



Two new taxa of *Euptychia* Hübner, 1818 (Lepidoptera: Nymphalidae: Satyrinae) from the Andes of Colombia and Peru

HANNIER W. PULIDO-B.¹, M. GONZALO ANDRADE-C.², CARLOS PEÑA^{3,4} & GERARDO LAMAS⁴

¹Universidad Pedagógica y Tecnológica de Colombia. Escuela de Biología, Tunja, Colombia. E-mail: hannierpulido@gmail.com

²Profesor Asociado, Instituto de Ciencias Naturales, Universidad Nacional de Colombia, Apartado 7495, Bogotá, D.C., Colombia. E-mail: mgandradec@unal.edu.co

³Department of Zoology, Stockholm University, S-106 91 Stockholm, Sweden. E-mail: carlosp420@yahoo.com

⁴Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Apartado 14-0434, Lima-14, Perú. E-mail: glamasm@unmsm.edu.pe

Abstract

We describe a new species and a new subspecies of *Euptychia* Hübner, 1818 from Colombia and Peru: *E. cesarense* Pulido, Andrade, Peña & Lamas **n. sp.** and *E. cesarense viloriai* Andrade, Pulido, Peña & Lamas **n. ssp.** This new species resembles *E. enyo* Butler, 1867 and *E. rufocincta* Weymer, 1911 but shows clear differences in the wing markings, ocellus pattern and the male genitalia morphology. The new subspecies can be distinguished from the nominotypical subspecies described herein by differences in wing pattern coloration. The nominate subspecies occurs in northern Colombia, and *E. c. viloriai* is known from eastern Peru.

Key words: Butterflies, Euptychiina, new species, taxonomy, Neotropical region

Introduction

The subfamily Satyrinae is a highly diverse group of butterflies that originated in the early Cenozoic (Peña & Wahlberg 2008) and in the present includes about 2400 species with a worldwide distribution (Ackery *et al.* 1999). The Euptychiina is one of the most species-rich subtribes in the Satyrinae containing over 400 species, distributed mainly in the Neotropical region (Lamas 2004) grouped in 43 genera, 13 of which are monotypic (Murray & Prowell 2005, Freitas *et al.* 2011, Marín *et al.* 2011). In South America, the Euptychiina inhabit mostly lowland forest habitats below 1000 m in elevation, with the exception of the diverse and largely Andean *Forsterinaria* Gray, 1973 (Peña & Lamas 2005, Pulido & Andrade 2008) and isolated species of other genera. Members of the related subtribe Pronophilina are predominant in high elevation Andean environments.

Historically, *Euptychia* Hübner, 1818 has been used as a “catch-all” genus to include a heterogeneous array of species (Murray & Prowell 2005, Freitas & Peña 2006), which reflects the difficulty in finding adult synapomorphies for the genus. Lamas’ (2004) recent checklist of Neotropical butterflies recognizes 13 described species and 16 undescribed species for the genus *Euptychia*. Like many other Euptychiina genera, *Euptychia* has not been rigorously delineated with diagnostic adult characters (Forster 1964; Miller 1968; Murray & Prowell 2005). However, the monophyly of the genus is supported by a recent study using molecular data (Murray & Prowell 2005).

The phylogenetic relationships of *Euptychia* with other genera in the Euptychiina are not completely clear. The molecular analysis of Murray & Prowell (2005) suggests that *Euptychia* does not share a common ancestor with the remaining genera of the subtribe, and appears in a basal position suggesting that *Euptychia* diverged early in Satyrinae evolution. Peña *et al.*’s (2006) molecular phylogenetic study, using an extensive sampling in Satyrinae, found a monophyletic Euptychiina where *Euptychia* is sister to all other euptychiines.

The new species *E. cesarense* is described in *Euptychia* because it shares distinctive characteristics with other species currently placed in this genus. In general, the genus can be distinguished from other Euptychiina by the small-sized adults, the arrangement of lines and ocelli in the wing pattern and the presence of a superuncus in the male genitalia.

Material and methods

Adults of the new species were examined from ICN-MHN-L and MUSM and we report eight collecting localities in Colombia and Peru (Fig. 1).

Wing pattern and morphology of genitalia of nine male and seven female specimens were examined and compared with other species included in *Euptychia* by Lamas (2004). The male genitalia were extracted using hot KOH 10% after placing them in this solution for 10 minutes. Genitalia were observed using a Zeiss Stemi 2000-C stereoscope and conserved in vials with alcohol and glycerin. Photographs of genitalia with the aedeagus extracted were taken in lateral and dorsal view using a digital Nikon Coolpix 8700 camera. We used AxioVision 3.1 for the measurement of genitalia and Photoshop CS3 to compose the pictures. Color descriptions in Photoshop CS3 follow the RGB color model in the "Lab space" in which a broad array of colors can be precisely described by the combination of Red (R), Green (G) and Blue (B). We follow this model because it is a device-independent color space.

We also extracted, for comparison, the male genitalia of *Euptychia westwoodi*, *E. meta*, *E. rufocincta*, *E. enyo* and *Euptychoides griphe*.

We used a KOH 10% and alcohol 70% treatment for clearing the wings and revealing the venation.

Genitalia terminology follows Klots (1970) and Peña & Lamas (2005), from which the terminology of the genital characters (Fig. 3) and wing markings (Fig. 2) is taken. Wing terminology follows Miller (1970).

The following abbreviations are used throughout the text:

FW	Forewing
DFW	Dorsal forewing
VFW	Ventral forewing
HW	Hindwing
DHW	Dorsal hindwing
VHW	Ventral hindwing
Gen.	Genitalia
ICN-MHN-L	Instituto de Ciencias Naturales, Colección de Lepidoptera, Universidad Nacional de Colombia, Bogotá, Colombia
MUSM	Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú
KWJH	Keith Willmott & Jason Hall collection, Gainesville, FL, USA
MECN	Museo Ecuatoriano de Ciencias Naturales, Quito, Ecuador.
RGB	Color model based on Red, Green and Blue

Results and discussion

Euptychia cesarensis Pulido, Andrade, Peña & Lamas, new species

(Figs. 2–5)

Euptychia [n. sp.]: Lamas, 2004

Description. MALE, FW length: 17.1 mm (n=4) (Figs. 2, 3, 5A)

Head: Labial palpi twice the eye diameter (1.5 mm), with long scales (3 mm), antennae yellowish, total length (9.03 mm) a little less than half of costal vein length.

Thorax: Dorsally blackish brown (R40, G42, B31), ventrally yellowish (R105, G92, B48), covered with dense light yellowish hair.

Abdomen. Dorsally blackish brown (R40, G42, B31), ventrally yellowish (R105, G92, B48).

Genitalia (Fig. 3): Uncus has the same length (0.48 mm) of the tegumen; superuncus is long (0.28 mm) in comparison with other species of the genus (Forster 1964); gnathos absent; fultura superior (ft) very elongated (0.36 mm); valva elongated (1.26 mm) with pointed end and plain internal margin; saccus (0.39 mm) rounded and short in ventral view; aedeagus (1.5 mm) tubular and curved upwards without cornuti.



FIGURE 1. *E. cesarensis* distribution in the Andes. A, Río de Oro (Cesar, Colombia); B, Pozuzo (Pasco, Perú); C, Mina Pichita (Junín, Perú); D, Santa Isabel, Río Cosñipata (Cuzco, Perú).

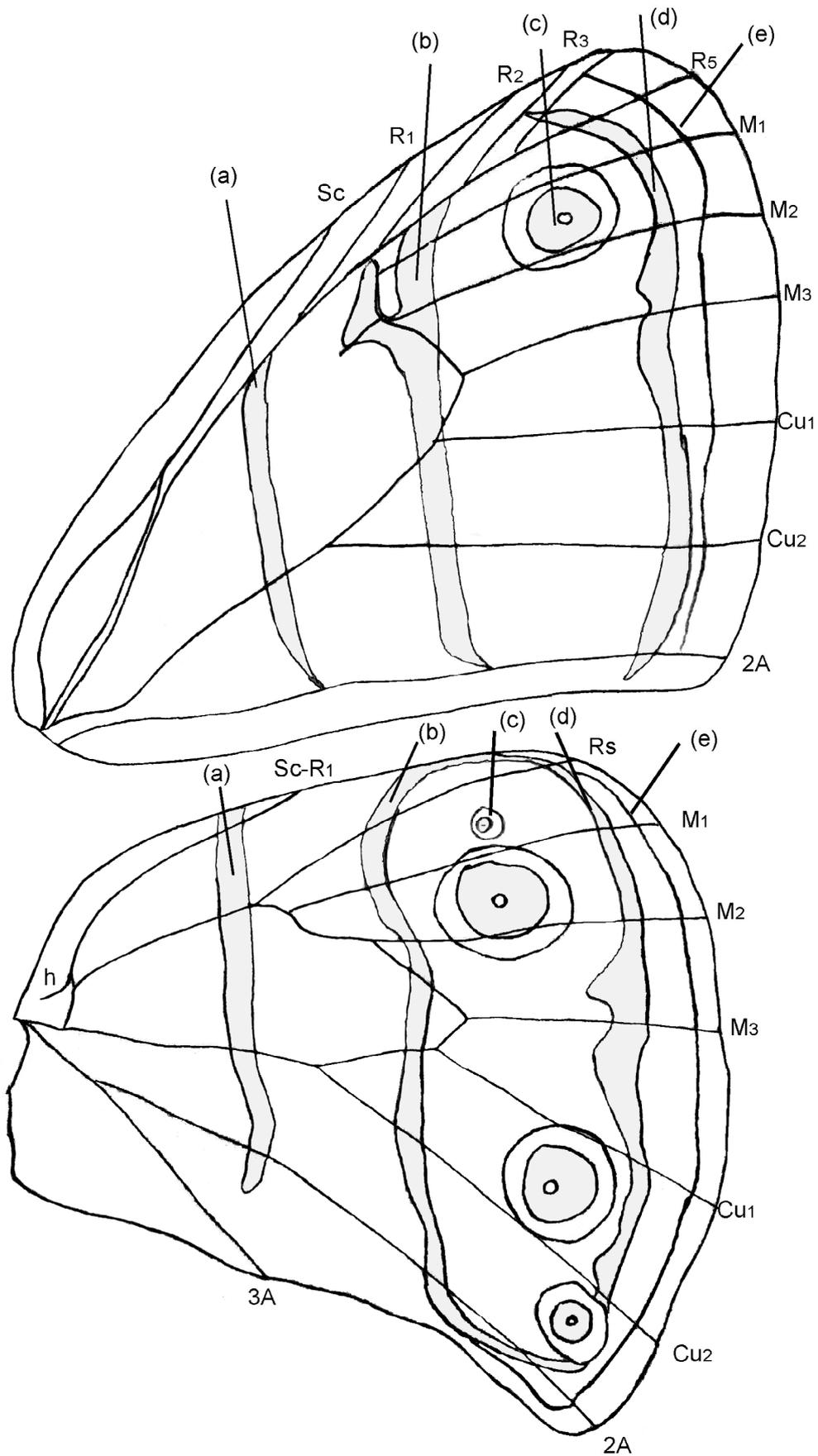


FIGURE 2. Male wing venation of *E. cesarensis* showing line and ocellus pattern, forewing above and hindwing below. (a), discal line; (b), postdiscal line; (c), submarginal ocelli; (d), submarginal line; (e) marginal line.

Forewing (FW). Apex rounded; outer margin covered with long scales. Dorsal ground color dark brown (R130, G112, B62), darker (R71, G59, B35) and diffused discal, postdiscal marginal and submarginal lines are evident in DFW, the same as a submarginal dot in M_1 - M_2 , discal and postdiscal lines are much diffused and darker (R86, G62, B34) than the ground. VFW color light brown (R150, G129, B66); discal, postdiscal, submarginal and marginal lines reddish brown (R104, G67, B25), straight discal line extending from discal cell to 2A, the postdiscal line is branched at the top of the discal cell and it extends from R_5 base to 2A, slightly undulated submarginal line from R_3 to 2A, and a narrower marginal line from R_4 to 2A. A single postdiscal black ocellus with a white pupil and encircled with a yellowish (R170, G140, B52) ring and an external reddish brown ring between R_5 and M_2 , the center of the ocellus is in M_2 - M_1 , but its extent into neighbouring cells may vary; two dark yellow patches between postdiscal and submarginal lines in M_3 - Cu_1 and Cu_1 - Cu_2 .

Hindwing (HW). Anal apex rounded. Dorsal ground color the same as DFW, discal and postdiscal lines fade out from costa to anal margin, marginal and submarginal lines darker (R62, G56, B34) than in DFW, with a submarginal dark (R86, G62, B34) dot in M_1 - M_2 , a black ocellus with a white pupil and encircled by a yellowish (R167, R131, B43) ring in cell Cu_1 - Cu_2 . VHW ground color the same as VFW, discal, postdiscal submarginal and marginal lines the same brown color as VFW, straight discal line from costal margin to 2A-3A, postdiscal line undulated from costal margin to M_2 and stays straight from M_2 to 2A-3A, where it branches reaching submarginal ocellus in Cu_2 -2A, submarginal line with an irregular undulated pattern from costal margin to ocellus in Cu_2 -2A, slightly undulated marginal line, thinner than remaining lines, from R_s to 2A-3A, four black ocelli between postdiscal and submarginal lines, smallest in cell R_s - M_1 , largest in cells M_1 - M_2 and Cu_1 - Cu_2 , and medium-sized in cell Cu_2 -2A, all of them with a white pupil and encircled by a yellowish (R170, G140, B52) ring and an external reddish brown ring.

FEMALE: FW length: 17.3 mm (n=4) (Figs. 2, 4, 5B): General color and pattern very similar to male, but in general paler and with more rounded wings.

Genitalia (Fig. 4): Papillae anales long and hairy adorned with setae, ductus bursae (du.bu) not sclerotized and not spirally twisted, long and narrow distally, corpus bursae (crp.bu) rounded with two sclerotized lineal signa (sig) longer than broader.

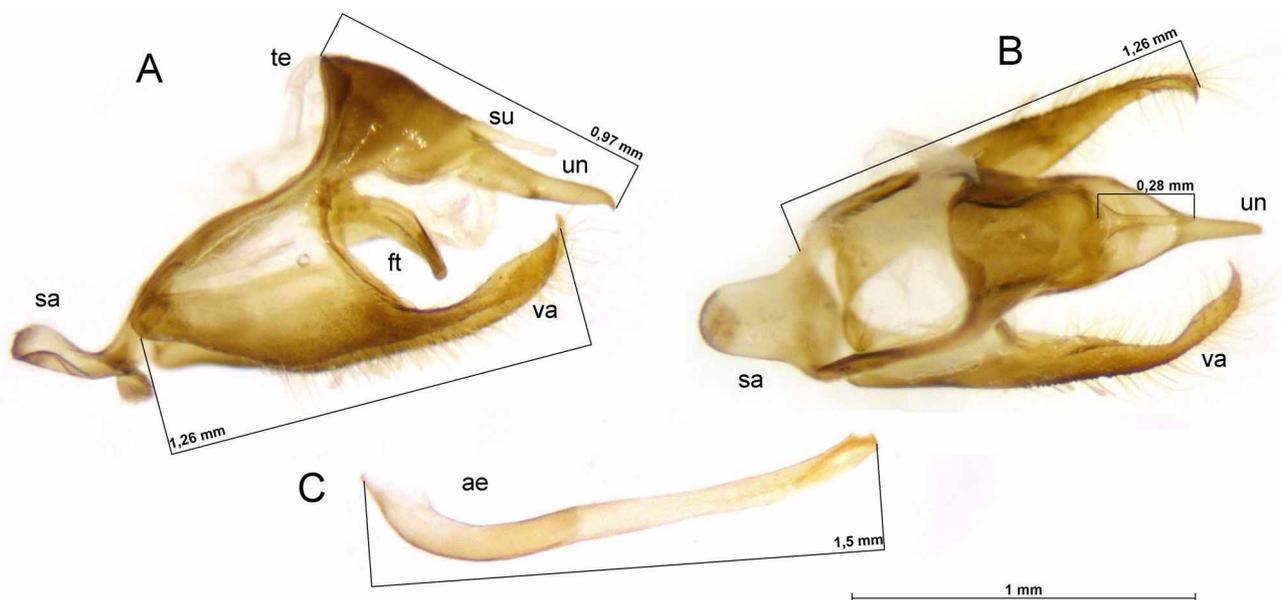


FIGURE 3. Male genitalia of *E. cesarensis*. A, lateral view; B, dorsal view; C, aedeagus (lateral view); ae: aedeagus; un: uncus; te: tegumen; ft: fultura superior; sa: saccus; va: valva; su: superuncus.

Forewing (FW). Dorsal ground color paler (R147, G115, B66) than of male, an ocellus between R_5 and M_2 with a white pupil and encircled by a yellowish ring. This ocellus and the discal, postdiscal, submarginal and marginal lines are more clearly defined than those of the male. VFW color pale yellowish brown (R179, G161, B99). In general, the lines are lighter colored and their relative position is the same as the male, the submarginal line with

an undulated pattern from R_3 to M_3 that continues with an irregular pattern reaching 2A, with a continuous darker yellow (R155, G115, B47) patch from M_3 - Cu_1 to Cu_2 -A2.

Hindwing (HW). Dorsal ground color the same as DFW, two postdiscal ocelli with a little white pupil and encircled by a yellow ring in cells M_1 - M_2 and Cu_1 - Cu_2 , submarginal line a little wider than of male. VHW ground color the same as VFW, lines and ocellus pattern the same as the male, but in some specimens the ocellus in Rs - M_1 is connected with the ocellus in M_1 - M_2 .

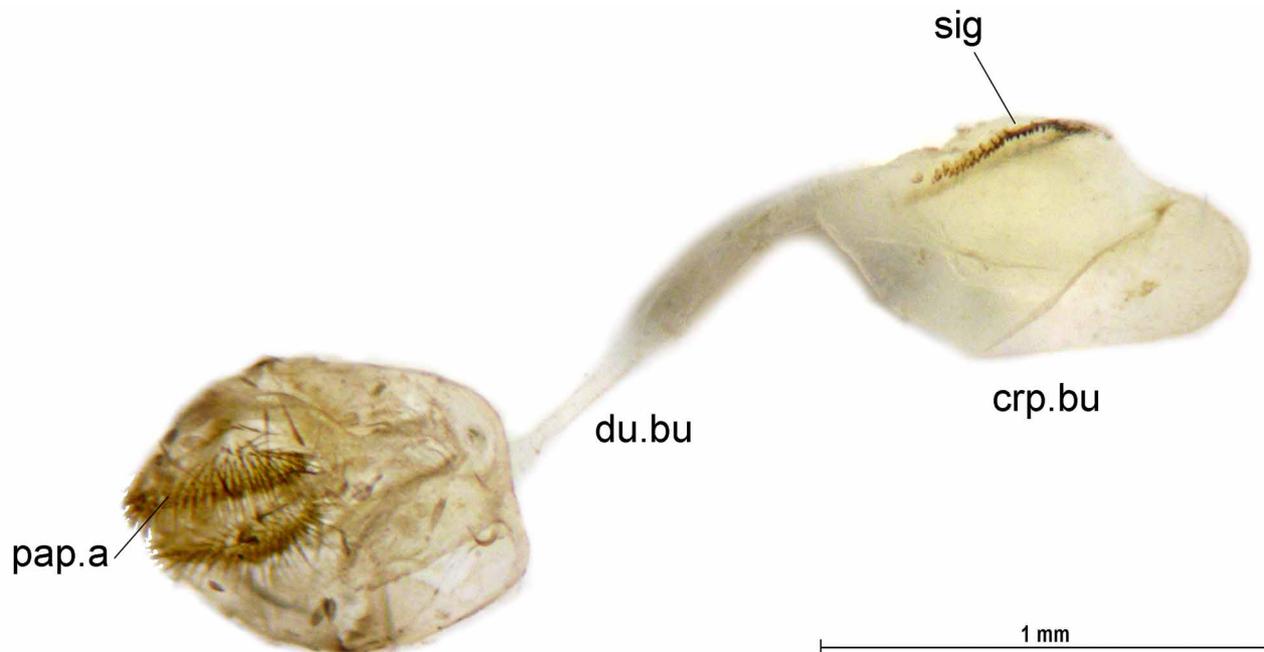


FIGURE 4. Female genitalia of *E. cesarensis*; pap.a: papillae anales; du.bu: ductus bursae; crp.bu: corpus bursae; sig: signa.

Early stages and host plants. Unknown for the new species, but Singer *et al* (1971) and Beccaloni *et al.* (2008) report plants of the Selaginellaceae as host plants for some species of *Euptychia*.

Etymology. The name *cesarensis* refers to the type locality.

Type locality. Colombia, Cesar, Río de Oro, Vereda El Salobre, 8°19'43.4''N, 73°24'19.3''W, 1300 m.

HOLOTYPE: Male, with the following labels: **COLOMBIA**, Cesar, Río de Oro, Vereda El Salobre, 8°19'43.4'' N, 73°24'19.3'' W, 1300 m, 6 March 2007, Hannier Pulido-B. leg., HP 1654, Gen No. 1461, ICN-MHN-L 20417.

ALLOTYPE: Female, with the following labels: **COLOMBIA**, Cesar (same data as HT), HP 1653, ICN-MHN-L 20419.

PARATYPES: **COLOMBIA**, Cesar, González, Vereda San Cayetano, 8°17'21'' N, 73°24'60'' W, 1800 m, 23 June 2007, H. Pulido-B. leg, HP 1979, Gen No. 1462, ICN-MHN-L 21429 (1 female) same data as HT, 1 female (HP 1653, ICN-MHN-L 20419); Cesar, Río de Oro, Vereda Saninvilla, 8°16'2.2'' N, 73°24'23'' W, 1550 m, 4 March 2007, H. Pulido-B. Leg., HP 1396, Gen No. 1457, ICN-MHNL 20420 (1 male); Cesar, Río de Oro, Vereda El Gitano, 8°18'34.5'' N, 73°24'44'' W, 1600 m, 5 March 2007, H. Pulido-B. Leg., HP 1528, Gen No. 1458, ICN-MHN-L 20421 (1 male); Cesar, Río de Oro, Vereda El Gitano, 8°19'27.1'' N, 73°24'34.5'' W, 1370 m, 5 March 2007, H. Pulido-B. Leg., HP 1527, Gen. No. 1460, ICN-MHN-L 20276 (1 male).

Diagnosis. The most obvious unique feature of the species is having a tornal ocellus in 2A- Cu_2 . The genitalia of *E. cesarensis* have the futura superior and the superuncus longer than *E. met and*, *E. enyo*. Forster's (1964) genitalia drawings of *Euptychia* show the internal margin of the valva is plain without any dorsal processes or teeth. This species can be readily distinguished from *E. rufocincta*, *E. enyo*, *E. hilara*, *E. insolata*, *E. jesia*, *E. meta*, *E. rufocincta* and *E. westwoodi* by having, on the VHW, four black ocelli with a white pupil encircled by a yellowish ring and an external reddish brown ring between the postdiscal and submarginal lines in Rs - M_1 , M_1 - M_2 , Cu_1 - Cu_2 and 2A- Cu_2 .

E. cesarensis is perhaps most similar to *E. rufocincta*, but can be separated because *E. rufocincta* has three ocelli on the VHW and the postdiscal line on the VFW is not branched at the costa as in *E. cesarensis*.



FIGURE 5. Adults of *E. cesarensis*, A. Holotype from Río de Oro (Cesar, Colombia), B. Allotype from González (Cesar, Colombia). D: Dorsal view; V: Ventral view.

In general aspect, the wing pattern of *E. cesarensis* resembles *Euptychia enyo* and *Euptychia rufocincta*. *E. cesarensis* can be distinguished from *E. enyo* by lacking the two ocelli between M_2 - M_3 and M_3 - Cu_1 in VHW, and lacking the three non-pupilled ocelli in M_2 - M_3 , M_3 - Cu_1 and Cu_1 - Cu_2 in VFW. The ground color in *E. cesarensis* is darker and the lines on the ventral side are narrower. The new species can be distinguished from *E. rufocincta* because in ventral side the lines are narrower and in VFW the postdiscal line is branched. The genitalia of *E. cesarensis* is compared with Forster's (1964) genitalia drawings of *Euptychia* species and with *E. meta* and *E. enyo*, showing notable differences: the superuncus is very long, being the half of uncus length, the fultura superior is longer and slightly ventrally curved and the valvae are elongated with a pointed end and a smooth internal margin.

Distribution and ecology. Only known from the type locality in the Serranía del Perijá. The species flies in secondary-growth Andean and subandean forest with species of the genus *Alfaroa*, *Hedyosmum*, *Weinmannia* and *Clusia* from 1300 to 1800 m.

Discussion. Although there is no consensus about the adult morphological characters that define *Euptychia*, the new species is described in this genus because it shows several similarities in ventral markings with other species currently placed in this genus. The relationships among *Euptychia* and other euptychiines are not clear (Murray & Prowell 2005; Peña *et al.* 2006), however it is possible to differentiate *Euptychia* from related genera (Forster 1964). The male genitalia in *Euptychia* exhibit a smaller uncus, absent gnathos and very elongated fultura superior. *Euptychia* can be separated from *Euptychoides* Forster, 1964 because male genitalia in *Euptychoides* have a well developed gnathos and the aedeagus has cornuti (Forster 1964), while these structures are not present in *Euptychia* species. *Forsterinaria* species present undulated dark brown discal, postdiscal, submarginal and marginal lines and submarginal ocelli in ventral view in both wings (Peña & Lamas 2005); *Erichthodes* Forster, 1964, in ventral view, present ocelli with bigger white pupils, and some species present white lines instead of those brown lines in *Euptychia*; *Magneuptychia* includes bigger sized adults and wider uncus.

***Euptychia cesarensis viloriai* Andrade, Pulido, Peña & Lamas, new subspecies**
(Figs. 2, 6)

Euptychia [n. sp.]: Lamas, 2004

Description. MALE, FW length: 17 mm (n=4) (Fig. 6A).

Similar to nominotypical subspecies but DHW with an additional white-pupilled faint black ocellus in Cu_2 -2A, the lines below are narrower and the ventral ground color is paler (R194, G175, B86), in VFW the ocellus between R_5 and M_2 is smaller and the dark yellow patches between postdiscal and submarginal lines in M_3 - Cu_1 and Cu_1 - Cu_2 are nearly inconspicuous, in VHW the anal area between the inner margin and the postdiscal line is dusted with white scales. Ventrally, the discal, postdiscal, marginal and submarginal lines are thinner than those of nominotypical subspecies and submarginal line in both wings is more undulated in M_2 - Cu_1 .



FIGURE 6. Adults of *E. cesareense viloriai*, A. Holotype, B. Allotype; both from Mina Pichita (Junín, Peru). D: Dorsal view; V: Ventral view.

Genitalia as in *E. cesareense cesareense*.

FEMALE, FW length: 17.2 mm (n=7) (Fig. 6B): Ground color in both wings paler and more yellowish than in *E. cesareense cesareense*. DFW with a white pupilled black ocellus in M1-M2. DHW with white-pupilled black ocelli in M₁-M₂, Cu₁-Cu₂, and a faint one in Cu₂-2A. Ventrally, the lines are wider than in *E. c. cesareense*, and the VFW patch between postdiscal and submarginal lines is more conspicuous.

Genitalia as in *E. cesareense cesareense*.

Early stages and host plants. Unknown.

Etymology. This subspecies is named after our friend and colleague Angel Viloria, in recognition of his important work on Andean Lepidoptera.

Type locality. Perú, Junín, Mina Pichita, 11°05' S, 75°25' W, 2100 m.

HOLOTYPE: Male, with the following labels: **PERU**, Junín, 1 Km S Mina Pichita, 11°05' S, 75°25' W, 2100 m, 21 August 2003, C. Peña Leg., MUSM-ENT-003934, GENITALIA #HWPB-01.

ALLOTYPE: Female, with the following labels: **PERU**, Junín, 1 Km S Mina Pichita, 2100 m, 22 August 2003, C. Peña Leg., MUSM.

PARATYPES: **PERU**, Junín, 1 Km S Mina Pichita, 11° 05' S, 75° 25' W, 2100 m, 12 November 2003, C. Peña Leg, MUSM, DNA Sample 04-55 Carlos Peña (1 male); Junín, 1 Km S Mina Pichita, 11° 05' S, 75° 25' W, 2100 m, 22 August 2003, C. Peña Leg, MUSM (2 females); Junín, 1 Km S Mina Pichita, 11° 05' S, 75° 25' W, 2100 m, 9 September 2002, J. Grados Leg, MUSM (1 male); Junín, 1 Km S Mina Pichita, 11° 05' S, 75° 25' W, 2100 m, 9 August 2002, J. Grados Leg, MUSM (1 female); Junín, 1 Km S Mina Pichita, 11° 05' S, 75° 25' W, 2100 m, 13 August 2002, C. Peña Leg, MUSM (2 females); Junín, 1 Km S Mina Pichita, 11° 05' S, 75° 25' W, 2100 m, 21 August 2003, J.J. Ramirez Leg, MUSM, Genitalia HWPB-03, MUSM-ENT-003937 (1 male); Junín, 1-3 Km S Mina Pichita, 2100 m, 24 August 1988, G. Lamas Leg, MUSM (1 female); Junín, 1 Km S Mina Pichita, 11° 05' S, 75° 25' W, 2100 m, 12 August 2002, A. Guanllo Leg, MUSM (1 female); Junín, 1-3 Km S Mina Pichita, Hda. Naranjal, 2100 m, 17 October 1989, G. Lamas Leg, MUSM (1 female); Junín, 0-1 Km E, Mina Pichita, Hda. Naranjal 2000 m, 18 November 1984, G. Lamas & J.E Pérez Leg, MUSM (1 female)

ADDITIONAL MATERIAL: **PERU**, Pasco, 18 Km S Pozuzo, 10° 16' S, 75° 33' W, 1200 m, 29 November 1997, G. Lamas Leg, MUSM (1 male); Cuzco, Cerca Santa Isabel, Río Cosñipata, 1200 – 1500 m, 5-11 February 1975, G. Lamas leg., MUSM-ENT-003941 (1 female); Cuzco, Río Cosñipata, Qbda. Quitacalzón, 1050m, 1-3 Septiembre 1989, G. Lamas Leg. (1 female); **ECUADOR**, Tungurahua, Río Blanco, 01°23' S, 78°20' W, 1000 m, 07 July 1966, S.E. Velástegui Leg, MUSM (1 female); Río Machay, 1° 23.75' S, 78° 16.30' W, 1700 m, 4-5 July 1993, J. Hall, leg, KWJH (1 male); Río Machay, 1° 23.75' S, 78° 16.30' W, 1700 m, 19-20 August 1993, K. Willmott & J. Hall, leg, KWJH (1 female); Río Machay, 1° 23.75' S, 78° 16.30' W, 1700 m, 19-20 August 1993, K. Willmott & J. Hall, leg, MECN (1 female).

Diagnosis. *Euptychia cesareense viloriai* males are distinguished from the nominotypical subspecies by having a pupilled ocellus between Cu₂-2A of DHW, the VHW anal area dusted with white scales, ventral ground color

paler, ventral lines narrower, VHW discal line more oblique and submarginal line in the VFW apex in zigzag, rather different from the smoothly rounded line in the *cesarensis*. Females can be separated by a general paler color, a pupilled ocellus in cell Cu₂-2A of DHW and wider VW submarginal lines are evident.

Distribution and ecology. Known from Junín, Pasco and Cuzco in Peru. The subspecies flies from 1200 to 2100 m.

The existence of the species in several localities of Peru, and northern Colombia, suggests that *Euptychia cesarensis* is a rare but widely distributed species in the Andes, with additional subspecies likely to be discovered in regions where it is currently unknown (Fig. 1). We compared additional material from Ecuador sharing features with *cesarensis* and *viloriai*, which seems to be a different subspecies, but the status of these specimens must be reviewed.

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Literature cited

- Ackery, P.R., de Jong, R. & Vane-Wright, R.I. (1999) The butterflies: Hedyloidea, Hesperioidea and Papilionoidea. In: Kristensen, N.P. (Ed), *Lepidoptera: Moths and Butterflies. 1. Evolution, Systematics and Biogeography*. Handbook of Zoology, vol. IV. Walter de Gruyter, Berlin. Part 35. 263–300 pp.
- Beccaloni, G.W., Viloria, A.L., Hall, S.K., & Robison, G.S. (2008) Catalogue of the hostplants of the Neotropical butterflies. *Catálogo de las plantas huésped de las mariposas neotropicales*. Sociedad Entomológica Aragonesa m3m: Monografías Tercer Milenio Vol. 8. S. E. A., Zaragoza, 536 pp.
- DeVries, P.J. (1987) *The butterflies of Costa Rica and their natural history*, vol. I: Papilionidae, Pieridae, and Nymphalidae. Princeton University Press, 327 pp.
- Forster, W. (1964) Beiträge zur Kenntnis der Insektenfauna Boliviens XIX. Lepidoptera III. Satyridae. *Veröffentlichungen der zoologischen Staatssammlung München* 8, 51–188, pls. 27–35.
- Freitas, A.V.L., Mielke, O.H.H., Moser, A., Silva-Brandão, K.L. & Iserhard, C.A. (2011) A New Genus and Species of *Euptychiina* (Lepidoptera: Nymphalidae: Satyrinae) from Southern Brazil. *Neotropical Lepidoptera*, 40(2), 231–237.
- Freitas, A.V.L. & Peña, C. (2006) Description of genus *Guaianaza* for “*Euptychia*” *pronophila* (Lepidoptera: Nymphalidae: Satyrinae) with a description of the immature stages. *Zootaxa*, 1163, 49–59.
- Klots, A.B. (1970) Lepidoptera. In: Tuxen S.L. (Ed.), *Taxonomist’s Glossary of Genitalia in Insects*. Ed. 2. Munksgaard, Copenhagen, pp. 115–130.
- Lamas, G. (2004) *Atlas of Neotropical Lepidoptera*. Checklist part 4A. Hesperioidea-Papilionoidea. Association for tropical Lepidoptera, Florida, 439 pp.
- Marín, M.A., Peña, C., Freitas, A.V.L., Wahlberg, N. & Uribe, S.I. (2011) From the Phylogeny of the Satyrinae Butterflies to the Systematics of *Euptychiina* (Lepidoptera: Nymphalidae): History, Progress and Prospects. *Neotropical Lepidoptera*, 40(1), 1–13.
- Miller, L.D. (1968) The higher classification, phylogeny and zoogeography of the Satyridae (Lepidoptera). *Memoirs of the American Entomological Society*, 24, 1–174.
- Miller, L.D. (1970) Nomenclature of wing veins and cells. *Journal of Research on the Lepidoptera*, 8 (2), 37–48.
- Murray, D. & Prowell, D.P. (2005) Molecular phylogenetics and evolutionary history of the Neotropical Satyrinae Subtribe *Euptychiina* (Nymphalidae: Satyrinae). *Molecular Phylogenetics and Evolution*, 34, 67–80.
- Peña, C. & Lamas, G. (2005) Revision of the butterfly genus *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae, Satyrinae). *Revista peruana de Biología*, 12, 5–48.
- Peña, C., Wahlberg, N., Weingartner, E., Kodandaramaiah, U., Nylin, S., Freitas, A.V.L. & Brower, A.V.Z. (2006) Higher level phylogeny of Satyrinae butterflies (Lepidoptera: Nymphalidae) based on DNA sequence data. *Molecular Phylogenetics and Evolution*, 40, 29–49.
- Peña, C. & Wahlberg, N. (2008) Prehistorical climate change increased diversification of a group of butterflies. *Biology Letters*, 4, 274–278.
- Pulido-B., H.W. & Andrade-C., M.G. (2008) A new species of *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae: Satyrinae) from the Serranía del Perijá, Cesar, Colombia. *Caldasia*, 30, 189–195.
- Singer, M.C., Ehrlich, P.R. & Gilbert, L.E. (1971) Butterfly feeding on Lycopsid. *Science*, 172, 1341–1342.