



Natural history of the mistletoe-feeding *Thereus lomalarga* (Lepidoptera, Lycaenidae, Eumaeini) in Colombia

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Abstract

The natural history and morphology of the immature stages of the butterfly *Thereus lomalarga* Robbins, Heredia & Busby are described and illustrated. The food plant is *Oryctanthus alveolatus* (H.B.K.) Kuijt (Loranthaceae). Chaetotaxy of the first instar is described and compared with that of three locally studied *Thereus* species. Larvae have four instars, and the dorsal nectary organ becomes functional in the third instar. They are facultatively tended by ants belonging to seven genera that are attracted to *O. alveolatus* by floral disc nectaries, honeydew producing Hemiptera, and secretory wounds produced by Hemiptera on the fleshy inflorescence rachis. The average period from egg to eclosion under lab conditions was 35.68 days. Females emerged before males. Adults of both sexes feed on nectar from the flowers of the food plant and on hemipteran secretions; adults were not observed feeding on other flowers. Campopleginae and Chalcidinae were the most important parasitoids.

Key words: Chaetotaxy, crypsis, honeydew, immatures, life cycle, Loranthaceae, myrmecophily, protogyny, *Thereus ortalus*

Resumen

Se describen e ilustran la historia natural y la morfología de los estados inmaduros de la mariposa *Thereus lomalarga* Robbins, Heredia & Busby. Se documenta la chaetotaxia de primer instar y se compara en tres especies del género estudiadas localmente. Las larvas tienen cuatro instares y desde el tercero es funcional el órgano dorsal de néctar. Son atendidas facultativamente por hormigas que pertenecen a siete géneros y que llegan a su hospedero, *Oryctanthus alveolatus* (H.B.K.) Kuijt (Loranthaceae), atraídas por los nectarios del disco floral, por hemípteros productores de honeydew, y por heridas ocasionadas por hemípteros en el raquis carnoso de la inflorescencia. El promedio de duración del ciclo de vida fue 35.68 días y las hembras nacieron antes que los machos. Adultos de ambos sexos se alimentaron del néctar de las flores de su hospedero y de las secreciones de los hemípteros; nunca se observaron libando de otras flores. Los principales parasitoides fueron Campopleginae y Chalcidinae.

Palabras clave: Chaetotaxia, cripsis, estados inmaduros, ciclo de vida, Loranthaceae, mirmecofilia, protoginia, *Thereus ortalus*

Introduction

The newly described hairstreak butterfly *Thereus lomalarga* Robbins, Heredia, & Busby is found from Costa Rica to the western slope of the Andes in Ecuador, and occurs in the great variety of forested habitats from sea level to 1600m elevation. The males are exceedingly rare. They have been collected at only one site despite more than a century of butterfly collecting in Costa Rica, Panama, western Colombia, and western Ecuador (Robbins *et al.* 2015).

Thereus contains 35 Neotropical species, of which two are included provisionally because of divergent morphology (Robbins 2004, Robbins *et al.* 2015). The genus *Rekoa* Kaye appears to be the closest relative of

Thereus (Robbins 1991, Quental 2008) and is a polyphagous genus, with two of its species each reared from about 20 plant families (Monteiro 1991, Robbins 1991). In contrast, all listed *Thereus* food plant records (Table 1) are in the family Loranthaceae except for one polyphagous species, which is one of the species that is provisionally included in *Thereus*.

The plant order Santalales, which includes the mistletoes, is the second most important caterpillar food plant after Fabales for the Lycaenidae (Fiedler 1995). Following the plant classification in Nickrent *et al.* (2010), mistletoe-feeding Lycaenidae worldwide primarily eat Viscaceae and the subtribe Psittacanthinae of the Loranthaceae (Atsatt 1981a, Whittaker 1984a, Ackery 1991, Fiedler 1995, Congdon & Bampton 2000, Ballmer 2008, Beccaloni *et al.* 2008). In the New World, lycaenid genera that specialize on mistletoes belong to *Thereus* Hübner (Table 1), *Atlides* Hübner, *Brangas* Hübner, *Callophrys* Billberg, and *Thepytus* Robbins (Sepp 1829–1843, Haskin 1933, Zikán 1956, D'Araujo e Silva 1967–1968, Whittaker 1984a, Ballmer & Pratt 1988, Fiedler 1995, Uchôa & Caires 2000, Beccaloni *et al.* 2008, Robbins *et al.* 2010, 2015, Uchôa *et al.* 2012, Janzen & Hallwachs 2015).

Oryctanthus alveolatus (Loranthaceae) is the most abundant hemiparasite, especially on *Miconia* (Melastomataceae) and *Vernonanthura* (Asteraceae) (Fig. 25) at Loma Larga (the study site for which the butterfly is named). Eggs and caterpillars of *T. lomalarga* were discovered on *O. alveolatus*; we document their life history. Additionally, knowledge of the food plant facilitated observations of adults in the field. In other words, discovery of the immatures allowed us to study the biology of both immatures and adults. Our results show that oviposition, larval feeding, adult feeding, and interspecific interactions, are centered on the mistletoe plants.

This paper presents observations on the morphology and behavior of the immature stages of *T. lomalarga*, its host plant, length of its life cycle, behavior of adults, and mortality factors. We also describe for the first time the chaetotaxy of the first instar of a species of *Thereus*. We compare our data on eggs and first instars, whose characters are considered to be more conservative at the genus level than later instars (Kitching 1985), with those of other Eumaeini (Ballmer & Pratt 1992) and two other *Thereus* species at Loma Larga (unpublished data). The life history of only one species, *T. pseudarcula* (Giacomelli), has been published (Walkmann & Núñez 2014) but it is not sufficiently detailed to allow comparison with *T. lomalarga*. The present work also discusses some aspects of conservation, such as the effectiveness of encouraging and protecting natural regeneration as a management practice in Loma Larga.

Materials and methods

The Loma Larga study area is in Pance, Cali, Valle del Cauca, southwestern Colombia (1200 m, 3°19'N, 76°34'W). It is located in the foothills of the eastern slope of the Western Andes on the outskirts of the Farallones de Cali Natural National Park. It is part of a suburban housing project that includes 62 ha of forest in several stages of natural regeneration, on soils formerly degraded by fire and cattle ranching. The Holdridge Life Zone is Premontane Humid Forest with a mean annual temperature of 17–24°C and average total annual precipitation of 2000–4000 mm (Espinal 1968). Vegetation is mostly early successional forest along steep slopes and creek margins where *Schefflera morototoni* (Araliaceae), *Miconia* (Melastomataceae), *Vernonanthura patens* (Asteraceae), *Myrsine pellucida* (Primulaceae), *Eugenia* (Myrtaceae), *Persea caerulea* (Lauraceae), *Ocotea aurantiadora* (Lauraceae), and *Cupania latifolia* (Sapindaceae) are common trees and shrubs.

On 19 April 2009 a second instar of *T. lomalarga* was found feeding on an early inflorescence of the hemiparasitic *O. alveolatus* that grew on a branch of *Miconia minutiflora* (Bonpl.) D. C. at 2.0 m above ground at the forest border. Observations and collections of life stages of *T. lomalarga* were made primarily from October 2010 to June 2011, although additional observations have continued, but 80% of the immatures of *T. lomalarga* were collected from March to June 2011 thanks to an improved search image. Hundreds of *O. alveolatus* plants were inspected at all heights above the ground. The most efficient way to locate larvae was to look for recently hatched eggs because the first instars are then found on the same spike. Later on, larvae disperse and are difficult to find, but pre-molt larvae were often found on top or underneath the leaf blade, near the base's border (Figs. 43, 47, 48). Only four 4th instars and one pupa were found in the field.

Eggs, larvae, and pupae were kept in glass containers at local ambient conditions, with a 12L/12D photoperiod and an average temperature about 23°C. Larvae were provided fresh food *ad libitum*. Early stages were examined with a Nikon SMZ 745 stereomicroscope at magnifications up to 100X. They were measured with 0.01mm

precision grids. Larval stages were identified by head capsule width (mean width and its standard deviation are reported). Caterpillar length was measured at the beginning and end of each stadium from the anal border to the T2 cephalic border. Pictures were taken with a Nikon Coolpix P80 digital camera; eggs, first instars, and exuviae, were photographed through the stereomicroscope's ocular lens. Figures 13 and 14 were taken with a Canon T3i camera and Helicon Focus program through an illuminated Nikon Eclipse microscope. Exuviae of second, third, and fourth instars were processed (Hinton 1956, Stehr 1987: 15) using 25% acetic acid to follow the development of the dorsal nectary organ (Figs. 20–24). Vouchers of immatures are deposited in the Museo de Entomología de la Universidad del Valle, Cali, Colombia. Finally, adult behavior was observed in the field with binoculars.

Immature stages of *Thereus ortalus* (Godman & Salvin) and an undescribed species of *Thereus* (Robbins in prep.) were also observed (unpublished data). We follow Stehr (1987) for morphological aspects in general, and Ballmer and Wright (2008) for first instar chaetotaxy. However, due to its position, we changed SD3 to D3 to refer to the "extra" seta associated with D1 and D2 in the Lycaenidae (Fig. 13). Setae and lenticles are mentioned only for half the body.

Lengths and development times are reported by their mean, standard deviation, and sample size, represented by X, SD, and N, respectively. Differences between males and females were analyzed using the non-parametric Mann Whitney U test and G test.

Results

The larva food plant. *Oryctanthus alveolatus* (Figs. 25–27) occurs widely in Colombia below 1500m elevation in the western Chocó, the inter-Andean valleys, and in the eastern Orinoco and Amazon drainages (Dueñas & Franco 2001). In the study area *O. alveolatus* is the most abundant hemiparasite, growing on almost all trees and shrubs at a variety of heights above the ground. Its flowers and fruits are borne in linear cavities (grooves) of a fleshy rachis. Few or many spikes may grow along the racemose inflorescence, in the axillae of the leaves, or from terminal buds. The spikes may be relatively young with a few fruits in a single row or may be relatively old with 25 fruits or more, of which a majority may have already been removed by birds: *Mionectes oleaginous* (Lichtenstein), *Myiozetetes cayanensis* (Linneo), *Phaeomyias murina* (Spix), *Phyllomyias griseiceps* (P.L. Sclater & Salvin), *Carduelis xanthogastra* (du Bus de Gisignies), *Tangara cyanicollis* (Orbigny & Lafresnaye), *Tiaris obscurus* (Orbigny & Lafresnaye), *Tyrannulus elatus* (Latham) and *Zimmerius viridiflavus* (Tschudi) among the more frequent ones. There are almost always ants at food sources such as floral nectar deposited in nectariferous disks, the exudates at the "wounds" made by insects on the fleshy rachis, and the "honeydew" excretions of Hemiptera (Membracidae, Coccidae, and Pseudococcidae) (Figs. 28–33, 34–38, 43 and 47). Ants of nine genera were collected, some of which also make their nests in branches of the mistletoe or its host plant. Inflorescences of *O. alveolatus* do not last very long in the laboratory. About two days after collection, the spikes fall off with larvae lodged in flowers and fruits, making it necessary to move the larvae to fresh food. To successfully rear caterpillars of *T. lomalarga*, a nearby source of *O. alveolatus* is necessary.

Morphology of immatures

Eggs (Fig.1). The freshly laid egg of *T. lomalarga* is hemispheric and yellowish-white, but turns white a few hours later. Eggs are usually laid singly on the sides of flower buds near the tip of an inflorescence of *O. alveolatus* (Figs. 25, 26). In one instance two eggs were laid on the same flower. The micropylar area is slightly depressed. The egg surface is smooth with minute cells without tubercles, and a minute pit in each one. The chorion is thick, and the developing head is never visible through it. The egg's base has a thin chorion sculpted throughout with polygonal cells. Larvae consume the micropylar area and the part of the egg just around it. Diameter 0.52–0.60mm (X=0.56mm, SD=0.02, N=28); height 0.27–0.40mm (X=0.35mm, SD=0.04, N=16). Duration 4–6 days (X=4.58 days, SD=0.61, N=17). The data on duration of the egg stage were obtained from five eggs that we observed being laid and from 12 eggs that we found while checking marked spikes of *Oryctanthus*.

First instar (Figs. 2, 13, 14). The head capsule of *T. lomalarga* is light brown with darker mandibles and black stemmata. The body is yellowish like the mistletoe flower buds. In contrast, the prothoracic shield, anal shield, lenticles (also called *pore cupola organs*, PCOs), and chalazae are brown. The larva gradually becomes green, but an area from A6 through A10 has a light reddish-brown tinge. The caterpillar has a trapezoidal shape when feeding because the head capsule and prothorax are "hidden" inside the floral buds. It has a similar trapezoidal shape during

pre-molt phases because the head capsule and prothorax are retracted inside segment T2. When stretched, the length of the "retracted area" is about one third of the total length of the larva. Dorsally, the larva is concave from segments T2 through A6 with well-marked brown chalaza in the dorsal border. Towards maturity the line between segments is sinuous, and inside each segment lateral sinuses give the cuticle a corrugated aspect.

The first instar of *T. lomalarga* appears to have few setae in contrast to larvae of other lycaenid genera. For example, with low power optics setae are seen only in the dorsal region and around the ventral and anal borders (Fig. 2). There are cream-colored D1 setae, which are spiculated and decumbent, associated with the chalazae. These setae are directed backwards, except at T2, where setae at its cephalic border are directed forwards. Both dorsal and border setae are 0.15mm long. At higher magnifications, other minute setae are observed (Figs 13, 14).

Lenticles are dorsal (DL) on segments T2, A7, and A8 and are subdorsal (SDL) on T3–A6. Ventrally, there are other, smaller lenticles (SVL).

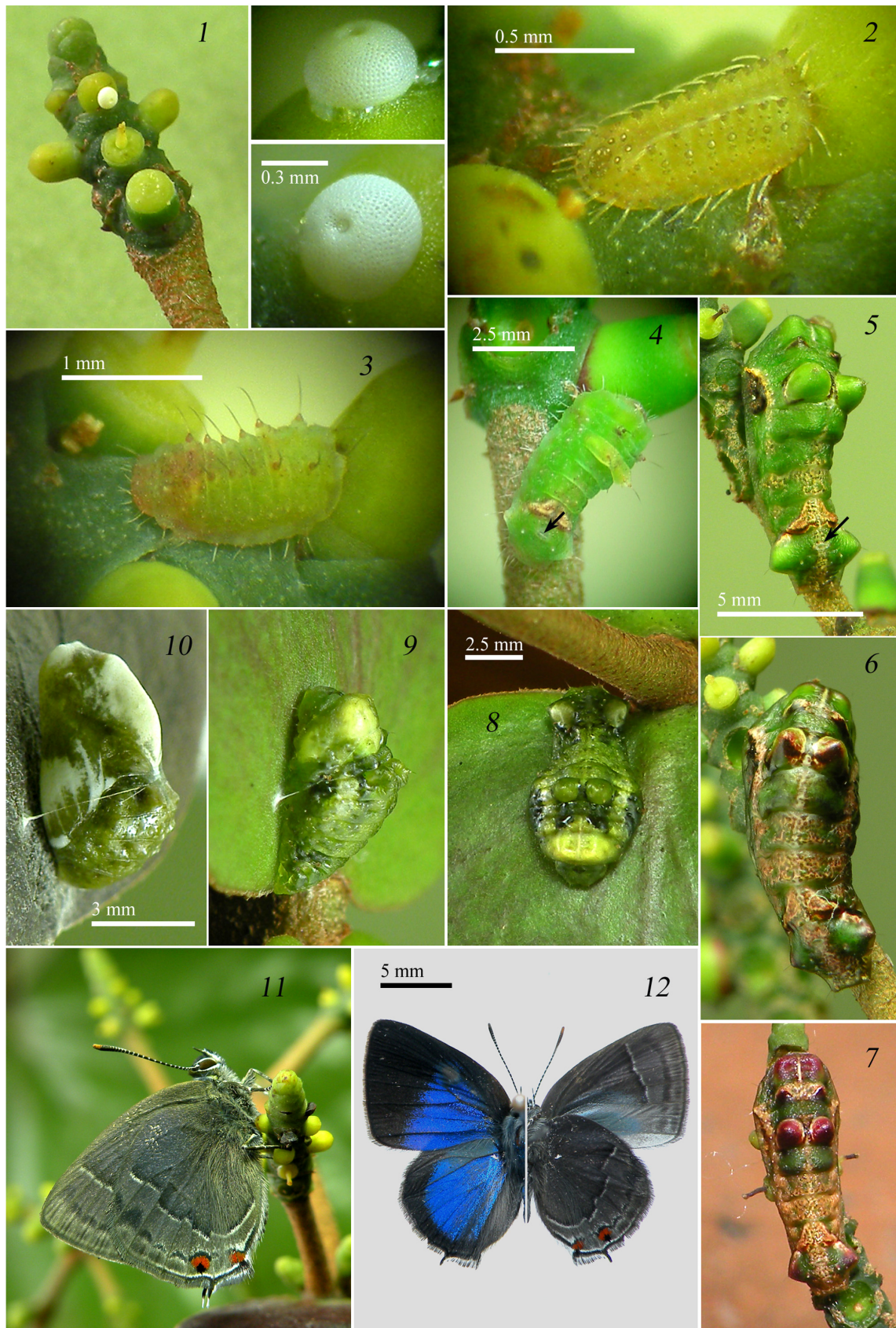
Thorax. T1. Prothoracic shield brown, 0.10mm wide, 0.34mm long. Only XD1 and XD2 setae are visible and are equally long, 0.05mm, on the anterior border and at each side of DL (dorsal lenticle). D1, D2, and SD1 are not visible with 100X. Anterior to the cephalic border of the shield and ventral to XD2 there are three setae in a straight line, the "fringe setae" F1, F2, and F3. F2 is the longest and the same size as XD1 and XD2. Only one lateral seta, L, is anterior of the spiracle, as are two subventral setae SV1 and SV2. **T2.** With D1, D2, and D3, directed forwards from well-developed chalazae, one DL, SD1 from a chalaza and SD2 a small spot, L1 from a chalaza and L2 a small spot, SV1 and SV2. **T3.** Has one SDL (subdorsal lenticle) and only D1 from a chalaza, D2 and D3 small spots, SD1 from a chalaza, and SD2 a small spot; L1 from a chalaza, L2 a small spot; SV1 and SV2.

Abdomen. A1. With two subdorsal lenticles, one large SDL above and a smaller SDL2 ventrally; only D1 from a chalaza, D2 and D3 small spots; SD1 and SD2 small spots; one LL (lateral lenticle); four L setae, three like small spots, and only one from a chalaza L1; SV1 and V1. **A2** is similar to A1, has no LL, but has one SVL (subventral lenticle). **A3–A6** is similar to A2 but with two ventral setae, V1 and V2. **A7** has one DL and one SDL; D1 from a chalaza; SD1 and SD2 as small spots; L1 from a chalaza, and L2, L3, and L4, as small spots. SVL and SV1. **A8** is similar to A7 but has only one SD1 and one L1. **A9–A10** with D1, L1, L2, L3, L4 from chalazae; PP1, PP2, and SV1, SV2, SV3, SV4.

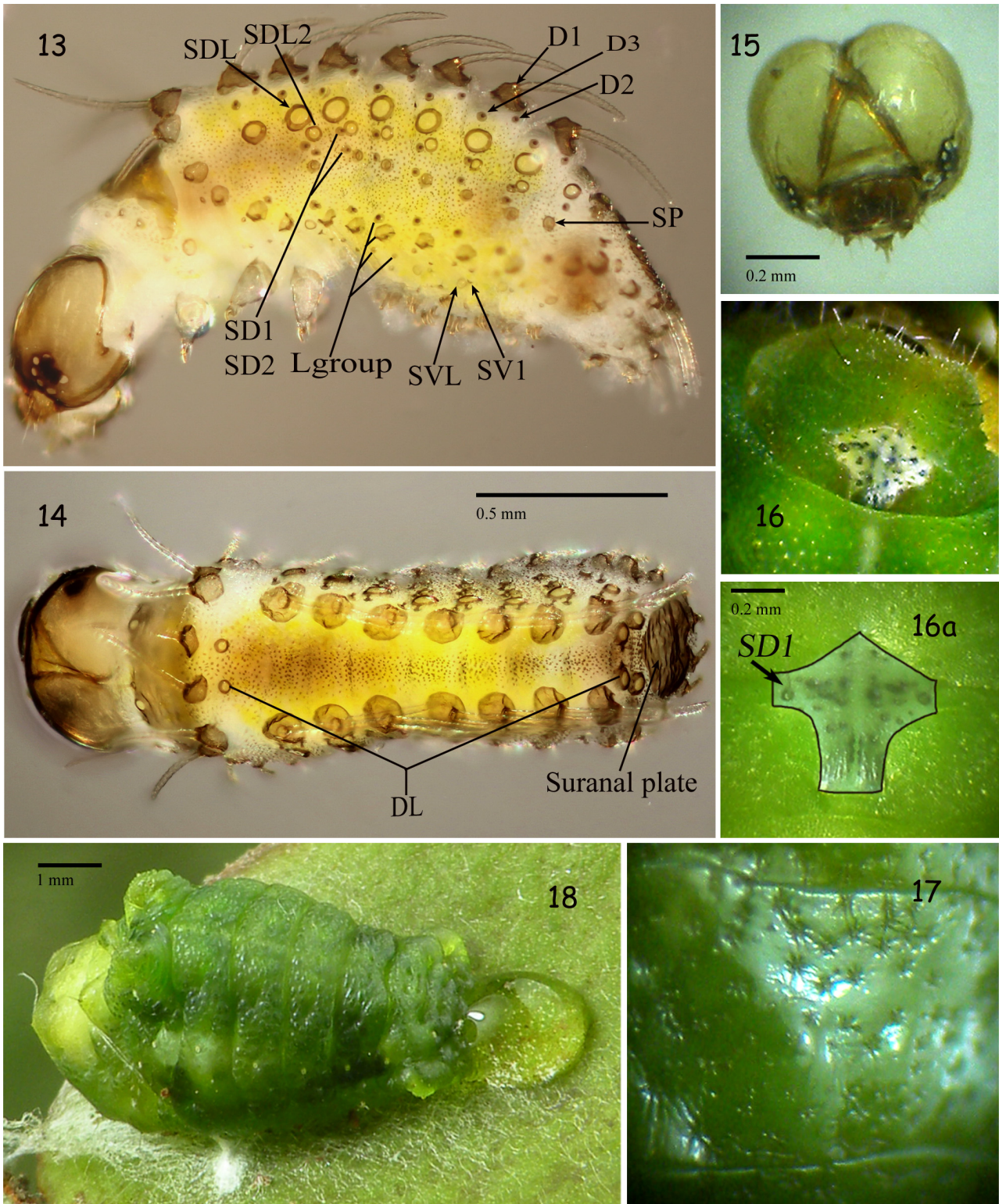
The larva has a lateral height of 0.70mm at its highest point on A3. Head capsule width 0.20–0.25 mm ($X=0.22$ mm, $SD=0.01$, $N=14$). Minimum body length 0.60–0.85 mm ($X=0.74$ mm, $SD=0.07$, $N=19$). Maximum body length 1.50–1.80 mm ($X=1.65$ mm, $SD=0.09$, $N=19$). Duration 5–6 days ($X=5.53$ days, $SD=0.51$, $N=19$).

Second instar (Fig. 3). In *T. lomalarga*, SD1 ("sensory setae" *sensu* Ballmer & Pratt 1988) is filiform, 0.07mm long, and located on the brown prothoracic shield, which measures 0.27mm by 0.15mm. The larva is greenish with dorsal reddish-brown shading from A6 to A10. The dorsal chalazae are located at the vertex of a conic protuberance from T3 to A6, except for A1, and the setae are longer, 0.25mm, vertical and grayish. The other segments lack protuberances and vertical setae. The ventral border, as in the first instar, is surrounded by cream-colored setae up to 0.20mm long. Dorsally and laterally the body has dispersed lenticles and dark spots that correspond to minute setae. The dorsal nectary gland (DNO) is not functional, lacking the outlet rings of the glandular bladders. There are six grouped lenticles (diameter 0.02mm) and four bifurcated setae surround the DNO area (Fig. 20). The cream-colored spiracle of A8 is the most conspicuous; at the ventral border between segments A7 and A8 there is a lateral conic protuberance (which persists in the remaining instars). Towards the end of this instar in A6, a yellowish brown pattern appears. Head capsule width 0.35–0.40 mm ($X=0.37$ mm, $SD=0.02$, $N=14$). Minimum body length 1.40–2.20 mm ($X=1.72$ mm, $SD=0.19$, $N=27$). Maximum body length 2.60–3.50 mm ($X=2.99$ mm, $SD=0.23$, $N=29$). Duration 3–6 days ($X=3.79$ days, $SD=0.68$, $N=29$).

Third instar (Figs. 4, 15). The prothoracic shield of *T. lomalarga* is 0.37mm by 0.33mm, and SD1 is 0.18mm long. The body is greenish with scattered lenticles and minute dark spots, as in the previous instar. All spiracles are cream-colored and fully visible. The distribution of dorsal chalazae in this instar is variable. The most common pattern has chalazae on T3, A2, and A6 with 0.35mm setae. There are larvae that additionally have dorsal chalazae with slightly shorter setae (0.25mm) on A3–A5 or only on A3 or A5. The setae are sometimes on one side only. Rarely there are chalazae on A1. On T3 there is a slight protuberance that on some larvae may be reddish or brown. On A2 this protuberance is well-developed. On A6 there is a dorsal triangular cream-brown patterning, caudally fringed with dark brown. As this instar progresses, a dark brown crescent, fringed above by a white band, appears in the subspiracular region from T3 to A2. There are short light setae on the ventral border along the body. Starting with this instar, the dorsal nectary gland on A7 is visible (arrow, Fig. 4) and functional, with 2 internal rings



FIGURES 1–12. Immature stages of *Thereus lomalarga*. 1. Egg on a flower bud of *Oryctanthus alveolatus*. 2. 1st instar. 3. 2nd instar. 4. 3rd instar. 5. 4th instar, green morph. 6. 4th instar, brown morph. 7. 4th instar, reddish morph. 8. At the end of 4th instar all morphs are green. 9. Prepupa. 10. Pupa. 11. Freshly emerged male. 12. Adult male. In figs. 4 and 5 arrow points to the dorsal nectary organ in segment A7.



FIGURES 13–18. Morphological details of immatures. 13. 1st instar, lateral view; arrows point to setae, lenticles and spiracles. 14. Idem, dorsal view. 15. 3rd instar epicranium. 16. 4th instar prothoracic shield. 16a arrow points to SD1 (sensory setae). 17. Star shaped sculpture of the pupa's cuticle. 18. Prepupa with excretion fluid.

corresponding to two glandular bladders (0.05mm), and externally with 10 to 15 lenticles (0.025mm) and 12 setae (Fig. 21). Head capsule width 0.57–0.65 mm ($X = 0.61$ mm, $SD = 0.03$, $N = 18$). Minimum body length 2.70–4.30 mm ($X = 3.20$ mm, $SD = 0.43$, $N = 31$). Maximum body length 4.70–6.20 mm ($X = 5.20$ mm, $SD = 0.45$, $N = 21$). Duration 3–5 days ($X = 3.81$ days, $SD = 0.65$, $N = 31$).

Fourth instar. The phenotype of the fourth instar caterpillar of *T. lomalarga* is variable (Figs. 5–7). Green larvae are most common and are cryptic when feeding on flower buds or fruits. Differences among morphs are due to the color of the protuberances, segment T2, and a greater dispersion of brown marbling, which sometimes develops as early as the second instar. Dorsal protuberances on A2 are conspicuous, with a diameter of 1.10mm and a height of 0.90mm. They closely resemble two fruits of *O. alveolatus*. There also are lateral protuberances on T3 and A8, with the maximum distance between them 3.0mm. All protuberances have an apical chalaza and gray setae, which are shorter than in the former instars. The body has scattered lenticles and pinnacles with minute setae that are visible at 100X (Fig. 24). The prothoracic shield (0.60mm by 0.60mm, Figs. 16, 16a) is cream-colored with a few dispersed dark spots and with an SD1 seta 0.35mm. Segment T2 in dorsal aspect is widest and is crossed by a whitish midline. Mainly from segments A4–A6, morphs show light brown marbling dorsally and laterally, very much like the colors of the trichomes on the mistletoe fleshy rachis of the spike. The brown subspiracular crescent between segments T3 and A2 is conserved, and, depending on the position of the larva, it resembles the hollow cavities left by the fruits when they fall from the spike. The spiracles are cream-colored, and the A7 DNO gland is surrounded by a cream-colored oval, which makes it conspicuous, with 20–22 lenticles (0.02mm), 18–22 setae, and four internal rings corresponding to four glandular bladders (0.06mm) (Figs. 19, 22, 23). Head capsule width 0.87–0.90 mm (N=2). Minimum body length 4.60–7.50 mm (X= 5.51mm, SD= 0.61, N= 25). Maximum body length 8.50–10.80 mm (X= 9.57 mm, SD= 0.61, N= 19).

Three days before pupating the larva turns green and stops feeding. The cream color on the T2–T3, protuberances on A8, and some subdorsal areas, becomes accented. The larva then prepares to pupate. In dorsal aspect the A2–A3 area is wide, being about half of its length, and from A4 to A10 there is a continuous narrowing. Laterally the segments are gradually higher from T2 to A3, and then they become lower from A4 to A10 (Fig. 8). After a pupation site is selected, the prepupa turns 180°, fixes the cremaster parallel to the substrate, and one day later produces the silk “girdle” that holds it to the substrate (Fig. 9). While still a prepupa, the larvae anally excrete a clear fluid like other Lycaenidae (Fig. 18). Length of prepupa with silk 6.30–7.80mm (X = 7.03mm, SD = 0.47, N = 14). Duration fourth instar 5–8 days (X = 6.69 days, SD = 0.79, N = 36).

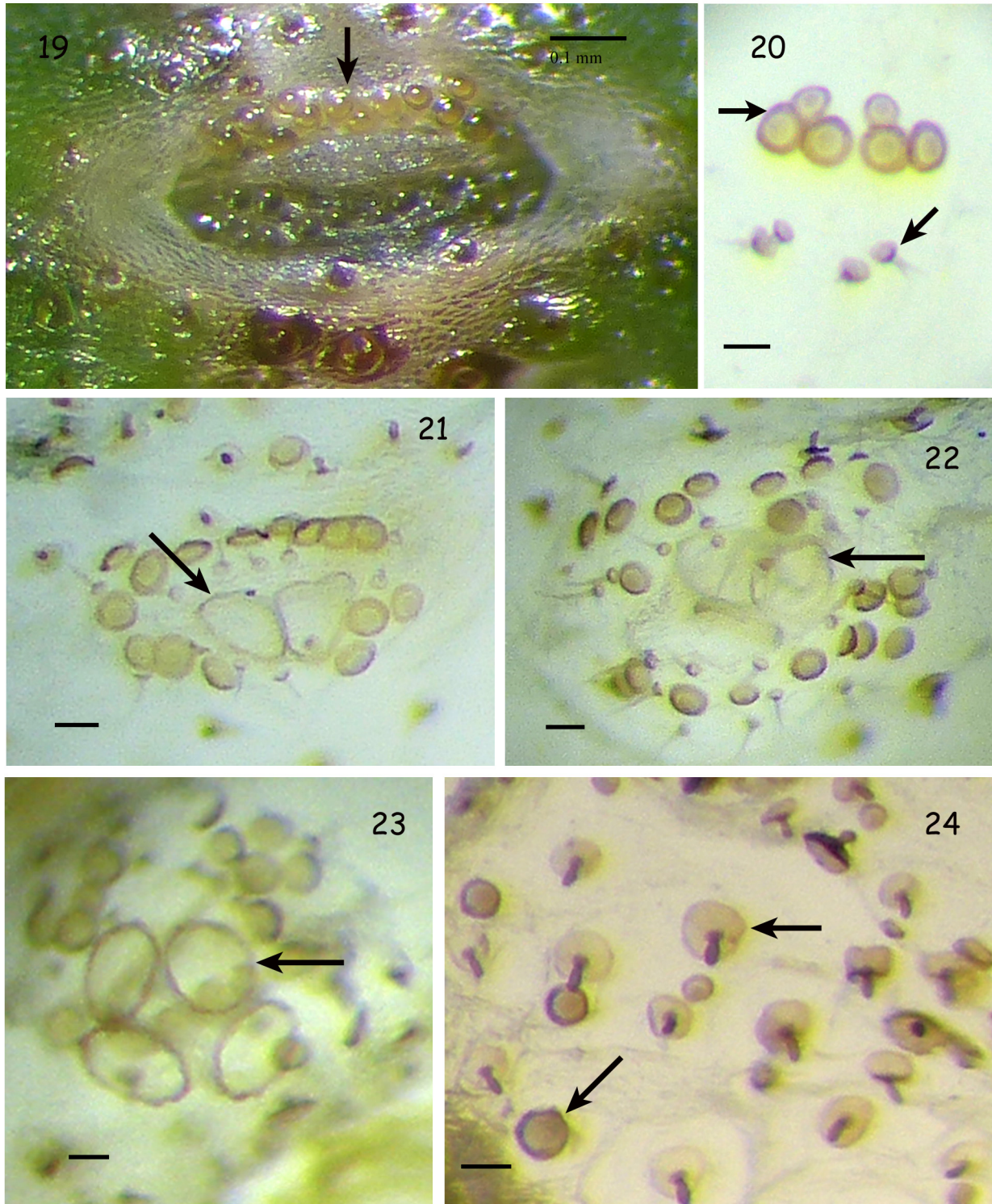
Pupa (Fig. 10). The pupa of *T. lomalarga* is dorsally green. It is cream-colored on the cephalic border of T1 and its spiracle, T2, mid line of T3 and A1, A9–A10, along the inner border of the wings, most of the outer border and on a wide band that covers the median and postmedian regions. The texture is smooth but with dispersed spots (lenticles) and star-shaped sculptures of the same color as the cuticle (Fig. 17). Spiracles, except those of T1, are less visible because they are green like the cuticle. Between A5 and A6 there is a cleft that corresponds to the stridulation area. Sometimes, when disturbed, the pupa produced an audible click. Both sides of the mid line of segments A1–A4 have slight green protuberances, and the silk girdle passes between segments A1 and A2. Ventrally, the pupa is a creamy-green color. Pupa length 6.00–7.60 mm (X= 6.69 mm, SD= 0.43, N= 35). Pupa width on segment (A3) 3.50–4.20 mm (X= 3.97 mm, SD= 0.19, N= 35). Duration 9–13 days (X= 11.35 days, SD= 1.04, N=34). Male pupae are significantly longer than those of females (U = 23.50, P < 0.0001). There are no differences in width of the pupa (U = 91.00, P = 0.29) or the wing length of males and females (U = 104.00, P = 0.26). In the lab adults of both sexes always emerged in the middle of the day before 1400 hours.

Development time. Larval and pupal development time for *T. lomalarga* was 27–34 days (X = 31.10 days, SD = 1.74, N = 20), but differs between the sexes. Males take 30–34 days (X = 31.55 days, SD = 1.29, N = 11) to develop, and females take 27–34 days (X= 30.56, SD = 2.13, N = 9). In other words, females, on average, develop one day faster than males, but the difference is not significant (U = 35.50, P = 0.28). The only life stage in which the more rapid development of females is statistically significant is the pupa (N = 34, 19 males, 15 females, G = 13.18, df = 2, P = 0.0014). The average time from oviposition to adult emergence is 35.68 days.

Mortality factors. Of 22 second and third instars found in the field and brought to the lab, 59.09% were parasitized by Campopleginae (Ichneumonidae) (Figs. 46, 46a). Additionally, a pupa and three larvae (one third and two fourth instars) were parasitized by Chalcididae (Fig. 47). Of 41 eggs collected, four did not hatch. Parasitoids did not emerge from collected eggs, although during the collecting period two eggs showed signs of parasitism. A fourth instar in the lab ate an egg of *T. lomalarga* that was accidentally collected with plant food that it was given. A third instar bored into a newly pupated individual. As noted above, many bird species at Loma Larga eat the fruits of *O. alveolatus*, and in so doing, are a potential source of predation.

Larval behavior. After eclosing, larvae of *T. lomalarga* fed on the closest flower bud, sometimes on the opposite side of the same flower on which the egg was laid. In both the laboratory and field, pre-molt larvae moved

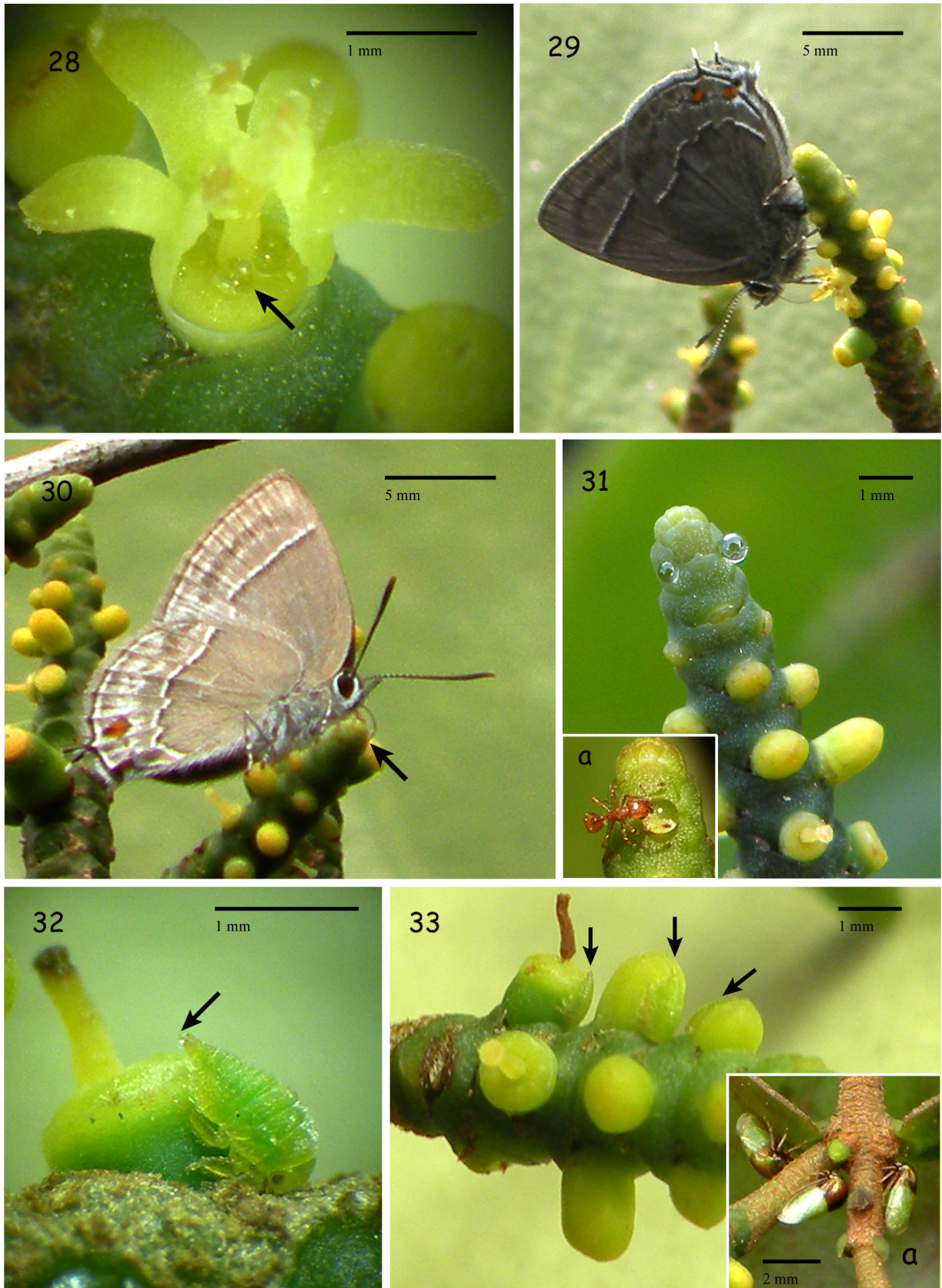
away from the flower spike on which they were feeding and onto the closest leaf, where they remained on or under the base of the leaf (Fig. 43, 47, 48). (As noted, this behavior facilitated finding pre-molt larvae). Pre-molt larvae make a silk base and remain there for a day before molting, with the head capsule and T1 retracted under T2. After molting, larvae consume the cast larval skin and sometimes also the part of the head capsule that sticks to it. Third instar onwards, feed mostly on fruits and sometimes also on the fleshy base of a fruits' rachis. One pupa was found on a leaf of the mistletoe's host plant.



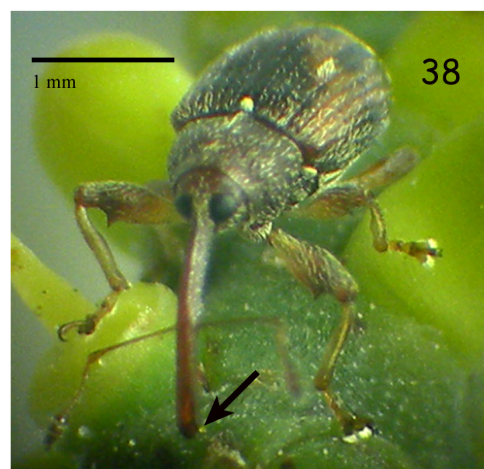
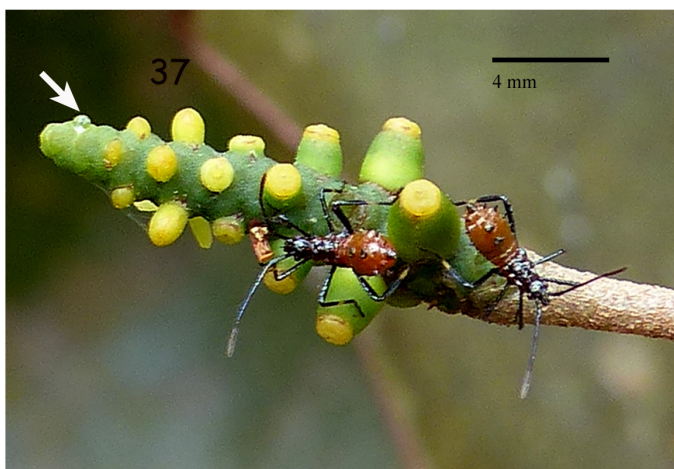
FIGURES 19–24. Segment A7, sugar gland (DNO). 19. 4th instar. 20. 2nd instar molt; arrows point to lenticles and setae. 21. 3rd instar molt; arrow points to glandular bladder (two). 22. 4th instar molt; arrow points to glandular bladder from the outside. 23. Idem, internal view (four). 24. Arrows point to lenticles and setae in 4th instar molt. Scale on molts 0.02 mm.



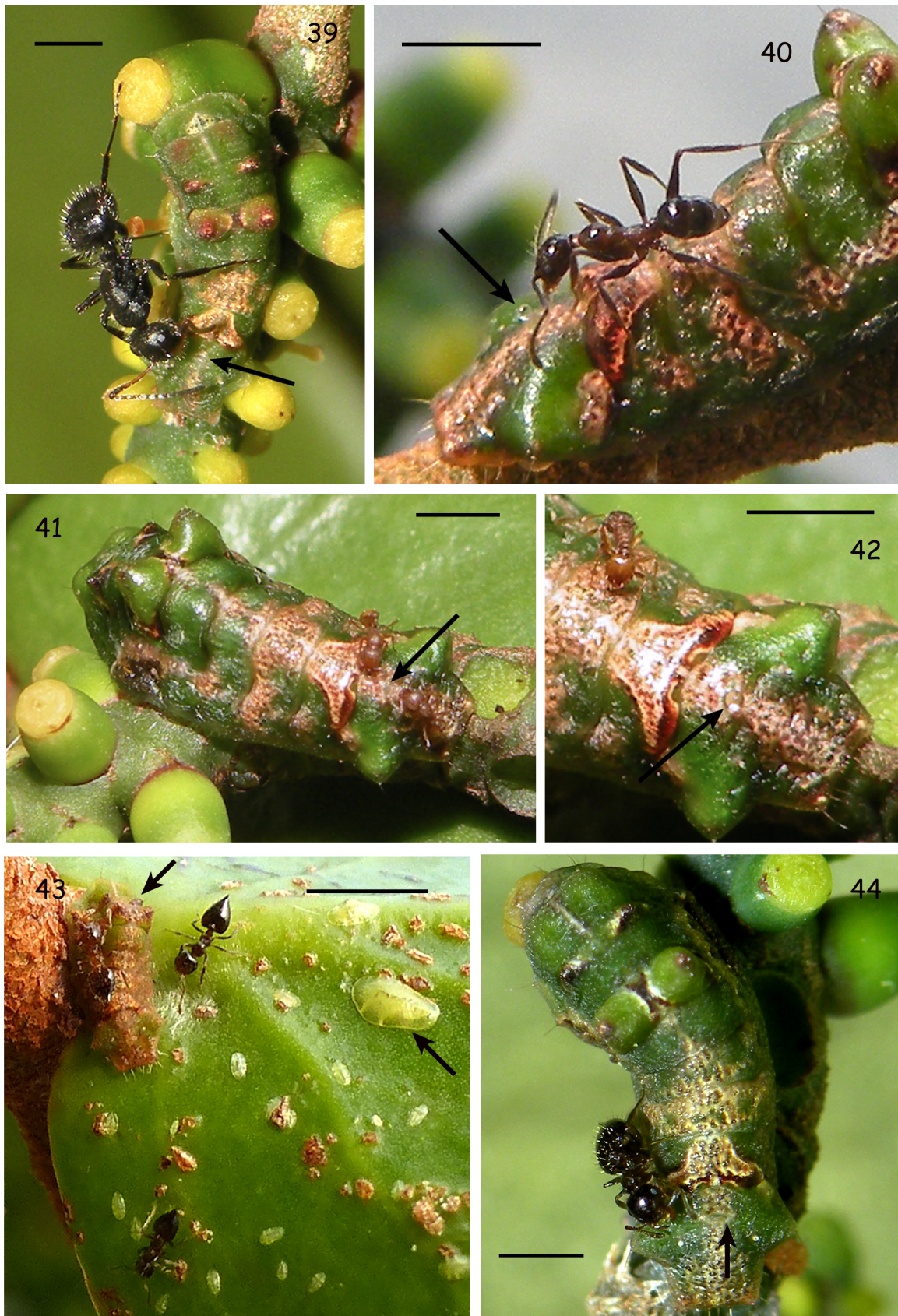
FIGURES 25–27. Mistletoes, *Oryctanthus alveolatus*. 25. *O. alveolatus* growing on *Vernonanthura patens*. 26. Racemose inflorescence; black arrows point to spikes with fruits removed by birds, and white arrows point to apical spikes where *T. lomalarga* often lay eggs. 27. Oviposition. 27 a. Egg laid on the side of flower bud.



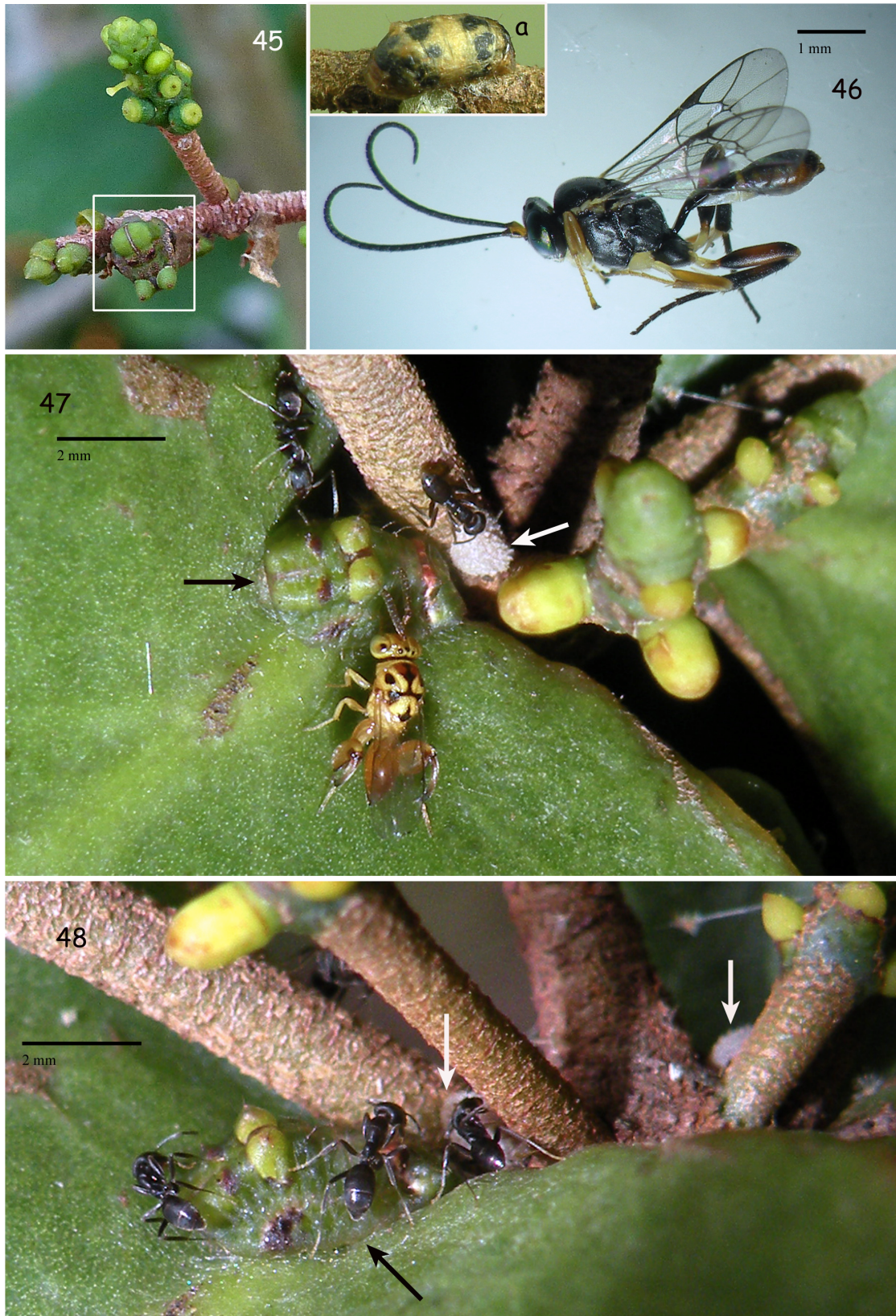
FIGURES 28–33. Food resources of *T. lomalarga*. 28. *O. alveolatus* flower; arrow points to floral disc nectaries. 29. Male feeding on flowers. 30. Female feeding on sugary drop of the fleshy rachis. 31. Spike of *O. alveolatus* with sugary drops at its tip. 31a. *Wasmania* sp ant feeding on sugary drop. 32. Membracidae nymph on an immature fruit; arrow points to anal excretion (honeydew). 33. Arrows point to cryptic Membracidae nymphs on *O. alveolatus* spike. 33a Adults of Membracidae in fig. 33.



FIGURES 34–38. Organisms that produce sugary drops by perforating the fleshy rachis and fruits of *O. alveolatus*; arrows point to the tips of the sucking organs. 34. Coreidae adult frequently visits the spikes. 35. Alydidae nymph (*Camponotus* ant mimic). 36. Reduviidae nymph, a predatory assassin bug that also perforate the fleshy rachis of *O. alveolatus*. 37. Coreidae nymphs; arrow points to secretion droplet left by them. 38. Some Curculionidae also draw sugary droplets.



FIGURES 39–44. *T. lomalarga*-ants interactions. Scale 2mm; arrow points to DNO. 39. 4th instar with *Camponotus*. 40. Idem, with *Pheidole*. 41. Idem, with *Wasmannia*. 42. Secretion droplet. 43. *Crematogaster* ants tending both early 3rd instar of *Th. lomalarga* brown morph and scale insects. Larva of *T. lomalarga* is close to a stem at the base of the inflorescence; arrows point to larva and Coccidae. 44. 4th instar with *Crematogaster*.



FIGURES 45–48. Cypsis, parasitoids, ants, and Coccidae. 45. 4th instar camouflaged in the tip of an inflorescence. 46. The most common morpho-species of Campopleginae. 45a. Campopleginae cocoon inside cuticle of 3rd instar of *T. lomalarga*. 47. 3rd instar pre-molting larva (black arrow points to edge of segment T2) tended by *Linephitema* that also milks scale insects (white arrows). 48. *Linephitema* ants surround the larva of fig. 47 at the arrival of a Chalcidinae, which flies off. In spite of the defense by ants, this larva became parasitized by the same morpho-species of Chalcidinae.

Caterpillars are facultatively tended by ants in the field during the last two instars. At Loma Larga, patrolling ants were almost always seen, while checking inflorescences of *O. alveolatus*. *Camponotus*, *Crematogaster*, and *Pseudomyrmex* were the most common genera. These ants fed on the floral disks, on excretions of Coccidae, Pseudococcidae, and Membracidae, and on exuded droplets from “wounds” made by sucking Hemiptera (Alydidae and Coreidae), and by Coleoptera (Curculionidae) that bite into the fleshy rachis (Figs. 28–33, 34–38). Several times, larvae were brought from the lab to the field and placed on spikes of *O. alveolatus* with ants, which were growing on a *Miconia* plant. As soon as an ant discovered a larva, it walked about it and repeatedly touched the dorsal nectary gland (A7) with its antennae until it stimulated a secretion (Figs. 39–44). Sometimes a secretion was not stimulated at first contact, and the ant continued foraging, but it came back to the larva and repeated the behavior until a secretion was obtained.

Four individual were followed in the field during February 2015 from the egg to prepupa. The eggs had been laid on different *O. alveolatus* bushes growing on the same host plant. *Crematogaster* ants tended Coccidae on leaves and inflorescences of the mistletoe (Fig.43). Second instars on would sometimes walk several meters along stems and roots from one mistletoe bush to another, and did so even when food on the original bush was still plentiful. The only movements observed in the lab were during the pre-molt period, in contrast to those seen in nature. Wandering caterpillars were observed using stems, roots, and stem-knots for refuge, probably avoiding exposure to predators and parasitoids and/or seeking a preferred microclimate. A second instar fed at the tip of a mistletoe root, and a third instar chewed a hole under a stem knot. Although the larvae had fresh spikes available, they also fed on floral buds, fruits and fleshy rachis, but did not eat leaves. Third and fourth instars were tended by *Crematogaster* ants.

Adult behavior. An egg-lying *T. lomalarga* was first seen on 27 March 2011 at 1048 hours under partially sunny skies. The female fluttered around an *O. alveolatus* bush growing on *Miconia minutiflora*, two meters above the ground at a forest border. She walked on several spikes within each inflorescence in different places on the plant, nearly always with an extended proboscis, occasionally stopping to bask with her head facing downwards. She also walked circular paths on the upper surface of some leaves at the base of the inflorescence while basking. After 35 min, the female laid one egg. Four more females were seen ovipositing between 1200 and 1400 hours with the same behavior, but they laid their eggs within the first 10 minutes of observation. Females of *T. lomalarga* always laid their eggs at the tip of a flower spike, and placed them laterally on the flower buds. They oviposited both on young inflorescences with few spikes and on old ones with many branches and long spikes that had lost most of their fruits (but which still had floral buds at the apex). Usually, there was one egg per inflorescence. However, a large bush of *O. alveolatus* might have eggs and larvae, including those of other *Thereus* species. Once two first instars and one egg were found on a single inflorescence. Two eggs were found together once also. They hatched the same day, and the two first instars fed side by side on flower buds. Eggs of *T. lomalarga* were found on bushes of *Oryctanthus* at heights of 1m–4m above the ground. At lower heights the eggs of *T. lomalarga* were more abundant than those of the other *Thereus* species. Copulation was not seen.

At midday of 27 June 2011 several *T. lomalarga* adults gathered on an *O. alveolatus* bush growing on *M. minutiflora*, 3.5m above the ground. Three males and a female walked among spikes of different inflorescences with extended proboscises, and once in a while they flew to another inflorescences and basked. Over the ensuing 15 days, this adult behavior was observed repeatedly. Males and females gathered to feed on mistletoe flowers, on exudates on the rachis, and on excretions of treehopper nymphs on the lateral side of fruits (Fig. 28–33). Using their proboscises, adults seemed to stimulate treehopper nymph excretions in much the same as the ants do with their antennae. Photographs of this adult behavior were not obtained because of the height of the shrub coupled with the small size of the nymph. Many adult butterflies could be recognized individually by the pattern of wing damage and were seen visiting daily until 1800 hours. Treehopper adults, other Hemiptera, and Curculionidae beetles, fed on the fleshy rachis of the *O. alveolatus* spikes, mostly on its tender tips. When these sucking insects leave, drops keep flowing from the wounds, which attracted *T. lomalarga* adults, ants, ichneumonid wasps, Diptera, and others (Figs. 31, 34–38). Solitary males and females of *T. lomalarga* were also seen feeding on exudates on *O. alveolatus* bushes high above the ground, at the end of the morning. Adults did not visit other nectar sources such as *Lantana* L. (Verbenaceae), *Stachytarpheta* Vahl (Verbenaceae), and some Asteraceae. These flowers were abundant and were used by other butterflies. At sundown adults took refuge for the night on the host tree or flew to a nearby one.

TABLE 1. Summary of food plant records for *Thereus*. MIZA-Museo del Instituto de Zoología Agrícola (Maracay, Venezuela). MUSENUV-Museo de Entomología de la Universidad del Valle (Cali, Colombia). PJD-P.J. DeVries, University of New Orleans, USA. UCR-University of California at Riverside, USA. USNM-United States National Museum (Washington, DC, USA).

Species	Food plant	Family	Locality	Reference, current voucher depository
<i>T. cithonius</i> (Godart)	<i>Sruthanthus condensatus</i>	Loranthaceae	México	Leg. G. Ballmer. <i>Ex. pupa</i> . In UCR
<i>T. guianivaga</i> (Johnson)	<i>Phoradendron</i> sp.	Viscaceae	Ecuador	Beccaloni <i>et al.</i> 2008
<i>T. lomalarga</i> Robbins, Heredia, & Busby	<i>Oryctanthus abveolatus</i>	Loranthaceae	Colombia	This paper and Robbins <i>et al.</i> (2015)
<i>T. oppia</i> (Godman & Salvin)	<i>Sruthanthus orbicularis</i>	Loranthaceae	Costa Rica	Robbins <i>et al.</i> (2015), Janzen & Hallwachs (2015). <i>Ex. pupa</i> . In USNM
<i>T. orasus</i> (Godman & Salvin)	<i>Sruthanthus condensatus</i>	Loranthaceae	México	Robbins <i>et al.</i> (2015), Leg. G. Ballmer. <i>Ex. larva</i> . In UCR
<i>T. ortalus</i> (Godman & Salvin)	<i>Sruthanthus</i> sp.	Loranthaceae	Costa Rica	Leg. L. D. Gomez. <i>Ex. larva</i> . In USNM
	A mistletoe with small round leaves.	Loranthaceae	Costa Rica	Leg. W. Haber. <i>Ex. pupa</i> . In USNM
	<i>Oryctanthus abveolatus</i>	Loranthaceae	Colombia	Leg. M. D. Heredia. <i>Ex. ova and larvae</i> . In MUSENUV
<i>T. pedusa</i> (Hewitson)	<i>Oryctanthus occidentalis</i>	Loranthaceae	Panamá	Leg. P. J. DeVries. <i>Ex. ova and larvae</i> . In PJD and USNM.
<i>T. praxis</i> (Godman & Salvin)	<i>Oryctanthus occidentalis</i>	Loranthaceae	Panamá	Leg. P. Davidar. <i>Ex. larvae</i> . In USNM
	The Venezuelan common name “guatepajarito” (on the voucher data label) refers to <i>Phthirusa</i> sp.	Loranthaceae	Venezuela	Leg. C. J. Rosales. <i>Ex. larvae</i> . In MIZA, cf. web site: agris.fao.org/agris-search/search.do?recordID=VE2007400200 for common name in Venezuela (accessed 30 Sep 2015)
<i>T. pseudarcula</i> (Giacomelli)	<i>Tripodanthus flagellaris</i>	Loranthaceae	Argentina	Volkman & Núñez Bustos 2014
<i>T. enenia</i> (Hewitson) ?, the uncertain specific identification is discussed in Robbins & Aiello (1982)	<i>Licania arborea</i>	Chrysobalanaceae	Costa Rica	Janzen & Hallwachs (2015). <i>Ex. larvae</i> . In USNM.
	<i>Zygia longifolia</i>	Fabaceae	Costa Rica	Janzen & Hallwachs (2015). <i>Ex. larvae</i> . In USNM.
	<i>Mascagnia hippocrateoides</i>	Malpighiaceae	Panamá	Robbins & Aiello (1982). In USNM
	<i>Stigmaphyllon</i>	Malpighiaceae	Panamá	Leg. P. J. DeVries. <i>Ex. larva</i> . In USNM

Discussion

The mistletoe food plant. Mistletoes at Loma Larga appear to be a keystone species, as has been shown elsewhere (Whittaker 1984b, Watson 2001, Watson & Herring 2012). At Loma Larga, *O. alveolatus* supports a complex network of ecological relationships among Lepidoptera, Hemiptera, Hymenoptera (ants and parasitoids), Coleoptera, birds, and its own host plants. On mistletoe, we have reared seven species of Lycaenidae, among them *Thereus lomalarga*, *T. ortalus*, and an undescribed species of *Thereus*. We have also reared four species of Riodinidae and several moth species. *Thereus* caterpillars and Hemiptera on *O. alveolatus* are myrmecophilous. As detailed, adults of *T. lomalarga* feed on mistletoe flowers, on the excretions of nymphs of a cryptic Membracidae, and on drops of liquid oozing from the fleshy inflorescence rachis.

During times of fruit scarcity, mostly of *Miconia*, the fruits of *O. alveolatus* are alternate foods for many species of birds, so that every mat of *Oryctanthus* becomes a center that recruits seeds of species that belong to more advanced stages of plant succession in this area. The Loma Larga suburban housing project has allowed this tract of land to regenerate naturally as a management practice (Kattan & Álvarez-López 1996, Fig. 25) and might serve as a model for other such efforts. While fifteen years ago the study area was a treeless grazed and burned pasture, it has developed a mistletoe community that hosts undescribed butterfly species, such as the recently named *T. lomalarga* (Robbins *et al.* 2015).

Immatures biology of *T. lomalarga*. The exocorion pattern is similar in *T. lomalarga*, *T. ortalus*, and *Thereus sp.* at Loma Larga, but quite different from other genera of Eumaeini in which most of the eggs are echinoid, of spinous appearance (Downey and Allyn 1981, 1984; Duarte *et al.* 2005; unpublished data). This pattern, which covers most of the chorion's surface in the tubercle-aeropyle zone (*sensu* Downey & Allyn 1984) gives the egg its typical appearance. The eggs of these *Thereus* species were always laid on younger plant parts or on flower buds (or areas close to the later).

Freshly hatched larvae of the three *Thereus* species possess the same chaetotaxy: prothoracic shield with only XD1 and XD2 visible; along the body one well-developed dorsal seta D1; D2, D3, SD1, SD2 visible as small spots; from the L group only one seta is developed, of equal length as D1 (Figs. 13, 14); lenticles (PCO) are in the same position in the three species, but are more conspicuous in *T. lomalarga*. This sharp reduction of tactile setae differentiates the first instar of *Thereus* from first instars of other genera like *Rekoa*, *Arawacus*, and *Kolana*, and more generally from the Eumaeini model (Ballmer & Pratt, 1992), where the prothoracic shield has 10 well developed setae, D1 and D2 the longest; in the other segments D2, D3, SD1, and SD2 are well developed, as in the L group which frequently has an additional seta, L4. After their first stadium, larvae of the three *Thereus* species are very different from each other in shape, and sometimes in color pattern, even when they feed on the same substrate.

Crypsis is widespread among eumaeine caterpillars (e.g., Monteiro 1991, Duarte *et al.* 2005, Kaminski & Freitas 2010, Kaminski & Freitas 2012, Schmid *et al.* 2010), including the larvae of *T. lomalarga*. The green morph has dorsal protuberances similar to the fruits of *O. alveolatus*. The other morphs are not so well-camouflaged while on the fruits, but the brown morph is similar in color to resting places on the stem, and the reddish morph closely resembles the color of young leaves on the food plant. Singer *et al.* (2014) experimentally showed that “dietary specialization of herbivores increases the antipredator effects of camouflage and aposematism”. The cryptic color pattern (Fig. 45), shape, and mobility of these larvae point to their host specificity and to a possible selection pressure exerted by visual predators such as birds.

The dorsal nectary organ of *T. lomalarga* (Figs. 19, 22) becomes functional at the start of the third instar. The lenticles (PCO) and setae around the gland increase from the second to fourth instar. From the third to fourth instar the glandular bladders increase their numbers (see Newcomer 1912, fig. 9 and 10; Malicky 1970, fig. 2; Vengliante & Hasenfuss 2012). Tending ants eat the larval secretions of this gland and protect caterpillars against predators and parasitoids (Figs. 39–44, 47, 48) (Atsatt 1981a,b; Pierce & Mead 1981; Fiedler 1991; Pierce & Nash 1999; Pierce *et al.* 2002; Kaminski *et al.* 2010). Patrolling ants of genera *Camponotus*, *Crematogaster*, and *Pseudomyrmex*, and less frequently *Wasmannia*, *Tapinoma*, *Solenopsis*, and *Linepitema*, are a constant presence on inflorescence spikes of *O. alveolatus* at Loma Larga. They feed on the floral disks of the mistletoe flowers. They tend and eat the excretions of Hemiptera (Coccidae, Pseudococcidae, and Membracidae) and Lepidoptera (Lycaenidae). They feed on the liquid that oozes from “wounds” made by sucking Hemiptera (Alydidae and Coreidae) and Coleoptera (Curculionidae) on the fleshy rachis of *O. alveolatus*. Eggs of *T. lomalarga* were

frequently laid near Coccidae and Pseudococcidae, less often near Membracidae. The presence of the last three groups presumably enhances the number of ants on the mistletoes and increases the number of ant-caterpillar encounters. Parasitism on the egg stage was very low in contrast to other Eumaeini (Kaminski *et al.* 2012, Bächtold *et al.* 2014, unpublished data). Only two eggs found showed signs of parasitism, and none of the eggs brought to the laboratory were parasitized.

Parasitism on the larvae was rather high: 59.09% of the collected early instars larvae, with only one exception, were parasitized by one species of Ichneumonidae (Campopleginae). All late instar larvae monitored in the field were also parasitized by Chalcididae (Chalcidinae) although they were tended by *Wasmania*, *Linepithema*, and *Crematogaster* ants, that were also tending Coccidae and Pseudococcidae. One larva, close to a coccid tended by *Linepithema*, was discovered by a chalcidine; the ants shifted their attention toward the larva and temporarily left the coccid they were milking (Figs. 47, 48). During this observation the parasitoid did not land on the larva, but later on, when collected at the end of its 4th instar, it had been parasitized by the same species of Chalcidinae. Nevertheless, studies designed to measure the effectiveness of the relationship with ants, have shown that percentages of parasitism decrease significantly in the presence of ants (Atsatt 1981a, Pierce & Mead 1981, Pierce & Nash 1999, Kaminski *et al.* 2010), and that not all the species of ants are equally effective in the defense of larvae (Fraser *et al.* 2001, Kaminski & Rodrigues 2011).

Fruits of *O. alveolatus* are consumed by larvae of *T. lomalarga* as well as by many species of birds (listed in the Results), for which reason incidental predation of caterpillars might be expected. However, the birds and *T. lomalarga* largely feed at different parts of the inflorescence. The birds preferentially feed on ripe fruits near the base of the older spikes, which in turn are close to the first pair of leaves. These leaves and the thicker base of the older spikes are used by the birds as perching supports while feeding. For their first two stadia, caterpillars of *T. lomalarga* feed on floral buds closest to the tip of the inflorescence (Figs. 26, 27) and then on the closest ripe fruits.

Adult biology of *T. lomalarga*. Although our sample size is small, the trend of all three *Thereus* species is that females emerge before males (protogyny), contrary to the general protandry in butterflies (Wiklund & Fagerström 1977, Morbey 2013). Studies on several species of *Calycopis* (Duarte *et al.* 2005, Duarte & Robbins 2009), and observations on *Lamprospilus* (unpublished data) have found the same trend. In *T. lomalarga* the shorter time of female development is due to a shorter pupal stage; in other stages there were no significant differences. Male pupae were significantly longer in overall length than those of females, but wing length was similar. Perhaps the weight of pupae and adults would have been a better variable (Chen *et al.* 2014).

Adults of *T. lomalarga* obtain nutrients from mistletoe flowers, from droplets on the mistletoe's fleshy inflorescence rachis, from oozing "wounds" made by Hemiptera and Coleoptera that suck on mistletoes, and from the excretions of Hemiptera feeding on the mistletoes. The adults have not been observed visiting flowers of other plants, unlike adults of the closely related *T. oppia* (Godman & Salvin) (Robbins *et al.* 2015). It has long been known that miletine lycaenid adults feed on excretions of Hemipteran nymphs (Maschwitz *et al.* 1985, 1988, Fiedler & Maschwitz 1989, Fiedler 1993, Youngsteadt & DeVries 2005, Lohman and Samarita 2009), and Wagner and Gagliardi (2015) suggested that eumaeine adults might also exploit various alternate sources of liquid nutrition. The data on *T. lomalarga* in this paper support this idea, and we have additionally observed males of *Michaelus jebus* (Godart) at Loma Larga milking aphids in a citrus tree patrolled by *Camponotus* ants.

In a taxonomic work on *Thereus*, it was noted that adults of *T. lomalarga* are rare in museum collections (Robbins *et al.* 2015). The results in this paper show that female oviposition, larval feeding, and adult feeding are centered on the mistletoe plants. Male territorial behavior, which occurs widely in eumaeines (Prieto & Dahners 2009), has been recorded in *T. lomalarga* only at the top of a small tree (Robbins *et al.* 2015). In other words, *T. lomalarga* does not obtain resources at ground level. The low height of the trees at Loma Larga—the mistletoes are mostly growing within five meters of the ground—facilitated our study of this community. The lack of adult resources at ground level may explain the rarity of this species in museums. It was also noted that adult females of *T. lomalarga* are far more frequently encountered—at least by butterfly collectors—than are adult males (Robbins *et al.* 2015). One possible explanation for this observation is that the sex ratio of adults is skewed in favor of females. However, among the 44 reared individuals in this study, 27 were males, a result that falsifies this hypothesis. A possible alternative is that females of *T. lomalarga* more readily disperse than males with the purpose of finding other patches of mistletoe.

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References

- Ackery, P.R. (1991) Hostplant utilization by African and Australian butterflies. *Biological Journal of the Linnean Society*, 44 (4), 335–351.
<http://dx.doi.org/10.1111/j.1095-8312.1991.tb00624.x>
- Atsatt, P.R. (1981a) Ant-dependent food plant selection by the mistletoe butterfly *Ogyris amaryllis* (Lycaenidae). *Oecologia*, 48 (1), 60–63.
<http://dx.doi.org/10.1007/BF00346988>
- Atsatt, P.R. (1981b) Lycaenidae butterflies and ants: selection for enemy-free space. *American Naturalist*, 118, 638–654.
<http://dx.doi.org/10.1086/283859>
- Ballmer, G.R. & Pratt, G.F. (1988) A survey of the last instar larvae of the Lycaenidae (Lepidoptera) of California. *Journal of Research on the Lepidoptera*, 27 (1), 1–80
- Ballmer, G.R. & Pratt, G.F. (1992) *Loranthomitoura*, a new genus of Eumaeini (Lepidoptera: Lycaenidae: Theclinae). *Tropical Lepidoptera*, 3 (1), 37–46.
- Ballmer, G.R. (2008) Life history of *Purlisa gigantea* in South Thailand. *Tropical Lepidoptera*, 18 (1), 32–39.
- Ballmer, G.R. & Wright, D.M. (2008) Life history and larval chaetotaxy of *Ahmetia achaja* (Lepidoptera, Lycaenidae, Lycaeninae, Theclini, Cheritrina). *Zootaxa*, 1845, 47–59.
- Beccaloni, G.W., Hall, S.K., Vilorio, A.L. & Robinson, G.S. (2008) Catalogue of the hostplants of the Neotropical butterflies / Catálogo de las plantas huésped de las mariposas Neotropicales. In: m3m—Monografías Tercer Milenio. Vol. 8. Zaragoza (Spain): S.E.A., RIBES-CYTED, The Natural History Museum, Instituto Venezolano de Investigaciones Científicas.
- Caires, C.S. (2012) Estudos taxonômicos aprofundados de *Oryctanthus* (Griseb.) Eichler, *Oryctina* Tiegh. e *Pusillanthus* Kuijt (Loranthaceae). Available from: http://repositorio.unb.br/bitstream/10482/11106/1/2012_Claudenir_Simoes_Caires.pdf (accessed July 2014)
- Congdon, C. & Bampton, I. (2000) Provisional notes on the foodplants of the Iolaini (Lepidoptera, Papilionoidea, Lycaenidae). *Metamorphosis*, 11 (1), 33–42.
- Chen, C., Xia, Q.W., Xiao, H.J., Xiao, L. & Xue, F.S. (2014) A comparison of the life-history traits between diapause and direct development individuals in the cotton bollworm, *Helicoverpa armigera*. *Journal of insect science*, 14 (1), 19.
<http://dx.doi.org/10.1093/jis/14.1.19>
- D'Araujo e Silva, A.G., Gonçalves, C.R., Galvão, D.M., Gonçalves, A.J.L., Gomes, J., Silva, M.N. & Simoni, L. (1967–1968) Quarto catálogo dos insetos que vivem nas plantas do Brasil. Seus parasitas e predadores. *Ministério da Agricultura*, Rio de Janeiro, Part I, Vol.1, 422 pp., Vol.2, 906 pp., Part II, Vol.2, 265 pp.
- Downey, J.C. & Allyn, A.C. (1981) Chorionic sculpturing in eggs of Lycaenidae. Part I. *Bulletin of the Allyn Museum*, 61, 1–29.
- Downey, J.C. & Allyn, A.C. (1984) Chorionic sculpturing in eggs of Lycaenidae. Part II. *Bulletin of the Allyn Museum*, 84, 1–44.
- Duarte, M., Robbins, R.K. & Mielke, O.H. (2005) Immature stages of *Calycopsis caulonia* (Hewitson, 1887) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini), with notes on rearing detritivorous hairstreaks on artificial diet. *Zootaxa* 1063, 1–31.
- Duarte, M. & Robbins, R.K. (2009) Immature stages of *Calycopsis bellera* (Hewitson) and *C. janeirica* (Felder) (Lepidoptera, Lycaenidae, Theclinae, Eumaeini): taxonomic significance and new evidence for detritivory. *Zootaxa*, 2325, 39–61.
- Dueñas Gomez, H.D.C. & Franco Roselli, P. (2001) Sinopsis de las Loranthaceae de Colombia. *Caldasia*, 23 (1), 81–99.
- Espinal, L.S. (1968) Visión Ecológica del Departamento del Valle del Cauca. Universidad del Valle, Cali.
- Fiedler, K. & Maschwitz, U. (1989) Adult myrmecophily in butterflies: the role of the ant *Anoplolepis longipes* in the feeding and oviposition behaviour of *Allotinus unicolor* (Lepidoptera, Lycaenidae). *Tyô to Ga*, 40 (4), 241–251.
- Fiedler, K. (1991) Systematic, evolutionary, and ecological implications of myrmecophily within Lycaenidae (Insecta: Lepidoptera: Papilionoidea). *Bonner Zoologische Monographien*, 31, 1–210.
- Fiedler, K. (1993) The remarkable biology of two Malaysian lycaenid butterflies. *Nature Malaysiana*, 18 (2), 35–42.

- Fiedler, K. (1995) Lycaenid butterflies and plants: is myrmecophily associated with particular hostplant preferences? *Ethology ecology & evolution*, 7 (2), 107–132.
<http://dx.doi.org/10.1080/08927014.1995.9522960>
- Fraser, A.M., Axén, A.H. & Pierce, N.E. (2001) Assessing the quality of different ant species as partners of a myrmecophilous butterfly. *Oecologia*, 129 (3), 452–460.
<http://dx.doi.org/10.1007/s004420100744>
- Haskin, J.R. (1933) *Thecla halesus*, its life cycle and habits. *Entomological News* 44, 72–74.
- Janzen, D.H. & Hallwachs, W. (2015) Dynamic database for an inventory of the macrocaterpillar fauna, and its food plants and parasitoids, of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica [Internet]. Philadelphia: University of Pennsylvania. Available from: <http://janzen.sas.upenn.edu> (accessed september 2015)
- Kaminski, L.A. & Freitas, A.V. (2010) Natural history and morphology of immature stages of the butterfly *Allosmaitia strophius* (Godart) (Lepidoptera: Lycaenidae) on flower buds of Malpighiaceae. *Studies on neotropical Fauna and Environment*, 45 (1), 11–19.
<http://dx.doi.org/10.1080/01650520903495826>
- Kaminski, L.A., Freitas, A.V. & Oliveira, P.S. (2010) Interaction between mutualisms: ant-tended butterflies exploit enemy-free space provided by ant-treehopper associations. *The American Naturalist*, 176 (3), 322–334.
<http://dx.doi.org/10.1086/655427>
- Kaminski, L.A. & Rodrigues, D. (2011) Species-specific levels of ant attendance mediate performance costs in a facultative myrmecophilous butterfly. *Physiological Entomology*, 36 (3), 208–214.
<http://dx.doi.org/10.1111/j.1365-3032.2011.00785.x>
- Kaminski, L.A., Rodrigues, D. & Freitas, A.V. (2012) Immature stages of *Parrhasius polibetes* (Lepidoptera: Lycaenidae): host plants, tending ants, natural enemies and morphology. *Journal of Natural History*, 46 (11–12), 645–667.
<http://dx.doi.org/10.1080/00222933.2011.651630>
- Kattan, G. & Álvarez-López, H. (1996) Preservation and management of biodiversity in fragmented landscapes in the Colombian Andes. pp 3–18 In Schelhas, J. & Greenberg R. (Eds.) *Forest Patches in Tropical Landscapes*. Island Press, Washington D. C.
- Kitching, I.J. (1985) Early stages and the classification of the milkweed butterflies (Lepidoptera, Danaeinae). *Zoological Journal of the Linnean Society*, 85 (1), 1–97.
<http://dx.doi.org/10.1111/j.1096-3642.1985.tb01516.x>
- Lohman, D.J. & Samarita, V.U. (2009) The biology of carnivorous butterfly larvae (Lepidoptera: Lycaenidae: Miletinae: Miletini) and their ant-tended hemipteran prey in Thailand and the Philippines. *Journal of Natural History*, 43 (9–10), 569–581.
<http://dx.doi.org/10.1080/00222930802610485>
- Malicky, H. (1970) New aspects of the association between lycaenid larvae (Lycaenidae) and ants (Formicidae, Hymenoptera). *Journal of the Lepidopterists' Society*, 24 (3), 190–202.
- Maschwitz, U., Dumpert, K. & Sebastian, P. (1985) Morphological and behavioural adaptations of homopterophagous blues (Lepidoptera: Lycaenidae). *Entomologia generalis*, 85–90.
- Maschwitz, U., Nässig, W.A., Dumpert, K. & Fiedler, K. (1988). Larval carnivory and myrmecoxeny, and imaginal myrmecophily in miletine lycaenids (Lepidoptera, Lycaenidae) on the Malay Peninsula. *Tyô to Ga*, 39 (3), 167–181.
- Monteiro, R.F. (1990) Cryptic larval polychromatism in *Rekoa marius* Lucas and *R. palegon* Cramer (Lycaenidae: Theclinae). *Journal of Research on the Lepidoptera*, 29 (1–2), 77–84.
- Morbey, Y.E. (2013) Protandry, sexual size dimorphism, and adaptive growth. *Journal of theoretical biology*, 339, 93–99.
<http://dx.doi.org/10.1016/j.jtbi.2013.05.009>
- Newcomer, E.J. (1912) Some observations on the relations of ants and lycaenid caterpillars, and a description of the relational organs of the latter. *Journal of the New York Entomological Society*, 31–36.
- Nickrent, D.L., Malécot, V., Vidal-Russell, R. & Der, J.P. (2010) A revised classification of Santalales. *Taxon*, 59 (2), 538–558.
- Pierce, N.E. & Mead, P.S. (1981) Parasitoids as selective agents in the symbiosis between lycaenid butterfly larvae and ants. *Science*, 211, 1185–1187.
<http://dx.doi.org/10.1126/science.211.4487.1185>
- Pierce, N.E. & Nash, D.R. (1999) The imperial blue, *Jalmenus evagoras* (Lycaenidae). *Monographs on Australian Lepidoptera*, 6, 279–315.
- Pierce, N.E., Braby, M.F., Heath, A., Lohman, D.J., Mathew, J., Rand, D.B. & Travassos, M.A. (2002) The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). *Annual Review of Entomology*, 47 (1), 733–771.
<http://dx.doi.org/10.1146/annurev.ento.47.091201.145257>
- Prieto, C. & Dahners, H.W. (2009) Resource utilization and environmental and spatio-temporal overlap of a hilltopping Lycaenid butterfly community in the Colombian Andes. *Journal of Insect Science*, 9 (1), 16.
<http://dx.doi.org/10.1673/031.009.1601>
- Quental, T.B. (2008) Systematics, sexual selection and evolution of secondary sexual characters in Neotropical Eumaeini butterflies (Lepidoptera: Lycaenidae). Dissertation, Harvard University, Cambridge, MA, 226 pp.
- Robbins, R.K. & Aiello, A. (1982) Foodplant and oviposition records for Panamanian Lycaenidae and Riodinidae. *Journal of the Lepidopterists Society*, 36(2), 65–75.

- Robbins, R.K. (1991) Evolution, comparative morphology, and identification of the eumaeine butterfly genus *Rekoa* Kaye (Lycaenidae: Theclinae). *Smithsonian Contribution to Zoology*, 498, 1–64.
<http://dx.doi.org/10.5479/si.00810282.498>
- Robbins, R.K. (2004) Lycaenidae. Theclinae. Eumaeini. In: Lamas G, editor. *Checklist: Part 4A. Hesperioidea—Papilionoidea*. In Heppner JB, editor. *Atlas of Neotropical Lepidoptera. Volume 5A*. Gainesville (IL): Association for Tropical Lepidoptera, Scientific Publishers. pp. 118–137.
- Robbins, R.K., Busby, R. & Duarte, M. (2010) Phylogeny and Taxonomy of the Neotropical *Thepytus* (Lepidoptera: Lycaenidae: Theclinae). *Arthropod Systematics & Phylogeny*, 68 (1), 35–52.
- Robbins, R., Heredia, M.D. & Busby, R.C. (2015) Male secondary sexual structures and the systematics of the *Thereus oppia* species group (Lepidoptera, Lycaenidae, Eumaeini). *ZooKeys*, 520, 109–130.
<http://dx.doi.org/10.3897/zookeys.520.10134>
- Schmid, S., Schmid, V.S., Kamke, R., Steiner, J. & Zillikens, A. (2010) Association of three species of *Strymon* Hübner (Lycaenidae: Theclinae: Eumaeini) with bromeliads in southern Brazil. *Journal of Research on the Lepidoptera*, 42, 50–84.
- Sepp, J. (1829–1843) *Natuurlijke Historie van Surinaamsche Vlinders, naar het leven geteekend. Papillons de Surinam dessinés d'après nature*. Amsterdam, Jan Christian Sepp en Zoon. 108 pages, 50 plates.
- Singer, M.S., Lichten-Marck, I.H., Farkas, T.E., Aaron, E., Whitney, K.D. & Mooney, K.A. (2014) Herbivore diet breadth mediates the cascading effects of carnivores in food webs. *Proceedings of the National Academy of Sciences*, 111 (26), 9521–9526.
<http://dx.doi.org/10.1073/pnas.1401949111>
- Stehr, F.W. (1987) Order Lepidoptera. In: Stehr FW, editor. *Immature insects. Vol. 1*. Dubuque (IA): Kendall-Hunt Publishing Company. pp. 288–305.
- Uchôa, M.A. & Caires, C.S. (2000) Candidate insects for the biocontrol of the plant phytoparasite *Psittacanthus* sp. (Loranthaceae) in the region of the Pantanal, Mato Grosso do Sul State, Brazil. In *XXI Int. Congress Entomol. Foz do Iguassu, Brazil, Abstract*, Vol. 1683.
- Uchôa, M.A., Caires, C.S., Nicácio, J.N. & Duarte, M. (2012) Frugivory of *Neosilba* species (Diptera: Lonchaeidae) and *Thepytus echelta* (Lepidoptera: Lycaenidae) on *Psittacanthus* (Santalales: Loranthaceae) in ecotonal cerrado-South Pantanal, Brazil. *Florida Entomologist*, 95 (3), 630–640.
<http://dx.doi.org/10.1653/024.095.0314>
- Vegliante, F. & Hasenfuss, I. (2012) Morphology and diversity of exocrine glands in lepidopteran larvae. *Annual review of Entomology*, 57, 187–204.
<http://dx.doi.org/10.1146/annurev-ento-120710-100646>
- Wagner, D.L. & Gagliardi, B.L. (2015) Hairstreaks (and Other Insects) Feeding at Galls, Honeydew, Extrafloral Nectaries, Sugar Bait, Cars, and Other Routine Substrates. *American Entomologist*, 61 (3), 160–167.
<http://dx.doi.org/10.1093/ae/tmv045>
- Watson, D.M. (2001) Mistletoe—a keystone resource in forests and woodlands worldwide. *Annual Review of Ecology and Systematics*, 219–249.
<http://dx.doi.org/10.1146/annurev.ecolsys.32.081501.114024>
- Watson, D.M. & Herring, M. (2012) Mistletoe as a keystone resource: an experimental test. *Proceedings of the Royal Society B-Biological Sciences*, 279, 3853–3860.
<http://dx.doi.org/10.1098/rspb.2012.0856>
- Whittaker, P.L. (1984a) Population biology of the great purple hairstreak, *Atlides halesus*, in Texas (Lycaenidae). *Journal of the Lepidopterists' Society*, 38 (3), 179–185.
- Whittaker, P.L. (1984b) The insect fauna of mistletoe (*Phoradendron tomentosum*, Loranthaceae) in southern Texas. *The Southwestern Naturalist*, 435–444.
<http://dx.doi.org/10.2307/3670996>
- Wiklund, C. & Fagerström, T. (1977) Why do males emerge before females? *Oecologia*, 31 (2), 153–158.
<http://dx.doi.org/10.1007/BF00346917>
- Wolkman, L. & Núñez Bustos, E. (2014) Observaciones sobre la biología de *Thereus pseudarcula* (Giacomelli 1914) (Lepidoptera: Lycaenidae: Theclinae). *Historia Natural*, Vol. 4 (2), 113–121.
- Youngsteadt, E. & Devries, P.J. (2005) The effects of ants on the entomophagous butterfly caterpillar *Feniseca tarquinius*, and the putative role of chemical camouflage in the *Feniseca*–Ant Interaction. *Journal of chemical ecology*, 31 (9), 2091–2109.
<http://dx.doi.org/10.1007/s10886-005-6079-2>
- Zikán, J.F. (1956) Beitrag zur biologie von 12 Theclinen-arten. *Dusenja*, 7 (3), 139–148.