A review of the *Argyrogrammana* fauna of the eastern Andes (Lepidoptera: Riodinidae: Symmachiini)

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**Abstract:** The montane *Argyrogrammana* Strand, 1932, fauna (Riodinidae: Symmachiini) of the eastern Andes is reviewed. There are five described species from the region, and an additional three species are described here from Ecuador and Peru: *A. janiceae* Ahrenholz & Hall, n. sp., *A. aurora* Hall & Willmott, n. sp. (both *occidentalis* group), and *A. cosnipata* Hall, n. sp. (*amalfreda* group). A ninth species, known from only a single Peruvian female, is figured but not described. These nine east Andean endemics range in elevation from 550 to 2200 m.

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

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**INTRODUCTION**

*Argyrogrammana* Strand, 1932, is a Neotropical riodinid genus (Symmachiini) of notably rare and beautiful species that has attracted significant taxonomic attention in recent decades (e.g., Brévignon & Gallard, 1995; Hall & Willmott, 1995, 1996; Dolibaina *et al.*, 2015; Gallard, 2017). Hall (2023) provided a comprehensive phylogenetic framework and taxonomic overview for the genus, recognizing 55 species in six species groups. With more than 20% of these species undescribed, we deemed it to be a worthwhile undertaking to review several of the most poorly known regional faunas. This paper treats the east Andean *Argyrogrammana* fauna, which is defined here as containing those species in the region with a majority of their elevational range above 1000 m. Nine species meet this criterion, in the *trochilina*, *occidentalis*, and *amalfreda* groups, including five described species, three that are described here, and one that is figured but not described as it is known from only a single female. Only one species outside of the east Andean region is currently known to have such a clear montane-limited distribution, the newly described Transandean *A. cana* Hall & Willmott, 2023. About a dozen lowland Amazonian species have been recorded at elevations above 1000 m, with nearly half of these known to range up to or above 1300 m, but none meets the montane-limited criterion. Prior to the mid-1990s, only a single *Argyrogrammana* species had been described from the eastern Andes, namely *A. subota* (Hewitson, 1877), which was not collected again for more than a century. Early discoveries on the east Andean *Argyrogrammana* fauna of Ecuador were published in papers by Hall & Willmott (1995, 1996, 1998), and some additional montane locality data were published in papers on the Colombian *Argyrogrammana* fauna by Constantino *et al.* (2012) and the riodinid fauna of southern Peru’s Cosñipata valley by Lamas *et al.* (in press). This review describes the more recently discovered species, definitively matches males and females for all the previously described species for the first time, 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 (2023). Female genitalia were not studied for the reasons discussed by Hall (2023). *Argyrogrammana* specimens were studied in the 27 personally visited institutional and private collections listed in Hall (2018), and the type specimens were examined for all available names. The distributional data presented here are based on these collections, except for the Colombian data, which are based on the records reported by Constantino *et al.* (2012). 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 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’ collections 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; 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.

SPECIES ACCOUNTS

trochilia group

Argyrogrammana subota (Hewitson, 1877)
(Figs. 1A,B)

Charis subota


Identification and Taxonomy: For over a century, A. subota remained known from a single ragged female specimen (figured by d’Abera (1994: 1052) and Hall & Willmott (1996: Figs. 8A,B)), until the species was rediscovered in Ecuador in the late 1990s. Discovery of the male allows the species to be phylogenetically placed near the base of the trochilia group, between the Transandean A. leptographia (Stichel, 1911) and Amazonian A. rameli (Stichel, 1930) (Hall, 2023). As in the other trochilia group species positioned from A. subota onward, male A. subota possesses a continuous dark band between the third and fourth blue bands from the base of the dorsal forewing, pale bands on the ventral wings, and whitish scaling on the ventral surface of the abdomen, and the female has pale diagonal bands on the dorsal forewing. However, unlike in the more derived species, both sexes of A. subota lack a continuous dark band between the second and third pale bands from the base of the forewing (with two separate interdigitating dark spots present in the middle of the discal cell instead of a single fused band) and largely smoothly continuous discally, postdiscal, and submarginally positioned bands on both ventral wings (with the bands consisting of more distinct and disjointed spots).

The male of A. subota can readily be separated from that of all similar trochilia group species by having four instead of three dark spots in the discal cell on the dorsal forewing and a relatively jagged series of whitish bands instead of relatively smooth yellow bands on the ventral wings. The male genitalia of A. subota are most similar to those of A. leptographia and A. rameli (both illustrated in Hall & Willmott (1996: Figs. 17 and 20)). They differ from the former by having a straighter ventral margin to a slightly longer upper posterior valve process, a slightly shorter aedeagus, and a shorter string of tiny aedeagal cornuti, and from the latter by having a slightly shorter and ventrally narrower saccus, a slightly broader upper posterior valve process, and a much shorter string of much smaller aedeagal cornuti. Notable intrapopulational wing pattern variation in A. subota males includes the exact (i.e., minor variation) width of all the blue bands and the yellowish submarginal band on both dorsal wings, and the size and prominence of the dark spot within the pale bar near the discal cell end on the ventral forewing.

The female of A. subota is unique in the genus in having cream-colored wings with a spotted pattern. The other cream-colored females in the trochilia group have more crisply banded patterns, and the other spotted females in the genus have yellow to orange wings. The holotype female is practically white, but this seems to be the result of it being an old and faded specimen. There is no significant wing pattern variation among the examined Ecuadorian A. subota females, but the examined Peruvian females (Amazonas and San Martín) differ by having slightly smoother dark postdiscal and submarginal bands on both wings, most notably with the dark postdiscal spot in the forewing cell M₁ aligned with the two neighboring spots instead of being slightly distally displaced (we have not examined any males from Peru).

Biology: This rare species is known to inhabit montane forest from 1300 to 1700 m. The type locality of Gima (= Jima), a high Andean village (c. 2800 m) in Azuay province that is located on the old trail from Cuenca (and the western lowlands) to Gualalaquiza at the base of the eastern Andes (850 m), is clearly inaccurate and at most represented a way station on the collector Clarence Buckley’s journey down into the Amazonian lowlands. The natural history specimens accumulated by Mr. Buckley on his third Ecuador expedition from 1876 to 1879/80 are well known to be vaguely or erroneously labeled (Chapman,
1926; Willmott & Vitale, 2008; Hämaläinen, 2021), a situation no doubt exacerbated by his use of independent collectors such as Manuel Villagomez and, at least in the case of the birds he collected, the fact that locality labels were only added by his agent, the dealer Edward Gerrard, after they arrived in London (Chapman, 1926). Most of the nine riodinid taxa proposed by Hewitson (1877) from Gima seem likely to have originated from the area below this village in neighboring Morona-Santiago province at elevations between 1000 and 2000 m.

In Ecuador, a solitary male was encountered perching 4 m above the ground at the forest edge along a broad ridgetop track at 1225 hrs. Males were also found in subcanopy traps baited with rotting fish and on fermento (a mixture of rotting fish and urine) placed on low leaves in ridgetop and hillside lightgaps. On four occasions during a three-year period, solitary females were encountered resting 3 to 4 m above the ground beneath leaves of the same tree, just below a forested hilltop, between 1100 and 1250 hrs. This unusual pattern of behavior suggests that either the food plant or a male perching lek was present very nearby.

**Distribution:** *Argyrogrammana subota* is known to range from central Ecuador (Morona-Santiago) to central Peru (San Martín), but may well also occur in Colombia and Bolivia.

**Argyrogrammana pastaza** Hall & Willmott, 1996 (Figs. 2A,B)


**Identification and Taxonomy:** *Argyrogrammana pastaza* can be phylogenetically placed between *A. rameli* and *A. trochilia* (Westwood, 1851). The five members of the *trochilia* group from *A. pastaza* onward all have a fourth blue band from the base of the male dorsal forewing that is broadened below vein Cu₁ instead of being of approximately even width throughout, and apical segments (in cells M₁ and R₄-₅) to the silver submarginal line on the male ventral forewing that are prominently inwardly directed instead of being vertically oriented to slightly inwardly directed. The character uniting the four most derived *trochilia* group species in Hall’s (2023) phylogenetic analysis of the genus, from *A. trochilia* onward, namely yellow distal bands on the male ventral forewing that are narrower rather than similar in width to or broader than the alternating dark bands, is certainly a rather weak one. However, *A. pastaza* and *A. trochilia* also both lack the two characters that would seem to more convincingly unite the terminal *trochilia* group clade containing *A. johannismarci* Brévignon, 1995, *A. brevignonii* Dolibaina & Dias, 2015, and *A. saphirina* (Staudinger, 1887), namely a consistent “2-2 pattern” of blue in cell 2A on the male dorsal forewing (one horizontal blue bar joining blue bands one and two and another joining blue bands three and four) and the consistent complete absence of a yellowish submarginal band on the male dorsal forewing.

In the lower portion of its elevational range, *A. pastaza* is sympatric with both of its closest relatives, the predominantly lowland *A. rameli* and *A. trochilia* (recorded from sea level up to 1500 m and 1400 m, respectively), although these two hilltopping species do not appear to be ecologically sympatric with the streamside-inhabiting *A. pastaza*. The male of *A. pastaza* can most readily be distinguished from the males of both these species by having blue scaling proximal to the costal portion of the yellow presubmarginal band on the ventral forewing, a character shared only by the otherwise dissimilar *A. brevignonii*, which was described and is only known from Acre, in western Brazil (Dolibaina et al., 2015). However, male specimens of *A. pastaza* that have only minimal such blue scaling, especially if they are old and worn, can easily be confused with broad-banded montane males of *A. rameli*; they differ by having a dorsal forewing with a more unevenly shaped fourth blue band from the wing base, typically a continuous blue bar across cell 2A (a “4-0 pattern”) that only rarely has the dark medial break always present in *A. rameli* (a “2-1 pattern”), and typically a less prominent and darker yellowish submarginal band, and a ventral forewing with a dark spot within the yellow bar near the discal cell end and a silver submarginal line that is much more prominently kinked inward in the apex (also visible dorsally), often dividing a narrower and similarly kinked yellow proximal band near vein M₁. *Argyrogrammana trochilia* males are best distinguished by their unique “3-1 pattern” of blue in cell 2A on the male dorsal forewing, as well as by their darker blue dorsal banding that is slightly more vertically oriented on the forewing. The male genitalia of *A. pastaza* are somewhat intermediate between those of *A. rameli* and *A. trochilia* (all illustrated in Hall & Willmott (1996: Figs. 16, 17, and 19)), differing from the former by having a shorter, broader, laterally flared, and more upwardly curved upper posterior valve process, an indistinctly rounded instead of prominently angular ventro-posterior valve corner, a narrower transtilla joining the valve tips, and a slightly longer string of aedeagal cornuti, and from the latter by having a slightly longer and laterally flared upper posterior valve process and a ventro-posterior valve corner that is less prominent and straight instead of ventrally and inwardly curved.

We have not observed any significant geographic wing pattern variation in *A. pastaza* males, but notable intrapopulational variation includes the pattern of blue in cell 2A on the dorsal forewing, which typically consists of a solid blue bar that may have some medial black scaling intruding into it but sometimes is completely divided by a black band extending to the anal margin, the exact width and shape of the distal blue (dorsal) and yellow (ventral) bands on both wings, the prominence of the yellow-orange submarginal band on both dorsal wings (but particularly the forewing, where it is sometimes completely absent), the size of the dark spot within the yellow bar near the discal cell end on the ventral forewing, and the extent and shape of the blue scaling proximal to the yellow presubmarginal band on the ventral forewing, which varies from extending along the entire costal half of the band to being restricted to a small spot in cell R₄-₅.

The females of *A. pastaza*, *A. rameli*, and *A. trochilia*, as well as *A. johannismarci*, all have confusingly similar white to cream banded wing patterns, and are generally jumbled together in collections. The female of *A. trochilia* is the most...
distinctive, and, like the male, can be distinguished by being slightly larger on average and having more vertically oriented whitish forewing bands and a variably solid whitish bar in dorsal forewing cell 2A joining the three most basal whitish bands (part of a “3-1 pattern”). The females of the three other species have more diagonally oriented pale forewing bands and a variably solid pale bar in dorsal forewing cell 2A joining the two most basal pale bands, with an obvious dark gap before an isolated third pale band (a “2-1 pattern”). The female of *A. johannismarci* (a species recorded from sea level up to 1200 m) has narrower cream to pale yellow colored bands, and it additionally differs from more cream-colored specimens of *A. rameli* by having a silver submarginal line in the apex of the ventral forewing that is more prominently kinked inward. The allotype female of *A. johannismarci* figured by Brévignon & Gallard (1995: Fig. 30) is *A. trochilha*, as subsequently noted by Brévignon & Gallard (1998), but the female specimen figured by Brévignon & Gallard (1998: Figs. 45-46) and Gallard (2017: Pl. 18, Fig. 12) is genuine *A. johannismarci*. The female of *A. pastaza* is most similar to that of *A. rameli*, particularly certain montane specimens of *A. rameli* that have similarly broad white bands, and only characters in the ventral forewing apex seem to consistently distinguish females of the two species, with female *A. pastaza* having a silver submarginal line that is more prominently kinked inward in cells M₁ and R₃₋₄, resulting in the immediately proximal pale band being abruptly narrowed or broken and similarly kinked near vein M₁ instead of being smoothly curved and of approximately even width in this zone. Some *A. pastaza* females, like that figured by Hall & Willmott (1996: Figs. 5C,D), also have a dark spot within the white bar near the discal cell end on the ventral forewing, which never seems to be present in *A. rameli* females. Additional intrapopulational wing pattern variation in *A. pastaza* females involves the exact width and shape of the pale distal bands on *A. pastaza* n. sp. is difficult to place phylogenetically, both because of its autopomorphic wing pattern and its evidently basal position within the genus. The morphological phylogenetic analysis of *Argyrogrammana* presented by Hall (2023) tentatively placed *A. janiceae* at the base of the *occidentalis* group, which contains most of the species in the genus with dorsally orange and black-spotted males. The species group is now recognized to contain twelve species, including nine in the *A. occidentalis* (Godman & Salvin, 1886) clade and a sister-species pair in the *A. placibilis* (Stichel, 1910) clade. *Argyrogrammana janiceae* is hypothesized to be sister to these two well-supported clades based on possessing a predominantly grayish discal cell with orange scaling across the cells below on the male ventral forewing (lost twice in the *A. occidentalis* clade) and a dark submarginal band on the female dorsal forewing that is more or less entirely separated from the silver submarginal line (independently derived in a scattered handful of *amalfreda* group species), but lacking a full to nearly full complement of dark postdiscal spots on the male dorsal forewing (universally present in the *A. placibilis* and *A. occidentalis* clades, but also the *stilbe*, barine, and
When the wing pattern characters for this female specimen were coded and added to Hall’s (2023) phylogenetic analysis, the taxon came out as sister to *A. janiceae*, predominantly on the basis of their shared possession of a forewing fringe with broad sections of prominent white scaling in all distal cells instead of typically just cells Cu, M₁, M₂, and R₄₋₅, a character that occurs elsewhere in the genus only in the two dissimilar *stilbe* group species. Confirmation of this taxon’s new species status and its description must await discovery of the male.

The male of *A. janiceae* (Fig. 3A) is most similar to that of *A. crocea*, with which it shares largely absent dark postdiscal spots on both dorsal wings and an orange and black banded dorsum to the abdomen (at least in some specimens of *A. crocea*), but it can immediately be distinguished from this and all other species in the genus by having alternating orange and black rays along the distal margin of both wings. The male genitalia of *A. janiceae* (Fig. 12) do not closely resemble those of any of its closest relatives, differing from those of *A. crocea* and *A. caesarion* by having a quite differently shaped upper posterior valve process, a rounded instead of prominently angular ventroposterior valve corner, a shorter string of aedeagal cornuti, and a slight ventral kink in the middle of the aedeagal pedicle, and from those of the two *A. placibilis* clade species by having an upper posterior valve process that is more medially than dorsally positioned, less upwardly and inwardly curved, and more broadly rounded in ventral view. Male wing pattern variation in *A. janiceae* males from the only known locality is limited to the prominence of the orange markings along the forewing costal margin, the exact width of the orange distal rays on both wings, and the presence or absence of small dark postdiscal marks in the tornus and apex of the hindwing.

The female of *A. janiceae* (Fig. 3B) is likewise quite unlike that of any other described species. It differs from the females of *A. crocea*, *A. caesarion*, and the *A. placibilis* clade species by being significantly larger, lacking most dark postdiscal spots on both wings, having orange scaling on both wings that becomes paler at the outer margins, and having white distal fringe elements in every cell on both wings. It additionally differs from all of these except *A. placibilis* by having a dark submarginal band on both dorsal wings. The female of the sympatric *A. natalita* Hall & Willmott, 1995 (Fig. 10B) has the most similar dorsal surface, but is instantly separated by the largely blue ventral surface possessed by many of the most derived *amalfreda* group species. The aforementioned female representing an undescribed potential sister species from Peru (Fig. 4) is the most similar overall, but differs from female *A. janiceae* by being smaller and having dark yellow instead of orange scaling on both wings that does not become paler toward the outer wing margins (but, unusually, does also become paler at the wing bases), more prominent dark basal spots on both wings, including a fully visible medially-divided spot toward the base of cell Cu₁ below the middle of the discal cell on both forewing surfaces, a full complement of dark postdiscal spots on both wings, and a dark presubmarginal spot in cell Cu₁ on the forewing that is more proximally positioned. The examined females of *A. janiceae* do not differ from each other except for the variable presence or absence of tiny faint dark postdiscal marks in the tornus and apex of the hindwing.

trochilia groups), a dark submarginal band on the male dorsal forewing that is more or less entirely separated from the silver submarginal line (uniquely present in the *A. placibilis* and *A. occidentalis* clades, and universal except for *A. willmotti* Dolibaina & Dias, 2015), and a dark submarginal band on the male dorsal hindwing that is more or less entirely separated from the silver submarginal line (universally present in the *A. placibilis* and *A. occidentalis* clades except for *A. willmotti*, but also widely present in sections of the *amalfreda* group). Also seemingly closely related to *A. janiceae* are two other orange and black-spotted species, the Transandean *A. crocea* (Godman & Salvin, 1878), which although preliminarily found by Hall (2023) to be the most basal member of the genus could plausibly be positioned a node away, as sister to the *occidentalis* + *amalfreda* groups, and the southeast Brazilian *A. caesarion* Lathy, 1958, which is tentatively hypothesized to be positioned at the very base of the *amalfreda* group. The closest relative to *A. janiceae* actually appears to be an undescribed species that is known to us from a single female, from a similar elevation in central Peru (Naranjos, San Martin [1700 m]) (see Fig. 4).
Biology: This rare and localized species is known to inhabit montane forest at 1650 m. Males were encountered in Ecuador along the forest edge of a ridgetop forest fragment during the early afternoon. They flew with a weak fluttering flight and landed under leaves 2 to 4 m above the ground at multiple locations, making it difficult to determine with certainty whether or not they were perching. Males were also attracted to fermento placed on low leaves along the forest edge. Females were found flying at the same time and place as the males. The wing pattern of male *A. janiceae* in particular, with its orange ground color, bold dark basal spots and dark distal rays, is sufficiently divergent from that of its congeners to suggest that the species may be involved in a mimicry ring with other similarly patterned Lepidoptera, particularly in the Riodinidae and day-flying moth families such as the Erebidae (Arctiinae) and Geometridae. Similar sympatric montane riodinids include both sexes of *Symmachia calderoni* Hall & Lamas, 2001, and *Mesene ingrumaensis* Callaghan & Salazar, 1999 (Symmachini).

Distribution: *Argyrogrammana janiceae* is currently known only from the type locality in southern Ecuador (Morona-Santiago), but it seems likely to range at least into northern Peru and possibly southern Colombia.

*Argyrogrammana aurora* Hall & Willmott, new species
(Figs. 5; 13)

Description: MALE: Forewing length HT 15 mm; PTs 13.5-15 mm. Wings: see Fig. 5. Head: Eyes dark brown and bare, with a darker brown transverse basal 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 dark 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. 13; posterior portion of valvae in ventral view weakly asymmetrical, with a relatively broad gap between tips; sclerotized transtilla forms a long, upwardly curved, “hook”-like posterior process that is broad 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: Unknown.

Types: HOLOTYPE male: ECUADOR: Zamora-Chinchipe, ridge above Zamora, 4°04.04’S 78°57.88’W, 1450 m, 13 Jan 2002 (J. P. W. Hall) (USNM). PARATYPES: ECUADOR: Napo, 2 males: km. 49 Tena-Loreto rd., 0°42.7’S 77°44.4’W, 1350 m, 15 Feb 2013 (D. H. Ahrenholz) (DA); Morona-Santiago, 1 male: Sopladora ridge, km. 10 Guarumales-Méndez rd., 2°35.5’4”S 78°27’23”W, 1650 m, 6-9 Nov 2010 (K. R. Willmott) (JH); Zamora-Chinchipe, 1 male: ridge above San Luis, 3 km. W. of Guayaguyme Alto, 3°55’14”S 78°54’49”W, 1500 m, 23 Jun 2013 (JH1706) (K. R. Willmott) (JH); same locality data as HT, 1 male: 20 May 2000 (K. R. Willmott) (JH); 2 males: 26 Sept 2003 (D. H. Ahrenholz) (DA).

Etymology: This species name is based on the Latin word “aurora”, which means “dawn”, and also refers to the goddess of dawn in Roman mythology. The name alludes to the orange wings of this butterfly and its occurrence on the eastern slope of the Andes.

Diagnosis: *Argyrogrammana aurora* n. sp. can be placed in the *A. occidentalis* clade of the *occidentalis* group, a clade of nine species that is strongly supported by three unique and universal characters, namely a dark presubmarginal band on the male dorsal forewing with spots above vein Cu, 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 (Hall, 2023). The *A. sublimis* Brévignon & Gallard, 1995, subsclade contains four very similar orange (males)/yellow (females) and black-spotted species, *A. sublimis*, with which the name iracyi P. & J. Jauffret, 2007, was tentatively synonymized by Hall & Willmott (2023), *A. saulensis* Gallard, 2008, the newly described *A. vespertina* Hall & Willmott, 2023, and *A. aurora*. These species all share a medially-divided dark spot near the base of cell Cu, below the base of the discal cell on the male dorsal forewing (in addition to the medially divided spot below the middle of the discal cell), a character that has evolved elsewhere in the genus only in the newly described *A. occidentalis* subsclade species *A. eura* Hall, 2023, which otherwise exhibits the multiple male wing pattern characters typical of that subsclade (see Hall & Willmott, 2023). The more derived trio of *A. sublimis* subsclade species can be externally separated from the basal *A. sublimis*, which appears to be sympatric throughout much of Amazonia with *A. saulensis*, by being larger, with male forewing lengths ranging from 11.5 to 15 mm compared to 10 to 11.5 mm in *A. sublimis*, lacking a broad, contrasted, darker orange distal band around the silver submarginal line on both male dorsal wings, and having smaller dark presubmarginal spots on the male dorsal hindwing that are surrounded by larger faint dark markings (reflecting much larger such spots on the ventral surface). In the male genitalia, the derived trio have a longer hook-like posterior transtilla process that extends to or beyond the dorsal margin of the valvae in lateral view and has approximately two-thirds instead of half its length beyond the posterior margin of the valvae in ventral view, and a broader gap between the valve tips in ventral view that is approximately twice as wide instead of the same width as the valve tip.

*Argyrogrammana aurora* belongs to a trio of previously unrecognized sibling species that are allo- or parapatrically distributed, with *A. aurora* (Fig. 5) confined to east Andean elevations above 1350 m, *A. saulensis* (Fig. 6) occurring across lowland Amazonia up to 1200 m, and *A. vespertina* (Fig. 7) confined to the lowland southern Transandean region. *Argyrogrammana aurora* is tentatively hypothesized to be sister to *A. vespertina* based on both subtle male wing pattern similarities, including the derived possession of dark submarginal spots on the dorsal wings that are smaller, narrower, and more widely spaced compared to those of *A. occidentalis* clade relatives, and mitochondrial COI DNA barcode data that were generated for Ecuadorian exemplars of these taxa. The barcoded male paratype of *A. aurora* from San Luis (Zamora-Chinchipe) (JH1706) was found to have a sequence divergence of 1.9% from a male paratype of *A. vespertina*.
from San Francisco (Esmeraldas) (JH1710), but 4.5% from the Lumbaqui (Sucumbios) male of *A. saulensis* (JH1709) in Fig. 6 (Hall & Willmott, 2023), implying that *A. aurora* has a closer phylogenetic and biogeographic relationship to its Transandean rather than Amazonian relative. We long regarded these three phenotypes as belonging to a single widespread taxon, while harboring suspicions that the montane phenotype at least might represent a distinct species, but the preliminary molecular sequence data combined with subtle external and male genitalia differences suggest that they represent three separate species. The *A. occidentalis* clade is the only one in the genus within which size is a genuinely important criterion for species identification, and indeed *A. aurora* most obviously externally differs from *A. vespertina* and *A. saulensis* by being larger, having a male forewing length range of 13.5 to 15 mm compared to 11.5 to 13.5 mm. There are no wing pattern differences that consistently separate these three species, but *A. aurora* has spots in the costal half of the presubmarginal band on the dorsal forewing that are smaller than those in nearly all specimens of *A. vespertina* and in many specimens of *A. saulensis*, a typically orange rather than orange-yellow ventral surface, dark vertical streaks in the costal third of the ventral forewing that are absent to sparsely present instead of typically densely present in *A. vespertina* and nearly always absent in *A. saulensis*, dark presubmarginal spots in cells M₁ and M₂ on the ventral forewing that are typically more arrow shaped than those in *A. vespertina*, a dark presubmarginal spot in cell Cu₁ on the ventral forewing that is typically slightly more proximally positioned compared to that in *A. saulensis*, and dark submarginal spots in the tornal half of the ventral forewing and on the ventral hindwing that are nearly always fused with the silver submarginal line, whereas these are typically separated in *A. saulensis* (although not in the heavily patterned Fig. 6 specimen). Additional notable intrapopulational wing pattern variation in *A. aurora* males includes the size of the dark presubmarginal spots on both dorsal wings and the prominence of gray scaling at the base of both ventral wings. At least two males of each of the three species were dissected, and several subtle but consistent genitalia differences were found, with *A. aurora* (Fig. 13) having weakly asymmetrical valve tips in ventral view instead of approximately symmetrical (*A. saulensis*, Fig. 14) or prominently asymmetrical (*A. vespertina*, Fig. 15) valve tips, a broad and curving hook-like transtilla process in ventral view instead of a broad and approximately straight (*A. saulensis*) or narrow and curving (*A. vespertina*) transtilla, and an approximately straight saccus in ventral view instead of one that curves to the left (*A. saulensis*) or angles to the right (*A. vespertina*). The female of *A. aurora* is not yet known, but can be expected to look like a larger version of the female of *A. vespertina* figured by Hall & Willmott (2023).

**Biology:** This uncommon to rare species is known to inhabit montane forest from 1350 to 1650 m. Solitary males or small groups of males were encountered in Ecuador perching on and around tree-trunk epiphytes in the sun-dappled subcanopy 6 to 15 m above the ground on hillslopes and ridge-tops from 1230 to 1415 hrs.

**Distribution:** *Argyrogrammana aurora* is known from most of Ecuador’s east Andean slope (Napo to Zamora-Chinchipe), and it seems likely to range at least into Colombia and Peru.

### amalfreda group

*Argyrogrammana caelestina* Hall & Willmott, 1995  
(Figs. 8A,B)


**Identification and Taxonomy:** *Argyrogrammana caelestina* belongs to a derived clade within the *amalfreda* group that contains all of that group’s montane members, including *A. pacsa* Hall & Willmott, 1998, *A. natalita*, and the new species *A. cosnipata* (Hall, 2023). This *A. natalita* clade, which is sister to the lowland Amazonian *A. nurtia* (Stichel, 1911) clade (*A. nurtia, A. alstonii* (Smart, 1979), *A. pulchra* (Talbot, 1929), and *A. sticheli* (Talbot, 1929)), is characterized by a large solid area of dark orange to orange-brown scaling at the base of the male dorsal wings, an entirely blue (between the dark spots) ventral hindwing in males (also in *A. pulchra* and *A. sticheli*), blue ventral scaling in the forewing discal cell and across the hindwing in females (also in *A. sticheli*), and whitish instead of yellowish scaling on the ventral surface of the male abdomen. *Argyrogrammana caelestina* appears to be sister to the elevationally parapatric *A. pacsa*, data that are suggestive of the pattern of repeated upward parapatric speciation that was reported for the riodinid genus *Ithomiola* C. & R. Felder, 1865 (Hall, 2005), in this case from a lowland ancestor similar to *A. amalfreda* (Staudinger, 1887) and *A. nurtia*. However, the additional presence at montane elevations of the sister-species pair of *A. natalita* and *A. cosnipata* indicates a more complex pattern of speciation.

The male of *A. caelestina* can readily be separated from that of *A. pacsa*, as well as *A. natalita*, by having darker and redder orange-brown scaling on the dorsal wings that is reduced in extent on the forewing, a broader and more elongate blue postdiscal patch on the dorsal forewing that extends into cell Cu₂, with commensurately longer blue postdiscal rays on the ventral forewing, a more complete set of dark presubmarginal spots on the dorsal hindwing, an inwardly diagonal dark postdiscal band on the ventral forewing, and a straighter dark postdiscal band on the ventral hindwing. The main evidence for the sister relationship between *A. caelestina* and *A. pacsa* is their very similar male genitalia, which share an aedeagal pedicel that laterally broadens medially, is significantly constricted in width anteriorly, extends ventrally to posteriorly anterior to this constriction (creating a concave shape), and is displaced to the left of the aedeagus (see Fig. 5K in Hall (2023)), a character state that is seen elsewhere in the genus only in the unrelated *trochilia* group species *A. saphirina*. The male genitalia of *A. caelestina* (see Fig. 15 in Hall & Willmott (1995)) potentially differ from those of *A. pacsa* (see Fig. 8 in Hall & Willmott (1998)) only by having a more sinusuous ventral section to the vinculum, a slightly longer saccus, and a slightly shorter string of aedeagal
East Andean, Stichel (1910-11) included the distal half of the forewing. A. caelestina is quite unlike those of its closest relatives, being unique in the genus in having a single broad yellow band across the ventral forewing (typically absent), and dark presubmarginal and submarginal bands on the dorsal hindwing that vary from a continuous solid band to a broken series of spots. The female of A. caelestina is quite unlike those of its closest relatives, being unique in the genus in having a single broad yellow band across the distal half of the forewing. Notable intrapopulational wing pattern variation in A. caelestina males includes the presence in 5-10% of individuals of a small blue spot at the discal cell end on the dorsal forewing, the variable presence of orange-brown submarginal scaling in the tornus of the dorsal forewing (typically absent), and dark presubmarginal and submarginal bands on the dorsal hindwing that vary from a continuous solid band to a broken series of spots. The female of A. caelestina is quite unlike those of its closest relatives, being unique in the genus in having a single broad yellow band across the distal half of the forewing. Notable intrapopulational wing pattern variation in A. caelestina males includes the presence in 5-10% of individuals of a small blue spot at the discal cell end on the dorsal forewing, the variable presence of orange-brown submarginal scaling in the tornus of the dorsal forewing (typically absent), and dark presubmarginal and submarginal bands on the dorsal hindwing that vary from a continuous solid band to a broken series of spots. The female of A. caelestina is quite unlike those of its closest relatives, being unique in the genus in having a single broad yellow band across the distal half of the forewing.
5C,D), who suggested that it could be the female of *A. natalita*. However, the subsequent discoveries in Ecuador of *A. pacsa*, and then of females clearly matching with the males of both *A. pacsa* and *A. natalita*, indicate that the female paraleotype of *A. nurtia* belongs to *A. pacsa*. The female of *A. pacsa* differs from that of *A. natalita* by being larger and having darker orange scaling in the basal half of both dorsal wings, a prominent band of dark postdiscal spots on both dorsal wings, more proximally positioned dark presubmarginal and submarginal bands on both dorsal wings, with a submarginal band that is largely separated from instead of entirely fused with the silver submarginal line, orange instead of blue scaling between the discal cell end and the dark postdiscal band on the ventral forewing, a more elongate and inwardly directed silver submarginal marking in cell M₁ on the ventral forewing, and more convex dark presubmarginal spots on the ventral hindwing. The female of *A. pacsa* differs from that of the new species *A. cosnipata* in many of the same ways, as detailed in that species account. Intrapopulational wing pattern variation in *A. pacsa* females includes the exact position of the dark postdiscal spot in cell M₁ on the forewing (typically more distally positioned than in the female in Fig. 9B), the size of the dark distal spots on both dorsal wings, whether the apical portion of the dark submarginal band on the dorsal forewing is separated from or fused with the silver submarginal line, the prominence of the blue scaling within the medial orange postdiscal spots on the ventral forewing, and the presence or absence of orange scaling in the apex of the ventral hindwing. The examined *A. pacsa* females from the southern Andes have less convex dark presubmarginal spots on the ventral hindwing compared to those from the central Andes (we have not examined any males from the southern Andes).

**Biology:** Moderately extensive locality data (seven localities) from the central Andes (Ecuador and C. Peru) indicate that this uncommon to rare species inhabits montane forest there from 1550 to 2100 m, apparently parapatrically replacing *A. caelestina* at higher elevations. However, in the southern Andes (S. Peru and Bolivia) *A. pacsa* has been recorded as low as 1200 m, suggesting that there, where *A. caelestina* has not been recorded and may not occur, the lower elevational limit for the species is lower. In Ecuador, a solitary male of *A. pacsa* was encountered perching 1 to 2 m above the ground at the edge of a ridge at 1100 hrs, and a small group of males was found perching 6 to 8 m above the ground on a sunlit bush beside a wide hillside trail from 1145 to 1300 hrs. Males were also found in subcanopy fish-baited traps and on fermento placed on low leaves on ridgetops between 1130 and 1215 hrs. One female was encountered resting beneath a leaf 8 m above the ground on the aforementioned hillside male perching bush at 1045 hrs, and others were found 3 to 9 m above the ground on ridgetops between 0930 and 1430 hrs.

**Distribution:** *Argyrogrammana pacsa* is known to range from central Ecuador (Morona-Santiago) to northern Bolivia (La Paz).

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**Argyrogrammana natalita** Hall & Willmott, 1995

(Figs. 10A,B)


**Identification and Taxonomy:** *Argyrogrammana natalita* is externally most similar to *A. pacsa*, but it actually appears to be sister to the new species *A. cosnipata*. It is distinguished from both in those species accounts. Notable intrapopulational wing pattern variation in *A. natalita* males includes the shade of the orange dorsal scaling, the prominence of dark spots in cell Cu₂ below the discal cell on the dorsal forewing, the width of the blue distal patch on the dorsal forewing, which in about 5% of individuals has an additional tiny distally displaced spot in cell R₄₊⁵, the prominence of dark spots at the base of the dorsal hindwing, the width of the dark submarginal band on the dorsal hindwing, and the arrangement of the two dark spots in the middle of the discal cell on the ventral forewing, which varies from separate closely interdigitating spots (typical character state for the genus and *A. natalita* clade) to partially fused spots that form a jagged band across the cell. Intrapopulational variation in *A. natalita* females includes the shade of the orange dorsal scaling, the exact size of the dark presubmarginal and submarginal spots on the dorsal forewing, the prominence of the dark postdiscal spots on the dorsal hindwing (typically absent to faint), and the prominence of the blue scaling within the orange postdiscal spots on the ventral forewing.

**Biology:** This uncommon to rare species is known to inhabit montane forest from 1300 to 1800 m, at least in the central Andes, and near the respective limits of its elevational distribution it is sympatric with *A. caelestina* and *A. pacsa*. In Ecuador, solitary males or pairs of males were encountered perching in the subcanopy, at the edge of lightgaps 8 to 12 m above the ground, on ridgetops and ridgetops from 1330 to 1440 hrs. A male was attracted to fermento placed on low leaves on a hilltop at 1430 hrs. Females were encountered flying or resting under low leaves at the edge of ridgetops between 1110 and 1145 hrs. In southern Peru, males were found perching 6 to 7 m above the ground between 1245 and 1320 hrs (Lamas et al., in press).

**Distribution:** *Argyrogrammana natalita* specimens have been examined from the area between northern Ecuador (Sucumbios) and central Peru (San Martin), although Lamas et al. (in press) additionally report it from southern Peru’s Cuzco department, meaning it is almost certain also to occur in both Colombia and Bolivia.

**Argyrogrammana cosnipata** Hall, new species

(Figs. 11A,B; 16)

**Description:** MALE: Forewing length HT 13.5 mm. Wings: see Fig. 11A. Head: Eyes dark brown and bare, with a darker brown transverse medial band and gray marginal scaling; frons black, with a broad dirty white transverse band
medially and three dirty white dorsal marks below base of antennae; labial palpi banded black and dirty white; antennal length approximately 55% of forewing length, segments black with vertical dirty white lateral bands, clubs black. **Body**: Dorsal surface of thorax dark orange and black, ventral surface gray, dorsal surface of abdomen black dorsally with a narrow dark orange band along posterior margin of all but posterior-most segment and a mixture of dark orange and black scaling laterally, ventral surface black with a narrow dirty white band along posterior margin of all segments; all legs banded dark brown and dirty white. **Genitalia**: see Fig. 16; sclerotized transf stigma between closely spaced valve tips concave and ventrally posteriorly directed in lateral view, projecting significantly above and below valve tips in lateral view; ductus ejaculatorius enters anterior tip of aedeagus to right; vesica exits posterior tip of aedeagus to right, conical complex on unverted vesica consists of a long, dorsally curved “braided rope” of numerous small (becoming slightly larger posteriorly), slightly convex, posteriorly (in anterior third of series) to ventroposteriorly (in posterior two-thirds of series) directed spine-like cornuti; eighth tergite and sternite rectangular. **FEMALE**: Forewing length PT 12 mm. **Wings**: see Fig. 11B. **Head**: Eyes dark brown and bare, with a darker brown transverse medial band and orange marginal scaling; frons black, with a broad pale orange transverse band medially and three pale orange dorsal marks below base of antennae that at lateral edges of frons extend ventrally to connect with medial band; labial palpi banded brown and pale orange; antennal length approximately 55% of forewing length, segments black with vertical dirty white lateral bands, clubs black. **Body**: Dorsal surface of thorax dark orange and black, ventral surface gray and blue, dorsal surface of abdomen black with a dark orange band along posterior margin of all but posterior-most segment, ventral surface black with a narrow pale orange band along posterior margin of each segment; all legs banded brown and pale orange.


**Etymology**: This species is named after the broader type locality, the Cosñipata valley in southeastern Peru.

**Diagnosis**: The morphological phylogenetic analysis of Argyrogrammana presented by Hall (2023) indicates that A. cosnipata n. sp. belongs to a derived clade within the amalfreda group. This species group is most readily characterized by its members possessing orange and blue dorsal wings and gray to blue ventral wings in males, although A. cosnipata is the only amalfreda group member to have clearly secondarily lost blue dorsal coloration. Argyrogrammana cosnipata belongs to the well-supported A. natalita clade, which contains all four montane members of the amalfreda group, including A. caelestina, A. pacsa, and A. natalita. All four species are unique in the genus in possessing a large solid area of dark orange to orange-brown scaling at the base of the male dorsal wings. They are also highly unusual in having an entirely blue (between the dark spots) ventral hindwing in males (independently derived in the closely related A. pulchra and A. sticheli), blue ventral scaling in the forewing discaal cell and across the hindwing in females (independently derived in A. sticheli), and whitish instead of yellowish scaling on the ventral surface of the male abdomen (also present in the derived majority of trochilida group species).

Argyrogrammana cosnipata (Figs. 11A,B) is most similar to and appears to be the sister species of A. natalita (Figs. 10A,B). The two species are unique in the genus in possessing lilac-blue spots immediately distal to the dark postdiscal band on the ventral forewing in males and blue scaling between the discaal cell end and the dark postdiscal band on the ventral forewing in females. They are also unusual in having a relatively distally positioned postdiscal band across cells M₁ to M₄ on the male ventral forewing (derived elsewhere in the amalfreda group in the three A. sebastiani Brévignon, 1995, subclade members and A. talboti Brévignon & Gallard, 1998). The highly autapomorphic male of A. cosnipata can readily be separated from the males of all of its close relatives in the A. natalita clade by having widespread orange-brown scaling across the dorsal forewing, with no large dark distal area containing a blue patch, and a fuller complement of dark basal, postdiscal, and submarginal spots on both dorsal wings. It is perhaps superficially more similar to two species positioned at the very base of the amalfreda group, the southeast Brazilian A. caesarion, and the newly described lowland Peruvian A. lamasí Ahrenholz & Hall, 2023, which similarly lack dorsal blue, but these species can quickly be separated by their gray rather than blue ventral surface. The male genitalia of A. cosnipata (Fig. 16) and A. natalita (see Fig. 14 in Hall & Willmott 1995)) are very similar, with those of A. cosnipata potentially differing only by having a less protruding ventroposterior corner to the valvae below the elongated upper posterior process. The male genitalia of A. caelestina and A. pacsa are very similar to each other, but rather distinct from those of A. cosnipata and A. natalita, differing by having a saccus that is significantly longer, anteriorly pointed instead of angular, and narrower in ventral view, valvae with a more prominently projecting and inwardly curved ventroposterior corner, a broader, slightly upturned, and ventrally convex upper posterior process that is more angular in ventral view, and a significantly longer vertical section between the two processes, an aedeagal cornutal complex that occupies about 50-60% instead of 100% of the distance between the aedeagal junction of the pedicel and the posterior tip of the aedeagus, and consists of significantly larger and more uniformly sized spine-like cornuti, and an aedeagal pedicle that mediially forms a laterally broadened pad with a significantly narrowed concave section anteriorly.

The female of A. cosnipata is much more similar to that of A. natalita, but seems to differ by having slightly darker and more reddish-brown dorsal wings, a complete set of dark postdiscal spots on both dorsal wings, a broken silver submarginal line on both dorsal wings, and potentially slightly more extensive orange scaling in the distal half of the ventral forewing. The female of A. cosnipata differs from that of A. pacsa by being smaller and having a more distally positioned dark postdiscal band on both wings, dark submarginal spots on both dorsal wings that are entirely fused with instead of largely separated from the silver submarginal line, blue instead of orange scaling between the discaal cell end and the dark postdiscal band on the ventral forewing, less convex dark presubmarginal spots on the ventral hindwing, and lilac scaling at the submargin of the ventral hindwing that more obviously contrasts with the caerulean blue scaling across the remainder of the wing.

**Biology**: This rare species is known to inhabit montane forest at about 1700 m. Given the apparent elevational parapatry of A. pacsa and A. caelestina, it is possible that A. cosnipata is also elevationally parapatric above its sister species A. natalita,
which has been recorded in southern Peru from about 1600 m (Lamas et al., in press). However, much more locality data are needed for both species from this region before any firm conclusions can be drawn. Nothing is known about the biology of *A. cosnipata*, although label data indicate that both sexes were collected at a hilltop locality.

**Distribution:** *Argyrogrammana cosnipata* is currently known only from the type locality in southern Peru (Cuzco), but it seems certain to range into neighboring Bolivia.

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**LITERATURE CITED**


