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Life Woven in Mist: Immature stages and morphology of Andean Pronophilina butterflies from the Eastern Cordillera of Colombia (Satyrinae: Satyrini)

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The subtribe Pronophilina comprises the most diverse lineage of Andean butterflies, with 59 genera and approximately 650 described species. Most studies on this group have focused on adults, highlighting a substantial gap in knowledge regarding the immature stages of the majority of species. Here, we document immatures stages of five Pronophilina species (*Idioneurula erebioides*, *Daedalma drusilla*, *Pedaliodes ochrotaenia*, *P. nebris*, *P. guicana*) for the first time. Additionally, we document immature stages of two additional species (*Lymanopoda samius*, *Junea doraete*) from the Eastern Cordillera in Colombia, building on earlier studies on these two taxa. The methodology involved systematic searches for eggs and larvae on potential host plants in the field. Collected larvae were photographed and monitored in the laboratory. Data on their interactions with host plants and parasitoids are presented. This approach allowed a comprehensive characterization of the life cycles, host plant associations, and larval behavior of each instar, providing valuable insights into the biology and ecology of this group of butterflies.

Keywords: High-elevation ecosystems, Host plant use, Larval development, Life history, Ontogeny, Parasitoid associations, Plant-insect interactions

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BACKGROUND

The subtribe Pronophilina Reuter, 1896 (Nymphalidae, Satyrinae, Satyrini) comprises more than 650 described butterfly species (Lamas 2004; Lamas et al. 2004; Pyrcz et al. 2024) however, we estimate that there are currently nearly 900 species when considering undescribed taxa (Pyrcz et al. in prep). This group exhibit a high level of endemism and diversity in Páramos and cloud forests of the tropical Andes (Pyrcz and Rodríguez 2006 2007) and consists of small to relatively large butterflies with predominantly dull brown and black patterned wings, however also a considerable ratio of brightly coloured blue, white, red or orange species (Pyrcz 2010). Studies on this subtribe encompass a wide spectrum, ranging from alpha diversity (Adams and Bernard 1977; Prieto 2003; Pyrcz 2004; Pyrcz and Viloria 2007; Marín et al. 2014), taxonomic and systematic revisions (Huertas and Arias 2007; Pyrcz 2004; Pyrcz and Rodríguez 2006 2007; Pyrcz and Viloria 2007 2009 2012; Pyrcz et al. 2017; Mahecha-J. et al. 2021; Pyrcz et al. 2023), biogeographic research (Adams 1985; Pyrcz and Rodríguez 2007; Pyrcz et al. 2009; Pyrcz 2010; Pyrcz et al. 2016; Mahecha et al. 2019), ecological studies (Mahecha-Jiménez et al. 2011; Marín et al. 2015; Montero and Ortíz 2013a; Díaz-Suárez et al. 2022; Cerdeña et al. 2024), patterns of vertical distribution turnover (Pyrcz 2004; Pyrcz and Wojtusiak 2002; Pyrcz et al. 2009; Pyrcz and Garlacz 2012), and phylogeny (Casner and Pyrcz 2010; Pyrcz et al. 2025).

The immature stages of Pronophilina have been associated with the plant family Poaceae as host plants, and it was inferred that they mainly exhibit oligophagous habits on mountain bamboos, especially in woody bamboos of the genus *Chusquea* Kunth and related (Pyrcz 2004; Montero and Ortíz 2013a; Padrón et al. 2019), excluding most Neosatyriti that feed on grasses (Benyamini et al.

2025) and isolated cases within the genus *Steremnia* Thieme, 1905 (Brown 1941) and the infratribe Pedaliodití (Montero and Ortíz 2014a; Viloria et al. 2015). For the subtribe Pronophilina, considering published observations and descriptions, less than 10% of immatures stages of the species are recorded, making it evident that the biology, life history, and ecology of most species in the subtribe remain unexplored and unknown (Pyrcz and Fratello 2005). This contrasts sharply with Neotropical butterflies overall, for which host plant records are available for approximately 26% of species (Beccaloni et al. 2008) and underscores the considerable gap in our understanding of the biology and life history of these Andean butterflies.

Data on the immature stages, both their host plants and morphology, of a group of insects has high phylogenetic value as they can provide taxonomically informative characters in phylogeny and evolutionary history (Costa 2006; Costa and Ide 2008). These stages are also crucial for understanding population dynamics, allowing us to assess the population structure and comprehend how environmental factors, climate changes, or disturbances may affect their abundance and distribution over time and space (Goh and Lange 1980; Päivinen et al. 2005; Välimäki and Itämies 2005). Furthermore, understanding the group's interaction in the ecosystem, including its relationships with other species, is fundamental to comprehend its role in ecosystem functioning and stability.

Here, we describe the immature stages of seven species of Pronophilina in the northern Andes and we discuss the taxonomical implication. The aim is to gather data on their interactions with host plants and other organisms such as parasites. These data will provide essential information for the management, protection, and conservation of Andean butterflies. Moreover, the obtained results will serve as a solid foundation for future investigations that seek to elucidate and understand the aspects of the biology, taxonomy, and ecology of this group of butterflies.

MATERIALS AND METHODS

Study Site and Collection

All immature stages were collected in 2024 at Páramo El Verdillo or Páramo Los Venados (Fig. 1). Both sites are in the Eastern Cordillera of the Northern Andes situated in Colombia. Previous expeditions have indicated the presence of Pronophilina species of interest that lack life cycle records and are endemic to the Eastern Cordillera.

El Verdillo Páramo (Fig. 1B–C) is situated within the southeastern zone of the Bosque Oriental de Bogotá Forest Reserve. It is located at 4°29'60.0"N, 74°04'41.8"W, at an elevation ranging from 3000 to 4000 m a.s.l. The reserve comprises Andean forests, high-Andean forests, and Páramo, with conserved ecosystems, fragmented areas, and some pasturelands. The area experiences a bimodal pattern of precipitation in May and October-November, with an average annual rainfall of 916 mm and an annual average temperature ranging from 8.4°C to 13°C (Camelo et al. 2009). The dominant flora includes tall vegetation such as *Chusquea* aff. *scandens*, associated with *Weinmannia tomentosa* L. f., *Chaetogastra grossa* (L. f.) P.J.F. Guim. and Michelang., *Ageratina tinifolia* (Kunth) R.M. King and H. Rob., *Eugenia* L., *Eucalyptus* L'Hér. The understory is characterized by Poaceae, *Elaphoglossum* Schott ex J. Sm., and *Arcytophillum* Willd. ex Schltdl. species. The Páramo Los Venados (Fig. 1C–D) is located south of the Serranía del Cocuy National Natural Park in the department of Boyacá, at 6°10'17.7"N, 72°23'32.4"W, with a maximum altitude of 3500 m a.s.l. Precipitation varies according to the analyzed slope, ranging from 700 mm/year to 1500 mm/year with an average of 1080 mm/year. The site is important as it is the origin of several streams and is considered a groundwater recharge area. The predominant habitats in the site are Páramo, subpáramo, and high-Andean forests, where species such as *Chusquea tessellata* Munro, *Calamagrostis effusa* (Kunth) Steud., *Espeletia grandiflora* Bonpl., *Espeletia argentea* Bonpl., *Arcytophyllum muticum* (Wedd.) Standl., among others, are dominant.

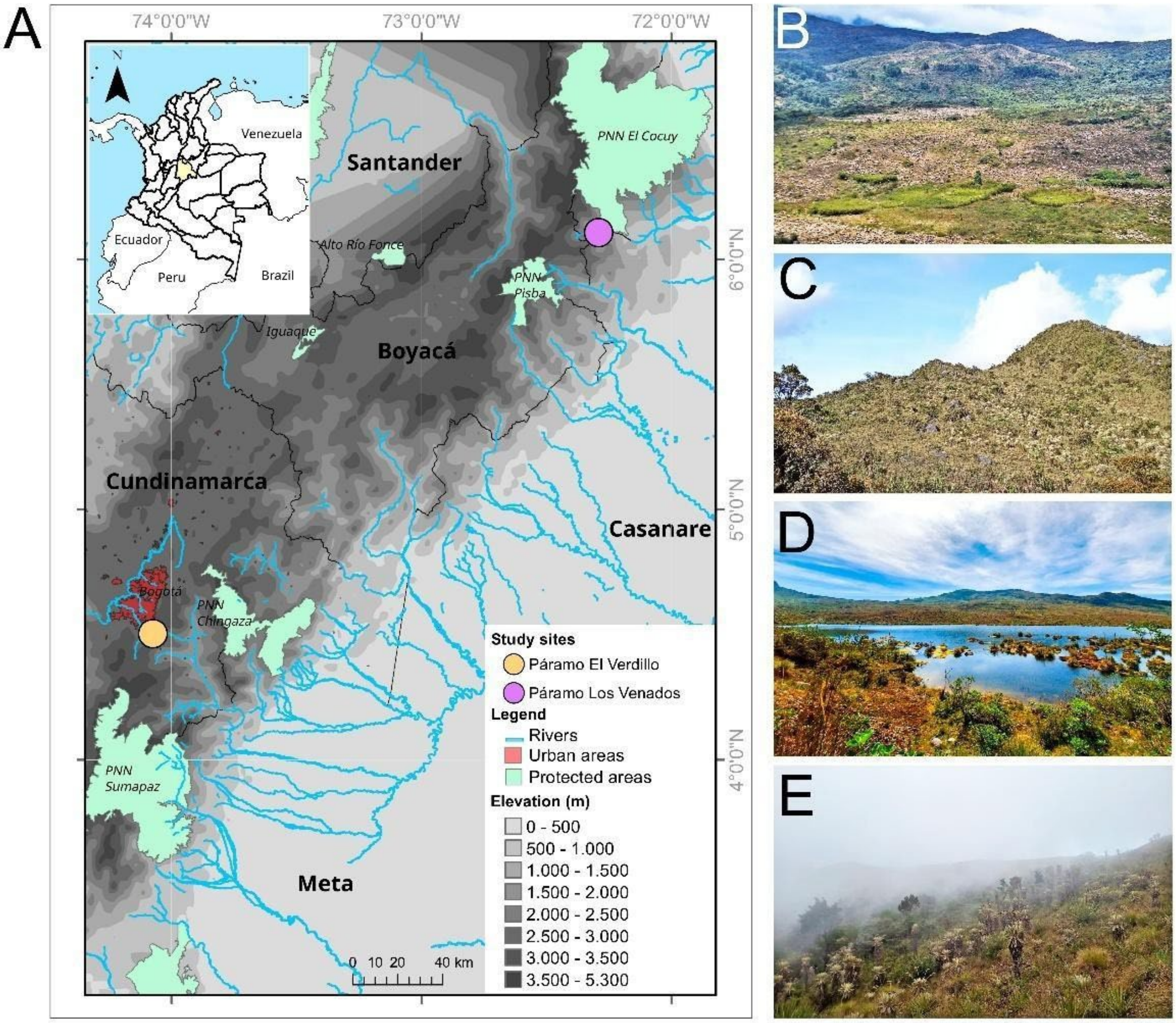

Fig 1. Location of the collection sites of Pronophilina immatures. A, Geographic location. B and C, Páramo El Verdillo, Cundinamarca, Colombia. D and E, Páramo Los Venados, Boyacá, Colombia.

The search and collection of immature stages was focused on *Chusquea* plants from the Poaceae family, which has been reported as the host plant for Pronophilina. This choice significantly increases the chances of finding the immature stages, as an association with these plants has facilitated the radiation of species within the subtribe. The eggs of *Pedaliodes guicana* Adams, 1986, *P. nebris* (Thieme, 1905), *L. samius* Westwood, 1851 and *Idioneurula erebioides* (C. Felder & R. Felder, 1867) were obtained from gravid females confined in a plastic bag with leaves of their possible host plant (following Freitas 2002; Pyrcz et al. 2018). Subsequently, each immature stage was transferred to the laboratory and kept at room temperature at 3,000 m.a.s.l in Bogotá, carrying out photographic documentation and periodic monitoring of its life cycle. The host plants were photographed, georeferenced, and regularly revisited to feed the larvae with fresh leaves. Specimen collection was conducted under the '*Permiso Marco de Recolección de Especímenes de Especies Silvestres de la Diversidad Biológica con Fines de Investigación*

Científica No Comercial', granted to the Universidad Distrital Francisco José de Caldas (Resolution No. 0738, July 8, 2014; ANLA).

Rearing

All immature stages were kept in a 1 L plastic container sealed with a soft cloth secured by a rubber band. The host plant leaves were kept hydrated using floral water tubes and were continuously replaced to ensure the immature stages have fresh leaves to feed on. Similarly, each container was replaced daily to prevent fungal or bacterial infections. Each individual was photographed using a digital camera Canon EOS Rebel T7 DSLR Camera with a Venus Laowa 100mm f/2.8 Ultra Macro every two or three days; some photographs were taken with Olympus OM-D E-M5 Mark II with Venus Laowa 50 mm X2 Super Macro by OJ. All photographs had a scale in mm for subsequent measurements. The emerged adults were stored at the Nature Education Centre (formerly the Zoological Museum) of the Jagiellonian University in Kraków, Poland (CEPUJ).

Morphology

Measurements for all stages were conducted using ImageJ 1.54d (Schneider et al. 2012) by counting pixels based on high-resolution photographs. The measurement of the egg was measured as the maximum diameter, the length of the larvae and pupa was estimated in dorsal view from the head to the posterior end of the 10th segment, reporting the measurement close to the change of instar. The observation of the head capsules was performed using a Stereomicroscope Leica M205A with Camera MC170 HD. Subsequently, the head capsules were illustrated using Krita 5.2.11 software based on the photographs. The width of the head capsule was measured as the distance between the most external stemmata. The description of the egg followed the works of García-Barros and Martin (1995); the approach of Stehr (1987) was followed for the larvae and pupa description.

RESULTS

The dates corresponding to key life-cycle events are presented in table 1, with exception of *P. nebris*, *I. erebioides* and *J. doraete* (Hewitson, 1858), which died at the first instar or whose life cycle was documented in a previous study.

Table 1. Dates of important life history events recorded for Pronophilina immatures

Voucher	Species	Date of coll.	Egg hatch	L1 to L2	L2 to L3	L3 to L4	L4 to L5	Pupation	Adult	Died
2024-IMM-LV-003	*Daedalma drusilla*	21-Mar-2024	23-Mar-2024	30-Mar-2024	7-Apr-2024	14-Apr-2024	22-Apr-2024	6-May-2024	27-May-2024	n/a
2024-IMM-LV-012	*Daedalma drusilla*	29-Apr-2024	n/a	n/a	6-May-2024	12-May-2024	20-May-2024	3-Jun-2024	21-Jun-2024	n/a
2024-IMM-LV-013	*Daedalma drusilla*	4-May-2024	n/a	n/a	n/a	n/a	12-May-2024	25-May-2024	14-Jun-2024	n/a
2024-IMM-LV-024	*Daedalma drusilla*	27-Apr-2024	n/a	n/a	n/a	n/a	n/a	n/a	n/a	05-May-2024
2024-IMM-LS-002	*Lymanopoda samius*	21-Feb-2024	10-Mar-2024	2-Apr-2024	20-Apr-2024	11-May-2024	n/a	n/a	n/a	11-May-24
2024-IMM-LV-012	*Lymanopoda samius*	29-Apr-2024	n/a	n/a	n/a	n/a	n/a	23-May-2024	11-Jun-2024	n/a
2024-IMM-LS-023	*Pedaliodes ochrotaenia*	30-Mar-2024	19-Mar-2024	2-May-2024	14-May-2024	23-May-2024	03-Jun-2024	17-Jun-2024	11-Jul-2024	n/a
2024-IMM-LS-001	*Pedaliodes guicana*	20-Feb-24	8-Mar-24	25-Mar-24	7-Apr-24	28-Apr-24	n/a	n/a	n/a	6-May-24
2024-IMM-LV-001	*Idioneurula erebioides*	17-Feb-24	8-Mar-24	n/a	n/a	n/a	n/a	n/a	n/a	17-Mar-24
2024-IMM-LV-014	*Junea doraete*	28-Apr-24	30-Apr-24	14-May-24	23-May-24	3-Jun-24	14-Jun-24	26-Jun-24	n/a	12-Jul-24
2024-IMM-LV-015	*Junea doraete*	7-May-24	8-May-24	24-May-24	3-Jun-24	15-Jun-24	26-Jun-24	n/a	n/a	12-Jul-24
2024-IMM-LV-016	*Junea doraete*	29-Apr-24	10-May-24	n/a	n/a	n/a	n/a	n/a	n/a	11-May-24
2024-IMM-LV-003	*Pedaliodes nebris*	11-Jan-24	21-Jan-24	n/a	n/a	n/a	n/a	n/a	n/a	4-Feb-24

Description of immatures stages

Lymanopoda samius Westwood, 1851

Vouchers: 2024-IMM-LS-002; 2024-IMM-LV-009.

Egg (Fig. 2A, B) (*n* = 3): Elongated, ends rounded. White after oviposition; light brown to slightly pink after 4 days. Chorion with multiple, regularly spaced longitudinal ridges. Head capsule and body visible through the chorion close to hatching. Young larva consumes part or entire chorion (Fig. 2B). Oviposition not observed under natural conditions. Duration: 18 days from oviposition (*n* = 1).

First instar (Fig. 2C, D, E) (*n* = 3): Head capsule (Fig. 3A, B) width 0.65 mm (*n* = 1), appearing creamy, with copper-colored pitted sculpturing, except from stemma 1 to mouthparts and lower half of frontoclypeus; head rounded, epicranial notch insignificant. Epicranial suture old copper. Mouthparts dark brown. Upper margin of each side with four semi-hyaline setae (L1, P1-P3), curved anteriorly; becoming dark gray with whitish tip as instar progresses. Head chaetotaxy in figure 3A, B. Labrum with five setae on each side. Four stemmata visible frontally; stemma 1 translucent and barely visible; stemma 3 largest. Body tubular, translucent to pale orange, with longitudinal striated pattern. Three longitudinal dorsal lines, faint reddish orange-brown. Subdorsal line more pronounced, same coloration of dorsal lines; creamy white areas between striation. Spiracle prominent on T1 and A8 as brown spots. Body chaetotaxy in figure 3F. Cuticle smooth, shiny, without long hairs. Caudal filaments bifid, pale orange, darkening distally with whitish tips. Later instar: Body translucent and light green; reddish lines fading to white, with fine light-brown longitudinal margins. Maximum length: 6.5 mm (*n* = 1). Duration: 23 days (*n* = 3).

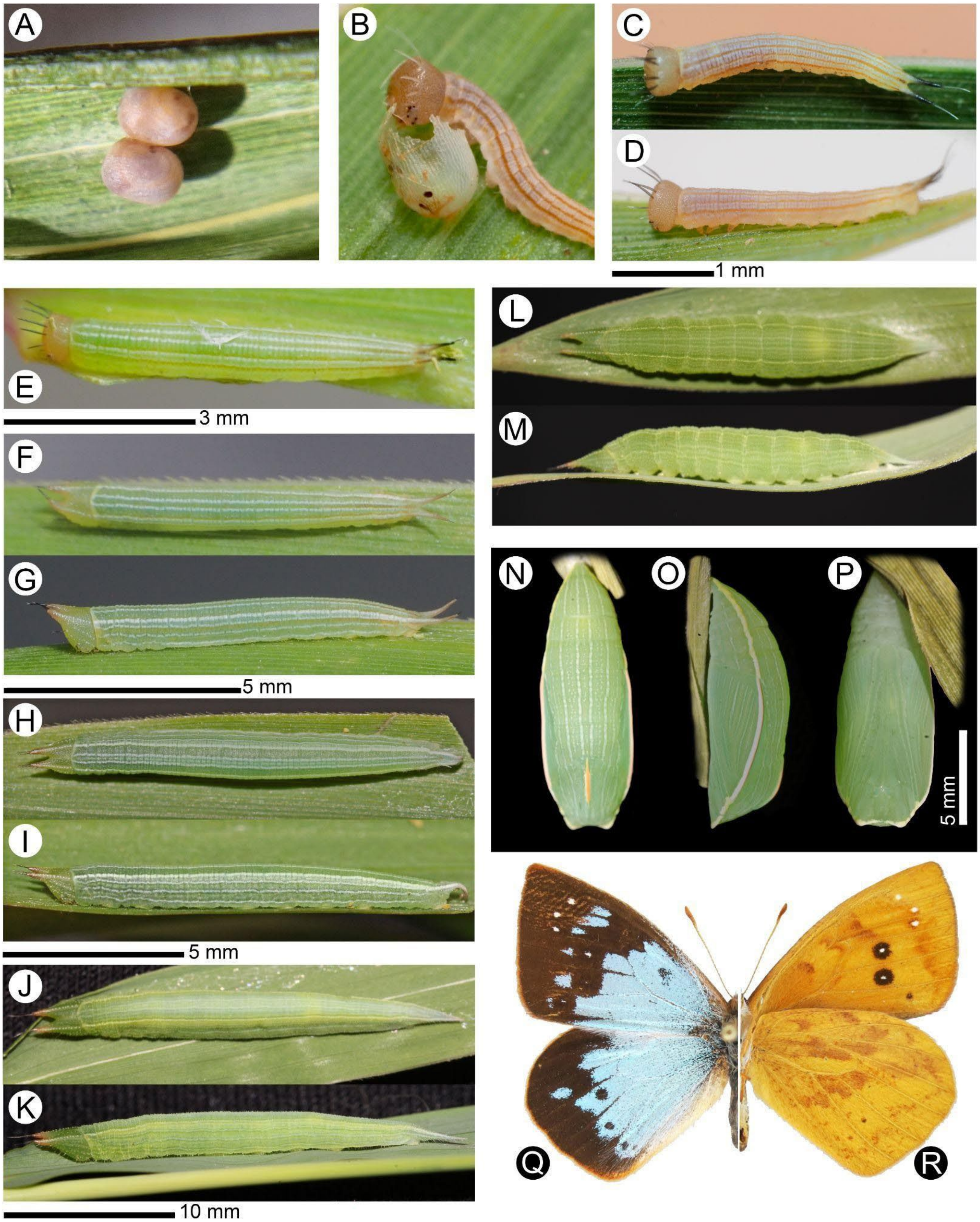

Fig. 2. *Lymanopoda samius* life stages: A, eggs in lateral view; B, first instar larva feeding chorion; C and D, early first instar in dorsal and lateral view; E, late first instar in dorsal view; F and G, second instar in dorsal and lateral view; H and I, third instar in dorsal and lateral view; J and K, fourth instar in dorsal and lateral view; L and M, prepupa in dorsal and lateral view; N, O, and P, pupa in dorsal, lateral and ventral view; Q and R, adult in dorsal and ventral view (photo of the adult does not correspond to that of the emerged adult).

Second instar (Fig. 2F, G) (*n* = 1): Head capsule width 0.84 mm (*n* = 1). Head capsule (Fig. 3C) light green; sutures and mouthparts slightly darker; pitted sculpting, granular textures. Scoli pale orange-brown with short black setae; each scolus terminates in a pair of long, thick setae with whitish tips. Thin white line on posterior part of scoli. Setal bases thickened, tuberculate. Four stemmata visible frontally; stemma 1 translucent and barely visible; stemma 3 largest. Labrum with five setae visible on each side. Lateral view with three diagonal rows of small white protuberances. Body smooth, semitranslucent, light olive green. Paired white mid-dorsal longitudinal lines; white subdorsal line, slightly wider, becoming ochre yellow from A6 onward. White supraspiracular and subspiracular lines. Spiracles yellowish-green spots with dark border; prominent on T1 and A8; abdominal spiracles as tiny black spots. Caudal filaments bifid, tending to erect and slightly upturned; pale creamy brown, each tip with a short black seta. Body length: 10 mm (*n* = 1). Duration: 18 days (*n* = 1).

Third instar (Fig. 2H, I) (*n* = 1): Head capsule (Fig. 3D) width 0.97 mm (*n* = 1); similar to immediately preceding instar, but dark olive green. Scoli longer and more pronounced; base olive green-brown, becoming dark reddish brown apically; short setae along surface; apical pair of characteristic long thick setae present. Labrum with five setae on each side. Body similar in coloration and patterns to immediately preceding instar, but ochre yellow almost invisible; ground color slightly opaquer. Supraspiracular and subspiracular lines more evident. Spiracles dark greenish-brown spots with creamy yellow border. Caudal filaments bifid, as in immediately preceding instar. Body length: 16 mm (*n* = 1). Duration: Unknown, approximately 21 days (*n* = 1).

Fourth instar (Fig. 2J, K) (*n* = 1): Head capsule (Fig. 3E) width 2.0 mm (*n* = 1), appearing dark green, slightly more opaque, faint striping with small white protuberances. Scoli bright orange-reddish, elongated, horn-like, with multiple short setae. Thin white-yellowish dotted line on posterior part of scoli; formed by small protuberances, aligned with subdorsal body line. Several translucent setae with broadened white bases, protuberance-like, distributed over entire head capsule. Body yellowish-green; line pattern similar to immediately preceding instar but less defined than instar 3; mid-dorsal line weak; whitish lines thinner; region from subdorsal to subspiracular yellowish green with corresponding thin whitish lines. Whitish microgranulations across body. Caudal filaments bifid, positioned touching each other, appearing fused. Body length: 22.7 mm (*n* = 1). Duration: Unknown, prepupa 11 days after collection (*n* = 1). In Prepupa (Fig. 2L, M) (*n* = 1), body more yellowish, compressed, plump. Subdorsal lines well defined, aligned with posterior scoli lines. Faint pale-yellow mark between A6–A7. Larva positioned abaxially on leaf, not suspended (*i.e.*, hanging) from terminal segments. Duration: 2 days (*n* = 1).

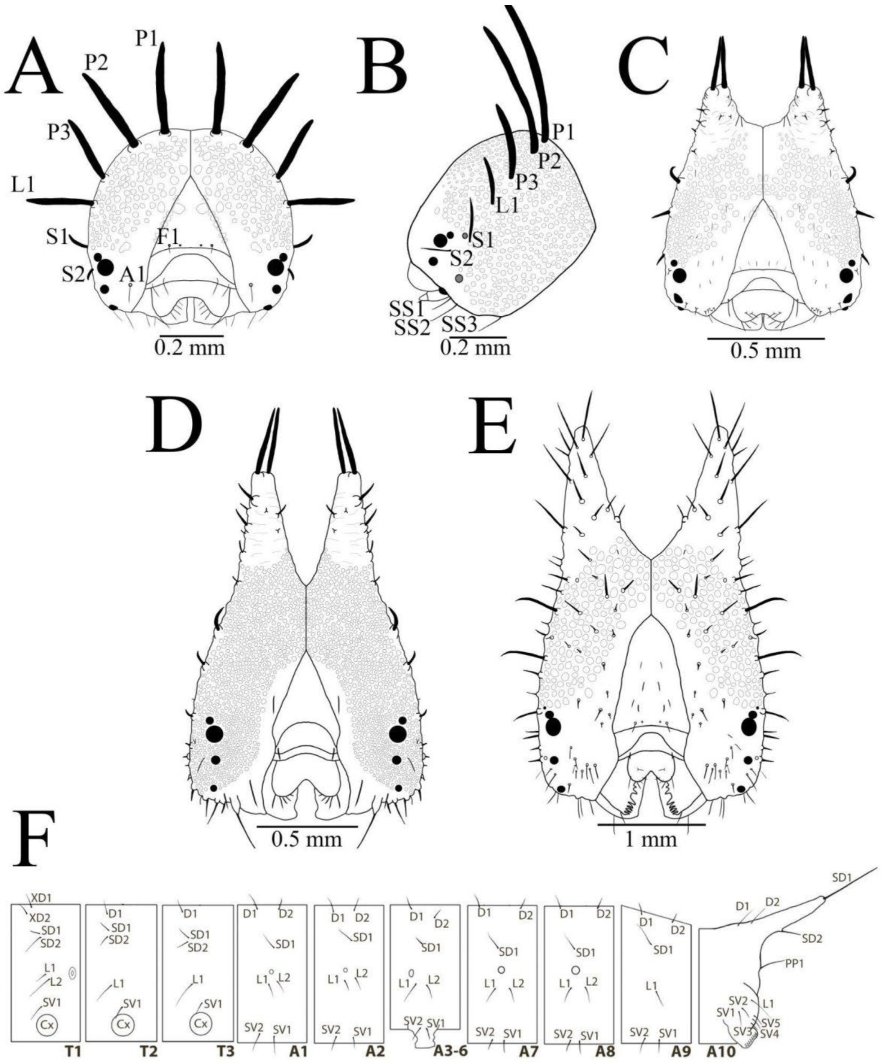

Fig. 3. *Lymanopoda samius* larval head capsules: A and B, first instar in frontal and lateral view; C, second instar; D, third instar; E, fourth (ultimate) instar; F, body chaetotaxy in lateral view (first instar).

Pupa (Fig. 2N, O, P) (*n* = 1): (Figure based on 2024-IMM-LV-009) Elongate, conical; tapering from A4 to A10; cremaster slightly oval. Body light olive green and matte. Six well-defined creamy white longitudinal lines; additional dotted dorsal lines. Squared ocular caps, edged with whitish-cream line. Mid-thoracic projection slight, yellowish cream. Posterior margin of wing cases slightly projected, bordered by whitish-yellow band, continuous with slightly more yellowish lateral abdominal band. Wing veins creamy white, distinct. Spiracles pale yellow, visible from A4 to A7. Body length: 14.2 mm (*n* = 1). Duration: 20 days (*n* = 1).

Hostplant: *Chusquea scandens* Kunth (Poaceae: Bambusoideae: Chusqueinae) (Fig. 4).

Remarks: The immatures from Páramo Los Venados (2024-IMM-LS-002; three eggs) were obtained from a gravid female confined in a plastic bag with its host plant and died at the end of the third instar. The remaining documentation of the fourth instar (the last instar according to Schultze 1929) and pupa was based on an additional individual found in Páramo El Verdillo in the ultimate instar (2024-IMM-LV-009). All larvae were fed *Chusquea scandens*, but the specimens obtained from Páramo Los Venados were fed with leaves from the bamboo population at Páramo El Verdillo. Contrary to the presence of only four stemmata reported for *L. caracara* Pyrcz, Willmott & J. Hall, 1999 (Padrón et al. 2019), we observed six stemmata in *L. samius*, with stemma 1 and 6 translucent and weakly developed, and stemma 3 larger than the others (Fig. 3). This configuration agrees with the general pattern described for Satyrinae (Stehr 1987). We consider that the presence of four stemmata within *Lymanopoda* Westwood, 1851, *i.e.*, a reduction in the number of stemmata as reported in Padrón et al. (2019), is improbable, based on larval behavior (*i.e.*, not a leaf miner), our own observations, and the fact that this character shows little variation at this hierarchical level.

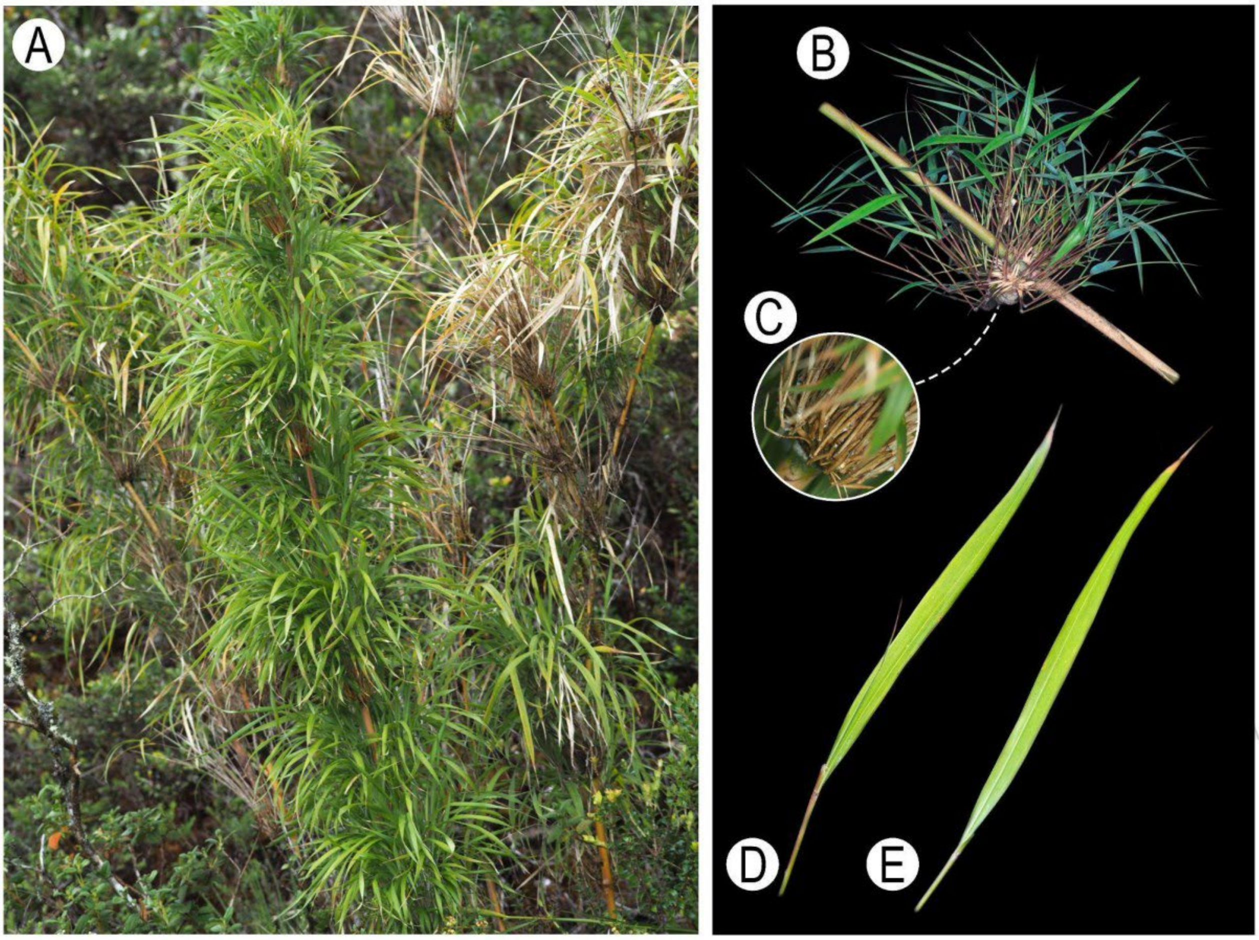

Fig. 4. *Chusquea scandens*, host plant for *Lymanopoda samius*, *Daedalma drusilla*, and *Pedaliodes ochrotaenia*: A, habit; B, mid-culm section; C, nodal region; D, adaxial view of the leaf; E, abaxial view of the leaf.

Idioneurula erebioides (C. Felder and R. Felder, 1867)

Voucher: 2024-IMM-LV-001.

Egg: (Fig. 5A, B) (n = 10): Diameter: 0.7 mm, height: 0.8 mm (n = 2). Subelliptical, ends rounded; attached to leaf by narrower surface. Green, turning slightly yellow a few days before hatching. Chorion with multiple, regularly spaced longitudinal ridges. Head capsule not visible near hatching. Larvae consume entire chorion or part of it. Oviposition not observed under natural conditions. Duration: 20 days from oviposition (*n* = 10).

First instar (Fig. 5C, D) (*n* = 10): Head capsule appearing light brown, slightly reticulated, with pitted sculpturing; vertex without noticeable scoli or projection. Primary setae translucent with black bases; with P1-P3 and L1 directed forward. Third stemma slightly larger than others. Body pale yellow; light brown longitudinal lines along mid-dorsal, subdorsal, and supraspiracular regions. Short black setae, slightly longer on posterior abdominal segments. Spiracles black. Caudal filaments paired, short, distinctly separated. Body length: 2.8 mm (*n* = 1), a few days after emergence. Duration: unknown.

Posterior *stages*: Unknown.

1. Hostplant: Unknown.

Remarks: The immatures were obtained from gravid females confined in a plastic bag, where they oviposited the 10 eggs reported above. All were treated under the same voucher (2024-IMM-LV-001). Newly hatched larvae were exposed to grasses, rushes, and sedges commonly found in the habitat frequented by *I. erebioides* (open areas with flooded patches). The larvae died before changing instar and they accepted feeding on a species of Cyperaceae that grows in swampy areas.

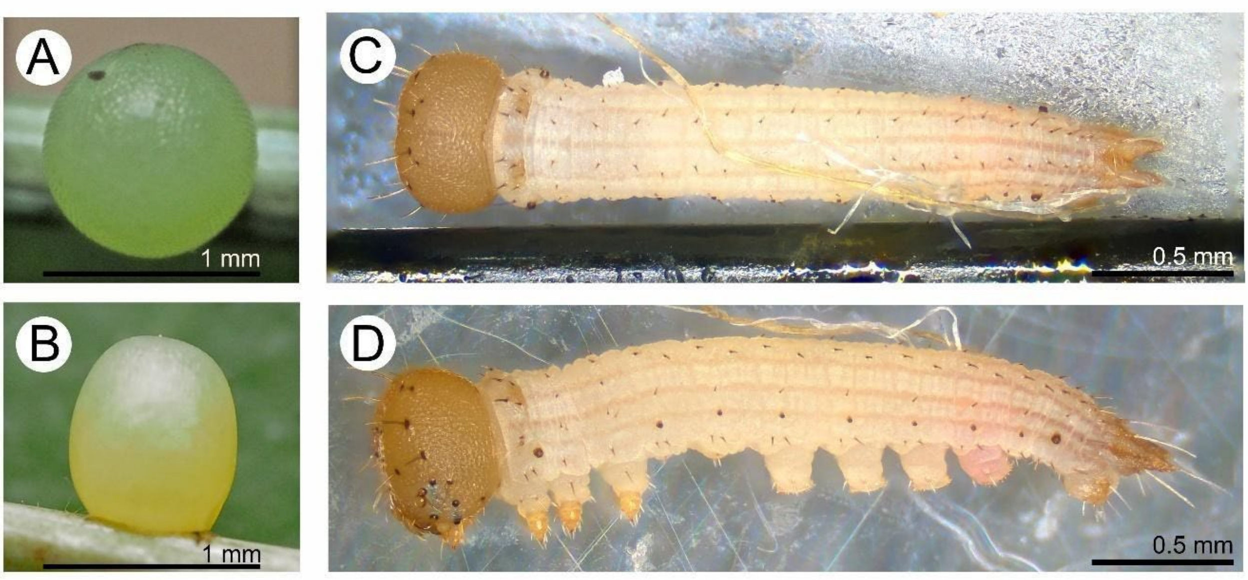

Fig. 5. Idioneurula erebioides partial life stages: A and B, egg in dorsal and lateral view; C and D, preserved first instar in dorsal and lateral view.

Daedalma drusilla **Hewitson, 1858**

Vouchers: 2024-IMM-LV-003, 012, 013, 024.

Egg (Fig. 6A, B, C) (*n* = 33): (Figure based on 2024-IMM-LV-003). Diameter 0.89–0.97 mm; height 0.61–0.83 mm (*n* = 33). Sub-spherical. Pale green with slight yellowish tint after oviposition; opaque black near hatching. Head capsule not visible near emergence. Chorion striated; cell edges thickened forming polygonal network; multiple elevated longitudinal ribs, fading near micropylar area. Micropyle elevated; micropylar rosette tuberculate. Young larvae usually do not consume eggshell; hatching via longitudinal slit in distal third of egg. Gregarious oviposition, in groups of 12 and 33 eggs (based on 2024-IMM-LV-003 and 024). Laid on abaxial surface of mature leaves. Duration: 2 days from collection.

First instar (Fig. 6D, E) (*n* = 33): (Figure based on 2024-IMM-LV-003). Head capsule (Fig. 7A, B) width 0.63–0.68 mm (*n* = 4), appearing dark brown, smooth; stemmata region, epicranial suture, clypeus, and mouthparts dark brown. Epicranial notch insignificant; vertex rounded, without scoli or projection. Head capsule chaetotaxy in figure 7A, B. Stemmata equal in size; stemma 4 closer to stemma 3 than to stemma 5. Newly emerged larva with ash-gray thoracic segments; abdominal segments pale yellow with short black setae. Later instar: body integument light green with creamy-white subdorsal band; spiracles black; tracheal system not discernible. Body turning yellow-orange a few days before molting. Two light-brown prothoracic plates: one dorsal, semi-rectangular; one subdorsal, smaller, semi-elliptical. Prolegs with black elliptical shields. Chaetotaxy in figure 7G. Caudal filaments short, not evident. Body length: 3.5–4.8 mm (*n* = 8). Duration: 7 days (*n* = 9).

Second instar (Fig. 6F, G) (*n* = 9): (Figure based on 2024-IMM-LV-012). Head capsule (Fig. 7C) width 0.82–0.94 mm (*n* = 3), appearing brown, rough; vertex flat with a pair of slightly pronounced, rounded scoli. Creamy brownish spots of variable shape and size: triangular on upper frons; ellipsoidal on upper lobe; elongated ellipsoidal between stemma 5 and adfrontal area on gena; elongated from posterior part of scoli to stemmata region; spot narrower or less evident among individuals. Body light brown; dark brown mid-dorsal longitudinal band; creamy-whitish subdorsal band well defined throughout the body; paired dark brown bands in supraspiracular region (discontinuous, forming small bands from A1) and spiracular region. Spiracles black, prominent on T1. Ventral region and prolegs slightly grayish. Caudal filaments short, bifid but barely distinguishable. Late instar: dorsal region becomes slightly pinkish; longitudinal band darker, especially anteriorly and posteriorly. Body length: 6.0–7.0 mm (*n* = 9). Duration: 8 days (*n* = 5).

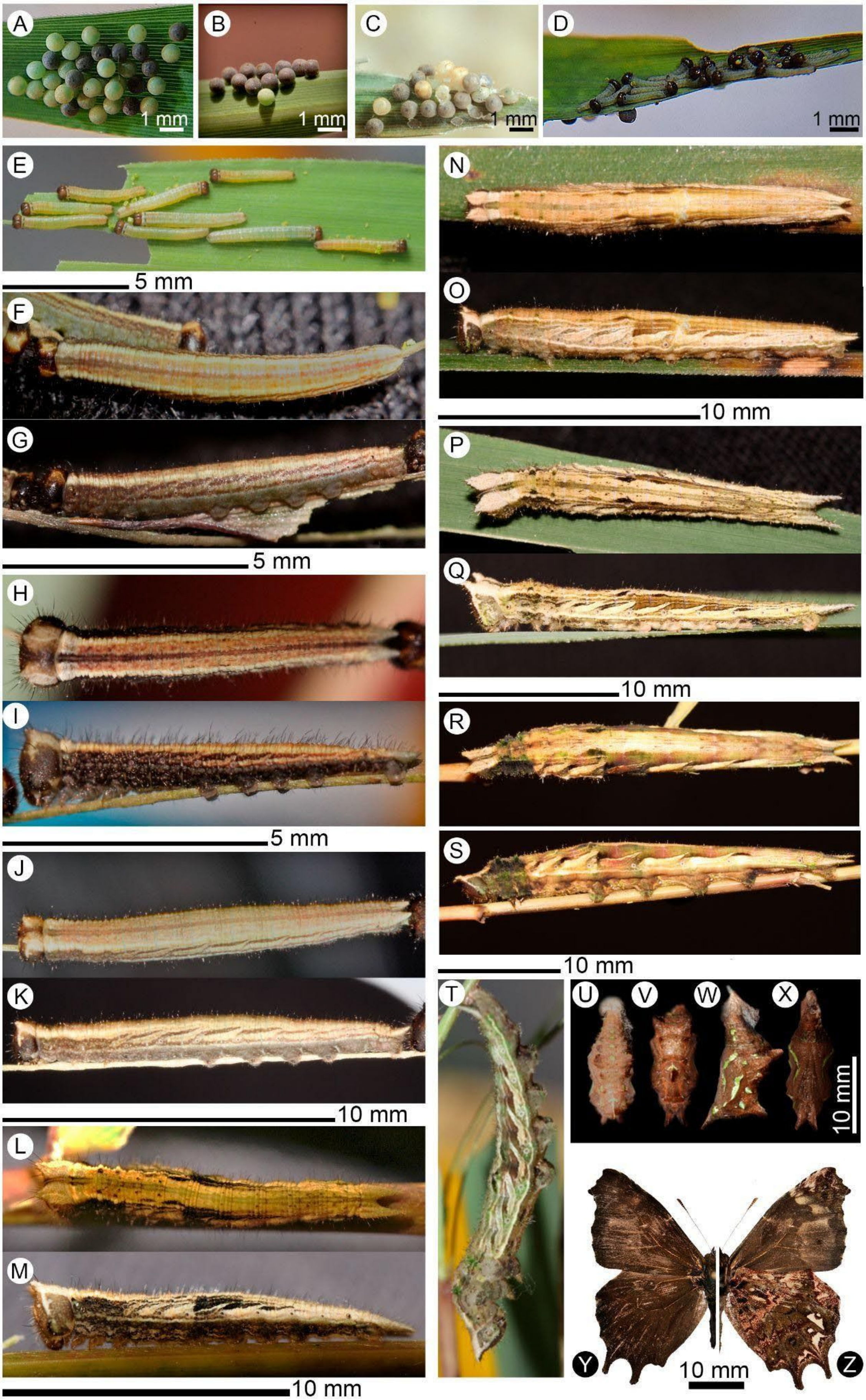

Fig. 6. *Daedalma drusilla* life stages: A, B) eggs in dorsal view; C) Hatched eggs, note the opening in the distal third; D) early first instar in group; E) late first instar; F, G) second instar in dorsal and lateral view; H, I) early third instar in dorsal and lateral view; J, K) late third instar in dorsal and

lateral view; L, M) early fourth instar in dorsal and lateral view; N, O) late fourth instar in dorsal and lateral view; P, Q) early fifth instar in dorsal and lateral view; R, S) late fifth instar in dorsal and lateral view; T)prepupa in lateral view; U, V, W, X) pupa in dorsal, lateral and ventral view; Y, Z) adult in dorsaland ventral view (photo of the adult does not correspond to that of the emerged adult).

Third instar (Fig. 6H, I, J, K) (*n* = 14): (Figure based on 2024-IMM-LV-012). Head capsule (Fig. 7D) width 1.34–1.37 mm (*n* = 3), light brown with creamy spots, position and shape as in immediately preceding instar; pitted sculpturing. Vertex with two creamy, rounded scoli bearing seven setae each; four long, thick, thread-like setae at base and apex (scolus length 0.15–0.17 mm). Two thin whitish lines posterior to scoli. Dark brown midline on vertex extending posteriorly. Labrum with four setae on each side. Body brown-reddish with numerous black setae; mid-dorsal line dark on anterior and posterior segments, reddish medially; creamy white subdorsal line. Lateral region from subdorsal to ventral dark brown; light reddish-brown supraspiracular stripe from A3 to A9; spiracles light brown to grayish. Late instar: body light brown-creamy; lateral areas paler, slightly grayish; supraspiracular line broken into distinct, oblique stripes from A1, ascending towards subdorsal region, fading posteriorly; tracheal system light-brown. Caudal filaments creamy, bifid; length similar to A8 in early instar, but appearance becoming less conspicuous later. Body length: 12.5–14.5 mm (*n* = 5). Duration: 6–7 days (*n* = 13).

Fourth instar (Fig. 6L–O) (*n* = 26): (Figure based on 2024-IMM-LV-012 and 013): Head capsule (Fig. 7E) width 1.70–2.03 mm (*n* = 3); more elongated than in immediately preceding instar; coloration similar, except scoli brown-creamy. Scoli triangular with rounded tips, more pronounced; five long, thick setae plus multiple smaller setae (scolus length: 0.4 mm). Faint green spot in stemmata region, more evident in late instar. Body pale brown; small circular protuberances on T2-T3; irregular black spots on T2-T3, A2-A3, and A7-A9. T1-T3 and subspiracular region black in lateral view, with scattered light brown spots. Creamy subdorsal longitudinal band; A3-A5 with black diagonal band laterally. Caudal filaments slightly longer than A8. Late instar: body light brown; protuberances on T2-T3 green; diagonal bands on A3-A5 brown; caudal filaments shortening. Body length: 20.2–23.1 mm (*n* = 2). Duration: 8 days (*n* = 13).

Fifth instar (Fig. 6P–S) (*n* = 21): (Figure based on 2024-IMM-LV-003 and 013): Head capsule (Fig. 7F) width 2.68 mm (*n* = 1); elongated, dark brown, with creamy-brownish spot on upper lobe. Scoli triangular, slightly lighter than head capsule (scolus length: 0.8 mm), with small protuberances at bases of setae. Posterior area of head capsule pale brown, with brown transverse band between scoli. Green stemmata spot more evident than immediately preceding instar. Body light brown; mid-dorsal band darker. Dark fleshy brown dorsolateral protuberances on T2-T3. A2 with black subdorsal spot; discontinuous brown triangular spots from A3 to A6. Caudal filaments deeply bifurcated. Late instar: mossy green spots developing, especially in subdorsal region, prolegs, spiracular region and T2-T3 protuberances; triangular spots merging, forming crenulated lateral patterns. Body length: 31–35 mm (*n* = 3). Duration: 14 days (*n* = 17). In prepupa (Fig. 6T) (*n* = 9) (Figure based on 2024-IMM-LV-003), shape and coloration similar, but slightly paler. Larva suspended (*i.e.*, hanging) from terminal segments, does not assume typical Satyrini G-shape; body slightly bent from T2. Duration: 2 days (*n* = 9).

Pupa (Fig. 6U–X) (*n* = 9): (Figure based on 2024-IMM-LV-013). Body reddish-brown with bright metallic green markings typically on wing cases, thoracic protrusions, keels, and spiracular area; variable among individuals (Fig. 8). Cephalic projections paired, dorsoventrally flattened. Multiple dorsal setae on T1-T2. Mid-dorsal thoracic keel distinct, forward-curved, flattened on T2; thorax with lateral triangular projections on T1-T3. Abdomen with subdorsal triangular protrusions decreasing in size toward cremaster; A2 with flattened keel bearing black-tipped projection on each side. Protrusions and keels with multiple light-brown setae. Spiracles dark brown. Cremaster brown, slightly orange dorsally; short, robust, semi-rectangular. Body length: 16.7 mm (*n* = 2). Duration: 20 days (*n* = 7).

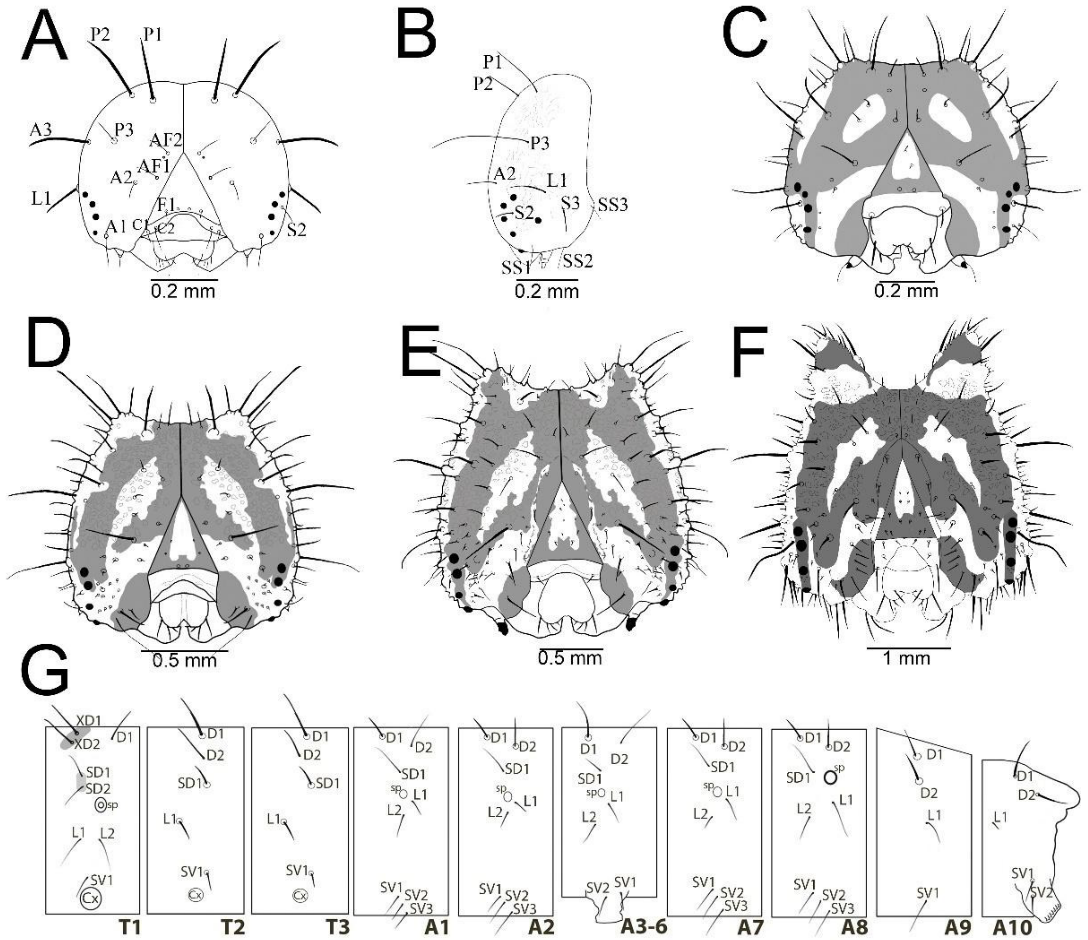

Fig. 7. *Daedalma drusilla* larval head capsules: A, B) first instar in dorsal and lateral view; C) second instar; D) third instar; E) fourth instar; F) fifth (ultimate) instar; G) body chaetotaxy in lateral view (first instar), thoracic plates illustrated in gray.

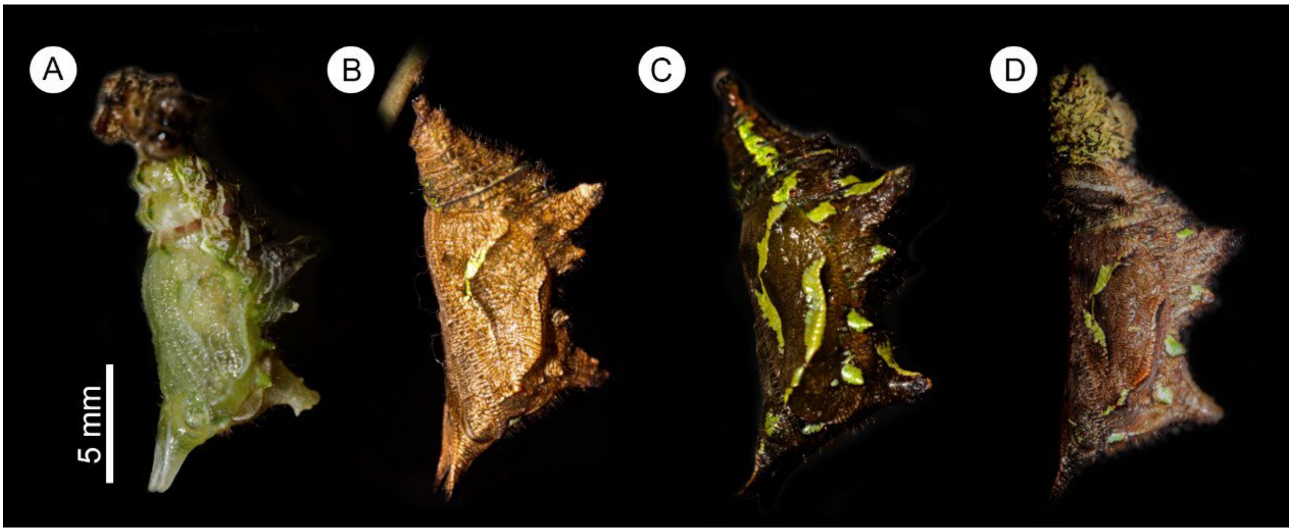

Fig. 8. Variation in pupal coloration of *Daedalma drusilla*: A) recently formed pupa; B) pupa with reduced metallic green markings; C) pupa with metallic green spots (most common phenotype); D) pupa with restricted metallic green spots.

Hostplant: *Chusquea scandens* Kunth (Poaceae: Bambusoideae: Chusqueinae) (Fig. 4).

Remarks: The larvae fed on the entire leaf lamina, excluding the main vein, and exhibited gregarious behavior, feeding together from the first instar until the end of the final instar. During the early instars, larvae dispersed while feeding and subsequently aggregated on the skeletal veins of previously consumed leaves to rest. In later instars, gregariousness was less pronounced; however, small groups of two larvae were observed feeding on the same leaf. When not feeding, final-instar larvae rested at the base of the stems. Parasitized larvae ceased growth at the beginning of the final instar, remaining exclusively on the skeletal vein without feeding until the emergence of the parasitoid larva to pupate. Additionally, the larvae of *D. drusilla* develop greenish patches on the body in the later instars, resembling mosses, as previously documented for *D. dinias emma* Pyrcz & Greeney, 2011, *D. rubroreducta* Pyrcz & Willmott, 2011, and *Mygona irmina* (E. Doubleday, [1849]) (Greeney et al. 2011; Pyrcz et al. 2011); similar patches are also present in the pupae of all four species, albeit to a lesser extent in *M. irmina*, and the last instar bear fleshy protuberances that currently appear to be a unique characteristic of the genus. A notable characteristic is the gregarious oviposition similar with what has been suggested for *D. rubroreducta*, based on the gregarious behavior of first instar larvae (Pyrcz et al. 2011). Gregariousness is maintained in the larvae up to the last instar in which larvae remain aggregated along the main vein of skeletonized leaves, as reported for *D. rubroreducta* (Pyrcz et al. 2011), raising the possibility that this condition may be recurrent within the genus.

Parasitoids: The eggs of *D. drusilla* were parasitized by Proctotrupoidea wasps (Fig. 9G); all eggs (n = 12) from a single clutch were parasitized, turning black, a coloration similar to that of larvae about to emerge. In addition, larvae were parasitized by Campopleginae (Ichneumonidae)

(Fig. 9F). We observed that the parasitoid larva emerges from A3 when the *D. drusilla* larva has just molted into the final instar (Fig. 9A). Subsequently, it constructs its cocoon beneath the host larva, using the remaining larval integument as a base (Fig. 9B, C). The adult parasitoid emerged after eight days (*n* = 3). Following parasitization, the behavior of the *D. drusilla* larva changed markedly: it ceased feeding and remains perched on the skeletal veins of the host plant, even when other larvae aggregate nearby. Notably, the same ichneumon parasitoid wasp was also found at Páramo El Verdillo in larvae of *Corades dymantis* Thieme, 1907 and Noctuidae (Fig. 9D, E), collected during the field work for the present study, exhibiting the same behavior described above.

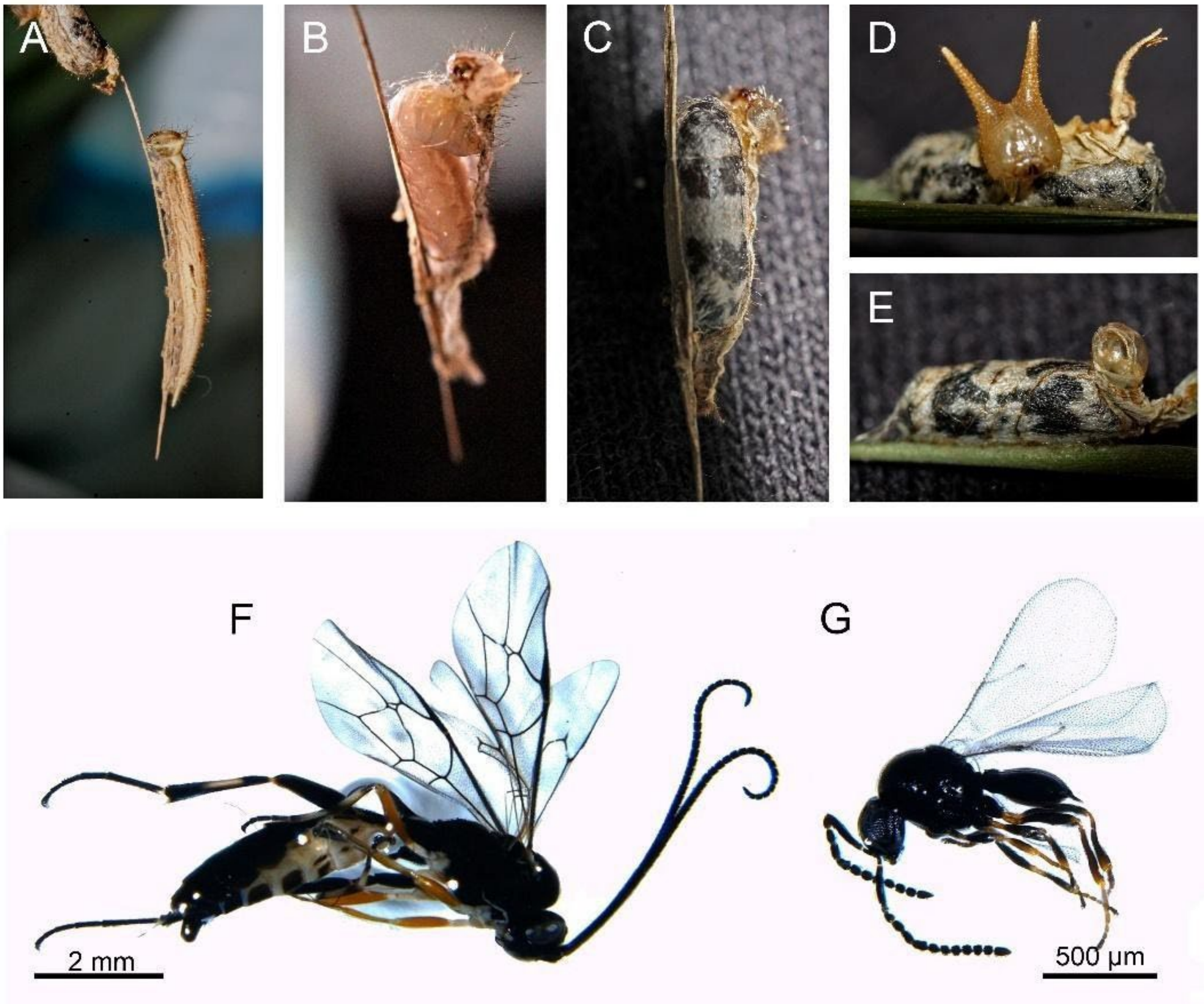

Fig. 9. Parasitism in eggs and larvae of *Daedalma drusilla*. A, early fifth-instar larva parasitized, resting on a skeletal vein of *Chusquea*; B, emerged parasitoid larva (Ichneumonidae) constructing the cocoon; C, parasitoid pupa in *Daedalma drusilla*; D, parasitoid pupa in *Corades dymantis* larva; E, parasitoid pupa in Noctuidae larva; F, adult larval parasitoid; G, adult egg parasitoid.

***Junea doraete* (Hewitson, 1858)**

Voucher: 2024-IMM-LV-014, 015, 016.

Egg: Not described here, see Montero and Ortíz (2012b).

First instar (Fig. 10A, B): Head capsule width 0.84 mm (n = 1); orange, slightly striated, striation less evident dorsally near epicranial suture. Epicranial notch slightly concave. Head chaetotaxy in figure 10A; setae P1-P3 and L1 directed forward, aligned along upper margin in dorsal view. Stemmata equal in size. Body with short black setae, slightly longer on posterior segments. Body chaetotaxy in figure 10B. For a description of the coloration and duration of the instar, see Montero and Ortíz (2012b).

Second to Fifth Instar: Not described here, see Montero and Ortíz (2012b).

Hostplant: *Chusquea scandens* (Poaceae: Bambusoideae: Chusqueinae).

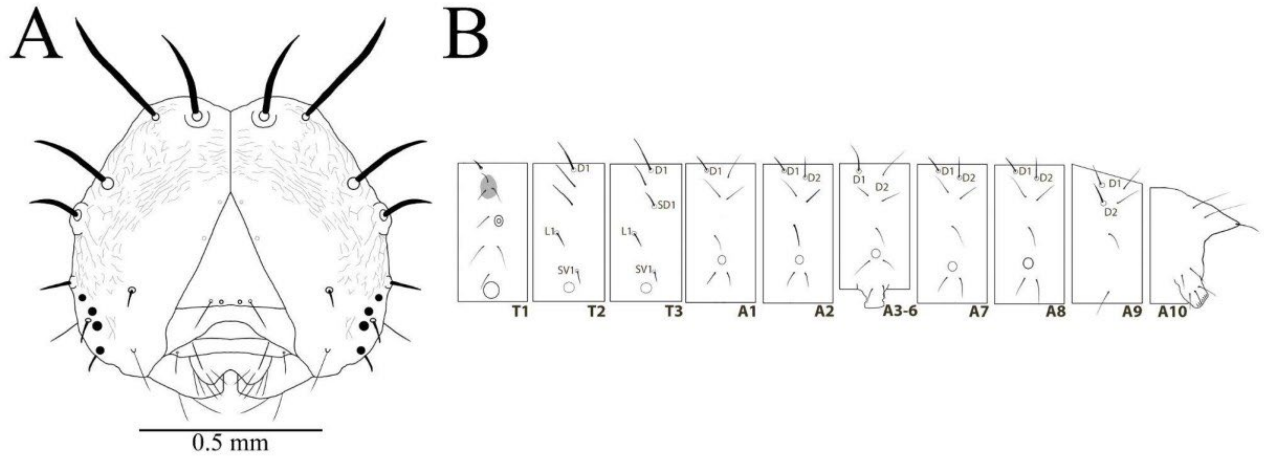

Fig. 10. *Junea doraete* chaetotaxy: A, head capsule; B, body chaetotaxy.

Pedaliodes nebris (Thieme, 1905)

Voucher: 2024-IMM-LV-002.

Egg (Fig. 11A, B) (n = 12) (Figure based on 2024-IMM-LV-002): Spherical; becoming flattened near hatching; pale yellow. Chorion striated with multiple raised longitudinal ribs; micropylar area slightly darker. Head capsule visible through chorion a few days before hatching. Laid on abaxial surface of mature leaves; oviposition not observed under natural conditions. Duration: 17 days.

Fig. 11. *Pedaliodes nebris* partial life stages: A and B, egg in dorsal and lateral view; C and D, preserved first instar in dorsal and lateral view; E and F, preserved first instar in dorsal and lateral view.

First instar (Fig. 11C, F) (*n* = 12) (Figure based on 2024-IMM-LV-003): Head capsule dark brown, striated, forming irregular reticulate pattern. Epicranial notch insignificant; vertex rounded, without scoli or projection. Primary setae semi-translucent. Six stemmata present; stemma 3 slightly larger. Newly emerged larva with pale yellow body; mid-dorsal band slightly darker, faint and discontinuous. After feeding, body slightly greenish to pale ochre; light brown longitudinal bands more evident on mid-dorsal, subdorsal, supra-spiracular, and subspiracular. Spiracles light brown. Setae black, slightly longer on A9–A10. Caudal filaments bifid, short, barely discernible. Body length: 4.3 mm (*n* = 1). Duration: unknown.

Posterior stages: Unknown.

Hostplant: *Poa* sp. (Poaceae: Pooideae: Poinae) (Fig. 12).

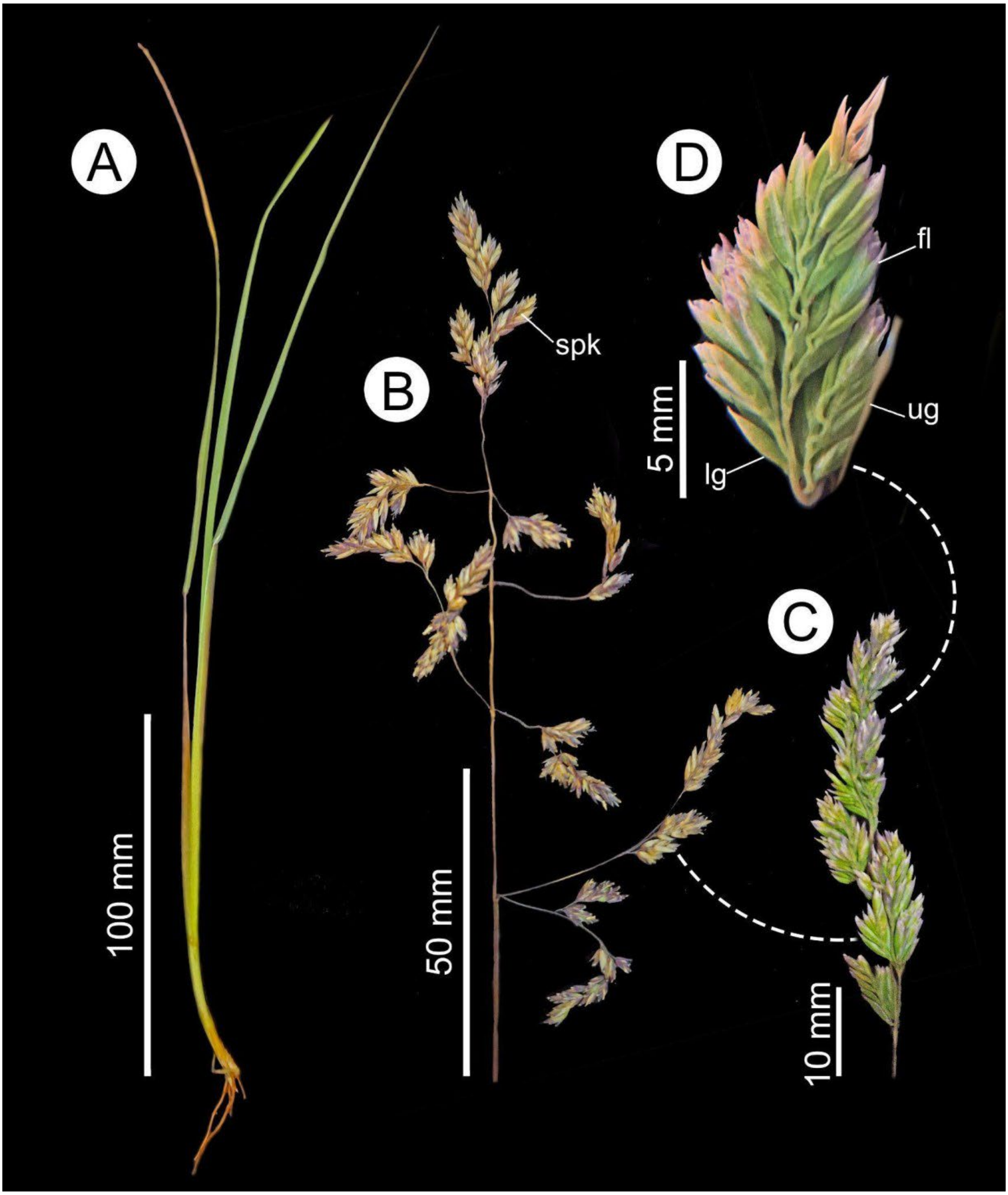

Fig. 12. *Poa* sp., host plant for *Pedaliodes nebris*: A, habit; B, synflorescence; C, detail of a branch of the synflorescence; D, spikelet. fl: florets, lg: lower glume, spk: spikelet, ug: upper glume.

Pedaliodes ochrotaenia (C. Felder and R. Felder, 1867)

Voucher: 2024-IMM-LV-0023.

Egg (n = 3): Spherical; yellowish. Chorion striated with multiple raised longitudinal ribs. Head capsule visible through chorion one day before emergence. Oviposition not observed under natural conditions. Duration: 20 days (n = 2).

First instar (Fig. 13A, B): Head capsule (Figs. 14A, B) width 0.69 mm (n = 1); dark brown to black, rounded, with irregular reticulations; epicranial and ecdysial sutures slightly darker. Epicranial notch insignificant; vertex rounded, without scoli or projections. Primary setae dark brown (Fig. 14A); labrum with five setae on each side. Stemma 3 slightly larger than others. Body slightly flattened, light brown, with reddish-brown longitudinal lines; mid-dorsal line being slightly thicker. Setae black with white tips, slightly longer caudally. Caudal filaments not evident. Body length: 6 mm. Duration: 13 days (n = 2).

Second instar (Figs. 13C, D) (n = 2): Head capsule (Fig. 14C) width 1.11 mm (n = 1); brown, with dark brown dorsal patch on upper half extending posteriorly; surface with pitted sculpturing. Scoli short, rounded. Multiple semi-translucent setae with broadened bases, tuberculate. Body cream-colored; reddish-brown longitudinal bands; whitish subdorsal and subspiracular lines. Paired brown spots on each side of A1-A2. Caudal filaments bifid, short. Body length: 13 mm. Duration: 12–13 days (n = 2).

Third instar (Figs. 13E, F) (n = 2): Head capsule (Fig. 14D) width 1.57 mm (n = 1); similar in coloration and patterns than preceding instar, but slightly less rounded; narrow band posterior to scoli. Scoli slightly more elongated, with increased number of protuberances and secondary setae. Body similar to immediately preceding instar; black subdorsal band with diffuse margins on T1–T3; paired irregular black subdorsal spots on A6 and A7. Caudal filaments short. Body length: 15 mm. Duration: 11–14 days (n = 2).

Fourth instar (Figs. 13H, I) (n = 2): Head capsule (Fig. 14E) width 2.10 mm (n = 1); shape and coloration patterns as to immediately preceding instar; line posterior to scoli slightly thicker. Black convex spot near epicranial suture, positioned higher; in one individual reduced to scoli bases, divided laterally and dorsally. Body similar to immediately preceding instar; dorsal zigzag pattern more pronounced; subdorsal brown line, more evident on anterior and posterior segments. Caudal filaments short. Body length: 15 mm (n = 2). Duration: 9 days (n = 2).

Fifth instar (Figs. 13J, K) (n = 2): Head capsule (Fig. 14F) width 2.90 mm (n = 1); dull brown, slightly more oval than in immediately preceding instars. Black spot restricted dorsally to stemmata region, narrowing toward adfrontal area. Multiple translucent secondary setae. Body opaque cream-brown with numerous minute black dots; T1 white dorsally; T2–T3 slightly darker. Mid-dorsal line diffuse; thin light-brown subdorsal zigzag lines with black dots on each segment; dark-brown subdorsal line discontinuous, limited to A5–A8. Subspiracular region and prolegs dark brown. Caudal filaments short. Body length: 33 mm (n = 1). Duration: 14–15 days (n = 2).

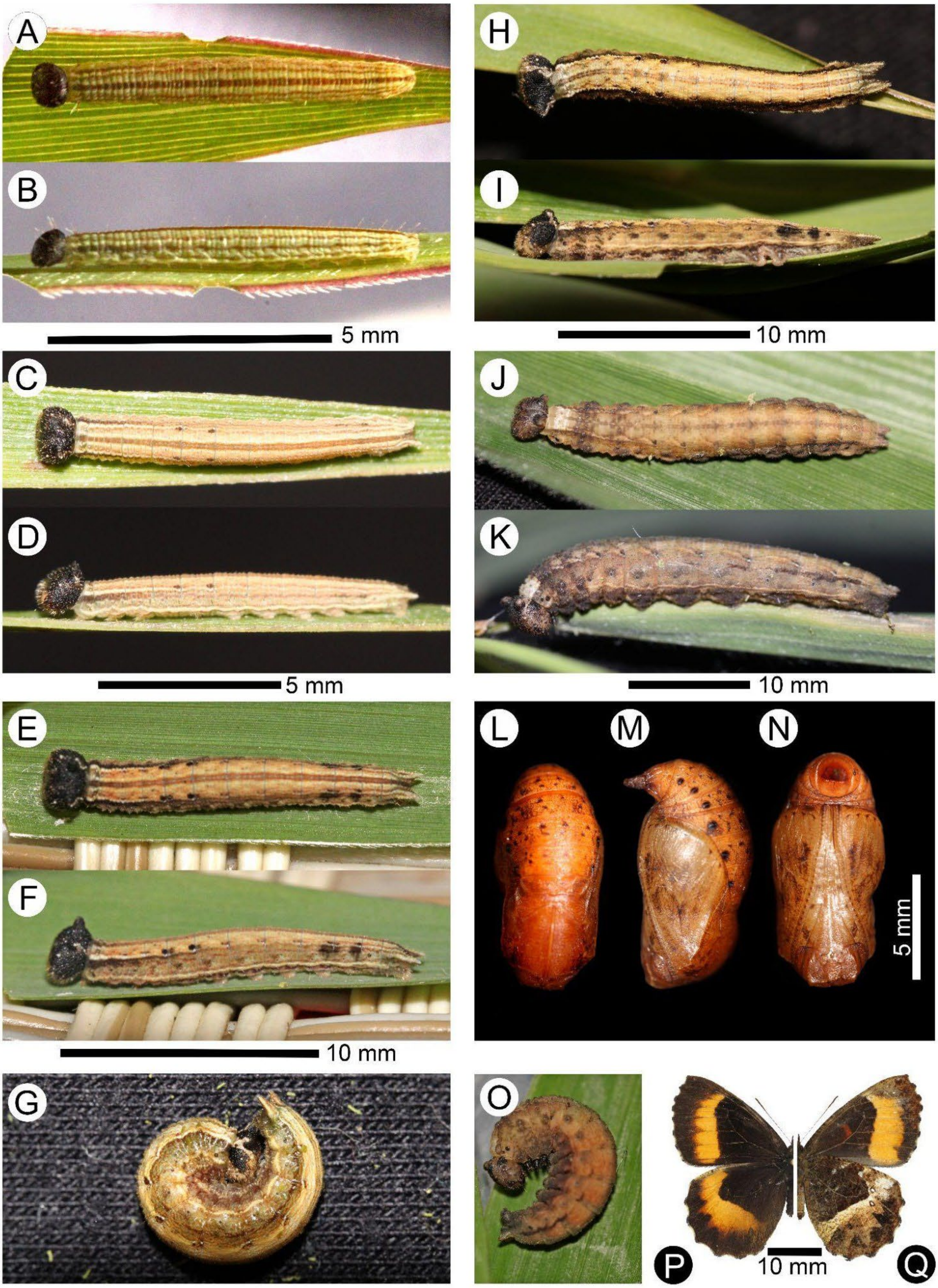

Fig. 13. *Pedaliodes ochrotaenia* life stages: A and B, first instar in lateral and dorsal view; C and D, second instar in lateral and dorsal view; E and F, third instar in lateral and dorsal view; G, fourth instar larva displaying defensive behavior; H and I, fourth instar in lateral and dorsal view; J and K,

fifth (ultimate) instar in lateral and dorsal view; L, M and N, pupa in dorsal, lateral and ventral view; O, prepupa in lateral view; P and Q, adult in dorsal and ventral view (photo of the adult does not correspond to that of the emerged adult).

Pupa (Figs. 13L, M, N) (n = 2): Robust, rounded; surface apparently smooth. Overall light brownish; dark-brown patches on wing case, leg case, and abdomen. Ocular caps squared. Abdomen slightly paler; spiracles black. Cremaster reddish-brown, triangular, rugose. Body length: 13 mm (n = 1). Duration: 24 days (n = 2).

Hostplant: *Chusquea scandens* (Poaceae: Bambusoideae: Chusqueinae).

Remarks: From the fourth instar onward, the larvae exhibited a defensive behavior in which, when exposed to an external stimulus, they drop from the plant and remain curled up on the ground for several minutes (Fig. 13G). Likewise, the pupa of neither of the two reared individuals suspended itself by the cremaster from any structure; instead, the larva stayed curled up on the ground and pupated in the same place after a couple of days (Fig. 13O). In all instars, the larvae prefer to feed at night, and no gregarious behavior was observed at any stage, and they rested abaxially, near the leaf margin.

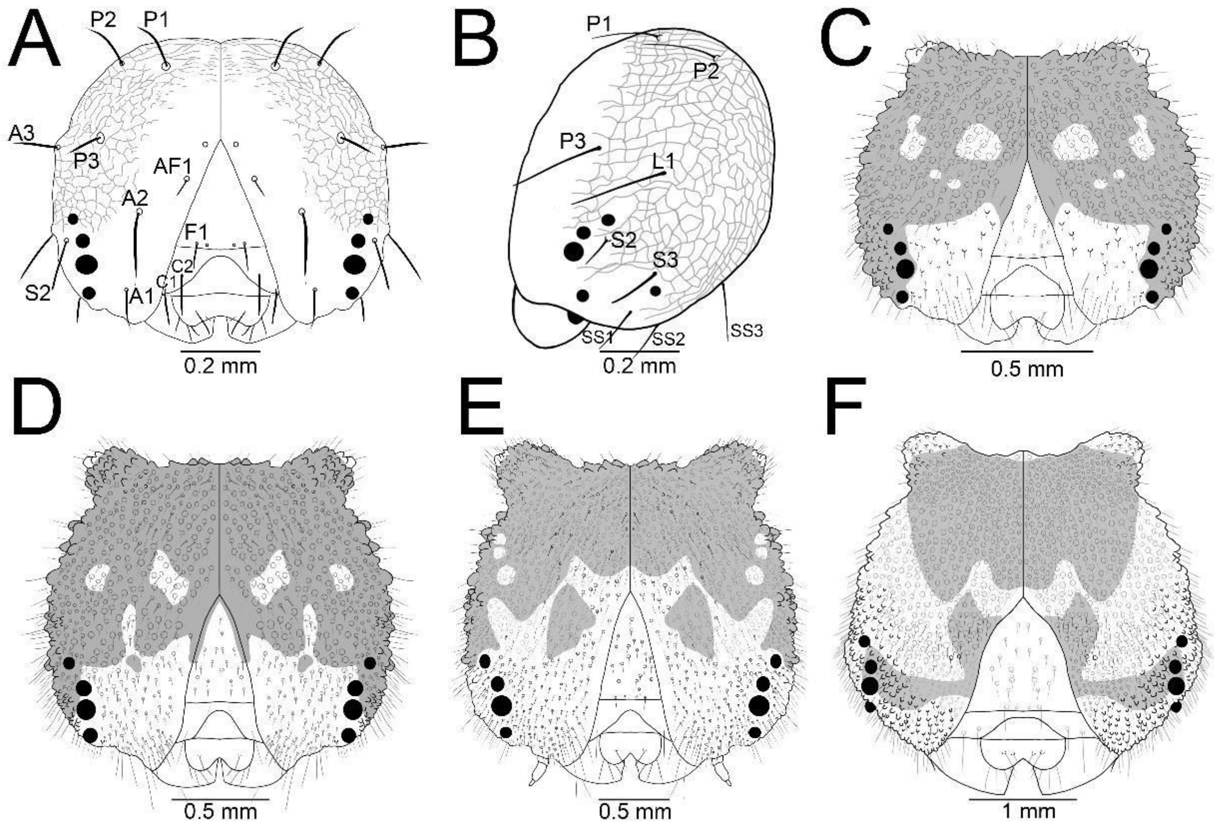

Fig. 14. *Pedaliodes ochrotaenia* larval head capsules: A and B, first instar in dorsal and lateral view; C, second instar; D, third instar; E, fourth instar, F, fifth (ultimate) instar.

Pedaliodes guicana **Adams, 1986**

Voucher: 2024-IMM-LS-001.

Egg (Fig. 15A, B) (*n* = 9): Diameter 1.21–1.26 mm (*n* = 3). Spherical; pale yellow. Chorion with multiple slightly sinuous meridians composed of small, irregularly sized circular cells. Head capsule visible 3 days before hatching; color changing from light brown to dark brown one day before emergence. Duration: 15–20 days (*n* = 9).

First instar (Fig. 15C, D) (*n* = 9): Head capsule (Figs. 16A, B) width 0.82–0.85 mm (*n* = 2); dark brown to shiny black, nearly round; irregular superficial reticulation, more evident laterally and posteriorly. Primary setae in figure 16A, B; head capsule setae light brown, slightly yellowish. Stemma 3 slightly larger than others. Newly emerged larva pale yellow; slightly darker dorsal longitudinal; setae light brown. Later instar: body light green with light brown longitudinal stripes; dorsal stripe longitudinal darkened; cream-colored subdorsal stripe present. Chaetotaxy in figure 16F. Caudal filaments bifid, short, barely visible. Body length: 5.0–6.0 mm (*n* = 6). Duration: 16–18 days (*n* = 6).

Second instar (Fig. 15E, F) (*n* = 5): Head capsule (Fig. 16C) width 1.10 mm (n = 1); wider than body; vertex with two short, rounded scoli; pitted sculpturing. Head capsule dark brown, lighter posterior to scoli; creamy spots on upper frons lateral region, and adfrontal area extending toward stemmata. Multiple light brown secondary setae over entire head capsule; genal tubercles present. Labrum with five setae on each side. Stemmata equal in size. Body light green; dark brown mid-dorsal longitudinal band, more evident from A5; discontinuous light brown subdorsal and supraspiracular bands. Body surface with scattered whitish spots. Caudal filaments short, more evident than in immediately preceding instar. Body length: 7.0–10.0 mm (*n* = 5). Duration: 15 days (*n* = 5).

Third instar (Fig. 15G, H) (*n* = 2): Head capsule (Fig. 16D) width 1.48 mm (*n* = 2); similar to immediately preceding instar; dark brown with broader, more defined creamy spots, especially near ecdysial line. Scoli rounded, slightly more elongated; anteriorly dark brown. Body reddish brown; mid-dorsal brown longitudinal band from T1, darker from A5-A6 to caudal region; paired circular brown spots flanking mid-dorsal band on segments A1-A7. Subdorsal dark brown band from T1 to A1, diffuse on T2-T3; thin, diffuse reddish-brown subspiracular. Spiracles dark brown; tracheal system yellow-cream. Body with numerous short translucent setae. Caudal region yellow-cream; caudal filaments paired, short, more evident than in immediately preceding instar. Body length: 9.0–11.0 mm (*n* = 2). Duration: 21–23 days (*n* = 2).

Fourth instar (Fig. 15I, J) (*n* = 2): Head capsule (Fig. 16E) width 1.93 mm (*n* = 1); similar to immediately preceding instar, slightly more elongated. Body similar in shape and coloration to immediately preceding instar; faint reddish-brown subdorsal zigzag pattern from T2 to A8 on each side. Body length: 13.0–14.0 mm (*n* = 2) until death. Duration: unknown.

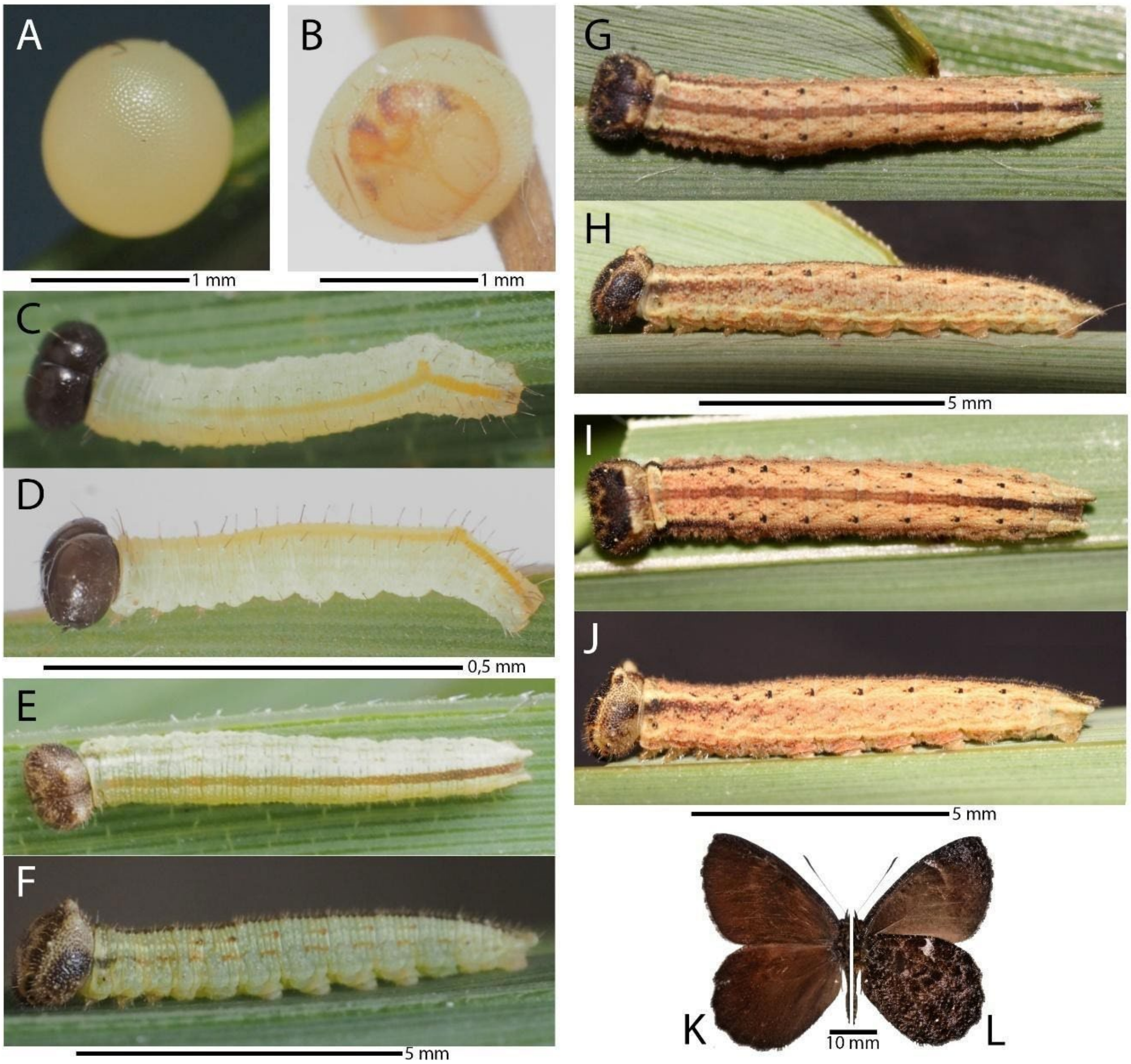

Fig. 15. *Pedaliodes guicana* partial life stages: A and B, Egg in lateral and dorsal view; C and D, first instar in dorsal and lateral view; E and F, second instar in dorsal and lateral view; G and H, third instar in dorsal and lateral view; I and J, fourth instar larva in dorsal and lateral view; K and L, adult in dorsal and ventral view (photo of the adult does not correspond to that of the emerged adult).

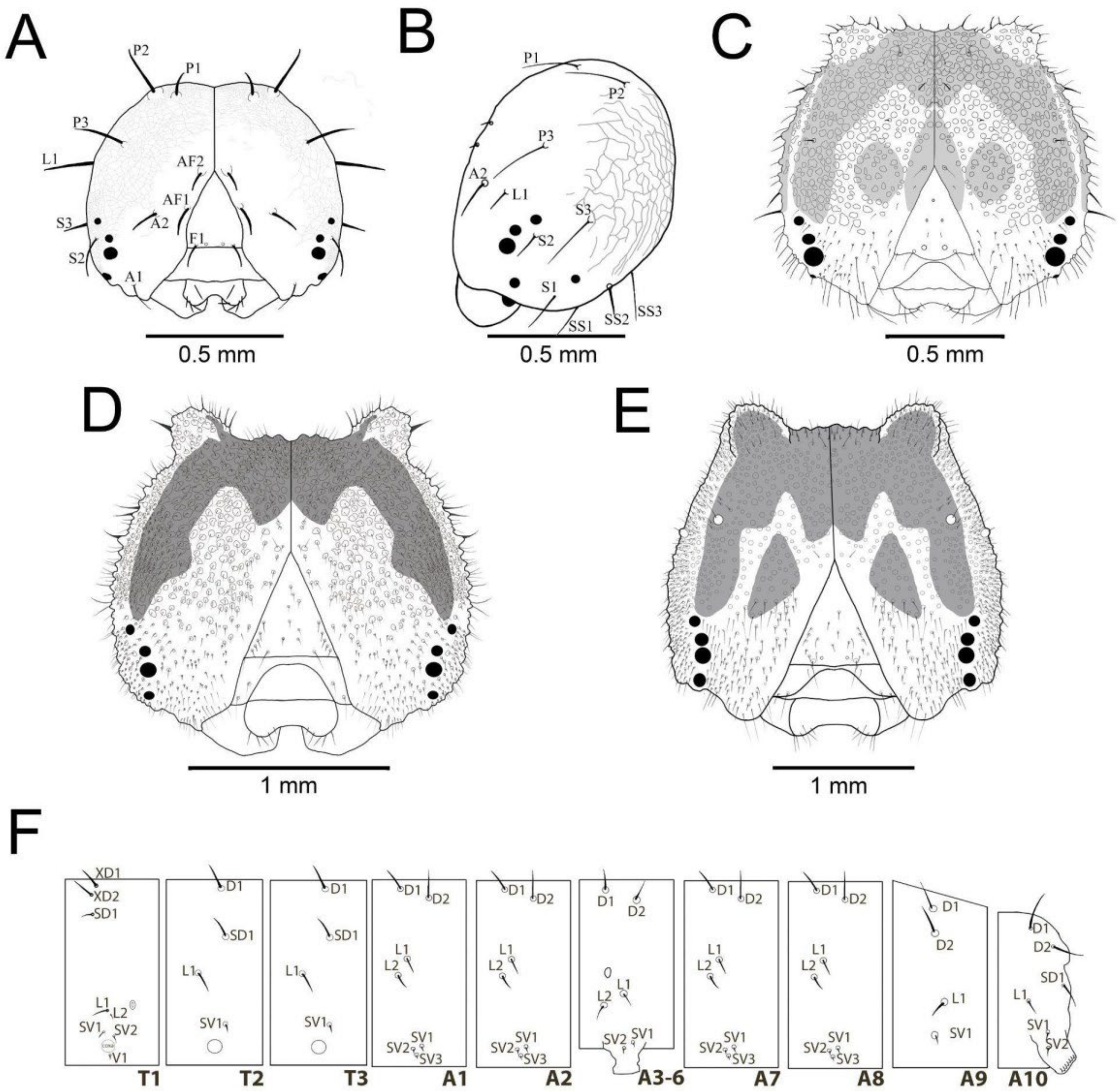

Fig. 16. *Pedaliodes guicana* larval head capsules: A and B, first instar in dorsal and lateral view; C, second instar; D, third instar; E, fourth instar; F, body chaetotaxy in lateral view (first instar).

Posterior stages: Unknown.

Hostplant: *Chusquea tessellata* Munro (Poaceae: Bambusoideae: Chusqueinae) (Fig. 17).

Remarks: Newly hatched larvae do not eat the chorion or do so only partially. In the early instars, they prefer to feed at the base of the leaves, and throughout all documented stages, they prefer young leaves and rest on the abaxial side of the leaf. When threatened, the larvae react violently by moving the anterior part of their body from side to side. If the stimulus persists, they curl up, protecting their head, drop from the leaf, and remain in that position for several minutes. The larvae died at the beginning of the fourth instar. The larvae were transferred and fed with leaves from populations of *Chusquea tessellata* from Páramo El Verdillo.

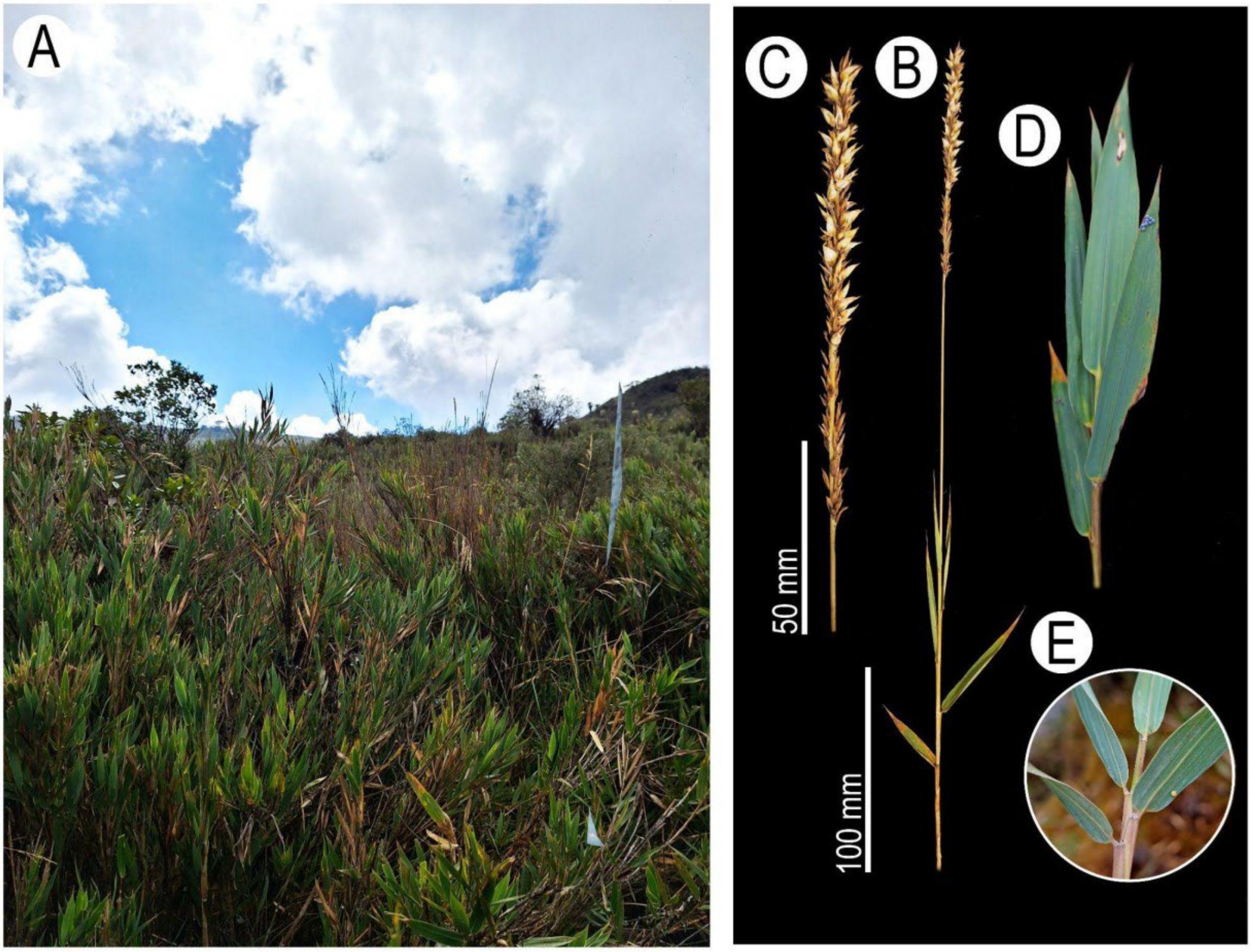

Fig. 17. *Chusquea tessellata*, host plant for *Pedaliodes guicana*: A, plant in habitat; B, synflorescence; C, detail of the synflorescence; D, leafs; E, phyllotaxis.

DISCUSSION

Documentation of immature stages of Lepidoptera has proven to be key for refining phylogenetic hypotheses, studying ecological relationships, identifying cryptic species, and understanding evolutionary adaptations (Kitching et al. 1985; Harvey 1991; Freitas and Brown 2004; Burns et al. 2008; Hernández-Roldán et al. 2012; Duque et al. 2014; Medina et al. 2020; Travesino et al. 2023). However, for the subtribe Pronophilina, there is still no comprehensive approach within any of these research areas that incorporates characters derived from immature stages. This is due to the limited knowledge of life cycles, which remain unknown in more than 90% of the species, clearly illustrating the Haeckelian shortfall proposed by Faria et al. (2020) for this group. The descriptions we present herein and the work of Benyamini et al. (2025), are both recent attempts aimed at reducing this gap in knowledge regarding the ontogeny of Pronophilina.

Eggs within Pronophilina exhibit highly disparate morphologies, potentially diagnostic at the generic level. For example, the egg of *L. samius* is elongate, with multiple longitudinal ribs and a faint pinkish hue, as reported by Schultze (1929). The egg closely resembles that of *L. schmidti* Adams, 1986 (Montero & Ortíz 2012a), *L. viventieni* (Apolinar, 1924), and *L. shefteli* Dyar, 1913 (pers. obs.) (Fig. 18). Therefore, it is probably that in *Lymanopoda*, the oval shape and the light brown coloration with a slight pinkish tone of the chorion surface may be characteristic. Similarly, the morphology, the surface of chorion, and the black coloration acquired by the eggs of *D. drusilla* are unique among known pronophiline butterflies, exhibits a markedly striated chorion with longitudinal ribs, a pale green surface that turns black prior to eclosion, and the larval head capsule is not visible before emergence. A striated chorion is also present in the genera *Corades* Doubleday, [1849], *Eteona* Doubleday, 1848, *Junea* Hemming, 1964, and *Mygona* Thieme, 1907, but in these taxa the feature is much more subtle than in *D. drusilla* (Freitas 2002; Greeney et al. 2010; Montero and Ortiz 2012b 2014b). Likewise, eggs of these genera are generally whitish-translucent, with the exception of *Junea*, in which the surface is yellowish, and in all cases both the head capsule and the larva become visible a few days before hatching (Montero and Ortiz 2012b).

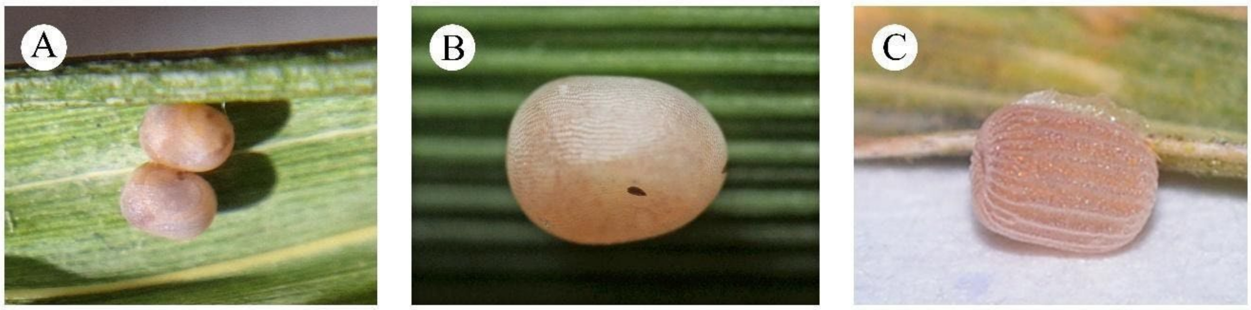

Fig. 18. *Lymanopoda* eggs: A, *L. samius* near to Páramo Los Venados, Boyacá, Colombia; B, *L. vivienteni* from Guasca, Cundinamarca, Colombia; C, *L. shefteli* from Puente río San Miguel, La Convención, Cusco, Peru.

An interesting fact is that this black coloration resembles that of parasitized eggs of *D. drusilla*. A similar coloration of viable eggs resembling parasitized eggs has been documented in some species of *Pareuptychia* Forster, 1964 (Murray 2001; Freitas et al. 2016a). On the other hand, in *Idioneurula* Strand, 1932, the green, subelliptical chorion could be diagnostic at the generic level, while regarding the *Pedaliodes* clade, we found that spherical white or yellow eggs are a constant feature among species and are therefore poorly informative to discriminate among genera.

We observed that after hatching, larvae may partially consume the chorion (*L. samius*, *P. guicana*), consume it entirely (*P. ochrotaenia*, *J. doraete*), or in some cases not consume it at all (*I. erebioides*, *D. drusilla*). This behavior may vary even among genera; for instance, *L. schmidti* has been reported as not consuming the chorion (Montero and Ortiz 2012a), while our observations show that *L. samius* does consume it (Fig. 2B). The underlying cause of the plasticity of this behavior in larvae remains uncertain, but it may represent an initial source of nutrients that allows the larva to move along the petiole toward the leaf, thereby reducing the period of vulnerability to parasitoids or predators (García-Barros 2006).

Larvae of some genera exhibit similarities that we consider not to be linked to the evolutionary history of a particular group, but rather to represent convergent adaptations in response to similar environmental conditions. For example, larvae of *Lymanopoda*, *P. nebris* and *Idioneurula* exhibit whitish longitudinal bands. This pattern may represent a form of crypsis with the hostplant leaves, possibly functioning as a disruptive strategy that breaks up the larval outline and reduces detectability (Stevens and Merilaita 2009; McLellan et al. 2023; Robinson et al. 2023). Similar patterns have been documented in multiple species of Euptychiina (*e.g.*, Murray 2001; Freitas 2003; Freitas et al. 2016b; Willmott et al. 2019), in *Corades* (Greney et al. 2010; Montero and Ortíz 2014) and *Eteona tisiphone* (Boisduval, 1836) (Freitas 2002), and even in other families of Lepidoptera such as Pyralidae (Vega et al. in prep). Furthermore, the brown coloration in larvae of *D. drusilla* and in the final instar of *Pedaliodes* Butler, 1867 may be linked to crypsis strategies that mimic their surroundings (Perveen and Khan 2024). This can be associated with their observed behaviors of resting on dry leaves or dropping to the ground when threatened, where dead *Chusquea* spp. leaves predominate.

We highlight that first-instar larvae, in several genera of Pronophilina, bear eight broad forward-directed setae, tapering toward the apex and aligned from the vertex to the gena except for the *Pedaliodes* complex, *Eretris* Thieme, 1905, and some genus of Neosatyriti such as *Neomaenas* Wallengren, 1858, *Argyrophorus* Blanchard, 1852, *Auca* Hayward, 1953, and *Quilaphoetosus* Herrera, 1966 (e.g., Montero and Ortiz 2012a; Montero et al. 2020; Benyamini et al. 2025). Notably, other Satyrini groups also exhibit this character such as Coenonymphina (Herbinson-Evans and Crosslet 2024) and Ypthimina (van der Poorten and van der Poorten 2012), perhaps representing a case of convergent evolution across multiple lineages. Additionally, one of the characters that may prove to be diagnostic between genera is the texture of the head capsule: in *Lymanopoda* it is clearly pitted sculptured, especially pronounced in the first instar, whereas in other genera (*Corades*, *Eretris*, *Junea*, *Idioneurula*, *Mygona*, *Lasiophila* C. Felder & R. Felder, 1859) it tends to be smoother or only slightly reticulate. On the other hand, larvae from the second instar onward in *Lymanopoda* and large pronophiline (e.g. *Corades*, *Lasiophila*, *Mygona*, and *Pronophila* Doubleday, [1849]) exhibit well-developed scoli (with the exception of *Daedalma* Hewitson, 1858), whereas the *Pedaliodes* clade is characterized by short, rounded scoli (Pelz 1997; Heredia and Viloria 2004; Greeney et al. 2009; Montero and Ortiz 2013a 2013b 2014a 2014d). In contrast, *Eretris* and the genera of Neosatyriti all lack scoli (Montero et al. 2020; Benyamini et al. 2025).

This separation is also evident when considering the pupa: large pronophilines (including *Daedalma*) have pupae with multiple structures and ornamentations (Greenet et al. 2011; Montero and Ortiz 2014c), whereas in *Pedaliodes* complex the pupae are short, robust, and smooth (*e.g.*, Montero and Ortiz 2012a), in Neosatyriti and *Eteona tisiphone* they are elongated and likewise smooth (Shapiro 1982; Freitas 2002; Benyamini et al. 2025). We consider that variation in the presence, shape, coloration, and ornamentation of these structures in larvae and pupae may be phylogenetically informative. However, at the infratribal level, the available data do not appear to support this pattern, as Pedalioditi is the sister infratribe of Pronophiliti rather than Lymanopoditi, and neither Eretriti nor Neosatyriti show direct affinities (Pyrcz et al. in prep).

Regarding the host plant association, we found that *P. nebris* feeding on a species of *Poa* occurring above 3300 m in the study area, an interesting finding considering that available records indicate that *Pedaliodes* larvae usually feed on species of *Chusquea*, with the exception of *Neopedaliodes zipa*, which was found feeding on *Carex jamesonii* Boott (Cyperaceae) (Montero and Ortíz 2013b). This observation is unusual as no other species of Pronophilina is known to use Cyperaceae as a host plant, and the rearing site was highly disturbed, therefore, this record may not be the plant that is commonly used by this species in nature. Likewise, our record of *I. erebioides* may indicate an accidental case of sedge consumption, in which the larvae, when exposed to different grasses and plants typical of flooded habitats, had no alternative but to consume this plant, especially considering that all larvae died after feeding on it. Given that *I. erebioides* is common in open areas with abundant grasses, it is plausible that this species may feed on an invasive grass species typical of fragmented habitats, potentially representing an adaptation to this type of environment.

Such discrepancies from the typical bamboo-feeding habit of the *Pedaliodes* clade highlight striking contrasts in host plant use across Pronophilina lineages. For example, in temperate and subarctic Pronophilina lineages, the use of grasses as host plants is frequent (Benyamini et al. 2025), whereas the use of bamboos is restricted to a fewer species, chiefly of the genus *Neomaenas* (Pyrcz and Boyer pers. obs.). In contrast, the use of grasses is rather exceptional in Neotropical lineages, occurring in particular within the *Pedaliodes* clade (*e.g.*, Pelz 1999; Montero and Ortíz 2014b; Viloria et al. 2015) and in some species of *Steremnia* (Brown 1941).

Similarly, we consider the behavior of gravid females upon capture to be rather peculiar and noteworthy. After capture, the females readily laid multiple eggs without apparent effort, a pattern observed in all captured females. This suggests that the oviposition strategy may involve mass laying on grass bunches, given that although oviposition of *P. nebris* was not observed, the eggs showed no adhesive that would indicate a specific placement on a particular part of the plant, which has also been reported for *Steromapedaliodes leukasmena* (Viloria & Camacho, 2015) and *S.*

castellana (Viloria et al. 2015). We emphasize the observation by Benyamini et al. (2025), who reported under laboratory conditions that oviposition of *Auca barrosi* (C. Silva, 1917) was carried out on items with a rough texture (paper towel, porous plastic plates, and porous stones). It is possible that in some Pronophilina species associated with grasslands and Páramo-like habitats, where *Chusquea* plants are uncommon, a host shift occurred toward Poaceae forming tussocks, with eggs being free of adhesive material.

CONCLUSIONS

Overall, the comparative analysis of the immature stages across Pronophilina highlights the substantial morphological, behavioral, and ecological diversity within the subtribe, while also revealing recurrent patterns of convergence associated with shared habitats and host plants. At the same time, the limited number of taxa for which immature stages are known severely constrains broader evolutionary interpretations. Moreover, available data are unevenly distributed among major Pronophilina clades, with relatively good coverage in the lineage including *Etcheverrius* (Guerin, 1832) and allies (Benyamini et al. 2025), partial representation in several large-bodied lineages as *Lasiophila*, *Mygona*, *Corades*, *Pedaliodes*, or *Junea* (*e.g.*, Greeney et al. 2011; Montero and Ortiz 2014), and almost complete gaps in others (*e.g.*, *Eretris*), some of which are represented by a single historical record (e.g., *Steremnia*) or remain entirely unknown (*e.g.*, *Manerebia* Staudinger, 1897) with respect to their immature stages.

Expanding life-history studies to poorly known genera and integrating morphological, behavioral, and molecular evidence will be essential to refine our understanding of character evolution within Pronophilina and to assess the phylogenetic signal of immature stage traits in Andean satyrine butterflies. We consider it essential, both for species conservation and for research purposes, to increase efforts to document the life cycles of pronophiline butterflies.

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REFERENCES

Adams MJ. 1985. Speciation in the Pronophiline butterflies (Satyridae) of the Northern Andes. J Res Lepid Supplement **1:**33–49.

Adams MJ, Bernard GI. 1977. Pronophiline butterflies (Satyridae) of the Sierra Nevada de Santa Marta, Colombia. Syst Entomol **2:**263–281. doi:10.1111/j.1365-3113.1977.tb00376.x.

Beccaloni GW, Viloria AL, Hall SK, Robinson GS. 2008. Catalogue of the Hostplants of the Neotropical Butterflies. Monografías del Tercer Milenio, Vol. 8. Sociedad Entomológica Aragonesa, Zaragoza.

Benyamini D, Ugarte A, Timer O, Benyamini A, Barriga JE et al. 2025. Pioneering travels in Chile to study the life histories of Satyrinae butterflies (Lepidoptera: Nymphalidae: Satyrinae: Pronophilina). Rev Chilena Entomol **51:**675–712.

Brown FM. 1941. Notes on Ecuadorian butterflies I: *Steroma*, *Pseudosteroma* and *Steremnia*. Ann Entomol Soc Am **34:**432–436. doi:10.1093/aesa/34.2.432.

Burns JM, Janzen DH, Hajibabaei M, Hallwachs W, Hebert PDN. 2008. DNA barcodes and cryptic species of skipper butterflies in the genus *Perichares* in Area de Conservación Guanacaste, Costa Rica. Proc Natl Acad Sci USA **105:**6350–6355. doi:10.1073/pnas.0712181105.

Camelo D, Pineda J, Vicente J, López J, Jiménez M et al. 2009. Reserva forestal protectora bosque oriental de Bogotá. Inventario de fauna. CAR, Bogotá D.C.

Casner KL, Pyrcz TW. 2010. Patterns and timing of diversification in a tropical montane butterfly genus, *Lymanopoda* (Nymphalidae, Satyrinae). Ecography **33:**251–259. doi:10.1111/j.1600-0587.2010.06306.x.

Cerdeña J, Mahecha-J O, Garlacz R, Arivilca-Pari J, Farfán J et al. 2024. A rapid assessment of Pronophilina Reuter, 1896 community structure and diversity in the upper most cloud forest near timberline in Manu National Park, Peru (Lepidoptera: Nymphalidae, Satyrinae). SHILAP **52:**235–250. doi:10.57065/shilap.899.

Costa C. 2006. Coleta, criação e identificação. In:Costa C, Ide S, Simonka CE. (eds), Insetos imaturos:metamorfose e identificação. Holos, Ribeirão Preto.

Costa C, Ide S. 2008. Importância e significado taxonômico e filogenético dos caracteres dos imaturos de Insecta em especial dos Coleoptera. *In*: Llorente J, Lanteri AA. (eds), Contribuciones taxonómicas en órdenes de insectos hiperdiversos. UNAM, México D.F.

Díaz-Suárez V, Mahecha-J. O, Andrade-C. MG, Pyrcz TW. 2022. Perturbación antrópica y patrones de diversidad en Satyrinae de montaña Pronophilina Reuter, 1896 en un bosque altoandino en Colombia (Lepidoptera:Nymphalidae). SHILAP **50:**709–728. doi:10.57065/shilap.263.

Duque PV, Vélez AB, Marin ADU, Flores EMB, Castillo DL, Wolff M. 2014, Estados inmaduros e historia natural de *Actinote callianthe amoena* (Jordan, 1913) (Nymphalidae:Heliconiinae, Acraeini). Trop Lepid Res **24:**87–95.

Faria LRR, Pie MR, Salles, F.F, Soares EDG. 2020. The Haeckelian shortfall or the tale of the missing semaphoronts. J Zool Syst Evol Res **59:**359–369. doi:10.1111/jzs.12435.

Freitas AVL. 2002. Immature stages of *Eteona tisiphone* (Nymphalidae:Satyrinae). J Lepid Soc **56**:286–288.

Freitas AVL. 2003. Description of a new genus for "*Euptychia*" *peculiaris* (Nymphalidae: Satyrinae):immature stages and systematic position. J Lepid Soc **57:**100–106.

Freitas AVL, Brown KS. 2004. Phylogeny of the Nymphalidae (Lepidoptera). Syst Biol. 53, 363–383. doi:10.1080/10635150490445670

Freitas AVL, Barbosa EP, Marín MA. 2016a. Immature stages and natural history of the Neotropical satyrine *Pareuptychia ocirrhoe interjecta* (Nymphalidae: Euptychiina). J Lepid Soc **70:**271–276.

Freitas AVL, Carreira JYO, Santos JP, Barbosa EP. 2016b. Immature stages and natural history of two species of *Forsterinaria* from southeastern Brazil (Lepidoptera: Nymphalidae). Trop Lepid Res **26:**13–18.

García-Barros E, Martín J. 1995. The eggs of European satyrine butterflies (Nymphalidae): external morphology and its use in systematics. Zool J Linn Soc **115:**73–115. doi:10.1006/zjls.1995.0034.

García-Barros E. 2006. Within and between species scaling in the weight, water, carbon and nitrogen contents of eggs and neonate larvae of twelve satyrine butterflies (Lepidoptera: Nymphalidae). Eur J Entomol **103:**559–568. doi:10.14411/eje.2006.076.

Goh KS, Lange WH. 1980. Spatial distribution patterns and sampling plans for immature stages of the artichoke plume moth. J Econ Entomol **73:**113–116. doi:10.1093/jee/73.1.113.

Greeney HF, Pyrcz TW, DeVries PJ, Dyer LA. 2009. The early stages of *Pedaliodes poesia* (Hewitson, 1862) in eastern Ecuador (Lepidoptera: Satyrinae: Pronophilina). J Insect Sci **9:**1–10. doi:10.1673/031.009.3801.

Greeney HF, Pyrcz TW, Dyer LA, Sánchez M, Walla T. 2010. The early stages and natural history of *Corades medeba* Hewitson, 1850 (Lepidoptera: Nymphalidae: Satyrinae: Pronophilina). Trop Lepid Res **20:**8–13.

Greeney HF, Dyer LA, Pyrcz TW. 2011. First description of the early stage biology of the genus *Mygona*:the natural history of the satyrine *Mygona irmina* in eastern Ecuador. J Insect Sci **11:**1–12. doi:10.1673/031.011.0105.

Harvey DJ. 1991. Higher classification of the Nymphalidae. *In*: Nijhout HF (ed) The Development and Evolution of Butterfly Wing Patterns. Smithsonian Institution, Washington.

Herbinson-Evans D, Crossley S. 2024. Some caterpillars of Satyrinae in Australia. Available at: https://lepidoptera.butterflyhouse.com.au/nymp/saty-cats.html (Feb. 2026).

Heredia MD, Viloria AL. 2004. Description and life history of *Pedaliodes zingara*, a new satyrine species from Colombia (Nymphalidae). J Lepid Soc **58:**80–87.

Hernández-Roldán JL, Munguira ML, Wagner W, Vila R. 2012. Comparative analysis and taxonomic use of the morphology of immature stages and natural history traits in European species of *Pyrgus* Hübner (Lepidoptera: Hesperiidae: Pyrginae). Zootaxa **3470:**1–71. doi:10.11646/zootaxa.3470.1.1

Huertas B, Arias JJ. 2007. A new butterfly species from the Colombian Andes and a review of the taxonomy of the genera *Idioneurula* Strand, 1932 and *Tamania* Pyrcz, 1995 (Lepidoptera: Nymphalidae: Satyrinae). Zootaxa **1652:**27–40. doi:10.11646/zootaxa.1652.1.2.

Kitching IJ. 1985. Early stages and classification of the milkweed butterflies (Lepidoptera: Danainae). Zool J Linn Soc. 85, 1–97. doi:10.1111/j.1096-3642.1985.tb01516.x.

Lamas G. 2004. Checklist:Part 4A. Hesperioidea – Papilionoidea. *In*: Heppner JB (ed) Atlas of Neotropical Lepidoptera, Vol. 5A. Association for Tropical Lepidoptera, Gainesville.

Lamas G, Viloria AL, Pyrcz TW. 2004. Subtribe Pronophilini. *In*: Lamas G (ed) Atlas of Neotropical Lepidoptera, Checklist:Part 4A. Association for Tropical Lepidoptera, Gainesville.

Mahecha-Jiménez OJ, Dumar-Rodríguez JC, Pyrcz TW. 2011. Efecto de la fragmentación del hábitat sobre las comunidades de mariposas de la tribu Pronophilini a lo largo de un gradiente altitudinal en un bosque andino en Bogotá (Colombia) (Lepidoptera: Nymphalidae, Satyrinae). SHILAP **39:**117–126.

Mahecha O, Garlacz R, Andrade MG, Prieto C, Pyrcz TW. 2019. Island biogeography in continental areas: inferring dispersal based on distributional patterns of Pronophilina butterflies (Nymphalidae: Satyrinae) in the north Andean massifs. Rev Mex Biodivers **90:**e902796. doi:10.22201/ib.20078706e.2019.90.2796.

Mahecha-J O, Florczyk K, Willmott KR, Cerdeña J, Zubek A et al. 2021. Solving the cryptic diversity of the genus *Manerebia* Staudinger in northern Peru:description of new species and considerations on the biogeographical role of the Huancabamba Deflection (Nymphalidae: Satyrinae: Pronophilina). Zootaxa **5072:**201–237. doi:10.11646/zootaxa.5072.3.1.

Marín MA, Álvarez CF, Giraldo CE, Pyrcz TW, Uribe SI et al. 2014. Mariposas en un bosque de niebla andino periurbano en el valle de Aburrá, Colombia. Rev Mex Biodivers **85:**200–208. doi:10.7550/rmb.36605.

Marín MA, Giraldo CE, Marín AL, Álvarez CF, Pyrcz TW. 2015. Differences in butterfly (Nymphalidae) diversity between hillsides and hilltop forest patches in the northern Andes. Stud Neotrop Fauna Environ **50:**194–203. doi:10.1080/01650521.2015.1099379.

McLellan CF, Cuthill IC, Montgomery SH. 2023. Pattern variation is linked to anti-predator coloration in butterfly larvae. Proc R Soc B **290:**20230811. doi:10.1098/rspb.2023.0811.

Medina, I, Vega-Trejo R, Wallenius T, Symonds MRE, Stuart-Fox D. 2020. From cryptic to colorful: evolutionary decoupling of larval and adult color in butterflies. Evol Lett **4:**34–43. doi:10.1002/evl3.149.

Montero F, Ortíz M. 2012a. Estados inmaduros e historia natural de algunas especies de la subtribu Pronophilina (Nymphalidae: Satyrinae) presentes en el Páramo del Tablazo, Colombia. II. *Lymanopoda schmidti* (Adams, 1986). Trop Lepid Res **22:**100–109.

Montero F, Ortíz M. 2012b. Estados inmaduros e historia natural de algunas especies de la subtribu Pronophilina (Nymphalidae: Satyrinae) presentes en el Páramo del Tablazo, Colombia. I. *Junea doraete doraete* (Hewitson, 1858). Trop Lepid Res **22:**32–41.

Montero F, Ortíz M. 2013a. Aporte al conocimiento para la conservación de las mariposas (Hesperioidea y Papilionoidea) en el Páramo del Tablazo, Cundinamarca, Colombia. Bol Cient Mus Hist Nat Univ Caldas **17:**197–226.

Montero F, Ortíz M. 2013b. Estados inmaduros e historia natural de algunas especies de la subtribu Pronophilina (Nymphalidae: Satyrinae) presentes en el Páramo del Tablazo, Colombia. III. *Neopedaliodes zipa* (Adams, 1986). Trop Lepid Res **23:**54–61.

Montero F, Ortíz M. 2014a. Ciclo de vida y ecología de *Panyapedaliodes drymaea* Hewitson, 1858 (Nymphalidae: Satyrinae: Pronophilina) en Cundinamarca, Colombia. Bol Cient Mus Hist Nat Univ Caldas **18:**284–296.

Montero F, Ortíz M. 2014b. Ciclo de vida de *Corades chelonis* Hewitson y *Corades dymantis* Thieme (Nymphalidae: Satyrinae: Pronophilina) y aspectos de su biología. Insecta Mundi **345:**1–29.

Montero F, Ortíz M. 2014c. Estados inmaduros e historia natural de algunas especies de la subtribu Pronophilina (Nymphalidae: Satyrinae) presentes en el Páramo del Tablazo, Colombia. IV. *Lasiophila circe circe* C. Felder & R. Felder, 1859. Trop Lepid Res **24:**37–43.

Montero F, Ortíz M. 2014d. Ciclo de vida y ecología de *Pedaliodes pallantis* Hewitson, 1862 (Nymphalidae: Satyrinae: Pronophilina) en Cundinamarca, Colombia. Trop Lepid Res **24:**81–86.

Montero F, Ortíz M, Viloria AL. 2020. Ciclo de vida de *Eretris catargyrea* (Staudinger, 1887), stat. rev. (Lepidoptera: Nymphalidae: Satyrinae). Anartia **30:**25–34.

Murray DL. 2001. Systematics of euptychiine butterflies (Nymphalidae: Satyrinae: Euptychiina) based on larval morphology and DNA sequence data and the evolution of life history traits. PhD thesis, Louisiana State University, USA.

Padrón P, Boyer P, Vélez A, Pyrcz TW. 2019. Description of the immature stages of a rare Andean Páramo butterfly *Lymanopoda caracara* Pyrcz, Willmott & J. Hall, 1999 (Lepidoptera: Nymphalidae). Zool Syst **44:**316–324. doi:10.11865/zs.201930.

Päivinen J, Grapputo A, Kaitala V, Komonen A, Kotiaho JS et al. 2005. Negative density-distribution relationship in butterflies. BMC Biol **3:**1–13. doi:10.1186/1741-7007-3-5.

Pelz V. 1997. Life history of *Pedaliodes parepa* from Ecuador (Lepidoptera: Nymphalidae: Satyrinae). Trop Lepid Res **8:**41–45.

Perveen FK, Khan A. 2024. Masters of camouflage and mimicry:Unusual world of Lepidoptera. In:Biodiversity and Ecology of Lepidoptera – Insights and Advances. IntechOpen. doi:10.5772/intechopen.1004166

Prieto CH. 2003. Satírinos (Lepidoptera: Nymphalidae: Satyrinae) del Parque Nacional Natural Munchique, diversidad de especies y distribución altitudinal. Rev Colomb Entomol **29:**203–211. doi:10.25100/SOCOLEN.V29I2.9606

Pyrcz TW. 2004. Pronophiline butterflies of the highlands of Chachapoyas in northern Peru:faunal survey, diversity, and distribution patterns (Lepidoptera: Nymphalidae: Satyrinae). Genus **15:**455–622.

Pyrcz TW. 2010. Wybrane zagadnienia z taksonomii, zoogeografii i ewolucji faun górskich na przykładzie grupy modelowej motyli z plemienia Pronophilini (Nymphalidae). Wydawnictwo Mantis, Olsztyn.

Pyrcz TW, Garlacz R. 2012. The presence–absence situation and its impact on the assemblage structure and interspecific relations of Pronophilina butterflies in the Venezuelan Andes (Lepidoptera: Nymphalidae). Neotrop Entomol **41:**186–195. doi:10.1007/s13744-012-0031-2

Pyrcz TW, Fratello S. 2005. Cloud forest butterfly fauna of the Pantepui – poor or poorly known? Description of new species and records of new genera of Pronophilina: *Eretris agata* and *Oxeoschistus romeo* (Nymphalidae: Satyrinae). J Lepid Soc **59:**201–212.

Pyrcz TW, Rodriguez G. 2006. Description of a new remarkable species of *Lymanopoda* Westwood and identification of a centre of endemism of cloud forest butterflies in Belmira, northern Central Cordillera, Antioquia, Colombia (Lepidoptera: Nymphalidae: Satyrinae). Genus **17:**291–297. doi:10.14411/eje.2018.039

Pyrcz TW, Rodríguez G. 2007. Mariposas de la tribu Pronophilini en la Cordillera Occidental de los Andes de Colombia (Lepidoptera: Nymphalidae: Satyrinae). SHILAP **35:**455–489.

Pyrcz TW, Wojtusiak J. 2002. The vertical distribution of pronophiline butterflies (Nymphalidae: Satyrinae) along an elevational transect in Monte Zerpa (Cordillera de Mérida, Venezuela) with remarks on their diversity and parapatric distribution. Glob Ecol Biogeogr **11:**211–221. doi:10.1046/j.1466-822X.2002.00285.x.

Pyrcz TW, Greeney HF, Willmott KR, Wojtusiak J. 2011. A taxonomic revision of the genus *Daedalma* Hewitson with the descriptions of twenty new taxa and the immature stages of two species (Lepidoptera: Nymphalidae: Satyrinae). Zootaxa **2898:**1–68. doi:10.11646/zootaxa.2898.1.1.

Pyrcz TW, Clavijo A, Uribe SI, Marín MA, Alvarez CF, Zubek A. 2016. Páramo de Belmira as an important centre of endemism in the northern Colombian Andes:new evidence from Pronophilina butterflies (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). Zootaxa **4179:**77–102. doi:10.11646/zootaxa.4179.1.3.

Pyrcz TW, Lorenc-Brudecka J, Zubek A, Boyer P, Carolaing-Gabaldon M et al. 2017. Taxonomy, phylogeny and distribution of the genus *Steromapedaliodes sensu novo* in the Cordillera de Mérida, Venezuela (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). Arthropod Syst. Phylogeny **75:**195–243. doi:10.3897/asp.75.e31899.

Pyrcz TW, Freitas AVL, Boyer P, Días FMS, Dolibaina DR et al. 2018. Uncovered diversity of a predominantly Andean butterfly clade in the Brazilian Atlantic Forest:a revision of the genus *Praepedaliodes* Forster (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). Neotrop Entomol **47:**211–255. doi:10.1007/s13744-017-0543-x.

Pyrcz TW, Willmott K, Lachowska-Cierlik D, Mrozek A, Florczyk K et al. 2023. Phylogeny and systematics of the "*Pronophila* clade", with two new genera to resolve the formerly polyphyletic genus *Pseudomaniola* (Lepidoptera: Nymphalidae: Satyrinae). Insect Syst Divers **7:**1–20. doi:10.1093/isd/ixad020.

Pyrcz TW, Boyer P, Petit JC, Garlacz R, Zajac-Garlacz K et al. 2024. Bedazzled:a new, striking species of *Corades* from the outskirts of Quito questions our knowledge of Andean cloud forest butterflies (Lepidoptera: Nymphalidae: Satyrinae). Zootaxa **5453:**255–262. doi:10.11646/zootaxa.5453.2.6.

Pyrcz TW, Mahecha-J. O, Lachowska-Cierlik D, Boyer P, Freitas AVL et al. 2025. Evolutionary history of Neotropical butterflies of the infratribe Neosatyriti based on target enrichment (Lepidoptera: Nymphalidae: Satyrinae: Satyrini: Pronophilina). Invertebr Syst **39.** doi:10.1071/IS24038.

Pyrcz TW, Wojtusiak J, Garlacz R. 2009. Diversity and distribution patterns of Pronophilini butterflies (Lepidoptera: Nymphalidae: Satyrinae) along an altitudinal transect in north-western Ecuador. Neotrop Entomol **38:**716–726. doi:10.1590/s1519-566x2009000600003.

Pyrcz TW, Viloria AL. 2007. Pronophiline and Erebiine butterflies in the Tamá range, Venezuela–Colombia border (Nymphalidae: Satyrinae). Trop Lepid Res **15:**18–52.

Pyrcz TW, Viloria AL. 2009. Systematics, zoogeography and bionomics of high Andean pedaliodines, Part 11: a new subspecies of *Pedaliodes ornata* Staudinger from the Cordillera de Mérida (Lepidoptera: Nymphalidae: Satyrinae). Genus **20:**13–22.

Pyrcz T, Viloria AL. 2012. Revalidation of *Pedaliodes lithochalcis* Butler & Druce, description of a new species from Peru and Bolivia and of a new subspecies of *P. napaea* Bates from Honduras (Lepidoptera: Nymphalidae: Satyrinae). Genus **23:**133–152.

Robinson ML, Weber MG, Freedman MG, Jordan E, Ashlock SR et al. 2023. Macroevolution of protective coloration across caterpillars reflects relationships with host plants. Proc R Soc B **290:**20222293. doi:10.1098/rspb.2022.2293.

Schultze RA. 1929. Die erste Stande von drei kolumbischen hochandinen Satyriden. Dtsch entomol Z Iris **43:**157–165.

Schneider C, Rasband W, Eliceiri K. 2012. NIH Image to ImageJ: 25 years of image analysis. Nat Methods **9:**671–675. doi:10.1038/nmeth.2089.

Shapiro AM. 1982. Notas sobre los estadios inmaduros de la mariposa plateada, *Argyrophorus argenteus* Blanchard (Lepidoptera: Satyridae). Rev Soc Mex Lepid **7:**29–31.

Stehr FW. 1987. Order Lepidoptera. *In*: Stehr FW (ed) Immature Insects, Vol. I. Kendall/Hunt Publishing, Dubuque.

Stevens M, Merilaita S. 2009. Defining disruptive coloration and distinguishing its functions. Philos Trans R Soc B Biol Sci **364:**481–488. doi:10.1098/rstb.2008.0216..

Travesino DG, Beccacece HM, Zapata AI. 2023. Description of life cycle and immature stages of *Yphthimoides celmis* (Godart, [1824]) (Lepidoptera: Nymphalidae: Satyrinae):a contribution to the taxonomic status of the genus. Zootaxa **5361:**125–134. doi:10.11646/zootaxa.5361.1.7

Välimäki P, Itämies J. 2005. Effects of canopy coverage on the immature stages of the Clouded Apollo butterfly [*Parnassius mnemosyne* (L.)] with observations on larval behaviour. Entomol Fenn **16:**117–123. doi:10.33338/ef.84244.

Van der Poorten G, van der Poorten N. 2012. New and revised descriptions of the immature stages of some butterflies in Sri Lanka and their larval food plants (Lepidoptera: Nymphalidae). Part 2:Subfamily Satyrinae. Trop Lepid Res **22:**80–92.

Viloria AL, Ferrer-Paris JR, Camacho J, Costa M. 2015. New satyrine butterflies from the Venezuelan Andes (Lepidoptera: Nymphalidae). Anartia **25:**95–160.

Willmott KR, Marín MA, Nakahara S, Pomerantz T, Lamas G et al. 2019. A revision of the new Andean butterfly genus *Optimandes* Marín, Nakahara & Willmott, n. gen., with the description of a new species (Nymphalidae: Satyrinae: Euptychiina). Trop Lepid Res **29:**29–44.