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.

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

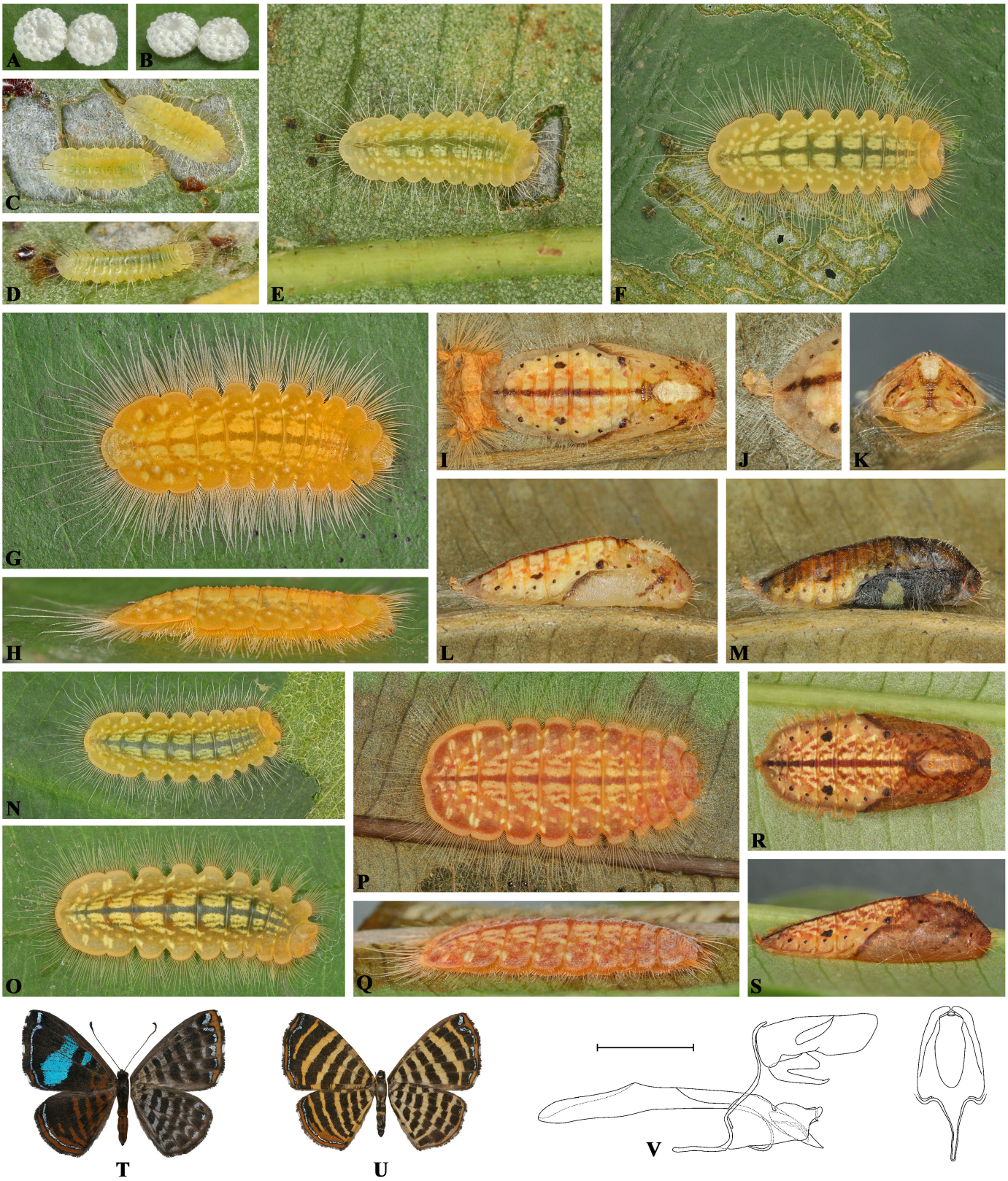

Fig. 1. Life history of *Argyrogrammana glaucopis* (Bates) from Santiago, Ecuador. Rearing #2: **A,B**. A pair of eggs in dorsal (A) and dorsolateral (B) views. **C,D**. Pre-prepenultimate instar caterpillars in dorsal (C) and dorsolateral (D) views, showing early instar feeding damage. **E**. Prepenultimate 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).

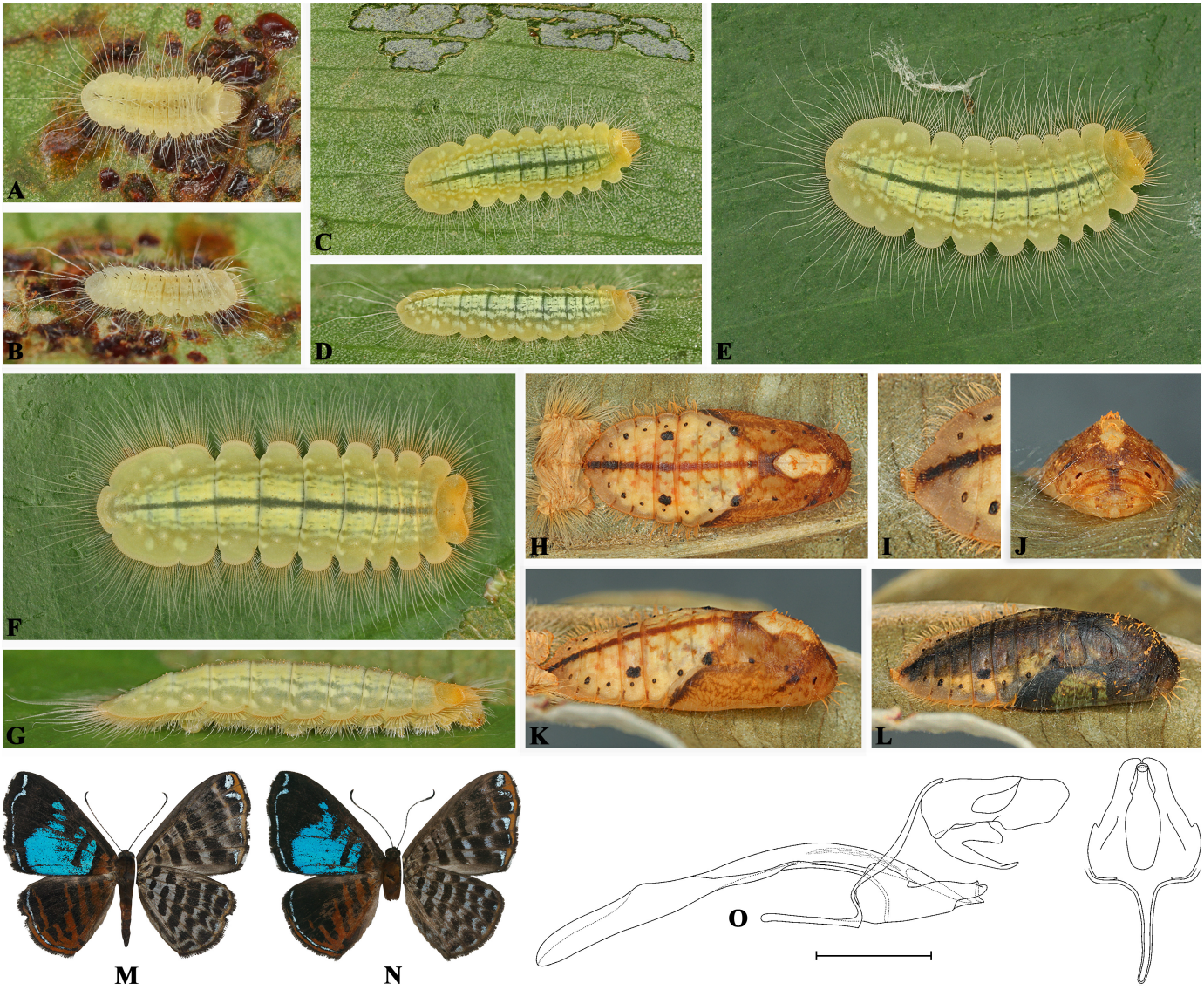

Fig. 2. Life history of *Argyrogrammana caerulea* Hall, **n. sp.** from El Recinto Arenal, Ecuador. **A,B**. Pre-prepenultimate instar caterpillar in dorsal (A) and dorsolateral (B) views, showing early instar feeding damage. **C,D**. Prepenultimate instar in dorsal (C) and dorsolateral (D) views, showing 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**. Eclosed 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. 1I-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. 1I) 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. 1I,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 Sucumbíos 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. glaucopis* are very similar. However, the single reared caterpillar of *A. caerulea* differed from the multiple examined caterpillars of *A. glaucopis* 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. glaucopis* 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 Riodinini (Downey & Allen, 1980; DeVries, 1997), with the most similar eggs that I have seen belonging to the symmachiine genus *Pirascca* 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. glaucopis* 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: *Sucumbíos*, 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, Cu_2, and Cu_1 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 uneverted 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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LITERATURE CITED

APG (Angiosperm Phylogeny Group). 2009. An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG III. *Botanical Journal of the Linnean Society* 161(1): 105-121.

Brévignon, C., Gallard, J.-Y. 1995. Contribution a l'étude des Riodinidae de Guyane Française (Lepidoptera). Le genre *Argyrogrammana*. *Lambillionea* 95(3): 393-406.

Comstock, J. H., Needham, J. G. 1898. The wings of insects. Chapter III. The specialization of wings by reduction. *American Naturalist* 32: 231-257.

Condit, R., Pérez, R., Daguerre, N. 2011. *Trees of Panama and Costa Rica*. Princeton, Princeton University Press. 494 pp.

DeVries, P. J. 1997. *The Butterflies of Costa Rica and Their Natural History. Volume II: Riodinidae*. Princeton, Princeton University Press. 288 pp.

DeVries, P. J., Chacón, I. A., Murray D. 1994. Toward a better understanding of host use and biodiversity in riodinid butterflies (Lepidoptera). *Journal of Research on the Lepidoptera* 31(1/2): 103-126.

Dick, C. W., Abdul-Salim, K., Bermingham, E. 2003. Molecular systematic analysis reveals cryptic tertiary diversification of a widespread tropical rain forest tree. *The American Naturalist* 162(6): 691-703.

Dolibaina, D. R., Dias, F. M. S., Mielke, O. H. H., Casagrande, M. M. 2015. *Argyrogrammana* Strand (Lepidoptera: Riodinidae) from Parque Nacional da Serra do Divisor, Acre, Brazil, with the description of four new species. *Zootaxa* 4028(2): 227-245.

Downey, J. C., Allyn, A. C. Jr. 1980. Eggs of Riodinidae. *Journal of the Lepidopterists' Society* 34(2): 133-145.

Eliot, J. N. 1973. The higher classification of the Lycaenidae (Lepidoptera): A tentative arrangement. *Bulletin of the British Museum of Natural History (Entomology)* 28: 373-506.

FM (Field Museum). 1999-2022. *Environmental and Conservation programs: Tropical Plant Guides*. https://www.fm2.fieldmuseum.org/plantguides. Date cited is when website version began to last accessed date October 2022.

Gallard, J.-Y. 2017. *Les Riodinidae de Guyane*. Sofia, Tezida. 191 pp.

Gentry, A. H. 1996. *A Field Guide to the Woody Plants of Northwest South America (Colombia, Ecuador, Peru) with Supplementary Notes on Herbaceous Taxa*. Chicago, University of Chicago Press. 895 pp.

Greeney, H. F. 2009. A revised classification scheme for larval hesperiid shelters, with comments on shelter diversity in the Pyrginae. *Journal of Research on the Lepidoptera* 41: 53-59.

Greeney, H. F., Jones, M. T. 2003. Shelter building in the Hesperiidae: A classification scheme for larval shelters. *Journal of Research on the Lepidoptera* 37: 27-36.

Hall, J. P. W. 2018. *A Monograph of the Nymphidiina (Lepidoptera: Riodinidae: Nymphidiini): Phylogeny, Taxonomy, Biology, and Biogeography*. Washington, The Entomological Society of Washington. 990 pp.

Hall, J. P. W. 2023. A morphological phylogenetic analysis of *Argyrogrammana* Strand (Lepidoptera: Riodinidae: Symmachiini). *Tropical Lepidoptera Research* 33(Supplement 1): 1-18.

Hall, J. P. W., Willmott, K. R. 1995. Notes on the genus *Argyrogrammana*, with descriptions of five new species (Lepidoptera: Riodinidae). *Tropical Lepidoptera* 6(2): 136-143.

Hall, J. P. W., Willmott, K. R. 1996. Notes on the genus *Argyrogrammana*, part 2, with one new species (Lepidoptera: Riodinidae). *Tropical Lepidoptera* 7(1): 71-80.

Hall, J. P. W., Willmott, K. R. 2023. A review of the *Argyrogrammana* fauna of the Transandean region (Lepidoptera: Riodinidae: Symmachiini). *Tropical Lepidoptera Research* 33(Supplement 1): 28-48.

Hall, J. P. W., Willmott, K. R., Ahrenholz, D. H. 2023a. A review of the *Argyrogrammana* fauna of the eastern Andes (Lepidoptera: Riodinidae: Symmachiini). *Tropical Lepidoptera Research* 33(Supplement 1): 49-60.

Hall, J. P. W., Willmott, K. R., Ahrenholz, D. H. 2023b. A review of the *Argyrogrammana amalfreda* group fauna of the western Amazon (Lepidoptera: Riodinidae: Symmachiini). *Tropical Lepidoptera Research* 33(Supplement 1): 61-85.

Harvey, D. J. 1987. *The Higher Classification of the Riodinidae (Lepidoptera)*. Ph.D. Thesis. Austin, University of Texas.

Janzen, D. H., Hallwachs, W. D. 2009-22. *Dynamic Database for an Inventory of the Macrocaterpillar Fauna, and its Food Plants and Parasitoids, of Area de Conservación Guanacaste (ACG), Northwestern Costa Rica*. https://www.janzen.sas.upenn.edu/caterpillars/database.lasso. Date cited is when website version began to last accessed date October 2022.

Kaminski, L. A. 2008. Immature stages of *Caria plutargus* (Lepidoptera: Riodinidae), with discussion on the behavioral and morphological defensive traits in nonmyrmecophilous riodinid butterflies. *Annals of the Entomological Society of America* 101(5): 906-914.

Klots, A. B. 1956. *Lepidoptera*, pp. 97-110. *In*: Tuxen, S. L. (Ed.), *Taxonomists' Glossary of Genitalia in Insects.* Copenhagen, Munksgaard.

MBG (Missouri Botanical Garden). 2022. *Tropicos*. https://www.tropicos.org. Date cited is last time of access (October 2022) as date when website began is unknown.

Mota, L. L., Kaminski, L. A., Freitas, A. V. L. 2014. Last instar larvae and pupae of *Ourocnemis archytas* and *Anteros formosus* (Lepidoptera: Riodinidae), with a summary of known host plants for the tribe Helicopini. *Zootaxa* 3838(4): 435-444.

Robbins, R. K., Aiello, A. 1982. Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. *Journal of the Lepidopterists' Society* 36(2): 65-75.

Seraphim, N., Kaminski, L. A., DeVries, P. J., Penz, C., Callaghan, C., Wahlberg, N., Silva-Brandão, K. L., Freitas, A. V. L. 2018. Molecular phylogeny and higher systematics of the metalmark butterflies (Lepidoptera: Riodinidae). *Systematic Entomology* 43(2): 407-425.

Stehr, F. W. (Ed.). 1987. *Immature Insects*. Dubuque, Kendall-Hunt Publishing Company. 754 pp.