

Complete immature stages of the euptychiine butterfly *Taygetis cleopatra* (C. Felder & R. Felder, 1862) (Lepidoptera: Nymphalidae: Satyrinae) in southeastern Peru

Thalia Hurtado^{1,2}, Shinichi Nakahara^{3,4}, Maryzender Rodríguez-Melgarejo^{4,6}, Rafael Tejeira^{1,5}, Joseph See¹, Rodrigo Ccahuana^{1,5} and Geoffrey Gallice^{1,3}

1. Alliance for a Sustainable Amazon, Hanover, MD 21076, USA; 2. Facultad de Ciencias Naturales y Matemática, Universidad Nacional Federico Villarreal, Jr. Río Chepén, El Agustino, Lima, Perú; 3. McGuire Center for Lepidoptera and Biodiversity, Florida Museum of Natural History, University of Florida, Gainesville, FL 32611, USA; 4. Departamento de Entomología, Museo de Historia Natural, Universidad Nacional Mayor de San Marcos, Apartado 14-0434 Lima-14, Perú; 5. Universidad Nacional de San Antonio Abad del Cusco, Av. de La Cultura 773, Cusco 08000, Perú; 6. Laboratorio de Entomología, Instituto Argentino de Investigaciones de las Zonas Áridas (IADIZA, CCT CONICET, Mendoza), Casilla de Correo 507, 5500 Mendoza, Argentina. *Correspondence: info@sustainableamazon.org

Date of issue online: 17 December 2021

Electronic copies (ISSN 2575-9256) in PDF format at: <http://journals.fcla.edu/tropolep>; <https://zenodo.org>; archived by the Institutional Repository at the University of Florida (IR@UF), <http://ufdc.ufl.edu/ufir>; **DOI:** 10.5281/zenodo.5777169

© The author(s). This is an open access article distributed under the Creative Commons license CC BY-NC 4.0 (<https://creativecommons.org/licenses/by-nc/4.0/>).

Abstract: Here we document the complete life cycle of the Neotropical nymphalid butterfly *Taygetis cleopatra* (C. Felder & R. Felder, 1862) based on two individuals collected and reared in Madre de Dios, Peru, including the morphology and duration of each life stage. We also report this species' natural hostplant at the study site, a species of herbaceous bamboo, *Olyra latifolia* L. (Poaceae: Bambusoideae: Olyreae). Our study confirms existing information regarding the partial life history of this species in Ecuador, as well as its use of *O. latifolia* as a hostplant in southeastern Peru, while adding new information regarding its immature biology.

Key Words: Euptychiina, hostplant, immature stages, natural history, Poaceae

Resumen: Documentamos aquí el ciclo de vida completo de la mariposa ninfálica Neotropical *Taygetis cleopatra* (C. Felder & R. Felder, 1862) con base en dos individuos recolectados y criados en Madre de Dios, Perú, incluyendo la morfología y duración de cada etapa del ciclo de vida. También se reporta su planta hospedera en el sitio de estudio, una especie de bambú herbáceo, *Olyra latifolia* L. (Poaceae: Bambusoideae: Olyreae). Nuestro estudio confirma la información existente sobre el ciclo de vida parcial de esta especie en Ecuador, así como el uso de *O. latifolia* como planta hospedera en el sureste de Perú, y se agrega nueva información sobre la biología de los estadios inmaduros de *T. cleopatra*.

Palabras clave: Euptychiina, estadios inmaduros, historia natural, planta hospedera, Poaceae

INTRODUCTION

The nymphalid subfamily Satyrinae is one of the most widespread and diverse groups of diurnal Lepidoptera in the world (Ackery *et al.*, 1999). The satyrine subtribe Euptychiina includes some 70 genera and more than 500 species, with a number still undescribed (Corahua-Espinoza *et al.*, in review), and the group is considered one of the most diverse Neotropical butterfly radiations (Murray & Prowell, 2005; Matos-Maraví *et al.*, 2013). Within the subtribe, the so-called “*Taygetis* clade” (*sensu* Murray & Prowell, 2005) is composed of 10 genera and over 60 described species, although the clade's known species diversity will likely increase as our knowledge of it increases (e.g., Matos-Maraví *et al.*, 2013; Nakahara *et al.*, 2021a, b). The members of the “*Taygetis* clade” occur exclusively in the Neotropical region, with their habitats ranging from lowland rainforest to cloud forest (e.g., Peña & Lamas, 2005; Nakahara

et al., 2019a). The genus *Taygetis* Hübner, [1819] includes some 30 described species (Lamas, 2004) with a number of undescribed species (unpublished data). Adults of some *Taygetis* species appear to be crepuscular (Young, 1984; DeVries, 1987; Murray, 2001) and both sexes are attracted to fermenting fruit (pers. obs.).

Despite steadily improving understanding of Euptychiina species diversity (see <https://www.floridamuseum.ufl.edu/museum-voices/euptychiina>), very little information is available on their early stage biology, with a complete life cycle known for less than 10% of species and host plant data available for a mere 20% of the species in the subtribe (Nakahara *et al.*, 2020; Corahua-Espinoza *et al.*, in review). This basic life history information is not only important for finding morphological synapomorphies based on immature stages (as in Willmott & Freitas, 2006), but knowing the natural hostplant also provides crucial data towards understand trophic interactions in the

biodiverse forests of the Neotropics (Baine *et al.*, 2019). Many Euptychiina butterflies are known to be closely tied to species in the plant family Poaceae (e.g., Ackery, 1988; Murray, 2001), an important group in both natural and agricultural ecosystems (Ackery, 1988; Murray, 2001; Marín *et al.*, 2011). However, some euptychiine species are also known to feed on other plant families such as Arecaceae, Marantaceae, Heliconiaceae, Cyperaceae, Commelinaceae and Selaginellaceae (Beccaloni *et al.*, 2008; Janzen & Hallwachs, 2018). Despite our rather limited understanding of euptychiine immature stages and their natural hostplants, recent years have seen an increase in studies focusing on these immature stages (e.g., Cosmo *et al.*, 2014; Freitas *et al.* 2016; Freitas, 2017; See *et al.*, 2018; Baine *et al.*, 2019; Nakahara *et al.*, 2020; Tejeira *et al.*, 2021; Corahua-Espinoza *et al.*, in review).

The present study contributes to our understanding of euptychiine immature stage biology and is based on field work carried out at the Finca Las Piedras (FLP) biological station in Madre de Dios, Peru, following preceding related studies on butterfly biology conducted at the site (See *et al.*, 2018; Baine *et al.*, 2019; Nakahara *et al.*, 2020; Tejeira *et al.* 2021; Ccahuana *et al.*, in press). Here we describe the immature stages of *Taygetis cleopatra* (C. Felder & R. Felder, 1862) and report its natural hostplant in the Peruvian Amazon, confirming findings of a partial life history study of the same taxon conducted in eastern Ecuador (Murray, 2001). Although this is not the first documented life history for this species, we add new information regarding its immature stages and provide data from a different region of the Neotropics, important for understanding stability and variability in morphology and biology.

MATERIALS AND METHODS

Study Site. The study site is Finca Las Piedras (FLP), a biological research station located ca. 48 km north of Puerto Maldonado in the department of Madre de Dios, southeastern Peru (-12.22789, -69.11119; ca. 240 m). The site is situated at the edge of an extensive upland “*terra firme*” rainforest dominated by emergent Brazil nut (*Bertholletia excelsa* Humb. & Bonpl.) and *Eschweilera* Mart. ex DC. spp. (Lecythidaceae), multiple species of hardwood trees in the family Fabaceae (e.g., *Dipteryx* Schreb. spp., *Apuleia leiocarpa* (Vogel) J.F.Macbr.), and abundant large palms of the family Arecaceae (especially *Euterpe precatória* Mart. and *Iriarteia deltoidea* Ruiz & Pav.), among others; the rainforest understory has a notable abundance of small palms (e.g., *Geonoma* spp. Willd. (Arecaceae)) and dense stands of low-growing Piperaceae. Also in the area are multiple palm swamps dominated by the palms *Mauritia flexuosa* L. f. and *Oenocarpus bataua* Mart., both in the family Arecaceae, as well as active and abandoned agricultural land to the west of the site. More information on FLP can be found in related studies such as See *et al.* (2018) and Baine *et al.* (2019). Field work was conducted between January and March 2020 at FLP as part of an ongoing, long-term project entitled ‘Lepidoptera Diversity and Biology’ that is being carried out by the Alliance for a Sustainable Amazon (<https://www.sustainableamazon.org/>).

Rearing. For this study, two specimens were reared on their respective, individual hostplants belonging to the same species (description below). Upon initial collection, the two eggs were taken to the field laboratory to continue the rearing process. The immatures were kept individually in a 1 L plastic container covered with a nylon mesh fabric fastened by an elastic band. Each container was labelled with its corresponding voucher code, (2020-FLP-IMM-0009) and (2020-FLP-IMM-0014) for the first and second immature discovered, respectively. Larvae were given hostplant leaves when necessary and the leaves were kept hydrated using floral water tubes (Aquapic, Floral Supply) which were filled daily with clean water. The immatures were taken out of the container for morphological observations and photographed daily (using a Nikon D7000 digital camera with Tokina Macro 100 F2.8 D AT-X Pro lens). All measurements were taken from photographs with a scale included and measured in millimeters. The containers were cleaned daily to avoid any fungal growth. After emergence, the adults were mounted, photographed, and stored.

Morphological study. Measurements of total length of each instar included the caudal filaments and were made in Photoshop CS6 from unprocessed photographs with a scale (ruler) included. Photographs of cephalic capsules were taken with a Leica LED2500 stereomicroscope with magnifications from 10x to 160x. Illustrations of the cephalic capsules were made by MRM using Adobe Illustrator CC 2015. A photograph of the capsules and observations made with the stereomicroscope were used as a reference for illustrations. Morphological examinations of the cephalic capsule of this study were performed at the Museo de Historia Natural de la Universidad Nacional Mayor de San Marcos, Lima, Peru (MUSM); all other examinations were performed at Finca Las Piedras. All voucher specimens are deposited in the collection of the Alliance for a Sustainable Amazon in Puerto Maldonado, Madre de Dios, Peru.

Molecular work. We sequenced the DNA barcoding region (*sensu* Hebert *et al.*, 2003) of one of the reared individuals (voucher code for the specimen: 2020-FLP-IMM-0014; DNA voucher code: LEP-34002) in order to confirm and clarify the species-level identification. The first half of the mitochondrial gene *cytochrome oxidase I* (COI) was amplified using primer pairs LCO (forward, GGTCACAAATCATAAAGATATTGG) and K699 (reverse: WGGGGGGTAAACTGTTCATCC), as well as Ron (forward: GGATCACCTGATATAGCATTCCC) and Nancy (reverse, CCTGGTAAAATTAATAAATAAACTTC) (see Nakahara *et al.* 2019b for primer information). Otherwise, DNA extraction, PCR and sequencing methods followed standard protocols with Qiagen’s DNeasy Blood & Tissue Kit used for DNA extraction from legs removed from the above individual. The obtained sequence provided below was incorporated into a dataset including >1,100 relevant COI sequences for the “*Taygetis* clade” compiled from unpublished data, in addition to available sequences from GenBank and BOLD. We performed neighbor-joining analysis based on the aforementioned dataset in accordance with Baine *et al.* (2019) in order to confirm the identification.

RESULTS

Both of the reared individuals passed through four larval stages. Dates for the first collected individual (2020-FLP-IMM-0009) are as follows: egg collection date: 21 January 2020; egg hatching: 24 January 2020; first to second instar: 30 January 2020; second to third instar: 6 February 2020; third to fourth instar: 15 February 2020; pupation: 1 March 2020; adult eclosion 14 March 2020. Dates for the second collected individual (2020-FLP-IMM-0014) are as follows: egg collection date: 27 January 2020; egg hatching: 29 January 2020; first to second instar: 6 February 2020; second to third instar: 12 February 2020; third to fourth instar: 21 February 2020; pupation: 8 March 2020; adult eclosion: 20 March 2020.

The COI ‘barcode’ sequence for 2020-FLP-IMM-0014 (GenBank Accession MZ645949, molecular voucher LEP-34002, 657 base pairs) is as follows:

```
ACTTTATATTTTTATTTTTGGTATTTGAGCAGGTATAGTAGG
AACATCTCTTAGTTTAATTATTCGAATAGAATTAGGTAATC
CAGGATTTTTAATTGGGGACGACCAAATTTATAATTC AATT
GTTACAGCTCATGCTTTTTATTATAATTTTTTTTTATAGTTAT
ACCAATTATAAATTGGAGGATTTGGTAATTGATTAGTACCTT
TAATATTAGGAGCTCCTGATATAGCWTTCCACGTATAAAT
AATATAAGATTTTGATTGCTCCCCCTTCATTAATTTTTATT
AATTTCTAGTAGTATTGTTGAAATGGTGCTGGTACAGGAT
GAACAGTTTATCCCCCTCTTTCATCTAATATTGCTCATAGT
GGATCCTCAGTTGATTTAGCTATTTTTTCTCTACATTTAGC
TGGAATTTTCATCAATTTTAGGAGCAATTAATTTTTATTACAA
CAATTATTAATATACGTATTAATAATATATCTTATGATCAA
ATACCTCTATTTATTTGAGCTGTTGGAATTACAGCTCTTCT
TTTACTTCTCTCCTTACCTGTTTTAGCAGGAGCAATTACCA
TACTTTTAAACAGATCGAAATCTAAATACATCATTTTTTGGAC
CCTGCAGGAGGAGGAGATCCTATTTTTATATCAACATTTATT
T
```

Hostplant. The hostplant *Olyra latifolia* L. (Poaceae: Bambusoideae: Olyreae) (Fig. 1) is a species of herbaceous bamboo that occurs in the study region in “*terra firme*” rainforest at edges and in disturbed areas such as light gaps. This species ranges from Mexico to Brazil and has a wide distribution in Peru; in the Amazon basin it occurs up to 700 m (Tovar, 1993). The plant is a perennial type of bamboo, generally 1-3.5 m tall; leaf blades ovate-oblong, 13-25 cm long by 3-10 cm wide, acuminate; the flower is unisexual with a female spikelet in the apical part of the branches and a male spikelet generally in the lower part. The hostplants (georeferenced and vouchered as HP332 for 2020-FLP-IMM-0009 and HP337 for 2020-FLP-IMM-0014) were located about 40 m from the forest edge at FLP, adjacent to a narrow path in an area with a closed canopy and low light incidence. At the time of egg collection, the plants were each roughly 1.3 m (n = 2) tall. For the images used in Fig. 1, a plant of the same species was chosen near the hostplant HP337 with the same overall characteristics but which had an inflorescence and was in somewhat better condition.

Behavior and description of immature stages. Eggs were found deposited individually, both on the abaxial side of a

mature leaf, near the midrib, medial portion of the leaf, at a height of approximately 0.8 m above the ground. Caterpillars moved relatively slowly. Larvae built a transparent silk carpet along their path on which they moved. At night, larvae were usually seen feeding near the leaf midrib; during the day larvae were usually found near the ligule. We avoided moving the caterpillar when changing the leaf by adding the new leaf near the ligule of the leaf currently in use.

Egg (Fig. 2A, B). All measurements are approximate: diameter 2.4 mm (n=1); spherical, smooth, cream-colored, with polygonal markings covering surface (n = 1). Duration 2 days (n = 2) after collection.

First instar (Figs. 2C, 3A). Head capsule semi-translucent, light brown, with two scoli present, each scolus with rounded, flattened, spatula-like setae; six chalazae, three on each side, each with a primary seta; three secondary setae present on one side of labrum and epicranial suture; stemma 1, 2, and 4 of same size, third stemma larger than other stemmata; forehead and clypeus slightly fused; 4 setae present on labrum, head capsule width 1.4-1.6 mm (n = 2), scoli length 0.8 mm (n = 1), inter-scoli distance 0.2 mm (n = 1). Body dark green, with a pair of thin whitish longitudinal stripes on each side, located in supraspiracular area; caudal filaments very short, bifid and whitish. Body length, including caudal filaments, 13.0 mm (n = 1). Duration 6-9 days (n = 2).

Second instar (Fig. 2D). Head capsule pale brown, with dark markings visible on entire lateral area of epicranium and “m-shape” marking on frontal part of epicranium, epicranium slightly porous; two developed scoli present (more pronounced than previous instar), each with two fine setae; six chalazae present, three on each side each with one primary seta; position of stemmata similar to previous instar, forehead and clypeus slightly fused; width of head capsule 1.9 mm (n = 2), scoli length 0.5-0.6 mm (n = 2); inter-scoli distance 0.4-0.5 mm (n = 2). Body dark green then pale green during final days of instar, with whitish longitudinal stripes arranged as follows: a pair of irregular thin stripes dorsally, a pair of thick stripes together, and a separate thin stripe on each side, supraspiracular. Caudal filaments short, bifurcated and pale pink. Body length 20.0 mm (n = 1). Duration 6-7 days (n = 2).

Third instar (Fig. 2E, 3C). Head capsule morphologically similar to previous instar, dark markings visible throughout lateral area of epicranium and frontal part of epicranium; two scoli, each with two setae; six chalazae present, each with one primary seta; stemmata distribution same as previous instar; frons and clypeus fused; capsule width 2.7-2.8 mm (n = 2), scoli length 0.7-0.8 mm (n = 2), inter-scoli distance 0.6-0.7 mm (n = 1). Body larger but overall similar in appearance to second instar; caudal filaments short, forked, and lilac-colored. Body length 34.1 mm (n = 1). Duration 8-9 days (n = 2).

Fourth instar (Fig. 2F, 3B). Head capsule pale green to cream-colored, with gray markings visible throughout lateral area of epicranium and “m-shaped” on frontal part of epicranium; with two scoli, each with 2 setae; four chalazae, two on each side, each with single primary seta; distribution of stemmata same as previous instar, but accompanied by 44 secondary setae (n=1; 22 on each side), acuminate along stemmata near mandible; frons and clypeus fused, labrum reduced; width of capsule 4.4-4.6 mm (n = 2), scoli length 1 mm (n = 2), inter-scoli distance 0.9-1.1 mm (n = 2). Body cryptic in color, with irregular patterns of brown, gray and black shades, from dorsal to supraspiracular area; longitudinal stripes light brown and faint, patterned similar to previous stage; caudal filaments short relative to body length, bifurcated and pale brown. Body length 48.6 mm (n = 1). Duration 15-16 days (n = 2).

Pupa (Fig. G). Broad, short, green and smooth; with reduced eyecaps; thin whitish band on wing case, row of reddish spots along abdomen, cremaster broad and short. Length 23.5 mm (n = 1). Duration 12-13 days (n = 1).

Adult (Fig. H). 2020-FLP-IMM-0009 is male and 2020-FLP-IMM-0014 is female. Figure H is based on this latter specimen, with dorsal and ventral views of wings.

DISCUSSION

Despite the documentation of immature stages of *T. cleopatra* by Murray (2001), we believe our study nevertheless provides important insights into the life history of this taxon. Firstly, Murray (2001) did not illustrate the immature stages except for drawings of the head capsule and a single dorsal photo of the mature instar (instar number not indicated) in monotone. We complement Murray’s (2001) study by

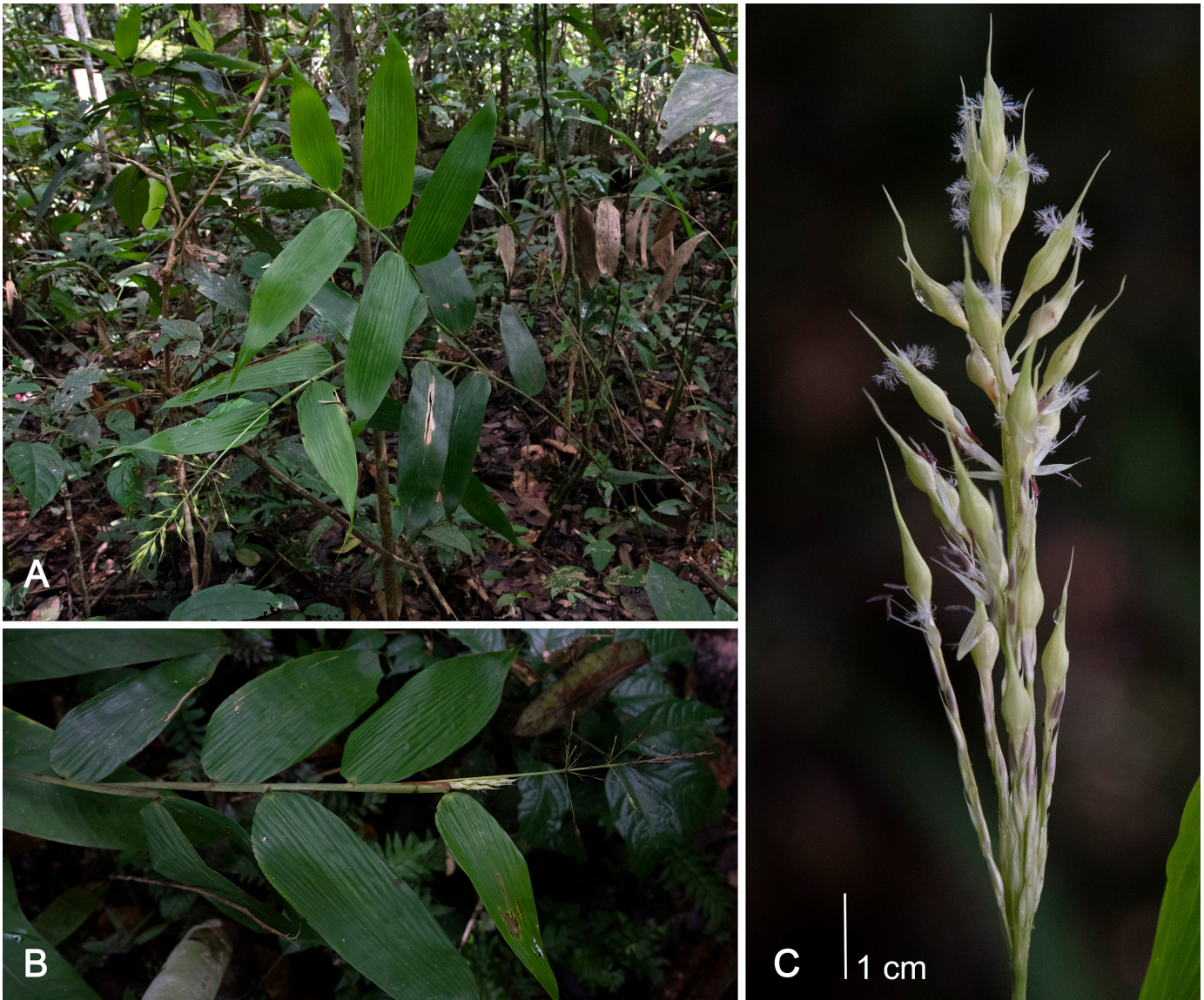


Figure 1. Hostplant of *Taygetis cleopatra*, *Olyra latifolia* L. (Poaceae: Bambusoideae), on 10 March 2020 at FLP: A) hostplant *in situ*; B) details of leaves and node; C) details of inflorescence materials. All figures belong to the same hostplant.

providing color photos of all stages, as well as head capsule illustrations and hostplant photos. Secondly, the lack of images or specimens of the adult vouchers for all of the five species of *Taygetis* studied in Murray (2001), including *T. cleopatra*, makes the species identification in that article impossible to verify, particularly because of the close resemblance of many *Taygetis* species and the existence of cryptic species supported by molecular data (pers. obs.). *Taygetis cleopatra* was described from “Río Negro” [=Peru] by Felder & Felder (1862: 176). Two syntypes, for which the images are available online (see <https://www.butterfliesofamerica.com/>; note the described year for this species has been erroneously listed as “1867” on the website) match the eclosed adult figured herein (Fig. 2H). The species identification in our study was also confirmed and clarified by obtaining a DNA barcode and comparing it with to over 1,100 relevant sequences compiled for taxa in the “*Taygetis* clade”. Based on unpublished data, the sequence provided above for 2020-FLP-IMM-0014 grouped together with a

number of sequences originating from specimens identified as *T. cleopatra* spanning its range, thus excluding the possibility of representing a cryptic undescribed species. However, the distinctive “m-shaped” marking and the dark lateral marking on the head capsule (i.e., features to key out *T. cleopatra* according to Murray (2001)) are visible in head capsule images of the second to fourth instars (third instar head capsule picture for 2020-FLP-IMM-0009 is provided in Fig. 3C) of *T. cleopatra* that we reared, thus somewhat supporting Murray’s (2001) identification. The number of larval instars is also consistent with Murray’s (2001) observation, namely passing only four larval instars, a common phenomenon for euptychiine butterfly larva (see Nakahara *et al.*, 2020 for discussion regarding larval instar numbers).

The natural hostplant of *T. cleopatra* that we report in Peru, *O. latifolia*, agrees with that recorded as a natural hostplant in Ecuador by Murray (2001), although Murray (2001) also reported another herbaceous bamboo species, *Pariana* sp.

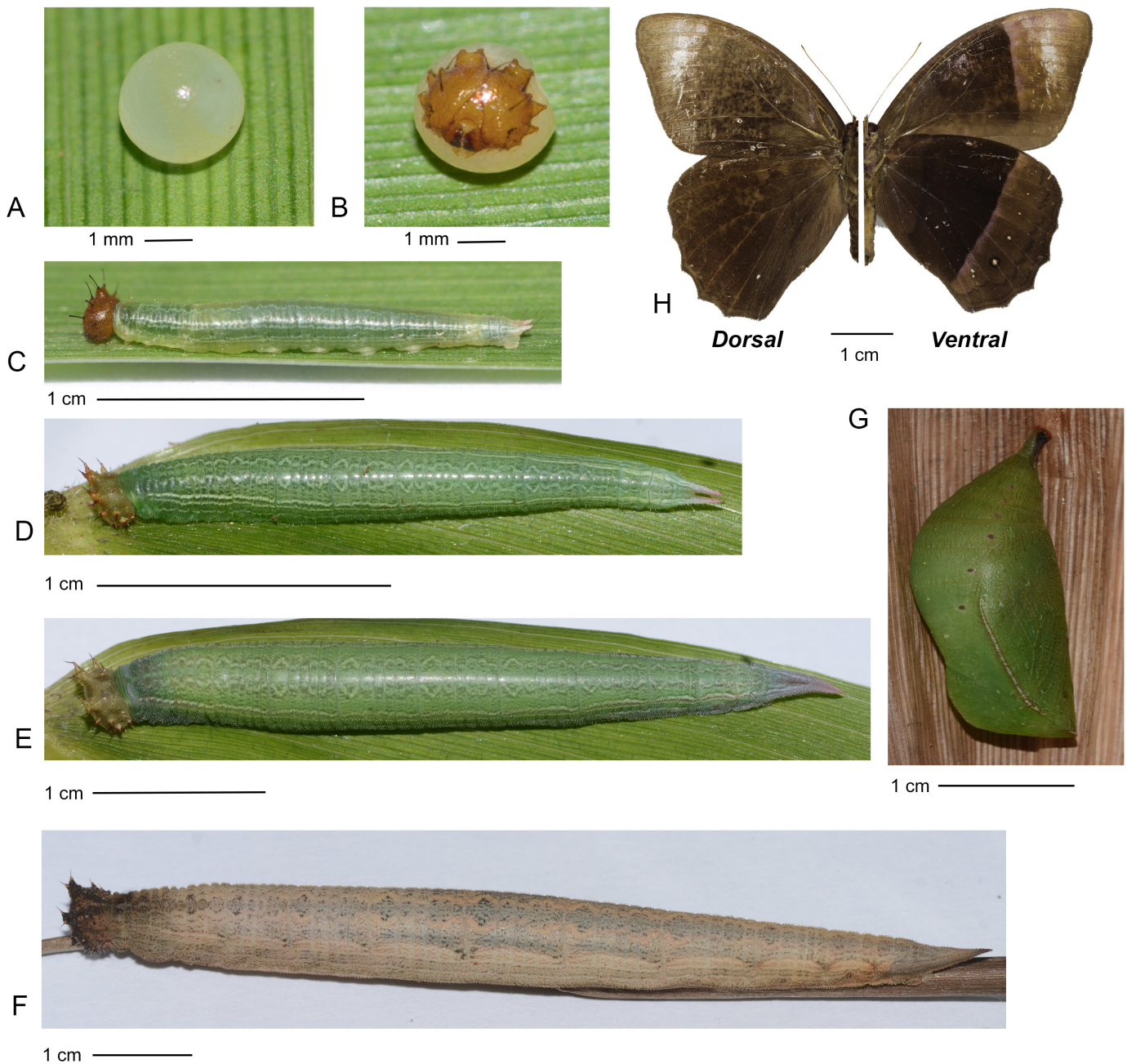


Figure 2. Life cycle of *Taygetis cleopatra* (egg, first instar, second instar, and third instar based on 2020-FLP-IMM-0014; fourth instar, pupa and adult based on 2020-FLP-IMM-0009): A) dorsal view of egg; B) dorsal view of egg with visible head capsule prior to hatching; C) dorso-lateral view of first instar; D) dorsal view of second instar; E) dorsal view of third instar; F) dorso-lateral view of fourth instar; G) lateral view of pupa; H) both sides of adult (dorsal on left, ventral on right).

(Poaceae: Bambusoideae: Olyreae), as an additional natural hostplant in Ecuador. Based on existing available information, many *Taygetis* species also feed on herbaceous bamboo species (Murray, 2001; Janzen & Hallwachs, 2018; Baine *et al.*, 2019). Nevertheless, grass species (e.g., *Lasiacis lingulata* Hitchcock & Chase for *T. rufomarginata* as in Baine *et al.* (2019)) and woody bamboo species (e.g., *Guadua angustifolia* Kunth for *T. virgilia* (Cramer, 1776) and *T. mermeria* (Cramer, 1776) as in Murray (2001)) are also reported as natural hostplants. Furthermore, plant families such as Cyperaceae and Commelinaceae are also recorded as hostplants for *Taygetis* species, although these represent a small fraction (24/1243;

less than 2%) of the available records for the genus provided in Janzen & Hallwachs (2018) and the remaining records for *Taygetis* in the Janzen & Hallwachs (2018) database all belong to the family Poaceae. This is consistent with the majority of known euptychiine hostplants, which are generally in the Poaceae, as mentioned above.

Life history information revealed by the above-mentioned studies represents only the proverbial tip of the iceberg regarding insights into *Taygetis* taxonomy. Considering the number of species in the “*Taygetis* clade” with unknown early stage biology, coupled with the existence of multiple undescribed species yet to be named and inconclusive morphological

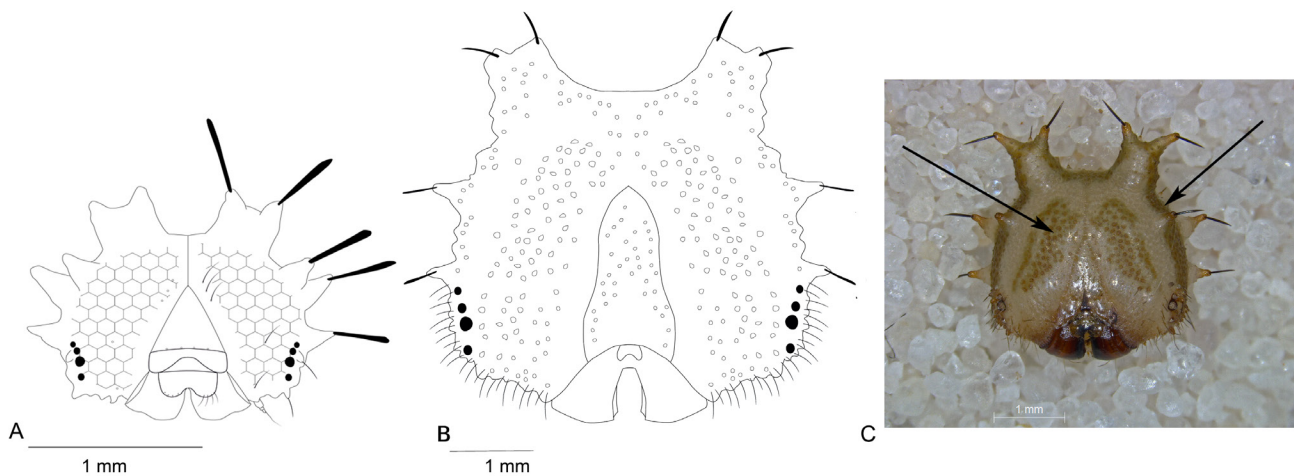


Figure 3. Head capsules of *Taygetis cleopatra*: A) first instar frontal view based on 2020-FLP-IMM-0014; B) fourth instar frontal view based on 2020-FLP-IMM-0009; C) frontal view of third instar showing two diagnostic characters mentioned in Murray (2001) based on 2020-FLP-IMM-0009.

information, much data remains to be gathered. As discussed in some relevant phylogenetic studies (e.g., Nakahara *et al.*, 2019a), we further affirm that the genus *Taygetis*, as currently conceived, is not monophyletic. A study is underway to describe a new genus for *T. ypthima* Hübner, [1821] and several other closely related taxa to achieve a monophyletic *Taygetis*. Müller (1886) documented the immatures of *T. ypthima* and illustrated its head capsule, although the information provided in that work is not sufficient to identify genus-level morphological differences between known *Taygetis* immatures and *T. ypthima*. Furthermore, Müller (1886) stated that he was unable to observe the eclosion of the adult, thus the identity of the taxon in that work is questionable. Besides species in *Taygetis* and *T. ypthima*, our knowledge regarding immature stages of other members of the “*Taygetis* clade” is very limited. Freitas & Peña (2006), Freitas *et al.*, (2016), and Nakahara *et al.* (2021a) provided some information on immature stage morphology of *Forsterinaria* Gray, 1973 and *Pseudodebis* Forster, 1964, although life history information revealed by these studies is limited considering the number of species in the “*Taygetis* clade” with unknown early stage biology, coupled with the existence of multiple undescribed species.

Based on published works on immature stages of species in the “*Taygetis* clade” (references cited herein) and other euptychiine taxa (e.g., Cosmo *et al.*, 2014), it is highly likely that the spatula-like primary setae of the first instar head capsule is a potential synapomorphy for the “*Taygetis* clade”. The debate will likely continue as to how universal this morphological character is across taxa in the “*Taygetis* clade” and whether this feature evolved independently in euptychiine species in other clades. There exists some evidence that these spatula-like setae may not represent a universal synapomorphy for the “*Taygetis* clade” since at least one species in the *Pseudodebis* “*celia* clade” (*sensu* Nakahara *et al.*, 2021a) apparently does not possess setae of such form in the first instar (Nakahara *et al.* in prep). On the other hand, the first instar head capsule of *Zischkaia arenisca* Nakahara, Willmott & Hall, 2019 (a taxon in the so-called “*Amphidecta* clade” *sensu* Espeland *et al.*, 2019) does

exhibit this feature (Nakahara *et al.*, 2019b), indicating that this character might be homoplasious. In addition, mature larvae of *Taygetis* possess separable bifid caudal filaments which are 1.5 times longer than A8 in dorsal view and seemingly fused most of the time (Janzen & Hallwachs, 2018; pers. obs.). However, our knowledge regarding euptychiine immature stages is far too incomplete to draw any firm conclusion as to the taxonomic significance of these character states, although recently obtained immature data for a number of *Taygetis* taxa may provide some further insights (Corahua-Espinoza *et al.*, in prep.). Clearly, in-depth studies of immature stage morphology and recording natural hostplants of caterpillars are worthwhile endeavors that provide useful information to support phylogenetic studies and increase our knowledge of the early stage biology of Neotropical butterflies.

ACKNOWLEDGMENTS

We thank Lynn Clark for identifying the hostplant; Marianne Espeland and Pilar Herrera for German translation of relevant literature; two anonymous reviewers for helpful comments which improved the manuscript; the authors would like to thank Peru’s Servicio Nacional Forestal y de Fauna Silvestre (SERFOR) for granting permission to conduct the field research (permit number:187-2017-SERFOR/DGGSPFFS). SN acknowledges University of Florida’s Entomology and Nematology Department and Alliance for a Sustainable Amazon for support. MRM thanks Diana Silva and Gerardo Lamas for allowing the use of the facilities and equipment of the Entomology Department (MUSM) and Consejo Nacional de Investigaciones Científicas y Técnicas – CONICET. TH thanks the team of the Alliance for a Sustainable Amazon for training, supporting and encouraging young students to enter the world of scientific publications and all the friends who gave moral support during the writing of the manuscript, because moral support also counts.

LITERATURE CITED

- Ackery, P. R.** 1988. Hostplants and classification: a review of nymphalid butterflies. *Biological Journal of the Linnean Society* 33: 95-203.
- Ackery, P. R., de Jong, R., Vane-Wright, R. I.** 1999. *The Butterflies: Hedyloidea, Hesperioidea and Papilionoidea*, pp. 263-300. In: Kristensen, N. P. (Ed.), *Lepidoptera: Moths and Butterflies. 1. Evolution, Systematics and Biogeography*. Handbook of Zoology, vol. IV. Part 35. Berlin, Walter de Gruyter.
- Baine, Q., Polo-Espinoza, G., Nakahara, S., Gallice, G.** 2019. Immature stages and new host record of *Taygetis rufomarginata* Staudinger, 1888 (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera Research* 29(2): 79-86.
- Beccaloni, G. W., Vilorio, Á. L., Hall, S. K., Robinson, G. S.** 2008. *Catalogue of the Hostplants of the Neotropical Butterflies / Catálogo de las Plantas Huésped de las Mariposas Neotropicales*. m3m-Monografías Tercer Milenio, Volume 8. Zaragoza, Spain: Sociedad Entomológica Aragonesa (SEA)/Red Iberoamericana de Biogeografía y Entomología Sistemática (RIBES)/Ciencia y Tecnología para el Desarrollo (CYTED)/Natural History Museum, London, U. K. (NHM)/Instituto Venezolano de Investigaciones Científicas, Venezuela (IVIC). 536 pp.
- Corahua-Espinoza, T., Nakahara, S., Kabir, J., Shellman, B., Tejeira, R., Ccahuana, R., Gallice, G.** Immature stages and new host plant records for four satyrine species feeding on herbaceous bamboos in southeastern Peru (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). *In review*.
- Cosmo, L. G., Barbosa, E. P., Freitas, A. V. L.** 2014. Biology and morphology of the immature stages of *Hermeuptychia atalanta* (Lepidoptera: Nymphalidae: Satyrinae). *Annales de la Société Entomologique de France* 50(1): 82-88.
- DeVries, P. J.** 1987. *The butterflies of Costa Rica and their Natural History. Papilionidae, Pieridae, Nymphalidae*. Princeton, Princeton University Press. xxii + 327 pp.
- Espeland, M., Breinholt, J., Barbosa, E. P., Casagrande, M., Huertas, B., Lamas, G., Marín, M. A., Mielke, O. H.H., Miller, J. Y., Nakahara, S., Tan, D., Warren, A. D., Zacca, T., Kawahara, A. Y., Freitas, A. V. L., Willmott, K. R.** 2019. Four hundred shades of brown: higher level phylogeny of the problematic Euptychiina (Lepidoptera, Nymphalidae, Satyrinae) based on hybrid enrichment data. *Molecular Phylogenetics and Evolution* 131: 116-124.
- Felder, C., Felder, R.** 1862. Specimen faunae lepidopterologicae riparum fluminis Negro superioris in Brasilia septentrionali. *Wiener entomologische Monatschrift* 6(3): 65-80.
- Freitas, A. V. L.** 2017. Immature stages of the Neotropical satyrine butterfly *Taygetis acuta* (Nymphalidae: Euptychiina). *Tropical Lepidoptera Research* 27(1): 1-5.
- Freitas, A. V. L., Peña, C.** 2006. Description of genus *Guaianaza* for “*Euptychia*” *pronophila* (Lepidoptera: Nymphalidae: Satyrinae) with a description of the immature stages. *Zootaxa* 1163: 49-59.
- Freitas, A. V. L., Carreira, J. Y. O., Santos, J. P., Barbosa, E. P.** 2016. Immature stages and natural history of two species of *Forsterinaria* from southeastern Brazil (Lepidoptera: Nymphalidae). *Tropical Lepidoptera Research* 26(1): 13-18.
- Hebert, P. D. N., Cywinska, A., Ball, S. L., deWaard, J. R.** 2003. Biological identifications through DNA barcodes. *Proceedings of the Royal Society of London B* 270: 313-321.
- Janzen, D. H., Hallwachs, W.** 2018. Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of Area de Conservacion Guanacaste (ACG), northwestern Costa Rica (nn-SRNP-nnnnn voucher codes) <<http://janzen.sas.upenn.edu>>. [accessed: June 2021]
- Lamas, G.** 2004. *Nymphalidae. Satyrinae. Tribe Satyrini. Subtribe Euptychiina*, pp. 217-223. In: Lamas, G. (Ed.), *Checklist: Part 4A. Hesperioidea - Papilionoidea*. In: Heppner, J. B. (Ed.), *Atlas of Neotropical Lepidoptera. Volume 5A*. Gainesville, Association for Tropical Lepidoptera; Scientific Publishers.
- Marin, M. A., Peña, C., Freitas, A. V. L., Wahlberg, N., Uribe, S.** 2011. From the phylogeny of the Satyrinae butterflies to the systematics of Euptychiina (Lepidoptera: Nymphalidae): history, progress and prospects. *Neotropical Entomology* 40(1): 2-14.
- Matos-Maraví, P. F., Peña, C., Willmott, K. R., Freitas, A. V. L., Wahlberg, N.** 2013. Systematics and evolutionary history of butterflies in the “*Taygetis* clade” (Nymphalidae: Satyrinae: Euptychiina): towards a better understanding of Neotropical biogeography. *Molecular Phylogenetics and Evolution* 66: 54-68.
- Müller, W.** 1886. Südamerikanische Nymphalidenraupen. Versuch eines natürlichen Systems der Nymphaliden. *Zoologische Jahrbücher (Systematik)* 1(3/4): 417-678.
- Murray, D.** 2001. Immature stages and biology of *Taygetis* Hübner (Lepidoptera: Nymphalidae). *Proceedings of the Entomological Society of Washington* 103(4): 932-945.
- Murray, D., Prowell, D. P.** 2005. Molecular phylogenetics and evolutionary history of the neotropical Satyrine Subtribe Euptychiina (Nymphalidae: Satyrinae). *Molecular Phylogenetics and Evolution* 34(1): 67-80.
- Nakahara, S., Barbosa, E. P., Willmott, K. R., Lamas, G., Freitas, A. V. L.** 2019a. Two new species of *Taygetina* Forster, 1964 with a possible case of “juxta loss” in butterflies (Lepidoptera: Nymphalidae: Satyrinae). *Insect Systematics and Diversity* 3(6): 9; 1-13.
- Nakahara, S., Hoffman, A., F., Hoffman, L., F., Gallice, G.** 2020. Immature stages of *Magneuptychia harpyia* (C. Felder & R. Felder, 1867) (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera Research* 30(1): 33-38.
- Nakahara, S., Matos-Maraví, P., Schwartz, J., Willmott, K. R.** 2021a. Assessing a generic synapomorphy of *Pseudodebis* Forster, 1964 (Lepidoptera: Nymphalidae: Satyrinae) and a recent speciation with a shift in elevation between two new species in the western Andes. *Invertebrate Systematics* 35(2): 158-180.
- Nakahara, S., Matos-Maraví, P., Willmott, K. R., Nakamura, I., MacDonald, J. R.** 2021b. Description of a new species of *Pseudodebis* Forster, 1964 from Central America. (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera Research* 31(1): 35-41.
- Nakahara, S., Zacca, T., Dias, F. M. S., Dolibaina, D. R., Xiao, L., Espeland, M., Casagrande, M. M., Mielke, O. H. H., Lamas, G., Huertas, B., Kleckner, K., Willmott, K. R.** 2019b. Revision of the poorly known Neotropical butterfly genus *Zischkaia* Forster, 1964 (Lepidoptera, Nymphalidae, Satyrinae), with descriptions of nine new species. *European Journal of Taxonomy* 551: 1-67.
- Peña, C., Lamas, G.** 2005. Revision of the butterfly genus *Forsterinaria* Gray, 1973 (Lepidoptera: Nymphalidae, Satyrinae). *Revista Peruana de Biología* 12: 5-48.
- Peña, C., Nylín, S., Freitas, A. V. L., Wahlberg, N.** 2010. Biogeographic history of the butterfly subtribe Euptychiina (Lepidoptera: Nymphalidae: Satyrinae). *Zoologica Scripta* 39(3): 243-258.
- See, J., Nakahara, S., Gallice, G.** 2018. Immature stages of *Splendeuptychia quadrina* (Butler, 1869) (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera Research* 28(2): 49-53.
- Tejeira, R., Ccahuana, R., Hurtado, T., Nakahara, S., See, J., Rodríguez-Melgarejo, M., Corahua-Espinoza, T., Gallice, G.** 2021. Immature stages of *Chloreuptychia marica* (Weymer, 1911) (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). *Tropical Lepidoptera Research* 31(2): 96-100.
- Tovar, O.** 1993. *Las Gramíneas (Poaceae) del Perú (Vol. 13)*. Editorial CSIC-CSIC Press.
- Willmott, K. R., Freitas, A. V. L.** 2006. Higher-level phylogeny of the Ithomiinae (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonisation and diversification. *Cladistics* 22: 297-368.
- Young, A. M.** 1984. Natural history notes for *Taygetis andromeda* (Cramer) (Satyridae) in Eastern Costa Rica. *Journal of the Lepidopterists' Society* 38: 102-113.