N. 102
May 31, 2004

MILWAUKEE PUBLIC MUSEUM
CONTRIBUTIONS in Biology and Geology

The early stages of *Apodemia paucipuncta* (Riodinidae): myrmecophily, a new caterpillar ant-organ and consequences for classification

By P.J. DeVries,
Bérites C. Cabral,
and Carla M. Penz

Milwaukee Public
MUSEUM

N. 102
May 31, 2004

MILWAUKEE PUBLIC MUSEUM
CONTRIBUTIONS in Biology and Geology

The early stages of *Apodemia paucipuncta* (Riodinidae): myrmecophily, a new caterpillar ant-organ and consequences for classification

By P.J. DeVries
Center for Biodiversity Studies
Milwaukee Public Museum
800 West Wells Street
Milwaukee, WI 53233, USA

Bérites C. Cabral
Departamento de Zoologia
Universidade de Brasilia
P.O. Box 04525
Brasilia, Distrito Federal 70919-970, Brazil

Carla M. Penz
Department of Invertebrate Zoology
Milwaukee Public Museum
800 West Wells Street,
Milwaukee, WI 53233, USA

Milwaukee Public
MUSEUM

Milwaukee Public Museum Contributions in Biology and Geology

Paul Mayer, Editor

Reviewer for this Publication:
André Victor Lucci Freitas, Museu de História Natural, Instituto de Biologia, Universidade Estadual de Campinas

This publication is priced at $6.00 and may be obtained by writing to the Museum Shop, Milwaukee Public Museum, 800 West Wells Street, Milwaukee, WI 53233. Orders must include $3.00 for shipping and handling ($4.00 for foreign destinations) and must be accompanied by money order or check drawn on U.S. bank. Money orders or checks should be made payable to the Milwaukee Public Museum, Inc. Wisconsin residents please add 5% sales tax.

ISBN 0-89326-215-3

Abstract

The early stages of *Apodemia paucipuncta* are described for the first time. This species forms symbiotic associations with *Crematogaster* ants in central Brazil, and possesses four sets of ant-organs: tentacle nectary organs, vibratory papillae, balloon setae and for the first time in the Riodinidae, a cervical gland that is used in myrmecophily. Larval morphology and behavior indicate that *paucipuncta*: (1) is misclassified in the genus *Apodemia*, (2) it is not a member of the Emesini, and (3) it should be classified in the tribe Nymphidiini.

Key words: Brazil, *cerrado*, cervical gland, myrmecophilly, symbiosis, *Crematogaster*.

Introduction

Symbiotic associations between butterfly caterpillars and ants occur in two monophyletic lycaenoid groups - the lycaenids and the riodinids (DeJong *et al.* 1996, Campbell *et al.* 2000, Campbell & Pierce 2003). Consideration of the specialized caterpillar ant-organs used to mediate and maintain ant symbionts has had a major influence on our understanding of the evolution of butterfly-ant symbioses (Cottrell 1984, DeVries 1988, 1991a,b,c, 1997, Pierce *et al.* 2002, Campbell & Pierce 2003). Available evidence suggests that minimally myrmecophilous caterpillars possess ant-organs for production of (1) food secretions, (2) acoustical signals, and (3) chemical signals, and the apparent differences in structure and homology among riodinid and lycaenid caterpillar ant-organs have been important to the classification of the lycaenoid butterflies (Cottrell 1984, Harvey 1987a, DeVries 1991b, 1997, Campbell *et al.* 2000, Pierce *et al.* 2002).

Riodinid caterpillar ant-organs may be briefly summarized as follows. While all myrmecophilous riodinid caterpillars possess paired tentacle nectary organs (TNOs) on segment A8 that provide food secretions, caterpillars may produce acoustical signals in at least two ways (DeVries 1991b, 1997, DeVries & Penz 2002, Travassos *et al.* in press). Members of the tribe Nymphidiini (*sensu* Penz & DeVries 1999) have paired vibratory papillae on segment T1 that rasp against a granulated area on the epicranium to produce substrate borne calls (DeVries 1988). The Eurybiini (*sensu* Harvey 1987a) lack vibratory papillae, and appear to produce calls by rubbing granulations and a sclerotized plate located in the cervical membrane against epicranial granulations (DeVries & Penz 2002, Travassos *et al.* in press). Some Nymphidiini possess ant-organs that appear to produce semiochemicals, and when employed can alter ant behavior (DeVries, 1988, 1997). Two types of ant-organs appear to be involved in chemical signaling. Some taxa (e.g., *Thisbe*, *Lemonias*, *Synargis*, *Juditha*) have paired, eversible anterior tentacle organs (ATOs) on segment T3, while others (e.g., *Nymphidium*, *Theope*) possess a corona of balloon setae on the anterior edge of segment T1 (DeVries 1997). Due to their importance for caterpillar survival (DeVries 1991c), it is not surprising that possessing particular types of ant-organs has been used in riodinid classification and phylogeny reconstruction (e.g., Harvey 1987a).

Despite occupying nearly 22% of Brazil's land area, the vegetation type termed cerrado remains a little known, largely threatened biome (Oliveira & Marquis 2002). Embracing high soil and elevational heterogeneity and bordered by four different vegetation types (Amazon and Atlantic forests, *caatinga* and *pantanal*), the biota of *cerrado* is a diverse mixture of endemic species plus those occurring in neighboring biomes (e.g., Eiten 2001, Motta *et al*. 2002, Brown & Gifford 2002). For example, of 172 species of *cerrado* riodinid butterflies, 42 species (24%) are endemic while the remaining 130 species occur in surrounding areas (Brown & Gifford 2002).

The tiny butterfly *Apodemia paucipuncta* Spitz, 1930 is an obscure, little known riodinid that appears to be endemic to Brazilian *cerrado* (Brown & Gifford 2002, Motta 2002). Given the tribal placement of the genus *Apodemia* Felder & Felder, 1865 within the Emesiini, the early stages of *A. paucipuncta* and its congeners are considered to be non-myrmecophilous. However, our recent observations establish that *A. paucipuncta* caterpillars are, in fact, myrmecophilous. This report has two purposes. The first is to describe and illustrate the mature caterpillar and pupa of *A. paucipuncta*, including a caterpillar ant-organ that is recognized for the first time in riodinids. We also provide observations on *A. paucipuncta* caterpillar associations with ants. Secondly, we show evidence based on comparisons with caterpillars of nine other riodinid species in four tribes that forces the reevaluation of *A. paucipuncta* classification. Detailed systematic analyses and formal taxonomic changes to *A. paucipuncta* are presented elsewhere (Penz & DeVries in preparation).

Materials and Methods

Study site

Fieldwork was conducted intermittently by BCC from July 1997 to 2003, and by PJD, CMP and BCC during April-May 2002 at Fazenda Água Limpa of the University of Brasilia (FAL, 15° 55' S 47° 55' W, 1100 m), Brasilia, Distrito Federal, Brazil. Climate data for the Distrito Federal region during 1961-1980 (Eiten 2001) show that temperatures range from 6 to 34.5° C, and a mean annual rainfall of 1,526 mm (driest months, June - August = 10.5 mm; wettest months, November - January = 770 mm).

Species and characters examined

Based on their generic and tribal placement (Spitz 1930, Harvey 1987a,b), natural history (DeVries 1997, Opler 1984, Scott 1986), and availability, the following caterpillar species were compared to those of *A. paucipuncta*: **Eurybiini**, *Alesa amesis* (n=3; Ecuador, Sucumbios, La Selva), *Eurybia lycisca* (n=3; Costa Rica, Puntarenas, Las Cruces); **Emesini**, *Apodemia mormo* (type-species of *Apodemia*; n=1; USA, California), *Calydna sturnula* (n=4, Costa Rica, Guanacaste, Area de Conservación Guanacaste), *Emesis tenedia* (n=1; Costa Rica, Puntarenas, Las Alturas); **Helicopini**, *Helicopis cupido* (n=1; Ecuador, Sucumbios, La Selva); **Nymphidiini**, *Nymphidium haematostictum* (n=2; Panama, Panama, Barro Colorado Isl.), *Nymphidium mantus* (n=2; Panama, Panama, Barro Colorado Isl.); *Catocyclotis adelina* (n=2, Costa Rica, San Jose, San Pedro); *Theope matuta* (n=1; Panama, Panama, Soberania National Park), *Theope virgilius* (n=1; Panama, Panama).

As in previous work (DeVries & Penz 2002) we examined a variety of characters including general body chaetotaxy, position of the abdominal spiracles, and ant-organs.

Results

Early stages

Fifth instar larva (Fig. 1-3): **Head** black, primary setae long, secondary short, all transparent. **Body** flattened dorso-ventrally; green dorsally, whitish ventrally; dorsal surface covered with small, brown, club-shaped secondary setae that bear a minute terminal point; cervical gland well developed, extendable for about one-half of head height; prothoracic shield black with long, barbed, transparent setae projecting anteriorly, one pair of dark brown vibratory papillae, and up to 11 pairs of dark brown balloon setae (balloon setae detach easily in live and preserved specimens); thoracic legs brown; T3 without anterior tentacle organs; T2 and A8 bearing dark brown saddles with faint green spots near the midline; T3-A7 with a dorso-lateral stripe, well defined on T3 and A7 (contiguous to adjacent saddles), faint on T4-A6; T2-A8 with a row of paired, long, green setae dorsally near midline, two setae on T2-A1, three on A2-A7, one on A8, all broad at tip and with sparse minute barbs; ventro-lateral flanges in segments T2-A8 with long (ca. one-half body width), transparent barbed setae that also surround anal plate; spiracle position on A1 ventral and close to anterior edge of segment, spiracles positioned dorsally on A2-8; tentacle nectary organs (TNOs) located dorso-laterally on A8, eversible from flat, unadorned slits on body cuticle; anal plate dark brown, flattened, oval, narrower than A8.

Pupa

(Fig. 3B): Cuticle brown, smooth, lacking ornamentation, tracheae not visible; three scattered rows of short, goblet-shaped setae: a dorsal row which expands laterally to the edge of the wing pads and covers the surface of the eyes, vertex and frons, two ventro-lateral rows (one on each side) below spiracular line; a cluster of long, barbed setae (presumably equivalent to those in the larval ventro-lateral flanges) at the edges of T3, A1-2 and above the spiracles on A4-7; spiracles on A6-7 slightly raised; cremaster scoop-like and terminating in a blunt point, with irregular slits dorsally, concave ventrally; cremaster hooks small, sparsely distributed along the entire ventral surface of cremaster.

General biology

In the Distrito Federal *A. paucipuncta* is known to feed on the young leaves of 12 genera of plants in nine families (Diniz & Morais 1997, Diniz et al. 2001) - here we report the flowers of *Stigmaphyllon* sp. (Malphigiaceae) as a host for the first time. Given the geographic area and diversity of *cerrado* (Olivera & Marquis 2002), we suspect even more host plants may be found for *A. paucipuncta* as its biology becomes better known.

In general appearance *A. paucipuncta* caterpillars are reminiscent of members of *Nymphidium* (Fig. 1) - the body is pale green and bears brownish balloon setae divided on either side of a subtle thoracic shield. Typical of riodinid-ant symbioses, ants persistently antennated caterpillar segments A8 to solicit delivery of food secretion from the TNOs. Depending on the circumstances, the TNOs would evert singly (Fig. 1C), as a pair, or not at all. Like other riodinid taxa possessing vibratory papillae (DeVries 1991b, 1997; Fig. 2C), *A. paucipuncta* caterpillars produced a chirping, substrate-borne call. Attendant ants repeatedly antennated the balloon setae on segment T-1, but ant behavior did not alter noticeably (Fig. 1C, 3). Of potential interest is that we found only *Crematogaster* sp. (Myrmicinae) ants tending *A. paucipuncta* caterpillars, despite the presence of other secretion-harvesting ant genera at our study site. This potentially indicates an obligate symbiotic association. However, at this point *A. paucipuncta* departs from all other known riodinid caterpillars.

When ants were antennating the balloon setae, an individual *A. paucipuncta* caterpillar occasionally raised its thoracic segments above the substrate, turned its body to one side, and quickly extruded and retracted a conspicuous cervical gland that curved laterally outward and slightly backward (Fig. 3A). The caterpillar would repeatedly extrude the gland while turning its body in alternating directions. We estimate the cervical gland remained extruded for no longer than 0.5 seconds. After extruding the cervical gland approximately 6-10 times the caterpillar lowered its thorax to the substrate and remained quiescent.

There was a marked ant response to the cervical gland. Attending ants responded immediately to the extruded cervical gland by extending their sting, becoming more animated, and antennating the anterior end of the caterpillar, particularly the balloon setae (Fig. 3). Animated behavior in ants lasted from 2-5 seconds, and was reinitiated each time the cervical gland was extruded. Animated ant behavior became quieter when the caterpillar's cervical gland was no longer extruded. In a few instances we observed an attending ant elevate its abdomen to a near vertical position with the sting extended (something also observed in some *Crematogaster-Nymphidium* symbioses (Fig. 1B & C), but we never observed ants behave aggressively to the caterpillar. In *Crematogaster* the spatulate sting is modified to disseminate semiochemicals (E. O. Wilson, pers. com.), and extending the sting in the circumstances described here may coincide with the production of air-borne recruitment pheromones among nestmates (J. Longino, pers com.).

We found no indication that the cervical gland functioned to repel ants. Rather, our observations suggested that ants became more alert when exposed to the cervical gland, much like ants exposed to the extruded ATOs in *Thisbe irenea* caterpillars (DeVries 1988). However, we never observed *A. paucipuncta* caterpillars extruding ATOs. We conclude that, in concert with their other ant organs, the cervical gland in *A. paucipuncta* likely produced semiochemicals that enhanced and maintained the caterpillar-ant symbiosis.

Comparison with other taxa

Comparing *A. paucipuncta* caterpillars to members of the tribes Emesini, Helicopini, and Nymphidiini (Table 1) provided information critical to evaluating the generic and tribal classification of *A. paucipuncta*. For example, we found that the prolegs of *A. paucipuncta* bear a lateroseries of crochets, and that their mesoseries is interrupted. In *Apodemia mormo* (type species of *Apodemia*) the lateroseries is absent and the mesoseries is continuous (see Harvey 1987b). We found both *Apodemia mormo* and *Emesis tenedia* possessed well-developed verrucae, whereas these are absent in *A. paucipuncta*. These characters indicate that *A. paucipuncta* is not a member of *Apodemia*.

Table 1 also presents characters relevant to the tribal classification of *A. paucipuncta*. As in members of *Nymphidium*, caterpillars of *A. paucipuncta* bear vibratory papillae, balloon setae, and TNOs (Fig. 1-2). Possessing vibratory papillae appears to be shared by all caterpillars of Nymphidiini, but these are absent in those of Eurybiini (Table 1; Harvey 1987a, DeVries 1997, DeVries & Penz 2002). We note that *A. paucipuncta*, *Catocyclotis*, *Nymphidium* and *Theope* all possess balloon setae. However, unlike *Nymphidium* and *Theope*, *Catocyclotis* and *A. paucipuncta* have their spiracles positioned dorsally on segments A3-7. Finally, *A. paucipuncta* caterpillars are unique among riodinids by possessing a well-developed cervical gland that is employed in myrmecophily (Fig. 3). In concert, these characters strongly suggest that *A. paucipuncta* is a member of the tribe Nymphidiini, not Emesini.

Discussion

Caterpillars of *A. paucipuncta* have one of the broadest diet breadths of any *cerrado* riodinid butterfly (Diniz & Morais 1997, Diniz *et al.* 2001), and this represents encounters with a wide assortment of secondary chemical compounds and leaf textures. Given the magnitude and diversity of Brazilian *cerrado* (Olivera & Marquis 2002), we would not be surprised if more *A. paucipuncta* host plants were found as its biology becomes better known.

In contrast to a varied diet, *A. paucipuncta* caterpillars were found only in association with *Crematogaster* sp. ants. Various riodinid genera (*Juditha*, *Synargis*, *Alesa*, *Theope*) contain species known to be host plant generalists and ant specialists (DeVries 1997, DeVries & Penz 2000). Our observations suggest *A. paucipuncta* may have an obligate symbiosis with *Crematogaster* sp. ants, and use the presence of these ants as an oviposition cue. However, such a relationship remains to be demonstrated.

The cervical gland of *A. paucipuncta* is a fleshy, eversible structure located midventrally between the larval head capsule and first pair of legs (Fig. 3). Caterpillars from several families of Lepidoptera have been reported to possess a cervical gland, and available evidence suggests they function as defense organs to repel potential enemies (Scudder 1889, Stehr 1987, Weatherston et al. 1986, DeVries 1987, Attygalle *et al.* 1993). Here we report that the extruded cervical gland of *A. paucipuncta* elicited a marked behavioral response in their ant symbionts; *Crematogaster* sp. ants were attracted to the cervical gland, extruded their sting, and gathered near the anterior portion of the caterpillar. When other riodinid caterpillars (*Thisbe*, *Synargis*, *Juditha*) extrude their ATOs there is generally an immediate acceleration of activity by attendant ants (DeVries 1988, 1997). Despite differences in intensity of ant response, caterpillar and ant behaviors suggest the cervical gland of *A. paucipuncta* and ATOs of other taxa serve an analogous function in maintaining symbiotic association. Therefore, this study is the first demonstration of a riodinid caterpillar possessing a well-developed cervical gland, and the first time it has been reported as a myrmecophilous organ in any group of Lepidoptera.

Balloon setae are poorly understood as ant-organs, yet in myrmecophilous riodinid caterpillars (e.g., *Nymphidium*, *Theope*, *Catocyclotis* and *A. paucipuncta*) they appear to disseminate semiochemicals that enhance symbioses with ants (DeVries 1997, this study, K. Nishida unpublished). Of particular interest is that possession of ATOs and balloon setae by known Nymphidiini caterpillars appears to be mutually exclusive, possibly pointing to distinct evolutionary events. Although potentially useful for elucidating phylogenetic relationships and caterpillar-ant symbioses, the evolution and function of balloon setae can only be understood when many more riodinid early stages become available.

In conclusion, by having a myrmecophilous caterpillar complete with ant-organs, it is clear that *paucipuncta* is not a member of the genus *Apodemia*, and also that it belongs to the tribe Nymphidiini. However, amending the generic classification of *A. paucipuncta* extends beyond the scope of the present work. Therefore a detailed systematic analysis of *A. paucipuncta* and relatives is presented elsewhere (Penz & DeVries in preparation).

Acknowledgments

For assisting our fieldwork and accommodation we thank Ivone R. Diniz, Helena C. Morais (Universidade de Brasilia, Brazil). For thoughts and discussions on ant chemical defenses we thank J. T. Longino, P. S Ward and E. O. Wilson. We also thank K. Nishida for fruitful discussions and sharing his unpublished field observations. This work was supported in part by NSF grant DEB 0316505. We dedicate this paper to the lyrical imagery of the Lee and Maria Friedlander family, and to the early stage biologist Ivan de Lima e Silva Penz

Literature Cited

Attygalle, A.B., S.R. Smedley, J. Meinwald & T. Eisner. 1993. Defensive secretion of two notodontid caterpillars (*Schizura unicornis*, *S.badia*). Journal of Chemical Ecology. 19:2089-2104

Brown Jr., K.S. & D.R. Gifford. 2002. Lepidoptera in the cerrado landscape and the conservation of vegetation, soil, and topographical mosaics. pp 201-222 *In*: P.S. Oliveira & R.J. Marquis (eds.) The Cerrados of Brazil, Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. 398 pp.

Campbell, D.L., A.V.Z. Brower & N.E. Pierce. 2000. Molecular evolution of the Wingless gene and its implications for the phylogenetic placement of the butterfly family Riodinidae (Lepidoptera: Papilionoidea). Molecular Biology and Evolution. 17: 684-696.

Campbell, D.L. & N. E. Pierce. 2003. Phylogenetic relationships of the Riodinidae: implications for the evolution of ant association. pp. 395-408 *In*: C. L. Boggs, W. B. Watt & P. R. Ehrlich (eds.). Butterflies; ecology and evolution taking flight. University Chicago Press, Chicago.

Cottrell, C. B. 1984. Aphytophagy in butterflies: its relationship to myrmecophily. Zoological Journal of the Linnean Society. 80:1-57.

de Jong R., R.I. Vane-Wright & P.R. Ackery. 1996. The higher classification of butterflies (Lepidoptera): problems and prospects. Entomologica Scandinavica 27:65-101.

DeVries, P.J. 1987. The Butterflies of Costa Rica and their Natural History. Vol I. Papilionidae, Pieridae, Nymphalidae. Princeton University Press, New Jersey. 327 pp.

———. 1988. The larval organs of *Thisbe irenea* (Riodinidae) and their effects upon attending ants. Zoological Journal of the Linnean Society. 94:379-393.

———. 1991a. Ecological and evolutionary patterns in riodinid butterflies. pp 143-156 *In*: C. Huxley & D.F. Cutler (eds.) Ant-plant interactions. Oxford University Press, Oxford.

———. 1991b. Call production by myrmecophylous riodinid and lycaenid butterfly caterpillars (Lepidoptera): morphological, acoustical, functional, and evolutionary patterns. American Museum Novitates 3025:1-23.

———. 1991c. The mutualism between *Thisbe irenea* and ants, and the role of ant ecology in the evolution of larval-ant associations. Biological Journal of the Linnean Society. 43: 179 - 195.

———. 1997. The Butterflies of Costa Rica and their Natural History. Vol II. Riodinidae. Princeton University Press, New Jersey. 288 pp.

DeVries, P.J. & C.M. Penz. 2002. The early stage morphology of *Alesa amesis* (Riodinidae: Eurybiini), a carnivorous butterfly. Journal of the Lepidopterists' Society, 265-271.

Diniz. I.R. & H.C. Morais. 1997. Lepidopteran caterpillar fauna on cerrado host plants. Biodiversity and Conservation, 6:817-836.

Diniz. I.R., H.C. Morais & A.J.A. Camargo. 2001. Host plants of lepidopteran caterpillars in the cerrado of the Distrito Federal, Brazil. Revista Brasileira de Entomologia, 45:107-122.

Eiten, G. 2001. Vegetação Natural do Distrito Federal. Editora UnB, Brasilia, Brazil. 162 pp.

Harvey, D. J. 1987a. The higher classification of the Riodinidae (Lepidoptera). Ph.D. Dissertation. University of Texas, Austin, Texas.

Harvey, D. J. 1987b. Riodinidae. pp 446-447 *In*: F. W. Stehr (ed.) Immature Insects. vol. 1. Kendal/Hunt, Dubuque, Iowa.

Motta, P. C. 2002. Butterflies from the Uberlandia region, Central Brazil: species list and biological comments. Brazilian Jounal of Biology. 62: 151-163.

Motta, P.E.F., N. Curi & D.P. Franzmeier. 2002. Relation of soils and geomorphic surfaces in the Brazilian Cerrado. pp 13- 32 *In*: P.S. Oliveira & RJ. Marquis (eds.) The Cerrados of Brazil, Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. 398 pp.

Penz, C. M. & P. J. DeVries. 1999. The higher level phylogeny of the tribe Lemoniini (Lepidoptera: Riodinidae): a preliminary assessment using adult morphology. American Museum Novitates 2384: 1- 32.

Pierce, N.E., M.F. Braby, A. Heath, D.J. Lohman, J. Mathew, D.B. Rand & M.A. Travassos. 2002. The ecology and evolution of ant association in the Lycaenidae (Lepidoptera). Annual Review of Entomology 47: 733-771.

Oliveira, P.S. & RJ. Marquis (eds.). 2002. The Cerrados of Brazil, Ecology and Natural History of a Neotropical Savanna. Columbia University Press, New York. 398 pp.

Opler, P. A. & G.O. Krizek 1984. Butterflies east of the great plains. Johns Hopkins Press, Baltimore.

Scott, J. A. 1986. The Butterflies of North America. A natural history field guide. Stanford University Press, Stanford.

Scudder, S. H. 1889. The butterflies of the Eastern United States and Canada with special reference to New England. Vol 1. Published by the author, Cambridge, Massachussets.

Spitz, R. 1930. Über neue brasilianische Insektenformen. Entomologische Rundschau 47:39-43.

Stehr, F. W. (ed.). 1987. Immature Insects. vol. 1. Kendal/Hunt, Dubuque, Iowa. 754 pp.

Travassos, M., P. J. DeVries & N. E. Pierce. *In press*. A novel organ and mechanism for larval sound production in butterfly caterpillars: *Eurybia elvina* (Lepidoptera: Riodinidae). Tropical Lepidoptera.

Weatherston, I., J.A. MacDonald, D. Miller, G. Riere, J.E. Percy-Cunningham & M.H. Benn. 1986. Ultrastructure of exocrine prothoracic gland of *Datana ministra* (Drury) (Lepidoptera: Notodontidae) and the nature of its secretion. Journal of Chemical Ecology. 12:2039-2050.

SPECIES	LS	MS	VER	VP	BS	TNOs	SPR
Eurybiini							
Alesa amesis	present	interrupted	absent	absent	absent	present	dorsal
Eurybia lycisca	present	interrupted	absent	absent	absent	present	dorsal
Helicopini							
Helicopis cupido	present	interrupted	absent	absent	absent	absent	dorsal
Emesini							
Emesis tenedia	present	interrupted	present	absent	absent	absent	dorsal
Apodemia mormo	absent	continuous	present	absent	absent	absent	dorsal
Apodemia paucipuncta	present	interrupted	absent	present	present	present	dorsal
Calydna sturnula	present	interrupted	absent	absent	present	absent	dorsal
Nymphidiini							
Nymphidium haematostictum	present	interrupted	absent	present	present	present	ventral
Nymphidium mantus	present	interrupted	absent	present	present	present	ventral
Theope virgilius	present	interrupted	absent	present	present	present	ventral
Theope matuta	present	interrupted	absent	present	present	present	ventral
Catocyclotis adelina	present	interrupted	absent	present	present	present	dorsal

TABLE 1 Comparison between *Apodemia paucipuncta* and nine riodinid species in four tribes indicating key characters for generic and tribal placement. Abreviations: LS = lateroseries of crochets; MS = mesoseries of crochets; VER = verrucae; VP = vibratory papillae; BS = balloon setae; TNOs = tentacle nectary organs; SPR = spiracle placement on A3-7.

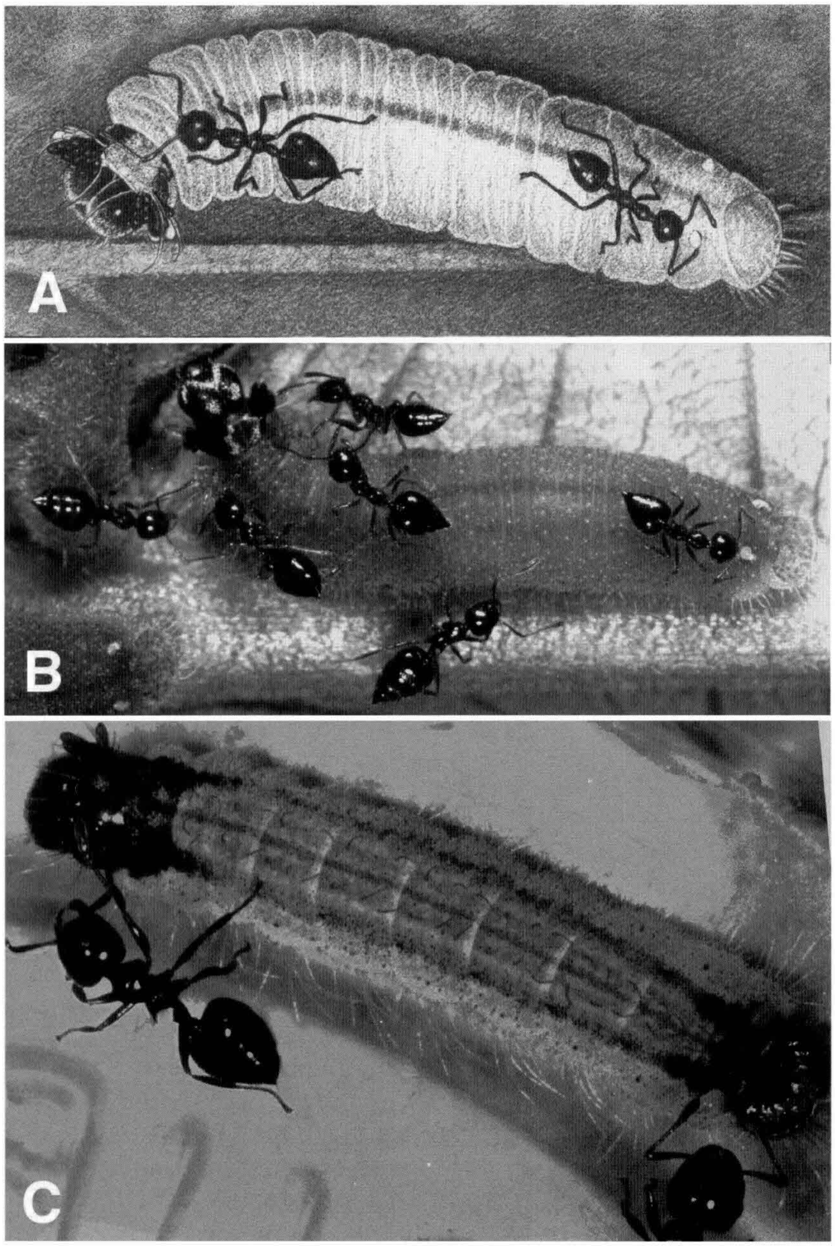
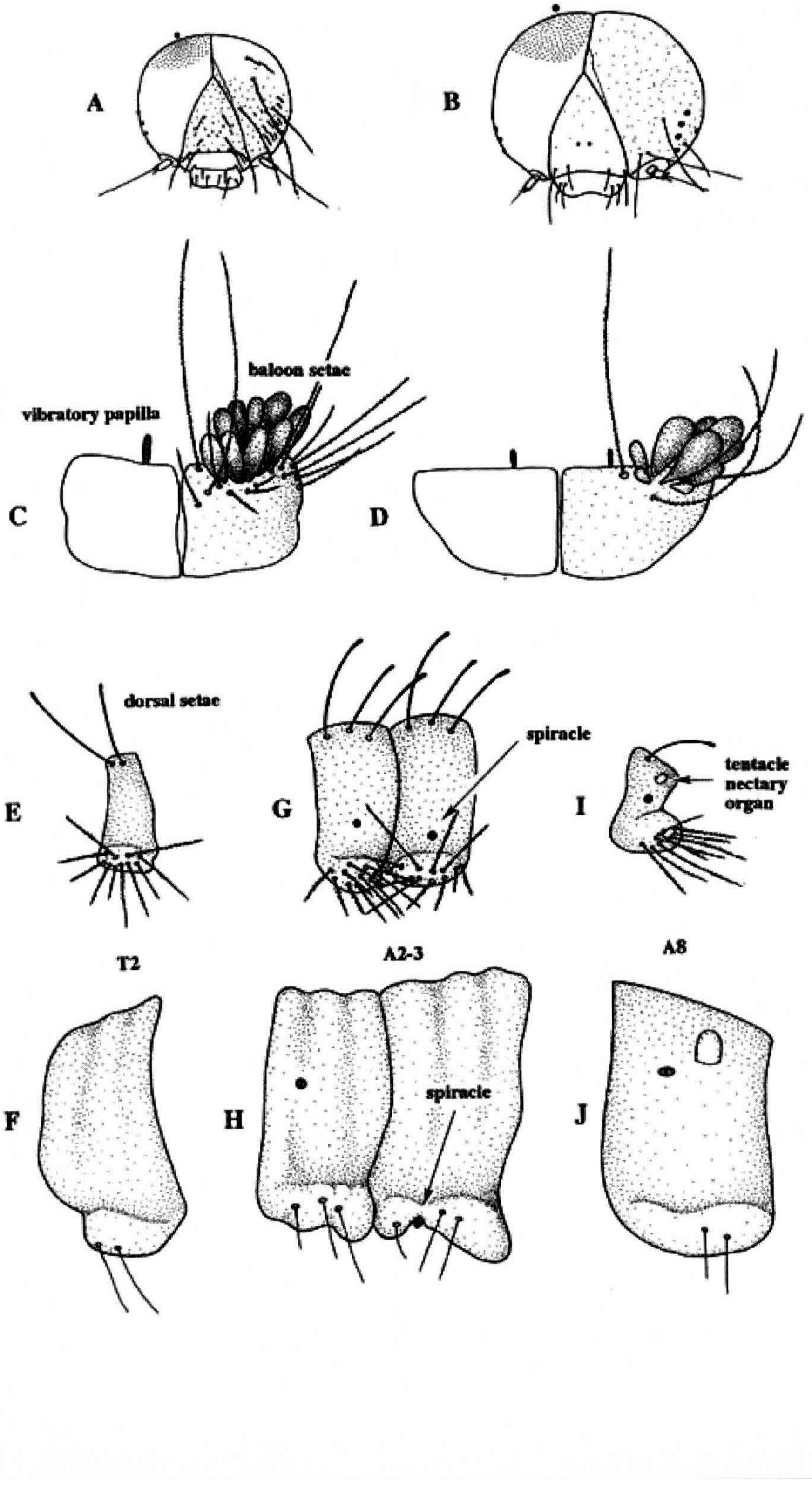


FIGURE 1 General perspectives of caterpillars. **A**, Drawing of fifth instar *Nymphidium ascolia* being tended by *Crematogaster* ants. (*after* Jennifer Clark, in DeVries 1997). **B**, Photo of fifth instar *Nymphidium leucosia* being tended by *Crematogaster* ants. Note that some ants have their stings extended. **C**, Fifth instar *Apodemia paucipuncta* tended by *Crematogaster* ants. Note ant with the sting extended.


A
B
baloon setae
vibratory papilla
C
D
dorsal setae
spiracle
tentacle
nectary
organ
E
G
I
T2
A2-3
A8
spiracle
F
H
J

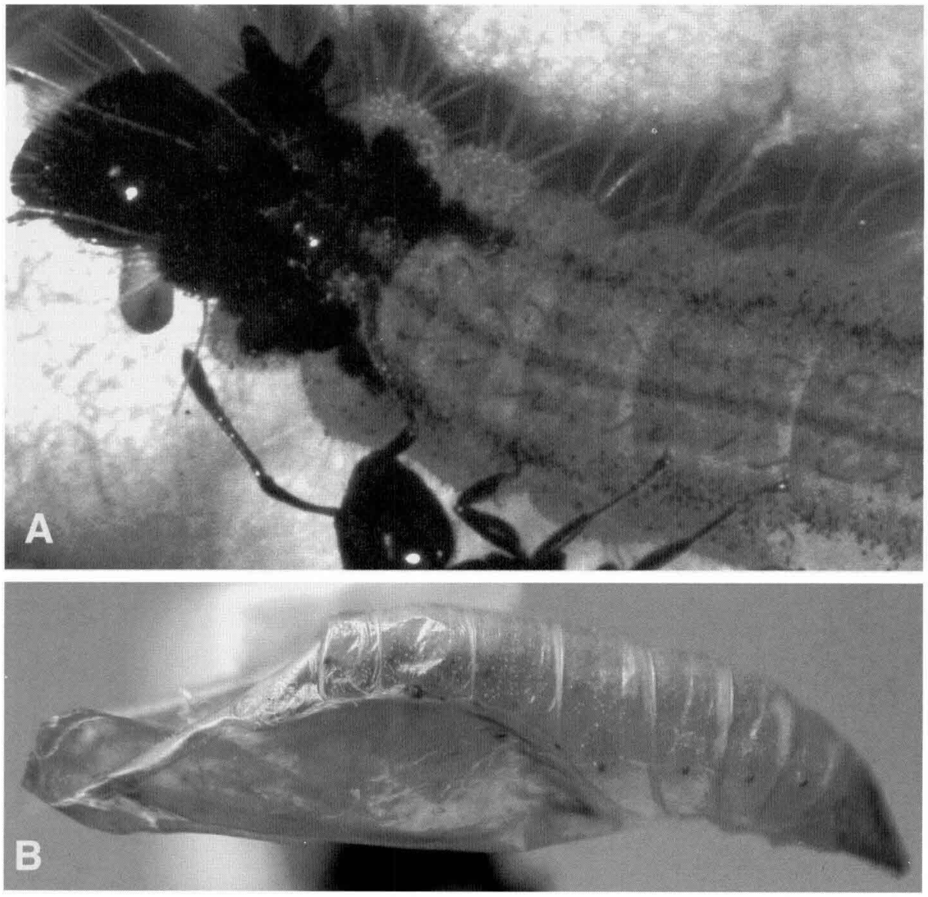


FIGURE 3 Fifth instar caterpillar and pupa of *Apodemia paucipuncta*. **A**, Fifth instar caterpillar showing extruded cervical gland and reaction of the *Crematogaster* ant. **B**, Lateral view of pupal exuvia.

FIGURE 2 Comparisons of fifth instar *Apodemia paucipuncta* and *Nymphidium haematostictum* caterpillars. Head in frontal view, black dot on right side shows the position of the vibratory papilla above head, shaded area represents the highest density of cuticle granulations: **A**, *A. paucipuncta*; **B**, *N. haematostictum*. Prothoracic shield in dorsal view, setae were omitted from left side to show vibratory papilla position: **C**, *A. paucipuncta*; **D**, *N. haematostictum*. Body segments in lateral view, note the dorsal setae and the position of the spiracle on A3, legs and small secondary setae were omited: **E**, T2, *A. paucipuncta*; **F**, T2, *N. haematostictum*; **G**, A2-3, *A. paucipuncta*; **H**, A2-3, *N. haematostictum*; **I**, A8, *A. paucipuncta*; **J**, A8, *N. haematostictum*.