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

# André V. L. Freitas

Departamento de Biologia Animal and Museu de Diversidade Biológica, Instituto de Biologia, Universidade Estadual de Campinas (Unicamp), Campinas, São Paulo, Brazil. baku@unicamp.br

Date of issue online: 1 June 2022

Electronic copies (ISSN 2575-9256) in PDF format at: https://journals.flvc.org/troplep; https://zenodo.org; archived by the Institutional Repository at the University of Florida (IR@UF), http://ufdc.ufl.edu/ufir; DOI: 10.5281/zenodo.6588532
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:** The immature stages are described for *Splendeuptychia ambra* (Weymer, [1911]). The eggs are rounded, pale yellow, smooth, and lack markings. The caterpillars pass through four instars; the first instar is pale cream with reddish longitudinal stripes and the head is black bearing a pair of very short scoli; the last (fourth) instar is beige with a pair of short caudal filaments on the last segment, laterally striped with thin lines and a darker dorsal stripe; the head is olive-brown with a pair of short scoli. The pupae are short and smooth, mostly light brown, mottled with dark brown stripes, with short rounded ocular caps and with very short paired subdorsal projections on the abdominal segments. The immature stages of *S. ambra* are compared with those of other species of the non-monophyletic genus *Splendeuptychia* that belong to three different clades within the subtribe Euptychina.

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

Key words: Atlantic Forest, Brazil, Satyrinae, Satyrini

Palavras chave: Brazil, Mata Atlântica, Satyrinae, Satyrini

## INTRODUCTION

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

Forster, 1964, among others (e.g. DeVries, 1987; Kaminski & Freitas, 2008; Freitas *et al.*, 2016a,b, 2019a; See *et al.*, 2018; Janzen & Hallwachs, 2021).

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



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

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

#### MATERIAL AND METHODS

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

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



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

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

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

# RESULTS

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

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

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

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

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

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

**Behavior and natural history.** *Splendeuptychia ambra* is known from a few localities of montane rain forest in the Atlantic Forest of southeastern Brazil, at elevations from 800-1400 m, with the exception of one record at lower elevation (220-250 m) from northern Argentina (Bustos, 2008; see additional records in Santos et al., 2018). Oviposition behavior was not observed in the field, and the natural host plant is unknown. In the laboratory, larvae easily accepted the small bamboo *Chusquea* 

cf. *ramosissima*, a native species from the region of Campinas, São Paulo (about 200 km far from the collecting site). Larvae are solitary and moved slowly and passed through four larval instars. Adults (Figs. 1D, E) are seldom observed in nature; in another study, only seven individuals (six males and a single female) were captured in baited traps over 36,000 trap-hours at the study site (Uehara-Prado *et al.*, 2005), all in areas where bamboos were common inside a large block of well-preserved forest. Behaviors such as territorialism and courtship were not observed.

#### DISCUSSION

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

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

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



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

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

The slender larvae with long head horns and the elongated pupae of the *Splendeuptychia* species belonging to the

*Amphidecta* clade' could benefit from camouflage when resting on narrow, elongated bamboo leaves that they feed on, as appears to be the case for the Pronophilina species *Eteona tisiphone* (Boisduval, 1836) (Freitas, 2002). Similar cases were reported in other species of Euptychiina and Hesperiidae, whose larvae feed on bamboos and other plants with thin leaves or leaflets, and have larvae slender bodies and a color patterns that suggest camouflage (Freitas, 2018, 2020; Freitas *et al.*, 2019b). However, the present data show that bamboo-feeding Euptychiina do differ in some specific morphological structures

horns and pupal shape (including the species of *Splendeuptychia* discussed here), suggesting that a number of factors are involved in the evolution of the morphology of Euptychiina immature stages (see also Corahua-Espinoza *et al.*, 2022). A promising way to study the evolution of the early stages of Euptychiina is by mapping the major morphological characteristics onto the comprehensive and well supported phylogenies that are now available. In this way, as more information from immature stages becomes available, understanding of morphological and ecological evolution in the Euptychiina will be improved, opening new avenues of investigation in this species-rich and diversified butterfly clade.

## ACKNOWLEDGMENTS

To Marcio Uehara-Prado, Danilo B. Ribeiro and Keith S. Brown Jr. for helping in field work and to Keith S. Brown Jr. for helping with photos of the immature stages. Special thanks to Luan Felipi P. de Andrade and to Ronaldo B. Francini, who kindly provided the images of the live adult from Teresópolis and of the study area in Morro Grande, respectively. Luisa L. Mota kindly revised the last version and made valuable suggestions in the text. The final text was revised by Geoff Gallice and Keith Willmott, who contributed with valuable corrections and suggestions. The author acknowledges support from FAPESP (Biota-Fapesp - grants 2011/50225-3, 2012/50260-6, 2013/50297-0, 2021/03868-8), from the Brazilian Research Council - CNPq (fellowship 302585/2011- 7, 421248/2017-3, 304291/2020-0) and from the National Science Foundation (DEB-1256742). This publication is part of the RedeLep 'Rede Nacional de Pesquisa e Conservação de Lepidópteros' SISBIOTA-Brasil/CNPq (563332/2010-7). Thanks to the ICMBio for the permits (#10438-1, 10438-2, 10438-3, 10438-4). Butterfly species are registered in the "Sistema Nacional de Gestão do Patrimônio Genético e do Conhecimento Tradicional Associado" (National System for the Management of Genetic Heritage and Associated Traditional Knowledge) SISGEN (A82149A).

#### LITERATURE CITED

- **Bustos, E. O. N.** 2008. Diversidad de mariposas diurnas en la Reserva Privada Yacutinga, provincia de Misiones, Argentina (Lepidoptera: Hesperioidea y Papilionoidea). *Tropical Lepidoptera Research* 18(2): 78-87.
- Corahua-Espinoza, T., Nakahara, S., Kabir, J., Shellman, B., Tejeira, R., Ccahuana, R., Gallice, G. 2022. Immature stages and new host plant records for four satyrine species feeding on herbaceous bamboos in southeastern Peru (Lepidoptera: Nymphalidae: Satyrinae: Satyrini). *Zootaxa* 5125(1): 37-62.
- **DeVries, P. J.** 1987. The butterflies of Costa Rica and their natural history. Papilionidae, Pieridae, Nymphalidae. Princeton, Princeton University Press, 327 pp.
- Espeland, M., Breinholt, J. W., Barbosa, E. P., Casagrande, M. 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.

- Freitas, A. V. L. 1991. Variação morfológica, ciclo de vida e sistemática de *Tegosa claudina* (Eschscholtz) (Lepidoptera, Nymphalidae, Melitaeinae) no Estado de São Paulo, Brasil. *Revista Brasileira de Entomologia* 35(2): 301-306.
- Freitas, A. V. L. 2002. Immature stages of *Eteona tisiphone* (Nymphalidae: Satyrinae). *Journal of the Lepidopterists' Society* 56(4): 286-288.
- Freitas, A. V. L. 2003. Description of a new genus for "Euptychia" peculiaris (Nymphalidae: Satyrinae): Immature stages and systematic position. Journal of the Lepidopterists' Society 57(2): 100-106.
- Freitas, A. V. L. 2004. Immature stages of Amphidecta reynoldsi (Nymphalidae: Satyrinae). Journal of the Lepidopterists' Society 58(1): 53-55.
- Freitas, A. V. L. 2007. A new species of *Moneuptychia* Forster (Lepidoptera: Satyrinae, Euptychiina) from the highlands of southeastern Brazil. *Neotropical Entomology* 36: 919-925.
- Freitas, A. V. L. 2018. Immature stages of the Neotropical skipper Lychnuchoides ozias ozias (Hewitson, 1878) (Lepidoptera: Hesperiidae). Tropical Lepidoptera Research 28(1): 25-28.
- Freitas, A. V. L. 2020. Immature stages of the Neotropical skipper Saliana longirostris (Sepp, [1840]) (Lepidoptera: Hesperiidae). Tropical Lepidoptera Research 30(2): 81-85.
- Freitas, A. V. L., Brown, Jr., K. S. 2004. Phylogeny of the Nymphalidae (Lepidoptera). Systematic Biology 53(3):363-383.
- Freitas, A. V. L., Barbosa, E. P., Marín, M. A. 2016a. Immature stages and natural history of the Neotropical satyrine *Pareuptychia ocirrhoe interjecta* (Nymphalidae: Euptychiina). Journal of the Lepidopterists' Society 70(4): 271-276.
- Freitas, A. V. L., Carreira, J. Y. O., Santos, J. P., Barbosa, E. P. 2016b. Immature stages and natural history of two species of *Forsterinaria* from southeastern Brazil (Lepidoptera: Nymphalidae). *Tropical Lepidoptera Research* 26(1): 13-18.
- Freitas, A. V. L., Barbosa, E. P., Zacca, T., Marín, M. A., Beirão, M. V., Silva, A. R. M., Casagrande, M. M., Espeland, M., Willmott, K. R. 2018. Before it is too late: description of a new genus and species of butterfly from a highly threatened Brazilian biome. *Revista Brasileira de Entomologia* 62(2): 148-158.
- Freitas, A. V. L., Mota, L. L., Barbosa, E. P., Carreira, J. Y. O. 2019a. Immature stages of the *Selaginella*-feeding *Euptychia mollina* (Nymphalidae: Satyrinae) from the Brazilian Amazon. *Zoologia* 36: e32053.
- Freitas, A. V. L., Mota, L. L., Zacca, T., Barbosa, E. P. 2019b. Description of a new and highly distinctive genus and species of Euptychiina (Lepidoptera: Nymphalidae: Satyrinae) from the Brazilian southern Amazon. *Revista Brasileira de Entomologia* 63(3): 254-261.
- Freitas, A. V. L., Barbosa, E. P., Carreira, J. Y. O. 2021a. Immature stages and natural history of *Yphthimoides borasta* (Nymphalidae: Euptychiina). *Tropical Lepidoptera Research* 31(1): 42-47.
- Freitas, A. V. L., Rosa, A. H. B., Kaminski, L. A. 2021b. Immature stages of *Stegosatyrus ocelloides* (Nymphalidae: Euptychiina), a grassland specialist butterfly *Tropical Lepidoptera Research* 31(2): 127-133.
- García-Barros, E., Martín, J. 1995. The eggs of European satyrine butterflies (Nymphalidae): external morphology and its use in systematics. *Zoological Journal of the Linnean Society* 115: 73-115.
- Janzen, D. H., Hallwachs, W. 2021. Dynamic Database for an Inventory of the Macrocaterpillar Fauna, and its Food Plants and Parasitoids, of the Area De Conservacion Guanacaste (acg), Northwestern Costa Rica. http:// janzen.sas.upenn.edu. Accessed 3 November 2021.
- Kaminski, L. A., Freitas, A. V. L. 2008. Immature stages of the butterfly Magneuptychia libye (L.) (Lepidoptera: Nymphalidae, Satyrinae). Neotropical Entomology 37: 169-172.
- Kendall, R. 1978. Larval foodplants, life history and temporal distribution for *Splendeuptychia kendalli* (Satyridae) from Mexico. *Journal of the Lepidopterists' Society* 32(2): 86-87.
- Lamas, G. 2004. Euptychiina, pp. 217-223. In: Lamas, G. (Ed.), Checklist: Part 4A. Hesperioidea - Papilionoidea. In: Heppner, J. B. (Ed.), Atlas

of Neotropical Lepidoptera. Vol. 5A. Gainesville, Scientific Publishers/ Association for Tropical Lepidoptera.

- Marín, M. A., Peña, C., Uribe, S. I., Freitas, A. V. L. 2017. Morphology agrees with molecular data: phylogenetic affinities of Euptychiina butterflies (Nymphalidae: Satyrinae). *Systematic Entomology* 42: 768-785.
- Nakahara, S., Hoffman, F. L. A., Hoffman, F. L., 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., Rodríguez-Melgarejo, M., Kleckner, K., Corahua-Espinoza, T., Tejeira, R., Espeland, M., Casagrande, M. M., Barbosa, E. P., See, J., Gallice, G., Lamas, G., Willmott, K. R. 2022. Systematic revision of a new butterfly genus, *Cisandina* Nakahara & Espeland, n. gen., with descriptions of three new taxa (Lepidoptera: Nymphalidae: Satyrinae). *Insect Systematics and Diversity* 6(1): 1-30.
- Peña, C., Nylin, S., Freitas, A.V. L., Wahlberg, N. 2010. Biogeographic history of the butterfly subtribe Euptychiina (Lepidoptera, Nymphalidae, Satyrinae). Zoologica Scripta 39: 243-258.
- Rosa, A. H. B., Huertas, B., Willmott, K. R., Barbosa, E. P., Machado, P. A., Mielke, O. H. H., Canaan, C. H. P., Freitas, A. V. L. 2021. Fifty years without a name: a new species of *Splendeuptychia* Forster (Lepidoptera: Nymphalidae: Satyrinae). *Zootaxa* 5061(1): 95-114.
- Santos, J. P., Freitas, A. V. L., Brown, K. S., Carreira, J. Y. O., Gueratto, P. E., Rosa, A. H. B., Lourenço, G. M. ... Ribeiro, M. C. 2018. Atlantic butterflies: A data set of fruit-feeding butterfly communities from the Atlantic forests. *Ecology* 99(12): 2875.
- See, J., Nakahara, S., Gallice, G. 2018. Immature stages of *Splendeuptychia quadrina* (Butler, 1869) (Lepidoptera: Nymphalidae: Satyrinae). *Tropical Lepidoptera Research* 28(2): 49-53.
- Singer, M. C., DeVries, P. J., Ehrlich, P. R. 1983. The Cissia confusa speciesgroup in Costa Rica and Trinidad (Lepidoptera: Satyrinae). Zoological Journal of the Linnean Society 79(2): 101-119.
- Stehr, F. W. 1987. Order Lepidoptera, pp. 288-305. In: Stehr F. W. (Ed), Immature Insects. Volume 1. Dubuque, Kendall-Hunt Publishing Company.
- 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.
- Triplehorn, C. A., Johnson, N. F. 2005. Borror and Delong's Introduction to the Study of the Insects. Belmont, Thomson Brooks/Cole. 864 pp.
- Uehara-Prado, M., Freitas, A. V. L., Francini, R. B., Brown Jr., K. S. 2004. Guia das borboletas frugívoras da Reserva Estadual do Morro Grande e região de Caucaia do Alto, Cotia (São Paulo). *Biota Neotropica* 4(1): 1-25.
- Uehara-Prado, M., Brown Jr., K. S., Freitas, A. V. L. 2005. Biological traits of frugivorous butterflies in a fragmented and a continuous landscape in the South Brazilian Atlantic Forest. *Journal of the Lepidopterists' Society* 59(2): 96-106.
- Uehara-Prado, M., Brown, Jr., K. S., Freitas, A. V. L. 2007 Species richness, composition and abundance of fruit-feeding butterflies in the Brazilian Atlantic Forest: comparison between a fragmented and a continuous landscape. *Global Ecology and Biogeography* 16(1): 43-54.
- Willmott, K. R., Freitas, A. V. L. 2006. Higher-level phylogeny of the Ithomiinae (Lepidoptera: Nymphalidae): classification, patterns of larval hostplant colonization and diversification. *Cladistics* 22: 297-368.
- Zacca, T., Barbosa, E. P., Freitas, A. V. L. 2021. *Euptychiina Species Checklist.* https://www2.ib.unicamp.br/labor/site/?page\_id=1020. Accessed 7 April 2022.