

Immature stages of *Adeloneivaia fallax* (Lepidoptera: Saturniidae)

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Abstract

Details of the egg, larval, and pupal morphology of *Adeloneivaia fallax* (Boisduval) (Lepidoptera: Saturniidae) are described and illustrated and compared with other species of Saturniidae, more specifically with other Ceratocampinae. Egg ultrastructure is described for the first time in Ceratocampinae; larval chaetotaxy is documented for the first time in *Adeloneivaia*; and few pupal characters are evaluated for their potential phylogenetic use. Biological and behavioral aspects of captive rearing are discussed, and larval host plant records for *A. fallax* are provided.

Key Words: Atlantic Forest; Ceratocampinae; larva; morphology; neotropical

Resumen

Son descritos e ilustrados detalles de la morfología de huevo, larva e pupa de *Adeloneivaia fallax* (Boisduval) (Lepidoptera, Saturniidae) y comparados con otras especies de Saturniidae, más específicamente con otros Ceratocampinae. Por primera vez se documenta la chaetotaxia larval en *Adeloneivaia*. Son proporcionados aspectos biológicos e comportamentales de la cría en cautiverio, así como registros de las plantas hospederas de *A. fallax*.

Palabras Clave: Mata atlántica; Ceratocampinae; larva; morfología; neotropical

The Saturniidae comprise medium–large, colorful moths that attract large numbers of admirers, breeders and professionals. Their immature stages are well known compared with other families of Lepidoptera. Though nearly 100 articles describing the immature stages of saturniids were published between 1985 and 2003 (Rougerie & Estradel 2008), only a few addressed egg and larval ultrastructure, or larval chaetotaxy, or discussed morphological variation in an evolutionary context (Balcázar–Lara & Wolfe 1997; Deml & Dettner 2002; Rougerie & Estradel 2008).

Only about 380 of the approximately 2,350 worldwide species of Saturniidae (van Nieukerken et al. 2011) are recorded from Brazil (Duarte et al. 2012). Among the four subfamilies, Hemileucinae are the most diverse in the country, followed by Ceratocampinae. Because of the high species diversity in the Hemileucinae, and the medical and economic importance of this group, studies dealing with the biology and morphology of the immature stages are concentrated in that subfamily, as noted by Specht et al. (2008). In contrast, only a few species of Ceratocampinae have well–known immature stages, and in many cases the life cycle of these species is only partially described. However, as Balcázar–Lara & Wolfe (1997) showed in their cladistic study of Ceratocampinae, the characters of the immatures proved to be of great importance in resolving a number of issues for which adult morphological characters proved inadequate. For example, they discovered that two of the three synapomorphies for the subfamily were derived from characters of the immatures, demonstrating the undeniable importance of studying these semaphoronts.

There is a great need for an up–to–date review to assess the current state of ceratocampine taxonomy. In the most recent revision of the subfamily, Lemaire (1988) recognized 170 species belonging to 27 genera, but in the last decade a significant number of new taxa has been described (Brechlin & Meister 2011). For Brazil, 85 species belonging to 21 genera are recorded from various biomes (Lemaire 1998, M. Duarte unpublished data).

Adeloneivaia Travassos, 1940 is the only genus of Ceratocampinae whose male genitalia have the posterior portion of the valva membranous. Of the 30 species in this genus, 14 occur in Brazil (Lemaire 1988; Brechlin & Meister 2011), and seven are recorded from remnants of Atlantic Forest in the state of São Paulo: *A. acuta* (Schaus, 1896), *A. boisduvalii* (Doûmet, 1859), *A. catharina* (Bouvier, 1927), *A. fallax* (Boisduval, 1872), *A. jason* (Boisduval, 1872), *A. schubarti* Rêgo–Barros & Mielke, 1970 and *A. subangulata* (Herrich–Schäffer, [1855]). It is in those forest remnants that efforts are being directed by the team of the Lepidoptera Laboratory of the Museu de Zoologia da Universidade de São Paulo, with the aim of increasing the biosystematic knowledge of these moths.

The genus *Adeloneivaia* was created to include 10 species originally described in *Othorene* and *Adelocephala* (*sensu* Herrich–Schäffer [1854]), and which had been placed in *Syssphinx* by later authors (e.g., Draudt 1929–1930; Bouvier 1930; Schüssler 1936). According to Lemaire (1988), *Adeloneivaia* is closely related to *Syssphinx*, differing from this genus in the morphology of the male and female genitalia and the presence of a pair of lateral capsules on the distal segments of

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the abdomen, which is covered with tufts of long piliform setae that obscure the valves in males and the ovipore in females. These characters appear to be exclusive to this genus. After mating, adults lose their lateral capsules, making it difficult to recognize this structure in specimens collected in the field. In order to observe the lateral capsules intact, one must rear specimens in the laboratory.

The immature stages of *Adeloneivaia* are still poorly known. Information is available in the literature for only four species: *A. jason*, *A. isara* (Dognin, 1905), *A. subangulata* and *A. schubarti*. The first of these was studied by Lampe (1987), the next two by Packard (1905: only *A. subangulata*) and Lemaire (1988), and the fourth by Furtado (2001). Although Balcázar-Lara & Wolfe (1997) did not include any information on the immature stages of *Adeloneivaia* in their cladistic study, their placement of the genus as a sister-group of the clade formed by *Adelowalkeria*–*Citioica* (*sensu* Balcázar-Lara & Wolfe, 1997) makes the prospect of obtaining and studying their immature stages even more attractive.

In the present study, we describe the immature stages (egg, larvae, and pupa) of *A. fallax*, with the chaetotaxy of the first instar. Additionally, we discuss some biological and behavioral aspects of captive breeding, and report larval host plants. We compare the data obtained here with information available in the literature on other ceratocampine species. Last, we comment on morphological description concerning the immature stages of Saturniidae.

The wide distribution of *A. fallax* in Brazil includes the states of Espírito Santo, Rio de Janeiro, São Paulo, Paraná, Santa Catarina and Rio Grande do Sul (Lemaire 1988). Similarly to many other Ceratocampinae,

adults of this species resemble a hawk moth. The wings are yellowish with well-marked veins, and in some cases, the postmedian area of the forewing is pinkish dorsally, with a brown discal band (in females, more conspicuous ventrally); the hindwing has less-marked veins, and is more evenly yellowish in females and yellow or orange in males, with a darker anal region, reddish or orange, respectively; in females, the forewing outer margin is more rounded than in males (Suppl. Figs. 1–4).

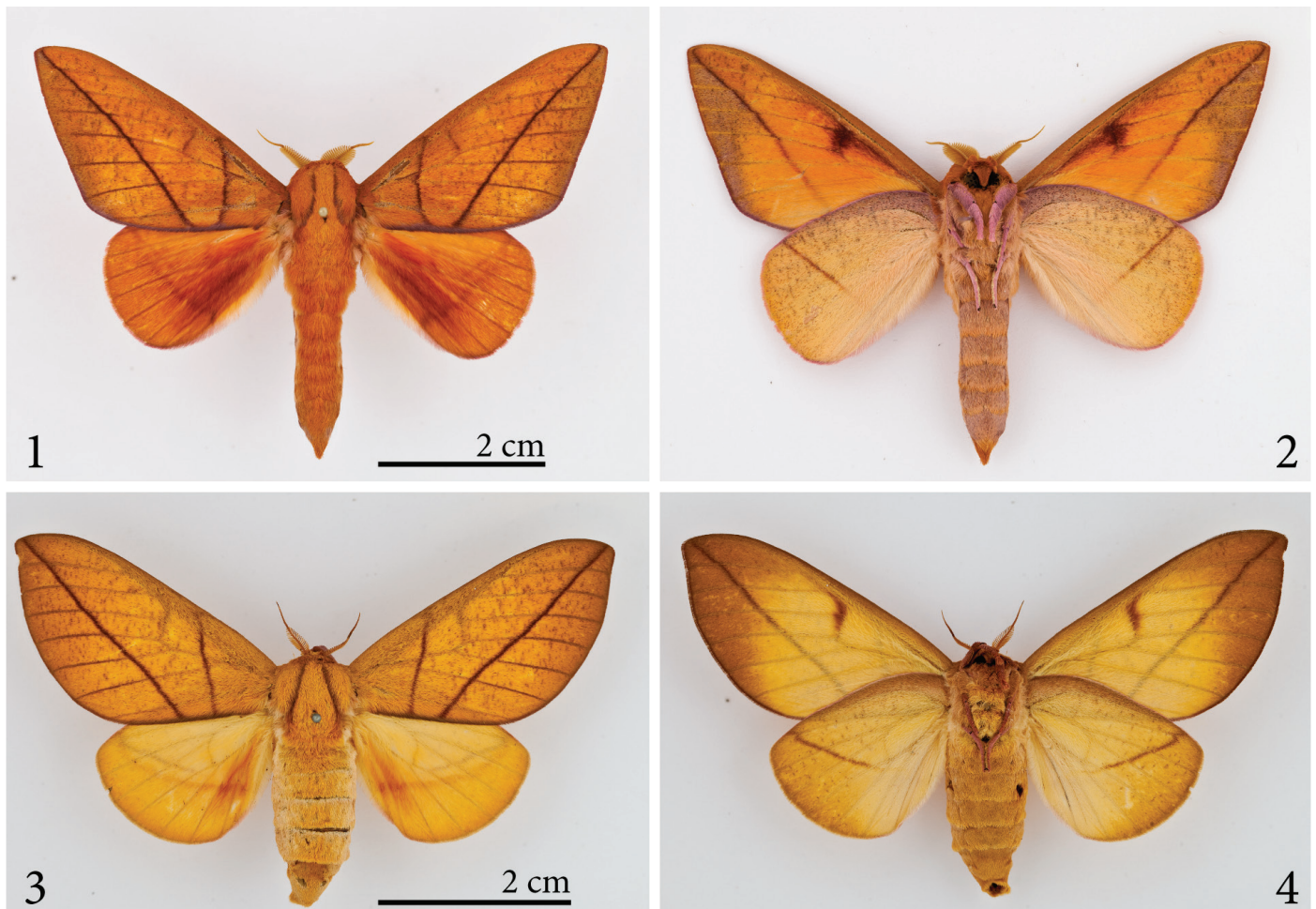
Materials and Methods

This study is part of the project “Faunistic analysis of Saturniidae (Insecta, Lepidoptera) in a fragment of Atlantic Forest of the state of São Paulo, Brazil,” supported by the State of São Paulo Research Foundation (FAPESP).

The classification used for Saturniidae follows Lemaire & Minet (1998). The nomenclature used for plants is in accordance with the website of the Missouri Botanical Garden (<http://www.tropicos.org> accessed on 11 April 2014). Supplementary figures for this article in Florida Entomologist 98(1) (March 2015), including color images of the adult and immature stages, are online at <http://purl.fcla.edu/fcla.edu/fcla/entomologist/browse>.

STUDY AREA

The samples were collected at the Boraceia Biological Station (EBB), which is located in the Municipality of Salesópolis, State of São



Figs. 1–4. *Adeloneivaia fallax*, adult. 1 and 2. Male, dorsal and ventral views, respectively. 3 and 4. Female, idem.

Paulo, Brazil (S 23°38' W 45°52'; 900 m a.s.l.). This area has 96 ha of montane Atlantic Forest, and is located within a reserve of 16,450 ha. The climate is humid tropical (Köppen CFA), with uniform rainfall (annual mean 2018.84 mm) throughout the year and warm summers (annual mean temperature 17.9 °C; see also Custódio Filho 1989).

The Ombrophilous Dense Forest vegetation covering the area comprises palm trees (mainly *Euterpe edulis* Mart.), ferns and large bamboos. Plants of the genus *Heliconia* L., which are characteristic of the region, occur along the streams (Bertoluci & Rodrigues 2002).

SAMPLING AND REARING PROTOCOL

Sampling was performed monthly, using mixed mercury–vapor lamps installed around one of the station lodges. The moths were collected either with entomological nets or manually as they landed on the white walls of the lodge. To obtain eggs of *A. fallax*, a female was collected and kept alive in a plastic container measuring 32 × 21 × 15 cm, with a 60 W bulb placed next to it to provide warmth and stimulate oviposition. Almost all eggs were laid on the second day.

The larvae were reared in containers covered with voile fabric. They were fed mainly with leaves of *Wisteria* cf. *sinensis* (Sims) DC. (Leguminosae: Papilionoideae), because this plant was abundant where the larvae were reared, and occasionally with leaves of *Inga* sp. (Fabaceae: Mimosoideae) (see also Lemaire 1988), and accepted both plants with no apparent preference. Initially, the leaves were replaced every two days, and from the fourth instar on, they were changed daily. Larvae in the pre-pupal stage were maintained on host plants in a soil layer of approximately 4 cm deep.

Eggs, larvae and pupae to be preserved were fixed with boiling water and then placed in 80% ethanol. Vouchers are deposited at the Museu de Zoologia da Universidade de São Paulo, Brazil (MZSP).

TREATMENT AND STUDY OF THE MATERIAL

To photograph the fixed first instars and pupa, a Canon EOS 5D Mark II was used, with Canon MP-E 65–mm 1–5x Macro and Canon EF 100–mm F2.8 L IS USM Macro lenses attached. The photographs were adjusted in the Adobe Lightroom 3.4 program and merged in the Helicon Focus 5.3.12 X64 program.

For scanning electron microscopy (SEM), the larvae were washed with a brush and soapy water, dehydrated in increasing concentrations of ethanol, critical point dried, and then coated with gold. The same procedure was performed with the egg, which was subjected to ultrasound for 3 min before the critical point drying and metallization procedures. The images were prepared at the MZSP Microscopy Laboratory, with a Carl Zeiss LEO 440 scanning electron microscope.

The terminology used for larval description and chaetotaxy follows Duarte et al. (2005, 2009), Pinheiro et al. (2011), and references therein. Pease (1960) and Snodgrass (1935) were followed for mouth parts and some specific structures, and García-Barros & Martín (1995) for the ultrastructure of the egg. Morphological terminology of the pupa is based on studies by Mosher (1914, 1916a, b), with a few changes to the abbreviations. Mosher's (1916a) abbreviations for the thoracic and abdominal pupa segments, as well for the antenna, were changed to (Mosher abbreviations are in parentheses): A1–10 – abdominal segment 1–10 (a1–a10); T1 – prothorax (p); T2 – mesothorax (ms); T3 – metathorax (mt); and ant – antenna (a). The capital abbreviations for the thoracic and abdominal segments have been adopted in several previous articles for larva, pupa and imago. The abbreviation «ant» stands for antenna and has been widely used in several studies.

Material examined of A. fallax. BRAZIL, State of São Paulo, Salesópolis, Boraceia Biological Station, 19–X– 2012, F.F. Albertoni & M.A. Ulys-

seá leg., S 23°38' W 45°52', 900 m, 1 female; from the material reared in laboratory we preserved: 15 eggs, 10 larvae of first instar, 6 of second, 3 of third, 2 of fourth, 1 of fifth, and 1 of sixth instar, 1 male and 1 female pupa, head capsules of all instars, 3 exuviae of mature larvae, 1 one dead prepupal larva (MZSP).

Material examined of the host plant Wisteria cf. *sinensis* (Sims) DC.: BRAZIL, State of São Paulo, São Paulo, Vila Madalena, 5–XII–2012, 1 exsiccate with leaves and flowers, F.F. Albertoni leg. (voucher deposited at the Herbarium of the Botany Department, Universidade de São Paulo, Brazil).

Results

LIFE CYCLE (SUPPL. FIGS. 5–15)

The single female collected in the field produced 96 eggs on 20 and 21 Oct 2012, of which many (approximately 30) were aborted (i.e., they did not hatch). Larvae emerged from 8 to 12 days after oviposition. Most larvae ate their eggshells, and after the third molt (fourth instar), they also ate their exuviae, except the head capsule. They remained, on average, 6 days in each of the first 4 larval stadia, and between 8 and 16 days in the 5th. The 6th instars ate for about 10 days and then migrated to the soil to prepare a pupation site. Pupation took place about 3 to 4 days later. The period from cessation of eating to actual molting was about 2 days for the first 3 larval molts, and at least 3 days for subsequent molts.

BEHAVIOR

The female laid eggs on the surfaces of leaves and on the wall of her container. The eggs were nearly all oriented in the same direction (Suppl. Fig. 5). Larvae were solitary and relatively aggressive toward each other. At rest, the thoracic scoli were held together and directed forward. With any disturbance, even if generated by another larva, they separated the thoracic scoli and occasionally raised the anterior half of the body. This behavior was observed especially in 1st and 2nd instars. Aggression towards each other involved biting with the mandibles; however, there was no evidence that they caused urtication damage to each other or to human skin at any stage of development.

Third and subsequent instars frequently cut part way through the leaflet rachis, weakening it to be able to pull and eat the leaflet while still clinging to the main rachis (Suppl. Fig. 13). Mature larvae burrowed into the soil for pupation without building a pupal chamber. In one case, a larva did not burrow, but instead pupated under a piece of wood measuring approximately 8 × 5 cm.

DESCRIPTION OF THE IMMATURE STAGES (SUPPL. FIGS. 5–70)

Eggs (Suppl. Figs. 5–7, 16–27). Ellipsoid, flattened, with the narrow ends concave. Translucent green, banded with yellow and dark brown a few days after oviposition. Corium with leathery appearance, micro-sculptured with abundant small punctuations and “pore-like openings” (or aeropyles *sensu* García-Barros & Martín 1995) (Suppl. Figs. 23, 24); cells present only in the micropyle region (Suppl. Figs. 18–21). Micropylar axis parallel to the substrate, typically 236–280 µm in diameter, with a rosette of 17 or more elongate obovate cells, each at least twice as long as wide; these surrounded in turn by numerous ranks of polygonal to rounded cells (Suppl. Figs. 16, 25–27).

First instar (Suppl. Figs. 8–9, 28–61). Length 7.5 mm ($n = 1$). Body whitish, yellowish ventrally, with yellow horizontal bars laterally on the metathorax and abdomen. After a few days of feeding the entire body becomes greenish above (Suppl. Fig. 9); ventrally yellow; uniformly

beige after preservation; edges of thoracic spiracles brown; abdominal spiracles whitish. Head length 1.37 mm (SD = 0.02; $n = 13$), width 1.16 mm (SD = 0.02), and length/width ratio 1.18 mm (SD = 0.02); oblong, longer than wide, reddish brown; occiput slightly emarginate, adfrontal arms shorter than epicranial suture; maxillary stipe longer than length of lobes and membranous palpomeres together, maxillary palps with 3 palpomeres, terminal papilla well developed; labrum emarginate medially; 5 stemmata forming a crescent around the S1 seta, the 6th below them, just lateral to the insertion of antenna. Antenna with 3 segments; second antennomere with long apical seta, about 3 times longer than length of antenna. Thorax wider than head, with 5 pairs of dorsal scoli, 1 pair on prothorax, 2 longer pairs on each of meso- and metathorax; scoli long, slender, almost one and a half times length of thorax, with globular apex; dark reddish-brown, with black spines along their length and 3 smaller spines on the globular apex; legs light brown; prothorax with pair of scoli projecting from prothoracic shield, slightly smaller than scoli of meso- and metathorax; legs slightly darkened basally, reddish. Abdomen with prolegs on segments A3–6 and A10 bearing uniserial, uniordinal crochets; A3–6 prolegs dark brown basally, medially and apically translucent yellow; A1–7 with 3 pairs of lateral scoli, these scoli yellow with black apices; all dorsal scoli bifurcated apically; anterior projection spiniform, with one seta longer than posterior seta; internal base of bifurcation usually with small spine transverse to anterior spines; subspiracular scoli with 2 opposing setae and 3 spines; supraspiracular scoli simple, with 1 seta on A1, 1 seta and 1 spine on A2, and 1 seta and 2 spines on each of segments A3–7; A8 with large mid-dorsal scoli (D1 and D2 fused), similar to those of the thorax, but slightly thicker and shorter; A9 with 1 dorsal scoli (D1 and D2 fused) longer than those of A1–7, with 2 opposing apical setae and 2 spines, and 1 supraspiracular scoli similar to subspiracular scoli on segments A3–7; anal plate semi-elliptical, with 3 pairs of scoli on each side: anterior pair each with 3 setae, median pair with single seta, and posterior pair with 1 seta and 1 spine.

Analysis of SEM images (Suppl. Figs. 37–61). Head capsule smooth, bearing primary setae. Stemmata partially projected beyond surface of head. Distal stipe with roughened surface; 3rd maxillary palpomere with 8 sensory cones. Base of hypopharynx densely covered with short setae and apical margin with rough surface; labial palps reduced to 1 pair of papillae with 1 seta each; apex of second antennal segment with 3 sensory cones, 2 close to border and 1, smaller, centrally at the apex of segment; third antennomere very small, with 4 sensory organs at apex. Thoracic scoli covered with warts and micro-setae. Scolus of segment A8 with similar texture but with more widely spaced warts on distal half. Spiracular peritreme (Suppl. Fig. 55) of segment A8 with lateral apparatus, absent from prothoracic spiracle (Suppl. Fig. 54); spiracles of T1 and A8 bearing filter in atrium orifice, consisting of spines with multiple tips. Prolegs of A3–6 and A10 with external surface of plantae micro-sculptured; crochets hidden in central region, when not in use, by a smooth membranous “pad.”

Chaetotaxy. Head with 20 pairs of tactile and microscopic setae (terminology *sensu* Hinton 1946) and 9 pairs of pores (Suppl. Figs. 28–32). Labrum (Suppl. Fig. 31) with 6 pairs of primary setae and 1 pair of pores, distributed as follows: 3 pairs of medial setae (M1, M2, and M3), M1 and M2 subequal in length and nearer midline; M3 shortest, nearer ventral margin of labrum; pore Ma (= puncture *P sensu* Peterson 1962) dorsal and equidistant to setae M1 and M2; 3 pairs of lateral setae (LA1, LA2 and LA3): LA1 dorsal and about half length of LA2, LA3 most ventral. Body chaetotaxy as illustrated in Suppl. Fig. 33.

Second instar (Suppl. Fig. 10). Length 17.24 mm (SD = 1.35; $n = 3$). Very similar to the 1st instar, differing in the following aspects: body greenish with yellow lateral protuberances in subspiracular area of segments A2, A4 and A6; prolegs reddish; spiracles white; abdominal

scoli red with black apices. Head: length 1.67 mm (SD = 0.13; $n = 3$), width 1.52 mm (SD = 0.04) and length/width ratio 1.10 mm (SD = 0.7); greenish with many secondary setae, shorter and finer than primary setae. Prolegs red at base, orange in middle and with row of chalazae at apex. Prothoracic scoli smaller and thinner than those of meso- and metathorax; this size difference being more pronounced in this instar. Dorsal scoli of segments A1, A3, A5 and A7 similar to those of the 1st instar; however, the scoli of A2, A4 and A6 are much more developed, with opposing apical setae and several shorter setae on stem; supra-spiracular scoli red, arising from a yellow, swollen base; subspiracular scoli with several setae, inserted in slight longitudinal protuberance; A8 and A9 with scoli very similar in shape and distribution to those of first instar. Anal plate very similar to first instar, but with 2 medial chalazae. Prolegs of A10 with small protuberances on ventral margin of posterior plate and on anterior margin of leg base.

Third instar (Suppl. Fig. 11). Length 20.32 mm (SD = 2.78; $n = 3$). Differing from the previous instar in the following aspects: prothoracic scoli significantly smaller than those of meso- and metathorax; supra-spiracular and dorsal scoli of segments A2, A4 and A6 pinkish, slightly metallic on latero-external surface, red at apex; scoli of segments A1, A3, A5 and A7 greenish with red apices; spiracles pale green. Head: length 2.95 mm (SD = 0.05; $n = 3$), width 2.46 mm (SD = 0.05), and length/width ratio 1.20 mm (SD = 0.4); with 2 poorly defined whitish stripes; labrum medial notch more pronounced than in previous instars. Legs yellowish at base and reddish at apex. Prothoracic spiracle green. Prolegs with purple base and black chalazae, red apex with chalazae better developed than in previous instars; apices of thoracic scoli and the scoli of A8 slightly expanded and forming slight bulge, with numerous micro-setae. A9 with scoli proportionally smaller than in 2nd instar, more robust and with small anal horn; anal plate with scoli proportionally smaller and more abundant than the 2nd instar, red with dark apices.

Fourth instar (Suppl. Figs. 12, 13). Length 32.67 mm (SD = 3.91; $n = 2$). Differing from the previous instars in the following aspects: prothoracic scoli as small as those of A1, A3, A5 and A7, light green; meso- and metathoracic scoli with bluish spines; supra- and subspiracular scoli varying from light green to bluish; supraspiracular and dorsal scoli of segments A2, A4 and A6 pinkish, metallic on external surfaces, with yellowish apices. Head: length 4.75 mm (SD = 0.33; $n = 2$), width 3.93 mm (SD = 0.25) and length/width ratio 1.21 mm (SD = 0.01); whitish green, with 2 latero-frontal longitudinal stripes, whiter than rest of head; labrum red, twice more deeply emarginate than previous instars. Thoracic legs green. Prolegs bright blue basally, with black, red-tipped chalazae. Scolus of A8 robust, greenish yellow, with pale blue spines; A9 scoli blue-tipped and better developed than previously; apices of A8 and A9 scoli not prominent; anal plate green, bordered with stout tubercles that are orange on lateral margins, blue on apical margin; A10 prolegs with anterior and posterior tubercles blue and orange, respectively.

Fifth instar (Suppl. Fig. 14). Length 54 mm ($n = 1$). Similar to the previous instar, differing in the following aspects: paler, greenish yellow body; thoracic scoli with spines yellowish apically; dorsal scoli of segments A2, A4 and A6 similar in size and color to previous instar; abdominal intersegmental membranes light salmon; A1, A3, A5 and A7 with scoli proportionally more developed than on A2, A4 and A6; dorsal and supra-spiracular scoli metallic, with external surface blue and internal surface yellow; with an elongate, white and blue marking that begins at the supra-spiracular scoli and extends downward to ventral surface of abdomen. A9 and A10 as in fourth instar, but more developed. Head: length 7.87 mm, width 5.63 mm and length/width ratio 1.40 mm; whitish and as rough as in previous instars, with a longitudinal and central greenish stripe (Suppl. Fig. 14).

Sixth instar (Suppl. Fig. 15). Length 54 mm ($n = 1$). Predominantly green with parts almost entirely uniform yellow, including intersegmental membranes; after fixed in boiling water, uniformly beige; thoracic spiracles pale green. Head: length 9 mm, width 7.36 mm ($n = 1$), and length/width ratio 1.22 mm; oblong and finely punctuated, laterally whitish with a longitudinal and central greenish stripe; occipital region with transverse depression and epicranial notch in a deep groove, especially between vertex and occiput; frons medially depressed; labrum well developed with 5 protuberances; clypeus bifurcated; stemmata region dark brown; mandibles black, strongly sclerotized on apical half, basal half lighter and less sclerotized. Prothorax with well-developed spiracles; 2 pairs of short dorsal scoli, green with yellowish apex, with 1 verruca anterior to spiracle and 1 chalaza below it; a protuberance with 3 chalazae near base of prothoracic legs and a smaller chalaza posteriorly. Meso- and metathorax with vestigial spiracles; a pair of long dorsal scoli, inner scoli between 6.5–8.0 mm, and outer scoli approximately 1 mm shorter, with only 1 small chalaza anterior to spiracles; mesothorax with 2 chalazae near base of legs: anterior chalaza long, posterior chalaza less than half length of the former; metathorax protuberance with 2 chalazae near base of legs; upper area of legs dark brown (fixed material in ethanol). Abdomen with dark-green spiracles, and dorsal scoli of segments A2, A4 and A6 as long as dorsal scoli of meso- and metathorax; dorsal and supraspiracular scoli of these abdominal segments yellow or metallic blue, with 1 white and 1 blue marking between supraspiracular scoli and ventral surface of segments; subspiracular scoli typically small with setae at apices; A1, A3, A5 and A7 with well-developed dorsal scoli; A1 and A2 with 3 pairs of ventral chazae; A8 with 1 dorsal scoli larger than dorsal scoli of meso- and metathorax; A9 with short scoli, blue or greenish at apices; anal plate with several reduced scoli, orange laterally, green in middle region, and all blue at apex; posterior margins of prolegs on A10 orange and with small tubercles.

Pupa (Suppl. Figs. 62–70). Integument dark metallic brown, paler on abdominal intersegmental membranes; A10 and cremaster darker than rest of the body. Length (female) 38 mm, width at metathorax 5.8 mm, width at A3 6.7 mm. Body cylindrical, narrowing abruptly from segment A8 to apex of abdomen. Head with several spiniform tubercles, 2 of which are well developed on the frons; vertex not visible dorsally; epicranial suture well marked; frontoclypeal suture weak; gena with row of tubercles and few setae; eyes with meso-external area with small tubercles and few setae (sculptured eye-piece); glazed eye-piece yellowish and glabrous; frontoclypeus with less-developed tubercles; antennae with wide base, wider at end of first 3rd, narrowing abruptly and ending before midlength of hindlegs; base of antennae with few small tubercles and row of cylindrical tubercles extending longitudinally, decreasing in size toward apex; short row of very small tubercles near dorsal border, extending from base to region of abrupt narrowing; elliptical labrum with pair of tubercles; pilifer not clearly visible; maxilla with few small tubercles, short and wide at base, ending beyond two-thirds length of prothoracic legs. Prothorax quite short, and seen clearly only in anterior view; anteriorly with row of tubercles, 2 pairs of well-developed spiniform tubercles in addition to small setae extending laterally; median sagittal line well marked from the mesothorax; prothoracic spiracles elongated and narrow and not clearly visible. Mesothorax well developed, with several spiniform tubercles and sparse setae. Metathorax short, with pair of large rounded dorsal tubercles, black and strongly sclerotized, with smaller and spiniform lateral tubercles. Mesothoracic wings with apex extending almost to posterior margin of A4, anal angle between A3 and A4 rounded, with row of spiniform tubercles on costal margin, with well-marked veins. Metathoracic wings not visible in ventral view and nearly reaching anal angle of forewings, with some robust tubercles on base and

a row of small tubercles; base of wings with many setae. Prothoracic legs relatively enlarged in all its extension, with small tubercles, slightly exceeding midlength of forewings; mesothoracic legs with some small tubercles, longer than anterior legs, ending slightly beyond anal angle of forewings. First 3 abdominal segments visible only in dorsal view, each with 2 transverse lines of tubercles (most apical tubercles distinctly developed), and with several short setae; spiracles of A1 not visible; segments A2–7 with well-developed spiracles with white filter apparatus (*sensu* Schmitz & Wasserthal 1999), those of A2 and A3 with lateral crescent of tubercles; segments A4–7 have 2 bands of spiniform tubercles, anterior band – aligned with the spiracles – better developed than posterior band; segments A5 and A6 freely moving; ventrally with conspicuous scars of prolegs; intersegmental areas of A4–6 pale brown and striated; anterior margin of A5–7 with dorso-lateral band of carenae; A8 with spiracles larger and slightly higher (more dorsal) than other segments, ventral surface smooth, except for the genital pore (in females), laterally with 2 rows of spiniform tubercles; dorsally with tubercles in same position as anterior line; A9 with dorsal and lateral row of well-developed spiniform tubercles, ventrally smaller and interrupted near anal-pore region of A10; A10 with lateroventral setae and pair of spiniform tubercles laterally. Cremaster 5 mm long, with apical fork, and many short, forked setae distally.

Discussion

Few studies have discussed general aspects of the morphology of the egg, larvae and pupa, and development patterns in Saturniidae (Packard 1905; Crotch 1956; Furtado 2000, 2001; Fronza et al. 2005). The morphology and biology of the immature stages of *A. fallax* are discussed and compared with other species of the genus and subfamily of these little-known moths.

LIFE CYCLE

The duration of each larval stadium differed markedly between *A. schubarti* and *A. fallax*. In the former species, each of the first 5 larval stadia lasted 3 days, about half the time observed for *A. fallax*. The duration of the final larval feeding period was roughly the same for both species. Other behavioral characteristics of *A. fallax* resembled some notes on *A. schubarti* by Furtado (2001).

Pupae were found buried a few millimeters beneath the surface of the ground. Pupation occurred in the soil, without a well-defined pupal chamber. Similar behavior was observed in *A. schubarti* and *Megaceresa pulchra* (Bouvier, 1923) (see also Furtado 1999, 2001). In contrast, larvae of *Psilopygida (Psigida) walkeri* (Grote, 1867) use debris and their own secretions to fashion a pupation chamber (Furtado 2000).

Lemaire (1988) referred to *Inga* sp. as a larval host plant of *A. fallax*. In the present study, in addition to *Inga* sp., we offered the larvae *Wisteria* cf. *sinensis* (Sims) DC. (Leguminosae: Papilionoideae), an Asian plant that has been cultivated worldwide, and is popularly known in Brazil as glicinia.

MORPHOLOGY

The egg of *A. fallax* does not differ greatly from eggs of other Ceratocampinae, such as *A. schubarti*, *P. walkeri* and *M. pulchra*, sharing with these species the greenish coloration and discoidal shape (Furtado 1999, 2000, 2001). As far as we know, the present study is the first detailed description of the egg ultrastructure of a ceratocampine moth.

In general, larvae of *A. fallax* are very similar to those of *A. schubarti* described by Furtado (2001), differing in few aspects. The 1st in-

stars of both species are alike, but differences appear in subsequent stadia, and become more accentuated in mature instars. The 1st instar *A. schubarti* can be distinguished by the presence of a narrow yellowish stripe along the spiracular area; thoracic and A8 scoli with bifurcated apices (instead of the globular apex with two spines of *A. fallax*) (Suppl. Figs. 8–9, 34–36, 51–52).

From the 2nd larval stadium on, *A. fallax* and *A. schubarti* differ in a number of characteristics (those of *A. schubarti* are in parentheses). The 2nd instar is characterized by a green head (green with yellow bands); thoracic scoli uniformly reddish, with black spines (reddish with apical yellow ring); spiracular furrows yellow only on A2, A4 and A6 (same color pattern, but extending laterally to the end of each segment); abdominal scoli of A2, A4 and A6 red (yellow). Third instar characterized by head capsule with faint white bands (bands yellow); metallic markings on T3, A2, A4, A6 and A8 pink (yellow); dorsal scoli of A2, A4 and A6 pink and red apically (golden yellow and brownish yellow on the outer and inner surface, respectively); lateral stripe of the anal plate reddish and with scoli (lateral stripe yellow, without scoli). Fourth instar characterized by prothoracic scoli green (yellow), smaller than those on the meso- and metathorax of *A. schubarti*; meso- and metathoracic scoli green with lateral spines (scoli reddish with paler color at apex); outer and inner dorsal scoli on T3 identical (outer dorsal scoli silver); scoli of A2, A4 and A6 with external lateral surface metallic pink, followed by a pink stripe (silver on the external lateral surface, followed by a yellow stripe); supraspiracular scoli vestigial (absent); scoli on A8 green with blue lateral spines (reddish with green and yellow base); prolegs differently colored blue, orange, green and red (same color pattern as integument, with reddish macules). Fifth instar characterized by indistinct longitudinal stripes on the head (green head with distinct yellow stripes); thoracic scoli green as on the integument, with yellow apices and lateral microspines (differently colored, with meso- and metathoracic scoli orange, green apically); base of meso- and metathoracic scoli and of segment A8 with micro-spines.

In his extensive work, Lemaire (1988) presented a series of photographs of final instars of various ceratocampines, including *A. isara* and *A. subangulata*. The final instar of these 2 species matches the 5th and 6th instars of *A. fallax* reared in our laboratory. In *A. isara* the thoracic and abdominal dorsal, supra- and subspiracular scoli are relatively larger than in *A. fallax* and *A. schubarti*, with no significant differences in size among the scoli of A1, A3, A5 and A7 and A2, A4 and A6, as observed in the larvae of *A. fallax* and *A. schubarti*.

Howse & Wolfe (2011) illustrated the presumptive final instar of *Syssphinx quadrilineata* (Grote & Robinson, 1867). It resembles larvae of *Adeloneivaia* (except *A. isara*), *Psilopygida* (*Psigida*) oiticica, 1959 and *Megaceresa* Michener, 1949 (in the 4th instar). However, the final instar of *S. quadrilineata* differs in the presence of numerous small scoli throughout the body, and a band of short, rounded scoli on the prothorax. Howse & Wolfe (2011) also illustrated a larva of *Syssphinx molina* (Cramer, 1780), which differed in general appearance from *S. quadrilineata*, in having the meso- and metathoracic scoli shorter, similar to each other in shape, and with a metallic appearance on segments A4 and A6.

The pupae of Ceratocampinae are characterized by having a bifurcate cremaster, the body covered with stout spines, a pair of tubercles on each side of the metanotum, and pupation occurring just beneath the soil surface (Mosher 1914). Although Mosher (1914) did not study pupae of *Adeloneivaia* or even species belonging to the most closely related genera such as *Adelocephala*, *Othorene* or *Syssphinx*, which later were transferred to *Adeloneivaia* (see Lemaire 1988), the general description used to characterize the subfamily is consistent with subse-

quent studies (Dias 1978, 1981, 1982, 1986, 1991; Lampe 1987, 2010; Furtado 1999, 2000, 2001) and with the results of the present study.

Comparing the pupa of *A. fallax* with the descriptions and illustrations available for *A. schubarti*, *M. pulchra* and *P. walkeri*, which are Neotropical Ceratocampinae, the one that least resembles the pupa of *A. fallax* is *P. walkeri*, which differs in having a rough integument (smooth in *A. fallax*) and in lacking spiniform projections or projections as long as those that occur in *A. fallax*, especially those of the prothorax, head, and abdominal segments.

The pupa of *M. pulchra* differs from *A. fallax* by having the 4 largest projections of the pronotum and the pair of frontal projections on the head long and acute; as well, these projections are oriented differently from those of *A. fallax*; mesonotum with 2 long sharp lateral projections (*A. fallax* has a short robust projection with a narrow apex, but not elongated), 1 large and 4 small projections on the dorsum (*A. fallax* has a pair of robust projections and 2 additional pairs of projections similar to, but smaller than the first pair).

The pupal morphology of *A. schubarti* does not differ significantly from *A. fallax*. The specimen illustrated by Furtado (2001) has all spiniform projections proportionately larger than those of *A. fallax*. This size difference is clearly visible in the projections on the frontal area of the head, and also in the 4 largest projections on the pronotum, with the orientation of the external pair differing; both members of the pair are oriented forward in *A. schubarti*, and face the opposite sides of the body in *A. fallax*. Both *A. schubarti* and *M. pulchra* have a pair of long sharp projections laterally on the mesonotum, the anterior pair being larger than the posterior, and, the integument of the wings has a rough and grainy appearance.

Remarks

Some morphological characters of the pupa of *A. fallax*, here compared with the data available for other saturniid species, particularly other Ceratocampinae, proved to be potentially useful for phylogenetic studies, as discussed below.

Body integument glabrous with a polished appearance, contrasting with a rough or rugged condition. The glabrous integument is shared with 3 species of *Adeloneivaia*: *A. fallax*, *A. jason* and *A. schubarti*. *Megaceresa pulchra* also has a polished glabrous integument. In *P. walkeri* and *Anisota dissimilis* (Boisduval, 1872) the integument may be mat, rugged or rough (Lampe 1987; Furtado 2001).

A row of well-developed projections along the length of the antennae, and positioned ventral to a row of minute projections. According to Mosher (1914), antennae with 2 rows of projections occur in *Syssphinx bicolor* (Harris, 1841) (but with the developed projections positioned dorsally), *Anisota virginensis* (Drury, 1773) and *A. senatoria* (J. E. Smith, 1797) (with 2 rows of minute projections positioned medially). Notably, *Adelocephala* and *Anisota* both include species with only 1 row of projections on the antennae. The pupa of *A. jason* may have more than 2 rows of projections (Lampe 2010), as in *Adelowalkeria flavosignata* (Walker, 1865) (Dias 1986). A row of minute projections was observed in *Procitheronia principalis* (Walker, 1855) (Dias 1991) and a row of medium-sized projections in *Citheronula armata* (W. Rothschild, 1907) (cited as *Citheronia armana* by Dias 1981). The absence of projections or a vestigial condition is shared with *Citheronia laocoon* (Cramer, 1777) and *Citheronia hamifera* W. Rothschild, 1907 (see Dias 1981, 1982).

Antennae not extending the length of the mesothoracic legs and with divergent apices. This seems to be a universal characteristic in pupae of Ceratocampinae, occurring also in many other members of Saturniidae. However, in some species of Bunaeini (Saturniinae) (see Rougerie & Estradel 2008), the antennae may touch or almost touch apically.

Galeae not extending the length of the mesothoracic legs, a characteristic shared with *A. fallax* and 3 other species of *Adeloneivaia*: *A. jason*, *A. schubarti* and *A. flavosignata* (information available in Dias 1986; Lampe 1987, 2010; Furtado 2001). However, the length of the galeae may vary in Ceratocampinae; in some species they end either at the apex of the mesothoracic legs or exceed this limit, as observed by Dias (1978, 1982, 1991) and Lampe (2010) in species of *Citheronula* Michener, 1949 and *Citheronia* Hübner, [1819].

Presence of 4 pointed spines on the median line of the prothorax. These spines can be observed in pupae of several Ceratocampinae; in some species the spines are well-developed and pointed as in *M. pulchra* (see Furtado 1999), poorly developed as in *A. jason* and *A. subangulata* (see Lampe 2010), or absent as in *P. walkeri* (see Furtado 2000), *A. dissimilis* (see Wolfe & Peigler 1993), plus a number of other species of the subfamily, particularly those species that belong to the clade Eac–Sch *sensu* Balcázar–Lara & Wolfe (1997: 6) (see also Dias 1978, 1981, 1982, 1991; Lampe 2010).

Forewing pad with projections on the costal margin. With respect to this characteristic, *A. fallax* is similar to *A. subangulata*, but differs from many other species including *A. jason*, *A. schubarti* and *A. flavosignata*, which have several rows of short projections on the wing surface (Dias 1986; Lampe 1987, 2010; Furtado 2001).

Pair of rounded tubercles on the metathorax. These tubercles have been recorded for a number of ceratocampine moths, and are relatively well developed. To be considered a synapomorphy of the subfamily, this characteristic should be analyzed in a larger number of species.

Anterior and posterior margins of segments A1–3 with a row of small projected tubercles. These tubercles are not observed in *A. schubarti*, except for some spiniform projections on the anterior margin of A1–3. More information on other species of *Adeloneivaia* is still needed.

Cremaster projected, apically forked, with A10 bearing a pair of shallow invaginations at the base of the cremaster. Apparently, the cremaster is not forked in *Neocarnegia basirei* (Schaus, 1892) (see Lampe 2010); however, the cremaster projected and with a bifid apex was considered a synapomorphy of Ceratocampinae in the study of Balcázar–Lara & Wolfe (1997), and occurs in virtually all known pupae of the subfamily. Additionally, the characters of *N. basirei* were previously considered plesiomorphic, hypothetically being the sister-species of other Ceratocampinae (Balcázar–Lara & Wolfe 1997), and also considered by Lemaire (1988) as a species whose taxonomic position was difficult to place within the subfamily.

In addition to this list of characters, other morphological aspects of the pupal stage vary in Ceratocampinae. The glazed eye-piece, which may represent the pupal eye, is not found in all species, nor are the bands of spiniform projections near the anterior and posterior margins of the abdominal segments. The anterior margin of segment A8 may show a variable and dense punctation, which was used by Dias (1991) to distinguish pupae of *Procitheronia* and *Citheronia*.

Finally, Rougerie & Estradel (2008) pointed out a number of characters for the pupa of *Bunaeopsis licharbas* (Maassen & Weyding, 1885) (Saturniinae), and compared them with other species of the same subfamily. Thus, with potentially informative characters existing among some members of suprageneric groups within the Saturniinae, comparisons with characters observed in the pupae of *A. fallax* were feasible. Pupae of Arsenurinae, Hemileucinae, Oxyteninae and Saturniinae (Aiello & Balcázar–Lara 1997; Mosher 1914, 1916a, b; Rougerie & Estradel 2008; Specht et al. 2007, 2008, 2009, 2011) differ from each other and from species of Ceratocampinae. Additionally, there are characters with less-discernible variation found among related species representing categories between suprageneric and family level.

CONSIDERATIONS ON STUDIES WITH IMMATURE STAGES OF SATURNIIDAE

Our knowledge of holometabolous insects should not be limited to the adult semaphoront. It is essential to know in detail all stages of the life cycles of species in order to provide maximum support for phylogenies. Unfortunately, it is not as common to use of morphological characters of the immature stages as it is to use adult characters, even though immature characters tend to provide better-resolved topologies (Meier & Lim 2009).

The immature stages of Lepidoptera can provide an abundance of characters, not only their morphology, but the behaviors of the living animals. Thus, it is essential that the entire life cycle be described in detail. The position in which the eggs are laid varies in different subfamilies and genera of Saturniidae; the pupal chambers, when present, have significantly different forms: some are hung and attached by silken threads, as observed in *Rothschildia hesperus* (Linnaeus, 1758), *Attacus atlas* (Linnaeus, 1758) (Saturniinae), and in some other species (see Crotch 1956); the pupal chambers may also be defined as a net, with thicker threads and perforated by relatively large spaces as in *Cricula trifenestrata* (Helfer, 1837), *Cricula agria* Jordan, 1909 and *Saturnina simla* Westwood, 1847 (Crotch 1956; Lampe 2010). Cocoons may be constructed with a double, single, or solid wall; composed of entire or perforated leaves, larval feces, or soil particles; and the pupal chambers may be constructed above or below ground.

Other important information includes the larval color and pattern as well as accurate records of the collecting site, the host plant(s), and the part of the plant used as larval food. The color pattern of the larval integument may vary intraspecifically in several members of Saturniidae, and this depends both on which part of the plant the larvae eat, and where the species occurs (Nentwig 1985; Rougerie & Estradel 2008; Lampe 2010).

In addition to the variation in the cocoon shape and larval color pattern, the morphology of immatures must be analyzed carefully, thoroughly illustrated, and described in detail. Last, we applaud the words of encouragement of Rougerie & Estradel (2008) for those researchers dealing with descriptions of the immature stages of saturniids, to develop their articles in the richest possible way, with detailed illustrations and descriptions, and providing the scientific community with good data for use in future phylogenetic studies involving Saturniidae and other groups of Lepidoptera.

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