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RESEARCH

Larval Biology of Anthophagous Eumaeini (Lepidoptera: Lycaenidae, Theclinae) in the Cerrado of Central Brazil

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ABSTRACT. The biology and morphology of the early stages of 22 species of Eumaeini (Lepidoptera: Lycaenidae, Theclinae) are presented. Observations were collected through the inspection of inflorescences in the field and the rearing of 214 larvae in laboratory. *Allosmaitia strophius* (Godart) associated with Malpighiaceae species and the polyphagous *Strymon mulucha* (Hewitson) were the most frequently collected species. Detritivory was observed in two species, *Electrostrymon endymion* (F.) and *Kisutam syllis* (Godman & Salvin), and myrmecophily in four other species, *A. strophius*, *Ministrymon azia* (Hewitson), *Parrhasius polibetes* (Stoll), and *S. mulucha*. Cannibalism was observed in *A. strophius*; in addition, the pupa of this and of three other species produced audible sounds. *Paiwarria aphaca* (Hewitson) was highlighted because of the great difference observed between its first and last instars, as well as the marked difference between that species and the larvae of *Paiwarria umbratus* (Geyer) documented in Costa Rica. Larvae of *Calycopis mimas* (Godman & Salvin) displayed "bungee jumping" behavior when stimulated. Parasitoids (Diptera, Hymenoptera) attacked 21 larvae of eight species, *A. strophius*, *K. syllis*, *M. azia*, *Pai. aphaca*, *P. polibetes*, *Rekoa marius* (Lucas), *S. mulucha*, and *Tmolus venustus* (H.H. Druce). Illustrations of immatures and parasitoids are provided.

Key Words: inflorescences, caterpillar, morphology, detritivory, cannibalism

The tribe Eumaeini (Theclinae) is one of the most diverse groups of Lycaenidae (Lepidoptera), comprising >1,000 known species in the Neotropical region, the majority occurring in South America (Robbins 2004a). Eumaeini larvae are commonly anthophagous but can also be found in young leaves and fallen flowers and fruits (D'Araújo e Silva et al. 1968; Chew and Robbins 1984; Fiedler 1995; Calvo 1998; Feinstein et al. 2007; Duarte and Robbins 2010; Silva et al. 2011). The larvae of several species are cryptically polychromatic (Monteiro 1991). Myrmecophilic associations are documented for many of these Lepidoptera (Malicky 1970, Ballmer and Pratt 1988, Monteiro 1990, DeVries 1990, Fiedler 1991, Duarte et al. 2005, Kaminski and Freitas 2010).

Because of the extraordinary species richness of Eumaeini, the taxonomy of many species is still unclear. Butterflies of this group exhibit intraspecific variations (geographical and phenological), which, in combination with interspecific similarities observed in some genera (e.g., *Calycopis*, see also Duarte and Robbins 2010), make them a group with interesting questions despite the difficulties of identification (Robbins and Aiello 1982, Robbins 1991a, Robbins and Duarte 2005, Lamas 2006, Robbins 2010a). Knowledge of the biology and morphology of immature stages can provide vital information to clarify some taxonomic issues (Duarte et al. 2005). For example, for some genera reviewed, the biogeography and use of certain resources by larvae plus adult behavior have been used to organize species into certain groups (Nicolay and Robbins 2005, Duarte and Robbins 2010, Robbins 2010b).

Although, the importance of information on immature stages for resolving taxonomic and phylogenetic groups has been established (Duarte et al. 2005, Duarte and Robbins 2010), such data are generally unavailable, especially in the Neotropics, which has the highest richness of these species (Calvo 1998, Pierce et al. 2002, Robbins 2004a, Duarte and Robbins 2009, Badenes-Pérez et al. 2010, Kaminski et al. 2012).

Here, we present morphological and biological data on Eumaeini larvae obtained from inflorescences in central Brazilian Cerrado. Illustrations of the larvae are provided and can be used as a field guide to assist data collection, which usually requires significant effort (Silva et al. 2011). The information presented in this study is the first data obtained in situ as regards the biology of the majority of the included species. The data provided have not been standardized for all species nevertheless it can be regarded as necessary first step to a better understanding of the Cerrado fauna and is a rich source for the development of further research.

Materials and Methods

The study took place at the Fazenda Água Limpa (FAL) (15° 55′ S, 47° 55′ W) with occasional data also being obtained at the Reserva Ecológica do Roncador of Instituto Brasileiro de Geografia e Estatística (RECOR/IBGE) (15° 56′ S, 47° 53′ W) and in fragments of Cerrado which forms part of the campus of the Universidade de Brasília (UnB) (15° 46′ S, 47° 50′ W), Distrito Federal (DF), Brazil. FAL is an experimental farm of the UnB and forms part of the 20,000 ha Gama and Cabeça de Veado Environmental Protection Area. The region, at an altitude of ∼1,050 m, has two clearly defined seasons, one dry (May to September) and the other wet (October to April), with a mean annual temperature of 22°C and mean annual precipitation of 1,417 mm (RECOR/ Reserva Ecológica do Roncador 2005).

The Cerrado biome covers a range of plant communities from practically treeless grasslands to heavily forested areas, including gallery forests surrounding riparian zones (Goodland 1971, Eiten 1972, Furley 1999, Oliveira-Filho and Ratter 2002).

Larvae were collected in areas of Cerrado sensu stricto and "campo sujo" vegetation (Cerrado grasslands), which are common vegetation physiognomies at the FAL (Ratter 1980, Munhoz and Felfili 2005). The campo sujo are predominantly herbaceous but may also contain several shrubs and semishrubs with an "herb-like" appearance; the woody

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Table 1. List of anthophagous Eumaeini butterflies (Lepidoptera: Lycaenidae, Theclinae) from the Cerrado of central Brazil, including information about number of eggs, larvae, and adults reared under laboratory conditions, with the period of the year when immatures were collected/observed in the field

Eumaeini species	No. of eggs and larvae	No. of parasitized individuals	No. of individuals not reaching the adult stage	No. of individuals reaching the adult stage	Month
A. strophius	66	7	13	46	April to Nov.
Ca. mimas	1	0	0	1	Feb.
C. telea	2	0	0	2	May, June, and Sept.
Cy. herodotus	5	0	0	5	May to Oct.
E. endymion	1	0	0	1	Dec.
Erora aff. *gabina*	3	0	0	3	Aug. to Oct. and Dec.
K. syllis	6	1	0	5	Dec. and Jan.
Ko. ergina	2	0	1	1	Mar., May, June, Aug., and Nov.
Mich. thordesa	1	0	0	1	Aug. and Oct.
M. azia	23	1	3	19	Jan. to Mar.
N. socia	1	0	0	1	May, Mar., and June to Oct.
O. empusa	2	0	0	2	May to Aug., and Oct.
Pai. aphaca	9	3	5	1	Mar., May, and Aug.
P. polibetes	22	4	2	16	April to Feb.
R. marius	5	1	0	4	June to Sept., and Dec.
R. palegon	5	0	1	4	April, May, July, and Nov.
S. bazochii	8	0	0	8	Aug.
S. bubastus	1	0	0	1	July
S. cyanofusca	5	0	0	5	July
S. crambusa	1	0	0	1	Aug.
S. mulucha	37	3	1	33	Mar. to Nov.
T. venustus	8	1	0	7	April and June to Aug.
Total	214	21	26	167	Jan. to Dec.

forms frequently occupy <2% of total vegetational cover. Woody savannahs with 15–30% tree cover are referred to as Cerrado sensu stricto. In these two vegetation physiognomies, flowering occurs throughout the year (Oliveira and Gibbs 2002, Munhoz and Felfili 2006).

Between March 2009 and December 2010, usually between 0900 h and 1200 h, inflorescences in the study areas were examined for Lycaenidae eggs and larvae after first inspecting the structures for the presence of ants. Very crowded inflorescences were collected for closer inspection in the laboratory. The eggs and larvae found on inflorescences were reared without temperature or humidity control in individual plastic containers. The peduncle of those inflorescences hosting an egg or larva was inserted into a small glass vial containing water, sealed with plastic wrap to prevent larvae drowning. This setup was placed in a plastic pot lined with paper towel and protected by a thin cloth. Larvae were supplied with inflorescences of the host plant ad libitum, noting their preference for buds or flowers. The immature stages and the parasitoids were photographed using a Canon Powershot A95 and Powershot SX20 digital cameras (Lake Success, NY). Images of the eggs and initial larval instars were taken with the camera attached to the stereomicroscope.

Observations on larval behavior were recorded at the time of collection and during periodic inspections of the rearing pots. Morphological features were observed under a stereomicroscope. Parasitoids of larvae and pupae were stored in 70% alcohol, as were ants found in association with larvae at the time of collection. Larvae that died during the rearing process were preserved following the procedure described by Duarte et al. (2005). Voucher specimens of both immatures and adults were deposited in the Coleção Entomológica do Departamento de Zoologia, UnB, and in the Lepidoptera collection of the Museu de Zoologia da Universidade de São Paulo. The taxonomic nomenclature follows Robbins (2004b).

Results

Inflorescences examined at the study sites resulted in 214 larvae distributed among 22 Eumaeini (Theclinae) species being collected and reared in the laboratory (Table 1). Eggs and larvae were found in 36 species from 18 botanical families, especially Malpighiaceae and Fabaceae, which were common in the study areas. Data concerning these host plants and other Theclinae species of the Cerrado of central Brazil are available in Silva et al. (2011).

During larval rearing, 15 larvae perished, mostly during egg eclosion. Five were preserved according to standard procedures to provide specimens for reference, two suffered cannibalism, and four were pupae from which adults did not emerge. Parasitoids (Diptera and Hymenoptera) attacked 21 larvae of eight species, which corresponded to 10% of total larvae collected. In total, 167 adults were successful reared in the laboratory.

It was not possible to determine the number of larval instars in this study, but it has been considered, and it is almost a common sense among the specialists, to be four instars in most Eumaeini, with some exceptions known in species of *Callophrys* Westwood (subgenus *Mitoura* Scudder) with five to seven instars and of *Calycopis* Scudder with five instars (Ballmer and Pratt 1988, Duarte et al. 2005, Duarte and Robbins 2009, respectively). To inform the periods of occurrence of the larvae in the study areas, data from previous collections were also included (Table 1; see also Silva et al. 2011).

General Biological and Morphological Aspects of the Eumaeini Immatures in the Cerrado. Eggs and larvae were found in isolation on inflorescences. Four species were observed interacting with ants (Formicidae: Myrmicinae, Formicinae): *Allosmaitia strophius* (Godart), *Ministrymon azia* (Hewitson), *Parrhasius polibetes* (Stoll), and *Strymon mulucha* (Hewitson). In most of the final-instar larvae reported in this study, the opening of the dorsal nectary organ (DNO) in the seventh abdominal segment (A7) and nearby pore cupola organs (PCOs) were observed under a stereomicroscope (e.g., Fig. 3D and E). In Lycaenid larvae, these appear to be the primary organs related to myrmecophily with the addition of the dendritic setae on the tegument of some species (Malicky 1970; Ballmer and Pratt 1988, 1991; Duarte et al. 2001, 2005). In this study, the presence of the DNO is cited for the first time in *Chlorostrymon telea* (Hewitson), *Cyanophrys herodotus* (F.), *Kisutam syllis* (Godman & Salvin), *M. azia*, *Nicolaea socia* (Hewitson), *Strymon crambusa* (Hewitson), *Strymon cyanofusca* K. Johnson, Eisele & MacPherson, *Ostrinotes empusa* (Hewitson), and

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Table 2. Summary of 22 anthophagous Eumaeini species from the Cerrado of central Brazil with notes on their adaptations related to myrmecophily

Species	Myrmecophilic adaptation	References
A. strophius	DNO, PCOs, dendritic setae	Kaminski and Freitas (2010)
Ca. mimas	Not observed	None
C. telea	DNO, PCOs	Present study
Cy. herodotus	DNO	Present study
E. endymion	Not observed	None
Erora aff. *gabina*	Not observed	None
K. syllis	DNO	Present study
Ko. ergina	DNO absent	Present study; L. A. Kaminski (unpublished data)
Mich. thordesa	DNO, PCOs	Present study; Kaminski et al. (2010b)
M. azia	DNO	Present study
N. socia	DNO	Present study
O. empusa	DNO	Present study
Pai. aphaca	Not observed	None
P. polibetes	DNO, PCOs	Kaminski et al. (2012)
R. marius	DNO, PCOs	Monteiro (1991)
R. palegon	DNO, PCOs	Monteiro (1991)
S. bazochii	Not observed	None
S. bubastus	Not observed	None
S. cyanofusca	DNO, PCOs	Present study
S. crambusa	DNO, PCOs	Present study
S. mulucha	DNO, PCOs	Present study; Monteiro (1990)
T. venustus	DNO, PCOs	Present study

Tmolus venustus (H.H. Druce) (Table 2). It is noteworthy to mention that it was not performed scanning electron microscopy to observe the presence of dendritic setae or others organs in these larvae.

During feeding, the larvae commonly moved only their head, with the rest of the body remained practically motionless. Feeding activity also occurred during the night. During locomotion, the larvae left traces of silk on the plant (Fig. 14D), and a fine-silk mesh was also deposited on the wall of the rearing container, as observed in *A. strophius*, *Cy. herodotus*, *K. syllis*, *Michaelus thordesa* (Hewitson), *P. polibetes*, *Rekoa marius* (Lucas), and *S. mulucha*.

Several early-instar larvae (L1–L2) exhibited different characteristics from later instars. In general, larvae chromatism was variable, reflecting the color of the inflorescence consumed (polychromatism is diet induced according to Monteiro 1991). A more uniform species-specific coloration was typically acquired during pupation. When the pupation site was chosen, a silk mesh was woven on the substrate, on which pupae generally remained immobile until metamorphosis occurred. Pupae have a general appearance that is common to Eumaeini, and most remained ventrally attached to the silk mesh connected by a silk girdle between the first- and second-abdominal segments (A1, A2) and the cremaster on the ventral region (details Duarte et al. 2005). No pupae were found during collections in the study sites, with exception to *Rekoa palegon* (Cramer) on *Lantana* L. (Verbenaceae) inflorescence collected in the campus. The adults showed typical coloration regardless of the larval coloration.

A. strophius (Godart). Sixty-six larvae were collected, the majority ($N = 21$) on *Peixotoa goiana* C. E. Anderson (Malpighiaceae) (see also Silva et al. 2011). Eggs were found (Fig. 1A) deposited at the base of closed buds and on the peduncle of inflorescences. *A. strophius* was only recorded on Malpighiaceae inflorescences. In fact, all larval food plant records for *Allosmaitia* Clench are in this family (Dewitz 1879, Gundlach 1881, Armas 2004, Kaminski and Freitas 2010). According to Kaminski and Freitas (2010), the development period of *A. strophius* from egg to adult is <40 d with four larval instars. The behavior of larvae in inflorescences is also in agreement with the description of these authors. The larvae (Fig. 1B–D) pierce and consume the interior of the buds, or possibly the entire bud, as well as flowers and young fruits. The results from this study differed from those in Kaminski and Freitas (2010); five larvae were observed in the field interacting with ants: *Camponotus* Mayr (Formicinae) and *Crematogaster* Lund (Myrmicinae) but no observations included exudates emission by larvae. One larva was parasitized by a fly (Diptera: Tachinidae) (Fig. 23Q). This larva and larvae of *S. mulucha*, both species foraging on *Heteropteris* sp. (Malpighiaceae), were attended by a single ant (*Camponotus* sp.) (Figs. 1C and 21L). *A. strophius* larvae hosted the braconid *Rogas* Nees (Hymenoptera: Braconidae, Rogadinae) (Fig. 23E and F), with adults emerging from the host body during molting from second to third instar; a species of *Conura* Spinola (Hymenoptera: Chalcididae) emerged from pupae after 31 ± 6.8 d from formation ($N = 3$) (Fig. 23C and D), and a species of Ichneumoninae (Hymenoptera: Ichneumonidae) emerged 27 d after pupal formation (Fig. 23A and B). Cannibalism was observed in two occasions, when larvae were kept in groups of two individuals in the same rearing container. Attacks seemed to occur on the most vulnerable individuals in prepupal and pupal phases. The predacious larva attacked the prepupa in the region of the DNO and fed accordingly from the inside through a circular hole (Fig. 1D). In the case of predation of pupae, most likely due to the restricted food source, the interior of the pupa was totally consumed by the larva via a large side opening (Fig. 1E). The adult cannibal larva emerged noticeably smaller than noncannibals. There is no information about the formation of the pupa in the natural environment, but in the laboratory, pupation tended to occur both on the inflorescence and on the wall of the rearing container, head uppermost. Two pupae emitted an intermittent noise when the container was moved. Kaminski and Freitas (2010) document details of the stridulation area (Fig. 1F) but did not comment on the production of sound by the pupae. Mean duration of pupal stage13.41 ± 4.28 d ($N = 46$). This species is widely distributed in the Neotropics (D'Abrera 1995, Prieto and Dahners 2006).

Calycopis mimas (Godman & Salvin). A final instar (Fig. 2) was found on inflorescence of *Diplusodon* sp. (Lythraceae) (but see also Silva et al. 2011, for occurrence in inflorescences of Melastomataceae). Larva fed on petals and reproductive structures within the calyx, where it remained in repose. On being touched, larva reacted with a "bungee jumping" behavior, suspended by a silk thread (Fig. 2C–E); later returning to the inflorescence, following the silken threads using its head in a zig-zag manner. In some species of this genus, larvae are detritivores (Duarte et al. 2005, Duarte and Robbins 2009, Robbins et al. 2010). The small quantity of setae visible on larval tegument differentiated it from *Calycopis caulonia* (Hewitson), *Calycopis bellera* (Hewitson), and *Calycopis janeirica* (C. Felder) larvae figured by Duarte et al. (2005) and Duarte and Robbins (2009), suggesting that *Ca. mimas* may

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Fig. 1. *A. strophius*. (A) egg; (B, C) last-instar larvae; (C) larva in interaction with ants *Camponotus* sp.; (D) cannibalism in prepupal and (E) pupal phases; (F) pupa, arrow indicating stridulation area.

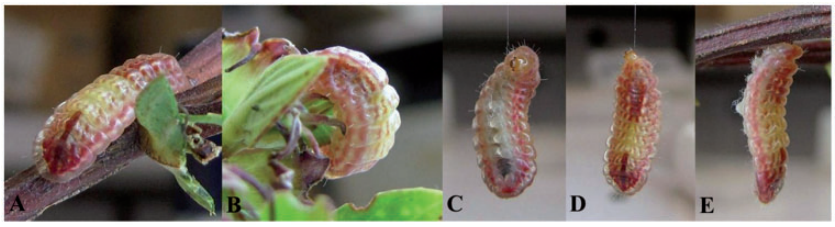

Fig. 2. *Ca. mimas*. (A–E) Last-instar larva.

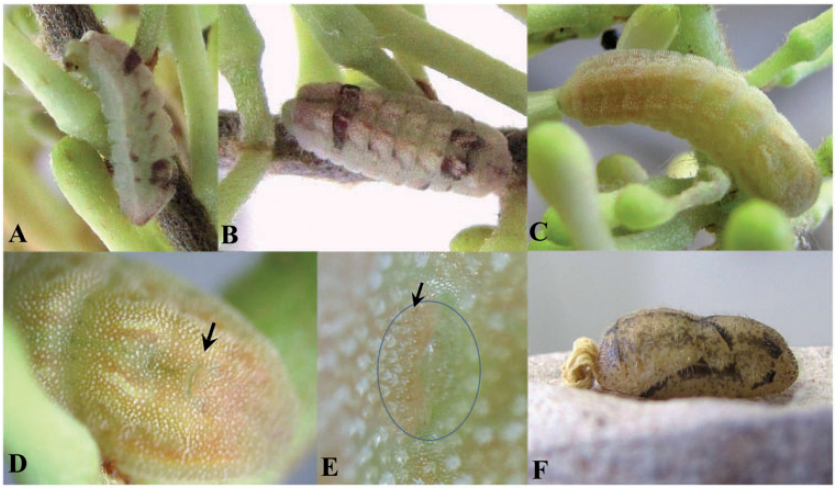

Fig. 3. *C. telea*. (A–C) last-instar larvae; (D) arrow indicating A7 segment with DNO and PCOs (E); (F) pupa with the larval exuvia joined to the abdomen.

belong to a different lineage within *Calycopis* (M.D. and R. K. Robbins, unpublished data). Pupation occurred in a small leaf near the inflorescence attached by a silk girdle and cremaster. Pupal stage lasted about 20 d. Myrmecophillous behavior is not documented in *Calycopis* larvae; however, for other species of the genus, Duarte et al. (2005) described the presence of organs and setae related to myrmecophily. This species is documented in Panama and South America (D'Abrera 1995, Robbins 2004b, Warren et al. 2012). In Brazil, it is poorly known, cited in Pará state by Godman and Salvin (1885–1888).

C. telea (Hewitson). Two last-instar larvae (Fig. 3) were found in inflorescences of *Roupala montana* Aublet (Proteaceae) eating the floral buds (but see also Silva et al. 2011, for occurrence in inflorescences of Sapindaceae). A larva creamy-green with dorsal purple patches on the first and sixth abdominal segments (A1 and A6) and other with uniformed coloration. DNO and PCOs present (Fig. 3D and E). A larva of this species was illustrated by Janzen and Hallwachs (2010) on flowers of *Guazuma ulmifolia* Lamarck (Sterculiaceae). The same authors also did not observe interaction with ants. Pupation occurred at the bottom of the rearing container attached by a silk girdle and cremaster hooks, with the larval exuvia joined to the abdomen (Fig. 3F). The adults emerged in 12 d. The species is widely distributed from extreme southern United States to Argentina (Johnson 1989, Janzen and Hallwachs 2010).

Cy. herodotus (F.). Five larvae (Fig. 4) were taken on *Chomelia ribesioides* Bentham ex. A. Gray (Rubiaceae), *Schefflera macrocarpa*

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Fig. 4. *Cy. herodotus*. (A) second-instar larva; (B–E) last-instar larvae; (E) arrow indicating DNO; (F) pupa.

Fig. 5. *E. endymion*. (A, B) second-instar larva; (C, D) last-instar larva.

(Chamisso & Schlechtendal) (Araliaceae) and *Ro. montana*. The larvae fed with the body extended or occasionally curled over the food. Larval data on *Ch. ribesioides* included buds, flowers, and new leaves being consumed, while those on *Ro. montana* primarily ate floral buds. In newly opened buds of *Sc. macrocarpa,* the reproductive parts were consumed, leaving only the calyx and bracts (Fig. 4A) intact. This species has been reared repeatedly in Brazil and other countries (Lima 1928, 1930, 1936; Monte 1934; Biezanko et al. 1974; Robbins and Aiello 1982). DNO present (Fig. 4E), however, no myrmecophilous interaction was observed. Pupation occurred on paper towel attached by a silk girdle (Fig. 4F); larval exuvia free, not attached to end of the abdomen. Pupal stage lasted in average 14.2 ± 3.7 d ($N = 5$). Larva of *Cy. herodotus* has body with conspicuous divisions accentuated by prominences subdorsais and subspiracular making it morphologically distinct from that of *Cyanophrys bertha* (Jones) with tegument "smooth" (Kaminski et al. 2010b), and *Cyanophrys fusius* (Goldman and Salvin) found in Costa Rica (Janzen and Hallwachs 2010). The species is widely distributed throughout the Neotropics, primarily in habitats <1,500 m (Robbins and Duarte 2005).

Electrostrymon endymion (F.). A second-instar larva (L2) (Fig. 5A and B) was found on *Qualea grandiflora* Martius (Vochysiaceae) inflorescence on ground. On being stimulated, the larva remained curled and immobile. In laboratory, it fed on *Q. grandiflora* petals in an intermediate stage of decomposition and remaining nestled in the petal folds. Pupation at the base of the rearing container. Pupa attached by a silk girdle and cremaster, with larval exuvia free. Imago emerged approximately after 10 d. Larvae of *Electrostrymon endymion* (Fig. 5C and D) and *K. syllis* (Fig. 7) are similar in both appearance and behavior and can be easily confounded. Both species belong to the subtribe Calycopidina, in which facultative detritivory has been recorded (Duarte and Robbins 2010). Despite the high sampling effort of immatures in *Q. grandiflora* inflorescences on the plant as opposed to on the ground ($N = 851$) (Silva et al. 2011), we did not find larvae of these two eumaeines, which reforces the detritivorous habit of those species. Both larvae of *Electrostrymon* Clench and *Kisutam* K. Johnson & Kroenlein have been found in fallen Lecythidaceae flowers (Feinstein et al. 2007, Duarte and Robbins 2010). *E. endymion* occurs from southern Brazil north to Santarem (PA) and north to Tarapoto, Peru.

Erora *aff.* gabina (Godman & Salvin). Three final-instar larvae (Fig. 6A–D) were found on *Q. grandiflora* (Vochysiaceae), *Miconia pohliana* Cogniaux, and *Miconia albicans* (Swartz) Steudel (Melastomataceae) inflorescences. Under laboratory conditions, larvae fed up on *Q. grandiflora* petals, on *Miconia* spp. calyx, buds, and young fruits and showed cryptic pattern with the calyx and peduncle of the inflorescences. According to the general descriptions of Klots and dos Passos (1981), caterpillars of *Erora laeta* (Edwards) and *Erora quaderna sanfordi* (dos Passos) are somewhat similar to those of *E. aff. gabina*. These authors did not find DNO and PCOs but describe dendritic setae related to myrmecophily (for illustration of dendritic setae see Duarte et al. 2001, 2005). Prepupae green-brownish (Fig. 6E); pupae attached to the inflorescences by a silk girdle, with the larval exuvia joined to the end of the abdomen (Fig. 6F). Klots and dos Passos (1981) noted pupae of *Er. laeta* and *Er. quaderna sanfordi* having silk mesh connected to cremaster and thenceforth to substrate no silken girdle. Mean duration of pupal stage 11.66 ± 1.15 d ($N = 3$).

K. syllis (Godman & Salvin). Six larvae (Fig. 7A and B) were found in *Q. grandiflora* petals taken on ground. In the laboratory, larvae either fed on petals in intermediate stage of decomposition or consumed fresh petals. Silk threads observed on petal folds, but, apparently, the larvae did not build shelters. Larvae similar to *E. endymion* (Fig. 5), both of which are considered to be facultative detritivores (Duarte and Robbins 2010). DNO present, no myrmecophilous interaction observed. Pupation (Fig. 7C) occurred on paper towel and on petals; mean duration of pupal stage 10 ± 0.70 d ($N = 5$). One larva was parasitized by the hymenopteran *Aprostocetus* sp. (Eulophidae, Tetrastichinae) (Fig. 23L), which emerged through a lateral hole of the pupa tegument. *K. syllis* is widely distributed and considered to be one of the commonest Eumaeini, with adults being found in abundance close to fallen fruits in rain forests (Duarte and Robbins 2010).

Kolana ergina (Hewitson). One larva, possibly third instar, was found on inflorescence of *Sc. macrocarpa* (Araliaceae), feeding in the interior of floral buds through a circular opening, moving only its retractable head with the rest of the body exposed. Differing from other

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Fig. 6. *Erora* aff. *gabina*. (A–D) last-instar larvae; (E) prepupa; (F) pupa.

Fig. 7. *K. syllis*. (A, B) last-instar larvae and (C) pupa.

Fig. 8. *Ko. ergina*. (A, B) last-instar larva, with details of verrucae (A) and (C, D) pupa.

Eumaeini species described in this study, mature larva of *Kolana ergina* showed dorsal and subspiracular extensions with bold colors on the extremities of the elongations. On *Sc. macrocarpa*, tegument white burgundy distally (Fig. 8A and B). In the central portion of the abdomen (A2–A4), the verrucae were orange and covered with spines (Fig. 8A). DNO absent. *Mico. pohliana* (Melastomataceae) floral buds and *Byrsonima coccolobifolia* Kunth (Malpighiaceae) are also cited as host-plants of *Ko. ergina* (Silva et al. 2011). On those plants, the larvae are reddish, verrucae distally blackened. Flinte et al. (2006) describe larva of *Ko. ergina*: yellow and reddish coloration while on leaves of *Byrsonima sericea* de Candolle in coastal habitat ("*restinga*") area of Rio de Janeiro state. Despite being apparently aposematic, larvae do exhibit polychromatism as per food-plant. Pupal pigmentation distinct, differing from other known pupae of Eumaeini by having a silvery brown with two pairs of black spots on the dorso (Fig. 8C and D). In the laboratory, pupa assumes head downmost position attached to inflorescence peduncle by silken girdle and cremaster with larval exuvia free; adult emergence after ∼20 d. *Ko. ergina* is a widespread species in South American lowlands (Robbins 2004b, Silva et al. 2011).

Mich. thordesa (Hewitson). Two eggs together were taken on *Bauhinia* sp. (Fabaceae) inflorescence peduncle (Fig. 9A); one eclosed after 5 d. Larval stage lasted 20 d ($N = 1$). Final instar (Fig. 9B and E) is highly cryptic on *Bauhinia* floral buds. Although feeding, larva remains twisted or curved on the inflorescence. Zikán and Zikán (1968) reared *Mich. thordesa* in Itatiaia from *Pyrostegia* Presl(cipó São João) (Bignoniaceae) under the name *Thecla pyrostegia* (voucher in Fundação Instituto Oswaldo Cruz, Rio de Janeiro, RJ) (see also Silva et al. 2011). DNO and PCOs present (Fig. 9C). Prepupa brown; pupation on rearing container wall (Fig. 9F), on being disturbed pupa emits intermittent sound reminiscent to that of a cicada (Hemiptera). Shortly before emergence, the brown pupa becomes blackish laterally; adult emerges after ∼13 d. Behavior and morphology apparently similar to the larva of *Michaelus jebus* (Godart) found in cultivated fruits of *Phaseolus* sp. (Fabaceae) (Gallo et al. 2002, N.A.P.S., personal observation). *Mich. thordesa* has been recorded from southeastern Mexico to Bolivia and southeastern Brazil (Nicolay 1979).

M. azia (Hewitson). Twenty-three larvae were collected on *Mimosa foliolosa* Bentham, *Mimosa lanuginosa* (Glaziou) Burkart, and *Mimosa radula* Bentham (Fabaceae) inflorescences, most larvae ($N = 18$) observed on *Mim. foliosa* (Fig. 10). It is of note that both species of *Mimosa* analyzed were herbaceous shrubs <1 m in height. At FAL, the majority of *Mim. foliosa* individuals occurred along the border of a gallery forest. *Mimosa claussenii* Bentham, is a shrub <2 m tall, was abundant in the study area and was intensively sampled

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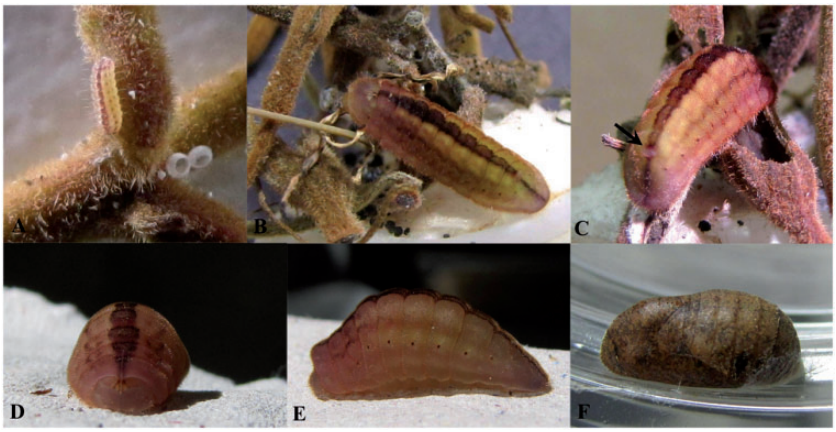

Fig. 9. *Mich. thordesa*. (A) Eggs and first-instar larva; (B–E) last-instar larva; (C) arrow indicating DNO; and (F) pupa.

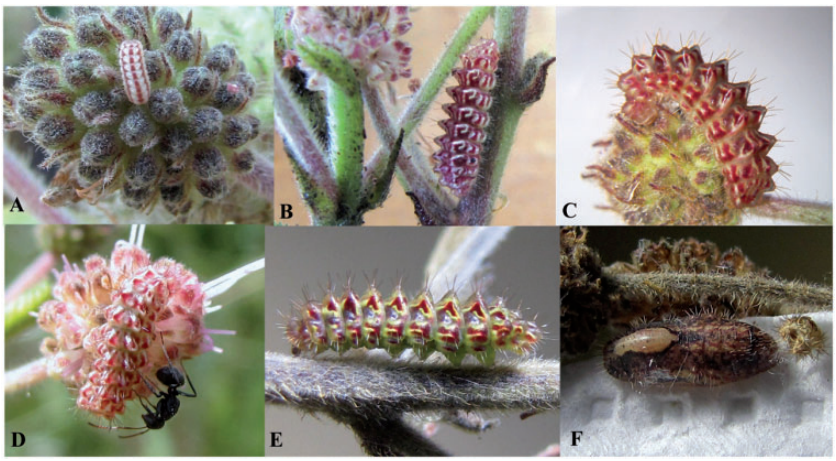

Fig. 10. *M. azia*. (A) First-instar larvae; (B–E) last-instar larvae; (D) larva in interaction with ants *Camponotus* sp.; and (F) pupa.

(~450 inflorescences); however, no *M. azia* larvae were found on this plant. The results of this study suggest that Fabaceae is the primary host plant family for *M. azia* (Robbins and Lamas 2004, Vargas and Parra 2009); however, there are records of butterfly on Anacardiaceae in Florida (Miller et al. 1997), but this record requires confirmation. We were unable to follow all larval instars in the laboratory, but we did note that first-instar larvae (Fig. 10A) differ from subsequent instars in having small conical projections and a mixed darker coloration on the dorso, which make them cryptic in regard to the inflorescence (Fig. 10B–E). The larvae fed on inflorescence reproductive structures of *Mimosa* spp., leaving the calyx in the glomerule. In the laboratory, pupation (Fig. 10F) was observed on the inflorescence, on the rearing container, and under paper towel attached by silken girdle and cremaster, frequently with larval exuvia joined to the end of the abdomen; mean duration 9.42 ± 2 d ($N = 19$). One larva was parasitized by *Conura* sp. (Chalcididae) (e.g., Fig. 23D); an adult parasitoid emerged from pupa after 20 d. Myrmecophilous interactions were observed between final instar ($N = 2$) of *M. azia* and individuals of *Camponotus* (Formicinae) on *Mim. foliosa* in March 2012 (N.A.P.S., personal observation). In constant motion, the ants performed antennal palpation in the DNO region (Fig. 10D), foraged on the inflorescences and then returned to the larva to repeat the same activity. It is a widely distributed species occurring from United States to South America (Chile, Brazil, Paraguay, and Argentina) (Robbins and Lamas 2002, 2004).

N. socia (Hewitson). A last instar was found on inflorescence of *Ro. montana* (Proteaceae) and monitored in laboratory. This species has been recorded in the Cerrado (Brown 1993, D'Abrera 1995), although there have been previous records on plants in the DF (Silva et al. 2011), this study illustrates for the first time a larva in situ. The cryptic light green larva changes to a pinkish tone when consuming older flowers (Fig. 11A and B) and soon pupated. DNO present, but no myrmecophilous interaction was observed in situ. Pupa attached to the base of the rearing container by silken girdle. Adult emerged after ~20 d. Biology unknown.

O. empusa (Hewitson). Two larvae found on inflorescences of Malpighiaceae (*B. coccolobifolia* and *Pe. goiana*). The green and pink coloration of the larvae was the same on both plants (Fig. 12A–D). Larvae consumed flowers, buds, and young fruits. When moving, the larvae leave silken trail, one occasion when a larva was touched, it "jumped" and remained suspended by a thread, returning only slowly to the plant. Prior to pupation (prepupae), the larvae assume a uniform hue (greenish or pinkish) (Fig. 12E). Pupation at base of rearing container, with mean duration 13.5 ± 0.7 d ($N = 2$). Ants of the genus *Crematogaster* (Myrmicinae) were observed on one of the inflorescences collected. DNO present. The only information regarding larvae of this genus was found in Kirkpatrick (1954) that described the larvae and pupae and noted that they are attended by ants. *O. empusa* is rare species that occurs from Tocantins and Pará south to Rio Grande do Sul, Paraguay, and Argentina. Misidentifications in the cited references are massive.

Paiwarria aphaca (Hewitson). Eggs and larvae taken on *Salacia* sp. (Celastraceae). One egg, deposited on the stalk close to the

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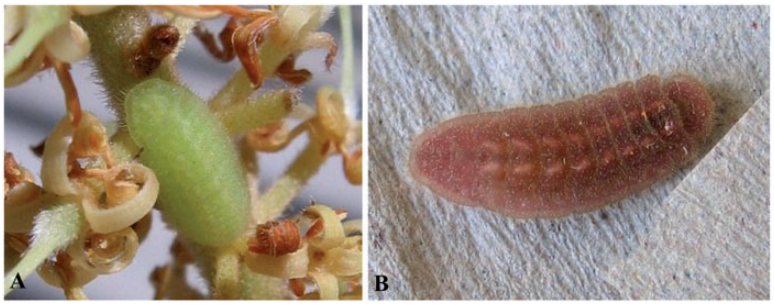

Fig. 11. *N. socia*. (A, B) Last-instar larva.

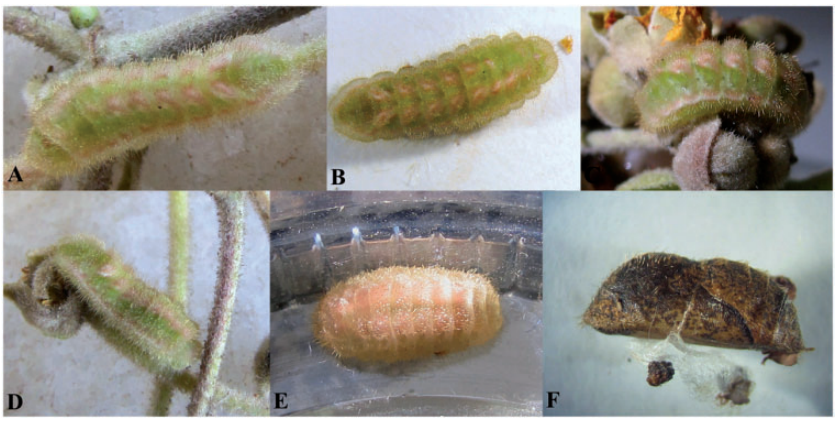

Fig. 12. *O. empusa*. (A–D) Last-instar larvae; (E) prepupa; and (F) pupal exuvia.

inflorescence, eclosed after 5 d; development from larva to adult emergence ∼30 d. In the initial instars, larvae are onisciform, tegument dorsally covered with small protuberances (see also Duarte et al. 2005), conspicuous coloration (Fig. 13A and B) with subsequent instars differing due to the presence of subdorsal and subspiracular elongations (Fig. 13C and D). Larvae consume buds, flowers, and eventually leaves of the host plant. Pupation occurred on a piece of leaf, attached firmly by a silk girdle and cremaster. Pupa brown, with white stripes and dorsal and subdorsal tubercles typical of the genus (Fig. 13E). Emergence ∼after 10 d. Three larvae parasitized by Camplopleginae wasps (Ichneumonidae) (Fig. 23I). The formation of the hymenopterans' cocoons occurred within the caterpillars before they reached the last instar, remaining only the head, prothorax, and spikes of saliences of the host (Fig. 23G and H). Parasitoids emerged 10.33 ± 2.88 d ($N = 3$). Larvae of *Paiwarria aphaca* and *Paiwarria venulius* (Cramer) feeding on leaves of *Salacia* sp. (N.A.P.S., personal observation; Fig. 13F) show phenotypic similiarities, differing from larvae of *Paiwarria umbratus* (Geyer) found on Sapotaceae leaves in Costa Rica (Janzen and Hallwachs 2010), in having elongations on the tegument or conspicuous coloration. Distribution includes Brazil, Paraguay, and Argentina (D'Abrera 1995, Núñez Bustos 2009).

P. polibetes (Stoll). Information on the morphology, behavior of the larvae, and their interactions with ants and Hemiptera are found in Kaminski et al. (2012) (but see also Silva et al. 2011 for additional larval host plant records). Larvae reared on *Sc. macrocarpa* (Araliaceae) (Fig. 14B) and *Miconia ferruginata* de Candolle (Melastomataceae) did not pierce the buds, as observed on other host plants (Silva et al. 2011). Larvae feed on the reproductive parts of newly opened buds and cutting the base of the buds to reach the ovary. This approach may be an alternative adopted to reduce mandible wear in contrast to the consumption of rigid parts of unopened buds (Rodrigues et al. 2010). In addition, it is possible that water loss occurs faster in the laboratory, drying out samples, and when faced with open versus closed buds, the larva "choose" the less costly source. In *Ro. montana*, an early-instar larva also fed on young fruits, acquiring a reddish color only at this stage (Fig. 14A). Pupation (Fig. 14F) occurred on the bottom or wall of the container or, in only two cases, on the inflorescence. External stimuli resulted in pupal stridulation. Average duration of pupal stage 13.81 ± 2.4 d ($N = 11$). On *Qualea parviflora* Martius (Vochysiaceae) (Fig. 14C), two *P. polibetes* larvae were parasitized by a Tetrastichinae (Hymenoptera: Eulophidae) (Fig. 23K); dozens of adult hymenopterans emerged through a hole in the thorax of the pupa (Fig. 23J) after ∼20 d. One larva resembling a second-instar foraging on *Mico. ferruginata* was parasitized by *Apanteles* sp. (Braconidae, Microgastrinae) (Fig. 23M); a single cocoon produced by the parasite was deposited under the host last segments; emergence approximately after 30 d. A larva on *Sc. macrocarpa* was parasitized by a tachnid fly (Diptera), which emerged as a larva from the pupa of *P. polibetes* (see cocoon Fig. 23P). Myrmecophilous interactions (with production of exudate) were observed between this parasitized larva of *P. polibetes* and an ant of the genus *Camponotus* (Formicinae) (Fig. 14E).

R. marius (Lucas). Distribution, host plants, and biology of *Rekoa* species, *R. marius* and *R. palegon* (Cramer), according to Monteiro (1990) and Robbins (1991a). Monteiro (1991) reported four instars and a larval–adult development period of ∼30 d for these species and provided illustrations and details of myrmecophilous interactions as well as with parasitoids (Diptera, Hymenoptera). Feeding behavior observed in this study is similar to that described by Monteiro (1991). A larva was observed on an unidentified Fabaceae species feeding on petals and young fruit; on *Ro. montana* (Proteaceae), larvae consumed buds and flowers, while on *Ouratea hexasperma* Baillon (Ochnaceae) and on a species of Malpighiaceae, larvae (Fig. 15A–E) fed on floral buds, perforating them, and consuming the interior. Pupal metamorphosis on inflorescence of Fabaceae and on the base or wall of the rearing container, secured by a silk girdle. Except for the pupa on Malpighiaceae that remained green until emergence (Fig. 15F), the

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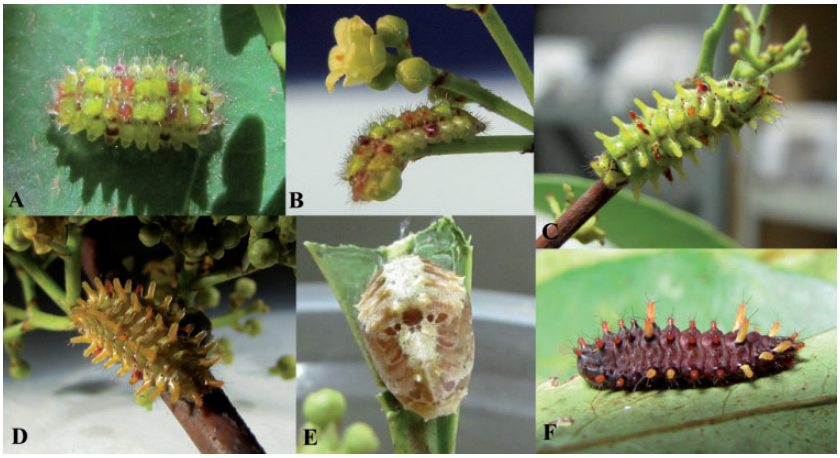

Fig. 13. *Pai. aphaca*. (A, B) Initial instars larvae; (C, D) last-instar larva; (E) pupa; and (F) last-instar larva of *Pai. venulius*.

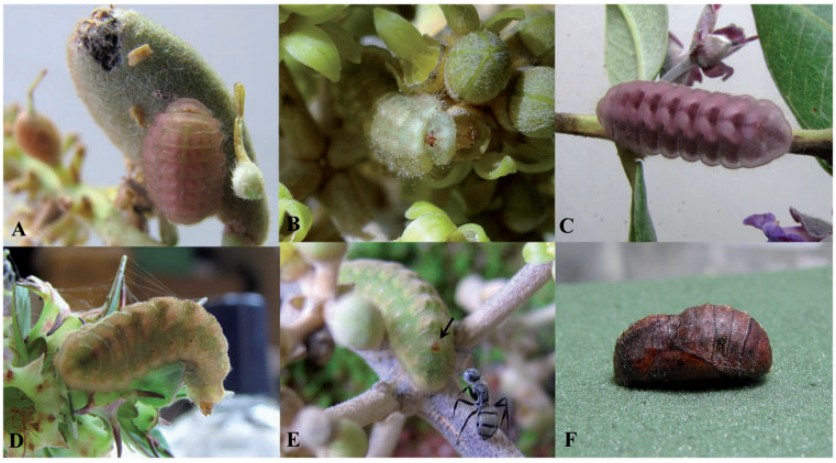

Fig. 14. *P. polibetes*. (A) Early-instar larva; (B–E) last-instar larvae; (F) larva in interaction with ants *Camponotus* sp., arrow indicating DNO; and (F) pupa.

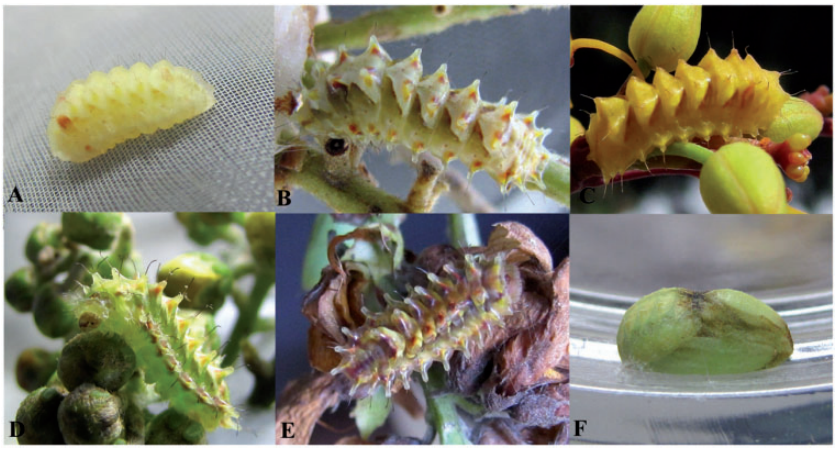

Fig. 15. *R. marius*. (A) Early-instar larva; (B–E) last-instar larvae; and (F) pupa.

pupae retained a predominantly yellow-brown coloration. The larval exuvia was attached to only one of the pupae; mean duration of pupal stage 13.33 ± 2.30 d ($N = 3$). One larva on *Ro. montana* was parasitized by a hymenopteran. The larva, with characteristics of an early instar (Fig. 15A), consumed flowers and buds voraciously, differing from the feeding behavior exhibited by other individuals. In just 5 d, this larva showed final instar characteristics (Fig. 15B), and after 6 more days, it pupated. The formation of the pupa occurred on the vertical wall of the rearing pot. After 30 d, 24 adult *Baryscapus* sp. (Eulophidae, Tetrastichinae) emerged through a hole on the side of the

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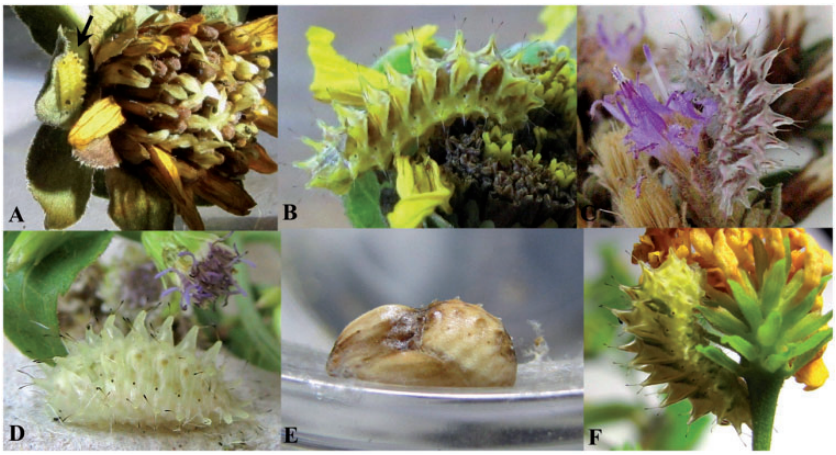

Fig. 16. *R. palegon*. (A) Arrow indicating first-instar larva; (B, C) last-instar larvae; (D) prepupa; (E) pupa; and (F) last-instar larvae on *Lantana* (Verbenaceae).

Fig. 17. *S. bazochii*. (A, B) Last-instar larvae; (C) prépupa; and (D) pupa.

host pupa (Fig. 23N and O). These suggest that the eulophid was altering the larval behavior in some way, so that it pupated before time. *R. marius* is distributed from Texas to Argentina (Robbins 1991a).

R. palegon (Cramer). Five larvae taken, each one on different species of Asteraceae: *Aspilia foliacea* Baker (Fig. 16A and B), *Baccharis dracunculifolia* de Candolle, *Chromolaena pedunculosa* (Hooker & Arnott) King & H. Robinson, *Lepdaploa* sp. (Fig. 16C), and an unidentified Eupatorieae. They fed preferentially on the capitulum, where a circular hole was made, and the reproductive structures were consumed internally (Monteiro 1991). An egg was found deposited on the semi-closed bract of *As. foliacea*. The larval–adult development time ~30 d. The larvae initially (first instar, Fig. 16A) fed on the bracts, and as they grew, they went on to feed on the reproductive structures, acquiring a cryptic pattern. Prepupae with uniform color, yellowish or white (Fig. 16D). Two larvae and two pupae of *R. palegon* were observed on a species of *Lantana* (Verbenaceae) (Fig. 16F) grown in gardens at the UnB campus; pupae on surface of leaf and on senescent inflorescence (N.A.P.S., personal observation). In the laboratory, pupal formation occurred on the wall (Fig. 16E) and base of container and on paper towel, attached to substrate by a silk girdle and cremaster hooks, and did not maintain the larval exuvia attached to the end of the abdomen. Pupal duration 9.75 ± 1.70 d ($N = 4$). When disturbed, the pupa reared on Eupatorieae produced a short sound with a frequency differing from other species, *A. strophius* and *P. polibetes*, studied in this article with audible sound production. Larvae of *R. palegon* possess myrmecophilous organs and maintain facultative associations with ants (Malicky 1970, DeVries 1990, Monteiro1991, Robbins 1991a) similar to those of *R. marius*, but no myrmecophilous interaction was observed.

Strymon bazochii (Godart). Six larvae and two eggs found on inflorescences of *Hypenia brachystachys* (Pohl ex Bentham) Harley (Lamiaceae) (cited as inflorescencens of an herbaceous Verbenaceae in Silva et al. 2011) in a "campo sujo" area of FAL. Eggs laid on calyx and peduncle of floral bud. Eclosion in 4 d. Period of development from larva to adult in 36 d. The larval cuticle was distinctly marked by distinctive tonality of purple and green (Fig. 17A and B). The cryptic larvae fed on floral buds and on the ovary by perforating the calyx. Prepupae purple-greenish (Fig. 17C). Pupation on senescent inflorescences being cryptic, attached by a silk girdle, usually without the larval exuvia joined to the abdomen (Fig. 17D). Pupal duration 12.75 ± 2.31 d ($N = 8$). The immatures are somewhat similar to those described by Dauphin (2011). *S. bazochii* is perhaps the first American butterfly to be introduced for biological control. It was introduced in 1902–1903 from Mexico to Hawaii to control *Lantana* (Verbenaceae), but it also consumes Lamiaceae in Hawaii (Swezey 1913, Perkins and Swezey 1924, Zimmerman 1958, Pallmer and Pullen 1995, Beccaloni et al. 2008). *S. bazochii* is widely distributed, extending from the southern United States to southern Brazil (D'Abrera 1995, Iserhard and Romanowski 2004, Dauphin 2011).

Strymon bubastus (Stoll). A last-instar larva was found on inflorescence of *Galactia* sp. (Fabaceae) in a "campo sujo" area. It was cryptic (Fig. 18A and B), feeding on calyx, making a hole to consume the inner tissues, as well as petals and young fruit (see also Silva et al. 2011). Pupation on inflorescence peduncle loosely attached by a silk thread on the cremaster (Fig. 18C) without the attachment of the larval exuvia; pupal period ~10 d. Although *Strymon bubastus* has been reared in other families of hostplants (Boraginaceae, Convolvulaceae, Malvaceae, and Portulacaceae), the biology of this butterfly is still unknown (Hallman 1979a,b,c; Beccaloni et al. 2008). The species is widely distributed in South America (Austin and Johnson 1997, Nicolay and Robbins 2005, Prieto and Dahners 2006).

S. crambusa (Hewitson). Early-instar larvae (L1/L2) with a uniform color, as the larvae developed this pattern was somewhat similar to that of the larvae of *S. mulucha* (see Fig. 21G), with two white lines oblique on seventh segment (Figs. 19A–C). Larva taken on *Oxalis densifolia* Zuccarini (Oxalidaceae) in "campo sujo" area. Because of the lack of this plant in field, after ~10 d in the laboratory, the larva accepted well buds and flowers of *Chamaecrista claussenii* (Bentham) Irwin & Barneby and other Fabaceae species, reaching to the adult stage. DNO and PCOs present. The larva pupated on the inflorescence (Fig. 19D), precariously attached via a silk thread on the cremaster. The adult

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Fig. 18. *S. bubastus*. (A, B) Last-instar larva and (C) pupal exuvia.

Fig. 19. *S. crambusa*. (A) Early-instar larva; (B, C) last-instar larva; and (D) pupa.

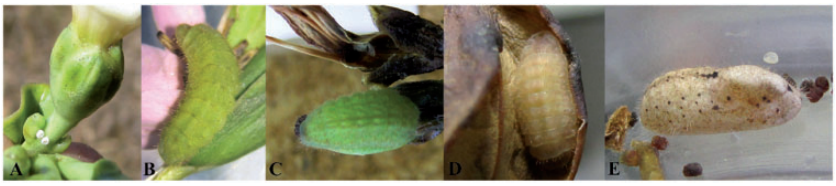

Fig. 20. *S. cyanofusca*. (A) Eggs on the peduncle of floral bud; (B, C) last-instar larvae; (D) prepupa; and (E) pupa.

emerged after 10 d. Larvae of *S. crambusa* were observed recently on *Oxalis cordata* A. Saint-Hilaire in FAL. This species is known only in xeric areas from Argentina, Bolivia (found on the border with Peru), Bolivia, and Chile (Johnson et al. 1990). Biology unknown, it is not commonly sampled in surveys. There is no other larval hostplant record available in the literature (see also Silva et al. 2011).

S. cyanofusca (Johnson, Eisele & MacPherson). Eggs and larvae were found on inflorescences of *Calolisianthus speciosus* (Chamisso & Schlechtendal) Gilg. (Gentianaceae) in "campo sujo" area. Eggs were laid together on the peduncle of floral bud (Fig. 20A). Eclosion in 5 d. Mean period of development from larva to adult 30.5 ± 3.53 d ($N = 2$). The cryptic larvae (Fig. 20B and C) foraging on the calyx fed on floral buds and on reproductive structures ignoring anthers. The coloration of the larvae did not change with the consumption of lilac-colored petals of host plant. One specimen showed a distinct color pattern with short pale green lines oblique distally (Fig. 20C). DNO and PCOs present. Prepupae pinkish (Fig. 20D). Pupal metamorphosis (Fig. 20E) on plant and base of container, attached with silken girdle and by the cremaster, larval exuvia joined to the abdomen. Mean duration of pupal stage 8 ± 1.9 d ($N = 5$). In May 2012, larvae of *S. cyanofusca* were observed on a species of *Deianira* Chamisso & Schlechtendal (Gentianaceae) (N.A.P.S., personal observation). Biology unknown. Records of occurrence have been reported in in dry areas of Brazil (Robbins and Nicolay 2001, Nicolay and Robbins 2005), Argentina and Peru (Robbins 2004b, Conservation International 2012).

S. mulucha (Hewitson). Thirty-seven larvae (Fig. 21A–H and L) were reared on seven host plant families (see Silva et al. 2011). Eggs were laid on calyx and peduncle of floral buds of *Calliandra dysantha* Bentham, *Bauhinia* sp., and *Galactia* sp. (Fabaceae). Eggs eclosed 4.6 ± 0.54 d, and mean period of development from larva to adult was 30.4 ± 3.04 d ($N = 5$). Feeding was observed on reproductive structures inside the floral buds, petals, and consuming also young fruit of Fabaceae and Malvaceae. A larva reacted by lifting the thorax and abdomen tip when it was touched on the dorsal surface. DNO and PCOs present. In laboratory, pupation (Fig. 21J and K) occurred on the plant, on the wall, or at the base of the rearing container, and on paper towel, attached to substrate by silken girdle and cremaster hooks. Mean duration pupal stage 13 ± 2.63 d ($N = 32$). During field work, one last-instar larva was observed being attended by *Camponotus* sp., the same ant (individual) that attended larvae of *A. strophius* on *Heteropteris* sp. (Malpighiaceae) (Figs. 1C; 21L); however, we did not observe larval exudations. This larva was also parasitized by a dipteran (Tachinidae) that emerged from the butterfly pupa after 10 d (Fig. 23Q). *S. mulucha* larvae also hosted two different morphospecies of Ichneumoninae (Hymenoptera: Ichneumonidae) and *Conura* sp. (Hymenoptera: Chalcididae), on *Casearia sylvestris* Swartz (Salicaceae) and Fabaceae, respectively. These hymenopterans emerged through a hole in the thorax of the pupa (e.g., Fig. 23A–D) after ~25 d. Monteiro (1990) cited larva–ant interactions but did not comment on the parasitoid species. Superficially, larvae of several species of *Strymon* Hübner have strong morphological similarities (Ballmer and Pratt 1988, Wagner 2005). *S. mulucha* is widely distributed in the Neotropics (Brown 1993, D'Abrera 1995, Robbins and Nicolay 2001, Warren et al. 2012).

T. venustus (H.H. Druce). Eight larvae were found on five plant species, *Galactia* sp. (Fabaceae), *Ou. hexasperma* (Ochnaceae), *Pe. goiana*, *Pterandra pyroidea* A. Jussieu, and an unidentified Malpighiaceae. Tegument color pattern (Fig. 22A–E) varied from tones of green to orange-brown between larvae that consumed the same structures on the same plant species, except on *Pt. pyroidea* where the larva was pink. The larvae fed on floral buds, petals, and on the ovary by perforating the calyx in Fabaceae; occasionally fed on elaiophores present in the calyx of Malpighiaceae. DNO and PCOs present. Pupation on the container and on the paper towel attached by silken girdle, usually without the larval exuvia joined to the abdomen (Fig. 22F and G). Pupal duration 14.16 ± 2.13 ($N = 6$) days. One larva on Malpighiaceae was parasitized by *Baryscapus* sp. (Eulophidae) (Fig. 23O) and did not produce a silk girdle for the pupa, which was sustained only by silk threads on the cremaster; after 35 d, 25 adult hymenopteran emerged. Biology of the *T. venustus* is unknown. *Tmolus echion* (L.) consumes reproductive structures of *Lantana* flowers, which are invasive species in certain

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Fig. 21. *S. mulucha*. (A–H) last-instar larvae; (I) prepupa; (J, K) pupae; and (L) *A. strophius* (above) and *S. muluca* (below) in interaction with ants *Camponotus* sp.

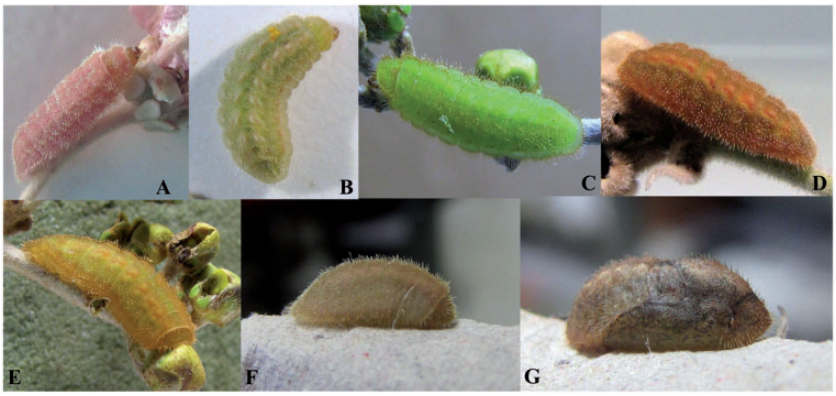

Fig. 22. *T. venustus*. (A–E) Last-stage larvae; (F) prepupa; and (G) pupa.

regions (Robbins and Aiello 1982, Palmer and Pullen 1995). Distribution of the *T. venustus* includes Brazil, French Guiana, Venezuela, and Colombia (D'Abrera 1995, Robbins 2004b, Emery et al. 2006, Gaviria-Ortiz and Henao-Bañol 2011, Warren et al. 2012).

Discussion

In this study, we have presented data on the biology for 22 Eumaeini species. Given the difficulties of finding the immatures in nature (Silva et al. 2011) and associating larvae with adults, it was not possible to conserve individual larvae to describe the larval chaetotaxy. Although lacking such details, the information presented in this study includes first records about the biology (food-plants, parasitoids, and phenology) of most of these species with novel larval illustrations.

Morphological and Behavioral Aspects of Immatures. The illustration of larvae raises important questions about the immature characteristics of the genera *Cyanophrys* Clench and *Paiwarria* Kaye. The larvae of *Cy. herodotus* (Fig. 4) shown in this study are quite different from those illustrated for *Cy. bertha* (Jones) by Kaminski et al. (2010b) and *Cy. fusius* (Godman & Salvin) provided by Janzen and Hallwachs (2010). The characteristic traits of these larvae may help clarify the position of these species in the phylogeny of the group discussed in Robbins and Duarte (2005).

Larvae of *Pai. aphaca* (Fig. 13A–D) differ considerably from those depicted as *Pai. umbratus* in Janzen and Hallwachs (2010). As expected, there are variations among larval instars (Downey 1987), which became clear in *Pai. aphaca*. Nevertheless, no larval instars reared in this study were similar to that *Pai. umbratus*. This species reared in Costa Rica fed on Sapotaceae and co-occured on the same leaves with the caterpillars of *Evenus regalis* (Cramer) (Janzen and Hallwachs 2010, Sermeño-Chicas et al. 2013). Fascinatingly, the differences between the larvae of *Pai. umbratus* and *Pai. aphaca* could be due to mimicry between *Pai. umbratus* and *Ev. regalis* on Sapotaceae. *Paiwarria* belongs to the *Eumaeus* Section (sensu Robbins 2004b), which includes aposematic species (Bowers and Larin 1989, Smith 2002, Contreras-Medina et al. 2003). The conspicuous coloration of early instars of *Pai. aphaca* (Figs. 13A) may indicate an aposematic species; however, this characterization requires further investigation. It is possible that the development of protrusions and extensions with spines is related to the defense mechanisms of these species, as appear to be the case for *Ko. ergina* (Fig. 8) (see Kaminski et al. 2009, 2010b). In fact, bristles and spines are important for deterring invertebrate predators, such as sucking Hemiptera, ants, and wasps (Dyer 1997, Gentry and Dyer 2002). These studies underscore the importance of characterizing the early instars.

The cannibal behavior observed among larvae of *A. strophius* in laboratory demonstrates the fragility of these insects during the pupal and prepupa stage. In one case, there was food restriction and a pupa was attacked (Fig. 1E); in other case, there was no restriction of food, and yet the prepupa was consumed (Fig. 1D). There are no previous reports of cannibalism in *A. strophius*, but this behavior is already known for many other Lycaenidae (Mattson 1980, Pierce and Easteal 1986, Fiedler 1990, Monteiro 1991, Duarte et al. 2005), and one explanation is that cannibalism occurs due to dietary deficiency suffered by the larvae. Mattson (1980) suggests that the tendency to cannibalism in

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Fig. 23. Parasitoids of lycaenid larvae; arrows indicate way to emerge from their hosts. (A) Pupal exuvia of *A. strophius* parasitized by (B) Ichneumoninae sp. (Ichneumonidae); (C) pupal exuvia of *A. strophius* parasitized by (D) *Conura* sp. (Chalcididae); (E) mummified larva of *A. strophius* parasitized by (F) *Rogas* sp. (Braconidae, Rogadinae); (G–H) cocoons of (I) Campopleginae sp. (Ichneumonidae) in *Pai. aphaca* larva; (J) pupal exuvia of *P. polibetes* parasitized by (K) Tetrastichinae sp. (Eulophidae); (L) *Aprostocetus* sp. (Eulophidae, Tetrastichinae) in *K. syllis*; (M) *Apanteles* (Braconidae, Microgastrinae) in *P. polibetes* larva; (N) pupal exuvia of *R. marius* parasitized by (O) *Baryscapus* sp. (Eulophidae, Tetrastichinae); (P) cocoons of fly (Tachinidae) (left) and pupal exuvia of *P. polibetes* (right); and (Q) cocoon and adult of Tachinidae parasite of the *A. strophius* and *S. mulucha*.

lycaenids may be related to the content of nitrogen present in the prey, given that the group feeds preferably on plant tissues rich on these compounds (e.g., inflorescences). Nonetheless, it is not recommended that the larvae be confined together in the laboratory, even though they were found near the field where they would probably have greater resource availability and mobility.

Moreover, no defence reaction was detected in larvae reared in a laboratory setting, with the exception of one *S. mulucha* larva that raised its thorax and abdomen ("beat reflex"), a single *E. endymion* that remained still and curled on being touched (Fig. 5B), a *Ca. mimas* larva that "jumped" from the inflorescence and returned via a silken thread (Fig. 2C–E) and *O. empusa*, which also "jumped" but returned slowly via a silken thread. The behavior of "beat reflex" and "bungee jumping," although common in Lepidoptera larvae, was not expected in the Lycaenidae (Malicky 1970, Kaminski et al. 2009). One possibility is that there are different responses to myrmecophilous contact and with other organisms. The production of silken threads occurs in many Lepidoptera with various functions, especially defense and the construction of shelters (Diniz et al. 2000, Monteiro et al. 2007, Rota and Wagner 2008, Greeney 2009). In Eumaeini, it was not possible to assess the role of the silk threads scattered throughout the inflorescence, but apparently, as in other Lepidoptera, this adaptation is a means whereby larvae can move safely around the substrate.

One possible defensive behavior is the production of sounds by larvae and pupae of Lycaenidae species (Downey 1966, DeVries 1990, Hill 1993, Calvo 1998). In this study, pupae of *A. strophius*, *Mich. thordesa*, *P. polibetes*, and *R. palegon* emitted audible noises when the container was moved. In reviewing this behavior, Pierce et al. (2002) observed that larvae and pupae make different types of sounds (usually inaudible to humans) depending on the function required, such as defence or to attract attendant ants.

Many of the larvae found in this study showed evidence of the organs related to myrmecophily (*C. telea*, *Cy. herodotus*, *K. syllis, M. azia*, *N. socia*, *O. empusa*, *S. crambusa, S. cyanofusca,* and *T. venustus*) or are already recognized as facultative myrmecophiles (*A. strophius, Mich. thordesa*, *P. polibetes, R. palegon*, *R. marius*, and *S. mulucha*) (Table 2). However, few interactions were observed per se between the Cerrado larvae and ants, possibly due to the focus being on obtaining larvae for identification and rearing, rather than monitoring individuals at the study sites. Furthermore, although facultative myrmecophily occurs in several species, it is often not recorded by researchers during field studies (Robbins and Aiello 1982, Robbins 1991b, Kaminski and Freitas 2010, Kaminski et al. 2010b, Rodrigues et al. 2010), possibly due to the influence of environmental conditions on the species involved (Ballmer and Pratt 1991, DeVries 1991, Pierce et al. 1991, Wagner and Kurina 1997, Fraser et al. 2001, Kaminski et al. 2012). The observation of DNO functioning outside of the laboratory is complicated by larval morphology and where it is on the host plant (see Fig. 21L), this would lead to the conclusion that controlled observations in the laboratory are a requisite (Kaminski and Freitas 2010).

Eumaeini Larvae and the Parasitoids. The protection of ants acting apparently against larval parasitoids (Pierce and Mead 1981, Pierce and Easteal 1986, Monteiro 1991, Fraser et al. 2001, Kaminski et al. 2010a) could not be evaluated here. Interestingly, however, three of the larvae visited by ants (*A. strophius*, *S. mulucha*, *P. polibetes*) at the collection sites were parasitized by Diptera. These observations suggest that parasitized larvae can produce communication and reward substances for ants, depending on the level of tissue damage (Pierce and Mead

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1981, Fiedler et al. 1992, Hanson and Gauld 1995). Conversely, braconids in the genus *Cotesia* Cameron (Braconidae, Microgastrinae) can use attendant ants to guide their oviposition (Pierce and Mead 1981, Pierce et al. 1987, Seufert and Fiedler 1999). Parasitoids can also use visual cues (frass or the arrangement of leaf shelters or silken threads, Sugiura and Yamazaki 2006) and chemicals to find their host (Price et al. 1980, Gentry and Dyer 2002, Santos et al. 2004). This approach may have been the case for the *K. syllis* specimen that was taken in the folds of flowers on the ground.

Another interesting feature of endoparasitoids is how they emerge from their hosts. In *A. strophius,* larvae parasitized by *Rogas* sp. (Braconidae, Rogadinae) showed a "mummified" posthatch aspect (Fig. 23E and F) that is typical of this wasp subfamily (Zaldívar-Riverón et al. 2008, Townsend and Shaw 2009). The adults of the genus *Conura* Spinola (Chalcididae) commonly emerge from the pupa of their lycaenid host (Monteiro 1991, Badenes-Pérez et al. 2010, Kaminski et al. 2010a,b), and in this study, all wasps of this genus emerged through an oval opening at the lateral of the thorax (Fig. 23C and D). Some species of this group can be restricted to certain families of Lepidoptera (Hanson and Gauld 1995). The color of the cocoon of Camplopleginae (Ichneumonidae) parasitizing *Pai. aphaca* (Fig. 23G–I) resembles the feces of birds, which seems to be a strategy of this subfamily of wasps against potential predators (Hanson and Gauld 1995, Fernandes et al. 2010) and can be easily recognized in the field.

The effects of parasitism by Tetrastichinae reported in *R. marius* and *T. venustus* suggest that parasitized larvae may exhibit altered behavior and development time. Here, it was not possible to observe hyperparasitoidism, but Eulophidae (Hymenoptera) is a cosmopolitan group composed of species that behave as hyperparasitoid, with several biological aspects little known for the neotropical species, including those belonging to Tetrastichinae (e.g., *Baryscapus* Förster and *Aprostocetus* Westwood; Fig. 23K, L, and O) (Delvare and LaSalle 1993, Zanuncio et al. 2009, Hansson and LaSalle 2010, Hansson 2010).

Variation in parasitoid associations may be influenced by the ecology of the host species and the phylogenetic relationships among parasitoids and their hosts (Shaw 1997, Wagner and Kurina 1997, Fraser et al. 2001, Stireman and Singer 2003, Stireman et al. 2009). The relationship between Lycaenidae, their host plants, and parasitoids is poorly explored. For example, behavioral observations of the parasitoid and the preservation of the remnants of larvae and pupa can be useful for identifying different Hymenoptera species and, when necessary, for identifying the lepidopteran (Shaw 1997, Townsend and Shaw 2009). Because of the importance of parasitoids in regulating the populations of various insects (Hanson and Gauld 1995, Jordão and Silva 2006), knowledge and documentation, at least in part, of their biology is essential to understand multitrophic parasitoid-host interactions (Price et al. 1980, Schurian et al. 1993, Santos et al. 2004, Fernandes et al. 2010).

Importantly, for more than half of the species presented in this study, no biological records or illustrations of the larvae were found in the existing bibliography, and for certain species, these are the first records of host plants (complementary to the information presented in Silva et al. 2011). Based on these records, experimental analyses should be proposed, and the ultrastructural evaluation of the identified larvae, as well as electron microscopy and descriptions of chaetotaxy, can be more reliably performed. Additionally, future comparisons of different localities should be made to investigate possible variations. It is noteworthy that the knowledge of life histories of these species and their host plants in the Cerrado may assist in designing measures for their conservation and management, as many Eumaeini species have suffered from severe habitat reduction in this biome.

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