

# A review of the *Argyrogrammana* fauna of the Transandean region (Lepidoptera: Riodinidae: Symmachiini)

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**Abstract:** The *Argyrogrammana* Strand, 1932, fauna (Riodinidae: Symmachiini) of the Transandean region is reviewed. Thirteen species are reported from this region, including four new species that are described here from Costa Rica, Panama, and Ecuador: *A. smalli* Hall, **n. sp.** (*barine* group), *A. vespertina* Hall & Willmott, **n. sp.**, *A. janzeni* Hall, **n. sp.**, and *A. cana* Hall & Willmott, **n. sp.** (all *occidentalis* group). An additional extralimital *occidentalis* group species, *A. eura* Hall, **n. sp.**, is described from the Guianas. Three names are elevated to the rank of species: *A. holosticta* (Godman & Salvin, 1878) from a subspecies of *A. stilbe* (Godart, [1824]) (**rev. stat.**), *A. juanita* (Staudinger, 1887) from synonymy with *A. occidentalis* (Godman & Salvin, 1886) (**rev. stat.**), and *A. phyton* (Stichel, 1911) from a subspecies of *A. physis* (Stichel, 1911) (**n. stat.**). Three names are synonymized: *A. leptographia magdalenae* Constantino *et al.*, 2012, with *A. leptographia* (Stichel, 1911), *A. iracyi* P. & J. Jauffret, 2007, with *A. sublimis* Brévignon & Gallard, 1995, and *A. saulensis tunari* Gallard, 2008, with *A. saulensis* Gallard, 2008 (**n. syn.**). Lectotypes are designated for the names *Argyrogramma trochilia leptographia*, *Charis perone* Westwood, 1851, *Lemonias juanita*, and *Charis occidentalis*.

**Key words:** Colombia, male perching, Neotropics, species description, taxonomy.

## INTRODUCTION

The Neotropical riodinid genus *Argyrogrammana* Strand, 1932 (Symmachiini) has already received significant taxonomic attention in recent decades (e.g., Brévignon & Gallard, 1995; Hall & Willmott, 1995, 1996; Dolibaina *et al.*, 2015; Gallard, 2017), but more than 20% of the known species in the genus still remain undescribed. Hall (2023a) established a comprehensive phylogenetic framework for the genus and provided an updated taxonomic overview, recognizing 55 species in six species groups. This is the first of three papers to review the most poorly known regional *Argyrogrammana* faunas, in this case treating the Transandean fauna. This biogeographic region encompasses the entire tropical zone west of the Andes, from Mexico to western Ecuador and northern Venezuela. Thirteen species are reported here from the Transandean region, including nine described species, of which two are returned to the rank of species from synonymy (*A. juanita* (Staudinger, 1887)) or subspecies status (*A. holosticta* (Godman & Salvin, 1878)), and four new species that are described here from Costa Rica, Panama, and Ecuador.

The Transandean region is unique in harboring members of all six *Argyrogrammana* species groups and in having two endemic species groups, the small *crocea* and *barine* groups, suggesting that it has played a pivotal geographic role in the diversification of the genus. This paper focuses in particular on the *occidentalis* group, which is shown here to be significantly more species rich than previously understood in the Transandean

region, where its diversity unusually matches that of the much larger Amazonian region. An additional extralimital species in this group, heretofore confounded with *A. occidentalis* (Godman & Salvin, 1886), is described from the Guianas. Only four Transandean *Argyrogrammana* species are moderately widespread, namely *A. crocea* (Godman & Salvin, 1878), *A. holosticta*, *A. leptographia* (Stichel, 1911), and *A. physis* (Stichel, 1911), the last of which is unique in ranging east of the Andes. The remaining species all have unusually small ranges, with several appearing to be geographically or elevationally allo/parapatric with respect to their closest relatives, meaning that they are likely to be of higher conservation concern than most *Argyrogrammana* species from elsewhere in the Neotropics.

Previous publications to treat the Transandean *Argyrogrammana* fauna include the broad review papers by Hall & Willmott (1995, 1996), the Costa Rican treatment by DeVries (1997), and the Colombian review paper by Constantino *et al.* (2012). Although many new *Argyrogrammana* species have been described from Amazonia in recent decades, none has been described from the Transandean region in nearly a century. This review paper describes all of the unnamed species known to us, matches males and females for nearly all species, reports many new country records, and for each taxon provides new or updated information on phylogenetic placement, identification, variation, elevational range, male perching behavior, and geographic distribution.

## MATERIALS AND METHODS

Morphology was studied using standard techniques, with the dissection methods used following those outlined in Hall (2018). The terminology for male genital structures follows Klots (1956), Eliot (1973), and Harvey (1987), and the nomenclature for venation follows Comstock & Needham (1898), with cells named for the vein above. The phylogenetic and character data presented here for *Argyrogrammana* are based on the analysis conducted by Hall (2023a). Female genitalia were not studied for the reasons discussed by Hall (2023a). *Argyrogrammana* specimens were studied in the 27 personally visited institutional and private collections listed in Hall (2018), and the type specimens or illustrations (for a few recently described taxa) were examined for all available names. The distributional data presented here are based on the aforementioned collections, augmented by additional records reported in the literature by Constantino *et al.* (2012) for Colombia. Because museum data for *Argyrogrammana* were recorded with an uneven level of detail over a period of three decades, most of the distributional data for previously described species are reported at the province and country level, which in part is why this work is presented as a review rather than a revision. The detailed biological data presented here for Ecuador are based on thirty years of observations by the authors in that country. The figured specimens, which represent material currently in the authors' collection unless otherwise stated, are reproduced at approximately 145% of life size.

The following collection acronyms are used throughout the text, with some older acronyms retained to maintain continuity: BMNH: Natural History Museum (NHMUK) (formerly British Museum of Natural History), London, United Kingdom; DA: David H. Ahrenholz collection, Landrum, SC, USA; FLMNH: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL, USA; GR: Gabriel Rodríguez collection, Mitú, Colombia; INABIO: Instituto Nacional de Biodiversidad, Quito, Ecuador; JH: Jason P. W. Hall collection, Washington, DC, USA; USNM: National Museum of Natural History (NMNH) (formerly United States National Museum), Smithsonian Institution, Washington, DC, USA; ZMHU: Museum für Naturkunde (MfN) (formerly Zoologisches Museum, Humboldt Universität), Berlin, Germany.

To help inform taxonomic decisions concerning similar allopatric taxa, the first half of the mitochondrial gene cytochrome oxidase I (COI), or the “barcode region”, was sequenced for several specimens using legs removed from dried *Argyrogrammana* material. DNA extraction, PCR, and sequencing techniques were the same as those described by Willmott *et al.* (2017), using the primer pairs LCO1490 (Folmer *et al.*, 1994)/K699 and Ron/Nancy to amplify the barcode region in two halves. Sequences were edited and aligned to a length of 402 bp using *BioEdit v. 7.1.3* (Hall, 1999), and pairwise distances between sequences were calculated using *MEGA v. 7.0* (Kumar *et al.*, 2016) with p-distance as the substitution model and other default settings. New sequences are deposited in Genbank, and metadata for all discussed sequences are provided in Table 1.

## SPECIES ACCOUNTS

*crocea* group

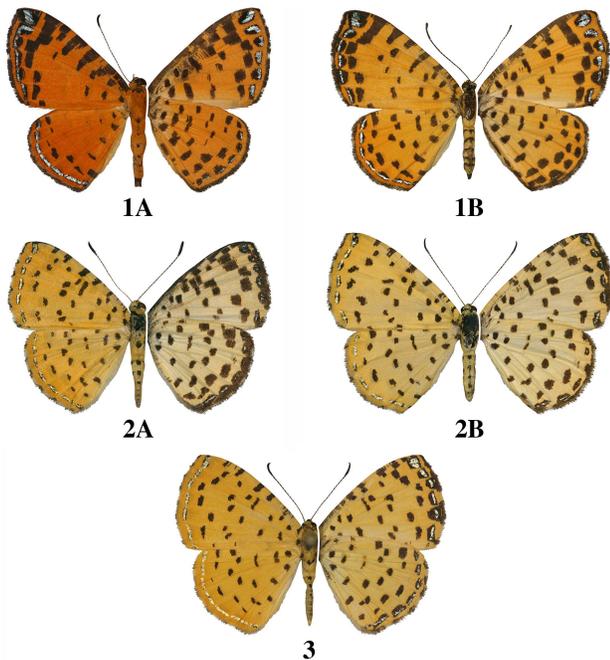
*Argyrogrammana crocea* (Godman & Salvin, 1878)  
(Figs. 1A,B)

*Charis crocea* Godman & Salvin, 1878. *Proc. Zool. Soc. Lond.* 1878(2): 364. TL: Calobre, Veraguas, Panama. Syntype male BMNH [examined].

**Identification and Taxonomy:** There are no synapomorphies grouping *A. crocea* with any individual species or clade within the genus, and, as a result, this species was recovered in Hall's (2023a) phylogenetic analysis of *Argyrogrammana* as the most basal member of the genus and placed in its own monotypic species group. Only two character states (symplesiomorphies) of limited distribution within the genus are possessed by *A. crocea*. A male abdomen with dark transverse dorsal bands (evident in only some specimens) is shared with the newly described east Andean *A. janiceae* Ahrenholz & Hall, 2023, at the base of the *occidentalis* group, and a metallic submarginal line on the male dorsal forewing divided into dashes by significant gaps at each vein is shared with the *stilbe* group, basal members of the *occidentalis* group, and mostly basal members of the *amalfreda* group (Hall, 2023a). While *A. crocea* is strongly supported as one of the most basal *Argyrogrammana* species,

**Table 1.** Voucher specimen data and Genbank/BOLD numbers for three sets of *Argyrogrammana* COI barcode sequences. Voucher numbers beginning with “JH17” represent sequences newly published in this study.

<i>Argyrogrammana</i> species	Locality (decimal latitude and longitude)	DNA voucher	Genbank/BOLD sequence
<i>A. stilbe</i>	Ecuador: Morona-Santiago, km. 14 Chigüinda-Gualaquiza rd. (-3.263, -78.651)	JH1707	OQ611065 (Genbank)
<i>A. holosticta</i>	Ecuador: Esmeraldas, Alto Tambo (0.912, -78.547)	JH1713	OQ611070 (Genbank)
<i>A. holosticta</i>	Panama: Panamá, Barro Colorado Is. (9.155, -79.848)	YB-BCI167217	BCIBT2013-19 (BOLD)
<i>A. holosticta</i>	Costa Rica: Guanacaste, Sendero Manguera (10.996, -85.398)	14-SRNP-70414	MHMYK5224-15 (BOLD)
<i>A. saulensis</i>	Ecuador: Sucumbios, Lumbaquí (0.004, -77.337)	JH1709	OQ611066 (Genbank)
<i>A. vespertina</i>	Ecuador: Esmeraldas, San Francisco (1.107, -78.699)	JH1710	OQ611067 (Genbank)
<i>A. vespertina</i>	Ecuador: Esmeraldas, El Durango (1.041, -78.634)	JH03R040	KT286503.1 (Genbank); GBMIN87881-17 (BOLD)
<i>A. vespertina</i>	Ecuador: Esmeraldas, “Lita” (0.888, -78.438)	LEP-78347	MW807629.1 (Genbank); AYK079-19 (BOLD)
<i>A. aurora</i>	Ecuador: Zamora-Chinchipe, San Luis (-2.387, -78.120)	JH1706	OQ611064 (Genbank)
<i>A. phytion</i>	Ecuador: Morona-Santiago, Santiago (-3.062, -78.015)	JH1712	OQ611069 (Genbank)
<i>A. physis</i>	Ecuador: Esmeraldas, San Francisco (1.107, -78.699)	JH1711	OQ611068 (Genbank)



**Figs. 1-3.** Transandean *Argyrogrammana crocea* (Fig. 1) and *stilbe* group (Fig. 2) adults, with an extralimital taxon included for comparison (Fig. 3) (dorsal surface on left, ventral surface on right). **1A.** *A. crocea* (Godman & Salvin, 1878) male, Piña, Colón, Panama (USNM). **1B.** *A. crocea* female, Lita, Carchi, W. Ecuador. **2A.** *A. holosticta* (Godman & Salvin, 1878) male, Alto Tambo, Esmeraldas, W. Ecuador. **2B.** *A. holosticta* female, Lita, Carchi, W. Ecuador. **3.** *A. stilbe* (Godart, [1824]) male, Santiago, Morona-Santiago, E. Ecuador.

its placement at the very base of the hypothesized tree may have been influenced by its similarity to the chosen outgroup taxon, *Symmachia phaedra* (Bates, 1868), and *A. crocea* could also plausibly be positioned one or two nodes away, as sister to the *occidentalis* + *amalfreda* groups or the *occidentalis* group (Hall, 2023a).

The sexes of *A. crocea* exhibit limited dimorphism compared to those of most congeners. The species is most similar to *occidentalis* group taxa such as the new species *A. vespertina* and *A. janzeni*. The male is distinguished by having multiple dark bars along the costal margin of the dorsal forewing, and both sexes most notably differ by having a solid instead of medially divided dark spot toward the base of cell  $Cu_2$  below the middle of the discal cell on the dorsal forewing, a dark presubmarginal band above vein  $M_2$  on the dorsal forewing that consists of a solid band instead of individual spots, and a dark submarginal band on both dorsal wings that is fused to instead of completely separated from the silver submarginal line. The male genitalia of *A. crocea* (see Fig. 26 in Hall & Willmott (1996)) are rather non-descript and unhelpfully dissimilar to those of its apparently closest relatives. The most similar male genitalia probably belong to certain distantly related *trochilia* group species, particularly *A. trochilia* (Westwood, 1851).

Notable intrapopulational wing pattern variation in males of *A. crocea* includes the prominence of the dark basal and postdiscal spots on both dorsal wings, the width and spacing of the dark presubmarginal spots on both dorsal wings, the presence or absence of dark submarginal spots along the

proximal margin of the silver submarginal line on the dorsal hindwing, and the amount of orange versus brown scaling in the discal cell on the ventral forewing. The dark markings on the dorsum of the abdomen also vary from small spots to larger transverse bands. The females are less variable, but exhibit similar variation in the dark distal bands and also in the shade of yellow-orange wing coloration.

**Biology:** This uncommon species is known from sea level to 1400 m. In Ecuador, a male perching lek has yet to be located, with non-perching males and females encountered along the forest edges of ridgetops, hillsides, and streams from mid morning to early afternoon. In Costa Rica, solitary males were encountered perching 1 to 3 m above the ground along hillside forest edge from 0730 to 0900 hrs, with females observed along forest edges and streams from 0800 to 1130 hrs (DeVries, 1997). This species has been reared in Costa Rica and Panama on *Garcinia intermedia* (Pittier), *Clusia cylindrica* Hammel, *Clusia quadrangula* Bartlett (all Clusiaceae), and *Calophyllum brasiliense* Cambessèdes (Calophyllaceae) (Robbins & Aiello, 1982; Janzen & Hallwachs, 2009-22).

**Distribution:** *Argyrogrammana crocea* occurs throughout the southern Transandean region, where it is known to range from southern Nicaragua to central Colombia and northwestern Ecuador.

#### *stilbe* group

*Argyrogrammana holosticta* (Godman & Salvin, 1878) **rev. stat.**

(Figs. 2A,B)

***Charis holosticta*** Godman & Salvin, 1878. *Proc. Zool. Soc. Lond.* 1878(2): 364. **TL:** Veraguas, Panama. Syntype male BMNH [examined].

**Identification and Taxonomy:** Godman & Salvin (1878) described *A. holosticta* as a species, from Veraguas, Panama (syntype male shown in Figs. 10C,D in Hall & Willmott (1996)), and it was subsequently maintained as such (e.g., Stichel, 1910-11, 1930-31) until being downgraded to a subspecies of *A. stilbe* by Hall & Willmott (1996). Although the type material of *A. stilbe*, a species described by Godart (1819-[24]) from Brazil, appears to be lost (Hall & Willmott, 1996), that of its accepted junior synonym *perone* (Stichel, 1930-31; Hall & Willmott, 1996; Callaghan & Lamas, 2004), a name proposed by Westwood (1850-52) from Belém, in east Amazonian Brazil, is extant. As detailed by Hall & Willmott (1996), there is an undetermined number of apparent syntypes of *perone* in the BMNH that represent both *A. stilbe* and *A. placibilis* (Stichel, 1910). One such syntype, a male of *A. placibilis*, was erroneously labeled by Julia Pope in 1993 as the holotype of *perone*. This specimen was figured by d'Abrera (1994: 1051) (under the name *A. stilbe*) and Hall & Willmott (1996: Figs. 9E,F). To ensure nomenclatural stability for *perone* (and hence *A. stilbe*), we here designate as its lectotype the unlabeled female syntype specimen in the BMNH that seems to

have formed the basis for Hewitson's illustration in Westwood (1850-52) (discussed and reproduced in Fig. 10G in Hall & Willmott (1996)). We do not have the verbatim label data for this specimen, but it is double pinned on a white strip of foam, and bears a Hewitson label and no locality data. This newly designated lectotype specimen was figured by d'Abreu (1994: 1051) (under the name "*Argyrogrammana* ? sp.", following *A. holosticta*) and Hall & Willmott (1996: Figs. 10A,B).

The Transandean *A. holosticta* (Figs. 2A,B) and Amazonian *A. stilbe* (Fig. 3) are very similar, almost sexually monomorphic taxa, but they do seem to exhibit a few consistent differences throughout their respective geographic ranges, with the former differing from the latter by having a slightly paler yellow dorsal surface, a noticeably paler yellow instead of yellow-orange ventral surface, a dark spot inside the costal edge of the discal cell end on the ventral forewing that always seems to be absent in *A. stilbe* males although present as a small faint spot in *A. stilbe* females, and heavier dark ventral spotting, especially of the presubmarginal band, which has the effect of creating semi-darkened halos around the dark presubmarginal spots on the dorsal wings (most noticeable in males). The first author dissected four males of *A. holosticta* from throughout its geographic range and three males of *A. stilbe* from the western Amazon, and found several potentially consistent differences in the male genitalia between the two taxa. Those of *A. holosticta* (see Fig. 23 in Hall & Willmott (1996)) have a slightly longer saccus that angles to the left instead of to the right in ventral view, valve tips that are slightly inwardly instead of slightly outwardly curved in ventral view, and aedeagal cornutal spines that are approximately 50% longer. To help decide whether these two allo/parapatrically distributed taxa should be treated as subspecies or species, we sequenced the barcode region of the mitochondrial gene COI for Ecuadorian exemplars. The results showed that a male of *A. holosticta* (JH1713), from Alto Tambo in Esmeraldas province, had a sequence divergence of 4.7% from a male of *A. stilbe* (JH1707), from km. 14 Chigüinda-Gualaquiza rd. in Morona-Santiago province. When comparing publicly available sequences (see metadata in Table 1), we also found a mean sequence divergence of 1.4% among three specimens of *A. holosticta* from western Ecuador, Panama (YB-BCII167217), and Costa Rica (14-SRNP-70414). Additional sequence data, particularly of *A. stilbe* from the eastern Amazon, are needed to provide a more definitive answer on taxonomic status. However, the significant DNA barcode difference between the sequenced individuals of *A. holosticta* and *A. stilbe*, combined with the subtle wing pattern and male genitalia differences reported here, would seem to support the recognition of two distinct species, and we tentatively return *A. holosticta* to species status (**rev. stat.**).

Hall's (2023a) phylogenetic analysis of *Argyrogrammana* placed *A. holosticta* and *A. stilbe* in a bitypic *stilbe* group, characterized by males having a prominently convex distal forewing margin, yellow dorsal wings, an entirely yellow frons, and genitalia with a triangular, distally finely pointed and upturned upper posterior valve process, and both sexes having a metallic submarginal line on both dorsal wings that is greenish gold instead of silver and a forewing fringe with broad sections of prominent white scaling in all distal cells instead

of typically just cells  $Cu_2$ ,  $M_3$ ,  $M_1$ , and  $R_{4+5}$  (also present in the newly described *occidentalis* group species *A. janiceae*). The *stilbe* group was recovered by Hall (2023a) as sister to the *barine* group + *trochilia* group clade. The males of all species in these three species groups are unique in the genus in possessing widespread yellow to white scaling across the ventral forewing, whereas the *crocea* group has orange scaling, the *occidentalis* group orange to gray scaling, and the *amalfreda* group typically gray to blue scaling across the male ventral forewing.

Both sexes of *A. holosticta* are often confused in collections of Transandean material with the similarly yellow female of *A. leptographia*, from which they are distinguished in that species account. Notable intrapopulational variation in *A. holosticta* includes the shade of the yellow dorsal coloration, the heaviness of the spotting on both wings, the extent to which the dark postdiscal spot in cell  $Cu_1$  on the forewing is proximally displaced compared to the two postdiscal spots in cell  $Cu_2$ , the arrangement of the dark postdiscal spots across cells  $M_3$  to  $M_1$  on the forewing, which varies from weakly to prominently semicircular in shape, the exact (i.e., minor variation) width of the dark presubmarginal band on both ventral wings, and the extent of dark scaling along the distal margin of both ventral wings.

**Biology:** This somewhat uncommon species is known with certainty from sea level to 1400 m, although Constantino *et al.* (2012) cite it as occurring as high as 2200 m in Caldas, Colombia. In Ecuador, small groups of males were encountered perching along streams from 1345 to 1530 hrs, typically between 5 and 8 m above the ground. However, on one occasion, males were observed from a canopy cable car perching atop canopy vegetation about 25 m above a stream. Males have an unusually weak and fluttering flight, but persistently defend their territories, particularly against other yellow riordinids such as those of *Baeotis* Hübner, [1819]. A female was encountered flying low to the ground along the forest edge of a ridgetop in the early afternoon. This species has been reared in Costa Rica on *Mosquitoxylum jamaicense* Krug & Urban (Anacardiaceae) (Janzen & Hallwachs, 2009-22).

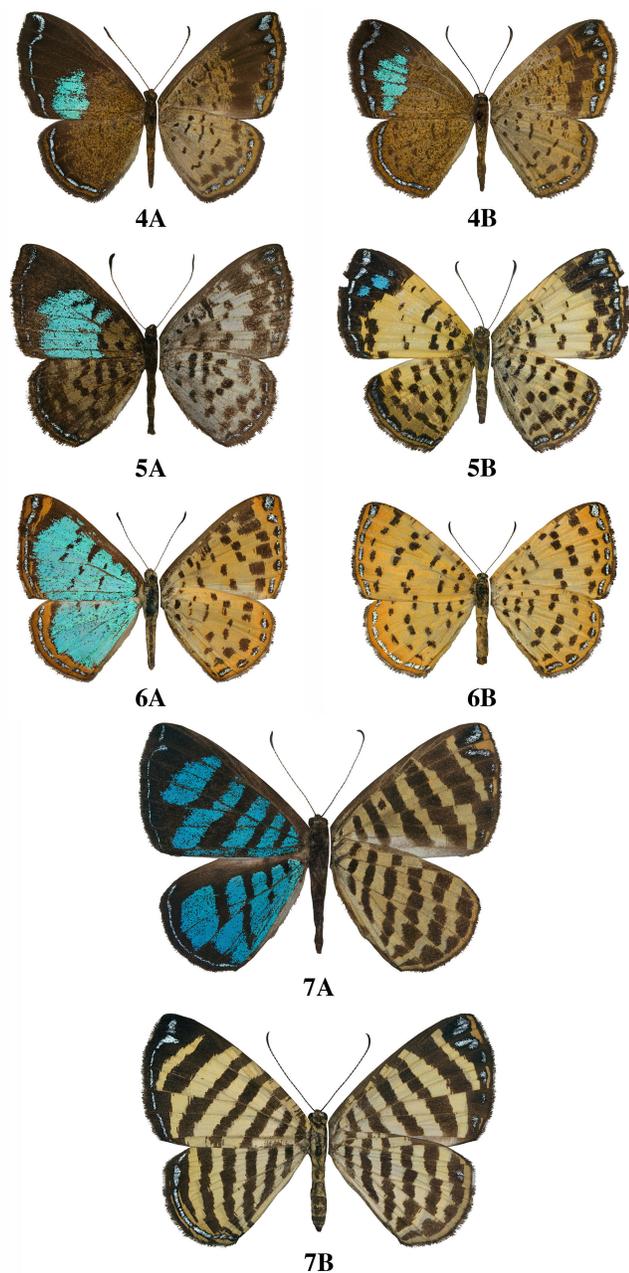
**Distribution:** *Argyrogrammana holosticta* is the most widespread Transandean species in the genus, occurring from southern Mexico to northwestern Ecuador and northern Venezuela. It is replaced throughout the Amazon by *A. stilbe*.

#### *barine* group

*Argyrogrammana barine* (Staudinger, 1887)  
(Figs. 4A,B)

**Charis barine** Staudinger, 1887. *Exot. Schmett.* 2(19): pl. 91; 1(20): 256 (1888). **TL:** Río San Juan, Chocó, W. Colombia. Syntype male and female ZMHU [examined].

**Identification and Taxonomy:** Hall's (2023a) phylogenetic analysis of *Argyrogrammana* placed *A. barine* and the new species *A. smalli* in a bitypic *barine* group, characterized by males having yellow-brown scaling across the base of both



**Figs. 4-7.** Transandean *Argyrogrammana barine* (Figs. 4-5) and *trochilia* group (Figs. 6-7) adults (dorsal surface on left, ventral surface on right). **4A.** *A. barine* (Staudinger, 1887) male, Hcda. Santa Isabel, Pichincha, W. Ecuador. **4B.** *A. barine* female, Lita, Carchi, W. Ecuador. **5A.** *A. smalli* Hall, n. sp., HT male, Fortuna Dam, Chiriquí, Panama (USNM). **5B.** *A. smalli* PT female, P. N. Braulio Carrillo, San José, Costa Rica (USNM). **6A.** *A. leptographia* (Stichel, 1911) male, El Encanto, Esmeraldas, W. Ecuador. **6B.** *A. leptographia* female, Uimbi, Esmeraldas, W. Ecuador. **7A.** *A. saphirina* (Staudinger, 1887) male, El Encanto, Esmeraldas, W. Ecuador. **7B.** *A. saphirina* female, Río Chuchuví, Esmeraldas, W. Ecuador.

dorsal wings, a greenish-blue medial patch extending to the anal margin on the dorsal forewing, and genitalia with a broad, distally rounded and upturned, inwardly tilted upper posterior valve process and a large vertically semicircular transtilla process, and females having blue presubmarginal spots on the dorsal forewing. The *barine* group was recovered in Hall's

(2023a) analysis as sister to the *trochilia* group. The males of all species in this clade possess a blue postdiscal patch on the dorsal forewing that extends to the anal margin, a character that occurs elsewhere in the genus only in the *amalfreda* group sister pair of *A. glaucopis* (Bates, 1868) and the newly described *A. caerulea* Hall, 2023.

The weakly sexually dimorphic *A. barine* is similar only to its sister species *A. smalli*, from which it is distinguished in that species account. Notable intrapopulational variation in *A. barine* includes the exact width and height of the greenish-blue postdiscal (male)/presubmarginal (female) band on the dorsal forewing, the width of the dark presubmarginal band on both surfaces of the hindwing, the width of the dark submarginal band on the dorsal hindwing in males, and the extent of yellow-brown scaling proximal to the silver submarginal line on the ventral forewing.

**Biology:** We have examined specimens of this not uncommon species from near sea level to 1200 m, although Constantino *et al.* (2012) refer to it as occurring up to 1700 m in Colombia. In Ecuador, males were encountered perching singly or in small groups 2 to 5 m above the ground in shady hilltop and ridgetop lightgaps from 1120 to 1400 hrs. Females were observed flying low to the ground along forest edges and in lightgaps on ridgetops and in flat forest, including streamsides, from 1130 to 1500 hrs.

**Distribution:** *Argyrogrammana barine* is known to range from west central Panama (Coclé) to northwestern Ecuador, and is seemingly replaced in western Panama and Costa Rica by the new species *A. smalli*. Literature references to *A. barine* occurring in Costa Rica (e.g., DeVries, 1997; Glassberg, 2017) are based on material of *A. smalli*.

#### *Argyrogrammana smalli* Hall, new species

(Figs. 5A,B; 18)

**Description:** MALE: Forewing length holotype (HT) 14 mm. *Wings:* see Fig. 5A. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and yellow and brown marginal scaling; frons dark brown, with a broad yellow transverse band ventromedially, a narrow vertical yellow band dorsally, and small yellow marks dorsolaterally below base of antennae; labial palpi dirty yellow with brown tips; antennal length approximately 55% of forewing length, segments black with vertical cream lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dark yellow brown and black, ventral surface gray, dorsal surface of abdomen dark yellow brown, ventral surface gray with a narrow dark brown medial band; all legs banded brown and pale dirty yellow. *Genitalia:* see Fig. 18; sclerotized transtilla forms a large, vertically semicircular, ventrally outwardly flared "hood"-like process between widely spaced valve tips and aedeagus, with a laterally compressed, anteriorly curved dorsal "fin"; ductus ejaculatorius enters anterior tip of aedeagus to right; vesica exits posterior tip of aedeagus to right, cornutal complex on unverted vesica consists of a very long and slightly curved series of numerous posteriorly directed spine-like cornuti occupying three-quarters length of aedeagus that are predominantly small and slightly curved but tiny and straight toward anterior tip of series; eighth tergite and sternite rectangular. FEMALE: Forewing length paratype (PT) 13.5 mm. *Wings:* see Fig. 5B. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and yellow marginal scaling; frons brown, with a broad yellow transverse band ventromedially, a few yellow scales ventrally, a narrow vertical yellow band dorsally, and small yellow marks dorsolaterally below base of antennae; labial palpi yellow with brown tips; antennal length approximately 55% of forewing length, segments black with vertical cream lateral bands, clubs black with orange-brown tips. *Body:*

Dorsal surface of thorax dark dirty yellow with a broken black medial band, ventral surface yellow gray, dorsal surface of abdomen brown with scattered dark dirty yellow scaling that is particularly dense along posterior margin of each segment, ventral surface yellow gray with a narrow brown medial band; all legs banded brown and dirty yellow.

**Types:** HOLOTYPE male: PANAMA: *Chiriquí*, continental divide N. of Fortuna Dam, 1100 m, 15 May 1985 (G. B. Small) (USNM).

PARATYPES: COSTA RICA: *San José*, 1 female: Parque Nacional Braulio Carrillo, 1050 m, 29 Jun 1980 (G. B. Small) (USNM).

**Etymology:** This species is named for the late Gordon B. Small, who collected both of the known specimens while amassing a critically important collection of riodinids from Panama as well as Costa Rica.

**Diagnosis:** The morphological phylogenetic analysis of *Argyrogrammana* presented by Hall (2023a) indicates that *A. smalli* **n. sp.** is sister to *A. barine* in the bitypic *barine* group, whose synapomorphies are listed in the previous species account. Both sexes of *A. smalli* (Figs. 5A,B) differ from those of *A. barine* by being slightly larger and having a broader forewing shape, more prominent dark basal, postdiscal, and submarginal spotting on both surfaces of both wings, a less prominently outwardly curved apical element to the silver submarginal line on the dorsal forewing, a more prominent white fringe element in forewing cell  $M_1$  as well as in all cells along the hindwing margin, a dark postdiscal band on the ventral forewing that consists of a more inwardly directed element across cells  $Cu_2$  and  $Cu_1$  and a more prominently semicircular element across cell  $M_3$  to  $M_1$ , a broader pale postdiscal band on the ventral forewing, and less extensive pale submarginal scaling on both ventral wings. The male of *A. smalli* additionally differs by having a slightly greenish tint to the yellow-brown scaling on both dorsal wings, a much larger greenish-blue band on the dorsal forewing that extends up to vein  $M_1$  and proximally into the discal cell, and pale gray to cream instead of grayish-yellow to brownish-yellow scaling across both ventral wings. The male genitalia of the two species do not differ from each other, but have valve and transtilla shapes that are unique in the genus (see Fig. 18).

The female of *A. smalli* additionally differs from that of *A. barine* by having gray-brown to pale yellow instead of dark yellow-brown scaling across both dorsal wings, small blue subapical spots in dorsal forewing cells  $R_{4+5}$  to  $M_2$  (with a few additional blue scales visible in dorsal forewing cell  $M_3$  and ventral forewing cells  $R_{4+5}$  and  $M_1$ ) rather than a large and more proximally positioned greenish-blue band extending from cell  $R_{4+5}$  to the anal margin, and gray to pale yellow instead of dark grayish yellow to brownish yellow scaling across both ventral wings. The female of *A. smalli* is actually more similar to that of the unrelated *amalfreda* group species *A. pulchra* (Talbot, 1929), but most obviously differs by being smaller and having more rounded wings, paler and duller yellow scaling on all wings that includes extensive grayish scaling across the hindwing, two separate interdigitating dark spots in the middle of the forewing discal cell instead of a single dark bar crossing the width of the cell, a fainter and more proximally positioned dark postdiscal spot in forewing cell  $M_1$ , yellow presubmarginal scaling on the dorsal forewing that does not extend into the apex,

three blue presubmarginal instead of one blue submarginal spot on the dorsal forewing, and a broader and discontinuous silver submarginal line on both dorsal wings.

**Biology:** This evidently rare species is known to date only from 1050 to 1100 m. Nothing is known about its biology.

**Distribution:** *Argyrogrammana smalli* is currently known only from Costa Rica and western Panama, and may be limited to this small area, apparently being replaced by *A. barine* farther to the east.

#### *trochilia* group

#### *Argyrogrammana leptographia* (Stichel, 1911)

(Figs. 6A,B)

*Argyrogramma trochilia leptographia* Stichel, 1911. *In*: Wytzman (ed.), *Gen. Insectorum* 112B: 247, pl. 26, fig. 64. **TL**: Río San Juan, Chocó, W. Colombia. Lectotype male ZMHU [designated].

= *Argyrogrammana leptographia magdalenae* Constantino, Rodríguez & Salazar, 2012. *Bol. Cient. Mus. Hist. Nat.* 16(1): 283, fig. 1. **TL**: Amalfi, Antioquia, C. Colombia. Holotype male GR; paratype illustration [examined]. **n. syn.**

**Identification and Taxonomy:** Hall's (2023a) phylogenetic analysis of *Argyrogrammana* placed *A. leptographia* as sister to the remainder of the *trochilia* group, with the east Andean *A. subota* (Hewitson, 1877) then sister to the clade containing the remaining species. Males of the eight *trochilia* group species are characterized by having no yellow to orange scaling along the base of the costal margin on the dorsal forewing (independently derived in the majority of *amalfreda* group species), a medially disjointed and isolated yellowish submarginal band on the dorsal forewing (secondarily lost in the three most derived group members), five blue bands on both dorsal wings, and a dorsally black instead of yellow to orange abdomen.

*Argyrogrammana leptographia* is phylogenetically interesting because its wing pattern is so obviously and unusually intermediate between species in the *stilbe* and *barine* groups, and the remaining members of the *trochilia* group to which it is sister. Dorsally, the male of *A. leptographia* is similar to those of the other *trochilia* group species, although it still typically has a discontinuous series of dark spots between the third and fourth blue bands from the base of the dorsal forewing instead of a continuous dark band. However, its ventral surface retains the ancestral yellow and dark-spotted pattern of the *stilbe* and *barine* groups that has yet to evolve the bold bands of the more derived *trochilia* group species. The female of *A. leptographia* has a yellow and dark-spotted pattern on both wing surfaces, thus closely resembling both sexes of the *stilbe* group species *A. holosticta* and *A. stilbe* rather than other *trochilia* group females, which have yellow to white bands on both wings. Female *A. leptographia* is thus frequently confused with *stilbe* group specimens in collections, but can readily be separated by having a less rounded wing shape, a noticeably shorter forewing discal cell, a more distally positioned dark postdiscal

band on the forewing, slightly more closely aligned spots in the dark postdiscal and presubmarginal bands on the forewing, a silver instead of greenish-gold submarginal line on both dorsal wings, white fringe elements in only some rather than all of the distal forewing cells, and no dark marginal markings on either ventral wing.

The male of *A. leptographia* is the most variable *Argyrogrammana* phenotype in the Transandean region. Males from Colombia have the narrowest and most well defined turquoise blue bands on both dorsal wings and the most prominent intervening dark bands, whereas males from Ecuador (Fig. 6A) and Central America have broader blue bands and narrower and more disjointed dark bands. Males from Ecuador tend to have such dark markings on the dorsal hindwing restricted to the costal margin, and the one examined male from Costa Rica has the dark markings within the dorsal blue patches reduced to just a single discal cell end mark on the forewing. Males from central Colombia, Panama, and Costa Rica seem to have the broadest yellowish submarginal band on both dorsal wings, with the forewing band in particular narrowest in males from western Colombia and Ecuador. The submarginal band tends to be orange in South American males, and a paler yellow orange in Central American males. Males from all of the above countries were dissected, and no significant differences were observed in the male genitalia (see Fig. 20 in Hall & Willmott (1996)). Given that the observed geographic variation in *A. leptographia* is neither discrete nor concordant, the recognition of subspecies does not seem warranted, and the subspecies name *magdalenae*, described by Constantino *et al.* (2012) from the middle Magdalena valley of central Colombia, is newly synonymized here with *A. leptographia* (**n. syn.**). All of the above wing pattern characters also vary to some degree locally, but the extent of the yellowish submarginal and marginal scaling on the dorsal forewing is the most locally variable character. Additional noteworthy intrapopulational variation in *A. leptographia* males includes the shade of the turquoise blue dorsal coloration, the exact lateral placement and shape of the dark postdiscal band on the forewing, and the width of the dark presubmarginal and submarginal bands on both ventral wings. The wing pattern of female *A. leptographia* is geographically stable, and intrapopulational variation is largely limited to the shade of the yellow coloration and the width of the dark distal bands on both wings.

*Argyrogrammana leptographia* was described by Stichel (1910-11) as a subspecies of *A. trochilia* (raised to species status by Hall & Willmott (1996)) from one male from Río San Juan, W. Colombia, in the ZMHU, and one male from "Colombia", in the BMNH. To restrict the type locality to a single more precise location, the male syntype in the ZMHU is designated here as the lectotype. It bears the following labels: "Type", "Río San Juan / Columb. / Tr.", "leptographia / Stich.", and "Coll. / Staudinger".

**Biology:** This somewhat uncommon species is known from sea level to 1600 m. In Ecuador, males were found perching singly or in pairs 2 to 4 m above the ground along forest edges and in lightgaps on ridgetops and in flat forest, including streamsides, from 1345 to 1500 hrs. Females were encountered flying low

to the ground along forest edges on ridgetops from 1100 to 1300 hrs, and one individual was also found in a subcanopy trap baited with rotting fish. In Costa Rica, females were found along forest edges and streams from 0630 to 1200 hrs, as well as visiting the white flowers of an asteraceous vine (DeVries, 1997). Foodplant records in the Clusiaceae were listed by DeVries (1997) under the name *A. leptographia*, but the accompanying text suggests that they are probably referable to *A. trochilia*, a species that was reared on the same plants in eastern Ecuador (DeVries *et al.*, 1994) and until that time period was treated as conspecific with *A. leptographia* (Hall & Willmott, 1996).

**Distribution:** *Argyrogrammana leptographia* is known to range from Costa Rica to central Colombia and northwestern Ecuador.

*Argyrogrammana saphirina* (Staudinger, 1887)  
(Figs. 7A,B)

*Charis saphirina* Staudinger, 1887. *Exot. Schmett.* 2(19): pl. 91; 1(20): 256 (1888). **TL:** Río San Juan, Chocó, W. Colombia. Syntype males (3) and female ZMHU [examined].

**Identification and Taxonomy:** This is the largest species of Transandean *Argyrogrammana*, and its banded wing pattern in both sexes makes it utterly distinct from any regional congeners. It seems to belong in a terminal derived clade of the *trochilia* group with the Amazonian *A. johannismarci* Brévignon, 1995, and *A. brevignoni* Dolibaina & Dias, 2015. The males of all three species are unique in the group in always lacking (or almost always in the case of *A. johannismarci*) yellow submarginal scaling on the dorsal forewing, and having a fourth blue band from the base of the dorsal forewing that is abruptly distally broadened below vein  $Cu_1$  and a consistent "2-2 pattern" of blue scaling in anal cell 2A on the dorsal forewing, with one bar below blue bands one and two and another below bands three and four. The sister species of *A. saphirina* seems likely to be the recently described *A. brevignoni*, whose male shares a fourth blue band from the base of the dorsal forewing that is both abruptly broadened and of uniform width below vein  $Cu_1$ , and a dark spot within the distal-most yellow band in the discal cell of the ventral forewing, a character that is only very rarely expressed in *A. johannismarci*.

The male of *A. saphirina* differs most obviously from the unique male holotype of *A. brevignoni*, from Acre, western Brazil, by being considerably larger and having broader blue bands on both dorsal wings, no orange marginal scaling on both dorsal wings, and a fifth yellow band from the base of the ventral forewing that has no iridescent blue scaling inside the apex and is distally displaced at vein  $Cu_1$ . The male genitalia of *A. saphirina* (see Fig. 15 in Hall & Willmott (1996)) are quite distinct from those of all other *trochilia* group species, most notably in having an aedeagal pedicel that is medially prominently ventrally bent and a transtilla that forms a medium-length horn-like process between the valve tips. Both of these characters appear to be incipiently present in the male genitalia

illustration for *A. brevignoni* in Dolibaina *et al.* (2015: Fig. 58), further supporting the sister hypothesis for the two species. The female of *A. saphirina* should be separable from all the other *trochilia* group females, including the as yet unknown female of *A. brevignoni*, by its larger size and medially disjunct fifth yellow band on the forewing.

Intrapopulational variation in *A. saphirina* is minimal. Male variation includes the exact width of the bands on both wings, the presence or absence of a small dark orange submarginal spot in the tornus of the dorsal hindwing, and the size of the dark spot within the distal-most yellow band in the discal cell of the ventral forewing. Female variation includes the exact width and shape of the bands on both wings, and the extent of yellow submarginal and marginal scaling on the dorsal hindwing.

**Biology:** This uncommon to rare species is known from near sea level to 900 m. In Ecuador, solitary males were encountered perching 3 to 4 m above the ground along forest edges and in lightgaps on ridgetops and in flat forest from 1120 to 1400 hrs. A female was observed flying around a shady hilltop tree trunk 3 to 4 m above the ground at 1545 hrs, probably searching for a perching male.

**Distribution:** *Argyrogrammana saphirina* appears to be restricted to the broader Chocó region, ranging from far eastern Panama to northwestern Ecuador.

#### *occidentalis* group

#### *Argyrogrammana vespertina* Hall & Willmott, new species

(Figs. 8A,B; 19)

**Description:** MALE: Forewing length HT 12 mm; PTs 12-13 mm. *Wings:* see Fig. 8A. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and orange marginal scaling; frons orange, with narrow dark brown transverse bands ventrally and dorsally and a dark brown “horizontal figure of eight” band medially; labial palpi orange with dark brown tips; antennal length approximately 50% of forewing length, segments black with vertical cream lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dirty orange with some black dorsal scaling, ventral surface pale orange gray, dorsal surface of abdomen dirty orange with a rectangular black mark at middle of anterior margin of all segments that becomes smaller on posterior segments, ventral surface pale orange gray with a narrow and broken brown medial band; all legs banded brown and pale dirty orange. *Genitalia:* see Fig. 19; posterior portion of valvae in ventral view prominently asymmetrical, with a relatively broad gap between tips; sclerotized transtilla forms a long, upwardly curved, “hook”-like posterior process that is narrow and curved to right in ventral view; ductus ejaculatorius enters anterior tip of aedeagus anteriorly; vesica exits posterior tip of aedeagus to right, cornutal complex on unverted vesica consists of a bundle of very long, thin, approximately straight, parallel, posteriorly directed “hair”-like cornuti; eighth tergite and sternite rectangular. FEMALE: Forewing length PT 12 mm. *Wings:* see Fig. 8B. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and dirty yellow marginal scaling; frons dirty yellow, with dark brown transverse bands ventrally and dorsally and a dark brown rectangular spot medially; labial palpi dirty yellow with dark brown tips; antennal length approximately 50% of forewing length, segments black with vertical cream lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dark dirty yellow with some dark brown dorsal scaling, ventral surface dirty yellow, dorsal surface of abdomen dark dirty yellow with rectangular dark brown dorsal and lateral marks at anterior margin of all segments that become smaller on posterior segments, ventral surface banded brown and dirty yellow; all legs banded brown and dirty yellow.

**Types:** HOLOTYPE male: ECUADOR: *Esmeraldas*, El Durango, km. 40 Lita-San Lorenzo rd., 1°02'45"N 78°38'06"W, 300 m, 27 Aug 2002 (J. P. W. Hall)

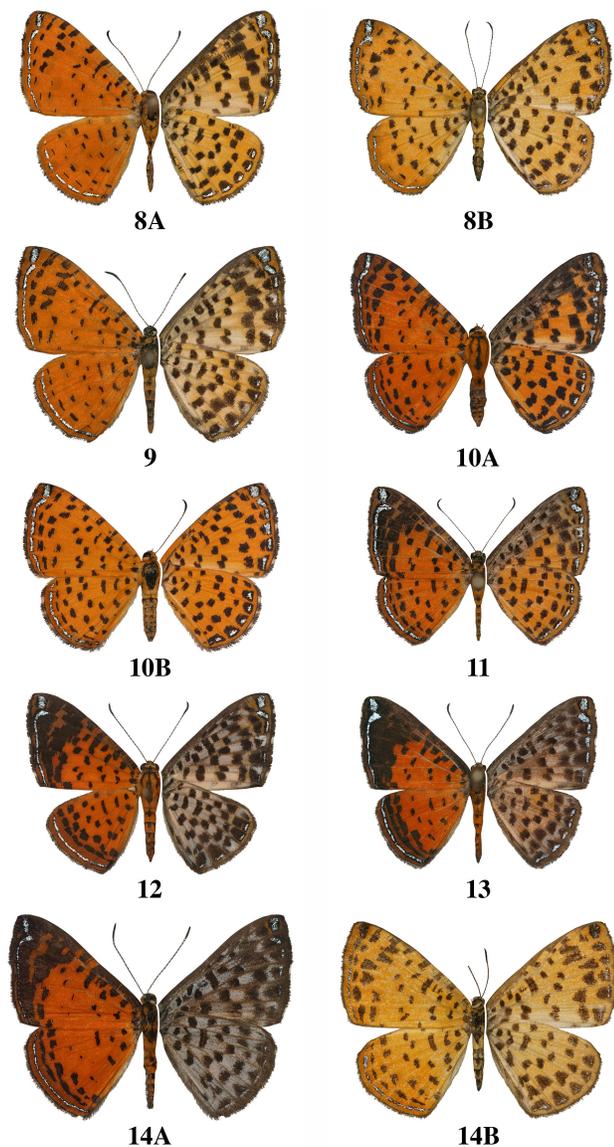
(USNM).

PARATYPES: PANAMA: *Panamá*, 1 male: Altos de Pacora, 650 m, 14 Mar 1975 (USNM); 1 male: Altos de Pacora, 600 m, 29 Mar 1975 (G. B. Small) (USNM); *Darién*, 1 female: Cana, 750 m, 14 Jul 1981 (G. B. Small) (USNM). ECUADOR: *Esmeraldas*, 1 male: same locality data as HT, 23 Mar 1995 (J. P. W. Hall) (JH); ridge above San Francisco, km. 17 San Lorenzo-Lita rd., 1°06'26"N 78°41'55"W, 200 m, 3 males: May 2008 (R. Aldaz) (INABIO); 1 male: 9-12 Aug 2016 (JH1710) (J. P. W. Hall) (JH); 2 males: Feb 2008 (E. Aldaz) (DA); 2 males: Oct 2016 (I. Aldas) (DA); 1 male: “Lita”, 650 m, Jul 2009 (LEP-78347) (FLMNH).

**Etymology:** The name is based on the Latin word “vespertina”, meaning “evening”, in reference to the restriction of this species to the west of the Andes, in contrast to its newly described sister species *A. aurora* Hall & Willmott, 2023, whose name refers to its distribution on the eastern slope of the Andes.

**Diagnosis:** The morphological phylogenetic analysis of *Argyrogrammana* presented by Hall (2023a) indicates that *A. vespertina* n. sp. belongs in the *occidentalis* group. This species group contains most of the species with males that have orange and black-spotted dorsal wing patterns, and many of them are confusingly similar and thus frequently confounded in collections and the literature. As recently as the 2004 checklist by Callaghan & Lamas, only three of the species in this group were recognized, namely *A. occidentalis*, *A. placibilis*, and *A. sublimis* Brévignon & Gallard, 1995. However, the group is here recognized to contain 12 species, half of which are described as new in this and a related paper (Hall *et al.*, 2023a), including nine species in the widely distributed *A. occidentalis* clade, two Amazonian species in the *A. placibilis* clade (*A. placibilis* and *A. willmotti* Dolibaina & Dias, 2015), and, tentatively, the newly described east Andean *A. janiceae* at the base.

The stem node of the *occidentalis* group is supported by males having a predominantly grayish discal cell on the ventral forewing with orange scaling across the cells below (unique to the group, but lost twice in the *A. occidentalis* clade), and females having a dark submarginal band on the dorsal forewing that is more or less entirely separated from the silver submarginal line (universal within the group, but independently derived in a scattered handful of *amalfreda* group species). The sister group relationship between the *A. placibilis* and *A. occidentalis* clades is supported by males having a full to nearly full complement of dark postdiscal spots on the dorsal forewing (universal within the clade, but also present in the *stilbe*, *barine*, and *trochilia* groups), a dark submarginal band on the dorsal forewing that is more or less entirely separated from the silver submarginal line (unique to the clade, but absent in *A. willmotti*), and a dark submarginal band on the dorsal hindwing that is more or less entirely separated from the silver submarginal line (universal within the clade except for *A. willmotti*, but also widely present in sections of the *amalfreda* group). *Argyrogrammana vespertina* belongs in the *A. occidentalis* clade, which is strongly supported by three unique and universal characters, namely a dark presubmarginal band on the male dorsal forewing with spots above vein Cu<sub>1</sub> that are significantly enlarged compared to the spots below, male genital valvae with a large, upwardly curved, hook-like posterior transtilla process, and a male genital aedeagus with a bundle of thin, straight, parallel “hair”-like cornuti.



**Figs. 8-14.** Transandean *Argyrogrammana occidentalis* group adults (Figs. 8, 10-11, 13-14), with extralimital taxa included for comparison (Figs. 9, 12) (dorsal surface on left, ventral surface on right). **8A.** *A. vespertina* Hall & Willmott, n. sp., HT male, El Durango, Esmeraldas, W. Ecuador (USNM). **8B.** *A. vespertina* PT female, Cana, Darién, Panama (USNM). **9.** *A. saulensis* Gallard, 2008, male, Lumbaquí, Sucumbíos, E. Ecuador. **10A.** *A. janzeni* Hall, n. sp., HT male, ACG Sector San Cristóbal, Alajuela, Costa Rica (USNM). **10B.** *A. janzeni* PT female, ACG Sector San Cristóbal, Alajuela, Costa Rica (USNM). **11.** *A. juanita* (Staudinger, 1887) male, San Francisco, Esmeraldas, W. Ecuador. **12.** *A. eura* Hall, n. sp., HT male, Roura, Cayenne, French Guiana (USNM). **13.** *A. occidentalis* (Godman & Salvin, 1886) male, San Francisco, Esmeraldas, W. Ecuador. **14A.** *A. cana* Hall & Willmott, n. sp., HT male, Serranía de Pirre, Darién, Panama (1500 m) (USNM). **14B.** *A. cana* PT female, Serranía de Pirre, Darién, Panama (1500 m) (USNM).

The *A. occidentalis* clade can be further divided into an *A. occidentalis* subclade of five species that are primarily distributed to the west of the Andes, and an *A. sublimis* subclade of four species that are primarily distributed to the east of the Andes. *Argyrogrammana vespertina* belongs in the *A. sublimis*

subclade as its only Transandean member, and seems to be sister to the newly described east Andean *A. aurora*, with *A. saulensis* Gallard, 2008, sister to them, and *A. sublimis* positioned at the base of the subclade. These four very similar species all share a medially divided dark spot near the base of cell  $Cu_2$  below the base of the discal cell on the male dorsal forewing, a character that has evolved elsewhere in the genus only in the new *A. occidentalis* subclade species *A. eura*, which otherwise exhibits the multiple male wing pattern characters typical of that subclade.

Before further discussing *A. vespertina*, we take this opportunity to try to clarify the taxonomy and identification of the *A. sublimis* subclade names proposed to date. Brévignon & Gallard (1995) introduced the name *A. sublimis* as a subspecies of the distantly related *A. stilbe*, which at the time they apparently believed was a senior synonym of *A. placibilis* (see the discussion of the name *perone* in the species account for *A. holosticta*), based on both sexes from French Guiana (forewing lengths of males illustrated in the literature 11-11.5 mm). The taxon actually seems to have been first figured by Cock (1981) from Trinidad, under the name *A. occidentalis*. Hall & Willmott (1996) subsequently elevated *A. sublimis* to species status, using the name to refer to similar specimens ranging in origin from Costa Rica to Amazonia that are here recognized as belonging to multiple species. The Costa Rican male that was figured as *A. sublimis* is included here as a paratype of the new species *A. janzeni*, and the Brazilian female that was figured as *A. sublimis* seems to belong to *A. saulensis*. Hall & Willmott (1996) also noted that in the figures published by Brévignon & Gallard (1995), the allotype female of *A. sublimis* belonged to *A. placibilis* and the female of *A. occidentalis* actually belonged to *A. sublimis* (in addition, the female figured as *A. amalfreda* (Staudinger, 1887) seems to belong to *A. saulensis*). The name *iracyi* was proposed by P. & J. Jauffret (2007) based on a single small male (forewing length 10.5 mm) from the Belém area of east Amazonian Brazil, although the specimen previously figured by Jauffret & Martins (2006) from a nearby locality as a female paratype of the *amalfreda* group species *A. danieli* P. Jauffret & Martins, 2006, appears to be conspecific with the *iracyi* holotype. Gallard (2008) subsequently proposed the taxa *A. iracyi saulensis*, based on large males from French Guiana (a female was later figured by Gallard (2017)), and *A. iracyi tunari*, based on similarly large males from Bolivia (forewing lengths of male types of these taxa 13-13.5 mm). In a paper on the *Argyrogrammana* fauna of Cerro Divisor, Acre, western Brazil, Dolibaina *et al.* (2015) recognized that two similar *A. sublimis* subclade species occurred sympatrically there, and they grappled with the issue of which names to apply. They correctly realized that the larger *saulensis* was not conspecific with *iracyi*, and they raised *A. saulensis* to species status, with *tunari* as a west Amazonian subspecies, and treated the smaller species as *iracyi*. However, Dolibaina *et al.* (2015) introduced some confusion with their figures for the females of the two *sublimis* subclade species, which seem to belong to the *amalfreda* group. Hall *et al.* (2023b) provided evidence for the specimen in Figs. 37 and 38 in Dolibaina *et al.* (2015), identified as *iracyi*, being the female of *A. danieli*, and the specimen in Figs. 41 and 42, identified as *A. saulensis tunari*,

being the female of *A. aparamilla* Hall & Willmott, 1995.

Although the aforementioned taxonomic arrangement adopted by Dolibaina *et al.* (2015) is logical and represents an improvement in the taxonomy of the subclade, we propose two further changes. There are two identifiable *A. sublimis* subclade species that may occur at any given locality throughout much of lowland Amazonia, with broad sympatry specifically recorded in French Guiana, east and west Amazonian Brazil, and Ecuador. The name *A. saulensis* certainly seems to apply to the larger of the two species, which has a known male forewing length of 11.5-13.5 mm. Examination of a large series of *A. saulensis* males from Ecuador shows this to be a variable species even within populations, most notably in the dorsal coloration, which varies from yellow orange to orange, the prominence of the dark spotting on both wing surfaces, the extent of grayish scaling across the base of both ventral wings, the presence or absence of whitish-gray submarginal scaling in cell  $M_3$  on both ventral wings variably obscuring the silver line, and whether or not the dark submarginal spots on the ventral hindwing and tornal half of the ventral forewing are separate from or fused to the silver submarginal line. Males from French Guiana differ from those known from the remainder of Amazonia by having slightly broader dark presubmarginal and submarginal spots in the forewing apex compared to even the most heavily marked specimens from elsewhere, such as the east Ecuadorian male in Fig. 9. However, given the variability of the species and the lack of known material from the area between French Guiana and the Rio Amazon, this modest difference seems insufficient to justify the recognition of subspecies, and we suggest that *tunari* be treated as a synonym of *A. saulensis* (**n. syn.**). The smallest Amazonian *A. sublimis* subclade specimens, those with a male forewing length of 10 to 11.5 mm, also seem to exhibit some geographic variation. The west Brazilian male figured by Dolibaina *et al.* (2015: Figs. 35-36) very closely matches the east Brazilian holotype male of *iracyi* figured by P. & J. Jauffret (2007: Figs. 3-4) in having a slightly more compact wing shape and cleaner orange ventral surface than males known from elsewhere. The lone male known from Ecuador has the same evenly spotted wing pattern as the Brazilian males, but the slightly more elongate wings and dirtier orange ventral surface of the French Guianan population. French Guianan males are themselves variable, with the males figured by Gallard (2008 [Pl. 2, Fig. 12, from inland Saül], 2017 [Pl. 18, Fig. 9, locality not stated]) differing from the holotype male of *A. sublimis* figured by Brévignon & Gallard (1995: Fig. 3, from coastal Galion) by having broader dark presubmarginal and submarginal spots in the apex of the dorsal forewing (mirroring the Saül population of *A. saulensis*). Overall, French Guianan males have less evenly spotted dorsal wings than males from elsewhere, with fainter spotting sometimes present in the middle of both wings and heavier spotting always present in the forewing apex. Notably, similar variation in the heaviness of apical forewing spotting that is clearly intraspecific occurs in other *occidentalis* group species, such as *A. placibilis*, *A. juanita*, and *A. saulensis*. We thus tentatively suggest that all of the above-discussed small Amazonian males belong to a single species, *A. sublimis*, resulting in *iracyi* being treated for now as a synonym of *A. sublimis* (**n. syn.**). Although males of *A. sublimis* are externally

primarily characterized by their small size, they also seem to differ from males of *A. saulensis* (as well as *A. vespertina* and *A. aurora*) by having a broad, contrasted, darker orange distal band around the silver submarginal line on both dorsal wings, and they typically have larger dark presubmarginal spots on the dorsal hindwing that are never surrounded by larger faint dark markings (reflecting larger such spots on the ventral surface). At least in the western Amazon, *A. sublimis* is a considerably rarer species than *A. saulensis*.

The male genitalia differences between *A. sublimis* subclade species are subtle, and the most important diagnostic characters can only be seen in ventral view. It is thus unfortunate that the male genitalia illustrations for *A. sublimis* from French Guiana by Brévignon & Gallard (1995: Fig. 2) and Gallard (2008: Pl. 3, Fig. 10) and for the holotype of *iracyi* by P. & J. Jauffret (2007: Fig. 5) are shown in lateral view only. The male genitalia illustrations for *A. saulensis* from French Guiana by Gallard (2008: Pl. 3, Fig. 11) include both ventral and lateral views, but these are insufficiently detailed and accurate to be very diagnostically helpful. The genitalia of the aforementioned Ecuadorian male identified here as *A. sublimis* differ from those of two dissected Ecuadorian males of *A. saulensis* (see Fig. 20) by having a saccus that is weakly angled instead of prominently curved to the left in ventral view, prominently asymmetrical instead of approximately symmetrical valve tips in ventral view (similar to those of *A. eura* in Fig. 23), a narrower gap between the valve tips in ventral view that is approximately the same width as instead of twice as wide as the valve tip, and a slightly shorter hook-like posterior transtilla process that does not extend beyond the dorsal margin of the valvae in lateral view, has approximately half instead of two-thirds its length beyond the posterior margin of the valvae in ventral view, and is relatively narrow, tapered, and curved to the right in ventral view (and thus similar to that of *A. janzeni* in Fig. 21) instead of relatively broad, angular, and straight. Most of these transtilla differences are also reflected in the genitalia illustrations by Dolibaina *et al.* (2015: Figs. 61-62) for west Brazilian specimens of these two species, although it is important to note that the characters involving asymmetry are absent only because all of the ventral genitalia illustrations in that paper lack inclusion of the asymmetries that are widespread in the genus. These asymmetries are generally unimportant, but in the *occidentalis* group they happen to provide some critical diagnostic characters. More definitive proof regarding the conspecificity of the names *sublimis* and *iracyi* must await a detailed genital examination of multiple *A. sublimis* males from the Guianas, which were not readily available for study.

With *A. saulensis* clearly differentiated above from *A. sublimis*, the new species *A. vespertina* can now be distinguished from its closest relatives *A. saulensis* and *A. aurora*. This trio of allo/parapatrically distributed sibling species was long regarded by us as belonging to a single widespread taxon. However, more detailed recent study has revealed that in addition to subtle external characters, these three phenotypes exhibit consistent male genitalia differences and significant DNA barcode differences, suggesting that they represent separate species. Externally, *A. vespertina* (Figs. 8A,B) is similar in size to the lowland Amazonian *A. saulensis* (Fig. 9), with a known

male forewing length range of 12-13 mm compared to 11.5 to 13.5 mm, while being noticeably smaller than the east Andean *A. aurora* (male forewing length 13.5 to 15 mm) (see Fig. 5 in Hall *et al.* (2023a)). There are no wing pattern differences that consistently separate these three species, but *A. vespertina* males have spots in the costal half of the presubmarginal band on the dorsal forewing that are typically larger than those in *A. aurora*, dark submarginal spots on both dorsal wings that tend to be smaller, narrower, and more widely spaced than those in *A. saulensis*, a ventral surface that is less orange colored than in *A. aurora* and has less basal grayish scaling than is often present in *A. saulensis*, dark vertical streaks in the costal third of the ventral forewing that are typically densely present instead of absent to sparsely present in *A. aurora* and nearly always absent in *A. saulensis*, dark presubmarginal spots in cells  $M_3$  and  $M_2$  on the ventral forewing that are rectangular rather than typically arrow shaped as in *A. aurora* and *A. saulensis*, a dark presubmarginal spot in cell  $Cu_1$  on the ventral forewing that tends to be slightly larger and more proximally positioned compared to that in *A. saulensis*, and dark submarginal spots on the ventral hindwing that are nearly always fused with the silver submarginal line rather than typically separated as in *A. saulensis* (although not in the heavily patterned Fig. 9 specimen). There is an insufficient series of females of *A. vespertina* and *A. saulensis* to determine whether they exhibit any moderately consistent wing pattern differences, and, with the female of *A. aurora* currently unknown, locality data are the best means of identifying these females. Additional notable intrapopulational wing pattern variation in *A. vespertina* males includes the prominence of the dark presubmarginal spots in the tornus of the dorsal forewing and dark submarginal spots on the dorsal hindwing (rarely absent), and the extent to which the dark submarginal spots in the tornus of the ventral forewing are separated from the silver submarginal line. Another species very similar to *A. vespertina*, *A. janzeni*, currently known only from Costa Rica, is distinguished in that species account.

Three males of *A. vespertina* were dissected from western Ecuador (Fig. 19) and one from Panama, and multiple males of both *A. saulensis* (Fig. 20) and *A. aurora* (see Fig. 13 in Hall *et al.* (2023a)) were dissected from eastern Ecuador, revealing several subtle but seemingly consistent genitalia differences between the species. The male genitalia of *A. vespertina* have a saccus in ventral view that angles to the right instead of being approximately straight (*A. aurora*) or curving to the left (*A. saulensis*), prominently asymmetrical valve tips in ventral view instead of weakly asymmetrical (*A. aurora*) or approximately symmetrical (*A. saulensis*) valve tips, and a narrow and curving hook-like transtilla process in ventral view instead of a broad and curving (*A. aurora*) or broad and approximately straight (*A. saulensis*) transtilla process. We sequenced the barcode region of the mitochondrial gene COI for Ecuadorian exemplars of these taxa, and the results showed that a male paratype of *A. vespertina* (JH1710), from San Francisco in Esmeraldas province, had a sequence divergence of 1.9% from a male paratype of *A. aurora* (JH1706), from San Luis in Zamora-Chinchipe province (1500 m), and 3.8% from the male of *A. saulensis* (JH1709) in Fig. 9, from Lumbaquí in Sucumbíos province (*A. saulensis* and *A. aurora* had a sequence divergence

of 4.5%). When comparing publicly available sequences (see metadata in Table 1), we also found a sequence divergence of no more than 0.2% among three male specimens of *A. vespertina* from western Ecuador (incl. LEP-78347 and JH03R040 [= "*A. sublimis*" in Espeland *et al.* (2015)]). Although more sequence data would clearly be desirable, particularly for *A. saulensis* from the eastern Amazon, these preliminary DNA barcode data are supportive of the species status hypothesis for these three taxa.

**Biology:** This uncommon to rare species is known from about 200 to 800 m. In Ecuador, solitary males or pairs of males were encountered perching 2 to 8 m above the ground on tree-trunk epiphytes from 1400 to 1515 hrs, primarily in shady hilltop lightgaps but also on one occasion inside the forest edge in flat forest.

**Distribution:** *Argyrogrammana vespertina* is known with certainty only from eastern Panama and northwestern Ecuador, but specimens listed by Constantino *et al.* (2012) under the name *A. sublimis* from the El Dovio-upper Río Garrapatas rd. and Río Calima, in Valle del Cauca, western Colombia, are also probably referable to this species. It is replaced throughout lowland Amazonia by *A. saulensis* and in the eastern Andes by *A. aurora*.

#### *Argyrogrammana janzeni* Hall, new species

(Figs. 10A,B; 21)

**Description:** MALE: Forewing length HT 12 mm. *Wings:* see Fig. 10A. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and orange marginal scaling; frons orange, with narrow black transverse bands ventrally and dorsally and a broad central black band medially; first and second segments of labial palpi orange with black scaling at distal tips, third segment black; antennal length approximately 55% of forewing length, segments black with vertical yellow lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dark orange with a black medial stripe and faint black lateral stripes, ventral surface pale orange gray, dorsal surface of abdomen dark orange with rectangular black dorsal and lateral marks at anterior margin of all segments that become smaller on posterior segments, ventral surface banded pale black and pale orange; all legs banded brown and pale orange. *Genitalia:* see Fig. 21; posterior portion of valvae in ventral view very weakly asymmetrical, with a narrow gap between tips; sclerotized transtilla forms a medium-length, upwardly curved, "hook"-like posterior process that is tapered and curved to right in ventral view; ductus ejaculatorius enters anterior tip of aedeagus anteriorly and slightly to right; vesica exits posterior tip of aedeagus to right, cornutal complex on unverted vesica consists of a bundle of very long, thin, approximately straight, parallel, posteriorly directed "hair"-like cornuti; eighth tergite and sternite rectangular. FEMALE: Forewing length PTs 11.5 mm. *Wings:* see Fig. 10B. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and orange marginal scaling; frons orange, with narrow dark brown transverse bands ventrally and dorsally and a small, vertically narrow dark brown spot medially; labial palpi orange with dark brown tips; antennal length approximately 55% of forewing length, segments black with vertical yellow lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax orange with some black scaling, ventral surface pale orange, dorsal surface of abdomen orange with rectangular black dorsal and lateral marks at anterior margin of all segments that become smaller on posterior segments, ventral surface pale orange with brown and orange lateral scaling at posterior margin of each segment; all legs banded brown and pale orange.

**Types:** HOLOTYPE male: COSTA RICA: *Alajuela*, Área de Conservación Guanacaste Sector San Cristóbal, 2012 (coll. as caterpillar) (ACG#: 12-SRNP-5583) (USNM).

PARATYPES: COSTA RICA: *Alajuela*, 2 females: Sendero Huerta, Área de Conservación Guanacaste Sector San Cristóbal, 10.9305°N 85.3722°W, 550 m, 29 Mar 2012 (coll. as caterpillars) (ACG#: 12-SRNP-1232 and 12-SRNP-1244) (USNM); 2 males: “Costa Rica” (BMNH).

**Etymology:** This species is named for Daniel H. Janzen, whose team of parataxonomists reared it in Costa Rica among many other important new rearings of riordinid species from the Área de Conservación Guanacaste (ACG).

**Diagnosis:** The morphological phylogenetic analysis of *Argyrogrammana* presented by Hall (2023a) indicates that *A. janzeni* n. sp. belongs in the *A. occidentalis* clade of the *occidentalis* group, where it seems to be phenotypically close to the ancestor of the *A. occidentalis* and *A. sublimis* subclades. The species can be excluded from the *A. sublimis* subclade because it has a solid instead of medially divided dark spot near the base of cell  $Cu_2$  below the base of the discal cell on the male dorsal forewing, and it seems to be the most basal member of the *A. occidentalis* subclade. It shares with the other members of that subclade a more or less continuous silver submarginal line on the male dorsal forewing instead of one that is divided into dashes by significant gaps at each vein, but lacks the multiple wing pattern synapomorphies possessed by the derived majority of subclade members (see the species account for *A. juanita*).

The male of *A. janzeni* (Fig. 10A) is most similar to that of its closest relative *A. juanita*, as well as males of *A. sublimis* subclade members such as *A. vespertina*. A worn male of *A. janzeni* was actually figured by Hall & Willmott (1996: Figs. 11A,B) under the name *A. sublimis* (now restricted to a small Amazonian taxon, as detailed in the species account for *A. vespertina*), but the reared specimens of *A. janzeni* figured here are in near perfect condition and much better highlight the diagnostic features of the species. The male of *A. janzeni* shares with the male of *A. juanita* a rich orange ventral surface with prominent grayish scaling along the costal margin of the ventral forewing, but it differs by being considerably larger and having a more or less unicolorous orange dorsal surface without noticeably darker and duller orange around the distal margins of both wings, dark presubmarginal and submarginal spots on the dorsal forewing that are all separate instead of typically fused above at least vein  $Cu_1$ , a weakly instead of prominently inwardly curved element to the silver submarginal line in cell  $M_1$  on the dorsal forewing, and less extensive darker orange scaling along the proximal margin of the silver submarginal line on the ventral forewing. The male genitalia of *A. janzeni* (Fig. 21) are very similar to those of *A. juanita*, potentially differing only by having a saccus in ventral view that is approximately straight instead of curved to the left and a transtilla process that is slightly narrower, more tapered, and less prominently curved to the right. The male of *A. janzeni* differs from that of *A. vespertina* by having a darker orange dorsal surface, a solid instead of medially divided dark spot near the base of cell  $Cu_2$  on the dorsal forewing, slightly heavier dark presubmarginal and submarginal bands on both dorsal wings, a more solid and continuous silver submarginal line on both dorsal wings, a darker orange ventral surface, and a solid band of grayish scaling along the costal margin of the ventral forewing. The male genitalia of *A. janzeni* differ from those of *A. vespertina*

by having a saccus in ventral view that is approximately straight instead of angled to the right, valve tips in ventral view that are very weakly instead of prominently asymmetrical and have a much narrower gap between them, and a slightly shorter hook-like posterior transtilla process that does not extend beyond the dorsal margin of the valvae in lateral view and is more laterally displaced to the left and distally tapered in ventral view.

The female of *A. janzeni* (Fig. 10B), which was recently figured by Glassberg (2017) under the name *A. leptographia*, can be distinguished from the females of most Transandean congeners by having orange instead of yellow to yellow-orange wings, and from the orange female of *A. physis* by having a medially divided instead of solid dark spot toward the base of cell  $Cu_2$  below the middle of the discal cell on the dorsal forewing and no grayish scaling across the ventral hindwing. It can additionally be separated from the females of at least some of the other *A. occidentalis* subclade species by having unicolorous wings without noticeably darker orange around the distal margins, smaller dark presubmarginal and submarginal spots on the dorsal forewing, and a more weakly inwardly curved element to the silver submarginal line in cell  $M_1$  on the dorsal forewing, although this last character is a much weaker indicator of phylogenetic position and identity in females than it is in males. No significant intrapopulational variation has been observed in this restricted-range species.

**Biology:** Nothing is known about the adult biology of this evidently rare species, which has been recorded from about 550 m. Most of the type series was reared to adults from caterpillars found feeding on *Calophyllum brasiliense* (Calophyllaceae) (Janzen & Hallwachs, 2009-22).

**Distribution:** *Argyrogrammana janzeni* is currently known only from Costa Rica. It may occur farther westward, as well as in western Panama, but is potentially replaced by its closest relative, *A. juanita*, from the environs of the Canal Zone of central Panama eastward.

*Argyrogrammana juanita* (Staudinger, 1887) **rev. stat.**  
(Figs. 11; 22)

*Lemonias juanita* Staudinger, 1887. *Exot. Schmett.* 2(19): pl. 92; 1(20): 258 (1888). **TL:** Río San Juan, Chocó, W. Colombia. Lectotype male ZMHU [designated].

**Identification and Taxonomy:** The names *occidentalis* and *juanita* were introduced in quick succession from the same type locality in western Colombia (Godman & Salvin, 1885-86; Staudinger, 1884-88), and the latter was soon synonymized with the former by Stichel (1910), an arrangement followed by all subsequent authors (e.g., Stichel, 1910-11, 1930-31; Hall & Willmott, 1996; Callaghan & Lamas, 2004). However, our field work in western Ecuador has led to the discovery that these names represent two distinct Transandean species, exhibiting multiple subtle wing pattern and genital differences, that perch in the same hilltop lightgaps during sequential time periods in the late afternoon. Therefore, *A. juanita* is returned here to the rank of species (**rev. stat.**).

*Argyrogrammana juanita* belongs to the derived section of the *A. occidentalis* subclade in the *A. occidentalis* clade, which in addition to *A. occidentalis* includes the new species *A. eura* (northeastern South America) and *A. cana* (montane Chocó). These four species are unique in the genus in having males with a dark presubmarginal band on the dorsal forewing containing spots above vein  $Cu_1$  that are significantly enlarged compared to the spots below and fused into a continuous band, two-tone orange scaling on the dorsal forewing encompassing orange scaling distal to the dark presubmarginal band that is darker than the orange scaling proximally, and a dark submarginal band of defined spots on the dorsal forewing that is formed into a broad and continuous band. They are also unique in the *occidentalis* group in having males with a prominently inwardly curved element to the silver submarginal line in cell  $M_1$  on the dorsal forewing, and unusual in having a broad and contrasted orange distal band around the silver submarginal line on the dorsal hindwing (also present in *A. placibilis* and *A. sublimis*).

The illustration by Seitz (1916-20: Pl. 135, row c) labeled as "*A. occidentalis*" seems to have been based on a male of *A. juanita*, but the male specimen shown here in Fig. 11 seems to be the first photograph of this species in the literature. The male of *A. juanita* differs from that of *A. occidentalis* by being consistently slightly smaller (10-11.5 mm versus 12-12.5 mm) and having a slightly more compact and less pointed wing shape, slightly paler and browner orange dorsal scaling, a more evenly spotted dorsal hindwing with dark presubmarginal and submarginal bands consisting of small individual spots instead of larger spots that are partially to completely fused into bands, pale scaling across the ventral hindwing and anal half of the ventral forewing that is a pure bright orange instead of a darker orange gray and extends from the wing base to the distal margin instead of largely stopping at the dark presubmarginal band, a narrower dark presubmarginal band on the ventral hindwing, and a dark submarginal band on the ventral hindwing consisting of small rectangular spots that are partially to completely separated from the silver submarginal line instead of larger triangular spots that are completely fused to that line. The male genitalia of the two species are very similar (Figs. 22 and 24), but those of *A. juanita* have slightly asymmetrical instead of approximately symmetrical valve tips in ventral view, and seem to have a slightly more curved transtilla process in ventral view. The male of *A. juanita* is separated from that of the considerably larger but ventrally more similar *A. janzeni* in that species account.

The single male of *A. juanita* examined from Panama (Cerro Campana) differs slightly from the examined Chocó males by having a dorsal forewing with individually defined dark presubmarginal spots and a dark submarginal band that is narrower and consists of separated spots. However, the width of these two bands also varies locally within the Chocó to a significant extent. At the opposite end of the variability spectrum (e.g., in the lectotype of *A. juanita*), these two bands can be so broad that the orange scaling between them is almost absent. Intrapopulation variation is otherwise largely limited to the exact width of the dark presubmarginal and submarginal bands on the hindwing, the width of the gap between the dark submarginal band and the silver submarginal line on the dorsal

hindwing, and whether or not the dark submarginal band on the ventral hindwing is completely separated from or partially fused to the silver submarginal line. We have not with certainty examined a female of *A. juanita*, although it is possible that one exists among the *A. occidentalis* material in European collections. It would be expected to differ from that of *A. occidentalis* by being slightly smaller, and having a narrower dark presubmarginal band on the hindwing, and a narrower dark submarginal band on both wings that is better separated on the ventral surface from the silver submarginal line.

*Argyrogrammana juanita* was described by Staudinger (1884-88) from a series of males and at least one female (of undetermined identity) from Río San Juan, W. Colombia, now in the ZMHU. We do not have photographs of the full type series, but, from the discussion of male wing pattern variation in Staudinger's original description of *A. juanita*, it is apparent that his syntype series is mixed and includes one or more males of *A. juanita* and two males of *A. occidentalis*, which was described (and not figured) only a year earlier by Godman & Salvin (1885-86) and not mentioned by Staudinger. Therefore, the male syntype illustrated by Staudinger (1884-88) is designated here as the lectotype. It bears the following labels: "Origin.", "abgebildet", "Río San Juan / Columb. / Tr.", "occidentalis / Godm & Salv. / (juanita Stgr.)", and "Coll. / Staudinger".

**Biology:** This rare species is known from near sea level to 750 m. In Ecuador, males were encountered perching on just a single hilltop, where one to three individuals could regularly be found flying 2 to 8 m above the ground around one or two tree trunks in a shady lightgap at the edge of the hill from 1500 to 1610 hrs, only rarely landing on epiphytes.

**Distribution:** *Argyrogrammana juanita* is known to range from the Canal Zone of central Panama to northwestern Ecuador. It seems to be replaced by *A. janzeni* farther to the west.

*Argyrogrammana occidentalis* (Godman & Salvin, 1886)  
(Figs. 13; 24)

*Charis occidentalis* Godman & Salvin, 1886. *Biol. Centr.-Amer., Lepid. Rhop.* 1(44): 431. **TL:** San Pablo, Río San Juan, W. Colombia. Lectotype male BMNH [designated].

**Identification and Taxonomy:** This was the first described member of the *occidentalis* group, and the name has heretofore been used in collections and the literature to refer to a single seemingly variable and moderately widespread species encompassing all those orange and dark-spotted male specimens with a two-tone orange dorsal surface, a dark dorsal forewing apex, a prominently inwardly curved element to the silver submarginal line in cell  $M_1$  on the dorsal forewing, and significant grayish ventral scaling. However, we show here that the name *A. occidentalis* of prior usage actually refers to a complex of four closely related, more range-restricted species in the *A. occidentalis* subclade that includes the reinstated *A. juanita* (sympatric with *A. occidentalis* in the lowlands of the

southern Transandean region), and the new species *A. eura* (northeastern South America) and *A. cana* (montane Chocó), all of which are separated from *A. occidentalis* in those species accounts. *Argyrogrammana occidentalis* was reported from Trinidad by Cock (1981), but the males in his Figs. 6 and 7 appear to be *A. sublimis*. The male of that Amazonian *A. sublimis* subclade species most notably externally differs from the male of *A. occidentalis*, as well as that of the partially sympatric *A. eura*, by having a dark presubmarginal band above vein  $Cu_1$  and a dark submarginal band on the dorsal forewing that are composed of separate spots instead of being broad and continuous, a much less prominently inwardly curved element to the silver submarginal line in cell  $M_1$  on the dorsal forewing, and a more orange ventral surface. It additionally differs from the male of *A. occidentalis* by having a medially divided dark spot near the base of cell  $Cu_2$  below the base of the discal cell on the dorsal forewing, and dark presubmarginal and submarginal bands on the dorsal hindwing that are composed of separate instead of partially to completely fused spots.

Notable intrapopulational dorsal wing pattern variation in males of *A. occidentalis* includes the width of the dark presubmarginal and submarginal bands on the forewing, the extent of the orange marginal scaling on the forewing, the prominence of the dark postdiscal spots on the hindwing, the continuity of the dark presubmarginal band on the hindwing, and the width of the gap between the dark submarginal band and the silver submarginal line on the hindwing. On the ventral surface, variation includes the prominence of the orange scaling across the basal portion of the forewing and basal two-thirds of the hindwing, which is typically moderately prominent (e.g., see Fig. 13) but is sometimes barely visible (e.g., in the lectotype of *A. occidentalis*), the extent to which the tornal half of the dark submarginal band on the forewing is separated from the silver submarginal line, the extent and prominence of the orange scaling either side of the silver submarginal line on the forewing, and the exact width of the dark presubmarginal band on the hindwing. A female of *A. occidentalis* was figured by Constantino *et al.* (2012: Fig. 21).

*Argyrogrammana occidentalis* was described by Godman & Salvin (1885-86) from an undetermined number of males and females from Río San Juan, W. Colombia, now in the BMNH. Given the great similarity of this species to the sympatric *A. juanita*, and the possibility of a mixed type series, of which we do not have a full photographic record, a lectotype designation seems prudent to ensure nomenclatural stability. The labeled male syntype in the BMNH is designated here as the lectotype, and it bears the following labels: "Type / H.T.", "S. Pablo, /R. San Juan, /W. Colombia. / Trotsch.", "male", "S. Pablo / Río San Juan / W. Colombia", and "B.C.A. Lep. Rhop. / Charis / occidentalis, / G. & S. / Godman-Salvin / Coll. 1914.-5.". Note that the historical addition of a holotype label to this specimen was a curatorial error.

**Biology:** This rare species is known from sea level to 200 m. In Ecuador, males were encountered perching on only a single hilltop, where solitary individuals were found flying 2 to 7 m above the ground around a tree trunk in a shady lightgap at the edge of the hill from 1630 to 1740 hrs, only rarely landing on

epiphytes. Males of *A. vespertina*, *A. juanita*, and *A. occidentalis* were found perching in the same hilltop lightgap during short and almost sequential time periods, with *A. vespertina* perching in the mid afternoon, *A. juanita* in the late afternoon, and *A. occidentalis* in the gloaming before dusk.

**Distribution:** *Argyrogrammana occidentalis* is currently known only from the Chocó region of western Colombia and northwestern Ecuador, but it seems likely to range into eastern Panama. It is replaced in northeastern South America by the new species *A. eura*.

### *Argyrogrammana cana* Hall & Willmott, new species (Figs. 14A,B; 25)

**Description:** MALE: Forewing length HT 14.5 mm; PTs 14.5-15 mm. *Wings:* see Fig. 14A. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and dark brown (inner) and yellow (outer) marginal scaling; frons yellow, with a dark brown transverse band at ventral margin and a large "U"-shaped dark brown mark dorsally; first and second segments of labial palpi pale yellow with dark brown scaling at distal tips, third segment dark brown; antennal length approximately 55% of forewing length, segments black with vertical dirty white lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dark orange with a broken black medial stripe, ventral surface gray, dorsal surface of abdomen dark orange with a rectangular black mark at middle of anterior margin of all segments that becomes smaller on posterior segments, ventral surface banded brown and gray; all legs banded brown and cream. *Genitalia:* see Fig. 25; posterior portion of valvae in ventral view approximately symmetrical, with a narrow gap between tips; sclerotized transtilla forms a medium-length, upwardly curved, "hook"-like posterior process that is narrow and curved to right in ventral view; ductus ejaculatorius enters anterior tip of aedeagus anteriorly; vesica exits posterior tip of aedeagus to right, cornutal complex on unevverted vesica consists of a bundle of very long, thin, approximately straight, parallel, posteriorly directed "hair"-like cornuti; eighth tergite and sternite rectangular. FEMALE: Forewing length PT 13 mm. *Wings:* see Fig. 14B. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and yellow marginal scaling; frons yellow, with a dark brown transverse band at ventral margin and a large "U"-shaped dark brown mark dorsally; first and second segments of labial palpi yellow with dark brown scaling at distal tips, third segment dark brown; antennal length approximately 55% of forewing length, segments black with vertical cream lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dark dirty yellow with a broken dark brown medial stripe, ventral surface cream, dorsal surface of abdomen dark dirty yellow with rectangular dark brown dorsal and lateral marks at anterior margin of all segments that become smaller on posterior segments, ventral surface banded pale brown and cream; all legs banded brown and cream.

**Types:** HOLOTYPE male: PANAMA: *Darién*, above Cana, Serranía de Pirre, 1500 m, 10 Apr 1983 (G. B. Small) (USNM).

PARATYPES: PANAMA: *Darién*, 5 males: same locality data as HT, 1300 m, 14-15 Apr 1983 (G. B. Small) (USNM); 1 female: same locality data as HT, 1500 m, 15 Apr 1983 (G. B. Small) (USNM). ECUADOR: *Esmeraldas*, 1 male: Río Chuchuví, km. 12.5 Lita-San Lorenzo rd., 0°52'51"N 78°30'54"W, 800-900 m, Mar 2001 (I. Aldas) (DA); *Pichincha*, 1 male: Mashpi Lodge, W. of Pacto, 0°09'45"N 78°52'28"W, 950 m, 30 July 2017 (A. Medina) (JH); 1 male: km. 21 Pacto-Guayabillas rd., 0°11'48"N 78°51'30"W, 900 m, 24 May 2004 (D. H. Ahrenholz) (DA); 1 male: km. 23 Pacto-Guayabillas rd., 0°11'48"N 78°51'54"W, 900 m, Apr 2005 (I. Aldas) (DA).

**Etymology:** This species is named after the type locality of Cana, which lies in a remote region of Panama's Darién province.

**Diagnosis:** Hall's (2023a) morphological phylogenetic analysis of *Argyrogrammana* indicates that *A. cana* n. sp. belongs in the *occidentalis* group, where it seems to form the terminal

sister pair with *A. occidentalis* in the *A. occidentalis* subclade of the *A. occidentalis* clade (characterized in previous species accounts). These two species possess a proximally broadened element in cell  $Cu_2$  to the dark submarginal band on the male dorsal hindwing, and, together with the new species *A. eura*, are unique in the *occidentalis* group in having widespread grayish scaling across both male ventral wings.

The male of *A. cana* (Fig. 14A) most obviously differs from that of *A. occidentalis* by being considerably larger (14.5-15 mm versus 12-12.5 mm), but it also has a slightly more rounded wing shape, absent to very faint instead of faint to prominent dark postdiscal spots in the anal half of the dorsal forewing and on the dorsal hindwing, slightly more discontinuous dark presubmarginal and submarginal bands on the dorsal hindwing, spots in the costal half of the dark presubmarginal band on the ventral forewing that are typically broader and more triangular in shape, and no orange scaling across the basal two-thirds of the ventral wings. The male genitalia of the two species (Figs. 24 and 25) do not significantly differ. However, *A. cana* and *A. occidentalis* are ecologically distinct, with the former seemingly confined to lower montane forest, where males perch in the early afternoon, and the latter to lowland forest, where males perch in the very late afternoon. *Argyrogrammana cana* is distinguished from *A. eura* in that species account.

Notable intrapopulational wing pattern variation in *A. cana* males includes the prominence of the dark basal spots in cell  $Cu_2$  on the dorsal forewing and across the base of the dorsal hindwing, the exact prominence of the dark postdiscal spots in the anal half of the dorsal forewing and on the dorsal hindwing, which vary from being entirely absent to partially weakly present, the width of the dark presubmarginal and submarginal bands on the dorsal forewing (the latter is entirely separated from the silver submarginal line in one of the Panamanian paratypes), the extent to which the silver submarginal line element in cell  $M_1$  on the forewing is inwardly curved, the extent of the orange marginal scaling on both surfaces of the forewing, the exact width of the dark presubmarginal and submarginal bands on the dorsal hindwing, and the width of the dark presubmarginal band on the ventral forewing.

The female of *A. cana* (Fig. 14B) is very similar to that of *A. occidentalis*, and seems to be best distinguished by its larger size and more convex distal forewing margin, combined with elevational data. The female of *A. cana* is also very similar to that of *A. vespertina*, but differs by being larger, and having a solid instead of partially medially divided dark spot near the base of cell  $Cu_2$  on the dorsal forewing, and dark submarginal spots on both wings that are heavier on the dorsal surface and more completely fused to the silver submarginal line on the ventral surface. Local variation in *A. cana* females is largely limited to the exact width and shape of the dark presubmarginal spots on the dorsal forewing and both ventral wings.

**Biology:** This rare species is known from 800 to 1500 m, seemingly replacing *A. occidentalis* at higher elevations. It is currently the only member of the Transandean *Argyrogrammana* fauna that genuinely appears to have a montane-limited distribution. In Ecuador, solitary males were encountered perching on a ridgetop during the early afternoon (D. Ahrenholz,

pers. comm.), and a male was found in a trap baited with rotting shrimp set 6 m above the ground in a ridgetop lightgap at 1530 hrs. A female seemingly belonging to this species (but not included in the type series) was encountered flying low to the ground along the forest edge of a ridgetop at 0900 hrs.

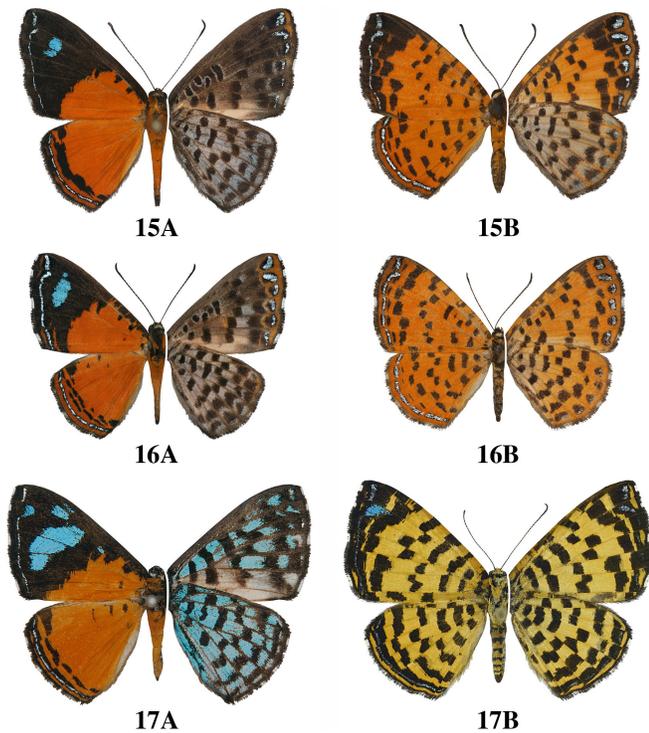
**Distribution:** *Argyrogrammana cana* is currently known only from far eastern Panama and northwestern Ecuador, but it presumably also occurs in western Colombia.

#### *amalfreda* group

#### *Argyrogrammana physis* (Stichel, 1911) (Figs. 15A,B)

*Argyrogramma physis* Stichel, 1911. In: Wytsman (ed.), *Gen. Insectorum* 112B: 246. TL: Río San Juan, Chocó, W. Colombia. Holotype male ZMHU [examined].

**Identification and Taxonomy:** Stichel (1910-11) described *A. physis* from a single west Colombian male (see Figs. 3A,B in Hall & Willmott (1995)), and on the same page of *Genera Insectorum* described *A. phyton* as a subspecies of *A. physis*, from a single west Brazilian male (see Figs. 3C,D in Hall & Willmott (1995)), and the two taxa have been treated as conspecific by all subsequent authors (e.g., Stichel, 1930-31; Hall & Willmott, 1995; Callaghan & Lamas, 2004; Dolibaina *et al.*, 2015). The two taxa do indeed seem to have exclusive, presumably parapatric, geographic distributions, with *A. physis* (Figs. 15A,B) ranging from the southern Transandean region to the eastern Amazon, and *A. phyton* (Figs. 16A,B) ranging throughout the western Amazon. Dolibaina *et al.* (2015) noted the significant differences that exist between the published illustrations of the male genitalia for *A. physis* from French Guiana (Fig. 8 in Brévignon & Gallard (1995)) and *A. phyton* from western Amazonia (Fig. 19 in Hall & Willmott (1995) and Fig. 51 in Dolibaina *et al.* (2015)). However, the illustration for *A. physis* is highly inaccurate. The first author has examined the male genitalia of *A. physis* specimens from throughout the taxon's geographic range, and the only potentially consistent difference identified was a slightly longer saccus in *A. physis* compared to *A. phyton*. The two taxa exhibit more obvious external differences, with *A. physis* males differing from *A. phyton* males by being slightly larger (typical forewing length is 12.5-13 mm versus 11.5-12 mm) and dorsally having a less prominent small dark spot around vein 2A at the very base of the forewing, a variably smaller orange patch on the forewing that does not extend to the costal margin, no orange submarginal and marginal scaling on the forewing, no dark basal spots on both wings, and dark presubmarginal and submarginal bands on the hindwing that consist of continuous partially to completely fused bands instead of separate bands of individual spots. On the ventral surface, *A. physis* males have no orange scaling proximal to the dark postdiscal band on the forewing, orange submarginal scaling on the forewing that is only rarely present (in Amazonian specimens) proximal to the silver submarginal line as traces in the apex instead of being consistently present in a band along the entire proximal length of the silver line,



**Figs. 15-17.** Transandean *Argyrogrammana amalfreda* group adults (Figs. 15, 17), with an extralimital taxon included for comparison (Fig. 16) (dorsal surface on left, ventral surface on right). **15A.** *A. physis* (Stichel, 1911) male, San Francisco, Esmeraldas, W. Ecuador. **15B.** *A. physis* female, El Durango, Esmeraldas, W. Ecuador. **16A.** *A. phyton* (Stichel, 1911) male, Finca San Carlo, Napo, E. Ecuador. **16B.** *A. phyton* female, Lumbaquí, Sucumbíos, E. Ecuador. **17A.** *A. pulchra* (Talbot, 1929) HT male, “Bogotá”, Colombia (BMNH). **17B.** *A. pulchra* female, Uimbicito, Esmeraldas, W. Ecuador (DA).

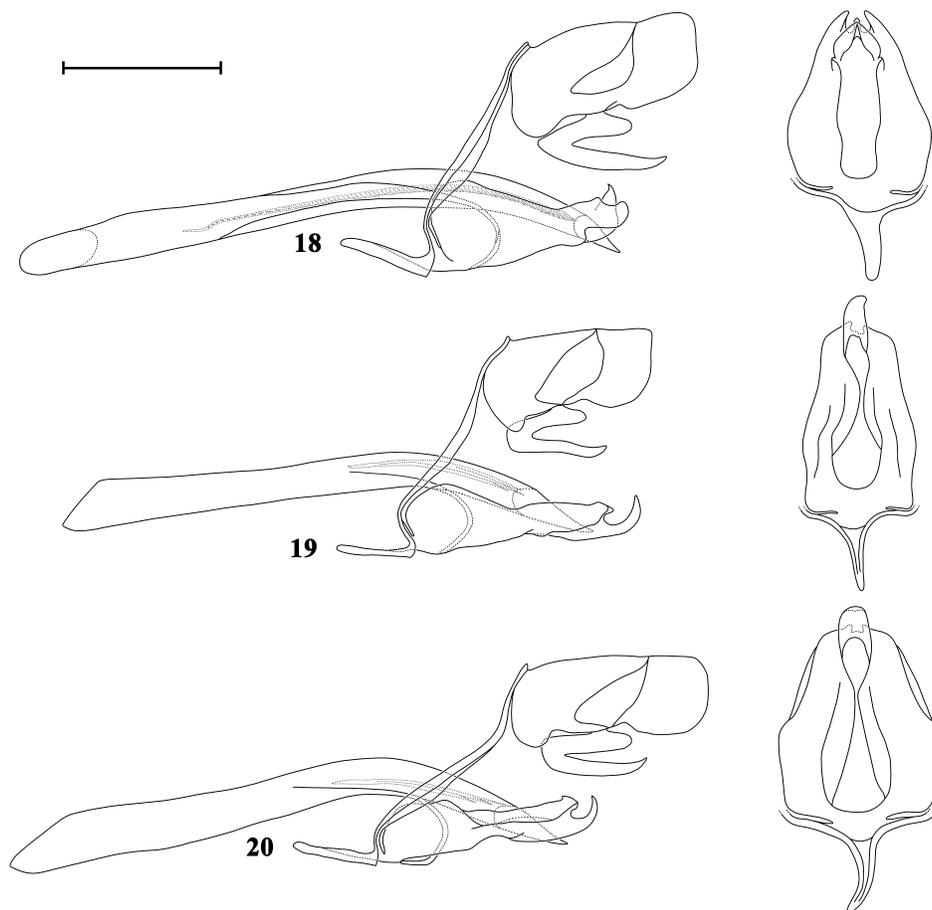
and blue-gray rather than grayish scaling on the hindwing. The female of *A. physis* differs from that of *A. phyton* by having a dorsal forewing with a broader dark presubmarginal band that consists of a partially fused band instead of individual spots and a broader dark submarginal band that is fused to instead of partially to completely separated from the silver submarginal line, and more extensive pale scaling across the ventral hindwing. Although *A. physis* specimens of both sexes from the eastern Amazon are more similar to *A. phyton* than are *A. physis* specimens from the more distant Transandean region, the above listed differences are consistent between nearly all of the examined specimens of the two taxa. To assist in deciding whether to treat these taxa as subspecies or species, we sequenced the barcode region of the mitochondrial gene COI for Ecuadorian exemplars of these taxa. The results showed that a male of *A. physis* (JH1711), from San Francisco in Esmeraldas province, had a sequence divergence of 5.1% from a male of *A. phyton* (JH1712), from Santiago in Morona-Santiago province. More sequence data would clearly be desirable, particularly from the eastern Amazon, but given the significant DNA barcode and wing pattern differences reported here between the two taxa, we tentatively raise *A. phyton* to species status (**n. stat.**). Hall’s (2023a) phylogenetic analysis of *Argyrogrammana* placed *A. physis* in a non-monophyletic

assemblage of similar species in the basal half of the *amalfreda* group, between *A. phyton* and the clade containing *A. bonita* Hall & Willmott, 1995, *A. chicomendesi* Gallard, 1995, and *A. halli* Dolibaina & Dias, 2015. However, this placement is supported by just a few homoplasious male wing pattern characters, and *A. physis* seems just as likely to be sister to *A. phyton*.

Transandean males of *A. physis*, which can not be confused with any sympatric congeners, possess a consistent wing pattern, with intrapopulation variation limited to the exact size and shape of the orange patch on the dorsal forewing, the size of the blue postdiscal spot in cell  $M_2$  on the dorsal forewing, the apical extent of the orange submarginal and marginal scaling on the dorsal hindwing, and the prominence of the blue-gray scaling distal to the dark postdiscal band on the ventral forewing. East Amazonian males of *A. physis* differ from Transandean males by having on average a slightly smaller orange patch on the dorsal forewing, a blue postdiscal patch on the dorsal forewing that consistently extends a variable distance across cell  $M_3$  and frequently includes a small spot in cell  $R_{4+5}$ , on average slightly more extensive and complex dark distal markings on the dorsal hindwing, and apical traces of orange submarginal scaling occasionally present proximal to the silver submarginal line on the ventral forewing. Because the wing pattern differences between the Transandean and east Amazonian populations of *A. physis* are minor, and no specimens are known to us from Venezuela, where individuals with intermediate wing patterns might be expected to occur, the recognition of subspecies does not seem warranted at present.

Within the Transandean region, the female of *A. physis* is perhaps most similar to that of *A. crocea*, but differs most notably by having a darker, more orange than yellow, dorsal surface, broader dark presubmarginal and submarginal bands on the dorsal forewing, a dark submarginal band on the dorsal hindwing that is separated instead of fused to the silver submarginal line, and a pale grayish ventral hindwing. The females of *occidentalis* group species can quickly be separated from female *A. physis* by having a medially divided instead of solid dark spot toward the base of cell  $Cu_2$  below the middle of the discal cell on the dorsal forewing, and they also typically have a proximally displaced dark presubmarginal spot in forewing cell  $M_1$ . There is no significant wing pattern variation in the examined Transandean females of *A. physis*. The French Guianan females of *A. physis* figured by Brévignon & Gallard (1995) and Gallard (2017) differ from Transandean females by having a broader band of orange scaling between the apical sections of the dark presubmarginal and submarginal bands on the forewing and less prominent pale grayish scaling on the ventral hindwing.

**Biology:** This uncommon to rare species is known from sea level to 900 m. In Ecuador, males were encountered perching singly or in pairs 1 to 3 m above the ground at the shady edges of hilltop lightgaps from 0800 to 1015 hrs. Females were observed flying near these male perching leks from 1300 to 1400 hrs. In French Guiana, males were found perching 2 to 5 m above the ground in the vicinity of hilltop tree trunks from 0730 to 0850 hrs (Brévignon & Gallard, 1995; Gallard, 2017).



**Figs. 18-20.** *Argyrogrammana* male genitalia, with genital capsule in lateral view, and valvae and saccus in ventral view. **18.** *A. smalli* n. sp. HT (USNM). **19.** *A. vespertina* n. sp. PT, El Durango, Esmeraldas, W. Ecuador. **20.** *A. saulensis*, Lumbaquí, Sucumbíos, E. Ecuador. Scale bar = 0.5 mm.

**Distribution:** *Argyrogrammana physis* is known to range from the Canal Zone of central Panama to northwestern Ecuador and central Colombia, as well as throughout the Guianas and into eastern Brazil as far south as Bahia, and it presumably also occurs in northern Venezuela and perhaps Trinidad. It is replaced in the western half of Amazonia by *A. phytion*, although the exact whereabouts of the contact zones between the two taxa remain to be determined.

*Argyrogrammana pulchra* (Talbot, 1929)  
(Figs. 17A,B)

*Argyrogramma pulchra* Talbot, 1929. *Bull. Hill Mus.* 3(2): 145, pl. 4, figs. 3, 4. TL: “Bogotá”, C. Colombia. Holotype male BMNH [examined].

**Identification and Taxonomy:** *Argyrogrammana pulchra* belongs in the derived *A. nurtia* clade of the *amalfreda* group, where it forms the terminal sister-species pair with the Amazonian *A. sticheli*, described in the same paper by Talbot (1929). The males of the two species most notably uniquely share a blue submarginal spot in cell  $M_1$  on the dorsal forewing that forms part of the silver submarginal line, a character that is

also present in the females of this species pair plus its sister *A. alstonii* (Smart, 1979) (see Hall *et al.*, 2023b).

The unique Colombian male holotype of *A. pulchra* (Fig. 17A) differs from the known males of *A. sticheli* by being slightly larger and having a slightly larger orange patch at the base of the dorsal forewing, a blue postdiscal band on the dorsal forewing that ends at vein  $Cu_2$  instead of extending into cell  $Cu_2$ , a smaller blue submarginal spot in cell  $M_1$  on the dorsal forewing, more extensive orange presubmarginal and marginal scaling on the dorsal hindwing, slightly paler iridescent blue scaling across both ventral wings, and a slightly more distally positioned dark postdiscal band on the ventral forewing with a slightly broader band of iridescent blue spots distally. *Argyrogrammana pulchra* is the only species in the genus whose male genitalia have not been examined by the first author.

The female of *A. pulchra* is more different from the female of *A. sticheli* (figured for the first time by Hall *et al.* (2023b)), differing by having yellow instead of orange dorsal patterning, a more distally positioned dark postdiscal band on the forewing, a triangular instead of rectangular blue submarginal spot in cell  $M_1$  on the dorsal forewing, yellow instead of orange and iridescent blue ventral patterning, and more prominent silver submarginal markings on both ventral wings, with a silver instead of blue submarginal mark in cell  $M_1$  on the ventral

forewing. The recently collected Ecuadorian female of *A. pulchra* in Fig. 17B differs only slightly from the Colombian female paratype (figured by d'Abrera (1994: 1051) and Hall & Willmott (1995: Figs. 7C,D)) by having a broader dark submarginal band on both surfaces of both wings, a slightly larger blue/silver submarginal mark in cell  $M_1$  on the forewing, and more yellow marginal scaling on the dorsal forewing.

**Biology:** This is a very rare species, with the only modern specimen collected in wet lowland forest at 150 m. Nothing is known about its biology.

**Distribution:** *Argyrogrammana pulchra* was described by Talbot (1929) from a male and female pair from “Bogotá”, central Colombia, a generalized historical label applied to specimens that may have originated from a range of different biogeographic regions and elevations, most commonly the eastern slope of the Andes or central valleys, but also more rarely the Chocó. The presence of multiple close relatives in lowland Amazonia and the lack of any modern material long suggested to us that *A. pulchra* was most likely a montane or Transandean species. The discovery of a female specimen in the lowlands of Esmeraldas province in northwestern Ecuador confirms the latter theory, and the species clearly occurs in western Colombia and may also range into central Colombia, as well as eastern Panama. This species is replaced in the Amazon by *A. sticheli*, and the male specimen figured by Dolibaina *et al.* (2015) from Acre, western Brazil, under the name *A. pulchra* belongs to *A. sticheli*.

### Extralimital New Species Description

#### *Argyrogrammana eura* Hall, new species (Figs. 12; 23)

**Description:** MALE: Forewing length HT 12 mm; PTs 11-11.5 mm. *Wings:* see Fig. 12. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and yellow-orange marginal scaling; frons yellow orange, with a dark brown transverse band at ventral margin and a large “U”-shaped dark brown mark dorsally; first and second segments of labial palpi yellow orange with dark brown scaling at distal tips, third segment dark brown; antennal length approximately 55% of forewing length, segments black with vertical cream lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dark orange with a black medial stripe and faint black lateral stripes, ventral surface gray, dorsal surface of abdomen dark orange with rectangular black dorsal and lateral marks at anterior margin of all segments that become smaller on posterior segments, ventral surface banded brown and pale yellow; all legs banded brown and pale yellow. *Genitalia:* see Fig. 23; posterior portion of valvae in ventral view prominently asymmetrical, with a narrow gap between tips; sclerotized transtilla forms a medium-length, upwardly curved, “hook”-like posterior process that is narrow and prominently curved to right in ventral view; ductus ejaculatorius enters anterior tip of aedeagus anteriorly and slightly to right; vesica exits posterior tip of aedeagus to right, cornutal complex on uneverted vesica consists of a bundle of very long, thin, approximately straight, parallel, posteriorly directed “hair”-like cornuti; eighth tergite and sternite rectangular. FEMALE: see Figs. 12C,D in Hall & Willmott (1996) and Fig. 7 on Pl. 18 in Gallard (2017).

**Types:** HOLOTYPE male: FRENCH GUIANA: *Cayenne*, Roura, 100 m, 10 Mar 1993 (J.-Y. Gallard) (USNM).

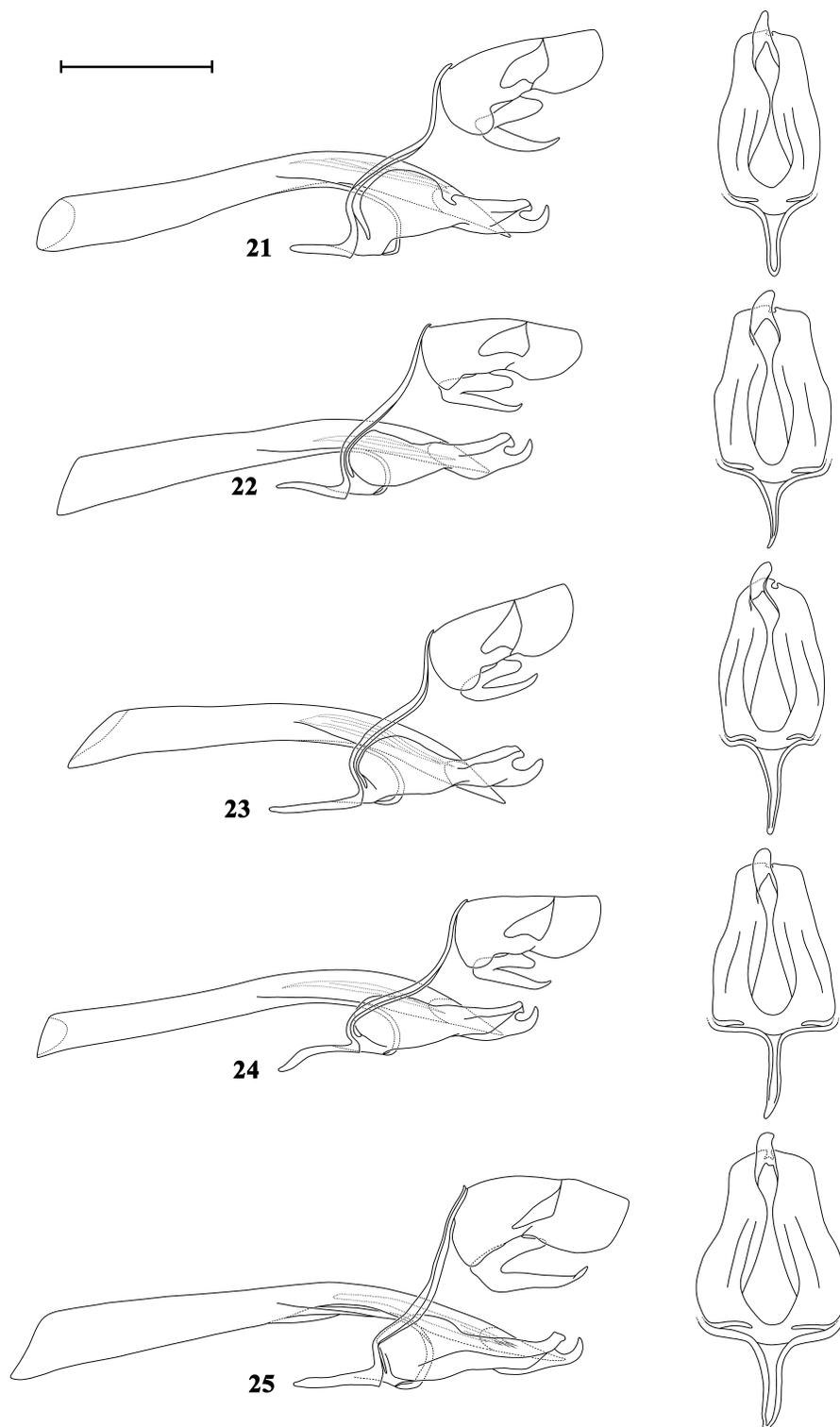
PARATYPES: GUYANA: *Upper Takutu-Upper Essequibo*, 2 males: ridge above Sipu River, Acarai Mountains, 1°22.2'N 58°57.9'W, 750-900 m, 31 Oct-10 Nov 2000 (S. Fratello *et al.*) (USNM). FRENCH GUIANA: *Cayenne*, 1 male: Montsinéry, 0-100 m, 21 Nov 1988 (D. J. Harvey) (USNM); 1 male:

Galion, 12 Oct 1986 (J.-Y. Gallard) (USNM); 1 male: Comté, 1 Nov 1988 (C. Brévignon) (USNM); 1 male: km. 35 on Route Nationale 2, 1 Nov 1989 (C. Brévignon) (USNM).

**Etymology:** The name is derived from the Latin word “eurus”, meaning “east wind” or “northeast wind”, in reference to the restriction of this species to northeastern South America, in contrast to the closely related *A. occidentalis*, whose name refers to its distribution to the west of the Andes.

**Diagnosis:** The morphological phylogenetic analysis of *Argyrogrammana* presented by Hall (2023a) indicates that *A. eura* n. sp. belongs to the *A. occidentalis* subclade of the *A. occidentalis* clade in the *occidentalis* group, each of which is characterized in the previous species accounts. It seems to be most closely related to *A. occidentalis* and the new species *A. cana*, with the males of all three species being unique in the group in having widespread grayish scaling across both ventral wings. These three species have previously been lumped together in the literature and/or collections, and are allo/parapatrically distributed, with *A. eura* occupying northeastern South America, and *A. occidentalis* and *A. cana* occurring at lowland and montane elevations, respectively, in the southern Transandean region. *Argyrogrammana eura* lacks the proximally broadened element in cell  $Cu_2$  to the dark submarginal band on the male dorsal hindwing possessed by the other two species, and is thus perhaps sister to them.

*Argyrogrammana eura* has previously been figured in the literature multiple times under the name *A. occidentalis*, by d'Abrera (1994: ventral male on p. 1051), Brévignon & Gallard (1995: male in Fig. 1), Hall & Willmott (1996: female in Figs. 12C,D), and Gallard (2008: male in Fig. 13; 2017: both sexes in Fig. 7 on Pl. 18). However, these two species (Figs. 12 and 13) exhibit multiple subtle wing pattern and genitalia differences. The most important wing pattern difference between them concerns the dark spot near the base of cell  $Cu_2$  below the base of the discal cell on the dorsal forewing, which in all examined *A. eura* males consists of a medially divided spot with the two elements situated at the margins of the cell (a character state shared with the four *A. sublimis* subclade species), and in all examined *A. occidentalis* males consists of a single solid spot in the middle of the cell. The male of *A. eura* additionally differs from that of *A. occidentalis* by having a discontinuous instead of typically continuous dark presubmarginal band on the dorsal hindwing, a typically discontinuous instead of continuous dark submarginal band on the dorsal hindwing that lacks a proximally broadened element in cell  $Cu_2$ , a grayish ventral surface that never has orange scaling across the basal portion of the forewing and basal two-thirds of the hindwing, broader and more rectangular dark submarginal spots on the ventral hindwing, and a “U”-shaped whitish-gray submarginal mark in cell  $M_3$  on both ventral wings largely obscuring the silver line. The male of *A. eura* most notably differs from that of *A. cana* by being much smaller and having the aforementioned medially divided spot near the base of cell  $Cu_2$  on the dorsal forewing, more evenly spotted dorsal wings with consistently prominent dark postdiscal spots, consistently prominent whitish-gray submarginal scaling in cell  $M_3$  on both ventral wings, and larger rectangular instead of triangular dark submarginal spots



**Figs. 21-25.** *Argyrogrammana* male genitalia, with genital capsule in lateral view, and valvae and saccus in ventral view. **21.** *A. janzeni* n. sp. HT (USNM). **22.** *A. juanita*, San Francisco, Esmeraldas, W. Ecuador. **23.** *A. eura* n. sp. PT, Montsinéry, Cayenne, French Guiana (USNM). **24.** *A. occidentalis*, San Francisco, Esmeraldas, W. Ecuador. **25.** *A. cana* n. sp. HT (USNM). Scale bar = 0.5 mm.

on the ventral hindwing. The male genitalia of *A. eura* (Fig. 23) are relatively distinctive, and differ from those of all its *A. occidentalis* subclade relatives (Figs. 21-22, 24-25) by having prominently asymmetrical instead of weakly asymmetrical

to symmetrical valve tips in ventral view, with an obviously more enlarged, posteriorly extended, and inwardly curved left valve tip, and a transtilla process in ventral view that is more prominently laterally displaced to the left and more prominently

curved to the right.

Notable intrapopulational wing pattern variation in males of *A. eura* includes the width of the dark presubmarginal and submarginal bands on the dorsal forewing, the extent of the orange marginal scaling on the dorsal forewing, the width and continuity of the dark submarginal band on the dorsal hindwing, the width of the gap between the dark submarginal band and the silver submarginal line on the dorsal hindwing, the exact lateral placement of the dark postdiscal band on the ventral forewing, and the width of the dark presubmarginal band on the ventral forewing.

The female of *A. eura* differs from those of *A. occidentalis* and *A. cana* by having a partially medially divided instead of solid dark spot near the base of cell  $Cu_2$  on the dorsal forewing, more extensive dark orange scaling around the silver submarginal line on both dorsal wings, and broader and more rectangular dark submarginal spots on the ventral hindwing. It additionally differs from the female of *A. cana* by being much smaller and having more heavily spotted wings, a more proximally positioned dark postdiscal band on both wings, spots in the costal half of the dark presubmarginal band on the forewing that are more rectangular than triangular in shape, and a more prominently inwardly curved element to the silver submarginal line in cell  $M_1$  on the forewing. The only significant variation observed in *A. eura* females is the extent to which the dark submarginal spots on the ventral forewing are separate from or fused to the silver submarginal line.

**Biology:** This not uncommon species is known from sea level to about 900 m. In French Guiana, where this is apparently the most common member of the genus, males were found perching 1 to 2 m above the ground on tree trunk epiphytes and lianas on hilltops from 1300 to 1600 hrs (Brévignon & Gallard, 1995; Gallard, 2017).

**Distribution:** *Argyrogrammana eura* is currently known only from Guyana and French Guiana, but it presumably occurs throughout northeastern South America. It is replaced in the lowlands to the west of the Andes by *A. occidentalis*.

#### ACKNOWLEDGMENTS

We thank all those museum curators in Europe and the Americas who gave access to the riodinid collections in their care (see list in Hall (2018)); all those who contributed to collecting recent *Argyrogrammana* material, especially David Ahrenholz, who shared data and images; the National Science Foundation (DEB grants #0103746 and #0639977), the National Geographic Society (Research and Exploration grant #5751-96), and the Turner Molecular Research Fund at the University of Florida for financial support of museum and field research; the Instituto Nacional de Biodiversidad (formerly Museo Ecuatoriano de Ciencias Naturales) (most recently Santiago Villamarín and Sofía Nogales) and Ministerio del Ambiente, Agua y Transición Ecológica for arranging the necessary permits for research in Ecuador; and Curtis Callaghan and Mario Marín for helpful comments on the manuscript.

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