Immature stages of *Stegosatyrus ocelloides* (Nymphalidae: Euptychiina), a grassland specialist butterfly

André V. L. Freitas[1*], Augusto H. B. Rosa[1] and Lucas A. Kaminski[2]

1. Departamento de Biologia Animal and Museu de Diversidade Biológica, Instituto de Biologia, Universidade Estadual de Campinas (Unicamp), Campinas, São Paulo, Brazil; 2. Departamento de Zoologia, Instituto de Biociências, Universidade Federal do Rio Grande do Sul (UFRGS), Porto Alegre, Rio Grande do Sul, Brazil. *corresponding author: baku@unicamp.br.

Date of issue online: 29 October 2021
Electronic copies (ISSN 2575-9256) in PDF format at: http://journals.fcla.edu/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.5600441

Abstract. The immature stages are described for *Stegosatyrus ocelloides* (Schaus, 1902), a butterfly species associated with open vegetation formations, such as grasslands and savannas, in the southern Neotropics, and additional information on the eggs and first and second instars of *Stegosatyrus periphas* (Godart, [1824]) are provided. In both species the eggs are barrel-shaped, with the chorion poorly marked with small concavities giving it a "golf ball" appearance, and light cream, with conspicuous broad darker stripes that turn to bright red after few days. The first instars are light cream with reddish longitudinal stripes and the head is black bearing a pair of very short scoli. The caterpillars of *S. ocelloides* pass through four instars, and occasionally show an additional fifth instar. The last instars are slender with a pair of short caudal filaments on the last segment, laterally striped with white and dark and light brown longitudinal lines and a dark brown head with a pair of short scoli. The pupae are elongated, rusty brown with silvery patches on the dorsal and lateral abdomen, with pointed projections on the head and insertion of the alar caps and marked dorsal carinae on the first abdominal segments. In general, the immature stages are distinct from all other species of the "*Megisto* clade", of which the genus *Stegosatyrus* Zacca, Mielke & Pyrcz, 2013 is part.

Key words: Atlantic Forest, Brazil, Campo de Altitude, Pampa, Satyrinae, Satyrini

Resumo. São descritos os estágios imaturos de *Stegosatyrus ocelloides* (Schaus, 1902), uma espécie de borboleta associada com habitats de vegetação aberta como campos e savanas, e informações complementares de ovos, primeiro e segundos instares de *Stegosatyrus periphas* (Godart, [1824]) são apresentadas. Nas duas espécies os ovos têm forma de barril e tem o córion marcado por pequenas concavidades, dando a aparência de "bolas de golf", são de cor creme, com faixas largas de vermelho vivo se formando após os primeiros dias. Os primeiros instares são claros com faixas longitudinais avermelhadas e cápsula escura com dois escolos curtos. As lagartas de *S. ocelloides* passam por quatro instares, com possibilidade de ocorrência de um quinto instar. Os instares finais são alongadas com cauda bífida curta, apresentando um padrão lateral estriado, com faixas longitudinais de cor branca e tons claros e escuros de marrom e possuem cabeça marrom escura com dois escolos curtos. As pupas são alongadas, marrom avermelhadas com áreas prateadas dorsal e lateralmente no abdômen, com projeções pontiagudas na cabeça e nas inserções das capas alares e os primeiros segmentos abdominais com carenas salientes. De modo geral, os imaturos são distintos de todos os outros conhecidos para o 'clado *Megisto*', do qual o gênero *Stegosatyrus* Zacca, Mielke & Pyrcz, 2013 faz parte.

Palavras chave: Brazil, Mata Atlântica, Campo de Altitude, Pampa, Satyrinae, Satyrini

INTRODUCTION

Butterflies (Lepidoptera: Papilionoidea) are among the best known insect groups (Boggs, 2003), but nevertheless the immature stages have been described for only a small fraction of species, with entire genera lacking any information concerning their life cycle. In the well-studied family Nymphalidae, for example, although data of immature stages have been described for most lineages and genera in some groups, such as the Ithomiini (Danainae) (Brown & Freitas, 1994; Willmott & Freitas, 2006) and Heliconiini (Heliconiinae) (Beebe *et al*., 1960; Fleming, 1960; Alexander, 1961a,b; Brown, 1981), other groups remain largely unknown, such as the species-rich Neotropical subtribe Euptychiina (Satyrinae). At present, detailed descriptions of immature stages are available for about a third of its 60 described genera, and for about 50 of the 432 described species (data from Zacca *et al*., 2021).

In recent years, a large collaborative international project has aimed to fill gaps in the knowledge of Euptychiina, resulting in over 50 publications on the ecology, natural history, taxonomy and evolution of this group (see details in http://www.floridamuseum.edu/neotropica/research/euptychiina/). However, although the early stages of several species have been described since the beginning of the above project, there are many genera where the early stages are still unknown or not described in detail. This is the case for *Stegosatyrus* Zacca,

Mielke & Pyrcz, 2013, a small genus with four described species restricted to the southern Neotropics.

All known species of *Stegosatyrus* are associated with open vegetation habitats, such as savannas and grasslands (including the Brazilian pampa and the Andean puna), and some species share some superficial similarities with species of *Megisto* Hübner, [1819] and *Pampasatyrus* Hayward, 1953 (Satyrini: Pronophilina), with which they were previously misplaced (Zacca *et al.*, 2013). The systematic position of *Stegosatyrus* remained undefined until recently, when morphological and molecular data showed that the genus is part of the '*Megisto* clade' of Peña *et al.* (2010) (Marín *et al.*, 2017; Espeland *et al*., 2019; Barbosa *et al*., unpublished).

In the study of Zacca *et al*. (2013) the genus *Stegosatyrus* was described and revised, with the inclusion of most available information for all the species in this genus. That study illustrated the egg and first instar of *Stegosatyrus periphas* (Godart, [1824]), but the complete life cycle has yet to be described for any species in the genus. Accordingly, the present study describes in detail the early stages of *Stegosatyrus ocelloides* (Schaus, 1902) and compares them with other Euptychiina, in addition to providing further information for *S. periphas*.

MATERIAL AND METHODS

Adults and immatures of *S. ocelloides* (Figs. 1E-F, 2) were studied based on material collected in two localities: 1) Trilha da Serrinha, São Francisco de Paula, Rio Grande do Sul, southern Brazil (*ca*. 900 m elevation; 29º29'11''S, 50º15'02''W) in December 2002; 2) Serra da Bocaina Cunha, São Paulo, southeastern Brazil (*ca*. 1600 m elevation; 22º48'15''S, 44º45'59''W) in January and February, 2021. These study sites are mainly covered by high altitude grasslands (locally known as "Campos de Altitude" or "Campos de cima da serra"), including dry and wet grassland areas interspersed with patches of high-altitude montane forest (Fig. 1A-D). In both localities, the climate is mild and wet all year round, with a warm summer and a very cold winter, where frosts are common, and temperatures usually drop near to 0ºC during the autumn and winter nights.

Adults and immature stages of *S. periphas* (Fig. 3B-F) were studied based on material collected in Parque Estadual do Espinilho, Barra do Quarai, Rio Grande do Sul, southern Brazil (*ca*. 55 m elevation; 30º12'00''S, 57º29'31''W) in March 2003 (Fig. 3A). This area has typical Pampa grasslands with the dominance of *Vachelia caven* (Molina) Seigler & Ebinger and *Prosopis* spp. (Fabaceae); for more details of the study site see Veloso & Góes-Filho (1982) and Marchiori & Romanowski (2006).

Eggs were obtained from wild-captured females confined in plastic bags (Freitas, 1991) and provided with leaves of several species of grasses accepted by other Euptychiina. 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 for all immature 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 in the AVLF 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 immature stages and morphology was studied using a Leica®MZ7.5 stereomicroscope equipped with a micrometric scale. Pictures of immature stages were obtained using a Nikon®Coolpix950. Egg size is presented as height and diameter, and head capsule size is the distance between the most external stemmata (as in Freitas, 2007). The terminology for larval and pupal characters follows Stehr (1987).

RESULTS

Immature stages description for *Stegosatyrus ocelloides*

Egg (Figs. 2A-C). Barrel-shaped, light cream, with conspicuous broad darker stripes as a laterally compressed loop that turn to bright red after a few days (Fig. 2C); chorion poorly marked with small concavities giving it a "golf ball" appearance. Height 0.82-0.90 mm (mean=0.872 mm, SD=0.032 mm, n=8); diameter 0.82-0.90 mm (mean=0.855 mm; SD=0.026 mm; n=8); duration 5-7 days (n=15).

The red bands are variable, and can either form single loops (Figs. 2A, B) or the external curved ends can touch, giving an appearance of crossing bands (Fig. 2C).

First instar (Figs. 2D, E). Head capsule width 0.62-0.68 mm (mean=0.647 mm, SD=0.024 mm, n=6); head scoli 0.08-0.10 mm (mean=0.083 mm, SD=0.008 mm, n=6). Head black, bearing a pair of very short scoli on vertex, each with two long narrow black setae. Third stemma larger than other stemmata. Body bluish green with reddish longitudinal stripes; a pair of short caudal filaments on last segment. Legs and prolegs light brown. Maximum length 7 mm. Duration 7-8 days (days, n=8).

Second instar (Figs. 2F, G). Head capsule width 0.90-0.96 mm (mean=0.930 mm, SD=0.021 mm, n=6); head scoli 0.16-0.20 mm (mean=0.173 mm, SD=0.016 mm, n=6). Head dark brown, with two short scoli on vertex. Body brown, dark ventrally, laterally striped with white and dark and light brown longitudinal lines; caudal filaments short. Legs and prolegs brown. General profile slender, much longer than broad. Maximum length 10 mm. Duration 8-13 days (n=9).

Third instar (Figs. 2H, I). Head capsule width 1.34-1.56 mm (mean=1.460 mm, SD=0.077 mm, n=6); head scoli 0.22-0.26 mm (mean=0.230 mm, SD=0.017 mm, n=6). Similar to second instar in color and general shape, but presenting a poorly marked dorsolateral zigzag pattern from segments A1 to A7. Maximum length 18 mm. Duration 7-11 days (n=5). Heads of two larvae that passed through five instars measured 1.14 and 1.20 mm, both with head scoli of 0.2 mm.

Fourth (last) instar (Figs. 2J, K). Head capsule width 2.10-2.22 mm (mean=2.176 mm, SD=0.048 mm, n=5); head scoli 0.30-0.32 mm (mean=0.304 mm, SD=0.009, n=5). Similar to third instar but larger and with broader lateral stripes; dorsolateral zigzag pattern is more marked, creating a pattern of "X"-shaped dorsal markings centered on intersegmental ridges from A1 to A7. Maximum length 26 mm. Duration 15-22 days (n=4).

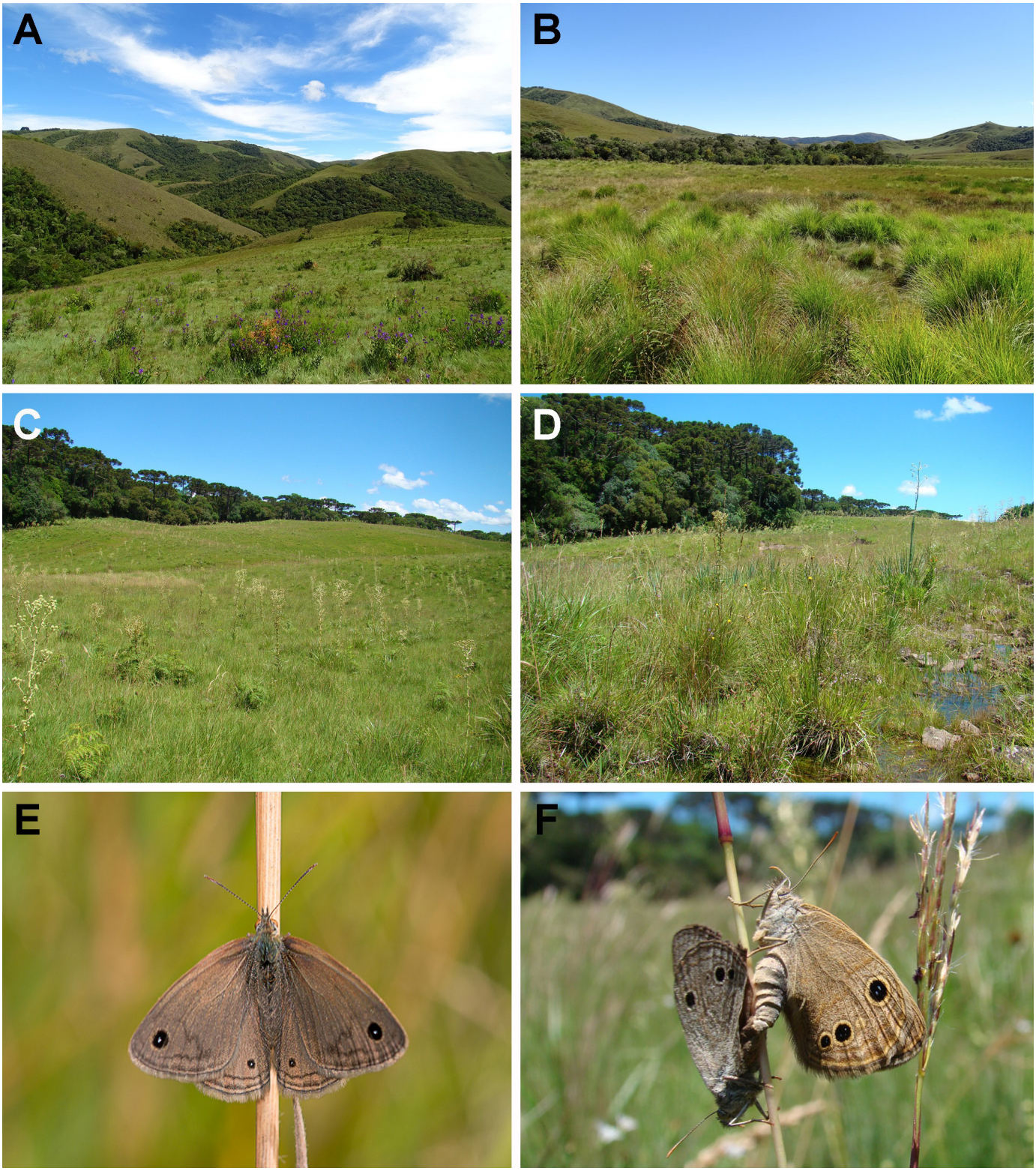
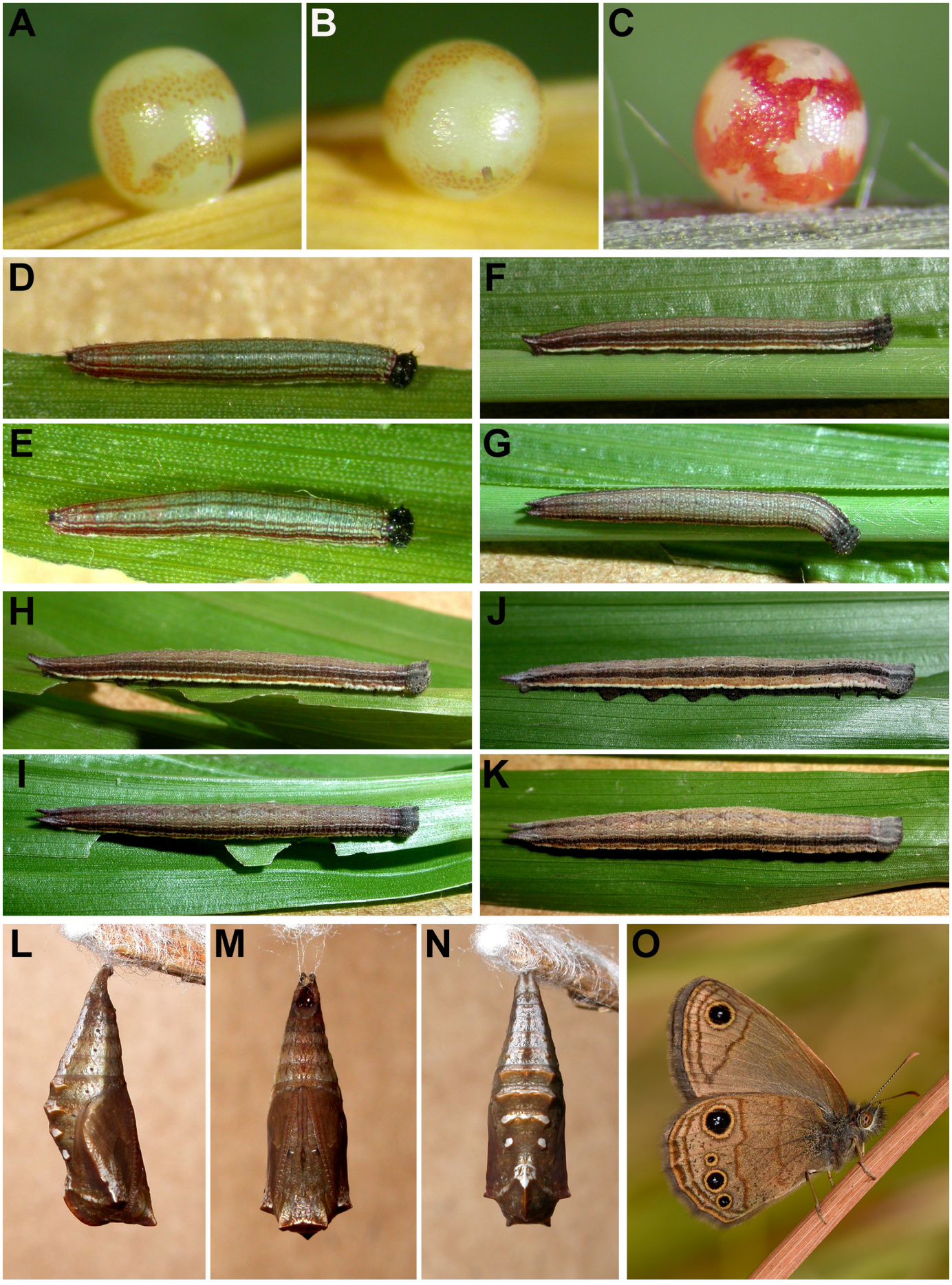


Figure. 1. Habitats and adults of *S. ocelloides*. **A.** Grassland, Serra da Bocaina, Cunha, SP; **B.** Wet grassland, Serra do Papagaio, Alagoa, MG; **C.** Grassland, São Francisco de Paula, RS; **D.** Wet grassland, São Francisco de Paula, RS; **E.** Dorsal view of *S. ocelloides*, Cunha, SP (photograph by Ricardo Costa); **F.** Mating pair of *S. ocelloides*, São Francisco de Paula, RS (Kaminski, 2021a). Abbreviations for Brazilian states: SP = São Paulo; MG = Minas Gerais; RS = Rio Grande do Sul.

Pupa (Figs. 2L-N). General profile elongated, with conspicuous pointed ocular caps and pointed processes in insertion of wing caps; abdominal segments forming a straight conical structure towards cremaster; dorsal abdomen with marked carina on A2 and A3; ground color light rusty brown (dark brown in some individuals) with silvery patches on dorsal and lateral abdomen; cremaster broad. Total length 9-12 mm. Duration 8-12 days (n=2).


A
B
C
D
F
E
G
H
J
I
K
L
M
N
O

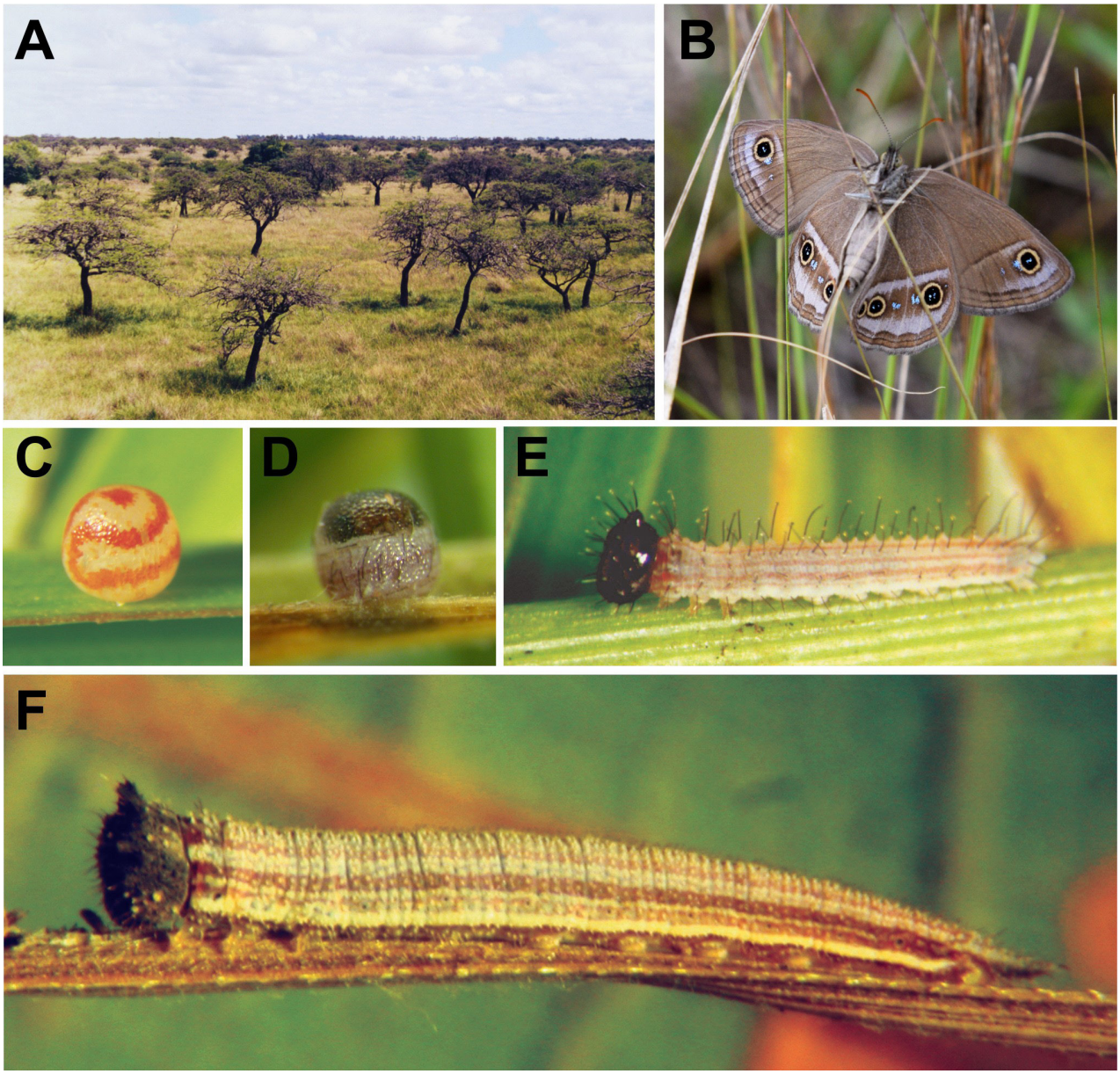


Figure. 3. Habitats and life stages of *S. periphas*. **A.** Open vegetation in Parque Estadual do Espinilho, Barra do Quarai, Rio Grande do Sul, Brazil; **B.** Adult female of *S. periphas* (Kaminski, 2021b; Copina, Córdoba, Argentina); **C, D.** Eggs, showing the broad bright red stripes and the nearly hatching larvae, respectively; **E.** First instar (lateral); **F.** Second instar (lateral).

Behavior and natural history of *Stegosatyrus ocelloides*

Oviposition behavior was not observed in the field, and the natural host plant is unknown. In the laboratory, larvae easily accepted cultivated broadleaf carpetgrass *Axonopus compressus* (Sw.) P. Beauv. ("grama missioneira") (Poaceae), a grass species native to Brazil, and early instars also accepted the common ornamental bamboo *Bambusa gracilis* Hort. ex Rivière & C. Rivière, both plants largely accepted by other Euptychiina larvae in the laboratory (Freitas, 2003; Kaminski & Freitas, 2008; Freitas *et al*., 2012). Larvae were isolated and moved slowly and passed through four larval instars (although two out of eight individuals presented an extra fifth instar). Adults (Figs. 1E, F; 2O) are mostly distributed in several areas of open vegetation, including cerrado savannas and high-altitude grasslands in the Atlantic Forest domain in southern and southeastern Brazil, at elevations from sea level to above 1600 m; further details of habitat and geographic distribution are available in Zacca *et al*. (2013). Curiously, although *S. ocelloides* is locally abundant in Serra da Bocaina, the species is absent in similar high-altitude grassland habitats in the main portion of the neighboring Serra da Mantiqueira mountain chain, including the well sampled regions from Campos do

Figure. 2 (p. 130, facing page). Life stages of *S. ocelloides* from Serra da Bocaina, Cunha, São Paulo. **A, B.** Early egg (lateral, dorsal); **C.** late egg showing the broad bright red stripes (lateral); **D, E.** First instar (lateral, dorsal); **F. G.** second instar (lateral, dorsal); **H, I** third instar (lateral, dorsal); **J, K.** fourth (last) instar (lateral, dorsal); **L, M, N.** Pupa (lateral, ventral, dorsal); **O.** adult male (photograph by Ricardo Costa).

Jordão, São Paulo, to Itatiaia National Park, Itatiaia, Rio de Janeiro (except for new records of Serra do Papagaio, Alagoa, Minas Gerais) (Zikán & Zikán, 1968; AVLF and AHBR, pers. obs.). Behaviors such as territorialism and courtship were never directly observed, but a pair was observed *in copula* in São Francisco de Paula (Fig. 1F). Based on museum specimens and field work, adults are present all year round.

Additional data on the immature stages of *Stegosatyrus periphas*

Egg (Figs. 3C, D). Barrel-shaped, light cream, with conspicuous broad darker stripes as a laterally compressed loop and a dark micropylar spot that turn to bright red after few days (Fig. 3C); chorion poorly marked with small concavities giving it a "golf ball" appearance. Height 1.042-1.10 mm (mean=1.064 mm, SD=0.026 mm, n=5); diameter 0.94-1.00 mm (mean=0.984 mm; SD=0.026 mm; n=5).

The red bands are variable, and can either form single loops (Fig. 3C) or the external curved ends can touch, giving an appearance of crossing bands (Zacca *et al.*, 2013: Figs. 67-69).

First instar (Fig. 3E). Head capsule width 0.64-0.68 mm (mean=0.652 mm, SD=0.018 mm, n=5); head scoli 0.10-0.12 mm (mean=0.112 mm, SD=0.009 mm, n=5). Head black, bearing a pair of very short scoli on vertex, each with two long narrow black setae. Third stemma larger than other stemmata. Body light cream with reddish longitudinal stripes; caudal filaments very short. Legs and prolegs light brown. Duration 7-8 days (days, n=8).

Second instar (Fig. 3F). Head capsule width 0.86-0.94 mm (mean=0.896 mm, SD=0.029 mm, n=5); head scoli 0.16-0.20 mm (mean=0.18 mm, SD=0.014 mm, n=5). Head dark brown, with two short scoli on vertex. Body brown, dark ventrally, laterally striped with white and dark and light brown longitudinal lines; caudal filaments short. Legs and prolegs brown. General profile slender, much longer than broad.

Behavior and natural history of *Stegosatyrus periphas*

Details of oviposition behavior were not observed in the field, but like *S. ocelloides*, females easily oviposited in the laboratory. Most eggs were fertile and hatched, and caterpillars accepted an unidentified species of grass (Poaceae) that was collected in the same place as the adults. Due to the lack of an adequate host plant, some alternative species of grasses were tested as food, but the larvae did not accept them and died in the second instar. In Argentina, Volkmann & Núñez-Bustos (2013) cite the annual bluegrass *Poa annua* L. (Poaceae) as a natural host plant. Despite the wide distribution of the species in Argentina, Brazil, Paraguay and Uruguay, this species is quite localized, occurring in small patches of habitat. In general, these butterflies occur in areas of preserved native Pampean grasslands and high-altitude grasslands with low grazing intensity in the southern Atlantic Forest domain. Adults visit several flower species, especially Asteraceae (Volkmann & Núñez-Bustos, 2013; Kaminski, 2021a). Based on museum specimens and field work, adults are present all year round.

DISCUSSION

Based on recent morphological and molecular evidence, the genus *Stegosatyrus* is part of the '*Megisto* clade' of Peña *et al*. (2010), although its relationships with other genera in this clade are uncertain (see Marín *et al*., 2017; Espeland *et al*., 2019; Barbosa *et al*., unpublished). However, the immature stages here described are quite distinct from other species in this clade, and accordingly, they are not of help to clarify the systematic position of the genus within the '*Megisto* clade'. For example, the larvae of *Stegosatyrus* are very thin and elongate, quite distinct from the stubby larvae of other members of the clade, such as *Moneuptychia* Forster, 1964, *Carminda* Ebert & Dias, 1998, *Yphthimoides* Forster, 1964, *Pharneuptychia* Forster, 1964, *Cissia* E. Doubleday, 1848 and *Megisto* (Scudder, 1888-89; Freitas *et al*., 2021, and references therein, and AVLF unpublished data). The pupa is also quite distinct from those of all other members of the '*Megisto* clade'; while pupae of all of the above genera are smooth, stubby, with short rounded ocular caps and presenting a marked curve in the end of the abdominal segments near the cremaster, the pupae of *S. ocelloides* are elongated, with pointed ocular caps and having pointed projections at the insertion of the wing caps, marked carinae in the dorsal abdomen, and lacking the curved abdomen near the cremaster.

Maybe the most remarkable feature are the broad, bright red stripes observed in the eggs of both species of *Stegosatyrus*. These are unique among the '*Megisto* clade' and represent a possible synapomorphy for this genus within the Euptychiina. Curiously, conspicuous broad red stripes (including spots in the micropylar area), are present in the eggs of the pronophilines *Pampasatyrus reticulata* (Weymer, 1907) and *Pampasatyrus gyrtone* (Berg, 1877) (Satyrini: Pronophilina) (Zacca & Freitas, unpublished data), species that are distantly related to *Stegosatyrus* but inhabit the same grassland habitats and show several superficial similarities in adult behavior. Besides the differences in color (bright red in *Stegosatyrus* and dark red in *Pampasatyrus*) and shape (laterally compressed loops in *Stegosatyrus* and transverse rings in *Pampasatyrus*), this morphological convergence suggest that similar selective pressures might be shaping the functional traits of these grassland specialist butterflies, both in the immature and adult stages.

Finally, an open question remains concerning the size of the primary setae in the first instar of *S. periphas*: in the present study, body setae are long, very similar to those also reported to *S. ocelloides*. Conversely Zacca *et al.* (2013) illustrated a first instar of *S. periphas* with very short body setae in segments T2 though A8. Determining whether these are consistent differences or just represent a rare anomaly requires future studies on both populations of *S. periphas*.

As additional data of Euptychiina immature stages and well supported phylogenies become available, it will become possible to draw a better picture of the distribution and evolution of morphological characters in this group. However, at present, the lack of adequate data for the majority of species and genera in Euptychiina precludes such studies even in the best known groups, such as the '*Megisto* clade'. Accordingly, the

description of immature stages for any species of Euptychiina should be strongly encouraged.

ACKNOWLEDGMENTS

We thank Ricardo Costa who provide pictures of live adults of *S. ocelloides*. Keith Willmott and Thamara Zacca revised and made valuable contributions to the submitted version. LAK was supported by CNPq (106325/2001-9, 478787/2001-4), Programa Nacional de Pós-Doutorado (PNPD-CAPES), National Geographic Society (WW-224R-17), and Fundação Romanowski. AHBR thanks Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) - Finance code 001. AVLF acknowledges support from FAPESP (Biota-Fapesp - grants 2011/50225-3, 2013/50297-0), 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). The authors also thank the ICMBio for the permits (#10438-3, #10802-26). Butterfly species are registered in the Brazilian 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 (A6C0E33).

LITERATURE CITED

Alexander, A. J. 1961a. A study of the biology and behavior of the caterpillars, pupae and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. Part I. Some aspects of larval behavior. *Zoologica NY* 46: 1-24.

Alexander, A. J. 1961b. A study of the biology and behavior of the caterpillars, pupae and emerging butterflies of the subfamily Heliconiinae in Trinidad, West Indies. Part II. Molting, and the behavior of pupae and emerging adults. *Zoologica NY* 46: 105-123.

Beebe, W., Crane, J., Fleming, H. 1960. A comparison of eggs, larvae and pupae in fourteen species of Heliconiine butterflies from Trinidad, W.I. *Zoologica NY* 45: 111-154.

Boggs, C. L., Watt, W. B., Ehrlich, P. R., Ehrlich, P. R. (Eds.). 2003. *Butterflies: Ecology and Evolution Taking Flight*. Chicago, University of Chicago Press. 756 pp.

Brown, K. S. 1981. The biology of *Heliconius* and related genera. *Annual Review of Entomology* 26: 427-456.

Brown, K. S., Freitas, A. V. L. 1994. Juvenile stages of Ithomiinae: overview and systematics (Lepidoptera, Nymphalidae). *Tropical Lepidoptera* 5: 9-20.

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. 2003. Description of a new genus for "*Euptychia*" *peculiaris* (Nymphalidae: Satyrinae): Immature stages and systematic position. *Journal of the Lepidopterists' Society* 57: 100-106.

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., Kaminski, L. A., Mielke, O. H. H., Barbosa, E. P., Silva-Brandão, K. L. 2012. A new species of *Yphthimoides* (Lepidoptera: Nymphalidae: Satyrinae) from the southern Atlantic Forest region. *Zootaxa* 3526: 31-44.

Freitas, A. V. L., Barbosa, E. P., Carreira, J. Y. O. 2021. Immature stages and natural history of *Yphthimoides borasta* (Nymphalidae: Euptychiina). *Tropical Lepidoptera Research* 31(1): 42-47.

Fleming, H. 1960. The first instar larvae of the Heliconiinae (butterfiies) of Trinidad, W. I. *Zoologica NY* 45: 91-110.

Kaminski, L. A. 2021a. https://www.iNaturalist.org/observations/73867218. (Accessed: 19 September 2021).

Kaminski, L. A. 2021b. https://www.iNaturalist.org/observations/81184825. (Accessed: 19 September 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.

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.

Marchiori, M. O., Romanowski, H. P. 2006. Borboletas (Lepidoptera, Papilionoidea e Hesperioidea) do Parque Estadual do Espinilho e entorno, Rio Grande do Sul, Brasil. *Revista Brasileira de Zoologia* 23: 1029-1037.

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.

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.

Scudder, S. H. 1888-1889. *The butterflies of the Eastern United States and Canada with special reference to New England*. Cambridge, Author. 1: xxvi + 766 pp., frontisp.; 2: xii + 767-1774, frontisp., figs.; 3: viii + 1775-1958, frontisp., pls. 1-89, 3 maps.

Stehr, F. W. 1987. *Order Lepidoptera*, pp. 288-305. *In*: Stehr F. W. (Ed), *Immature Insects*. *Volume 1*. Dubuque, Kendall-Hunt Publishing Company. 754 pp.

Triplehorn, C. A., Johnson, N. F. 2005. *Borror and Delong's Introduction to the Study of the Insects*. Belmont, Thomson Brooks/Cole. 864 pp.

Veloso, H. P., Góes-Filho, L. 1982. Fitogeografia Brasileira: Classificação Fisionômico-Ecológica da vegetação Neotropical. *In*: Ministério de Minas e Energia. Projeto RADAMBRASIL, Boletim Técnico. Série Vegetação 1, Salvador. 85 pp.

Volkmann L., Núñez-Bustos E. 2013. Mariposas serranas de Argentina Central. Tomo II: Nymphalidae y Hesperiidae. Huerta Grande, Equipo Gráfico. 192 pp.

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 13 April 2021).

Zacca, T., Mielke, O. H. H., Pyrcz, T. W., Casagrande, M. M., Freitas, A. V. L., Boyer, P. 2013. *Stegosatyrus*, a new genus of Euptychiina from the grasslands of neotropical realm (Lepidoptera: Nymphalidae: Satyrinae). *Zootaxa* 3692 (2): 331-350.

Zikán, J. F., Zikán, W. 1968. Inseto-fauna do Itatiaia e da Mantiqueira. III. Lepidoptera. *Pesquisa Agropecuária Brasileira* 3: 45-109.