Life History of *Calydna sturnula* with a Review of Larval and Pupal Balloon Setae in the Riodinidae (Lepidoptera)

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ABSTRACT The immature stages of *Calydna sturnula*, from the second instar onwards, are described and illustrated from tropical dry forest in the Area de Conservación Guanacaste in northwestern Costa Rica. The foodplant in all cases was *Schoepfia schreberi* (Olacaceae). Only six of the 219 individual caterpillars and pupae collected during the last 15 yr were parasitized by braconid and chalcid wasps and a tachinid fly. The larval ultrastructure of *C. sturnula* was studied by means of scanning electron microscopy, with emphasis placed on their prothoracic balloon setae, rare structures in the Riodinidae. The occurrence of larval and pupal balloon setae in the Riodinidae is reviewed. Larval balloon setae are currently known from all three genera of the Helicopini, at least *Calydna* in the *incertae sedis* section of the Riodininae, and at least three genera of the Nymphidiini. Larval material was examined for all but one of these genera, and the macro and ultrastructure of their balloon setae are described, illustrated, and compared. Pupal balloon setae are currently known only from *Helicopis* and *Calydna*. The balloon setae of *Calydna* and the genera of the Helicopini are found to be more similar to each other than to those of the Nymphidiini genera. Because balloon setae occur in nonmyrmecophilous (such as *Calydna*) as well as myrmecophilous species, we hypothesize that they are used to store and disperse a noxious chemical when the caterpillar or pupa is grabbed by a predator, rather than to facilitate a symbiotic relationship with ants, as previously suggested. Internally, balloon setae are filled with a spongy yellowish material that consists of a dense latticework of tiny strands. We suggest that as these strands enter the otherwise hollow external acanthae, the acanthae discharge the noxious chemical when the balloon setae are squeezed.

KEY WORDS balloon setae, *Calydna*, Helicopini, larval defenses, Nymphidiini

THE IMMATURE STAGES OF the Riodinidae remain perhaps the most poorly known of all the butterfly families. By 1987, Harvey (1987a) was able to report that, after 150 yr of study, information on the food plants and/or the morphology of the early stages was known for only ≈100 riodinid species, or 8–9% of the total familial diversity. After more intensive subsequent searching, as reported in DeVries et al. (1994), DeVries (1997), and Janzen and Hallwachs (2002), this number now totals 170–180 species. However, this still represents only 13–15% of the family. Unfortunately, the life histories of very few of even these species have been described and illustrated in any detail (e.g., *Aricoris hubrichi* by Bruch 1926; *Lemonias caliginea* by Ross 1964, 1966; *Menander felsina* by Callaghan 1977; *Thisbe irenea* by DeVries 1988a, 1991; and *Juditha caucana* by Hall and Harvey 2001).

Herein we describe and illustrate the early stages of the riodinid *Calydna sturnula* (Geyer) (the adults are illustrated in Fig. 1) from the second instar onward. This represents the first published life history for the genus, and makes *Calydna* Doubleday the fourth genus to be reared in the *incertae sedis* section (of Harvey 1987a) of the Riodininae, after *Argyrogrammana* Strand, *Apodemia* C. and R. Felder, and *Emesis* Fabricius. *Calydna sturnula* is the most common and widespread species in the genus and ranges from northern Mexico to Argentina, Paraguay, and southeastern Brazil. It occurs in a wide variety of lowland habitats, from dry *Acacia* scrub to wet rainforest, and appears to be most common in Central America, where it has been erroneously referred to in past literature under the names *hegias* R. Felder and *sinuata* R. Felder (Hall 2002).

The most remarkable feature of *Calydna* caterpillars is their large cluster of balloon setae on the prothoracic shield. Such structures were first reported by Guppy (1904) in two species of *Theope* Doubleday from Trinidad (see Fig. 2), and they are now also known from other myrmecophilous genera in the Nymphidiini and from the nonmyrmecophilous genera of the Helicopini (Harvey 1987a; Hall 1998, 1999). Herein we review the occurrence of balloon setae in the Riodinidae, compare the macro and ultrastructure of these setae across different genera and tribal groupings, and, in the context of these findings, discuss the possible function of balloon setae. Also, by examining

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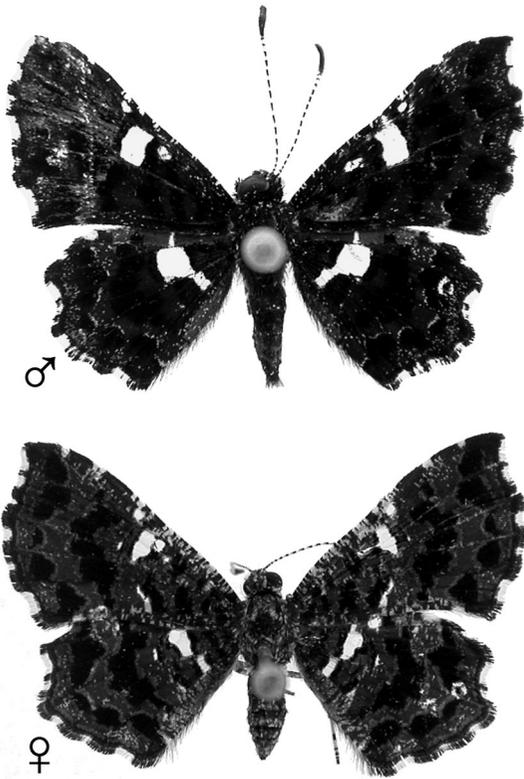
Fig. 1. Dorsal surface of *Calydna sturnula* adults reared from caterpillars collected in dry forest of the ACG, northwestern Costa Rica (♂ 95-SRNP-6705; ♀ 94-SRNP-6057).

an additional character system, we hoped to shed further light on the phylogenetic position of *Calydna*, which is currently not placed in any tribe of the Riodininae (Hall 2002).

Materials and Methods

Rearing of *Calydna sturnula*. *Calydna sturnula* was reared in the lowland dry forest of the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica, as part of the macrocaterpillar inventory of the ACG that began in 1978 (e.g., Janzen 1988, 1993; Burns and Janzen 2001; Schauff and Janzen 2001; Janzen and Hallwachs 2002). Between 1987 and 2001, D.H.J. and several resident parataxonomists amassed 219 rearing records for *C. sturnula* from 13 separate rearing events. Wild-caught caterpillars and pupae were reared individually in foliage-filled plastic bags at ambient temperatures and any resulting parasitoids collected. Voucher specimens of early stage material (01-SRNP-15826, 15831, 15838, 15849, 15851; all codes refer to those used in the ACG inventory web site of Janzen and Hallwachs 2002), as well as pinned and spread reared adults (87-SRNP-1329, 94-SRNP-6057, 95-SRNP-6705), have been deposited in the National Museum of Natural History, Smithsonian Institution, Washington, DC (USNM).
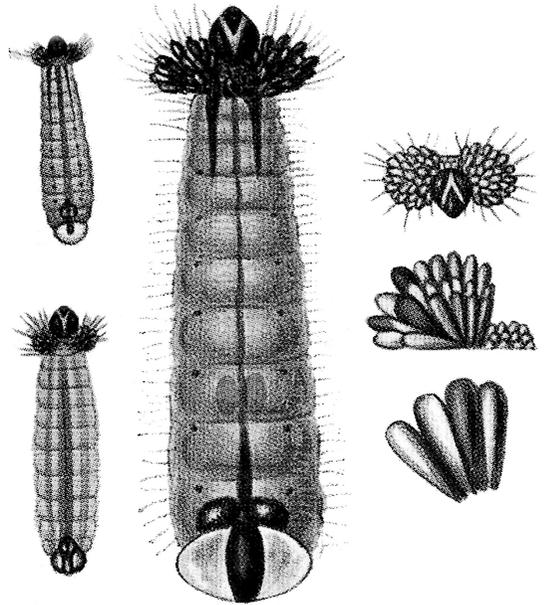
Fig. 2. An adaptation of Guppy's (1904) original illustrations of the larval balloon setae in *Theope foliorum* Bates (bottom left) and *Theope eudocia* Westwood (remaining figures) from Trinidad.

Morphology. The early stage material used in this study came from The Natural History Museum, London, United Kingdom (BMNH) and the collections of the authors. All images were taken or prepared by the authors unless otherwise stated in the figure captions. The images in Fig. 3 (more of which can be found on the ACG inventory web site of Janzen and Hallwachs 2002) were taken with Kodachrome 25. Light microscopy was done with an Olympus SZH, and digital images were taken using a Nikon HC-300Zi attached to a Wild M400 microscope. Scanning electron microscopy (SEM) was conducted by means of an ISI Super IIIA and a Leica Stereoscan 440, with material mounted on aluminum stubs using carbon tape, and sputter coated with gold/palladium. Alcohol preserved larval material was critical point dried in a Samdri 790 machine before mounting. The terminology for larval and pupal morphology follows Stehr (1987).

Results and Discussion

Life History of *Calydna sturnula*. All *C. sturnula* caterpillars were found resting or feeding on mature foliage of the small tree *Schoepfia schreberi* (Olacaceae). The egg and first-instar caterpillar remain unknown, and below we describe in detail only the fifth-instar caterpillar and the pupa. The early-instar caterpillars differ primarily from the later instars by having longer, lateral, filamentous setae and prominent brown markings extending through the middle of the white dorsal band of the thorax and abdomen.

Description of fifth-instar caterpillar (total length 15.7 mm) (Figs. 3C–G, 4A–M, and 5A–C): the head
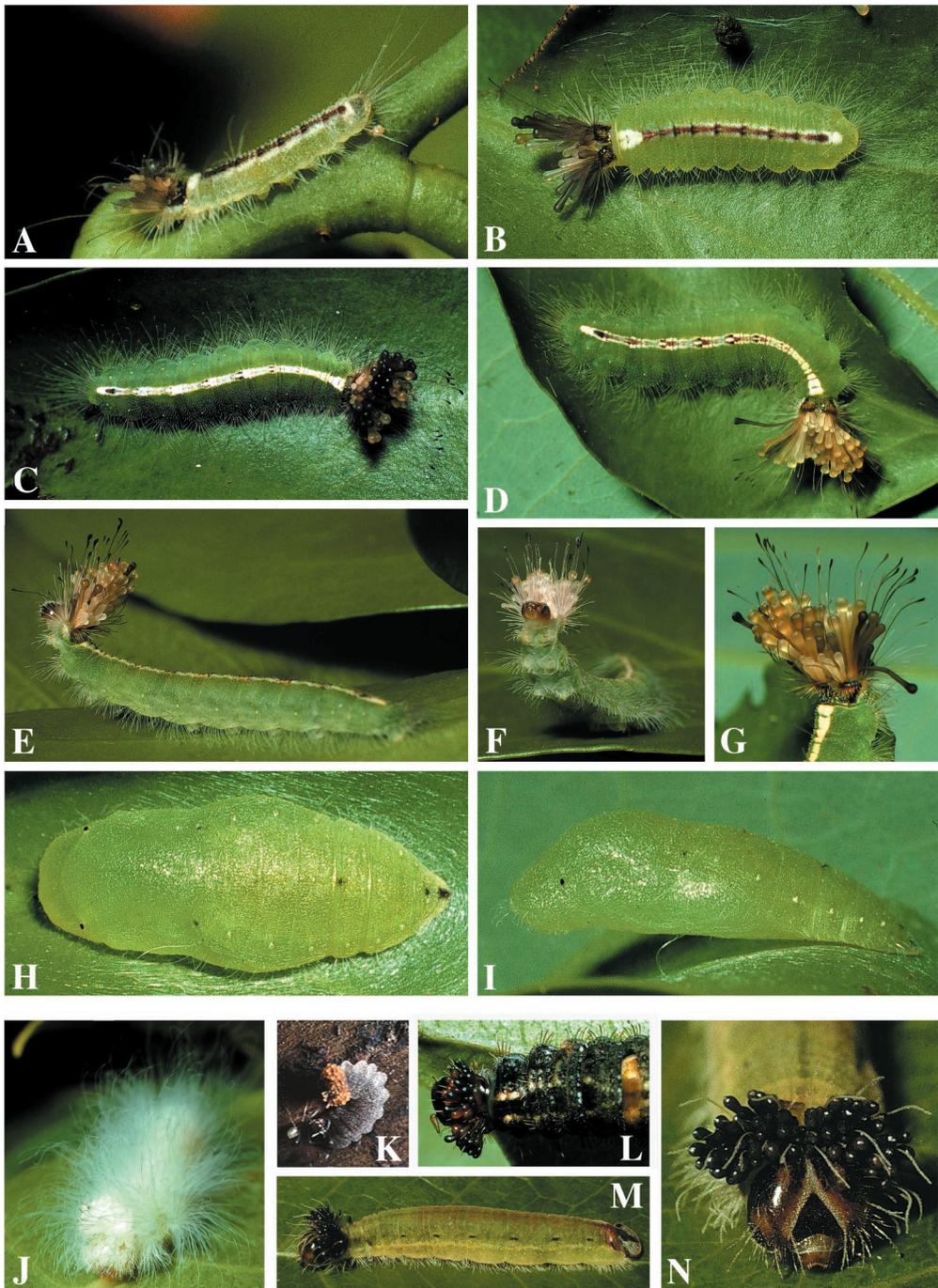
Fig. 3. Immature stages. Lateral view of a third instar caterpillar (A) (01-SRNP-15826), dorsal view of a fourth instar caterpillar (B) (01-SRNP-15838), dorsal (C, D, G), lateral (E), and ventral (F) views of fifth-instar caterpillars (87-SRNP-1329, 01-SRNP-15831), and dorsal (H) and lateral (I) views of a pupa (01-SRNP-15849) of *Calydna sturnula* from the dry forest of the ACG, Costa Rica; (J) dorsofrontal view of a fifth-instar *Anteros carausius* Westwood caterpillar (01-SRNP-17279) from the dry forest of the ACG, Costa Rica; (K) an unidentified probable Nymphidiina caterpillar in an *Azteca* ant nest from Corcovado, Costa Rica (photo by J. Longino); (L) an unidentified probable *Theope* caterpillar (01-SRNP-9759) from the wet forest of the ACG, Costa Rica; lateral (M) and dorsofrontal (N) views of a fifth-instar *Theope virgilius* caterpillar (97-SRNP-4889) from the dry forest of the ACG, Costa Rica.
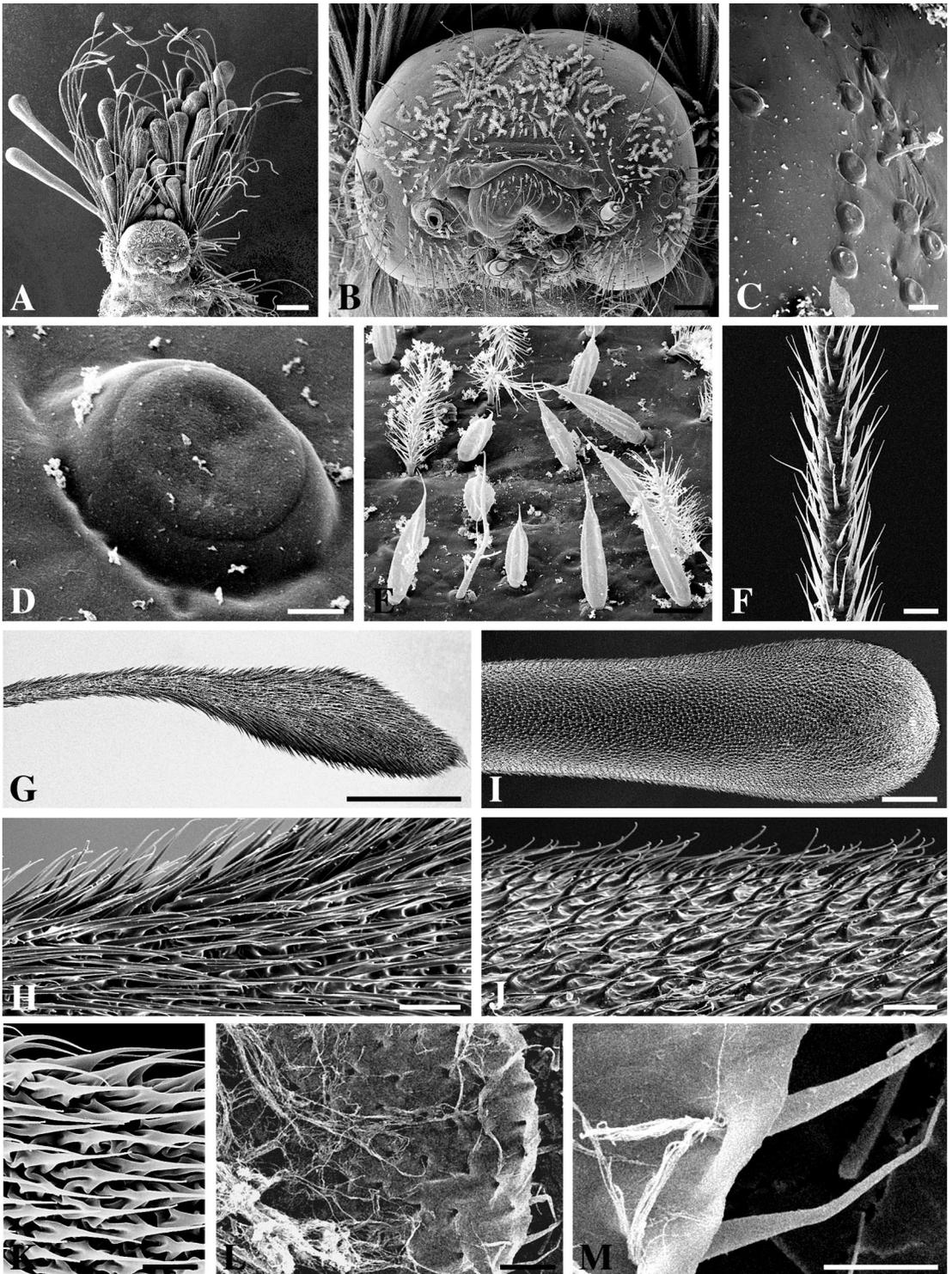
Fig. 4. Morphology of *Calydna sturnula* larval head and prothorax (01-SRNP-15831). (A) frontal view of head and prothoracic balloon setae; (B) frontal view of head at higher magnification; (C) overview of perforated cupola organs (PCOs) on left dorsal side of head; (D) a single PCO on head at higher magnification; (E) high magnification view of three different setal types on frons of head; (F) high magnification view of a long plumose seta from prothorax; (G) distal portion of a spatulate-tipped seta from prothorax; (H) high magnification view of seta in (G); (I) distal portion of a balloon seta from prothorax; (J) high magnification view of seta in (I); (K) high magnification view of a different, more shriveled balloon seta; (L) inner surface of a balloon seta, showing network of spongy strands; (M) high magnification view of strands in (L) entering external acanthae of a balloon seta. Scale bars: A: 500 μm; B, G, I: 100 μm; C, E: 20 μm; F, H, J, L: 10 μm; D, K, M: 5 μm.
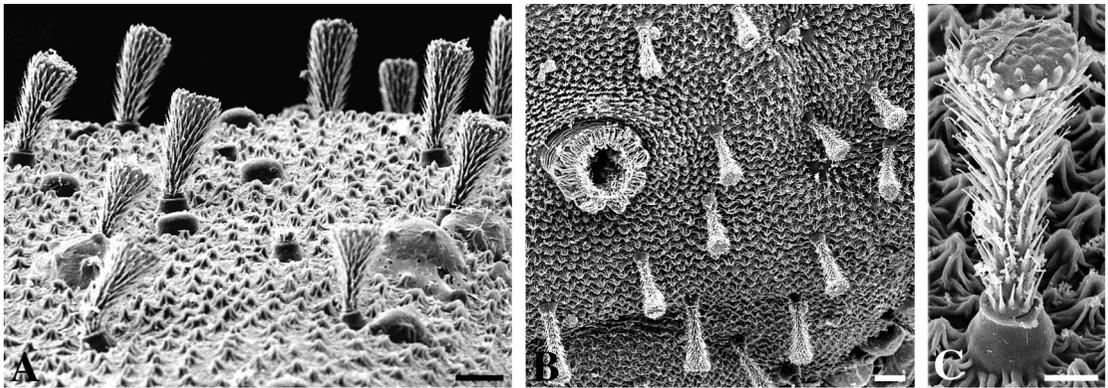
Fig. 5. Morphology of *Calydna sturnula* larval body (01-SRNP-15831). (A) High magnification view of dorsal section of abdominal segment eight, showing PCOs and wedge-like setae; (B) lateral view of abdominal segment eight, showing a spiracle and wedge-like setae; (C) high magnification view of a single wedge-like seta from (B) (note encrusted tip of seta). Scale bars: A, B: 20 μm; C: 10 μm.

(width 1.3 mm) (Fig. 4A–E) is approximately circular in outline and black except for the white trimmed clypeus; the labrum, mandibles and antennae are brown; the surface of the head contains three setal types (Fig. 4B and E): (1) a few largely lateral, long, slender setae, (2) largely frontal, short, ribbed, apically pointed setae, and (3) short, plumose setae; the perforated cupola organs (PCOs) are arranged in two dorsal clusters of twelve and have sieve plates with minute pores (Figs. 4C and D).

The thoracic shield (width 1.9 mm) is black, medially desclerotized dorsally, and bears three types of setae anteriorly that form a corona over the head (Figs. 3C–G and 4A): (1) cream-yellow to brown balloon setae of variable length (0.4–2.9 mm) that are expanded distally to a rounded tip (max. width 0.4 mm) (Figs. 3C–G and 4A, I–M); (2) slightly longer setae (max. length 4.3 mm) with spatulate tips (Figs. 3C–G, and 4G and H); and (3) long, slender, plumose setae (Fig. 4A and F), including intergrades to setal type (2); setal types (1) and (2) are densely covered externally with short, slightly curved acanthae (Fig. 4H and J, K) (these are more densely clumped in dried and shriveled setae [4K] than in expanded alcohol preserved ones [4J]), and setal type (1) is filled internally with a spongy yellowish white material that enters the hollow acanthae (Fig. 4L and M); T2 and T3 are green, with a median, white, longitudinal stripe, long lateral setae (max. length 1.8 mm), evenly scattered, spiky, wedge-shaped setae (note encrusted tip of setae, implying setae are used for dispersal of a chemical), and a few scattered PCOs (Fig. 3C–G).

The abdomen (max. width 3.3 mm) (Figs. 3C–F and 5A–C) is green, with a dorsal, white, longitudinal stripe continuing to the posterior edge of A9 that contains a variable scattering of brown markings, and a lateral fringe of long, simple setae on all segments; the dorsal surface is generally smooth, with scattered, spiky, wedge-shaped setae as on T2–3 (Fig. 5A–C), and a few scattered PCOs (Fig. 5A); the spiracles are white, and those on A1 are displaced anteriorly and ventrally (i.e., in line with lateral fringe of setae)

compared with those on A2–8; the prolegs on A3–6 have planta, and a lateroseries and interrupted mesoseries of multiordinal, uniserial crochets.

Description of pupa (total length 9.4 mm, width at A1 4.0 mm) (Fig. 3H and I): green and dorsoventrally compressed, with long, lateral setae on thoracic and abdominal segments as in caterpillars, and very short, sparsely scattered, mushroom-shaped setae dorsally (not illustrated); the prothoracic and mesothoracic legs are both in contact with the eyes; T3 extends posteriorly to A2, separating A1 from T2; a silk girdle is present, crossing A1; the environs of the spiracle on T1 is black; the abdominal spiracles are cream and exposed on A2–A7; the cremastral area extends anteriorly to the posterior edge of A6, squeezing A7 laterally; A9 and A10 are fused dorsally.

Parasitoids. Only six (3%) of the 219 individual wild-caught caterpillars and pupae collected were later found to have been parasitized. Five braconid wasp larvae in the genus *Apanteles* emerged from a fifth-instar caterpillar to form white cocoons next to it that were tightly affixed to the leaf substrate. On two occasions, a single braconid wasp larva in the genus *Hypomicrogaster* emerged from a fourth-instar caterpillar to form a similar cocoon. A single unidentified chalcid wasp adult emerged from a host pupa and, on two occasions, a solitary tachinid fly larva emerged from a host pupa to eventually pupate in the leaf litter or soil.

Systematics. Because *Calydna* has not yet been placed in any tribe of the Riodininae, we briefly discuss what, if anything, the morphology of immature *C. sturnula* suggests for the systematic placement of the genus. The position of spiracle A1, and the presence of planta and an interrupted mesoseries of crochets in the caterpillars, is typical for the Riodininae (Harvey 1987a, 1987b). Larval balloon setae are found elsewhere only in the Helicopini and Nymphidiini, and the ultrastructure of balloon setae in *Calydna* is essentially the same as that in all Helicopini genera, but quite different to that in most nymphidiine genera. The absence of long secondary setae in mature larval
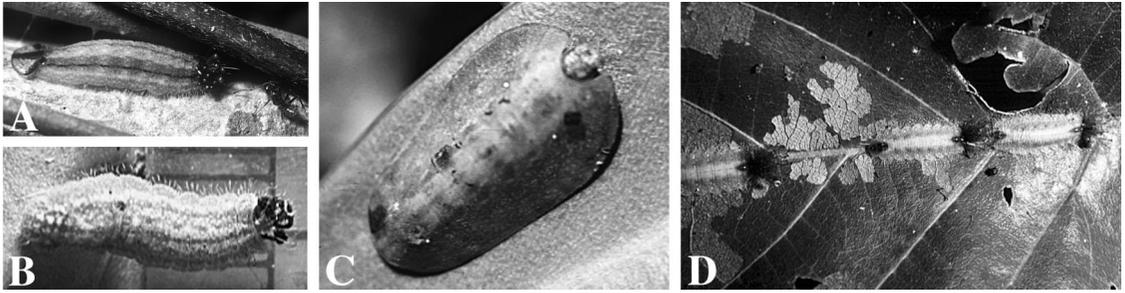
Fig. 6. Immature stages. (A) An unidentified probable *Theope* caterpillar from northern Venezuela (photo by J. Longino); (B) a late-instar *Nymphidium baeotia* Hewitson caterpillar from Timehri, Guyana (photo by J. Longino); (C) a late-instar *Menander pretus* (Cramer) caterpillar from La Selva, Costa Rica (photo by P. DeVries); (D) three unidentified caterpillars, similar to but distinct from *Calydna*, from La Selva, Costa Rica, feeding on *Persea* (Lauraceae) (photo by L. Gilbert).

instars is generally characteristic only of myrmecophilous caterpillars, but *C. sturnula* caterpillars are not ant-attended and do not have the "ant organs" common to all members of the two myrmecophilous riodinid tribes, Eurybiini and Nymphidiini (Harvey 1987a). *Argyrogrammana,* another genus in the riodinine *incertae sedis* section, also has nonmyrmecophilous caterpillars that are devoid of long setae (Robbins and Aiello 1982).

Two other *incertae sedis* genera, *Apodemia* and *Emesis,* have the pupal silk girdle crossing at the junction of abdominal segments one and two, but the silk girdle of *Calydna* pupae is typical for the Riodininae in crossing abdominal segment one (Harvey 1987a). The fusion of abdominal segments nine and ten in *Calydna* pupae is also typical of the derived majority of the Riodininae (Hall 2003). However, *C. sturnula* pupae do exhibit three anomalous characters: (1) the ventral compression of abdominal segment seven is not known in any other riodinid pupa; (2) the spiracle on abdominal segment three is exposed rather than concealed beneath the wing case, a condition typical of the Nemeobiinae and Euselasiinae, but known in the Riodininae only in *Emesis emesia* (Hewitson) and *Argyrogrammana crocea* (Godman and Salvin) (Harvey 1987a, unpublished data); and (3) abdominal segment 2, but not 1, is in contact with the mesothorax, a condition typical of the Nemeobiinae and Euselasiinae, but previously unknown in the Riodininae (Harvey 1987a, Hall 2003). It should also be mentioned that the pupa of the recently reared *Calydna venusta* Godman and Salvin, which belongs in a different species group to *C. sturnula* (Hall 2002), bears balloon setae laterally on the mesothorax (Cock and Hall 2004). Pupal balloon setae are currently known elsewhere in the Riodinidae only from *Helicopis* Fabricius, in which they occur as a single cluster on the prothorax.

In summary, the morphological information gleaned from immature *C. sturnula* is somewhat ambiguous and inconclusive regarding the phylogenetic placement of *Calydna.* This is partly because insufficient representatives from genera hypothesized to be closely related to *Calydna* based on adult morphology, such as *Echydna* Hall, have been reared. However, when considering genera from which species have been reared, *Calydna* caterpillars and pupae are, on balance, most similar to those of *Argyrogrammana* and the genera of the Helicopini. Given their great structural similarity, it is possible that larval balloon setae have evolved only once outside of the Nymphidiini. These setae may thus eventually prove to be a character that unites *Calydna,* the genera of the Helicopini, and an unknown number of additional genera from the riodinine *incertae sedis* section (e.g., see Fig. 6D), into a single clade. Now that a comprehensive species-level phylogeny for the Nymphidiini is nearly completed (Hall 2002, unpublished data; Hall and Harvey 2002), it is clear that larval balloon setae have evolved multiple times in that tribe. Because larval balloon setae are apparently absent in the basal subtribes of the Nymphidiini, namely the Aricorina and Lemoniadina (Hall and Harvey 2002), the evolution of balloon setae within the Nymphidiini appears to be independent from their evolution outside of that tribe, as originally suggested by Harvey (1987a).

Structural Review of Balloon Setae in the Riodinidae. Larval balloon setae are now known from multiple genera in each of three tribal groupings in the Riodininae, namely the *incertae sedis* section, Helicopini and Nymphidiini, as detailed in Table 1. Within the *incertae sedis* section, the macro and ultrastructure of these setae in *Calydna* were described in the previous section. However, Fig. 6D would seem to provide evidence that larval balloon setae are present in an additional genus closely related to *Calydna.* The three unidentified caterpillars depicted there can clearly be seen to have dorsally positioned white spiracles on the lateral flanges, thus excluding them from the derived Nymphidiini (Nymphidiina + Theopeina), whose caterpillars possess ventrally positioned spiracles on abdominal segments three to seven, hidden from dorsal view (Harvey 1987a; Hall 1999, 2002). Their green, largely naked, bodies also exclude them from the Helicopini. Because both Costa Rican *Calydna* species, *C. sturnula* and *C. venusta,* have been reared (Janzen and Hallwachs 2002, Hall 2002, Cock and Hall 2004), and both differ from the Costa Rican caterpillars in Fig. 6D by having slightly narrower bodies, paler balloon setae, and a prominent black and white dorsal band along the entire body instead of

Table 1. Overview of the occurrence and structure of larval balloon setae in the Riodinidae

Taxon	Balloon setae	References	Figures
Helicopini: (3/3)			3, 7
Helicopis (2/3)	Large, dense, medially positioned cluster of yellowish-white balloon setae on prothorax totally obscures head from above; external surface of balloon setae densely covered with short, slightly curved spines; numerous long, white, plumose setae also present on prothorax	Sepp (1829-1852); Harvey (1987a); DeVries et al. (1994)	7A-E
Anteros (≥4/≥18)	Same as *Helicopis*, but balloon setae also reddish in one species	Moss (unpubl. data); Kendall (1976); DeVries et al. (1994); Janzen and Hallwachs (2002)	3J, 7F-H
Sarota (1/20)	Same as *Helicopis*	DeVries (1988b)	none
incertae sedis: (4/12)			3-6
Calydna (2/18)	Large, dense cluster of yellow or pale brown to dark brown balloon setae across prothorax (balloon setae longer laterally) totally obscures head from above; external surface of balloon setae densely covered with short, slightly curved spines; a few long, white, plumose setae and numerous longer, spatulate-tipped setae also present on prothorax	Janzen and Hallwachs (2002); this paper; Cock and Hall (2004)	3A-I, 4, 5
Unidentified genus	Same as *Calydna*, but balloon setae darker, ultrastructure of balloon setae unknown	This paper	6D
Nymphidiini: (11/>27)			2, 3, 6, 8
Theopeina (2/5)			2, 3, 6, 8
Theope (≥8/68)	Two distinct, variably sized, dorsolateral clusters of generally short, dark red and purple to brown or black balloon setae on prothorax generally only partially obscure head from above; external surface of balloon setae densely covered with small, oval platelets; sparsely distributed, very long, white plumose setae also present on prothorax	Guppy (1904); Kirkpatrick (1954); Harvey (1987a); DeVries et al. (1994); DeVries (1997); Janzen and Hallwachs (2002)	2, 3L-N, 6A, 8A-D
Nymphidiina (4/>16)			3, 6, 8
Nymphidium (≥12/30)	Two distinct, variably sized, dorsolateral clusters of short, dark red and purple to black (usually dorsally) or pale brown (usually ventrally) balloon setae on prothorax generally only partially obscure head from above; external surface of balloon setae densely covered with short spines that have expanded oval base; long plumose setae on prothorax absent	Sepp (1829-52); Mallet (unpubl. data); Harvey (1987a); Callaghan (1989, 1999); DeVries et al. (1994); Brévignon and Gallard (1999); Janzen and Hallwachs (2002); Hall (unpubl. data)	6B, 8E-G
Menander (4/12)	A pair of small, dark, lateral, paddle-like setae (incipient balloon setae?) on prothorax; external surface of paddle-like setae densely covered with small, oval platelets; long plumose setae on prothorax absent	Callaghan (1977); Donahue (1979); Harvey (1987a); DeVries et al. (1994); Dyer and Gentry (2002)	6C, 8H-I
Unidentified genus	Large, dense, medially positioned cluster of bright orange balloon setae on prothorax partially obscures head from above, ultrastructure of balloon setae unknown; long plumose setae on prothorax absent	This paper	3K

Numbers in parentheses after tribal groupings represent the number of genera from which at least one species has been reared, out of the total number of genera in the group. Numbers in parentheses after genera represent the number of species reared, out of the total number of species in the genus.

broad black areas at either end of the body only, we believe that the caterpillars in Fig. 6D belong to another genus. However, because the hypothesized closest relatives of *Calydna* based on adult morphology, namely *Echydna* Hall, *Callistium* Stichel, *Petrocerus* Callaghan, *Imelda* Hewitson, and *Echenais* Hübner (Hall 2002), do not occur in Costa Rica, the generic placement of these caterpillars remains unclear. Notably, the feeding damage in Fig. 6D is similar to that left by *Argyrogrammana* caterpillars, which also have largely naked bodies (Robbins and Aiello 1982).

Representatives from all three genera in the Helicopini (*Ourocnemis* Bethune-Baker should probably be regarded as a synonym of *Anteros* Hübner (Hall 1998)) have been reared, and all are now known to possess larval balloon setae. Sepp (1829–1852) was the

first to rear a *Helicopis* species, but Harvey (1987a) was the first to note the yellowish-white balloon setae on the caterpillars, based on material collected by J. Mallet in Guyana. Harvey (1987a) was also the first author to note that *Helicopis* is the only genus in the tribe to additionally have a cluster of balloon setae on the prothorax of the pupae. Two species of *Helicopis* have been reared, and crude paintings of *H. endymiaena* (Hübner) caterpillars are given by Sepp (1829–1852). Kendall (1976) was the first to rear an *Anteros* species, vaguely referring to the presence of balloon setae as "a verrucose patch on the first segment." At least four species of *Anteros* have been reared, and their caterpillars, which have yellowish to reddish balloon setae, are illustrated in DeVries (1997), Janzen and Hallwachs (2002) and here in Fig. 3J. DeVries (1988b) was
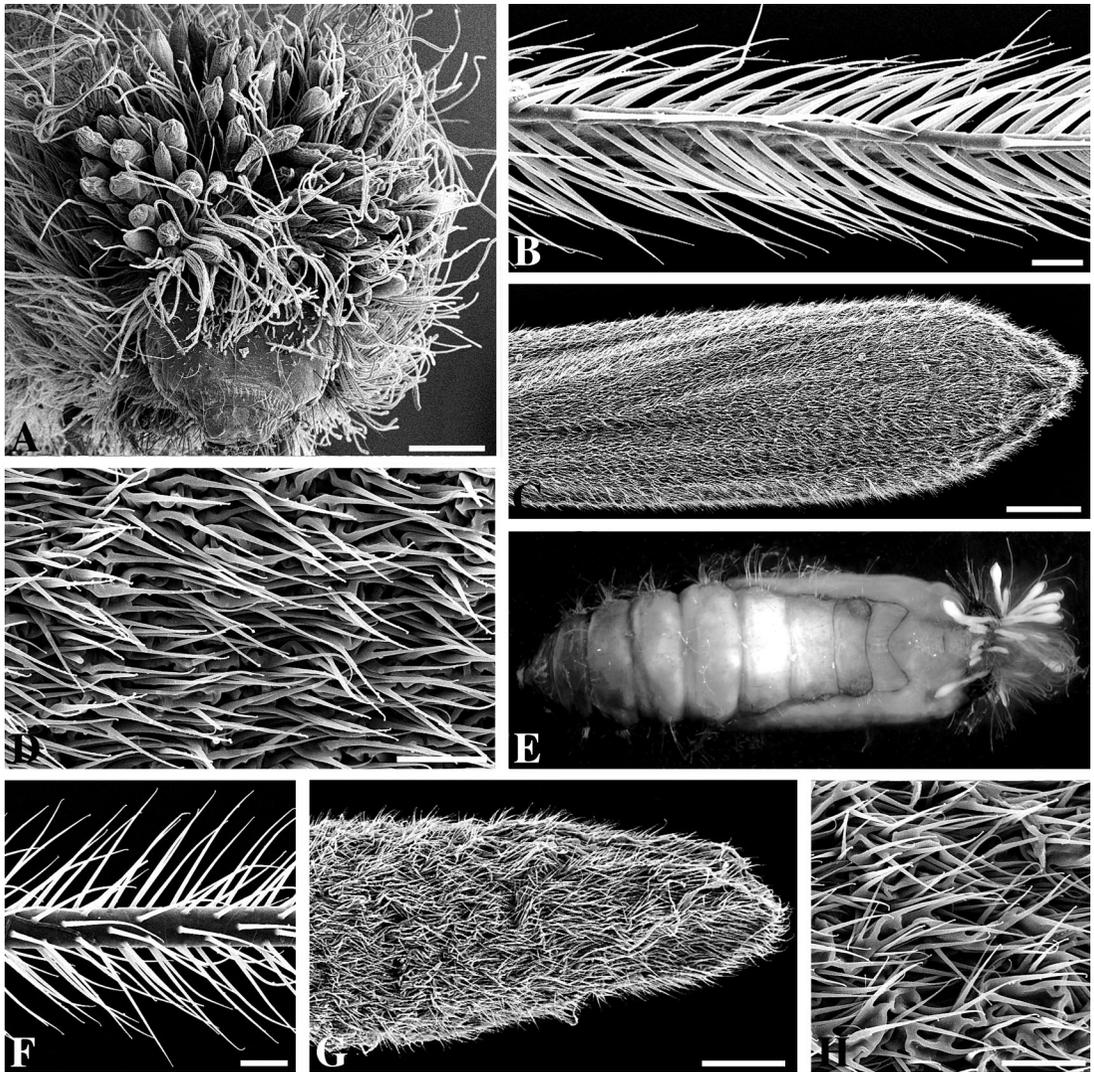
Fig. 7. Immature stage morphology of the Helicopini. Late-instar *Helicopis cupido* caterpillar (A–D) and pupa (E) from Georgetown, Guyana (ex. J. Mallet): (A) frontal view of head and prothoracic balloon setae; (B) high magnification view of a plumose seta from prothorax; (C) distal portion of a balloon seta from prothorax; (D) high magnification view of seta in (C); (E) dorsal view of a pupa, showing prothoracic balloon setae. Last instar *Anteros renaldus* caterpillar (F–H) from Pará, Brazil (M. Moss, BMNH): (F) high magnification view of a plumose seta from prothorax; (G) distal portion of a balloon seta from prothorax; (H) high magnification view of seta in (G). Scale bars: A: 500 μm; C, G: 50 μm; B, D, F, H: 10 μm.

the first to rear a *Sarota* Westwood species, referring to their balloon setae by stating "segments T1–2 [sic] have a dense dorsal topknot." Only *S. acantus* (Stoll) (not *gyas* Cramer as stated by DeVries 1988b, 1997 (Hall 1998)) has been reared through to the adult, and illustrations of the caterpillar, which has yellow-white balloon setae, are given by DeVries (1988b, 1997) and Hall (1998).

The balloon setae of *Helicopis cupido* (Linnaeus) and *Anteros renaldus* (Stoll) were studied in detail (Fig. 7). Caterpillars of both genera have a large, dense, medially positioned cluster of balloon setae on the prothorax that totally obscures the head from above (Fig. 7A). At high magnification, the external

surface of the larval balloon setae in both genera is seen to be densely covered with short, slightly curved spines or acanthae (acellular projections) (Fig. 7C, D, G, and H). These spines are slightly more densely clumped in the illustrations here than they would be in life, because the balloon setae depicted were dried and slightly shriveled. The balloon setae are internally filled with a spongy yellowish white material. Caterpillars of both genera also have numerous long, white, filamentous setae distributed among the balloon setae. These filamentous setae are densely covered with tiny, distally directed spines (Fig. 7B and F). *Helicopis* is the only genus in the Helicopini to also have the same, presumably homologous, balloon setae and longer plu-

mose setae on the prothorax of the pupae. In the illustrated *Helicopis* pupa (Fig. 7E), the balloon setae have become diaphanous, and the yellowish material within is clearly visible.

Species from only a small fraction of the genera in the Nymphidiini have been reared, and only a few of these, in the subtribes Theopeina and Nymphidiina (*sensu* Hall 1999, 2002; Hall and Harvey 2002), have larval balloon setae (Fig. 8). Within the Theopeina, species of only two genera have been reared, *Protonymphidia* Hall and *Theope*, and only members of the latter genus have larval balloon setae (Harvey 1987a; DeVries 1997; Hall 1999, 2000, 2002). Guppy (1904) was the first to rear species of *Theope* and to realize its caterpillars had these setae. At least eight species of *Theope* have been reared (Hall 1999), and illustrations of the caterpillars are given by Guppy (1904) (reproduced here in Fig. 2), DeVries and Hall (1996), DeVries (1997), Janzen and Hallwachs (2002) and here in Figs. 3L–N and 6A. DeVries and Poinar (1997) and Poinar and Poinar (1999) illustrate what is probably a *Theope* caterpillar, complete with prominent balloon setae, in 15–20 million year old Dominican amber, graphically demonstrating the evolutionary antiquity of these organs.

Balloon setae in *Theope* caterpillars are prominent but generally do not completely obscure the head from above (*T. bacenis* Schaus is an obvious exception) and are darkly colored, from dark red and purple to brown or black (Figs. 3L–N and 8A). We were able to study in detail the balloon setae of *T. virgilius* (Fabricius), and the balloon setae of *T. bacenis* were well illustrated by DeVries (1997). The external surface of the balloon setae in these species is densely covered with small oval platelets that are tightly appressed to the surface (Fig. 8B and C). The apices of the setae, where the platelets slightly overlap, bring to mind the external body armor of an armadillo or pangolin. Internally, the setae are filled with a spongy yellowish material. Sparsely distributed among the balloon setae are very long, whitish, filamentous setae that are themselves densely covered with small, distally curved spines (Fig. 8D).

Within the species-rich Nymphidiina, species from only four genera have been reared (13% of the species), namely *Nymphidium* Fabricius, "*Calospila*" Geyer, *Menander* Hemming and *Setabis* Westwood (Sepp 1829–52; Kaye 1921; Callaghan 1977; Harvey 1987a, 1987b; DeVries 1997). Larval balloon setae have been reported only in the first of these genera. Sepp (1829–1852) was the first to rear a *Nymphidium* species, but balloon setae were not reported for the genus until recently (Harvey 1987a). Approximately twelve species of *Nymphidium* have been reared (J.P.W.H., unpublished data), and illustrations of their caterpillars are given in Sepp (1829–1852), Callaghan (1989), DeVries (1994, 1997), Brévignon and Gallard (1999) and here in Fig. 6B. The larval prothorax generally has two small, well-defined, dorsolateral clusters of short balloon setae, although the balloon setae are much more numerous in *N. mantus* (Cramer). The dark purple and red to black setae are generally positioned

dorsally, with the paler setae positioned more ventrally and laterally.

We were only able to study in detail the balloon setae of *N. cachrus* (Fabricius), but intrageneric variation in riodinid balloon setae ultrastructure does seem to be limited. The external surface of the balloon setae in *N. cachrus* caterpillars is densely covered with small spines that have enlarged oval-shaped bases (Fig. 8E–G). Instead of having numerous filamentous setae, the prothorax of *Nymphidium* caterpillars bears only a few long and stout, spine-like setae.

We suggest that the pair of short, broad and flattened, paddle-like setae on the prothorax of *Menander* caterpillars may represent setae that are evolutionarily intermediate between the typical spine-like larval prothoracic setae of other nymphidiine genera and true balloon setae. Callaghan (1977) was the first to rear a *Menander* species and note the presence of these paddle-like setae in the second instar onwards of *M. felsina* (Hewitson). Four species of *Menander* have been reared, and illustrations of the caterpillars are given by Callaghan (1977), Donahue (1979), DeVries (1997), Brévignon and Gallard (1999), Dyer and Gentry (2002) and here in Fig. 6C. We were able to study in detail a *M. menander* (Stoll) caterpillar. Its paddle-like prothoracic setae are entirely covered with nonoverlapping oval platelets (Fig. 8H and I) much like those on the balloon setae of *Theope* caterpillars.

Figure 3K provides a tantalizing glimpse into the unknown majority of riodinid life histories. This distinctive, small, gray caterpillar with bright orange balloon setae, which probably belongs to a species in the Nymphidiina, was found in an *Azteca* ant nest at Corcovado, Costa Rica, by J. Longino. To further our understanding of nymphidiine life histories, it will be vital to search ant's nests, as well as foliage, to seek out those many species suspected of being aphytophagous (Hall 1999, unpublished data; Hall and Harvey 2002).

What is the Function of Balloon Setae? The function of balloon setae has been an unsolved mystery for nearly 100 yr. The only hypothesis put forward thus far is that by DeVries (1997), who, in the context of discussing the balloon setae of the myrmecophilous nymphidiine caterpillars of *Theope* and *Nymphidium*, stated "*Azteca* ants will frequently antennate the balloon setae of *Theope* and then briefly seize one of the setae with their mandibles. After biting a seta the ant will run about for a few moments in an agitated manner and cause a markedly increased activity in nearby ants-an analogous behavior can be simulated by crushing an individual ant near its nestmates. This suggests that the balloon setae secrete some chemical substance that causes a brief alarm response in the attending ants and thus function in a manner similar to the anterior tentacle organs." However, we see several problems with this hypothesis. First, balloon setae also occur in nonmyrmecophilous caterpillars, a fact that was overlooked by DeVries (1997). Second, nymphidiine caterpillars, like those of the Lycaenidae, already have organs, the anterior tentacle organs, that are believed to emit a volatile chemical similar to an ant alarm pheromone (Clark and Dickson 1956; Malicky
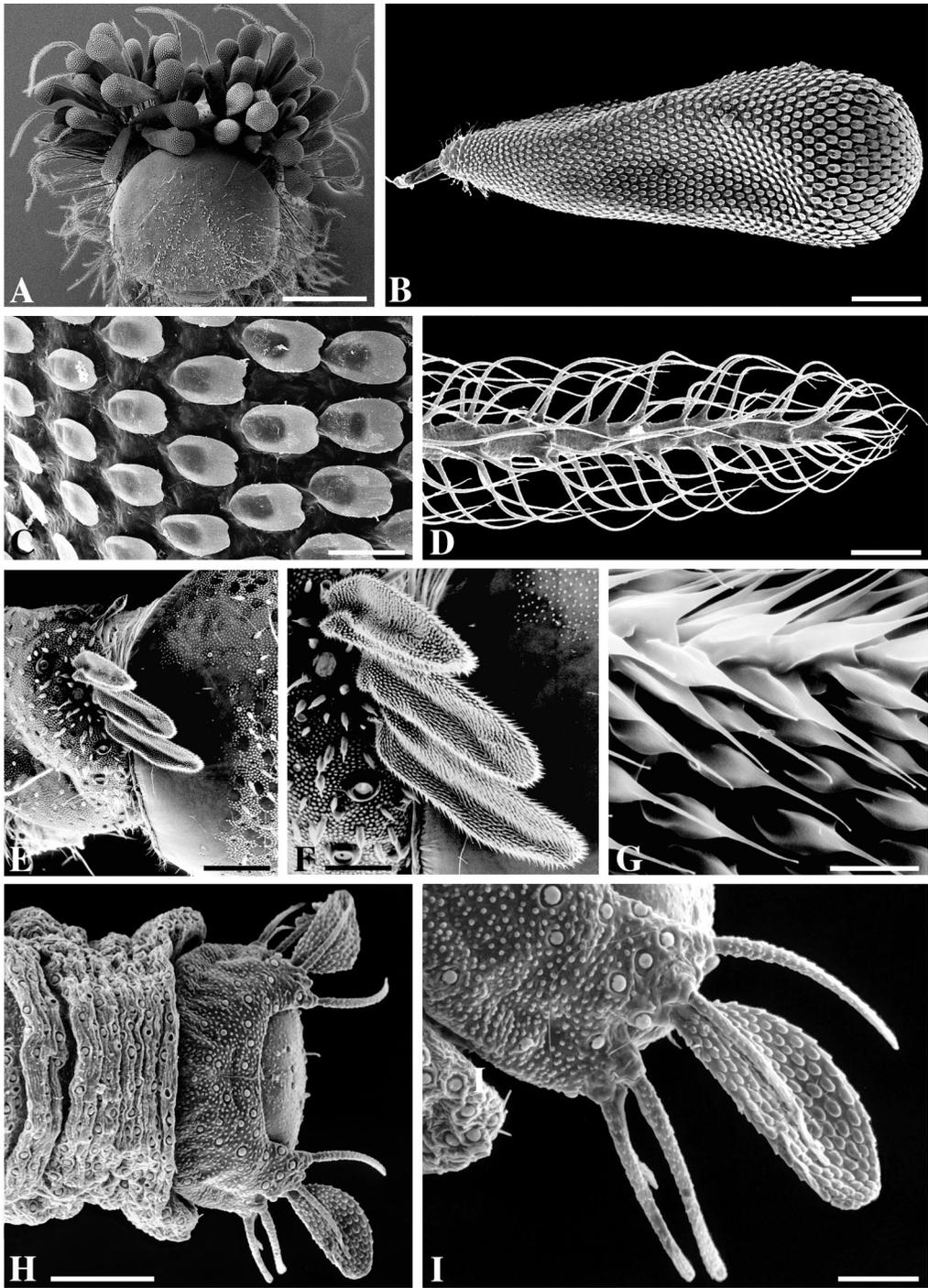
Fig. 8. Larval morphology of the Nymphidiini. Late-instar *Theope virgilius* caterpillar (A–D) from the dry forest of the ACG, Costa Rica (89-SRNP-714): (A) frontal view of head and prothoracic balloon setae; (B) a single balloon seta from prothorax; (C) high magnification view of balloon seta in (B); (D) high magnification view of a plumose seta from prothorax. Late-instar *Nymphidium cachrus* caterpillar (E-G) from Timehri, Guyana (ex. J. Mallet): (E,F) dorsolateral views of prothoracic balloon setae (note in E the empty sockets where a few balloon setae have become detached, and the single small vibratory papilla dorsally); (G) high magnification view of a single seta in (E, F). Late-instar *Menander menander* caterpillar (H, I) from Veracruz, Mexico (ex. C. Horvitz): (H) dorsal and (I) dorsolateral views of anterior portion of caterpillar, showing paddle-like setae on prothorax. Scale bars: A: 500 μm; E, H: 250 μm; B, F, I: 100 μm; C, D: 20 μm; G: 10 μm.

1969, 1970; Claassens and Dickson 1977; Cottrell 1984; DeVries 1988a). Only rarely does an organism go to the physiological expense of maintaining two organs with the same function. Third, an organ that one organism uses to manipulate another organism into defending it would most likely be under total control of the manipulating organism, as is the case with anterior tentacle organs. However, it seems that balloon setae must be squeezed (and perhaps also broken) by an external force to function. Finally, the ant "alarm" response could just as well be a "stress" reaction created by a chemical that is obnoxious to the ant that bit the seta, as the ant response described is the same as that of ants that are sprayed or dosed with a variety of defensive chemicals released by insects.

We propose the alternative hypothesis that riodinid balloon setae serve to deter invertebrate and vertebrate predators from eating caterpillars or pupae that are molested or handled as potential prey by releasing a noxious chemical. We believe the field observations of DeVries (1997) outlined above are equally well explained by this hypothesis. Larval prothoracic glands are commonly used as defensive organs elsewhere in the butterflies. In papilionid caterpillars, a bifid gland termed an osmeterium is everted from the mid-dorsal region of the prothorax when the caterpillar is threatened. The everted gland can readily be seen to glisten with its defensive secretion, which Eisner and Meinwald (1965) found to contain isobutyric and 2-methylbutyric acid in an exemplar species. A similar eversible gland used in defense is present ventrally on the prothorax of caterpillars in the Hesperiidae, Nymphalidae, and Pieridae (Tolliver 1987). Although no such eversible prothoracic glands are known in the Lycaenidae and Riodinidae, their caterpillars have a substantially thicker cuticle than do similarly sized caterpillars in the other butterfly families (Malicky 1969, 1970).

We have found that the balloon setae of exemplar species in five genera discussed in detail above (*Calydna, Helicopis, Anteros, Theope,* and *Nymphidium*), representing all three tribal groupings, are filled with a spongy yellowish material. Without preserved *Menander* caterpillars, we could not examine the internal structure of their paddle-like prothoracic setae. This finding explains the field observations of DeVries (1997) that when a balloon seta is gently squeezed and then released it immediately regains its former shape. Under the SEM, this material, which presumably stores the soon-to-be released chemical(s), can be seen to consist of innumerable tiny strands. These are clustered together to form bundles of strands, which near the inner surface of the balloon seta extend weblike between and into the otherwise hollow acanthae (Fig. 4L and M). These acanthae on the external surface of the balloon setae, which take the form of spines in the *incertae sedis* section and Helicopini, and oval platelets with or without a spine at their posterior tip in the Nymphidiini, thus appear to serve two functions. First, they presumably protect the setal membrane from being broken when the seta is handled, and second, especially in the absence of any obvious pores

on the setal membrane itself, they appear to be the conduits through which the chemical is expelled to the outside.

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