A distinctive new species of cloud forest Euptychiina (Lepidoptera: Nymphalidae: Satyrinae) from Ecuador and Peru

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Abstract: A new species of Euptychiina, *Erichthodes eremita* Lamas, Willmott & Radford, **n. sp.**, is described and illustrated. DNA sequence data suggest that the new species is sister to a species currently placed in *Erichthodes* Forster, 1964, although ongoing revision of the generic taxonomy of the subtribe might result in the reclassification of both of these species in future. The new species is known from the eastern Andes of southern Ecuador and adjacent northern Peru, where it is a rare inhabitant of stunted, 'elfin' cloudforest confined to ridge and mountain tops.

Key words: inventory, Andes, species description, taxonomy

INTRODUCTION

Ongoing field work in Andean cloud forests has uncovered a remarkable number of new, often distinctive, butterfly species in the last few decades (e.g., Salazar & Constantino, 1993; Hall & Willmott, 1995; Eitschberger & Racheli, 1998; Willmott *et al*., 2001; Pyrcz, 2004). This is true even for groups that have their center of diversity in lowland forests, such as the satyrine subtribe Euptychiina (e.g., Peña & Lamas, 2005; Nakahara *et al.*, 2015a). Euptychiina has been the subject of intensive research during the last decade with numerous papers published (see Nakahara *et al*., 2018), and after being one of the most poorly known groups of butterflies, a reasonable understanding of its diversity, evolution and distribution is beginning to emerge. Building on previous molecular studies (Murray & Prowell, 2005; Peña *et al.*, 2010), a combination of morphological (Marín *et al*., 2017) and molecular (Espeland *et al*., unpubl. data) phylogenetic study is ongoing, which will contribute towards revising the generic classification of the group. As such, several notable new species have recently been described, whose inclusion in research focused on particular clades is needed to clarify generic limits (e.g., Zacca *et al.*, 2014; Huertas *et al.*, 2016; Nakahara *et al*., 2018). In this paper, we therefore describe a distinctive, new cloud forest Euptychiina species of uncertain generic affinities that has been recorded during long-term faunistic studies of the butterflies of Ecuador and Peru.

MATERIALS AND METHODS

The authors and colleagues have been conducting field work throughout Ecuador and Peru for many years to collect butterfly material for taxonomic study and document distribution and behavior. In addition, most of the type specimens of the new species described here were collected during targeted surveys of the Cordillera del Cóndor in Ecuador by the Cambridge University Lepidoptera Expedition to the 'Tercera Cordillera' (see Radford & Willmott (2013) for more details). Specimens were studied in public and private collections in the Americas and Europe to examine type specimens, study variation and record distribution data. The following collection acronyms are used: **FLMNH**: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, USA; **FRPI**: Francisco Piñas personal collection, Quito, Ecuador; **INABIO**: Instituto Nacional de Biodiversidad, Quito, Ecuador (formerly Museo Ecuatoriano de Ciencias Naturales, MECN); **MUSM**: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru.

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 Comstock & Needham (1918). We use the abbreviations DFW, VFW, DHW and VHW for dorsal and ventral forewing and hindwing.

We extracted genomic DNA from legs removed from dried Euptychiina specimens 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 and annealing temperatures are provided in Table 1. PCR reactions were conducted in a 20 ul volume containing 2 ul DNA, 0.4 ul of each primer (10 uM), 0.5 ul of Bovine Serum Albumin (BSA, 20 mg/mL), 6.7 ul of ddH_2O, and 10 ul of OneTaq® Hot Start Quick-Load® 2X Master Mix or Platinum™ Green Hot Start PCR Master Mix (2X).

Single strands of the PCR products were sequenced by University of Florida's Interdisciplinary Center for Biotechnology Research Sanger Sequencing Group using the same primers as in the PCR. Sequences of the taxon described here were incorporated into a large dataset comprising >2000 previously published and new, unpublished Euptychiina sequences, representing >420 species, and included in ongoing analyses (Espeland, unpubl. data) to provisionally determine the closest relatives, as described in Nakahara *et al*. (2015b). New sequences are deposited in Genbank (Table 2).

Table 1. Primers and reaction conditions.

Gene	Primer	Sequence (5'-3')	Direction	Annealing temp./°C	Source
COI	LCO_nym	TTTCTACAAATCATAAAGATATTGG	forward	51	Neild *et al*. (2015)
COI	HCO_nym	TAAACTTCAGGATGACCAAAAA	reverse	51	Neild *et al*. (2015)
EF-1α	ef44	GCYGARCGYGARCGTGGTATYAC	forward	58	Monteiro & Pierce (2001)
EF-1α	efrcM4	ACAGCVACKGTYTGYCTCATRTC	reverse	58	Monteiro & Pierce (2001)
GAPDH	Frigga	AARGCTGGRGCTGAATATGT	forward	46	Wahlberg & Wheat (2008)
GAPDH	Burre	GWTTGAATGTACTTGATRAGRTC	reverse	46	Wahlberg & Wheat (2008)
RpS5	rpS5degF	ATGGCNGARGARAAYTGGAAYGA	forward	46	Wahlberg & Wheat (2008)
RpS5	rpS5degR	CGGTTRGAYTTRGCAACACG	reverse	46	Wahlberg & Wheat (2008)

Table 2. Voucher specimen information and Genbank numbers for DNA sequence data. Sequences with Genbank numbers beginning 'MH-' are newly deposited as part of this study.

Taxon	Locality (decimal latitude and longitude)	DNA voucher	COI	EF-1α	GAPDH	RpS5
Erichthodes julia	Peru: Junín: Quebrada Siete Jeringas (-11.2, -75.4)	CP04-65	GU205834	GU205890	GU205946	GU206006
Erichthodes julia	Peru: Cuzco: El Mirador (-13.067, -71.55)	KW-15-112	MH347473			
Erichthodes julia	Peru: Junín: Cerro Pichita, N side trail (-11.09, -75.434)	LEP-18583	MH347474			
Erichthodes eremita	Ecuador: Zam.-Chinchipe: km 20.3 Loja-Zamora rd. (-3.988, -79.106)	KW-081120-01	MH347470	MH347475	MH347477	MH347478
Erichthodes eremita	Ecuador: Zam.-Chinchipe: km 20.3 Loja-Zamora rd. (-3.988, -79.106)	KW-081120-02	MH347471			
Erichthodes eremita	Ecuador: Zam.-Chinchipe: km 20.3 Loja-Zamora rd. (-3.988, -79.106)	KW-081120-03	MH347472	MH347476		
Neonympha areolatus	USA	CP22-03	GU205856	GU205912	GU205967	GU206028
Satyrotaygetis satyrina	Costa Rica: Puntarenas	DNA97-006	AY508575	AY509101		
Pareuptychia ocirrhoe	Peru: Madre de Dios: Tambopata Research Center (-13.133, -69.6)	CP01-66	DQ338805	DQ338951	GQ357444	GQ357573
Erichthodes antonina	Peru: Madre de Dios: Albergue Posada Amazonas (-12.783, -69.233)	CP02-24	DQ338792	DQ338935	GQ357429	GQ357558
Megeuptychia monopunctata	Peru: Amazonas: Cordillera del Cóndor, Qda Kegkem (-3.633, -78.3)	CP06-70	GU205852	GU205908	GU205964	GU206024
Taydebis peculiaris	Brazil: São Paulo: Campos do Jordão	NW149-11	GQ864811	GQ864905	GQ865036	GQ865499

RESULTS

Erichthodes eremita Lamas, Willmott & Radford, **n. sp.**
Figs. 1-3

Yphthimoides sp. n.: Lamas (1997: 93, 97, 217); Lamas (2004: 223).
Taygetis blanda Möschler: Piñas (2004: 19, figs. 93, 94) [misidentification]

Diagnosis and identification: Analysis of available DNA sequence data show that *E. eremita* **n. sp.** is the sister species of *Erichthodes julia* (Weymer, 1911) (Fig. 1E,F), with 100% bootstrap support (Fig. 4). The two species occur in east Andean cloud forests and have somewhat similar VHW ocelli, in terms of number and arrangement of pupils. The male of *E. julia* has faint darker scaling in the middle of the DFW, similar to the more conspicuous black androconial patch of *E. eremita*, while both sexes have a white VHW postdiscal band similar to that of female *E. eremita*. Otherwise the two species are very distinct, with males of *E. eremita* being larger (*E. eremita*: FW length 23-25 mm, mean 24.3 mm, n=14; *E. julia*: FW length 20-22 mm, mean 21.4 mm, n=7) and having a dark brown dorsal ground color (not grayish brown), reddish scaling in the distal part of the ventral wings and no paler shading near the distal margins, no complete white ventral postdiscal band, smaller VHW ocelli, a postdiscal ocellus on the VFW in cell M_1-R_5, in addition to numerous other differences. The females of both species likewise differ, except that the dorsal coloration and white ventral postdiscal band are similar. The male genitalia of *E. eremita* and *E. julia* (figured by Forster, 1964: 118, Fig. 129) differ in the posterior dorsal 'shoulder' of the valva being more pronounced and angled in the latter, and more gently curving in the former (the female genitalia of *E. julia* were not available for study).

Erichthodes eremita is also probably closely related to *Erichthodes jovita* (C. Felder & R. Felder, 1867), from Colombia, based on the very similar male genitalia, although no DNA sequence data have yet been obtained for the latter species. Genitalic similarities include the shape of the valva, the brachia being approximately aligned with the uncus in lateral view, and the similarly shaped aedeagus with two patches of cornuti. The type of *E. jovita* is figured in Warren *et al.* (2018) and *E. eremita* is easily distinguished from it and all other euptychiines by the combination of a two-tone ventral ground color, which is darker basally and paler distally, with a VHW that has whitish postdiscal scaling centered on the veins (in the

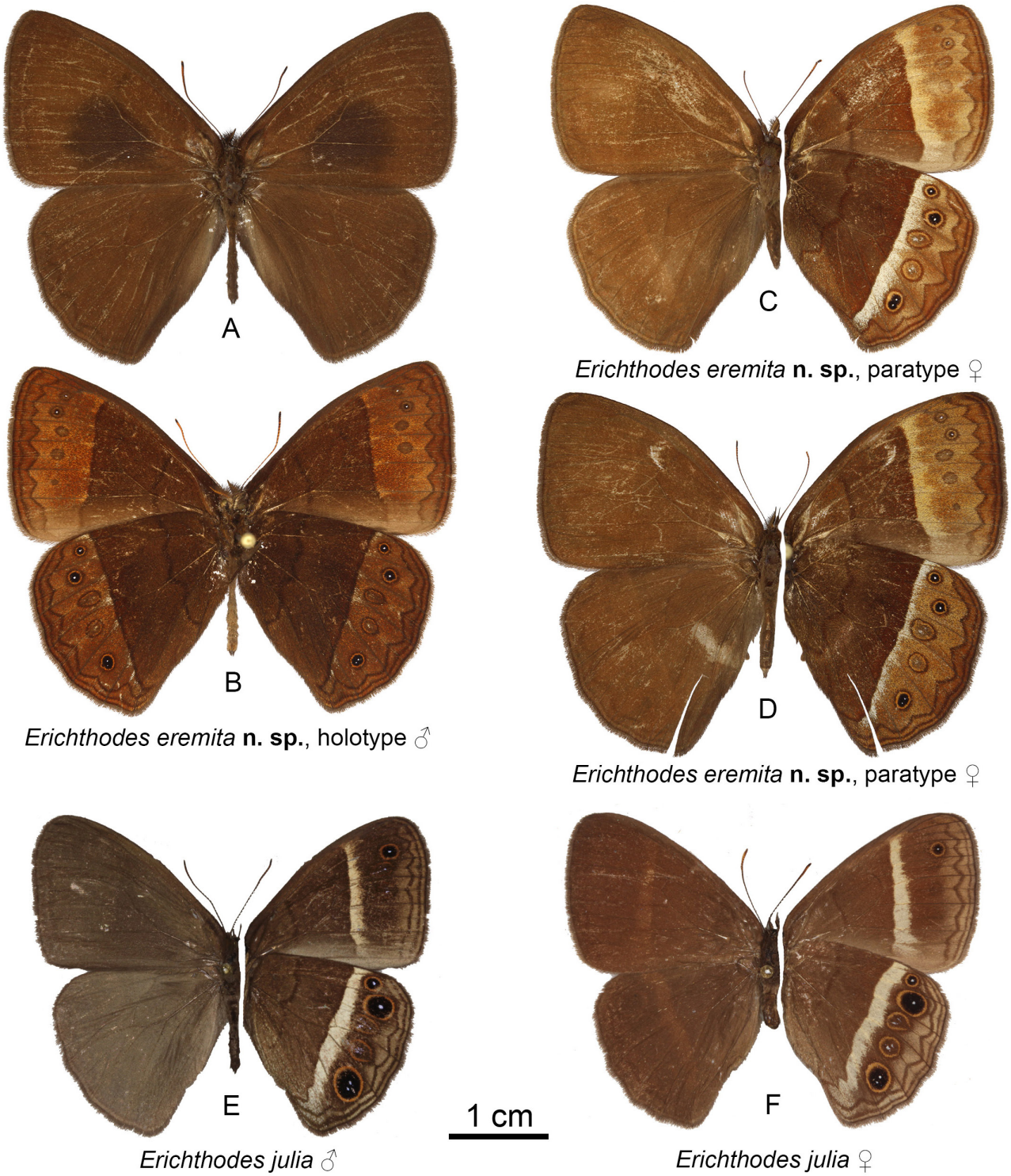

Fig. 1. A, B. *Erichthodes eremita* **n. sp.**, holotype ♂ (PAT47), Ecuador: **A**, dorsal surface, **B**, ventral surface. **C.** *Erichthodes eremita* **n. sp.**, paratype ♀ (FLMNH-MGCL-112620), Ecuador (left dorsal, right ventral). **D.** *Erichthodes eremita* **n. sp.**, paratype ♀ (PAN198), Ecuador (left dorsal, right ventral). **E.** *Erichthodes julia* ♂, Peru, Cuzco, El Mirador. **F.** *Erichthodes julia* ♀, Peru, Pasco, 18 km S Pozuzo.

male) or forming a band (in the female) at the distal edge of the dark brown postdiscal line. *Erichthodes narapa* (Schaus, 1902), from southern Brazil and Argentina, has, like *E. eremita*, pale scaling along the distal edge of the dark ventral postdiscal line, but it otherwise differs in many respects. In particular, the ventral surface of *E. narapa* lacks reddish coloration and has more prominently yellow-ringed ventral ocelli, and DNA sequence data indicate that the two species are likely unrelated (Espeland *et al*., unpubl. data). Likewise, *Harjesia blanda* (Möschler, 1877) has a superficially similar wing pattern (to the female and to more continuously white-banded males) but is easily distinguished by numerous characters, especially the scalloped (not smoothly convex) HW distal margin, lack of reddish brown scaling in the ventral ground color, and single (not double) pupil in the ocellus in VHW cell Cu_2-Cu_1.

As implied above, there is some variation among specimens collected at the same time and place in the expression of the white postdiscal band on the VHW, which in males varies from being present only as scattered white scaling around the veins (e.g., Fig. 1B) to forming a more or less continuous band, similar to the female in Fig. 1D. In females, the band ranges from a thin, continuous line as in Fig. 1D, to a broader band extending to the postdiscal ocelli, as in Fig. 1C. The ventral ground color ranges from a rich reddish brown to a more muted dark brown, and the contrast in lightness between the wings basal and distal of the dark postdiscal line varies, being pronounced in some specimens and more subtle in others. Too few specimens are known to determine whether there is any geographic variation between individuals from the Cordillera del Cóndor and the adjacent Andes, while some of the variation in ground color seems to be associated with the age and wear of specimens. Worn male specimens with limited white ventral scaling appear more uniformly brown on the ventral surface and thus may appear somewhat similar to co-occurring *Forsterinaria* Gray, 1973 (which lack VHW ocelli) and *Eretris* Thieme, 1905 (which have a very irregular rather than straight dark brown VHW postdiscal line).

Description: MALE (Fig. 1A,B): Forewing length of holotype 25 mm (23-25 mm, mean 24.3 mm, n=14). *Wings*: FW triangular, apex rounded, distal margin slightly convex, anal margin straight, most of subcostal vein swollen, base of cubitus swollen, recurrent vein absent, origin of M_2 nearer M_1 than M_3, vein R_2 arising just distally of origin of R_3+R_4+R_5; HW approximately triangular, distal margin rounded, anal margin slightly indented basal of tornus, humeral vein developed. *Dorsal surface*: Ground color brown. DFW with an approximately circular patch of black androconial scales in middle of wing, in middle of cell 2A-Cu_2, basal portion of cells Cu_2-M_3, and extending slightly into adjacent discal cell - androconial scales similar in shape to typical wing scales but more densely packed, overlapping one another by *c.* 50% instead of 25% in remainder of wing; entire distal portion of both wings also covered with sparse, paler brown, slightly curved hair-like scales. DHW with two thin, indistinct dark brown submarginal lines, more basal line wavy and more distal line straighter, wing margin lined with dark brown. *Ventral surface*: Ground color slightly darker brown than dorsal surface in basal half, becoming paler on FW towards anal margin, distal half (distal of dark brown postdiscal line) with paler, reddish-brown scaling throughout. VFW with thin, slightly convex dark brown discal line from costal vein extending across discal cell just basal of base of vein Cu_2 into middle of cell 2A-Cu_2; thin, approximately straight dark brown postdiscal line from cell M_1-R_5 to vein Cu_2, bending slightly distally and becoming diffuse in cell 2A-Cu_2; indistinct, triangular patches of paler scaling at distal edge of dark brown postdiscal line centered on veins; five postdiscal ocelli in cells Cu_2-Cu_1 (tiny brown spot), Cu_1-M_2 (circular brown spots encircled by very indistinct darker brown ring), M_2-M_1 (circular brown spot encircled by darker brown ring, with central black spot and white pupil), and M_1-R_5 (similar to preceding except white pupil almost covers black central area); two thin, indistinct dark brown submarginal lines, more basal line wavy and more distal line straighter, wing margin lined with dark brown. VHW similar to VFW except dark brown discal line more irregular, crossing middle of discal cell; triangular patches of paler scaling at distal edge of dark brown postdiscal line centered on veins brighter and more prominent; ocellus in cell Cu_2-Cu_1 well-developed, black center and encircled with orange, with two central white pupils, ocelli in cell Cu_1-M_2 slightly elongate, brown encircled with faint orange ring and with central white pupil, ocelli in cell M_2-Rs similar to that in cell Cu_2-Cu_1 but with only a single white pupil in each. *Head*: Eyes brown with dense, long, golden setae; antennae *c.* two fifths FW length and with *c.* 32 segments, distal *c.* 11 segments comprising club, dark brown with sparse white scales at ventral base of segments in basal part of antennae; labial palpi dark brown with sparse paler grayish brown scales laterally and long dark brown hair-like scales ventrally, terminal segment in length slightly shorter than width of eye, second segment *c.* twice as long as width of eye, basal segment *c.* one third length of second segment; head covered with dark brown scales and hair-like scales. *Thorax*: Thorax dark brown, dorsally with long, dense greenish and orangish hair-like scales; foreleg tibia about two thirds of tarsus in length, femur slightly longer, dark brown; mid- and hindlegs dark brown, slightly paler grayish dorsally, with spines ventrally on tarsus and tibia, pair of tibial spurs at distal end of tibia. *Abdomen*: Dark brown, ventral surface slightly paler grayish brown. *Genitalia* (Fig. 2A-G): As illustrated, notable features include eighth tergum unsclerotized except for narrow anterior band and slightly broader posterior patch; brachia aligned with uncus in lateral view, laterally flared in dorsal view, uncus distally tapering and ending in a single point; valva rather broad throughout except tapering distally to an upturned tip; aedeagus with anterior tip protruding beyond ductus ejaculatorius, with two patches of teeth-like cornuti; juxta approximately heart-shaped and very weakly sclerotized.

FEMALE: (Fig. 1C,D): Forewing mean length 25.2 mm (24-26 mm, n=5). *Wings*: as illustrated, similar to male except more rounded, paler, lacking black androconial scales on DFW, with white ventral postdiscal scaling more extensive, typically fused to form a band. *Head*, *thorax*, *abdomen*: similar to male except more extensive pale brown scaling laterally on labial palpi and on ventral surface of legs. *Genitalia* (Fig. 2H-L): inter-segmental membrane between 7th and 8th abdominal segments pleated and expandable (Fig. 2H-J), as in many other euptychiines; lamella postvaginalis forming broad lateral plates almost touching ventral edge of eighth tergum (Fig. 2H); antrum a sclerotized tube broadening distally (Fig. 2J,L); ductus bursae slightly curved just anterior of antrum, ductus seminalis inserts dorsally just anterior of antrum (Fig. 2L); corpus bursae with two elongate spiny signa (Fig. 2K,L).

Types: HOLOTYPE ♂: **ECUADOR**: *Zamora-Chinchipe*: Destacamento Paquisha Alto, [3°54'5"S,78°28'59"W], 2324 m, (Radford, J.), 8 Sep 2010, [PAT47], (genitalic dissection KW-17-19; CULEPEX Expedition, 2010) (FLMNH, to be deposited in INABIO).

PARATYPES (22 ♂, 8 ♀): **Ecuador**: *Morona-Santiago:* Cóndor Mirador, [3°37'41"S,78°23'42"W], 1984 m, (Hartley, E.), 22 Aug 2010, 1 ♂ [CON11], (FLMNH) (CULEPEX Expedition, 2010); Cóndor Mirador, [3°37'43"S,78°23'40"W], 1972 m, (Radford, J.), 21 Aug 2010, 1 ♂ [CON5], (FLMNH) (CULEPEX Expedition, 2010); *Zamora-Chinchipe:* above Destacamento Paquisha Alto, [3°54'S,78°28'32"W], 2300 m, (Robinson Willmott, J. C.), 5 Aug 2009, 1 ♀ [FLMNH-MGCL-149625], (FLMNH); Destacamento Paquisha Alto, [3°53'50"S,78°28'49"W], 2425 m, (Radford, J.), 4 Sep 2010, 1 ♂ [PAN147], (FLMNH) (CULEPEX Expedition, 2010); Destacamento Paquisha Alto, [3°53'51"S,78°28'48"W], 2421 m, (Radford, J.), 4 Sep 2010, 1 ♂ [PAN146], (FLMNH) (CULEPEX Expedition, 2010); Destacamento Paquisha Alto, [3°53'53"S,78°28'50"W], 2376 m, (Buckland, K.), 8 Sep 2010, 1 ♂ [PAT54], (FLMNH) (CULEPEX Expedition, 2010); Destacamento Paquisha Alto, [3°53'53"S,78°29'2"W], 2444 m, (Radford, J.), 6 Sep 2010, 1 ♂ [PAN167], 1 ♀ [PAN166], (FLMNH) (CULEPEX Expedition, 2010), 7 Sep 2010, 1 ♂ [PAN170], 1 ♂ [PAN171, to be deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC, USA], 1 ♂ [PAN172], 1 ♂ [PAN173], 1 ♂ [PAT31], 1 ♀ [PAN174], 1 ♀ [PAN175], (FLMNH) (CULEPEX Expedition, 2010), 8 Sep 2010, 1 ♂ [PAN199], 1 ♂ [PAN200, to be deposited in the Natural History Museum, London, UK], 1 ♂ [PAN203], 1 ♂ [PANW], 1 ♂ [PANZ], 1 ♀ [PAN198], 1 ♀ [PAN201], 1 ♀ [PAN202], (FLMNH) (CULEPEX Expedition, 2010); Destacamento Paquisha Alto, [3°54'5"S,78°28'59"W], 2324 m, (Radford, J.), 7 Sep 2010, 1 ♂ [PAN169], (FLMNH) (CULEPEX Expedition, 2010); km 20.3 Loja-Zamora rd., [3°59'17"S,79°6'22"W], 2420 m, (Aldaz, R.), 2 Nov 2006, 1 ♀ [FLMNH-MGCL-112620], (FLMNH), (Willmott, K. R.), 16 Oct 2006, 1 ♂ [FLMNH-MGCL-112618], (FLMNH), 17 Oct 2006, 1 ♂ [FLMNH-MGCL-112619], (FLMNH); km 20.3 Loja-Zamora rd., [3°59'17"S,79°6'22"W], 2450 m, (Willmott, K. R.), 22 Sep 2007, 1 ♂ [FLMNH-MGCL-113702], (FLMNH); km 20.3 Loja-Zamora rd., [3°59'17"S,79°6'22"W], 2500 m, (Willmott, K. R., Hall, J. P. W.), 24 Nov 1997, 1 ♂, (FLMNH). **Peru**: *Amazonas:* Alfonso Ugarte, [3°55'S,78°26'W], 2100 m, (Wust, W.), 18 Jul 1994, 1 ♂ [MUSM-LEP-105632], (MUSM).
Other records: **Ecuador**: *Zamora-Chinchipe:* Parque Nacional Podocarpus, [3°59'18"S,79°5'42"W], 2000 m, (Kling, M.), 1 May 1999, 1 ♀, (FRPI) (Piñas (2004: 19, f. 93, 94, as '*Taygetis blanda*')) (specimen not examined in person and therefore excluded from type series).

Etymology: The name is derived from the Latin masculine noun 'eremita', meaning a hermit, in reference to the remote and isolated habitats where this species lives. It is treated as a noun in apposition.

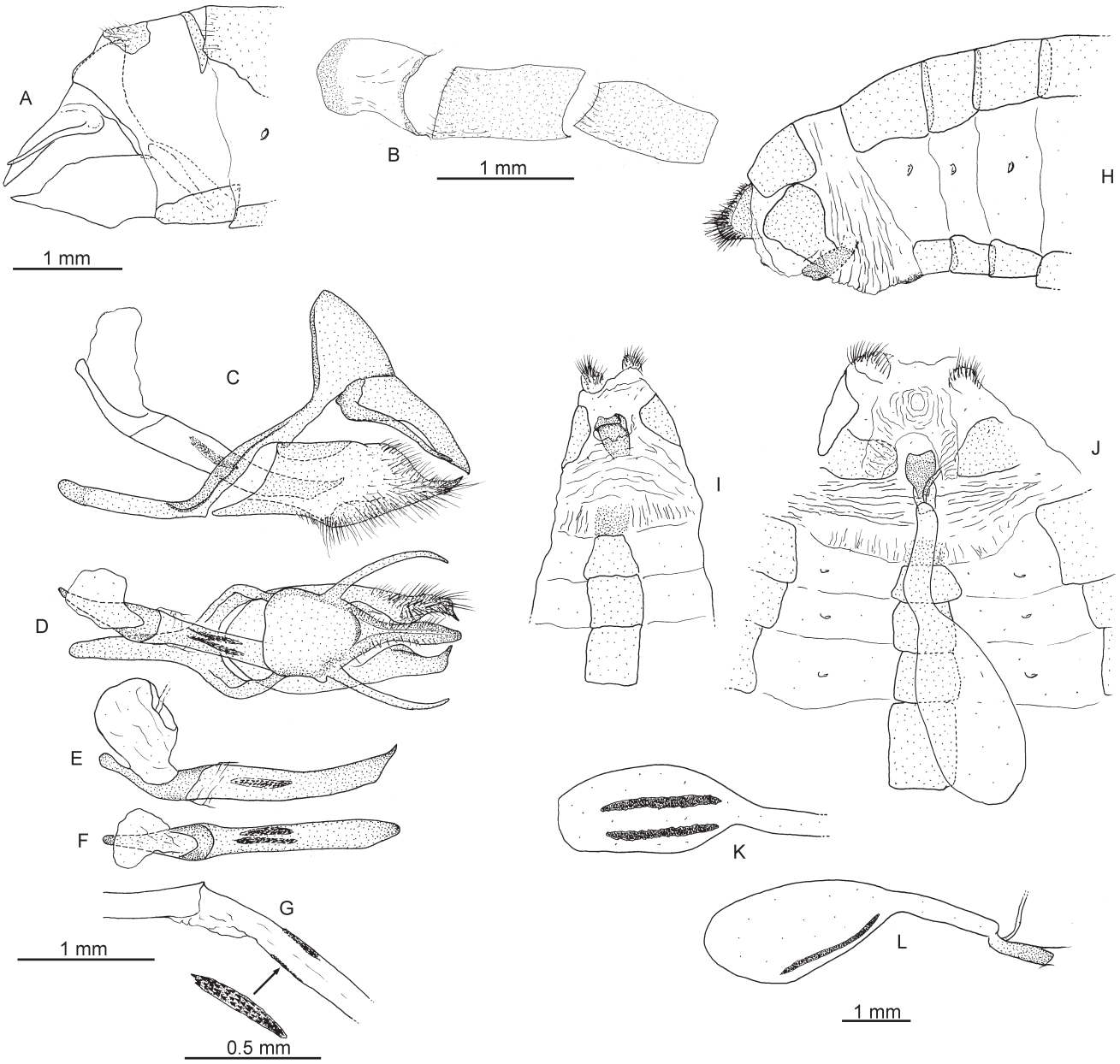

Fig. 2. A-G, *Erichthodes eremita* **n. sp.**, male genitalia (HT, dissection KW-17-19). **A.** Genitalia *in situ* at posterior tip of abdomen, lateral view. **B**. Dorsal view of posterior tip of abdomen. **C.** Genitalia, lateral view. **D**. Genitalia, dorsal view, setae omitted from left valva to better indicate valva shape. **E**. Aedeagus, lateral view. **F**. Aedeagus, dorsal view. **G.** Everted vesica, lateral view, with perpendicular view of ventral cornutal patch. **H-L,** *Erichthodes eremita* **n. sp.**, female genitalia (dissection KW-17-23). **H.** Abdomen posterior tip, lateral view. **I**. Abdomen posterior tip, ventral view. **J**. Genitalia, dorsal view. **K**. Corpus bursae, view perpendicular to signa. **L**. Corpus bursae, ductus bursae and ductus seminalis, lateral view.

Taxonomy: This species is described here in the genus *Erichthodes* Forster, 1964, based on DNA sequence data that consistently place it as sister to *E. julia* (Espeland *et al*., unpubl. data; Fig. 4). However, molecular and morphological support for a monophyletic *Erichthodes*, with type species *E. antonina* (C. Felder & R. Felder, 1867), is weak, and a new genus might therefore be needed for *E. eremita* and *E. julia*, perhaps also including *E. jovita* (see discussion under Diagnosis above). The broader clade containing *E. eremita*, *E. julia*, *E. jovita*, *E. antonina* and related genera is under study by M. Marín and collaborators to resolve these taxonomic issues. This species was listed as '*Yphthimoides* n. sp.' by Lamas (1997, 2004) and was figured by Piñas (2004: 19, figs. 93, 94) as '*Taygetis blanda*' (=*Harjesia blanda*), an unrelated but phenotypically somewhat similar species that also occurs in Ecuador and Peru.

Distribution and natural history: This species is known only from the upper Río Zamora valley in southeastern Ecuador, and in the nearby Cordillera del Cóndor, where it occurs on both Ecuadorian and Peruvian sides of that mountain range (Fig. 3A). As currently known, it is allopatric with respect to its apparent closest relatives, *E. jovita* from central Colombia and *E. julia* from central Peru to Bolivia. In addition to its restricted geographic range, *E. eremita* is also a habitat specialist.

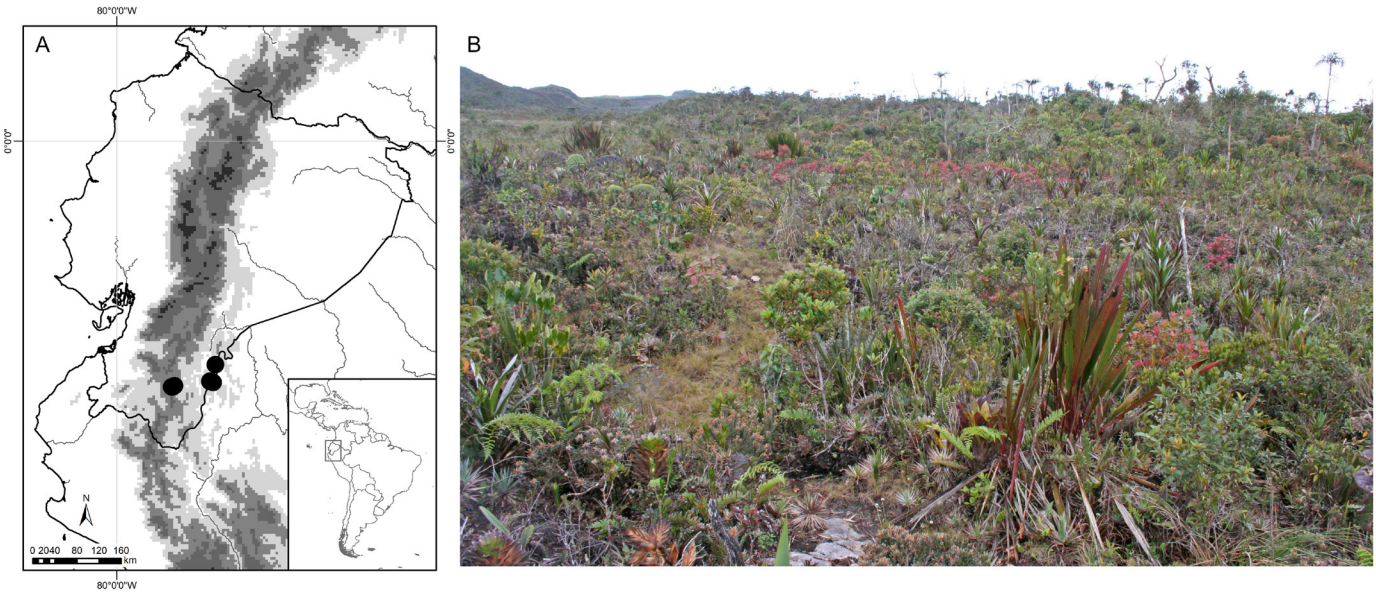

Fig. 3. A, distribution records for *Erichthodes eremita* **n. sp. B**, top of plateau above Destacamento Paquisha Alto (Ecuador, Zamora-Chinchipe), type locality for *E. eremita*.

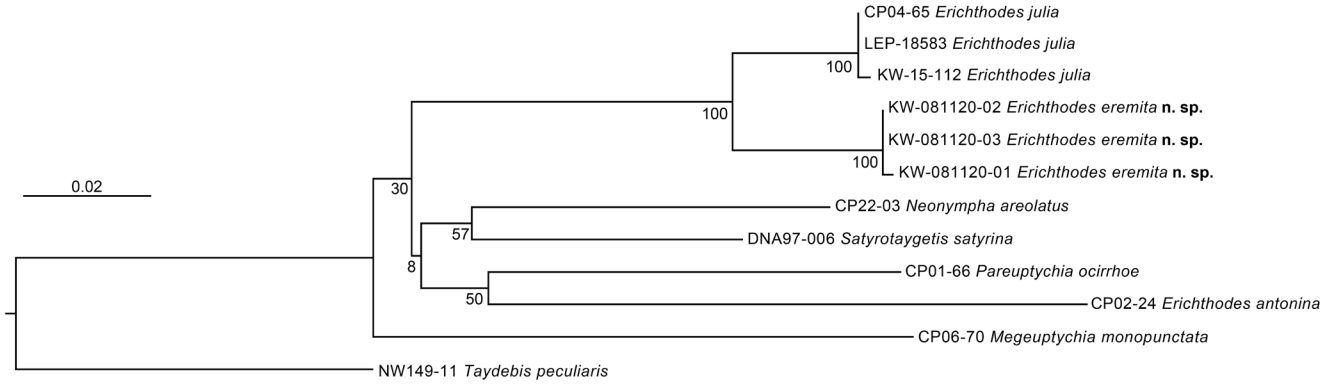

Fig. 4. Maximum likelihood tree for *Erichthodes* and other close relatives with bootstrap support inferred using IQ-TREE, based on sequences of four genes available from Genbank and newly generated for this study (Table 2). The tree was extracted from a much larger dataset for Euptychiina (Espeland *et al*., unpubl. data).

Although the species has been recorded from 1970-2500 m, it occurs only on or near the tops of ridges and mountains where nutrient-poor soils result in a covering of stunted, 'elfin' forest and/or montane scrub (Fig. 3B), and the species has not been found inside tall cloud forest on nearby slopes at similar elevations. For example, despite spending several months conducting an intensive survey of cloud forest butterflies at the Reserva Arcoiris beside the Loja-Zamora road in southern Ecuador, the species was not recorded, yet walking 20 m off the same road onto a ridge covered with elfin scrub resulted in the collection of several individuals. Males have been recorded attracted to rotting fish placed in traps 1 m above the ground, and both sexes were found flying within 1 m of the ground in open areas and along trails.

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LITERATURE CITED

Comstock, J. H., Needham, J. G. 1918. The wings of insects. *American Naturalist* 32: 231-257.

Eitschberger, U., Racheli, T. 1998. *Catasticta* studies (Lepidoptera: Pieridae). *Neue entomologische Nachrichten* 41: 4-94.

Hall, J. P. W., Willmott, K. R. 1995. Five new species and a new genus of riodinid from the cloud forests of eastern Ecuador (Lepidoptera: Riodinidae). *Tropical Lepidoptera* 6(2): 131-135.

Hebert, P. D. N., Cywinska, A., Ball, S. L., deWaard, J. R. 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B* 270: 596-599.

Huertas, B., Lamas, G., Fagua, G., Mallet, J., Nakahara, S., Willmott, K. R. 2016. A remarkable new butterfly species from western Amazonia (Lepidoptera: Nymphalidae: Satyrinae). *Conservación Colombiana* 24: 5-11.

Klots, A. B. 1956. *Lepidoptera*, pp. 115-130. *In*: Tuxen, S. L. (Ed.), *Taxonomist's glossary of genitalia in insects*. Munkssgard, Copenhagen.

Lamas, G. 1997. Lepidoptera of the Cordillera del Cóndor, pp. 90-98, 212-230. *In*: Schulenberg, T. S., Awbrey, K. (Eds.), The Cordillera del Cóndor Region of Ecuador and Peru: A biological assessment. *RAP Working Papers* 7: 1-231.

Lamas, G. 2004. *Nymphalidae. Satyrinae. Tribe Satyrini. Subtribe Euptychiina*, pp. 217-223. *In*: Lamas, G. (Ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea*. *In*: Heppner, J. B. (Ed.), *Atlas of Neotropical Lepidoptera. Volume 5A*. Gainesville, Association for Tropical Lepidoptera, Scientific Publishers.

Marín, M. A., Peña, C., Uribe, S. I., Freitas, A. V. L. 2017. Morphology agrees with molecular data: phylogenetic affinities of Euptychiina butterflies (Nymphalidae: Satyrinae). *Systematic Entomology* 42(4): 768-785.

Monteiro, A., Pierce, N. E. 2001. Phylogeny of *Bicyclus* (Lepidoptera: Nymphalidae) inferred from COI, COII and EF-1α gene sequences. *Molecular Phylogenetics and Evolution* 18(2): 264-281.

Murray, D. L., Prowell, D. P. 2005. Molecular phylogenetics and evolutionary history of the Neotropical satyrine subtribe Euptychiina (Nymphalidae: Satyrinae). *Molecular Phylogenetics and Evolution* 34(1): 67-80.

Nakahara, S., Hall, J. P. W., Lamas, G., Willmott, K. R. 2015a. Seven new species and one new subspecies of *Euptychia* Hübner, 1818 (Lepidoptera: Nymphalidae: Satyrinae) from the tropical Andes. *Tropical Lepidoptera Research* 25(2): 63-79.

Nakahara, S., Janzen, D. H., Hallwachs, W., Espeland, M. 2015b. Description of a new genus for *Euptychia hilara* (C. Felder & R. Felder, 1867) (Lepidoptera: Nymphalidae: Satyrinae). *Zootaxa* 4012(3): 525-541.

Nakahara, S., Willmott, K. R., Mielke, O. H. H., Schwartz, J., Zacca, T., Espeland, M., Lamas, G. 2018. Seven new taxa from the butterfly subtribe Euptychiina (Lepidoptera: Nymphalidae: Satyrinae) with revisional notes on *Harjesia* Forster, 1964 and *Pseudeuptychia* Forster, 1964. *Insecta Mundi*, in press.

Neild, A. F. E., Nakahara, S., Zacca, T., Fratello, S. A., Lamas, G., Le Crom, J.-F., Dolibaina, D. R., Dias, F. M. S., Casagrande, M. M., Mielke, O. H. H., Espeland, M. 2015. Two new species of *Euptychia* Hübner, 1818 from the Upper Amazon basin (Lepidoptera, Nymphalidae, Satyrinae). *ZooKeys* 541: 87-108.

Peña, C., Lamas, G. 2005. Revision of the butterfly genus *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae, Satyrinae). *Revista Peruana de Biología* 12(1): 5-48.

Peña, C., Nylin, S., Freitas, A. V. L., Wahlberg, N. 2010. Biogeographic history of the butterfly subtribe Euptychiina (Lepidoptera, Nymphalidae, Satyrinae). *Zoologica Scripta* 39(3): 243-258.

Piñas, F. 2004. *Mariposas del Ecuador. Vol. 11b. Familia: Nymphalidae. Subfamilia: Satyrinae.* Quito, Compañía de Jesús. v + 90 pp.

Pyrcz, T. W. 2004. Pronophiline butterflies of the highlands of Chachapoyas in northern Peru: faunal survey, diversity and distribution patterns (Lepidoptera, Nymphalidae, Satyrinae). *Genus* 15(4): 455-622.

Radford, J., Willmott, K. R. 2013. A distinctive new subspecies of *Catasticta poujadei* from the Cordillera del Cóndor in eastern Ecuador (Lepidoptera: Pieridae: Pierinae). *Tropical Lepidoptera Research* 23(2): 86-91.

Scoble, M. 1992. *The Lepidoptera: Form, Function and Diversity*. London, Oxford University Press. ix + 352 pp.

Salazar, J. A., Constantino, L. M. 1993. Descripción de cuatro nuevas especies de Riodininae para Colombia (Lepidoptera: Lycaenidae). *Shilap* 21(81): 13-18.

Wahlberg, N., Wheat, C. W. 2008. Genomic outposts serve the phylogenomic pioneers: designing novel nuclear markers for genomic DNA extractions of Lepidoptera. *Systematic Biology* 57(2): 231-242.

Warren, A. D., Davis, K. J., Stangeland, E. M., Pelham, J. P., Grishin, N. V. 2018. *Illustrated Lists of American Butterflies (North and South America) 21-XI-2017.* www.butterfliesofamerica.com, accessed 8th May 2018.

Willmott, K. R., Hall, J. P. W., Lamas, G. 2001. Systematics of *Hypanartia* (Lepidoptera: Nymphalidae: Nymphalinae), with a test for geographical speciation mechanisms in the Andes. *Systematic Entomology* 26(4): 369-399.

Zacca, T., Siewert, R. R., Mielke, O. H. H., Casagrande, M. M. 2014. A new species of *Magneuptychia* Forster, 1964 (Lepidoptera: Nymphalidae: Satyrinae) from Brazilian savanna. *Zootaxa* 3795(1): 71-78.