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NEW SPECIES OF *EUHAPIGIODES*, new genus, AND *HAPIGIODES* IN HAPIGIINI, new tribe, FROM COSTA RICA, WITH NOTES ON THEIR LIFE HISTORY AND IMMATURES (LEPIDOPTERA: NOTODONTIDAE)

J. S. MILLER[1], D. H. JANZEN[2], and J. G. FRANCLEMONT[3]

[1]Dept. of Entomology, American Museum of Natural History, Central Park West at 79th St., New York, New York 10024;
[2]Dept. of Biology, University of Pennsylvania, Philadelphia, Pennsylvania 19104;
[3]Dept. of Entomology, Comstock Hall, Cornell University, Ithaca, New York 14853, USA

ABSTRACT.– Two new species of Notodontidae from the lowland dry forests of the Area de Conservación Guanacaste, northwestern Costa Rica are described: *Hapigiodes sigifredomarini* **n. sp.** and *Euhapigiodes hallwachsae* **n. sp.** in *Euhapigiodes*, **n. gen**. The larvae of both feed on *Lonchocarpus* (Fabaceae). *Pseudhapigia misericordia* Dyar is moved to *Hapigiodes* as a new combination. *Hapigiodes* and *Euhapigiodes* are relatives of *Hapigia*, and would previously have been placed in the tribe Hemiceratini of Forbes, but comparison of adults and larvae of *Hapigiodes*, *Euhapigiodes* and *Hapigia* with *Hemiceras* yields the result that the Hemiceratini is polyphyletic. Thus, Hapigiini is erected as a new tribe of 9 genera, provisionally placed in the notodontid subfamily Heterocampinae. The larvae and adults of 8 hapigiine species from Costa Rica are figured, and their hostplants (all Fabaceae) are listed. These are the first life histories and food plants described for the Hapigiini.

KEY WORDS: *Anita*, *Antaea*, biology, *Canodia*, Central America, *Chliara*, *Colax*, distribution, Dudusinae, eggs, ***Euhapigiodes hallwachsae*** n. sp., Fabaceae, *Hapigia*, ***Hapigiodes sigifredomarini*** n. sp., *Hemiceras*, Hemiceratini, Heterocampinae, immatures, larvae, Leguminosae, Mesoamerica, Mexico, Neotropical, Nicaragua, Oriental, Panama, *Phalera*, Phalerinae, *Procolax*, *Pseudhapigia*, pupae, *Rhapigia*, South America, systematics.

The two new species described in this paper, *Hapigiodes sigifredomarini* Franclemont & Miller, n. sp., and *Euhapigiodes hallwachsae* Franclemont & Miller, n. sp., were reared as part of an on-going inventory (75,000 records, 1978-96) of the caterpillar fauna of the lowland dry forest of the Area de Conservación Guanacaste (ACG) in northwestern Costa Rica (Janzen and Hallwachs, 1997; Fig. 1). They are described so as to be able to refer to them during biodiversity development of the ACG (Janzen 1988, 1993, 1996), and because consideration of their larvae and other notodontid larvae reared in this same inventory leads us to erect the new tribe Hapigiini within the heterocampine Notodontidae.

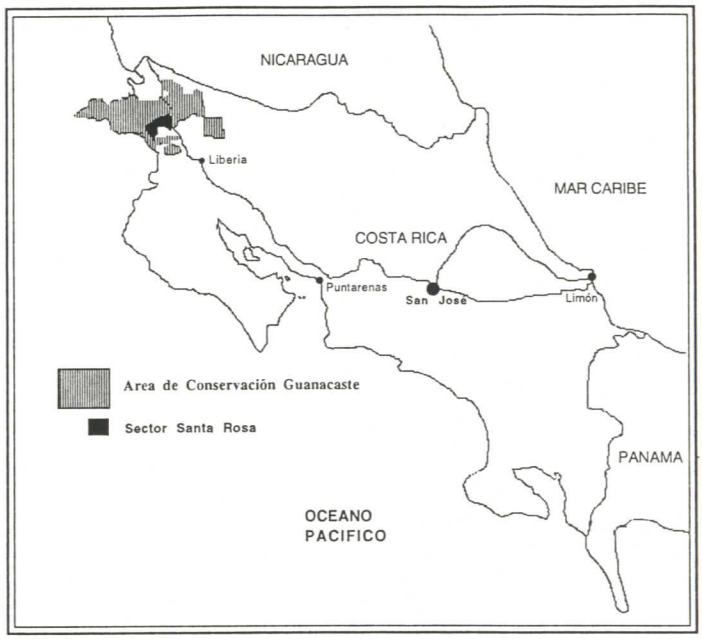


Fig. 1. Map of Costa Rica showing the Area de Conservación Guanacaste and Sector Santa Rosa, where most of the larval collections for this study were made.

TAXONOMY

Although *E. hallwachsae* and *H. sigifredomarini* show numerous superficial similarities, such as in general wing shape, wing pattern and antennal structure, we have concluded that they do not belong in the same genus. The new species *H. sigifredomarini* is congeneric with *Hapigiodes xolotl* Schaus, the type of *Hapigiodes*, while *E. hallwachsae* does not fit in any existing notodontid genus. For it we erect the genus name *Euhapigiodes*.

Beyond these simple statements, the taxonomic waters become extremely murky. For example, our preliminary investigation into the systematics of *Hapigiodes* Dyar reveals that the genus is not monophyletic. We dissected the male genitalia of *Hapigiodes arpi* Draudt from Brazil and found that this species differs substantially from *Hapigiodes xolotl*. The three taxa described in *Hapigiodes* by Thiaucourt (1978, 1987) also differ from *Hapigiodes xolotl*; for example, males of *Hapigiodes descimoni* Thiau-

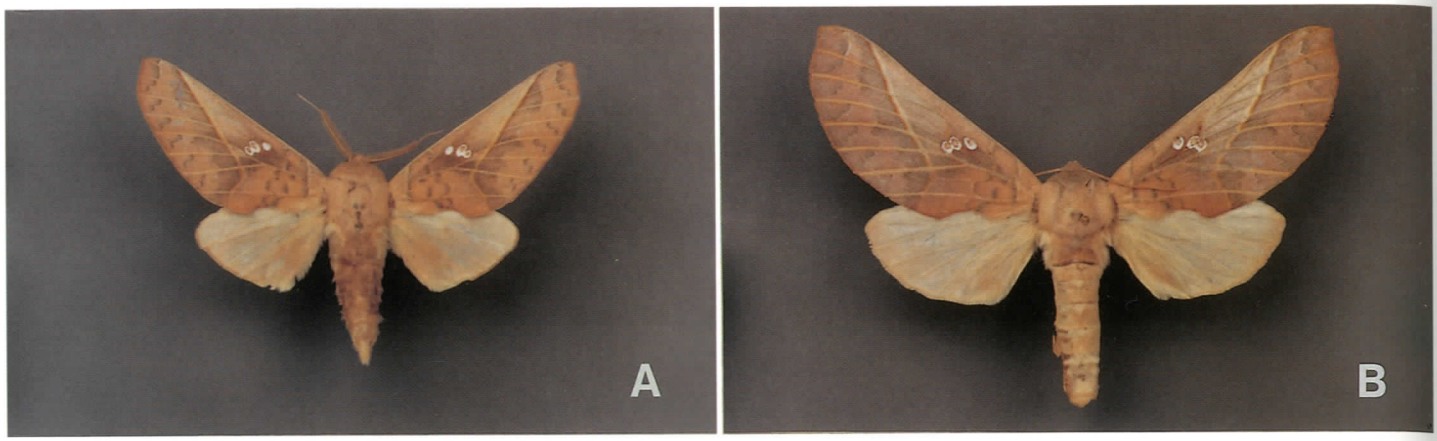


Fig. 2. Adults of *Euhapigiodes hallwachsae*, n. sp., Santa Rosa National Park, Prov. Guanacaste, Costa Rica: A) holotype ♂ (collected at light, D. H. Janzen & W. Hallwachs, 300m, July 1984, INBio). B) paratype ♀ (collected at light, D. H. Janzen & W. Hallwachs, 11 Jan 1996, INBio).

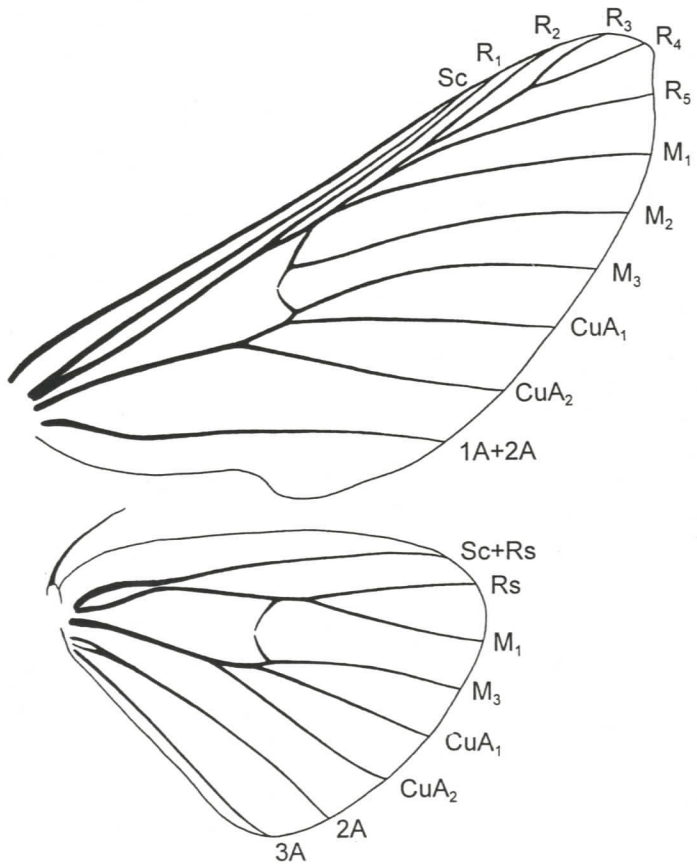


Fig. 3. Wing venation of *Euhapigiodes hallwachsae* n. sp., ♂ (slide #JSM-804). Symbols: A = anal vein; CuA = cubital vein; M = medial vein; R = radial vein; Rs = radial sector; Sc = subcostal vein.

court from Ecuador and Peru have genitalia (Fig. 16A-B) more similar to those of *Colax apulus* Cramer (pers. observ.), a large notodontid with superficial resemblance to *Hapigia* (Fig. 13) and here placed with it in the Hapigiini.

Resolving the species composition of *Hapigiodes* and related genera is beyond the scope of this paper. Nevertheless, we attempt to provide a framework for future systematic work. After describing the two Costa Rican notodontids, we outline the boundaries of the new tribe Hapigiini, placing it in the subfamily Heterocampinae. We also provide a preliminary list of diagnostic characters for the tribe. It is our hope that by doing these things, we will encourage future systematists to focus on what is clearly a fascinating problem.

We use standard sources for morphological terminology. Adult morphology and wing pattern nomenclature are according to Forbes (1954). Larval chaetotaxy follows Hinton (1946). Pupal morphology follows Mosher (1916).

EUHAPIGIODES Franclemont & Miller, new genus

Diagnosis.– Adult moths in this genus, so far known to include only the new species *E. hallwachsae*, can be distinguished from other Hapigiini by the generally yellowish brown color and gray-brown wing markings. The forewing postmedial (pm) line is distinctive in having the portion above the posterior bend running at a steep oblique angle toward the apex (Fig. 2). This portion also forms a fairly straight line, rather than being convex as in other hapigiine species where a pm line occurs (Fig. 8, 12-13). The male and female genitalia (Fig. 5) show features unique among the Hapigiini we have examined, examples being the lateral processes on segment A8 of the female, and the long, dentate dorsal processes at the base of the transtilla in males. Based on the hapigiine larvae so far known (Fig. 14-15), the caterpillar of *Euhapigiodes* bears close superficial resemblance to *Hapigia* in having pinkish stripes on the head, prothoracic plate and lateral line (Fig. 14A-B,E-G, 15A). Although there are numerous differences in primary setal characters between *Euhapigiodes* and *Hapigiodes* (compare Fig. 6, 10), we have not made detailed comparisons of setal patterns among other hapigiine larvae, and therefore cannot yet offer diagnostic traits for caterpillars of *Euhapigiodes*.

Description.– MALE.– *Head*: slightly retracted; eyes naked; a conspicuous, spreading tuft of long, hairlike scales partially covering eye, arising laterally, tuft half the width of eye; labial palpi relatively short, porrect, segment 2 the longest, scales below forming a sharp ventral ridge, segment 3 small and round; haustellum well developed; front clothed with a tight mass of narrowly spatulate scales, except a narrow scaleless region near clypeus; scales of front meeting apices of palpi to form a small tuft; antennae broadly pectinate for basal four fifths, terminal fifth simple; scape with a small, triangular ventral tuft; ocelli inconspicuous but present. *Thorax*: densely clothed with hairlike scales; tibial spurs in

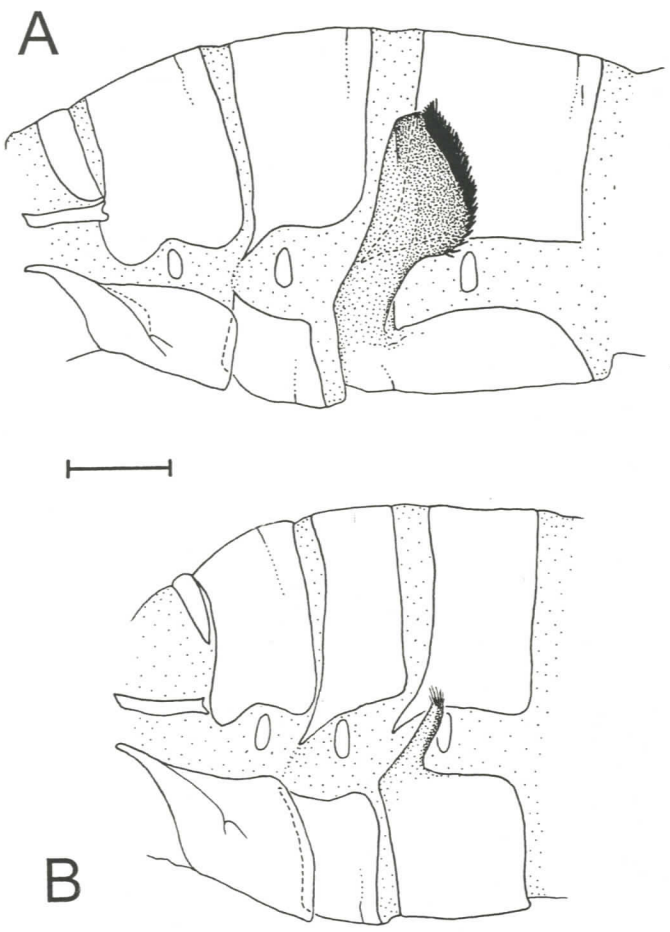


Fig. 4. Adult ♂ abdominal segments 1-4 in lateral view (anterior at left), showing the cteniophore on sternum 4: A) *Hapigia raatzi* Möschler. B) *Euhapigiodes hallwachsae* n. sp. Scale line = 2mm.

the formula 0-2-4; epiphysis broad, slightly shorter than tibia; a prominent triangular tuft immediately behind collar arising from base of each tegula, these tufts erect when the moth is at rest; tegulae covered with long, hairlike scales. *Wings* (Fig. 2A, 3): forewing with accessory cell absent, R_{2-5} stalked, M_1 short-stalked with Rs; FW posterior margin excavated half way out, forming a blunt tooth beyond excavation; outer margin convex, with a slight excavation near apex. Hindwing with Sc and Rs touching near basal third of cell, then separate; vein M_2 absent. *Abdomen*: clothed with hairlike scales; a small cteniophore present on anterior margin of segment 4, composed of a relatively short lobe (Fig. 4B), without the coarse spines typical of *Hapigia* and others (Fig. 4A); an inconspicuous caudal tuft. *Genitalia* (Fig. 5A-D): anterior margin of sternum 8 without apophyses, posterior margin sclerotized, with a U-shaped medial excavation and bifurcate lateral processes; uncus and socii short; valve broad, lower margin of costa expanded inward almost to sacculus to form a wide, sclerotized plate bearing short teeth along ventral margin, valve apex denticulate; transtilla with a pair of large, dentate dorsal processes; juxta strongly sclerotized; aedeagus relatively thick, curved; vesica bearing deciduous cornuti, a group of 5-6 large basal cornuti, each with a short, thick stalk leading to three long spines, the apex of each spine club-shaped (Fig. 5D).

FEMALE.– *Head*: as in male, except antennal segments with blunt lobes rather than pectinations. *Thorax*: similar to males, tufts behind collar less pronounced (Fig. 14H). *Wings* (Fig. 2B): broader than in male. *Genitalia* (Fig. 5E): anterior and posterior apophyses long and thin; ostium relatively simple; pleural region of tergum 8 with broad, sclerotized lateral processes; lamella postvaginalis a large triangular plate, bearing a transverse row of setae on posterior margin; ductus bursae greatly elongate, sclerotized only near ostium; ductus seminalis arising from ductus bursae just below ostium; corpus bursae oval-shaped, with a small scobinate signum near middle and a second one distally.

EGG.– Somewhat flattened and slightly ovoid spheres.

FIRST INSTAR LARVA.– *Head*: clypeus and anteclypeus greatly produced. *Thorax*: setae of prothoracic plate on small tubercles; SV setae in the formula 2-2-2. *Abdomen*: dorsal setae on small tubercles; each segment with a horizontal row of 4 setae in the L3 position; A7 and A8 with numerous secondary setae in the SV and V regions; A8 with each D1 seta on a large, sclerotized tubercle.

LAST INSTAR LARVA.– *Head*: setal pattern (Fig. 6C) as in most other Notodontidae (Forbes, 1910; Miller, 1991); labrum deeply notched, anteclypeus deeply cleft in middle. *Thorax* (Fig. 6A): SV setae in the formula 2-2-2; tarsal setae spatulate, with minute longitudinal striations (as in Heterocampinae; see Miller, 1991: fig. 479, 486). *Abdomen* (Fig. 6B): L3 location multisetose on segments A2-A6; SV and V setae multisetose on A7-A9; A8 without a mid-dorsal tubercle.

PUPA.– Generally broad and blunt. *Head*: proximo-lateral angles of proboscis extending to eye-pieces; anterior suture of proboscis arching sharply forward at midline; labial palpus sclerite absent. *Thorax*: caudal margin of mesothorax with a transverse row of striae, separated by raised ridges. *Abdomen*: anterior margin of each moveable segment (A5-A7) with a diffuse row of pits; cremaster (Fig. 7A) lacking setae, with a central series of knoblike processes, these surrounded by a prominent ring of raised striae.

Type species.– *Euhapigiodes hallwachsae* Franclemont & Miller, by present designation.

Euhapigiodes hallwachsae Franclemont & Miller, new sp.

Fig. 2-4B, 5-7A, 14A-B, 14H

Diagnosis.– This is the only species so far known in the genus. Distinguishing characteristics are given in the generic diagnosis.

Description.– MALE (Fig. 2A).– Forewing length: 29-32mm. *Head*: front densely clothed with a mixture of buff and orange-brown scales; labial palpi concolorous; antenna with shaft covered in buff and scattered brown scales, pectinations golden-brown. *Thorax*: clothed with a mixture of buff, orange-brown and a few gray-brown scales; each tuft behind collar with anterior margin gray-brown, the rest uniformly buff and orange-brown; femur and tibia covered with the same scale mixture as thorax; each tarsal segment with buff and brown scales, and a distal buff-colored ring. *Wings*: forewing ground color a mixture of buff and orange-brown scales, scales in discal cell and near postmedial line light gray-brown; veins yellowish-buff; faint gray-brown basal and antemedial lines with a third discontinuous line between them, antemedial line sinuate; three ringlike spots at distal margin of discal cell, each shiny white with fuscous margins, anterior spot separate and more basal, lower two confluent and located along discocellular vein; postmedial line obliquely angled from near apex to vein CuA_2, then bending outward to anal margin, line yellow-buff on inner margin, orange-brown beyond; subterminal line a series of faint gray-brown, S-shaped maculations; fringe golden-brown; ventral surface uniformly yellow-buff. Hindwing uniformly whitish-buff above and below. *Abdomen*: orange-brown to buff above and below; an inconspicuous terminal tuft. *Genitalia* (Fig. 5A-D) as in generic description.

FEMALE (Fig. 2B, 14H).– Forewing length: 37-39mm. *Head*: similar to male. *Thorax*: similar to male, but with a greater preponderance of gray-brown scales; tufts behind collar with anterior margins not as contrasting. *Wings*: dark markings generally less distinct than in male; discal spots larger. *Abdomen*: as in male. *Genitalia* (Fig. 5E): as in generic description.

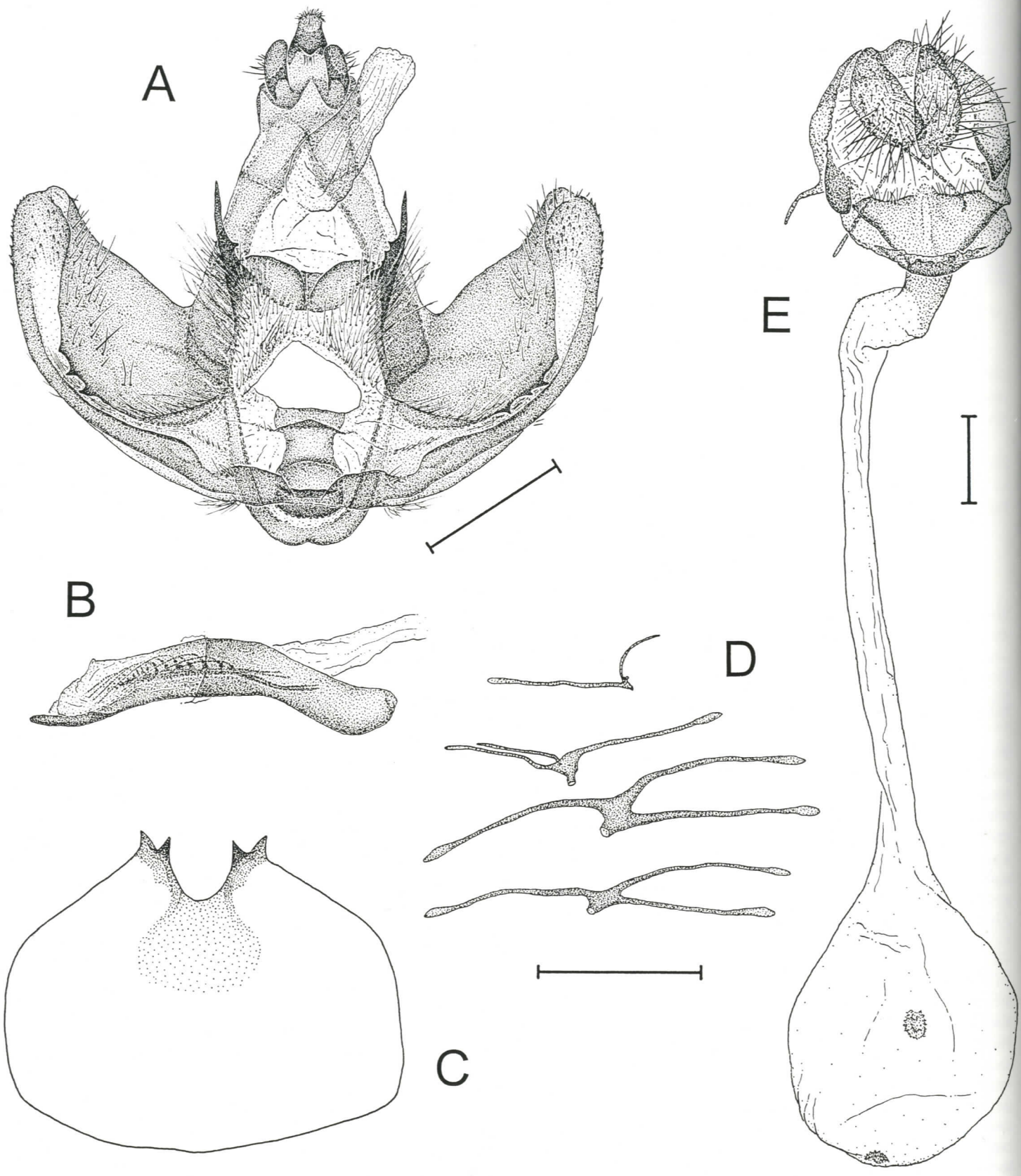


Fig. 5. Genitalia of *Euhapigiodes hallwachsae* n. sp.: A) ♂ genitalia, posterior view (slide #JGF-6809). B) aedeagus, lateral view. C) sternum 8, ventral view. D) deciduous cornuti of the vesica, enlarged. E) ♀ genitalia, ventral view with posterior at top (slide #JGF-7948). Scale lines: A-C, E = 2mm; D = 1mm.

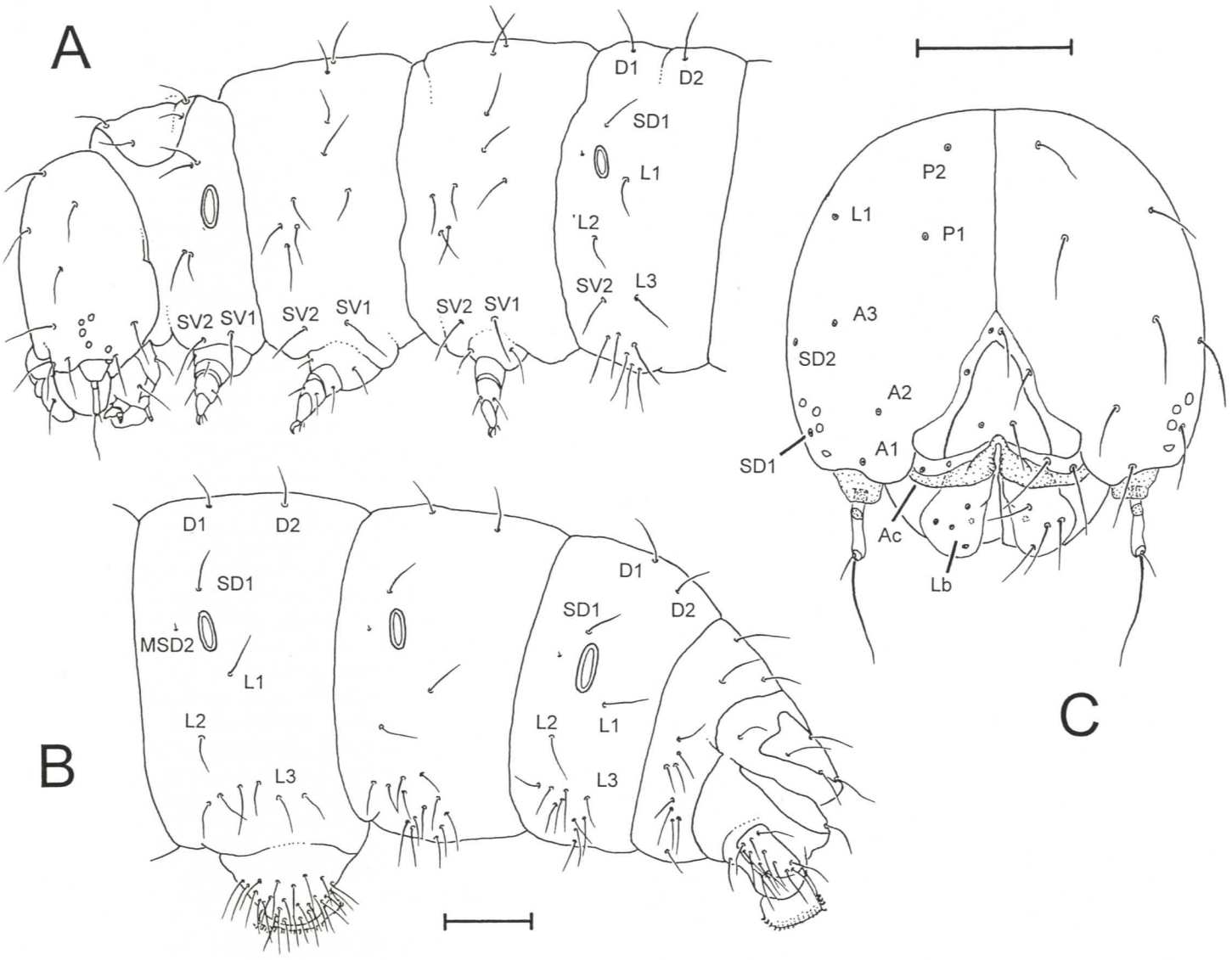


Fig. 6. Last instar larva of *Euhapigiodes hallwachsae* n. sp.: A) Head, thorax and abdominal segment 1, lateral view. B) abdominal segments 6-10, lateral view. C) head, frontal view. Scale lines = 2mm. Symbols: A = anterior seta; Ac = anteclypeus; D = dorsal seta; L = lateral seta; Lb = labrum; MSD = subdorsal proprioceptor seta; P = posterodorsal seta; SD = subdorsal seta; SV = subventral seta.

EGG.– Diameter: 2mm, somewhat flattened and slightly ovoid sphere. Leaf green on upper surface, gray white-green on sides and below, turning from green to purple one day before hatching. First instar emerges 6 days after egg is laid. Eggs glued singly on upper or lower side of leaflets of full-sized leaves.

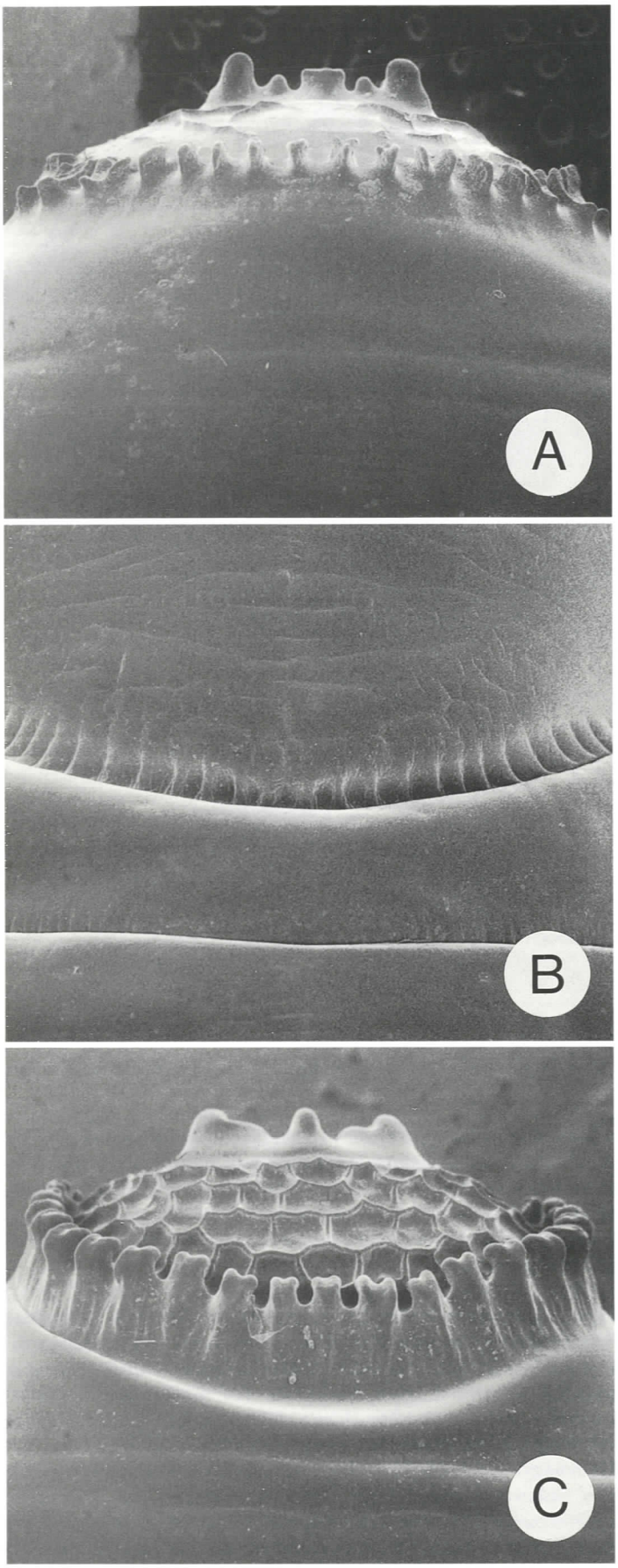
FIRST INSTAR LARVA.– *Head*: width 1.1-1.2mm. Light brown mottled with dark brown. *Thorax*: light yellow-green. *Abdomen*: a longitudinal, lemon yellow lateral stripe passing through spiracular line; region above lateral line with a series of irregular diagonal, yellow lines; a yellow mid-dorsal stripe. Larvae are yellowish upon emergence, becoming leaf green as they fill with their first meal.

LAST INSTAR LARVA (Fig. 6, 14A-B).– *Head*: width approximately 5.5mm; green with a broad stripe extending from antenna to near vertex, stripe pink with buff margins, labrum and surrounding region pink to light brown. *Thorax*: dark lime green above, reticulate blue-green below; lateral stripe extending from spiracle upward to anterior margin of prothoracic plate; a pink transverse stripe along anterior margin of prothoracic plate in front of white stripe. *Abdomen*: dark lime green above, reticulate blue-green below, these two regions separated by a thin lateral stripe passing through lower margin of each spiracle, stripe pink above and white below; thorax and abdomen with a white to buff mid-dorsal, longitudinal stripe, and a series of fainter diagonal lines, each extending from spiracle of one segment to dorso-posterior margin of following segment.

PUPA.– See generic description.

Types.– Holotype male (Fig. 2A): Santa Rosa National Park, Guanacaste Prov. COSTA RICA, July 1984, 300m, D. H. Janzen and W. Hallwachs. Deposited at Instituto Nacional de Biodiversidad (INBio). Paratypes deposited in AMNH (New York), the JGF Collection (in Cornell University Insect Collections, Ithaca, NY), BMNH (London), USNM (Washington), and INBio (San Jose).

Etymology.– This species is named in honor of Winifred Hallwachs, who discovered both *Euhapigiodes hallwachsae* and *Hapigiodes sigifredomarini*, and who has dedicated her life to insuring that the habitat of these moths and thousands of other species survives into perpetuity.



Distribution.– *Euhapigiodes hallwachsae* is known only from the lowland dry forests of Guanacaste Province in northwestern Costa Rica (Fig. 1). Specific collecting sites include: Sector Santa Rosa and Sector El Hacha of the Area de Conservación Guanacaste; Parque Nacional Barra Honda; Parque Nacional Palo Verde; and Carmona. The species has not been encountered elsewhere despite extensive collecting at lights in the remainder of the country by the National Biodiversity Inventory (INBio) and by D. H. Janzen and W. Hallwachs.

Hostplants.– In nature, larvae of *Euhapigiodes hallwachsae* have been found feeding only on *Lonchocarpus costaricensis* and *L. rugosus* (Fabaceae: Papilionoideae) despite the fact that there are 10 other species of *Lonchocarpus* growing in these dry forest habitats (Janzen and Liesner, 1980). Over 100 species of *Lonchocarpus* are known worldwide (Gentry, 1993). In captivity, the larvae will readily eat the leaves of *Lonchocarpus minimiflorus*, *Lonchocarpus orotinus* and *Lonchocarpus phlebophyllus*, appearing to grow even more rapidly on them than on *Lonchocarpus costaricensis* or *Lonchocarpus rugosus*. The larvae rejected *Lonchocarpus acuminatus*. All of these tree species are common where *Euhapigiodes hallwachsae* occurs, and four additional species grow in the periphery of the moth's known distribution. These have not been offered to the larvae. Given the intense search for large caterpillars that has occurred in this forest (1,965 individual caterpillar captures on *Lonchocarpus* spp.), it is likely that *Euhapigiodes hallwachsae* is restricted to *Lonchocarpus costaricensis* and *L. rugosus*.

Lonchocarpus costaricensis is found in dry northwestern Costa Rica and dry western Nicaragua (N. Zamora, pers. comm.). Although moth collections from this region of Nicaragua are lacking, it may well turn out that *Euhapigiodes hallwachsae* occurs there.

Biology.– Adults come frequently to lights, with females appearing in the first 2-4 hours after sunset (at which time they are flying to oviposit) and males appearing between about 10pm (2200h) and 2am (0200h), at which time they are apparently searching for newly-eclosed females. There is no indication that moths of either sex visit flowers at night or day. *Euhapigiodes hallwachsae* was not captured by early collectors of Costa Rican moths (e.g., William Schaus), probably because these collectors did not visit the northwestern part of Costa Rica, which was remote until the construction of the Interamerican Highway in the 1940's.

Based on collections of moths from lights placed in the forest and on forest edges, *Euhapigiodes hallwachsae* co-occurs with a typical Costa Rican dry forest fauna of large notodontids. Other Hapigiini with which it flies include *Hapigia repandens* Schaus, *Hapigia simplex* Walker, *Antaea lichyi* Franclemont, *Antaea licormas* Cramer, *Chliara croesus* Cramer, *Colax apulus* Cramer and *Hapigiodes sigifredomarini*. Caterpillars of all these feed on the leaves of various fabaceous shrubs and trees in this forest (see Discussion and Table 4; see also Janzen 1988, 1993).

The life history of *Euhapigiodes hallwachsae* has been studied only in the dry forests of the eastern end of Sector Santa Rosa (200-300m elevation) of the Area de Conservación Guanacaste, which straddles the Interamerican Highway in northwestern Costa Rica. The first larvae appear in the second half of May during the first 1-2 weeks after the rainy season begins. Second-generation larvae appear on foliage in August-September (3rd to 4th month of the rainy season), and occasionally there is a third generation in December-January. Apparently the second-generation pupae remain dormant in the litter throughout the dry season (December to early May). Far more larvae are present during the first

Fig. 7. Scanning electron micrographs of hapigiine pupae: A) *Euhapigiodes hallwachsae* n. sp., terminal segments in dorsal view showing cremaster (26X). B) *Hapigiodes sigifredomarini* n. sp., dorsal view showing junction of the meso- and metathorax (23X). C) *Hapigiodes sigifredomarini* n. sp. cremaster, dorsal view (25X).

generation than in subsequent generations. Caterpillars of *Euhapigiodes hallwachsae* have not yet been abundant enough to defoliate their hosts (e.g., see Janzen, 1988), but they are annually present in low and highly variable numbers. There is no hint that they breed elsewhere and invade the Santa Rosa forest.

Eggs have been found only on new, but full-sized *Lonchocarpus* leaves. As with most notodontid larvae (Godfrey et al., 1989), first instars feed near the middle of the leaf while later instars feed at the leaf margin. In *Euhapigiodes hallwachsae*, first instar caterpillars eat 1mm diameter holes through the leaflet and later instars eat large bays from the margin of the leaflet blade, usually starting at the tip on one side of the midrib. The caterpillars consume leaflets of all ages and perch on the leaf midrib on the underside when not feeding. Larvae use approximately 20 days to attain the prepupal stage.

Prepupae drop out of the tree crown or crawl down to the litter and pupate in a soil-surface chamber made by pushing litter to the sides of a small space. There is no cocoon, and the larva does not burrow deeply into the soil. The pupal stage lasts 18-20 days in the rainy season, or 5-6 months for pupae that remain dormant during the long dry season. Adults eclose 1-2 hours after sunset, and climb 20-100cm above the ground to harden their wings. Males then fly off. Staying at the place where her wings hardened, the female mates between 10pm (2200h) and 2am (0200h) with a single male, who leaves her within an hour of mating. She begins oviposition the next evening shortly after dark. Confined to an empty plastic bag, she lays 10-20% of her eggs each night until she dies after about 10 nights, usually with the abdomen empty of eggs. In captivity, eggs are glued singly to the sides of the plastic bag and laid without requiring any larval food plant stimulus. A large female contains 200-300 eggs.

HAPIGIODES Dyar, 1911

Hapigiodes Dyar, 1911:259
Hapidiodes Nijhout, 1978:132, missp.

Diagnosis.– Dyar (1911) distinguished this genus from *Pseudhapigia* Schaus by having "veins 3 and 4 of hind wings apart and the antennae pectinated on the basal two-thirds only." Our own study suggests that the configuration of hind wing veins 3 and 4 (equivalent to CuA_1 and M_3) is identical in these two genera. The remaining trait seems to hold true. The male antennae in *Pseudhapigia brunnea* Schaus (from Mexico and Arizona) are pectinate almost to the end, while in *Hapigiodes* the terminal 30 or more segments are simple. According to Draudt (1933), forewing vein M_1 is more clearly separated from Rs in *Hapigiodes* than in *Pseudhapigia*. Dyar noted that *Hapigiodes* would key out to *Colax* Hübner in Schaus' (1901) key to American notodontid genera, but the two genera are easily separated; *Colax* species are extremely large (FW length approximately 40-50mm) and they have a concave rather than convex outer margin near the forewing apex (Fig. 13).

Adults of *Hapigiodes* can be distinguished from *Euhapigiodes* by the absence of a cteniophore in males, and by having the postmedial line arching outward rather than being straight (compare Fig. 2, 8). Genitalic differences are numerous (see descriptions and figures). The sinuate shiny white marking of the forewing apex, characteristic of many Hapigiini (Fig. 12-13), is present in *Hapigiodes* but absent in *Euhapigiodes*. Caterpillars of *Hapigiodes* and *Euhapigiodes* differ in a suite of characters (compare Fig. 6, 10). The most obvious include: Thoracic SV setae 2-1-1 in *Hapigiodes*, 2-2-2 in *Euhapigiodes*; *Hapigiodes* with a mid-dorsal protuberance on A8, absent in *Euhapigiodes*.

Below we present a redescription for *Hapigiodes* based on examination of adults of *Hapigiodes xolotl* and *Hapigiodes sigifredomarini*, and immatures of *Hapigiodes sigifredomarini*.

Description.– MALE.– *Head*: generally similar to *Euhapigiodes*; slightly retracted; eyes naked; a relatively small spreading tuft covering lateral portion of eye, tuft one fourth the width of eye; labial palpi porrect, segment 1 short, segment 2 large and laterally compressed, segment 3 small and round; vertex and front clothed with spatulate scales, except a scaleless patch from clypeus to near middle of frons; antennae pectinate for basal two thirds, simple beyond; base of antenna with small, inconspicuous tufts above and below; ocelli very small. *Thorax*: vestiture similar to *Euhapigiodes*; conical tuft at base of tegula small, not prominent; tegula covered with hairlike scales. *Wings* (Fig. 8A-C): venation as in *Euhapigiodes*; other features similar except forewings generally broader, outer margin more convex with a slight excavation near apex; posterior margin excavated half way out to form a blunt "tooth"; a small, sinuate silver mark present near apex. Hindwing as in *Euhapigiodes*. *Abdomen*: cteniophore absent; a small, pointed caudal tuft. *Genitalia* (Fig. 9A–D, 11A–C, 16C-D): anterior margin of sternum 8 with a shallow excavation, posterior margin with a deep, sclerotized notch; uncus short and broad, socii narrow; valve broad, costa expanded outward, apex membranous; distum of valve with a broad, sclerotized denticulate plate, expanded ventro-laterally; lower margin of transtilla dentate; juxta very wide, with a cup-shaped lower portion, a transverse fold, and a wide upper portion; aedeagus dorso-ventrally compressed, base rounded, apex with two sclerotized prongs; vesica bearing deciduous cornuti, a set of basal cornuti, each with a short, thick stalk leading to three long, curved spines, their apices acute (Fig. 9D).

FEMALE.– *Head*: similar to male; antennal pectinations somewhat shorter. *Thorax*: similar to males; tuft behind collar slightly smaller. *Wings*: as in male, except forewing broader and outer margin more convex (Fig. 8B). *Abdomen*: wider than in male. *Genitalia*: (Fig. 9E, 11D) generally as in other Hapigiini (Table 3); anterior apophysis relatively short, posterior apophysis extremely long and thin; ostium complex, comprising two broad sclerites with antlerlike processes along outer margins, upper plate with a deep medial notch; ductus bursae and corpus bursae similar to *Euhapigiodes*.

EGG.– As in *Euhapigiodes*, a somewhat flattened and slightly ovoid sphere.

FIRST INSTAR LARVA.– As in *Euhapigiodes*, except SV setae in the formula 2-1-1, and only a single seta in the L3 position on abdominal segments.

LAST INSTAR LARVA.– *Head*: without dorso-ventral stripes (Fig. 14D). *Thorax*: SV setae in the formula 2-1-1 (Fig. 10A); tarsal setae similar to Heterocampinae. *Abdomen*: extra anterior L seta on A2–A6 (typical of most Notodontidae) absent; a small, mid-dorsal tubercle present on A8 (Fig. 10B, 14C).

PUPA.– Similar to *Euhapigiodes*, but differing by the characters listed in the description of *H. sigifredomarini* (below).

Type species.– *Hapigia xolotl* Schaus (1892:339), original designation by Dyar (1911).

Distribution.– Our male genitalia dissections confirm that *H. xolotl*, *H. sigifredomarini*, and *Pseudhapigia misericordia* Dyar are congeneric (Fig. 9A–D, 11A–C, 16C-D). Other so-called *Hapigiodes* from South America (Fig. 16A-B) are of doubtful placement, leading us to believe that when delimited through

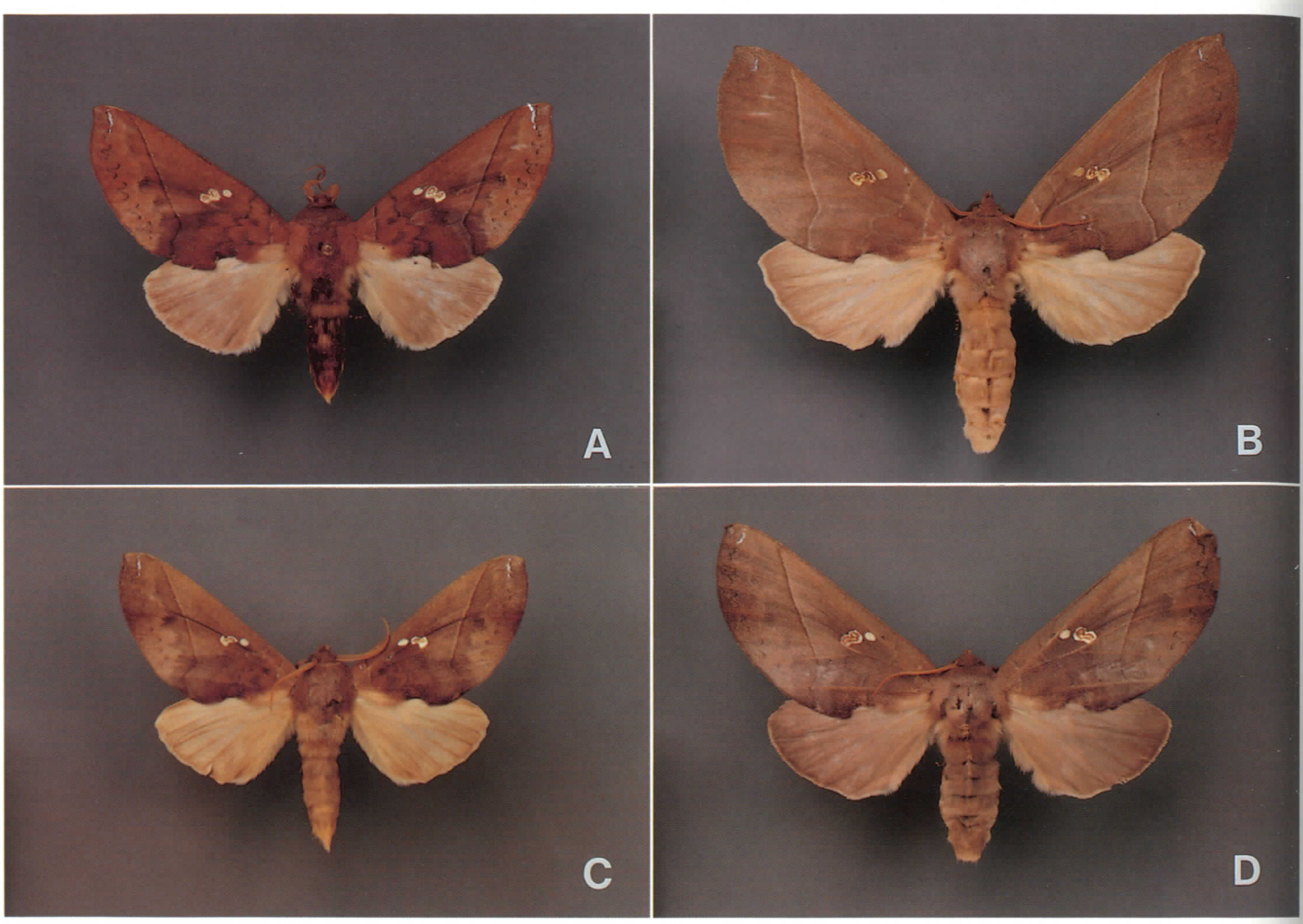


Fig. 8. Adults of *Hapigiodes sigifredomarini* n. sp., Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (voucher numbers refer to Janzen and Hallwachs rearing record database): A) holotype ♂ (collected at light, D. H. Janzen & W. Hallwachs, 25-29 July 1981, INBio). B) ♀ (90-SRNP-1533, eclosed 6 Aug 1990, host *Lonchocarpus minimiflorus*). C) ♂ (90-SRNP-1541, eclosed 31 Aug 1990, host *Lonchocarpus minimiflorus*). D) ♀ (95-SRNP-4515, eclosed 26 June 1995, host *Lonchocarpus costaricensis*).

more intense study, *Hapigiodes* will be restricted to Mexico and Central America.

Hapigiodes xolotl has been captured in dry forest at the Chamela Biological Station (Ceballos and García, 1995) in Colima, western Mexico (A. Pescador, pers. com.), and specimens of *Hapigiodes sigifredomarini* are known from as far south as Corcovado on the Osa Peninsula of Costa Rica (collections in INBio). Although we have seen no specimens, species of *Hapigiodes* related to *H. xolotl* almost certainly occur in Panama.

Biology.– See description of *Hapigiodes sigifredomarini* to follow, the only species of this genus reared to date.

Hapigiodes sigifredomarini Franclemont & Miller, new sp.

Fig. 7B-C, 8-10, 14C-D

Diagnosis.– *Hapigiodes sigifredomarini* is extremely similar to *Hapigiodes xolotl*. Males are difficult to separate based on wing pattern. However, in *H. sigifredomarini* the body and forewings are generally darker and the wing markings more distinct. Although our sample size is small, it also appears that *H.sigifredomarini* is somewhat smaller than *H. xolotl*; forewing length of the latter is 28-29mm (2 AMNH males). Females of the two species are easier to distinguish. In *H. sigifredomarini*, the female forewing tends to be gray and that of males is reddish brown (Fig. 8), while in *H. xolotl* both sexes are reddish brown. Another character useful for separating females is in the antennae; *H. sigifredomarini* has pectinations almost as long as those of males, while in *H. xolotl* the pectinations are very short. The most clear-cut features for distinguishing the two species are found in the male and female genitalia (see description below and Figs. 9, 10).

Description.– MALE (Fig. 8A, 8C).– Forewing length: 24–28mm. *Head*: clothed with gray-brown or slightly reddish gray-brown scales; labial palpi with a few scattered white scales; scape of antenna with some white scales, shaft with a dorsal covering of white scales and brown scales along lateral margins. *Thorax*: collar light gray to reddish gray-brown, dorsum light gray, tegula clothed with light reddish brown, hairlike scales; pleural and ventral regions buff to reddish brown; femur and tibia concolorous with tegula, a few scattered white scales; each tarsal segment dark brown with white scales in a distal ring and on ventral surface. *Wings*: forewing ground color mostly an uneven dark brown, outer fifth reddish brown from below M_3 to apex, whitish brown from M_3 to lower angle; basal line straight, composed of a white inner line and a dark brown outer one; antemedial line sinuate, poorly defined, composed of a dark gray-brown inner line and sometimes a whitish outer

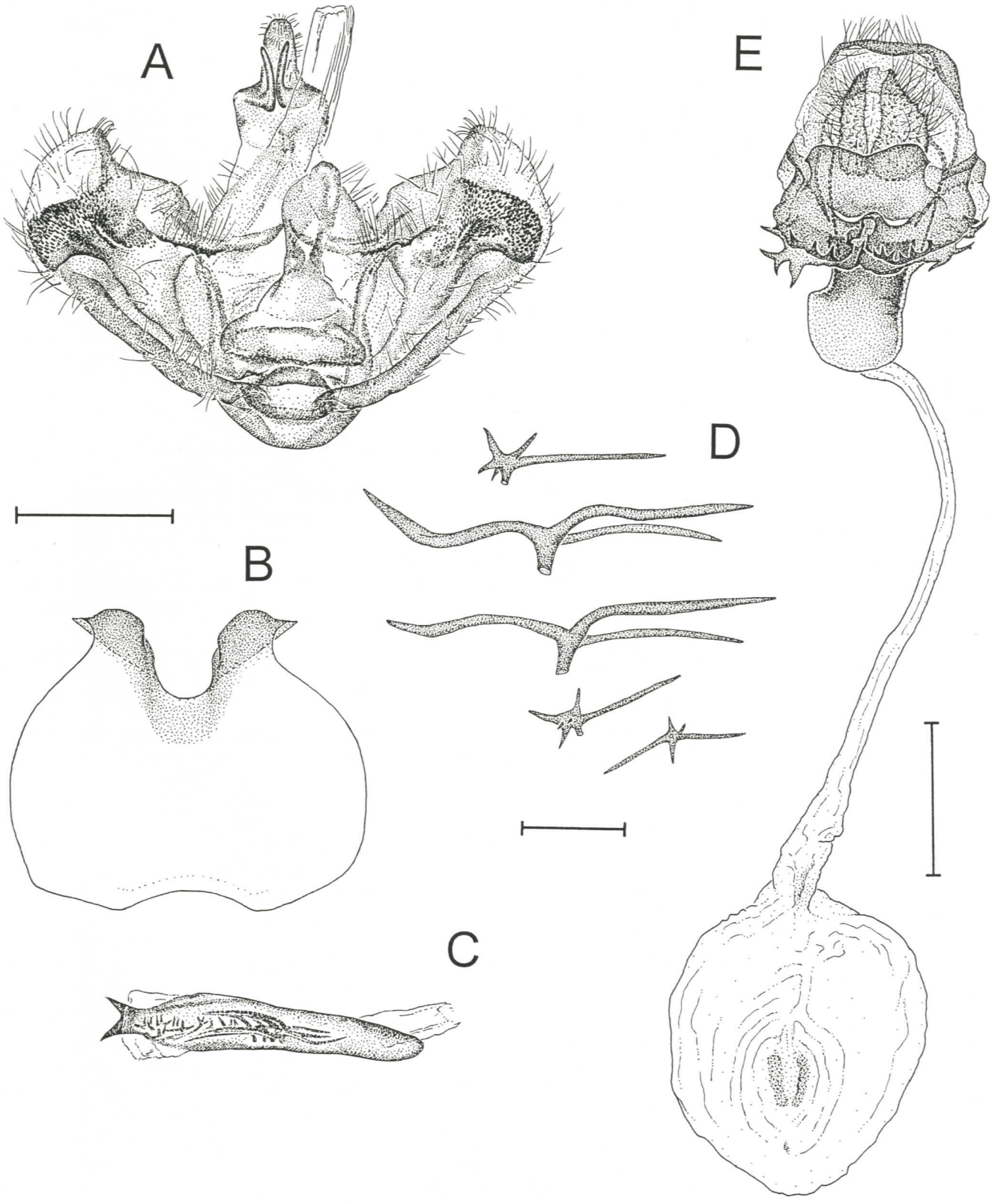


Fig. 9. Genitalia of *Hapigiodes sigifredomarini* n. sp.: A) ♂ genitalia, posterior view (slide #JGF-6808). B) sternum 8, ventral view. C) aedeagus, lateral view. D) deciduous cornuti of the vesica, enlarged. E) ♀ genitalia, ventral view with posterior at top (slide #JSM-801). Scale lines: A-C, E = 2mm; D = 0.5mm.

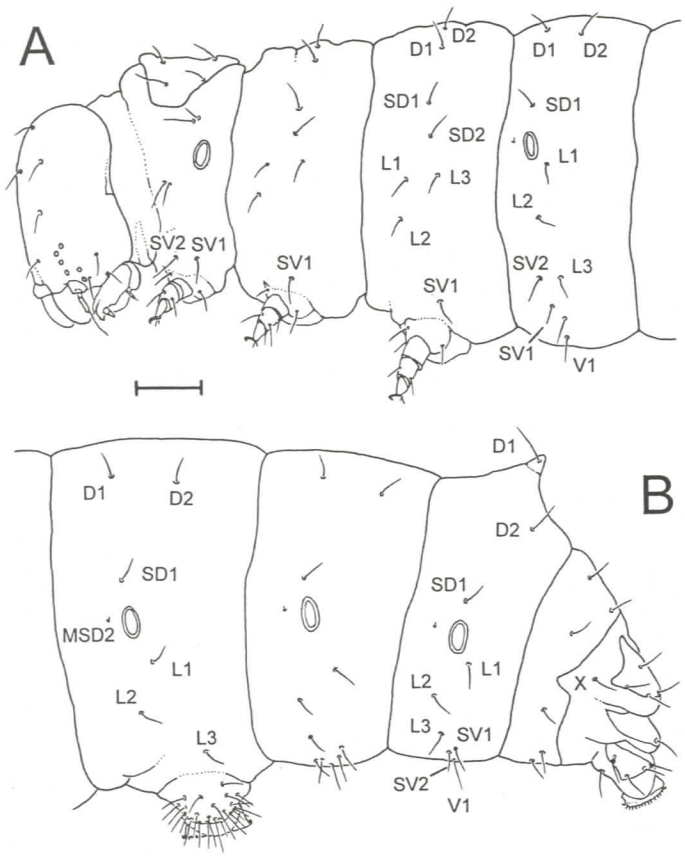


Fig. 10. Last instar larva of *Hapigiodes sigifredomarini* n. sp.: A) Head, thorax and abdominal segment 1, lateral view. B) abdominal segments 6-10, lateral view. Scale line = 2mm. For key to symbols see Fig. 6.

one; location and color of three discal spots as in *Euhapigiodes hallwachsae*, except all slightly smaller and white scales of each ring shinier, anterior ring sometimes fused with others; postmedial line similar to *E. hallwachsae*, but not as obliquely angled and line slightly convex rather than straight; pm line composed of a buff-colored inner line and a dark greenish-brown outer one; subterminal line a series of dark brown, S-shaped maculations; a sinuate, shiny white marking near apex; fringe golden brown; ventral surface buff to light brown, with contrasting dark brown fringe. Hindwing ground color yellow-buff to light gray-brown, with scattered brown scales; ventral surface uniformly light buff. *Abdomen*: each segment with base covered in short, silvery gray scales, and posterior margin with long, gray hairlike scales; dorsum of A1 slightly darker. *Genitalia* (Fig. 9A–D): sclerotized posterior notch of sternum 8 slightly constricted rather than U-shaped as in *H. xolotl* (Fig. 11C), notch narrower; costa of valve with irregular upper margin, costa wider and rounded outward in *H. xolotl* (Fig. 11A); broad spiculate process of valve with raised lobe located medially in *H. sigifredomarini*, rather than on upper margin as in *H. xolotl*; aedeagus in lateral view with a very slight curve in *H. sigifredomarini*, a more pronounced curve in *H. xolotl*.

FEMALE (Fig. 8B, 8D).– Forewing length: 29–36mm. Females are variable, but tend to be almost completely gray, including the fore and hind wings; there is little of the reddish color found in males. *Head*: similar to male, but scales light gray to gray, occasionally a slight reddish tint. *Thorax*: completely gray except disc, which is light gray. *Wings*: forewing ground color uneven gray, outer fifth lighter gray, sometimes with a faint reddish brown tint in upper portion; markings less distinct than in male; ventral surface uniformly gray. Hindwing mostly gray, covered with shiny hairlike scales; ventral surface light gray. *Abdomen*: covered with light gray scales. *Genitalia* (Fig. 9E): similar to *xolotl* (Fig. 11D), except lower sclerite of ostium with projections more acute, ductus bursae with a sharp bend near base, and a single large signum rather than a large one and a second small one.

EGG.– Similar in shape and color to *Euhapigiodes hallwachsae*, but about 1.8mm diameter.

FIRST INSTAR LARVA.– See description for *Hapigiodes*.

LAST INSTAR LARVA (Fig. 10, 14C-D).– *Head*: width approximately 5.5mm; dark green to blue-green; labrum brownish; mandibles yellow-brown. *Thorax*: whitish green above, darker lime green below; white lateral stripe extending from below spiracle and curving upward to form a wide, white transverse stripe along anterior margin of prothoracic plate; T1 spiracle with margin pink. *Abdomen*: light whitish green above, darker lime green below, these two regions separated by a thin lateral stripe passing through the lower margin of each spiracle, stripe dark green above and white below; ventral margins of T2–A4 spiracles pink; thorax and abdomen with a white, mid-dorsal longitudinal stripe, and a series of faint, whitish-green diagonal lines, each extending from just above spiracle of one segment to near dorso-posterior margin of following segment.

PUPA.– *Head*: as in *Euhapigiodes*, except front with a small, blunt protuberance between eyes. *Thorax*: similar to *Euhapigiodes*, a transverse row of striae along caudal margin of mesothorax (Fig. 7B). *Abdomen*: as in *Euhapigiodes*, but cremaster (Fig. 7C) with dorsal semicircle of raised striae and knoblike central processes much larger; a highly reticulate area between semicircle and central processes (only slightly crenulate in *Euhapigiodes*).

Types.– Holotype male (Fig. 8A): Santa Rosa National Park, Guanacaste Prov., COSTA RICA, 25-29 Jul 1981, D. H. Janzen & W. Hallwachs. Deposited at Instituto Nacional de Biodiversidad (INBio). Paratypes (all from Area de Conservación Guanacaste) deposited in AMNH (new York), the JGF Collection (in Cornell University Insect Collections, Ithaca, NY), BMNH (London), USNM (Washington), and INBio (San Jose).

Etymology.– This species is named in honor of Sr. Sigifredo Marín Zuñiga, the Director of the Area de Conservación Guanacaste, in recognition of more than two decades of diligent and enthusiastic effort by him and his family to construct a permanent system of conserved wildlands for the country of Costa Rica.

Distribution.– We have made genitalia dissections for a series of INBio specimens from different Costa Rican localities. These include examples ranging from the southern Pacific coast (Corcovado, Osa Peninsula) to the northern Atlantic region (Tortuguero) and the dry northwest. Although there is some variation in genitalic morphology, all appear to be *H. sigifredomarini*. As far as we are able to determine, there have been no true *H. xolotl* collected in Costa Rica. Much more material would be required, including specimens from Panama, Nicaragua and other Central American countries, in order to fully document the distributions of *H. sigifredomarini*, *H. xolotl* and other *Hapigiodes* species.

Hostplants.– This species has a broader diet breadth within *Lonchocarpus* than does *Euhapigiodes hallwachsae*; *Hapigiodes sigifredomarini* has been recorded from six *Lonchocarpus* species, whereas *Euhapigiodes hallwachsae* has been found only on *Lonchocarpus costaricensis* and *L. rugosus* (Table 4).

Biology.– In the Santa Rosa dry forests of the Area de Conservación Guanacaste, the biology of *Hapigiodes sigifredomarini* as known to date (Janzen and Hallwachs, 1997) is essentially identical to that described earlier for *Euhapigiodes hallwachsae*,

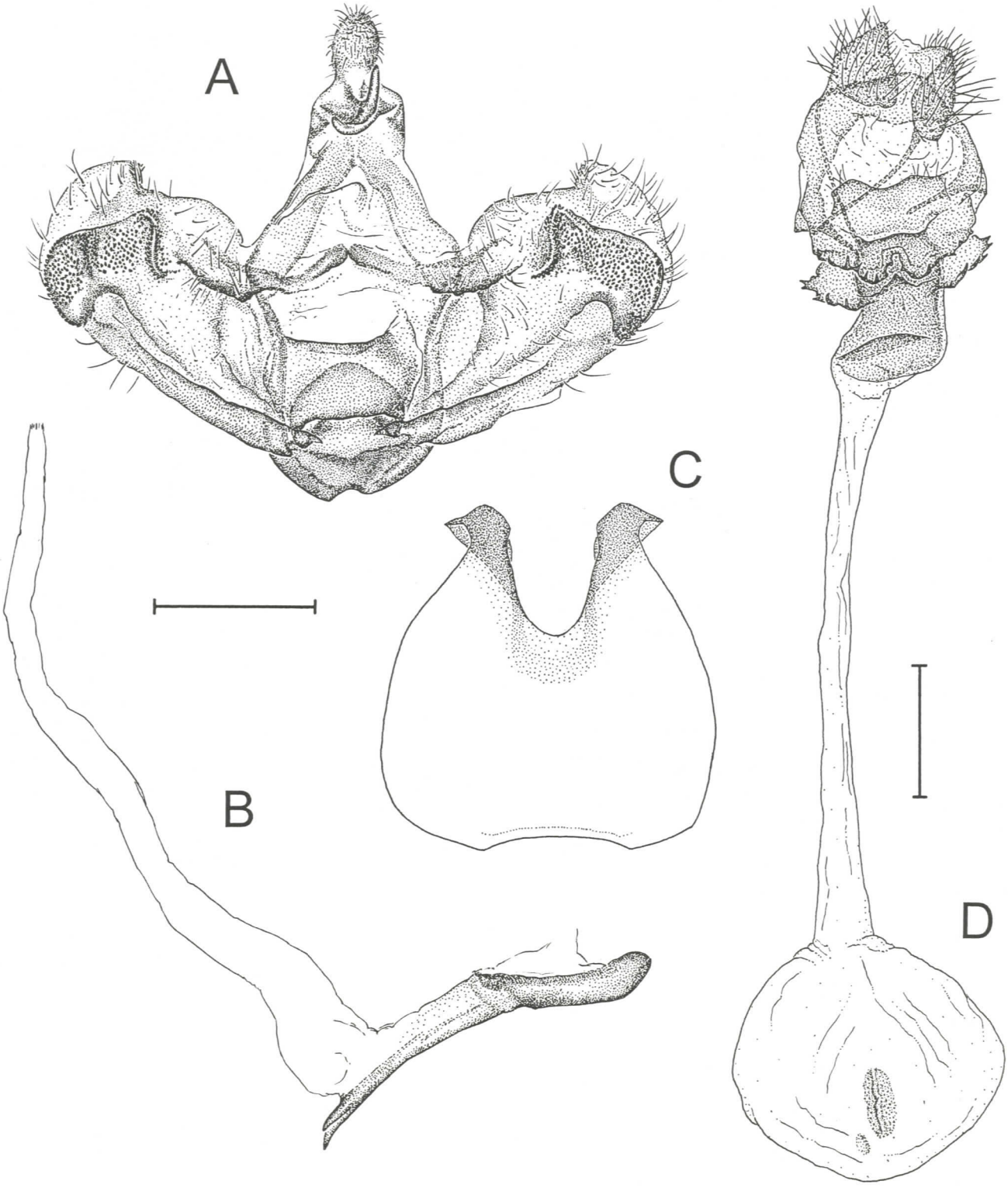


Fig. 11. Genitalia of *Hapigiodes xolotl* Schaus: A) ♂ genitalia (USNM slide # 42,602; Morelos, Mexico), posterior view. B) sternum 8, ventral view. C) aedeagus, lateral view with vesica everted. D) ♀ genitalia of *Hapigiodes xolotl* holotype (USNM slide #42603; Coatepec, Mexico), ventral view with posterior at top. Scale lines = 2mm.

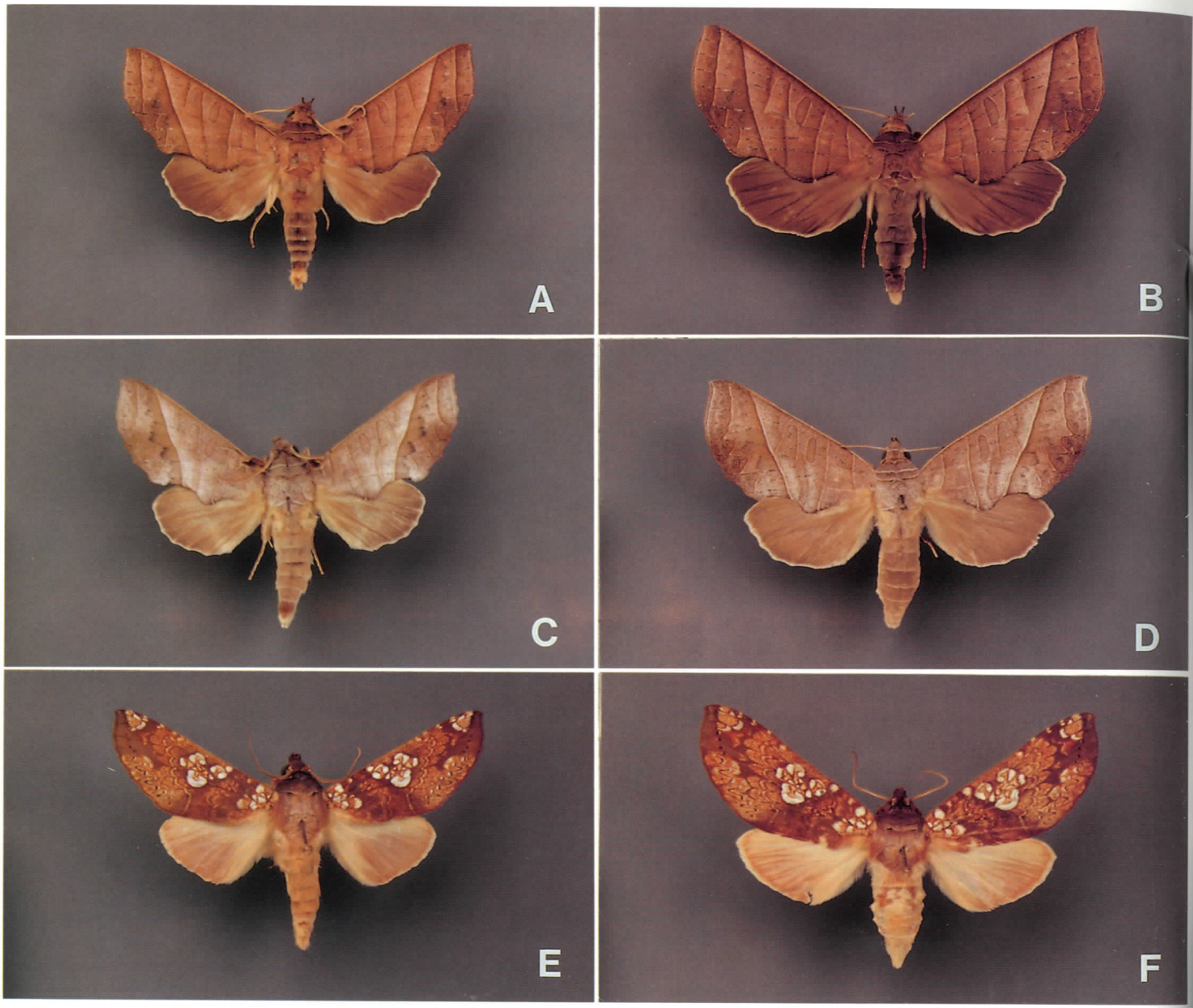


Fig. 12. Adult Hapigiini from Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (voucher numbers refer to Janzen and Hallwachs rearing record database): A) ♂ of *Antaea lichyi* Franclemont (84-SRNP-1323, eclosed 23 July 1984, host *Machaerium acuminatum*). B) ♀ of *Antaea lichyi* Franclemont (95-SRNP-9006, eclosed 5 Oct 1995, host *Machaerium acuminatum*). C) ♂ of *Antaea licormas* Cramer (91-SRNP-1428, eclosed 29 July 1991, host *Machaerium biovulatum*). D) ♀ of *Antaea licormas* Cramer (82-SRNP-314.1, eclosed 12 Aug 1982, host *Machaerium biovulatum*). E) ♂ of *Chliara croesus* Cramer (93-SRNP-3052, eclosed 17 July 1993, host *Andira inermis*). F) ♀ of *Chliara croesus* Cramer (95-SRNP-6095, eclosed 17 July 1995, host *Andira inermis*).

except for the former's use of more species of *Lonchocarpus* species as larval food plants.

Hapigiodes misericordia (Dyar), new comb.

Fig. 16C-D

Pseudhapigia misericordia Dyar, 1911:258.

Our dissections for this study included a male of *Pseudhapigia misericordia* from Guerrero, Mexico (USNM). Dyar (1911), in his original description, recognized a close relationship between *H. misericordia* and *Hapigiodes xolotl*, but chose nevertheless to place *H. misericordia* in *Pseudhapigia*. The male genitalia (Fig. 16C-D) show that it belongs in the same genus as *Hapigiodes xolotl* (Fig. 11A–C), and we hereby formalize that change.

According to Dyar (1911), *H. misericordia* can be distinguished from *H. xolotl* in being "larger, darker and without silvery scales on the discal marks, which are also further apart and more obliquely placed." Also according to him, "The antennae of the female have shorter pectinations than in *xolotl*." We have not examined enough Mexican material to either confirm or reject these statements, and we have not examined Dyar's USNM holotype of *H. misericordia*.

DISCUSSION

CLASSIFICATION

One of the more difficult problems in the higher classification of the Notodontidae has been the position and composition of the so-called "Hemiceratini" (Miller, 1991). The group was originally

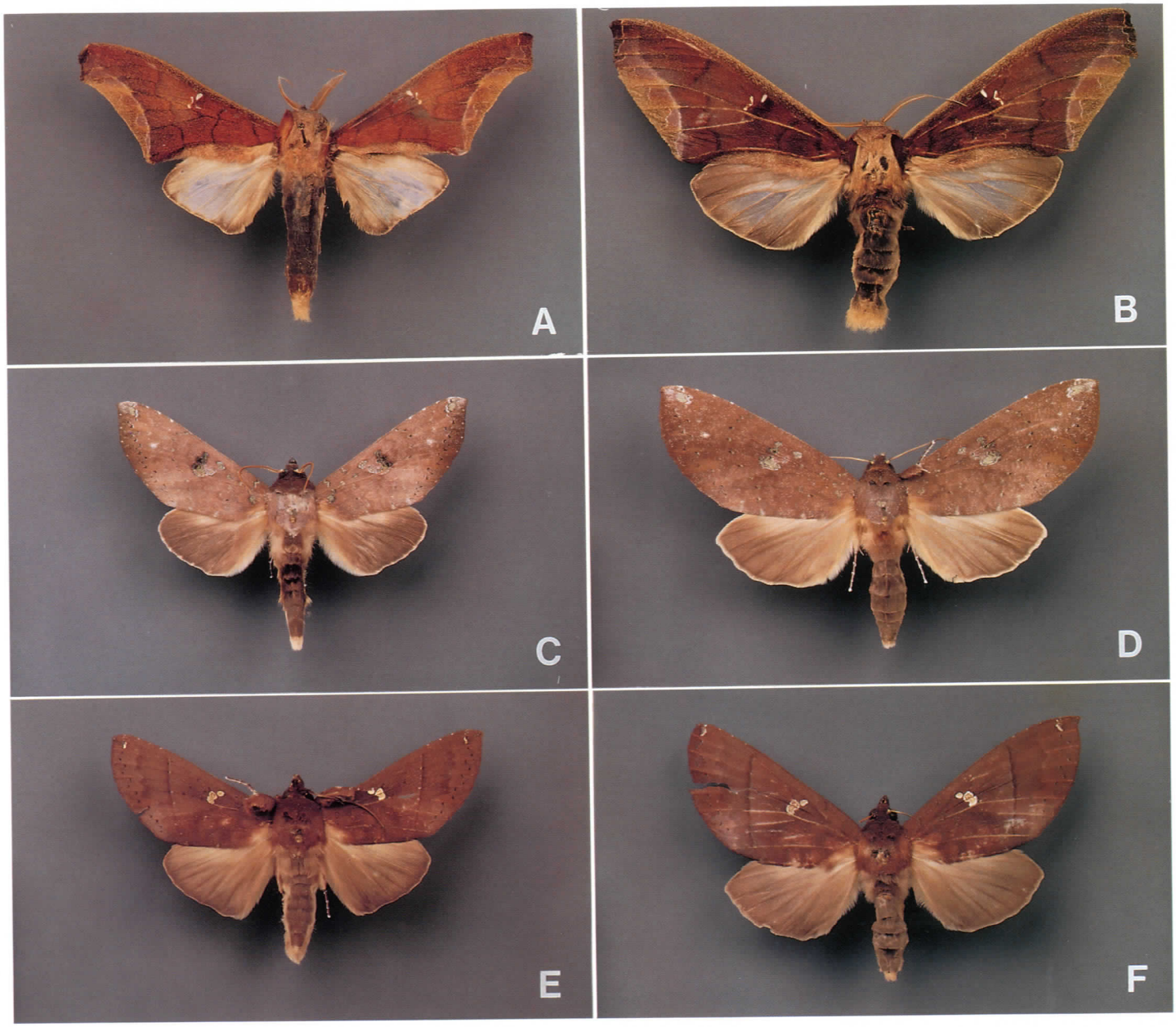


Fig. 13. Adult Hapigiini from Sector Santa Rosa, Area de Conservación Guanacaste, Costa Rica (unless noted otherwise) (voucher numbers refer to Janzen and Hallwachs rearing record database): A) ♂ of *Colax apulus* Cramer (collected at light, G. E. Martinez, Aug 8 1991, between Playa Pirikiki and Playa Chiquita, Prov. Limón, Costa Rica, AMNH). B) ♀ of *Colax apulus* Cramer (93-SRNP-4132, eclosed 6 Sep 1993, host *Pterocarpus rohrii*). C) ♂ of *Hapigia repandens* Schaus (95-SRNP-11236, eclosed 20 Dec 1995, host *Machaerium acuminatum*). D) ♀ of *Hapigia repandens* Schaus (91-SRNP-1552, eclosed 5 Aug 1991, host *Machaerium biovulatum*). E) ♂ of *Hapigia simplex* Walker (93-SRNP-7515, eclosed 29 Nov 1993, host *Inga vera*). F) ♀ of *Hapigia simplex* Walker (93-SRNP-7513, eclosed 29 Nov 1993, host *Inga vera*).

erected by Guenée (1852) to include *Hemiceras* and *Canodia*, both Notodontidae, as well as several genera now removed to the Noctuidae (e.g., *Gonodonta*). Forbes (1939) later expanded the concept by adding neotropical genera characterized by relatively large adult body size, and by the absence of hind wing vein M_2. His tribe Hemiceratini (Table 1) included *Hapigia*, and would almost certainly have included *Hapigiodes* were the genus known from Barro Colorado Island, Panama, the area where Forbes' study was based. It was actually Schaus who laid the groundwork for the Hemiceratini; the taxa separated out at couplet "B.b." in Schaus' (1901) key to the genera of American Notodontidae correspond almost exactly with the hemiceratine genera listed by Forbes. These were distinguished by having M_2 of the hind wing absent, and by lacking a forewing accessory cell (Fig. 3). Miller (1991) questioned monophyly of the Hemiceratini, noting that hind wing vein M_2 has apparently been lost by convergence in at least five notodontid subfamilies. In his attempt to reclassify the major groups of Notodontidae, Miller was unable to find a clear subfamily affiliation for *Hemiceras*, and placed the genus incertae sedis.

Examination of the species described in this paper, especially their immature stages, allows reevaluation of the Hemiceratini. We conclude that *Hapigiodes* and *Euhapigiodes* are not closely related to *Hemiceras* but instead belong, along with *Hapigia*,

TABLE 1. Genera in the tribe Hemiceratini of Guenée (1852) and Forbes (1939). Species numbers from Gaede (1934).

Genus	No. species
Hemiceras Guenée	167
Canodia Guenée	2
Anita Schaus	10
Colax Hübner	2
Hapigia Guenée	23
Rhapigia Schaus	5
Chliara Walker	6
Antaea Hübner	5

TABLE 2. Genera in the new tribe Hapigiini based on presence of specialized deciduous cornuti in the male genitalia, and an elongate ductus bursae in the female genitalia. Species numbers are summarized from the publications of Draudt (1933), Gaede (1934), Forbes (1942) and Thiaucourt (1978, 1987). Presence (+) or absence (–) of a cteniophore was determined by dissection of representative species only.

Genus	No. species	Cteniophore
Antaea Hübner	5	+
Chliara Walker	6	+
Colax Hübner	2	+
Euhapigiodes Franc. & Miller	1	+
Hapigia Guenée	24	+
Hapigiodes Dyar	10	–
Procolax Schaus	2	+
Pseudhapigia Schaus	3	+
Rhapigia Schaus	5	+

Total number of described species = 58

TABLE 3. Diagnostic traits for the Hapigiini based on a preliminary morphological survey of representative taxa. Of the characters listed, only numbers 5 and 12 are likely to be exclusive to the Hapigiini.

1) Adult with a large, triangular tuft behind collar near base of each tegula.
2) Forewing falcate.
3) Dorsal surface of forewing often with three small, shiny ocelli near end of discal cell.
4) Forewing accessory cell absent.
5) Vesica of male genitalia bearing large, deciduous cornuti, each with a thick base and three elongate arms.
6) Aedeagus of male genitalia with an elongate ductus ejaculatorius.
7) Female genitalia with ductus bursae greatly elongate.
8) Anterior and posterior apophyses of female genitalia long and thin.
9) Caterpillar with a series of lateral stripes extending from spiracle of one segment to dorso-posterior margin of the following segment.
10) Labrum of larva deeply cleft, anteclypeus with a dorso-medial notch.
11) Pupa with a row of dorsal striations along posterior margin of mesothorax.
12) Cremaster of pupa lacking setae, surrounded by a striate ring.

Chliara, *Colax*, and additional genera, in the new tribe Hapigiini. After removal of these hapigiine genera, the Hemiceratini reverts to a group closely resembling Guenée's original formulation, comprising only the genera *Hemiceras* and *Canodia*. Its position in the notodontid classification remains obscure.

HAPIGIINI Franclemont & Miller, new tribe

Type-genus: *Hapigia* Guenée, 1852

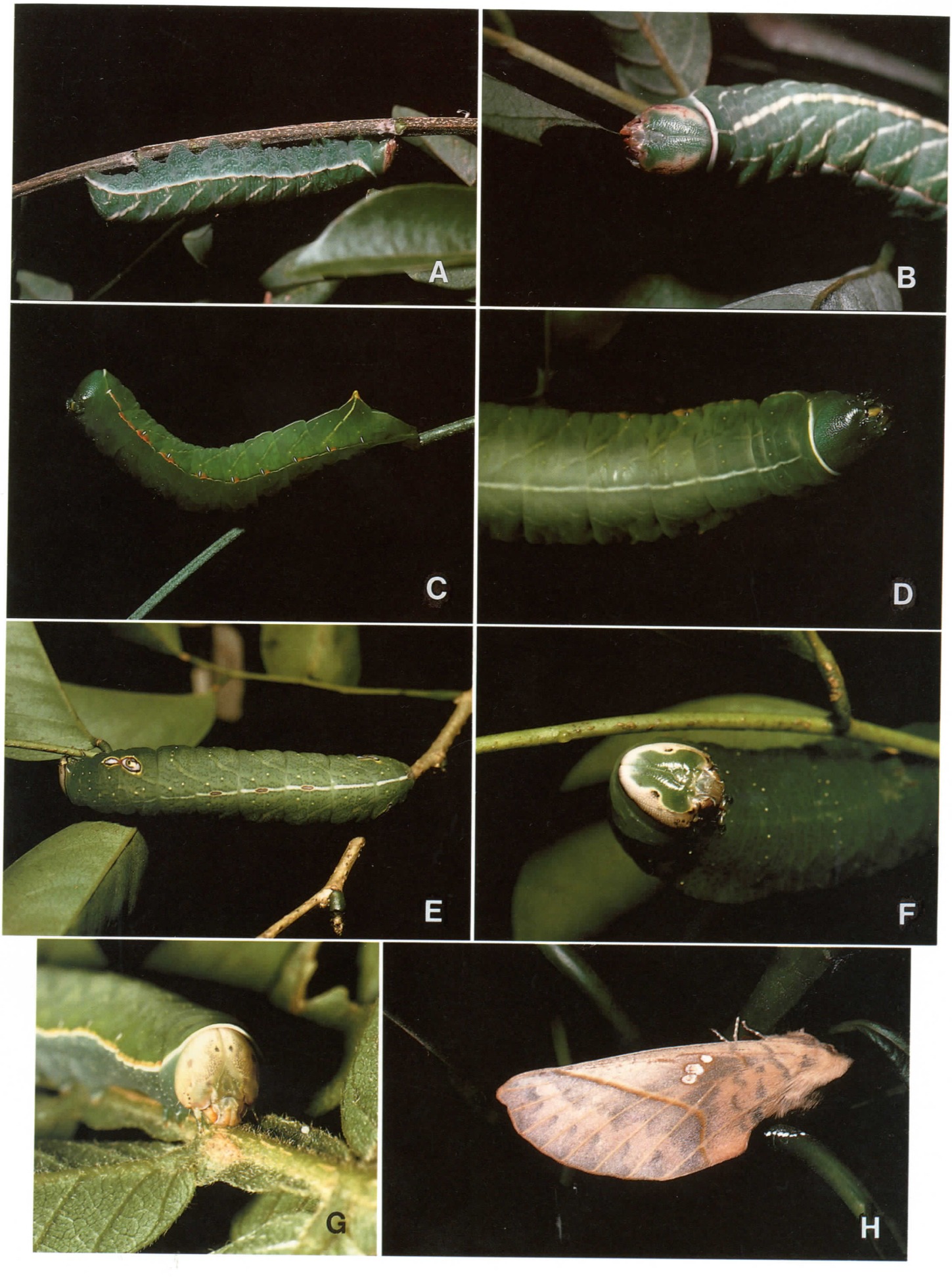
Description.– See Table 3 for diagnostic characters of the tribe.

Comparison of larvae and adults of *Hemiceras* (see Miller, 1991) with those of *Hapigiodes* and *Euhapigiodes* demonstrates that the Hemiceratini as previously conceived is not a monophyletic tribe. Our research shows that nine genera, most of which were placed by Forbes in the Hemiceratini, form a clade defined by a suite of derived characters. These genera, including *Hapigia*, *Hapigiodes*, and *Euhapigiodes*, we hereby remove from the Hemiceratini and recognize as the new tribe Hapigiini (Table 2). In Table 3 we present a list of diagnostic traits for the Hapigiini, exemplified by the morphology of *Euhapigiodes hallwachsae* and *Hapigiodes sigifredomarini*. As far as we know, these 12 apomorphic features do not occur together elsewhere in the Notodontidae, and none of them are found in *Hemiceras*.

Perhaps the most useful identifying characteristics for members of the Hapigiini include: relatively large adult body size; the presence of falcate wings, especially in males; the presence of three silvery white, often ring-shaped, discal spots (not present in all *Antaea* and *Hapigia* species); the presence of a blunt tooth on the posterior margin of the forewing (though found elsewhere in Notodontidae); a series of light-colored diagonal lines on the dorso-lateral region of the caterpillar; pupal cremaster lacking setae, but with a dorsal semicircle of raised processes. The most reliable trait, presence of highly unusual deciduous cornuti on the male vesica (Fig. 5D, 9D; see also fig. 68b in Forbes, 1942), requires dissection. For species identification of adults, Forbes (1939, 1942) provides useful keys covering five of the nine hapigiine genera.

During the course of the extensive survey of Lepidoptera foodplants for the Area de Conservación Guanacaste, caterpillars of eight hapigiine species have been discovered (pictured in Fig. 14-15; corresponding adults are shown in Fig. 2, 8, 12-13). These are the first published host records, and the first larval photographs ever presented for representatives of this moth tribe. Although more study is required, our observations suggest that hapigiine larvae can be characterized by their rather large, sphingidlike appearance. In all species, the contrasting lateral line passes through the spiracles, dividing the body into a light upper portion and a darker lower portion. This is a classic disruptive pattern of caterpillars that perch upside down from their substrate. There is considerable color pattern variation among the larvae of different hapigiines, and some features, such as the presence or absence of a dorsal tubercle on A8, vary. An unusual feature of *Colax* caterpillars, noted by Forbes (1939), is the enlarged, paddle-shaped primary setae on the anterior and posterior portion of the larva (Fig. 15D–F). All Costa Rican hapigiines so far known feed on Fabaceae, though they occur on at least six diff-

Fig. 14. Last instar larvae and adult of Hapigiini from Sector Santa Rosa, Area de Conservación Guanacaste, northwestern Costa Rica (voucher numbers refer to Janzen and Hallwachs rearing record database): A) *Euhapigiodes hallwachsae* n. sp., 90-SRNP-24 (habitus). B) *Euhapigiodes hallwachsae* n. sp., 90-SRNP-24 (head). C) *Hapigiodes sigifredomarini* n. sp., 81-SRNP-1029 (habitus). D) *Hapigiodes sigifredomarini* n. sp., 90-SRNP-1466 (head). E) *Hapigia repandens*, 93-SRNP-7065 (habitus). F) *Hapigia repandens*, 93-SRNP-7065 (head). G) *Hapigia simplex*, 93-SRNP-7499 (head). H) *Euhapigiodes hallwachsae* n. sp., 90-SRNP-24 (adult ♀). All photos by D. H. Janzen.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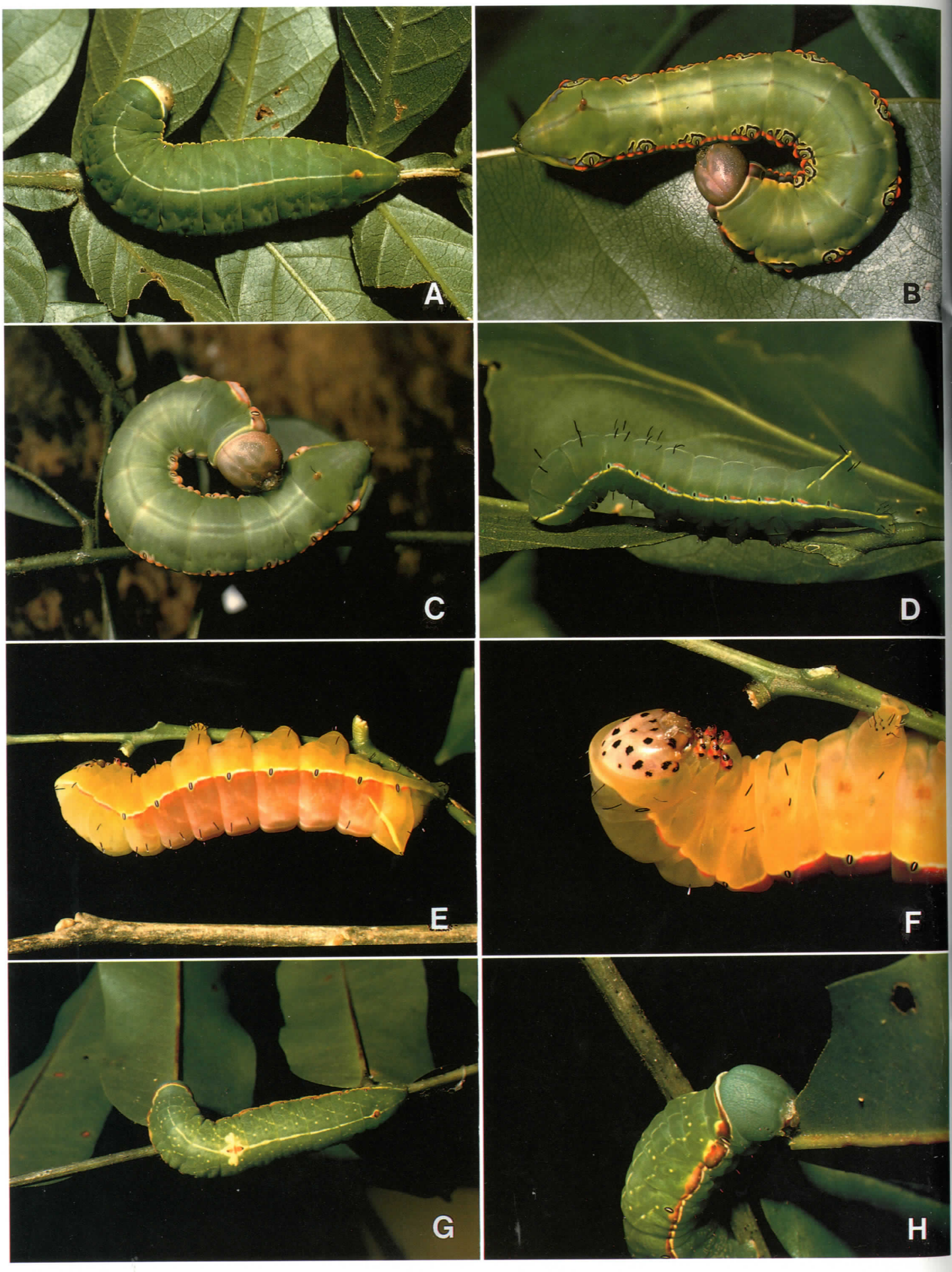
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B
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H

TABLE 4. Larval food plant records for Hapigiini in tropical dry forest (Area de Conservación Guanacaste) (source: Janzen and Hallwachs, 1997). All larval food plants are trees in the family Fabaceae.

Hapigiine species	Hostplant species
Antaea lichyi Franclemont	*Machaerium acuminatum* *Machaerium biovulatum* *Machaerium kegelii*
Antaea licormas Cramer	*Machaerium biovulatum* *Dalbergia retusa*
Chliara croesus Cramer	*Andira inermis*
Colax apulus Cramer	*Pterocarpus rohrii*
Euhapigiodes hallwachsae n. sp.	*Lonchocarpus costaricensis* *Lonchocarpus rugosus*
Hapigia repandens Schaus	*Machaerium acuminatum* *Machaerium biovulatum*
Hapigia simplex Walker	*Machaerium biovulatum* *Inga punctata* *Inga vera*
Hapigiodes sigifredomarini n. sp.	*Lonchocarpus acuminatus* *Lonchocarpus costaricensis* *Lonchocarpus guatemalensis* *Lonchocarpus minimiflorus* *Lonchocarpus phlebophyllus* *Lonchocarpus rugosus*

erent fabaceous genera (Table 4). Among Notodontidae, Fabaceae-feeding is certainly not exclusive to the Hapigiini (e.g., Janzen and Hallwachs, 1997). Fabaceae have been colonized separately by members of at least six different subfamilies, making this perhaps the most evolutionarily labile hostplant association in the Notodontidae (Miller, 1992a).

Understanding the systematics of the Hapigiini will require extensive research. Redefinition of the genera is essential. However, at present we feel confident in the following taxonomic statements: The Hapigiini is almost certainly restricted to the New World, with by far the greatest diversity being found in Central and South America; only a single species, *Pseudhapigia brunnea* Schaus, occurs north of the US-Mexican border. The tribe is relatively small, with 58 described species (Table 2). We are much less certain about the subfamily affiliation of the Hapigiini. We hereby provisionally place it in the subfamily Heterocampinae. Our rationale is based on the presence of two characters, one from adults and one from larvae. Pupal characters are suggestive, but not conclusive.

Fig. 15. Last instar larvae of Hapigiini from Sector Santa Rosa, Area de Conservación Guanacaste, northwestern Costa Rica (voucher numbers refer to Janzen and Hallwachs rearing record database (Janzen and Hallwachs, 1997)): A) *Hapigia simplex*, 93-SRNP-7499 (habitus). B) *Antaea lichyi*, 95-SRNP-7199 (habitus). C) *Antaea licormas*, 95-SRNP-4828 (habitus). D) *Colax apulus*, 93-SRNP-4502 (green form, habitus). E) *Colax apulus*, 93-SRNP-4155 (yellow form, habitus). F) *Colax apulus*, 93-SRNP-4155 (yellow form, head). G) *Chliara croesus*, 93-SRNP-3828 (habitus). H) *Chliara croesus*, 93-SRNP-3828 (head). All photos by D. H. Janzen.

A character that has caused considerable confusion among notodontid taxonomists is the cteniophore. This structure, first described by Jordan (1923), is a lateral lobe, usually with a compliment of robust, often toothlike distal setae, arising from the antero-dorsal margin of the A4 sternum in adult males (Fig. 4). Its function is unknown. Miller (1991), summarizing the taxonomic distribution of the cteniophore, observed that it is widespread but not universal among Heterocampinae, and has also been reported in some Oriental *Phalera* species (Phalerinae), and in *Hapigia*, at that time regarded as a member of the Hemiceratini.

Based on our preliminary survey, a cteniophore occurs in all hapigiine genera except *Hapigiodes* (Table 2). In some genera the structure is small, *Euhapigiodes* being an example (Fig. 4B), while in others, such as *Hapigia*, it is hugely developed (Fig. 4A; see also fig. 9-13 in Jordan, 1923). With placement of Hapigiini in the Heterocampinae, the number of notodontid subfamilies in which the cteniophore occurs is only two: the Heterocampinae and Phalerinae (Oriental *Phalera*). Nevertheless, within Heterocampinae there appears to have been considerable loss and/or gain of the structure (Miller, 1991).

Another interesting characteristic of the Heterocampinae occurs on the larval thoracic legs. In many Lepidoptera caterpillars, the tarsal setae are highly modified (Miller, 1991). There is considerable variation in setal morphology within the Notodontidae, and shape differences can provide useful diagnostic characters. In Heterocampinae, the tarsal setae are spatulate with a series of minute longitudinal grooves (Miller, 1991: figs. 479, 486). The tarsal setae of *Hapigiodes* and *Euhapigiodes* are of this same type.

The pupae of Hapigiini are unusual. The anterior margin of each moveable abdominal segment (A5-A7) bears a diffuse row of pits, a feature of Heterocampinae (Miller, 1992b). However, the forked cremaster typical of North American Heterocampinae (Packard, 1895; Mosher, 1916, 1918; Miller, 1992b) does not occur in the Hapigiini. The hapigiine cremaster (Fig. 7A, 7C) is unlike that of any other Notodontidae. Sculpturing along the caudal margin of the mesothorax is characteristic of only two notodontid subfamilies, the Heterocampinae and Dudusinae (Miller, 1992b). The sculpturing in Hapigiini (Fig. 7B) more closely resembles the latter. Pupae of Hapigiini key to couplet "8(7)" in Miller's (1992b) key to notodontid subfamilies, with the next dichotomy, a choice between Heterocampinae and Dudusinae, being inconclusive.

Taken together, these morphological traits indicate placement of the Hapigiini within Heterocampinae. While our hypothesis is not based on an overwhelming body of evidence, we feel that it currently represents the best estimate of relationships.

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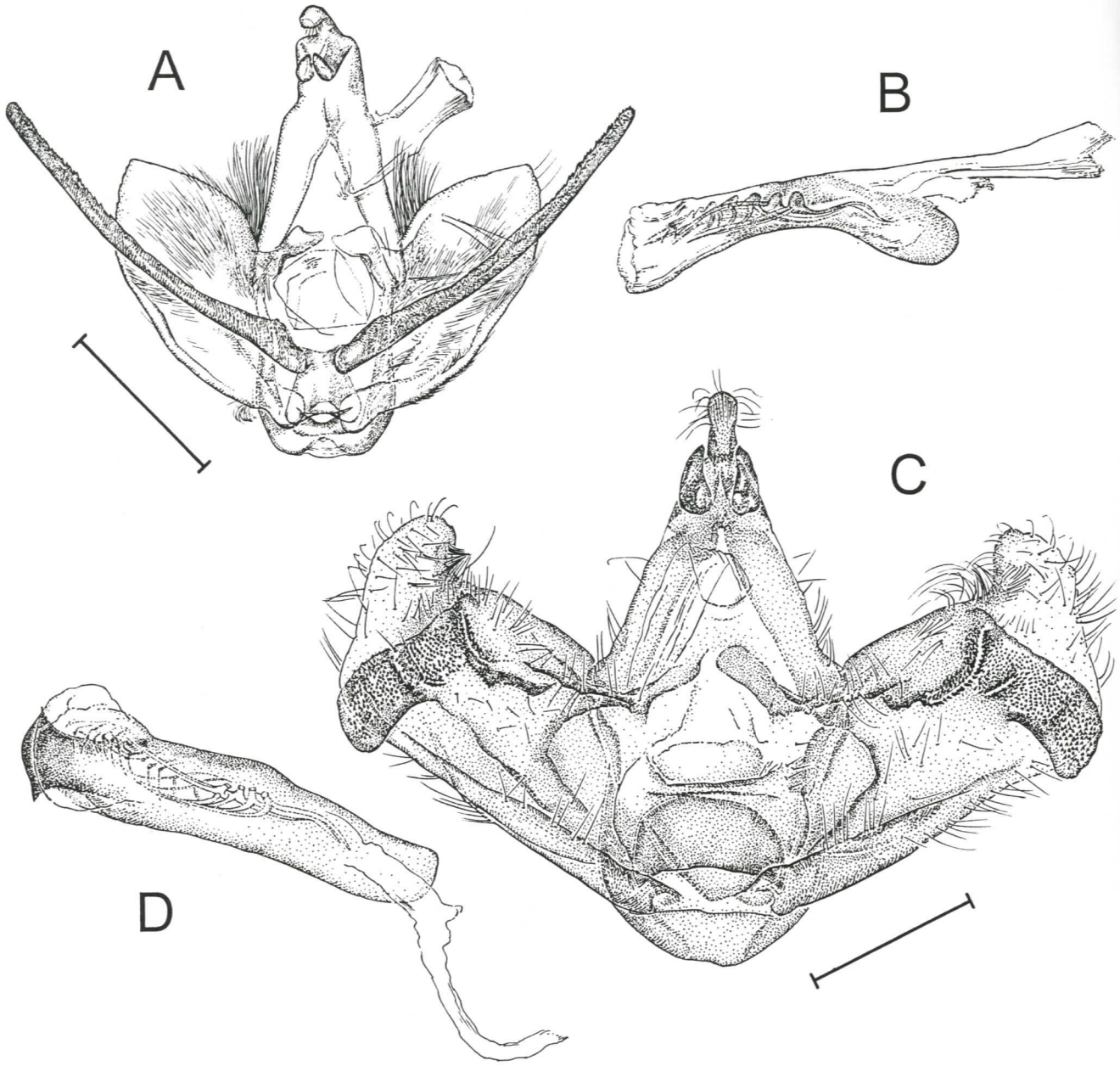

Fig. 16. ♂ genitalia of Hapigiini: A) *Hapigiodes descimoni* Thiaucourt (slide #JGF-2323; Peru), posterior view. B) aedeagus of *Hapigiodes descimoni*, lateral view (anterior at left). C) *Hapigiodes misericordia* Dyar (slide #JGF-2207; Guerrero, Mexico), posterior view. D) aedeagus of *Hapigiodes misericordia*, lateral view (anterior at left). Scale lines = 2mm.

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