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First record of the enigmatic tribe Anaeomorphini (Lepidoptera, Nymphalidae, Charaxinae) outside of the Amazon basin: a new species of *Anaeomorpha* Rothschild, 1894, from the Chocó region of western Ecuador

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Abstract. We describe a new butterfly species, *Anaeomorpha mirifica* Simon and Willmott, **n. sp.** (Lepidoptera, Nymphalidae, Charaxinae), from premontane rain forest of the Chocó region of northwestern Ecuador. This represents the second known species and the first record outside of the Amazon basin for this taxonomically and biologically enigmatic genus. Although the two species are not known to be sympatric, we identified 21 characters in the external color pattern, wing shape and male genitalia that together support distinct species status. Most notably, the new species possesses an ocellus in the ventral hind wing tornus, a character which occurs in the Neotropical Charaxinae only in the genus *Prepona* Boisduval, 1836. A mean divergence of 6.8% in the COI 'barcodes' between the two species underlines their taxonomic distinctness.

Key Words. Anaeini, COI DNA barcode, endemism, fieldwork, Preponini, taxonomy

Resumen. Describimos una nueva especie de mariposa, *Anaeomorpha mirifica* Simon and Willmott, **n. sp.** (Lepidoptera, Nymphalidae, Charaxinae), nativa del bosque pluvial de las montañas del Chocó en el noroeste de Ecuador. Este taxón representa la segunda especie de este género cuya taxonomía y biología es poco conocida y además es el primer registro fuera de la región Amazónica. Aunque las dos especies no se conocen en simpatría hasta la fecha, hemos identificado 21 caracteres en el patrón de color alar, la forma del ala, y la genitalia del macho, que juntos apoyan el estatus de especies diferentes. Mas específicamente, la nueva especie tiene un ocelo en el torno del ala posterior ventral, un carácter que ocurre en los Charaxinae neotropicales solamente en el género *Prepona* Boisduval, 1836. Una divergencia de 6,8% en los códigos de barra del gen COI entre las dos especies enfatiza su diferenciación taxonómica.

Palabras Clave. Anaeini, código de barras de ADN de COI, endemismo, trabajo de campo, Preponini, taxonomía

Introduction

The genus *Anaeomorpha* (Nymphalidae, Charaxinae) was described by Rothschild (1894) for a single new species of Neotropical butterfly which was, at that time, and has remained until this day, one of the most distinctive butterfly species in the world. The genus currently contains a single species, *Anaeomorpha splendida*, and two subspecies, which occur in lowland rain forests of the upper Amazon basin (Salazar 1999; Lamas 2004; Attal and Büche 2008; Salazar 2011). *Anaeomorpha splendida* is very rare in the field, and the great majority of known specimens in collections are males captured by commercial dealers, almost certainly using rotting carrion baits to which males are attracted (Checa et al. 2009; pers. obs.). The female remained unknown until its discovery in Peru only a few years ago (Salazar 2011; Schäffler and Frankenbach 2011).

Our knowledge of the relationships of *Anaeomorpha* is almost as limited as it is of the species' biology. Based on a recent molecular phylogenetic analysis, the relationships of *Anaeomorpha* with respect to the two Neotropical charaxine tribes, Anaeini and Preponini, and other Old World charaxine lineages, are still unresolved, and the genus is currently placed in its own tribe, the Anaeomorphini (Ortiz-Acevedo and Willmott 2013). Morphological characters provide similarly equivocal information as to the true relationships of the genus (Marconato 2008; Salazar 2011) and, more than a century since its description, adding to our knowledge of the genus is a slow process. The purpose of this paper is to report the first record of *Anaeomorpha* outside of the Amazon basin, and to describe the second known species in the genus.

Materials and Methods

Fieldwork was conducted by the authors and colleagues throughout Ecuador over the last 25 years, including at the type locality. While not resulting in the capture of any specimens of the new species described here, such field work provided information about the rarity and distribution of its sister species, *Anaeomorpha splendida.* Charaxine collections were studied by KRW and JPWH in numerous public and private collections in the Americas and Europe while gathering data for a forthcoming series of books on the butterflies of Ecuador. Collections containing specimens illustrated here include the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (FLMNH), and the Mark Simon collection, Gainesville, FL, USA (MASI). Photographs of type specimens of all described names in *Anaeomorpha* (listed in Lamas 2004) were examined in Attal and Büche (2008), Salazar (1999) and Warren et al. (2017).

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 and Needham (1918). We use the abbreviations DFW, VFW, DHW and VHW for dorsal and ventral forewing and hind wing.

We extracted genomic DNA from a leg removed from the holotype of the new species of *Anaeomorpha* using Qiagen's DNeasy Blood & Tissue Kit following the manufacturer's protocol, incubating the sample overnight (24 hr) and using a final elution volume of 50 µl. We amplified the first half of the mitochondrial gene cytochrome c oxidase I (COI), also known as the barcode region for animals (Hebert et al. 2003), in two fragments, using primer pairs LCO_nym (forward, TTTCTACAAATCATAAAGATATTGG) and K699 (reverse, WGGGGGGTAAACTGTTCATCC), and Ron (forward, GGATCACCTGATATAGCATTCCC) and Nancy (reverse, CCTGGTAAAATTAAAATATAAACTTC) (Monteiro and Pierce 2001; Elias et al. 2007). All PCR reactions were conducted in a 20 µl volume comprising 2 µl DNA, 6.7 µl ddH2O, 0.4 µl of each primer (10uM), 0.5 µl of Bovine Serum Albumin (BSA, 20 mg/mL), and 10 µl One*Taq*® Quick-Load 2X Master Mix. 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°C, followed by 35 cycles of 30 s at 94°C, 40 s at 51°C, 1 min at 68°C, followed by 5 min at 68°C. Single strands of the PCR products were sequenced in both directions by University of Florida's Interdisciplinary Center for Biotechnology Research Sanger Sequencing Group using the same primers as in the PCR.

Fragments of the *A. mirifica* sequence were assembled into a composite sequence and aligned using BioEdit v. 7.1.3 (Hall 1999) with three sequences for *Anaeomorpha splendida* obtained from GenBank. Those three sequences had the following data: EU528313.1, voucher CP05-41, Peru, Loreto, Tierra Hermosa (Wahlberg et al. 2009); KC132999.1, LEP-03551 and KC 132981.1, LEP-03346, both Ecuador, Orellana, Estación Científica Yasuní (Ortiz-Acevedo and Willmott 2013). The final aligned sequences were checked by eye and were of length 663 bp. To estimate divergence within and between taxa, we used 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 sequence from *A. mirifica* is deposited in GenBank (accession KY609921).

Results and Discussion

Anaeomorpha mirifica Simon and Willmott, **new species**
(Fig. 1A,B, 2A–E, 3)

Diagnosis and identification. *Anaeomorpha mirifica* **n. sp.** differs most obviously from *A. splendida*, the only other member of the genus, on the ventral surface, in particular by the darker ventral ground color, the less conspicuous black postdiscal line that is lined distally with white on the HW, and by the presence of a marginal ocellus on the VHW in cell Cu_2-Cu_1. The male genitalia differ most notably in the more elongate uncus and in the more symmetrical, less distally pointed, and smooth-sided aedeagus. Other differences are listed in Table 1, and illustrated in Fig. 1 and 2.

Description. MALE (Fig. 1A,B, 2A–E): Forewing length 44 mm (n=1). *Wing shape and color pattern*: as illustrated (Fig. 1), and described in comparison with *A. splendida* (Table 1). Hind wing discocellular vein apparently absent, as in *A. splendida*. *Head*: eyes brown, bare; antennae with c. 50 segments, a little darker brown than in *A. splendida* with a slightly reddish tinge and unscaled except for pale brown scales ventrally on basal 10 segments; labial palpi pale brown, with dense, slightly longer, darker brown scales on inner edge, dorso-lateral scales near tip dark brown. *Thorax*: dorsal surface black, ventral surface medium brown, forelegs pale brown, mid- and hind legs pale brown except for ring of dark brown scales at distal end of tibia. *Abdomen*: dorsal surface black, ventral surface gray-brown. *Genitalia* (Fig. 2A–E): as illustrated and described in comparison with *A. splendida* (Table 1). Notable features include the gnathos arms, which are lightly curving, recessed and directed anteroventrally, the elongate, curving ductus ejaculatorius, which opens dorsally, and the symmetrical aedeagus in dorsal view, which lacks spines on the left side. FEMALE: Unknown.

COI barcode. Holotype of *A. mirifica*: tissue voucher LEP-16998; GenBank accession number KY609921:

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AGCAGGAATAGTAGGAACTTCTCTTAGCCTTATTATTCGTACTGAATTAGGCAATCCAGGTTCTTTAATTGGTAA
TGATCAAATTTATAATACTATTGTAACAGCCCATGCCTTTATTATAATTTTTTTTATAGTAATACCTATTATAAT
TGGAGGATTTGGTAATTGACTAGTCCCCTTAATACTAGGAGCTCCTGATATAGCWTTCCCTCGAATAAATAATAT
AAGATTTTGACTTTTACCCCCGTCATTAGTTCTTTTAATTTCGAGTAGAATTGTAGAAAATGGAGCTGGAACAGG
ATGAACAGTTTACCCCCCTTTATCCTCTAATATCGCCCATAGAGGCTCATCAGTTGATTTAGCCATTTTTTCTCT
TCATTTAGCAGGAATTTCCTCAATTTTAGGAGCAATTAATTTTATTACAACAATTATTAATATACGAATTAATAG
CTTATCTTATGATCAAATACCCCTATTTGTTTGATCTGTTGGGATTACTGCTTTACTTCTTCTTCTTTCATTACC
TGTTTTAGCAGGAGCTATTACAATATTATTAACTGATCGAAATTTAAATACTTCTTTTTTTGACCCTGCAGGAGG
AGGAGATCCAATTTTATATCAACATTTATTTTGATTTTTTGGCCACCCAGAAGTTTATATTTT
```

Types. HOLOTYPE MALE: **ECUADOR**: *Esmeraldas*: [Río] Chuchuví [c. 0°53'01"N, 78°31'31"W], 700 m, August 2008, (local collector), [tissue voucher# LEP-16998; genitalia dissection# KW-15-167], (in the MASI, to be deposited in the FLMNH).

Etymology. The species name is derived from the Latin feminine adjective 'mirifica', meaning wonderful or miraculous.

Taxonomy and variation. This taxon shares numerous distinctive morphological characters with *A. splendida*, the type species of *Anaeomorpha*. Among others, these include the unique pattern of green scaling on the DFW, the medially divided two-tone ventral ground color and the recessed and anteriorly directed gnathos in the male genitalia. A BLAST search (https://blast.ncbi.nlm.nih.gov/Blast.cgi) of GenBank confirmed that the *Anaeomorpha splendida* sequences deposited there were the closest match for the COI barcode sequence of this taxon. Although allopatric with respect to the only other known species in the genus, we treat *A. mirifica* **n. sp.** as a distinct species for several reasons. Firstly, there are a large number of wing pattern and genitalic characters that differ between the two taxa (Table 1). While it is impossible to assess variation within *A. mirifica* given that there is only a single known specimen, none of these characters differ between the two subspecies of *A. splendida* (Attal and Büche 2008; Schäffler and Frankenbach 2011; see legend for Fig. 1), with wing patterns examined in 10 specimens and male genitalia examined in four specimens of that species (two dissected, two illustrated in Bonfantti et al. (2013) and Salazar (2011)). It is therefore reasonable to suppose that at least the majority represent taxonomically consistent characters. In particular, the morphology of the uncus and aedeagus are characters that, in our experience, typically only vary between species. Given that most diverse tropical butterfly genera have examples of sister species or species complexes that differ only in wing pattern and not in other aspects of morphology (e.g., *Adelpha* Hübner, Willmott (2003); numerous Ithomiini genera, Willmott (unpubl. data)), we feel that these differences are taxonomically significant. Furthermore, the differences in wing pattern are greater than those between many other closely related, sympatric species of Neotropical charaxines (pers. obs.). We also regard the presence of an ocellus on the VHW as important; ocelli on the VHW are a key character that varies between genera in the Neotropical charaxine tribe Preponini, but such ocelli are typically very stable and show little variation within or between congeneric species. Finally, the mean divergence of 6.8% observed between the DNA barcode sequence of *A. mirifica* and three Amazonian individuals of *A. splendida*, which showed a mean divergence of 0.2%, is also supportive of species status.

Distribution. This species is currently known only from a single specimen captured by a local collector in northwestern Ecuador. A colleague who was in the field with the collector of the holotype on the day of its capture, but along another trail, reported to us that the specimen was collected along a trail heading west from where the Ibarra-San Lorenzo road crosses the Río Chuchuví. The bridge is at c. 700 m elevation, while the ridge that lies c. 1 km west of the bridge ranges from c. 950–1080 m elevation. Since the specimen was reported to have been collected on a ridge, we surmise that the latter range represents the most likely capture elevation.

Habitat and adult ecology. The type locality lies in very wet rainforest on steep slopes. The holotype was most likely captured when attracted to rotting fish or rotting banana bait, which is employed extensively by local collectors in the region.

Discussion. The discovery of this new species is remarkable and it adds another rare, recently discovered charaxine to the Chocó fauna (Constantino 1999; Willmott and Hall 2004; Choimet 2009). Although the type locality, Río Chuchuví, supports more recently described species of butterflies than almost any other in Ecuador, it is also extremely well sampled by resident butterfly collectors, and the absence of additional specimens in collections is a mystery. According to local collectors, an additional specimen was captured at the same site within a year of the capture of the holotype, but its whereabouts are currently unknown and we know of no further specimens. *Anaeomorpha splendida* also appears to be typically very rare; although M. Checa (Checa et al. 2009) captured three individuals during a study in 2006 at a single site in eastern Ecuador, despite using the same trapping methods and sampling the same trails for c. 6000 trap-days over the past three years, we have not recorded the species. It therefore seems likely that *Anaeomorpha* species occur at very low density, with populations periodically appearing and disappearing at any particular site. Another possibility is that *A. mirifica* is not a lowland species like *A. splendida*, but a lower montane species; the montane forests of northwestern Ecuador between 1000–1800 m are much more poorly sampled than the adjacent lowlands, and no doubt hold additional, as yet undiscovered, butterfly taxa.

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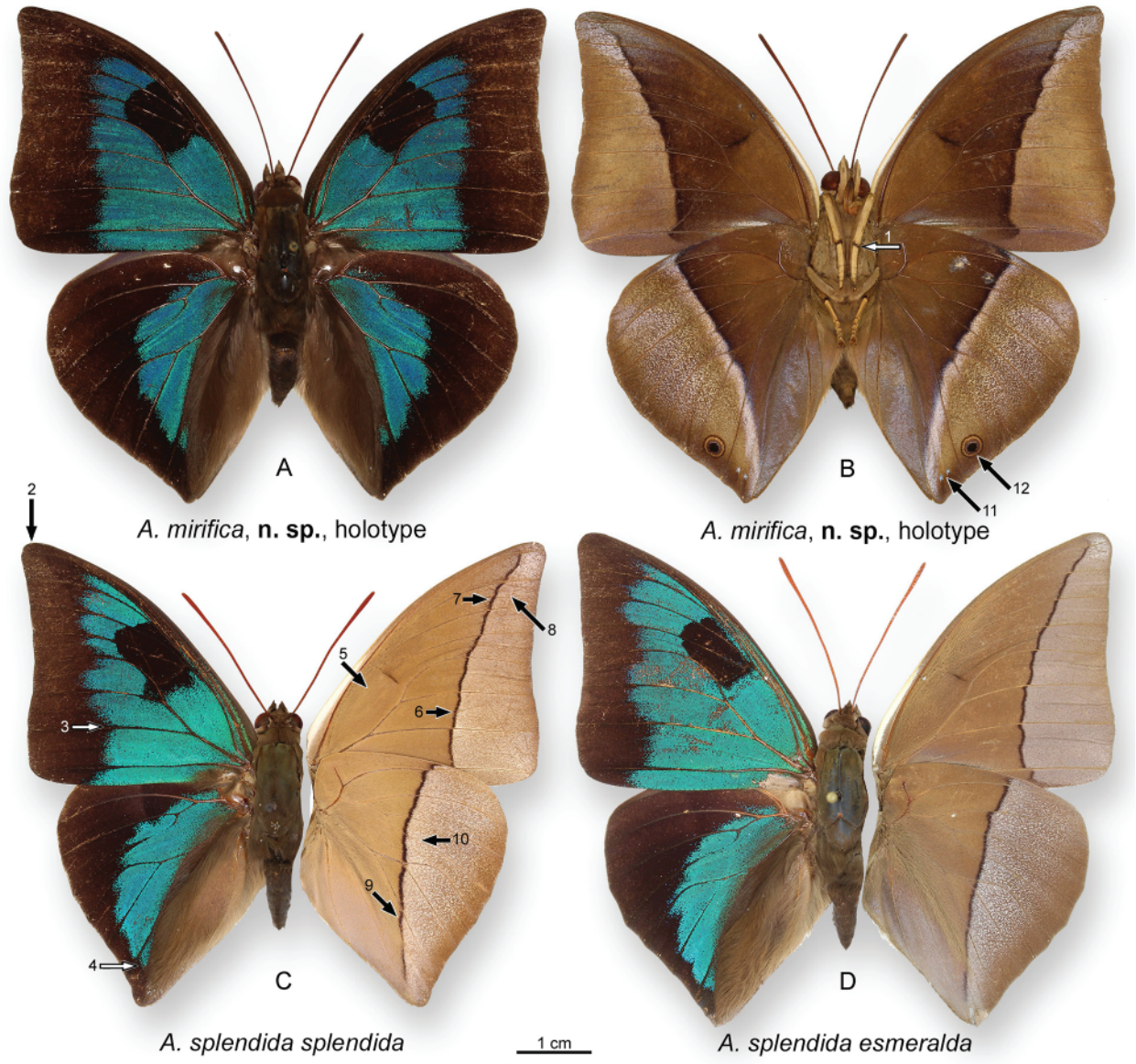

Figure 1. *Anaeomorpha* males. **A–B.** *A. mirifica* **n. sp.**, **holotype**, Ecuador, Esmeraldas, Río Chuchuví: A, dorsal surface; B, ventral surface. **C.** *A. splendida splendida*, Ecuador, Orellana, Río Tiputini: left, dorsal surface, right, ventral surface. **D.** *A. splendida esmeralda*, Peru, Huánuco, "Tingo María": left, dorsal surface, right, ventral surface. Apparently stable differences between *A. s. esmeralda* and the nominate subspecies include, in the former, the broader DFW green area, the darker brown ventral color, the black VFW medial line extending cleanly to the anal margin, and the slightly reduced white scaling towards the VHW distal margin (Attal and Büche 2008).

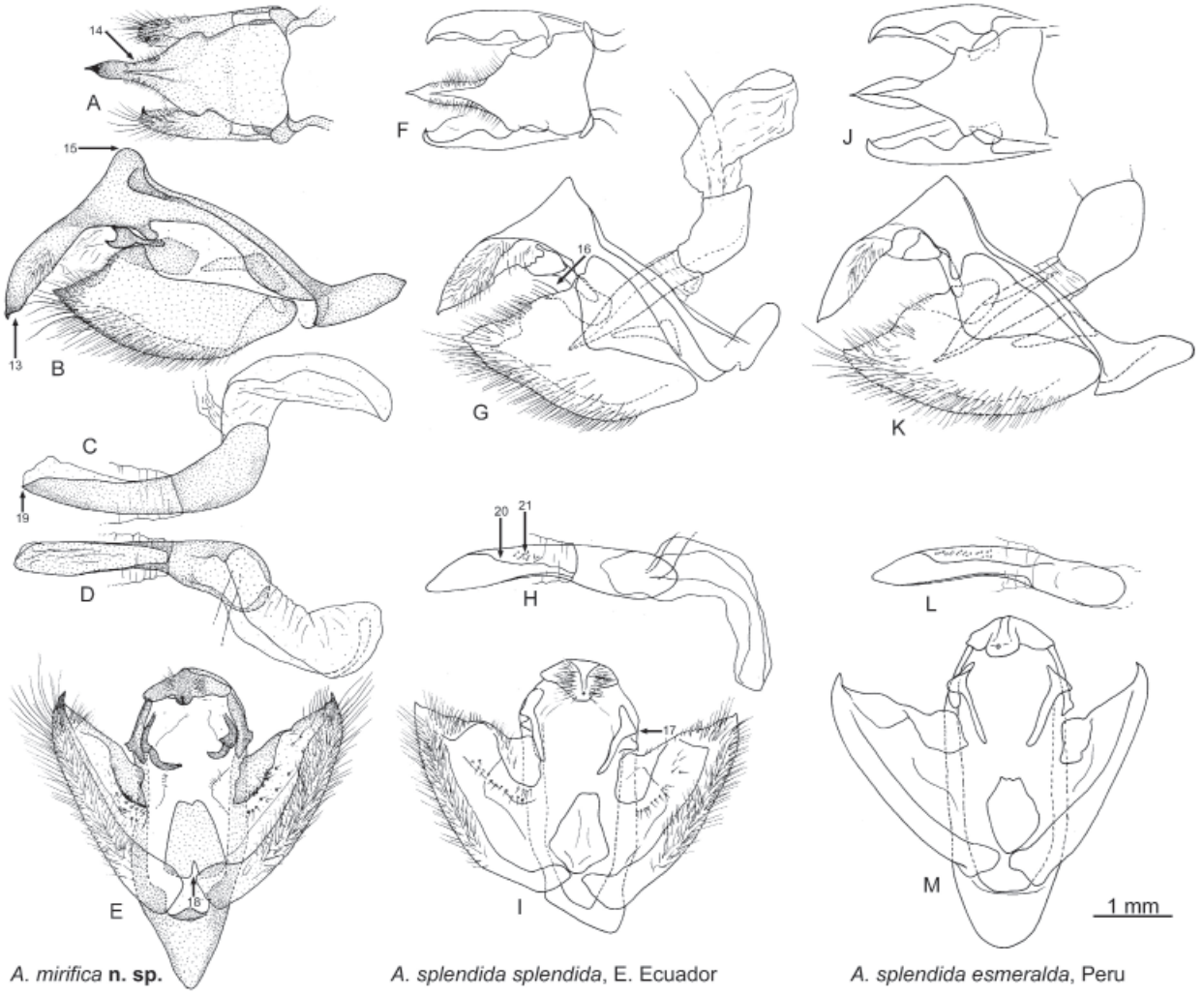

Figure 2. *Anaeomorpha* male genitalia. **A–E**. *A. mirifica* **n. sp.**, **holotype**, Ecuador, Esmeraldas, Río Chuchuví (genitalic dissection KW-15-167): A, dorsal view; B, lateral view (aedeagus omitted); C, aedeagus, lateral view; D, aedeagus, dorsal view; E, genitalia, posteroventral view. **F–I**. *A. splendida splendida*, Ecuador, Orellana, Estación Científica Yasuní (genitalic dissection KW-15-163): F, dorsal view (setae omitted from valvae); G, lateral view; H, aedeagus, dorsal view; I, genitalia, posteroventral view. **J–M**. *A. splendida esmeralda*, Peru, 'San Martín' (genitalic dissection GM-07-61): J, dorsal view (setae omitted); K, lateral view; L, aedeagus, dorsal view; M, genitalia, posteroventral view (setae omitted).

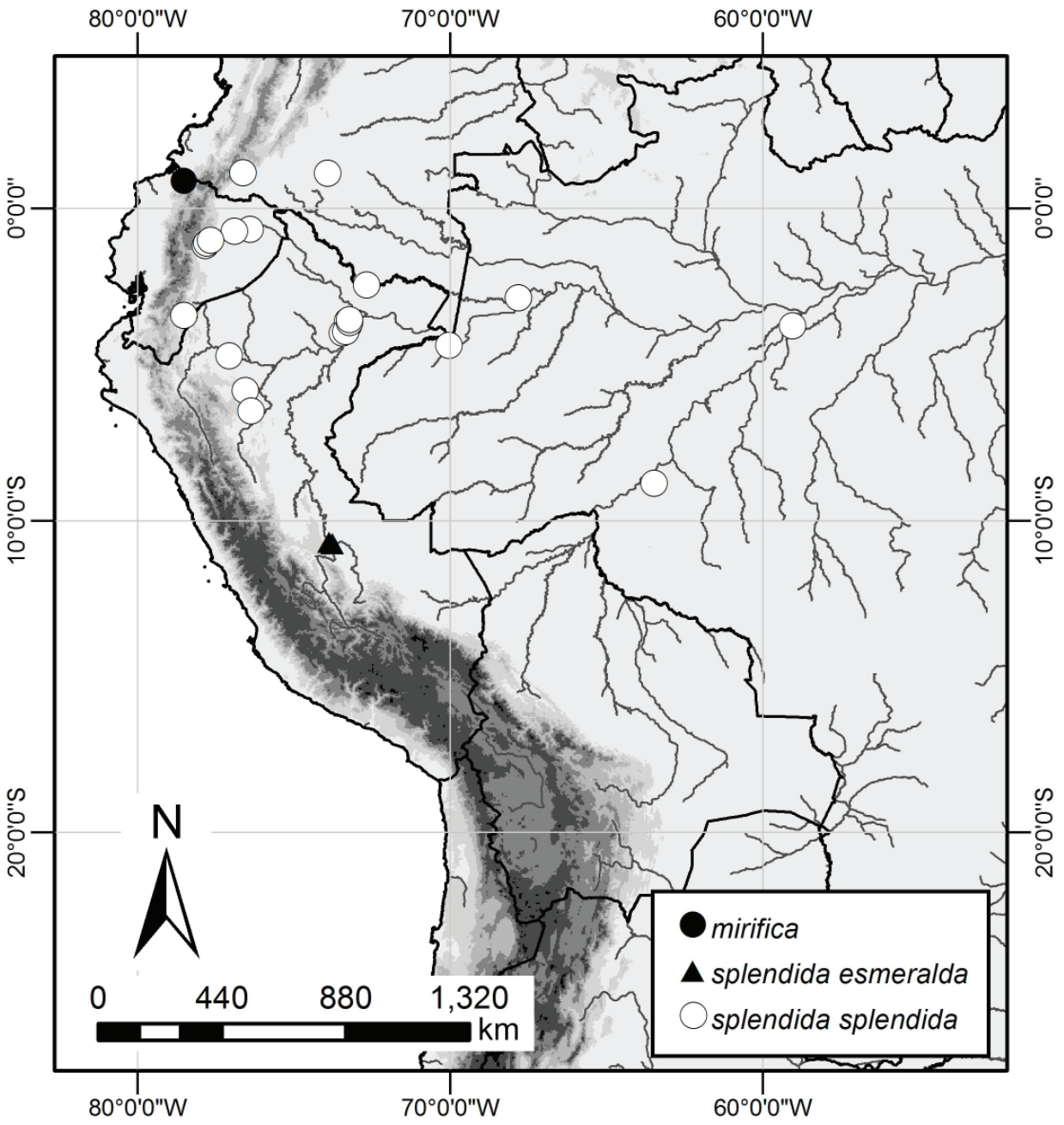

Figure 3. Distribution of *Anaeomorpha*, based on research in Ecuador by KRW and JPWH, and on additional localities in Salazar (2011), Schäffler and Frankenbach (2011), and May et al. (2014).

Table 1. Characters showing variation between *A. mirifica* **n. sp.** and *A. splendida*. Characters are illustrated in Fig. 1 and 2 with arrows numbered according to the character numbers in the table.

No.	Character	*A. splendida*	*A. mirifica* n. sp.
1	Mid- and hind leg color	Uniformly pale brown	Pale brown with ring of dark brown scales at distal edge tibia
2	Wing shape	Elongate, with more pointed FW apex and HW tornus	Broader, with less pointed FW apex and HW tornus
3	DFW: distal edge green area	Indented at veins Cu_2 and M_3	Approximately straight
4	DHW: green area	Extending almost to tornus	Not extending so far towards tornus
5	Ventral ground color basal of black postdiscal line	Uniformly pale brown to medium brown	Darker brown, becoming slightly paler in discal and basal areas both wings
6	Black postdiscal line	Basal edge clearly defined	Basal edge not clearly defined, merging into brown ground color
7	Black postdiscal line, VFW	Almost straight within each cell, anterior of vein M_3	Slightly undulate within each cell, anterior of vein M_3
8	Ventral ground color distal of black postdiscal line, VFW	Uniformly pale brown overlaid with scattered whitish scales	Pale brown, becoming darker along distal margin and towards anal margin, conspicuous whitish scaling along distal edge black line towards apex only
9	Black postdiscal line, VHW	Continuous and approximately even in strength from costa to vein 2A	Becoming more indistinct from costa towards tornus, overlaid with pale whitish scales in cell 2A-Cu_2
10	Ventral ground color distal of black postdiscal line, VHW	Uniformly pale brown overlaid with scattered whitish scales, except for brown marginal border	Uniformly pale brown, overlaid with scattered whitish scales in middle of brown area from vein Cu_1 to apex, conspicuous whitish line along distal edge of black line, brown marginal border
11	Tornus, cell Cu_2-2A, VHW	No visible ocelli or pupils	Two pale bluish pupils aligned parallel to distal margin
12	Tornus, cell Cu_2-Cu_1, VHW	No visible ocelli or pupils	Conspicuous ocellus consisting of black central spot edged with scattered white scales basally, then brown ring, then pale buff ring, then thinner black ring, slightly compressed parallel to distal margin
13	Male genitalia: uncus shape in lateral view	Relatively deep and short, tip aligned with continuation of ventral edge of valva distal portion	Relatively long and narrow, tip extending significantly past continuation of ventral edge of valva distal portion
14	Male genitalia: uncus shape in dorsal view	Base of uncus with sides of uncus vertical and dorsal keel prominent	Base of uncus more rounded with dorsal keel less prominent
15	Male genitalia: tegumen	Anterior-dorsal edge more pointed	Anterior-dorsal edge more rounded
16	Male genitalia: gnathos	Ventral edge further from dorsal edge of valva	Ventral edge almost touching dorsal edge of valva
17	Male genitalia: gnathos	In posterior view, strongly angled in midpoint	In posterior view, not strongly angled in midpoint
18	Male genitalia: juxta	Tapering distally, pointed/rounded at ventral anterior edge	Less tapering distally, cleft at ventral anterior edge
19	Male genitalia: aedeagus in lateral view	Tapering to a point at distal tip	More rounded at tip
20	Male genitalia: aedeagus in dorsal view	Asymmetrical, with sclerotized left side broader than right side	Symmetrical, sclerotized sides almost equal in size
21	Male genitalia: aedeagus middle, left dorsal side	With numerous tiny spines	Smooth, lacking spines