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Immature stages and biology of the Neotropical skipper *Artines angelica* Medeiros, 2019 (Hesperiidae: Hesperiinae: Hesperiini: Moncina)

Yeison VEGA[1,2,*], Carolina FLORES BANCAYAN[2,3], Antuané CORDOVA VELAZCO[2,4], Zunilda ESCALANTE ARTEAGA[2,5], Geoffrey GALLICE[6, 7, 8], Shinichi NAKAHARA[9]

[1] Grupo de Investigación Biología de Organismos Tropicales (BIOTUN), Departamento de Biología, Universidad Nacional de Colombia, Bogotá, Colombia
[2] Alianza para una Amazonía Sostenible, Madre de Dios, Perú
[3] Laboratorio de Ecología y Biodiversidad Animal, Facultad de Ciencias Naturales y Matemática, Universidad Nacional Federico Villarreal, Lima, Perú
[4] Facultad de Ciencias Biológicas, Universidad Nacional Mayor de San Marcos, Lima, Perú
[5] Universidad Nacional de San Antonio Abad del Cusco, Cusco, Perú
[6] Departamento de Ingeniería, Pontificia Universidad Católica del Perú, Lima, Perú
[7] Alliance for a Sustainable Amazon, Potomac, MD, USA
[8] Department of Natural History, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA
[9] Museum of Comparative Zoology and Department of Organismic and Evolutionary Biology, Harvard University, Cambridge - MA, USA
* correspondence: yevegag@unal.edu.co

ABSTRACT

In this study, we describe the immature life stages and two natural host plant associations of the neotropical skipper butterfly *Artines angelica* Medeiros, 2019 (Hesperiidae), in southeastern Peru. This represents the first published information regarding the basic biology of this species, and only the second for the genus *Artines*, highlighting our general lack of knowledge of this group. Specimens were collected at the Finca Las Piedras research station in Peru's Madre de Dios department, where immatures were found and reared on two herbaceous bamboo species, *Taquara micrantha* (Kunth) I.L.C. Oliveira and R.P. Oliveira and *Olyra latifolia* L. (both Poaceae). The life cycle of the only individual *A. artines* found and reared from the egg stage spanned 55 days, during which the species went through six larval instars. The life and natural history information we provide may be useful in understanding the species diversity of the skipper subtribe Moncina, which is extremely diverse yet poorly studied to date.

KEY WORDS: Bionomy, life cycle, natural history, terra-firme rainforest, Neotropical region, Poaceae

Estados inmaduros y biología de la mariposa neotropical *Artines angelica* Medeiros, 2019 (Hesperiidae: Hesperiinae: Hesperiini: Moncina)

RESUMEN

En este estudio se describe por primera vez los estados inmaduros y la asociación con dos plantas hospederas de la mariposa neotropical *Artines angelica* Medeiros, 2019 (Hesperiidae) en el sureste de Perú. Esto representa la primera información publicada sobre la biología básica de esta especie, y solo la segunda para el género *Artines*, lo que resalta nuestro desconocimiento general sobre este grupo. Los especímenes fueron recolectados en la estación biológica Finca Las Piedras en el departamento de Madre de Dios, Perú, hallando los huevos en dos especies de Poaceae, *Taquara micrantha* (Kunth) I.L.C. Oliveira and R.P. Oliveira y *Olyra latifolia* L. Según el presente estudio, el ciclo de vida comprende 55 días desde huevo a la emergencia del adulto, basado en sólo un individuo, durante el cual la especie pasa por seis estadios larvales. La información aquí consignada sobre la historia natural de la especie puede ser útil en nuestra comprensión de la diversidad de hespéridos de la subtribu Moncina, los cuales son extremadamente diversos y, a la fecha, pobremente estudiados.

PALABRAS CLAVE: Bionomía, ciclo de vida, historia natural, bosque tropical de tierra firme, región Neotropical, Poaceae

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INTRODUCTION

With over 800 valid species-group names in more than 100 genera (Warren *et al.* 2024), the skipper subtribe Moncina is a highly diverse radiation within the subfamily Hesperiinae. Despite their high abundance and widespread distribution throughout the Neotropics, Moncina diversity, ecology, biogeography, and life and natural history remain poorly understood, due in part to the group's extremely high species richness, as well as difficult identification (Dolibaina *et al.* 2015, 2017). In addition, in recent years new Moncina species have been described at a high rate (e.g., Dolibaina *et al.* 2015; Medeiros *et al.* 2019; Brockmann *et al.* 2022; Zhang *et al.* 2023), suggesting that our understanding of the species diversity of the subtribe is far from complete.

Information regarding immature stage biology is one potential tool for improving our understanding of Hesperiidae diversity, particularly highly diverse groups such as Moncina. For example, combining natural history data with other independent sources of evidence such as genetic, ecological and systematic data, can lead to new classification proposals, clarify the phylogenetic relationships among species, delimit and distinguish taxa, and improve our understanding of the group's evolutionary history (e.g., Hebert *et al.* 2004; Burns *et al.* 2010; Janzen *et al.* 2011; Bertrand *et al.* 2014; Núñez *et al.* 2021). However, basic biological information is scattered and available for only approximately 113 species within the subtribe (representing ca. 14% of the total currently known species; Beccaloni *et al.* 2008; Greeney and Warren 2009; Cock 2009; Cock 2011; Cock 2012; Janzen and Hallwachs 2023; Sousa *et al.* 2023), severely hampering detailed study. Furthermore, such information provides an opportunity for addressing the so-called "Haeckelian shortfall" (Faria *et al.* 2020), which emphasizes that gaps in our knowledge of biodiversity, including both ecology and evolution, can be improved by the inclusion of information derived from the study of the early developmental stages of organisms.

The genus *Artines* has a complex taxonomic history and remains in a state of rapid change. Initially, the genus was established in 1901 by Frederick DuCane Godman in his "*Biologia Centrali-Americana Insecta. Lepidoptera-Rhopalocera.*" (Godman 1901). Godman followed Watson's (1893) classification and recognized three subfamilies in Hesperiidae: Pyrrhopyginae, Hesperiinae and Pamphilinae, with *Artines* in this latter subfamily (Godman 1901: 608). The current higher-level classification of Hesperiidae, including tribal and subtribal classification, largely builds upon Brigadier William Evans' monumental work based on adult external morphology (Evans 1949, 1951, 1952, 1953, 1955) where *Artines* was placed in the subfamily Hesperiinae (Evans 1955: 106).

With the rise of molecular techniques, several genomic studies in recent years have revised Evans' classification by producing resolved phylogenetic hypotheses, providing insights into generic relationships of *Artines* (e.g., Zhang *et al.* 2022). However, despite the description and addition of new species by Evans (1955), Mielke (1968, 1992), Steinhauser and Austin (1993), and Dolibaina *et al.* (2015), no phylogenetic hypothesis has been proposed for *Artines*. Recent cladistic analyses focused on other genera and based on morphological characters suggest that *Artines* represents a polyphyletic lineage (Carneiro *et al.*, 2015), prompting a revision of the genus by Medeiros *et al.* (2019). This revision established that the genus comprises 15 known species distributed across forested habitats from Central America to the Cerrado ecosystem in Brazil.

Given the diversity of the genus *Artines*, which is distributed across various Neotropical habitats, as well as the existence of faunistic studies (e.g., Murray 2000), it is notable that the only reported life or natural history information for the genus is for *A. rica* Steinhauser and Austin, 1993, in Costa Rica (Janzen and Hallwachs 2023). This information is not presented in a formal description, rather it is part of the research database of the authors and includes only partial documentation of later instars and several host plants. This limited knowledge underscores the uncertainty surrounding the basic biology of *Artines* and highlights the broader knowledge gaps within the subtribe Moncina.

In this study, we present the first descriptions of the immature stages of *Artines angelica* Medeiros, 2019, including detailed photographs and descriptions of the egg, six larval instars, and pupa. Additionally, we document the species' natural host plants for the first time.

MATERIALS AND METHODS

Study site and Field Collection

All specimens were collected at Finca Las Piedras (FLP) research and education center in Madre de Dios, located approximately 48 km from Puerto Maldonado in southeastern Peru (12°13'40" S, 69°6'40" W; 240 m asl). FLP spans 74 hectares of upland, terra firme rainforest, swamps dominated by the palm *Mauritia flexuosa* L. (Arecaceae), regenerating secondary forests, and active and abandoned agricultural lands (for more information about FLP see Baine *et al.*, 2019). The collection of specimens was authorized by research permit number D000443-2021-MIDAGRI-DGGDPFFS from Peru's Servicio Nacional Forestal y de Fauna Silvestre (SERFOR). This project is part of a long-term initiative to document the diversity and biology of Lepidoptera in southeastern Peru.

Rearing

Rearing followed the standard protocol established at FLP (e.g., Baine *et al.* 2019; Ccahuana *et al.* 2021; Corahua-Espinoza *et al.* 2022). Each immature was found by searching potential host plants in the field and subsequently transported from the field to the laboratory at FLP for rearing to adulthood under controlled conditions; immatures were photographed periodically (see below) and their life cycles monitored until eclosion. Host plants on which immatures were found in the field were marked, photographed, georeferenced, and regularly visited to provide fresh leaves for feeding larvae. Immatures were fed with their respective natural host plant species throughout the larval stages.

The immatures were collected on three different occasions. The first collection was on February 11, 2022, where a last instar larva was collected (voucher 2022-FLP-IMM-0057); the second collection of a penultimate instar took place on March 31, 2022 (voucher 2022-FLP-IMM-0172); the third collection of an egg occurred on February 7, 2023 (voucher 2023-FLP-IMM-0117) (Table 1). All immatures were kept in individual 1 L plastic containers sealed with a soft nylon cloth secured with a rubber band, to prevent escape and keep parasitoids out while maintaining airflow. The host plant leaves were kept hydrated using floral water tubes and were replaced as needed to ensure that the immature had fresh leaves to feed on. Each individual was photographed using a Nikon D7100 digital camera and Tokina (AT-X PRO macro 100 F 2.8 D) macro lens every two or three days, or when a discarded head capsule was observed inside or outside the shelter (indicating a larval molt), by opening its shelter. This frequency was chosen to facilitate the documentation of each life stage while minimizing stress to shelter-building larvae. All photographs included a scale in mm for subsequent measurements by pixel counting. Eclosed adults were papered or mounted and stored in the Lepidoptera collection of the Alliance for a Sustainable Amazon in Puerto Maldonado, Peru.

Morphology

Measurements for all life stages were gathered by counting pixels calibrated to scale in high resolution digital photographs using ImageJ 1.54d. Measurements included the maximum diameter of the egg, length of the larvae, and length of the pupae from the front of the head to the posterior end of the abdomen while in dorsal view. Observations and photography of the head capsules were carried out using a Nikon ECLIPSE Si optical trinocular microscope with a 12Mpx Sony IMX183 CMOS camera, subsequently illustrated with CorelDRAW Graphics Suite 2021 software. Head capsules of *A. rica* and *Eutocus facilis* (Plötz, 1884) were drawn based on the photographs available in Janzen and Hallwachs (2023), following the same procedure as above. These species were chosen to illustrate the variation in the characteristics of the head capsule of phylogenetically closely related genera.

The only recovered first instar head capsule was damaged and thus not illustrated. The width of the head capsule was considered as the distance between the outermost parts. The description of the egg and larvae followed the terminology in Minno (1994), except for the terms frontoclypeus and epicraneal notch, which are in accordance with Stehr (1987); the description of the pupa was based on Mosher (1915). The nomenclature for setae and pores was based on the terminology by Stehr (1987).

Identification

The identification of the three reared adult specimens was carried out based on the diagnostic characters for *Artines* species provided by Medeiros *et al.* (2019). For the two male specimens, we confirmed that the cornutus has multiple conspicuous short and pointed spines extending from the distal end of the vesica. In the case of the female, the presence of a sclerotized plate wider than the ostium, located at the proximal end of the postvaginal lamella was verified. These diagnostic characters for *A. angelica* were originally detailed in Medeiros *et al.* (2019), where the holotype specimen was also illustrated.

The host plants are common understory plants at FLP that have been identified by previous studies at the site (*Olyra latifolia*, see Hurtado *et al.* 2021; *Taquara micrantha*, see Corahua-Espinoza *et al.* 2022). Likewise, the botanical identification was verified following the taxonomic keys and descriptions in Oliveira and Oliveira (2020).

RESULTS

Description of immature stages

Artines angelica Medeiros, 2019

Vouchers: 2022-FLP-IMM-0057, 0172; 2023-FLP-IMM-0117

ZooBank register: urn:lsid:zoobank.org:pub:359CE411-CBB9-4501-A356-F8B292D33F39

Table 1. Dates of important life history events recorded for *Artines angelica* at FLP.

Voucher	Date of col.	Egg hatch	L1 to L2	L2 to L3	L3 to L4	L4 to L5	L5 to L6	Pupation	Adult
2022-FLP-IMM-0057	11/02/2022	n/a	n/a	n/a	n/a	n/a	11/02/2022	17/02/2023	28/02/2022
2022-FLP-IMM-0172	31/03/2022	n/a	n/a	n/a	n/a	31/03/2022	07/04/2022	20/04/2023	30/04/2023
2023-FLP-IMM-0117	07/02/2023	08/02/2023	13/02/2023	18/02/2023	26/02/2023	04/03/2023	09/03/2023	22/03/2023	03/04/2023

Egg (Figure 1a, based on 2023-FLP-IMM-0117, N=1). Diameter 0.97 mm (N=1). Semi-spherical shape resembling a dome or cup. Creamy colored with a slight yellowish tint, featuring a central brown spot of approximately 0.58 mm, corresponding to the cephalic capsule of the individual nearing hatching. Chorion marked by a series of hexagonal ribs covering the entire surface of the egg, dissipating near the micropylar area. Laid on the abaxial side of mature leaves.

First instar (Figure 1b-c, based on 2023-FLP-IMM-0117, N=1). Head capsule width 0.60 mm, black with pitted sculpturing, rounded vertex, and insignificant epicranial notch. Frontoclypeus smooth, setae F1, AF1, AF2, C1, C2, A1, A2, S1, S2, S3, P1, P2, MD1, MD2, and L1, as well as pores Fa and AFa present. Light green body, darker on the dorsal side due to feeding, smooth, with a black prothoracic shield present, A10 with a somewhat whitish coloration. Short translucent setae scattered across body, longer on A10. Anal plate not differentiated from the integument. Body length: 3.7 mm.

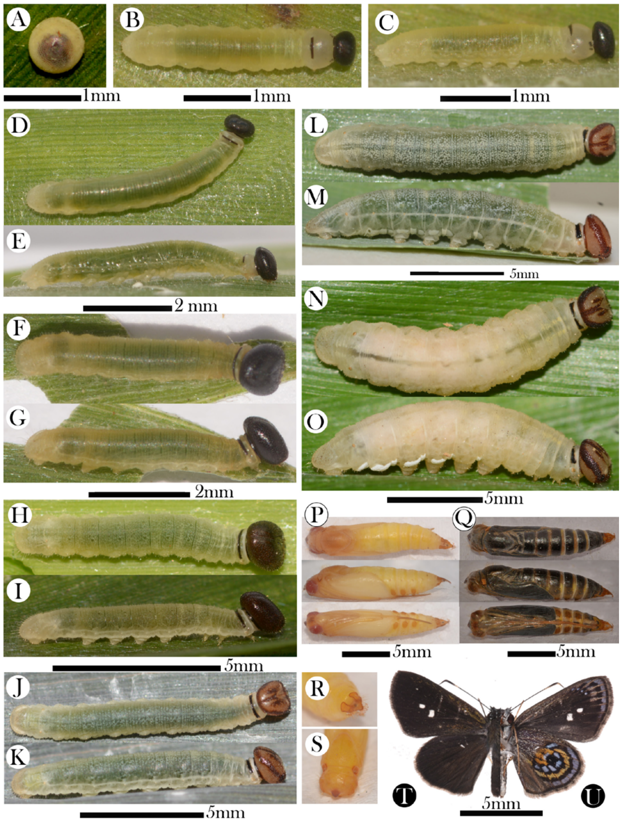

Figure 1. Life stages of *Artines angelica*. **A.** Egg with head capsule visible (dorsal); **B, C.** First instar (dorsal, lateral); **D, E.** Second instar (dorsal, lateral); **F, G.** Third instar (dorsal, lateral); **H, I.** Fourth instar (dorsal, lateral); **J, K.** Fifth instar (dorsal, lateral); **L, M.** Sixth instar (dorsal, lateral); **N, O.** Prepupa, the white masses on the ventral region of the last segments are wax in an early stage of the prepupa; **P.** Pupa at an intermediate stage of development; **Q.** Pupa in the final stage, about to emerge as an imago; **R.** Detail of the cremaster; **S.** Detail of the frontal region of the pupa; **T.** Dorsal view of the adult; **U.** Ventral view of the adult.

Second instar (Figure 1d-e, based on 2023-FLP-IMM-0117, N=1). Head capsule width 0.79 mm; slightly brown head capsule without pitted sculpturing, transitioning to a web-like sculpture, with a slightly pronounced epicranial notch, and 5 setae visible on one side of the labrum (Figure 2a). Six stemmata visible, stemma 5 slightly closer to stemma 6 than stemma 4. Body smooth with a darker coloration than the previous instar, with dark green intersegmental lines; legs, prolegs, and the last three abdominal segments in white-yellow. Tracheal system visible as white on the lateral side of the body along spiracles. Anal plate sclerotized with multiple white-yellow setae. Towards the end of this instar, the body becomes more yellowish and slightly shrinks. Body length: 4.0 – 5.2 mm.

Third instar (Figure 1f-g, based on 2023-FLP-IMM-0117, N=1). Head capsule width 1.09 mm. Head capsule similar to the previous instar in texture and color, with a slightly less prominent epicranial notch (Figure 2b). It retains a shape similar to the second instar, with a darker green dorsal side than the previous instar and a yellowish granular texture. Body length: 5.2 mm - 7.2 mm.

Fourth instar (Figure 1h-i, based on 2023-FLP-IMM-0117, N=1). Head capsule width 1.38 mm. Head capsule brown, with five setae visible on one side of the labrum, a slightly less noticeable epicranial concavity, and a more rounded structure with a texture similar to the third instar (Figure 2c). Body coloration similar to the previous stage, with a whitish integument on the legs, prolegs, and the last three

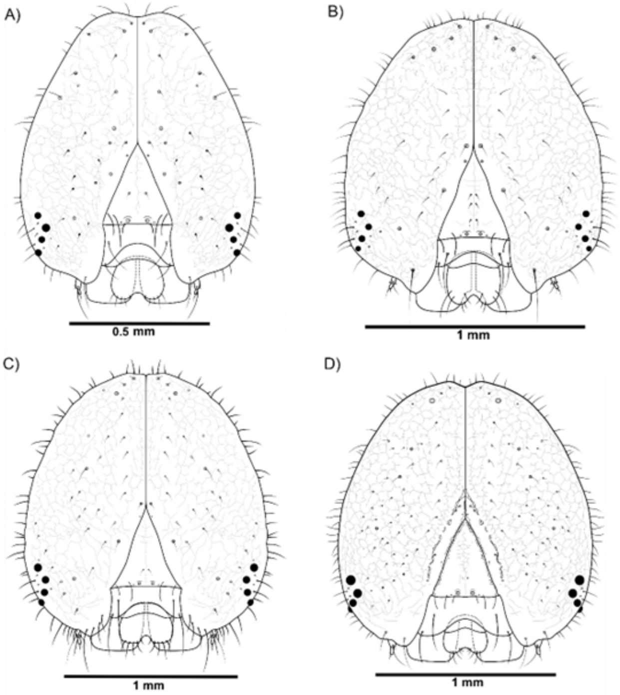

Figure 2. Illustrations of the head capsules of *Artines angelica*, based on voucher 2023-FLP-IMM-0117. **A.** Second instar; **B.** Third instar; **C.** Fourth instar; **D.** Fifth instar.

abdominal segments. Dorsally, thorax exhibits three faint whitish longitudinal lines, two lines closer to the subdorsal region, and one central line extending from the first thoracic segment (T1) to the ninth abdominal segment. In the abdominal region, there are two small dark green parallel spots on each abdominal segment, except for A8, A9, and A10. Body length: 8.3 - 12.0 mm.

Fifth instar (Figure 1j-k, based on 2022-FLP-IMM-0172, description based on N=2). Head capsule width 1.87 mm. Pebbly sculptured texture in the head capsule. Light brown adfrontal area and dark brown adfrontal and epicranial sutures. Dark brown stripe adjacent to the ecdysial line in the postfrontal region, extending longitudinally to the vertex; two parallel yellow stripes on each side in the outer region of the epicranial suture and the ecdysial line, forming a interrupted circular pattern linearly arranged as they approach the midline of the frons; two yellow spots starting from the base of the frons, near the clypeus, appearing to continue the previously mentioned yellow stripes, extending towards the sides of the head and becoming sharper as they approach the stemmata. Light brown frontoclypeus with a central dark brown longitudinal stripe. Dark brown lateral band extending from the vertex to stemmata 1-4. Light brown labrum and mandible, dark brown maxillae, labrum with five visible setae on one side (Figure 2d). Smooth body similar to the previous instar but with more noticeable longitudinal thoracic lines, dorsally more yellowish, and the dorsal abdomen exhibiting a granular pigmentation with irregularly distributed green dots, denser from A3 to A6. Dark green spiracular and subspiracular region with small white dots. White tracheal system forming a longitudinal line connecting the spiracles. Light green legs and prolegs. Body length: 12.0 – 18.0 mm.

Sixth instar (Figure 1 l-m, based on 2022-FLP-IMM-0172, description based on N=3). Head capsule width 2.4 mm. The texture and shape of the head capsule are similar to the previous instar. The epicranial and lateral bands become darker brown, although the intensity of pigmentation varies among individuals, ranging from very dark brown (almost black) to reddish-brown. Pale yellow frontal spot becomes more defined. Body smooth with a more yellowish coloration on the dorsum, extending to the subdorsal area. A dark green longitudinal line appears medially from the prothoracic shield to the caudal region. Ventrolateral area between the segments A3-A4, A4-A5, A5-A6, and A6-A7, as well as the segments A5, A6, and A7, exhibit white wax glands. Spiracles pale yellow. Body length: 22 mm - 25.4 mm.

Prepupa (Figure 1n-o, based on 2022-FLP-IMM-0057, description based on N=3). Body contracts and turns pale yellow overall. Dorsal longitudinal line becomes yellowish-ochre. Wax present on the intersegments A3-A4, A4-A5, A5-A6, and A6-A7, as well as on the segments A5, A6, A7, and A8. As the instar progresses, both the larva and the leaf on which it creates its shelter become covered in wax. Body length: 16.5 mm - 18.0 mm.

Pupa (Figure 1p-q, based on 2023-FLP-IMM-0117, description based on N=3). Head and thorax yellowish-ochre. The maxillae extends to segment a9+a10. There is a short red-brown pointed process on the frons (Figure 1s). Yellowish setae are present in the ocular, supraocular, and frons regions. Body elongated, fusiform, and tapers towards the cremaster. The prothorax with two spaced bands of yellowish setae. Mesothorax covered with yellowish marginal setae and a pair of pale orange eye-pieces. Mesothoracic wing yellowish-ochre in the proximal region and pale yellow in the distal region. Abdominal segments pale yellow, with oval-shaped yellowish-ochre spots on segments a5, a6, and a7. The a9+a10 segment with pale orange setae in the ventral view. Triangular cremaster reddish-brown with laterally positioned setae of the same color, including more than 20 hooked setae with a rounded and thickened tip (Figure 1r). As development progresses, the pupal eyes become reddish, and the mesothoracic wings, thorax, legs, and maxilla change to a light brown color. As the adult emergence approaches, the pupa turns black, except for the structures resembling eyes on the prothoracic region, the dorsal view of the abdominal intersegments, the ventral view of the abdominal segments, and the cremaster, which retain their original coloration (Figure 1q). Body length: 14.6 - 15.6 mm.

Bionomics

The life cycle spanned a maximum of 55 days (N=1, 2022-FLP-IMM-0057) from egg to adult emergence, although we note that the egg was not collected at the time of oviposition and development time may have been influenced by captive conditions. The egg was collected close to the larva's emergence, taking only 1 day to hatch. Six larval instars were observed and exhibited variable durations. The first and second instars lasted 4–5 days (N=1 each), while the third instar spanned 8 days (N=1). The fourth instar lasted 5 days (N=1). The fifth and sixth instars (N=2 and N=3, respectively) displayed the longest durations, each lasting for 13 days. The prepupal stage was brief, lasting only 1–2 days (N=3), whereas the pupal stage spanned 10–13 days before eclosion (N=3).

Host plants and behavior

The host plant was identified as *Olyra latifolia* L. (Poaceae: Bambusoideae: Olyreae) for both 2022-FLP-IMM-0057 and 2023-FLP-IMM-0117; both of the individuals were found on the same plant. This perennial herbaceous bamboo reaches up to approximately 3 meters in height at the study site, and has been described by Sonderstrom and Zuloaga 1989. The egg (2023-FLP-IMM-0117) was found at a height of 0.5 meters above the ground on the abaxial side of the leaf, near the base of the blade and close to the midrib. The second individual (larva, voucher code 2022-FLP-IMM-0057) was found at a height of 0.4 meters above the ground on the abaxial side of the leaf, in the middle part of the leaf, between the midrib and the leaf margin (Figure 4a-j).

The host plant of the remaining larva (2022-FLP-IMM-0172) was identified as *Taquara micrantha* (Kunth) I.L.C. Oliveira and R.P. Oliveira (Poaceae: Bambusoideae: Olyreae). This plant is a perennial and erect herbaceous bamboo, described by Oliveira *et al.* 2019 and Oliveira and Oliveira 2020. It is worth noting that this species exhibits high morphological variation, primarily concerning the indumentum of the leaves. The larva was found at a height of 0.25 m above the ground, on the abaxial side of the leaf, near the apex and the midrib of the blade (Figure 4k-q).

In all instars, the larvae constructed tubular shelters by weaving several silk threads on the abaxial side of the leaf (Figure 3), with the tension from these threads causing a section of the leaf to fold. The extent of leaf folding varies depending on the instar and the individual. This type of shelter belongs to Group I, Type II, according to the classification by Greeney and Jones (2003). The same type of shelter (Group I, Type II) was built both in the laboratory and in the field based on the observations made in the present study. It is noteworthy that after opening the shelter, the larva immediately constructed a new shelter.

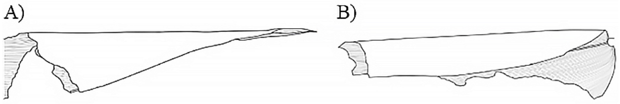

Figure 3. Tubular shelters created by the larvae of *A. angelica*. **A)** the shelters are constructed at the apex of the leaf, or **B)** at the margin of the blade, by folding a section of the leaf, depending on the size of the larva. The shaded area represents the underside of the leaf.

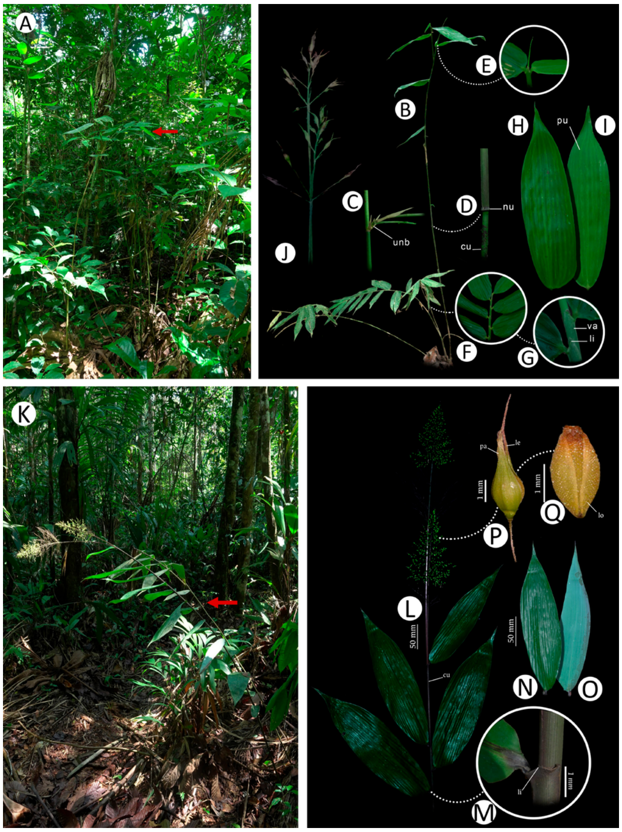

Figure 4. Host plants for *Artines angelica*. **A)** *Olyra latifolia* in situ, **B)** Habit, **C)** Detail of the culm showing branching, **D)** Nodal area, **E)** Apex, **F)** Phyllotaxis, **G)** Ligular area, **H)** Adaxial leaf surface, **I)** Abaxial leaf surface, **J)** Synflorescence, **K)** *Taquara micrantha* in situ, **L)** Habit, **M)** Ligular area, **N)** Adaxial leaf surface, **O)** Abaxial leaf surface, **P)** Spikelet, **Q)** Immature flower. cu: culm, le: lemma, li: ligule, lo: lodicule, nu: node, pa: palea, pu: pubescence, unb: upper node branching, va: sheath. The red arrow indicates the host plant. For the composition of this *Olyra latifolia* plate (B-J), different individuals from FLP were taken.

DISCUSSION

The single larva of *A. angelica* reared from the egg stage passed through six instars in the present study. Morphological changes between instars other than size are rather trivial, except for the last two instars where a change in the coloration of the head capsule occurs (Figure 1). In general, the immature stages of *A. angelica* are similar to those of *A. rica*, the only other species of *Artines* with documented life stages. Differences in the coloration of the head capsule are evident between *A. angelica* and *A. rica*, especially the markings anterior to the stemmata in the frontal area (Figure 5). For instance, in *A. angelica* the marking is horizontal (Figure 5a-c), while it is oblique in *A. rica* (Figure 5d). However, as illustrated in Figure 5, notable intraspecific variation is also present in *A. angelica*, and it is possible that *A. rica* also exhibits similar variation that is not visible from the limited published information.

The patterns of head capsule markings proved to be consistent across several species of *Taygetis* Hübner, [1819] (Satyrinae) in Ecuador and are used as a diagnostic character to identify larvae (Murray 2001). Clearly, documenting additional individuals of *A. angelica* spanning the species' range is necessary to assess the reliability of the coloration patterns of the head capsule for species recognition. If this characteristic proves to be consistent across *Artines* species, it may be informative and thus useful to support taxonomic changes in skippers. Therefore, documenting the immature stages of the other 13 known species of *Artines*, as well as of sister genera, could contribute significantly to our understanding of the evolutionary relationships of these taxa.

Comparing the larval morphology of *Artines* with its sister genera (Zhang *et al.* 2022) reveals small yet nevertheless informative differences. For instance, the immature stages of *A. angelica* and *A. rica* broadly resemble those of *Eutocus facilis* (Plötz, 1884) and *E. vetulus* (Mabille, 1883) (Janzen and Hallwachs 2023), with notable differences in the extent of the lateral band on the head capsule, the shape of the epicranial

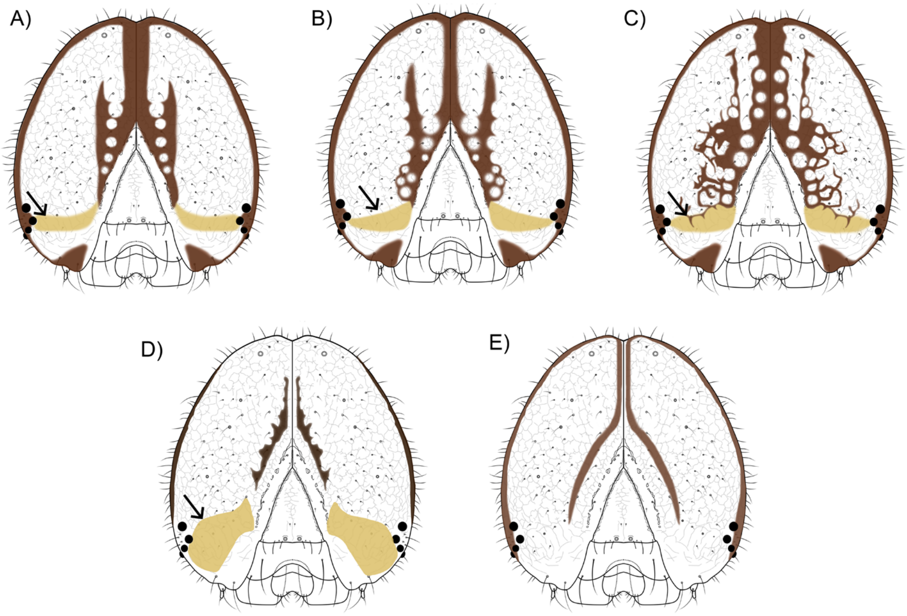

Figure 5. Comparison of the coloration of the cephalic capsule of *Artines angelica* with other closely related species. **A, B, C.** Head capsules of *A. angelica* (voucher 2022-FLP-IMM-0057, 2022-FLP-IMM-0172, 2023- FLP-IMM-0117, respectively); **D.** Head capsule of *A. rica*; E. Head capsule of *Eutocus facilis*. The arrows show the anterior darker markings.

suture pattern, the ecdysial line, and the dorsal body line in the final two instars (Figure 5). Thus, it is evident that Hesperiidae immatures have multiple characteristics that could provide an additional line of evidence to support classification hypotheses (e.g., Waterhouse 1932; Atkins 1973; Warren *et al.* 2008). To date, this strategy of complementing adult morphological and genetic characters in taxonomic and systematic studies has been under-utilized because life cycles are unknown for many species (Wahlberg *et al.* 2005).

According to Calixto Moraga (pers. comm.), the life cycle of *A. rica* in Guanacaste (Costa Rica) has been documented from the second instar with an average duration of 47 days (n=5) until the emergence of the adult. In the present study, the life cycle for *A. angelica* spanned a total of 55 days (N=1) from the egg stage (from the time of discovery of the egg in the field) until reaching the adult stage. It should be noted that for *A. rica*, there is no equivalent duration data reported from the egg, but there might not be a significant difference in development times given similar durations of development from the second instar for both species and the similar climatic conditions in both regions. However, it is important to consider that only one record of *A. angelica* was obtained from the egg in this study, requiring greater sample sizes for both species and further study of other factors that may influence development times to make an informative comparison.

Like all species within Moncina for which host plant records are available (e.g., Fukuda *et al.* 1984; Opler and Krizek 1984; Warren 1996; Brock and Kaufman 2003; Beccaloni *et al.* 2008; Janzen and Hallwachs 2023; Warren *et al.* 2009), *A. angelica* uses species from the family Poaceae as host plants. This is consistent with the general dietary preferences of Hesperiinae, the majority of which use monocots as their larval host plants (Warren *et al.* 2009). Regarding one of the congeneric species, *A. rica*, it shares *Olyra latifolia* as a host plant, and other reported species include *O. caudata* Trin., *Bambusa vulgaris* Schrad. ex Wendl., and an unidentified Poaceae (Janzen and Hallwachs 2023). Our observations constitute the first record for *Artines* using *Taquara micrantha* as a host plant, revealing a preference for this plant in the southwestern Amazon in Peru. Given the variety of plants consumed by *A. rica* and the closely-related genus *Eutocus*, it is likely that *A. angelica* uses other Poaceae species in the area as larval host plants. This ability could allow the exploitation of different plants throughout the year, possibly as an adaptation to the strong seasonality of the region (e.g., Lattin 1995; Pérez-Contreras 1999; Martínez-Hernández *et al.* 2020).

Changes across instars in shelter structure were not observed, except for the folded lamina portion that correlates with larval size, in accordance with other studies (e.g., Duerr *et al.* 2022). Other studies have reported changes in the structure and number of shelters constructed by Hesperiidae larvae (e.g., Young 1993; Moraes *et al.* 2012; Lepesqueur *et al.* 2017) due to controlled laboratory conditions, and we do not rule out the possibility of similar effects in the current study. However, the individual *A. angelica* collected as a mature larva in the present study (2022-FLP-IMM-0172) was found in the same type of shelter built in the laboratory setting (Group I, Type II) by the immature collected from the egg (2023-FLP-IMM-0117), suggesting that the conditions in captivity and/or the frequent opening of the shelter likely did not influence the shelter structure in the present study (e.g., Bächtold *et al.* 2012, 2017).

Furthermore, it is possible that *A. angelica* constructs only one type of shelter throughout its ontogeny under natural conditions considering that we have only observed one type of shelter in the present study. Therefore, given the limited sample size in this study, as well as the potential contribution of accurate and detailed data regarding larval behavior and shelter structures to studies of hesperiid taxonomy, systematics, and ecology, we recommend further work to confirm our findings and to document the basic biology of other species in this diverse group of butterflies.

It is important to emphasize that the significance of documenting life stages and natural history goes beyond providing crucial characters for understanding the evolution and systematics of tropical Lepidoptera. Given that the overwhelming majority of the Earth's species are plants and their insect herbivores, especially in the tropics, understanding plant-insect interactions in hyper-diverse ecosystems such as the Amazon can contribute greatly to our broader understanding of ecosystem functioning. Furthermore, considering that climate change and other human activities are having accelerating impacts on ecosystems globally, establishing baselines of the basic biology of representative groups such as Lepidoptera will be important to evaluate the biological impacts of these changes.

CONCLUSIONS

We do not know to within even an order of magnitude how many insect species exist on Earth (Stork 2018; Mora *et al.* 2011), to which our lack of understanding of the natural history of most species is added. Although Lepidoptera have been better studied than most other groups of arthropods in the tropics, we still know almost nothing about the immature stages, host plants, and other ecological interactions of the majority of species. Therefore, we strongly urge further research in the immature stage biology of groups such as Moncina and other diverse groups of insect herbivores, especially in diverse and poorly studied tropical ecosystems.

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DATA AVAILABILITY: Data available upon request – The data that support the findings of this study are available, upon reasonable request from Alliance for a Sustainable Amazon. The dataset is not publicly available because work is being done on the online repository and it is not yet available.