♀ [dissection, 9051; ‘Songo Stgr./Salona Stgr./Río Songo (1,200 m) Bolivia (Yungas) 1895–1896. Garlepp//LECTOTYPE ♂ *Euptychia fida* Weymer designated by Lee D. Miller 1989//genitalia vial M-9051 ♂ Lee D. Miller’], (MNHU); Yungas, [16°17’13”S, 66°48’33”W], 1,200 m, 1 ♂ [BMNH(E)-1267787; ‘Salona Stgr. Bolivia/Yungas//

Fruhstorfer Coll. B. M. 1937-285//BMNH(E) 1267787], (NHMUK); Zongo, [16°5'46"S, 68°3'9"W], (Garlepp), 2 ♂ [‘Songo Bol. Garl.// LECTO-PARATYPE ♂ *Euptychia fida* Weymer, des. Lee D. Miller 1989’], (MNHU), 1 ♂ [BMNH(E)-1267786; dissection, B.M.(N.H.) Rhopalocera vial No. 9531], (NHMUK), 1 ♂ [dissection, SA19; ‘Präparat Nr. SA 19 Zoolog. Staatssammlung München’//‘Songo Bol. Garl.’//‘Para-Typus *Euptychia fida* Weym.’//‘*fida* Weym.’//‘Original!’], (ZSM).

Distribution and natural history: The nominate race of *C. fida* n. comb. is known to date only from Bolivia (Fig. 8)

***Cisandina fida directa* Nakahara & Willmott, New Subspecies**

(Figs. 1, 2m and n, 3p and q, 4h and i, 8)

Description and Diagnosis:

Male: Forewing length 23.5–24.5 mm ($n = 2$): Differs from the nominotypical subspecies in the following respect: VHW postdiscal band rather straight; this band traverses distally after passing Cu_2 and bends back half way between Cu_2 and 2A (Fig. 2m).

Female: Forewing length 24.5–25.0 mm ($n = 2$): Differs from the nominotypical subspecies by the same ventral forewing character provided for the male (Fig. 2n); differs from the male by having more broad and rounded wing shape; two small ocelli present in VFW cells M_2 and M_3 in one female (from Zamora, ridge to west, 13 Jan 2002), whereas the ocelli are absent in these cells in the other examined female (FLMNH-MGCL-145742).

Type material. Holotype male, with the following labels separated by double-forward slashes://ECUADOR: Zamora-Chinchipec Zamora, ridge to west, 1,400–1,450 m 4°4.50'S, 78°58.12'W 18.v.2000, K. Willmott/DNA voucher LEP-14657//Genitalic vial SN-20-42 S. Nakahara// (FLMNH, to be deposited in INABIO).

Paratypes (2 ♂, 2 ♀): **Ecuador:** *Zamora-Chinchipec*: km 10 Los Encuentros-El Panguí, ridge E San Roque, [3°42'11"S, 78°35'36"W], 1,050 m, (Willmott, K. R., Hall, J. P. W.), 4 Aug 2009, 1 ♀ [FLMNH-MGCL-145742] [dissection, SN-15-180], (FLMNH); km 14 Yacuambi-Saraguro rd., Juyapa, [3°34'48"S, 78°57'2"W], 1,740 m, (Willmott, K. R., J. I. R., J. C. R.), 21 Jun 2013, 1 ♂ [FLMNH-MGCL-157449], (FLMNH); *Zamora*, ridge to west, [4°4'30"S, 78°58'7"W], 1,400–1,450 m, (Willmott, K. R.), 13 Jan 2002, 1 ♀, (FLMNH), 20 May 2000, 1 ♂, (FLMNH).

Other records: **Peru:** *Ucayali*: Río Aguaytía, Previsto, [9°3'S, 75°38'W], 420–500 m, Oct 2006, 1 ♂ [FLMNH-MGCL-281611; MGCL Accession #2016-40 E. C. Knudson/Bordelon], (FLMNH) [this locality is doubtful, and the specimen probably originated further west, in Huánuco department].

Etymology. This species-group name is a feminine Latin adjective meaning ‘straight, not curved’, in reference to the smoother VHW postdiscal band compared with the nominate race.

Distribution and natural history. This subspecies is known from southern Ecuador (Zamora-Chinchipec) and central Peru (Fig. 8). In Ecuador, it occurs in cloud forest from 1,050 to 1,740 m, where it is

rare and only known from ridge top localities. Males were attracted to rotting fish in canopy bait traps or to similar bait placed on leaves 1 m above the ground, and one female was found flying along the edge of a road through a secondary forest with abundant bamboo during the middle of the day.

***Cisandina sanmarcos* (Nakahara & Lamas, 2018), New Combination**

(Figs. 1, 2o and p, 3r–t, 4i–k, 8)

Magneuptychia sp. n.: Lamas & Grados [1997]: 58

Magneuptychia n. sp. Lamas, MS: Lamas 2004: 220

Euptychoides sanmarcos Nakahara & Lamas, in Nakahara et al. 2018a: 12–14, figs. 10–11, 16.

Systematic placement and diagnosis: As discussed in Nakahara et al. (2018a), this species is closely related to *C. fida* n. comb. (Fig. 1). *Cisandina sanmarcos* n. comb. forms a strongly supported clade with *C. fida* n. comb. in the present study (Fig. 1; SH-aLRT/UFBoot=100/100), which is also strongly supported as sister to four species discussed above (Fig. 1; SH-aLRT/UFBoot=96.9/95). Nevertheless, the placement of *C. sanmarcos* n. comb. results in *C. fida* n. comb. being paraphyletic, as mentioned under the corresponding section of that species, and further discussion and justification as to its specific status can be found below. See corresponding section of *C. fida* n. comb. for diagnostic characters to distinguish these two taxa.

Taxonomy: Nakahara et al. (2018a) described *Euptychoides sanmarcos* based on three males and eight females, including the male holotype. As mentioned in the original description, we were aware of the fact that the generic classification regarding this species would need subsequent revision, albeit due to its distinctiveness and the goal of Nakahara et al. (2018a) to describe ‘miscellaneous taxa’ to further future investigation of their relationships, we went ahead and named it prior to its ultimate generic assessment. The sole reason for describing this species under *Euptychoides* was because of its sister relationship with ‘*Euptychoides fida*’, although knowing that ‘*Euptychoides fida*’ was distantly related to *Euptychia saturnus* Butler, 1867, the type species of *Euptychoides*. Nevertheless, the holotype male of *Cisandina sanmarcos* n. comb. from Madre de Dios, Peru figured in the original description (Fig. 10), evidently possesses characters discussed in the original description that separate the species from its sister species, *Cisandina fida* n. comb. Note that the holotype of *E. sanmarcos* was deposited at MUSM in October 2019 subsequent to its description, as indicated in the original description. Additionally, the female specimen housed at the MZUJ listed below was not included in the type series as this individual was not known to the authors during the course of preparing Nakahara et al. (2018a).

Specimens examined (3 ♂, 10 ♀): **Bolivia:** *La Paz*: Río Zongo, [16°3'40"S, 68°1'2"W], 1,200 m, (Garlepp), 1895–1896, 1 ♂ [dissection, M-9141 Lee D. Miller], (MNHU). **Peru:** *Cuzco*: Cosñipata Valley, Quebrada Quitacalzón, [13°1'35"S, 71°29'57"W], 1,050 m, (Harris, B.), 12 Aug 2009, 1 ♀ [MUSM-LEP-103661; dissection, genitalic vial SN-14-18 MUSM], (MUSM), (Kinyon, S.), 25 Sep 2011, 1 ♀ [MUSM-LEP-103662], (MUSM); Cosñipata Valley, Quebrada Quitacalzón, [13°1'35"S, 71°29'57"W], 1,100 m, (Gibson, L.), 10 May 2012, 1 ♀ [MUSM-LEP-103663], (MUSM), (Kinyon, S.), 22 Sep 2014, 1 ♀ [MUSM-LEP-103666], (MUSM), (Lamas,

G.), 22 Sep 2014, 1 ♀ [MUSM-LEP-103664; dissection, genitalic vial SN-16-17 MUSM], (MUSM), (Lamas, G.), 23 Oct 2010, 1 ♀ [MUSM-LEP-103667], (MUSM); Gallito de las Rocas conservation area [13° 04.513' S 71° 25.133' W], 1,000–1,100 m, (G. Gallice), 9 Jul 2019, 1 ♀ [2019-GR-0077], (ASA); *Huánuco*: Cordillera del Sira, [9°25' S, 74°45' W], 1,380 m, (Exp. Universidad Viena), Sep 1987–Aug 1988, 1 ♀ [MUSM-LEP-103660], (MUSM); *Madre de Dios*: Cerro Pantiacolla, E Slope nr. summit, ca. 4-km ENE Shintuya, [12°38'19"S, 71°17'19"W], 960–1,030 m, (Douglass, J. F.), 25 Jul 1980, 1 ♂ [dissection, SN-14-149; HT *sanmarcos*], (MUSM); *Puno*: Tambopata – Candamo, Río Távara, [13°26'S, 69°38'W], 450–1,050 m, (Baynes, H.), 1 Aug 1995, 1 ♂ [MUSM-LEP-103659], (MUSM), (Grados, J.), 9 Aug 1995, 1 ♀ [MUSM-LEP-103665], (MUSM); *San Martín*: Jorge Chávez, [5°41'S, 77°40'W], 1,200–1,400 m, (Calderón, B.), 2003, 1 ♀, (MZUJ).

Distribution and natural history: *Cisandina sanmarcos* n. comb. ranges from northern Peru (San Martín department) to La Paz, Bolivia (Fig. 8). All known sites are along the slopes of the eastern Andes in an altitudinal zone between 960 and 1,380 m. It is worth mentioning that an additional specimen of this species was collected subsequent to its description by GG at Gallito de las Rocas conservation area, Cosñipata Valley, Cuzco, Peru (13°04.513'S, 71°25.133'W) in July 2019, bringing the total number of known specimens of *C. sanmarcos* n. comb. to 11. GG sprayed the understory plants along the ridge with urine. This particular individual was patrolling, but it is unclear whether it was attracted to the urine or not. The forest along the ridge was primary, with remarkably extensive patches of bamboo (probably *Guadua* sp.) on the slopes that had most likely colonized landslides. Nothing otherwise notable was recorded in terms of its behavior.

Cisandina trinitensis (Brévignon & Benmesbah, 2012), New Combination

(Figs. 1, 2q and r, 3u–w, 4l and m, 8)

Euptychia? sp.: D'Abrera 1988: 780, figs.

Magneuptychia trinitensis Brévignon & Benmesbah, 2012: 47, pl. 3, Figs. 1–4, pl. 4, Figs. 8, 8a.

Systematic placement and diagnosis: *Cisandina trinitensis* n. comb. is moderately to strongly supported as sister to the remainder of *Cisandina* n. gen. (Fig. 1; SH-aLRT/UFBoot=91.9/92), with three sequenced individuals (LCB251, LCB356, MB_1708_15) forming a well-supported clade (Fig. 1; SH-aLRT/UFBoot = 100/100). *Cisandina trinitensis* n. comb. is readily distinguished from other species in the genus by the lack of an ocellus in VHW cell Cu₂, coupled with the presence of four submarginal ocelli on the VFW (in cells M₁, M₂, M₃, and Cu₁). However, it must be noted that some ocelli on the VFW may appear as faint or only a trace, and with the limited number of specimens examined this character may prove unreliable.

Taxonomy: Brévignon and Benmesbah (2012) described *Magneuptychia trinitensis* based on two males and two females, including the male holotype, all collected in French Guiana. The holotype was examined prior to deposition in MOBE, and it was also figured in the original description (pl. 3, Figs. 1 and 2), where the aforementioned characters are visible. We also incorporated sequences from the holotype in our molecular phylogeny (Fig. 1; LCB 251), thus leaving no doubt as to its rather distinctive identity,

which is also indicated as being sister to the rest of the genus according to the maximum likelihood tree (Fig. 1).

Distribution and natural history: *Cisandina trinitensis* n. comb. is so far known from a handful of sites all situated in French Guiana (Fig. 8).

Specimens examined (3 ♂, 2 ♀): **French Guiana:** *Cayenne:* Montagne de la Trinité, [4°36'2"N, 53°24'43"W], (Benmesbah, M.), 10 Nov 2010, 1 ♀ [AT *trinitensis*], (LBCB), (Hermier, B.), 30 Oct 2008, 1 ♀ [PT *trinitensis*], (LBCB); Nouragues Station, [4°5'N, 52°41'W], (Benmesbah, M.), 6 Sep 2010, 1 ♂, (MOBE); *St-Laurent du Maroni:* Maripasoula, Antecume-Pata, 'filet', [3°17'53"N, 54°4'16"W], (Benmesbah, M.), 13 Mar 2012, 1 ♂ [HT *trinitensis*], (MOBE); *Not located:* 'French Guiana', 1 ♂ [PT *trinitensis*], (MOBE).

Other records: **French Guiana:** *Cayenne:* Cayenne, [4°56'N, 52°20'W], 1 ♂, 1 ♀, (NHMUK) (D'Abrera (188: 780, '*Euptychia?* sp.)); *St-Laurent du Maroni:* Maripasoula, Antecume-Pata, 'filet', [3°17'53"N, 54°4'16"W], (Benmesbah, M.), 13 Mar 2012, 1 ♀ [PT *trinitensis*], (MOBE) (Brévignon and Benmesbah (2012)).

Discussion

We here introduce another new euptychiine genus, *Cisandina* n. gen., to accommodate five existing species previously associated with *Magneuptychia* and *Euptychoides*, as well as describe three new taxa within the new genus. The highly polyphyletic natures of *Magneuptychia* and *Euptychoides* have been indicated by a number of other studies (e.g., Peña et al. 2010, Nakahara et al. 2016, Espeland et al. 2019), and our multi-locus phylogeny justifies these taxonomic changes as discussed above. Here, we considered several possible generic arrangements for these seven species, including recognizing three genera for the three phenotypically compact groups of *Cisandina* species, namely the *C. lea* subgroup, *C. fida* subgroup and *C. trinitensis* subgroup. In fact, our initial approach was to describe two genera, one for the *C. lea* subgroup and the other for the *C. fida* subgroup. Nevertheless, as DNA sequence data supported *M. trinitensis* as the sister to both of these genera, we decided instead to describe a single genus to harbor this morphologically relatively compact group of seven species. Indeed, the male genitalia and female genitalia can be considered as rather homogeneous among these seven species, with some characteristic features such as 1) reduced appendices angulares, 2) broad base of brachia, 3) large antero-dorsal opening of phallus, 4) sclerotized portion of manica, and 5) heavily sclerotized wrinkled lamella antevaginalis partially fused with lateral plate of eighth abdominal segment. These traits (1) to (5) are apparently not shared with other species in the '*Archeuptychia* clade', except for the sclerotized region of manica, which is apparently also present in *Erichthodes arius* and *Yphthimoides eriphule*, and these characters (1) to (4) can be considered as rare character states even among the entire subtribe Euptychiina. Although the support is not high for its monophyly (Fig. 1; SH-aLRT/UFBoot=86.7/69), the potential sister group (*Erichthodes arius* + *Yphthimoides eriphule*) of *Cisandina* n. gen. also has rather distinctive genitalic characters. Apart from the manica being sclerotized at the juncture of the phallus and aedeagus, the male genitalia of these two species possess a broad, band-like juxta (in lateral and ventral view), a narrow uncus (of width similar to the brachia) which curves downwards, and the basal portion of the valva is tapering, and a study is underway by SN and EPB to describe a

new genus for this clade. The distinctive genitalia of its sister group reinforces the taxonomic significance of the homogenous genitalic features of *Cisandina* n. gen., although we have not been able to examine the female genitalia of *E. arius*. Coupled with these genitalic characters, the slightly displaced VHW ocellus in cell M_2 serves as a diagnostic character to separate these seven species from *E. arius* and *Y. eriphule*, and virtually all other members of the ‘*Archeuptychia* clade’. Despite genitalic characters suggesting that a single genus is the best taxonomic solution, there are some significant biological and distributional differences between species in the *lea* and *fida* subgroups, which are worth emphasizing. As summarized above, all four species in the *lea* subgroup inhabit lowland forests of the Amazon basin, Guianas, Trinidad, and Atlantic coastal forest of Brazil, being recorded from elevations up to 1,400 m. On the other hand, the two species in the *fida* subgroup are residents of tropical east Andean middle elevation cloud forests from southern Ecuador to Bolivia, confined to an altitudinal zone between 960 and 1,740 m. Thus, species in the *lea* and *fida* subgroups occur in allopatry with somewhat different habitat preferences, which may result in different biological traits, although the lack of natural history information for taxa recognized in the *fida* subgroup prevents further recognition of such differences. In fact, the immature stage morphology of two species in the *lea* subgroup, *C. castanya* n. sp. and *C. philippa* n. comb. & reinst. stat. further supports our taxonomic proposal of establishing *Cisandina* n. gen. by their short, rounded and stubby head scoli in the last instar larvae, transforming from the well-developed bifurcating head scoli of the penultimate instar, which is a unique feature for euptychiines, as explained above. The overall phenotype of species in the *lea* subgroup is different from species in the *fida* subgroup in exhibiting iridescent blue or greenish wing coloration, whereas the wings of the latter subgroup are basically brownish without any lilac reflection. These phenotypic and ecological differences might merit generic recognition, but in that case a monotypic genus would be required for *M. trinitensis*, which seems unreasonable given the number of shared unique genitalic features with species in the *lea* and *fida* subgroups. We, therefore, decided to resolve this subjective issue by establishing a single genus for these seven species.

Nakahara et al. (2019b) made a judgement of accepting paraphyletic species, a situation presents in this article as well. We are fully aware of ‘the untenability of paraphyletic groups’ for taxonomic purposes (e.g., de Queiroz and Gauthier 1990), and the advantages of recognizing clades as taxa. Nevertheless, many ‘species’ (i.e., specific epithets) are established without testing their monophyly and it is not uncommon that they do not represent monophyletic entities due to the mode of speciation (e.g., Nosil et al. 2002), a situation also discussed in Nakahara et al. (2019a). Furthermore, multiple molecular markers should ideally be used to provide reliable evidence of monophyly or paraphyly of a species. *Cisandina fida* n. comb. and *C. sanmarcos* n. comb. are phenotypically readily distinguishable and their broad sympatry in central Peru and Bolivia refutes the possibility of subspecific status of the latter taxon. We were unable to obtain genetic data for the nominate race of *C. fida* n. comb., so this lack of data also might have contributed towards the unexpected result of recovering *C. fida* n. comb. as paraphyletic.

In summary, we contributed to resolving the systematics of two polyphyletic genera, *Magneuptychia* and *Euptychoides*, by removing five species in total and erecting a new genus to accommodate them. We further described two new species and one subspecies related to these taxa, and provided a phylogenetic hypothesis for all the species discussed in this study. Throughout this article and in other studies on taxa associated with *Magneuptychia* (Nakahara et al. 2020a), we have highlighted the importance of a biological classification

supported by a phylogenetic hypothesis. We continue to revise the systematics of Euptychiina by following this trend, including a forthcoming study on a clade collapsed in Fig. 1.

Author Contributions

SN wrote the paper and performed morphological work; SN, KK, ME, and KRW performed relevant molecular lab work and analysis; MRM, TCE, RT, JS and GG contributed towards obtaining life history information and incorporating into the paper; EPB and MMC assisted with specimens under their care; SN, MRM, KK, TCE, ME, MMC, EPB, GG, GL, and KRW edited and revised the paper.

Acknowledgments

We would like to express our gratitude to all curators and collectors who allowed access to or provided information about specimens under their care, including Gerald Legg (BMB), Wolfram Mey (MNHU), Mike J. Perceval (MIPE), Mohamed Benmesbah (MOBE), Tomasz Pyrcz (MZUJ), Blanca Huertas (NHMUK), Robert Robbins and Brian Harris (USNM), Axel Hausmann (ZSM), and André V. L. Freitas (ZUEC); Hajo Gernaat for translating relevant parts of the original description; Ulf Drechsel for allowing us to use his photograph of *C. esmeralda* n. sp.; Ezequiel Núñez for photographing relevant specimens; Lynn Clark and Fabrício Ferreira for generously identifying the host plants; all those who contributed to digitizing specimen data, especially Robyn Crowther and Evelyn Gamboa; three anonymous reviewers for conducting post-submission reviews and providing numerous helpful comments and suggestions. SN acknowledges University of Florida’s Entomology Department and Alliance for Sustainable Amazon for support. MRM thanks Diana Silva for their continuous support, and Consejo Nacional de Investigaciones Científicas y Técnicas – CONICET for doctoral fellowship. EPB (2016/15873-8, 2018/21432-0) thanks Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP) and Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) (162673/2020-5). MMC (CNPq302084/2017-7) thanks Conselho Nacional de Desenvolvimento Científico e Tecnológico. KRW acknowledges the US National Science Foundation (DEB-1256742) for support. Rearing relevant to the present study at Finca Las Piedras was conducted under permit no. 187-2017-SERFOR/DGGSPFFS; Brazilian butterfly species are registered in the Brazilian Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado (National System for the Management of Genetic Heritage and Associated Traditional Knowledge) SISGEN (A37D0EF).

References Cited

- Andrade, M. G., A. L. Vilorio, E. R. Henao-Bañol, and J.-F. LeCrom. 2019. Generic reassignments of satyrine butterflies from Colombia and Venezuela (Lepidoptera: Nymphalidae). *Anartia* 28: 26–46.
- Baine, Q., G. Polo-Espinoza, S. Nakahara, and G. Gallice. 2019. Immature stages and new host record of *Taygetis rufomarginata* Staudinger, 1888 (Lepidoptera: Nymphalidae: Satyrinae). *Trop. Lepid. Res.* 29: 79–86.
- Beccaloni, G. W., A. L. Vilorio, S. K. Hall, and G. S. Robinson. 2008. Catalogue of the host plants of the Neotropical butterflies. *Catálogo de las plantas huésped de las mariposas Neotropicales*. Sociedad Entomológica Aragonesa, Zaragoza (Monografías del Tercer Milenio, vol. 8).
- Brévignon, C., and M. Benmesbah. 2012. Complément à l’inventaire des Satyrinae de Guyane (Lepidoptera: Nymphalidae), pp. 36–52. In D. Lacomme, and L. Manil (eds.), *Lépidoptères de Guyane*, Tome 7, Nymphalidae. Association des Lépidoptéristes de France, Paris.
- Butler, A. G. 1867. A monograph of the genus *Euptychia*, a numerous race of butterflies belonging to the family Satyridae; with descriptions of sixty species new to science, and notes to their affinities, etc. *Proc. Zool. Soc. Lond.* 1866: 458–504.
- Butler, A. G. 1868. Catalogue of diurnal Lepidoptera of the family Satyridae in the collection of the British Museum. Taylor and Francis, London, United Kingdom.

- Butler, A. G. 1877. On new species of the genus *Euptychia*, with a tabular view of those hitherto recorded. J. Linn. Soc. Lond. (Zool.) 13: 116–128.
- Chainey, J. E. 2005. The species of Papilionidae and Pieridae (Lepidoptera) described by Cramer and Stoll and their putative type material in the Natural History Museum in London. Zool. J. Linn. Soc. 145: 283–337.
- Cong, Q., and N. V. Grishin. 2014. A new *Hermeuptychia* (Lepidoptera, Nymphalidae, Satyrinae) is sympatric and synchronic with *H. sosybius* in southeast US coastal plains, while another new *Hermeuptychia* species – not hermes – inhabits south Texas and northeast Mexico. Zookeys 379: 43–91.
- Costa, M., A. L. Viloria, S. Attal, A. F. E. Neild, S. A. Fratello, and S. Nakahara. 2016. Lepidoptera del Pantepui. Parte III. Nuevos Nymphalidae Cyrestinae y Satyrinae. Bull. Soc. Entomol. France. 121: 179–206.
- Cramer, P. 1777. De uitlandsche Kapellen voorkomende in de drie Waereld-Deelen Asia, Africa en America. Papillons exotiques des trois parties du monde l'Asie, l'Afrique et l'Amérique, vol. 2. Utrecht, Barthelemy Wild and J. Van Schoonhoven & Comp, Amsterdam, S. J. Baalde.
- Cramer, P. 1780. De uitlandsche Kapellen voorkomende in de drie Waereld-Deelen Asia, Africa en America. Papillons Exotiques des Trois Parties du Monde l'Asie, l'Afrique et l'Amérique, vol. 4. Utrecht, Barthelemy Wild and J. Van Schoonhoven & Comp, Amsterdam, S. J. Baalde.
- D'Abbrera, B. 1988. Butterflies of the Neotropical Region—Part V. Nymphalidae (Concl.) & Satyridae. Black Rock, Hill House, Victoria.
- Espeland, M., J. W. Breinholt, E. P. Barbosa, M. M. Casagrande, B. Huertas, G. Lamas, M. A. Marín, O. H. H. Mielke, J. Y. Miller, S. Nakahara, et al. 2019. Four hundred shades of brown: Higher level phylogeny of the problematic Euptychiina (Lepidoptera, Nymphalidae, Satyrinae) based on hybrid enrichment data. Mol. Phylogenet. Evol. 131: 116–124.
- Forster, W. 1964. Beiträge zur Kenntnis der Insektenfauna Boliviens XIX. Lepidoptera III. Satyridae. Veröff. Zool. Staatssammlung München 8: 51–188.
- Gaede, M. 1931. Familia Satyridae. Lepidopterorum Catalogus. 43: 1–320, 46: 321–544, 48: 545–759.
- Gernaat, H. B. P. E., B. G. Beckles, and T. V. Andel. 2012. Butterflies of Suriname: A Natural History. Amsterdam, KIT Publishers.
- Geyer, C. 1832. Pp. 1–48. In Hübner, J., (ed.), Zuträge zur Sammlung exotischer Schmetterlinge, bestehend in Bekanntmachung einzelner Geschlechter neuer oder seltener nichteuropäischer Arten, 4. Jacob Hübner, Augsburg.
- Godart, J. B. 1824. 329–706, 708–711, 794–828. In P. A. Latreille, and J. B. Godart, (eds.), Encyclopédie Méthodique. Histoire naturelle des animaux veuve Agasse, Paris.
- Hebert, P. D., A. Cywinska, S. L. Ball, and J. R. deWaard. 2003. Biological identifications through DNA barcodes. Proc. Biol. Sci. 270: 313–321.
- Horn, W., and I. Kahle. 1935. Über entomologische Sammlungen, Entomologen & Entomo-Museologie. I. Kapitel. Sammlungen, welche ihren Eigentümer gewechselt haben [Part]. Entomol. Beih. Berlin-Dahlem 2: 1–160.
- ICZN (International Commission on Zoological Nomenclature). 1999. International Code of Zoological Nomenclature, 4th Edition. International Trust for Zoological Nomenclature, London, United Kingdom.
- de Jong, R. 1982. Rediscovery of the type of *Papilio phineus* Cramer and its bearing on the genera *Phemiades* Hübner and *Propertius* Evans (Hesperiidae). J. Lepid. Soc. 36: 279–289.
- Kalyaanamoorthy, S., B. Q. Minh, T. K. F. Wong, A. von Haeseler, and L. S. Jermiin. 2017. ModelFinder: fast model selection for accurate phylogenetic estimates. Nat. Methods. 14: 587–589.
- Kirby, W. F. 1871. A synonymic catalogue of diurnal Lepidoptera. John Van Voorst, London, United Kingdom.
- Kirby, W. F. 1879. Catalogue of the collection of diurnal Lepidoptera formed by the late William Chapman Hewitson of Oatlands, Walton-on-Thames; and bequeathed by him to the British Museum. John Van Voorst, London, United Kingdom.
- Lamas, G. 2004. Nymphalidae. Satyrinae. Tribe Satyrini. Subtribe Euptychiina, pp. 217–223. In G. Lamas (ed.), Checklist: Part 4A. Hesperioidea – Papilionoidea. In Heppner, J. B. (ed.), Atlas of Neotropical Lepidoptera, vol. 5A. Scientific Publishers, Association for Tropical Lepidoptera, Gainesville.
- Lamas, G., and J. Grados. [1997]. Mariposas de la Cordillera del Sira, Perú (Lepidoptera: Papilionoidea y Hesperioidea). Rev. Peru. Entomol. 39: 55–61.
- Lavinia, P. D., E. O. Núñez Bustos, C. Kopuchian, D. A. Lijtmaer, N. C. García, P. D. N. Hebert, and P. L. Tubaro. 2017. Barcoding the butterflies of southern South America: species delimitation efficacy, cryptic diversity and geographic patterns of divergence. PLoS One. 12: e0186845.
- Marín, M. A., C. Peña, S. I. Uribe, and A. V. L. Freitas. 2017. Morphology agrees with molecular data: phylogenetic affinities of Euptychiina butterflies (Nymphalidae: Satyrinae). Syst. Entomol. 42: 768–785.
- Miller, L. D. 1968. The higher classification, phylogeny and zoogeography of the Satyridae (Lepidoptera). Mem. Am. Entomol. Soc. 24: [6] + iii + 174.
- Minh, B. Q., H. A. Schmidt, O. Chernomor, D. Schrempf, M. D. Woodhams, A. von Haeseler, and R. Lanfear. 2020. IQ-TREE 2: New models and efficient methods for phylogenetic inference in the genomic era. Mol. Biol. Evol. 37: 1530–1534.
- Murray, D., and D. P. Prowell. 2005. Molecular phylogenetics and evolutionary history of the neotropical Satyrine Subtribe Euptychiina (Nymphalidae: Satyrinae). Mol. Phylogenet. Evol. 34: 67–80.
- Nakahara, S., D. H. Janzen, W. Hallwachs, and M. Espeland. 2015. Description of a new genus for *Euptychia bilara* (C. Felder & R. Felder, 1867) (Lepidoptera: Nymphalidae: Satyrinae). Zootaxa. 4012: 525–541.
- Nakahara, S., E. P. Barbosa, M. A. Marín, A. V. Freitas, T. Pomerantz, and K. R. Willmott. 2016. *Graphita* gen. nov., a New Genus for *Neonympha griphe* C. Felder & R. Felder, 1867 (Lepidoptera, Nymphalidae, Satyrinae). Neotrop. Entomol. 45: 675–691.
- Nakahara, S., K. R. Willmott, O. H. H. Mielke, J. Schwartz, T. Zacca, M. Espeland, and G. Lamas. 2018a. Seven new taxa from the butterfly subtribe Euptychiina (Lepidoptera: Nymphalidae: Satyrinae) with revisional notes on *Harjesia* Forster, 1964 and *Pseudeuptychia* Forster, 1964. Insecta Mundi 639: 1–38.
- Nakahara, S., T. Zacca, B. Huertas, A. F. E. Neild, J. P. W. Hall, G. Lamas, L. A. Holian, M. Espeland, and K. R. Willmott. 2018b. Remarkable sexual dimorphism, rarity and cryptic species: a revision of the 'aegrota' species group' of the Neotropical butterfly genus *Caeruleuptychia* Forster, 1964 with the description of three new species (Lepidoptera, Nymphalidae, Satyrinae). Insect. Syst. Evol. 49: 130–182.
- Nakahara, S., G. Lamas, S. Tyler, M. A. Marín, B. Huertas, K. R. Willmott, O. H. H. Mielke, and M. Espeland. 2019a. A revision of the new genus *Amiga* Nakahara, Willmott & Espeland, gen. n., described for *Papilio amaca* Fabricius, 1776 (Lepidoptera, Nymphalidae, Satyrinae). ZooKeys 821: 85–152.
- Nakahara, S., T. Zacca, F. M. S. Dias, D. R. Dolibaina, L. Xiao, M. Espeland, M. M. Casagrande, O. H. H. Mielke, G. Lamas, B. Huertas, et al. 2019b. Revision of the poorly known Neotropical butterfly genus *Zischkaia* Forster, 1964 (Lepidoptera, Nymphalidae, Satyrinae), with descriptions of nine new species. Eur. J. Taxon. 551: 1–67.
- Nakahara, S., K. Kleckner, G. Lamas, B. Huertas, and K. R. Willmott. 2020a. Contribution towards the systematics of *Magneuptychia* Forster, 1964: *Caeruleuptychia francisca* (Butler, 1870), n. comb. (Lepidoptera: Nymphalidae: Satyrinae). Tijdschr. Entomol. 163: 51–61.
- Nakahara, S., G. Lamas, K. Willmott, and M. Espeland. 2020b. Description of a new genus and species for a common and widespread Amazonian satyrine butterfly (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). PeerJ. 8: e10324.
- Nosil, P., B. J. Crespi, and C. P. Sandoval. 2002. Host-plant adaptation drives the parallel evolution of reproductive isolation. Nature. 417: 440–443.
- Peña, C., S. Nylin, A. V. L. Freitas, and N. Wahlberg. 2010. Biogeographic history of the butterfly subtribe Euptychiina (Lepidoptera, Nymphalidae, Satyrinae). Zool. Scripta. 39: 243–258.
- de Queiroz, K., and J. Gauthier. 1990. Phylogeny as a central principle in taxonomy: phylogenetic definitions of taxon names. Syst. Zool. 39: 307–322.
- Riley, N. D., and A. G. Gabriel. 1924. Catalogue of the type specimens of Lepidoptera Rhopalocera in the British Museum. Part I. Satyridae. Oxford University Press, London, United Kingdom.
- Robbins, R. K., G. Lamas, O. H. H. Mielke, D. J. Harvey, and M. M. Casagrande. 1996. Taxonomic composition and ecological structure of the species-rich butterfly community at Pakitza, Parque Nacional del Manu, Perú, pp. 217–252. In D. E. Wilson and A. Sandoval (eds.), Manu. The biodiversity of southeastern Peru. Smithsonian Institution, Washington, DC.

- Roepke, W. 1941. Over de vlinder-collectie Verloren van Themaat. Entomol. Ber. 10: 373–375.
- Singer, M. C., and P. R. Ehrlich. 1993. Host specialization of satyrine butterflies, and their responses to habitat fragmentation in Trinidad. J. Res. Lepid. 30: 248–256.
- Smit, P., A. P. M. Sanders, and J. P. F. van der Veer. 1986. Hendrik Engel's alphabetical list of Dutch zoological cabinets and menageries. Nieuwe Nederlandse Bijdragen tot de Geschiedenis der Geneeskunde en der Natuurwetenschappen 19: i–x, 1–340.
- Warren, A. D., K. J. Davis, E. M. Stangeland, J. P. Pelham, K. R. Willmott, and N. V. Grishin. 2017. Illustrated Lists of American Butterflies [accessed April 2020]. <http://www.butterfliesofamerica.com>
- Westwood, J. O. 1851. Pp. 363–374. In E. Doubleday, (eds.), The genera of diurnal Lepidoptera: comprising their generic characters, a notice of their habits and transformations, and a catalogue of the species of each genus. Longman, Brown, Green & Longmans, London, United Kingdom.
- Weymer, G. 1911. 4. Familie: Satyridae, pp. 173–192. In A. Seitz (ed.), Die Gross-Schmetterlinge der Erde 5. A. Kernen, Stuttgart.
- Willmott, K. R., M. A. Marín, S. Nakahara, T. Pomerantz, G. Lamas, B. Huertas, M. Espeland, L. Xiao, J. P. W. Hall, J. I. R. Willmott, and A. V. L. Freitas. 2019. A revision of the new Andean butterfly genus *Optimandes* Marín, Nakahara & Willmott, n. gen., with the description of a new species (Nymphalidae: Satyrinae: Euptychiina). Trop. Lepid. Res. 29: 29–44.
- Zacca, T., M. M. Casagrande, O. H. H. Mielke, B. Huertas, E. Barbosa, A. V. L. Freitas, G. Lamas, M. Espeland, C. Brévignon, S. Nakahara, et al. 2021. Systematics of the Neotropical butterfly genus *Paryphthimoides* Forster, 1964 (Lepidoptera: Nymphalidae: Satyrinae), with descriptions of seven new taxa. Insect Syst. Evol. 52: 42–96.