Immature stages of *Mechanitis lysimnia nesaea* (Nymphalidae: Danainae: Ithomiini)

Douglas Henrique Alves Melo[1] **and André Victor Lucci Freitas**[2,*]

1. Departamento de Zoologia, Universidade Federal de Pernambuco - UFPE, Recife, Pernambuco, Brazil. 2. Departamento de Biologia Animal e Museu de Diversidade Biológica, Instituto de Biologia, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. *Corresponding author: baku@unicamp.br.

Date of issue online: 7 April 2023
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.7790105.

Abstract: The immature stages (eggs, larvae and pupae), larval behavior, oviposition and host plant of *Mechanitis lysimnia nesaea* Hübner, [1820] are described for the first time. Eggs are laid in clusters on the upper side of leaves of its solanaceous hostplants. The larvae are gregarious and undergo five instars. The first instar head capsule is black and the body is translucent yellow. From the second instar on, the body changes to bluish gray with yellow stripes, with colors becoming more vivid in the last instar. Initially, the pupa is yellow, turning reflective (silvery/golden) with dark contours on the wing cases and abdomen after the first day. A comparison with other species of *Mechanitis* shows that, despite their similarities, the early stages are informative at the species level, and could help to understand the species limits in the currently non-monophyletic species in this genus.

Key words: host plant, immatures stages, life cycle, Mechanitina, Solanaceae.

Resumo: Os estágios imaturos (ovos, larvas e pupas), comportamento larval, oviposição e planta hospedeira de *Mechanitis lysimnia nesaea* Hübner, [1820] são descritos pela primeira vez. Os ovos são depositados em grupos na parte superior das folhas de suas plantas hospedeiras (solanáceas). As larvas são gregárias e passam por cinco instares. A cápsula cefálica do primeiro instar é preta e o corpo é amarelo translúcido. A partir do segundo instar, o corpo muda para cinza azulado com faixas amarelas, com cores mais vívidas no último instar. A pupa é amarela inicialmente, tornando metálica (prateada/dourada) com contornos escuros na região das asas e no abdome após o primeiro dia. Comparações com outras espécies de *Mechanitis* mostram que, além das semelhanças, os estágios iniciais são informativos em nível de espécie e podem ajudar a entender os limites das espécies não monofiléticas deste gênero.

Palavras-chave: planta hospedeira, estágios imaturos, ciclo de vida, Mechanitina, Solanaceae.

INTRODUCTION

Distributed from Mexico to northern Argentina, the Neotropical tribe Ithomiini (Nymphalidae: Danainae) includes about 390 species occurring in several forested habitats from sea level to 3,000 meters (Brown & Freitas, 1994; Lamas, 2004; Willmott & Freitas, 2006; Brower *et al.*, 2014). The adults are all aposematic and unpalatable and are involved in numerous Müllerian mimicry rings (Brown & Benson, 1974; Beccaloni, 1997). Ithomiini larvae are usually very host-specific to plant family and genus, feeding mostly on plants of the family Solanaceae, with a few exceptions using Apocynaceae and Gesneriaceae (Drummond & Brown, 1987; Beccaloni *et al.*, 2008).

The tribe Ithomiini is currently divided into ten subtribes supported by morphological and molecular data (Willmott & Freitas, 2006; Brower *et al.*, 2006, 2014; Garzon-Orduña *et al.*, 2015). The subtribe Mechanitina contains five genera, including *Mechanitis* Fabricius, 1807, a small genus containing five described species and over 50 subspecies distributed throughout the Neotropics (Fox, 1967; Brown, 1977, 1979; Lamas, 1987, 2004; Dasmahapatra *et al.*, 2010; Hill *et al.*, 2012; Giraldo *et al.*, 2014), and with a reputation for being taxonomically 'difficult' (Fox, 1967). Occurring from Mexico to Argentina, *Mechanitis lysimnia* (Fabricius, 1793) is the most widespread species, with at least 14 described subspecies and several unnamed local forms (Brown, 1979; Lamas, 2004; Mota *et al.*, 2022). One of these subspecies, *Mechanitis lysimnia nesaea* Hübner, [1820], is common in northeastern Brazil, occurring in well-preserved and secondary forests especially on the coast, but also present in forest patches in semi-arid regions (Caatinga) (Kesselring & Ebert, 1979; Nobre *et al.*, 2008; Paluch *et al.*, 2011; Zacca & Bravo, 2012; Kerpel *et al.*, 2014; Melo *et al.*, 2019).

Species of *Mechanitis* are common components of most lowland Neotropical forests, and although the immature stages have been described for one or more populations of most species, only a few subspecies and/or populations have been studied in this respect (Carvalho *et al.*, 2019, and references therein). Detailed information on immature stages from different populations could assist in conservation and help to understand species limits and help to identify cryptic taxonomic diversity. Accordingly, the present paper describes in detail the immature stages of *M. lysimnia nesaea*, aiming to improve the understanding of species limits and variation in *Mechanitis* immature stages.

MATERIAL AND METHODS

Study Sites

Adults and immatures of *M. lysimnia nesaea* were studied from August to September 2014, from January to March 2016, and in November 2022, in Parque Estadual Dois Irmãos (08º00'48" S, 34º56'42.9" W; altitude 40-60 m), a forest fragment of 1,157.72 hectares located in the metropolitan region of Recife, Pernambuco, Brazil (Fig. 1A, B). Solanaceous hostplants were searched for eggs and larvae of *M. lysimnia nesaea*, along forest edges, trails and at the margins of streams near weirs, where the host plant is common. Additional data was obtained in August 2006 in Serra Negra District, Bezerros Municipality, Pernambuco, Brazil (08º10'45" S, 35º46'57" W; altitude 800-900 m).

Rearing, Morphology, and Behavior

Descriptions here are mostly based on material from Parque Estadual Dois Irmãos, with larvae reared on *Solanum stramoniifolium* Jacq. (Solanaceae) (Fig. 1 B, C). Eggs and larvae were reared in the laboratory in plastic pots under ambient conditions, cleaned daily, and with food available *ad libitum* following Carvalho *et al.* (2019). Leaves were kept fresh by immersing their petioles in small vials with clean water. Data were recorded on behavior and development time for all stages. Dry head capsules and pupal exuviae were retained in glass vials. Measurements were obtained 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 lateral stemmata (as in Carvalho *et al.*, 2019). Maximum length was measured one or two days before each molt (when larvae reach maximum length). Immature stages were fixed in Kahle-Dietrich solution and then preserved in 70% ethanol. The specimens were deposited at the Zoological Collection (ZUEC) of the Museu de Diversidade Biológica, Universidade Estadual de Campinas, Campinas, São Paulo, Brazil. Adult behavior, including oviposition and the flight activities of butterflies were studied in the field from 08:00 to 16:00 at forest edges and in the forest interior. The taxonomy follows Lamas (2004) modified after Hill *et al.* (2012), where *M. mazaeus* and *M. messenoides* are considered as distinct species (see also Warren *et al.*, 2019). Accordingly, data discussed here for the immature stages of *M. messenoides* correspond to a population belonging to "haplogroup A" of Hill *et al.* (2012).

RESULTS

Hostplants, oviposition and larval behavior

Based on field observations, the main host plant of *M. lysimnia nesaea* is *Solanum stramoniifolium*, popularly known as "Jurubeba" in Recife. In addition, four unidentified species of Solanaceae (three *Solanum* and one unidentified genus) were recorded in the field (e.g. Fig. 1D). Eggs are laid in groups of variable size (from five to more than 130 eggs) (Fig. 1E, 2A, B), always on the upper leaf surface near the apex of both young and mature leaves of *Solanum stramoniifolium* (Fig. 1B, C), and on mature leaves of the unidentified Solanaceae from Bezerros (Fig 1D). The total duration of the oviposition process was not recorded, but females were observed to spend up to three hours in the process of laying eggs, until flying away when disturbed by the wind.

Larvae consume the egg corion just after hatching (Fig. 2C) and soon start feeding on the leaf blade, producing small holes nearby the oviposition site. Subsequently, larvae move to the under surface of the leaf where they preferentially stay until the last instar (although some larvae were observed on the upper surface during nocturnal feeding). First instars weave a silken thread, using it as a "platform" to move around among the thorns and trichomes of the hostplant. The first instars feed on almost the entire leaf, avoiding only the trichomes. From the second instar on, larvae start to feed on the leaf edges, consuming also the secondary veins. Only from the third instar on are the thorns are eaten, while the central leaf vein is not consumed in any instar.

Larvae are gregarious in all instars, participating in all the activities such as feeding, resting, and movement between the leaves and molting, at the same time. When handled, the larvae are able to regurgitate recently eaten food. In the field, pupation occurs off the host plants, and pupae were never observed on the host plant, but in the laboratory, pupation can occur on the leaf underside and on the lid of the plastic containers.

Description of the immature stages

Egg (Fig. 2A, B): Diameter 0.64-0.70 mm (mean = 0.66 mm, SD = 0.025, n = 8); height 1.10-1.24 mm (mean = 1.17 mm, SD = 0.063, n = 8). White and elongated with a pointed apex. Eggs become transparent near hatching making it possible to visualize the dark head capsule of larvae (Fig. 2C). Egg surface sculptured with 10-11 horizontal ridges and 12-14 vertical ridges (n = 15). Duration: 5 days (n = 77).

First instar (Fig. 2C, D, E): Head capsule width 0.48-0.50 mm (mean = 0.48 mm, SD = 0.017, n = 11). Head capsule black and smooth, without any projections; body translucent yellow with visible intestinal contents; prothoracic segment with two dorsolateral small protuberances; a pair of short rounded lateral projections from A1 to A8; legs black; prolegs light yellow with a lateral gray plate (Fig. 2D). A triangular dark patch is present in anal plate. Maximum body length 3.5 mm (n =10). Duration: 3-4 days (n = 155).

Second instar (Fig. 2F, G): Head capsule width 0.70-0.76 mm (mean = 0.74 mm, SD = 0.017, n = 14). Head capsule black and smooth; body light green, with a pair of short lateral projections from A1 to A8; prothoracic protuberances and abdominal lateral projections more conspicuous than in first instar; legs black, prolegs light cream; lateral dark plates absent on proleg (Fig. 2F). Maximum body length 9.5 mm (n = 10). Duration: 2-3 days (n = 100).

Third instar (Fig. 2H, I): Head capsule width 1.0-1.12 mm (mean = 1.07 mm, SD = 0.035, n = 16). Similar to previous instar, darker, with lateral projections more developed, pointed and with a yellow patch at base. Prolegs light cream; lateral dark plates absent on proleg (Fig 2H). Maximum body length 15.5 mm (n = 10). Duration: 2-3 days (n = 210).

Fourth instar (Fig. 2J, K): Head capsule width 1.44-1.64 mm (mean = 1.55 mm, SD = 0.068, n = 15). Head capsule black with frons and mouthparts pale; in some individuals head capsule is predominantly light cream or brown (Fig. 2K), with a black patch restricted to the stemmatal region. Body light bluish grey, a dorsal light-yellow stripe from T2 to A8; prothorax white with a pair of short dorsolateral protuberances; lateral abdominal projections longer than in previous instar, white, each yellow at base with a black circled spiracle; legs black; prolegs light cream; lateral dark plates absent on proleg (Fig. 2J). Maximum body length 29.0 mm (n = 10). Duration: 2-3 days (n = 145).

Fifth (last) instar (Fig. 3A-F): Head capsule width 2.0-2.1 mm (mean = 2.04 mm, SD = 0.033, n = 7). Head capsule black with frons and mouthparts

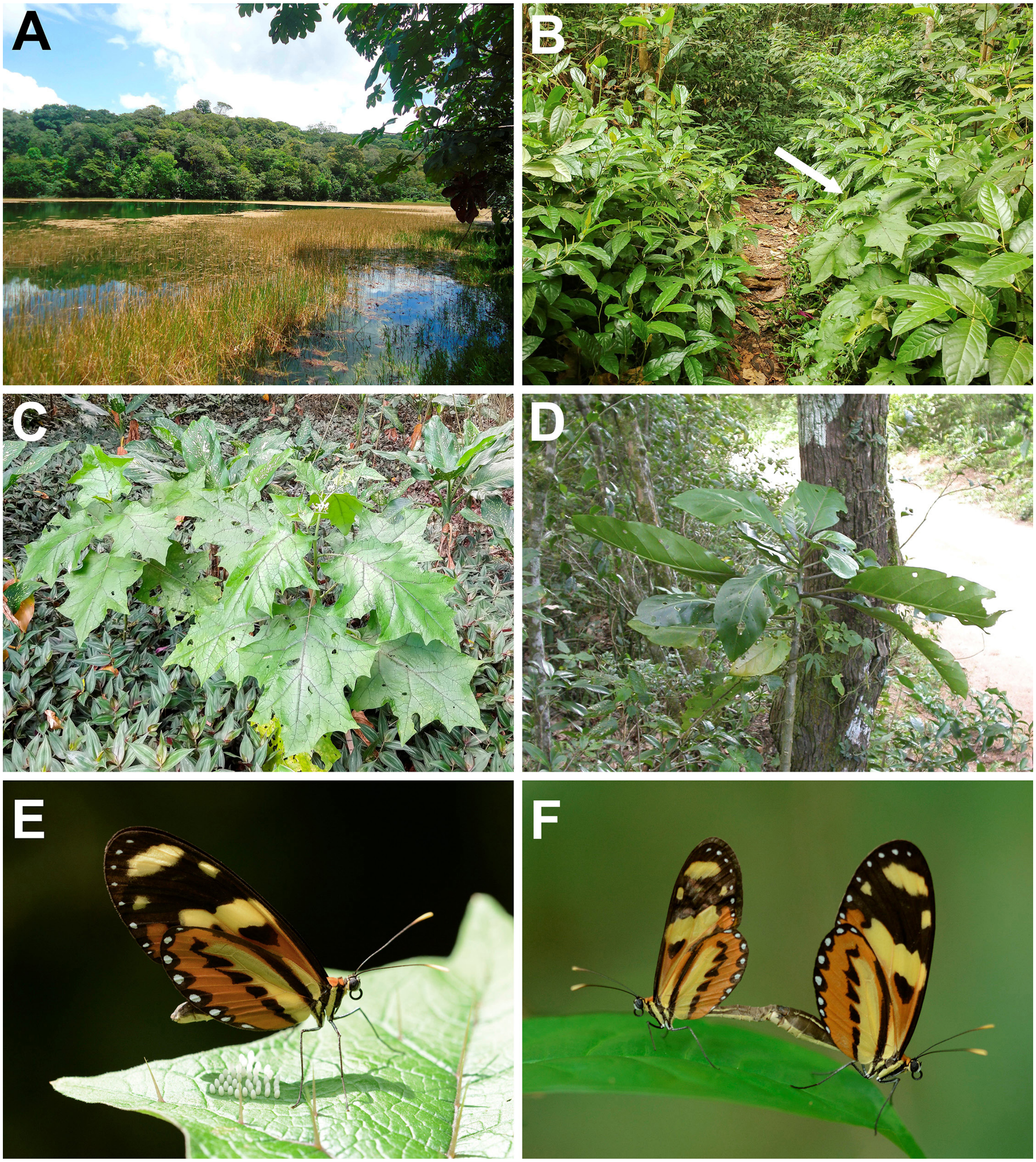

Figure 1. Habitat, host plants and adults of *Mechanitis lysimnia nesaea* in Parque Estadual Dois Irmãos, Recife, Pernambuco, Brazil. **A**. general view of the habitat; **B.** trail inside the area where *Solanum stramoniifolium* (white arrow) occurred; **C.** close view of a shrub of *Solanum stramoniifolium*; **D**. unidentified Solanaceae used as host plant in Bezerros municipality; **E.** Ovipositing female, showing newly laid eggs; **F.** mating pair (male on left).

pale (Fig. 3C, D) or predominantly light cream, with a black patch restricted to the stemmatal region (Fig. 3A, B, E). Just after molt, body similar to previous instar; color then becomes vivid, having a dark bluish green background with three bright yellow stripes, the first dorsal from T2 to A8 and a pair of subdorsal stripes from T2 o A9; prothorax white, with well-developed prothoracic protuberances; lateral abdominal projections very long, yellow, white at distal half and with a conspicuous black circled spiracle near the body insertion. Legs black; prolegs light cream; lateral black plates can be present (fig. 3B, D) or absent (Fig. 3A, F); anal prolegs lacking lateral dark plates (Fig. 3A, B, D). Larvae change to entire yellow just before pupation (Fig. 3F). Maximum body length 32.0 mm (n = 10). Duration: 3-4 days (n = 90).

Pupa (Fig. 3G-J): Pendant, reflective metallic, general profile elongated. Translucent yellow initially, changing to metallic with dark contours at wing cases and abdomen after 24 h; cremaster black; a slightly protruding dorsal edge on dorsal A3 and short pointed ocular caps. Pupa loses reflections at maturity close to adult emergence revealing the body and wing pattern of adult (Fig. 3J). Maximum length 17.0 mm (n = 10). Duration: 5-7 days (n = 30).

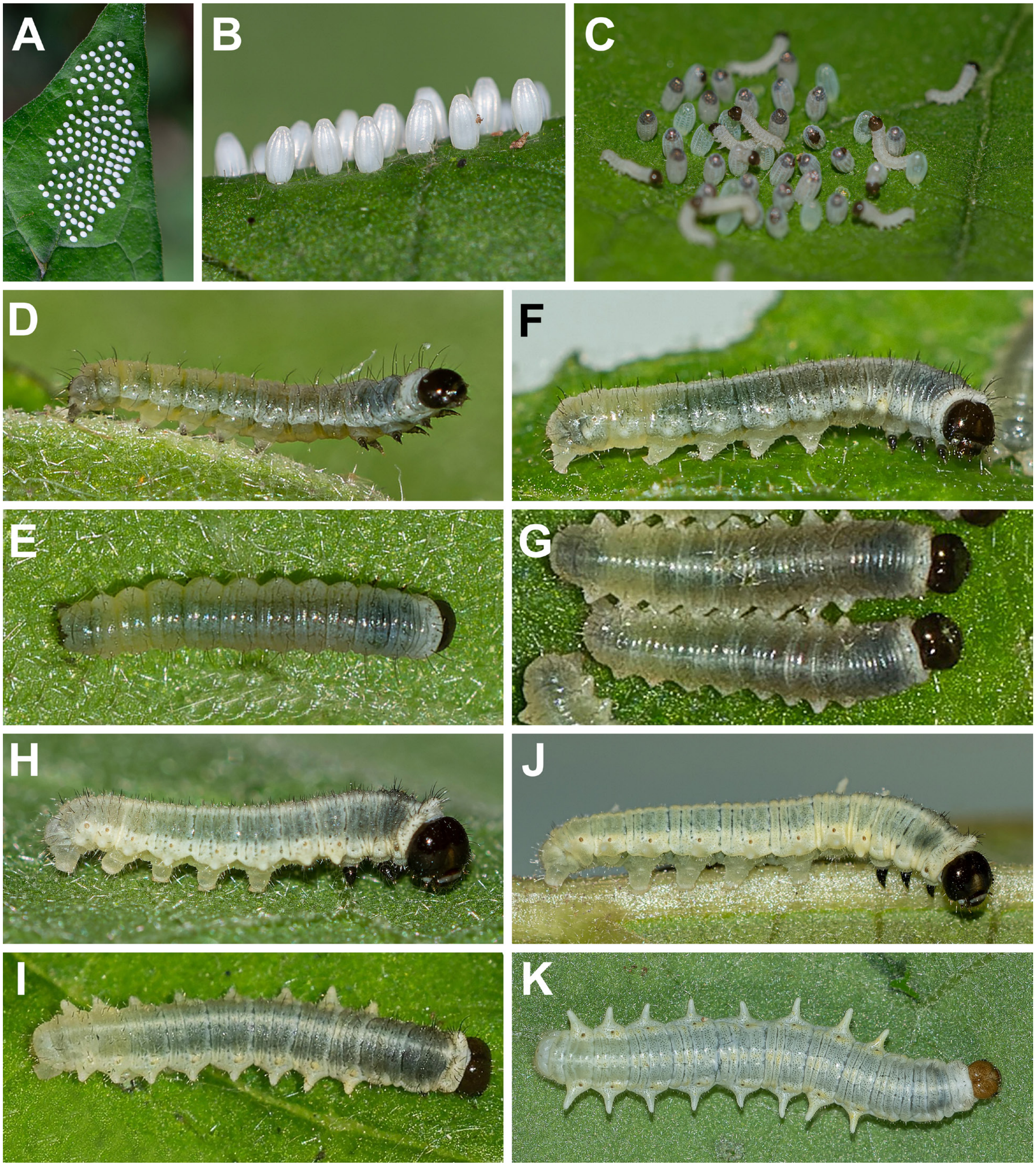

Figure 2. Immature stages of *Mechanitis lysimnia nesaea* from Parque Estadual Dois Irmãos, Recife, Pernambuco, Brazil. **A, B.** oviposition pattern; **C**. a newly hatched clutch of eggs with first instars consuming the eggshells; **D, E.** first instar (lateral, dorsal); **F, G.** second instar (lateral, dorsal); **H, I.** third instar (lateral, dorsal); **J, K.** fourth instar (lateral, dorsal).

Adult behavior

Adults remain in the dark forest interior most of the day. In the early morning, males can be observed flying in sunny clearings and forest edges visiting flowers, and females search these same open habitats in warm hours of the day for host plants (Fig. 1E). Adults fly low, near the ground from 30 cm to 1.5 m. They can be locally abundant, forming large groups in wet areas inside the forest described as "ithomiine pockets", which usually contain other sympatric tiger-patterned ithomiine co-mimics such as *Hypothyris ninonia daetina* (Weymer, 1899) and *Hypothyris euclea laphria* (E. Doubleday, 1847). Larger co-mimics in the pockets include the nymphalids *Lycorea halia discreta* Haensch, 1909 (Danainae, Danaini), *Heliconius ethilla flavomaculatus* Weymer, 1894 and *Eueides isabella dianasa* (Hübner, 1806) (Heliconiinae, Heliconiini). *Mechanitis lysimnia nesaea* is multivoltine, with adults flying all year round. Mating pairs (Fig. 1F) were only observed in the forest interior.

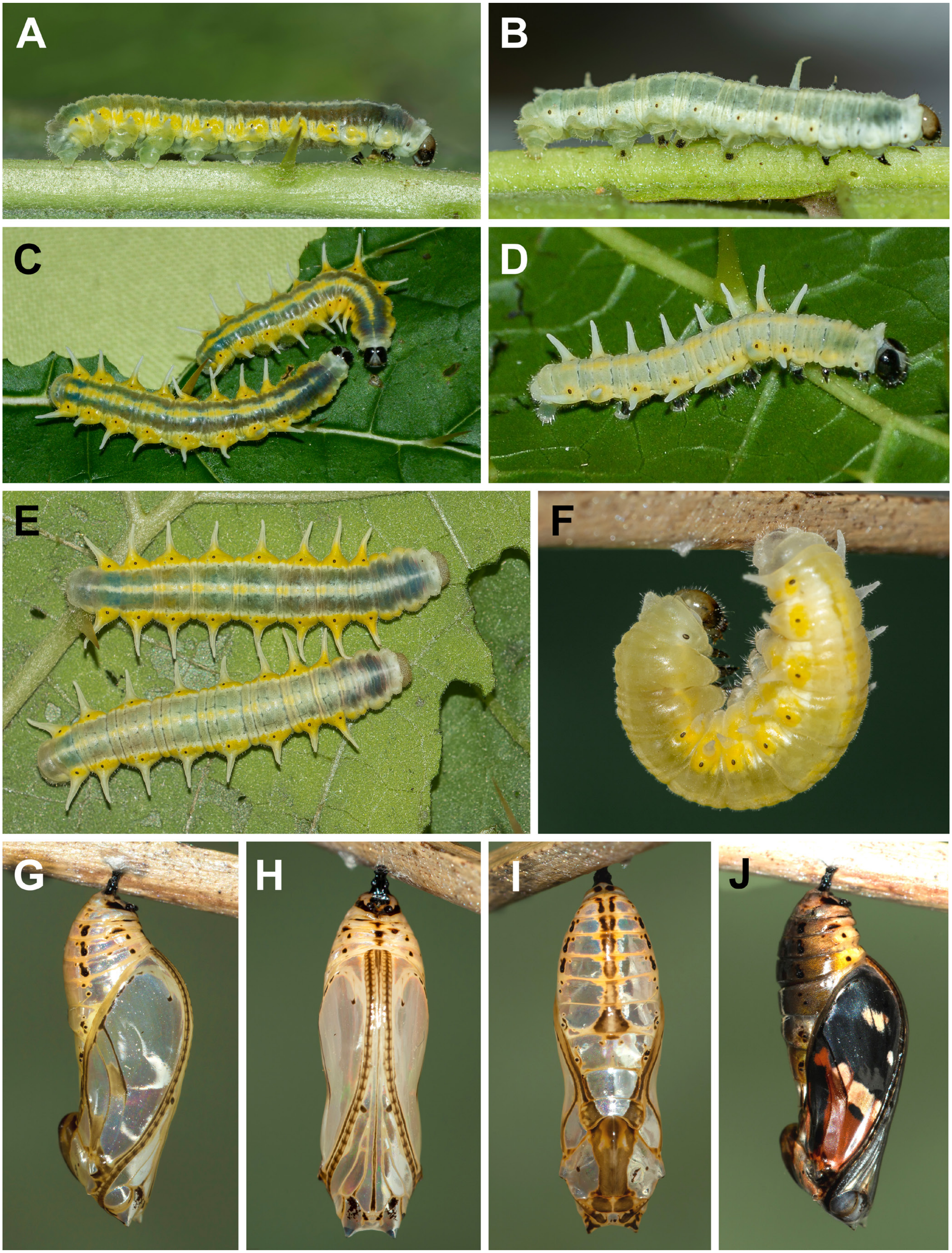

Figure 3. Immature stages of *Mechanitis lysimnia nesaea* from Parque Estadual Dois Irmãos, Recife, Pernambuco, Brazil. **A, B.** fifth (last) instars, lateral view; **C, D, E.** Fifth (last) instars, dorsal view; **F.** pre pupa; **G, H, I.** pupa (lateral, ventral, dorsal, respectively); **J.** pupa near eclosion.

DISCUSSION

All life stages of *M. lysimnia nesaea* are similar to those of other known *Mechanitis*, including the tall, ellipsoid eggs, laid in clusters on the upper leaf surface of the host plants, the larvae being gregarious in all instars, the pair of short dorsolateral protuberances on the prothorax and the presence of long fleshy lateral projections on the abdominal segments (Brown & Freitas, 1994; Motta, 1989; Giraldo & Uribe, 2010a,b, 2012; Anteparra *et al*., 2011; Hill *et al*., 2012; Giraldo *et al*., 2014; Ruiz *et al*., 2015; Carvalho *et al*., 2019; Santacruz *et al.*, 2019). The lateral abdominal projections are one of the clear synapomorphies of the subtribe Mechanitina (Willmott & Freitas, 2006), but only in *Mechanitis* are they long and pointed in the last instar; they are short in *Thyridia* Hübner, 1816, *Sais* Hübner, 1816, and *Scada* Kirby, 1871, and can be short or absent in *Forbestra* R. Fox, 1967 (Brown & Freitas, 1994; Freitas & Brown, 2002; Brévignon, 2003; Hill, 2006; Carvalho *et al*. 2019; Freitas *et al*., 2020). The paired, short, dorsolateral protuberances on the prothorax are present in all known *Mechanitis* and in *Forbestra olivencia* and can be considered a synapomorphy of the clade *Forbestra* + *Mechanitis*, with a possible loss in *F. equicola* (Brévignon, 2003). However, these structures are relatively shorter in *M. lysimnia nesaea* and *M. lysimnia lysimnia* compared to other species of *Mechanitis* (see references above).

The eggs of *M. lysimnia nesaea* have 10-11 horizontal ridges, fewer than *M. polymnia casabranca* (13-16 ridges, Carvalho *et al*., 2019; Motta, 1989), *M. polymnia caucaensis* (about 14 ridges, Giraldo & Uribe, 2010a), and *M. polymnia* ca. *dorissides* (11-13 ridges in a population from Acre, north Brazil, AVLF pers. obs.). The number is lower than that observed in *M. lysimnia lysimnia* in southeastern Brazil (15-16 ridges, Motta, 1989; AVLF pers. obs.) and *Mechanitis lysimnia elisa* (18 ridges, Ajmat-de Toledo & Terán, 1970). Concerning the vertical ridges, the pattern is not the same: these comprise 12-14 in *M. lysimnia nesaea* (present study), fewer than *M. lysimnia elisa* (15 ridges, Ajmat-de Toledo & Terán, 1970) and *M. menapis* (13-15 ridges, Giraldo & Uribe, 2010b; Santacruz *et al.* 2019). However, in this case the number of vertical ridges is similar to that reported for *M. lysimnia lysimnia* (13-14 ridges; AVLF pers. obs.), *M. polymnia casabranca* (13-14 ridges, Carvalho *et al*., 2019; Motta, 1989), and higher than reported for *M. polymnia* ca. *dorissides* (11-13 ridges, AVLF pers. obs.), *M. mazaeus* and *M. messenoides* (10-14 ridges for both species, with averages of 11.7 and 12.0 ridges, respectively; R. Hill, pers. comm.).

Comparison of known *Mechanitis* immature stages clarifies similarities and highlights differences. Compared to other species and populations of *Mechanitis*, fifth instars of *M. lysimnia nesaea* are very distinct from those of *Mechanitis polymnia* (Linnaeus, 1758), whose larvae present a light gray body and brown head capsule (Giraldo & Uribe, 2010a; Anteparra *et al*., 2011; Ruiz *et al*., 2015; Carvalho *et al*., 2019). Conversely, in these two respects, fifth instars of *M. lysimnia nesaea* are more similar to those of *Mechanitis menapis* Hewitson, [1856], *Mechanitis mazaeus* Hewitson, 1860, *Mechanitis messenoides* C. Felder & R. Felder, 1865, and the nominal subspecies, *M. lysimnia lysimnia* (Fabricius, 1793), with the body more richly colored and head capsules predominantly black or cream with black areas (D'Almeida, 1922; Giraldo & Uribe, 2010b, 2012; Giraldo *et al*., 2014; Hill *et al*., 2012; Santacruz *et al*., 2019; AVLF unpublished). However, the variation in the color of the head capsule in the fourth and fifth instar of *M. lysimnia nesaea* is interesting and distinguishes it from the nominal subspecies, where such variation has never been reported (D'Almeida, 1922; AVLF, unpublished). These differences are equivalent to the species-level differences reported among other species of *Mechanitis*, and this is an interesting topic for future research. The lateral abdominal projections also vary in relative size in the different species of *Mechanitis*, being longer in *M. menapis* (Giraldo *et al*., 2010b; Santacruz *et al.*, 2019) and comparatively short in *M. mazaeus* (Hill *et al*., 2012), whereas in *M. polymnia*, and *M. messenoides*, *M. lysimnia lysimnia* and *M. lysimnia nesaea* they are more intermediate in length (Giraldo & Uribe, 2010a; Hill *et al*., 2012; Carvalho *et al*., 2019, present study and AVLF unpublished). The paired short dorsolateral protuberances on the prothorax are relatively shorter in *M. lysimnia nesaea* and *M. lysimnia lysimnia* compared to other species of *Mechanitis* (see references above).

As indicated with the addition of *M. lysimnia nesaea* here and as previously mentioned by Carvalho *et al*. (2019), comparative studies of immature stages could gain in robustness as more species, subspecies, and populations are described in detail. Previous studies have shown that the ultrastructure of eggs and first instar larvae, for example, are broadly informative at the species level in Danainae (Motta, 1989, 2003; Kitching, 1984, 1985), and other aspects of immature stages have been informative for clarifying species differences (Hill *et al*., 2012). For example, study of the immature stages of sympatric *Mechanitis* revealed differences in clutch size, larval host plant use, and fifth instar morphology in *M. messenoides* and *M. mazaeus*, clarifying their species status. Thus, knowledge about additional subspecies and populations could help to understand the species limits within the several non-monophyletic species of *Mechanitis* revealed by molecular evidence, as shown by Hill *et al*. (2012) and Giraldo & Uribe (2012). Accordingly, the detailed description of life stages of more subspecies and populations of *Mechanitis*, especially the nominal subspecies, could provide valuable data to better understand the taxonomy and species limits of this iconic ithomiine genus.

ACKNOWLEDGMENTS

We are indebted to all the staff of the "Parque Estadual Dois Irmãos" for allowing research in the area. AVLF thanks the CNPq (process304291/2020-0) and the National Science Foundation (DEB-1256742). Carlos E. Giraldo and Ryan Hill read the manuscript and made valuable suggestions that improved the final text. This publication is part of the RedeLep 'Rede Nacional de Pesquisa e Conservação de Lepidópteros' SISBIOTABrasil/ CNPq (563332/2010-7), and of the BIOTA-FAPESP Program (grants 2011/50225-3 and 2021/03868-8). The present study is registered at the SISGEN (A59BC58).

LITERATURE CITED

Ajmat de Toledo, Z. D., Terán, H. 1970. Fauna del noroeste argentino - contribución al conocimiento de los lepidópteros Argentinos I. *Mechanitis lysimnia elisa* (Guérin-Méneville) (Rhopalocera - Ithomiidae). *Acta Zoologica Lilloana* 26: 33-48.

Anteparra, M. E., Ayvar, J. C., Granados, L. B. 2011. Algunos aspectos sobre la biología de *Mechanitis polymnia proceriformis* Bryk, 1953 (Lepidoptera: Nymphalidae) asociado con la cocona (Solanum sessiliflorum Dunal) en Tingo María. *Aporte Santiaguino* 4(1): 64-74.

Beccaloni, G. W. 1997. Ecology, natural history and behaviour of ithomiine butterflies and their mimics in Ecuador (Lepidoptera: Nymphalidae: Ithomiinae). *Tropical Lepidoptera* 8: 103-124.

Beccaloni, G. W., Viloria, Á. L., Hall, S. K, Robinson, G. S. 2008. *Catalogue of the host plants of the Neotropical butterflies. Catálogo de las plantas huésped de las mariposas neotropicales.* Zaragoza, Sociedad Entomológica Aragonesa. (Monografías del Tercer Milenio, Vol. 8). 536 pp.

Brévignon, C. 2003. Inventaire des Ithomiinae de Guyane Française (Lepidoptera, Nymphalidae). *Lambillionea* 103: 41-58.

Brower, A. V. Z., Freitas, A. V. L., Lee, M. -M., Silva-Brandão, K. L., Whinnett, A., Willmott, K. R. 2006. Phylogenetic relationships among the Ithomiini (Lepidoptera: Nymphalidae) inferred from one mitochondrial and two nuclear gene regions. *Systematic Entomology* 31: 288-301.

Brower, A. V. Z., Willmott, K. R., Silva-Brandão, K. L., Garzón-Orduña, I. J., Freitas, A. V. L. 2014. Phylogenetic relationships of ithomiine butterflies (Lepidoptera: Nymphalidae: Danainae) as implied by combined morphological and molecular data. *Systematics and Biodiversity* 12(2): 133-147.

Brown Jr., K. S. 1977. Geographical patterns of evolution in Neotropical Lepidoptera: differentiation of the species of *Melinaea* and *Mechanitis* (Nymphalidae: Ithomiinae). *Systematic Entomology* 2: 161-197.

Brown Jr., K. S. 1979. *Ecologia Geográfica e Evolução nas Florestas Neotropicais.* PhD Thesis. Campinas, Universidade Estadual de Campinas. xxxi + 385 p.

Brown Jr., K. S., Benson, W. W. 1974. Adaptive polymorphism associated with multiple Müllerian mimicry in *Heliconius numata* (Lepid. Nymph.). *Biotropica* 6: 205-228.

Brown Jr., K. S., Freitas, A. V. L. 1994. Juvenile stages of Ithomiinae: overview and systematics. *Tropical Lepidoptera* 5(1): 9-20.

Carvalho, M. R. M., Barbosa, E. P., Freitas, A. V. L. 2019. Immature stages of *Mechanitis polymnia casabranca* (Nymphalidae, Danainae). *Tropical Lepidoptera Research* 19(1): 12-18.

D'Almeida, R. F. 1922. *Mélanges lépidoptérologiques. Études sur les lépidoptères du Brésil*. Berlin, R. Friedländer & Sohn. viii + 226 pp.

Dasmahapatra, K. K., Elias, M. E., Hill, R., Hoffman, J. I., Mallet, J. 2010. Mitochondrial DNA barcoding detects some species that are real, and some that are not. *Molecular Ecology Resources* 10: 264-273.

Drummond, B. A., Brown Jr., K. S. 1987. Ithomiinae (Lepidoptera: Nymphalidae): summary of known larval food plants. *Annals of the Missouri Botanical Garden* 74: 341-358.

Fox, R. M. 1967. A monograph of the Ithomiidae (Lepidoptera) Part III The tribe Mechanitini Fox. *Memoirs of the American Entomological Society* 22: 1-190.

Freitas, A. V. L., Brown Jr., K. S. 2002. Immature stages of *Sais rosalia* (Nymphalidae, Ithomiinae). *Journal of the Lepidopterists' Society* 56: 104-106.

Freitas, A. V. L., Rosa, A. H. B., Nobre, C. E. B., Melo, D. H. A., Mota, L. L., Silva-Brandão, K. L., Machado, P. A., Carreira, J. Y. O. 2020. Immature stages, natural history, systematics and conservation of an endangered Neotropical butterfly: the case of *Scada karschina delicata* (Nymphalidae: Ithomiini). *Neotropical Entomology* 49: 685-695.

Garzón-Orduña, I. J., Silva-Brandão, K. L., Willmott, K. R., Freitas, A. V. L., Brower, A. V. Z. 2015. Incompatible ages for clearwing butterflies based on alternative secondary calibrations. *Systematic Biology* 64(5): 752-767

Giraldo, C. E., Uribe, S. I. 2010a. Registro de *Mechanitis polymnia* (Lepidoptera: Ithomiinae) en *Solanum jamaicense* y ciclo de vida en laboratorio. *Revista Colombiana de Entomología* 36(1): 165-168.

Giraldo, C. E., Uribe, S. I. 2010b. *Solanum hirtum* as a host plant for *Mechanitis menapis menapis* (Lepidoptera: Ithomiinae) in Colombia. *Revista Colombiana de Entomología* 36(1): 169-171.

Giraldo, C. E., Uribe, S. I. 2012. Taxonomy of *Mechanitis* (F.) (Lepidoptera, Nymphalidae) from the west Colombian Andes: an integrative approach. *Neotropical Entomology* 41: 472-484.

Giraldo, C. E., Ramírez-Restrepo, L., Escobar, F., Uribe, S. I. 2014. Life cycle and host plants of *Mechanitis menapis doryssus* (Danainae: Ithomiini) in Mexico. *Southwestern Entomologist* 39(4): 761-771.

Hill, R. I. 2006. Life history and biology of *Forbestra olivencia* (Bates, 1862) (Nymphalidae, Ithomiinae). *Journal of the Lepidopterists' Society* 60: 203-210.

Hill, R. I., Elias, M., Dasmahapatra, K. K., Jiggins, C. D., Koong, V., Willmott, K. R., Mallet, J. 2012. Ecologically relevant cryptic species in the highly polymorphic Amazonian butterfly *Mechanitis mazaeus s.l.* (Lepidoptera: Nymphalidae; Ithomiini). *Biological Journal of the Linnean Society* 106: 540-560.

Kerpel, S., Zacca, T., Nobre, C. E. B., Júnior, A. F., Xavier, M., Fonseca, A. 2014. *Borboletas do Semiárido, conhecimento atual e contribuições do PPBio*, pp. 245-275. *In*: Bravo, F., Calor, A. (Eds.), *Artrópodes do Semi-Árido: biodiversidade e conservação*. Feira de Santana, Printmídia.

Kesselring, J., Ebert, H. 1979. Relação das borboletas encontradas na "Mata do Buraquinho", João Pessoa, Estado da Paraíba, Brasil. *Revista Nordestina de Biologia* 2: 105-118.

Kitching, I. J. 1984. The use of larval chaetotaxy in butterfly systematics, with special reference to the Danaini (Lepidoptera: Nymphalidae). *Systematic Entomology* 9: 49-61.

Kitching, I. J. 1985. Early stages and classification of the milkweed butterflies (Lepidoptera: Danainae). *Zoological Journal of the Linnean Society* 85: 1-97.

Lamas, G. 1987. The identity of *Mechanitis doryssus* Bates and *M. saturata* Godman (Lepidoptera: Nymphalidae; Ithomiinae). *Revista Peruana de Entomología* 30: 48-50.

Lamas, G. (Ed.) 2004. *Ithomiinae*, pp. 172-191. *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.

Melo, D. H. A., M. Duarte, O. H. H. Mielke, R. K. Robbins, Freitas, A. V. L. 2019. Butterflies (Lepidoptera: Papilionoidea) of an urban park in northeastern Brazil. *Biota Neotropica* 19(1): e20180614.

Mota, L. L., Vasconcellos, L. R., Willmott, K. R., Freitas, A. V. L. 2022. A new subspecies of *Mechanitis lysimnia* from southern Amazonia (Nymphalidae: Danainae: Ithomiini). *Tropical Lepidoptera Research* 32(1): 47-51.

Motta, P. C. 1989. *Análise filogenética de Ithomiinae (Lep.: Nymphalidae) com base nos ovos: Relação com plantas hospedeiras*. MSc Dissertation. Campinas, Universidade Estadual de Campinas.

Motta, P. C. 2003. *Phylogenetic relationships of Ithomiinae based on first-instar larvae*, pp. 409-429. *In*: Boggs, C., Ehrlich, P., Watt, W.B. (Eds.), *Butterflies: Ecology and Evolution Taking Flight.* Chicago, Chicago University Press.

Nobre, C. E. B., Schlindwein, C., Mielke, O. H. H. 2008. The butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of the Catimbau National Park, Pernambuco, Brazil. *Zootaxa* 1751: 35-45.

Paluch, M., Mielke, O. H. H., Nobre, C. E. B., Casagrande, M. M., Melo, D. H. A., Freitas, A. V. L. 2011. Butterflies (Lepidoptera: Papilionoidea and Hesperioidea) of the Parque Ecológico João Vasconcelos Sobrinho, Caruaru, Pernambuco, Brazil. *Biota Neotropica* 11(4): 229-238.

Ruiz, E., Vásquez, J., Zárate, R., Pinedo, J. 2015. Aspectos biológicos de *Morpho helenor theodorus* (Fruhstorfer) (Lepidoptera: Nymphalidae; Morphinae) y *Mechanitis polymnia* (Linnaeus), (Lepidoptera: Nymphalidae; Ithomiinae), en la Amazonía baja del Perú. *Folia Amazónica* 24(1): 45-54.

Santacruz, P. G., Despand, E., Giraldo, C. E. 2019. Ciclo de vida y enemigos naturales de *Mechanitis menapis* (Lepidoptera: Ithomiini)**.** *Revista de Biología Tropical* 67(6): 1488-1504.

Warren, A. D., Davis, K. J., Stangeland, E. M., Pelham, J. P., Grishin, N. V. 2019. *Illustrated Lists of American Butterflies.* http://www.butterfliesofamerica.com. Accessed November 2022.

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(4): 297-368.

Zacca, T., Bravo, F. 2012. Borboletas (Lepidoptera: Papilionoidea e Hesperioidea) da porção norte da Chapada Diamantina, Bahia, Brasil. *Biota Neotropica* 12(2). https://doi.org/10.1590/S1676-06032012000200012.