

A new species and eight new subspecies of high elevation *Actinote* from Colombia, Ecuador and Peru (Nymphalidae, Heliconiinae, Acraeini)

Keith R. Willmott^{1,2}, Gerardo Lamas³, Jason P. W. Hall⁴, Pierre Boyer⁵, Tomasz Pyrcz⁶ and Klaudia Florczyk⁷

1. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, Florida, USA; kwillmott@flmnh.ufl.edu; 2. Instituto Nacional de Biodiversidad, Quito, Ecuador; 3. Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Perú; 4. Department of Entomology, National Museum of Natural History, Smithsonian Institution, Washington, DC 20560-0127, USA; 5. Le Puy Sainte Réparate, France; 6. Department of Invertebrate Evolution, Institute of Zoology and Biomedical Research, Jagiellonian University, Gronostajowa 9, 30-387 Kraków, Poland; 7. Nature Education Centre, Jagiellonian University, Gronostajowa 5, 30-387 Kraków, Poland

Date of issue online: 27 October 2023

Zoobank Registered: urn:lsid:zoobank.org:pub:426852BA-EA23-4F2D-BBCD-25968FC91D69

Electronic copies (ISSN 2575-9256) in PDF format at: <https://journals.flvc.org/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.10027609.

© The author(s). This is an open access article distributed under the Creative Commons license CC BY-NC 4.0 (<https://creativecommons.org/licenses/by-nc/4.0/>).

Abstract: We describe one new species and eight new subspecies of high elevation *Actinote* Hübner, [1819] (Nymphalidae, Heliconiinae, Acraeini) from Colombia, Ecuador and Peru: *Actinote pyrrhosticta* Lamas, Willmott & Hall, **n. sp.**, *Actinote pyrrhosticta quintecocha* Lamas & Willmott, **n. ssp.**, *Actinote pyrrhosticta apurimac* Lamas & Willmott, **n. ssp.**, *Actinote pyrrhosticta alfamayo* Lamas & Willmott, **n. ssp.**, *Actinote eresia albesia* Lamas & Willmott, **n. ssp.**, *Actinote eresia canyaris* Pyrcz & Lamas, **n. ssp.**, *Actinote hilaris arcoiris* Willmott & Hall, **n. ssp.**, *Actinote hilaris sourakovi* Willmott & Lamas, **n. ssp.**, and *Actinote trinacria alegria* Boyer & Willmott, **n. ssp.** We treat *Actinote binghamae* Dyar, 1913 as a new synonym of *Actinote eresia eresina* (Hoffer, 1874) **n. syn.**, and treat *Altinote santamarta* Winhard, 2017 as a subspecies, *Actinote trinacria santamarta* **rev. stat.** We illustrate adult specimens of all described taxa of *A. pyrrhosticta* **n. sp.**, *A. eresia* (C. Felder & R. Felder, 1862) and *A. hilaris* Jordan, 1910, and representatives of *A. trinacria* (C. Felder & R. Felder, 1862). We also provide illustrations of male and female genitalia for select taxa, distribution maps, and a revised, annotated synonymic list for all four species.

Resumen: En este trabajo describimos una especie nueva y ocho nuevas subspecies altoandinas de *Actinote* Hübner, [1819] (Nymphalidae, Heliconiinae, Acraeini) encontradas en Colombia, Ecuador y Perú: *Actinote pyrrhosticta* Lamas, Willmott & Hall, **n. sp.**, *Actinote pyrrhosticta quintecocha* Lamas & Willmott, **n. ssp.**, *Actinote pyrrhosticta apurimac* Lamas & Willmott, **n. ssp.**, *Actinote pyrrhosticta alfamayo* Lamas & Willmott, **n. ssp.**, *Actinote eresia albesia* Lamas & Willmott, **n. ssp.**, *Actinote eresia canyaris* Pyrcz & Lamas, **n. ssp.**, *Actinote hilaris arcoiris* Willmott & Hall, **n. ssp.**, *Actinote hilaris sourakovi* Willmott & Lamas, **n. ssp.**, y *Actinote trinacria alegria* Boyer & Willmott, **n. ssp.** Consideramos a *Actinote binghamae* Dyar, 1913 como un nuevo sinónimo de *Actinote eresia eresina* (Hoffer, 1874) **n. syn.**, y a *Altinote santamarta* Winhard, 2017 como una subespecie, *Actinote trinacria santamarta* **rev. stat.** Además, ilustramos especímenes adultos de todos los taxa descritos de *A. pyrrhosticta* **n. sp.**, *A. eresia* (C. Felder & R. Felder, 1862) y *A. hilaris* Jordan, 1910, y algunos representantes de *A. trinacria* (C. Felder & R. Felder, 1862). También presentamos ilustraciones de las genitales masculinas y femeninas de algunos taxones seleccionados, junto con mapas de distribución, y una lista de sinonimos revisada para las cuatro especies.

Key words: Andes; COI barcode; morphology; taxonomy.

INTRODUCTION

The Neotropical Acraeini comprises over 50 described species and a half-dozen or more known, undescribed species (Lamas, 2004; Francini *et al.*, 2004; Paluch *et al.*, 2006; Neild, 2008; Willmott *et al.*, 2009; Winhard, 2017; Willmott *et al.*, 2017; Freitas *et al.*, 2018). The generic classification of these butterflies has remained remarkably unstable in recent decades, with Pierre (1987) placing all Neotropical species within the pantropical genus *Acraea* Fabricius, 1807, and Lamas (2004) recognizing three genera for these species, *Actinote* Hübner,

[1819], *Altinote* Potts, 1943, and *Abananote* Potts, 1943. Silva-Brandão *et al.* (2008) showed that neither *Altinote* nor *Abananote* was monophyletic and suggested treating all Neotropical species within a single genus, *Actinote*, a decision followed by Willmott *et al.* (2017) and Carvalho *et al.* (2021; albeit as a subgenus of *Acraea*), and formalized by Zhang *et al.* (2021) with the synonymy of Potts's generic names and recognition of *Actinote* as the sole genus of American Acraeini (see also Williams & Henning, 2023).

Actinote are relatively large, conspicuous, colorful and slow-flying butterflies, distributed throughout the Neotropics,

mostly in forest habitats, from sea level to 4050 m. Although several species are very common, a number are very rare, and new species continue to be described from the two centers of diversity for the genus, the Atlantic forest (e.g., Francini *et al.*, 2004; Freitas *et al.*, 2018) and the Andes (e.g., Neild, 2008; Willmott *et al.*, 2009; Winhard, 2017; Willmott *et al.*, 2017). The uppermost forests of the Andes, in particular, contain several species that are poorly represented in most collections, with a number of distinctive populations scattered throughout this tropical montane region. To contribute to ongoing faunistic studies in the Andes, we here describe a new species and eight new subspecies of high Andean *Actinote*.

MATERIALS AND METHODS

Actinote specimens and information on distribution and natural history were collected by the authors and colleagues throughout Ecuador and Peru, and in numerous collections, over many years. Morphological and molecular methods follow Willmott *et al.* (2017), and are described only briefly here. The following collection acronyms are used: AWLW: Allan & Lesley Wolhuter collection, United Kingdom; CAS: California Academy of Sciences, San Francisco, USA; HAWA: Haydon Warren-Gash collection, Pressac, France; INABIO: Instituto Nacional de Biodiversidad, Quito, Ecuador; JEPE: Jean-Claude Petit collection, Ducy, France; MGCL: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, USA; MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; CEPUI: Nature Education Centre, Jagiellonian University (formerly Zoological Museum, MZUJ); NHMUK: Natural History Museum, London, UK; PIBO: Pierre Boyer collection, Le Puy Sainte Réparate, France; RCCP: Research Collection of Carlos Prieto, Cali, Colombia; USNM: National Museum of Natural History, Smithsonian Institution, Washington, DC, USA.

Adult abdomens were soaked in hot 10% KOH for 10-15 minutes, dissected and subsequently stored in glycerine. Body morphology and dissections were studied using a binocular microscope at up to 100x magnification. The terminology for male genitalic and abdominal structures follows Scoble (1992), and nomenclature for venation follows Comstock & Needham (1898). We use the abbreviations DFW, VFW, DHW and VHW for dorsal and ventral forewing and hindwing, and HT and LT for Holotype and Lectotype, respectively.

For most specimens, genomic DNA was extracted from legs removed from *Actinote* 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 50 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), using primers and methods described by Willmott *et al.* (2017). Single strands of the PCR products were sequenced by the University of Florida's Interdisciplinary Center for Biotechnology Research Sanger Sequencing Group or by Eurofins Genomics, using the same primers as in the PCR. Two new sequences were obtained using methods described by Kawahara *et al.* (2023).

Where necessary, fragments were assembled into composite sequences and all 18 new sequences were aligned using BioEdit v. 7.1.3 (Hall, 1999), with 26 additional sequences obtained from GenBank (Appendix 1). The final aligned sequences were of length 633 bp, and new sequences are deposited in GenBank (Appendix 1). To examine relationships among taxa we conducted a phylogenetic analysis using the Maximum Likelihood (ML) method in MEGA11 (Tamura *et al.*, 2021). The best substitution model (lowest Bayesian Information Criterion score) was TN93+G+I, and this model was used in the ML search with 100 bootstrap replicates to estimate branch support. The tree was rooted with a sequence from *Telchinia issoria* (Hübner, [1819]), a member of the clade sister to *Actinote* (Carvalho *et al.*, 2021). We also calculated mean within-group and between-group genetic divergence using MEGA11, with partial deletion of missing data with 90% cut-off, p-distance as the substitution model, and other default options.

RESULTS AND DISCUSSION

DNA barcodes and relationships among *Actinote* taxa

The ML analysis of COI barcode sequences (Fig. 1) recovered three main clades as in Carvalho *et al.* (2021), with strong support (100% bootstrap) for a clade containing *A. pyrrhosticta* **n. sp.**, *A. eresia* (C. Felder & R. Felder, 1862) and *A. hilaris* Jordan, 1910, and with weak support (57% bootstrap) for *A. pyrrhosticta* being sister to the other two species. Although the relationships among the three main clades differ from those in Carvalho *et al.* (2021), in which *A. eresia*+*A. hilaris* were placed as sister to all other *Actinote*, this discrepancy likely reflects the lack of nuclear gene data in our analysis that would be needed to confidently resolve deeper nodes. In terms of species relationships, in our analysis *Actinote eresia canyaris* **n. ssp.** formed a strongly supported clade with *A. eresia eresia* and *A. eresia leptogramma* Jordan, 1913 (92% bootstrap), and *A. hilaris arcoiris* **n. ssp.** and *A. hilaris sourakovi* **n. ssp.** formed a strongly supported clade with *A. hilaris desmiala* Jordan, 1913 (99% bootstrap; the nominate subspecies of *A. hilaris* was not sampled). *Actinote eresia eresina* (Hopffer, 1874) did not form a clade with other *A. eresia*, but instead was moderately well supported as sister to *A. hilaris*, a result discussed below in the annotated checklist.

Taxonomy

Actinote pyrrhosticta Lamas, Willmott & Hall, new species

Figs. 2A-C, 6A,D-H, 9A, 10A-D, 11A,B

Diagnosis and identification: Analysis of multiple nuclear and mitochondrial gene sequences showed that *A. eresia* and *A. hilaris* form a clade that is sister to all other Neotropical Acraeini (Carvalho *et al.*, 2021; Chazot *et al.*, 2021). Our analysis of COI sequence data shows that *A. pyrrhosticta* **n. sp.** is also a member of this clade, and sister to these two species (Fig. 1). These three species share a distinctive VHW pattern, with a thin, only slightly kinked brown discal line bordered distally by a pale postdiscal band (Figs. 2-5). The definition of the discal line and the expression of the pale postdiscal band are rather variable,

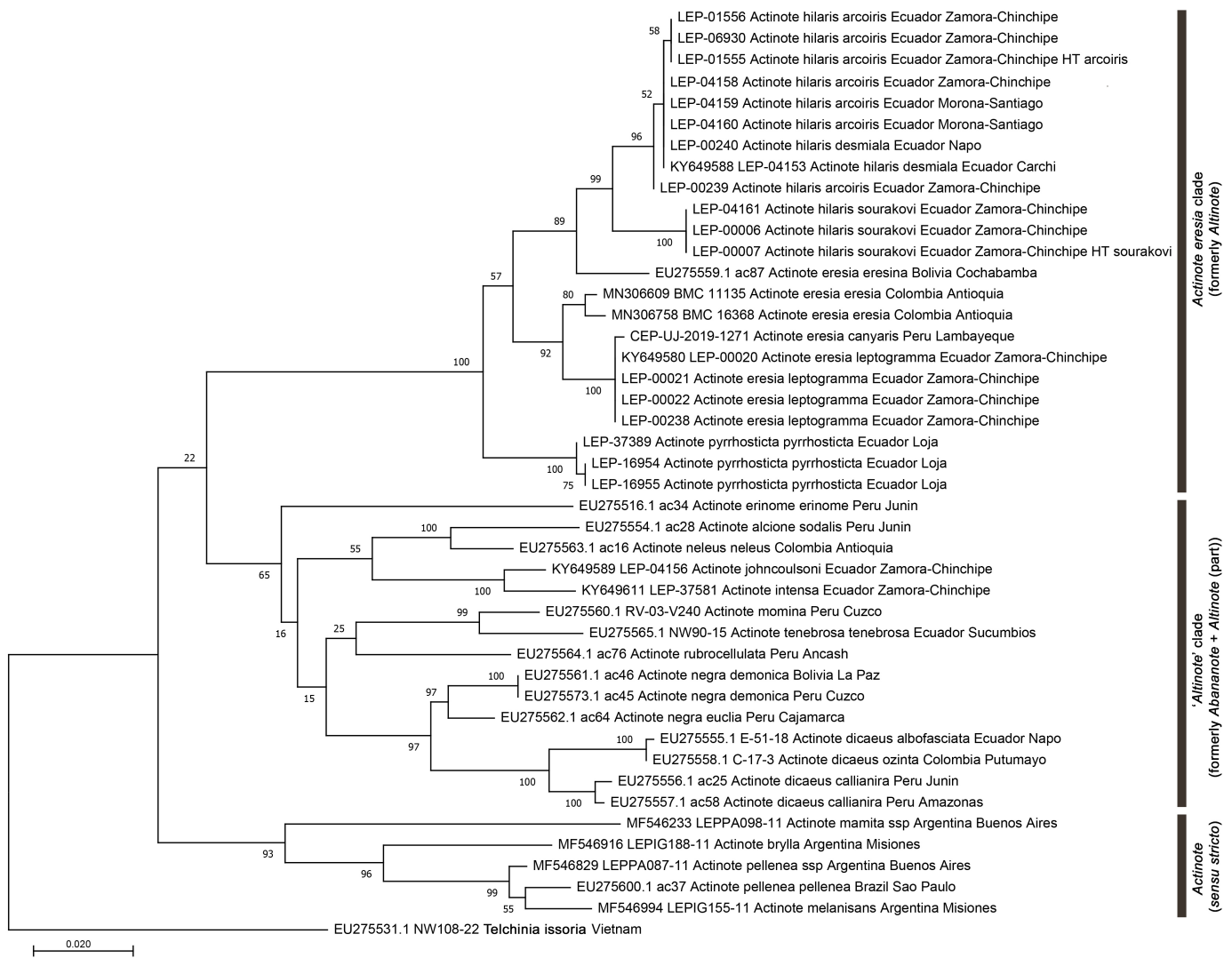


Figure 1. Maximum-Likelihood tree for the *Actinote eresia* clade and exemplar species of *Actinote* based on 663 bp of COI (barcode region). Numbers by nodes indicate bootstrap support based on 100 replicates. Black vertical bars at right indicate the three main clades of *Actinote* referred to in the text.

but together they nevertheless enable ready recognition of almost all specimens of these three species, in comparison with all other Neotropical Acraeini. Perhaps the most superficially similar species are *A. rubrocellulata* Hayward, 1960 (central Peru) and *A. mamita* (Burmeister, 1861) (Atlantic forest), but the former lacks the brown VHW discal line and pale postdiscal band, while the latter has a brown VHW discal line but it is more strongly kinked, as in other *Actinote sensu* Lamas (2004), and lacks the pale postdiscal band. Both *A. rubrocellulata* and *A. mamita* were included in recent molecular phylogenetic studies (Carvalho *et al.*, 2021) and were not recovered as being closely related to the *A. eresia* clade.

Actinote pyrrhosticta n. sp. can be consistently distinguished from *A. eresia* by the following characters: **1)** The black 'S'-shaped discocellular bar on the FW extends as a continuous line through the base of vein Cu_2 to the anal margin; in *A. eresia*, the line is more distally placed in the discal cell, and the black marking in cell 2A- Cu_2 is reduced to a small spot or absent, not meeting the discocellular line (Figs. 2-4). **2)** The

black postdiscal line in VFW cell Cu_2-Cu_1 in *A. pyrrhosticta* is placed directly in a line with that in cell Cu_1-M_3 , while in *A. eresia* it is displaced distally or absent; overall, the curving black postdiscal line on the VFW of *A. pyrrhosticta* is more basally positioned than it is in *A. eresia* (Figs. 2-4). **3)** The distinct block of pale scaling in *A. pyrrhosticta* at the base of the VHW in cell $Rs-Sc+R_1$ contrasts with the darker coloring of the anterior half of the discal cell; in *A. eresia*, the anterior half of the discal cell is similarly pale-colored. In *A. hilaris*, the black FW postdiscal line and cell-end bar are fused, forming a broad black band in the middle of the wing (Figs. 2-5). **4)** A series of orange dorsolateral spots is present along the abdomen in *A. pyrrhosticta* (a single lateral spot in the middle of each tergite, e.g. Figs. 2J, 11A,F,H,I), which is absent or, at most, barely visible in only some tergites (e.g., *A. e. eresia*) in the two related species (e.g., Fig. 11J,L). **5)** The sphragis of *A. pyrrhosticta* barely protrudes beyond the ventral edge of the abdomen (Fig. 2J), in contrast to the protruding sphragis of *A. eresia* (Fig. 2K) and *A. hilaris* (Fig. 2L). The tapering male genitalic valva of *A.*

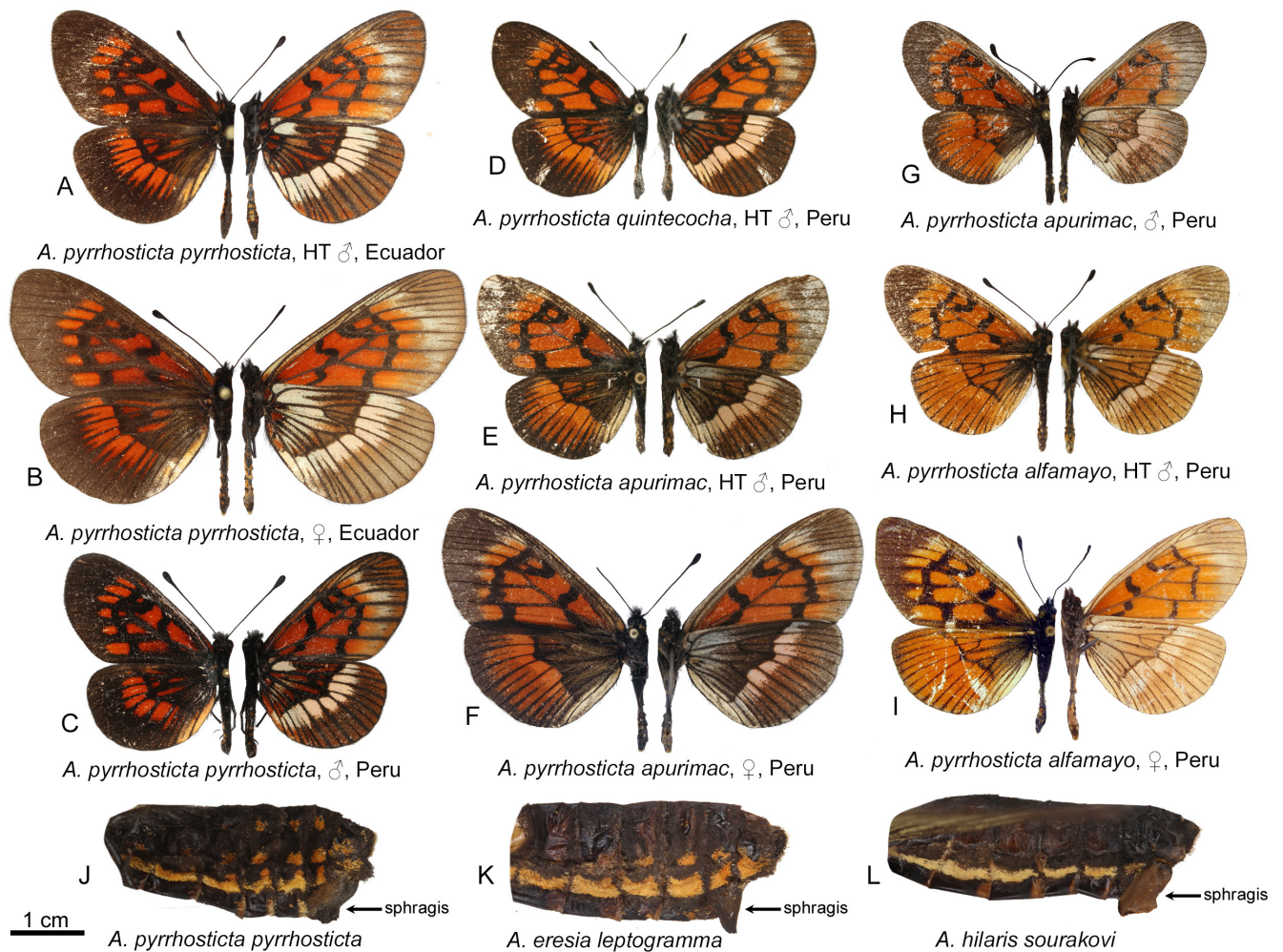


Figure 2. *Actinote* specimens (A-F), left half dorsal surface, right half ventral surface. **A)** *A. pyrrhosticta* n. sp., HT ♂, Ecuador, Loja, km 13.2 Jimbura-San Andrés rd. (FLMNH-MGCL-209919); **B)** *A. pyrrhosticta* n. sp., ♀, Ecuador, Loja, km 13.2 Jimbura-San Andrés rd. (FLMNH-MGCL-209929); **C)** *A. pyrrhosticta* n. sp., ♂, Peru, Cajamarca, N El Pargo (MZUJ); **D)** *A. pyrrhosticta quintecocha* n. ssp., HT ♂, Peru, Amazonas, Quintecocha (MUSM-ENT-007883); **E)** *A. pyrrhosticta apurimac* n. ssp., HT ♂, Peru, Apurímac, Laguna Angascocha (MUSM-ENT-007885); **F)** *A. pyrrhosticta apurimac* n. ssp., ♀, Peru, Apurímac, Laguna Uspacocha (MUSM); **G)** *A. pyrrhosticta apurimac* n. ssp., ♂, Peru, Apurímac, vía Huanipaca km 8 (MZUJ); **H)** *A. pyrrhosticta alfamayo* n. ssp., HT ♂, Peru, Cuzco, Río Santa María (MUSM-ENT-007887); **I)** *A. pyrrhosticta alfamayo* n. ssp., ♀, Peru, Cuzco, ‘Kiteni’, (PIBO). *Actinote* ♀ abdomen, lateral view (J-L). **J)** *A. pyrrhosticta pyrrhosticta* (FLMNH-MGCL-109926); **K)** *A. eresia leptogramma* (FLMNH-MGCL-119804); **L)** *A. hilaris sourakovi* (FLMNH-MGCL-145578).

pyrrhosticta (Fig. 6A-C) is distinct from the broader, blunter valva of *A. eresia leptogramma* (Fig. 7B), but similar to that of *A. eresia eresina* (Fig. 7C) and *A. hilaris* (Fig. 7E,F). Other characters distinguishing subspecies of *A. pyrrhosticta* from those of *A. eresia* occurring in the same region are discussed under the accounts of each taxon.

Description: MALE (Fig. 2A,C): Forewing length of HT 24.5 mm (23-25 mm, mean 23.9 mm, n=10). *Wings:* as illustrated. VHW with long, black hair-like scales (‘bristles’ of Jordan (1913) and Potts (1943)) along veins, including location of vestigial vein 1A (vein visible in distal fifth of wing). *Head:* eyes black, bare; antennae black with sparse black needle-like scales dorsally, 35 antennomeres with terminal 9 antennomeres comprising club; labial palpi with sparse, long, black, hair-like scales ventrally (much shorter, similar scales dorsally) on basal and middle segment, sparse black scales laterally on middle and terminal segment; top of head black, frons with sparse, long, black, hair-like scales, two tufts of orange hair-like scales dorsolaterally on patagia. *Thorax:* black with sparse, long black and brown hair-like scales, except ventrally

with lateral orange spot on meso- and metathorax approximately in region of epimeron and katepisternum, forelegs, mid- and hindlegs black. *Abdomen:* dorsal surface black except for orange spot in middle of each tergite laterally, ventral surface black except for spots of orange scaling in middle of each sternite in anterior half, laterally with line of orange scaling dorsal of sternites and orange dashes ventral of tergites. *Genitalia* (Fig. 6A): as illustrated, notable features include broad-based, upwardly tapering valva with indented basal edge, and relatively broad aedeagus. Juxta is a rather elongate, approximately ‘V’-shaped plate.

FEMALE: (Fig. 2B,J): Forewing length mean 28.1 mm (26.5-29.5 mm, n=7). *Wings:* similar to male except FW slightly broader. *Dorsal surface:* similar to male. *Ventral surface:* similar to male except whitish scaling in basal third of VHW more extensive, reaching posteriorly to vein 3A. *Head, thorax, abdomen:* similar to male in coloration. Out of six examined females, all possessed a sphragis, a curving, rectangular plate closely appressed to tip of abdomen, not protruding ventrally beyond terminal sternite (Fig. 2J). *Genitalia* (Fig. 6D-H): Notable features include strongly sclerotized eighth tergite with invaginated antero-ventral corner, lamella antevaginalis forming a roughly U-shaped, curving plate, with a separate, horseshoe-shaped lamella postvaginalis that

protrudes postero-ventrally (Fig. 6E); ductus bursae very short, broad, merging into amorphous, small corpus bursae, similar in size to lamella antevaginalis plus lamella postvaginalis (Fig. 6F), ductus seminalis narrow; subpapillary glands similar in size to papillae anales (Fig. 6G,H).

Types: HOLOTYPE ♂: **ECUADOR:** *Loja:* nr. Amaluza, km 13.2 Jimbura-San Andrés rd., [4°42'32"S,79°26'47"W], 2970 m, (Willmott, K. R., J. I. R., J. C. R.), 12 Jun 2014, [FLMNH-MGCL-209919; LEP-37390; dissection, KW-15-164], (MGCL, to be deposited in INABIO).

PARATYPES (18 ♂, 13 ♀): **ECUADOR:** *Loja:* 'Cordillera Lagunillas, E Jimbura', 2600-3000 m, (Jasinski, A.), 14 May 1998, 1 ♂, (CEPUJ); 'Cordillera Lagunillas, E Jimbura', 3300 m, (Jasinski, A.), 1 ♂, (CEPUJ); nr. Amaluza, km 13.2 Jimbura-San Andrés rd., [4°42'32"S,79°26'47"W], 2900 m, (Willmott, K. R., J. I. R., J. C. R.), 12 Jun 2014, 1 ♂ [FLMNH-MGCL-209921], (MGCL); 'Nord de Laguna Negra, Jimbura-Zumba 3060m', [4°42'32"S,79°26'47"W], 3030 m, (Boyer, P.), 4-6 Aug 2017, 2 ♀, (PIBO), (Petit, J.-C.), 4-6 Aug 2017, 1 ♂, 1 ♀, (JEPE); nr. Amaluza, km 13.2 Jimbura-San Andrés rd., [4°42'32"S,79°26'47"W], (Willmott, K. R., J. I. R., J. C. R.), 12 Jun 2014, 1 ♂ [FLMNH-MGCL-195746], 1 ♂ [FLMNH-MGCL-209918], 1 ♂ [FLMNH-MGCL-209920], 1 ♂ [FLMNH-MGCL-209922], 1 ♂ [FLMNH-MGCL-209923], 1 ♂ [FLMNH-MGCL-209924], 1 ♂ [FLMNH-MGCL-209925], 1 ♀ [FLMNH-MGCL-195747], 1 ♀ [FLMNH-MGCL-209926], 1 ♀ [FLMNH-MGCL-209927], 1 ♀ [FLMNH-MGCL-209928], 1 ♀ [FLMNH-MGCL-209929], 1 ♀ [FLMNH-MGCL-209930], (MGCL), 4 ♂, 2 ♀, (INABIO), (Boyer, P.), 4 Aug 2017, 1 ♀, (PIBO). **PERU:** *Cajamarca:* Llama-'Uambos' [=Huambos], N 'Pargo' [=El Pargo], [6°27'20"S,79°42'W], 3000-3050 m, (Pyrz, T. W.), 9 Jun 2018, 1 ♂, (CEPUJ); *Piura:* Ayabaca, Ramos, [4°42'S,79°28'W], 2900 m, (Zelada, W.), 2 Jun 2007, 1 ♂, (MUSM), 4 Jul 2007, 1 ♀ [dissection, MUSM-2010-11-26-06], (MUSM), 5 Jul 2007, 1 ♂ [dissection, MUSM-2010-11-26-05], (MUSM).

Etymology: The species name is derived from the Latinized Greek words *pyrrhos*, meaning flame-colored, and *stiktos*, meaning spotted, in reference to the coloration of the wings and orange dorsal abdominal spots that are distinctive for this species. The name is treated as a feminine adjective.

Taxonomy and variation: This species is geographically variable and four subspecies are recognized. These four taxa are grouped on the basis of the diagnostic wing and abdominal color pattern characters discussed above, in the absence of molecular data for all but the nominate subspecies, and the lack of clear morphological differences to separate *A. eresia* from *A. pyrrhosticta* n. sp. The three species in the *A. eresia* clade are broadly sympatric from southern Ecuador to southern Peru, but they appear typically to replace one another from lower to higher elevations in the order *A. hilaris*, *A. eresia*, and *A. pyrrhosticta*, and are rarely collected in microsympatry.

DNA sequence data would be useful to test the taxonomic hypothesis proposed here, given the large gap between the currently known locations of *A. pyrrhosticta* in southern Ecuador and northern Peru, and southern Peru (Fig. 9A). That gap seems most likely to represent a sampling artifact resulting from the rarity and restricted elevational range of this species. Mean sequence divergence within sampled *A. pyrrhosticta* was 0.1%, with mean divergence between *A. pyrrhosticta* and *A. eresia* being 3.6%, and between *A. pyrrhosticta* and *A. hilaris* being 4.5%.

No notable differences were observed between the genitalia of the male holotype from Ecuador and a dissected specimen from Peru (MUSM-2010-11-26-05).

Distribution and natural history: The nominate subspecies is known from the western slope of the Andes in extreme southern Ecuador, within a few km of the Peru border, to northwestern Peru (Cajamarca, Piura) (Fig. 9A). The taxon was first collected in Ecuador by A. Jasinski, during his pioneering trips to the Jimbura-San Andrés road (e.g., Jasinski, 1996, 1998a,b), but his two specimens, now in the CEPUJ, were labeled with imprecise data. We made a number of visits to the same road before finally observing the species flying along the edge of undisturbed forest from 2900-3030 m on the west Andean slope. On 12 June, 2014, both sexes were observed in approximately equal numbers, flying in the vicinity of a small stream (Fig. 10A) on a sunny morning from 10:20-11:30. Individuals of both sexes were observed flying over the low forest canopy and repeatedly descending to 1-2 m above the ground, with males occasionally landing on the ground. A pair was observed *in copula* from 11:20 to 15:00, resting on the ground on rocks along the stream and road edge (Fig. 11A,B); additional males and females were observed to fly frequently down to within 0.5 m of the mating pair before flying off. In August 2017, PB observed this species at the same stream, in a short period of bright sun at 13:30. Several individuals were seen flying over the canopy, and two females were observed resting near water. The species was only seen during a few minutes with bright sun and was not abundant, and was neither observed subsequently, nor seen again during visits to the stream over a 4-5 day period.

The lack of previous observations coupled with the abundance of the species during our observations on 12 June 2014, when multiple individuals were visible at any one time, are consistent with a synchronous emergence of adults from gregarious immature stages along with a relatively short adult life span (see also notes under *A. pyrrhosticta apurimac* n. ssp.).

Actinote pyrrhosticta quintecocha Lamas & Willmott, new subspecies

Figs. 2D, 6B, 9A

Diagnosis and identification: This taxon differs from the nominate in having paler, less reddish orange dorsal markings, which are also expanded in each cell, with a notably thin black postdiscal line on the DHW (Fig. 2D). The DFW orange marking at the base of cell Cu_2 - Cu_1 is broader and the similarly colored postdiscal markings in this cell and cell Cu_1 - M_3 are reduced or absent.

Description: MALE (Fig. 2D): Forewing length 21.0 mm (n=1). *Wings:* as illustrated. *Head, thorax, abdomen* as in nominate subspecies. *Genitalia* (Fig. 6B): similar to nominate subspecies.

FEMALE: unknown.

Types: HOLOTYPE ♂: **PERU:** *Amazonas:* Quintecocha, [6°51'30"S,77°42'W], 3150 m, (Gallusser, S.), 20 Nov 2003, [MUSM-ENT-007883], (MUSM).

PARATYPES (3 ♂): **PERU:** *Amazonas:* Quintecocha, [6°51-52'S,77°42'W], 3150 m, (Gallusser, S.), 20 Nov 2003, 1 ♂ [MUSM-ENT-007884; dissection, MUSM-2010-11-26-07], (MUSM); same collection data, but 20 Sep 2004, 2 ♂, (MUSM).

Etymology: The name is derived from that of the type locality, and it is treated as a feminine noun in apposition.

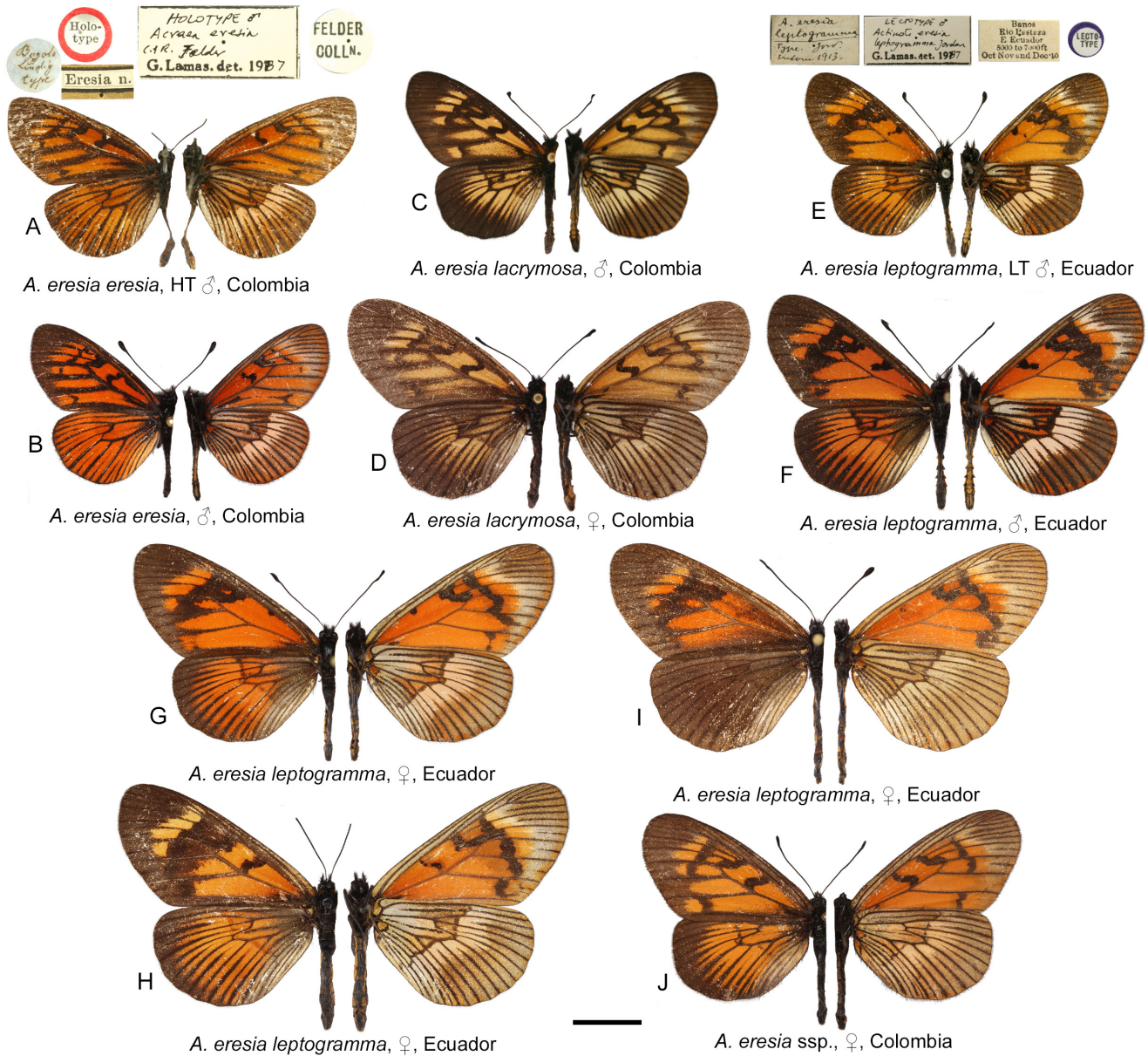


Figure 3. *Actinote eresia* specimens, left half dorsal surface, right half ventral surface. **A)** *A. eresia eresia*, HT ♂, Colombia, ‘Bogotá’ (NHMUK); **B)** *A. eresia eresia*, ♂, Colombia, Cundinamarca, La Floresta (CEPUJ); **C)** *A. eresia lacrymosa*, ♂, Colombia, Caldas, Manizales (MUSM); **D)** *A. eresia lacrymosa*, ♀, Colombia, Caldas, Manizales (MUSM); **E)** *A. eresia leptogramma*, LT ♂, Ecuador, Tungurahua, Baños (NHMUK); **F)** *A. eresia leptogramma*, ♂, Ecuador, Zamora-Chinchipe, Quebrada Navidades (FLMNH-MGCL-113370); **G)** *A. eresia leptogramma*, ♀, Ecuador, Zamora-Chinchipe, Quebrada Navidades (FLMNH-MGCL-113360); **H)** *A. eresia leptogramma*, ♀, Ecuador, Zamora-Chinchipe, Casa Simpson (JR-07-2A); **I)** *A. eresia leptogramma*, ♀, Ecuador, Zamora-Chinchipe, Quebrada Navidades (FLMNH-MGCL-113359); **J)** *A. eresia* ssp., ♀, Colombia, Cauca, Tambito (CEPUJ).

Taxonomy and variation: Characters supporting recognition of this taxon as conspecific with *A. p. pyrhosticta* **n. sp.** are discussed under the description of the nominate subspecies. It was not possible to assess variation in this subspecies since only four specimens are known. Nevertheless, the stability of the diagnostic characters of the nominate subspecies in the relatively large series examined, from multiple sites, supports recognition of *A. p. quintecocha* **n. ssp.** as a distinct taxon.

Distribution and natural history: This subspecies is known only from four specimens collected at the type locality at 3150 m in the Department of Amazonas in northern Peru (Fig. 9A).

Actinote pyrhosticta apurimac Lamas & Willmott, **new subspecies**

Figs. 2E-G, 6C, 9A, 11C-H

Diagnosis and identification: This subspecies is distinguished from *A. p. quintecocha* **n. ssp.** by having broader dorsal orange markings on both wings, with postdiscal spots present in cells Cu_2 - M_3 on the FW, and a much broader postdiscal band on the DHW, extending almost to the distal margin near the tornus (Fig. 2E-G). Conversely, the orange markings basal of the thin, dark postdiscal line on the DHW are reduced in the discal cell and anal margin area, with this area of the wing mostly dark

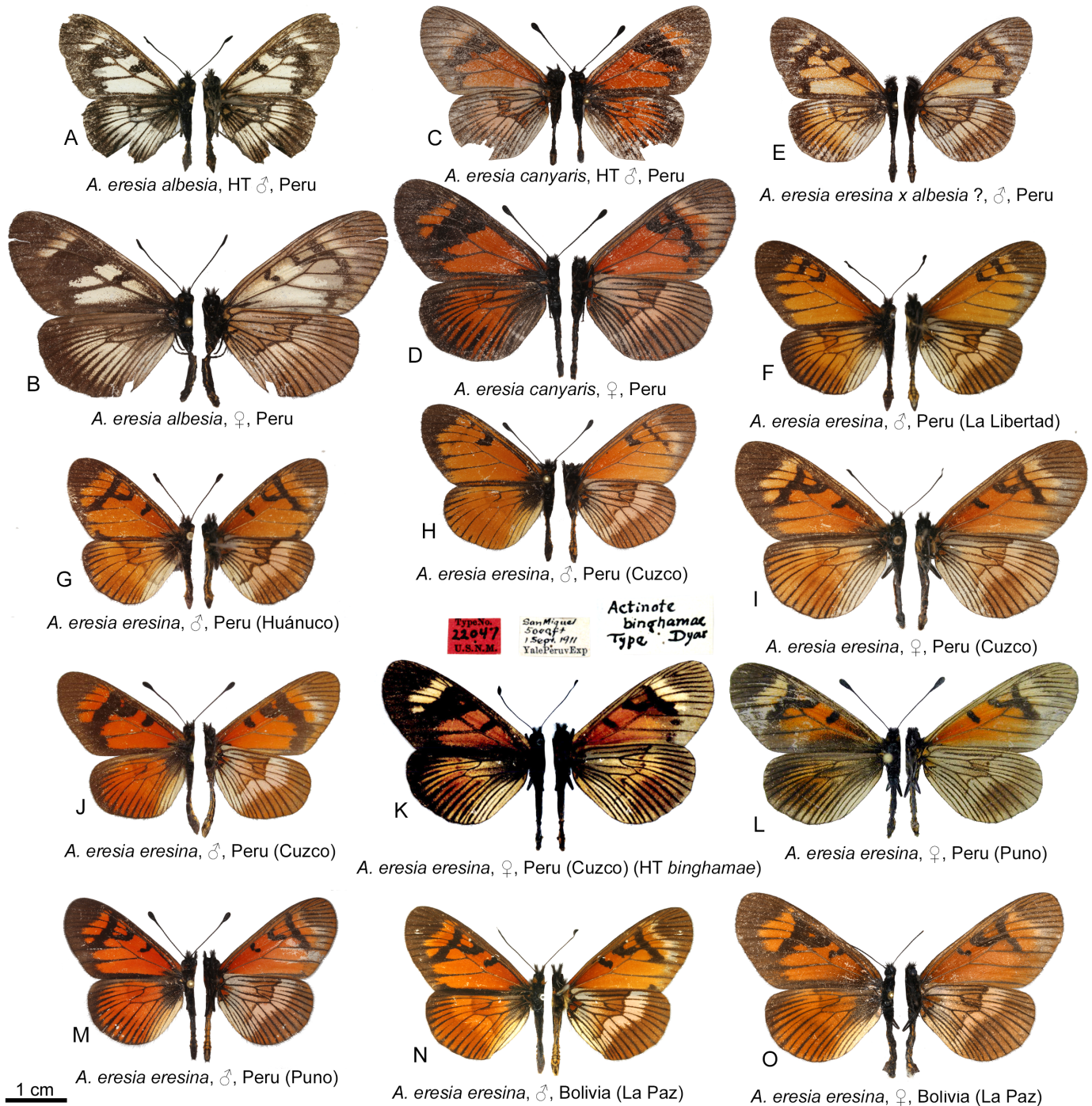


Figure 4. *Actinote eresia* specimens, left half dorsal surface, right half ventral surface (reverse for C). **A)** *A. eresia albesia* n. ssp., HT ♂, Peru, Amazonas, Quebrada Chido (MUSM); **B)** *A. eresia albesia* n. ssp., ♀, no data (CEPUJ); **C)** *A. eresia canyaris* n. ssp., HT ♂, Peru, Lambayeque, via 'Kañaris' (CEPUJ); **D)** *A. eresia canyaris* n. ssp., ♀, Peru, Lambayeque, via 'Kañaris' (CEPUJ); **E)** *A. eresia eresina*, transitional to *albesia* n. ssp.?, ♂, Peru, Amazonas, Molinopampa (CEPUJ); **F)** *A. eresia eresina*, ♂, Peru, La Libertad, Tayabamba-Ongón (MUSM-ENT-07483); **G)** *A. eresia eresina*, ♂, Peru, Huánuco, Diez Canseco (MUSM-ENT-07489); **H)** *A. eresia eresina*, ♂, Peru, Cuzco, Quebrada Tocchohuayco-Pillahuata (CEPUJ); **I)** *A. eresia eresina*, ♀, Peru, Cuzco, San Pedro (MUSM-ENT-07526); **J)** *A. eresia eresina*, ♂, Peru, Cuzco, Abra Malaga-Santa María (Quillabamba road) (PIBO); **K)** *A. eresia eresina*, ♀, Peru, Cuzco, San Miguel (USNM; HT of *binghamae*); **L)** *A. eresia eresina*, ♀, Peru, Puno, Río Jerusalén, Río Sina (PIBO; left-right wings reversed for easier comparison); **M)** *A. eresia eresina*, ♂, Peru, Puno, 3 km E Sina (PIBO); **N)** *A. eresia eresina*, ♂, Bolivia, La Paz, Coroico (NHMUK); **O)** *A. eresia eresina*, ♀, Bolivia, La Paz, Unduavi (CEPUJ).

brown (instead of orange). The paler orange color of the dorsal markings, broad DHW postdiscal band, and reduced orange in the basal half of the DHW, are the most obvious characters distinguishing this taxon from the nominate subspecies.

Description: MALE (Fig. 2E,G): Forewing length 23.1 mm (n=1). *Wings:* as illustrated. *Head, thorax, abdomen:* as in nominate subspecies. *Genitalia* (Fig. 6C): similar to nominate subspecies.

FEMALE: (Fig. 2F): Forewing length 28.4 mm (n=1). *Wings:* as illustrated, differing from male most notably in having broader white scaling in basal

third of VHW, as in other subspecies. *Head, thorax, abdomen*: similar to male. *Genitalia*: not examined.

Types: HOLOTYPE ♂: **PERU:** *Apurímac*: S[antuario]. N[acional]. Ampay, Laguna Angascocha, [13°35'S, 72°53'W], 3200 m, (Curo, J. L.), 21 Jul 2001, [MUSM-ENT-007885], (MUSM).

PARATYPES (9 ♂, 2 ♀): **PERU:** *Apurímac*: S[antuario]. N[acional]. Ampay, vía Huanipaca km 8, [13°32'12"S, 72°51'56"W], '3800' m, (Pyrcz, T. W.), 7 Sep 2008, 1 ♂, (CEPUJ), 3950 m, (Boyer, P.), 7 Sep 2008, 5 ♂, (PIBO); S[antuario]. N[acional]. Ampay, Laguna Angascocha, [13°35'S, 72°53'W], 3200 m, (Curo, J. L.), 21 Jul 2001, 1 ♂ [MUSM-ENT-007886; dissection, MUSM-2010-11-26-08], (MUSM); S[antuario]. N[acional]. Ampay, Explana[da], 3600 m, (Curo, J., Mayorga, R., Samanez, O., Astete, C.), 25 Jul 2007, 1 ♂, (MUSM); S[antuario]. N[acional]. Ampay, Laguna Uspacocha, [13°34'38"S, 72°53'10"W], 3750 m, (Curo, J., Mayorga, R., Samanez, O., Astete, C.), 25 Jul 2007, 1 ♂, 1 ♀, (MUSM); S[antuario]. N[acional]. Ampay, 3350 m, (Baiker, J.), 19 Apr 2009, 1 ♀, (MUSM).

Other records (photographs of live specimens): **Peru:** *Cuzco*: above Mollepata, [13°24'53"S, 72°34'7"W], 3600 m, (Geale, D.), 20 Jul 2021, 1 ♀, (<https://www.inaturalist.org/observations/97049333>), 1 ♀, (<https://www.inaturalist.org/observations/97049334>), 1 ♂, (<https://www.inaturalist.org/observations/97049336>), 1 ♂, (<https://www.inaturalist.org/observations/97049339>), 1 ♂, (<https://www.inaturalist.org/observations/97049345>), 27 Jun 2013, 1 ♂, (<https://www.inaturalist.org/observations/97049346>); Soraypampa, [13°24'4"S, 72°34'22"W], 3850 m, (Galiano, W.), 25 Jul 2010, 1 ♂, (Galiano, W. (17 Nov 2011, pers. comm. to KRW, with photo)).

Etymology: The name is derived from that of the type locality, and it is treated as a masculine noun in apposition.

Taxonomy and variation: Characters supporting recognition of this taxon as conspecific with *A. p. pyrrhosticta n. sp.* are discussed under the description of the nominate subspecies. In comparison with the holotype from Apurímac, male specimens from Cuzco have slightly more extensive orange in the basal area of the DHW, with only a narrow black line separating that area from the broader orange in the remainder of the wing.

Distribution and natural history: This taxon is known from 3200-3950 m in southern Peru, in the headwaters of the Apurímac valley in the department of that name and adjacent Cuzco (Fig. 9A), where it occurs in the uppermost cloudforest, with records of adults from April to September. David Geale (see iNaturalist references above) photographed both sexes nectaring on two Asteraceae species (Fig. 11F-H), as well as a single moribund larva (Fig. 11C) and clusters of hundreds of pupae (Fig. 11D,E), assumed to be this species based on the abundance of adults, lack of other species, and a freshly emerged adult female (Fig. 11D). PB also observed males nectaring on Asteraceae along the Huanipaca road.

Actinote pyrrhosticta alfamayo Lamas & Willmott, **new subspecies**

Figs. 2H,I, 9A

Diagnosis and identification: This subspecies is distinguished from *A. p. apurimac n. sp.* by the more extensive orange dorsal markings, including postdiscal markings on the FW in cells Cu_2-M_3 that are broader than the orange marking at the base of cell Cu_1-M_3 , and orange covering almost the entire DHW, except for the veins in the basal half of the wing, a dark

postdiscal line, and black intervenal stripes intruding from the distal margin (Fig. 2H,I).

Description: MALE (Fig. 2H): Forewing length 22.1 mm (n=1). *Wings*: as illustrated. *Head, thorax, abdomen*: as in nominate subspecies. *Genitalia*: somewhat intermediate between those of *A. pyrrhosticta quintecocha n. sp.* (Fig. 6B) and *A. pyrrhosticta apurimac n. sp.* (Fig. 6C), in other words not showing notable differences from either taxon.

FEMALE: (Fig. 2I): Forewing length 22 mm (n=1). *Wings*: as illustrated. *Head, thorax, abdomen*: similar to male. *Genitalia*: not examined.

Types: HOLOTYPE ♂: **PERU:** *Cuzco*: Río Santa María, 7-14 km E Alfamayo, [13°5'S, 72°23'W], 2700-3000 m, (Lamas, G.), 6 Oct 1981, [MUSM-ENT-007887], (MUSM).

PARATYPES (1 ♂, 1 ♀): **PERU:** *Cuzco*: Río Santa María, 7-14 km E Alfamayo, [13°5'S, 72°23'W], 2700-3000 m, (Lamas, G.), 6 Oct 1981, 1 ♂ [MUSM-ENT-007888; dissected], (MUSM); 'Kiteni', (Weiss, J.-C.), [19-22] Jul 1978, 1 ♀, (PIBO).

Etymology: The name is derived from that of the type locality, and it is treated as a masculine noun in apposition.

Taxonomy and variation: Characters supporting recognition of this taxon as conspecific with *A. p. pyrrhosticta* are discussed under the description of the nominate subspecies. Obviously it would be desirable to obtain additional material of this taxon and *A. pyrrhosticta apurimac*, to better assess geographic variation. Available data show these taxa to be allopatric and consistently different in the small series examined. To our knowledge, no specimens of *A. pyrrhosticta alfamayo* have been collected in the last 42 years, and thus we prefer to name this taxon now rather than wait in the hope that further material might become available for study.

Distribution and natural history: Label data for this taxon suggest that it occurs from 2700-3000 m, at lower elevations than the neighboring *A. p. apurimac n. sp.*, in the upper headwaters of the Río Urubamba (Fig. 9A). The collector of the female specimen, Jean-Claude Weiss, reported to PB (pers. comm.) that he collected at Kiteni on 20-21 July 1978, and thus the specimen was most likely collected between Abra Málaga and Quillabamba on his way to or from Kiteni, the elevation of which (approximately 600 m) is clearly too low for this taxon.

Actinote eresia albesia Lamas & Willmott, **new subspecies**

Figs. 4A,B, 9B

Diagnosis and identification: This subspecies is distinguished from all other *A. eresia* subspecies by the typically orange wing areas instead being very pale whitish gray (Fig. 4A,B). In wing pattern, it is perhaps most similar to *A. e. leptogramma*, except for having slightly broader dark borders on the DHW.

Description: MALE (Fig. 4A): Forewing length 22.0 mm (n=1). *Wings*: as illustrated. *Head, thorax, abdomen*: similar to *A. pyrrhosticta n. sp.* except with tufts of hair-like scales dorso-laterally on patagia yellowish, lacking conspicuous orange subdorsal spots on abdomen, and with pale yellowish (instead of orange) spots ventrally on thorax. *Genitalia*: not examined.

FEMALE: (Fig. 4B): Forewing length 29.5 mm (n=1). *Wings*: as illustrated. *Head, thorax, abdomen*: similar to male. *Genitalia*: not examined.

Types: HOLOTYPE ♂: **PERU:** Amazonas: Quebrada 'Chiro' [=Chido], [ca. 5°49'S, 78°02'W], 2300-2500 m, (Lamas, G.), 24 Aug 1998, (MUSM).

PARATYPES (8 ♂, 1 ♀): **PERU:** Amazonas: Alto Nieva, [ca. 5°40'S, 77°47'W], 2000-2500 m, (local collector), Apr 2005, 2 ♂, (PIBO); Quebrada Chido, [5°50'S, 78°00'W], 2300-2500 m, (Calderón, B.), Nov 1999, 1 ♂, (MUSM); San Lorenzo, [5°48'S, 77°58'W], 2300 m, (Pintado, J.), Feb 2011, 1 ♂, (MUSM); Oso Perdido, [5°43'S, 77°50'W], 2125 m, (Pintado, J.), Apr 2015, 2 ♂, (MUSM); Pomacochas, [5°49'S, 77°58'W], 2200 m, (Pyrz, T. W.), 17 Aug 1998, 2 ♂, (CEPUJ); **Country unknown:** *Not located:* no data, 1 ♀, (CEPUJ).

Etymology: The name is an amalgam of the feminine Latin adjective *alba*, meaning white, and the species name *eresia*, and it is treated as a feminine noun in apposition.

Taxonomy and variation: Characters supporting recognition of this taxon as conspecific with *A. eresia eresia* are discussed under the description of *A. pyrrhosticta* n. sp. A male specimen from Peru, Amazonas, Molinopampa, in the CEPUJ has a narrow black DHW border (as in *A. eresia eresina*) but washed-out orange markings, especially in FW cell 2A-Cu₂ (Fig. 4E), and perhaps represents a transitional phenotype between *A. e. albesia* n. ssp. and *A. eresia eresina*.

Distribution and natural history: This taxon is known only from northeastern Peru in Amazonas (Fig. 9B), where label data suggest it occurs from 2000-2500 m.

Actinote eresia canyaris Pyrcz & Lamas, new subspecies
Figs. 4C,D, 7A, 9B

Diagnosis and identification: This subspecies differs from *A. eresia leptogramma* by having darker dorsal orange markings, a broader black area separating the basal orange area of the DFW from the orange postdiscal band (resulting from loss of the orange postdiscal spots that are present in *A. e. leptogramma* in the basal part of cell Cu₁-M₃ and just distal of the discocellular veins), no dark spot in the middle of the FW discal cell orange area, a very indistinct dark discal line within the DHW orange area, and less contrasting ventral coloration (Fig. 4D,E).

Description: MALE (Fig. 4C): Forewing length 22.5 mm (n=1). *Wings:* as illustrated. *Head, thorax, abdomen:* as in *A. eresia albesia* except with dark orange scale tufts on patagia and ventral thorax spots orange. *Genitalia* (Fig. 7D): similar to nominate subspecies (Fig. 7A) except valva broader and blunter, as in *A. eresia leptogramma*.

FEMALE: (Fig. 4D): Forewing length 26.2 mm (n=1). *Wings:* as illustrated. *Head, thorax, abdomen:* similar to male. *Genitalia:* not examined.

Types: HOLOTYPE ♂: **PERU:** Lambayeque: Pucará, vía 'Kañaris' [=Cañaris], [6°3'43"S, 79°15'8"W], 2700-2800 m, (Pyrz, T. W.), 14 Jun 2018, [dissection, prep. genit. 1910, 15/12/2019 K. Florczyk], (CEPUJ, to be deposited in MUSM).

PARATYPES (1 ♀): **PERU:** Lambayeque: Pucará, vía 'Kañaris' [=Cañaris], [6°3'43"S, 79°15'8"W], 2700-2800 m, (Pyrz, T. W.), 14 Jun 2018, 1 ♀, (CEPUJ).

Etymology: The subspecies name is derived from that of the type locality and is treated as a feminine noun in apposition.

Taxonomy and variation: Characters supporting recognition of this taxon as conspecific with *A. eresia eresia* are discussed

under the description of *A. pyrrhosticta* n. sp., and this hypothesis is supported by analysis of DNA barcode sequence data (Fig. 1). With only two specimens known it is not possible to reasonably assess variation.

Distribution and natural history: This is the only representative of *A. eresia* so far known from the western Andes in Peru (Fig. 9B), where it is known only from the type locality from 2700-2800 m.

Actinote hilaris arcoiris Willmott & Hall, new subspecies
Figs. 5C-H, 7E, 9B, 11J

Diagnosis and identification: This new subspecies (Fig. 5C-H) is perhaps superficially most similar to the nominate subspecies (Fig. 5K,L), which occurs from central Peru (Pasco) to the northern Andes of Bolivia. It may be distinguished from that subspecies by having slightly paler orange coloration, and, in the male, by the basal half of the VHW being dark orange, rather than being predominantly yellowish white. Females may be superficially similar to those of *A. eresia leptogramma*, but can be distinguished by the broad, even black band separating the basal orange area from the orange postdiscal band on the VFW, instead of having a thin, irregular black line which appears to fork at the costa. Although this taxon is also superficially similar to other less closely related Andean *Actinote*, the whitish band through the middle of the VHW distinguishes this species.

Description: MALE (Fig. 5C): Forewing length of HT 27.5 mm (22.0-27.7 mm, mean 25.8 mm, n=10). *Wings:* as illustrated. *Head, thorax, abdomen:* as in *A. pyrrhosticta* n. sp., except with 39 antennomeres, frons with dense, long, black, hair-like scales, patagia black, ventral spots on thorax orange, mesothorax meron with patch of very long, yellow, hair-like scales, abdomen black except for scattered ventral orange scaling in middle of sternites and thin lateral line of yellow scales just dorsal of sternites. *Genitalia* (Fig. 7E): similar to nominate subspecies (pers. obs.).

FEMALE: (Fig. 5D-H): Forewing length mean 30.5 mm (26.3-32.5 mm, n=4). *Wings:* as illustrated, variable with respect to color of basal half of DFW and width and color of DFW postdiscal band. *Head, thorax, abdomen:* similar in color to male, sphragis present in two examined specimens as a broad, blunt rectangular plate extending beyond ventral edge of sternites, similar to *A. hilaris sourakovi* n. ssp. (Fig. 2L). *Genitalia:* not examined.

Types: HOLOTYPE ♂: **ECUADOR:** Zamora-Chinchipec: km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S, 79°5'42"W], 2100 m, (Willmott, K. R.), 25 Nov 2003, [DNA voucher LEP-01555; Genitalic dissection KW-19-065], (MGCL, to be deposited in INABIO).

PARATYPES (12 ♂, 12 ♀): **ECUADOR:** Morona-Santiago: Guarumales/Hidropaute, [2°34'34"S, 78°30'46"W], 1800 m, (Petit, J.-C.), 29 Oct 2009, 1 ♀, (JEPE); km 22 Limón-Gualaceo rd., [3°0'30"S, 78°32'20"W], 2100 m, (Willmott, K. R.), 10 Nov 2010, 1 ♂ [FLMNH-MGCL-146472], 1 ♀ [FLMNH-MGCL-145576], 1 ♀ [FLMNH-MGCL-145577], (MGCL); km 50-60 Gualaquiza-Chigüinda rd., (Boyer, P.), 3 Dec 1998, 1 ♀, (PIBO); Quebrada Nueva de Octubre, [2°15'42"S, 78°12'54"W], 1600 m, (Petit, J.-C.), 26 Oct 2008, 1 ♂, (JEPE); Zamora-Chinchipec: km 18 Yacuambi-Saraguro rd., Cascada Hampik Yaku, [3°33'56"S, 78°58'16"W], 2000 m, (Willmott, K. R., J. I. R., J. C. R.), 21 Jun 2013, 1 ♀ [FLMNH-MGCL-157856], (MGCL); 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, 1 ♂, (MGCL), (Willmott, K. R., Aldaz, R.), 9 Nov 2006, 1 ♀ [FLMNH-MGCL-119805], (MGCL); km 24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S, 79°5'42"W], 2100 m, (Willmott, K. R.), 25 Nov 2003, 3 ♂, (MGCL); km 25 Loja-Zamora rd., [3°59'18"S, 79°5'42"W], 2000 m, (Boyer, P.), 21 Nov 1996, 1 ♂, (PIBO); km 32 Loja-Zamora rd., Quebrada Zurita, [3°58'18"S, 79°6'12"W], 1900

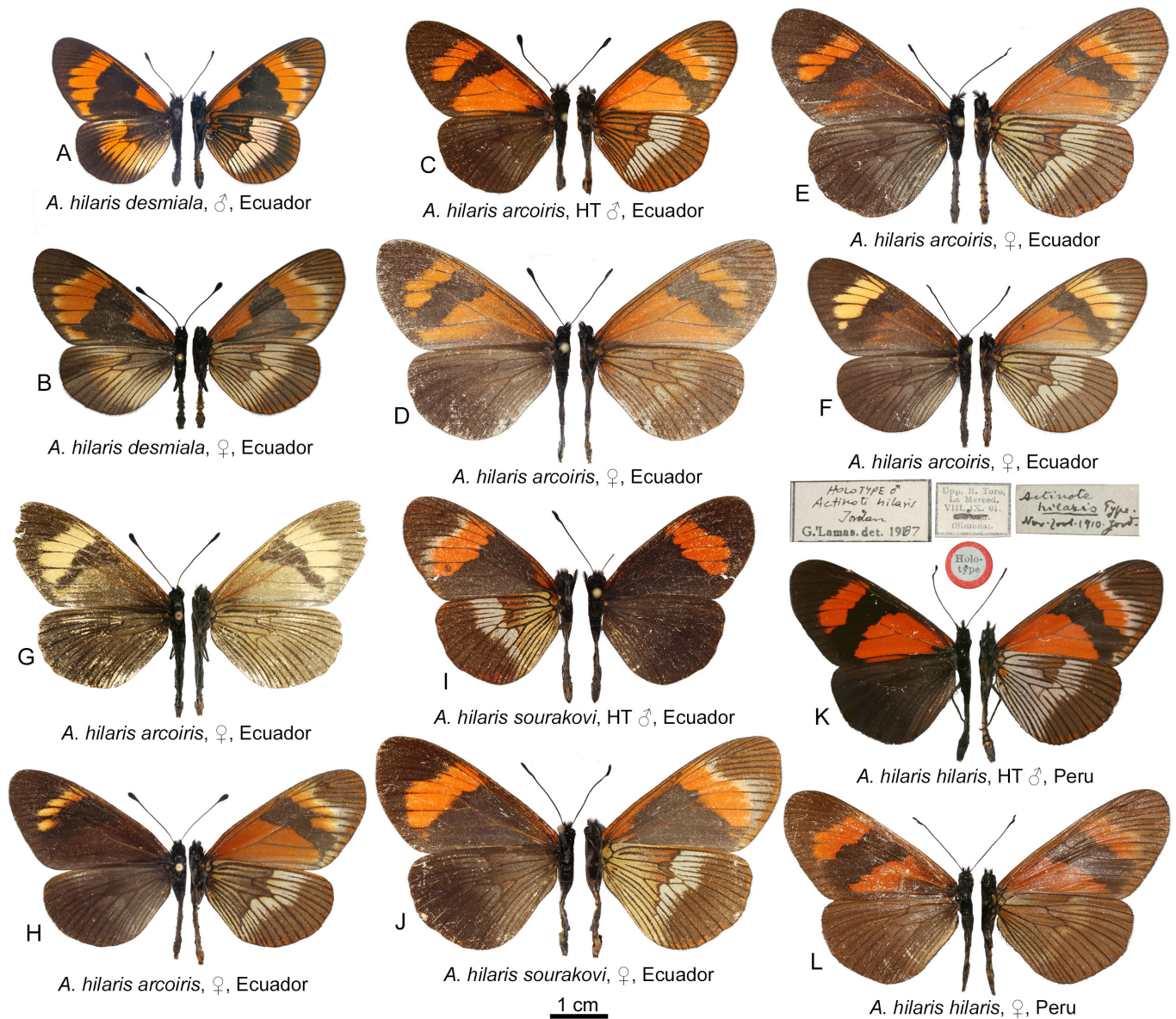


Figure 5. *Actinote hilaris* specimens, left half dorsal surface, right half ventral surface (reverse for I). **A)** *A. hilaris desmiala*, ♂, Ecuador, Napo, Río Jatun Tinahua (MGCL); **B)** *A. hilaris desmiala*, ♀, Ecuador, Napo, Yanayacu (CEPUJ); **C)** *A. hilaris arcoiris n. ssp.*, HT ♂, Ecuador, Zamora-Chinchipe, San Francisco (MGCL, LEP-01555); **D)** *A. hilaris arcoiris n. ssp.*, ♀, Ecuador, Zamora-Chinchipe, Cascada Hampik Yaku (FLMNH-MGCL-157856); **E)** *A. hilaris arcoiris n. ssp.*, ♀, Ecuador, Zamora-Chinchipe, San Francisco (FLMNH-MGCL-119805); **F)** *A. hilaris arcoiris n. ssp.*, ♀, Ecuador, Morona-Santiago, km 22 Limón-Gualaceo rd. (FLMNH-MGCL-145577); **G)** *A. hilaris arcoiris n. ssp.*, ♀, Ecuador, Zamora-Chinchipe, Loja-Zamora old rd. (PIBO); **H)** *A. hilaris arcoiris n. ssp.*, ♀, Ecuador, Morona-Santiago, Guarumales (PIBO); **I)** *A. hilaris sourakovi n. ssp.*, HT ♂, Ecuador, Zamora-Chinchipe, Quebrada Honda (FLMNH-MGCL-111075); **J)** *A. hilaris sourakovi n. ssp.*, ♀, Ecuador, Zamora-Chinchipe, above Valladolid (MGCL); **K)** *A. hilaris hilaris*, HT ♂, Peru, Junín, upper Río Toro (NHMUK); **L)** *A. hilaris hilaris*, ♀, Peru, Pasco, Cushi (NHMUK).

m, (Willmott, K. R.), 14 Nov 2010, 1 ♂ [FLMNH-MGCL-145575], 1 ♂ [FLMNH-MGCL-146469], 1 ♂ [FLMNH-MGCL-146470], 1 ♂ [FLMNH-MGCL-146471], (MGCL); Loja-Zamora old rd., [3°58'30"S, 79°7'30"W], 2000-2700 m, (Boyer, P.), Jun 1998, 1 ♂, (PIBO); Loja-Zamora old rd., [3°58'30"S, 79°7'30"W], 2200-2700 m, (Boyer, P.), 25 Nov 1998, 2 ♀, (PIBO), Jun 1998, 1 ♀, (PIBO); 'Zamora valley', (Los, K.), May 1997, 1 ♀, (CEPUJ); *Not located*: 'Ecuador', 1 ♀ ['Ecdre'], 1 ♀ ['Ecuador'], (NHMUK).

Other records: Ecuador: *Morona-Santiago*: Alshi, [2°13'47"S, 78°13'11"W], (Wolhuter, A. & L.), 19 Sep 2002, 1 ♂, (AWLW) (Wolhuter, A. & L. (pers. comm. with CD of images to KRW)); Guarumales/Hidropaute, [2°34'16"S, 78°30'56"W], 2000 m, (Petit, J.-C.), 1 ♂, (JEPE) (<http://www.sangay.eu>, no 1508), 1 ♀, (JEPE) (<http://www.sangay.eu>, no 734), 1 ♂, (JEPE) (<http://www.sangay.eu>,

no 897); Guarumales/Hidropaute, [2°34'34"S, 78°30'46"W], (Petit, J.-C.), 1 ♀, (JEPE); *Loja*: c. 3 km ESE Loja, Escuela Amauta, [4°2'38"S, 79°10'24"W], 2300 m, (Piedra, V.), 30 Apr 2022, 1 ♂, (photograph of live specimen) (<https://www.inaturalist.org/observations/114043083>).

Etymology: The subspecies name is derived from that of the type locality and is also the Spanish word for 'rainbow'. It is treated as a masculine noun in apposition.

Taxonomy and variation: Characters supporting recognition of this taxon as conspecific with *A. hilaris hilaris* are discussed

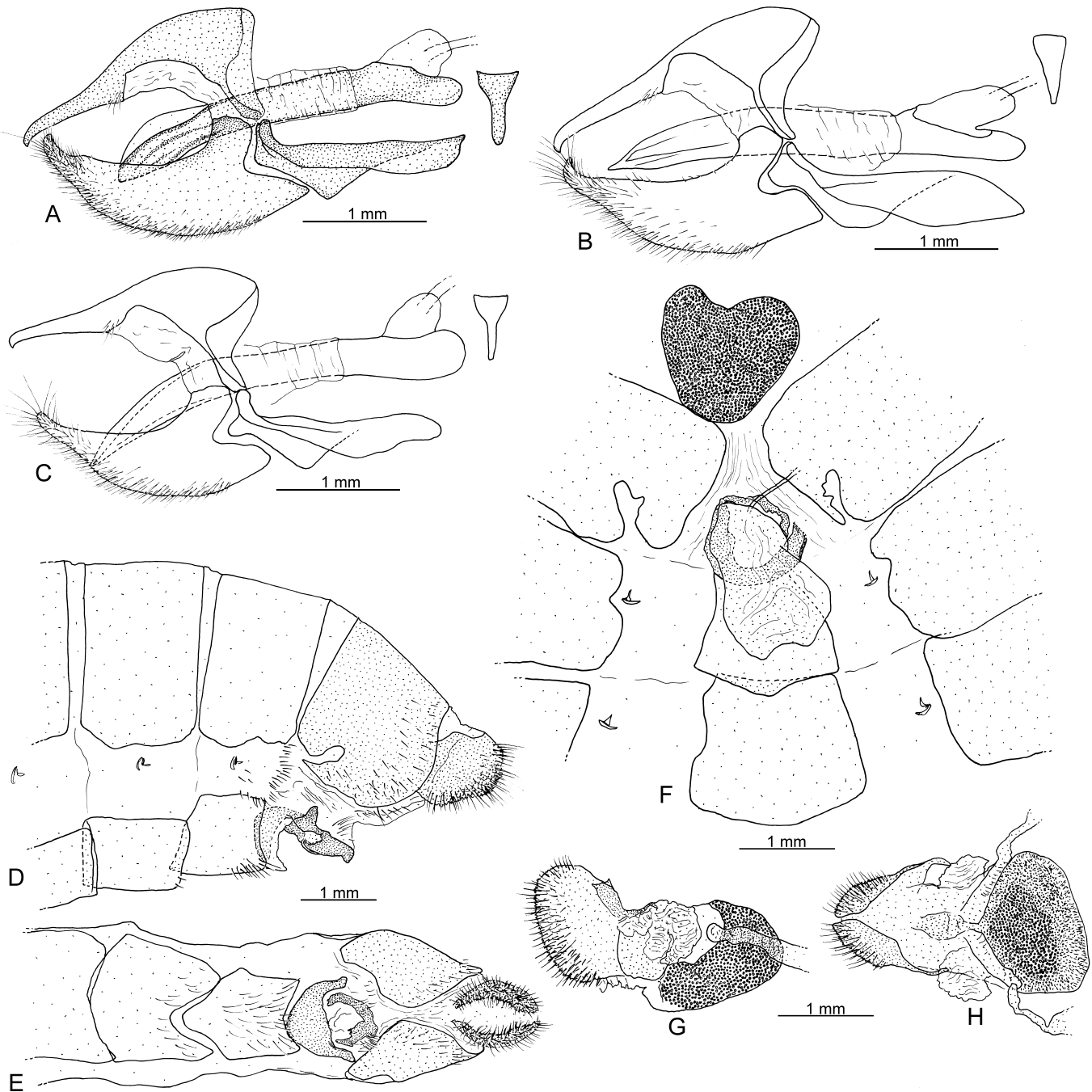


Figure 6. Genitalia of *Actinote pyrrhosticta* n. sp. **A)** *A. pyrrhosticta pyrrhosticta* n. sp., HT ♂, Ecuador, lateral view genitalia and posterior view juxta (upper right); **B)** *A. pyrrhosticta quintecocha* n. ssp., ♂, Peru (MUSM-2010-11-26-07), lateral view genitalia and posterior view juxta (upper right); **C)** *A. pyrrhosticta apurimac* n. ssp., ♂, Peru (MUSM-2010-11-26-08), lateral view genitalia and posterior view juxta (upper right); **D-H):** *A. pyrrhosticta pyrrhosticta* n. sp., ♀ (FLMNH-MGCL-209927; KW-16-63): **D)** lateral view posterior tip abdomen; **E)** ventral view posterior tip abdomen; **F)** abdomen interior and genitalia dorsal view; **G)** papillae anales and subpapillary glands lateral view; **H)** same as F, dorsal view.

under the description of *A. pyrrhosticta* n. sp. DNA barcode sequence data support conspecificity of this taxon with *A. hilaris sourakovi* n. ssp. and *A. hilaris desmiala* (Fig. 1). Mean pairwise sequence divergence within *A. hilaris* was 0.9%, and mean between-group divergence was 3.9% (*A. hilaris/A. eresia*) and 4.5% (*A. hilaris/A. pyrrhosticta*). The female of this taxon is rather variable in the tone of the FW orange markings, the extent to which the orange DFW basal area is obscured with black scaling, and in the color of the DFW postdiscal band, which

may be a pale cream color (Fig. 5D-H). We have not examined a sufficient number of specimens to determine whether females of *A. hilaris arcoiris* n. ssp. can be consistently distinguished from those of the nominate subspecies (Fig. 5L), but these two taxa are widely disjunct.

Distribution and natural history: This subspecies is known from central to southeastern Ecuador in the provinces of Morona-Santiago and Zamora-Chinchipe, where it is rather

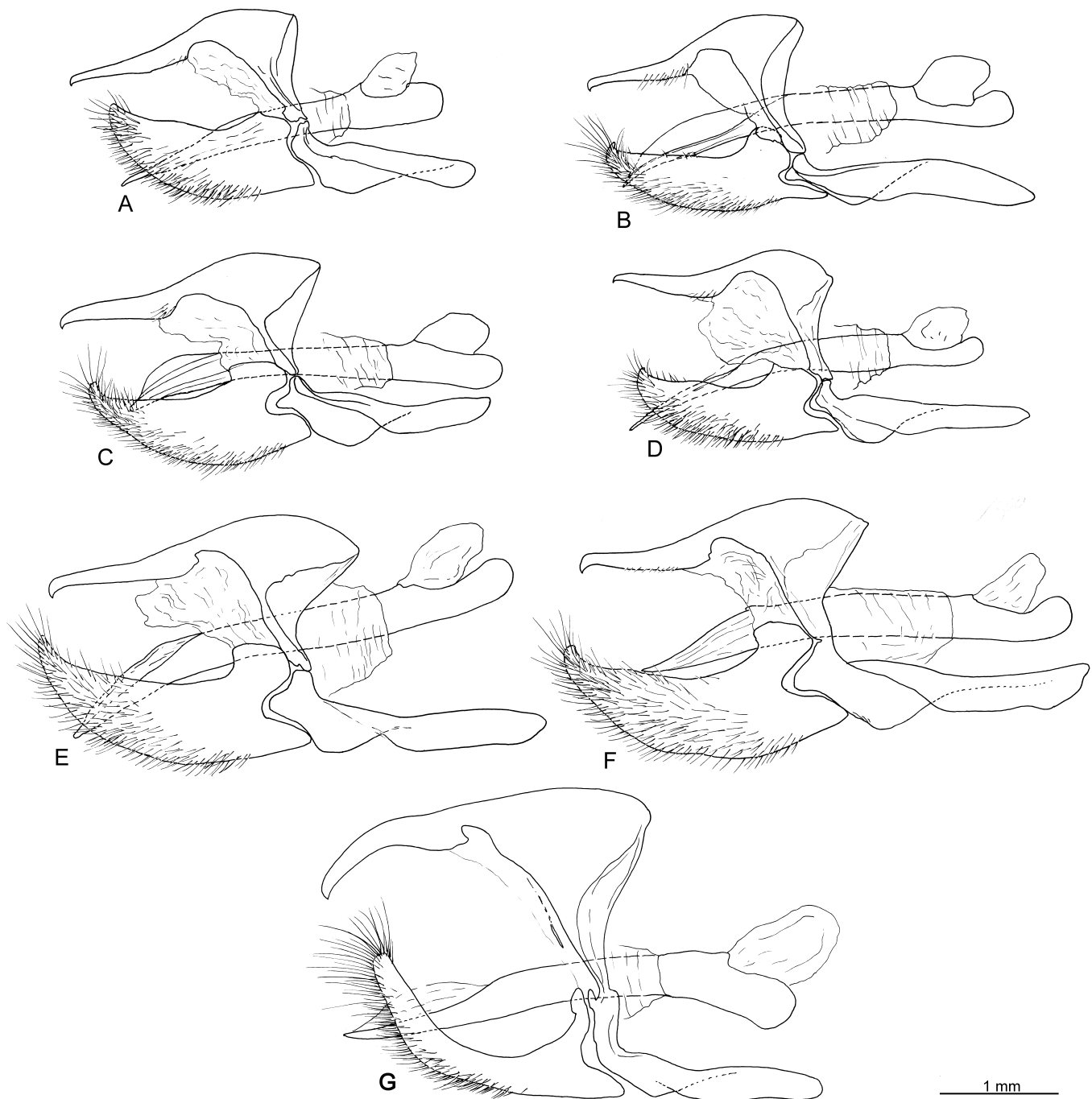


Figure 7. Male genitalia of *Actinote eresia*, *Actinote hilaris* and *Actinote trinacria*, lateral view. **A)** *A. eresia eresia*, ♂, Colombia (CEPUJ); **B)** *A. eresia leptogramma*, ♂, Ecuador (FLMNH-MGCL-113366; KW-15-157); **C)** *A. eresia eresina*, ♂, Peru (MUSM-2010-11-26-03); **D)** *A. eresia canyaris* n. ssp., HT ♂, Peru; **E)** *A. hilaris arcoiris* n. ssp., HT ♂, Ecuador; **F)** *A. hilaris sourakovi* n. ssp., HT ♂, Ecuador; **G)** *A. trinacria alegria* n. ssp., HT ♂, Ecuador.

rare and typically found in relatively undisturbed cloud forest from 1600-2300 m. In Ecuador, males were found feeding on flowers in the forest canopy 20 m above the ground from 10:00-11:00 hr and 14:00-16:00 hr, and were also observed flying 2-3 m above a forested river in bright sun from 10:00-11:00 hr. A female was encountered flying 4 m above the ground over a ridgetop road through forest at 13:00 hrs, and two others were observed puddling solitarily in the morning at damp sand, not in the company of males.

***Actinote hilaris sourakovi* Willmott & Lamas, new subspecies**

Figs. 2L, 5I,J, 7F, 9C, 11K,L

Diagnosis and identification: This subspecies is easily distinguished from all other taxa within *A. hilaris*, *A. eresia* and *A. pyrrhosticta* n. sp. by the entirely black DFW basal area (Fig. 5I,J). The VHW is similar to that of *A. hilaris hilaris* in having pale yellowish white scaling extending from the base

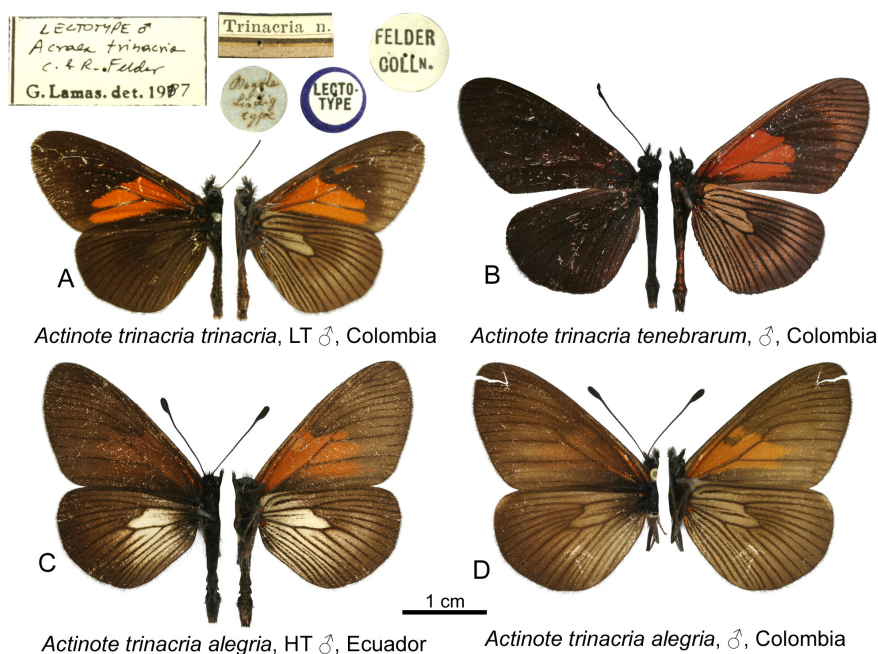


Figure 8. *Actinote trinacria* specimens, left half dorsal surface, right half ventral surface. **A)** *A. trinacria trinacria*, LT ♂, Colombia, ‘Bogotá’ (NHMUK); **B)** *A. trinacria tenebrarum*, ♂, Colombia, Antioquia, Valdivia (NHMUK); **C)** *A. trinacria alegria* n. ssp., HT ♂, Ecuador, Sucumbíos, El Calvario-La Alegría rd. (PIBO); **D)** *A. trinacria alegria* n. ssp., ♂, Colombia, Cauca, Leticia to Puracé (NHMUK).

to the edge of the pale postdiscal band in the posterior half of the wing, and in this respect it differs (in males) from *A. hilaris arcoiris* n. ssp.

Description: MALE (Fig. 5I): Forewing length of HT 27.9 mm (27.9-31.4 mm, mean 29.8 mm, n=4). *Wings:* as illustrated. *Head, thorax, abdomen:* as in *A. hilaris arcoiris* n. ssp., except ventral thoracic spots on katapisternum and epimeron orange (not yellow). *Genitalia* (Fig. 7F): similar to *A. hilaris arcoiris* (Fig. 7E) and nominate subspecies (pers. obs.).

FEMALE: (Fig. 5J): Forewing length mean 34.3 mm (32.8-36.7 mm, n=3). *Wings:* as illustrated. *Head, thorax, abdomen:* similar to *A. hilaris arcoiris* n. ssp., including sphragis (Fig. 2L) (present in three specimens). *Genitalia:* not examined.

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchipe:* Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S, 79°7'18"W], 1900 m, (Willmott, K. R.), 30 Nov 2005, [FLMNH-MGCL-111075]; DNA voucher LEP-00007; Genitalia dissection KW-19-064], (MGCL, to be deposited in INABIO).

PARATYPES (12 ♂, 11 ♀): **ECUADOR:** *Loja:* ‘above Yangana’ [=La Entrada], [4°25'6"S, 79°9'18"W], 2500 m, (Aldas, I.), May 2000, 1 ♂, (PIBO), (Boyer, P.), May 2000, 3 ♂, (PIBO); *Zamora-Chinchipe:* above Valladolid, [4°31'18"S, 79°7'48"W], (Sourakov, A.), 17-21 May 1993, 1 ♀ [FLMNH-MGCL-281001], (MGCL); above Valladolid, [4°31'18"S, 79°7'48"W], 2000 m, (Sourakov, A.), 17-21 May 1993, 1 ♀, (MGCL); km 4.3 San Andrés-Jimbura rd., [4°47'59"S, 79°18'18"W], 2020 m, (Willmott, K. R.), 13 Oct 2010, 1 ♂ [FLMNH-MGCL-146473], (MGCL); km 5.3 San Andrés-Jimbura rd., Finca San Carlos, [4°47'53"S, 79°18'34"W], 2000 m, (Willmott, K. R.), 15 Oct 2010, 1 ♀ [FLMNH-MGCL-145578], (MGCL); km 8 Valladolid-Tapala rd., [4°32'22"S, 79°6'21"W], 1600 m, (Willmott, K. R.), 1 Dec 2005, 1 ♂ [FLMNH-MGCL-111076], (MGCL); Reserva Tapichalaca, Quebrada Honda trail, [4°28'21"S, 79°7'18"W], 1900 m, (Willmott, K. R.), 30 Nov 2005, 1 ♀ [FLMNH-MGCL-111074], (MGCL). **PERU:** *Amazonas:* 2 km NW Ocol, [6°15'S, 77°35'W], 2550 m, (Grados, J.), 19 Aug 1998, 1 ♀ [MUSM-ENT-7540], (MUSM); 3 km N Nueva Esperanza, Quebrada Piruro,

[6°23'S, 77°26'W], 1700 m, (Wojtusiak, J.), 19 Sep 1999, 1 ♀, (CEPUJ); 5 km N Molinopampa, [6°10'S, 77°39'W], 3000 m, (Grados, J.), 20 Aug 1998, 1 ♂ [MUSM-ENT-7538], 1 ♂ [MUSM-ENT-7539], (MUSM); Rodríguez de Mendoza, ‘Hingil Pata’ [=Inguilpata], [6°14'S, 77°57'W], 2300 m, (Calderón, B.), 2 Sep 1998, 1 ♂, (CEPUJ); Rodríguez de Mendoza, ‘Llanoico’ [=Quebrada Yanahuayco], [6°24'S, 77°26'W], 1600-2000 m, (Pyrcz, T. W.), Sep 1998, 1 ♂, (CEPUJ); Molinopampa-El Tingo, [6°13'15"S, 77°38'37"W], 2400 m, (Pyrcz, T. W.), 26 Jun 1998, 1 ♂, (CEPUJ); Pomacochas, [5°49'S, 77°58'W], 2200 m, (Calderón, B.), 18 Aug 1998, 1 ♀, (CEPUJ); Quebrada La Florida, [5°45'27.86"S, 78°04'34"W], 2133 m, (Quispe, E. R.), 16 Nov 2019, 1 ♀, (MUSM); *Cajamarca:* Naranja, [6°16'S, 78°51'W], 2300 m, (Grados, J.), 18 Oct 1998, 1 ♀ [MUSM-ENT-7541], (MUSM); Prov[incia]. San Ignacio, nr. C[entro]. P[oblado]. Pueblo Libre, [5°06'02"S, 79°14'12"W], 2070 m, (Sánchez, P.), 9 Oct 2017, 1 ♀, (MUSM); *San Martín:* ‘Jorge Chávez’ - (error), (Calderón, B.), Jul 2005, 1 ♂, (PIBO); Puente Nieva, [5°41'S, 77°47'W], 2025 m, (Lamas, G.), 9 Nov 1998, 1 ♀ [MUSM-ENT-7542], (MUSM).

Other records: **Peru:** *Amazonas:* Abra Patricia, [5°42'S, 77°48'W], 2150 m, (Geale, D.), 4 Dec 2022, 1 ♀, (photograph of live specimen) (Geale, D. (May 2023, pers. comm. to KRW with photo)). *Pasco:* ‘Camino del Pichis, ‘Tambo Eneñas’ [= Eneñas] to Dos de Mayo’ - (error), (Cornell University Expedition), 5 Jul 1930, 1 ♀ [Lot 607 Sub 126, R. W. L. Potts Collection], (CAS).

Etymology: This distinctive taxon is named for Andrei Sourakov, in recognition of many years of friendship, wit, lively debate and forthright criticism. Andrei also collected the first known specimens of this subspecies from Ecuador, during a remarkably successful expedition to the Valladolid region (KRW, JPWH).

Taxonomy and variation: Characters supporting recognition of this taxon as conspecific with *A. hilaris hilaris* are discussed under the description of *A. pyrrosticta* n. sp. DNA barcode sequence data support conspecificity of this taxon with *A.*

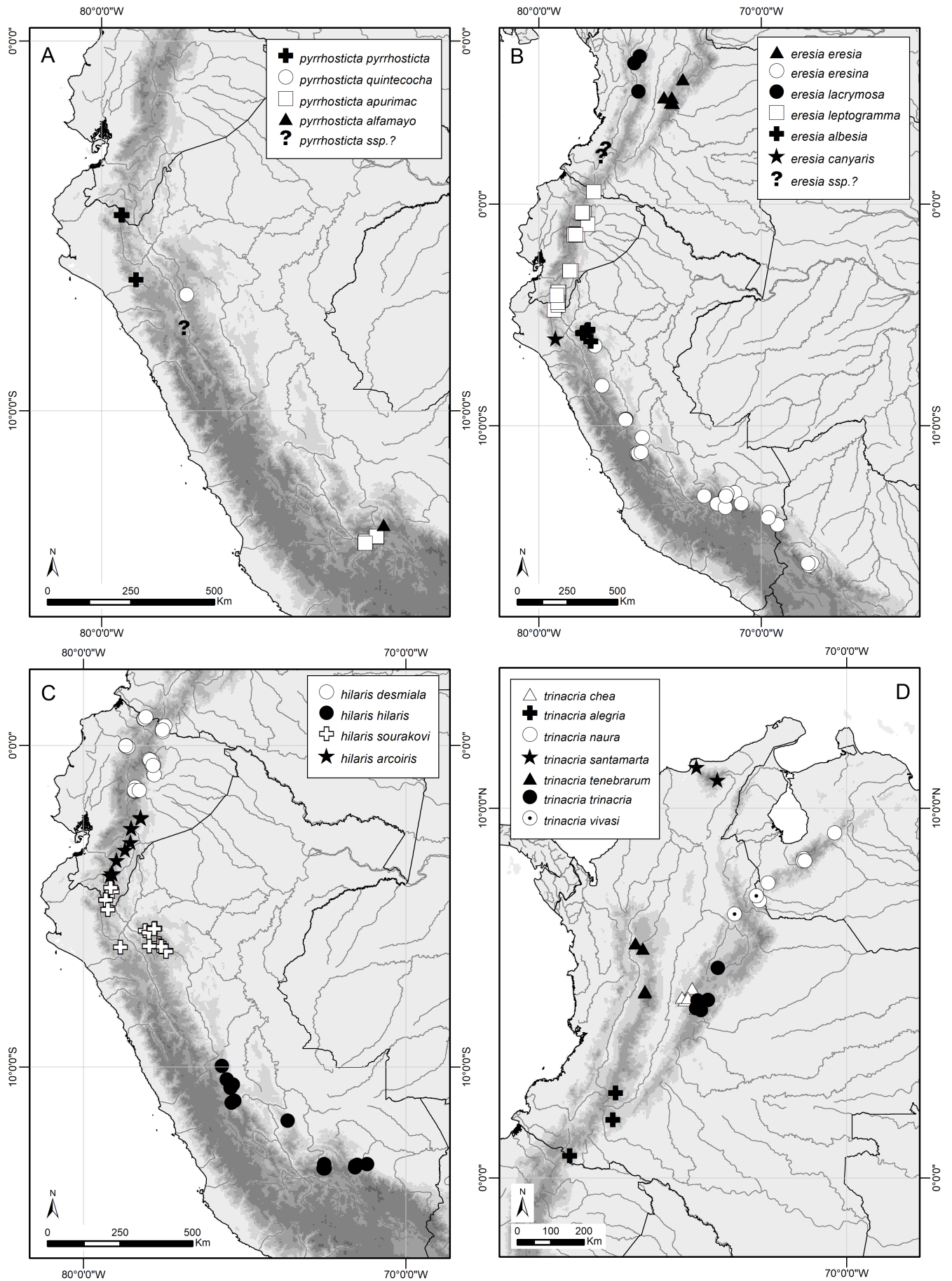


Figure 9. Maps depicting recorded localities for *Actinote* taxa. A) *A. pyrhosticta* n. sp.; B) *A. eresia*; C) *A. hilaris*; D) *A. trinacria*.

hilaris arcoiris n. ssp. and *A. hilaris desmiala* (Fig. 1). The width of the FW orange band is slightly variable.

Distribution and natural history: This subspecies occurs from extreme southern Ecuador (Zamora-Chinchiipe, in the upper valleys of rivers that flow into the Río Marañón) through northern Peru as far south as San Martín (Fig. 9C). A historical specimen from Pasco, within the distribution of the nominate

subspecies, seems likely to be mislabeled. The taxon is found in relatively undisturbed cloud forest from 1600-2550 m (with one record from 3000 m), where it is uncommon. In Ecuador, both sexes were found feeding on flowers along the edges of rivers and roads in the mid-morning. One little-damaged male was found in early December dead on the ground by a stream in the morning, during a period of unusually clear and cold nights.



Figure 10. Habitats of new *Actinote* taxa. **A)** Ecuador, Loja, Jimbura-San Andrés road, type locality of *Actinote pyrrhosticta* n. sp., stream gully and road where numerous individuals were observed on the morning of 12 June 2014; **B)** Peru, Cajamarca, El Pargo, habitat of *A. pyrrhosticta* n. sp. **C)** Peru, Apurímac, Santuario Nacional Ampay, Laguna Angasocha, type locality of *A. pyrrhosticta apurimac* n. ssp. **D)** Peru, Apurímac, Santuario Nacional Ampay, Laguna Uspacocha, habitat of *A. pyrrhosticta apurimac* n. ssp. **E)** Peru, Lambayeque, Cañaris, type locality of *A. eresia canyaris* n. ssp. **F)** Ecuador, Zamora-Chinchiipe, San Francisco, type locality of *Actinote hilaris arcoiris* n. ssp.

Actinote trinacria alegría Boyer & Willmott, **new subspecies**
Figs. 7G, 8C,D, 9D

Diagnosis and identification: This subspecies is distinguished from other *A. trinacria* (C. Felder & R. Felder, 1862) taxa by the dark DFW, lacking any orange markings in the discal cell (otherwise occurring only in *A. trinacria tenebrarum* Oberthür, 1917), and by the unique whitish patches in the basal third of the DHW (Fig. 8C,D). The ground color of the wings is dark brown, rather than black as in other subspecies of *A. trinacria*.

Description: MALE (Fig. 8C): Forewing length 24.2 mm (n=1). *Wings:* as illustrated, veins M_1 and Rs fused near their base. *Head, thorax, abdomen:* as in nominate subspecies, including spots of orange-yellow scales on ventral thorax near base of legs which appear to be smaller than in nominate subspecies, and no orange-red line down middle of ventral abdomen, in contrast to *A. t. trinacria* and *A. t. naura*. *Genitalia* (Fig. 7G): uncus curving downwards, valvae elongate, narrow, of even width throughout most of length, upwardly curved in middle.

FEMALE: unknown.

Types: HOLOTYPE ♂: **ECUADOR:** *Sucumbios:* El Calvario-La Alegría rd., [0°36'N, 77°28'36"W], 2800 m, (Boyer, P.), 26 Nov 1999, (PIBO, to be deposited in CEPUIJ).

Other specimens examined (see discussion under Taxonomy and variation) (2 ♂): **COLOMBIA:** *Cauca:* eastern slopes of Cordillera Central, [Santa Leticia to Puracé, [2°17'53"N, 76°13'57"W], 2650-2700 m, (Adams, M. J., Hardy, P. J.), Aug 1979, 1 ♂, (NHMUK); San Juan de Villalobos km 90, [1°29'53"N, 76°22'32"W], 1800 m, (Prieto, C.), 22 Jun 2013, 1 ♂ [g 066], (RCCP) (photograph examined).

Etymology: The subspecies name is derived from that of the type locality, and is also, appropriately, the Spanish word for 'happiness', given the serendipity of the collection of the holotype (see below). The name is treated as a feminine noun in apposition.

Taxonomy and variation: This taxon is associated with other taxa currently treated as subspecies of *A. trinacria* on the basis of several shared characters, including: relatively small size, whitish gray VHW discal cell contrasting with reddish spots at the base of the wing anterior and posterior of the discal cell, and indistinct whitish-gray VHW postdiscal band tapering anteriorly (e.g., Fig. 8A,B). The genitalia of the holotype of *A. trinacria alegría n. ssp.* are similar to those of a dissected specimen of *A. trinacria trinacria* (Colombia, Boyacá, vic. Arcabuco, in MGCL) in having narrow, upwardly curving valvae, a character that may prove to be distinctive for this species. We examined two Colombian specimens (Fig. 8D) that are similar to this taxon in lacking conspicuous orange DFW markings and in the pale shading in the basal half of the DHW, although both differ from the holotype of *A. t. alegría n. ssp.* in having more muted whitish gray coloring on the HW, especially the specimen from Leticia-Puracé, and in the orange on the VFW being reduced (absent in cell Cu_1-M_3 and reduced in cell 2A- Cu_2). In addition, the figured Colombian specimen from Leticia to Puracé (Fig. 8D) differs from the holotype of *A. trinacria alegría n. ssp.* (Fig. 8C) in having HW veins M_1 and Rs separate at their bases. Although the fusion or not of the bases of these two veins can be taxonomically important

in *Actinote* (e.g., see description of *Actinote balletae* Neild & Romero, 2008 (Neild, 2008: 32)), in this case the difference seems to represent intraspecific variation, since the other Colombian specimen has these veins touching where they leave the discal cell, intermediate between the two states discussed above. Furthermore, we observed similar variation in other species of *Actinote*, such as *A. johncoulsoni* Willmott, Lamas & Hall, 2017 and *A. stratonicæ* (Latreille, [1813]). The two Colombian specimens are regarded at present as representing the same taxon as the Ecuadorian holotype, but were excluded from the type series and may ultimately prove to represent a distinct subspecies.

Distribution and natural history: This taxon is the southernmost representative of *A. trinacria*, occurring in northeastern Ecuador in Sucumbios, potentially to southern Colombia in Cauca on the eastern slopes of the Cordilleras Central and Oriental (Fig. 9D). The three specimens discussed here were collected between 1800-2800 m. The holotype was found crawling across a damp, dirt road through cloud forest on a very cool, overcast morning.

Annotated checklist of relevant species

A single dash before a name indicates a valid subspecific name and two dashes indicates a synonym. All distributions from Ecuador to Bolivia are on the eastern slopes of the Andes unless otherwise noted.

pyrrhosticta Lamas, Willmott & Hall, **n. sp.** [Fig. 2A-C; S.W. Ecuador (Loja) to N.W. Peru (Cajamarca, Piura)]
- *quintecocha* Lamas & Willmott, **n. ssp.** [Fig. 2D; N. Peru (Amazonas)]
- *apurimac* Lamas & Willmott, **n. ssp.** [Fig. 2E-G; S. Peru (Apurimac, Cuzco)]
- *alfamayo* Lamas & Willmott, **n. ssp.** [Fig. 2H,I; S. Peru (Cuzco)]
- *n. ssp.?* [Fig. 11I; Peru (La Libertad)]; photographs of live butterflies taken by Jonathan Newman (Fig. 11I) and Remco Hofland (<https://observation.org/observation/175942503/>) on the same day at Cochorco, La Libertad, Peru (7°45'28"S, 77°46'20"W) may represent an additional undescribed subspecies not yet represented in any collection. These specimens are similar to the nominate subspecies but the outer edges of the orange postdiscal bands on both wings are tinged pale yellowish. Hofland (pers. comm.) reported seeing approximately 20 adults in the early afternoon of 7 July 2019 at Cochorco, which is also one of the few known sites for the extremely localized endemic Peruvian hummingbird Purple-backed Sunbeam (*Aglaeactis aliciae* Salvin). Given the large gaps within the distribution of *A. pyrrhosticta*, additional undescribed taxa seem likely.

eresia (C. Felder & R. Felder, 1862) [Fig. 3A,B; E. Colombia (Cordillera Oriental)]
- *lacrymosa* Oberthür, 1917 [Fig. 3C,D; C. Colombia (Cordillera Central)]



Figure 11. Images of new *Actinote* taxa in nature. **A,B**) Mating pair of *Actinote pyrrosticta* n. sp., female in foreground (A), and male (B), resting on rocks and low vegetation near edge of stream gully at type locality; **C-H**, *Actinote pyrrosticta apurimac* n. ssp., Peru, Cuzco, above Mollepata (photographs by David Geale). **C**) Last instar; **D**) Pupal case with freshly emerged adult adjacent; **E**) Cluster of pupae; **F,G**) Males nectaring on Asteraceae flowers; **H**) Female nectaring on Asteraceae flowers; **I**) *Actinote pyrrosticta* n. ssp.?, Peru, La Libertad, Cochorco (photograph by Jonathan Newman); **J**) *A. hilaris arcoiris* n. ssp. female, puddling on damp gravel, Ecuador, Morona-Santiago, Cebadas-Macas road; **K,L**) *Actinote hilaris sourakovi* n. ssp. female, dorsal (K) and ventral (L), Peru, Amazonas, Abra Patricia (photographs by David Geale).

- *leptogramma* Jordan, 1913 [Fig. 3E-H; Ecuador (Sucumbíos to Zamora-Chinchipe)]; the valva of the male genitalia in *A. e. leptogramma* (Fig. 7B) is noticeably broader and blunter than that of *A. e. eresina* (Fig. 7C) and the nominate subspecies (Fig. 7A), but it is similar to that of *A. e. canyaris* (Fig. 7D). Furthermore, the single available sequence of *A. eresia eresina* (AC87), from Cochabamba, Bolivia, did not form a clade with the remaining *A. eresia* sequences from Colombia and Ecuador (Fig. 1). Finally, in the few examined specimens, the sphragis of *A. e. eresina* was squared at the tip, and blunter than the pointed sphragis of *A. e. leptogramma*. Collectively, these observations suggest that *A. e. eresina* might perhaps be considered a species distinct from remaining *A. eresia* taxa, but the relatively close allopatry of known taxa suggests that they should conservatively be treated as conspecific until more data are available. Two specimens of *A. eresia* from west Colombia (Cauca) in the CEPUIJ (Fig. 3J) and RCCP are somewhat intermediate in wing pattern between *A. e. leptogramma* and typical *A. e. lacrymosa*, and may represent an undescribed subspecies, but given the variability within *A. e. leptogramma* and *A. e. lacrymosa*, we feel that more material is needed to clarify the taxonomy. Similarly, the southernmost known specimen of *A. e. leptogramma*, a female from the Jimbura-San Andrés road on the southern Ecuador-northern Peru border (PIBO), might represent a distinct subspecies, although it only differs from that shown in Fig. 3I in having more reduced orange at the base of the DFW.
- *albesia* Lamas & Willmott, **n. ssp.** [Fig. 4A,B; N. Peru (Amazonas)]
- *canyaris* Pycrz & Lamas, **n. ssp.** [Fig. 4C,D; N.W. Peru (Lambayeque)]
- *eresina* (Hopffer, 1874) [Fig. 4E-O; N. Peru (Amazonas, an apparently intermediate specimen to *albesia* Fig. 4E) to Bolivia (Cochabamba)]; Lamas (2004) listed several additional undescribed subspecies from Peru, which we here provisionally treat as *A. eresia eresina*. There is substantial variation within *A. eresia eresina*, both geographic (clinal?) and local, which includes, in particular: the presence or absence of a black spot in the middle of the FW discal cell, the separation or fusion of the DFW orange postdiscal band with the immediately basal orange area, the width of the dark margin in the DFW tornus and on the DHW, and the overall dorsal color, which varies from pale orange to a darker reddish orange (Fig. 4F-O). At least some locally distinctive phenotypes seem to be stable, but overall the picture is complex. Furthermore, the lack of DNA sequence data hinders recognition of genetically well-defined populations that might correspond with wing pattern differences, and the fact that the single available sequence for *A. e. eresina* does not group with other *A. eresia* (see discussion above under *leptogramma*) suggests that a thorough molecular and morphological study of *A. eresia* would be valuable, to determine both species and subspecies limits.
- - *binghamae* Dyar, 1913, **n. syn.** [Fig. 4K]; Lamas (2004) retained *Actinote binghamae* Dyar, 1913 as a valid subspecies, but the type locality (San Miguel, Cuzco, Peru) lies within the range of *A. eresia eresina*. A somewhat similar specimen in the PIBO from Peru, Puno, Sina (Fig. 4L), and another from Peru, Huánuco, E Acomayo (not figured) suggests that the holotype of *binghamae* is a form of *A. eresia eresina*, and we therefore place the name in synonymy (**n. syn.**).
- hilaris* Jordan, 1910 [Fig. 5K,L; C. Peru (Pasco) to Bolivia (Santa Cruz)]
- *desmiala* Jordan, 1913 [Fig. 5A,B; N.W. Ecuador (Carchi to Pichincha), N.E. Ecuador (Sucumbíos to Tungurahua)]
- - *culoti* (Oberthür, 1916)
- - *brownorum* (Potts, 1943)
- *arcoiris* Willmott & Hall, **n. ssp.** [Fig. 5C-H; S. Ecuador (Morona-Santiago to Zamora-Chinchipe)]
- *sourakovi* Willmott & Lamas, **n. ssp.** [Fig. 5I,J; S. Ecuador (Zamora-Chinchipe) to C. Peru (San Martín)]
- trinacria* (C. Felder & R. Felder, 1862) [Fig. 8A; E. Colombia (E. slope Cordillera Oriental)]
- - *iguaquensis* Andrade & Restrepo, 1992
- *naura* (Druce, 1875) [Venezuela (Cordillera de Mérida)]
- *chea* Druce, 1903 [E. Colombia (W. slope Cordillera Oriental)]; three males in the HAWA from Colombia, Cundinamarca, Chicaque road, resemble *A. t. trinacria* but have reduced red on the DFW, and may represent a distinct subspecies. A male specimen with similar wing pattern in the HAWA was collected further north, in Boyacá, thus leap-frogging the distribution of *A. trinacria chea* on the western slopes of the Cordillera Oriental. There is thus the possibility that these specimens represent transitional forms between subspecies, and we refrain from describing new taxa until the distribution of these forms becomes better known.
- *tenebrarum* Oberthür, 1917 [Fig. 8B; C. Colombia (Cordillera Central)]
- - *unicolor* Talbot, 1932
- *vivasi* Neild & Romero, 2008 [N. Colombia (Santander) to Venezuela (Sierra de El Tamá)]
- *santamarta* (Winhard, 2017) [N. Colombia (Sierra Nevada de Santa Marta)], **rev. stat.** Winhard (2017) introduced the name *Actinote santamarta* with a simple description of the taxon, without a diagnosis, which only arguably makes the name available under Article 13.1 of the ICZN (ICZN, 1999) since the characters described were not explicitly “purported to differentiate the taxon”. Lamas (2004) listed this taxon as “*Actinote trinacria* n. ssp. [2]”, since it shares a number of wing pattern characters with other taxa currently treated as subspecies of *A. trinacria*, as discussed under the description of *A. t. alegria*, and we here place it as a subspecies of *Actinote trinacria*. *Actinote trinacria santamarta* is most similar in wing pattern to *A. trinacria naura* and *A. trinacria vivasi*, but differs from both in having a reddish mark at the end of the DFW discal cell, and a DFW subapical band of three reddish marks in cells M₃-R₅.
- *alegria* Boyer & Willmott, **n. ssp.** [Fig. 8C,D; S. Colombia (Cauca) to N. Ecuador (Sucumbíos)]

ACKNOWLEDGMENTS

We thank the museum curators who allowed us to examine the Acraeini collections under their care, and individuals who provided access to or shared information from their private collections or field work, including Allan & Lesley Wolhuter, Carlos Prieto, Jere Schweikert, Steven Heydon, Jeff & Cathy Smith, Lynn Kimsey, Haydon Warren-Gash, Jamie Radford, Jean-Claude Petit, Phil Ackery, Blanca Huertas, Bob Robbins, and Axel Hausmann. We thank the Trustees of the Natural History Museum, London, for permission to publish images of specimens in that collection. We thank Santiago Villamarín, Sofia Nogales, Diego Inclán, the INABIO and Ecuadorian Ministerio del Ambiente, Agua y Transición Ecológica for arranging the necessary permits for research in Ecuador, most recently under the project ‘Diversity and Biology of Lepidoptera in Ecuador’ (No. MAATE-DNB-CM-2023-0298). Museum and field work was funded in part by the Leverhulme Trust, the Darwin Initiative, the FLMNH Museum Associates, the National Geographic Society (Research and Exploration Grant #5751-96), and the US National Science Foundation (NSF) (DEB-0103746, DEB-0639977, DEB-0639861, DBI-0847582, DEB-1256742). The fieldwork of Tomasz Pyrzc in Peru was supported by NCN grant Harmonia-10 2018/30/M/NZ8/00293 “Evolutionary biogeography and diversification of the predominantly Andean butterfly subtribe Pronophilina (Nymphalidae, Satyrinae) based on phylogenetic data generated using modern molecular methods”. We thank the owners and/or managers of Parque Nacional Podocarpus, Reserva Tapichalaca, and Fundación Arcoiris for providing access to their properties and facilities for research. For their companionship and assistance in the field, and/or providing specimen data and images, we thank Julia and Jamie Robinson Willmott, Kim Garwood, Andrew Neild, David Geale, Jonathan Newman, Remco Hoffland, Washington Galiano, and Raúl Aldaz. We thank the numerous people who contributed to databasing museum specimens, and Akito Kawahara, Becky Messcher and the ButterflyNet project (NSF DEB # 1541557) for providing two of the sequences used in the analysis. Finally, we thank Marlon Paluch and Carlos Prieto for their helpful comments on the manuscript.

LITERATURE CITED

- Carvalho, A. P. S., St Laurent, R. A., Toussaint, E. F. A., Storer, C., Dexter, K. M., Aduse-Poku, K., Kawahara, A. Y. 2021. Is sexual conflict a driver of speciation? A case study with a tribe of brush-footed butterflies. *Systematic Biology* 70(3): 413-420.
- Chazot, N. et al. 2021. Conserved ancestral tropical niche but different continental histories explain the latitudinal diversity gradient in brush-footed butterflies. *Nature Communications* 12(5717): 1-10.
- Comstock, J. H., Needham, J. G. 1898. The wings of insects. Chapter III. The specialization of wings by reduction. *American Naturalist* 32(376): 231-257.
- Francini, R. B., Freitas, A. V. L., Penz, C. M. 2004. Two new species of *Actinote* (Lepidoptera, Nymphalidae) from southeastern Brazil. *Zootaxa* 719: 1-10.
- Freitas, A. V. L., Francini, R. B., Paluch, M., Barbosa, E. P. 2018. A new species of *Actinote* Hübner (Nymphalidae: Heliconiinae: Acraeini) from southeast Brazil. *Revista Brasileira de Entomologia* 62(2): 135-147.
- Hall, T. A. 1999. BioEdit: a user-friendly biological sequence alignment editor and analysis program for Windows 95/98/NT. *Nucleic Acids Symposium Series* 41: 95-98.
- 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.
- ICZN (International Commission on Zoological Nomenclature) 1999. *International Code of Zoological Nomenclature. Fourth Edition*. London, The International Trust for Zoological Nomenclature.
- Jasinski, A. 1996. Description of three new subspecies of *Perisama* Doubleday from Ecuador and Northern Peru (Lepidoptera: Nymphalidae: Eurytelinae: Catagrammini). *Genus* 7(3): 503-514.
- Jasinski, A. 1998a. Description of a new species of *Catasticta* from Ecuador (Lepidoptera: Pieridae). *Genus* 9(3): 399-404.
- Jasinski, A. 1998b. Description of a new species of *Hypanartia* from southern Ecuador and northern Peru (Lepidoptera: Nymphalidae). *Genus* 9(3): 405-410.
- Kawahara, A. Y., et al. 2023. A global phylogeny of butterflies reveals their evolutionary history, ancestral hosts, and biogeographic origins. *Nature Ecology & Evolution* 7(6): 903-913.
- Lamas, G. 2004. *Nymphalidae. Heliconiinae*, pp. 261-274. 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.
- Neild, A. F. E. 2008. *The Butterflies of Venezuela. Part 2: Nymphalidae II (Acraeinae, Libytheinae, Nymphalinae, Ithomiinae, Morphinae)*. *A Comprehensive Guide to the Identification of Adult Nymphalidae, Papilionidae, and Pieridae*. London, Meridian Publications.
- Paluch, M., Casagrande, M. M., Mielke, O. H. H. 2006. Três espécies e duas subespécies novas de *Actinote* Hübner (Nymphalidae, Heliconiinae, Acraeini). *Revista Brasileira de Zoologia* 23(3): 764-778.
- Pierre, J. 1987. Systématique cladistique chez les *Acraea* (Lepidoptera, Nymphalidae). *Annales de la Société Entomologique de France* (N. S.) 23(1): 11-27.
- Scoble, M. 1992. *The Lepidoptera: Form, Function and Diversity*. London, Oxford University Press. ix + 352 pp.
- Silva-Brandão, K. L., Wahlberg, N., Francini, R. B., de Azeredo-Espin, A. M. L., Brown, K. S., Paluch, M., Lees, D. C., Freitas, A. V. L. 2008. Phylogenetic relationships of butterflies of the tribe Acraeini (Lepidoptera, Nymphalidae, Heliconiinae) and the evolution of host plant use. *Molecular Phylogenetics and Evolution* 46(2): 515-531.
- Tamura, K., Stecher, G., Kumar, S. 2021. MEGA11: Molecular Evolutionary Genetics Analysis version 11. *Molecular Biology and Evolution* 38(7): 3022-3027.
- Williams, M. C., Henning, G. A. 2023. Taxonomic revision of the tribe Acraeini Boisduval, 1833 (Papilionoidea: Nymphalidae: Heliconiinae). *Metamorphosis* 34: 35-49.
- Willmott, K. R., Freitas, A. V. L., Hall, J. P. W., Silva-Brandão, K. L., Paluch, M. 2009. A new species of *Actinote* Hübner from the eastern Andes of Ecuador (Lepidoptera: Nymphalidae: Heliconiinae). *Proceedings of the Entomological Society of Washington* 111(1): 47-56.
- Willmott, K. R., Lamas, G., Hall, J. P. W. 2017. Notes on the taxonomy of *Actinote intensa* Jordan (Lepidoptera: Nymphalidae: Heliconiinae) and the description of a new sibling species from eastern Ecuador. *Tropical Lepidoptera Research* 27(1): 6-15.
- Winhard, W. 2017. Neue tagfalterarten und -unterarten aus Kolumbien und Ecuador (Lepidoptera: Papilionidae, Pieridae et Nymphalidae). *Atalanta* 48(1-4): 261-274.
- Zhang, J., Cong, Q., Shen, J., Opler, P. A., Grishin, N. V. 2021. Genomics-guided refinement of butterfly taxonomy. *The Taxonomic Report of the International Lepidoptera Survey* 9(3): 1-54.

Appendix 1. Voucher specimen information for DNA sequence data.

Taxon	Locality (decimal latitude and longitude)	DNA voucher number	GenBank number
<i>Acraea (Telchinia) issoria</i>	Vietnam	NW108-22	EU275531
<i>Actinote alcione sodalis</i>	Peru: Junin: no specific locality	ac28	EU275554
<i>Actinote brylla</i>	Argentina: Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Seccional Yacui (-25.675, -54.169)	LEPIG188-11	MF546916
<i>Actinote dicaeus albofasciata</i>	Ecuador: Napo: no specific locality	E-51-18	EU275555
<i>Actinote dicaeus callianira</i>	Peru: Amazonas: 'Rodríguez de Mendoza' [= Mendoza] (-6.4, -77.483)	ac58	EU275557
<i>Actinote dicaeus callianira</i>	Peru: Junin: no specific locality	ac25	EU275556
<i>Actinote dicaeus ozinta</i>	Colombia: Putumayo: no specific locality	C-17-3	EU275558
<i>Actinote eresia eresia</i>	Colombia: Antioquia: Alto El Indio	BMC_16368	MN306758
<i>Actinote eresia eresia</i>	Colombia: Antioquia: Montañitas	BMC_11135	MN306609
<i>Actinote eresia eresia</i>	Bolivia: Cochabamba: no specific locality	ac87	EU275559
<i>Actinote eresia leptogramma</i>	Ecuador: Zamora-Chinchi: Quebrada Navidades (-3.975, -79.125)	LEP-00021	OR570623
<i>Actinote eresia leptogramma</i>	Ecuador: Zamora-Chinchi: Quebrada Navidades (-3.975, -79.125)	LEP-00022	OR570624
<i>Actinote eresia leptogramma</i>	Ecuador: Zamora-Chinchi: Quebrada Navidades (-3.975, -79.125)	LEP-00020	KY649580
<i>Actinote eresia leptogramma</i>	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-00238	OR570625
<i>Actinote eresia canyaris n. ssp.</i>	Peru: Lambayeque: vía 'Kañaris' [=Cañaris] (-6.057, -79.251)	CEP-UJ-2019-1271	OR570620
<i>Actinote erinome erinome</i>	Peru: Junin: no specific locality	ac34	EU275516
<i>Actinote hilaris desmiala</i>	Ecuador: Carchi: Santa Rosa (0.827, -78.128)	LEP-04153	KY649588
<i>Actinote hilaris desmiala</i>	Ecuador: Napo: Estación Científica Yanayacu (-0.59, -77.883)	LEP-00240	OR570627
<i>Actinote hilaris arcoiris n. ssp.</i>	Ecuador: Morona-Santiago: km 22 Limón-Gualaceo rd. (-3.008, -78.539)	LEP-04159	OR570631
<i>Actinote hilaris arcoiris n. ssp.</i>	Ecuador: Morona-Santiago: km 22 Limón-Gualaceo rd. (-3.008, -78.539)	LEP-04160	OR570632
<i>Actinote hilaris arcoiris n. ssp.</i>	Ecuador: Zamora-Chinchi: Quebrada Zurita (-3.972, -79.103)	LEP-04158	OR570630
<i>Actinote hilaris arcoiris n. ssp.</i>	Ecuador: Zamora-Chinchi: Quebrada Zurita (-3.972, -79.103)	LEP-06930	OR570634
<i>Actinote hilaris arcoiris n. ssp.</i>	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-00239	OR570626
<i>Actinote hilaris arcoiris n. ssp.</i>	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-01555	OR570628
<i>Actinote hilaris arcoiris n. ssp.</i>	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-01556	OR570629
<i>Actinote hilaris sourakovi n. ssp.</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-04161	OR570633
<i>Actinote hilaris sourakovi n. ssp.</i>	Ecuador: Zamora-Chinchi: Quebrada Honda trail (-4.472, -79.122)	LEP-00006	OR570621
<i>Actinote hilaris sourakovi n. ssp.</i>	Ecuador: Zamora-Chinchi: Quebrada Honda trail (-4.472, -79.122)	LEP-00007	OR570622
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-37581	KY649611
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-04156	KY649589
<i>Actinote mamita</i>	Argentina: Buenos Aires: Partido de Magdalena, Estancia El Destino (-35.125, -57.375)	LEPPA098-11	MF546233
<i>Actinote melanisans</i>	Argentina: Misiones: Departamento de Iguazú, Parque Nacional Iguazú, Seccional Yacui (-25.675, -54.169)	LEPIG155-11	MF546994
<i>Actinote momina</i>	Peru: Cuzco: no specific locality	RV-03-V240	EU275560
<i>Actinote negra demonica</i>	Bolivia: La Paz: Coroico (-16.226, -67.737)	ac46	EU275561
<i>Actinote negra demonica</i>	Peru: Cuzco: Santa Teresa (-13.187, -72.588)	ac45	EU275573
<i>Actinote negra euclia</i>	Peru: Cajamarca: no specific locality	ac64	EU275562
<i>Actinote neleus neleus</i>	Colombia: Antioquia: Sabaneta	ac16	EU275563
<i>Actinote pellenea pellenea</i>	Brazil: São Paulo: Santos (-23.967, -46.333)	ac37	EU275600
<i>Actinote pellenea ssp</i>	Argentina: Buenos Aires: Partido de Magdalena, Estancia El Destino (-35.125, -57.375)	LEPPA087-11	MF546829
<i>Actinote p. pyrrhosticta n. sp.</i>	Ecuador: Loja: km 13.2 Jimbura-San Andrés rd. (-4.709, -79.446)	LEP-16954	OR570635
<i>Actinote p. pyrrhosticta n. sp.</i>	Ecuador: Loja: km 13.2 Jimbura-San Andrés rd. (-4.709, -79.446)	LEP-16955	OR570636
<i>Actinote p. pyrrhosticta n. sp.</i>	Ecuador: Loja: km 13.2 Jimbura-San Andrés rd. (-4.709, -79.446)	LEP-37389	OR570637
<i>Actinote rubrocellulata</i>	Peru: Ancash: no specific locality	ac76	EU275564
<i>Actinote tenebrosa tenebrosa</i>	Ecuador: Sucumbios: La Bonita (0.474, -77.54)	NW90-15	EU275565