A revision of the new Andean butterfly genus *Optimandes* Marín, Nakahara & Willmott, n. gen., with the description of a new species (Nymphalidae: Satyrinae: Euptychiina)

Keith R. Willmott[1], Mario A. Marín[2], Shinichi Nakahara[1,3], Tatiana Pomerantz[1], Gerardo Lamas[3], Blanca Huertas[4], Marianne Espeland[5], Lei Xiao[1], Jason P. W. Hall[6], James I. Robinson Willmott[1], André V. L. Freitas[2]

1. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA: kwillmott@flmnh.ufl.edu
2. Departamento de Biologia Animal and Museu de Zoologia, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.
3. Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.
4. Natural History Museum, Cromwell Road, London, United Kingdom.
5. Arthropoda Department, Zoological Research Museum Alexander Koenig, Germany.
6. Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Date of issue online: 3 May 2019
Zoobank Registered: urn:lsid:zoobank.org:pub:9DED7FED-83FB-49FA-9B49-D3177A9F93A8
Electronic copies (ISSN 2575-9256) in PDF format at: http://journals.fcla.edu/troplep; https://zenodo.org; archived by the Institutional Repository at the University of Florida (IR@UF), http://ufdc.ufl.edu/ufir; **DOI**: 10.5281/zenodo.2650482

Abstract: A new genus, *Optimandes* Marín, Nakahara & Willmott, **n. gen.**, is described to contain the type species *Neonympha eugenia* C. Felder & R. Felder, 1867, its junior subjective synonym *Euptychia phineus* Butler, 1867, and its subspecies *Euptychia transversa* Weymer, 1911, which are transferred from the genus *Euptychoides* Forster, 1964. The sister species to *Optimandes eugenia* **n. comb.** is a distinctive new species which is here described and named as *Optimandes mocha* Willmott, Hall & Lamas, **n. sp.** Figures of wings, genitalia and distribution maps are provided for both species and the immature stages of *Optimandes eugenia* are described for the first time. Both species are uncommon to rare inhabitants of Andean cloud forest, with *O. eugenia* widespread throughout the tropical Andes, and *O. mocha* occurring from southern Ecuador to Bolivia.

Key words: Andes, *Chusquea*, immature stages, inventory, mimicry, species description, taxonomy

INTRODUCTION

The butterfly family Nymphalidae has been intensively studied over the last couple of decades, including broad, comprehensive phylogenetic studies (Brower, 2000; Freitas & Brown, 2004; Wahlberg *et al.,* 2009), as well as taxonomic revisions. However, some nymphalid groups have still remained poorly understood until recently, such as the diverse subtribe Euptychiina (Satyrinae). This group of more than 400 described species (Lamas, 2004) has been neglected for almost four decades, since the pioneering taxonomic work of Forster (1964) and Miller (1968). Research over the last decade on the phylogenetics and generic classification of the Euptychiina has uncovered a remarkable number of para- or polyphyletic genera (e.g., Murray & Prowell, 2005; Peña *et al*., 2010; Nakahara *et al*., 2015; Marín *et al*., 2017; Zacca *et al*., 2018). One of the most notable is the genus *Euptychoides* Forster, 1964, whose members appear in six different clades based on both morphological (Marín *et al*., 2017) and molecular (Espeland *et al*., 2019; unpublished data) research. One monotypic genus, *Graphita* Nakahara, Marín & Barbosa, 2016, was recently described (Nakahara *et al*., 2016), while another clade consists of *Euptychoides eugenia* (C. Felder & R. Felder, 1867) and a distinctive, undescribed species from the eastern Andes collected by the authors during long-term surveys of the butterflies of Ecuador and Peru. We therefore here describe a new genus for *E. eugenia*, describe its sister species, and review and summarize the taxonomy and biology of both species.

MATERIALS AND METHODS

The authors and colleagues have been conducting field work throughout Ecuador and Peru for many years to collect material for taxonomic study and document distribution and behavior. Standard hand-netting was supplemented with the use of bait-traps, baited with rotting fish and suspended from 1-20 m above the ground, and observations were made using single rope climbing techniques (Hall & Willmott, 2010). Immature stages were located by searching potential host plants in Ecuador, in this case bamboos (Poaceae), and eggs and larvae were reared in plastic cups that were cleaned and provided with fresh host plant leaves daily. Observations of behavior and development were recorded and photographs were taken with a Canon EOS Rebel T4i with 60 mm macro lens and a Canon Macro Ring Lite MR-14EXII, and a Canon EOS 60D with an MP-E 65 mm macro lens and the same ring flash. Size was estimated using the ApproximateFocusDistance as recorded in the image EXIF data to estimate total image width, and thereby enable

pixel distances to be converted to mm, with measurements from multiple images (and potentially caterpillars) being combined to provide lower and upper estimates of head capsule and body size. Voucher specimens of the immature stages are deposited in the Florida Museum of Natural History, University of Florida, Gainesville, USA.

Public and private collections in the Americas and Europe were visited to examine type specimens, study morphological variation and record distribution data of *Euptychoides* and other genera under study. The following collection acronyms are used: **ANNE**: Andrew F. E. Neild collection, London, United Kingdom; **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); **JARA**: James Radford collection, Cambridge, UK; **MNHU**: Museum für Naturkunde, Leibniz-Institut für Evolutions- und Biodiversitätsforschung an der Humboldt Universität, Berlin, Germany; **MUSM**: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; **MZUJ**: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland; **NHMUK**: Natural History Museum, London, UK (formerly BMNH); **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, São Paulo, Brazil.

Morphology was studied using standard techniques, with adult abdomens being soaked in hot 10% KOH for 10-15 minutes, dissected and subsequently stored in glass tubes in glycerine. Body morphology and dissections were studied using a stereomicroscope at up to 100x magnification. The terminology for genitalic and abdominal structures follows Scoble (1992), with use of the term brachia following Klots (1956), and nomenclature for venation follows the Comstock & Needham (1898) system as in Comstock (1918). We use the abbreviations DFW, VFW, DHW and VHW for dorsal and ventral forewing and hindwing. The taxonomic classification follows Lamas (2004), modified following Peña *et al.* (2006, 2010), Wahlberg *et al.* (2009) and Nakahara *et al*. (2016).

We extracted genomic DNA from legs removed from dried Euptychiina specimens, and from two thoracic legs dissected from caterpillars preserved in 70% ethanol, using Qiagen's DNeasy Blood & Tissue Kit following the manufacturer's protocol, incubating samples overnight (24 h) and using a final elution volume of 100 ul. We amplified the first half of the mitochondrial gene cytochrome oxidase I (COI), also known as the barcode region for animals (Hebert *et al.*, 2003), and the nuclear genes EF-1α, GAPDH and RpS5, which have proved successful in resolving relationships among euptychiines in previous studies (Peña *et al*., 2010). Primer information, PCR reaction conditions and sequencing were as described in Willmott *et al*. (2018). New sequences were deposited in Genbank and were incorporated into a dataset of published Euptychiina sequences (Murray & Prowell, 2005; Peña *et al.*, 2006, 2010, 2011; Wahlberg *et al.*, 2009; Freitas *et al.*, 2011, 2018a; Nakahara *et al*., 2016) to identify close relatives (sequence information is provided in Appendix 1).

The concatenated dataset (3,930 base pairs) was partitioned to gene and codon positions, and the maximum-likelihood tree was inferred in IQ-TREE v1.6.9 (Nguyen *et al*., 2015), using the edge-linked partitions (-spp) (Chernomor *et al*., 2016) and obtaining the best-fit model using ModelFinder (-m MFP) (Kalyaanamoorthy *et al*., 2017). Twenty likelihood searches were performed, and the tree with the maximum likelihood was selected. Branch support was calculated using ultrafast bootstrap with 2000 replications, optimized with nearest neighbor interchange (-bnni) (Hoang *et al*., 2018).

RESULTS

Optimandes Marín, Nakahara & Willmott, **new genus**
Type species: *Neonympha eugenia* C. Felder & R. Felder, 1867

Diagnosis and identification: Genetic sequence data show that *Optimandes* **n. gen.** is a member of the *Pareuptychia* clade (Murray & Prowell, 2005), where it is sister to *Nhambikuara* Freitas, Barbosa & Zacca, 2018 (Espeland *et al*., 2019) (Fig. 1), albeit with only moderate ultrafast bootstrap support (83%). Aside from *Nhambikuara cerradensis* Freitas, Barbosa & Zacca, 2018, the type of *Nhambikuara* and related species forming the sister clade to *Optimandes* all have distinctive, oval submarginal ocelli on the VHW with pale scaling offset from the center of each ocellus. In contrast, both *Optimandes* species have circular or slightly oval submarginal VHW ocelli with a single, well-marked central white pupil in each, in addition to two well-developed subapical ocelli on the VFW in cells M_2-M_1 and M_1-R_5 (the latter reduced in *O. e. eugenia* and barely visible or absent in *Nhambikuara*). The combination of the two subapical ocelli in the VFW apex, and single-pupilled VHW ocelli, which fill cells Cu_2-Cu_1 and M_2-M_1 on the VHW, distinguish this genus from most other euptychiines. *Magneuptychia tiessa* (Hewitson, 1869) has these characteristics also, and is also a member of the *Pareuptychia* clade based on genetic data, but the species is sister to *Satyrotaygetis satyrina* (Bates, 1865) and both are more closely related to *Pareuptychia* than they are to *Optimandes*. The male genitalia of *M. tiessa* likewise shows no obvious similarities to those of *Optimandes*.

Description: MALE (Fig. 2,3,4): Forewing length 23-24 mm (n=5). *Wings*: FW triangular, distal and anal margins straight and almost perpendicular, vein R_2 arising just basally of origin of vein R_{3+4+5} (Fig. 3); HW approximately triangular, distal margin rounded, anal margin slightly indented basal of tornus. *Dorsal surface*: Ground color gray-brown to reddish brown, slight darker blackish brown marginal line on both wings, and indistinct submarginal line on DHW. *Ventral surface*: Ground color grayish to reddish brown, a little paler than dorsal surface, with scattered to solid white scaling in posterior basal half of VHW, discal area, and surrounding more anterior ocelli in one taxon. VFW with a discal and a postdiscal line/band, darker brown, latter bordered distally with paler ground scales followed by darker ground scales and two to four postdiscal ocelli in cells Cu_1-M_3, with those in M_2-R_5 black spots encircled by clear yellowish brown rings with a single central white pupil in each ocellus, remaining ocelli smaller but similar, or simple yellow rings, or obsolete; two broad, dark brown submarginal lines, more basal line wavy and bordered basally by band of paler ground scaling, more distal line straighter, wing margin lined with black. VHW with dark brown discal and postdiscal lines from costa to anal margin, postdiscal line bordered distally with paler ground scaling; five to six postdiscal ocelli, black with yellow ring and central white pupil in cells 2A-Cu_2 and M_1-Rs (half width of cell) and Cu_2-Cu_1 and M_2-

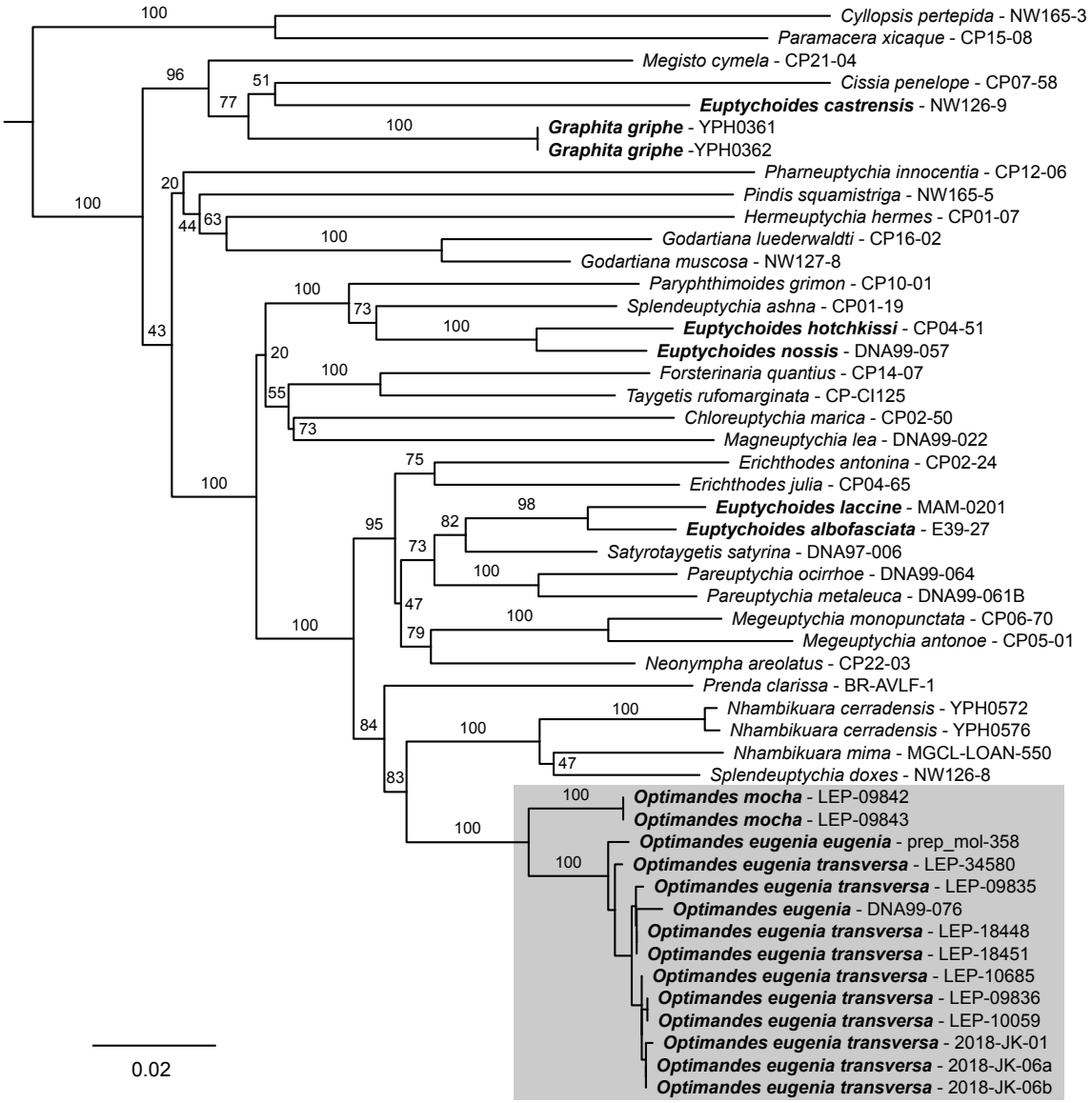

Fig. 1. Maximum likelihood tree (log-likelihood: -26562.376) showing the phylogenetic relationships among *Optimandes* **new genus** and relatives within the subtribe Euptychiina. Numbers beside branches are ultrafast bootstrap values. Names in bold were included in *Euptychoides* in Lamas (2004).

M_1 (almost filling cell), ocelli in cells Cu_1-M_2 similar to others but reduced in size, or more indistinct and lacking central pupil, or obsolete; two broad, dark brown submarginal lines, more basal line wavy and bordered basally by band of paler grayish scaling, wing margin lined with black. *Head*: eyes brown with dense, long setae; antennae with *c.* 33 antennomeres, distal *c.* 10 comprising club (n=4), dark brown with sparse white scales at ventral base of antennomeres in basal part of antennae; labial palpi (Fig. 3B) dark brown with long dark brown hair-like scales ventrally, with *O. eugenia* having cream-colored scales laterally; head covered with dark brown scales and hair-like scales. *Thorax*: thorax, forelegs (Fig. 3C), mid- and hindlegs dark brown (mid- and hindlegs ventrally with sparse cream-colored scales in *O. eugenia*), mid- and hindlegs with pair of tibial spurs. *Abdomen*: dark brown dorsally, paler brown ventrally, eighth tergite unsclerotized except for narrow anterior band and slightly broader posterior patch; eighth sternite appearing as single plate, in contrast to several species currently placed in *Euptychoides* (e.g., *E. pseudosaturnus* Forster, 1964). *Genitalia* (Fig. 4): notable features in comparison with other Euptychiina include aedeagus relatively broad, curving upwards anteriorly and containing two conspicuous elongate patches of teeth-like cornuti; uncus with broad basal half in lateral view with a prominent dorsal 'keel'; brachia directed upwards with respect to uncus; valva tapering with distal tip pointed.

FEMALE (known only for *O. eugenia*) (Fig. 2,3,5): Forewing length 25 mm (n=1). *Wings*: similar to male except more rounded, paler. *Head*, *thorax*, *abdomen*: similar to male except with sparse cream-colored hair-like scales among dark brown hair-like scales on ventral palpi, foreleg tarsus not reduced (Fig. 3E), covered with cream-colored scales and hair-like scales. *Genitalia* (Fig. 5): inter-segmental membrane between 7th and 8th abdominal segments pleated and expandable, as in many other euptychiines; lamella postvaginalis forming broad lateral plates extending close to (*E. e. eugenia*, Fig. 5A) or fused with (*E. e. transversa*) anterioventral edge of eighth tergum; posteriorly-directed, 'scoop'-like plate ventral of ostium bursae (Fig. 5A,B); no sclerotized antrum, ductus bursae relatively long and broadening gradually into poorly defined corpus bursae that bears two elongate spiny signa (Fig. 5D), ductus seminalis joins ductus bursae dorsally very close to ostium bursae.

Etymology: The generic name is derived from the masculine Latin noun *optimas*, an aristocrat, combined with 'Andes', to which mountain range the genus is largely endemic, and it is considered masculine. The name is in reference to *O. eugenia*, whose specific name means 'well-born', as well as being a feminine given name; the Felders may have named the species after Empress Elisabeth Amalia Eugenia of Wittelsbach ("Sissi") (1837-1898).

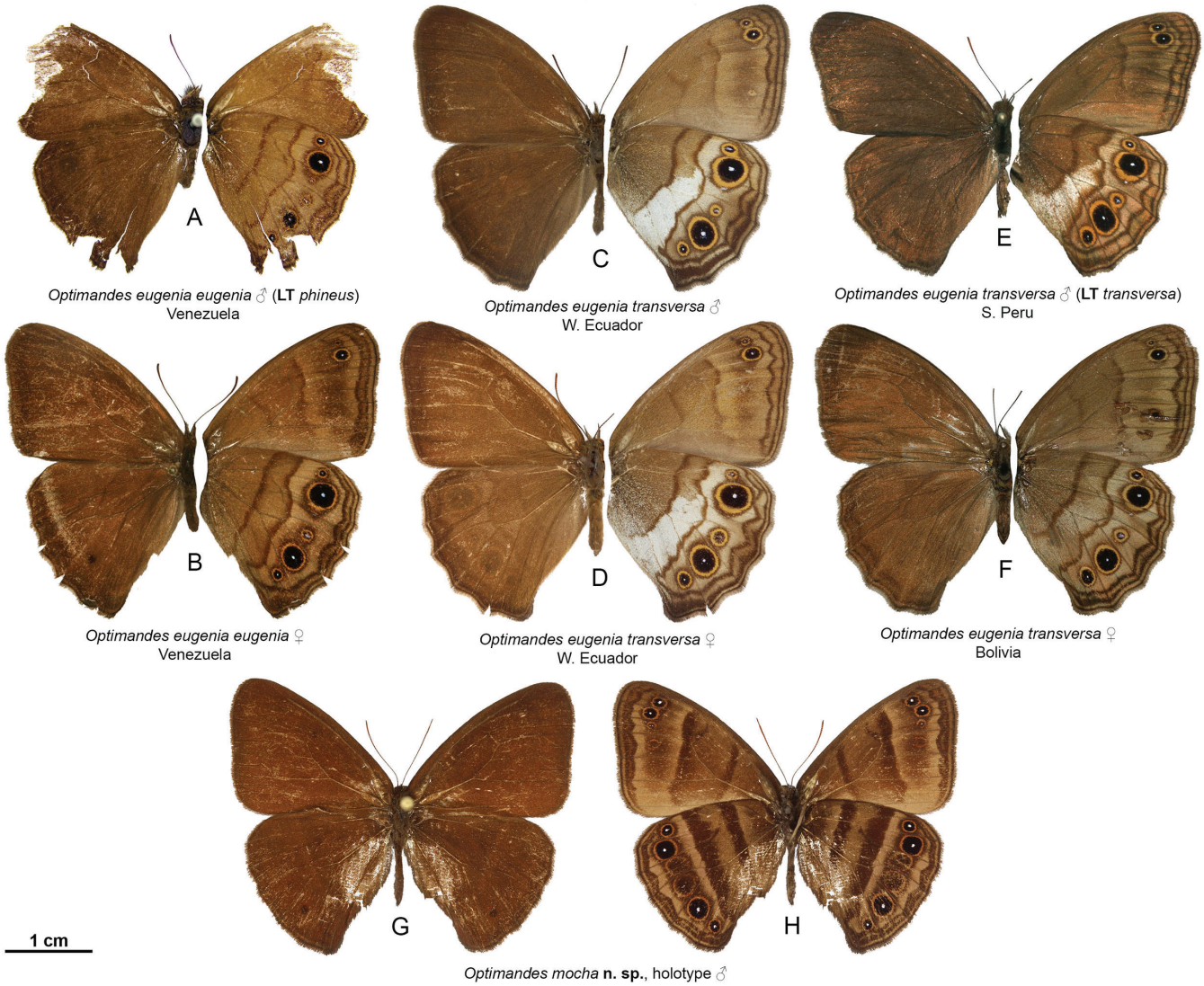

Fig. 2. *Optimandes*, adults, left side dorsal, right side ventral, unless stated otherwise. **A,B** *Optimandes eugenia eugenia*. **A.** ♂, Venezuela (lectotype *Euptychia phineus*). **B**. ♀, Venezuela (Aragua). **C-F**, *Optimandes eugenia transversa*. **C**. ♂, W. Ecuador (Pichincha). **D**. ♀, W. Ecuador (Carchi). **E**. ♂, Peru (Cuzco) (lectotype *Euptychia transversa*). **F**. ♀, Bolivia (Cochabamba). **G,H**, *Optimandes mocha* **n. sp.**, holotype ♂, Ecuador. **G.** Dorsal surface. **H**. Ventral surface.

Relationships and taxonomy: Genetic sequence data show that *Optimandes* **n. gen.** is a member of the *Pareuptychia* clade (Murray & Prowell, 2005), where it is strongly supported as monophyletic (100%) and moderately well supported (83%) as sister to *Nhambikuara* (Espeland *et al*., 2019) (Fig. 1). This result was also confirmed in ongoing analyses aimed at generating as comprehensive a phylogeny as possible for the Euptychiina, incorporating a much larger dataset including additional unpublished sequences, comprising >2000 sequences and representing >420 species (Espeland, unpublished data). This dataset includes the type species of 59 of the 61 available generic names for Euptychiina, and species closely related (based on morphology) to the remaining two type species.

As discussed above under Diagnosis and identification, *Optimandes* and *Nhambikuara* do not closely resemble one another in wing pattern or morphology, and the two seem ecologically rather distinct, with *Nhambikuara* predominantly a lowland genus and *Optimandes* confined to cloud forest. We therefore believe that they are best treated as distinct genera. The type species of *Euptychoides*, *Euptychia saturnus* Butler, 1867 (=*Euptychoides laccine* (C. Felder & R. Felder, 1867)), is also a member of the *Pareuptychia* clade, but it is not close to *Optimandes*, instead being more closely related to *Satyrotaygetis* Forster, 1964 and *Pareuptychia*. Although a comprehensive phylogenetic anlaysis of the *Pareuptychia* clade based on morphological data has not been published, *E. laccine* does not show any obvious characters in the genitalia that might suggest a close relationship to *Optimandes eugenia* **n. comb.** The male genitalia of *E. laccine* differ from those of *O. eugenia* in having a much narrower uncus (in lateral view), with its dorsal edge more smoothly aligned with the dorsal edge of the tegumen, narrower valvae with a small dorsal projection just basal of the posterior tip, and the aedeagus becoming narrower anteriorly. These characters are also shared with *E. pseudosaturnus* and *Euptychoides albofasciata* (Hewitson, 1869), consistent with molecular data that show a close relationship among these species (Fig. 1, and Marín, unpublished data).

Optimandes eugenia has had a somewhat unstable history

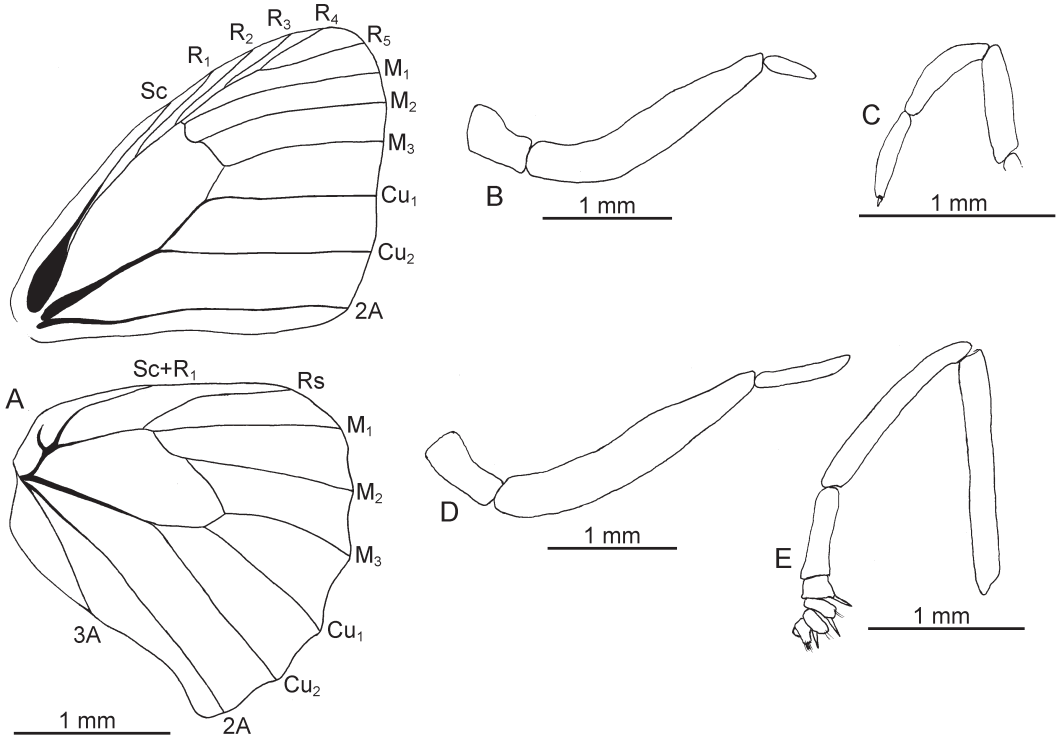

Fig. 3. A. *Optimandes eugenia*, morphology. **A-C**, *O. e. transversa*, ♂ (FLMNH-MGCL-112616). **A**. Wing venation. **B**. Lateral view of labial palpus. **C.** Lateral view of foreleg. **D-E,** *O. e. eugenia*, ♀ (FLMNH-MGCL-298582). **D**. Lateral view of labial palpus. **E.** Lateral view of foreleg.

of generic classification. Butler (1877) considered *O. eugenia eugenia* (as '*Euptychia phineus*') as a member of his '*E. harmonia* group', which included *Euptychia gulnare* Butler, 1870, *E. harmonia* Butler, 1867, *Neonympha yphthima* C. Felder & R. Felder, 1867, *E. nebulosa* Butler, 1867, and *E. oreba* Butler, 1870. These five species are currently placed in five different genera. Weymer (1911) placed *O. e. transversa* in his 'Saturnus Group', which also included three species later placed in *Euptychoides* by Forster (1964) and Lamas (2004), namely *Euptychoides laccine* (referred to as '*E. saturnus*' by Weymer), *Euptychoides fida* (Weymer, 1911) and *Graphita griphe* (C. Felder & R. Felder, 1867). However, Weymer (1911) placed *O. eugenia eugenia* (as '*E. phineus*') in his 'Harmonia Group', corresponding to *Hermeuptychia* Forster, 1964, of later authors, and evidently confused it with several other true *Hermeuptychia* occurring throughout the eastern Andes. Forster (1964) placed *O. e. eugenia* in *Yphthimoides* Forster, 1964, and *O. e. transversa* in *Euptychoides*, apparently influenced by the presence or absence of white on the VHW. This character seems to perhaps be involved in mimicry, as we discuss further below, and based on molecular and morphological data we regard the two taxa as conspecific, following Lamas (2004).

Distribution and natural history: The genus is known from the Cordillera de la Costa in northern Venezuela, from both Andean slopes of Ecuador, and south of Ecuador along the eastern Andes to Bolivia (Fig. 6). Both known species are uncommon to rare inhabitants of cloud forest, ranging from 1000-2200 m in elevation. The immature stages of *O. eugenia transversa* are described below.

Optimandes eugenia (C. Felder & R. Felder, 1867), **n. comb.**
Figs. 1-6

Diagnosis and identification: *Optimandes eugenia* **n. comb.** is easily distinguished from the only other member of the genus, *Optimandes mocha* **n. sp.**, as described under that species. It is superficially similar to a number of other euptychiines, but the very pronounced, single-pupilled VHW ocelli in cells Cu_2-Cu_1 and M_2-M_1 and highly reduced ocelli between them, coupled with the undulate dark postdiscal line on the VHW, are distinctive.

Taxonomy: *Optimandes eugenia* contains two subspecies that were formerly placed in different genera until united by Lamas (2004). The two taxa show little divergence in the DNA barcode (Fig. 1), share a distinctive, sclerotized plate ventral of the ostium bursae (Fig. 5B; male genitalia of the nominate subspecies were not examined), occur at similar elevations, and share a number of distinctive wing pattern characters that suggest they are conspecific. These wing pattern characters include the very similar arrangement of submarginal ocelli on the VHW that is unique within the Euptychiina in terms of the relative size and shape of ocelli in different cells, namely very large ocelli in cells Cu_2-Cu_1 and M_2-M_1, a small but distinct ocellus in cell Cu_1-M_3 and a virtually obsolete ocellus in cell M_3-M_2 (in some otherwise very similar *Hermeuptychia*, the ocelli in cells Cu_1-M_3 and M_3-M_2 may be small but distinct, or virtually obsolete, but are similar in both cells), and a small ocellus in cell 2A-Cu_2 (absent, for example, in *E. nossis*); in addition, the ocelli that are each surrounded by a yellow ring

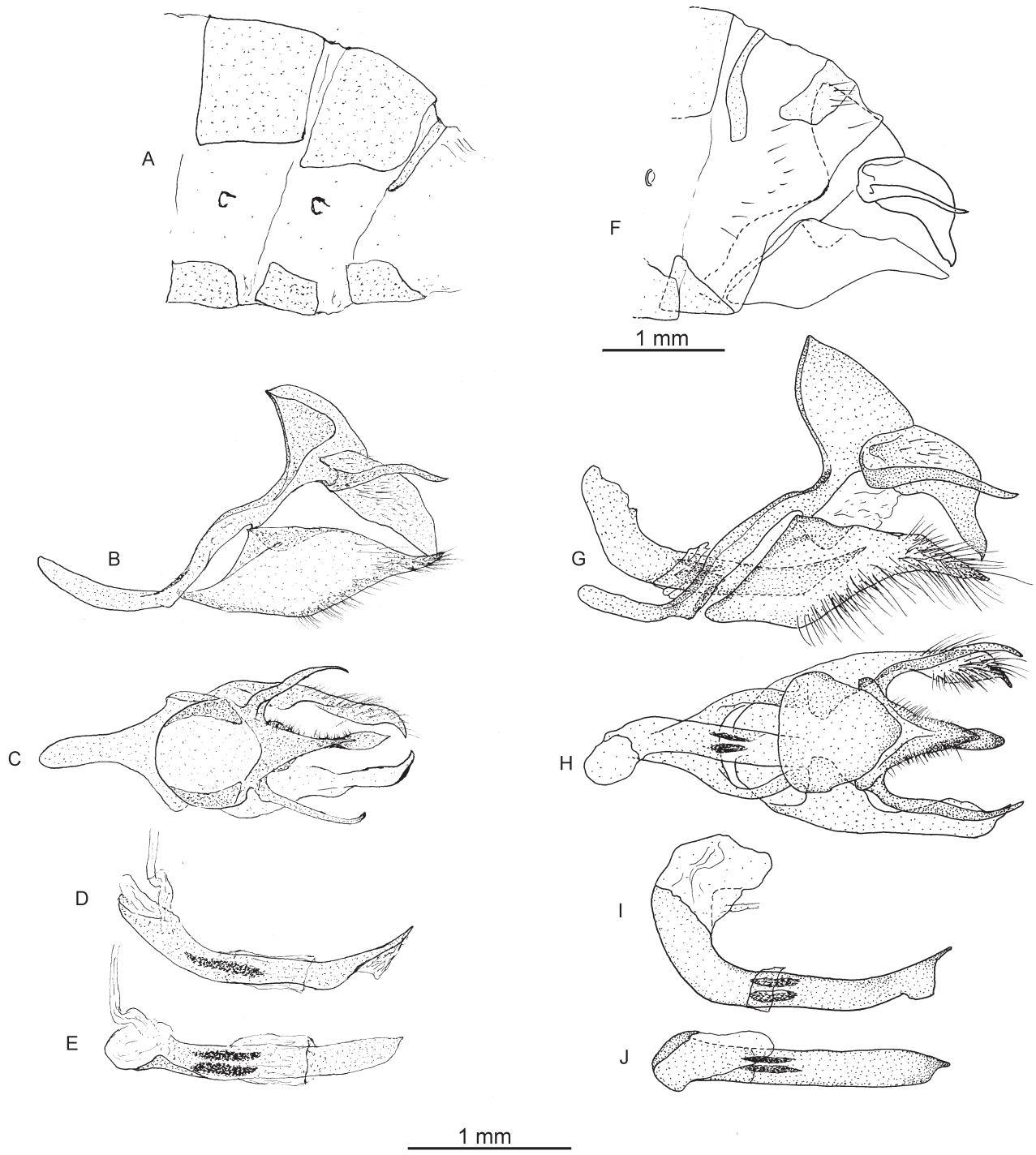

Fig. 4. *Optimandes*, male genitalia. **A-E,** *O. eugenia transversa* (FLMNH-MGCL-112616, dissection KW-14-30). **F-J,** *O. mocha* **n. sp.** (HT, dissection KW-17-20). **A,F**. Lateral view terminal abdominal segments. **B,G**. Lateral view genitalic capsule. **C,H**. Dorsal view genitalic capsule. **D,I.** Lateral view aedeagus. **E,J.** Dorsal view aedeagus.

that is well-defined and narrow, and have a single central white pupil (Fig. 2), are further useful distinguishing characters. The undulate dark postdiscal line on the VHW is also distinctive and shared between the taxa, although the nominate subspecies has a straighter dark VHW discal line than *O. e. transversa*. Mimicry with other cloud forest euptychiines is a possible explanation for the principal difference between the two taxa, namely the large white patch of scaling on the VHW of *O. e. transversa*, as discussed further below.

Distribution and natural history: This species is known from northern Venezuela, western Ecuador and from the east Andean slopes of Ecuador south to Bolivia, in cloud forest from 1000-2200 m elevation (Fig. 6). The immature stages of *O. e. transversa* are described under that taxon.

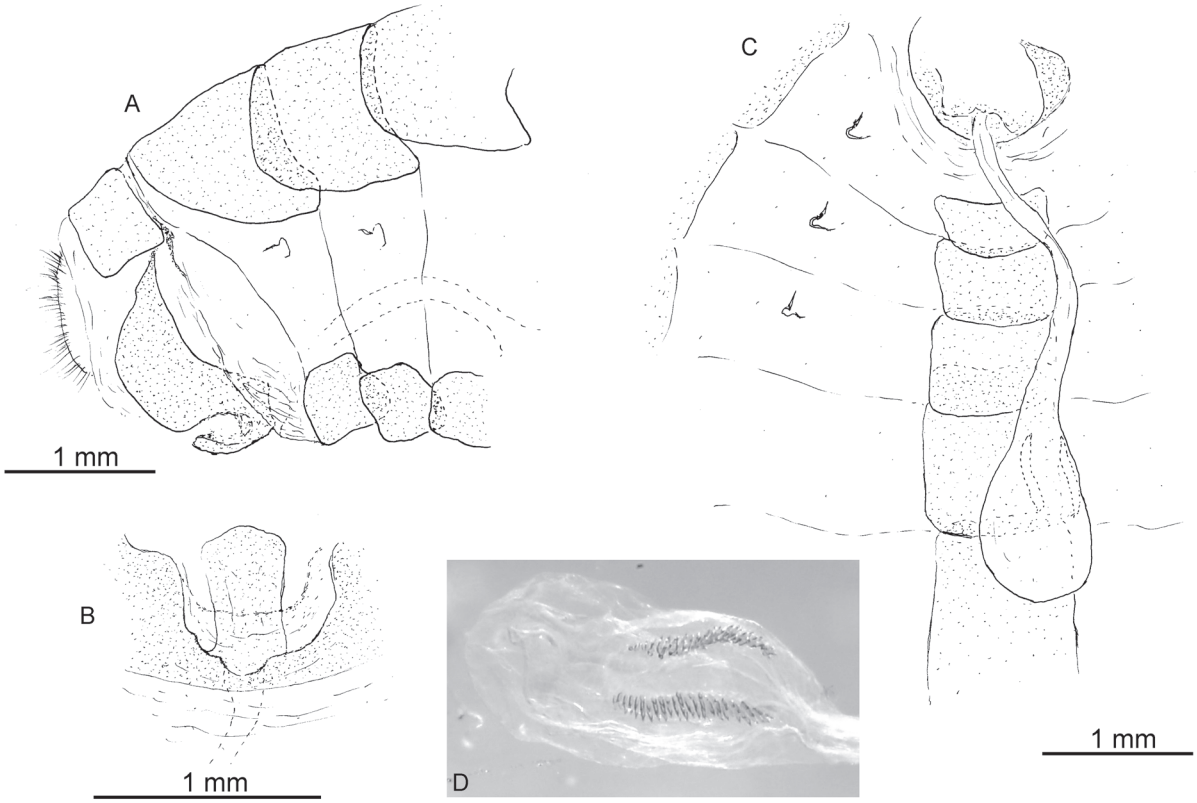

Fig. 5. *Optimandes e. eugenia*, female genitalia (FLMNH-MGCL-298582, dissection SN-17-205). **A**. Lateral view of terminal abdominal segments. **B**. Ventral view of sclerotized plate ventral of ostium bursae. **C**. Dorsal view of genitalia. **D**. Perpendicular view of signa.

Optimandes eugenia eugenia (C. Felder & R. Felder, 1867), **n. comb.**
Figs. 1, 2A,B, 5, 6

Neonympha eugenia Felder & Felder (1867: 476). **Lectotype** ♀ [here designated]: "Euptychia Eugenia Mor[itz]//Venezuela type//Type// FELDER COLLN.//Rothschild Bequest B. M. 1939-1.//Type of N. eugenia, Feld = Eup. Phineus, Butler. Comp. with Type. NDR.//BMNH(E) 1499239" (NHMUK, examined).

=*Euptychia phineus* Butler (1867: 478, pl. 39, fig. 18). **Lectotype** ♂ [here designated]: "Euptychia Phineus. Butler. Monog.//Venezuela//Venezuela Pur. from Dyson. 47-9.//Type//B. M. TYPE No. Rh 3232 Euptychia phineus ♂ Butl.//Comp. w. Type of N. eugenia Feld. NDR.//BMNH(E) 1267047/NHMUK013376550" (NHMUK, examined).

Euptychia ('*E. harmonia* group') *phineus*: Butler (1877: 120)
Euptychia ('Harmonia Group') *phineus*: Weymer (1911: 209)
Yphthimoides phineus: Forster (1964: 105)
Euptychia phineus: D'Abrera (1988: 777, ♀ V)
Euptychoides eugenia eugenia: Lamas (2004: 219)

Diagnosis and identification: This taxon is distinguished from *O. e. transversa* by the lack of white scaling in the VHW discal and postdiscal areas and by having a straighter dark discal line on the VHW, which does not curve basally towards the anal margin (Fig. 2). It is superficially similar to several *Hermeuptychia* species, but may be distinguished by its larger size, lack of submarginal ocelli in the middle of the VFW, paler scaling distal to the dark VHW postdiscal line, and narrower dark yellow rings around the VHW ocelli.

Taxonomy: Felder & Felder (1867) described *Neonympha eugenia* based on an unspecified number of female specimens in the Felder collection, collected by Johann Wilhelm Karl Moritz in Venezuela, most likely at Colonia Tovar. The original description mentioned the parallel, curving lines in the middle of the VHW and six ocelli on the VHW, with the second and fifth much larger than the remainder. A syntype corresponding to this description is in the NHMUK and is here designated as **lectotype** to fix the identity of the name, given the existence of other superficially similar species (e.g., *Hermeuptychia* spp.). Butler (1867) described *Euptychia phineus* based on an unspecified number of specimens from Venezuela, in the NHMUK, and figured the ventral surface. A syntype corresponding to this description is in the NHMUK and is here designated as **lectotype** to fix the identity of the name (Fig. 2A). Each author was clearly unaware of the publication of the other and we follow Weymer (1911) and Lamas (2004) in considering the two names as subjective synonyms. The name *eugenia* is deemed to have been established on [25 April] 1867 (Lamas *et al*., 1995), whereas Butler's (1867) description of *phineus* was published in 'April' 1867, defaulting to the last day of that month (ICZN, 1999, Article 21.3.1), therefore making *eugenia* the older name by 5 days.

Distribution and natural history: This taxon is known only from the Cordillera de la Costa of northern Venezuela from 1000-1650 m (Fig. 6), and it is rare in collections. Ríos-Málaver (pers. comm.) collected three individuals in the forest of the Centro de Ecología of the Instituto Venezolano de Investigaciones Científicas, Caracas, between July and October, during the rainy season, flying from 10:58 to 15:10, on both sunny and cloudy days.

Specimens examined (3 ♂, 4 ♀): **Venezuela**: *Aragua:* Parque Nacional Henri Pittier, Portochuelo Pass, [10°20'54"N,67°41'16"W], 1150 m, (Miller, L. D), 24 Jul 1981, 1 ♀ [FLMNH-MGCL-298583; cloud forest], (FLMNH); no specific locality, (Sullivan, J. B.), 22 Mar 1972, 1 ♀ [FLMNH-MGCL-297243], (FLMNH); *Miranda:* Río Chacaito, [10°25'N,66°55'W], 980-1080 m, (Lichy, R.), 3 Jul 1937, 1 ♀ [FLMNH-MGCL-298582], (FLMNH); *Not located:* 'Venezuela', 1 ♂ [BMNH(E) 1420244; "Agrees exactly with female type of N. eugenia, Feld"], 1 ♂ [BMNH(E) 1420245], (NHMUK), 1 ♂ [BMNH(E) 1267047; Lectotype *E. phineus*], (NHMUK), (Moritz), 1 ♀ [BMNH(E) 1499239; Lectotype *N. eugenia*], (NHMUK).
Other records (sight records and photographs of live individuals): **Venezuela**: *Miranda:* Altos de Pipe, IVIC, 1600-1650 m, (Pyrcz, T. W.), 16 Dec 2005, 1 ♀ [prep. mol. 358/16.III.2018] (MZUJ) [photograph examined], 27 Jul 2012, [15:10, 21.1°C, 85.3% humidity, flying, cloudy], 9 Oct 2012, [11:05, 26.3°C, 77.8% humidity, flying, sunny], 28 Aug 2012, [10:58, 25.1°C, 89.3% humidity, flying, sunny], (Ríos-Málaver, I. C., pers. comm.); above km 11 turn off Caracas to Los Teques rd., Altos de Pipe (IVIC site), 1550-1650 m, (Neild, A. F. E.), 13-14 Oct 2000, 1 ♀, (ANNE) [photograph examined].

Optimandes eugenia transversa (Weymer, 1911), **n. comb.**
Figs. 1, 2C-F, 3, 4A-E, 6, 7, 8

Euptychia transversa Weymer (1911: 197, pl. 47a) **Lectotype** ♂ [here designated]: "transversa Weym.//Original ?//Para-Typus Euptychia transversa Weym.//Marcap.//Peru Marcapata Staatsamml. München// Präparat Nr. SA20 Zoolog. Staatssammlung München" (ZSM, examined). **Paralectotype** ♂: "Lectotype ♂ Euptychia transversa Weymer designated by: Lee D. Miller 1989//genitalia vial M-9138 ♂ Lee D. Miller//Marcapata Cuzco" (MNHU, examined).

Euptychoides transversa: Forster (1964: 97, fig. 85)
Euptychia phineus: D'Abrera (1988: 777, ♂ V), misidentification
Euptychoides eugenia transversa: Lamas (2004: 219)
Euptychoides phineus: Piñas (2004: 22, fig. 129, 130), misidentification
Euptychoides eugenia [*transversa*]: Murray & Prowell (2005); Espeland *et al.* (2019: 122)

Diagnosis and identification: Diagnostic characters of this taxon are discussed under the nominate subspecies. This taxon is superficially similar to a number of sympatric cloud forest euptychiines, particularly *Euptychoides fida* and *Hermeuptychia* species, but may be distinguished by the very reduced VHW ocelli in the middle of the wing and the undulating VHW dark discal line, in addition to other distinguishing characteristics of the genus.

Taxonomy: Weymer (1911) described this taxon based on an unspecified number of specimens from Marcapata in Peru, stating that it also occurred at Río 'Vitaca' (=Río Bitaco) in Valle del Cauca, Colombia. The figure of the ventral surface corresponds closely to a syntype specimen in the ZSM that is here designated as **lectotype** to fix the identity of the name (Fig. 2E); a male paralectotype from the same locality is in the MNHU. We follow Lamas (2004) in treating this taxon as a subspecies of *O. eugenia* since the two share very similar wing patterns, except for white scaling on the VHW, as discussed above under Diagnosis and identification. There is some variation throughout the Andes in the extent of the white scaling on the VHW and expression of the dark lines on the VHW. Specimens from western Ecuador (Fig. 2C,D) have pure white scaling lacking scattered brown scales, narrow discal and postdiscal lines and a broad outer submarginal line that remains broad into M_3-M_2. East Andean specimens (Fig. 2E) have broader, more indistinct discal and postdiscal lines, narrower submarginal lines and more diffuse white scaling, which is reduced even further in Bolivian specimens (Fig. 2F) to the extent that they resemble the nominate subspecies (D'Abrera, 1988: 777, figured a Bolivian male specimen under the name *Euptychia phineus*). Deciding whether any of this variation merits taxonomic recognition requires more comprehensive material from more intervening regions; nonetheless, based on specimens we have examined, the variation appears to be insufficiently stable or marked. DNA barcode sequences from east and west Andean specimens show no significant divergence (Fig. 1).

Distribution and natural history: In western Ecuador, this subspecies is known to date from Carchi to Pichincha. There are single records from Cañar (collected by R. de Lafebre) and Bolívar (collected by M. de Mathan) that require confirmation, since specimens of numerous other butterfly taxa with the same labels in the FLMNH and NHMUK, respectively, are evidently mislabeled. The Bolívar specimen, in particular, has a ventral wing pattern similar to east Ecuadorian specimens. The subspecies is also known in the eastern Andes from Ecuador (Napo) south to Bolivia (Cochabamba). The species presumably also occurs throughout the montane areas of Colombia and in the Venezuelan Cordillera de Mérida, although we have seen no records from these areas aside from Weymer's (1911) report of the taxon from Río Bitaco (Colombia, Valle del Cauca). Despite being rather rare in historical collections (e.g., a total of 14 specimens in the three largest European collections, NHMUK, MNHU and ZSM), we have found it to be merely uncommon, or even locally common, in the field in Ecuador and Peru, where it occurs in cloud forest from 1000-2200 m. The rarity of specimens in collections may be due to the tendency of the species to fly high in the canopy. In Ecuador, males were frequently attracted to traps 8-10 m above the ground baited with rotting fish and were observed flying and perching 15 m above a stream in a small light gap from 13:00-14:00. Females were not attracted to baits and were therefore much more rarely encountered in the field, with one individual observed resting at 0.5 m on a stand of bamboo in a forest light gap at 12:30.

Immature stages (Figs. 7, 8): The following description of the immature stages of *E. eugenia transversa* is based on two lots collected in Zamora-Chinchipe, eastern Ecuador, in July-August 2018. These lots include: 2018-JK-01, comprising four 1st instars from the ridge E of San Roque, of which one survived until 3rd instar and was barcoded to confirm identification; 2018-JK-06, comprising eight 3rd instars from km 20 Los Encuentros-Zarza (3°50'14"S,78°35'31"W), with four surviving until 4th instar, of which two were barcoded to confirm identification, and with the remaining four producing 2 adult males (Fig. 8C), 1 female and 1 of undetermined sex (failed to completely eclose). JK-01 was collected feeding on an unidentified species of *Chusquea* (Poaceae, Fig. 8D-F, identified by Lynn Clark, pers. comm.) *c.* 1 m above the ground growing along the edge of forest along a ridge top road, and JK-06 was collected *c.* 2 m above the ground on what appears to have been the same plant species (Fig. 8G) growing at the edge of forest along a river.

1st instar (Fig. 7A-E): The 1st instar fed from the edge of the leaf near the leaf base, making a characteristic elongate hole along the leaf edge (Fig. 7A,B). Body green, slightly darker dorsally, with an indistinct dorsolateral pale

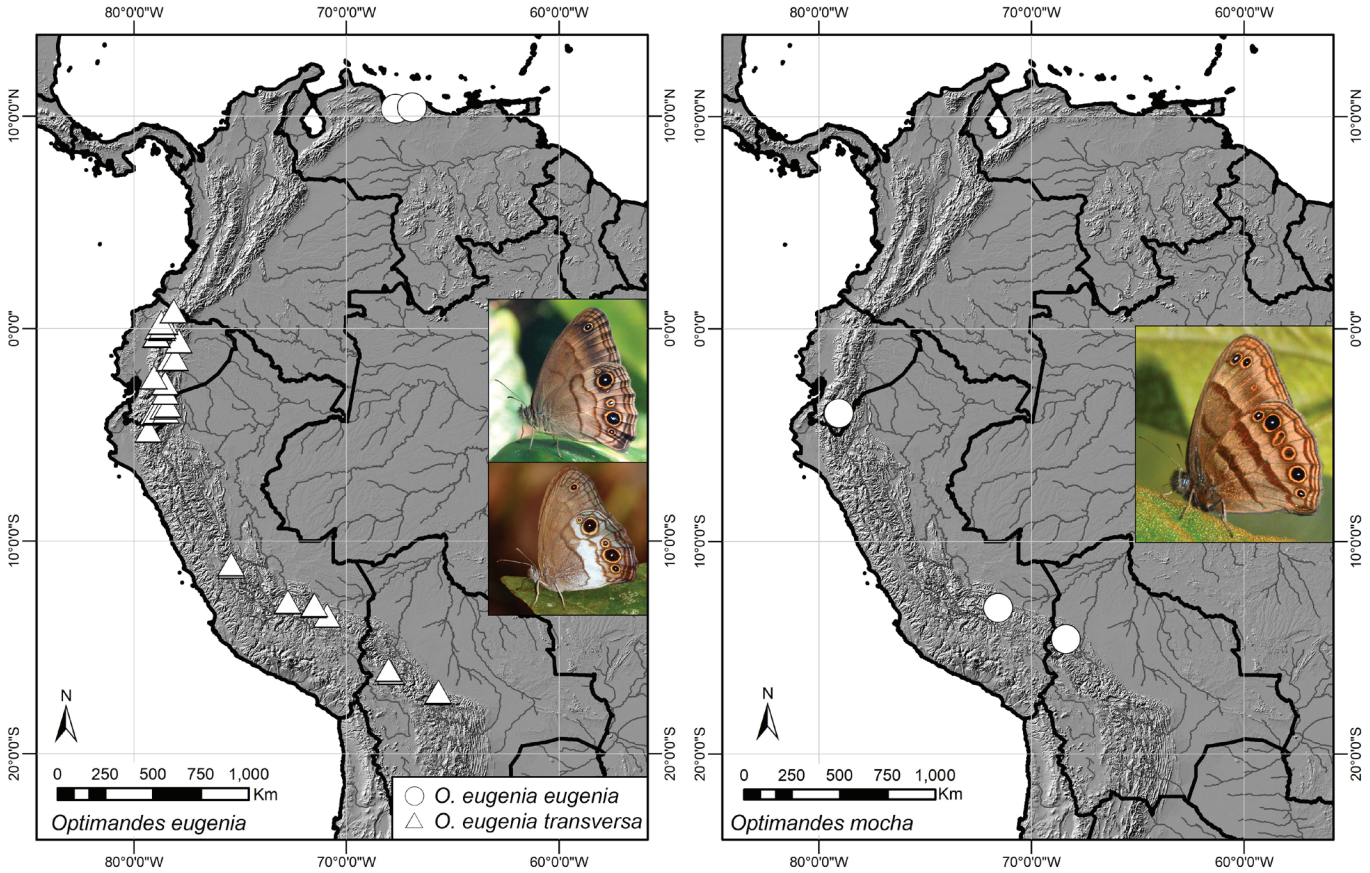

Fig. 6. Distributions of species of *Optimandes* **n. gen.**: *O. eugenia* (left, with inset images of *O. e. eugenia*, above [photographed by I. Cristóbal Ríos-Málaver], and *O. e. transversa*, below [photographed by A. F. E. Neild]) and *O. mocha* **n. sp.** (right, photographed by K. Kertell).

line, very short caudal filaments, legs and prolegs pale green, body covered with short, club-tipped setae, and with a black head capsule bearing setae and a pair of short, rounded dorsal scoli on vertex. Molted to 2nd instar 3 days after collection (n=4). Maximum length *c.* 5.3-5.9 mm, head capsule width *c.* 0.7-0.9 mm.

2nd instar (Fig. 7F-I): Body pale green on molting, becoming darker reddish brown in anterior half in later part of instar, with pale yellowish green dorsolateral line and three similar but thinner lateral lines, pair of stubby caudal filaments, legs and prolegs pale green, and with a black head capsule bearing a pair of longer (*c.* half head height), tapering, blunt scoli on vertex. Molted to 3rd instar after 5-9 days (exact duration not recorded) (n=1). Maximum length *c.* 9.9-10.1 mm, head capsule width *c.* 1.0-1.2 mm.

3rd instar (Fig. 7J-L): Body pale bluish green, with pale yellowish green dorsolateral line and three similar but thinner lateral lines, spiracles yellowish brown, pair of stubby caudal filaments, legs and prolegs pale green, and with a green head capsule bearing a pair of shorter (*c.* one third head height), tapering, pointed orange scoli on vertex and black stemmata. Molted to 4th instar 5-9 days after collection (exact duration not recorded) (n=6). Maximum length *c.* 15.9-16.5 mm, head capsule width *c.* 1.5-1.7 mm.

4th (last) instar (Fig. 7M-O): Body bright green, with pale green dorsolateral line and three similar but thinner lateral lines, spiracles yellowish brown, pair of longer caudal filaments, legs and prolegs pale green, and with a green head capsule bearing a pair of short (*c.* one fifth head height), conical orange scoli on vertex (relatively shorter than in previous instar) and black stemmata. Duration at least 6 days (exact duration not recorded) (n=5). Maximum length *c.* 28.0 mm, head capsule width *c.* 2.4-2.5 mm.

Pupa (Fig. 8): Short and smooth, with rounded ocular caps, bright green except for few scattered small black and brown spots on abdomen, continuing as single dorsolateral black spots onto thorax, edge of wing case delineated with thin white line bordered dorsally by thin brown line, cremaster short and broad. Adults eclosed after 11-12 days (n=4).

Overall, the immature stages are morphologically simple and similar to those of several other Euptychiina with green immatures, such as *Pareuptychia*, *Cepheuptychia* Forster, 1964 and *Taydebis* Freitas, 2003 (Freitas *et al*., 2016a), all members of the *Pareuptychia* clade. In particular, the green last instar with orange head scoli and the short green pupa are remarkably similar to those of *Pareuptychia* (Freitas *et al*., 2016a). Although the immature stages of Euptychiina are known for relatively few taxa, an entirely green last instar is apparently uncommon, with predominantly brown larvae being far more widespread in the subtribe (Freitas *et al*., 2016a, b, 2018b and references therein). Although camouflage in Euptychiina larvae has been suggested as a major strategy for escaping from predators (Freitas, 2017; Freitas *et al.*, in press), it would be interesting to investigate why green larvae (and pupae) are especially prevalent in the *Pareuptychia* clade.

Specimens examined (38 ♂, 20 ♀): Ecuador: *Carchi:* Reserva Las Golondrinas, N of La Carolina, Nariz del Diablo, [0°49'39"N,78°7'29"W], 1900 m, (Willmott, K. R.), 28 Nov 1996, (FLMNH); *Imbabura:* km 26 Chontal Bajo-Chontal Alto, Chontal Alto, [0°17'48"N,78°42'3"W], 1550-1650 m, (Willmott, K. R., Hall, J. P. W.), 10 Aug 2011, 1 ♀, (INABIO); *Pichincha:* [Alluriquín], Río Toachi, [0°19'6"S,78°57'13"W], 800 m, Sep, 1 ♀ [FLMNH-MGCL-193438], (FLMNH); [Salto de] Napac, [0°20'6"S,78°53'24"W], 1000 m, (Nicolay, S. S.), 23 Sep 1975, 1 ♀ [FLMNH-MGCL-193439], (FLMNH); 12 km SW Las Tolas, [0°3'3"N,78°50'18"W], 1200 m, (Willmott, K. R., Hall, J. P. W.), 1,3 Aug 2011, 1 ♂ [FLMNH-MGCL-157244], 1 ♂ [FLMNH-MGCL-157245], 1 ♀ [FLMNH-MGCL-157246], (FLMNH), 1 ♀, (INABIO); km 85 Quito-Sto. Domingo old rd., 1372 m, (Hyatt, J.), 2 Jul 1980, 1 ♀ [FLMNH-MGCL-193437], (FLMNH); NW Quito, Alamo valley, 1800 m, (Adams, M. J. & J.), 6 Aug 1986, 1 ♀ [BMNH(E) 1420248], (NHMUK); Quito-Sto. Domingo old rd., Hacienda Santa Isabel, [0°18'48"S,78°56'W], 1200 m, (Willmott, K. R.), 2 Sep 1996, 1 ♂, (FLMNH); Río Alambi, Reserva Maquipucuna, [0°5'42"N,78°38'W], 1250-1350 m, (Willmott, K. R., Hall, J. P. W.), 16,17 Aug 1993, (FLMNH); Tandayapa Bird Lodge, [0°0'7"N,78°40'41"W], 1700 m, (Willmott, K. R., Hall, J. P. W.),

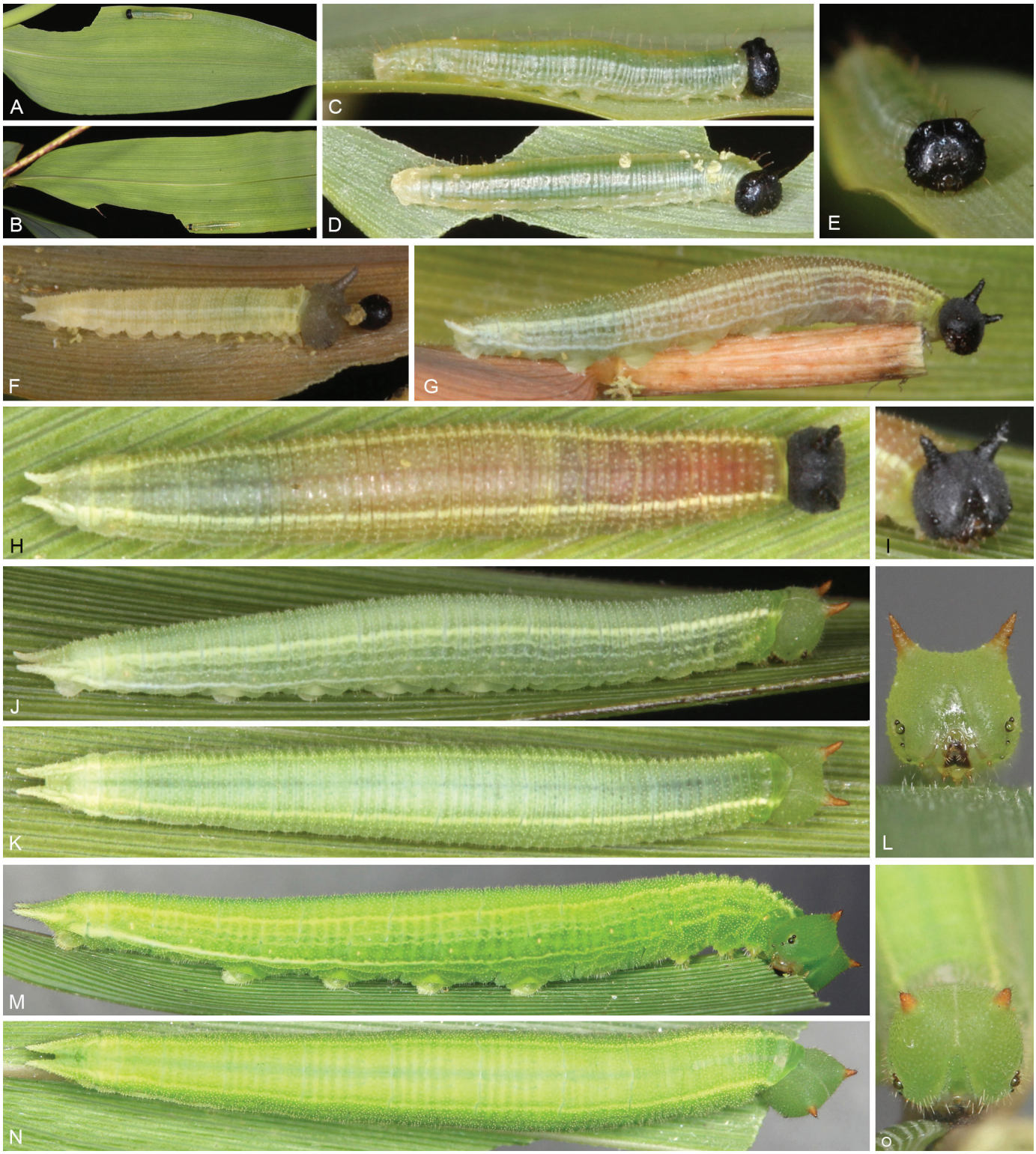

Fig. 7. Immature stages of *O. eugenia transversa* from eastern Ecuador. **A-E**. 1st instar (lot 2018-JK-01), showing leaf damage (A,B), lateral (C) and dorsal (D) views of larva, and frontal view of head capsule (E). **F-I**. 2nd instar (lot 2018-JK-01), showing freshly molted instar (F), lateral (G) and dorsal (H) views of larva, and frontal view of head capsule (I). **J-L**. 3rd instar, showing lateral (J) and dorsal (K) views of larva (lot 2018-JK-01), and frontal view of head capsule (L, lot 2018-JK-06). **M-O**. 4th (final) instar (lot 2018-JK-06), showing lateral (M) and dorsal (N) views of larva, and frontal view of head capsule (O).

2-5 Aug 2011, 1 ♂ [FLMNH-MGCL-157247], 1 ♂ [FLMNH-MGCL-157248], (FLMNH); *Bolívar*: Balzapamba - (mislabeled?), [1°47'S,79°10'W], (Mathan, M. de), Sep 1893-Feb 1894, 1 ♂ [NHMUK012824432], (NHMUK); *Cañar:* Río Angas, nr. Huigra, Angas - (mislabeled?), [2°18'S,79°3'W], 1000 m, (Lafebre, R. de), Jul 1974, 1 ♂ [FLMNH-MGCL-193440], (FLMNH); *Napo:* nr. Cosanga, Estación Científica Yanayacu, [0°35'24"S,77°53'W], 2000 m, (Willmott, K. R.), 24 Nov 2006, 1 ♂ [FLMNH-MGCL-112612], (FLMNH); *Pastaza:* km 11 Mera-Río Anzu rd., [1°25'15"S,78°3'8"W], 1200 m, (Hall, J. P. W., Willmott, K. R., J. C. R., J. I. R), 31 Jul 2015, 1 ♀ [FLMNH-MGCL-209655], (FLMNH); *Tungurahua:* Reserva Cerro Candelaria, Fundación Ecominga, [1°25'30"S,78°17'59"W], 2200 m, (Radford, J.), 19 Aug 2008 [JR-08-350], (JARA), 20 Aug 2008 [JR-08-374], (JARA), 21 Aug 2008 [JR-08-128],

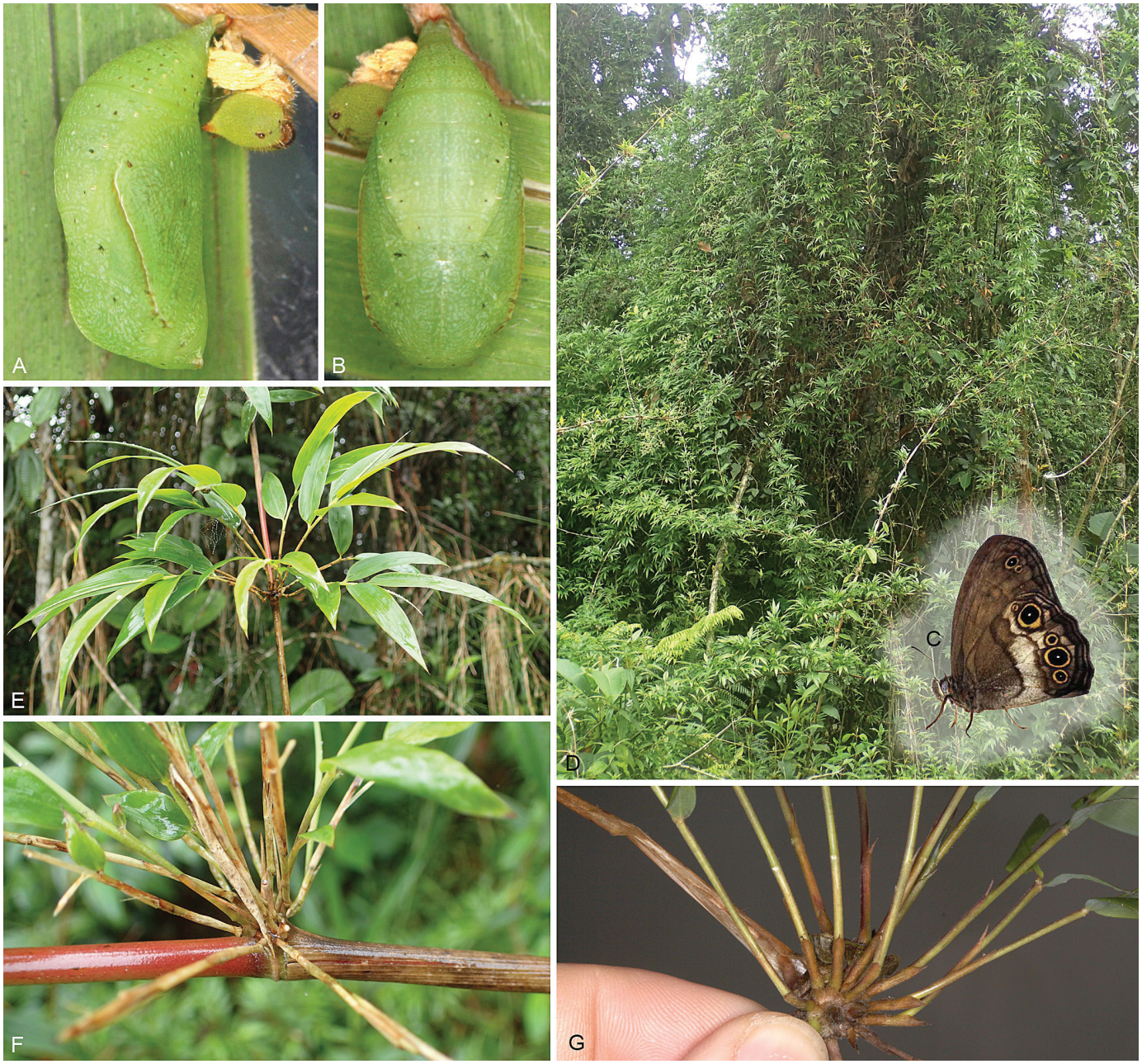

Fig. 8. Immature stages, host plant and habitat of *O. eugenia transversa* from eastern Ecuador. **A,B**. Pupa (lot 2018-JK-06), lateral (A) and dorsal (B) views. **C**. Adult male (lot 2018-JK-06). **D**. Large stand of *Chusquea* sp., host plant of lot 2018-JK-01, at edge of forest along road on ridge E of San Roque, Zamora-Chinchipe. **E,F**. *Chusquea* sp. host plant, as in D. **G**. *Chusquea* sp. host plant of lot 2018-JK-06 from Río Blanco, near El Zarza, Zamora-Chinchipe.

(JARA); *Morona-Santiago:* Cóndor Mirador, [3°37'42"S,78°23'41"W], 1974 m, (Radford, J.), 23 Aug 2010, 1 ♀ [CON91], (FLMNH) (CULEPEX Expedition, 2010); Guarumales/Hidropaute, [2°34'9"S,78°30'49"W], 1900 m, (Willmott, K. R.), 7 Nov 2010, 1 ♂ [FLMNH-MGCL-146103], (FLMNH); km 14 Limón-Gualaceo rd., [3°0'36"S,78°30'W], 1900 m, (Willmott, K. R.), 11 Nov 1996, 1 ♂, (FLMNH); *Zamora-Chinchipe:* km 10 Los Encuentros-El Panguí rd., ridge E San Roque, [3°42'11"S,78°35'36"W], 1050 m, (Willmott, K. R., Hall, J. P. W.), 4 Aug 2009, 1 ♀ [FLMNH-MGCL-145733], 18 Jul 2018, 1 individual [larva lot 2018-JK-01, barcoded], (FLMNH); km 20 Los Encuentros-Zarza rd., [3°50'14"S,78°35'31"W], 1450 m, (Hall, J. P. W., Willmott, K. R., J. I. R), 22 Jul 2018, 2 ♂, 1 ♀ [larvae, lot 2018-JK-06, 1 ♂ eclosed 18 Aug 2018, 1 ♂, 1 ♀ eclosed 22 Aug 2018], 2 individuals [larvae lot 2018-JK-06, barcoded], (FLMNH); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Aldaz, R.), 3 Oct 2006, 1 ♂ [FLMNH-MGCL-112616], (FLMNH), (Willmott, K. R.), 2 Dec 2006, 1 ♂ [FLMNH-MGCL-112617], (FLMNH), (Willmott, K. R., Aldaz, R.), 11 Oct 2006, 1 ♂ [FLMNH-MGCL-112614], (FLMNH), 1 ♂ [FLMNH-MGCL-112613], 1 ♂ [FLMNH-MGCL-112615], (INABIO); km 4.3 San Andrés-Jimbura rd., [4°47'59"S,79°18'18"W], 2020 m, (Willmott, K. R.), 13 Oct 2010, 1 ♀, (INABIO); *Not located:* 'Ecuador', 1 ♂ [BMNH(E) 1420249; Joicey Bequest 1934-120], (NHMUK)**. Peru**: *Junín:* 1 km S Mina Pichita, [11°5'28"S,75°24'58"W], 2100 m, (Lamas, G.), 22 Aug 2003, 1 ♂ [MUSM-LEP-101616], (MUSM), (Peña, C.), 22 Aug 2003, 1 ♂ [MUSM-LEP-101615], (MUSM); 1-3 km SE Mina Pichita, [11°5'28"S,75°24'58"W], 2100 m, (Lamas, G.), 26 Aug 1988, 1 ♂ [MUSM-LEP-101614], (MUSM); Quebrada Siete Jeringas, [11°12'S,75°24'W], 1700 m, (Peña, C.), 15 Nov 2003, 1 ♂ [MUSM-LEP-101617], 1 ♀ [MUSM-LEP-101621], (MUSM); *Cuzco:* Cosñipata rd., San Pedro Lodge, 1375 m, (Kinyon, S.), 22 Oct 2013, 1 ♂, (USNM), 23 Sep 2011, 1 ♂, (USNM); Cosñipata, Quebrada Quitacalzón, [13°1'S,71°30'W], 1100 m, (Lamas, G.), 23 Oct 2010, 1 ♂ [MUSM-LEP-101618], (MUSM); Marcapata, [13°30'34"S,70°53'57"W], 1800 m, 1 ♂ ['LECTOTYPE ♂ Euptychia transversa Weymer designated by: Lee D. Miller 1989//genitalia vial M-9138 ♂ Lee D.

Miller//Marca-pata Cuzco'], (MNHU), 1 ♂ ['Original ?'//'Para-typus Euptychia transversa Weym.'//'marcap'//'Peru Marcapata Staatsamml. München'//'Präparat Nr. SA20 Zoolog. Staatssammlung München'//'transversa Weym.'], (ZSM); San Pedro, [13°3'S,71°33'W], 1400 m, (Lamas, G.), 10 Nov 2007, 1 ♀ [MUSM-LEP-101624], (MUSM), 13 Nov 2012, 1 ♀ [MUSM-LEP-101626], (MUSM), 23 Sep 2011, 1 ♂ [MUSM-LEP-101619], 1 ♀ [MUSM-LEP-101625], (MUSM), (West, F. & A.), 4-8 Nov 2007, 1 ♀ [MUSM-LEP-101623], (MUSM); San Pedro, [13°3'S,71°33'W], 1400-1650 m, (Lamas, G.), 7 Nov 2001, 1 ♀ [MUSM-LEP-101622], (MUSM); upper Río Urubamba, Río Vilcanota, 3000 m - (mislabeled), (Garlepp, O.), 1898, 1 ♂, (MNHU); El Mirador, [13º 4'S, 71º33'W], 1720 m, (Kinyon, S.), 28 Oct 2018, 1 ♂, (MUSM). **Bolivia**: *La Paz:* Río Zongo, [16°3'40"S,68°1'2"W], 1200 m, (Garlepp), 1896, 1 ♂, (MNHU); Sandillani, [16°12'S,67°54'W], 2000 m, (Lamas, G.), 4 Dec 2007, 1 ♂ [MUSM-LEP-101620], (MUSM); *Cochabamba:* Alto Palmar, [17°9'2"S,65°42'47"W], 1100 m, (Baumann), Nov 1960, 1 ♀, (ZSM); Yungas del Espíritu Santo, [17°6'S,65°40'W], (Germain, P.), 1888-1889, 1 ♂ [NHMUK012824433], 1 ♂ [NHMUK012824430], 1 ♀ [BMNH(E) 1420246], 1 ♀ [BMNH(E) 1420247], (NHMUK); no specific locality, 1 ♂ [NHMUK012824431], (NHMUK).

Other records (sight records and photographs of live individuals; "W & H, SR" indicates sight records by Willmott and Hall): **Ecuador**: *Carchi:* Reserva Las Golondrinas, N of La Carolina, Santa Rosa, [0°49'38"N,78°7'42"W], 1700 m, (Willmott, K. R., Hall, J. P. W.), 4,5 Sep 1996, (W & H, SR); *Imbabura:* Selva Alegre-Otavalo rd., Mina Selva Alegre, [0°17'3"N,78°32'44"W], 2020 m, (Willmott, K. R., Hall, J. P. W.), 11 Aug 2011, (W & H, SR); *Zamora-Chinchipe: c.* 3 km W Guayguayme Alto, ridge above San Luís, [3°55'14"S,78°54'49"W], 1470 m, (Neild, A.), Nov 2015, 1 ♂, (photograph live specimen) (Neild, A., pers. comm. (10 Nov 2015 by email to KRW with photo)); Destacamento Paquisha Alto, [3°54'28"S,78°29'5"W], 2100 m, (Radford, J.), 1 Sep 2010, 1 ♂/♀ [PAN56], (sight record) (CULEPEX Expedition, 2010); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 28 Nov 2003, (W & H, SR).

Optimandes mocha Willmott, Hall & Lamas, **n. sp.**
Figs. 1G,H, 3A-E, 4, 6

Diagnosis and identification: DNA sequence data suggest that this species is sister to *Optimandes eugenia*, from which it may easily be distinguished by the straight and very broad dark brown ventral discal and postdiscal lines and large VHW ocelli in cells Cu_1-M_2 (similar in size to those in Cu_2-Cu_1 and M_2-M_1). In addition, *O. eugenia transversa*, which is sympatric with *O. mocha* **n. sp.**, has a broad white postdiscal band on the VHW. The male genitalia of the two species differ as follows: in *O. mocha*, the uncus is sharply constricted near the posterior tip rather than just narrowing gradually, the valva posterior tip slants downwards rather than curving slightly upwards, and the aedeagus curves upwards more strongly in the anterior half. *Optimandes mocha* is distinguished from all other euptychiines by the combination of very broad, straight brown ventral postdiscal lines and a tornal ocellus on the VHW in cell 2A-Cu_2; *Magneuptychia tiessa* (Hewitson, 1869) has similarly broad VHW postdiscal lines but is larger and has a more scalloped HW margin and no VHW tornal ocellus, among other differences.

Description: MALE (Fig. 2G,H): Forewing length 22.5 mm (mean 23 mm, n=2). *Wings*: FW triangular, distal and anal margins straight and almost perpendicular, vein R_2 arising just basally of origin of vein R_{3+4+5}; HW approximately triangular, distal margin rounded, anal margin slightly indented basal of tornus. *Dorsal surface*: Ground color brown. DFW with costa and distal margin very slightly darker than remainder of wing. DHW with indistinct black postdiscal ocellus encircled by very diffuse orange ring in cell Cu_2-Cu_1, margin lined diffusely with black, very indistinct darker submarginal line visible in tornal region. *Ventral surface*: Ground color grayish brown, a little paler than dorsal surface. VFW with broad, straight dark brown discal line from costal vein extending across discal cell basal of base of vein Cu_2 almost to vein 2A; discocellular veins lined with dark brown; broad, approximately straight dark brown postdiscal line from cell M_1-R_5 to vein 2A, slightly kinked in cells 2A-Cu_2 and M_1-R_5, basally diffusing into wing background, distally bordered sharply by band of paler grayish scaling; four postdiscal ocelli in cells Cu_1-M_3 (indistinct black spot encircled by yellowish brown ring), M_3-M_2 (similar to preceding but with central white pupil), and M_2-R_5 (black spots encircled by clear yellowish brown rings with single central white pupils in each ocellus); two broad, dark brown submarginal lines, more basal line wavy and bordered basally by band of paler grayish scaling, more distal line straighter, lines close or touching at each wing vein, wing margin lined with black. VHW with broad, straight dark brown discal line from costa extending across discal cell just basal of base of vein Rs, tapering towards anal margin to a thin line in middle of cell 3A-2A; broad, straight dark brown postdiscal line tapering from costa to tornal indentation on anal margin, bordered distally with pale grayish band; discocellular vein 2d lined with dark brown; six postdiscal ocelli, in cells 2A-Cu_2 (half width of cell, black spot encircled by clear yellowish brown ring with single central white pupil), Cu_2-Cu_1 (similar to preceding except larger, almost filling cell), Cu_1-M_3 and M_3-M_2 (similar to preceding except dark brown central spot, diffuse yellow brown ring and no white pupil), M_2-M_1 (similar to that in Cu_2-Cu_1, filling cell) and M_1-Rs (similar to preceding but not quite filling cell); two broad, dark brown submarginal lines, more basal line wavy and bordered basally by band of paler grayish scaling, more distal line straighter, lines close or touching at each wing vein, wing margin lined with black. *Head*: eyes brown with dense, long setae; antennae with *c.* 33 antennomeres, distal *c.* 10 comprising club, dark brown with sparse white scales at ventral base of antennomeres in basal part of antennae; labial palpi dark brown with long dark brown hair-like scales ventrally on basal segment, remaining segments missing in specimens studied; head covered with dark brown scales and hair-like scales. *Thorax*: thorax, forelegs, mid- and hind legs dark brown, mid- and hind legs with pair of tibial spurs. *Abdomen*: dark brown. *Genitalia* (Fig. 4F-J): as illustrated, notable features include eighth tergite unsclerotized except for narrow anterior band and slightly broader posterior patch; brachia directed upwards with respect to uncus, uncus curving downwards, in lateral view broad in basal two-thirds then sharply constricted and narrow in distal third; valva tapering throughout, with distal tip pointed and directed downwards; aedeagus with anterior portion curved upwards and smoothly joining ductus ejaculatorius, distal portion ending with a point on right side, two elongate, parallel patches of teeth-like cornuti visible in middle of aedeagus.

FEMALE: unknown.

Types: HOLOTYPE ♂: **ECUADOR**: *Zamora-Chinchipe:* nr. Sabanilla, Loja-Zamora rd., Quebrada San Ramón, power station, [3°58'12"S,79°3'42"W], 1850 m, (Willmott, K. R., Aldaz, R.), 28 Oct 2006, [FLMNH-MGCL-112631], (genitalic dissection KW-17-20), (FLMNH, to be deposited in INABIO).
PARATYPES (3 ♂): **Ecuador**: *Zamora-Chinchipe:* km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R.), 3 Dec 2006, 1 ♂ [FLMNH-MGCL-112632], (FLMNH). **Peru**: *Cuzco:* Rocotal, [13°7'S,71°34'W], 1970 m, (Harris, B.), 15 Aug 2009, 1 ♂ [MUSM-LEP-101305], (MUSM). **Bolivia**: *La Paz:* Yungas, San Antonio [de Chicalulu], [14°35'S,68°23'W], 1800 m, (Garlepp, G.), 1895-1896, 1 ♂, (MNHU).

Etymology: The species name is derived from the English word 'mocha', meaning a mixture of coffee and chocolate, in reference to the rich dark brown colors of the ventral surface of this species. It is treated as a feminine noun in apposition.

Distribution and natural history: This species is known to occur from southern Ecuador to Bolivia on the east Andean slopes, between 1800 m and 2100 m elevation (Fig. 6). It is very rare in collections as well as in nature; despite collecting for 57 days spread over 7 months and 5 years at the Reserva Arcoiris in southeastern Ecuador, using hand-nets and up to 32 bait-traps, only a single individual was recorded at that site. That individual was collected in a trap baited with rotting fish 1 m above the ground, in tall cloud forest on a steep slope *c.* 50 m from a stream (Quebrada de las Pavas), on a day of bright sun. The holotype was collected between 11:00 and 14:00 in bright sun at or near the upper Quebrada San Ramón, in well-preserved cloud forest. Ken Kertell photographed a male (Fig.

6) at Rocotal, Cuzco, Peru, at approximately 12:00 on 17 Nov 2015, feeding on rotting fish bait sprayed onto roadside leaves (Kertell, K., pers. comm.).

DISCUSSION

Euptychoides as circumscribed by Lamas (2004) is one of the most dramatically polyphyletic genera within the Euptychiina, with ongoing phylogenetic study indicating that the 11 species listed by Lamas potentially belong to six different genera. Figure 1 includes five of the six clades of species formerly included within *Euptychoides*, while *Euptychoides fida* (Weymer, 1911) and *Euptychoides sanmarcos* Nakahara & Lamas, 2018 form the sixth clade, likely also unrelated to remaining *Euptychoides* (Espeland *et al*., unpublished data). Although the type species of *Euptychoides*, *Euptychia saturnus* (currently considered a junior subjective synonym of *E. laccine*), and *Optimandes eugenia* are both members of the *Pareuptychia* clade, they are not closely related within this clade (Fig. 1), supporting the description of *Optimandes*. The appropriate generic classification for the remaining three clades of *Euptychoides* (containing *E. castrensis*, *E. hotchkissii*+*E. nossis*, and *E. fida*+*E. sanmarcos*) is the subject of ongoing research.

Evidently, the striking white ventral hindwing band that characterizes most of the taxa formerly placed in *Euptychoides*, along with their predominance in cloud forest habitats, are not good indicators of phylogenetic relationship. Nevertheless, the co-occurrence of these two characters may not be random; such coincidence in distinctive wing patterns among unrelated sympatric butterfly species is typically interpreted as resulting from mimicry. *Optimandes eugenia transversa* is sympatric with a number of superficially similar euptychiines, which closely resemble one another at rest and in flight. On the western slopes of the Andes these include *Euptychoides nossis* (Hewitson, 1862) and *Forsterinaria pallida aurita* Peña & Lamas, 2005, and on the eastern slopes *Euptychia cesarense viloriai* Andrade *et al*., 2011, *Caeruleuptychia trembathi* Willmott *et al*., 2017 (female), *Graphita griphe*, *Euptychoides fida*, *Euptychoides albofasciata*, *Hermeuptychia* species (e.g., D'Abrera, 1988: 777), *Forsterinaria boliviana* (Godman, 1905), *Forsterinaria pallida pallida* Peña & Lamas, 2005, *Rareuptychia clio* (Weymer, 1911) (at lower elevations), and several species of *Splendeuptychia* Forster, 1964. *Optimandes eugenia eugenia* is not strikingly colored, but nevertheless is so superficially similar to several montane *Hermeuptychia* species that Weymer (1911) treated them in the same species group. Furthermore, *O. eugenia* and several of the species it resembles show analogous geographic variation (e.g., *E. cesarense* Pulido *et al*., 2011), a phenomenon that is most parsimoniously explained by mimicry (Willmott, 2003).

Notwithstanding the circumstantial evidence discussed above, the basis for potential mimicry in these euptychiines is not clear, with satyrines in general being regarded as universally palatable (e.g., DeVries, 1987; Larsen, 1991; but see Murillo-Hiller, 2009), despite scant published empirical data (Bowers & Wiernasz, 1979; Chai, 1986). As a result, satyrine species that show apparent convergence in wing pattern with members of other butterfly subfamilies have long been regarded as Batesian mimics (e.g., Vane-Wright, 1971; Wei *et al*., 2017). Nevertheless, a hypothesis of presumably Müllerian mimicry within the Satyrinae has been discussed for brassolines (e.g., Bristow, 1981, 1982, 1991; Penz, 2017), pronophilines (Viloria, 2007) and haeterines (Murillo-Hiller, 2009), despite the lack of an obvious mechanism driving wing pattern convergence.

An alternative explanation is that similar color patterns represent adaptation to some unknown environmental factor. Interestingly, a white VHW band is also present in some montane euptychiines in localities far from the Andes. For example, in the Brazilian Atlantic Forest this pattern is found in *Moneuptychia montana* Freitas, 2015, *Forsterinaria pronophila* (Butler, 1867), *Carminda umuarama* Ebert & Dias, 1997, in some individuals of *Carminda griseldis* (Weymer, 1911) (especially those from higher altitudes), in some species of *Splendeuptychia* Forster, 1964 (e.g. *Splendeuptychia* ca. *ambra*) and *Euptychoides castrensis* (Schaus, 1902) (a complex including several undescribed species that are part of *Moneuptychia* Forster, 1964; Freitas *et al.*, in preparation). All of the above taxa are sympatric in several localities in the high mountains of southeastern Brazil.

As knowledge improves of the phylogenetic relationships among euptychiines it seems likely that more cases of phenotypic convergence among the more colorful members of this subtribe will be revealed. Such cases could provide new opportunities to investigate the intriguing possibility of mimicry, as well as phenotypic convergence arising from adaptation to local environments, among these otherwise largely cryptic butterflies.

ACKNOWLEDGMENTS

We thank the museum curators who allowed us to examine the Euptychiina collections under their care. We thank Santiago Villamarín, Sofía Nogales, the MECN/INABIO and Ecuadorian Ministerio del Ambiente for arranging the necessary permits for research in Ecuador (MAE-DNB-CM-2016-0045), and Tomasz Pyrcz and Ichiro Nakamura for providing important tissue samples. Museum and field work was funded in part by the National Geographic Society, the Leverhulme Trust, the Darwin Initiative, the National Science Foundation (# 0103746, 0639861, #1256742), the FLMNH Museum Associates, the Florida Museum of Natural History and the University of Florida. SN acknowledges University of Florida's Entomology and Nematology Department for support. We thank Fundación Arcoiris, the members of CULEPEX, Fundación Ecominga and Tandayapa Bird Lodge for their invaluable support in the field. For their company in the field and for collecting specimens of Euptychiina we thank Raúl Aldaz and Julia Robinson Willmott. We also thank Indiana Cristóbal Ríos-Málaver, Andrew Neild and Ken Kertell for allowing us to include their photographs of live butterflies in Fig. 6 and for sharing their field observations. We thank Gebreyes Kassu and Karunakar Kallam for helping to obtain DNA sequence data and Lynn Clark for identifying the host plant of *O. e. transversa*. MAM thanks the Fundação de Amparo à Pesquisa do Estado de São Paulo - FAPESP (fellowship 2018/11910-1). AVLF acknowledges support from FAPESP (Biota-Fapesp - grant 2011/50225-3), from the

Brazilian Research Council - CNPq (303834/2015-3), from the National Science Foundation (DEB-1256742) and from the United States Agency for International Development - USAID / the U.S. National Academy of Sciences (NAS), under the PEER program (Sponsor Grant Award Number: AID-OAA-A-11-00012) (Mapping and Conserving Butterfly Biodiversity in the Brazilian Amazon). This publication is part of the RedeLep 'Rede Nacional de Pesquisa e Conservação de Lepidópteros' SISBIOTA-Brasil/CNPq (563332/2010-7). Finally, we thank two reviewers whose comments significantly improved the manuscript.

Author contributions

KRW, SN and TP performed dissections and prepared drawings, KRW, SN and MAM wrote the descriptions, KRW, TP, MAM, SN, GL, BH, JPWH and JIRW contributed to collecting and digitizing specimen data, ME, MAM, AVLF, KRW and LX conducted the molecular phylogenetic work, with ME focusing on the Euptychiina and MAM/AVLF on the *Pareuptychia* clade, and JPWH, JIRW and KRW collected, reared, photographed and barcoded immature stages. KRW and SN prepared the first draft of the manuscript and all authors read, offered comments and approved the paper.

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Appendix 1. Voucher specimen information and Genbank numbers for DNA sequence data. Sequences newly published in this study are highlighted in bold.

Taxon	Locality (decimal latitude and longitude)	DNA voucher number	COI	EF-1α	GAPDH	RpS5
Optimandes eugenia eugenia	Venezuela: Miranda: Altos de Pipe, IVIC	prep_mol_358	**MK416253**	-	-	-
Optimandes eugenia transversa	Ecuador: Pichincha	DNA99-076	AY508538	AY509064	-	-
Optimandes eugenia transversa	Ecuador: Zamora-Chinchipe: ridge E San Roque (-3.703, -78.593)	2018-JK-01 (larva)	**MK416242**	-	-	-
Optimandes eugenia transversa	Ecuador: Zamora-Chinchipe: km 20 Los Encuentros-Zarza (-3.837, -78.592)	2018-JK-06a (larva)	**MK416243**	-	-	-
Optimandes eugenia transversa	Ecuador: Zamora-Chinchipe: km 20 Los Encuentros-Zarza (-3.837, -78.592)	2018-JK-06b (larva)	**MK416244**	-	-	-
Optimandes eugenia transversa	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-09835	**MK416245**	**MK416254**	**MK416258**	**MK416261**
Optimandes eugenia transversa	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-09836	**MK416246**	-	-	-
Optimandes eugenia transversa	Ecuador: Morona-Santiago: Guarumales/Hidropaute (-2.569, -78.514)	LEP-10059	MK305306	**MK416256**	**MK416260**	**MK416263**
Optimandes eugenia transversa	Ecuador: Zamora-Chinchipe: ridge E San Roque (-3.703, -78.593)	LEP-10685	MK305305	**MK416257**	-	**MK416264**
Optimandes eugenia transversa	Ecuador: Pichincha: 12 km SW Las Tolas (0.051, -78.838)	LEP-18448	**MK416249**	-	-	-
Optimandes eugenia transversa	Ecuador: Pichincha: Tandayapa Bird Lodge (0.002, -78.678)	LEP-18451	**MK416250**	-	-	-
Optimandes eugenia transversa	Ecuador: Pastaza: km 11 Mera-Río Anzu rd. (-1.421, -78.052)	LEP-34580	**MK416251**	-	-	-
Optimandes mocha n. sp.	Ecuador: Zamora-Chinchipe: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-09842	**MK416247**	-	-	-
Optimandes mocha n. sp.	Ecuador: Zamora-Chinchipe: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-09843	**MK416248**	**MK416255**	**MK416259**	**MK416262**
Chloreuptychia marica	Peru: Madre de Dios	CP02-50	GU205831	GU205887	GU205943	GU206003
Cissia penelope	Peru: Junín: La Solitaria	CP07-58	GU205833	GU205889	GU205945	GU206005
Cyllopsis pertepida	Mexico: Guanajuato	NW165-3	GQ357204	GQ357274	GQ357428	GQ357557
Erichthodes antonina	Peru: Madre de Dios	CP02-24	DQ338792	DQ338935	GQ357429	GQ357558
Erichthodes julia	Peru: Junín: Quebrada Siete Jeringas	CP04-65	GU205834	GU205890	GU205946	GU206006
Euptychoides albofasciata	Ecuador: Sucumbíos	E-39-27	AY508540	AY509066	-	-
Euptychoides castrensis	Brazil: São Paulo: Riberão das Pedras	NW126-9	DQ338798	DQ338942	GQ357434	GQ357563
Euptychoides hotchkissi	Peru: Junín: 1 Km S Mina Pichita	CP04-51	GU205836	GU205892	GU205949	GU206009
Euptychoides laccine	Colombia: Antioquia: Venecia (5.962, -75.708)	MAM-0201	**MK416252**	-	-	**MK416265**
Euptychoides nossis	Ecuador: Pichincha	DNA99-057	AY508539	AY509065	-	-
Forsterinaria quantius	Brazil: São Paulo: São Luiz do Paraitinga	CP14-07	GQ864772	GQ864866	GQ864972	GQ865442
Godartiana luederwaldti	Brazil: Distrito Federal: Brasilia	CP16-02	GU205828	GU205884	GU205940	GU206000
Godartiana muscosa	Brazil: São Paulo: Serra do Japi	NW127-8	DQ338582	DQ338944	GQ864974	GQ865443
Graphita griphe	Colombia: Valle del Cauca: San Antonio	YPH0361	KU340866	-	KU340915	KU340948
Graphita griphe	Colombia: Valle del Cauca: San Antonio	YPH0362	KU340867	-	-	KU340949
Hermeuptychia hermes	Peru: Madre de Dios	CP01-07	GQ357207	GQ357276	GQ357438	GQ357567
Magneuptychia lea	Peru: Madre de Dios	DNA99-022	AY508554	AY509080	-	-
Megeuptychia antonoe	Peru: Amazonas: Cordillera del Cóndor	CP05-01	GU205851	GU205907	-	GU206023
Megeuptychia monopunctata	Peru: Amazonas: Cordillera del Cóndor	CP06-70	GU205852	GU205908	GU205964	GU206024
Megisto cymela	USA: Rhode Island: Valley Falls	CP21-04	GQ357208	GQ357277	GQ357439	GQ357569
Neonympha areolatus	USA	CP22-03	GU205856	GU205912	GU205967	GU206028
Nhambikuara cerradensis	Brazil: Minas Gerais: Santana do Riacho	YPH0572	MF489984	-	MF490004	MF490017
Nhambikuara cerradensis	Brazil: Mato Grosso do Sul: Aquidauana	YPH0576	MF489988	-	MF490007	MF490021
Nhambikuara mima	Brazil: Rondônia: Porto Velho	MGCL-LOAN-550	MF489994	-	MF490009	MF490025
Paramacera xicaque	Mexico: Distrito Federal	CP15-08	GQ357210	GQ357279	GQ357442	GQ357571
Pareuptychia metaleuca	Ecuador: Pichincha	DNA99-061B	AY508566	AY509092	-	-
Pareuptychia ocirrhoe	Ecuador: Napo	DNA99-064	AY508568	AY509094	-	-
Paryphthimoides grimon	Brazil: São Paulo: Sete Barras: Saibadela	CP10-01	DQ338806	DQ338952	GQ865015	GQ865483
Pharneuptychia innocentia	Brazil: Minas Gerais: Serra do Cipó	CP12-06	DQ338808	DQ338954	GU205974	GU206035
Pindis squamistriga	Mexico: Guanajuato	NW165-5	GQ357211	GQ357280	GQ357445	GQ357574
Prenda clarissa	Brazil: Rio Grande do Sul: São Francisco de Paula	BR-AVLF-1	HQ444284	HQ444285	-	-
Satyrotaygetis satyrina	Costa Rica: Puntarenas	DNA97-006	AY508575	AY509101	-	-
Splendeuptychia ashna	Peru: Madre de Dios	CP01-19	GU205865	GU205921	GU205979	GU206040
Splendeuptychia doxes	Brazil: São Paulo: Atibaia	NW126-8	GU205867	GU205923	GU205981	GU206042
Taygetis rufomarginata	Peru: Madre de Dios: CICRA	CP-CI125	GU205872	GU205928	GU205986	GU206047