

NOTES ON THE GENUS *CALISTO*, WITH DESCRIPTIONS OF THE IMMATURE STAGES (PART 1) (LEPIDOPTERA: NYMPHALIDAE: SATYRINAE)

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ABSTRACT.— Immature stages of eight species of the genus *Calisto* Hübner (*Calisto grannus dilemma* González, *C. hysius* Godart, *C. obscura* Michener, *C. confusa confusa* Lathy, *C. confusa debarriera* Clench, *C. batesi* Michener, *C. archebates* Ménétériès, *C. sommeri* Schwartz and Gali, and *C. pulchella* Lathy) are illustrated, described, and compared. Characters of immature stages, such as egg, larval, and pupal structures and color patterns, are found to be of taxonomic value. Correlations between these characters and ecological strategies employed by immature stages of different *Calisto* species are found. On the basis of these observations, taxon *debarriera* is synonymized with *confusa* and assigned a form status, while *C. grannus grannus* and *C. grannus dilemma* are confirmed to be conspecific. In contrast, *C. batesi* and *C. hysius*, as well as *C. sommeri* and *C. grannus*, are proved to be separate species. Immature stages of *C. pulchella* proved to be morphologically very distinct from the other *Calisto* species, supporting observations on the adults. Foodplant records and observations on egg and first instar larval morphology are provided for *C. galii* Schwartz, *C. tasajera* González, Schwartz & Wetherbee, *C. schwartzi* Gali, and *C. arcas* Bates.

KEY WORDS: *Calisto*, Caribbean, Central America, Diptidae, eggs, Gramineae, Poaceae, Hispaniola, hostplants, larval morphology, Neotropical, pupae, systematics, West Indies.

The study of lepidopteran immature stages has proved to be important for both alpha and beta taxonomy, as well as for recreating the evolutionary history and understanding the ecological strategies employed by species (e.g., Dantchenko *et al.*, 1995; Kitching, 1985; Miller, 1991; Balmer and Pratt, 1992). The vast majority of mortality in a species occurs in the egg, larval and pupal stages. Therefore, these stages are subject to intensive natural selection. Natural selection in stable environments usually works to protect the phenotypic status quo, unless the mortality factors change for a species. As a consequence, so-called sibling species, whose adults remain superficially similar under similar environmental conditions, can differ in characters of the eggs, larvae, and pupae, which occupy different ecological niches and are likely to change phenotypically as a result of different selective factors. Studying these stages might lead to discovery of sibling species complexes. Some characters could be conservative and therefore useful for grouping species into species groups and genera. Finally, the correlation of the morphology of immatures with their ecological strategies is poorly studied and is of interest.

Most of the existing applications of the morphology of immature stages to systematics compare members of higher taxa such as genera and tribes. There are practically no works that include thorough comparison of the immature stages on the intrageneric level. Such an attempt is made here in respect to the genus *Calisto*, which is obviously monophyletic and at the same time a highly diverse genus, yet immatures of which are likely to show differences.

In the last revision of the genus *Calisto*, Munroe (1951) recognized only 20 species. Since then, the number of described

species has increased to 38, giving a total of 47 valid names available for the group, when combined with existing subspecific names (Smith *et al.*, 1994).

The diversity of habitats and climatic conditions found in the relatively tiny area of the island of Hispaniola, where most of the *Calisto* species occur, may play an even larger role in the speciation process than does geographic isolation within the island, and may have stimulated adaptive radiation. Previous works on the fauna of the West Indies showed that they are a very appropriate area for an evolutionary process of this kind (Liebherr, 1988; Woods, 1989).

In the present work, the immature stages of eight different species of the genus *Calisto* (Satyrinae) from the Dominican Republic, West Indies, are described and compared.

MATERIALS AND METHODS

After a trip to the Dominican Republic in June 1994, an attempt was made to raise *Calisto* species on Kentucky Blue grass, *Poa pratensis*. Several relatively common species, such as *C. grannus grannus*, *C. grannus dilemma*, *C. batesi*, *C. confusa*, and *C. obscura* initially seemed to accept the substitute food plant. However, most of the larvae died in the early stages, and only *C. grannus grannus* was reared to the last instar (Sourakov and Emmel, 1995). *Calisto galii*, *C. schwartzi*, *C. arcas*, and *C. pulchella* did not accept the substitute food plant at all. That finding led to the supposition that many of the rare and extremely localized species of *Calisto* are hostplant specific, and that their unique distributions might be reflecting not only evolutionary history, but their hostplants' present distributions as well.

On a subsequent trip to the Dominican Republic in September 1995, eggs from the above species as well as those of *C. archebates*, *C. hysius*, *C. sommeri*, *C. confusa debarriera*, and *C. tasajera* were obtained. Larvae of *C. confusa confusa*, *C. confusa debarriera*, *C. obscura*, *C. hysius*, *C. grannus dilemma*, *C. batesi*, *C. sommeri*, and *C. archebates* were raised to the pupal stage on a mixed diet of St. Augustine grass (*Stenotaphrum secundatum*) and Bermuda grass (*Cynodon dactylon* (L.) Pers.). Their complete life histories are recorded here. A female of *C. grannus dilemma* was observed placing an egg underneath the leaf of *Panicum xalapense* HBK (Poaceae). There is no doubt, however, that all of the above species, except *C. archebates*, utilize more than one species of grass. *C. archebates* is a localized species, found in a few localities of the Southern Island in hardwood forest. The only grass abundant in their native habitat is *Isachne rigifolia* (Poir.) Urb. Females seem to be closely associated with it, and often spend time on this plant. This behavior is typical for other *Calisto* females as well, so that they are rarely seen in flight, even when the species is abundant. The larvae of *C. archebates* accepted *I. rigifolia*, but were raised on St. Augustine grass due to its availability. All larval instars of *Calisto pulchella* were collected on sugar cane. This *Calisto* is an agricultural pest of cane on Hispaniola (Smyth, 1920; Rincones *et al.*, 1989; Holloway, 1933). They were subsequently raised to pupa on sugar cane leaves, stored in the refrigerator.

Females of all species laid eggs in 8 oz plastic containers. Only *C. pulchella*, *C. tasajera*, and *C. archebates* lay their eggs loose, without attaching them to the plant, the netting, or the walls of the container. A female of *C. tasajera* was observed sitting on a leaf and dropping the egg into the middle of an unidentified bunch grass (see back cover figures), on which it feeds in Valle de Bao, in the Cordillera Central. The grass is so tough and dry that the larva evidently feeds at the very base of the grass stem, where it is soft and moist, but where a female cannot gain access because of the thickness of the grass. Larvae of *Calisto grannus* raised in a pot with growing grass spent all the time at the bases of the grass. This behavior may provide protection from predators. *C. pulchella* drops the egg into the deep pocket between the stem and the leaf of the sugar cane, where the larva feeds, scraping the soft surface of the stem. It is completely hidden by the leaf, and comes out onto the leaves at night only in later instars. Turner (in Brown and Heineman, 1972) described *C. zangis* females in Jamaica dropping eggs while flying over grass. No such behavior was observed in Hispaniolan *Calisto*.

All of the reared species had five larval instars. In Dethier's (1940) description of the life history of *C. herophile* Hübner from Cuba, he observes only four instars. The description of *C. zangis* (Fabricius) by Turner does not specify the number of instars. Collecting localities for the specimens, from which eggs were obtained and immature stages described, are in Table 1:

Taxon	Locality
<i>C. archebates</i>	5.5 km north of Los Arroyos, Sierra de Baoruco, Pedernales Province, 1300m
<i>C. sommeri</i>	5.5 km north of Los Arroyos, Sierra de Baoruco, Pedernales Province, 1300m
<i>C. hysius</i>	1.5 km south of Los Arroyos, Sierra de Baoruco, Pedernales Province, 1300m
<i>C. obscura</i>	San José de Las Matos, Santiago Province, 600m
<i>C. grannus dilemma</i>	Above Mata Grande, Santiago Province, Cordillera Central, 1200m
<i>C. batesi</i>	Above Mata Grande, Santiago Province, Cordillera Central, 1200m
<i>C. confusa confusa</i>	Above Mata Grande, Santiago Province, Cordillera Central, 1200m
<i>C. confusa debarriera</i>	Above Mata Grande, Santiago Province, Cordillera Central, 1200m
<i>C. pulchella</i>	Above Mata Grande, Santiago Province, Cordillera Central, 1200m

IMMATURE STAGES

Calisto confusa confusa Lathy and *C. c. debarriera* Clench: (front cover, upper right and lower right)

Egg: 0.85mm wide, 0.82mm high, rounded, slightly tapered toward micropyle (Fig. 17H); surface with hexagonal facets; interstices between facets bear pores, one to each side of facet (Fig. 17P); micropyle rosette-shaped with irregular pentagonal and hexagonal facets (Fig. 17A); white when laid; subsequently brown patterned if fertile (Fig. 11U).

First instar larva (Fig. 9A,B): Head (Fig. 12G-1) 0.60mm wide, 0.46mm high, black; entire surface, except clypeus and narrow area of frons immediately above clypeus covered with fine irregular raised reticulation (Fig. 14L); pair of horns, each 12% of head height; when newly hatched, larva pure white, brown striped (Fig. 11P). Spiracular stripe relatively weak. After feeding, ground color becomes dark greenish. Stripes become wider and darker (Fig. 11O).

Second instar (Fig. 9C-F): Head 0.80mm wide, 0.64mm high, ground color pure white, extensively brown patterned (Fig. 12G-2); body, prolegs and abdomen pale brown; a complex body pattern maintained to last instar, with minor changes; spiracular stripe broad, pale brown, subdorsal stripe convex which, when combined across all segments, appears as a zigzagged white line running between spiracular and supraspiracular stripes; mid-dorsal stripe on each segment broadening to an anterior diamond-shaped mark; subspiracular stripe narrow, pale brown; between it and spiracular stripe a white line; spiracles white, surrounded by ring of white.

Third instar (Fig. 9G,H): Head (Fig. 12G-3) 1.40mm wide, 1.24mm high. Other features are identical to those of second instar.

Fourth instar (Fig. 9I-L; 10A-C): Head (Fig. 12G-4, 12H-4) 1.58mm wide, 1.42mm high; subdorsal body spots become darker and smaller, turning into dots. Some specimens have large black spots next to spiracles on abdominal segments 3-6 (Fig. 9K).

Fifth instar (Fig. 9M-S; 10D-L): Head (Fig. 12G-5, 12H-5) 2.21mm wide, 2.13mm high; mid-dorsal body stripe turns white in first two thoracic segments, extending into a white median stripe in occipital part of head. Some individuals show contrasting coloration, especially immediately after molting (Fig. 9M,N), while others are dull (Fig. 9O,P). In the last instar larva almost doubles in size (Fig. 10J-K). However, towards pupation, it becomes smaller and turns translucent green, with the entire pattern preserved (Fig. 9S, 10L). Some prepupae are marked more extensively than others (Fig. 9S and Fig. 10L).

Pupa (Fig. 9T, Fig. 10 M-O and Fig. 13B): 10mm long, 4mm wide dorso-ventrally, 5mm across, pale green. Occasional individuals have black markings (only one of several dozen pupa); firmly attached to grass stem; abdomen bent almost at a right angle, as the larva pupates on vertically oriented grass leaves and stem; before hatching turns yellowish with black eyes (Fig. 9T), and later entirely black.

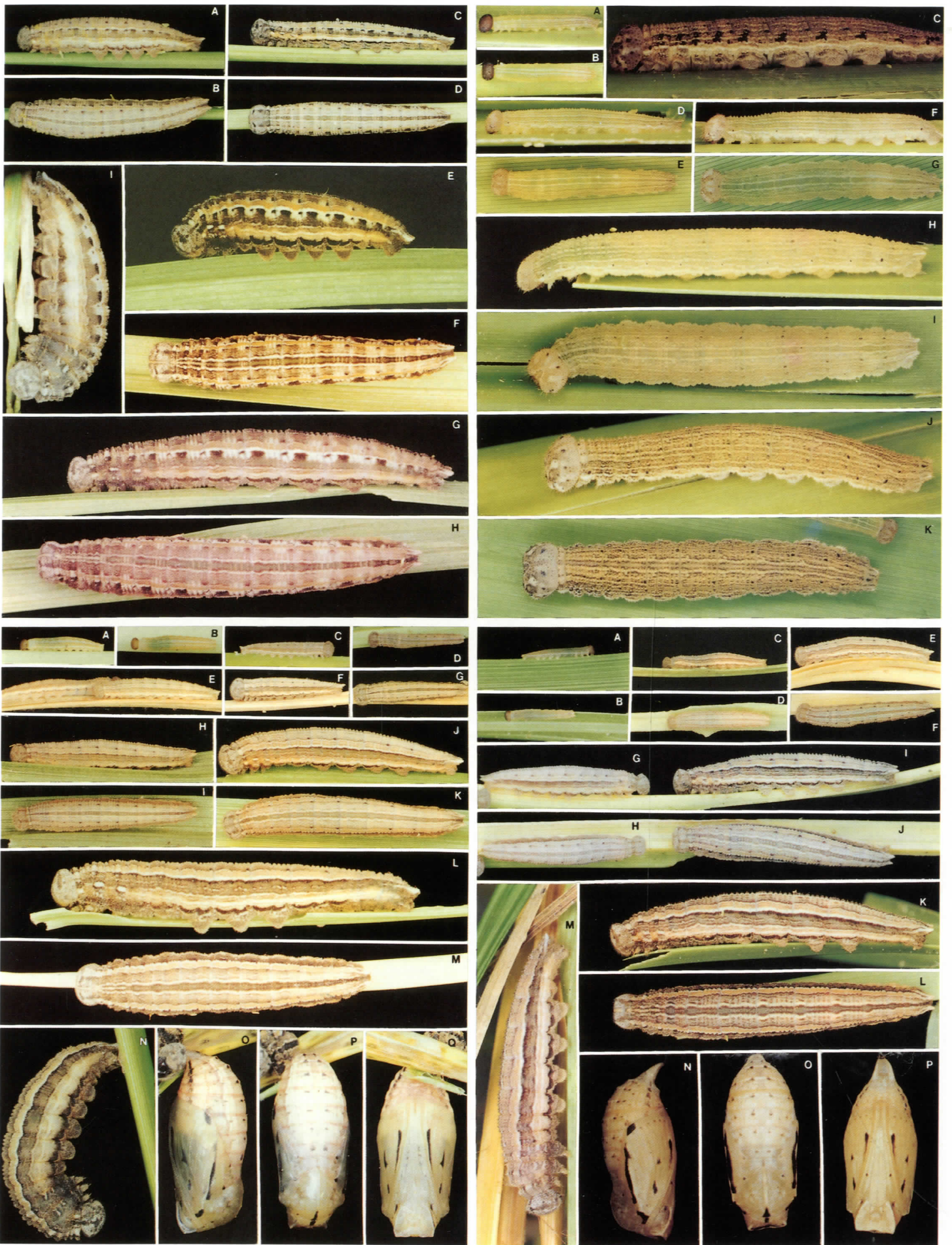
Adults: Two forms are found in adults of *C. confusa*, the most widespread and common *Calisto* species in Hispaniola: *C. confusa debarriera* (Front cover, lower right), which lacks white coloration on the underside, and *C. confusa confusa* (front cover, upper right), in which all dark stripes are bordered by white stripes of different width and intensity.

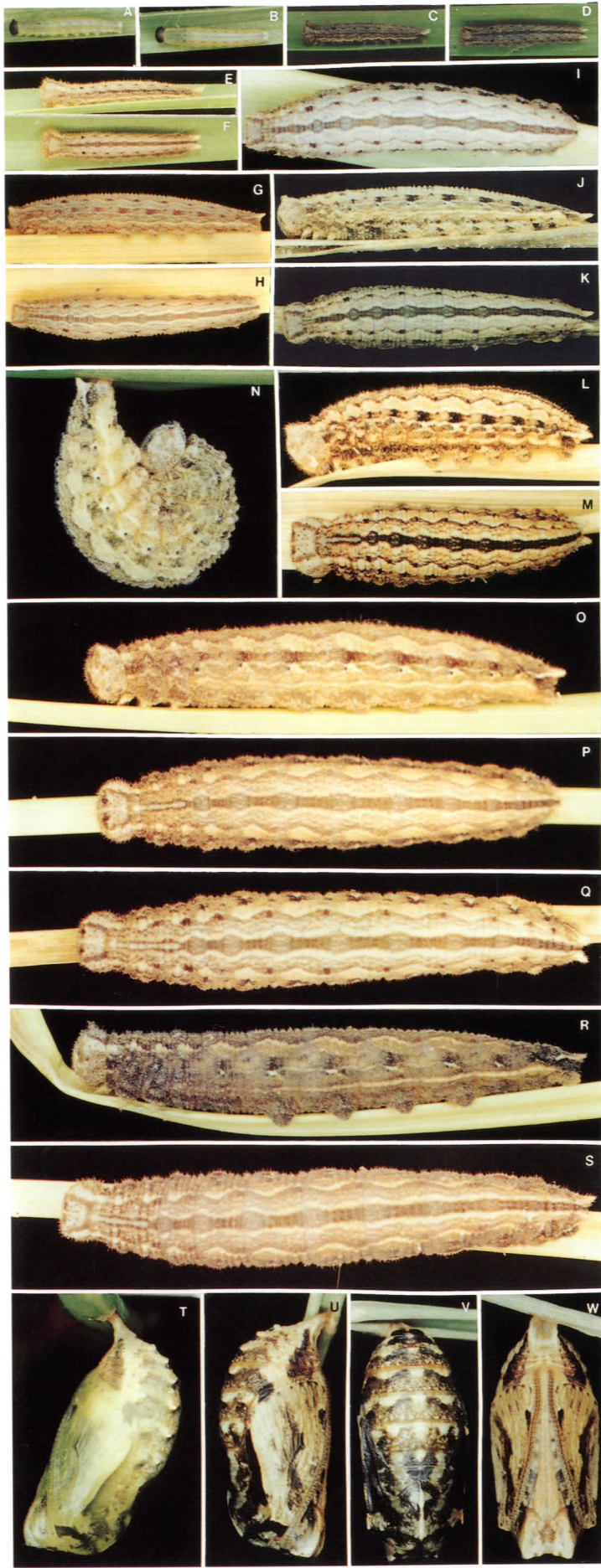
Fig. 1 (upper left). Larvae of *Calisto sommeri*, "spotted" form: (A)-(B) Third instar; (C)-(D) Fourth instar; (E)-(H) Fifth instar; (I) Prepupa.

Fig. 2 (upper right). Immature stages of *C. pulchella*: (A)-(B) First instar; (D)-(E) Second instar; (F)-(G) Third instar; (H)-(I) Fourth instar; (C), (J)-(K) Fifth instar.

Fig. 3 (lower left). Immature stages of *Calisto sommeri*, "striated" form: (A)-(B) First instar; (C)-(E) Second instar; (F)-(I) Third instar; (J)-(K) Fourth instar; (L)-(M) Fifth instar; (N) Prepupa; (O)-(Q) Pupa.

Fig. 4 (lower right). Life history of *Calisto grannus dilemma*: (A)-(B) First instar; (C)-(D) Second instar; (E)-(H) Third instar; (I)-(J) Fourth instar; (K)-(L) Fifth instar; (M) Prepupa; (N)-(P) Pupa.





This character is stronger in females, and varies significantly from one population to another. These forms, originally described as subspecies, are considered as species by some authors. In general, *C. c. confusa* is found at lower elevations than *C. c. debarriera*. I found some individuals of either form mixed in the populations of the other form. The distribution of these forms is parapatric, which eliminates the possibility that these are geographic subspecies. Both forms from the same population were reared under similar conditions and their life histories recorded. Even though differences in coloration are noticeable, no other significant differences were found (Fig. 9 and Fig. 10). These differences are within normal intrapopulation variation and cannot serve for separating species. Furthermore, one of the four reared offspring of *C. c. confusa* fell within the range of *C. c. debarriera* variation, and two of twenty offspring of *C. c. debarriera* showed some white coloration, which could be considered intermediate. Considering all of the above, I conclude that *C. c. confusa* and *C. c. debarriera* are conspecific, and therefore assign the status of ecological forms to these taxa.

***Calisto obscura* Michener:** (front cover, lower left).

Egg: No eggs available for study.

First instar larva: Head (Fig. 12F-1), 0.67mm wide, 0.50mm high; black; structure similar to that of *C. confusa* (Fig. 14M); pair of horns, each 18% of the head height.

Second instar (Fig. 6A,B): Head (Fig. 12F-2) 0.90mm wide, 0.74mm high; body striation olive colored; mid-dorsal stripe wide, broadening on each segment to an anterior diamond-shaped mark; other stripes thin; spiracular stripe separated from pale grey prolegs and abdomen by a white stripe.

Third instar (Fig. 6C-F): Head (Fig. 12F-3) 0.80mm wide, 0.80mm high; body coloration similar to that of second instar larva of *C. confusa*.

Fourth instar (Fig. 6G-H): Head (Fig. 12F-4) 0.98mm wide, 0.98mm high; spiracular stripe concave; zigzagged white line between spiracular and supraspiracular stripes found in *C. confusa*, in *C. obscura* expands into a chain of white rhombuses; subspiracular stripe becomes distinct and dark in late fourth instar.

Fifth instar (Fig. I-M): Head (Fig. 12F-5) 1.53mm wide, 1.49mm high; black spots in subdorsal body stripe less noticeable due to overall darkening of the body; cream-colored supraspiracular chain of rhombuses distinct in segment 3-8; mid-dorsal stripe white in first two segments of the body, extending to occiput of head (Fig. 6K), widening in segments 3-7; subspiracular stripe black. Two types of ground coloration of larva were observed: dark brown to almost black (Fig. 6I), and olive-brown (Fig. 6J-K). Prepupae (Fig. 6L,M) gray or brown. In some prepupae, subspiracular stripe disappeared (Fig. 6M).

Pupa (Fig. 6N-O and Fig. 13A): 10.3mm long, 4.5mm wide dorsoventrally, 5mm across, pale brown with a few black markings.

C. obscura, for which the life history is illustrated, was collected at the San Jose de las Matas area in the Cordillera Central, at an elevation of 700 m above sea level. The larvae of *C. obscura* from the foothills of the Sierra de Baoruco at sea level were reared earlier. Their coloration was lighter than the examples described above, and the head of the fifth instar larva (Fig. 12D-6) was smaller, with obscured pattern. The *C. obscura* populations of the northern and southern islands have possibly been isolated for a long time and became distinct.

Fig. 5 (left column). Life history of *Calisto archebates*: (A)-(B) First instar; (C)-(D) Second instar; (E)-(H) Third instar; (I)-(K) Fourth instar; (L)-(M) Fifth instar immediately after molting; (O)-(S) Different forms of fifth instar; (N) Prepupa; (T) Pupa, green form; (U)-(W) Pupa, brown form.

Fig. 6 (upper right). Immature stages of *Calisto obscura*: (A)-(B) Second instar; (C)-(F) Third instar; (G)-(H) Fourth instar; (I)-(K) Fifth instar; (L)-(M) Prepupa; (N)-(O) Pupa.

Fig. 7 (lower right). Immature stages of *Calisto hysius*: (A)-(B) Second instar; (C)-(D) Third instar; (E)-(F) Fourth instar; (G)-(J) Fifth instar; (K) Prepupa; (L)-(N) Pupa.

***Calisto hysius* Godart:** (front cover, middle left).

Egg: 0.7mm wide, 0.7mm high; wider at base, tapered toward micropyle (Fig. 17I); surface bearing equidistantly positioned, rounded sunken facets with pores on elevated interstices between them (Fig. 17M).

First instar larvae (Fig. 11D,E): Head (Fig. 12D-1) pale brown, 0.59mm wide, 0.53mm high; reticulation much less dense than in *C. confusa*, resembling a spider web laid over smooth surface of head (Fig. 14J); pair of horns, each 11% of head height; body striations pale brown.

Second instar (Fig. 7A,B): Head (Fig. 12D-2) 0.71mm wide, 0.80mm high; color pattern of head X-shaped, with arms of "X" connecting in middle of occipital area; upper arms of "X" very weakly expressed; a black stripe extends on top of head and down its sides, ending at stigmatal areas and outlining shape of head, if looked at full face; stripes come off tips of head horns and continue into subdorsal body stripes; body striping same as in *C. obscura*, except that subventral stripe narrow instead of wide; broadenings of mid-dorsal stripe oval rather than diamond-shaped.

Third instar (Fig. 7C,D): Head (Fig. 12D-3) 1.28mm wide, 1.24mm high; subdorsal body spots darker and more noticeable than in second instar.

Fourth instar (Fig. 7E,F): Head (Fig. 12D-4) 1.84mm wide, 1.82mm high; body stripes dark brown; subdorsal spots black; zigzag-shape of outside margin of subdorsal stripe repeated by very thin supraspiracular stripe.

Fifth instar (Fig. 7G-J): Head (Fig. 12D-5) 2.51mm wide, 2.34mm high; subdorsal body stripe becomes much darker, especially on outside, where it almost matches color of subdorsal spots; supraspiracular stripe almost disappears; spiracular stripe narrows in middle of each segment and widens on edges, which creates white chain of rhombuses throughout body segments 3-9; color pattern varies from almost black (Fig. 7G,H) to brown (Fig. 7I-J). Prepupa dark green (Fig. 7K).

Pupa (Fig. 7L-M, and Fig. 13I-K): 11mm long, 5.25mm wide dorsoventrally, 5.25mm across; ground color dark green with black markings which vary in intensity (Fig. 13I); row of black dots goes along mid-dorsal line, one dot in each abdominal segment; lateral sides of eye-pieces and base of wing black; two rows of black spots on each side of spiracular line; wings and forelegs bear a few black markings.

***Calisto batesi* Michener:** (front cover, upper middle).

Egg: Rounded, flattened on top and bottom (Fig. 17D), 0.74mm wide, 0.67mm high; surface ridged, with pores on top of ridges (Fig. 17L); stay white until larvae hatch.

First instar larva (Fig. 11B,C,J): Head (Fig. 12E-1) brown, 0.58mm wide, 0.46mm high; structure as in *C. hysius* (Fig. 11K); body striation pale brown; spiracular stripe well expressed (Fig. 11J); supraspiracular stripe becomes zigzagged (Fig. 11B,C). After feeding, ground color turns green.

Later instars: In general these similar to *C. hysius*. Spiracular stripe in last instar wider than in *C. hysius*; larva appears almost entirely black; subspiracular stripe paler than rest of body (Fig. 19F); head smaller than in other *Calisto* in all instars (Fig. 12E); pigmentation of last instar head more intensive, so that dominant color black (Fig. 12E-5). For head sizes, see Table 1.

Pupa: No pupa available for description.

***Calisto archebates* Ménétriers:** (front cover, middle right).

Egg: Surface covered with sunken circular facets (Fig. 17N), with six equidistantly positioned pores for each facet on surrounding elevated interstices.

First instar larva (Fig. 5A,B): Head (Fig. 12A-1) black, 0.74mm wide, 0.65mm high; intensity of reticulation (Fig. 14B) between those of *C. confusa* and *C. hysius*; two horns, each 13% of head height; subdorsal

body stripe zigzagged (Fig. 11H); posterior reddish spot on body segments 3-10, among which first spot larger than rest; mid-dorsal stripe vague.

Second instar (Fig. 5C,D): Head (Fig. 12A-2) bears extensions of each, but mid-dorsal, olive colored stripes; 1.14mm wide, 0.98mm high; mid-dorsal body stripe becomes darker, with oval anterior broadenings on segments 3-9.

Third instar (Fig. 5E,H): Head (Fig. 12A-3) 1.49mm wide, 1.39mm high; all but subdorsal stripes on head become vague; supraspiracular body stripe becomes darker towards middle of each segment appearing broken; thin white zigzagged stripe divides spiracular stripe in two.

Fourth instar (Fig. 5I-K): Head (Fig. 12A-4) 2.14mm wide, 2.14mm high. Two forms noticeable in this instar: black (Fig. 5J,K) and olive colored (Fig. 5I); mid-dorsal stripe white in first 2 segments; previously described pattern becomes more contrasted.

Fifth instar (Fig. 5L-S): Head 3.00mm wide, 2.79mm high. Immediately after molting (Fig. 5L,M), body pattern very contrasted. When larva grows, pattern becomes less noticeable. Several forms found in this instar: colored almost entirely and evenly black (Fig. 5R) or olive (Fig. 5S). These may have strong contrast and may bear earlier described pattern with subdorsal spots and broken spiracular stripe present (Fig. 5Q); or they may be contrasted, but with less pigmentation, with supraspiracular stripe wide and pale (Fig. 5O,P). In all forms, mid-dorsal stripe white in first three segments. Prepupa (Fig. 5N) grayish-brown.

Pupa (Fig. 5T-W and Fig. 13L-O): 12mm long, 6mm wide dorso-ventrally, 5.7mm across; wings green after pupation (Fig. 13O), but turn gray in time in most individuals; prothorax and mesothorax dark green with an intense black pattern; abdomen dark gray with a white stripe just ventrally of spiracular line, pale mid-dorsal stripe, and subdorsal line of whitish spots; intensity of black coloration varies in different individuals (Fig. 13L).

***Calisto grannus dilemma* González:** (front cover, upper left).

The life history of *C. grannus grannus*, of which *dilemma* might be a low elevation form rather than a subspecies, has been described (Sourakov and Emmel, 1995). Even though no significant differences were observed between the two subspecies, here a new description is provided, which includes the third instar, the fourth instar, and the pupa, which were not described earlier.

Egg (Fig. 11R): 0.89mm wide, 0.86mm high, almost perfectly round, being a little flattened in micropylar area (Fig. 17G); surface reticulate; interstices between hexagonal facets elevated significantly; facets connected with each other by a deep gorge (Fig. 17O); color pattern brown (Fig. 11R).

First instar larva (Fig. 4A,B): Head (Fig. 12C-1) 0.61mm wide, 0.53mm high; dark brown, darker than in nominate subspecies, reticulation like that in *C. archebates*, not different from that of nominate subspecies (Fig. 14D); body stripes straight and brown (Fig. 11A,I).

Second instar (Fig. 4C,D): Head (Fig. 12C-2) 0.87mm wide, 0.84mm high; anterior broadenings of mid-dorsal body stripe in segments 4-11 oval; subdorsal stripe thin with dark posterior spots in segments 3-9; spiracular stripe becomes dominant; subdorsal stripe inconspicuous; subventral stripe darker than tan prolegs.

Third instar (Fig. 4E,H): Head (Fig. 12C-3) 1.24mm wide, 1.14mm high; body coloration similar to second instar larva.

Fourth instar (Fig. 4I,J): Head (Fig. 12C-4) 1.77mm wide, 1.61mm high; head pattern, mid-dorsal, spiracular, supraspiracular and subventral body stripes dark brown, almost black; ground color between stripes brown.

Fifth instar (Fig. 4K,M): Head (Fig. 12C-5) 2.36mm wide, 2.13mm high; spiracular, mid-dorsal, and subventral stripes coffee-colored; subdorsal stripe pale brown; subdorsal spots disappear; sub- and

supraspiracular stripes vague and tan colored; all stripes straight; mid-dorsal stripe with anterior oval broadenings in body segments 4-11. All stripes in prepupa (Fig. 4M) paler than in larva.

Pupa (Fig. 4N-P and Fig. 13F): 11.8mm long, 4mm wide dorso-ventrally, 4mm across; ground color whitish-brown with black spot on foreleg and wing; ventral margin of wing black.

***Calisto sommeri* Schwartz & Gali:** (front cover, center).

Egg: Surface structure similar to that of *C. confusa* (Fig. 17K).

First instar larva (Fig. 3A,B): Head (Fig. 12B-1) amber-colored, 0.72mm wide, 0.58mm high, unusually rounded in shape, compared to heads of *Calisto* species described above; reticulation very shallow, almost absent (Fig. 14F); pair of small horns, each 0.7% of head height; body as in *C. grannus*, with pale brown striations (Fig. 11L); stripes wider than in *C. grannus dilemma*. After feeding coloration of striations remains pale brown, and subdorsal spots become noticeable.

Second instar (Fig. 3C-E): Head (Fig. 12B-2) 1.11mm wide, 0.87mm high; with pale brown X-pattern. Two persistent patterns in body coloration appear: "striated", similar to coloration of *C. grannus*, and "spotted", with broken spiracular stripe. These two patterns persist into later instars.

Third instar (Fig. 3F-I and Fig. 1A,B): Head 1.34mm wide, 1.15mm high; color pattern becomes more noticeable (Fig. 12B-3). Some larvae remain very similar to those of *C. grannus* (Fig. 3F-I). Others (Fig. 1A,B) show vertical white stripes, corresponding with secondary body segmentation, crossing darkened spiracular stripe and creating broken pattern.

Fourth instar (Fig. 1C,D and Fig. 3J,K): Head (Fig. 12B-4) 1.90mm wide, 1.77mm high; difference in color patterns becomes sharper; two elongated white spots on second and third thoracic segment below spiracular line.

Fifth instar (Fig. 1E-I and Fig. 3L-N): Head (Fig. 12B-5) 2.59mm wide, 2.28mm high, more rounded than in *C. grannus*; difference in two body color patterns increases: in "spotted" larvae, vertical white stripes invade subdorsal body stripe and become wider in spiracular stripe; remaining upper margin of spiracular stripe becomes darker than rest of stripe (Fig. 1E,G), forming line of black spots throughout body on top of spiracular stripe; thoracic spots below spiracular stripe become more noticeable in both patterns. "Striated" larvae (Fig. 3L) can be distinguished from fifth instar of *C. grannus dilemma* (Fig. 4K) only by shape and size of head and thoracic white spots. In prepupa (Fig. 3N), all stripes become darker.

Pupa (Fig. 3O-Q and Fig. 13C-E,G,H): 12.5mm long, 5-5.5mm wide dorso-ventrally, 5.25mm across; wings bluish (Fig. 13G,H) rather than brown as in *C. grannus* (Fig. 13F (side view)) right after pupation; later turn silver-brown with generally more extensive black spotting (Fig. 13C) than in *C. grannus*.

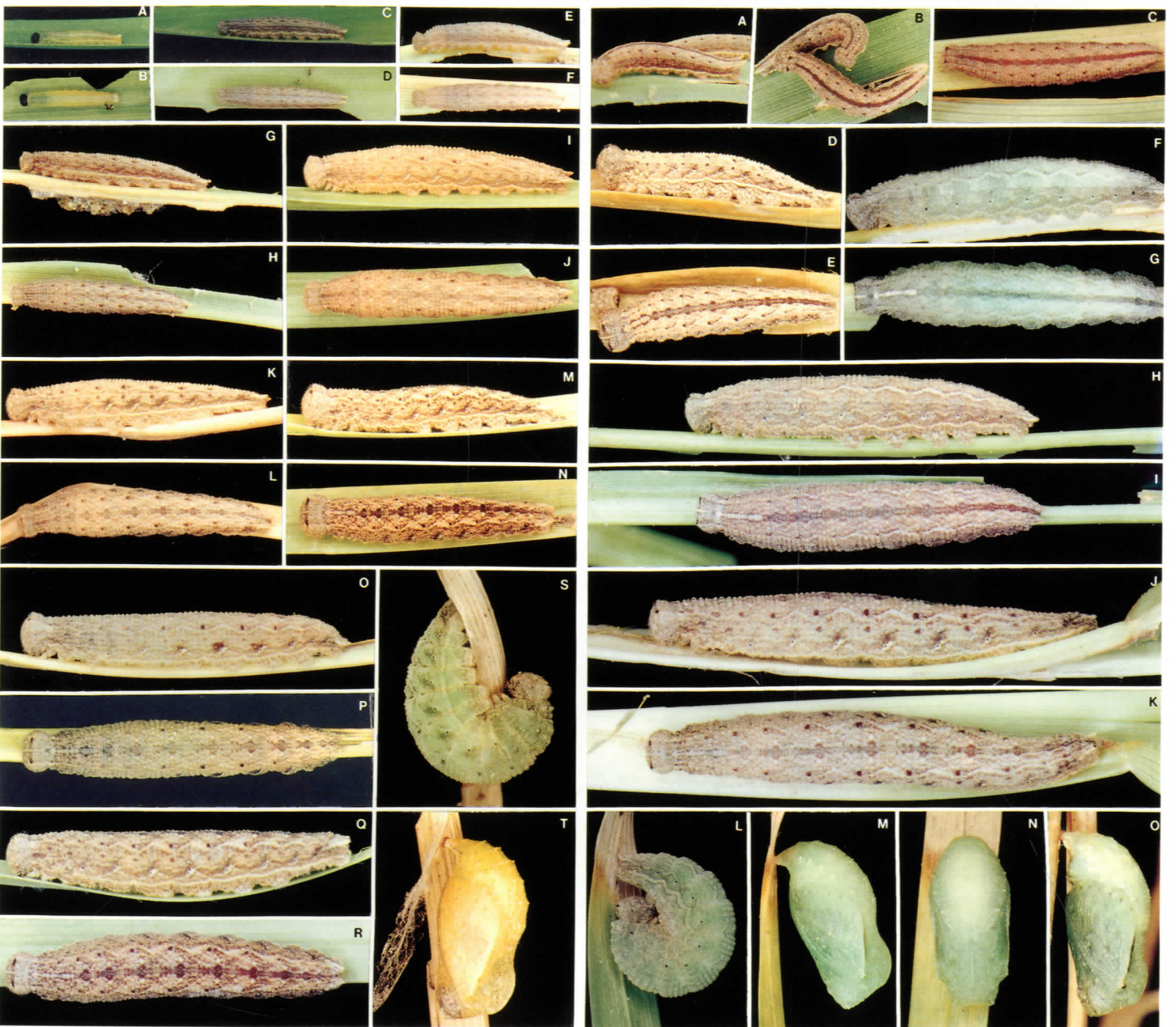
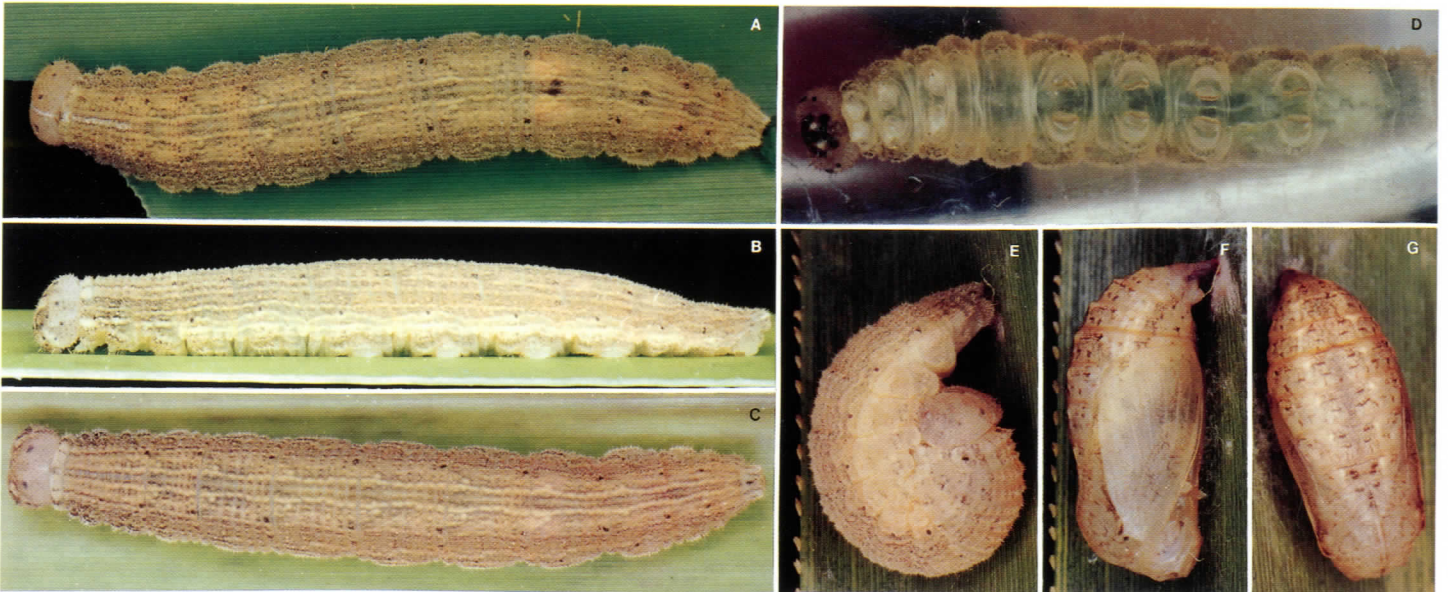
***Calisto pulchella* Lathy:** (front cover, lower middle).

Egg: 1.35mm in diameter; round (Fig. 17F), surface divided into unevenly sized, irregular hexagonal facets with rounded angles (Fig. 17R); six porous facets surround a poreless facet located in the middle; all facets much smaller than in other species, especially relative to egg size; white when laid and shows dark brown extensive pattern if fertile (Fig. 11F).

Fig. 8 (upper third). Immature stages of *C. pulchella* (continues from Fig. 2): (A)-(D) Fifth instar larva; (E) Prepupa; (F)-(G) Pupa.

Fig. 9 (lower left). Immature stages of *Calisto confusa debarriera*: (A)-(B) First instar; (C)-(F) Second instar; (G)-(H) Third instar; (I)-(L) Fourth instar; (M)-(R) Fifth instar; (S) Prepupa; (T) Pupa immediately before hatching.

Fig. 10 (lower right). Immature stages of *Calisto confusa confusa*: (A)-(C) Fourth instar; (D)-(E) Fifth instar immediately after molting; (H)-(K) Fifth instar; (F)-(G), (L) Prepupa; (M)-(O) Pupa.



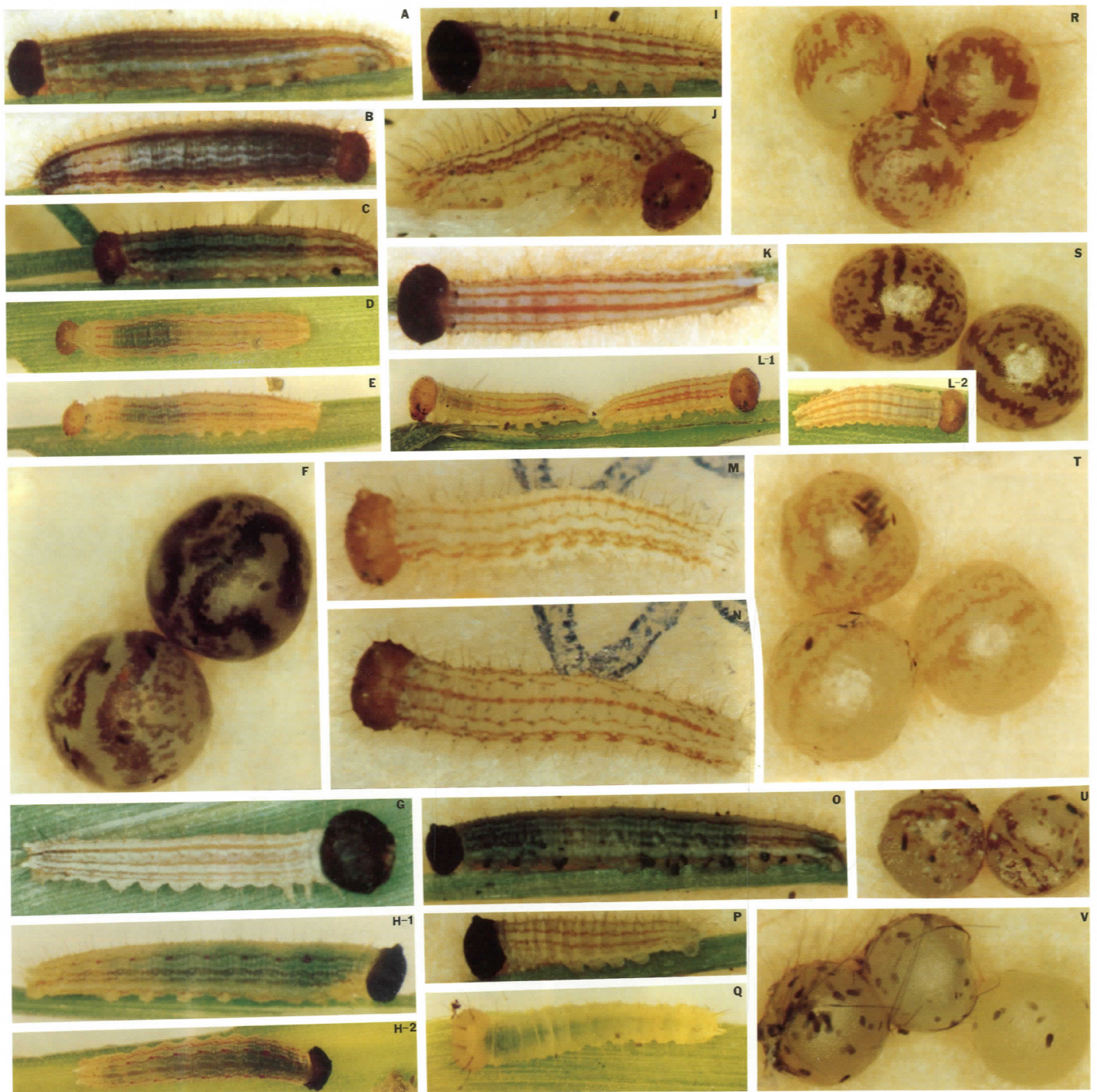


Fig. 11. First instar larva after feeding: (A) *C. grannus dilemma*; (B)-(C) *C. batesi*; (D)-(E) *C. hysius*; (H) *C. archebates*; (O) *C. confusa*; (Q) *C. galii*. First instar before feeding: (G) *C. pulchella*; (I) *C. grannus dilemma*; (J) *C. batesi*; (K) *C. schwartzi*; (L) *C. sommeri*; (M)-(N) *C. arcas*; (P) *C. confusa*. Eggs: (F) *C. pulchella*; (R) *C. grannus dilemma*; (S) *C. schwartzi*; (T) *C. arcas*; (U) *C. confusa*; (V) *C. galii*.

First instar larva (Fig. 2A,B): Head (Fig. 12I-1) 1.30mm wide, 1.10mm high, dark brown; prognathous; reticulation extensive, covers entire head except clypeus; horns absent, with unreticulated plate remaining in their place; an additional setum above first stemma (Fig. 14I); striations of newly hatched larva resemble other *Calisto* (Fig. 11G); after feeding, body pale green, with striations only slightly darker than rest of body (Fig. 2A,B).

Second instar (Fig. 2D,E): Head (Fig. 12I-2) 1.77mm wide, 1.43mm

high, white with a pale brown X-shaped brown pattern; no body stripes below spiracular line; spiracular stripe thin; supraspiracular stripe wider than spiracular stripe; anterior broadenings in segments 3-8 of mid-dorsal stripe small.

Third instar (Fig. 2F,G): Head (Fig. 12I-3) 2.22mm wide, 1.90mm high; body color similar to second instar; subdorsal spots more noticeable.

Fourth instar (Fig. 2H,I): Head (Fig. 12I-4) 3.06mm wide, 2.65mm high, with additional occipital black spots (Fig. 2I); subspiracular body

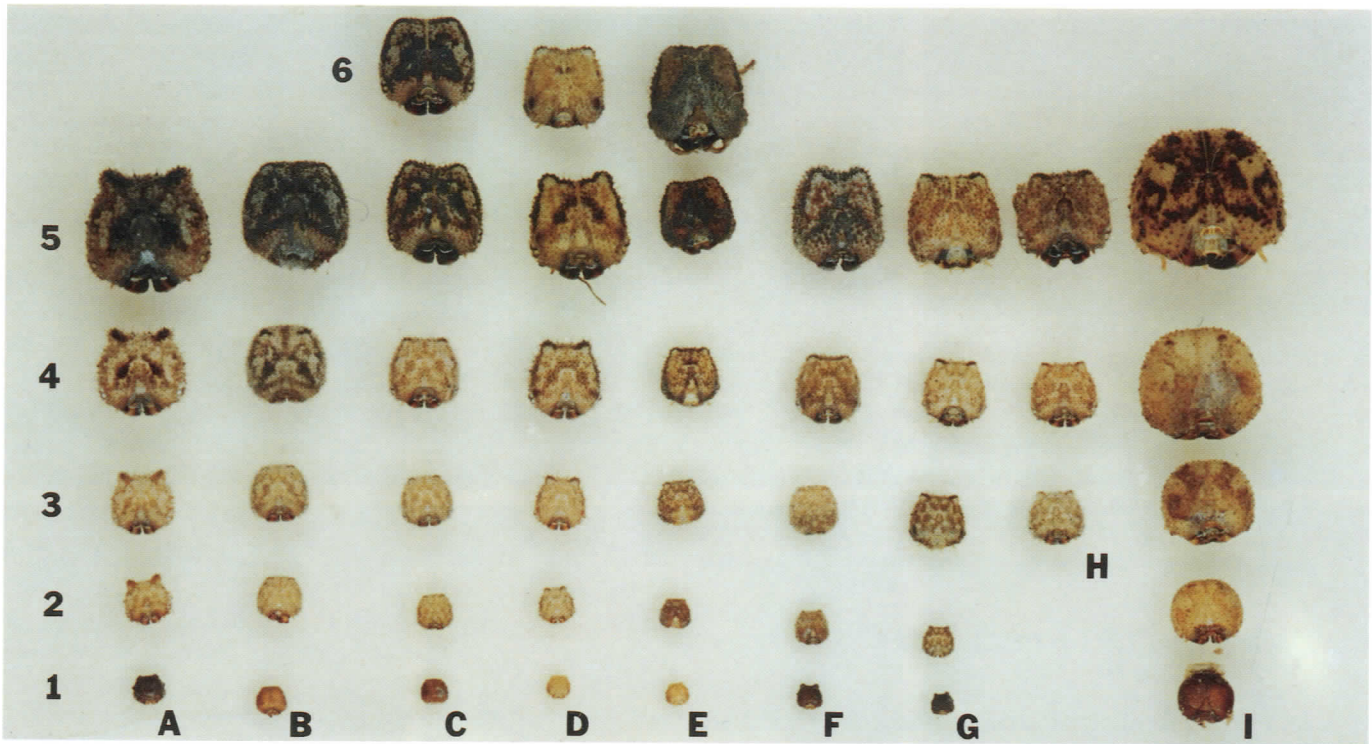


Fig. 12 (upper half). Larval head capsules: (1) First instar; (2) Second instar; (3) Third instar; (4) Fourth instar; (5) Fifth instar: (A) *Calisto archebates*; (B) *C. sommeri*; (C) *C. grannus dilemma*; (D) *C. hysius*; (E) *C. batesi*; (F) *C. obscura*; (G) *C. confusa confusa*; (H) *C. confusa debarriera*; (I) *C. pulchella*. (6C) Fifth instar of *C. grannus grannus*; (6D) Fifth instar of *C. obscura* from Sierra de Baoruco; (6E) Aberrant sixth instar of *C. batesi*.

Fig. 13 (lower half). Pupae: (A) *C. obscura*; (B) *C. confusa*; (C)-(E), (G), (E) *C. sommeri*; (F) *C. grannus dilemma*; (I)-(K) *C. hysius*; (L)-(O) *C. archebates*; (P)-(R) *C. pulchella*.

stripe darker than in third instar; subdorsal stripe wide, with only a thin white line between it and mid-dorsal stripe; subdorsal spots increase from being dots to well developed black spots; interstices between stripes narrow; mid-dorsal stripe wide and dark; rose-colored testes noticeable through integument of male larvae (Fig. 2I).

Fifth instar (Fig. 2C,J,K and Fig. 8A-E): Head (Fig. 12I-5) 3.72mm wide, 3.12mm high; X-shaped color pattern elaborated by ring-shaped spots on sides of "X" and black median stripe; four pairs of black spots on side of head (Fig. 8B); in some individuals, color pattern very pale, hardly noticeable; body color pattern remains same as in fourth instar, although pigmentation increases; dark spots appearing around spiracles, in supraspiracular stripe, and sometimes in mid-dorsal stripe; mid-dorsal stripe white, bordered by black lines. Overall, body becomes more pigmented, less transparent, so that testes in male larvae almost invisible; intensity of body pigmentation varies between individuals.

Pupa (Fig. 8F,G and Fig. 13P-R): 14mm long, 6mm wide dorso-ventrally, 6mm across, greenish-gray with a few small black spots on abdomen.

DISCUSSION OF CHARACTERS

EGGS

While the eggs do not show superficial diversity of shapes and patterns, there are useful characters that can be seen with the help of Scanning Electron Microscopy. Although eggs were not illustrated for all of the species described, representatives are figured for divergent species groups of *Calisto*, such as *C. grannus dilemma* (Fig. 11R), *C. schwartzi* (Fig. 11S), *C. arcas* (Fig. 11T), *C. pulchella* (Fig. 11F), *C. confusa* (Fig. 11U), and *C. galii* (Fig. 11V). Except for those of *C. galii*, which is probably the most divergent species of *Calisto*, all are superficially similar in appearance. Variables include egg size and color pattern. Intensity and shape of the color spots varies between individuals of the same species, and are therefore difficult to compare. Eggs of most of the species are not perfectly round. When the micropyle is observed and the egg is oriented vertically, differences in shape become noticeable. Thus, the eggs of *C. pulchella* (Fig. 17F), *C. schwartzi*, and *C. tasajera* are spherical; *C. batesi* is flattened on both poles (Fig. 17D); *C. grannus dilemma* is flattened in the micropylar area and is slightly tapered toward it (Fig. 17G); *C. arcas* (Fig. 17E), *C. hysius* (Fig. 17I), and *C. confusa* are round, slightly tapered toward the micropyle (Fig. 17H). The shape of the eggs corresponds with the way they are laid: in *C. pulchella* eggs are dropped in the leaf pocket, while in *C. tasajera* and, probably, in *C. schwartzi* they are dropped into the middle of the bunch grass. In other species, eggs are glued to the grass, therefore requiring a larger surface of contact with the substrate, which is provided by a wider and flatter base.

A study of the egg surface at high magnification reveals unique structures for each species. The basic structure is exemplified by *C. confusa* (Fig. 17P), where hexagonal facets are separated from the interstices by a furrow. The interstices carry pores, one for each side of a facet. Some furrows are connected. *C. sommeri* (Fig. 17K) has a structure similar to *C. confusa*. In *C. tasajera* the interstices are divided into a pattern similar to the original facets, so that the original facets can be identified only by the absence of pores (Fig. 17Q). In all of the above species, the interstices are level with the facets. In *C. archebates* (Fig. 17N) and *C. hysius* (Fig. 17M), facets are sunken and the interstices are elevated. Similarly, in *C. arcas* (Fig. 17J) and *C. grannus*

dilemma (Fig. 17O), the facets are sunken, but they are also interconnected by a narrow furrow. This configuration is exaggerated in *C. batesi*, with the surface being covered by alternating ridges and furrows (Fig. 17L). In *C. pulchella* (Fig. 17R), interstices are divided into facets only slightly smaller than the original (poreless) facets and distinct from the latter by the presence of large pores. All facets of *C. pulchella* tend to lose their hexagonal shape, instead appearing as irregular circles. They are much smaller relative to egg size than in the other species studied.

Micropylar structures are similar in all species studied (Fig. 17A-C and Fig. 22F,I,J).

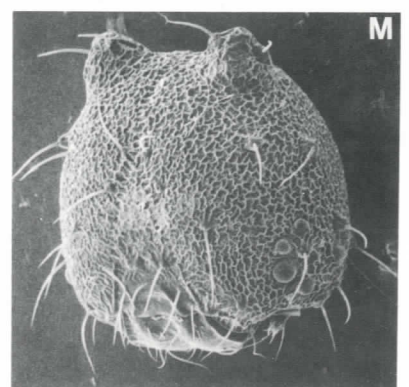
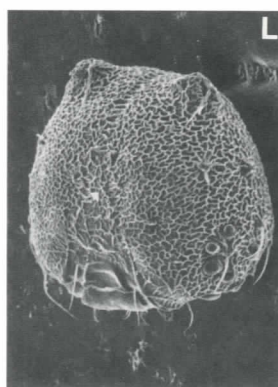
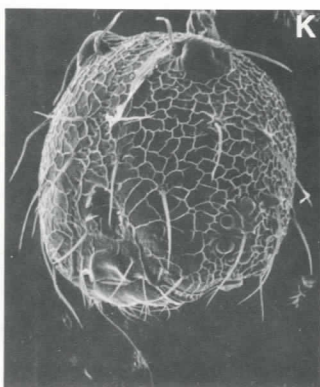
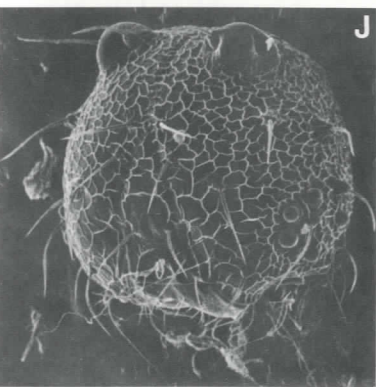
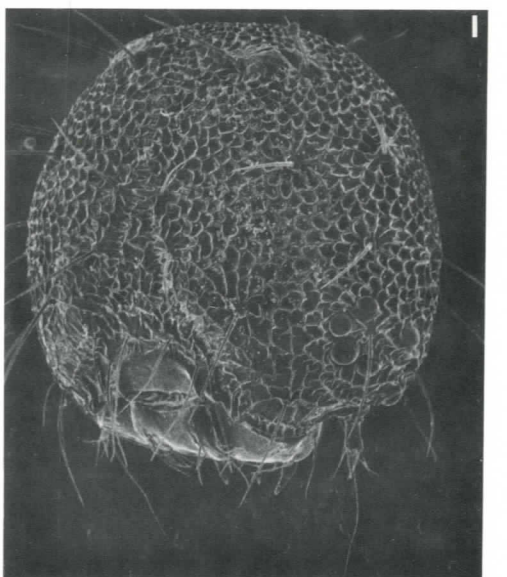
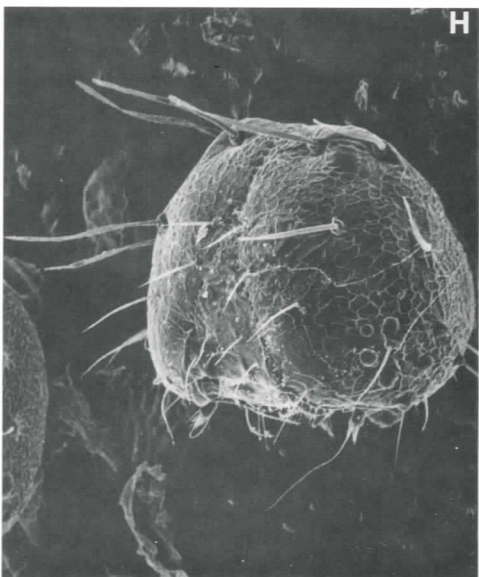
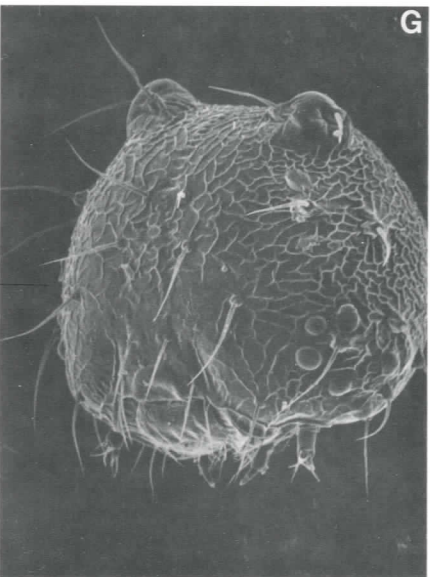
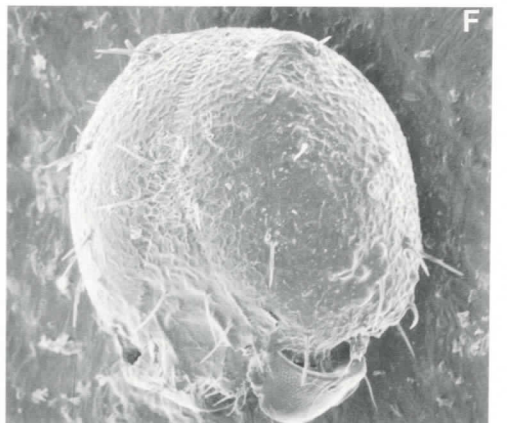
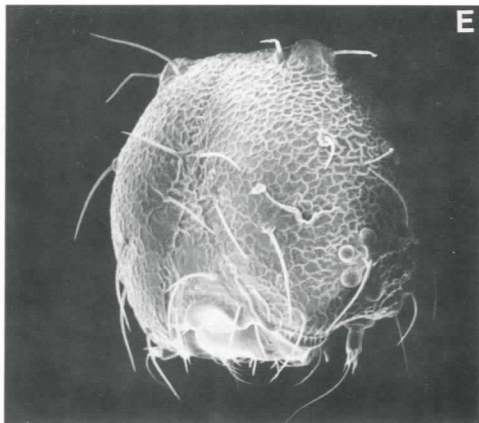
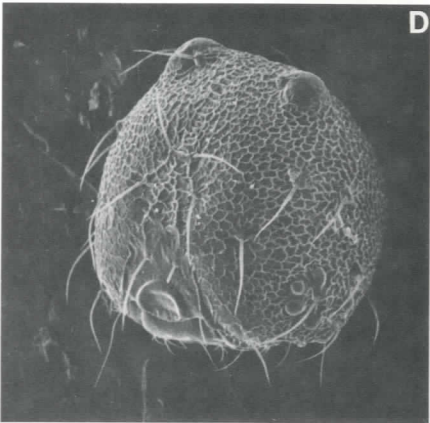
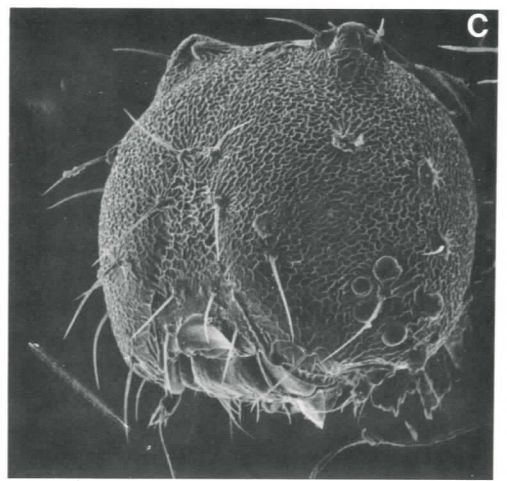
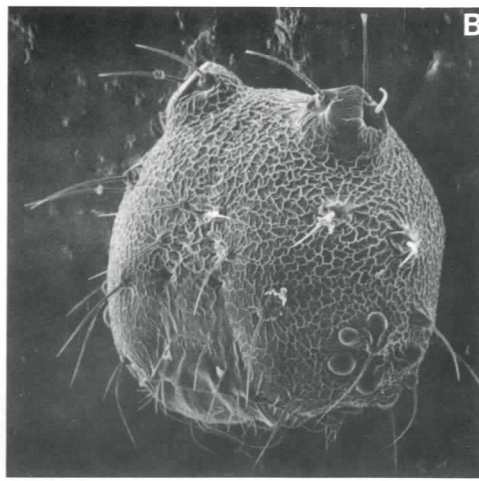
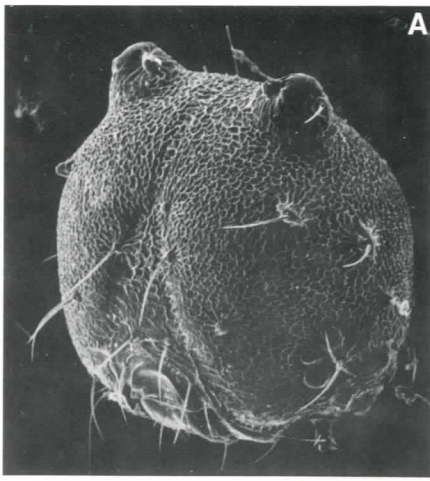
LARVAE

First instar: As with eggs, superficial observation of first instar larvae shows a few differences. Exceptions include the larvae of *C. pulchella*, which have a disproportionately large head without typical horns (Fig. 11G and Fig. 14I), and larvae of *C. galii* which have long head setae (more than twice the normal) and no body striations (Fig. 11Q and Fig. 14H). Otherwise, differences are restricted to the color of the body striations, color and surface structure of the head, and the size of the head horns. Micrographs of head capsules (Fig. 14) show differences in shape, and reticulation. Thus, *C. tasajera* (Fig. 14A), *C. schwartzi* (Fig. 14C), *C. grannus* (Fig. 14E), *C. sommeri* (Fig. 14F), *C. confusa* (Fig. 14L), *C. obscura* (Fig. 14M), and *C. pulchella* (Fig. 14I) have dense reticulation, while *C. batesi* (Fig. 14K), *C. hysius* (Fig. 14J), *C. arcas* (Fig. 14G), and *C. galii* (Fig. 14H) have a web-shaped, loose reticulation. *C. archebates* (Fig. 14B) falls between these two types. The morphology of *C. sommeri* is puzzling: being superficially very similar to the *C. grannus* group, this species differs from the latter, by almost completely lacking head horns and any raised reticulation, and by the overall rounded shape of the head. *C. pulchella*, besides lacking head horns, has an extremely large head, when compared to similarly sized species such as *C. archebates* or *C. arcas*.

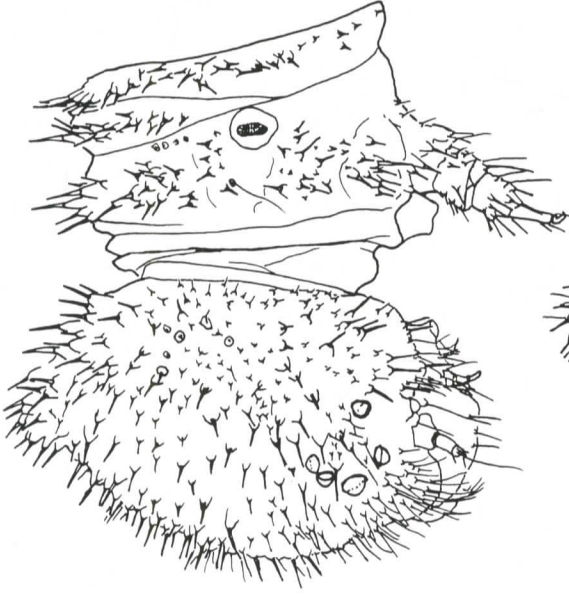
C. galii is a deep forest butterfly associated with bamboo, *Chusquea abietifolia* Griseb. (Bambusoideae). The differences in its first instar larva support its early diversification from other *Calisto*. Utilizing bamboo as a food plant is common in satyrids of the Neotropical mainland, and may be a primitive character.

Last instar: Heads and first thoracic segments of the eight species described are illustrated in Fig. 15. The general appearance of all but *C. pulchella* is similar, even though differences in head shape, as well as size, thickness and length of covering setae do occur. The number of setae also varies. Thus, *C. confusa* (Fig. 15H) and *C. pulchella* (Fig. 15A) have fewer setae than the other six species, and the setae are thinner. *C. sommeri* (Fig. 15C) has short, thick setae and a rounded head shape. *C. confusa*, *C. obscura*, (Fig. 15G), *C. hysius* (Fig. 15F), and *C. batesi* (Fig. 15B) have a bump anterior to the stemmatal area. The number of secondary setae on the body varies as well. *C. pulchella* (Fig. 15A) has a head significantly larger than in the remaining species, and it is prognathous rather than hypognathous. The head bears

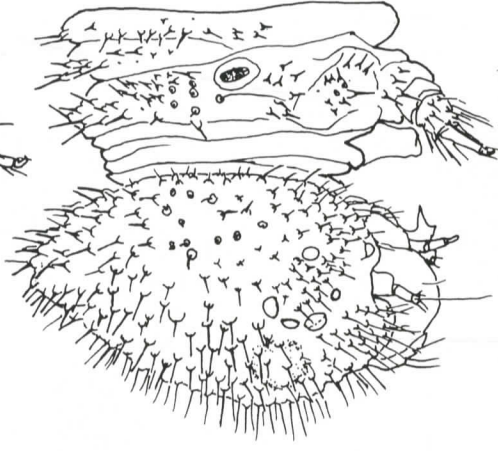
Fig. 14. Head of the first instar larva: (A) *Calisto tasajera*; (B) *C. archebates*; (C) *C. schwartzi*; (D) *C. grannus dilemma*; (E) *C. grannus grannus*; (F) *C. sommeri*; (G) *C. arcas*; (H) *C. galii*; (I) *C. pulchella*; (J) *C. hysius*; (K) *C. batesi*; (L) *C. confusa*; (M) *C. obscura*; (I)-X 75; The rest-X100.



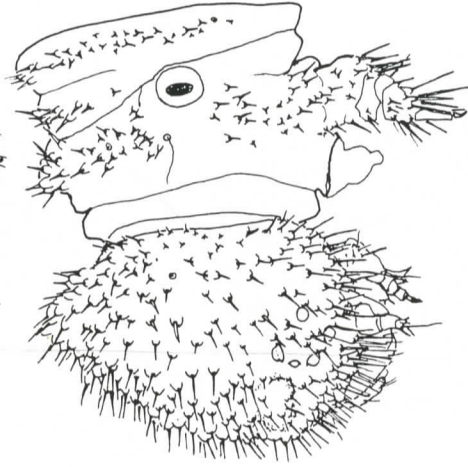
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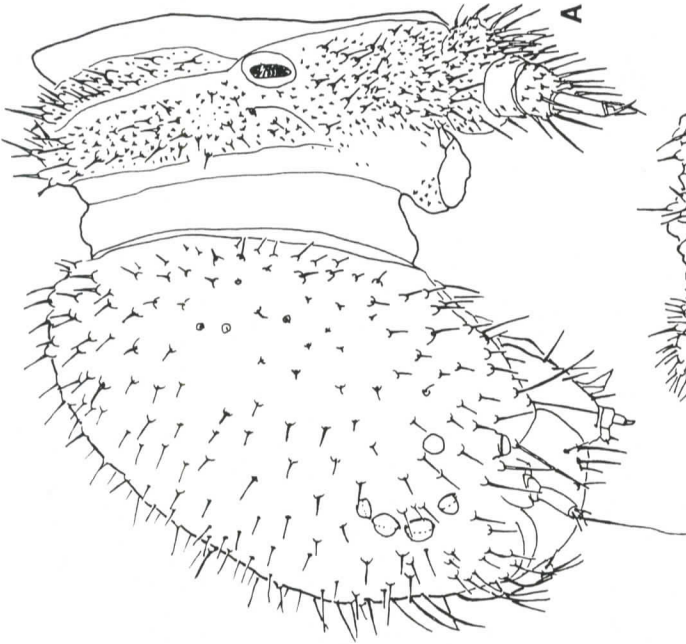
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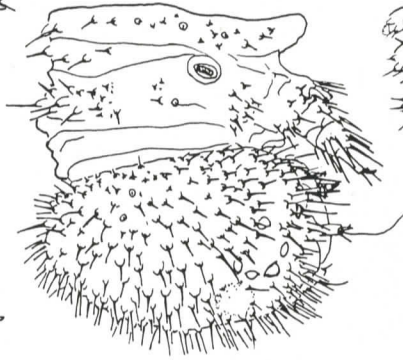
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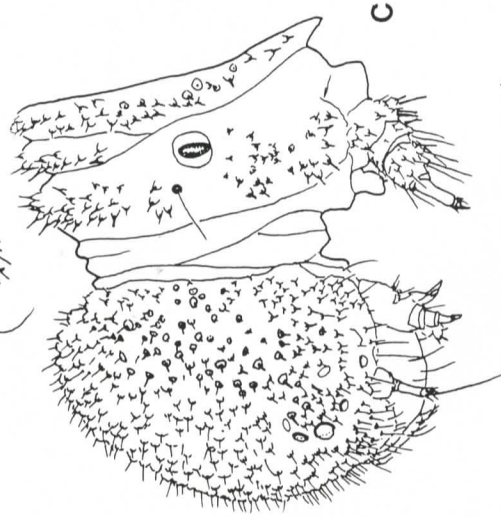
A



B



C



D

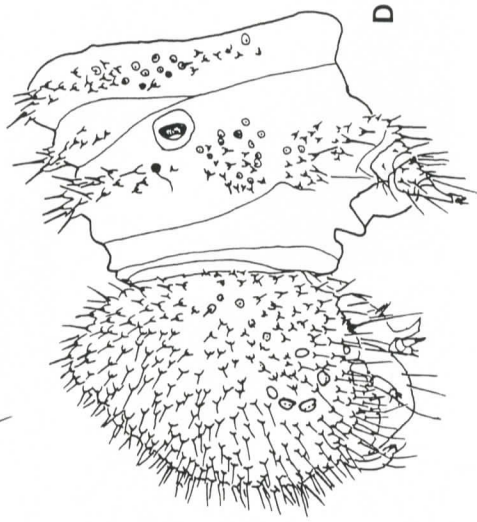


TABLE 2. Head size in *Calisto* larvae.

Taxon/Instar	Fifth	Fourth	Third	Second	First
	width/height	width/height	width/height	width/height	width/height
<i>C. archebates</i>	3.00/2.79	2.14/2.14	1.49/1.39	1.14/0.98	0.74/0.65
<i>C. sommeri</i>	2.59/2.28	1.90/1.77	1.34/1.15	1.11/0.87	0.72/0.58
<i>C. grannus dilemma</i>	2.36/2.13	1.77/1.61	1.24/1.14	0.87/0.84	0.61/0.53
<i>C. hysius</i>	2.51/2.34	1.84/1.82	1.28/1.24	0.71/0.80	0.59/0.53
<i>C. batesi</i>	2.00/1.62	1.47/1.32	1.17/1.02	0.80/0.69	0.58/0.46
<i>C. obscura</i>	1.53/1.49	0.98/0.98	0.80/0.80	0.90/0.74	0.67/0.50
<i>C. confusa confusa</i>	2.21/2.13	1.58/1.42	1.40/1.24	0.80/0.64	0.60/0.46
<i>C. confusa debarriera</i>	2.21/1.95	1.80/1.42	1.29/1.19		
<i>C. pulchella</i>	3.72/3.12	3.06/2.65	2.22/1.90	1.77/1.43	1.30/1.10

a few relatively thin, lightly colored setae, some of which lack pinacula. Besides the secondary setae found in other species, the entire body of *C. pulchella* is covered with additional minute spines.

Head capsule coloration persists from the second to the last instar, becoming darker in mature larvae. All species are characterized by an X-shaped black marking. It is most strongly expressed in the last instar of *C. archebates* (Fig. 12A-5). Two wide black lower arms of the "X" come up from the stemmatal area along the frontoclypeal suture, and join above the frontoclypeus. From this point, two thinner arms radiate into the black tips of the head horns and continue on the occiput of the head, going backwards and integrating into the subdorsal body stripes (Fig. 5M). In *C. hysius* (Fig. 12D-5), a similar pattern is elaborated by two additional black stripes coming down from the tips of the horns along the sides of the head and disappearing in the stemmatal area (Fig. 7G,I). The lower arms of the "X" are elevated, so that there is an unpigmented space between them and the frontoclypeal suture. In *C. obscura* the tips of horns are connected by a strong black stripe (Fig. 6K), and its frontoclypeal suture is colored black (Fig. 12F-5). In *C. confusa* (Fig. 12G-5) the whole pattern is similar to that of *C. obscura*, but is very vague. In *C. batesi*, on the contrary, the pattern is intensified, so that the middle of the head seems to bear a large black triangle (Fig. 12E-5). In *C. sommeri* (Fig. 12B-5) and *C. grannus dilemma* (Fig. 12C-5), the pattern described above is slightly modified: the thick lower arms of the "X" are parallel to the darkly colored frontoclypeal suture. The upper arms turn to the outside and backwards, reaching only halfway to the tips of the head horns, and connect to the middle of the lower arms. The lateral stripe is present and reaches the stemmatal area where it connects to the lower arms of the "X". In *C. pulchella* (Fig. 12I-5), the "X" pattern is present as well. However, the lower arms begin higher than in the other species. They become wider on reaching their crossing point, and even wider upper arms rise to the highest points of the head (no horns are present). A stripe extends halfway down each side to the middle of the frontoclypeal suture, where stripes go towards the stemmatal areas. In addition, there are two circular spots above and medially of the stemmatal areas.

The body color patterns of the last instar larvae are elaborate and quite difficult to describe. A schematic drawing of the second thoracic segment coloration for each species was therefore produced (Fig. 19). All of the stripes are present in all of the species; however, their thickness, intensity, color, and configura-

tion create different patterns. Thus, in *C. grannus* (Fig. 19D), the spiracular stripe is wide, dark and straight; in *C. sommeri* (Fig. 19H), it is convex in both lower and upper margins, so that the whole stripe appears broken. In *C. confusa* (Fig. 19C), this stripe is wide and lightly colored, dominating the body coloration. It also is convex in its upper margin and forms a zigzagged line. However, in *C. obscura* (Fig. 19B) the upper margin of the spiracular stripe is concave in each segment, so that, together with the convex subdorsal stripe, it forms a chain of pale rhomboids. In *C. hysius* (Fig. 19A), the spiracular stripe is similar to that of *C. confusa*, but the upper part of the stripe is paler than the rest, so that there is also a chain of lightly colored rhomboids between the spiracular and subdorsal stripes, but less conspicuous than in *C. obscura*. In *C. archebates* (Fig. 19G), the spiracular stripe is divided in two by a thin white zigzagged stripe at the level of the spiracular line. In *C. batesi* (Fig. 19F), this stripe is dark, giving the body an overall dark coloration. It narrows towards the posterior end of each segment. This creates a characteristic pale uneven subspiracular stripe. In *C. pulchella* (Fig. 19E), this stripe is narrow, pale, and straight.

Micrographs of the mandiblar cutting surface for each species were made (Fig. 16). Comparison of mandibles is useful in newly molted larvae before feeding (Fig. 16A,E). After just a few days of feeding, the teeth show wear (Fig. 16C,F,M). By the time of pupation, the chewing surface is significantly reduced (Fig. 16G,K) or completely smooth (Fig. 16B,G,I,L,N). The degree of mandibular wear by the end of the instar differs in different species. Thus, in *C. pulchella* (Fig. 16I), *C. hysius* (Fig. 16L), *C. archebates* (Fig. 16G), and *C. sommeri* (Fig. 16J) the toothed cutting edge completely disappears. In *C. obscura* (Fig. 16B), *C. confusa* (Fig. 16D), and *C. grannus* (Fig. 16K) a trace of the teeth is left. This probably reflects the original structure of the mandible: in the latter species, the cutting sides of the teeth extend into grooves (on both the inside and outside surfaces) (Fig. 16C,K,O) that create uneven wear of the cutting edge, preserving the toothed shape of the cutting edge even in the badly worn mandibles. The mandible of *C. pulchella* (Fig. 16P) seems to be broader than *C. confusa* (Fig. 16O) at the beginning of the fifth instar. By the end of the instar (Fig. 16I), its chewing surface is completely flat and it is relatively narrower than in other species (Fig. 21). This can perhaps be attributed to tougher food plant leaves.

These observations lead to the supposition that larval molting possibly is stimulated not only by excessive stretching of the integument, but also by the necessity to "replace" the mandibles. That would explain the occasional molting to the artifact sixth instar observed in *C. batesi*, *C. pulchella*, and *C. sommeri*, which happened when the quality of the food was low, and therefore more food was needed for the larva to reach pupation size. Interestingly, there are consistently six instars in the dioptine moth genus *Tithraustes* (Dioptidae), that feed on palms, which have even higher content of silicon than grass and, therefore, are tougher. Other species of the subfamily have only four instars. Additional instars may be an adaptation to tough host plant leaves, which require the frequent renewal of the mandibles (Cal Snyder, pers. com.).

Fig. 15. The head and the first thoracic segment in fifth instar larva: (A) *C. pulchella*; (B) *C. batesi*; (C) *C. sommeri*; (D) *C. grannus dilemma*; (E) *C. archebates*; (F) *C. hysius*; (G) *C. obscura*; (H) *C. confusa*.

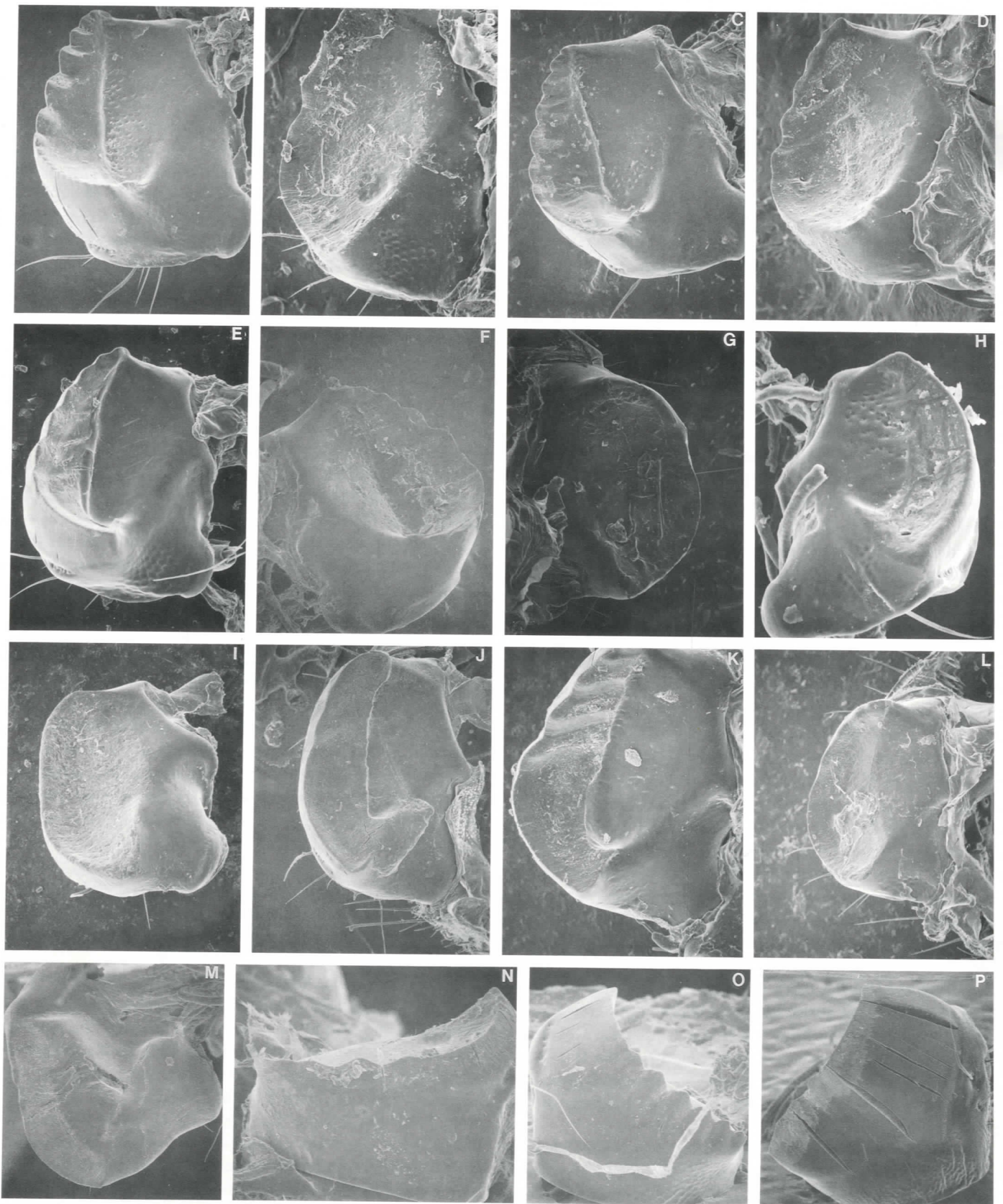


Fig. 16. Chewing surface of the mandible: (A) *C. obscura*, beginning of instar 5 (X150); (B) *C. obscura*, end of instar 5 (X200); (C) *C. confusa*, beginning of instar 5 (X150); (D) *C. confusa*, end of instar 5 (X150); (E) *C. batesi*, beginning of instar 5 (X150); (F) *C. archebates*, beginning of instar 5 (X100); (G) *C. archebates*, end of instar 5 (X100); (H) *C. galii*, beginning of instar 1 (X500); (I) *C. pulchella*, end of instar 4 (X100); (J) *Calisto sommeri*, end of instar 5 (X100); (K) *C. grannus dilemma*, end of instar 5 (X150); (L) *C. hysius*, end of instar 5 (X100); (M) *C. pulchella*, beginning of instar 5 (X75); External surface of the mandible: (N) *C. obscura*, end of instar 5 (X150); (O) *C. confusa*, beginning of the instar 5 (X100); (P) *C. pulchella*, beginning of instar 5 (X75).

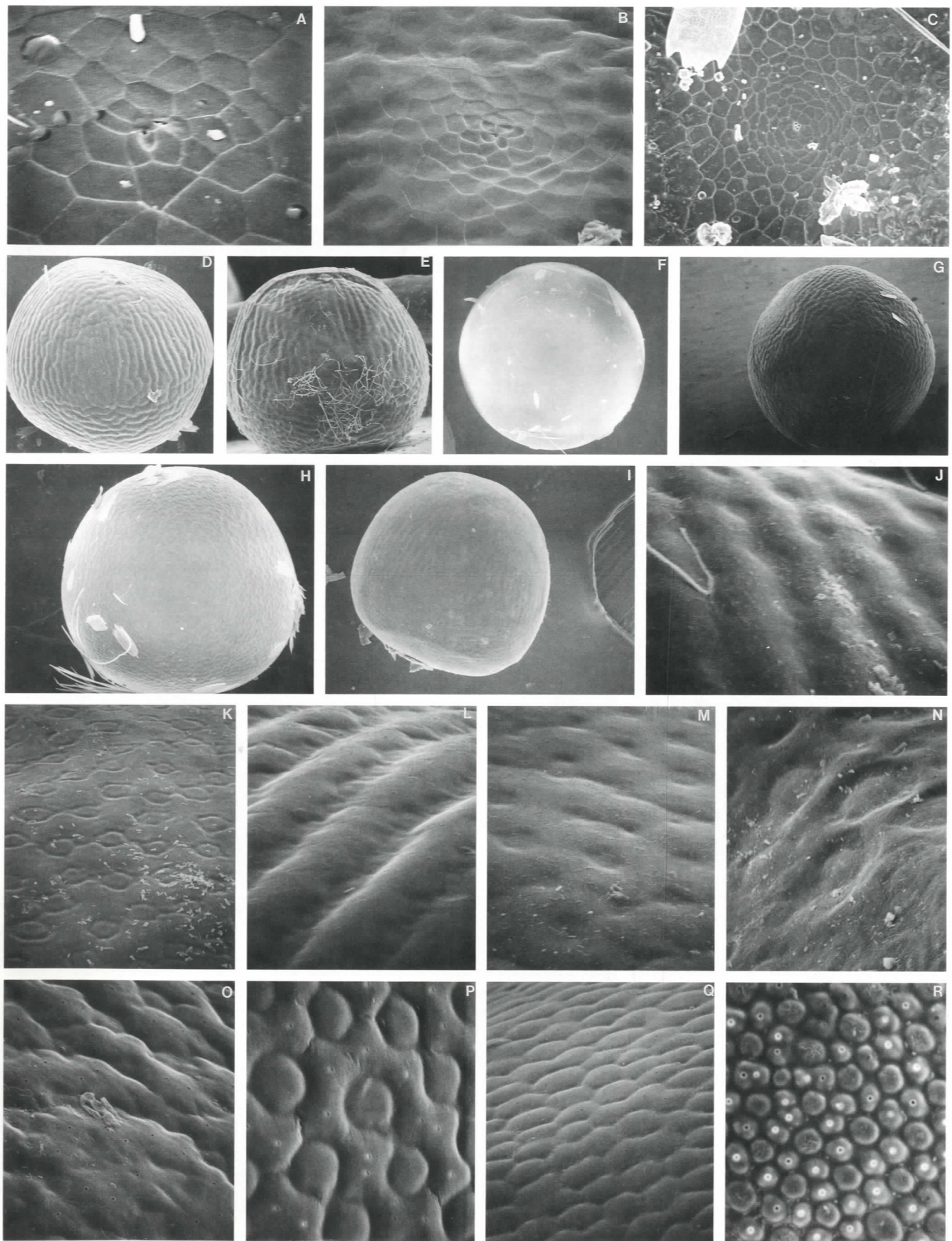


Fig. 17. Egg micropyle of: (A) *C. confusa* (X1500); (B) *C. batesi* (X750); (C) *C. pulchella* (X380); Side view of the egg of: (D) *C. batesi* (X100); (E) *C. arcas* (X100); (F) *C. pulchella*; (G) *C. grannus dilemma*; (H) *C. confusa*; (I) *C. hysius*; Egg surface of (J) *C. arcas* (X1000); (K) *C. sommeri* (X1000); (L) *C. batesi* (X1000); (M) *C. hysius* (X1000); (N) *C. archebates* (X1000); (O) *C. grannus dilemma* (X1000); (P) *C. confusa* (X1000); (Q) *C. tasajera* (X1000); (R) *C. pulchella* (X1000).

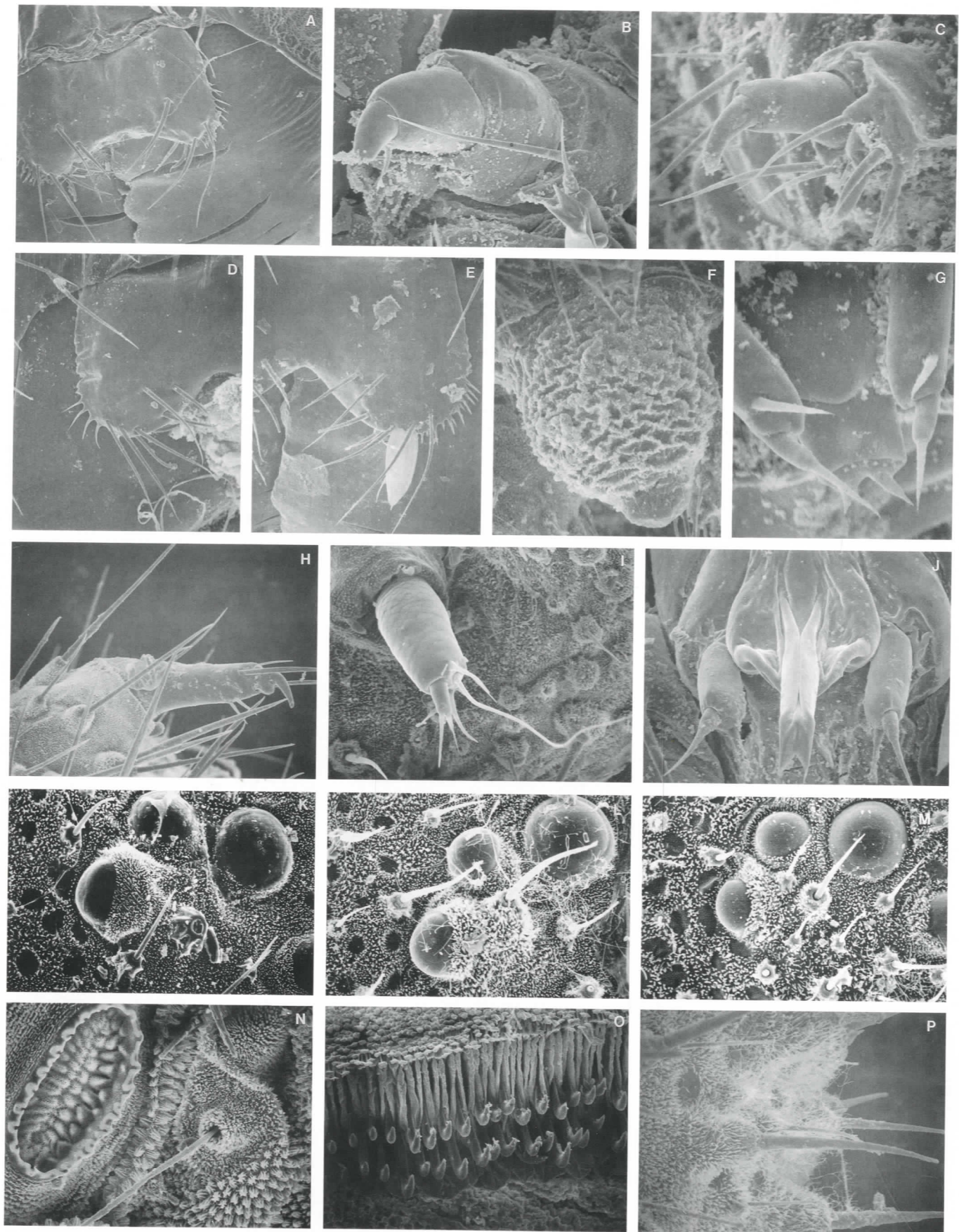


Fig. 18. (A) Labrum of *C. pulchella* (X100); (B) Maxilla of *C. pulchella* (X380); (C) Maxilla of *C. grannus* (X500); (D) Labrum of *C. grannus* (X500); (E) Labrum of *C. archebates* (X200); (F) Prothoracic gland of *C. grannus* (X300); (G) Spinnerett of *C. grannus* (X1000); (H) Prothoracic leg of the fifth instar larva of *C. archebates* (X250); (I) Antenna of the fifth instar larva of *C. hysius* (X300); (J) Spinnerett of *C. pulchella* (X500); (K) Stemmata of *C. pulchella* (X380); (L) Stemmata of *C. archebates* (X500); (M) Stemmata of *C. sommeri* (X500); (N) Spiracle and body surface of the fifth instar larva of *C. archebates* (X380); (O) Crochets of the proleg of *C. pulchella* (X380); (P) Head horns area in the fifth instar larva of *C. archebates*.

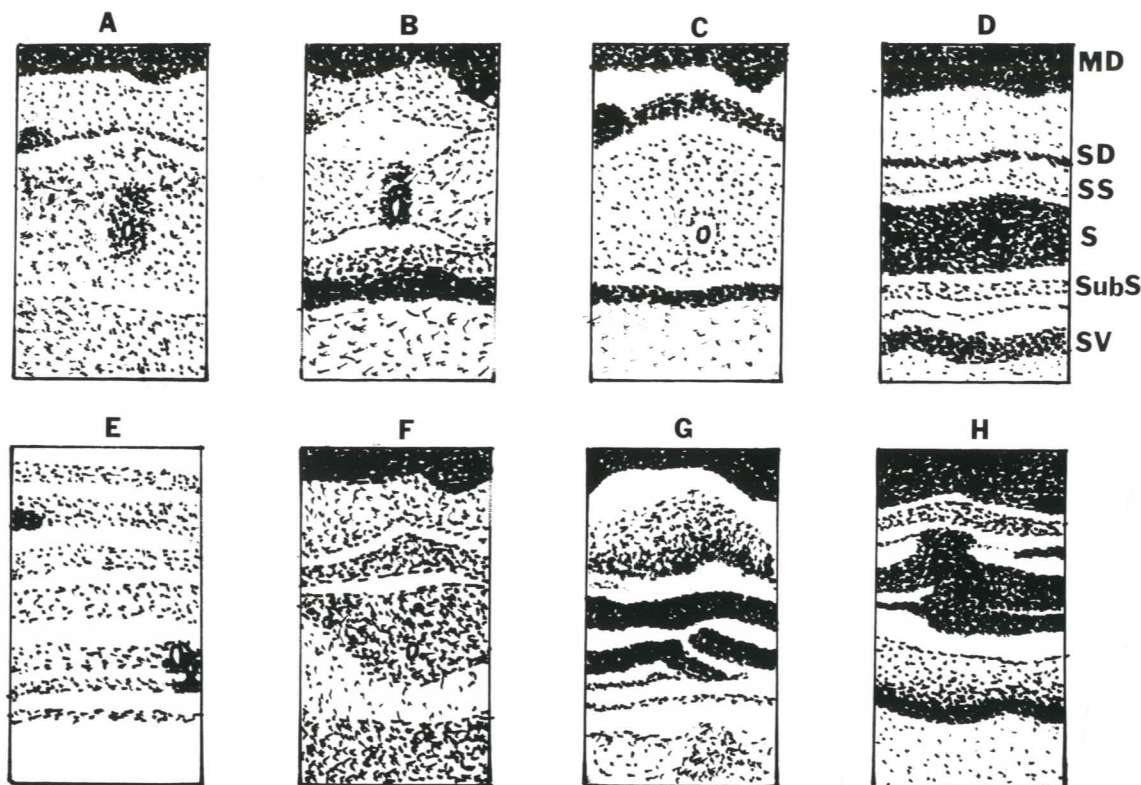


Fig. 19. Scheme of the pigmentation of the second abdominal segment of the fifth instar larva: (A) *C. hysius*; (B) *C. obscura*; (C) *C. confusa*; (D) *C. grannus dilemma*; (E) *C. pulchella*; (F) *C. batesi*; (G) *C. archebates*; (H) *C. sommeri*; MD - mid-dorsal stripe; SD - subdorsal stripe; SS - supraspiracular stripe; SubS - subspiracular stripe; SV - subventral stripe.

At present there are no intact mandibles available for most of the species, which makes thorough comparison impossible. However, those species for which adequate material is available, such as *C. batesi* (Fig. 16E), *C. obscura* (Fig. 16A), and *C. confusa* (Fig. 16C), show certain differences in teeth number and structure as well as in porousness of the chewing surface.

A close study of the labrum shows differences in the position and number of setae as well as number and length of spines on the latero-ventral margin. There are six setae and eight spines in *C. pulchella* (Fig. 18A), eight setae and five spines in *C. grannus* (Fig. 18D), and nine setae and twelve spines in *C. archebates* (Fig. 18E). The shape of the labrum itself varies as well. For example, in *C. pulchella* the notch is shallow, in *C. grannus* it is U-shaped, and in *C. archebates* it is V-shaped.

The maxilla of *C. pulchella* (Fig. 18B) differs from other species (e.g., Fig. 18C and 22H). The palpus of *C. pulchella* has shorter and wider segments. The mesal lobe is positioned dorsally from the palpus and reduced. The number and position of the sensillae on the annular sclerites is different as well. Differences in lacinogaleal sensillae can be correlated with larval ecology: larvae of *C. pulchella* are nearly endophagous, spending most of their life in the tight pocket between the leaf and the stem of the cane. Sensillae in this case may carry mostly properties of mechanoreceptors. In other *Calisto*, which during their larval development undoubtedly eat several host plants and need to find new ones, sensillae may serve an olfactory function as well (Scoble 1994).

The spinneret in *C. pulchella* (Fig. 18J) is narrower and longer

than in other *Calisto*, such as *C. grannus* (Fig. 18G). The prementum of *C. pulchella* is wider and longer.

The surface of the head is reticulate in all species (Fig. 18K-M). However, in some species, such as *C. sommeri* (Fig. 18M), there are more setae and they are shorter than in others, such as *C. archebates* (Fig. 18L). In *C. pulchella*, there are relatively few setae and, unlike other species, their pinacula are smooth rather than reticulate.

The legs (Fig. 18H), antennae (Fig. 18I), head (Fig. 18P), and body surface (Fig. 18N) showed no significant differences. The crochets of the prolegs are in a biordinal mesoseries. In the crochets of *C. pulchella* (Fig. 18O), the difference between short and long crochets is greater than in other species.

The shape of the body proved to be similar in all of the species; therefore, only *C. obscura* (Fig. 20) is illustrated.

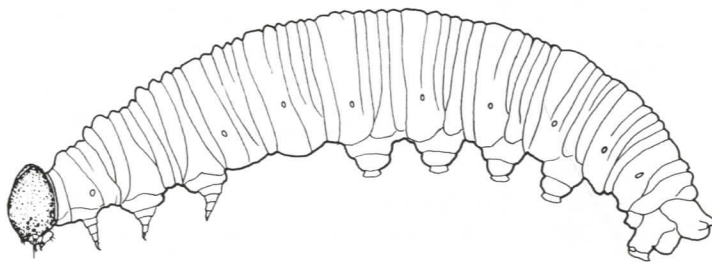


Fig. 20. True and false segmentation in the fifth instar larva of *C. obscura*.

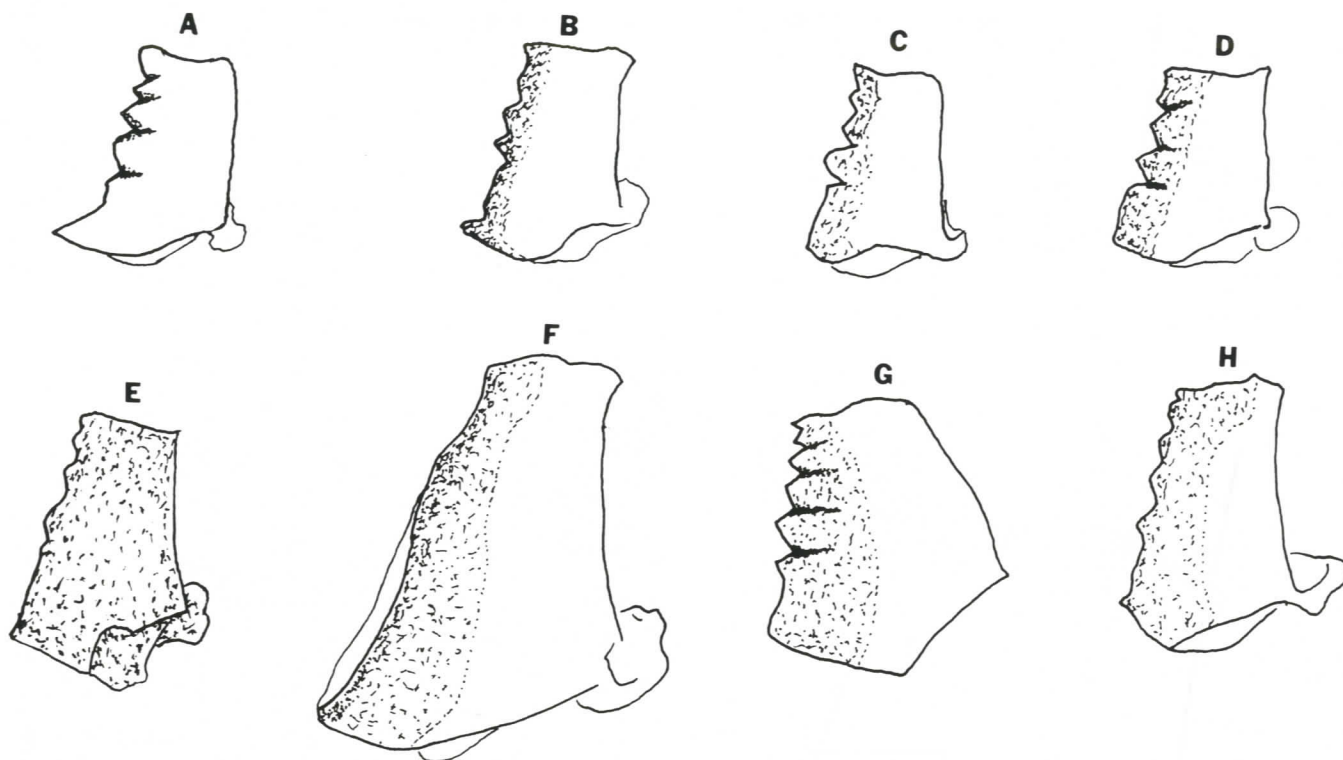


Fig. 21. Front view of the left mandible of the fourth instar larva: (A) *Calisto hysius*; (B) *C. obscura*; (C) *C. batesi*; (D) *C. confusa*; (E) *C. grannus dilemma*; (F) *C. pulchella*; (G) *C. sommeri*; (H) *C. archebates*.

PUPAE

Several ecological strategies are found to be employed by pupae. Coloration is one of these strategies. It has been shown (e.g., West and Hazel, 1982, 1985) that visually-hunting predators, such as birds, are capable of developing a search pattern for pupae. Probably as a consequence, pupae often employ cryptic coloration. Thus, the pupae of *C. confusa* are entirely green (Fig. 10M-O and Fig. 13B) and so firmly attached to the grass stems that it is difficult to pull them off without damaging them. Pupae of *C. obscura* (Fig. 6N,O and Fig. 13A), *C. grannus* (Fig. 4N-P and Fig. 13F), and *C. sommeri* (Fig. 3O-Q and Fig. 13C-E) are pale brown with black markings of varying intensity. They would be extremely inconspicuous on a background of dry grass and leaves. Indeed, after pupation, pupae either immediately fall off onto the ground, or do so when the slightest vibration is applied, and become lost to view. *C. hysius* (Fig. 7L-N and Fig. 13I-K) employs both strategies at once: its pupae vary in color from green to gray, with different amounts of dark markings (Fig. 13I). They are also attached to the grass with different strengths. Similarly, *C. archebates* varies from green to almost black (Fig. 5T-W and Fig. 13L-O). Its pupae are attached to the substrate with different degrees of firmness, but most of them would fall off with a strong vibration. These are practically invisible when they pupate between the grass roots and dry stems. *C. pulchella* is greenish and attaches firmly to a cane surface, on which it is fairly unnoticeable (Fig. 13P-R).

The different "behavior" of the pupae described above is attributable to the differences in their cremasters. In some species, such as *C. confusa* (Fig. 22D), *C. archebates* (Fig. 22C), and *C.*

pulchella, more hook-shaped cremaster setae are present. In others, such as *C. dilemma* (Fig. 22E) or *C. obscura* (Fig. 22A), only a few hooks are present. These provide a weak attachment and also break off easier, releasing pupa at the slightest vibration. In *C. hysius* (Fig. 22G) and *C. sommeri* (Fig. 22B), some or all of the cremaster setae are spinose, so that they do not hold the pupa firmly attached to the silk, allowing it to fall off after pupation.

Structurally (Fig. 23) pupae are rather similar. However, a few minor differences can be pointed out. In *C. sommeri* (Fig. 23F), *C. obscura* (Fig. 23E), and *C. grannus* (Fig. 23C), the last abdominal segment is long and pointed. In *C. pulchella* (Fig. 23G) and *C. confusa* (Fig. 23D), it is relatively short and coming to a wide cremaster area. In *C. hysius* (Fig. 23A) and *C. archebates* (Fig. 23B), the shape of the last abdominal segment is intermediate of the described above. In *C. pulchella*, *C. confusa*, and to some degree in *C. archebates*, the next to last abdominal segment is narrower ventrally than dorsally: that creates a sharper angle between the cremaster and the abdomen. The thickened posterior margins of the abdominal segments create a wave-shaped dorsal surface in *C. pulchella*, *C. archebates*, and *C. confusa*. Segmentation of antennae is expressed stronger in *C. archebates* and *C. hysius* than in other species.

The time of development from egg to adult is different in all of the species and is shown in Table 3. The information on the size of eggs, last instar larvae, and pupae is also summarized there.

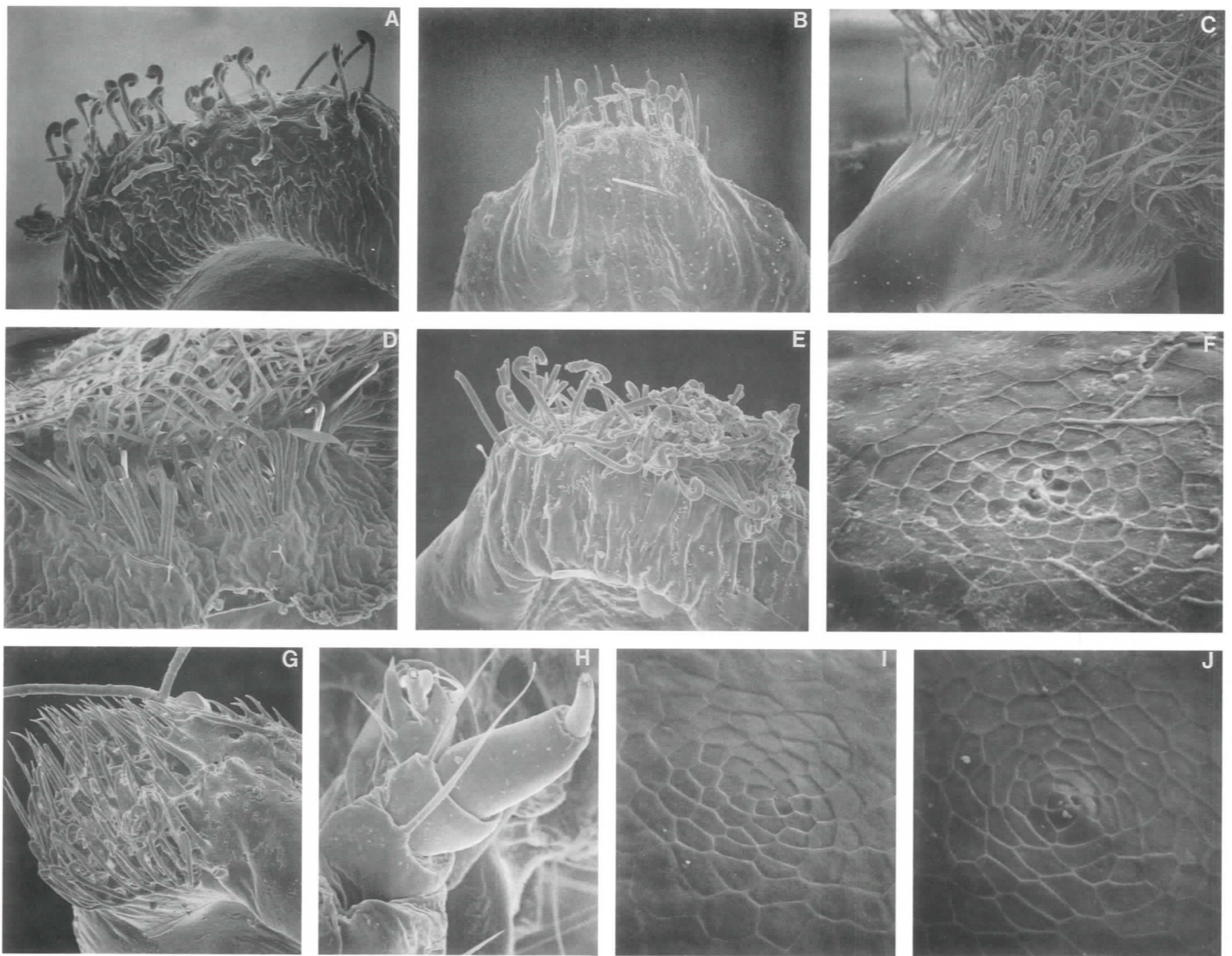


Fig. 22. (A)-(E), (G) Cremaster of the pupae: (A) *C. obscura* (X200); (B) *C. sommeri* (X150); (C) *C. archebates* (X150); (D) *C. confusa* (X200); (E) *C. grannus dilemma* (X200); (G) *C. hysius* (X150); (F), (I)-(J) Micropyle of the egg: (F) *C. arcas* (X1000); (I) *C. grannus dilemma* (X500); (J) *C. tasajera* (X750); (H) Maxilla of *C. confusa* (X380).

TABLE 3. Data on development time and sizes of eggs, larvae, pupae, and adults.

Taxon	egg size width/height	length of 5th instar larva	length of pupa	width of pupa dorso-ventrally	width of pupa side to side	wing span	time of development
<i>C. archebates</i>	?	26	12	6	5.7	21-23	95 days
<i>C. sommeri</i>	?	24	12.5	5.25	5.25	17-18	105 days
<i>C. hysius</i>	0.7/0.7	25	11	5.25	5.25	16.5-17.5	77 days
<i>C. obscura</i>	?	20	10.3	4.5	5	14-15	73 days
<i>C. grannus dilemma</i>	0.89/0.86	21	11.8	4	4	16-17	85 days
<i>C. batesi</i>	0.74/0.67	?	?	?	?	13-15	?
<i>C. confusa confusa</i>	0.85/0.82	22	10	4	5	14-16	60 days
<i>C. pulchella</i>	1.35/1.35	35	14	6	6	22-25	?

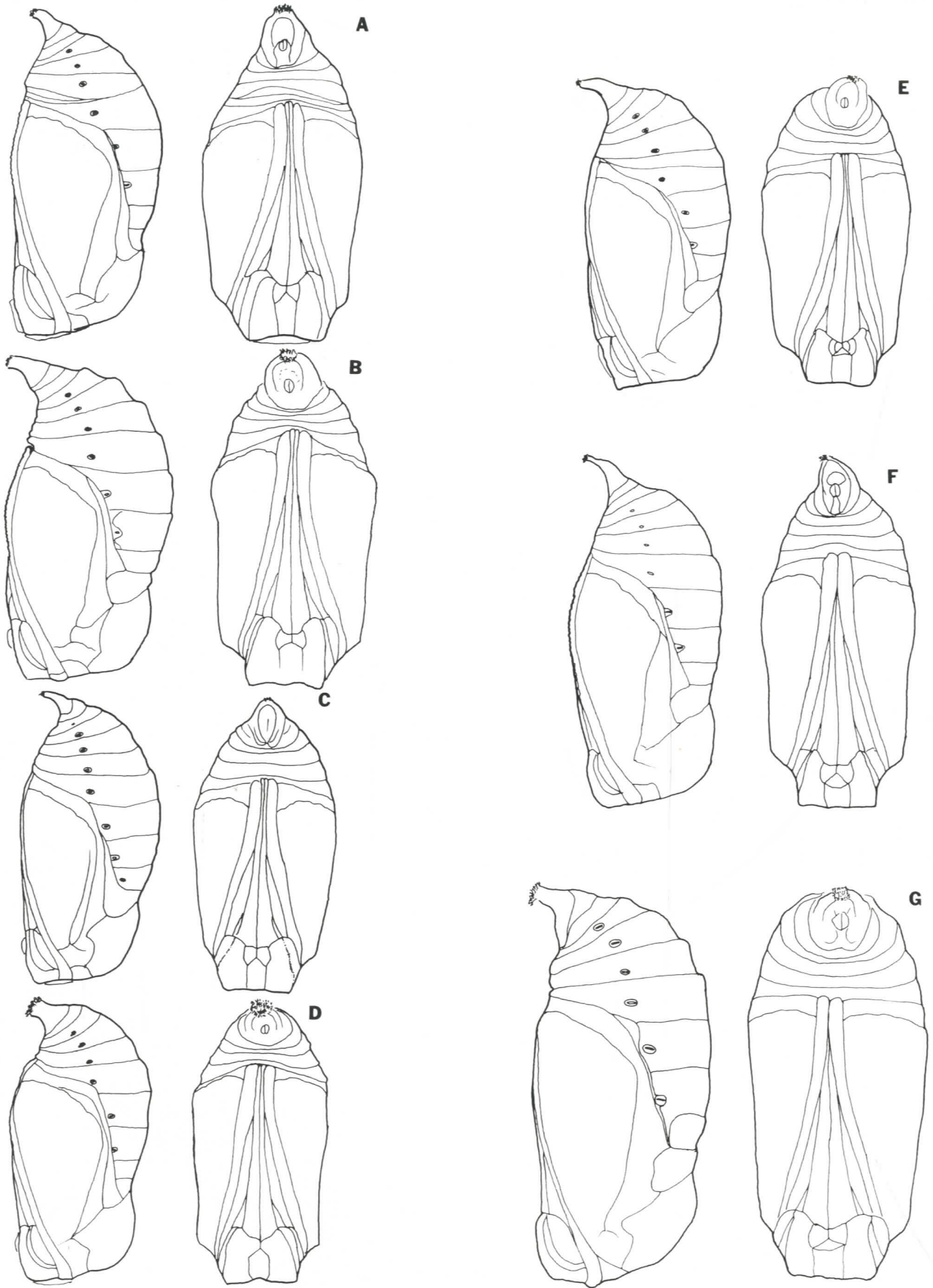


Fig. 23. Structure of the pupa: (A) *C. hysius*; (B) *C. archebates*; (C) *C. grannus dilemma*; (D) *C. confusa*; (E) *C. obscura*; (F) *C. sommeri*; (G) *C. pulchella*.

CONCLUSIONS

In previous cases, characters of satyrine immature stages were shown to be conservative at the intrageneric level (e.g., Sourakov, 1995). Observations on *Calisto* support the view of the early diversification of the genus, as well as the idea that characters of immature stages can evolve faster than those of adults. *C. confusa* and *C. obscura*, sympatric cosmopolitan species, were referred to by Munroe as a "compact group," based on wing pattern. Their immatures, however, show significant differences. Their sympatry and wide geographic distribution suggest prolonged reproductive isolation. *C. sommeri* and *C. batesi*, which were considered by some as subspecies of *C. grannus* and *C. hysius*, respectively, showed sufficient differences in their immature stage to consider them separate species. *C. archebates*, despite the distinctness of its adults (front cover, middle right), appears to be close to *C. hysius*. The adults of *C. galii* and *C. pulchella* are extremely different from other Hispaniolan *Calisto*, ecologically as well as morphologically. They are even more divergent in their immature stages than in their adults, and could be placed in separate genera (or subgenera) on the bases of these characters.

As in adults, colors of larvae and pupae seem to be the least conservative characters, varying even intraspecifically. Elaborate shape in color pattern, however, seems to be unique for each species and might serve for species identification. Most of the taxonomically useful characters were found in the sclerotized structures of the larval head. The differences in egg surface structures were found to be substantial and can be used as well for determining evolutionary relationships within *Calisto*.

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