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CONTENTS

Front Cover Photo - *Faunis sappho* (Nymphalidae, Satyrinae), Philippines, Bohol Island. Photo by Keith Wolfe.
Inside Back Cover Photo - *Melanolycaena altimontana* (Lycaenidae, Lycaeninae), Papua New Guinea, Mt. Hagen. Photo by Keith Willmott.
Back Cover Photo - *Cicadoforma ocelotus* (Noctuidae, Pantheinae), Colombia, Cundinamarca. Photo by Joe Martinez.

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Pseudogyris gen. nov. (Lepidoptera: Lycaenidae), a new genus for two rare thecline butterflies from New Guinea, including the description of a new species

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Abstract: The lycaenid tribe Ogyrini Waterhouse & Lyell, 1914 is endemic to the Australian Region, where it is restricted to mainland New Guinea and Australia. It currently includes 15 species, all assigned to the genus *Ogyris* Angas, 1847, and most of these are endemic to Australia. One species, *Ogyris meeki* (Rothschild, 1900) from mainland New Guinea, has been rarely collected, being previously known only from nine specimens (7 ♂, 2 ♀). However, comparative study of the morphology, including adult wing structure and genitalia, and wing color pattern elements based on examination of existing and additional material (9 ♂, 3 ♀), indicate that *O. meeki* comprises a complex of two species, and differs fundamentally from *Ogyris* by 14 unique characters, many of which are considered to be synapomorphies. We therefore propose a new genus, *Pseudogyris* **gen. nov.**, and a new species to classify this unusual pair of species, which are among the largest and perhaps most spectacular theclines. Unlike *Ogyris*, *Pseudogyris meeki* (Rothschild, 1900) **comb. nov.** and *Pseudogyris brandti* **sp. nov.** are restricted to mainland New Guinea (West Papua and Papua of Indonesia, and Papua New Guinea) and the neighboring island of New Ireland (PNG), where they occur in tropical lowland rainforest and lower montane forest. The two species of *Pseudogyris* are allopatric, being separated by the Central Cordillera, with *P. meeki* **comb. nov.** restricted to the southern lowlands and *P. brandti* **sp. nov.** to the northern lowlands and New Ireland.

Resumen: La tribu Ogyrini Waterhouse & Lyell, 1914 de la Lycaenidae es endémica de la región Australiana, donde está restringida a la parte continental de Nueva Guinea y Australia. Actualmente incluye 15 especies del género *Ogyris* Angas, 1847, y la mayoría de éstas son endémicas de Australia. La especie, *Ogyris meeki* (Rothschild, 1900) de la parte continental de Nueva Guinea, ha sido recolectada pocas veces, y sólo se conocían nueve especímenes (7 ♂, 2 ♀). Sin embargo, el estudio comparativo de la morfología, incluyendo la estructura del ala y las genitalias de los adultos y los elementos del patrón de color del ala, basados en el examen de material existente y adicional (9 ♂, 3 ♀), indica que *O. meeki* comprende un complejo de dos especies y difiere fundamentalmente de *Ogyris* por 14 caracteres únicos, muchos de los cuales se consideran sinapomórficos. Por lo tanto, proponemos el nuevo género *Pseudogyris* **gen. nov.** y una nueva especie para dar cabida a este inusual conjunto de especies, las cuales se encuentran entre las más grandes y quizás más espectaculares theclines. A diferencia de *Ogyris*, *Pseudogyris meeki* (Rothschild, 1900) **comb. nov.** y *Pseudogyris brandti* **sp. nov.** están restringidas a la parte continental de Nueva Guinea (Papua Occidental y Papua de Indonesia, y Papua Nueva Guinea) y la vecina isla de Nueva Irlanda (PNG), donde se encuentran en la selva tropical de tierras bajas y en la selva montana baja. Las dos especies de *Pseudogyris* son alopátricas y están separadas por la Cordillera Central, con *P. meeki* **comb. nov.** restringida a las tierras bajas del sur y *P. brandti* **sp. nov.** a las tierras bajas del norte y Nueva Irlanda.

Key words: Australian zoogeographic region, biosystematics, taxonomy, Theclinae, tropical forest, vicariance biogeography

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INTRODUCTION

The lycaenid genus *Ogyris* Angas, 1847 belongs to the monotypic tribe Ogyrini Waterhouse & Lyell, 1914 and is endemic to the Australian Region (Eliot, 1973). It currently includes 15 species, of which 13 are restricted to the Australian mainland and the adjacent islands of Melville and Kangaroo Islands (Field, 1999; Braby, 2000; Williams & Hay, 2001; Schmidt & Hughes, 2006; Schmidt, 2007; Braby & Douglas, 2008; Grund, 2010; Braby *et al.*, 2011). Only two species occur on mainland New Guinea (Parsons, 1998), one of which, *O. zosine* (Hewitson, 1853), also occurs widely in western, central, northern and eastern Australia (Braby *et al.*, 2014; Braby *et al.*, 2018), whereas the other, *O. meeki* (Rothschild, 1900) (Fig. 1), is restricted to mainland New Guinea (Papua and Papua New Guinea) (Parsons, 1998). The adults are robust and of medium

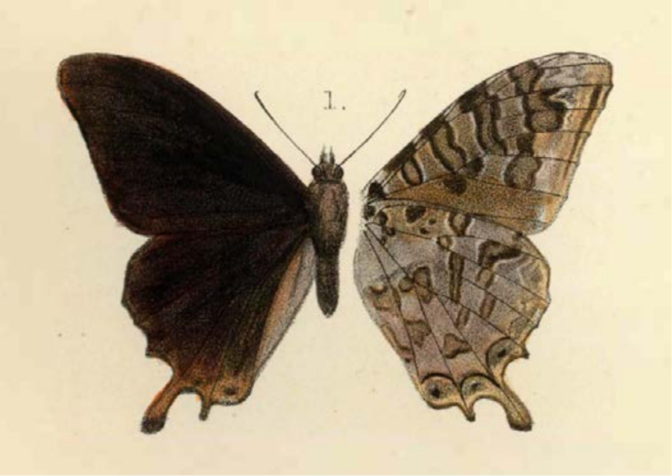

Figure 1. Syntype male of *Ogyris meeki* illustrated by Rothschild (1900).

to large size, and their flight is rapid and powerful. Many of them are brilliantly colored. The male lacks androconia (sex-scales), and a few species are strongly sexually dimorphic. All species in Australia occur in eucalypt open-forest, or eucalypt and acacia woodland or shrubland, with several species adapted to low rainfall areas of the semi-arid and arid zones (Braby, 2000). Only *O. meeki* occurs in rainforest, where it has been collected from lowland areas up to 800 m (Parsons, 1998).

Waterhouse & Lyell (1914) and Eliot (1973) provided a diagnosis of Ogyrini, noting that the forewing has 11 veins, with the radial branches R_4 and R_5 fused into a single vein R_{4+5} which reaches the costa just before the apex; vein Sc reaches the costa before the end of the discal cell; veins R_1 and R_2 are separated and not anastomosed; vein M_2 arises closer to vein M_1 than M_3; veins M_1 and $R_3 + R_{4+5}$ are connate at the apex of the discal cell in some species; the hind wing is generally without a tail and has the termen highly dentate and sometimes strongly produced at the end of vein CuA_2; the tornal lobe (between veins CuA_2 and 1A+2A) is present but weakly developed; the eye is smooth; the labial palpus is clothed with long appressed scales, with the third (apical) segment very short; and the male fore tarsus is fused into a single segment, terminating in a short down-turned point. Bethune-Baker (1905) provided illustrations of the male genitalia for 10 species of *Ogyris* and summarized their comparative differences; however, he did not examine the genitalia of *O. meeki*. The male genitalia of *Ogyris* possess juxta and brachia, and Parsons (1998) noted that the genitalia are simple and similar to those of *Arhopala* Boisduval, 1832, but the valva is shorter with the distal margin bearing a concave, U-shaped indentation. The female genitalia of *Ogyris* are also simple in which the ostium bursae is broad and weakly sclerotized, the ductus bursae is membranous, non-sclerotized and moderately long and expands into the corpus bursae, which is rounded and membranous without signa (Field, 1999). Braby (2000) observed that the antenna is about half or less than half the length of the forewing costa (nudum segments about 45 - Eliot, 1973); the flagellum of the antenna generally expands gradually into a slender club, but in the *O. olane* species-group it expands abruptly into a conspicuous club.

Bethune-Baker (1905), Parsons (1998) and Braby (2000) all independently noted that *O. meeki* is distinctive on account of fundamental differences in wing shape and pattern, including the presence of a long, clubbed tail on vein CuA_1, rather than a tornal projection on CuA_2. Indeed, Rothschild (1900, p. 274) stated "This is the largest and most aberrant species of the genus…" Braby (2000) remarked that *O. meeki* appears to be misplaced in this genus. Moreover, Parsons (1998, p. 395) perceptively stated that "…the ♂ und is somewhat variable, although this variability may eventually be found to correlate somewhat with geographical position when longer series of the species become available." However, comparative morphological studies of the adults, including the genitalia and other structures, have so far been lacking due to the paucity of material. D'Abrera (1971) and Parsons (1998) noted that the species was known only from a total of nine specimens (7 ♂, 2 ♀) in museum collections. Since that publication a further 11 specimens (8 ♂, 3 ♀) have come to our attention, preserved in three private collections (AYC, CJMC, MFBC; see Materials and Methods below). There is also an additional specimen (1 ♂) in KSP (Schröder, 2021). The purpose of this study is to examine the morphology of *O. meeki* and critically reassess its generic placement and taxonomic status based on these new acquisitions. Based on this comparative study we demonstrate that *O. meeki* comprises a complex of two species, one of which is new, and that both belong in a new genus distinct from *Ogyris*.

MATERIALS AND METHODS

There has been taxonomic confusion regarding the nomenclature of the genus-group name *Ogyris* because it was introduced twice by different authors, first by Angas (1847) with *O. amaryllis* Hewitson, 1862 as type species by subsequent monotypy, and then by Westwood (1851) in Doubleday and Westwood (1846-1852) with *O. abrota* Westwood, 1851 as type species by monotypy (Edwards, 1996; Edwards *et al.*, 2001). *Ogyris* Angas, 1847 was introduced for two undescribed species and thus the name was established without a nominal type species. Tepper (1893) was the first to correctly identify one of the figures illustrated by Angas (1847) as *Ogyris amaryllis*. This action was accepted by Edwards (1996) as the first reviser to include a valid species in *Ogyris* Angas; hence, *O. amaryllis* is the type species of *Ogyris* Angas by subsequent monotypy. Thus, prior to 1996, all published literature refers to *Ogyris* Westwood, 1851, which is a junior subjective synonym of *Ogyris* Angas, 1847.

Ogyris includes a number of informal species-groups according to similarities in adult phenotype, antennal structure and life history (Bethune-Baker, 1905; Braby, 2000). These groups are the *O. aenone* species-group of at least three species (*O. aenone* (Waterhouse, 1902), *O. ianthis* (Waterhouse, 1900) and *O. iphis* (Waterhouse & Lyell, 1914)), the *O. olane* species-group of three species (*O. oroetes* (Hewitson, 1862), *O. olane* (Hewitson, 1862) and *O. barnardi* (Miskin, 1890)), the *O. genoveva* species-group of two species (*O. genoveva* (Hewitson, [1853]) and *O. zosine* (Hewitson, [1853])), and the *O. idmo* species-group of four species (*O. otanes* (C. & R. Felder, 1865), *O. halmaturia* (Tepper, 1890), *O. idmo* (Hewitson, 1862) and *O. subterrestris* Field, 1999), which is closely related to the *O.*

genoveva species-group. *Ogyris amaryllis* (Hewitson, 1862) and *O. abrota* (Westwood, [1851]), as well as *O. meeki*, appear to be more isolated from these species-groups but their exact phylogenetic relationships are unclear.

Although Bethune-Baker (1905) illustrated the male genitalia of 10 species of *Ogyris* and provided diagnoses for each, his drawings are insufficient for modern comparative purposes. Since that publication the male genitalia have been illustrated for *O. genoveva* (Eliot, 1973), *O. subterrestris* (Field, 1999) and *O. halmaturia* (Braby & Douglas, 2008), whereas the female genitalia have been described and illustrated only for *O. subterrestris* (Field, 1999). We therefore dissected and examined the genitalia of both sexes of one species representing each of the various species-groups noted above, notably *O. abrota*, *O. aenone*, *O. amaryllis*, *O. olane*, *O. zosine* and *O. idmo*, for comparison with *O. meeki*. Dissection of the genitalia was performed using standard techniques: the entire abdomen was removed and placed in 10% KOH and boiled for 20 minutes, and then transferred to 30% ethanol for cleaning, dissection and examination. Completed dissections were fixed in 95% ethanol and then 100% isopropanol. The genitalia were placed in an alcohol-based gel in an excavated glass block and photographed using a Leica M205A microscope and were stacked using Helicon Focus 5.3 according to the technique of Su (2016). Terminology for genitalia follows Klots (1970) and Eliot (1973).

Adult size was estimated by measuring the length of the forewing, that is, the straight-line distance between the apex and base (i.e., the point of attachment of the wing with the thorax), using digital photographs or a digital caliper to an accuracy of 0.1 mm. Geo-coordinates (latitude and longitude) for each location were determined using Google Earth, converted to decimal degrees with a precision of approximately 10–100 km, and then plotted in ArcGIS version 10.7.1 using a projected coordinate system (WGS84_MGA_zone 55).

For species concept we follow Mayr's biological species concept based on phenotypic or morphological criteria, especially the reproductive structures, as a surrogate of reproductive isolation.

The following acronyms refer to repositories where specimens have been examined or deposited: **ANIC**: Australian National Insect Collection, Canberra, Australia; **AYC**: Akira Yagishita private collection, Japan; **NHMUK**: Natural History Museum, London, England (formerly British Museum of Natural History); **CJMC**: Chris J. Müller private collection, Sydney, Australia; **KONE**: National Insect Collection, Port Moresby, Papua New Guinea; **KSP**: Koleksi Serangga Papua, Jayapura, Indonesia (see Gassó Miracle, 2017); **MCZ**: Pierce Lab, Museum of Comparative Zoology, Harvard University, USA; **MFBC**: Michael F. Braby private collection, Canberra, Australia (now largely incorporated into ANIC); **MfN**: Museum für Naturkunde, Berlin, Germany (formerly Zoologisches Museum der Humboldt-Universität); **NMW**: Naturhistorisches Museum Wien, Vienna, Austria (The Natural History Museum Vienna).

TAXONOMY

Pseudogyris gen. nov.

(Figs. 1-45)

http://zoobank.org/urn:lsid:zoobank.org:act:4C727BD8-3594-4669-8436-AE109F743B43

Type species. *Ogyris meeki* Rothschild, 1900 (designated here)

Diagnosis: Adults of *Pseudogyris* differ structurally from *Ogyris* in several fundamental ways. Although the wing venation (Figs. 23, 24) is similar to *Ogyris* (see Waterhouse & Lyell, 1914, Fig. X, p. 115), the forewing of male *Pseudogyris* differs in shape, being more strongly arched with the apex produced and termen distinctly concave. The hindwing of *Pseudogyris* has a prominent tail, which is long (ca. 6 mm) and spatulate at the end of vein CuA_1, whereas in *Ogyris* tails are absent. Although in three species of *Ogyris* (*O. genoveva*, *O. zosine* and *O. aenone*) there is a pronounced tornal projection at the end of vein CuA_2 and in two of these species (*O. genoveva* and *O. zosine*) there is an additional conspicuous projection at the end of vein M_3, in *Pseudogyris* there is no broad tornal projection but, rather, a small, narrow projection at the end of vein CuA_2, as well as a series of three smaller projections at the ends of veins M_1 to M_3. In contrast, in most species of *Ogyris* there is a series of five small projections from veins M_1 to CuA_2, giving the termen of the hindwing a dentate pattern. Also, the wings are larger than *Ogyris*: in male *Pseudogyris*, the forewing length (from base to apex) ranges from 30.3–36.5 mm (mean = 32.7 mm, n = 15), whereas in the four largest species of *Ogyris* (*O. genoveva*, *O. zosine*, *O. idmo* and *O. halmaturia*) the male forewing never exceeds 30 mm in length. The body (thorax and abdomen) of *Pseudogyris* is not as large or as robust relative to the size of the wings compared with *Ogyris*.

In addition, *Pseudogyris* differs from *Ogyris* by the following six wing color pattern characters. (1) The upperside of the wings in the male (Figs. 2, 5, 11, 13, 17, 19) have a different color pattern. In *Pseudogyris*, the color is uniformly dark brown with a deep purple suffusion, whereas in *Ogyris* the color is brighter purple, purplish-bronze, or metallic pale blue. (2) The upperside of the wings in the female (Figs. 8, 15, 21) have a different color pattern. In *Pseudogyris*, the ground color is bright orange, with the forewing possessing a broad black transverse band that extends from the base through the discal cell to the broad black termen with which it connects between veins M_2 and M_3, whereas the basal and central areas in females of most species of *Ogyris* are bright iridescent blue or purple. The inner edge of the black terminal band on the forewing in *Pseudogyris* is dentate, extending proximally along veins CuA_1 and CuA_2, whereas in *Ogyris* it is straight or evenly curved. In *Ogyris*, pronounced sexual dimorphism in which the female lacks iridescence scales occurs only in two species (*O. abrota* and *O. ianthis*), but these species do not have the broad black transverse band on the forewing that effectively divides the orange or yellow area into two separate patches, a pattern element which is unique to *Pseudogyris*. (3) The underside of the forewing in both sexes (Figs. 3, 6, 9, 12, 14, 16, 18, 20, 22) has a different color pattern. In *Pseudogyris*, there is


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3


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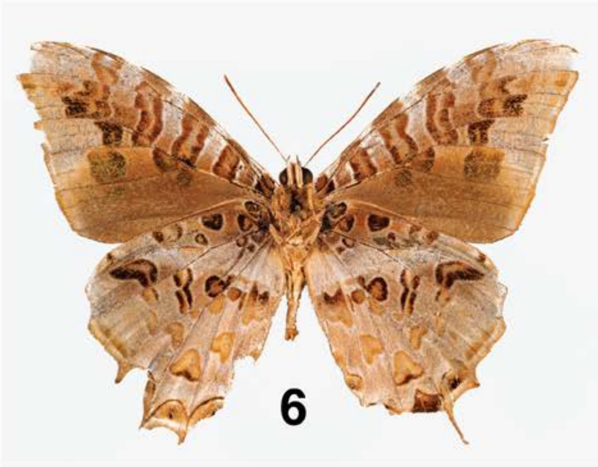
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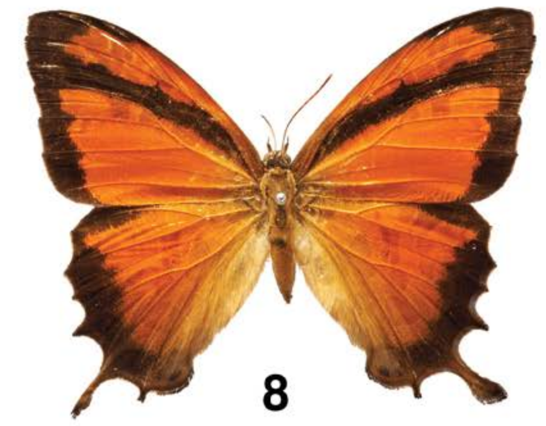
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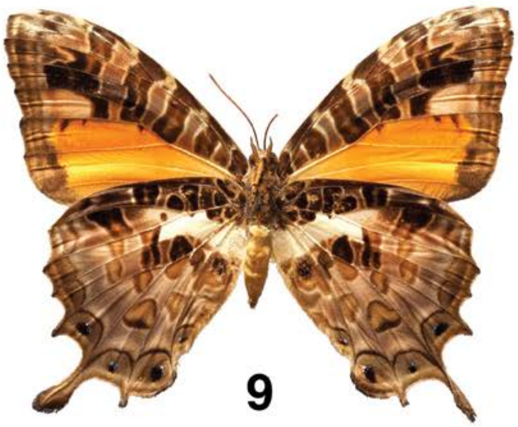
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Milne Bay,
Brit. N. G.,
II. 99.
(A. S. Meek).

Type

Ogyris
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4


Coll.
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10

Figures 2-10. Type material of *Pseudogyris meeki* comb. nov.: (2-4) lectotype male of *Ogyris meeki*, showing upperside, underside and labels (NHMUK), © The Trustees of the Natural History Museum London; (5-7) paralectotype male of *Ogyris meeki*, showing upperside, underside and labels (MfN), © Museum für Naturkunde Berlin; (8-10) holotype female of *Ogyris aurantiaca*, showing upperside, underside and labels (NMW), © H. Bruckner photo collection. Scale bar = 10 mm.

Figures 11-16. Adults of *Pseudogyris meeki* comb. nov., showing: (11, 12) male upper- and underside, Yahukimo, Papua (AYC); (13, 14) male upper- and underside, Yahukimo, Papua (CJMC); (15, 16) female upper- and underside, Timika, Papua (AYC). Scale bar = 10 mm.

a basal spot followed by a series of three conspicuous broad brown bars in the discal cell, followed by a broad but variable postmedian band. The cell bars occur from the subbasal area to the discocellulars, and each bar extends from the costa to the cubital vein. The bars form a complex pattern, with each bar comprising a paler brown band or line broadly edged with darker chocolate brown and then narrowly edged with white or grey. In contrast, in *Ogyris* the basal spot is absent or reduced

Figures 17-22. Adults of *Pseudogyris brandti* sp. nov., showing: (17, 18) holotype male upper- and underside, Torricelli Mountains, Mokai, Papua New Guinea (ANIC); (19, 20) paratype male upper- and underside, Sorong, Doberai Peninsula, West Papua (AYC); (21, 22) paratype female upper- and underside, Avona, Kaimana, West Papua (AYC). Scale bar = 10 mm.

to a minute dot, and the cell bars are narrower, dark brown or black and usually edged with iridescent blue, with the two outer bars sometimes enclosing a narrow dark blue line. Moreover, the bars in *Ogyris* are shorter in length, extending between the radial and cubital veins and do not reach the costa. (4) The underside of the hind wing in both sexes (Figs. 3, 6, 9, 12, 14, 16, 18, 20, 22) has a different color pattern. In *Pseudogyris*, there is a series of variable but conspicuous discrete brown spots and markings which are edged with dark brown or black and then narrowly with grey, somewhat similar to the pattern of *Arhopala antharita* Grose-Smith, 1894, whereas in *Ogyris* the pattern is far more complex, with the markings typically comprising a mosaic of irregularly shaped brown bands, edged narrowly with black, from the subbasal area to the postmedian area. In the *O. aenone* species-group, the markings are more discrete but faintly developed and less well defined. (5) The underside of the hindwing of *Pseudogyris* has a broad transverse submedian band, a pattern element which is absent in *Ogyris*. In *Pseudogyris*, the band is grey (male) or cream (female) and it extends from vein Rs through the discal cell to the dorsum. (6) The underside of the hindwing of *Pseudogyris* has a series of terminal lunules or crescent-shaped marks, with three of those between veins M_3 and 1A+2A, each enclosing a conspicuous black spot each of which has a patch of iridescent bluish-white scales; the largest of these spots comprises the tornal lobe. There is also a similar but smaller spot along the dorsum between veins 1A+2A and 3A. In *Ogyris*, these terminal and tornal marks and spots are absent.

The male genitalia of *Pseudogyris* (Figs. 30, 31, 39–44) are similar to those of *Ogyris*, but the valvae are more deeply divided or excavated apically into two long processes. In *Ogyris* (Figs. 33–38), the processes, when present, are more asymmetrical, with the lower process generally much shorter and the apex rounded posteriorly. The valvae in *Ogyris* are variable in shape: the apical indentation and bifurcated processes are well developed in *O. abrota* (Fig. 33), the *O. aenone* (Fig. 34) and *O. genoveva* (Fig 37) species-groups, less pronounced in *O. amaryllis* (Fig. 35), and poorly developed or absent in the *O. idmo* species-group (Fig. 38). In the *O. olane* species-group (Fig. 36), the valvae are long and narrow with the lower process residual or absent.

The female genitalia of *Pseudogyris* (Fig. 32) are similar to those of *Ogyris* with respect to the form of the sterigma of the ostium bursae, which comprises a simple sclerotized column. However, in *Pseudogyris*, the corpus bursae is exceptionally enlarged and elongated with the posterior half sclerotized, whereas in *Ogyris* the corpus bursae comprises a membranous rounded or oval-shaped sack that is not sclerotized. The corpus bursae is comparatively short in the *O. idmo* species-group; in *O. abrota*, there is a pair of weakly sclerotized signa located posteriorly. The shape of the ductus bursae is variable: in *Pseudogyris*, *Ogyris abrota*, *O. aenone* species-group and *O. olane* species-group it is relatively long and narrow and usually weakly sclerotized, in *O. amaryllis* it is short and narrow and weakly sclerotized, but in the *O. genoveva* and *O. idmo* species-groups it is relatively short and broad. In *Pseudogyris*, the ductus seminalis is located approximately midway between the ostium bursae and corpus bursae, whereas in *Ogyris* it is usually located near the anterior end of the ductus bursae close to the corpus bursae.

The morphology of the wing venation (Figs. 23, 24), antenna (Fig. 25), labial palpus (Fig. 26) and legs (Figs. 27-29) is similar to *Ogyris*. The number of segments of the flagellum in *Pseudogyris* ranges from 52-55, whereas in *Ogyris* it varies from 38 (*O. idmo* species-group - Field, 1999), 46 (*O. abrota*, *O. amaryllis*, *O. olane* species-group) to 56 (*O. genoveva* species-group).

Variation: The underside pattern of *Pseudogyris* varies among males, particularly the ground color, the form and extent of the brown markings and spots, and the shape of the brown postmedian band on the forewing. Available data suggest the underside pattern varies geographically and partitions into two distinct groups: (1) areas to the south of the Central Cordillera or Central Highlands of mainland New Guinea; and (2) areas to the north of the Central Cordillera. Investigation of these pattern differences indicates that there are in fact two species in the complex, with the latter group warranting specific status and a new name (see below).

Etymology: The genus-group name *Pseudogyris* is derived from the Greek word pseudos or pseudes, which means false, and refers to the fact that *Pseudogyris* is similar and closely related to, but otherwise taxonomically distinct from, *Ogyris*.

Distribution: *Pseudogyris* was previously known only from mainland New Guinea (Papua Province of Indonesia, and Papua New Guinea). However, over the past 20 years material has been collected from West Papua (AYC and MFBC) and New Ireland of Papua New Guinea (CJMC). Thus, spatial data of the known 21 specimens (16 ♂, 5 ♀) indicates that the geographical distribution of *Pseudogyris* (Fig. 45) extends from West Papua (including Sorong, Kaimana and Wasior), through Papua (including Timika, Lower Oetakwa River, Yahukimo and Jayapura) to Papua New Guinea (mainland PNG and New Ireland). In Papua New Guinea, it has been collected on the mainland from the Prince Alexander Range (CJMC), Torricelli Mountains (ANIC), Amahop near Maprik, Rawlinson Mountains Huon Peninsula, Mamai plantation near Port Glasgow (Parsons, 1998), and Milne Bay (Rothschild, 1900). It may also occur in New Britain, which lies between the New Guinea mainland and New Ireland. Most specimens appear to have been collected from lowland areas (<500 m) dominated by tropical forest; however, the altitudinal range is uncertain because the labels of most specimens do not report altitude. The highest recorded altitudes on the mainland include two males collected from the West Sepik Province: at approximately 650 m in the Prince Alexander Range (CJMC), and at 760 m (2,500 ft) from Mokai in the Torricelli Mountains by WW Brandt (ANIC). In central New Ireland, a male was collected in lower montane forest at approximately 1,100 m in the Schleinitz Mountains (CJMC). Thus, available spatial data suggests *Pseudogyris* is absent from the higher elevated mid-montane forest (1,600-2,100 m). As far as is known it does not occur together with *Ogyris zosine faciepicta* Strand, 1911, which is known from two males from the East Sepik and Northern Provinces (Parsons, 1998). *Ogyris zosine faciepicta* is the only taxon of *Ogyris* known to occur on mainland New Guinea.

Biology: Little is known of the biology of *Pseudogyris*. Adults have been collected in each month from September to April, as well as in June. Two males captured by one of us (CJM) were flying rapidly in the lower canopy approximately 6-8 m above the ground during the afternoon.

Pseudogyris meeki (Rothschild, 1900) comb. nov.

(Figs. 1, 2-10, 11-16, 39-41, 45)

Ogyris meeki Rothschild, 1900: p. 274, pl. V fig 1. [genus *Ogyris* Westwood, 1851]

Ogyris meeki Rothschild. - Bethune-Baker (1905), pp. 271, 278; Rebel (1912), pp. 219-220; Meek (1913), p. 238; Seitz (1926), p. 940, fig. 161g; D'Abrera (1971), p. 321; D'Abrera (1990), p. 321; Common and Waterhouse (1972), p. 336; Common and Waterhouse (1981), p. 471; Parsons (1998), pp. 395-396, pl. 60 Figs. 1633-1635. [genus *Ogyris* Westwood, 1851]

Ogyris meeki (Rothschild, 1900). - Braby (2000), p. 693; Tennent (2006), pp. 39, 161. [genus *Ogyris* Angas, 1947]

Ogyris aurantiaca Rebel, 1912: pp. 219-221, Figs. 2, 3. [genus *Ogyris* Westwood, 1851]

Ogyris aurantiaca Rebel. - Seitz (1926), p. 941; D'Abrera (1971), p. 321; D'Abrera (1990), p. 321; Parsons (1998), p. 395. [genus *Ogyris* Westwood, 1851]

Material examined:

Lectotype: ♂ **PAPUA NEW GUINEA:** "Milne Bay, Brit. N. G., II. 99, (A. S. Meek).", "Ogyris meeki Type! R., N. z. 00.", "Type", "NHMUK 010923731" (NHMUK).

Paralectotype: ♂ **PAPUA NEW GUINEA:** "Milne Bay, südl. Nue Guinea, 1896-7, Eichh.", "Coll. Staudinger", "*Orgyris* [sic], sec. Jordan n. sp.", "http://coll.mfn-berlin.de/u/ca880d" (MfN).

Other material: 6♂, 3♀. **INDONESIA:** 1 ♂, 1 ♀ "Lower Oetakwa R., Dutch South N.G., 17.-28. Nov. 1910., (A.S. Meek)", "Specimen photographed by B. D'Abrera, 1970" (NHMUK); 1 ♀ "Timika, Irian Jaya, INDONESIA, NOV. 2001", "Genitalia No. MFB-125, P. meeki ♀" (AYC); 1 ♂ "Timika, Irian Jaya, INDONESIA, MAR. 2003" (AYC); 1 ♂ "Timika, Irian Jaya, INDONESIA, NOV. 2018" (AYC); 1 ♂ "Yahukimo, central Irian Jaya, INDONESIA, JAN. 2013", "Genitalia No. MFB-136, P. meeki ♂" (AYC); 1 ♂ "INDONESIA, Yahukimo Regency, JAN, 2013", "CJM-21-3225" [DNA leg voucher in MCZ] (CJMC). **PAPUA NEW GUINEA:** 1 ♀ "Brit. N. guinea", "Phot. Orig.", "Ogyris aurantiaca Rbl, Type" (NMW) [holotype of *Ogyris aurantiaca*]; 1 ♂ "Mamai Estate, near Amazon Bay, CeP" (KONE) as illustrated in Parsons (1998).

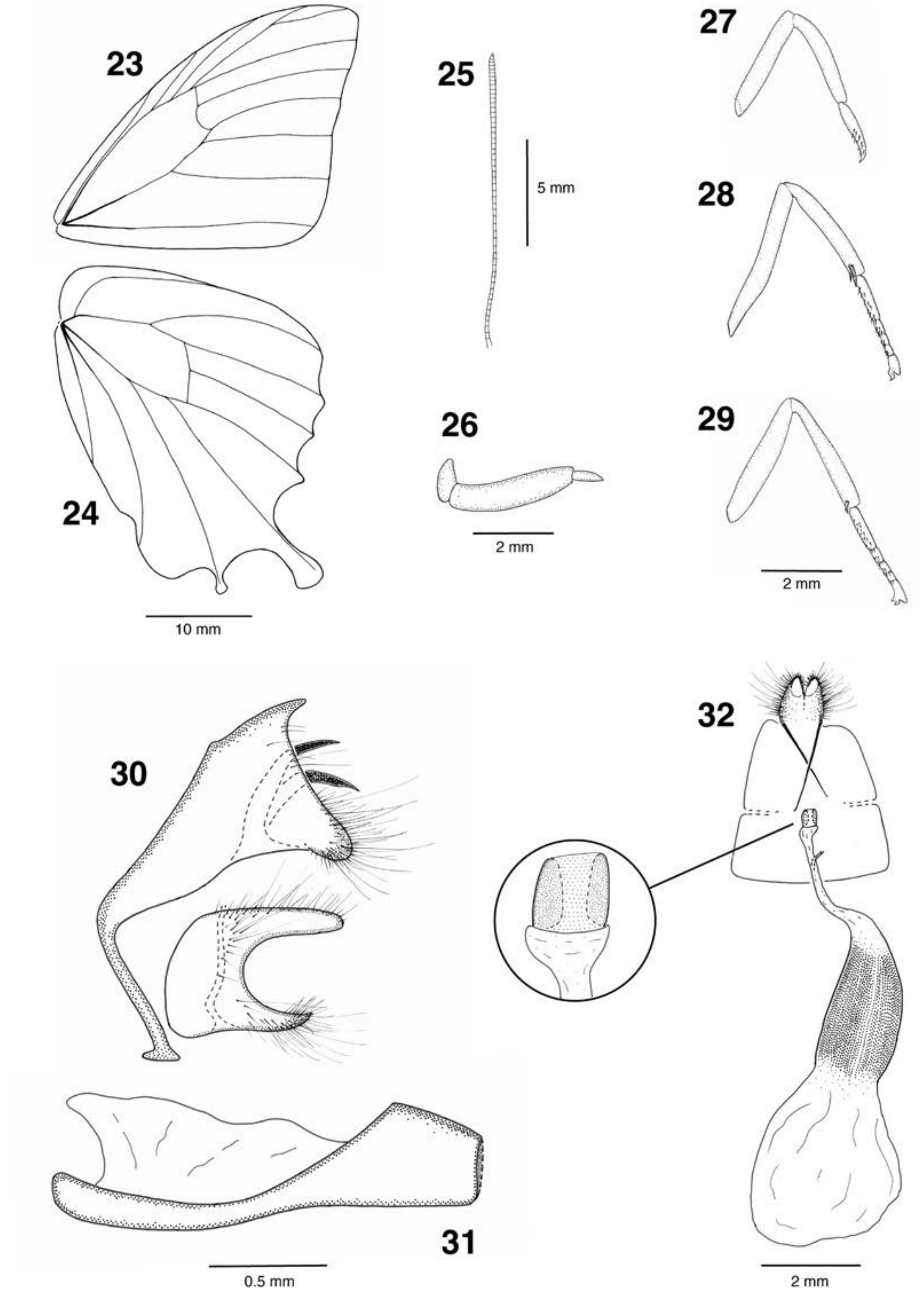
Diagnosis: *Pseudogyris meeki* males (Figs. 11-14), compared with *P. brandti* sp. nov. males, have the underside ground color darker purple or purplish-brown, the underside markings larger and more distinct (i.e., darker brown with pronounced white edges), a broader transverse submedian band on the hindwing, and the postmedian band on the forewing extended distally towards the termen between veins M_1 and M_3. The lower section of the forewing postmedian band between veins M_1 and CuA_1 is narrower and about half the width of the section between veins CuA_1 and CuA_2. Also, the double postmedian mark between veins M_3 and Rs on the underside of the hindwing has the outer edge distinctly curved (concave) in *P. meeki* males, whereas it is relatively straight in *P. brandti* sp. nov. males. In addition, adult males appear to be smaller in size (forewing length: 30.3-32.5 mm; mean = 31.4 mm, *n* = 8). The male genitalia of *P. meeki* (Figs. 39-41) differ fundamentally from those of *P. brandti* sp. nov. (Figs. 42-44) in the following respects: the apical processes of the valvae (in lateral view) are more widely divergent from one another, with the lower (ventral) process rounded apically and the upper (dorsal) process of uneven width; the uncus (in posterior view) is obtuse rather than rounded; the uncus lobes (in lateral view) are shorter and narrower and (in posterior view) relatively straight; the brachia are broader throughout their length and enlarged near the base; and the anterior margin of the tegumen (in dorsal view) is sinuate without the middorsal projection. Females of the two species are difficult to distinguish, but in *P. meeki* the cream transverse submedian band on the underside of the hindwing is slightly broader with a relatively straight posterior margin.

Remarks: Rothschild (1900) originally illustrated (Fig. 1) and described *Ogyris meeki* Rothschild, 1900 based on two syntype males from Milne Bay, Papua New Guinea, one of which was collected by A. S. Meek, but he did not designate a holotype. Of the two syntypes, one is housed in NHMUK (Figs. 2-4) and the other in the MfN Staudinger collection (Figs. 5-7). Parsons (1998) referred to the syntype in NHMUK as the 'holotype'. We interpret Parsons' (1998) incorrect reference to a holotype as a lectotype designation according to Article 74 of the ICZN (1999). It therefore follows that the second specimen in MfN automatically becomes a paralectotype.

Association of the sexes of *P. meeki* was first hypothesized by Meek (1913) and then later by D'Abrera (1971) and Parsons (1998), but to date has not been confirmed by captive breeding of the immature stages or by field observations on adult courtship or mating. However, we consider that the male and female illustrated here from Papua to belong to the same species given their similarities in size, underside pattern and the shape of the hindwing. At the time of description of *P. meeki* the female was unknown (Bethune-Baker, 1905; Seitz, 1926). Meek (1913, p. 97) collected a female some years later, noting that "I did not get a female specimen until the year 1910." Meek's female (as well as a second male) was collected from the Lower Oetakwa River, Papua, and is housed in NHMUK; it was subsequently illustrated by both D'Abrera (1971; 1990) and Parsons (1998).

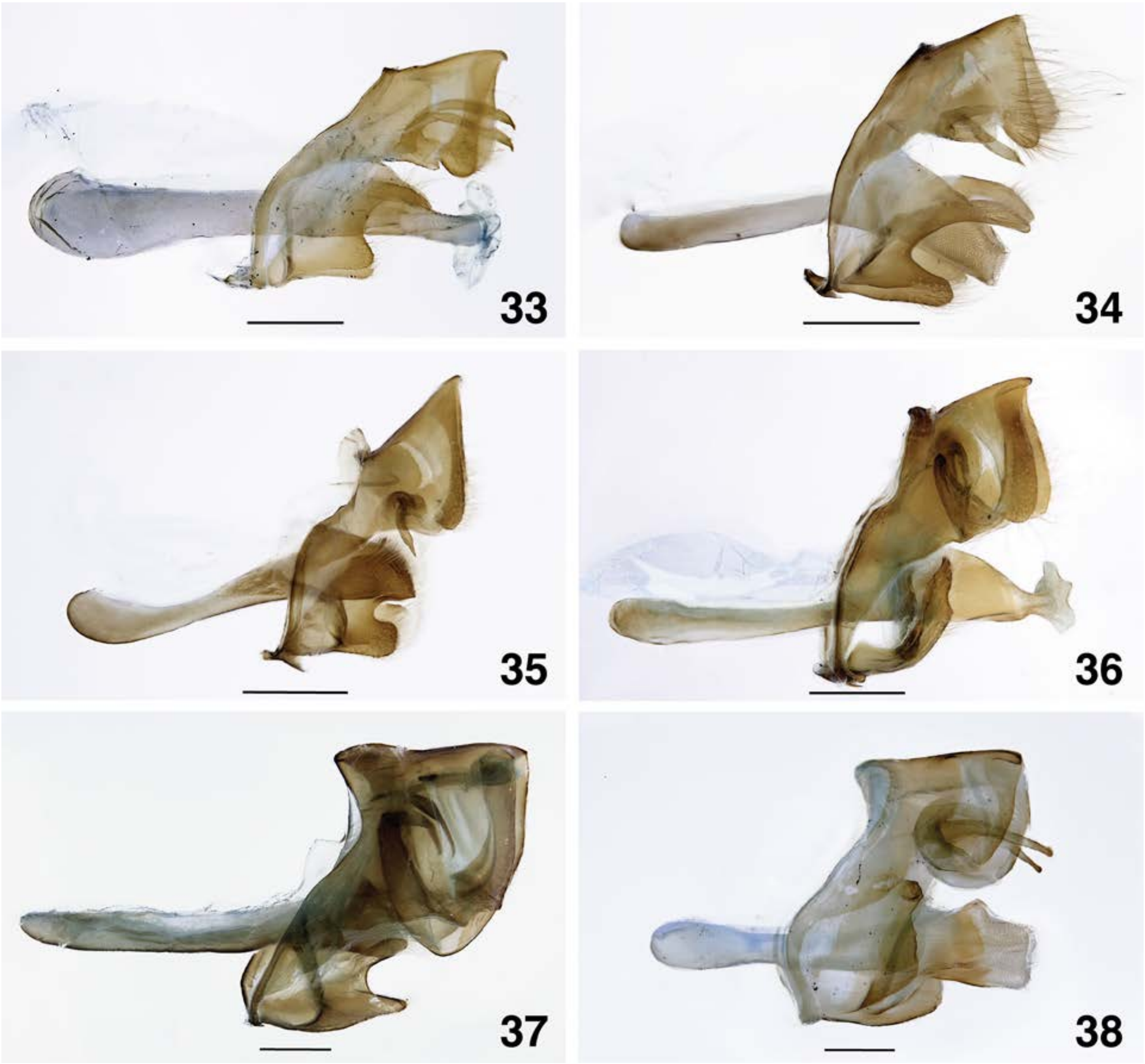
Hans Rebel (1861-1940) described and illustrated the species *Ogyris aurantiaca* Rebel, 1912 based on a single female from an unspecified location in southern Papua New Guinea (given as 'British New Guinea') (Rebel, 1912). Parsons (1998) considered the holotype female of *Ogyris aurantiaca* (Rebel, 1912) to be the opposite sex of the lectotype male of *Pseudogyris meeki* (Rothschild, 1900); he therefore synonymized *O. aurantiaca* as an objective junior synonym of *P. meeki*. Parsons (1998) stated that the whereabouts of the holotype female of *O. aurantiaca* is not known, but we have traced it in NMW (Figs. 8-10). Since *P. meeki* is restricted to areas south of the Central Cordillera and the far east of Papua New Guinea (see below), and British New Guinea refers to this same area of Papua New Guinea, it can be safely assumed that Rebel's type specimen came from within the distribution of *P. meeki*. Moreover, the *O. aurantiaca* holotype female agrees with two females of *P. meeki* from Papua south of the Central Cordillera, bearing a prominent, broad cream transverse submedian band on the underside of the hindwing. Therefore, we agree with Parsons in that *O. aurantiaca* is indeed synonymous with *P. meeki*.

The exact locality from which the *O. aurantiaca* holotype female was obtained, and the person responsible for the collection, may never been known. Rebel was an Austrian entomologist who specialized in Lepidoptera (Hermkens, 2013). He was keeper of the Lepidoptera collection of the Naturhistorisches Museum in Vienna, a post he held from 1897



Figures 23-32. Adult morphology of *Pseudogyris brandti* sp. nov., showing: (23, 24) wing venation of fore- and hindwings; (25) antenna; (26) labial palpus; (27-29) male fore-, mid- and hindlegs, (30, 31) male genitalia, lateral view with phallus removed, and phallus, lateral view; (32) *P. meeki* comb. nov. female genitalia, ventral view.

to 1932. He directed the Department of Zoology in 1923 and was the museum's Director General in 1925. Rebel secured vast acquisitions for the museum, and this included four accessions from New Guinea, between 1906 and 1912, though information for two of the purchases is unknown. The annual reports of the museum from 1906 to 1912 indicate that Karl Rechinger (botanist) and Rudolf Pöch (doctor, anthropologist and ethnologist) donated specimens they collected from New Guinea, in 1906 and 1911, respectively (Sabine Gaal-Haszler, pers. comm. 2021). It appears that Rechinger collected in German New Guinea, whereas Pöch spent nearly two years (1905-1906) in New Guinea, including three months in British New Guinea where he visited areas just north of Milne Bay (Goodenough and Collingwood Bays). In addition to anthropological objects, Pöch gathered geological data as well as biological specimens, such as mammals, birds, shells and reptiles (Hermkens, 2013). Thus, it is possible that the *O. aurantiaca* type was collected by Pöch in 1905/1906, possibly somewhere near Milne Bay, and



Figures 33-38. Male genitalia of *Ogyris*, lateral view: (33) *O. abrota*; (34) *O. aenone*; (35) *O. amaryllis*; (36) *O. olane*; (37) *O. zosine*; (38) *O. idmo.* Scale bars = 0.5 mm.

deposited by Pöch in NMW when he donated his collection in 1911; the species was subsequently described by Rebel in 1912.

Distribution: *Pseudogyris meeki* occurs on mainland New Guinea where it is known from lowland areas south of the Central Cordillera (Fig. 45). It has been recorded from Milne Bay, PNG (type locality) (Rothschild, 1900), Mamai plantation near Port Glasgow, PNG (Parsons, 1998), Lower Oetakwa River (NHMUK), Timika and Yahukimo (AYC, CJMC), Papua, Indonesia. Two females from Timika (AYC) and the Lower Oetakwa River, Papua (illustrated in D'Abrera, 1971; 1990; Parsons, 1998) are considered to belong here. Adults have been collected in the months of November and from January to March.

***Pseudogyris brandti* sp. nov.**

(Figs. 17-22, 23-31, 42-44, 45)

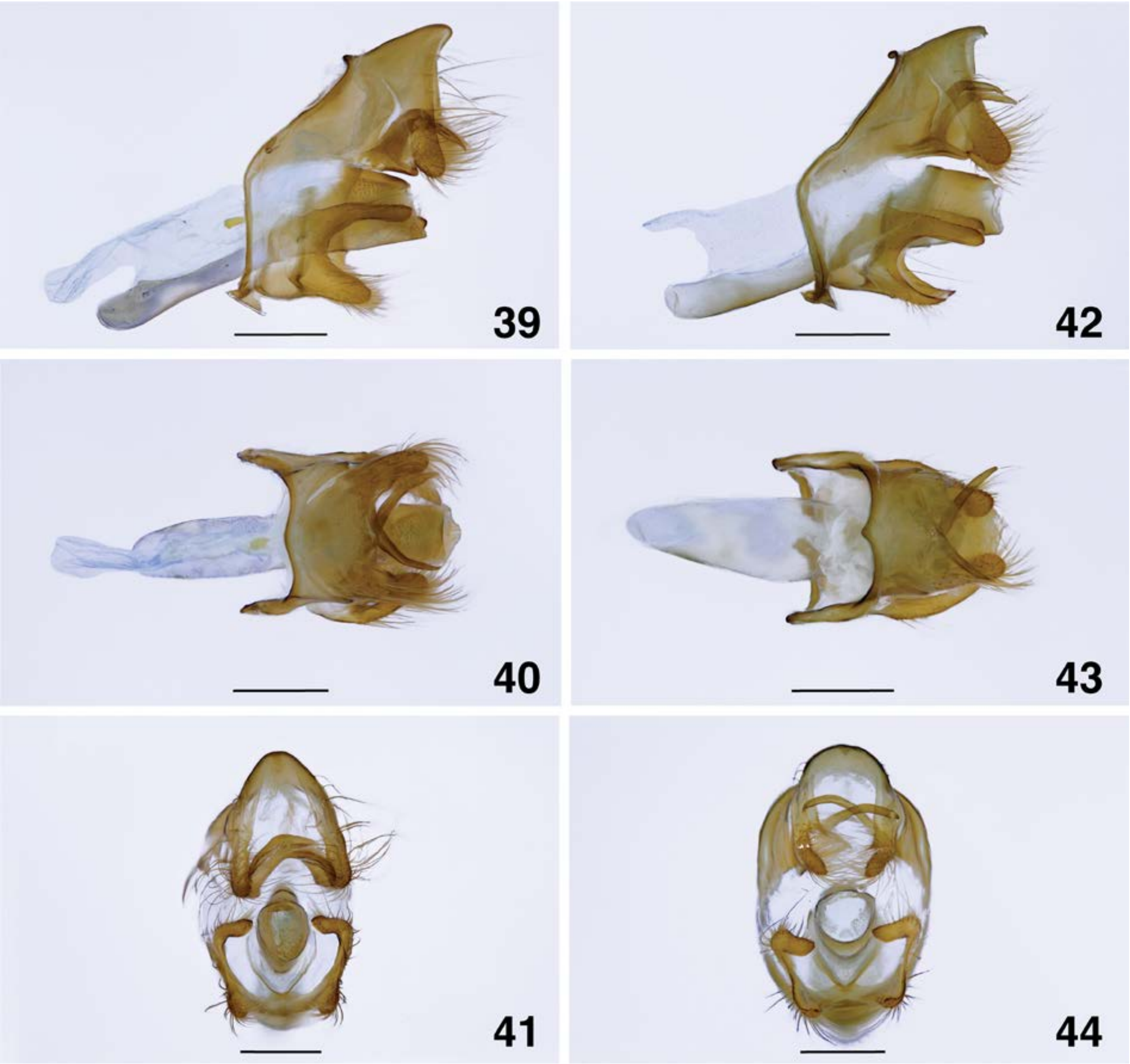
http://zoobank.org/urn:lsid:zoobank.org:act:436E93CB-8F3E-4207-91C4-585C20CC6DFE

Ogyris meeki Rothschild. - D'Abrera (1971), p. 321; D'Abrera (1990), p. 321; Parsons (1998), p. 395, pl. 60, Figs. 1628-1632. [genus *Ogyris* Westwood, 1851]

Material examined:

Holotype: ♂ **PAPUA NEW GUINEA:** "NEW GUINEA, Torricelli Mountains, Mokai, 2500 ft., 8 Dec. 1958-23 Jan. 1959, W. W. Brandt" (ANIC).

Paratypes: 5♂, 2♀. **INDONESIA:** 1 ♂ "Sorong, W-Irian, Nov. 1999", "Genitalia No. MFB-120, P. brandti ♂", "MFB-13-P039" [DNA leg voucher in MCZ], "M.F. Braby Collection, Donated ANIC 2020" (MFBC); 1 ♂ "Sorong, Doberai Pen., Irian Jaya, INDONESIA, Apr. 2005" (AYC); 1 ♀ "Avona, Kaimana. Etna, INDONESIA, Sep. 2006 (AYC); 1 ♀ "Wasior, Wondiwoi Mts., Wandammen Pen, Irian Jaya, INDONESIA, Dec. 2013" (AYC). **PAPUA NEW GUINEA:** 1 ♂ "Rawlinson Mts, inland Huon Gulf, (Keysser)", "Specimen



Figures 39-44. Male genitalia of *Pseudogyris*: (39-41) *P. meeki* comb. nov., showing lateral, dorsal and posterior views, Yahukimo, Papua (AYC); (42-44) *P. brandti* sp. nov., showing lateral, dorsal and posterior views, Sorong, West Papua (MFBC). Scale bars = 0.5 mm.

photographed by B. D'Abrera, 1970", "NHMUK 014047073" (NHMUK); 1 ♂ "PAPUA NEW GUINEA, Schleinitz Mts, New Ireland Province, ca. 1100m, 3.33 S, 151.94 E, Oct, 2005, C.J. Müller", "CJM-21-3223" [DNA leg voucher (RE-05-D041) in MCZ] (CJMC); 1 ♂ "PAPUA NEW GUINEA, Prince Alexander Range, West Sepik Province, ca. 650m, 3.52 S, 142.97 E, Jun. 2012, C.J. Müller", "CJM-21-3224" [DNA leg voucher in MCZ] (CJMC).

Other material: 2 ♂. **INDONESIA:** 1 ♂ "Jayapura, Papua" (KSP) as illustrated in Schröder (2021). **PAPUA NEW GUINEA:** 1 ♂ "Amahop, near Maprik, ESP" (KONE) as illustrated in Parsons (1998).

Diagnosis: *Pseudogyris brandti* males (Figs. 17-20), compared with *P. meeki* males, have the underside ground color paler lilac or lilac-grey with the underside markings smaller and less contrasted, a narrower transverse submedian band on the hindwing, and the postmedian band on the forewing of approximately even width but frequently displaced proximally between veins M_3 and CuA_2. This displaced, lower section of the forewing postmedian band is of even width, whereas in *P. meeki* the section between veins CuA_1 and CuA_2 is about twice the width of the adjacent section between veins M_3 and CuA_1. Also, the double postmedian mark between veins M_1 and Rs on the underside of the hindwing has the outer edge relatively straight in *P. brandti* males, whereas it is distinctly curved (concave) in *P. meeki* males. In addition, adult males appear to be larger (forewing length: 32.7-36.5 mm; mean = 34.3 mm, *n* = 7). The male genitalia of *P. brandti* (Figs. 42-44) differ fundamentally from those of *P. meeki* (Figs. 39-41) in the following respects: the apical processes of the valvae (in lateral view) are parallel with one another, with the lower process terminating in a spine and the upper process of uniform width; the uncus (in posterior view) is evenly curved rather than obtuse; the uncus lobes (in lateral view) are longer and broader and (in posterior view) inwardly curved towards their apices; the brachia are narrower and more slender throughout their length; and the anterior margin of the tegumen (in dorsal view) has a middorsal projection. Females of the two species are difficult to distinguish, but in *P. brandti* the cream transverse

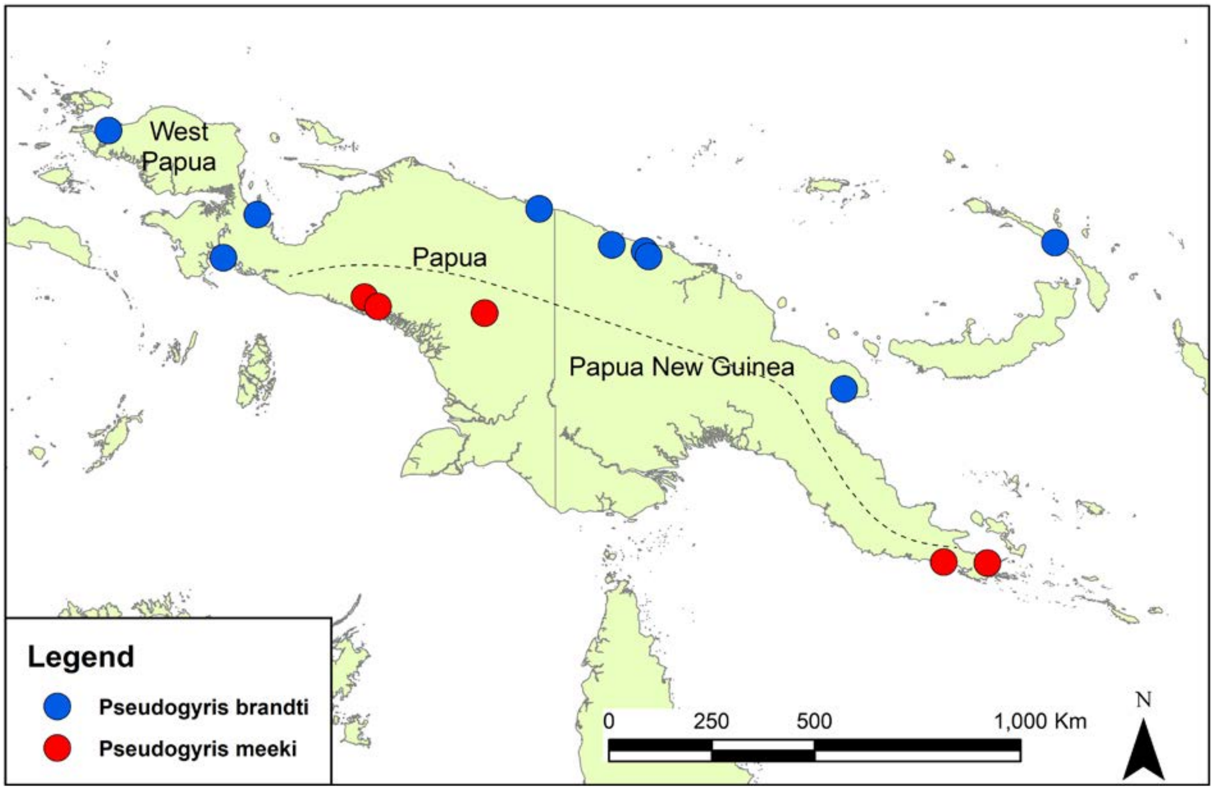


Figure 45. Distribution map of *Pseudogyris* and the geographical distribution of its two species *P. meeki* comb. nov. and *P. brandti* sp. nov. based on vouchered specimens in museum and private collections. Dashed line indicates approximate location of the Central Cordillera, a biogeographic barrier that divides the lowland areas of northern and southern mainland New Guinea.

submedian band on the underside of the hindwing is slightly narrower and constricted with the posterior margin concave.

Description:

Male: *Head*: eyes black; frons brown; labial palp clothed with brown piliform scales, a paler brown narrow mid-ventral line, third (apical) segment short and slender, second (middle) segment four times longer than third segment; antenna 14-15 mm long, flagellum with 52-55 segments (shaft 39-42, club 13-14), shaft gradually expands into club, shaft orange, club black tipped with orange. *Thorax*: dorsal surface black, ventral surface brown; legs brown; foreleg with tarsus fused into a single segment, terminating in a point; mid- and hindlegs each with a pair of tibial spurs. *Forewing*: length 36.5 mm (holotype); upperside uniformly dark brown with a deep purple suffusion (iridescent under white light), a narrow black terminal line, termen slightly concave; underside ground color lilac or lilac-grey, with posterior third of wing (below cubitus and CuA$_2$) brown, discal cell with a basal spot, followed by a series of three conspicuous broad purplish-brown subbasal, submedian and median bars extending from costa to cubital vein, each bar comprises a paler band broadly edged with darker purplish-brown and then narrowly with white or grey, a purplish-brown submedian spot between veins CuA$_2$ and 1A+2A below submedian bar, a purplish-brown median spot between veins CuA$_1$ and CuA$_2$ distal to submedian bar, median bar extends along discocellular veins into space between veins M$_3$ and CuA$_1$, a broad postmedian band from costa to vein CuA$_2$ often displaced proximally at vein M$_3$, pattern of postmedian band similar to discoceullar cell bars, a narrow purple subterminal line from veins M$_1$ to CuA$_2$, followed by a darker and broader terminal line from veins M$_1$ to just below CuA$_2$. *Hindwing*: upperside uniformly dark brown with a deep purple suffusion (iridescent under white light), a black terminal band that widens towards tornus, costa and dorsum paler brown, termen concave between veins with slight projections at end of veins Rs, M$_1$, M$_2$ and M$_3$, the largest of these projections on M$_3$, end of vein CuA$_1$ with a prominent spatulate tail, end of vein CuA$_2$ with a conspicuous projection, tornal lobe between veins CuA$_2$ and 1A+2A; underside ground color lilac or lilac-grey, a series of three subbasal spots, two or three submedian spots just below costa between veins Sc+R$_1$ and Rs, a broad grey transverse submedian band from vein Rs through discal cell to dorsum, a complex series of brown median and postmedian spots and markings frequently edged with dark brown or black, an irregular faint whitish subterminal line from veins Rs to 1A+2A, followed by a series of dark brown terminal lunules or crescent-shaped marks, those marks between veins M$_3$ and CuA$_1$, CuA$_1$ and CuA$_2$, CuA$_2$ and 1A+2A, and 1A+2A and 3A each enclose a brown area centered with a conspicuous black spot bearing a patch of iridescent bluish-white scales, the largest of these spots comprises the tornal lobe. *Abdomen*: dorsal surface black, ventral surface brown. *Genitalia*: vinculum (in lateral view) relatively straight but bent at an internal angle of ca. 135º approximately two-fifths along its length; saccus short; tegumen relatively large, broad and sclerotized; uncus evenly rounded (in posterior view) with a pair of lateral lobes, uncus lobes broad and long, extending beyond ventral surface of tegumen, and sclerotized with numerous setae; brachium (=gnathos) long and narrow, strongly curved, heavily sclerotized and terminating in a spine; valva deeply divided with a U-shaped indentation and bifurcated into two long apical sclerotized processes furnished with numerous setae, with upper (dorsal) process longer and of uniform width and inwardly curved, lower (ventral) process terminating in a spine; phallus (in lateral view) very broad posteriorly, coecum narrower beyond alula, cornutus absent.

Female: *Head*: similar to male; antenna 12-13 mm long, flagellum with 53 segments (shaft 39, club 14). *Thorax*: dorsal surface orange-brown, ventral surface brown; legs brown. *Forewing*: length 30.2-31.0 mm (*n* = 2); upperside orange, costa narrowly black, apex and termen broadly black with inner edge extending proximally along veins CuA$_1$ and CuA$_2$, a broad black curved transverse band extending from base through discal cell to termen between veins M$_2$ and M$_3$, termen slightly concave; underside ground color purplish-grey, with posterior third of wing (below cubitus and CuA$_1$) orange except for termen which is broadly brown, markings and pattern similar to male except spots and bands darker, postmedian band shorter (stops at vein CuA$_1$) with section between veins M$_1$ and M$_3$ broadly edged distally with dark purplish-brown, a broad whitish rectangular spot between veins M$_3$ and CuA$_1$ distal to postmedian band. *Hindwing*: upperside orange, costa and termen broadly black, dorsum paler orange, margin of wing similar shape to male but projections at the end of veins Rs, M$_1$, M$_2$ and M$_3$ more pronounced so that termen appears dentate; underside ground color purplish-grey, markings and pattern similar to male except spots and marks darker, broad transverse submedian band cream. *Abdomen*: dorsal surface orange-brown, ventral surface pale brown.

Remarks: This species has previously been confused with *P. meeki*. For example, a male specimen from the Rawlinson Mountains illustrated by D'Abrera (1971; 1990) and Parsons (1998) (plate 60, fig. 1632) and a further two males from Mokai and Amahop illustrated as *Ogyris meeki* by Parsons (1998) (plate 60, Figs. 1628-1631) are in fact *P. brandti*.

Etymology: The species-group name *brandti* is in honor of William Waldemar Brandt (1904-1982), who collected a fine specimen of this species, in 1958-59. Brandt spent many years (1949-1963) conducting field work throughout Papua New Guinea and he made a substantial contribution to knowledge of the entomology of the country, especially Lepidoptera (Upton, 1997).

Distribution: *Pseudogyris brandti* occurs on mainland New Guinea and New Ireland where it is restricted to lowland and lower montane areas (up to 1,100 m) north of the Central Cordillera (Fig. 45). It has been recorded from Sorong, West Papua (MFBC, AYC), Jayapura, Papua (KSP) (Schröder, 2021), and in Papua New Guinea from the Prince Alexander Range (CJMC), Mokai Torricelli Mountains (type locality) (ANIC) (also illustrated in Parsons, 1998), Amahop near Maprik (KONE) (illustrated in Parsons, 1998), the Rawlinson Mountains Huon Peninsula (NHMUK) (illustrated in D'Abrera, 1971; 1990; Parsons, 1998), and the Schleinitz Mountains in central New Ireland (CJMC). Two females from Avona, Kaimana and Wasior, Wondiwoi Mountains, Wandammen Peninsula, West Papua (AYC) are considered to belong here.

Adults have been collected in the months of June, from September to December and in April. The relatively long flight season suggests the species is multivoltine.

DISCUSSION

Two genera are now included in the tribe Ogyrini, which is endemic to the Australian region (Eliot, 1973). Morphology of the wing venation, labial palpus and male and female genitalia clearly place *Pseudogyris* in the Ogyrini. Although a phylogenetic hypothesis of all members of the tribe is required to determine their evolutionary relationships and confirm monophyly of *Ogyris*, the large number of unique phenotypic characters observed in the two sister species *meeki* and *brandti* (total of at least 14 characters - 5 morphological based on wing/body features, 6 wing color pattern elements, and 3 morphological based on genitalia) strongly suggests they fall outside the *Ogyris* lineage. The relationships of the Ogyrini are somewhat uncertain, but the tribe appears to be closely related to the *Lucia* section of the polyphyletic Luciini Waterhouse & Lyell, 1914 (Espeland *et al.*, 2018 and unpublished data). The *Lucia* section of the Luciini includes four genera: *Lucia* Swainson, 1833, *Paralucia* C. & R. Felder, 1860, *Pseudodipsas* Waterhouse & R.E. Turner, 1905 and *Acrodipsas* Sands, 1980 (Eliot, 1973; Sands, 1980). The likely phylogenetic hypothesis of genera of these two tribes is: ((*Lucia* + *Paralucia*) + (*Pseudodipsas* + *Acrodipsas*)) + (*Ogyris* + *Pseudogyris*).

Compared with *Ogyris*, character states unique to *Pseudogyris* include the large body size (forewing length); the elongated and almost falcate forewing of the male; the prominent spatulate tail on vein CuA_1 of the hindwing; the broad black transverse band on the forewing upperside of the female; the broad and long discal cell bars with filled (brown) color pattern on the forewing underside; the broad cream or grey transverse submedian band on the hindwing underside; the series of conspicuous discrete brown spots and markings on the hind wing underside; and the series of four terminal crescent-shaped marks enclosing a black spot overlaid with iridescent bluish-white scales between veins M_3 and 3A on the hindwing underside, with one of these marks and spots being particularly pronounced on the tornal lobe between veins CuA_2 and 1A+2A. These eight character-states are absent in the *Lucia* section of the Luciini and thus they may be considered synapomorphies for *Pseudogyris*. The polarity of the other characters that differentiate *Pseudogyris* from *Ogyris*, such as morphology of the genitalia, await further study. The single, conspicuous spatulate tail on the hindwing of *Pseudogyris* is most unusual and reminiscent of the tail of papilionids, such as *Graphium weiskei* (Ribbe, 1900), except it is located on vein CuA_1 instead of CuA_2. In the Theclinae and Polyommatinae, the tail, when present, is filamentous and always located on vein CuA_2 adjacent to the tornal lobe (Eliot, 1973; Ackery *et al.*, 1999), whereas in *Pseudogyris* the tail is of a different shape and on a different vein. In some thecline genera there is a second filamentous tail on vein 1A+2A or, very occasionally, on CuA_1, such as in the Neotropical Eumaeini (e.g., *Arcas* Swainson, 1832, *Evenus* Hübner, 1819, *Paiwarria* Kaye, 1904 and *Pseudolycaena* Wallengren, 1858). Pronounced sexual dimorphism in *Pseudogyris* is remarkable and, to some extent, parallels that observed in *Ogyris ianthis* but is even more striking.

Pseudogyris is considered to be polytypic, containing two allopatric species, *P. meeki* and *P. brandti*, hypothesized to have diverged vicariantly by the uplift of the Central Cordillera of mainland New Guinea during the Pliocene-Pleistocene (Toussaint *et al.*, 2014). As such, the genus adds to the growing number of cases of butterflies endemic to mainland New Guinea that have putative vicariant, sister taxa on either side of the Central Cordillera. Examples of species pairs which have allopatric, lowland distributions on the northern and southern sides of the Cordillera, respectively, include: *Ornithoptera paradisea* + *O. meridionalis*; *Chaetocneme critomedia* + *C. caristus*; *Parantica kirbyi* + *P. schenkii*; *Parthenos sylvia* + *P. tigrina*; *Mydosama durga* + *M. bazochii*; *Praetaxila satraps* + *P. albiplaga*; *Hypochrysops thesaurus* + *H. cleonides*; and *Hypochrysops heros* + *H. herdonius*.

Ogyris has radiated on the Australian continent (14 species are now recognized) where they mainly specialize on parasitic plants in the family Loranthaceae growing in dry, non-rainforest habitats (Braby, 2000). The larvae of one species (*O. otanes*) feeds on related Santalaceae (Burns & Angel, 1952; Williams *et al.*, 1992; Hart & Powell, 1997; Williams & Hay, 2001), but three species are myrmecophagous and specialize on ants (Pierce, 1995; Hunt *et al.*, 1998; Moore, 1999; Field, 1999; Douglas & Allen, 2002; Braby & Douglas, 2008; Schmidt *et al.*, 2014; Williams *et al.*, 2020). In addition, three species-groups of *Ogyris* have specific, obligate associations with ants: the *O. aenone* species-group with Dolichoderinae, and the *O. genoveva* and *O. idmo* species-groups with Formicinae (*Camponotus*) (Eastwood & Fraser, 1999). The remaining five species (*O. amaryllis*, *O. abrota* and the *O. olane* species-group) have non-specific, facultative associations with ants. In contrast, *Pseudogyris* is largely allopatric, containing two putative vicariant species restricted to tropical lowland rainforest and lower montane forest in mainland New Guinea and New Ireland, but the extent to which it associates with ants is not known. Limited diversification of the lineage implies *Pseudogyris* may not be associated with Loranthaceae, unlike the pierid genus *Delias* Hübner, 1819 which appears to have radiated explosively on aerial hemi-parasites in the Santalales (especially Loranthaceae and Viscaceae) in montane New Guinea (Braby, 2006; Braby & Pierce, 2007; Müller *et al.*, 2013). This lack of diversification, together with its relatively small spatial distribution and habitat association, suggests *Pseudogyris* may be a relict. An investigation into the historical biogeography and divergence times of these lineages in the context of the drying of Australia during the Tertiary would make a fascinating study. Espeland *et al.* (2018) estimated the stem group of the Ogyrini to have evolved in the Eocene, which is well before the major period of aridification of the Australian continent and concomitant contraction of the Gondwanan rainforests (White, 1994, 1998).

Further work on the life history, biology, and host plant specialization of *Pseudogyris* may provide additional evidence supporting the distinctiveness of this lineage. On recounting his adventures in New Guinea and the discovery of *P. meeki* at Milne Bay, Meek (1913, p. 98) reminisced that "I had taken… one male specimen of the large blue butterfly (*Orgyris* [sic] *meeki*) which pupates under the ground at the trunk of the food-plant (the tree on which the mistletoe lives)." However, given that the life history of *P. meeki* is unknown it is likely that Meek was referring more generally to the biology of the genus *Ogyris* rather than to the species *P. meeki* in particular. Before working in New Guinea, Meek had spent time as a cattleman with G. Barnard on the pastoral property at Coomooboolaroo Station (near Duaringa), QLD, in the 1890s (Tennent, 2021). George Barnard was the first naturalist to discover the life history of *Ogyris*, and his observations and descriptions of the immature stages of *O. genoveva* (and *O. zosine*, see Waterhouse, 1941), together with a beautifully colored plate illustrating the life histories of these two butterflies, was published by Miskin (1883). Thus, Meek would have been aware that the larvae of *Ogyris* feed on Loranthaceae and that those of *O. genoveva* and *O. zosine* often pupate beneath the surface of the ground at the base of the trunk of the host tree.

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Life history of the Philippine endemic butterfly *Faunis sappho* (Nymphalidae, Satyrinae, Amathusiini) on Bohol island, with the first record of a dipteran parasitoid (Tachinidae, Exoristinae, Eryciini) for the genus and a listing of hostplant families utilized by the tribe

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Abstract: The early stages of *Faunis sappho sappho* Semper, 1878 are described for the first time, including images of ova, all instars, and pupae, from livestock occurring in a private garden on Bohol island, Philippines. The numerous monocotyledon hostplants confirmed to be naturally used by this poorly understood butterfly are enumerated, and the first record of a parasitic fly for the genus is reported. References to the published immature stages and comparisons to final-instar larvae of the other eight species of *Faunis* are presented, plus a list of all known host genera for the tribe Amathusiini is detailed from the second author's personal database. Thus, this paper represents the most comprehensive account of the juvenile biology of any *Faunis* species as well as probably the Amathusiini.

Pagbubuod: Sa kauna-unahang pagkakataon, ang iba't ibang yugto ng life cycle ng paruparong *Faunis sappho sappho* Semper, 1878 ay nailarawan mula sa isang pribadong hardin sa isla ng Bohol sa Pilipinas. Kabilang sa mga naobserbahan at nakuhanan ng larawan ay ang itlog, lahat ng instar ng uod, at pupa. Ang ilan sa mga monocotyledon na halamang pagkain nitong hindi pa gaanong napag-aaralang species ng paruparo ay nakumpirma, at naitala rin sa unang pagkakataon ang isang parasitikong langaw para sa genus ng *Faunis*. Iprinesenta rin dito ang mga sanggunian na tumatalakay sa iba't ibang yugto ng life cycle ng paruparo at ang paghahambing sa huling instar ng uod ng walo pang species ng *Faunis*. Nakadetalye na rin ang listahan ng lahat ng kilalang genera ng halamang pagkain ng tribung Amathusiini mula sa personal na rekord ng ikalawang may-akda. Ang sulating ito ay naglalahad ng pinakakomprehensibong ulat ukol sa life cycle ng mga species ng *Faunis* maging na rin ng tribung Amathusiini.

Additional key words: Arecaceae, Asia, Asparagaceae, biogeography, *Drino*, Heliconiaceae, *Isosturmia*, Odonata, Pandanaceae

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INTRODUCTION

The genus *Faunis* Hübner, 1819 contains nine species, all of which occur only in southeastern Asia: *Faunis aerope* Leech, 1890; *Faunis canens* Hübner, 1826; *Faunis eumeus* Drury, 1773; *Faunis gracilis* Butler, 1867; *Faunis kirata* de Nicéville, 1891; *Faunis menado* Hewitson, 1863; *Faunis phaon* Erichson, 1834; *Faunis sappho* Semper, 1878; and *Faunis stomphax* Westwood, 1858 (Brower, 2009; Nakamura *et al.*, 2010; Savela, 2022). Two of these species, *F. phaon* and *F. sappho*, are restricted to the Philippines, with *F. stomphax* narrowly extending into Palawan from Borneo (Igarashi & Fukuda, 2000). Regarding the former two endemics, *F. phaon* is widely distributed across the country except Palawan Province (Aoki *et al.*, 1982), while *F. sappho* is known only from the East Visayan-Mindanao biogeographic/faunal region (*sensu* Vane-Wright, 1990). Treadaway & Schroeder (2012) record four subspecies for the Philippine Islands: nominate *F. s. sappho* on Bohol, the subject of this report; *Faunis sappho ameinokleia* Fruhstorfer, 1911, on Camiguin de Mindanao; *Faunis sappho dinagatensis* Aoki & Uémura, 1982, on Dinagat; and *Faunis sappho kleis* Semper, 1878, on Biliran, Camotes, Homonhon, Leyte, Panaon, Samar, and Siargao (Fig. 1).

The early stages of six species of *Faunis*, commonly called "fauns", have been published in color by such authors as Igarashi & Fukuda, 2000 (*F. menado* and *F. stomphax*); Lang, 2011 (*F. aerope*); Leong, 2011 (*F. canens*); Wolfe & Feurtado, 2021 (*F. phaon*); and Young *et al.*, 2007 (*F. eumeus*). Larval images of what are almost certainly *F. gracilis* from Malaysia and *F. kirata* from Borneo and Malaysia are in the possession of KVW thanks to like-minded colleagues and photographers, thus leaving *F. sappho* presented here as the last member of the genus to have its mature caterpillar illustrated. It should be noted that *F. sappho* has the most limited range of any *Faunis* (Fig. 1), which does not overlap (is allopatric with) that of *F. phaon*, the other endemic Philippine faun.

STUDY LOCATION AND METHODS

Faunis sappho was reared at Habitat Bohol Highland

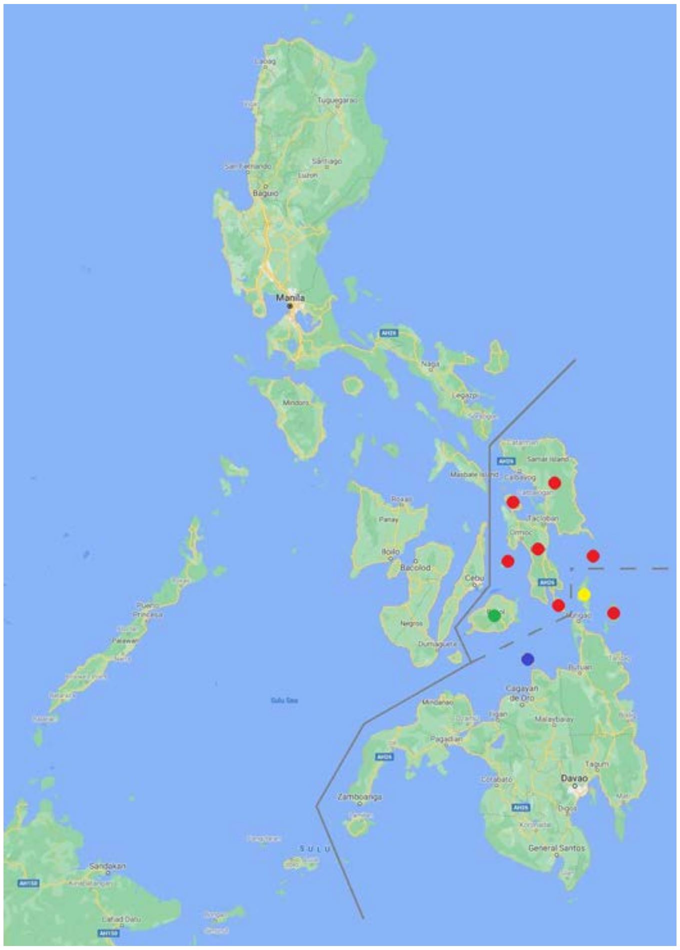

Figure 1. Consensus map ex Vane-Wright, 1990, Fig. 6 showing East Visayan-Mindanao faunal region and distribution of *Faunis sappho* subspecies (Treadaway & Schroeder, 2012): ssp. *sappho*, green; ssp. *ameinokleia*, blue; ssp. *dinagatensis*, yellow; and ssp. *kleis*, red. Note that *F. phaon*, the other Philippine endemic, occurs almost everywhere else excluding Palawan, where *F. stomphax* flies.

Nature Resort (9°41'52.0"N 124°06'01.0"E), a biodiversity and conservation project located in Bilar municipality, Bohol island-province, Philippines, where the species is common year-around in the private specialty garden. The climate type there is classified as tropical monsoon at an elevation of ~300 m. The decision to raise this secretive butterfly was made in October 2020 after many larvae were discovered on several different naturally growing local plants that had been recently moved from outside into large plastic pots and then placed in a big open-air restaurant. These transplanted caterpillars were not monitored due to seemingly large numbers of predatory ants, spiders, etc., but rather a controlled breeding program was developed that would document the immature biology of *F. sappho* utilizing the same species of plants that were now known to be eaten in the wild. Indeed, on one subsequent occasion, a female flew into the unenclosed restaurant and deposited eight eggs on a *Heliconia psittacorum* L.f., 1782 (Heliconiaceae), at 11:30 h. Thus, beginning in May 2021, four females were briefly confined inside a netted basket with five different live plants, viz *Areca catechu* L., 1753 (Arecaceae); *Bambusa multiplex* (Lour.) Raeusch. ex Schult. & Schult.f., 1830 (syn. *B. glaucescens*) (Poaceae, Bambusoideae) - unlike the others, merely a suspected possibility; *Dracaena aubryana* Brongn. ex É.Morren, 1860 (syn. *D. thalioides*) (Asparagaceae); *H. psittacorum*; and *Pandanus amaryllifolius* Roxb. ex Lindl., 1829 (Pandanaceae). Rearing was accomplished under ambient conditions (daily average 28° C, 77% RH) on open potted plants, sleeved potted plants, and with cut rain-cleansed fresh leaves replenished every day in carefully maintained, covered, translucent plastic containers. All resulting adult butterflies were promptly released unharmed back into the garden, with a few at first temporarily relaxed in a chiller for sexing purposes. Two voucher specimens, a male and female, were frozen and, along with a selection of shed larval head capsules, all of which are currently in the first author's possession, will be bequeathed to the National Museum of Natural History in Manila.

RESULTS AND DISCUSSION

With the exception of the tested *Bambusa*, which received no ova, seven groups consisting of 49 individual eggs were laid on the other four plants: *A. catechu*, 7 eggs in two groups of three and four; *D. aubryana*, 12 eggs in one group; *H. psittacorum*, 8 eggs in one group; and *P. amaryllifolius*, 22 eggs in three groups of six, seven, and nine. In the interest of efficiency, it was decided to focus the remaining breeding efforts on only *A. catechu*, *H. psittacorum*, and *P. amaryllifolius*, as the young caterpillars that resulted from the 12 eggs oviposited on *D. aubryana* had difficulty feeding on that plant's hard, thick leaves and soon died. Previous observations in the same location suggest that older *F. sappho* larvae, perhaps in their fourth instar, may fare better on this particular *Dracaena*, while an unidentified congener with softer leaves that is not part of the present study is readily eaten by all instars of *F. sappho*.

Besides the five plant species presented to females as described above, *F. sappho* juveniles seen in the outside garden during the end of 2020 and later were also recorded on four additional hostplants, namely a second and third palm, *Chamaedorea seifrizii* Burret, 1938 and *Heterospathe elata* Scheff., 1876 (both Arecaceae); a second *Dracaena*, the so-called lucky bamboo, *Dracaena braunii* Engl., 1892 (syn. *D. sanderiana*) (Asparagaceae); and a second lobster-claw, *Heliconia latispatha* Benth., 1846 (Heliconiaceae). Information from these earlier *in situ* wild eggs and/or caterpillars is included below in the descriptions of immatures. In all, at least eight different hosts from four monocot families are naturally used by *F. sappho* on Bohol, a hostplant trait common in the genus *Faunis*, while related genera in the tribe Amathusiini feed upon a wide variety of these and other monocots plus one gymnosperm (see addendum). Notably, of the aforesaid eight plants, only two of the palms, *A. catechu* and *H. elata*, are native to the Philippines, while the others are exotics from the Americas and western Africa or introduced from Indonesia (Pelser *et al.*, 2011; POWO, 2021).

Faunis sappho early stages

The following findings are a consolidation of the data obtained from livestock raised on open potted plants, sleeved potted plants, and cut fresh leaves inside covered, translucent

Figure 2. Ova of *Faunis sappho sappho* on *Heliconia psittacorum* (Heliconiaceae) with larval heads clearly visible one day before hatching.

Figure 3. Dorsal view of first instars of *Faunis sappho sappho* on *Pandanus amaryllifolius* (Pandanaceae) five days after emerging and showing considerable plant material within their translucent bodies.

Figure 4. Dorsal view of second instars of *Faunis sappho sappho* on *Areca catechu* (Arecaceae) three days after molting.

Figure 5. Dorsal view of third instars of *Faunis sappho sappho* on *Pandanus amaryllifolius* one day after molting.

Figure 6. Dorsal view of fourth instars of *Faunis sappho sappho* on *Heliconia psittacorum* four days after molting.

Figures 7-8. Dorsal [7, above] and lateral [8, below] views of fifth instar of *Faunis sappho sappho* on *Pandanus amaryllifolius* four days after molting and five days prior to becoming prepupal.

plastic containers. Body measurements were of resting caterpillars and did not include the caudal “tails” and head “horns”, which were progressively longer with each successive molt and thus could have easily added as much as five millimeters to their length by the final instar. All such measurements were made opportunistically and do not necessarily represent results from the same individuals.

Ova: Round, smooth, and creamy greenish blue when newly laid. Eggs are placed in closely spaced groups of 3-12 with a brownish latitudinal “ripening ring” - essentially the outline of the developing larval head within - appearing on the second day. Measured diameter 1.5 mm (n = 1), duration ~8 days (Fig. 2).

Eggs were deposited on either the underside or upperside of expanded hostplant leaves, the preferred location being along or

Figure 9. Lateral view of prepupa of *Faunis sappho sappho* ex *Pandanus amaryllifolius* nine days into its fifth instar and one day before pupating.

Figures 10-11. Dorsal [10, left] and lateral [11, right] views of wild pupae of *Faunis sappho sappho* on *Areca catechu* four days after pupating and nine days prior to eclosing.

near the center length of the midrib. Only one ovum (infertile) out of 49 did not hatch, with one monitored group emerging before 05:30 h. Eggshells were partially to fully consumed.

First-instar larvae: Upon hatching, caterpillars are cream color with long, white, fine body hairs, smooth light brown heads with scattered shorter black hairs, and two tiny, dark pointed tails. Their cream bodies gradually turn yellowish green as ingested hostplant becomes increasingly visible through the shiny translucent cuticle. Day four saw development of four thin, light, longitudinal dorsal lines and what looks like a row of lateral dark spots. Maximum measured body length ~8 mm (n = 6), weighted average duration 7 days (Fig. 3).

Second-instar larvae: Similar to preceding instar, but their bodies are now dark green with the four longitudinal dorsal lines clearly white and distinct, and a black end to the abdomen. The white body hairs are much longer, while the prolegs and spiracular spots are light orange with the true legs and short tails appearing paler. Heads are now a richer shade of brown and, in addition to the earlier black hairs, crowned with a pair of concolorous, short, truncated spinose horns. Maximum measured body length ~21 mm (n = 4), shed head capsule maximum width 1.4 mm (n = 5), duration 6-9 days (Fig. 4).

Third-instar larvae: Similar to preceding instar, but their bodies are now black with all other colors being brighter, while the white body hairs are much longer and more dense. A thick creamy white line below and thinner wavy white line above the spiracles are now prominent. The truncated head horns, which face forward, are stouter with the top setae arranged in a five-point star with a sixth spine in the middle of the array. Maximum measured body length 30 mm (n = 7), shed head capsule maximum width 2.1 mm (n = 5), duration ~6 days (Fig. 5).

Fourth-instar larvae: Similar to preceding instar, but their body hairs are now longer, denser, and more brownish, especially on the thoracic segments. The four white longitudinal dorsal lines are now centered with three greenish lines and the abdominal end is no longer black. The tails and head horns are proportionally bigger, while the prolegs have taken on a pinkish hue. Maximum measured body length ~41 mm (n = 9), shed head capsule maximum width 3.0 mm (n = 1), duration 6-8 days (Fig. 6).

Fifth/last-instar larvae: Similar to preceding instar, but with their tails, horns, and dense now auburn-and-white long hairs well developed, as is a rich body patterning. Beginning in the late fourth instar but more prevalent in the fifth, a triangular black patch appears below the horns on both sides of the coronal sulcus that is accompanied by a similar darkening of the adfrontal area and around the stemmata. Maximum measured body length 55 mm (n = 17), shed head capsule maximum width per Dyar's Rule 4.5 mm, weighted average duration 9 days (Figs. 7 & 8).

Gregarious throughout their caterpillar development but staying in no consistent formation, the first instars remained together near where they hatched for feeding, resting, and molting, while in subsequent instars up to maturity, larvae

Figure 12. Female parasitoid fly *Drino* sp. or *Isosturmia* sp. (Tachinidae) "waiting" very close to group of mature caterpillars of *Faunis sappho sappho* resting only slightly out of frame on *Heliconia psittacorum* leaf (see text).

Figure 13. Newly emerged well-marked ♀ *Faunis sappho sappho* ex *Pandanus amaryllifolius* resting on non-hostplant leaf.

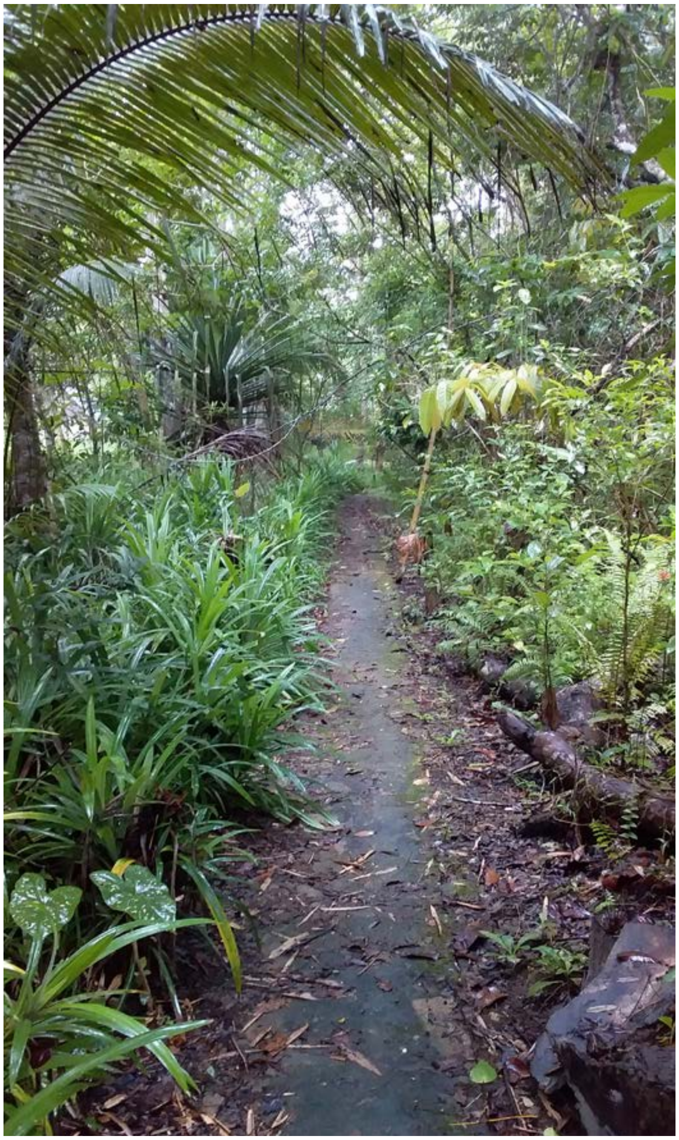

Figure 14. Typical habitat where *Faunis sappho sappho* is often observed in study area on Bohol island. This shady path, which is roughly 50 m long and damp most of the year, is bordered by stands of *Pandanus*, various palms, and *Heliconia*, but not many flowering plants. Other butterflies seen here include *Papilio rumanzovia*, *Eurema hecabe*, *Parantica vitrina*, *Elymnias congruens*, and *Yoma sabina*.

could be found either with the original number of individuals or in smaller groups on either surface of the hostplant leaf. Presumably, resting and molting would most often take place on the underside of leaves in the wild. The caterpillars on all hostplants ate mainly in the afternoon starting about 14:00 h and through the night, though eating in the morning between 08:30 and 09:30 h was sometimes seen. Neonates traveled to the edge of their natal leaf to initiate feeding, which is also where the larvae usually regrouped after molting or moving to a new hostplant leaf. As is normal with many butterfly species, caterpillar colors faded considerably prior to each ecdysis. The shed exuviae were eaten in the earlier instars but not in later ones, which is perhaps due to the increased amount of dense body hairs. No active defensive behavior was noticed when the larvae were occasionally touched or moved during routine husbandry, at which time they did not seem to react in any significant manner, but rather simply fell freely and curled upon landing. Besides the parasitoid discussed in the next section, the only other predator encountered was a small spider that ate a batch of very young first instars being reared inside a container.

Prepupae: Coloration is the same as last instar, but they are now substantially paler (faded) and their bodies look contracted. Measured body length 38 mm (n = 1), duration 1 day (Fig. 9).

Regardless of their hostplant, all larvae pupated between late evening (~20:00 h) and early the next day (~06:00 h), with the latter period appearing to be the usual time judging from the freshness of pupae in the morning. The open potted and sleeved caterpillars chose the underside of leaves, rachises, framing, and other supports, while the container larvae suspended themselves from the top lid.

Pupae: Hanging vertically by their cremasters from fashioned silk pads, they are unmarked, smooth, and apple-green after hardening, with whitish spiracles and bifurcated head projections that taper to golden points. Measured end-to-end length 29 mm, width 10 mm, distance between horn tips 4.5 mm (n = 1), duration 12-13 days (Figs. 10 & 11).

Although pupation sometimes occurred side by side in confinement, such a situation is unlikely to happen in the wild where caterpillars were observed to wander away from their hostplant in search of a safe place to pupate. Both sexes typically emerged overnight and during the early morning hours, with an occasional adult eclosing later; Fig. 13 shows such a newly emerged female at 13:29 h. Of the first 19 ex *A. catechu* and ex *P. amaryllifolius* imagoes to eclose (the *H. psittacorum* larvae died of a probable virus in their final instar), five were males and 14 were females. The total developmental time from oviposition to adult emergence was roughly 63 days, with the faster growing *P. amaryllifolius* caterpillars (potted host and container fed) taking 57 days and the slower growing *A. catechu* larvae (container fed) requiring 69 days. No conclusion was reached whether this disparity of approximately 12 days was due to the hostplant or breeding regime.

Tachinidae parasitoid

Two separate adult fly parasitoids were recorded during this study, which represents the first documentation of a Tachinidae-*Faunis* association (James O'Hara, pers. comm.). On 24 June 2021, four last-instar *F. sappho* that had been naturally developing on an open potted *P. amaryllifolius* began behaving differently and thus were suspected of being parasitized. These caterpillars were moved into individual, covered, translucent plastic containers where on 27 June 2021, three days later, an unrecorded number of fly larvae and puparia were found on the container bottoms. Images were available for only one such unfortunate caterpillar, a close examination of which showed the characteristic large blackened spot on abdominal segments two and four. One of the maggots was chosen for completion, with a female fly eclosing on 15 July 2021 and photographically identified by three tachinid specialists as either *Drino* Robineau-Desvoidy, 1863 or *Isosturmia* Townsend, 1927 (formerly a subgenus of *Drino*). This adult specimen was not retained.

The second encounter occurred nearby on 28 June 2021 when a female Tachinidae was seen to remain stubbornly next to a group of final instars resting on an open potted *H. psittacorum*. During the brief period of observation, the fly was not seen to land upon nor interact with the caterpillars in any manner. An image of this subsequent tachinid (Fig. 12) was sent to the same three experts who had unanimously agreed on its determination - *Drino* sp. or *Isosturmia* sp.

Comparison with congeners

Compared to the other eight species of *Faunis*, mature *F. sappho* larvae are very similar to those of *F. canens* (Malaysia; Leong, 2011) and *F. phaon* (Luzon; Wolfe & Feurtado, 2021) in being dark brown with lighter longitudinal dorsal and lateral lines, while *F. menado* and *F. stomphax* (Sulawesi and Palawan respectively; Igarashi & Fukuda, 2000) are black with indistinct longitudinal dorsal stripes and prominent orangish spiracular marks. In contrast, *F. gracilis* (Malaysia; KVW, pers. image) has black dorsal and subdorsal patches separated by shades of brown, white, and/or yellow, while *F. kirata* (Borneo; KVW, pers. image) looks even more atypical in being brown with a middorsal line of broken black streaks bordered by broad whitish bands. The only Chinese congeners, *F. aerope* (Lang, 2011) and *F. eumeus* (Young *et al.*, 2007), are distinctive in having reddish orange dorsums. With the exception of *F. gracilis* and *F. kirata* whose pupae are presently unknown, the pupae of the other six species appear almost identical to what is pictured here for *F. sappho*. The amount of coverage and detail in the foregoing six published reports varies greatly.

Adult behavior

On Bohol island, *Faunis sappho* is found in shady humid habitats where the hostplants grow nearby. They can also be seen in thinly forested areas flying along narrow trails (Fig. 14) or around small clearings that have an accumulation of old damp leaves. Sunny, drier environments and thick woodlands are avoided, apparently due to a lack of suitable hostplants in those locations, as are wide-open places. The butterfly is fairly active all year and for much of the day, but more so in the morning about 08:00 h than in the afternoon around 16:00 h; later sightings are most likely females searching for hostplants. Even during cloudy, cool weather, adults are still regularly observed.

Faunis sappho is normally encountered as single individuals, though occasionally when high emergence has occurred in a preferred area with many hostplants due to optimal seasonal conditions, up to half a dozen adults can be seen at the same time along such favored trails. The first author has photographed them resting on a leaf 0.5 m high at 13:34 h and basking in a sunny spot on the ground at 14:18 h. Their flight is always low to the ground, below 0.5 m and mainly then just skimming the forest floor. It is swift and purposeful, lasting only a short distance before the butterfly stops and rests for a while until continuing, thus it never travels far. Females, presumably intent on laying eggs, spend only about two or three seconds on an inappropriate leaf before flying to the next.

Faunis sappho adults have been photographed feeding on what appear to be civet dung at 08:31 h, a fallen cracked seedpod at 08:43 h, a damp forest-floor leaf at 08:54 h, bird excreta at 10:28 h, smashed possible figs at 10:29 h, a broken coconut at 12:07 h, and a fallen ripe "chico" (sapodilla) fruit at 14:15 h. Neither sex has been observed visiting flowers. They are predated by the widespread dragonfly *Orthetrum serapia* Watson, 1984 (Libellulidae), a lone such encounter being photographed at 10:07 h in an open garden where the subject butterfly rarely flies.

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Addendum: The following list of Amathusiini hostplant families was gleaned by the second author from many dozens of books, reports, personal communications, scientific websites, etc., over the course of 25+ years of study. Although often included in the tribe by a number of well-known sources, the genera *Morphopsis* (on Pandanaceae) and *Xanthotaenia* (on Zingiberaceae) are excluded here because of their very atypical (for Amathusiini) larvae (lack of hirsuteness and characteristic head horns) and pupae. The tribe is confined to Asia and utilizes only monocots except for a lone gymnosperm.

AMATHUSIINI GENERA AND HOSTPLANT FAMILIES REPORTEDLY USED

Aemona (3 spp.) > viz. *amathusia*, *lena*:
* Arecaceae
* Poaceae
* Smilacaceae

Allaemona (1 sp.)
* unknown

Amathusia (14 spp.) > viz. *phidippus*:
* Arecaceae
* Musaceae

Amathuxidia (3 spp.) > viz. *amythaon*:
* Arecaceae

Discophora (11 spp.) > viz. *celinde*, *lepida*, *necho*, *ogina*, *sondaica*, *timora*:
* Arecaceae
* Poaceae, Bambusoideae
* Poaceae, Panicoideae

Enispe (5 spp.) > viz. *euthymius*, *lunatum*:
* Poaceae, Bambusoideae

Faunis (9 spp.) > *aerope*, *canens*, *eumeus*, *gracilis*, *kirata*, *menado*, *phaon*, *sappho*, *stomphax*:
* Araceae
* Arecaceae
* Asparagaceae
* Cycadaceae
* Heliconiaceae
* Hypoxidaceae
* Musaceae
* Orchidaceae
* Pandanaceae
* Smilacaceae

Hyantis (1 sp.) According to the species-level phylogeny generated by Chazot *et al.* (2021), *Hyantis* groups outside the Amathusiini.
* unknown

Melanocyma (1 sp.) > *faunula*:
* Arecaceae

Stichophthalma (10 spp.) > viz. *howqua*, *neumogeni*, *suffusa*:
* Arecaceae
* Poaceae, Bambusoideae
* Poaceae, Micrairoideae
* Poaceae, Panicoideae

Taenaris (27 spp.) > viz. *artemis*, *butleri*, *catops*, *dimona*, *gorgo*, *honrathi*, *horsfieldii*, *mailua*, *myops*, *onolaus*, *phorcas*:
* Arecaceae
* Asparagaceae
* Costaceae
* Cycadaceae GYMNOSPERM
* Flagellariaceae
* Hypoxidaceae
* Musaceae
* Orchidaceae
* Pandanaceae
* Poaceae, Micrairoideae
* Poaceae, Panicoideae
* Smilacaceae

Thaumantis (4 spp.) > viz. *diores*, *odana*:
* Arecaceae
* Poaceae, Bambusoideae

Thauria (2 spp.) > viz. *aliris*:
* Arecaceae

Zeuxidia (10 spp.) > viz. *amethystus*, *aurelius*, *doubledayi*:
* Arecaceae

AMATHUSIINI HOSTPLANT FAMILIES USED BY GENERA IN RANK ORDER

* Arecaceae - 11
* Poaceae, Bambusoideae - 4
* Musaceae - 3
* Poaceae, Panicoideae - 3
* Smilacaceae - 3
* Asparagaceae - 2
* Hypoxidaceae - 2
* Orchidaceae - 2
* Pandanaceae - 2
* Poaceae, Micrairoideae - 2
* Araceae - 1
* Costaceae - 1
* Flagellariaceae - 1
* Heliconiaceae - 1
* Cycadaceae GYMNOSPERM (only non-monocot) - 1

Life history of the jaguar moth *Cicadomorphus falkasiska* Martinez (Noctuidae: Pantheinae) with notes on behavior

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Abstract: We here describe the life history of one of the rarest jaguar moths, *Cicadomorphus falkasiska* Martinez, 2020. We provide information on host plant association and behavioral characteristics based on rearing *in situ* (Oxapampa, Peru) and *ex situ* (Göttingen, Germany). This is the first study where the life history of a jaguar moth species is completely illustrated, including immature and adult habitus and larval head capsules from the first to the last instar.

Key words: Host plant, immatures, Neotropics, Noctuoidea, UV reflective.

INTRODUCTION

The Neotropical jaguar moths (Noctuidae: Pantheinae) are a poorly studied, recently described member of the *Lichnoptera* Herrich-Schäffer clade (Martinez, 2020). Jaguar moths are characterized by their similar appearance to tiger moths and tussock moths (Erebidae: Arctiinae), and comprise the genus *Cicadomorphus* Martinez along with other genera such as *Bathyra* Walker, *Cicadoforma* Martinez, *Gaujonia* Dognin, *Gaujoptera* Martinez, *Lichnoptera*, *Millerana* Martinez, and *Oculicattus* Martinez. *Cicadomorphus* was described after determining that the genus *Gaujonia* was not monophyletic and was thus separated into five genera (*Cicadoforma*, *Cicadomorphus*, *Gaujonia*, *Millerana*, and *Oculicattus*) based on molecular and morphological data (Martinez, 2020).

Cicadomorphus is a small genus with four species distributed in the Andes from Colombia to Bolivia. As mentioned above, this genus is remarkably similar to *Cicadoforma* externally and internally, but several morphological characters that can diagnose both genera were described by Martinez (2020). The genus is sexually dimorphic, mainly in size, with females almost twice as large as males and slightly paler. Although similar to other genera in the *Gaujonia* group, *Cicadomorphus* is characterized by the semi-hyaline wings, especially in males which have scales only on the veins and margins, resulting in resemblance to members of Cicadidae (Hemiptera) and inspiring the generic name.

The species *Cicadomorphus falkasiska* Martinez is endemic to Peru, occurring at high altitudes above 2000 m (Martinez, 2020). Unfortunately, like other Neotropical noctuoid groups, the immature stages of jaguar moths are practically unknown, with exception of two species that have been reported as pests in the pine tree industry (Bollino & Onore, 2001; Guevara & Romero, 2008). Existing life cycle descriptions are incomplete and usually poorly illustrated. Martinez (2020) superficially described the other two species, one of which was *C. falkasiska* Martinez, illustrating only the last instar and adults of each. We here describe and illustrate in detail the complete life cycle of *C. falkasiska*, and provide discussion of its biology, host plant association, and chemical defense.

MATERIALS AND METHODS

On 21 February 2018, Falk Zahlaus collected a female of *Cicadomorphus falkasika* in a light trap in Oxapampa, Peru, which laid about 200 eggs, and he contacted the authors to rear them (Fig. 1, Fig. 2A,B). The eggs were fertile, but no host plants were known for the species. We contacted local people in Peru to collect more larvae or females to lay eggs, which helped to determine the host plant of this species. Eggs were laid in captivity and were shipped to Germany to be reared by the second author (facilities were not available where the eggs were collected). The eggs were placed in petri dishes and when they hatched the larvae were fed leaves of *Quercus aquifolioides* Rehder & E.H. Wilson (Fagaceae) (most pantheines feed on members of this plant family). Later, other larvae in Peru were collected on *Prunus subcorymbosa* Ruiz ex Koehne (Rosaceae) by local people, and we thus added leaves of *Prunus laurocerasus* L. to their diet. Leaves were changed every three

Figure 1. First collected female with recently laid eggs (at far left).

Figure 2. A-B. Area where the first female was collected in the montane forest of Oxapampa, Peru.

days to avoid mold accumulating. Life cycle and measurements were recorded daily with a triangle protractor. Photographs were taken with a Nikon D7000 camera equipped with a Sigma APO 150mm f/2.8 EX DG OS HSM Macro lens. To document head capsules, we employed a StackShot automated focus stacking macro rail with a Canon EOS 6D camera and an Infinity long-distance microscope Model K2 DistaMax™. At least one larva was euthanized from each instar to be deposited in the immature stages collection at the McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL, USA (MGCL). Unfortunately, we could not conduct a larval chaetotaxy comparison due the lack of sufficiently preserved specimens available to us, so that study will have to wait until more specimens are available. Finally, pupae were placed in collapsible butterfly rearing cages until emergence of the adults, which were euthanized and pinned and also deposited at MGCL. The host plant was identified by using the Missouri Botanical Garden website (Missouri Botanical Garden, 2020) and the works of Pérez-Zabala (2007) and Achá-Macias and Fuentes (2011). In order to record reproductive aspects of this species we placed some of the previously collected male and female adults in collapsible butterfly rearing cages, with each containing a small branch of *P. subcorymbosa*, while the rest were placed in petri dishes in an attempt to collect eggs.

RESULTS

Life stages description

Egg (~1 mm wide and high; duration: ~16-19 days). Sulfur yellow with a semi-circular dome-shape and smooth chorion with rather inconspicuous transverse and longitudinal ribs. Eggs became dark gray close to time of eclosion. Immediately before hatching chorion became transparent with the ribs practically disappeared (Fig. 1).

Neonate first instar (Body length: ~1.22-1.31 mm; duration: ~6 hours). *Head*. Head capsule black, covered with long primary setae and wider than rest of body. *Thorax*. Brownish gray with a narrow black band in prothorax dorsally and presenting black secondary setae arising from dark-brown verrucae; adenosma in ventral prothoracic area absent; lateral prothoracic verrucae remarkably larger than others with longer setae; spiracles same color as rest of thorax. *Abdomen*. Brownish gray with dark brown verrucae, which present long black secondary setae; spiracles same color as rest of abdomen. *Legs*. Same color as thorax and claws pale brown. *Prolegs*. Same color as abdomen and crochets pale brown (Figs. 3A, 6).

Later first instar (Body length: ~1.31-2.98 mm; duration: ~6-8 days). *Head*. Black with long primary setae. *Thorax*. Brownish gray with dorsal prothoracic verrucae forming an oval marking presenting two small verrucae, paler one on each side of marking; adenosma in ventral prothoracic area absent; subdorsal verrucae brown with black hair-like and spine-like setae; mid-dorsal verrucae brown with black spine-like setae only; prothoracic and lateral verrucae also presenting long hair-like setae; spiracles slightly darker than rest of thorax. *Abdomen*. Brownish gray with A1-A4 and A6-A8 darker dorsally; verrucae brown with spine-like setae, and other hair-like setae only laterally; spiracles barely darker than rest of abdomen. *Legs*. Dark brownish gray and claws pale brown. *Prolegs*. Slightly darker than rest of abdomen and crochets pale brown (Figs. 3A, 6).

Second instar (Body length: ~2.95-5.53 mm; duration: ~6-8 days). *Head*. Black head capsule with short secondary setae. *Thorax*. Brownish white with a brown trapezoidal marking on prothorax formed by dorsal verrucae; brown verrucae except by those on each side of marking, which are brownish white; adenosma in ventral prothoracic area well developed and functional; verrucae with brown and white spine-like setae, which are longer and hair-like on prothorax near head; lateral prothoracic verrucae prominent; spiracles pale brown. *Abdomen*. Brownish white with A1-A4 and A6-A8 brown dorsally; verrucae brown with brown and white spine-like setae, but lateral verrucae and those in A9 presenting long hair-like setae; pale-brown spiracles. *Legs*. Brown with claws brown. *Prolegs*. Brownish white with a brownish shade on subventral area; crochets pale brown (Figs. 3B, 6).

Third instar (Body length: ~4.31-11.05 mm; duration: ~6-8 days). *Head*. Black with short secondary setae. *Thorax*. Brownish yellow with gray coloration and a wide semi-circular marking formed by prothoracic verrucae on dorsum; adenosma well developed and functional; wide dark brown verrucae except for a small dark brown verruca on each side of semi-circular marking; dark brown and white spine-like setae on verrucae longer near head; lateral verrucae in prothorax with few very long dark-brown hair-like setae, while rest of lateral verrucae have white long hair-like setae; spiracles dark brownish yellow. *Abdomen*. Brownish yellow with dorsum brown excluding A5, which is gray; A8-A9 brighter coloration than rest of body; wide verrucae brown with dark and white spine-like setae; lateral verrucae and A9 showing also long white hair-like setae; dark-brownish spiracles. *Legs*. Dark brown with claws brown. *Prolegs*. Dark brown with lower subventral area gray; crochets brown (Figs. 3C, 6).

Fourth instar (Body length: ~7.11-15.02 mm; duration: ~5-7 days). *Head*. Black showing short secondary setae. *Thorax*. Brownish orange slightly darker on dorsum except for prothorax which is dark brown; adenosma well developed and functional; dark brown semi-circular marking on prothorax near head almost imperceptible; verrucae dark brown with dark brown spine-like secondary setae; lateral verrucae with long white hair-like setae thicker on lateral prothoracic verrucae; dorsal mesothoracic and metathoracic verrucae presenting also dark-orange spine-like setae; spiracles dark yellowish orange. *Abdomen*. Dark brown dorsally, and brownish orange laterally excluding A9-A10, which are bright whitish orange; dark brown verrucae with similarly colored secondary setae; dorsal verrucae have also some dark orange setae; lateral verrucae and those in A9 with long white hair-like setae; dark yellowish-orange spiracles. *Legs*. Dark brown. *Prolegs*. Dark brown with lower subventral area grayish brown and reddish-brown crochets (Figs. 3D, 6).

Fifth instar (Body length: ~9.07-19.18 mm; duration: ~8-12 days). *Head*. Black with short secondary setae. *Thorax*. Dark brown with similarly colored

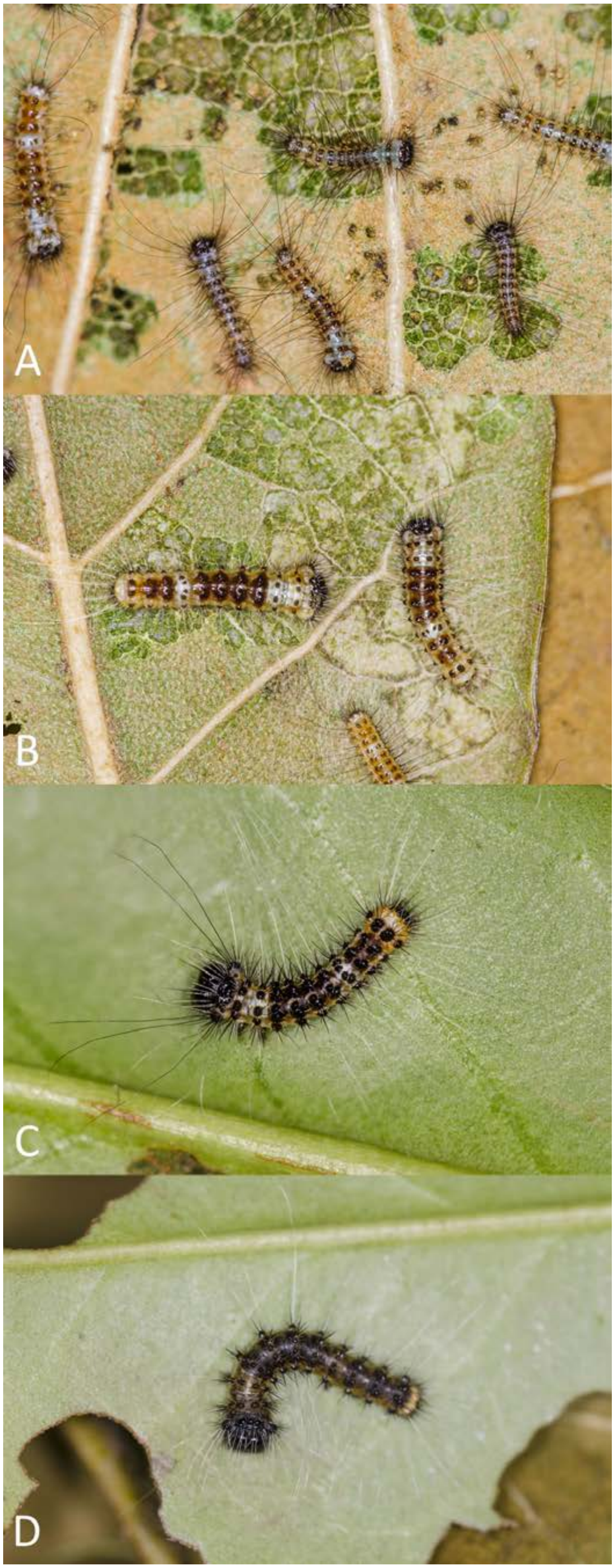

Figure 3. A-D. Immature stages of *Cicadomorphus falkasiska*. A. Neonate and later first instar. B. Second instar. C. Third instar. D. Fourth instar.

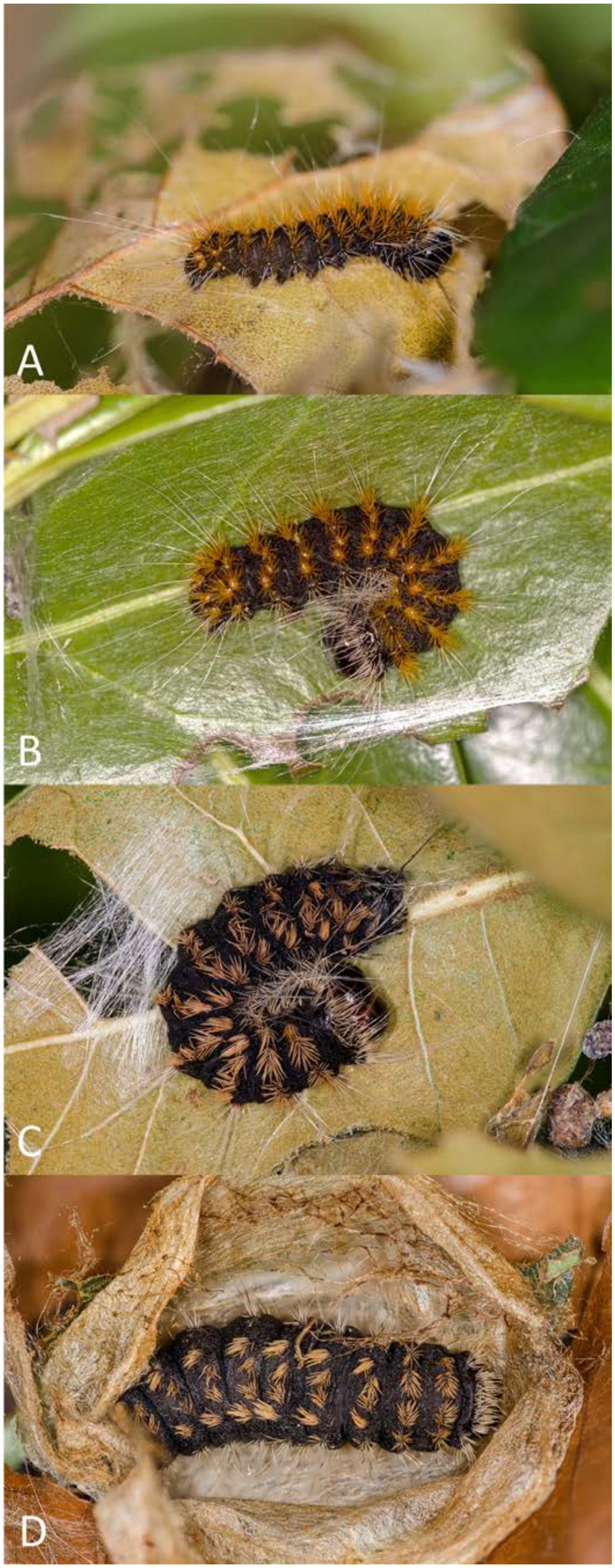

Figure 4. A-D. Immature stages of *Cicadomorphus falkasiska*. A. Fifth instar. B. Sixth instar. C. Seventh instar. D. Pre-pupa.

verrucae; marking formed by dorsal prothoracic verrucae inconspicuous; adenosma well developed, but non-functional; wide, orange secondary spine-like setae and narrower, dark brown setae; prothoracic and lateral verrucae also showing long white hair-like secondary setae; spiracles whitish orange. *Abdomen*. Dark brown and verrucae with same color except on A8-A9, which are orange; wide, orange secondary spine-like setae and narrower, dark brown setae; lateral verrucae and those on A9-A10 presenting white long hair-like setae; whitish-orange spiracles. *Legs*. Dark brown. *Prolegs*. Dark brown with lower subventral area in grayish brown and crochets dark reddish brown (Figs. 4A, 6).

Sixth instar (Body length: ~15.89-28.36 mm; duration: ~5-8 days). *Head*. Dark brown displaying short secondary setae. *Thorax*. Dark brown with verrucae in same color except for those in dorsal area in metathorax, which are orange; wide adenosma, but non-functional; orange spine-like secondary setae; long white hair-like secondary setae on prothoracic and lateral verrucae; spiracles whitish orange. *Abdomen*. Dark brown with dorsal verrucae orange except those in lateral area and A10 that are brown; spine-like secondary setae in orange, and lateral verrucae and those on A8-A10 with long white hair-like secondary setae; spiracles whitish orange. *Legs*. Dark brown. *Prolegs*. Dark brown with dark red crochets (Figs. 4B, 6).

Seventh instar (Body length: ~26.13-30.08 mm; duration: ~10-14 days). *Head*. Dark brown exhibiting short secondary setae. *Thorax*. Dark brown with whitish orange verrucae, except for dorsal prothoracic verrucae which are dark brown; adenosma wide and non-functional; verrucae with bright orange and spine-like secondary setae, long white hair-like setae on prothorax and laterally; spiracles whitish brown. *Abdomen*. Dark brown with whitish-orange verrucae; bright orange spine-like secondary setae slightly paler in lateral verrucae; lateral verrucae with long white hair-like setae; whitish-brown spiracles. *Legs*. Brown paler on claws. *Prolegs*. Dark brown with dark reddish-brown crochets (Figs. 4C, 6).

Pre-pupa (Body length: ~27.04-29.15 mm; duration: ~4-6 days). *Head*. Dark brown presenting very short secondary setae. *Thorax*. Slightly swollen and dark brown in color, including verrucae; adenosma inconspicuous; pale orange spine-like secondary setae with some white on lateral verrucae; some long hair-like secondary setae on prothoracic and lateral verrucae, but mostly lost during this stage; pale-orange spiracles. *Abdomen*. Slightly swollen with dark brown coloration as well as verrucae; secondary setae spine-like, pale orange and marbled in brown and pale orange laterally; lateral verrucae with long white hair-like secondary setae, which are also mostly lost during this stage. *Legs*. Dark brown, brighter than rest of thorax. *Prolegs*. Dark brown, brighter than rest of abdomen with crochets also dark brown (Figs. 4D, 6).

Pupa (Body length: male ~27.01-28.06 mm; female ~27.42-29.05 mm; duration: ~19-21 days). *Head*. Sutures smooth, almost imperceptible, except by antennae, palpi and maxillae; palpi and maxillae are concealed; antennae ending at ¾ of forewing, maxillae ending at middle of forewing. *Thorax*. Oval prothoracic plate two and one third times shorter than mesothoracic plate; metathoracic plate narrow and M-shaped. *Wings*. Both wings ending on A4; hindwings concealed by forewings, only visible in small space between both forewings. *Legs*. Prothoracic legs concealed by mesothoracic legs. *Abdomen*. A1-A4 covered by wings ventrally; A4-A10 segments greatly swollen with A8-A10 fused; spiracles conspicuous and well developed; secondary setae in positions occupied by verrucae in larval stages; trapezoidal cremaster short and rugose with two pairs of long hooks and 8-10 pairs of small hooks. *Cocoon*.

Figure 5. A-C. Immature stages of *Cicadomorphus falkasiska*. A. Cocoon. B. Pupa, ventral side. C. Pupa, lateral side.

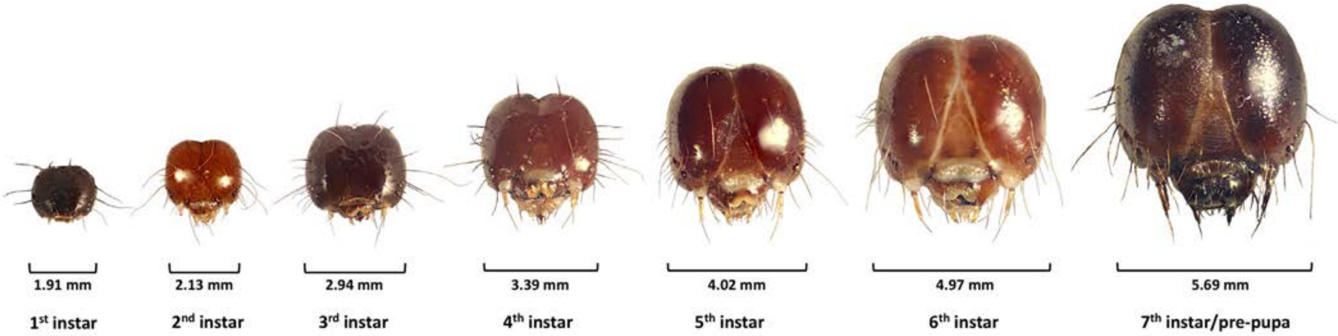

Figure 6. Cephalic capsules of *Cicadomorphus falkasiska*.

Thick and like a tear-drop in shape; its construction includes copper-colored silk threads and secondary setae (Figs. 5A-C).

Adult (Forewing length: male 23-25 mm; female 30-32 mm). *Head*. Palpi pale-yellow with last segment black with a pale-yellow stripe ventrally, and a dot of same color dorsally; dark-yellow frons; dark brown antennae. *Thorax*. Pale yellow with few blurred spots in black, more visible in males than females. *Wings*. Forewings pale yellow; hyaline areas in male nearly without scales, but more scales in female; postmedial and subterminal lines inconspicuous in male, whereas basal, antemedial, and medial lines well defined; females present all line patterns poorly defined; large and elongate orbicular spot; reniform spot narrow, outlined in black and showing a black dot in middle; hindwings hyaline in males, semi-hyaline in females with fringe paler yellow than forewing in both sexes. *Legs*. Pale yellow except for prothoracic legs, which have some brown patches. *Abdomen*. Whitish gray with few tufts on middle of abdomen; A1-A3 with tufts yellow with A2 showing a small black dot, and remaining tufts black on other segments with some yellow and long white scales; female with yellow tufts only on A1-A4 (Figs. 7, 8).

Larval behavior: The larvae are completely nocturnal. When neonate larvae are ready to hatch, they begin to eat the center of the upper side of the chorion, leaving the rest intact, and stay on the egg cluster for several hours. In the first four instars the larvae are gregarious, and feed on the cuticle and epidermis of the leaf. From the second to the fourth instar the adenosma is functional, producing a highly alkaline compound (Figs. 9B, C). Subsequently, from the fifth to seventh instar, the larvae are more scattered and feed on the entire leaf, leaving almost nothing uneaten. Additionally, the integument and secondary setae harden in these late instars and take on a bright, presumably warning coloration similar to some larvae of tiger moths (Erebidae: Arctiinae) (Fig. 9D). After being disturbed larvae arch their backs inward to exhibit their bright orange secondary setae (Fig. 9). Finally, during the pre-pupal stage, the larvae stop eating and begin cocoon construction, producing copper-colored silk and adhering some of their secondary setae.

Adult behavior: Adults occur at high altitudes (above 2000 m) and at relatively low temperatures (17-18°C). *Cicadomorphus falkasiska* is mainly nocturnal and flies all year round, but adults are more common from late September to middle December (spring and summer). Both sexes fly near the ground, but females are short-distance fliers, perhaps because of their heavier bodies, whereas males are lighter and seemingly able to maintain longer flights. Females, and less often males, have been observed feeding on rotten fruit, tree sap, or mud (Fig. 10). Interestingly, despite being nocturnal, the entire bodies of the adults are highly UV reflective in both sexes (Fig. 11).

Reproductive aspects: As mentioned above, the first female was collected during middle February (mid-summer) of 2018 in central Peru above 2500 m. Subsequently collected females and larvae were found from late February to late March (late summer to early fall). The courtship is very short, with the male approaching the female and fluttering its wings constantly, and after few minutes the male positions itself behind the female and inserts its genitalia towards those of the female. Mating lasts about 30-45 min, and during mating the female covers the male almost entirely with its wings, because the abdomen in most pantheines is short. After mating, the female stays resting, whereas the male frequently flies away.

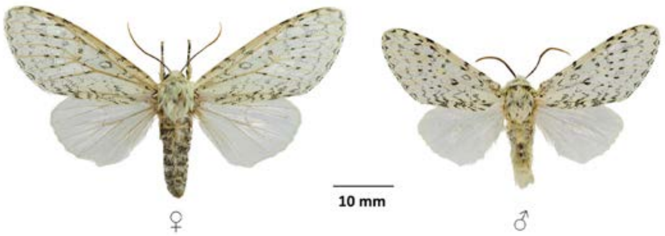

Figure 7. Adult habitus of *Cicadomorphus falkasiska*.

Figure 8. Female of *Cicadomorphus falkasiska* resting on *Quercus aquifolioides*.

Oviposition behavior: Oviposition was recorded only once, inside of the collapsible butterfly rearing cages, because most females died before laying eggs, perhaps because they did not copulate. The only fertilized female carefully laid a cluster of eggs on the leaves of the *Prunus subcorymbosa* branch that was previously set into the cage. In contrast, females that were placed in petri dishes just laid eggs randomly. Interestingly, the female uses her haustellum to probe the ideal place to lay her eggs.

Host plant: Larvae of *Cicadomorphus falkasiska* were found naturally feeding on *Prunus subcorymbosa* Ruiz ex Koehne (Fig. 12), which is a plant of the family Rosaceae distributed in Central and South America. This plant can reach a height up to 30 m and can be differentiated from other species of the genus

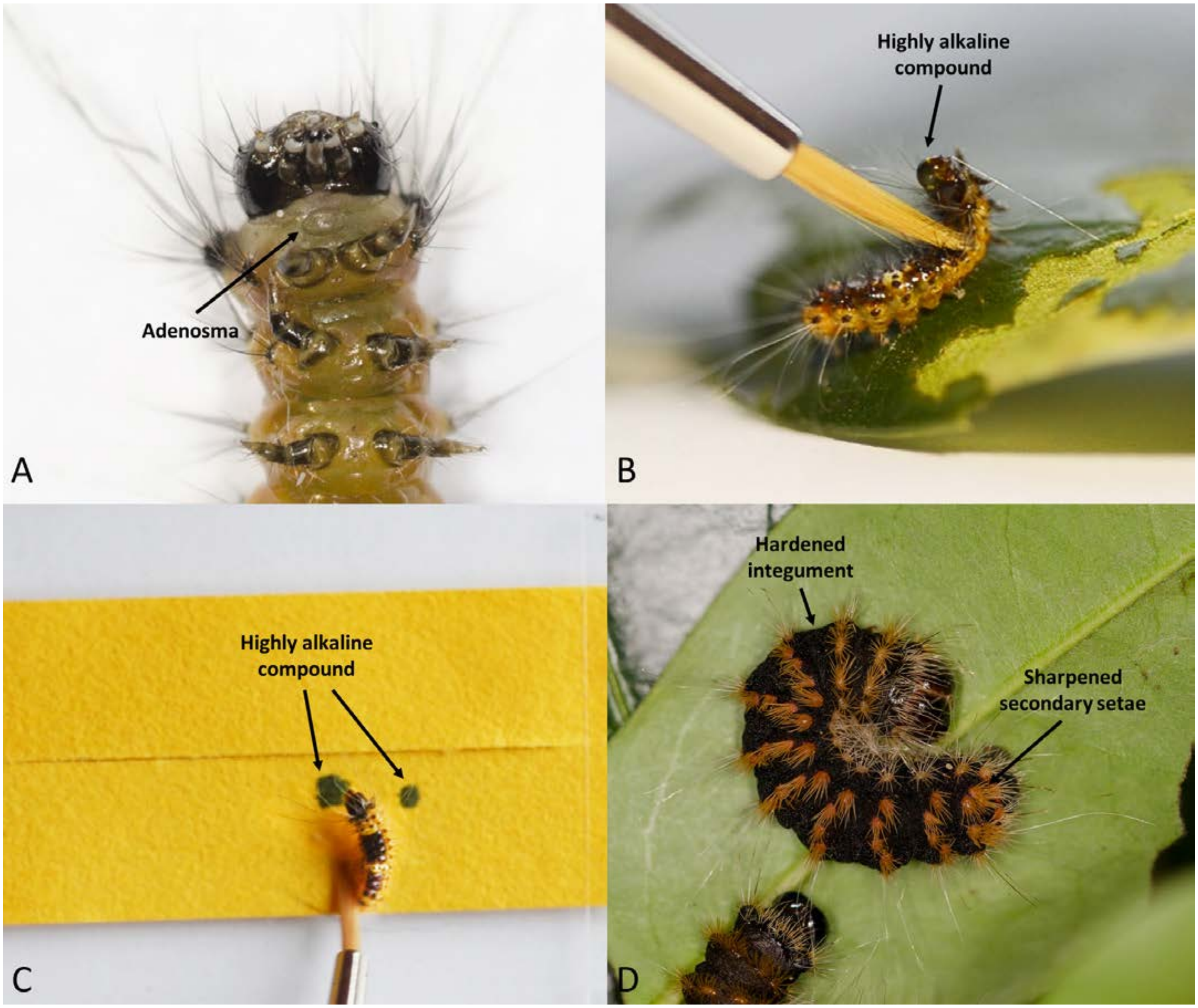

Figure 9. A-D. Types of defenses in larvae of *Cicadomorphus falkasiska*. A. Adenosma. B-C. Highly alkaline compound mixed with the regurgitation. D. Physical defense.

Prunus by the chartaceous or subcoriaceous leaves with waxy undersides mainly visible on the midrib. In addition, another important character is the dense cover of trichomes on the leaf, inflorescence, fruit buds, and hypanthium. The larvae feed mainly on leaves, but sometimes during the earlier instars they feed on inflorescence buds. During the day, larvae rest on the tree branches or trunk until sundown.

DISCUSSION

This study represents the first complete life cycle description of one of the 38 known species of jaguar moths distributed in the Americas (Hampson, 1913; Seitz, 1919-1944; Schmidt & Anweiler, 2020; Martinez, 2020). As mentioned above, many assumptions have been made about the biology, behavior, and life history of pantheines. One of those assumptions is that supposedly the adults do not feed, based on the reduced haustellum (Anweiler, 2009; Behounek et al., 2011; Schmidt & Anweiler, 2020). However, despite the fact that the haustellum is reduced, it is still developed, and we have found that it is functional, as has been observed in other genera such as *Charadra* Walker, *Colocasia* Ochsenheimer, and *Panthea* Hübner (Martinez, personal observation).

The reproductive behavior of noctuids is poorly studied, with only a few works such as Birch *et al.* (1989), Cibrian-Tovar & Mitchell (1991), and Nakano *et al*. (2009). However, most of these studies have been performed using pheromones or acoustic communication. In the case of *Cicadomorphus falkasiska*, neither acoustic communication nor pheromone release was observed during reproductive behavior, but we may have missed such sexual behaviors since we began observations right after the male approached the female. Otherwise, it has been hypothesized that UV-reflectance could play an important role in the sexual selection (Lyytinen *et al*., 2004) and all species of the genus *Cicadomorphus* are UV-reflective. It is possible that they evolved the ability to detect this UV pattern, instead of using pheromones for mate recognition, possibly implying an extra cost in production.

Figure 10. Adult of *Cicadomorphus falkasiska* feeding on fruit juice.

Figure 11. Adult habitus of *Cicadomorphus falkasiska* under UV light.

Another important observation is that the first four larval instars, which appear to be the most vulnerable, have developed some mechanisms that may help to avoid predators, including: a) production of silk threads to move from one leaf to another and hanging from the leaves while resting, and b) production of a highly alkaline compound that is produced in the adenosma and mixed with the regurgitation and expelled when the larva is disturbed, with the exception of the first instar (Figs. 9A, B, C). The adenosma is reduced and non-functional in the first and from the fifth to seventh instar, possibly because they depend more for defense on visual mimicry and mechanical defense than on chemical defense (Fig. 9D).

A remarkable observation concerning *Cicadomorphus* is the potential mimicry in adults and larvae, which resemble aposematic tiger moths (Erebidae: Arctiinae), not only morphologically but behaviorally (Martinez, personal observation). However, *Cicadomorphus* is not the only genus in Pantheinae potentially engaging in this kind of behavior, with, for example *Colocasia*, *Anacronicta* Warren, *Panthea*, and *Trisuloides* Butler being similar to tussock moth species (Erebidae: Lymantriinae) in both larval and adult stages. Some species even feed on some of the same host plants (Kitching & Rawlins, 1999; Yasuda *et al*., 2012). Willmott and Mallet (2004) observed a similar phenomenon in ithomiine butterflies and they suggested that mimicry between species sharing hostplants is promoted by the shared microhabitat of the adults. Other genera, like *Gaujonia* Dognin and *Arctioptera* Schmidt & Anweiler, look more similar to tiger moths in both larval and adult stages, such as *Hypercompe* spp. or *Estigmene* spp. (Chacón & Montero, 2007; Martinez, 2020; Schmidt & Anweiler, 2020). On the other hand, while members of the genus *Trichosea* Grote mimic tiger moths in the adult stage, the larvae resemble a totally different family, Lasiocampidae, which is not related to the Noctuoidea (Sugi & Nakamura, 1986; Yasuda *et al*., 2014).

Figure 12. A-B. *Prunus subcorymbosa*, host plant of *Cicadomorphus falkasiska*. A. Habitus. B. Leaves and inflorescences.

Finally, a host plant relationship between Pantheinae and Rosaceae, as reported here, is not previously unknown. There are some genera that are known to feed on *Prunus* and other rosaceous plants such as *Trichosea* Grote and *Arctioptera* Schmidt & Anweiler (Matov & Kononenko, 2012; Kononenko, 2005; Schmidt & Anweiler, 2020). A curious note is that all these pantheine genera not only share similar host plants, but also external morphology, which is astonishing considering that the three genera are globally allopatric. *Trichosea* is restricted to Eurasia, *Arctioptera* is limited to North and Central America, and *Cicadomorphus* is confined to the Andes in South America (Hampson 1913; Sugi & Nakamura, 1986; Martinez, 2020; Schmidt & Anweiler, 2020).

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Grouping as a strategy to mitigate top-down and bottom-up pressures for survival and growth in *Methona confusa* (Butler, 1873) (Nymphalidae, Ithomiini)

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Abstract: This study tests the advantages of group-living in the gregarious aposematic caterpillars of *Methona confusa* (Butler, 1873), a Neotropical clearwing butterfly (Ithomiini). Larvae were reared on their host plant *Brunfelsia grandiflora* (D. Don, 1829) (Solanaceae) both in isolation and in groups, in the field and in a greenhouse in two experiments: the first, from hatching to pupation, and the second, from the third instar to pupation. In Experiment 1, almost all larvae placed in the field died within the first days of the experiment, suggesting strong pressures from abiotic factors (e.g., rain) and/or predators on early-instar larvae. In the greenhouse, survival was higher in grouped larvae compared to isolated larvae, suggesting that aggregation benefits larvae in the absence of predation and abiotic factors. In Experiment 2, survival was higher in the greenhouse than in the field. Grouping did not affect mortality rate, but it did speed up development with no cost in terms of pupal mass. Together, these results suggest that group-living can confer benefits to aposematic larvae that are not related to predation and that these benefits may be greater in earlier than in later instar larvae.

Key words: Aggregation, aposematism, feeding facilitation, gregarious behavior.

INTRODUCTION

Gregarious behavior occurs in various forms in several orders of insects. Most Lepidoptera lay their eggs singly and their larvae have a solitary behavior (Clark & Faeth, 1997), but gregarious behavior is exhibited across at least 20 families (Costa, 2006; Stamp, 1980). Most groups exhibit a simple social structure, consisting of larval herds that feed together during the early stages of larval development, generally dispersing before pupating (Allen, 2010). Although gregarious behavior could present some disadvantages, such as smaller adults (Wiklund & Persson, 1983), intraspecific competition, probability of disease transmission, cannibalism, parasitism (mostly egg and pupa) (Reader & Hochuli, 2003; Lawrence, 1990), several advantages have been proposed to explain gregarious behavior: broadly speaking, benefits of group-living include anti-predator defense, thermoregulation, and overcoming plant defenses (Stamp, 1980). Advantages are usually more important early in development, explaining why larvae often disperse as they mature (Despland, 2013).

Grouping can be favored by top-down selection pressures as it decreases the risk of predation or parasitism (in the larvae) via several mechanisms, including dilution of risk and active defense (Hunter, 2003; McClure & Despland, 2011). Most notably, aposematic colouration is often combined with group-living, and grouping enhances the strength of warning signals (Ruxton *et al.*, 2004).

However, multiple studies also show benefits of group-living in the absence of predators (Tsubaki & Shiotsu, 1982; Lawrence, 1990; Stamp & Bowers, 1990; Clark & Faeth, 1997; Fordyce & Agrawal, 2002; Denno & Benrey, 2003; Reader & Hochuli, 2003; Inouye & Johnson, 2005; Pescador-Rubio, 2009; Allen, 2010; Fiorentino *et al.*, 2014; Rosa *et al.*, 2017; Despland, 2019). These results suggest that gregarious larvae feed more efficiently than solitary ones because they can overcome plant defenses, including trichomes (Despland, 2019), leaf toughness (Fiorentino *et al.*, 2014) or toxic compounds (Denno & Benrey, 2003).

These bottom-up advantages to grouping have been observed in chemically-defended aposematic caterpillars of several species (e.g., *Chlosyne lacinia* (Geyer, 1837) (Nymphalidae) Clark & Faeth, 1997; *Chlosyne janais* (Drury, 1782) Denno & Benrey 2003; *Chlosyne poecile* (Felder, 1867) Inouye & Johnson, 2005; *Battus philenor* (Linnaues, 1771) (Papilionidae) Fordyce, 2003; *Doratifera casta* (Scott, 1864) (Limacodidae) Reader & Hochuli, 2003). One hypothesis is based on the fact that feeding on the toxic plant compounds required to back up an aposematic signal with chemical defense is costly, even for specialists (Zalucki *et al.*, 2012), and suggests that aggregation can help mitigate those costs (Despland, 2019). In this scenario, aggregation driven by bottom-up selection pressures increases conspicuousness (Despland & Simpson, 2005) and can explain the adaptive value of aposematism early in development, when these bottom-up pressures are generally stronger (Despland, 2013).

Gregariousness is common among larvae of the butterfly family Nymphalidae, including aposematic species (Inouye & Johnson 2005). In particular, the subfamily Danainae (which includes the legendary Monarch and Neotropical clearwings) is characterized by chemically-defended adult butterflies with warningly coloured wings; many larvae are also aposematic and gregarious (Massuda & Trigo, 2009). These larvae feed on toxic plants and are chemically defended, but also suffer costs associated with plant defense: consumption of plant compounds mediates a trade-off between anti-predator protection and toxicity (e.g., *Danaus plexippus* (Linnaeus, 1758) (Danainae) Zalucki *et al.*, 2012). Danaine caterpillars that specialize on toxic plants show adaptations to circumvent plant defenses (Zalucki *et al.*, 2012), including gregarious collective feeding to overwhelm those defenses (Despland, 2019).

Methona confusa (Butler, 1873) (Nymphalidae, Danainae, Ithomiini) have an aposematic colouration in the larval stage (the body is black with yellow rings) and are gregarious throughout larval development (Hill & Tipan, 2008) (Fig.1). *Methona* species feed on alkaloid-laden *Brunfelsia* (Solanaceae) plants, and are likely chemically defended against vertebrates (Tavares *et al*., 2013; Hill & Tipan, 2008). Indeed, other ithomiine larvae sequester *Brunfelsia* defensive compounds for defense in the larval and adult stages (Trigo & Motta, 1990).

This study aims to evaluate the advantages of group-living in the absence of predators in the gregarious aposematic caterpillars of *Methona confusa*. Specifically, we compare the development, growth and survival of *Methona confusa* larvae when reared in groups or in isolation, in both field and greenhouse (i.e.,, protected from predators) conditions.

MATERIALS AND METHODS

Study site and organism: The study was conducted at Mashpi Reserve, Ecuador (0°09’59.3”N, 78°52’47.6”W) an evergreen cloud forest at 850 m elevation on the western slope of the Andes (Sierra, 1999). Rearings were conducted in a greenhouse and outdoors, along a transect following the road, in the forest ecotone, in semi-shaded habitat.

Methona confusa has a broad but discontinuous distribution in South America east of the Andes (Lamas, 2004; Hill & Tipan, 2008), with records inside the Chocó Biogeographic Region (Andrade-Correa, 2002). Its main host plant is *Brunfelsia grandiflora* (Solanaceae) (Hill & Tipan, 2008), shrubs and small trees that grow in light woodlands, disturbed habitats and forest ecotones, distributed from Central America to northern South America (Colombia, Brazil, Ecuador, Peru and Bolivia) (Luzuriaga *et al.*, 2018). *Methona confusa* oviposits clusters of 18-46 eggs (Hill & Tipan, 2008) (Santos *et al*., 2017), the eggs hatch after approximately five days, and the larvae go through five instars (Hill & Tipan, 2008; Massuda & Trigo, 2009).

In both field and greenhouse treatments, the larvae were placed on cut *Brunfelsia grandiflora* branches placed in water. The branches were about 30 cm long; their leaves were mature but not old or damaged. It was ensured that both gregarious and solitary larvae had enough branches on which to feed. New branches were placed alongside the old ones every day, allowing the larvae to move onto the new foliage. Old branches were removed when larvae moved to new ones.

Experimental design: Two experiments were conducted between 12 March 2018 and 4 April 2018, and each was done in both field and greenhouse environments. In Experiment 1, first instar larvae were placed in both the field and the greenhouse treatment either alone (N=16) or in groups of 10 (N=10 groups). However, most of the first instar larvae in the field treatment disappeared within the first five days of the experiment, possibly due to environmental conditions (rainstorms). In Experiment 2, larvae were reared in the greenhouse in groups until the third instar. At the second molt, larvae weighing between 30 and 59 mg were placed in the four treatments: alone in the field (N=28), in groups of ten in the field (N= 10 groups), alone in the greenhouse (N=20) and in groups of ten in the greenhouse (N=10 groups).

The larvae were inspected every day, recording deaths and disappearances as mortality. Larval mass was recorded every four days using a portable balance (Ohaus Scout SPX123). Finally, pupae were weighed 24 hours after pupation. Data loggers for temperature and humidity were placed in the forest transect and in the greenhouse.

Data analysis: All statistical analyses were done with R 3.5.3 software. Individuals within the grouped treatment were pooled to generate a single value per replicate. Survivorship between treatments within each experiment was compared with Cox proportional hazard models (survival 2.44-1 package).

Data from Experiment 1 was split between an early developmental period corresponding to the first two instars (first seven days of the experiment) and a later one representing the third instar onward (day 8 to 14) in order to examine ontogenetic shifts in mortality rates. A generalized linear model with a binomial link function (function glm) was used to compare mortality rates between solitary and grouped insects kept indoors both early and late in development.

Larval mass at each measurement date was compared between treatments using a linear mixed model (package lme4) with grouping and location as fixed effects and time as a random effect. Pupal mass and development time were analyzed with linear models including grouping and location (function lm). Data were tested for linear model assumptions by visual examination of residuals prior to analysis.

RESULTS

Survival rates: In Experiment 1, survival was much higher in the greenhouse than in the field (Cox survival analysis $z = 4.82$; $p < 0.001$): in the field, only one insect from the grouped treatment (and none from the solitary treatment) survived to pupation. In the greenhouse, larval survival from hatching to pupation was higher in grouped than in solitary individuals (Cox survival analysis $z = -1.91$; $p = 0.04$) (Figure 2).

In Experiment 2, larval survival from the third instar onward was higher in the greenhouse than in the field (Cox survival analysis $z = -1.99$; $p = 0.04$) but did not depend on grouping (Cox survival analysis $z = 0.70$; $p=0.48$) (Figure 2). During the

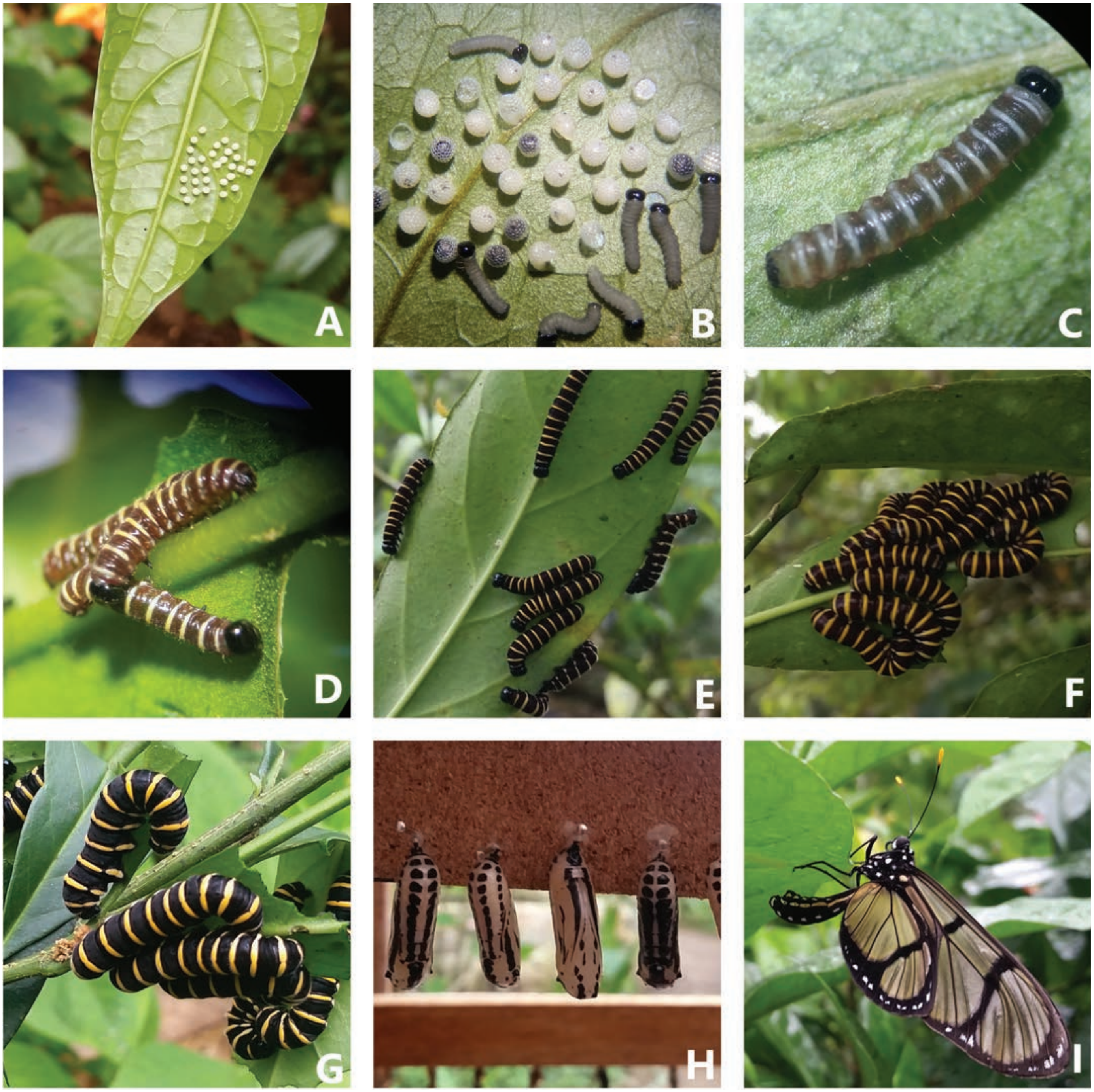

Figure 1. *M. confusa* life cycle. **A.** Egg batch under host plant leaf (*B. grandiflora). ***B.** Neonate larvae emerging from an egg mass. **C.** First instar. **D.** Second instar. **E.** Third instar. **F.** Fourth instar. **G.** Fifth instar. **H.** *M. confusa* pupae. **I.** Adult *M. confusa* ovipositing on *B. grandiflora.*

course of the experiment, the temperature was slightly higher in the greenhouse (mean=22.12°C, sd=2.06) than outdoors (mean=20.6°C, sd=0.97). Humidity was consistently above 90% in both the field and the greenhouse.

Splitting the Experiment 1 mortality data from the greenhouse between early and later in development showed differential effects of grouping: the early development period binomial GLM showed higher mortality in isolated than in grouped larvae (df = 22, p=0.01). However, later-instar mortality (both experiments together) did not differ significantly, either between experiment 1 and 2 (df = 38, p=0.98) or between isolated and grouped larvae (df = 37, p=0.63). All datasets fit the assumptions of the binomial distribution.

Growth and development: Linear mixed models of larval mass failed to detect a difference between grouped and solitary insects at any stage in development, in the three contexts for which there was sufficient data (Experiment 1 in the greenhouse, Experiment 2 in the greenhouse and in the field). Mean caterpillar mass across all treatments increased from 1.11 mg (+/- 0.06 S.E.) at hatching to 5.77 mg (+/- 0.64 SE) on day 4, to 44.13 mg (+/- 6.68 SE) on day 8, to 156.37 mg (+/-10.37 S.E.) on day 12, to 385.26 mg (+/-24.02 S.E.) on day 16 and finally 756.07 mg (+/-14.22 S.E.) on day 20 of the experiment.

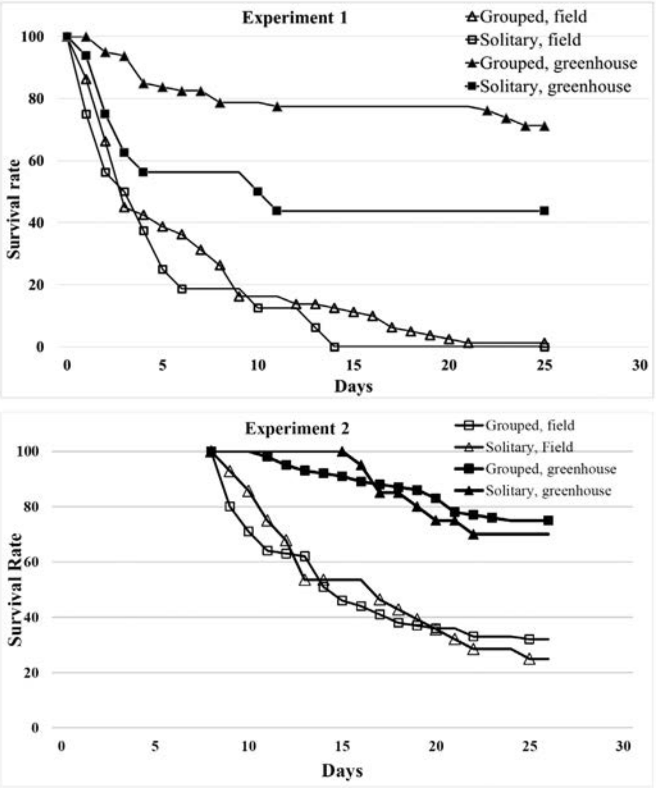

Figure 2. Survivorship curve of larvae in the different treatments in Experiments 1 (from hatching onward), and 2 (beginning at the molt to the third instar). Measurements in Experiment 2 were started on day eight, when larvae molted to the third instar and were placed outdoors.

Experiment 2 showed that development time was longer for solitary caterpillars than grouped individuals (F1,33 = 20.3, p<0.0001; solitary median: 19 days (quartiles 18, 19), grouped median: 17 days (quartiles 16.5, 18)), but that there was no associated effect on pupal mass (F1,33 = 0.114, p = 0.73; solitary median: 0.78 g (quartiles 0.69, 0.82), grouped median: 0.76 g (quartiles 0.73; 0.79)). Survival rates for solitary larvae in Experiment 1 were too low for analysis.

DISCUSSION

The results from our study show a high mortality rate outdoors, particularly in the early instars, and so high that, in Experiment 1, all but one of the first instar larvae placed outdoors died, most of them within the first five days of the experiment (Figure 2). The source of this mortality cannot be reliably measured but observations suggest predators, rainfall and wind. Conditions like heavy rainfall or winds storms can easily dislodge small larvae and restrict the feeding time (Despland, 2018), causing an increase in mortality (Kamata & Igarashi, 1994), especially in larvae that are artificially placed and that have not been able to attach firmly to the plant. In the present experiment, larvae fed on the underside of leaves, sheltered from the rain, but some were found dead under the plants following heavy rains and winds, especially first instar larvae, suggesting that they had been dislodged. Spiders were also frequently seen on the plants and may have predated larvae.

Among larvae reared in the greenhouse, mortality rate was considerably higher in the first two instars than from the third instar (L3) onwards (Table 1). Indeed, type III survivorship curves (with most mortality occurring in the early stages) are very common in lepidopteran life histories (Itô & Miyashita, 1968; Deevey, 1947; Despland, 2018). For instance, survival rates of first instar Monarch caterpillars (*D. plexippus*) vary between 3% and 40% depending on host plant (Zalucki *et al.*, 2012). Another example is *Dendrolimus spectabilis* (Butler, 1877) (Lasiocampidae), where first instar survival rates vary between 10 % and 26.4% depending on the place and time of year (Kanamitsu, 1962).

Our results further show that grouping improved survival of early instar larvae reared indoors (Table 1). That this effect was observed indoors, where the larvae were protected from natural enemies, suggests that the group-living advantages did not only involve anti-predator defense. Similar improved performance in groups away from predation has been observed in other species, including several aposematic Neotropical nymphalids (*Chlosyne lacinia*, see Clark & Faeth, 1997; *Chlosyne janais*, see Denno & Benrey 2003; *Chlosyne poecile*, see Inouye & Johnson, 2005). One possible explanation is thermoregulation, but, given that temperatures were between 20-24°C during our experiment, a more likely advantage conferred by group-living is overcoming plant defenses and establishing a feeding site (Clark & Faeth, 1997). Enhanced feeding efficiency in groups has been tied to collective piercing of tough foliar cuticle in *C. lacinia* (Clark & Faeth, 1997), overwhelming induced allelochemical responses in *C. janais* (Denno & Benrey, 2003), and social facilitation of feeding in *C. poecile* (Inouye & Johnson, 2005). *Brunfelsia* leaves are highly chemically defended (Trigo & Motta, 1990), bear only few trichomes and are tough (personal observation). Leaf toughness and chemical defenses can prevent early-instar insect herbivores with small mandibles from piercing the leaf cuticle and accessing the nutritious tissues underneath (Zalucki *et al.*, 2012). Chemical defenses might be compromised in

Table 1. Average mortality rate for larvae in the early (L1-L2) and later (L3-) instars, compared between locations and grouping treatments. Mortality rate is given as the mean proportion of caterpillars that died within a seven-day period, shown with standard error.

Treatment	**Expt 1 L1-L2**		**Expt 1 L3-**		**Expt 2 L3-**	
	mean	**S.D.**	**mean**	**S.D.**	**mean**	**S.D.**
grouped, field	0.69	0.18	0.60	0.16	0.49	0.19
solitary, field	0.81	0.21	0.67	0.21	0.54	0.22
grouped, greenhouse	0.18	0.04	0.08	0.03	0.07	0.02
solitary, greenhouse	0.44	0.13	0.13	0.12	0.09	0.07

the cut branches used in our experiments but would be equal among field and greenhouse experiments. Aggregation and collective feeding could facilitate establishment of feeding (Despland, 2019) by early instar *M. confusa* larvae, but this cannot be tested directly with our data. The difference in indoor survival rate between grouped and solitary insects was greater in the first larval instars than later in development (Table 1), suggesting that this benefit to grouping is more important in the early larval instars.

Grouping increases effectiveness of warning signals against predators (Sillén-Tullberg, 1988; Clark & Faeth, 1998; Ruxton *et al*., 2004; Pinheiro *et al*., 2008), and recent work suggests that aposematic larvae can also benefit from bottom-up advantages of grouping, as they tend to feed on chemically defended plants (Karban & Agrawal, 2002; Despland, 2020). For instance, Monarch caterpillars feed on a range of *Asclepias* (Linnaeus, 1753) (Apocynaceae), plants with variable chemical defenses, and mortality from bottom-up and top-down sources varies between hosts (Zalucki *et al*., 2012).

Finally, larvae in Experiment 2 showed faster growth rate in groups, with no trade-off on final size. Gregarious larvae have often been shown to pupate faster than solitary ones (Inouye & Johnson, 2005), and the slow-growth-high-mortality hypothesis proposes that this faster development should improve survival by decreasing exposure to natural enemies (Williams, 1999). However, empirical support for this hypothesis is mixed at best (Williams, 1999; Chen & Chen, 2018), and it has not received much attention in aposematic species. One study (Fordyce & Agrawal, 2002) shows that grouping in warning-coloured *Battus philenor* (Papilionidae) accelerates development and improves survival.

Selection pressures vary throughout larval ontogeny, and our data show that *M. confusa* mortality in early instars is very high; grouping ameliorates survival even in the absence of predation and abiotic factors, raising the possibility of collective overcoming plant defenses (Despland, 2019), like the toughness and chemical defenses in *Brunfelsia* leaves. *Methona confusa* combines group-living and aposematism from the beginning of larval development; aggregation amplifies aposematic signals in small organisms (Sillén-Tullberg, 1988; Clark & Faeth, 1998; Ruxton *et al*., 2004; Pinheiro *et al*., 2008) and our data suggests it also mitigates bottom-up pressure from plant defenses. These findings suggest a developmental strategy whereby aggregation allows first instar caterpillars to feed on a defended plant that might be inaccessible to solitary larvae.

Additional experiments might clarify and complement our findings. For instance, observations of early instar larvae in the field could clarify causes of mortality, since larvae were found dead presumably due to heavy rains or wind. Instead of artificial experimental groupings, another complementary experiment could use naturally occurring clutch size variation to examine the effect of gregarism in relation to different natural clutch sizes.

Based on this study, *Methona confusa* joins the ever-growing list of caterpillar species that have been shown to benefit from grouping in the absence of predation and parasitism (see references in introduction). Results further suggest that aggregation in *M. confusa* mitigates both top-down and bottom-up pressures, demonstrating how the strategy of this species integrates in a tritrophic context (Stireman & Singer, 2018). However, many questions remain, for instance about the exact mechanism of countering plant defenses or about the role of parasitoids, which have been shown in other Neotropical ithomiines to be important mortality sources that interact with host plants (Despland & Santacruz, 2020; Santacruz *et al*., 2019). Moreover, other species do not share the same gregarious behavior as *Methona confusa*; most species of Lepidoptera, and many ithomiines, are solitary, and *Methona* itself includes solitary species that feed from the same host plant, such as *Methona curvifascia* (Weymer, 1883). Compared with *M. confusa*, *M. curvifascia* is morphologically similar, but has larger first instar larvae (Hill & Tipan, 2008), and this greater size could perhaps help the larvae overcome the leaf toughness alone. Gregarious and solitary species show different strategies linked to variation in costs and benefits of group living; investigating these in a phylogenetic context, in conjunction with larval host plant specialization (Willmott & Freitas, 2006), could further our understanding of diversification in the Ithomiini.

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Author contributions

All authors contributed to the study conception and design. Material preparation and data collection were performed by Janeth Rentería, data analyses were performed by Janeth Rentería and Emma Despland. The first draft of the manuscript was written by Janeth Rentería and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

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Early stage biology of two euptychiine butterfly species in the Peruvian Amazon (Lepidoptera: Nymphalidae: Satyrinae: Satyrini)

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Abstract: The immature stages of two euptychiine butterflies (Nymphalidae: Satyrinae), *Paryphthimoides terrestris* (Butler, 1867) and *Magneuptychia iris* (C. Felder & R. Felder, 1867), are described herein and their natural host plants are documented. Notes on the immature stages of these two species were included previously in an unpublished dissertation, although our work is the first to provide satisfactory illustrations of the immature stages of these two taxa. Based on the population found and studied in Madre de Dios, Peru, both species utilize plant species in the family Poaceae. We provide illustrations of immatures, head capsules, and host plants for both species.

Key Words: Euptychiina, Finca Las Piedras, host plant, life history, Madre de Dios.

Resumen: Los estadios inmaduros de dos mariposas euptychiinas (Nymphalidae: Satyrinae), *Paryphthimoides terrestris* (Butler, 1867) y *Magneuptychia iris* (C. Felder & R. Felder, 1867) se documentan y describen, así como también sus plantas hospederas naturales. Los estadios inmaduros de estas dos especies fueron documentados previamente en una disertación no publicada; no obstante, nuestro estudio es el primero en proporcionar ilustraciones de los estadios inmaduros de estos dos taxones. Basado en la población encontrada y estudiada en Madre de Dios, Perú, ambas especies utilizan especies de plantas de la familia Poaceae. Proporcionamos ilustraciones de inmaduros, cápsulas cefálicas y plantas hospederas para estas dos especies.

Palabras clave: Planta hospedera, Finca Las Piedras, historia de vida, Madre de Dios, Euptychiina.

INTRODUCTION

The nymphalid subtribe Euptychiina is a diverse radiation found predominantly in the Neotropical lowlands, with more than 440 described species (excluding synonyms), with true species-richness estimated to exceed 500 species (Hurtado *et al*., 2021; unpublished data). Members of the subtribe are common elements of butterfly fauna throughout Central and South America, as several inventories focused on different habitat types have shown (e.g., Beltrami *et al*., 2014; Lamas *et al*., 1991; Yoshimoto *et al*., 2018). In particular, the southwestern Amazon basin (i.e., Madre de Dios department in Peru and adjacent state of Acre in Brazil) harbors a particularly high diversity of euptychiines, rivaled only by the slopes of the tropical Andes in terms of its community diversity (unpublished data). Many euptychiine species utilize plants in the family Poaceae, commonly known as grasses, in addition to several species known to feed on plant families such as Arecaceae, Marantaceae, Heliconiaceae, and Selaginellaceae (Beccaloni *et al*., 2008; Janzen & Hallwachs, 2018). Despite many species being a common component of butterfly communities in the Neotropical region, our knowledge of euptychiine immature stages and their natural host plant remains highly fragmentary, with approximately 80% of the members lacking any host plant records (Corahua-Espinoza *et al*., 2022). It is worth investigating this topic because Lepidoptera life history information serves as the basis for understanding species diversity due to their close links with plant distribution and diversity (Brown, 1991; New, 2014), and for developing appropriate conservation strategies that account for species interactions.

The southwestern Amazon rainforest, including Madre de Dios department, is one of the most biodiverse regions on earth, evidenced by a survey of butterflies (Lamas *et al*., 1991), as well as faunistic studies focused on other vertebrate and invertebrate groups (e.g., Barthem *et al*., 2003; von May *et al*., 2008). It is worth noting that while this region is the heart of diversity for euptychiine butterflies, it is also home to many euptychiine taxa that are not known elsewhere in the Neotropics (e.g., *Caeruleuptychia scripta* Nakahara, Zacca & Huertas, 2017; Nakahara *et al*., 2018). The southwestern Amazon basin, therefore, offers an ideal setting to explore the early stage biology of euptychiine species and to generate valuable natural host plant records for future studies. Climate change and other anthropogenic threats, such as road proliferation and associated resource extraction and deforestation (Gallice *et al*., 2019; Finer & Novoa, 2016; Finer & Mamani, 2021), make documenting the biodiversity of southwestern Amazonia ever more urgent.

The Alliance for a Sustainable Amazon (ASA) (https://www.sustainableamazon.org/) is a nonprofit organization working to conserve biodiversity in the Madre de Dios region by conducting research to generate baseline information for science-based conservation. One of ASA's long-term research projects is focused on Lepidoptera diversity and biology, and the study reported here was conducted under the auspices of this project. Fieldwork is primarily conducted at ASA's research facility, Finca Las Piedras (FLP), located approximately 48 km north of Puerto Maldonado in Madre de Dios department, Peru (-12.22789, -69.11119; ca. 240 m). This study is part of an ongoing series of publications that document complete immature stages of butterflies and their host plants, with seven of them focused on euptychiine species (See *et al*., 2018; Baine *et al*., 2019; Nakahara *et al*., 2020, 2022; Tejeira *et al*., 2021; Ccahuana *et al*., 2021a, b; Hurtado *et al*., 2021; Corahua-Espinoza *et al.*, 2022). Following the precedent set by these studies we here report life history information for two additional euptychiine species with their natural host plant records. The generic classification of one species discussed herein, *Magneuptychia iris* (C. Felder & R. Felder, 1867), changed recently, and a new generic arrangement has been proposed for this taxon in Andrade *et al*. (2019). As stated in previous relevant studies (e.g., Nakahara *et al*., 2022), however, this taxonomic change was not supported by a phylogenetic hypothesis of any kind and ongoing molecular work suggests the proposal to be invalid (unpublished data). We thus follow the most widely accepted Neotropical butterfly classification (Lamas, 2004) and use this specific epithet in combination with *Magneuptychia* Forster, 1964. Although we do not provide complete information regarding the life history of *Paryphthimoides terrestris* (Butler, 1867), we nevertheless consider this a valuable contribution to our understanding of euptychiine butterfly biology for the reasons outlined above.

MATERIALS AND METHODS

As mentioned above, the study was conducted at FLP field station, a 54-ha property of mature "*terra firme*" rainforest, regenerating secondary forest, active and abandoned agricultural plots, and *Mauritia* L. f. (Arecaceae) palm swamps. The "*terra firme*" or upland forest at FLP is characterized by emergent, tall *Bertholletia excelsa* Humb. & Bonpl. (Lecythidaceae) (i.e. Brazil nut trees) and other species in the family Lecythidaceae such as *Eschweilera coriacea* (DC.) S.A. Mori, *Couratari guianensis* Aubl., and *Couratari macrosperma* A. C. Sm.; *Aspidosperma parvifolium* A.DC. (Apocynaceae); *Hymenaea oblongifolia* Huber, *Tachigali* sp., and *Dipteryx micrantha* Harms (Fabaceae); and *Iriartea deltoidea* Ruiz & Pav., *Euterpe precatoria* Mart. (Arecaceae); the understory consists of a variety of herbaceous bamboo species and other grasses such as *Pharus virescens* Döll. as reported herein. Samples were collected and processed using procedures published by See *et al*. (2018), Baine *et al*. (2019), Nakahara *et al*. (2020), and Ccahuana *et al*. (2021a, b). Fieldwork was conducted from February to July 2021, in which larvae were collected from mature forest. The larvae were reared in the laboratory at FLP in 500 mL and 1 L plastic containers with mesh covers to monitor growth and development. The containers were cleaned and searched for head capsules daily, photographs were taken frequently (at least twice per instar), and the larvae were provided with fresh leaves from their respective host plants kept fresh using floral water tubes. The samples were vouchered (2021-FLP-IMM-0102; 0242; 0314; 0382; 0386), and head capsules were observed using a Novel NSZ-608T microscope at the Arachnology and Zoology laboratory of the Universidad Nacional de San Antonio Abad del Cusco, Peru (UNSAAC). The head capsule graphics were made with Adobe Illustrator version 2019.23.0. Measurements of the larvae and pupae were determined based on a ruler photographed with immatures and rounded to the nearest tenth of a millimeter. Body length for larvae was measured from the frons to the posterior tip of the caudal filament; pupae length was measured from the base of the cremaster to the anterior tip of the head. Larval terminology follows Stehr (1987). After examination, the preserved adult specimens were deposited in the ASA's Lepidoptera collection in Puerto Maldonado, Peru.

We obtained the first half of mitochondrial gene *cytochrome oxidase I* (COI), the so-called "barcoding region" (*sensu* Hebert *et al.*, 2003) for 2021-FLP-IMM-0314 in order to aid the identification. DNA was extracted from thoracic tissue cut out by scalpel and homogenized using magnetic beads. Subsequent extraction procedures largely followed the protocols of Qiagen's DNeasy Blood & Tissue Kit with 50 µl as an elution volume. The COI barcoding region was amplified using primer pairs LCO (forward, GGTCAACAAATCATAAAGATATTGG) and HCO (reverse, TAAACTTCAGGGTGACCAAAAAATCA), with PCR reaction conditions as in Nakahara *et al.* (2020). This PCR product was purified by the addition of Exonuclease I (New England BioLabs) and rAPid Alkaline Phosphatase (Roche Diagnostics) and incubated with the following thermocycler conditions: 15 min at 37C, 15 min at 80C, hold at 10C. Subsequently, the purified product was submitted for direct Sanger sequencing at Eurofins Genomics in Louisville, Kentucky, USA. The raw sequence was trimmed and manually edited using 4Peaks software and the NCBI Open Reading Frame Finder (ORFfinder). To verify identity, the sequence was aligned with 96 other euptychiines in Geneious Prime (v 2021.2.2, Biomatters Ltd.) using the MUSCLE plug-in (Muscle 3.8.425) set at 10 iterations. The sequences used in alignment were first selected for closely-related euptychiine taxa within the "*Pareuptychia* clade" (*sensu* Murray & Prowell (2005)) plus an outgroup (*Amiga* Nakahara, Willmott & Espeland, 2019 spp.) (unpublished data) and then selected for high coverage of our sequenced region. A neighbor-joining tree was constructed using the Jukes-Cantor genetic distance model through Geneious Tree Builder. The GenBank accession number for 2021-FLP-IMM-0314 is OM524555.

RESULTS

Larvae of the two euptychiine species were collected on leaves of plant species in the family Poaceae, between February and July 2021. Both species were found on different host plant species. Dates for key life history events for each species are summarized in Table 1. Table 2 provides the host plant conditions observed and recorded.

Description of the immature stages

***Paryphthimoides terrestris* (Butler, 1867)**
(Voucher: 2021-FLP-IMM-0102)

Murray (2001) reported five larval stages for *P. terrestris*, although considering the variable infra-specific larval instar numbers observed in euptychiine species (e.g., *Splendeuptychia furina* (Hewitson, 1862); Corahua-Espinoza *et al*., 2022), we decided not to draw conclusions regarding the number of larval stages of this species based on our incomplete life history information.

Penultimate instar (Figs. 1 A, B; 4 A). Head capsule width: 1.4 mm (n=1). Head capsule dark beige with numerous secondary setae and two short scoli terminating in rather rounded tips (scolus length 0.52 mm (n=1)); three semi-transparent chalazae visible on lateral side (M1-3), with primary seta on each of these three chalazae; dark band-like marking visible on frontal part of head capsule, as well as inner side of scoli and vertex; six setae visible on one side of labrum; six stemmata visible, with first and sixth somewhat semi-transparent and thus insignificant, third stemma largest and closer to second stemma than fourth stemma. Body chartreuse in color with dark brown discoloration dorsally along upper abdominal segments; dark green band extending along middorsal area, well-defined along thorax and absent or insignificant in upper abdominal segments, more defined and brownish along A7-A10; dark brown spiracles, prominent on T1 and A8; ventral prolegs present on A3 to A6, caudal prolegs present on A10; bifid caudal filaments similar in length to A8 in dorsal view. Body length: 12.2 mm (n=1). Duration: Unknown; larva molted four days after collection.

Ultimate instar (Figs. 1 C, D; 4 B). Head capsule width: 1.8 mm (n=1). Head capsule morphologically similar to previous instar (scolus length 0.62 mm (n=1)). Body morphologically similar to previous instar, except coloration; body light beige with gray dorsal discoloration; middorsal band dark brown and more defined along thorax than in previous instar; indistinct, light brown subdorsal stripes extending from base of scoli to T3; jagged subserosal band more defined from A3 to A6. Body length: 19.7 mm (n=1). Duration: 13 days.

Pupa (Figs. 1 E, F). Body and wings cream in color and mottled with dark brown; body short and round with squared ocular caps; spiracles appearing light brownish; small two-toned cream and brown protuberances present in two rows along dorsal area of abdomen; dark brown cremaster, details not discernable based on images. Body length: 8.8 mm (n=1). Duration: 11 days.

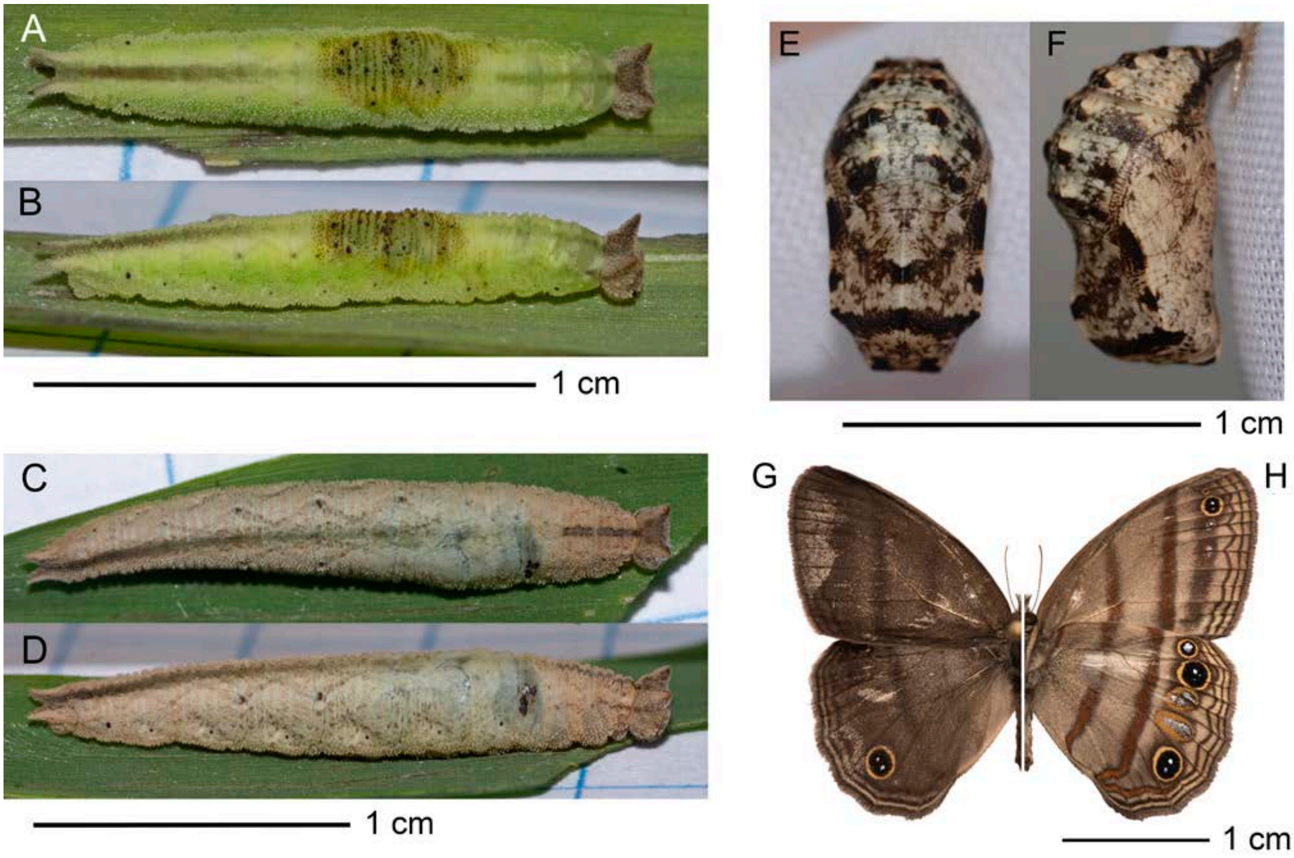

Figure 1. *Paryphthimoides terrestris* life stages: A, B) penultimate instar in dorsal view, lateral view; C, D) ultimate instar in dorsal view, lateral view; E, F) pupa in dorsal view, lateral view; G, H) adult in dorsal view, ventral view.

Table 1. Dates of important life history events recorded for the two euptychiines: *Paryphthimoides terrestris* and *Magneuptychia iris*.

Voucher	Taxon	sex	Date of collection	Egg hatch	L1 to L2	L2 to L3	L3 to L4 (Penultimate to ultimate)	Pupation	Adult	Died
2021-FLP-IMM-0102	*Paryphthimoides terrestris*	male	09/02/2021	no data	no data	no data	13/02/2021	25/02/2021	07/03/2021	N/A
2021-FLP-IMM-0242	*Magneuptychia iris*	female	17/03/2021	no data	no data	no data	25/03/2021	04/04/2021	13/04/2021	N/A
2021-FLP-IMM-0382	*Magneuptychia iris*	male	15/05/2021	no data	16/05/2021	26/05/2021	04/06/2021	16/06/2021	01/07/2021	N/A
2021-FLP-IMM-0314	*Magneuptychia iris*	no data	08/04/2021	12/04/2021	19/04/2021	26/04/2021	06/05/2021	N/A	N/A	10/05/2021
2021-FLP-IMM-0386	*Magneuptychia iris*	male	15/05/2021	no data	no data	no data	no data	27/05/2021	07/06/2021	N/A

Table 2. Details of host plant conditions, location and sampled immature stages. Abbreviations: abaxial (AB); adaxial (AD); distal (D); middle (M); proxima (P); midrib (B); middle (E); margin (IN).

IMM ID	HOST PLANT ID	PLANT GENUS	PLANT SPECIES	DISTANCE FROM GROUND (meters)	LEAF SURFACE (AB/AD)	LF PROXIMITY TO BASE (D/M/P)	LF BLADE PROXIMITY (B/E/IN)	FOUND AS:	LATITUDE	LONGITUDE	FLOWER
2021-FLP-IMM-0102	482	*Lasiacis*	*ligulata*	0.3	AB	D	B	larva	-12.22643	-69.11414	no
2021-FLP-IMM-0242	545	*Pharus*	*virescens*	0.2	AB	M	E	larva	-12.22792	-69.11108	no
2021-FLP-IMM-0314	558	*Pharus*	*virescens*	0.5	AB	P	N	egg	-12.22510	-69.11045	yes
2021-FLP-IMM-0382	558	*Pharus*	*virescens*	0.8	AB	P	B	larva	-12.22510	-69.11045	yes
2021-FLP-IMM-0386	558	*Pharus*	*virescens*	0.3	AB	M	E	larva	-12.22510	-69.11045	yes

Host plant. *Lasiacis ligulata* Hitchc. & Chase (Fig. 3 A, B, C). Habit: herb, belongs to plant family Poaceae: subfamily Panicoideae: tribe Paniceae. Culms: branched; woody. Culm nodes: glabrous. Leaves: glabrous on adaxial surface and pubescent on abaxial surface; blade base asymmetrical; linear to ovate or lanceolate; blade margins scabrous; blade apex acuminate. Inflorescence: raceme with spherical calyxes surrounding reduced white petals. Fruits: similar size to mature flower and dry, brown, and spherical (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:135703-2). Phenology: flowering early between April and June, and fruiting between July and August (Baine *et al*., 2019), both in dry season. Distribution: from Caribbean to northern and western South America, between 0-2000 m (Tovar-Serpa, 2009; Bernal *et al*., 2020).

The plant on which the larva was found was located at the edge of the forest, where this plant species is usually found in the highest abundance at the field site (Baine *et al*., 2019). At the time of larva collection (2 February 2021), the plant was approximately 1.3 m tall; the larva was found at a distance of 0.3 m from the ground; situated on the abaxial surface of the leaf, near the apex of the blade, in the midrib of the leaf (see Table 2).

Magneuptychia iris **(C. Felder & R. Felder, 1867)**

(Vouchers: 2021-FLP-IMM-0242, 2021-FLP-IMM-0314, 2021-FLP-IMM-0382, 2021-FLP-IMM-0386)

Murray's (2001) descriptions of egg, five larval stages and pupa for "*Magneuptychia ayaya*" (Butler, 1867) is largely in agreement with life stages of *M. iris* documented and illustrated herein. Currently, *Euptychia ayaya* is regarded as a junior subjective synonym of *Neonympha iris* (e.g., Lamas, 2004). Unlike the present study, *Magneuptychia iris* went through five larval stages based on individuals from eastern Ecuador (Murray, 2001). However, despite this discrepancy, we believe the in-depth morphological study of immatures conducted in Murray (2001) will complement our documentation of *M. iris* based on a population from southeastern Peru.

Although 2021-FLP-IMM-0314 did not reach the adult stage (see Table 1), the larva closely resembled other known larvae of *Magneuptychia iris* studied herein at all stages and was found to utilize the same host plant species as these other three individuals. In addition, our neighbor-joining analysis of the COI barcode sequence from this specimen resulted in identity matches of 99.844%, 97.738%, and 97.738% respectively with three sequenced individuals identified as *M. iris* based on comparison with the syntype of *Neonympha iris* (images available at: https://www.butterfliesofamerica.com/), and thus we consider this individual to be conspecific.

Egg (Fig. 2 A, B). Spherical, semi-transparent, pearl-like, and whitish in color, with polygonal markings covering the entire surface; head capsule visible via translucence 1 day prior to hatching. Diameter: 1.1 mm (n=1). Duration: Unknown, hatched 4 days (n=1) after collection .

First instar (Figs. 2 C, D. 4 C). Head capsule width: 0.74 mm (n=1). Head capsule black; head capsule smooth, with two rectangular scoli (scolus length 0.19 mm (n=1)), each with two primary setae dilated at tip; six chalazae visible (three on each side) in frontal view, each accompanied primary seta dilated at tip; five setae visible on one side of labrum; six stemmata visible, third stemma largest and closer to second stemma than fourth stemma. Body integument creamy-white and appearing semi-translucent thus presumably gut content visible, influencing light green body color; pair of white stripes in subdorsal area, more visible late during first instar; chaetotaxy not fully discernible based on pictures but primary setae bulbous at apex ("weakly bulbed" *sensu* Murray, 2001: Fig. 3.13C), XD1 and XD2 visible on T1; D1, D2, SD1 and L1 apparently present from T1 to A10, D1 and D2 rather short except for terminal abdominal segments, D1 apparently considerably longer than D2 on A8 and A9; ventral prolegs present on A3 to A6, caudal prolegs present on A10; caudal filament short (shorter than A8 in dorsal view). Body length: 5.9 mm (n=1). Duration: 7 days (n=1).

Second instar (Figs. 2 E, F). Head capsule width: 1.1 mm (n=1). Head capsule dark brown; head scoli developed and tapered (compared to first instar; scolus length = 0.49 mm (n=1)), resembling those of the immediately following instar; no visible chalazae; five setae visible on one side of labrum; six stemmata, with first and sixth somewhat semi-transparent and thus insignificant. Body dark-green; pair of white stripes in subdorsal area, indistinct stripe visible laterally, just below white subdorsal stripe; spiracles whitish, prominent on T1

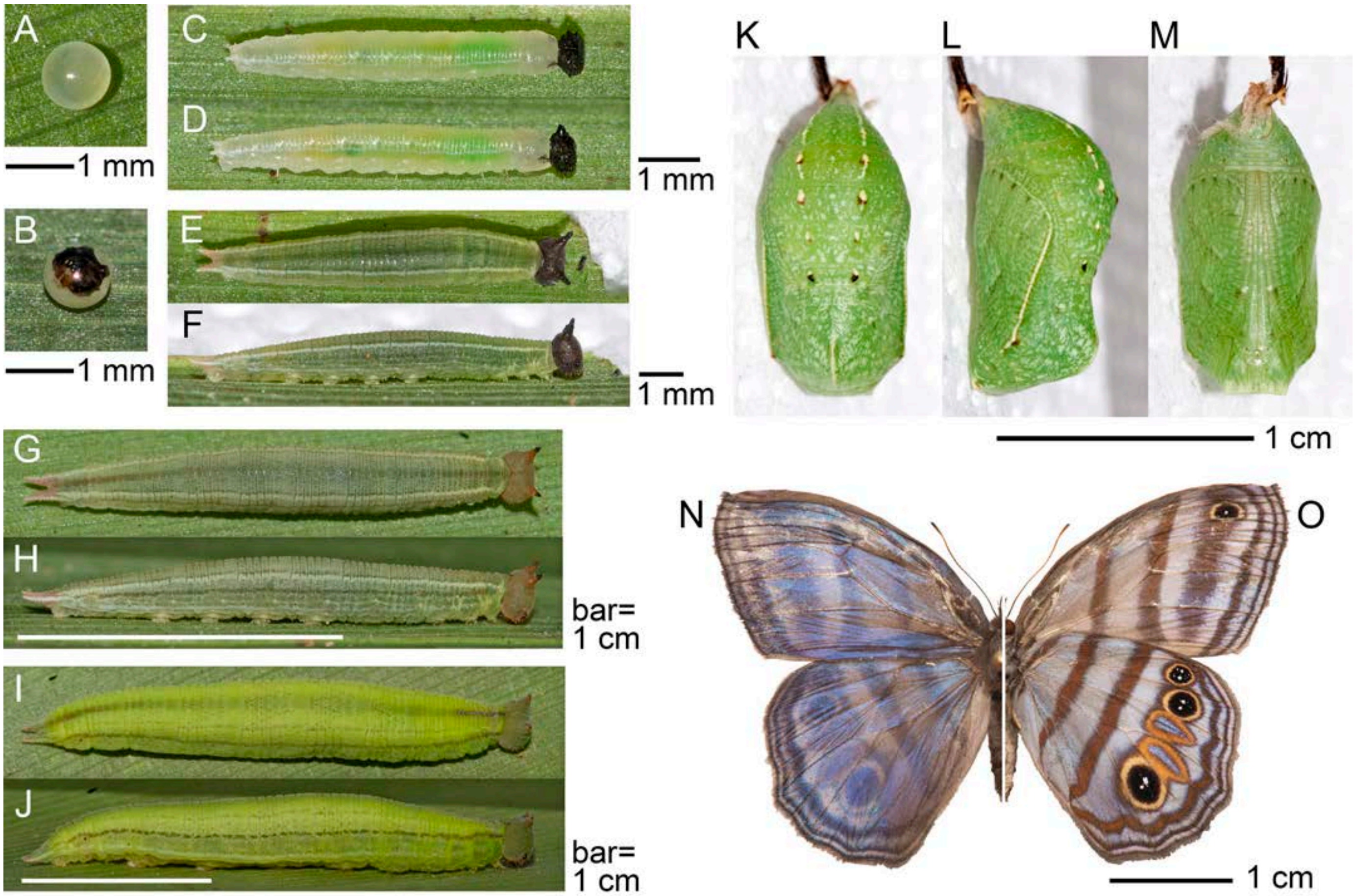

Figure 2. *Magneuptychia iris* life stages: A, B) egg in dorsal view, head capsule visible before hatching C, D) first instar in dorsal view, lateral view; E, F) second instar in dorsal view, lateral view; G, H) third instar in dorsal view, ventral view; I, J) fourth (ultimate) instar in dorsal view, lateral view; K, L, M) pupa in dorsal view, lateral view, ventral view; N, O) adult in dorsal view, ventral view. Figures A and B are based on 2021-FLP-IMM-0314; figures C-O are based on 2021-FLP-IMM-0386.

and A8; ventral prolegs present on A3 to A6, caudal prolegs present on A10; caudal filament pink-ish and appearing as equal in length to A8 in dorsal view. Body length: 9.0 mm (n=1). Duration: 7-11 days (n=2).

Third instar (Figs. 2 G, H. 4 D). Head capsule width: 1.8 mm (n=1). Head capsule light olive in color with mild iridescence; scoli short (scolus length 0.74 mm (n=1)) terminating in rather pointy ends, tipped in orange; five setae visible on one side of labrum; six stemmata, with first and sixth somewhat semi-transparent and thus insignificant. Body yellow-green with mild wart projections; dark green longitudinal band along mid-dorsal area of abdomen, fading to maroon along the thorax and near caudal filaments; white and dark green subdorsal longitudinal lines extending from the head to caudal filaments; two pairs of dark green spots along white subdorsal line between abdominal segments A3 and A4 and A4 and A5; maroon spiracles; bifid caudal filaments tipped with orange. Body length: 13.0-15.1 mm (n=2). Duration: 9-10 days (n=2).

Fourth (ultimate) instar (Figs. 2 I, J; 4 E). Head capsule width: 2.2 mm (n=1). Morphology of head capsule similar to previous instar except for darker coloration and scoli appearing stubby compared to head capsule width and terminating in pointy anterior ends (scolus length 0.62 mm (n=1)). Body morphologically similar to previous instar; body brighter in color; middorsal band more well-defined along prothoracic plate to metathorax and white outlined with maroon in color; bottom subdorsal line and pair of spots along white subdorsal line appear more maroon than previous instar; spiracles brownish, prominent on T1 and A8. Body length: 26.8-28.7 mm (n=2). Duration: 11-12 days (n=2).

Pupa (Figs. 2 K, L, M). Body bright green with scattered white speckles; body overall short, wide and rounded with squared ocular caps; spiracles present as yellow spots; protuberances present in two rows along dorsal area of abdomen as two-toned brown and white dots; cremaster appearing paler, somewhat elongate and gradually narrowing towards distal end. Some hours prior to emergence, the wing shell color changed dramatically from green to black. Body length: 11-11.9 mm (n=2). Duration: 9-15 days (n=3).

Host plant. *Pharus virescens* Döll. (Figs. 3 D, E, F). Habit: herb, belongs to the plant family Poaceae: subfamily Pharoideae: tribe Phareae. Culms: decumbent; 50-100 cm long; rooting from lower nodes. Leaves: elliptic; blade venation oblique from midrib; with well-defined transverse veins; apex acuminate. Inflorescence: in the form of an open panicle; pubescent; spikelets with male and female flowers. Fruits: Caryopsis with adherent pericarp (https://powo.science.kew.org/taxon/urn:lsid:ipni.org:names:415723-1). Phenology: early

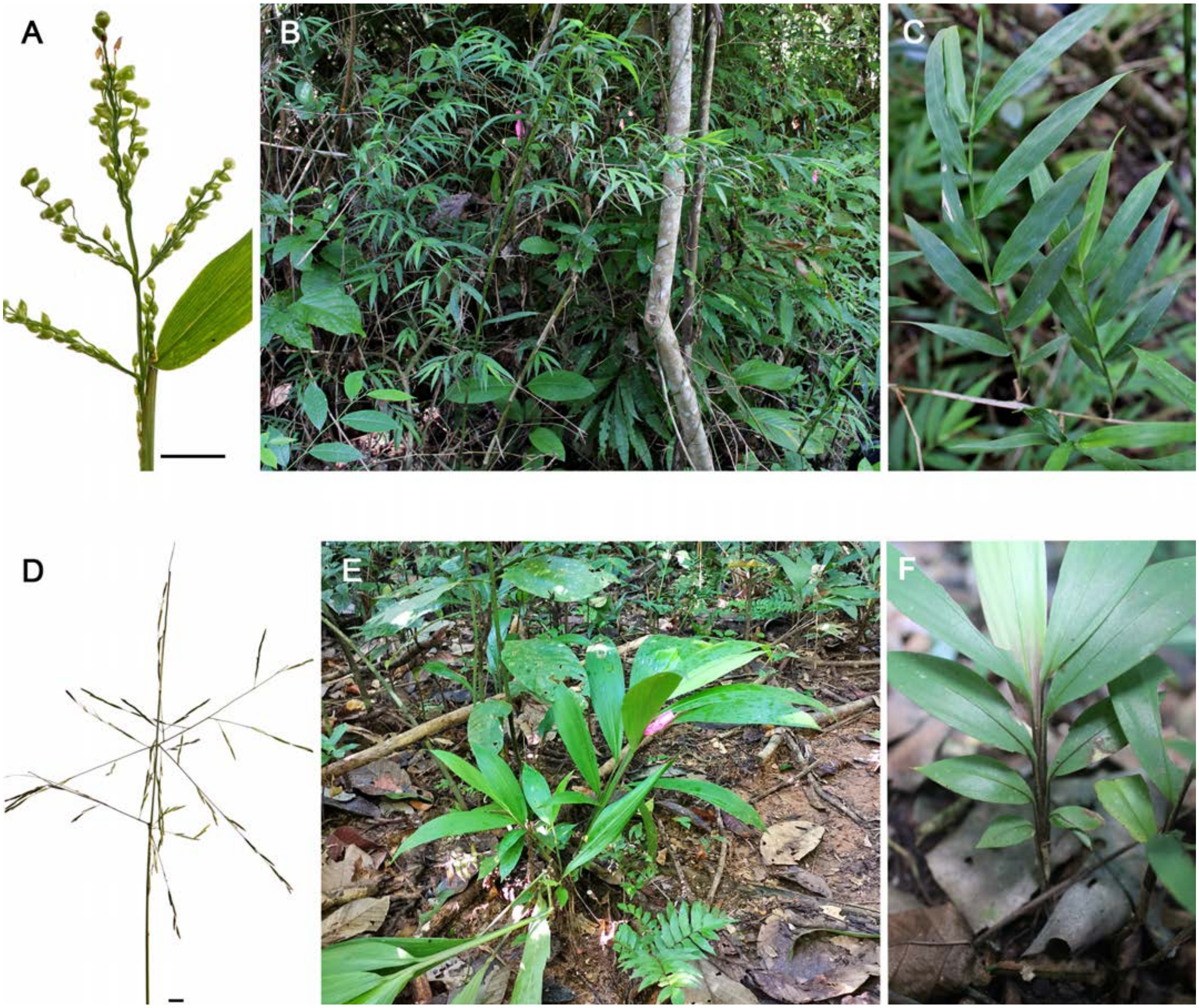

Figure 3. Host plants of two satyrine butterfly species in the Peruvian Amazon. *Lasiacis ligulata*: A) details of inflorescence, B) host plant *in situ* view, C) close-up view of the leaves; *Pharus virescens*: D) details of inflorescence; E) host plant *in situ*; F) close-up view of the leaves and node. Scale bar = 1 cm for figures A & D.

flowering from April; fruiting between May and July (in the dry season), the plants dry up as an annual species at the end of June and in July (in FLP). Distribution: Mesoamerica, northern South America, western South America, and Brazil, between 230-500 m altitude (Bernal *et al*., 2020).

The plant on which the larva was found was located in an area with a closed canopy and low light incidence. This plant species is typically found along trails and in light gaps within the forest at FLP, but usually not at the forest edge, which likely explains the fact that adults are often found flying in the forest understory away from the edge. At the time of larva collection (March 17, 2021; based on 2021-FLP-IMM-0242), the plant was approximately 0.5 m tall. The larva was found at a distance of 0.2 m from the ground, situated on the abaxial surface of the leaf, in the middle of the blade, between the midrib and the margin of the leaf (see Table 2).

DISCUSSION

Singer & Ehrlich (1991) reported the following host plant records for *Paryphthimoides terrestris* (as *Cissia terrestris*) based on plant material accepted by the females in captivity in oviposition trials in Trinidad: *Cyperus* L. and *Scleria* Bergius (both Cyperaceae); *Lasiacis sloanei* (Griseb.), *Ichnanthus pallens* (Sw.), *Panicum pilosum* Sw., *Panicum polygonatum* Schrad (Panicoideae: Paniceae), *Paspalum conjugatum* Bergius, *Paspalum decumbens* Stapf (Panicoideae: Paspaleae), *Setaria paniculifera* (Steud.) (Panicoideae: Paniceae) and *Tripsacum* L. (Panicoideae: Andropogoneae) (summarized in Beccaloni *et al*. (2008)). However, these records do not reflect the host plant of this species in the natural environment. Murray's (2001) dissertation reported "many grass species" as host plants for *P. terrestris* found in the field in eastern Ecuador (as *Cissia terrestris* or "*Marissa*" *terrestris*), which includes grass genera such as *Eleusine* Gaertn. (Chloridoideae: Cynodonteae),

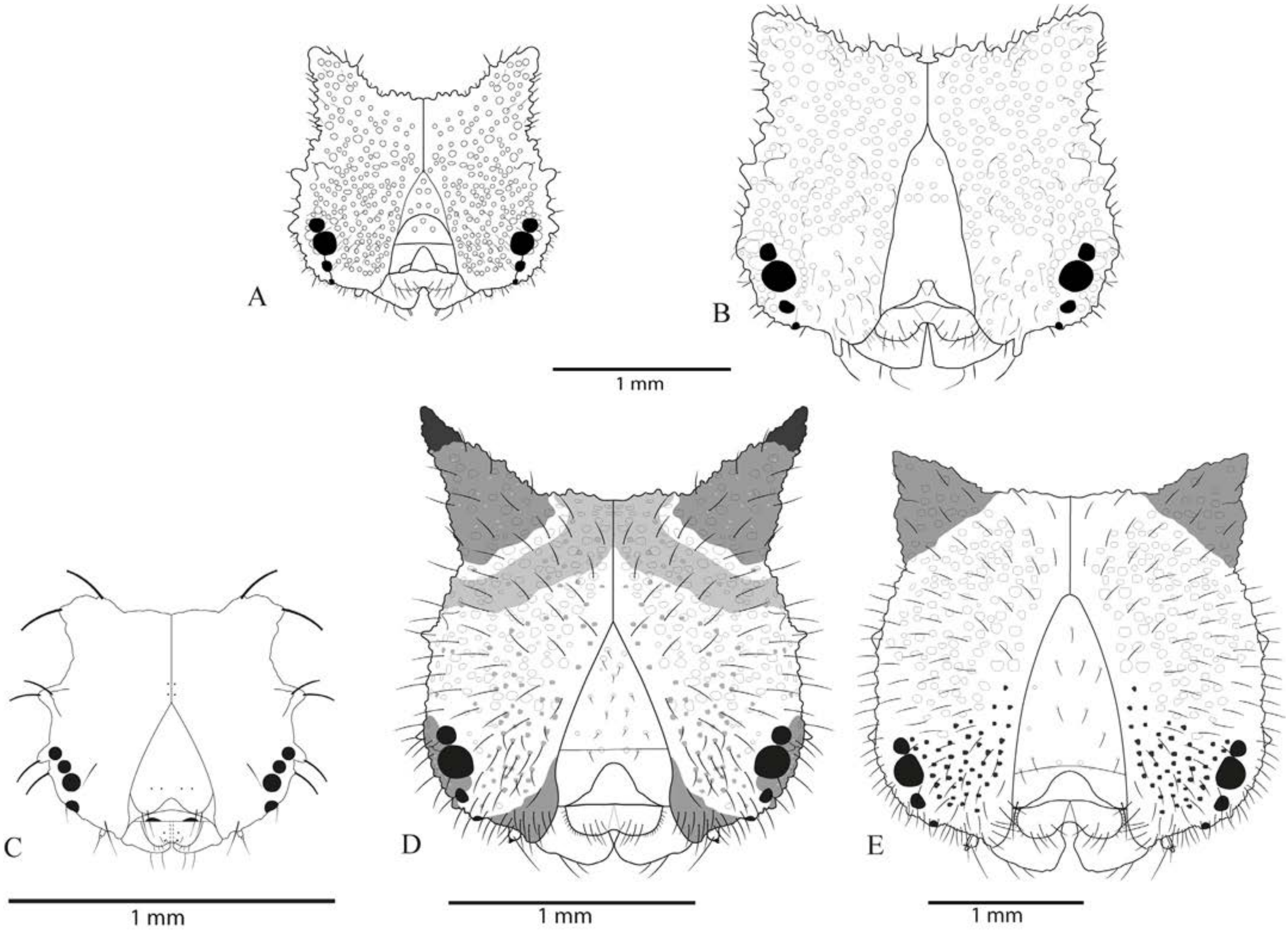

Figure 4. Illustrations of the head capsules: A, B) penultimate and ultimate instar in frontal view of *Paryphthimoides terrestris* (based on 2021-FLP-IMM-0102); C, D, E) first, third and fourth (ultimate) instar in frontal view of *Magneuptychia iris* (based on 2021-FLP-IMM-0382).

Ichnanthus Beauvois (Panicoideae: Paspaleae), *Lasiacis* Hitchc., *Andropogon* L. (Panicoideae: Andropogoneae), *Paspalum* L. (Panicoideae: Paspaleae), *Pharus* P. br., *Orthoclada* P. Beauvois (Panicoideae: Zeugiteae), and *Guadua* Kunth (Bambuseae: Guaduinae). However, the study does not explicitly state which of the genera were utilized by *P. terrestris* and adult images of reared materials were not available to confirm their identification. Notwithstanding this situation, it is reasonable to assume that *P. terrestris* was correctly identified in Murray (2001) considering that the identification of this taxon appears to be correct in the same author's subsequent work, Murray & Prowell (2005). Therefore, our record of *Lasiacis ligulata* as a natural host plant for *P. terrestris* at FLP is the first species-level record of a natural host plant for this taxon. This record is consistent with many other host plant records for euptychiine species, most of which are in the plant family Poaceae. *Lasiacis ligulata* grows in abundance along forest edges at FLP, and this grass species is recorded as a natural host plant for some euptychiine taxa (e.g., *Taygetis rufomarginata* Staudinger, 1888; Baine *et al*., 2019); it is also accepted in captivity by some species known to feed on other Poaceae species at the study site (e.g., *Paryphthimoides brixius* (Godart, [1824]; Corahua-Espinoza *et al*., 2022). This observation suggests *P. terrestris* may well be found on other host plants at FLP. However, based on our field observations, a given euptychiine species appears to be repeatedly found on the same species in the family Poaceae at the study site, such as *Magneuptychia iris* documented herein (four individuals all found on *P. virescens*), and further sustained fieldwork is required to provide insights into the diet breadth of *P. terrestris*. We were unable to find any host plant records for *Magneuptychia iris* in existing studies, including Murray (2001) where this species is documented under the specific epithet *ayaya*, thus, to our knowledge, *Pharus virescens* is the first reported host plant record for this taxon. *Pharus virescens* is not reported as a host plant for any euptychiine taxa in Beccaloni *et al.* (2008) nor Janzen & Hallwachs (2018); however, several additional euptychiine species have been documented on this grass species at FLP (Corahua-Espinoza *et al*., in prep.). *Pharus virescens* is not present throughout the year at the study site, as it dies back during the dry season; therefore, this observation suggests that this taxon may utilize different host plants which await confirmation based on future fieldwork. Therefore, there remains much to explore in terms of natural host plant use of these two euptychiine species, and the generation of further natural host plant records for euptychiines in the southwestern Amazonian euptychiine diversity hotspot would be extremely valuable towards exploring this group's diet breadth and in understanding their diversity in the region.

The two euptychiine species in this study are scattered across two major clades recovered within Euptychiina, and our study shows some morphological affinities by comparing taxa with known immature stages within these clades. For example, *Magneuptychia iris* is recovered as a member of the so-called "*Pareuptychia* clade" (*sensu* Murray & Prowell (2005)) in Espeland *et al.* (2019), and the ultimate instar and pupa overall resemble those stages of *Optimandes eugenia transversa* (Weymer, 1911) and species in *Pareuptychia* Forster, 1964 (Murray, 2001; Willmott *et al.*, 2019), mainly by sharing these following characters: 1) greenish body with a dorsal stripe; 2) head capsule with a pair of short and conical orangeish scoli on vertex; 3) black stemmata (based on live pictures); 4) pupa greenish, short and smooth, with few scattered spots on abdomen. It must be noted that several morphological characters are also discussed in Murray (2001) to support a similar relationship found in that work ((((*Pareuptychia occirhoe* (Fabricius, 1776) + *Pareuptychia hesionides* (Forster, 1964)))) + *Pareuptychia metaleuca* (Boisduval, 1870))) + *Cepheuptychia cephus* (Fabricius, 1775)) + *Magneuptychia ayaya*). For example, the pore Pb being located postero-basal to P2 (i.e., distal primary seta on scolus) in the first instar is considered as synapomorphic for *Pareuptychia* - *M*. "*ayaya*" clade in Murray (2001). Albeit there is a limited number of satyrine taxa coded for cladistic analysis in Murray (2001), a matrix consisting of more than 150 characters based on immature stages is remarkable and the work undoubtedly serves as a baseline, as well as a vital foundation, for exploring satyrine immature morphology. *Paryphthimoides terristris* is a taxon recovered in the so-called "*Splendeuptychia* clade", which is perhaps the most species-rich major clade within the subtribe, only rivaled by the "*Taygetis* clade" (*sensu* Murray & Prowell (2005)) in terms of its species diversity, with both of these two clades containing over 80 described species each. Nevertheless, the available life history information for taxa in the "*Splendeuptychia* clade" remains sparse, reflecting our poor knowledge of euptychiine early stage biology as a whole. For example, despite *Paryphthimoides* Forster, 1964 being recovered as a monophyletic entity accommodating eight species (Zacca *et al*., 2020), the present study is one of the few sources of information for its natural host plant and immature stages. Murray's (2001) findings on *P. terrestris* and Corahua-Espinoza's (2022) report on *Paryphthimoides brixius* (Godart, [1824]) are the two other existing works that contribute towards knowledge of the early stage biology of *Paryphthimoides*. Nevertheless, Murray's (2001) mature larva image for *P. terrestris* (Fig. 2.12B) is insufficient to discern any characters for consistency and we herein discuss features based solely on a single individual described above. Based on some available studies, as well as unpublished data, on early stage biology regarding taxa in the "*Splendeuptychia* clade" (e.g., Singer *et al*., 1983; DeVries, 1987; Murray, 2001; Corahua-Espinoza *et al*., unpublished data), there appear to be two recurring characters observed in this clade: 1) first instar having a semi-translucent body with orangeish stripes; 2) somewhat mottled pupa with bright protuberances along the dorsal surface of the abdomen. Collectively, sustained effort aimed at documenting immature stages of butterflies in the Neotropics, particularly in diverse regions such as the Peruvian Amazon, is extremely valuable towards filling in gaps where our knowledge lags far behind. Some relevant studies on euptychiine immature stages have shown several putative synapomorphic characters based on caterpillar morphology to refine taxonomic hypotheses (e.g., Corahua-Espinoza *et al*., 2022; Nakahara *et al*., 2022), and we continue to contribute towards a better understanding of Neotropical butterfly taxonomy, ecology, and evolution by revealing the life history of butterflies in one of the most diverse regions on the planet.

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A new subspecies of *Mechanitis lysimnia* from southern Amazonia (Nymphalidae: Danainae: Ithomiini)

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Abstract: A new ithomiine butterfly, *Mechanitis lysimnia tapajona* Freitas & Mota **ssp. nov.**, is described from four localities in southern Amazonia. This taxon is very similar to the subspecies *Mechanitis lysimnia nesaea*, but can be distinguished by the orange hindwing discal cell (which is yellow in *M. l. nesaea*). The recognition of *Mechanitis lysimnia tapajona* **ssp. nov.** is significant since it represents a subspecies of *Mechanitis lysimnia* occupying the 'Tapajós center of endemism', filling the largest distribution gap for this species in South America.

Key words: Amazon Forest, butterfly, Mechanitina, Solanaceae.

INTRODUCTION

The genus *Mechanitis* Fabricius, 1807 (Nymphalidae: Danainae: Ithomiini) includes five species and 48 described subspecies distributed in forest throughout the Neotropical region, from Mexico to northern Argentina (Fox, 1967; Brown, 1979; Brévignon, 2007; Hill *et al.*, 2012). Species of *Mechanitis* are in general associated with open and sunny habitats, such as forest edges, clearings and secondary vegetation, with some species commonly found in urban areas (Brown, 1992; Giraldo *et al.*, 2014, Carvalho *et al.*, 2019 and references therein). All known species in the genus lay clustered eggs and larvae are gregarious, feeding on several species of Solanaceae (Drummond & Brown, 1987; Willmott & Freitas, 2006; Hill *et al.*, 2012).

With 13 described subspecies, *Mechanitis lysimnia* (Fabricius, 1793) is the most widespread species, ranging from central Mexico to the province of Buenos Aires and the east Andean slopes of the Argentinian provinces of Jujuy to Mendoza (Brown, 1979). Although *M. lysimnia* is common and broadly distributed, a large gap with no records is present in northern Mato Grosso and southern Pará, in a region that partially overlaps the 'Tapajós center of endemism' (Brown, 1977a,b, 1979).

Recently, a specimen of *Mechanitis lysimnia* collected by LLM in Alta Floresta (northern Mato Grosso) showed a color pattern different from any described subspecies. Subsequently, three additional specimens from "Igarapé XV de Novembro" collected by K. S. Brown Jr. and three from Alvorada da Amazônia collected by LRV (both in southwestern Pará, about 114 km northwest and 240 km north of Alta Floresta, respectively), a photograph of a live adult in Alta Floresta and a photograph of a live adult from Parauapebas (Pará, about 800 km northeast of Alta Floresta), confirmed that this is a well-defined, undescribed subspecies. Accordingly, the present paper describes this new subspecies of *Mechanitis lysimnia* from southern Amazonia.

MATERIALS AND METHODS

Adult specimens of the new taxon were examined in two collections in Brazil: **MNRJ**: Museu Nacional, Universidade Federal do Rio de Janeiro, Rio de Janeiro, Rio de Janeiro, Brazil; **ZUEC**: Zoological Collection, Museu de Diversidade Biológica da Universidade Estadual de Campinas, Campinas, São Paulo. Approximately 1400 specimens of *Mechanitis lysimnia* subspecies were also examined in multiple public and private collections in South America, USA and Europe. In addition, photographs of Neotropical butterfly type specimens taken by Gerardo Lamas and available in Warren *et al.* (2017) and the photographs of *Mechanitis lysimnia neukircheni* Neild, 2008 (Neild, 2008), *Mechanitis lysimnia bipuncta* W. Forbes, 1948 and *Mechanitis lysimnia solaria* W. Forbes, 1948 (Forbes, 1948, Brown 1977b) were also consulted and compared with the new taxon described here.

Field work was conducted by LLM and LRV in two forested regions in the Brazilian states of Mato Grosso and Pará (from 2015 to 2021), respectively, when adult habitats and behavior were studied. Photographs of live individuals available on the

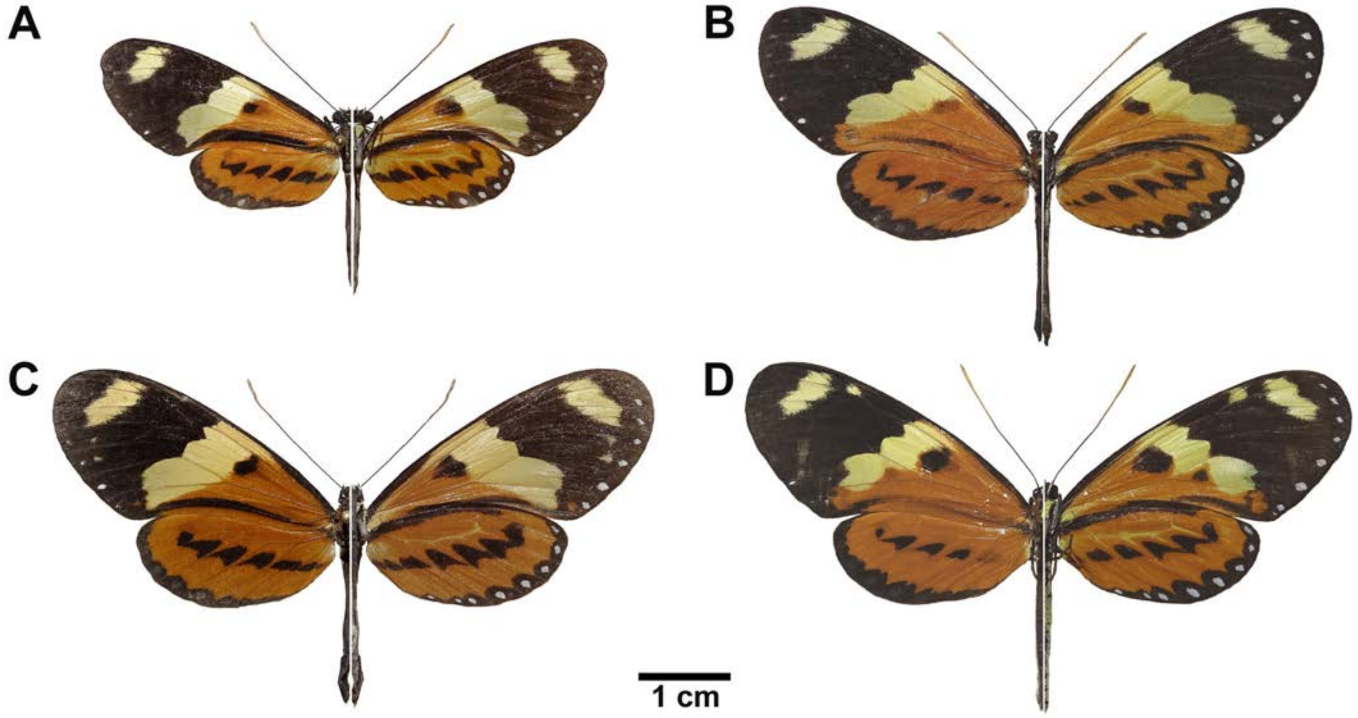

Figure. 1. *Mechanitis lysimnia tapajona* **ssp. nov.** A. Holotype male; B, C, D. Three female paratypes (MN-LEP 2741, MN-LEP 2742 and ZUEC-LEP 11198, respectively). Left= dorsal; Right = ventral. Scale bar = 1 cm.

internet were also examined from three websites (iNaturalist, Flickr and Facebook social media) using the name of the species "*Mechanitis lysimnia*" in an exhaustive search, and for Facebook this search was focused on groups related to insect photography.

Mechanitis lysimnia tapajona Freitas & Mota, **ssp. nov.**

Figs. 1-3

Description and diagnosis. Male (Fig. 1A, 2C). Antennae basal half black and apical half yellow, 13-14 mm in length (n=2), with 34 antennomeres; club with 11 antennomeres, not conspicuously developed (n=1). Thorax black with a thin white dorsal line; patagium orange. Forewing length 26-28 mm (n=3); hindwing length 16-17 mm (n=3). Forewing pattern similar on both surfaces: basal third orange with a central black spot (triangular in some individuals) in discal cell, middle section yellow, last third black with a large apical yellow spot; a series of small marginal white dots in intervenal spaces from apex to CuA_1-CuA_2 on ventral side. Hindwing ground color orange, including discal cell (an additional smaller black spot at stalk of CuA_2 near discal cell is present in one individual); on ventral surface, discal veins are covered by yellow scales; a costal black bar from anal margin to apex, merging to a broad marginal scalloped black border from M_1 to 3A, these with marginal white dots in intervenal spaces on ventral surface; a series of postdiscal black trapezoidal spots extend from basal inner margin to end of discal section; a single beige hair pencil typical of species at dorsal costal region. **Female** (Figs. 1B-D, 2D). Very similar to male, with more rounded forewings. On forewing, smaller yellow postmedian and/or marginal spots, in addition to a large apical spot, are present in two out of three examined individuals. Antennal length 15-16 mm (n=4), with 37-39 antennomeres; club with 13-14 antennomeres, not conspicuously developed (n=3). Forewing length 32-34 mm (n=4); hindwing length 20-22 mm (n=4).

Mechanitis lysimnia tapajona **ssp. nov.** is very similar to *Mechanitis lysimnia nesaea* Hübner, [1820], particularly individuals resembling the form *sulphurescens* Haensch, 1905, which has a single subapical yellow spot, lacking the yellow postmedian spots. The main difference is the predominantly orange hindwing discal cell of *M. lysimnia tapajona* **ssp. nov.**, which is completely yellow in *M. lysimnia nesaea*.

Type material. Holotype (Fig. 1A): Male, deposited in the Zoological Collection of the Museu de Diversidade Biológica da Universidade Estadual de Campinas (ZUEC), Campinas, São Paulo, Brazil. Labels on the holotype (Five labels separated by transverse bars): /HOLOTYPUS / Brazil, Pará, Novo Progresso, Alvorada da Amazônia, Córrego rio Quico/ Arco-íris, -7.291835° -55.311290°, 20.VII.2021, L[ucius]. R[abello]. Vasconcellos *leg*. / LBR1923/ AHBR 427/ Holotypus *Mechanitis lysimnia tapajona* Freitas & Mota *det*. 2021 / ZUEC LEP 11197/. **Paratypes** (all from Brazil) (Figs. 1B-D): *Mato Grosso*: Alta Floresta, Cristalino Lodge, 9.VI.2016, 1 female, L[uísa]. L[ima]. Mota *leg*., LLM720, plot7, 15:51, ZUEC-LEP 11198 (ZUEC). *Pará*: Novo Progresso, Alvorada da Amazônia, Córrego rio Quico/Arco-íris, -7.291835° -55.311290°, 21.VII.2021, 1 female (LBR 1924, AHBR 428, MN-LEP 2742), 23.VII.2021, 1 female, L[ucius]. R[abello]. Vasconcellos *leg*., (LBR1925, AHBR 429, MN-LEP 2741) (MNRJ); Novo Progresso, Região XV de Novembro, Serra do

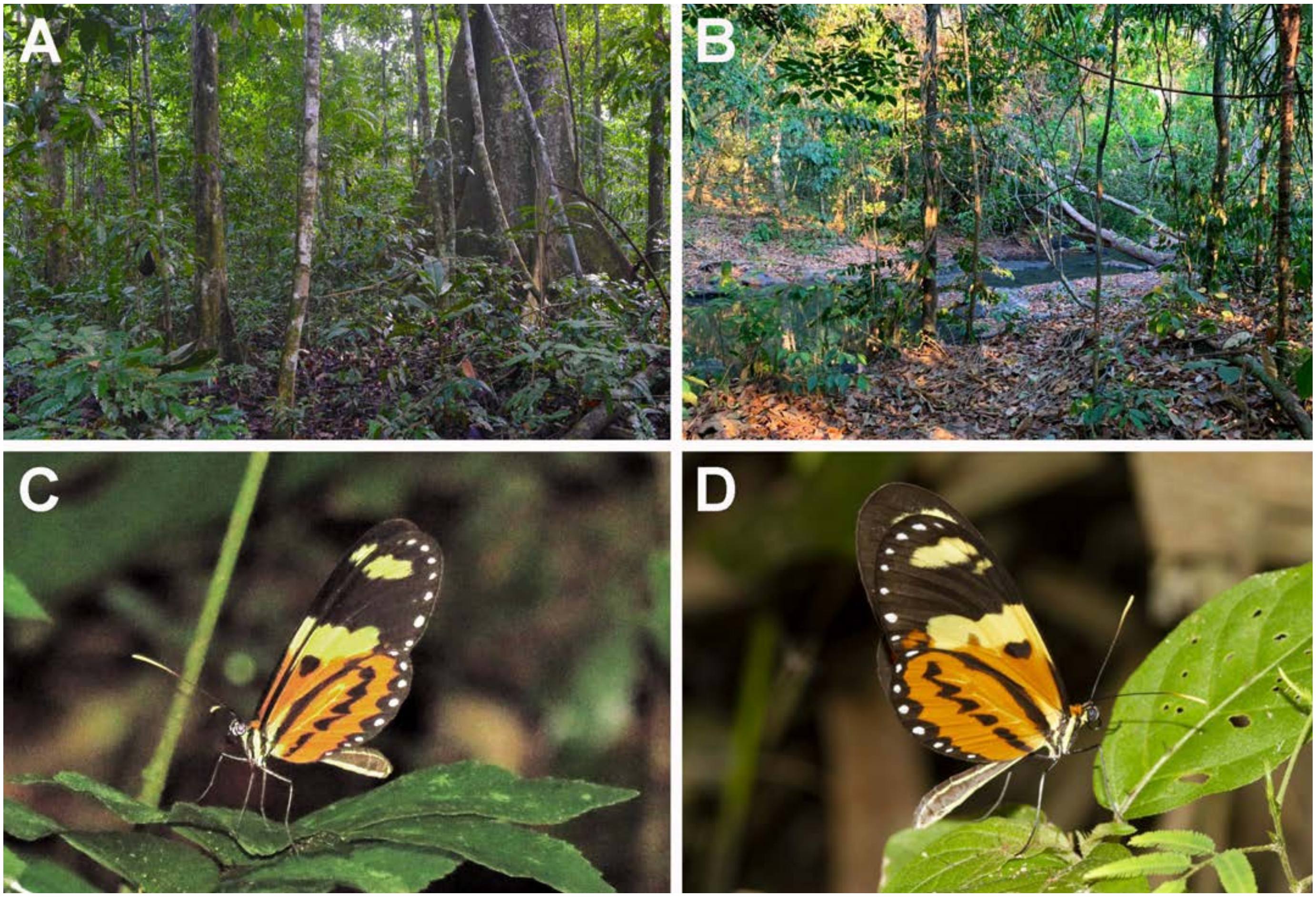

Figure. 2. Habitats and adults of *Mechanitis lysimnia tapajona* **spp. nov**. A. View of the interior of "Terra firme" Forest at Cristalino Lodge, Mato Grosso; B. Riparian Forest in the region of Alvoradada Amazônia, Novo Progresso, Pará (photograph by Clair Royer). C. Adult male from Cristalino, Mato Grosso (photograph by Sidnei Dantas); D. adult female from Parauapebas, Pará (photograph by Filho "Manfredini").

Cachimbo, 9°27'41.7"S 54°51'30.2"W, 22.X.1977, 2 males and one female, K[eith]. S[palding]. Brown Jr. *leg*., (ZUEC LEP 11273, 11274, 11275) (ZUEC).

Etymology. This subspecies name is treated as a noun in apposition and refers to the association of this taxon with the 'Tapajós center of endemism' (*sensu* Brown 1977a, 1979).

Taxonomy and variation. Based on the few known individuals (seven specimens and two images), variation in the forewing includes the size of the yellow apical spot, the presence of additional small yellow postmedian and/or marginal spots, the size and shape of the black discal spot in the orange basal area, and the presence of an additional black spot at the base of vein CuA_2 near the discal cell. In one of the paratypes the black discal spot is present only on the ventral surface (Fig. 1B); in the anal angle, a spot of variable size may be present or absent. On the hindwing, the size of the postdiscal black trapezoidal spots varies, and in some individuals, these are loosely connected, almost forming a continuous postdiscal black bar.

Distribution. This subspecies is known from only four localities in southern and southeastern Amazonia: 1) the region of "Cristalino Lodge" (9°35'51"S, 55°55'52"W), located near the west banks of the Cristalino River, Alta Floresta, northern Mato Grosso State (near the border with Pará State); 2) the riparian forests of the stream "Córrego rio Quico/Arco-íris" (7°17'30.6"S, 55°18'40.6"W), Alvorada da Amazônia, Novo Progresso, southern Pará State; 3) the riparian forests near the "Igarapé XV de Novembro", near the Mato Grosso/Pará border (9°27'41.7"S 54°51'30.2"W), Novo Progresso, southern Pará State; and 4) Carajás National Forest, Parauapebas, Pará State (6°04'02.8"S, 49°55'00.4"W) (https://www.inaturalist.org/observations/50786492) (Fig. 3).

Habitat and behavior. The few known individuals were captured in forest habitats not far from water bodies (Fig. 2A, B). The host plant and immatures are unknown, although it is expected that larvae will be gregarious and feed on Solanaceae, as with other species of *Mechanitis*, including several other subspecies of *M. lysimnia* (Drummond & Brown, 1987; Willmott & Freitas, 2006; Hill *et al.*, 2012).

DISCUSSION

The discovery of this new subspecies of *Mechanitis lysimia* within the area known as the 'Tapajós center of endemism' is an important finding, since this was one of the

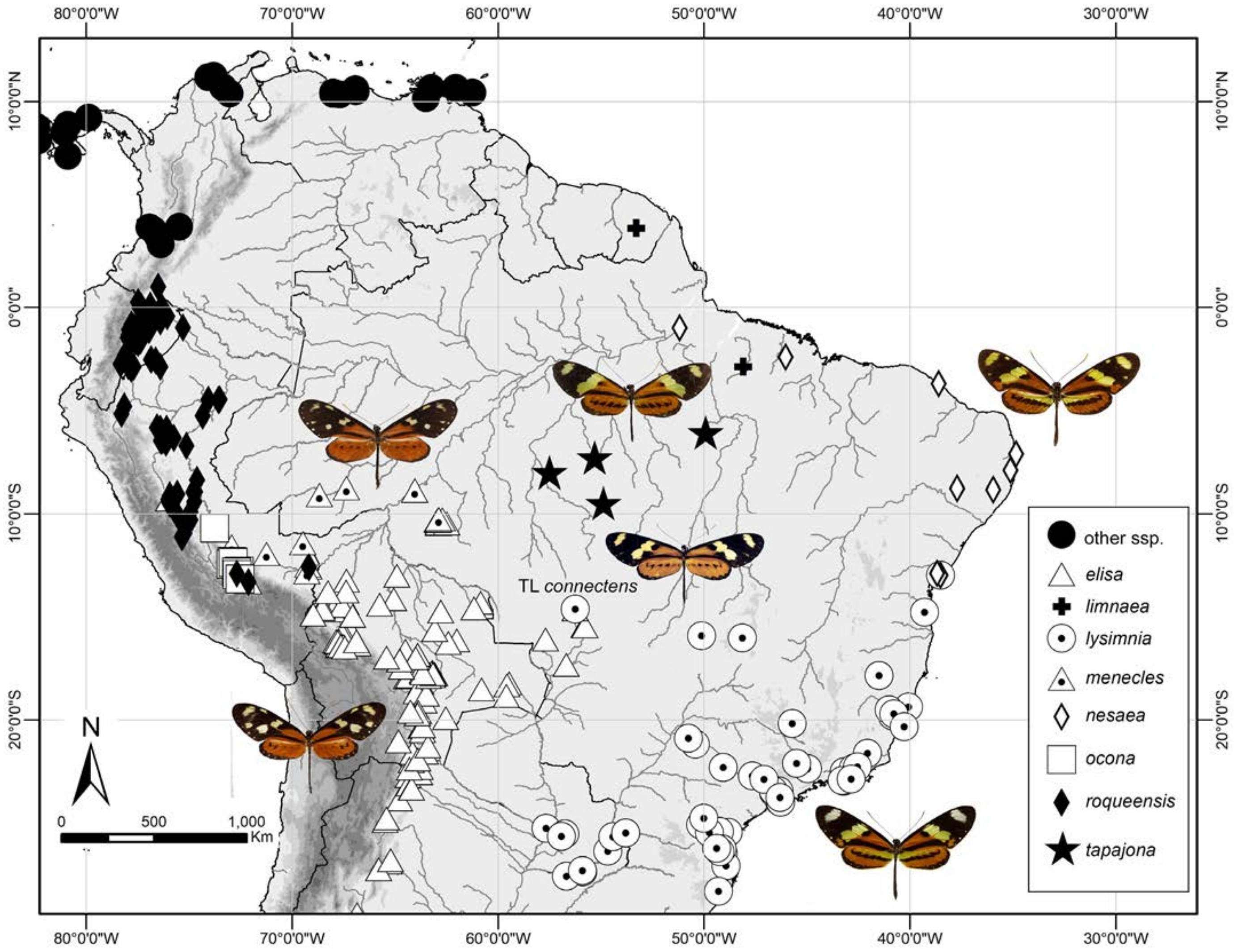

Figure 3. Distribution map showing the geographic distribution of *M. lysimnia tapajona* **ssp. nov.** in relation to other known subspecies of *M. lysimnia*. The image of "*connectens*" is of its holotype, illustrated in the website "Butterflies of America" (Warren *et al.,* 2017).

few centers of butterfly endemism where a local form of *M. lysimnia* was unknown, representing the largest distribution gap for this species in South America. The fact that this subspecies was unknown until now may relate to it being an uncommon butterfly in the region; a single individual was collected in the region of the Cristalino River after more than 700 hours of field work (LLM and AVLF), including a whole year of sampling by the first author. Therefore, although *M. lysimnia tapajona* **ssp. nov.** is known from only four localities in southern and southeastern Amazonia, it could potentially occur at similarly low density throughout the large area defined by the upper courses of the rivers Tapajós and Araguaia, in the Brazilian states of Pará and northern Mato Grosso.

Some phenotypes similar to *M. lysimnia tapajona* **ssp. nov.** have been previously reported, but they were considered to be part of the variation in the hybrid populations previously known as *M. elisa connectens* Talbot, 1928 (= *Mechanitis lysimnia elisa* (Guérin-Méneville, [1844])). In his revision of "Mechanitini" (now Mechanitina), Fox (1967) stated that: "As the name suggests, *connectens* links *elisa* [including populations currently named as *Mechanitis lysimnia menecles* Hewitson, 1860] with *nesaea* and *lysimnia*; dark individuals are quite similar to *elisa* and light individuals are very close to *nesaea*" (see all subspecies in Fig. 3). However, the present results show that, in spite of the low number of known individuals, *M. lysimnia tapajona* **ssp. nov.** represents a relatively stable phenotype ranging from northern Mato Grosso to east Pará, and the lighter phenotypes mentioned by Fox (1967) likely represent intergrades with the new subspecies here described.

In this study we show that the apparent Brazilian gap in the distribution of the widespread species *M. lysimnia* may be a sampling artifact, as suggested for several putative rare butterfly species that have been described or reported in new Brazilian localities in recent years (e.g., Greve *et al.*, 2013; Rosa *et al.*, 2017, 2021; Barbosa *et al.*, 2020 and references therein), including a Satyrini described from individuals also collected at Cristalino Lodge (Freitas *et al.*, 2019). As such, this study shows the importance of continuous sampling of butterflies in the Neotropical region, including both well sampled and poorly known regions, to better document the distribution of both relatively common as well as rarely observed species.

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Immature stages of *Splendeuptychia ambra* (Nymphalidae: Euptychiina) and the diversity of immature morphology within *Splendeuptychia*

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Abstract: The immature stages are described for *Splendeuptychia ambra* (Weymer, [1911]). The eggs are rounded, pale yellow, smooth, and lack markings. The caterpillars pass through four instars; the first instar is pale cream with reddish longitudinal stripes and the head is black bearing a pair of very short scoli; the last (fourth) instar is beige with a pair of short caudal filaments on the last segment, laterally striped with thin lines and a darker dorsal stripe; the head is olive-brown with a pair of short scoli. The pupae are short and smooth, mostly light brown, mottled with dark brown stripes, with short rounded ocular caps and with very short paired subdorsal projections on the abdominal segments. The immature stages of *S. ambra* are compared with those of other species of the non-monophyletic genus *Splendeuptychia* that belong to three different clades within the subtribe Euptychiina.

Resumo: Os estágios imaturos de *Splendeuptychia ambra* (Weymer, [1911]) são descritos. Os ovos são esféricos, amarelo claros, lisos e sem marcas. As lagartas passam por quatros instares; o primeiro instar é bege com faixas longitudinais avermelhadas e a cabeça é preta com um par de escolos muito curtos; o quarto e último instar é bege com um par de filamentos caudais curtos no último segmento, com padrão de finas estrias laterais e uma faixa dorsal escura; a cabeça é marrom olivácea com um par de escolos curtos. A pupa é curta e lisa, predominantemente marrom claro marcada com faixas e pintas marrom escuras, com capas oculares curtas e pares de projeções laterais muito curtas nos segmentos abdominais. Os estágios imaturos de *S. ambra* são comparados com aqueles de outras espécies do gênero não monofilético *Splendeuptychia* pertencendo a três diferentes clados dentro de Euptychiina.

Key words: Atlantic Forest, Brazil, Satyrinae, Satyrini

Palavras chave: Brazil, Mata Atlântica, Satyrinae, Satyrini

INTRODUCTION

With 437 described species (Zacca *et al*., 2021), the subtribe Euptychina (Nymphalidae: Satyrinae) is one of the most species-rich butterfly groups, but also one of the less well known. Despite a recent large collaborative international project aiming to fill several knowledge gaps in Euptychiina (http://www.flmnh.ufl.edu/museum-voices/euptychiina/), there are still important areas beyond taxonomy and systematics that need study, such as behavior, ecology and natural history. One of these areas concerns the description of their immature stages, and even considering a number of recent efforts (e.g. Freitas *et al*., 2019a,b, 2021a,b; Nakahara *et al*., 2020, 2022; Tejeira *et al*., 2021 and references therein), immature stages are mostly unknown for the subtribe, with entire genera lacking any information concerning their life cycle, such as *Caeruleuptychia* Forster, 1964, *Emeryus* Zacca, Casagrande & Mielke, 2020 and *Malaveria* Viloria & Benmesbah, 2021. Moreover, for some large genera, immature stages are described for only a couple of species, for example *Euptychia* Hübner, 1818, *Forsterinaria* Gray, 1973, *Magneuptychia* Forster, 1964 and *Splendeuptychia* Forster, 1964, among others (e.g. DeVries, 1987; Kaminski & Freitas, 2008; Freitas *et al*., 2016a,b, 2019a; See *et al*., 2018; Janzen & Hallwachs, 2021).

The genus *Splendeuptychia* currently includes 25 described species and a similar number of undescribed species occurring from Mexico to northern Argentina (Lamas, 2004; Rosa *et al*., 2021 and references therein, Zacca *et al*., 2021). As with several other large Euptychiina genera, *Splendeuptychia* is non-monophyletic with species spread over three different clades within the tribe (Peña *et al*., 2010; Marín *et al*., 2017; Freitas *et al*., 2018; Espeland *et al*., 2019, Rosa *et al*., 2021). Published information on the immature stages of *Splendeuptychia* is surprisingly limited considering it contains almost 50 species, with detailed accounts only available for *Splendeuptychia quadrina* (Butler, 1869) (See *et al*., 2018) and *Splendeuptychia furina* (Hewitson, 1862) (Corahua-Espinoza *et al*., 2022), and a brief textual description of *Splendeuptychia kendalli* Miller, 1976 (Kendall, 1978). Accordingly, in an attempt to improve knowledge of the immature stages of *Splendeuptychia*, the present paper describes for the first time the immature stages of *Splendeuptychia ambra* (Weymer, [1911]), an uncommon

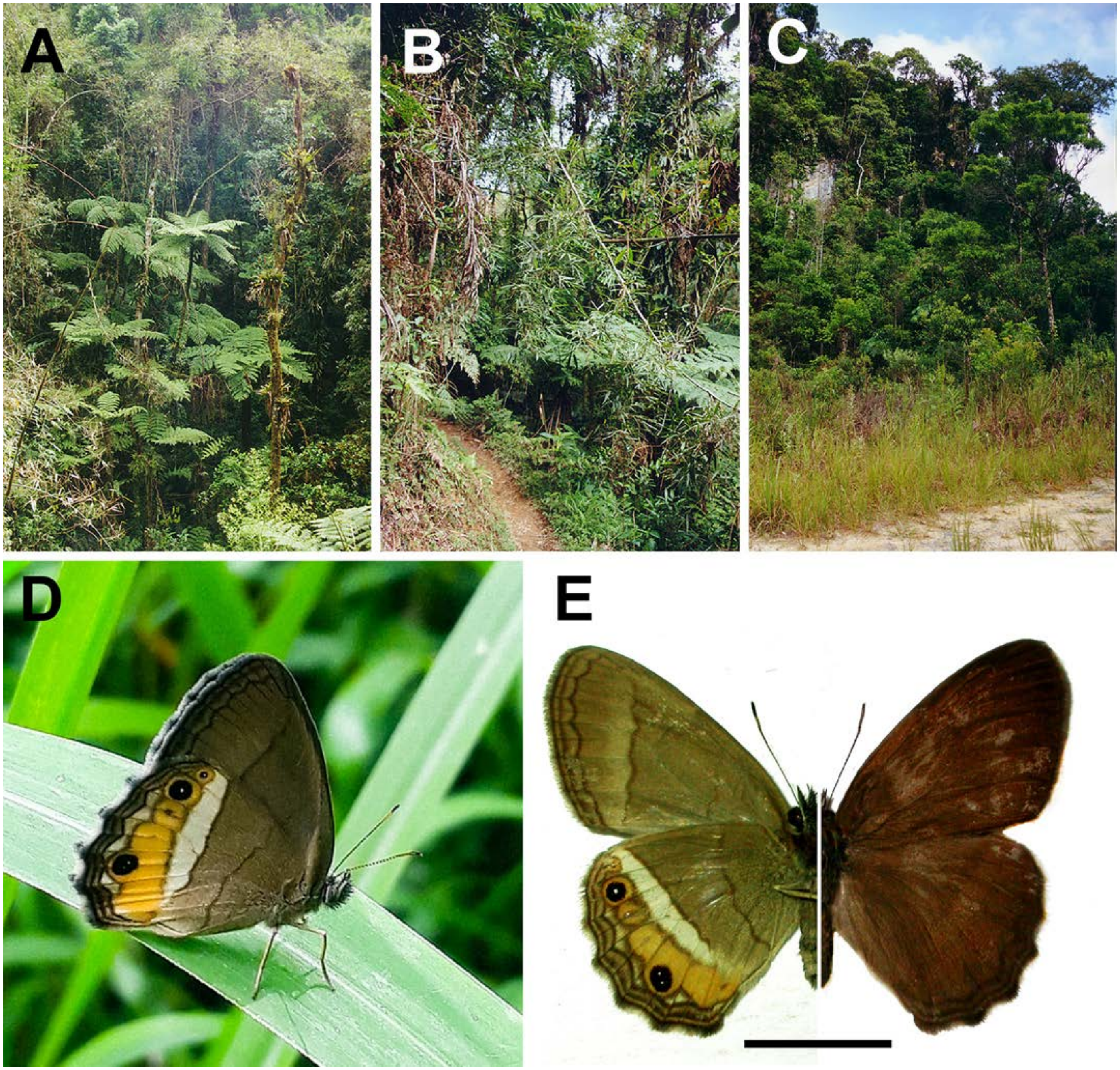

Figure. 1. Habitats and adults of *S. ambra*. **A, B, C.** Three views of the wet montane forests in the region of Morro Grande State Reserve, Cotia, São Paulo; **D.** Live adult of *S. ambra* from Teresópolis, Rio de Janeiro (photograph by Luan Felipi P. de Andrade); **E.** A reared adult of *S. ambra* (present study), ventral left, dorsal right (black bar = 1 cm).

species from the Atlantic Forest in southeastern Brazil, and compares them with other species of Euptychiina.

MATERIAL AND METHODS

Adults and immatures of *S. ambra* (Figs. 1, 2) were studied in April 2002 in Morro Grande State Reserve (23°39’−23°50’ S, 46°55’−47°01’ W) in the Atlantic Forest of southeastern Brazil, a large block of forest (> 10,000 ha) mostly in advanced stages of succession, but also containing large patches of well-preserved original montane forest (Fig. 1A, B, C). Elevation varies from 900 to 1000 m, average monthly temperatures vary from 11°C to 27°C and the average rainfall is 1400 mm (see details of the study area in Uehara-Prado *et al*., 2004, 2007).

Eggs were obtained from a wild-captured female kept in a plastic bag and provided with leaves of a Brazilian native bamboo species (Poaceae), following Freitas (1991). Larvae were reared in plastic containers cleaned daily and provided with fresh plant material every two or three days (following Freitas, 2007). Data were recorded on morphology and development time were recorded for all stages. Dry head capsules and pupal cases were retained in glass vials. Immature stages were fixed in Kahle-Dietrich solution (Triplehorn & Johnson, 2005). Voucher specimens of the immature stages and adults were deposited

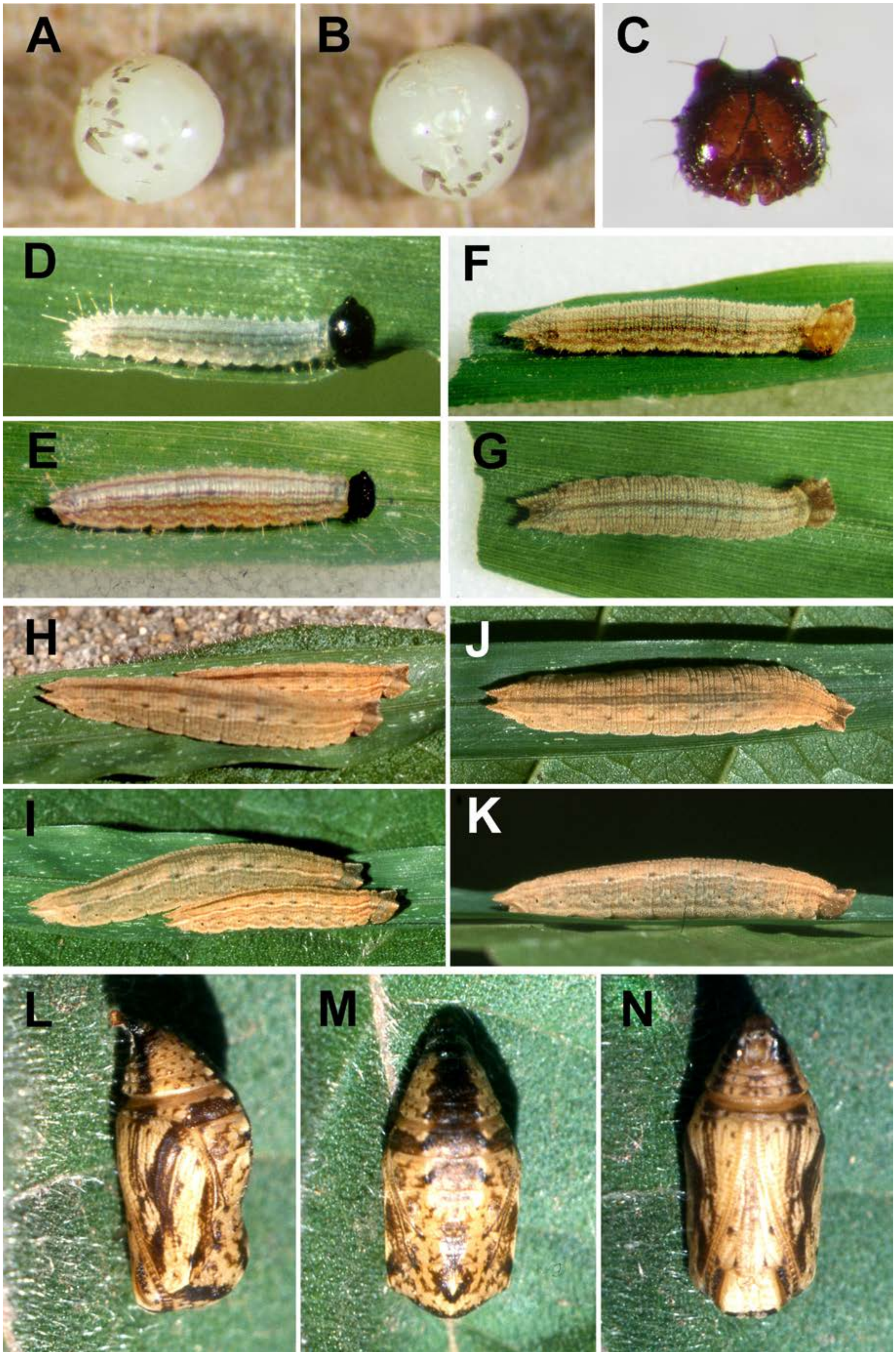

Figure. 2. Life stages of *S. ambra*. **A, B.** Egg fixed in Kahle-Dietrich solution (lateral, dorsal); **C.** First instar head capsule; **D, E.** First instar (early lateral and late dorsal, respectively); **F, G.** second instar (lateral, dorsal); **H, I, J, K.** fourth (last) instars in different views; **L, M, N.** Pupa (lateral, dorsal, ventral).

in the André V. L. Freitas collection, part of the Zoological Collection of the Museu de Diversidade Biológica (ZUEC-AVLF), Universidade Estadual de Campinas, Campinas, São Paulo, Brazil.

Measurements were taken for all life stages and morphology was studied using a Leica®MZ7.5 stereomicroscope equipped with a micrometric scale. Egg size is presented as height and diameter, and head capsule size is the distance between the most external stemmata (as in Freitas, 2007). Terminology for the early stages description follows García-Barros & Martín (1995) for eggs and Stehr (1987) for larvae and pupae.

RESULTS

Egg (Fig. 2A, B). Rounded, pale yellow, smooth, with no visible markings and ridges (Fig. 2). Height and diameter 1.3 mm (n = 1); duration 6 days (n = 5) and 2 days (n = 1).

First instar (Fig. 2C, D, E). Head capsule width 0.72-0.8 mm; head scoli 0.10-0.12 mm (n = 4). Head pale brown, bearing a pair of very short scoli on vertex, each with two long narrow black setae. Third stemma larger than other stemmata. Body beige with reddish longitudinal stripes; a pair of short caudal filaments on last abdominal segment. Legs and prolegs light brown. Maximum length 5 mm. Duration 7-8 days (n = 4).

Second instar (Fig. 2F, G). Head capsule width 1.02-1.08 mm; head scoli 0.22-0.28 mm (n = 3). Head dark brown, with two short scoli on vertex. Body brown, laterally striped with dark brown longitudinal lines, including a conspicuous dorsal stripe; caudal filaments short. Legs and prolegs light brown. Maximum length 10 mm. Duration 5-6 days (n = 4).

Third instar. Head capsule width 1.40-1.50 mm; head scoli 0.34-0.40 mm (n = 4). Similar to second instar in color and general shape. Maximum length 16 mm. Duration 8 days (n = 4).

Fourth (last) instar (Fig. 2H, I, J, K). Head capsule width 1.96-2.00 mm; head scoli 0.58-0.60 mm (n = 3). Head olive-brown with pale cream rounded markings. Body similar to third instar but larger; beige, with a weakly marked pattern of longitudinal thin lines; a subdorsal pale undulating stripe with dark patches in the intersegmental regions and a dorsal dark stripe. General profile thick and stout; a pair of short caudal filaments on last abdominal segment. Maximum length 22 mm. Duration 17 days (n = 2).

Pupa (Fig. 2L, M, N). Very short and smooth; mostly pale brown, mottled with dark brown stripes, with very short rounded ocular caps; cremaster broad and dark laterally; abdomen with a broad dorsal dark brown stripe, with very short paired subdorsal projections, slightly curved in last segments. Total length 9 mm. Duration 13 days (n = 2).

Behavior and natural history. *Splendeuptychia ambra* is known from a few localities of montane rain forest in the Atlantic Forest of southeastern Brazil, at elevations from 800-1400 m, with the exception of one record at lower elevation (220-250 m) from northern Argentina (Bustos, 2008; see additional records in Santos *et al*., 2018). Oviposition behavior was not observed in the field, and the natural host plant is unknown. In the laboratory, larvae easily accepted the small bamboo *Chusquea* cf. *ramosissima*, a native species from the region of Campinas, São Paulo (about 200 km far from the collecting site). Larvae are solitary and moved slowly and passed through four larval instars. Adults (Figs. 1D, E) are seldom observed in nature; in another study, only seven individuals (six males and a single female) were captured in baited traps over 36,000 trap-hours at the study site (Uehara-Prado *et al*., 2005), all in areas where bamboos were common inside a large block of well-preserved forest. Behaviors such as territorialism and courtship were not observed.

DISCUSSION

As previously mentioned, the genus *Splendeuptychia* is clearly non-monophyletic, with the species in this genus appearing in three distinct lineages of Euptychiina, namely: 1) the ‘*Splendeuptychia* clade’, which includes the type species of the genus, *Splendeuptychia ashna* (Hewitson, 1869); 2) the ‘*Pareuptychia* clade’; and 3) the ‘*Amphidecta* clade’ (clades names and composition following Espeland *et al*., 2019, and Rosa *et al*., 2021). Considering that the immature stages of butterflies usually provide important evidence of systematic relationships (e.g. Freitas & Brown, 2004, and Willmott & Freitas, 2006), the genus *Splendeuptychia* could be a good model group for testing this pattern within the Euptychiina.

Morphology and molecular data indicate that *S. ambra* is closely related to *S. ashna* within the ‘*Splendeuptychia* clade’ (Barbosa & Freitas, unpublished). Consistent with this hypothesis, its immature stages present several similarities with those of other species in this clade, such as the thick larvae, beige to brownish colored, bearing short head horns and a short stubby pupa with also short ocular caps and short paired lateral abdominal projections. These features are quite similar to those of other species in the ‘*Splendeuptychia* clade’, such as *Splendeuptychia* sp. (Fig. 3A-C), *Magneuptychia libye* (Linnaeus, 1767), “*Cissia*” *confusa* (Staudinger, 1887), “*Magneuptychia*” *pallema* (Schaus, 1902), *Paryphthimoides poltys* (Prittwitz, 1865) and *Malaveria grimon* (Godart, [1824]) (Singer *et al*., 1983; DeVries, 1987; Kaminski & Freitas, 2008; Janzen & Hallwachs, 2021; AVLF, unpublished).

In contrast, while the immature stages of *S. ambra* are similar to those of other members of the ‘*Splendeuptychia* clade’, they are quite distinct from other known species of *Splendeuptychia* belonging to the other two clades. For example, the immature stages of *Splendeuptychia doxes* (Godart, [1824]), *Splendeuptychia furina* (Hewitson, 1862), and *Nhambikuara mima* (Butler, 1867), all closely related and members of the ‘*Pareuptychia* clade’, have slender larvae bearing short head horns, and the pupae are slender, with short ocular caps (Fig. 3D-G; Corahua-Espinoza *et al*., 2022; AVLF, unpublished). These are reminiscent of the immature stages of *Taydebis melobosis* (Capronnier, 1874) and *Pareuptychia ocirrhoe* (Fabricius, 1776), both from the same clade (Freitas, 2003; Freitas *et al*., 2016). Finally, the immature stages of the *Splendeuptychia* species belonging to the ‘*Amphidecta* clade’ are distinct from all of the above. In *Splendeuptychia libitina* (Butler, 1870), *S. pagyris* (Godart, [1824]), *Splendeuptychia hygina* (Butler, 1877) and *Splendeuptychia quadrina* (Butler,

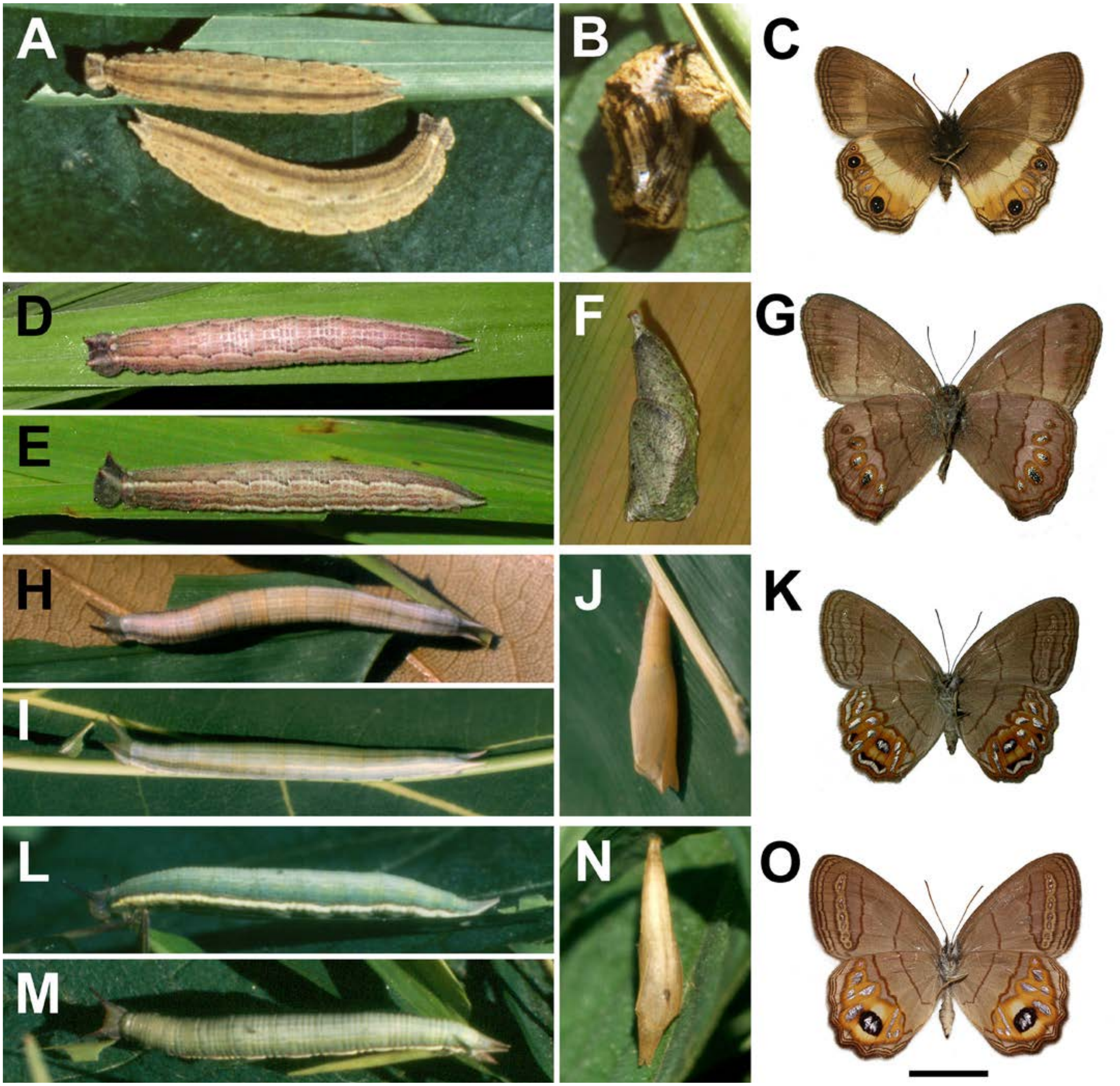

Figure. 3. Immature stages of *Splendeuptychia* species (all from Brazil). **A, B, C.** *Splendeuptychia* sp., fourth (last) instar, two larvae, pupa (lateral), reared adult (ventral), Alta Floresta, MT; **D, E, F, G.** *Splendeuptychia doxes*, fourth (last) instar (dorsal, lateral), pupa (lateral), São Luiz do Paraitinga, SP, adult (ventral), Caucaia do Alto, SP; **H, I, J, K.** *Splendeuptychia libitina*, fourth (last) instar (two dorsal views), pupa (latero-ventral), reared adult (ventral), Morro do Diabo State Park, Teodoro Sampaio, SP; **L, M, N, O.** *Splendeuptychia pagyris*, fourth (last) instar (lateral, dorsal), pupa (dorsal), reared adult (ventral), Morro Grande State Reserve, Cotia, SP. Acronyms for Brazilian states: SP = São Paulo, MT = Mato Grosso. All adults to scale; black bar = 1 cm.

1869), larvae are very slender and elongate, usually with greenish tones, bearing long head horns and long caudal filaments and their pupae are slender with conspicuous pointed ocular caps (Fig. 3H-O, See *et al*., 2018; AVLF, unpublished). However, although these characteristics roughly match those observed in *Amphidecta reynoldsi* Sharpe, 1890 (Freitas, 2004), there is not enough knowledge of the immature stages of the '*Amphidecta* clade' to allow more thorough comparisons.

The slender larvae with long head horns and the elongated pupae of the *Splendeuptychia* species belonging to the '*Amphidecta* clade' could benefit from camouflage when resting on narrow, elongated bamboo leaves that they feed on, as appears to be the case for the Pronophilina species *Eteona tisiphone* (Boisduval, 1836) (Freitas, 2002). Similar cases were reported in other species of Euptychiina and Hesperiidae, whose larvae feed on bamboos and other plants with thin leaves or leaflets, and have larvae slender bodies and a color patterns that suggest camouflage (Freitas, 2018, 2020; Freitas *et al*., 2019b). However, the present data show that bamboo-feeding Euptychiina do differ in some specific morphological structures of their larvae and pupae, such as body profile, size of the head horns and pupal shape (including the species of *Splendeuptychia* discussed here), suggesting that a number of factors are involved in the evolution of the morphology of Euptychiina immature stages (see also Corahua-Espinoza *et al*., 2022). A promising way to study the evolution of the early stages of Euptychiina is by mapping the major morphological characteristics onto the comprehensive and well supported phylogenies that are now available. In this way, as more information from immature stages becomes available, understanding of morphological and ecological evolution in the Euptychiina will be improved, opening new avenues of investigation in this species-rich and diversified butterfly clade.

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Scientific Note: The discovery of a second species of moth-butterfly (Lepidoptera: Hedylidae) in Jamaica, West Indies

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Abstract: The recent discovery of the moth-butterfly *Macrosoma cascaria* (Schaus, 1901), together with the already recognized *M. stabilinota* (Prout, 1932), results in a total of two species of *Macrosoma* (Hübner) known from Jamaica. Neither of these species are known to be present on either Cuba or Hispaniola, and there is no evidence so far of these being introduced accidentally to the island. Jamaica now lies far from any other landmasses, suggesting a possible Late Miocene origin, when the island was in closer proximity to Central America. The property on which *M. cascaria* was found is a protected wildlife haven, where the forested areas have been left virtually untouched for the last 150 years.

Key words: Blue Mountains, Jamaica, *Macrosoma*, Mandeville, mesic forest.

Species of *Macrosoma* (Hübner, 1818) (Hedylidae) are found from central Mexico south through Central America to northern South America, where they range from Colombia east to the Guianas, Surinam, and northern Brazil, south to Ecuador, Peru and central Bolivia and southeastern Brazil. Peru is the biological epicenter for *Macrosoma*, with some twenty-six species recorded. Although most Hedylidae are nocturnal, a few species are diurnal and are superficially similar in appearance to some butterflies, such as the Wood White (*Leptidea sinapis* (Linnaeus, 1758)), Pieridae, while also sharing some other structural and life history similarities with that butterfly family (Scoble, 1986; Scoble & Aiello, 1990).

Around the Caribbean, *Macrosoma rubedinaria* (Walker, 1862) (Fig. 1) is found in western and southern Mexico, through Central America to Colombia, east to northeastern Brazil, and south to Amazonian northern Peru and Bolivia, as well as Cuba, Trinidad, and Tobago. At one time this species was erroneously believed to occur in Jamaica (Barnes, 2001), and an unconfirmed report also suggested this insect was present on Hispaniola.

Trinidad has three additional species: *M. conifera* (Warren, 1897), *M. subordinata* (Warren, 1904), and *M. ustrinaria* (Herrich-Schäffer, 1854), (Cock, 2014; Cock & Alston-Smith, 2017b). Trinidad is faunistically aligned with South America, thus these records are not surprising, but they demonstrate the possible capability of some *Macrosoma* to disperse over water, reaching both Trinidad and Tobago from the mainland, a distance of not less than 11 km across the Gulf of Paria and an additional 30 km between Trinidad and the island of Tobago. However, these islands may have been connected during the late Pleistocene, permitting movement when sea levels would also have been lower during the height of the last glaciation from 11,000 to 13,000 years ago (Mychajliw *et al*., 2020). There has, however, been no direct connection between Cuba and the Yucatán, thus for *M. rubedinaria* to reach Cuba from the Yucatán would, at present, mean a flight of not less than 200 km. If this species has indeed reached Hispaniola, this would have required a second ocean crossing of 80 km across the Windward Passage; unlikely for this tiny moth, which has a wingspan of approximately 38 mm and a relatively weak flight.

As described in *Discovering Jamaican Butterflies and their Relationships around the Caribbean* (Turner & Turland, 2017), the first *Macrosoma* collected in Jamaica was a male *M. stabilinota* (Figs. 2-4) at Bath, St. Thomas Parish, by André Avinoff in 1937 (Fig. 5). The male of this species is superficially similar to the male and female of *M. rubedinaria*, with which it was first confused. However, *M. rubedinaria* displays a pair of small black discal spots on the dorsal forewing and a minute black discal spot on the dorsal hindwing. These markings are not present in *M. stabilinota*. Male and female *M. rubedinaria* are similar in appearance. The two species are further differentiated by the four small white subapical spots on the forewing, which are present only on the male of *M. stabilinota*. Also, the female of *M. stabilinota* displays a large forewing subapical arrowhead-shaped white spot, with two additional micro-spots above it, which are not present on the male of this species.

The first Jamaican female of *M. stabilinota* was collected at Jacks Hill, Kingston & St. Andrew Parish, by Ronald Bengry (from the Institute of Jamaica) in 1957. In 1963, Bernard Heineman, coauthor of *Jamaica and its Butterflies* (1972), collected a male and female in Port Antonio, Portland Parish. A fifth specimen, another male, was collected by Matthew Barnes, near Mavis Bank, St. Andrew Parish, in 1988 (Barnes, 2001). A further six specimens were observed and photographed near

Figure 1. *Macrosoma rubedinaria* at Matias Romero, Oaxaca, Mexico (photo courtesy of Juan Carlos García Morales).

Figure 2. ♂ *Macrosoma stabilinota* at Silver Hill Gap, St. Andrew Parish, 11 August 2018.

Silver Hill Gap, St Andrew Parish, between 2012 and 2014 (Turner & Turland, 2017). Finally, VT photographed a male *M. stabilinota* at 23:50 h on 3 December 2021, on an overcast night with a temperature of 19°C, in a forest clearing around 600 m from the site in Manchester Parish where *M. cascaria* was photographed. This represents the first specimen of *M. stabilinota* to be observed so far to the west in Jamaica.

A search for *Macrosoma* on the south side of the Cockpit Country north of Quickstep, Trelawny Parish, in west central Jamaica, was conducted in late July 2011. A further four nights were spent searching for this genus on the north side of the Cockpit Country near Windsor but without success. More extensive investigations are required.

There seems little reason why members of this genus should not be present in humid forested areas across the island, thus it was perhaps not surprising when VT and AH-S photographed a second species of *Macrosoma* at the site of Marshall's Pen, later identified as *M. cascaria* Schaus, 1901 (Figs. 6-7), representing the first record for this species in Jamaica. On 9 August 2021, heavy rain showers fell in the afternoon, but later cleared, leaving a partially overcast night sky with stars visible between clouds. The *Macrosoma* was observed at 19:59 h at a light source produced from a Honda Ex 350 generator with 110/350VA output, ballast and regulator, and 125W clear bulb placed in front of a large white collection sheet. The light was set up before sunset at 18:38 h and remained in place until 22:30 h. No further specimens were observed that evening. The insect was photographed using a Nikon D850 camera with a Micro Nikkor AF-S 105 mm lens and Nikon SB 800 Speedlight.

Figure 3. ♂ *Macrosoma stabilinota*, detail of right forewing of specimen at Figure 2.

Figure 4. ♀ *Macrosoma stabilinota* at Silver Hill Gap, St. Andrew Parish, 16 August 2014.

On the mainland, *M. cascaria* is found in Mexico from Mislanta, Veracruz and west central Tabasco, south through Central America to northern Venezuela, where species of *Croton* L. (Euphorbiaceae) and *Conostegia* D. Don (Melastomataceae) have been identified as larval food plants. Both of these genera are well represented in Jamaica (Adams, 1972). While possible accidental introductions of immature stages on plants from Central America to Jamaica cannot be discounted, the larval food plants and immature stages of these two species in Jamaica have not yet been discovered but are expected to be native plant species. It seems unlikely that there would be two separate introductions of this genus to the island, both of which would have had to survive on a relatively small number of imported plant seedlings or immediately adapt to using local larval food plants. Usually, the process of adapting to utilize unfamiliar native species of these plants would be expected to take place only over time. It is far more likely that both species of *Macrosoma* are native Jamaican species.

In summary, there are now two species of *Macrosoma* known from Jamaica; *M. stabilinota*, and the recently discovered *M. cascaria*. The nearest distance from Jamaica to the closest

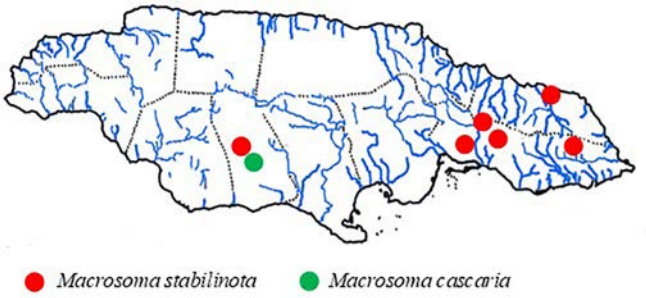

Figure 5. Distribution map of *Macrosoma* species in Jamaica.

Figure 6. *Macrosoma cascaria* at Marshall's Pen, Manchester Parish, 9 August 2021.

Figure 7. *Macrosoma cascaria*, right dorsal forewing detail from specimen depicted in Fig. 6.

Figure 8. Mesic forest and cattle pasture habitat at the moth trapping site, Marshall's Pen, Manchester Parish.

point of land in Honduras, where both these species occur, is approximately 1,027 km, a distance considered unlikely for such tiny moths to fly. Alternatively, these species may perhaps have reached the island when it was separated by as little as 200 km from the landmasses comprising the Nicaraguan Rise in the late Miocene, between about 23 and 5 million years ago (Iturralde-Vinent, 2006). For this reason, the DNA of both species of Jamaican *Macrosoma* should be investigated to determine if, over time, there has been enough divergence to support subspecific recognition.

The site where *M. cascaria* was recorded, Marshall's Pen (Fig. 8), is of significant ecological interest, being surrounded by habitations and lands degraded through quarrying for limestone and farming. Typical of a cattle property in Jamaica, Marshall's Pen property comprises a Great House, still used as a residence by the owner, Ann Haynes-Sutton, which is positioned among forested hills and a mostly linked network of pastures for grazing of beef cattle. More than 60 percent of the 125-hectare property is covered by mid-level mesic forest. The property is a declared Protected National Heritage Site, and it supports undisturbed forested areas and wildlife, including 330 plant species identified by the Institute of Jamaica's botanist George Proctor. These include rare species that may be indicators of old growth forests, such as *Pilostyles blanchetii* (Gardner) R. Br. (Apodanthaceae). Since 2018, more than 150 species of larger moths, some of these new Jamaican records, have been identified on this property. This total includes twenty-one species of Sphingidae, more than thirty species of Arctiinae, and seven species of Uraniidae (Epipleminae). Fifteen endemic species of butterflies are also known to be present. Among other fauna at Marshall's Pen are endemic species of Hylidae, including the endangered Jamaican Green Tree Frog (*Osteopilus wilderi* Dunn), Jamaican Laughing Frog (*Osteopilus brunneus* Gosse), Jamaican Snoring Frog (*Calyptahyla crucialis* Harlan), the endemic crab *Metopaulias depressus* Rathbun (Sesarmidae), whose life cycle is confined to bromeliads, and five anoles (Dactyloidae): *Anolis garmani* Stejneger, *Anolis valencienni* Duméril & Bibron, *Anolis grahami* Gray, *Anolis lineatopus* Gray, and *Anolis opalinus* Gosse. The property is also one of the most important sites for birds in Jamaica, with more than one hundred species observed, including twenty-three of the thirty Jamaican endemics. Less common species, crested quail dove (*Geotrygon versicolor* Lafresnaye) (Colombidae), and greater Antillean elaenia (*Elaenia fallax* (Sclaterare) (Tyrannidae), are present. The property is an overwintering site for migratory and vagrant bird species (Haynes-Sutton *et al.*, 2009).

This relative abundance of fauna and flora at Marshall's Pen property is a result of the fact that many of the forested hills have not been cleared in the last 150 years (although some have been subjected to selective harvesting of timber, sticks and posts) and some thickly forested often impenetrable rocky limestone outcrops, mostly at elevations between 650-690 m, have never been cleared, still largely retaining their original vegetation. Canopy heights within the forested areas reach up to 15-20 m. Undulating pasture lands between the outcrops are mostly at an elevation of 650 m. Selective and ongoing rewilding of the estate, together with best farming practices, where herbicides and insecticides are minimally used for management of pasture lands, potentially contribute to the enduring presence of endemic species. In spite of serious degradation of Jamaica's forests during the last 350 years, there are still many areas of primary forest or forest that have been allowed to regenerate with very little disturbance for long periods. This reveals that important habitat niches still exist in Jamaica where unexpected new species can still be found.

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Distribution and observations on the biology of *Telchin atymnius futilis* (Walker, 1856) (Castniidae: Castniinae) in Mexico

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Abstract: *Telchin atymnius futilis* (Walker, 1856) is one of the few Castniidae with distribution in Mexico that is not endemic to the country. Starting from greater knowledge of its geographical distribution and field studies carried out in recent years, bionomic details as well as previously unknown information on its ecology, plant associations and behavioral aspects are provided. Likewise, the taxon's variability and geographical distribution in Mexico is analyzed.

Key words: biogeography, bionomics, distribution, Lepidoptera, Mexico, variability.

Resumen: *Telchin atymnius futilis* (Walker, 1856) es uno de los pocos Castniidae con distribución en México que no es endémico para el país. Teniendo ahora mayores conocimientos sobre su distribución geográfica y gracias a estudios de campo realizados en los últimos años, se proporcionan detalles bionómicos, así como sobre su ecología, asociaciones con plantas y aspectos de comportamiento previamente desconocidos. De igual forma se analiza la variabilidad del taxón y su distribución geográfica en México.

Palabras clave: aspectos bionómicos, biogeografía, distribución, Lepidoptera, México, variabilidad.

INTRODUCTION

In the Americas, the family Castniidae is distributed from Mexico to Argentina, including the Caribbean (Miller, 1986; González & Cock, 2004; López-Godínez & Porion, 2012; García-Díaz *et al.*, 2020). In general, the family is poorly represented in entomological collections worldwide (Vinciguerra *et al.*, 2011; Moraes & Duarte, 2014; Worthy *et al.*, 2017; González & Domagała, 2019). Nevertheless, interest in Castniidae by Mexican collectors and researchers has increased considerably in the past two decades (García-Díaz *et al.*, 2019); as a result, we now have better representation in Mexican collections, both institutional and private. In Mexico, most taxa that are distributed in rainforests, semideciduous forests and cloud forests on the Gulf of Mexico slope are not endemic to the country. Among them is *Telchin atymnius futilis* (Walker, 1856), a taxon that is considered the most ‘common’ in Mexico.

Castnia atymnius Dalman, 1824, was described based on material from Brazil, while *Castnia futilis* Walker, 1856, and *Castnia salasia* Boisduval, [1875] were described from material from Nicaragua and Mexico, respectively; however, the last name is considered to be a synonym of *C. futilis*. Houlbert (1918) considered *Castnia atymnius* in the genus *Castniomera* Houlbert, 1918, without mentioning *Castnia futilis*. Both taxa were considered two different species until Miller (1986), based on morphological similarities between them, determined that *Castniomera atymnius* is a valid species and that *Castniomera futilis* is not; however, she placed *futilis* as a subspecies of *atymnius*. This subspecific position was maintained in Miller (1995), Lamas (1995) and subsequent publications to this date. For their part, Moraes & Duarte (2009) synonymized *Castniomera* with *Telchin*, Hübner, 1825.

Currently, *T. atymnius* includes seven recognized subspecies throughout the continent (*atymnius*, *drucei* (Schaus, 1911), *ecuadorensis* (Houlbert, 1917), *futilis*, *humboldti* (Boisduval, [1875]), *immaculata* (Lathy, 1922), *newmanni* (Houlbert, 1917)), distributed from Mexico to Brazil, with *T. a. futilis* being the one with the northernmost distribution (Mesoamerica). *Telchin atymnius* is a species often associated with heliconias (*Heliconia* spp.: Heliconiaceae) and banana trees (*Musa* spp.: Musaceae), which are its host plants (Gallego, 1946, 1963; Lara, 1964a; Miller, 1986; González & Cock, 2004; González *et al.*, 2010; González *et al.*, 2017; González & Domagała, 2019). Consequently, some subspecies are of great economic and commercial importance since they are pests of banana plantain crops. The subspecies *Telchin atymnius humboldti* is cited by Lara (1964a, 1964b, 1965, 1966a, 1966b), who described and analyzed in great detail the taxon’s adult morphology, its complete life cycle and the damage it causes in banana plantations in Costa Rica.

Starting from a compilation of localities where *T. atymnius futilis* has been observed in Mexico, a map of its distribution in the country was prepared. Additionally, through the author’s collecting and personal observations, and information provided by Roberto G. de la Maza, Filiberto Mora and Alejandro González, relevant bionomic aspects of this subspecies are discussed, and its different host plants in Mexico are documented.

MATERIALS AND METHODS

Telchin atymnius futilis distribution records were located while searching the following institutional and private collections: Private collection of José de Jesús García-Díaz, Tehuacán, Puebla, Mexico (JJGD); Private collection of the Haghenbeck Family, Tehuacán, Puebla, Mexico (CFH); Private collection of the De la Maza Family, Mexico City, Mexico (CDM); Private collection of Bernardo López-Godínez, Guadalajara, Mexico (BLG); Private collection of the Turrent Family, Mexico City, Mexico (CFT); Private collection of the Villarreal Family, Oaxaca, Oaxaca, Mexico (CFV); Private collection of Robert Worthy, Caterham, Surrey, U.K. (RW); Private collection of Dirk Casteleyn, Brugge, West Flanders, Belgium (DC); Private collection of Daniel J. Curoe, Mexico City, Mexico (DJCC); Colección Entomológica del Instituto de Biología de la Universidad Nacional Autónoma de México, Mexico City, Mexico (IBUNAM); Museo de Historia Natural de la Ciudad de México, Mexico City, Mexico (MHNCM); Colección Entomológica de la Facultad de Ciencias Agronómicas de la Universidad Autónoma de Chiapas, Villaflores, Chiapas, Mexico (UNACH); Yale Peabody Museum of Natural History, New Haven, USA (YPM); Museum für Naturkunde, Berlin, Germany (ex-ZMHB: Zoologisches Museum der Humboldt Universität zu Berlin, Germany) (MfNB); American Museum of Natural History, New York, USA (AMNH).

Bionomic information was obtained based on the author's personal observations in San Felipe Jalapa de Díaz, Oaxaca, and El Vigía, Veracruz; also from Roberto G. de la Maza in the ADVC (Área Destinada Voluntariamente a la Conservación) Kolijke, Puebla; Filiberto Mora (in Santiago Yancuitlalpan, Puebla); and Alejandro González-Castillo (in Xilitla, San Luis Potosí).

The distribution map of *T. atymnius futilis* was prepared using SimpleMappr (Shorthouse, 2010). Georeferencing of localities was done by means of Google Earth. The photos of the specimens illustrated in Figure 4 were taken with a Fujifilm FinePix HS20EXR camera. Adobe Photoshop 2020 was used for figures editing.

RESULTS

Biogeographical comments and distribution. In Mexico, north of the Isthmus of Tehuantepec, *Telchin atymnius futilis* has a restricted distribution within rainforests, semideciduous forests and cloud forests of the central and northern slopes facing the Gulf of Mexico. South of the Isthmus of Tehuantepec, in the states of Chiapas and Oaxaca, it has been located on both the Gulf and the Pacific slopes. Its northernmost known distribution point is Xilitla, San Luis Potosí; however, its distribution possibly extends through the state to humid regions of northern Veracruz or southern Tamaulipas, although Irmin García-Morales & Jesús García-Jiménez (pers. comm.) point out that it has not been observed in the El Cielo Biosphere Reserve (RBEC), in Tamaulipas. The following is a list of localities where the taxon has been sighted and collected: **Campeche:** Calakmul; **Chiapas:** Bonampak, Cerro Cebú, Chajul, Cintalapa, El Ocote, Frontera Corozal, Huixtla, La Granja, Laguna Bélgica, Mazatán, Ocuilapa, Palenque, San Quintín, Selva Negra, Tapachula, Yajalón; **Hidalgo:** Puerto del Caballo; **Oaxaca:** Arroyo de Banco, La Esperanza, La Soledad, La Trinidad, Metates, Rancho San Carlos, San José Chiltepec, San Felipe Jalapa de Díaz, San Pedro Tapanatepec, Santa María Chimalapa, Soyolapam, Valle Nacional; **Puebla:** ADVC Kolijke, Barranca de Patla, Cuetzalan, La Ceiba, Mazatzongo de Guerrero, Presa La Soledad, Tlaxcalantongo, Xicotepec de Juárez, Yancuitlalpan; **Querétaro:** Río Tancuilín; **San Luis Potosí:** Tamazunchale, Xilitla; **Tabasco:** Huimanguillo, Santa Rosalía, Teapa; **Veracruz:** Atoyac, Cerro El Vigía, Coatepec, Coatzacoalcos, Córdoba, Dos Amates, Fortín de las Flores, Hacienda El Mirador, Ixtaczoquitlán, Misantla, Orizaba, Presidio, Reserva Ecológico Santa Gertrudis, Tezonapa, Volcán San Martín, Volcán Santa Martha, Xico (Fig. 3). Likewise, there are records of the taxon in various localities in Central America: Belize, Guatemala, El Salvador, Honduras, Nicaragua, Costa Rica and Panama (Miller, 1986; Miller, 1995; Lamas, 1995; González & Hernández-Baz, 2012; van den Berghe *et al.*, 2020). Druce (1883) illustrated a specimen of '*Castnia futilis*' from Costa Rica; however, it is evident that this specimen corresponds to *Telchin atymnius drucei*. It is possible that in other bibliographical sources there are confusions or erroneous references between subspecies (*e.g.*, Westwood, 1877).

Ecology and behavior. *Telchin a. futilis* coexists with different castniid species in various localities in Mexico. In the great majority of these localities, it is sympatric with *Athis inca orizabensis* (Strand, 1913), while in a few it flies together with *A. delecta* (Schaus, 1911), *A. inca inca* (Walker, 1854), *T. evalthe viryi* (Boisduval, [1875]) or *Telchin diva diva* (Butler, 1870), depending on the region. The elevations of the localities where it is distributed ranges from 0-1900 m above sea level; however, it is most frequently observed between 400-1200 m. It is recorded from mid-March to mid-November, depending on the locality, and the beginning and duration of the rainy season. There is a record of the taxon from Palenque, Chiapas (January). Its flight period is longer than that of the other castniid species with distribution in Mexico; its extensive distribution in different ecosystems favors a long flight period, unlike other species. It does not show a particular preference with respect to its flight zone, since it often flies in open sunny places such as ravines or the banks of rivers and streams, and open areas shaded by trees over 15 m high, always in proximity to one of its host plants. Roberto de la Maza (pers. comm.) points out that the host plant species at ADVC Kolijke (Puebla) are *Heliconia latispatha* Benth. (Fig. 2G), *H. bourgaeana* Petersen (Fig. 2F), *H. collinsiana* Griggs (Fig. 2E) and *H. rostrata* Ruiz & Pav. (Heliconiaceae). Moreover, Filiberto Mora (pers. comm.) indicates that *T. atymnius futilis* is associated with various host plants in Yancuitlalpan, Puebla; he has observed several females ovipositing on *H. bourgaeana* (Fig. 2F) and *H. rostrata* (Heliconiaceae), *Canna tuerckheimii* Kraenzl. (Cannaceae), and on one occasion on *Etlingera elatior* (Jack) R.M.Sm. (Zingiberaceae). Also, Lugo-Cruz *et al.* (2020) indicate that this subspecies attacks crops of *H. psittacorum* L.f., *H. bihai* (L.) L. and *H. stricta* Huber in a Cárdenas, Teapa, Tabasco, plantation. As with the other castniid species in Mexico, *T. a.*

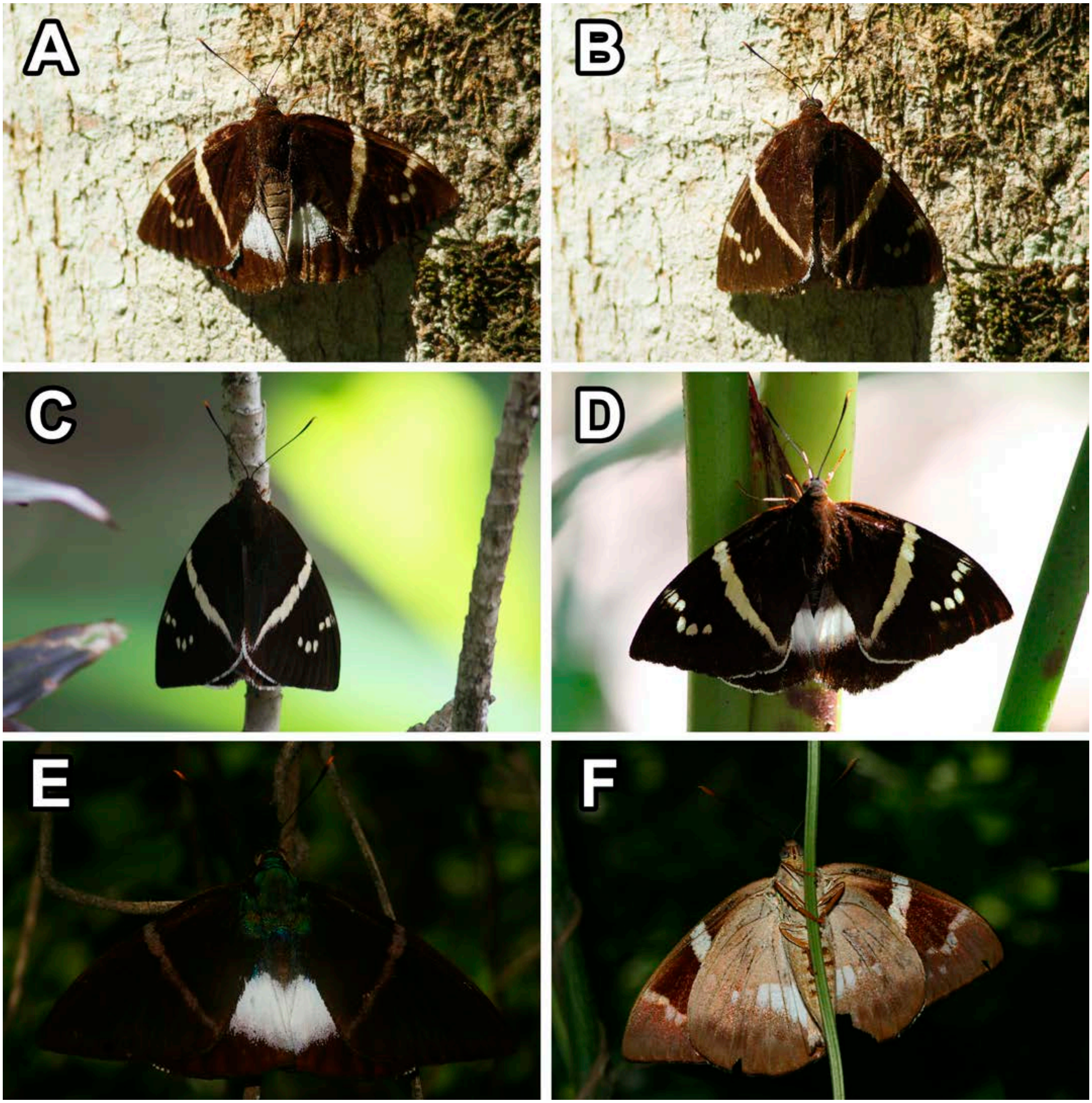

Figure 1. Males and females of *Telchin atymnius futilis* in several localities in Mexico, resting in stegopterous position. A-B) Female, dorsal view (Palenque, Chiapas, 17-I-2019, Manuel Hernández-Ancheita); C) dorsal view of a resting female (Palenque, Chiapas, 02-VIII-2018, Manuel Hernández-Ancheita); D) dorsal view of a female apparently feeding on *Heliconia* sp. (Palenque, Chiapas, 29-V-2018, Manuel Hernández-Ancheita); E) dorsal view of a male blending in with its surroundings (ADVC Kolijke, Puebla, 24-V-2009, Roberto G. de la Maza E.); F) male, ventral view (ADVC Kolijke, Puebla, 28-V-2006, Roberto G. de la Maza E.).

futilis adults have not been observed feeding on flowers, mud or decomposing fruits; however, there is a record of a female that seemed to be feeding on damaged plant tissue of a *Heliconia* sp. (Manuel Hernández-Ancheita, pers. comm.) (Fig. 1D).

Males eclose 10-20 days before females. The taxon is seldom observed on cool or cloudy days as it prefers to fly in warm and sunny surroundings. Males begin to fly at 10:00 on sunny days with temperatures that fluctuate between 22 and 28 °C, and at 11:00 on overcast days, whereas females are most frequently observed on warm days between 12:00 and 14:00. Both males and females have been occasionally observed until 17:00 on sunny days. Males become more active at higher temperatures, making frequent monitoring flights in the vicinity of their perching zone, whereas when the temperature decreases, they become less active and cease to fly. Unlike other Mexican castniid species such as *A. flavimaculata* (Miller, 1972), *A.*

hechtiae (Dyar, 1910), *A. inca* (Walker, 1854), *A. miastagma* (Dyar, 1925) or *A. thysanete* (Dyar, 1912), large numbers of specimens are not observed in a single day; typically, about 2-3 males and one female have been observed per day. Neither males nor females fly in drizzle or light rain.

Telchin a. futilis males are territorial and fly faster than *futilis* females and the majority of *Athis* species in Mexico; their flight is rapid and straight, slightly erratic. As with the great majority of Mexican castniids, male *T. a. futilis* often perch in stegopterous position on some dry twig, branch, tree trunk or on the leaves of one of its host plants to wait for a female to fly nearby (Figs. 1E, 1F, 2D). When a medium-sized or large butterfly flies near the perching zone of a male, it will be chased for several meters until they disappear and the intruder has been driven away from the zone; the male will then immediately return to (or near) the same spot where it was initially perched. Sometimes males have been observed chasing small birds. After males perch on the middle of a dry twig, they walk slowly (and with the middle pair of legs moving in a rapid ‘shuffling’ manner) toward the tip. If people pass nearby, they are often easily startled and can take flight and perform a patrol flight of the perching zone, or simply disappear from its initial location. On rare occasions males have attacked people who walk near them; for a few seconds they will whirl intensely near the person’s body, sometimes hitting them with their wings (Roberto de la Maza, pers. comm.). Fights between males, when one invades the perching zone of another, are frequently observed. When these happen, pursuing flights take place in and out of the perching zone at different heights, up to 15 m. At the end of a fight, the winning male remains in the desired area while the loser withdraws. This can be repeated several times in a day.

Females, on the other hand, are on average larger and slightly slower than males. They are infrequently observed in April, May and June, and more commonly seen in July and August. Occasionally they can be seen resting during cloudy days or during the first hours of warm days (between 10:30 and 12:00); they can sometimes be observed perching in stegopterous position. They are often seen near one of their host plants, with the intention of ovipositing. When this occurs, they land on and flutter around the plant up to 50 cm above the ground, apparently determining where to deposit the egg; after that they land on the lower part of the plant and walk for 30 s to decide the exact spot where they will oviposit, usually close to the ground (Figs. 2A, 2B). After oviposition, they fly off in search of another plant on which to oviposit. Sometimes a female will deposit up to two eggs per plant. Females do not oviposit on plants which have already been used as host plants by another female. When the larva hatches, it makes a hole in the inferior part of the plant (usually 10 cm from the ground) and begins its life cycle inside the plant. Filiberto Mora (pers. comm.) indicates that the hole in which the larva penetrates the interior of the plant is always covered by a gelatinous substance; however, its composition is unknown. According to Lugo-Cruz *et al.* (2020), in the case of *Heliconia* spp., *T. a. futilis* larvae bore galleries in the pseudostems and corms, causing the plants to weaken; these plants display a descending pattern of withering symptoms, turning dark brown from the apex to the base. The entrance and exit wounds and the damage to the plants favors the entry of pathogens, leading to the death of the plants a few months after the adults have emerged. When a female flies near a male, it will be chased for several meters until they disappear. The only copulation that has been documented for this taxon in Mexico was observed at the Edward James Sculpture Garden, in the vicinity of Las Pozas, Xilitla, San Luis Potosí (Fig. 2C); there, a male and a female were found copulating on a rocky path near the La Conchita stream, at 14:30 on a sunny day (Alejandro González, pers. comm). The copulation lasted approximately 10 minutes, and most of the time the pair’s heads were pointing in opposite directions in a way similar to the description by García-Díaz *et al.* (2020) for *Athis hechtiae*. During that time period the moths were mostly still, without moving, in stegopterous position. Nevertheless, on five occasions, the male (with the female attached and motionless) attempted to fly toward the vegetation but didn’t succeed since they managed only small hopping flights that didn’t exceed 30 cm in height and ended on the same spot where they were initially copulating. At the end of the copulation, both individuals’ abdomens became detached and they flew off in different directions. The complete life cycle of the taxon remains unknown; nevertheless, it is evident that the third and fifth instar larvae resemble those illustrated by Lara (1964a), in reference to *Telchin atymnius humboldti* (Filiberto Mora, pers. comm.). Adults eclose in the morning between 9:00-10:00; after a few hours they spread their wings and begin to fly.

Material examined. Data from 193 specimens (144♂♂, 49♀♀) were recorded from the several collections under scrutiny: **Chiapas:** 1♂, VI-1997 (DC); 1♀, Ocosingo, Bonampak, VII-1964 (IBUNAM); 3♂♂, 1♀, Tapachula, Tapachula, *leg.* J. C. García (IBUNAM); 1♂, Marqués de Comillas, Chajul, 02-VII-1980, *leg.* J. de la Maza E. (CFT); 1♂, Ocosingo, Río Lacanja, Bonampak, Reserva de la Cojolita, 16º46’06”N 91º07’33”W (329 m), *leg.* P Jakubek (RW); 1♀, San Quintín, 10-IX-2007 (RW); 2♂♂, Comitán, 27 km SE Santa Rosa, Rancho Santa Ana, IX-1969, *leg.* Peter Hubbell (YPM); 1♂, Huixtla, 08-VI-1963, *leg.* A. Díaz F. (CFH); 2♂♂, La Trinidad (CFH); 1♀, Marqués de Comillas, Chajul, 17-VIII-1981, *leg.* J. de la Maza E. (CDM); 2♂♂, Marqués de Comillas, Chajul, 17-VII-1981, *leg.* J. de la Maza E. (CDM); 1♂, La Concordia, Cerro Cebú, 19-VIII-2016, *leg.* J. de la Maza E. (CDM); 1♂, La Concordia, Cerro Cebú, 22-VIII-2015, *leg.* J. de la Maza E. (CDM); 1♂, La Granja, 26-VII-1930 (AMNH); **Hidalgo:** 1♀, Puerto del Caballo (high elevation cloud forest), 19-VII-1981, *leg.* William H. Howe (AMNH); **Oaxaca:** 1♂, San Felipe Jalapa de Díaz, 4km NE San Bartolomé Ayautla, 14-VIII-2017, *leg.* J. J. García D. (JJGD); 2♂♂, Santiago Comaltepec, Soyolapam, VI-1967, *leg.* A. Díaz F. (IBUNAM); 3♂♂, Santa María Chimalapa, Chalchijapa, 30-V-1995, *leg.* J. L. Salinas G. (IBUNAM); 1♂, Santa María Chimalapa, Chalchijapa, 26-V-1995, *leg.* J. L. Salinas G. (IBUNAM); 1♀, San Juan Bautista Valle Nacional, Valle Nacional, 11-IX-1982, *leg.* A. Ibarra (IBUNAM); 3♀♀, San José Chiltepec, Chiltepec, VIII-1964, *leg.* A. Díaz F. (IBUNAM); 1♂, Santa María Chimalapa, Chalchijapa, 27-V-1995, *leg.* J. L. Salinas G. (IBUNAM); 1♂, Santa María Chimalapa, Chalchijapa, 25-V-1995, *leg.* J. L. Salinas G. (IBUNAM); 1♂, Santiago Comaltepec, Soyolapam, V-1967, *leg.* A. Díaz F. (IBUNAM); 3♂♂, Santiago Comaltepec, Puerto Eligio, 07-IX-1987, *leg.* O. Villarreal (CFV); 1♂, San Juan Bautista Valle Nacional, Cerro La Soledad, 03-VI-1990, *leg.* O. Villarreal (CFV); 2♂♂, Santiago Comaltepec, Cerro Metate, 17º40’06”N 96º19’38”W (1165 m), 16-V-2008, *leg.* P. Jakubek (RW); 1♂, Santiago Comaltepec, Cerro Metate, 17º40’06”N 96º19’38”W (1165 m), 06-V-2006, *leg.* P. Jakubek (RW); 1♂, Santiago Comaltepec, Cerro Metate, 17º40’06”N 96º19’38”W (1165 m), 26-V-2006, *leg.* P. Jakubek (RW); 1♀, Santiago Comaltepec, Cerro Metate, 17º40’06”N 96º19’38”W (1165 m), 15-V-2006, *leg.* P. Jakubek (RW); 1♀, La Esperanza (1780 m), VII-2017 (RW); 1♂, 1♀, Tuxtepec, El Naranjal-Chiltepec, VIII-1969, *leg.* Peter Hubbell (YPM); 2♂♂, Cintalapa, La Pilar, 11-VIII-2001, *leg.* C. Morales L. (UNACH); 1♂,

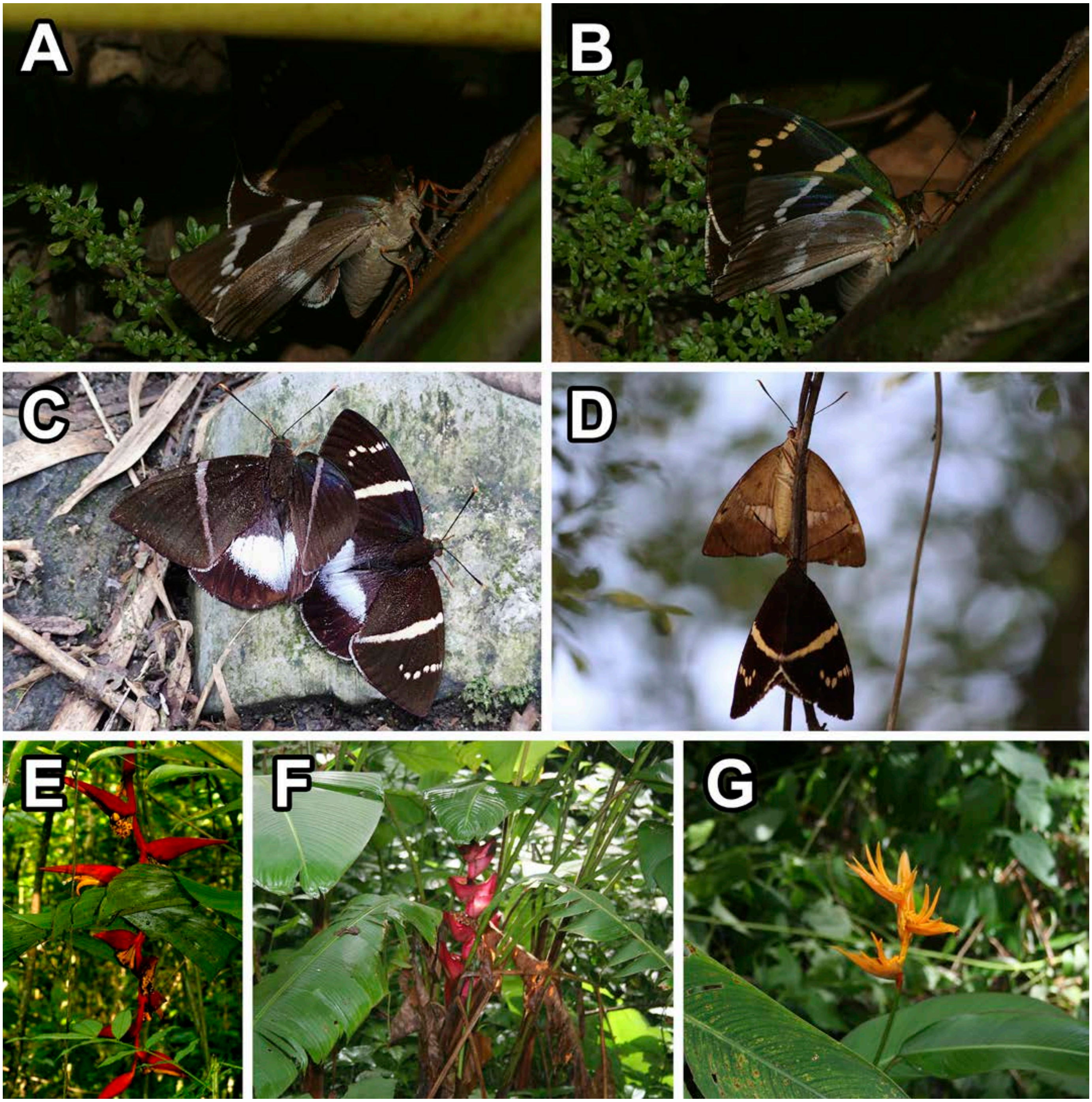

Figure 2. Aspects of *Telchin atymnius futilis* ecology in Mexico. A-B) Female ovipositing on *Heliconia* sp. (ADVC Kolijke, Puebla, 24-V-2009, Roberto G. de la Maza E.); C) male (left) and female (right) copulating (Edward James Sculpture Garden, Xilitla, San Luis Potosí, 21-VII-2021, Alejandro González-Castillo); D) resting male (top) and female (bottom) (Palenque, Chiapas, 22-XI-2017, Manuel Hernández-Ancheita); E) *Heliconia collinsiana*, a host plant of the taxon (ADVC Kolijke, Puebla, 15-X-2010, Roberto G. de la Maza E.); F) *H. bourgaeana*, a host plant of the taxon (ADVC Kolijke, Puebla, 07-VII-2013, Roberto G. de la Maza E.); G) *H. latispatha*, a host plant of the taxon (ADVC Kolijke, Puebla, 07-VII-2013, Roberto G. de la Maza E.).

Ocozocoautla, Laguna Bélgica, 23-VIII-1991, *leg.* C. J. Morales (UNACH); 4♂♂, Ocozocoautla, Ocuilapa de Juárez, 22-VIII-1997, *leg.* C. J. Morales (UNACH); 1♀, Sierra de Juárez, Metates, VII-2013, *leg.* L. Haghenbeck C. (CFH); 1♂, Sierra de Juárez, Metates, VI-2000, *leg.* L. Haghenbeck C. (CFH); 1♂, Sierra de Juárez, Metates, 28-III-1996 (CFH); 1♂, San Felipe Jalapa de Díaz, Jalapa de Díaz, IX-2009, *leg.* L. Haghenbeck C. (CFH); 1♀, Tapanatepec, Las Minas, 04-VI-1979, *leg.* J. de la Maza E. (CDM); 1♂, Rancho San Carlos, VIII-1968, *leg.* Peter Hubbell (AMNH); **Puebla:** 1♂, La Ceiba, La Junta, 01-VII-2019, *leg.* E. Yañez (JJGD); 1♂, Zihuateutla, Barranca de Patla, 12-VIII-2019, *leg.* E. Yañez (BLG); 1♂, Zihuateutla, Barranca de Patla, 11-VI-2016, *leg.* E. Yañez (BLG); 1♂, Venustiano Carranza, El Ajengibre, 16-V-1953 (IBUNAM); 2♂♂, Zihuateutla, Barranca de Patla, 05-IX-1978, *leg.* A. Ibarra (IBUNAM); 1♂, Xicotepec, Villa Juárez, 05-VI-1966, *leg.* C. Beutelspacher B. (IBUNAM); 1♀, Cuetzalan del Progreso, Santiago Yancuitlalpan, 15-V-1982, *leg.* F. Mora (CFV); 1♂, San Sebastián Tlacotepec, Mazatzongo de Guerrero, 15-V-1984, *leg.* O. Villarreal (CFV); 1♂, Zihuateutla, ADVC Kolijke, 03-V-2020, *leg.* A. Turrent C. (CFT); 1♂, 1♀, Zihuateutla, ADVC Kolijke, 25-VIII-2018, *leg.* A. Turrent C. (CFT); 1♂, Zihuateutla, Barranca de Patla, 28-VI-

Figure 3. Geographic distribution of *Telchin atymnius futilis* in Mexico.

1998, *leg.* A. Turrent C. (CFT); 1♂, Zihuateutla, Barranca de Patla, 08-V-1997, *leg.* A. Turrent C. (CFT); 1♂, Zihuateutla, Barranca de Patla, 20-XI-1997, *leg.* R. Turrent D. (CFT); 1♂, Tlatlauquitepec, Presa La Soledad, 08-IX-2018, *leg.* A. Turrent C. (CFT); 1♀, Villa Juárez, Dos Caminos, 11-VII-2014, *leg.* A. Sampayo (RW); 2♂♂, Cuetzalan del Progreso, Cuetzalan, IX-1997, *leg.* F. G. Haghenbeck F. (CFH); 1♂, Cuetzalan del Progreso, Cuetzalan, 28-VII-1996, *leg.* F. G. Haghenbeck F. (CFH); 1♂, Zihuateutla, Barranca de Patla, 12-VIII-1980, *leg.* D. J. Curoe (DJCC); 1♂, Zihuateutla, Barranca de Patla, 20-V-1974, *leg.* R. J. Boué Peña (IBUNAM); 1♂, Zihuateutla, Barranca de Patla, 18-V-1977, *leg.* R. J. Boué Peña (IBUNAM); 1♂, Zihuateutla, Barranca de Patla, 28-V-1977, *leg.* R. J. Boué Peña (IBUNAM); 1♂, Zihuateutla, Barranca de Patla, 27-V-1978, *leg.* R. J. Boué Peña (IBUNAM); 1♂, Xicotepex, Tlaxcalantongo, *leg.* R. J. Boué Peña (IBUNAM); 1♂, Xicotepex, Tlaxcalantongo, 18-VI-1978, *leg.* R. J. Boué Peña (IBUNAM); 1♂ Puebla, Tehuacán, 1000m, VII 2015 (RW) [the locality of this specimen is doubtful, since *T. a. futilis* is not present in arid ecosystems and none of its host plants is distributed in the Tehuacán-Cuicatlán Valley, see discussion below]; **San Luis Potosí:** 1♂, Tamazunchale, El Sol (400 ft), 24-VI-1941, *leg.* J. & R. Potts (AMNH); **Tabasco:** 1♀, Teapa, 2-VII-1964, *leg.* John Pallister (AMNH); **Veracruz:** 1♂, Santiago Tuxtla, El Vigía, 20-VII-1995, *leg.* F. G. Haghenbeck F. (JJGD); 2♂♂, Santiago Tuxtla, El Vigía, 11-VIII-2013, *leg.* J. J. García D. (JJGD); 1♀, Santiago Tuxtla, El Vigía, 11-VIII-2013, *leg.* J. J. García D. (JJGD); 1♂, Santiago Tuxtla, El Vigía, 15-VII-2017 (JJGD); 1♂, Santiago Tuxtla, El Vigía, 01-VIII-2017 (JJGD); 2♂♂, 1♀, Santiago Tuxtla, El Vigía, 20-VI-2019 (JJGD); 1♂, Santiago Tuxtla, El Vigía, 01-VII-2019 (JJGD); 4♂♂, 1♀, Santiago Tuxtla, El Vigía, 05-VII-2019 (JJGD); 1♂, 1♀, Santiago Tuxtla, El Vigía, 20-VIII-2019 (JJGD); 1♀, Santiago Tuxtla, El Vigía, 10-IX-2019 (JJGD); 1♂, San Pedro Soteapan 500m, VII/VIII-2006 (DC); 1♂, Santiago Tuxtla, El Vigía, 16-VI-2017 (BLG); 1♂, Santiago Tuxtla, El Vigía, 19-VI-2018 (BLG); 1♂, Santiago Tuxtla, El Vigía, 09-VII-2019 (BLG); 1♀, Santiago Tuxtla, El Vigía, 11-VIII-2018 (BLG); 1♂, Santiago Tuxtla, El Vigía, IV-1964, *leg.* R. F. de la Maza R. (IBUNAM); 2♂♂, Coatzacoalcos, Pajaritos, VII-1944, *leg.* R. F. de la Maza (IBUNAM); 1♂, Catemaco, Dos Amates, 15-IX-1963, *leg.* R. F. de la Maza (IBUNAM); 1♂, 1♀, Veracruz, Veracruz, VI-1961 (IBUNAM); 1♂, Santiago Tuxtla, El Vigía, VI-1964, *leg.* R. F. de la Maza R. (IBUNAM); 1♂, Orizaba, Orizaba (IBUNAM); 1♂, Catemaco, Dos Amates, X-1963, *leg.* R. F. de la Maza R. (IBUNAM); 1♀, Catemaco, Dos Amates, 17-X-1976, *leg.* A. Ibarra (IBUNAM); 1♂, San Andrés Tuxtla, Volcán Santa Martha, 20-VI-1982 (IBUNAM); 1♀, Santiago Tuxtla, El Vigía, III-2017 (CFT); 1♂, Centro de Veracruz [possibly Orizaba], ex *leg.* Mario del Toro (CFT); 1♂, Santiago Tuxtla, Volcán San Martín (1200 m), VII-2005 (RW); 2♂♂, 2♀♀, San Andrés Tuxtla, Catemaco, VII-2016 (RW); 1♀, San Andrés Tuxtla, Catemaco, 18º22'36"N 95º07'35"W (345 m), 20-IX-2003, *leg.* P. Jakubek (RW); 7♂♂, 1♀, Dos Amates, between Catemaco and Laguna Sontecomapan, IX-1969, *leg.* Peter Hubbell (YPM); 2♂♂, Dos Amates, between Catemaco and Laguna Sontecomapan, X-1969, *leg.* Peter Hubbell (YPM); 1♂, San Andrés Tuxtla, Laguna Encantada, 03-VII-1985, *leg.* Robert A. Raguso (YPM); 1♀, Santiago Tuxtla, El Vigía, 15-IX-1998, *leg.* F. G. Haghenbeck F. (CFH); 1♀, Catemaco, Dos Amates, 04-IX-1996, *leg.* F. G. Haghenbeck F. (CFH); 1♀, Santiago Tuxtla, El Vigía, 03-X-2013 (CFH); 3♀♀, Santiago Tuxtla, El Vigía, VI-1996, *leg.* F. G. Haghenbeck F. (CFH); 1♀, Atoyac, 11-VI-1987, *leg.* F. G. Haghenbeck F. (CFH); 2♂♂, Santiago Tuxtla, El Vigía, 03-VI-2002, *leg.* F. G. Haghenbeck F. (CFH); 5♂♂, Santiago Tuxtla, El Vigía, 21-III-1997 (CFH); 1♀, Dos Amates, Catemaco, 19-IX-1970, R. F. de la Maza R. (CDM); 1♀, Santiago Tuxtla, El Vigía, 15-VIII-1963, R. F. de la Maza R. (CDM); 1♂, Santiago Tuxtla, El Vigía, 12-IX-1964, R. F. de la Maza R. (CDM); 1♂, Dos Amates, Catemaco, 18-VI-1965, R. F. de la Maza R. (CDM); 1♂, Dos Amates, Catemaco, 07-VI-1964, R. F. de la Maza R. (CDM); 6♂♂, 2♀♀, Coatzacoalcos, Pajaritos, VII-1944, M. Guerra Coll., Frank Johnson Donor (AMNH); 1♂, Tezonapa, Tezonapa, XI, W. L. Tower Collection (AMNH); 1♂, Km. 25 sureste, VII-1944, M. Guerra Coll., Frank Johnson Donor (AMNH); 1♂, Presidio, V-1940, *leg.* C. C. Hoffmann (AMNH); 1♂, Presidio, VIII, *leg.* C. C. Hoffmann (AMNH); 1♂, Orizaba, VII-1907, *leg.* C. C. Hoffmann (AMNH); 2♂♂, Presidio, VIII-1913, *leg.* C. C. Hoffmann (AMNH); 1♂, Jalapa, Collection Hy. Edwards (AMNH); 1♂, Misantla, VI-1909, *leg.* C. C. Hoffmann (AMNH); 1♂, Presidio, IX-1939, *leg.* C. C. Hoffmann (AMNH); 1♀, Presidio, IX-1940, *leg.* C. C. Hoffmann (AMNH); 1♀, No. 2887, Presidio, *leg.* R. Müller (MHNCM); 1♀, No. 2888, Mirador, *leg.* R. Müller (MHNCM); 1♂, No. 2701, Mirador, *leg.* R. Müller (MHNCM); 1♂, No. 2700, Orizaba, *leg.* R. Müller (MHNCM). Additionally, seven specimens were analyzed without information on their locality: 1♂, Mexico, 2-91 (DC); 1♀, Mexico, *leg.* Paul Buxbaum (YPM); 2♂♂, 2♀♀, Mexico, Friedrich Hist. Coll. (MfNB); 1♀, *leg.* R. J. Boué Peña (IBUNAM).

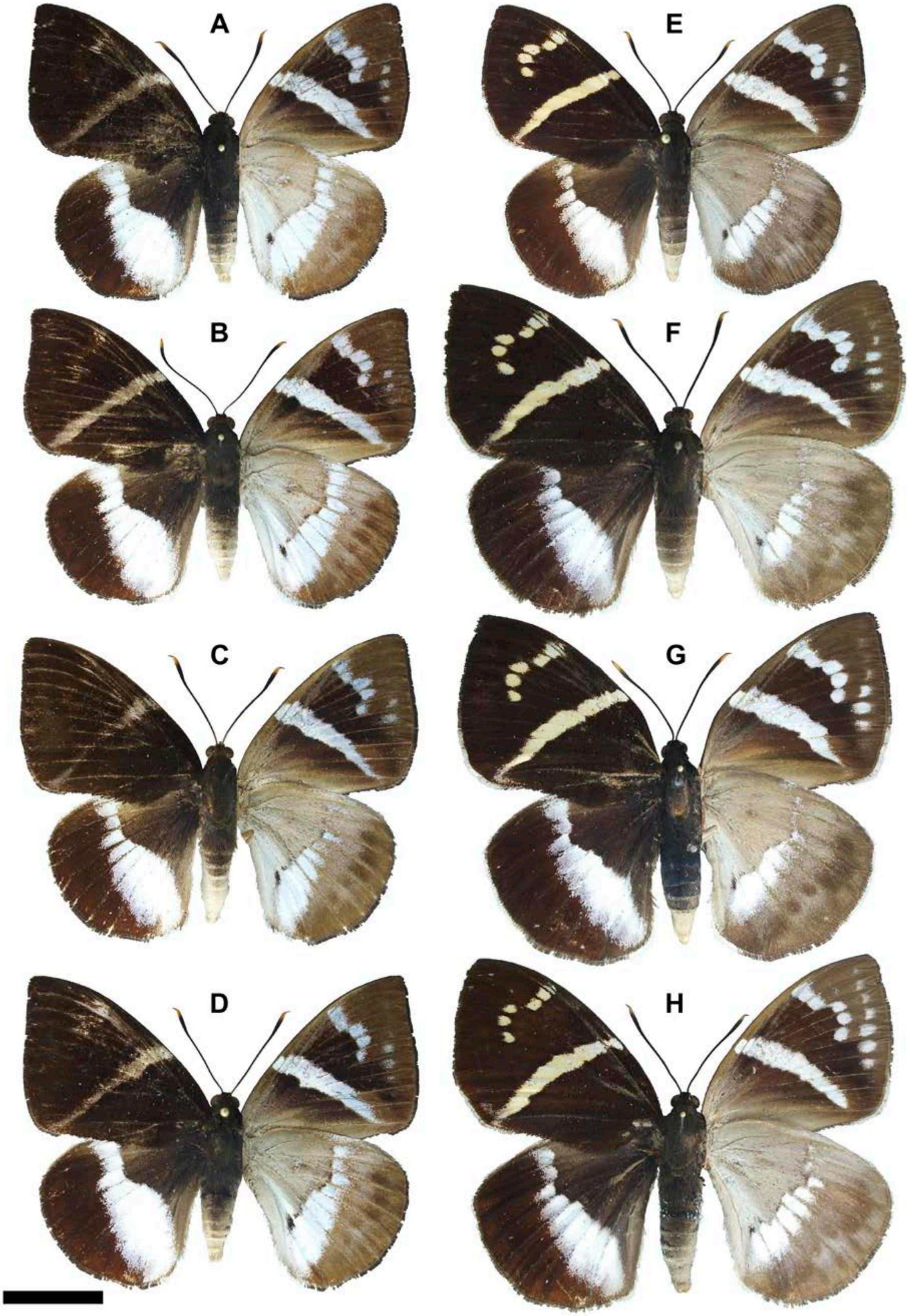

Figure 4. Dorsal (left) and ventral (right) variation of *Telchin atymnius futilis* males (A-D) and females (E-H). A) Male from Veracruz, Santiago Tuxtla, El Vigía, 20-VI-2019 (JJGD); B) male from Veracruz, Santiago Tuxtla, El Vigía, 20-VI-2019 (JJGD); C) male from Oaxaca, San Felipe Jalapa de Díaz, 4 km NE San Bartolomé Ayautla, 14-VIII-2017, *leg*. J. J. García D. (JJGD); D) male from Veracruz, Santiago Tuxtla, El Vigía, 01-VII-2019 (JJGD); E) female from Veracruz, Santiago Tuxtla, El Vigía, 10-IX-2019 (JJGD); F) female from Veracruz, Santiago Tuxtla, El Vigía, 11-VIII-2013, *leg*. J. J. García D. (JJGD); G) female from Veracruz, Santiago Tuxtla, El Vigía, 20-VIII-2019 (JJGD); H) female from Veracruz, Santiago Tuxtla, El Vigía, 20-VI-2019 (JJGD). Scale bar = 2 cm.

Variation. This castniid subspecies exhibits clear sexual dimorphism but little variation within each sex (Fig. 4). In addition to size, the main difference between males and females can be seen in dorsal view: on the forewings, the subapical spot band is always present in females, never (or barely suggested) in males; the diagonal band is often slightly wider in females. Ventrally, the main difference can be observed on the hindwings: the white band is wider in males, mainly near the costal margin.

Concerning variation between individuals, in some males, dorsally, the nearly imperceptible forewing costal band disappears completely. In both males and females, the forewing diagonal band and the hindwing white band exhibit variations in each specimen on both surfaces; some specimens have a narrowed white band (dorsal view) near the costal margin. Ventrally, the length and width of the submarginal spots on the forewings is variable in both sexes.

DISCUSSION

Telchin atymnius futilis is a very common taxon, frequently observed in Mexico and Central America (Miller, 2000; González, 2008; González & Hernández-Baz, 2012; van den Berghe *et al.*, 2020). Considering the taxon's presence in the Mexican states mentioned by Morales-Morales *et al.* (2015), the records in this work for Campeche, Hidalgo, Oaxaca, Puebla, Querétaro, San Luis Potosí and Tabasco constitute new state records which broaden considerably its known distribution in the country. Of all the castniid species in Mexico, the complete range of this subspecies seems to be evolving relatively recently, which agrees with what was noted by Miller (1986). This suggestion is supported by the following facts: (1) it is not endemic to the country, thus its distribution is not restricted to Mexico; (2) north of the Isthmus of Tehuantepec, it is only distributed on the Gulf slope, whereas south of the Isthmus it is distributed on both slopes (and in both cases without presenting subspeciation); (3) it does not occur in arid regions, unlike other castniid species in the country; (4) it does not have a sister species on the Pacific slope of the Sierra Madre del Sur or the Balsas River basin, since these regions would seem to be natural barriers that prevent its expansion toward the northern Pacific regions. *Telchin evalthe viryi* and *Telchin diva diva* are two taxa with a distribution relatively similar to that of *T. atymnius futilis*; however, the latter's distribution is more northerly.

Its broad distribution on the Gulf of Mexico slope could be explained by its high food adaptive plasticity, because nine host plant species belonging to three genera (*Heliconia*, *Canna* and *Etlingera*) are known for this subspecies in Mexico. It is worth noting that one of the host plants, *Etlingera elatior*, is Asiatic in origin (Juwita *et al.*, 2018) and *Heliconia rostrata* is native to South America (Banerjee *et al.*, 2020); however, the latter species has been recorded growing wild in Chiapas, in the Chajul region (Santos *et al.*, 2009). Additionally, some subspecies of *Telchin atymnius* have been recorded to feed on sugar cane (*Saccharum officinarum*: Poaceae) (Aya *et al.*, 2021), with *T. a. futilis* being one of them (Miller, 2000; González *et al.*, 2010; González & Domagała, 2019; van den Berghe *et al.*, 2020). In Costa Rica, *Telchin licus* (Drury, 1773) has been recorded as an important pest of sugarcane monocultures in some localities of the country (Coto & Saunders, 2004; LAICA, 2016). However, it has recently been confirmed that the taxa studied in these works correspond to *T. a. futilis* and *T. a. drucei* (LAICA, 2017; Salazar-Blanco *et al.*, 2018; Cadet-Piedra *et al.*, 2019; José Daniel Salazar, pers. comm.). This type of confusion is frequent between subspecies of *T. licus* and *T. atymnius*, which has resulted in misidentifications in various works (Aya *et al.*, 2021). Curiously, *futilis* and *drucei* fly together in sugar cane fields in the region of San Carlos, Huetar Norte, Costa Rica (where both taxa have been collected) (LAICA, 2016; José Daniel Salazar, pers. comm.). Miller (2000) comments that *Telchin atymnius* also feeds on banana tree (*Musa* spp.: Musaceae) but doesn't specify whether *futilis* feeds on that plant. The remarks by González *et al.* (2010), González & Domagała (2019) and van den Berghe *et al.* (2020) concerning the banana tree (*Musa* spp.) as the host plant of *Telchin atymnius futilis* come from Miller (2000); however, there are no other publications documenting this subspecies' host plant associations. Considering the above mentioned, it is evident that there has been confusion concerning some host plants of this subspecies. However, by examining the information provided in the present work together with the cited bibliography, it can be inferred that *T. atymnius* is a species that does feed on *Saccharum officinarum* and that the subspecies *T. a. futilis* does not feed on nor attack *Musa* spp. monocultures. It is curious that the preference of this subspecies for sugar cane has not, to date, been documented in Mexico. The great number of *Heliconia* species in the country on the Gulf slope may explain why it has not required a similar adaptation. *Telchin atymnius futilis* is, without doubt, the Mexican castniid with the greatest number of host plant species. There is also the possibility that it uses other hostplants, especially Heliconiaceae native to Mexico and Central America.

Among the specimens studied for this work, the record of *T. atymnius futilis* from Tehuacán, Puebla, seems doubtful because: (1) it is the only record in which the collecting locality is not within a humid region such as rainforest, semideciduous forest or cloud forest; (2) the Tehuacán-Cuicatlán Valley is an arid region with a high degree of endemism, located south of the Trans-Mexican Volcanic Belt and which has xeric scrublands vegetation in its northern part and deciduous forest in the south (Rzedowski, 1973, 1978; Canseco-Márquez & Gutiérrez-Mayén, 2010; Rojas *et al.*, 2013; García-Díaz *et al.*, 2021); (3) there are no records of any of its host plants in the Tehuacán-Cuicatlán Valley (Valiente-Banuet *et al.*, 2009; Bolaños-Bautista & González-Bernal, 2016). Similar cases of doubtful or erroneous information on Lepidoptera have been noted by De la Maza-Elvira *et al.* (2017), García-Díaz & Turrent-Carriles (2019) and González *et al.* (2021), among others.

Unlike other castniid species with distribution in Mexico, such as *Athis hechtiae*, *A. thysanete*, *Escalantiana chelone* (Hopffer, 1856) or *Mexicastnia estherae* (Miller, 1976), *Telchin atymnius futilis* is not narrowly distributed within the country; thus, it is likely less vulnerable than those other species. In addition, it has nine confirmed host plants in Mexico. However, some of its populations might be affected in various parts of the country due to deforestation. Host plants of *T. atymnius futilis* are, for the most part, ornamental plants that thrive in different types of forest thus helping prevent local extinctions of this subspecies and, at the same time, helping to broaden its distribution in Mexico.

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TROPICAL LEPIDOPTERA
Research

VOLUME 32, NUMBER 1 June 2022

TABLE OF CONTENTS