

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

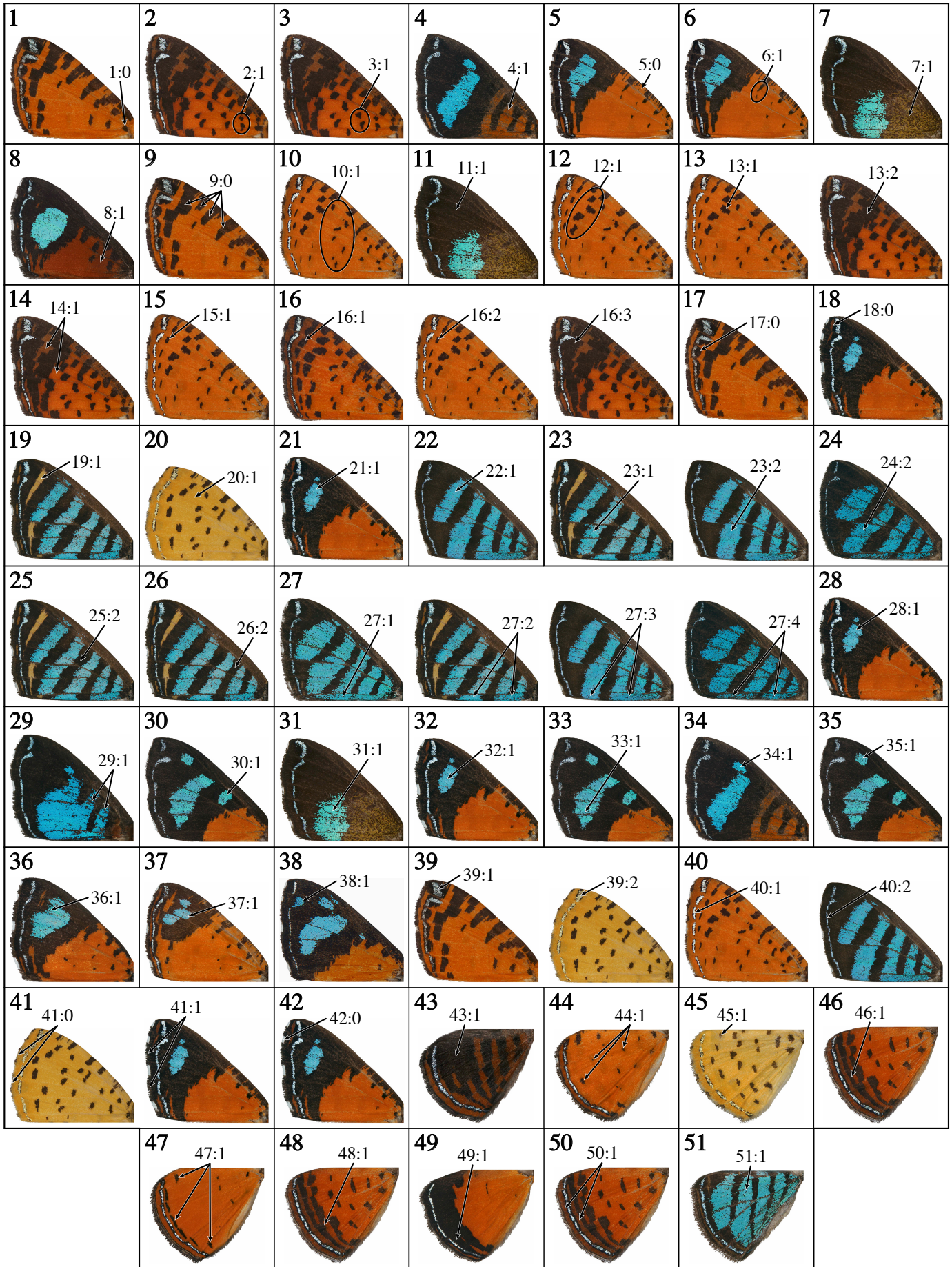
One hundred and ten characters were identified from a morphological study of *Argyrogrammana* adults (55 species), as listed below, from the wing pattern (87 [77 male, 10 female]) (Figs. 1-3), head and body (six) (Fig. 4), and male genitalia (17) (Fig. 5) (see Table 1 for the character matrix). Two of 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.

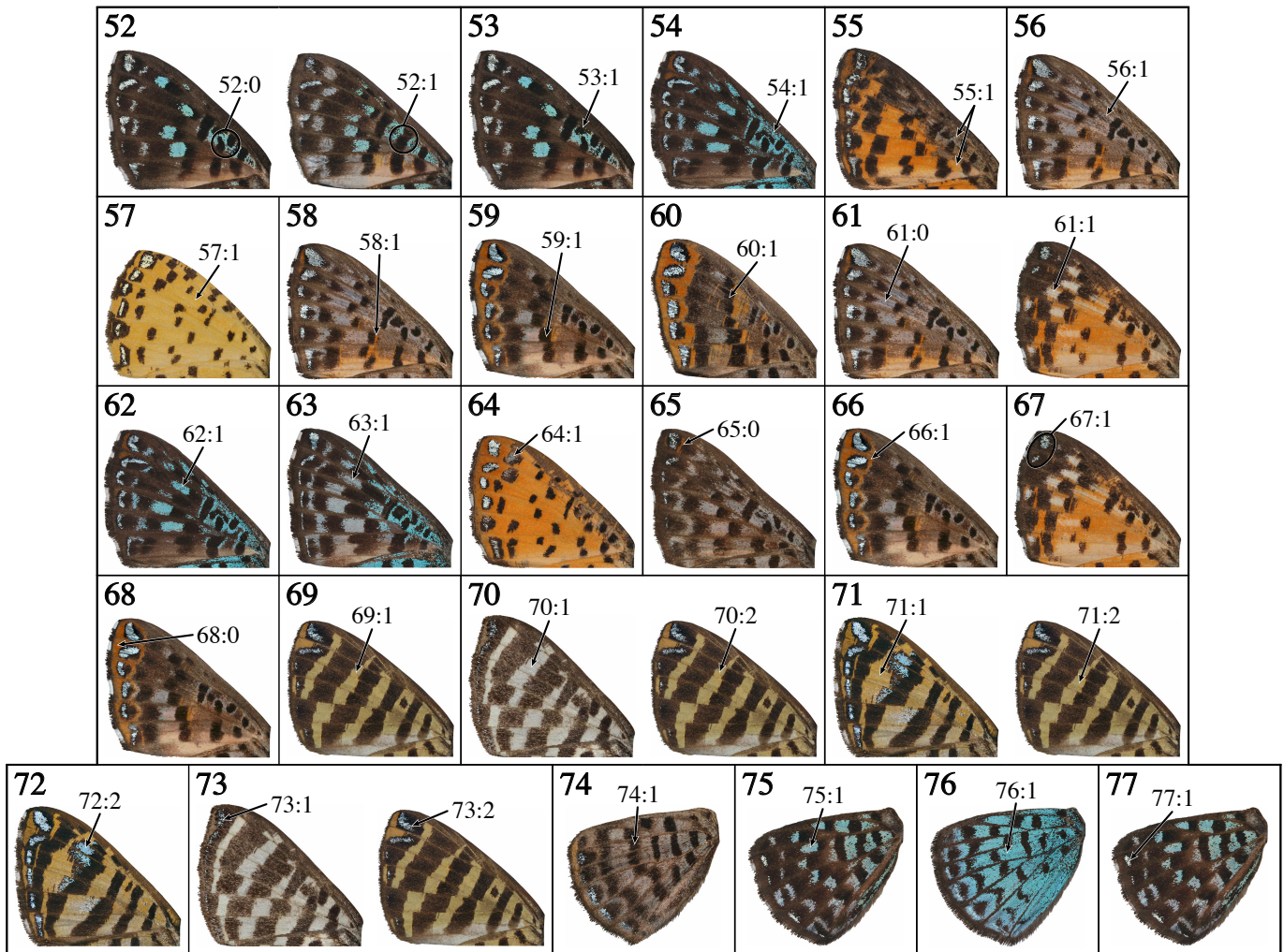


Fig. 2. Characters of the male ventral wing pattern in *Argyrogrammana* (characters 52-73 forewing, 74-77 hindwing). Each box depicts a single character (numbered at top left), with the relevant character state(s) indicated by one or more arrows or a circle. Wings in character boxes: 52(0), 53, 75, 77 = *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 ($< 45^\circ$ angle); (2) prominently inwardly directed ($> 45^\circ$ 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.

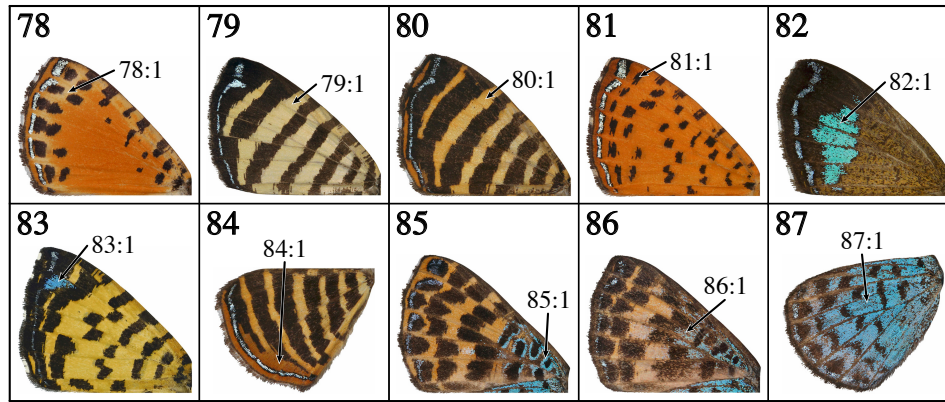


Fig. 3. Characters of the female wing pattern in *Argyrogrammana* (characters 78-83 dorsal forewing, 84 dorsal hindwing, 85-86 ventral forewing, and 87 ventral hindwing). Each box depicts a single character (numbered at top left), with the relevant character state indicated by an arrow. Wings in character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

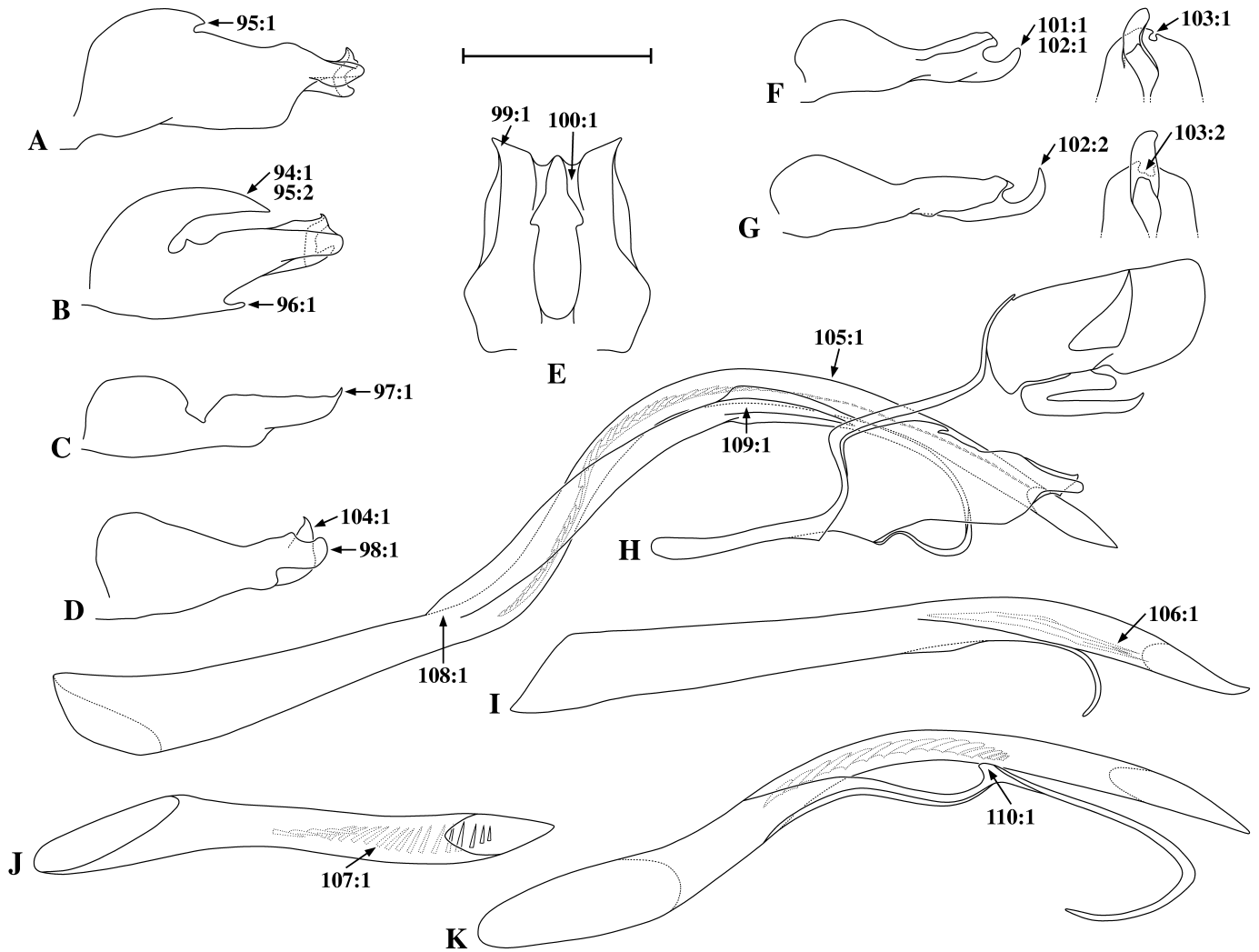


Fig. 5. Characters of the male genitalia in *Argyrogrammana* (characters 94-104 valvae and transtilla, 105-110 aedeagus, cornuti, and pedicel). Relevant character states are indicated by an arrow. A-D, F-G (left): valve in lateral view; E: valvae in ventral view; F-G (right): distal tip of valvae in ventral view; H: entire genital capsule in lateral view; I, K: aedeagus and pedicel in dorsal view; J: aedeagus in ventral 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 *Argyrogrammana* 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 *Baetis 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

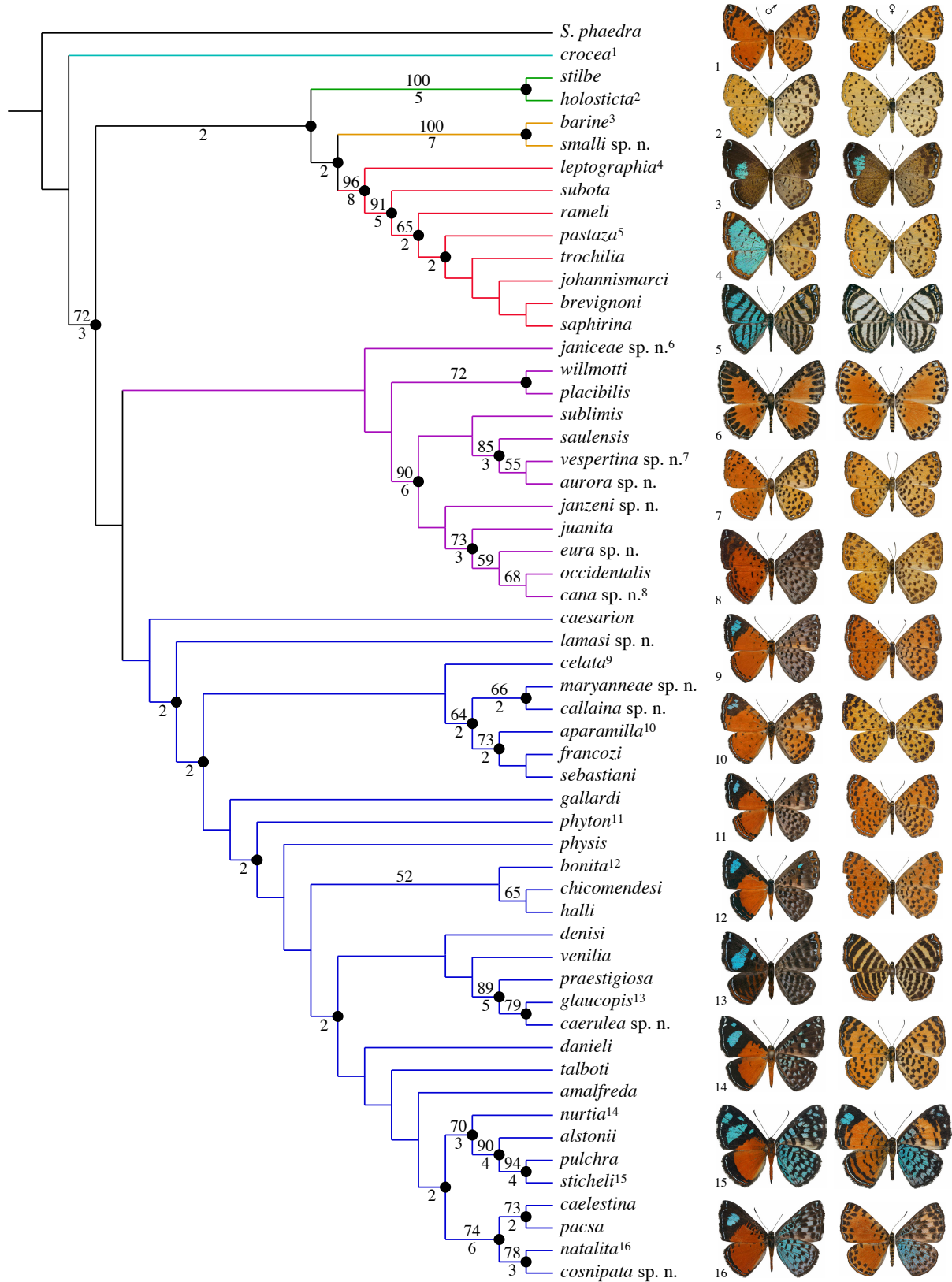


Fig. 6. Single most parsimonious cladogram resulting from the heuristic analysis of 110 morphological characters for all 55 species of *Argyrogrammana*. The six recognized species groups are indicated through the use of colored branches: turquoise = *crocea* group (1 species); green = *stilbe* group (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.

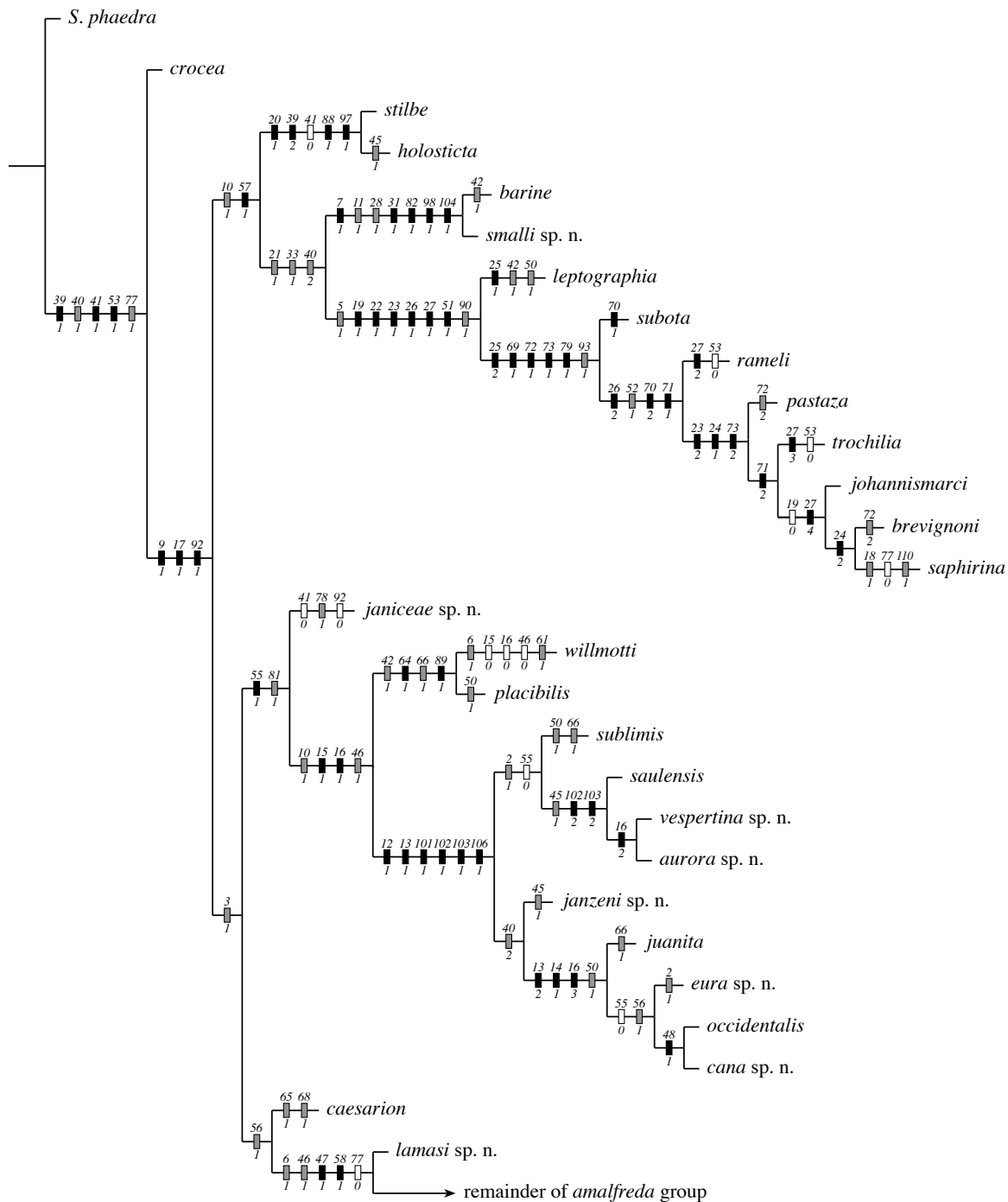


Fig. 7. Top half of cladogram from Fig. 6 (*Argyrogrammana crocea*, *stilbe*, *barine*, *trochilia*, and *occidentalis* groups, and basal two taxa in *amalfreda* group) illustrating the distribution of character states. Black bars indicate unique apomorphies, gray bars homoplasious apomorphies, and white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

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*

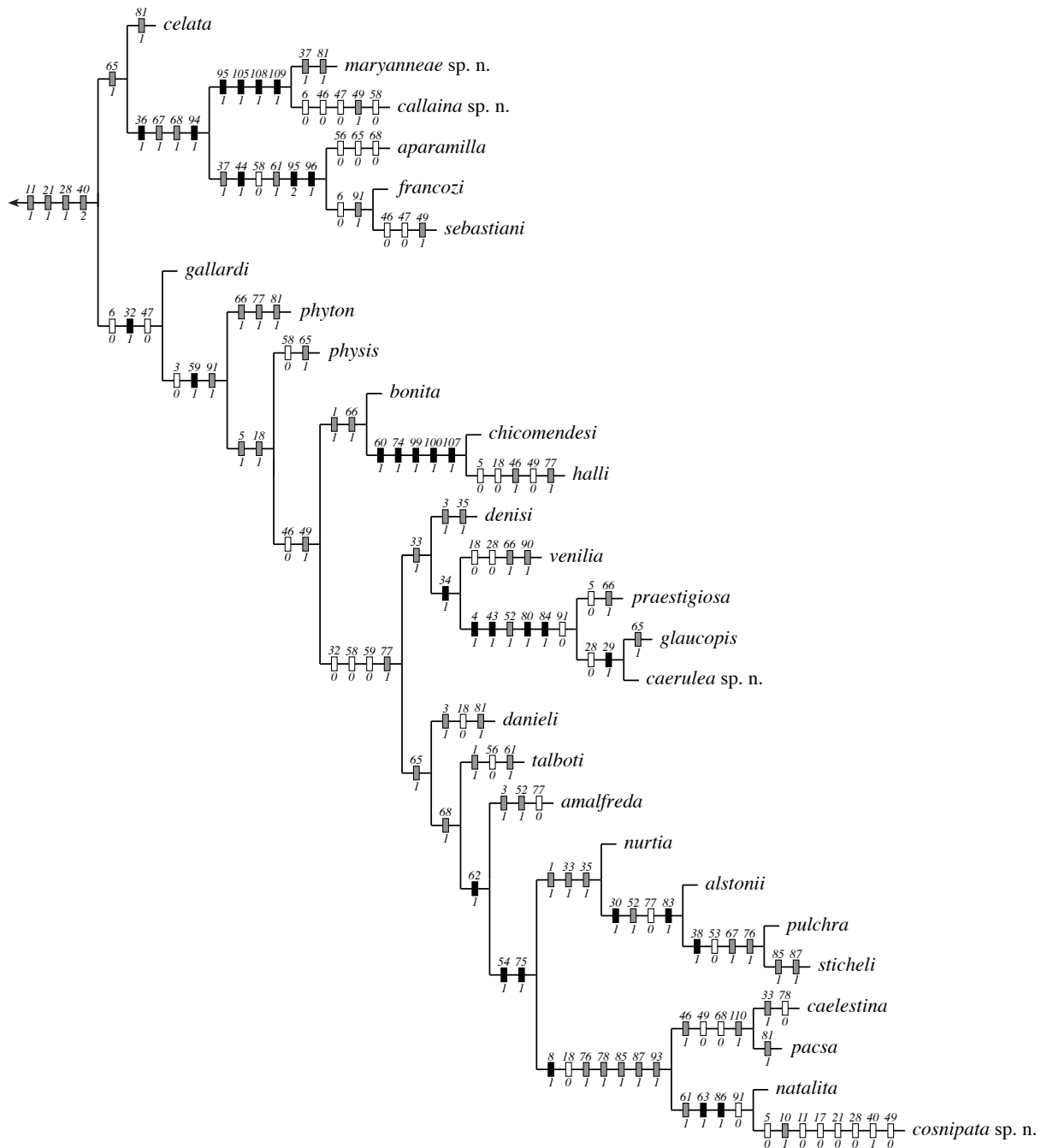


Fig. 8. Bottom half of cladogram from Fig. 6 (derived majority of *Argyrogrammana amalfreda* group) illustrating the distribution of character states. Black bars indicate unique apomorphies, gray bars homoplasious apomorphies, and white bars reversals.

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. glaucopsis* is removed. This analysis shows

that *A. glaucopsis* 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. pacsia</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. pacsia</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*

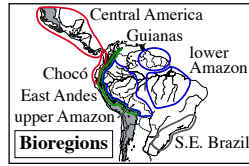
group (*A. holosticta*), and twice each in the *trochilia* group (*A. leptographia* (Stichel, 1911) and *A. saphirina* (Staudinger, 1887)), *occidentalis* group (*A. vespertina* Hall & Willmott, 2023, and the *A. occidentalis* subclade) and *amalfreda* group (*A. physis* and *A. pulchra*). The only example 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

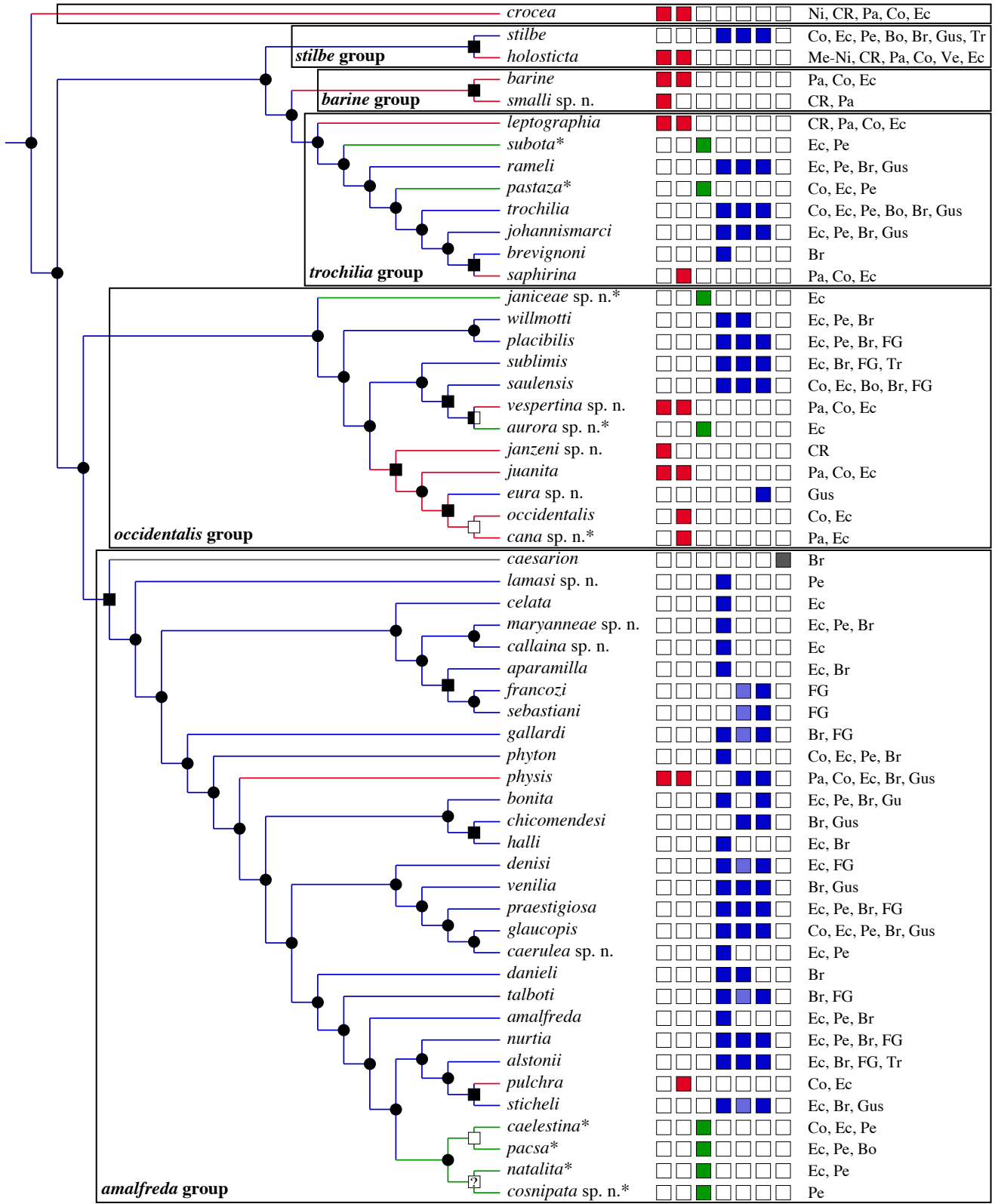


Bioregions

- Central America
- Chocó
- East Andes
- Upper Amazon
- Lower Amazon
- Guianas
- Southeast Brazil

Country codes:

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

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