

# NOTES ON THE GENUS *CALISTO*, WITH DESCRIPTIONS OF THE IMMATURE STAGES (PART 2) (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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**ABSTRACT.**— The biology of *Calisto crypta* Gali, *C. nubila* Lathy, and *C. tasajera* Gonzalez, Schwartz & Wetherbee is described for the first time and the taxonomic implications of these data for the genus are discussed. Characters supporting relatedness of these species to each other and to other species complexes of *Calisto* are found in immature stages and in the structures of male and female genitalia. The latter are illustrated for the members of the *lyceia* species complex and relationships between these species are suggested. *C. hendersoni* Gali is suggested to be a synonym of *C. franciscoi*. A little known species, *C. raburni* Gali is found to be the most distinct member of the complex, and an additional locality for it (Dominican Republic: Polo, Barahona Prov.) is provided. New collecting data for the recently discovered *C. tasajera* add to the knowledge of this species' natural history. Finally, a theory of diversification is proposed for the *lyceia* complex.

**KEY WORDS:** Caribbean, Dominican Republic, eggs, Gramineae, Hispaniola, hostplants, larvae, Neotropical, Puerto Rico, pupae, taxonomy, West Indies.

The term "lyceia complex" was coined by Gali when he described five new species of the satyrine genus *Calisto* Hübner from Hispaniola, characterized by diffused red coloration of the underside of the wing (Gali, 1985). The term was subsequently used by Gonzalez *et al.* (1991), Hedges and Johnson (1994), and by Smith *et al.* (1994). This group of Hispaniolan *Calisto* includes seven species, of which four (*C. crypta* Gali, *C. lyceia* Bates, *C. hendersoni* Gali, and *C. franciscoi* Gali) are lowland desert dwellers, while *C. tasajera* Gonzalez, Schwartz & Wetherbee, *C. raburni* Gali, and *C. schwartzi* Gali inhabit mountain habitats. Based on the new data presented in this paper, the *lyceia* complex is likely to represent an artificial group; however, I continue for convenience to use this term.

All species but *C. lyceia* were described very recently and are little known to lepidopterists. They are sometimes hard to distinguish from each other based on the wing patterns, which are subdued, variable and fragile, and are best observed in freshly emerged, live specimens (Fig. 1). A key to the members of the complex based on these characters is provided in Hedges and Johnson (1994).

Based on currently available information, all species are allopatric and therefore the identification is usually based on the collecting locality rather than on external characters. Thus, *C. crypta* is found only in the north of the island, *C. lyceia* in the southeast on two small islands off the coast of Hispaniola, and *C. franciscoi* in the southern desert habitats of the island. *C. hendersoni* and *C. raburni* are known only from their type localities in Valle de Neiba and Massif de la Selle, respectively, while very similar *C. schwartzi* and *C. tasajera* inhabit different mountain systems (*C. schwartzi* – Sierra de Baoruco; *C. tasajera* – Cordillera Central). As more collecting data become available, the distribution of all these species might prove to be more extensive.

Johnson *et al.* (1987) concluded that female genitalia are extremely useful for classification of *Calisto* and for determining their evolutionary relationships. This study called attention to the previously neglected internal characters. Smith *et al.* (1991) illustrated the female genitalia for the newly described island isolate *C. anegadensis* Smith, Miller & McKenzie, found exclusively on Anegada Island. Both male and female genitalia of *C. anegadensis* suggest close aff-

inity to *C. nubila* Lathy of Puerto Rico, the species that is also the closest geographically. Simultaneously, the diffused red coloration of the underside of both species and the association of *C. anegadensis* with *Uniola virgata* bunch grass in a xeric habitat on Anegada relate both species to the *lyceia* complex on Hispaniola (*U. virgata* in the lowland desert and *Danthonia domingensis* in the high Cordillera Central are host plants of Hispaniolan *Calisto* (Sourakov, 1996)). Therefore, discussion of these species in the context of *lyceia* complex seems appropriate.

Here, illustrations of male and female genitalia for the members of the complex are provided, as these characters allow to distinguish species better than wing pattern and indicate relationships among them. New information on life histories presented here should contribute to understanding of phylogenetic relationships among members of the genus. I find it important to publish even this fragmented information because of the importance of *Calisto* for understanding the speciation process as a whole: their remarkable diversification in the tiny land area of West Indies (with 56 named taxa there, according to Smith *et al.*, 1994) deserves as much attention from students of the evolutionary biology as the 13 species of Darwin's finches in the Galapagos Islands once have received.

## Materials and Methods

*C. crypta* is found in the desert around Monte Cristi in the northwestern part of Dominican Republic. The habitat where it was collected in June 1996 is located on the coast of the large bay (Bahia de Icaquitos) just north of the town of Monte Cristi at the foothill of the El Morro mountain. Thomas C. Emmel of the University of Florida and his research assistants visited different desert localities around Monte Cristi six times in different years, but were able to obtain only half a dozen males (Emmel, pers. com.). His most successful trip was in June 1988, when he caught four males of *C. crypta* along with several rare species of Hesperidae. Most specimens taken by Schwartz are from May and were collected south of Monte Cristi (the southernmost specimen of *C. crypta* comes from the foothill of Cordillera Central, 40 km S. of Monte Cristi) (Schwartz, 1989).

The emergence and breeding of *C. crypta* apparently are correlated with rains, which are sporadic in the deserts of Hispaniola. The butterflies are closely associated with *Uniola virgata* and much of

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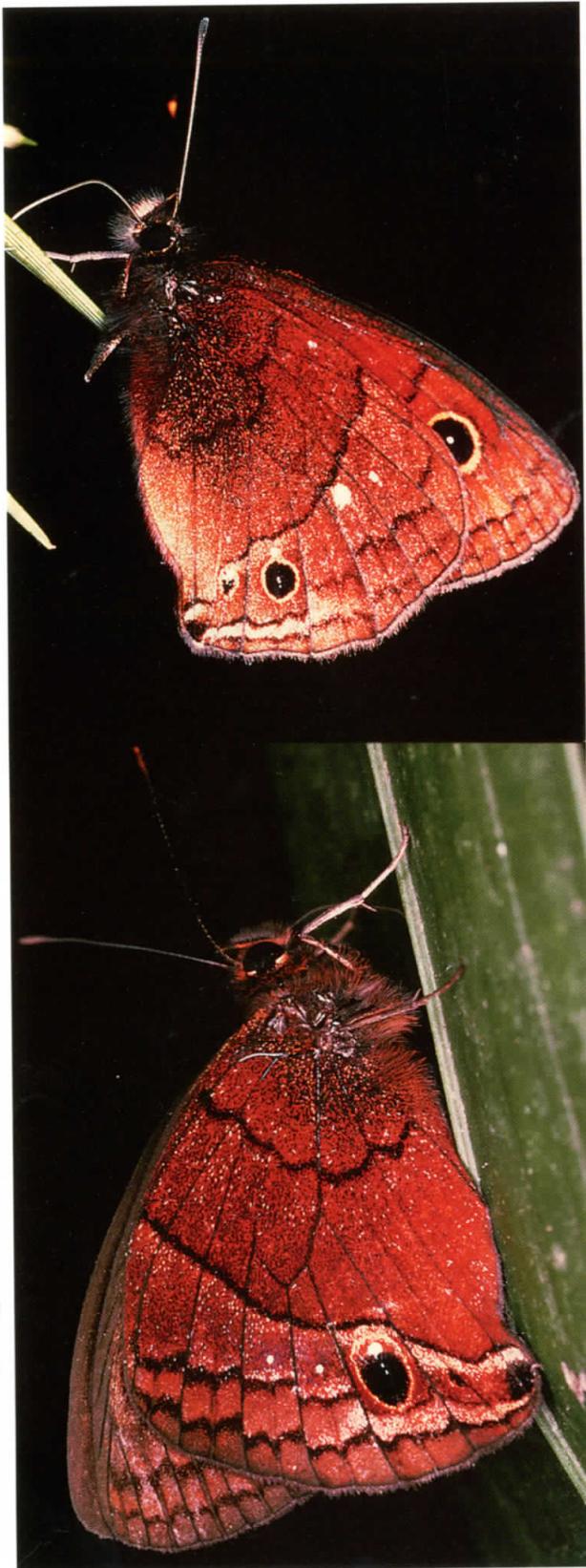


Fig. 1. Adults of *Calisto tasajera* (upper left), *C. nubila* (lower left), *C. raburni* (upper right), and *C. crypta* (lower right).

their time is spent hiding in the shade of these tall, spherically shaped, bushy grasses. Males occasionally fly between the bushes looking for females. Females stay inside the grass clumps, but can be chased out, or will come out to feed on desert wildflowers occasionally. All of the observed butterfly activity happened between 0900 and 1200h in the morning, before the desert heat became intolerable (temperatures above 40°C are not uncommon in this habitat).

Three June days that I spent in this habitat yielded 43 males and 6 females. The latter laid many eggs while being kept alive in plastic containers with netting tops, and fed daily with 25% sugar solution. The larvae were then reared through the fourth instar on St. Augustine grass, *Stenotaphrum secundatum*, at which point the last larva died.

Eggs of *C. tasajera* were obtained from numerous females collected in September 1998 at and above Valle de Bao (6300'), located at the foothill of Pico Duarte in the Cordillera Central. Butterflies were flying in association with *Danthonia domingensis* bunch grass. Many different grasses were offered to larvae, and while most larvae died before they started feeding, about 10% of the larvae (not more than 20 individuals) accepted the lawn Rye Grass. Almost all feeding larvae molted to second instars, but after molting only three larvae continued feeding. Of the latter, only one larva developed to the third instar, at which point it died.

Eggs of *C. nubila* were obtained from a single female collected in El Yunque, Puerto Rico, in September 1998. This species, though endemic to the latter island, is relatively common there. Twelve out of 20 first instar larvae that accepted Rye Grass developed normally to the last instar, at which point most were preserved, while some were allowed to pupate.

In all three of the above species, larvae were exposed to the wide variety of grasses for at least four days, before any of them began feeding. No such delay in feeding was observed in common and polyphagous Hispaniolan *Calisto* (*C. grannus* Bates and *C. confusa* Lathy). These species as well as *C. arcas* Bates, *C. nubila*, and *C. tasajera* were offered food concurrently, clearly demonstrating previously noted (Sourakov, 1996) host plant specificity (NB! *C. arcas* did not accept food at all).

Dissections were conducted using standard procedure: the abdomens of dry specimens were kept overnight in 10% KOH, genitalia removed and, in case of females, placed under a cover glass to flatten them. Then the shape of genitalia was traced with the help of an Olympus CH-2 microscope, equipped with a camera lucida.

Eggs were subject to a critical drying procedure prior to SEM. Larvae were photographed alive and preserved after boiling in 70% ethanol. Head capsules were collected after molting and studied under SEM. Color photography was conducted with a Nikon macro lens, extension tubes, and a ring flash. In case of first instar larval head capsules (Fig. 3), a digital camera and a computer program "Auto-montage" were employed to enhance depth of field.

### Morphology of Immature Stages

**Eggs:** *C. crypta* eggs are 0.8mm in diameter, perfectly round; brown fertility pattern appears within 24 hours in fertile eggs; under SEM, the level structure of the hexagonal facets could be observed, similar to that found in *C. tasajera* eggs (illustrated in Sourakov, 1996, p. 105). Unlike the above two species, eggs of *C. nubila* are attached to the substrate with glue secreted by female; they, therefore, are flatter at the base.

**First instar:** Body striations are typical of other *Calisto*, olive in color in *C. crypta* and *C. tasajera* (Fig. 4A), brown in *C. nubila* (Fig. 4D), with seven red subdorsal spots in the first two species, which makes them similar to *C. archebates* Ménétrières and *C. hysius* Godart. The main differences are restricted to the head. In *C. crypta* and *C. nubila* (Fig. 3), the ground color is light (white and cream color, respectively). Brown X-shaped markings that are typical of larvae of later instars in other *Calisto* species are strongly expressed in *C. crypta*, where they are complemented with dark head horns and numerous dark spots, located at the setal bases and throughout the head. In *C. nubila* the x-shaped markings are lighter, and are restricted to the front of the head. In *C. tasajera* (Fig. 3), the head is uniformly pigmented black, as it is in, for example, *C. confusa*, *C. obscura* Michener, and *C. archebates*. The head of all species is covered with fine reticulation, more dense in *C. tasajera* than in other two species. The characteristic head shape for each species and the differences described above are shown in Fig. 3. There are five extra setae on the head of *C. crypta*, compared to most other species (Fig. 2), and one such seta in *C. nubila*. The chaetotaxy of *C. tasajera* is typical of other *Calisto*, whose biology has been previously described (Sourakov, 1996).

**Later instars:** Differences in head shape between species become more profound. In *C. crypta*, it is rounded, with only traces of horns present in a form of enlarged setal base. In this character, *C. crypta* resembles *C. sommeri* Schwartz & Gali (Sourakov, 1996, p. 102). Head of *C. nubila*, on the other hand, is flattened in front and bears large head horns, similar to those of *C. hysius* and *C. archebates*. Shape of *C. tasajera*'s head is an intermediate of the above two species (Fig. 5). Coloration of the head in Hispaniolan species is pale, with only horn areas marked black, and several small dark spots throughout the head. In *C. nubila*, head is of the same color as the body, with black occipital band connecting the horns and descending on the lateral side of the head towards stemmata.

For *C. crypta* and *C. tasajera*, no larvae are available beyond the third instar. Body color pattern in this instar (Fig. 4B-C) resembles *C. grannus*

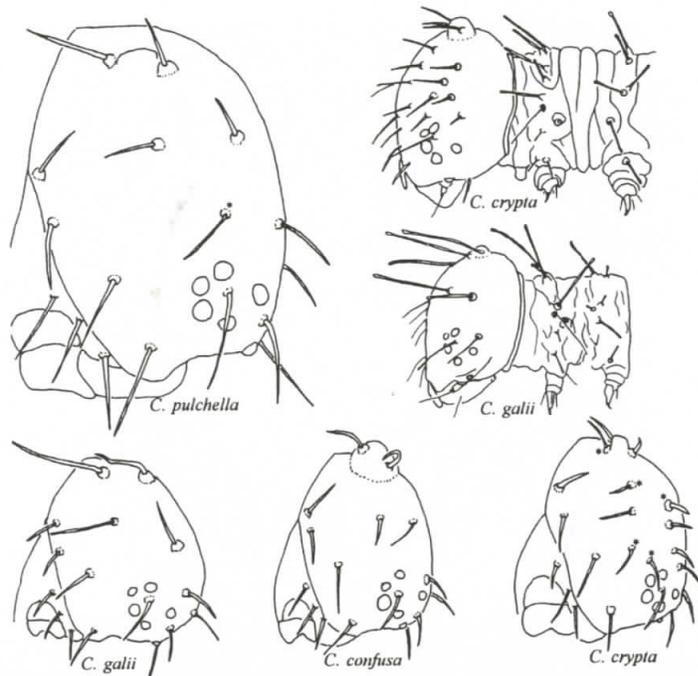


Fig. 2. Chaetotaxy of the first instar larva's head and first thoracic segments; \* - indicates extra setae.

(Sourakov, 1996, p. 93), with straight, dark brown and olive, longitudinal stripes and rhomboid widenings of mid-dorsal stripe; paradorsal spots are present.

In the last instar, *C. nubila*'s color pattern and prominent head horns (Fig. 4I-G) resemble the last instar larvae of *C. hysius* or *C. archebates* (illustrated in Sourakov, 1996, p. 94). However, even more than in above species, the light-brown striations blend with the larva's ground color. Still, slightly darker mid-dorsal stripe and zigzagged subdorsal stripes could be identified. The latter bear even darker paradorsal spots in segments 3-10, with a white large setal base giving an eye-like appearance to each spot. A cream-colored stripe separates light-brown sub-spiracular and sub-ventral/ventral areas.

**Pupae:** No pupae are available for *C. crypta* and *C. tasajera*. Pupa of *C. nubila* is olive-brown with black markings, whose extent varies between individuals (Fig. 4K-L). Thickened posterior margin of the abdominal segment creates ridges across the dorsal side of the abdomen. The pointed laterally cremaster is wide and highly setose, similarly to *C. confusa* and *C. pulchella* Lathy.

**Discussion:** The appearance of additional head setae and of a x-shape color pattern are interesting features of *C. nubila*'s and *C. crypta*'s first-instar larval morphology. *C. crypta* is particularly striking in its difference from the basic generic chaetotaxy with its five additional head setae. It is possible to speculate based on this observations that the highland member of the *lyceia* complex, *C. tasajera*, which shares a "normal" chaetotaxy and pigmentation of the head with the rest of *Calisto*, is the ancestral member of the complex, while *C. crypta* is a more recently derived one. Similarity of first instar head color patterns links *C. crypta* (and, therefore, the *lyceia* complex) to *C. nubila*, while presence of one suprastematal seta ties the latter species to *C. pulchella* Lathy (both of these species are also large, compared to other *Calisto*, and share similarities in shape and color of pupae).

While the contrast of *C. crypta*'s head chaetotaxy with that of other *Calisto* might appear extraordinary, one can only speculate on why such difference has evolved. The first instar larva of *C. crypta*, with its "pseudo-secondary" setae (normally secondary setae do not appear until the second instar), and with its color pattern typical of the later instars, is a mere morphological intermediate between the typical first and second instars of *Calisto*. *C. crypta*'s unusual morph-

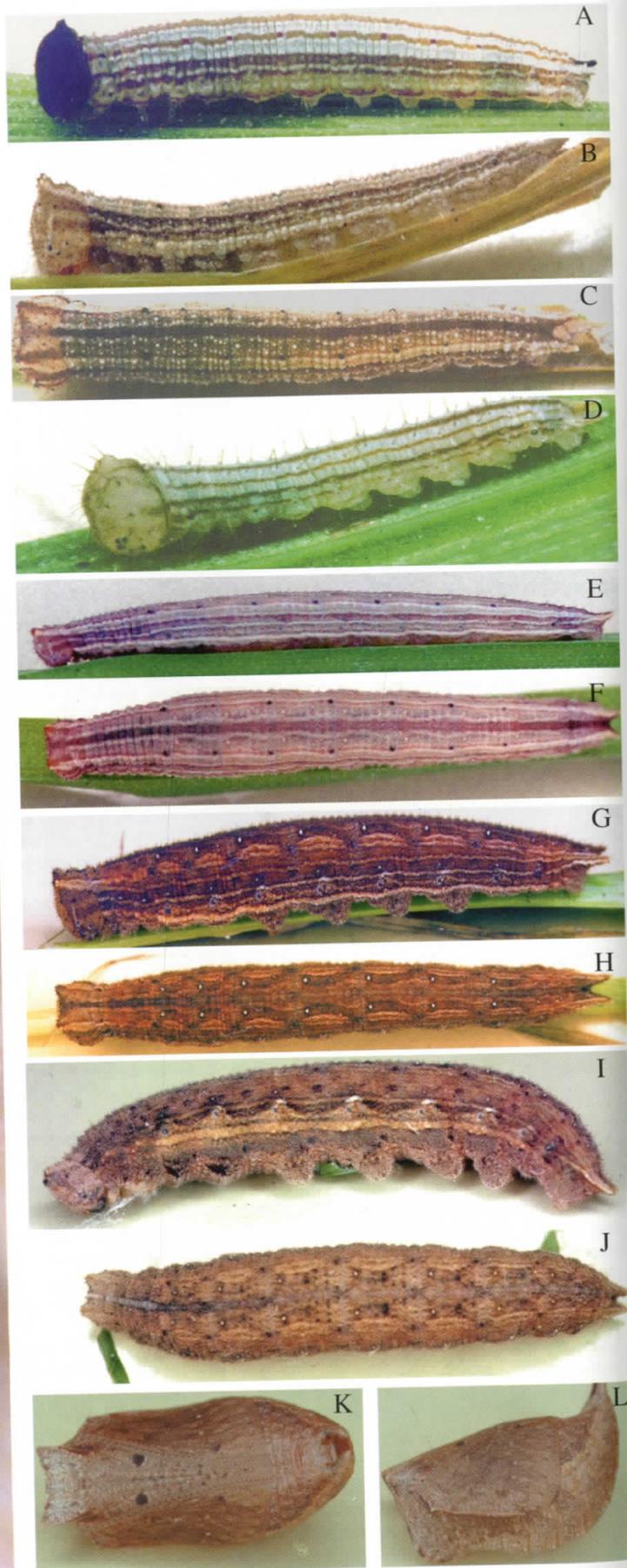
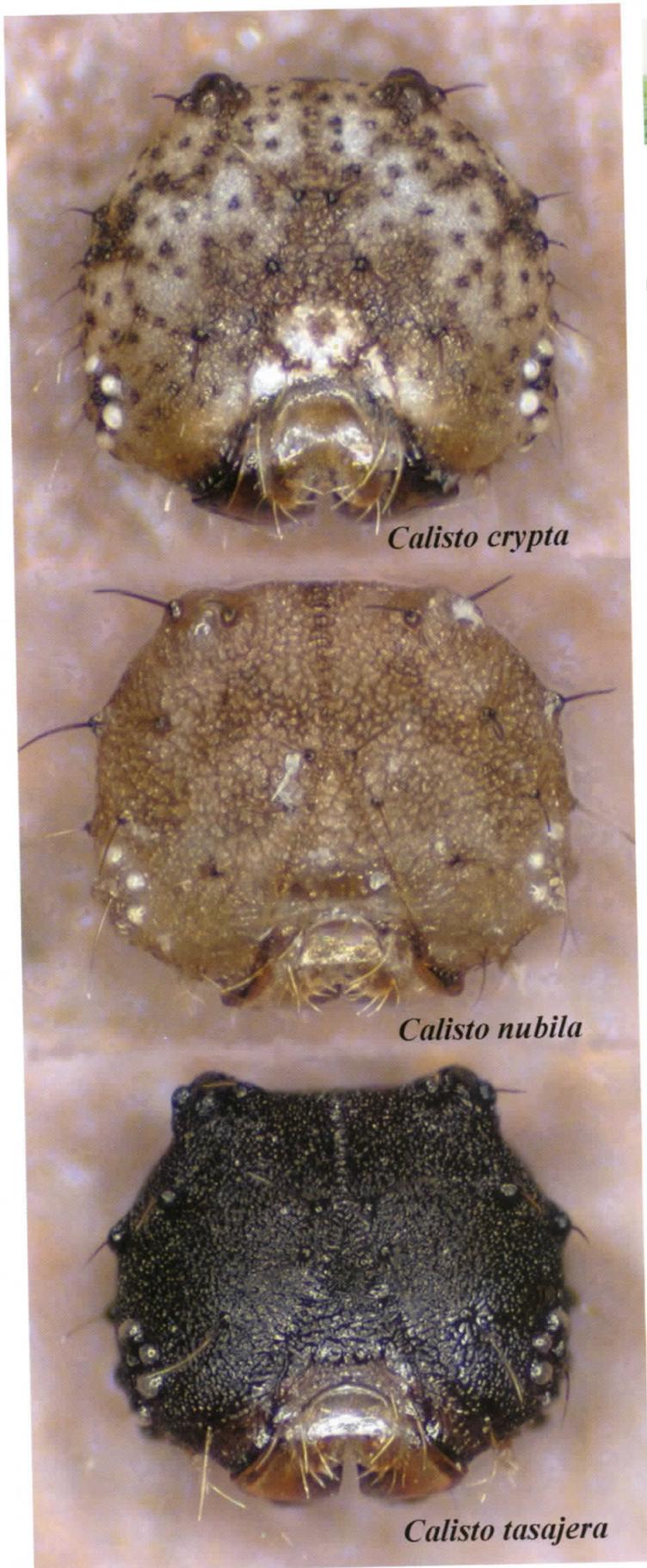


Fig. 3. Heads of the first instar larvae of *Calisto*.

Fig. 4. Immature stages of *Calisto*: (A)-(C) *C. tasajera*, (A) First instar; (B)-(C) Third instar; (D)-(L) *C. nubila*, (D) First instar; (E)-(F) Second instar; (G)-(H) Fourth instar; (I)-(J) Fifth instar; (K) Pupa, ventral view; (L) Pupa, lateral view.

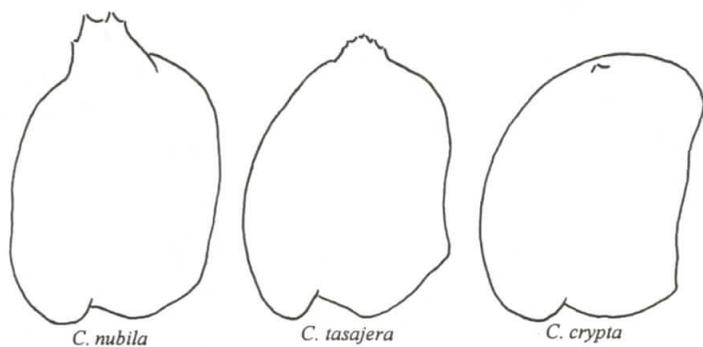


Fig. 5. Heads of the second instar larvae of *Calisto* (lateral view).

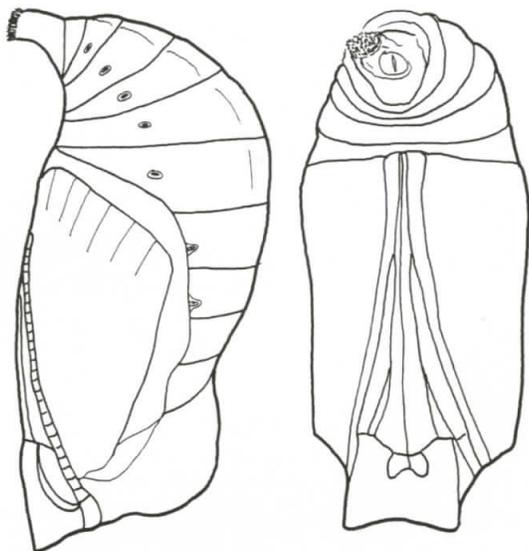


Fig. 6. Diagram of *C. nubila*'s pupa: lateral view (left), ventral view (right).

ology could be viewed as an unfolding within an egg of a genetic development program which normally happens outside an egg in other *Calisto* species.

The resemblance between late instar larvae and pupae of *C. nubila* those of other Hispaniolan *Calisto* species outside the *lyceia* complex indicates either *C. nubila*'s sister position towards the complex (Fig. 8), or convergent evolution.

### Review of Genital Structures

No extreme differences in female genitalia as illustrated in Johnson *et al.* (1987) for the members of the *lyceia* complex were found. The most noticeable characters in the female genital apparatus are in the posterior wall of the copulatory cavity. The cavity is a membranous sac, which opens internally into the ductus bursae and externally through the copulatory pore. The structures of the posterior genital plate were emphasized the most by Johnson *et al.* (1987), and the terms *sclerotized ring*, *dorsal crown*, and *internal loop* are applied to these structures.

Following the above terminology, it could be noted in all species studied (with the exception of *C. raburni*) that the differences are restricted to the size of the crown, length of the loop and shape of the ring (Fig. 7). The differences between *C. franciscoi*/*C. hendersoni* and *C. crypta* are slim, while those between *C. tasajera* and *C. schwartzi* are more substantial (these species pairs can hardly be distinguished based on wing pattern). In *C. raburni* (whose wing pattern suggests affinity to the latter species pair), the ring is

incomplete ventrally, and the loop is thick, asymmetrical and bears small, heavily sclerotized projection. The dorsal crown in this species is much narrower than in others. There is also a large sclerite in the middle of the posterior wall of the copulatory cavity. This sclerite is detached from the ring, and is not found in any other member of the genus. Thus, female genitalia (as well as male genitalia, as it is shown below) do not suggest close relationships of *C. raburni* to the *lyceia* complex, despite its external appearance.

The sclerotized portion of the anterior wall of the copulatory cavity previously overlooked by students of the genus (and indicated in Fig. 7 as the anterior genital plate) also is of taxonomic value. In *C. franciscoi*/*C. hendersoni* and *C. crypta*, the anterior plate is rounded and depressed inward, closely aligned to the posterior plate, while in *C. raburni*, *C. tasajera*, and *C. schwartzi*, it is of different shapes and protrudes outwards. The projections of the sclerotized ring towards the anterior genital plate are absent in *C. raburni*, wide and triangular in *C. tasajera*, and narrow and long in other species.

The shape of sclerotized parts of male genitalia can be used for identification of the species, while the position of uncus and brahia towards each other is non-important, as they are not firmly fused to the tegumen. Here, I illustrated only protruding parts of male genitalia (Fig. 7). *C. tasajera* and *C. schwartzi* differ by the presence of a sharp dorsal prong in which the valvae terminate in the first species, while being rounded in the second species. In *C. raburni*, the uncus is covered with long setae, there are no brahia, and the valvae are rounded. In *C. crypta*, *C. lyceia*, and *C. franciscoi*/*C. hendersoni*, the shape of the valvae might serve as a distinguishing character. In *C. crypta*, the terminus is right-angled; in *C. lyceia* it is rounded, while in *C. franciscoi*/*C. hendersoni* it protrudes dorsally in a short prong. Dissection of a large number of specimens from different localities will show whether this latter character is useful for delineating the taxa or whether it can be attributed to variation. Even based on the current information, *C. hendersoni* appears to be a synonym of *C. franciscoi*, as these two species have overlapping geographic ranges and show no distinguishing characters in either male, or female genitalia.

Previously published comparative drawings of male genitalia for the *lyceia* complex are only those found in original descriptions (Gali, 1985), and these differ dramatically from my observations. However, the structures illustrated in the above work are also often anatomically impossible (*C. franciscoi* has the valvae and aedeagus reversed 180°, *C. lyceia* lacks a saccus, etc.), so I attribute the differences to the poor quality of Gali's illustrations. In the second appendix to this work, I provide collecting data for the specimens studied.

### Relationships of the *lyceia* complex to other *Calisto*

*Calisto raburni* might be more closely related to some other living species of *Calisto* than to the *lyceia* group. This can be concluded based on the genitalic characters, despite the similarities with the wing pattern of the *tasajera*/*schwartzi* complex. The structure of the uncus, the absence of brahia (male genitalia), and a small sclerotized projection on the dorsum of the internal loop (female genitalia) of *C. raburni* are found also in *C. elelea* Bates, while an incomplete sclerotized ring is found only in *C. clydoniata* Schwartz & Gali (Sourakov, unpubl.). No biological information is available for the above three species to support the morphological characters relating adults.

Larval morphology of *C. crypta* and *C. tasajera* indicates these species' closeness to *C. grannus*, the wide-spread butterfly of the Central Cordillera. *Calisto grannus* and *C. tasajera* are sympatric in the Cordillera Central and there utilize the same host, *Danthonia domingensis*.

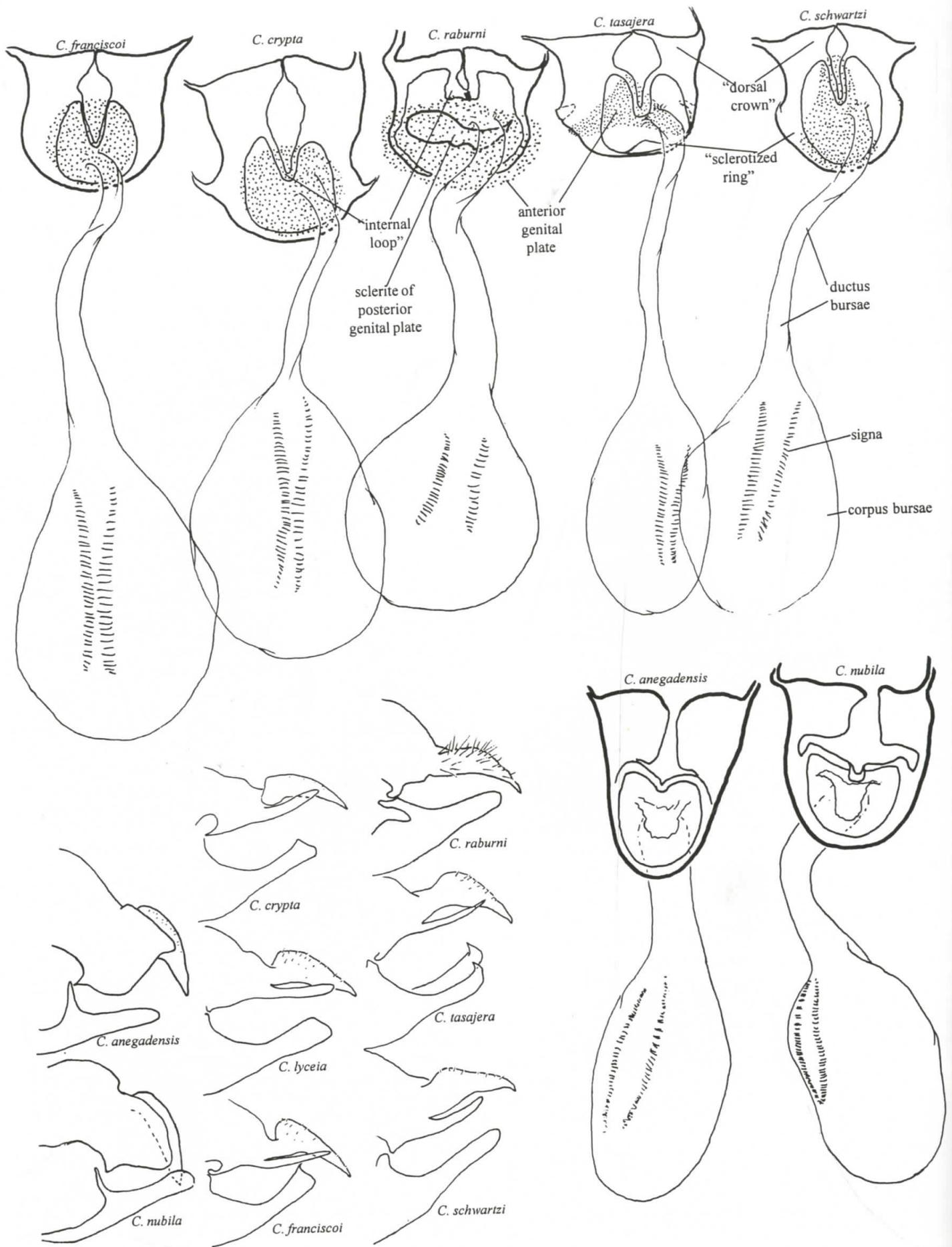


Fig. 7. Female and male genitalia in *Calisto* of *lyceia* species complex.

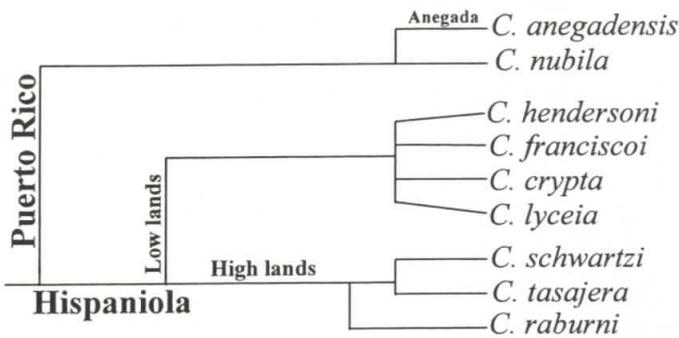


Fig. 8. A schematic cladogram of hypothetical evolutionary relationships of the *Calisto lyceia* complex.

Presence of a suprastematal seta in *C. nubila*'s first instar larva relates this species to *C. pulchella*, with which it also shares similar size, wing shape and shape and color of the pupa. The atypical genitalia of *C. pulchella* made some workers even consider it a separate genus (Johnson, pers. comm.), but new data presented herein help to link this species to the rest of the genus.

The schematic cladogram in Fig. 8 reflects my current perception of the evolutionary relationships within the *lyceia* complex. More work, including molecular studies, will be essential for understanding speciation in this fascinating group of butterflies.

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#### Appendix I

The present publication is an appropriate place to report collecting data concerning little known members of the *lyceia* complex. On my April 1995 trip to the top of the Pico Duarte (10,300'), I collected *C. tasajera*, which was present in very large numbers on the first days of the month at Valle de Bao, located at the northern foothills of the mountain (6300'). In September 1998, the species was noted again in great numbers, flying up between 6300' and 8700' on both southern and northern slopes. This species was first discovered by David Wetherbee and described by Gonzalez *et al.* (1991). Hedges and Johnson (1994) reported this species from Valle de Bao from 1 August. Two females of this species were also taken by Emmel and me on 23-25 June 1994 at mid-morning on the road to Valle Nuevo, 21-22 km SE of Constanza, 6350', where they fed on flowers, together with *C. arcas* Bates, *C. galii* Schwartz, and *C. grannus*. The UHW color of the latter specimens is gray, as it is in *C. schwartzi* (sister species of *C. tasajera* from the Southern paleoisland of Hispaniola), rather than red, as it is in the Valle de Bao population. Though the distance between two *C. tasajera* localities is only 40 km straight line, the isolation in high mountain refugia must have led to appearance of these distinct populations. The new data indicate *C. tasajera*'s multiple broods and wide distribution.

On the trip through Barahona Province, in the south of Hispaniola, Emmel and I stopped to collect on the outskirts of the town of Polo (foothills of Sierra de Baoruco). Among abundant *C. hysius*, Emmel netted a male of *C. raburni*. This specimen was found on 9 April 1995, flying at noon approximately 1 km south of Polo town center, in a valley heavily planted in coffee. This is a second locality known for this species, which was described from a single male collected much further to the west. Ten more specimens (4 females) of this species from its type locality collected by Gonzalez are in the Milwaukee Public Museum collection.

#### Appendix II

Specimens examined are from the collection of A. Schwartz donated to the Milwaukee Public Museum. All specimens in this collection have a unique number.

*C. tasajera* female 25034 (paratype), Rep. Dom.: San Juan, Loma de Tasajera, 2142m; male 27871 Rep. Dom.: Santiago, Loma de Tambor, 2000m.

*C. schwartzi* females 11333 and male 11354 (paratypes), Rep. Dom.: Pedernales, 1 km N. Aceitillar, 4200 ft.; female 27722 and male 27690, Rep. Dom.: Independencia, 16.7km SE Puerto Escondido, 1350m

*C. raburni* females 118398, 18403, and males 18391, 18399, Rep. Dom.: Independencia, 7km NE El Aguacate, Path to El Limon, 1700-1900ft.

*C. crypta* female 17648, Rep. Dom.: Santiago Rodriguez, 3.6km S. Zamba, 700ft.; male 17254 Rep. Dom.: 1km SE Monte Cristi

*C. franciscoi* female 10432 (paratype), Rep. Dom.: Independencia, 2km S. Duverge; male 13417 (paratype) Rep. Dom.: Barahona, 8km ESE Canoa

*C. hendersoni* female 13153 (paratype) and male 18258, Rep. Dom.: Independencia, 4km E. El Limon, sea level.

*C. lyceia* males 7425, 7426 Rep. Dom.: Isla Catalina, nr. Naval Base.