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Immature stages and new host plant records for four satyrine species feeding on herbaceous bamboos in southeastern Peru (Lepidoptera: Nymphalidae: Satyrinae: Satyrini)

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Abstract

We here document the immature stages of three euptychiine butterflies, *Nhambikuara mima* (Butler, 1867), *Splendeuptychia furina* (Hewitson, 1862), and *Paryphthimoides brixius* (Godart, [1824]), all found feeding on a species of herbaceous bamboo, *Taquara micrantha* (Kunth) I.L.C.Oliveira & R.P.Oliveira (Poaceae: Bambusoideae: Olyreae) in Madre de Dios, Peru. This study is the first to report the life history of these three taxa with their natural host plant. We provide illustrations of immatures, head capsules, and the host plant for each of these three species. The immature morphology of these taxa supports recent generic arrangements of these three species in comparison with their close relatives, namely *Splendeuptychia furina* to *Nhambikuara mima* and *Paryphthimoides brixius* to *Paryphthimoides terrestris* (Butler, 1867), a species documented in our successive study. Thus, the present study includes taxonomic implications based on immature stages by discovering putative synapomorphic characters of larvae and pupae. These pairs of closely related species occur in micro-sympatry at the study site in southeastern Peru, and our observations possibly suggest niche partitioning between sibling species. Additionally, we report two herbaceous bamboo species, *Olyra latifolia* L. and *Taquara micrantha* (Kunth) I.L.C.Oliveira & R.P.Oliveira as the first known natural host plants for *Magneuptychia harpyia* (C. Felder & R. Felder, 1867).

Key words: Euptychiina, life history, Madre de Dios, Olyreae

Resumen

Aquí documentamos los estadios inmaduros de tres mariposas euptychiina, *Nhambikuara mima* (Butler, 1867) Splendeuptychia furina (Hewitson, 1862) y *Paryphthimoides brixius* (Godart, [1824]), todas encontradas alimentándose de una especie de bambú herbáceo, *Taquara micrantha* (Kunth) I.L.C.Oliveira & R.P.Oliveira (Poaceae, Bambusoideae, Olyreae) en Madre de Dios, Perú. Este estudio es el primero en reportar la historia de vida de estos tres taxones con su planta hospedera natural. Proporcionamos ilustraciones de inmaduros, cápsulas cefálicas y la planta hospedera para cada una de estas tres especies. La morfología de los inmaduros de estos taxones apoya los recientes arreglos genéricos de estas tres especies al compararlos con sus parientes cercanos, a decir que *Splendeuptychia furina* (Hewitson, 1862) a *Nhambikuara mima* (Butler, 1867) y *Paryphthimoides brixius* (Hewitson, 1862) a *Paryphthimoides terrestris* (Butler, 1867), una especie documentada en nuestro sucesivo estudio. Por lo tanto, el presente estudio incluye implicaciones taxonómicas basadas en estadios inmaduros al descubrir caracteres sinapomórficos putativos de larvas y pupas. Estos pares de especies estrechamente relacionadas ocurren en micro-simpatría en el sitio de estudio en el sureste de Perú, nuestras observaciones tal vez sugieren una partición de nicho entre las especies hermanas. Además, informamos de dos especies de bambú herbáceos, *Olyra latifolia* L. y *Taquara micrantha* (Kunth) I.L.C.Oliveira & R.P.Oliveira como las primeras plantas hospederas naturales conocidas para *Magneuptychia harpyia* (C. Felder & R. Felder, 1867).

Palabras clave: Euptychiina, historia de vida, Madre de Dios, Olyreae

Introduction

The nymphalid subtribe Euptychiina is a diverse radiation in the Neotropical lowlands, with its diversity currently estimated to exceed 500 species in about 70 genera (unpublished data). Janzen & Hallwachs (2018) provide one of the most comprehensive datasets for euptychiine life history to date, providing 185 natural host plant records for over 30 euptychiine species based on more than 2,000 reared individuals at their study site in northwestern Costa Rica. Nevertheless, our knowledge of euptychine life history is highly fragmentary besides the aforementioned database, with any kind of host plant records at the generic or species-level lacking for approximately 80% of the subtribe (Nakahara & Corahua-Espinoza, in prep.). For example, Beccaloni et al.'s (2008) comprehensive host plant catalog for Neotropical butterflies lists 251 host plant records for 81 euptychiine species. Out of these 251 host plant records listed in Beccaloni et al. (2008), 56 records for 32 species are not accompanied with generic or species-level identification regarding their host plants, namely as "Unidentified species [of Gramineae]", "bamboo(s)" or "grass". There also exist 71 host plant records in Beccaloni et al. (2008) based on accepted host plants in captivity, with five species represented only by such data. Furthermore, 46 (>50%) species listed in this catalog are represented only with a single host plant record, which is probably not reflective of their true diet breadth in nature. The degrees of polyphagy in herbivores can range from strict specialists to extreme generalists, and this level of polyphagy can potentially influence the diversification of lineages, as indicated by a study on a generalist group of Lepidoptera (Wang et al. 2017). Arriving at a firm understanding of euptychiine diversity, along with the accumulation of their native host plant records, could greatly enhance our understanding of their level of polyphagy and diversification processes in the lowland Neotropical region.

The grass (Poaceae) tribe Olyreae represents a monophyletic entity commonly known as the herbaceous bamboos (Clark & Oliveira 2018; Oliveira et al. 2020), which is also a diverse group predominantly found in the Neotropical region. More than 120 species in 23 genera are documented (e.g., 125 species in Clark et al. 2015; 123 species in Oliveira et al. 2020), and the discovery of new species has increased known species diversity in recent years (Ferreira et al. 2020a, b, c; Dias et al. 2021). Unlike woody bamboo species in the tribe Bambuseae, Olyreae species exhibit seasonal or annual flowering patterns, and herbaceous bamboos are readily distinguishable morphologically from woody bamboos based on differences in spikelets, culms, and leaves (Judziewicz et al. 1999). Herbaceous bamboos are known to be an important component of understory and forest edge plant communities in the lowland Neotropics, although some species, such as Olyra standleyi Hitchc., can be found at elevations above 2,500 m (Clark 1990; Judziewicz et al. 1999; Oliveira et al. 2020). Despite molecular evidence suggesting its polyphyly (e.g., Oliveira et al. 2020), the genus Olyra is one of the most diverse herbaceous bamboo genera with 25 species recognized (Clark & Oliveira 2018), rivaled only by Pariana Aublet, in terms of species-richness within the tribe. Members of Olyra occur from northeastern Mexico to northern Argentina, including the West Indies, with a single species (O. latifolia L.) recorded to occur in Africa and Sri Lanka (Judziewicz et al. 1999). Initially introduced as a member of Olyra, Olyra micrantha Kunth, was transferred to Parodiolyra Soderstr. & Zuloaga, based solely on comparative morphology without any supporting phylogenetic hypotheses (Zuloaga & Davides 1999). Subsequently, Oliveira et al.'s (2014) molecular phylogenetic study suggested Parodiolyra may not be monophyletic since "Parodiolyra" micrantha did not form a clade with the type species of Parodiolyra, Olyra ramosissima Trin. Recently, with increased taxon sampling and additional molecular markers, Oliveira et al. (2020) corroborated the paraphyly of *Parodiolyra*, and simultaneously described a new genus *Taquara* I.L.C.Oliveira & R.P.Oliveira to accommodate P. micrantha and P. colombiensis Davidse & Zuloaga, maintaining the monophyly of Parodiolyra. Taquara micrantha is currently conceived as a widely distributed species in South America, with notable variation documented in its morphology (Zuloaga & Davides 1999; Oliveira et al. 2020).

Recent studies conducted in southeastern Peru have recorded herbaceous bamboo species as natural host plants for euptychiines (Tejeira *et al.* 2021; Hurtado *et al.* 2021; Nakahara *et al.* 2022; Corahua-Espinoza *et al.* in press). The aforementioned database and host plant catalog list relatively few herbaceous bamboos as euptychiine host plants, although ongoing research by the authors in the Peruvian Amazon suggests a greater abundance of these bamboos as natural host plants, as discussed below. In the present study, we document the immature stages and natural host plants for three euptychiines feeding on herbaceous bamboos following our preceding studies and report *Taquara micrantha* as a natural host plant record for *Nhambikuara mima* (Butler, 1867), *Splendeuptychia furina* (Hewitson, 1862), and *Paryphthimoides brixius* (Godart, [1824]). We further compare our findings of *Splendeuptychia furina* (Hewitson, 1862) to *Nhambikuara mima*; and *Paryphthimoides brixius to Paryphthimoides terrestris* (Butler, 1867), a species documented in our successive study (Corahua-Espinoza *et al.* in press), to find generic diagnostic characters based on immature stages. We further report two herbaceous bamboo species, *Olyra latifolia* and *Taquara micrantha* as the first known host plants utilized in nature for *Magneuptychia harpyia* (C. Felder & R. Felder, 1867).

Materials and methods

The present study was mainly carried out at Finca Las Piedras (FLP), a 54 ha research station located approximately 48 km north of Puerto Maldonado, Madre de Dios department, Peru (-12.22789, -69.11119; ca. 240 m). The study site consists mostly of mature '*terra firme*' or upland rainforest, although abandoned agricultural fields, regenerating secondary forest, and *Mauritia* palm swamps also occur in the area. *Terra firme* rainforest at the site is dominated by emergent *Bertholletia excelsa* (i.e. Brazil nut) and *Eschweilera coriacea*, both in the Lecythidaceae, as well as multiple Fabaceae species (e.g., *Apuleia leiocarpa, Dipteryx micrantha, Hymenaea* spp.), among others; the understory is characterized by abundant small palms, Piperaceae spp., and herbaceous bamboos (Poaceae: Bambusoideae: Olyreae). Additional information regarding FLP is summarized in Baine *et al.* (2019) and See *et al.* (2018), and is also available at: https://www.sustainableamazon.org/. The larva of *M. harpyia* (2021-FLP-IMM-0352) was obtained from comparable rainforest within a concession of the extraction of Brazil nuts located approximately 15 km east of FLP (-12.22726, -68.97076).

The fieldwork relevant to this study was carried out between April–December 2021, as well as February 2020 at FLP. The sampled larvae were taken into the field laboratory at FLP to monitor their growth (dates summarized in Table 1) after condition assessments of the host plants in the field (Table 2). The immatures were kept at ambient temperature in 1 L plastic containers covered with a nylon mesh cloth held in place by an elastic band. The larvae were photographed frequently (at least twice per instar) and received fresh leaves from their host plants as needed, which were kept fresh using floral water tubes, and the container was cleaned daily. The larva of Paryphthimoides brixius was fed with Lasiacis ligulata Hitche. & Chase in its last three instars. During the rearing period, temperature and precipitation information were recorded daily at 8 am (GMT-5) and summarized in Appendix. Examination of the head capsules were made using a Novel NSZ-608T microscope and stereoscope 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 were determined based on the ruler photographed with immatures and rounded off to the tenth of 1 mm. Head capsule width was calculated by measuring the widest point of the capsule, including the chalazae. Body length for larvae was measured from the anterior portion of the head to the posterior tip of the caudal filament; pupa length was measured from the base of the cremaster to the anterior tip of the head. We follow Stehr (1987) for terminology related to immature stages. Due to its potential for containing a phylogenetic signal, and with no apparent standardized terminology for chalazae observed in the euptychiine group, we termed principle chalazae herein to aid description and recognition of homologous chalazae in the group (Fig. 6c). The examined individuals were vouchered (2021-FLP-IMM-0486, 0489, 0520, 0521, 0528, 0536, 0537, 0538, 0539, 0542, 0316, 0467, 0553, 0554, 0556, 0557, 0558, 0395, 0352, 0555 and 2020-FLP-IMM-0073) and these materials are deposited in the collection of the Alliance for a Sustainable Amazon (ASA), Puerto Maldonado, Peru.

TABLE 1. Voucher information	iion and dates recorded for four eu	uptychiine spec	ies studied herein.				
voucher	Taxon	sex	date of coll.	egg hatch	L1 to L2	L2 to L3	L3 to L4
							(antepenultimate to
							penultimate)
2021-FLP-IMM-0486	Nhambikuara mima	female	23/7/2021	no data	no data	no data	24/7/2021
2021-FLP-IMM-0489	Nhambikuara mima	male	23/7/2021	no data	no data	no data	28/7/2021
2021-FLP-IMM-0520	Nhambikuara mima	no data	1/9/2021	5/9/2021	no data	no data	no data
2021-FLP-IMM-0521	Nhambikuara mima	no data	1/9/2021	5/9/2021	no data	no data	no data
2021-FLP-IMM-0528	Nhambikuara mima	no data	6/9/2021	8/9/2021	no data	no data	no data
2021-FLP-IMM-0536	Nhambikuara mima	no data	14/9/2021	17/9/2021	no data	no data	no data
2021-FLP-IMM-0537	Nhambikuara mima	no data	14/9/2021	18/9/2021	no data	no data	no data
2021-FLP-IMM-0538	Nhambikuara mima	female	14/9/2021	18/9/2021	25/9/2021	2/10/2021	9/10/2021
2021-FLP-IMM-0539	Nhambikuara mima	no data	14/9/2021	18/9/2021	no data	no data	no data
2021-FLP-IMM-0542	Nhambikuara mima	female	19/9/2021	25/9/2021	2/10/2021	9/10/2021	15/10/2021
2020-FLP-IMM-0073	Splendeuptychia furina	female	27/2/2020	no data	no data	no data	no data
2021-FLP-IMM-0316	Splendeuptychia furina	male	08/04/2021	no data	no data	no data	no data
2021-FLP-IMM-0467	Splendeuptychia furina	male	12/7/2021	no data	no data	no data	no data
2021-FLP-IMM-0553	Splendeuptychia furina	male	28/10/2021	no data	no data	no data	31/10/2021
2021-FLP-IMM-0554	Splendeuptychia furina	female	28/10/2021	30/10/2021	7/11/2021	13/11/2021	19/11/2021
2021-FLP-IMM-0556	Splendeuptychia furina	male	5/11/2021	8/11/2021	17/11/2021	21/11/2021	26/11/2021
2021-FLP-IMM-0557	Splendeuptychia furina	female	7/11/2021	10/11/2021	15/11/2021	21/11/2021	26/11/2021
2021-FLP-IMM-0558	Splendeuptychia furina	female	8/11/2021	10/11/2021	16/11/2021	21/11/2021	28/11/2021
2021-FLP-IMM-0395	Paryphthimoides brixius	male	23/5/2021	no data	no data	30/5/2021	7/6/2021
2021-FLP-IMM-0352	Magneuptychia harpyia	female	18/4/2021	no data	no data	no data	no data
2021-FLP-IMM-0555	Magneuptychia harpyia	male	4/11/2021	11/11/2021	18/11/2021	26/11/2021	3/12/2021
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TABLE 1. (Continued)							
voucher	Taxon	sex	L4 to L5	L5 to L6	pupation	adult	died
			(penultimate to ultimate)				
2021-FLP-IMM-0486	Nhambikuara mima	female	9/8/2021	n/a	22/8/2021	3/9/2021	n/a
2021-FLP-IMM-0489	Nhambikuara mima	male	11/8/2021	n/a	23/8/2021	5/9/2022	n/a
2021-FLP-IMM-0520	Nhambikuara mima	no data	no data	no data	no data	no data	11/9/2021
2021-FLP-IMM-0521	Nhambikuara mima	no data	no data	no data	no data	no data	11/9/2021
2021-FLP-IMM-0528	Nhambikuara mima	no data	no data	no data	no data	no data	21/9/2021
2021-FLP-IMM-0536	Nhambikuara mima	no data	no data	no data	no data	no data	23/9/2021
2021-FLP-IMM-0537	Nhambikuara mima	no data	no data	no data	no data	no data	1/10/2021
2021-FLP-IMM-0538	Nhambikuara mima	female	16/10/2021	n/a	27/10/2021	7/11/2021	n/a
2021-FLP-IMM-0539	Nhambikuara mima	no data	no data	no data	no data	no data	28/9/2021
2021-FLP-IMM-0542	Nhambikuara mima	female	23/10/2021	n/a	2/11/2021	15/11/2021	n/a
2020-FLP-IMM-0073	Splendeuptychia furina	female	no data	no data	no data	11/3/2020	n/a
2021-FLP-IMM-0316	Splendeuptychia furina	male	no data	no data	13/4/2021	26/4/2021	n/a
2021-FLP-IMM-0467	Splendeuptychia furina	male	16/7/2021	n/a	2/8/2021	16/8/2021	n/a
2021-FLP-IMM-0553	Splendeuptychia furina	male	6/11/2021	n/a	15/11/2021	28/11/2021	n/a
2021-FLP-IMM-0554	Splendeuptychia furina	female	26/11/2021	n/a	5/12/2021	16/12/2021	n/a
2021-FLP-IMM-0556	Splendeuptychia furina	male	2/12/2021	n/a	10/12/2021	22/12/2021	n/a
2021-FLP-IMM-0557	Splendeuptychia furina	female	n/a	n/a	5/12/2021	16/12/2021	n/a
2021-FLP-IMM-0558	Splendeuptychia furina	female	n/a	n/a	7/12/2021	18/12/2021	n/a
2021-FLP-IMM-0395	Paryphthimoides brixius	male	16/6/2021	n/a	1/7/2021	16/7/2021	n/a
2021-FLP-IMM-0352	Magneuptychia harpyia	female	no data	no data	27/4/2021	14/5/2021	n/a
2021-FLP-IMM-0555	Magneuptychia harpyia	male	10/12/2021	18/12/2021	2/1/2022	14/1/2022	n/a

TABLE 2. Details of sampled materials with information on the host plant conditions. Abbreviations: abaxial (AB); adaxial (AD); distal (D); middle (M); proximal (P); midrib

	~ ()(
	Stage egg(s)/ larva(E)	larva	larva	egg	larva	larva	larva	larva	egg	egg	egg	egg	larva	larva	egg							
	LF damage (NO/L/ MI/H)	Г	NO	Н	NO	IMI	L	NO														
	LF age (N/MA/O)	MA	Z	MA																		
	LF blade proximity (B/E/IN)	н	N	В	В	Щ	В	В	Щ	В	В	Ц	В	N	Е	Е	ц	Е	Щ	N	В	Е
	LF proximity to base (D/M/P)	M	D	Μ	Μ	Μ	Μ	Μ	Μ	Μ	Μ	Μ	D	Μ	Μ	Р	Μ	Μ	Μ	Μ	Μ	Μ
eavy (H).	Leaf surface (AB/ AD)	AB																				
VO); light (L); mid (MI); he	Distance from ground (meters)	0.4	0.2	0.1	0.15	0.1	0.2	0.1	0.2	0.1	0.1	0.25	0.9	0.1	0.2	0.1	0.1	0.1	0.15	0.2	0.8	0.1
	Plant species	micrantha	latifolia	micrantha																		
); old (O); none (]	Plant genus	Taquara	Olyra	Taquara																		
V); mature (MA)	Plant family	Poaceae																				
IN); new (N	Host plant ID	594	594	611	611	611	577	591	575	608	575	389	560	585	614	614	591	591	577	495	544	614
(B); middle (E); margin (.	Voucher	2021-FLP-IMM-0486	2021-FLP-IMM-0489	2021-FLP-IMM-0520	2021-FLP-IMM-0521	2021-FLP-IMM-0528	2021-FLP-IMM-0536	2021-FLP-IMM-0537	2021-FLP-IMM-0538	2021-FLP-IMM-0539	2021-FLP-IMM-0542	2020-FLP-IMM-0073	2021-FLP-IMM-0316	2021-FLP-IMM-0467	2021-FLP-IMM-0553	2021-FLP-IMM-0554	2021-FLP-IMM-0556	2021-FLP-IMM-0557	2021-FLP-IMM-0558	2021-FLP-IMM-0395	2021-FLP-IMM-0352	2021-FLP-IMM-0555

Results

Table 1 provides information for all recorded dates, sex (if discernible), and voucher codes associated with individuals studied in the present article. Information regarding the condition of the host plants at the time of sampling for each immature is available in Table 2, and temperature and precipitation data for the rearing period in 2021 are provided in Appendix.

Description of the immature stages

Nhambikuara mima (Butler, 1867)

(2021-FLP-IMM-0486, 0489, 0520, 0521, 0528, 0536, 0537, 0538, 0539, 0542)

Egg (Fig. 1: 1a, b). Spherical, semi-transparent, pearl-like and whitish in color, with polygonal markings covering the surface. Black patchy irregular spots appear two days prior to hatching (Fig.1: 1b). Diameter: 1.1–1.2 mm (n=2). Duration: Unknown, hatched 2–6 days (n=8) after collection.

First instar (Fig. 1: 2a, b; Fig. 5: a). Head capsule width: 0.92 mm(n=1). Head capsule appearing black with rectangular scolus, with two rather broad seta (scolus length 0.16 mm(n=1)); three chalazae visible in frontal view, M1, M2, M3, with seta on each of M1-3; five setae visible on one side of labrum; six stemmata visible, with stemma 1 and 6 somewhat paler and thus insignificant, stemma 3 largest, closer to stemma 2 than 4. Body integument creamy-white and semi-transparent, influencing dark green (T1 to A5) to light green (A6 to A8) body color due to gut content; pair of white stripes in subdorsal area; tracheal system barely visible; chaetotaxy not fully discernible based on photographs, primary setae weakly bulbed at apex (*sensu* Murray (2001)), XD1 and XD2 visible on T1; D1, D2, SD1 and L1 apparently present from T1 to A10 (D1 approximately 1.5 times longer than D2 on A8 and A9); short, bifid caudal filaments. Body length: 4.0 mm (n=1). Duration: 7 days (n = 2).



FIGURE 1. Life history of *Nhambikuara mima*: 1a) egg, 1b) black patches present on egg two days prior to hatching; 2a, b) first instar in dorsal and lateral view; 3a, b) second instar in dorsal and lateral view; 4a, b) third instar in dorsal and lateral view; 5a, b) fourth instar in dorsal and lateral view; 6a, b) fifth (ultimate) instar in dorsal and lateral view; 7a, b, c) pupa in dorsal, lateral and ventral view; 8a, b) adult in dorsal and ventral view. Figure 1a based on 2021-FLP-IMM-0542; 1b, 2a, b, 3a, b are based on 2021-FLP-IMM-0538; otherwise illustrations based on 2021-FLP-IMM-0489.

Second instar (Fig. 1: 3a, b; Fig. 5: b). Head capsule width: 1.1 mm (n=1). Head capsule appearing light olive with numerous secondary setae and "antler-like" bifurcating scolus, inner short fork positioned perpendicular to horizontal plane, appearing darker distally, with seta on both tips (scolus length 0.64 mm (n=1)); seven chalazae visible on lateral side, M1, M2, M3, P1, P2, P3, P4, with primary seta on each of M1-3, P1,2; five setae visible on one of labrum; six stemmata visible, arrangement similar to previous instar. Body light green, dorsally with rather broad, white, parallel bands delineating the mid-dorsal region; four dorso-lateral stripes lateral to white bands, first band broadest and extending towards base of caudal filament, fourth narrow and somewhat insignificant; spiracles visible as dark green spots; short, bifid caudal filaments, dorsally pink. Body length: 6.4-8.0 mm (n=2). Duration: 7 days (n = 2).

Third instar (Fig. 1: 4a, b). Head capsule width: 1.5 mm (n=1). Head capsule appearing light olive with numerous secondary setae "antler-like" bifurcating scolus, inner short fork positioned perpendicular to horizontal plane, appearing darker distally, with seta on both tips (scolus length 0.4 mm (n=1)); seven chalazae visible on lateral side, M1, M2, M3, P1, P2, P3, P4, with primary seta on each of M1-3; five setae visible on one of labrum; six stemmata visible, arrangement similar to previous instar. Body light green, dorsally with rather broad, white, parallel bands delineating the mid-dorsal region; four dorso-lateral stripes lateral to white bands, first band broadest and extending towards base of caudal filament, fourth narrow and somewhat insignificant; spiracles visible as dark green spots; short, bifid caudal filaments, dorsally pink. Body length: 9.6–12.8 mm (n=4). Duration: 6–7 days (n = 2).

Fourth instar (Fig. 1: 5a, b). Head capsule width: 2.0 mm (n=1). Head capsule appearing olive with numerous secondary setae and "antler-like" bifurcating scolus, inner short fork positioned perpendicular to horizontal plane, appearing darker distally, with seta on both tips (scolus length 0.6 mm (n=1)); seven chalazae (M1-3, P1-4) visible on lateral side, developed compared to previous instar, with primary seta on each of these seven chalazae, as well as on two chalazae posterior of scolus; dark band-like marking visible on frontal part and lateral side of head capsule (as illustrated); five setae visible on one of labrum; six stemmata visible, arrangement similar to previous instar. Body pinkish dorsally and olive laterally; general pattern similar to previous instar except for inner margin of broad dorsal white band appearing thicker and thus delineating pink mid-dorsal region with contrast. Body length: 12.3–18.7 mm (n=4). Duration: 7–16 days (n=4).

Fifth (ultimate) instar (Fig. 1: 6a, b; Fig 5: c, d). Head capsule width: 3.1 mm (n=1). Head capsule appearing olive with numerous secondary setae and "antler-like" bifurcating scolus, similar to previous instar except for appearing shorter in proportion to head capsule height (scolus length 0.5 mm (n=1)); seven chalazae (M1-3, P1-4) visible on lateral side, overall arrangement similar to previous instar; dark band-like marking visible on frontal part and lateral side of head capsule (as illustrated); five setae visible on one of labrum; six stemmata visible, arrangement similar to previous instar; labrum appearing reduced. Body pink, dorsally with dark rose mid-dorsal region delineated with creamy-white narrow band adjacent to pink broad dorsal region; stripes dorso-lateral to lateral bands appearing creamy-white and somewhat insignificant, except for thick creamy-white ventral margin; dark reddish, rounded spots present along posterior margin of dorso-lateral region from A1 to A6, as well as A7 but rather insignificant; spiracles visible as dark brownish spots; short, bifid caudal filaments, dorsally pink. Body length: 22.7–26.7 mm (n=4). Duration: 10–13 days (n=4).

Pupa (Fig. 1: 7a, b, c). Body light brown, mottled with dark brown especially prominent on thorax, head appearing rather pale ventrally except for antennae; body overall appearing slender with squared ocular caps; small brown protuberances present in two rows along dorsal area of abdomen (appearing darker on A1); paired shoulder-like protuberances present on the mesothorax; light brown cremaster, short and gradually narrowing towards distal end in posterior view, with rounded pitted sculptures. Body length: 12.0–12.8 mm (n=2). Duration: 11–13 days (n=3).

Host plant (Fig 4: 1a-d; 2a-d). *Taquara micrantha* (Kunth) I.L.C.Oliveira & R.P.Oliveira (Poaceae: Bambusoideae: Olyreae).

This is a species of herbaceous bamboo, usually found grouped with other individuals of the same species in understory light gaps, as well as along the forest edges at FLP. *Taquara micrantha* is a species characterized by considerable variation (Oliveira *et al.* 2020), which appears to be the case at FLP. The larvae were found feeding on two variations of *Taquara micrantha*, characterized by presence or absence of pubescence on the stem and leaves, during different months of the year.

Two larvae (2021-FLP-IMM-0486 and 2021-FLP-IMM-0489; July 2021) were found on a single T. micrantha

plant growing in a gap near the edge of the forest. This plant had prominent pubescence on the stem and on the abaxial surface of the leaves (Fig. 4: 1a-d; one variation of *Taquara micrantha*). Eight eggs (2021-FLP-IMM-0520, 0521, 0528, 0536, 0537, 0538, 0539, 0542; September 2021) were found on plants near a palm swamp. These plants had lacked pubescence on the stem and scabrous abaxial surface (Fig. 4: 2a-d; another variation of *Taquara micrantha*).

Based on 2021-FLP-IMM-0489 at the time of larva collection for *Nhambikuara mima* (July 23, 2021), the plant was 0.4 m tall. The larva was found at a distance of 0.2 m from the ground, on the abaxial surface of the leaf, near the leaf apex, at the margin of the blade (Table 2).

Splendeuptychia furina (Hewitson, 1862)

(2020-FLP-IMM-0073; 2021-FLP-IMM-0316, 0467, 0553, 0554, 0556, 0557, 0558)

As indicated in Table 1, this taxon goes through either four or five larval instars. The description below is based mainly on 2021-FLP-IMM-0554, which passed through five larval instars.

Egg (Fig. 2: 1a, b). Spherical, semi-transparent, pearl-like and whitish in color, with polygonal markings covering the surface. Brown irregular short stripes, partially delineating polygonal markings, appearing two days prior to hatching (Fig. 2: 1a); head capsule visible day prior to hatching (Fig. 2: 1b). Diameter: 1.0–1.1 mm (n=2). Duration: Unknown, hatched 2–3 days (n=4) after collection.

First instar (Fig. 2: 2a, b; Fig. 5: e). Head capsule width: 0.9 mm (n=1). Head capsule appearing black with rectangular scolus, with two rather broad setae (scolus length 0.1 mm (n=1)); three chalazae visible in frontal view, M1, M2, M3, with seta on each of M1-3; five setae on one side of labrum; with stemma 1 and 6 somewhat paler and thus insignificant, stemma 3 largest, closer to stemma 2 than 4. Body integument creamy whitish and semi-transparent, thus influencing dark green (anterior half of abdomen and occasionally thorax) to light green (towards terminal abdominal segments) body color due to gut content; pair of white stripes in subdorsal area; tracheal system barely visible; chaetotaxy not fully discernible based on photographs, primary setae weakly bulbed at apex (*sensu* Murray (2001)), XD1 and XD2 visible on T1; D1, D2, SD1 and L1 apparently present from T1 to A10 (D1 approximately 1.5 times longer than D2 on A8 and A9); ventral prolegs present on A3 to A6, caudal prolegs present on A10; caudal filaments short (shorter than A8 in dorsal view). Body length: 4.6–5.5 mm (n=2). Duration: 5–9 days (n=4).

Second instar (Fig. 2: 3a, b; Fig. 5: f). Head capsule width: 1.3 mm (n=1). Head capsule appearing black with numerous secondary setae and "antler-like" bifurcating scolus, entirely blackish, inner fork positioned almost perpendicular to horizontal plane, with seta on both tips (scolus length 0.4 mm (n=1)); seven whitish chalazae visible on lateral side, M1, M2, M3, P1, P2, P3, P4, with primary seta on each of M1-3, and P1, seta on P2 not discernable; six setae on one side of labrum, six stemmata visible, arrangement similar to previous instar. Body dark green; dorsally with white, band-like rows of spots somewhat delineating the mid-dorsal region (more defined from T1 to T3); broad and whitish pair of sub-dorsal stripes, extending towards base of caudal filament, with narrow concolorous lateral stripe present below; spiracles visible as light brownish spots, prominent on T1 and A8; caudal filaments, dorsally pink, shorter than A8 in dorsal view. Body length: 7.7 mm (n=1). Duration: 4–6 days (n = 4).

Third instar (Fig. 2: 4a, b). Head capsule width: 1.6 mm (n=1). Head capsule appearing black with numerous secondary setae; "antler-like" bifurcating scolus, entirely blackish, inner fork positioned almost perpendicular to horizontal plane, with seta on both tips (scolus length 0.6 mm (n=1)); seven whitish chalazae visible on lateral side, M1, M2, M3, P1, P2, P3, P4, with primary seta on each of M1-3; six setae on one side of labrum; six stemmata visible, arrangement similar to previous instar. Body dark green, dorsally with pair of white, narrow, parallel bands delineating the mid-dorsal region; broad and whitish pair of sub-dorsal stripes, extending towards base of caudal filament, with narrow concolorous lateral stripe present below; spiracles visible as light brownish spots, prominent on T1 and A8; caudal filaments, dorsally pink, similar in length to A8 in dorsal view. Body length: 9.5-11.1 mm (n=2). Duration: 5-7 days (n = 4).

Fourth instar (Fig. 2: 5a, b; Fig. 5: g). Head capsule width: 2.3 mm (n=1). Head capsule appearing olive with numerous secondary setae and "antler-like" bifurcating scolus, appearing orangish, inner fork positioned perpendicular to horizontal plane, appearing darker distally, with seta on both tips (scolus length 0.7 mm (n=1)); seven whitish chalazae (M1-3, P1-4) visible on lateral side, developed compared to previous instar, with primary

seta on each of these seven chalazae, as well as on two chalazae posterior of scolus; dark band-like marking visible on frontal part and lateral side of head capsule (as illustrated); six setae on one side of labrum; six stemmata visible, with first and sixth somewhat semi-transparent and thus insignificant, third stemma largest. Body lighter than previous instar; general pattern similar to previous instar except for spiracles appearing whitish. Body length: 19.0-19.5 mm (n=2). Duration: 6-7 days (n=2).



FIGURE 2. Life history of *Splendeuptychia furina*: 1a) egg with brown stripes and mandibles showing through translucence, 1b) head capsule showing through translucence two days prior to hatching; 2a, b) first instar in dorsal and lateral view; 3a, b) second instar in dorsal and lateral view; 4a, b) third instar in dorsal and lateral view; 5a, b) fourth instar in dorsal and lateral view; 6a, b) fifth (ultimate) instar in dorsal and lateral view; 7a, b) ultimate instar exhibiting purple colouration a day prior to pupation, dorsal and lateral view; 8a, b, c) pupa in dorsal, lateral and ventral view; 9a, b) adult in dorsal and ventral view. Figure 2b, 3b are based on 2021-FLP-IMM-0556; otherwise illustrations based on 2021-FLP-IMM-0554.

Fifth (ultimate) instar (Fig. 2: 6a, b; 7a, b; Fig. 5: h). Head capsule width: 2.6 mm (n=1). Head capsule appearing olive with numerous secondary setae and "antler-like" bifurcating scolus, similar to previous instar except for appearing shorter in proportion to head capsule height (scolus length 0.8 mm (n=1)); seven chalazae (M1-3, P1-4) visible on lateral side but appearing orangish compared to previous instar and less developed; six stemmata visible, arrangement similar to previous instar; four setae discernable on one side of labrum with few other small setae, labrum appearing reduced. Body mint green (turns purplish a day prior to pupation, mobile but does not feed; Fig. 2: 7a, b); general pattern similar to previous instar except for stripes somewhat insignificant by blended into mint green body color except for T1, spiracles appearing creamy orangish. Body length: 25.8–26.0 mm (n=2). Duration: 8–9 days (n=2).

Pupa (Fig. 2: 8a, b, c). Body dark chestnut brown and mottled with cream spots; body overall appearing slender with squared ocular caps; small dark brown protuberances present in two rows along dorsal area of abdomen; paired shoulder-like protuberances present on the mesothorax; pale cremaster, short and gradually narrowing towards distal end in posterior view, with rounded pitted sculptures. Body length: 11.6–13.2 mm (n=2). Duration: 11–14 days (n=7).

Host plant (Fig 4: 2a–d). *Taquara micrantha* (Kunth) I.L.C.Oliveira & R.P.Oliveira (Poaceae: Bambusoideae: Olyreae).

See corresponding section of previous species for further detail. All the larvae of *S. furina* collected in 2021 were sampled from *Taquara micrantha*, and all individuals shared characteristics of absence of pubescence on the abaxial leaf surface (another variation of *T. micrantha*).

Based on 2021- FLP-IMM-0554, the individual associated with S. furina was located near a palm swamp, in a

small forest area. At the date of collection the plant was 0.4 m tall. The egg was found at a distance of 0.1 m from the ground, on the abaxial surface, proximal to the leaf base, and between the midrib and margin of the leaf.

Paryphthimoides brixius (Hewitson, 1862)

(2021-FLP-IMM-0395)

Second instar. Head capsule width: 0.8 mm (n=1). Head appearing dark brown scattered with secondary setae and "horn-like" scolus, slightly curving outwards in frontal view (scolus length 0.3 mm (n=1)); single, whitish chalazae visible on lateral side (M1) (based on head capsule image), with primary seta on each of these chalazae; six stemmata visible, with first and sixth somewhat semi-transparent and thus insignificant, third stemma largest. Body not described and illustrated. Duration: Unknown; molted 7 days after collection.

Third instar (Fig 3: 1a, b; Fig 5: i). Head capsule width: 1.0 mm (n=1). Head appearing light olive with numerous secondary setae, apparently thicker, denser, and increased in number compared to previous instar; "horn-like" scolus appearing dark brown except for posterior side and basal half of anterior side (scolus length 0.4 mm (n=1)); dark colouration on vertex extending to scolus, as well as present laterally and partially on frontal part, as illustrated; three whitish chalazae visible on lateral side (M1-3), with primary seta on each of these three chalazae; six stemmata visible, with stemma 1 and 6 somewhat semi-transparent and thus insignificant, stemma 3 largest, closer to stemma 2 than 4. Body whitish; dark purple band extending along mid-dorsal area, well-defined along thorax and A5 onwards, insignificant from A1 to A4; concolourous jagged band traversing along previous mid-dorsal band; similar jagged band present laterally, roughly parallel to previous band; spiracles visible as creamy-white spots; short, bifid caudal filaments, dorsally white, inner side purple resulting from continuation of mid-dorsal band. Body length: 8.2 mm (n=1). Duration: 8 days (n=1).



FIGURE 3. Life history of *Paryphthimoides brixius*: 1a, b) third instar in dorsal and lateral view; 2a, b) fourth instar in dorsal and lateral view; 3a, b) fifth (ultimate) instar in dorsal and lateral view; 4a, b, c) pupa in dorsal, lateral and ventral view; 5a, b) adult in dorsal and ventral view. All illustrations based on 2021-FLP-IMM-0395.

Fourth instar (Fig 3: 2a, b). Head capsule width: 1.5 mm (n=1). Head appearing olive with numerous secondary setae, apparently thicker and increased in number compared to previous instar; head scolus overall similar to previous instar except somewhat shorter (scolus length 0.5 mm (n=1)) and distally (apex) orangish; patterns of darker markings on head capsule similar to previous instar except for area increasing in frontal part and reduced laterally around chalazae; arrangement and appearance of stemmata and chalazae similar to previous instar. Body color pattern similar to previous instar; spiracles appearing darker compared to previous instar; caudal filaments similar to previous instar. Body length: 13.4 mm (n=1). Duration: 9 days (n=1).

Fifth (ultimate) instar (Fig 3: 3a, b; Fig 5: j). Head capsule width: 1.9 mm (n=1). Head appearing olive with numerous secondary setae, apparently thicker and denser compared to previous instar; head scolus overall similar to previous instar except shorter (scolus length 0.4 mm (n=1)); patterns of dark brown markings on head capsule increasing on frontal side as well as laterally, as illustrated; arrangement and appearance of stemmata and chalazae similar to previous instar; five setae on one side of labrum, labrum appearing reduced. Body flesh-coloured; middorsal band and jagged dorso-lateral to lateral bands as in previous instar except for appearing somewhat brownish; spiracles appearing dark brownish and more prominent compared to previous instars; bifid caudal filaments, dorsally brownish, with inner side dark brownish resulting from continuation of mid-dorsal band, and terminating in pink posterior tip. Body length: 17.5 mm (n=1). Duration: 15 days (n=1).

Pupa (Fig 3: 4a, b, c). Body cream in color and mottled with dark brown; wing case overall cream scattered with dark brown markings; body overall appearing short and rounded, with squared ocular caps; small cream and dark brown protuberances present in two rows along dorsal area of abdomen; brown cremaster, gradually narrowing towards distal end but appearing broader than previous two species. Body length: 6.8 mm (n=1). Duration: 15 days (n=1).

Host plant. Taquara micrantha (Kunth) I.L.C.Oliveira & R.P.Oliveira (Poaceae: Bambusoideae: Olyreae).

See corresponding section of previous species for further detail. At the time of larval collection for *Paryphthimoides brixius*, (May 23, 2021), the plant was 0.4 m tall. The larva was found at a distance of 0.2 m from the ground, on the abaxial surface of the leaf, in the middle part (between the base and the apex) just at the margin of the leaf (Table 2).



FIGURE 4. Host plant, two variations of *Taquara micrantha*. *Taquara micrantha* with pubescence on the abaxial surface as a host plant for *Nhambikuara mima* and *Paryphthimoides brixius*: 1a) leaves; 1b) close-up view of the node and abaxial part showing pubescence; 1c) inflorescence materials; 1d) host plant in situ. *Taquara micrantha* lacking pubescence for *Splendeuptychia furina*: 2a) leaves and inflorescence *in situ*; 2b) close-up view of nodes; 2c) close-up view of abaxial surface showing lack of pubescence; 2d) host plant *in situ*.



FIGURE 5. Illustrations of head capsules: a, b, c) first, second, and fifth (ultimate) instar of *Nhambikuara mima*, in frontal view; d) fifth (ultimate) instar of *N. mima*, lateral view indicating labeled chalazae; e–h) first, second, fourth and fifth instar of *Splendeuptychia furina*, in frontal view; i, j) third and fifth (ultimate) instar of *Paryphthimoides brixius*, in frontal view. Figure a, b are based on 2021-FLP-IMM-0538; c, d are based on 2021-FLP-IMM-0489; e, f, g are based on 2021-FLP-IMM-0554; h are based on 2021-FLP-IMM-0316; i, j are based on 2021-FLP-IMM-0395.



FIGURE 6. Host plants for *Magneuptychia harpyia*: *Olyra latifolia* L.: 1a) leaves; 1b) close-up view of the nodes; 1c) close-up view of inflorescence materials; 1d) host plant *in situ*. 1e) *Taquara micrantha in situ* 2a, b) adult of *Magneuptychia harpyia* in dorsal and ventral view (based on 2021-FLP-IMM-0352).

Magneuptychia harpyia (C. Felder & R. Felder)

(2021-FLP-IMM-0352, 0555)

Host plants. *Olyra latifolia* L. (Poaceae: Bambusoideae: Olyreae) (Fig. 6: 1a–d). Based on 2021-FLP-IMM-0352, the larva was found on a plant in a primary forest located on a property adjacent to FLP (Monterrey). This plant species is typically found in areas of limited light availability and usually grows in groups of a few individuals, near other species of herbaceous plants of similar size. The collection was made when the plant was 0.8 m tall. The larva was found at a distance of 0.8 m from the ground, on the abaxial leaf surface, at the base of the leaf blade, just at the margin of the leaf (Table 2).

Taquara micrantha (Kunth) I.L.C.Oliveira & R.P.Oliveira (Poaceae: Bambusoideae: Olyreae) (Fig. 4: 2a–c. 6: 1e).

See corresponding section of previous species for further detail. Based on 2021-FLP-IMM-0555, the egg was sampled from *T. micrantha* with variation of absence of pubescence in the abaxial part of the leaf. The individual associated with *M. harpyia* was located near a palm swamp, in a small forest area. At the date of collection the plant was 0.4 m tall. The egg was found at a distance of 0.1 m from the ground, on the abaxial surface, in the middle part of the leaf, between the midrib and margin of the leaf.

Discussion

We here report novel life history information for four satyrine species in the nymphalid subtribe Euptychiina based on populations studied in Madre de Dios, Peru. All four species documented herein utilize herbaceous bamboo species in nature. As discussed above, Janzen & Hallwachs (2018) and Beccaloni *et al.* (2008) list relatively few herbaceous bamboos as host plants for euptychiine species. Beccaloni *et al.* (2008) referred to only two (out of 251) herbaceous bamboo records representing euptychiine host plants based on DeVries (1986) and Janzen & Hallwachs (2000 [2018]) (both for *Taygetis laches* Fabricius, 1793), as well as a single record for *Taygetis virgilia* (Cramer, 1776) based on personal communication. These records are all based on the herbaceous bamboo genus *Olyra*. Janzen & Hallwachs (2018) further report three records (out of 185) of *O. latifolia* being a euptychiine natural host plant based on 330 individuals for *Vareuptychia themis* (Butler, 1867) (as *Cissia themis*) (n=2), *Taygetis laches* (n=325), and *Taygetis thamyra* (Cramer, 1779) (n=3). Although identification of taxa in these two sources needs further verification, it is highly suggestive that these herbaceous bamboo records represent just the tip of the iceberg of known euptychiine host plant records in existing literature.

Considering the total diversity of Poaceae, with approximately 11,500 species in about 750 genera currently known (Soreng et al. 2017), one can interpret that underrepresented Olyreae host plant records for euptychiine species, as summarized above, simply reflect the species-richness of herbaceous bamboos (>120 species, see above) compared to the overall diversity of grasses. However, it must be taken into account that Olyreae diversity peaks in the Atlantic coastal forest of Brazil (Soderstrom et al. 1988), whereas Janzen & Hallwachs' (2018) database is based strictly on Costa Rican materials. The present study reported four euptychiine species in total, so far known only to utilize species of the tribe Olyreae in the Peruvian Amazon. Tejeira et al. (2021) and Nakahara et al. (2022) also reported a herbaceous bamboo species as a natural host plant for three euptychiine species based on a study conducted at FLP. These seven euptychiine species: Splendeuptychia furina (Hewitson, 1862), Paryphthimoides brixius (Godart, [1824]), Nhambikuara mima (Butler, 1867), Magneuptychia harpyia (C. Felder & R. Felder, 1867), Chloreuptychia marica (Weymer, 1911), Cisandina philippa (Buter, 1867), and Cisandina castanya Lamas & Nakahara, 2022 are uncommon at FLP (pers. obs.). Materials for these taxa are also less represented in public/ private collections compared to more widespread and common species known to feed on a wide range of species in the family Poaceae, such as Magneuptychia libye (Linneaus, 1767), which uses a species of herbaceous bamboo in the genus Piresia Swallen, as well as species in the family Cyperaceae (Singer & Ehrlich 1991; Beccaloni et al. 2008; Checa & Torres 2019).



FIGURE 7. Immature stages with some notable characters indicated with arrows, *Nhambikuara mima* compared to *Splendeuptychia furina*; *Paryphthimoides brixius* compared to *Paryphthimoides terrestris*: 1a, b) *Paryphthimoides brixius* ultimate instar in dorsal view and lateral view; 2a, b) *Paryphthimoides terrestris* ultimate instar in dorsal view and lateral view; 3a, b) *Nhambikuara mima* ultimate instar in dorsal view and lateral view and lateral view; 4a, b) *Splendeuptychia furina* ultimate instar prior to pupation in dorsal view and lateral view. 1c, 2c) *Paryphthimoides brixius* ultimate instar head capsule and *Paryphthimoides terrestris* ultimate instar head capsule; 3c, 4c) *Nhambikuara mima* ultimate instar head capsule; 3d–f, 4d, e) pupa of *Paryphthimoides brixius* and *Paryphthimoides terrestris*; 3d–f, 4d, e) pupa of *Nhambikuara mima* compared to *Splendeuptychia furina*. All images for *Nhambikuara mima*, *Splendeuptychia furina*, and *Paryphthimoides brixius* are reproduced from the present article; All images for *Paryphthimoides terrestris* from Corahua-Espinioza *et al.* (in press).

Since its initial proposal by Walsh (1864), the influence of host plant shifts on phytophagous insect diversification has stimulated a wealth of evolutionary research (e.g., Matsubayashi *et al.* 2010). The present study, coupled with our successive study at FLP, also suggests niche partitioning related to host plants may potentially play a key role in euptychiine diversification. For instance, two congeneric closely related species, *Paryphthimoides brixius* and *P. terrestris* occur in micro-sympatry at FLP and these two species are documented to utilize two distantly related plant species scattered in two different subfamilies of the Poaceae family (*Taquara micrantha* and *Lasiacis ligulata*). This is also reinforced by another pair of closely related euptychiine species in a distantly related genus, *Cisandina philippa* and *C. castanya*, which are found to be affiliated with two different herbaceous bamboo species (*Taquara micrantha* and *Olyra latifolia*) at the same study site (Nakahara *et al.* 2022). On the contrary, *Nhambikuara mima* and *Splendeuptychia furina* (see below for their relationships) were both found associated with *Taquara micrantha*, although immatures were sampled at different times of the year. Despite the fact that *Taquara micrantha* is the host plant for both *Nhambikuara mima* and *Splendeuptychia furina*, we report noticeable variation in the presence and absence of pubescence on the leaf. *Nhambikuara mima* was found on both variations of *T. micrantha* (2021-FLP-

IMM-0486, 0489 on leaf with pubescence; 2021-FLP-IMM-0520, 0521, 0528, 0536, 0537, 0538, 0539, 0542 on leaf without pubescence), whereas all larvae of *Splendeuptychia furina* collected in 2021 were only sampled from individuals with leaves which lacked pubescence (2021-FLP-IMM-0316, 0467, 0553, 0554, 0556, 0557, 0558). We are unable to provide information on presence or absence of pubescence for *T. micrantha* which the larva of *S. furina* was sampled in 2020.

Acquisition of inflorescent materials was key to identifying the host plant of *Nhambikuara mima*, which was identified previously as a species in the genus Pariana Aublet, rather than T. micrantha. This information highlights the highly variable nature of T. micrantha, whilst also suggesting subtle niche requirement differences may exist between these two taxa associated with variation within T. micrantha when additional data becomes available. We also report here that a single individual of S. furina from Mato Grosso, Brazil (Cristalino River, Alta Floresta municipality) was reared based on an egg obtained in captivity in June 2000, and subsequently reared on native bamboo in the region and Bambusa textillis McClure (Poaceae: Bambusoideae: Bambuseae) (A. Freitas, pers. comm.). Reduced competition for larval food plants has been suggested for two sympatric sibling satyrine species in North America (Shapiro & Cardé 1970), and our observation remains to be further tested with additional natural host plant data. Although here we report O. latifolia and T. micrantha as the first known natural host plants for Magneuptychia harpyia, this species accepted a different grass species (Lasiacis ligulata) throughout five larval stages in captivity (Nakahara et al. 2020). Paryphthimoides brixius also accepted Lasiacis ligulata in captivity in the present study. These observations suggest the herbaceous bamboo-feeding euptychiine taxa may potentially utilize a variety of Poaceae species in nature; therefore, whether our observation is reflecting a shift into a narrow niche associated with their host plants or not, further assessment by sustained fieldwork and species-level identification of their natural host plants is warranted. It is worth mentioning that a total of 15 individuals of *Chloreuptychia marica* were recorded to utilize only Pariana lunata Ness (Olyreae) for two consecutive years at FLP, encompassing somewhat different seasonalities (June-August 2020 and March-May 2021; Tejeira et al. (2021); Corahua-Espinoza et al. unpublished data), perhaps suggesting its narrow host plant preference at this study site. If their rarity can partially be explained by their narrow diet breadth, it would be interesting to explore the natural host plants of these species, spanning the range of the neotropics, as well as temporally throughout the year to encompass both dry and rainy seasons. As mentioned above, host plant records are available for about a mere 20% of the total euptychiine diversity (Nakahara & Corahua-Espinoza, in prep). Thus, compiling published and unpublished euptychiine host plant data into a single dataset to assess the role of host plant utilization and diet breadth in the evolution of euptychiines (based on the degree of polyphagy) will be extremely valuable in terms of our understanding of biogeography of this species-rich group. This research will provide insight into the factors contributing to the diversification of insects in the Amazon basin (Nakahara & Corahua-Espinoza, in prep.).

Nhambikuara mima and Paryphthimoides brixius are recovered as members of the so-called "Pareuptychia clade" (sensu Murray & Prowell 2005) and "Splendeuptychia clade" (sensu Peña et al. 2010), respectively. The generic classification of these two species changed recently from the comprehensive Lamas (2004) checklist of Neotropical butterflies, based on molecular data with support from adult external morphology (Espeland et al. in prep.). Despite the fact that they are not currently considered congeneric, *Nhambikuara mima* and *Splendeuptychia* furina form a strongly supported clade together with a few other species presently associated with Splendeuptychia (unpublished data). The present study further provides some immature characters which support this close relationship of Nhambikuara mima and Splendeuptychia furina: 1) ultimate instar of both species possess somewhat bifurcating "antler-like" head scolus with inner short fork positioned perpendicular to horizontal plane; 2) scolus orangish and darker distally; 3) seven rather developed chalazae (M1-3, P1-4) present (each apparently accompanied with seta); 4) pupa with paired shoulder-like protuberances present on the mesothorax; 5) pupa appearing slender and elongated, overall appearing two-toned by thorax and head mottled with darker colour. We also compare immature stages of Paryphthimoides brixius with Payphthimoides terrestris documented in Corahua-Espinoza et al. (in press) and provide these following characters to support their congeneric treatment: 1) vertex, scolus, and lateral side of head marked with darker colouration throughout penultimate and ultimate instars; 2) three whitish chalazae (M1-3) present (each apparently accompanied with seta); 3) mid-dorsal band well-defined along thorax and A5 onwards, insignificant from A1 to A4, coupled with concolourous jagged band traversing along mid-dorsal band; 4) pupa cream and mottled with dark brown, with two-toned protuberances. These aforementioned characters can be assessed based solely on photographs, being inexpensive and time efficient. Therefore, we consider these features to be worth listing for practical reasons, especially since immature stages are often not known for both sister species

pairs or two closely related species especially in the tropics. We were unable to study more than one individual for two species out of these four taxa discussed above, thus assessing variation, as well as exploring and comparing larval chaetotaxy, was not possible. Nevertheless, we argue that the infraspecific stability of these features discussed herein can be reasonably justified based on relevant euptychiine immature stages studies where multiple individuals were available for examination (e.g., Tejeira *et al.* 2021; Hurtado *et al.* 2021; present study). Clearly, an in-depth study of larval chaetotaxy is desirable to explore species-level differences, as evidenced by Hill & Tipan (2008), when additional materials become available for study.

To provide baseline information for future research on euptychiine diversity (as discussed above), we consider providing generic or species-level identification of their natural host plants, illustrations, and duration for documented immature stages, as well as head capsule illustrations to fulfill this purpose. We further report black, patchy spots which appear two days prior to hatching in the eggs of *N. mima* (Fig. 1: 1b); in some individuals, these black patches formed a stripe. Murray (2001) reported a similar character state for three *Pareuptychia* species, in which the egg turns entirely black, and determined that the inner chorion layer causes this phenomenon. Given that *N. mima* and *Pareuptychia* are both members of the same "*Pareuptychia* clade", the development of black coloration, observed in eggs of these taxa, may appear in other species of this clade as well; this conclusion is also somewhat supported by our observation of *S. furina* developing multiple brownish stripes at a similar development stage of the egg (Fig. 2: 1a).

In summary, coupled with our successive work (Corahua-Espinoza *et al.* in press), we here illustrate that our gap in knowledge regarding euptychiine systematics and biology can be improved based on intensive fieldwork combined with collaborative efforts. We continue to explore the early-stage biology of these common, but cryptic, members of the Neotropical butterfly community at FLP, in order to contribute to our understanding of the highly diverse Amazonian biodiversity.

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APPENDIX. Temperature (in Celsius) and precipitation (mm) data measured daily at FLP for the period when the rearing was conducted at this site. Maximum and minimum temperature represents those of the previous day.

date	max.temp	min.temp	current.temp.	current.time	precip.
08/04/2021	27.0	22.5	23.5	7:50	11
09/04/2021	28.0	22.5	24.5	8:05	1
10/04/2021	26.0	23.0	23.5	7:51	2
11/04/2021	26.5	22.0	23.0	8:12	5
12/04/2021	27.0	22.0	24.0	8:05	0
13/04/2021	25.0	20.5	22.0	8:13	0
14/04/2021	26.5	22.0	23.0	7:50	0
15/04/2021	27.5	22.5	23.5	7:58	0
16/04/2021	27.5	22.5	23.5	8:03	0
17/04/2021	28.0	23.5	24.0	7:58	0
18/04/2021	25.0	23.0	24.0	8:05	8
19/04/2021	27.0	23.5	25.0	9:06	10
20/04/2021	26.0	22.5	24.5	7:57	6
21/04/2021	26.5	23.0	24.0	7:54	4
22/04/2021	27.0	23.0	24.0	7:57	7
23/04/2021	27.5	23.5	25.0	8:01	1
24/04/2021	28.0	23.5	24.5	7:53	1
25/04/2021	28.0	23.5	24.5	7:55	0
26/04/2021	27.5	20.0	20.0	7:57	84
27/04/2021	23.0	20.5	21.5	8:01	8.5
28/04/2021	24.0	21.5	22.0	7:56	0
29/04/2021	29.5	23.5	25.0	7:50	0
30/04/2021	23.5	17.0	19.0	8:02	0
01/05/2021	24.5	18.0	19.0	7:51	0
02/05/2021	25.5	18.5	20.0	8:04	0

date	max.temp	min.temp	current.temp.	current.time	precip.
03/05/2021	27.0	20.0	22.0	7:56	0
04/05/2021	27.0	21.5	22.5	8:03	0
05/05/2021	28.0	22.0	23.0	7:55	0
06/05/2021	28.0	22.5	24.0	7:54	0
07/05/2021	24.0	16.0	16.5	7:50	1
08/05/2021	20.5	16.0	17.0	7:54	0
09/05/2021	23.0	16.5	17.5	7:49	0
10/05/2021	25.0	17.5	19.5	8:06	0
11/05/2021	26.0	19.0	21.0	8:03	0
12/05/2021	27.0	21.0	23.0	7:51	0
13/05/2021	24.0	19.5	20.0	7:53	0
14/05/2021	22.5	18.0	20.0	8:05	0
15/05/2021	24.0	19.5	21.5	7:59	0
16/05/2021	25.5	20.0	21.0	8:05	0
17/05/2021	26.5	21.0	23.0	8:03	0
18/05/2021	27.0	21.5	22.5	7:50	0
19/05/2021	27.0	20.5	22.0	8:05	18
20/05/2021	26.5	21.0	22.0	7:59	0
21/05/2021	27.0	21.5	23.0	7:55	0
22/05/2021	27.5	22.5	24.0	7:57	0
23/05/2021	28.0	23.5	24.0	8:10	7
24/05/2021	26.0	16.0	16.0	8:07	19
25/05/2021	18.5	15.5	17.0	8:04	0
26/05/2021	22.5	17.0	19.0	7:50	0
27/05/2021	21.5	18.5	20.0	7:49	0
28/05/2021	26.0	20.0	21.0	7:58	0
29/05/2021	27.0	20.5	21.5	9:30	0
30/05/2021	27.5	21.5	23.0	8:20	0
31/05/2021	28.0	23.0	23.0	9:57	0
01/06/2021	24.0	21.0	20.0	7:58	0
02/06/2021	23.0	20.0	21.0	7:58	0
03/06/2021	26.0	21.0	24.0	8:05	0
04/06/2021	26.0	22.5	23.0	7:48	24
05/06/2021	26.0	23.0	23.0	8:10	0
06/06/2021	27.0	21.5	23.0	8:23	0
07/06/2021	26.5	22.5	23.5	7:50	0
08/06/2021	26.0	22.5	23.5	8:00	6
09/06/2021	26.0	22.0	23.0	7:55	11
10/06/2021	27.0	23.0	22.0	8:01	3
11/06/2021	27.0	22.5	23.5	7:50	0
12/06/2021	25.0	17.0	18.0	8:03	10
13/06/2021	21.5	16.5	17.5	8:03	0
14/06/2021	23.0	16.5	17.5	8:01	0
15/06/2021	24.0	18.0	20.5	7:45	0

date	max.temp	min.temp	current.temp.	current.time	precip.
16/06/2021	25.0	19.0	20.5	7:55	0
17/06/2021	25.5	18.5	20.0	7:58	0
18/06/2021	24.5	19.5	19.5	7:58	0
19/06/2021	22.0	19.0	20.0	8:00	0
20/06/2021	21.0	18.0	18.0	8:00	1
21/06/2021	19.0	18.0	19.0	7:59	0
22/06/2021	24.0	19.0	21.0	7:54	0
23/06/2021	24.5	20.0	21.0	7:54	0
24/06/2021	25.5	19.0	20.0	7:55	0
25/06/2021	26.5	20.0	21.0	8:00	1
26/06/2021	27.0	20.0	21.0	7:53	0
27/06/2021	27.5	21.0	22.0	7:55	0
28/06/2021	27.5	16.5	17.0	7:59	4
29/06/2021	17.0	11.0	12.0	7:55	1
30/06/2021	16.0	12.0	14.0	8:00	0
01/07/2021	19.0	9.5	11.0	8:00	0
02/07/2021	20.5	11.0	13.0	8:00	0
03/07/2021	23.0	12.5	16.0	8:03	0
04/07/2021	24.0	15.0	17.0	8:01	0
05/07/2021	24.0	16.0	17.0	7:58	0
06/07/2021	25.0	16.0	18.5	8:00	0
07/07/2021	26.0	17.5	19.0	8:01	0
08/07/2021	26.0	19.0	20.0	8:03	0
09/07/2021	26.5	19.5	20.5	7:56	0
10/07/2021	26.5	21.0	22.0	8:09	0
11/07/2021	27.0	20.0	23.0	8:00	0
12/07/2021	25.0	20.0	21.0	7:59	2
13/07/2021	27.0	20.5	21.5	7:50	0
14/07/2021	27.0	21.5	23.0	8:00	1
15/07/2021	28.0	21.0	22.5	8:00	0
16/07/2021	28.0	22.0	22.5	7:55	0
17/07/2021	28.0	21.5	21.5	8:08	0
18/07/2021	25.0	21.0	21.0	7:45	0
19/07/2021	no data	no data	no data	no data	11
20/07/2021	22.0	13.0	15.0	8:04	0
21/07/2021	22.0	13.5	15.0	7:59	0
22/07/2021	23.0	15.0	16.0	7:54	0
23/07/2021	25.0	15.5	17.0	8:00	0
24/07/2021	26.0	17.5	18.0	8:05	0
25/07/2021	27.0	18.0	20.0	8:00	0
26/07/2021	27.5	19.5	20.0	8:00	0
27/07/2021	28.0	20.0	22.0	7:53	0
28/07/2021	28.0	17.0	17.0	8:01	0
29/07/2021	17.5	12.5	14.0	7:59	0

date	max.temp	min.temp	current.temp.	current.time	precip.
30/07/2021	19.5	11.0	12.0	7:50	0
31/07/2021	22.0	12.0	14.0	8:00	0
01/08/2021	24.0	14.0	17.5	8:25	0
02/08/2021	26.0	15.5	17.0	7:55	0
03/08/2021	25.0	15.0	17.0	7:57	0
04/08/2021	25.5	15.5	17.0	7:52	0
05/08/2021	27.0	15.0	16.0	7:48	0
06/08/2021	26.5	15.5	17.5	7:58	0
07/08/2021	27.5	17.0	18.5	7:56	0
08/08/2021	28.0	18.0	21.0	8:20	0
09/08/2021	29.0	19.5	21.0	7:59	0
10/08/2021	29.0	20.5	22.0	8:04	0
11/08/2021	29.0	19.0	20.0	8:04	0
12/08/2021	26.5	16.5	17.5	8:00	0
13/08/2021	25.0	15.0	13.0	7:50	0
14/08/2021	25.0	15.5	12.0	7:53	0
15/08/2021	27.0	17.0	19.0	7:56	0
16/08/2021	28.0	18.0	21.0	8:00	0
17/08/2021	30.0	21.5	22.0	7:43	0
18/08/2021	31.0	22.0	23.5	7:59	0
19/08/2021	31.0	22.0	23.5	7:58	0
20/08/2021	31.5	22.5	23.5	7:45	4
21/08/2021	29.0	23.0	24.5	8:00	0
22/08/2021	30.0	22.5	24.0	8:00	0
23/08/2021	31.0	23.0	24.5	7:47	0
24/08/2021	31.5	23.5	25.0	7:53	0
25/08/2021	32.0	24.0	25.0	7:57	0
26/08/2021	33.0	24.0	26.0	8:00	0
27/08/2021	33.0	16.5	17.5	7:54	3
28/08/2021	23.5	17.0	19.0	7:54	0
29/08/2021	28.0	19.0	22.0	7:47	0
30/08/2021	30.0	22.0	23.5	7:56	0
31/08/2021	31.0	22.0	24.0	7:59	0
01/09/2021	32.5	23.5	25.0	7:47	0
02/09/2021	33.0	23.0	25.0	8:00	0
03/09/2021	32.0	22.5	24.0	8:07	0
04/09/2021	33.0	23.0	24.5	7:43	0
05/09/2021	32.0	23.0	25.5	7:59	0
06/09/2021	34.0	23.5	25.0	7:46	3
07/09/2021	31.5	23.0	24.5	7:51	0
08/09/2021	33.0	22.0	25.0	8:08	0
09/09/2021	34.0	22.5	23.5	7:44	9
10/09/2021	31.0	17.0	17.0	7:44	1
11/09/2021	18.5	16.0	18.5	7:55	2

date	max.temp	min.temp	current.temp.	current.time	precip.
12/09/2021	27.5	18.0	22.5	8:01	0
13/09/2021	31.0	21.5	23.5	7:50	0
14/09/2021	32.5	21.5	24.5	7:46	0
15/09/2021	33.0	23.5	25.0	7:52	0
16/09/2021	30.0	20.0	21.0	7:58	1
17/09/2021	25.0	20.0	22.0	7:53	0
18/09/2021	31.5	21.0	24.0	8:00	0
19/09/2021	33.0	23.0	25.0	7:51	0
20/09/2021	33.0	24.0	26.0	7:46	0
21/09/2021	34.0	24.5	27.0	7:51	0
22/09/2021	32.0	22.0	23.0	7:46	0
23/09/2021	31.0	22.0	24.0	7:45	0
24/09/2021	33.5	23.0	25.0	7:45	0
25/09/2021	31.0	22.0	24.0	7:51	0
26/09/2021	32.5	23.0	25.0	7:47	0
27/09/2021	33.0	24.0	26.0	7:54	0
28/09/2021	33.5	24.5	27.5	8:08	0
29/09/2021	34.5	24.5	27.5	8:02	0
30/09/2021	32.5	22.5	19.5	7:59	10
1/10/2021	31.5	22.5	20.0	7:53	0
2/10/2021	32.5	23.0	26.0	7:54	0
3/10/2021	33.5	23.0	27.0	8:19	0
4/10/2021	32.5	23.5	24.0	7:50	9
5/10/2021	28.0	22.0	21.5	8:06	0
6/10/2021	22.0	19.0	21.5	8:05	0
7/10/2021	29.5	21.5	25.0	7:53	0
8/10/2021	31.5	22.5	25.0	7:47	0
9/10/2021	33.0	25.5	24.0	7:53	0
10/10/2021	31.5	24.0	26.5	7:52	0
11/10/2021	34.5	24.5	27.5	8:00	0
12/10/2021	35.5	24.0	24.0	8:00	0
13/10/2021	29.0	24.0	29.0	8:02	25
14/10/2021	31.0	24.0	27.5	8:00	0
15/10/2021	33.0	25.0	27.0	7:56	0
16/10/2021	33.0	24.5	24.0	7:53	5
17/10/2021	26.0	19.5	21.0	7:48	0
18/10/2021	26.0	21.0	23.0	7:56	33
19/10/2021	28.5	22.0	22.0	7:47	1
20/10/2021	23.0	20.0	23.0	8:08	0
21/10/2021	30.0	22.0	25.0	8:02	0
22/10/2021	32.0	24.0	25.0	8:10	0
23/10/2021	32.0	24.5	27.0	8:00	0
24/10/2021	33.0	24.5	28.5	7:59	0
25/10/2021	32.5	27.0	19.0	8:10	20

date	max.temp	min.temp	current.temp.	current.time	precip.
26/10/2021	23.5	19.0	21.0	7:53	1
27/10/2021	25.0	20.0	22.0	8:10	0
28/10/2021	29.5	22.0	25.5	7:52	0
29/10/2021	31.0	23.0	25.0	7:52	0
30/10/2021	32.0	22.5	26.0	7:57	0
31/10/2021	32.5	23.0	27.0	8:02	0
1/11/2021	33.0	24.0	27.0	7:44	0
2/11/2021	33.0	22.0	25.5	7:56	0
3/11/2021	30.5	23.0	23.0	8:01	0
4/11/2021	25.0	22.0	23.0	8:00	0
5/11/2021	no data	no data	no data	no data	no data
6/11/2021	no data	no data	no data	no data	no data
7/11/2021	31.0	19.5	20.0	7:33	18
8/11/2021	22.0	20.0	22.0	8:00	7
9/11/2021	26.0	22.0	24.0	7:58	0
10/11/2021	26.5	23.0	25.0	7:50:00	0
11/11/2021	29.0	24.0	26.0	8:05:00	0
12/11/2021	25.0	23.0	22.0	8:02:00	15
13/11/2021	26.0	24.0	23.0	7:54:00	4
14/11/2021	27.0	24.0	26.0	8:10	0
15/11/2021	29.0	24.0	25.0	7:50:00	0
16/11/2021	30.0	25.0	26.0	7:55:00	0
17/11/2021	27.0	24.0	24.5	7:50:00	0
18/11/2021	27.0	21.0	21.0	7:58:00	43
19/11/2021	22.5	21.5	22.0	7:58:00	21
20/11/2021	23.5	22.0	22.0	8:10:00	18
21/11/2021	26.0	22.0	26.5	7:55:00	0
22/11/2021	29.0	23.5	25.0	7:45:00	0
23/11/2021	29.5	25.0	26.0	7:55:00	0
24/11/2021	33.0	22.0	23.0	7:55:00	21
25/11/2021	28.5	23.5	25.0	7:57:00	0
26/11/2021	29.5	23.5	25.5	7:55:00	3
27/11/2021	29.5	23.0	23.5	7:55	1
28/11/2021	24.0	22.5	24.0	7:59	8
29/11/2021	27.5	23.0	25.5	8:48	19
30/11/2021	28.5	23.5	24.0	7:55	42
1/12/2021	27.5	23.5	25.0	7:54	0
2/12/2021	29.0	23.5	25.5	7:46	0
3/12/2021	28.5	23.0	25.0	7:55	18
4/12/2021	28.5	24.0	25.5	7:57	4
5/12/2021	28.5	24.5	25.0	7:40	0
6/12/2021	27.5	23.0	23.5	8:04	36
7/12/2021	26.0	23.5	24.5	7:55	18
8/12/2021	27.0	23.0	24.0	7:51	33

date	max.temp	min.temp	current.temp.	current.time	precip.
9/12/2021	28.5	23.0	23.5	7:53	1
10/12/2021	26.0	23.0	24.0	7:49	10
11/12/2021	28.0	24.0	24.5	7:54	0
12/12/2021	28.5	24.5	25.0	7:46	0
13/12/2021	28.0	24.4	26.0	7:51	2
14/12/2021	27.0	24.5	25.5	7:54	0
15/12/2021	28.5	23.5	25.5	9:00	0
16/12/2021	27.0	22.5	23.5	7:54	16
17/12/2021	27.0	22.5	25.0	7:40	1
18/12/2021	27.5	23.5	25.0	8:00	3