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A collection of papers on *Argyrogrammana* Strand (Riodinidae: Symmachiini)
by Jason P. W. Hall, K. R. Willmott, and D. H. Ahrenholz

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Front cover: *Argyrogrammana nurtia* male, Santiago, Morona-Santiago, E. Ecuador (photo by D. H. Ahrenholz).

Back cover: *Argyrogrammana johannismarci* male, km. 53 Santiago-Puerto Morona rd., Morona-Santiago, E. Ecuador (top); *Argyrogrammana rameli* male, km. 2 Santiago-Puerto Morona rd., Morona-Santiago, E. Ecuador (bottom) (photos by D. H. Ahrenholz).

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A morphological phylogenetic analysis of *Argyrogrammana* Strand (Lepidoptera: Riodinidae: Symmachiini)

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Abstract: A phylogenetic analysis for all 55 known species of *Argyrogrammana* Strand, 1932 (Riodinidae: Symmachiini) is presented using 110 characters of adult morphology, all of which are illustrated. A single most parsimonious cladogram was generated that is fully resolved. Six species groups are recognized, which are hypothesized to be related as follows: (*crocea* group ((*stilbe* group (*barine* group + *trochilia* group)) + (*occidentalis* group + *amalfreda* group))). The *stilbe* complex of prior usage is found to be polyphyletic, with species distributed in the monotypic *crocea* group, *stilbe* group (2 species), and *occidentalis* group (12 species); the *amalfreda* complex of prior usage is found to be a monophyletic *amalfreda* group (30 species) once *A. barine* (Staudinger, 1887) is removed to the *barine* group (2 species); and the *trochilia* complex of prior usage is found to be a monophyletic *trochilia* group (8 species) once *A. glaucopis* (Bates, 1868) is removed to the *amalfreda* group. A synonymic checklist for *Argyrogrammana* is presented. *Argyrogrammana* appears to have had eight separate colonization and speciation events from Amazonia into the Transandean region (involving all species groups), one such event from the Transandean region back into Amazonia, and one such event from Amazonia into southeastern Brazil. Six vertical speciation events have occurred from the lowlands up into the montane elevations of the Andes, mostly from lowland Amazonia into the eastern Andes, where there has been a small intra-Andean species radiation in the *A. natalita* Hall & Willmott, 1995, clade (*amalfreda* group). Overall, 31% of species in the genus appear to be allo- or parapatrically distributed with respect to their closest relatives, and 98% are restricted to just one of the three major biogeographic regions, with 76% occurring in Amazonia and 24% in the Transandean region.

Key words: biogeography, Neotropics, phylogeny, species richness.

INTRODUCTION

The genus *Argyrogrammana* Strand, 1932, is one of the largest in the Riodinidae, ranging from Mexico to southeastern Brazil. Its small but aesthetically charismatic butterflies are among the rarest in the family, with more than half of the species recognized here described in just the last 30 years (e.g., Brévignon & Gallard, 1995; Hall & Willmott, 1995, 1996a, 2023; Dolibaina *et al.*, 2015; Hall *et al.*, 2023a,b). The distinctive genus was placed by Stichel (1910-11, 1930-31) in his subtribe Mesenini, which largely corresponds to the tribe Symmachiini of current usage. Although this would prove to be a rather prescient placement, no morphological evidence was given to support it, and Harvey (1987) subsequently treated *Argyrogrammana* in a four-forewing-veined *incertae sedis* section containing genera that did not possess the synapomorphies for any of the established riodinine tribes. More recently, molecular phylogenies for the family have suggested that *Argyrogrammana* is sister to the Symmachiini (*sensu* Harvey, 1987), and should perhaps be included within it (Espeland *et al.*, 2015; Seraphim *et al.*, 2018; Zhang *et al.*, 2021). Based on its hypothesized age and morphological and molecular distinction from the Symmachiini *sensu stricto*, *Argyrogrammana* might reasonably be treated in its own tribe

or at least as a subtribe of the Symmachiini *sensu lato*, but resolution of this issue should probably await the completion of more comprehensive phylogenies and be addressed in the context of finalizing a higher classification for the family.

The wing pattern of *Argyrogrammana* species, as the name suggests, most obviously differs from those of the Symmachiini *sensu stricto* by having a distinctive metallic (typically silver) submarginal line on both dorsal wings and typically both ventral wings that is variably proximally kinked in the forewing subapex (Hall & Willmott, 1996a). Similar metallic submarginal markings can be found in a number of genera in the related tribes Calydnini, Emesidini, Helicopini, and particularly the Riodinini, but in none of those genera do they form a single line on both wing surfaces that is subapically kinked on the forewing. *Argyrogrammana* species also externally differ by having two interdigitating dark spots in the middle of the discal cell on the ventral forewing, a character state that is secondarily lost through fusion into a single bar in a few derived species, and a dark transverse band across the middle of the eyes (Hall & Willmott, 1996a). Morphologically, *Argyrogrammana* differs most definitively from all genera in the Symmachiini *sensu stricto* by lacking concealed abdominal androconia. These longitudinally ribbed androconial scales surrounded by acanthae on one or more of male abdominal

tergites four to seven are unique in the family, and are often associated with androconial brush organs at the anal margin of the dorsal hindwing (Harvey, 1987; Hall & Harvey, 2002). The male genitalia of *Argyrogrammana* species, compared to those in the *Symmachiini sensu stricto*, have a simple uncus that always lacks a triangular projection from the middle of the posterior margin, valvae that are almost always entire rather than frequently bifurcate, a transtilla dorsally joining the valve tips that is typically more structurally complex and consistently sclerotized, an aedeagus that is consistently long and narrow rather than short and broad, an aedeagal cornutal arrangement that involves a single long and often “braided rope”-like series of typically very small spines instead of one or more clusters of variably sized but often larger spines near the base of the everted vesica, and an aedeagal pedicel that is much longer and often asymmetrically positioned.

My interest in and involvement with *Argyrogrammana* dates to a pair of coauthored review papers in the 1990s (Hall & Willmott, 1995, 1996a). Since that time, many additional new species have been described, mostly from Brazil and French Guiana (Brévignon & Gallard, 1998; Hall & Willmott, 1998; Jauffret & Martins, 2006; Gallard, 2008, 2017; Dolibaina *et al.*, 2015), and many others have been discovered by myself and collaborators in Ecuador, as well as uncovered in collections from elsewhere in the Neotropics. With 12 new species in need of description, amounting to more than a quarter of the heretofore recognized total, and a substantial amount of new taxonomic, geographic, and biological data to report, an updated review of the genus seemed warranted, targeting the least well known taxa and faunas. The results of this project are presented in three faunal reviews, of the Transandean region (Hall & Willmott, 2023), the east Andean region (Hall *et al.*, 2023a), and the *amalfreda* group of the west Amazonian region (Hall *et al.*, 2023b), and in a paper on new *Argyrogrammana* life histories (Hall, 2023). The purpose of this paper is to provide a phylogenetic and taxonomic framework for these reviews, by conducting a comprehensive phylogenetic analysis for *Argyrogrammana* that tests the monophyly of informal species groupings which have now been in largely unchanged usage for more than a century (Stichel, 1910-11, 1930-31). The resulting phylogenetic hypothesis also provides the opportunity to examine in more detail the biogeography of the genus.

MATERIALS AND METHODS

The phylogenetic analysis presented here was based on adult morphological characters, derived from the wings, head, body, and male genitalia. Female genitalia characters were not included in the analysis for multiple reasons, including the lack of known females for some rarer species, the uncertainty in matching the sexes of some species, and the unavailability of females for dissection of many species given their often great rarity in and wide dispersion among the world’s collections. The homogeneity found in the male genitalia seems likely to be reflected in the females, meaning that only a small number of additional codable characters would likely result from a female genital study. As an example, Hall’s (2005a) morphological phylogenetic study of the riodinid subtribe Napaeina, which

included a similar number of taxa and characters and exactly the same percentage of male genitalia characters, produced only a single codable female genital character after an exhaustive survey. Immature-stage characters were not included in the analysis because only a handful of *Argyrogrammana* species have been reared (Hall, 2023). Similarly, DNA characters were not incorporated because sequence data are currently available for only a small fraction of the species. A few species exhibit notable variation in a few of the coded characters (almost entirely in the male wing pattern), and in such cases a species was coded with the derived character state if at least 20% of the examined specimens possessed that state (i.e., it was present in an apparently significant proportion of the population, well beyond a level attributable to unusual forms and aberrations). Phylogenetically uninformative autapomorphic characters were excluded from the analysis. Morphology was studied using standard techniques, with the dissection methods used following those outlined in Hall (2018). The terminology used here 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 ingroup for the phylogenetic analysis encompassed all 55 of the *Argyrogrammana* species known to me from males, including 12 species newly described in the series of associated papers by Hall (2023), Hall & Willmott (2023), and Hall *et al.* (2023a,b). One undescribed east Andean species was excluded because it is currently known from only a single female, although a provisional phylogenetic placement is discussed by Hall *et al.* (2023a). The synonymic checklist that formed the taxonomic basis for the analysis is given in an Appendix. *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, mostly recently described taxa) were examined for all available names. The outgroup taxon selected for this analysis was the Amazonian *Symmachia phaedra* (Bates, 1868). Zhang *et al.* (2021) recently transferred this species to the small new genus *Tigria* Grishin, 2021, based on molecular genomic data, but, despite this being a monophyletic grouping for which there has also long been known to be morphological support (Hall & Willmott, 1996b; Hall & Harvey, 2002), such a placement seems somewhat premature given that only about a third of the known species in *Symmachia* Hübner, [1819] *sensu lato* and the broader *Symmachiini sensu stricto* have any molecular sequence data. Although *S. phaedra* does not appear to be positioned at the very base of the *Symmachiini sensu stricto* (Zhang *et al.*, 2021), in a tribe of predominantly aposematic and mimetic species, its fully spotted wing pattern is probably the most similar to those of *Argyrogrammana* species, and wing pattern characters form the great majority of the characters in the analysis. As the male genitalia of *Argyrogrammana* are rather homogeneous, and it was clear that none of the genitalia characters in the analysis would impact the deeper cladogram nodes, close genital similarity was rendered a minimal factor in outgroup choice.

A single character matrix was constructed using *MacClade v. 3.05* (Maddison & Maddison, 1995), and a

maximum parsimony analysis was then performed using *PAUP v. 4.0b10* (Swofford, 2002). A heuristic search was performed with tree bisection-reconnection (TBR) branch swapping and 500 random-addition-sequence replicates. All characters were equally weighted and unordered, thus making no *a priori* assumptions about their relative importance or the transformation series of their component states. The strength of branch support was estimated by means of 1000 bootstrap replicates (Felsenstein, 1985) in *PAUP*, and by calculating decay indices (Bremer, 1988, 1994) using *Autodecay v. 4.0* in combination with *PAUP* (Eriksson, 1998). Such branch support measures are based on the level of character homoplasy and quantity, rather than character quality, but they do allow a quick, crude assessment of branch support strength, although there is no substitute for a careful study of the distributions of individual characters. Character evolution was studied using *MacClade*. In the few instances when the optimization of a character on a portion of the cladogram was ambiguous (all involving the *A. placibilis* (Stichel, 1910), *A. sebastiani* Brévignon, 1995, *A. venilia* (Bates, 1868), and *A. natalita* Hall & Willmott, 1995, clades), the most plausible evolutionary scenario was adopted (Agnarsson & Miller, 2008), with the program's ACCTRAN option (accelerated transformation, favoring secondary losses) applied to the cladogram depiction of some characters (6, 15, 16, 46, 68, and 78), and the DELTRAN option (delayed transformation, favoring parallel gains) applied to others (28, 37, 49, 58, 66, and 81).

RESULTS

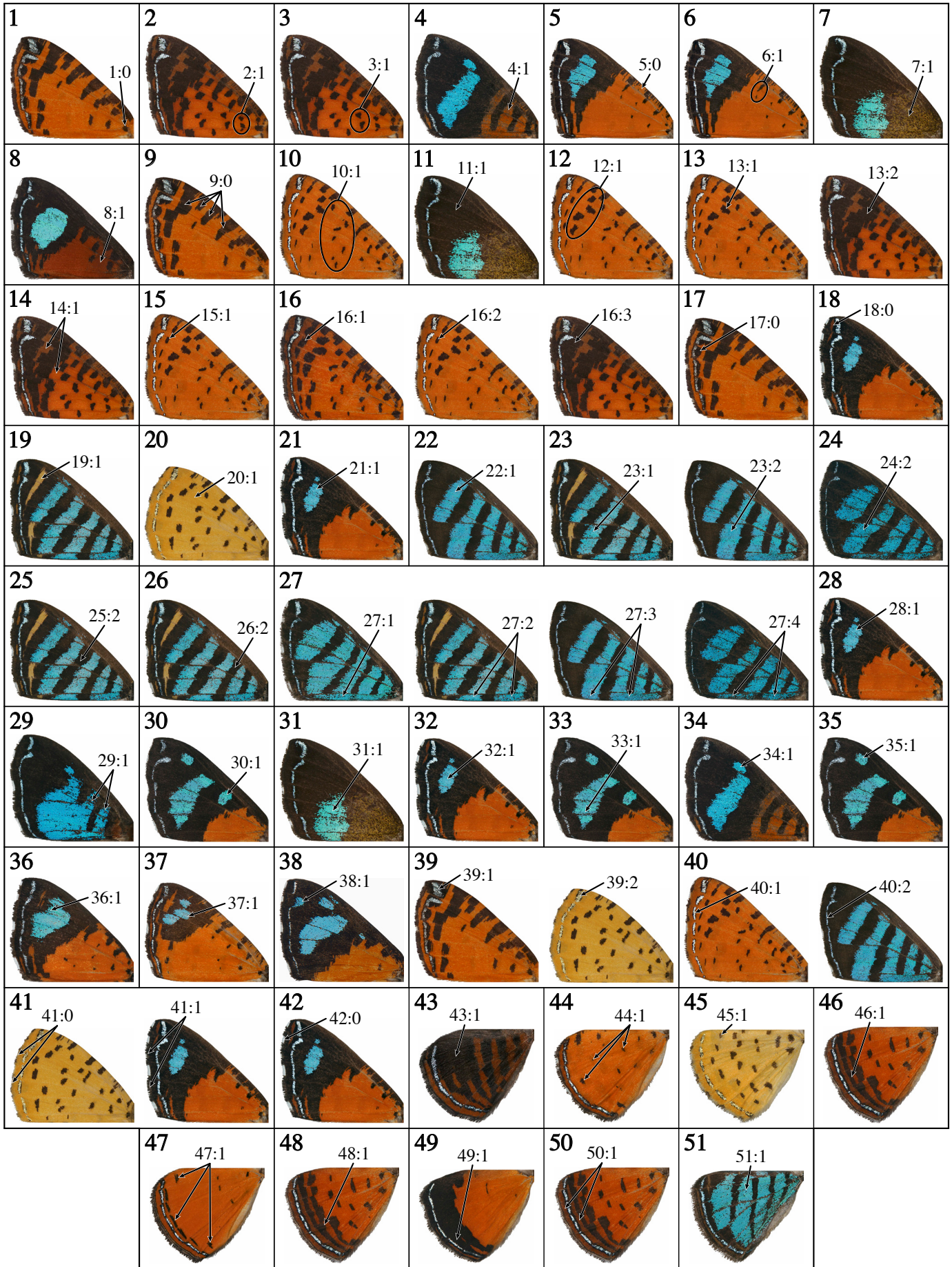
One hundred and ten characters were identified from a morphological study of *Argyrogrammana* adults (55 species), as listed below, from the wing pattern (87 [77 male, 10 female]) (Figs. 1-3), head and body (six) (Fig. 4), and male genitalia (17) (Fig. 5) (see Table 1 for the character matrix). Two of them are multistate characters and the remainder are binary characters. The character to taxon ratio of exactly 2:1 was sufficient to generate a fully resolved phylogenetic hypothesis. The majority of codable characters came from the males, particularly the forewing wing pattern, with 42 characters coded from the male dorsal forewing, 22 from the male ventral forewing, nine from the male dorsal hindwing, and four from the male ventral hindwing. In the females, only six additional characters could be coded from the dorsal forewing, two from the ventral forewing, and one each from the dorsal and ventral hindwing. The male genitalia of *Argyrogrammana* species are rather homogeneous, and even those character systems that do exhibit significant interspecific variation produced disappointingly few codable characters because of the phenomenon of merging potential character states across comprehensively studied large genera. As a result, the male genitalia contributed an unusually small percentage of the overall codable characters, certainly compared to the phylogenetic analyses of riodinid genera such as *Theope* Doubleday, 1847, and *Nymphidium* Fabricius, 1807 (Hall, 2002, 2018). The codable variation in the male genitalia was observed in the valvae (six characters), an unusually interspecifically variable and sometimes morphologically complex transtilla (five), and the aedeagus, cornuti, and pedicel

(six). Unfortunately, most of these characters only provided support for sister-species relationships, and only three characters provided support for deeper nodes, character 94 for the derived majority of the *A. sebastiani* clade in the *amalfreda* group (5 species) and characters 101 and 106 for the *A. occidentalis* (Godman & Salvin, 1886) clade in the *occidentalis* group (9 species). The two standard measures of character homoplasy, the consistency index (CI) and retention index (RI), are given for each character in the analysis. Homoplasy in the wing pattern data set was high, with a third of the coded characters having a CI of 0.33 or less, but many of these characters nonetheless provided important support for certain cladogram nodes, and more than three-quarters of the wing pattern characters have an RI of at least 0.7. Almost no homoplasy was evident in the coded male genitalia characters.

The heuristic search generated a single most parsimonious cladogram, with a length of 256 steps, an overall CI of 0.50, and an overall RI of 0.81. This cladogram is shown in Figs. 6-8, with branch support values indicated in Fig. 6 and the distribution of character states depicted in Figs. 7-8.

Male dorsal wing pattern (Fig. 1):

1. *A dark spot around vein 2A at very base of dorsal forewing (next to thorax) in male:* (0) present; (1) absent. CI = 0.33; RI = 0.71.
2. *A medially divided dark spot near base of cell Cu₂ (below base of discal cell) on dorsal forewing in male:* (0) absent; (1) present. CI = 0.5; RI = 0.75.
3. *A medially divided dark spot toward base of cell Cu₂ (below middle of discal cell) on dorsal forewing in male:* (0) absent; (1) present. CI = 0.2; RI = 0.83.
4. *Multiple orange bands at base of dorsal forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
5. *Yellow to orange scaling along base of costal margin (above discal cell) on dorsal forewing in male:* (0) present; (1) absent. CI = 0.2; RI = 0.83.
6. *A medially divided dark spot at end of discal cell on dorsal forewing in male:* (0) absent; (1) present. CI = 0.2; RI = 0.
7. *Yellow-brown scaling across base of dorsal wings in male:* (0) absent; (1) present. CI = 1; RI = 1.
8. *A large solid area of dark orange to orange-brown scaling at base of dorsal wings in male:* (0) absent; (1) present. CI = 1; RI = 1.
9. *Four dark bars along costal margin of dorsal forewing in male distal to discal cell that extend from costa to at least vein M₁:* (0) present; (1) absent. CI = 1; RI = 1.
10. *A full to nearly full complement of dark postdiscal spots visible on dorsal forewing in male:* (0) absent; (1) present. CI = 0.33; RI = 0.91.
11. *A large contiguous area of dark apical scaling encompassing dark postdiscal to submarginal bands on dorsal forewing in male:* (0) absent; (1) present. CI = 0.33; RI = 0.92.
12. *A dark presubmarginal band on dorsal forewing in male with spots above vein Cu₁ significantly enlarged compared to spots below (i.e., at least twice as wide):* (0) absent; (1) present. CI = 1; RI = 1.
13. *If a dark presubmarginal band on dorsal forewing in male with spots above vein Cu₁ significantly enlarged compared to spots below present (12:1), spots:* (1) separate; (2) fused into a continuous band. CI = 1; RI = 1.
14. *Two-tone orange scaling on dorsal forewing in male, with orange scaling distal to dark presubmarginal band darker than orange scaling proximally:* (0) absent; (1) present. CI = 1; RI = 1.
15. *A dark submarginal band on dorsal forewing in male more or less entirely separated from metallic submarginal line by yellow to orange distal scaling:* (0) absent; (1) present. CI = 0.5; RI = 0.89.
16. *If a dark submarginal band on dorsal forewing in male more or less entirely separated from metallic submarginal line by yellow to orange distal scaling present (15:1), spots:* (1) large, rectangular, and closely spaced; (2) small, narrow, and widely spaced; (3) formed into a broad and continuous band. CI = 0.75; RI = 0.86.
17. *Oval dark submarginal spots surrounded by orange scaling on dorsal forewing in male that are submarginally positioned (i.e., for*



Argyrogrammana species entirely centered over rather than proximal to metallic submarginal line): (0) present; (1) absent. CI = 0.5; RI = 0.5.

- 18. Yellow to orange scaling at submargin to margin of dorsal forewing in male: (0) present; (1) absent. CI = 0.17; RI = 0.62.
- 19. A medially disjointed, isolated yellowish submarginal band on dorsal forewing in male: (0) absent; (1) present. CI = 0.5; RI = 0.75.
- 20. Yellow dorsal wings in male: (0) absent; (1) present. CI = 1; RI = 1.
- 21. Blue scaling on dorsal wings in male: (0) absent; (1) present. CI = 0.33; RI = 0.89.
- 22. Five diagonal blue bands on dorsal forewing in male: (0) absent; (1) present. CI = 1; RI = 1.
- 23. If five diagonal blue bands on dorsal forewing in male present (22:1), fourth blue band from wing base: (1) of approximately even width throughout; (2) broadened below vein Cu_1 . CI = 1; RI = 1.
- 24. If five diagonal blue bands on dorsal forewing in male present, with fourth band from wing base broadened below vein Cu_1 (23:2), a fourth blue

band that is both abruptly distally broadened below vein Cu_1 (i.e., at least twice as wide) and of even width across cells Cu_1 and Cu_2 : (1) absent; (2) present. CI = 1; RI = 1.

- 25. If five diagonal blue bands on dorsal forewing in male present (22:1), a continuous dark band (from vein 2A to costa) between third and fourth blue bands from wing base: (1) absent; (2) present. CI = 1; RI = 1.
- 26. If five diagonal blue bands on dorsal forewing in male present (22:1), a continuous dark band (from vein 2A to costa) between second and third blue bands from wing base: (1) absent; (2) present. CI = 1; RI = 1.
- 27. If five diagonal blue bands on dorsal forewing in male present (22:1), blue anal scaling in cell 2A forms: (1) one long continuous bar below bands one to four (as counted from wing base) (a "4-0 pattern"); (2) one bar below bands one and two and another below band three (a "2-1 pattern"); (3) one bar below bands one to three and another below band four (a "3-1 pattern"); (4) one bar below bands one and two and another below bands three and four (a "2-2 pattern"). CI = 1; RI = 1.

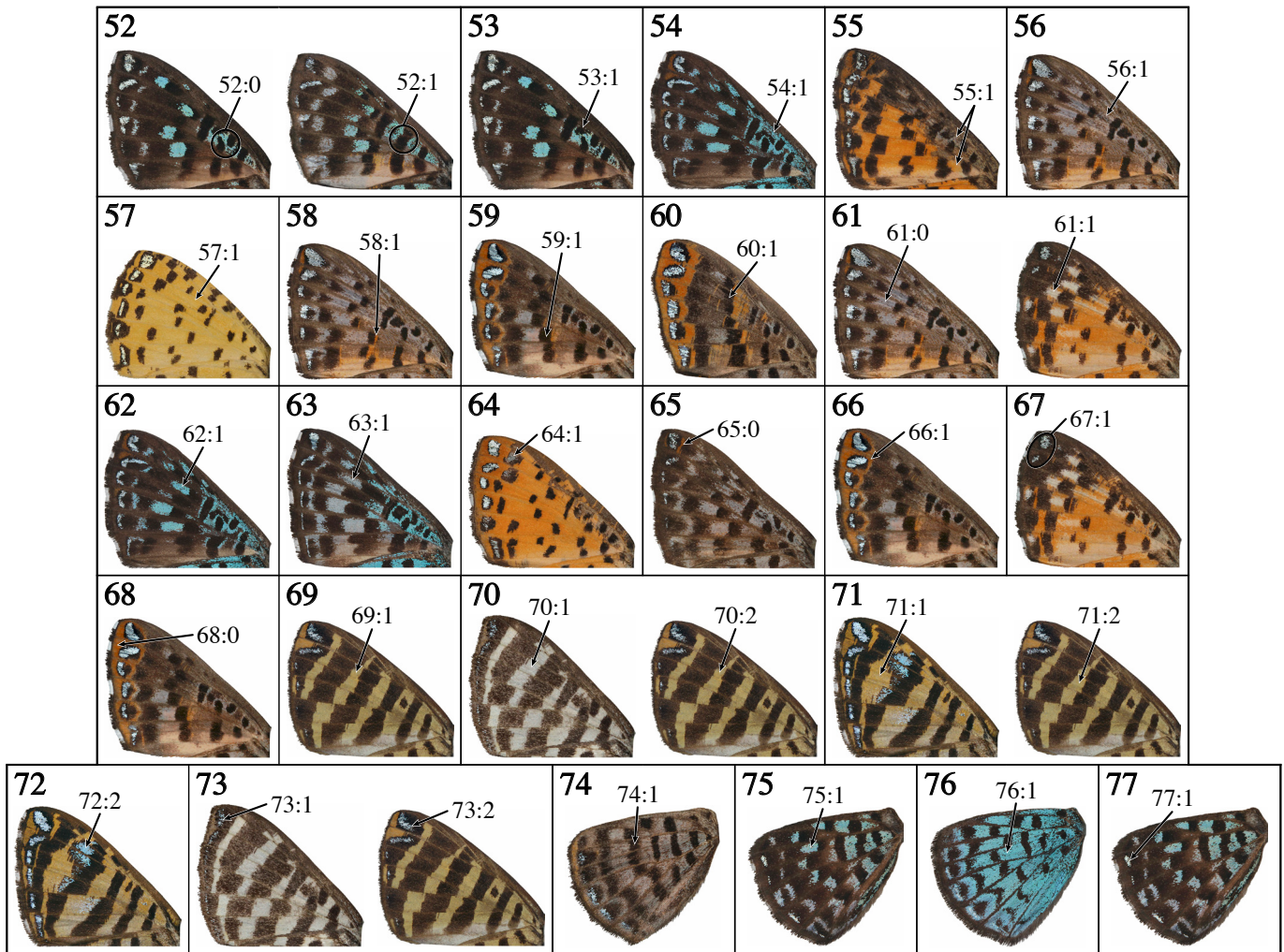


Fig. 2. Characters of the male ventral wing pattern in *Argyrogrammana* (characters 52-73 forewing, 74-77 hindwing). Each box depicts a single character (numbered at top left), with the relevant character state(s) indicated by one or more arrows or a circle. Wings in character boxes: 52(0), 53, 75, 77 = *A. nurtia*; 52(1) = *A. alstonii*; 54, 62, 76 = *A. pacsa*; 55 = *A. janzeni*; 56, 58, 61(0) = *A. celata*; 57 = *A. stilbe*; 59, 66, 68 = *A. phyton*; 60, 74 = *A. halli*; 61(1), 67 = *A. aparamilla*; 63 = *A. natalita*; 64 = *A. placibilis*; 65 = *A. cana*; 69, 70(2), 71(2), 73(2) = *A. saphirina*; 70(1), 73(1) = *A. subota*; 71(1), 72 = *A. pastaza*. Wings not to scale.

Fig. 1 (p. 4, facing). Characters of the male dorsal wing pattern in *Argyrogrammana* (characters 1-42 forewing, 43-51 hindwing). Each box depicts a single character (numbered at top left), with the relevant character state(s) indicated by one or more arrows or a circle. Wings in character boxes: 1, 9, 17, 39(1) = *A. crocea*; 2, 3, 13(2), 14, 16(3) = *A. eura*; 4, 34 = *A. praestigiosa*; 5, 6, 47 = *A. celata*; 7, 11, 31 = *A. barine*; 8 = *A. pacsa*; 10, 12, 13(1), 15, 16(2), 40(1) = *A. vespertina*; 16(1) = *A. janzeni*; 18, 21, 28, 32, 41(1), 42 = *A. phyton*; 19, 23(1), 25, 26, 27(2) = *A. rameli*; 20, 39(2), 41(0) = *A. stilbe*; 22, 23(2), 27(3), 40(2) = *A. trochilia*; 24, 27(4) = *A. saphirina*; 27(1), 51 = *A. pastaza*; 29 = *A. caerulea*; 30, 33, 35 = *A. alstonii*; 36 = *A. callaina*; 37, 44 = *A. aparamilla*; 38 = *A. pulchra*; 43 = *A. glaucopis*; 45 = *A. holosticta*; 46, 48, 50 = *A. occidentalis*; 49 = *A. nurtia*. Wings not to scale.

28. *Blue scaling in distal two-thirds only of dorsal forewing in male:* (0) absent; (1) present. CI = 0.2; RI = 0.84.
29. *Two blue spots only in middle of discal cell on dorsal forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
30. *A blue spot near end only of discal cell on dorsal forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
31. *A greenish-blue medial patch extending to anal margin on dorsal forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
32. *An approximately evenly rectangular blue postdiscal patch within cells M_3 to M_1 (with a smaller spot commonly present in cell R_{4+5}) on dorsal forewing in male:* (0) absent; (1) present. CI = 0.5; RI = 0.8.
33. *A blue postdiscal patch that extends to at least vein Cu_2 on dorsal forewing in male:* (0) absent; (1) present. CI = 0.25; RI = 0.84.
34. *A blue postdiscal patch on dorsal forewing in male with a distally displaced (but generally contiguous) costal spot in cell R_{4+5} compared to both neighboring spots in cells M_2 and M_1 :* (0) absent; (1) present. CI = 1; RI = 1.
35. *A blue postdiscal patch on dorsal forewing in male with a significantly distally disjunct (and always isolated) costal spot in cell R_{4+5} :* (0) absent; (1) present. CI = 0.5; RI = 0.75.
36. *A blue postdiscal patch on dorsal forewing in male with a distal margin that has spot in cell M_1 proximally displaced compared to both neighboring spots:* (0) absent; (1) present. CI = 1; RI = 1.
37. *A blue postdiscal patch on dorsal forewing in male with a proximal margin that has spot in cell M_1 proximally displaced compared to both neighboring spots:* (0) absent; (1) present. CI = 0.5; RI = 0.67.
38. *A blue submarginal spot in cell M_1 on dorsal forewing in male that forms part of metallic submarginal line:* (0) absent; (1) present. CI = 1; RI = 1.
39. *Metallic submarginal line on both dorsal wings in male:* (0) absent; (1) silver; (2) greenish gold. CI = 1; RI = 1.
40. *If a metallic submarginal line on both dorsal wings in male present (39:1 or 2), line on dorsal forewing:* (1) divided into dashes by significant gaps at each vein; (2) more or less continuous except for a possible apical break at vein M_1 . CI = 0.4; RI = 0.75.
41. *Forewing fringe in either sex contains broad sections of prominent white scaling:* (0) in all distal cells; (1) only in some distal cells (typically Cu_2 , M_3 , M_1 , and R_{4+5}). CI = 0.33; RI = 0.33.
42. *A white fringe element in forewing cell M_1 in either sex:* (0) present; (1) absent. CI = 0.33; RI = 0.33.
43. *A dorsal hindwing in male with orange scaling that is largely confined to basal and anal regions of wing, leaving a large dark apex:* (0) absent; (1) present. CI = 1; RI = 1.
44. *Tiny dark basal, postdiscal, and presubmarginal spots surrounded by larger faint dark markings across dorsal hindwing in male (reflecting much larger dark spots on ventral surface):* (0) absent; (1) present. CI = 1; RI = 1.
45. *Dark presubmarginal spots only surrounded by larger faint dark markings on dorsal hindwing in male (reflecting larger dark spots on ventral surface):* (0) absent; (1) present. CI = 0.33; RI = 0.5.
46. *A dark submarginal band on dorsal hindwing in male more or less completely separated from metallic submarginal line by yellow to orange distal scaling:* (0) absent; (1) present. CI = 0.13; RI = 0.65.
47. *A dark submarginal band surrounded by yellow to orange scaling on dorsal hindwing in male with dark presubmarginal band confined to single dark spots in apex and tornus:* (0) absent; (1) present. CI = 0.25; RI = 0.25.
48. *A continuous to nearly continuous (with a possible break at vein Cu_1) dark submarginal band on dorsal hindwing in male with orange scaling on both sides (darker distally) and a proximally broadened element in cell Cu_2 :* (0) absent; (1) present. CI = 1; RI = 1.
49. *A continuous dark submarginal band on dorsal hindwing in male between basal yellow to orange patch and most of metallic submarginal line:* (0) absent; (1) present. CI = 0.17; RI = 0.67.
- Several species are assigned a “?” because they do not have a yellow to orange basal patch on the dorsal hindwing.
50. *A broad, contrasted orange distal band around metallic submarginal line on dorsal hindwing in male:* (0) absent; (1) present. CI = 0.25; RI = 0.5.
51. *Five blue bands on dorsal hindwing in male:* (0) absent; (1) present. CI = 1; RI = 1.
- Male ventral wing pattern (Fig. 2):
52. *Center of discal cell on ventral forewing in male contains:* (0) two dark spots; (1) one dark spot. CI = 0.25; RI = 0.75.
- Throughout the genus *Argyrogrammana*, state (0) consists of two interdigitating spots, with one extending half way across the cell from its upper margin and the other half way across the cell from its lower margin. State (1) consists of the two spots in state (0) aligning to form a single bar extending across the entire width of the cell. An intermediate state can be seen in some specimens of *A. nurtia* (Stichel, 1911) and *A. natalita*.
53. *A dark spot visible inside end of discal cell on ventral forewing in either sex:* (0) absent; (1) present. CI = 0.25; RI = 0.25.
54. *Blue scaling in discal cell on ventral forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
55. *A predominantly grayish discal cell with orange scaling across cells below on ventral forewing in male:* (0) absent; (1) present. CI = 0.33; RI = 0.5.
56. *Widespread gray to blue scaling across ventral forewing in male:* (0) absent; (1) present. CI = 0.25; RI = 0.88.
57. *Widespread yellow to white scaling across ventral forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
58. *Isolated orange scaling along most of proximal margin of dark postdiscal band (i.e., at least beyond vein Cu_1) on ventral forewing in male:* (0) absent; (1) present. CI = 0.2; RI = 0.43.
59. *A vertical component to dark postdiscal band across cells Cu_2 and Cu_1 on ventral forewing in male:* (0) absent; (1) present. CI = 0.5; RI = 0.75.
60. *A straight and approximately vertical component to dark postdiscal band across cells M_3 to R_2 on ventral forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
61. *Postdiscal band across cells M_3 to M_1 on ventral forewing in male:* (0) relatively proximally positioned (i.e., distance from discal cell end to middle of pale spot distal to dark postdiscal spot in cell M_2 approximately equal to or less than distance from middle of pale spot to distal margin); (1) relatively distally positioned (i.e., first aforementioned distance significantly greater than second distance). CI = 0.25; RI = 0.5.
62. *A full complement of blue spots immediately distal to dark postdiscal band on ventral forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
63. *Lilac-blue spots immediately distal to dark postdiscal band on ventral forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
64. *Dark presubmarginal spots with gray to silver scaling within and orange scaling proximally and distally in subapex of ventral forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
65. *Yellow to orange scaling immediately proximal to metallic submarginal line on ventral forewing in male:* (0) present; (1) absent. CI = 0.17; RI = 0.72.
66. *A contrasted orange band along entire proximal length of metallic submarginal line on ventral forewing in male:* (0) absent; (1) present. CI = 0.14; RI = 0.33.
67. *A metallic submarginal line on ventral forewing in male largely confined to apex, with metallic scaling barely visible to absent in cells Cu_2 to M_2 :* (0) absent; (1) present. CI = 0.5; RI = 0.83.
68. *Yellow to orange scaling distal to metallic submarginal line on ventral forewing in male:* (0) present; (1) absent. CI = 0.2; RI = 0.67.
69. *Pale bands on ventral forewing in male:* (0) absent; (1) present. CI = 1; RI = 1.
70. *If pale bands on ventral forewing in male present (69:1), bands:* (1) white; (2) yellow. CI = 1; RI = 1.
71. *If pale bands on ventral forewing in male present and yellow (70:2), pale distal bands:* (1) similar in width to or broader than alternating dark bands; (2) narrower than alternating dark bands. CI = 1; RI = 1.
72. *If pale bands on ventral forewing in male present (69:1), a patch of blue scales proximal to costal portion of fifth pale band from wing base:* (1) absent; (2) present. CI = 0.67; RI = 0.8.
73. *If pale bands on ventral forewing in male present (69:1), apical segments of metallic submarginal line in cells M_1 and R_{4+5} :* (1) approximately vertically oriented to slightly inwardly directed (< 45° angle); (2) prominently inwardly directed (> 45° angle). CI = 1; RI = 1.
74. *A straight component to a continuous (below vein Rs) dark postdiscal band across cells M_3 to Rs on ventral hindwing in male:* (0) absent; (1) present. CI = 1; RI = 1.
75. *Blue spots immediately distal to dark postdiscal band on ventral hindwing in male:* (0) absent; (1) present. CI = 1; RI = 1.
76. *An entirely blue ventral hindwing in male (between dark spots):* (0) absent; (1) present. CI = 0.5; RI = 0.8.
77. *A metallic submarginal line on ventral hindwing in male:* (0) mostly to completely absent; (1) mostly to completely present. CI = 0.13; RI = 0.56.



Fig. 3. Characters of the female wing pattern in *Argyrogrammana* (characters 78-83 dorsal forewing, 84 dorsal hindwing, 85-86 ventral forewing, and 87 ventral hindwing). Each box depicts a single character (numbered at top left), with the relevant character state indicated by an arrow. Wings in character boxes: 78 = *A. janiceae*; 79 = *A. saphirina*; 80, 84 = *A. glaucopsis*; 81 = *A. janzeni*; 82 = *A. barine*; 83 = *A. pulchra*; 85, 87 = *A. pacs*; 86 = *A. natalita*. Wings not to scale.

Female dorsal wing pattern (Fig. 3):

- 78. *A dorsal forewing in female with orange scaling that becomes paler toward costal and distal margins:* (0) absent; (1) present. CI = 0.33; RI = 0.33.
Several species are assigned a “?” for characters 78 to 87 because their females remain unknown.
- 79. *White to pale yellow diagonal bands on dorsal forewing in female:* (0) absent; (1) present. CI = 1; RI = 1.
- 80. *Dark yellow to orange diagonal bands on dorsal forewing in female:* (0) absent; (1) present. CI = 1; RI = 1.
- 81. *A dark submarginal band on dorsal forewing in female more or less entirely separated from metallic submarginal line by yellow to orange distal scaling:* (0) absent; (1) present. CI = 0.17; RI = 0.62.
- 82. *Blue presubmarginal spots on dorsal forewing in female:* (0) absent; (1) present. CI = 1; RI = 1.
- 83. *A blue submarginal spot in cell M_1 on dorsal forewing in female that forms part of metallic submarginal line:* (0) absent; (1) present. CI = 1; RI = 1.
- 84. *A dark orange band proximally lining anal portion only of metallic submarginal line on dorsal hindwing in female:* (0) absent; (1) present. CI = 1; RI = 1.

Female ventral wing pattern (Fig. 3):

- 85. *Blue scaling in discal cell on ventral forewing in female:* (0) absent; (1) present. CI = 0.5; RI = 0.75.
- 86. *Blue scaling between discal cell end and dark postdiscal band on ventral forewing in female:* (0) absent; (1) present. CI = 1; RI = 1.
- 87. *Blue scaling across ventral hindwing in female:* (0) absent; (1) present. CI = 0.5; RI = 0.75.

Head and Body (Fig. 4):

- 88. *An entirely yellow male frons:* (0) absent; (1) present. CI = 1; RI = 1.
- 89. *An orange male frons with a central dark spot:* (0) absent; (1) present. CI = 1; RI = 1.
- 90. *Dorsum of male abdomen:* (0) yellow to orange; (1) blackish. CI = 0.5; RI = 0.88.
- 91. *If dorsum of male abdomen yellow to orange (90:0), dorsal spots or bands:* (0) present; (1) absent. CI = 0.25; RI = 0.82.
- 92. *Transverse dark bands along dorsum of male abdomen:* (0) present; (1) absent. CI = 0.5; RI = 0.5.
- 93. *Pale scaling on ventral surface of male abdomen:* (0) yellowish; (1) whitish. CI = 0.5; RI = 0.9.

The recently described *A. francozi* Gallard, 2017, is assigned a “?” because the ventral surface of the male abdomen was not available for examination.

Male genitalia (Fig. 5):

- 94. *A posterior process at anterodorsal corner of valvae:* (0) absent; (1) present. CI = 1; RI = 1.

Argyrogrammana pulchra (Talbot, 1929) is assigned a “?” for characters 94 to 110 because the male genitalia were not available for examination.

- 95. *If a posterior process at anterodorsal corner of valvae present (94:1), process:* (1) very short; (2) long. CI = 1; RI = 1.
- 96. *A short, inwardly curved, and dorsoventrally flattened lower posterior process at ventral margin of valvae with a straight margin ventrally and a deep notch dorsally:* (0) absent; (1) present. CI = 1; RI = 1.
- 97. *A triangular, distally finely pointed and upturned upper posterior valve process:* (0) absent; (1) present. CI = 1; RI = 1.
- 98. *A broad, distally rounded and upturned, inwardly tilted upper posterior valve process:* (0) absent; (1) present. CI = 1; RI = 1.
- 99. *An upwardly and outwardly curved upper posterior valve process:* (0) absent; (1) present. CI = 1; RI = 1.
- 100. *A transtilla consisting of broad lateral bands posteroventrally that are only connected dorsally, with no medial sclerotization posteroventrally:* (0) absent; (1) present. CI = 1; RI = 1.
- 101. *A large, upwardly curved, hook-like posterior transtilla process:* (0) absent; (1) present. CI = 1; RI = 1.
- 102. *If a large, upwardly curved, hook-like posterior transtilla process present (101:1), transtilla:* (1) relatively short (i.e., not extending to dorsal margin of valvae in lateral view and having approximately half of its length beyond posterior margin of valvae in ventral view); (2) relatively long (i.e., extending to or beyond dorsal margin of valvae in lateral view and having approximately two-thirds of its length beyond posterior margin of valvae in ventral view). CI = 1; RI = 1.



Fig. 4. Characters of the head and body in *Argyrogrammana* (characters 88-89 male frons, 90-92 dorsal male abdomen, 93 ventral male abdomen). Each box depicts one or more characters (numbered at top left), with the relevant character state(s) indicated by an arrow. Heads/bodies in character boxes: 88 = *A. stilbe*; 89 = *A. willmotti*; 90-93: 90(0) = *A. nurtia*; 90(1) = *A. saphirina*; 91(0) = *A. aparamilla*; 92(0) = *A. janiceae*; 93(0) = *A. willmotti*; 93(1) = *A. pacs*. Bodies not to scale.

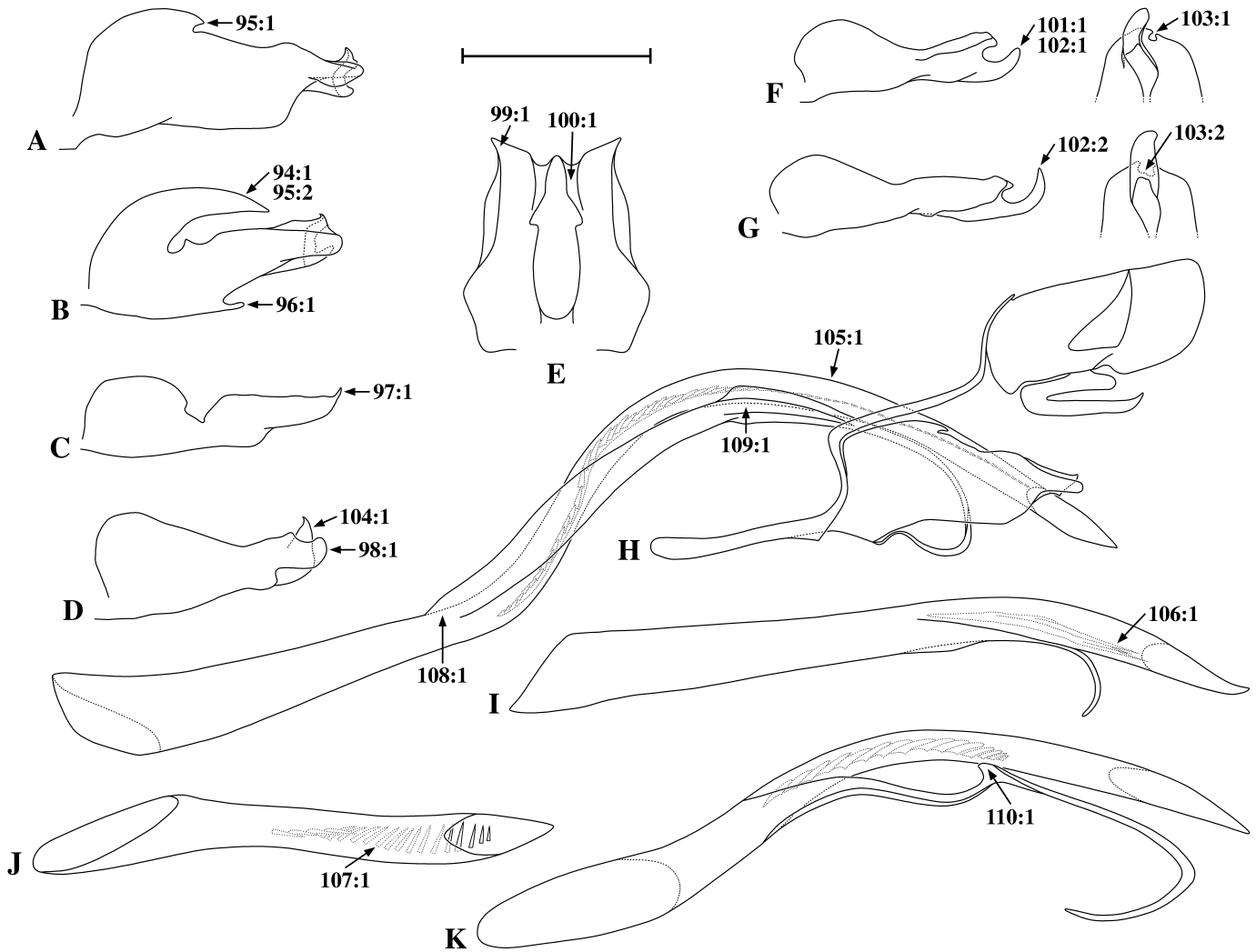


Fig. 5. Characters of the male genitalia in *Argyrogrammana* (characters 94-104 valvae and transtilla, 105-110 aedeagus, cornuti, and pedicel). Relevant character states are indicated by an arrow. A-D, F-G (left): valve in lateral view; E: valvae in ventral view; F-G (right): distal tip of valvae in ventral view; H: entire genital capsule in lateral view; I, K: aedeagus and pedicel in lateral view; J: aedeagus in dorsal view. A = *A. callaina*; B = *A. aparamilla*; C = *A. stilbe*; D = *A. smalli*; E = *A. chicomendesi*; F = *A. eura*; G = *A. vespertina*; H = *A. maryanneae*; I = *A. aurora*; J = *A. chicomendesi*; K = *A. caelestina*. Scale bar = 0.5 mm.

103. If a large, upwardly curved, hook-like posterior transtilla process present (101:1), gap between valve tips in ventral view: (1) relatively narrow (i.e., approximately same width as valve tip in ventral view); (2) relatively broad (i.e., approximately twice as wide as valve tip in ventral view). CI = 1; RI = 1.
104. A large vertically semicircular transtilla process: (0) absent; (1) present. CI = 1; RI = 1.
105. A prominently sigmoidal aedeagus: (0) absent; (1) present. CI = 1; RI = 1.
106. A bundle of thin, straight, parallel "hair"-like aedeagal cornuti: (0) absent; (1) present. CI = 1; RI = 1.
107. A twisted series of medium length spine-like aedeagal cornuti that in posterior half (on uneverted vesica) form a "comb"-like pattern, with widely spaced cornuti perpendicular to aedeagus: (0) absent; (1) present. CI = 1; RI = 1.
108. A pedicel that joins aedeagus dorsally: (0) absent; (1) present. CI = 1; RI = 1.
109. A pedicel that laterally broadens medially, with heavy sclerotization posteriorly and weak sclerotization anteriorly: (0) absent; (1) present. CI = 1; RI = 1.
110. A pedicel that laterally broadens medially, is significantly constricted in width anteriorly (to no more than one-third width in ventral view), extends ventrally or even posteriorly anterior to constriction (creating a concave shape), and is displaced to left of aedeagus: (0) absent; (1) present. CI = 0.5; RI = 0.5.

DISCUSSION

Cladograms: Stichel (1910) proposed the generic name *Argyrogramma* for a small group of species that had previously largely been treated in *Charis* Hübner, [1819], with *A. stilbe* (Godart, [1824]) as its type species, but as this name was a homonym of Hübner's noctuid moth genus, Strand (1932) introduced the replacement name *Argyrogrammana*. Stichel (1910-11, 1930-31) subsequently recognized 13 (first catalog) to 17 (second catalog) species in the genus in three species groups: the Stilbiformes for the species with males that have yellow to orange and dark-spotted wings (including the misplaced riodinines *Baeotis sulphurea* (R. Felder, 1869) and *B. macularia* (Boisduval, 1870)), the Bariniformes for the species with males that have yellow to orange scaling at the base of both dorsal wings and one or more distal blue patches on the dorsal forewing, and the Trochiliiformes for the species with males that have blue bands across one (*A. glaucopis* (Bates, 1868)) or both dorsal wings. When reviewing the genus

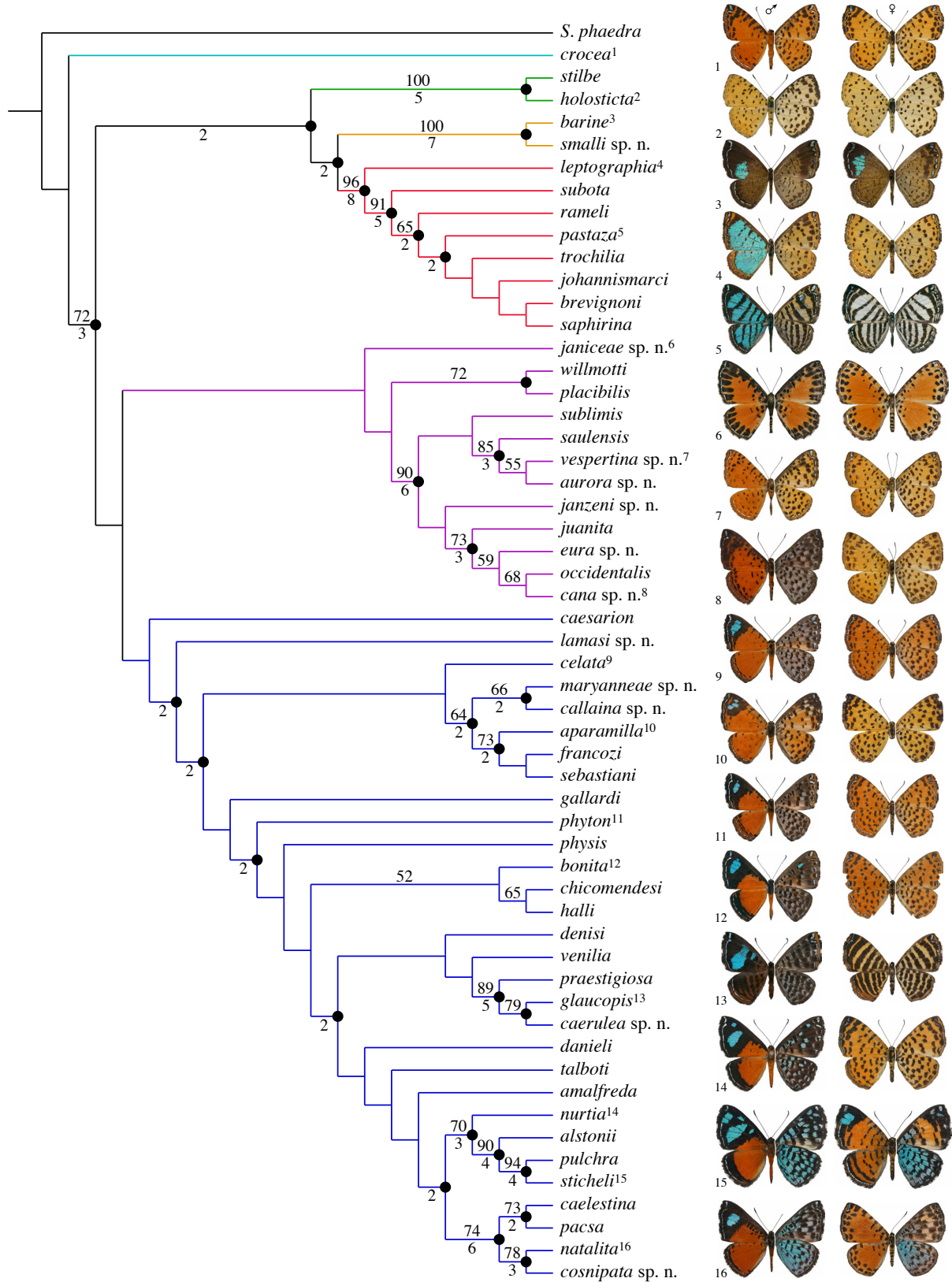


Fig. 6. Single most parsimonious cladogram resulting from the heuristic analysis of 110 morphological characters for all 55 species of *Argyrogrammana*. The six recognized species groups are indicated through the use of colored branches: turquoise = *crocea* group (1 species); green = *stilbe* group (2); yellow = *barine* group (2); red = *trochilia* group (8); purple = *occidentalis* group (12); and blue = *amalfreda* group (30). Branch support is shown in the form of bootstrap values higher than 50 above branches and decay index values higher than one below branches. The best-supported nodes, with a bootstrap value of 70 or higher and/or a decay index value of two or higher, are indicated with a black circle. Both sexes (male on left, female on right) of exemplars from each species group are shown to the right of the cladogram (at two-thirds life size), with numbers (1-16) matching images to species names.

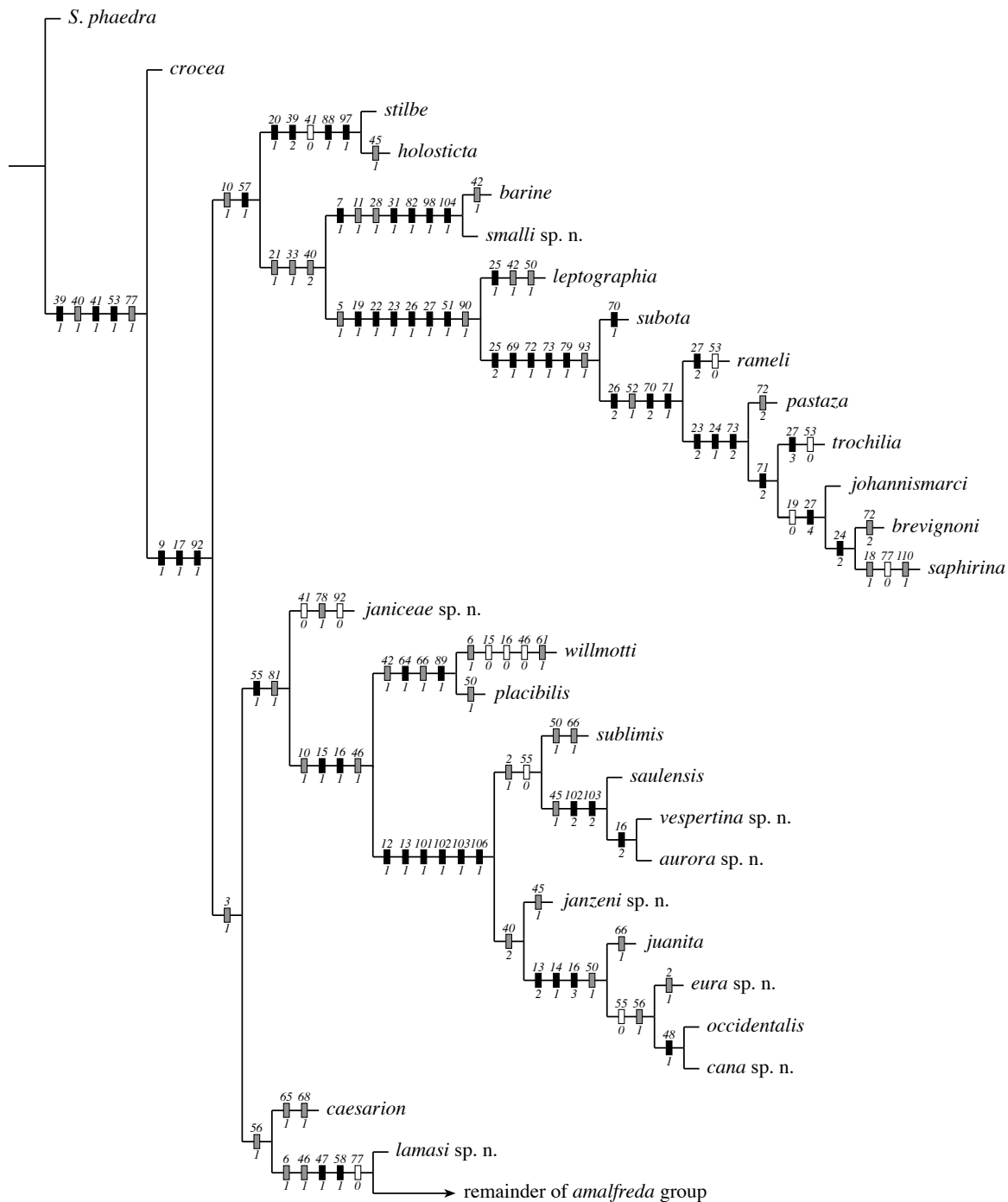


Fig. 7. Top half of cladogram from Fig. 6 (*Argyrogrammana crocea*, *stilbe*, *barine*, *trochilia*, and *occidentalis* groups, and basal two taxa in *amalfreda* group) illustrating the distribution of character states. Black bars indicate unique apomorphies, gray bars homoplasious apomorphies, and white bars reversals.

Argyrogrammana, Hall & Willmott (1995, 1996a) recognized 31 species in the same three species groups, which were referred to as the *stilbe*, *amalfreda*, and *trochilia* complexes, and used to clarify communication about the group rather than imply monophyly. These groups were used in much the same way as Stichel had used them, although *A. venilia* was treated in the *amalfreda* complex, based on its male ventral wing pattern, rather than the *stilbe* and *trochilia* complexes (as the female-based name *venilia* and the synonymous male-based name *boyi* Röber, 1926, respectively), and *A. glaucopis*

and *A. praestigiosa* (Stichel, 1929) were recognized as closely related species exhibiting wing pattern elements common to both the *amalfreda* and *trochilia* complexes, rendering their phylogenetic affinities uncertain.

Based on the results of the phylogenetic analysis presented here, I adopt a revised species group classification for *Argyrogrammana*, recognizing six morphologically and/or phenotypically distinct monophyletic species groups. The hypothesized phylogenetic relationships among them are as follows: (*crocea* group ((*stilbe* group (*barine* group + *trochilia*

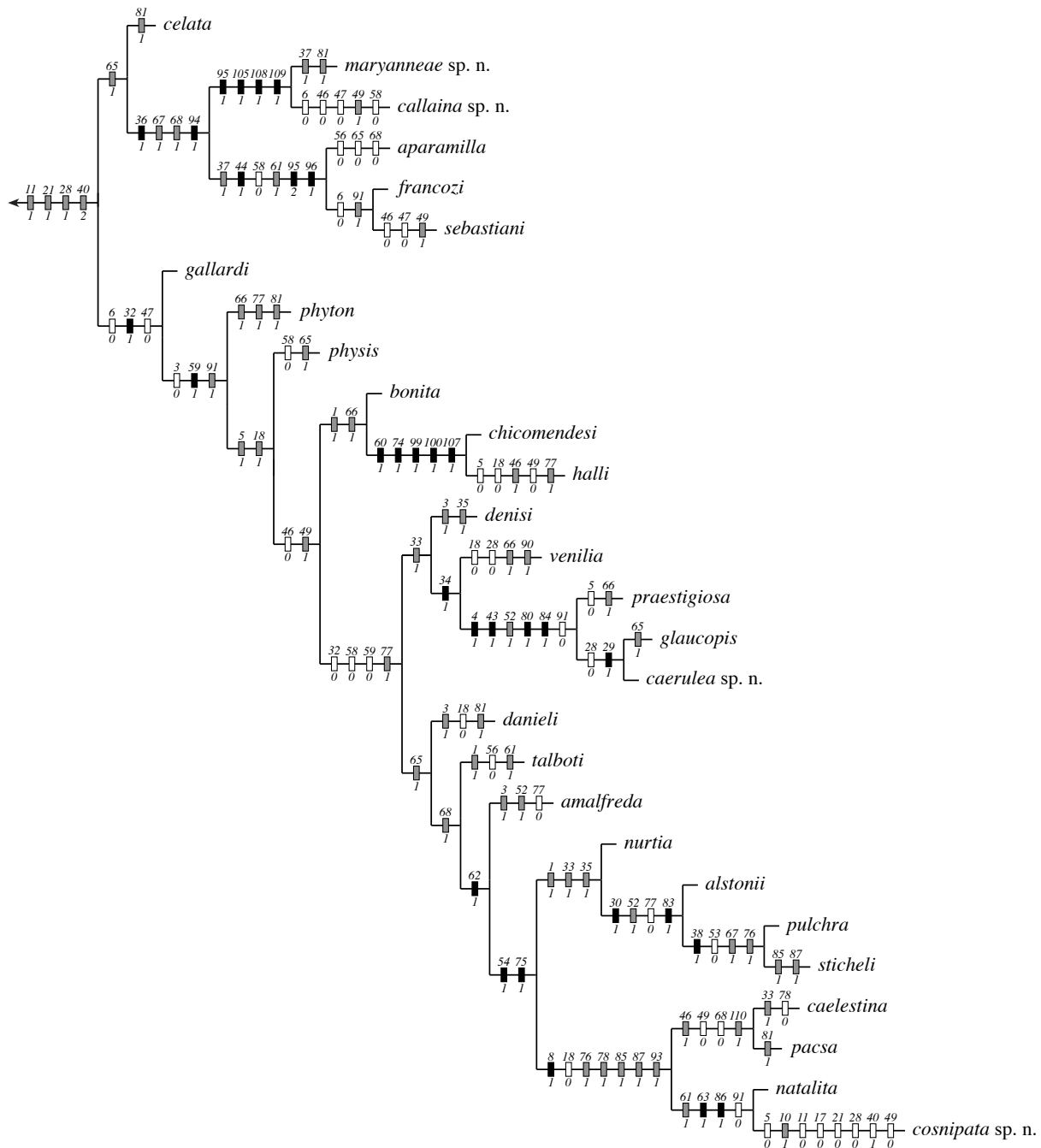


Fig. 8. Bottom half of cladogram from Fig. 6 (derived majority of *Argyrogrammana amalfreda* group) illustrating the distribution of character states. Black bars indicate unique apomorphies, gray bars homoplasious apomorphies, and white bars reversals.

group)) + (*occidentalis* group + *amalfreda* group))). The *stilbe* complex of prior usage is found here to be polyphyletic, and to contain several basal lineages, with species distributed in the monotypic *crocea* group, *stilbe* group (2 species), and *occidentalis* group (12 species). The *amalfreda* complex is found here to be a monophyletic *amalfreda* group (30 species) once the distantly related *A. barine* (Staudinger, 1887) is removed to the *barine* group (2 species). The *trochilia* complex is also found here to be a monophyletic *trochilia* group (8 species) once *A. glaucopis* is removed. This analysis shows

that *A. glaucopis* and *A. praestigiosa* belong in the derived half of the *amalfreda* group, with the banded ventral pattern of the males and orange-banded pattern of the females having evolved independently from similar wing patterns in *trochilia* group species.

The characters supporting the six species groups are shown in Table 2. Note that although the *crocea* group has no apomorphies, characters 9, 17, and 92 are unique or nearly unique symplesiomorphies within the genus (character 17 is also present in *A. cosnipata* Hall, 2023, and 92 in *A. janiceae*

Ahrenholz & Hall, 2023) that would be apomorphies if a different outgroup taxon were used. The characters supporting each of the nodes within the polytypic species groups are discussed in the series of associated faunal review papers, with *occidentalis* group characters discussed primarily in Hall & Willmott (2023) but also Hall *et al.* (2023a), *trochilia* group characters discussed in Hall & Willmott (2023) and Hall *et al.* (2023a), and *amalfreda* group characters discussed primarily in Hall *et al.* (2023b) but also Hall & Willmott (2023) and Hall *et al.* (2023a).

Branch support for the smaller and more morphologically and phenotypically homogeneous *stilbe*, *barine*, and *trochilia* groups is very strong, with bootstrap values ranging from 96 to 100 and decay index values from 5 to 8. Branch support in the derived half of the *trochilia* group is weak (i.e., bootstrap values below 50 and decay index values of 1) because of a paucity of characters that are predominantly multistate rather than binary. The three species groups form a single clade, with intergroup branch support that is moderately good (decay index values of 2). The *barine* group + *trochilia* group clade

is best characterized by its males universally having a blue postdiscal patch on the dorsal forewing that extends to the anal margin, a character (see 33) that occurs elsewhere in the genus in only a handful of derived *amalfreda* group species. The clade containing all three of the *stilbe*, *barine*, and *trochilia* groups is uniquely and universally characterized by its males having widespread yellow to white scaling across the ventral forewing (character 57). Branch support for the larger and more heterogeneous *occidentalis* and *amalfreda* groups is weak, but mostly because of the inclusion of unusual basal taxa. The *occidentalis* group is composed of a very strongly supported core *A. occidentalis* clade of nine species (bootstrap value of 90 and decay index value of 6), a bitypic *A. placibilis* clade whose apparent sister relationship to the *A. occidentalis* clade generates weak branch support because of probable character reversals in *A. willmotti* Dolibaina & Dias, 2015, and a highly autapomorphic *A. janiceae* that was recovered as sister to the two other clades and is tentatively included in the group. The core of the *amalfreda* group, excluding *A. caesarion* Lathy, 1958, has moderately good branch support (decay index value

Table 2. A list of synapomorphies for the six species groups recognized here in *Argyrogrammana*. All characters are unique for and universal within each group, unless indicated otherwise. Wing pattern characters that do not reference a particular sex may apply to either sex. The numbers in brackets after each species group represent the number of species it contains, and those after each character refer to the character number and state in the phylogenetic analysis.

Species groups	Synapomorphies
<i>crocea</i> group [1]	<ul style="list-style-type: none"> • None
<i>stilbe</i> group [2]	<ul style="list-style-type: none"> • Yellow dorsal wings in males [20:1] (Fig. 1) • A greenish-gold metallic submarginal line on dorsal wings [39:2] (Fig. 1) • A forewing fringe with broad sections of prominent white scaling in all distal cells [41:0] (Fig. 1) (also <i>A. janiceae</i> in <i>occidentalis</i> group) • An entirely yellow frons in males [88:1] (Fig. 4) • A triangular, distally finely pointed and upturned upper posterior valve process in male genitalia [97:1] (Fig. 5C)
<i>barine</i> group [2]	<ul style="list-style-type: none"> • Yellow-brown scaling across base of dorsal wings in males [7:1] (Fig. 1) • A greenish-blue medial patch extending to anal margin on dorsal forewing in males [31:1] (Fig. 1) • Blue presubmarginal spots on dorsal forewing in females [82:1] (Fig. 3) • A broad, distally rounded and upturned, inwardly tilted upper posterior valve process in male genitalia [98:1] (Fig. 5D) • A large vertically semicircular transtilla process in male genitalia [104:1] (Fig. 5D)
<i>trochilia</i> group [8]	<ul style="list-style-type: none"> • A medially disjointed, isolated yellowish submarginal band on dorsal forewing in males [19:1] (Fig. 1) (lost in clade of <i>A. johannismarci</i>, <i>A. brevignoni</i>, and <i>A. saphirina</i>) • Five diagonal blue bands on dorsal forewing in males [22:1] (Fig. 1) • Five blue bands on dorsal hindwing in males [51:1] (Fig. 1) • White to yellow bands on ventral forewing in males [69:1] (Fig. 2) (not <i>A. leptographia</i>) • White to pale yellow diagonal bands on dorsal forewing in females [79:1] (Fig. 3) (not <i>A. leptographia</i>) • A dorsally blackish abdomen in males [90:1] (Fig. 4) (also <i>A. venilia</i> in <i>amalfreda</i> group) • Whitish ventral scaling on abdomen in males [93:1] (Fig. 4) (not <i>A. leptographia</i>; also <i>amalfreda</i> group clade of <i>A. caelestina</i>, <i>A. pacsa</i>, <i>A. natalita</i>, and <i>A. cosnipata</i>)
<i>occidentalis</i> group [12]	<ul style="list-style-type: none"> • A dark submarginal band more or less entirely separated by yellow to orange distal scaling from metallic submarginal line on dorsal forewing in males [15:1] (Fig. 1) (not <i>A. janiceae</i> and <i>A. willmotti</i>) • A predominantly grayish discal cell with orange scaling across cells below on ventral forewing in males [55:1] (Fig. 2) (lost in clade of <i>A. sublimis</i>, <i>A. saulensis</i>, <i>A. vespertina</i>, and <i>A. aurora</i>, and clade of <i>A. eura</i>, <i>A. occidentalis</i>, and <i>A. cana</i>) • A dark submarginal band more or less entirely separated by yellow to orange distal scaling from metallic submarginal line on dorsal forewing in females [81:1] (Fig. 3) (also at least <i>A. celata</i>, <i>A. maryanneae</i>, <i>A. phyton</i>, <i>A. danieli</i>, and <i>A. pacsa</i> in <i>amalfreda</i> group)
<i>amalfreda</i> group [30]	<ul style="list-style-type: none"> • Widespread orange scaling across dorsal wings with blue scaling on dorsal forewing in males [see 28:1] (Fig. 1) (not <i>A. caesarion</i> and <i>A. lamasi</i> [no blue], and lost in <i>A. venilia</i> [no orange] and <i>A. cosnipata</i> [no blue]) • Widespread gray to blue scaling across ventral forewing in males [56:1] (Fig. 2) (lost in <i>A. aparamilla</i> and <i>A. talboti</i>; also <i>occidentalis</i> group clade of <i>A. eura</i>, <i>A. occidentalis</i>, and <i>A. cana</i>)

of 2), and only five of these 29 species lack one of the two group synapomorphies listed in Table 2. In the case of *A. lamasi* Ahrenholz & Hall, 2023, *A. aparamilla* Hall & Willmott, 1995, and *A. cosnipata*, their male genital morphology unequivocally links them to close relatives in the group, and in *A. venilia* the preponderance of wing pattern data strongly suggest that it is a derived member of the group. Only the unusually patterned *A. talboti* Brévignon & Gallard, 1998, which has no clear extant relatives and a potentially unique geography and ecology within the genus (see Hall *et al.*, 2023b), engenders some genuine uncertainty as to its gross phylogenetic placement. The uniquely dorsally red *A. caesarion* was included in the *amalfreda* group by Hall & Willmott (1995), and it was recovered here as sister to the core *amalfreda* group. It is tentatively included here in the *amalfreda* group, based on its gray ventral wings, although it is possible that *A. caesarion* occupies an even more basal position within the genus. Branch support in the middle of the *amalfreda* group is weak because of a paucity of characters that are mostly homoplasious. The hypothesized sister relationship between the *occidentalis* and *amalfreda* groups is supported by just a single but significant character, a medially divided dark spot toward the base of cell Cu_2 (below the middle of the discal cell) on the dorsal forewing in males (character 3), which occurs in all *occidentalis* group species and across the basal third of the *amalfreda* group (as well as in three other more derived species) but nowhere else in the genus.

Biogeography: The generation of a well-resolved phylogenetic hypothesis for *Argyrogrammana* allows a more detailed discussion on the biogeography of the genus than has previously been possible. Figure 9 melds the available phylogenetic and geographic data for the genus, and forms the basis for this discussion. It is notable that the apparently most basal extant members of *Argyrogrammana*, namely *A. crocea* (Godman & Salvin, 1878) (Transandean), *A. stilbe/A. holosticta* (Godman & Salvin, 1878) (Amazonian/Transandean), *A. janiceae* (east Andean), and *A. caesarion* (southeast Brazilian) together occupy the entire known geographic range of the genus from southern Mexico to southeastern Brazil. This observation suggests that *Argyrogrammana* had a very broad Neotropical distribution even in the very earliest stage of its diversification, which molecular clock methods have estimated to be between 25 and 45 million years ago (Espeland *et al.*, 2015; Seraphim *et al.*, 2018). Colonization and speciation (except in the case of *A. physis* (Stichel, 1911)) from Amazonia into the Transandean region, presumably around the northern margin of the Andes, has been a frequent event, apparently occurring twice to form the *crocea* and *barine* groups, once in the *stilbe*

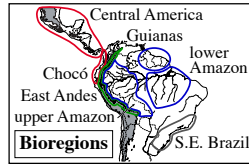
group (*A. holosticta*), and twice each in the *trochilia* group (*A. leptographia* (Stichel, 1911) and *A. saphirina* (Staudinger, 1887)), *occidentalis* group (*A. vespertina* Hall & Willmott, 2023, and the *A. occidentalis* subclade) and *amalfreda* group (*A. physis* and *A. pulchra*). The only example of this process in reverse, Amazonian colonization and speciation from the Transandean region, is the *occidentalis* group species *A. eura* Hall, 2023, which is restricted to neighboring northeastern South America.

Overall, 31% of species in the genus appear to be allo- or parapatrically distributed with respect to their closest relatives, which is about average when compared to the figures for the other large riodinid groups for which there are phylogenetic revisions (summarized in Hall (2018)). However, these species are not evenly phylogenetically distributed across the genus, with the highest rates of sympatry among close relatives being in the *amalfreda* and *trochilia* groups, which overwhelmingly contain Amazonian species (90% and 75%, respectively), and the lowest rates being in the other four species groups, which all contain a significant Transandean fauna (42-100%). Within lowland Amazonia, only a single sister-species pair, *A. chicomendesi* Gallard, 1995, and *A. halli* Dolibaina & Dias, 2015, has a seemingly parapatric distribution, divided between the upper and lower Amazon. In the Transandean region, two sister-species pairs seem to have parapatric distributions, *A. smalli* Hall, 2023, and *A. barine*, which are predominantly premontane species that appear to have been historically separated by the lowland forests of central Panama, and *A. occidentalis* and *A. cana* Hall & Willmott, 2023, which appear to be elevationally parapatric across the broader Chocó region. The great majority of *Argyrogrammana* species occur at lowland elevations, and only nine described species (16%) have montane-limited distributions (up to 2200 m), with most of their range above 1000 m, the aforementioned *A. cana* on the western slope of the Andes and the remainder on the east Andean slope. Speciation up into the eastern Andes from the lowlands has occurred on five separate occasions, including twice each in the *trochilia* group (*A. subota* (Hewitson, 1877) and *A. pastaza* Hall & Willmott, 1996) and *occidentalis* group (*A. janiceae* and *A. aurora* Hall & Willmott, 2023), and once in the *amalfreda* group (the *A. natalita* clade). In most of these events, colonization has happened from lowland Amazonia, but, in the case of *A. aurora*, it seems to have happened from the Transandean lowlands, presumably through the inter-Andean valleys of Colombia. Only in the *amalfreda* group (*A. natalita* clade) has there been a subsequent species radiation within the eastern Andes. The sister-species pair of *A. caelestina* Hall & Willmott, 1995, and *A. pacsa* Hall & Willmott, 1998, is

Fig. 9 (p. 15, facing). Biogeographic data for *Argyrogrammana* overlaid onto the cladogram from Fig. 6 (with the six species groups delineated by boxes). The symbols at each cladogram node indicate whether the species in the two clades are sympatric or allo/parapatric, and, if the latter, whether they are geographically or elevationally allo/parapatric. Montane-limited species that have the majority of their elevational range above 1000 m are indicated with an asterisk. To the right of the cladogram, the biogeographic subregion(s) occupied by each species is indicated with a dark-color-shaded box for recorded occurrence and a pale-color-shaded box for expected occurrence (only necessary for the lower Amazon). The colors on the cladogram branches, in the bioregions map, and in the subregional boxes reference the broader biogeographic regions (red = Transandean region; green = eastern Andes; blue = Amazonia; and gray = southeastern Brazil). On the far right, the list of countries that each species has been recorded from is based on material examined in the 27 personally visited collections listed in Hall (2018), augmented by the literature (Gus refers to the recorded presence of a species in two or more of the Guianan countries).

Clade members:

- Sympatric
- Geographically allo- or parapatric;
- Elevationally parapatric;
- or both
- * Montane



Central America

Chocó

East Andes

Upper Amazon

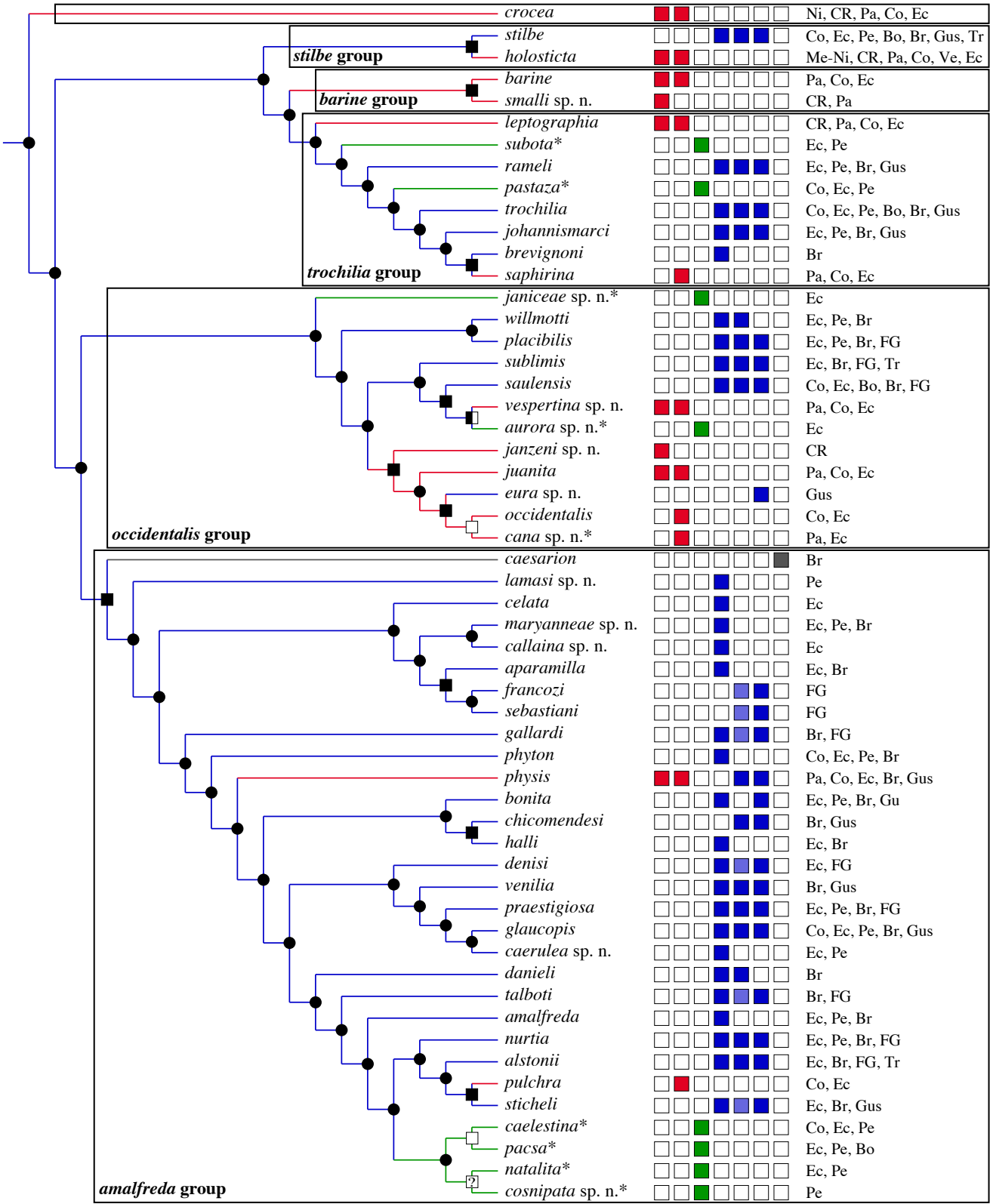
Lower Amazon

Guianas

Southeast Brazil

Country codes:

Me = Mexico Pe = Peru
 Ni = Nicaragua Bo = Bolivia
 CR = Costa Rica Br = Brazil
 Pa = Panama Gu = Guyana
 Ve = Venezuela FG = Fr. Guiana
 Co = Colombia Gus = Guianas
 Ec = Ecuador Tr = Trinidad



Subregional totals	9	11	8	29	22	2	1
Subregional endemics	2	4	8	10	0	1	1
Regional totals / Regional endemics	13/12		34/33				

elevationally parapatric, suggesting a similar pattern of repeated upward parapatric speciation that was reported for the riodinid genus *Ithomiola* C. & R. Felder, 1865 (Hall, 2005a,b), in this case from a lowland ancestor similar to *A. amalfreda* (Staudinger, 1887) and *A. nurtia*. The sister-species pair of *A. natalita* and *A. cosnipata* may also be elevationally parapatric in the southern Andes, but there are currently insufficient elevational data to verify this hypothesis. The two pairs are partially sympatric, with *A. pacsá* and *A. natalita* geographically widespread, but *A. caelestina* known only from the north to central Andes and *A. cosnipata* from the southern Andes. This distribution pattern is suggestive of a geographically allopatric speciation event within the eastern Andes for the ancestor of the two pairs followed by vertical speciation within potentially both pairs and subsequent partial dispersal. Dispersal to more southerly latitudes by the lower montane *A. caelestina* may have been impeded by increased competition from lowland congeners resulting from a climate-induced lowering and/or contracting elevational range, and, conversely, dispersal north to more equatorial latitudes by the upper montane *A. cosnipata* may have been prevented by habitat unsuitability resulting from a rising elevational range.

Argyrogrammana diversity is overwhelmingly concentrated in the Amazon, where 76% of species occur (42), with eight species confined to the eastern Andes and 34 primarily distributed in lowland Amazonia. The upper Amazon is the most diverse subregion with 29 species (recorded and expected), and the lower Amazon and Guianas are both expected to harbor 22 species (only 16 recorded for the lower Amazon). Fourteen lowland Amazonian species (41%) are widespread throughout the region, while 11 species (32%) seem likely to be endemic to the upper Amazon (including *A. bonita* Hall & Willmott, 1995, which ranges to southern Guyana), two (6%) to the combined upper and lower Amazon, six (18%) to the combined lower Amazon and Guianas (including *A. venilia* and *A. talboti*, which range to the edge of western Amazonia but apparently not throughout it, and *A. physis*, which also ranges west of the Andes), one (3%) to the Guianas, and none to the lower Amazon. Thirteen species occur in the Transandean region (24%), with diversity peaking in the Chocó (11) and tapering abruptly north through Central America. Only *A. holosticta* is known to occur north of Nicaragua. Incredibly, for such a species-rich genus, only a single species is known from the Atlantic Forest region of southeastern Brazil, which highlights the intolerance by *Argyrogrammana* species of the drier Cerrado and Caatinga habitats that separate the region from similarly wet Amazonian forests. The restriction of virtually all *Argyrogrammana* species to not only wet but also relatively undisturbed forest habitats (*A. talboti* might be an exception, as discussed by Hall *et al.* (2023b)), as well as their relatively weak flight capabilities and proclivity for shady microhabitats, explains why a very unusually high 98% of species are confined to just one of the three major biogeographic regions. With recent morphological and molecular study resulting in the splitting of *A. stilbe*/*A. holosticta* and *A. saulensis* Gallard, 2008/*A. vespertina* (Hall & Willmott, 2023), which were both previously regarded as widespread species, *A. physis* is now the only species in the genus known to range between the Transandean and Amazonian regions. At the national level, Ecuador has by

far the highest number of recorded *Argyrogrammana* species (41), followed by Brazil (27), Peru, French Guiana (both 21), and Colombia (17). However, once collection-effort biases are minimized through the use of predicted range data, the likely country rankings for expected numbers of species are found to be as follows: Ecuador and Colombia first (both c. 44), followed by Brazil and Peru (both c. 35), Bolivia (c. 33), and the Guianan countries and Venezuela (all c. 21-22). These data imply *Argyrogrammana* recording rates of perhaps 100% for French Guiana and 93% for Ecuador, while on the other end of the spectrum only about 39% for Colombia, 9% for Bolivia, and 5% for Venezuela. For the former category of countries, such high rates of faunal knowledge have resulted from decades of dedicated, geographically thorough, and specialist study by teams of lepidopterists. For the latter category of countries, even if some additional untallied species records exist in their national and local collections, and predicted species numbers for the most biogeographically peripheral countries are slightly overestimated, it is clear that inventory work there on rare butterfly genera such as *Argyrogrammana* is still in its infancy.

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APPENDIX

Synonymic checklist for the genus *Argyrogrammana* (55 species). Single dashes represent subspecies, and double dashes represent synonyms. The 12 new species (n. sp.) are described, and the taxonomic changes (n. syn., n. stat., and rev. stat.) made and justified, in the associated papers by Hall (2023), Hall & Willmott (2023), and Hall *et al.* (2023a,b).

<i>Argyrogrammana</i> Strand, 1932	<i>natalita</i> Hall & Willmott, 1995
-- <i>Argyrogramma</i> Stichel, 1910	<i>nurtia</i> (Stichel, 1911)
<i>alstonii</i> (Smart, 1979)	-- <i>ludibunda</i> Brévignon & Gallard, 1995 n. syn.
<i>amalfreda</i> (Staudinger, 1887)	<i>occidentalis</i> (Godman & Salvin, 1886)
<i>aparamilla</i> Hall & Willmott, 1995	<i>pacsa</i> Hall & Willmott, 1998
<i>aurora</i> Hall & Willmott, 2023 n. sp.	<i>pastaza</i> Hall & Willmott, 1996
<i>barine</i> (Staudinger, 1887)	<i>physis</i> (Stichel, 1911)
<i>bonita</i> Hall & Willmott, 1995	<i>phyton</i> (Stichel, 1911) n. stat.
<i>brevignoni</i> Dolibaina & Dias, 2015	<i>placibilis</i> (Stichel, 1910)
<i>caelestina</i> Hall & Willmott, 1995	<i>praestigiosa</i> (Stichel, 1929)
<i>caerulea</i> Hall, 2023 n. sp.	-- <i>sonazul</i> P. Jauffret & Martins, 2006 n. syn.
<i>caesarion</i> Lathy, 1958	<i>pulchra</i> (Talbot, 1929)
<i>callaina</i> Hall & Ahrenholz, 2023 n. sp.	<i>rameli</i> (Stichel, 1930)
<i>cana</i> Hall & Willmott, 2023 n. sp.	-- <i>boyi</i> (Meier-Ramel, 1928), preocc.
<i>celata</i> Hall & Willmott, 1995	<i>saphirina</i> (Staudinger, 1887)
<i>chicomendesii</i> Gallard, 1995	<i>saulensis</i> Gallard, 2008
<i>cosnipata</i> Hall, 2023 n. sp.	-- <i>tunari</i> Gallard, 2008 n. syn.
<i>crocea</i> (Godman & Salvin, 1878)	<i>sebastiani</i> Brévignon, 1995
<i>danieli</i> P. Jauffret & Martins, 2006	<i>smalli</i> Hall, 2023 n. sp.
<i>denisi</i> Gallard, 1995	<i>sticheli</i> (Talbot, 1929)
<i>aura</i> Hall, 2023 n. sp.	<i>stilbe</i> (Godart, [1824])
<i>francozi</i> Gallard, 2017	-- <i>perone</i> (Westwood, 1851)
<i>gallardi</i> Dolibaina & Dias, 2015	-- <i>orientalis</i> Brévignon & Gallard, 1995
<i>glaucopis</i> (Bates, 1868)	<i>sublimis</i> Brévignon & Gallard, 1995
-- <i>virgata</i> Brévignon & Gallard, 1995 n. syn.	-- <i>iracyi</i> P. & J. Jauffret, 2007 n. syn.
<i>halli</i> Dolibaina & Dias, 2015	<i>subota</i> (Hewitson, 1877)
<i>holosticta</i> (Godman & Salvin, 1878) rev. stat.	<i>talboti</i> Brévignon & Gallard, 1998
<i>janiceae</i> Ahrenholz & Hall, 2023 n. sp.	- <i>naranjilla</i> Hall & Furtado, 1999
<i>janzeni</i> Hall, 2023 n. sp.	<i>trochilia</i> (Westwood, 1851)
<i>johannismarci</i> Brévignon, 1995	<i>venilia</i> (Bates, 1868)
<i>juanita</i> (Staudinger, 1887) rev. stat.	-- <i>boyi</i> (Röber, 1926)
<i>lamasi</i> Ahrenholz & Hall, 2023 n. sp.	-- <i>amazonica</i> (Meier-Ramel, 1928)
<i>leptographia</i> (Stichel, 1911)	<i>vespertina</i> Hall & Willmott, 2023 n. sp.
-- <i>magdalena</i> Constantino <i>et al.</i> , 2012 n. syn.	<i>willmotti</i> Dolibaina & Dias, 2015
<i>maryanneae</i> Ahrenholz & Hall, 2023 n. sp.	

Immature stages of *Argyrogrammana glaucopis* (Bates) and the new sister species *A. caerulea* (Lepidoptera: Riodinidae: Symmachiini)

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Abstract: The immature stages of two species in the *Argyrogrammana amalfreda* group (Riodinidae: Symmachiini) are described and illustrated for the first time. Immatures of both species, *A. glaucopis* (Bates, 1868) and the here-described sister species *A. caerulea* Hall, n. sp., were found on *Symphonia globulifera* Linnaeus f. (Clusiaceae) in separate lowland rainforest localities in eastern Ecuador. The current state of knowledge on *Argyrogrammana* food plants and immature stages is summarized.

Key words: caterpillars, eggs, Neotropics, Peru, pupae, species description, taxonomy.

INTRODUCTION

The Neotropical riodinid genus *Argyrogrammana* Strand, 1932 (Symmachiini) is now known to be one of the largest in the family, containing at least 55 species (Hall, 2023). However, because most species are rare, with more than half described in just the last 30 years (e.g., Brévignon & Gallard, 1995; Hall & Willmott, 1995, 1996, 2023; Dolibaina *et al.*, 2015; Hall *et al.*, 2023a,b), *Argyrogrammana* food-plant and immature-stage data remain limited. To date, such information exists for only four species, belonging to four of the six species groups proposed by Hall (2023), as summarized in Table 1. Robbins & Aiello (1982) published the first early-stage data for *Argyrogrammana* in a paper on lycaenid and riodinid rearings in Panama. They reported finding a caterpillar of *A. crocea* (Godman & Salvin, 1878) (*crocea* group) on *Garcinia intermedia* (Pittier) (originally cited under the synonym *Rheedia edulis* (Seemann)), a medium-sized primary forest tree in the family Clusiaceae, and provided a brief description of the mature caterpillar and pupa. DeVries *et al.* (1994) subsequently reported food plants for *A. trochilia* (Westwood, 1851) (*trochilia* group) from eastern Ecuador that were also in the Clusiaceae (*Garcinia* L. and *Chrysochlamys* Poeppig (under *Tovomitopsis* Planchon & Triana, which MBG (2022) treats as a junior synonym)). The mature caterpillar and pupa were later briefly described by DeVries (1997) (under the species account for *A. leptographia* (Stichel, 1911)), and photographs of these early stages from French Guiana, on an unidentified Clusiaceae species, were published by Gallard (2017). Janzen & Hallwachs (2009-22), through their Costa Rican caterpillar-rearing-project website, have provided the most significant trove of *Argyrogrammana* food-plant records. Additional records are given for *A. crocea*, in the genera *Clusia* L. (Clusiaceae) and *Calophyllum* L. (long

included within the Clusiaceae but more recently placed in the separate closely related family Calophyllaceae (APG, 2009)), and the same *Calophyllum* species is also reported as the food plant for the newly described *A. janzeni* Hall, 2023 (*occidentalis* group) (Hall & Willmott, 2023). Somewhat surprisingly, the food-plant record reported by Janzen & Hallwachs (2009-22) for *A. holosticta* (Godman & Salvin, 1878) (a *stilbe* group taxon returned to species status by Hall & Willmott (2023)) is *Mosquitoxylum* Krug & Urban, a monotypic Transandean tree genus in the Anacardiaceae, a family that belongs to a different rosid order (Sapindales) than the families Clusiaceae and Calophyllaceae (Malpighiales). It is noteworthy that the *stilbe* group forms one of the most basal clades within *Argyrogrammana*, and its members exhibit among the most divergent wing patterns in the genus, most notably uniquely possessing bright yellow rather than yellow-brown, orange, or blue male dorsal wings and gold rather than silver submarginal markings (Hall, 2023). Also, the two *stilbe* group members, along with *A. pastaza* Hall & Willmott, 1996 (*trochilia* group), are the only *Argyrogrammana* species confirmed to perch in streamside rather than hilltop microhabitats (Hall & Willmott, 1996, unpubl. data). Janzen & Hallwachs (2009-22) provide multiple photographs of the mature caterpillar and pupa of *A. crocea* and *A. holosticta*, which represent the most detailed documentation to date of *Argyrogrammana* life histories.

The purpose of this paper is twofold, to report food-plant and immature-stage data for *A. glaucopis* (Bates, 1868) and its sister species, and to describe that sister species. Knowledge of *Argyrogrammana* early stages is expanded by providing the first rearing information for the *amalfreda* group, by far the largest in the genus, as well as more complete life histories, including eggs and early instars, than have previously been published.

Table 1. A list of all known original rearing records for the genus *Argyrogrammana*, giving the species, genus (both where known), and family of food plants, the rearing location, and the original bibliographic reference(s). Plant taxonomy and the spelling of plant names follow the Missouri Botanical Garden's online Tropicos database (MBG, 2022). Note that in some instances the corrected/updated names of the taxa given here differ from those listed in the original publications. Early stage information provided by authors is indicated in the Reference section as follows: D = description of, and F = figures of, (e) egg, (c) caterpillar, and (p) pupa.

<i>Argyrogrammana</i> taxon	Plant taxon	Location	Reference
<i>crocea</i> group			
<i>A. crocea</i> (Godman & Salvin, 1878)	CLUSIACEAE		
	<i>Garcinia intermedia</i> (Pittier) Hammel, 1989	Panama	Robbins & Aiello (1982) (D:c,p)
	<i>Clusia cylindrica</i> Hammel, 1986	Costa Rica	Janzen & Hallwachs (2009-22)
	<i>Clusia quadrangula</i> Bartlett, [1907]	Costa Rica	Janzen & Hallwachs (2009-22)
	CALOPHYLLACEAE		
	<i>Calophyllum brasiliense</i> Cambessèdes, [1828]	Costa Rica	Janzen & Hallwachs (2009-22) (F:c,p)
<i>stilbe</i> group			
<i>A. holosticta</i> (Godman & Salvin, 1878)	ANACARDIACEAE		
	<i>Mosquitoxylum jamaicense</i> Krug & Urban, 1895	Costa Rica	Janzen & Hallwachs (2009-22) (F:c,p)
<i>trochilia</i> group			
<i>A. trochilia</i> (Westwood, 1851)	CLUSIACEAE		
	<i>Garcinia</i> sp.	Ecuador	DeVries <i>et al.</i> (1994) DeVries (1997) (D:c,p)
	<i>Chrysochlamys</i> sp. unidentified sp.	Ecuador French Guiana	DeVries <i>et al.</i> (1994) Gallard (2017) (D,F:c,p)
<i>occidentalis</i> group			
<i>A. janzeni</i> Hall, 2023	CALOPHYLLACEAE		
	<i>Calophyllum brasiliense</i> Cambessèdes, [1828]	Costa Rica	Janzen & Hallwachs (2009-22)
<i>amalfreda</i> group			
<i>A. glaucopsis</i> (Bates, 1868)	CLUSIACEAE		
	<i>Symphonia globulifera</i> Linnaeus f., [1782]	Ecuador	Hall (this paper) (D,F:e,c,p)
<i>A. caerulea</i> Hall n. sp.	CLUSIACEAE		
	<i>Symphonia globulifera</i> Linnaeus f., [1782]	Ecuador	Hall (this paper) (D,F:c,p)

MATERIALS AND METHODS

Standard rearing methods were employed, with caterpillars kept at approximately ambient temperatures in small plastic containers that were cleaned daily and replenished with fresh food-plant leaves as needed every two or three days. Photographs of immatures were taken using a Canon EOS 60D with an MP-E 65 mm macro lens and a Canon MR-14EX ring flash mounted on a portable copy stand. Preliminary plant identifications were made in the field using Gentry (1996) and Condit *et al.* (2011), which were later confirmed using various on-line resources, particularly the Missouri Botanical Garden's Tropicos database (MBG, 2022) and the Field Museum's Tropical Plant Guides website (FM, 1999-2022).

Morphology was studied using standard techniques, with the dissection methods used following those outlined in Hall (2018). The terminology for immature-stage structures follows Stehr (1987) and Harvey (1987), and that for male genital structures follows Klots (1956), Eliot (1973), and Harvey (1987). The nomenclature for venation follows Comstock & Needham (1898), with cells named for the vein above. *Argyrogrammana* specimens were studied in the 27 personally visited institutional and private collections listed in Hall (2018), and the type specimens or illustrations were examined for all available names.

LIFE HISTORIES

Argyrogrammana glaucopsis (Bates, 1868) (Figs. 1A-S)

Location and food plant: In February 2017, while randomly searching understory plants for butterfly caterpillars on a forested hill behind the town of Santiago, in Morona-Santiago province, eastern Ecuador (400 m) (3°02'23"S, 78°00'33"W), I found a single penultimate instar caterpillar that would later prove to be *A. glaucopsis* on *Symphonia globulifera* L. f. (rearing #1). This is a widespread Neotropical and Afrotropical forest tree species in the family Clusiaceae that is geographically and ecologically variable but currently recognized as representing the sole member of the genus outside of Madagascar (Dick *et al.*, 2003; MBG, 2022). The smallish leaves are opposite, long, narrow, thick, and shiny, with faint, parallel, closely spaced secondary veins, and exude yellow latex when damaged. Unlike similar *Garcinia* species, *S. globulifera* has an apical bud between the terminal pair of leaves. The mature tree is tall, with numerous long, above-ground stilt roots (Condit *et al.*, 2011), but in the understory at this location the plant was encountered as 1-3 m tall saplings. Approximately half a dozen such saplings were located on the top and sides of the hill, which was covered with primary forest that had been selectively logged in decades past. Potential caterpillar feeding damage was noted on one of these other plants, but no additional immature stages were located. The plant species was searched for but seemed to be absent in

the more degraded ridgetop forest that had to be traversed to access the hilltop location. In August 2018, the same hilltop *S. globulifera* plants were checked again for immature stages, and four *A. glaucopsis* eggs and three first or second instar (pre-prepenultimate) caterpillars were found on a single leaf (rearing #2). No immature stages were found during a check of the same plants in July 2021.

Egg (Figs. 1A,B): Two closely spaced pairs of small white eggs were found along the upper edge of a *S. globulifera* leaf, and faint basal remains of several hatched eggs were detected nearby. The intact eggs were probably damaged or infertile, as they never hatched during over a month of observation. The eggs are dorsoventrally flattened and tire shaped, with a rather small and deeply recessed dorsal micropylar region and prominently dimpled hexagonal chorionic sculpturing, creating the overall impression of a squashed golf ball. The two vertical sides of the hexagons are about half the length of the diagonal sides, with an aeropyle present at each corner.

Early instars (Figs. 1C-E): The three pre-prepenultimate caterpillars found with the eggs (rearing #2) were feeding on the ventral side of a leaf that was loosely overlapping another. However, the lone penultimate instar caterpillar (rearing #1) was found between two precisely overlapping leaves that had been partially silked together, a behavior also reported for other *Argyrogrammana* species (Robbins & Aiello, 1982; DeVries, 1997; Gallard, 2017). Unlike the very obvious folded leaf shelters of the HesperIIDae (e.g., Greeney & Jones, 2003; Greeney, 2009) or the semi-natural looking rolled leaf shelters of riodinid genera such as *Anteros* Hübner, [1819], and *Caria* Hübner, 1823 (e.g., DeVries, 1997; Kaminski, 2008; Mota *et al.*, 2014; Hall, unpubl. data), this *Argyrogrammana* leaf shelter was remarkably natural in appearance, resembling two leaves that had become stuck together after a rainstorm. Under laboratory rearing conditions, all caterpillars from the prepenultimate instar onwards fed between two closely appressed silked-together leaves. The caterpillars only graze the internal surface of their leaf shelters, so their feeding damage is not externally visible to predators. Because the food plant exudes a significant amount of latex when damaged, the caterpillars graze between the leaf veins, creating a distinctive pattern of windows or panels in the leaf epidermis. The early instars seem to be particularly careful, avoiding eating through even minor veins (Figs. 1C-E), whereas the later instars avoid only the more major veins (Figs. 1F,N). The latex is yellow when fresh but becomes reddish when dried (Figs. 1C,D). Because of their tight living space, traces of latex can sometimes become smeared on the caterpillars' bodies, but, at least in the case of later instars, this does not seem to be unduly harmful, with the latex being discarded in the next molt. It is noteworthy that latex-filled Clusiaceae leaves can retain their turgidity and freshness when cut from the source plant for as long as three or four weeks (when appropriately stored in a sealed high humidity environment), compared to a week or so for most collected food-plant leaves, meaning that *Argyrogrammana* caterpillars can successfully be reared through long after leaving an area where the food plant is known to grow.

The head capsule is a pale brownish-green color, with tiny sparsely distributed whitish setae across its frontal and dorsofrontal regions. The body is dorsoventrally flattened, particularly laterally and posteriorly, with semicircular lateral flanges that are most prominent from thoracic segment two (T2) to abdominal segment five (A5). The body is green to yellow green along the dorsal midline, becoming yellowish laterally and posteriorly. The pre-prepenultimate instar (Figs. 1C,D) is slightly transparent and without patterning, but the prepenultimate instar (Fig. 1F) has a pair of speckled, rectangular, pale yellowish-green blotches on each body segment along the edge of the darker dorsal midline, with a broken, uneven, and undulating pale yellowish-green band immediately laterally, and an undulating line of pale yellowish-green spots along the lateral margin (overlying the spiracles). The prepenultimate instar has tiny, very sparsely distributed, flattened white setae along the lateral portion of each body segment. Pairs of thick, short black setae are present along the dorsal midline of the body at the anterior margin of T2 (dorsoanteriorly directed) and A1-A8 (dorsoposteriorly directed), with the pair on A8 more than twice as long as the remainder. These setae are prominent in the pre-prepenultimate instar, but barely visible in the prepenultimate instar except on A7 and particularly A8. Pairs of medium-sized, posteriorly directed white setae are present along the dorsal midline of the body at the posterior margin of segments T3-A8, which are proportionately shorter in the prepenultimate instar. The lateral margins of all thoracic and abdominal segments have long setae that are anteriorly to anterolaterally directed on the prothorax, laterally directed on segments T2-A8, and very long and posteriorly directed on the abdominal anal plate. The pre-prepenultimate instar has relatively sparse lateral setae, with five setae in an arc on segments T2-A8, with a short white-tipped black seta near the anterior segment edge, a longer black seta posteroventrally, and three variably longer white setae posteroventrally. The prepenultimate instar has approximately twice as many lateral setae, with a similar color scheme except that there are one or two white setae between the black ones on segments T2-A8.

Late instars (Figs. 1F-H,N-Q): The penultimate instar (Figs. 1F,N) differs from the prepenultimate instar by having more densely distributed tiny white setae on the head, more prominently semicircular lateral flanges on body segments T1-A6, an orange tinge to the head and body color that is most prominent on the thoracic segments, slightly more prominent pale body patterning, faint reddish-brown speckling along the dorsal midline of the body, a noticeably defined paler rim around the lateral margin of the body, more densely distributed tiny flattened white setae along the lateral portions of the body, no black dorsal setae, shorter and less prominent white dorsal setae, and approximately twice as many lateral setae that are all basally yellow to orange and distally whitish. The early last instar (Fig. 1O) is similar to the penultimate instar but has a slightly darker and more orange color, even less prominent white dorsal setae, and approximately 50% more lateral setae that are all orangish. By the end of the last instar (Figs. 1G,H,P,Q), the caterpillar is broader and has lost all traces of green coloration, developing a ground color that is entirely orange to red and

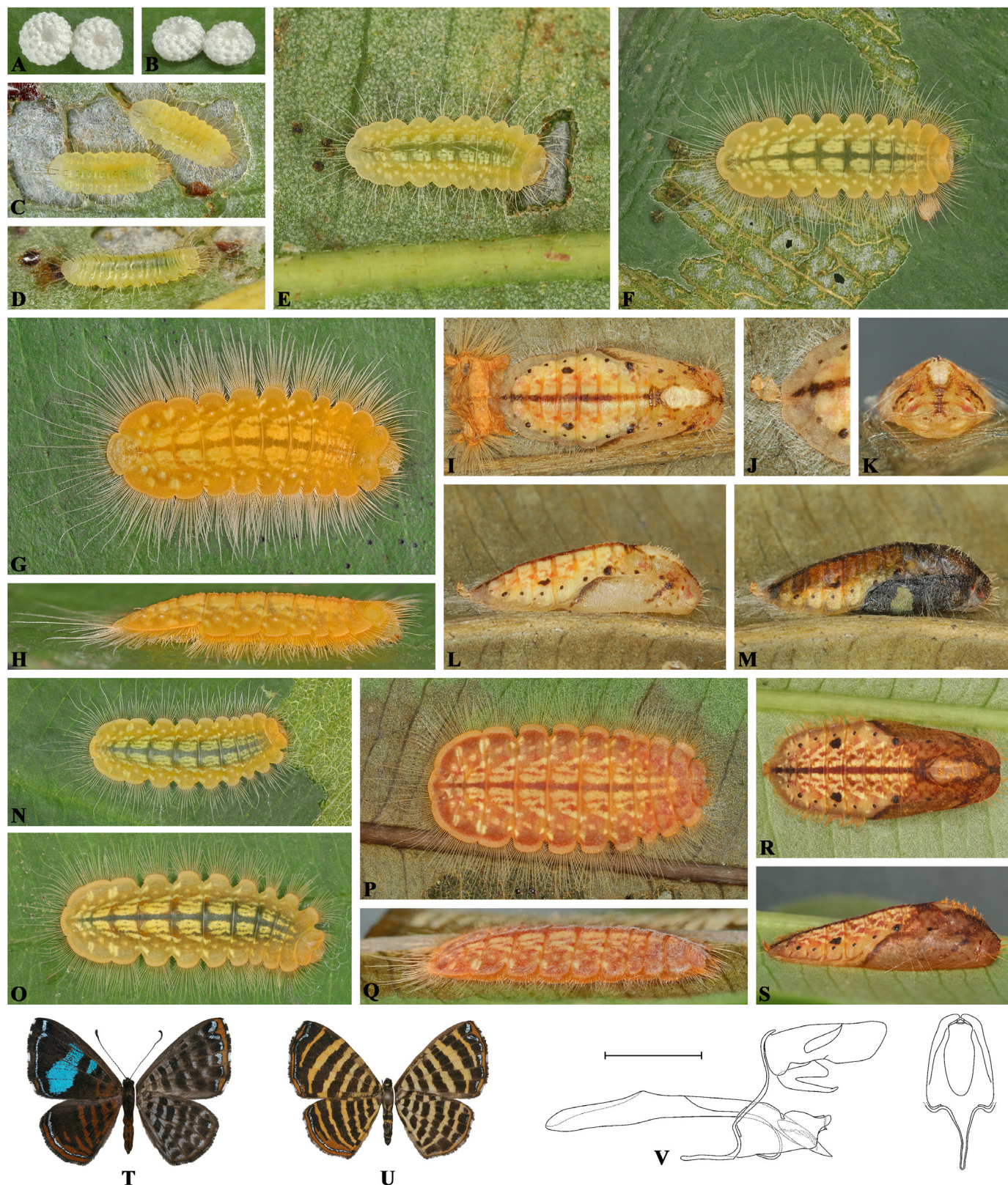


Fig. 1. Life history of *Argyrogrammana glaucopis* (Bates) from Santiago, Ecuador. Rearing #2: **A,B.** A pair of eggs in dorsal (A) and dorsolateral (B) views. **C,D.** Pre-prepenultimate instar caterpillars in dorsal (C) and dorsolateral (D) views, showing early instar feeding damage. **E.** Prepenultimate instar in dorsal view. **F.** Penultimate instar in dorsal view, showing late instar feeding damage. **G,H.** Last instar in dorsal (G) and lateral (H) views. **I-M.** Pupa in dorsal (I), frontal (K), and lateral (L) views, with a magnified view of the terminal abdominal segments and cremaster (J) and lateral view of the darkened pre-eclosion pupa (M) with the male's narrow blue dorsal forewing patch visible. Rearing #1: **N.** Penultimate instar in dorsal view. **O.** Early last instar in dorsal view. **P,Q.** Late last instar in dorsal (P) and lateral (Q) views. **R,S.** Pupa in dorsal (R) and lateral (S) views. **T,U.** Eclosed adult male from rearing #1 (T) and a female from Pakitza, Peru (U). **V.** Male genitalia, Lumbaquí, Ecuador (scale bar = 0.5 mm).

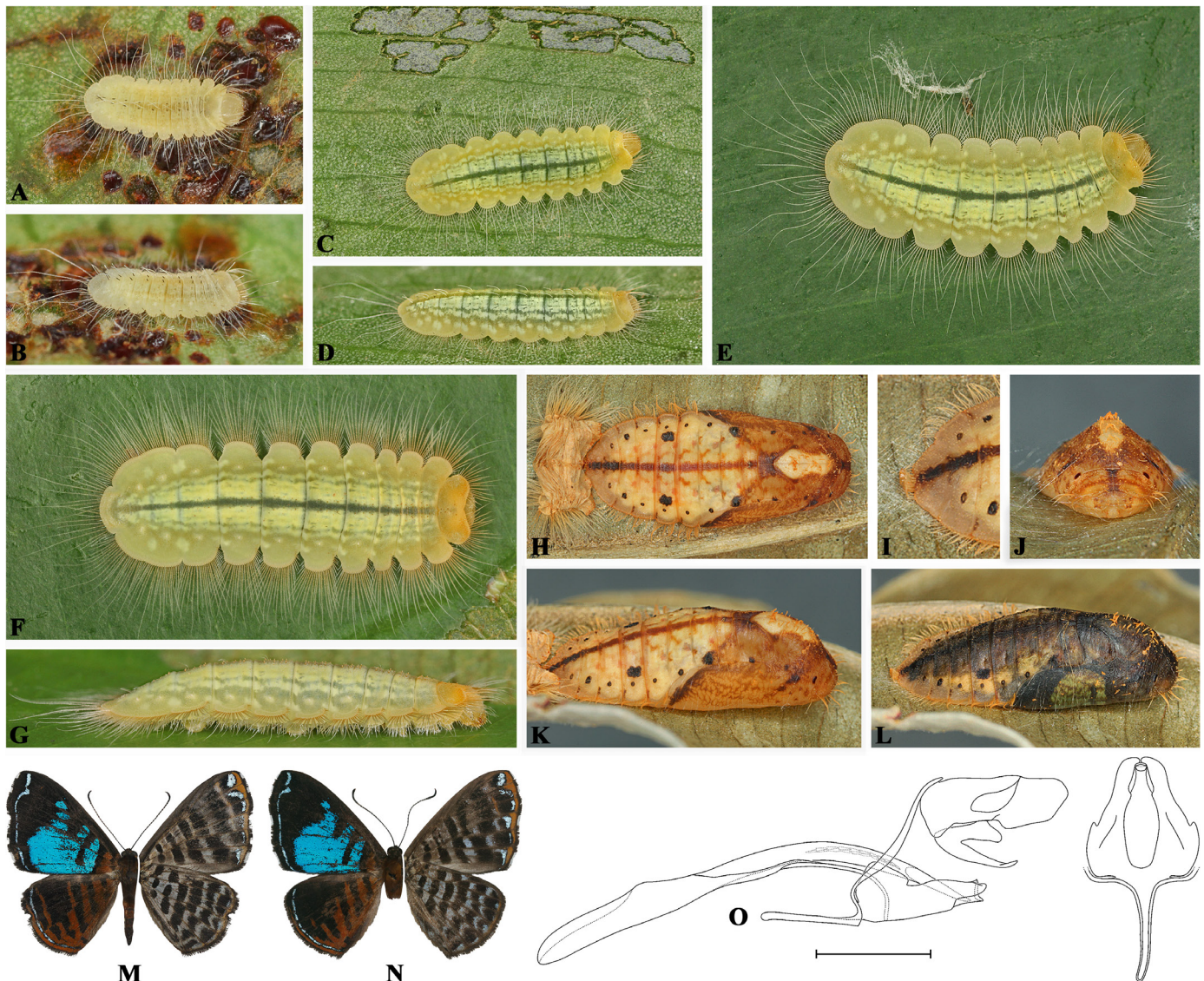


Fig. 2. Life history of *Argyrogrammana caerulea* Hall, n. sp. from El Recinto Arenal, Ecuador. **A,B.** Pre-prepenultimate instar caterpillar in dorsal (A) and dorsolateral (B) views, showing early instar feeding damage. **C,D.** Prepenultimate instar in dorsal (C) and dorsolateral (D) views, showing mid-instar feeding damage. **E.** Penultimate instar in dorsal view. **F,G.** Last instar in dorsal (F) and lateral (G) views. **H-L.** Pupa in dorsal (H), frontal (J), and dorsolateral (K) views, with a magnified view of the terminal abdominal segments and cremaster (I) and dorsolateral view of the darkened pre-eclosion pupa (L) with the male's large blue dorsal forewing patch visible. **M,N.** Enclosed adult paratype male (M) and holotype male from Explornapo-ACEER, Peru (N). **O.** Holotype male genitalia (scale bar = 0.5 mm).

paler patterning that is entirely yellow to orange. The maximum length of the last instar was approximately 13-14 mm (n=2). The duration of the penultimate instar was 13 days (n=1) and that of the last instar was 13-15 days (n=2).

Pupa (Figs. 11-M,R,S): At least under laboratory rearing conditions, pupation occurred within the leaf shelter, beneath the dorsal leaf beside the midrib. However, under more natural rearing conditions, Gallard (2017) reported that pupation in *A. trochilia* occurred on a leaf at the base of the food plant. The cast larval skin remained attached to the pupal cremaster (Fig. 11) by means of a large upwardly curved hook (Fig. 1J). The pupa is cylindrical, broadest at its middle (A3-A4), tallest from T2-A2, and dorsoventrally flattened, particularly around the lateral margins of the abdomen. The head and thoracic segments vary

from pale tan (Figs. 11,K,L) to reddish brown (Figs. 1R,S), and the thorax has a sparse dorsal scattering of tiny yellow to orange setae. The prothorax has a darker brown dorsal band, a pink to purple-brown transverse band, and a posterior to lateral rim of stiff, medium-length yellow to orange setae. The mesothorax has a broad and uneven paler brown dorsal band sparsely filled with short, thick, curved yellow to orange setae, a variably narrow darker brown area surrounding this pale band that at its anterior tip extends posteroventrally as a series of broken blotches, a semicircular red spiracle at the lateral anterior margin, a few short and thick orange setae over mostly the middle of the wing pad, and a darker brown area along the anterior margin of the wing pad. The metathorax has a darker brown dorsal band, dark brown splotching laterally, and a round black mark at the ventral margin. The abdomen varies from yellowish to pale brown and

has a dark brown dorsal midline (becoming darker posteriorly), a double row of dark, broken, inwardly diagonal dorsal bands lined proximally with paler areas on A1-A8, a small and round black area surrounding the spiracles on A2-A8 (including a spiracle that, for the Riodininae, is unusually visible on A3) that is slightly larger on A7 and about three times as large on A2, a medium-sized black blotch proximal to the spiracle on A5, a variably prominent short and dark brown lateral line along the posterior margin of segments A4-A7, and a slightly darker and transparent lateral rim on A4-A10 edged with stiff, medium-length yellow to orange setae. A multi-stranded silk girdle predominantly crosses A1 (Figs. 1K,M,R,S). The pupal length was approximately 11.5-12 mm, and the duration of this stage was 17-18 days (n=2). In the days prior to eclosion, the pupae darkened significantly and the forewing wing pattern became evident (Fig. 1M), allowing both individuals to be identified as males. The eclosed male from rearing #1 is shown in Fig. 1T.

Argyrogrammana caerulea Hall, new species

(Figs. 2A-L)

Location and food plant: In August 2018, I found a single late first or second instar (pre-prepenultimate) caterpillar that would later prove to be an undescribed species similar to *A. glaucopis* while searching a sapling of *Symphonia globulifera* in the understory of actively logged ridgetop forest above the village of El Recinto Arenal, near Lumbaquí, in Sucumbios province, eastern Ecuador (600 m) (0°01'11"S, 77°17'24"W). No additional plants were found during a brief search of the area.

Early instars (Figs. 2A-D): The pre-prepenultimate caterpillar was found on the ventral side of a leaf that was loosely overlapping another, and all instars showed the same feeding behaviors (Figs. 2A-C) as described above for *A. glaucopis*. The head capsule is pale yellowish brown, becoming orange brown in the prepenultimate instar, with tiny sparsely distributed whitish setae across its frontal and dorsofrontal regions. The body is dorsoventrally flattened, particularly laterally and posteriorly, with semicircular lateral flanges that are most prominent from T1-A5. The pre-prepenultimate instar (Figs. 2A,B) is pale yellowish brown and laterally slightly transparent, with a darker dorsal midline and darker dorsolateral speckling. The prepenultimate instar (Figs. 2C,D) is dark green along the dorsal midline, becoming yellowish green laterally and posteriorly (with a hint of orange on T1), with a pair of speckled, rectangular, pale green blotches on each body segment along the edge of the darker dorsal midline, an uneven and undulating pale green band immediately laterally, and an undulating line of pale yellowish-green spots along the lateral margin (overlying the spiracles). Tiny, very sparsely distributed, flattened white setae are present along the lateral portion of each body segment. Pairs of thick, short black setae are present along the dorsal midline of the body at the anterior margin of T2 (dorsoanteriorly directed) and A1-A8 (dorsoposteriorly directed), with the pair on A8 more than twice as long as the remainder. These setae are prominent in the pre-prepenultimate instar, but barely visible in the prepenultimate

instar except on A7 and particularly A8. Pairs of medium-sized, posteriorly directed white setae are present along the dorsal midline of the body at the posterior margin of segments T3-A8, which are proportionately shorter in the prepenultimate instar. The lateral margins of all thoracic and abdominal segments have long setae that are anteriorly to anterolaterally directed on the prothorax, laterally directed on segments T2-A8, and very long and posteriorly directed on the abdominal anal plate. The pre-prepenultimate instar has relatively sparse lateral setae, with eight setae in an arc on segments T2-A8, with a short white-tipped black seta near the anterior segment edge, longer white and black setae posteroventrally, and then five variably longer white setae posteriorly. The prepenultimate instar has approximately 50% more lateral setae, with two short black setae near the anterior segment edge, one or two longer white setae posteroventrally, and then one variably longer brown seta followed by numerous white setae posteriorly. The duration of the prepenultimate instar was 10 days.

Late instars (Figs. 2E-G): The penultimate instar (Fig. 2E) differs from the prepenultimate instar by having slightly more prominently semicircular lateral flanges on body segments T1-A6, a slightly paler and plainer green body color with a more prominent orange tinge to the prothorax, slightly paler and less speckled pale green patterning along the dorsum of the body, faint and sparse reddish-brown speckling along the dorsal midline of the body, a noticeably defined paler rim around the lateral margin of the body, more densely distributed tiny flattened white setae along the lateral portions of the body, no black dorsal setae, shorter and less prominent white dorsal setae, and approximately 50% more lateral setae that are predominantly yellow to orange basally and whitish distally. The last instar (Figs. 2F,G) is very similar to the penultimate instar but has more orange coloring across the thoracic segments and faint orange coloring around the lateral rim of the body, even less prominent white dorsal setae, and approximately 50% more lateral setae that are all orangish basally and yellow to white distally. The maximum length of the last instar was approximately 14 mm. The duration of the penultimate instar was 11 days and that of the last instar was 12 days.

Pupa (Figs. 2H-L): Pupation occurred within the leaf shelter, beneath the dorsal leaf beside the midrib. The cast larval skin remained attached to the pupal cremaster (Fig. 2H) by means of a large upwardly curved hook (Fig. 2I). The pupa is cylindrical, broadest at its middle (A3-A4), tallest from T2-A2, and dorsoventrally flattened, particularly around the lateral margins of the abdomen. The head and thoracic segments are reddish brown with extensive darker brown speckling, and the thorax has a sparse dorsal scattering of tiny orange setae. The prothorax has a darker brown dorsal band, an orange-brown transverse band, and a posterior to lateral rim of stiff, medium-length orange setae. The mesothorax has a broad and uneven paler brown dorsal band sparsely filled with short, thick, curved orange setae, a variably narrow darker brown area surrounding this pale band that at its anterior tip extends posteroventrally as a series of broken blotches, a semicircular black spiracle at the lateral anterior margin, a few short and thick orange setae

over the wing pad, and a darker brown area along the dorsal and anterior margin of the wing pad. The metathorax has a darker brown dorsal band, dark brown splotching laterally, and a round black mark at the ventral margin. The abdomen is pale yellow brown and has a dark brown dorsal midline (becoming darker posteriorly), a double row (outer row faint) of dark, broken, inwardly diagonal dorsal bands on A1-A8, a small and round black area surrounding the spiracles on A2-A8 that is slightly larger on A7 and about three times as large on A2, a medium-sized black blotch proximal to the spiracle on A5, a short and dark brown lateral line along the posterior margin of segments A4-A7, and a slightly darker and transparent lateral rim on A4-A10 edged with stiff, medium-length orange setae. A multi-stranded silk girdle predominantly crosses A1 (Figs. 2J-L). The pupal length was approximately 12 mm, and the duration of this stage was 18 days. In the days prior to eclosion, the pupa darkened significantly and the forewing wing pattern became evident (Fig. 2L), allowing the individual to be sexed. The eclosed male is shown in Fig. 2M.

Discussion: The immature stages of *A. caerulea* and *A. glaucopsis* are very similar. However, the single reared caterpillar of *A. caerulea* differed from the multiple examined caterpillars of *A. glaucopsis* by being predominantly shades of green instead of yellow green (early instars) or yellow to orange (late instars), and by having a slightly narrower dark dorsal midline, much narrower intersegmental dark lines perpendicular to this dorsal midline, and an undulating but continuous instead of discontinuous pale dorsolateral line distal to the much broader pale dorsal band. Additionally, the single examined pupa of *A. caerulea* differed from the two examined pupae of *A. glaucopsis* by having a black instead of red mesothoracic spiracle.

Argyrogrammana eggs were previously unknown. They are most similar to those of other genera in the Symmachiini as well as some genera in the Riordini (Downey & Allen, 1980; DeVries, 1997), with the most similar eggs that I have seen belonging to the symmachiine genus *Pirascia* Hall & Willmott, 1996 (Hall, unpubl. data), although knowledge of eggs in this tribe remains very limited.

Photographs of *Argyrogrammana* caterpillars and pupae have previously been published for three species, *A. crocea*, *A. holosticta*, and *A. trochilia* (Janzen & Hallwachs, 2009-22; Gallard, 2017). Overall, the form and color patterning of these stages seems to be relatively uniform throughout the genus, although the immatures of the *barine* and *occidentalis* groups have yet to be photographically documented. The immatures of the *amalfreda* group species *A. caerulea* and *A. glaucopsis* are most similar to those of *A. crocea* (*crocea* group) and *A. trochilia* (*trochilia* group), but differ by having caterpillars with a green instead of reddish-brown dorsal midline and pale green to yellow/orange instead of blackish markings overlying the abdominal spiracles. The Anacardiaceae-feeding immatures of *A. holosticta* (*stilbe* group) are the most distinctive of those known. The caterpillar differs from those of the four previous species by having a medially divided pale dorsal band, resulting in three narrow parallel bands traversing the length of the body either side of the dark green dorsal midline. Pale markings overlie the abdominal spiracles, as in the *amalfreda*

group species. The pupa of *A. holosticta* is pale yellow green instead of brown, with sparser reddish-brown instead of dark brown to black markings that are largely confined to a large rectangular area at the posterolateral portion of the prothorax and anterolateral portion of the mesothorax, a semicircular area at the lateral margins of abdominal segments four to six, and highlighting the spiracles.

DeVries (1997) reported the presence of a pair of orifices similar to tentacle nectary organs on the eighth larval abdominal segment of the non-myrmecophilous *Symmachia rubina* Bates, 1866 (Symmachiini), and Kaminski (in Seraphim *et al.*, 2018) made reference to such “nonfunctional tentacle nectary organ openings” also occurring in *Argyrogrammana* caterpillars. I have observed these interesting structures, of unknown function, in *Symmachia* caterpillars that I have reared myself. They are situated near the posterior margin of the eighth abdominal segment, slightly proximal to the spiracles, and are similar in size to and only slightly less conspicuous than the spiracles. However, no similar structures are evident in any of the high-definition larval photographs of the two *Argyrogrammana* species whose rearings are reported here, although no preserved caterpillars were available for microscopic examination.

SPECIES DESCRIPTION

Argyrogrammana caerulea Hall, new species (Figs. 2M-O)

Description: MALE: Forewing length holotype 13.5 mm; paratypes 13-13.5 mm. *Wings:* see Figs. 2M,N. *Head:* Eyes brown and bare, with a darker brown transverse medial band and rufous-brown marginal scaling; frons black, with a broad dirty yellowish transverse medial band and three dirty yellowish dorsal spots below base of antennae; labial palpi banded dark brown and dirty white; antennal length approximately 55% of forewing length, segments black with vertical white lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax dark rufous brown, ventral surface gray, dorsal surface of abdomen dark rufous brown with an indistinct triangular blackish mark at middle of anterior margin of all segments, ventral surface with a dark brown ventral stripe and alternating dark brown and dirty white lateral bands; all legs banded dark brown and dirty white. *Genitalia:* see Fig. 2O; sclerotized transtilla between closely spaced valve tips concave in lateral view, with posteriorly directed ventral portion attached to valvae by membranous tissue; ductus ejaculatorius enters anterior tip of aedeagus dorsally and slightly to right; vesica exits posterior tip of aedeagus to right, cornutal complex on uneverted vesica consists of twelve small (becoming smaller posteriorly) posteriorly directed spine-like cornuti arranged along a gently dorsally curved sclerotized rod; eighth tergite and sternite rectangular. FEMALE: Unknown.

Types: HOLOTYPE male: PERU: *Loreto*, Río Sucusari, Explornapo-ACEER, 3°14'S 72°55'W, 140 m, 12 Sept 1995 (G. Lamas) (National Museum of Natural History, Smithsonian Institution, Washington, DC, USA).

PARATYPES: ECUADOR: *Sucumbios*, 1 male: nr. Palma Roja, km. 23 Puerto El Carmen de Putumayo-Tarapoa rd., 0°06.26'N 76°02.58'W, [250 m], 31 Dec 2016 (I. Aldas) (collection of David H. Ahrenholz, Landrum, SC, USA); 1 male: above El Recinto Arenal, km. 12 Lumbaquí-Coca rd., 0°01'11"S 77°17'24"W, 600 m, 17 Aug 2018 (coll. as caterpillar) (J. P. W. Hall) (collection of Jason P. W. Hall, Washington, DC, USA).

Etymology: This species name is based on the Latin word “caerulea”, meaning “sky blue”, in reference to the very large blue patch on the male dorsal forewing.

Systematic placement and diagnosis: The morphological phylogenetic analysis of *Argyrogrammana* presented by Hall

(2023) indicates that *A. caerulea* n. sp. can be placed in the central portion of the large *amalfreda* group, which is most readily characterized by its members possessing orange and blue dorsal wings and gray to blue ventral wings in males. *Argyrogrammana caerulea* belongs to a well-supported clade of three species that also contains *A. praestigiosa* (Stichel, 1929) and *A. glaucopis*. All three species are unique in the genus in possessing multiple orange bands at the base of the male dorsal forewing and orange scaling on the male dorsal hindwing that is largely confined to the basal and anal wing regions. Additionally, the center of the discal cell on the male ventral forewing in these three species has a single dark bar extending across the entire width of the cell instead of two interdigitating spots, a character state that has independently evolved elsewhere in the genus only in the six most derived *trochilia* group species and four derived *amalfreda* group species, namely *A. amalfreda* (Staudinger, 1887) and the clade containing *A. alstonii* (Smart, 1979), *A. pulchra* (Talbot, 1929), and *A. sticheli* (Talbot, 1929) (Hall, 2023). The females of *A. praestigiosa*, *A. glaucopis*, and presumably *A. caerulea* (currently unknown) are also unusual in the genus in having banded instead of spotted wing patterns. The derived majority of *trochilia* group species have independently evolved banded females, but these are white to pale yellow banded whereas *A. glaucopis* clade females are dark yellow to orange banded (Hall, 2023).

Argyrogrammana caerulea (Figs. 2M,N) is most similar to and appears to be the sister species of *A. glaucopis* (Figs. 1T,U), the two species being unique in the genus in possessing two blue spots only in the discal cell of the male dorsal forewing (the second, central discal spot is very occasionally reduced or absent in *A. glaucopis*). Within the *amalfreda* group, *A. venilia* (Bates, 1868) has three such blue discal spots, and *A. alstonii*, *A. pulchra*, and *A. sticheli* have a single such blue discal spot at the cell end. The male of *A. caerulea* differs most obviously from that of *A. glaucopis* by having a much larger blue medial patch on the dorsal forewing, which in cells 2A, Cu₂, and Cu₁ extends basally to form a contiguous patch with the two blue spots in the discal cell. The spotting pattern on the male ventral surface of the two species is the same, but in all three of the examined *A. caerulea* males there is orange scaling proximal to the dark submarginal spots in the apex of the ventral forewing, whereas this scaling is entirely blue gray in the examined males of *A. glaucopis*. The only significant wing pattern variation observed in the known *A. caerulea* males involves the orange bands on the dorsal hindwing, which vary slightly in the distal half of the wing in their shape and length, intraspecific variation that also occurs in *A. glaucopis*. Given the external similarity of the two species, the male genitalia of *A. caerulea* (Fig. 2O) and *A. glaucopis* (Fig. 1V) differ to a surprising extent, with those of *A. caerulea* having dorsoventrally narrower valvae with a much more elongate upper posterior process, a proportionately longer saccus and aedeagus, and a different arrangement of aedeagal cornuti. In *A. caerulea*, the cornutal complex is more anteriorly positioned on the unevverted vesica, and is longer and more shallowly convex, consisting of about a dozen spine-like cornuti that become smaller posteriorly instead of about a half dozen such cornuti that become larger

posteriorly. The female of *A. caerulea* remains unknown with any certainty, but it is presumed to look very much like that of the more common *A. glaucopis*. In the eastern Amazon at least, the female of *A. praestigiosa* seems to be distinguishable from that of *A. glaucopis* on the basis of having more orange than yellow dorsal bands, no yellow-orange submarginal band in the apex of the dorsal forewing, and a broken instead of continuous yellow submarginal band in the apex of the ventral forewing (Brévignon & Gallard, 1995; Gallard, 2017). However, because of insufficient material, it is not yet clear how useful these characters will prove to be in separating females of the three *A. glaucopis* clade species in the western Amazon.

Biology: This species is known to inhabit wet lowland rainforest from 150 to 600 m. Nothing is known about its adult biology.

Distribution: *Argyrogrammana caerulea* is currently known only from the central western Amazon, in Ecuador (Sucumbíos) and northern Peru (Loreto), but it surely also occurs in at least neighboring southern Colombia.

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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. phytion* (Stichel, 1911) from a subspecies of *A. physis* (Stichel, 1911) (**n. stat.**). Three names are synonymized: *A. leptographia magdalena* 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

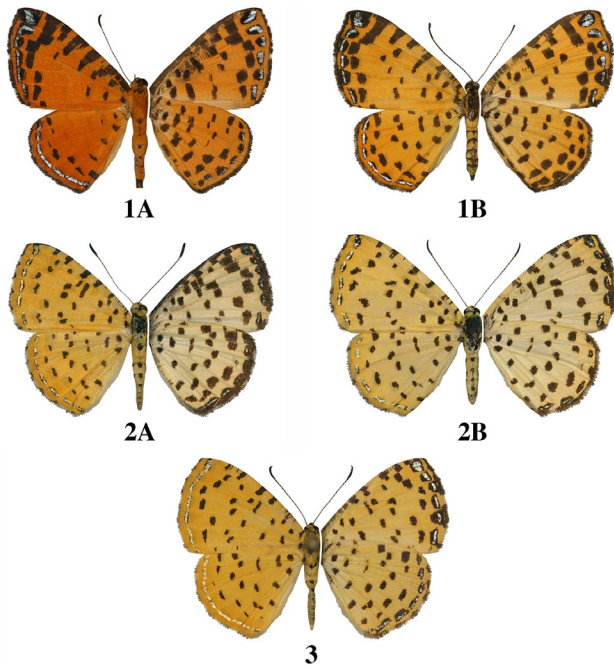
Argyrogrammana crocea (Godman & Salvin, 1878)
(Figs. 1A,B)

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-BCII67217), 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).

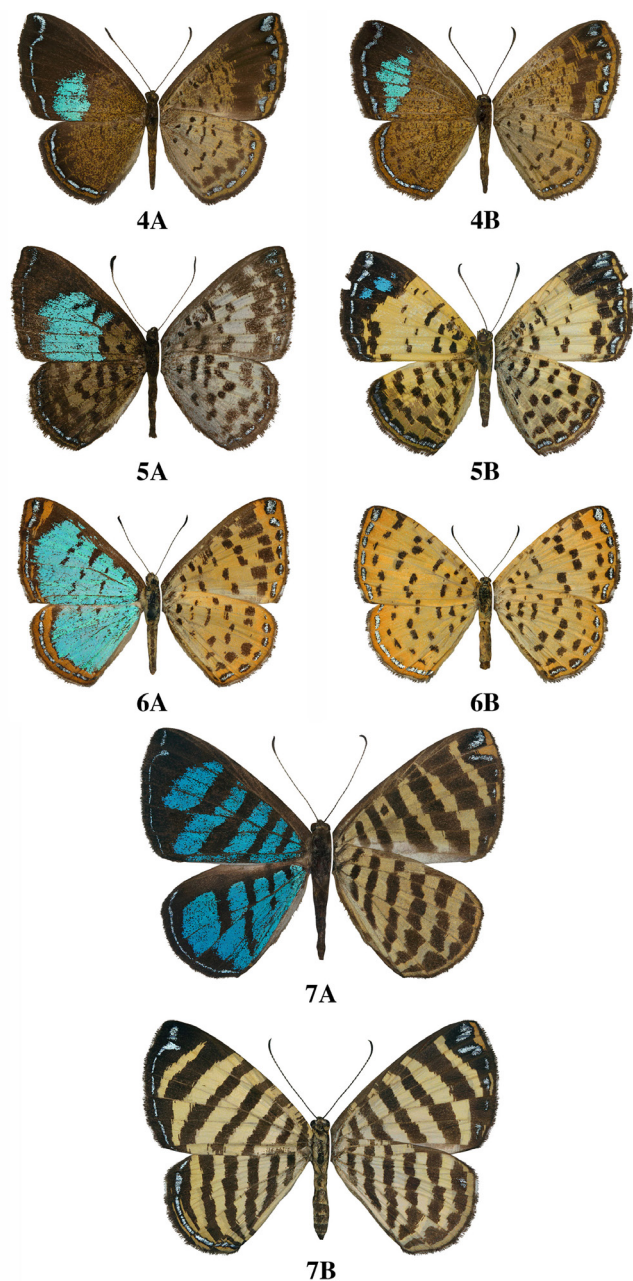
Distribution: *Argyrogrammana holosticta* is the most widespread Transandean species in the genus, occurring from southern Mexico to northwestern Ecuador and northern Venezuela. It is replaced throughout the Amazon by *A. stilbe*.

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. brevigioni* 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. brevigioni*, 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)

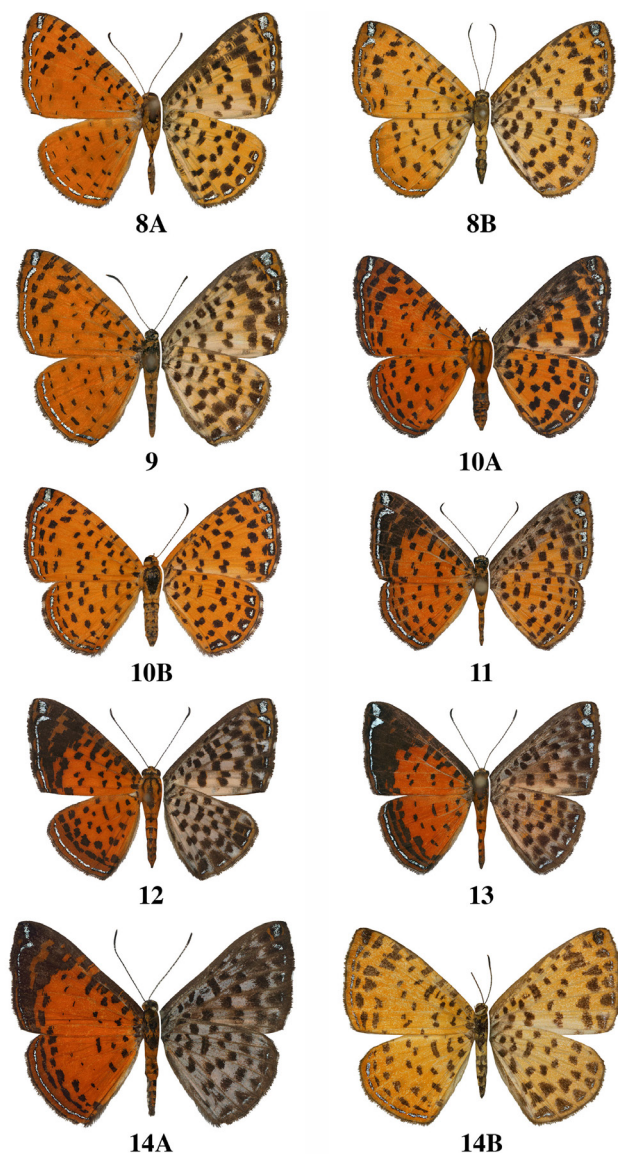
(USNM).

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 Cu₁ 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 uneverted 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.

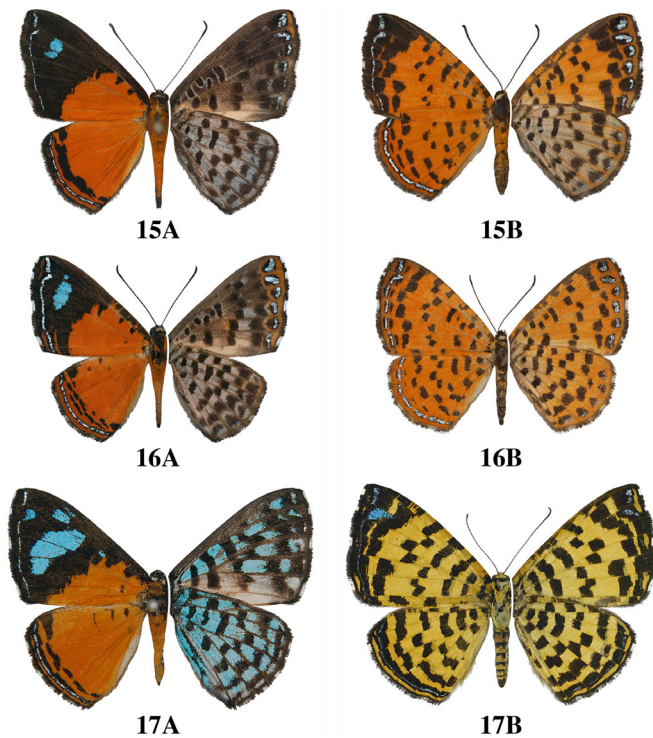
Distribution: *Argyrogrammana cana* is currently known only from far eastern Panama and northwestern Ecuador, but it presumably also occurs in western Colombia.

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).

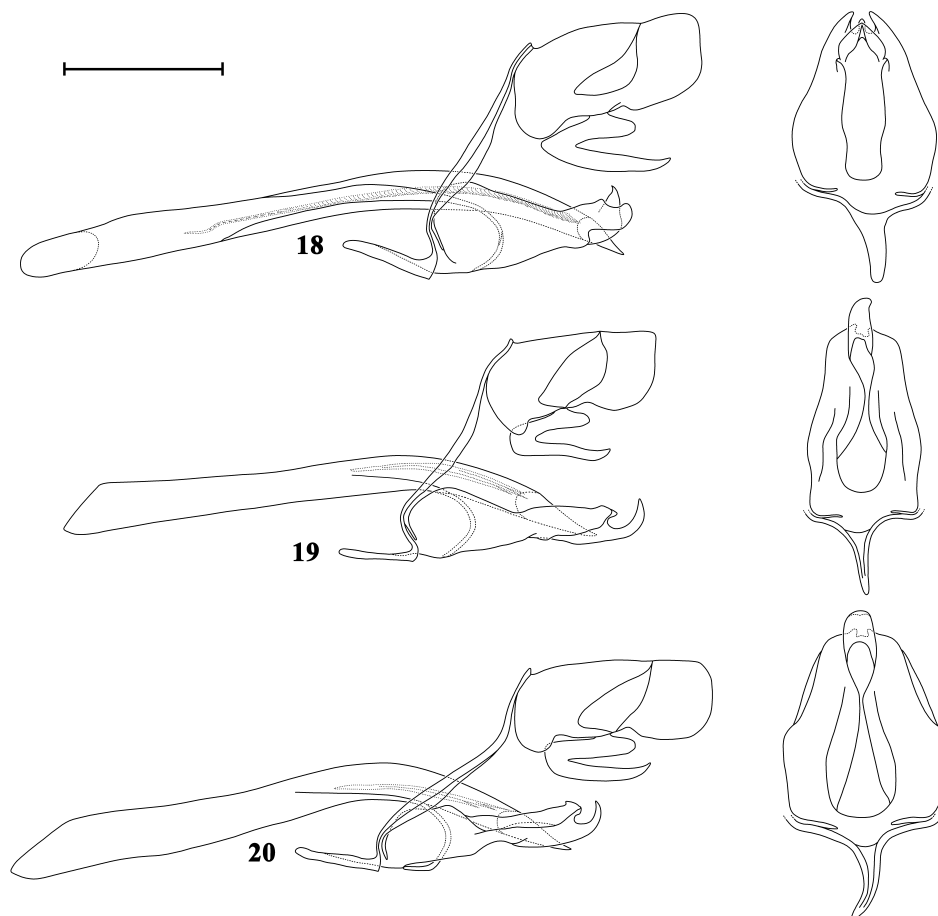
and blue-gray rather than grayish scaling on the hindwing. The female of *A. physis* differs from that of *A. phyton* by having a dorsal forewing with a broader dark presubmarginal band that consists of a partially fused band instead of individual spots and a broader dark submarginal band that is fused 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).

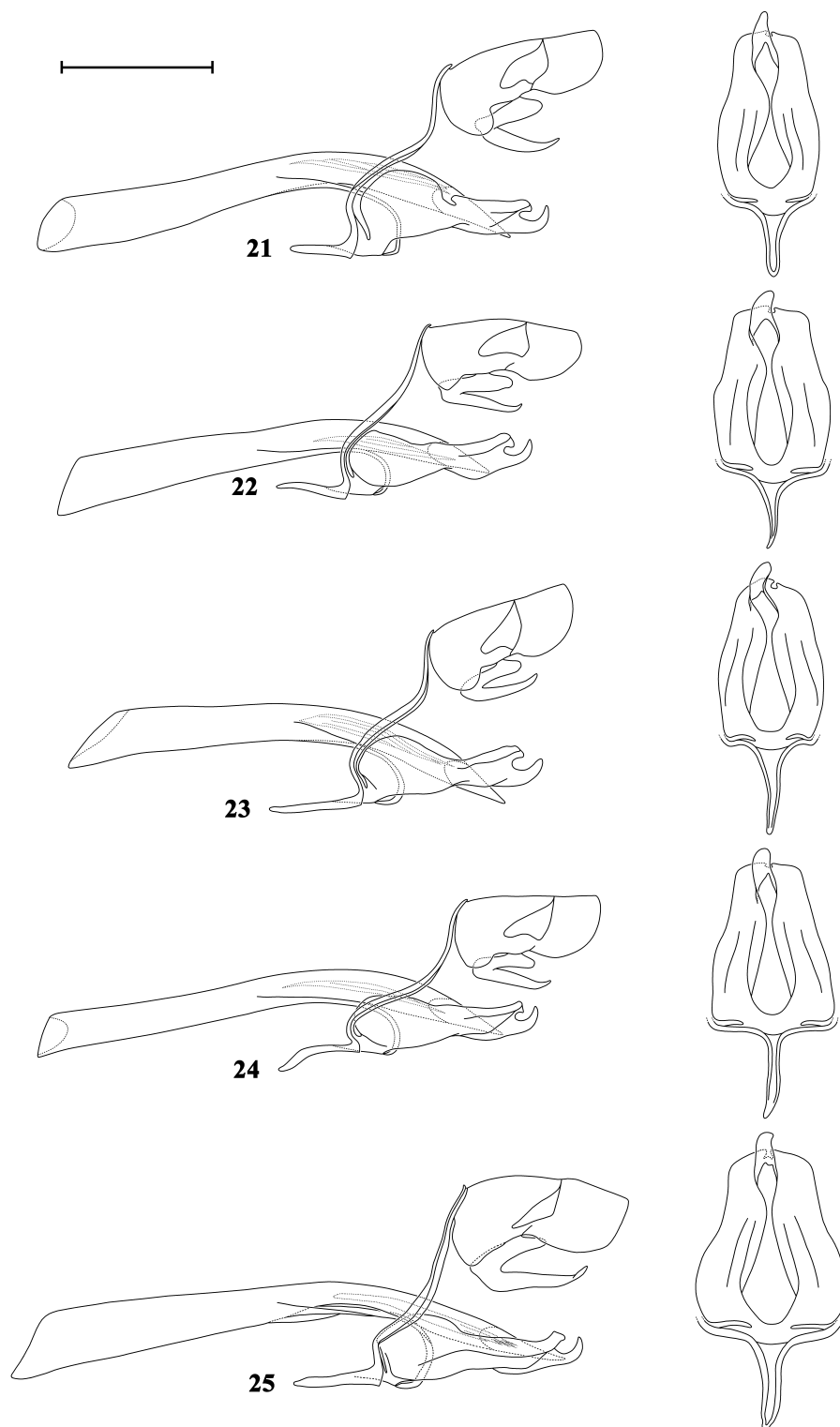
PARATYPES: GUYANA: *Upper Takutu-Upper Essequibo*, 2 males: ridge above Sipu River, Acarai Mountains, 1°22.2'N 58°57.9'W, 750-900 m, 31 Oct-10 Nov 2000 (S. Fratello *et al.*) (USNM). FRENCH GUIANA: *Cayenne*, 1 male: Montsinéry, 0-100 m, 21 Nov 1988 (D. J. Harvey) (USNM); 1 male:

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*.

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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.

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 *trochilia*, *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

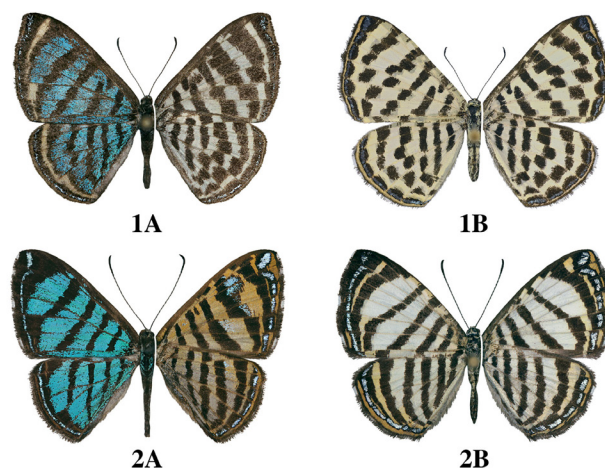
trochilia group

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

Charis subota Hewitson, 1877. *Equa. Lepid. Buckley* 5: 95.
TL: "Gima", E. Ecuador. Holotype female BMNH [examined].

Identification and Taxonomy: For over a century, *A. subota* remained known from a single ragged female specimen (figured by d'Abrera (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, postdiscally, 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



Figs. 1-2. East Andean *Argyrogrammana trochilia* group adults (dorsal surface on left, ventral surface on right). **1A.** *A. subota* (Hewitson, 1877) male, Río Abanico, Morona-Santiago, E. Ecuador (1600 m). **1B.** *A. subota* female, Río Abanico, Morona-Santiago, E. Ecuador (1600 m). **2A.** *A. pastaza* Hall & Willmott, 1996, male, Río Llandia, Pastaza, E. Ecuador (900 m). **2B.** *A. pastaza* female, Condor Mirador, Zamora-Chinchipe, E. Ecuador (1750 m).

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 intrapopulation 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 forewing cell M_2 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 Gualaquiza 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; Hämäläinen, 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 riordinid 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)

Argyrogrammana pastaza Hall & Willmott, 1996. *Trop. Lepid.* 7(1): 72, figs. 5A-D. TL: Río Llandia, km. 25 Puyo-Tena rd., Pastaza, E. Ecuador. Holotype male BMNH [examined].

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 Cu_1 instead of being of approximately even width throughout, and apical segments (in cells M_1 and R_{4+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. brevignoni* 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. brevignoni*, 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 M_1 . *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 ventroposterior 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 ventroposterior 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 intrapopulation 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 R_{4+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. trochilia*, 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 M_1 and R_{4+5} , resulting in the immediately proximal pale band being abruptly narrowed or broken and similarly kinked near vein M_1 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 both wings, including the complete absence in some specimens of the yellow band immediately proximal to the silver submarginal line on the dorsal forewing.

Biology: This not uncommon species is known to inhabit premontane and montane forest from 800 to 2200 m. It is the most commonly encountered of the Andean *Argyrogrammana* species, and the only one to be substantially represented in historical museum collections, presumably because it is the only one known to inhabit more accessible and frequented streamside rather than hilltop environments. In Ecuador, pairs or small groups of males were encountered perching 3 to 8 m above the ground along streams and nearby forest edges from 1345 to 1630 hrs. Females were found flying low to the ground along streams in the vicinity of male perching leks in the early to mid afternoon. In southern Peru, males were found perching 2.5 to 5 m above the ground between 1230 and 1400 hrs (Lamas *et al.*, in press).

Distribution: *Argyrogrammana pastaza* is known to range from southern Colombia (Caquetá) to southern Peru (Cuzco), and seems certain also to occur in Bolivia.

occidentalis group

Argyrogrammana janiceae Ahrenholz & Hall, new species

(Figs. 3A,B; 12)

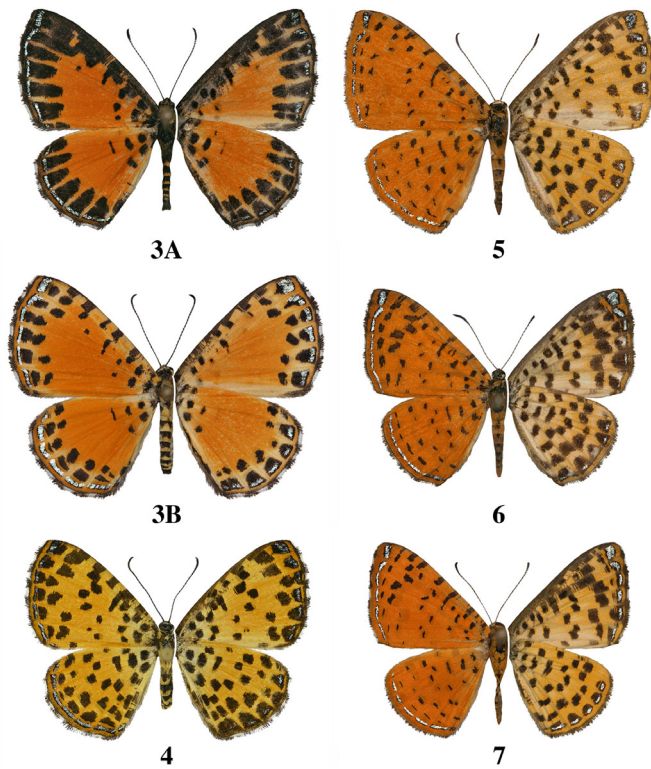
Description: MALE: Forewing length holotype (HT) 14.5 mm; paratypes (PTs) 14-14.5 mm. *Wings:* see Fig. 3A. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and orange marginal scaling; frons dark yellow orange, with a narrow black transverse band ventrally and a broad black transverse band dorsally; labial palpi dirty yellow with black tips; antennal length approximately 55% of forewing length, segments black with vertical cream lateral bands, clubs black. *Body:* Dorsal surface of thorax dark orange and black, ventral surface orange gray, dorsal surface of abdomen black with a narrow orange band along posterior margin of all but posterior-most segment, ventral surface pale orange gray with a variably prominent narrow pale black band along posterior margin of all segments; all legs banded black and pale orange. *Genitalia:* see Fig. 12; sclerotized transtilla between closely spaced valve tips slightly concave and ventrally posteriorly directed in lateral view, projecting slightly above and below valve tips in lateral view; ductus ejaculatorius enters anterior tip of aedeagus dorsally and slightly to right; vesica exits posterior tip of aedeagus to right, cornutal complex on uneverted vesica consists of a slightly dorsally curved “braided rope” of 13 small (becoming larger posteriorly), slightly convex, ventroposteriorly directed spine-like cornuti; eighth tergite and sternite rectangular. FEMALE: Forewing length PTs 13.5-14 mm. *Wings:* see Fig. 3B. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and yellow-orange marginal scaling; frons yellow orange, with narrow black transverse bands ventrally and dorsally; labial palpi yellow with black tips; antennal length approximately 55% of forewing length, segments black with vertical cream lateral bands, clubs black. *Body:* Dorsal surface of thorax yellow orange and black, ventral surface dirty yellow, dorsal surface of abdomen pale black with a yellow-orange band along posterior margin of all but posterior-most segment that is broad on anterior segments but becomes narrower posteriorly, ventral surface yellow with a variably prominent narrow pale black band along posterior margin of each segment; all legs banded pale black and yellow orange.

Types: HOLOTYPE male: ECUADOR: *Morona-Santiago*, Plan de Milagro, km. 15 Limón-Gualaquiza rd., 03°01.93'S 78°28.74'W, 1650 m, 21 Sept 2016 (D. H. Ahrenholz) (to be deposited in INABIO).

PARATYPES: ECUADOR: *Morona-Santiago*, 4 males, 2 females: same data as HT (R. C. Busby, I. Aldas, and D. H. Ahrenholz) (DA).

Etymology: This species is named for my beloved sister Janice Ahrenholz Dunkerton (D. Ahrenholz).

Diagnosis: *Argyrogrammana janiceae* n. sp. is difficult to place phylogenetically, both because of its autapomorphic 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



Figs. 3-7. East Andean *Argyrogrammana occidentalis* group adults (Figs. 3-5), with extralimital taxa included for comparison (Figs. 6-7) (dorsal surface on left, ventral surface on right). **3A.** *A. janiceae* Ahrenholz & Hall, n. sp., HT male, Plan de Milagro, Morona-Santiago, E. Ecuador (1650 m) (INABIO). **3B.** *A. janiceae* PT female, Plan de Milagro, Morona-Santiago, E. Ecuador (1650 m). **4.** *A. sp. nr. janiceae* female, Naranjos, San Martín, Peru (1700 m). **5.** *A. aurora* Hall & Willmott, n. sp., HT male, Zamora, Zamora-Chinchipec, E. Ecuador (1450 m) (USNM). **6.** *A. saulensis* Gallard, 2008, male, Lumbaquí, Sucumbios, lowland E. Ecuador (950 m). **7.** *A. vespertina* Hall & Willmott, 2023, HT male, El Durango, Esmeraldas, lowland W. Ecuador (300 m) (USNM).

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 Martín [1700 m]) (see Fig. 4).

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_2 , M_3 , M_1 , and R_{4+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 pedicel, 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 Cu_2 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 Cu_1 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.

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 (*Symmachiini*).

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 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. 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 uneverted 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°35'54"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 Guayguayme 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_1 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, subclade 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_2 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* subclade species *A. eura* Hall, 2023, which otherwise exhibits the multiple male wing pattern characters typical of that subclade (see Hall & Willmott, 2023). The more derived trio of *A. sublimis* subclade 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 Lumbaquí (Sucumbíos) 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 genital 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 M_3 and M_2 on the ventral forewing that are typically more arrow shaped than those in *A. vespertina*, a dark presubmarginal spot in cell Cu_1 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 hilltops and ridgetops from 1230 to 1415 hrs.

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

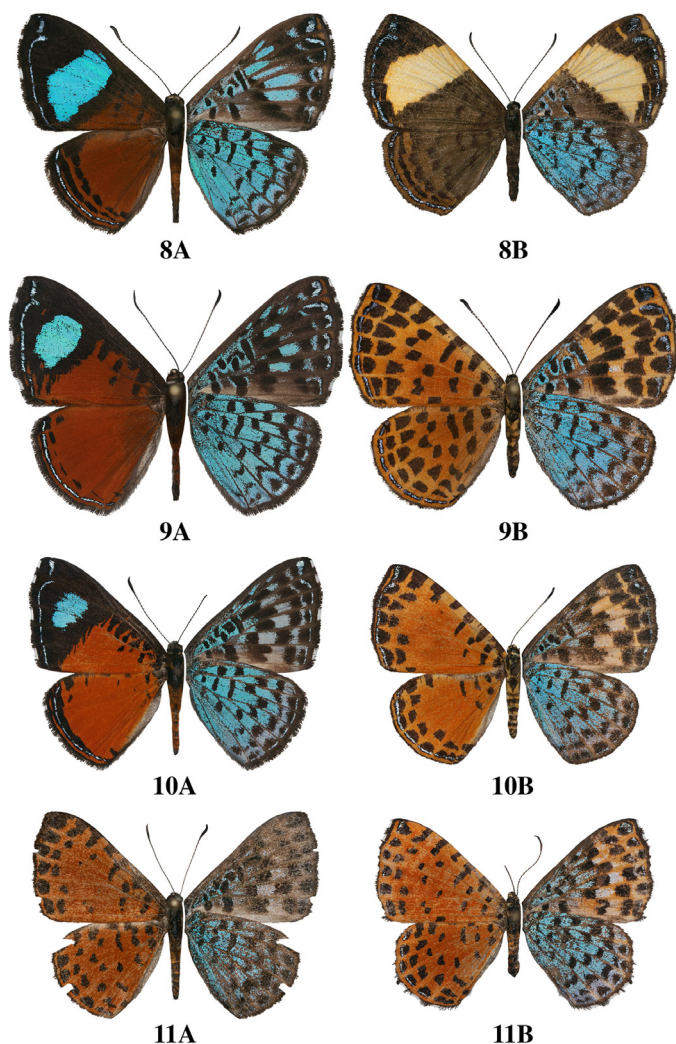
amalfreda group

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

Argyrogrammana caelestina Hall & Willmott, 1995. *Trop. Lepid.* 6(2): 140, figs. 10A, 10B. **TL:** km. 49 Tena-Loreto rd., Napo, E. Ecuador. Holotype male BMNH [examined].

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 riordinid 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 Cu_2 , 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 sinuous ventral section to the vinculum, a slightly longer saccus, and a slightly shorter string of aedeagal



Figs. 8-11. East Andean *Argyrogrammana amalfreda* group adults (dorsal surface on left, ventral surface on right). **8A.** *A. caelestina* Hall & Willmott, 1995, male, km. 49 Tena-Loreto rd., Napo, E. Ecuador (1350 m). **8B.** *A. caelestina* female, km. 49 Tena-Loreto rd., Napo, E. Ecuador (1350 m). **9A.** *A. pacsa* Hall & Willmott, 1998, male, Yakunk-Cutucú trail, Morona-Santiago, E. Ecuador (1550 m). **9B.** *A. pacsa* female, San Francisco, Zamora-Chinchipe, E. Ecuador (1900 m). **10A.** *A. natalita* Hall & Willmott, 1995, HT male, La Bonita, Sucumbíos, E. Ecuador (1550 m) (BMNH). **10B.** *A. natalita* female, Yakunk-Cutucú trail, Morona-Santiago, E. Ecuador (1550 m). **11A.** *A. cosnipata* Hall, n. sp., HT male, El Mirador, Cuzco, Peru (1700 m) (USNM). **11B.** *A. cosnipata* PT female, El Mirador, Cuzco, Peru (1700 m) (USNM).

cornuti, although an insufficient series has been examined to know whether these represent consistent differences. 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.

Biology: This uncommon species is known to inhabit premontane and lower montane forest from 550 to 1500 m. It is the most commonly encountered of the Andean *amalfreda* group species. In Ecuador, small to medium-sized groups of up to six males were encountered perching on and around tree-trunk epiphytes 2 to 5 m above the ground at the edge of hilltop and ridgetop lightgaps from 1315 to 1615 hrs. Males were attracted to fermento placed on low leaves in these same habitats. Females were found resting beneath leaves 1 to 3 m above the ground along ridgetops in the vicinity of male perching leks in the late morning to early afternoon. The yellow and blue wing pattern of female *A. caelestina* is sufficiently divergent from that of its closest relatives to suggest that this female may be involved in a mimicry ring with other similarly patterned Lepidoptera, particularly in the Nymphalidae and Riodinidae, and, among day-flying moths, in the Erebidae (Arctiinae). Examples of sympatric premontane riodinids with similar yellow and blue ventral patterning include *Lucillella camissa* (Hewitson, 1870) (both sexes) (Symmachiini) and *Ancyluris cacica* (C. & R. Felder, 1865) (female) (Riodinini).

Distribution: *Argyrogrammana caelestina* is known to range from southern Colombia (Cauca) to central Peru (San Martín).

Argyrogrammana pacsa Hall & Willmott, 1998
(Figs. 9A,B)

Argyrogrammana pacsa Hall & Willmott, 1998. *Lambillionea* 98(3)(1): 325, figs. 1A-D. **TL:** Romerillos, Zamora-Chinchipe, E. Ecuador. Holotype male BMNH [examined].

Identification and Taxonomy: *Argyrogrammana pacsa* seems to be the sister species of *A. caelestina*, from which it is distinguished in that species account. However, the male is actually externally more similar to that of *A. natalita*, from which it most obviously differs by being larger and having darker orange-brown scaling on the dorsal wings that typically extends further into the tornus on the forewing, fewer dark spots in the discal cell of the dorsal forewing, a larger blue distal patch on the dorsal forewing that extends into cell Cu_1 , a dark submarginal band on the dorsal hindwing that is separate from instead of fused with the silver submarginal line, blue instead of lilac-blue spots on the ventral forewing that are more proximally positioned, orange scaling distal to the silver submarginal line on the ventral forewing, and a broader band of blue rather than lilac spots along the submargin of the ventral hindwing. Notable intrapopulational wing pattern variation in *A. pacsa* males includes the presence or absence of two dark spots in cell Cu_2 below the middle of the discal cell on the dorsal forewing, the extent of orange-brown submarginal scaling on the dorsal forewing, and the prominence of the dark presubmarginal band on the dorsal hindwing.

When describing *A. nurtia*, Stichel (1910-11) included a non-conspecific female as a syntype, which is now a paralectotype after the male lectotype designation by Hall *et al.* (2023). This female specimen in the ZMHU from Río Zongo, Bolivia, was figured by Hall & Willmott (1995: Figs.

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 paralectotype 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 M_1 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 M_2 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).

Argyrogrammana natalita Hall & Willmott, 1995
(Figs. 10A,B)

Argyrogrammana natalita Hall & Willmott, 1995. *Trop. Lepid.* 6(2): 138, figs. 9A, 9B. TL: km. 12 La Bonita-Rosa Florida rd., Sucumbíos, E. Ecuador. Holotype male BMNH [examined].

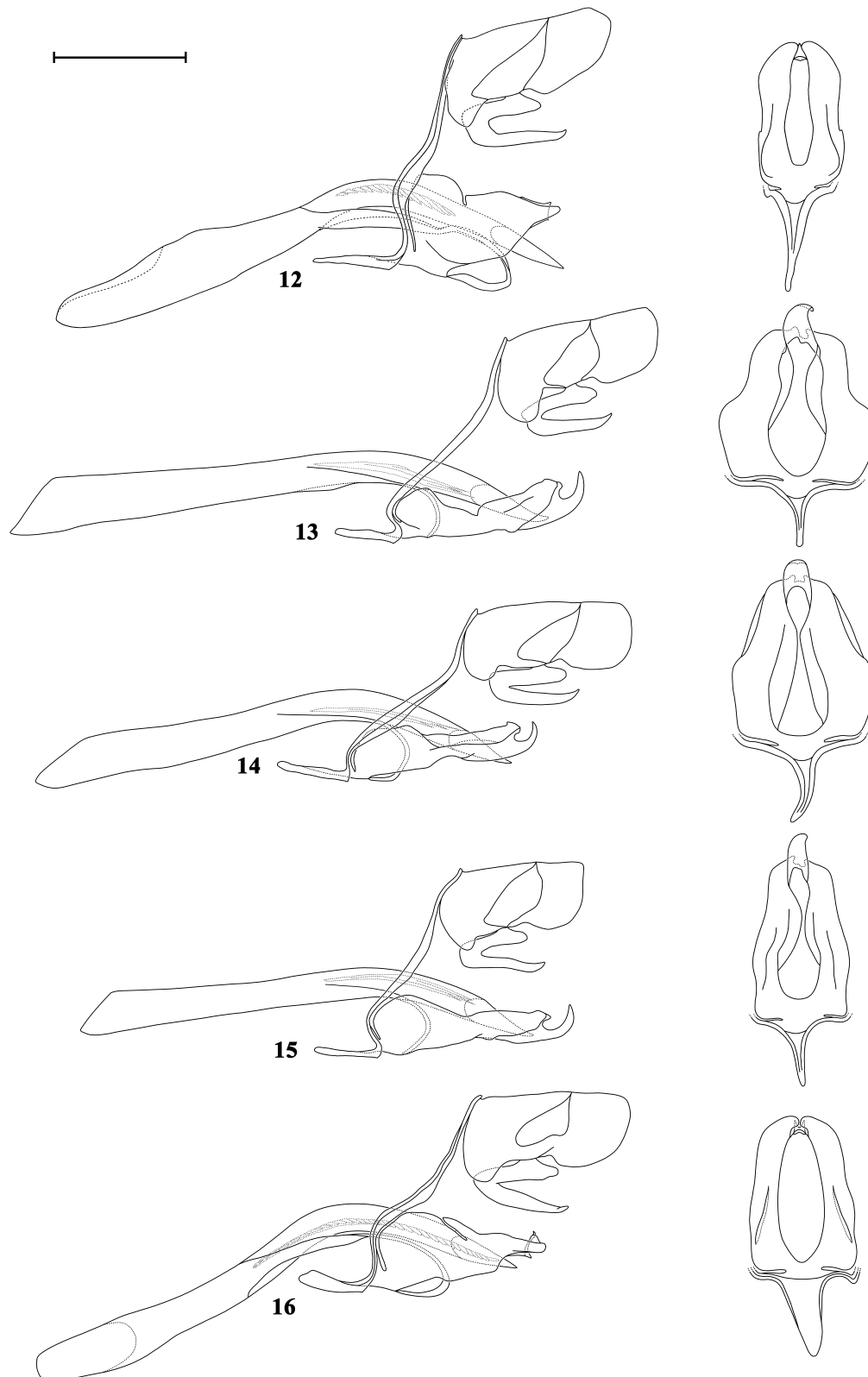
Identification and Taxonomy: *Argyrogrammana natalita* is externally most similar to *A. pacsa*, but it actually appears to be sister to the new species *A. cosnipata*. It is distinguished from both in those species accounts. Notable intrapopulational wing pattern variation in *A. natalita* males includes the shade of the orange dorsal scaling, the prominence of dark spots in cell Cu_2 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 R_{4+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 hilltops 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 (Sucumbíos) and central Peru (San Martín), 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



Figs. 12-16. *Argyrogrammana* male genitalia, with genital capsule in lateral view, and valvae and saccus in ventral view. **12.** *A. janiceae* n. sp. HT (INABIO). **13.** *A. aurora* n. sp. PT, Zamora, Zamora-Chinchipe, E. Ecuador. **14.** *A. saulensis*, Lumbaquí, Sucumbíos, E. Ecuador. **15.** *A. vespertina* PT, El Durango, Esmeraldas, W. Ecuador. **16.** *A. cosnipata* n. sp. HT (USNM). Scale bar = 0.5 mm.

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 transtilla 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, cornutal complex on unevverted 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.

Types: HOLOTYPE male: PERU: *Cuzco*, El Mirador, Paucartambo-Pilcopata rd., Cosñipata valley, 13°04'S 71°33'W, 1720 m, 22 Oct 2013 (S. Kinyon) (USNM).

PARATYPES: PERU: *Cuzco*, 1 female: same locality data as HT, 11 Feb 2011 (B. Harris) (USNM).

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 discal 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 *trochilia* 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 discal 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 M_3 to M_1 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. lamasi* 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 pedicel that medially 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 discal 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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A review of the *Argyrogrammana amalfreda* group fauna of the western Amazon (Lepidoptera: Riodinidae: Symmachiini)

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Abstract: The *Argyrogrammana amalfreda* group (Riodinidae: Symmachiini) fauna of the western Amazon is reviewed. Eighteen species are reported from the region, including three new species that are described here from Ecuador and Peru: *A. lamasi* Ahrenholz & Hall, n. sp., *A. maryanneae* Ahrenholz & Hall, n. sp., and *A. callaina* Hall & Ahrenholz, n. sp. Three names are synonymized: *A. sonazul* P. Jauffret & Martins, 2006, with *A. praestigiosa* (Stichel, 1929), *A. glaucopis virgata* Brévignon & Gallard, 1995, with *A. glaucopis* (Bates, 1868), and *A. nurtia ludibunda* Brévignon & Gallard, 1995, with *A. nurtia* (Stichel, 1911) (n. syn.). A lectotype is designated for the name *Argyrogramma nurtia*.

Key words: Brazil, Colombia, French Guiana, male perching, Neotropics, species description, taxonomy.

INTRODUCTION

The Neotropical riodinid genus *Argyrogrammana* Strand, 1932 (Symmachiini) epitomizes the outstanding beauty of the butterflies in this family, and the rare and elusive nature of its markedly sexually dimorphic species, most of which are denizens of the forest canopy and were unknown to science until recent decades, has combined to create an alluring target for taxonomic attention (e.g., Brévignon & Gallard, 1995; Hall & Willmott, 1995, 1996; Dolibaina *et al.*, 2015; Gallard, 2017). Hall (2023a) provided a comprehensive phylogenetic framework and updated taxonomic overview for the genus, recognizing 55 species in six species groups. With more than 20% of these species undescribed, reviews of several of the most poorly known regional faunas seemed to be worthwhile. Within Amazonia, the *trochilia* group has become well known and the *occidentalis* group has heretofore become reasonably well known (Brévignon & Gallard, 1995; Hall & Willmott, 1996; Gallard, 2008, 2017; Dolibaina *et al.*, 2015), with additional taxonomic clarity provided in Hall & Willmott (2023). However, the much larger *amalfreda* group (30 species), which is most readily characterized by its members possessing orange and blue dorsal wings and gray to blue ventral wings in males, remains incompletely understood. The *amalfreda* group fauna of the eastern Amazon, particularly the Guianas, is now rather well known, thanks to the work of C. Brévignon, J.-Y. Gallard, and others in French Guiana, which culminated in the phenomenal work by Gallard (2017) that correctly matched nearly all the sexes of the species known from that region.

Therefore, this paper is restricted to reviewing the *amalfreda* group fauna of the western Amazon, encompassing the lowland Amazonian territories of Colombia, Ecuador, Peru, Bolivia, and western Brazil (western Amazonas, Acre, and western Rondônia).

Eighteen *amalfreda* group species are reported here from the western Amazon, including 15 described species and three that are described here from Ecuador and Peru. Two additional species are considered geographically peripheral members of the fauna. Prior to the mid-1990s, only seven of the 18 species had been described and only four of the seven were known from the western Amazon (*A. phyton* (Stichel, 1911), *A. glaucopis* (Bates, 1868), *A. amalfreda* (Staudinger, 1887), and *A. nurtia* (Stichel, 1911)). Early discoveries on the lowland *amalfreda* group fauna of Ecuador were published by Hall & Willmott (1995), additional species were described by Dolibaina *et al.* (2015) in their review of the *Argyrogrammana* fauna of Parque Nacional da Serra do Divisor in Acre, western Brazil, and species that were described by Brévignon & Gallard (1995) and Jauffret & Martins (2006) from the eastern Amazon have subsequently been recorded in the western portion of the basin. This review describes the more recently discovered species, includes one species that was recently reared and described by Hall (2023b), matches males and females of many species for the first time, reports many new country records from Ecuador and elsewhere, 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 Brévignon & Gallard (1995) and Gallard (2017) for French Guiana, Constantino *et al.* (2012) for Colombia, and Dolibaina *et al.* (2015) for Acre, western Brazil. 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 (rare species) or country (more common species) 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; DZUP: Departamento de Zoologia, Universidade Federal do Paraná, Curitiba, Brazil; FLMNH: McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, Gainesville, FL, USA; INABIO: Instituto Nacional de Biodiversidad, Quito, Ecuador; LCB: Lalita and Christian Brévignon collection, Matoury, French Guiana; MNHN: Muséum National d'Histoire Naturelle, Paris, France; MPEG: Museu Paraense Emílio Goeldi, Belém, Brazil; MS: Mark J. Simon collection, Gainesville, FL, USA; MUSM: Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Lima, Peru; 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

***Argyrogrammana lamasi* Ahrenholz & Hall, new species**
(Figs. 1; 19)

Description: MALE: Forewing length holotype (HT) and paratype (PT) 12

mm. *Wings:* see Fig. 1. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and yellow marginal scaling; frons yellow, with a broad black transverse band medially, some brown scaling near ventral margin, and a very narrow black transverse band at dorsal margin; labial palpi yellow, with black scaling at ventral tip of first segment and covering distal majority of third segment; antennal length approximately 55% of forewing length, segments black with vertical white lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax orange, ventral surface gray, dorsal surface of abdomen orange with a triangular black mark at anterior margin of all but posterior-most one or two segments, ventral surface pale black with dirty yellow scaling along posterior margin of all segments; all legs banded dark brown and dirty yellow. *Genitalia:* see Fig. 19; sclerotized transtilla between closely spaced valve tips small, medially more heavily sclerotized, slightly concave, and ventrally posteriorly directed in lateral view; ductus ejaculatorius enters anterior tip of aedeagus to right; vesica exits posterior tip of aedeagus to right, cornutal complex on uneverted vesica consists of a straight series of eight medium-sized, slightly convex, ventroposteriorly directed spine-like cornuti; eighth tergite and sternite rectangular. FEMALE: Unknown.

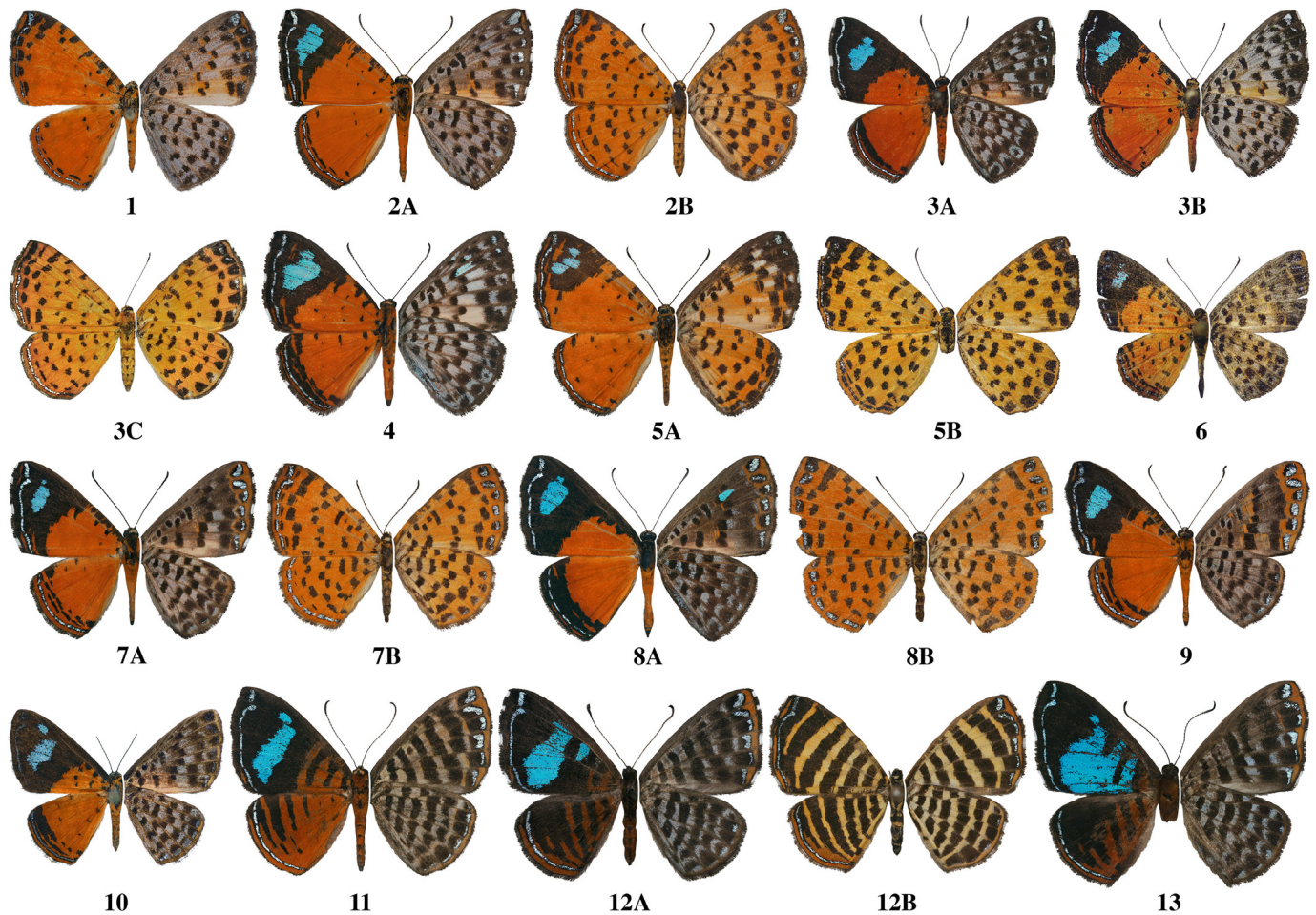
Types: HOLOTYPE male: PERU: *Junin*, Río Venado, Satipo, 11° 15'S 74° 38'W, 650-950 m, Sept 2010 (USNM).

PARATYPES: PERU: *Junin*, 1 male: same data as HT (DA).

Etymology: This species is named for Gerardo Lamas to honor his extraordinary and incomparable contribution to the study of Peruvian Lepidoptera.

Diagnosis: The morphological phylogenetic analysis of *Argyrogrammana* presented by Hall (2023a) indicates that *A. lamasi* n. sp. belongs at the base of the *amalfreda* group, although uncertainty remains about its exact phylogenetic placement. The core of the *amalfreda* group contains 29 species that can nearly all be characterized by the males uniquely possessing widespread orange scaling across both dorsal wings with blue scaling on the dorsal forewing, and by having widespread gray to blue scaling across both ventral wings. Within this group, only the males of *A. aparamilla* Hall & Willmott, 1995, and *A. talboti* Brévignon & Gallard, 1998, lack gray to blue scaling on the ventral surface, which in both cases has been secondarily lost in favor of orange scaling that reflects the dorsal pattern. Elsewhere in the genus, widespread gray to blue ventral scaling is present only in the clade containing *A. occidentalis* (Godman & Salvin, 1886) and the newly described *A. eura* Hall, 2023, and *A. cana* Hall & Willmott, 2023, which have genital morphology unequivocally placing them in the *occidentalis* group, and in *A. caesarion* Lathy, 1958, a species discussed below. Within the core *amalfreda* group, only the male of *A. venilia* (Bates, 1868) lacks widespread orange dorsal scaling, with blue scaling having expanded to occupy most of both dorsal wings, and only the males of *A. lamasi* and the newly described montane *A. cosnipata* Hall, 2023, lack a blue patch on the dorsal forewing. This latter character has obviously been secondarily lost in *A. cosnipata*, which is sister to *A. natalita* Hall & Willmott, 1995, but the polarity of this character with respect to *A. lamasi* remains unclear due to its imprecisely known basal position in the *amalfreda* group (see below).

Argyrogrammana caesarion is biogeographically unique in being the only member of the genus known to inhabit southeastern Brazil, morphologically unique in having widely separated and prominently laterally flared male genital valve tips, and phenotypically unique in having uniformly red dorsal wings in both sexes. It has no obvious close extant



Figs. 1-13. West Amazonian *Argyrogrammana amalfreda* group adults I (dorsal surface on left, ventral surface on right). **1.** *A. lamasi* Ahrenholz & Hall, **n. sp.**, HT male, Río Venado, Junín, Peru (USNM). **2A.** *A. celata* Hall & Willmott, 1995, HT male, Finca San Carlo, Napo, E. Ecuador (BMNH). **2B.** *A. celata* female, Finca San Carlo, Napo, E. Ecuador. **3A.** *A. maryanneae* Ahrenholz & Hall, **n. sp.**, HT male, Finca San Carlo, Napo, E. Ecuador. **3B.** *A. maryanneae* male, P. N. da Serra do Divisor, Acre, W. Brazil (DZUP). **3C.** *A. maryanneae* female, Reserva Nacional Allpahuayo-Mishana, Iquitos, Loreto, Peru (MUSM). **4.** *A. callaina* Hall & Ahrenholz, **n. sp.**, HT male, Pitirishca, Pastaza, E. Ecuador (USNM). **5A.** *A. aparamilla* Hall & Willmott, 1995, HT male, Finca San Carlo, Napo, E. Ecuador (BMNH). **5B.** *A. aparamilla* female, P. N. da Serra do Divisor, Acre, W. Brazil (DZUP). **6.** *A. gallardi* Dolibaina & Dias, 2015, HT male, P. N. da Serra do Divisor, Acre, W. Brazil (DZUP). **7A.** *A. phyton* (Stichel, 1911) male, Finca San Carlo, Napo, E. Ecuador. **7B.** *A. phyton* female, Lumbaquí, Sucumbíos, E. Ecuador. **8A.** *A. bonita* Hall & Willmott, 1995, male, Finca San Carlo, Napo, E. Ecuador. **8B.** *A. bonita* female, Lumbaquí, Sucumbíos, E. Ecuador. **9.** *A. halli* Dolibaina & Dias, 2015, male, Santiago, Morona-Santiago, E. Ecuador. **10.** *A. denisi* Gallard, 1995, male, Coca-Taracoa rd., Orellana, E. Ecuador. **11.** *A. praestigiosa* (Stichel, 1929) male, Reserva Tambopata, Madre de Dios, Peru (USNM). **12A.** *A. glaucopsis* (Bates, 1868) male, Santiago, Morona-Santiago, E. Ecuador. **12B.** *A. glaucopsis* female, P. N. Manu, Pakitza, Madre de Dios, Peru (USNM). **13.** *A. caerulea* Hall, 2023, HT male, Río Sucusari, Explornapo-ACEER, Loreto, Peru (USNM).

relatives, making it difficult to place phylogenetically. In Hall's (2023a) phylogenetic analysis, *A. caesarion* was sister to the core *amalfreda* group, and for convenience it was tentatively included in that species group. However, its placement there is primarily based on its gray male ventral surface, a character that is known to have evolved at least twice in the genus and could be more homoplasious, raising the possibility that *A. caesarion* could occupy an even more basal position in the genus. It is interesting to note that the four species occupying the most basal positions in the hypothesized phylogeny of *Argyrogrammana*, the Transandean *A. crocea* (Godman & Salvin, 1878) at the very base of the tree, the Amazonian *A. stilbe* (Godart, [1824]) at the base (with *A. holosticta* (Godman & Salvin, 1878)) of the *stilbe* group (*barine* group + *trochilia* group) clade, the newly described east Andean *A. janiceae* Ahrenholz & Hall,

2023, at the base of the *occidentalis* group, and the southeast Brazilian *A. caesarion* at the base of the *amalfreda* group, are all allopatrically distributed throughout most of the geographic range of the genus, perhaps providing further support for the hypothesis that these are relictual taxa closely related to the widespread ancestor(s) of the genus. Hall's (2023a) phylogeny recovered *A. lamasi* as sister to the remaining core of the *amalfreda* group, between *A. caesarion* and the *A. sebastiani* Brévignon, 1995, clade. However, this placement is based on a constellation of linked characters stemming from its entirely orange dorsal wings that lack a blue forewing patch, and it is possible that *A. lamasi* is actually sister to *A. celata* Hall & Willmott, 1995, at the base of the *A. sebastiani* clade. *Argyrogrammana lamasi* seems to be most closely related to *A. celata*, having the same male genitalia as that species and

sharing two male wing pattern synapomorphies with most members of the *A. sebastiani* clade, namely a medially divided dark spot at the end of the discal cell on the dorsal forewing (independently derived in *A. willmotti* Dolibaina & Dias, 2015) and a dark submarginal band surrounded by orange scaling on the dorsal hindwing with a dark presubmarginal band confined to single dark spots in the apex and tornus (unique).

The male of *A. lamasi* (Fig. 1) is most obviously separable from that of *A. celata* (Fig. 2A) by having an entirely orange dorsal forewing, with no blue patch and defined dark postdiscal, presubmarginal, and submarginal spots. The ventral surfaces of the two species are similar, but that of *A. lamasi* has more extensive orange scaling proximal to the dark postdiscal band on the forewing than in any examined specimen of *A. celata*, orange scaling proximal to the silver submarginal line on the forewing (absent in all *A. sebastiani* clade members except *A. aparamilla*), and certain dark presubmarginal and submarginal spots on both wings, most notably in cells M_2 and M_1 on the forewing and cell Cu_1 on the hindwing, that are rounded instead of pointed. The male genitalia of the *A. lamasi* holotype (Fig. 19) fall within the range of variation observed in the male genitalia of two examined *A. celata* specimens (see Fig. 20). The male of *A. lamasi* most notably differs from that of *A. caesarion* by having an orange instead of red dorsal surface, a medially divided dark spot at the end of the discal cell on both dorsal wings, an incomplete dark presubmarginal band on both dorsal wings, a dark submarginal band on both dorsal wings, orange postdiscal and submarginal scaling on the ventral forewing, and a largely absent silver submarginal line on the ventral hindwing. Wing pattern variation in the male type series of *A. lamasi* is very limited, and, compared to the figured holotype, the paratype has a dark submarginal band in cells M_2 to Cu_2 on the dorsal forewing that is slightly more separated from the silver submarginal line, and a dark spot visible inside the discal cell end on the ventral forewing. The female of *A. lamasi* is unknown, but can be expected to look very much like that of *A. celata*.

Biology: Nothing is known about the biology of this evidently very rare species, as the type specimens were acquired from a commercial source. The types bear a locality label of “Río Venado, Satipo”. The Peruvian town of Satipo is situated at about 650 m on the Río Satipo, whereas a nearby village with the name Río Venado lies at about 950 m. Satellite imagery of the area reveals that the valley bottoms are deforested, and the topography suggests that the types of *A. lamasi* were most likely collected on a forested hilltop between 700 and 1200 m.

Distribution: *Argyrogrammana lamasi* is currently known only from the type locality in central Peru (Junín), but it seems likely to range at least into Bolivia and perhaps neighboring areas of the southwest Brazilian Amazon.

Argyrogrammana celata Hall & Willmott, 1995
(Figs. 2A,B; 20)

Argyrogrammana celata Hall & Willmott, 1995. *Trop. Lepid.* 6(2): 142, figs. 12A, 12B. TL: Finca San Carlo, km. 12 Tena-

Puyo rd., Napo, E. Ecuador. Holotype male BMNH [examined].

Identification and Taxonomy: *Argyrogrammana celata* is positioned in Hall’s (2023a) phylogeny at the base of the basal *A. sebastiani* clade, which also includes the new species *A. maryanneae* and *A. callaina*, as well as *A. aparamilla*, *A. sebastiani*, and *A. francozi* Gallard, 2017. However, *A. celata* has the same male genitalia as the new species *A. lamasi* (see Figs. 19 and 20), and may be most closely related to that species, as discussed in the previous species account. Externally, the male of *A. celata* is most similar to that of *A. maryanneae*, from which it differs by being larger and having a vertically broader wing shape, more extensive orange submarginal scaling in the tornus of the dorsal forewing, a blue postdiscal patch on the dorsal forewing that has a slightly wider spot in cell R_{4+5} , a less proximally displaced spot in cell M_1 , and a typically slightly smaller and/or narrower spot in cell M_3 , a dark submarginal band on the dorsal hindwing that consists of a typically discontinuous series of narrow spots instead of a broader solid band, gray rather than blue-gray ventral scaling, a less prominently semicircular set of dark postdiscal spots across cells Cu_2 and Cu_1 on the ventral forewing, much more prominent silver submarginal markings on both ventral wings including traces on the hindwing, orange scaling distal to the silver submarginal line on the ventral forewing, and a more prominent white fringe element in forewing cell M_1 that extends to the edge of the fringe. The male genitalia of *A. celata* (Fig. 20) differ from those of *A. maryanneae* (Fig. 21) by having a saccus that is shorter, slightly undulating in lateral view, much broader basally in ventral view, and anteriorly pointed instead of slightly bulbous, valvae with no tiny posterior process at the anterodorsal corner and a slightly broader and distally more inwardly and upwardly curved upper posterior process, a transtilla between the valve tips that has a slightly posteriorly directed and heavily sclerotized ventral section rather than being a plain uniformly sclerotized band, a much shorter, broader, and straighter aedeagus, a very much shorter series of much larger aedeagal cornuti, and an aedeagal pedicel that is posteriorly more angular, medially only gradually slightly broadened instead of abruptly laterally flared, evenly sclerotized instead of more weakly sclerotized anterior to the medial flare, and anteriorly joins the aedeagus on its left side instead of dorsally.

Notable intrapopulational wing pattern variation in *A. celata* males includes the prominence of the dark postdiscal spots on both dorsal wings, which are typically absent but are rarely partially visible, the extent of the orange submarginal scaling in the tornus of the dorsal forewing, which typically extends across cells Cu_2 and Cu_1 but is sometimes confined to cell Cu_2 , the exact (i.e., minor variation) width and shape of the blue distal patch on the dorsal forewing, which extends a variable distance across cell M_3 , the prominence of the dark submarginal band on the dorsal hindwing, which typically forms a discontinuous series of spots but rarely forms a nearly continuous band, and the prominence of black spots on the dorsum of the abdomen.

The female of *A. celata*, associated here with the male for the first time, is most similar to those of *A. maryanneae* and *A. phyton* of the known *amalfreda* group females (females of *A.*

lamasi and *A. callaina* are unknown but are also expected to be very similar), with all three having a complete dark submarginal band on both dorsal wings that is entirely separated from the silver submarginal line. The female of *A. celata* differs from that of *A. maryanneae* by being larger and having a vertically broader wing shape, darker orange wings, a weakly rather than prominently semicircular set of dark postdiscal spots across cells Cu_2 and Cu_1 on the forewing, and a more prominent silver submarginal line on both ventral wings. It differs from that of *A. phyton* by having medially divided dark spots at the discal cell end and toward the base of cell Cu_2 below the middle of the discal cell on the dorsal forewing, a weakly semicircular rather than nearly vertical set of dark postdiscal spots across cells Cu_2 and Cu_1 on the forewing, smaller and separated dark presubmarginal spots on the dorsal forewing, and a silver submarginal line on the ventral forewing that has a less inwardly directed element in cell M_1 and a larger element in cell R_{4+5} . The females of several *occidentalis* group species are also very similar, but they can most quickly be separated from female *A. celata* by having a solid instead of medially divided dark spot at the discal cell end on the dorsal forewing. The two examined *A. celata* females differ only slightly in the shade of the orange wings.

Biology: This very rare species is known from 550 to 800 m. Solitary males were encountered in Ecuador perching at the edge of shady hilltop lightgaps 2 to 4 m above the ground from 1330 to 1600 hrs. A female was encountered flying low to the ground in a male perching lek at 1430 hrs.

Distribution: *Argyrogrammana celata* remains known only from a small area in central eastern Ecuador (Napo), but it seems likely to range at least into Colombia, northern Peru, and perhaps neighboring western Brazil.

***Argyrogrammana maryanneae* Ahrenholz & Hall, new species**
(Figs. 3A-C; 21)

Description: MALE: Forewing length HT 11.5 mm. *Wings:* see Fig. 3A. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and dark yellow marginal scaling; frons black, with a broad dark yellow transverse band ventrally, some yellow scaling at ventral margin, and a dark yellow transverse band dorsally consisting of yellow triangles in dorsal corners and a broad area of sparse yellow scaling in between; labial palpi yellow, with black scaling at ventral tip of first segment and covering distal majority of third segment; antennal length approximately 55% of forewing length, segments black with vertical white lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax orange, ventral surface grayish, dorsal surface of abdomen orange with a triangular black mark at anterior margin of all but entirely black posterior-most segment, ventral surface black with dirty yellow scaling along posterior margin of all segments; all legs banded black and dirty yellow. *Genitalia:* see Fig. 21; sclerotized transtilla between closely spaced valve tips a plain, very slightly concave, uniformly sclerotized band that projects slightly above and below valve tips in lateral view; ductus ejaculatorius enters anterior tip of aedeagus anteriorly and to right; vesica exits posterior tip of aedeagus to right, cornutal complex on uneverted vesica consists of a very long, sinuous ribbon of numerous small (becoming tiny in posterior half of series), largely posteriorly directed spine-like cornuti; eighth tergite and sternite rectangular. FEMALE: Not known with certainty, but see Fig. 3C.

Types: HOLOTYPE male: ECUADOR: Napo, Finca San Carlo, km. 12 Tena-

Puyo rd., 1°05.59'S 77°46.98'W, 550 m, 3 Jan 2010 (D. H. Ahrenholz) (USNM).

Etymology: This species is named for my beloved sister Marianne Ahrenholz Rutzmoser (D. Ahrenholz).

Diagnosis: The morphological phylogenetic analysis of *Argyrogrammana* conducted by Hall (2023a) indicates that *A. maryanneae* n. sp. belongs near the base of the *amalfreda* group, in the *A. sebastiani* clade. It appears to be sister to the new species *A. callaina*, both species uniquely having male genitalia with a very short posterior process at the anterodorsal corner of the valvae, a prominently sigmoidal aedeagus, and a pedicel that joins the aedeagus dorsally and laterally broadens medially, where there is heavy sclerotization posteriorly and weak sclerotization anteriorly. This sister-species pair seems to be sister to the *A. sebastiani* subclade, containing *A. aparamilla*, *A. sebastiani*, and *A. francozi*. All five species uniquely have a blue postdiscal patch on the male dorsal forewing with a distal margin that has the spot in cell M_1 proximally displaced compared to both neighboring spots, and a posterior process at the anterodorsal corner of the male genital valvae (a long process in the *A. sebastiani* subclade), and all five species also have a silver submarginal line on the male ventral forewing that is largely confined to the apex (independently derived in *A. sticheli* (Talbot, 1929) and *A. pulchra* (Talbot, 1929)). In addition, all but *A. callaina* have a blue postdiscal patch on the male dorsal forewing with a proximal margin that has the spot in cell M_1 proximally displaced compared to both neighboring spots, and all but *A. aparamilla* lack orange scaling both distal and proximal to the silver submarginal line on the male ventral forewing (independently derived in *A. caesarion* and most *amalfreda* group species phylogenetically positioned from *A. talboti* onward).

The male of *A. maryanneae* (Figs. 3A,B) is distinguished from the male of its sister species *A. callaina* in that species account. It is actually externally more similar to the male of *A. sebastiani*, known only from French Guiana, and it only subtly differs by having less prominent dark postdiscal spots on both dorsal wings, a broader blue postdiscal patch on the dorsal forewing with a less prominently proximally displaced spot in cell M_1 , no larger faint marks surrounding the fewer dark spots on the dorsal hindwing, a dark submarginal band on the dorsal hindwing that is separated from the silver submarginal line by orange scaling instead of being directly adjacent to it, orange scaling proximal to the dark postdiscal band on the ventral forewing, a slightly more proximally positioned dark/pale postdiscal band across cells M_3 to M_1 on the ventral forewing, more horizontally elongate submarginal spots on both ventral wings, a slightly more prominent silver submarginal line on the ventral forewing, and a reduced white fringe element in forewing cell M_1 that does not extend to the edge of the fringe (the basal row of fringe scales on the ventral forewing is white and the distal row is black). The male of the recently described *A. francozi*, also known only from French Guiana, is similar to that of *A. sebastiani*, and, based on the figured holotype (Gallard, 2017: Pl. 17, Fig. 11), seems to differ from it by having a slightly more pointed wing shape with an angular forewing apex, slightly more extensive orange scaling on the dorsal

forewing, a slightly broader blue postdiscal patch on the dorsal forewing, a dark submarginal band on the dorsal hindwing that is separated from the silver submarginal line by orange scaling as in *A. maryanneae* but consists of separate spots instead of a continuous band, a slightly more proximally positioned dark bar at the discal cell end on the ventral forewing, yellow instead of gray scaling proximal to the dark postdiscal spot in ventral forewing cell Cu_1 , and a slightly broader blue-gray postdiscal band on both ventral wings. The holotype male of *A. maryanneae* is so superficially similar to male *A. sebastiani* that prior to closer study and dissection it was believed to represent that species. However, the male genitalia of *A. maryanneae* (Fig. 21) clearly highlight the phylogenetic affinity of this species with *A. callaina*, whereas the male genitalia of *A. sebastiani* and *A. francozi* are very similar to those of *A. aparamilla*. These last three species form the genitally distinct *A. sebastiani* subclade, with male genitalia that differ from those of *A. maryanneae* by having a shorter saccus, tri-pronged valvae with a much longer anterodorsal process, a more gradually tapered and triangular upper posterior process, and an additional short lower posterior process, a much shorter aedeagus with a much shorter series of larger cornuti, and a more typical *Argyrogrammana* aedeagal pedicel that is evenly tapered and joins the aedeagus on its left side instead of dorsally. The male of *A. maryanneae* is also rather similar to that of *A. celata*, at the base of the *A. sebastiani* clade, from which it is distinguished in that species account.

Dolibaina *et al.* (2015) figured a male specimen (one of seven) from Acre, western Brazil, under the name *A. celata* that is shown here in Fig. 3B. This male differs phenotypically and genitally in numerous ways from that of *A. celata* (see that species account and Figs. 2A and 20), and it is identified here as being conspecific with the Ecuadorian holotype of *A. maryanneae* (Fig. 3A) based on sharing the same wing size and shape, the same fundamental wing pattern, including subtle elements such as the same arrangement of silver submarginal markings on the ventral forewing and the same uniquely reduced white fringe element in forewing cell M_1 detailed above, and the same male genitalia (allowing for some minor artistic differences) (Fig. 53 in Dolibaina *et al.*, 2015). The figured Acre male does exhibit some notable wing pattern differences from the holotype of *A. maryanneae*, including slightly paler orange dorsal scaling, a noticeably larger orange patch on the dorsal forewing that extends from the tornus to the middle of the costal margin, a slightly narrower blue postdiscal patch on the dorsal forewing with a slightly less prominently proximally displaced spot in cell M_1 , more orange marginal scaling on the dorsal forewing, more extensive and grayer blue-gray scaling on the ventral surface, orange scaling proximal to the dark postdiscal band on the ventral hindwing, and slightly narrower presubmarginal spots on both ventral wings. However, given that these two male phenotypes have somewhat distant geographic origins, and most of the differences are typical of intraspecific, even intrapopulational, variation in the genus, we conservatively treat them as belonging to a single variable species.

A female specimen from the Iquitos area of northern Peru in the MUSM (Fig. 3C) is tentatively identified here as *A. maryanneae* based on similarities in wing size, shape, and pattern, again including the same arrangement of silver

submarginal markings on the ventral forewing and seemingly the same reduced white fringe element in forewing cell M_1 . A more definitive assignment of females to males in the basal section of the *amalfreda* group must await the discovery of females for *A. lamasi* and *A. callaina*. The putative female of *A. maryanneae* shares with females of some *amalfreda* and *occidentalis* group species a dark submarginal band on both dorsal wings that is entirely separated from the silver submarginal line, but it can be distinguished from all of these except *A. celata* (among known females) by having a medially divided dark spot at the discal cell end on both dorsal wings. It is separated from female *A. celata* in that species account.

Biology: This very rare species is known from 150 to 550 m. In Ecuador, a solitary male was encountered resting beneath a leaf less than a meter above the ground on a hilltop at 1545 hrs. In western Brazil, males were found perching 6 m above the ground on a hilltop at 1800 hrs (Dolibaina *et al.*, 2015).

Distribution: *Argyrogrammana maryanneae* is currently known only from Ecuador (Napó), Peru (Loreto), and western Brazil (Acre), but it likely occurs more broadly across the western Amazon.

Argyrogrammana callaina Hall & Ahrenholz, new species (Figs. 4; 22)

Description: MALE: Forewing length HT 12.5 mm; PTs 12-12.5 mm. *Wings:* see Fig. 4. *Head:* Eyes dark brown and bare, with a darker brown transverse medial band and yellow marginal scaling; frons black, with a broad yellow transverse band ventrally, some yellow scaling at ventral margin, and a yellow transverse band dorsally consisting of yellow squares in dorsal corners and a narrow area of sparser yellow scaling in between; labial palpi yellow, with black scaling around tip of first and second segments and covering third segment; antennal length approximately 55% of forewing length, segments black with vertical white lateral bands, clubs black with orange-brown tips. *Body:* Dorsal surface of thorax orange, ventral surface gray, dorsal surface of abdomen orange with a triangular black mark at anterior margin of anterior segments and a black tip, ventral surface pale black with dirty yellow scaling along posterior margin of all segments; all legs banded dark brown and dirty yellow. *Genitalia:* see Fig. 22; sclerotized transtilla between closely spaced valve tips prominently concave and ventrally posteriorly directed in lateral view, ventrally bi-pronged in ventral view, and projecting significantly above and below valve tips in lateral view; ductus ejaculatorius enters anterior tip of aedeagus anteriorly and to right; vesica exits posterior tip of aedeagus to right, cornutal complex on uneverted vesica consists of a long, dorsally curved “braided rope” of numerous spine-like cornuti that are small and posteriorly directed in anterior half of series, becoming tiny and ventroposteriorly directed in posterior half of series; eighth tergite and sternite rectangular. FEMALE: Unknown.

Types: HOLOTYPE male: ECUADOR: *Pastaza*, Pítitirshca, Puyo-Macas rd., 1°48'18"S 77°49'15"W, 1000 m, 9 Sept 2001 (R. C. Busby) (USNM).

PARATYPES: ECUADOR: *Napó*, Finca San Carlo, km. 12 Tena-Puyo rd., 1°05.59'S 77°46.98'W, 550 m, 1 male: Mar 2019 (MS); 1 male: 24 Sept 2011 (D. H. Ahrenholz) (DA); 1 male: 24 Feb 2011 (D. H. Ahrenholz) (DA); 1 male: Apuya, km. 14 Tena-Puyo rd., 1°06.00'S 77°46.60'W, 600 m, 17 Dec 2016 (I. Aldas) (to be deposited in INABIO); 1 male: “Tena”, 650 m, Oct 2010 (FLMNH); *Morona-Santiago*, 1 male: N. of San Isidro, nr. Macas, 2°11'54"S 78°09'24"W, 1250 m, 29 Jan 2014 (I. Aldas) (DA); 1 male: km. 2 Santiago-Puerto Morona rd., 450 m, 3°2.14'S 78°00'W, 7 Jan 2012 (D. H. Ahrenholz) (DA).

Etymology: The name is derived from the Latin word “callaina”, meaning “turquoise”, in reference to the sizeable turquoise blue patch on the dorsal forewing in this species.

Diagnosis: The morphological phylogenetic analysis of *Argyrogrammana* conducted by Hall (2023a) indicates that *A. callaina* n. sp. belongs near the base of the *amalfreda* group, in the *A. sebastiani* clade, where it appears to be sister to the new species *A. maryanneae*, as detailed in that species account. The male of *A. callaina* (Fig. 4) differs from that of *A. maryanneae* by being larger and having a vertically broader wing shape, a solid instead of medially divided dark spot (when visible) at the discal cell end on the dorsal forewing, a broader blue postdiscal patch on the dorsal forewing with a spot in cell M_1 whose proximal margin is typically less proximally displaced compared to the spot in cell M_2 , a dark presubmarginal band on the dorsal hindwing that is complete and often continuous instead of being confined to small spots in the tornus and apex, and a dark submarginal band on the dorsal hindwing that is directly adjacent to the silver submarginal line instead of being separated from it by orange scaling. On the ventral surface, *A. callaina* has no orange scaling proximal to the dark postdiscal band on the forewing, slightly paler and bluer blue-gray scaling that forms a broader postdiscal band on both wings with contrasted iridescent pale blue spots in forewing cells R_2 , R_{4+5} , and M_1 , a less jagged and even more reduced silver submarginal line on the forewing, and a larger white fringe element in forewing cell M_1 that extends to the edge of the fringe. The male genitalia of *A. callaina* (Fig. 22) differ from those of *A. maryanneae* (Fig. 21) by having a vertically instead of horizontally elongate uncus that is distally concave instead of convex, a more anteroventrally elongate tegumen, an anteriorly pointed instead of slightly bulbous saccus, valvae with a more prominent posterior process at the anterodorsal corner, a smaller angular base at the anteroventral corner, a broader and more angular upper posterior process, and a prominently concave and ventrally bi-pronged transtilla between the valve tips instead of a plain transtilla band, a slightly shorter, broader, and less sigmoidal aedeagus, a shorter ribbon of slightly larger aedeagal cornuti, and an aedeagal pedicel that is posteriorly less sinuously curved, medially less prominently laterally flared, and anteriorly joins the aedeagus closer to its anterior tip.

The male of *A. callaina* is also similar to the males of the *A. sebastiani* subclade species *A. sebastiani* and *A. francozi*, from French Guiana, but most notably differs by being larger and having a slightly vertically broader and more rounded wing shape, a much broader blue postdiscal patch on the dorsal forewing that typically extends into cell Cu_1 and has a spot in cell M_1 whose proximal margin is not significantly proximally displaced compared to the proportionately broader spot in cell M_2 , barely any dark postdiscal spots on the dorsal hindwing, a complete dark presubmarginal band on the dorsal hindwing, slightly paler blue-gray scaling on both ventral wings, a slightly more proximally positioned dark/pale postdiscal band across cells M_3 to M_1 on the ventral forewing, a broader blue-gray postdiscal band on both ventral wings with iridescent pale blue spots in forewing cells R_2 , R_{4+5} , and M_1 , and slightly different submarginal markings on both ventral wings including a small

dark spot within instead of a larger dark band across the blue-gray submarginal spot on the hindwing. The male genitalia of *A. callaina* are very different from those of *A. sebastiani* and *A. francozi*, which differ in the same ways from *A. maryanneae* as detailed in that species account.

Notable intrapopulational wing pattern variation in *A. callaina* males includes the prominence of the dark spotting in cell Cu_2 within the orange patch on the dorsal forewing, the exact width and shape of the blue distal patch on the dorsal forewing, which typically extends into the upper half of cell Cu_1 , the extent of the orange submarginal scaling on the dorsal forewing, which typically extends from the anal margin to about vein Cu_2 but is sometimes less extensive and rarely more extensive (in the holotype uniquely also appearing distal to the blue patch), and the width of the dark presubmarginal and submarginal bands and the continuity of the former on the dorsal hindwing. The female of *A. callaina* remains unknown.

Biology: This very rare species is known from 450 to 1250 m. A male perching lek has yet to be located, and all of the known males were encountered in subcanopy traps baited with rotting fish and on fermento (a mixture of rotting fish and urine) placed on low leaves in ridgetop, hilltop, and hillside lightgaps.

Distribution: *Argyrogrammana callaina* is currently known only from Ecuador (Napó to Morona-Santiago), but it seems likely to extend at least along the east Andean foothills into Colombia and Peru.

Argyrogrammana aparamilla Hall & Willmott, 1995
(Figs. 5A,B)

Argyrogrammana aparamilla Hall & Willmott, 1995. *Trop. Lepid.* 6(2): 142, figs. 11A, 11B. TL: Finca San Carlo, km. 12 Tena-Puyo rd., Napó, E. Ecuador. Holotype male BMNH [examined].

Identification and Taxonomy: *Argyrogrammana aparamilla* belongs to the *A. sebastiani* subclade, within the *A. sebastiani* clade, which also includes *A. sebastiani* and *A. francozi*, currently known only from French Guiana. The males of these three species are unique in having a narrow and prominently zigzagging blue postdiscal band on the dorsal forewing, a series of tiny dark basal, postdiscal, and presubmarginal spots on the dorsal hindwing that are surrounded by larger faint dark markings (reflecting much larger dark spots on the ventral surface), and tri-pronged male genital valvae, with a long anterodorsal process, a gradually tapered and triangular upper posterior process, and a short, inwardly curved, dorsoventrally flattened, and dorsally deeply notched lower posterior process (see Fig. 5B in Hall (2023a)). They are also unusual in having a relatively distally positioned dark/pale postdiscal band across cells M_3 to M_1 on the ventral forewing, with the distance from the discal cell end to the middle of the pale postdiscal spot in cell M_2 being significantly greater than the distance from the middle of this spot to the distal margin, a character state that has independently evolved in only a handful of other, unrelated

Argyrogrammana species. The phylogenetic relationships within the *A. sebastiani* subclade are not completely clear, but Hall's (2023a) phylogeny recovered *A. sebastiani* and *A. francozi* as sister species based on them sharing a solid instead of medially divided dark spot at the discal cell end on the male dorsal forewing and a male abdomen that is entirely orange dorsally without black spots.

The male of *A. aparamilla* represents one of the most distinctive phenotypes in the genus and can readily be separated from males of its closest relatives, as well as all other *amalfreda* group species, by having an orange and dark-spotted ventral surface. The only other member of the species group to have orange instead of gray to blue ventral scaling, the distantly related *A. talboti*, lacks dark spotting and is otherwise phenotypically and morphologically very different. The male genitalia of *A. aparamilla* (see Fig. 16 in Hall & Willmott (1995) and Fig. 55 in Dolibaina *et al.* (2015)) are very similar to those of *A. sebastiani* and *A. francozi* (see Fig. 3 in Brévignon & Gallard (1995) and Fig. 32 in Gallard (2017)), differing from the former by having a slightly longer saccus, and from the latter by having a longer anterodorsal valve process and a longer series of aedeagal cornuti.

Notable intrapopulation wing pattern variation in Ecuadorian males of *A. aparamilla* includes the exact width of the blue distal patch on the dorsal forewing, which has a variably present spot in cell M_3 , the extent of the orange submarginal scaling on the dorsal forewing, which varies from more or less continuous in the holotype to medially discontinuous, the prominence of the dark postdiscal spots on both dorsal wings and the variable presence of some dark presubmarginal and submarginal spots on the dorsal hindwing, the exact width and shape of the whitish postdiscal spots on the ventral forewing, the extent of the orange submarginal and marginal scaling in the apex of the ventral forewing, the variable presence of faint silver submarginal scaling in ventral forewing cells M_3 and M_2 , and the variable presence of very faint whitish postdiscal marks on the ventral hindwing. The male specimen figured by Dolibaina *et al.* (2015: Figs. 21-22) from Acre, western Brazil, differs from Ecuadorian males by having slightly larger dark spots on the ventral hindwing (particularly postdiscally), and reduced, more yellowish orange scaling on both ventral wings, with more grayish scaling visible in the basal half of the discal cell on the forewing and across the basal third of the hindwing.

Dolibaina *et al.* (2015) figured a female specimen from Acre, western Brazil, under the name *A. saulensis* Gallard, 2008, that is shown here in Fig. 5B. This female differs in numerous ways from that of *A. saulensis* and similar females in the *occidentalis* group, for example by lacking a dark submarginal band on the dorsal forewing that is separated from the silver submarginal line and a complete silver submarginal line on both ventral wings. It is suggested here to be the first known female of *A. aparamilla*, based on it sharing with the male of that species a very similar wing size, shape, and pattern, including a relatively distally positioned dark postdiscal band across cells M_3 to M_1 on the forewing and silver submarginal markings on the ventral surface that are confined to the forewing apex. This combination of characters is unique within west Amazonian *Argyrogrammana* to *A. aparamilla*. The Acre

female does have a solid dark spot at the discal cell end on the dorsal forewing rather than the medially divided spot found in the known males, but a similar discrepancy between the sexes in a spotting character of the forewing discal cell also occurs in *A. amalfreda*, suggesting that this difference alone is insufficient to cast serious doubt on its identification as *A. aparamilla*. The female of *A. aparamilla* is most similar to that of *A. francozi*, differing from the unique female figured by Gallard (2017: Pl. 17, Fig. 11) only by being slightly paler yellow and having a slightly narrower, more discontinuous dark presubmarginal band on the dorsal forewing. The female of *A. sebastiani* is smaller and has a more rounded forewing shape, darker orange wings, and a more proximally displaced dark postdiscal spot in forewing cell Cu_1 .

Biology: This very rare species is known from 450 to 950 m. In Ecuador, solitary males were encountered perching 1 to 5 m above the ground in shady hilltop lightgaps from 1430 to 1515 hrs. In western Brazil, solitary males were similarly found perching 1 to 2 m above the ground in hilltop lightgaps from 1430 to 1500 hrs, with a female encountered flying low to the ground on the same hilltop in the late afternoon (Dolibaina *et al.*, 2015).

Distribution: *Argyrogrammana aparamilla* is currently known only from Ecuador (Sucumbíos to Morona-Santiago) and western Brazil (Acre), but it presumably occurs more broadly across the western Amazon.

Argyrogrammana gallardi Dolibaina & Dias, 2015
(Fig. 6)

Argyrogrammana gallardi Dolibaina & Dias, 2015. *Zootaxa* 4028(2): 235, figs. 17-20. TL: Rio Moa, P. N. Serra do Divisor, Mâncio Lima, Acre, W. Brazil. Holotype male DZUP; type illustrations [examined].

Identification and Taxonomy: *Argyrogrammana gallardi* seems to be phylogenetically positioned between the *A. sebastiani* clade and the remainder of the *amalfreda* group. The next most derived section of the *amalfreda* group, the phylogenetically ladderized *A. physis* (Stichel, 1911) grade, includes *A. phyton*, *A. physis*, *A. bonita* Hall & Willmott, 1995, *A. chicomendesi* Gallard, 1995, and *A. halli* Dolibaina & Dias, 2015, and *A. gallardi* uniquely shares with these five species an approximately evenly rectangular blue postdiscal patch within cells M_3 to M_1 on the male dorsal forewing (with a smaller spot commonly present in cell R_{4+5}). However, *A. gallardi* still retains the medially divided dark spot toward the base of cell Cu_2 below the middle of the discal cell on the male dorsal forewing that is possessed by all *occidentalis* group species and all of the more basal *amalfreda* group species but is lacking in nearly all of the more derived *amalfreda* group species (the exceptions are *A. denisi* Gallard, 1995, *A. danieli* P. Jauffret & Martins, 2006, and *A. amalfreda*). It also lacks the unique vertical component to the dark postdiscal band across cells Cu_2 and Cu_1 on the male ventral forewing that is possessed by all

A. physis grade species, and still retains dark spots along the dorsum of the male abdomen that are present in nearly all of the more basal *Argyrogrammana* species (absent in *A. sebastiani* + *A. francozi*) but absent in nearly all of the more derived *amalfreda* group species (present in the three *A. glaucopis* subclade species and *A. natalita* + *A. cosnipata*).

The first known male of this species was collected in French Guiana, and figured by Brévignon & Gallard (1995: Fig. 11) under the name *A. amalfreda*, before two additional males were collected in Acre, western Brazil, and the species was described by Dolibaina *et al.* (2015) as *A. gallardi* (one of these latter males, the holotype, is shown in Fig. 6). This small species can only be confused with *A. amalfreda* and *A. danieli*, which together constitute the smallest members of the *amalfreda* group, with forewing lengths of 10.5 to 11 mm. The male of *A. gallardi* differs from the males of these two species by having a larger orange patch on the dorsal forewing that includes submarginal orange in the tornus, a smaller and rectangular rather than square blue postdiscal patch on the dorsal forewing, prominent dark postdiscal spots on both dorsal wings, distinct and discontinuous dark presubmarginal and submarginal bands on the dorsal hindwing, dark spots on the dorsum of the abdomen, and a prominently proximally displaced dark postdiscal spot in cell Cu_1 on the ventral forewing. It additionally differs on the ventral forewing from the male of *A. amalfreda* by having two separate interdigitating dark spots in the middle of the discal cell instead of a single dark bar crossing the width of the cell, lacking iridescent blue spots distal to the dark postdiscal band, and having orange submarginal and marginal scaling (traces are also present elsewhere ventrally in the holotype). The male genitalia of these three species are all quite distinct, both from each other and from those of their remaining congeners, with those of *A. gallardi* (see Fig. 54 in Dolibaina *et al.* (2015)) having a slightly longer saccus, broader valvae with a broader upper posterior process and no lower posterior process, a longer aedeagus, and a longer series of aedeagal cornuti. The west Brazilian holotype male of *A. gallardi* differs minorly from the French Guianan male figured by Brévignon & Gallard (1995) and Gallard (2017: Pl. 17, Fig. 9) by having a slightly larger orange patch on the dorsal forewing, a blue postdiscal patch on the dorsal forewing that does not extend into cell M_3 , and scattered orange scaling across both ventral wings, primarily proximal to the dark postdiscal band.

The female specimen figured by Dolibaina *et al.* (2015) under the name *A. gallardi* is identified here as *A. amalfreda*, and no females of *A. gallardi* are known to us from the western Amazon. However, Gallard (2017: Pl. 17, Fig. 9) figured a clearly genuine female of *A. gallardi* from French Guiana (the female originally associated with a male *A. gallardi* specimen in Brévignon & Gallard (1995) seems to be *A. saulensis*). The female of *A. gallardi* is probably most similar to that of *A. amalfreda*, but is darker orange and has a medially divided dark spot toward the base of cell Cu_2 below the middle of the discal cell on the dorsal forewing, the same prominently proximally displaced dark postdiscal spot in forewing cell Cu_1 as the male, a broader dark presubmarginal band on the dorsal forewing that is continuous between cell M_3 and the costal margin and has a more proximally positioned spot in cell Cu_1 , a visible dark

submarginal band on the dorsal hindwing, and noticeably darker orange scaling along the distal margin of the ventral forewing.

Biology: This very rare species is known from near sea level to 450 m. In western Brazil, solitary males were encountered perching 2 to 5 m above the ground on a hilltop from 1530 to 1800 hrs (Dolibaina *et al.*, 2015). Although both sexes are known from French Guiana, no biological data have been reported in association with these specimens (Gallard, 2017).

Distribution: *Argyrogrammana gallardi* is currently known only from western Brazil (Acre) and French Guiana, but it seems likely to be widespread throughout Amazonia.

***Argyrogrammana phyton* (Stichel, 1911)**
(Figs. 7A,B; 23A)

Argyrogramma physis phyton Stichel, 1911. In: Wytzman (ed.), *Gen. Insectorum* 112B: 246. TL: São Paulo de Olivença, Amazonas, W. Brazil. Holotype male ZMHU [examined].

Identification and Taxonomy: *Argyrogrammana phyton* belongs to an apparently non-monophyletic assemblage of similar species referred to here as the *A. physis* grade, which includes *A. physis*, *A. bonita*, *A. chicomendesii*, and *A. halli*. These five species are characterized by having a plain rectangular blue postdiscal patch within cells M_3 to M_1 on the male dorsal forewing (with a smaller spot commonly present in cell R_{4+5}) (also present in the closely related *A. gallardi*), a vertical component to the dark postdiscal band across cells Cu_2 and Cu_1 on the male ventral forewing, and significant orange scaling along the proximal length of the silver submarginal line on the male ventral forewing (not present in *A. physis*, and also present in some specimens of *A. venilia* and *A. praestigiosa* (Stichel, 1929), as well as some *occidentalis* group species). All of these species except *A. physis* also retain the orange scaling proximal to the dark postdiscal band on the male ventral forewing that is present in many of the more basal but none of the more derived *amalfreda* group species. Hall's (2023a) phylogenetic analysis of *Argyrogrammana* recovered *A. phyton* as the most basal member of the *A. physis* grade, with *A. physis* one node removed. However, this arrangement is supported by just a few homoplasious wing pattern characters, and *A. phyton* seems just as likely to be sister to the apparently parapatrically distributed *A. physis*.

Stichel (1910-11) described *A. phyton*, from a single west Brazilian male (see Figs. 3C,D in Hall & Willmott (1995)), as a subspecies of *A. physis*, which was simultaneously described from a single west Colombian male (see Figs. 3A,B 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). However, these two taxa exhibit several consistent wing pattern differences, and with single Ecuadorian exemplars of *A. phyton* (Morona-Santiago province) and *A. physis* (Esmeraldas province) showing a significant sequence divergence of 5.1% in their mitochondrial COI DNA barcodes,

Hall & Willmott (2023) tentatively raised *A. phyton* to species status.

The male of *A. phyton* differs from that of *A. physis* by being slightly smaller and dorsally having a more prominent small dark spot around vein 2A at the very base of the forewing, a variably larger orange patch on the forewing that extends to the costal margin, significant orange submarginal and marginal scaling on the forewing instead of none, on occasion some dark basal spots on both wings, dark presubmarginal and submarginal bands on the hindwing that consist of separate bands of individual spots instead of continuous partially to completely fused bands, and a completely orange instead of typically black and orange margin on the hindwing. On the ventral surface, *A. phyton* males have orange scaling proximal to the dark postdiscal band on the forewing that is always absent in *A. physis* males, orange scaling along the distal forewing margin that consistently forms a prominent band along the entire proximal length of the silver submarginal line instead of rarely being present as traces in the apex, and grayish rather than blue-gray scaling on the hindwing. The male genitalia of *A. phyton* (see Fig. 19 in Hall & Willmott (1995) and Fig. 51 in Dolibaina *et al.* (2015)) and *A. physis* (there is an inaccurate illustration in Brévignon & Gallard (1995: Fig. 8)) are very similar. The first author dissected several specimens of each species, and the only potentially consistent difference that was observed between them was a slightly shorter saccus in *A. phyton*. The male of *A. phyton* is also similar to that of *A. halli*, from which it is distinguished in that species account.

Notable intrapopulational wing pattern variation in *A. phyton* males includes the exact size and shape of the orange patch on the dorsal forewing, the exact width and length of the blue postdiscal patch on the dorsal forewing, which variably extends into cell R_{4+5} and is rarely absent from cell M_3 , the extent of the orange submarginal scaling on the dorsal forewing, which typically extends across cells Cu_2 and Cu_1 but more rarely occurs only in cell Cu_2 or extends in a broken band toward the costal margin, the extent of orange marginal scaling on the dorsal forewing, the occasional presence of some dark basal spots on both dorsal wings, the prominence of the dark presubmarginal band on the dorsal hindwing, the prominence of the orange scaling proximal to the dark postdiscal band and elsewhere across the basal two-thirds of the ventral forewing, the exact width of the orange band along the distal margin of the ventral forewing, and the extent of orange scaling along the distal margin of the ventral hindwing.

The female of *A. phyton*, associated here with the male for the first time, differs from the female of *A. physis* by having a narrower dark presubmarginal band on the dorsal forewing that consists of individual spots instead of a partially fused band, a narrower dark submarginal band on the dorsal forewing that is partially to completely separated from instead of fused to the silver submarginal line, and less extensive pale scaling across the ventral hindwing. The female of *A. phyton* is also similar to those of *A. celata* and *A. bonita* of the known *amalfreda* group females, from which it is distinguished in those species accounts. The females of *occidentalis* group species are also rather similar, but they can most quickly be separated from female *A. phyton* 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 . Wing pattern variation in *A. phyton* females is largely limited to the dark submarginal band on the dorsal forewing, which is typically completely separated from the silver submarginal line but is sometimes fused to it in the tornal half of the wing, and the dark submarginal band on the ventral hindwing, which is typically completely fused with the silver submarginal line but is sometimes partially separated from it.

Biology: This uncommon species is known from near sea level to 1400 m. In Ecuador, solitary males or pairs of males were encountered perching 1 to 4 m above the ground around tree trunks in shady hilltop lightgaps from 0900 to 1045 hrs and then again, much more rarely, from 1500 to 1600 hrs. Females were found flying low to the ground on ridgetops and hilltops from 1150 to 1515 hrs. Both sexes were also attracted to fermento placed on low leaves on hilltops, a male at 1450 hrs (Fig. 23A) and a female at 1510 hrs. In western Brazil, males were found perching 2 m above the ground in a hilltop lightgap at 0900 hrs (Dolibaina *et al.*, 2015).

Distribution: *Argyrogrammana phyton* is widespread across western Amazonia, where it is known to range from Colombia to Peru, and into western Brazil (Amazonas, Acre, and Rondônia). It is replaced in the eastern Amazon and to the west of the Andes by the closely related *A. physis*, although the locations of the contact zones between the two taxa in Colombia and Brazil remain unclear. An historical male specimen of *A. phyton* in the BMNH labeled as originating from Cananche, Cundinamarca, on the western slope of the eastern cordillera in Colombia (figured by d'Abrera (1994: 1051) under the name *A. physis*), may have been mislabeled from the eastern, Amazonian slope. Constantino *et al.* (2012) reported an *A. phyton* male from Villavicencio in central eastern Colombia (Meta) and an *A. physis* male from Puerto Triunfo in the Magdalena valley of central Colombia (Antioquia).

Argyrogrammana bonita Hall & Willmott, 1995
(Figs. 8A,B; 23B)

Argyrogrammana bonita Hall & Willmott, 1995. *Trop. Lepid.* 6(2): 143, figs. 13A, 13B. **TL:** Finca San Carlo, km. 12 Tena-Puyo rd., Napo, E. Ecuador. Holotype male BMNH [examined].

Identification and Taxonomy: *Argyrogrammana bonita* belongs to the *A. physis* grade and seems to be sister to *A. chicomendesi* and *A. halli*. The males of all three species completely lack a small dark spot around vein 2A at the very base of the dorsal forewing, a character state that occurs elsewhere only in *A. talboti* and the four *A. nurtia* clade members, and typically have an orange band along the proximal length of the silver submarginal line on the ventral forewing, which is consistently present elsewhere in the *amalfreda* group only in *A. phyton*.

The male of *A. bonita* is most similar to those of *A. physis*

and *A. chicomendesi*, east Amazonian species with which it is known to be sympatric in Guyana. The most characteristic wing pattern element of male *A. bonita*, which separates it from the males of all other *amalfreda* group species, is its contrasted, iridescent turquoise postdiscal mark in ventral forewing cell M_1 . Additional characters separating it from the males of both *A. physis* and *A. chicomendesi* are a squatter and less pointed forewing shape, a slightly broader blue postdiscal patch on the dorsal forewing, typically more extensive orange scaling proximal to the silver submarginal line on the ventral forewing, and more bluish blue-gray scaling on both ventral wings. The male of *A. bonita* further differs from that of *A. physis* by having broader and more completely fused dark presubmarginal and submarginal bands on the dorsal hindwing, orange scaling proximal to the dark postdiscal band on the ventral forewing, a narrower band of typically less prominent blue-gray scaling distal to the dark postdiscal band on the ventral forewing, and a broader dark presubmarginal band on the ventral forewing; and from that of *A. chicomendesi* by having a slightly larger basal orange patch on both dorsal wings, slightly more extensive orange submarginal and marginal scaling on the dorsal hindwing, a jagged rather than straight series of dark postdiscal spots between cell M_3 and the costal margin on the ventral forewing, and a jagged rather than straight series of dark postdiscal and presubmarginal spots between cells M_3 and R_{4+5} on the ventral hindwing. The male genitalia of *A. bonita* (see Fig. 18 in Hall & Willmott (1995) and Fig. 49 in Dolibaina *et al.* (2015)) differ from those of the other *A. physis* grade species by having a ventral notch in the valvae immediately anterior to the ventroposterior corner, an upper posterior valve process that is much longer, broader, more upwardly directed, and posteriorly instead of inwardly (*A. phyton* and *A. physis*) or outwardly (*A. chicomendesi* and *A. halli*) directed, a more posteriorly projecting transtilla, and a shorter series of aedeagal cornuti.

Notable intrapopulational variation in dorsal wing pattern in *A. bonita* males includes the exact shape of the orange patch on both wings, the exact width and length of the blue postdiscal patch on the forewing, which rarely extends into cell Cu_1 , the occasional presence of orange tornal submarginal scaling and rare presence of orange marginal scaling on the forewing, the rare presence of a dark cell end mark on the hindwing, and the prominence of the orange submarginal and marginal scaling on the hindwing. Local ventral variation includes the size and shape of the turquoise postdiscal mark in forewing cell M_1 , which rarely is either barely visible or accompanied by an additional smaller spot in the cell above, the prominence of the orange scaling proximal to the dark postdiscal band and elsewhere across the basal two-thirds of the forewing (very rarely absent), the prominence of the blue-gray scaling distal to the dark postdiscal band on the forewing, the width and extent of the orange scaling proximal to the silver submarginal line on the forewing, which typically extends along nearly the entire length of the wing but is occasionally confined to the apex and very rarely absent, and the rare presence of orange scaling proximal to the costal portion of the dark postdiscal band and along the margin on the hindwing.

The female of *A. bonita*, which is associated here with the male for the first time, can readily be confused with those of *A.*

phyton and *A. physis*, but differs from both by lacking a dark submarginal band on the dorsal hindwing. It additionally differs from female *A. phyton* by being slightly larger and having a dark submarginal band on the dorsal forewing that is completely fused to instead of partially to completely separated from the silver submarginal line, and from female *A. physis* by having narrower dark presubmarginal and submarginal bands on the dorsal forewing that largely consist of individual spots instead of partially fused bands. No significant wing pattern variation has been observed in *A. bonita* females.

Biology: This uncommon species is known from near sea level to 1100 m. In Ecuador, males were encountered perching singly or in groups of up to three individuals 1 to 3 m above the ground on and around tree trunks in shady hilltop and ridgetop lightgaps from 1300 to 1500 hrs, although most commonly in the final half hour of this period. Females were observed flying into hilltop male perching lek areas about 3 m above the ground between 1330 and 1445 hrs. Both sexes were also attracted to fermento placed on low leaves on hilltops, males from 1115 to 1530 hrs (Fig. 23B) and a female at 1100 hrs. In western Brazil, males were similarly found perching 2 m above the ground in hilltop lightgaps at 1500 hrs (Dolibaina *et al.*, 2015).

Distribution: *Argyrogrammana bonita* is known to range from Ecuador to Peru, and into western Brazil (Amazonas and Acre), and there is also an outlying record from Guyana. This is one of a handful of otherwise west Amazonian riordinid species that were recently collected in the mountains of southern Guyana by Steve Fratello (material in the USNM), with other examples including *Minotauros lampros* (Bates, 1868), *Livendula pauxilla* (Stichel, 1911), and *Mesenopsis pulchella* Godman, 1903 (Hall, 2018).

***Argyrogrammana halli* Dolibaina & Dias, 2015**
(Fig. 9)

***Argyrogrammana halli* Dolibaina & Dias, 2015.** *Zootaxa* 4028(2): 233, figs. 13, 14. **TL:** Rio Moa, P. N. Serra do Divisor, Mâncio Lima, Acre, W. Brazil. Holotype male DZUP; type illustrations [examined].

Identification and Taxonomy: *Argyrogrammana halli* is sister to the east Amazonian *A. chicomendesi*, with males of the two *A. physis* grade species uniquely sharing a straight and approximately vertical component to the dark postdiscal band across cells M_3 to R_2 (in addition to cells Cu_2 and Cu_1) on the ventral forewing, a straight component to a continuous (below vein R_s) dark postdiscal band across cells M_3 to R_s on the ventral hindwing, and very distinctive genitalia. The male genitalia have an upwardly and outwardly curved upper posterior valve process, a transtilla that consists of broad lateral bands posteroventrally which are only connected dorsally with no medial sclerotization posteroventrally, and a twisted series of medium length spine-like aedeagal cornuti that in the posterior half of the uneverted vesica form a “comb”-like pattern with the widely spaced cornuti perpendicular to the aedeagus (see Figs. 5E,J in Hall (2023a)).

The male of *A. halli* differs from that of *A. chicomendesi* by having an angular forewing apex, a larger orange basal patch on the dorsal forewing that extends to the costal margin, a slightly broader blue postdiscal patch on the dorsal forewing, orange submarginal and marginal scaling on the dorsal forewing, a dorsal hindwing that is entirely orange except for the narrow dark presubmarginal and submarginal bands instead of being orange in the basal three-fifths and almost entirely black in the distal two-fifths, a more consistently straight dark postdiscal band on the ventral forewing, a consistently thick band instead of a variably narrow line of orange scaling proximal to the silver submarginal line on the ventral forewing, and a prominent silver submarginal line on the ventral hindwing. The male genitalia of *A. halli* (see Fig. 52 in Dolibaina *et al.* (2015)) are very similar to those of *A. chicomendesi*, but the lateral illustration for the latter species in Brévignon & Gallard (1995: Fig. 9) is too crude to show any of the (mostly ventral) diagnostic characters, explaining why Dolibaina *et al.* (2015) were unable to identify correctly the closest relative to their new species. The genitalia of *A. halli* differ only by having a slightly more prominently projecting ventroposterior corner to the valvae, an upper posterior valve process that is slightly broader in lateral view and slightly more prominently upwardly and outwardly curved, a transtilla that dorsally has a straight instead of slightly posteriorly projecting posterior margin, and a slightly shorter series of aedeagal cornuti. The male of *A. halli* is also similar to that of *A. phyton*, but differs by having an angular forewing apex, no small dark spot around vein 2A at the very base of the dorsal forewing, typically a slightly smaller orange patch on the dorsal forewing with typically slightly less submarginal scaling in the tornus, a slightly different blue postdiscal patch on the dorsal forewing that is typically slightly broader, much more rarely extends into cell R_{4+5} , and typically extends to the vicinity of vein Cu_1 instead of the middle of cell M_3 , and a slightly broader and more continuous dark presubmarginal band on the dorsal hindwing. It differs ventrally by having a virtually straight dark postdiscal band on the forewing with more extensive orange scaling typically present proximally and less prominent grayish scaling present distally, typically a broader area of orange scaling proximal to the silver submarginal line on the forewing, and straighter dark postdiscal and presubmarginal bands across cells M_3 to R_s on the hindwing. The male genitalia of the two species are very different. In addition to the diagnostic genital characters listed in the previous paragraph, the male genitalia of *A. halli* (and *A. chicomendesi*) differ from those of *A. phyton*, *A. physis*, and *A. bonita* by having an aedeagal pedicel that is medially laterally flared.

Notable intrapopulational wing pattern variation in *A. halli* males includes the size and shape of the orange patch on the dorsal forewing, including the extent of orange submarginal scaling in the tornus, the exact width and shape of the blue postdiscal patch on the dorsal forewing, which can rarely extend slightly into cell Cu_1 and/or cell R_{4+5} , the extent of orange marginal scaling on the dorsal forewing, the width and continuity of the dark presubmarginal band and prominence of the dark submarginal band on the dorsal hindwing, the prominence of the orange scaling proximal to the dark postdiscal band and elsewhere across the basal two-thirds of the ventral

forewing, the exact width of the orange band along the distal margin of the ventral forewing, and the extent of orange scaling along the distal margin of the ventral hindwing. The female of *A. halli* remains unknown, but can be expected to look similar to the female of *A. chicomendesi*, which has more of a banded wing pattern than the other known *A. physis* grade females.

Biology: This rare species is known from 400 to 1100 m. In Ecuador, solitary males or pairs of males were encountered perching 2 to 5 m above the ground on tree-trunk lianas and epiphytes in shady hilltop lightgaps from 1430 to 1500 hrs. Males were also attracted to fermento placed on low leaves on hilltops. In western Brazil, a pair of males was found perching 2 m above the ground on a hilltop at 1000 hrs (Dolibaina *et al.*, 2015), suggesting that this species, like the closely related *A. phyton*, may have discrete morning and afternoon perching phases.

Distribution: *Argyrogrammana halli* is currently known only from Ecuador (Pastaza and Morona-Santiago) and western Brazil (Acre), but it is likely to be widespread across the western Amazon, where it seems to replace the east Amazonian *A. chicomendesi*.

Argyrogrammana denisi Gallard, 1995
(Fig. 10)

Argyrogrammana denisi Gallard, 1995. In: Brévignon & Gallard, *Lambillionea* 95(3): 395, figs. 9, 10. TL: Galion, Roura, Cayenne, French Guiana. Holotype male MNHN [examined].

Identification and Taxonomy: *Argyrogrammana denisi* seems to belong near the base of the derived half of the *amalfreda* group, but the species exhibits a curious blend of characters, making its phylogenetic placement hard to pinpoint definitively. Hall's (2023a) phylogenetic analysis of *Argyrogrammana* recovered *A. denisi* as the most basal member of the *A. venilia* clade, containing the phenotypically highly derived and generally dissimilar *A. venilia* and *A. glaucopis* and relatives, based on all five clade members having males with a blue postdiscal patch on the dorsal forewing that extends to at least vein Cu_2 , but *A. denisi* having a blue postdiscal patch with a costal spot in cell R_{4+5} that is significantly distally disjunct and isolated instead of merely distally displaced and generally contiguous. Both of these dorsal wing pattern characters have also evolved, apparently independently, in the *A. nurtia* clade, which belongs in the terminal crown of the *amalfreda* group, whose species share several characters associated with their blue ventral wing patterns. *Argyrogrammana denisi* also seems to be closely related to *A. danieli* and, to a lesser extent, *A. amalfreda*, with which it uniquely shares among derived *amalfreda* group species a medially divided dark spot toward the base of cell Cu_2 below the middle of the discal cell on the male dorsal forewing, a character otherwise possessed by basal *amalfreda* group species and *occidentalis* group members.

The male of *A. denisi* is not very similar to that of any other species, but overall it most closely approaches that of

A. danieli, most obviously differing by having the elongate composite blue postdiscal patch on the dorsal forewing described above instead of a simpler and smaller square patch. The wing patterns are otherwise remarkably similar, with that of male *A. denisi* most notably having orange scaling proximal to the silver submarginal line on the ventral forewing and a narrower dark submarginal band on the ventral hindwing. The arrangement of distal black markings on the dorsal hindwing is also remarkably stable in male *A. denisi*, with two separate dark presubmarginal spots present in cells Cu_2 and Cu_1 in all examined specimens, whereas in male *A. danieli* this area of the dorsal hindwing is variable, with the holotype having a largely black distal third to the wing and the male figured here having a continuous dark presubmarginal line across cells Cu_2 and Cu_1 on a wing that is otherwise practically the same as in *A. denisi*. The male genitalia of *A. denisi* (see Fig. 4 in Brévignon & Gallard (1995)) are rather non-descript, perhaps most similar to those of *A. physis* and *A. phyton*, whereas the male genitalia of *A. danieli* are distinctive for their very long and narrow upper posterior valve process, posteriorly elongate transtilla, and short aedeagus.

Notable intrapopulational wing pattern variation in *A. denisi* males includes the exact size of the orange patch on the dorsal forewing, the exact width and shape of the blue postdiscal patch on the dorsal forewing, which extends a variable amount across cell Cu_1 , the exact extent of the orange submarginal and marginal scaling on the dorsal hindwing, the prominence of the orange scaling proximal to the silver submarginal line on the ventral forewing, and the extent of orange scaling along the distal margin of the ventral hindwing. One Ecuadorian male has slight traces of orange scaling proximal to the dark postdiscal band on the ventral forewing, which is absent in all other examined *A. denisi* males. The known Ecuadorian males differ only very slightly from French Guianan males by having slightly less prominent dark spotting within the orange dorsal patches and on average a slightly broader blue postdiscal patch on the dorsal forewing. The male genitalia of the two populations were examined and found to be the same.

No females of *A. denisi* are known to us from the western Amazon, but Brévignon & Gallard (1995: Fig. 10) and Gallard (2017: Pl. 17, Fig. 5) figured females from French Guiana. It is most similar to the females of *A. sebastiani*, *A. francozi*, and *A. gallardi*, which all share a medially divided dark spot toward the base of cell Cu_2 below the middle of the discal cell on the dorsal forewing and a broad dark submarginal band on the dorsal forewing that is fused to the silver submarginal line. However, the female of *A. denisi* can be separated from those of all three species by having a relatively straight instead of semicircular component to the dark postdiscal band across cells Cu_2 and Cu_1 on the forewing, and a prominent silver submarginal line on the ventral hindwing. These two characters are shared by the putative female of *A. danieli*, but the female of that species has a narrower dark submarginal band on the dorsal forewing that is entirely separated from the silver submarginal line, a largely absent dark submarginal band on the dorsal hindwing, and a broader dark submarginal band on both ventral wings. The three *A. denisi* females figured in the literature do not significantly differ from each other.

Biology: This species is known from sea level to 1100 m, where it is rare (Guianas) to very rare (remainder of Amazonia). In Ecuador, a solitary male was encountered perching 5 m above the ground below the canopy of a hilltop's tallest tree at 1400 hrs. A male was also attracted to fermento placed on low leaves on a hilltop at 1600 hrs. In French Guiana, small groups of males were found perching 4 to 7 m above the ground on and around hilltop tree trunks from 1230 to 1430 hrs (Brévignon & Gallard, 1995; Gallard, 2017).

Distribution: *Argyrogrammana denisi* is reported here from the western Amazon for the first time. It is now known from Ecuador (Orellana, Morona-Santiago, and Zamora-Chinchipec) as well as French Guiana, implying that it is widespread throughout much of Amazonia.

Argyrogrammana praestigiosa (Stichel, 1929)

(Fig. 11; 23C)

Argyrogrammana praestigiosa Stichel, 1929. *Mitt. Zool. Mus. Berl.* 15(1): 19. **TL:** No locality data. Holotype male ZMHU [examined].

= *Argyrogrammana sonazul* P. Jauffret & Martins, 2006. *Lambillionea* 106(3)(1): 398, figs. 7, 8. **TL:** Granja Sonho Azul, Reserva Klagesi, Santo Antônio do Tauá, Pará, E. Brazil. Holotype male MPEG; type illustrations [examined]. **n. syn.**

Identification and Taxonomy: *Argyrogrammana praestigiosa* belongs to the well-defined *A. glaucopsis* subclade, within which it is sister to *A. glaucopsis* and the newly described *A. caerulea* Hall, 2023. The males of all three species uniquely share a dorsal forewing with multiple orangish bands at the wing base and a dorsal hindwing with orangish scaling that is largely confined to the basal and anal regions of the wing. They are also unusual in having a single dark bar across the middle of the discal cell on the ventral forewing instead of two separate interdigitating dark spots, a character state that occurs elsewhere only in the more derived *amalfreda* group species *A. amalfreda*, *A. alstonii* (Smart, 1979), *A. pulchra*, and *A. sticheli*, as well as in the derived majority of *trochilia* group species, and a more banded ventral pattern than is present elsewhere in the *amalfreda* group but is reminiscent of the *trochilia* group. The females of the *A. glaucopsis* subclade species uniquely share a dorsal forewing with dark yellow to orange diagonal bands and a dorsal hindwing with a dark orange band proximally lining the anal portion only of the silver submarginal line. The derived, banded wing patterns of *A. glaucopsis* subclade species make determining their phylogenetic placement difficult. They have previously been suspected to be closely related to the *trochilia* group (e.g., Hall & Willmott, 1996), but Hall's (2023a) phylogenetic analysis of *Argyrogrammana* conclusively showed that any resemblance is superficial and the *A. glaucopsis* subclade belongs in the derived half of the *amalfreda* group. Hall's (2023a) analysis placed the *A. glaucopsis* subclade within a broader *A. venilia* clade, with the dorsally blue-banded *A. venilia* as sister and *A. denisi* at the base of the clade, although there is certainly limited evidence to support this arrangement. All of the *A. venilia* clade species

share the homoplasious character of a blue postdiscal patch on the male dorsal forewing that extends to at least vein Cu_2 , and *A. venilia* and the *A. glaucopis* subclade can be united based on uniquely possessing a blue postdiscal patch on the male dorsal forewing with a costal spot in cell R_{4+5} that is distally displaced (compared to both neighboring spots in cells M_2 and M_1) yet generally contiguous, and uniquely for the *amalfreda* group having multiple blue markings in (and sometimes below) the discal cell on the male dorsal forewing (not present in *A. praestigiosa*). *Argyrogrammana chicomendesi* and *A. halli* possess some less derived banded elements to their ventral wing patterns, but the preponderance of evidence suggests that they are closely related members of the *A. physis* grade rather than *A. venilia* clade members, implying that banded wing patterns have independently evolved twice in the *amalfreda* group in addition to the *trochilia* group.

The male of *A. praestigiosa* can readily be separated from those of *A. glaucopis* and *A. caerulea* by having orange scaling on both dorsal wings that is typically paler and more extensive, no blue markings in or below the discal cell on the dorsal forewing, and a variably narrower blue postdiscal patch on the dorsal forewing. The ventral wing pattern of all three species is virtually the same, although that of *A. praestigiosa* is more variable (see below). The male genitalia of *A. praestigiosa* (see Fig. 10 in Brévignon & Gallard (1995) and Fig. 56 in Dolibaina *et al.* (2015)) differ from those of *A. glaucopis* and *A. caerulea* by having larger aedeagal cornuti and a medially flared aedeagal pedicel. They additionally differ from the former by having a slightly longer and posteriorly rather than slightly upwardly directed upper posterior valve process, a longer aedeagus, and a longer series of more anteriorly positioned aedeagal cornuti (on the unverted vesica), and from the latter by having a slightly shorter saccus, dorsoventrally much broader valvae, and a slightly shorter upper posterior valve process.

Notable intrapopulation wing pattern variation in *A. praestigiosa* males includes the presence or absence of orange scaling along the costal margin on the dorsal forewing, the prominence of a third main orange discal band near the discal cell end on the dorsal forewing, the exact width, length, and shape of the blue postdiscal band on the dorsal forewing, which extends a variable amount across cell Cu_2 and includes a costal spot in cell R_{4+5} that varies from merely distally displaced but contiguous to distally disjunct and isolated, the presence (rare) or absence (seemingly always absent in the Guianas) of orange marginal scaling in the tornus on the dorsal forewing, the extent of orange submarginal and marginal scaling on the dorsal hindwing, the exact width and shape of the pale bands on both ventral wings, and the prominence of the orange marginal scaling on the ventral forewing. *Argyrogrammana praestigiosa* males also exhibit significant geographic variation. Males from French Guiana rarely have even a partial third (distal) orange discal band on the dorsal forewing, always have a narrow blue postdiscal band on the dorsal forewing that rarely enters cell Cu_2 , consistently have a large black area in the apex of the dorsal hindwing devoid of orange scaling, always have grayish banding on both ventral wings with no orange scaling proximal to the silver submarginal lines, seem to have more proximally pointed dark submarginal spots on the ventral hindwing, and

always have an entirely orange dorsum to the abdomen. The holotype male of *A. praestigiosa* (see Fig. 1 in Hall & Willmott (1995)) lacks locality data, but its wing pattern closely matches that of this population and it seems likely to have been collected in the Guianas. West Amazonian males, in contrast, always have a partial to fully formed third orange discal band on the dorsal forewing, typically have a broader blue postdiscal band on the dorsal forewing that always crosses most or all of cell Cu_2 , consistently have some orange postdiscal, presubmarginal and submarginal scaling extending into the apex on the dorsal hindwing, always have variably prominent orange scaling within the grayish band proximal to the silver submarginal line on both ventral wings with faint orange scaling typically present in association with many of the remaining grayish bands, seem to have more proximally rounded dark submarginal spots on the ventral hindwing, and consistently have variably prominent black spots along the orange dorsum of the abdomen. The male genitalia of these two populations were examined and found not to differ. Males from the east Brazilian Amazon, one of which from Belém was figured by d'Abrera (1994: 1051) under the name *A. barine* (Staudinger, 1887), have intermediate wing patterns, with a partial third orange forewing band, a blue forewing band like west Amazonian males, a hindwing apex like Guianan males, a ventral surface that is intermediate, and a dorsally orange abdomen. Jauffret & Martins (2006) proposed the name *A. sonazul* based on one such male from near Belém, which has an aberrationally narrowed blue forewing band in cells M_2 and M_1 but otherwise seems typical of the regional population. Dolibaina *et al.* (2015) raised the possibility that *A. sonazul* might be conspecific with *A. praestigiosa*, and, given the above-presented evidence suggesting that geographic variation in *A. praestigiosa* is clinal rather than discrete, the name *A. sonazul* is newly synonymized here with *A. praestigiosa* (**n. syn.**).

No clearly identifiable females of *A. praestigiosa* are known to us from the western Amazon, but Brévignon & Gallard (1995: Fig. 24) and Gallard (2017: Pl. 18, Fig. 14) figured females from French Guiana. It is very similar to the female of *A. glaucopis* (female *A. caerulea* is unknown) but differs by having darker and more orange than yellow dorsal bands, no yellow-orange submarginal band in the apex of the dorsal forewing, and a broken instead of continuous yellow submarginal band in the apex of the ventral forewing. However, given the geographic variation evident in males of *A. praestigiosa*, it is not clear whether or how well these differences will serve to distinguish females of the two species in the western Amazon. Local variation in *A. praestigiosa* females includes the exact width, shape, and angle of the pale bands, particularly the postdiscally positioned band on the forewing.

Biology: We have examined specimens of this rare species from sea level to 600 m, although Lamas *et al.* (in press) report it occurring up to 1050 m in southern Peru. In Ecuador, a male perching lek has yet to be located, and all of the known males were encountered on fermento placed on low leaves (Fig. 23C), mostly on hilltops but also once in flat forest. In western Brazil, an apparently non-perching male was encountered flying 4 m above the ground at 1300 hrs (Dolibaina *et al.*, 2015). In eastern

Brazil, a male was collected on low *Cordia schomburgkii* DC. flowers (Cordiaceae) near the edge of flat forest at 1330 hrs (Jauffret & Martins, 2006). In French Guiana, large groups of males of up to 12 individuals were found perching 4 to 10 m above the ground around a hilltop tree trunk from 1600 to 1630 hrs (Brévignon & Gallard, 1995; Gallard, 2017).

Distribution: *Argyrogrammana praestigiosa* appears to be widespread throughout much of Amazonia, where it is known to range from Ecuador to Peru, and along the length of the Brazilian Amazon into French Guiana.

Argyrogrammana glaucopis (Bates, 1868)
(Figs. 12A,B; 23D)

Charis glaucopis Bates, 1868. *J. Linn. Soc. Lond. Zool.* 9(39): 393. **TL:** Tefé, Amazonas, W. Brazil. Syntype male BMNH [examined].

= *Argyrogrammana glaucopis virgata* Brévignon & Gallard, 1995. *Lambillionea* 95(3): 398, figs. 31, 32. **TL:** km. 35 on Route Nationale 2, Roura, Cayenne, French Guiana. Holotype male LCB; type illustrations [examined]. **n. syn.**

Identification and Taxonomy: *Argyrogrammana glaucopis* is most similar to and appears to be the sister species of the newly described *A. caerulea*, with the males of the two species being unique in the genus in possessing two blue spots only in the discal cell of the dorsal forewing, and having darker, more orange-brown dorsal bands than in the other *A. glaucopis* subclade species *A. praestigiosa*. The male of *A. glaucopis* primarily differs from that of *A. caerulea* by having a blue postdiscal band on the dorsal forewing that is separated from the blue discal spots instead of a much larger blue medial patch that from the postdiscal area extends basally in cells 2A, Cu₂, and Cu₁ to form a contiguous patch with the two blue spots in the discal cell. It also seemingly consistently lacks orange scaling proximal to the dark submarginal spots on the ventral forewing. The male genitalia of the two species are surprisingly distinct, with those of *A. glaucopis* (see Fig. 11 in Brévignon & Gallard (1995), Fig. 21 in Hall & Willmott (1996), and Fig. 1V in Hall (2023b)) differing from those of *A. caerulea* (see Fig. 2O in Hall (2023b)) by having dorsoventrally broader valvae with a much shorter upper posterior process, a proportionately shorter saccus and aedeagus, and a shorter, more convex, and more posteriorly positioned series of aedeagal cornuti (on the uneverted vesica) that become larger rather than smaller posteriorly.

Notable intrapopulational wing pattern variation in *A. glaucopis* males includes the shade of the orange bands on both dorsal wings, which vary from medium orange (atypical) to orange brown (typical), the extent of orange scaling at the very base of the dorsal forewing, the width of the blue spot at the discal cell end and the size of the blue spot in the middle of the discal cell on the dorsal forewing (which rarely can be barely visible, as in Fig. 12A, or even absent), the exact width and shape of the blue postdiscal band on the dorsal forewing, which sometimes includes an additional tiny costal spot in cell R₂, has a spot in

cell R₄₊₅ that extends a variable distance distally compared to the spot below it, and is particularly variable in width in cells Cu₂ and Cu₁ (rarely contacting the silver submarginal line), the presence (very rare) or absence of orange marginal scaling on the dorsal forewing, the extent of the orange banding on the dorsal hindwing, which varies from being confined to just the very wing base and anal margin to the entire basal half of the wing and tornal two-thirds of the distal half of the wing (with an intermediate state being most typical), the exact width, shape, and bluish color of the blue-gray bands on both ventral wings, and the presence or absence of orange marginal scaling on the ventral hindwing. Males from premontane elevations in Ecuador have a blue-gray postdiscal band on the ventral forewing that is about three times broader than in lowland males. Curiously, males from premontane elevations of the lowland *trochilia* group species *A. rameli* (Stichel, 1930), *A. trochilia* (Westwood, 1851), and *A. johannismarci* Brévignon, 1995, also have broader banding patterns than lowland males. Males of *A. glaucopis* from the Guianas have on average a slightly narrower blue postdiscal band on the dorsal forewing than males from the remainder of Amazonia (a syntype male from Tefé, western Brazil, was figured by Hall & Willmott (1996: Figs. 7B,C)), but this character is not close to being geographically consistent, with narrow-banded males occurring throughout Amazonia. With no other significant or consistent differences separating Guianan specimens of *A. glaucopis*, the subspecies name *virgata*, described by Brévignon & Gallard (1995) from French Guiana, is newly synonymized here with *A. glaucopis* (**n. syn.**).

The female of *A. glaucopis* is separated from the similar female of *A. praestigiosa* in that species account, while the presumably similar female of *A. caerulea* is not yet known. The females of certain sympatric *trochilia* group species, *A. johannismarci* in particular, but also *A. rameli* and *A. trochilia*, can easily be confused with *A. glaucopis* subclade females, but these *trochilia* group females have white or cream to pale yellow instead of dark yellow to orange bands, lack dark orange scaling proximally lining the silver submarginal line on the dorsal hindwing, typically have discontinuous yellowish instead of continuous orange scaling along the margin of the ventral forewing, and have dark spots in the basal half of the ventral hindwing that form smoothly continuous bands instead of discontinuous to partially continuous bands. Local variation in *A. glaucopis* females includes the exact width, shape, angle, and color (dark yellow to yellow orange) of the pale bands, with the postdiscally positioned band on the forewing being the most variably shaped, and the extent of the orange scaling immediately proximal to the silver submarginal line on the dorsal hindwing.

There is an interesting unidentified female specimen in the BMNH from Tefé, western Brazil, which is worth mentioning here, as Seitz (1916-20: Pl 142, line g) seems to have illustrated it to represent the female of *A. glaucopis* in his influential *Die Gross-Schmetterlinge der Erde*. It does indeed probably most closely approximate female *A. glaucopis*, having a dark yellow banding pattern and an orange band along the margin of both dorsal wings that is very broad on the hindwing, although the costal half of the yellow postdiscal band on the forewing and

the entire yellow postdiscal band on the hindwing are greatly thickened, with the dark postdiscal band on the hindwing much reduced. Other unique features of the BMNH female include a proximally displaced silver submarginal line on the hindwing and a complete absence of silver submarginal markings on both ventral wings, both indicators that it might be a somewhat aberrant individual. Because this female lacks a significant orange band proximally lining the silver submarginal line on the dorsal hindwing (admittedly hard to code with such a proximal silver line) and has smoothly continuous broad dark bands at the base of the ventral hindwing, our suspicion is that it does not belong to the *A. glaucopsis* subclade but rather the *trochilia* group. So, rather than being a potential female for *A. caerulea*, whose male does not share many similar ventral pattern elements, it could be a potential female for the recently described west Brazilian *A. brevignoni* Dolibaina & Dias, 2015, whose male shares a more similar (though far from identical) ventral wing pattern, including an uncannily similar dark presubmarginal band on the ventral forewing with a very elongate spot in cell Cu_1 . Alternatively, the BMNH female may belong to yet another undescribed species.

Biology: This uncommon species is known from sea level to 1300 m. In Ecuador, solitary males or pairs of males were encountered perching on and around tree trunks in shady hilltop and ridgetop lightgaps from 1415 to 1640 hrs. In the lowlands, males were observed to perch between 1 and 3 m above the ground, but at premontane elevations, beyond the upper elevational limit of most lowland congeners, they perched as high as 8 m above the ground. Males were also attracted to fermento placed on low leaves on hilltops from 1030 to 1215 hrs (Fig. 23D). Females were encountered landing under low leaves on hilltops from 1310 to 1420 hrs. The species was reared on *Symphonia globulifera* L. f. (Clusiaceae) by Hall (2023b). In French Guiana, small to large groups of males, of up to at least six individuals, were found perching 1 to 3 m above the ground on and around hilltop tree trunks from 1530 to 1630 hrs (Brévignon & Gallard, 1995; Gallard, 2017).

Distribution: *Argyrogrammana glaucopsis* is widespread throughout Amazonia, and is known to range from Colombia to Peru, and along the length of the Brazilian Amazon into the Guianas.

Argyrogrammana caerulea Hall, 2023
(Fig. 13)

Argyrogrammana caerulea Hall, 2023. *Trop. Lepid. Res.* 33(Suppl. 1): 25, figs. 2M, 2N. **TL:** Río Sucusari, Explornapo-ACEER, Loreto, Peru. Holotype male USNM [examined].

Identification and Taxonomy: The newly described *A. caerulea* is most similar to its sister species *A. glaucopsis*, from which it is separated in that species account (see also Hall, 2023b). The three examined males exhibit minimal wing pattern variation, with the orange bands on the dorsal hindwing varying slightly in the distal half of the wing in their shape and

length. The female of *A. caerulea* is not yet known, but it can be anticipated to be hard to differentiate from that of *A. glaucopsis* given that the males of the two species have the same ventral spotting pattern.

Biology: This very rare species is known from 150 to 600 m. Nothing is known about its adult biology, but the species was reared on *Symphonia globulifera* (Clusiaceae) in Ecuador by Hall (2023b).

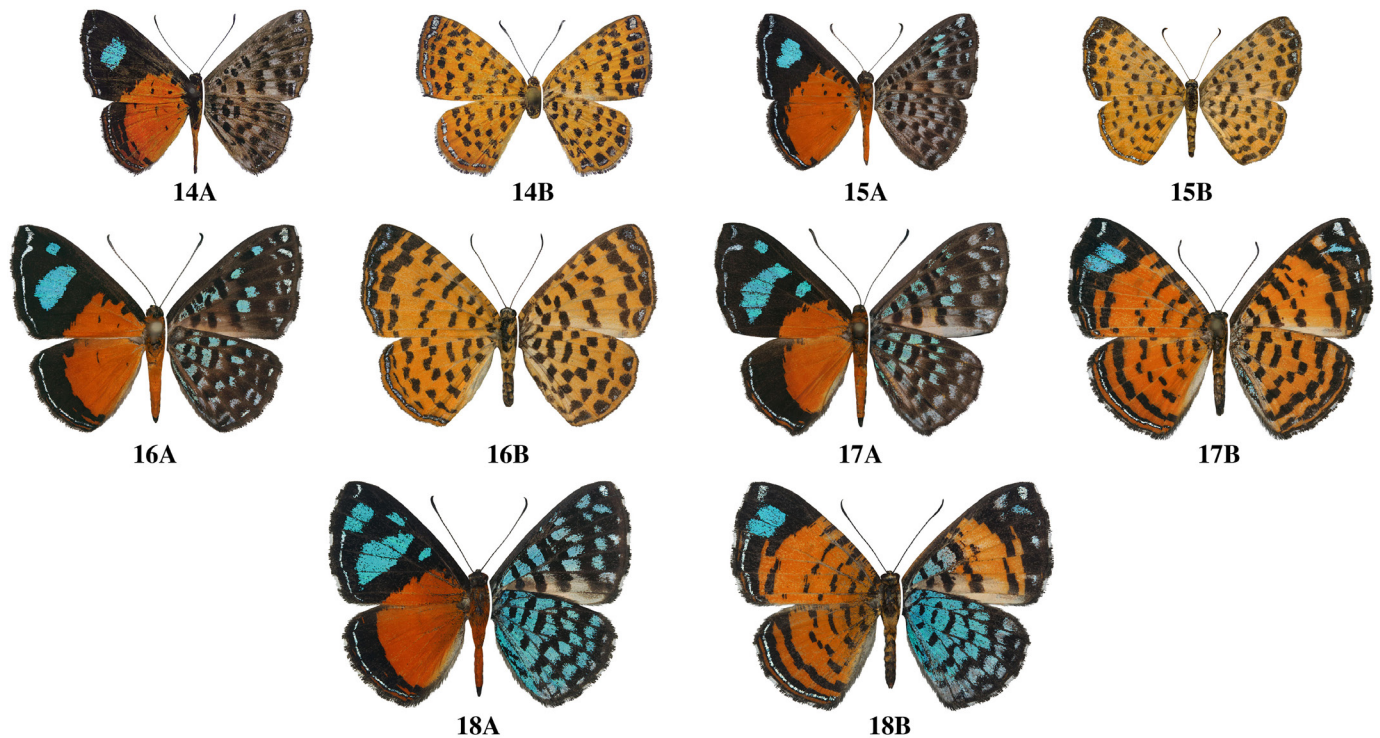
Distribution: *Argyrogrammana caerulea* is currently known only from Ecuador (Sucumbíos) and Peru (Loreto), but it also surely occurs in at least neighboring southern Colombia and probably western Brazil.

Argyrogrammana danieli P. Jauffret & Martins, 2006
(Figs. 14A,B)

Argyrogrammana danieli P. Jauffret & Martins, 2006. *Lambillionea* 106(3)(1): 397, figs. 3-6. **TL:** Igarapé do Tubo, Santo Antônio do Tauá, Pará, E. Brazil. Holotype male MPEG; type illustrations [examined].

Identification and Taxonomy: *Argyrogrammana danieli* seems to be phylogenetically positioned between the *A. venilia* and *A. nurtia* clades, although character support for this placement is not strong (Hall, 2023a). It seems to be very closely related to and is most similar to *A. denisi*, situated at the base of the *A. venilia* clade, and the more derived *A. amalfreda*, with the males of all three species being unique in the derived half of the *amalfreda* group in having a medially divided dark spot toward the base of cell Cu_2 below the middle of the discal cell on the dorsal forewing. The males of derived *amalfreda* group species from *A. danieli* onward all lack orange scaling proximal to the silver submarginal line on the ventral forewing, a character also exhibited by some other, mostly basal, *amalfreda* group members. However, the male of *A. danieli* still possesses orange scaling distal to the silver submarginal line on the ventral forewing, which has been lost in all of the more derived species except for a reversal in the montane sister pair of *A. caelestina* Hall & Willmott, 1995, and *A. pacsa* Hall & Willmott, 1998 (also lost in a handful of basal *amalfreda* group species).

The male of *A. danieli* is similar in size and dorsal wing pattern to the male of *A. amalfreda*, and it differs dorsally only by having a slightly smaller orange patch on the forewing with fewer dark spots visible in the discal cell, a dark presubmarginal band on the hindwing that is variably broad and continuous instead of largely absent, and a dark submarginal band on the hindwing that continues to the anal margin instead of typically stopping near vein Cu_2 . However, the ventral surface of *A. danieli* is more distinct, having two separate interdigitating dark spots in the middle of the discal cell on the forewing instead of a single dark bar crossing the width of the cell, an approximately straight instead of semicircular set of inwardly directed dark postdiscal spots across cells Cu_2 and Cu_1 on the forewing, more consistently sized and grayish instead of iridescent blue spots distal to the dark postdiscal band on the forewing with



Figs. 14-18. West Amazonian *Argyrogrammana amalfreda* group adults II (dorsal surface on left, ventral surface on right). **14A.** *A. danieli* P. Jauffret & Martins, 2006, male, P. N. da Serra do Divisor, Acre, W. Brazil (DZUP). **14B.** *A. danieli* female, P. N. da Serra do Divisor, Acre, W. Brazil (DZUP). **15A.** *A. amalfreda* (Staudinger, 1887) male, Santiago, Morona-Santiago, E. Ecuador. **15B.** *A. amalfreda* female, Santiago, Morona-Santiago, E. Ecuador. **16A.** *A. nurtia* (Stichel, 1911) male, Finca San Carlo, Napo, E. Ecuador. **16B.** *A. nurtia* female, Finca San Carlo, Napo, E. Ecuador. **17A.** *A. alstonii* (Smart, 1979) male, Lumbaquí, Sucumbios, E. Ecuador. **17B.** *A. alstonii* female, Lumbaquí, Sucumbios, E. Ecuador. **18A.** *A. sticheli* (Talbot, 1929) male, Sumak Yaku, Zamora-Chinchi, E. Ecuador. **18B.** *A. sticheli* female, Sumak Yaku, Zamora-Chinchi, E. Ecuador.

grayish rather than blue-gray scaling across the remainder of both wings, a more prominent silver submarginal line in the tornal half of the forewing and on the hindwing, a longer and inwardly curved instead of directed silver submarginal element in forewing cell M_1 , and orange scaling along the margin of both wings. The male of *A. danieli* is similar in size and ventral wing pattern to the male of *A. denisi*, and is also similar in size to the male of *A. gallardi*, from both of which it is distinguished in those species accounts. The distinctive male genitalia of *A. danieli*, which were not figured in the original description (Jauffret & Martins, 2006) but were subsequently illustrated by Dolibaina *et al.* (2015: Fig. 50) under the name *A. amalfreda*, differ from those of its similar relatives by having a longer and narrower upper posterior valve process, a more posteriorly elongate transtilla, and a shorter aedeagus.

Only two males of *A. danieli* are known to us, the holotype from near Belém, in the east Brazilian Amazon, and a male from Acre, in western Brazil, which was figured by Dolibaina *et al.* (2015) under the name *A. amalfreda* (reproduced here in Fig. 14A). This Acre male differs slightly on the dorsal surface from the holotype by having a slightly squarer blue postdiscal patch on the forewing, with a broader blue spot in cell M_3 and blue extending into cell Cu_1 , a slightly broader and more continuous dark presubmarginal band on the hindwing, and a broader dark submarginal band on the hindwing, with no orange scaling distally and less orange scaling at the wing margin. The ventral

surfaces of the two specimens do not significantly differ.

The female specimen figured by Jauffret & Martins (2006) as a paratype of *A. danieli* is not conspecific with the male holotype, and appears to be the female of the *occidentalis* group species *A. sublimis* Brévignon & Gallard, 1995. Dolibaina *et al.* (2015) figured a female specimen from Acre, western Brazil, under the name *A. iracyi* P. & J. Jauffret, 2007 (tentatively synonymized with *A. sublimis* by Hall & Willmott (2023)), that is shown here in Fig. 14B as a possible first known female of *A. danieli*. This female certainly differs in several subtle but critical ways from that of *A. sublimis* and relatives, by having a notably more distally positioned dark postdiscal band on both wings, an approximately straight instead of semicircular set of inwardly directed dark postdiscal spots across cells Cu_2 and Cu_1 on the forewing, square instead of rectangular to triangular dark presubmarginal spots in forewing cells M_2 and M_1 with a less proximally displaced spot in cell M_1 , a nearly absent instead of partially to fully complete dark submarginal band on the dorsal hindwing, a dark submarginal band on the ventral forewing that is entirely fused to instead of at least partially separated from the silver submarginal line, and a longer and more inwardly directed silver submarginal element in cell M_1 on the ventral forewing. In contrast, all of the above ventral characters match quite well with the ventral pattern of the sympatrically collected male of *A. danieli*. The remaining ventral pattern elements also match well, including the unusually broad and rectangular dark

submarginal spots on both wings, and all of the other small *amalfreda* group species already have females matched to the males. The female of *A. danieli* is separated from the females of *A. denisi* and *A. amalfreda* in those species accounts.

Biology: This very rare species is known from sea level to 450 m. In western Brazil, a solitary male was encountered perching 6 m above the ground on a hilltop at 1600 hrs, and a female was found flying low to the ground in flat forest at 1700 hrs (Dolibaina *et al.*, 2015). In eastern Brazil, an apparently non-perching male was found on a hot day resting beneath a leaf 4 m above the ground by a flat forest stream at 1300 hrs (Jauffret & Martins, 2006).

Distribution: *Argyrogrammana danieli* is currently known only from Brazil (Acre and Pará), but its occurrence across the entire width of the Brazilian Amazon suggests that it probably has an even wider Amazonian distribution.

Argyrogrammana amalfreda (Staudinger, 1887)
(Figs. 15A,B; 23E)

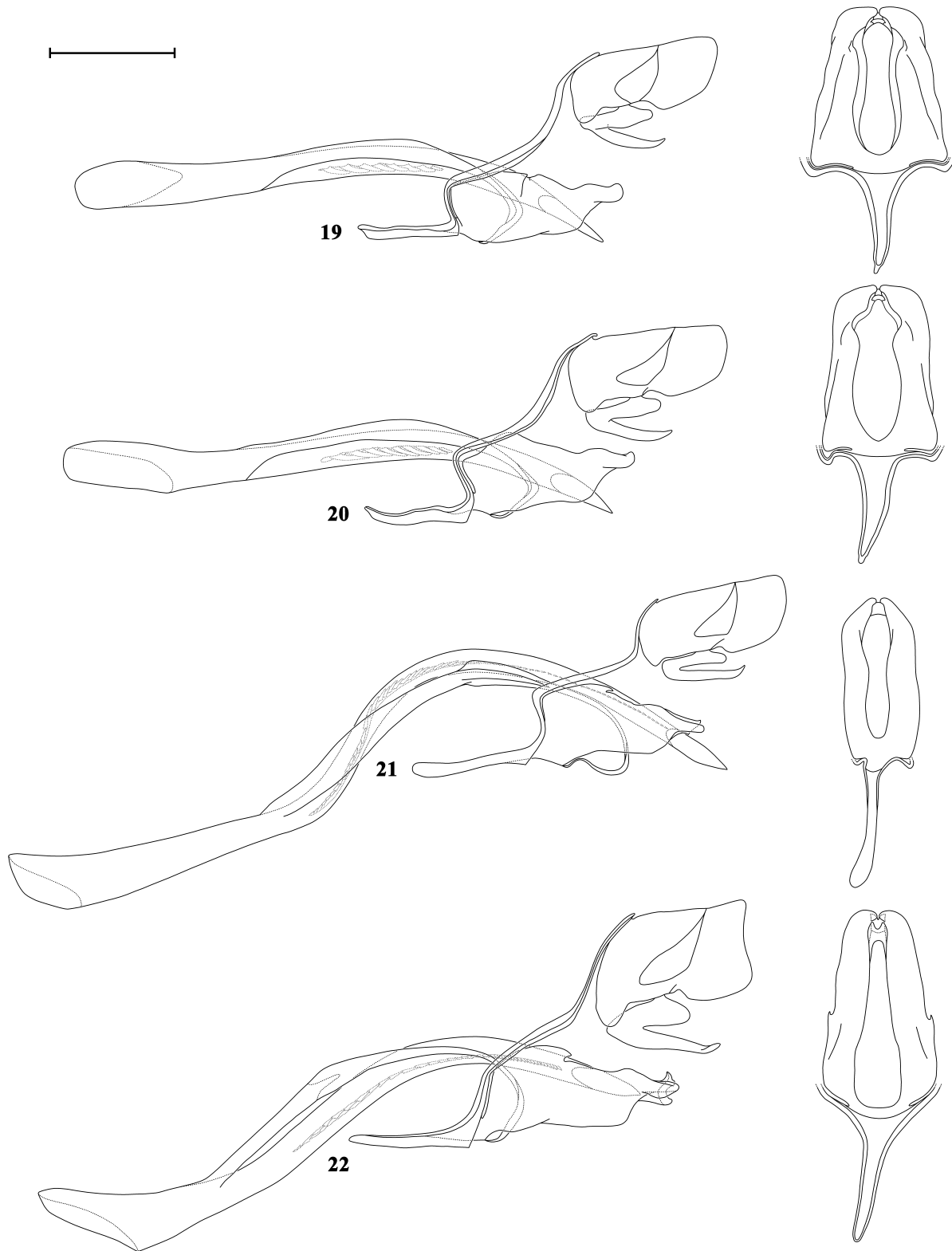
Charis amalfreda Staudinger, 1887. *Exot. Schmett.* 2(19): pl. 91; 1(20): 256 (1888). TL: Pebas, Loreto, Peru. Holotype male ZMHU [examined].

Identification and Taxonomy: *Argyrogrammana amalfreda* was recovered in Hall's (2023a) phylogenetic analysis of the genus as sister to the terminal *A. nurtia* clade + *A. natalita* clade, based on all nine clade members uniquely having males with a full complement of iridescent blue spots immediately distal to the dark postdiscal band on the ventral forewing, as well as all but two clade members having no orange scaling either proximal or distal to the silver submarginal line on the male ventral forewing (a character state also exhibited by *A. talboti* and independently derived in a handful of basal *amalfreda* group species). However, the male of *A. amalfreda* lacks the more widespread iridescent blue scaling present on both ventral wings in males of all the more derived *amalfreda* group species, and the species also seems to be closely related to *A. danieli*, whose male shares a dorsal forewing with a medially divided dark spot toward the base of cell Cu_2 below the middle of the discal cell and a square blue postdiscal patch.

Argyrogrammana amalfreda has at times been confused in the literature with the other small *amalfreda* group species *A. gallardi* and *A. danieli* (Brévignon & Gallard, 1995; Dolibaina *et al.*, 2015), whose males are distinguished from the actually rather phenotypically and morphologically distinctive male of *A. amalfreda* in those species accounts. The species was known for more than a century only from the male holotype from Pebas, northern Peru (see Fig. 4 in Hall & Willmott (1995)), but it was rediscovered by the authors in southern Ecuador, where a long series of males has now been collected. The male genitalia of *A. amalfreda* (see Fig. 20 in Hall & Willmott (1995)) differ from those of all other *amalfreda* group species by having a ventroposterior corner to the valvae that forms a broadly triangular and prominently posteriorly projecting lower process.

Intrapopulation wing pattern variation in *A. amalfreda* males is relatively limited, and includes the exact shape of the orange patch on the dorsal forewing, the prominence of the dark basal spotting on both dorsal wings, the exact width and shape of the blue postdiscal patch on the dorsal forewing, which sometimes extends slightly into cell Cu_1 and has a variably straight to undulating distal margin, the exact width of the dark submarginal band on the dorsal hindwing, which is often fused with the dark presubmarginal spot in the wing apex, the extent of the orange marginal scaling on the dorsal hindwing, the shape of the middle dark spot in the discal cell on the ventral forewing, which varies from a straight bar to a slightly jagged one (reflecting a fusion of the two separate spots that are present in the closest relatives), and the exact width of the pale postdiscal band on both ventral wings. The Peruvian holotype has a dark submarginal band on the dorsal hindwing that extends nearly to the anal margin, whereas all of the known Ecuadorian males have a band that stops near vein Cu_2 .

Dolibaina *et al.* (2015: Figs. 19-20) figured a small female specimen from Acre, western Brazil, which they tentatively identified as *A. gallardi*. However, a different phenotype that undoubtedly represents the genuine female of *A. gallardi* was subsequently figured by Gallard (2017) from French Guiana, and we suggest that the Acre specimen represents the first known female of *A. amalfreda*. A second, practically identical female (see Fig. 15B) was collected in Ecuador at the same locality where *A. amalfreda* males are rather common (see Biology section below). This female phenotype has an arrangement of dark spots and ventral silver submarginal markings that match well with those of male *A. amalfreda*. There are two notable discrepancies, with the female having a solid (although medially constricted) instead of medially divided dark spot toward the base of cell Cu_2 below the middle of the discal cell on the dorsal forewing, and two separate dark spots instead of a single bar in the middle of the discal cell on the ventral forewing. However, both of these character states tend to be less pronounced in *Argyrogrammana* females compared to males, and some *A. amalfreda* males do have a jagged (partially fused) medial discal cell bar. Given that males of the other small *amalfreda* group species, namely *A. gallardi*, *A. denisi*, and *A. danieli*, already have females assigned to them, these discrepancies would seem to cast only minor doubt on the identification of female *A. amalfreda*. The female of *A. amalfreda* is probably most similar to that of *A. gallardi*, from which it is distinguished in that species account. It is also similar to the female of *A. danieli*, but is slightly smaller and has an angular forewing apex, a more prominently semicircular set of dark postdiscal spots across cells Cu_2 and Cu_1 on the forewing, a dark submarginal band on the dorsal forewing that is entirely fused to instead of separated from the silver submarginal line, no visible dark submarginal band on the dorsal hindwing, a narrower dark submarginal band on both ventral wings, an inwardly directed instead of curved silver submarginal element in cell M_1 on the ventral forewing, and a less prominent silver submarginal line on the ventral hindwing. The dark postdiscal band on both wings in the only known putative female of *A. danieli* is more distally positioned compared to that in the *A. amalfreda* females, but, as this position is not reflected in the



Figs. 19-22. *Argyrogrammana amalfreda* group male genitalia, with genital capsule in lateral view, and valvae and saccus in ventral view. **19.** *A. lamasi* n. sp. HT (USNM). **20.** *A. celata* PT, Finca San Carlo, Napo, E. Ecuador. **21.** *A. maryanneae* n. sp. HT (USNM). **22.** *A. callaina* n. sp. HT (USNM). Scale bar = 0.5 mm.

male of *A. danieli*, it is not likely to be a consistent feature of the female.

Biology: This rare species is known from 100 to 600 m. In Ecuador, a male perching lek has yet to be located, and all of the

known males were encountered in subcanopy fish-baited traps and on fermento placed on low leaves on hilltops and ridgetops from 1030 to 1530 hrs (Fig. 23E). Although generally a very rare and localized species, on one particular hilltop near Santiago, *A. amalfreda* is the most commonly attracted *Argyrogrammana* to

fermento, with as many as half a dozen individuals sometimes observed during a single day. A female was also once attracted to fermento on this same hilltop at 1415 hrs. In western Brazil, a female was found flying low to the ground in flat forest at 1630 hrs (Dolibaina *et al.*, 2015).

Distribution: *Argyrogrammana amalfreda* is currently known only from Ecuador (Napo and Morona-Santiago), Peru (Loreto), and western Brazil (Acre), but it seems likely to have a broader west Amazonian distribution.

Argyrogrammana nurtia (Stichel, 1911)
(Figs. 16A,B; 23F,G)

Argyrogramma nurtia Stichel, 1911. In: Wytzman (ed.), *Gen. Insectorum* 112B: 246. TL: Río Pachitea, Huánuco, Peru. Lectotype male ZMHU [designated].

= *Argyrogrammana nurtia ludibunda* Brévignon & Gallard, 1995. *Lambillionea* 95(3): 396, figs. 15, 16. TL: Maripasoula, Saint Laurent du Maroni, French Guiana. Holotype male LCB; type illustrations [examined]. **n. syn.**

Identification and Taxonomy: *Argyrogrammana nurtia* belongs at the base of the derived *A. nurtia* clade, which also includes *A. alstonii*, *A. pulchra*, and *A. sticheli*. The males of all four species share a completely absent small dark spot around vein 2A at the very base of the dorsal forewing (also lost in the clade containing *A. bonita*, *A. chicomendesi*, and *A. halli*, as well as in *A. talboti*), and a blue postdiscal patch on the dorsal forewing that extends to at least vein Cu_2 (also present elsewhere in the *amalfreda* group in the *A. venilia* clade and *A. caelestina*) and has a costal spot in cell R_{4+5} that is always significantly distally disjunct and isolated (also present in *A. denisi*). Hall's (2023a) phylogenetic analysis of *Argyrogrammana* recovered the *A. nurtia* clade as sister to the east Andean *A. natalita* clade in the terminal crown clade of the *amalfreda* group, based on the males of all eight species uniquely having widespread iridescent blue patterning across both ventral wings.

The male of *A. nurtia* is most similar to that of its closest relative *A. alstonii*, differing by being slightly smaller on average and dorsally having a typically slightly larger basal orange patch on both wings, no blue spot at the end of the discal cell on the forewing, a blue postdiscal patch on the forewing that has an approximately straight rather than concave proximal margin across cells M_3 to M_1 and typically extends to the vicinity of vein Cu_2 instead of variably across cell Cu_2 , a silver submarginal line on the forewing that typically has a less prominently inwardly curved element in cell M_1 , and typically more orange scaling in the distal portion of the hindwing. Ventrally, it has two separate interdigitating dark spots in the middle of the discal cell on the forewing instead of a single dark bar crossing the width of the cell, typically a slightly more distally positioned postdiscal band on both wings, typically a slightly narrower blue-gray band distal to the dark presubmarginal band on both wings, and a less prominent silver submarginal line on the hindwing. The male genitalia of *A. nurtia* (see Fig. 5 in Brévignon & Gallard (1995), Fig. 21 in Hall & Willmott (1995), and Fig. 47

in Dolibaina *et al.* (2015)) differ from those of *A. alstonii* by having a lower posterior section to the valvae that protrudes posteriorly, is slightly outwardly flared, and has a concave inner margin in ventral view, an upper posterior valve process that is longer, more upwardly directed, gradually instead of abruptly inwardly curved, and ventrally slightly concave, and a longer and broader "keel"-like transtilla. The male of *A. nurtia* is also dorsally somewhat similar to that of *A. denisi*, but it is considerably larger and has quite a different ventral pattern that includes iridescent blue spots.

Notable intrapopulational wing pattern variation in *A. nurtia* males dorsally includes the exact size and shape of the basal orange patch on both wings, the presence or absence (typical) of limited dark basal spotting on both wings, the exact width and shape of the blue postdiscal band on the forewing, which extends a variable distance across cell Cu_1 and has a costal spot in cell R_{4+5} that varies in size and the extent to which it is distally disjunct from the remainder of the band, the presence (very rare) or absence of orange submarginal scaling in the tornus of the forewing, the extent to which the silver submarginal element in cell M_1 on the forewing curves inward, and the extent of the orange submarginal and marginal scaling on the hindwing. Ventral variation includes the arrangement of the two middle dark spots in the discal cell on the forewing, which varies from completely separated to partially fused spots, the exact lateral placement of the dark postdiscal band on both wings and the exact width of the distal iridescent blue spots, which may be present or absent in forewing cells M_2 (typically absent) and M_1 (nearly always present), the exact width of the blue-gray band distal to the dark presubmarginal band on both wings, and the prominence of the silver submarginal markings on both wings. Males of *A. nurtia* from the eastern Amazon consistently have a small orange basal patch on both dorsal wings and minimal distal orange scaling on the dorsal hindwing, whereas those from the western Amazon exhibit considerable local variation in these two characters, while on average having larger orange patches and more distal hindwing orange. Male specimens from the highest elevations at the base of the Andes seem to have the most extensive dorsal orange scaling. Males from most of Amazonia also quite consistently have a relatively narrow blue postdiscal band on the dorsal forewing, whereas males from the far western Amazon on average have a broader blue forewing band, a pattern of geographic variation repeated in most *amalfreda* group species. The latter phenotype is exemplified by the lectotype male of *A. nurtia* (designated below) from Río Pachitea, at the base of the Andes in central Peru (see Figs. 5A,B in Hall & Willmott (1995)). Because the observed geographic variation in this species is neither concordant nor discrete, the subspecies name *ludibunda*, described by Brévignon & Gallard (1995) from French Guiana, is newly synonymized here with *A. nurtia* (**n. syn.**).

The female of *A. nurtia* was first correctly associated with the male by Brévignon & Gallard (1995). It can readily be separated from that of the closely related *A. alstonii* by lacking a blue patch in the dorsal forewing apex, but also consistently differs by having two separate interdigitating dark spots instead of a single jagged dark bar in the middle of the discal cell on the ventral forewing and a silver instead of iridescent blue

submarginal mark in cell M_1 on the ventral forewing. Overall, in terms of both size and wing pattern, the female of *A. nurtia* is perhaps most similar to that of *A. aparamilla*, but it differs 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 forewing, a dark postdiscal band on the forewing with a typically straighter section across cells Cu_2 and Cu_1 and a more proximally positioned section across cells M_3 to M_1 , and prominent silver submarginal markings on both ventral wings.

Intrapopulation wing pattern variation in *A. nurtia* females is mostly limited to the exact shape and lateral placement of the dark postdiscal band on the forewing, the width of the dark presubmarginal and submarginal bands on both wings, and the extent to which the silver submarginal element in cell M_1 on the forewing curves inward. Females of *A. nurtia* figured by Brévignon & Gallard (1995: Fig. 16) and Gallard (2017: Pl. 17, Fig. 6) from French Guiana differ from the few examined west Amazonian females by being more heavily marked, most notably having a broader dark submarginal band on both wings that on the forewing is partially fused with the dark presubmarginal band. The female specimen figured by Gallard (2017: Pl. 17, Fig. 8) as *A. alstonii* is identified here as also being *A. nurtia* (see the species accounts for *A. alstonii* and *A. sticheli*).

Argyrogrammana nurtia was described by Stichel (1910-11) from one male from Río Pachitea, Peru, and one female from Río Zongo, Bolivia, now in the ZMHU. As these specimens constitute a mixed type series, with the female syntype representing the Andean *A. pacsá* (see Hall *et al.*, 2023), the male syntype is designated here as the lectotype. It bears the following labels: “Type”, “Pachitea / Peru”, “nurtia / Stich.”, and “Coll. / Staudinger”.

Biology: This uncommon species is known from sea level to 1150 m. The montane elevational range reported by Lamas *et al.* (in press) in southern Peru is based on female specimens that seem likely to be referable to the montane *A. pacsá* (see Hall *et al.*, 2023). In Ecuador, males were encountered perching singly or in groups of up to three individuals on tree-trunk epiphytes in shady hilltop lightgaps from 1545 to 1745 hrs. At the beginning of this time period, males fly as low as 1 to 4 m above the ground, but, as the sun drops toward the horizon and its rays gradually move higher up into the subcanopy, the males’ perching activity follows, and by the end of the day males were typically observed perching about 7 to 11 m above the ground. Males were also found in subcanopy fish-baited traps and on fermento placed on low leaves from 1445 to 1730 hrs (Fig. 23F), mostly on hilltops and ridgetops but also once in flat forest. A female was once observed being chased by two males 11 m above the ground in a hilltop perching lek area at 1740 hrs (female in Fig. 16B), another female was encountered flying low to the ground across a hilltop at 1545 hrs, and another was attracted to fermento on a hilltop at 1600 hrs (Fig. 23G). In western Brazil, males were found perching 1 m above the ground on a hilltop at 1500 hrs (Dolibaina *et al.*, 2015). In French Guiana, solitary males or pairs of males were found perching 3 to 10 m above the ground around hilltop tree trunks from 1715 to 1800 hrs (Brévignon & Gallard, 1995; Gallard, 2017).

Distribution: *Argyrogrammana nurtia* appears to be widespread throughout much of Amazonia, where it is known to range from Ecuador to Peru, and along the length of the Brazilian Amazon into French Guiana.

Argyrogrammana alstonii (Smart, 1979)
(Figs. 17A,B)

Argyrogrammana alstonii Smart, 1979. *The Aurelian* 1(3): 9, fig. TL: Cumberland Hill, Diego Martin, Trinidad. Holotype male FLMNH [examined].

Identification and Taxonomy: *Argyrogrammana alstonii* belongs in the *A. nurtia* clade, where it is sister to *A. pulchra* and *A. sticheli*. These three species uniquely share a blue spot near the end only of the discal cell on the dorsal forewing in males and a blue submarginal spot in cell M_1 on the dorsal forewing in females that forms part of the silver submarginal line. They are also unusual in having a single dark bar across the middle of the discal cell on the ventral forewing in both sexes instead of two separate interdigitating dark spots, a character state that occurs elsewhere in the *amalfreda* group only in the three *A. glaucopis* subclade species, as well as a mostly to completely absent silver submarginal line on the ventral hindwing in males, which elsewhere in the derived half of the *amalfreda* group occurs only in *A. amalfreda*.

Males of *A. alstonii* that have a particularly small blue spot at the discal cell end on the dorsal forewing can be confused with males of *A. nurtia*, and the two species are distinguished in that species account. The male of *A. alstonii* differs from that of *A. sticheli* by being slightly smaller on average and having a blue postdiscal band on the dorsal forewing that is narrower, more vertically oriented, and proximally more concave across cells M_3 to M_1 , no blue submarginal spot(s) in the apex of the dorsal forewing, a dark spot inside the end of the discal cell on the ventral forewing, a slightly more distally positioned dark postdiscal band on the ventral forewing, less extensive iridescent blue scaling across the base of both ventral wings, a blue-gray instead of iridescent blue band distal to the dark presubmarginal band on both ventral wings, and more prominent silver submarginal markings on the ventral forewing, including a silver instead of iridescent blue mark in cell M_1 .

Notable intrapopulation wing pattern variation in *A. alstonii* males dorsally includes the size and shape of the basal orange patch on both wings, the presence or absence of dark basal spotting on both wings, the size of the blue spot near the discal cell end on the forewing, the exact width and shape of the blue postdiscal band on the forewing, which extends a variable distance across cell Cu_2 , has a costal spot in cell R_{4+5} that varies slightly in size and the extent to which it is distally disjunct from the remainder of the band, and sometimes includes an additional tiny blue spot in cell R_2 , the extent to which the silver submarginal element in cell M_1 on the forewing curves inward, and the extent of the orange submarginal and marginal scaling on the hindwing. Ventral variation includes the prominence of the dark spot inside the discal cell end on the forewing, the exact lateral placement of the dark postdiscal band on both wings, the width of the iridescent blue spots distal to the dark

postdiscal band on both wings and the prominence of the blue spots on the hindwing, the exact width of the blue-gray band distal to the dark presubmarginal band on both wings, and the presence (very rare) or absence of traces of orange marginal scaling in the forewing apex. Males of *A. alstonii* from the eastern Amazon and Trinidad have on average more prominent dark basal spotting within the orange patches on both dorsal wings and a slightly narrower blue postdiscal band on the dorsal forewing compared to west Amazonian males, and males from the eastern Amazon additionally have smaller blue discal cell end and costal spots on the dorsal forewing (the former sometimes no more than a tiny dot) and a shorter blue forewing postdiscal band that rarely extends much beyond vein Cu_2 compared to males from elsewhere. Because geographic variation in *A. alstonii* is incompletely understood, with no material currently known from the central Amazon, and, at least in males, discordant and relatively insignificant, no subspecies seem warranted.

The discovery of the true female of *A. sticheli* in Ecuador has revealed that the female specimens figured by Brévignon & Gallard (1995: Fig. 18) and Gallard (2017: Pl. 17, Fig. 7) from French Guiana under the name *A. sticheli* actually belong to *A. alstonii*, and the female figured by Gallard (2017) as *A. alstonii* is a heavily marked specimen of *A. nurtia*. The female of *A. alstonii* is intermediate in appearance between those of its close relatives *A. nurtia* and *A. sticheli*. It is distinguished from them in detail in those species accounts, but most obviously differs from the former by having an area of blue submarginal scaling in the apex of the dorsal forewing, and from the latter by lacking widespread blue ventral scaling. The female of *A. alstonii* is actually perhaps most similar to that of the Transandean *A. pulchra*, but has orange instead of yellow patterning on both wing surfaces, a less prominently semicircular section to the dark postdiscal band across cells M_3 to M_1 on the forewing, a rectangular instead of triangular blue submarginal spot in cell M_1 on the dorsal forewing, and a blue instead of silver submarginal mark in cell M_1 on the ventral forewing.

Intrapopulation wing pattern variation in the known *A. alstonii* females is minimal. The two known females from Ecuador have a dark postdiscal band on the dorsal forewing that exhibits a variably semicircular element across cells Cu_2 and Cu_1 and a variably prominent element across cells M_3 to M_1 , a slightly variably shaped dark presubmarginal band on the dorsal hindwing, and a variably broad dark submarginal band on the dorsal hindwing. The two known females from French Guiana have a variably broad blue submarginal spot in cell M_1 on the dorsal forewing, and a variably broad costal section to the dark presubmarginal band on the ventral forewing. Compared to each other, these females from opposite sides of the Amazon differ in one striking way, with the Ecuadorian females having two blue submarginal spots (cells M_2 and M_1) in the dorsal forewing apex compared to one (cell M_1) in the French Guianan females. However, given the significant variation observed in this character even at the local level among a longer series of *A. sticheli* males, this character seems likely to vary both locally and clinally once a larger number of *A. alstonii* females becomes known from a wider range of Amazonian localities, much as the blue forewing postdiscal band varies slightly in

size in *A. nurtia* clade males. The Ecuadorian females of *A. alstonii* also have a prominent orange presubmarginal spot in cell R_{4+5} on both surfaces of the forewing, a little iridescent blue scaling along the anal margin of the ventral hindwing, and more marginal orange scaling on both surfaces of both wings.

Biology: This rare species is known from sea level to 950 m. In Ecuador, males were encountered perching singly or in small groups, on one occasion numbering up to five individuals, 4 to 10 m above the ground around tree trunks in shady hilltop lightgaps from 1430 to 1645 hrs. Like *A. nurtia* males, those of *A. alstonii* adjust their perching height based on the angle of the sun, moving higher up into the trees later in the afternoon. Once, in undulating flat lowland forest, a male was encountered on the steps of a canopy tower flying in to perch on a mid-canopy tree-trunk epiphyte about 25 m above the ground at 1750 hrs (in an area of the emergent tree where other tree-trunk perching riordinids had been perching earlier that afternoon). A male was also attracted to fermento placed on low leaves on a hilltop at 1230 hrs. Two females were found 2 m above the ground near a male perching lek on a hilltop, one flying along the forest edge at 1320 hrs and the other resting under a leaf in a lightgap at 1450 hrs. In western Brazil, males were found perching 7 m above the ground on a hilltop from 1600 to 1800 hrs (Dolibaina *et al.*, 2015). In French Guiana, males were found perching 3 to 10 m above the ground around hilltop tree trunks from 1630 to 1745 hrs, one female was found flying on a hilltop at 1300 hrs and another was attracted to a hilltop light trap (Brévignon & Gallard, 1995; Gallard, 2017).

Distribution: *Argyrogrammana alstonii* is currently known from Ecuador, the length of the Brazilian Amazon, French Guiana, and Trinidad, and it is clearly widespread throughout much of the Amazon region.

Argyrogrammana sticheli (Talbot, 1929)
(Figs. 18A,B; 23H)

Argyrogramma sticheli Talbot, 1929. *Bull. Hill Mus.* 3(2): 146, pl. 4, figs. 1, 2. **TL:** Saint Laurent, Saint Laurent du Maroni, French Guiana. Holotype male BMNH [examined].

Identification and Taxonomy: The Amazonian *A. sticheli* and Transandean *A. pulchra* form the terminal sister-species pair in the *A. nurtia* clade. The males of the two species uniquely have a blue submarginal spot in cell M_1 on the dorsal forewing that forms part of the silver submarginal line, uniquely for the *amalfreda* group have no dark spot inside the end of the discal cell on the ventral forewing, and unusually have a silver submarginal line on the ventral forewing that is largely confined to the apex (also present in most *A. sebastiani* clade species) and widespread iridescent blue scaling across both ventral wings (also present in members of the closely related *A. natalita* clade).

The male of *A. sticheli* differs from the unique Colombian male holotype of *A. pulchra* (figured by d'Abrera (1994), Hall & Willmott (1995, 2023), and Constantino *et al.* (2012)) by

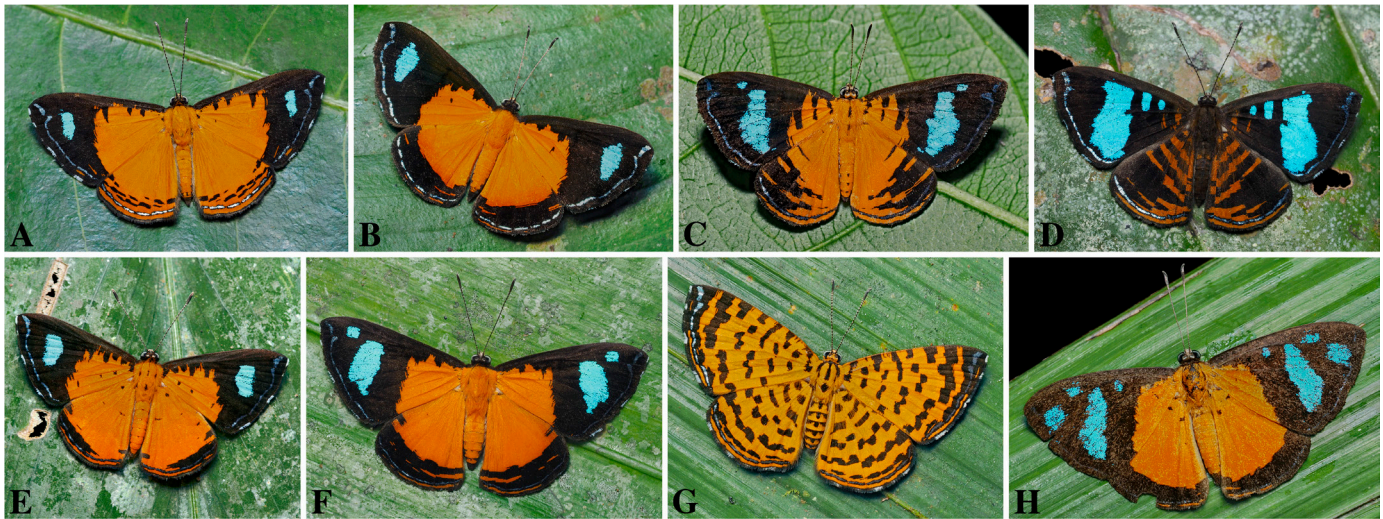


Fig. 23. *Argyrogrammana amalfreda* group adults (A-F, H: males; G: female) feeding on fermento bait (a mixture of rotting fish and urine) in eastern Ecuador (A-F: Santiago, Morona-Santiago; G-H: Finca San Carlo, Napo). A. *A. phyton*. B. *A. bonita*. C. *A. praestigiosa*. D. *A. glaucopis*. E. *A. amalfreda*. F, G. *A. nurtia*. H. *A. sticheli*. Photos by D. H. Ahrenholz.

being slightly smaller and having a slightly smaller orange patch at the base of the dorsal forewing, a blue postdiscal band on the dorsal forewing that extends into cell Cu_2 instead of ending at vein Cu_2 , a larger blue submarginal spot in cell M_1 on the dorsal forewing, less extensive orange presubmarginal and marginal scaling on the dorsal hindwing, slightly darker iridescent blue scaling across both ventral wings, and a slightly more proximally positioned dark postdiscal band on the ventral forewing with a slightly narrower band of iridescent blue spots distally. The male of *A. sticheli* is distinguished from the male of *A. alstonii* in that species account.

Notable intrapopulational wing pattern variation in *A. sticheli* males from Ecuador, the only country from which multiple specimens are known from multiple localities, includes the limited presence or absence (typical) of dark basal spotting on both dorsal wings, the exact size of the blue spot near the discal cell end on the dorsal forewing, the length of the blue postdiscal band on the dorsal forewing, which extends a variable distance across cell Cu_2 , the width of the blue submarginal spot in cell M_1 on the dorsal forewing, the size and shape of the blue submarginal spot in cell M_2 on the dorsal forewing, which in the specimen in Fig. 18A forms a full-sized rectangular spot but in all the remaining known specimens forms a smaller triangular spot (in the upper left corner of the space occupied by the rectangular spot) that is one-third to two-thirds the size (see Fig. 23H), and the extent of the orange marginal scaling on the dorsal hindwing. The holotype male of *A. sticheli* from French Guiana was figured by d'Abrera (1994: 1051) and Hall & Willmott (1995: Figs. 8A,B), and a second, recently collected French Guianan male, was figured by Gallard (2017: Pl. 17, Fig. 7). Ecuadorian males of *A. sticheli* differ from these two French Guianan males by having slightly darker orange scaling at the base of both dorsal wings, a more elongate orange patch at the base of the dorsal forewing that extends further along the anal margin, less prominent dark basal spotting on both dorsal wings, a broader blue postdiscal band on the dorsal forewing that on average extends further

across cell Cu_2 , an additional blue submarginal spot in cell M_2 on the dorsal forewing, a larger orange patch on the dorsal hindwing, some orange presubmarginal and marginal scaling on the dorsal hindwing, and broader discal, postdiscal, and presubmarginal bands of iridescent blue spots on both ventral wings. A photograph of an *A. sticheli* male on the *inaturalist.org* website from Tapanahony, Surinam, has a similar dorsal wing pattern to the French Guianan males, but completely lacks a blue spot near the forewing discal cell end. The only other male of *A. sticheli* known to us was figured by Dolibaina *et al.* (2015: Figs. 5-6) from Acre, western Brazil, misidentified as *A. pulchra*. This male is intermediate between those known from Ecuador and the Guianas, having orange dorsal patches the same size and shape as in Ecuadorian males, a blue postdiscal band on the dorsal forewing of intermediate width, only a single blue submarginal spot (in cell M_1) on the dorsal forewing, and iridescent blue bands on both ventral wings of intermediate width. Geographic variation in *A. sticheli* males thus appears to be clinal.

When describing *A. sticheli*, Talbot (1929) tentatively assigned as the female a non-conspecific French Guianan specimen that was described by Brévignon & Gallard (1998) as *A. talboti*, and later shown by Gallard (2017) to be a male rather than a female. Brévignon & Gallard (1995) figured what they believed to be the first genuine female of *A. sticheli*, also from French Guiana, quite understandably matching a female with a blue submarginal spot in forewing cell M_1 with the male of the only Amazonian species to possess this same spot. However, females have been collected in Ecuador during courtship flights with males of *A. sticheli* that have closely matching wing patterns and are clearly conspecific. This discovery reveals that the female phenotype heretofore believed to belong to *A. sticheli* actually belongs to *A. alstonii*, and that *A. alstonii* exhibits sexual dimorphism in the expression of a blue submarginal spot in forewing cell M_1 . The female of *A. sticheli* differs most strikingly from that of *A. alstonii* by having iridescent blue scaling across the base of the ventral forewing

and entire ventral hindwing, a character that has independently evolved in females of the closely related *A. natalita* clade. The known *A. sticheli* females additionally differ from those of *A. alstonii* by being slightly larger and having slightly darker, duller, and browner orange dorsal scaling, particularly at the wing bases, a slightly more proximally positioned dark postdiscal band on the forewing, iridescent blue rather than gray or orange presubmarginal spots in cells M_1 and R_{4+5} on the ventral forewing, and less prominent silver submarginal markings on both ventral wings. Given the similarity of the males, the females of *A. sticheli* and *A. pulchra* are surprisingly different, with the former most notably differing from the latter by having orange instead of yellow dorsal patterning, a more proximally positioned dark postdiscal band on the forewing, a rectangular instead of triangular blue submarginal spot in cell M_1 on the dorsal forewing, orange and iridescent blue instead of yellow ventral patterning, and less prominent silver submarginal markings on both ventral wings, with a blue instead of silver submarginal mark in cell M_1 on the ventral forewing. The two known Ecuadorian females of *A. sticheli* do not differ notably from each other. However, *A. sticheli* females can be expected to exhibit geographic variation similar to that observed in *A. alstonii*, with Guianan females likely to have only a single blue submarginal spot in the dorsal forewing apex.

Biology: This very rare species is known from sea level to 1100 m. In Ecuador, a small group of males was encountered perching just below the stunted canopy of a hilltop's tallest tree (above *A. nurtia*), flying rapidly around the open space below the canopy and occasionally landing on tree-trunk epiphytes 5 to 8 m above the ground from 1345 to 1500 hrs. Males were also found on fermento placed on low leaves on hilltops at 1530 hrs (Fig. 23H). Individual females were observed being chased by one or two males in the above-described male lekking area throughout most of the perching period. In western Brazil, a solitary male was found perching 5 m above the ground on a hilltop at 1300 hrs (Dolibaina *et al.*, 2015). In French Guiana, the only male collected in modern times there was attracted to the odor of a camp waste bin in the Réserve des Nouragues at 1700 hrs (Gallard, 2017).

Distribution: *Argyrogrammana sticheli* is currently known only from Ecuador (Napo, Pastaza, and Zamora-Chinchipe), western Brazil (Acre), Surinam, and French Guiana, but it is probably widespread throughout much of Amazonia. It is replaced to the west of the Andes by *A. pulchra* (Hall & Willmott, 2023).

Geographically Peripheral Species

Two additional species, *A. venilia* (Bates, 1868) and *A. talboti* Brévignon & Gallard, 1998, are known from the geographical periphery of the west Amazonian region, but because both appear to be essentially east Amazonian species and both sexes of these distinctive species are well illustrated elsewhere (Brévignon & Gallard, 1995; Hall & Furtado, 1999; Gallard, 2017), they are only briefly discussed here.

Argyrogrammana venilia (= *boyi* Röber, 1926, and *amazonica* Meier-Ramel, 1928) is known to range across the

Guianas and the central and eastern Amazon of Brazil as far west as the Tefé region, in the central west Brazilian Amazon, where it is not uncommon for an *amalfreda* group species, perching on hilltops in the early afternoon (Gallard, 2017). Hall & Willmott (1995) cited this species as occurring in Ecuador, but this was an error, based on the misidentification of a female specimen. The fact that *A. venilia* has never been found in a country as intensively surveyed as Ecuador suggests that it truly does not range into the core of the west Amazonian region. This species is unique in the *amalfreda* group in having a male with blue patterning on both dorsal wings, thus superficially somewhat resembling males in the *trochilia* group. However, the preponderance of morphological evidence suggests that *A. venilia* is sister to the *A. glaucopis* subclade, containing *A. praestigiosa*, *A. glaucopis*, and *A. caerulea* (Hall, 2023a).

Argyrogrammana talboti is a much rarer and more enigmatic species that is currently known only from the southwest Brazilian Amazon (southern Amazonas, Rondônia, and Mato Grosso) and French Guiana, with an orange phenotype named *A. t. naranjilla* Hall & Furtado, 1999, occurring in the former region, and the yellow nominotypical subspecies occurring in the Guianas. We tentatively retain two subspecies for now because these taxa may have disjunct geographic ranges and be involved in mimicry with other similarly patterned butterflies and day-flying moths, both factors that could result in discontinuous wing pattern variation. This is the largest species in the genus, with females having a forewing length of up to 21 mm, and its largely sexually monomorphic wing pattern (females do lack the males' small blue patch in the subapex of the forewing) is quite unlike that of any other congener, being a simpler, spotless, largely yellow/orange and black pattern that is the same on both wing surfaces. The morphological phylogenetic analysis of *Argyrogrammana* conducted by Hall (2023a) tentatively placed *A. talboti* in the derived half of the *amalfreda* group, between the *A. venilia* clade and the terminal *A. nurtia* clade + *A. natalita* clade. However, given its autapomorphic wing pattern and the lack of phylogenetic clues in the genitalia, more precisely pinpointing its closest relatives on the basis of morphology alone is not possible. Gallard (2017) reported that the only *A. talboti* specimen collected in French Guiana in modern times, a male, was encountered during the morning flying around a bush in "rock savanna" in the southwestern Massif du Mitaraka. This low, scrubby, dry vegetation type, which, interestingly, includes the predominant *Argyrogrammana* food-plant family Clusiaceae (see Hall, 2023b) as one of its dominant floral elements, is characteristic of the granite inselbergs that are scattered across the Guiana Shield region (de Granville & Sastre, 1973; Sarthou *et al.*, 2003, 2017). These island-like inselbergs appear to be xeric floral refuges, sharing much of their flora with savanna-like vegetation types throughout Amazonia (de Granville, 1982), and, if *A. talboti* is, or historically was, unique among *Argyrogrammana* species in being closely associated with such drier forest types, it could explain both its divergent wing pattern and disjointed distribution pattern that seems to exclude the wettest parts of the Amazon. If it does occur in the far western Amazon, the most likely locations would be far eastern Bolivia and perhaps northeastern Colombia.

Four additional *amalfreda* group species are known from Amazonia. *Argyrogrammana physis* ranges from the southern Transandean region to the Guianas and eastern Brazil (as far south as Bahia), and is replaced in western Amazonia by *A. phyton*. *Argyrogrammana chicomendesi* is restricted to the eastern Amazon, and is replaced in western Amazonia by *A. halli*. The very rare *A. sebastiani* and *A. francozi* are currently known only from French Guiana, and they seem somewhat unlikely to range into the western Amazon given that the closely related *A. aparamilla* is apparently endemic there.

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