

Notes on the taxonomy of *Actinote intensa* Jordan (Lepidoptera: Nymphalidae: Heliconiinae) and the description of a new sibling species from eastern Ecuador

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Abstract: We review the taxonomy of *Actinote intensa* Jordan **stat. rest.** and describe a new sibling species, *Actinote johncoulsoni* Willmott, Lamas & Hall, **n. sp.**, from the east Andean slopes of central and southern Ecuador. The species are broadly sympatric, occur in the same sites throughout the more restricted range of the new species, and differ in a number of wing pattern characters, supported by a mean 2% pairwise divergence in their COI DNA barcodes.

Resumen: Revisamos la taxonomía de la especie *Actinote intensa* Jordan **stat. rest.** y describimos una nueva especie relacionada, *Actinote johncoulsoni* Willmott, Lamas & Hall, **n. sp.**, de las vertientes orientales de los Andes en el centro y sur del Ecuador. Las especies son simpátricas y ocurren en los mismos sitios en el rango más restringido de la especie nueva, y tienen una variedad de caracteres diferentes en el patrón del ala, apoyados por una divergencia promedio de 2% en sus códigos de barra del gen COI.

Key words: Acraeini, Andes, cloud forest, cryptic species, DNA barcoding, Peru, wing pattern

INTRODUCTION

Although not nearly as diverse as their Old World relatives, the Neotropical Acraeini contains more than fifty species and the group has been the subject of a number of recent taxonomic studies. The generic classification of these species is currently unresolved, with Pierre (1987) placing all Neotropical species within the pantropical genus *Acraea* Fabricius, 1807, and the most recent classification (Lamas, 2004) dividing the same species among three genera, *Actinote* Hübner, [1819], *Altinote* Potts, 1943, and *Abananote* Potts, 1943. Potts (1943), partly following Jordan (1913), used characters of the scale morphology on the ventral wing surfaces to separate *Actinote* and *Altinote*, placing *Abananote* as a subgenus of the latter. The monophyly of these taxa remained untested, however, until Silva-Brandão *et al.* (2008) showed that although *Actinote* as conceived by Lamas (2004) represented a single clade, neither *Altinote* nor *Abananote* was monophyletic. Silva-Brandão *et al.* (2008: 528) therefore suggested that “*Actinote* Hübner, [1819] should be expanded to include all Neotropical Acraeini”, and we follow that suggestion here, referring to *Actinote* in the sense of Lamas (2004) as *Actinote sensu stricto* (*s. s.*).

Actinote has also been the subject of a notable number of new species descriptions in recent years (e.g., Penz & Francini, 1996; Francini *et al.*, 2004; Paluch *et al.*, 2006; Neild, 2008; Willmott *et al.*, 2009). All of those species have been within *Actinote s. s.*, which reaches its highest diversity in southeastern Brazil and the periphery of the Amazon basin (Silva-Brandão *et al.*, 2008). In Andean cloud forest habitats, however, the dominant species are those that were placed by Lamas (2004) in the genera *Abananote* and *Altinote*. Within those groups

a number of species are very restricted in distribution and poorly represented in collections, and Lamas (2004) listed two undescribed species under those generic names from Peru. Otherwise, no new species outside of *Actinote s. s.* have been described for more than 50 years, the most recent being *Actinote rubrocellulata* Hayward, 1960 (Lamas, 2004).

During a long-term survey of the butterflies of Ecuador, we noticed that series from single sites of the species formerly known as “*Actinote radiata*” (e.g., Jordan, 1913; D’Abrera, 1987; Lamas, 2004) often apparently contained two distinct phenotypes. However, substantial wing pattern variation within each of those phenotypes complicated the identification of diagnostic characters and the correct application of described names. Here, we use DNA “barcodes” to clarify species limits, investigate possible relationships with allopatric taxa, review the identity of existing names, and describe a new sibling species that is widespread and locally common from central to southeastern Ecuador.

MATERIALS AND METHODS

Field work was conducted by the authors and colleagues throughout Ecuador and Peru over many years to collect material for taxonomic study and document distribution and behavior. Material was studied in numerous 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; JEPE: Jean-Claude Petit collection, Ducey, France; KWJH: Keith R.

Willmott & Jason P. W. Hall collection, Gainesville, FL, USA; INABIO: Instituto Nacional de Biodiversidad, Quito, Ecuador; MZUJ: Muzeum Zoologiczne Uniwersytetu Jagiellońskiego, Kraków, Poland; NHMUK: Natural History Museum, London, UK; PIBO: Pierre Boyer collection, Le Puy, France.

Morphology was studied using standard techniques, with adult abdomens being 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 (1918). We use the abbreviations DFW, VFW, DHW and VHW for dorsal and ventral forewing and hind wing.

We extracted genomic DNA 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 50-100 ul with the smaller elution for older specimens. 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 primer pairs LCO (forward, GGTCACAAATCATAAAGATATTGG) and HCO (reverse, TAAACTTCAGGGTGACCAAAAAATCA) (Folmer *et al.*, 1994), or LCO_nym (forward, TTTCTACAAATCATAAAGATATTGG) and HCO_nym (reverse, TAAACTTCAGGATGACCAAAAA) (Neild *et al.*, 2015), or LepF1 (forward, ATTCAACCAATCATAAAGATAT) and LepR1 (reverse, AACTTCTGGATGTCCAAAAA) (Hebert *et al.*, 2004). For recalcitrant samples we amplified the gene region in two fragments, using primer pairs LCO_nym and K699 (reverse, WGGGGGGTAAACTGTTCATCC), and Ron (forward, GGATCACCTGATATAGCATTTCC) and Nancy (reverse, CCTGGTAAATATAAATATAAACTTC) (Monteiro & Pierce, 2001; Elias *et al.*, 2007). All PCR reactions were conducted in a 20 ul volume comprising 2 ul DNA, 0.4 ul of each primer (10 uM), 0.5 ul of Bovine Serum Albumin (BSA, 20 mg/mL) (for older samples), MgCl₂ catalyst and *Taq* DNA polymerase. Typical reaction conditions were as follows: 1 min at 94°C followed by 5 cycles of 30 s at 94°C, 40 s at 45°C, 1 min at 68-72°C (depending on the *Taq* mix), followed by 35 cycles of 30 s at 94°C, 40 s at 51°C, 1 min at 68-72°C, followed by 5 min at 68-72°C. 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.

Where necessary, fragments were assembled into composite sequences and all 43 new sequences were aligned using BioEdit v. 7.1.3 (Hall, 1999), with 17 additional sequences obtained from GenBank (Appendix 1). The final aligned sequences were of length 666 bp. To test for consistent genetic differences between phenotypes we conducted a neighbor-joining analysis using MEGA 7.0 (Kumar *et al.*, 2016), with the Kimura 2-parameter substitution model, partial deletion of sites with missing data, and other default settings. The same settings were used to compute mean pairwise distances between sequences, between and within groups. New sequences are deposited in GenBank.

RESULTS AND DISCUSSION

DNA barcodes

The neighbor-joining analysis of the DNA barcode sequences showed a single clade containing specimens with the "*A. radiata*" wing pattern, which was split into two distinct clades corresponding to the two phenotypes initially recognized within series of sympatric specimens (Fig. 1). Examination of specimens within each clade allowed the identification of diagnostic wing pattern differences (see Table 1) that enabled us to associate relevant type specimens with one of the clades, *A. intensa*, while the other clade represents the new species described here, *A. johncoulsoni* n. sp.. The mean pairwise distance between the two species was 2%, while within-group mean pairwise distances were 0.5% (*A. intensa*) and 0.1 % (*A. johncoulsoni* n. sp.). Within *A. intensa*, three Peruvian specimens (LEP-04012, LEP-04014, LEP-04015) formed a somewhat isolated clade along with a specimen (LEP-04013) putatively from Tungurahua province in Ecuador. The latter specimen has a similar wing pattern to the Peruvian specimens (different from other Tungurahua *A. intensa*) and comes from the same collection, so we assume that it represents a labeling error. The clade containing *Actinote intensa* and *A. johncoulsoni* was relatively distant from the nearest other included sequences.

Actinote intensa Jordan, 1910, stat. rest. (Figs. 2A-I, 3A, 4, 5D,E)

Actinote radiata intensa Jordan (1910: 463). **Type locality:** Peru, [Pasco], Cushi, 1800-1900 m. **Types:** **Lectotype** ♂: "LECTOTYPE ♂ *Actinote radiata intensa* Jordan G. Lamas. det. 1987//Cushi, Prov. Huanuco, Peru, 1900 m (W. Hoffmanns)//*A. radiata intensa* Type. Jord. Nov. Zool. 1910./LECTOTYPE//Type"; **Paralectotypes** (6 ♂): 3 ♂, same collection data as lectotype; 3 ♂, same collection data as lectotype except 1820 m, 1904; (NHMUK) (all examined).
=*Acraea radiata* Hewitson (1868: [32], pl. [18], figs. 39-41), junior primary homonym of *Acraea zitja* var. *radiata* Guenée, 1865. **Type locality:** Ecuador. **Types:** **Lectotype** ♂: "LECTOTYPE ♂ *Acraea radiata* Hewitson G. Lamas. det. 1987//Ecuador Hewitson Coll. 79.-69. *Acraea radiata*, Hew. 3//B. M. Type No. Rh 7721 *Acraea radiata*, ♂ Hew./LECTOTYPE//Type H. T."; **Paralectotypes** ♀: "PARALECTOTYPE ♀ *Acraea radiata* Hewitson G. Lamas. det. 1987//Ecuador Hewitson Coll. 79.-69. *Acraea radiata*, Hew. 4//B. M. Type No. Rh 7722 *Acraea radiata*, ♀ Hew./Paralectotype//Type H. T.//BMNH(E) #808382"; **Paralectotypes** (2 ♂): 1 ♂: "Ecuador Hewitson Coll. 79.-69. *Acraea radiata*, Hew. 2" [= *A. johncoulsoni* n. sp.]; 1 ♂: "Ecuador Hewitson Coll. 79.-69. *Acraea radiata*, Hew. 1" [= *A. johncoulsoni* n. sp.]; (NHMUK) (all examined).
=*Acraea (Abananote) intensa gerardolamas* Kemal & Koçak (2007: 2), replacement name, n. syn. **Type locality** and **Types** as for *Acraea radiata* above.

Actinote radiata radiata Hewitson: Jordan (1913); D'Abrera (1987: 436 – figured specimen is *A. johncoulsoni*)

Actinote radiata intensa Jordan: Jordan (1913); D'Abrera (1987)

Abananote radiata radiata (Hewitson): Lamas ([1997]); Lamas (2004)

Abananote radiata intensa (Jordan): Lamas ([1997]); Lamas (2004)

Acraea (Abananote) intensa Jordan: Kemal & Koçak (2007)

Acraea (Abananote) intensa intensa Jordan: Kemal & Koçak (2007)

Diagnosis: Identification of this species with respect to *A. johncoulsoni* n. sp. is discussed under the latter species. *Actinote intensa* and *A. johncoulsoni* are otherwise easily identified from other species in the genus by the long, black hair-like scales present on the VHW in the basal half of cell Cu1-M3 (shared

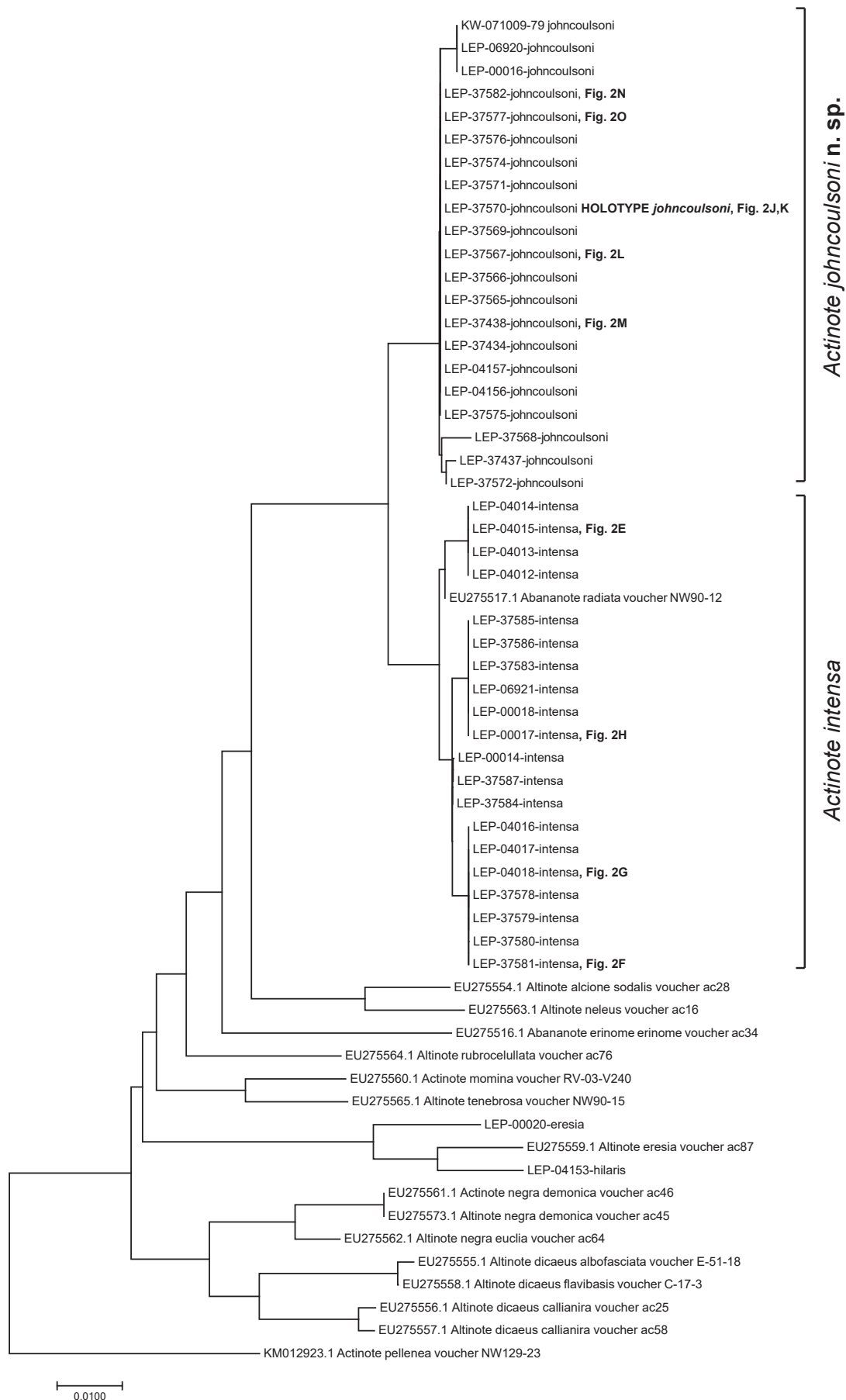


Fig. 1. Neighbor-joining tree (Kimura 2-parameter) for *Actinote intensa* and relatives based on 666 bp of COI (barcode region).

with *A. erinome* (C. Felder & R. Felder, 1861) and *A. abana* (Hewitson, 1868) and noted by Jordan (1913)), the orange DFW band composed of rays, and by the thin orange scaling lining the edges of the veins on the VHW. The male genitalia of *A. intensa* and *A. johncoulsoni* most closely resemble that of *A. abana*, but differ in having a sclerotized band around the aedeagus immediately anterior of the attachment of the manica.

Taxonomy and variation: Hewitson (1868) described *Acraea radiata* from an unspecified number of specimens in his collection from Ecuador. He described both sexes, and figured the upperside and underside of presumably the same specimen in figs. 39 and 40, and the upperside of another specimen in fig. 41. The lectotype specimen in the NHMUK (Fig. 2C,D) designated by Lamas ([1997]) matches figs. 39 and 40, while the second figured specimen, fig. 41, matches the paralectotype female in the NHMUK (Fig. 2I). Both of these types have the diagnostic wing pattern characters of *A. intensa* as defined here (see under Diagnosis for *A. johncoulsoni* n. sp.). However, an additional two specimens in the NHMUK from Hewitson's collection that are also paralectotypes represent *A. johncoulsoni*.

Jordan (1910) described a new subspecies, *Actinote radiata intensa*, based on a series of male specimens from Cushi, [Pasco], Peru in the NHMUK. The lectotype was designated by Lamas ([1997]) and is illustrated in Fig. 2A,B. Jordan (1910) stated that the dorsal ground color was darker than in Ecuadorian specimens, and that the orange postdiscal streaks were narrower on the DFW and more pinkish on the VFW. Although these features are apparent in the majority of specimens examined, there is also substantial variation in the width of the orange DFW band even within Ecuador (Fig. 2F,G,H), and we feel that the differences are not sufficiently consistent or marked to merit subspecific recognition. Within Ecuador there seems to be an approximate cline in the width of the orange DFW band, which is broadest in Tungurahua, moderate in Morona-Santiago, and narrowest in Zamora-Chinchipec provinces. However, we feel that there are no easily defined discontinuities in this variation that would allow the recognition of subspecies.

Actinote radiata was widely used as the name for this species until Kemal & Koçak (2007) noted that it was a junior primary homonym of *Acraea zitja* var. *radiata* Guenée, 1865, and provided the replacement name *Acraea (Abanote) intensa gerardolamas*. *Actinote intensa* therefore becomes the oldest name for the species (**stat. rest.**) and we treat the name

gerardolamas, which applies to Ecuadorian specimens, as a junior subjective synonym (**n. syn.**).

Distribution: *Actinote intensa* occurs along the eastern Andes from the Río Pastaza valley (Tungurahua) in Ecuador, to central Peru (Junín) (Fig. 4). A single specimen in the MZUJ was supposedly collected along the Tena-Loreto road, Napo province, at 1400 m by H. Greeney. We have seen no other specimens from this rather well-sampled road, the elevation is unusually low for the species, and the wing pattern resembles that of Peruvian specimens rather than those from nearby Tungurahua, so the record requires confirmation.

Habitat and ecology: *Actinote intensa* occurs in intact cloud forest habitats, from 1600-2500 m in Ecuador and 1360-3000 m in Peru (Fig. 5A). Males are locally common along rivers and wide streams, flying from 2-6 m, where they also congregate to feed at damp gravel and rock faces (Fig. 5D,E), particularly wherever there is urine or rotting carrion. We have also recorded several males in mid-storey and canopy traps baited with rotting fish inside forest. We have never seen the female in nature and it is very rare in collections.

Actinote johncoulsoni Willmott, Lamas & Hall, new species
(Figs. 2J-O, 3B-H, 4, 5B,C)

Diagnosis and identification: *Actinote johncoulsoni* n. sp. can be consistently distinguished from its sister species *A. intensa* by a number of wing pattern characters. Firstly, the two orange-pink spots in the VFW tornus of *A. intensa* are approximately equal in size, such that an imaginary line connecting their basal edges is parallel to the wing distal margin (see Fig. 2B,D,F). In *A. johncoulsoni*, the anterior spot is about twice the width of the posterior, and the aforementioned imaginary line is not parallel to the wing margin (see Fig. 2K,L). This is the only wing pattern character that seems to be stable throughout the range of both species. Nevertheless, based on the DNA barcode analysis, in localities where the two species are sympatric several other characters are useful in concert to identify them. These include, in particular, the more pinkish VFW postdiscal band and greater basal extension of this band in cell M1-R5 in *A. johncoulsoni*, while other useful characters are described in Table 1 and illustrated in Fig. 2F,L. No consistent genitalic characters were found to distinguish the species from *A. intensa*.

Table 1. Wing pattern characters differentiating *Actinote intensa* and *A. johncoulsoni* n. sp. Only character 7 is consistent in all examined specimens, but the presence of a majority of the other characters helps to confirm identification. Less obvious characters are indicated on Fig. 2F,L.

No.	Character	<i>A. intensa</i>	<i>A. johncoulsoni</i> n. sp.
1	Dorsal ground color	Brownish black	Grayish black
2	DFW postdiscal band color	Orange	Pinkish orange
3	DHW dark intervenal stripes	Hardly visible, instead veins on DHW more conspicuously marked	Darker intervenal strips more conspicuous
4	VFW postdiscal band color	Orange	Pinkish orange
5	VFW postdiscal band extent	Not extending to base of cell M1-R5 or notably more basally than in adjacent cell M2-M1	Extending to base of cell M1-R5 and notably more basally than in adjacent cell M2-M1
6	VFW costa	Black with scattered orange scales	Black with few or no orange scales
7	VFW orange paired tornal spots	Similar in size	Anterior spot larger



A



C



J



B



D



K

LECTOTYPE ♂
Actinote radiata
intensa Jordan
G.Lamas, det. 1987



A. radiata
intensa
Type. fort.
Nov. 1910.

Cuzhi,
Prov. Huancayo,
Peru, 1900 m
(W. Hoffmann).

LECTOTYPE ♂
Acraea radiata
Hewitson
G.Lamas, det. 1987

Ecuador
Hewitson Coll.
798 ♂.
Acraea
radiata, New
3

B.M. TYPE
No. Rh7721
Acraea
radiata
♂ New.



ECUADOR: Zamora-Chinipe
nr. Sabanilla, Loja-Zamora rd.,
Quebrada San Ramón, power
station
1700-1850m,
13.viii.2009, K.R. Willmott & J. P.
W. Hall
FLMNH# 145142

DNA voucher
LEP-37570

A. intensa, LT ♂, Peru

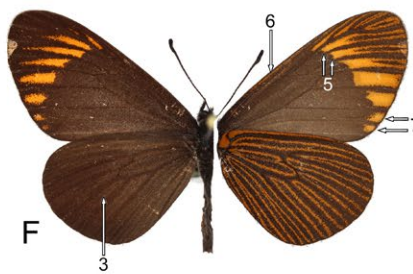
A. intensa, (LT *Acraea radiata*) ♂, Ecuador

A. johncoulsoni n. sp., HT ♂



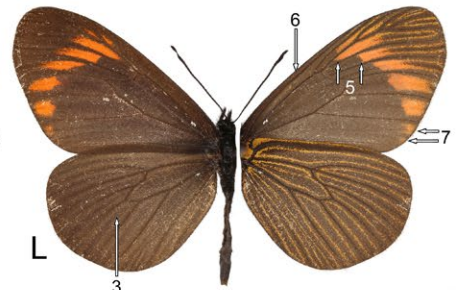
E

A. intensa, ♂, Peru



F

A. intensa, ♂, Ecuador



L

A. johncoulsoni, ♂, Ecuador



G

1 cm

A. intensa, ♂, Ecuador



H

A. intensa, ♂, Ecuador



M

A. johncoulsoni, ♂, Ecuador



I

1 cm *A. intensa*, ♀, Ecuador



N

A. johncoulsoni, ♀, Ecuador



O

A. johncoulsoni, ♀, Ecuador

Description: MALE (Fig. 2J,K): Forewing length of holotype 25 mm (21-26 mm, mean 24.1 mm, n=28). *Wing shape and color pattern:* very similar to *A. intensa*, as illustrated (Fig. 2J,K) and described in comparison with *A. intensa* (Table 1). VHW with long, black hair-like scales ('bristles' of Jordan (1913) and Potts (1943)) along veins and in cells except for distal half of cells anterior of vein Cu1. *Head:* eyes black, bare; antennae black with sparse black needle-like scales dorsally, 31 antennomeres with terminal 9 antennomeres comprising club; labial palpi with very sparse, long, black, hair-like scales perpendicular to palpus surface on basal and middle segment, very sparse black scales laterally on middle segment; top of head black, frons with sparse, long, black, hair-like scales. *Thorax:* dorsal surface black, ventral surface black, forelegs, mid- and hind legs black. *Abdomen:* dorsal surface black, ventral surface black except for spots of orange scaling in middle of each sternite in anterior half, and line of orange scaling laterally dorsal of sternites. *Genitalia* (Fig. 3B): as illustrated (Fig. 3B). Notable features include the gently curving uncus, lack of gnathos, sharply curving valvae, and the aedeagus with a sclerotized ring just anterior of the manica attachment. The juxta is a rather irregular, approximately "V"-shaped plate.

FEMALE: (Fig. 2N,O): Forewing length 27-28 mm, mean 27.4 mm (n=5). *Wing shape and color pattern:* similar to male except wings slightly more elongate, orange markings typically more extensive. *Head, thorax, abdomen:* similar to male in coloration. Four out of six examined females with a sphragis, a curving, rectangular plate, terminating ventrally in a tuft of scales perpendicular to abdomen (Fig. 3H); dissected specimen lacked a sphragis. *Genitalia* (Fig. 3C-G): as illustrated (Fig. 3C-G). Notable features include lamella ante- and postvaginalis fused into a single approximately circular plate with circular ostium bursae (Fig. 3D); lamella antevaginalis wrinkled and covered with tiny protuberances and spines; antrum a weakly sclerotized, small band; ductus bursae very short, ductus seminalis thin, corpus bursae small, similar in size to lamella antevaginalis plus lamella postvaginalis (Fig. 3E); subpapillary glands similar in size to papillae anales (Fig. 3E,G).

Types: HOLOTYPE ♂: **ECUADOR:** *Zamora-Chinchipe:* nr. Sabanilla, Loja-Zamora rd., Quebrada San Ramón, power station, [3°58'12"S,79°3'42"W], (K.R. Willmott & J. P. W. Hall), 13 Aug 2009, 1 ♂ [FLMNH-MGCL-145142], (FLMNH, to be deposited in INABIO).

Paratypes (66 ♂, 7 ♀): **ECUADOR:** *Loja:* km 15 Loja-Zamora rd., 2600-2800 m, 20 Feb 1996, 1 ♂, (PIBO); 'Loja' - (error), 1 ♂, (NHMUK); *Morona-Santiago:* 42 km W Méndez, 1600 m, (Petit, J.-C.), 14 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-145572], 1 ♂ [FLMNH-MGCL-146406], (FLMNH); km 25 Macas-Nueve de Octubre rd., [2°15'42"S,78°12'54"W], 1600-2100 m, (Boyer, P.), 6 Dec 1998, 1 ♂, (PIBO); km 44.5 Gualaceo-Limón rd., Río Gualaceño, [3°1'26"S,78°38'7"W], 2175 m, (Willmott, K. R.), 7 Oct 2007, 1 ♂ [FLMNH-MGCL-113346], 1 ♂ [FLMNH-MGCL-113348], 1 ♂ [FLMNH-MGCL-113350], (FLMNH); Limón-Gualaceo rd., [3°0'30"S,78°34'6"W], 2200 m, (Wojtusiak, J., Pyrcz, T.), 31 Aug 2003, 1 ♂, (MZUJ); San Martín, Chigüinda, [3°13'41"S,78°41'59"W], 2030 m, (Willmott, K. R.), 11 Oct 2007, 1 ♂ [FLMNH-MGCL-113347], (FLMNH); *Zamora-Chinchipe:* Destacamento Paquisha Alto, [3°54'28"S,78°29'5"W], 2100 m, (Radford, J.), 3 Sep 2010, 1 ♀ [PAN112], (FLMNH) (CULEPEX Expedition, 2010); km 17.6 San Andrés-Zumba rd., Quebrada de los Rubies, [4°52'37"S,79°12'34"W], 1660 m, (Willmott, K. R., J. C. R., J. I. R.), 22 Jun 2014, 1 ♂ [FLMNH-MGCL-280790], (FLMNH); km 18 Yacuambi-Saraguro rd., Cascada Hampik Yaku, [3°33'56"S,78°58'6"W], 2000 m, (Willmott, K. R., J. C. R., J. I. R.), 21 Jun 2013, 1 ♀ [FLMNH-MGCL-157825], (FLMNH); km

24 Loja-Zamora rd., San Francisco, casa de Arcoiris, [3°59'18"S,79°5'42"W], 2000-2100 m, (Willmott, K. R., Aldaz, R.), 23 Oct 2006, 1 ♀ [FLMNH-MGCL-119807], (FLMNH); km 30 Loja-Zamora rd., 'station électrique', [3°58'12"S,79°3'42"W], 1800 m, 20 Feb 1996, 1 ♂, (PIBO); 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-146465], (FLMNH); 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-145574], 1 ♂ [FLMNH-MGCL-146462], 1 ♂ [FLMNH-MGCL-146464], 1 ♂ [FLMNH-MGCL-146466], 1 ♂ [FLMNH-MGCL-146467], 1 ♀ [FLMNH-MGCL-145573], 1 ♀ [FLMNH-MGCL-146461], 1 ♀ [FLMNH-MGCL-146463], (FLMNH), 1 ♂, (INABIO); km 6 San Andrés-Jimbura rd., Quebrada Troya, [4°47'32"S,79°18'42"W], 2050 m, (Willmott, K. R., J. C. R., J. I. R.), 20 Jun 2014, 1 ♂ [FLMNH-MGCL-280788], 1 ♂ [FLMNH-MGCL-280791], (FLMNH), 5 ♂, (INABIO), 21 Jun 2014, 1 ♂ [FLMNH-MGCL-195833], 1 ♂ [FLMNH-MGCL-195834], 1 ♂ [FLMNH-MGCL-195835], 1 ♂ [FLMNH-MGCL-195836], (FLMNH), 5 ♂, (INABIO), 29 May 2013, 1 ♂ [FLMNH-MGCL-157826], 1 ♂ [FLMNH-MGCL-157827], (FLMNH), 8 ♂, (INABIO); km 7 San Andrés-Jimbura rd., trail to Río Bolívar, [4°47'11"S,79°18'50"W], 2050 m, (Willmott, K. R., J. C. R., J. I. R.), 31 May 2013, 1 ♂, (INABIO); Loja-Zamora rd., [3°59'30"S,79°8'12"W], 2700-2800 m, Jun 1998, 2 ♂, (PIBO); Loja-Zamora rd., Río San Francisco, [3°58'42"S,79°6'6"W], 1900 m, (Willmott, K. R.), 28 Oct 1997, 1 ♂, (KWJH); nr. Sabanilla, Loja-Zamora rd., Quebrada San Ramón, power station, [3°58'12"S,79°3'42"W], (Willmott, K. R., Hall, J. P. W.), 13 Aug 2009, 1 ♂ [FLMNH-MGCL-145143], 1 ♂ [FLMNH-MGCL-145144], 1 ♂ [FLMNH-MGCL-145145], 1 ♂ [FLMNH-MGCL-145146], 1 ♂ [FLMNH-MGCL-145147], (FLMNH); Quebrada Zurita, old Loja-Zamora rd., [3°58'1"S,79°6'53"W], 2100 m, (Willmott, K. R., J. C. R., J. I. R.), 1 Jul 2014, 1 ♂ [FLMNH-MGCL-280789], (FLMNH); Río Sabanilla, [3°58'12"S,79°3'42"W], 1300 m, (Jasinski, A.), 19 May 1996, 1 ♂, (MZUJ); "Zamora, 915-1220 m", (Baron, O.), 9 ♂, (NHMUK); Zamora-Loja rd., San Francisco, canal subterráneo, [3°58'44"S,79°5"W], 1800 m, (Willmott, K. R.), 04 Feb 2002, 1 ♂, (KWJH).

Other examined specimens (3 ♂): **Ecuador:** 'Ecuador', 1 ♂ ['Ecuador Hewitson Coll. 79-69 *Acraea radiata*, Hew. 1./Ecuad.'], 1 ♂ ['Ecuador Hewitson Coll. 79-69 *Acraea radiata*, Hew. 2./Ecuad.'], (paralectotypes of *Acraea radiata*, NHMUK); 'S Ecuador', 1 ♂, (NHMUK).

Etymology: This species is named for Kenneth John Coulson, who has been for many years a firm and generous friend with a great spirit of adventure and a boundless sense of humor (KRW).

Taxonomy and variation: The first question to be addressed is whether the two apparently distinct wing pattern phenotypes seen in sympatric series from Ecuador represent variation or distinct species. The DNA barcode data strongly support the latter (Fig. 1). Barcoded specimens of both species were collected in micro-sympatry at four sites, and in broader sympatry throughout the range of *A. johncoulsoni*, and these grouped into two distinct clusters with a mean between-group pairwise distance of 2%, and mean within-group pairwise distance of 0.1% (*A. johncoulsoni*) and 0.5% (*A. intensa*).

Fig. 2 (facing page). *Actinote intensa* and *A. johncoulsoni* n. sp. Numbered arrows refer to characters in Table 1. **A-I, *Actinote intensa*.** Split specimens show dorsal surface on left, ventral surface on right. **A,B: Lectotype** male of *Actinote radiata intensa*, Peru, [Pasco], Cushi, NHMUK: A, dorsal surface, B, ventral surface and specimen labels (Courtesy of the Trustees of the Natural History Museum). **C,D: Lectotype** male of *Acraea radiata* and *Acraea (Abananote) intensa gerardolamas*, Ecuador: C, dorsal surface, D, ventral surface and specimen labels (Courtesy of the Trustees of the Natural History Museum). **E:** male, Peru, Amazonas, Pomacochas (LEP-04015). **F:** male, Ecuador, Zamora-Chinchipe, Quebrada San Ramón (LEP-37581). **G:** male, Ecuador, Zamora-Chinchipe, Quebrada San Ramón (LEP-04018). **H:** male, Ecuador, Morona-Santiago, Río Retiro (LEP-00017). **I:** paralectotype female of *Acraea radiata*, Ecuador, NHMUK (Courtesy of the Trustees of the Natural History Museum). **J-O, *Actinote johncoulsoni*.** **J,K. Holotype** male of *Actinote johncoulsoni* n. sp., Ecuador, Zamora-Chinchipe, Quebrada San Ramón: J, dorsal surface, K, ventral surface and specimen labels. **L:** male, Ecuador, Zamora-Chinchipe, Quebrada Troya (LEP-37567). **M:** male, Ecuador, Zamora-Chinchipe, Quebrada Troya (LEP-37438). **N:** female, Ecuador, Zamora-Chinchipe, San Francisco (LEP-37582). **O:** female, Ecuador, Zamora-Chinchipe, Finca San Carlos (LEP-37577).

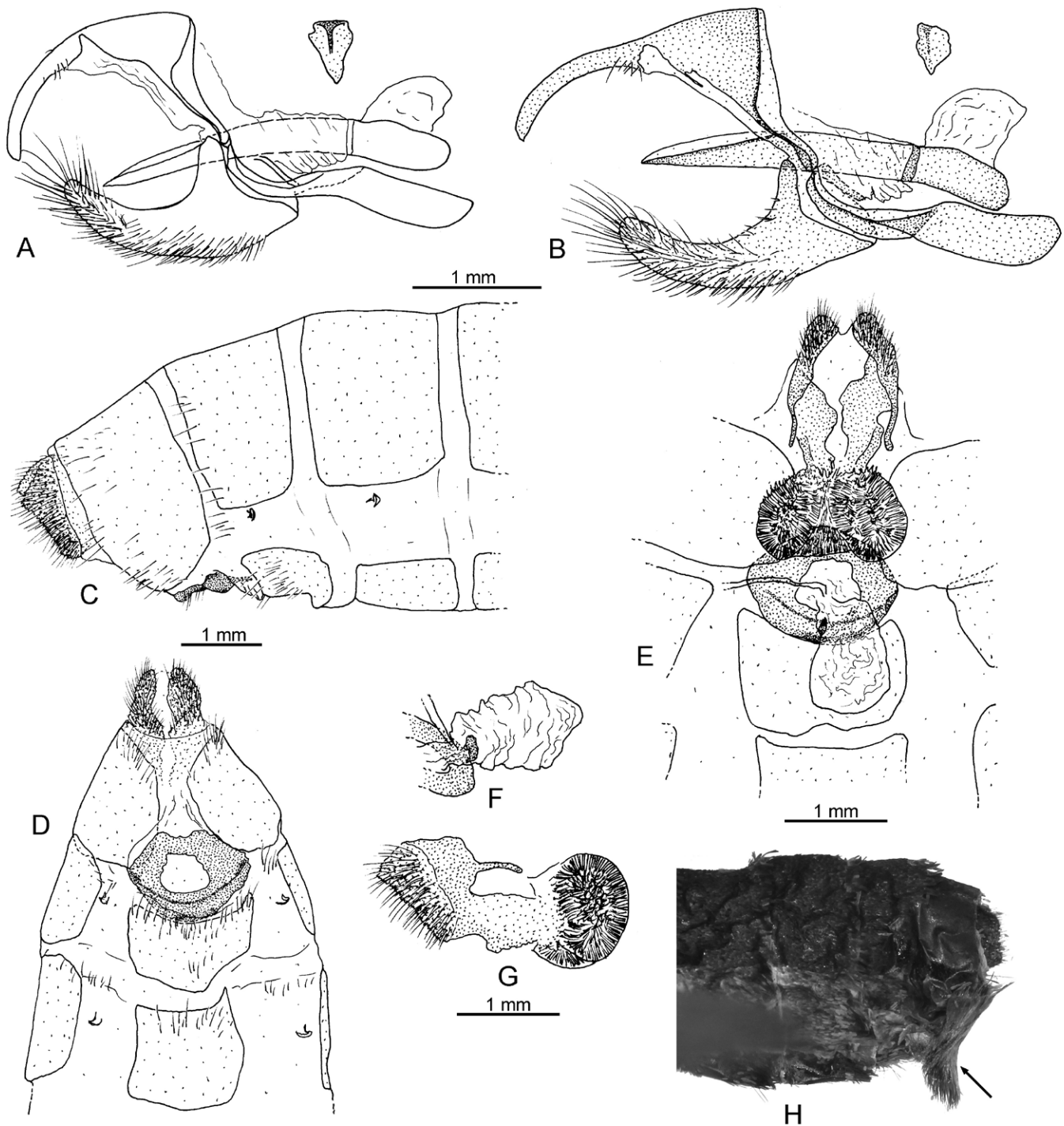


Fig. 3. Genitalia of *Actinote intensa* and *A. johncoulsoni* n. sp. **A:** *A. intensa*, ♂, lateral view genitalia and posterior view juxta (upper right), dissection # KW-15-142, Ecuador, Quebrada San Ramón. **B:** *A. johncoulsoni*, holotype ♂, lateral view genitalia and posterior view juxta (upper right), dissection# KW-15-146, Ecuador, Quebrada San Ramón. **C-G:** *A. johncoulsoni*, ♀ (KW-15-146; LEP-04156): **C:** lateral view posterior tip abdomen. **D:** ventral view posterior tip abdomen. **E:** abdomen interior and genitalia dorsal view; **F:** lamella antevaginalis, corpus bursae and ductus bursae lateral view. **G:** papillae anales and subpapillary glands lateral view. **H:** *A. johncoulsoni*, ♀ (LEP-37434): lateral view abdomen tip showing sphragis (indicated by arrow).

The second question is how to apply existing names to the two species. The barcoded groups enabled the identification of a number of wing pattern characters (Table 1) that allowed us to assign the names *intensa*, *radiata* and *gerardolamas* to one species, leaving the second species to be described here. The

type of *intensa* and, to a greater extent, more recently collected Peruvian specimens tend to have more pinkish coloration in the FW band than Ecuadorian specimens, thus more closely resembling *A. johncoulsoni*. However, other characters, especially the equally sized, paired orange VFW tornal spots,

point to Peruvian specimens being conspecific with Ecuadorian specimens identified here as *A. intensa*. Furthermore, barcoded specimens from northern Peru (e.g., Fig. 2E) that are phenotypically similar to the type of *intensa* grouped with Ecuadorian *A. intensa* and not *A. johncoulsoni*.

The final question is whether *A. johncoulsoni* could be a subspecies of an existing species. *Actinote johncoulsoni* and *A. intensa* share a number of morphological characters, as discussed in the diagnosis of *A. intensa*, suggesting that they are sister species. Based on the very similar genitalia (shape of valva and uncus), and shared black hair-like scales on the VHW, the closest relative to *A. intensa*+*A. johncoulsoni* is likely to be *A. abana*, a species sympatric with *A. johncoulsoni*. *Actinote erinome* is distributed allopatrically with respect to *A. johncoulsoni*, from northern Peru to Bolivia, but both genetic data (Fig. 1) and male genitalic characters (straighter uncus with hooked tip, more up-turned valva, lack of sclerotized band around aedeagus anterior of manica, examined in specimens of *A. erinome mathani* Oberthür, 1917, *A. erinome erinome*, and *A. erinome testacea* (Salvin & Godman, 1868)) suggest that these are distinct species.

Both the width and pinkish tinge of the DFW band in *A. johncoulsoni* vary (Fig. 2J,L,M), without any apparent geographic correlation.

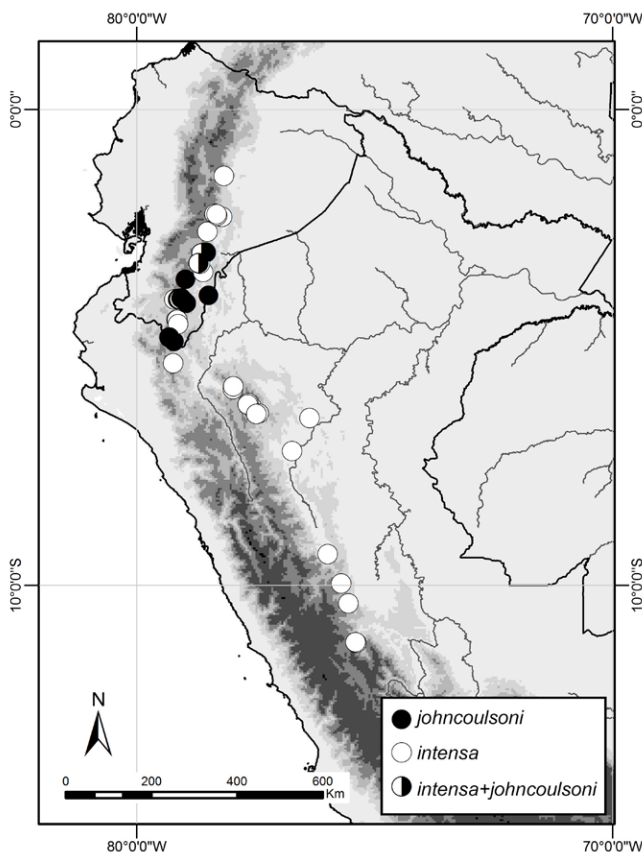


Fig. 4. Distribution of *Actinote intensa* and *A. johncoulsoni* n. sp.

Distribution: *Actinote johncoulsoni* has been recorded in Morona-Santiago and Zamora-Chinchipe provinces in eastern Ecuador (Fig. 4). Its presence at sites in Ecuador that are within 5 km of the Peru border suggest that it almost certainly occurs in the latter country.

Habitat and ecology: *Actinote johncoulsoni* occurs in the same cloud forest habitats (Fig. 5A) as its sister species *A. intensa*, from 1600-2200 m, and the two species are often found together. Like *A. intensa*, males may be found flying 2-6 m above streams, puddling at damp sand and gravel (Fig. 5B,C), especially where there is urine or rotting carrion, and are occasionally found in traps baited with rotting fish. Females are much rarer in nature; single individuals have been observed flying across open ridge tops and along rivers (J. Radford, pers. comm.; pers. obs.), and we collected one individual (Fig. 2N) puddling along a river.

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Fig. 5. Habitat and live *Actinote*. **A:** Ecuador, Zamora-Chinchipe, upper valley of Río San Francisco, the vicinity of the type locality, where both *A. intensa* and *A. johncoulsoni* occur. **B,C:** *A. johncoulsoni* n. sp., Ecuador. **D,E:** *A. intensa*, Ecuador. Photographs B,C by Maris Midgley.

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Appendix 1. Voucher specimen information for DNA sequence data. Sequences with DNA voucher numbers beginning “LEP-” or “KW-” are newly deposited in GenBank, the remainder were available in GenBank prior to this study. Taxon names for samples obtained from GenBank are reproduced unaltered from the sequence title.

Taxon	Locality (decimal latitude and longitude)	DNA voucher number	GenBank number
<i>Actinote johncoulsoni</i>	Ecuador: Morona-Santiago: km 22 Limón-Gualaceo rd. (-3.008, -78.539)	LEP-06920	KY649591
<i>Actinote johncoulsoni</i>	Ecuador: Morona-Santiago: Río Gualaceño (-3.024, -78.635)	KW-071009-79	KY649575
<i>Actinote johncoulsoni</i>	Ecuador: Morona-Santiago: San Martín, Chigüinda (-3.228, -78.7)	LEP-00016	KY649577
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Cascada Hampik Yaku (-3.566, -78.968)	LEP-37434	KY649593
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-04156	KY649589
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-04157	KY649590
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-37571	KY649602
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-37572	KY649603
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-37574	KY649604
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-37576	KY649606
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Finca San Carlos (-4.798, -79.309)	LEP-37577	KY649607
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: km 4.3 San Andrés-Jimbura rd. (-4.8, -79.305)	LEP-37575	KY649605
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-37569	KY649600
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-37570	KY649601
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada Troya (-4.792, -79.312)	LEP-37437	KY649594
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada Troya (-4.792, -79.312)	LEP-37438	KY649595
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada Troya (-4.792, -79.312)	LEP-37565	KY649596
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada Troya (-4.792, -79.312)	LEP-37566	KY649597
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada Troya (-4.792, -79.312)	LEP-37567	KY649598
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: Quebrada Troya (-4.792, -79.312)	LEP-37568	KY649599
<i>Actinote johncoulsoni</i>	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-37582	KY649612
<i>Actinote eresia leptogramma</i>	Ecuador: Zamora-Chinchi: Quebrada Navidades (-3.975, -79.125)	LEP-00020	KY649580
<i>Actinote hilaris desmiala</i>	Ecuador: Carchi: Reserva Forestal Golondrinas (0.826, -78.112)	LEP-04153	KY649588
<i>Actinote intensa</i>	Ecuador: Loja: Quebrada Gurunamaca (-4.422, -79.143)	LEP-00014	KY649576
<i>Actinote intensa</i>	Ecuador: Morona-Santiago: Guarumales/Hidropaute (-2.569, -78.514)	LEP-06921	KY649592
<i>Actinote intensa</i>	Ecuador: Morona-Santiago: Quebrada Cugusha, km 37 Macas-Cebadas rd. (-2.225, -78.291)	LEP-00018	KY649579
<i>Actinote intensa</i>	Ecuador: Morona-Santiago: Río Gualaceño (-3.024, -78.635)	LEP-37583	KY649613
<i>Actinote intensa</i>	Ecuador: Morona-Santiago: Río Retiro, km 42 Macas-Cebadas rd. (-2.2, -78.317)	LEP-00017	KY649578
<i>Actinote intensa</i>	Ecuador: Morona-Santiago: Río Retiro, km 42 Macas-Cebadas rd. (-2.2, -78.317)	LEP-37585	KY649615
<i>Actinote intensa</i>	Ecuador: Morona-Santiago: Río Retiro, km 42 Macas-Cebadas rd. (-2.2, -78.317)	LEP-37586	KY649616
<i>Actinote intensa</i>	Ecuador: Morona-Santiago: San Martín, Chigüinda (-3.228, -78.7)	LEP-37584	KY649614
<i>Actinote intensa</i>	Ecuador: Tungurahua: Baños-Ponchoa (presumed mislabeled from Peru)	LEP-04013	KY649582
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: km 12 old Zamora-Loja rd. (-4.022, -79.013)	LEP-04017	KY649586
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-04016	KY649585
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-04018	KY649587
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-37578	KY649608
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-37579	KY649609
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-37580	KY649610
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: Quebrada San Ramón, power station (-3.97, -79.062)	LEP-37581	KY649611
<i>Actinote intensa</i>	Ecuador: Zamora-Chinchi: San Francisco, casa de Arcoiris (-3.988, -79.095)	LEP-37587	KY649617
<i>Actinote intensa</i>	Peru: Amazonas: Pomacochas (-5.817, -77.967)	LEP-04015	KY649584
<i>Actinote intensa</i>	Peru: Amazonas: 'Rodríguez de Mendoza' [= Mendoza] (-6.4, -77.483)	LEP-04012	KY649581
<i>Actinote intensa</i>	Peru: Amazonas: 'Rodríguez de Mendoza' [= Mendoza] (-6.4, -77.483)	LEP-04014	KY649583
<i>Abananote erinome erinome</i>	Peru: Junín (Silva-Brandão <i>et al.</i> , 2008)	AC34	EU275516.1
<i>Abananote radiata</i>	Ecuador: Morona-Santiago: Macas-Guamote rd. (Silva-Brandão <i>et al.</i> , 2008)	NW90-12	EU275517.1
<i>Altinote alcione sodalis</i>	Peru: Junín (Silva-Brandão <i>et al.</i> , 2008)	AC28	EU275554.1
<i>Altinote dicaeus albofasciata</i>	Ecuador: Napo (Silva-Brandão <i>et al.</i> , 2008)	E-51-18	EU275555.1
<i>Altinote dicaeus callianira</i>	Peru: Junín (Silva-Brandão <i>et al.</i> , 2008)	AC25	EU275556.1
<i>Altinote dicaeus callianira</i>	Peru: Junín (Silva-Brandão <i>et al.</i> , 2008)	AC58	EU275557.1
<i>Altinote dicaeus flavibasis</i>	Colombia: Putumayo (Silva-Brandão <i>et al.</i> , 2008)	C-17	EU275558.1
<i>Altinote eresia</i>	Bolivia: Cochabamba (Silva-Brandão <i>et al.</i> , 2008)	AC87	EU275559.1
<i>Actinote momina</i>	Peru: Cuzco (Silva-Brandão <i>et al.</i> , 2008)	RV-03-V240	EU275560.1
<i>Actinote negra demonica</i>	Bolivia: Yungas: Coroico (Silva-Brandão <i>et al.</i> , 2008)	AC46	EU275561.1
<i>Altinote negra euclia</i>	Peru: Cajamarca (Silva-Brandão <i>et al.</i> , 2008)	AC64	EU275562.1
<i>Altinote neleus</i>	Colombia: Antioquia: Sabaneta (Silva-Brandão <i>et al.</i> , 2008)	AC16	EU275563.1
<i>Altinote rubrocelullata</i>	Peru: Ancash (Silva-Brandão <i>et al.</i> , 2008)	AC76	EU275564.1
<i>Altinote tenebrosa</i>	Ecuador: Sucumbios: La Bonita (Silva-Brandão <i>et al.</i> , 2008)	NW90-15	EU275565.1
<i>Altinote negra demonica</i>	Peru: Cuzco: Santa Teresa (Silva-Brandão <i>et al.</i> , 2008)	AC45	EU275573.1
<i>Actinote pellenea</i>	Brazil: São Luis de Paratiga (www.nymphalidae.net/db.php)	NW129-23	KM012923.1