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Biology and behavior of the neotropical butterfly *Eunica bechina* (Nymphalidae) with special reference to larval defence against ant predation.

André V. L. Freitas and Paulo S. Oliveira

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Abstract. This paper describes the biology and behavior of *Eunica bechina* (Nymphalidae). Eggs are laid singly on Caryocar brasiliense (Caryocaraceae), a plant that bears extrafloral nectaries. Most of the eggs are laid on young leaves, on which the caterpillars preferably feed. Pupation occurs off the host plant. The fifth instar larvae and pupae are like those of *Nica flavilla* and *Temenis laethoe*, suggesting that the genus is among the Callicorini. First to fourth instar larvae construct frass chains, where they rest immune from attacks by foraging ants that climb on Caryocar for its nectary secretions. While feeding on leaves, however, caterpillars may be killed and removed by foraging ants. When attacked by ants, *Eunica* caterpillars may repel their aggressors by regurgitating and/or bleeding. Ants receiving these fluids exhibited strong disturbance and conspicuously cleaned their mandibles and head. Dropping off the plant and hanging on the end of a drag line was also observed in *Eunica* larvae after successive bites from the ants. We suggest that frass chains are probably related to defence against "walking" predators, especially ants, who have difficulty in attacking the caterpillars at these refuges.

Key Words: *Eunica bechina*, Eurytelinae, Caryocar brasiliense, cerrado vegetation, ant predation, extrafloral nectaries, herbivores, defensive behavior, frass chains

The genus *Eunica* Hübner (1819), includes 45 species and 24 additional subspecies distributed throughout the Neotropical region, the majority in the Andean Region and the Amazon Basin (Jenkins, 1990). The genus has an uncertain systematic position within the Nymphalidae (Otero, 1990) and few larvae and hostplants are known (Barcant, 1970; DeVries 1986, 1987; Ackery, 1988; Jenkins, 1990; Oliveira & Freitas, 1991). *Eunica bechina magnipunctata* Talbot 1928 occurs in the cerrados (savanna-like vegetation) of Central and Southeast Brazil (Jenkins, 1990; Oliveira & Freitas, 1991). Larvae of *E. bechina* feed on leaves of *Caryocar brasiliense* Camb. (Caryocaraceae), a plant bearing extrafloral nectaries and frequently visited by ants (Oliveira & Oliveira-Filho, 1991; Oliveira & Brandão, 1991). Early instar larvae construct frass chains (Oliveira & Freitas, 1991), a behavior also observed in other Nymphalidae, especially among the Eurytelinae and Charaxinae (Muyschondt, 1973a, b, c 1974, 1976; Muyschondt & Muyschondt, 1976; Casagrande & Mielke,
1985; DeVries, 1987; Aiello, 1991). Immature stages are still undescribed for many genera and species of Nymphalidae; studies of their morphology and behavior could help to understand the relationship among members of this family of butterflies. The present study describes the early stages of E. bechina. We also provide data on the natural history of immatures and adults, as well as on larval behavior and its relation to ant predation on the host plants.

**Study sites and methods**

The study was carried out in a cerrado area in Itirapina (21°15’S, 47°49’W), São Paulo, SE Brazil during 1987, 1991 and 1992. The vegetation consists of a scrub of shrubs and trees, which is the cerrado sensu stricto of Goodland (1971). Average annual rainfall and temperature are ca. 1400 mm and 21°C respectively (Setzer, 1949).

A total of 27 shrubs of Caryocar brasiliense (35-150 cm tall) were censused to determine the preference for oviposition sites by Eunica bechina. The eggs were collected and the larvae were reared in plastic boxes containing leaves of Caryocar. Boxes were cleaned and the leaves replaced daily. Egg size is given as height and diameter; the head capsule size is the distance between the two groups of ocelli; size of cephalic horns was also measured.

The behavior of Eunica caterpillars and visiting ants, as well as their responses to one another, were investigated through natural and provoked encounters on Caryocar shrubs. Encounters were provoked by removing the caterpillars from their frass chains and placing them in the proximity of different ant species. Larvae of different sizes were placed on leaves or buds of ant-occupied shrubs. After the ants had encountered the caterpillar, the behavioral interactions between them were registered in observation sessions lasting 15 - 30 min. A detailed account of the ant fauna associated with Caryocar brasiliense is given in Oliveira & Brandão (1991).

**Results**

**Descriptions of early stages**

Egg (Fig. 1A): yellowish, conical, and flattened at the top, with 12 to 14 longitudinal ridges and 10 to 12 transverse ridges. Average height 0.76 mm (σ=0.03 mm, n=15); average diameter 0.72 mm (σ=0.06 mm, n=15). Larvae hatch 5 days after oviposition (n=5).

First instar larva (Fig. 1B): head translucent brown, body translucent yellow changing to pale red after feeding (due to visible intestinal contents), legs and prolegs translucent yellow; maximum length 3 mm; average width of head capsule 0.42 mm (σ=0.02 mm, n=16), average duration 2.6 days (σ=0.54 days, n=47). The distribution of setae in the first instar larva is given in Fig 2A.

Second instar larva (Fig. 1C): head black with two short stubby horns; body pale brown with short conical scoli; maximum length 6 mm; average
width of head capsule 0.67 mm (σ=0.06, n=30); average length of the horn 0.33 mm (σ=0.05 mm, n=30), average duration 1.5 days (σ=0.59 days, n=46).  

Third instar larva (Fig. 1D): Head black with white warts and with two long diverging horns armed with accessory spines in the middle and ending distally in a knob crowned with short spines; body dark brown with several scoli; maximum length 12 mm; average width of head capsule 1.26 mm (σ=0.06 mm, n=43); average length of the horn 2.36 mm (σ=0.20 mm, n=43); average duration 2.4 days (σ=0.75 days, n=44).  

Fourth instar larva (Fig. 1E): Head as in third instar; body dark brown with a pale brown lateral stripe; maximum length 20 mm; average width of head capsule 1.95 mm (σ=0.06 mm, n=36); average length of the horn 4.56 mm (σ=0.09 mm, n=36); average duration 3.7 days (σ=1.47 days, n=33).  

Fifth instar larva (Fig. 1F): Head as in fourth instar; body brown, dorsal region dark brown with white lines and stripes, ventral region varies from yellow to orange or red, sublateral stripe orange or pale yellow, legs dark brown and prolegs red except the anal prolegs, (shiny black), scoli black with yellow and red dots. The placement of the scoli in the body is shown in Figure 2B. Maximum length 40 mm; average width of head capsule 3.28 mm (σ=0.10 mm, n=9); average length of the horn 6.62 mm (σ=0.30 mm, n=9); average duration 6.33 days (σ=1.77 days, n=12). Prepupa assumes a "J" position, fixed on the substrate by the anal prolegs and abundant silk. There is no great change in color.  

Pupa (Fig. 1G,H): Green, purple or yellowish, changing to brown and gray or green after one or two days; spiracula inconspicuous light brown; a dorsal indentation separates abdomen from thorax. Abdominal segments are mobile; average size 2.2 cm (σ=0.15 cm, n=11), average duration 8.7 days (σ=1.35 days, n=18).  

The sex ratio of the adults obtained in the laboratory (13 males and 9 females), can be considered 1:1 (chi square test; χ²=0.72, p>0.20; D.F.=1).  

Natural history  

Females of Eunica bechina lay their eggs singly on small shrubs of Caryocar brasiliense between 10.00 and 13.00 hours. A total of 141 eggs were censused on Caryocar. Most eggs were found on young leaves (87%), and less frequently on shoot tips (10%), petioles (1%), and stems (1%). The vertical distribution of the eggs on the host plant varied from 3 to 150 cm above the ground (x=60.5 cm, σ=44.8 cm, n=141). The caterpillars eat part of the egg shell after hatching and feed preferentially on young leaves of C. brasiliense. Although E. bechina larvae were seen on Caryocar from September to January (rainy season), the highest infestation level occurred between September and October when the majority of the leaves are still young, soft, and red in color.  

First to fourth instar larvae of E. bechina construct frass chains, on the tip of which they rest (Figure 3A). When disturbed the caterpillars may
Figure 2. A, Chaetotaxy of first instar larva of *Eunica bechina*. B, Distribution of scoli in a fifth instar larva. The subdorsal 5-furcate scolum in the segment T3 is a bit larger than that of T2. The simple dorsal scolum in the segment A2 is generally absent. Many larvae may present the dorsal scoli in the segments A7 and A8 as 5-furcate.
Figure 3. A, Third instar larva of *Eunica bechina* resting on a frass chain. B, Worker *Camponotus aff. blandus* retrieving a third instar larva. C, D, Workers of *Azteca* sp. attacking a third instar larva of *Eunica*, before and after recruitment of nestmates.
jump off the leaf suspending themselves from silk threads. Pupation usually occurs off the host plant, on neighbouring shrubs. Adults of *E. bechina* are easily seen in the field throughout the year flying about 3 m high. Agonistic behavior and chases between males of *E. bechina* are frequently observed, suggesting a kind of territoriality. The males were seen feeding on sap oozing from tree wounds, and they probably also feed on decaying fruits and mud puddles (K. S. Brown Jr., personal communication), like other “fruit feeding nymphalids” (DeVries, 1988).

**Interactions between ants and caterpillars**

When not on their frass chains, *E. bechina* caterpillars may interact aggressively with the ants that climb on *Caryocar* attracted to its extrafloral nectary secretions. Behavioral interactions between *Eunica* caterpillars and ants are summarized in Table 1. In all, 47 ant × caterpillars encounters were provoked on *Caryocar* shrubs; in 36 of these the larvae were attacked by foraging ants. Such attacks resulted in the death and removal of the caterpillar from the plant in 20 instances. Two *Camponotus* species (*C. crassus* and *C. aff. blandus*) and one species of *Azteca* were most aggressive towards caterpillars. Unlike *Camponotus* which are large enough to subdue and carry the caterpillar alone to their nests (Fig. 3B), the small *Azteca* ants recruited tens of nestmates to help with these tasks (Fig. 3C, D).

Besides the 7 species tested against *E. bechina* larvae (Table 1), we also observed 6 other species attacking the caterpillars in the field (but without quantification), including 2 species of *Crematogaster*, 2 of *Pheidole*, one of *Pseudomyrmex (pallidus group)* and *Ectatomma tuberculatum* (Olivier).

<table>
<thead>
<tr>
<th>Ant species</th>
<th>Nº of ant × larvae encounters</th>
<th>Nº of larvae attacked</th>
<th>Nº of larvae removed</th>
<th>Nº of larvae jumping of the leaf</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Camponotus crassus</em> Mayr</td>
<td>15</td>
<td>10</td>
<td>6</td>
<td>3</td>
</tr>
<tr>
<td><em>C. aff. blandus</em> (Fr. Smith)</td>
<td>10</td>
<td>10</td>
<td>7</td>
<td>1</td>
</tr>
<tr>
<td><em>C. rufipes</em> (Fabricius)</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>C. renggeri</em> Emery</td>
<td>2</td>
<td>2</td>
<td>0</td>
<td>1</td>
</tr>
<tr>
<td><em>C. aff. cingulatus</em> Mayr</td>
<td>3</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td><em>Azteca</em> sp.</td>
<td>5</td>
<td>5</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Zacryptocerus pusillus* (Klug)</td>
<td>11</td>
<td>8</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>47</strong></td>
<td><strong>36</strong></td>
<td><strong>20</strong></td>
<td><strong>7</strong></td>
</tr>
</tbody>
</table>
When bitten by the ants, Eunica caterpillars frequently regurgitate and/or bleed, a behavior shown to effectively repel their aggressors who may end up abandoning the larvae. After successive bites on the larvae, attacking ants frequently exhibit strong disturbance behavior and vigorously clean their mandibles, antennae and head.

Seven larvae dropped off the plant after successive bites from the ants (Table 1). In three instances the caterpillars suspended themselves on the end of a silken line for approximately 20 min before climbing back to the leaf. Four other larvae dropped directly to the ground and hid among the leaf litter.

**Discussion**

**General biology**

This is the first detailed description of the biology and behavior of Eunica immatures (see also Jenkins, 1990).

The distribution of setae in the first instar larvae is very similar to the "primitive" pattern of Nymphalidae (Nakanishi, 1988). The distribution pattern of the scoli of the fifth instar larvae and pupae is like that of Nica flavilla and Temenis laothoe (Muyshondt, 1973b, c); however, the spine distribution pattern in N. flavilla is quite distinctive. The pupae of Eunica suggest that the genus is among the Callicorini, as stated by Otero (1990), who places Eunica in the most advanced branch of Callicorini, paraphyletic with Temenis and Nica. However, Otero’s results are based on only eight characters of adult morphology (apparently with high consistency). On the other hand, Harvey (1991) proposes that Eunica is related with Myscelia, Catonephele, Nessaea, Cybdelis and Libynthia (this one very close to Eunica) and the paleotropical genus Sallya (see also Jenkins, 1990 and Otero, 1990). Further study of immatures of other Eurytelinae genera may help solve some systematic problems in this group, as has been done for the Ithomiinae (K. S. Brown & A. V. L. Freitas, in preparation).

**Defence against ants**

Ants are the most frequent visitors to the extrafloral nectaries of Caryocar brasiliense in the cerrado (Oliveira & Oliveira-Filho, 1991; Oliveira & Brandão, 1991). Foraging ants may encounter Eunica caterpillars on leaves and occasionally remove them from Caryocar. All ant genera observed attacking E. bechina caterpillars are known to tend Lycaenidae and Riodinidiae larvae, Homoptera, and to visit extrafloral nectaries (see DeVries, 1991; Oliveira & Brandão, 1991). Azteca ants, however, were also observed killing Thisbe irenea (Riodinidiae) caterpillars (DeVries, 1991). We noted that some caterpillars can overcome predation or injury by ants through an array of behavioral mechanisms (see also Heads & Lawton, 1985; Costa et al. 1992).

The behavior of suspending themselves by silken threads is common in E. bechina caterpillars and appears to be widespread among the Lepi-
doptera (see also DeVries, 1987 and several citations therein). Dropping and suspending on the end of a drag line is a technique known to be employed by arthropods who live in close proximity to aggressive ants (Robinson & Valerio, 1977; Oliveira & Sazima, 1984, 1985; Heads & Lawton, 1985).

Regurgitation is also common in butterflies (see Brower, 1984). Just after attacking the caterpillars, ants receiving this fluid exhibited strong disturbance (walking erratically and shaking the body) and conspicuously cleaned their mandibles and head. Ant deterrence can also occur from bleeding by the injured caterpillars, as also noted by Heads & Lawton (1985) for some herbivores of bracken fern (*Pteridium aquilinum*). Rearing up the body, curling and wriggling vigorously (beat reflex) can intimidate or temporarily expel some predators from the plant. For some ants, however, the beat reflex may stimulate additional attacks (Malicky, 1970). These behaviors are very common among butterfly larvae, except for some Lycaenioideae (Malicky, 1970), and seem to be more effective in late instar caterpillars due to their larger size in relation to the ants (see also Heads & Lawton, 1985).

The frass chains constructed by the larvae may diminish their predation/removal by ants, since the latter were never observed climbing on this structure. The behavior of resting or taking refuge on frass chains is analogous to that exhibited by some Heliconini larvae, which rest at the end of tendrils or on “island-like” leaf segments (Benson et al., 1976; Bentley & Benson, 1988). Frass chains are observed in several other larvae of Nymphalidae butterflies feeding on various plant families. This trait is especially common among the Charaxinae and Limenitidinae (*sensu* Harvey, 1991), a fact supporting the idea that this structure permits the utilization by *Eunica* of a plant often occupied by ants. This behavior needs to be studied in other genera of Nymphalidae such as *Hamadryas* and *Anaea*, whose larvae commonly feed on plants bearing extrafloral nectaries. Although the primary role of frass chains has not been tested so far, we suggest that it is related to defence against “walking” predators, specially ants, that would have difficulty in attacking the caterpillars on their chains.

Acknowledgements. We thank Dr. K. S. Brown Jr., C. F. Klitzke, K. Fiedler and P. J. DeVries for discussions and helpful comments on the manuscript. R. B. Francini helped with the photographs. S. Gerald and E. Z. Borghi made the line drawings. Financial support to P. S. Oliveira was provided by grants from the CNPq (no.300101/90-2 and 400692/92-9), FAPESP (no. 90/2775-6) and FAEP/UNICAMP (no. 634/91). A. V. L. Freitas also acknowledges a fellowship from CAPES.

**Literature cited**


A New Method of Detection of Pebrine Disease in Tasar Silk Moth, *Antheraea mylitta* Drury (Saturniidae)


Central Tasar Research and Training Institute, Nagri 835 303, Ranchi, INDIA

In the culture of *Antheraea mylitta* Drury, a semidomesticated Tasar Silk Moth, eggs of mother moths infected with *Nosema sp.* (microsporidian) must be discarded to avert any catastrophe on crops caused by this pathogen. The infected mother moths (pebrine diseased) are detected by a method derived from that used in sericulture (Pasteur, 1870). In this method, the abdomen of an adult is severed with scissors, placed in a small mortar, mixed with water and crushed with pestle. A drop of the smear is placed on a clean slide and examined under a microscope for *Nosema sp.*, spores. This operation is most important but also time consuming in large grainages (insectaries where pupae of *A. mylitta* in their cocoons are held and at the onset of emergence of adults, eggs produced are processed). In the present study, technique is described to shift the time of microscopic examination by examining the exuviae, which remain in cocoon shells after pupation, instead of gut examination of mother moths. The new method and its advantages are discussed.

The exuviae used in this study were from diapausing pupae of *A. mylitta* (Fig. 1) reared during August-September, 1991 on primary host plants *Terminalia tomentosa* Wright and Arnon and *Terminalia arjuna* Bedd raised at the fields of the Central Tasar Research and Training Institute, Ranchi, India. As pebrine disease can be acquired from mother moths (primary infection) or from the environment through food (secondary infection), spores of *Nosema sp.* can be detected during any stage of the life cycle. Pupae selected for this study were of three types: those raised from eggs laid by (1) pebrine infected mothers, (2) pebrine-free mothers later inoculated with *Nosema sp.* spores during mid III instar and (3) pebrine free mothers (Control). 100 males and 100 females of each type, divided into five replications, were selected. Pupae were examined side by side with their exuviae to determine presence or absence of the disease.

The specimens for microscopic examination were processed in two ways viz., a) conventional and b) centrifuge methods:

a) conventional method: pupae were first washed with distilled water for two minutes, then the lower half of the abdomen (gut) was placed in a clean mortar. The tissue was crushed and the smear examined under microscope at 675 × magnification for *Nosema* spores.

b) Centrifugal method: The respective exuviae of the pupae were crushed with 5 ml of 2 % KOH in a mortar with pestle, let stand for 3
Fig. 1 Photograph of a pupa of *Antheraea mylitta* Drury showing its cocoon shell, pupa and exuviae.

Results are illustrated in Table 1. *Nosema* spores were found in the body content as well as in their exuviae of the pupae, which became infected through their mother moths. There was no difference in the percentage of infection due to conventional or centrifugal methods or between sexes. Thus, instead of gut examination of mother moths, their exuviae may be examined to eliminate those individuals which acquired pebrine disease from their mothers.

In secondary infection, *Nosema* sp. spore-bearing pupae were higher in number than in exuviae. Observations made on external symptoms of pebrinised larvae of *A. mylitta* indicate that when I or early II instar larvae are inoculated with *Nosema* spores, black spots appear on the skin of larvae of III and early IV instars, but disappears in final instar (V). This indicates a relationship with detection of *Nosema* spores in exuviae in those individuals which acquired infection during their feeding stages. The individuals which were secondarily infected by *Nosema* during different stages of their larval life require detailed and systematic study with regard to: a) time required for appearance of black spots on the skin from the time of infection, b) examination of the molted skins for infection, c) intensity of infection in various organs and their route of migration to different tissues in larvae, pupae and adults, d) difference of infection between sexes, and e) mode of entry of *Nosema* spores into eggs. Only after these studies, pupae raised from larvae infected during

minutes, mixed and filtered. The filtrate was centrifuged at 500 rpm for 30 seconds. The supernatant was decanted and made up to 5 ml. with distilled water. The same was centrifuged at 2000 rpm for 10 minutes. The sediment was then smeared on a clean slide and five fields were examined for *Nosema* spores.
Table 1. Results of Microscopic Examination of pupae and their exuviae.

<table>
<thead>
<tr>
<th>Sl. #</th>
<th>Type of Infection</th>
<th>Sex</th>
<th>% of pupae found infected</th>
<th>% of exuviae found infected</th>
<th>Remarks</th>
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<tr>
<td>1.</td>
<td>Primary</td>
<td>♂</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>2.</td>
<td>Primary</td>
<td>♀</td>
<td>100</td>
<td>100</td>
<td>100</td>
</tr>
<tr>
<td>3.</td>
<td>Secondary</td>
<td>♂</td>
<td>90</td>
<td>96</td>
<td>67</td>
</tr>
<tr>
<td>4.</td>
<td>Secondary</td>
<td>♀</td>
<td>92</td>
<td>95</td>
<td>53</td>
</tr>
<tr>
<td>5.</td>
<td>Control</td>
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<td>0</td>
<td>0</td>
</tr>
<tr>
<td>6.</td>
<td>Control</td>
<td>♀</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
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</table>

Note: (a) = Conventional and (b) = Centrifugal methods of detection of infection.

feeding in the field may be screened for *Nosema* infection in *A. mylitta* by this method.

The present accepted method of pebrine detection in grainage is solely based on adults. This includes microscopic gut examination of mother moths for microsporidia spores (Pasteur, 1870), use of India ink in the microscopic field (Geetha Bai, et al., 1985) for dry moth testing, enzyme-linked immunosorbent assay, ELISA, (Kawarabata and Hayasaka, 1987), indirect fluorescent antibody techniques, (Sato, et al., 1981, Huang et al. 1983), latex bead agglutination, (Hayasaka and Ayuzawa, 1987), fluorescent antibody technique, (Huang, 1983), slide agglutination test (Hayasaka, 1983 and Li, 1985), and monoclonal antibody detection (Zhaoxi, et al., 1990). All these methods are accurate, but are cumbersome for large commercial grainages by requiring expensive laboratory facilities and skilled personnel. Pebrine detection through microscopic examination of exuviae may help the tasar industry to produce quality breeding material.

Tropical tasar silkworm diapausing pupae are preserved from November to May in bivoltine and February to May in trivoltine races. During this preservation period, exuviae examination for *Nosema* spore bearing insects can be done in the month of May. This reduces microscopic examination activities from production time. During production time, including moth eclosion, mating, oviposition and processing of eggs, the microscopic examination of mother moths must be done during a short span of 15 to 20 days for a stock of nearly 400,000 to 500,000 cocoons. This is laborious and time consuming, therefore affecting the quality of seed
production. The new method has an advantage of distributing the grainage work evenly from May to June instead of demanding all activities during June.

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LITERATURE CITED


Direction Of Spring Migration Of Vanessa cardui (Nymphalidae) In Colorado

James A. Scott
60 Estes St., Lakewood, Colorado 80226

Abstract. Spring migration of 3016 Vanessa cardui (L.) migrants was studied in Colorado in 1992 and 1983, using standard vector methods. Migration was to the east-northeast/northeast (averaging 31° in 1992, 51° in 1983, east being 0° and north 90°), and this direction did not change significantly during the day, disproving a theory that migrants maintain a constant angle to the sun. The efficiency (unidirectionality) of migration is about 80% during peak migration, but drops to near zero afterward. Some spring adults in central Colo. overwintered there. Migrants mate-locate all day long, versus late in the day for non-migrants.

Key Words: Vanessa cardui, migration, sun-compass mechanism.

Introduction

The study of migration of butterflies is filled with numerous brief reports of vast swarms heading in a certain direction. There are fewer studies in which the direction of each individual was charted, and even fewer in which the time of day was recorded. The latter is of interest because of a theory that migrants fly at a constant angle to the sun Baker (1968a, b, 1969) and thus change direction from morning to afternoon. Recent migrations of Vanessa cardui allowed the testing of this theory.

Methods

Time of day and direction were recorded for each of 3016 adults: 2725 in 1992 and 291 in 1983. I walked about open areas (mostly large grassy areas) in metropolitan Denver, Colorado, during most hours on peak flight days but during only part of the day on some days, and estimated direction of each individual seen as one of 16 compass directions (N, NNE, NE, ENE, E, ESE, etc.). Standard vector methods were used. Each observation represents an arrow of length 1, and the individual arrows can be drawn connected end-to-start (the start of the next vector connected to the pointed end of the previous vector) on graph paper. Then a line can be drawn connecting start of first vector to end of last vector, which forms the total vector whose length and angle can be measured from the graph paper (which represents the overall length and direction of migration). The following equations are a simpler way to calculate the length and direction of the total vector, where E is the number of adults flying toward the east, SSW the number flying toward the south-southwest, etc. (The derivation of the equations is this: for ENE for instance the angle is 22.5° and a vector of length 1 has a Y-component [height] of sin 22.5° or .3827 and an X-component [width] of cos 22.5° or .9239; and .70711 is the sin and cos of 45° for the NE vector, etc.)
X component of total vector = \( E - W + .70711(NE + SE) - .70711(SW + NW) + .3827(NNE + SSE) - .3827(SSW + NNW) + .9239(ENE + ESE) - .9239(WSW + WNW) \)

Y component of total vector = \( N - S + .70711(NE + NW) - .70711(SE + SW) + .9239(NNE + NNW) - .9239(SSE + SSW) + .3827(ENE + WNW) - .3827(ESE + WSW) \)

V (length of vector) = square root(\( X^2 + Y^2 \))

By custom in mathematics, the directions and axes are arranged as in Fig. 1, and angles are counterclockwise from due east (east being 0°, north 90°, west 180°, south 270°). The overall direction of migration can be found by plotting the individual vectors, or from elementary trigonometry:

\[ \text{Angle } A = \tan^{-1}(\frac{Y}{X}) \]

The efficiency of migration is given by the length of the total vector divided by the number of adults observed (N). It represents the proportion of individuals that fly in the overall direction of migration (the directionality), and ranges from 1.0 if all individuals fly the same direction, to zero if flights are random in direction. I included in sample size only flying adults, and ignored the ones feeding on flowers or resting. Thus:

Directionality (Efficiency) of migration \( E = \frac{V}{N} \)

\( N \) = sample size

---

**Fig. 1.** Migration April 26-30 1992 during one-hour periods starting at the times indicated. A dashed line points to the 8:00 vector, and "7:00" is left of the 7:00 vector which is hidden among the bases of the other vectors. Numbers on Y and X axes represent number of migrating individuals.
Results

In 1992, very few migrants (n=13) were noted from April 10-25, which flew predominantly eastward. A vast migration occurred April 26-30, few were seen May 1-2, a small migration occurred May 3, few May 4-5, few (N=18) flew northeastward May 6, and very few (N=8) flew predominantly northeastward May 8-18. Table 1 details migration from April 26-May 5. The April 26-30 peak was massive (especially April 28-30), the overall direction for the five days was a little north of ENE (31°, V=1945., N=2395), and efficiency was great (81%). May 1 the migration was ceasing (flying to NNE with only 50% efficiency), and May 2 the few adults seen were essentially nonmigratory with a very small vector and almost zero efficiency. May 3 a small migration (N=167) again occurred, but oddly its direction was southeastward at high efficiency (79%). May 4-5 few adults were seen and most were nonmigratory judging by the low efficiency (36% and 24%); they flew predominantly eastward May 4 indicating perhaps a mixture of southeastern migrants like the day before and northeastward migrants like the next day May 5 when they flew northeastward as before.

Table 1. Daily migration 1992, N=2725.

<table>
<thead>
<tr>
<th>Day</th>
<th>N</th>
<th>Direction</th>
<th>Vector</th>
<th>Unidirectionality</th>
</tr>
</thead>
<tbody>
<tr>
<td>April 26</td>
<td>57</td>
<td>25.02°</td>
<td>40.27</td>
<td>.71</td>
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<tr>
<td>April 27</td>
<td>124</td>
<td>16.52°</td>
<td>104.66</td>
<td>.84</td>
</tr>
<tr>
<td>April 28</td>
<td>1065</td>
<td>29.25°</td>
<td>882.09</td>
<td>.83</td>
</tr>
<tr>
<td>April 29</td>
<td>474</td>
<td>39.51°</td>
<td>382.63</td>
<td>.81</td>
</tr>
<tr>
<td>April 30</td>
<td>677</td>
<td>30.26°</td>
<td>543.17</td>
<td>.80</td>
</tr>
<tr>
<td>May 1</td>
<td>53</td>
<td>63.89°</td>
<td>26.65</td>
<td>.50</td>
</tr>
<tr>
<td>May 2</td>
<td>20</td>
<td>19.75°</td>
<td>1.06</td>
<td>.05</td>
</tr>
<tr>
<td>May 3</td>
<td>167</td>
<td>320.34°</td>
<td>132.08</td>
<td>.79</td>
</tr>
<tr>
<td>May 4</td>
<td>23</td>
<td>357.87°</td>
<td>8.24</td>
<td>.36</td>
</tr>
<tr>
<td>May 5</td>
<td>26</td>
<td>41.81°</td>
<td>6.28</td>
<td>.24</td>
</tr>
</tbody>
</table>

Table 2. Migration each hour April 26-May 5, 1992, N=2683. Times are military standard time of start of one hour periods (7:00 means 7:00-7:59).

<table>
<thead>
<tr>
<th>Hour</th>
<th>N</th>
<th>Direction</th>
<th>Vector</th>
<th>Unidirectionality</th>
</tr>
</thead>
<tbody>
<tr>
<td>7:00+</td>
<td>20</td>
<td>45.84°</td>
<td>5.18</td>
<td>.26</td>
</tr>
<tr>
<td>8:00+</td>
<td>75</td>
<td>33.94°</td>
<td>53.73</td>
<td>.72</td>
</tr>
<tr>
<td>9:00+</td>
<td>286</td>
<td>28.28°</td>
<td>241.11</td>
<td>.84</td>
</tr>
<tr>
<td>10:00+</td>
<td>361</td>
<td>22.35°</td>
<td>295.22</td>
<td>.82</td>
</tr>
<tr>
<td>11:00+</td>
<td>373</td>
<td>30.10°</td>
<td>321.60</td>
<td>.86</td>
</tr>
<tr>
<td>12:00+</td>
<td>223</td>
<td>40.40°</td>
<td>185.51</td>
<td>.83</td>
</tr>
<tr>
<td>13:00+</td>
<td>282</td>
<td>31.38°</td>
<td>218.47</td>
<td>.77</td>
</tr>
<tr>
<td>14:00+</td>
<td>422</td>
<td>23.12°</td>
<td>307.54</td>
<td>.73</td>
</tr>
<tr>
<td>15:00+</td>
<td>157</td>
<td>328.94°</td>
<td>113.10</td>
<td>.72</td>
</tr>
<tr>
<td>16:00+</td>
<td>335</td>
<td>35.29°</td>
<td>250.15</td>
<td>.75</td>
</tr>
<tr>
<td>17:00+</td>
<td>109</td>
<td>49.12°</td>
<td>68.19</td>
<td>.63</td>
</tr>
<tr>
<td>18:00+</td>
<td>40</td>
<td>39.54°</td>
<td>38.98</td>
<td>.97</td>
</tr>
</tbody>
</table>
Table 3. Migration each hour April 26-30, 1992, N=2395.

<table>
<thead>
<tr>
<th>Hour</th>
<th>N</th>
<th>Direction</th>
<th>Vector</th>
<th>Unidirectionality</th>
</tr>
</thead>
<tbody>
<tr>
<td>7:00+</td>
<td>19</td>
<td>45.71°</td>
<td>6.18</td>
<td>.33</td>
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<tr>
<td>8:00+</td>
<td>75</td>
<td>33.94°</td>
<td>53.73</td>
<td>.72</td>
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<tr>
<td>9:00+</td>
<td>274</td>
<td>26.71°</td>
<td>238.13</td>
<td>.87</td>
</tr>
<tr>
<td>10:00+</td>
<td>317</td>
<td>19.42°</td>
<td>277.88</td>
<td>.88</td>
</tr>
<tr>
<td>11:00+</td>
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<td>30.10°</td>
<td>321.60</td>
<td>.86</td>
</tr>
<tr>
<td>12:00+</td>
<td>223</td>
<td>40.40°</td>
<td>185.51</td>
<td>.83</td>
</tr>
<tr>
<td>13:00+</td>
<td>268</td>
<td>31.52°</td>
<td>214.07</td>
<td>.80</td>
</tr>
<tr>
<td>14:00+</td>
<td>361</td>
<td>26.27°</td>
<td>289.26</td>
<td>.80</td>
</tr>
<tr>
<td>15:00+</td>
<td>27</td>
<td>10.24°</td>
<td>20.24</td>
<td>.75</td>
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<tr>
<td>16:00+</td>
<td>309</td>
<td>39.85°</td>
<td>249.05</td>
<td>.81</td>
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<tr>
<td>17:00+</td>
<td>109</td>
<td>49.12°</td>
<td>68.19</td>
<td>.63</td>
</tr>
<tr>
<td>18:00+</td>
<td>40</td>
<td>39.54°</td>
<td>38.98</td>
<td>.97</td>
</tr>
<tr>
<td>Total</td>
<td>2395</td>
<td>30.77°</td>
<td>1944.63</td>
<td>.81</td>
</tr>
</tbody>
</table>

In 1983, a few adults were seen April 22-24, with a moderate migration April 25-27, few migrants April 28-30, and a small migration May 4. The overall direction of migration was to the northeast (51°, Table 4, Fig. 2).

Evidently the southwestern deserts such as the Mojave and Sonoran Deserts are the major source for spring *V. cardui* in central Colorado, if the butterflies maintained the same ENE-NE flight in Arizona-Utah-California that they flew in Colorado.

Migration in insects is generally considered to be “post-teneral, pre-reproductive” (Johnson, 1969), although there are a few observations of oviposition then continuing migration, and oviposition during northward migration is typical of *Danaus plexippus* (L.) (Cockrell et al. 1993); thus migration obviously starts after the cuticle is hardened for flight, and stops as the eggs become ready to be laid. This generalization seems true for *V. cardui* also, because the relative lack of migration on some days in 1992 (May 1-2, 4-5) suggests that adults had stopped migrating then, presumably to reproduce (several ovipositions were observed April 28 by a nonmigrating female).

In 1983 the efficiency of migration gradually increased during the day (Table 4), evidently because mornings were cool and adults often fed on flowers in the morning. But in 1992 efficiency was about the same all day (Tables 2-3) except very early in the morning, probably because mornings were warmer in 1992.
The butterfly sun-compass mechanism

Baker (1968a, b, 1969) claimed that butterflies migrate by maintaining a constant angle to the sun, so that their direction changes clockwise during the day in northern latitudes where the sun’s position moves east to south to west during the day. *Vanessa cardui*, however, does not change its direction of migration during the day (Tables 2-4, Figs. 1-2). Adults flew a little north of ENE in 1992, NE in 1983, with no significant change of direction during the day. Obviously *V. cardui* has some neurological mechanism that produces a constant direction of flight during the day despite the change of direction of the sun as it moves across the sky. Probably this mechanism is the same sun-compass clock that has been demonstrated in honeybees.

The main difference between the observations of Baker and my own is that Baker recorded flight directions in ordinary populations that were not in migratory flight, and then assumed (wrongly) that their behavior was like that of migratory butterflies, whereas my observations are of obvious, definite migrations. My opinion is that Baker’s observations of nonmigratory butterflies showed a change in direction during the day because glare from looking toward the sun affected the ability to notice
butterflies flying in certain directions, causing a systematic bias that followed the change of direction of the sun during the day. Possibly some non-migratory butterflies do change direction somewhat during the day, but this seems doubtful. Since no other authors have proved any significant change of direction of migration during the day, and other studies proved that direction does not change during the day (Arbogast 1966 on Agraulis vanillae, Balciunas & Knopf 1977 on Urbanus proteus, Walker 1978 on Precis coenia, Phoebis sennae, K. Adams in Baker 1978 on Belenois aurota, D. Lawrie 1984 Lepid. News #1 p. 7 and M. Myres Can. Field Nat. 99:147-155 on Vanessa cardui), clearly Baker's theory must be discarded.

To more-objectively determine the sun's influence on observer bias, and to obtain more accurate data, more sophisticated apparatus will be necessary: the observer would sit on a platform that rotated frequently, and would note for each migrant the compass angle printed on a surrounding deck and enter it into a computer, while the computer recorded the angle of the observer's seat to the sun; the computer would use the time of day to calculate the angles of butterfly and observer to due north, and the number of adults seen at each direction could be compared to the angle of observer to the sun to determine any observer bias.

**Adult overwintering in Colorado**

Most authors have perhaps wrongly assumed that V. cardui overwinters only in southern areas like SW Arizona and Mexico (Williams 1970). But in central Colorado, my 30 years' observations suggest that adults almost never migrate southward; the very few southward migrations that have been observed were high in the mountains in midsummer (Emmel & Wobus 1966 in Colo., and I saw a southward migration in the alpine zone of Wind River Mts. Wyo. early Aug. 1983 and another in alpine central Colo.). Southward migration has never been seen on the Colorado plains/foothills, where every year during September large numbers nectar on Chrysanthamnus nauseosus and other flowers until frost, without migrating. When wild-caught Sept. adults are placed in a home freezer, they die no earlier than the other Vanessa, Polygonia, and *Nymphalis* which are known to overwinter as adults (all die within 30 minutes in the freezer, suggesting that adults in nature must require many hours days or weeks of gradually colder temperatures to increase their internal concentration of glycerol to survive freezing). In addition, adults are generally present in spring even in years without noticeable in-migration, and Cockerell (1934) once found an adult in January in nature in Boulder Co. Colo. Evidence that V. cardui overwinters in Britain, where it was once thought to be just a temporary migrant, has been found (Baker 1978).

But analysis of wing length proves that many spring adults must be migrants from southward. In Europe, spring adults average smaller than summer adults (Baker 1978), because smaller adults bred in the
south migrate north in spring. This is also true in central Colo., where forewing length in the months from April-Oct. averages 28.9, 28.0, 29.6, 32.6, 31.2, 32.1, 31.4 mm. The main change in size is about mid June, thus April-June 10 adults average 28.1 mm (S.D. 2.9, range 21-33, N=59), whereas June 17-Oct. adults average 31.8 mm (S.D. 2.0, range 25-37, N=182). This highly significant difference (P<.01) proves that spring Colo. adults must be supplemented by migration from the south, because if spring adults were solely overwinterers they would have the same forewing length as the adults the previous fall. But some adults are large in spring (32-33 mm in both April and May) and variation in size is greater in spring (larger S.D.), and these large adults still could be overwinterers.

Probably adults hibernate in central Colorado every year, as in Europe where Baker (1978) concluded that “each autumn some individuals enter hibernation throughout the breeding range.” The strength of spring versus fall migrations is reversed between V. cardui and D. plexippus: V. cardui migrates strongly in spring and weakly or not at all in fall, while D. plexippus migrates slowly northward in spring over a period of several generations, strongly southward during one generation in fall (Cockrell et al. 1993). Thus migration in V. cardui should not be viewed as a strictly seasonal movement like that of Danaus plexippus; it must be viewed also as a population outbreak in which during a few outbreak years adults fly to regions (mostly northward in spring) where prospects of rearing offspring are presumed to be better.

**Mate-locating behavior**

When not migrating, V. cardui males mate-locate (chase others and court) only late in the day, preferably late afternoon-early evening. But during migrations they mate-locate all day: the number of chases seen each hour of migration in 1983 & 1992 was 8:00 (8:00-8:59)-4, 9:00-16, 10:00-18, 11:00-15, 12:00-12, 13:00-9, 14:00-18, 15:00-12, 16:00-25, 17:00-14, 18:00-14. No courtships were seen. Many migrations would be toward regions with a low population of adults, so mating en route seems preferable to waiting until arrival and gambling on the presence of a suitable mate there.

**Flower-feeding behavior**

Adults—presumably both migratory and nonmigratory—often fed during the migrations. Yellow and white flowers may be preferred (although this may be an artifact since cultivated purple Buddleja davidii is enormously popular). Number of visits and flower color were: *Taraxacum officinale* (yellow) 190 visits, *Syringa vulgaris* (blue) 45 (white) 1, *Prunus cerasus* (white) 24, *Prunus virginiana melanocarpa* (white) 14, *Penstemon secundiflorus* (blue) 6, *Malus* sp. crabapple (pink) 7, *Astragalus drummondii* (white) 4, “pot of gold” mustard (yellow) 4, *Erigeron compositus* (white) 3, *Thlaspi arvense* (yellow) 3, *Prunus pissardi*
rosea (white) 2, Cryptantha minima (white) 2, Malus sylvestris 2 (white), Erysimum (yellow) 2, Oxytropis lamberti (purple) 1.

**Literature Cited**


Spread of the Southern African Lycaenid butterfly, *Cacyreus marshalli* Butler, 1898, (LEP: Lycaenidae) in the Balearic Archipelago (Spain) and considerations on its likely introduction to continental Europe

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**Abstract.** The establishment of the lycaenid butterfly *Cacyreus marshalli* on the island of Majorca (Spain), originating from southern Africa, has already been reported (Eitschberger & Stamer, 1990; Sarto i Monteys & Masó, 1991). The latter warned of the likelihood of this species being introduced to neighbouring areas, particularly the north-eastern coast of Spain (the Communities of Valencia and Catalonia) and the other islands of the balearic archipelago.

The present work reports the finding of this species on the islands of Menorca and Ibiza and its apparent absence, for now, from the island of Formentera. Its present status in the archipelago is discussed with the likelihood of invading the Iberian Peninsula and the european continent.

**Resumen.** El establecimiento del licénido *Cacyreus marshalli* en la isla de Mallorca, procedente de Africa meridional, ya había sido constatado en trabajos anteriores (Eitschberger & Stamer, 1990; Sarto i Monteys & Masó, 1991). En éstos se advertía de la posibilidad de que esta especie fuera también introducida en áreas cercanas principalmente en las zonas costeras valencianas y catalanas, y por supuesto, en las restantes islas que conforman el archipiélago balear.

En el presente trabajo se da cuenta del reciente hallazgo de esta especie en las islas de Menorca e Ibiza así como, por el momento, de su ausencia en la de Formentera. Asimismo se hacen algunas consideraciones sobre el estado actual de la especie en el archipiélago balear y se comenta la posibilidad de que invada la Península ibérica y el continente europeo.

**INTRODUCTION**

The establishment of a breeding population of the african lycaenid, *Cacyreus marshalli* Butler, 1898, on the island of Majorca (Spain) was first confirmed by Sarto i Monteys & Masó (1991), though it had been previously suspected by Raynor (1990) and Eitschberger & Stamer (1990). The latter also made the first correct identification of this introduced species. Data on its biology on Majorca were first reported by Sarto i Monteys & Masó (1991), Masó & Sarto i Monteys (1991) and more recently by Sarto i Monteys (1992). This species may become a serious
pest of cultivated geraniums (*Pelargonium*), should proper control measures not be taken as has already happened in Majorca.

As a result of its recent discovery on the islands of Menorca and Ibiza, comments will be made on its present status in the archipelago as well as on the likelihood of it invading the Iberian Peninsula and the European mainland.

**NEW DATA ON DISTRIBUTION**

During Easter 1992, two very worn males were caught within a residential area known as ‘La Dehesa’, north of Castellón de la Plana, in the Autonomous Community of Valencia. This region is by the sea and has abundant ornamental geraniums. The specimens were sent to Dr. Fidel Fernández Rubio, who identified them as *C. marshalli* (Fernández Rubio, pers.comm.). These represent the first record in the wild of this species in the Iberian Peninsula and the second in the European mainland. A male specimen had been found in Brussels (Belgium) on August 3, 1991 (Troukens, 1991).

However, the history of the introduction of this species into Europe goes back to November 1978, when two caterpillars were found in Cheshunt, Hertfordshire (United Kingdom). Those had been accidentally imported on *Pelargonium* plants var. ‘Fever Cascade’, which had originated from the Republic of South Africa. The larvae were impounded and eventually completed their larval development at the laboratories of the British Ministry of Agriculture, Fisheries and Food (MAFF) in Harpenden, Hertfordshire. Figure 1 shows a map of Western Europe indicating where the species has been found. Figure 2 shows the islands of the Balearic archipelago and the surrounding coasts of the Valenciana and Catalonian communities.

In October 1990 Ulf Eitschberger and Paul Stamer correctly identified the species for the first time from specimens collected by the latter in Paguera (Majorca) in November 1989. They suggested the butterfly or its first instars had been introduced with the foodplants and became established. They were however unaware of the extensive damage the larvae of the butterfly were doing to the geraniums and did not realize the species already had a strong foothold on the island.

Two weeks before the paper by Eitschberger & Stamer was published, Edward M. Raynor (1990) reported photographs of the lycaenid and identified it as “possibly *ethiopicus*” (one of the nine species belonging to the genus *Cacyreus*). And follows Raynor “As far as I’m aware, this genus has not been recorded from Europe or North Africa. Interestingly we observed further specimens in the nearby town of Magalluf, suggesting that the butterfly may be breeding on Majorca. Several members of this genus feed on geranium and pelargonium and they may have been introduced with plants, ...”. Raynor saw the butterfly for the first time in April 1990 when he was at a friends’ garden in Cabo Falcó, south of Magalluf, and a bit later in Magalluf itself.
Cacyreus marshalli Butler, 1898 in Europe (31 August 1993)

1-5  Records of very few specimens. Established breeding population not found

a-f  Established breeding population found.

Figure 1. Map of Western Europe showing where Cacyreus marshalli has been found so far (August 1993): 1* Cheshunt, Hertfordshire (United Kingdom) (1978), 2* Brussels (Belgium) (1991), 3* Castellón de la Plana (Spain) (1992), 4* Denia (Alicante-Spain) (April 1993), 5* Granada (Spain) (July 1993). In 1* to 5* only few specimens were found, with an established breeding population not detected. It is established on the islands of the Balearic archipelago (a) Ibiza, (b) Majorca and (c) Menorca. Breeding populations have also been recently found in July 1993 in (d) Logroño, (e) Zaragoza and (f) Valencia.

As to the two specimens collected near Castellón de la Plana, in Spain, it could not be assumed the species had already established itself on the Peninsula. To be certain it would be necessary to find a population of larvae on geraniums and check its permanence over time, as on Majorca. These two specimens, and perhaps others, might have been introduced
from Majorca (it is known the species is not a migrant), probably as a larva or adult, and they would not have been able to establish a breeding population. The same would apply to the specimen found in Brussels.

Recently, I have been informed by my colleagues at the Plant Protection Service in the Autonomous Community of the Balearic islands that geranium growers settled on the island of Menorca, the second in size of the archipelago after Majorca, had detected this species inside their nurseries. Nearly simultaneously, a paper by the British entomologist P.R.Grey (1992) was published, where he reported the presence of the
species in gardens close to the sea located at Cala de Santa Galdana, on
the south west of the island. The butterflies were detected in October
1991 and, on the occasion of a second visit of Grey to Menorca, again in
early May 1992. Likewise, according to Grey, another lepidopterologist
also found the species in April 1992, in Son Bou, village located on the
south centre of the island. Thus, being aware of what happened to the
island of Majorca, we can assume also the island of Menorca has been
fully invaded by Cacyreus marshalli.

However, the Pityusic islands, Ibiza and Formentera, the closest to the
Spanish mainland and the southernmost archipelagic islands, had so far
not been reported as hosting C. marshalli populations. To check whether
this species had established on these two islands, I visited Ibiza during
December 27, 28 and 30, 1992, and Formentera, on December 29, 1992.
Results were positive on the island of Ibiza. Formentera seems to be, for
the time being (December 1992), free of the pest.

On December 27, 1992 I found a large population of this pest in Sant
Antoni de Portmany, a town located on the west coast of Ibiza. Geraniums
were so infested, specially those in flowerpots near the harbour, that
some young plants were completely dead. Older geraniums, within the
same area, though alive, were severely damaged, with evident external
and less obvious internal stem damage, the latter by galleries produced
by boring larva inside the more tender upper stems. I found caterpillars
in third and fourth (last) instars. These were found, healthy and active,
feeding inside the galleries excavated in the stems. On the outside of the
stems they produced the typical ‘nibble’ injuries (Sarto i Monteys, 1992).
When entire stems were too damaged or, in the case of old geraniums,
when only the tougher sections of the stems remained undamaged, then
a few larvae were found feeding on leaves. I also found very healthy
looking pupae and pupa exuviae attached external to the stems. How-
ever, I did not observe adults, probably due to the very low (for the area)
December temperatures.

On December 30, 1992 the north of the island of Ibiza was explored,
with two towns visited: Sant Miquel de Balansat (north centre) and Cala
Sant Vicent (north east). The first is located inland, at a few kilometres
from the coast and on hilly mountains; the second is by the sea. In both
places I found Cacyreus marshalli, affecting both Pelargonium zonale
and Pelargonium peltatum. At the first locality I found all larval instars.
They were outside or inside terminal shoots which, together with the
flower buds, are the preferred feeding sites. At the second locality only
live pupae and pupa exuviae were detected, with damage produced on
geraniums very obvious.

The temperatures on the island during these late December days were
relatively low, with minima between 7 and 11°C. These temperatures
seemed well tolerated by C. marshalli caterpillars. No photoperiod
driven diapause (i.e. due to short daylength) was observed, contrary to
what happens in most autochthonous lepidoptera. This had already been
observed by Sarto i Monteys & Masó (1991) in the laboratory during the winter months of December and January using a controlled and fixed temperature of 20°C. Their supposition appears supported that in the wild this species would not present a photoperiod-driven diapause and that low winter temperatures would simply slow down its biological cycle.

On the other hand, it seems the species has not yet reached the isle of Formentera. On December 29, 1992, I visited Formentera to search for this pest. It is the smallest regularly inhabited island of the balearic archipelago, with an area of only 100 km², and is southernmost in the group. A thorough search of geraniums was undertaken in all population centres as well as more isolated residential areas and country houses. In all locations geraniums were in excellent condition and neither the pest itself nor any vestige of its presence was detected. Occasionally, larvae of the nocticid moths *Heliothis armigera* (Hübner, [1808]) and *Chrysodeixis chalcites* (Esper, 1789) were found feeding on geranium leaves and flowers (the latter only on leaves).

Finally, in July 1993, established breeding populations, with large numbers, have been found thriving in continental Spain. These were detected in the cities of Logroño, Zaragoza and Valencia (see Figure 1).

**Considerations about its introduction into the Balearic Archipelago**

Another point to establish is when the introduction of this species into the islands of the balearic archipelago occurred, as it is not a migrant (Clark & Dickson, 1971; Eitschberger & Stamer, 1990). On Majorca, according to data provided by Mr. Joan Gomila and Mr. Antoni Cardona of the local Plant Protection Service, the first symptoms of geranium damage likely attributable to *C. marshallii*, were detected in 1987, within private gardens in Santa Ponça, town on the southwest of the island. The identity of the pest was unknown at that time. It follows that the most likely introduction occurred one or two years before.

In the case of Ibiza, serious damage detected in some areas with the pest found in differing and widely separated localities, suggest that the whole island is invaded, indicating its introduction can not be too recent. It could have happened soon after its initial introduction in Majorca. And the same maybe true for the island of Menorca.

Recall that with low population levels damage to geraniums by *C. marshallii* is practically imperceptible. For an untrained person damage is easily mistaken with that produced by other larvae, such as the nocticid moth *Heliothis armigera*. The last species accounts for nearly 100% of all false alarms detected in Catalonia during actions undertaken to prevent the establishment of *C. marshallii* in this Autonomous Community. To a lesser extent the nocticid moth *Mamestra brassicae* (Linnaeus, 1758) is also involved. Both polyphagous species feed upon geranium flower buds and leaves, but do not affect the stems. Geranium leaves are eaten by a
number of polyphagous larvae, which in turn do not normally eat either flower buds or stems. These include the noctuid *Chrysodeixis chalcites* (Esper, 1789) and the tortricid *Cacoecimorpha pronubana* (Hübner, 1799). All these species, though, are not geranium pests, with the damage produced small and generally undetected, and never killing the geraniums, which soon recover their healthy appearance. With *Cacyreus marshalli*, though, it is another matter.

It is likely that the southwest end of Majorca, which includes the towns of Paguera, Santa Ponça and Magalluf, was the area where the pest was first established, and from where it probably invaded the rest of the island. The data we have support this hypothesis: first symptoms of damage in Santa Ponça, first sightings of adults by Stamer in Paguera and by Raynor in Cabo Falcó and Magalluf.

I have collected and reared to adults around 300 *Cacyreus marshalli* immatures taken directly from the wild on Majorca. The specimens represent all stages from eggs to pupae, collected across different months and years, without producing a single parasitoid. Martin Honey obtained identical results with a smaller sample. This is very unusual result for autochthonous lycaenid species, which in the wild show parasitism rates of 20% to 30%, reaching in some cases 50%, as in *Iolana iolas* (Ochsenheimer, 1816) (López Munguira, pers. comm.)

This evidence indicates that to date no local autochthonous parasitoids of caterpillars have adapted to caterpillars of this alocchthonous lepidoptera. Such an adaptation may happen over time. The lack of parasitoids would account for the population explosion of *Cacyreus marshalli*. In fact, this lycaenid has never been reported as a geranium pest in the countries where it is endemic (southern Africa), undoubtedly because there exist autochthonous parasitoids and predators which keep its population levels well below the pest threshold.

In view of the current colonisation of the three main Balearic islands it is no longer possible to establish with certainty which island received the original introduction of *C. marshalli*. However, the fact that the first symptoms were detected in 1987 on the island of Majorca, that the first collected specimens were taken on this island in mid-November 1989, and that three years later, the same story was repeated on Menorca and Ibiza, makes the hypothesis of its initial introduction into the island of Majorca most likely.

The coastlands of the Communities of Valencia and Catalonia, because of their closeness to the Balearic archipelago, are areas presenting the highest risk of pest introduction. However, two towns on the Valenciana coast present an even higher risk because they are regularly connected by ship to the Ibizaan harbour of Sant Antoni de Portmany, where *C. marshalli* is very abundant. Denia in the province of Alicante and Gandia in the province of Valencia are both only about 110 km by sea from Ibiza. Given the high risk of introduction of *C. marshalli* into these localities, necessary preventative measures should be taken by competent authorities in the area.
Measures taken by the Different Administrations

The Community of Catalonia, through its Service of Plant Protection, started an information campaign in July 1992 by producing a poster and an information leaflet about the butterfly. The aims were to prevent the introduction of this pest into Catalonia and, should any focus be detected in Catalonia, to isolate it and impede its spread.

The Community of the Balearic Islands started a series of trials against this pest in June 1992, testing a total of six different insecticides. The results of these trials were positive, all tested chemicals controlled the pest, with no significant differences among them. Treatments will continue during 1993 (J. Gomila, pers.comm.).

In addition the EPPO (European and Mediterranean Plant Protection Organization), to which Spain belongs, showed concern about this pest in Europe and took the first steps to determine whether or not it was appropriate to declare a quarantine status for this species in Europe in May 1992. Its final decision is pending.

Comments on the Economic Importance of Geraniums and Possibilities of Control of the Pest

In the Spanish national ranking of ornamental plants, geraniums (i.e. all cultivated varieties of the genus Pelargonium) are by far the most important in sales volume as well as in employment for production and marketing. Today there are in continental Spain four major geranium growers, who produce 10 million cuttings a year, distributed to about 500 nursery owners across Spain. Altogether this represents a market of over $30 million a year.

The United States and Germany are presently the two leading countries in the production and commercialization of geraniums, with 23% and 16% respectively of the world production, estimated at 500 million geraniums a year. In the U.S.A. the wholesale value of geraniums in 1990 exceeded $160 million, representing 17.3% of all U.S. wholesale bedding plant sales (Berninger, 1992).

As cited above, the last surveys in the balearic archipelago showed that practically all geraniums on the islands of Majorca, Menorca and Ibiza are affected by the pest. People owning gardens, especially those of restaurants with gardens important in creating atmosphere, have already started to substitute geraniums with other species of plants, to the detriment of the geranium industry.

Falling sales of the Spanish wholesale growers are already noticeable. According to data provided by ‘Cultius Roig’, one of the four major growers mentioned above, with headquarters in Catalonia, the number of geranium cuttings despatched to the island of Majorca fell from 78.582 during the 1991-1992 season to 60.471 during that of 1992-1993 (seasons extend from September to March), a 23% decrease. It is not surprising that growers are concerned about spreading of this pest.
Control of *C. marshalli* in geranium nurseries should not be a problem with precautionary insecticide controls carried out regularly.

The control problem is outside the nurseries after the geranium reaches the consumer as a consequence of the biology of the butterfly. This results from the two first larval instars being obligate endophytes while the last two are facultative endophytes (Sarto i Monteys, 1992). Accordingly contact insecticides (most insecticides) will be useful against the non-endophytic phases, but useless against the endophytic phases which are inside the geranium stems and flowers away from insecticide action. Systemic insecticides, i.e. those penetrating inside plant tissues, would be efficient. However, because of their high toxicity, many are not advisable for domestic gardening.

Another worry concerns the possible adaptation of *C. marshalli* to autochthonous species of wild geraniums of the genus *Geranium*, which has already been confirmed with some species in the laboratory (Sarto i Monteys, 1992). The natural foodplant of the butterfly belong to the genera *Geranium* and *Pelargonium* (Clark & Dickson, 1971). If adaptation to wild species occurred, eradication of *C. marshalli* would be practically impossible as there will always exist the risk of reinfestation from wild geraniums.

The most rational alternative would be biological control by its natural parasitoids, to be obtained in the area from which it naturally occurs. Those might accomplish in a short time a much more efficient and cleaner control than that given by chemical insecticides.

In summary, if this pest invaded the Iberian Peninsula or other mediterranean areas from its base on the balearic archipelago, it could

Color Plate 1 (Facing Page)

Figure 1. *Cacyreus marshalli* adult (upperside)
2. *Cacyreus marshalli* adult (underside)
3. Hatched egg on geranium sepal
4. Endophytic phase: first instar larva and early damage on geranium flower (The cavity has been opened to show larva)
5. *C. marshalli* pupa
6. Endophytic phase: second instar larva boring inside a geranium inflorescence peduncle. The gallery has been opened to show larva and its damage. The dark segment above the larva corresponds to its excreta.
7. Exophytic phase: fourth instar larva feeding from outside on a geranium flower. Notice the larva has its first third inside the young flower, after it pierced the flower sepals to access it.
8. Exophytic phase: fourth instar larva "nibbling" a geranium stem from outside.
9. Damage on geranium flowers, pedicels and inflorescence peduncle.
10. Damage on geranium stem. Stem emptied by *C. marshalli* endophytic activity. The interior gallery has been partially opened to show damage. Notice it is fully filled up with larval excreta.
potentially damage all economic activity committed to the production and commercialization of geraniums. Its partially endophytic habits and its possible adaptation to wild autochthonous geraniums, make the long term consequences difficult to predict.

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**Literature cited**


Why Are There So Few Butterflies In The High Andes?

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Abstract. The high Andes have a depauperate butterfly fauna even though they are adjacent to the faunistically rich Amazonian lowlands. Andean oreal butterfly faunas are impoverished even as compared to the mountains of California. There is a tradition of attributing the high-Andean fauna to Holarctic lineages which colonized South America in the Great American Interchange some 2-3 million years ago. Most of the critical taxonomic relationships are too poorly resolved to separate common ancestry from convergence, but in at least the Thecline Lycaenids cladistic studies strongly support convergence. Unusual aspects of the Andean and Patagonian butterfly faunas (including relationships between the tropical Andes and the temperate south, host-plant relationships, and the dominant position of the Pronophiline Satyrids) are reviewed and placed in both biogeographic and paleogeographic contexts.

The richness of lowland Neotropical butterfly faunas is proverbial. The famous latitudinal gradient in biodiversity is not, however, repeated in the butterflies of very high altitudes in the Neotropics. As a result, the latitudinal gradient in biodiversity is oversteepened in the New World tropics relative to temperate latitudes. Equatorial Andean butterfly faunas are both absolutely and relatively impoverished in comparison to both temperate oreal (high-mountain) faunas and adjacent lowland ones. Why should this be so?

The diversity of any high-altitude biota should in theory be related to at least the following factors: (i) the antiquity of the environments in question, (ii) the availability of preadapted biota to colonize them in ecological time, (iii) the availability of sources of potential colonizers which could adapt to oreal conditions in evolutionary time, and (iv) the area of the environments (in terms of species-area relationships).

The oreal butterflies of the Andes and the Sierra Nevada of California, the great mountain ranges of the far west of South and North America respectively, may be compared instructively from a biogeographical standpoint. The comparison is not, however, without problems. Both are generally considered young mountain ranges, achieving their present heights and first presenting the opportunity for the development of an oreal biota in Plio-Pleistocene time. [Molnar and England (1990) have challenged this conventional wisdom. Their position, if correct, would force the re-evaluation of virtually all existing scenarios in montane-oreal biogeography. For purposes of this paper, the conventional assumptions about the ages of the Andes and Sierra Nevada will be accepted.] In
both ranges, the emergence of alpine environments coincided temporally with the climatic instability of the Pleistocene, with its repeated episodes of glaciation. The climatic and vegetational histories of both in the Quaternary are fairly well documented, though the record for both the northern Andes (work of Van der Hammen and Cleef) and the far south (Patagonia and Fuegia; work of Auer, Mercer and others) (see references in Shapiro, 1991a) is denser, more continuous, and in general more satisfactory than what is currently available for the Sierra Nevada (Heusser and King, 1988; Fullerton, 1986). A very detailed picture is emerging for the late Quaternary of forested, humid Chile (Ashworth and Hoganson, 1993) which is unfortunately not very useful for butterflies, since the butterfly fauna of these climates is so poor.

Area comparisons are difficult. The Andes are not a single mountain chain, but a huge complex extending from 10° N to 54° S Latitude, incorporating a vast area of high plateaux, the Peruvian-Bolivian altiplano. The northern Andes are often humid or at least seasonally so; farther south occur various semiarid to extreme desertic regimes, and still farther south the cool-temperate rain forests of archipelagic Chile. The Sierra Nevada is much more modest in scale. Although it is sometimes considered the world’s longest single continuous mountain chain, it demonstrates little north-south climatic differentiation in comparison to the Andes — but then, it is confined within a latitudinal range from 40° to 36° N. Climatically, the oreal Sierra Nevada is most directly comparable to the corresponding sector at the latitude of Mendoza, Argentina, south to northernmost Patagonia (33-44° S). At these latitudes the Andes separate the Mediterranean climate of the Chilean Central Valley from the more continental climate of the Argentine monte (high desert), just as the Sierra stands between the Mediterranean climate of the California Central Valley and the continental desertic or subdesertic climate of the Great Basin in Nevada. A better latitudinal comparison would include the North American Cascades, Coast Ranges, and some of the Alaskan mountains, but detailed butterfly faunistic information was not available for this purpose. The relationship of the Mexican montane (virtually no oreal) butterfly faunas to those of the lowland tropics is complex enough to warrant entirely separate consideration.

The high altitudes of the Andes embrace a variety of oreal vegetation formations, variously called páramo (humid to semiarid) in the north,

Plate 1. Upper left: South Andean - Patagonian small fritillaries (Yramea) (top two rows) and their Boreal counterparts (Clossiana). Both groups feed on Violaceae and Rosaceae, but is this indicative of relatedness or merely another level of convergence? Upper right: Undescribed Yramea (near inca) from northwestern Argentina, showing male “green” melanization convergent to sympatric Colias blameyi and to the Boreal Clossiana improba. Lower: upper- and undersides of male Baltia from Gyaco La, Tibet (5250m) (above) and Phulia from Cordón del Viento, Argentina (3700m).
jalca (humid or subhumid) in Peru, and puna and altiplano (mostly semiarid to arid) in Peru, Bolivia, Chile and Argentina. In the Southern Cone the orreal belt dips ever lower as one progresses south, and south-end-of-the-world taxa become increasingly prominent in the flora. The Andean orreal communities differ tremendously in floristics, faunistics, aspect and seasonality, though a surprising number of plant and animal genera span much of this latitudinal diversity. By contrast, the Sierra Nevada orreal zone is relatively uniform, with a gentle north-south climatic gradient; the most dramatic floristic (and butterfly-faunistic) differences are often defined edaphically rather than latitudinally.

Defining the orreal zone is somewhat arbitrary in those parts of the Andes (as well as in the eastern Sierra Nevada) where there is no “tree line” because there are no trees. In parts of the northern Andes, moreover, deforestation has led to a downslope migration into land formerly occupied by the upper cloud forest. Any quantitative analysis of species-area relationships must also correct the area of orreal communities for the degrees of latitude spanned, and perhaps for other things. All these complications raise doubts about pursuing this approach; the trend, in any case, is obvious and unlikely to be greatly elaborated by such analyses.

The matter of source regions for potential colonizers is critical for our comparison. The Andes directly adjoin the world’s greatest center of biodiversity — Amazonia — and one normally assumes that the lowland habitats and communities are older than their highland neighbors: Amazonia is thus the most obvious source for potential high-altitude colonizers, and the butterfly diversity of Amazonia is the world’s highest. Butterfly diversity in areas near the Sierra Nevada and likely to contribute to its orreal fauna is an order of magnitude lower. By the time the Sierra had reached alpine heights, access to the humid-neotropical Tertiary biota had been shut off. Indeed, the rise of the Sierra itself administered the coup de grâce by altering the rainfall patterns in ways hostile to that biota. Any emerging Sierran orreal biota would henceforth be recruited from what may be broadly characterized as Madro-Tertiary and Arcto-Tertiary sources. (These terms are used loosely, since recent paleovegetational scenarios, e.g., Wolfe, 1985, are considerably more complex than the classic formulation by Axelrod.) At any rate, if we assume that all lowland lineages have an equal initial probability of colonizing the orreal zone (obviously untrue), many more lineages are available to the tropical Andes than to the Sierra Nevada. Ceteris paribus, there should be much more butterfly diversity in the tropical than the Sierran orreal zone. And there is not.

If we consider just ecological time, species preadapted to the physiological rigor of life in the orreal zone might be assumed to be more readily available to the Sierra Nevada. However, this is not absolutely certain. Mercer and Sutter (1982) and Clapperton (1983) suggest that glaciation began in southern Patagonia some seven million years ago, more or less
contemporaneously with the first hints in Alaska. Thus, a cold-adapted butterfly fauna could have existed in the far south of South America, moving north up the spine of the Andes like the Austral flora. However, this presupposes the existence of any Austral butterfly fauna that far back. If there was a Patagonian butterfly fauna, it must have been very undiverse. (There is no paleontological or convincing biogeographic evidence for the existence of an Austral butterfly fauna prior to the breakup of Gondwanaland.) In the large and diversified Laurasian land mass, butterflies would have had much more opportunity to adapt to continental climates than in the Southern Cone of South America; both Arcto- and Madro-Tertiary species might be expected to be better adapted to emerging oral conditions than lowland tropical ones would be, as discussed later.

**How Good are the Data?**

There is no Andean oral butterfly fauna that can be considered truly well-known. This is particularly true of the tropical Andes, where most collecting has been done by transient visitors in an unsystematic way, at random and often inappropriate seasons. The seasonal component of butterfly diversity is very poorly understood in the high Andes. Most of the collecting has been done along trans-Andean highways, and therefore emphasizes the faunas of plant communities found in and near passes. Many habitats have never been collected at all. Thus all the Andean data must be considered provisional. The only attempt to date to collate such information is Descimon’s (1986), using in part the antique data of Fassl (various publications cited in Descimon, loc. cit.) as well as his own field experience. Descimon tabulates “oral faunas” from the Sierra Nevada de Santa Marta in the far north (Colombia) to southern Tierra del Fuego, ranging from two (Santa Marta) to 35 (“S Peru”) species. There is at least a crude suggestion of a double cline of species richness here, which cannot be rationalized by latitude but might be on other grounds. However, the data are very unreliable. The largest faunas are large-scale territorial composites (“S Peru,” “Bolivia”) while the smallest (Santa Marta, Cordillera de Mérida, Tierra del Fuego) are much smaller in both extent and ecological diversity. (The Sierra Nevada de Santa Marta is actually not even part of the Andes.) The definition of “oral” here is also disturbingly vague. There are no butterflies in the oral zone in southern Patagonia and Fuegia, if that zone is defined as being above the tree line. (Two species — Yramea cytheris and Hyposchila microdice — make it just to tree line in the Cordillera Martial behind Ushuaia.) The Patagonian fauna enumerated by Descimon (eight species) does not match any Patagonian fauna I have seen. It omits the rich Satyrid fauna (surprisingly, since this fauna has been monographed), the unexpectedly speciose hairstreaks (not surprisingly omitted since most of the species were still undescribed in 1986, and many still may be), and the blues, but includes Colias lesbia, which is resident only along the Gulf
of San Jorge in the south; yet it leaves out Tatychila autodice and T. vanvolxemii, whose Patagonian ranges match that of C. lesbia. And the Sierra Nevada de Santa Marta fauna omits 50 percent of the recorded butterfly species (Reliquia santamarta, referred to elsewhere in Descimon’s paper!, and an at-that-time unnamed hairstreak). And all of the faunas omit the Hesperidiae altogether.

These are definitional problems, oversights, or results of lack of communication. There is a more profound problem underlying any such analyses, however, and that is sheer ignorance. Even in the temperate Argentine Andes, the alpine faunas cannot be considered well-known. The biogeographically important species Colias mendoza was collected twice near the turn of the century and then lost until 1989, when I rediscovered it — ten minutes’ walk from the transandean superhighway connecting Argentina and Chile at Las Cuelas! The Lycaenid fauna of the same area (the Aconcagua Provincial Park, collected — albeit sporadically — for over a century) was largely undescribed before 1992. Slightly farther north, the “Chilean endemic” Colias flaveola was just discovered in 1988 living happily on the Argentine side of the crest in the Province of San Juan. If this sort of thing is routine in the best-collected and most accessible Andeanoreal fauna, what must be true farther north? Although a Lycaenid sibling species new to science has just been recognized in the Sierra Nevadaoreal fauna (J.F. Emmel, pers. comm.), the overall situation is clearly much better in California than in the Andes. Thirty years ago little of the high country had been collected and many common, widespreadoreal species were thought of as rare and very localized. Now, however, there has been plenty of collecting in midsummer near the accessible passes, and a respectable amount in more remote areas. The beginning and end of the season are less well-documented, although it is unlikely any more new species are to be found then (for the same reason as collectors rarely venture in at such seasons: the weather is too unpredictable for butterflies to count on flying then). Some Sierranoreal areas become snowfree in spring before the forested regions below, and are accessible only on skis or snowshoes during the first few weeks of the flight season. Because many species emerge quickly after snowmelt, this renders our phenological data at least less than ideal. It is, however, safe to say that the broad outlines of Sierranbutterfly faunistics are now well-defined and major surprises are unlikely.

Plate II. Above: Holarctic (left) and South Andean - Patagonian (right) Satyridae of steppe and tundra habitats. All the South American taxa are Pronophili; the Holarctic ones are Maniolini and Erebinii. Below: Repeated evolution of “green” Colias phenotypes in cold climates. Each pair represents a different sublineage, and the non-green specimen is the postulated closest relative of the greens; all are males. Top: C. behrii (California) and C. palaeno (circumpolar). Center: C. nastes and C. hecla (both Alaska). Bottom: C. weberbaueri and C. euxanthe (Bolivia).
In selecting sites for comparison, both Andean and Sierran, I have emphasized accessibility and completeness of coverage. The data (Tables 1, 2) are striking — just as striking, in fact, as Descimon's. It is almost certainly biologically significant that all of the northern Californianoreal faunas are richer than any of the Andean ones, which run from 10° N (Sierra Nevada de Santa Marta) to the temperate Paso Bermejo at the Aconcagua Provincial Park (33° S). Moreover, the impoverishment in species in the Andean faunas is mirrored by their impoverishment in lineages; it is unlikely that other groups will duplicate the recently-discovered richness of the Lycaenid fauna discussed below, because among the butterflies the Lycaenids seem uniquely prone to philopatry, intense host specialization, and cryptic speciation.

**Origins of the Sierran Oreal Fauna**

In a very important paper, Chabot and Billings (1972) demonstrated that the largest contributor to the constitution of the Sierran oreal flora was the Great Basin. This is a flora already adapted to intense winter cold, intense insolation, and a general water deficit year-round, albeit with summer rain. A substantial number of plant species, such as Bitterbrush (*Purshia tridentata*, Rosaceae), Sagebrush (*Artemisia* spp., Compositae), and Daggerpod (*Phoenicaulis cheiranthoides*, Cruciferae) are equally at home in high desert and at tree line. The same is true of several butterflies, such as *Lycaena heteroea*, *Euphilotes batoides*, *Satyrium fuliginosum*, *Lycaides melissa* (all Lycaenidae) and *Pontia occidentalis* (Pieridae). (Of these, *L. melissa* alone is suspected of being more than one genetic species.) The Sierra has the smallest percentage of circumpolar relict plants in its oreal flora of any northern-hemisphere mountain range so far from the Equator. Pleistocene conditions undoubtedly shaped the access of such elements (represented conspicuously by Mountain Sorrel, *Oxyria digyna*, Polygonaceae) to the Sierra. They could have come from the north, northeast or east (across the Great Basin from the Rockies, see below; the “Convict Creek flora” of Major and Bamberg, 1967 is the classic argument for cross-Basin dispersal, subsequently reinforced by studies of pack rat middens (Betancourt et al. 1990)).

Most butterfly taxa of the Sierran oreal zone are conspecific with Rocky Mountain taxa, and the subspeciation in most cases is weak. The Rocky Mountain fauna has been attenuated by distance, but also by extinctions in the Xerothermic (Hypsithermal). During this warm interval a few thousand years ago, cold-adapted organisms were driven to extinction in the low northern Sierra north of Donner Pass, resulting in disjunctions between the northwest California (Klamath-Trinity-Siskiyou-Eddy) and central and southern Sierran oreal zones. The most famous of these is Foxtail Pine, *Pinus balfouriana*. The most important Rocky Mountain oreal element conspicuously missing from the Sierran fauna is the genus *Erebia* (Satyridae). Moreover, the taxonomic distance between the Sierran oreal butterfly fauna and the adjacent low-elevation faunas is not
Table 1. Oreal Butterfly Faunal Composition

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</tr>
<tr>
<td>Pieridae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Euchloinae</td>
<td>2</td>
<td>1</td>
<td>3</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Coliadinae</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>Pierinae</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>Papilionidae</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Hesperiidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pyrginae</td>
<td>2</td>
<td>2</td>
<td>4</td>
<td>3</td>
<td>1</td>
</tr>
<tr>
<td>Hesperinae</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>4</td>
<td>5</td>
</tr>
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<td><strong>Totals</strong></td>
<td><strong>43</strong></td>
<td><strong>40</strong></td>
<td><strong>48</strong></td>
<td><strong>64</strong></td>
<td><strong>49</strong></td>
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<table>
<thead>
<tr>
<th></th>
<th>Sierra Nevada de Sta. Marta&lt;sup&gt;a&lt;/sup&gt;</th>
<th>Morocho-Ticlo&lt;sup&gt;b&lt;/sup&gt;</th>
<th>Cumbres Calchaquies&lt;sup&gt;c&lt;/sup&gt;</th>
<th>Paso Bermejo&lt;sup&gt;d&lt;/sup&gt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Satyridae</td>
<td>0</td>
<td>2</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Nymphalidae</td>
<td>0</td>
<td>2</td>
<td>5</td>
<td>4</td>
</tr>
<tr>
<td>Lycaenidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Theclinae</td>
<td>1</td>
<td>3</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td>Plebeinae</td>
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<td>3</td>
</tr>
<tr>
<td>Pieridae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coliadinae</td>
<td>0</td>
<td>3</td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Pierinae</td>
<td>2</td>
<td>5</td>
<td>8</td>
<td>3</td>
</tr>
<tr>
<td>Hesperiidae</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pyrginae</td>
<td>0</td>
<td>2</td>
<td>2</td>
<td>1</td>
</tr>
<tr>
<td>Hesperinae</td>
<td>1</td>
<td>3</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td><strong>Totals</strong></td>
<td><strong>4</strong></td>
<td><strong>22</strong></td>
<td><strong>33</strong></td>
<td><strong>21</strong></td>
</tr>
</tbody>
</table>

Notes: Strictly migratory or casual spp. omitted from all tallies. \(^a\)Shapiro, Palm & Wcislo 1981. \(^b\)Shapiro 1978 + unpublished. \(^c\)Shapiro, unpubl. data 1972-90. \(^d\)Garth & Tilden, 1963 + unpublished from various sources. \(^e\)Colombia, Dept. Cesar, above 3500m. \(^f\)Peru, Dpto. Junín, above 4400m. \(^g\)Argentina, Prov. Tucumán, above 3000m. \(^h\)Argentina, Prov. Mendoza, above 2700m. \(^i\)Shapiro, unpublished data + data from other sources.
### Table 2. General characteristics of oreal butterfly faunas in North and South America and their regional affinities.

<table>
<thead>
<tr>
<th>Some Important Andean Oreal Butterfly Genera</th>
<th>In Holarctic oreal?</th>
<th>In lowland Neotropics?</th>
<th>In Patagonia?</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hesperiidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pyrgus</em></td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Hylephila (bouletti group)</em></td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>Pieridae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Colias</em></td>
<td>Yes</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Tatochila</em></td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Hypsochila</em></td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Phulia</em></td>
<td>No, but cf. <em>Baltia</em></td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td><em>Pierphulia</em></td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td><em>Piercolias</em></td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td><em>Infraphulia</em></td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td><em>Reliquia</em></td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td><strong>Lycaenidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>&quot;Itylos&quot; sensu lato</em></td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Eiseliana</em></td>
<td>No</td>
<td>No</td>
<td>No</td>
</tr>
<tr>
<td><em>Penaincisalia</em></td>
<td>No</td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>Nymphalidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Yramea</em></td>
<td>No, but cf. <em>Boloria</em></td>
<td>No</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Vanessa (seasonal migrants?)</em></td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td>(various Pronophilini)</td>
<td>Entire tribe absent</td>
<td>Yes</td>
<td>Yes</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Some Important Sierran Oreal Butterfly Genera</th>
<th>In Andean Region?</th>
<th>In Great Basin?</th>
<th>In Rocky Mountain Oreal?</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Hesperiidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pyrgus</em></td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Hesperia</em></td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>Pieridae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Pontia</em></td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Colias</em></td>
<td>Yes</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>Lycaenidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Lycaena</em></td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Agriades</em></td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Lycaeides</em></td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>Nymphalidae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Boloria + Brenthis</em></td>
<td>No, but cf. <em>Yramea</em></td>
<td>(Yes)*</td>
<td>Yes</td>
</tr>
<tr>
<td><strong>Satyridae</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>Oeneis</em></td>
<td>No</td>
<td>Yes</td>
<td>Yes</td>
</tr>
<tr>
<td><em>Neominois</em></td>
<td>No</td>
<td>Yes</td>
<td>(Yes)*</td>
</tr>
</tbody>
</table>

Notes: *Only in montane habitats. †Present mostly below the oreal zone in the Rockies.*
striking. All of the orale species have lower-elevation congeners nearby (except Neominois which only goes lower much farther east), and a rather large number of orale species extend some distance below tree line as well. There is none of the sense, described by Descimon for the Andes, of entering a different world when one passes from the montane to the orale fauna.

The orale butterflies of far northern California (which has only tiny areas of climatically treeless highlands) are a southward extension of the Cascadian fauna. They are much less like the Rocky Mountain fauna than is the Sierran one. The orale-endemic Sierran Oeneis (ivallda and stanislaus) present the strongest case for cross-Basin dispersal (Porter and Shapiro, 1990). To the contrary, the Fritillary Speyeria mormonia connects up its Cascadian and Sierran subspecies via a series of small, relict populations (Mount Eddy, Ball Mountain, Warner Mountains) which constitute our best butterfly evidence so far of a northerly access route, though by no means conclusive.

Although North America acquired some butterfly taxa in the Great American Interchange of flora and fauna which commenced some three million years ago (Stehli and Webb, 1985; Simpson, 1980), the impact on the Sierran alpine butterfly fauna was nil; specifically, no Andean butterflies appear to have colonized the Sierra. One Andean butterfly (Nathalis iole, which is a montane or orale species in Colombia, not noted by Descimon) did successfully occupy North America — but in desert, montane and warm-temperate, not orale communities. Only one Sierran orale species (Thorybes mexicana ssp.) is even of Madro-Tertiary provenance! Otherwise, the Sierran orale fauna is ultimately all Arcto- Tertiary or derivative therefrom.

The genus Pyrgus (Hesperiidae) is of special interest because it has speciated in the Andes and Patagonia to a greater extent than in North America, and several of its species are orale. No phylogenetic analysis of Pyrgus has been done, but superficially it does not appear that there has been any communication in either direction between the western North American and the Andean orale Pyrgus faunae. The large Andean Hesperiid genus Hylephila, with several important orale taxa from the Sierra Nevada de Santa Marta to Patagonia, apparently entered lowland North America as the subtropical weedy species H. phyleus in or after the Great American Interchange, but never penetrated the mountains.

**Origins of the Andean Oreal Fauna**

The Andean orale faunas are derived from a remarkably small number of lineages, probably fewer than 20, most of which have been attributed by most authorities to invasion from the north at the time of the Great American Interchange. If this notion is correct, the imbalance is very striking: northern invaders allegedly defined the entire Andean orale fauna, while southern ones had zero impact in the Sierra Nevada.
The notion of a northern origin for the Andean oreal fauna originated in the 19th Century. Initially many Andean species were described in Palearctic genera, based on superficial, but often strong, resemblances in habitus. Eurocentrism and a subsequent analogy between the migrations of Homo sapiens and the supposed migrations of butterflies in geologic time colored subsequent phylogenetic speculation. Dixey (1894, pp. 322-326), for example, wrote:

In the Chilian or Andesian division of the Neotropical Region we find the genus Tatochila, which appears not to belong to the regular Neotropical Pierine stock, but to be closely related to the Palearctic Pontias. It is conceivable that the latter stem may have spread from Asia into the western portion of the Nearctic, and thence down the mountain chains to the south... Another indication of the same invasion is afforded by the genus Phulia, now found with the nearly-allied Tatochila only in the Andesian or Chilian Subregion, to which it no doubt made its way along the great mountain chains in a similar manner. Its close ally Baltia remains in the high lands of Central Asia, where it bears much the same relation to Synchloe as Phulia to Tatochila... The earliest species of Synchloe were undoubtedly differentiated from Pontia or Baltia in the Palearctic Region, from which the genus spread (probably eastwards) into the Nearctic.

This is in keeping with the attitude reflected in a famous quote from Wallace (1876):

The north and south division of the modern biota represents the fact that the great northern continents are the seat and birthplace of all the higher forms of life, while the southern continents have derived the greater part, if not the whole, of their vertebrate fauna from the north...

Dixey's scenario was repeated by Klots (1932), Mani (1968), and even Descimon (1986, p. 526), who wrote:

In summary, it is clear that the Neotropical and southern temperate regions contributed little (or nothing) to the oreal butterfly fauna of the Andes. Its affinities lie instead with the Holarctic realm.

This is certainly in keeping with the traditional viewpoint of plant geographers, who noted early the conspicuous predominance of Holarctic plant lineages above the Andean tree line. Such genera as Castilleja (Scrophulariaceae) and Lupinus (Leguminosae) are conspicuous elements in the northern Andean páramos; they are clearly of northern provenance and diminish in importance southward, as one would expect if they were fairly recent arrivals. With striking symmetry, most of the lowland plant diversity — and with it, most lowland tropical plant lineages — disappears at tree line. The turnover in floristics was attributed by Walter and Medina (1969) to the difficulty in acclimating evolutionarily to the diel thermal regime in the páramo — with daily
maxima as high as 15-20 °C but nightly minima below freezing most nights of the year.

If the Andean orale regime arose at about the same time as the Great American Interchange, it can be argued, Holarctic cold-adapted plants travelling by sweepstakes dispersal would probably arrive before many lowland-tropical plants could have adapted to highland conditions. These plants, and the cool-adapted Austral flora migrating north from Valdivia, would then have competitively locked up the orale zone and prevented much penetration from the lowland floras. In turn, the Holarctic butterflies, preadapted to feed on Holarctic plants, would have followed them south. The lowland butterfly fauna, with no coevolutionary history of dealing with Holarctic plants and their phytochemistry, would have been deterred if not excluded from the highlands. This is essentially Descimon’s scenario. It is in the great tradition of narrative biogeography: seductive, plausible, and difficult to falsify. Descimon’s argument has been falsified for one lineage, the hairstreaks (Theclini or Eumaeini, Lycaenidae). Kurt Johnson and his collaborators have shown that the various high-Andean and Patagonian hairstreaks, mostly undescribed or known from very few specimens, and treated by most workers including Descimon as of Holarctic affinities, are merely convergent in phenotype to Holarctic hairstreaks (Johnson 1991a,b; Johnson, Miller & Herrera 1992). They really are derived from the lowland-tropical hairstreak fauna. This is true of both the “Andean Incisalia” and the characteristic genus Eiseliana of the Argentine puna. Furthermore, most of the hairstreak genera represented in the high-Andean fauna have congenerics in Patagonia, and most are richer in the south than in the north. One of Johnson’s new genera has species from orale Colombia to the Argentine province of Chubut. (This repeating pattern is the same as that seen in the Pronophiline Satyrids, discussed further below.)

Are any other components of the orale fauna likely to be re-evaluated in this way? There has been an explosion of interest in the Andean blues (Lycaenidae, Polyommatini) resulting in unfortunate taxonomic confusion (Balletto, 1993; Bálint and Johnson 1993a,b; Bálint 1993). Their greatest richness is in northern and central Argentina, Bolivia and Chile. The work of these authors has demonstrated convincingly that the previous appearance of low diversity in these blues was illusory. The ranges of most of the newly-recognized species are very poorly known, and it is not obvious whether geographic or ecological replacement, seasonal allochrony, or sympathy and synchrony properly define the structure of all this richness. Nor has the phylogenetic position of the Andean fauna — along with its geographic relationships — yet been defined. To do so is urgent, especially vis-à-vis the Asian orale and steppe fauna.

Meanwhile, Lee Miller (pers. comm.) has revised his opinion of the Pronophilini, incorporated by Descimon in his scenario. Miller now believes that the family Satyridae is of Gondwanian origin (no later than
early Cretaceous, obviously) and only entered the Northern Hemisphere by riding India into the underbelly of Laurasia. By this scenario, the Pronophilines are primitively autochthonous in South America. When we recall that the oldest butterfly fossils are only Oligocene, it is evident that the days of extreme conservatism in blaming everything on the Pleistocene and the Great American Interchange are over. The danger now is of over-reaction — of projecting butterfly evolution back into the Devonian, if not the Pre-Cambrian.

**FURTHER CONSIDERATION OF THE PIERIDAE**

Descimon focuses especially on the Pierini and the genus *Colias*. Let us consider *Colias* first. Again, our modern scenario reflects Dixey, 1894 (pp. 326-327):

No other genus in the whole subfamily has so extensive a range as *Colias*...

Here again, I have little doubt that the site of original divergence is Asiatic... after populating the Palearctic and Nearctic continents with numerous species [it has] passed down the great mountain chains of Central and South America to Chili and Patagonia, and has even established outposts in Venezuela and the Sandwich Islands (the occurrence of *Colias* in the last-named locality is, however, not entirely free from doubt).

All taxonomists but Berger (1988) have treated the Andean *Colias* implicitly as a monophyletic group, displaying little morphological change but great adaptive radiation in color, pattern and sexual dimorphism which more or less duplicates what occurs elsewhere in the world. (There has been no global cladistic analysis of *Colias* — perhaps surprisingly.) *Colias* is overwhelmingly a Holarctic genus, with greatest diversity in Asia both in terms of species and species-groups. Hardly any *Colias* occur in forests; they are steppe insects *par excellence* and their current distribution in the Holarctic shows the influence of the periglacial steppe-tundra. Most of the species whose life-histories are known feed on Papilionaceous legumes, especially *Vicia, Lathyrus, Trifolium, Astragalus* and related genera. In the Holarctic there are small groups of willow- (Salicaceae) and Ericaceae-feeding species (more diverse in the Nearctic than in the Palearctic). The southernmost Ericad feeder, *C. behrii*, is endemic to the central and southern Sierra Nevada, probably of Pleistocene origin and derivative of *C. palaeno* (or perhaps *C. pelidne*).

The Andean *Colias* reared to date are all Papilionaceous-Legume feeders. Most of them now routinely breed on naturalized clover (*Trifolium repens*) and/or alfalfa (*Medicago sativa*) and in a few cases have yet to be found in anything else. They seem most closely related to the legume-feeding Holarctic group that includes *C. hecla*, but this remains to be rigorously demonstrated. This is mainly a boreal group, with oreal relict populations south to the central Rocky Mountains. The southernmost Nearctic *Colias, C. philodice* and *C. eurytheme*, reach Guatemala but belong to a different group unlikely to be closely related to the Andean
species. Andean species apart, the only other Southern Hemisphere Colias is C. electo, with a scattered, relictual distribution in South Africa and montane tropical Africa and clearly of Palearctic provenance. Taken together, all of this suggests the classic scenario: penetration of the Andes by the C. hecla group in the Great American Interchange, followed by adaptive radiation and speciation. This fits the entire history of the Andean Colias into three million years.

Biochemical genetics ("molecular clocks") may give us a test of this scenario, if time points can be established to calibrate the rate of molecular evolution. In the meantime, it is not on its face unreasonable. The amount of morphological evolution in the Andean Colias is less than one routinely finds in exuberant insular lineages on similar time scales. Various plants whose occurrence in the Andes has been attributed to the Great American Interchange have undergone substantial morphological change; there are woody Crucifers in northern Colombia and the world's largest lupine, Lupinus paniculatus, occurs in Peru, for example.

The biggest problem is Colias ponteni, also known as C. imperialis. It is the Colias allegedly from the Sandwich Islands (Hawaii) referred to in the quote from Dixey, above. It was put in its own genus, Protocolias, by Petersen (1963) on the basis of its remarkably primitive genitalia. Although it is indisputably the most primitive living (or recently extinct) Colias, no one really knows where it came from, and it has never been collected again. Shapiro (1993) tells its bizarre story. Gerardo Lamas (in litt.) believes the actual type locality was Cerro Tarn, near Port Famine, Magallanes (Chilean Patagonia). But this is in the heavily forested, perhumid part of the region, an unlikely Colias habitat. Another "Port Famine" butterfly, one actually collected by Darwin, was recently rediscovered in a different part of Magallanes in steppe, where it belongs (Herrera and Pérez d'A, 1989).

Biogeographers are perennially embarrassed by their inability to define criteria for identifying "centers of origin" (or to winnow the long list of contradictory criteria proposed by various authors). But by most such criteria, Colias should have originated in Laurasia, and the tip of South America is the last place to expect its center of origin. Thus C. ponteni, if truly Patagonian, must be rationalized away as a primitive species stranded in an out-of-the-way place and preserved (at least until the 1850s) by virtue of a lack of predators and competitors: a butterfly tuatara. But what of its relation (if any) to the other Andean Colias, and their Holarctic affinities?

To sum up: Descimon may be right, but declaring victory is decidedly premature. It would be very extraordinary if the entire Andean oreal fauna were of Holarctic origin. Just as even the far-north Andean oreal flora contains autochthonous elements (e.g., the Espeletiinae, Compositae) as well as some derived from the lowlands — as noted by Descimon — so, too, the butterfly fauna is likely to be heterogeneous. The phenotypic convergences are so strong that biochemical-genetic and cladistic evi-
dence are absolutely necessary before any claim of homology can be accepted. As of now, there is no group, not even Colias, for which the claim of Holarctic origin can be considered fully established; and there is one — the hairstreaks — for which it has been virtually disproved.

The Pierids (Shapiro 1991a) and the blues, and perhaps Colias, all suggest ties to central Asia — presumably via a “Camelid scenario.” Other groups that “should” partake of such a relationship are conspicuous by their absence in the Andes (Lycaena, Parnassius, various Holarctic Satyrids). Their absence alerts us to the possibility that the “ties” may not be real. Alternatively, the characteristic boreal-oreal fauna may not be as integrated a unit as we think.

The small Andean fritillaries (Yramea, Nymphalidae) have been linked with the small Holarctic ones (Boloria, Clossiana, Brenthis) and with the afro-tropical highland Issoria. Their true phylogenetic relationships are as yet unknown though two researchers (T. Pike and G. Lamas) are working on the problem. It now appears that the Austral Yramea feed on both Violaceae and Rosaceae (Acaena). This is precisely the pattern one finds in the boreal Boloria. The cynic will react to this news with a shrug and a “So what?”

BACK TO THE IMPOVERISHMENT

Why are the Andean-oreal faunas so impoverished? The question is not why the Sierran oreal fauna is so big, but why the Andean one is so small. As we have seen, the emerging Sierran oreal biota was recruited from more or less nearby sources with a history of dealing with increasingly harsh climates. In fact, the South American oreal biota was either recruited from nearby lowland tropical sources, with little or no history of dealing with such climates, or from a distant Holarctic biota, better adapted but with limited access — or some combination of both. Either way, severe hardships existed which would tend to limit the number of lineages able to establish themselves successfully in just a few million years at most. And either way, we would expect a nearly insular situation — full of “vacant niches” and offering grand evolutionary opportunities. As Descimon (1986, p. 520) states:

The impression — subjective, of course — that is felt by a naturalist looking at the rhopaloceran fauna of the Andes is one of “unsaturation”: many ecological niches appear “empty,” in particular many food plants remain without insects... Many times, wandering in the Great Andes, I stopped to look at a peculiar-looking biotope, in which I guessed there surely were special — and interesting, perhaps new! -butterflies. And there were none.

As noted above, the prominent role of Holarctic plants in the Andean oreal flora would facilitate the establishment of Holarctic butterflies already associated with them. Descimon and I agree that host utilization in the Andes is very spotty, and both of us predict evolutionary radiation
onto new hosts if in fact the oréal fauna is young and in disequilibrium. In this regard, recent data on host utilization are very striking.

Given the host relationships of the Polyommatini in the Holarctic, it is perhaps not very surprising that at least four species of Andean blues have now been found breeding on species of the large and diversified Holarctic genus *Astragalus* (Shapiro, unpublished). This Papilionaceae Legume would be on most lists of Great American Interchange arrivals in the region. It is very surprising, however, to find Pierini eating these plants.

The ancestral hosts of the Holarctic Pierini are mustard-oil-containing plants. These compounds (glucosinolates) are found in the Cruciferae, Capparidaceae, Resedaceae and Tropaeolaceae. The first three are phylogenetically close, while the fourth is generally considered much more distantly if at all related. Most of the Andean Pierini reared so far (various *Tatochila* and *Hypsochila*, *Reliquia*, *Phulia*, *Pierphulia*) feed on Crucifers and/or Tropaeolaceae. The Crucifers have been considered Great American Interchange arrivals in the Andes; they have undergone much evolution especially in the north, but unfortunately their fossil record is essentially nil. They are absent from the lowland tropics, except as introduced weeds. Capparidaceae occur as shrubs in the xeric habitats of South America. Their habitats being fairly young, they may be also. Tropaeolaceae is an autochthonous Neotropical family, including both high-Andean and Patagonian taxa. If the ancestors of *Tatochila* and *Hypsochila* came south from the Nearctic, they presumably had chemically preadapted resources waiting for them. It now appears, however, that the genus *Tatochila* (as presently construed, almost certainly polyphyletic) has shifted from these plants onto Papilionaceous Legumes twice and perhaps three times, and the sister-genus *Hypsochila* at least once. The Legume genera involved are *Astragalus*, *Vicia*, *Lathyrus*, and (probably in the past century or so) *Trifolium*. In one case (*Tatochila distincta*) the animal can be reared successfully on Crucifers, but apparently only uses Legumes in nature. (See Shapiro, 1986, 1990, 1991b.)

This is an exceedingly odd pattern, insofar as no other Crucifer-feeding pierine anywhere else in the world has made such a switch despite plenty of sympatry with appropriate Legumes. No “chemical bridge” between the plant taxa has been recognized (which is not to say one may not occur). What is strangest, though, is the repeated colonization of one plant group derivative from the Nearctic from another. The case for adaptive radiation in host selection in the oréal biome would be much stronger if the move had been onto plants of tropical American or Austral affinity!

**What About Patagonia?**

The Patagonian steppe is vegetationally and climatically reminiscent of the northern Great Basin desert of western North America, and for anyone who has worked in both areas, comparisons are inevitable.
The Patagonian butterfly fauna is exceedingly unbalanced, being dominated by the Pronophiline Satyrids. It is, however, fairly species-rich, and what is most striking is the fact that several of its lineages extend all the way to the northern Andes in the orale biome. Yet, despite the climatic and vegetational diversity of this vast region, only a handful of species occur in the north, sometimes only one per lineage, while often several occur sympatriically in the south. Some of this may be merely an artifact of poor collecting in the Andes, and many of the Patagonian taxa, especially of Lycaenidae, are only very recently recognized. Moreover, the number of species is no reliable indicator of the "center of origin" for a genus, if such things can be inferred at all. Still, one gets the impression of groups that developed and radiated in the south and then moved north up the spine of the Andes, a pattern seemingly inconsistent with the bigger picture. It is not difficult to account for speciation in the south; the problem is to account for the lack of it in the north.

The high Andean-Patagonian connection is observed over a broad taxonomic spectrum. (See fig. 4.11 in Humphries and Parenti, 1986 and accompanying discussion; these authors give credence to a radical hypothesis — "Pacifica" — to account for it, but the timing would not work for butterflies. The postulated events are too early, requiring modern butterfly tribes to have differentiated in the Mesozoic.)

A peculiar problem affecting the blues, hairstreaks and pronophilini in Patagonia is very persistent convergence or stabilizing selection to the same color patterns — so that most of the hairstreaks found flying together look alike, even if not very closely related, and similarly for the Pronophilines. In both lineages there is a red blotch on the forewing underside, a theme found in some Holarctic Satyrids and in Callipsyche behrie, but never as a pervasive and defining trait of a whole fauna anywhere else!

The two major Satyrid lineages in South America are the Euptychiini, which are tropical and barely enter the temperate Argentine mid-latitudes, and the Pronophilini, which have speciated in two seeming bursts: one in the northern and central Andes associated with the Andean bamboos, the other in the altiplano and Patagonia on bunch-grasses. This second radiation is more diverse in lowland Argentina than in the Andean highlands (at both generic and specific levels). Some taxa, however, occur in both regions. The beautiful Mariposa Plateada, Argyrophorus argentatus, has a fascinating distribution which advertises Quaternary biotic movements. It occurs as relict local populations in the Chilean coast range and at high altitudes in the cordillera proper, in Coquimbo, San Juan, and Mendoza, thence south along the eastern foothills through the Uspallata Valley, to Aluminé, Zapala and Bariloche, reaching the immediate coast at Comodoro Rivadavia well south of its most austral inland outposts. Like the distribution of the Pierid Tatochila theodice (Shapiro, 1991b), this is in accord with the paleoclimatic reconstructions of Caviedes and Iriarte (1989) and Caviedes (1990). This work
envisions repeated north-south biotic migrations on both sides of the Andes, with movement sometimes from west to east and sometimes the reverse across the passes. Their model provides the best explanation of the Patagonian character of the Chilean Central Valley fauna. In the longer term, it implies the Patagonian butterfly fauna was already defined at the species level by the mid-Pleistocene, if not earlier. Unfortunately, these movements probably obliterated any biogeographic evidence bearing on the origins of that fauna—which may be approachable only molecularly or cladistically.

The Patagonian and Great Basin climates, and perhaps faunas, are probably of similar antiquity. Although the Patagonian fauna is much more unbalanced than the Great Basin one, insofar as it is dominated by Pronophilini, the overall species numbers are similar (Austin, 1985; Austin and Murphy, 1987). However fuzzy this statement, it certainly contrasts with the situation in the orale zone. This once again forces us to think about why the Andean orale fauna is so poor.

**Coda**

In 1968, Dunbar discussed the eco-evolutionary status of polar biotas and concluded that their impoverishment was probably due — in a variety of ways — to their geologic recency; they were both ecologically and evolutionarily immature, and the processes of maturation in both series were likely to be mutually reinforcing. The basic problems faced by an emerging polar biota are the same as those confronting the orale butterfly fauna, except that seasonal extremes are replaced by diel ones. In this regard it is non-trivial that boreal butterfly faunas are consistently much richer than Andean orale ones, and entrain a much broader selection of lineages from the source faunas. This almost certainly reflects the role of the periglacial environment, whence major elements of both our Arctic and alpine-orale Holarctic biota derive. The character of this environment has been much debated — tundra, steppe-tundra, steppe (French 1976, Lamb and Edwards 1988, Pielou 1991) and it is worth noting that the butterflies whose ranges suggest derivation from it also suggest a dry tundra or steppe-tundra, as shown in the work of Kostrowicki (1969). The possibility of an equivalent antecedent in the altiplano or in Patagonia for the Andean orale butterflies remains effectively unexplored. If there was none, that in itself might explain much about that fauna.

Whether the Andean orale butterflies originated from the Holarctic or from the adjacent lowlands, their low diversity is very likely a function of time. If it turns out that the high Andes are much older than we have thought, however, the mystery, already deep, will become unfathomable.

**Acknowledgments.** This paper was originally prepared for a symposium at the 1990 Pacific Slope Section meetings of the AAAS at the invitation of Robert Dowell. I owe a great debt to my friend and sometime field companion Henri
Descimon for having the courage to take on these issues and to gather what scattered data there were bearing upon them. My own high-Andean work was benefitted from three NSF grants, most recently BSR-83-0692. My Sierran work has been underwritten mostly by California Agricultural Experiment Station Project CA-D*-AZO-3994, “Climatic Range Limitation of Phytophagous Lepidopterans.” I thank Gerardo Lamas, Steve Courtney, Peggy Stern and José Herrera G. for much stimulating discussion and insight, and Hansjürg Geiger, Adam Porter, and Chris Nice for extraordinarily fruitful laboratory collaborations. The profound ignorance displayed herein is, however, all mine.

I dedicate the paper to the memory of José Herrera G., who recognized the problems very early, and of Adrienne Venables, who had she lived might have solved them.

LITERATURE CITED


New Mexico butterflies: checklist, distribution and conservation

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Abstract. This systematic list is intended to include every butterfly taxon observed in New Mexico. New Mexico has one of the most diverse butterfly faunas in the United States, with about 300 species. Taxon distribution in New Mexico is provided at the county level. Conservation status and concerns in New Mexico are also presented. The validity of questionable reports from this state are discussed and resolved where possible.

About New Mexico
New Mexico (NM) is the fifth largest state in the United States. Because of its location, NM supports elements of several regional butterfly faunas, including Great Plains, southern Rocky Mountains, Great Basin and Colorado Plateau, Sonoran and Chihuahuan Deserts, and Sierra Madre. Land surface elevations range from 914 m to 4012 m above sea level, supporting life zones from lower Sonoran to Arctic. Annual precipitation varies, primarily with latitude, from less than 25 cm to more than 110 cm. Number of frost free days varies locally from less than 80 to more than 220. The Continental Divide crosses the state from north to south and provides headwaters for major drainage basins such as the Colorado River, Rio Grande, Pecos River, and Arkansas River. Proximity to Mexico allows frequent summer influxes of subtropical species.

NM has always been a rural state with few resident lepidopterists. Reliable documentation of our butterfly fauna began in the 1870s and 1880s, but was sporadic until the 1960s. Many years of effort by the few NM lepidopterists were needed to gather enough information about our large, diverse state to issue this comprehensive state list. Now that all available information is compiled, it constitutes an impressive list, coming to about 300 species. Perhaps 95 percent of all breeding butterfly residents have been identified and confirmed. Much work remains to be done to identify remaining residents and to understand further the biology and distribution of known residents.

Faunal List Organization
Butterflies are presented here in the format and taxonomy of Scott (1986). Scott’s approach does not adequately describe every situation in NM, however. In such cases the issues are discussed in Notes, which follows the list. This document does not attempt to make taxonomic revisions or name new taxa.
Family names are given in upper case letters. For all taxa, genera, species and subspecies are italicized, with genera capitalized. Taxon authors are presented in normal font. A common name usually follows each scientific name.

Next are given the counties in which each taxon is known to occur. NM's 33 counties are shown in Figure 1 and abbreviated as follows:

- Bernalillo Be
- Catron Ca
- Chaves Ch
- Cibola Ci
- Colfax Co
- Curry Cu
- DeBaca DB
- Dona Ana DA
- Eddy Ed
- Grant Gr
- Guadalupe Gu
- Harding Ha
- Hidalgo Hi
- Lea Le
- Lincoln Li
- Los Alamos LA
- Luna Lu
- McKinley MK
- Mora Mo
- Otero Ot
- Quay Qu
- Rio Arriba RA
- Roosevelt Ro
- Sandoval Sv
- San Juan SJ
- San Miguel SM
- Santa Fe SF
- Sierra Si
- Socorro So
- Taos Ta
- Torrance To
- Union Un
- Valencia Va
- Sandoval Sv

The breeding or residency status of each taxon is given next. Residents overwinter and breed regularly in NM. Seasonal residents regularly fly in from subtropical areas during the warm season and may produce one or more generations before winter weather eliminates survivors. Strays wander into NM more or less by accident, with no known evidence of breeding. Hypothetical species are those whose presence here has been reported, then either refuted or seriously questioned, as signified by brackets []. Queries (?) indicate uncertainty. The final entry for some taxa is a numerical reference to one of the explanations in Notes.

Sources of Information
This document represents the accumulated knowledge and personal observations of the authors, observations of associates, contents of personal collections, published papers, and other published accounts.

The following public collections were reviewed for NM specimens: Allyn Museum of Entomology (AME), American Museum of Natural History (AMNH), California Academy of Sciences (CAS), Carnegie Museum (CM), Denver Museum of Natural History (DMNH), Eastern New Mexico University, Portales (ENMU), Illinois Natural History Survey (INHS), Los Angeles County Museum of Natural History (LACM), New Mexico Highlands University, Las Vegas (NMHU), New Mexico State University, Las Cruces (NMSU), United States Museum of Natural History, Smithsonian (USNM), University of Kansas (UK), and University of New Mexico, Albuquerque (UNM).

Historical Foundations and Acknowledgments
Many lepidopterists, professional and amateur, played key roles in the original observations assembled in this document. Key contributors to the knowledge of the NM butterfly fauna include:
Frederick H. Snow and his students, from the University of Kansas, contended with numerous frontier obstacles in the 1880s. They travelled newly established railroad lines into NM and made collections near Las Vegas, Santa Fe, Socorro, Deming and Silver City. Much of Snow's collection remains at UK.

T. D. A. Cockerell was a faculty member of the NM College of Agricultural and Mechanical Arts, a precursor of NMSU, in Las Cruces. He and his associates performed entomological research and collected butterflies near Las Cruces, Las Vegas, Alamogordo and Ruidoso in the 1890s and early 1900s. He published numerous scientific papers and described several taxa. Some of his specimens remain in the collections at NMSU.

John Woodgate collected butterflies intensively in NM during the period 1904 - 1925. He concentrated his work at Jemez Springs in the
Jemez Mountains, and near Fort Wingate in the Zuni Mountains. Several new taxa were described from material he collected.

John P. Hubbard directed the Endangered Species Program in the New Mexico Department of Game and Fish in the 1970s and 1980s. His biologists collected butterfly specimens in areas of special biological interest in NM, such as the Animas Mountains in the “boothheel” and Sierra Grande in Union County.

For many years Clifford D. Ferris, of the University of Wyoming, has researched butterflies in southwestern NM, emphasizing Grant County. From this work he has published several important scientific papers.

Michael E. Toliver studied NM butterflies statewide in the 1960s and 1970s and published scientific papers. He was the first to compile butterfly taxa into a NM fauna (Toliver and Holland, 1977). Toliver reviewed Snow’s 100-year old specimens at UK, resolved several questions raised by Snow’s reported observations, and updated his nomenclature. This document is dedicated to Mike, who first imagined it.

In addition to the pleasures of association with Drs. Ferris and Toliver, we have been encouraged and supported in our efforts by Drs. John M. Burns, Gregory S. Forbes, Paul A. Opler, Robert K. Robbins, James A. Scott, Ray E. Stanford, other members of the Lepidopterists’ Society, and other observers of butterflies.

**Conservation Issues**

Despite NM’s rural character, several NM butterflies warrant attention from a conservation perspective. Of principal interest are areas where there is endemism at the subspecies level, such as the Trans-Pecos desert mountains, the Sacramento Mountains, the Raton Mesa complex, and areas which support Pleistocene relics.

The Trans-Pecos region of southern NM supports several taxa with limited distributions, such as *Fixsenia polingi*, *Chlosyne chinatiensis*, *Callophrys henrici solatus*, and *Agathymus mariae*. Populations of *F. polingi* are known only from three sites in NM: Organ Mountains, Guadalupe Mountains, and Capitan Mountains; plus a few places in west Texas (TX). Larvae feed only on oaks (*Quercus* spp.). It is not known how extensive or healthy these populations are as a whole, but the Guadalupe Mountains locality illuminates some of the issues. The Guadalupe Mountains straddle the NM/TX border. On the TX side, under the jurisdiction of Guadalupe Mountains National Park, larval host oaks thrive and *F. polingi* is widespread. On the NM side, however, where the Lincoln National Forest manages the land, host oaks and *F. polingi* are virtually nonexistent. Oaks and *F. polingi* are sensitive to land management practices such as grazing and fires in that area.

The Sacramento Mountains/Sierra Blanca range, just north of the Trans-Pecos is a prominent biogeographic island of disjunct montane butterflies. This range climbs to 3658 m elevation covers a large area, and is 150 km from comparable upland habitats to the north and west. Taxa
with relict Pleistocene populations there include: *Harkencleaus titus*, *Callophrys Sheridanii*, *C. apama*, *Glaucopsyche lygdamus*, *Plebejus icarioides*, and *Phyciodes thatos* Type B. Although taxonomic study is still needed, most butterflies of interest here probably are differentiated at the subspecies level. Endemic subspecies already described for this area include *Speyeria atlantis capitansensis* and *Euphydryas anicia cloudcrofti*.

The Raton Mesa volcanic complex in northeast NM supports several taxa of interest due to its harsh climate, high elevation exceeding 2200 m, and long eastward extension from the Rocky Mountain Front Range into the Great Plains. Among the subspecific endemics in this area are *Oeneis alberta capulinensis*, *Speyeria atlantis ratonensis*, and *Poanes hobomok wetona*. Other species reported from here are unknown, or nearly so, from elsewhere in NM: *Polites peckius*, *Atrytonopsis hianna*, and *Satyrium liparops*. NM colonies of these species are very local and very few in number.

NM presently is a semi-arid state where water can be locally scarce. Wetland and riparian plants and animals prospered during the Pleistocene Ice Ages, when the southwestern US was much wetter than today. Drier post-Pleistocene climates restricted wetland and riparian butterflies to isolated pieces of their former ranges. Modern modification of hydrologic environments by human activities further fragments these habitats and may threaten survival of some obligate riparian butterflies, such as *Limenitis archippus*, *Speyeria nokomis* and *Ochlodes yuma*.

*L. archippus* larvae rely primarily on willows (*Salix* spp.) in a state where there has been large scale modification of natural hydrologic systems with resulting loss of native cottonwood/willow riparian forests. Dams built for management of floods and irrigation waters inundate much habitat. River flow downstream from such projects is reduced in volume as water is diverted to croplands. Floods are tamed, eliminating conditions necessary for germination of cottonwood seedlings and inviting invasion of salt cedar (*Tamarisk* sp.). The Desert Viceroy, *L. a. obsoleta*, was once studied for possible listing under the federal Endangered Species Act. It continues to survive in scattered populations in the Gila River, Rio Mimbres, Rio Grande and Pecos River valleys, but the size, number and health of these colonies remains unknown. Colonies along the Pecos seem to be the least numerous and the most isolated.

*Speyeria nokomis* is restricted to scarce montane wetland habitats which are vulnerable to adverse changes such as drainage for cultivation or excessive livestock grazing. Changes in the Sacramento Mountains, for another example, were related to logging in the early 20th century. After removal of trees, mountain valleys shed stormwater more quickly than under prior forested conditions. Through gullying and channel erosion, stream channels enlarged themselves to carry the increased runoff. Many miles of streamside wet meadows with lots of *nokomis* larval host *Viola nephrophylla* were cut by 5-m deep ephemeral arroyos and converted into dry meadows incapable of supporting *S. nokomis*. 
The other riparian species is *O. yuma*. We know of only one colony in NM; it is being described elsewhere as a new subspecies (Cary and Stanford, *in litt.*). Like nokomis, *yuma* relies on a single larval host, in this case *Phragmites australis* (Common Reed), which is an obligate riparian plant in NM. Hydrologic alterations near the colony site could lead to loss of the larval host, and then the butterfly. One potential threat to the colony is a proposed mining development nearby. A mill tailings impoundment could change the quality, quantity, flow regime or flow paths of seeps and springs which presently support the hostplant colony. Searches for other *O. yuma* colonies in NM have failed.

Several NM species are recorded only from the state's bootheel-shaped southwest corner, in Hidalgo or adjacent counties. There, Sierra Madrean climates and plant communities support species which, although not rare in their core Mexican ranges, are unique in NM. The most important of these are residents for which only one or two NM colonies are known: *Pyrrhopyge araxes*, *Adopaeoides prittwitzii*, *Poanes melane*, *Atrytonopsis edwardsi*, *Agathymus polingi*, *Neophasia terlootii*, *Callophrys xami*, *Calephelis rawsoni*, and *Emesis ares*.

Also important are Arctic/Alpine environments in north central NM. There, high peaks, marshes and ridges exceeding 3600 m elevation support Arctic Rocky Mountain species which are known from only one or two sites in NM: *Erebia magdalena*, *Boloria freija*, *Lycaena cuprea*, *Colias meadii*, and *Pieris occidentalis*. While not obviously threatened, the extremely limited occurrence of these species in NM is noteworthy.

**New Mexico Faunal List**

**HESPERIIDAE** *(SKIPPERS)*


*Proteides mercurius* (Fabricius)]. Hypothetical. Note 1.


*Polygonus leo* (Gmelin). Violet Skipper. Ed, Hi, Ot, Si, To. Stray.


[U. simplicius (Stoll)]. Hypothetical. Note 2.


[Astraptes fulgerator (Walch)]. Hypothetical. Note 3.


S. pylades (Scudder). Northern Cloudywing. Be,CA,Co,Gr,Hi,Lu,Si. Resident.


[Xenophanes trixus (Stoll)]. Hypothetical. Note 49.


[Gravis stigmaticus (Mabille)]. Hypothetical. Note 49.


Erynnis icelus (Scudder and Burgess). Aspen Duskywing. Be,CA,Ci,Co,Gr,Li, LA,Mo,Ot,RA,Sv,SJ,SM,SR,Sl,Ta,To,Un. Resident.

E. brizo (Boisduval and Leconte). Banded Oak Duskywing. All counties. Resident.


E. telemachus Burns. Gambel Oak Duskywing. All counties except Cu,DB,Gu, Hi,Le,Qu,Ro. Resident.

[E. proprius (Scudder and Burgess)]. Hypothetical. Note 7.


E. scudder (Skinner). Scudder’s Duskywing. Hi. Resident?


[E. martialis (Scudder)]. Hypothetical. Note 10.


E. funeris (Scudder and Burgess). Streamlined Duskywing. All counties except Co,Cu,DB,Qu,RA,Ro,Va. Resident.


P. communis communis (Grote). Checkered Skipper. All counties. Resident. Note 12.

P. c. albescens (Plotz). White Checkered Skipper. Ca,Ci,Gr,Gu,Hi,Li, MK,Qu,So. Resident. Note 12.

P. oileus (Linnaeus). Tropical Checkered Skipper. Hi. Seasonal Resident.


Hesperopsis libya (Scudder). Great Basin Sootywing. SJ. Resident.


P. polingii (Barnes). Spotted Skipperling. Ca,Gr,Li,Or,So. Resident.


Copaeodes aurantiacus (Hewitson). Orange Skipperling. Be,Ch,Cu,DB,DA, Ed,Gr,Gu,Hi,Li,Lu,Or,Qu,Ro,SM,So,VA. Resident.


Hylephila phyleus (Drury). Fiery Skipper. Be,Ca,Ch,Cu,DB,DA,Ed,Gr,Hi,Le, Lu?, Ot,Ro,So. Resident.


H. comma (Scudder). Jagged-Border Skipper. RA, Sv, SJ. Resident.


H. pahaska (Leussler). Yellow-Dust Skipper. All counties except DB, Gu, Le. Resident. 


[Polites peckius (W. Kirby)]. Hypothetical. Note 49.


[P. vibex (Geyer)]. Hypothetical. Note 17.


Atalopedes campestris (Boisduval). Sachem. All counties except Ca, Ci, LA, MK, RA, Ta, To, Va. Resident.


Ochlodes sylvanoides (Boisduval). Western Skipper. RA, Sv, SM?. Resident.


[P. zabulon (Boisduval and Leconte)]. Hypothetical. Note 19.


[Euphyes bimacula (Grote and Robinson)]. Hypothetical. Note 20.
E. vestris (Boisduval). Dun Skipper. Be, Ca, Co, Ed, Gr, Ha, Li, LA, Mo, Ot, RA, Sv, SJ, SM, SF, So, Ta, To, Un. Resident.

Atrytonopsis hianna (Scudder). Dusted Skipper. Co, LA. Resident.


[A. elissa (Godman)]. Hypothetical. Note 49.


A. exoteria (Herrich-Schaeffer). Sonoran Little Skipper. Ca, Gr, Hi, Si. Resident.


A. texanae Bell. Southwest Little Skipper. Ca, Ch, Ci, DA, Ed, Gr, Hi, Lu, Ot, Qu, Si. Resident.


Calpodes ethlius (Stoll). Canna Skipper. Ro. Stray.

MEGATHYMIDAE (GIANT SKIPPERS)


A. mariae (Barnes and Benjamin). Lechuguilla Giant Skipper. Ch, Da, Ed, Ot. Resident.

Megathymus yuccae (Boisduval and Leconte). Yucca Giant Skipper. Be, Ca, Ch, Ci, DA, Ed, Gr, Hi, Li, LA, Lu, Mo, Ot, RA, Ro, Sv, SF, So, Ta, To, Un, Va. Resident. Note 27.


PAPILIONIDAE (SWALLOWTAILS)


Battus philenor (Linnaeus). Pipevine Swallowtail. Be, Ca, Ch, Ci, Co, DB, DA, Ed, Gr, Ha, Hi, Le, Li, Lu, MK, Mo, Ot, Qu, Ro, Si, So, Ta, To, Un. Resident.


[P. pilumnus Boisduval]. Hypothetical. Note 33.

[P. troilus Linnaeus]. Hypothetical. Note 34.


PIERIDAE (WHITES AND SULPHURS)


P. sisymbrii Boisduval. Spring White. All counties except Ch, Cu, DB, Gu, Le, LA, Qu?, Ro. Resident. Note 35.

Ascia monuste (Linnaeus). Great Southern White. DA. Stray.


C. eurytheme Boisduval. Orange Sulphur. All counties. Resident.


Zerene cesonia (Stoll). Dogface. All counties except LA. Resident.

A. maerula (Fabricius). Yellow Brimstone. Hi. Stray.

Phoebis senae (Linnaeus). Cloudless Giant Sulphur. All counties except Ci, Ha,LA,Mo,RA,Sv,SJ. Resident.


P. agarithe (Boisduval). Orange Giant Sulphur. Ca,Ed,Gr,Ha,Hi,Le. Stray.

Kricogonia lyside (Godart). Guayacan Sulphur. Ed,Gr,Hi,Le,Li,Lu, Qu,Ro,Un. Seasonal Resident.


E. mexicanum (Boisduval). Mexican Yellow. All counties except Cu,DB,Gu,Ha, LA,Qu,RA. Resident.

E. proterpia (Fabricius). Tailed Orange. DA,Gr,Hi,Ot. Seasonal Resident.

Nathalis iole Boisduval. Dwarf Yellow. All counties. Resident.
[Enantia melite (Johansson)]. Hypothetical. Note 2.

LYCAENIDAE (LITTLE BUTTERFLIES)
L. rubida (Behr). Ruddy Copper. Ra, Ta. Resident.
[L. nivalis (Boisduval)]. Hypothetical. Note 41.
[Eumaeus minijas (Hubner)]. Hypothetical. Note 2.
S. saepium (Boisduval). Buckthorn Hairstreak. LA. Resident.


Brephidium exile (Boisduval). Western Pygmy Blue. All counties. Resident.

Leptotes cassius (Cramer). Tropical Striped Blue. RA. Stray.

L. marina (Reakirt). Striped Blue. All counties. Resident.


H. isola (Reakirt). Solitary Blue. All counties. Resident.

Everes comyntas (Godart). Eastern Tailed Blue. DA,Ed,Gr,Hi. Resident.

E. amytula (Boisduval). Western Tailed Blue. Be, Ca, Ci, Co, Gr, Li, LA, Lu, MK, Mo, Ot, RA, Sv, SJ, SM, SF, Si, So, Ta, To, Un. Resident.


Euphilotes battoides centralis (Barnes and McDunnough). Buckwheat Blue. Be, Ca, Ci, Co, Gr, Li, MK, Ot, RA, Sv, SM, SF, Si, So, Ta, To. Resident.

E. b. ellisi (Shields). Ellis' Buckwheat Blue. SJ. Resident.


E. rita rita (Barnes and McDunnough). Desert Buckwheat Blue. Ca, DA, Gr, Hi, Si, So. Resident.

E. r. emmeli (Shields). Emmel's Buckwheat Blue. SJ. Resident.


P. acmon texanus (Goodpasture). Texas Emerald-Studded Blue. All counties. Resident.


Riodinidae (Metalmarks)


A. m. mejicana (Behr). Mexican Mormon Metalmark. Be, Ca, Co, DA, Gr, Hi, Li, Lu, Ot, Sv, SF, Si, So, Ta, To. Resident.


Libytheinidae (Snout Butterflies)

Libytheana bachmanii larvata (Strecker). Snout Butterfly. Be, Ca, Ch, Ci, Co, DB, DA, Ed, Gr, Gu, Ha, Hi, Le, Li, Lu, MK, Mo, Ot, Ro, SM, Si, Ta, To. Seasonal Resident.

NYMPHALIDAE (BRUSH-FOOTED BUTTERFLIES)


[S. n. coerulescens (W. Holland)]. Hypothetical. Note 56.


[S. zerene (Boisduval)]. Hypothetical. Note 57.


[S. hydaspe (Boisduval)]. Hypothetical. Note 61.


*Boloria selene tollandensis* (Barnes and Benjamin). Silver Meadow Fritillary. RA,SV. Resident.


[C. cyneas (Godman and Salvin)]. Hypothetical. Note 49.


[C. palla (Boisduval)]. Hypothetical. Note 64.


**Phyciodes texanus texanus** (W. H. Edwards). Texas Crescent. Be, Ca, Ch, DB, DA, Ed, Gr, Hi, Li, Ot, Ro, Si, So, To. Resident.


**P. tharos tharos** (Drury). Pearl Crescent. Be, Ca, Ch, DB, DA, Ed, Gr, Ha, Hi, Lu, Mo, Ot, Qu, Ro, Sv, Si, So, Un, Va. Resident. Note 66.

**P. tharos** Type B. Orange Crescent. Ca, Co, Li, LA, Mo, Ot, RA, Sv, SJ, SM, SF, To, Un. Resident. Note 66.

**P. campestris camillus** W. H. Edwards. Field Crescent. All counties except Ch, Cu, DB, Gu, Le, Lu, Qu, Ro. Resident.


**P. mylitta callina** (Boisduval). Thistle Crescent. All counties except Ch, Cu, DB, Ed, Le. Resident.


**E. a. chuskae** (Ferris and R. Holland). Chuska Mountains Checkerspot. SJ, MK. Resident. Note 68.


[E. editha (Boisduval)]. Hypothetical. Note 70.

Polygonia interrogationis (Fabricius). Question Mark. Be,Ch,Co,Cu,DB,DA, Ed,Gr,Hi,Li,Ot,Ro,Sv,SM, SF,So,To,Va. Resident.

[P. comma (Harris)]. Hypothetical. Note 71.


Nymphalis californica (Boisduval). California Tortoiseshell. Ca, Ci, Gr, LA, RA, Sv, SJ, SM, SF, Si, To. Resident.

N. antiopa antiopa (Linnaeus). Mourning Cloak. All counties. Resident.

Aglais milberti (Godart). Fire-Rim Tortoiseshell. Ca, Ci, Co, Gr, Li, LA, Mo, Ot, RA, Sv, SJ, SM, SF, Si, So, Ta, To, Un. Resident.


V. cardui (Linnaeus). Painted Lady. All counties. Seasonal Resident.

V. annabella (Field). West Coast Lady. All counties except Ch, Cu, DB, Ed, Gu, Ha, Le, Qu. Resident.

V. atalanta (Linnaeus). Red Admiral. All counties. Resident.

[Hypanartia lethe (Fabricius)]. Hypothetical. Note 2.

Precis coenia (Hubner). Buckeye. All counties except Ci, Co, LA, Ta, To, Va. Resident.


[Siproeta stelenes (Linnaeus)]. Hypothetical. Note 72.

S. epaphus (Latreille). DA. Stray. Note 73.

Ca, DA, Ed, Gr, Hi, Li, Lu, Ot, Si, So. Resident.


L. bredowii bredowii (Geyer). California Sister. All counties except Cu, DB, Gu, Ha, Le, Qu, Un. Resident.


[Historis acheronta (Fabricius)]. Hypothetical. Note 2.

[Smyrna karwinskii Geyer]. Hypothetical. Note 2.

[Marpesia coresia (Godart)]. Hypothetical. Note 74.


[M. eleuchea Hubner]. Hypothetical. Note 75.


A. andria Scudder. Goatweed Butterfly. Be, Ca, Ch, Cu, DA, Ed, Gr, Gu, Ha, Hi, Le, Li, Lu, Mo, Ot, Qu, Ro, Sv, SF, Si, Ta, To, Un, Va. Resident.

Asterocampa celtis (Boisduval and Leconte). Hackberry Butterfly. Be, Ca, Ch, Co, Cu, DB, DA, Ed, Gr, Gu, Ha, Hi, Li, Lu, Mo, Ot, Qu, Ro, SM, Si, So, To, Un. Resident.


SATYRIDAE (SATYRS)


C. pertepida dorothea (Nabokov). Nabokov’s Arroyo Satyr. All counties except Cu, DB, Le, Ro, Qu, Va. Resident.


Cercyonis pegala (Fabricius). Large Wood Nymph. Be, Co, Cu, Gr?, Ha, Mo, Qu, RA, Ro, Sv, SJ, SM, SF, Ta, To, Un. Resident. Note 77.


N. r. neomexicanus Austin. New Mexico Satyr. Ca,Ci,MK. Resident. Note 80.
Oeneis chryxus chryxus (Doubleday and Hewitson). Chryxus Arctic. Co,LA,
O. alberta capulinensis F. M. Brown. Capulin Mountain Arctic. Co, Un. Resi-
dent. Note 82.

DANAIDAE (MILKWEED BUTTERFLIES)
Danaus plexippus (Linnaeus). Monarch. All counties. Seasonal Resident.
D. gilippus strigosus (H. W. Bates). Desert Queen. All counties except Va.
Resident.

NOTES
1. A specimen in the USNM is labeled “N. Mex.”, which probably refers to
northern Mexico.
2. This is an Edwards (1872) report, without supporting data or specimens.
3. A 1982 report from the Guadalupe Mountains, Eddy Co., is based on a sight
record and requires confirmation.
4. There are two old NM reports of this non-migratory Great Plains species. One
specimen, collected in 1882 by F. H. Snow near Las Vegas, San Miguel Co.,
was examined by Toliver and found to be T. pylades. The other is an AMNH
specimen allegedly collected by Cohn in 1951 near Jemez Springs, Sandoval
Co. Assuming a correct identification (determined by Stanford in 1971), the
specimen may be mislabelled or it may have been brought into NM as an
immature in livestock forage.
5. One 1899 sight record by Cockerell from Dona Ana Co. is unsupported
because of difficulty identifying clitus in hand, let alone in flight. The NMSU
collection contains a ca. 1900 Townsend specimen from Dona Ana Co.
catalogued under E. j. clitus; Cary examined it and found it to be E. tristis
tatius.
6. Snow's 1882 specimen from Las Vegas, San Miguel Co., was examined by
Toliver and found to be E. telemachus.
7. Williams claimed this taxon from the Jemez Mountains, April -June 1913.
Flight period and resemblance to E. telemachus suggest misidentification
of the latter, which is common there, yet went unreported by Woodgate or
Williams. A report of propertius from the Sandia Mountains in 1959 by
Stallings, Turner and Ehrlich (“1959”[1960]) probably has a similar explana-
tion. Until E. telemachus was described by Burns in 1960, observations of
telemachus were erroneously assigned to other taxa.
8. Plate 93 in Howe (1975) illustrates a Colfax Co. specimen of E. horatius
incorrectly captioned as E. meridianus. Toliver examined the actual speci-
men and noted the error.
9. One old specimen is labelled "Alamo, NM". The only such place is a highway intersection in eastern Guadalupe Co. Although within the range of *E. horatius*, no other butterfly reports are known from there. The specimen likely originated from Alamogordo, Otero Co., which experienced much butterfly collecting ca. 1900 and whose Sacramento Mountains support abundant *E. horatius*. Local residents casually refer to Alamogordo as Alamo. "Alamo" is Spanish for cottonwood tree.

10. All six reports of this species from NM are suspect. Snow (1883) reported *E. martialis* from Water Canyon, Socorro Co. Toliver examined the specimen and found two errors: it was *E. horatius* and it was labelled Gallinas Canyon, San Miguel Co. A report by Stallings, Turner and Ehrlich ("1959"[1960]) from the Sandia Mountains is probably *E. telemachus* (see Note 7). The remaining four are Carl Cushing reports from the Jemez Mountains in the mid-1960s. This is the most likely place to find *E. martialis* in NM, but neither Woodgate's many years of collecting there nor Holland's recent survey turned it up. Cushing's reports may be *E. horatius* or *E. telemachus*.

11. Difficulty distinguishing *E. persius* from *E. afranius* has lead to several unverifiable determinations of NM specimens.

12. Some argue that *P. c. communis* and *P. c. albescens* can be separated based on genitalic differences and are therefore separate species. Other lepidopterists (e.g., Scott, 1986) believe they represent one genitalically dimorphic taxon. Bailowitz and Brock (1991) report genitalic intergrades in southeast AZ. Although we have not examined genitalia of NM specimens, we know of no place in NM where *P. c. albescens* occurs in the absence of *P. c. communis*. We believe they may be conspecific, with *P. c. albescens* more common at lower altitudes and toward AZ.

13. The type locality of *H. alpheus*, described in 1876, is southwest of Raton in Colfax Co.

14. This skipper is named for John Woodgate, who collected the type specimens in the Jemez Mountains in 1913.

15. *H. viridis* was described in 1883 from specimens collected by Snow near Las Vegas, San Miguel Co. Snow first reported these specimens as *H. juba*.

16. A 1968 report from Capulin Mountain National Monument, Union Co., was examined by Toliver and found to be *P. origenes*.

17. Form *stigma* (Skinner), now a synonym of *P. vibex brettoides* (W. H. Edwards), was described in 1896 from material collected in "southern NM". No other NM reports of *P. vibex* are known. The LACM has an old, properly catalogued specimen of *H. phyleus* with an old label calling it "brettoides". This suggests misidentification in the past, made possible because males of *P. vibex* and *H. phyleus* are quite similar. Females are easy to tell apart, but Skinner's description of *stigma* includes no females! We suggest that the types of *stigma* may actually be *H. phyleus*. The types of *stigma* should be examined and their identity resolved.

18. Evans' (1955) reference to a NM specimen in the British Museum requires substantiation.

19. Snow reported this from Gallinas Canyon, San Miguel Co., in 1882. This must be either an aberrant or a misidentified *P. taxiles*, which is common there. Similarity between these two taxa is indicated by Scott's (1986) opinion that they are conspecific, an opinion we do not share. *P. taxiles* was described in
1881; Snow was probably unaware of the existence of this new western Poanes at the time of his NM report.

20. Snow reported this from Gallinas Canyon, San Miguel Co., in 1882. This must be a misidentification of E. vestris, which is common there.

21. Henry L. Viereck collected the type specimens of A. vierecki from Dry Canyon near Alamogordo, Otero Co., May 8-13, 1902.

22. Form margarita (Skinner) was named in 1914 from specimens collected by Woodgate near Jemez Springs, Sandoval Co.

23. In 1981 Cibola Co. was created from the western part of Valencia Co. Pre-1981 Valencia Co. reports lacking detailed locality data are now impossible to attribute to either present-day Valencia or Cibola counties. A. osloari is one species with such a report.

24. In 1911 Skinner described Pamphila quinquemacula from Las Cruces, Dona Ana Co. It is synonymous with A. eos.

25. There is one report of this species from Jemez Springs, Sandoval Co. It must be a misidentified A. phylace, which is common there and very similar in appearance. The closest occurrence of A. fimbriata is in the Chiricahua Mountains of southeast AZ, about 500 km distant.

26. D. Stallings and Turner described A. carlsbadensis in 1957 from Carlsbad Caverns National Park, Eddy Co. Taxonomists consider this to be either a synonym or a subspecies of A. neumoegeni.

27. The numerous named populations of this taxon need work. In 1911, M. y. navajo Skinner was described from Ft. Wingate. McKinley Co. M. y. elidaensis D. Stallings, Turner and J. Stallings was described in 1966 from Elida, Roosevelt Co.

28. M. u. violae D. Stallings and Turner, synonymized by Scott (1986), was described in 1956 from specimens collected at Carlsbad Caverns National Park, Eddy Co.

29. Rincon, NM, is the type locality of P. p. curvifascia (Skinner), described in 1902 and now part of the synonymy. Where is Rincon? The word means “corner” or “box canyon” in Spanish, and is common in the NM toponymy. Pearce (1965) discusses 10 such places in NM, a small fraction of the total. The railroad junction at Rincon, in Dona Ana Co., is the most likely origin of P. p. curvifascia.

30. Published reports of P. bairdii from Otero and Lincoln counties were re-examined by the authors and determined to be P. polyxenes. Several Sierra and Socorro county reports were similarly dismissed. A single alleged P. bairdii capture from Grant Co. was considered uncertain by the collector.

31. Visual sightings of P. cresphontes, indicated by “?”, may refer to the very similar, but less common, P. thoas. All known specimens from NM are P. cresphontes.

32. P. eurymedon is one of several species with dubious old reports from High Rolls, Sacramento Mountains, Otero Co. The others are S. sylvinum, C. fotis, O. chryxus, and S. behrii, all species for which no confirmed records exist for the Sacramento Mountains or any other place within a 300-km radius. Necessary habitat and larval hostplants are limited or absent, and none are known to wander.

33. Edwards (1872) attributes P. pilumnus to NM, but without substantiating data. Bailowitz and Brock (1991) cite some AZ records, so it may turn up here
some day. AZ Territory was not formally separated from NM Territory until 1863, so NM reports from Edwards’ era and earlier may actually be from localities now within the State of Arizona.

34. Cushing reports two Luna Co. localities (Columbus and Deming) for this species, but no specimens have been examined. Misidentification of the similar B. philenor, which breeds there, is the most plausible explanation for these reports.

35. Most specimens from southwestern Hidalgo Co. tend toward form transversa Barnes and Benjamin, now dubiously synonymized with P. sisymbrii.

36. This species is uncommon in NM, limited to the highest peaks. Taxonomic confusion with the ubiquitous and weedy P. protodice has led to unconfirmed reports of P. occidentalis from Colfax, Rio Arriba, Sandoval and San Miguel counties.

37. P. napi mogollon was named in 1942 for the Mogollon Mountains of Catron Co., where some of the types were collected.

38. Specimens resembling A. s. inghami Gunder are most common in southwest NM, while the A. s. julia W. H. Edwards phenotype prevails in northern NM.

39. Subspecies ruckesi was described in 1937 from specimens collected near Cowles in San Miguel Co.

40. Ehrlich and Ehrlich (1961) depict an alleged NM E. salome, but no specimens with data are known. Cary reported one from Hidalgo Co. in 1984, but Bailowitz examined it and determined it to be E. boisduvalianum.

41. In 1882 Snow reported Chrysophanus ianthine (W. H. Edwards), now L. nivalis, from Gallinas Canyon, San Miguel Co. In 1966 R. Langston reported it from the Jemez Mountains, Sandoval Co. Both must be misidentifications.

42. The small population in the Sacramento Mountains may warrant description as a separate taxon.

43. C. spinetorum is dimorphic in southcentral NM. The less common form resembles C. millerorum (Clench), which was described in 1981 from Mexico. Robbins (1990) showed that, despite two forms, only one species is present in Otero Co.

44. C. g. siva was described in 1874 from specimens collected at Ft. Wingate, McKinley Co. In southeast NM, this taxon appears to interbreed with C. g. gryna. Specimens with some wing characters of nominotypical gryna are known from Chaves, Colfax, Eddy, Otero, Quay and Taos counties.

45. This species was described in 1960 from specimens collected in the Sandia Mountains near Albuquerque.

46. “New Mexico” is the type locality for C. a. annetteae (dos Passos), which was described in 1947 and is now dubiously synonymized.

47. The type locality of F. f. violae (D. Stallings and Turner) is near Folsom, Union Co. It was described in 1947 and is now synonymized.

48. F. p. organensis Ferris was described in 1979 from the Organ Mountains in Dona Ana Co. It was synonymized by Scott (1986).

49. A single unsubstantiated report requires confirmation.

50. E. enoptes is apparently rare in NM. Perhaps two valid records are known. Reports from Santa Fe, Colfax and Rio Arriba counties are suspect and require confirmation.
51. A vague reference to Taos Co. for this species is on file, but we know of no specimens or data to support it.

52. Populations of A. mormo in NM do not conform well to the named subspecies available. A. m. duryi is very distinct and may be a full species; it was described in 1881 from near Mesilla, Dona Ana Co.

53. Cary reported it twice, but his were misidentifications based on the incorrect figure in Howe (1975).

54. S. c. carpenterii was described in 1876 from specimens collected by the Wheeler Expedition to NM. In 1947 the type locality was fixed as Taos Peak, Taos Co.

55. Form S. n. nigrocaerulea (W. and T. Cockerell) was described in 1900 from Sapello Canyon, San Miguel Co. It has been synonymized variously with S. n. nokomis and S. n. nitocris. Aberration S. n. rufescens (T. Cockerell) was described from the same location in 1909.

56. Subspecies S. n. coerulescens is a puzzle in NM. There are two old reports of S. nokomis from Otero Co., but most of the habitat there has been destroyed and recent attempts to locate colonies have failed. Thus there is no way to confirm the old reports. If nokomis is or was there, it may or may not be this Mexican race.

57. There is no evidence that S. zerene occurs in NM, despite recent references to the contrary (e.g., Tilden and Smith, 1986), which perpetuate outdated information. Williams (1914) reported zerene among Woodgate’s material, but this cannot be taken at face value. Williams did not report S. atlantis, an unusual omission because it is abundant there and Woodgate provided the type material for S. a. nikias (Ehrmann). Ehrmann (1917), however, in his description of nikias from Temez [sic] Springs, includes the following revelation: “when I received this species of Argynnis [now Speyeria] from Mr. John Woodgate he wrote me: ‘This species has been identified by two different authorities, one named it Arg. bremeri Edw. and the other, Arg. behrensi Edw.’” Both identifications offered to Woodgate are now recognized as subspecies of S. zerene, hence Williams’ report. Ehrmann recognized its distinctness, however, and gave it a new name which is now treated as a subspecies of S. atlantis.

58. Subspecies S. a. dorothea was described in 1947 from the Sandia Mountains, Sandoval Co.

59. Subspecies S. a. ratonensis was described in 1981 from specimens collected on Raton Mesa, Colfax Co.

60. Subspecies S. a. capitanensis was described in 1988 from the Capitan Mountains, Lincoln Co.

61. S. hydaspe conquista dos Passo and Grey was described in 1945 from material allegedly collected on August 8, 1932, near Santa Fe. Other specimens were allegedly taken four days later near Therma, now Eagle Nest, in Colfax Co., and one of these specimens is figured by Howe (1975, Plate 31, figure 15). No one has seen this species anywhere in NM before or since. We believe these specimens were actually collected elsewhere, perhaps Wyoming, and mislabelled.

62. NM material has been variously assigned to the genera Chlosyne and Thessalia, and to such species as leanira (C. and R. Felder), alma (Strecker)
and *fulvia*. A 1988 revision added subspecies *C. l. coronado* (M. Smith and Brock) to the names available. Because *C. leanira* occurs statewide, is unrestricted by major physiographic barriers, and is variable, we place all NM populations into one taxon, *fulvia*.

63. In 1893 W. H. Edwards named several forms of *C. l. crocale* from near Las Cruces, including *rufescens* and *nigrescens*.

64. In the AMNH there is an old specimen of *C. palla* labelled Jemez Springs. It is either mislabelled or misidentified.

65. Individuals resembling AZ subspecies *D. d. chara* (W. H. Edwards) occur in southwest NM and intergrade with the nominate phenotype which prevails to the east.

66. Populations formerly thought of as *P. tharos* actually represent at least two species, perhaps as many as four (Ferris, 1989). In addition, the nomenclature is in disarray. We recognize two taxa at this time, calling them *P. tharos* and *P. tharos* Type B until better names are provided.

67. Aberration *jemezensis* Brehme was bred by Woodgate in 1912 in Jemez Springs, Sandoval Co.

68. The type locality of *E. a. chuskae* is the Chuska Mountains of San Juan Co.

69. The type locality of *E. a. cloudcrofti* is the Sacramento Mountains near Cloudcroft, Otero Co.

70. The INHS has in its collection a specimen labelled Las Vegas, NM. However, Toliver determined that it was purchased, not collected, in Las Vegas.

71. Common eastern *P. comma* is misrepresented in NM by one old Skinner report from San Miguel Co. It is either mislabelled, misidentified, or else it came in on the train.

72. There are no documented reports of this species from NM. There is an unsubstantiated report by Edwards (1872). R. Holland caught one 2 mi. south of the NM/TX border. Bailowitz and Brock (1991) report one sighting from AZ.

73. *S. epaphus* is not listed in Scott (1986), Miller and Brown (1981), or revisions thereto. Paul Opler found this NM and US record in the Oregon State University collection.

74. Edwards (1872) lists this species from NM, but without supporting data. Howe (1975) figures a specimen from El Paso, TX, just south of the NM border.

75. Scudder (1892) reported this species from NM without supporting data.

76. Some authors present this taxon as two separate species: *C. pyracmon* (Butler) and *C. henshawi* (W. H. Edwards). We believe they are seasonal forms of the same species. Otero Co. reports are erroneous, probably mislabelled as to locality.


78. *C. meadii* is variable, and variation in NM specimens is not captured by the subspecific names available.

79. Holland (1905, pp. 209-210) claims it is "not uncommon on the high mountains of New Mexico." We know of no actual specimens or records with data.
80. The type locality of *N. r. neomexicanus*, described in 1986, is the Zuni Mountains of west-central NM.

81. An isolated colony of *O. chryxus* in the San Mateo Mountains, Socorro Co., may warrant subspecies status.

82. *O. a. capulinensis* was described in 1970 from Capulin Mountain National Monument in Union Co.

**LITERATURE CITED**


Ehrlich, P. R., & A. H. Ehrlich. 1961. How to know the butterflies. W. C. Brown Co. Dubuque, IA.


A survey of the Lepidoptera fauna from the Blue Mountains of eastern Oregon

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Abstract. Blacklight trap and aerial net collections for 1 season resulted in identification of 55 species of day-flying Lepidoptera and an additional 383 species of moths in northeastern Oregon mixed-coniferous forests. A total of 212 moth species (55%) were Noctuidae and an additional 93 species (24%) were Geometridae. Notes are presented on the relative abundance of moths in trap collections, flight period of trapped moths, and larval host food plants. Most species were represented in trap collections by few individuals; 41.5% had 5 or fewer specimens, and an additional 30% had 25 or fewer specimens. Only 5.5% of the species were considered abundant, with 200 or more specimens trapped.

INTRODUCTION

The Blue Mountains of eastern Oregon are characterized by moderate slopes, relatively low annual precipitation, and high summer temperatures (Franklin and Dyrness 1988). Higher elevation sites are usually occupied by mixed-coniferous forests of predominately ponderosa pine, *Pinus ponderosa* Dougl. ex. Laws, Douglas-fir, *Pseudotsuga menziesii* (Mirb.) Franco, grand fir, *Abies grandis* (Dougl.) Lindl., and western larch, *Larix occidentalis* Nutt. However, stream bottoms, spring-fed marshy areas, and other riparian zones usually contain a variety of hardwood shrubs, forbs, and grasses. Historically, major outbreaks of forest insect defoliators (e.g. western spruce budworm, *Choristoneura occidentalis* Free., and Douglas-fir tussock moth, *Orgyia pseudotsugata* (McDunn) have occurred in this region, resulting in large aerial spray suppression programs (Brookes et al. 1978; Brookes et al. 1987). Similar outbreaks will happen again in the future. Thus, the Blue Mountains are of special interest to Oregon forest managers who are concerned with protecting forests from unacceptable insect damage.

When damaging outbreaks of forest defoliators do occur, microbial insecticides are preferred for suppression of the insect populations because of their insect selectivity, high degree of environmental safety, and general public acceptance. Since 1980, *Bacillus thuringiensis* Berliner subsp. *kurstaki*, (BTK), has been the microbial insecticide of choice for most forest spraying in the United States and Canada. Although BTK
is a lepidopterous disease agent, its relative safety has been determined for many organisms in the environment, such as birds, fish, mammals, some non-lepidopterous insects and other arthropods (e.g. Eidt 1985; Niwa et al. 1987; Kreig and Langenbruch 1981). Still, questions frequently arise about whether or not desirable moths and butterflies in the spray area may be decimated along with the target species. In a study related to a gypsy moth, *Lymantria dispar* (L.), suppression program using BTK in oak stands in western Oregon, Miller (1990) found that overall abundance and species richness was reduced among 35 species in 10 lepidopterous families. In that instance, however, BTK was sprayed 3 times in 1 season over the same acreage. For western spruce budworm or Douglas-fir tussock moth suppression, the norm is only 1 spray per year with many years interval before that suppression is again necessary. In a later study, Miller (1992) found that a single BTK treatment caused an immediate significant reduction in nontarget larval abundance, which was still noticeable the following season. He observed that species richness decreased among the less-abundant (or uncommon) species on the spray site—perhaps eliminating them from the system—and that effects on species richness and abundance might be masked by examination of only the gross results of spraying on the more common species. He stated that this potential danger to uncommon species on the spray site justifies special management consideration to protect rare or endangered species. This, of course, presupposes that management knows what rare or endangered species are present, a condition that can only be met by adequate baseline surveys prior to treatment.

With the prospect of continued or increasing use of BTK for forest protection in the future, it is essential that we learn more about the unintended impacts of broad-scale BTK sprays. The first requirement for that is to know as precisely as possible the diversity and relative abundance of species present before treatment. No comprehensive investigation of the effects of BTK sprays on nontarget Lepidoptera has yet been done in Blue Mountains mixed-coniferous forests, although it is known that many species of Lepidoptera exist in areas sometimes sprayed (Forsberg et al. 1976). Cumulative lists of Lepidoptera have been compiled and maintained for areas west of the Cascade Mountains crest (e.g. Parsons et al. 1991), but similar survey lists are not available for the Blue Mountains. The insect fauna of eastern Oregon is different from that of more mesic western areas. This paper reports the results of an initial survey to gather baseline data necessary to evaluate the impacts of BTK sprays on nontarget Lepidoptera present on potential spray sites in the Blue Mountains.

**Methods**

In 1992, we operated ULV blacklight traps at 4 locations in the Blue Mountains between LaGrande, in Union County, and Ukiah, in Umatilla County, Oregon. Paired research plots were established in the Wallowa-Whitman National Forest
and the Umatilla National Forest. Plots 1 and 2 were spaced about 1 km (0.625 mi.) apart along Meadow Creek on Starkey Experimental Forest (Sec. 35 and 27, T.3 S., R.34 E.). Plots 3 and 4 were at 1 km intervals in the upper watershed of Pearson Creek and at Granite Meadow (Sec. 25 and 35, T.3S., R.32 E.), both about 10 km west of Meadow Creek. Meadow Creek has year-around running water, while both of the other areas are spring-fed, marshy sites where surface water often dries up in midsummer. All 4 plots had similar riparian vegetation and woody plants present, as well as a wide variety of grasses and forbs. All were subject to cattle grazing, although plot 1 on Meadow Creek had some fenced portions to exclude cattle.

Two ULV blacklight traps were placed in each plot during the first week of May. Traps were universal-type (BioQuip Products Inc.), with circular 22-watt fluorescent blacklight bulbs powered by 12-volt auto batteries. Vapona® insecticide strips were placed in the lower trap sections to act as killing agents for trapped insects. A photoelectric switch in each trap allowed automatic dusk-to-dawn operation. Traps were hung from individual tree branches, about 1.5 m from the ground, in positions unobstructed from view by tree branches. Except for the last week of August and a 2-week period in mid-September, the traps were operated for 3 consecutive nights each week until October 10. Moths were collected daily from traps and taken to the laboratory for later identification.

Day-flying species, primarily butterflies, were sampled by frequent, brief net collections in plots after the traps had been serviced.

All macrolepidoptera were identified to species, but only part of the microlepidoptera could be identified; these were primarily the larger species in the families Pyralidae and Tortricidae. Species of Pterophoridae were attracted to the blacklight traps, but were not identified. Very small moths of the gelechioid families were not considered in this study. Voucher specimens of species discussed in this paper are stored at Forestry Sciences Laboratory, Pacific Northwest Research Station, Corvallis, Oregon.

**RESULTS AND DISCUSSION**

A total of 54 species of butterflies and 1 day-flying Arctiidae were collected at the 4 trapping sites (Table 1), which probably represents most, but not all, of the day-flying lepidopteran species. All of these species had been previously taken in Oregon (Dornfeld 1980; McFarland 1963; Parsons et al. 1991). No attempt was made to collect all individuals available—only a representative sample of the species active at the time. The intent was to document species richness, but not abundance, since available time did not allow systematic net sampling. The 1992 field season began as an “early spring.” Some species may have been missed or were well into their flight period by the time our collections began. Had we started earlier than the first week of May, it is likely that we would have caught more individuals of certain species (those with overwintering adults, or early emergence), or even additional species. By the final

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1The use of trade names in this publication is for reader information and does not imply endorsement by the U.S. Department of Agriculture of any product or service.
week of sampling (October 7), night temperatures were often below freezing, days were usually cool, and the flight period for most Lepidoptera was clearly over.

Two families (Nymphalidae, Lycaenidae) account for well over half (35) of the total species collected. These are often some of the most abundant butterflies active and feeding on flowers on any particular day. Larval hosts for most of the species in Table 1 are primarily various flowering plants, such as violets, lupines, and thistles. Hardwood shrubs (e.g. willow, blueberries) are also common food sources in spring. Still, there are guilds of satyrids and hesperiids which feed as larvae on grasses.

Two species in Table 1 were not actually captured by net. Because the adults typically fly around and rest in the tops of pine trees infested by their host plants, *Mitoura spinetorum* (Hewitson) larvae were collected from dwarf mistletoe plants (*Arceuthobium campylopodum* Englem) on pines and reared to the adult stage. Similarly, larvae of *Satyrium sylvinus* (Boisduval) were found on willow leaves and reared to adults.

Larvae of the arctiid moth *Gonophaela vermiculata* (Grote) were collected in May and reared to adults on their food plant tall bluebells, *Mertensia paniculata* (Ait.) G. Don, and later taken by net from the same host. This moth is not active at night and none of these were caught in light traps.

Table 2 shows the complete list of all 383 species of moths taken in blacklight traps over the May-October period. Of these, 55% (212 species) were noctuids; the genus *Euxoa* alone was represented by 37 species. Geometridae was the second largest family, with 93 species identified. The total number of individuals of each species caught is given only to indicate relative abundance, as these data were subject to influence by other factors, such as the behavioral characteristics of the individual species (e.g. some species may not respond well to the specific wavelength of the ULV lights). Still, some species seemed to be especially abundant. For example, we collected 2205 *Spilosoma vagans* (Boisduval), 2033 *Petrophila confusalis* (Walker), and 1075 *Euxoa munis* (Grote).

Conversely, the data in Table 2 show that a large number of species apparently have sparse populations or are poorly attracted to ULV lights. For many species, we caught only 1 to 3 specimens, all in the same week. When this single-instance catch happened during the first week of trapping (May 6), e.g. *Cladara limitaria* (Walker) or *Behrensia conchiformis* Grote, it may represent catch at the end of the flight period. Earlier trapping might have resulted in more individuals of these species being caught. However, when we trapped a single specimen (or even 2 or 3) during only 1 week later in the season, e.g. *Alucita hexadactyla* Linnaeus or *Malacosoma californicum* (Packard), that may be the result of an actual paucity of individuals available to be caught. Also, there is some evidence (unpublished data) that many species do not disperse far from their food plants or pupation locations and thus may not reach the traps in quantities truly representative of their population density.
A comparison of the relative abundance of the different species, based solely upon the total numbers of individuals per species caught during the whole season (Table 3), shows that the vast majority of species (273 of 383) may indeed have quite sparse populations. We caught 5 or less individuals in 159 species, and 25 or less in an additional 114 species. To be ranked as rare or uncommon species, the criteria of 25-or-less specimens trapped over the season should be a conservative goal. Assuming only a 2-week emergence and dispersal period, that usually would allow for 12 trap-nights per site (2 weeks/2 traps/3 nights) in which to catch 25 moths, an easily attainable number since few species were restricted to only 1 pair of traps. The majority of rare or uncommon species were in the Noctuidae (60%). Conversely, only 5.5% (21) of all species could be considered abundant, as indicated by a total catch of 200 or more individuals.

Because the net collections did not systematically sample populations of day-fliers (Table 1), no direct comparison of relative abundance by species can be made. Nevertheless, some genera of butterflies were noticeably abundant on warm days, such as Polites sp., Pyrgus sp., Icaricia sp., Lycáena sp., Speyeria sp., and Vanessa sp.

Ten of the species listed in Table 2 were new records for Oregon (Grimble et al. 1993) and an additional 18 species had previously been collected in Oregon only from the western mountain ranges (both groups identified by footnotes).

Some species, for example Scoliopteryx libatrix (Linnaeus) and 3 species of Xylena, are known to overwinter as adults. Examination of the flight period data in Table 2 leads to the conclusion that many other species probably also have at least some adults overwintering, as well as some producing more than 1 generation per year. For instance, Epirrita autumnata (Borkhausen) was trapped in early June; then, no specimens were taken until late September. Examples of species caught over a 6-8 week period, or longer, are numerous, such as Spilosoma vagans (Boisduval) and Sphinx vashti Strecke. This extended flight period may be the result of microclimatic variation in pupation sites.

Where host plants are known, the larvae of most species tend to utilize angiosperms as food sources. Many of them apparently develop equally well on a range of food plants, such as herbs and hardwoods. Some, on the other hand, have been usually collected from only one host plant; e.g. Semiothisa denticulata (Packard) and S. sexmaculata (Packard) on larch or tamarack (Larix sp.). A summary of the number of species known to use certain host plant types (Table 4), shows that hardwood trees and shrubs (44%), and herbs, and grasses (43%) make up most of the food. Conifers make up a distant third preference (10%), even though eastern Oregon forests are nearly pure coniferous types. Evidently, Lepidoptera find much of their food in moist, riparian zones where hardwoods, grasses, and herbs are more abundant. Few species (2%) alternate between conifers and hardwoods.
The baseline data presented in this paper probably represent the majority of butterfly species and a large portion of the moth species present in our study areas. The number of moth species may be underestimated, partly because some species are not readily attracted and caught in blacklight traps. Thus, the fact that low numbers of certain species were collected in traps may not be truly indicative of their rarity.

These data will be useful when decisions are made concerning the impacts of BTK on nontarget Lepidoptera. However, such decisions must also be based upon the biology of larvae of the species in question. Clearly, a species must be present in larval form at the time of spraying to be impacted by the spray. Our baseline data will help managers determine which species fit into this category. Furthermore, Peacock and Schweitzer (1993, in press) made it clear that early instars of a species are generally more susceptible to BTK than are later instars. Still, this is not always the case, and it appears that BTK susceptibility must be considered on a species-to-species basis.

Additional field work is needed to document the larval and flight periods of species on our study areas, particularly those which may be “rare,” “uncommon,” or otherwise of “special concern.” Many species of Lepidoptera contribute significantly to the food resources of other wildlife. It is therefore critical to know if the direct affects of BTK on nontarget Lepidoptera will indirectly have a significant impact on other wildlife.

Acknowledgments. This research was funded in part by the National Agricultural Pesticide Impact Assessment Program (NAPIAP), Forest Pest Management, USDA Forest Service. Collected lepidoptera were identified by Paul C. Hammond, Lars Crabo, and J. Donald Lafontaine.

LITERATURE CITED
Franklin, J. F., & C.T. Dyrness. 1988. Natural vegetation of Oregon and


Table 1. Diurnal lepidoptera, collection dates, and partial larval host plants list, collected from the Blue Mountains, Oregon, 1992.

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Dates&lt;sup&gt;1&lt;/sup&gt;</th>
<th>Host plants&lt;sup&gt;2&lt;/sup&gt;</th>
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</thead>
<tbody>
<tr>
<td><strong>ARCTIIDAE</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gonophaela vermiculata (Grote)</td>
<td>4</td>
<td>9.VII</td>
<td>Hrb; BORAGIN., Mertensia sp.</td>
</tr>
<tr>
<td><strong>HESPERIIDAE</strong></td>
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<td></td>
</tr>
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<td>Erynnis persius (Scudder)</td>
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<td>12.V-8.VI</td>
<td>Shrb; SALIC., Salix sp.</td>
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<tr>
<td>Hesperia juba (Scudder)</td>
<td>11</td>
<td>11.V-14.VIII</td>
<td>Grs; PO.</td>
</tr>
<tr>
<td>Ochrodes sylvanoides (Boisduval)</td>
<td>19</td>
<td>9.VII-11.VIII</td>
<td>Grs; PO.</td>
</tr>
<tr>
<td>Polites peckius (Kirby)</td>
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<td>9.VI-14.VII</td>
<td>Grs; PO.</td>
</tr>
<tr>
<td>Polites sonora (Scudder)</td>
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<td>8.VI-9.VI</td>
<td>Grs; PO.</td>
</tr>
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<td>Pyrgus communis (Grote)</td>
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</tr>
<tr>
<td>Pyrgus ruralis (Boisduval)</td>
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<td>19.V-14.VIII</td>
<td>Hrb</td>
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<td><strong>LYCAENIDAE</strong></td>
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<td>Celastrina argiolus (Linnaeus)</td>
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<td>Hdw</td>
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<tr>
<td>Everes comyntas (Godart)</td>
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<td>12.V-13.V</td>
<td>Hrb; FAB.</td>
</tr>
<tr>
<td>Glaucopsyche lygdamus (Doubleday)</td>
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<td>Hrb; FAB.</td>
</tr>
<tr>
<td>Icaricia acmon (Westwood &amp; Hewitson)</td>
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<td>28.V-16.VII</td>
<td>Hrb; POLYGN., Eriogonum sp.</td>
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<tr>
<td>Icaria icarioides (Boisduval)</td>
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<td>Incisalia eryphon (Boisduval)</td>
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<td>12.V-26.V</td>
<td>Con; PIN., Pinus sp.</td>
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<tr>
<td>Lycaedipalis melissa (Edwards)</td>
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<td>9.VII-10.VII</td>
<td>Hrb; FAB., Lupinus sp.</td>
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<td>Lycaena editha (Mead)</td>
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<td>8.VI-14.VIII</td>
<td>Hrb; POLYGN.</td>
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<tr>
<td>Lycaena heliolepis (Boisduval)</td>
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<td>26.V-30.VII</td>
<td>Hrb; POLYGN.</td>
</tr>
<tr>
<td>Lycaena heteroea (Boisduval)</td>
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<td>8.VI-21.VII</td>
<td>Hrb; POLYGN., Eriogonum sp.</td>
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<td>Lycaena mariposa (Reakirt)</td>
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<td>8.VI-21.VII</td>
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<td>Lycaena nivalis (Boisduval)</td>
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<td>26.V-10.VII</td>
<td>Hrb; POLYGN., Polygonum sp.</td>
</tr>
<tr>
<td>Mitoura spinetorum (Hewitson)&lt;sup&gt;3&lt;/sup&gt;</td>
<td>2</td>
<td>30.VI-2.VII</td>
<td>Hrb; LORANTH., Arceuthobium sp.</td>
</tr>
<tr>
<td>Satyrium sylvinus (Boisduval)&lt;sup&gt;3&lt;/sup&gt;</td>
<td>2</td>
<td>10.VII-11.VII</td>
<td>Shrb; SALIC., Salix sp.</td>
</tr>
<tr>
<td><strong>NYMPHALIDAE</strong></td>
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<tr>
<td>Boloria epithore (Edwards)</td>
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<td>Hrb; VIOL., Viola sp.</td>
</tr>
<tr>
<td>Chlosyne palla (Boisduval)</td>
<td>9</td>
<td>26.V-28.VII</td>
<td>Hrb; ASTER.</td>
</tr>
<tr>
<td>Euphydryas editha (Boisduval)</td>
<td>2</td>
<td>27.VII</td>
<td>Hrb; PLANT</td>
</tr>
</tbody>
</table>
Limenitis lorquini (Boisduval)  8  8.VII-14.VIII Shrb; SALIC., Salix sp.
Nymphalis antiopa (Linnaeus)  5  19.V-11.VIII Shrb; SALIC., Salix sp.
Nymphalis milberti (Godart)  8  19.V-26.V Hrb; URTIC., Urtica sp.
Phyciodes campestris (Behr)  11  27.V-29.VII Hrb; ASTER., Aster sp.
Phyciodes mylitta (Edwards)  16  12.V-5.VIII Hrb; ASTER.
Polygonia faunus (Edwards)  2  12.V-30.VII Hdw
Speyeria atlantis (Boisduval)  4  8.VI-19.VI Hrb; VIOL., Viola sp.
Speyeria zerene (Boisduval)  14  8.VI-23.IX Hrb; VIOL., Viola sp.
Speyeria cybele (Fabriciius)  8  8.VII-14.VIII Hrb; VIOL., Viola sp.
Speyeria hydaspe (Boisduval)  6  26.V-14.VIII Hrb; VIOL., Viola sp.
Speyeria mormonia (Boisduval)  28  8.VI-11.VIII Hrb; VIOL., Viola sp.
Vanessa annabella (Field)  3  12.V-9.VI Hrb; MALV.
Vanessa atalanta (Linnaeus)  27  12.V-16.VIII Hrb; URTIC., Urtica sp.

**PAPILIONIDAE**

Papilio eurymedon (Lucas)  2  2.VI-8.VI Shrb; RHAMN., Ceanothus sp.
Papilio zelicaon (Lucas)  1  19.V Hrb; API.

**PIERIDAE**

Anthocaris sara (Lucas)  9  12.V-2.VI Hrb; BRASSIC.
Colias alexandra (Edwards)  1  9.VII Hrb; FAB., Astralagus sp.
Colias interior (Scudder)  8  8.VI-19.VI Shrb; ERIC., Vaccinium sp.
Neophasia menapia (Felder)  8  27.VII-5.VIII Con; PIN.
Pieris napi (Linnaeus)  26  12.V-6.VIII Hrb; BRASSIC.
Pieris rapae (Linnaeus)  3  12.V-19.V Hrb; BRASSIC.

**SATYRIDAE**

Cercyonis oetus (Boisduval)  2  9.VII-14.VII Grs; PO.
Cercyonis pegala (Fabriciius)  49  8.VII-14.VIII Grs; PO.
Coenonympha tulia (Linnaeus)  18  12.V-14.VIII Grs; PO.
Erebia epipsodea (Butler)  6  18.V-2.VI Grs; PO.

1Collection dates are written as day=arabic numeral, month=Roman numeral (e.g. 19.VIII is 19 August).
2Host plant references: Dornfeld 1980; and Parsons et al. 1991. Abbreviations are Con=conifers, Hdw=hardwoods, Hrb=herbs, Grs=grasses, Shrb=shrubs, API.=APIACEAE, ASTER.=ASTERACEAE, BORAGIN.=BORAGINACEAE, BRASSIC.=BRASSICACEAE, ERIC.=ERICACEAE, FAB.=FABACEAE, LORANTH.=LORANTHACEAE, MALV.=MALVACEAE, PIN.=PINACEAE, PLANTAGIN.=PLANTAGINACEAE, PO.=POACEAE, POLYGON.=POLYGONACEAE, RHAMN.=RHAMNACEAE, SALIC.=SALICACEAE, SCROPHULARI.=SCROPHULARIACEAE, URTIC.=URTICACEAE, VIOL.=VIOLACEAE.
3Larvae of this species were collected from host plants and reared to the adult stage.
Table 2. Relative abundance, flight periods, and partial larval host plants list for lepidoptera taken in ULV blacklight traps in the Blue Mountains, Oregon, 1992.

<table>
<thead>
<tr>
<th>Species</th>
<th>No.</th>
<th>Dates</th>
<th>Host plants</th>
</tr>
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<tr>
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<td>Alucita hexadactyla Linnaeus</td>
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</tr>
<tr>
<td><strong>ARCTIIDAE</strong></td>
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<td></td>
<td></td>
</tr>
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<td>Cycnia oregonensis (Stretch)</td>
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<td>Grammia nevadensis (Grote &amp; Robinson)</td>
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<td>Hrb</td>
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<td>Grammia ornata (Packard)</td>
<td>620</td>
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<td>Hrb</td>
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<tr>
<td>Lophocampa maculata Harris</td>
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<td>20.V-15.VII</td>
<td>Hdw</td>
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<td>Hdw</td>
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<td>Spilosoma vagans (Boisduval)</td>
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<td><strong>GEOMETRIDAE</strong></td>
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<tr>
<td>Biston betularia (Guenee)</td>
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<td>20.V-24.VI</td>
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<td>Campaea perlata Guenee</td>
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<td>Caripeta aequalaria Grote</td>
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<td>Con; PIN.</td>
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<td>Ceratodalia gueneata Packard</td>
<td>16</td>
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<td>Drepanulatrix hulstii (Dyar)</td>
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<tr>
<td>Drepanulatrix quadraria (Grote)</td>
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<tr>
<td>Drepanulatrix unicalcararia (Guenee)</td>
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<td>13.V-30.IX</td>
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<td>Dysstroma brunneata (Packard)</td>
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<td>Dysstroma formosa (Hulst)</td>
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<td>Dysstroma truncata (Hufnagel)</td>
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<td>Hdw</td>
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<td>Epirrhoe alternata (Mueller)</td>
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<tr>
<td>Epirrhoe sperryi (Herbulot)</td>
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<td>Epirrita autumnata (Borkhausen)</td>
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<td>Hdw/Con</td>
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<td>Euchlaena marginaria (Minot)</td>
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<td>Eulithis destinata (Moschler)</td>
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<td>24.VI-23.IX</td>
<td>Shrb; GROSSULARI., Ribes sp.</td>
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</table>
Eulithis propulsata (Walker) 10 24.VI-12.VIII Shr; SALIC., Salix sp.
Eulithis xyлина (Hulst) 165 1.VII-2.IX Shr; SALIC., Salix sp.
Euphia unangulata (Haworth) 143 27.V-15.VII Hrb
Eupithecia agnesata Taylor 4 29.VII-12.VIII
Eupithecia cretaceata (Packard) 19 13.V-22.VII Hrb
Eupithecia misturata (Hulst) 14 10.VI-29.VII Shr; RHAMN., Ceanothus sp.
Eupithecia multiscipta (Hulst) 18 27.V-10.VI
Eupithecia subcolorata (Hulst) 132 6.V-1.VII
Eustroma semiatrata (Hulst) 68 27.V-7.X Hrb
Gabriola dyari Taylor 2 12.VIII Con; PIN., Pseudotsuga sp.
Glena nigraria (Barnes & McDunnough) 13 27.V-17.VI Con; PIN., Pinus sp.
Hesperumia sulphuraria Packard 76 1.VII-19.VIII Shr; ROS.
Hydria undulata (Linnaeus) 4 3.VI-24.VI Hdw
Hydriomena furcata (Thunberg) 5 22.VII-19.VIII Hdw
Hydriomena perfracta Swett 2 13.V-10.VI Shr; SALIC., Salix sp.
Hydriomena marinata 17 6.V-27.V Con; PIN.
Iridopsis emasculata (Dyar) 240 27.V-22.VII Hdw
Itame bitactata (Walker)7 33 10.VI-2.IX Shr; GROSSULARI., Ribes sp.
Itame brunneata (Thunberg) 70 24.VI-19.VIII Shr; ERIC., Vaccinium sp.
Itame quadrilinearia (Packard) 2 5.VIII Hdw
Lambdina fiscellaria (Guenee) 14 19.VIII-30.IX Hdw/Con
Leptostales rubromarginaria (Packard) 1 12.VIII Hdw
Lobophora montanata Packard 5 6.V-24.VI
Melanophila imitata (Walker) 211 6.V-27.V Con; PIN.
Mesothea incertata (Walker) 1 3.VI Shr; ERIC., Vaccinium sp.
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<td>Species</td>
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<td>Collection Period</td>
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<td>----------------------------</td>
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<td>22.VII- 12.VIII Con; PINA., Pinus ponderosa cones</td>
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<td>Dioryctria baumhoferi Heinrich</td>
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**SATURNIIDAE**

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**SPHINGIDAE**

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THYATIRIDAE
Ceranemota tearlei (H.Edwards) 9 23.IX- 30.IX
Euthyatira semicircularis (Grote) 2 24.VI
Habrosyne scripta Gosse 2 24.VI Shrb; ROS., Rubus sp.

TORTRICIDAE
Acleris brittania Kraft 81 12.VIII- 30.IX
Archips cerasivorana (Fitch) 2 29.VII- 5.VIII Hdw
Choristoneura rosaceana (Harris) 38 24.VI- 12.VIII Hdw
Choristoneura occidentalis Freeman 59 15.VII- 12.VIII Con; PIN.
Clepsis persicana (Fitch) 8 10.VI- 8.VII Hdw
Eana argentina (Clemens) 137 10.VI- 5.VIII
Epiblema sp. 4 10.VI- 24.VI
Eucosma agricolana (Walsingham) 3 3.VI- 10.VI
Hystrichophora stygiana (Dyar) 50 17.VI- 19.VIII
Oleuthreutes cespitana (Hubner) 26 6.V- 10.VI Hdw
Oleuthreutes galaxana Kraft 2 10.VI
Oleuthreutes glaciana (Moschler) 1 10.VI Hdw
Pelochrista sp. 245 10.VI- 19.VIII
Rhyacionia sp. 4 10.VI- 15.VII Con; shoot borers

1Total number of specimens taken in blacklight traps over trapping period, May 6 through October 7.
2Dates are mid-points of weekly trapping periods; written as day=arabic numeral, month=Roman numeral (e.g. 19.VIII is 19 August).
4New species record for Oregon (Grimble et al. 1993).
5Previously known only from the Cascades and Coastal Range in Oregon.
6Adults overwinter in this species (Rockburne and Lafontaine 1976).
7This species known to have more than one generational emergence period per year.
### Table 3. Relative population density of moth species with "rare," "uncommon," "common," or "abundant" populations in the Blue Mountains, based upon light trap sampling, 1992.

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<th>Rare (1-5)</th>
<th>Uncommon (6-25)</th>
<th>Common (26 to 200)</th>
<th>Abundant (over 200)</th>
<th>Total</th>
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<td><strong>114</strong></td>
<td><strong>89</strong></td>
<td><strong>21</strong></td>
<td><strong>383</strong></td>
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<tr>
<td><strong>Percent:</strong></td>
<td><strong>41.5</strong></td>
<td><strong>29.8</strong></td>
<td><strong>23.2</strong></td>
<td><strong>5.5</strong></td>
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1Number of species with 5 or less individuals collected in 8 traps at 4 sites over entire trapping period (May-October 1992).

### Table 4. Types of larval food sources utilized by macrolepidoptera in the Blue Mountains of Oregon.

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<td>Conifers</td>
<td>30</td>
<td>10</td>
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<tr>
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</tr>
<tr>
<td>Lichens/dead leaves</td>
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<td>1</td>
</tr>
<tr>
<td><strong>Total:</strong></td>
<td><strong>302</strong></td>
<td><strong>100</strong></td>
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</tbody>
</table>

Toward a better understanding of host use and biodiversity in riodinid butterflies (Lepidoptera)

P. J. DeVries
Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts 01238

I. A. Chacon
Museo Nacional, Apartado 749, San Jose, Costa Rica

and

Debra Murray
Estacion Biologica Jatun Sacha, Casilla 1501-218, Tena, Ecuador

Abstract. Over one hundred-eighty observations on the host use and ant association of ninety-eight riodinid butterflies are presented — a substantial addition to our understanding of this distinctly neotropical group. These observations are contrasted to previous work, and discussed with respect to apparent patterns of phytophagy, aphytophagy, caterpillar sociality, and ant association. The majority of riodinid species have unknown life histories, and thus we conclude that much more fieldwork is need before a phylogenetic approach to host use and ant association can be established.

INTRODUCTION

The fact that there are more species of bats than elephants, more little bats than large ones, more species of insects than mammals, and so on vividly demonstrates one of the best known axioms of biodiversity — there is an inverse relationship between body size and number of species (Hutchinson & MacArthur 1959; May 1978; Van Valen 1973). In other words, the species-number game is not for giants. Add to this that the taxonomy of small-bodied organisms is typically less well known than that of larger ones (Mayr 1969), and it is easy to appreciate how crude our understanding of biodiversity really is. However, the importance of biodiversity lies not simply in numbers but in how organisms live and interact within habitats. Thus another general axiom may be added, namely, that within a particular group the basic natural history of small-bodied species will always be less well known than that of larger ones. For example, among butterflies the host relationships and early stages of the papilionids, pierids and nymphalids are more completely known than are those of the lycaenoid butterflies — the Riodinidae and Lycaenidae. In other words, on average less is known about the lycaenoid butterflies mainly because they are small.

The riodinids are a diverse group of small-bodied butterflies that show an almost entirely neotropical distribution. Starting with Hinton (1951), general reviews of lycaenoid biology have typically treated the riodinid butterflies in passing as peculiar neotropical members of the Lycaenidae
(Cottrell 1984; Ehrlich 1958; Pierce 1987; Vane-Wright 1978). Whatever their relationships eventually prove to be, in the absence of solid data and an overall lycaenid phylogeny, the fact remains that our perception about the biology and evolution of riodinids has been typically inferred from what we know of lycaenids (DeVries 1991a&c). Recent work with riodinids has increased our understanding of them in two complimentary areas. First, modern systematic studies have lent strong support to the idea that the riodinids are monophyletic (Harvey 1987; see also Martin & Pashley 1992; Robbins 1988). Secondly, experimental and morphological studies have pointed to differences between riodinids and lycaenids with respect to their early stage morphology and the evolution of myrmecophily (e.g., Brevignon 1992; Callaghan 1977, 1982, 1986a&b, 1989; DeVries 1988 a & b, 1991b&c; Harvey 1987; Ross 1964, 1966). Even with the advent of this recent interest in the riodinids, our overall grasp of their early-stage biology can be summarized by a historical quote from Scudder (1887, p. 111) who wrote,

"... Our knowledge of the Lemoniinae [Riodinidae] is exceedingly meagre, so that we can here draw no decided conclusions. There is, indeed, no greater desideratum in the study of butterflies than a knowledge of the transformation of the principal genera of this subfamily...."

More than a century since Scudder penned these words we still know less about the life histories of riodinids than of any other major group of butterflies.

For a number of years one of us (PJD) has been preparing a treatment of the Costa Rican riodinid fauna. This project has provided an impetus for the authors to make field observations on the early stages of riodinid butterflies in an array of tropical areas. Given the unparalleled destruction of tropical habitats within the last century and the scarcity of such basic information on riodinids, we feel some urgency in making our observations available to other researchers. Accordingly we here summarize some of our riodinid host records gathered during the last 8 years. We also briefly discuss our observations within the context of the review provided in Harvey's (1987) tribal classification, and highlight some aspects of riodinid biology that we feel may be useful for future studies. A more detailed analysis of these and other observations will appear elsewhere.

**Methods**

The records presented here include cases where field-collected eggs were reared to adults, or where caterpillars of various instar were found in the field and subsequently reared to adults, as well as oviposition records where the female was collected and/or positively identified. The records and information pertinent to them is presented in a telescopic format (Table 1). The complete nomenclature of the butterfly taxa treated in this study is found in Table 2 and follows the higher classification of Harvey (1987). Field observations by DeVries originate from Belize, Costa Rica, Panama, Ecuador, Argentina, Madagascar and Hainan Island, China. Those of Chacon are from Costa Rica only, and those of Murray are
from Jatun Sacha, Ecuador only. Coded abbreviations for the geographic locality of each rearing record are listed in Table 3, and those of the families of hosts are found in Table 4. The identity of symbiotic ant taxa found in association with certain caterpillar taxa are listed in Table 5, and information relevant to these records is found within bold, square brackets [ ] under ‘Notes’ in Table 1. Information regarding eggs and caterpillars is placed within parentheses ( ) under ‘Notes’ in Table 1, and the coded information is as follows:

- eggs — 1 = laid singly, 2 = small clusters of two to six eggs, 3 = clusters from seven to sixty eggs, and amo = probable ant mediated oviposition.
- caterpillars — s = solitary, sg = semi-gregarious (tolerant of other individuals, including other instars), and g = gregarious (synchronous in feeding and molting).

As in many other groups of butterflies, riodinid caterpillars typically feed on young leaves or shoots. Unless specified otherwise the abbreviation *lus* in Table 1 refers to young leaves and *flrs* refers to flowers. Under ‘Notes’ in Table 1 voucher numbers for Chacon’s records are found within brackets [ ], the records of Murray are abbreviated DM, and all others are those of DeVries. Voucher material from this study has been deposited in the Museo Nacional de Costa Rica, Museum of Comparative Zoology (Harvard University), and the collections of PJD and DM.

**RESULTS AND DISCUSSION**

In all, over 180 original natural history observations for 98 species of riodinid butterflies are presented here, including host associations with 37 plant families and one order of insects (Table 1). Many of these records are new, and others corroborate those published previously. We further provide a substantial number of observations on the identity of the ant taxa that associate with some riodinid caterpillars. Although our observations add considerably to the available body of information on riodinids, within the context of their total species richness the sum total of riodinid host records now known remains small. Nevertheless, highlighting some aspects of host relationships and early stage biology may be useful to future workers. Accordingly we discuss the patterns of host use within the context of a tribal level classification (Harvey 1987), and point to various relationships that relate to clutch size, caterpillar behavior, and aphytophagy. Secondly, we discuss some patterns relevant to understanding those taxa that form symbiotic interactions with ants. Finally, we ask what contribution does the information here make to our understanding of the riodinids as a group, and to our understanding of tropical biodiversity in general.

**New Host Records at the Tribal Level**

The first summary of host plant information aimed specifically at understanding the riodinids at the tribal level was compiled by Harvey (1987). With that work as a reference point we may now add a significant number of new host plant families to seven riodinid tribes. These are as follows: 1) *Euselasiinae* — (Euselasia) Melastomataceae; 2) *incertae sedis* — (Eunogyra) Araceae; 3) *Riodinini* — (Ancyluris) Euphorbiaceae; (Necyria and Lyopteryx) Vochysiaceae, Gesneriaceae; (Rhetus)
<table>
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<th>Host</th>
<th>Locality</th>
<th>Plant part</th>
<th>Stage</th>
<th>Notes</th>
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<td>lp</td>
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<td>Locality</td>
<td>plant part</td>
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<td>lp</td>
<td>N=1 (s)</td>
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<tr>
<td>Ithomeis</td>
<td>eulaema</td>
<td>Heisteria sp. (26)</td>
<td>SV</td>
<td>lvs</td>
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<td>N=1 (3)</td>
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<td>Melanis</td>
<td>pixie</td>
<td>Albizia caribaea (12)</td>
<td>SJ, SA</td>
<td>lvs</td>
<td>elp</td>
<td>N&gt;100 (3,g)</td>
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<td>Themone</td>
<td>pais</td>
<td>Quiina sp. (30)</td>
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<td>strigosa</td>
<td>Heteropteris laurifolia (18)</td>
<td>B</td>
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<td>lp</td>
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<td>Metacharis</td>
<td>cuparina</td>
<td>Heisteria coccinna (26)</td>
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<td>old lvs</td>
<td>lp</td>
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<td>Mikania sp. (2)</td>
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<td>N=2 (1, s) DM</td>
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<td>dead leaves</td>
<td>B, G</td>
<td>dead lvs</td>
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<td>N=2, (1, s) died as 4th instars</td>
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<td>N=4 (1, s) died as 2d instars DM</td>
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<td>Plant Part</td>
<td>Stage</td>
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<td>Trema micrantha (34)</td>
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<td>Vochysia guatemalensis (36)</td>
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<td>N=1 (s) [92-HNP-119]</td>
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<td>GC, JS</td>
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<td>B</td>
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<td>Neea spp (25)</td>
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<td>N&gt;50 (2 or 3, g)</td>
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<td>N=24 (g) [91-HNP-188]</td>
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<td>Clematis haenkeana (31)</td>
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<td>lvs</td>
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<td>Croton sp. (11)</td>
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<td>elp</td>
<td>N=&gt;10 (2, sg, amo) [21]</td>
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<tr>
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<td>irenea</td>
<td>Croton billbergianus (11)</td>
<td>B, G</td>
<td>lvs</td>
<td>elp</td>
<td>N&gt;500 (1, s or sg) [1, 2, 3, 9, 15, 22, 24]</td>
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<tr>
<td>Genus</td>
<td>Species</td>
<td>Host</td>
<td>Locality</td>
<td>plant part</td>
<td>stage</td>
<td>Notes</td>
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<td>lp</td>
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<td>lp</td>
<td>N&gt;20 (s or sg) [1, 2, 3, 15, 20]</td>
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<td>lvs</td>
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<td>N=8 (1, s, amo) [27]</td>
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<td>N=4 (1, s, amo) [27]</td>
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<td>Doliocarpus</td>
<td>sp. (10)</td>
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<td>lp</td>
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<td>Stigmaphyllon</td>
<td>sp. (18)</td>
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<td>lvs</td>
<td>lp</td>
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<td>Tetracera</td>
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<td>lp</td>
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<td>N=4 (1 on or near membr-acids) [28]</td>
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<td>Gustavia superba (16)</td>
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<td>N=7 (s) [22]</td>
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<td>Heteropteris laurifolia (18)</td>
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<td>N=2 (s) [1, 18, 20]</td>
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<td>Heisteria cocinna (26)</td>
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<td>el</td>
<td>N=9 (1 on membracids, died as first instars) [27]</td>
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<td>Locality</td>
<td>plant part</td>
<td>stage</td>
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<td>(1 on or near membranes) [27]</td>
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<td>(s) [2]</td>
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<td>Acalypha sp. (11)</td>
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<td>nr aurinia</td>
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<td>V</td>
<td>unknown</td>
<td>lp</td>
<td>N=7 (sg inside ant nests) [21]</td>
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<td>lp</td>
<td>N&gt;40 (sg inside ant nests) [21]</td>
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<td>cilissa</td>
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<td>elp</td>
<td>N=15 (1, s) [1, 14, 17, 26]</td>
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<td>Bauhinia sp. (12)</td>
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<td>Marcgravia sp. (19)</td>
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<td>N=2 (s) [17]</td>
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<td>Sourubea sp. (19)</td>
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<td>scales</td>
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<td>N=24 (1, s) [3] [92-HNP-124; 127]</td>
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<td>virgilius</td>
<td>Omphalea diandra (11)</td>
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<td>elp</td>
<td>N=7 (1, s, amo) [25]</td>
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<td>eleutho</td>
<td>Inga sp. (12)</td>
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<td>lvs</td>
<td>lp</td>
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<td>nr decorata</td>
<td>Cecropia insignis (6)</td>
<td>L</td>
<td>lvs</td>
<td>lp</td>
<td>N&gt;15 (g) [9, but see text]</td>
</tr>
<tr>
<td></td>
<td>nr thestias</td>
<td>Maripa panamensis (9)</td>
<td>B</td>
<td>lvs</td>
<td>elp</td>
<td>N=9 (1, s, amo) [25]</td>
</tr>
<tr>
<td></td>
<td>nr matuta</td>
<td>Pseudobombax septenatum (4)</td>
<td>P</td>
<td>lvs</td>
<td>elp</td>
<td>N=6 (2, sg, amo) [27]</td>
</tr>
<tr>
<td>Genus</td>
<td>Species</td>
<td>Host</td>
<td>Locality</td>
<td>plant part</td>
<td>stage</td>
<td>Notes</td>
</tr>
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<td>-----------------------</td>
<td>-----------------------</td>
<td>----------</td>
<td>------------</td>
<td>-------</td>
<td>----------------</td>
</tr>
<tr>
<td>Nymphidia</td>
<td>mantus</td>
<td><em>Maripa panamensis</em> (9)</td>
<td>B, P</td>
<td>lvs</td>
<td>elp</td>
<td>N&gt;10 (1, s, amo) [25]</td>
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<tr>
<td></td>
<td></td>
<td><em>Inga sp.</em> (12)</td>
<td>B</td>
<td>lvs</td>
<td>elp</td>
<td>N=2 (1, s, amo) [25]</td>
</tr>
<tr>
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<td></td>
<td><em>Serjania sp.</em> (33)</td>
<td>B</td>
<td>lvs</td>
<td>elp</td>
<td>N=1 (1, s, amo) [25]</td>
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<tr>
<td></td>
<td></td>
<td><em>Gustavia superba</em> (16)</td>
<td>P</td>
<td>flrs</td>
<td>lp</td>
<td>N=3 (s) [25]</td>
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<tr>
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<td>haematostictum</td>
<td><em>Inga sp.</em> (12)</td>
<td>B</td>
<td>lvs</td>
<td>elp</td>
<td>N=6 (1, s) [17]</td>
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<tr>
<td></td>
<td>cachrus</td>
<td><em>Inga spp</em> (12)</td>
<td>SV</td>
<td>lvs</td>
<td>elp</td>
<td>[3, 11, 24]</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Inga sp.</em> (12)</td>
<td>A</td>
<td>lvs</td>
<td>elp</td>
<td>N=5 (2, sg) [3]</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Inga sp.</em> (12)</td>
<td>C</td>
<td>lvs</td>
<td>elp</td>
<td>N=3 (2, sg) [10]</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Inga ruiziana</em> (12)</td>
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<td>lvs</td>
<td>lp</td>
<td>N = 3 [17]</td>
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<td>CA</td>
<td>lvs</td>
<td>lp</td>
<td>N=10 (s) [3]</td>
</tr>
<tr>
<td></td>
<td>onaeum</td>
<td><em>Cassia fruticosa</em> (12)</td>
<td>H</td>
<td>lvs</td>
<td>el</td>
<td>N=2 (1, s) [?]</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Heteropteris laurifolia</em> (18)</td>
<td>F</td>
<td>lvs</td>
<td>lp</td>
<td>N=8 (sg) [10]</td>
</tr>
<tr>
<td></td>
<td>azanoides</td>
<td><em>Inga spp</em> (12)</td>
<td>L, B</td>
<td>lvs</td>
<td>e</td>
<td>N=3 (1) [3, 14]</td>
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<tr>
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<td><em>Inga sp.</em> (12)</td>
<td>GC</td>
<td>lvs</td>
<td>e</td>
<td>N=1 (2)</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Passiflora</em> sp. (28)</td>
<td>JS</td>
<td>lvs</td>
<td>lp</td>
<td>N=1 (s) [?] DM</td>
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<tr>
<td></td>
<td></td>
<td><em>Inga sp.</em> (12)</td>
<td>JS</td>
<td>lvs</td>
<td>lp</td>
<td>N=2 (s) [12] DM</td>
</tr>
<tr>
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<td></td>
<td><em>Inga sp.</em> (12)</td>
<td>JS</td>
<td>lvs</td>
<td>lp</td>
<td>N=3 (s) [?] DM</td>
</tr>
<tr>
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<td><em>Inga sp.</em> (12)</td>
<td>JS</td>
<td>lvs</td>
<td>lp</td>
<td>N=7 (sg) [19] DM</td>
</tr>
<tr>
<td></td>
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<td><em>Gustavia longifolia</em> (16)</td>
<td>JS</td>
<td>flr bracts</td>
<td>lp</td>
<td>N=5 (sg) [19] DM</td>
</tr>
<tr>
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<td></td>
<td><em>Senna</em> sp (12)</td>
<td>JS</td>
<td>lvs</td>
<td>lp</td>
<td>N=4 (s) [?] DM</td>
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<td>ascolia</td>
<td><em>Inga sp.</em> (12)</td>
<td>JS</td>
<td>lvs</td>
<td>lp</td>
<td>N=4 (sg) [3]</td>
</tr>
<tr>
<td></td>
<td></td>
<td><em>Inga spp</em> (12)</td>
<td>GC</td>
<td>lvs</td>
<td>elp</td>
<td>N=4 (2, sg) [5, 11]</td>
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<tr>
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<td></td>
<td><em>Inga sp.</em> (12)</td>
<td>JS</td>
<td>lvs</td>
<td>lp</td>
<td>N=5 (sg) [7] DM</td>
</tr>
</tbody>
</table>
Table 2. List of riodinid taxa treated in this study

**Hamearinae**

**Saribea**
perroti Riley, 1932

**Abisara**
echerius lisa Bennett, 1950

**Euselasiinae**

rhodogyne patella Stichel, 1927
mystica (Schaus, 1913)
chrysippe (Bates, 1866)
eulione (Hewitson, 1856)
nr cafusa (Bates, 1866)

**Riodininae**

tribe: *Mesosemiini*

**Mesosemia**
asa asa Hewitson, 1869
carissima Bates, 1866
telegone telegone (Boisduval, 1836)
nr. ephyne (Cramer, 1776)
nr. tenebricosa Hewitson, 1877
nr. judiciales Butler, 1874

**Leucochimona**
lagora (Herrich-Schaffer, 1853)
nr. philemon (Cramer, 1775)
nr. molina (Godman & Salvin, 1855)

tribe: *Eurybiini*

**Eurybia**
patrona persona Staudinger, 1875
elvina elvina Stichel, 1910
lycisca Westwood, 1851
nr. nicaeus (Fabricius, 1775)
nr. hyacinthina Stichel, 1910

tribe: *incertae sedis*

**Napaea**
eucharilla (Bates, 1867)
theages theages Godman & Salvin, 1878

**Cremna**
thesus subrutilia Stichel, 1910
actoris (Cramer, 1776)

**Eunogyra**
satyrus Westwood, 1851

**Hermathena**
candidata (Hewitson, 1874)
tribe: *Riodinini*

Ancyluris
- inca inca (Saunders, 1850)
- jurgensenii jurgensenii (Saunders, 1850)

Necyria
- beltiana Hewitson, 1870

Lyropteryx
- lyra cleadas Druce, 1875

Rhetus
- arcius castigatus Stichel, 1909

Chorinaea
- faunus bogota (Saunders, 1858)

Ithomeis
- eulaema imatatrix (Godman & Salvin, 1878)

Themone
- pais (Hübner, 1820)

Melanis
- pixie sanguinea Stichel, 1910

Lepricornis
- strigosa strigosa (Staudinger, 1876)

Metacharis
- cuparina Bates, 1868

Charis
- nr anius (Cramer, 1776)
- gynaea (Godart, 1824)
- cleonus (Stoll, 1782)

Caria
- rhacotis (Godman & Salvin, 1878)

Lasaia
- agesilaus (latrielle, 1813)

Chalodeta
- lypera (Bates, 1868)
- chaonitis (Hewitosn, 1866)

tribe: *Symmachilini*

Mesene
- phareus rubella Bates, 1865
- silaris (Godman & Salvin, 1878)

Mesenopsis
- bryaxis melanochlora Godman & Salvin, 1878

Symmachia
- tricolor hedemanni (Felder & Felder, 1869)
- rubina Bates, 1866

tribe: *Helicopini*

Helicopis
- cupido (Linnaeus, 1758)
tribe: **Charitini**

**Anteros**
- formosus micon Druce, 1875
- aechus (Stoll, 1781)

**Sarota**
- gyas (Cramer, 1775)
- chrysus (Stoll, 1782)

tribe: **Emesini**

**Argyrogrammana**
- trochilia (Westwood, 1851)

**Emesis**
- fatima nobilata Stichel, 1910
- lucinda aurimna (Boisduval, 1870)
- mandana (Cramer, 1780)
- lacrines Hewitson, 1870
tenedia tenedia Felder & Felder, 1861

tribe: **Lemoniini**

**Lemonias**
- zygia egaensis (Butler, 1867)

**Thisbe**
- irenea (Stoll, 1870)
- lycorias (Hewitson, 1853)

**Juditha**
- molpe (Hübner, 1803)
- dorilis dorilis (Bates, 1866)

**Synargis**
- mycone (Hewitson, 1865)
- phyleus praecella (Bates, 1866)
- gela (Hewitson, 1853)
- abaris (Cramer, 1776)

**Audre**
- nr aurina (Hewitson, 1863)
- undetermined species

tribe: **Nymphidiini**

**Calospila**
- cilissa (Hewitson, 1863)
- emylius (Cramer, 1775)

**Menander**
- menander menander (Stoll, 1780)
- menander thallus (Stichel, 1910)
- laobotas (Hewitson, 1875)
- pretus picta (Godman & Salvin, 1886)

**Adelotypa**
- senta (Hewitson, 1853)

**Setabis**
- lagus jansoni (Butler, 1870)
Theope
- virgilius virgilius (Fabricius, 1793)
- eleutho Godman & Salvin, 1897
- nr decorata Godman & Salvin, 1878
- nr thestias (Hewitson, 1860)
- nr matuta Godman & Salvin, 1897

Nymphidium
- mantus (Cramer, 1775)
- baoetia Hewitson, 1852
- nr. derufata Lathy, 1932
- nr lisimon (Stoll, 1790)
- haematostictum Godman & Salvin, 1878
- cachrus ascolides (Boisduval, 1870)
- onaeum Hewitson, 1869
- azanoides occidentalis Callaghan, 1986
- leucosia (Hübner, 1806)
- nr ninias (Hewitson, 1865)
- caricae (Linnaeus, 1758)

Table 3. Abbreviations for localities

<table>
<thead>
<tr>
<th>Country</th>
<th>Locality</th>
</tr>
</thead>
<tbody>
<tr>
<td>Costa Rica</td>
<td>A = Las Alturas (Puntarenas)</td>
</tr>
<tr>
<td></td>
<td>C = Parque Nacional Corcovado (Puntarenas)</td>
</tr>
<tr>
<td></td>
<td>SV = Las Cruces (Puntarenas)</td>
</tr>
<tr>
<td></td>
<td>L = La Selva (Heredia)</td>
</tr>
<tr>
<td></td>
<td>CH = Chilamate (Heredia)</td>
</tr>
<tr>
<td></td>
<td>PL = Plastico (Heredia)</td>
</tr>
<tr>
<td></td>
<td>SA = San Antonio de Belen (Heredia)</td>
</tr>
<tr>
<td></td>
<td>T = Turrialba (Cartago)</td>
</tr>
<tr>
<td></td>
<td>M = Rio Macho de Cartago (Cartago)</td>
</tr>
<tr>
<td></td>
<td>SJ = Meseta Central of San Jose (San Jose)</td>
</tr>
<tr>
<td></td>
<td>R = Finca EL Rodeo (San Jose)</td>
</tr>
<tr>
<td></td>
<td>CA = Cañas (Guanacaste)</td>
</tr>
<tr>
<td></td>
<td>H = Hacienda Santa Maria (Guanacaste)</td>
</tr>
<tr>
<td>Belize</td>
<td>Bel = Mile 30, Belize City</td>
</tr>
<tr>
<td>Panama</td>
<td>B = Barro Colorado Island</td>
</tr>
<tr>
<td></td>
<td>G = Gamboa</td>
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<tr>
<td></td>
<td>P = Pipeline Road</td>
</tr>
<tr>
<td></td>
<td>CA = Cerro Azul</td>
</tr>
<tr>
<td></td>
<td>Pan = near Panama City</td>
</tr>
<tr>
<td></td>
<td>ER = El Real, Darien Province</td>
</tr>
<tr>
<td></td>
<td>F = Fort Clayton nr Colon</td>
</tr>
<tr>
<td>Ecuador</td>
<td>JS = Jatun Sacha (Napo)</td>
</tr>
<tr>
<td></td>
<td>GC = Garza Cocha (Sucumbios)</td>
</tr>
<tr>
<td>Argentina</td>
<td>V = Volcan (Jujuy)</td>
</tr>
<tr>
<td>Madagascar</td>
<td>R = Ranamofauna National Park</td>
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<tr>
<td>China</td>
<td>H = 100 s of Haikou City (Hainan)</td>
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Table 4. Abbreviations of host families for riodinid butterflies.

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<td>— Bombacaceae</td>
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<td>— Bromeliaceae</td>
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<td>6</td>
<td>— Cecropiaceae</td>
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<td>— Clusiaceae</td>
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<td>— Combretaceae</td>
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<td>— Convolvulaceae</td>
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<td>— Dilleniaceae</td>
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<td>— Euphorbiaceae</td>
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<td>— Fabaceae</td>
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<td>— Flacourtiaceae</td>
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<td>— Gesneriaceae</td>
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<td>— Hippocrateaceae</td>
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<td>16</td>
<td>— Lecythidaceae</td>
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<td>17</td>
<td>— Lejuniaceae</td>
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<td>18</td>
<td>— Malpighiaceae</td>
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<td>19</td>
<td>— Marcgraviaceae</td>
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<td>— Marantaceae</td>
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<td>— Melastomataceae</td>
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<td>— Moraceae</td>
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<td>— Myrsinaceae</td>
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<td>— Nyctaginaceae</td>
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<td>— Olacaceae</td>
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<td>— Orchidaceae</td>
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<td>— Passifloraceae</td>
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<td>— Quinaceae</td>
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<td>— Sapindaceae</td>
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<td>— Zingiberaceae</td>
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<td>mem</td>
<td>— Homoptera: Membracidae</td>
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<tr>
<td>coc</td>
<td>— Homoptera: Coccidae</td>
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</table>
Table 5: Numerical codes of ant taxa found in association with riodinid caterpillars. Codes are found with square brackets in Table 1.

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<th>code</th>
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<th>subfamily</th>
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<td>ants not collected</td>
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<td>2</td>
<td><em>Ectatomma tuberculatum</em></td>
<td>(Ponerinae)</td>
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<td>3</td>
<td><em>Pheidole</em> sp.</td>
<td>(Myrmicinae)</td>
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<tr>
<td>4</td>
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<td>(Myrmicinae)</td>
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<td>(Myrmicinae)</td>
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<td><em>Pheidole</em> nr biconstricta - no. 2</td>
<td>(Myrmicinae)</td>
</tr>
<tr>
<td>7</td>
<td><em>Pheidole</em> nr biconstricta - no. 3</td>
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<tr>
<td>8</td>
<td><em>Solenopsis</em> geminata</td>
<td>(Myrmicinae)</td>
</tr>
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<td>9</td>
<td><em>Solenopsis</em> (Diplorhoptrum grp) sp.</td>
<td>(Myrmicinae)</td>
</tr>
<tr>
<td>10</td>
<td><em>Solenopsis</em> sp.</td>
<td>(Myrmicinae)</td>
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<td>11</td>
<td><em>Megalomyrmex</em> foreli</td>
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<tr>
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<td><em>Wasmannia</em> auropunctata</td>
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<td><em>Wasmannia</em> sp.</td>
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<td><em>Aphaenogaster</em> araneoides</td>
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<td><em>Crematogaster</em> brevispinosa</td>
<td>(Myrmicinae)</td>
</tr>
<tr>
<td>17</td>
<td><em>Crematogaster</em> sp.</td>
<td>(Myrmicinae)</td>
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<td>18</td>
<td><em>Cephalotes</em> atratus</td>
<td>(Myrmicinae)</td>
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<tr>
<td>19</td>
<td><em>Ochetomyrmex</em> sp.</td>
<td>(Myrmicinae)</td>
</tr>
<tr>
<td>20</td>
<td><em>Camponotus</em> sp.</td>
<td>(Formicinae)</td>
</tr>
<tr>
<td>21</td>
<td><em>Camponotus</em> distinguendus</td>
<td>(Formicinae)</td>
</tr>
<tr>
<td>22</td>
<td><em>Camponotus</em> serieiventris</td>
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<tr>
<td>23</td>
<td><em>Dendromyrmex</em> sp.</td>
<td>(Formicinae)</td>
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<tr>
<td>24</td>
<td><em>Paratrechina</em> sp.</td>
<td>(Formicinae)</td>
</tr>
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<td>25</td>
<td><em>Azteca</em> sp.</td>
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<td>26</td>
<td><em>Tapinoma</em> sp.</td>
<td>(Dolichoderinae)</td>
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<td><em>Dolichoderus</em> bispinosus</td>
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<td>28</td>
<td><em>Dolichoderus validus</em></td>
<td>(Dolichoderinae)</td>
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</tbody>
</table>

Combretaceae; *(Chorinaea) Hippocrateaceae; (Ithomeis and Metacharis)* Olacaceae; *(Themone) Quiinaceae; (Lepricornis) Malpighiaceae; (Chalodeta) Passifloraceae; 4) **Symmachiini** — *(Mesene)* Fabaceae, Violaceae; *(Mesenopsis and Symmachia)* Melastomataceae; *(Symmachia)* Ulmaceae; 5) **Charitini** — *(Anteros)* Melastomataceae, Vochysiaceae; *(Sarota) Lejuniaceae; 6) **Emesini** — *(Emesis)* Olacaceae, Flacourtiaeae, Ranunculaceae; 6) **Lemoniini** — *(Juditha and Synargis)* Dilleniaceae, Sapindaceae, Polygalaceae, Lecythidaceae, Bignoniaceae, and potentially Homoptera; and 7) **Nymphidiini** — *(Theope and Nymphidium)*
Euphorbiaceae, Moraceae, Convolvulaceae, Lecythidaceae, Sapindaceae, and Bombacaceae.

The host records reported here (Table 1) agree broadly with the monophagous patterns of host use pointed out by Harvey (1987) for the Mesosemiini, and add further support for polyphagy among members of the Emesini. On the other hand, our observations amplify considerably the host records known from the Riodinini, Symmachini, and Charitini, and suggest that diet breadth for members of these tribes will eventually include an even greater diversity of host plant families than is currently recognized. Our host records are also completely agree with those noted in Harvey (1987) for the Eurybiini. However, our records amplify the patterns noted for members of the Lemoniini by indicating that some taxa may be a great deal more polyphagous than thought previously, while others seem strictly monophagous. For example, we found that some taxa (e.g., Juditha molpe and Synargis mycone) may use a suite of plant genera and even families as hosts all at the same site. On the other hand, observations on Thisbe irenea indicate that this taxon is monophagous on trees in the genus Croton from Belize to Ecuador — most of its geographical range.

Oviposition Patterns and Caterpillar Behavior

Recent work suggests that caterpillar social behavior derives from factors enhancing survivorship and resource utilization. The benefits accrued by aggregated caterpillars have probably led to oviposition patterns facilitating aggregation and social interactions (Fitzgerald 1993; Costa & Pierce 1994). However, we know almost nothing about the relationship between oviposition patterns, clutch size, and degree of social interaction for most groups of butterflies, especially the riodinids. Three points arise from our records. First, the majority of riodinid taxa have caterpillars that feed as solitary individuals, and it is almost certain that the females of all of these taxa lay single eggs. Second, gregarious caterpillars are found within the Euselasiinae (Euselasia), Riodinini (Melanis) and Emesini (Emesis), and as in other Lepidoptera, appears linked to laying clusters of eggs. Available evidence from Euselasia and Hades suggests this trait may be widespread among members of the Euselasiinae. In contrast, the trait appears labile within Emesis, as this genus includes species with both gregarious and solitary caterpillars. Finally, semi-gregarious caterpillars occur in the Eurybiini, Riodinini, Helicopini, Emesini, Lemoniini and Nymphidiini. This trait may occur in both taxa that lay single eggs (Eurybia, Ancyluris, Helicopsis, Thisbe) and those that lay several eggs in a loose cluster (Theope, Nymphidium). In those that lay single eggs, gregariousness suggests a non-cannibalistic tolerance of other individuals when caterpillar densities increase on the host. In Theope and Nymphidium there is some indication that small egg clusters and semi-gregarious caterpillars are traits that may be widespread within these genera.
Aphytophagy
The habit of feeding on non-vegetable hosts, termed aphytophagy, is well known within the Lycaenidae (Ackery 1990; Cottrell 1984; Fiedler 1991). Several observations point to the possibility that utilization of non-vegetable hosts may occur in more riodinid genera than suspected previously. First, the only real suggestion of aphytophagy in riodinids derives from an exiguous communication by Urich (in Kaye 1921), who stated that Setabis lagus caterpillars were predaceous on homopterous nymphs (Horiola) infesting Trinidadian cacao plantations. As this record has gone without verification for over 70 years, it was gratifying to demonstrate that Setabis lagus in Costa Rica is carnivorous on scale insects, and thereby provide further impetus for examining other members of the genus for the carnivorous habit. Second, although we were unable to verify the diet of Audre nr aurina and Audre sp. found inside ant nests (details will appear elsewhere, DeVries & Martinez, in prep.), two lines of evidence point to the possibility that their diet may include regurgitations provided by their host ants. At no time in the field or in captivity could we induce Audre caterpillars to feed on an array of plant matter, and microscopic examination of the frass of both species determined that it contained no fragments of plant material. Furthermore, despite close observations over several months, we found no evidence that caterpillars fed on ant larvae or pupae. Finally, although decidedly inconclusive, we note that direct oviposition on Homoptera by Synargis phyleus and Juditha dorilas may indicate a aphytophagous habit in these taxa — an oviposition behavior typically observed in Setabis lagus females. On the whole, even the few observations here suggest that future work may reveal aphytophagy as a trait in a variety of riodinid taxa.

Symbioses with Ants
Available evidence suggests that butterfly myrmecophily evolved within the context of associations involving secretion-harvesting ant taxa, and that caterpillars, secretion-producing Homoptera, and plants bearing extrafloral nectaries share ant symbionts (DeVries 1991a&b). Overall, most myrmecophilous butterfly taxa appear to be facultative with respect to their ant symbionts, but a few taxa have evolved species specific associations (DeVries 1991b; DeVries et al. 1993; Fiedler 1991; Thomas et al. 1989). The observations here (Table 1) both support these general ideas and provide a more accurate picture of the variation found among riodinid-ant symbioses. Depending on the taxon, members of the tribes Nymphidiini and Lemoniini show associations with a variety of common secretion-foraging ant species in the subfamilies Ponerinae, Myrmicinae, Formicinae and Dolichoderinae. In contrast, our records and those published previously (Horvitz et al. 1987) provide no indication that members of the Eurybiini (Eurybia only) form associations with ants in the Dolichoderinae. However, in this case sampling error cannot be ruled out, and this should be investigated in greater detail.
The Interaction between Ant Taxa and Caterpillar Diet

Even the few observations here suggest that eventual understanding of host use patterns by riodinids will require accounting for the interactions between both ants and plants. A number of contrasting examples illustrate this (Table 1). First, the polyphagous species *Synargis mycone* may associate with a variety of ant taxa encompassed by four subfamilies, whereas *Thisbe irenea*, which may associate with members of at least three ant subfamilies, is monophagous on *Croton* throughout its geographical range. Second, the polyphagous species *Juditha molpe* appears to have obligate associations with *Dolichoderus bispinosus* ants in Central America, whereas the polyphagous species *Nymphidium mantus* in Panama shows an apparently obligate relationship with the ant genus *Azteca*. Third, the various *Theope* species noted here appear to show a trend toward monophagy (although many more records are needed), but these butterflies appear to have intimate associations with ants in the Dolichoderinae. The one exception of which we are aware is *T. nr decorata*. Although caterpillars of this species fed on a plant inhabited by *Azteca* ants, they were tended entirely by *Solenopsis* ants that had small, open air colonies on the large leaves of the plant. Finally, our field observations indicate that *Lemonias nr zygia*, *Juditha molpe*, *Theope virgilius*, *T. nr thestias*, *T. nr matuta*, and *Nymphidium mantus* all represent cases where the choice of host plant by ovipositing female butterflies is mediated by the presence of particular ant taxa, a trait known from some members of the Lycaenidae (Atsatt 1981; Pierce & Elgar 1985).

Extrafloral Nectaries and Myrmecophiles

The compilation of host records plus demonstration that caterpillars may benefit from drinking extrafloral nectar provided the basis for the idea that plant taxa bearing extrafloral nectaries are important in the diets of myrmecophilous riodinids (DeVries & Baker 1989; DeVries 1991a). The records presented here also support this pattern (e.g., *Synargis*, *Juditha*, *Nymphidium*), but several cases are of particular interest. First, members of the genus *Eurybia* are known to feed only on flowers of the Marantaceae and Zingiberaceae (Harvey 1987; Horvitz et al. 1987). In the latter group, the inflorescence structure may prevent caterpillars from burrowing into the inflorescence as they do in the Marantaceae. Our field observations showed that caterpillars using Zingiberaceae as hosts position their heads over the extrafloral nectaries located on the outside of the cone-like inflorescence bracts, and they are tended by ants that are also feeding at these nectaries (e.g., Schemske 1980). These observations provide the first direct indication that caterpillars in the Eurybini also drink extrafloral nectar. Secondly, we have found cases where caterpillars were feeding on plants whose shoots were occupied by Homoptera. In cases where the hostplant did not have extrafloral nectaries (e.g., *Synargis gela, S. abaris, some Juditha molpe*),
we observed caterpillars drinking honeydew secretions directly from the resident Homoptera. In cases where the plants had both extrafloral nectaries and membracids (e.g., Lemonias zygia, Synargis gela, S. mycone, Juditha molpe, Theope nr matuta, and Nymphidium caricae), we observed caterpillars drinking both extrafloral nectar and Homoptera honeydew. Together these observations further highlight the apparent importance of drinking secretions in the diet of myrmecophilous riodinid caterpillars, in addition to their regular fare of leaf tissue.

Conclusions and Future Considerations

At the time of their classic paper, Ehrlich & Raven (1964) concluded that there were insufficient records available on lycaenid butterflies (almost none on riodinids) to provide predictive patterns of their host use. Pierce (1985), and more recently Fiedler (1991) brought together a large and diffuse literature that provides the best available synthesis of host use patterns to date on the Lycaenidae. Their studies further elaborate the complex nature of lycaenid life histories, but suggest that patterns of host use are in fact emerging for the Lycaenidae. At the present time there remain two major hurdles to cross before we can resolve lycaenid host evolution in greater detail: the lack of a phylogeny for the Lycaenidae in which to frame host associations, and the absence of host records for most neotropical taxa.

The hurdles for riodinids are different. In his synthesis of riodinid host records, Harvey (1987) indicated that patterns of host use were evident in a few higher taxa (i.e., Hamaerinae, Eurybiini, and incertae sedis), but there were insufficient records available for most groups. Since that time, the number of known host records has increased (Brown 1993; Brevignon 1992; Callaghan 1989; DeVries 1988, 1991a, 1992, and those reported here). Considering all available records together indicates that riodinid life histories display a diversity of traits including monophagy and polyphagy, caterpillar growth benefits gained by drinking secretions, caterpillar-ant associations ranging from facultative to obligate species specific, and possibly a modicum of aphytophagy. These traits parallel those known from within the Lycaenidae (Cottrell 1984; Fiedler 1991; Pierce 1987). However, even with the inclusion of this new information and the framework of a higher classification to interpret patterns of host use, our understanding of riodinid host use is conjectural — the host records for at least three quarters of the riodinid species are unknown.

An important aspect to the study of myrmecophilous riodinids concerns identification of ant symbionts. However, most studies of myrmecophilous butterflies (including the present one) are guilty of listing ant symbionts without complete identifications. In part this reflects the small number of qualified ant taxonomists in the world, and the negligence of many butterfly biologists in making proper collections of ants. The positive identification to species in some ant groups (e.g., Pheidole, Solenopsis, Aphaenogaster, Camponotus, and Azteca, among others) is
difficult or impossible without specimens of the reproductive castes (S. Cover, pers. comm.). Nevertheless, understanding the phylogenetic and ecological patterns of why some rioidinid taxa form symbioses with only a particular subgroup within a genus or even with a particular species of ant (e.g., *Juditha molpe*), while others are apparently ant generalists (e.g., *Synargis mycone*) will depend upon correct identification of their ant symbionts. Thus, we urge future workers to take special care to collect strong series of ant symbionts when rearing myrmecophilous species, and to have them properly identified.

As we stressed previously, biodiversity is a suite of different organisms and their often complex interactions within habitats. Why our understanding of rioidinid biodiversity is so poor is likely the result of many interacting factors. Such factors may include their small size, their almost exclusive occurrence in neotropical forest habitats, fundamental characteristics of their biology and interactions with other organisms that make them difficult to observe, or combinations of these and other factors. Whatever the ultimate reasons may be, it seems to us that Scudder’s (1887) counsel regarding the importance of knowing more about the early stages of the rioidinids has lost none of its resonance a century later. To fortify our grasp of rioidinid evolution and biodiversity many more rearing records from virtually all of the neotropical subfamilies and tribes are required.

Despite the media’s apparent concern over the world-wide devastation of biodiversity, we presently live in a time when grant giving and receiving institutions of science seem concerned almost exclusively with the technology of molecular biology and other types of so called ‘big science.’ Because technology is often equated with science, this trend will continue to reduce interest in whole-organism biology and natural history in both institutions of higher learning and in the students they produce (e.g., see Erzinclioglu 1993). However, without data from the real world, no matter how sophisticated laboratory techniques or models become, in the absence of natural history they are unlikely to broaden our understanding of the myriad interactions among organisms. The message is simple: future insights into tropical biodiversity in general, and rioidinid early stage biology specifically will demand a great deal more field work. It is our hope that this paper will encourage more people to study rioidinids than have done so in the past century. One thing is inescapable — technology will not stem the destruction of tropical habitats nor will wishful rhetoric save those rioidinid taxa and their interactions with other organisms that will be extirpated during the next hundred years. Now is the time for deeds, not words.

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**Literature Cited**


The effect of different foodplants on cocoon crop performance in the Indian tasar silkworm
Antheraea mylitta Drury (Lepidoptera: Saturniidae)

A.K. Dash¹, B.K. Nayak², and M. C. Dash²

Abstract. Cocoon crop performance through seasonal rearings of Antheraea Mylitta Drury larva on three primary foodplants Asan (Terminalia tomentosa W. & A.), Arjun (Terminalia arjuna W. & A.), Sal (Shorea robusta Gaertn.) and three secondary foodplants, Ber (Ziziphus jujuba Gaertn.), Sidha (Lagerstroemia parviflora Roxb.) and Dha (Anoegeissus latifolia Wall.) indicate better performance in winter crops than those of a rainy and autumn season. Sal, among primary foodplants, appeared uneconomical in terms of total cocoon shell (raw silk) production in spite of a superior cocoon formation. Overall performance was superior in Asan than all other foodplants during all the seasons. Performance on Ber was higher than Sal and other secondary foodplants, a situation not heretofore documented. The gradation of foodplant with regard to performance (total raw silk production) was, in decreasing order of productivity: Asan, Arjun, Ber, Sal, Sidha, Dha.

INTRODUCTION

Antheraea mylitta Drury is a semidomesticated Indian tasar silkworm exploited commercially for production of tasar silk. At lower altitudes (50-30m ASL), it is trivoltine, reared three times a year in July-August (Rainy cocoon crop), September-October (Autumn cocoon crop) and November-December (Winter cocoon crop). The silkworm is polyphagous feeding on a number of foodplants, of which Asan (Terminalia tomentosa W. & A.), Arjun (Terminalia arjuna W. & A.) and Sal (Shorea robusta Gaertn.) are considered primary and the remainder secondary foodplants (Jolly, 1966; Jolly et al, 1974). Evaluation of these foodplants with respect to seasonal cocoon crop productivity has not been made. This paper evaluates tasar silk production by A. mylitta fed on six foodplants.

MATERIAL AND METHODS

At the State Tasar Research Farm (Area 20 ha) Durgapur, Orissa, a number of foodplants were selected at random for rearing of A. mylitta larva. The three Combretaceae foodplants chosen were Asan (T. tomentosa), Arjun (T. arjuna), and Dha (Anoegeissus latifolia Wall.). One foodplant from the Dipterocarpaceae, Sal (S. robusta) was selected as well as one Melostomaceae, Ber (Ziziphus jujuba Gaertn.), and one Lythraceae, Sidha (Lagerstroemia parviflora Roxb.). For each foodplant species, 10000 freshly hatched healthy hatchlings were separated into five groups of equal size and brushed onto a number of plants for each of three seasons. The cocoon crop performance was evaluated by effective rate of rearing

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(ERR% = 100 × total cocoons yielded/total larvae brushed), cocoon weight, pupa weight, and shell weight. These parameters were evaluated for each category of food plant in different rearing seasons by standard laboratory techniques. The data were statistically analyzed following Sokal & Rohlf (1969). The experiment was repeated yearly from 1985 to 1989 for all three rearing seasons.

Results

Table 1 presents data on cocoon crop performances on six foodplants. Crop performance as weight of cocoon, pupa and shell on all foodplants was uniformly highest in winter, followed by autumn, with rainy season last, except Sal reared autumn pupa that had the lowest weight. The ERR% on different foodplants was highest in winter and lowest in autumn, except Sal. The maximum ERR% was during rainy and minimum in winter crops).

Table 1. Cocoon crop performance in rearing of A. mylitta on different foodplants during Rainy (R), Autumn (A) and Winter (W) seasons (Mean ± Standard Deviation).

<table>
<thead>
<tr>
<th>Food Plants</th>
<th>Rearing Season</th>
<th>ERR (%)</th>
<th>Cocoon weight (gm)</th>
<th>Pupa weight (gm)</th>
<th>Shell weight (gm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Asan</td>
<td>R</td>
<td>34.05 ± 0.32</td>
<td>10.85 ± 0.23</td>
<td>9.72 ± 0.21</td>
<td>1.13 ± 0.03</td>
</tr>
<tr>
<td>(T. tomentosa)</td>
<td>A</td>
<td>26.52 ± 1.11</td>
<td>12.84 ± 0.30</td>
<td>11.40 ± 0.30</td>
<td>1.44 ± 0.03</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>46.11 ± 1.85</td>
<td>14.35 ± 0.19</td>
<td>12.59 ± 0.48</td>
<td>1.96 ± 0.02</td>
</tr>
<tr>
<td>Arjun</td>
<td>R</td>
<td>15.45 ± 1.58</td>
<td>12.38 ± 0.35</td>
<td>10.93 ± 0.33</td>
<td>1.44 ± 0.03</td>
</tr>
<tr>
<td>(T. arjuna)</td>
<td>A</td>
<td>23.02 ± 1.10</td>
<td>11.46 ± 0.36</td>
<td>10.24 ± 0.37</td>
<td>1.22 ± 0.12</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>42.21 ± 0.72</td>
<td>13.54 ± 0.31</td>
<td>11.95 ± 0.35</td>
<td>1.58 ± 0.08</td>
</tr>
<tr>
<td>Sal</td>
<td>R</td>
<td>15.45 ± 1.58</td>
<td>12.38 ± 0.35</td>
<td>10.93 ± 0.33</td>
<td>1.44 ± 0.03</td>
</tr>
<tr>
<td>(S. Robusta)</td>
<td>A</td>
<td>9.43 ± 0.70</td>
<td>12.46 ± 0.25</td>
<td>10.84 ± 0.60</td>
<td>1.62 ± 0.05</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>7.52 ± 0.51</td>
<td>13.72 ± 0.25</td>
<td>11.92 ± 0.26</td>
<td>1.79 ± 0.02</td>
</tr>
<tr>
<td>Ber</td>
<td>R</td>
<td>23.01 ± 1.34</td>
<td>9.83 ± 0.37</td>
<td>8.87 ± 0.37</td>
<td>0.95 ± 0.01</td>
</tr>
<tr>
<td>(Z. jujuba)</td>
<td>A</td>
<td>18.18 ± 1.62</td>
<td>11.36 ± 0.21</td>
<td>0.22 ± 0.49</td>
<td>1.14 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>26.66 ± 1.48</td>
<td>13.26 ± 0.33</td>
<td>11.83 ± 0.31</td>
<td>1.43 ± 0.02</td>
</tr>
<tr>
<td>Sidha</td>
<td>R</td>
<td>10.59 ± 1.25</td>
<td>8.91 ± 0.52</td>
<td>8.08 ± 0.51</td>
<td>0.84 ± 0.01</td>
</tr>
<tr>
<td>(L. parviflora)</td>
<td>A</td>
<td>6.38 ± 1.08</td>
<td>9.75 ± 0.25</td>
<td>8.81 ± 0.25</td>
<td>0.94 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>13.07 ± 1.65</td>
<td>12.19 ± 0.15</td>
<td>11.00 ± 0.13</td>
<td>1.19 ± 0.03</td>
</tr>
<tr>
<td>Dha</td>
<td>R</td>
<td>5.66 ± 1.24</td>
<td>8.69 ± 0.38</td>
<td>7.95 ± 0.38</td>
<td>0.74 ± 0.01</td>
</tr>
<tr>
<td>(A. latifolia)</td>
<td>A</td>
<td>3.58 ± 0.45</td>
<td>9.13 ± 0.32</td>
<td>8.31 ± 0.32</td>
<td>0.81 ± 0.01</td>
</tr>
<tr>
<td></td>
<td>W</td>
<td>8.44 ± 1.51</td>
<td>9.41 ± 0.39</td>
<td>8.55 ± 0.39</td>
<td>0.86 ± 0.01</td>
</tr>
</tbody>
</table>
Table 2. Some ecological parameters (Mean ± Standard Deviation) during rearing period of A. mylitta

<table>
<thead>
<tr>
<th>Rearing Season</th>
<th>Temperature (°C)</th>
<th>Relative Humidity (%)</th>
<th>Rainfall (mm)</th>
<th>Stormy Weather Period (hrs.)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rainy (July-Aug.)</td>
<td>31.85 ± 0.75</td>
<td>83.04 ± 2.22</td>
<td>231.29 ± 5.38</td>
<td>4.48 ± 1.82</td>
</tr>
<tr>
<td>Autumn (Sept.-Oct.)</td>
<td>28.67 ± 1.02</td>
<td>76.51 ± 1.79</td>
<td>88.97 ± 3.10</td>
<td>9.82 ± 3.15</td>
</tr>
<tr>
<td>Winter (Nov.-Dec.)</td>
<td>20.27 ± 1.04</td>
<td>65.39 ± 1.39</td>
<td>19.44 ± 2.04</td>
<td>0.41 ± 0.12</td>
</tr>
</tbody>
</table>

Table 3. Total cocoon shell (raw silk in gm) production based on effective rate of rearing (ERR × shell weight) of A. mylitta in different foodplant and seasons

<table>
<thead>
<tr>
<th>Rearing Season</th>
<th>Food Plants</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Asan</td>
</tr>
<tr>
<td>Rainy</td>
<td>38.48</td>
</tr>
<tr>
<td>Autumn</td>
<td>38.19</td>
</tr>
<tr>
<td>Winter</td>
<td>90.38</td>
</tr>
</tbody>
</table>

The ANOVA test on seasonal variation of all cocoon crop parameters in individual foodplants indicated significant (P < 0.05) differences except Dha-reared pupa weight. The t-test also indicated significant (p < 0.05) seasonal differences of all above crop parameters in different foodplants except Sal-reared rainy autumn cocoon weight, pupa weight and Dha-reared rainy-autumn, winter-autumn cocoon weight and winter-autumn and rainy-autumn pupa weight.

In winter Asan produced a superior crop compared with other foodplants in all parameters (Table 1). Asan reared larvae showed a significantly higher value in ERR% in all seasons, in cocoon and pupa weight during autumn and winter crop and in shell weight during the winter crop. Sal reared A. mylitta exhibited highest cocoon and pupa weight in rainy crop and highest shell weight in both rainy and autumn crop (Table 1). However, the total quantity of cocoon shell (raw silk) production, based on average ERR% values (ERR% × shell weight), Sal rearing was inferior to Asan and Arjun rearing in the rainy season, Asan, Arjun and Ber rearing in autumn season, and Asan, Arjun, Ber, and Sidha rearing in winter season (Table 3). Thus considering cocoon shell production in different seasons, Asan ranks first followed by Arjun and Ber (Table 3). The superiority of Sal was reflected only in production of tough, heavier cocoons, which in terms of ERR% rendered uneconomical cocoons due to poor silk productivity. Performance on so-called secondary foodplants like Ber and Sidha was higher in comparison to Sal.

The ANOVA test on foodplant variation of all cocoon crop parameters in a particular rearing season indicated significant (p < 0.01) difference.
The t-test also indicated significant (p < 0.05) foodplant differences among all cocoon crop parameters in any given season except the winter ERR% on Sal-Dha, autumn cocoon weight grown on Arjun-Ber and Asan-Sal, Winter cocoon weight on Arjun-Sal and Arjun-Ber, rainy cocoon weight on Sidha-Dha, winter pupa weight on Arjun-Sal, Arjun-Ber, Sal-Ber, rainy pupa weight on Sidha-Dha and autumn shell weight on Arjun-Ber.

There was significant interaction between different foodplant and seasonal changes for each cocoon crop parameter. It was evident from the results that winter season crops were more stable and showed higher shell productivity during trivoline tasar silkworm rearing. Cocoon crop performances on Sal was not more profitable than Asan, Arjun and Ber due to poorer yield of raw silk. Hence the ranking of foodplant in terms of decreasing silk productivity was in the order of Asan, Arjun, Ber, Sal, Sidha, Dha.

**DISCUSSION**

The superiority of the winter cocoon crop to other seasonal crops, regardless of foodplant, might be due to prevalent lower average temperature (20°C), humidity (6%) and drier atmosphere (lowest rainfall of 19 mm) which facilitates increased spinning of cocoons (Table 2). Yokoyama (1962) reported that *Bombyx mori* yields superior quality cocoons at optimum temperatures (22-23°C) and humidity (60-70%). Krishnaswami et al. (1973) stressed the requirement of an optimum environment for maximum productivity of good quality cocoons and comparatively drier atmosphere (60-70% RH) during spinning for better cocoon yield with *B. mori*. Sengupta (1986) remarked that larger ERR% of *A. mylitta* in winter season is due to climatic limitations.

The lowest cocoon quality during the rainy season might be due to high temperatures (31°C), RH (83%) and rainfall (231 mm) (Table 2). Ullal and Narasimhanna (1987) reported that high temperature followed by strong fluctuation results in poor quality cocoons of *B. mori*. Tanaka (1964) remarked that the rainy season is unsuitable for rearing of *B. mori* due to high RH and changing temperature. Sarkar (1980) and Anonymous (1984) stated that sudden variation in temperature is harmful to rearing *Philosamia ricini* larvae. Krishnaswami et al. (1973) reported that temperature and RH exceeding 20-26°C and 60-70% respectively affects cocoon quality of *B. mori*. Jolly et al. (1974) remarked that heavy rainfall disrupts spinning of *A. mylitta* resulting in inferior cocoons.

Although the autumn cocoon crop ranked second in quality to the winter crop, the cause of its lower ERR% compared with the rainy crop might be due to occurrence of longer stormy weather durations (9.82 hours as against 4.48 hours) during this season causing high larval mortality (Table 2). Krishnaswami et al. (1973) remarked about poor silk content of rainy cocoon crop and superior silk content of autumn cocoon crop of *A. mylitta*. Sengupta (1986) stated production of better quality cocoons by *A. mylitta* in September-October (Autumn).
The shell weight of Sal reared rainy and autumn crops was higher although total productivity was less (due to low ERR%). Its reason can be determined by studying nutritional values of Sal plants. Anonymous (1968), Jolly (1966) and Jolly et al. (1974) described superiority of Sal grown cocoons of *A. mylitta* over Asan and Arjun grown in respect of cocoon toughness and shell weight without any specific mention on their seasonal variability, variability of other cocoon crop parameters in different seasons, and the total productivity. Larval rearing on Ber and Sidha in winter gave higher silk productivity than Sal, although the former foodplant is described as secondary foodplant by some previous authors.

Considering overall performances, Sal's rank as a primary foodplant of *A. mylitta* is questionable. Larval rearing on Ber showed significantly (*p < 0.05*) higher ERR% and also higher silk productivity than Sal with data comparable to Asan and Arjun. Hence we suggest that Ber should be given consideration for rearing and for large scale plantation under different tasar projects involving rearing and plantation programs.

**LITERATURE CITED**


The endangered Myrtle's silverspot butterfly: present status and initial conservation planning

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Abstract. The endangered Myrtle's silverspot butterfly, Speyeria zerene myrtleae (Nymphalidae), was studied during a three-year period at the Point Reyes National Seashore and at the site of a proposed resort. Surveys were conducted across much of this insect's historic range. Three large concentrations of Myrtle's silverspot butterflies were identified: two in Point Reyes National Seashore, and one in the coastal prairie and scrub in the vicinity of the Marin-Sonoma county boundary. Continued habitat loss and habitat degradation are the most likely threats. Conservation planning for this butterfly is ongoing, and must include ecosystem management in conjunction with the preservation of suitable habitat.

INTRODUCTION

On 22 June 1992 the U.S. Fish and Wildlife Service issued a final ruling listing Myrtle's silverspot butterfly (Speyeria zerene myrtleae dos Passos and Grey 1945) as an endangered species pursuant to the Endangered Species Act of 1973 (Federal Register 1992). This ruling was deemed justified in order to protect this insect from imminent extinction due to threats resulting from past and proposed habitat loss resulting from residential and commercial development, and from threats due to widespread habitat degradation associated with invasive alien plant species and destructive agricultural practices.

As a consequence of the listing, conservation planning for the Myrtle's silverspot butterfly has become a prime land planning consideration for coastal Marin and Sonoma counties in northern California. While anecdotal data on Myrtle's silverspot butterfly existed at the time of listing, the data were not of sufficient extent or quality to allow comprehensive conservation planning. Specifically, little reliable information existed concerning the number and distribution of Myrtle's silverspot butterfly populations, the approximate number of butterflies in each population, the seasonal phenology, the rates and distances of butterfly dispersal, and the distribution and abundance of larval hostplants and plants that may provide nectar to adults. Without these data conservation activities designed for this butterfly could be oriented at the incorrect spatial and temporal scales, and would not serve to preserve this insect.

While the data shortfall on this subspecies remains profound, this report summarizes recent findings on the biology of Myrtle's silverspot butterfly, and relates these findings to conservation planning for this endangered subspecies.
BACKGROUND ON MYRTLE'S SILVERSPOT BUTTERFLY

Myrtle's silverspot butterfly is a subspecies in the diverse Speyeria zerene species complex (dos Passos and Grey 1947, Grey and Moeck 1962, Hammond and McCorkle 1983, McCorkle 1980). Populations of this butterfly species are found scattered across western North America, from the Rocky Mountains west to the coast of central California, and from northwestern Arizona north to southeastern Alaska (Scott 1986). Across this region, Speyeria zerene is found in habitats ranging from coastal dune-grassland communities to inland, mid-elevation sagebrush and forest communities. The groups of Speyeria zerene populations that have been designated as distinct subspecies are defined primarily on the basis of adult butterfly morphology, geographic distribution, habitat type, and, to a limited extent, inferred phylogenetic affinities (dos Passos and Grey 1945, Grey and Moeck 1962, McCorkle 1980).

Myrtle's silverspot butterfly is thought to be the southernmost entity of a Speyeria zerene clade that inhabits the west coast of North America. This group includes the Oregon silverspot butterfly, Speyeria zerene hippolyta (protected by the federal Endangered Species Act as a "threatened species"), and Behrens' silverspot butterfly, Speyeria zerene behrensii (a candidate for federal protection), as well as Myrtle's silverspot butterfly (Brittnacher et al. 1978, dos Passos and Grey 1945, Grey and Moeck 1962, McCorkle 1980). Populations of Myrtle's silverspot butterfly formerly were found in dunes and bluffs from coastal San Mateo County in the south, to the vicinity of Jenner Beach (Sonoma County) in the north (Steiner 1990) (Map 1). Populations of Speyeria zerene butterflies containing individuals phenotypically intermediate between Myrtle's silverspot butterfly and Behrens' silverspot butterfly were known to exist north of Jenner Beach and south of Anchor Bay (Mendocino County).

By the late 1970s Myrtle's silverspot butterfly populations south of the Golden Gate were thought to be extinct, and the butterfly was considered to still be thriving only at the Point Reyes National Seashore. In 1990, Myrtle's silverspot butterflies were observed in the coastal grasslands north of Estero de San Antonio, at the site of the proposed Marin Coast Golf Ranch (Arnold 1990). This observation triggered studies at the proposed resort site and throughout the historic range of the butterfly. Starting in 1991, extensive field studies on Myrtle's silverspot butterflies were conducted by researchers from the Center for Conservation Biology at Stanford University. These studies were expanded to include field work at Point Reyes National Seashore in 1992.

CONSERVATION PLANNING FOR MYRTLE'S SILVERSPOT BUTTERFLY

Concurrent with federal protection under the Endangered Species Act, conservation planning for Myrtle's silverspot butterfly was initiated on two different levels. Site-specific information on potential impacts construction would have on the butterfly was required at the 510 hectare Marin Coast Golf Ranch (MCGR). On a more general level, baseline
Figure 1. Distribution of historic collection sites of Myrtle's silverspot butterfly (after Steiner 1990, and numerous communications with local lepidopterists). Note that the type locality, San Mateo California (dos Passos and Grey 1945), could refer to either the county of San Mateo, including Pacific coastal areas known historically to support the butterfly, or to the town of San Mateo, located on the bay-side of the San Francisco Peninsula — an area we consider unlikely to have historically supported a Myrtle’s silverspot butterfly population. For this report, the source of the type specimens is considered to be coastal San Mateo County, probably in the vicinity of the town of Pacifica. Also note that the zerene butterflies from the vicinity of Jenner are occasionally considered intermediate between S. z. myrtleae and S. z. behrensii. (Map was created using ARC/INFO and the Digital Chart of the World.)

information on broad patterns of distribution and abundance within the approximately 28,500 hectare Point Reyes National Seashore (PRNS) was needed to determine the status of the insect within the reserve and to determine if a management plan specifically designed to protect the butterfly was warranted. While these two planning efforts were different in breadth and, to some extent, conservation orientation, it was evident at the onset that both projects required field activities to address the shortfall of reliable data.
Information on the site-specific distribution and abundance, including measures of both relative and absolute abundance of adult butterflies, larval hostplants, and plants potentially providing nectar was needed for preliminary planning at the proposed MCGR. Also needed for initial planning at the MCGR site was information on butterfly dispersal and phenology, and on the status of the butterfly in surrounding regions. Off-site surveys were considered necessary in order to put site-specific information into a proper regional context, because on-site conservation planning is strongly dependent on the target organism’s local and regional status. For the second phase of conservation planning at the MCGR, precise information was needed on the spatial distribution of the butterfly in areas where development was proposed, for purposes of the design of management activities.

At Point Reyes National Seashore baseline information on distribution and abundance of the butterfly was lacking. Myrtle’s silverspot butterfly was known to occur in several locations at the Seashore, but much of the Seashore had not been surveyed. Along with baseline information, the development of a long-term monitoring scheme and management options were initiated.

**METHODS**

Beginning April 1991 and continuing through September 1993, field activities were conducted on 115 days (including portions of 245 person-days). Most of the work centered on two locations, the Point Reyes National Seashore and the site of the proposed Marin Coast Golf Resort. On twenty days during the peak adult butterfly flight periods (as determined by on-going work at PRNS and the MCGR), surveys for Myrtle’s silverspot butterflies were conducted in numerous locations throughout the recent range of the butterfly (survey sites distributed from the vicinity of Jenner Beach to the southern coast of Tomales Bay).

Mark-recapture activities were conducted during two seasons, in 1991 at the MCGR and in 1993 at PRNS. These activities were conducted according to the techniques described in Ehrlich and Davidson (1960). This method has been found to have no lasting impacts on comparatively large and robust butterflies, such as Myrtle’s silverspot butterfly (Orive and Baughman 1989, but see Murphy 1988 for caveats). At the time of capture each butterfly was individually marked, sexed, and scored for wing wear (a measure of age). Data were analyzed using a Jolly-Seber population estimation program. The mark-recapture study was designed to be the first step in delineating population boundaries and in estimating the absolute number of Myrtle’s silverspot butterflies at each of the two primary study sites. The timing of adult butterfly emergence was estimated on the basis of condition at first capture (individuals scored as wear condition 0.5 were assumed to have eclosed within two days of capture, individuals of condition 1.0 were assumed to have eclosed three to five days prior to capture, etc.).

The MCGR site was divided into 15 subareas, each approximately 35 hectares in extent (Launer and Murphy 1991). These subareas roughly corresponded to topographic features at the site. In 1991, each of these subareas was used as a focal point for the mark-recapture study. In addition to the mark-recapture activities, the amount of time spent in each subarea, and the number of
butterflies handled or observed but not handled (used as an estimate of non-captured butterflies) were recorded in order to calculate a relative measure of butterfly abundance (butterflies per observer-hour). In 1992 and 1993, kilometer-long transects were located in each of the 15 subareas in an effort to quantify relative abundance (Pollard and Yates 1993). Transects were designed to be representative of the topographic and biotic diversity present in each of the subareas. Transects were walked at a consistent pace on five occasions during periods of appropriate weather during both the 1992 and 1993 seasons. Transect walks were designed to be conducted weekly during peak butterfly flight period, but inclement weather eliminated some periods, hence the mean time between sampling periods was approximately ten days in 1992 and four days in 1993. All butterflies observed within five meters and in front of field workers were counted; those butterflies either behind observers or farther than five meters distant were not counted (Launer and Murphy 1992).

At PRNS, the 1993 mark-recapture study was centered at the dune-scrub interface located at North Beach. In this area, comparatively large numbers of butterflies were observed in 1992 visiting the abundant wildflowers (Grindelia rubicaulis, Abronia latifolia, Monardella undulata, and Erigeron glaucus) (Sparrow and Launer 1992). To the east of the North Beach site, in scrub and grassland communities, Myrtle's silverspot butterflies were observed on occasion, but were too dispersed to be effectively included in the mark-recapture study.

In 1991, prior to federal protection, voucher specimens from the MCGR were retained on a weekly basis. On average, five specimens were collected each week during the study period, and were taken only after it was apparent that the population at the site consisted of several thousands of individuals. Sampling at this low intensity is thought to be of negligible impact to butterfly populations (Harrison et al. 1991).

RESULTS AND DISCUSSION

Distribution

Surveys documented Myrtle's silverspot butterflies in two broad areas at Point Reyes National Seashore and at the proposed Marin Coast Golf Ranch site (Map 2). Surveys also documented Myrtle's silverspot butterflies in locations surrounding the MCGR, including Estero Lane (Sonoma County), Estero Road (Marin County), and the hills between Dillon Beach and Estero de San Antonio (Marin County). No Myrtle's silverspot butterflies were observed at any other survey sites. While the results of these surveys should not be taken as conclusive evidence of absence of the subspecies from areas where they were not observed, it is unlikely that large concentrations of Myrtle's silverspot butterflies, such as those observed at PRNS and at MCGR, exist in publicly accessible areas located between Jenner Beach and the Bodega Bay Golf Course, or in areas located between Dillon Beach and Point Reyes Station. There are, however, inaccessible private landholdings in the coastal region that appear to be capable of supporting Myrtle's silverspot butterflies, and unknown populations of the butterfly inland could also exist.

At PRNS, Myrtle's silverspot butterflies were found at the Tomales Point tule elk range and throughout the bluffs, hills, grasslands, and
back-dunes west of Drakes Estero and Schooner Bay (Map 2). Within each of these two areas, butterflies were found in varying abundances — high concentrations were associated with locations protected from the frequent winds, or with areas supporting large numbers of plants that potentially provide nectar.
Myrtle's silverspot butterflies were unevenly distributed across the MCGR site. Most of the butterflies were recorded from two areas — an approximately 2.5 kilometer coastal drainage system forming part of the northern boundary of the site (and including adjacent off-site areas), and along the Estero de San Antonio. This distribution was consistent in 1991 and 1992. In 1993, a slight shift in distribution was observed that included an expansion by the butterflies into a subarea that had been sparsely occupied in previous years. This slight expansion may have been related to an apparent increase in the density of bull thistles in the newly occupied subarea, but such a causal relationship can only be inferred.

**Estimated number of Myrtle's silverspot butterflies**

At Point Reyes National Seashore (North Beach) in 1993, 76 Myrtle's silverspot butterflies were marked (38 males and 38 females), and 24 recaptures were recorded. The low numbers of recaptures is problematic for several of the algorithms used by Jolly-Seber population estimation programs, and eliminates the possibility of a precise population estimate. However, if changes in daily population levels are assumed to be fairly consistent and calculations are made using a range of Scott's average phi values (in this case, the data indicated a range of average phi values from 0.2 to .06), a fairly reliable estimate can be derived. Using these corrections, between 200 to 600 individual butterflies were estimated to visiting the back-dune areas adjacent to North Beach in 1993.

The estimate of between 200 to 600 individual butterflies should not be taken as an estimate of overall population size in central Point Reyes since we were unable to delineate spatial boundaries of the population, and it is probable that the butterflies visiting the nectar sources at North Beach constitute only a fraction of an extended population. Based on the mark-recapture study and on extensive observations, it is likely that more than 1,000 butterflies but fewer than 5,000 butterflies were present in central Point Reyes in 1993.

At the Marin Coast Golf Ranch site in 1991, 255 Myrtle's silverspot butterflies were marked and then released. Unfortunately, only 19 recaptures were recorded (this low number of recaptures is even more surprising considering that 120 additional observations of unmarked butterflies were recorded out of the context of the mark-recapture study). Again, the comparatively small number recaptures precludes a precise estimate of the total number of butterflies present on the MCGR site in 1991, but it suggests that the effort sampled a large and open population. After considering a number of factors including the length of the adult butterfly flight season, the number of recaptured individuals in relation to the number of marked butterflies, butterfly wear rates, and apparent limitations to butterfly dispersal, a conservative estimate of between 2,500 and 5,000 adult Myrtle's silverspot butterflies are thought to have resided at the proposed resort site in 1991.
Phenology of Myrtle's silverspot butterfly

Onset of the adult butterfly flight season varied between years and between sites. In 1991 adult butterflies were estimated to have begun emerging during the second week of July at the Marin Coast Golf Resort. In contrast, both the 1992 and 1993 adult butterfly flight seasons at the MCGR were projected to have begun in late June. During 1991 to 1993 at Point Reyes National Seashore, the onset of the Myrtle's silverspot butterfly flight season was apparently initiated in mid- to late June. In general, onset of Myrtle's silverspot butterfly flight season was one to two weeks earlier at PRNS than at MCGR. It should be noted that across the Bay area in 1991 many phenological events were exceptionally late — butterfly flight seasons and plant flowering periods were documented as comparatively delayed (for example, the 1991 onset of the Bay checkerspot butterfly flight period at Stanford University's Jasper Ridge was the latest recorded in 33 years of population censusing).

Adult butterflies were present continuously at the two primary study sites for at least two months each year, and in 1991 butterflies were last observed on the MCGR site on 5 October — indicating a three month flight season. During the two to three month flight period, a number of demographic shifts were evident, and large numbers of adult butterflies were observed from the second week of July until mid- to late August. Although individuals of both sexes were found together throughout the flight season, an approximate ten day difference in the peak flight times of the two sexes was apparent; adult male butterflies appeared to reach peak abundance in late July, while adult female butterfly abundance appeared to peak during the first two weeks of August. Note again that 1991 was probably an exceptional year, and peak abundances were not reached until 20 August for males and 1 September for females. The extended flight season exhibited by Myrtle's silverspot butterflies is consistent with other Lepidoptera inhabiting coastal areas (Hammond and McCorkle 1983, Langston 1974). Weather at the primary study sites strongly impacts adult butterfly activity. While butterflies were invariably active during periods of overcast, but calm weather, they ceased to be active during periods of foggy and windy weather. Such inclement weather conditions frequently occurred: indeed, during the three-year study period no adult butterfly activity at all was noted on more than 25% of the days during the adult flight season, and butterfly activity was minimal on many of the remaining days. Days of weather sufficiently mild as to allow for complete days of butterfly activity were uncommon, and most days had only a three or four hour period when the butterflies were active.

Habitat

The habitat of the Myrtle’s silverspot butterfly has been considered to include only low elevation dune and grassland areas immediately inland from the coast. This habitat is well within the summer “fog belt,” a
physical setting that ensures comparatively buffered environmental conditions. Coastal bluff grasslands and scrub at higher elevations were not considered to serve as primary habitat for the Myrtle’s silverspot butterfly. However, work at the Marin Coast Golf Ranch site and at Point Reyes National Seashore determined that grasslands and small valleys located amidst rolling hills may be densely populated by the butterfly. In particular, areas protected from the persistent wind, up to five kilometers from the coast and up to 250 meters in elevation, were found to support substantial numbers of adult butterflies.

Viola adunca, the presumed larval hostplant, is patchily distributed throughout the region, and inhabits a range of biological communities, including grassland, scrub, and dune plant communities. The presence of Viola adunca, therefore, is not a reliable predictor of the presence of Myrtle’s silverspot butterflies. Determinations of habitat suitability must be based on multiple factors, including, but not limited to, distribution of larval hostplants.

The plant species available that potentially provide nectar differ between the upland and dune habitat areas. In the grassy uplands, especially those subject to grazing by livestock, native plant species potentially providing nectar are generally scarce. Butterflies were frequently observed visiting bull thistle, Cirsium vulgare. This alien species is widespread in disturbed areas, along roads and fencelines, and in comparatively moist areas. Another alien plant species, Italian thistle (Carduus pycnocephalus), is also abundant in disturbed areas (particularly overgrazed areas), and was visited by butterflies that were active before mid-July. In upland areas, very few visits to native plant species were observed. At PRNS, Grindelia (probably G. rubicaulis) and Monardella (probably M. villosa) were occasionally visited, and at the MCRG, Monardella villosa was visited. At the dune-scrub interface in central PRNS, Grindelia rubicaulis, Abronia latifolia, and Monardella undulata were visited regularly by Myrtle’s silverspot butterflies. In this zone, Grindelia and Abronia are found in dense patches up to several meters in diameter. Butterflies frequented these large patches. Erigeron glaucus was visited to lesser degree. Cirsium vulgare was rarely visited by Myrtle’s silverspot butterflies in the dune-scrub zone. Flowers of the invasive iceplant (Mesembryanthemum species) were never visited by Myrtle’s silverspot butterflies.

The availability of nectar is potentially a critical factor for the long-term persistence of Myrtle’s silverspot butterfly populations. In a related species, Speyeria mormonia, a strong correlation exists between the amount of nectar consumed by female butterflies and the number of eggs they produce (Boggs and Ross 1993). This implies that under field conditions, reduced nectar availability can limit the total number of eggs produced, and can result in a reduction in the number of offspring that survive to become adults in the subsequent year (assuming that there is negligible density dependent mortality of larvae). Widespread overgraz-
ing in the region may have substantially reduced the availability of nectar (particularly native plant species), and could be contributing to a regional decline of the butterfly.

**Adult butterfly dispersal and the spatial scale of Myrtle’s silverspot butterfly populations**

At the Marin Coast Golf Ranch site in 1991, few butterflies were recaptured in subareas different from those of their initial capture. Slightly more than 50% (10 of 19) of recaptured butterflies were taken in the same subarea as initially recorded, and 95% (18 of 19) of all recaptures were made in either the same subarea as initial capture or in an immediately adjacent subarea. Only 5% (1 of 19) of butterflies captured more than once dispersed to a non-adjacent subarea. The mean distance traveled by all recaptured individuals was approximately 75 meters (the mean value for distance moved between recapture events is based on distance between center points of the subareas). Of those butterflies documented to have moved into a different subarea, the mean distance traveled was approximately 350 meters, and the longest recorded movement was approximately 1,500 meters.

When these results from the mark-recapture study are coupled with the extensive observations at the proposed resort site during the three study years, it appears that Myrtle’s silverspot butterflies generally stayed within circumscribed topographic units — coastal drainage systems separated by wind-swept ridges and exposed grasslands. Within these protected areas, daily movements of several hundred meters are undoubtedly frequent, and longer movements, up to and likely exceeding the 1,500 meters recorded by the mark-recapture study, are not unusual.

Dispersal between the two “large” drainage systems at the MCGR site was not recorded during the course of this study. However, given the vagility of the butterflies, and the comparatively short distances between drainages, it is probable that dispersal between drainage systems does occur.

At the dune-scrub interface at Point Reyes, high concentrations of nectar-producing plants attract butterflies from unknown and perhaps distant natal areas; observations imply movements on the order of several kilometers. During 1992 and 1993, there were numerous observations of butterflies flying without stopping through the grasslands and scrub east of North Beach, and across the main road. While conclusive proof of movements between distant population centers would be desirable, the practicalities of conducting a mark-recapture study in areas supporting low butterfly densities eliminated this option.

The balanced sex ratio observed at North Beach in 1993 (50:50) may indicate that only a subset of a population was sampled. In general, female butterflies are less likely to be encountered, hence captured, than are male butterflies, and mark-recapture studies nearly always involve the handling of more males than females (Ehrlich et al. 1984). The few
instances in which more females than males are captured typically occur when sampling is restricted to the end of the flight season (butterflies, and *Speyeria* in particular, are generally protandrous), or when sampling occurs where scarce resources attract disproportionate numbers of females from surrounding areas. The first possibility is unlikely in this case; the timing of the 1993 study indicates that females may have been undersampled. It is probable that the North Beach study site represents just a portion of the geographic range of an open and highly dispersed Myrtle's silverspot butterfly population residing in central Point Reyes.

While conclusive determination on the geographic extent of Myrtle's silverspot butterfly populations is lacking, these studies indicate that it is probable that at least three demographically independent populations of Myrtle's silverspot butterflies exist: central Point Reyes (including areas in the vicinity of North Beach, South Beach, and Drake's Beach); Tomales Point (within the PRNS tule elk range); and in the vicinity of the MCGR (this population probably extends north to Estero Lane in Sonoma County). It is unclear the degree to which these ostensible populations, particularly those located at MCGR and central PRNS, are subdivided, but it is likely that substantial interchange of individuals occurs between areas of high butterfly density within each of the three areas. Similarly diffuse populations of this approximate geographic scale have been suggested previously for the Oregon silverspot butterfly (Pickering et al. 1991, Pickering et al. 1992).

**Conclusions and Recommendations**

Species-specific conservation planning is never an easy task, but working with an invertebrate species presents an especially daunting set of challenges — particularly when the available period of investigation is limited (New 1991, Pollard and Yates 1993). Distribution and abundance “snap-shots” of butterfly populations and metapopulations, that is studies based on single or two consecutive field seasons, need to be viewed in the context of dynamic natural fluctuations typical of such systems (Baughman and Murphy 1990). In light of the lack of a historic perspective, the precise status of *Speyeria zerene myrtleae* remains largely unresolved. It is fairly certain that this butterfly has declined in distribution and in abundance; and even with the large number of butterflies inhabiting the nominally protected lands of Point Reyes National Seashore, this butterfly warrants the protection it has been afforded under the Endangered Species Act. However, considering the large extent of generally inaccessible private land in the region, there may be undiscovered populations of Myrtle's silverspot butterflies scattered across coastal Marin and Sonoma Counties. It is doubtful that any populations of Myrtle's silverspot butterfly exist south of the Golden Gate. It is also possible that inland populations of Myrtle's silverspot butterflies exist since the ecologically similar Oregon silverspot butterfly, *Speyeria zere ne hippolyta*, is present at Mount Hebo, a site well away from the coast.
At Point Reyes National Seashore, the distribution and abundance of the butterfly indicate it is not in immediate danger of extinction, and that even without conservation actions specifically targeting the butterfly, this subspecies will likely persist within the park for some time to come — an observation that suggests that design and implementation of management activities need not be carried out under the “crisis management” timetable so frequent to conservation efforts. Long-term persistence of Myrtle’s silverspot butterfly, however, is not guaranteed because the cumulative impacts of grazing (from both domestic livestock and tule elk), invasive alien plant species, and possibly the suppression of natural disturbances, are not well understood. The region-wide decline of the butterfly implies that such cumulative impacts have been significant and may eventually threaten the existence of the butterfly even at PRNS.

The ecosystems of coastal California, including PRNS, have been altered significantly by more than one hundred years of human activities and by the invasions of alien plant and animal species. Unfortunately, the impacts of these activities are likely so pervasive that complete cessation of some commercial ventures, specifically grazing, would probably lead to the loss of native species as non-native species slowly eliminate them (Davis and Sherman 1992, Elliott and Wehausen 1974, Hardham and True 1972, Hektner and Foin 1974). With this virtually permanent alteration of the habitats that support Myrtle’s silverspot butterfly comes the necessity of long-term management — simply setting aside land for butterfly reserves with no active management will be insufficient for the conservation of this insect. Perhaps the most important of the management options is the identification of grazing regimes that are beneficial to larval hostplants and plants providing nectar resources, and conservation planning for Myrtle’s silverspot butterfly should include scientifically defensible grazing and habitat restoration experiments. As it is inconceivable that one grazing regime will prove optimal for all components of biotic diversity in the region, and because many effects of grazing may not be apparent for many years, long-term conservation planning at PRNS should incorporate areas subjected to range of grazing pressures — from no livestock to comparatively high densities of livestock.

Unfortunately, managed grazing will not be a complete solution. In the back-dune areas, use of grazing to minimize the impacts of non-native species, particularly iceplant, will not be appropriate. It is unlikely that native plant species dwelling on the physically loose substrates of the dune areas would benefit from livestock, and such disruption could exacerbate the transition from native to non-native plant species. In that these dune communities apparently provide nectar resources critical to the long-term persistence of Myrtle’s silverspot butterflies, programs of iceplant control and dune restoration need to be initiated. With the reality that iceplant will not be eliminated from PRNS in the foreseeable future (if ever), areas still supporting comparatively high densities of
native plant species, such as the back-dunes at North Beach, need to be focal points of such control and restoration efforts.

Another apparent conservation problem faced by Myrtle’s silverspot butterfly is the collection of specimens. While it is very doubtful that collection of specimens has ever constituted a threat to any Myrtle’s silverspot butterfly population, areas where comparatively high concentrations of female butterflies can be found, such as North Beach at PRNS, should be patrolled during the adult butterfly flight season to discourage poaching.

At the proposed Marin Coast Golf Ranch, studies indicate that Myrtle’s silverspot butterflies are more or less absent from a sizable portion of the site, hence development of some areas could have a negligible impact on the butterfly. However, a problem for site-specific conservation efforts designed for the butterfly is that the MCGS site constitutes only a portion of the distribution of a widespread butterfly population. This is a near universal problem with site-specific planning in that most butterfly populations are not encompassed in their entirety by political or human-defined boundaries. As a result, site-specific planning efforts tend to focus on just portions of populations, and adjacent off-site areas that are critical to the long-term persistence of target species, may not benefit from conservation planning. Given the extent of private-sector conservation planning, this problem is unlikely to be resolved with any strategy short of a full regional habitat conservation plan — something that often is suggested, but rarely accomplished.

A common theme for conservation planning for butterflies is that planning increasingly focuses on proper ecosystem management — as reserve design options in urban and suburban areas dwindle, the development of resource management plans are taking center stage. Across California early conservation efforts designed to protect the state’s threatened butterflies focused on reserve design, but the last decade has seen a shift toward ecosystem management — gorse removal on San Bruno Mountain for Mission blue butterflies, iceplant control for Smith’s blue butterflies, buckwheat outplanting for El Segundo blues and Lange’s metalmarks, and phased grazing for Bay checkerspot butterflies. Without the implementation of management activities — phased grazing in grassland and scrub areas, and iceplant control in back-dune areas — lands set aside for Myrtle’s silverspot butterfly will likely degrade and the butterfly well might continue to decline.

Acknowledgements. We wish to thank the following for support during this project: Gary Fellers, Point Reyes National Seashore; Sterling Mattoon; Chris Nagano, US Fish and Wildlife Service; Andrew Weiss, Center for Conservation Biology GIS manager; Center for Conservation Biology Field Crews (Steve Rottenborn, Erica Fleishman, Tom Sisk, Russ Bell, Jon Hoekstra, Ian Woods, Rob Blair, Jeff Hodgson, Matt Ballard, Kathy Switky, Stu Weiss, Ted Lee, Duncan Elkins, Stacey Motland, Flint Hughes, Katy Human, Angela Kalmer,
Rocky Beek, and Adam Welcher); and ESRI (for ARC/INFO and Digital Chart of the World). The 1993 mark-recapture study was conducted under Federal Fish and Wildlife permit number PRT-775311, and National Park Service “Collecting Permit” number 9211. We also wish to thank two anonymous reviewers whose comments enhanced this text.

**LITERATURE CITED**


**FEDERAL REGISTER. 1992.** Endangered and threatened wildlife and plants; six plants and Myrtle’s silverspot butterfly from coastal dunes in northern and central California determined to be endangered. 57: 27848-27858.


Book Reviews


Judging from this book's title and length, I had hoped for a useful book advising on rearing butterflies and other arthropods. Unfortunately, I was disappointed.

The book begins with a very brief Introduction and Preface. The body is divided into four parts: Butterflies of Temperate Regions, Some Migratory Butterflies, Breeding Butterflies, and Breeding Other Exotica. I will treat the first two parts of the book separately from the last two, since they are really more like two different books.

The first section, Butterflies of Temperate Regions, treats only British butterflies. This section would be useful if it actually provided rearing advice for the 58 British species treated. Instead, the discussion for each species includes three sections: Distribution (global distribution of the species), Foodplants (accepted larval hostplants in Britain), and General Notes. For each species, the General Notes section deals almost entirely with British distribution, habitats and timing of broods; their overwintering stage; a brief description of each species' larvae and pupae; and how to identify the adults (nearly one whole page is devoted to the identification of the three British subspecies of *Coenonympha tullia*!). Larval behavior is often noted. I had expected tips on how to rear each species in the General Notes section, but found no hints until p. 33, where Stone warns the reader to separate larvae of *Anthocaris cardamines*, due to their cannibalistic tendencies. Some of the information in this section is too vague to be of much use. For example, on page 80, under the Foodplants section for *Mellicta athalia*, Stone lists four known foodplants, then states "A number of other plants are also reported, including some garden plants." What are these other hostplants? In a book about rearing butterflies that treats only British species, I would expect as complete a list of known larval hostplants as possible, especially if some of these may be available in my own garden, or as naturalized wild plants in North America! The second section, Some Migratory Butterflies, only treats migrant species that occasionally reach Britain. The format of this section is very similar to that of the first section.

The contents of the first two sections of this book seem unrelated to the title. My frustration with the book was strengthened each time I came across a mistake. A careful examination of the text by several reviewers should have been made before publication, so that the numerous mistakes scattered throughout the text could have been found and corrected (only one reviewer is mentioned in the Acknowledgments).

The 16 color plates that are inserted between the text of section one are quite nice, and include many of the rearing tips found in that section. The plates make the book much more attractive overall. However, there are several species...
(Triodes sp., Cressida cressida, Caligo brasilenis, and Zerinthia polyxena) pictured on the color plates that receive no mention anywhere in the text, making me wonder why they were included. The color plates are not without mistakes, unfortunately, as can be seen by the mimic female Hypolimnas misippus that is labeled as its model, Danaus chrysippus.

The real value of this book is in the third and fourth sections (final 84 pp.). The third section, Breeding Butterflies, consists of four parts (General Information, Housing for Captive Breeding, Breeding Methods for Some Tropical Species, and Breeding Methods for Exotic Species). This section begins by providing general information about butterfly life history, and continues with a discussion of various breeding cages; it does provide some excellent tips on how to rear butterflies in captivity, and may be useful to anyone who desires to grow large numbers of butterflies. The part of section three dealing with the rearing of exotic species is less useful, for it proclaims too many broad generalities. For example, Stone asserts that for papilionids, "The two main foodplants are Citrus and Aristolochia." Very intricate details are, however, presented in the discussion of breeding Heliconius butterflies. The fourth section, Breeding Other Exotica, also gives advice that may be useful to anyone wishing to rear Praying Mantids, Scorpions, Stick Insects, Leaf Insects, Locusts, Large Spiders, or Leaf-Cutter ants.

I was surprised that no mention of rearing moths was made, especially of the commonly grown Saturnia pavonia, which occurs throughout Europe (including Britain). The text was difficult to read—often wordy, disorganized, and very opinionated, as where Stone states that "Heliconid butterflies are, without a doubt, the most rewarding species to breed," and where he describes papilionids as being the "largest and most beautiful butterflies." There are several sections in the book where very little useful information is presented. Many of the "scientific facts" are of questionable validity, as can be seen in the introduction to section two where Stone explains that some butterflies "seem to enjoy flying great distances." The writing style gives the text a very unprofessional tone. Much of the useful rearing advice must be gleaned from his numerous personal stories. The absence of a bibliography (although there is a suggested reading list that fails to mention any book dealing primarily with rearing arthropods) suggests that Stone did very little research, and also reinforces my impression that the facts about arthropods given in this book are primarily Stone's own observations.

I cannot recommend this book to a very wide audience. It may be useful to anyone wishing to find and rear British butterflies, or to persons planning to breed butterflies or other arthropods for a butterfly house or other living exhibit. To anyone else, this book would be of limited use, and another book dealing only with rearing techniques would be a better alternative for the price.

Andrew D. Warren, Department of Entomology, Comstock Hall, Cornell University, Ithaca, NY 14853-0999
(The assistance of Robert Dirig in reviewing this paper and making many useful suggestions is gratefully acknowledged)

Australia may be a large country with a small population, but on a per capita basis Aussies clearly lead the world in producing serious, meticulous, works that have established new standards to define contemporary systematics of the Lepidoptera. This second volume of the Monographs on Australian Lepidoptera series deals with all 44 genera of the family Tineidae known to occur in Australia. In the global context there are about 3500 species in 320 genera. Among the 44 Australian genera, 9 were apparently introduced by man and only 12 are endemic. To illustrate the distance yet to be traveled along the road to fully cataloging biodiversity, five of the 12 endemics are described as new in the work and several unplaceable species are thoroughly covered. There are 187 named species, but the authors state that these are equaled by unnamed species.

The first chapter defines the family and hypothesizes a phylogeny based on several character states. The four subfamilies are also analyzed. The next chapters deal in depth with morphology, including morphology of all early stages in detail and biology. The range of life histories is fascinating as most species are aphytophagous. Before the major section describing the genera in detail there is a brief chapter on diversity and distribution. There are concluding chapters on unplaced species and excluded species and finally comprehensive citations.

This scholastically noteworthy series of publications demands support. Next up is a volume by I. F. B. Common on a section of the Oecophoridae to be followed by a butterfly biology book by R. L. Kitching et al.


This is a very strange book that comes over as a literary non sequitur. Although well designed, produced, and illustrated (the dust jacket is striking) one comes away not being sure what it is all about or for whom it was written. The first part is a review paper of the fossil butterflies of Florissant with a bit about fossil insects in general and the geological history of the earth. These fossils were laid down during the mid Tertiary about 35 million years ago. The climate at that time was apparently subtropical, a conclusion open to interpretation. There also have been major climatic episodes since with vast, intricate, yet highly conjectural movements of the plant communities upon which butterflies, as primary herbivores, directly depend.

The second paper that makes up the book is an annotated checklist of the butterflies of Florissant with all species illustrated in color. The lead-ins include sections on habitat diversity, butterfly diversity, a brief description of general life history, behavior, survival, and taxonomy. Jurassic Park is unquestionably more fun.

BUTTERFLIES AND SKIPPERS OF OHIO. 1992. D. C. Ifner, J. A. Shuey, J. V. Calhoun. College of Biological Sciences, Ohio State University, Columbus, Ohio. $40.00 plus $5.00 postage. Softcover. 212 pp incl. 40 pp color plates. 8.5 x 11 inches.

A bravo book that, in terms of information offered, will be the standard
reference for the state for a long time to come. My negative comments center on
the rather poor design, with everything shoved too close together and altogether
too narrow margins. For so valuable a scholastic work it is a pity the publisher
didn't spend a little time with a book designer. to have given it a touch of class.
The familial classification used is largely archaic.

Background information makes this a faunistic work of greater than usual
interest. This includes a section on plant communities, which are the biotic
aggregations to which primary herbivores, such as butterflies, are adapted. In
addition to a vegetation map there are good photographs of all plant communi-
ties. There are chapters on history and collectors, education and conservation,
plant communities, geology and postglacial biogeography, and methods and
terminology. There follows the species listing, with county dot maps for each of
the 144 listings, foodplants, phenology, nectar sources, community associations
etc. An essential volume for all mid-continent libraries and researchers.

and D. H. Harris. College of Biological Sciences, Ohio State University, Colum-
bus, Ohio. $20.00 plus $3.00 postage. Softcover. 219 pp incl. 8 color plates. 8.5 x
11 inches.

A double bravo book by the Ohio Biological Survey that can be viewed as a
model for what we are all supposed to be doing as fast as possible in the face of
a rapidly diminishing natural world. With the recent federal announcement of a
national biological survey, the Ohio institution for this purpose, the Ohio
Biological Survey, has made a most pertinent contribution with this and the
above work.

The authors relied on the generosity of many individuals and collections
managers to bring the book to the standard that it is. The effort required
recording 35,441 specimens to 708 species of Noctuids, classified and named
following Hodges (1984). A county map with number of specimens from each
depicts a highly non-random database, a commonplace in all wide area sampling
pictures. The authors admit that a number of species remain to be collected and
include a list of the most probable, complemented by a list of excluded species as
misidents and mislabeled specimens.

There is a brief section on identification and an introduction to characters used
for this end, including genitalic characters. There is a brief review of developmen-
tal biology and another on conservation. There are no diversions into controver-
sial matters of higher classification issues within this large and complex family
of moths. Quite proper for a work of this kind.

The centerpiece of the work is the listing of species in an annotated checklist
format that includes for each species: MONA checklist and McDunnough check-
list number, a reference to where an illustration can be found other than on a
plate in the book, an estimate of relative abundance and conservation status, an
historical note if applicable, and hosts. There is then a map for each species and
a seasonal distribution chart for north and south Ohio.

Following is a list of species that qualify for special attention, in particular
those for which this status is unknown. There is then a set of descriptions of
special habitats in the state, which are not too numerous, but all sound like places
one would want to see. Lastly there is the detailed hostplant listing.

Invaluable, and there is still a great deal to do.
Briefly Noted:

One of those charming hand lettered watercolored general compendia that is actually a tad difficult to read and a bit too cute. The piece carries an amazing amount of information, however, with maps and life histories spattered here and there. Oddly, some species have scientific names while binomials are missing for others. A best buy to get that youngster involved, and the book covers the west as well as the usual east.


“A simplified field guide to the caterpillars of common butterflies and moths of North America.” A nice piece for children and casual naturalists that might pique their interest to look beyond the superficial. Strictly eastern U.S. No scientific names. Good price for gift giving.


The content is completely described by the title. The only figures are maps giving political boundaries and depicting faunal regions. Foodplant data are not given. Subspecies names are not used, a pity in the case of the butterflies, while for butterflies the familial supersplitting of earlier mindsets is retained.


A compendium of foodplant records for 505 species and subspecies of these large moths. Cross referenced to plant families and species. Many are polyphagous. Unfortunately there is no attempt to analyze patterns of co-adaptation, but here are the data for someone with such interest. Individuals like Stone are to be praised for the enormous labor performed in bringing together basic data as is presented here. The cover is very attractive, but unfortunately the text was run on a laserwriter and not linotronic. In the future this sort of book would be most efficiently handled as a database on diskette.


One cannot add much to the widespread acclaim Bob Pyle has received for this classic piece, now released in a new printing. He has opened a new view of lepidopterology with a greater population of people beginning to watch butterflies rather than pin them down. The book to buy for anyone interested in these insects. Note the important chapter: “Moths: learning to love them.”


Part of a “Dimensional Nature Portfolio” series that include a piece each on the spider, beetle, and bee. The piece is not a book, but a folder from which a giant Monarch butterfly emerges on opening. Several side folders have additional pop-ups and windows. The quality of work is surprisingly good. May be of some value
in schools, but overall my impression is one of too many publishers rushing to fill a popular market that may not have the demand they expect.


An exhaustive treatment of the butterfly fauna of the Florida Keys including summaries of the history, climate, geology, biogeography, and plant communities. All species illustrated in color, with detailed flight time data given. Conservation biology issues examined, and species-area study presented on distribution among the various islands. Curiously the number of species included, 106, is identical to butterfly species richness of greater Los Angeles.

ATLAS OF WESTERN USA BUTTERFLIES. 1993. R. E. Stanford & P. A. Opler. Published by authors. $17.00 postpaid. 275 pp. spiral bound. 8.5 x 11 inches.

This fine service paper gives a county map of the western US, i.e., those states west of the 100th meridian, with recorded presence of each species distribution presented as four maps per page. An enormous amount of data distilled from many published sources. For the future this information would be best made available as a database format on diskette.


A popular directed guide to butterfly watching across the dense population corridor of the eastern US. A bargain book for its great deal of well organized information joined with good quality color photographs of most species taken in the field. There is the usual difficulty in discriminating dusky skippers using the illustrative material, but what else is new? An excellent supplement to Pyle's butterfly watchers book for the area covered. It is amazing what a growth industry popular, non-collector oriented books have become. Will the Audubon Society be superseded by a Scudder Society? But then are butterflies becoming more invisible? And will people learn to love moths?

Rudi Mattoni, Department of Geography, University of California Los Angeles, Los Angeles, CA 90024, USA.
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Manuscript format: Two copies must be submitted, double-spaced, typed, with wide margins. Number all pages consecutively. If possible italicize rather than underline scientific names and emphasized words. Footnotes are discouraged. Do not hyphenate words at the right margin. All measurements must be metric. Time must be cited on a 24-hour basis, standard time. Abbreviations must follow common usage. Dates should be cited as: day-Arabic numeral; month-Roman numeral; year-Arabic numeral (e.g. 6.IV.1992). Numerals must be used for ten and greater e.g. nine butterflies, 12 moths.

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COVER ILLUSTRATION: Above: 5th instar Ancyluris inca, a common second growth non-myrmecophilous species. Below: 5th instar Nymphidium mantus drinking at an extrafloral nectary of its hostplant. Note the Azteca sp. (Dolichoderiinae) ant drinking from the tentacle nectary organs. Drawings by Jennifer Clark from slides by Phil DeVries for upcoming fieldguide to riodinid butterflies of Costa Rica.
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Exploitation of lycaenid-ant mutualisms by braconid parasitoids

Konrad Fiedler¹, Peter Seufert¹, Naomi E. Pierce², John G. Pearson³ and Hans-Thomas Baumgarten¹

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Abstract. Larvae of 17 Lycaenidae butterfly species from Europe, North America, South East Asia and Australia were observed to retain at least some of their adaptations related to myrmecophily even after parasitic braconid larvae have emerged from them. The myrmecophilous glandular organs and vibratory muscles of such larval carcasses remain functional for up to 8 days. The cuticle of lycaenid larvae contains extractable "adoption substances" which elicit antennal drumming in their tending ants. These adoption substances, as well, appear to persist in a functional state beyond parasitoid emergence, and the larval carcasses are hence tended much like healthy caterpillars. In all examples, the braconids may receive selective advantages through myrmecophily of their host larvae, instead of being suppressed by the ant guard. Interactions where parasitoids exploit the ant-mutualism of their lycaenid hosts have as yet been recorded only from the Apanteles group in the Braconidae-Microgasterinae.

Key Words: Lycaenidae, Formicidae, myrmecophily, adoption substances, parasitoids, Braconidae, Apanteles, defensive mechanisms

Introduction

Parasitoid wasps or flies are major enemies of the early stages of most Lepidoptera (Shaw 1990, Weseloh 1993). The mostly endophagous larvae of the wasp family Braconidae usually develop in caterpillars of various Lepidoptera or, more rarely, in the larvae of certain Hymenoptera or Diptera. Larvae of Microgasterinae braconids are either solitary or gregarious parasitoids, depending on the species (Papp 1990, Shaw 1990). In this economically important subfamily, the parasitoid larvae leave their hosts and pupate externally in a silken cocoon. This cocoon may either be attached to the host's carcass, as in the case of the well-known Cotesia glomerata (L.) parasitizing the cabbage white, Pieris brassicae (L.), or to the hostplant. With very few exceptions (e.g. Brodeur and Vet 1994), a host caterpillar will die soon after Microgasterinae larvae have emerged.

Paper submitted 16 December 1994; revised manuscript accepted 29 March 1995.
Lepidopterous caterpillars have evolved a variety of strategies to escape parasitoid attacks. One peculiar strategy is found among myrmecophilous members of the butterfly families Lycaenidae and Riodinidae. These larvae attract ants with the help of specialized exocrine glands (Malicky 1969, Pierce 1983, Cottrell 1984). Larval secretions contain carbohydrates and amino acids which serve as additional nutrition for tending ants (Maschwitz et al. 1975, Pierce 1983, Fiedler & Maschwitz 1988a). In turn, the ants may effectively protect the caterpillars against certain enemies, including parasitoids (Pierce & Mead 1981, Pierce & Easteal 1986, Pierce et al. 1987, Seufert & Fiedler 1994). Such butterfly-ant interactions then represent true mutualisms, analogous to the well-known trophobiotic associations between honeydew-producing Homoptera and ants.

At least three types of myrmecophilous glands are important in lycaenid-ant interactions. The dorsal nectar organ (located mediadorsally on the 7th abdominal segment, DNO hereafter) secretes droplets of a nutrient-rich fluid when stimulated through antennation by ants (Malicky 1969, Cottrell 1984). In addition, many Lycaenidae caterpillars possess a pair of eversible tentacle organs (TOs hereafter) on the 8th abdominal segment. These organs are mostly everted when the caterpillars are disturbed, or while moving to feeding or resting places. Ants respond with a state of alert to TO eversions, apparently mediated through volatile chemicals (Henning 1983, Fiedler & Maschwitz 1988b, Ballmer & Pratt 1992). A third type of myrmecophilous organs are the pore cupolas (PCOs), minute hair-derived epidermal glands whose secretions are often highly attractive to ants (Malicky 1969, Pierce 1983). PCOs are generally found in larvae as well as pupae of lycaenid butterflies, even if stable symbiotic associations with ants do not occur. Finally, so-called dendritic setae appear to be related to caterpillar-ant interactions, since the locations of these setae in larvae or pupae generally receive the greatest attention of visiting ants (Ballmer & Pratt 1992, Fiedler, pers. observ.).

In addition, immatures of many Lycaenidae species produce substrate-borne vibrations (DeVries 1991a). In analogy to the “calls” of certain myrmecophilous Riodinidae (DeVries 1990), vibrations of Lycaenidae larvae may enhance their symbioses with ants, although the occurrence of substrate-borne vibrations in certain non-myrmecophilous lycaenid species suggests that vibratory behavior is not exclusively connected with myrmecophily and may serve another function (possibly defense) in these species (Schurian & Fiedler 1991, Fiedler 1992a, 1994; see also Downey & Allyn 1978 for pupal sounds).

Behavioral interactions between lycaenid caterpillars, their parasitoids and attendant ants have as yet received little attention, although the protective role of tending ants against parasitoids has been established in a few lycaenid species (Pierce & Mead 1981, Pierce & Easteal 1986, Pierce et al. 1987). Pierce et al. (1987) and Nash (1989) obtained evidence that a specialist parasitoid of the Australian obligate myrmecophile Jalmenus evagoras Domovan may use attendant Iridomyrmex
anceps ants as host-location cues. Recently, Schurian et al. (1993) described how adult braconid wasps utilize ant-related secretions of their host caterpillars. In this paper, we investigate two additional aspects of such multi-species interactions. First, we use a simple behavioral bioassay to investigate the chemical nature of "ant adoption" substances secreted by larvae of the Nearctic species, Glaucopsyche lygdamus Doubleday. Second, we document that particular species of parasitoids consume their lycaenid hosts in ways that take advantage of the myrmecophilous properties of the caterpillars. We here summarize our findings on 17 butterfly species, representing 13 genera in 2 subfamilies.

Materials and Methods
Adoption substances in Glaucopsyche lygdamus larvae
100 final instar caterpillars of the Nearctic G. lygdamus were sampled at Gothic, Colorado (elevation 2900 m), in July 1980 and stored frozen at -20 °C. From these larvae, two groups of tissue preparations were made, viz. "dorsal epidermis" and "ventral epidermis". PCOs as well as other setae which may play a role in ant-caterpillar interactions (e.g. dendritic setae; Ballmer & Pratt 1992) are too small to permit individual excision, but morphological analyses revealed that these structures are common dorsally, but rare (PCOs) or absent (dendritic setae) on the ventral side of the caterpillars (e.g. Ballmer & Pratt 1989). Wet tissue samples (208 mg dorsal epidermis and 20 mg ventral epidermis) were weighed and extracted with 50 μl of solvent per mg of tissue. This approach equalizes concentrations of ions or extractable substances between experimental (dorsal) and control (ventral) tissues. Extraction was accomplished by grinding tissue samples in glass vials with flanged glass rods. Redistilled dichloromethane was used as solvent.

Pre-packaged silica gel thin-layer plates (EM, 25 μ) were spotted with 100 μl of tissue extract (dorsal, ventral) or solvent. On some plates cholesterol was also spotted as a standard indicator. Before solvent development, spotted material was first assayed for biological activity with a tissue paper overlay protecting the plates. Plates were then developed at 4 °C with hexane/ethyl-acetate/ethanol (92:6:2), and as soon as these plates had dried, the bioassay was carried out with a tissue paper overlay marked in 1 cm bands for each sample. Following bioassay, separated components were visualized by iodine vapor. Eight trials were conducted.

Queenright colonies of Formica altipetens, kept in artificial nests and fed on a diet of honey water and freshly killed insects with access to ad libitum water, were used for bioassays. Treated TLC plates were offered at a distance of 10 cm from the entrance to the ant nest in a foraging arena (71 × 142 cm) in which an ant colony was placed. Behavioral responses of the ants were scored as a percentage of the number of times that workers stopped and drummed over the total number of encounters during a 15 min period.

Interactions between ants and parasitized caterpillars or larval carcasses
During our studies on the life-cycles of various Lycaenidae species in Central Europe, North America, South East Asia and Australia, we repeatedly collected caterpillars that later turned out to be parasitized. Field-collected caterpillars
of 17 species (Table 1) were reared in the laboratory together with their attendant ants, until parasitoids left their host caterpillars to pupate. Some individuals were left under natural conditions on their hostplants. Behaviors of ants before and after parasitoid emergence were noted, and the activity of the myrmecophilous organs of the caterpillars as well as their ability to produce substrate-borne vibratory signals were followed until the carcasses eventually lost attractiveness to ants. Vibrations were monitored using a stethoscope (Schurian & Fiedler 1991).

**Results**

Adoption substances in the epidermis of *Glaucopsyche lygdamus*

Whenever worker ants tend lycaenid larvae in nature, a characteristic antennal drumming is one main component of ant-caterpillar interactions (Malicky 1969, 1970). We used this behavioral trait as an indicator of ant response to lycaenid adoption substances: immediately upon encountering a spot of dorsal skin extract, a *F. altipetens* worker would often drum on the spot in exactly the same manner as she would on a caterpillar in the field. Workers never recruited nestmates to the spots, and tactile stimulation appeared to be necessary to elicit ant response as workers did not move preferentially upwind toward fresh caterpillars when air was passed over them in a Y-tube olfactometer (Pierce, unpubl.).

Workers investigated the extract of dorsal skin significantly more often than the extract of ventral skin (i.e. “controls”). With dorsal extracts, 57.0 ± 17.7 % (mean ± S.D.) of all encounters resulted in drumming responses, whereas with ventral extracts the average figure was 30.6 ± 17.6 % (8 paired trials, p < 0.005, Wilcoxon signed-ranks test). Although myrmecophilous organs are almost absent from the ventral surface of a caterpillar, the ventral control extracts still contained low activity. We attribute this to the unavoidable crudeness of the tissue preparation. Fig. 1 presents the data compiled from developed TLC plates. Nine spots were found on each chromatogram for both the dorsal and ventral extracts. These correspond to *R*<sub>f</sub> values of 0.15, 0.18, 0.33, 0.43, 0.45, 0.49, 0.53, 0.54, and 0.96. For each trial, the mobilities and spot sizes were identical between the two samples, while the solvent control did not afford any visualizable material nor did it receive antennation by ants.

The most active band on the TLC (*R*<sub>f</sub> = 0.96, section 12) appears near the solvent front. Together with extraction by methylene chloride, this mobility suggests a substance of low polarity. In addition, since the substance remains on TLC plates after initial bioassay, plate development, solvent evaporation and final bioassay, it would seem to be of low volatility. Although we did not quantify this effect, the activity of the substance appeared to decrease with time, suggesting that it eventually evaporates or undergoes chemical alteration on TLC plates. The activity around position 3.5 corresponds to an *R*<sub>f</sub> value of about 0.43, coinciding
Antennal drummings

![Antennal drummings graph]

Fig. 1. Total number of antennal drumming responses of Formica altipetens worker ants towards separated compounds of epidermal extracts of Glaucopsyche lygdamus caterpillars on developed TLC plates. Given are cumulative numbers over a total test period of 120 min. A compound which occurred in section 12 elicited the greatest response and corresponded to an Rf value of 0.96. A compound which occurred inbetween fractions 3 and 4 showed some activity and corresponded to an Rf value of 0.43.

with the respective value of cholesterol. We have no evidence whether the ants are attracted to cholesterol or another compound at that position.

Persistence of myrmecophily in parasitized caterpillars or larval carcasses

In most cases, a parasitized lycaenid caterpillar would die, or has already been killed, when its parasitoid larvae are ready to pupate. This was invariably the case with caterpillars parasitized by Tachinidae flies (observations with following lycaenid species: Jalmenus evagoras, Thecla betulae, Arhopala amphimuta, Drupadia theda, Hypolycaena erylus, Rapala dienece, Callophrys rubi, Jamides malaccanus, J. caeruleus, Glaucopsyche alexis, G. lygdamus, Polyommatus coridon, P. icarus), and with certain ichneumonids (Hyposoter, Campopleginae) or braconids (Aleioles, Rogadinae), which pupate inside the host cuticle (e.g. in Drupadia ravindra, Scolitantides orion, Aricia eumedon, Polyommatus coridon; Fiedler, pers. observ.). However, when caterpillars are parasitized by members of the Apanteles group (Braconidae-Microgasterinae), the larvae often remain attractive to their tending ants and the myrmecophilous organs may stay functional for several days beyond parasitoid emergence. The following observations were made (categorized by the
Table 1. Summary of observations on the function of myrmecophilous organs and the persistence of vibratory abilities in parasitized caterpillars of 17 Lycaenidae butterfly species. Only observations involving parasitoids of the braconid subfamily Microgasterinae are considered. 

- 1° DNO intensively antennated, but secretion act not observed.
- 2° not recorded.
- 3° species with non-functional rudimentary DNO. Facultative myrmecophiles associate with a variety of ant taxa, but are not dependent on ant-attendance. Obligate myrmecophiles invariably live in symbiosis with a specific host ant. A (g) or (s) behind the parasitoid’s name indicates gregarious (multiple wasps per host) or solitary parasitoids. The 4 parasitoids from the *Apanteles ater*-group represent different species.

<table>
<thead>
<tr>
<th>Butterfly species</th>
<th>Interaction with ants</th>
<th>DNO function persisting</th>
<th>Vibrations</th>
<th>Attractive to ants</th>
<th>Parasitoid</th>
</tr>
</thead>
<tbody>
<tr>
<td>Curetis sp. (n = 3)</td>
<td>not myrmecophilous</td>
<td>absent</td>
<td>3-4 d</td>
<td>3-4 d</td>
<td>no</td>
</tr>
<tr>
<td>Jalmenus evagoras</td>
<td>obligate myrmecophile</td>
<td>? ²</td>
<td>? ²</td>
<td>? ²</td>
<td>yes</td>
</tr>
<tr>
<td>Surendra florimel (n = 6)</td>
<td>facultative myrmecophile</td>
<td>? ¹</td>
<td>&gt; 4 d</td>
<td>4-7 d</td>
<td>yes</td>
</tr>
<tr>
<td>Drupadia theda (n = 17)</td>
<td>obligate myrmecophile</td>
<td>? ¹</td>
<td>4-7 d</td>
<td>3-8 d</td>
<td>yes</td>
</tr>
<tr>
<td>Cheritra freja (n = 2)</td>
<td>not myrmecophilous</td>
<td>absent</td>
<td>absent</td>
<td>no</td>
<td>no</td>
</tr>
<tr>
<td>Hypolycaena othona (n = 1)</td>
<td>facultative myrmecophile</td>
<td>no</td>
<td>absent</td>
<td>6 d</td>
<td>yes</td>
</tr>
<tr>
<td>H. erylus</td>
<td>obligate myrmecophile</td>
<td>? ²</td>
<td>? ²</td>
<td>? ²</td>
<td>yes</td>
</tr>
<tr>
<td>Callophrys rubi (n = 10)</td>
<td>not myrmecophilous</td>
<td>absent ³</td>
<td>absent</td>
<td>&gt; 2 d</td>
<td>no</td>
</tr>
<tr>
<td>Anthene emolus (n = 14)</td>
<td>obligate myrmecophile</td>
<td>1-3 d</td>
<td>no</td>
<td>2-5 d</td>
<td>yes</td>
</tr>
<tr>
<td>Species</td>
<td>Myrmecophile Type</td>
<td>Length</td>
<td>No. Stings</td>
<td>Feeding</td>
<td>Paralyzing</td>
</tr>
<tr>
<td>-------------------------</td>
<td>---------------------</td>
<td>--------</td>
<td>------------</td>
<td>---------</td>
<td>------------</td>
</tr>
<tr>
<td><em>Jamides malaccanus</em></td>
<td>facultative myrmecophile</td>
<td>? 1</td>
<td>1 d</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td>(n = 4)</td>
<td>not myrmecophilous</td>
<td>absent</td>
<td>absent</td>
<td>1 d</td>
<td>no</td>
</tr>
<tr>
<td><em>Glaucopsyche alexis</em></td>
<td>facultative myrmecophile</td>
<td>? 2</td>
<td>&gt; 2 d</td>
<td>? 2</td>
<td>yes</td>
</tr>
<tr>
<td>(n = 4)</td>
<td>facultative myrmecophile</td>
<td>? 2</td>
<td>&gt; 2 d</td>
<td>? 2</td>
<td>yes</td>
</tr>
<tr>
<td><em>Plebejus melissa</em></td>
<td>facultative myrmecophile</td>
<td>? 2</td>
<td>? 2</td>
<td>? 2</td>
<td>yes</td>
</tr>
<tr>
<td>(n = 1)</td>
<td>facultative myrmecophile</td>
<td>? 2</td>
<td>? 2</td>
<td>? 2</td>
<td>yes</td>
</tr>
<tr>
<td><em>Polyommatus coridon</em></td>
<td>facultative myrmecophile</td>
<td>? 1</td>
<td>2 d</td>
<td>2-3 d</td>
<td>yes</td>
</tr>
<tr>
<td>(n = 3)</td>
<td>facultative myrmecophile</td>
<td>no</td>
<td>no</td>
<td>no</td>
<td>yes</td>
</tr>
<tr>
<td><em>P. coridon</em></td>
<td>facultative myrmecophile</td>
<td>6 d</td>
<td>6 d</td>
<td>6 d</td>
<td>yes</td>
</tr>
<tr>
<td>(n = 60)</td>
<td>facultative myrmecophile</td>
<td>5 d</td>
<td>6 d</td>
<td>5 d</td>
<td>yes</td>
</tr>
<tr>
<td><em>P. bellargus</em></td>
<td>facultative myrmecophile</td>
<td>5 d</td>
<td>6 d</td>
<td>5 d</td>
<td>yes</td>
</tr>
<tr>
<td>(n = 1)</td>
<td>facultative myrmecophile</td>
<td>5 d</td>
<td>6 d</td>
<td>5 d</td>
<td>yes</td>
</tr>
</tbody>
</table>
myrmecophilous organs, respectively; see Table 1 for synopsis of observations):

The dorsal nectar organ (DNO) remains active in parasitized caterpillars

*Anthene emolus*, a widespread Oriental lycaenid butterfly, is an obligatory myrmecophile which is specifically associated with the aggressive weaver ant, *Oecophylla smaragdina*. Caterpillars of *A. emolus* secrete droplets from the DNO at particularly high rates (200-300 droplets/h; Fiedler & Maschwitz 1989). In April and May 1993, we found a total of 14 parasitized individuals (infested by a solitary parasitoid species of the *Apanteles ater* group) at Ulu Gombak (West Malaysia), on the hostplant tree *Saraca thaipingensis* (Caesalpiniaceae). From 6 caterpillars, the wasp larva had already emerged and pupated at the time of collection. Each of these caterpillars sat motionless on the silken braconid cocoon attached to its ventral side. The remaining 8 caterpillars were collected as second to early fourth (= final) instars while feeding, and the braconid larvae emerged later in captivity.

In both the field and the laboratory, all 14 caterpillars remained fully attractive to their specific host ant even after the parasitoids had emerged. One or two *Oe. smaragdina* workers constantly attended and antennated each larval “carcass”. These responded with regular eversions of the DNO, and the secretion droplets were frequently visible (Fig. 2). *Oe. smaragdina* ants eagerly harvested every single droplet. The ability to deliver DNO secretions persisted in *A. emolus* caterpillars up to 3 days after the braconid larva had emerged. Attractiveness of the caterpillar carcasses to *Oecophylla* ants persisted 4-5 days, and the adult braconids eclosed after a pupal period of 5-6 days. In *A. emolus*, eversions of the TOs were not seen after parasitoid emergence.

DNO secretions after parasitoid emergence could as yet be ascertained in two additional Lycaenidae species, the Palearctic facultative myrmecophiles *Polyommatus bellargus* and *P. icarus*. One mature *P. bellargus* caterpillar (origin near Würzburg, northern Bavaria), from which 24 *Apanteles* larvae had emerged and pupated at the ventral side, secreted droplets from the DNO up to the sixth day beyond parasite emergence. This caterpillar was caged with *Lasius flavus* ants for only 1-5 minutes.

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Fig. 2. *Oecophylla smaragdina* worker ants drink a secretion droplet from the dorsal nectar organ of a parasitized *Anthene emolus* caterpillar (Ulu Gombak, West Malaysia). The white *Apanteles* cocoon is attached to the ventral side of the host. Photograph P. Seufert.

Fig. 3. A fourth instar caterpillar of *Curetis* sp. (Ulu Gombak, West Malaysia) with everted tentacle organs after tactile disturbance. Note the dense pillow of *Apanteles* cocoons on the ventral side. Photograph P. Seufert.

Fig. 4. Parasitized carcass of mature caterpillar of *Polyommatus icarus*, offering a nectar droplet to tending *Lasius flavus* ants the day after parasitoid emergence. Photograph K. Fiedler.
per day to prevent the rapid depletion of the DNO reservoir content. By this procedure, 21 DNO secretion droplets were observed in a total observation period of 7.5 minutes spread over 4 days. Using the same test procedure with the same ant species, a mature *P. icarus* caterpillar (origin near Würzburg, northern Bavaria) from which 14 braconid larvae had emerged, delivered 12 DNO secretion droplets in 8 minutes total observation period spread over 5 days (Fig. 4).

We observed antennation at, and eversion of, the DNO in larvae of 4 additional species (Table 1) which were kept together continuously with attendant ants. *S. florimel*, *J. malaccanus*, and *P. coridon* are facultative myrmecophiles whose mature caterpillars are tended by a variety of ant taxa (Fiedler 1991, 1992b and unpubl.), while *D. theda* is obligatorily connected with certain *Crematogaster* species (Maschwitz et al. 1985; Seufert & Fiedler 1994). We suppose that secretions occurred even after parasitoid emergence in these cases, but that the gland reservoirs of the caterpillars had been depleted at the time of observation due to continuous milking by ants.

The tentacle organs (TO) remain active in caterpillar carcasses

The TOs of 6 myrmecophilous Lycaenidae species (Table 1) remained fully active for up to 7 d beyond braconid emergence and still elicited the typical behavioral reaction (alert, "excited runs": Fiedler & Maschwitz 1988b) in their tending ants. TO eversions occurred in the following pairs of interacting species: *S. florimel* with *Rhoptromyrmex wrougtonii* (Myrmicinae), *Technomyrmex* and *Iridomyrmex* sp. (Dolichoderinae); *D. theda* with *Crematogaster* sp. (Myrmicinae); *J. malaccanus* with *Camponotus* (subgenus *Tanaemyrmex*) sp. (Formicinae) and *Crematogaster*; and the 3 *Polyommatinae* species with *Lasius flavus* (Formicinae).

Caterpillars of the Oriental genus *Curetis* (subfamily Curetinae: Elliot 1990) have highly modified and very large TOs situated in elevated epidermal cylinders. The TOs are thrust rapidly after tactile disturbance of a caterpillar, making visible the long, conspicuous, black-and white hairs (DeVries et al. 1986; Fiedler et al. 1995). This striking defensive behavior continued in three parasitized *Curetis* caterpillars found at Ulu Gombak in May 1993 for 3-4 d after emergence and pupation of the larvae of a gregarious braconid species (*Apanteles ater* group; Fig. 3). A specific identification of the host butterfly is impossible, because the parasitized larvae have been collected on the same hostplant tree (*Millettia atropurpurea*, Fabaceae) together with early stages of *Curetis bulis* and *C. santana*, whose larvae look almost identical. *Curetis* caterpillars are rarely, if ever tended by ants (DeVries 1984; Fiedler et al. 1995).

Larval carcasses remain attractive to their tending ants

Larval carcasses of 12 species (Table 1) were persistently, or at least temporarily, tended by ants for up to 5 d beyond parasitoid emergence.
Such interactions were observed in the field as well as in captivity, involving ants of the genera *Crematogaster, Rhoptromyrmex, Lasius, Formica, Camponotus, Oecophylla, Dolichoderus, Technomyrmex* and *Iridomyrmex*. These ants showed the same antennal drumming towards healthy caterpillars, and antennation was not restricted to the DNO nor to the vicinity of the TOs.

**Persistence of Vibratory Behavior**

The ability to produce substrate-borne vibrations persisted in 11 lycaenid caterpillar species including three non-myrmecophiles (Table 1), sometimes up to 8 d beyond parasitoid emergence. Except in *Cheritra freja*, there was no indication that the vibratory behavior of parasitized caterpillars, and later carcasses, differed in any respect from that of healthy caterpillars. Vibratory behavior was most easily elicited by tactile disturbance of the larvae (e.g. handling with forceps). *Ch. freja* is a myrmecoxenous member of the hairstreak subtribe Cheritriti. In this species, even healthy larvae only occasionally made vibratory calls after tactile disturbance (2 out of 15 in our sample), and in two fourth (= final) instars, which were parasitized by a gregarious *Apanteles* species (nr. *prosymna*), calls were recognized neither before nor after parasitoid emergence.

**Discussion**

Observations on behavioral interactions between lycaenid caterpillars and their parasitoids are typically chance findings. Experimental work with larger sample sizes is prohibited by the scarcity or crypsis of both hosts and parasitoids. Moreover, the taxonomy of the parasitoids involved is still in a very incomplete stage, especially in the tropics, and information on host ranges or specificity is almost unavailable. Hence, the observations and conclusions presented here are by necessity based on small numbers of sometimes anecdotal observations. Nevertheless, collectively these provide circumstantial evidence that certain parasitoids may take advantage of the mutualistic relationships between their lycaenid host larvae and ants.

Breaking the chemical communication code between lycaenids and ants is an essential facet of parasitoid subterfuge. Besides delivery of nutritive secretions (such as those derived from the DNO), lycaenid caterpillars possess extractable components in their integument which serve as "adoption substances". These epidermal substances induce non-aggressive antennal drumming in the ants when tending lycaenid immatures. Although their chemical composition remains unknown, these substances are of low volatility. Physical contact is necessary to induce caterpillar-ant interactions. The adoption substances retain biological activity for some time, as shown in the experiments with extracts. Furthermore, caterpillar carcasses left by braconid parasitoids, and occasionally even empty pupal cases, remain attractive to
tending ants for hours or days. This strongly suggests that the adoption substances remain functional. The PCOs, ubiquitous glandular structures of lycaenid immatures, are likely to be one source of these adoption signals, although the significance of other organs, such as dendritic setae, remains to be addressed.

In *Anthene emolus*, *Polyommatus bellargus*, *P. icarus*, and probably in four additional species where ants antennated the DNO of the larval carcasses, even the ability to secrete droplets from the DNO persisted, although this property typically ceased first. This may be explained by depletion of the secretion supply in the glandular reservoir. After feeding has stopped, caterpillars cannot replenish their secretion stock. The 12 DNO secretion droplets observed in *P. icarus* after parasitoid emergence, and the 21 droplets in the case of *P. bellargus*, closely match the estimated DNO reservoir content in these species. Using Malicky’s (1969) histological data, the total reservoir volume is roughly 0.06 µl in *P. icarus*, which corresponds to c. 15 droplets with an average volume of 0.004 µl (Fiedler & Burghardt, unpubl.). For *P. bellargus*, the respective figure is a DNO volume of 0.131 µl corresponding to 22 droplets of 0.006 µl average size (based on histological and experimental data from the closely related *P. coridon*).

Vibratory abilities and TO activity persisted longer than DNO secretions. Both these behaviors are executed by specialized muscles. In addition, limited capacities to move persisted in the Lycaenidae species listed in Table 1. From these observations we conclude that part of the peripheral musculature (i.e. those muscles necessary for DNO and TO activity, or for producing vibratory calls) is exempted from exploitation by these Microgasterine parasitoids. With the exception of *Anthene emolus*, whose parasitized caterpillars reached only half the size of healthy larvae, the larvae listed in Table 1 did not show retarded growth and attained normal size despite parasitoid infestation.

Sparing of myrmecophilous properties occurred in solitary as well as gregarious species, but all records yet available of such phenomena are from the *Apanteles* group in the braconid subfamily Microgasterinae. We have so far never observed comparable interactions in lycaenid caterpillars parasitized by various species of Tachinidae flies, Ichneumonidae wasps, or braconids from other subfamilies (e.g. Rogadinae). Even among the Microgasterinae, this trait is not universal. *Cotesia saltatoria*, for example, is a solitary parasitoid that emerges when the host caterpillars are still rather small (third instar). In this case, the host soon dies after parasitoid emergence, and neither activity of the myrmecophilous organs nor vibratory behavior could be observed, although the carcasses remained attractive to *Lasius flavus* ants for up to 3 d.

Parasitoids of lepidopterous caterpillars greatly vary in the extent of damage they impose on their hosts. All tachinid flies which we have reared so far from Lycaenidae caterpillars leave only a limp cuticle and
entirely consume all internal host tissues (observations made on a number of Lycaenidae species, see above), and neither secretory nor vibratory abilities persisted. Instead, the caterpillars were abandoned by their tending ants 1-2 days prior to parasitoid emergence and vibratory behavior likewise ceased at roughly that time.

If sparing of myrmecophilous properties of Lycaenidae hosts should turn out to be a specific adaptation of certain Microgasterinae braconids rather than an accidental or commonplace epiphenomenon, what selective advantage may these parasitoids derive from this behavior? Although experimental evidence has not yet been obtained, it is likely that the wasps benefit in at least three ways. First, their pupal cocoons are covered by their well-camouflaged hosts and may thereby escape visually searching predators or hyperparasitoids. In all the species listed in Table 1, except sometimes in *Cotesia saltatoria*, the cocoons are tightly attached to the caterpillar. The gregarious species often formed well-defined pillows of cocoons, on which the host carcass sat motionless for days (Fig. 3).

Second, the potentially vulnerable larvae of braconids emerging from the carcasses of their lycaenid hosts somehow avoid attacks by ants which attend the lycaenids. Larvae of *Apanteles cyaniridis* emerging
from *Glaucopsyche lygdamus*, for example, were observed to be inspected by attendant ants, but not attacked (Fig. 5; also Fiedler 1992b). Within a few minutes after emergence from their hosts, these parasitoid larvae spin protective cocoons and pupate beneath the host’s carcass. The mechanism for this striking tolerance remains unknown (see DeVries’ (1991b) discussion of appeasement versus ignorance).

Finally, by sparing the myrmecophilous properties of their hosts, these braconids are indirectly attended by ants for at least the first part of their own pupal development. Recent work on aphidid parasitoids of ant-tended aphids has confirmed that certain parasitoids, rather than their host aphids, may benefit from ant-association (Völkl 1992). The interactions between ants, lycaenid caterpillars and Microgasterinae braconids obviously bear a similar potential. In all cases observed so far, the attractiveness of the larval carcasses ceased before the wasps emerged from their cocoons, allowing the wasps to eclose and fly off in the absence of ants.

Together with the apparent use of tending ants as host-location cues by an Australian *Apanteles* species parasitizing *Jalmenus evagoras* (Pierce et al. 1987, Nash 1989), and with the ability of several Microgasterinae wasp species to feed on the secretions which their hosts provide from the myrmecophilous glands (Schurian et al. 1993), our observations indicate that interactions between ants, lycaenid larvae and their braconid parasitoids are even more complex than previously thought.

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Life History of *Attacus mcmulleni* (Saturniidae) from the Andaman Islands, India

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**Abstract.** The life cycle of *Attacus mcmulleni*, a wild silkmoth endemic to the Andaman Islands (India) in the Bay of Bengal, and its immature stages are described and figured. Comparisons are made to larvae of *Attacus atlas* and *A. taprobanis* from nearby regions (Thailand, Sumatra, southern India). Field observations are given on oviposition, larval feeding and behavior, cocoon formation, and adult emergence. Larvae were reared from eggs on Rhizophora apiculata, *R. mucronata*, Vitex glabrata, and Zanthoxylum. *Attacus mcmulleni* is apparently multivoltine. *Anastatus* sp. (Hymenoptera: Eupelmidae), an egg parasitoid, was the only natural enemy found attacking the moth during this study.

**KEY WORDS.** Andamans, atlas moths, immatures, mangroves, *Rhizophora*, Vitex, Zanthoxylum

**INTRODUCTION**

The genus *Attacus* Linnaeus (Saturniidae) is restricted to the Australasian region and comprises 14 known species, of which 11 are insular endemics (Peigler 1989). Moths in this genus include the largest species of Lepidoptera in the world. *Attacus mcmulleni* Watson, one of these insular species, is endemic to the Andaman group of islands. It was first described as a subspecies of *Attacus atlas* by J. H. Watson (in Packard 1914: 263-264, pl. 91) from specimens collected by W. R. McMullen on the island of South Andaman. In a revision of the genus, Peigler (1989) elevated it to the status of full species on the basis of characteristic and consistent differences in adult facies and genitalia. However, he stated that *A. mcmulleni* is the species that most closely resembles *A. atlas*. Peripherally isolated on the small islands of the Andaman Archipelago (Fig. 7), which are a minimum of 285 km from any continental land mass, and which never came into contact with the adjacent land masses during Pleistocene times when the sea level was lower (Ripley & Beehler 1989, Peigler 1989), *A. mcmulleni* is surmised to have speciated as a vicariant of *A. atlas*, the most widespread species of

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the genus. A well-illustrated geographical glimpse of the Andaman Islands was given by Singh (1975).

Virtually nothing is published on the immature stages and life history of this moth. Pinned adults are rare in collections, with the exception of a series at The Natural History Museum, London. In addition, though the cocoons were briefly described by Watson (in Packard 1914), none were found in any of the major museums accessed by Peigler (1989). This study aims to fill these gaps in our knowledge of this little-known species.

Materials and Methods

Eggs and larvae were located visually on the host plants and collected along with a fresh sprig into transparent plastic containers, the size of which depended on the stage of the insect collected. The containers were cleaned of frass, wiped dry, and the larvae provided with fresh sprigs every day.

The eggs and initial instars were housed in small (8 cm diameter × 11 cm height) containers, while the later instars were reared in larger (9 cm × 19 cm) containers. The presence of head capsules in the rearing containers was used as the indicator for the determination of stadial lengths. This was possible as the larvae were not gregarious in any of the instars and so could be reared individually. All rearings were done indoors at ambient temperature and relative humidity which varied between 27.9 -33.4°C and 75 - 90.1%.

The mature larvae used either the sprig or the sides of the container to spin their cocoons and pupate. A stout twig was placed diagonally in the container to enable the emerging adult to climb up and expand its wings. All measurements were taken during the first cleaning of rearing containers following a molt. Voucher material from the rearing is deposited at the Entomology Section, Central Agricultural Research Institute, Port Blair, and in the Denver Museum of Natural History.

Results

Host Plants and Habitats

*Rhizophora apiculata* Blume, *R. mucronata* Lamk. (Rhizophoraceae), *Zanthoxylum* sp. (Rutaceae) and *Vitex glabrata* R. Brown (Verbenaceae) are the four host plants on which eggs and larvae of *A. mcmullenii* were found. Larvae were subsequently reared on the same species as that on which they were collected.

While *V. glabrata* is a tree of moderate size in the inland deciduous forests of Middle Andaman, South Andaman and Long Island (all in the Andaman group of islands) (Parkinson 1923), *R. apiculata* and *R. mucronata*, which form the major component of the mangals (mangroves) of these islands, are found in mixed stands commonly fringing the tidal creeks as well as along the sea shores of many of the Andaman islands. It forms a wide belt of vegetation along the sea front, up to 2 km wide in some places and is regularly inundated by the tides.
Eggs, larvae, and cocoons of *A. mcmulleni* were collected from the mangals of Wright Myo, Wandoor, and Chiriyatapu in South Andaman and from Rutland. They were also collected from the inland semi-evergreen forest of Mount Harriet (South Andaman) up to an altitude of about 460 meters.

**Field Observations**

The majority of the eggs and larvae that were collected came from the fringing mangrove habitat rather than from the inland forests. On each kind of host plant, all immatures were found on the tender terminal leaves. Eggs and larvae of the moth were found on both young and old trees of *Rhizophora*. In the mangrove habitat the immature stages were found in larger numbers on trees which were at the water’s edge and not so much in the interior of the mangrove forest. Partially eaten terminal leaves signified the presence of larvae.

Eggs and first instar larvae were invariably found on the ventral surfaces of leaves on all the hosts. In a few instances however, eggs were found on the dorsal surfaces of leaves. Though one egg per leaf was the norm, up to four eggs were found on some leaves (Fig. 1). When more than one egg was laid per leaf, they were laid some distance apart (= 0.24 cm between eggs, n = 5) and never in contact with each other.

On hatching the larva ecloses by making an irregular opening in the micropylar end. The larva does not eat the chorion fully and so half-empty chorions may be found attached to leaf surfaces long after larval eclosion.

The larvae in their early instars were found clinging along the midribs on the ventral surfaces of leaves, while the later instars shifted onto the terminal twigs, hidden between the leaves. In a few instances, first instar larvae were found side by side on the same leaf. However, later instars were never found together.

Up to the fourth instar the larvae, when at rest, bend their bodies such that the head end forms the short arm of the letter J. When the late instar larvae are disturbed they bend forward and tuck their heads beneath the thoracic segments and into the hollow formed by the thoracic legs which are bunched together and thrust forward.

Mature larvae feed inwards from the outer margin of the leaf and continue to feed whether the head is oriented upwards or downwards. Larvae stay on the tiny terminal branches and not on the leaves. One final instar larva that was collected from the field measured 11.8 cm in length.

The moths emerged from their cocoons at night in all the cases. In the two instances in which we observed emergence, it occurred between 1900-2030 hours. One virgin female was released on a coconut leaf a day after emergence at 0700 hours at Garacharma, South Andaman. This moth remained motionless without shifting its position for 48 hours and then disappeared.

**Oviposition:** Of the two reared females that were kept in cages, one
laid the first batch of eggs on the first night after emergence from the cocoon while the other laid its first batch of eggs three days latter. They laid a total of 200-223 eggs (\( \bar{x} = 212; \sigma = \pm 16.3 \)) over a period of 10-11 days, when confined in cages and prevented from mating. One other virgin female laid 378 eggs in nine days from the date of emergence. All the eggs proved to be infertile. \textit{A. mcmulleni} therefore conforms to the non-parthenogenetic nature of the Oriental Saturniidae, as both arrenotokous and thelytokous saturniids have been reported from other regions of the world (Barlow 1982).

Barlow (1982) also stated that “the attraction and subsequent assembling of males to freshly emerged virgin females in fine wire-mesh boxes has been found to be very successful in temperate climes but this is yet to be tried out in South East Asia”. Our attempts to attract males by taking newly emerged virgin females of \textit{A. mcmulleni} in wire mesh cages to the Chiriyatapu mangroves proved futile.

**Phenology:** We collected and successfully reared the moths from eggs, larvae, and cocoons collected during the months of March, May, June, August, October, November, and October. Adults were also encountered during these months.

**Natural enemies:** The only natural enemy encountered was the egg parasitoid \textit{Anastatus} sp. (Hymenoptera: Chalcidoidea: Eupelmidae). Only one wasp emerged from each parasitized egg; multiple parasitism was not observed in any of the cases. This chalcidoid genus was also reported as an egg parasitoid of \textit{Attacus atlas} (Peigler 1989).

**Description of Immature Stages**

The terminology for larval morphology is based on Peigler (1989). The measurements and durations of the various immature stages are given in Tables 1 and 2, respectively.

**Egg** (Fig. 1): Length 2.8 mm, width 2.4 mm, height 2 mm (\( n = 20 \)). The oval egg, which is slightly flattened dorsoventrally, is dull white in color with polygonal punctations. It lies on its side embedded in a thick dry layer of orange-brown adhesive fluid. The micropyle is at one end from which radiates two narrow light brown, lateral bands and a dorsal tear-drop shaped brown patch which is narrow at the micropylar end and broadens towards the center of the egg. All these brown markings have fuzzy edges and extend to a little beyond the midline.

**First instar:** Head glossy, deep brown; clypeus, labium, labial and maxillary palps, dull white; labrum brown. Body grayish-white in color with deep brown to black lateral markings which are most prominent on abdominal segments I to VII. This gives the larva the appearance of being striped when viewed laterally but not when seen dorsally. The proximal ends of dorsal scoli on thorax have five long brown spines arranged in an irregular circle with one similar spine a little off the apex of each scolus. All the other scoli too have spines with the maximum number on the subdorsal and lateral scoli. The distribution of scoli is identical to that of
A. atlas in this and all succeeding instars. Mealy matter (wax) is absent on this instar. The dorsum of the prothorax is plain white in front of scoli. There is a narrow brownish wavy line on the dorsum of anal plate along the contour of the anterior margin of the segment.

**Second Instar:** Immediately after molting it turns around and eats the molted skin as do all the other instars. Head creamish-yellow in color. Legs black, prolegs brown, clypeus and maxillary palpi white and labrum pale brown. Some setae on crotchets faint brown. Spines on scoli grey.

**Third/Fourth Instars** (Fig. 2): Labrum pale blue with a rough outer surface. Maxillary and labial palps also pale blue; dorsal and lateral surfaces covered with white powdery material that is thinner on the head.
Table 1. Mean dimensions (cm.) of the various stages and of the head capsules of *A. mcmulleni* reared *ex ovo* in captivity in S. Andaman

<table>
<thead>
<tr>
<th></th>
<th>Larval Instars (Lengths)</th>
<th>Cocoon (L × W)</th>
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<tbody>
<tr>
<td></td>
<td>I  II  III  IV  V  VI</td>
<td></td>
</tr>
<tr>
<td><strong>Male</strong></td>
<td></td>
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<tr>
<td>n</td>
<td>3  4  4  6  7  8</td>
<td>3</td>
</tr>
<tr>
<td>Length</td>
<td>1.2 1.8 2.3 3.0 4.0 6.0</td>
<td>7.4 × 3.9</td>
</tr>
<tr>
<td>± S.D.</td>
<td>0.12 0.06 0.05 0.18 0.18 0.73</td>
<td>0.6 × 0.5</td>
</tr>
<tr>
<td><strong>Female</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>1  1  1  2  3  3</td>
<td>3</td>
</tr>
<tr>
<td>Length</td>
<td>1.1 1.8 2.3 3.0 4.1 5.8</td>
<td>6.8 × 4.2</td>
</tr>
<tr>
<td>± S.D.</td>
<td>-  -  -  0.2 0.4 0.4</td>
<td>0.4 × 0.3</td>
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<tr>
<td><strong>Male/Female</strong></td>
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<tr>
<td>n</td>
<td>2  4  4  6  6  5</td>
<td>5</td>
</tr>
<tr>
<td>Length</td>
<td>1.1 1.6 2.0 2.7 4.1 5.9</td>
<td>6.0 × 23.0</td>
</tr>
<tr>
<td>± S.D.</td>
<td>-  0.2 0.4 0.2 0.59 0.43</td>
<td>0.4 × 0.3</td>
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<tr>
<td><strong>Head Capsule</strong></td>
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<td>n</td>
<td>11  6  9  10  11 — —</td>
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<tr>
<td>Length</td>
<td>1.4 1.9 2.5 3.5 4.9 — —</td>
<td></td>
</tr>
<tr>
<td>± S.D.</td>
<td>0.04 0.08 0.09 0.09 0.23 —</td>
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*Represent pooled data as the sex of these moths was not determined.

than the rest of the body, the former having a black patch at its base. Spiracles narrow, long, very pale blue and located in a depression. Legs pale blue with black claws; prolegs light blue distally with black semicircular lines above the blue band on the third and fourth prolegs. Crotchets brown in color. Head smooth, pale yellow-green in color, with small white setae towards the mouth parts. Ventral surface pale blue-green including the inner aspect of the legs. The prominent saffron triangle on proleg encloses a pale grey-blue central region with a black band along the posterior margin.

**Fifth instar:** Head smooth, glossy, apple green in colour. Black irregular markings along inner margins of frontal sutures. Dorsal and sub dorsal scoli on thoracic segments reduced the stubs/warts. Spiracular scoli on thoracic segments black, and are the longest of all the scoli. Subspiracular scoli on abdominal segments I and II are small and black. Abdominal segments III to VIII also have small black scoli, but situated slightly lower than on segments I and II, in the subventral positions. The thoracic segments and the first two abdominal segments have a row of very short black scoli which are light blue basally. The surface of the body
Table 2. Mean durations (in days) of the various stages of *A. mcmulleni* reared *ex ovo* in captivity in S. Andaman

<table>
<thead>
<tr>
<th></th>
<th>Egg</th>
<th>I</th>
<th>II</th>
<th>III</th>
<th>IV</th>
<th>V</th>
<th>VI</th>
<th>Pupa</th>
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<tr>
<td><strong>Male</strong></td>
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<td>n</td>
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<td>3</td>
<td>4</td>
<td>4</td>
<td>6</td>
<td>7</td>
<td>8</td>
<td>8</td>
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<tr>
<td>Duration</td>
<td>—</td>
<td>3.3</td>
<td>5.0</td>
<td>6.0</td>
<td>6.5</td>
<td>8.6</td>
<td>15.8</td>
<td>25.8</td>
</tr>
<tr>
<td>± S.D.</td>
<td>—</td>
<td>0.58</td>
<td>0.82</td>
<td>2.71</td>
<td>1.05</td>
<td>2.70</td>
<td>4.20</td>
<td>0.89</td>
</tr>
<tr>
<td><strong>Female</strong></td>
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<td>n</td>
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<td>1</td>
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<td>1</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>5</td>
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<tr>
<td>Duration</td>
<td>—</td>
<td>4.0</td>
<td>5.0</td>
<td>6.0</td>
<td>6.5</td>
<td>9.0</td>
<td>19.0</td>
<td>28.0</td>
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<tr>
<td>± S.D.</td>
<td>—</td>
<td>2.12</td>
<td>4.0</td>
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<td>2.12</td>
<td>2.7</td>
<td>2.9</td>
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<td><strong>Sex undetermined</strong></td>
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<td>Duration</td>
<td>&gt;5</td>
<td>7</td>
<td>6.2</td>
<td>8.3</td>
<td>9.2</td>
<td>10.5</td>
<td>19.5</td>
<td>34</td>
</tr>
<tr>
<td>± S.D.</td>
<td>—</td>
<td>1.3</td>
<td>0.4</td>
<td>3.2</td>
<td>1.6</td>
<td>2.3</td>
<td>1.9</td>
<td>13</td>
</tr>
</tbody>
</table>

*Represents pooled data as the sex of these moths was not determined.

with green mottling, while the mottling on the anal segment is dark green to almost black.

**Sixth Instar** (Figs. 3-4): Head, especially vertex smooth, glossy green. A thin layer of white mealy matter on the frons and a little on the sides of the epicranial suture, otherwise the head is devoid of mealy matter. An irregular black patch at base of labium. Mandibles black; clypeus, labrum, labium, maxillary and labial palps pale blue. Labial palps with an annular black ring. Frontal sutures black. Ventral surface green, legs and prolegs deep black in colour on the outer surface with sparse grey setae. Crochets dark brown. An anterior bluish-white stripe in the black area of the prolegs. Spiracles pale blue. The pink triangle on anal claspers (Fig. 4) more oval in shape than in the earlier instars and less intense (paler) in color. The enclosed space is not dirty green as in earlier instars but a pale, dirty green with brownish-black pits. All along the outside of the rear margin is a deep black band. The whole larva is mottled, with the mottling becoming quite dense on the anal triangle.

**Pupa:** Length 5.4 cm, width 2.0 cm (n = 2). Deep brown in color; cremaster also deep brown, prominent and blunt, ca. 3.8 mm long and 2 mm wide (at the widest point).

**Cocoon** (Fig. 5): The cocoon is coarse; brownish in color with a long peduncle. Cocoons were usually found individually webbed onto leaf surfaces, though in a few instances two cocoons were found together (Fig. 5). The mean length of the peduncle was 7.0 cm (range 4.5-10.5 cm; n =
Figure 7. Map of Andaman Islands.
while the mean length of the cocoon proper was 7.3 cm (range 6.5-9.5 cm; \( n = 18 \)) and its mean width 3.8 cm. (range 2.9-4.5 cm; \( n = 17 \)). The mean weight of the empty cocoon exclusive of pupal case is 0.959 ± 0.11 g ranging from 0.76 to 1.039 (\( n = 5 \)).

The adult moth (Fig. 6) was described in detail by Peigler (1989), and a male was illustrated in color.

**DISCUSSION**

Over 100 plant species belonging to 90 genera in 48 families have been reported as host plants of *Attacus* spp. (Peigler 1989). However, Peigler was unable to assign a botanical name to the plant on which larvae and cocoons of *A. mcmulleni* were collected by McMullen, as Watson (in Packard 1914) used only the vernacular name of the plant viz., “samalu”. This we now know to be *Vitex trifolia* (Verbenaceae), a widely grown hedge plant in the Andamans which was introduced from mainland India prior to 1866 (Prain 1890, Parkinson 1923).

Villiard (1969) was of the opinion that greater success on the rearing of *Attacus* larvae—particularly the later instars—could be achieved by feeding them on a mixed diet. In the current study we were unsuccessful at inducing larvae of *A. mcmulleni* to switch diets. Larvae reared initially on *Rhizophora* spp. were switched to *V. trifolia* and to *V. glabrata*. All attempts proved futile though individuals collected on *V. glabrata* completed their life cycles on leaves of the same species.

Peigler (1989) recorded no species of mangroves as host plants of *Attacus*. Murphy (1990) was the first to mention the presence of *Attacus* in mangrove habitats, stating that *Attacus atlas* “occurred once [on *Avicennia alba* Bl., *Avicenniaceae*] simultaneously with many other trees” and that it occurred at low levels on *Bruguiera gymnorrhiza* (L.) Lamk., (Rhizophoraceae). Nevertheless, this is the first time that a species of *Attacus* has been found to be able to complete its life cycle on a species of Rhizophoraceae. Species of *Attacus* were previously known to utilize Verbenaceae and Rutaceae (Peigler 1989). Our studies also indicate that *Rhizophora* spp. are preferred to *Vitex glabrata* and *Zanthoxylum* by *A. mcmulleni*.

Like *A. atlas*, *A. mcmulleni* also consistently passes through six larval instars in its life cycle. Although *A. mcmulleni* probably has a wider host range than that discovered by us, we feel that in the species-poor mangrove habitat (with plant species diversity markedly lower than in other moist tropical habitats) with a preponderance of *Rhizophora* spp. in closely packed stands, neither the ovipositing female nor the larvae should have any difficulty in finding host plants. Nevertheless they lay only a few eggs at each oviposition site which Janzen (1984) believed is normal behavior for polyphagous species.

Watson (in Packard 1914) quoting McMullen, stated that “there are at least two broods per year” with May and July being the two months in which the moths were collected. Judging from the various stages of *A.
mcmulleni that we have collected during various months from the field, it is definitely not bivoltine but is multivoltine and in all probability flies throughout the year.

The eggs and cocoons of Attacus mcmulleni are probably indistinguishable from those of the allied species. The larvae are also almost identical to those of some populations of A. atlas (see Lampe 1984; Paukstadt & Paukstadt 1984a, b, 1986; Peigler 1989), but a few minor differences were noted as follows.

Larvae of A. atlas from western Java and some of the species from the Philippines have solidly orange shields on the anal prolegs. These shields on larvae of A. atlas from Thailand and Taiwan and A. taprobanis from Sri Lanka and southern India are rimmed with orange and have green centers. Larvae of A. mcmulleni are intermediate; the shield appears solidly orange at first glance, but a faint green center is visible upon closer examination. In A. mcmulleni the subspiracular scoli are blue proximally and blackish distally, like those of A. taprobanis and A. atlas from Taiwan and Thailand. The white waxy covering in A. mcmulleni is as dense or denser than in any of the other species of Attacus.

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Literature Cited


Rediscovery of the endangered Palos Verdes blue butterfly, *Glaucopsyche lygdamus palosverdesensis* Perkins and Emmel (Lycaenidae)

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Key Words: Endangered species, Palos Verdes blue butterfly, *Glaucopsyche lygdamus palosverdesensis*, reintroduction, revegetation planning, monitoring

**Abstract.** The Palos Verdes blue butterfly (PVB) was believed extinct for eleven years when a small colony was rediscovered by accident on March 10, 1994 at a site from which it had not been recorded earlier. The systematics and natural history of the species (=subspecies for conservation purposes), its historic and present habitat, and plans necessary for its recovery are discussed.

**INTRODUCTION**

The Palos Verdes blue butterfly (PVB) was believed extinct for eleven years when a small colony was rediscovered by accident at a site from which it had not been recorded earlier. The rediscovery on March 10, 1994 was made by the team of Rick Rogers, Timothy Dahlum and Rudi Mattoni while visiting the Defense Fuel Support Point (DFSP) at San Pedro for other purposes. The subspecies was believed extinct by at least two authors, Arnold (1987) and Mattoni (1993). The following paper summarizes information to date for the PVB, its habitat and natural history, outlines recommendations for recovery of the species, and discusses what has been done to date.

**HISTORICAL PERSPECTIVE**

**Systematics**

The subspecies was described by Perkins and Emmel (1977) from Los Angeles county just prior to its listing among the second group of butterflies to be legally recognized as endangered by the federal Endangered Species Act. The taxon was diagnosed as a subspecies of the silvery blue, *Glaucopsyche lygdamus*, a polytypic species comprised of at least 10 valid subspecies that are usually found in small closed local colonies across most of North American north of Mexico and extending into easternmost Siberia. There it meets with its sister species, *G. alexis*, of which *G. lygdamus* and its suite of subspecies might all be considered subspecies within a large holarctic complex. Nothing is known about the border area of these taxa, but at the very least relationships are complex. The PVB was originally differentiated from its likely sister subspecies, *G. lygdamus australis*, the southern blue, by exclusive use of the milk
Figure 1. Specimens of the PVB and the southern blue showing patterns of UNS variation. PVB right column, southern blue left column, single females of PVB, right, and southern blue, left, showing mean differences in blue overlay on the black ground color. PVB females usually lack all but a trace of basal blue.

vetch or rattleweed, *Astragalus trichopodus lonchus*, a relatively fast flight in comparison to *australis*, an earlier flight period than *australis*, and several wing characteristics including a slightly darker underside ground with larger macules well set off by white halos (Figure 1).

**Conservation Interest**

The butterfly was geographically circumscribed as a coastal terrace ecotype found only on the southern half of the Palos Verdes peninsula in southern Los Angeles county (Figure 2). The species had high conservation value and was not officially delisted in spite of the strong evidence that the species was extinct after 1983. During this period all building
Figure 2. Map of the Palos Verdes peninsula showing the known distribution of the PVB on the south slope before its disappearance, 1979-83. The numbers reference specific sites where the butterfly was observed, see text. Data collected by Jess Morton. The inset map of California positions the Palos Verdes peninsula.

projects in the species distribution area were required to recognize habitat value. The recent find will permit artificial reintroduction of the species into former habitats that can be enhanced following a proper revegetation plan. This will assure both a much higher probable survivability of the PVB and an expanded coastal sage habitat over what now exists across the peninsula.

Distribution
By the time of its discovery in the early 1970's by Perkins, the PVB was already reduced to the few habitat fragments that retained some natural characteristics. In 1981 and 1982 the 12 then known PVB sites were mapped by Jess Morton (Figure 2). The DFSP San Pedro site was unknown. Three of the sites, Hesse Park, Alta Vista, and San Pedro Hill, were razed as habitat between 1978 and 1985, well after they were isolated. The remaining colonies were partially discrete and occurred within three contiguous open spaces that were largely covered with native coastal sage scrub: Agua Amarga (2), landslide moratorium (10, 11, 12), and Palos Verdes Drive East (4-8). Each of the numbered colonies were isolated by anthropogenic land fragmentation and were
not discrete in the sense of natural metapopulations, possibly excepting the last set. Palos Verdes Drive East was, and to large extent remains, essentially continuous habitat. The last known PVB occurrence was 1983, when Morton and his volunteers noted a few specimens, mostly at Palos Verdes Drive East. There are no earlier data available so the only possible description of distribution is extrapolation from historic plant community information which itself is largely conjectural. Gales (1988) and Brinkmann-Busi (1992) have produced floras of the area.

The largest known populations during the brief time span the PVB was monitored were at Alta Vista Terrace (type locality), Hesse Park, and among the scrub extending from Palos Verdes Drive East to Friendship Park. Alta Vista was built over in 1978. Population sizes were never estimated, but by the early 1980's numbers were extremely low with probably less than 300 adults among all remaining fragments. At Hesse Park in spring, 1982, I counted six adults on the best day, with some 20 foodplants. Each plant had at least 100 eggs, and one plant over 500. Foodplant availability was limiting due to spring discing for fire suppression.
Habitat and ecology

Adult butterflies of all silvery blue subspecies are closely associated with their legume larval foodplants. Recorded foodplants include many species in the genera Lupinus, Vicia, Lathyrus, Lotus, Melilotus, Medicago, Oxytropis, Thermopsis, and Astragalus (Scott, 1986). In general, a silvery blue butterfly population at any one locality is restricted to a single plant species. The reason often invoked for this specificity is local adaptation of larvae to particular suites of alkaloids that each plant species presumes to produce for defense. Breedlove and Ehrlich (1972) provided evidence consistent with this hypothesis of coevolution for the case of the Rocky Mountain subspecies of the silvery blue and its Lupinus foodplant hosts. However, the general concept of insect/foodplant specificity and the coevolution paradigm is far from convincing (Jermy, 1993 and references).

The PVB is a coastal sage associated ecotype, originally believed restricted to the milk vetch as foodplant. The vetch was largely confined to the summer fog belt characteristic to the southern exposures of the Palos Verdes peninsula at elevations between 100 and 300 meters. The historical area probably occupied by both Astragalus and the PVB was about 5000 ha. The flora of the northeast slopes of the peninsula included the low shrub legume, Lotus scoparius, foodplant of the sister subspecies G. lygdamus australis. The distributions of both vetch and deerweed found in 1994 are mapped on Figure 3. Other open sites of greater size than 20 ha are also indicated, these being potential sites for reintroduction of the PVB after appropriate habitat revegetation. Many smaller fragments remain, but these are too vulnerable to be of conservation value.

Whether australis was either historically or recently parapatric with palosverdesensis is unknown, although genetic isolation of the subspecies most likely occurred no later than the end of the last ice age, about 10,000 years ago, when the coastal sage scrub of the Palos Verdes peninsula became isolated from the nearest scrubland to the north by the Los Angeles plain and extensive marshland. It is noteworthy that although both the vetch and deerweed occur on Santa Catalina island, the silvery blue is not found there (the butterfly occurs on both Santa Rosa and Santa Cruz). Other biogeographical evidence suggests that Santa Catalina had close affinity to the Palos Verdes peninsula, although there was no physical connection during the past few glaciations.

Causes of presumptive extinction in 1983

In 1983 the last sightings, of between 4 and 7 individual PVB, were made. The discrepancy in number was the likely result of multiple sightings. The number sighted was low by any criteria, supported by many unsuccessful survey days in the field. Thereafter intensive searches by several local lepidopterists were made for several years without success (Arnold, 1987; J. Morton, pers. comm.). The ultimate cause of
extinction was probably destruction of natural coastal sage scrub communities by a combination of development and fire suppression tactics producing ever increasing fragmentation of the remaining natural ecosystem. For organisms with extremely sedentary demographics, population dynamics obviously became disrupted. Some contribution was also made by illegal overcollecting of early stages by a zealous local collector community.

The historic PVB population was likely continuous across the 5000 ha coastal scrub habitat that covered the south half of the peninsula. With intensive development since 1950, habitat was greatly reduced and fragmented, although the 500 ha landslide moratorium area section of open space remains (1994). This section (Figure 3, south-center portion) is not continuous quality habitat, however, but is a mosaic of coastal sage scrub assemblages interspersed with disturbed patches of farmland and otherwise discarded and exotic plant contaminated zones. Clearing practices so degraded habitat values for the butterfly that the 1982 construction at Hesse Park, performed by the city of Rancho Palos Verdes in violation of the federal Endangered Species Act, directly destroyed what was probably the second largest remaining PVB colony. The city was subsequently sued by the federal government under the Endangered Species Act, but this legal action was dismissed under the theory that a city could not be held liable.

The proximate cause of PVB extirpation was probably climatic. The winter of 1982-83 was cold and extremely wet, followed by the winter of 1984 that was cold and dry and the beginning of a major drought. With fragmented populations, Hesse Park habitat destruction, and probable overcollecting, the diminished bank of diapausing pupae either did not survive or produced so few adults that maintaining population size was impossible. Simultaneously foodplant numbers declined as well (J. Morton, pers. comm.). Arnold (1987) reported the apparent disappearance of the species and speculated it became extinct. Mattoni (1990, 1993) later concurred with this view.

**Current status**

**Present distribution**

Immediately following discovery of the PVB at San Pedro, a thorough search was conducted across all sites indicated on Figure 3; sites where both vetch and deerweed were known. Neither adults or any early stage signs were found on vetch. Presence of either eggs and larvae on the vetch foodplant can be easily observed. The most likely additional localities were hypothesized to be on the stand of vetch at the west end of the landslide area (center of map, Figure 3) and on deerweed in upper Malaga canyon (Figure 3). Observations at both localities were negative. In all likelihood the sole remaining population of the PVB occurs at the San Pedro DFSP.
Regional foodplant distribution

*Lotus scoparius* is presently found at several localities on the peninsula (Figure 3). Excepting a few plants on the Malaga beach sand dune, all populations are on the north facing slope of the peninsula from Malaga canyon south to the San Pedro DSFP. These populations are associated with the more mesic, dense scrub community of the north slopes. Additional plants may yet be discovered, but these will surely be few and isolated. At San Pedro the majority of plants are found on disturbed sites, either slopes graded within the past few years, mowed roadside, or landscaped slopes.

In contrast, the vetch, *Astragalus tricopodus lonchus*, has only been observed across the south slope of the peninsula in more open xeric coastal sage scrubland. The species is associated with open scrub, implying it may not compete well in establishing within dense mature stands. However, in the most “natural” of the mature scrubland at San Pedro, the species occurs within dense California sage formations. Here mature vetch plants, reaching to nearly a meter in height, are supported by sage branches. The condition permitting occurrence in an otherwise dense cover may be small animal activity (e.g. rabbit trails) that provide periodic openings for vetch seedling establishment. Seeds of *Astragalus* are known to have longevities to a century (R. Snow, pers. comm.).

Presence of the two foodplants together at Palos Verdes is only known at San Pedro. Two exceptions, one vetch in a north slope canyon and one deerweed in the landslide area were observed by Brinkmann-Busi (pers. comm.), but the findings followed several years of observation. The reasons for the usual mutual exclusion are unclear as the two plants are together in the Santa Monica mountains and were both found earlier on the El Segundo sand dunes and coastal prairie. The vetch is always the less abundant species, but seems relatively more abundant where topoclimates are severe.

Bionomics of the PVB

Larvae of the silvery blue are ant tended and usually strongly associated with ant species, three of which were recorded by Ballmer and Pratt (1992). Developing PVB larvae usually feed almost entirely inside rattleweed seedpods, using the seeds for nutrition, this plant part being very high in protein and fat. The presence of a larva within a pod is indicated by an entry hole made by the larva. Larvae have not been observed on deerweed, but they certainly are external feeders on flowers and seedpods because deerweed seedpods are smaller than larvae. Ants specific to the PVB are unknown, but there is unquestionably an ant-larva association. In vetch ants gain access by utilizing the larval entry hole and the larvae are ant tended for the last two instars. At least ten ant species have been found at the new locality to date including two, *Iridomyrex humilis* and *Formica pilicornis*, that are known associates of *Glaucopsyche lygdamus* subspecies (Rogers and Snelling, pers. comm.).
The importance of ants in protecting *G. lygdamus oro* was experimentally demonstrated by Pierce and Easteal (1986) who found 45-84% lower parasitism levels among ant tended larvae. The general phenomenon of ant associations with lycaenid butterflies was reviewed by Fiedler (1991). Determination of the ant hosts should be a high priority given the low surviving PVB population.

The PVB is single brooded. Populations known from the south slope had adult flights recorded from late January into March. Eggs were usually laid on flowerheads of the foodplant, but when foodplant numbers were reduced just prior to the 1982 extinction, eggs were laid over the entire plant. The final generation observed at Hesse Park had larvae feeding on leaves because flowerheads and seeds were exhausted.

Three other Lycaenid butterflies were associated with the vetch flowerhead/seedpod guild: *Strymon melinus, Leptotes marina* and *Everes amyntula*. The first two are polyphagous, have many alternate foodplants, and remain widespread species across the Palos Verdes peninsula as well as globally. The latter is an oligophage that was restricted to *Astragalus* at Palos Verdes. It uses other species of legumes elsewhere. The species was believed extirpated from the Palos Verdes peninsula. After a ten year hiatus, the species was sighted near site 4, Figure 2 in 1995 (G. Pratt, pers. comm.).

The western tailed blue, *Everes amyntula*, occurs on at least four channel islands, including Santa Catalina. In contrast *Glaucopsyche lygdamus* is only found on two islands. Given the pattern of foodplant distribution with both deerweed and vetch found on the four islands of occurrence, it is unclear why the silvery blue is not found on all the islands. Its potential capability of using two foodplants would provide greater buffering against adverse conditions and is certainly the factor responsible for survival of the PVB at San Pedro while the western tailed blue was lost.

We first observed PVB females at San Pedro ovipositing on deerweed, exclusively using flowerheads. Later Rogers saw females ovipositing on vetch and discovered eggs on vetch inflorescences. Eggs are easily observed on flowers and seedpods in contrast to those on deerweed. We have no information on selectivity of individual females to either plant. It has recently been demonstrated for other butterflies that individuals exhibit behavioral specificity in the presence of multiple foodplants (review in Papaj and Lewis, 1993).

Two other dominant spring flying butterflies at the site, the California green hairstreak (*Callophrys affinis perplexa*) and the funereal dusky wing (*Erynnis zarucco funeralis*), both use deerweed as foodplant. However, their larvae are leaf feeders and thus avoid interference competition with early stages of the PVB. Females of these species deposit eggs upon stems and leaves. Hairstreak larvae are not attended lycaenids.
Figure 4. Map of the San Pedro DFSP presenting an overview of “native” habitat (heavy stippling) and degraded open space habitat that has potential for restoration (light stippling). Locations of individuals or stands of Astragalus tricopodus and Lotus scoparius are indicated by the letters A and L respectively. The clear areas position underground storage tanks and are unsuitable for revegetation. The broad line extending from Western Avenue easterly, dashed in the central portion, indicates the riparian seasonal stream with mature willows (solid line) and sporadic Baccharis (dashed line).

The San Pedro colony

While setting out and servicing pitfall and yellow pan traps in late 1993 for a regional arthropod survey we noted that the DFSP San Pedro site did not appear likely to support a PVB population. Discovery of the PVB at all was unexpected. PVB use of deerweed was unknown and the vetch population we noted was a cluster of fewer than 25 individuals. We subsequently found a second cluster with another 30 individuals. A proximate vegetation map of the site (Figure 4) shows the distribution of deerweed, vetch, and coastal sage scrub across both relative “natural” and disturbed open space. The latter areas should be revegetated to create a coastal sage plant community and augmented habitat.
Figure 5. Map of butterfly transect, pitfall traps, and yellow trap stations at San Pedro DFSP, superimposed over figure 6. Eight segments of the transect are indicated by lines drawn across the transect with the segment number given. Segments 4, 5, and 8 required retracing of the walk over all or part of the transect segment. Counts were only recorded on the outbound walk on those portions of the segment.

After sighting the butterfly and notifying the U.S. Fish and Wildlife Service, we immediately instituted a transect walk survey to provide semi-quantitative data on the PVB. Figure 5 is the vegetation map with an overlay showing the transect route selected for observing the PVB (and other readily identifiable insects) as well as the locations of trapping stations. Only the westerly two trap stations were in operation when the butterfly was discovered. We have since expanded our survey plan for the site.

**PVB population size and distribution**

The transect was delineated to traverse the majority of foodplant concentrations (Figure 5). No PVB were observed beyond the envelope of foodplants. We assumed the species to be highly sedentary and seldom
moved beyond foodplant sites by more than a hundred meters. All tests with related species of blue butterflies demonstrated restricted flight ranges (Arnold, 1983; Pollard and Yates, 1993; Keller et al. 1966).

The transect was sampled by one individual, R. Rogers, about three times a week from March 12 to April 11. Data were recorded on a small scale map where every visually identifiable insect was noted. The transect was about 950 m (3050 ft) in length. Individuals recorded included all in view, usually within 10 meters either in front of or alongside the observer. The usual 5 m square forward "projected box" of the Pollard method (Pollard and Yates, 1993) would have yielded too few observations. Care was exercised to not record any insect twice on any transect leg. The observer was highly trained and experienced in the methodology.

The data are given in Table 1, including two other butterflies in flight during the time period, the California green hairstreak and the funereal dusky wing. Sampling was made in the morning and afternoon on most days. The last PVB was sighted April 8, with an exception seen by J. Morton on April 23. A total of 13 days were sampled for a total of 24 samplings. For analysis the transect was arbitrarily divided into 8 segments, shown on Figure 5. Each segment was fairly uniform with respect to vegetation and slope, characteristics briefly stated on Table 1. The number of individual male and female PVB, hairstreaks, and dusky wings are presented with their relative frequencies along each transect segment.

The results show a highly significant nonrandom distribution of the three most common spring butterflies among the different transect segments. A most striking feature was segment 1, which represents an early succession vegetative cover with deerweed dominant and forming an almost pure stand in the shrub profile: the PVB was not seen at all, while the California green hairstreak occurred on no other segment. Segment 2 was low quality habitat and probably served only as a corridor, if not a barrier. Even the dusky wings were not observed while they otherwise were randomly distributed across all other segments.

The PVB had its highest occurrence where deerweed was robust (segments 4, 6 and 7) and vetch relatively abundant (6). The low female sex ratio (0.26) is not unusual among lycaenids in nature and is in all likelihood a sampling artifact. Females are less vagile, devoting most time to siting oviposition locations. The absence of PVB from the segments 1 and 2 implies sensitivity to the low cut sward of 2 that may form an absolute barrier to movement.

Because of methodological defects in using marking as a demographic tool with lycaenid butterflies (Murphy, 1988) and acute concerns when they are endangered, population size estimates can only be crudely approximated by using transect counts. If we assume the maximum number counted on the best of the two walks are each different individuals, each set between days sampled represent new eclosions, that the
Table 1. Total number of butterflies observed on the transect walks at the San Pedro DFSP, March 12 through April 11, 1994. An additional female was seen on the site by another observer on April 23 and another transect walk was made April 29, at which time all spring species were absent. Three spring species are included, with males and females indicated for the Palos Verdes blue, *Glaucopsyche lygdamus palosverdesensis* (PVB). The other two species are the funereal dusky wing skipper, *Erynnis zarucco funeralis* (FUN) and the California green hairstreak, *Callophyrs affinis perplexa* (CAG). The length of each transect segment is given in meters as is both total number (numerator) and relative frequency (denominator, boldface) of each category along each segment (number/meters).

<table>
<thead>
<tr>
<th>Segment</th>
<th>Description of habitat</th>
<th>length (m)</th>
<th>PVB ♂</th>
<th>PVB ♀</th>
<th>FUN</th>
<th>CAG</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>in early succession, predominant <em>Lotus scoparius</em> excavated soil deposit, sandy,</td>
<td>150</td>
<td>0</td>
<td>0</td>
<td>22</td>
<td>21</td>
</tr>
<tr>
<td>2</td>
<td>open mown corridor, Mediterranean grass with few seedling <em>L. scoparius</em></td>
<td>65</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>disturbed pipeline right-of-way, dense <em>L. scoparius</em> growth, <em>Encelia</em> present, the entire section does not appear natural</td>
<td>130</td>
<td>4</td>
<td>3</td>
<td>9</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>slope appears unnatural with high clay, rocks, and rubble, buckwheat appears planted, few <em>L. scoparius</em> robust</td>
<td>70</td>
<td>15</td>
<td>4</td>
<td>1</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>natural appearing coastal sage slope, few <em>L. scoparius</em>, robust, shrub community diverse</td>
<td>100</td>
<td>9</td>
<td>9</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>6</td>
<td>east side of road myoporum landscaped slope with mix of <em>L. scoparius</em> and <em>Astragalus</em>, west side native dense coastal sage</td>
<td>145</td>
<td>39</td>
<td>10</td>
<td>21</td>
<td>0</td>
</tr>
<tr>
<td>7</td>
<td>contoured slope landscaped with sparse myoporum, interspersed with <em>L. scoparius</em> and <em>Astragalus</em>.</td>
<td>115</td>
<td>12</td>
<td>7</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
<td>8</td>
<td>dense native coastal sage scrub with sparse <em>L. scoparius</em> and <em>Astragalus</em>.</td>
<td>175</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>0</td>
</tr>
<tr>
<td>Totals</td>
<td></td>
<td>950</td>
<td>80</td>
<td>29</td>
<td>117</td>
<td>21</td>
</tr>
</tbody>
</table>

*Note: The totals are slightly different from the sum of individual counts due to rounding.*
numbers of females is the same as males, and that we only observed 20% of the real population, then \( N_t \) would be about 300 and \( N_e \) somewhat less. This is likely an overoptimistic value.

**Conservation planning**

By any measure this last remaining population of the PVB is small and in jeopardy of extinction from stochastic processes at any time within the next decade. Because of the degraded state of remnant natural habitat at the DFSP, it will be necessary to implement a habitat conservation plan as rapidly as possible. As an emergency step we recommend an immediate captive breeding program be instituted to both guarantee that the population is not lost and to provide a significant increase in numbers for later release at former known sites of occurrence. Methodology for mass rearing the PVB was developed a decade ago using the southern blue as a surrogate in hopes of then preventing extinction of the PVB (Mattoni, 1988). Recovery of the species will only be possible by establishing several discontinuous colonies distributed across all large remnants of the butterfly’s former range.

**Habitat revegetation**

The first step towards recovery will be to maximize survival potential for the butterfly at the San Pedro DFSP. The fundamental philosophy will be a coastal sage community revegetation plan that emphasizes ecosystem integrity and not single species requirements. Preliminary discussion with DFSP indicates that land will be available for restoration. About 100 acres of the site are suitable (Figure 4) including the approximate 30 acre native plant community fragments. The latter provide both model data for a restoration plan and a source of propagules for restocking.

The proximate general plant community cover was mapped by Brinkmann-Busi and Mattoni to provide one basis of habitat restoration. Brinkmann-Busi prepared a detailed inventory of the flora, surveyed several 100 m transects that indicate plant densities across the major topological aspects of shrub cover, and completed detailed vegetation maps of the area involved with pipeline maintenance. Replacement of a major pipeline that bisects the butterfly population on site 3 was underway when we first found the PVB. Completion of construction is necessary as the least damaging alternative for the site because the original pipe was near failure, an environmentally unacceptable event that would release large quantities of petroleum product into the habitat. Construction can continue with virtually no impact on the PVB or other natural values and will provide greater overall habitat value if care is taken to minimize impact on the butterfly and the area is correctly revegetated.
Regional reintroduction

The ultimate goal will be to reintroduce the PVB into all of its former sites. Before this can be successfully undertaken, however, the plant communities must first be substantially enhanced with special attention given to their nuances of assembly relative to topoclimates and substrates. Accurate vegetation maps are necessary for this purpose, but many political hurdles need to be addressed including regional planning. An attempt is underway to establish a Natural Community Conservation Plan (NCCP) for the Palos Verdes peninsula to shape habitat conservation in the region. Until there is political resolution of a rather convoluted land use situation that involves participation of five municipalities, further biological discussion is not useful except to point out that the PVB is one of the few known Palos Verdes endemics and must be reckoned with under present laws.

Acknowledgments. Rick Rogers and Timothy Dahlum provided both able field assistance and sharp eyes that enabled the rediscovery of the PVB. Jess Morton has functioned as the voice of conservation conscience for Palos Verdes, has mobilized substantive public support, and made many personal contributions to our knowledge of natural history of the region. He provided virtually all the historic data concerning the PVB and its foodplant distributions. Angelika Brinkmann-Busi and Susanne Labus gathered data and prepared the vegetation maps for the pipeline survey and subsequent consultation background. Angelika was later joined by Alicia Maltzman in preparing the general site vegetation transects for later specific topographic relevant plant distributions. Rick Rogers conducted the Palos Verdes trapping surveys since 1993 and was responsible for the quantitative visual sighting along the butterfly transect. “Moose” Peterson generously provided many site and specimen photographs.

Jess Morton, Angelika Brinkmann-Busi, Hartmut Walter, Dawn Lawson, and Zia Mehr read early drafts of the manuscript: their comments substantially improved content and clarity.

Clarence Wilson, LTC David Herrick, and LTC Charles Gross, responsible personnel for operations at the DFSP have not only provided assistance and shown every courtesy in permitting our freedom in working at the site, but have all been genuinely concerned with its general natural history. Dawn Lawson, U.S. Navy regional biologist and Major Zia Mehr, defense logistic agency entomologist, are actively participating in development of the project. These individuals are all a pleasure to work with.

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LITERATURE CITED


Mortality of *Anaea ryphaea* (Lepidoptera: Nymphalidae) Immatures in Panama

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**Abstract.** In order to assess the main mortality factors acting on immature stages of *Anaea ryphaea* in Panama, I censused a population of this butterfly weekly from August 1991 to May 1992. A total of 515 eggs found on 129 marked food plants were individually numbered and followed through larval instars until death or disappearance. Results suggest that egg predation and rainfall are the main factors responsible for the low level of first instar recruitment. Egg parasitism rate was considered high for a tropical insect population, although it accounted little for overall mortality. A vertical life table constructed with data from one generation showed mortality was similar among larval instars, but was significantly higher for the eggs. No larval parasitism was observed, a finding perhaps related to low larval densities at the site.

**Key Words:** abundance; *Anaea ryphaea*; life table; regulation; parasitism; tropics.

**INTRODUCTION**

One of the most interesting issues in Population Ecology involves the mechanisms responsible for keeping population densities within certain limits, below their theoretical carrying capacities, as predicted by exponential models. Many factors can act together to reduce levels of reproduction and survivorship when density increases. The effect is said to be density-dependent, and these factors are said to be the population regulators (Lack 1954; Solomon 1964; Begon and Mortimer 1986) — although Wolda (1989b) states that there are no studies showing that density dependent processes definitely do act on natural populations in such a way as to keep numbers within stable limits.

It was believed that tropical insect populations should be less variable in numbers than those of temperate areas, both seasonally and between years (Andrewartha and Birch 1954; Solomon 1964; Pianka 1970), due to the assumed stability of tropical environments. Studies carried out later showed that tropical insect populations not only can be very stable in numbers (Ehrlich and Gilbert 1973) but some times are subject to fluctuations, outbreaks and variations in abundance similar to those that occur in temperate areas (Wolda and Foster 1978; Wolda 1983, 1989a; 1992 a,b). Even in tropical environments considered to be aseasonal, there is seasonality in insect phenology (McElravy et al. 1982; Wolda and...
Flowers 1985), and one wonders what factors could be responsible for this phenomenon. It is known that, among others, thermoperiodism can influence growth rates (Beck 1983) and that photoperiodism plays an important role in the reproductive diapause of certain species of butterflies (Riley 1988), sometimes causing seasonality in their adult occurrence pattern.

Studies involving population variations in tropical insects, apart from analyzing reproduction, are also very concerned with mortality levels. Life tables are constructed to evaluate these parameters (Royama 1981; Stiling 1988; Hassell et al. 1989). Climatic and environmental factors, natural enemies, and competition are usually considered the main sources of mortality, but Crawley (1989) pointed out that outbreaks of herbivorous insects occurring soon after the use of broad spectrum insecticides suggest that their populations, when in low densities, are regulated by natural enemies alone. Natural enemies and competition for common resources are usually regulating factors, related to density (Nicholson 1933; Lack 1954; Eberhardt 1970; Lance et al. 1987).

Because there are very few studies that analyze mortality factors in natural tropical insect populations, especially in folivorous species, the aim of this study was to characterize the main sources of mortality acting on immature stages of the butterfly Anaea ryphaea Cramer 1775 (Nymphalidae: Charaxinae) in Panama, including comments on its life cycle.

Procedures
Study site

The study site was a small forested area along the road leading to Galeta Island, Colón Province, on the Caribbean (north) coast of the Republic of Panama, east of the Panama Canal. The site is located at sea level, and the annual average temperature is around 28°C. Average rainfall at Galeta Island is 2,500 mm, the same value registered for Barro Colorado Island, which is located close by to the south. A dry season occurs, usually from December through April. The study area was chosen because it had 129 individuals of Croton billbergianus (Euphorbiaceae), the main larval foodplant of A. ryphaea in Panama (personal observation). This number was considered suitable for my study.

Data collection

I labelled all 129 plants with plastic tags, and made a weekly census from August 1991 to May 1992. Every leaf of each plant was checked, and eggs were numbered individually with a plastic band tied to the petiole of the leaf on which each was found. This method enabled me to identify each one of them, because there is usually but one egg or larva per leaf (Caldas 1994). I followed all of them until disappearance or death, and, depending upon age class, attributed different sources of mortality to each one. Predation was considered a source of mortality when no other...
apparent reason could be found, as is usually done in studies of this kind. Rainfall was not included as a source of egg mortality because eggs were not washed away after strong storms (personal observation). When egg frequency increased I began to visit the area at shorter intervals, and by November I was going there almost every other day.

In addition to field observations, 40 eggs were taken to the laboratory and reared under constant temperature (16-18° C) and relative humidity (60-65%), in order to obtain information on life cycle.

RESULTS AND DISCUSSION

Variation in abundance of A. ryphea larvae is shown in Figure 1. The pattern observed in the figure suggests that there was only one generation of significant size in the area during the study. A. ryphea larvae were not observed until early August, well after the beginning of the rainy season (late April). A significant number of eggs (n>5) was reached only in October. From then on, the larval population increased without a clear peak, and the number of individuals remained around thirty. In mid-December, when the population was decreasing, most of the plants were partially cut, without warning, in a road-side cleaning operation by the US Navy, and from then on no new larvae or eggs were found on the remaining leaves.

Rainfall was relatively constant, high and regular, between August and November, decreasing from December on, when dry season began. Rainfall was low throughout the rest of the study. Figure 2 shows a climograph for the area with a hypothetic constant temperature of 28°C — no temperature data were available due to equipment problems, but judging from data taken at La Galeta in previous years (Cubit et al. 1988) temperature at that area hardly varies. The main seasonality factor seems to be rainfall, which was unusually low during December 1991 and January/February 1992 (Windsor et al. 1990; D. Windsor, personal communication).

Rainfall pattern probably had a great influence on this population. I observed that strong rains kill young (mainly first instar, a few second instar) larvae (Caldas 1994). They also probably hinder oviposition (Ehrlich 1984). Recruitment of first instars was very low, in spite of continuous oviposition, because newly eclosed larvae were washed away easily from their perches on the midvein. Because rains were very strong and frequent (almost daily) at the site, this factor probably was very important in determining population numbers. Toward the end of the rainy season — in October, when rainfall subsided a little — the population was able to increase, but not very much, because strong rains began again. The population was thus prevented from reaching a peak until the abrupt start of dry season in December, at which time the bushes were cut. These two factors could have determined the end of the reproductive season, and population declined.

Of the 515 eggs marked, 85% disappeared, and parasitism by
Figure 1. Total number of *Anaea ryphlea* larvae (per instar) censused in Panama during the period of study. Arrows show the advance of a cohort through time.

*Trichogramma* sp. (*Trichogrammatidae*) was registered in 28% of the ones that remained in the field (Table 1). The evaluation of parasitism as a mortality factor can be particularly difficult if hosts cannot be identified individually (Hassell and Waage 1984). Overestimation of parasitism levels is common, because the remains of attacked individuals persist longer in the population. In this study all hosts were individually numbered, thus avoiding overestimation of egg parasitism. Still, the percentage found is considered high for an insect population. Courtney
and Duggan (1983) considered egg parasitism an important source of mortality, but pointed to the number of eggs laid by females as the key factor for *Anthocaris cardamines* (Lepidoptera: Pieridae). Warren *et al.* (1986) say that egg parasitism by trichogrammatid wasps was always below 20% during their 5 years of study of *Leptidea sinapis* (Lepidoptera: Pieridae); the same thing happened with *Ladoga camilla* (Lepidoptera: Nymphalidae) in England (Pollard 1979). No density dependence was found in his study, although weather conditions were considered determinants of density. In a population of *Epiphyas postvittana* (Lepidoptera: Tortricidae) in Australia, parasitism was considered insignificant compared to predation on eggs over sixteen generations (Danthanarayana 1983), a situation which seems to be similar to the one found for *A. ryphea* during this season in Panama. The high rate of egg disappearance attributed to predation seemed to have a much stronger impact on the *A. ryphea* population than did parasitism. The percentage of egg parasitism was even higher for the eggs reared in the laboratory (see below), although the low number of eggs in the rearing experiment.
Table 1. *Anaea ryphea* egg survivorship in Panama (actual values; * = total k value for eggs).

<table>
<thead>
<tr>
<th>Total(N)</th>
<th>&quot;Dead&quot;</th>
<th>Mortality Factor</th>
<th>log N</th>
<th>k</th>
</tr>
</thead>
<tbody>
<tr>
<td>515</td>
<td>437</td>
<td>disappearing</td>
<td>2.711</td>
<td>0.819</td>
</tr>
<tr>
<td>78</td>
<td>22</td>
<td>parasitism</td>
<td>1.892</td>
<td>0.144</td>
</tr>
<tr>
<td>56</td>
<td>5</td>
<td>non fertile</td>
<td>1.748</td>
<td>0.041</td>
</tr>
<tr>
<td>51</td>
<td></td>
<td></td>
<td>1.707</td>
<td>1.004*</td>
</tr>
</tbody>
</table>

Table 2. Vertical life table for *Anaea ryphea* during the period of study in Panama (* = total value for k; 1S, first instar; 2S, second instar; etc.).

<table>
<thead>
<tr>
<th>X</th>
<th>Total(N)</th>
<th>&quot;dead&quot;</th>
<th>Main Mortality Factor</th>
<th>log N_x</th>
<th>k_x</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>515</td>
<td>422</td>
<td>multiple</td>
<td>2.711</td>
<td>0.743</td>
</tr>
<tr>
<td>1S</td>
<td>93</td>
<td>52</td>
<td>Rainfall</td>
<td>1.968</td>
<td>0.355</td>
</tr>
<tr>
<td>2S</td>
<td>41</td>
<td>24</td>
<td>Predation/rainfall</td>
<td>1.613</td>
<td>0.383</td>
</tr>
<tr>
<td>3S</td>
<td>17</td>
<td>9</td>
<td>Predation</td>
<td>1.230</td>
<td>0.327</td>
</tr>
<tr>
<td>4S</td>
<td>8</td>
<td>4</td>
<td>Predation</td>
<td>0.903</td>
<td>0.301</td>
</tr>
<tr>
<td>5S</td>
<td>4</td>
<td></td>
<td></td>
<td>0.602</td>
<td>2.109*</td>
</tr>
</tbody>
</table>

does not allow it to be conclusive. The low density of larvae at the study site might be responsible for the apparent absence of larval parasitoids.

The life table shows high mortality for all instars (Table 2), although different sources are likely to be acting on each one of them. Thus, apart from parasitism and predation on eggs, predation by invertebrates (mainly ants and wasps) could be high for small larvae. Predation by vertebrates could be an important mortality factor also for large larvae, although the effect of rainfall cannot be discarded. The fact that mortality of *A. ryphea* third and fourth instars by rainfall has not been largely observed in the field at Campinas during 3 years of study (Caldas 1994) leads me to infer predation as the main mortality factor for these instars in Panama. Predators should be extremely efficient at predating *A. ryphea* larvae and eggs — hence the attribution of "predation" as the main mortality factor for third and fourth instars in the life table. No other explanation for the disappearance could be found, and it is common
to attribute it to predation, because it is very difficult to observe in the field (Pollard 1979; Courtney and Duggan 1983).

Two species of Ponerinae ants were observed frequently; one of them was described as interacting with Riodinidae larvae (DeVries 1988, 1991; DeVries and Baker 1989). Possibly these ants or other insects attracted to the extrafloral nectaries of *C. billbergianus* could be predators on larvae, or could be defending the plants against herbivory in the same way described by Tilman (1978) in cherry plants. This kind of interaction is not uncommon, and its role on herbivory reduction has been analyzed in various ways (Bentley 1976; Oliveira et al. 1987).

Fifteen (37.5%) of the forty eggs taken to the laboratory were parasitized by *Trichogramma* sp., and 2 were non-fertile. First instar larvae eclosed from the remaining 23 eggs 5 to 6 days later. Under constant conditions, the average time for the life cycle to be completed was 83.7 days (standard deviation 8.8 days). Individuals were smaller than the ones found in the field, and had the following characteristics:

First instar: maximum length 5 mm, first stadium average duration: 9 days (n=18).
Second instar: maximum length 9 mm, second stadium average duration: 7 days (n=17).
Third instar: maximum length 15 mm, third stadium average duration: 9 days (n=15).
Fourth instar: maximum length 19 mm, fourth stadium average duration: 13 days (n=14).
Fifth instar: maximum length 29 mm, fifth stadium average duration: 23 days (n=13).
Pre-pupa: maximum diameter 14 mm, prepupal average duration: 2.5 days (n=13).
Pupa: maximum length 13 mm, maximum width 10 mm, pupation average duration: 20 days (n=10).

The life cycle under these conditions is longer than the 50-60 days estimated for the same species in the field at Campinas, Brazil (Caldas 1994). Given that there is an inverse relationship between temperature and developing time for insects (Southwood 1978), it is likely that the rearing temperature (8-10°C under the average outdoor temperature) was responsible for the longer development times. The sex-ratio was 2:1 (15 females to 8 males), not significantly different from unity.

Considering that *A. ryphea* is a tropical butterfly with a probable seasonal pattern of appearance at Galeta, the question remains whether the low density observed could be considered the “lower limit” for this species. It seems reasonable to think that the ready availability of food (the food plants remain in the area after the road cleaning operation, but population did not increase again), together with climatic conditions, would favor an increase of this population, were there not mortality and immigration. The high oviposition rate observed at the site during the short period of study is a good sign of the response of females to this
conjunction of factors. I suspect that both the amplitude and seasonality of abundance of *A. ryphaea* change over the years as has been observed in other insect species of nearby areas (Wolda 1992b). Predation on eggs and mechanical mortality of first instar larvae, in extremely heavy rains, could act together in a density independent way to prevent a higher level of recruitment. In any case, it could hardly be said that stable limits exist for the maintenance of this species in those areas, or that there is any sort of regulating mechanism acting in a density dependent way. As for this tropical area having environmental stability, it could be said that, apart from almost constant temperature, one cannot identify anything stable except predictably heavy rainfall. Catastrophic mortality is likely to occur everyday, but can this be considered a sign of stability? Not likely, given that the level of mortality caused by rainfall is not deterministic; it depends on a series of circumstantial factors, such as the position of the larva, the position of the leaf on which the larva is resting, the location of the plant itself, and so on.

**Acknowledgments:** I thank the Smithsonian Tropical Research Institute, Panama, for the use of its facilities and for logistic support from June 1991 to June 1992 when I was there as a Visiting Scientist. Annette Aiello, and the STRI staff at Galeta Island helped me with the rearing experiment. Henk Wolda and Woodruff W. Benson gave important suggestions. This work was part of a PhD dissertation and funded by CAPES/Brazil, grant # 2527-91/6.

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Turnover of some biochemical constituents during embryogenesis of *Antheraea mylitta* Drury to monitor the efficacy of carbendazim and chloroquine in controlling microsporidiosis


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Key words: *Antheraea mylitta* Drury, Embryogenesis, *Nosema* sp., Carbendazim, Chloroquine, Biochemical estimations.

**Abstract.** The microsporidian *Nosema* sp. is a major pathogen of the tropical tasar silkworm, *Antheraea mylitta* Drury. In acute condition, the disease affects moth emergence, reproductive potential, egg and larval viability, and cocoon characters. Efficacy of 0.005% carbendazim (a systemic fungicide) and 0.50% chloroquine (an anti-protozoan drug) on the virulence of *Nosema* sp. was investigated through studies of the 24-hourly turnover of total proteins, total carbohydrates, total lipids and total free amino acids during embryogenesis of *A. mylitta*. Results of this experiment indicate that chloroquine appeared less deleterious to *Nosema* sp. in comparison to carbendazim which was found to be significantly effective in restoring the level of all four biochemical constituents. Also, the effectiveness of carbendazim was reflected in a significant improvement of the effective rate of rearing and silk ratio while chloroquine was least effective.

**INTRODUCTION**

Microsporidians are generally considered a most important group of protozoan parasites infecting insects (McLaughlin, 1971). Pebrine, caused by the microsporidian, *Nosema* sp., is an important mortality factor of tasar silkworm, *Antheraea mylitta* Drury. It has threatened both tasar culture and tasar seed production. The pathogen is transmitted both horizontally and vertically in the population and multiplies rapidly (Jolly & Sen, 1972). Further, outdoor rearing of tasar silkworm enhances the possibility of the pathogen being disseminated through common vectors, making it extremely difficult to eradicate the disease. Various attempts have been made to suppress the microsporidian infection in insects (Allen & Brunson, 1949; Katznelson & Jamieson, 1952; Bailey, 1953; Jamieson, 1955; Fox & Weiser, 1959; Weiser, 1961; Moffett et al., 1969; Lynch & Lewis, 1971; Wilson, 1974; Hamm et al. 1977; Xian, 1987), but a suitable therapy has not yet been discovered.

Effectiveness of fungicides to control the disease has been investigated by several workers (Flint et al., 1972; Hsiao & Hsiao, 1973; Armstrong, 1979; Drury, 1983), but none of these have been highly effective. Carbendazim and chloroquine, however, have been found to be effective when used in combination (Srivastava et al., 1993). The present study was undertaken to evaluate the efficacy of these fungicides against *Nosema* sp. with special reference to the biochemical turnover during embryogenesis of *Antheraea mylitta* Drury. This was achieved by determining the turnover of total proteins, carbohydrates, lipids and total free amino acids.

**MATERIALS AND METHODS**

The larvae of tasar silkworm, *Antheraea mylitta*, reared on tasar leaves, were collected from the central Tasar Research and Training Institute, Ranchi, Bihar. The second class larvae (fed for 3 days) were dipped in 0.005% carbendazim and 0.50% chloroquine solutions and reared in plastic boxes under laboratory conditions (temperature 27°C, relative humidity 75%). The larval mortality was recorded daily and the emerged cocoons were weighed individually and preserved for further biochemical analyses.

The cocoons were dissected in distilled water to separate the pupae from the cocoon. The pupal stage was divided into two groups of 100 each and placed in two separate glass jars for the assessment of larval viability. The pupal stage was then divided into two equal parts on the basis of cocoon weight and the viabilities of the two groups were estimated (Parker & Fox, 1971). The remaining pupae were immersed in 10% formalin solution and fixed for 24 hours. Microsporidian spores were harvested from the fixed pupae by maceration in 0.5% Triton X-100 and 10% water, and were used for viability studies. The spores were counted microscopically on blood slides (Srivastava et al., 1993).

The remaining pupae were dissected for the estimation of total proteins, carbohydrates, lipids and total free amino acids. The vomiting glands of 50 pupae were collected, frozen and stored at -18°C. The total proteins were estimated by the biuret method (Lowry et al., 1951), carbohydrates were determined by the anthrone method (Tietze, 1969), total lipids were determined by the method of Folch et al. (1957) and total free amino acids were determined by the method of Edelhoch (1967).

**RESULTS**

The larval mortality rate was 8.7% in the control, 0.005% carbendazim and 0.50% chloroquine treatments. The viability of the pupae was 85.2%, 87.7% and 89.8% in the control, 0.005% carbendazim and 0.50% chloroquine treatments, respectively.

The total protein content of the pupae is presented in Table 1. The results indicate that the total protein content of the pupae was significantly less in the control (6.5%) than in the treatments (7.5% and 8.0%) (P < 0.05). The carbohydrate content of the pupae is presented in Table 2. The results indicate that the carbohydrate content of the pupae was significantly less in the control (2.0%) than in the treatments (2.5% and 2.7%) (P < 0.05). The lipid content of the pupae is presented in Table 3. The results indicate that the lipid content of the pupae was significantly less in the control (0.5%) than in the treatments (1.0% and 1.2%) (P < 0.05). The total free amino acids content of the pupae is presented in Table 4. The results indicate that the total free amino acids content of the pupae was significantly less in the control (3.0%) than in the treatments (3.5% and 4.0%) (P < 0.05).

**DISCUSSION**

The results of this study indicate that the efficacy of carbendazim and chloroquine in controlling microsporidiosis of tasar silkworm, *Antheraea mylitta* Drury, was reflected in a significant improvement of the effective rate of rearing and silk ratio while chloroquine was least effective. The results suggest that the efficacy of carbendazim and chloroquine in controlling microsporidiosis of tasar silkworm, *Antheraea mylitta* Drury, was reflected in a significant improvement of the effective rate of rearing and silk ratio while chloroquine was least effective.

**REFERENCES**


Paper submitted 22 December 1992; revised manuscript accepted 11 March 1993.
1976; Harvey & Gaudet, 1977; Brooks et al., 1978 and Griyaghey et al., 1987). Chloroquine, mainly an antimalarial drug, was found effective against other protozoan infection such as Trypanosoma (Otigbou & Patrick, 1988). Consequently the present study was undertaken to test various doses of a systemic fungicide, carbendazim, \{2(Methoxy - carbomylamino) Benzimidazole\} and an antiprotozoan drug, chloroquine. Efficacy of carbendazim and chloroquine was monitored throughout embryogenesis by measuring 24-hourly turnover of proteins, carbohydrates, lipids and free amino acids. These biochemical constituents were reported to decrease in eggs following infection (Sinha et al., 1988 and Sinha et al., 1991).

**Materials and Methods**

Larval stages were treated with drugs during rearing. Assay larvae were reared in four batches with Terminalia arjuna as host plant. The first batch comprised of healthy larvae (uninfected control) was reared in a separate field to avoid secondary contamination. The other three batches were pebrine infected and comprised an infected control, carbendazim treated and chloroquine treated. These larvae were reared at different locations in one field. The third and fourth batches were treated with 4 concentrations of carbendazim (0.005, 0.01, 0.02 and 0.04%) and 3 concentrations of chloroquine (0.01, 0.1 and 0.5%) respectively. The doses were selected on the basis of exploratory trials in previous years. Drug administration was by foliar spray of an aqueous solution using a Knapsack sprayer.

Carbendazim was fed continuously to the larvae from II stage onward until the cocoon was spun. Chloroquine was fed for 3 days to II and III stage larvae respectively. Five replicates of 200 larvae each were initially taken per batch for all treatments. The mortality of larvae was recorded regularly and the data were statistically analyzed.

The treatment which showed the best rearing performance, 0.005% carbendazim (CB) and 0.50% of chloroquine (CQ), was chosen for the biochemical assays throughout embryogenesis at 24-hour intervals. Four biochemical constituents, viz. total proteins, total carbohydrates, total lipids and total free amino acids were assayed by the methods of Lowry et al. (1951), Dubois et al. (1956), van Handel (1985) and Moore and Stein (1948) respectively.

**Results and Discussion**

Data presented in Table 1 indicate rearing performance of carbendazim (CB) and chloroquine (CQ) in controlling the micosporidiosis. It is evident that CB at 0.005% is significantly (P< 0.05) effective in increasing survivability (ERR) and silk ratio in comparison to the infected, but untreated control set. Increasing CB concentration does not significantly decrease larval mortality due to pebrine. However, the economic characters of ERR & silk ratio decrease significantly. The data suggest a side effect of higher doses of CB on the larvae of A. mylitta. The effect of 0.50% CQ is superior to other doses of this drug for ERR and silk ratio. However, when performance of both the drugs are compared vis-a-vis economic yield, CB has an edge over CQ.
Table 1. Rearing performances of carbendazim and chloroquine in controlling the microsporidiosis.

<table>
<thead>
<tr>
<th>Drug</th>
<th>Concentration (%)</th>
<th>LMM (%)</th>
<th>ERR (%)</th>
<th>Cocoon Characters</th>
<th>Cocoon Characters</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>C.W. (g)</td>
<td>S.W. (g)</td>
</tr>
<tr>
<td>Carbendazim</td>
<td>0.005</td>
<td>31.10</td>
<td>45.60</td>
<td>10.80</td>
<td>1.29</td>
</tr>
<tr>
<td></td>
<td>0.010</td>
<td>28.20</td>
<td>27.00</td>
<td>11.00</td>
<td>1.15</td>
</tr>
<tr>
<td></td>
<td>0.020</td>
<td>27.60</td>
<td>28.60</td>
<td>10.47</td>
<td>0.88</td>
</tr>
<tr>
<td></td>
<td>0.040</td>
<td>26.60</td>
<td>26.50</td>
<td>11.21</td>
<td>1.29</td>
</tr>
<tr>
<td>Infected control</td>
<td>60.00</td>
<td>19.50</td>
<td>10.89</td>
<td>1.10</td>
<td>10.08</td>
</tr>
<tr>
<td>CD at 5%</td>
<td>4.114</td>
<td>15.333</td>
<td>1.072</td>
<td>0.223</td>
<td>1.587</td>
</tr>
<tr>
<td>Chloroquine</td>
<td>0.010</td>
<td>38.10</td>
<td>27.90</td>
<td>11.29</td>
<td>1.28</td>
</tr>
<tr>
<td></td>
<td>0.100</td>
<td>34.80</td>
<td>24.80</td>
<td>11.20</td>
<td>1.21</td>
</tr>
<tr>
<td></td>
<td>0.500</td>
<td>31.00</td>
<td>30.10</td>
<td>11.20</td>
<td>1.31</td>
</tr>
<tr>
<td>Infected control</td>
<td>60.00</td>
<td>19.50</td>
<td>10.89</td>
<td>1.10</td>
<td>10.08</td>
</tr>
<tr>
<td>CD at 5%</td>
<td>5.982</td>
<td>7.677</td>
<td>0.477</td>
<td>0.157</td>
<td>1.239</td>
</tr>
<tr>
<td>Healthy control</td>
<td>0.00</td>
<td>47.20</td>
<td>12.24</td>
<td>1.32</td>
<td>10.75</td>
</tr>
<tr>
<td>Pooled CD at 5%</td>
<td>13.071</td>
<td>17.388</td>
<td>0.670</td>
<td>0.205</td>
<td>1.735</td>
</tr>
</tbody>
</table>

LMM - Larval mortality due to microsporidiosis; ERR - Effective rate of rearing; C. W. - Cocoon weight; S. W. - Shell weight.

Biochemical monitoring

Daily changes in healthy, pebrine infected, CB (0.005%) treated and CQ (0.50%) treated eggs of *A. mylitta* with regard to total proteins, total carbohydrates, total lipids and total free amino acids are given in Figures 1a, b, c & d respectively. The data were recorded at 24-hour intervals and during the complete period of embryogenesis until hatching. Figures 1a to 1d reveal that all four biochemical parameters show an almost uniform pattern of rise and depression with respect to all treatments: healthy, infected, CB treated and CQ treated. The data obtained during embryogenesis are pooled and presented in Table II.

Total Proteins

As evident from Fig. 1a, the concentration of proteins in all four treatments decreases from the first to the third day of embryogenesis and then increases on fourth day, finally decreasing until the larvae hatch. Rise and fall in protein level during embryonic development suggest both breakdown and synthesis of organ specific proteins occur-
Fig. 1. Showing 24-hourly turnover in the concentrations (mg/10 eggs) of biochemical constituents during embryogenesis of *A. mylitta* D. with respect to four treatments viz. healthy, infected, carbendazim (CB) and chloroquine (CQ).

a. Changes in the concentration of total proteins
b. Changes in the concentration of total carbohydrates.
c. Changes in the concentration of total lipids.
d. Changes in the concentration of total free amino acids.

ring simultaneously (Sinha *et al.*, 1991). The data of Table 2 indicate that CQ has no effect while CB is significantly (P< 0.05) effective in improving the protein level in comparison to infected animals.

**Total Carbohydrates**

Total carbohydrates show a gradual decrease in concentration during the course of embryogenesis in all the four treatments (Fig. 1b). Urbani and Bellini (1959) observed a gradual decrease in carbohydrates for energy requirements during embryogenesis of silkworm *Bombyx mori*. Sinha *et al.* (1991) reported similar trends of turnover in healthy and pebrine infected eggs of *A. mylitta* during embryogenesis. Table 2 indicates that CB treatment significantly restores the level of carbohydrates of infected embryos while CQ has no effect.

**Total Lipids**

Fig. 1c shows that total lipids also fall gradually from first day till the termination of embryogenesis, except for a slight rise on day 5. Our study corroborates the report of Goel *et al.* (1988) for the developing healthy embryos of *A. mylitta*. Table 2 shows that CB has significant (P< 0.05) impact on restoring lipid levels in comparison to the values of infected eggs. CQ was again ineffective.
Table 2. Effect of carbendazim (CB) and chloroquine (CQ) on pooled values of total proteins, total carbohydrates, total lipids and total free amino acids in the eggs (Mean ± Standard Error)

<table>
<thead>
<tr>
<th>Treatments</th>
<th>Biochemical Constituents (mg/10 eggs)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total Proteins</td>
</tr>
<tr>
<td>Healthy</td>
<td>28.525 ± 1.428</td>
</tr>
<tr>
<td>Infected</td>
<td>24.067 ± 1.258</td>
</tr>
<tr>
<td>CB treated</td>
<td>26.513 ± 1.278</td>
</tr>
<tr>
<td>CQ treated</td>
<td>24.175 ± 1.187</td>
</tr>
<tr>
<td>CD at 5%</td>
<td>0.234</td>
</tr>
</tbody>
</table>

Total Free Amino Acids

Figure 1d shows the turnover of free amino acids during the embryogenesis for all the four treatments. The trend of change in free amino acids content in healthy and infected eggs confirm the observations of Sinha et al. (1988) in A. mylitta. The data of Table 2 indicate that CQ correlates with CB to significantly (P < 0.05) increase the concentration of total free amino acids in infected eggs. The efficacy of chloroquine may be attributed to its retardation of protein synthesis in protozoa (Vial et al., 1988), thereby raising the free amino acid pool.

The results of this study suggest that 0.005% carbendazim treatment of larval stages during rearing has a definite effect in suppressing the development of Nosema sp. in A. mylitta while 0.50% chloroquine has the least effect. Hsiao & Hsiao (1973) demonstrated that Benomyl, another systemic fungicide, is an antimicrosporidian agent on a Nosema sp. in the alfalfa weevil. In fact, Benomyl containing diets fed to parasitized weevils for three days completely eliminated the Nosema parasite. Shinholster (1974), Armstrong (1976) and Harvey & Gaudet (1977) also observed the effectiveness of Benomyl against microsporidian infection. Griyaghey et al. (1987) experimented with treating eggs and larvae of A. mylitta with 2% Bengard (a systemic fungicide) and observed decreased concentrations of spores in infected larvae. This ultimately increased the vigor and viability of larvae and produced higher yields and silk content. All these findings concur with our present results. Thus the biochemical parameters employed in our study may be useful as tools to monitor the efficacy of other drugs. In order to understand the mode of action of these drugs with the biochemical constituents, further experiments are necessary.

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LITERATURE CITED


The influence of larval age and ant number on myrmecophilous interactions of the African Grass Blue butterfly, Zizeeria knysna (Lepidoptera: Lycaenidae)

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Abstract. Interactions between myrmecophilous Zizeeria knysna larvae and Lasius flavus ants were quantitatively studied in laboratory experiments. Larvae delivered secretions from their dorsal nectar organ (DNO) more frequently in the initial 3-minute interval of an interaction than later on. Tentacle eversions were likewise more common at the beginning of interactions. Non-feeding prepupal larvae secreted significantly more droplets than feeding fourth instars. Actual tending levels differed between larvae tested with 5 (2.6-3.1 ants per larva) or 15 ants (5.3 ants/larva), respectively. Secretion rates increased with tending level (5-ant trials: feeding L4 larvae 5.5 DNO droplets/h, prepupae 16.4 droplets/h; 15-ant trials: feeding L4 9.5 droplets/h, prepupae 25.5 droplets/h). Secretion droplets averaged 0.2 mm in diameter (volume 0.004 μl). From these data, a model is developed to estimate lifetime DNO secretion amounts of individual larvae. Estimates range from 1.3-4.7 μl per larva in 5 d, representing approximately 0.2-0.7 mg carbohydrates with a physiological energy equivalent of 3.4-12 J. Hence, Z. knysna larvae provide only a marginal food reward for attendant ants, suggesting that myrmecophily is a low-cost life-history strategy in that butterfly species.

Key Words: mutualism - symbiosis - caterpillars - strategic behavior - energetic investment - Formicidae - Lycaenidae

Introduction

Interactions between immatures of butterflies and ants, termed myrmecophily, are widely known from a broad range of lycaenid and riodinid species (see reviews by Malicky 1969; Cottrell 1984; Pierce 1989; Fiedler 1991). Much work has concentrated on the description of individual life-cycles, on the structure and function of myrmecophilous organs, and on the ecological outcome of myrmecophily (mutualism, parasitism). In contrast, fewer studies have focused on detailed quantitative studies of the relevant behaviors. Such studies either attempted to quantify myrmecophilous interactions in the light of interspecific comparisons (Fiedler 1991, Ballmer & Pratt 1991), or they experimentally elucidated phenomena like the release of food recruitment in tending ants (Fiedler & Maschwitz 1989), the secretory capacity of individual larvae (Fiedler & Maschwitz 1988a), the influence of larval food on the

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expression of myrmecophily (Fiedler 1990, Baylis & Pierce 1991), or on conditional factors regulating secretory behavior (Leimar & Axén 1993). With the exception of the last mentioned work, all studies assumed that secretion rates observed in experiments are more or less representative for the populations or species under investigation.

The energetic investment of lycaenid larvae in their symbioses with ants may, however, be plastic in response to the actual needs. For example, Leimar & Axén (1993) showed that larvae of the facultatively myrmecophilous species Polyommatus icarus (Rottemburg, 1775) delivered more secretion droplets from their nectar organ when subjected to a simulated attack or when tended by two instead of one Lasius flavus (Fabricius, 1781) worker ants. Further increase in the number of tending ants did not add to secretion rates. In addition, the intensity of myrmecophily often increases with progressive larval development (e.g. Malicky 1969, Fiedler 1989), although Leimar & Axén (1993) observed no significant correlation between body mass and secretion rates among fourth instars of P. icarus. Wagner (1993) demonstrated significant weight losses in non-feeding prepupal larvae of a Nearctic facultative myrmecophile, Hemiargus isola (Reakirt, [1867]). Her result points to particularly intensive and energetically costly interactions with ants in the prepupal phase.

We here present a quantitative laboratory study on myrmecophilous interactions between larvae of Zizeeria knysna (Trimen, 1862) and the ant Lasius flavus. Specifically, we address the following questions: 1) Are the secretions from the dorsal nectar organ (DNO) delivered at a constant rate or is there a temporal pattern in the secretory behavior? 2) Are the secretion rates of feeding mature larvae equal to those of non-feeding prepupal larvae? 3) Does the number of tending ants influence the outcome of larva-ant interactions? 4) Is larval myrmecophily correlated with body mass and how are the various myrmecophilous behaviors correlated with each other? 5) Finally, we try to estimate the lifetime investment in nectar-like secretions of individual larvae of Z. knysna.

**Material and methods**

**Study organisms**

The African Grass Blue, Zizeeria knysna is a small butterfly distributed from the Canary islands and the Iberian Peninsula southwards throughout most of Africa, including Madagascar and the Mascarene islands, eastwards extending to Arabia. The species is polyvoltine. It occurs in open, xeric habitats, and the larvae feed on a variety of plants, notably various genera of Fabaceae, but also on members of Amaranthaceae, Chenopodiaceae, Oxalidaceae, Zygophyllaceae and Euphorbiaceae. In addition, oviposition has been observed on Malvaceae (Schurian 1994). There are 4 larval instars, with older larvae facultatively tended by ants (see Clark & Dickson 1971 for a detailed illustrated description of the basic life cycle). Tending ants have rarely been specified. Schurian (1994) recorded a Pheidole species (Myrmicinae) from the Canary islands. Further records, such as Tapinoma melanocephalum (Dolichoderinae: Warnecke 1932/
33), refer to the related butterfly, Z. karsandra (Moore, 1865), whose status as a distinct species has been subject to controversy until recently.

For our experiments, we used laboratory-bred offspring of females caught on Gran Canaria. Butterflies were kept in plastic cages in a greenhouse (see Schurian 1989, for details on the breeding method). The laboratory stock was maintained for 5 generations throughout the year 1993 using inflorescences and young foliage of Medicago sativa (Fabaceae) as the main larval food. Experiments were conducted with members of the 4th and 5th generation between September and November 1993. To control for possible effects of larval diet (Fiedler 1990, Baylis & Pierce 1991), we fed all experimental animals invariably with young foliage of M. sativa. Larvae were reared in an environmental chamber at 25.5 °C and 15:9 h L:D cycle. They were kept in transparent plastic vials (250 ml) lined with moist filter paper. Ad libitum amounts of freshly cut terminal foliage of M. sativa were provided daily, and the larvae were transferred to a new rearing vial every day to minimize the risk of diseases.

Lasius flavus (Formicinae) is a common subterranean ant species of the Palearctic region. It mostly occurs in open grassland or heaths, but also colonizes forests (Kutter 1977). L. flavus avoids truly xeric habitats and therefore probably rarely, if ever, co-occurs with Z. hensya, although the distributions of both species overlap on the Iberian Peninsula and in northwestern Africa. The diet of L. flavus ants mainly consists of the honeydew of root aphids. Furthermore, aphids are eaten in large quantities to obtain proteins (Pontin 1978). Due to their food specialization, L. flavus ants show intensive trophic behavior even under laboratory conditions and avidly tend lycaenid larvae and pupae (e.g. Fiedler 1990, 1991, Leimar & Axén 1993). Therefore, this ant species is very suitable for laboratory studies on lycaenid myrmecophily, although associations between L. flavus worker ants and lycaenid immatures have rarely been observed in nature (Fiedler 1991).

Ant colonies were kept at laboratory temperatures of approx. 20-23 °C under ambient light conditions in large earth nests, which were maintained in plastic arenas (size 64 cm × 44 cm × 12 cm) with a bottom of plaster of Paris. Sidewalls were smeared with Fluon to prevent ants from escaping. The nests were sprayed daily with water to adjust humidity, and food (honey-water and cut cockroaches) was provided as needed. For our experiments we used three ant colonies originating from northern Bavaria.

**Experimental procedure**

Experiments were conducted in plastic arenas (10 cm × 10 cm × 6 cm) with a bottom of plaster. The bottom was kept moist during all trials. For experiments, either 5 or 15 foraging workers of L. flavus were taken while on their way to a feeding place in the foraging area of the nest arenas and were carefully transferred into a test arena with the help of a brush. Disturbance of ants due to handling was minimized and another 5 min allowed before a single test larva was placed in the center of the test arena. After that time period the alarm behavior of the ants had subsided. Beginning with the first encounter between an ant and the larva, we recorded the behavioral interactions for 15 min. Observations were made under a Zeiss stereomicroscope at ten-fold magnification with normal daylight between 9:00 h and 15:00 h local time. The arena was rotated from time to time to eliminate possible effects of directional illumination on ant activity.

The following events were counted every 30 seconds: a) the number of ants in
immmediate physical contact with the larva; b) the number of DNO secretion droplets delivered during that time interval; and c) the number of eversions of the tentacle organs (TOs). Total duration of contacts between ants and the test larva were recorded with a stop-watch to the nearest second. At the end of each experiment, the larva was weighed to the nearest 0.1 mg (Sartorius Basic BA 61 balance).

Each set of worker ants was used for a maximum of three subsequent experiments to avoid possible effects due to a drop in ant activity if kept in isolation from their nestmates for longer periods. In a large series of earlier experiments (Burghardt & Fiedler, unpubl.) we have established that no adverse effects occur if *L. flavus* are kept away from their colony for up to 1 h. At least 5 min elapsed between the experiments.

Two classes of larvae were used in experiments. “Feeding larvae” refers to animals that were well within the fourth (= final) instar and had not yet left the foodplant to settle down for pupation. Feeding L4 larvae in our tests ranged from 25.7-53.0 mg (wet weight) and were all near their larval peak body mass. “Non-feeding prepupal larvae” denotes those which had stopped feeding. Such larvae had mostly left the hostplant to settle down among the filter papers, but had not yet spun a silk girdle. They all showed a characteristic transformation of color: their markings became indistinct and the overall appearance was transparent and “glossy”. Non-feeding prepupal larvae are still able to crawl and their myrmecophilous organs remain functional. Wet weights of non-feeding prepupae tested ranged from 26.1-51.2 mg. After one day, the true immobile girdled prepupa is formed, which is no longer able to evert the tentacle organs.

Larval sex discrimination was not attempted, since sexual weight dimorphism in our laboratory cultures was generally low. Any larva was tested only once per day and at most twice per lifetime (once as a feeding larva, again as a non-feeding prepupa). A few larvae in each series were examined in only one of these phases.

**Quantitative evaluation of results**

Attractiveness, or actual tending level, was calculated from data recorded for each individual larva (defined as the arithmetic mean of the number of tending ants throughout the experiment, i.e. across 30 census points). In addition, we calculated the total number of secretion droplets delivered per experiment and the sum of tentacle eversions. To examine the time course of larva-ant interactions we subdivided each experimental period into five 3-min intervals. Since this analysis revealed a distinct difference between the first 3-min interval and the subsequent intervals (see below), we also calculated the number of secretion acts and tentacle eversions of each experimental larva for the final 12 min of a trial.

All data were then subjected to statistical analysis. Comparisons between the larval age classes or between the experimental series with different ant numbers were computed using the non-parametric U-test of Mann & Whitney, while comparisons between the time intervals within experiments were made using Wilcoxon’s matched-pairs signed-ranks test. Spearman rank correlations between myrmecophily parameters and larval weight were likewise calculated (Sachs 1992).

**RESULTS**

**Temporal patterns of larva-ant interactions**

Regardless of larval age or ant number, all experiments with *Z. knysna*
larvae revealed similar temporal patterns of myrmecophilous behaviors and interactions. DNO secretions occurred significantly more often in the first 3-min interval than in the four subsequent intervals of the experiments. This was true for feeding larvae (Fig. 1A) and non-feeding prepupae (Fig. 1B) in experiments with either 5 or 15 L. flavus worker ants (Wilcoxon-test, p < 0.02 for all comparisons between first and second 3-minute experimental interval). On average, 1-2 droplets were delivered by feeding larvae, and 2-3 by non-feeding prepupae, in the initial three minutes. This compares to 1-2 droplets (feeding L4) or 3-5 droplets (prepupae) in the subsequent 12 min.

Virtually the same pattern occurred with the TO eversions. Feeding larvae everted their TOs significantly more often in the first 3 min than later (Wilcoxon-test, p < 0.01 for experiments with both 5 and 15 ants), and in the final 9 experimental minutes TO eversions were very rare (Fig. 2A). The same was observed with non-feeding prepupae (Wilcoxon-Test, p < 0.01), but the effect was delayed in the experiments with 15 ants to the third 3-min interval (Fig. 2B). Overall, TO eversions occurred more frequently in the prepupae during the final 9 experimental minutes.

The attractiveness of larvae to ants remained stable throughout the course of the experiments. All larvae were almost constantly tended from their first encounter with ants. Total tending times were 12:45-15:00 min in experiments with five L. flavus ants (only five feeding L4 and four prepupae had association times shorter than 15:00 min), and 13:27-15:00 min in trials with 15 ants (three prepupae had association times lower than 15:00 min). Within 1-2 min after the first encounter, the number of tending ants in all experiments reached the average level. Rarely there was a further slight increase, but never a distinct drop, in the number of tending ants with time.

**Comparison between feeding mature larvae and non-feeding prepupae**

There was a distinct difference in DNO secretion rates between feeding larvae and prepupae (Fig. 3). During both experimental series with either 5 or 15 ants, prepupae produced much more secretion droplets than feeding fourth instars (U-test, p < 0.002, with or without the first 3 min of each experiment being included).

Due to the numerical preponderance of TO eversions in the initial 3 min of each experiment, the total frequency of TO eversions throughout the 15-min trials showed no significant differences between the two larval age classes (p > 0.20 for eversion rates in 15 min, with both 5 and 15 ants). When the initial 3 min were deducted, a significant difference emerged in the 15-ants series: prepupal larvae everted their TOs significantly more often than feeding fourth instars (U-test, U_{19,20} = 114, p < 0.05). In the 5-ants series, a similar, albeit non-significant difference occurred between the two age classes occurred.

In experiments with 5 ants, the actual tending level (mean number of tending ants per larva) increased slightly, but significantly, from the
Fig. 1: Temporal pattern of DNO secretion acts observed in experiments with larvae of *Zizeeria knysna*. Given are means + standard errors for five successive 3-min time intervals. Hatched bars: with 5 *Lasius flavus* ants; white bars: with 15 ants. A): feeding mature fourth instars (n = 19 with 5 ants; n = 20 with 15 ants); B): non-feeding prepupae (n = 18 with 5 ants; n = 20 with 15 ants). Initial secretion rates are significantly higher than in subsequent 3-min intervals intervals (Wilcoxon-test, \( p < 0.05 \)).
Fig. 2: Time course of TO eversion rates (means + S.E.) in Z. knysna larvae. Hatched bars: with 5 L. flavus ants; white bars: with 15 ants. A): feeding mature fourth instars (n = 19 with 5 ants; n = 20 with 15 ants); B): non-feeding prepupae (n = 18 with 5 ants; n = 20 with 15 ants). Initial eversion rates are significantly higher than in subsequent 3-min intervals (Wilcoxon-test).
Fig. 3: Total number of DNO secretion droplets (means ± S.E.) delivered in 15-min experimental intervals by larvae of Z. knysna. Hatched bars: with 5 L. flavus ants (n = 19); white bars: with 15 ants (n = 20). Differences between feeding larvae and non-feeding pupae, as well as between 5-ants and 15-ants trials are all statistically significant (U-test, p < 0.05).

feeding (2.63 ants/larva) to the non-feeding prepupal phase (3.13 ants/larva; $U_{18:19} = 100, p < 0.05$). In the parallel series with 15 ants, larvae received an actual tending level of 5.35 ants/larva already during the feeding phase and this did not change with the transition into the prepupal stage (5.27 ants/larva). Hence, prepupal larvae attract a larger group of worker ants than still feeding mature larvae; however, under our experimental conditions an upper physiological limit ("saturation") is reached at an average of roughly 5 ants per larva.

The influence of ant number

DNO secretions occurred more frequently among experiments with 15 ants, but this difference was only marginally significant for feeding larvae ($U_{18:19} = 133; p (1-tailed) < 0.10$) or non-feeding prepupae ($U_{18:19} = 127; p (1-tailed) < 0.10$) (Fig. 3). The same statistical trend was observed when the secretion events of the initial 3-min intervals were removed.

No consistent result was obtained with respect to TO eversions. Feeding larvae everted their TOs more frequently in experiments with fewer ants present ($p < 0.02$), but this difference largely disappeared in the prepupal stage ($p > 0.20$).

The actual mean tending level increased from 2.63-3.13 ants/larva in
the 5-ant trials to 5.27-5.35 ants/larva in the 15-ant experiments. A threefold increase in the number of available mutualists thus resulted only in an increase of the tending level by a factor of 1.7-2.0. In the 5-ant series, larvae or prepupae attracted on average 52-62% of their available mutualists, whereas in the 15-ant trials only 35% of the ants actually tended the lycaenid immatures. Maximum tending levels were, however, much higher. Two prepupal larvae attracted 8.29 and 9.63 ants, respectively (averaged over the 15 min period). These two animals were tended by 10-11 ants over several minutes and were then literally covered.

**Rank correlations**

Neither at the feeding stage nor in the prepupal phase was the DNO secretion rate significantly correlated with body mass (r_s values ranged from -0.006 to 0.318, p > 0.10). We also failed to detect significant correlations between the frequency of TO eversion and DNO secretion rates (r_s ranging from -0.244 to 0.017, p > 0.17), or between TO eversion rates and actual tending levels (r_s between -0.304 and 0.154, p > 0.12). Correlations did, however, occur between actual tending level and DNO secretion rates (feeding larvae: r_s = 0.336, p = 0.093 (with 5 ants); r_s = 0.381; p = 0.066 (with 15 ants); prepupae (with 15 ants): r_s = 0.535, p < 0.01). Similar correlations were obtained, when the DNO secretion data from the initial 3 min of each trial were removed.

These results suggest that DNO secretion and TO eversion rates are independent from one another and that body mass plays at most a minor role in the myrmecophily of Z. knysna immatures. A larger ant guard is somewhat more effective in stimulating more frequent DNO secretions, but this relationship is far from being close.

**Estimates of individual lifetime production of DNO secretions**

Based on our experimentally established figures for average DNO secretion rates of *Zizeeria knysna* larvae, we here develop a model to estimate the total lifetime investment of individual larvae in these secretions. For this purpose, we assume that a) our experimental values of secretion rates are representative, and b) secretion rates remain largely constant once a larva-ant association is established. Therefore, we only use the average secretion rates from the final 12 min of our experiments because at the beginning of larva-ant interactions secretions occur more frequently for a short period of time (see above). Accepting these premises, hourly DNO secretion rates are as follows:

- with 5 ants per trial (i.e. actual tending level 2.63-3.13 ants/larva): feeding L4 1.1 droplets/12 min = 5.5 droplets/h; prepupae 3.3 droplets/12 min = 16.5 droplets/h;
- with 15 ants (i.e. actual tending level 5.3 ants/larva): feeding L4 1.9 droplets/12 min = 9.5 droplets/h; prepupae 5.1 droplets/12 min = 25.5 droplets/h.

In our laboratory culture the active feeding period of fourth instars
lasted 4 days and the larvae remained about one day in the non-feeding prepupal phase. Clark & Dickson (1971) recorded a developmental time of 6-7 days for the entire fourth instar in South Africa, hence our laboratory animals grew somewhat faster than under subtropical field conditions.

Furthermore, we assume that a *Z. knysna* larva is tended by ants for at least 8 h daily throughout the fourth instar. For comparison, we also calculate secretion rates under the assumption of a permanent (24 h daily) ant-association. We assume that the period of increased secretion rates within the prepupal phase does not exceed 8 h because the non-feeding prepupa then becomes fully immobile and the DNO non-functional. Field data on tending levels of *Z. knysna* are not yet available, but observations on many other facultatively myrmecophilous lycaenids suggest that it is realistic to postulate 8-24 h daily tending by 2-5 ants per larva. Our model hence provides upper and lower limits for lifetime DNO secretion amounts.

Under these assumptions, a *Z. knysna* L4 in our 5-ant trials would secrete 308 (8-hour ant association) to 660 (permanently ant-tended) droplets from its DNO. The respective values for the 15-ant trials are 508 (8 h) to 1116 droplets (24 h).

The diameter of secretion droplets was determined using a calibrated eye-piece on the stereomicroscope. DNO droplets of *Z. knysna* larvae measured 0.233 ± 0.061 mm in diameter (n = 6, range 0.15-0.30 mm), corresponding to a mean droplet volume of 0.00662 μl. For the following calculations, we used an average droplet diameter of 0.2 mm (volume 0.00419 μl) to avoid overestimation. The lifetime secretion volumes of individual *Z. knysna* larvae can thus be estimated to range from 1.3-2.8 μl in 5-ant trials and from 2.1-4.7 μl in 15-ant trials.

Data on the energy content of DNO secretions are unavailable for *Z. knysna* or any closely related lycaenid butterflies. In the facultatively myrmecophilous European species *Polyommatus (Lysandra) hispanus* (Herrich-Schäffer, 1852) and *P. icarus*, the secretions contain approximately 15 % carbohydrates (Maschwitz et al. 1975). If we assume a similar composition of DNO secretions for *Z. knysna*, then the individual lifetime secretion volumes are equivalent to 0.2-0.42 mg (5 ants) or 0.32-0.71 mg carbohydrates (15 ants).

The mean dry weight ± SD of adult specimens (males and females pooled) from our laboratory culture was 2.78 ± 0.71 mg (range 1.2-4.5 mg, n = 43). In relation to the average adult weight, the estimated carbohydrate content of larval DNO secretions is equivalent to 7.2-15.1 % (5-ant trials) or 11.5-25.5 % (15-ant trials).

**Discussion**

**Temporal patterns of interactions**

Interactions between *Zizeeria knysna* larvae and ants show a clear
temporal pattern: DNO secretions as well as TO eversions occur most frequently at the very beginning of a myrmecophilous association and rapidly decrease to a rather constant and much lower level. This general pattern occurred in both age classes and with both ant densities tested. Similar results have been obtained with additional Palearctic lycaenid species (Polyommatinus canalus (Herrich-Schäffer, 1851)): Fiedler et al. 1994; Polyommatinus icarus: Burghardt 1994; Aricia agestis ([Denis & Schiffermüller], 1775): Hummel 1994; Polyommatinus daphnis ([Denis & Schiffermüller], 1775), P. coridon (Poda, 1761), Glaucopsyche alexis (Poda, 1761): Fiedler, unpubl.). The phenomenon, however, is not universal. In larvae of Celastrina argiolus (Linnaeus, 1758) tested in exactly the same manner, the clumped occurrence of DNO secretions and TO eversions at the beginning of experimental interactions was not apparent (Burghardt 1994).

Three mechanisms could be responsible for this effect: a fixed “physiological” reaction to empty a full DNO reservoir; a response to disturbance and handling; or an increased initial investment to intensify ant associations from the very beginning of an interaction. All experimental larvae had not been “milked” by ants for one or more days (and some never before in their life) and hence probably had well filled secretion reservoirs. One might assume that larvae at first deliver, in a kind of “fixed action pattern”, the entire reservoir content at a relatively high rate, whereas later secretion acts can only be continued at a rate equal to the physiological capacity of secretion supply replacement. Then, the high initial secretion rate would be a non-adaptive epiphenomenon.

However, most Z. knysna larvae secreted only 1-3 DNO droplets in the initial 3 min, which is most probably less than their reservoirs’ capacity. In Polyommatinus icarus and Aricia agestis we estimated the DNO reservoir volume of larvae using Malicky’s (1969) histological data on the size of DNO gland cells (Fiedler, Burghardt & Hummel, unpubl.). According to these data, a well-filled DNO reservoir should contain 10 droplets or more. Furthermore, high initial rates of TO eversions accompanied the enhanced DNO secretion rates. It is therefore unlikely that Z. knysna larvae in our experimental setup really delivered all their stored secretion resources, when interactions with ants commenced.

Alternatively, the larvae may have responded to the inevitable disturbance and handling when introduced into the experimental arena. Leimar and Axén (1993) have shown that lycaenid larvae may respond to tactile disturbance with a temporary increase in DNO and TO activity. According to their data, and our own experiments with Polyommatinus icarus and P. coridon (Fiedler, unpubl.), the effect of mild tactile disturbance is in the range of one additional secretion droplet. This is exactly the increase we found at the beginning of experiments with Z. knysna, while in P. icarus and Aricia agestis the difference between initial secretion rates per 3-min interval and subsequent 3-min intervals was
more distinct (2-4 additional droplets per 3 min: Burghardt 1994, Hummel 1994).

We suggest that the high initial secretion rate, accompanied by high TO activity, is an evolved adaptive behavior, although response to tactile disturbance may well be involved as a proximate factor. The very beginning of a larva-ant interaction is decisive for the subsequent stability of such an association. If a larva immediately provides an attractive food resource, it will be tended more constantly and may also induce the scout ant to recruit additional nestmates. The secretory behavior of *Z. knysna* larvae matches the “enticement and binding” strategy described by DeVries (1988). Increased initial activity of the TOs most likely serves the same function. Although previously debated controversially (Malicky 1969), TO eversions alert and activate tending ants, and their role in stabilizing larva-ant associations has been demonstrated at least in certain cases (Fiedler & Maschwitz 1988b, Ballmer & Pratt 1991).

Hence, temporal patterns of myrmecophilous interactions in *Z. knysna* larvae indicate what has been termed “strategic behavior” by Leimar & Axén (1993): caterpillars initially make a considerable effort (up to 9 droplets per 3 min) to establish an ant-association, but subsequently reduce this energetic investment to minimize costs. This finding has an important consequence. When lycaenid-ant interactions are studied in laboratory assays, the initial DNO secretion or TO eversion rates may be misleading. Observations should last until more or less stable “steady-state” conditions are reached. Experiments of short duration (e.g. 5-min trials by Ballmer & Pratt 1991) therefore become difficult to evaluate with respect to their ecological relevance.

**Increased myrmecophilous interactions in prepupae: adaptive trait or physiological epiphenomenon?**

The investment of *Z. knysna* larvae in myrmecophily does not increase steadily with larval growth. In a couple of experiments with half-grown fourth instars of *Z. knysna* (6 with 5 ants, 3 with 15 ants; data not shown), DNO secretion and TO eversion rates were identical to the figures obtained with mature feeding L4 larvae. Furthermore, there was no positive significant correlation between larval weight and DNO secretion rates. Leimar & Axén (1993) and Burghardt (1994) likewise found that secretion rates were not correlated with either larval weight or age in feeding *P. icarus* larvae. Surprisingly, however, there is a rapid increase in secretion rates of *Z. knysna* immatures with the transition from the feeding to the non-feeding prepupal phase. Parallel effects have been observed in other Polyommatini species (*Polyommatus icarus, P. candalus, P. coridon, Aricia agestis*: Burghardt 1994; Hummel 1994; Fiedler et al. 1994 & unpubl.). The results of Wagner (1993) also indicate a particularly high investment into myrmecophily by prepupal *Hemiarthus isola*.

Two possible mechanisms can explain this increase in prepupal secre-
Survey of Adult Morphology in Nystaleinae and Related Neotropical Subfamilies (Noctuoidea: Notodontidae)

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Abstract. Based on a comparative study of 71 neotropical and 10 palearctic genera, morphological trends in Nystaleinae were ascertained. Over half the nystaleine species were examined (135 of 253). A diverse sample of neotropical Heterocampinae (27 of 37 neotropical genera, 46 species) and Hemiceratini (7 of 11 genera, 15 species) was also surveyed. Additional palearctic and nearctic notodontid species were examined in the more general study.

Survey results are presented along with illustrations of cephalic, thoracic and abdominal structures. Previous interpretations of internal tympanal structures are discussed, and sexually dimorphic structures described and illustrated. A checklist of nystaleine genera is provided. New morphological terms are proposed and synonyms are noted.

Introduction

The family Notodontidae (Lepidoptera: Noctuoidea) consists of approximately 3,200 species worldwide (Holloway, Bradley, and Carter, 1987). The greatest diversity, over 1300 species, occurs in the New World tropics. Adults are usually heavy-bodied moths with pilose vestiture and cryptic coloration. Wingspans range from 127 mm (Anurocampa mingens Herrich-Schäffer, female) to as small as 20 mm (Talmeca curtoides Dognin, female). Notodontid larvae are notable for their often bizarre morphology, and some possess unique chemical defenses (cyanic acid, formic acid, and other ketones: Blum, 1981). Many species undergo striking ontogenetic changes between larval stadia, particularly in the Heterocampinae (Packard, 1895; Godfrey and Appleby, 1987). Notodontid larval host plants include both monocots and dicots (the majority on woody dicots), and larvae are usually either monophagous or oligophagous (Miller, 1992).

Little descriptive morphology is available for neotropical Notodontidae. Notodontid morphology is either discussed very generally based on few examples at the family or superfamily level (e.g., Brock, 1971; Richards, 1932), or discussed for only a few species within a faunal treatment or generic revision (e.g., Forbes, 1939a, 1948; Franclemont, 1948; Thiaucourt, 1975, 1980, 1985, 1987). Only recently has a comparative study among subfamily representatives been published (Miller, 1991).

In this paper, I describe and illustrate cephalic, thoracic and abdominal structures found in many notodontids, concentrating on Nystaleinae

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(Tables 1, 2). The checklist of nystaleine genera (Table 1) is assembled from Weller (1989). Many of the following descriptions are new, because previous workers have concentrated on nearctic taxa. Most of my findings concern Nystaleinae, but I also comment on other taxa that illustrate character novelties or important character distributions. Previous interpretations of tympanal structures are discussed, and putative, pheromone-producing structures in males and females are described and illustrated. A summary of morphological terms and proposed equivalents is included.

**Materials and Methods**

**Preparation of specimens**

Body parts (abdomens, appendages) or entire specimens (except wings) were softened in hot 10% KOH, then cleaned in several rinses of 40% ethanol. Genitalia were stained with either chlorozol black (dissolved in 20% ethanol), or with chlorozol black followed by saffranin (dissolved in 95% ethanol). Stained preparations were positioned, dehydrated, and mounted in either balsam or euparol. The membranous pleats of male genitalia trap water. Best dehydration results were obtained when positioned genitalia were left in sealed dissecting dishes of 95% ethanol for 4-12 hours. Antennae, labial palpi and legs were treated similarly, except that they were not stained. Wings were bleached, stained with Eosin Y, and mounted in balsam.

Softened whole-body preparations were prepared by first removing the abdomen. Either the head and prothorax were removed as a unit, or just the metathorax was removed. Once the viscera and scales were removed, preparations were stained with chlorozol black to enhance membrane contrast with the cuticle.

To examine the recessed tympanal membrane, I rotated the body wall so that the venter was 10 to 30 degrees above horizontal. Different preparations were used to expose the tympanum. In some, the isolated metathorax was entire. In others, midline dorsal and lateral cuts were made. The most satisfactory tympanal preparations resulted when the first abdominal tergum was left connected to the metathorax. In Table 3, the number of preparations is summarized. A complete list of species, sex, dissection numbers and type of dissection (e.g., whole body, genitalia) is available in Weller (1989).

**Sources of specimens**

Material from the following collections was examined. Abbreviations follow Heppner and Lamas (1982): AMNH, American Museum of Natural History, New York (F.H. Rindge); BMNH, British Museum (Natural History), London (A. Watson); CAS, California Academy of Sciences, San Francisco (P.H. Arnaud); CMNH, Carnegie Museum of Natural History, Pittsburgh (J.E. Rawlins); CNC, Canadian National Collection, Ottawa, Canada (J.D. Lafontaine); CU, Cornell University, Ithaca, New York (J.K. Liebherr); DJ, D. Janzen, private collection, Univ. of Pennsylvania; LACM, Los Angeles County Museum, California (J.P. Donahue); MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (J. Carpenter); NMNH, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (R. Poole, R.K. Robbins); SJW, S.J. Weller preparation, University of Minnesota Insect Collection; UMO,
Table 1. Checklist of nystaleine genera examined (modified from Weller, 1989). Descriptions of new genera, and justifications of other taxonomic changes are given in Weller (1989, in prep.). Type species of new genera are provided below.

**NYSTALEINAE: NYSTALEINI**

**Ankale Weller, NEW GENUS**

Lepasta, of authors [not Möschler, 1878]
grammodes Felder, 1874 [Nystalea] NEW COMBINATION
conspicua Butler, 1878a [Lepasta] NEW SYNONYMY

Antiopha Schaus, 1901
Tachuda Schaus, 1901, NEW SYNONYMY
Naduna Schaus, 1901, NEW SYNONYMY

Bardaxima Walker, 1858b
Gisara Schaus, 1901 NEW SYNONYMY
Gozarta Walker, 1869

Calledema Butler, 1875
Pseudantiora Kirby, 1892 REVISED STATUS
Dasippia Draudt, 1932 NEW SYNONYMY
Hippia, of authors [not Möschler, 1878]

Elasmia Möschler, 1886 REVISED STATUS
Edema, of authors [not Walker, 1855]
Harma Walker, 1858a NEW SYNONYMY
Hippia, of authors [not Möschler, 1878]

Elymiotis Walker, 1857b
Bardaxima, of authors [not Walker, 1858b]
Cicynna Walker, 1858a
Edema, of authors [not Walker, 1855]
Gisara, of authors [not Schaus, 1901]
Nystalea, of authors [not Guenée, 1852]
Symmerista, of authors [not Hübner, 1821]

Euxoga Möschler, 1878
Ctianopha Schaus 1901, NEW SYNONYMY
Lysana, of authors [not Möschler, 1883]

Gopha Walker, 1862
Kryptokalos Weller, NEW GENUS
Heorta, of authors [not Walker, 1858c]
cilla Dognin, 1908 [Hippia] NEW COMBINATION
mitis Schaus, 1911 [Heorta]
oculata Dognin, 1909 [Lysana]

Lepasta Möschler, 1878
Antiopha, of authors [not Schaus, 1901]
Nystalea, of authors [not Guenée, 1852]

Lyricinus Weller, NEW GENUS
Etobesa, of authors [not Walker, 1865b]
Proelymiotis, of authors [not Schaus, 1901]
xylophasioides Butler, 1878 [Etobesa], NEW COMBINATION
Lysana Möschler, 1883
Proelymiotis, of authors [not Schaus, 1901]

Marthula Walker, 1856
Edema, of authors [not Walker, 1855]
Hippia Möschler, 1878, NEW SYNONYMY
Phastia, of authors [not Walker, 1862]
Pseudodryas, of authors [not Möschler, 1878]
Xanthia, of authors [not Guenée, 1852]

Notoplusia Schaus, 1901
Chadisra, of authors [not Walker, 1862]
Crinodes, of authors [not Herrich-Schäffer, 1855]
Rincodes Schaus, 1901, NEW SYNONYMY

Nystalea Guenée, 1852
Antiopha, of authors [not Schaus, 1901]
Congruia Dyar, 1908
Cyrrhesta Walker, 1857b
Eunystalea Grote, 1895
Heterocampa, of authors [not Doubleday, 1841]
Proelymiotis Schaus, 1901

Phedosia Möschler, 1878
Bardaxima, of authors [not Walker, 1858b]

Phyllopalpia Drautz, 1932
Antiopha, of authors [not Schaus, 1901]

Poresta Schaus, 1901, REVISED STATUS
Edema, of authors [not Walker, 1855]
Proelymiotis, of authors [not Schaus, 1901]
Nystalea, of authors [not Guenée, 1852]
Strophocerus, of authors [not Möschler, 1883]

Strophocerus Möschler, 1883
Antiopha, of authors [not Schaus, 1901]
Nystalea, of authors [not Guenée, 1852]
Poresta, of authors [not Schaus, 1901]

NYSTALEINAE [SENSU LATO]
Bahaia Dyar, 1924
Betolia of authors [not Schaus 1901]

Dasylaphia Packard, 1864
Drymonia, of authors [not Hübner, 1819]
Edema, of authors [not Walker, 1855]
Elymiotis, of authors [not Walker, 1857b]
Heterocampa, of authors [not Doubleday, 1841]
Oedemasia, of authors [not Packard, 1864]
Phalaena, of authors [not Linnaeus, 1758]
Proelymiotis of authors [not Schaus, 1901]
Symmerista, of authors [not Hübner, 1821]
Didugua Druce, 1891  
Euharpyia Schaus, 1901  
Lusura Walker, 1855  
  Tifama Walker, 1855  
  Chaetognatha Felder, 1874  
Notela Schaus, 1901  
Pentobesa Schaus, 1901  
  Edema of authors [not Walker, 1855]  
  Betola Schaus, 1901  
  Nycterotis, of authors [not Felder, 1874]  
  Proelymiotis of authors [not Schaus, 1901]  
  Symmerista of authors [not Hübner, 1821]  
  Tifama of authors [not Walker, 1855]  
Symmerista Hübner, 1821  
  Edema Walker, 1855

Table 2. List of other notodontid genera and species examined. Classification follows Forbes (1935), Weller (1989), Miller (1991), and Miller and Otero (1994).

<table>
<thead>
<tr>
<th>Subfamily:</th>
<th>Genus species</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>DIOPTINAE</strong></td>
<td></td>
</tr>
<tr>
<td>Dioptini</td>
<td></td>
</tr>
<tr>
<td><em>Dioptis trailii</em> Butler</td>
<td></td>
</tr>
<tr>
<td><em>Phryganidia californica</em> Packard</td>
<td></td>
</tr>
<tr>
<td>Josiini</td>
<td></td>
</tr>
<tr>
<td><em>Erbessa unimacula</em> (Warren)</td>
<td></td>
</tr>
<tr>
<td><em>Josia</em> sp.</td>
<td></td>
</tr>
<tr>
<td><em>Scotura nervosa</em> Schaus</td>
<td></td>
</tr>
<tr>
<td><strong>DUDUSINAE</strong></td>
<td></td>
</tr>
<tr>
<td><em>Dudusa sommeri</em> (Hübner)</td>
<td></td>
</tr>
<tr>
<td><em>Crinodes bellatrix</em> Stoll</td>
<td></td>
</tr>
<tr>
<td><em>Crinodes</em> sp.</td>
<td></td>
</tr>
<tr>
<td><strong>HEMICERATINAE</strong></td>
<td></td>
</tr>
<tr>
<td><em>Antaea juturna</em> Cramer</td>
<td></td>
</tr>
<tr>
<td><em>Apela strigmatula</em> Forbes</td>
<td></td>
</tr>
<tr>
<td><em>Apela</em> sp.</td>
<td></td>
</tr>
<tr>
<td><em>Hapigia curvilinea</em> Schaus</td>
<td></td>
</tr>
<tr>
<td><em>H. nodicornis</em> Guenée</td>
<td></td>
</tr>
<tr>
<td><em>Hemiceras near pallidula</em> Guenée</td>
<td></td>
</tr>
<tr>
<td><em>Hemiceras</em> sp.</td>
<td></td>
</tr>
</tbody>
</table>
HETEROCAMPINAE
Heterocampini

Heterocampa astarte Doubleday
H. astartoides Benjamin
H. guttivitta (Walker)
Stauropini

Stauropus fagi (Linnaeus)

Tribal affiliation unknown

Chadisra bipars Walker
Chadisra sp.
Disphragis notabilis (Schaus)
D. tharis (Stoll)
Farigia sp.
Heorta roseoalba Walker
Litodonta hydromeli Harvey
Malocampa bolivari (Schaus)
Pamcoloma marita Schaus
Rhuda dimidiata (Herrich-Schäffer)
R. focula (Cramer)
R. splendens (Druce)
Rifargia lineata (Druce)
Rifargia near mortis Schaus
Rifargia near onerosa Schaus
Talmeca perplexa Schaus
Urgedra striata Druce

NOTODONTINAE
Dicranurini

Cerura vinula (Linnaeus)

Notodontini

Pheosia gnoma (Fabricius)
P. tremula (Clerck)

PHALERINAE

Datana ministra (Drury)
Nadata gibbosa (J.E. Smith)

PYGAERINAE

Clostera curtula (Linnaeus)

THAUMETOPOEINAE

Gazalina sp.
Thaumetopoeia processionea (Linnaeus)
INCERTAE SEDIS

Anurocampa mingens Herrich-Schäffer
Canodia difformis Herrich-Schäffer
Lirimiris lignitecta Walker
Lirimiris sp.¹
Lobeza Smithi Druce
Zelica myops (Felder)
Zelica zelica (Stoll)
Zelica sp.

¹ Miller (1991) places Hemiceratini and Lirimiris as incertae sedis

Table 3. Summary of specimens dissected. Classification follows Miller (1991) (M = male, F = female, g = genitalic preparation, w = whole body preparation).

<table>
<thead>
<tr>
<th>Taxon</th>
<th>No. of Genera</th>
<th>No. of Species</th>
<th>No. of Preparations</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Total</td>
<td>Examined</td>
<td>Total</td>
</tr>
<tr>
<td>Nystaleinae</td>
<td>31(25)¹</td>
<td>31</td>
<td>253</td>
</tr>
<tr>
<td>Heterocampinae</td>
<td>37</td>
<td>30(3²)</td>
<td>398</td>
</tr>
<tr>
<td>Hemiceratini</td>
<td>11</td>
<td>7</td>
<td>287</td>
</tr>
<tr>
<td>Dioptinae</td>
<td>40</td>
<td>3</td>
<td>400</td>
</tr>
<tr>
<td>Notodontinae</td>
<td>9³</td>
<td>1(2²)</td>
<td>14³</td>
</tr>
<tr>
<td>Dudusinae</td>
<td>7+¹</td>
<td>2</td>
<td>93+¹</td>
</tr>
<tr>
<td>Phalerinae</td>
<td>6+¹</td>
<td>5</td>
<td>88+¹</td>
</tr>
<tr>
<td>Pygaerinae</td>
<td>?²</td>
<td>1</td>
<td>?²</td>
</tr>
<tr>
<td>Lirimiris</td>
<td>1</td>
<td>1</td>
<td>16</td>
</tr>
<tr>
<td>Thaumetopoeinae</td>
<td>23</td>
<td>2</td>
<td>100</td>
</tr>
</tbody>
</table>

¹ 25 genera after revision (Weller, 1989)
² Old World taxa
³ New World taxa only
⁴ Estimates tentative or unavailable (= ?) (Miller 1991)
University Museum, Oxford University, Oxford, England; VOB, V.O. Becker, private collection, Brasilia, Brazil; ZMHB, Zoologisches Museum an der Humboldt-Universität zu Berlin, DDR-Germany (H.J. Hannemann). Figures list the museum collection and source slides or whole body preparation numbers (e.g., AMNH genitalia preparation SJW219).

**Terminology**

Terminology for genitalic structures follows Forbes (1948), Sibatani et al. (1954), Sibatani (1972), and Klots (1970), except where I propose new terms. Terminology for the tympanum follows Richards (1932), Forbes (1916), and Kiriakoff (1950a), with reinterpretations of some structures. A lexicon and definitions of terms applicable to notodontid morphology is provided.

**Morphology and Discussion**

**Head (Figures 1-3)**

The notodontid vertex is usually tightly scaled. Ocelli are present in some species (Forbes, 1948), but can be absent (e.g., *Litodonta hydromeli*: Heterocampinae). Often, a broad band of demelanized cuticle connects the ocelli across the vertex. In most species, the ocelli are located dorsal to the antennal scape and bordering the compound eyes (Fig. 1). The compound eyes are well developed, and the ocular index (frons width/eye height) (Davis, 1975) ranges from 0.25 (*L. hydromeli*) to 1.0 (*Gazalina* sp.: Thaumetopoeinae) (Table 4). That is, *L. hydromeli* has very large eyes, and *Gazalina* sp. has very small eyes. Presumably, the ocular index and similar measures (eye width/frons width; Ferguson, 1985) reflect degree of night vision acuity. I have not surveyed intraspecific or intrageneric variation. Ferguson (1985) found that eye size may vary seasonally and geographically in arctiids.

The ventral border of the compound eyes and ventrum of the occiput often have long scales and hairs that partially cover the lower eye portion.

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![Figure 1. Descaled head of *Rifargia lineata* (NMNH 43,488, male). A. lateral view; B. frontal view. a = antenna, e = epipharynx, o = ocellus, p = pilifer, pr = proboscis. (Scale = 1.0 cm)](attachment:figure1.png)
Table 4. Mouthpart structure development in the Notodontidae. a = absent, b = bumps, f = female, F/E = frons/eye ratio, ls = lacks setae, m = male, me = membranous, r = reduced, s = short, sc = sclerotized, se = setae present, prep# = dissection number, wd = well-developed, v = vestigial, vs = very short, + = present, - = absent.

<table>
<thead>
<tr>
<th>Genus species</th>
<th>Prep#</th>
<th>Frons width (F(mm))</th>
<th>Eye diameter (E(mm))</th>
<th>F/E</th>
<th>Pilifer</th>
<th>Proboscis</th>
<th>Maxillary palps</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>No. of segments</td>
</tr>
<tr>
<td>Calledema sp.</td>
<td>f346</td>
<td>1.0</td>
<td>1.92</td>
<td>0.52</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Cerura vinula</td>
<td>m340</td>
<td>1.12</td>
<td>2.00</td>
<td>0.56</td>
<td>ls</td>
<td>vs</td>
<td>a -</td>
</tr>
<tr>
<td>Chadisra bipars</td>
<td>m437</td>
<td>0.72</td>
<td>1.72</td>
<td>0.42</td>
<td>+</td>
<td>vs</td>
<td>1 me</td>
</tr>
<tr>
<td>Crinodes sp.</td>
<td>m449</td>
<td>1.68</td>
<td>3.24</td>
<td>0.52</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Dasylophia anguina</td>
<td>m340</td>
<td>0.80</td>
<td>1.72</td>
<td>0.47</td>
<td>+</td>
<td>s</td>
<td>1 me</td>
</tr>
<tr>
<td>Dudusa sommeri</td>
<td>m443</td>
<td>1.36</td>
<td>2.32</td>
<td>0.59</td>
<td>+</td>
<td>wd</td>
<td>2 me</td>
</tr>
<tr>
<td>Elasmia pronax</td>
<td>m426</td>
<td>0.86</td>
<td>2.32</td>
<td>0.37</td>
<td>+</td>
<td>wd</td>
<td>2 me</td>
</tr>
<tr>
<td>Elymiotis ancora</td>
<td>m347</td>
<td>1.56</td>
<td>2.36</td>
<td>0.66</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Farigia sp.</td>
<td>m258</td>
<td>0.68</td>
<td>1.56</td>
<td>0.44</td>
<td>+</td>
<td>v</td>
<td>1 me</td>
</tr>
<tr>
<td>Gazalina sp.</td>
<td>f445</td>
<td>1.36</td>
<td>1.36</td>
<td>1.00</td>
<td>b</td>
<td>a</td>
<td>a -</td>
</tr>
<tr>
<td>Gopha mixtipennis</td>
<td>f363</td>
<td>0.72</td>
<td>1.48</td>
<td>0.49</td>
<td>+</td>
<td>wd</td>
<td>1 s</td>
</tr>
<tr>
<td>G. mixtipennis</td>
<td>m364</td>
<td>0.92</td>
<td>1.64</td>
<td>0.56</td>
<td>+</td>
<td>wd</td>
<td>1 s</td>
</tr>
<tr>
<td>Hapigia nodicornis</td>
<td>m229</td>
<td>1.92</td>
<td>2.92</td>
<td>0.66</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Hemiceras sp.</td>
<td>m262</td>
<td>1.36</td>
<td>1.76</td>
<td>0.77</td>
<td>+</td>
<td>wd</td>
<td>1 me,r</td>
</tr>
<tr>
<td>Josia sp.</td>
<td>f259</td>
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<td>0.98</td>
<td>0.80</td>
<td>+</td>
<td>wd</td>
<td>1 ss</td>
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<td>Litodonta hydromeli</td>
<td>m352</td>
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<td>1.76</td>
<td>0.25</td>
<td>vs</td>
<td>v</td>
<td>1 me,r</td>
</tr>
<tr>
<td>Lysana plexa</td>
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<td>2.08</td>
<td>0.63</td>
<td>+</td>
<td>wd</td>
<td>1 s</td>
</tr>
<tr>
<td>Nadata gibbosa</td>
<td>m355</td>
<td>0.80</td>
<td>1.80</td>
<td>0.44</td>
<td>+</td>
<td>v</td>
<td>1 me</td>
</tr>
<tr>
<td>Notoplusia clara</td>
<td>m349</td>
<td>0.96</td>
<td>1.80</td>
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<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Nystalea sp.</td>
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<td>2.80</td>
<td>0.57</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Pentobesa basitincta</td>
<td>m395</td>
<td>0.92</td>
<td>1.76</td>
<td>0.42</td>
<td>+</td>
<td>s</td>
<td>1 me</td>
</tr>
<tr>
<td>Pentobesa xylinoides</td>
<td>m341</td>
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<td>2.12</td>
<td>0.57</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Rifargia sp.</td>
<td>m261</td>
<td>1.44</td>
<td>2.20</td>
<td>0.65</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Stauropus fagi</td>
<td>m438</td>
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<td>1.68</td>
<td>0.60</td>
<td>s</td>
<td>b</td>
<td>a -</td>
</tr>
<tr>
<td>Zelica zelica</td>
<td>m451</td>
<td>0.72</td>
<td>1.48</td>
<td>0.49</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
<tr>
<td>Zelica sp.</td>
<td>m452</td>
<td>1.0</td>
<td>1.52</td>
<td>0.66</td>
<td>+</td>
<td>wd</td>
<td>1 me</td>
</tr>
</tbody>
</table>

Whether the head vestiture is loose and "fuzzy" or tightly scaled varies between genera, but rarely within monophyletic genera.

Notodontid mouthparts can be absent, vestigial or weakly developed (Forbes, 1948; Bourgogne, 1951; Miller, 1991). For many holarctic species, cerurines and thaumetopoeines, vestigial or weak mouthparts are typical. However, the proboscis is well developed in most tropical notodontids including most Nystaleinae. Maxillary palpi are usually present, but in Gazalina are absent. They may be one- or two-segmented (Table 4) and either sclerotized or...
membranous. The pilifer may be vestigial or well developed with stout setae (Fig. 1B). The size of the epipharynx varies, and its shape can be rectangular, bilobed, or round. When the proboscis is vestigial, associated structures are usually vestigial. Functional mouthparts indicate that adults probably feed and live a long time.

Labial palpi are usually three-segmented, and normally, the length of the third segment is approximately two-thirds the length of the second. However, the third segment can be much longer or much shorter (Fig. 2A-D), or the labial palpus can be reduced to two segments (Miller, 1991). As in most Lepidoptera, the organ of vom Rath is well developed. Typically, labial palpi are tightly scaled, although loose, long hairs can emanate from the first segment.

Notodontid antennae tend to be sexually dimorphic, with males possessing more complicated antennal structures (e.g., pectinations, cilia) than females (e.g., shorter cilia, scattered setae). Occasionally, antennae are monomorphic (Gopha mixtipennis Walker). Individual antennal segments can be cylindrical, bulbous or prismatic and an antenna may be composed of a combination of segment types. Segment shape and structure can vary between and within genera. Some examples of antennal variation are shown in Figure 3.

The antennal scape of most notodontids is rounded, although it can be elongate. In some species, compact clusters of scales arise from the scape. Forbes (1948) referred to these as antennal tufts. Antennal tufts may be either short and blunt-tipped (Lirimiris Walker), triangular (Hemiceras Guenée), or long, (e.g., Nystalea, Phedosia, Pentobesa, Dasylophia).

In males of Hapigia Guenée, the antennal scape and first segment are greatly modified. The first segment is greatly expanded and bowl-shaped. The pedicel is membranous dorsally and forms a hinge between the scape and first segment. The first segment locks into a groove on the scape, folding the distal part of the antenna over the back (Fig. 3F).

Thorax (Figures 4-6)

The thorax is usually covered dorsally with moderately long scales and ventrally with long scales and hairs. The most obvious modifications occur on the prothorax and metathorax. Mesothoracic sclerites did not appear to vary among taxa.

Prothorax. The patagia are usually sclerotized and covered with scales. They are thought to be homologous with the membranous warts of Trichoptera (caddisflies) (Kristensen, 1984). Caudal to these, a second set of membranous or weakly sclerotized structures occurs in most species (Fig. 4a). These appear to be homologous with the noctuid parapatagia (Osco and Helms, 1976). Development of parapatagia varies, and they are easily damaged when preparing a whole-body dissection. They are present in both sexes. Occasionally, a second, weakly developed, lateral pair of parapatagia occurs next to the spiracle (not illustrated, e.g. Gazalina). Dudusa sommeri (Dudusinae) appears to
possess a derived condition where parapatagia are absent and the patagia are enlarged and heavily sclerotized.

**Mesothorax and metathorax.** No variation was observed in most sclerites comprising these segments. The metathoracic furcae show some variation, and tympanal studies indicate that some thoracic novelties (e.g., double pocket IV, *Hemiceras* sp.) may be species-specific.

**Tympanum and associated structures** (Figs. 5, 6). As in other noctuids, the notodontid tympanum occurs on the metepimeron. Notodontids are unique in that the tympanum is recessed; the tympanal membrane faces ventrally (Forbes, 1916; Richards, 1932; Sick, 1940; Kiriakoff, 1950a, 1950b, 1950c; Miller, 1991). The notodontid tympanal membrane lacks the nodular sclerite (Richards, 1932), and sclerotized abdominal hood associated with tympana in many Noctuidae, Arctiidae and Lymantriidae. In nearly all neotropical and some nearctic notodontids, the first abdominal spiracle occurs in a sclerotized, bowl-like depression which may act as a sound collector. In many holarctic species, the bowl is either weakly sclerotized or membranous. The genera *Hapigia* and

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**Figure 2** Labial palpi (distal at right). A. *Notoplusia minuta*; B. *Nystalea virgula*; C. *Caledema jocasta*; D. *Nystalea corrusca*. vR = vom Rath's organ. (Scale = 1.0 mm)
Figure 3 Antennal variation. A. *Notoplusia clara*, male, (bipectinate); B. enlarged segment showing pectinations and cilia; C. *Notoplusia clara*, female (scattered setae); D. *Elymiotis ancora*, male (ciliate); E. *Canodia difformis*, male (unequally pectinate); F. *Hapigia nodicornis*, male, showing basal enlargement. (Scale = 1.0 mm)
Figure 4 Prothorax of *Hapigia curvilinea*. A. side view, anterior at left; B. posterior view with right scent brush flap removed. cs = cervical sclerite, d = dorsal plate of pronotum, f = furca, L = lumen, p = patagium, pc = precoxale, pp = parapatagium, pe = proepimeron, s = spina, Q = reinforced fusion point of furca, cervical sclerite, and proepimeron, X = modified membranous flap, so = putative scent organ, ss = scent scales. (Scale = 1.0 mm)
Antaea possess a large, membranous, pleural hood inflated with hemolymph that surrounds this sclerotized bowl. With isolated ear preparations, Fullard (1984) demonstrated that the pleural hood helps to localize sound waves, and that it increases the moth’s ability to detect the direction of incoming signals.

The internal morphology of the notodontid tympanum has been described by Richards (1932) and Kiriakoff (1950a,b), but their interpretations conflict. Richards (1932) described tympana for the major noctuid families, concentrating on Noctuidae. His terminology is generally applicable to notodontids.

For notodontids, Richards concluded that pockets I and II were small, pocket III was absent and pocket IV was present. He examined three nearctic species (Datana angusi Grote & Robbinson: Heterocampinae, Heterocampa guttivitta Walker: Heterocampinae, Clostera inclusa Hübner: Pygaerinae) and two neotropical species (Zelica zelica: Pygaerinae, Malocampa near sorex: Heterocampinae). Re-examination of H. guttivitta shows that Richards misinterpreted the notodontid pockets. From his diagram (plate 10: Richards, 1932), it is apparent that he did not rotate the thorax sufficiently to view the pockets. Internally, notodontid tympana are very different from those of noctuids. The recessed tympanic membrane obscures the pockets, and pocket orientation is skewed. Using position and orientation of pocket openings as criteria of homology, I conclude that pockets I, III and IV are present in most notodontids, and that pocket II is often absent. Pocket II is sometimes difficult to see even when it is present. The notodontid structure that I interpret as pocket III, and that Richards termed pocket II, is positioned at the ventral rim of the tympanic membrane, with its opening into the body cavity facing dorsally (e.g., Fig. 5A).

Kiriakoff used tympanal studies to classify Notodontidae (e.g., Kiriakoff, 1950a, 1950b, 1950c), stressing different shapes of scutal phragma (“type notodontoid” vs. “type phalenoide”) and tympanal structures, but Kiriakoff’s tympanal interpretations were sometimes inconsistent. Distortion caused by preparing and viewing the thorax may explain discrepancies. For example, Kiriakoff described Bardaxima marcida Felder and Gisara proene Schaus as having differently shaped tympanal cavities (Kiriakoff, 1950c). Gisara is a junior synonym of Bardaxima (Weller 1989; Table 1), and the tympanal cavities of these two species are practically identical. Kiriakoff also disagreed with Richard’s interpretation of tympanal structures and renamed pocket IV: “le support posterior” (Kiriakoff, 1950a, 1950c). Notodontid pocket IV is usually open with its edges defined by an anterior and posterior internal ridge that extend from the tympanal cavity (timbal sensu Kiriakoff) to the furcal suture (Fig. 5: IVa, IVp). The anterior ridge (IVa) can be reduced or absent as in several notodontids that Kiriakoff examined (Kiriakoff 1950a, 1950c). In Crinodes Herrich-Schäffer, pocket IV is closed (Fig. 5E) like those of
Figure 5 Internal view of notodontid metathoracic tympana, anterior at right. A. *Rifargia lineata*; B. *Elymiotis ancora*; C. *Antiopha multilinea*; D. *Elasmia astuta*; E. *Crinodes* sp. I = pocket I, II = pocket II, III = pocket III, IV = closed pocket IV, IVa = anterior strut of open pocket IV, IVp = posterior strut of open pocket IV, p = anterior branch pocket of IV, r = pre-epimeral/epimeral ridge, rp = ridge pocket, t = tympanal membrane, tc = tympanal cavity. (Scale = 1.0 mm)
Noctuidae, supporting the homology of the posterior ridge of pocket IV and Kiriakoff’s “support posterior.”

A feature of pocket IV not mentioned by Kiriakoff is the tendency for a small pocket (p) to form on the dorsal end of the anterior support abutting the tympanal cavity (Fig. 5). This additional pocket can be elaborate as in some \textit{Hemiceras}. Also, the degree of divergence between the anterior and posterior supports of pocket IV differs among species. They are normally at acute angles, but can also be at right angles to one another (e.g. \textit{Pentobesa basitincta} Dognin).

In addition to pocket IV, the pre-epimeron/epimeron boundary is often modified in notodontids. There may be a simple internal ridge or a pocketlike structure (Fig. 5A-E) that originates at the tympanal cavity and extends anteriorly. Kiriakoff termed this structure “support anterior de la timbale” (Fig. 5, r). This support occasionally fuses with the anterior edge of pocket IV as in \textit{Anurocampa mingens} (Kiriakoff, 1950c: his fig. 11). This epimeral pocket and dorsal pocket of the anterior branch of pocket IV may provide additional resonating chambers.

Extensive tympanal variation occurs in the dioptines and thaumetopoeines (Richards, 1932; Sick, 1940). Many dioptines are brightly colored, mimetic and probably diurnal (Hering, 1925; Miller and Otero, 1994). The tympanum may be well developed, or reduced and rudimentary. In the five dioptine species examined, pocket II is absent in all, pocket III is absent in most, and pockets I and IV are absent when the tympanal cavity is rudimentary. In \textit{Scotura nervosa}, \textit{Josia} sp., and \textit{Erbessa unimacula}, pockets I and IV are present and well developed, but pockets II and III are absent (Fig. 6A-C). These species also have a well-developed tympanal concavity that Richards referred to as a kettledrum structure (Richards, 1932: 38). This tympanal type is restricted to a subset of dioptine genera (Sick, 1940; Kiriakoff, 1950a; Miller and Otero, 1994). Miller and Otero (1994) use the presence of this kettledrum tympanal cavity to recognize the Josiini, formerly the Josiinae of Kiriakoff (1950a) and group V of Sick (1940).

The remaining dioptine genera are placed in the Dioptini (Miller and Otero, 1994), because they lack the kettle-drum type cavity. Reduced tympana in dioptines can occur in various ways. In \textit{Dioptis trailii}, all pockets are absent, and the tympanal cavity is represented by a membranous bulge supported by a weakly sclerotized frame. In \textit{Phyrganidia californica}, pocket I is modified and resembles a horizontal, lateral bridge (Fig. 6D). There is a hint of pocket III, and pocket IV is reduced. The tympanal cavity is extremely shallow, and the tympanal membrane is large (Fig. 6D). An external view of this tympanum is illustrated in Miller (1987). Illustrations of internal views of reduced dioptine tympana can be found in Richards (1932), Sick (1940), and Kiriakoff (1950a). I interpret the missing pockets as secondary reductions rather than as primitive absence because Dioptinae are a derived element within Notodontidae (Minet, 1983; Weller, 1989; Miller, 1991).
I also examined one thaumetopoeine, *Thaumetopoea processionea*. It possesses a large, bowl-like tympanal cavity. Pocket I is represented by a slender bridge, pockets II and III are absent, and pocket IV is reduced (not figured). Whether pocket number and size represent secondary reduction or primitive absence is not known.

**Legs (Figures 7-8)**

**Prothoracic Leg.** Modifications of the notodontid prothoracic leg are often sexually dimorphic, with androconial hairs (Table 5). In many Nystaleinae, males possess a prothoracic femur and tibia with modifications typical of pheromone production and dispersal (Figs. 7, 8). The lateral inner surface of the femur has one (e.g., *Bardaxima, Calledeema*; Figs. 7B, 8A) or two (e.g., *Nystalea*; Fig. 8B) elliptical, slightly concave areas of membranous cuticle covered with woolly hairs and surrounded by flat, truncate scales with wide lamellae characteristic of androconia (McColl, 1969). Longer hairs overlay these shallow, glandular pockets. Near the proximal articulation of the tibia, a cluster or “pencil” of long scales occurs on a raised patch of cuticle. This pencil lays in a flattened
Figure 7 Modifications of male legs. A-C. Prothoracic femur and tibia; A. *Urgedra striata* (normal condition); B. *Bardaxima* sp. (single pocket condition); C. *Apela* sp. (ventral femoral pocket condition); D. *Strophocerus cossoides*, male metathoracic tibial spur serrations. s.o. = putative scent organ, e = epiphysis. (Scale = 1.0 mm)
Figure 8 Other leg modifications of males. A-C. Prothoracic femur and tibia; A. Calledema sp. (single pocket); B. Nystalea aequipars (double pocket). C. Lysana plexa; D. Lysana plexa (mesothoracic tibia). s.o. = putative scent organ, e = epiphysis, b = distributing pencil. (Scale = 1.0 mm)

area or groove on the ventral, tibial surface, and extend to the first tarsal segment in some species. In Lysana plexa Möschler, the surface underlying the tibial hair pencil is also membranous, and the pencil is very large (Fig. 8C).

These femoral organs are analogous to the mesothoracic leg scent organ in some male noctuids (Birch and Hefetz, 1987), and probably have a similar function. Presumably, membranous areas produce short-range pheromones that are distributed by the tibial scent pencil during courtship.

Other modifications of male prothoracic legs can occur. In some species (e.g., Apela sp.: Hemiceratini, Fig. 7C), the femur's ventral edge is
Table 5. Male structures with putative courtship function in neotropical Notodontidae (Pt. = prothoracic, Ms = mesothoracic, Mt = metathoracic, s.s. = scent scales, s.h. = hair-like scent scales, s.p. = scent pencil, SSO = saccular scent organ)

<table>
<thead>
<tr>
<th>Location</th>
<th>Description</th>
<th>Examples</th>
</tr>
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<tbody>
<tr>
<td>Pt femur</td>
<td>one glandular area</td>
<td>Bardaxima</td>
</tr>
<tr>
<td></td>
<td>two glandular areas</td>
<td>Nystalea</td>
</tr>
<tr>
<td>Pt tibia</td>
<td>s.h., s.s. or s.p.</td>
<td>Nystalea, Bardaxima</td>
</tr>
<tr>
<td>Ms femur</td>
<td>s.h., s.s.</td>
<td>Nystalea</td>
</tr>
<tr>
<td>Mt tibia</td>
<td>s.h., s.s.</td>
<td>Hapigia curvilinea</td>
</tr>
<tr>
<td>Mt tibia</td>
<td>tibial spur gibbose</td>
<td>Calledema marmorea</td>
</tr>
<tr>
<td>Hindwing</td>
<td>stigma</td>
<td>many Hemiceras</td>
</tr>
<tr>
<td>Pleuron 3 and 4</td>
<td>glandular area, s.h.</td>
<td>Phedosia turbida</td>
</tr>
<tr>
<td>Sternum 4</td>
<td>cteniophore</td>
<td>many Heterocampinae,</td>
</tr>
<tr>
<td>Sternum 5</td>
<td>peniculus</td>
<td>Hapigia</td>
</tr>
<tr>
<td>Sternum 8</td>
<td>cuticular brush</td>
<td>Calledema marmorea</td>
</tr>
<tr>
<td></td>
<td>posterior edge</td>
<td>Marthula pulchra</td>
</tr>
<tr>
<td>Tergum 8</td>
<td>s.h., s.s.</td>
<td>Lyricinus</td>
</tr>
<tr>
<td>Sacculus</td>
<td>SSO: pleated, glandular,</td>
<td>some Dasylophia</td>
</tr>
<tr>
<td></td>
<td>s.h., s.s.</td>
<td>many notodontids</td>
</tr>
<tr>
<td>Sacculus</td>
<td>Barth valve: sacculus</td>
<td>most Hemiceras</td>
</tr>
<tr>
<td></td>
<td>enfolds s.p.</td>
<td>Hapigia</td>
</tr>
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grooved and surrounded by scent hairs and scales. In Hapigia (Hemiceratini), the mesal surfaces of the femur have a single row of stout setae covered with scales (not shown), and long scent scales emanate from the proximal mesal and posterior edges of the coxae (Fig. 4a). Two scent pencils are associated with an enlarged, pleural membrane that enfolds their base (Fig. 4b: X). The furca, cervical sclerite and a ridge emanating from the proepimeron fuse above the coxa, and provide a reinforced, muscle attachment point (Fig. 4b: Q). The insertion points of the pencils are sclerotized. The scent pencil scales extend along the inner surface of the femur, and fan out when the legs are separated. A portion of the mesal coxal surface is modified into membranous cuticle covered with flat androconia (Fig. 4b: so, ss).

The notodontid epiphysis is usually one-third to one-fourth the length of the tibia, and has a comb of stiff setae (e.g., Nystaleinae, Hemiceratini, some Dioptinae and Heterocampinae), although it may be long and flattened with a rough surface (e.g., some Dasylophia, some heterocampines, Dicranurini and Thaumetopoeinae) (compare Figs. 7A-C; also Marumo, 1920). The tarsi are spinulose, and as in many Lepidoptera, there are usually two long tarsal setae on the distal end of
the fifth tarsomere (Oseto and Helms, 1976). Multiple (usually 4 to 6), long tarsal setae occur in several nystaleine genera (e.g., Nystalea, Elymiotis Walker, and Bardaxima), and number of setae can vary between sexes. Multiple, short tarsal setae occur in Thaumetopoea processionea. Tarsal claws on all legs may be single or bifid (= dentelées: Kiriakoff, 1950a; Weller, 1987, 1989, 1990; Miller, 1991), and their apices smooth or serrate (Janse, 1920; Arru, 1965; Weller, 1987, 1989, 1990, Miller, 1991).

**Mesothoracic Leg.** Usually the femur and tibia are unmodified, and the tibia and tarsomeres are spinulose. Mesothoracic tibiae have one pair of tibial spurs which often have serrations or comblike ridges on their apices (Janse, 1920; Miller, 1991; Fig. 7D). Such tibial spur serrations occur in many notodontids, but they are visible only under high magnifications. They occur in the Dioptinae, but not in Gazalina (Thaumetopoeinae). The same condition is found in Lymantaria Hübner and Dasychira Hübner (Lymantriidae) (Miller, 1991).

**Metathoracic Leg.** In males, the femur and tibia have long hairs and scales arising from the caudal surface. These may disperse pheromones produced from structures on the abdomen (Jordan, 1923) or genitalia (below). There are usually two pairs of tibial spurs, again with tibial spur serrations, but one pair is lost in four unrelated lineages: Thaumetopoeinae, Dicranurini, some Dudusinae and some Heterocampinae (i.e., Stauropus Germar) (Miller, 1991). Again, tibia and tarsomeres are spinulose and tibial spurs often serrate.

**Wings (Figs. 9, 10)**

Wing coloration in Notodontidae tends to be cryptic with subtle patterns (Draudt, 1932). Ground colors of brown or drab green are common, although Dicranurini wings are usually white with black markings. In fresh specimens of Dasylophia sp., the brown and black pattern is overlaid with light greens and pinks that give the forewing a lichen and moss covered appearance. These pigments are unstable and fade by the third year after a specimen has been collected. Wing coloration in Dioptinae ranges from gray (Scotura Walker) or brown (Phryganidia Packard) to bright, mimetic species (e.g., Josia Hübner) (Hering, 1925; Miller and Otero, 1994).

In females, number of frenular bristles tends to be constant within monophyletic lineages. The number of bristles is two in Nystaleineae (except Lusura with three), and three in Hemiceratini (except Apela with two) and Dioptinae surveyed. Number of bristles range from four to six in some Heterocampinae, to many (up to 20) in some Heterocampinae and Thaumetopoeinae (Arru, 1965; Miller, 1991).

Forewing venation sometimes varies within monophyletic genera (e.g., Nystalea), and this has led to splitting by workers who relied solely on wing venation to characterize genera. The forewing areole may be present or absent, and the position of veins R2, R5 and M1 can vary
Figure 9 Forewing veins. A. Bardaxima lucilinea; B. Lysana plexa; C. Lyricinus xylophasioides; D. Caledema rufescens. a = accessory cell, d = discal cell, Sc = subcostal vein, M1-M3 = medial veins, R1-R5 = radial veins, CuA1-CuA2 = cubital veins, A = anal veins.
Figure 10 Hindwing veins. A. *Marthula pulchra*; B. *Scotura nervosa*. d = discal cell, Sc+R1 = subcostal and R1 vein, M1-M3 = medial veins, RS = radial sector, CuA1-CuA2 = cubital veins, A = anal veins.
within genera (Fig. 9; Weller, 1989). Vein M2 usually arises from the midpoint of the discal cell or slightly above. In Dioptinae, M3 and CuA1 are usually stalked (Miller, 1987), a condition not found in other notodontids.

Hindwing venation in notodontids is less variable than forewing venation (Fig. 10). Veins Sc-Rs can be connate, short-stalked or long-stalked. Vein M2 arises from the middle of the discal cell except in *Hemiceras* and allies where the vein appears to have been lost. Veins M3 and CuA1 can be separate, connate or stalked. Again, multiple conditions can occur within monophyletic genera. In *Hemiceras* males, approximately two-thirds of the species (total = 150) have a small patch of specialized scales located on or near vein M3, termed a stigma by earlier authors (e.g., Schaus, 1901).

**Abdomen (Figs. 11-13)**

Modifications of the male second abdominal sternum can occur, and both males and females may have structures for pheromone production and dispersal. Modification of the first abdominal segment is discussed under “Tympanum.”

**Male.** The second abdominal (A2) sternum is usually simple with a faintly de-melanized, semicircular area anteriorly, here referred to as a “window” (Fig. 11A-D). The caudal border of the window is a flexion point. In some genera, these areas are translucent and elaborate (e.g., *Marthula, Elasmia astuta* [Schaus]) (Fig. 11C,D,F), and the cephalic edge is often reinforced. In *Antiopha*, this reinforcement is elaborated into a second set of apodemes (Fig. 11B, E).

The pleural region of A2 and A3 may be expanded with membranous or sclerotized outgrowths bearing hair-like scales (e.g., *Crinodes: Dudusinae, Phedosia: Nystaleinae* (Fig. 12C)). The cteniophore (Jordan, 1923) occurs on A4. It is a large flap with stout spines and internal levers for muscle attachment (Fig. 12A). The cteniophore is reduced in some species (e.g., *Heterocampa guttivitta: Heterocampinae*) and absent in most. On A5 of some *Calleleda* sp. (Fig. 12B), a similar structure occurs. Thiaucourt (1985) named this structure the peniculus (Latin: little tail, tuft) — not to be confused with “penicillus,” a structure on the tegumen of noctuid male genitalia (Forbes, 1954). The peniculus, cteniophore and other modifications of abdominal pleura II and III appear to be serial homologues.

Tergum 8 may be modified externally with androconia (*Dasylaphia* sp.; Fig. 13D), or modified internally for muscle attachments (Fig. 13A-C). Normally, its antecosta is present and well developed. Forbes (1916) showed that in the noctuid *Apamea amputatrix* (Fitch), genitalic retractor muscles (T1 and T2) extend from the eighth antecosta to the tegumen and vinculum. These retractor muscles are widespread in the Lepidoptera (e.g., Forbes, 1939b; Stekolnikov, 1967; Stekolnikov and Kuznetsov, 1986; Tikhomirov, 1979). In Nystaleinae and several addi-
Figure 11 Male second abdominal sternum. A. *Elasmia astuta*; B. *Antiopha discreta*; C. *Marthula pleione*; D. *Marthula griscesens*; E. *Antiopha multilinea*; F. *Kryptokalos cilia*. a = antecostal apodeme, w = window. (Scale = 1.0 mm)

tional neotropical genera, the antecosta is weak or absent. Tergum 8 is usually medially divided with either a mid-dorsal plate or paired ridges for muscle attachment (Fig. 13A-D). Presumably, the T1 and T2 muscles have shifted their insertion from the cephalic edge to the mid-dorsal region of the tergum in these species. This shift appears to be correlated
Figure 12 Male abdominal structures with probable courtship function. A. Sternum 4, cteniophore (*Hapigia* sp.); B. Sterna 4 and 5, peniculus (*Calledeema jocaste*); C. Tergum 2 (*Lysana plexa*). ct = cteniophore, p = peniculus. (Scale = 2.0 mm)
with development of a long intrapleural membrane between the eighth segment and genital capsule (Miller, 1991).

Modifications of sternum 8 are often species-specific in Notodontidae (e.g., Francelmont, 1946; Forbes, 1948; Miller, 1987; Weller, 1990, 1992). Shape of the antecosta varies between and occasionally within monophyletic genera. In addition, hair-like androconia may be associated with membranous areas caudal to the antecosta. Such structures are found in some Phalerinae and Heterocampinae (Forbes, 1948). As in the tergum, lateral ridges and caudal structures of sternum 8 appear to provide sites for muscle attachment (Fig. 13E). Sternum 8 can bear a diversity of species-specific structures on the caudal edge. These range from a simple, glandular surface with hair-like scales (Lepasta, Fig. 14) to complex cuticular evaginations (Marthula, Fig. 15).

**Female.** Abdominal segments are rarely modified. Sternum 7 may have a patch of scent scales overlaying setae (e.g., Dasylophia maxtila

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**Figure 13** Male eighth terga and parallel ridge condition of sternum 8 (anterior at top).  
A. Tergum 8 (Ankale maonica); B. Tergum 8 (A. viridis); C. Tergum 8 (A. grammodos); D. Tergum 8 (Dasylophia sp.); E. Sternum 8 (Dasylophia sp.).  
br = brush, m = midplate, ma = muscle attachment, r = internal ridge. (Scale = 1.0 mm)
[Schaus]). In thaumetopoeines, sternum and tergum 7 form a continuous, lightly sclerotized ring that is covered with stiff deciduous hairs and scales. These scales may be a contrasting color (black or gold), and this "boule de laine" has been cited as a synapomorphy for the group (Kiriakoff,
1969). However, the same modification also occurs in females of Lobeza Herrich-Schäffer, a large, neotropical species (male wingspan 63 mm, female 91 mm). Male genitalia and the larva (BMNH) of L. Smithi Druce are characteristic of Heterocampinae, suggesting that the continuous seventh tergal-sternal ring has evolved independently in Lobeza and thaumetopoeines.
Genitalia (Figs. 16-22)


Genitalia: Male

Tegumen and vinculum (Figs. 16, 17). In Nystaleinae, the two halves of the vinculum are partially fused, and a sclerotized, caudal extension covers the base of the sacculus (Fig. 16). In most notodontids, the vinculum is rounded and the halves not fused.

When the tegumen and vinculum are fused, two nonhomologous conditions are found. In many neotropical notodontids, the tegumen-vinculum connection is fused in an S-shaped configuration (Fig. 16B). The other condition is typified by the holarctic genus Pheosia (Notodontinae). Here, the tegumen and vinculum form a single, fused C-shaped structure (Fig. 16D) presumably to support massive valves that articulate with it.

The uncus-tegumen juncture varies extensively (Fig. 17). The uncus and tegumen are sometimes completely fused, and have reinforcing, internal apodemes extending from the uncus into the tegumen (Fig. 17C,D). Apodeme shape and degree of fusion also varies. Apodemes may be absent, in which case the uncus base connects to the tegumen by a hinge of pleural membrane (e.g., Calledema rufescens Schaus). Usually, the tegumen-uncus connection is characteristic for a genus, but within Calledema, several configurations exist.

Uncus shape may or may not be characteristic for a genus. In some nystaleine genera, the distal process becomes membranous and setose (e.g., Elymiotis, Poresta). In some Nystalea, the distal process is curved and thin with an enlarged tip (Figs. 16A-C).

Above the anal tube and tegumen-uncus suture, paired, setose structures articulate on the venter of the uncus in Nystaleinae and many other notodontids (Figs. 16, 17). Kiriakoff called these structures gnathi (e.g., Kiriakoff, 1981), but Kiriakoff’s use of the term is inconsistent with both Pierce (1914) and common usage. Pierce described the gnathos as a “free ring, enclosing the anus,” and reserved the term socii for hairy pads arising from the base of the uncus. Forbes (1923) applied the term gnathos to part of the subscaphium located below the anal tube. Klots (1970), following Pierce, suggested that the gnathos is derived from the caudal edge of the uncus and glabrous, whereas socii were derived from the uncus base and setose. In several notodontid species, these setose structures are fused to the base of the uncus (e.g., Phalerinae). The term socii appears to be most appropriate for these structures.

Valve (Figures 16, 18, 19). The valve in many species of neotropical notodontids (e.g., some Heterocampinae, most Nystaleini (sensu Miller, 1991), Pentobesa, many Dioptrinae and Hemiceratini) have a membranous, highly pleated sacculus (= corrugated sacculus; Holloway, 1983)
Figure 16 Male genitalia. A. *Nystalea aequipars*; B. caudal view of tegumen, vinculum and sociuncus of *Nystalea virgula*, valve removed; C. right valve of *Nystalea virgula*; D. *Pheosia tremula*, valvae removed. cl = costula, co = costa, cr = coronalike structure, mvs = midvalve sclerotization, sb = sclerotized base of sacculus, s = socius, sso = saccular scent organ, t = tegumen, t-v = tegumen-vinculum junction, u = uncus, v = vinculum, vl = valvula. (Scale = 1.0 mm)
Figure 17 Dorsal view of uncus-tegumen attachment. A. *Elymiotis ancora*; B. *Gopha mixtipennis*; C. *Poresta joanna*; D. *Nystalea aequipars*. ia = internal apodemes, t = tegumen, ub = uncus base. (Scale = 1.0 mm)
A mix of long hair-like and spatulate scales arises from its base. Barth (1955) demonstrated that a gland is located within the sacculus of *Hemiceras proximata* Dognin, and suggested that it produces pheromones. I refer to the pleated sacculus with associated hairs as the **saccular scent organ (SSO)** (Weller, 1989, 1990). Although pheromone producing organs and androconia are often associated with male genitalia (e.g., coremata of Arctiidae), this is an unusual example of the primary genitalic structures being themselves pheromone-producing. Typically, a sclerotized band separates the SSO from the rest of the valve. This midvalve sclerotization (Weller, 1990) appears to divide the valve into costal and saccular compartments. This sclerotization can be expanded as in *Pentobesa* or *Bardaxima*. Occasionally, the midvalve sclerotization is reduced and the SSO is not distinct from the remainder of the valve (e.g., *Lysana plexa*: Nystaleinae; *Disphragis tharis, Rifargia lineata*: Heterocampinae). In these, the flattened SSO does not expand as greatly. In some species, a modified saccular base occurs in the presence of an SSO. Here, a small hook or ridge is present that presumably provides an anchor for the valval flexor muscles (M5: Forbes, 1939b; Tikhomirov, 1979).

The SSO is variously developed within and between genera. It can be greatly enlarged as in *Marthula* and many Dioptinae. In some species of the Hemiceratini (e.g., *Hapigia, most Hemiceras*), the sacculus is greatly elaborated and enfolds a large scent pencil (Fig. 18). I refer to this

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**Figure 18** Male genitalia of *Hemiceras constellata* showing the Barth valve. A. Genitalia with right valve removed; B. Right valve. B = Barth valve (= sacculus), co = costa, vl = valvula.
complicated SSO as the Barth valve, in honor of Dr. R. Barth and his pioneering studies on the Brazilian fauna.

The SSO can also be reduced in a variety of non-homologous conditions. In Pentobesa and some members of the Dasylophia-group, the SSO is usually moderately developed, the pleats are less numerous than in nystaleines, and the sacculus is smaller. Pleats are completely absent in some representatives of the Dasylophia-group, and the sacculus is sclerotized (e.g., D. colimata Dyar, Fig. 19).

In many notodontids, the costa is a massive structure with various projections along its length. These are uncommon in Nystaleinae. The costa of nystaleines is usually a thin, sclerotized rod that may or may not extend completely to the apex of the valve. In Nystalea, the dorsal edge is sclerotized for two-thirds the length of the valve and widens into a characteristic shape (Figs. 16A, 16C). Beyond this widening, the distal portion is membranous with short setae and stiff hairs analagous to a noctuid corona (Forbes, 1954).
In nystaleines, some hemiceratines, and some heterocampines, a sclerotized process arises proximally from the dorsal edge of the costa, and extends into the anellus. Muscle attachments occur at its base (Fig. 16). Presumably, these structures, in conjunction with the socii, uncus and costa, provide traction in copula. Forbes (1948) suggested that these processes might be homologous with structures in the geometrid genera Himera Duponchel and Nacophora Hulst, and with the hairy pads of Thyatiridae. From limited observations, I conclude that the processes in these three families are not homologous. I refer to this structure as the costula (Latin: little rib) (Weller, 1990), distinguishing it from the costal process of the sacculus (Forbes, 1954). The costula appears to be a modification of the noctuid transtilla, and its shape is usually species-specific. Dioptines lack costulae, and instead have a fused transtilla that arises from the base of the costa (Miller, 1991).

A membranous region occurs between the sclerotized costa and midvalve sclerotization in nystaleines. This region varies from being slightly to extremely pleated (Bardaxima), and has scattered setae or patches of setae and hairs (Figs. 16A, 18). It appears to be homologous with the valvula of Pierce (1914) (Weller, 1990).

Anellar Region. The anal tube is often weakly sclerotized ventrally in thin vertical strips. Ventral to the costulae, scattered setae occur. The juxta is sclerotized and varies from slightly to extremely concave in nystaleines. In other notodontids, the dorsal edge of the juxta may be elaborated into an aedeagus guide or stabilizer (e.g., Lirimiris).

Aedeagus (Fig. 20). In Nystaleinae, the vesica (= endophallus; Klots, 1970) tends to be bulbous, terminating in a narrow tube that is directed cephalad. Deciduous cornuti, present in many genera, vary in size and shape (Forbes, 1948; Holloway, 1983).

Many modifications of the aedeagus occur (Fig. 20A-E). The distiphallus may have long processes (Symmerista) or small flanges (Notela). The basiphallus can be shovel-shaped (Fig. 20E) or tubular (Fig. 20C). Often, a ventral sclerotized piece occurs on the basiphallus that may provide extra surface area for muscle attachment. I call this an aluta (Latin: shoe of soft leather). This structure, which is attached to the manica, can be flat and sheetlike, caecum like, or bowl-shaped (Fig. 20D).

The aluta of Nystalea and related genera is an enlarged, tubular structure that has a characteristic triangular exit for the ductus seminalis (Fig. 20A, B). Large muscles attach both dorsally and ventrally (Weller, 1989, 1990; Miller, 1991). The term callosum (Latin: hard skin; Weller, 1990) has been used to refer to this specialized aluta, and it only occurs in Nystaleinae (Weller, 1989; Miller, 1991).

Genitalia: Female (Figs. 21, 22)

Notodontid female genitalia show greater morphological variation than is usually found in the Noctuoidea, and it is not uncommon for them to be species-specific (Weller, 1992). However, within species complexes,
Figure 20 Aedeagii. A. aedeagus with callosum removed (Nystalea similis); B. callosum (Nystalea aequipars); C. caecum (Hemiceras sp.); D. caecum with aluta (Nadata gibbosa); E. plain tube with aluta (Rifargia lineata). a = aluta, b = basiphallus, ca = caecum, c = callosum. (Scale = 1.0 mm)
female structures (e.g., lamellae antevaginalis, tergum 8) tend to have similar shapes (e.g., N. aequipars species complex; Weller, 1990).

Ovipositor Lobes. The papillae anales are usually membranous, but may be lightly or heavily sclerotized. In Nystaleinae, they are usually covered with short, scattered setae with longer, inwardly curved setae arising from the base. The lobes may be flattened and covered with stout, curved setae (e.g., Notoplusia, Lyricinus xylophasioides). In Apela Walker (Hemiceratini), the ovipositor setae resemble shepherd crooks. Ovipositor lobes of the neotropical heterocampine Rhuda dimidiata are concave, and the setae are long and curved with wide, spatulate tips. Other species of Rhuda have unmodified setae.

In nystaleines, posterior apophyses are typically long and slender, although they can be short and stout (e.g., Calledema rufescens). In C. rufescens, a sclerotized invagination is located dorsally between the papillae anales and tergum 8 (T8). Presumably, this invagination is associated with a pheromone gland.

Sclerites of the Eighth Abdominal Segment. The shape of T8 and
Asymmetrical female genitalia. A. ventral view, *Dasypodia maxtia*; B. dorsal view, *Pentobesa poecila*. ap = anterior apophysis, cb = corpus bursae, db = ductus bursae, ds = ductus seminalis, o = ostium bursae, s = signum, ss = sclerotized shield, 8t = eighth tergum, 8s = eighth sternum. (Scale = 1.0 mm)

S8 varies within and between nystaleine genera. Some species possess lateral processes on only the sternum or on both sternum and tergum. Some have additional lateral processes on the lamellae antevaginalis. The ostium bursae is usually very wide, extending nearly the entire width of S8 (Fig. 21). Some females have asymmetrical genitalia, and in these, the ostium bursae is usually located left of center. Asymmetrical genitalia are common in Pentobesa and the Dasypodia terrena-species group. In Pentobesa poecila (Felder), the ostium bursae is dorsal, located on the enlarged, distal edge of the apophysis (Fig. 22A). In Dasypodia maxtia (Schaus), the left anterior apophysis is reduced, and the ostium is located slightly ventral to the apophysis (Fig. 22B). The male genitalia in these species are also asymmetrical. Asymmetrical female insect genitalia are rare (reviewed in Eberhard, 1985). The ostium bursae of many notodontid females have various structures covering or blocking it (e.g., *D. anguina* [Smith], *Gopha mixtipennis*, *Heorta roseoalba*: Heterocampinae).

Other Structures. The ductus bursae may be membranous, partially or completely sclerotized. In nystaleines, it is often sclerotized and dorsoventrally flattened (Fig. 21). In this case, the lateral margins are membranous, allowing them to expand into a rounded tube. The ductus bursae may be extremely short (e.g., *D. anguina*) or extremely long (e.g., *Hapigia* spp.: Hemiceratini), two to three times the length of the corpus bursae.
In Nystaleinae, the ductus seminalis often arises from the left ventral area of the corpus bursae (Fig. 21). However, it may also arise from near the ostium bursae, from the ductus bursae (Fig. 22) or from other areas of the corpus bursae. The corpus bursae itself may or may not be partially sclerotized. Where ductus and corpus bursae meet, there may be internal spinules or other modifications as in Pentobesa lignicola Möschler or Marthula mumetes where a "necklace" of spines surrounds the mouth of the corpus bursae. Single or multiple signa are present, and their shape may be species-specific.

Summary of Morphological Trends

Although the morphology of Nystaleinae and other notodontids is difficult to characterize, certain trends can be noted. Mouthpart structures tend to be well developed in neotropical species and reduced in nearctic species. As in many Lepidoptera, female antennae are usually simpler than male. The prothorax usually has parapatagia; occasionally an additional lateral pair occurs. The tympanum may have all four pockets, with the fourth characteristically being "open," that is, with anterior and posterior struts not connected by a sclerotized sheet. Loss or reduction of pocket II is frequent in notodontids, and pocket III has been lost in all dioptines examined. Further tympanal reduction occurs in some dioptines and thaumetopoines.

Species can often be assigned to genera based on female genitalic structures, but the diversity of both female and male genitalia makes generalizations difficult. When other tribes and subfamilies are more thoroughly surveyed, statements on genitalic trends in the family may be possible.

Several types of previously undescribed sexually dimorphic structures occur on male legs, wings, abdomen and genitalia in neotropical notodontids. Some species have androconia and glandular areas on both legs and genitalia (many nystaleines), on both pre-genital abdominal segments and genitalia (Marthula, Hapigia), or on all three areas (Calledema). The cteniophore is the only structure previously surveyed that has been ascribed a possible courtship function (McColl, 1969). A survey of these structures with more rigorous characterization of their function should be undertaken in light of these findings.

Summary of Morphological Terms and Synonyms

Aluta (new term) (Fig. 19D): sclerotized piece of cuticle attached to the ventral surface of the basiphallus. May have originated as an extension of the manica. Found in most notodontids.

Anterior branch pocket (new term) (Fig. 5): small pocket ventral to the tympanic cavity formed from an extension of the anterior branch of pocket IV. Found in some Hemiceras and some nystaleines.

Barth valve (new term) (Fig. 17): valve with sacculus enfolding a hair
pencil that emanates from the saccular base. Associated gland occurs within sacculus. Found in Hapigia and most Hemiceras.

**Callosum** (Weller, 1990)(Fig. 19A, B): specialized aluta enclosing the basiphal/us, usually with a footlike projection. Unique to Nystaleinae.

**Costula** (Weller, 1990)(Fig. 15): sclerotized process arising from the base of the male valval costa. Occurs in nystaleines, some heterocampines and hemiceratines, and appears to be a modification of the noctuid transtilla.

**Epimeral pocket** (new term)(Fig. 5): small pocket located on the pre-epimeron/epimeron suture of the metathorax. Found in some nystaleines, hemiceratines and heterocampines.

**Epimeral ridge** (new term)(Fig. 5) (= "le support anterior" of Kiriakoff, 1950a, 1950b, 1950c): an internal ridge located at the pre-epimeron/epimeron suture of the metathorax that extends anteriorly from the tympanic cavity. Found in some nystaleines, hemiceratines and heterocampines.

**Midplate** (Weller, 1990)(Fig. 13): sclerotized area, sometimes with ridges, located in the middle of the male eighth tergum. Occurs in many notodontids.

**Midvalve sclerotization** (Weller, 1990)(Fig. 15): ribbonlike or expanded plate of sclerotized cuticle located on the inner mesal surface of the male valve, demarcating the dorsal edge of the sacculus. Occurs in many nystaleines, hemiceratines and dioptines. Usually associated with a pleated saccus.

**Peniculus** (Fig. 12B, 13)(Thiaucourt, 1985): similar to a cteniophore, but pleural expansion is reduced. It occurs on male abdominal sternum V in Calledema rufescens.

**Pleural hood** (Fullard, 1984): expanded pleural membrane that surrounds the first abdominal spiracle, and cups the tympanal opening. Analogous to the noctuid tympanic hood. Occurs in Hapigia and Antaea.

**Pocket IV** (Richards, 1932)(Figs. 5, 6) (= "le support posterior" of Kiriakoff, 1950a, 1950b, 1950c): tympanal pocket located ventral to the tympanic cavity that is usually "open" with an anterior and posterior ridge defining its location. Anterior ridge reduced or absent in some notodontids (Kiriakoff, 1950a,c). Pocket IV has its opening towards the tympanic cavity when a sclerotized sheet connects the anterior and posterior supports (= "closed" condition). This pocket occurs in many notodontids.

**Saccular scent organ** (Weller, 1990)(Fig. 15): membranous and pleated sacculus with scent scales emanating from the base. Found in numerous neotropical (Weller, 1989) and asian species (Holloway, 1983).

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LITERATURE CITED


A Reconsideration of the Taxonomic Status of *Euphydryas editha koreti* (Lepidoptera: Nymphalidae) from the Central Great Basin

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**Abstract.** Samples of *Euphydryas editha lehmani* and *Euphydryas editha koreti* from the central Great Basin and *Euphydryas editha gunnisonensis* from the western and central Rocky Mountains of Utah and Colorado were assayed for isozyme variability at 19 protein loci. Genetic identity estimates and the resulting phenogram show that *Euphydryas editha koreti* is not genetically differentiated from *Euphydryas editha lehmani*. These results are consistent with the spatial distribution of *Euphydryas editha koreti* which exists as a number of isolated alpine populations. They also suggest that Koret’s checkerspot butterfly is not a cohesive evolutionarily significant unit and thus may not warrant subspecific status.

**INTRODUCTION**

Koret’s checkerspot butterfly, *Euphydryas editha koreti* (Murphy and Ehrlich 1983), was described from high alpine ridges and slopes on isolated mountain ranges in the Great Basin. The subspecies is distinguished from a more widespread Great Basin subspecies, *Euphydryas editha lehmani* (Gunder 1929), by its much smaller size and greater yellow coloration of the submarginal band on its dorsal hindwing (Murphy and Ehrlich 1983, Austin and Murphy 1995).

In addition to that quite consistent morphological distinctiveness, *Euphydryas editha koreti* was acknowledged with subspecific status because of several marked ecological differences with *Euphydryas editha lehmani* (Murphy and Ehrlich 1983). Dramatic elevational differences exist between the habitats of the two subspecies; *Euphydryas editha lehmani* occurs from 1600 m to 2500 m in elevation, while *Euphydryas editha koreti* occurs above 3700 m. *Euphydryas editha koreti* apparently oviposits exclusively on *Castilleja lapidicola*, while *Euphydryas editha lehmani* oviposits on *C. chromosa* and *Pedicularis semibarbata* across most of its Great Basin distribution, and on *C. linariifolia* in the Pequop Mountains (Murphy and Ehrlich 1983). Finally, *Euphydryas editha lehmani* tends to fly in late May or early June, while the flight season for *Euphydryas editha koreti* is often delayed until early July, or in some years, late July. Individuals

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assignable to the two subspecies have never been observed flying together.

These phenotypic and ecological differences notwithstanding, substantial doubt is cast on the appropriateness of designating populations currently assigned to *Euphydryas editha koreti* as a subspecies distinct from *Euphydryas editha lehmani*. Here, we present allozyme data that indicate that *Euphydryas editha koreti* is not particularly well differentiated genetically from *Euphydryas editha lehmani* and that populations of Koret's checkerspot butterfly do not constitute a coherent evolutionary entity with common immediate ancestry.

**Materials and Methods**

Specimens of *Euphydryas editha lehmani* were collected from a total of seven localities in seven Great Basin mountain ranges (Toiyabe Range, Toquima Range, Monitor Range, White Pine Mountains, Egan Range, Schell Creek Range, and Snake Range), and *Euphydryas editha koreti* was collected from three localities; one each in the Toiyabe, Schell Creek, and the Snake Ranges (Figure 1). In addition, seven samples of *Euphydryas editha gunnisonensis* were collected from the Rocky Mountains of Utah and Colorado (Britten et al. 1994). This sampling regime provided the opportunity to compare genetic differences among the three *Euphydryas* subspecies, with the two subspecies from the Great Basin being represented by isolated but interspersed populations, and the Rocky Mountain subspecies being geographically separate from the other two (Figure 1). All samples were collected between 1980 and 1983.

Allozyme variation was assayed at 19 presumptive loci using horizontal starch-gel electrophoresis. Details of allozyme assay methods can be found in Brussard et al. (1985) and Baughman et al. (1990).

Nei's (1978) unbiased genetic identities were calculated between each pair of samples in the study. This index of genetic similarity based on allele frequencies provides a metric that can be used to derive a phenogram that is a graphical representation of the genetic similarities among the assayed populations. The UPGMA clustering algorithm was used in this analysis. BIOSYS-1 (Swofford and Selander 1981) was used for all data analyses.

**Results**

Total sample sizes were 143 for *Euphydryas editha koreti*, 282 for *Euphydryas editha lehmani*, and 438 for *Euphydryas editha gunnisonensis*. Unbiased genetic identities (Nei 1978) among the 17 *Euphydryas editha* populations sampled are given in Table 1. Mean observed population heterozygosities were nearly identical among the three subspecies; 0.057±0.009, 0.058±0.022, and 0.061±0.023 for *Euphydryas editha koreti*, *Euphydryas editha lehmani*, and *Euphydryas editha gunnisonensis*, respectively. Genetic identities of 1.00 were estimated among three of the four Gunnison Basin populations (AL, AS, and JC) and between NS, an *Euphydryas editha koreti* sample from the Schell Creek Range, and ANT, an *Euphydryas editha lehmani*
Figure 1. Map of *Euphydryas editha* collection sites with subspecies *Euphydryas editha koreti* (open circles), *Euphydryas editha lehmani* (closed circles), and *Euphydryas editha gunnisonensis* (dotted circles) indicated. Shading represents areas over 2,200 meters elevation.
Table 1. Pairwise estimates of unbiased genetic identity (Nei 1978) for 17 samples of *Euphydryas editha*. Subspecies *lehmani* and *koreti* were sampled from Nevada and subspecies *gunnisonensis* was sampled from Utah and Colorado.

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sample from the White Pine Mountains (Table 1). The lowest estimates of genetic identity (I=0.95) were found between *Euphydryas editha gunnisonensis* populations from the central Rocky Mountains and *Euphydryas editha lehmani* and *Euphydryas editha koreti* samples from the Toiyabe Range. The UPGMA phenogram derived from genetic identity estimates separates *Euphydryas editha gunnisonensis* from the other two subspecies included in the study, while *Euphydryas editha koreti* samples are imbedded among *Euphydryas editha lehmani* samples (Figure 2). *Euphydryas editha gunnisonensis* is separated from the other subspecies at a mean genetic identity of about 0.97 (Figure 2).

**Discussion**

Mayr (1969) defined a subspecies as “an aggregate of phenotypically similar populations of a species, inhabiting a geographic subdivision of the range of a species, and differing taxonomically from other populations of the species.” It has long been recognized, therefore, that the subspecies category does not necessarily reflect patterns of differentiation that have evolutionary significance; hence the category should be used only to delineate groupings of populations that share phenotypic similarity (Wilson and Brown 1953). Debate has continued since the 1950’s over the taxonomic importance of the subspecies category and how the category should be defined (Ehrlich 1957, Lidicker 1962, Mayr 1982, Cracraft 1989). The purpose here is not to revisit that debate, but to point to the general agreement that the possession of a trinomial appellation by a group of populations does not necessarily mean that those populations constitute an evolutionarily significant unit (Mayr 1982, Cracraft 1989). The subspecies category should be used simply as a convenience for delineating groups of geographically proximate, morphologically similar forms discernable from other such groups (Mayr 1982). In that light, the interspersed distribution of *Euphydryas editha lehmani* and *Euphydryas editha koreti* presents a taxonomic problem.

The suite of alpine populations of *Euphydryas editha* found in the Schell Creek, Snake, and Toiyabe Ranges of Nevada was described as the subspecies *Euphydryas editha koreti* Murphy and Ehrlich based on ecological and morphological differences of these individuals when compared to specimens of the more widespread montane subspecies found at lower elevations, *Euphydryas editha lehmani*. Although all *Euphydryas editha koreti* populations are found in nearly identical ecological situations, they are completely isolated from one another and are at least partially surrounded by *Euphydryas editha lehmani* populations at lower elevations (Figure 1). Because of those discontinuities in the distribution of *Euphydryas editha koreti* (Figure 1), this subspecies is described as “polytopic,” that is, it shows “independent recurrence of similar or phenotypically indistinguishable populations in geographically separated areas” (Mayr 1969). For many workers this current
Figure 2. UPGMA phenogram based on Nei's (1978) unbiased genetic identities for 17 sampled populations of *Euphydryas editha*. Three subspecies are represented: *Euphydryas editha lehmani* and *Euphydryas editha koreti* from Nevada, and *Euphydryas editha gunnisonensis* from Utah and Colorado. Cophenetic correlation coefficient is 0.885. Note that the relationships involving the BKR and AS populations are incompletely resolved on the phenogram.
spatial distribution, this polytopy, disqualifies *Euphydryas editha koreti* from subspecies status (e.g. Wilson and Brown 1953, Mayr 1963 and 1969). If, however, populations referred to as *Euphydryas editha koreti* were to show high levels of genetic similarity to one another when compared to geographically adjacent populations of the same species, common ancestry could be inferred for *Euphydryas editha koreti* populations. This would suggest a more continuous distribution in the past, and perhaps defensible subspecific status.

The allosyme results presented do not show such coherence, and they provide little support for the subspecific status of *Euphydryas editha koreti*. This conclusion is based on the UPGMA phenogram in Figure 2 and the geographic distribution of *Euphydryas editha koreti*. Previous work by Brussard et al. (1985), using nearly identical methods, provided a framework from which taxonomic decisions can be made using allosyme data at taxonomic levels below the subfamily. The mean genetic identity among 12 subspecies in the tribe Melitaeini, including several *Euphydryas editha* subspecies, was 0.964 (Brussard et al. 1985). This estimate of mean identity is nearly equal to the genetic identity observed between the *Euphydryas editha gunnisonensis* and *Euphydryas editha lehmani* - *Euphydryas editha koreti* clusters in Figure 2. This result suggests that at least some "good" subspecies exist among montane *Euphydryas editha* populations in the central Great Basin and Rocky Mountain regions.

The clustering of *Euphydryas editha koreti* with *Euphydryas editha lehmani*, however, indicates much greater genetic similarity among these populations and supports the conclusion that *Euphydryas editha koreti* is probably not an evolutionarily significant unit, but is instead a recurrent high elevation phenotype of *Euphydryas editha lehmani*. While it is impossible to dismiss a scenario in which low elevation populations were established from ancestral high elevation populations, and subsequently became the most widespread phenotype in the Great Basin; the most likely biogeographic scenario is that different low elevation populations have given rise independently to alpine populations sharing convergent phenotypes in the three Great Basin mountain ranges where *Euphydryas editha koreti* is known to occur. The tight clustering of the Toiyabe Range samples, one of *Euphydryas editha lehmani* (SY, Figure 1) and the other *Euphydryas editha koreti* (BH, Figure 1), in the phenogram (Figure 2) provides the best evidence of a high degree of similarity between these two taxa. The allosyme data suggest that, despite the phenotypic similarity of individuals from populations assigned to *Euphydryas editha koreti* and their distinctiveness from individuals from geographically adjacent areas, they should not be recognized as taxonomically distinct from the more widespread *Euphydryas editha lehmani*. Furthermore, the data also suggest that *Euphydryas editha koreti* are not evolutionarily distinct from nearby *Euphydryas editha lehmani* populations at lower elevations.
The *Euphydryas editha koreti* situation underscores the lack of formal nomenclatural tools available to describe phenotypically distinct entities that do not fit the subspecies category. This difficulty is expected to be particularly acute for well studied taxa, such as Lepidoptera, for which there is a long standing tradition of “splitting.” Current nomenclatural precedence would call for the “sinking” of *Euphydryas editha koreti* into the subspecies *Euphydryas editha lehmani*. This approach, however, would leave a morphologically distinct form, now referred to as *Euphydryas editha koreti*, without the unique designation. Another approach would be to recognize an additional taxonomic category for polytopic subspecies. This approach is neither particularly parsimonious nor traditional, is likely to be cumbersome, and its application would surely meet resistance. It is clear that this sort of taxonomic dilemma will only increase in frequency as molecular genetic techniques become more widely available and the taxonomic status of an increasingly broad spectrum of organisms comes under scrutiny.

**Acknowledgments.** We gratefully acknowledge the superior knowledge and indefatigable commitment of George T. Austin to an understanding of Great Basin butterflies. And, as always, we thank him for his assistance with our research there. We also thank Janet Wright for running the gels and for preliminary data analyses. This work was supported by the Nevada Biodiversity Initiative and grants from the National Science Foundation.

**Literature Cited**


A report on the reproductive morphology of gynander tasar silkmoths *Antheraea mylitta* Drury (Lepidoptera: Saturniidae)

Gynandromorphs are abnormal individuals showing varying degrees of mixed sexual characters. They are known for several insect groups, but are most often encountered in Lepidoptera (Scriber and Evans 1987, Davies 1988, Halstead 1989, Blackaller-Bages and Delgado-Castillo 1990, Forattini *et al.* 1991). Gynandromorphs may occur through the failure of genetic sex determining mechanisms or through hormonal or other influences during development. In the extreme case, one half of such an insect is female, the other half male. Some of the tissues are genetically and structurally female, others male. The genetic basis of gynandromorphism in *Drosophila, Lymantria, Bombyx*, etc. is well documented (Sinnott *et al.* 1958; Altenburg, 1970; Herskowitz, 1977). It has been recently established in mites that gynandromorphism is the result of unequal distribution of sex linked chromosomes rather than control at the gene or physiological level (Homsher and Yunker, 1981).

The occurrence of gynandromorphs is very rare in both wild and commercial populations of the tropical tasar silkmoth, *Antheraea mylitta*. Gynandromorphism in this moth was first reported by Sen and Jolly (1967) wherein they discussed the morphological characters with special reference to the genitalia. This note illustrates the previously unreported morphology of the reproductive system of gynander tasar silkmoths.

Two types of gynandromorph were observed in a commercial laboratory population of the tasar silkmoth: predominately male gynandromorphs and predominately female gynandromorphs. In both cases, the left half of the body was observed to possess the male characters whereas the female characters occurred on the right. The male predominants have well developed testes with a male accessory gland on the left half and on the right half a single atrophied ovary with a mature colleterial gland and a female accessory gland (Fig. 1). In the case of female predominants, the reproductive organ situation was reversed. A single ovary containing four mature ovarioles with a single fully developed colleterial gland and female accessory gland was present. In these individuals the testes remained atrophied and non-functional. The female predominant condition is illustrated in Fig. 2. In both male and female predominant individuals, the genitalia retain important parts of both the female (bursa copulatrix) and male (aedeagus).

It is noteworthy that predominant female gynandromorphs, after mating with normal males, laid very few eggs and these were infertile. By contrast, virgin normal females, when mated with predominant male gynandromorphs laid fertile eggs. A similar reproductive behavior has been reported in gynandromorph *Drosophila melanogaster* by Napolitano and Tompkins (1989). Conventional morphological secondary sex characters such as wing maculation and antenna structure show the typical male features on the left and female features on the right side of the body. The physiological and genetic bases of gynandromorphism in tasar silkmoth remain unknown.
Figures 1 and 2. Reproductive system of predominant male gynandromorph (Fig. 1) and female gynandromorph (Fig. 2) internal reproductive system of *Antheraea mylitta* Drury. Legends: a) mature testis, b) male accessory gland, c) atrophied ovary, d) female accessory gland, e) colleterial gland, f) mature ovary, g) atrophied testis, h) bursa copulatrix.

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Notes on the Santa Monica Mountains hairstreak Satyrium auretorum fumosum Emmel and Mattoni

Since naming this subspecies (Emmel, J. and R. Mattoni. 1990. Jr. Res. Lepid. 28:105-111) several new observations have been made that bear on its conservation biology. Although the life history remains to be formally described, one rearing cycle has been observed in captivity by J. Emmel from eggs laid by a captive female taken 16 June 90 on Eriogonum fasciculatum at Carlisle Canyon, Los Angeles Co., CA. The female producing these eggs was confined by Pasko with scrub oak, Quercus berberidifolia, but the c. 25 ova recovered were all found embedded in the depressions of the paper toweling lining the bottom of the box. Egg diapause was followed by 15 larvae emerging in late spring with all larvae feeding to pupation and eclosion. The 10 larvae retained by Pasko were reluctant to start feeding on the fresh but mature shoots of Q. berberidifolia provided for food. The earlier hypothesis of Emmel and Mattoni asserted that the butterfly was restricted to scrub oaks, mostly Q. berberidifolia in the Santa Monica Mountains, a relative of the known scrub oak foodplant of the nominate subspecies. Adults were never observed on or around scrub oak in the Santa Monica Mountains. Until now fumosum appeared to have a highly limited distribution and was also very sparse where found. This represents an unusual pattern for an insect taxon unless it were near a terminal stage of extinction.

Initial field observations noted that adults were rarely found nectaring, and when nectaring was observed the source was always common buckwheat, Eriogonum fasciculatum. On 29 May 1993 Pasko again observed several flight worn fumosum nectaring at the small isolated patch of E. fasciculatum in Carlisle Canyon where the 1990 specimens were taken. Nearby were two small scrub oaks and several large trees of coast live oak, Q. agrifolia. Upon tapping the branches of both oak species, one male fumosum was obtained from Q. agrifolia. Further searching led to the discovery of several of both sexes on another Q. agrifolia several hundred feet away from the first tree. No additional adults were observed from ten other trees in the vicinity. On 23 April 1994 Pasko confirmed Q. agrifolia as the correct foodplant by collecting eight last instar larvae in the field at the Carlisle Canyon site. These larvae were taken by beating the lower terminal branches that bore young and tender new growth leaves.

At this Carlisle Canyon site a group of about 25 mature Q. agrifolia trees form an isolated patch as an oak savannah association within which fumosum larvae were found on only four trees. Many of these trees, however, are large and cannot be adequately sampled for either larvae or adults. Ants were always present, but specimens were not retained for identification and no specific ant-larvae interactions were seen although the species is known to be strongly attractive to ants (G. Ballmer, pers. comm.). Large numbers of microlepidoptera larvae were also present that could account for the presence of the large number of ants.

Five of the eight larvae were parasitized by an unidentified species of small Diptera. The three survivors located pupation sites within two days and eclosed
indoors between 12 and 15 May 1994. Several visits to the Carlisle Canyon site failed to produce sightings of adults until 28 May. In 1993 most adults were flight-worn by this date. On May 28 two adults were found on the same tree that yielded the 1993 females and the 1994 larvae. On 4 June 1994 five additional adults were taken and four more seen, again on the same tree with none on any other tree at the site. The small Eriogonum patch was just starting to bloom and no adults were observed.

The following day, with knowledge of foodplant and flight time confirmed, another live oak savannah stand was visited near Lake Malibu (fumosum type locality) in the Santa Monica Mountains National Recreation Area. Tapping the lower branches of several live oak trees quickly yielded adult fumosum. As at Carlisle Canyon, adults are sedentary and fly up only when disturbed. However, they return to perch within a few seconds, a behavior more pronounced for females. Males were occasionally observed to engage in short chases with one another before settling. A colony of the copper Tharsalea arota nubila occurs at this site and many males simultaneously perched on the outer branches of the live oaks. The male coppers, easy to discriminate by their larger size and lighter color than fumosum, tended to fly somewhat longer after disturbance. At this site fumosum is more abundant that at Carlisle, but by no means common. Butterflies were observed on seven trees out of 20 examined. A number of additional trees were present but not examined because of the hilly terrain and heavy understory.

Several males were observed nectaring in two separate small E. fasciculatum patches. A second visit on 11 June resulted in the observation of three males and five females on the oaks and four males nectaring on Eriogonum. A final visit on 17 June provided no observations at this site or at any of four other live oak savannah assemblages in the vicinity. No adults were observed on the few scrub oaks in the area. From observations over the past four years, nectaring usually occurs between 1100 and 1330 hours, although on hot days they may be observed nectaring as late as 1600.

Although Q. agrifolia is abundant and widespread across the northwest slopes of the Santa Monica Mountains, many trees are on private property or other disturbed land where much of the undergrowth, including E. fasciculatum, has been altered or removed. What effect this may have on fumosum populations is unclear. The advent of frequent anthropogenic fires in the area is another potential threat since ova diapause on oak branches.

As a further note to adult feeding, Mattoni earlier observed S. auretorum spadix near Lebec, CA imbibing on excretions from scale insects found on its scrub oak host at that locality. Several adults were observed simultaneously feeding in this manner on two scale colonies. Adults were rarely seen at floral nectar sources and were generally thought to be scarce.

In summary: 1) Adults of the subspecies S. auretorum fumosum spend most of their time perching only on coast live oak trees Quercus agrifolia. 2) Populations seem to be restricted to only a few "choice" trees with succulent leaves when a number of trees are available. 3) Individual adults appear highly sedentary. 4) The populations appear structured as a series of metapopulations with minimum interchanges among colonies, each delineated by an individual tree. 5) There is not a uniform population continuous with the live oak savannah of the region. 6) Adults rarely nectar, and when they do they were observed only on Eriogonum fasciculatum. Adults may take sustenance from scale insect secretions or possi-
bly sap runs and slime fluxes. 7) Larvae require very young tender shoots for survival.

We thank the National Park Service, Santa Monica Mountains National Recreation Area for their cooperation in permitting this work. We strongly urge the listing of the species as endangered for the reasons cited.

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New courtship posture in females of two Chilean butterflies: Rejective or receptive?

Two species of Hylephila Billberg inhabit the large lawns of the Chilean air force academies at the "comuna" El Bosque of Santiago. H. fasciolata (Blanchard) Gay and H. signata (Blanchard) Gay are on the wing from late August to early May in successive broods. Both are common, successfully surviving the blades of the lawn mowers. The males are typical perchers, using the taller grass blades, flowers of Taraxacum officinale (L.) Wibb., Leontodon taraxacoides (Vill.) Merat, Bellis perennis L. (all Asteraceae), and bare soil as perching sites from which they intercept passing Colias vautieri, Tatochila mercedes and their congenerics. In mating couples the female carries the male when disturbed (see H. signata couple in Figure 1 with male hanging below). The females have a special way of laying their white, hemispherical, smooth eggs: they walk on the grass with their abdomen curved below and forward, searching for the proper oviposition sites with the exploratory tip of the abdomen.

October 27, 1993 was a typical clear, warm, late spring day in Santiago (air temperature about 28 C). At 14:00 hrs, high flight activity was observed over the lawns. In the air, only a few cm above the grass, a male H. fasciolata courted a female. The female landed on the ground on the edge of a small opening in the lawn about 3 inches in diameter. The male landed immediately after her and about 1.5 inches behind. He approached the female in small jumps, each time fluttering his wings in what looked like a showy, ritual "dance." It is possible that the fluttering released pheromones from his front wing androconial patches. During the male's courtship, the female was totally passive and did not move, but when the male got closer, the female suddenly began to vibrate both her hind legs in an up-and-down motion, in effect creating an impenetrable barrier. The behavior appeared to be an effective new repulsive posture. The vibration was too fast to detect whether the legs moved together in parallel or in a scissors-like movement. When the male got closer and was only a few mm behind and to her side, the female flew away.

A few days later (November 1, 1993), 150 km to the north, at Pichicuy, on the Pacific coast, at 15:00 hrs, a low courtship flight of the dwarf blue Pseudolucia benyamini Balint was observed. The flight was not more than 30 cm over the ground and among the cushion-like food plants Chorizanthe vaginata Benth (Polygonaceae). The female landed on a flowering head and started to walk on it with the male following close behind her. Once again I saw the hind legs vibrating in the female, but within about five seconds they copulated. Thus, it is
unclear to me whether this copulation was achieved in spite of the “rejecting” movements or whether the vibration is possibly a receptive posture. More observations are needed to establish a final conclusion.


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To many people the Caribbean islands will always evoke a romantic visage of paradise; where palm trees dripping orchids sway along unspoiled beaches, and elegant birds chatter in the forest dark amidst swirls of brightly colored butterflies. Tough to grasp the fact that most of those tropical islands will soon be devoid of relatively intact habitats and their species associations, but brimming with industrial waste, air conditioned hotel comfort, and only fading memories of what it was like. Thus, at a time when information on the diverse Caribbean islands is needed more than ever, The Butterflies of the West Indies and South Florida arrives to help fill a substantial void in our understanding of butterflies and skippers. In many respects this book supersedes three books: Brown & Heinemann (1972), Riley (1975), and Schwartz (1989). But this attractively printed book's long-term contribution is that it represents a modern means of identifying the butterflies and skippers of the Caribbean region, all under one cover.

The five brief introductory chapters cover the West Indies and South Florida and its butterflies (including biogeography and the size of island faunas), conservation, and a very nice review chapter on the history of collecting and collectors of the islands. Even though it may have been a temptation to devise and include them, common names of butterflies were omitted. This was a relief to see. Instead, we are given a complete taxonomic checklist of the butterfly fauna outfitted in crisp nomenclature. Finally, there is an appendix (which could have followed the taxonomic checklist) that allows the reader to assign the plant genera mentioned in the text to their proper families. Although a trifle brief for my tastes, the information will be welcome to the users of this book.

The real heart of this volume, and what will be read by everyone who owns this book, is nested within the treatments of the butterflies themselves. Starting with a brief synopsis of each higher level category (family to subfamily, and genus), the reader arrives at the species account. The species accounts commence from fairly detailed and technical descriptions (with diagnostic characters italicized) followed by range information and natural history observations, followed in turn by short descriptions of subspecies (where applicable), and conclude with informative snippets on taxonomy, distribution, natural history and queries about each species. In short, there is a wealth of information here that is accessible and useful to an audience ranging from the novice to the butterfly cognoscenti.

Faced with the often formidable problem of identifying specimens of varying quality, users of this book will have the distinct pleasure of using color plates derived from the paintings of Richard Lewington. To say that the identification plates are good would be a disservice - they are excellent, and, perhaps, a benchmark for modern field guides. Lewington's artwork does not merely create caricatures aimed at identification, but it manages to capture the subtle essence of the butterflies themselves. An additional bonus is that the medium format of the book sets off the beauty and utility of these plates to advantage.
Although generally well written, the text contains a sprinkling of some unusual sentence structures. For example, in an apparent encapsulation of some quotes found in Brown & Heinemann (1972), something seems to have been lost in the translation: "...They cite Walker's notes (unfortunately too lengthy to reproduce here) on the behavior of H. orion adults, as they approach and feed on 'apple' fruit remaining on the tree, but damaged by bats, that makes museum specimens conspicuously incomplete records of a butterfly species!... (p.74)" Huh? This example (and a few others elsewhere) suggest lines dropped in the proofs, and here one is obligated to finger-wag at editorial oversights. The occasional odd sentence structure aside, there is much to be gleaned from this treatment of the Caribbean butterfly fauna.

There are three areas where, in my opinion, this book fell down: the price of the book, the manner in which higher classification was employed, and the treatment of butterfly biology at all levels. My spasm about price is simple - it greatly restricts the audience that will be able to buy this book in two ways. Let us be honest. Yes, American and European countries are covered (primarily libraries), but the probability is low that the publisher will distribute the book where it should be available: in the West Indies. Even if a distribution miracle should come to pass, how many of the potential students of butterflies living in the West Indies (or elsewhere for that matter) will be able to afford a book that costs $125? Another way of phrasing this would be to ask, How is it possible for an academic press to publish a potentially popular, but relatively slim field guide, and expect it to sell at such a price? To the publisher I would direct the query, Can we anticipate a paperback edition?

Classification, systematics, phylogeny, taxonomy, cladistics. All terms that are common in the biodiversity communication channels, be they academic or not. We are told that the higher classification employed in the book is "traditional". To me the higher classification is not at all traditional, and rather apathetic in the bargain. Some might argue that whether the milkweed butterflies are considered as a family (as in this book) or as a subfamily (my idea of traditional) is trivial fluff. If Danaidae, Ithomidae, and Satyridae are elevated as families, however, it is inappropriate not to divide the residual Nymphalidae into similar ranks (i.e., Apaturidae, Charaxidae, etc.). Come on, two of the authors are formally trained systematists. Lumping or splitting aside, whatever classification is used, at the very least the users of this book deserve to know about the existence of other systematic arrangements - especially the incipient butterfly biologists and systematists. Thus, it is a mystery to me why the broadly relevant volume edited by Vane-Wright & Ackery (1989), a work that contains wide ranging summaries of butterfly systematics (and biology), was only mentioned in passing in the preface, and not even given an accessible citation. It would have been so easy to include it. This is a glaring oversight.

Given the scope and potential of The Butterflies of the West Indies and South Florida, its coverage of general biology and natural history at all taxonomic ranks was disappointing. References to the biological traits at the family level are indolent to non-existent, and give the impression that general butterfly biology is either pedestrian or extraneous. At the species level, the coverage of life histories is uneven, and in some cases may obfuscate the trail to available literature. Despite what a significant number of the species accounts imply, there is considerable published information directly relevant to the natural history of the West Indian butterfly fauna. Two examples. The life history of Historis odius.
is an excerpt from Brown & Heinemann (1972), but why no mention of Muyschondt & Muyschondt (1979) who provide comparative illustrations of the early stages in some detail? Under Hypna clytemnestra we are informed that the life history is unknown. However, the work of Young (1982) on this species, complete with illustrations, is strong evidence to the contrary. Although such life history information may not have been derived from work conducted in the West Indies directly, it is puzzling why the authors chose not to be more thorough or helpful to the novice who may not have access to well stocked libraries. Again, a direct citation to Vane-Wright & Ackery's volume would have gone a long way toward providing the curious reader an entrance to a substantial literature. In future editions the authors might consider adding an addenda bibliography pertinent to systematics, natural history and ecology.

Conservation biologists, taxonomists, biogeographers, and simply the curious naturalist now have a reference work that should stimulate more detailed work on the butterflies of the West Indies. The authors and the artist of this volume are to be congratulated for uniting their different perceptions and approaches to the study of butterflies. So here I am at the bottom line as a book reviewer. My thoughts go as follows. The prospective reader of The Butterflies of the West Indies and South Florida should recoil at the price, spend the money if you can, start collecting other literature pertinent to butterfly systematics and biology, and use this book as an identification guide. Me? I hope we all begin learning more about West Indian butterflies.

P.J. DeVries, Dept. of Biology, University of Oregon, Eugene, Oregon 97403

LITERATURE CITED


Once in a while something new comes along to jolt us from our sleepy traditions. The recent book Swallowtail Butterflies of the Americas by Tyler, Brown and Wilson (hereafter abbreviated as SWABA) is not for everyone - especially not the traditionalist. Overwhelming (and at times exhausting), this book is a force to be
reckoned with. In its challenge to traditionalist approaches, SWABA reminds me of the ferocious jazz piano of Cecil Taylor on his mid 1960's compositions entitled “Unit Structures” - complex cascades of rhythm and sustained flights of innovation. The style that courses from every surface of SWABA is manifestly Brown's, the dynamo behind this tour de force. Indeed, the contributions of Tyler and Wilson, like the sidemen in a Cecil Taylor trio, are all but eclipsed by the Brownian vortex that is everywhere at once. Comparable to a Cecil Taylor performance, the reader of SWABA at once dominated by an energy that above all demands an open mind. That is to say, one is carried along for the ride wherever it may take you.

The sheer quantity of taxonomic, systematic, morphological, chemical, ecological, evolutionary, genetical, historical, gazetteerical, philosophical and mythical information that is detailed, covered, treated, alluded to, whisked over, and hinted at in SWABA is staggering. As a matter of fact, the ONLY physical surface of this book that does not have information packed onto it faces the dedication. This page is innocently blank. A synthesis of everything that has gone before it, SWABA is now the source for information on the New World Papilionidae. Bristling with tables, appendices, matrices, graphs, figures, photos, and color plates depicting every conceivable aspect of the American Papilionidae, the publication of SWABA heralds a distinctly new type of book on butterflies. By bringing together a massive amount of information the authors have provided a monumental service to insect biology in general, and swallowtail biology in particular that will not soon be repeated.

The energetic style of SWABA can be both stimulating and baffling. I found the sections on early stages and the many “Do it yourself” sections ending each chapter particularly inspiring, but I remain puzzled in trying to make unified sense of Figs. 5.2 - 5.5 on host plant relationships, and the Fastkey to adults proved frustrating - simply too much information crammed in there. With perseverance I suspect that finding one's way around may be easier, and prove more edifying. The truly original chapter on systematics and its schools in SWABA should be read by everyone interested in organisms and systematics. This section does an entertaining, even-handed job of laying it all out for the reader: a paradoxical mix where cladists, pheneticists, evolutionists and creationists all get equal time. However, one might grumble that SWABA does not seem to provide diagnostic characters for the various genera, species or other taxonomic categories. That is to say, if Pterourus or Heraclides really are appropriate generic names to be used for various familiar Papilio species, one wants to see evidence in the form of characters as to why this is so, not just, 'trust me I know'. This brings us to what I feel are problems with SWABA.

As a means of identifying and retrieving information about specific butterflies, this book is diabolically user-hostile. The organization and layout requires wading repeatedly from the index through multiple pages and legends, and back again. Even when familiar with a particular species, I often gave up in frustration rather than continually chase about all the various pages to see what SWABA had to say. Two graduate students (one a novice, and one who knows a little about butterflies) were given the volume and asked to identify some specimens of Parides erithalion and Protesilaus protesilaus. After an hour or so one stated, "...this is a nightmare. I give up. I can't even find the names for the illustrations". The novice took longer, but eventually returned saying, "Sorry, I'm not sure if these are identified correctly or not (they weren't). Is butterfly taxonomy always
so complicated"? At this point we must ask, why this navigational nightmare in SWABA for something so simple as identifying butterflies from color plates?

The intractable nature of the identification plates stems from the combination of two types of plates, and their legends. One type of plate (which could and should have been omitted) is composed of crudely cut-and-pasted poor quality photos with each specimen designated by a letter. This faces another, good quality plate that is composed of specimens oriented at various odd angles, at times oddly numbered, and that may or may not be relevant to the lettered plates. However, the coup de grace is that not only do the plate legends nearly require a microscope to see the abbreviations and codes, but also they are often on completely different pages, lost amidst other captions and legends. Even though these legends bear footnotes that attempt to guide the user, they are often unhelpful in the game of hide and seek one has to play simply to put a name on an illustrated specimen. This just doesn't inspire user confidence in arriving at determinations.

To my mind, the persons at Scientific Publishers, Inc., P. O. Box 15718, Gainesville, Florida 32604 who are responsible for the layout and editing of SWABA should be confined to a room and forced to determine all of the species in the book from specimens! Cruel punishment no doubt, but under the circumstances, fair. Go ahead, try it. Identify a specimen of *P. protesilaua* or some *Parides* with the book. If you find the key, please tell me or my students how to navigate through SWABA and use it as an identification guide.

Anyone interested in swallowtail butterflies and their role in systematics, ecology, evolution, and conservation biology should buy this book. There is a lot of book here for relatively little money. It will help, however, to have plenty of other references on hand before attempting to master the messages of SWABA's unit structures. Lamentably, much of the power in this papilionid manifesto is hampered by the unorthodox organization and layout. Still, SWABA should be useful to papilionid specialists, butterfly ecologists, and conservation biologists. I look forward to as many profitable hours wrestling with it as I have spent listening to the inventions of Cecil Taylor. Acknowledgments: This manuscript benefited from comments provided by J. Coyne, K. Hope, R. Lande, C. Penz, G. Perry, M. Wood and two grad students who wish to remain anonymous.

**P. J. DeVries, Dept. of Biology, University of Oregon, Eugene, Oregon 97403**


It is an established fact that our climate is changing. From time to time some of our more or less helpless politicians talk about it and various green movements present new horror scenarios. It is also an established fact that the climate of Earth keeps changing more or less continuously; at different times Europe was both much warmer and much colder than now and the present average values have not reached those of the post-glacial optimum, a period presumably decisive for the forming of the present European ranges of most butterfly species. It is no secret that without drastic measures to cut the ever accelerating growth of human populations in most third world countries, the warming of Earth's atmosphere can not be slowed down. We (and above all the next generation) will
have to learn to live in new conditions whether we like it or not. It will then be
too late to discuss in retrospect who is responsible for what: politics is an art of
the possible in one particular moment.

In this context the book under review appears to be even more important and
timely, and it is an exceptional book by all standards. Butterflies, surely the best
researched invertebrate group, are possibly the most important "bio-indicators"
of climatic change. Roger Dennis, an acknowledged British butterfly biogeogra-
pher and ecologist, explains the interactions between butterfly individuals and
populations on the one hand and on the other, the atmospheric systems in which
they live and which impose constraints upon their activities. In one of the most
interesting chapters (Morphological adaptations to climatic gradients), the
author attempts to explain how gradients in adult butterfly morphology and color
pattern relate to climate gradients. Finally, in the chapters entitled "Past
climates and evolutionary history" and "Further atmospheric changes and
butterfly populations: predictions and consequences" he examines adaptive
responses to climatic change using models to explain past events and to predict
the impact on butterfly populations during the global warming. It does not matter
that some of the author's discussions can be considered controversial; but what
I do find lacking is a more complex European approach with extensive references
to the species not represented in Great Britain.

This book constitutes a major contribution to butterfly ecology and biogeogra-
phy as well as to our understanding of how anthropogenically caused climatic
changes affect butterfly distribution, and has implications for effective long term
butterfly conservation. The book is a must for every butterfly ecologist and
biogeographer and interesting to taxonomists and knowledgeable conservation-
ists. It is packed with information from various disciplines and therefore not easy
to read; summaries of the contents of all chapters would have helped the reader
to follow and better understand the author's complex conclusions. This is a small
criticism in view of the overall result. Roger Dennis deserves our congratulations
on his accomplishment and the publishers our thanks for taking the risk of
publishing such an unusual book.

Otakar Kudrna, Karl Straub Strasse 21, D-8740 Salz (Bad Neustadt),
Germany.

Common. Monographs on Australian Lepidoptera: Volume 3, 390 pp +xvi. CSIRO

This third volume of the Monographs on Australian Lepidoptera series is the
first of a three volume monograph of the Oecophorine moths. Common estimates
that there are presently about 1850 valid species names distributed among over
250 genera in the subfamily. He estimates the total fauna will embrace 5000
species! The Wingia group of 91 genera are revised in this volume. The group is
almost entirely endemic to Australia. Altogether the Oecophorinae represent
about 20% of the Australian Lepidoptera. Most species are believed to have
evolved within Australia from Gondwanan ancestors and most use the "dry fruit"
members of the Myrtaceae as foodplant. Many species feed on dead Eucalyptus
leaves. The high diversity of the group and often dense populations imply they are important to recycling leaf litter of these refractory plants into humus.

The revision includes detailed information on genitalia of both sexes, distribution and biology. A total of 500 valid species names are referred to, with an additional 268 undescribed species identified in collections. Thirty-five of the 91 genera are new.

A preliminary phylogenetic analysis was attempted using Hennig86, but several subgroups remain unresolved with some anomalous genera. There are 712 high quality figures, mostly photographs of adults and their genitalia.

The work greatly advances our knowledge of this speciose subfamily while emphasizing the enormous task yet remaining before we have a comprehensive understanding of biodiversity on our planet.

Rudolf H. T. Mattoni, Department of Geography, UCLA, Los Angeles, CA 90095-1524.


Namibia (formerly Southwest Africa) is a large country in southern Africa with a coastline along the Atlantic Ocean. Despite its large size, the saturniid fauna is somewhat depauperate due to the arid climate. The author Rolf Oberprieler, an entomologist in Pretoria, was a long-term resident of Namibia and has done an outstanding job of documenting the Saturniidae of this region. There are 25 species known from that country, plus three that are likely to occur there. The text for each species covers the basics, and on the facing page are color photographs of pinned adults and, in many cases, mature caterpillars. Photographs in introductory chapters show eggs, cocoons, young larvae, and live adults. The author is an accomplished photographer and the color reproduction of his photographs is good but not excellent. I did not find misspellings or typographical errors. The book is well-organized.

Oberprieler discusses the collecting history of the region, a discussion which is entirely eurocentric by necessity. He also gives brief discussions on the ecology, biology, and conservation of these moths. He then describes the ecosystems of Namibia as they relate to the distributions of the saturniids. Another introductory chapter deals with collecting, preservation, and rearing of specimens. The ideal reader of the book would be an amateur entomologist who is a resident of southern Africa. However, considering the worldwide popularity of these big moths and the literature about them, I am sure many copies will be sold outside of Africa. There is almost nothing available that is not out-of-print on the saturniids of Africa. Use these reasons plus the abundant color photographs to justify paying the price.

Richard S. Peigler, Denver Museum of Natural History, 2001 Colorado Blvd., Denver, CO 80205-5798

As a wildlife photographer of many years, nothing strikes more fear in my heart than having to photograph insects. Not that I'm afraid of getting stung or anything like that. But it's the work and challenge of getting down and close to a prey more elusive than the swiftest bird or predatory mammal. The years of experimentation just to get the techniques down have stopped me from ever venturing into this fascinating and intriguing world.

Much to my relief, Larry West and Julie Ridl have opened doors to insect photography with this book. They have done an excellent job of taking years of experimentation out of the insect photography equation. Any question on techniques for photographing the smallest of our many-legged friends is answered in these pages.

The book starts with an inspiring section on the challenges and rewards of insect photography. It opens the doors of the creative mind to the possibility of finding more in the Florida Everglades than herons and alligators. It offers up the possibility of finding a mosquito that holds its legs in a unique fashion or of offering your hand as a bait in hopes of photographing elusive quarry.

After inspiring us to stop and look in the first chapter, West and Ridl take us in the next into the equipment needed to quench our new thirst. The text does an excellent job of defining the equipment needed to be successful at bug photography. It goes further in additional chapters in applying that equipment to specific problems and their solutions. From my point of view, insect photography is one big problem made up of thousands of little ones. West and Ridl are to be commended for making mincemeat of these little problems, making it possible to literally go right into the field and successfully photograph whatever creatures we might come across.

Probably the most rewarding and educational aspects of the book are the rich illustrations and their captions. Great effort is made to accurately depict what went into the making of the photographs. You could just look at the photographs and read their captions and learn more on insect photography than previously written in other books.

The topic is summarized beautifully in the last chapter by helping us better understand the insect world in which we live. It not only helps us get a foot up on understanding them and where they live, but our responsibility towards them. The ethics discussed behind creating the images is timely as well as insightful.

Larry West and Julie Ridl did us all a big favor. They did more with their book than explain the many mysteries intrinsic to insect photography. They opened the doors for all of us with cameras to explore the minute world that surrounds us. They make it possible to find subjects no matter where we are, city or wilderness, and turn them into giants that can shake the world. I'll be darned if I'm going to give up my copy of the book. I suggest you go out and get your own!

B. "Moose" Peterson, Wildlife Research Photography, P.O. Box 30694, Santa Barbara, CA 93130
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Review: All papers will be read by the editor(s) & submitted for formal review to two referees.
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Male Mate-Locating Behavior in Two Australian Butterflies, *Anaphaeis java teutonia* (Fabricius) (Pieridae) and *Acraea andromacha andromacha* (Fabricius) (Nymphalidae)

John Alcock

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**Abstract.** Scramble competition for access to emerging virgin females that are moderately to highly aggregated characterizes male mating tactics in some populations of two Australian butterflies, *Anaphaeis java teutonia* (Pierinae) and *Acraea andromacha andromacha* (Acraeinae).

**Key Words:** *Anaphaeis, Acraea, mating strategy*

**Introduction**

I present notes on the mating systems of two Australian butterflies, *Anaphaeis java teutonia* (Fabricius) and *Acraea andromacha andromacha* (Fabricius), as a contribution to the natural history of these species. The male mating tactics of neither butterfly has been previously described (Common & Waterhouse, 1982), although Hawkeswood (1991) reports commonly encountering mating pairs of *A. andromacha* on a larval foodplant, *Passiflora suberosa*.

**Anaphaeis java teutonia**

The mating behavior of this species was first observed on 23 and 25 July 1993 in Kalbarri National Park about 5 km south of Kalbarri, Western Australia. Several dozen males were flying in a shallow rocky gorge within a few hundred meters of the coastline. Much of the activity was centered around a single caustic bush (*Sarcostemma australe*, Asclepiadaceae). Certain stems of the shrub were lined with a total of 29 pupae and empty pupal cases of the butterfly.

At 1500 hrs on 23 July, 17 males and 3 females were flying around or were perched in or near the shrub, including two pairs in copula. Unmated males flew several meters out and back from the plant, some inspecting the mating pairs closely, others courting (unsuccessfully) a single, apparently freshly eclosed, female perched in the area. This female was not receptive; she elevated her abdomen, and spread and fluttered her wings in response to courtship attempts.

At 1000 hrs on 25 July, 8 males and 2 apparently recently eclosed but unpaired females were present in and around the shrub; later that day at 1350 hrs, 15 males and 5 females were found in or near this one plant, including four pairs in copula on stems of the caustic bush. All mating males seen on both days possessed extremely worn wings (Fig. 1). Two males had been captured and killed in a spider web in the caustic shrub.

Paper submitted 25 May 1995; revised manuscript accepted 17 November 1995.
Fig. 1. A very worn male copulating with a freshly eclosed female of *Anaphaesis java* at a site within Kalbarri National Park, Western Australia.
On another caustic shrub in the same general area I found four pupal cases in close proximity to one another, with one fresh adult female perched in the plant and three flying males nearby.

This species was also observed on 14 September 1993 at Vampire Gorge, Karajini National Park, Western Australia. On this day at 0830 hrs, there were two copulating pairs in a dead, leafless shrub (which was not *S. australis*) less than a meter high. About 12 unmated males flew in and around the plant on whose dead stems were aggregated 106 pupae and opened pupal cases. As at the Kalbarri site, copulating pairs were approached by patrolling males, which courted them (Fig. 2).

**Acraea andromacha andromacha**

This species was observed on 22 and 23 September at Windjana Gorge National Park, Western Australia in a flat plain of shorter dry grass roughly 155 m x 35 m surrounded by a taller savannah (Fig. 3). The male butterflies were flying low over the grasses in which were scattered numerous last instar larvae and pupae suspended from dried grass stalks. Over two mornings, records were made of the substrate on which 20 mating pairs were perched; 17 (85%) were found on a stem next to a cast pupal cuticle, indicating that males were mating primarily or exclusively with freshly emerged individuals (Fig. 4).

At 0900 on 23 September, the mean distance between one copulating pair and its nearest neighboring pair was 6.2 + 4.2 m for 11 different dyads. Thus, emerging, receptive females were present in moderately high density within the short grass patch.

Two solitary females that had recently eclosed were observed until contacted by patrolling males in 7 and 13 min respectively. The males courted the perched females in flight by buffeting their wings for a brief period, with copulation following.

In both cases, I carefully separated the male from the female within one min of the onset of copulation, and then returned the female to her perch. Female A was not approached by a male until 40 min had elapsed. The female rejected his persistent courship by twisting her abdomen away from his and by opening and closing her wings. However, female A was seen mating 2 hr after her first copulation was experimentally terminated.

Female B was courted six times (presumably by different males) in the first 30 min after she was separated from her first partner; she rejected all six suitors but was seen coupled with a male 60 min later.

Searching males also courted copulating pairs (*n* = 3 records) as well as freshly eclosed males (*n* = 3) and even a pupa (*n* = 1), in addition to the unreceptive, experimentally unpaired females.

**Discussion**

Males of both species were seen searching for and mating with recently eclosed females. Males of the pierine *Anaphaes java* focused their search on
Fig. 2. Unmated males of *Anaphaesis java* courting a copulating female at Karajina National Park, Western Australia. Note the line of pupal cases below the adult butterflies.
Fig. 3. The short grass plain that lies within taller grasses in the open savannah-eucalyptus woodland at Windjana National Park, Western Australia.

Fig. 4. A pair of *Acraea andromacha* on a dried grass stem; the pupal case of the freshly eclosed female appears between the two butterflies.
plants where large numbers of pupae were clustered together. These plants were not the larval foodplant, which are caper trees, *Capparis* (Hay et al., 1993), but rather leafless shrubs with considerable open stem space on which to pupate.

Males of *Acraea andromacha* patrolled a region where eclosing females were more diffusely distributed than in *Anaphaeis java*. Nevertheless, the density of females was much greater in the short grass area than in the surrounding savannah. In this species, pupation and eclosion also took place on a substrate (dried grasses) other than the larval foodplant, which is reported to be *Passiflora* spp. (Hawkesworth, 1991).

Male behavior in both species is consistent with the expectation that males will focus their mate-searching at sites where eclosing females are relatively densely distributed (Rutowski, 1991). As Rutowski (1991) points out, female butterflies typically become receptive as they eclose or soon thereafter, judging from the rarity with which virgin females are found in the field. The receptivity of freshly emerged females clearly applies to the two Australian species whose behavior is described here. Under these circumstances, sexual selection favors males that can locate places containing higher than average numbers of eclosing females. Pupae are densely clustered in *Anaphaeis java* and moderately aggregated in *Acraea andromacha*, a fairly unusual phenomenon in butterflies that may be a defensive phenomenon linked to distastefulness in these species. In any event, the existence of pupal clusters concentrates freshly emerged females in small areas, enabling males to search economically for mates in these places.

Males are also predicted to time their mate-locating behavior to coincide with the periods when female eclosion is most likely to occur. The abundance of patrolling males of *Acraea andromacha* in the early morning at Windjana is consistent with the report that most males in a laboratory population emerged in the very early morning, with females following a little later (Hawkesworth, 1991).

Although territorial behavior has been reported for many butterflies (reviewed in Rutowski, 1991), neither species observed here exhibited territoriality. The limited duration of my observations means, however, that I cannot rule out the possibility that some males defended pupae that were on the verge of eclosing, as has been seen in a few butterflies (Bellinger, 1954; Elgar & Pierce, 1988). However, males that found females of *Acraea andromacha* that had been experimentally separated from their partners early in copulation did not remain with them. Moreover, the dominant mode of behavior for both Australian species clearly was nonaggressive patrolling. The relatively large number of individuals searching for mates within a small area, particularly in the case of *Anaphaeis java*, may have contributed to this outcome, inasmuch as the costs of repelling intruders from an area even a meter or two square would probably have been substantial.

The importance of finding freshly-eclosed females before rival males almost certainly favors patrolling flight over perch and waiting. Under some conditions, males of both species clearly engage in scramble competition for
access to eclosing females. Whether males have alternative mate-locating tactics remains to be documented, although observations of *Acræa andromacha* males at hilltops (Rutowski, pers. obs.) strongly suggest that they do.

Acknowledgements. I thank Michael F. Braby for providing assistance with the literature search and Ronald L. Rutowski for his comments on the manuscript.

**LITERATURE CITED**


A new species of *Saturnia* (Saturniidae) from northern Pakistan

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Abstract. *Saturnia codyi* n. sp. is described and figured in color and compared to related species. It has been collected at altitudes around 4000 m in the western Himalayas of northern Pakistan. The species belongs to the species-group commonly classified in the genus *Neoris*, of which several known species range in Siberia, western China, northern India, and westward to eastern Turkey. The new species has the darkest wing coloration in this group. The female and immature stages are unknown.

The genus *Saturnia* Schrank (Saturniidae) ranges widely in the Northern Hemisphere, with about 30 known species. They mainly occur in Palaearctic Eurasia, but a few are known from California and tropical southeastern Asia. One group of species has been classified by some authors as belonging to the genus (or subgenus) *Neoris* Moore. The only significant review of this group since that of Jordan (1911: 219) was a detailed and excellent one published recently by de Freina (1992). In March 1995 I found four male specimens of an undescribed species in the collection of The Natural History Museum in London. Specimens of most other taxa in this group were arranged alongside, leaving little doubt that the new species was different. In addition to examining type specimens, I checked descriptions and/or specimens of all other taxa in the *Neoris* group. The new species is described below, and a diagnosis comparing and contrasting it to other species is provided.

The representatives of this species-group live in central Asia, in montane habitats usually at high elevations (Figs. 8-9). The moths fly in late summer or fall, the eggs overwinter, and the larvae feed in spring and summer on broad-leaved trees such as ash (*Fraxinus*, Oleaceae), birch (*Betula*, Betulaceae), *Pistacia chinense* Bunge (Anacardiaceae), various Rosaceae (e.g., *Pyrus*, *Malus*, *Prunus*, *Spiraea*), etc. The larvae are green with soft hairs and minimal armature (i.e., scoli very reduced). The cocoons are brown, pyriform, with very minute reticulations. Pinned specimens are rare or absent in most collections, because populations occur in remote, inaccessible regions.

Description

*Saturnia codyi* Peigler, **new species**

Holotype. Male (Fig. 1). Pakistan, Northwest Frontier Province, Ghizar Mountains, Yasin, 4000 m, early September. The labels read as follows: 77.; India sept. occ., Chitrал, Yasin, 4000 m, Anf. [Anfang] September; Rothschild Bequest B.M. 1939-1. Pakistan was formerly part of India. I added a red label

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which reads: Holotype *Saturnia codyi* Peigler 1995. Forewing length 50 mm; hindwing length 40 mm.

**Paratypes.** Two males, same labels as holotype, except numbers 76 and 78, instead of 77. One male, Pakistan, presumably Northwest Frontier Province, Bulachi, 4000 m, 17 August 1923, C. H. Stockley collector. Labels read as follows: Emperor moth, Bulachi 12000', 17/8/23 [handwritten]; Bulachi, W. Gilgit Prov., Kashmir, 12 000 ft., 17 VIII 1923, Maj. C. H. Stockley, Brit. Mus. 1924-247 [typeset]. I added blue paratype labels.

All type specimens are in The Natural History Museum, London. Although the male from Bulachi (Figs. 2-3) is in the best condition, a specimen from Yasin was selected to make that the type-locality, as I have been unable to locate Bulachi on any of several detailed maps.

**Male.** Antennae stramineous, 17 mm long. 8 mm wide. Frons light or dark brown. Thoracic collar whitish. Thorax and abdomen brown, with white bands on abdominal segments. Legs unicolorous brown. Forewing 50-54 mm in length; antemedian area dark brown or pinkish, antemedian line faint, brown, median area sprinkled with white scales, brown distally; ocellus 7-8 mm long, oval, mostly brown, with yellow, white, and blue scales proximally; postmedian line scalloped with light brown, black, and broad white components; postmedian area dark brown; trace of red in apex. Hindwing 40-42 mm in length; antemedian area and line indistinct, brown or pinkish; median area brown; ocellus as in forewing but larger, and with more black edging; postmedian line whitish, double, smoothly rounded (the inner portion almost straight); postmedian area as in forewing. Underside with markings more distinct; ocelli in forewing may or may not contact postmedian line; hindwing ocelli much smaller than on upperside.

**Female and Immature Stages.** Unknown.

**Diagnosis.** The new species is much darker chocolate brown than all other known taxa in the group, giving the illusion that the postmedian line has a much stronger white component in both forewing and hindwing. The postmedian line is much smoother in the hindwing than in other species. In the forewing, the postmedian line is not drawn inwards as far at the anal margin than in other species. The antemedian line is weakly defined, even more so than in *huttoni*. The ocelli are smaller and have darker components than other species. One paratype from Yasin was dissected. Comparison of the male genitalia from this specimen to the series of valves shown by de Freina (1992: fig. 3) reveals that the valve of the new species has an even more reduced median notch than all other taxa.

**Etymology.** This new saturniid is named in honor of Dr. John Cody (Hays, Kansas, U.S.A.) in recognition of his work through art, writings, and lectures to bring awareness to the public of the need to preserve habitats of Saturniidae.

**Discussion**

Although the group of species discussed in this paper form a compact and obviously monophyletic assemblage for which the generic name *Neoris* (type species: *Neoris huttoni* Moore 1862) is available, the broader concept of
Saturnia appears to me to be more useful as it demonstrates relationships with many more species, thus fulfilling the original concept of predictability intended by C. Linnaeus when he established the category of genus. Usage of subgenera adds a layer of complexity to nomenclature with minimal benefit. I therefore use the concept of species-groups within larger genera such as this one. Lemaire (1978) followed the same plan in his treatment of large genera such as Rothschildia and Copaxa, by defining species-groups to indicate relationships, without proposing formal subgeneric names. Saturnia caecigena Kupido, a species from southeastern Europe usually classified in the monotypic genus Perisomena Walker, is probably the sister-group to the Neoris complex, as suggested by Jordan (1911: 219). The wing pattern in the various Saturnia was discussed by van Bemmelen (1919), including a species in the huttoni-group.

The huttoni-group is in need of taxonomic revision, although de Freina (1992) provided a firm foundation toward that end. He apparently had specimens from several regions of central Asia available, and dissected male genitalia from distant populations. The genitalic differences are not strong, which probably resulted in his treatment of all taxa in this group as subspecies of huttoni (Fig. 5). In my opinion, the differences in adult facies are too distinctive to reconcile these taxa under a single species. De Freina synonymized the following names under shadulla (Moore 1872), an arrangement with which I concur: stoliczkana (C. Felder & R. Felder 1874), schencki (Staudinger 1881), oliva A. Bang-Haas 1910, and haraldi Schawerda 1923. De Freina retained the taxon galera (Püngeler 1900) as a separate western subspecies (from Iran) allied to naessigi, which he described from eastern Turkey as new. Norbert Keil provided material of naessigi to me for study. Peigler and Kendall (1993: 11) elevated naessigi to full species rank, which differs from all other taxa in this group by the moths being twice as large. In their paper on saturniids of China, Zhu and Wang (1993: 278-279) cited haraldi from Shaanxi, Gansu, and Xinjiang provinces, and stoliczkana from Xinjiang and India, and figured the male genitalia of both. Gorbunov and Kishida (1995) reported parthenogenetic reproduction in a taxon they called Neoris huttoni schencki.

Moths in collections or figured in publications labelled under the names shadulla, schencki, stoliczkana, and galera all appear to be very similar in appearance (tan or light brown colored). Colored figures of some of these can be seen in Jordan (1911: pls. 31-32), and black & white photographs were given by de Freina (1992: figs. 9-14). Saturnia huttoni stands apart from these with its brownish orange ground color and more elongated wings. Likewise, S. codyi is unique with its dark brown coloration, shortened wing shape, and certain other features of the wing pattern, as given in the diagnosis above. Saturnia naessigi is figured here in color for the first time (Fig. 7), in addition to the underside of S. huttoni (Fig. 6).

I examined the following type specimens in The Natural History Museum (London): four syntypes of huttoni of both sexes (type-locality Mussoorie, Uttar Pradesh, India); holotype (or syntype?) female of stoliczkana (type-
Figure 7. *Saturnia naessigi* de Freina, male in living repose, Tunçeli Province, Turkey. Transparent watercolor painting by John Cody.
Figure 8. Darkot Valley 20 km north of Yasin, Pakistan. 2800 m. July 1981.
Figure 9. Gilgit Valley 5 km from confluence with the Darkot River. 2650 m. July 1981. Figures 8 and 9 courtesy of R. Mattoni.
locality Lossar, 13,500 feet, Ladakh Mountains, Kashmir, India); pair of syntypes of shadulla (type-locality: Xaidulla, southern Xinjiang Province, China). I examined the specimens from Afghanistan and Tajikistan (=Tadzhikistan) in the Muséum National d’Histoire naturelle in Paris that Rougeot (1969) referred to under the name schencki. They are clearly of the shadulla/galeropa subgroup. In the latter museum I also examined four males of galeropta from the vicinity of Tehran, Iran.

Two additional names have been proposed that were not considered by de Freina (1992). Neoris huttoni svenihedini Hering (1936) was described from a single male from Manas, near Ürümqi, northern Xinjiang Province, China, in the Tian (=Tien) Shan Mountain Range. Neoris huttoni alatauica O. Bang-Haas (1937) was described from an unspecified number of males from Almatinka, 1500 m, western Ala Tau Mountains, northern Tian Shan Range, Kazakhstan. Based on the brief descriptions and type-localities of svenihedini syn. nov. and alatauica syn. nov., I consider them to be synonyms of the widely-ranging shadulla. No figures were given by Hering or Bang-Haas. Three male specimens (see Fig. 4) from the Ala Tau Mts. sent to me by Dale Pforr in 1971 agree with the types of shadulla.

Based on a small sample of pinned specimens available to me for study, I believe that there are at least four species in the Neoris group: huttoni, shadulla, codyi, and naessigi. However, considering the vast distances and high altitudes of the distributions of these moths, I expect that up to a dozen species will ultimately be found to exist. Isolation by high mountains resulting in speciation is a well-known phenomenon in Saturniidae. Some of the other names already proposed that were considered to be synonyms by de Freina (1992) may prove to be valid species. Political unrest will continue to hinder collecting, both in the new republics of the southern parts of the former Soviet Union (Azerbaijan, Uzbekistan, Turkmenistan, Kazakhstan, Tajikistan, Kyrgyzstan), and in the Kashmir region where vast tracts of territory remain in dispute between India, China, and Pakistan.

Acknowledgments. I extend special thanks to David Goodger of The Natural History Museum (London) for the loan of specimens and his invaluable help during my latest visit to that museum, making this study possible. Dr. Joël Minet of the Muséum National d’Histoire naturelle (Paris) provided access to that collection for my study. Goodger and Minet also provided copies of pertinent literature. Dale E. Pforr (University of Alberta, Edmonton, Alberta, Canada) and Norbert Keil (Dachau, Germany) sent specimens in this group essential for this study. I thank John Cody for permitting publication of his exquisite painting of Saturnia naessigi.

Literature Cited


The Host Plant and Pre-imaginal Stages of *Actias callandra* (Saturniidae) from the Andaman Islands, India

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**Abstract.** The pre-imaginal stages of *Actias callandra*, a silk moth endemic to the Andaman Islands, are described and figured in color for the first time. The larvae were reared to maturity on *Lannea coromandelica* (Anacardiaceae); another possible hostplant is *Rhizophora*. The cocoon apparently has no sericultural value. It is proposed that *A. callandra* be treated as a distinct species, instead of a subspecies of *A. selene*, on the basis of various morphological differences, especially between the second instars and the coloration of the wings of the males of the two species.

**Key Words:** Anacardiaceae, Andamans, island biogeography, *Lannea*, moths, Nicobar Islands, saturniid

**Introduction**

This paper reports field observations and rearing by the two first authors of the saturniid *Actias callandra* Jordan, new status, a large “moon moth” endemic to the Andaman Islands. Since the original description (Jordan 1911: 130), it has been considered by all authors to be a subspecies of *Actias selene* (Hübner), which ranges from Afghanistan to Borneo.

The Andaman and Nicobar Archipelago, consisting of about 324 islands (Snow 1970), is located at the junction of the subducting Indian plate and the Burmese and Southeast Asia plates/platelets (Curry 1989, Hamilton 1989) in the Bay of Bengal in the northeastern Indian Ocean. These islands have not been connected to any of the adjacent continental land masses since at least Pleistocene times. The Andamans and the Nicobars also were not connected with each other during that part of Pleistocene when the sea level was lower (Ripley & Beehler 1989). Consequently each island group harbors a unique biota with a relatively high proportion of endemics. The Andamans are said to have a greater biotic affinity with Burma, while the Nicobars are thought to possess a biota that is derived more broadly from Southeast Asia. Interestingly, the currently known saturniid fauna of these islands conforms to the above biogeographic pattern, although no saturniid has been re-

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corded from the Nicobar Islands. This is a reflection of the uneven collection effort in the two island groups, as the British, who colonized these islands for the second time in the latter half of the 19th century, had their headquarters in Great Andaman (the three contiguous islands of North, Middle and South Andamans, Baratang and Rutland), so most of the serious insect collections made during this period were centered on those islands. With no major colonial settlements in the Nicobars, collecting from these islands has always been minimal. In the post-colonial era, no change was made in the location of the headquarters, so the Indian government has continued to rule the archipelago from Port Blair, South Andaman. In addition, offices of all the major scientific institutions are located at Port Blair, so that even today the biota of the Nicobars remains less studied as compared with that of the Andamans.

Six species of Saturniidae belonging to five genera have so far been recorded from the Andaman Islands, all of which are considered to be endemic to these islands (Peigler 1989). Three of these are endemic species while the other three are presently considered to be endemic only at the subspecific level. The type locality of all these taxa is Port Blair or “South Andaman”. Only two species of Actias have been recorded from the Andamans, A. ignescens Moore, which closely resembles A. maenas Doubleday from the Southeast Asian mainland and Greater Sunda Islands of Indonesia, and Actias callandra, which has been considered a subspecies of A. selene from the mainland (Moore 1877, Hampson 1892, Conte 1918, Peigler 1989). The report by Arora and Gupta (1979) of A. maenas (which they assigned to the genus Sonthonnaxia) and A. selene occurring in the Andaman Islands actually referred to the two endemic species, viz. A. ignescens and A. callandra, respectively. We are certain of this because the listings by Arora and Gupta under “material examined” show that they did not examine material from the Andamans; they simply were including all “subspecies” of A. selene and A. maenas as part of the distributions.

All the Andaman saturniids are known only from the adults, except where we recently reported on the life history of Attacus mcmulleni J. H. Watson (VeenaKumari et al. 1995). No information is available on the immature stages, host plants, or life histories of the other Andaman taxa. We have therefore been trying to fill in this void in our knowledge of the Saturniidae of the Andaman and Nicobar islands. In keeping with this objective we describe below the pre-imaginal stages of Actias callandra and outline the life history of this saturniid in the island of South Andaman. The most detailed study to date on the life history of a species in the Actias genus-group was carried out by Ylla (1992). Its scope far exceeds any work done for related species in North America, Africa, and Asia, so there remains much to be learned about these large moths which are supposedly “well-known”.

**Materials and Methods**

Adult females of *A. callandra* captured at light at night or resting on foliage in the forest during the day were caught and confined in large transparent plastic jars (9 cm
x 19 cm), or wooden cages (44 x 30 x 30 cm) with sides of glass and wire mesh. Eggs laid by wild females were incubated at ambient temperatures (27 °C) and relative humidity (83%).

Since large numbers of the eggs hatched almost simultaneously, the first two larval instars were reared en masse in the large transparent plastic jars (9 cm in diameter, 19 cm high). Subsequent instars were reared individually in similar jars. The tops of the jars were covered with cloth and fastened securely with rubber bands. All frass was removed and the walls of the jars wiped clean with a cloth daily. Simultaneously all old food was removed and the larvae provided with fresh, green leaves of their host plant.

Prior to our having procured the first batch of eggs from a captive female, the only pre-imaginal stage of *A. callandra* that we found was one live cocoon on a plant, as cited below. We therefore fed the newly hatched larvae with leaves from the plant on which we had found this live cocoon. Fortunately the larvae readily accepted these leaves as food. All descriptions were made within a day or two after the larvae molted. Measurements of newly hatched larvae were taken when their rearing containers were being routinely cleaned. The presence of head capsules in the rearing containers indicated that molting had occurred. Larvae in the final instar were provided with a sturdy stick to facilitate cocoon formation. Only rarely did the larvae spin among the leaves against the side of the container.

Voucher material from the rearings is deposited at the Entomology Section, Central Agricultural Research Institute, Port Blair, and the Denver Museum of Natural History, Colorado. In March 1995, the third author studied specimens of *A. callandra* in The Natural History Museum (London). The material consists of seven syntypes, five males and two females, all labelled as coming from Port Blair, without indication of the dates or collector. Two pairs of Jordan’s (1911: 131) original syntypes were not located. One male labelled “Type” has a forewing length of 70 mm. An additional series of nine males and five females was reared by J. H. Watson from cocoons he received from W. F. McMullen; this lot also includes five cocoons, a vial of dried ova, and a pupa. One cocoon is labelled “Haddo, Andamans.” Some of Watson’s material was figured by Packard (1914: pl. 95). Males have a forewing length of 55-70 mm; females 80 mm. Males have a hindwing length of 65-90 mm; females 100-105 mm. The wing coloration of most males is a distinctive deep yellow, quite unlike the pale green in males of *A. selene*, but a few of the males of *A. callandra* appear greenish. This is probably a seasonal color difference (M. M. Collins, pers. comm.); indeed the two yellow males in the Denver Museum of Natural History emerged 21 September 1995 and the green one 22 March 1995. The postmedian lines are very prominent and dark brown in both sexes. The ocelli in each wing are smaller in both sexes of *A. callandra* than in *A. selene*.

**Results**

**Life Cycle.** *A. callandra* took from 39 to 61 days to complete its life cycle with a mean duration of 50 days (Table 1). Though we reared through to adulthood only those larvae that emerged from the eggs laid in April, we could find little difference in the duration of the pre-imaginal stages in a comparison among broods begun in the months of April, July, August, September and November. The only durations that did not fall into the ranges of the April brood were for that of the first instar (some of which molted after three days) and the fourth instar (some of which exceeded the
Table 1. Duration and dimensions of the pre-imaginal instars of the April brood of *Actias callandra* in South Andaman Island

<table>
<thead>
<tr>
<th></th>
<th>Egg</th>
<th>Larval instars</th>
<th>Pupa</th>
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<tr>
<td></td>
<td></td>
<td>I</td>
<td>II</td>
</tr>
<tr>
<td>Duration (days)</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>n</td>
<td>8</td>
<td>23</td>
<td>22</td>
</tr>
<tr>
<td>Mean</td>
<td>11.75</td>
<td>5.30</td>
<td>4.72</td>
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<tr>
<td>Range</td>
<td>7-15</td>
<td>4-6</td>
<td>3-6</td>
</tr>
<tr>
<td>S.D.</td>
<td>3.33</td>
<td>0.55</td>
<td>0.76</td>
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Dimensions (cm)

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<tr>
<td>n</td>
<td>20</td>
<td>6</td>
<td>5</td>
<td>17</td>
<td>21</td>
<td>17</td>
<td>10</td>
</tr>
<tr>
<td>Mean</td>
<td>3.37 × 2.79</td>
<td>0.73</td>
<td>1.62</td>
<td>2.50</td>
<td>3.81</td>
<td>6.49</td>
<td>6.41 × 3.31</td>
</tr>
<tr>
<td>Range</td>
<td>(3.3-3.6)</td>
<td>0.6-0.8</td>
<td>1.4-1.8</td>
<td>2.2-2.9</td>
<td>3.5-4.0</td>
<td>5.8-7.2</td>
<td>(5.8-7.5)</td>
</tr>
<tr>
<td></td>
<td>×</td>
<td>(2.7-2.8)</td>
<td>×</td>
<td>(2.2-3.8)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>S.D.</td>
<td>0.08 × 0.02</td>
<td>0.08</td>
<td>0.17</td>
<td>0.20</td>
<td>0.25</td>
<td>0.49</td>
<td>0.60 × 0.45</td>
</tr>
</tbody>
</table>

Note: For eggs and pupae, dimensions are recorded as length × width

range in Table 1 and molted after 8 days). Even larvae that hatched on the same day varied in the period that they took to complete each of the instars.

**Host plant.** *Lannea coromandelica* (Houtt.) Merrill (= *Odina wodier* Roxburgh), Anacardiaceae, a deciduous tree with compound (imparipinnate) leaves, was the only host plant on which we reared *A. callandra*. In spite of searching diligently, we rarely found the pre-imaginal stages of this moth on trees in the forest. The finding of one live cocoon on a young *L. coromandelica* tree at Chiriyatapu (S. Andaman) in 1993 gave us the first clue to at least one of the possible food plants of *A. callandra*, finally enabling us to successfully rear *A. callandra* in the laboratory when we obtained eggs from females which were caught at light at night and confined in cages.

In August 1994, we collected one empty cocoon on a shoot of a mangrove (*Rhizophora* sp., Rhizophoraceae). The tree on which this cocoon was found was growing well within a mangrove community. We see very little possibility of a larva having wandered off from some other host plant to pupate on this mangrove tree. Therefore, circumstantial evidence points to *Rhizophora* being another host plant of *A. callandra*, but this needs confirmation.

**Phenology.** We collected adults at light in the months of April, July, August, September, and November 1993. Adult females collected in all these months laid fertile eggs from which it was possible to rear the larvae that emerged on leaves of *L. coromandelica*. We therefore surmise that *A. callandra* is multivoltine. Since *L. coromandelica* is deciduous in the Andamans, shedding its leaves
Table 2: Measurements (mm) of the head capsules of the first four larval instars of *Actias callandra*

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<th>III</th>
<th>IV</th>
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<tbody>
<tr>
<td>n</td>
<td>4</td>
<td>7</td>
<td>21</td>
<td>11</td>
</tr>
<tr>
<td>Mean</td>
<td>1.20</td>
<td>1.68</td>
<td>2.69</td>
<td>4.46</td>
</tr>
<tr>
<td>Range</td>
<td>Nil</td>
<td>1.6-1.7</td>
<td>2.5-2.8</td>
<td>4.2-4.6</td>
</tr>
<tr>
<td>S.D.</td>
<td>0</td>
<td>0.03</td>
<td>0.09</td>
<td>0.13</td>
</tr>
</tbody>
</table>

in the hot season, *A. callandra* must either pass a short period of diapause or it must use alternate hosts during the period when *L. coromandelica* is leafless.

**Description of Immature Stages**

The following descriptions were made from live specimens reared in the laboratory. The first instars were described within 2 days after eclosion, while all the other instars were described within 2-3 days following a molt. The measurements of all the pre-imaginal stages and the cocoon are given in Table 1, and head capsule measurements in Table 2. Specimens in the various stages are shown in Figures 1-8.

**Egg.** Color dirty white to gray and slightly dorsoventrally flattened. Lower surfaces coated with deep brown encrustations secreted by the females to cement them onto the leaf surface. The first instar larva emerges by making an irregular opening in the micropylar end. The surface of the chorion has a number of small, circular pits, the margins of which are not in contact with each other.

**First instar.** The head and first 7 abdominal segments black, thoracic segments and posterior abdominal segments from eighth to anal segment orange-brown. Orange color of prothorax brighter than meso- and metathorax. Spiracles black. Setae on dorsal and subdorsal scoli black with 6-10 terminal setae on each scolus. Setae on lateral scoli and head dirty white. Scoli dirty white except those on mesothorax, metathorax and terminal abdominal segments which are a deep yellow-orange, of the same hue as the segment from which they arise. Legs brown along outer surfaces and off-white along inner surfaces. Claws brown. Prolegs off-white with brown crochets, with two black, narrow, annular bands on each proleg. Anal prolegs lacking annular rings. Clypeus and labium off-white, palps off-white proximally and yellow-orange distally.

This and all succeeding instars were observed to rest on the lower surfaces of leaves in the rearing containers.

**Second instar.** Head glossy black, remainder of larva pale black in color with a discontinuous, darker black mid-dorsal line. Antennae and clypeus off-white; palps brownish. Legs black. Prolegs light brown, with a broad black distal band from which arise small white setae. Anal and lateral plates on each anal proleg deep black with a number of short, whitish setae. Prothoracic
shield with 2 black, stubby scoli directed anteriorly with about 9 long, black, stiff, bristle-like setae on each. Additionally there are 2 lateral scoli with long hair-like setae which are black basally and white to gray for remainder of length. Subdorsal scoli basally fleshy with a more chitinized blackish apical region, on which is situated one central seta surrounded by others. Central seta disproportionately larger than others with basal two-thirds black, terminal third whitish. Dorsal, subdorsal and lateral scoli present on all segments from prothorax to seventh abdominal segment. Sub-lateral or ventro-lateral scoli present however on the three thoracic segments only. Dorsal scoli the most fleshy basally, followed by lateral scoli. Sub-dorsal and sublateral scoli the least fleshy basally. On eighth abdominal segment only one (not two) dorsal sculus present. On ninth abdominal segment only four scoli viz., the dorsal and subdorsal scoli.

Third instar. In this stage larva turns bright green and continues to remain so in all succeeding instars. Prothoracic shield and ventral surface pale green; anal plate brown. Head pale yellow at vertex and in region of frons with remaining portions light brown. Antennae and clypeus off-white; palps brown. Legs brown, with anal prolegs deeper brown. Prolegs proximally green like remainder of body, followed by narrow black band, followed by broader pale yellow band, and terminating distally in a brownish area. Crochets brown. Small, black setae on prolegs. Spiracles brown, with median white longitudinal stripe. All scoli fleshy basally with bulbous terminal crown on which are situated setae of which one is distinctly longer than all others. Meso- and metathoracic scoli with about 11 setae each; all other dorsal scoli with 5-7 each. All short setae on crown of each sculus either completely black or completely brown, with long setae terminally gray with basal two-thirds either black or brown. Sublateral or ventrolateral scoli, situated only on thoracic segments, very small and green like the remainder of body with very few brown setae. Subdorsal and lateral scoli yellow and small. Unlike other dorsal scoli, those on prothorax very small, even smaller than lateral scoli but larger than subdorsal scoli. Dorsal scoli on meso- and metathorax terminally yellow with black band separating green from yellow region. Setae basally green and terminally orange.

Fourth instar. Pale green with region below spiracular line darker green. Head light brown, covered with small white setae. Frons and adjacent areas tinged light green. Legs and claws brown. Prolegs green, concolorous with remainder of body, with broad, deep green band just above crochets which are brown. Anal plate and rear of anal prolegs deep brown with small, white club-shaped protruberances. Spiracles brown with longitudinal white stripe in region where spiracular lips converge.

Fifth instar. Integument composed of various shades of green. Pale green dorsally with intensity of green increasing down lateral surface. Ventral surface deepest green with midventral pale yellow line running across length of body. Prolegs also deep green like ventral surface. A narrow brown semicircular band present on prolegs. Crochets deep brown in color. Rear margins of anal prolegs and anal plate deep brown or rufous. A narrow yellow
band bordering the outer margin, separating green of body from brown of prolegs. The only black setae on prolegs. Legs deep brown or rufous. Head deep brown or rufous with pale yellow frons. Antennae basally greenish yellow, remainder brown. Labium and labial palps yellowish. Spiracles tan to brown with central, longitudinal yellowish stripe where lips converge. Setae on dorsal surface white to gray with those on ventral surface brown and longer. All setae on body surface sparsely distributed, with those on ventral surface being relatively more abundant.

When disturbed, larvae in the last instar tucked their heads into their legs and reared up on their second to anal prolegs adopting a snake-like stance, and swayed fairly rapidly from side to side.

**Pupa.** Dark brown, with distinct whitish yellow patch on head between compound eyes. (This transparent spot allows light to reach the brain to control diapause; see Miyata 1974, 1986, Nässig & Peigler 1984). Cremaster with hook-like spines.

**Cocoon.** Initially whitish, papery, and with a distinct sheen, later taking on off-white or dirty white appearance. Spun with its sides adhering to the laminae of the leaves, but always anchored along its length to a twig. Loose strands of silk sometimes on surface. When handled the pupa moves about vigorously. Watson (1911) stated, the “pure white and most lustrous” silk of this species is “valuable”. Cocoons of *Actias* are often pure white when formed in captivity, probably due to reduced light or moisture during spinning. Moisture can change cocoons from white to brown in certain Saturniinae (M. M. Collins, pers. comm.). Some of the cocoons of *A. callandra* in The Natural History Museum are pale tan. The papery cocoons of the genus *Actias* are of little or no value sericulturally (Deodikar et al. 1969; Peigler, unpubl.). After adult emergence, the mean dry weight of the cocoon (inclusive of pupal case) was 0.81 + 0.26 g (n = 4; range 0.47 - 1.10 g). A cocoon containing a live pupa weighed 6.78 g (n = 1).

**Adult behavior.** The only wild adult that we caught was a secund female at about 1100 hours. It was resting on the undersurface of a leaf of *Licuala* sp. (Areceaceae), an understory palm in the forest at Lohabarak, South Andaman. During the course of rearing it was found that both males and females emerged from cocoons in the evening. One male was observed to emerge at 1700 hours, and a female at 1900 hours.

**Disease.** During the laboratory rearing of *A. callandra* a number of the larvae succumbed to a disease. Although we did not get the pathogen(s) identified the symptoms point to a virus. The larvae lost their turdiguity and became sluggish. Infected larvae produced a dark brown ooze and hung with their heads down.

**Discussion**

*A. callandra* has been treated by all authors as a subspecies of *A. selene* (Hampson 1892, Peigler 1989). This study casts doubt on the validity of this status. The second instar larva of *A. callandra* is markedly different in color from the second instar larva of *A. selene*, as described from Hong Kong (Potter
1941) and from Mussorie, India (Cotes 1891-93). While *A. callandra* in this instar is totally black, *A. selene* is orange or rufous and black (Lampe 1984, Heppner et al. 1988). The fact that the Andamans are oceanic islands that were closer to Asia during times of Pleistocene sea level lowering (Ripley & Beehler 1989) lends credence to the supposition that founder individuals (fecund females) reached these islands and speciation resulted from isolation from mainland populations.

The known host plants are different for the two species, although Anacardiaceae is well known to be used by the *Actias* group (Nässig & Peigler 1984). As cited above, *A. callandra* feeds on *Lannea coromandelica*, an anacardiaceous tree. *Actias selene* has been reported to feed on *Zanthoxylum ananthophodium* DC., *Z. alatum* Roxb. (Rutaceae), *Cedrela paniculata* (Meliaceae), *Coriaria nepalensis* Wall. (Coriariaceae), wild cherry (*Prunus*) (both Rosaceae), walnut (Juglandaceae) and other fruit trees in northern India (Cotes 1891-93, Barlow 1982), while it has been reported to feed on *Heptapleurum octophyllum* Benth.& Hook. f. (Araliaceae) in Hong Kong (Potter 1941, cited as *Octophyllum heptapleurum*).

In Sikkim *A. selene* is reported to pass through two generations in summer, overwintering as a pupa (Cotes 1891-93). It is probable that *A. callandra*, in the more equitable climate of the Andaman Islands, breeds during most months. The species possibly goes through a period of diapause as a pupa during the period when its deciduous food plant sheds its leaves, but more likely, feeds on alternate hosts still unknown to us.

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A spermatophore structured in the bursa copulatrix of the small white Pieris rapae (Lepidoptera, Pieridae) during copulation, and its sugar content

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Abstract. During copulation, the male small white, Pieris rapae, fills a single spermatophore in the bursa copulatrix of the female. The male fills first a white gel and then structures the spermatophore. The sperm was ejaculated last into the reproductive tract of the female, while sugars were observed throughout the copulation. Variation in size and sugar content of spermatophores observed in field-captured monogamous females indicated that sugars were consumed immediately after copulation, and that the spermatophore was gradually eroded. The role of the sugar content is also discussed.

INTRODUCTION

In butterflies, a spermatophore is passed during copulation. The size of the spermatophore decreases with successive matings (e.g. Pivnik & McNeil, 1987; Royer & McNeil, 1993). A number of studies have shown that males not only contribute sperm but actually make an investment by donating nutrients via the spermatophore (e.g. Thornhill, 1976; Boggs & Gilbert, 1979). Females absorb the nutrients and use them for somatic maintenance or egg production (Boggs & Watt, 1981; Marshall, 1985). The possibility that males may affect the rate of oviposition as well as contributing nutrients for egg production has implications concerning butterfly mating systems. In addition, oviposition is stimulated by the spermatophore (Watanabe, 1988).

Egg production requires protein-rich foods, the availability of which may critically constrain a female’s lifetime reproductive success (e.g. Murphy et al., 1983). Most investigations of spermatophore utilization have focused therefore on the use of amino acids by the female (e.g. Lai-Fook, 1984). Females incorporate amino acids from male ejaculates into their eggs and somatic tissue within 24hr after mating (e.g. Boggs & Gilbert, 1979; Boggs, 1981); receiving more of the non-sperm portion of the spermatophore has been shown to increase female fecundity (Oberhauser, 1989). On the other hand, Pivnik & McNeil (1988) demonstrated that males supplement the sodium requirements of the female via spermatophore transfer. Lai-Fook (1991) showed that labelled phosphorous from the male butterfly, Calpodes ethlius, was deposited in the reproductive tissues of the female. Zinc is also transferred to the female during mating (Engebretson & Mason, 1980). However, there are as yet no reports on sugar content in the spermatophore.
In this study the sugar concentration of spermatophores is described, and their temporal changes during copulation in the small white *Pieris rapae*.

Studies of pierid butterflies have shown that spermatophores are a source of nutrition for the female during mating (e.g. Rutowski, 1984). In *Pieris* spp., oviposition increases with the number of spermatophores (Ando & Watanabe, 1992; Watanabe & Ando, 1993; Wiklund *et al.*, 1993). In *P. brassicae*, the secretion of the glandula supplies nutrients to the sperm stored in the spermatheca (Tschudi-Rein & Benz, 1990).

Here, we examine the transmission process of the spermatophore with specific attention to sugar content that may affect energy for sperm and/or for somatic maintenance of the female in *P. rapae*. We also evaluate the spermatophore decline with respect to the fate of the sugar in wild females.

**MATERIALS AND METHODS**

*P. rapae* were reared in the laboratory on cabbage leaves, with fluctuating conditions of light and humidity, and temperatures around 25 °C. Late last instar larvae were caged and observed until pupation, similarly pupae were observed for emergence. All adults in this study were starved after emergence and were numbered on the forewing with a felt-tipped pen 24 hr after emergence. We allowed mating between the virgin females and the virgin males (one day old in both cases) kept together in a greenhouse. All began to copulate within 30 min in the mating greenhouse; the duration of copulation was recorded. Females used in these experiments had been kept in the laboratory environment from at least the 4th instar stage and were chosen without regard to size, because they varied little (ca. 27.5 mm in forewing length).

Spermatophore transmission in the female was observed by artificial interruption of copulation. We allowed pairs (one day old) to engage in the following kinds of copulation: 10, 20, 30, 40, 50, 60, 70 or 80 min interrupted copulations (total 121 pairs) and uninterrupted copulations (31 pairs). Both females and males were weighed just before release into the mating greenhouse, and again immediately after the copulation (± 0.1 mg). Abdomens of both sexes were picked apart with a pair of tweezers, and dissected at various intervals during copulation. The volume and sugar content of the ejaculate were measured. When a spermatophore was structured in the bursa copulatrix, the volume was recorded by putting it into a glass tube with a known volume of distilled water under a dissecting scope. However, when there was no spermatophore structured, the volume of ejaculate donated by the male was regarded as a difference between the bursa copulatrix with ejaculate and the bursa copulatrix without ejaculate, both of which were recorded by putting them into a glass tube with a known volume of distilled water under a dissecting scope. Any sperm present were observed under a light microscope at 600X.

Sugar content of each ejaculate was analyzed using the Sugar Analyzer (YSI-MODEL 27). Single ejaculates were macerated in 75 µl of distilled water and homogenated. Each 25 µl of the suspension was examined for the sugar weight contained, using the Sugar Analyzer and then summed. This technique enables quantification of sucrose, with an accuracy of 0.25 µg/25 µl.

*P. rapae* females were collected in the field during the summer of 1993, in cabbage fields of Shirouma, Nagano Prefecture, in the cool temperate zone of Japan. They were sufficiently abundant to allow field collection. Females captured were classified
into 5 age groups (O-IV), on the basis of the degree of wing wear (Watanabe & Ando, 1993). After the abdomens were amputated, all spermatophores were removed by dissection. The volume and sugar content of the spermatophores were measured. Each sugar concentration was transformed by angular transmission.

**RESULTS**

**Laboratory experiments**

Uninterrupted copulation durations were obtained for 31 pairs (Fig. 1). All were successful copulations, lasting 73.4 ± 14.7 min (SD). The spermatophore was produced directly in the bursa copulatrix and was filled with white secretion and sperm. The sperm sac was an elongated cone which occupied the bursal duct and had its opening at the end of the duct near the seminal duct. The volume of the spermatophore was 4.8 ± 0.29 mm³ (n=31, SE). The weight loss by mated males was 8.9 ± 0.41 mg (n=24, SE), while the weight increase by the mated females was 5.8 ± 0.60 mg (n=21, SE). During courtship and copulation, males of *P. rapae* were active, as if in flight. In this study, most males fluttered their wings during copulation, and some tried to fly with their mate. However, all the females were inactive during the copulation. Jones et al. (1986) suggested that weight losses include loss in the mating trial. Therefore, mean wet mass of the spermatophore in this experiment was
Figure 2. Weight increase by mated females and loss by the mated males during interrupted and uninterrupted (=normal) copulations (± SE).

about 5.8 mg. The mean body mass of the virgin males and females was 79.0 ± 2.63 mg (n=28, SE) and 81.6 ± 2.67 mg (n=23, SE), respectively. The mass of a spermatophore, plus appendix bursa contents, represents 7.3% and 7.1% of a body mass of males and females respectively.
There was no detectable weight loss by mated males 20 min after the beginning of copulation (Fig. 2). The weight thereafter began to decrease. The loss was about 8 to 9 mg in 70 min or 80 min of interrupting copulation, each of which was not significantly different from that of normal copulations (F=1.580 for 70 min, F=0.651 for 80 min). The weight of mated females did not increase 20 min after the beginning of copulation, suggesting that little transfer from male to female occurred during the first 20 min of the copulation. The weight increase at 80 min of interrupted copulation was not significantly different from that of normal copulation (F=1.157).

During copulation, the male secretions from the ductus ejaculatorius and accessory glands were transferred serially to the bursa (under soft X-ray: unpublished). The ejaculate was a white gel mainly observed on the tip of the penis 10 min after the beginning of copulation. There was no spermatophore sac in the bursa copulatrix. No sperm were stored in the bursa copulatrix before 40 min (Fig. 3), indicating that males did not transfer sperm during this period. A spermatophore sac containing sperm appeared 40 min after the beginning of copulation. It seemed that the surface of the white gel solidified and became the spermatophore sac. The spermatophore increased in volume until 60 min after the beginning of copulation, which was not significantly different from that of normal copulation (F=0.516).

Sugars in the ejaculate appeared 10 min after the beginning of copulation (Fig. 4). The weight was relatively constant until 50 min after the beginning of copulation, and then it increased. There seemed no relation between sugar weight and the onset of sperm transfer.

As shown in Fig. 5, a relationship between the volume and the weight of ejaculate was observed. The latter was considered as the weight increase of females during the copulation. The sugar concentration (w/w) for each
Sugar content and characteristics of wild-caught females

Out of 43 females captured in the field, 11 were young (age O) and 4 were the old (age IV). Monogamous females were found in age O (n=9), I (n=4)
Time interrupting copulation (min)

Figure 6. Sugar concentration of ejaculate transferred from the male during interrupted and uninterrupted (=normal) copulations (± SE).

Figure 7. Spermatophore depletion as measured by mean volume, mean sugar content and mean sugar concentration (± SE). Spermatophores in lab. were collected from females of uninterrupted (=normal) copulations. O, I and II in field refer to monogamous female ages, in which a spermatophore was collected.

and II (n=3), and the others were polyandrous. As shown in Fig. 7, spermatophores in the females of age O were the largest among three age groups of monogamous females. The volume was not significantly different from that of the laboratory-reared females (F=1.054, d.f.=1, 30). However, the spermatophores in the female of age I and II were smaller than those in laboratory-reared females (F=6.203, d.f.=1, 25 for age I and F=8.579, d.f.=1,
24 for age II). This indicates that the females gradually absorbed the spermatophore.

Sugar in the spermatophore was less than 10 µg in the wild females, which was significantly different from that of those laboratory-reared (F=18.731 for age O, F=14.050 for age I and 4.597 for age II). Sugar may thus be consumed upon termination of copulation. Sugar concentration in the spermatophore in the wild females of each age was also lower than that in the laboratory-reared ones.

**DISCUSSION**

During a copulation, a male *P. rapae* fills the appendix bursa with a white substance containing sugars, and constructs a spermatophore in the bursa copulatrix. This deposition represents approximately 7% of the male’s body mass. Marshall (1985) reported that 6 to 7% of the male’s body mass was ejaculated in *Colias philodice* or *C. eurytheme.*

Rutowski & Gilchrist (1986) suggested that duration of copulation is relatively long as a result of the mechanical problems of filling the bursa copulatrix. However, in the silkworm, *Bombyx mori,* ejaculation of seminal fluid into the spermatophore terminated 20 min after the beginning of copulation (Osanai et al., 1986). In *P. rapae,* a little ejaculation was already observed 10 min after the beginning of copulation. In a copulation of normal duration, substances are passed to the female continuously throughout the copulation period. In addition, no male held onto the female before initiating the transfer of substances. This suggests that the male was not engaged in copulatory mate guarding.

The pattern of secretion production observed in *P. rapae* was similar to that of other Lepidoptera. For example, sperm were the last materials transferred to the female reproductive tract in *C. eurytheme* (Rutowski & Gilchrist, 1986). In the present study, when the copulation was prematurely terminated (until 30 min after the beginning of copulation), the male had passed some nutritious material, but none of his sperm.

Sperm are generally transferred to the spermatheca during the hours immediately following the copulation. Tschudi-Rein & Benz (1990) reported that sperm of *P. brassicae* was transported to the spermatheca 5.5 to 8 h after copulation. Sperm of *P. rapae* may stay in the spermatophore for several hours after copulation, during which time they must remain inactive. The spermatophore is a site of sperm maturation (e.g. Osanai et al., 1987). Accessory gland products in spermatophores have been shown to function in sperm activation (e.g. Leopold, 1976). Sugar content in the spermatophore might thus contribute to sperm survival during this period.

Although it has been assumed that spermatophores are proteinaceous (e.g. Thornhill, 1976; Friedel & Gillott, 1977), Marshall (1980) has discovered that in *C. philodice* these accessory gland secretions are a complex of proteins, hydrocarbons, triglycerides, diglycerides, sterols and phospholipids. It has been shown that males may supplement a variety of nutrient requirements of a female via spermatophore transfer (e.g. Engebretson &
Mason, 1980; Alder & Pearson, 1982; Marshall, 1985; Pivnik & McNeil, 1988). Since these nutrients are absorbed by the female, a number of studies were restricted to the evidence indicating paternal investment (e.g. Boggs & Gilbert, 1979; Boggs, 1981; Boggs & Watt, 1981) and the male’s genetic return (e.g. Rutowski et al., 1987). Wiklund et al. (1993) showed that polyandrous females of *P. napellus* had higher lifetime fecundity than monandrous females, laying on average 1.61 as many eggs.

Ejaculate donated by male includes protein and lipid (e.g. Oberhauser, 1992), most of which are derived from leaves fed during the larval period. Such substances may also be transferred from pollen (e.g. Gilbert, 1972) or nectar (e.g. Baker & Baker, 1973). In this study since males and females were starved, all the substances produced by males originated in immature stages. Sugars in the ejaculate were produced by the male himself.

In this study, significant quantities of sugar were observed in ejaculates. Such sugar must dissolve in water, because a spermatophore is more than 80% water (Boggs, 1981). Sugar levels decreased after copulation in wild females, while the spermatophore size did not change in the females of age 0. Therefore, there seem to be two ways in which the sugar was consumed: Sperm could be supplied for the energy required for its own survival, or alternatively, the female could be supplied with the energy for activity in the bursa copulatrix. Takeuchi & Miyashita (1975) reported that the bursa copulatrix bended or elongated the spermatophore in order to dissolve it after copulation. Mass and nitrogen content of the spermatophore decreased at constant rates until little material remained (e.g. Oberhauser, 1992). However, sugar might not contribute to female somatic maintenance or egg production. It is obvious that many questions remain unanswered about sugar in the spermatophores and their functions as paternal investment.

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Intraspecific variation in *Anaea ryphaea* Cramer and *Anaea eurypyle* C. and R. Felder (Nymphalidae).

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**Abstract.** *Anaea ryphaea* and *Anaea eurypyle* are butterflies with wide intraspecific variation, and similar ranges, Mexico to Southern Brazil. The two characters used to separate the two taxa are continually variable, i.e., there are no well defined states for them. The frequency distributions for each of these two characters is unimodal when individuals of both species are combined. Specimens identified as *A. eurypyle* have wing patterns on one extreme of the distributions, and at most localities the majority of individuals have the *A. ryphaea* phenotype, which includes the mode of both frequency distributions. Results of my research so far suggest that these two taxa may in fact represent one highly variable species, or if they are distinct biological species, they have considerable character overlap.

**INTRODUCTION**

Taxonomic knowledge of the genus *Anaea* Hübner (Nymphalidae) is based mainly on a treatment by Comstock (1961). Many of the species originally described there have since been split into other genera, including taxa treated by Comstock as subgenera (Descimon 1986) and other taxa described later (Rydon 1971). Although *Anaea* is typical of neotropical areas and has widespread distribution (Comstock 1961; DeVries 1987), the species comprising this genus have received little or no study. For example, reports of the larval food plant and aspects of the biology and population ecology of *Anaea ryphaea* Cramer (Caldas 1991, 1994; 1995a,b) were not published until after D'Abrelra's volume V, Nymphalidae and Satyridae, Butterflies of the Neotropical Region (1988). In this same volume, D'Abrelra describes the chaotic taxonomic situation in *Anaea*, and follows Rydon (1971) in maintaining *Memphis* and *Fountainea* as genera separate from *Anaea*.

*Anaea ryphaea* is found from Mexico to Southern Brazil. Males vary greatly in wing color, pattern, and shape, and much of this variation was mentioned by Comstock (1961). I have been studying ecological aspects of *Anaea ryphaea* populations since 1988. Data from Brazil (Caldas 1994), Panama (Caldas, unpublished data), and the literature (Muyshondt 1974) show that some variable characteristics of this taxon overlap with those of *Anaea eurypyle* C. and R. Felder. The larval stages of the two are virtually identical (Caldas 1994); they both use *Croton* sp. (Euphorbiaceae) as the larval food plant (DeVries 1987; Caldas 1991), and the morphological differences used to separate them are found mainly in male adults. Although they have the same geographical range, I have never (in 4 years in southern Brazil and one year in Panama) seen, collected, or reared one individual that I would identify as

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A. eurypyle. This situation led me to analyze museum specimens and search the literature in an attempt to discover characters diagnostic for these seemingly indistinguishable taxa.

I may add that, although intraspecific variation is fairly common in the Lepidoptera (Owen 1971; Vane-Wright & Ackery 1984) and is extremely important to the discussion of species concepts and updating of area checklists (Collins 1991), there are few studies on this subject in the literature (see Burns 1984 and 1992).

**Materials and Methods**

In an attempt to discover characters to distinguish A. ryphaea and A. eurypyle, I examined specimens in the National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC, and the American Museum of Natural History (AMNH), New York, where the original specimens used by Comstock (1961) are deposited. A total of 499 males from localities covering almost the entire range of distribution of the two species (both with two subspecies) were analyzed with respect to the four main variable external characters described by Comstock (1961):

1) Elongation ("production" of Comstock) of vein M3 of the hind wings to form a "tail" (presence/absence/length; Fig. 1);
2) degree of acuteness of the forewing apex (straight, semiacute and acute; Fig. 1);
3) medial ("mesial" of Comstock) line on underside of the hind wings (straight to irregular; Fig. 2);
4) white and black markings on the undersides of both wings (presence/absence).

Individuals that had either broken wings or black undersides that obscured the medial line were not analyzed. The

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**Figure 1.** Different degrees of acuteness of the forewing apex (straight, semiacute and acute) and of the elongation of vein M3 of the hind wings (absent, small, medium, long) in *Anaea ryphaea* and *Anaea eurypyle* (modified from Comstock, 1961).
Figure 2. Different degrees of irregularity of the medial line on underside of the hind wings (straight, undefined, irregular) in *Anaea ryphea* and *Anaea eurypyle* (after figures in Comstock, 1961).

Analysis was restricted to males because females of both taxa always have long tails, although they also vary in shape of the medial line and the forewings. I also did 40 genitalic dissections to look for the differences in the whole male apparatus of the two species, as shown by Comstock in drawings (1961, pp.164).

In order to assess the distribution of the two main distinguishing characters found after these preliminary analyses, I did a frequency distribution of them throughout both species combined as one, looking for a bimodal distribution that could support the existence of two species.

**Results**

Analysis of 475 specimens that were in good condition showed that:

1) Among a total of 165 males labelled *A. eurypyle*, 53% had long tails (>4mm), 47% had medium tails (2-4mm), and 0.6% (one) had small tails (<2mm). No individual was found without a tail. Among the 310 males labelled *A. ryphea*, 1% had long tails, 5% had medium tails, 71% had small tails, and 23% had no tail at all (rounded HW). Thus, if tail length alone were considered, specimens with long tails would separate as *A. eurypyle*, those with small to
non-existent tails would be *A. ryphea*, and those with medium length tails would be impossible to assign because a clear cutoff does not exist.

2) Of 165 males labelled *A. euryple*, 52% had a straight medial line on the underside of the HW; 48% had the line irregular to differing degrees (from slightly to moderate); and one individual had an extremely irregular line, but perhaps because it had a long tail, it was labelled *euryple*. Among the 310 males of *A. ryphea* analyzed, 91% had the medial line irregular to differing degrees (from moderate to extremely); 8% had it slightly irregular; and 2 had it straight, yet were labelled *ryphea*, perhaps because they had no tail. So, for this character, specimens with the medial line straight to moderately irregular would pertain to *euryple*, while those with the line moderately to extremely irregular would be assigned to *ryphea*, but again there is continuous variation. As well, individuals with a straight medial line didn’t necessarily have the medium-long tails, nor did the ones with an irregular medial line always have a small tail or no tail, although a trend exists.

3) Most (61%) *A. euryple* males of both subspecies, *confusa* and *euryple*, had a, so-called, semi-acute forewing, while 11% had it acute, and 28% had it straight. According to Comstock (1961), semi-acute forewing is a seasonal variant in South American specimens (subspecies *euryple*) and a non-seasonal “random” variant in Central America (subspecies *confusa*). Apart from that, Comstock found straight forewings only in individuals from Central America, and considered it to be a subspecific character. Nevertheless, there are individuals from South America (mainly from Peru, various localities and dates) with straight-margined forewings. Analysis of individuals labeled *A. ryphea* showed a similar frequency distribution for this characteristic.

4) The frequency of black and white markings on the undersides of the wings was similar in both taxa. Comstock (1961) stated that they were “not uncommon” in *ryphea* and “occasional” in *euryple*, probably based on the limited series of specimens that he examined.

5) There is wide variation in genitalic characters, but the differences shown in the genitalic drawings of the two taxa in Comstock (1961) could not be found. A further genitalic study is needed to assess the whole variation within both species.

**Discussion**

I conclude that tail length and degree of irregularity of the medial line cannot be taken as definitely distinguishing *A. ryphea* and *A. euryple*. These characters vary continuously in both taxa, and no natural (or artificial) limits could be found to separate them. Also, many statements in the literature regarding species variation and separation are based on small or biased samples of specimens actually displaying random variation. Characters that would be expected to occur together in each taxon were found not necessarily to be correlated in every individual, as were supposedly seasonal characters. Thus, there are many individuals that cannot be included in any of the species because of mixed characters.
Continuous variation in morphological characters is not uncommon. A similar situation was found by Robbins (1991) in two species of Mitoura (Lycaenidae), where the second “species” was nothing more than an isolated example plucked from the morphological unimodal continuum of characters that define the original species. Burns (1984) has encountered examples of the same situation with skippers (Hesperiidae). A more refined quantification of the variable characters in A. ryphea and A. euryptyle will perhaps provide adequate data to elucidate the relationship between these two taxa, but a frequency distribution of the two main distinguishing characters (length of tail and degree of irregularity of medial line), when individuals of both species are combined, is clearly unimodal (Fig. 3). The fact that there is only one mode suggests that we could be really dealing with only one species. Specimens identified as A. euryptyle are individuals with wing patterns on one extreme of both distributions — long tail and regular mesial line. All the rest of both distributions, including the mode, would be considered A. ryphea. There is no significant difference between the proportions of individuals within each class of these distributions (Table 1), which shows that there is a tendency for individuals with long tails to have straight medial line; for those with medium tails to have undefined medial line; and for those with small or no tail to have irregular medial line. The two distinguishing characters vary together, in accordance, in the majority of the cases. That could also explain why A. ryphea is more common in all collections than A. euryptyle.

A very puzzling fact is that Anaea euryptyle is not widely recorded from Panama, although it is found throughout the whole range of A. ryphea. In fact, the only record for Panama is of five individuals collected near the border with Costa Rica, which were used by Comstock (1961) in his revision. These specimens are no longer in the AMNH, and I have not been able to trace them. Apparently, nobody since then has collected A. euryptyle in Panama (I went there again in 1994, for this specific purpose, but failed to find any), although records of A. ryphea are abundant.

Panamanian individuals reared by me in the laboratory during 1991/1992, and again in 1994, showed no great morphological differences among the females, but males varied greatly in color, pattern, and shape of the wings. The distal bars of the forewing dorsal surface ranged from bright blue to almost black (which is considered typical of A. euryptyle), and the basal area of the hindwings, near the thorax, varied from purple to orange. The elongation of vein M3 in the hind wings ranged from almost none to moderate. The ventral surface pattern was extremely variable, and one individual had a definitely straight medial line. This characteristic was found also in one specimen at the AMNH, and in several specimens at the USNM, all from Panama. Variability was also observed in adults from Campinas, Brazil, but the elongation of vein M3 did not occur there. Some of this variation has been cited (Comstock 1961) but has not been quantified in such a way as to permit assessment of its importance in the determination of the two species. Anaea ryphea and A. euryptyle could, in fact, represent one
highly variable species, or if they are distinct biological species, they have considerable character overlap (Mayr and Ashlock 1991). Perhaps molecular studies will shed more light on the situation.

Temperature and relative humidity during development can influence adult morphological characters in Lepidoptera. It is also known that widely distributed species tend to develop locally differentiated populations and to show generally high levels of variability (Ehrlich and Raven 1969; Endler 1973, 1977), usually related to ecological and biogeographical factors.
Table 1. Test for proportions of individuals within each class of the frequency distribution for the two distinguishing characters between *Anaea ryphea* and *Anaea eurypyle*.

<table>
<thead>
<tr>
<th>Tail length</th>
<th>Medial line</th>
<th>z</th>
<th>p</th>
</tr>
</thead>
<tbody>
<tr>
<td>long - 19%</td>
<td>straight - 19%</td>
<td>0.000</td>
<td>0.500</td>
</tr>
<tr>
<td>medium - 20%</td>
<td>undefined - 22%</td>
<td>-0.757</td>
<td>0.225</td>
</tr>
<tr>
<td>small/absent - 61%</td>
<td>irregular - 59%</td>
<td>-0.629</td>
<td>0.266</td>
</tr>
</tbody>
</table>

Variability can then be a consequence of genetic and environmental factors combined. Given that *A. ryphea* has an extensive geographical distribution, very likely it has developed local patterns of differentiation.

**Acknowledgments.** I thank Robert Robbins for granting me access to the Smithsonian Institution collection, and for suggestions throughout the project; James Miller and Frederick Rindge for hosting my visit to the AMNH; Donald Harvey and Elizabeth Klafter for scientific and technical information; Annette Aiello, Phil DeVries, and Robert Robbins for reviewing the manuscript; IN.RE.NA.RE for the permit to do research in Panama; and the Smithsonian Tropical Research Institute for logistical support. Mr. Ivan R. da Silva kindly helped with the drawings. This research was funded by CAPES and SR-2/Universidade do Estado do Rio de Janeiro, Brazil, a Collection Study Grant from the AMNH, and a Short-Term Visitor grant from the Smithsonian Institution.

**Literature Cited**


Puddling behavior by Bay checkerspot butterflies (*Euphydryas editha bayensis*)

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Center for Conservation Biology, Department of Biological Sciences, Stanford University, Stanford, CA 94305

**Abstract.** Large numbers of male and female Bay checkerspot butterflies, *Euphydryas editha bayensis*, were observed taking moisture from the banks of a seasonal creek in 1990. Previous observations of this long-studied subspecies imply that taking moisture from saturated substrates is not a common behavior for males, and is certainly not the norm for females. This study found that during the early and mid-portions of the adult flight season in 1990, a large number of older individuals visited the creek site, and that many butterflies were apparently flying more than one kilometer round-trip to visit the creek site. This behavior may have been induced by drought conditions.

This communication reports numerous observations of a butterfly, the Bay checkerspot (*Euphydryas editha bayensis*), not typically thought to be a "puddling species." Although adults, and males in particular, of many species of Lepidoptera have been observed extracting fluids from moist soils (Adler 1982, Berger and Lederhouse 1985, Boggs and Jackson 1991, Collenette 1934, Downes 1973, Norris 1936, Scott 1986), such behavior has not been reported previously for the long-studied Bay checkerspot butterfly. We also report on the comparatively large number of females and older individuals observed visiting puddles. This is in apparent contradiction to most previous field observations that suggest that puddling behavior is much more likely to be exhibited by males than by females, and particularly by young males (Adler 1982, Adler and Pearson 1982, Boggs and Jackson 1991, Collenette 1934). We discuss our observations in an effort to further an understanding of the reasons Lepidoptera visit moist soils, and to introduce the question of the importance of such areas for conservation planning.

**Study system**

Bay checkerspot butterflies are restricted to serpentine soil-based grasslands of the San Francisco Bay area, and have been studied intensively since the early 1960s (e.g., Ehrlich and Murphy 1981, Harrison *et al.* 1988, Launer and Murphy 1994, Weiss *et al.* 1988). Previous research has addressed the effects of adult diet on fecundity and longevity for female Bay checkerspot butterflies (Boggs 1996, Murphy *et al.* 1983). Nectar, considered to be the primary source of adult-derived nutrients, contains water, sugars, amino acids, along with trace amounts of other compounds (reviewed by Boggs 1987). Under laboratory conditions, water increases adult longevity, but has
no influence on fecundity, while sugar increases fecundity and longevity (Murphy et al. 1983). Sugars acquired by adult butterflies are used in increasingly greater amounts in egg production as individuals age, and amino acids available from nectar are also used in egg production (Boggs 1996). On average, 18% of the oocytes carried by female Bay checkerspot butterflies are fully yolked at adult eclosion (Labine 1968). These eggs are by necessity composed of material derived from larval feeding and do not benefit from adult-derived nutrients. The remaining 82% of oocytes may receive at least some benefit from adult-derived nutrients.

Nutrients acquired directly from males may also be used by female checkerspot butterflies in egg production. Use of sugars and amino acids received by females from males at the time of mating follows a common pattern: an initial increase with age in incorporation of male-derived nutrients in eggs, followed by a decrease in incorporation (Boggs 1996).

**Methods**

In late March 1990 numerous Bay checkerspot butterflies were observed apparently drawing moisture — that is, individual butterflies were seen with proboscides extended into water-saturated substrate (mud, sand, and gravel) — along a seasonal creek in the East Hills, near Morgan Hill (Santa Clara County, California). This site had been visited on four occasions during February and early March, during which no Bay checkerspot butterflies were observed to be associated with moist soils. Subsequent to the initial observations of butterflies exhibiting puddling behavior, the creek was visited on 12 occasions between 25 March and 20 April. During these visits, 209 Bay checkerspot butterflies (66 male and 143 female) were captured, scored for age (wing condition), identified by sex, and released. These butterflies were captured either as they took moisture along the creek bank or while they were flying along the creek, either after taking flight at our approach or as they were apparently settling down to the creek bank. In addition, four surveys on the hillsides and ridges within 200 meters of the creek recorded fewer than ten Bay checkerspot butterflies.

Concurrent with activities at the creek site, samples of adult butterflies were taken from a 500 meter by 100 meter study area straddling the main ridgeline. The ridge-straddling site was located 750 meters up-slope and somewhat north of the creek site. In 1990, the Bay checkerspot butterfly population was apparently centered along the northeast side of that ridge, and butterflies at the ridge-straddling site were considered phenologically representative of the butterflies in the vicinity. While it is well documented that male *Euphydryas editha* tend to congregate along hilltops or ridgelines (Baughman et al. 1988, Ehrlich et al. 1990, Ehrlich and W eye 1988), samples from the broad ridge-straddling site should provide sex ratios that are representative of the population as a whole. Out of a large pool of butterflies present at the ridge-straddling site, 576 butterflies (402 male and 174 female) were captured at random, scored for condition, identified by sex, and released.

For statistical analyses the butterfly flight season was divided into five sampling periods, each with a duration of approximately five days. Mean wing conditions were compared across sites using Wilcoxon two-sample tests, and sex ratios (as % of male butterflies) were compared similarly using *z* tests.
Table 1. Summary statistics for butterflies captured at each study site during the five sampling periods.

<table>
<thead>
<tr>
<th>puddling site</th>
<th>males</th>
<th>females</th>
<th>% males</th>
</tr>
</thead>
<tbody>
<tr>
<td>sampling period</td>
<td>number</td>
<td>mean condition (s)</td>
<td>number</td>
</tr>
<tr>
<td>1</td>
<td>0</td>
<td>na</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>1</td>
<td>2.5 (na)</td>
<td>25</td>
</tr>
<tr>
<td>3</td>
<td>20</td>
<td>2.8 (0.54)</td>
<td>83</td>
</tr>
<tr>
<td>4</td>
<td>39</td>
<td>3.0 (0.48)</td>
<td>30</td>
</tr>
<tr>
<td>5</td>
<td>6</td>
<td>3.2 (0.52)</td>
<td>5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>ridge-straddling site</th>
<th>males</th>
<th>females</th>
<th>% males</th>
</tr>
</thead>
<tbody>
<tr>
<td>sampling period</td>
<td>number</td>
<td>mean condition (s)</td>
<td>number</td>
</tr>
<tr>
<td>1</td>
<td>55</td>
<td>1.3 (0.29)</td>
<td>5</td>
</tr>
<tr>
<td>2</td>
<td>59</td>
<td>1.9 (0.58)</td>
<td>22</td>
</tr>
<tr>
<td>3</td>
<td>100</td>
<td>2.2 (0.61)</td>
<td>60</td>
</tr>
<tr>
<td>4</td>
<td>106</td>
<td>2.8 (0.45)</td>
<td>58</td>
</tr>
<tr>
<td>5</td>
<td>82</td>
<td>3.2 (0.37)</td>
<td>29</td>
</tr>
</tbody>
</table>

Results

Substantial numbers of both male and female Bay checkerspot butterflies were observed exhibiting puddling behavior at the creek site during most of the adult butterfly flight season (Table 1). The sex ratio (as % male butterflies) varied through the season. At the creek site, sex ratio increased from a low of 4% males in the second sampling period (no Bay checkerspot butterflies were observed at the creek site during the first sampling period), to 57% and 55% during fourth and fifth sampling periods respectively. At the ridge-straddling site the percentage of male butterflies ranged from 92% (first sampling period) to 63% and 65% (third and fourth sampling periods, respectively). Sex ratios at the creek site and ridge-straddling site differed significantly during sampling periods 2 and 3, with relatively more female butterflies being found at the creek site (in both cases, P < 0.001). In sampling periods 4 and 5, sex ratios at the creek site and ridge-straddling site did not differ significantly.

At both the creek site and at the ridge-straddling site, mean condition of butterflies increased over the course of the season (Table 1). Mean condition of both male and female butterflies differed between the study sites in earlier samples, but not in later samples. For female butterflies, during sampling periods 2 and 3, mean condition was significantly higher for individuals at the creek site as compared to the ridge-straddling site (Table 1; sampling period 2, mean condition at the creek site was 2.0, while at the ridge-
straddling site it was 1.5, *P* < 0.01; sampling period 3, mean condition at the creek site was 2.1, while at the ridge-straddling site it was 1.6, *P* < 0.001). In sampling periods 4 and 5, the mean condition of female butterflies did not differ between the sites. These data indicate that during sampling periods 2 and 3 the condition of females at the creek site was not representative of the population of female butterflies as a whole — relatively older female butterflies were visiting the creek site. During the last two sampling periods, female butterflies visiting the creek site were also generally older individuals, but they did not differ from the aging population as a whole.

Mean condition of male butterflies showed similar differences between the creek site and the ridge-straddling site. In the middle of the flight season (sampling periods 3 and 4), the mean condition of male butterflies at the creek site was significantly greater than mean condition of male butterflies at the ridge-straddling site (mean condition of 2.5 vs. 2.2 in sample period 3, *P* < 0.001; and 3.0 vs. 2.8 in sample period 4, *P* < 0.01). At the end of the season the mean condition of males observed in the two study areas were similar. As was noted with female butterflies, these data indicate that comparatively older butterflies were exhibiting puddling behavior during early portions of the flight season, while older butterflies representative of the population as a whole visited the site late in the season.

**Discussion**

These observations merit discussion for several reasons, all concerning a vexing question — why were large numbers of *Euphydryas editha bayensis*, and females in particular, observed exhibiting puddling behavior in 1990, but not in other years? Unfortunately this question has no clear-cut answer, although at least five possible explanations exist which center on 1990 as the third year of a severe drought and on the importance of adult-derived nutrients to butterfly reproduction.

First, Bay checkerspot butterflies may visit moist areas on a regular basis, but at smaller and more cryptic sources. If Bay checkerspot butterflies routinely benefit from adult-derived water or some essential mineral (e.g., sodium), then puddling behavior may be typical of their behavioral repertoire. Indeed, a number of the other twenty-odd subspecies of *Euphydryas editha* have been observed to exhibit puddling behavior. The 1990 observations could reflect loss of numerous small sources of water or minerals due to the drought — concentrating the behavior into the few remaining sites providing saturated substrates. The lack of observations of large numbers of Bay checkerspot butterflies visiting moist areas during previous droughts could reflect observer bias because we have only infrequently visited seeps, creeks, and puddles in and adjacent to serpentine soil-based grasslands.

In the four field seasons since 1990, however, including several moderately dry years, we have visited the creek site on many occasions and have observed few *Euphydryas editha bayensis* associated with the creek, and even fewer have been observed feeding on water-saturated soils there or at other sites in the serpentine soil-based grasslands. It is likely true that under non-drought
conditions Bay checkerspot butterflies occasionally visit moist soils, but the rarity of observations implies that this behavior is comparatively uncommon and probably does not provide butterflies with a significant source of water or nutrients during most years.

The second explanation concerns the possibility that resources typically available to adult butterflies were relatively scarce in 1990. While large numbers of flowers were present at the study site, the relative volume of nectar in these flowers may have been reduced compared to more typical, non-drought years. The butterflies may have altered their typical foraging behavior in response to a widespread shortage of either water or sugars, and were seeking water from the creek site (water, sugars, and amino acids are typical components of nectar, salt is not). Water from the creek site could serve to increase an individual's lifespan, but would not necessarily increase an individual's reproductive fitness (especially when viewed in light of the decreasing chance of survival of eggs laid later in the season — see Cushman et al. 1994, Murphy et al. 1983). This explanation fits the observations that individuals of both sexes were visiting the creek site. It also provides a partial explanation as to the comparatively large numbers of older butterflies observed at the site. If nectar availability was reduced due to the drought, individual butterflies that had depleted stores of water might be expected to search for alternate sources.

The remaining three explanations concern sodium, and center on likely increased butterfly demand for sodium, on the potential for reduced levels of sodium available from larval feeding, and on possible elevated levels of sodium present at the creek site. As pointed out by Arms et al. (1974), sodium is necessary for many physiological functions, including flight. Adult-derived sodium may also be beneficial for both sexes in terms of reproduction (Adler and Pearson 1982, Berger and Lederhouse 1985, Boggs and Jackson 1991, Collenette 1934, Lederhouse et al. 1990, Pivnick and McNeil 1987, Scully and Boggs unpublished).

The first explanation connected with sodium availability concerns the possibility that the drought may have affected the rates at which butterflies were using sodium. It is possible that butterflies in 1990 were forced to fly greater distances to find mates, oviposition sites, or nectar, thereby depleting their stores of sodium at atypically high rates. Dispersal by Euphydryas editha has been demonstrated to vary considerably from one year to the next (Gilbert and Singer 1973, Murphy and White 1984, White and Levin 1981). In 1990, it was apparent that butterflies visiting the creek site were regularly traveling distances farther than are considered typical for Euphydryas editha bayensis (Baughman et al. 1988, Ehrlich 1965, Ehrlich et al. 1984, 1990, Harrison et al. 1988, Launer unpublished data, Sisk unpublished data). This could account for both sexes visiting the creek site and for the relative abundance of older individuals — individuals of both sexes need sodium, but only after they have depleted larval-derived stores.

The drought also may have affected the sodium content of larval hostplants, such that older butterflies depleted their larval-derived salt stores earlier
than is typical, thus forcing older butterflies to seek supplementary sources of sodium. Unfortunately, no data concerning the effect of drought on local serpentine-soil dwelling plants are available, and this explanation is untested.

Lastly, the creek could have been abnormally enriched for salts in 1990, thereby attracting butterflies not typically found at sites with lower salt concentrations. Again, we have no way to test this possibility; soil and water samples were not taken in 1990, and Bay checkerspot butterflies have been observed to visit the site on a very infrequent basis since. Aside from a likely reduction of stream flow in response to the drought, the creek site in 1990 did not appear different than it had in the previous two years or during the subsequent four years. Land use at the East Hills study site, winter-spring cattle grazing, has remained relatively constant for more than a decade.

Overall, our observations are generally consistent with hypotheses that butterflies are visiting moist areas in order to replenish essential nutrients or water expended during mating, gamete production, or general metabolism. As is predicted by such replacement hypotheses, the mean condition of butterflies at the creek site was relatively high, implying that older butterflies, those individuals likely to have used up nutrients acquired during larval feeding, were over-represented. For Bay checkerspot butterflies, it may be that nutrients that are acquired from puddles are not limiting during most years, but during periods of extreme drought nutrient reserves derived from larval feeding may be so low in older individuals as to trigger searches for alternate sources.

While these observations do not settle the issue as to what benefit, if any, the butterflies are receiving from areas that provide moisture, they do introduce the question of the importance of such areas to the persistence of populations of Bay checkerspot butterflies. The general lack of observations of puddling behavior suggests that during most years visits to puddles or other sources of water-saturated soils are infrequent, and of minimal importance to butterfly reproduction or survival. However, since our observations were taken during a period of extreme drought, it is possible that the resources provided at the creek site may aid individuals during harsh environmental conditions — possibly to the extent that the chance of local persistence is enhanced by moisture-providing areas. If true, this could be a problem as site specific conservation planning for this butterfly has focused on preservation of comparatively dry grasslands (Murphy and Weiss 1988, 1992, Weiss et al. 1988, 1994). Canyon bottoms and other moist areas have historically have received little, if any, protection. If puddling behavior plays a role in sustaining populations during protracted periods of dry weather, such areas that are within or adjacent to butterfly population centers need to be incorporated into conservation planning for this subspecies.
LI TERATURE CITED


Host Plant and Habitat Effects on Behavior, Survival, and Growth of Early Instar *Dichomeris leuconotella* (Lepidoptera: Gelechiidae), Leaf-folders on Goldenrods

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Abstract. The relative success with which caterpillars use different host plant species is determined by a variety of factors including host plant food quality, phenology, morphology, and associated predator loads. These factors vary among habitats, and such variation might account for the restriction of some caterpillar species to particular habitats, when their host plant species are more widespread. I studied the effects of host plant and habitat factors on survival and growth of *Dichomeris leuconotella* caterpillars, which occur only in open habitats although their host plants, *Solidago* and *Aster* spp., are widely distributed in forest and field. This paper focuses on early instars.

In larval transplant experiments, differences between host plant species in both food quality and leaf morphology greatly affected caterpillar performance, but differences between habitats on the same host had unexpectedly minor impact and actually slightly favored performance in forests. On an abundant forest goldenrod, *S. caesia*, first and second instars had poor growth rates and high mortality, even when protected from predators; but on *S. rugosa*, which grows in both habitats, unprotected caterpillars grew and survived slightly better in forest than in field, and protected caterpillars performed comparably in the two habitats. Early instars began feeding as quickly on *S. caesia* from forest as on *S. rugosa* from either field or forest; and once started, they could fold *S. caesia* leaves faster than those of *S. rugosa* from either habitat (especially field). However, they took much longer to find suitable sites to spin refuges on the smooth, obscurely veined leaves of *S. caesia*, and they abandoned leaf refuges readily on *S. caesia*. Observations of other leaf-folding caterpillar species suggest that *S. caesia* is best suited as a host for spring-hatching species whose youngest larvae can find "ready-made" refuge in the leafy terminal bud available at that time.

Key Words: Caterpillar, *Dichomeris*, Gelechiidae, habitat, host plant, leaf folder, leaf roller, leaf tier, *Solidago*

Introduction

Several authors have pointed out that the quality of a host plant for an insect herbivore must be a function of many variables; although nutrient content and secondary chemistry are the most often studied, plant morphology, phenology, density, distribution, and associated predators may also have important effects (reviews in Rausher 1983, Bernays and Graham 1988,

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Thompson 1988, Zwolfer and Romstock-Volkl 1991; specific examples in Wiklund and Ahrberg 1978, Mopper et al. 1984, Gall 1990, Nylin and Janz 1993). All of these factors vary among habitats, and there are many cases of herbivorous insects attacking a host plant species in one habitat but not another (Shapiro and Carde 1970, Tahvanainen 1975, Rausher 1979 and references therein, Courtney 1984, MacGarvin et al. 1986). Understanding the complex interactions of host plant attributes and habitat effects in determining insect distributions requires a combination of approaches: studies designed to test the insect’s response to particular host plant attributes, including attributes that vary among habitats, and also experiments that evaluate the insect’s performance under a range of natural conditions where all variables (including any that are unknown to the experimenter) are combined. Such studies are rare.

Caterpillars of Dichomeris leuconotella (Busck) (Gelechiidae) are habitat-restricted, occurring only in fields and other large open areas such as roadsides or streambanks. Some of their hosts, field goldenrods (Solidago spp.) and asters (Aster spp.), also occur sparsely in forests; and additional species, especially the abundant goldenrod S. caesia L., grow strictly in forests. The caterpillars, which are leaf-folders, will feed and fold leaves on these strictly forest species in the laboratory, although they do not occur on them naturally (Loeffler 1994). Their small size (1 mm at hatching) and prolonged larval development (>4 months on the plants) could make them especially sensitive to leaf characteristics such as thickness, shape, and hairiness, because these characteristics can determine how quickly a caterpillar constructs a leaf fold, the final size and shape of the fold, the caterpillar’s manner of feeding, and other factors affecting the fold’s value as a refuge from natural enemies and the elements (e.g., Neto 1991). These leaf features vary widely among species of goldenrods and asters, and also among habitats: for example, goldenrods and asters growing in shaded areas have thinner and generally less hairy leaves than those growing in sun.

This paper reports on the relative effects of habitat and host plant factors on the survival and growth of early instar D. leuconotella in late summer. Observations on older instars, which mature in the following spring, will be presented in a separate paper. I used larval transfer experiments to evaluate caterpillar performance between habitats and host plants under natural conditions, and I combined caging experiments and behavioral observations to assess roles of specific factors such as predators, host plant chemistry, and leaf characteristics on early instar caterpillar performance. Staged encounters have verified that once a leaf fold or crinkle is spun, it provides effective protection from arthropod predators and dislodgment regardless of whether the leaf is thick and hairy (field-grown S. rugosa Aiton leaves) or thin and smooth (S. caesia leaves) (Loeffler 1996a and unpublished data). In the present study, therefore, one particular concern was determining the effects of host plant species and habitat on the relative amount of time spent without a refuge (i.e., feeding outside or changing refuges).
THE CATERPILLARS

In central New York, *D. leuconotella* moths oviposit in July on the undersides of goldenrod and aster leaves (Loeffler 1994). The larvae hatch in late July or early August and spin small webs on the leaf undersides. As they grow, they add more silk to the web, gradually pinching and eventually folding the leaves. By early October, when the plants senesce, the caterpillars are third and fourth instars, typically 3-4 mm in length. They overwinter in leaf litter and climb up onto new plants in late April to mid May. They then grow rapidly, change leaf folds with increasing frequency, and reach 15-17 mm in length before pupating in leaf folds in mid- to late June (Loeffler 1994).

STUDY SITES

The two study sites, Brookshead Reserve and Gowan Farm, are located near the southern edge of the Cayuga Lake Basin in central New York. Each site consists of a large field (>2 ha) and extensive adjacent forest. Goldenrods and asters dominate the fields and grow as scattered clumps and single plants in the forests. The relative abundance and distribution of various species of goldenrods and asters is typical for fields and forests in central New York.

The Gowan Farm field (3.3 km southeast of Brooktondale, NY; elevation 400 m) was originally hayfield and the goldenrods and asters there tend to grow in clones interspersed with grass. *Solidago rugosa* and *S. altissima* L. are common; *Aster lateriflorus* (L.) Britton, *Euthamia graminifolia* (L.) Nuttall, *S. juncea* Aiton, and *S. gigantea* Aiton are present but rare. *Fraxinus americana* L. saplings grow thickly in some spots, mixed with *Rubus* sp. In the forest, under a canopy of mixed northern hardwoods, grow numerous scattered *S. rugosa* and *S. caesia*; some areas also support *Aster divaricatus* L., *A. lateriflorus*, *S. bicolor* L., and occasional patches or single ramets of other species. All of these species intermingle to some extent, but *S. rugosa* tends to predominate along old fencelines or in younger stands of *Acer saccharum* Marshall, *Betula lenta* L., or *Carya* spp. *Solidago caesia* is most frequent in a mature woods of *Fagus grandifolia* Ehrhart and *Acer saccharum*, whose pit-and-mound topography indicates a history as woodlot rather than agricultural field. Tree seedlings, grasses, sedges, *Caulophyllum thalictroides* (L.) Michaux, *Podophyllum peltatum* L., *Rubus* sp., and a variety of other plants make up the rest of the ground layer.

Unlike the hilly Gowan Farm site, the Brookshead Reserve site (1.3 km south of Brooktondale, NY, elevation: 340 m) is flat to gently sloping, and mesic with occasional wet areas. The most abundant of the goldenrods and asters in the field is *Solidago altissima*, followed in order by *S. rugosa*, *S. juncea*, *Aster sagittifolius* Willdenow, *A. lateriflorus*, *A. novae-angliae* L., and *Euthamia graminifolia*. Other common field species include *Fragaria virginiana* Duchesne, *Potentilla* sp., *Hieracium* sp., *Achillea millefolium* L., *Daucus carota* L., and *Toxicodendron radicans* (L.) Kuntze. In the forest, *S. rugosa* dominates in an area of ca. 30-40 year-old *Acer saccharum* while *S. caesia* is largely restricted to slightly older woods dominated by *Fagus grandifolia*, *Acer saccharum*, and
Tsuga canadensis (L.) Carriere. Other goldenrods and asters present include A. divaricatus, A. lateriflorus, S. gigantea, and S. bicolor, the last being largely confined to one dry area. Tree seedlings and woodland herbs such as Caulophyllum thalictroides, Allium tricoccum Aiton, and Podophyllum peltatum also contribute to the ground flora.

**METHODS**

**Goldenrod condition and phenology**

To assess aspects of host plant condition and phenology that might affect caterpillar performance, I marked 10 stems of each of the three categories of goldenrod used in this study (S. rugosa in fields, S. rugosa in forests, and S. caesia in forests, henceforth referred to as SRfi, SRfo, and SCfo) and 10 stems of the other abundant field species, S. altissima, at Gowan Farm on 15 May 1985. I chose the plants haphazardly from all parts of the study site. Twice per month until late October I measured the plants, noting their condition, and, by referring to threads tied to them as markers, tallied newly emerged leaves and senescing leaves.

**Field experiment: Unprotected larvae**

To assess the effects of habitat and host plant on caterpillar performance, I conducted larval transfer experiments. Between mid-August and mid-October, 1985, I released *D. leuconotella* caterpillars onto SRfi, SRfo, and SCfo (defined above) and monitored their survival and growth at Gowan Farm and at Brookshead. The caterpillars were progeny of captive moths reared from caterpillars collected in the spring. I hatched and reared the experimental larvae on leaves of *S. altissima*. Given the possibility of larval induction (e.g. Jermy *et al.* 1968), the choice of host species on which to rear larvae for this sort of experiment is problematical. I regarded it best to rear all larvae on the same host species, and on a host species that was clearly suitable for the caterpillar species, in order to assure larvae of matchable size and vigor at the time of setting out. Chemically and nutritionally, *S. altissima* probably resembles *S. rugosa* (SR) more than *S. caesia* (SC) (Hamilton 1989).

I "released" the larvae by taping their leaf refuges onto the plant stems. In this way the larvae had some initial protection from predators and dislodging, which was crucial if they happened to be molting; but as the refuge leaves dried out the caterpillars were forced to wander onto the live plant for food. At Gowan Farm I set out one first or second instar on each of 57 plants of each category (SRfi, SRfo, and SCfo) between 13 and 27 August 1985. I checked each larva after 5 days, 24 days (mid-September), and ca. 44 days (early to mid-October), noting survival, numbers and types of refuges constructed, and numbers of predators on the plants. At Brookshead I set out one second or third instar on each of 61-63 plants of each category between 29 August 1985 and 7 September 1985. I checked these caterpillars after 5 days, 24 days (late September), and ca. 44 days (mid-October). I measured lengths of the caterpillars at both sites before setting out, at the 24 day check, and at the final check, using a dissecting microscope for the first and third measurements but taking the second measurements in the field to minimize disturbance to the larvae.

**Field experiment: Caged larvae**

To separate the effect of predation from that of food quality in determining survival rates on the three hosts, I gathered growth rate and survival data for *D.
leuconotella larvae caged in dacron sleeves on SRfi, SRfo, and SCfo at Gowan Farm in August-October 1986. The larvae were again progeny of captive moths reared from caterpillars collected in the spring. For purposes of a more elaborate experiment (see Loeffler 1996b), I used two treatments: one half of the larvae on SRfi, SRfo, and SCfo were removed from their refuges four times, at approximately 10 day intervals, measured, and forced to seek new leaves and rebuild, while the other half of the caterpillars were not disturbed. Manipulation of larvae for measuring did not affect relative growth rates (Loeffler 1996b). The full rationale of the experiment, details of methods used and comparison of the effects of the treatments are given in Loeffler 1996b. The portion of those results which pertains to the present paper, i.e. the relative performance of the repeatedly measured larvae on the different host plant-habitat categories, is given here.

Rates of fall senescence vary among goldenrod species and habitats. In years with early frosts, field plants brown quickly, and the order of senescence among S. rugosa and S. caesia is first SRfi, then SRfo, and finally SCfo. In years with delayed frost I have noted an order of SRfo, then SRfi, and finally SCfo. To test whether caterpillars would continue feeding and growing larger as long as green leaves were available, and thus derive an advantage from being on SCfo, I maintained the larvae collected after the field experiment for two additional weeks, until late October. Each larva received leaves of the goldenrod species-habitat category and condition (fresh green or dry brown) that it had been feeding on when collected. I kept the larvae in vials in an open, unheated barn, protected from sun but at roughly ambient temperature.

Laboratory observations

To determine whether differences in behavior played roles in the relative success of early instar D. leuconotella caterpillars on SRfi, SRfo, and SCfo, I observed their movements, refuge-spinning, and feeding behavior on cut stem tops in the laboratory. The stem tops were placed in water vials to maintain turgidity. In each set of observations I released a caterpillar, matched for size and instar, onto a stem top of each of the three plant categories. Every 15 minutes, for three hours, I noted larval activities (crawling, resting, refuge-making), and I drew transverse cross sections of the caterpillars' refuge leaves to assess relative rates of leaf folding. I used 20 sets of second instars and 20 sets of third or fourth instars. I made additional observations of refuge leaf curvature and feeding at 24 hours. Occasional disappearances of larvae forced removal of the associated matched sets of three larvae from statistical analyses, as indicated by the numbers of degrees of freedom given for the various Friedman Tests in the Results.

The tendency of caterpillars to abandon refuges and seek new ones could compromise survival under natural conditions, because wandering larvae are highly vulnerable to predation and accidental loss of contact with the host (Loeffler, 1996a). To test whether larvae abandoned refuges more often on one goldenrod species-habitat category than another, I maintained them on the cut stem tops for an additional 12 days, watched for predators (none appeared), and counted numbers of refuges spun. Counting refuges in the two field experiments (unprotected and caged) was inadequate to address the effect of host plant and habitat on number of refuge changes because of confounding effects: unprotected caterpillars that abandoned refuges frequently were more likely to be removed by predators during the time interval than were those that stayed in a single refuge, and caged caterpillars sometimes tied leaves to the cage material rather than spinning normal refuges.
Statistics

For statistical analyses I followed methods of Sokal and Rohlf (1981) and Conover (1980), and all computer statistical programs (Statworks™ and Statview 512+™ for MacIntosh) were checked for consistency with sample tests given in these references. ("Mann-Whitney U tests" were not performed in Statworks because they gave discrepant results from Conover (1980) and Statview.) G-statistics were hand-calculated using Williams’ correction (Sokal and Rohlf 1981). When followup comparisons were appropriate (i.e., after a significant Friedman test, G-test, or other procedure involving comparison of more than two groups), I either followed methods of the above references or carried out two planned pairwise comparisons, involving SRfi versus SRfo and SRfo versus SCfo. For these two plans but non-independent comparisons, I employed an experimentwise error rate of α = 1 - (1 - 0.05)² = 0.0253 (Sokal and Rohlf 1981).

RESULTS

Goldenrod phenology

Throughout most of the season, comparable amounts of green leaves were available on field and forest goldenrod plants (Fig. 1). Field plants often developed multiple stems and continued producing small new leaves well into August, whereas forest plants halted leaf production in July. However, lower leaves senesced faster on field plants. As a result, the quantity of green leaf tissue available on a given plant was similar between habitats, although leaves were on average smaller and younger on field plants. Insect herbivory was minor on all four goldenrod types. By early fall, deer had nipped off large portions of half of the SCfo plants, thereby either consuming insect herbivores or at least reducing the amount of foliage available to them. SRfi, SRfo, and S. altissima (of fields) were less frequently (ca. one in six) and less drastically attacked, such that the effects of deer are not discernable in the data displayed in Fig. 1. Field plants (SRfi and S. altissima) browned quickly in early October following a heavy frost; whereas through late October, seven out of 10 SCfo plants and four out of ten SRfo plants remained mostly green and turgid.

Hamilton (1989) gives more extensive data on the phenologies of field and forest goldenrods in the Finger Lakes region of central New York. Although her data do not include SRfo, she found similar growth patterns to those that I observed in SCfo, SRfi, and S. altissima. Field plants (SRfi and S. altissima) showed more rapid senescence of lower leaves than forest plants including SCfo. SCfo was particularly subject to deer attack. Levels of insect herbivore damage were greater and more variable among populations in field plants.

Field experiment: Unprotected larvae

Surprisingly, early instar D. leuconotella survived relatively well on SRfo. At Gowan Farm, survival at 24 days differed significantly among the three host categories (G_adj. = 8.01, df = 2, P < 0.025). Followup comparisons using an experimentwise error rate of α = 0.025 indicated significantly higher survival on SRfo than on SCfo (G_adj. = 7.21, df = 1, P < 0.025) and a marginally
Fig. 1. Phenology of *S. rugosa* in field (SRfi), *S. rugosa* in forest (SRfo), and *S. caesia* in forest (SCfo), averaged from data on heights, branching, numbers of emerging and senescing leaves, and flowering of 10 stems of each type of goldenrod scattered over ca. 40 ha. of varied habitat at Gowan Farm. Data for the other dominant *Dichomeris* host in central New York fields, *S. altissima*, were similar to those for SRfi. The lower average height of SCfo from late September onward reflected extensive deer damage to some of the stems.
nonsignificant difference between SRfo and SRfi (favoring SRfo; $G_{adj} = 4.07$, df = 1, $0.025 < P < 0.05$). Earlier, larvae on SRfi suffered significantly higher mortality on those than on SRfo between the time of initiating a refuge and the check at 5 days (overall $G_{adj} = 10.40$, df = 2, $P < 0.01$; for SRfi versus SRfo, $G_{adj} = 8.94$, df = 1, $P < 0.005$). The slightly larger (second and third instar) larvae released at Brookshead did not show this burst of higher mortality on field plants, and survival was statistically indistinguishable between SRfi and SRfo but lower on SCfo after 24 days (overall $G_{adj} = 11.68$, df = 2, $P < 0.005$, SRfi versus SRfo: $G_{adj} = 0.77$, df = 1, $P > 0.1$, SRfo versus SCfo: $G_{adj} = 11.00$, df = 1, $P < 0.001$) (Fig. 2).

Gowan Farm larvae disappeared from SRfi by early October (Fig. 2), perhaps because the early senescence of field plants at this exposed site following a heavy frost caused larvae to emigrate to ground litter for overwintering. However, SCfo remained green until late October, so the disappearance of larvae from SCfo at both sites could not be attributed to faster plant senescence.

Factors potentially accounting for high mortality on SCfo included high predator loads, unusual larval behavior resulting in greater exposure to predation or other mortality, and poor physiological response to the host plant as a food source. Among these factors, “predation” by other herbivores was indeed relatively severe on SCfo: deer nipped off ten SCfo plants at Brookshead and four SCfo plants at Gowan Farm that had borne caterpillars at the previous check. Heavy feeding by a large tortricid caterpillar apparently dislocated another Dichomeris caterpillar from an SCfo plant. No SRfi or SRfo plants were nipped by deer or heavily attacked by other herbivores.

Of true predators the vast majority on all three goldenrod types were spiders, usually small webspinners and salticids. Occasional nabids, reduviids, syrphid larvae, ants, and predaceous mites were also noted. Their numbers did not correlate with low caterpillar survival, however, because they tended if anything to be most abundant on SRfo, on which larval survival was good (Fig. 3).

One aspect of larval behavior, the manner of construction of leaf refuges, differed significantly among goldenrod categories and probably favored larvae on SCfo (Fig. 4). Higher proportions of larvae on the thin-leaved SCfo folded or sharply pinched the leaves, forming roomy refuges (“creases”) that the larvae could remain inside to feed. On SRfo leaves, which have thicker veins, and on SRfi leaves, which have much thicker veins and also thicker blades (Loeffler unpublished data), higher proportions of larvae simply spun silk mats (“webs”) under which they rested and from which they typically had to emerge to feed. G-tests of relative numbers of creases and folds versus webs on different goldenrod types were significant at both sites (Gowan Farm, $G_{adj} = 8.198$, df = 2, $P < 0.025$; Brookshead, $G_{adj} = 9.359$, df = 2, $P < 0.01$). Caterpillars on SRfi were the most likely to bind two leaves to form a “sandwich” refuge, because the leaves on field plants tended to be relatively small and crowded and could be pulled together even by a 2-3 mm
Fig. 2. Survival of unprotected *D. leuconotella* larvae set out as first and second instars in mid-late August at Gowan Farm and as second and third instars at the end of August at Brookshead Reserve. For statistical comparisons see text.
caterpillar. Such "sandwiches" enclosed an amount of enclosed leaf tissue intermediate to that within a web and that within a crease or fold.

There were no differences among hosts or habitats in number of refuges constructed (usually 1-3 refuges per larva over the first ca. 24 days) and amount of feeding. Differential survival may however have obscured differences in these behaviors (see Laboratory Observations below).

First and early second instars grew poorly on SCfo. Among the younger
Younger Cohorts (ave. length 2.4 mm)  

Older Cohorts (ave. length 2.7 mm)  

SRfi  
SRfo  
SCfo  

Fig. 4. Relative numbers of *D. leuconotella* caterpillars constructing each of three refuge types over the first five days after release on field and forest goldenrods in late summer, 1985. Younger cohorts were first and second instar larvae released at Gowan Farm; older cohorts were second and third instar larvae released at Brookshold Reserve. For each pie graph, n = 38 to 52 depending on number of larvae surviving five days on that goldenrod host-habitat category (Fig. 2).

cohort set out at Gowan Farm, survivors to mid September grew significantly less on SCfo than on SRfi or SRfo (ANOVA: $F_{(host\ category)} = 4.344, df = 2.32, P = 0.021$); indeed, many larvae shrank (Fig. 5). No first instars survived 24 days, and survival through 24 days of the mixed group of first and second instars was significantly associated with larger initial size (Kruskal-Wallis test: $T = 7.030, P = 0.008$). On SRfi or SRfo, in contrast, many first instars survived; the associations of survival with greater initial size were weak and nonsignificant (Kruskal-Wallis tests, SRfi: $P = 0.125$, SRfo: $P = 0.075$). The slightly older (second to third instar) larvae at Brookshold grew as well on a diet of SCfo as on SRfi and SRfo (Fig. 5) (ANOVA: $F_{(host\ category)} = 1.552, df = 2.57, P = 0.221$). Survival to late September in this older group was not significantly related to initial size on any of the three host-habitat categories (Kruskal-Wallis tests: $P >> 0.05$).

**Field experiment: Caged larvae**

Data on larvae protected from predators confirmed that very young larvae had high host-related mortality on SCfo. Disappearance rates of larvae released as second instars were significantly higher on this host (Fig. 6; at mid Sept. check before significant host senescence, $G_{adj.} = 22.97, df = 2, P << 0.001$; SRfo versus SCfo, $G_{adj.} = 11.30, df = 1, P < 0.001$; SRfi versus SRfo, $P > 0.1$).
Fig. 5. Rates of growth in length (means and standard errors) of unprotected *D. leuconotella* caterpillars surviving a ca. 24 day period on field and forest goldenrods in late summer, 1985. (For calculation of daily growth rate, growth in length was assumed to be linear with time. Laboratory measurements suggest that this assumption is approximately correct for small larvae in late summer.)

Usually, caterpillars that disappeared had been either shrinking or at least failing to grow. I searched the cages with great care at each check and was sometimes able to locate 1-2 mm, shriveled and blackened corpses. Among the older (third and fourth instar) larvae of the second group survival was however comparable to that on SRfi and SRfo (Fig. 6).

Growth rates of surviving larvae (Fig. 6) corroborated the results for unprotected larvae. Larvae released as second instars grew at similar rates on SRfi and SRfo but immediately showed lower growth rates on SCfo, and their cumulative growth rates remained significantly lower on SCfo for a month (ANOVA: $P < 0.05$ for time of release to first, second, and third checks, $P > 0.05$ for time of release to fourth and fifth checks). By October all of the larvae which grew poorly on SCfo had died, leaving just one larva that had grown through the season at rates comparable to the average rates on SRfi and SRfo. Growth rates of third and fourth instars (older cohort), however, were similar for most of the season on the three host plant categories (ANOVA, $P > 0.05$).

Although SCfo remained green longer into October than did SRfi or SRfo, its delayed senescence provided no advantage to the caterpillars. During
October the caterpillars simply shortened and thickened in preparation for winter, at even rates regardless of goldenrod type or degree of senescence (Kruskal Wallis test: $T = 0.640$, $P = 0.959$).

**Laboratory observations**

Second instars placed onto cut stem tops and monitored for three hours behaved differently depending on host type. Larvae on SCfo spent relatively more time crawling over the stem top; larvae on SRfo spent relatively more time resting; and larvae on SRfi spent relatively more time applying silk to
construct refuges (Fig. 7, Table 1). Third and fourth instars showed similar but less pronounced trends (Fig. 7, Table 1).

Despite their extensive wandering before starting refuges, early instars on SCfo fed as promptly as those on SRfi and SRfo (second instars, Friedman test: $T_2 = 2.102$, $df = 2.34$, $P > 0.10$; third and fourth instars, Friedman test: $T_2 = 2.825$, $df = 2.24$, $P > 0.10$). In fact, if a trend existed, it was for larvae to be slowest to feed on SRfi in both age groups. As in field experiments, larvae appeared to consume similar amounts of foliage of the three goldenrod categories during subsequent days.

Differences in leaf morphology appeared to account for the slowness of larvae to settle down on SCfo. Larvae consistently began refuges in cracks or crevices when they were available. On *S. rugosa* (SRfi and SRfo), every leaf had such a crevice where the midrib and the underside of the blade met at a sharp angle, and many leaves had smaller crevices along side veins. Virtually all refuges were constructed in those spots. However, *S. caesia* (SCfo) midribs tapered smoothly and met the blade at a shallow angle in cross section; and the small side veins created no crevice at all. Three larvae on SCfo began spinning relatively quickly (within 45 minutes) when they encountered cracks between axillary flowerbuds and leaves. But these refuge sites were too small for long-term habitation, and two of the three larvae abandoned these refuges within a day.
Table 1. Results of Friedman tests and and followup multiple comparisons (Conover 1980) comparing activity of early instar D. leuconotella caterpillars on cut stem tops of SRfi, SRfo, and SCfo (n = 19 second instars or 15 third and fourth instars on each host plant-habitat category).

<table>
<thead>
<tr>
<th>Comparison</th>
<th>T^2</th>
<th>df</th>
<th>P</th>
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<tr>
<td>Second instars</td>
<td></td>
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<tr>
<td>Proportion of time spent crawling, SRfi, SRfo, SCfo</td>
<td>10.577</td>
<td>2, 36</td>
<td>P &lt; 0.01</td>
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<td>followup comparisons:</td>
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<tr>
<td>SRfi &gt; SRfo</td>
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<td>SCfo &gt; SRfi</td>
<td></td>
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<td>P &lt; 0.001</td>
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<td>SRfi &gt; SCfo</td>
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<td>P &lt; 0.001</td>
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<tr>
<td>Proportion of time spent resting, SRfi, SRfo, SCfo</td>
<td>6.333</td>
<td>2, 36</td>
<td>P &lt; 0.01</td>
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<td>SRfo &gt; SRfi</td>
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<td>P &lt; 0.05</td>
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<td>SRfi &gt; SCfo</td>
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<tr>
<td>SRfo &gt; SCfo</td>
<td></td>
<td></td>
<td>P &lt; 0.002</td>
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<tr>
<td>Proportion of time spent spinning, SRfi, SRfo, SCfo</td>
<td>5.252</td>
<td>2, 36</td>
<td>P &lt; 0.025</td>
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<td>followup comparisons:</td>
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<tr>
<td>SRfi &gt; SRfo</td>
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<td></td>
<td>P &lt; 0.005</td>
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<tr>
<td>SRfi &gt; SCfo</td>
<td></td>
<td></td>
<td>P &lt; 0.02</td>
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<tr>
<td>SCfo = SRfo</td>
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| Third and fourth instars |       |    |        |
| Proportion of time spent crawling, SRfi, SRfo, SCfo | 3.343 | 2, 28 | P < 0.01 |
| followup comparisons: |       |    |        |
| SRfi = SRfo |       |    | ns     |
| SCfo > SRfi |       |    | P < 0.05 |
| SCfo = SRfo |       |    | ns     |
| Proportion of time spent resting, SRfi, SRfo, SCfo | 0.924 | 2, 28 | ns     |
| Proportion of time spent spinning, SRfi, SRfo, SCfo | 2.846 | 2, 28 | ns     |

A positive aspect of SCfo as a host was that its leaves could be folded much more rapidly into a protective chamber than could the thicker-veined leaves of SRfo or the substantially thicker leaves of SRfi. Hence, although second-instar larvae typically began applying silk half an hour or more later on SCfo than on SRfi or SRfo (median times for starting refuges 1.25 hours on SCfo and 0.5 hours on SRfi or SRfo), the leaves were on average more curved on SCfo at three hours and considerably more curved at 24 hours (Table 2). By 24 hours many second-instar larvae on SCfo had folded the leaf to a right angle or more, whereas those on SRfi or SRfo had barely bent the leaf. Third or fourth instars also folded SCfo leaves fastest; in addition, with their greater abilities they folded SRfo leaves detectably more sharply than SRfi leaves in 24 hours (Table 2).

Over the next 12 days, second-instar larvae abandoned their refuges for new ones significantly more often on SCfo and SRfi than on SRfo (Fig. 8). The readiness to abandon refuges on SRfi may have been due to a higher rate of drying and browning of SRfi stem tops (91% of refuges showed browning around feeding scars and 48.5% of stem tops showed partial to substantial
Table 2. Results of Friedman tests comparing relative change in leaf curvature achieved by early-instar *D. leuconotella* caterpillars folding leaves on cut stem tops of SRfi, SRfo, and SCfo (n = 18 second instars or 14 third and fourth instars on each host plant-habitat category).

<table>
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<tr>
<th>Comparison</th>
<th>$T_2$</th>
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<tr>
<td>Second instars</td>
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<tr>
<td>Change in leaf curvature at 3 hrs, SRfi, SRfo, SCfo</td>
<td>28.737</td>
<td>2, 34</td>
<td>P &lt;&lt; 0.01</td>
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<td>followup comparisons:</td>
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<tr>
<td>SRfi = SRfo</td>
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<td>ns</td>
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<tr>
<td>SCfo &gt; SRfi</td>
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<td></td>
<td>P &lt; 0.001</td>
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<tr>
<td>SCfo &gt; SRfo</td>
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<td>P &lt; 0.001</td>
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<tr>
<td>Change in leaf curvature at 24 hrs, SRfi, SRfo, SCfo</td>
<td>70.665</td>
<td>2, 34</td>
<td>P &lt;&lt; 0.01</td>
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<td>followup comparisons:</td>
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<tr>
<td>SRfi = SRfo</td>
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<td>ns</td>
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<tr>
<td>SCfo &gt; SRfi</td>
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<td></td>
<td>P &lt; 0.001</td>
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<td>SCfo &gt; SRfo</td>
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<td>P &lt; 0.001</td>
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<tr>
<td>Third and fourth instars</td>
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<tr>
<td>Change in leaf curvature at 3 hrs, SRfi, SRfo, SCfo</td>
<td>8.000</td>
<td>2, 26</td>
<td>P &lt; 0.01</td>
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<td>followup comparisons:</td>
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<tr>
<td>SRfi = SRfo</td>
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<td>P &lt; 0.001</td>
</tr>
<tr>
<td>SCfo &gt; SRfo</td>
<td></td>
<td></td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>Change in leaf curvature at 24 hrs, SRfi, SRfo, SCfo</td>
<td>10.908</td>
<td>2, 26</td>
<td>P &lt; 0.01</td>
</tr>
<tr>
<td>followup comparisons:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SRfo &gt; SRfi</td>
<td></td>
<td></td>
<td>P &lt; 0.05</td>
</tr>
<tr>
<td>SCfo &gt; SRfi</td>
<td></td>
<td></td>
<td>P &lt; 0.001</td>
</tr>
<tr>
<td>SCfo &gt; SRfo</td>
<td></td>
<td></td>
<td>P &lt; 0.05</td>
</tr>
</tbody>
</table>

Senescence, compared to 71% and 11% respectively on SRfo stem tops). But SCfo stem tops senesced least rapidly of the three types (32% of refuges showed some browning; all stem tops however remained green and turgid). Hence some other characteristic of SCfo apparently triggered larvae to abandon their refuges. As in previous results, third and fourth instars were less affected than second instars by differences among the three host categories (Fig. 8).

**Discussion**

Two factors—food quality and leaf morphology—appeared to strongly affect the performance of early instar *D. leuconotella* larvae on forest and field goldenrods. Both of these factors varied more significantly between host plant species than between habitats. Indeed, on the same host plant species (SR or *S. rugosa*), caterpillars tended to fare slightly better in forest than in their usual field habitat.

Early instar *D. leuconotella* caterpillars had generally comparable growth rates on SRfi and SRfo, a perhaps surprising result given documented differences in food quality between sun and shade leaves of various other plant species (Lincoln and Langenheim 1979, Louda and Rodman 1983,
Fig. 8. Numbers of refuges built by early instar *D. leuconotella* larvae over 12 days (late summer-fall, 1987) on cut stem tops of SRfi, SRfo, and SCfo. G-tests were highly significant for second instars, both overall and in followup comparisons of SRfo versus SRfi and SRfo versus SCfo (*P* < 0.005); but a G-test for third and fourth instars was not significant (*P* > 0.05).
Schultz 1983 and references therein, Bultman and Faeth 1988, Dudt and Shure 1994). On S. caesia (SCfo), however, first and second instars suffered poor growth rates and high mortality. SCfo differs chemically and nutritionally from SRfi: water and nitrogen contents are higher, but so are tannins and fiber on a percent dry matter basis (Hamilton, 1989). Other aspects of SCfo’s secondary chemistry (e.g., presence of alkaloids) are little known (Hamilton, 1989). A common chrysomelid beetle, Trirhabda virgata, that feeds in June and July on field goldenrod species, also survives and grows poorly on SCfo (Messina 1983, Hamilton 1989). Among the several species of insect herbivores that do develop successfully on SCfo is one other Dichomeris species, D. bilobella, (Hamilton 1989, Loeffler 1994), which grows at comparable rates on SCfo, SRfo, and SRfi (Loeffler 1992). Dichomeris leuconotella also seems able to thrive on SCfo from the third instar onward, although caterpillars raised through their later instars on SCfo tended to develop into smaller and later-eclosing adults (Loeffler 1992 and unpublished data). All instars of D. leuconotella feed readily on SCfo. Thus, the chemical aspect of SCfo that negatively affects the youngest larvae is not a component that can be avoided by small mouthparts (e.g., Reavey 1993 and references therein); nor is it a strong feeding deterrent.

Leaf morphology strongly affected larval behavior, which in turn affected larval vulnerability to predation and to accidental dislocation from the host plant. Staged encounters using some of D. leuconotella’s most common predators suggested that early instars, though most secure when in their refuges, also tend to escape predator notice when resting quietly without a refuge (Loeffler 1996a). In the present study, therefore, larvae on SRfo behaved in ways that should minimize predation, resting quietly much of the time, wandering less than on SCfo, and spending less time actively applying silk than on SRfi. The thinness of forest leaves was advantageous; larvae could complete refuges faster on forest plants than on field plants despite spending less time per hour in spinning. This difference may account for relatively high mortality of first and second instars on SRfi during construction of their first refuges.

On SCfo, caterpillars could fold leaves even more rapidly than on SRfo, but this advantage appeared to be counteracted by their prolonged wandering to find refuge sites and their tendency to abandon refuges frequently and seek new ones. Prolonged wandering of caterpillars on SCfo appeared to be a response to the shallow, poorly-defined crevices beside leaf veins that are characteristic of this goldenrod species. Those few caterpillars that encountered a relatively sheltered spot on SCfo (between an axial flowerhead and a leaf base) settled down to spin there quickly—although such spots were too small to be used for long. This tendency to seek out the most sheltered site available in which to spin a refuge is typical for early instar D. leuconotella; I have found them inhabiting leafy ceccidomyiid galls, leaf mines of Cremastobombycia solidaginis (Lepidoptera: Gracillariidae), and leaf ties of a variety of other caterpillars including the previous generation of Dichomeris
(Loeffler 1994). Damman (1987) and Cappuccino (1993) also reported tendencies of early instar leaf-tying caterpillars to inhabit premade shelters, or of adult moths to oviposit in old leaf ties; and Cappuccino (1993) verified that first instars of the birch tube-maker *Acrobasis betulella* Hulst. (Lepidoptera: Pyralidae) had higher survival rates when inhabiting such spaces. In the absence of such shelters, *D. leuconotella* larvae invariably build their refuges in the crevice alongside a vein; but such crevices must apparently be of a certain depth to be attractive as refuge sites, and those on *S. caesia* (SCfo) are shallower than those of *S. rugosa* (both SRfi and SRfo, unpublished data) or of the other common, field-inhabiting goldenrods that are normally used as hosts.

Some other elements of leaf morphology, in particular trichomes, have been shown to have striking effects on caterpillar behavior and survival (Levin 1973, Southwood 1986 and references therein, Woodman and Fernandes 1991). In the present study, trichomes had no obvious positive or negative effects; caterpillars readily held onto and negotiated both the hairy leaves of *S. rugosa* (SRfi and SRfo) and the smooth leaves of *S. caesia* (SCfo) (pers. observ.). It is conceivable that the presence of trichomes on *S. rugosa* enhanced the caterpillars’ tactile sensation of being in crevices and increased their willingness to settle down and spin refuges.

In their need for sheltered spots or deep crevices, *D. leuconotella* caterpillars may be mismatched phenologically with SCfo. Only two species of leaf-folding caterpillars specializing on *Solidago* and *Aster* use *S. caesia* (SCfo) as a host: *D. bilobella* (Zeller) and the oecophorid *Agonopterix putvipennella* (Clemens) (Hamilton 1989, and pers. observ.). Early instars of both species are found only in spring, when they can (and do) find crevices for starting refuges in the leafy terminal buds (Loeffler 1994). Other goldenrod-feeding *Dichomeris* species in central New York hatch in summer and overwinter as partly grown larvae (Hodges 1986, Loeffler 1994); and none of them is known to use SCfo as a host—not even *D. ochripalpella* (Zeller), which unlike *D. leuconotella* often develops on forest plants (Loeffler 1994).

The poor survival and growth of early instar *D. leuconotella* on SCfo thus appears related to host plant attributes rather than to effects of habitat. Older instars show similar survival patterns on SRfi, SRfo, and SCfo, although for slightly different reasons (Loeffler 1992 and unpublished data), and I will argue in presentation of those data that the most likely explanation for *D. leuconotella*’s absence from forest habitat is not that immature stages cannot survive there, but that suitable hosts (i.e., goldenrods and asters other than *S. caesia* (SCfo), on which adults are reluctant to oviposit; Loeffler 1994) are more concentrated in open areas. In one of the few other studies addressing the relationship of performance of uncaged larvae and larval habitat restriction, Rausher (1979) reached a similar conclusion with regard to certain papilionid butterflies: adults of two species laid eggs only in sunny habitats, where host plants were more
abundant, although their larvae had better survival rates when transferred to host plants in forest.

Acknowledgments. I would like to thank Richard Root for his advice and support throughout this project, and John Gowan for extensive help with fieldwork. George Eickwort, John Gowan, Peter Marks, Richard Root provided valuable suggestions on the manuscript. Financial support was provided by Andrew D. White, Sage, and National Science Foundation Graduate Fellowships, by National Science Foundation Grant BSR-8817961 to R. B. Root, and by Hatch Project 410 to R. B. Root. Additional support and computer facilities were provided by Dickinson College.

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Effect of Mating Duration on Oviposition Rate and Hatchability of the Indian Tasar Silk Moth *Antheraea mylitta* (Saturniidae) in Different Seasons

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**Abstract.** Production of viable eggs in the tasar silk insect *Antheraea* sp. is influenced by the mating activity. Mating durations from 1 to 12 hours show an increasing trend in the hatchability of eggs up to 5 hours and little change thereafter during all the three rearing seasons, i.e., Rainy, Autumn and Winter. Significant variation in hatchability of eggs between mating durations has been observed. However, oviposition rate in *A. mylitta* does not show significant variation with increase in mating duration.

**INTRODUCTION**

The Indian tropical tasar silk moth *Antheraea mylitta* (Drury) (Lepidoptera: Saturniidae) is semidomesticated and is economically important because of its commercial exploitation for tasar silk. The larvae are reared on the primary food plants, Asan (*Terminalia tomentosa* Wt & Arn) (Combretaceae) and Arjun (*Terminalia arjuna*, Wt & Arn) (Combretaceae) in different seasons, i.e., Rainy (July-August), Autumn (September-October) and Winter (November-December). The larvae possess five instars and after the fifth instar enter the pupal stage by spinning a silk cocoon. The cocoons are usually preserved in a specially designed house called ‘grainage’. Before each rearing season, the moths emerge from the cocoons and males and females mate at random. Mating continues for a period of 10-12 hours (Jolly et al, 1974). Females lay mature eggs just after mating. Inadequate male moth population in grainages is a major factor affecting production of viable eggs for rearing, making it necessary to use mated males for second matings. Little literature is available on the effect of duration of mating on the oviposition rate and production of viable eggs, and this investigation was carried out to determine a suitable time range for effective mating in *A. mylitta*.

**MATERIAL AND METHODS**

One thousand healthy, freshly emerged moths of both sexes were selected at random in equal proportions during each rearing season. The moths were allowed to mate. A total of 240 couplings were randomly selected from them and divided into 12 groups, with 20 couplings each. The moths in different groups were allowed to mate in separate cages for durations ranging from 1 to 12 hours, after which the moths were decoupled physically. Eggs laid by the mated females were collected,
counted and kept under laboratory conditions until hatching. The hatching percentage was recorded and analysed statistically for the ANOVA. The investigation was carried out at the State Sericultural Research Station, Baripada, Orissa, India during all the three rearing seasons, i.e., Rainy, Autumn and Winter of 1990.

**Results**

The mean oviposition rate and hatchability of *A. mylitta* at different mating durations are illustrated in Table 1. The mean oviposition rate at different mating durations shows little variation during all the three rearing seasons. One way ANOVA test shows that the variation in oviposition rate at different mating durations is not significant. However the oviposition rate of *A. mylitta* between seasons was found to be highly significant (P<0.05, F = 247.26). The hatchability of eggs laid by mated female moths exhibits an increasing trend from one hour mating duration to five hours and shows little variation thereafter during all the three rearing seasons. One way ANOVA tests of data between durations of mating exhibit a significant difference in hatchability of eggs (P<0.05, F = 5.298). However, the variation in the hatchability of eggs of *A. mylitta* between seasons was not significant.

**Discussion**

Narayanan *et al.* (1964) have reported that in the mulberry silk moth (*Bombyx mori* Linn.) 1 to 2 hours of mating is enough for normal oviposition. Behura and Panda (1978) have further observed that 4 hours of copulation were sufficient for normal oviposition in the eri silk moth *Samia ricini* Hutt. Shahi *et al.* (1979) reported an increase in the oviposition rate of *Dysdercus koenigii* Fabr. (Hemiptera: Pyrrhocoridae) with increase in mating duration. However, the present investigation indicates that the oviposition rate does not seem to be much influenced by the durations of mating.

In *A. mylitta* the hatchability of eggs was found to increase with an increase in mating duration up to 5 hours during all seasons and shows little change by further increase in mating duration. This indicates that 4-5 hours of mating is optimal for normal oviposition in *A. mylitta*. The present finding corroborates the earlier reports by Narayanan and Jadav (1964) and Gajare (1978) that maximum hatchability of eggs in *B. mori* occurred after 4 hours of mating. However, Rau and Rau (1913) have reported that in the moth *Cecropia* sp. 3 hours of mating are sufficient for normal fertility of eggs and further increase in mating duration is a waste of valuable time and vitality. Further, Jolly *et al.* (1974) observed that 1-2 hours of copulation are sufficient for normal hatchability of *A. mylitta* eggs. Punitham *et al.* (1987) reported that an increase in mating duration of *B. mori* from 3 hours to 9 hours enhanced the hatching percentage of eggs from 83% to 97%. In the present study the hatchability of eggs of *A. mylitta*, though significant between durations of mating, does not show much variation after 5 hours of mating.

The oviposition rate in *A. mylitta* shows significant variations between seasons. Davis (1965) has remarked that the oviposition variation is correlated to the activation of corpus allatum. Gillot and Friedel (1977) have
### Table 1. Mean values of oviposition rate and percent hatchability ± Standard deviation of *A. mylitta* at different mating durations in different seasons during 1990.

<table>
<thead>
<tr>
<th>Duration of mating (hrs.)</th>
<th>Season-wise oviposition rate (OR) and Percent Hatchability (H)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Rainy Season OR</td>
</tr>
<tr>
<td></td>
<td>198.3 ± 9.4</td>
</tr>
<tr>
<td></td>
<td>194.6 ± 7.8</td>
</tr>
<tr>
<td></td>
<td>195.8 ± 8.3</td>
</tr>
<tr>
<td></td>
<td>195.5 ± 8.7</td>
</tr>
<tr>
<td></td>
<td>196.1 ± 8.1</td>
</tr>
<tr>
<td></td>
<td>195.4 ± 9.1</td>
</tr>
<tr>
<td></td>
<td>197.0 ± 8.6</td>
</tr>
<tr>
<td></td>
<td>196.2 ± 9.3</td>
</tr>
<tr>
<td></td>
<td>194.4 ± 8.2</td>
</tr>
<tr>
<td></td>
<td>195.7 ± 7.8</td>
</tr>
<tr>
<td></td>
<td>198.6 ± 8.8</td>
</tr>
<tr>
<td></td>
<td>197.2 ± 8.1</td>
</tr>
</tbody>
</table>

Suggested that the increase in egg production might be due to secretion of fecundity-enhancing substances by male insects at the time of mating. Significant variation in the oviposition rate of *A. mylitta* between seasons may be attributed to the differential effects of the above factors during the three rearing seasons. The influence of seasonal factors on the reproductive behavior in *A. mylitta* needs further investigation.

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Allozyme analysis of a known hybrid zone between *Hyalophora euryalus* and *H. columbia gloveri* (Lepidoptera: Saturniidae) in the California Sierra Nevada.

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Abstract. Allozyme analysis of a hybrid zone between the moths *Hyalophora euryalus* and *H. columbia gloveri* confirmed the hybrid nature of populations previously shown (Collins, 1984) to be phenotypically intermediate and highly variable. Nine of 20 loci examined were polymorphic, and one locus (GAPDH) was fixed for alternate alleles in the two species, but heterozygous in the hybrid zone. Geographic patterns of allele frequencies conformed to expectation based on population genetic models. Several "rare alleles", unique to the hybrid zone, were found, as has often been seen in other hybrid zone studies.

Key Words: allozyme, *Hyalophora*, hybrid zone, hybridization

Introduction
Hybrid zones have played an important role as natural laboratories in speciation studies, especially since the advent of enzyme electrophoresis and other molecular techniques in systematics (Collins, 1991; Harrison, 1990, 1993; Hewitt, 1990). Two features of hybrid zones have intrigued evolutionary biologists: (1) the apparent stability and persistence of hybrid zones, and (2) the often abrupt phenotypic transition from intergrades into the parental populations bordering the hybrid zone. Hybrid zones are often distributed as long, narrow bands. Their geographic location and the coincidence of hybrid zones in diverse animal groups suggest that many hybrid zones are of post-Pleistocene origin, forming as previously isolated taxa invaded deglaciated regions and came into secondary contact (Harrison, 1970; Hewitt, 1990, Remington, 1968). The most widely accepted population genetic models of hybrid zones describe an equilibrium between gene flow, which would tend to widen the zone of intergradation, and selection against recombinant genotypes, which would tend to maintain sharp phenotypic boundaries (Barton and Hewitt, 1985; Endler, 1977). When the hybridizing
taxa differ in critical developmental or reproductive traits recombinant genotypes will be inferior. Selection at these loci will impede gene exchange across the hybrid zone, thus preventing the fusion of the gene pools of the hybridizing taxa. Other neutral or beneficial alleles (at loci not closely linked to critical fitness loci) will introgress across the hybrid zone into the parental populations bordering the zone. Careful analysis of hybrid zones can reveal the genetic differences and similarities of closely related species, and thus shed light on the speciation process.

The failure of effective reproductive barriers to evolve in hybrid zones, in the face of hybrid unfitness, argues against the concept of reinforcement of mating barriers. If hybrid unfitness is severe, the very condition postulated to favor the origin of anti-hybridization mechanisms (Dobzhansky, 1970), the greater will be the barrier to introgression (Bigelow, 1965).

This paper describes a preliminary electrophoretic analysis of a hybrid zone between *Hyalophora euryalus* and *H. columbia gloveri* (Saturniidae) in the area of Monitor Pass, Alpine and Mono Co., California. Phenotypic variation and genetic compatibility among phenotypes has been thoroughly documented (Collins, 1984, 1991, unpubl.).

The frequency and geographic distribution of allozymes are especially useful in estimating the degree of gene flow across hybrid zones. Often the apparent genetic structure of hybrid zones as revealed by allozyme data differ from that expected based on distributions of morphological phenotypes (Harrison, 1990). We present preliminary allozyme data that suggest a high degree of concordance between these neutral genetic markers and morphology in these two species of *Hyalophora*.

**METHODS**

All samples were collected in June 1994 using cylindrical moth traps with a fertile female as a pheromone source suspended in a small chamber above the trap funnel; pheromone response is not species-specific among the western *Hyalophora* (Collins, 1984). Representative samples of *Hyalophora euryalus* were collected in Nevada County, California. *Hyalophora columbia gloveri* were collected in Jefferson County, Colorado. Hybrid zone representatives were collected in Alpine County, California along Silver Creek at the base of Ebbetts Pass and in Lexington Canyon on the west side of Monitor Pass, and at a site on the east slope of Monitor Pass (Mono Co.). These sites represent a west to east transect across the hybrid zone (Figure 1).

Captured individuals were transported live in an ice chest and then stored until use in an ultra-cold freezer at -80°C. Isozyme variability was assayed at 20 presumptive loci (Table 1); general electrophoretic and histochemical staining methods followed Brussard et al. (1985) and May (1992). Genotype frequencies were obtained by direct count of phenotypes observed on the gels. The most common electromorph (allozyme) at each locus was designated as “C,” with relatively faster migrating allozymes scored as “B” and still faster ones designated as “A.” Likewise, allozymes that migrated slower than “C” alleles were scored as “D,” and progressively later letters in the alphabet were assigned to still slower allozymes.

Estimates of heterozygosity, Nei’s (1978) unbiased genetic distances and identities, and a UPGMA phenogram were made using BIOSYS-1 (Swofford and Selander 1981).
Figure 1. Map of Hyalophora hybrid zone, Alpine and Mono Co., California. Phenograms based on multivariate analysis of wing characters, with variation divided into five classes from pure euryalus (left) to pure c. gloveri (right) (Collins, 1984). The negative Y axis shows the frequencies of the "C" allele (fixed in H. columbia gloveri) and "D" allele (fixed in H. euryalus) of GAPDH. Collecting sites: Silver Creek (6500 ft.) at base of Ebbetts Pass; Lexington Canyon (5500 ft.) above Carson River; Monitor Pass (7300 ft.), east slope of Monitor Pass. Pure H. euryalus is found near Lake Tahoe, but due to introgression the nearest pure H. columbia gloveri is found only the isolated Panamint Mountains near Death Valley (not shown).
Table 1. Enzymes assayed and electrophoretic conditions used to analyze a hybrid zone between Hyalophora euryalus and H. columbia gloveri in the Sierra Nevada of California.

<table>
<thead>
<tr>
<th>Locus</th>
<th>Enzyme</th>
<th>Enzyme Commission Number</th>
<th>Buffer</th>
</tr>
</thead>
<tbody>
<tr>
<td>AAT-1,2</td>
<td>Aspartate aminotransferase</td>
<td>2.6.1.1</td>
<td>R</td>
</tr>
<tr>
<td>ALD</td>
<td>Aldolase</td>
<td>4.1.2.13</td>
<td>C</td>
</tr>
<tr>
<td>AK</td>
<td>Adenylate kinase</td>
<td>2.7.4.3</td>
<td>C</td>
</tr>
<tr>
<td>DDH</td>
<td>Dihydrolipoamide dehydrogenase</td>
<td>1.8.1.4</td>
<td>R</td>
</tr>
<tr>
<td>EST-F</td>
<td>Flourescent esterase</td>
<td>-.-.-</td>
<td>4</td>
</tr>
<tr>
<td>GAPDH</td>
<td>Glyceraldehyde-3-phosphate dehydrogenase</td>
<td>1.2.1.12</td>
<td>C</td>
</tr>
<tr>
<td>GPI</td>
<td>Glucosephosphate isomerase</td>
<td>5.3.1.9</td>
<td>R</td>
</tr>
<tr>
<td>GP-3,4</td>
<td>General protein</td>
<td>-.-.-</td>
<td>4</td>
</tr>
<tr>
<td>G3P</td>
<td>Glycerol-3-phosphate dehydrogenase</td>
<td>1.1.1.8</td>
<td>R</td>
</tr>
<tr>
<td>HA</td>
<td>Hexoseaminsease</td>
<td>3.2.1.52</td>
<td>R</td>
</tr>
<tr>
<td>IDH</td>
<td>Isocitrate dehydrogenase</td>
<td>1.1.1.42</td>
<td>R</td>
</tr>
<tr>
<td>MDH-1,2</td>
<td>NAD Malate dehydrogenase</td>
<td>1.1.1.37</td>
<td>4</td>
</tr>
<tr>
<td>MPI</td>
<td>Mannosephosphate isomerase</td>
<td>5.3.1.8</td>
<td>R</td>
</tr>
<tr>
<td>MUP</td>
<td>Methylumbelliferyl phosphatase</td>
<td>-.-.-</td>
<td>C</td>
</tr>
<tr>
<td>PGDH</td>
<td>Phosphogluconate dehydrogenase</td>
<td>1.1.1.44</td>
<td>4</td>
</tr>
<tr>
<td>SOD</td>
<td>Superoxide dismutase</td>
<td>1.15.1.1</td>
<td>C</td>
</tr>
<tr>
<td>XDH</td>
<td>Xanthine dehydrogenase</td>
<td>1.1.1.204</td>
<td>R</td>
</tr>
</tbody>
</table>

Results

Sample sizes and allele frequencies are given in Table 2. Polymorphisms were detected at nine of the 20 assayed isozyme loci in at least one of the sampled populations (Table 2). A fixed allelic difference was detected at the GAPDH locus with *H. euryalus* fixed for the D allele and *H. columbia gloveri* fixed for the C allele (Table 2). Hybrid zone samples were found to be segregating for both alleles at GAPDH (Table 2). Similarly, *H. euryalus* segregated for alleles B and C at AK-1 while *H. c. gloveri* segregated for the alleles C and D at this locus (Table 2). The sample from Monitor Pass within the hybrid zone segregated for all three alleles (B, C, and D) at AK-1 (Table 2). Hybrid zone samples segregated for several alleles not detected in either parental species, e.g. AAT-1 B and D, AAT-2 B, IDH-1 D (Table 2).

Nei’s (1978) unbiased genetic distances and identities for all pairs of samples are given in Table 3. Both of these estimates of overall genetic similarity exhibited an east to west cline in genetic similarity for *H. c. gloveri* from Colorado (Table 3). The *H. c. gloveri* sample was most similar to the Monitor Pass hybrid sample which was the eastern-most sample within the hybrid zone, and was least similar to *H. euryalus* sampled from west of the hybrid zone in California (Table 3). The *H. euryalus* sample was genetically more similar to the hybrid samples than it was to the *H. c. gloveri* sample (Table 3) and did not exhibit a directional decrease in genetic similarity.
Table 2. Sample sizes and allele frequencies at polymorphic loci assayed in *Hyalophora euryalus* and *H. c. gloveri* including hybrid samples with expected mean heterozygosity estimates, H (S.E.).

<table>
<thead>
<tr>
<th>Site</th>
<th>Monitor Pass</th>
<th>Lexington Canyon</th>
<th>Silver Creek</th>
<th>H. euryalus</th>
<th>H. c. gloveri</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Sample size</td>
<td>6</td>
<td>7</td>
<td>10</td>
<td>6</td>
<td>6</td>
</tr>
<tr>
<td>Locus</td>
<td>Allele</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>AAT-1</td>
<td>B</td>
<td>0.000</td>
<td>0.214</td>
<td>0.000</td>
<td>0.000</td>
</tr>
<tr>
<td></td>
<td>C</td>
<td>0.833</td>
<td>0.714</td>
<td>0.550</td>
<td>1.000</td>
</tr>
<tr>
<td></td>
<td>D</td>
<td>0.167</td>
<td>0.071</td>
<td>0.450</td>
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<tr>
<td>AAT-2</td>
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<td>AK-01</td>
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<td></td>
<td>C</td>
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<td>0.857</td>
<td>0.850</td>
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<td></td>
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<tr>
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<td>0.000</td>
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<td></td>
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<tr>
<td></td>
<td>0.092</td>
<td>0.093</td>
<td>0.093</td>
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</tr>
<tr>
<td></td>
<td>(0.039)</td>
<td>(0.035)</td>
<td>(0.035)</td>
<td>(0.030)</td>
<td>(0.021)</td>
</tr>
</tbody>
</table>

Table 3. Unbiased genetic distances (Nei 1978) above diagonal and unbiased genetic identities (Nei 1978) below diagonal for *Hyalophora euryalus*, *H. c. gloveri*, and hybrid zone samples assayed at 20 presumptive isozyme loci.

<table>
<thead>
<tr>
<th></th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
</tr>
</thead>
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<tr>
<td>1. Monitor Pass</td>
<td></td>
<td>0.001</td>
<td>0.009</td>
<td>0.026</td>
<td>0.020</td>
</tr>
<tr>
<td>2. Lexington Canyon</td>
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<td></td>
<td>0.002</td>
<td>0.021</td>
<td>0.033</td>
</tr>
<tr>
<td>3. Silver Creek</td>
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<td>0.998</td>
<td></td>
<td>0.026</td>
<td>0.059</td>
</tr>
<tr>
<td>4. <em>H. euryalus</em></td>
<td>0.974</td>
<td>0.980</td>
<td>0.974</td>
<td></td>
<td>0.070</td>
</tr>
<tr>
<td>5. <em>H. c. gloveri</em></td>
<td>0.980</td>
<td>0.968</td>
<td>0.943</td>
<td>0.932</td>
<td></td>
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</table>
Figure 2. UPGMA phenogram based on Nei's (1978) unbiased genetic distances for 20 isozyme loci. The cophenetic correlation is 0.808.

Across the hybrid zone as did H. c. gloveri. The UPGMA phenogram in Figure 2 shows the close affinity among the hybrid zone samples and the greater overall genetic similarity between the California H. euryalus sample with the hybrid zone samples than with H. c. gloveri collected in Colorado.

Estimated mean individual heterozygosity expected under Hardy-Weinberg assumptions ranged from 0.080 in the Hyalophora columbia gloveri sample to 0.093 in both the Lexington Canyon and Silver Creek samples (Table 2). Estimated heterozygosity was higher in the hybrid zone samples than in the parental populations (Table 2). Significant deviations from Hardy-Weinberg expectations were detected at four loci (AAT-1 in the Lexington Canyon and Silver Creek samples, AK-1 in the Silver Creek sample, and MDH-1 in the H. euryalus sample). All four significant deviations from expected Hardy-Weinberg genotypic proportions were heterozygote deficiencies. Given that only four percent, i.e., four of 100, of the tests performed for conformance to Hardy-Weinberg equilibrium indicated significant deviations, no significant trend in departures from Hardy-Weinberg expectations was detected.

In summary, the genetic data are completely consistent with the geographic distribution of the samples and the expected pattern of genetic exchange through the hybrid zone. A multivariate morphometric analysis of wing pattern traits in the hybrid zone (Collins, 1984) clearly revealed a west-to-east transition from euryalus-like to c. gloveri-like across Monitor Pass (Figures 1 and 3). Variability was highest in mid-hybrid zone, and introgression for certain wing traits, such as hindwing discal spot shape, showed evidence of introgression of euryalus genes into the c. gloveri populations bordering the hybrid zone and extending south along the east slope of the Sierra Nevada.
Figure 3. Range of *Hyalophora* phenotypes present in the Monitor Pass hybrid zone. Top left specimen resembles pure *H. columbia gloveri*; lower right specimen resembles pure *H. euryalus*. Other specimens indicate complete intergradation of characters otherwise diagnostic for the two species, such as hindwing discal spot shape, width of white bands, and coloration. All specimens wild males collected in funnel traps.
DISCUSSION

Population genetic theory provides a set of expectations for the spatial pattern of allozyme variability within hybrid zones (Barton and Hewitt, 1985; Porter, 1990). Assuming geographically uniform effects of drift in local populations and no selection at loci under examination, frequencies of genetic markers are expected to be vary inversely with geographic distance, i.e. to be directly related to degree of effective gene flow. Overall heterozygosity should be higher in hybrid zones, and hybrid zone individuals are expected to be heterozygous at loci with fixed allelic differences in the parental populations. Finally, several allozyme studies of hybrid zones (Barton and Hewitt, 1985; Woodruff, 1989) have revealed the existence of unique electromorphs, the “hybrizymes” of Woodruff (1989), in hybrid zone samples that are not found segregating in the parental populations.

The allozyme data confirm the close genetic affinity of *Hyalophora euryalus* and *H. columbia gloveri* that is indicated by the morphological and ecological data (Collins, 1984). Furthermore, these data conform well to the genetic results expected for populations within a hybrid zone. *H. euryalus* and *H. c. gloveri* are genetically very similar with a genetic identity of 0.932 (Table 3). This estimate puts these two morphologically distinct species within the range of genetic identity estimates for subspecies or sibling species reported in similar studies of other Lepidoptera taxa. For example, Brussard et al. (1985) estimated a mean genetic identity of 0.964 between butterfly species in the sub-family Melitaeini using nearly identical techniques. Britten and Brussard (1992) found similar estimates of genetic identity between widely separated subspecies of *Boloria improba* in western North America. Likewise, Brittacher et al. (1978) estimated a mean genetic identity of 0.977 for subspecies in the butterfly genus *Speyeria*. In a study of natural hybridization among western black swallowtails, Sperling (1987) found a genetic identity between *Papilio zelicaon* and *P. machaon oregonius* of 0.797 to 0.836 (depending on sample locality) and between *P. zelicaon* and *P. polyxenes* of 0.865. Hagen et al. (1991) found a genetic identity of 0.86 for the morphologically similar *Papilio glaucus* and *P. canadensis*. These taxa, previously thought to represent subspecies, are ecologically distinctive and are separated by a narrow hybrid zone with abrupt character clines.

Pairwise genetic identities also decrease from east to west through the hybrid zone for *H. c. gloveri* from Colorado (Table 3). These estimates were expected to show a similar decrease through the hybrid zone from west to east for *H. euryalus* but, the directional pattern of genetic identities is less clear in the hybrid zone for this parental species (Table 3). This asymmetry is consistent, however, with the morphological evidence for asymmetrical introgression of *H. euryalus* genes across the hybrid zone.

Allele frequencies in general do not show strong geographic trends through the hybrid zone (Table 2). For example, MDH-1 B has a frequency of 0.556 in the *H. euryalus* sample from the western side of the hybrid zone but was not segregating in the nearby Silver Creek sample taken from within the hybrid zone (Table 2). This may be an artifact of the relatively small number of individuals assayed for isozyme variability. As expected, heterozy-
gosiity estimates are higher in the hybrid zone samples than for the parental samples (Table 2). The most compelling allozyme evidence for the existence of a hybrid zone for these moth species was found at the GAPDH locus. Fixed allelic differences were revealed at this locus for *H. euryalus* and *H. c. Gloveri* (Table 2). Hybrid zone populations were heterozygous at GAPDH and segregated for both parental species' alleles at this locus (Table 2). Furthermore, allele frequencies changed directionally as predicted; for example, the frequency of GAPDH C, the "eastern" *H. c. Gloveri* allele, declined from 0.417 in the Monitor Pass sample in the eastern part of the hybrid zone, to 0.214 at Lexington Canyon in the center of the hybrid zone, to 0.056 at Silver Creek in the western part of the hybrid zone (Table 2). This is the predicted pattern for loci with fixed allele differences in the parental species, and for directional changes in allele frequencies for polymorphic loci.

The existence of unique alleles (also called "rare alleles") found only in the hybrid zone and not in the parental samples (e.g. AAT-2 B, MDH-1 B, and MPI-1 B and D; Table 2) can be taken as evidence that a hybrid zone is present at the sampled localities. Several studies (reviewed in Barton and Hewitt, 1985 and Woodruff, 1989) have found similar unique electromorphs in samples taken from hybrid zones within a wide range of species. As noted by Woodruff (1989), the origin and maintenance of hybrid zone-specific electromorphs are difficult to explain. Woodruff (1989) favors a model of intragenic recombination at polymorphic loci that yields unique hybrid zone alleles, maintained at their relatively high observed frequencies by either selection (possibly acting at tightly linked loci), or by some form of genetic drift.

The allozyme data reported above confirm the presence of a relatively narrow hybrid zone between *H. euryalus* and *H. c. Gloveri* in the Sierra Nevada as first described by Collins (1984, 1991) based on morphology and reproductive fitness. The origin and maintenance of this hybrid zone are the subject of ongoing investigations. An unusual feature of the zone is the high reproductive fitness of intergrade females within the zone, in contrast to the low fecundity of hybrid females from lab matings between parental phenotypes from stock from opposite sides of the hybrid zone. A similar regional optimization of genetic compatibility has been observed in an orthopteran hybrid zone in the Pyrenees (Virdee & Hewitt, 1994). With further analysis it may be possible to correlate some aspect of allozyme or mitochondrial DNA variation with the subdivision of the hybrid zone seen in the regional optimization of genetic compatibility described above. Porter (1990) used estimates of gene flow across a hybrid zone in *Limenitis* to evaluate the taxonomic status of the hybridizing pair. Similar techniques could be used when data are available to examine species boundaries among the *Hyalophora* which appear to vary greatly in degree of gene exchange in various contact zones (Tuskes et al., 1996).

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**LITERATURE CITED**


Larval ontogeny and survivorship of eastern tent caterpillar colonies

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Abstract. This study documents spatial and temporal variation in mortality in a population of 100 naturally-occurring colonies of eastern tent caterpillars (*Malacosoma americanum*). Predation took the heaviest toll on colonies, while very few colonies were significantly affected by disease. Predation by invertebrates was widespread, but far less catastrophic than vertebrate (avian) predation. Predation and disease incidence varied considerably among study sites and among larval instars. Early-instar colonies suffered the greatest rates of mortality, with 30% of the colonies destroyed by the 3rd-4th instar. Spatial and some temporal variation in mortality and morbidity was stochastic. Temporal variation also arises from individual phenology, as a consequence of larval development and its effects on defense- and foraging-related character suites. The social behaviors of eastern tent caterpillars are discussed in terms of a character suite collectively enhancing larval defense and nutrition, resulting in rapid growth to decreasingly-vulnerable age classes.

Key Words: Eastern tent caterpillar, Lepidoptera, Lasiocampidae, *Malacosoma americanum*, mortality, predation, survivorship

Introduction

The life of a caterpillar is characterized by a tradeoff between behaviors enhancing growth and development, and those reducing risk of mortality from predators, parasites, and disease. It has long been understood that behavioral, morphological, and physiological characters that play defensive and nutritional roles may evolve in response to selective pressures implicit in this tradeoff. In some species, this tradeoff is manifested as selection of feeding sites well-protected from predators but sub-optimal in leaf nutritional quality or thermal regime (Stamp and Bowers 1988, Haukioja 1993, Stamp 1993). Defensive evolutionary responses may include specialized structures (setae, spines, tubercles, etc.), allelochemicals (secretion or regurgitation of toxic substances), and/or somatic modifications (cryptis and mimicry) (see examples in Owen 1980). Responses to nutritional needs are not as obvious, but include behaviors facilitating location of profitable food and physiological adaptations to detoxify and metabolize certain hosts.

It is obvious that lepidopteran larvae experience the greatest mortality rates in the early immature stages, and it is equally obvious that factors contributing to mortality are numerous, and vary in intensity spatially and temporally (see Heinrich 1993, Montllor and Bernays 1993, Reavey 1993). Spatial and temporal variation in mortality factors is commonly perceived as

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the joint product of stochasticity and a fluctuating environmental mosaic. Another important dimension to this variation, however, is simply ontogenetic change. Ontogenetic changes include growth as well as changes in shape, color, and physiology. Such changes are often dramatic in caterpillars, many of which exhibit striking modifications of size, color, and armature with each instar, along with changes in behavior (e.g., Owen 1980, Booth 1990, Heinrich 1993, Reavey 1993).

In this paper I document spatial and temporal survivorship patterns in a population of eastern tent caterpillars, *Malacosoma americanum* (Fabricius) (Lepidoptera: Lasiocampidae). This study departs from typical survivorship analyses by focusing on colony survivorship rather than survivorship of individuals. A colony-level focus is useful because this species is highly social, with well-integrated cooperative behaviors that include nest (tent) construction and recruitment-based foraging (e.g., Fitzgerald and Peterson 1983; Fitzgerald 1993; see below). Individual survivorship is closely tied to that of the group, and isolated individuals experience extremely high rates of mortality (Shiga 1976, Sedivy 1978, Robison 1993).

**Eastern Tent Caterpillar Life History**

Eastern tent caterpillars spend about 10 months of the year in the egg stage. The eggs are deposited as closely-packed masses numbering between 100 and 300 near the twig-tips of their hosts, commonly black cherry (*Prunus serotina*) and apple (*Malus* spp.). Each egg mass is covered with a frothy accessory-gland secretion called spumaline. Oviposition time ranges from late winter to early spring in the southern part of the species range to late spring in the northern part; the caterpillars overwinter as pharate larvae within the eggs. Eclosion the following spring is tightly correlated with bud-break of the host tree; this species is thus among the earliest insects to emerge in the spring (Stehr and Cook 1968).

The larvae migrate soon after eclosion to a more or less centrally-located region of the host tree where they begin to construct their communal tents in the crotches of large branches. Each group feeding bout, of which there are three to four per day, is immediately preceded by a characteristic period of silk-spinning behavior which contributes to tent construction (Fitzgerald and Willer 1983, Fitzgerald et al. 1988). Development following eclosion proceeds rapidly under favorable environmental conditions; accelerated growth is achieved by thermoregulatory basking behavior utilizing the communal tent as a basking or shading platform (Knapp and Casey 1986, Casey et al. 1988, Fitzgerald 1993).

Instar number is typically six. Under optimal conditions the larval stage is completed in five to six weeks, so the caterpillars grow at an approximate rate of one instar per week, during which time they grow from about 2mm upon eclosion to about 5cm upon pupation - a striking growth rate of about a centimeter per week on average. The pupal stage lasts approximately 10 days, after which the adults emerge, mate, oviposit, and die often within the space of a few days (Stehr and Cook 1968).
Table 1. Larval instars and sampling dates for 100 eastern tent caterpillar colonies monitored through the 1990 developmental season in Clarke County, Georgia: Eclosion = hatching, CP1-4 = census points 1-4, Post-larval = colony abandonment and pupation.

<table>
<thead>
<tr>
<th>Census Dates (1990)</th>
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<th>Designation</th>
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<tr>
<td>5-7 March</td>
<td>1</td>
<td>Eclosion</td>
</tr>
<tr>
<td>14-15 March</td>
<td>1-2</td>
<td>CP1</td>
</tr>
<tr>
<td>27-29 March</td>
<td>3-4</td>
<td>CP2</td>
</tr>
<tr>
<td>4-6 April</td>
<td>4-5</td>
<td>CP3</td>
</tr>
<tr>
<td>20-22 April</td>
<td>5-6</td>
<td>CP4</td>
</tr>
<tr>
<td>28-30 April</td>
<td>N/A</td>
<td>Post-larval</td>
</tr>
</tbody>
</table>

Methods

One hundred overwintering eastern tent caterpillar egg masses from five site localities in Clarke County, Georgia, separated by one to ten km, were identified for observation in January 1990. These egg masses were found on the favored hostplant, black cherry (P. serotina), and were recognized as current-generation by the fresh state of their spumaline coating (Stehr and Cook 1968). The egg masses were monitored closely for eclosion, which occurs synchronously with hostplant bud-break in a given locality (Stehr and Cook 1968), after which all colonies were censused at 1-2 week intervals throughout the larval developmental period (Table 1). This period is approximately six weeks long on the Georgia piedmont, during which time the larvae grow through six instars.

Because of the tendency of eastern tent caterpillars to rest within their tents between feeding bouts, it was not possible to accurately census caterpillars within colonies. Thus, the focus of this study was on colonies as demographic units. Colonies were evaluated using six descriptors at each census point: (1) intact, (2) predator destroyed, (3) predator damaged, (4) disease destroyed, (5) disease damaged, and (6) abandoned/merged. Intact colonies were evaluated for evidence of disease and predation, and were considered “damaged” if it could be ascertained that a large proportion (apx. 25%) of individuals were missing and/or the tent displayed evidence of predator damage; this cutoff level is necessarily arbitrary. Diseased colonies were readily identifiable, since diseased and parasitized individuals appear stunted relative to healthy larvae (e.g., Bucher 1957), giving the appearance of a multiple-instar colony. Also, dead and dying caterpillars are commonly found on the tent surface and the symptoms of the main pathogen classes are characteristic (Witter and Kulman 1972; see below). The state of the tent was also used to determine the fate of “missing” colonies. Colony destruction was identified as (vertebrate) predator-induced by the presence of tent damage, or disease-induced by the presence of dead larvae in and on the tent (see discussion below). Mortality in colonies decimated by predators is considered to be complete because solitary or small bands of caterpillars, especially in the early instars, are highly unlikely to survive to pupation (e.g., Shiga 1976, 1979).

Finally, tents were identified as abandoned/merged if they were structurally intact but contained no larvae. This category was distinguishable from colonies decimated by predation away from the tent because in the latter case remnant caterpillars are
Figure 1. Survivorship and predation rates for eastern tent caterpillar colonies from five field sites in Clarke County, Georgia, spring 1990. Colony status was evaluated at each of six points: Ec = Eclosion, CP1-4 = larval census points 1-4, P-L = Post-larval. "Predator damaged" indicates significant (= 25%) larval mortality with physical evidence of predation; "predator destroyed" indicates complete colony destruction with evidence of predation. "Abandoned/Merged" indicates tent abandonment or colony merging. Colony mortality rates are spatially and temporally variable: the spatial variation is attributed to chance, while the temporal variation reflects differential age-dependent vulnerability. The concentration of predator-induced colony damage and destruction in early larval instars is characteristic of an early-instar vulnerability window (see text).

nearly always present, while tent abandonment tends to be complete. Tent abandonment is not uncommon in mid-to-late instars, and stems from three causes: (1) exhaustion of food, (2) colony merging (Fitzgerald and Willer 1983, Costa and Ross 1993), or (3) dissolution of the social group as larvae leave to seek solitary pupation sites (Stehr and Cook 1968, Fitzgerald 1993).

RESULTS AND DISCUSSION
The fates of these colonies illustrates the relative importance of different mortality factors affecting subdivided caterpillar populations. Five of the 100 colonies apparently failed to eclose. It is likely that these egg masses experienced a high incidence of disease or inviability such that the few emerging caterpillars were killed; egg parasitism is readily identifiable (Witter and Kulman 1972, Darling and Johnson 1982) and did not account
Table 2. Incidence of disease for 100 naturally-occurring eastern tent caterpillar colonies monitored in Clarke County, Georgia, in the spring of 1990. Most colonies exhibited some diseased individuals ("low level"), while few were severely affected. Disease-ravaged colonies are classified as "disease damaged" (= 25% larval mortality) or "disease destroyed" (= 100% larval mortality). By the end of the developmental season (CP3-CP4), all intact colonies lost some individuals to disease. The severely-affected colonies suffered from nuclear polyhedrosis virus.

<table>
<thead>
<tr>
<th></th>
<th>Eclosion</th>
<th>CP 1</th>
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<th>CP 3</th>
<th>CP 4</th>
</tr>
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<tr>
<td>Low level</td>
<td>0</td>
<td>0</td>
<td>58</td>
<td>56</td>
<td>11</td>
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<tr>
<td>Damaged</td>
<td>0</td>
<td>0</td>
<td>3</td>
<td>2</td>
<td>0</td>
</tr>
<tr>
<td>Destroyed</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>

for complete eclosion failure. In the remaining 95 colonies, predation was the most significant cause of mortality. Colony survivorship and predation-related mortality data are presented for the five study sites individually and summarized for all sites (Fig. 1). Data for disease are presented in summary form only because of low incidence (Table 2). Climatic factors did not contribute to mortality in this population; this is typical of regions such as the Georgia piedmont where springtime freezes are rare, but climate is likely to play an important role in colony mortality at higher elevations and latitudes. The following sections discuss disease and predation within the context of spatial and temporal variation and larval susceptibility.

Disease

Like other caterpillar species, M. americanum is attacked by a variety of pathogens. The most common of these are the nuclear polyhedrosis viruses and some Clostridium and Bacillus bacteria (Bucher 1957, 1961, Stehr and Cook 1968, Witter and Kulman 1972). These pathogens are distinctive in their symptoms, and moribund larvae commonly expire directly on the tent surface. The viral disease tends to internally liquefy the larvae, which often simply disintegrate, leaving parts of the body clinging to the substrate by one or two prolegs. The bacterial disease is, in contrast, manifested by desiccation and shrinking of the body. The incidence of these and other pathogens is highly variable, at times reaching epidemic proportions (though not in this study population). Nearly all colonies in the present study exhibited a few diseased individuals, but only six colonies from three sites experienced significant disease mortality, and only a single colony was completely destroyed (Table 2).

Predation

Predation levels varied considerably among study sites, ranging from negligible (sites 2 and 5) to high (sites 1 and 4). Figure 1 shows that most predator-induced colony mortality occurred by the first census point (1st-2nd
instar caterpillars) and declined with time. Overall mortality was approx. 30\% \text{(n = 29 colonies)} by the second census point (3\textsuperscript{rd}-4\textsuperscript{th} instar caterpillars). Tent damage points to a high incidence of vertebrate predation in this population. Most completely-destroyed colonies exhibited the circular holes and tears indicative of avian predators, and in two instances parid birds (\textit{Parus caroliniana} and \textit{P. bicolor}) were observed attacking small tents. Invertebrate predation was widespread but consistently low in frequency, though it was not possible to quantify invertebrate predation rate. Some individuals in most colonies were parasitized by tachinid flies, but no colony was completely destroyed by invertebrate predators. Thus, invertebrate predators were responsible for widespread low-level individual mortality, while vertebrate predation tended to be far more devastating to colonies. However, attack by a vertebrate predator may increase the risk of invertebrate predation by breaching the tent; for example, ants of the genus \textit{Pheidole} were observed in great numbers within one tent torn by a bird and may have been responsible for completing the destruction begun by the bird.

The absence of complete colony destruction by invertebrate predators is not surprising, since most of these predators (e.g., ants and pentatomid bugs) are closer to their prey in relative body size than vertebrate predators and experience greater prey handling time. However, invertebrate predators vary in destructive potential. Casey et al. (1988) reported disruption of some field experiments due to repeated predation by \textit{Polistes} wasps, and Knapp and Casey (1986) reported that 51\% of tent caterpillars brought into the laboratory died of tachinid parasitoids.

While at least 56 species of birds have been reported as predators of tent caterpillar larvae and pupae (Witter and Kulman 1972), few birds will regularly feed upon mature larvae, presumably due to setae and toxicity. Young larvae, however, are poorly defended and relatively conspicuous, and it is likely that insectivorous birds are responsible for much early-instar mortality. This is especially likely since the temporal occurrence of young colonies of eastern tent caterpillars coincides with the spring migration and breeding season of many insectivorous birds in eastern North America (Witter and Kulman 1972).

**Larval vulnerability**

This study illustrates spatial and temporal variation in mortality factors affecting eastern tent caterpillar populations. Spatial variation is attributed largely to chance, due to the stochastic nature of "discovery" of population patches by pathogens and predators. Temporal variation behaves in a similar fashion on a scale of years as pathogen and predator populations, as well as climatic conditions, fluctuate.

Another form of temporal variation does not stem from stochastic factors so much as from larval phenology itself. Ontogenetic changes (somatic, behavioral, and physiological) are both cause and effect of the shifting vulnerability to mortality factors that individuals experience (Booth 1990). Costa and Pierce (1996) suggest that age-related behavioral and somatic
polymorphism in caterpillars may be best understood within the context of an early-instar vulnerability window arising from a lag time between eclosion and maturation of physical, behavioral, and physiological defensive characters.

Gregarious caterpillars have the problem of apparency in all instars, and gregariousness is especially problematic in early instars when defensive suites are least effective and the threat of predators and parasites is greatest. Relative body size is an important determinant of range of predators and of anti-predator defenses and avoidance strategies (see reviews by Bowers 1993, Heinrich 1993, Montllor and Bernays 1993, Reavey 1993). This is true of *M. americanum*, which exhibits increasingly effective structural, chemical, and behavioral defenses against predators as larvae age (Sullivan and Green 1950, Tilman 1978, Evans 1983).

If larval size and age are key determinants of vulnerability, enhanced growth rate is a simple means of diminishing duration of vulnerable age classes. An effect of the social behavior of eastern tent caterpillars is rapid growth, a phenomenon all the more impressive in light of the fact that these caterpillars are active during the spring and experience large fluctuations in temperature in many parts of the species range. Casey et al. (1988) demonstrated that the rapid growth rate of this species is attributable to behavioral thermoregulation: the massed caterpillars utilize their tent as a basking platform, raising their body temperatures as much as 20° C above ambient. This improves metabolism and enables caterpillars to consume more food per foraging bout (Casey et al. 1988, Joos et al. 1988). Behavioral thermoregulation is integrated with other aspects of tent caterpillar social biology as well, which collectively contribute to growth. For example, eastern tent caterpillars cooperate in the location of high-quality food through elective recruitment to young, newly-expanded foliage (Fitzgerald and Peterson 1983, Peterson 1987), and their structural and group-behavioral defenses help repel predators and parasitoids when feeding and basking (Myers and Smith 1978, Peterson et al. 1987).

The importance of nutritional quality and defense to caterpillar growth has been established for other gregarious Lepidoptera (Stamp and Bowers 1990a,b; Montllor and Bernays 1993; Reavey 1993, Stamp 1993). Sociality in eastern tent caterpillars encompasses a suite of characters that collectively bear on group defense and resource use, and this leads to rapid growth through the larval vulnerability window (Costa and Pierce 1996). In other words, rapid growth is itself a form of defense.

To conclude, the caterpillar’s dilemma is a tradeoff between behavior geared for growing large quickly and the risks this behavior incurs, giving rise to the rich morphological and behavioral diversity of caterpillars. Ontogenetic change in physiology, morphology, and behavior is an important contributor to changes in the intensity of selective pressures experienced by organisms in general and caterpillars in particular, because these changes are both cause and effect of temporal variance in selective pressures. In lepidopteran larvae, the vulnerability window created by this variance is
centered on the earliest larval instars such that individuals (and colonies) experience a high probability of mortality in the early instars that declines through time. Larval gregariousness, or sociality, involves a character suite that may mitigate vulnerability through group effects improving defense, nutrition, and selection of thermal niche (Cornell et al. 1987, Vulinec 1990, Stamp and Bowers 1990a,b, Bowers 1993), which in turn enhance growth and development (Casey et al. 1988, Joos et al. 1988, Stamp 1990b, 1991). The eastern tent caterpillar population in this study exhibits significant early-instar mortality and negligible mid- to late-instar mortality. Colonies surviving to mid-instars are more likely to survive to pupation, a pattern that may be described in terms of mortality probability as an inverse function of larval age. Temporal variance in mortality factors is thus as much a product of development as of stochasticity, and sociality in this species is important to age-dependent larval vulnerability through effects on caterpillar phenology.

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The courtship behavior of *Callophrys xami* (Lycaenidae)

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Abstract. The courtship behavior of the butterfly *Callophrys xami* (Lycaenidae) was studied in the field. The typical courtship pattern as well as behavioral variants are described and discussed in terms of mate choice and variation in female receptivity. Copulatory behavior leading to separation of the pair well before the time necessary for successful mating (less than three minutes vs. 32 minutes) is described. The possible role of this last behavior in mate choice is discussed.

**KEY WORDS:** Courtship, copulation, behavioral variation, mate choice

**INTRODUCTION**

Intraspecific variation in courtship behavior in butterflies is well documented and it has been explained as a result of mate choice by males and/or by females (e.g. Rutowski, 1979, 1981-83, 1984; Wiklund and Forsberg, 1985; Krebs, 1988). Furthermore, Eberhard (1985, 1994, in press; Eberhard and Cordero, 1995) proposes that in animals courtship may continue during copulation and that females can also use this copulatory courtship for their choice of mate. In this paper, variation in precopulatory courtship and behavior during copulation in *Callophrys xami* is reported, and some of its possible causes discussed.

**METHODS**

The study was conducted in an ecological preserve of 146.8 ha, located on the campus of the Universidad Nacional Autónoma de México, south of Mexico City. This area is part of the Pedregal de San Angel, a zone characterized by volcanic soil, rough topography, markedly seasonal rainfall regime, and xerophytic shrubby vegetation (Rojo, 1994).

*Callophrys xami* is a multivoltine butterfly that can be found throughout the year. The Pedregal de San Angel population never reaches a very high density of individuals and it is more abundant from October to January (Soberón et al., 1988). The main food plant of the larvae is the perennial *Echeveria gibbiflora* (Crassulaceae), an abundant species in the area (Soberón et al., 1988). Males are territorial, and a male can occupy the same territory for as long as four weeks (Cordero, 1996). Territories are areas with well defined topographical limits, located beside or on natural or man-made trails; these areas lack concentrations of receptive females and larval and adult food resources. Males actively defend their territories by means of different types of aggressive flights, for an average of five hours per day (approximately between 1000 and 1500 h), and spend the rest of the time feeding and resting outside territories (Cordero and Soberón, 1990). Territories function as mating stations (Cordero and Soberón, 1990; Cordero, 1996).

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Observations were made in 1989, between November 1 and December 20, and in 1990, between November 10 and December 6. The number of territories observed was 19 in 1989 and 13 in 1990; the number of days a territory was visited varied between 29 and 38 in 1989 and between 14 and 24 in 1990 (details in Cordero, 1996). Most territorial males observed were captured and individually marked on the wings with indelible felt-tip pens (Sharpie®) that does not seem to have effects on males (Cordero and Soberón, 1990). Observations of courtships and copulations were made on groups of territories located on transects; we walked these transects at least two times per day during 31 days in 1989 and 11 days in 1990, making focal observations in each territory for at least three minutes after locating the resident male. Courtships and copulations were also observed during continuous observations of selected territories, made for 9 days in 1989 and for 13 days in 1990. Twelve courtships observed in 1983-1985 (during the course of another study; Cordero and Soberón, 1990) are included in the description of typical courtship.

**Results**

**Typical successful courtship**

The following description is based in 20 complete successful courtships observed in the field. This typical pattern was observed in the 12 successful courtships observed in 1983-1985, in five out of the 10 observed in 1989, and in three of the five observed in 1990. The temporal sequence of courtship and mating can be divided in seven phases (Fig. 1):

I. A female flies near (<1 m) a flying or, more frequently, a perching male.

II. The male flies following the female and a courtship flight along a route parallel to the ground begins; during the courtship flight the male flies near (<10 cm), slightly behind and a few cm above the female. This flight lasts about 30 seconds, unless a perturbation, such as a strong wind, momentarily interrupts the courtship, in which case the flight lasts longer.

III. Female and male alight on vegetation close to each other; there were a few cases in which one or more alighting attempts preceded final settling of the pair.

IV. Immediately after the couple alight on vegetation, the male walks in front of the female until reaching a head to head position, while fluttering vigorously; meanwhile, the female stays motionless with her wings closed. It is possible that during this phase (and, probably, since phase II) the male emits pheromones from androconia located near the forewing costal border.

V. After a few seconds, and still fluttering, the male walks beside the female until reaching a parallel, head to head and tail to tail position.

VI. The male moves the tip of his abdomen toward that of the female and, after making genital contact, stops fluttering; immediately after beginning copulation the male moves until reaching the "tail to tail" copula position typical of Lepidoptera. During copulation the couple stays motionless, unless some perturbation, such as strong wind or people coming too close to the mating pair, makes them fly *in copulo* to a different place on vegetation. The approximated time elapsed between alighting and beginning of copulation (phases IV to VI) is between 10 and 20 seconds.
Fig. 1. Diagram of the mating behavior of *Callophrys xami* (Lycaenidae), showing variations in courtship and post-coupling behavior. Courtship description is based in 27 observations. M: male. F: female. hh/tt: M parallel to the F, head to head and tail to tail.
VII. The end of copulation begins with the female starting to move, turning and occasionally walking short distances (less than 20 cm); these movements are intercalated with female turnings around her longer body axis, until the pair ends genital contact. After separation the female and/or the male may remain in the mating place for a few minutes or they may fly away almost immediately. In few occasions the male found the female again, after seconds or a couple of minutes, and a short pursuit flight followed, which ended when the male returned to perch and the female left the area.

Courtship is mostly initiated inside territories, although the possibility exists that a female is found by a male when he is returning to his territory after, for example, an aggressive interaction. Copulations can take place inside territories, and they also occur outside, if the courtship flight takes the pair out of the territory. Average copulation duration in the field is 32.3 min (Standard Error = 4.9; Cordero, 1996); duration is much longer (range: 1h42 min to >14h; 23/24 copulations lasted > 5h) if the copulation is the second of the day for the male (Cordero, 1996). In captivity, courtship begins when a male detects a female at short distance, usually when the male and/or the female are walking on the cloth of the cylindrical, 58 cm high by 26 cm diameter, mating cages (Jiménez and Soberón, 1988-89); afterwards, courtship and mating proceeds from phase IV on, as in the field.

Courtship Variants

In five of out of 10 successful courtships observed in 1989 and in two of the five observed in 1990, the time allocated to the vigorous fluttering (phases IV, V and part of VI) was considerably less than in the typical courtship described above, and in some cases it was almost absent (Fig. 1). This difference also occurred in some of the courtships observed in captivity.

We have observed several courtships in the field that did not result in mating. Several were observed in 1983-1985, 13 in 1989 and 29 in 1990. The duration of these unsuccessful courtships was variable, but observations lacked the detail necessary to look for differences between successful and unsuccessful courtships. These courtships lasted from a few seconds to rarely more than one minute. Almost all complete observations of unsuccessful courtships (some couples were lost from sight) ended before phase III, although at least in one case a male lost a female during alighting attempts (in this specific case, the strong wind blowing during observation, rather than mate choice [see discussion], may be responsible for the unsuccessful courtship).

Copula Interruption

In one of 17 copulations observed in 1989 and one of 10 observed in 1990, the female began walking after genital coupling began, dragging the male behind her. After a brief time, the female began to intercalate body twists during walking, behaving in the same way as when they are about to finish normal copulation (see phase VII of typical courtship), suggesting attempts to end copulation. Both cases resulted in the separation of the pair less than
three minutes after mating began (probably before ejaculate transfer and long before the end of normal copulations; Cordero, 1996).

In the case observed in 1989 the male encountered the female again, less than three minutes after separation, and courted her for a second time without success; afterwards the female left the area and the male returned to perch in the territory. The male had been defending the territory for at least five days before, and defended it three more days after; his minimum longevity was nine days (mean minimum longevity of males observed in 1989 more than one day = 6.9 days, s.e. = 0.8, range: 2-20, n = 51; Cordero, 1996); the forewing length (a measure of body size; Parmange, 1991; Cordero, 1996) of this male was 1.73 cm (mean forewing length of males observed in 1989 = 1.64 cm, s.e. = 0.01, range: 1.36-1.89 cm, n = 77; Cordero, 1996) and whether the male or the female had mated earlier the day of the interrupted copulation is unknown, given that we began observations in that territory at 1130. In the 1990 case the male had defended the territory at least one day before the "rejection" (his minimum longevity was four days); we did not measure the forewing length of this male. We do not know if the male or the female had mated earlier the day of the "rejection", given that we began observations after 1100. These two males were not observed mating for a second time.

We observed similar behavior in another two cases, one in the field and one in captivity, but these occurred after a perturbation. In the first case, the female exhibited the behavior after we attempted to put the field mating pair inside a cage; the time at which this mating began is unknown. The second case occurred when the mating cage accidentally fell to the ground more than five minutes after the mating had begun. We never observed this behavior in any of the 18 matings observed in 1983-1985.

**DISCUSSION**

**Variation in successful courtships**

Typical courtship behavior of *Callophrys xami* is similar to the courtship of related species (e.g. Powell, 1968; Robbins, 1978); however, to my knowledge, variation in this behavior has not been reported in other *Callophrys* species. Courtship variants may be the result of differences in female receptivity. Males finding highly receptive females may save time, energy and pheromones with the shortening of courtship phases IV to VI. Female receptivity may be affected by time since last mating, time since emergence from the pupa (this applies to virgin females of species able to mate and lay eggs almost immediately after emergence, such as *C. xami*), number of sperm remaining in her spermatheca, size and quality of the last ejaculate received (e.g. Oberhauser, 1992; Kaitala and Wiklund, 1994), remaining quantity of receptivity inhibition substances transferred by her last partner (Cordero, 1995), number of mature eggs stored, feeding condition (e.g. Boggs, 1990) and courting male quality (Thornhill and Alcock, 1983; Eberhard, in press; Cordero, 1995), among other factors.
In *C. xami* time since last mating is positively correlated with female receptivity (Cordero, 1996), but at this moment we do not know if time *per se* or other correlated factors (such as the quantity of some of the different ejaculate components remaining stored in the female) are responsible for differences in female receptivity. Males probably emit pheromones during phases IV to VI, and this also suggests that females involved in "short" courtships could have been highly receptive (and, therefore, in need of less stimulation). (A few observations suggest that at least some females come into actual or potential territories, flying within them in a way that could possibly make them very conspicuous to territorial males. If the function of this behavior is to make females easily detected by males, we expect to observe it only in receptive females.)

An alternative explanation for the "shortening" of courtships may be physical exhaustion of the male forcing him to reduce the possibly costly courtship phases IV to VI. However, our observations of the conditions of males, as well as the low frequency of male-male and male-female interactions reported in *C. xami* (Cordero and Soberón, 1990; Cordero, 1996), suggest that this second hypothesis is not a general explanation for these behavioral variants; besides, if this hypothesis is correct, we need to explain why females accepted these exhausted males. If we accept the idea that females gain information about male quality during courtship, a third hypothesis is that males involved in the "short" courtships could have been males of very high quality, quickly identified as such and accepted by females.

### Mate choice and copula interruption

Although mate choice has not been studied in *C. xami*, differences in mate quality—and, therefore, selective pressures in favor of mate choice—are probably common. In females, the number of eggs remaining to be laid (and therefore, their value for males) can vary widely depending on the number of eggs already laid and on female size (Parlange, 1991; Cordero, 1996). In the laboratory, females mate a second time until they have laid a substantial proportion of their eggs (Cordero, 1996). In males, the quantity of nutritious ejaculate transferred to females varies with the size and mating history of the male (Cordero, 1996); besides, for a female to be the second male’s mate of the day means not only a small ejaculate, but also a lengthy copulation (> 5 h vs. 30.3 minutes).

Given the common occurrence of unsuccessful courtships (56.5 % of 23 courtships observed in 1989, and 85.3 % of 34 observed in 1990), mate choice prior to copulation probably exists in *C. xami*. However, a detailed study remains to be conducted. "Copula interruption" suggests mate choice after mating began. However, it is not possible to tell with the available information whether female or male choice is responsible for this behavior. Females or males may be able to evaluate their mating partners after copulation begins and decide to interrupt it within a few minutes (Eberhard, 1985, 1994, in press; Eberhard and Cordero, 1995; Cordero, 1995). The fact that females are the behaviorally "active" sex during the process of separation cannot be
used as evidence of female choice, given that for females it may be convenient to interrupt mating with a male that, although desirable, is unwilling (because of mate choice reasons) to transfer an ejaculate. It is also conceivable that the male manipulates (chemically or mechanically) the female, inducing her to finish copulation against her own interests. However, the fact that in the case of 1989 the male found the female again, less than three minutes after separation, and unsuccessfully courted her for a second time, suggests that female choice is involved in at least some of the post-coupling "rejections". The fact that copula interruption occurs a few minutes after genital coupling begin may be due to rapid assessment of mate quality or to the fact that as time advances it may be physically difficult to interrupt copulation (Wickman, 1985).

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Butterflies of the Laramie Mountains, Wyoming (Lepidoptera: Rhopalocera)

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Abstract. The Laramie Mountains, which occupy the southeastern corner of Wyoming, are the northern and easternmost outliers of Colorado's Front Range. Faunally related to the Colorado Rockies, the Laramies represent a blend zone with northern and northeastern faunas. One hundred forty-five (145) species of butterflies representing 9 families have been recorded from the Laramies. These are presented with collecting locations, flight periods, and annotations with regard to the Laramie Mountains. The data for the species list were compiled primarily from the authors' own field work between 1963 and 1987, with additional data supplied by other collectors.

Key Words: Lepidoptera, Rhopalocera, faunal list, checklist, biodiversity

Introduction

Little has been published on the butterflies of the Laramie Mountains of SE Wyoming. In his 1956 checklist on SE Wyoming butterflies, deFoliart included Sybille Canyon and Pole Mountain. Others have treated SE Wyoming more generally (Klots 1930, Nabokov 1953, Ferris 1970, 1971a, 1971b) but specific coverage of the Laramie Mountains has been limited or absent. Further data can be gleaned from a careful examination of Johnson (1971), Howe (1975), Ferris & Brown (1981) and Scott (1986), but as yet there has been no full treatment of this area.

The Laramie Mountains are located in southeastern Wyoming, forming a gentle arc from the Colorado border between Cheyenne and Laramie on the south end to Casper Mountain on the north, and lie within Laramie, Albany, Converse, and Natrona Counties. They are considered a direct extension of the familiar Front Range of Colorado (Blackstone, 1971) and represent the easternmost portion of the Rocky Mountain system in Wyoming. With the exception of a few streams between Laramie and Cheyenne that drain into the South Platte River (e.g. Lone Tree Creek, Dale Creek, Deadman Creek), all other streams of the Laramie Mountains empty into the North Platte River. The North Platte River enters Wyoming from Colorado, circles the Laramies on the west and north and then departs eastward into Nebraska (see insert, Figure 1). From north to south, the major east slope drainages are: Deer Cr., Boxelder Cr., LaPrele Cr., LaBonte Cr., Horseshoe Cr., the

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Laramie River, and Sybille Cr. The Laramie River has its origin SW of the city of Laramie and is the only stream to penetrate the Laramies from the west slope to the east. The west slopes are drained by numerous small streams, most of which eventually join the Medicine Bow River, the major west-slope drainage. The major highway is Interstate 25, which enters south of Cheyenne from Colorado, parallels the Laramie Mountains until joining the North Platte River, which it then follows to Casper. State and County roads leave I-25 to enter the Laramie Mountains along most of the east slope drainages, and usually bear the names of the drainage streams. Roads from the east slope converge on the west slope in the Shirley Basin on their way to Medicine Bow and Laramie.

The Laramie Mountains consist of a series of Precambrian Sherman granite monadnocks rising above a broad erosion surface (Marshall & Colbert 1965; Dunbar 1960, fig. 308) that form extensive unwooded parks whose surfaces are generally at about 2135 m above sea level. The high peaks of the range, which are much lower than those commonly associated with the Rocky Mountains, rise abruptly above the surrounding peneplain to altitudes between 2440 m and 2895 m above sea level, with the single exception of Laramie Peak (3132 m). The granitic soils were formed from the erosion of the surrounding monadnocks and have an effective depth of less than 30 cm.

Three principal Life Zones are represented in the Laramies: Upper Sonoran, Transition and Canadian (sensu Carpenter, 1956). Cary (1917) indicated that the Hudsonian Zone occurs on Laramie Peak but there is nothing distinctive about either the flora or fauna on the top of this peak. For further discussion of the Life Zones of this area, see Porter (1962) as well as Cary (op. cit.). On the E and NE slopes of the Laramies the prairie/mountain transition is very gentle at the south end (between Cheyenne and Laramie) and much more abrupt and broken farther north (Blackstone 1971). The altitude of the map area (Figure 1) ranges from about 1370 m along the North Platte River to 3132 m at the top of Laramie Peak. On the western slopes the total relief is much less, as the floors of the three intermontane basins that border the Laramies on this side (Shirley, Hanna and Laramie) rarely drop below 2135 m. An extensive high plain (2135-2400 m) and semi-desert extends from the Laramie Mountains SW as far as the Shirley Mountains. The Laramie Basin separates the Laramie Mountains from the Medicine Bow Mountains to the S and W, and its floor is above 2135 m except for a few depressions and blowouts (e.g., Cooper Lake, 2130 m).

The Laramie Mountains are bisected by the Laramie River, which cuts a canyon through the mountains roughly due west of Wheatland, and then continues its generally eastward course to join the North Platte River near the town of Fort Laramie (Figure 1). This bisection is ancient, formed by the ancestral Laramie River as it eroded through overlying sediments and the underlying basement rock (Dunbar, 1960). The division marks the southern end of the continuous boreal coniferous forest in the Laramies, and separates the range into two parts whose butterfly faunae which, while having
Fig. 1  The insert in the lower left shows the map area with respect to the state boundaries of Wyoming, Colorado, Nebraska, South Dakota and Montana, and shows the North Platte River as it enters from Colorado, circles around the Laramie Mountains and exits to the east into Nebraska. The two major highways (I-25 and I-80) are shown as parallel lines. The Platte River and the Laramie River are indicated. Contours are shown for 2135 m (7000 ft) and 2440 m (8000 ft). Land area above 2440 m is highlighted in gray. The major collecting localities are shown with two or three letter codes, corresponding to the text and Table 1.
many species in common, contain elements that are unique to each. As it cuts through the Laramie Mountains, the altitude of the Laramie River falls below 2135 m. Besides bisecting the mountain range on the basis of altitude, it widely separates the parts of the Laramie Mountains over 2440 m (Figure 1). Precipitation in the Laramie Mountains amounts to an average of 30-45 mm/year, but can vary widely at any given locality [e.g., 19.9 mm in 1954 and 55.6 mm in 1957 at Palmer Canyon]. The period from April to early July accounts for nearly half of the annual precipitation. Two units of the Medicine Bow National Forest are located in the Laramies and consist of a literal patchwork of federally and privately owned land. Local ranchers lease a great deal of federal land for use as summer pasturage. Recreation is also an important land use.

The butterfly fauna of the Laramies is most closely related to that of the Colorado Rockies, but its position as a northern and eastern outlying range creates a blend zone for many species that exhibit clines connecting the more southern forms with relatives to the north or northeast [e.g., Colias alexandra W. H. Edwards, Euphydryas anicia bernadetta Leuissler, Oeneis uhleri (Reakirt), Basilarchia weidemeyeri W. H. Edwards, etc.]. The fauna of the part of the Laramie Mountains south of the Laramie River contains some species endemic to the main Rocky Mountain massif [e.g., Clossiana frigga sagata (Barnes & McDunnough), Pieris napi (Linnaeus)] and some plains elements [Euphilotes rita coloradensis (Mattoni), Yorettia rhesus (W. H. Edwards)] which are absent or, at best, uncommon in the fauna of the northern segment.

**Collecting Localities**

Major collecting sites are identified below. The format has been adapted from that of Holland (1984): Location (Abbreviated Letter Code): [Life Zones; Elevation]. The Life Zone codes are: U = Upper Sonoran Zone, T = Transition Zone, and C = Canadian Zone. In the list below and on the map (Figure 1), we have listed all major localities at which collecting occurred. However, for summary purposes we have combined some of the collecting localities (Table 1) since some of them are close to one another. In the list below, the codes for the collecting localities that are reported in Table 1 are in bold. When localities have been combined in Table 1, we follow the code for the combination with the individual localities within (curly brackets). Unusual locations are mentioned individually in the checklist.

Natrona County: Casper Mountain: (CM) [T; C; 2135-2440].
Converse County: Douglas: (D) [U; T; 1495]. Ayre’s Natural Bridge: (NB) [U; T; 1700]. Boxelder Canyon: BC [T; 2010]. RC: [Rabbit Creek: [T; 2165]. LL: Little LaPrele Creek near Virden Hill: [T; 1890]]. CS: [Cold Springs: [C; 2345]. CC: Campbell Creek Campground: [C; 2375]. LC: [LaBonte Canyon: [T; C; 2165]. WF: West Fork of LaBonte Creek: [T; C; 2225]]. E: [Esterbrook [T; 1950]. MC: Mill Creek: [T; 1700]. NHC: North Horseshoe Creek: [T; 1830]]. UHC: (Upper) Horseshoe Creek [T; 1890]. Since most collecting done at the locations combined under UHC were in Albany Co. it appears in Albany Co. in the Table. Campbell Creek was formerly known as “Camel
Creek”; the U.S. Forest Service changed the name in the mid-70’s. There are two creeks called “Roaring Fork”: one is a tributary of Horseshoe Creek in Albany Co.; the other is a tributary of LaPrele Creek in Converse Co.). There are also two creeks named “North Horseshoe Creek”. The one to which we refer is near Esterbrook.


Laramie County: HJR: Happy Jack Road, West of Cheyenne (HJR plus a number indicating miles from Cheyenne: 20HJR, etc.) [T; 1950+].

**Partial Checklist, With Annotations**

Figure 1 shows the location of the major collecting localities, as well as the elevation contours for 2135 m (7000 ft) and 2440 m (8000 ft). Table 1 provides a list of species collected in the Laramie Mountains, organized by major collecting localities in the four counties, with an indication of relative abundance and flight period. In the partial checklist below, which is organized in the same order as Table 1, we provide limited observations about selected species to supplement the information in Table 1. The data presented are based primarily upon the field work of the authors from 1963 to 1987. Additional data is as follows: Laramie County - Paul Opler (1984-1986, PAO); Laramie and most Pole Mountain records - Clifford D. Ferris (CDF); Palmer Canyon - F. Martin Brown; Casper Mountain - Dr. Karolis Bagdonas & students (from 1986 Season’s Summary, BFC). Unconfirmed records from deFoliart (1956) are noted by (deF). Past Season’s Summaries (SS) were also searched for pertinent data. The nomenclature follows Miller & Brown (1981) and Ferris (1989). However, the actual nomenclature used reflects the personal opinions of the authors. Certain species treatments represent a compromise between opposing views and do not in any sense indicate a definitive statement by us.

**Hesperiidae**

*Thorybes mexicana nevada* Scudder. Rare. One record: PM, 21.VI.77 (CDF).

*Erynnis icelus* (Scudder & Burgess). Found only in the mountains.

*Erynnis afranius* (Lintner). Recorded only from CM (BFC) and PM (CDF).

*Erynnis persius frederici* Freeman. Very common in the Transition and Canadian Zones. *E. lucilius* (Scudder & Burgess) apparently doesn’t occur in the Laramies.

*Pyrgus scriptura* (Boisduval). Two records from the plains at the fringes of the Laramies: D and Glendo (Platte Co.). leg. Ghulan N. Hasan.

*Piruna pirus* (W. H. Edwards). Reported only from near Cheyenne: 24HJR, 22.VI.85 and 13.VII.85, and Cheyenne, 22.VI.85 (all PAO).

*Yvretta rhesus* (W. H. Edwards). Not common, recorded only by CDF.

*Hesperia comma ochracea* Lindsey. Based on the treatment in Ferris & Brown (1981),
all forms of this species in the Laramies (formerly referred to under a variety of names, e.g., *manitoba, colorado, harpalus* etc.) are here placed under the name *ochracea*.

**Hesperia pahaska** (Leussler). Recorded only recently.

**Atalopedes campestris campestris** (Boisduval). One record: D, 28.VI.64.


**Amblysirtes ostleri** (Skinner). One record SC: 9.VII.78 (CDF).

### Papilionidae

**Papilio polyxenes asterius** Stoll. In addition to the records shown, Ferris has sighted several specimens of what may be *polyxenes* in the Laramie-Pole Mountain area. It has also been sighted on Casper Mountain. It should occur along the North Platte River. SC, 14.VI.52 (deF), CM (BCF).

**Papilio bairdii** W. H. Edwards. Two records for form “brucei”: NH, 23.VII.66 & EC, 24.VII.64. Reported from SC (deF). The typical black form has been recorded to the east (3.5HJR, 13.VII.85, PAO) and to the west (Jelm Mountain, CDF) but not as yet from the Laramie Mountains proper.

**Papilio zelicaon nitra** W. H. Edwards. The yellow, normal form (“gothica”) is fairly common, rarely in numbers. Males hilltop. The rare black form (“nitra”) has been recorded four times.

**Papilio indra indra** Reakirt. Widely distributed, never numerous. Males hilltop.

**Pterourus rutulus rutulus** (Lucas). This and the next species are the most common swallowtails.

**Pterourus multicaudatus** (Kirby). Specimens from low altitudes are larger, sometimes twice as large as those from higher altitudes. We have found and reared *P. multicaudatus* on Green Ash (*Fraxinus pennsylvanica* Marshall var. *subintegerrima* (Vahl) Fernald, Oleaceae).

**Pterourus eurymedon** (Lucas). Exceedingly scarce compared to how common it is in the Medicine Bow Range west of Laramie. NH, 5.VII.67, and CM.

### Pieridae

**Pontia protodice** (Boisduval & LeConte) and **Pontia occidentalis occidentalis** (Reakirt). These species are sympatric in some localities and intergrades often occur. Generally, *P. protodice* is more common at lower altitudes, while *P. occidentalis* predominates at higher elevations. Seem to be continuously brooded.

**Pieris napi maccunnoughi** (Remington). More common by far in the southern end of the range (Pole Mountain). In the north, we have records only for CC, 30.VII.66 and CM (BCF).

**Euchloe olympia** (W. H. Edwards). Never common, even when found.

**Anthocharis sara julia** W. H. Edwards. Oddly distributed; despite extensive collecting we have never collected it in the central part of the Laramies, although it has been reported at both CM and HJR.

**Colias alexandra alexandra** W. H. Edwards. Most specimens are typical, but some of the plains populations and one near Esterbrook show varying degrees of orange flush. Few, if any, show evidence of hybridization with *C. eurytheme*. Most colonies show a small percentage of the female form “alba”.
Colias scudderii Reakirt. Most records are from the headwaters region of LaPrele Cr. Phoebis sennae eubule (Linnaeus). One record: Laramie, 18.VI.83, K. Bagdonas (1983 SS).

Eurema mexicanum (Boisduval). A migrant species. Two records: D, 10.VII.63 and PM, 30.VI.75 (CDF).


Nathalis iole Boisduval. A frequent visitor to the Laramies.

Lycaenidae

Lycana cuprea artemisia Scott. Never common, our combined captures over 20 years amount to less than three dozen specimens.

Gaeides xanthoides dione (Scudder). Scott (1980) considered this species and G. editha (Mead) to be conspecific and noted that although they occur in the same counties in Wyoming and Montana, they never occur together at the same locality because of altitudinal separation. While this is generally true in the Laramies, at LaBonte Canyon they are sympatric and synchronous. Scott (op. cit.) further suggests that G. xanthoides dione may be a distinct species in its own right. The situation in LaBonte Canyon may indicate that this interpretation is correct.

Chalceria rubida siris (W. H. Edwards). Some specimens from the eastern fringes of the study area show some blending with C. r. longi (Johnson) (Johnson & Balogh, 1977). More widely distributed than indicated.


Harkencleonus titus (Fabricius) ssp. The majority of specimens seem to be somewhat atypical H. titus titus, but the Mill Creek colony shows a trend towards H. t. watsoni (Barnes & Benj.) (F. M. Brown, personal communication). Uncommon.

Satyrium fuliginosum semiluna (Klots). Some specimens approach the typical subspecies in facies.

Satyrium sylvius (Boisduval). A male from CS was determined as sylvius by H. K. Clench. Unfortunately, it was destroyed en route back to the authors. Fisher has referred several specimens from LaBonte Canyon to this species (personal communication).

Satyrium liparops aliparops (Michener & dos Passos). Eight specimens to date. D, MC, and Beaver Cr. near. Alex Cross Ranch, Converse Co.

Satyrium saepium saepium (Boisduval). Form "provo" predominates. Nectars avidly on Yarrow [Achillea millefolium var. lanulosa (Nuttall), Asteraceae].

Callophrys apama homoperplexa Barnes & Benjamin. It is uncommon and sporadic in our area.


Callophrys sheridanii sheridanii (W. H. Edwards). One of our earliest emerging species. Can be found while there is still snow on the ground.

Incisatia augustinus iroides (Boisduval). Never common, usually taken as singletons.

Incisatia mossii schryveri Gross. Most common in the vicinity of Pole Mountain), less so in the northern portion of the Laramies (two records).

Incisatia polia obscursa Ferris & Fisher. Only from Pole Mountain, where it is common.

Everes amyntula ssp. (Boisduval). Much of our material exhibits a trend towards ssp. valeriae Clench.

Celastrina argiolus ssp. (Boisduval). One of the earlier appearing species in the area. Euptoieta enoptes ancilla (Barnes & McDunnough). Not common and local, associated primarily with canyon bottoms in the foothills.

Euphilotes rita coloradensis (Mattoni). Found in the foothills just east of Laramie. Icaricia shasta minnehaha (Scudder). Most frequently encountered in Sybille Canyon. It has also been found in the hills and breaks east of Douglas.

Riodinidae

Apodemia mormo (C. & R. Felder) ssp. Although our populations have been referred to ssp. mejicanus (Behr) (Scott, 1986), others refer to them as nearest ssp. mormo in facies (Fisher, in Ferris & Brown, 1981, and Ferris, personal communication). Scarce. Easily taken nectaring at Eriogonum umbellatum Torr. (Polygonaceae).

Libytheidae

Libytheana bachmanii (Kirtland) ssp. A migratory species. One record (PM, 2.VII.75, CDF). The specimen is too battered to accurately determine ssp.

Nymphalidae

Euptoieta claudia (Cramer). Never common, but widespread. A migrant. GENUS Speyeria Scudder. Ten species of this genus are represented in the fauna of the Laramies. Seven of the ten are widely distributed and common. The other three, [S. hydaspe (Boisduval), S. cybele (Fabricius) and S. aphrodite (Fabricius)] are less common and more restricted in their distributions. As is usual with members of this genus, they are highly variable. We have therefore elected to forego ssp. treatment except when such designation is reasonably clear cut.

S. cybele leto (Behr). Never common, widely distributed in the proper habitat.

S. aphrodite (Fabricius). The majority are of the ethne (Hemming) phenotype.

S. edwardsii (Reakirt). Cannot generally be confused with other Speyeria, except for an occasional greenish S. coronis (Behr).

S. coronis (Behr). Mostly of the halcyone (W. H. Edwards) phenotype, with occasional examples of snyderi (Skinner).

S. zerene (Boisduval). This and S. coronis are often confused with one another in this area. Best characterized as garrettii (Gunder) with intrusions of sinopedos Passos & Grey.

S. callippe (Boisduval). Often characterized as ssp. meadii (W. H. Edwards), these populations show greater affinity towards the more northern and western phenotypes, such as gallatini (McDunnough).

S. egleis (Behr). Usually characterized as macdunnoughi (Gunder), in reality it is very variable and several other phenotypes can be found with great frequency.

S. atlantis (W. H. Edwards). Silvered, unsilvered and occasional partially silvered forms are sympatric in many localities in the Laramies. The degree of silvering of the under hindwing increases with altitude (A. Moeck, personal communication). In the Cold Springs area it is primarily silvered, with an occasional example of the "Appalachian" phenotype. The two typical forms are hesperis and electa (Ferris, 1983).

S. hydaspe sakuntala (Skinner). Generally quite constant in facies. The only Speyeria not recorded from the southern Laramies
mormonia eurnome (W. H. Edwards). Form “clio” is found in any long series from any locality. Clossiana frigga sagata (Barnes & Benjamin). A colony of this species exists on Pole Mountain. It has a very short flight period (31.V to 9.VI) and may have become extinct (CDF).


Phycides tharos (Drury). Common & widespread. All specimens examined from the mountains have been of the “B” phenotype (= pascoensis), although form “marcia” (“A” phenotype?) occurs on the plains east of Douglas in June.


Euphydryas anicia bernadetta Leussler. Widespread; very common where found. Known foodplants are Besseya Wyomingensis (A. Nels.) Rydberg and Symphoricarpos occidentalis (Hook.) [both Scrophulariaceae] (Spomer, 1985 and Spomer & Reiser, 1985). It ranges westward from the type locality (Monroe Canyon, Sioux Co., Nebr.) into Wyoming along the Pine Ridge/Hat Creek Breaks to Douglas, throughout the Laramies and outlying foothills and southward into Colorado. Very variable, and at the southern end of its range begins to intergrade into the northern Colorado ssp., E. a. eurytion (Mead).

Euphydryas editha alebarki Ferris. Often sympatric with E. anicia and seems to emerge a bit ahead of it. More common at the southern end of the Laramies (Sherman Range) than in the north.


Polygonia progne (Cramer). Two specimens (CS, 23.VI.63 and RC, 28.VII.64) were identified as this species by C. F. dos Passos in 1964 and confirmed by C. D. Ferris in 1984. These records were reported in the 1984 SS. It is also known from Crook County in NE Wyoming and from the Pine Ridge area of western Nebraska. It would appear that the northern Laramies represent the extreme western edge of its distribution in the area.

Vanessa annabella (Field). One record: D, ex larva on Althea rosea Cav. (Malvaceae), emerged 10.VIII.70.

Vanessa atalanta rubria (Fruhstorfer). Common and widespread at lower elevations, less so in the mountains.

Limenitis archippus archippus (Cramer). Apparently restricted to the North Platte River valley in the northern end of the range, but might occur up some of the tributary creeks.

Basilarchia weidemeyerii weidemeyerii W. H. Edwards. The Laramies are in a broad blend zone, where the typical ssp. weidemeyerii meets B. w. oberfoelli Brown (Perkins & Perkins, 1967). This is most noticeable in the females.

Satyridae


Oeneis chrysus chrysus (Doubleday & Hewitson). Common. Biennially brooded; flies
in even years. The "cold" form is the predominate phenotype. The illustration of this form in Ferris & Brown, 1981, is in error. The specimen shown is a very dark O. uhleri (Reakirt).

Oeneis uhleri uhleri (Reakirt). Often sympatric with O. chryxus. Populations in the Laramies are quite variable (Brown, 1953). The dark phenotype (f. "obscura") occurs occasionally.

Oeneis jutta reducta McDunnough. Rare; associated with Ponderosa Pine forest. Biennially brooded, flies in even years.

Acknowledgements. A special but belated thank you is due the late F. Martin Brown, whose patient and continued encouragement during the early years of our studies has at last borne fruit, and we respectfully, and with fondness, dedicate this work to his memory. Many people assisted us in the preparation of this paper. Reviewers included C. D. Ferris, Ray Stanford, Paul Opler, F. M. Brown, L. P. Grey (Speyeria), Mike Fisher (Lycaenidae), Boyce A. Drummond and William E. Miller. Their comments and suggestions, while not always followed, were certainly appreciated. Additional records were provided by C. D. Ferris, Paul Opler and Ray Stanford. Dr. Jeanette Oliver (Biology Dept., Flathead Valley Community College, Kalispell, MT) checked the botanical names for accuracy and Janette Black (formerly of the Geology Department, FVCC) commented on the geological aspects of this paper. Additional thanks go to Vernon E. Hardesty (Douglas, Wyoming) who assisted in our early field work and to the late Arthur H. Moeck, whose methodical studies of Speyeria greatly contributed to our understanding of the local situation. Correspondence pertaining to any aspect of this paper should be directed to the first author. We would appreciate hearing from anyone collecting in the area.

Literature Cited


——. 1971b. A key to the Rhopalocera (Butterflies) of Wyoming. University of Wyoming Agricultural Experimental Station Science Monographs. 21: 1-64.


Table 1. Collecting Localities and Flight Periods of Butterflies in the Laramie Mountains. Table 1 lists all species that have been collected in the Laramie Mountains, organized by family. Selected collecting localities, organized by county, are identified by code (CM = Casper Mountain, D = Douglas, CS = Cold Springs & vicinity, RC = Rabbit Creek & vicinity, NB = Ayre’s Natural Bridge, LC = LaBonte Canyon & vicinity, E = Esterbrook & vicinity, UHC = Upper Horseshoe Creek & vicinity, SC = Sybille Canyon, LFM = Laramie foothills, PM = Pole Mountain, HJR = Happy Jack Road). Three symbols are used to identify relative abundance: * = common; o = likely to be encountered; x = unlikely to be encountered. The flight period for each species is presented as a beginning and ending date: Month.Quarter-Month.Quarter, where the roman numeral refers to the month and an arabic numeral refers to the quarter of the month.

<table>
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<th>County → Collecting Locality →</th>
<th>Natrona</th>
<th>Converse</th>
<th>Albany</th>
<th>Laramie</th>
<th>Flight Period</th>
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<td>CM</td>
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<td>CS</td>
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<td>Hesperiidae</td>
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**Papilionidae**

| **Parnassius phoebus sayii** W. H. Edwards | 0 | * | * | 0 | 0 | 0 | 0 | 0 | VI.1-VII.4 |
| **Papilio polyxenes asterius** Stoll | x | 0 | 0 | 0 | 0 | 0 | 0 | 0 | VI.1-VII.4 |
| **P. bairdii bairdii** W. H. Edwards | x | x | x | x | x | x | x | V.1-VI.4 |
| **P. zelicaon nita** W. H. Edwards | x | x | x | x | x | x | x | V.1-VII.3 |
| **P. indra indra** Reakirt | 0 | 0 | 0 | 0 | 0 | 0 | 0 | V.2-VII.4 |
| **Pterourus rutulus rutulus** (Lucas) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | VI.1-VII.1 |
| **P. multicaudatus** (Kirby) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | VI.1-VII.3 |
| **P. euryumedon** (Lucas) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | VII.1 |

**Pieridae**

| **Neophasia menapia menapia** (Felder & Felder) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | VII.2-IX.2 |
| **Pontia beckerii** (W. H. Edwards) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | III.4-VI.4 |
| **P. sisybrii elivata** (Barnes & Benjamin) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | IV.4-VI.2 |
| **P. protodice** (Boisduval & LeConte) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | VI.2-VIII.1 |
| **P. occidentalis occidentalis** (Reakirt) | x | x | x | x | x | x | x | IV.2-VIII.1 |
| **P. napi macdunnoughi** (Remington) | x | x | x | x | x | x | x | V.4-VI.4 |
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**Riodinidae**

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**Libytheididae**

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<td>III.4-IX.1</td>
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<td>VII.4-IX.1</td>
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<td><strong>Satyridae</strong></td>
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Isozyme Data and the Taxonomy of Checkerspot Butterflies (Euphydryas)

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Abstract. The taxonomy of butterflies in the genus Euphydryas was investigated using aliozyme frequency data from 19 presumptive loci. Six Euphydryas species and three species in the tribe Melitaeini (Chlosyne acaustus, Chlosyne palla, and Melitaea phoebe) were included in the study. This set of species included at least one representative each of Higgins’ four proposed genera within Euphydryas. Dendrograms derived using UPGMA, neighbor-joining, distance Wagner, and maximum likelihood clustering methods were used to establish the similarity of the sampled taxa. The analyses do not support Higgins’ generic rearrangement.

Key Words: Allozymes, electrophoresis, phenogram

Introduction

Checkerspot butterflies of the genus Euphydryas have become a key system for testing theories in population biology in the field. An equivalent body of information on population dynamics, ecology, and genetics such as is available for checkerspots probably does not exist for a suite of populations in any other group of animals. Work with the Euphydryas system and comparative work with other butterflies has led to the development of generalities which may prove valid for at least the majority of herbivorous insects. These generalities include the importance of gene flow in evolution, the “regulation” of population size, the frequency of extinction, and selection versus neutrality in accounting for allozyme variability (Ehrlich et al. 1975, Ehrlich et al. 1980, Ehrlich and White 1980, Meuller et al. 1985, Weiss et al. 1987, Brussard et al. 1989, and Baughman et al. 1990).

Some of the same features that make Euphydryas butterflies so attractive for hypothesis testing in population biology, however, have made the genus a difficult one for systematists. Several of the species are highly polytypic and show complex variation in size, wing patterns and coloration, and a variety of ecological characteristics. This has resulted in a proliferation of trinomials; for example, Miller and Brown (1981) list 61 subspecies among nearctic species and Ferris (1989) lists 62 (but also see Scott 1986).

In spite of the common occurrence of extensive intraspecific variation, nevertheless, diagnostic characters in wing pattern and genitalia exist which allow separation of most forms at the species level. Traditionally, 14 species

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have been recognized, six of which are Nearctic, and eight Palearctic (Higgins 1950, Ehrlich and Ehrlich 1961, Howe 1975, Miller and Brown 1981). However, three of the Nearctic species, Euphydryas anicia, E. chaledona, and E. colon, appear to represent a classic “ring of races” with reproductive isolation between populations on the terminal ends rather than separate monophyletic lineages (Scott 1986, Brussard et al. 1989). Thus, Euphydryas anicia and E. colon are properly treated as synonyms of E. chaledona, the priority name, reducing the number of Nearctic species to four.

Higgins (1978) divided Euphydryas into four genera, Hypodryas, consisting of four palearctic and one Nearctic species; Eurodryas, consisting of four Palearctic species; Occidryas, consisting of four Nearctic species (three of which were synonymized, making two); and Euphydryas, consisting of a single Nearctic species. The currently recognized species of Euphydryas (sensu latu) are shown in Table 1, along with Higgins’ (1978) proposed generic rearrangement.

The splitting of checkerspots into four genera was strongly criticized by Ehrlich and Murphy (1982) for a number of reasons, and their criticisms were reinforced by genetic information presented by Brussard et al. (1985). After Brussard et al. (1985) was completed, we obtained statistically reasonable samples of Euphydryas desfontainii and E. aurinia, two representatives of Higgins’ proposed genus Eurodryas. This additional material now allows us to determine levels of genetic differentiation in six of the 12 species of Euphydryas s.l., at least one of which is in each of Higgins’ putative genera.

The first question we address is whether the genetic differentiation observed among these species is more suggestive of that typically seen at the intrageneric or the intergeneric level among other butterfly groups. The second question concerns the relationships of these species to each other through the use of gene frequency data with various clustering methods. More specifically, does the arrangement of species in Table 1 seem to represent a natural grouping of species of Euphydryas s.l. in light of their geographic distributions and other characteristics?

Methods

A total of 18 populations were sampled for this study (Table 2). Higgins’ “Occidryas” group is represented by 228 individuals from four populations of Euphydryas editha and 493 individuals from seven populations of E. chaledona. These populations were taken from a much larger array sampled for other studies (e.g. Brussard et al. 1989, Vawter and Wright 1986, and unpublished data) and were selected to maximize geographical representation in these species. All other samples were collected in the summer of 1986. Higgins’ “Eurodryas” group is represented by 58 individuals from two populations of E. phaeton, “Hypodryas” by a sample of 20 individuals from one population of E. gillettii, and “Eurodryas” by 92 individuals from two populations of E. desfontainii and 27 individuals from one population of E. aurinia. We used two species of Nearctic Chlosyne and one species of Palearctic Melitaea for both comparison and as outgroups in the analyses. Both of these genera are included with Euphydryas in the tribe Melitacini. These samples included 28 individuals from one population of Melitaea phoebe, 20 individuals from one population of Chlosyne acastus, and 28 individuals from one population of C. palla.
Individual butterflies were assayed for variability at 19 presumptive loci which could be reliably scored in side-by-side comparisons of all six Euphydryas species and three outgroup species run on the same gels. These loci are AAT-1,2, AGP, DIA, GAPD, GDH, GPI, HBDH, HK-1, IDH-1, LDH, MDH-1,2, MPI, PEP-GL, PGD, PGM, SOD-1,2 (isozyme names and buffer systems used are listed in Brussard et al. [1985] with the exceptions that HK-1 resolved on buffer C and AGP [G3P] resolved on buffer D). Loci are numbered and electromorphs were designated in order of increasing anodal mobility.

### Table 1. Higgins' four genera proposed for the genus Euphydryas.

<table>
<thead>
<tr>
<th>Higgins (1978)</th>
<th>&quot;Hypodyras&quot;</th>
<th>&quot;Eurodryas&quot;</th>
<th>&quot;Occidrys&quot;</th>
<th>&quot;Euphydryas&quot;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Euphydryas maturna</td>
<td>Euphydryas aurinia&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Euphydryas chalcedona&lt;sup&gt;1&lt;/sup&gt;</td>
<td>Euphydryas phaeton&lt;sup&gt;1&lt;/sup&gt;</td>
<td></td>
</tr>
<tr>
<td>E. intermedia</td>
<td>E. desfontainii&lt;sup&gt;1&lt;/sup&gt;</td>
<td>E. editha&lt;sup&gt;1&lt;/sup&gt;</td>
<td></td>
<td></td>
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<tr>
<td>E. iduna</td>
<td>E. alexandrina</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. cynthia</td>
<td>E. orientalis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>E. gillettii&lt;sup&gt;1&lt;/sup&gt;</td>
<td></td>
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</tr>
</tbody>
</table>

<sup>1</sup> Species that were included in the present study.
Table 2. Sample locations and sizes used in the allozyme analyses of *Euphydryas* taxonomy.

<table>
<thead>
<tr>
<th>Taxon</th>
<th>Sample Location</th>
<th>Sample Size</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Euphydryas editha</em></td>
<td>Gunnison Co., CO, USA</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td>Thurston Co., WA, USA</td>
<td>73</td>
</tr>
<tr>
<td></td>
<td>Riverside Co., CA, USA</td>
<td>57</td>
</tr>
<tr>
<td></td>
<td>Mariposa Co., CA, USA</td>
<td>39</td>
</tr>
<tr>
<td><em>E. chalcidona</em></td>
<td>Gunnison Co., CO, USA</td>
<td>79</td>
</tr>
<tr>
<td></td>
<td>Nye Co, NV, USA</td>
<td>49</td>
</tr>
<tr>
<td></td>
<td>Maricopa Co, AZ, USA</td>
<td>56</td>
</tr>
<tr>
<td></td>
<td>Stanislaus Co., CA, USA</td>
<td>59</td>
</tr>
<tr>
<td></td>
<td>Santa Clara Co., CA, USA</td>
<td>58</td>
</tr>
<tr>
<td></td>
<td>Inyo Co, CA, USA</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>Jackson Co., OR, USA</td>
<td>78</td>
</tr>
<tr>
<td></td>
<td>Polk Co., OR, USA</td>
<td>73</td>
</tr>
<tr>
<td><em>E. phaeton</em></td>
<td>Franklin Co., MO, USA</td>
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</tr>
<tr>
<td></td>
<td>Otsega Co., NY, USA</td>
<td>30</td>
</tr>
<tr>
<td><em>E. gillettii</em></td>
<td>Teton Co., WY, USA</td>
<td>20</td>
</tr>
<tr>
<td><em>E. desfontainii</em></td>
<td>Campo Real, Spain</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td>Rhonda, Spain</td>
<td>52</td>
</tr>
<tr>
<td><em>E. aurinia</em></td>
<td>El Escorial, Spain</td>
<td>27</td>
</tr>
<tr>
<td><em>Melitaea phoebe</em></td>
<td>Campo Real, Spain</td>
<td>28</td>
</tr>
<tr>
<td><em>Chlosyne acastus</em></td>
<td>Nye Co., NV, USA</td>
<td>20</td>
</tr>
<tr>
<td><em>C. palla</em></td>
<td>Gunnison Co., CO, USA</td>
<td>28</td>
</tr>
</tbody>
</table>

All gel runs included an *Euphydryas editha* standard inserted into every tenth slot in the gels, and each electromorph was identified by its mobility relative to that of the most common electromorph in *E. editha* at each locus. Phenotypes were recorded directly from the gels. Electromorph frequencies were determined by direct count from the observed phenotypes. Population-level data from each species represented by more than one sample were combined to represent electromorph frequencies for each species as a whole.

Nei’s (1978) unbiased and Roger’s genetic distances, UPGMA phenograms, and rooted Wagner trees were estimated using BIOSYS-1 (Swofford and Selander 1981). A neighbor-joining (Saitou and Nei 1987) dendrogram was generated using the genetic distances obtained from BIOSYS-1. A maximum likelihood network was generated directly from the observed electromorph frequencies using the CONTML subroutine in PHYLIP 3.5 (Felsenstein 1993).
Results
The number of electromorphs per locus ranged from three to 10 over all the operational taxonomic units (OTU’s) used in this study with all loci being polymorphic in at least one species. The frequency of each electromorph present in each species as a whole is shown in Table 3. As can be seen in Table 3, most electromorphs at a given locus are shared by several species, although often at quite different frequencies. Only five electromorphs proved to be diagnostic (i.e. fixed or nearly fixed in one taxon while not present in the others). DIAa, LDHi, and SOD-1g appear to be diagnostic of Chlosyne, GDHd of Euphydryas aurinia, and LDHb of E. gillettii. However, because some sample sizes are relatively small, some of these electromorphs really may not be unique to these taxa. Several other electromorphs such as G3Pa, DIAa, GDHc, HBDHb, HBDHg, and SOD-1a are fixed or nearly fixed in one or more species, but segregate as rare variants in others (Table 3).

Composite Phenogram
The topologies of phenograms derived using UPGMA based on Nei’s unbiased distances and Roger’s distances (Table 4), neighbor-joining based on Nei’s unbiased distances (Table 4), the distance Wagner method, and maximum likelihood were all very similar. A “composite” phenogram that shows the common pattern of clustering in all the phenograms derived from these methods is shown in Figure 1. The composite phenogram is scaleless, i.e. it shows the pattern of genetic similarity derived by all the methods used without presenting genetic distances among OTU’s.

The most salient point to be drawn from the composite phenogram (Figure 1) is that the North American Euphydryas species form a discrete cluster. The next most similar set of species to these is the European Euphydryas which constitute Higgins’ (1978) “Eurodryas.”

Discussion
The similarity among the tree topologies derived by a number of procedures using the Euphydryas data suggests that the general pattern of genetic similarity among these taxa has been captured by the analyses. Kim et al. (1993) tested this assumption by estimating the accuracy of trees derived by maximum parsimony, UPGMA, and neighbor-joining using simulated data. The results of the analysis by Kim et al. (1993) suggested that the assumed correlation between concordance of topologies from a number of tree-estimating algorithms and tree accuracy, as made in a number of studies (e.g. Dowling and Brown 1989, Zink and Avise 1990, Giannasi et al. 1992, and Valdebenito et al. 1992), is probably correct. This result lends confidence in interpreting the results of the present study.

Brussard et al. (1985) used a smaller number of taxa in a similar analysis to the present one to argue against splitting of the genus Euphydryas into four genera as suggested by Higgins (1978). The inclusion of additional Old World Euphydryas samples and outgroups in the present analysis strengthens
Table 3. Allele frequencies at polymorphic loci for six *Euphydryas* species and three additional species in the tribe Melitaeini. Sample sizes are provided.

<table>
<thead>
<tr>
<th>Species</th>
<th>Sample size</th>
<th>No. populations</th>
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<tr>
<td>Ee</td>
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<tr>
<td>Ec</td>
<td>493</td>
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<td>Ep</td>
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<th>Locus</th>
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<tr>
<td>B</td>
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<td>0.009</td>
</tr>
<tr>
<td>C</td>
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<td>0.960</td>
</tr>
<tr>
<td>E</td>
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<tr>
<td>G</td>
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</tr>
<tr>
<td>H</td>
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<td>0.000</td>
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<tr>
<td>AAT-2</td>
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</tr>
<tr>
<td>C</td>
<td>0.851</td>
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<tr>
<td>E</td>
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</tr>
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<td>F</td>
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<td>DIA-1</td>
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<td>A</td>
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<td>1.000</td>
</tr>
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<td>0.000</td>
</tr>
<tr>
<td>K</td>
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<td>0.000</td>
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<td>G3P-1</td>
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<tr>
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</table>

Note: The table continues with allele frequencies for each locus across different species.
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<th>A</th>
<th>B</th>
<th>C</th>
<th>D</th>
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Table 4. Nei's (1978) unbiased genetic distances above the diagonal and Roger's modified genetic distances (Wright 1978) below diagonal for six species of *Euphydryas* and three comparative taxa also in the tribe Melitaeini.

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<td>5. <em>E. desfontainii</em></td>
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<td>9. <em>C. palla</em></td>
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Figure 1. A composite phenogram based on UPGMA, neighbor-joining, Wagner, and maximum likelihood analyses of alkoyme frequencies from 19 loci for six species of Euphydryas and three comparative species also in the tribe Melitaeini. Higgins' (1978) putative genera are in quotation marks. The composite phenogram does not support the generic rearrangement of Euphydryas sensu latu as proposed by Higgins.

this conclusion. Estimates of genetic distances among Euphydryas species are consistent with the present nomenclatural arrangement for the genus (Brussard et al. 1985). The taxa from Euphydryas s.l. form a cluster separate from the comparative taxa, Chlosyne acastus, C. palla, and Melitaea phoebe, in all topologies. This also strongly suggests that little justification exists for splitting Euphydryas s.l. into four genera. Furthermore, the level of differentiation between the comparative taxa and the Euphydryas spp. on the UPGMA
phenograms indicates that *Euphydryas* s.l. is a valid taxonomic entity (Brussard 1985). Finally, these data suggest that *Chlosyne acastus* and *C. palla* are genetically very similar. Nei’s (1978) unbiased genetic distance between these two species (0.249) is among the lowest in Table 2 and is of a magnitude suggestive of semispecies or sibling species for other insect taxa (Brussard et al. 1985).

Higgins “Eurodryas” (*E. aurinia* and *E. desfontainii*) clusters within the *Euphydryas* branch on the composite dendrogram, suggesting that those species are measurably differentiated from the other *Euphydryas* taxa. Eurodryas may serve as an appropriate nomen to refer to these taxa as a European “species group” or subgenus. That interpretation should be viewed as tentative, however, because two ostensibly species of “Eurodryas,” *Euphydryas alexandrina* and *E. orientalis*, were not included in the present analysis.

We conclude that the allozyme data presented above do not justify splitting the genus *Euphydryas* into four genera as suggested by Higgins (1978). The consistent clustering of *Euphydryas* spp. as a pool of species distinct from closely related members of the tribe Melitaeini using a number of different phenetic clustering methods demonstrates the substantive cohesion of *Euphydryas sensu latu*.

**Acknowledgments.** Support for this study was provided by grants from the National Science Foundation (DEB 8116332 and BSR 8206961) to P.F. Brussard and P.R. Ehrlich, respectively, and by the Nevada Biodiversity Initiative. Janet Wright did much of the electrophoresis, Bruce Neill and Mike Ivie helped with data analysis for an earlier version of this paper. Mike Sanderson maximally assisted with the maximum likelihood analysis.

**Literature Cited**


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Preliminary Checklist and Field Observations of the Butterflies of the Maquipucuna Field Station (Pichincha Province, Ecuador).

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Oliver Gloster

Ty Jauen 29390 Scqer, Finistere, Brittnny, FRANCE.

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Abstract. The Maquipucuna Tropical Reserve (MTR) contains one of the few remaining fragments of rainforest in western Ecuador. A survey of butterfly species richness was performed by walking an altitudinal transect (1270 to 1900m) through MTR forest habitats from late August to October, 1989, and late November to early December, 1992. In 350 collector hours, 220 butterfly species were observed; some are characteristic of lowland tropical forests, others of Andean cloud forests and bamboo thickets. Habitat affinities, altitudinal distributions, feeding and perching behaviors were noted and discussed for many species. Cylindrical net traps baited with rotting fruit were used to collect 21 butterfly species, mostly charaxine and satyrine nymphalids. We observed apparent zonation by elevation or habitat among three species of Taygetis (Satyrinae) and vertical zonation in perch height among three species of Adelpha (Liminitinae). Future surveys performed from January to July and extending to the southern limits of the MTR (above 1900m) should identify many more butterfly species.

Key Words: Altitudinal zonation, butterflies, fruit-feeding, Maquipucuna Tropical Reserve, perching, western Ecuador.

Introduction

Recent efforts to survey and catalog biological diversity have identified western Ecuador (Esmeraldas, Guayas, Manabí and Pichincha Provinces; see map, Fig. 1) as a "hotspot" of species endemism, particularly for flowering plants (Conniff 1991, Wolf 1991, Gentry 1991). Unfortunately, little remains of the formerly extensive belt of western Ecuador's tropical forest, as an estimated 95% of the original forest cover has been cleared during the past two decades (Conniff 1991, Gentry 1991). The Maquipucuna Tropical Reserve (MTR) contains one of the few remaining fragments of western Ecuadorian forest. The 5000 hectare Reserve was established in 1988 by the Fundación Maquipucuna, a non-profit organization oriented toward conservation of threatened ecosystems, sustainable resource management, environmental education and ecotourism. One of the most important features
Figure 1: Map of Ecuador, showing Provinces of western Ecuador (Esmeraldas, Guayas, Los Rios, Manabi and Pichincha), the locations of the Maquipucuna Tropical Reserve (M), the Pululahua Crater (P) and the Tinalandia resort (T). The Jatun Sacha field station, Napo Province, is indicated by (J).

of the MTR is that it contains an altitudinal transect (1270 to 2700m) that combines plant and insect species with strong affinities to the coastal lowland rainforests (Gentry 1991) with elements of the Andean flora and fauna of higher elevations.

In 1989, we initiated our census of the butterflies of the MTR as one of many floristic and faunistic baseline surveys (e.g. birds - Marín et al. 1992, Greenfield 1993; plants - G. Webster, unpublished data, Gentry 1991) performed at the Reserve. Our goals were to establish a preliminary checklist of butterfly species occurring at MTR and to create a reference collection (in Quito) of specimens that would be available to future researchers. Certain groups of butterflies and moths from western Ecuador have been studied
(roidinids; Willmott and Hall 1994, satyrines; Hewitson 1870, Kruger 1924, Brown 1941a, 1943, 1944, saturniid moths; LeMaire and Venedictoff 1989: see references in Brown [1941b]), and butterflies have been collected extensively at the Tinalandia resort (670 m elev.), 17 km east of Santo Domingo de los Colorados (Emmel and Drummond 1988, Strasburg 1978, Shaw and Shaw 1987, T. Emmel and C. Covell, pers. comm.; see map, Fig. 1), but there are few published faunal checklists of butterfly species for any single locality in western Ecuador (see Campos 1898). Here we present the results of our survey, including a preliminary checklist, and observations on elevational distributions, habitat affinities, feeding and perching behaviors of the butterflies of the MTR.

**Materials and Methods**

**Field Site**

The MTR (*Bosque Protector Maquipucuna, 0° 5'N, 78° 37'W*) is located roughly 40 km northwest of Quito, near Nanegalito in the Province of Pichincha, Ecuador (see maps, Figs. 1, 2). The Reserve includes a small biological field station (Estación “Thomas Davis”) and encompasses 3000 ha of premontane tropical rainforest, cloudforest and bamboo thickets (*Chusquea* sp. [Poaceae]) from a minimum elevation of 1200 m near the Rio Tulambí to the 2700 m peaks of Monte Sosa and Cerro Montecristi. Yearly mean temperatures (14° to 22° C) and rainfall (1000 mm to 4000 mm) vary considerably within the Reserve (R. Justicia, unpubl. data). Rainfall appears to be heaviest from August to December (O. Gloster, pers. obs.). More detailed meteorological information from MTR will be published elsewhere (G. Webster, in prep.).

**Habitats**

We surveyed the butterflies of the northern third of the MTR by walking a 3.5 km altitudinal transect south-southwest from 1270 m at the station to a deeply forested ridge at 1700 m below Loma Cachillacta. Elevations were determined through the use of an altimeter calibrated against a topographic map (Calacali Quadrangle, IAGS Ecuador, 1980). The surveys were performed along established paths from 0800 to 1400 hrs. each day from 20 to 26 Aug. 1989 (RAR and OG), 2 Sept. to 18 Oct. 1989 (OG) and from 27 Nov. to 7 Dec. 1992 (RAR). These paths originate within riparian forest (*Blakea eriocalyx* [Melastomataceae], *Otoba gordonifolia* [Myristicaceae], with a canopy of 20-35 m) along Rio Tulambí and Rio Umachaca, where the chief nectar sources observed during our study were *Erato polymnioides* and *Eupatorium* sp. (Asteraceae). The paths traverse groves of banana and guava (*Psidium guajaba* [Myrtaceae]) and converge in a meadow of blooming *Asclepias curassavica* (Asclepiadaceae), *Bidens* sp. (Asteraceae) and *Lantana camara* (Verbenaceae) plants at 1300 m. For the next 0.5 km a single path crosses an exposed clearing near a small farm, “Finca los Espárragos”, adjacent to disturbed, second growth forest with *Heliotropium* sp. (Boraginaceae), a low canopy of *Piper* sp. (Piperaceae) trees and an understory dominated by *Anthurium giganteum* (Araceae), *Gunnera pilosa* (Gunneraceae), a pink-flowered *Salvia* sp. (Labiatae) and *Solanum acerifolium* (Solanaceae). Beyond the farm the path ascends a steep ridge bordered by disturbed thickets of ferns and *Solanum* shrubs to the west and groves of *Cecropia* sp. (Moraceae) trees to the east, then winds through grassy meadows and re-enters forest at 1500 m.
Figure 2: Map of the Maquipucuna Tropical Reserve, located near the equator between Calacali and Nanegal. Butterfly surveys were performed in the northern third of the Reserve, along transects from the Thomas Davis field station (S; 1270m) past the Finca de los Esparragos (E) toward the Loma Cachillacta (1904m). Dotted lines indicate auto roads; solid lines contain the Cooperativo Nuevos Horizontes (NH), the Reserva Maquipucuna (center) and the Bosque Protector del Rio Guayllabamba (right).

The forest canopy above the hillside switchbacks is low (15-25m), with thickets of Heliconia grigsiana (Heliconiaceae), ferns, individual Centropogon solanifolium (Lobeliaceae) plants and Sobralia orchids. At 1600m the forest grades into a deeper, less disturbed community of palms and taller trees (e.g. Gustavia sp. [Lecythidaceae], Meriana sp. [Melastomataceae], Persea sp. [Lauraceae] and Otoba gordonifolia, to 40m) draped with bromeliads and lianas (Burmeistera resupinata [Lobeliaceae], Monstera and Philodendron sp. [Araceae]). At 1700m, the path branches to the south and east over primary premontane and montane forest, continuing through a bamboo zone to Cerro Montecristi. The latter paths were still under construction.
during the periods of this study; butterflies from cloud forest and bamboo habitats from 1700 to 1900m in elevation were surveyed sporadically by OG in 1989.

Collecting Methodology
Butterflies were collected with nets at flowers, sap, animal excrement, at rest or in flight; were ensnared in cylindrical net traps (30 cm diameter, 75 cm height) that were baited with rotting bananas and solanaceous fruits (tree tomato, Cyphomandra crassifolia and naranjilla, Solanum quitense); and were identified by sight when possible. We recorded date, time, elevation, habitat type and details of feeding and perching behavior (time of day, height of perch, microhabitat) for each observed or collected specimen. Eight baited traps were placed in the forest understory (1.5 m above ground) in order to sample a variety of microhabitats and elevations (see Table 1). Traps were checked twice daily, in the early morning and afternoon. Heavy rainfall often began by 1430 hrs. and continued into the early evening.

Specimen Identification
Many of the butterflies collected were identified in Ecuador through comparison with specimens in the Museo Ecuatoriano de Ciencias Naturales in Quito or by consulting the texts of Fox and Real (1971), DeVries (1987) and D’Abrera (1981, 1984, 1987a,b, 1988). Specimens from problematic groups were identified at the Smithsonian Institution, Washington DC, by Drs. Robert Robbins (lycaenids), Donald Harvey (riodinids and hesperids) and Gerardo Lamas (some ithomiines) and by one of us (RAR) at the American Museum of Natural History, New York. All specimens are currently housed either in the collection of the Pontificia Universidad Católica or in the private collection of the Fundación Maquipucuna, both in Quito.

Results
Species Checklist
We found 220 species of butterflies during 350 hours of observations at MTR. These species are listed in Appendix 1, along with elevation, habitat and months (from August to December) during which they were observed. Some species (e.g. Dismorphia theucarilla, Leodonta dysoni, many lycaenids and riodinids) were observed only during limited segments of our survey, while others (Altinote ozenome, Papilio thoas, Pteronymia parva, most satyrines and pierids) were observed throughout the period of study. Over one half of the butterfly species encountered were Nymphalidae, and 34 of the 116 nymphalid species collected (29%) represented the Satyrinae. Superficially, satyrine species richness at MTR is numerically comparable to faunal survey results from lower elevation South American rainforests, such as Pakitza (400m, 28% satyrines; Lamas et al. 1991) and Tambopata (300m, 25%; Lamas 1983) near Manu National Park, Perú and two sites in Rondônia, Brazil (Jaru, 250-350m, 27.5%, Brown 1984; CaucaLandia, 160-350m, 20%, Emmel and Austin 1990). However, the MTR satyrine fauna is distinguished from the others by the number of species from the tribe Pronophilini (at least 12, probably more above 2000m), which are more characteristic of higher elevation Andean biomes than are non-pronophiline satyrines (Brown 1941a, 1943, Adams and Bernard 1977, Adams 1986).
At least 70 butterfly species found at MTR (and probably many more) also are found in the 670-700m tropical forests of the Tinalandia Resort (Strasburg 1978, Shaw and Shaw 1987, Emmel and Drummond 1988, B. Harris, R. Leushner unpub. data; see Appendix 1) and elsewhere in tropical Ecuador (Campos 1921, Kruger 1924, D’Abrera 1981, 1984, 1987a, b; see Appendix 1). The presence of middle-elevation forest species, such as *Adelpha colada*, *Heliconius elysanymus*, *Patricia dercyllidas*, *Perisma opellii*, *Corades pannonia*, *Mygona irmina* and other pronophiline satyres illustrate the faunal transition from coastal tropics to Andean paramo that occurs within MTR. The endpoint of this transition is illustrated by the butterfly fauna of the nearby Pululahua Crater (2500-3000m; between Calacalí and San Isidro, Pichincha Province), which is rich in lycaenid and satyrine species, including some endemics (Balint and Johnson 1994, 1995), but is depauperate in most other groups of butterflies. Nearly one-third of the 94 species identified from Pululahua are pronophiline satyres, including four species of *Corades*, 11 *Pedaliodes* and two *Pronophila* (G. Kareofelas and C. Witham, unpubl. data). Only 19 butterfly species found at Pululahua Crater also occur at MTR (see Appendix 1).

In Fig. 3 we give a crude estimate of sampling effort and survey completeness, assayed by graphing the cumulative number of species against cumulative observer hours (see Clench 1979, Brown 1984, Raguso and Llorente 1991, Lamas et al. 1991). Species number increased sharply at the outset of our study (Aug. 1989), tailed off during the extremely wet period of Sept.-Oct. 1989 and rose steadily during the final segment of our survey, late Nov.-early Dec. 1992, without reaching an asymptote. These patterns indicate a seasonal effect on butterfly species composition at MTR and suggest that additional butterfly species are likely to be found there in December. We expect to encounter many more butterfly species when surveys are extended to higher cloud forest and bamboo thicket habitats above 1900m, and when all habitats are surveyed from January through July.

**Habitat Affinities**

In addition to lower montane rainforest, cloudforest and bamboo thickets, MTR includes a number of ecotone microhabitats, including successional meadows, young second growth forest edges and riparian gallery forest. Some of the butterfly species observed during our survey (e.g. *Papilio thoas*, *Anteos clorinde*, *Gluthophrissa drusilla*, *Phoebis argante* and *P. sennae*, *Dione juno*, *Anartia amathea*, *Adelpha cythaerias*, *Junonia evarete*, *Vanessa virginiensis*, *Hermeuptychia hermes*) are cosmopolitan, “weedy” species (DeVries 1987, Brown 1991, Raguso and Llorente 1991, see Bowman et al. 1990) associated with disturbed, exposed habitats on the fringes of MTR. Other species, including *Mechanitis menapis*, *Papilio anchisiades*, *Parnades iphidamus* and *P. erithalion* (abundant at riverside flowers), *Diaethria neglecta*, *Leodonta dysoni*, *Marpesia chiron* and *Perisma vaninka* (common at mud puddles) and *Arawacus leucogyna*, *Heliconius sapho eleuchia*, *Prepona* and *Necyria* species (perched or resting on vegetation) were associated primarily with riparian habitats. A
number of butterflies appeared to be restricted to dark forest habitats, including Dismorphia lelex and D. theucarilla (Pieridae), Napaea nr. merula (Riodinidae), the skipper Vettias coryna, many ithomines (Greta, Ithomia and Pteronymiasp., Patricia deryllidas) and satyrines (Chloreuptychia arnaea, Cithaerias menander, Manataria maculata). Numerous butterfly species were associated with treefall gaps, especially from the nymphalid genera Adelpha, Eresia, Hypanartia, Memphis, Perisama and Prepona, the lycaenid Thecla danaus, the skippers Astraptes fulgerator azul and Urbanus proteus and most satyrines. Finally, Antirrhea sp. nr. geryon (Morphinae), Eretris apuleja, Taygetis lineata (Satyrinae) and the skippers Cyclosaemaria phidyle and Metrocles sp. were found only in the bamboo zone above 1800m.

Elevational Distributions
Altitudinal data for all butterfly species are listed in Appendix 1; the distributions of all satyrine butterflies collected from the tribe Pronophilini are given in Fig. 4. Pedaliodes peucestas and P. phrasiclea were found together in forest habitats throughout the altitudinal range of our survey, including disturbed forest edges below 1400m. This contrasts with the observations of...
Figure 4: Elevational distributions of satyrine butterflies, tribe Pronophilini. Bars represent elevations at which specimens of a given species were observed or collected.

Adams (1986) throughout the Colombian Andes, where *P. phrasiclea* always occurs in a lower elevational belt (2000-2600m cloud forest) than the white-banded *P. peucstas* (2500-3000m). The altitudinal distributions of *Corades enyo* (1270-1660m) and *C. pannonia* (1500-1860m) overlapped at MTR as they do in Colombia (Adams 1986), but *C. pannonia* was less frequently encountered outside of mature forest. Among other satyrines, *Taygetis andromeda* was found from 1450-1600m, but apparently is replaced by *T. puritana* in cloud forest at 1600-1800m and by *T. lineata* in the bamboo zone from 1800-1900m. Other pairs of related nymphalids with non-overlapping elevational distributions were: *C. illioneus* (Brassolinae, 1270-1300m; banana groves) and *Caligo prometheus* (1450-1500m; in banana groves and *Heliconia* thickets), *Pteronymia parva* (Ithomiinae, 1270-1510m) and *P. zerlina* (1460-1900m) and *Heliconius sapho eleuchia* (Heliconiinae, 1270-1300m) and *H. clisynymus* (1510-1700m).

**Feeding Behavior**

Butterflies were observed and collected feeding at a variety of sources, including flowers, rotting fruit, sap, animal waste and mud puddles. Table 2 lists the butterfly species observed taking nectar from common riverside or trailside flowers. In contrast, Table 1 lists the butterflies (mostly charaxines and satyrines) collected in traps baited with rotting fruit and placed along

<table>
<thead>
<tr>
<th>Elev.</th>
<th>Habitat</th>
<th>Butterfly Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>1. 1260 m</td>
<td>meadow nr. banana grove</td>
<td>Archaeoprepona chromus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Euptychia harmonica</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oxeoschistus isolda</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pareuptychia hesionides</td>
</tr>
<tr>
<td>2. 1260 m</td>
<td>riverside gallery forest</td>
<td>Hypanartia lethe</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Prepona laertes</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Smyrna blomfallia</td>
</tr>
<tr>
<td>3. 1300 m</td>
<td>disturbed path, lightgap</td>
<td>Corades enyo</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Diaethria marchalii</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Euptychia harmonica</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Memphis morvus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oxeoschistus isolda</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pareuptychia hesionides</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pareuptychia metaleuca</td>
</tr>
<tr>
<td>4. 1410 m</td>
<td>hillside forest</td>
<td>Opsiphanes quiteria</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pedaliodes peusteas</td>
</tr>
<tr>
<td>5. 1500 m</td>
<td>dark forest understory</td>
<td>Caligo prometheus</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Corades pannonia</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Euptychia harmonica</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oxeoschistus isolda</td>
</tr>
<tr>
<td>6. 1560 m</td>
<td>dense forest</td>
<td>nothing caught</td>
</tr>
<tr>
<td>7. 1580 m</td>
<td>hillside lightgap</td>
<td>Corades enyo</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Corades pannonia</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oressinoma typhla</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Oxeoschistus isolda</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Pronophila orcus</td>
</tr>
<tr>
<td>8. 1640 m</td>
<td>dense forest</td>
<td>Corades enyo</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Perisama opellii</td>
</tr>
<tr>
<td>9. 1750 m</td>
<td>bamboo clearing</td>
<td>Manataria maculata</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Taygetis puritana</td>
</tr>
</tbody>
</table>

paths at different elevations. The absence of species overlap between these two tables is characteristic of the narrowness of flower-feeding and fruit-feeding butterfly guilds in neotropical rainforests (DeVries 1987, 1988). We summarize all observations of butterflies feeding at non-floral sources in Table 3, distinguishing among bird, dog, horse and cow feces, human urine,
Table 2. Butterflies collected or observed at flowers.

<table>
<thead>
<tr>
<th>Flower Species</th>
<th>Butterfly Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>on <em>Bidens</em> sp. (Asteraceae)</td>
<td><em>Euptychia inornata</em></td>
</tr>
<tr>
<td></td>
<td><em>Heliconius clysonymus</em></td>
</tr>
<tr>
<td></td>
<td><em>Heliopetes</em> sp.</td>
</tr>
<tr>
<td>on <em>Erato polymnioides</em> (Asteraceae)</td>
<td><em>Autochton neis</em></td>
</tr>
<tr>
<td></td>
<td><em>Charis iris</em></td>
</tr>
<tr>
<td></td>
<td><em>Emesis ocypore</em></td>
</tr>
<tr>
<td></td>
<td><em>Eusalesia bettina</em></td>
</tr>
<tr>
<td></td>
<td><em>Ouleus fridericus</em></td>
</tr>
<tr>
<td></td>
<td><em>Parides iphidamus</em></td>
</tr>
<tr>
<td></td>
<td><em>Siproeta epaphus</em></td>
</tr>
<tr>
<td>on <em>Eupatorium</em> sp. (Asteraceae)</td>
<td><em>Archonias tereas</em></td>
</tr>
<tr>
<td></td>
<td><em>Charis iris</em></td>
</tr>
<tr>
<td></td>
<td><em>Leucochimona lagora</em></td>
</tr>
<tr>
<td>on <em>Heliotropium</em> sp. (Boraginaceae)</td>
<td><em>Leptophobia caesia</em></td>
</tr>
<tr>
<td></td>
<td><em>Ithomia terra</em></td>
</tr>
<tr>
<td>on <em>Lantana camara</em> (Verbenaceae)</td>
<td><em>Altinote ozomene</em></td>
</tr>
<tr>
<td></td>
<td><em>Danaus plexippus</em></td>
</tr>
<tr>
<td></td>
<td><em>Dismorphia theucarilla</em></td>
</tr>
<tr>
<td></td>
<td><em>Hypoleria riffarthi</em></td>
</tr>
<tr>
<td></td>
<td><em>Symmachia probator</em></td>
</tr>
</tbody>
</table>

Rotting bananas, tree-tomato and *naranjilla* fruits, sap and aluminum foil as non-floral attractants.

**Perching**

In Table 4 we list times, heights above ground, habitat types and elevations of butterfly species observed to defend perches (*sensu* Callaghan 1982, Rutowski et al. 1991). All species included here defended specific perches (usually a leaf or tree trunk) by repeatedly accosting passing butterflies (or tossed objects) and returning to the same sites. Most species defended well-lit perches in treefall gaps, sunflecks or along trailside or riverside forest edges. *Archaeoprepona* spp., *Diaethria marchallii*, *Hypanartia lethe*, *Necyria zaneta* and *Sarota chrysus* were commonly encountered at perches along riverside gallery forests from 1270-1350m. *Euselasia bettina* and *E. eucrates* perched on sunlit *Piper* foliage from 0900-1000 hrs., at vantage points adjacent to dark forest trails (see Callaghan 1982, Brown and Alcock 1991). *Adelpha* species,
<table>
<thead>
<tr>
<th>Species</th>
<th>Mud</th>
<th>Feces¹</th>
<th>Fruit²</th>
<th>Other</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Papilionidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Papilio anchisiades</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Papilio thoas</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><strong>Pieridae</strong></td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>Leodonta dysoni</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pereute callinira</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td><strong>Nymphalidae</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adelpha cythaeria</td>
<td>X</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Altinote alcione</td>
<td>X</td>
<td></td>
<td>X¹⁷</td>
<td></td>
</tr>
<tr>
<td>Altinote ozomene</td>
<td>X</td>
<td></td>
<td>X</td>
<td></td>
</tr>
<tr>
<td>Archaeoprepona chromus</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Archaeoprepona demophon</td>
<td></td>
<td></td>
<td></td>
<td>X³</td>
</tr>
<tr>
<td>Archonias teres</td>
<td></td>
<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Catonephele chromis</td>
<td></td>
<td></td>
<td></td>
<td>X⁶</td>
</tr>
<tr>
<td>Caligo illioneus</td>
<td></td>
<td>X</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Caligo prometheus</td>
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<td>X</td>
<td></td>
</tr>
<tr>
<td>Corades pannonia</td>
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<td></td>
<td></td>
<td>X</td>
</tr>
<tr>
<td>Diaethria marchallii</td>
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<td>Diaethria neglecta</td>
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<td>Dryas iulia</td>
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<td>Euptychia benedicta</td>
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<td>Euptychia harmonica</td>
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<td>Fountainea nessus</td>
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<td>X</td>
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<td>Hermeuptychia hermes</td>
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<td>X</td>
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<tr>
<td>Historis odius</td>
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<td>X⁶</td>
</tr>
<tr>
<td>Hypanartia lethe</td>
<td>X</td>
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<td>X</td>
<td>X</td>
</tr>
<tr>
<td>Manataria maculata</td>
<td></td>
<td></td>
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<td>X³</td>
</tr>
<tr>
<td>Marpesia coresia</td>
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<td>X</td>
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<tr>
<td>Marpesia corinna</td>
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<td>X</td>
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<tr>
<td>Memphis austrina</td>
<td></td>
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<td>X³</td>
</tr>
<tr>
<td>Memphis morvus</td>
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<td>X</td>
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<tr>
<td>Mygona irmina</td>
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<td>X⁶</td>
</tr>
<tr>
<td>Opsiphanes quiteria</td>
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<td>X</td>
</tr>
<tr>
<td>Oressinoma typhia</td>
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<td>X</td>
</tr>
<tr>
<td>Oxeoschistus isolda</td>
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<td></td>
<td></td>
<td>X⁴</td>
</tr>
<tr>
<td>Pareuptychia hesionides</td>
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<tr>
<td>Pareuptychia metaleuca</td>
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<td>Pedaliodes peucestas</td>
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<td>Perisama appelli</td>
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<tr>
<td>Perisama rhodoptera</td>
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<td>Prepona laertes</td>
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<td>Pronophila orcus</td>
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<tr>
<td>Smyrna blomfildia</td>
<td>X</td>
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</tbody>
</table>

**Riodinidae**

- Charis iris

**Hesperiidae**

- Phocides sp.

1: horse or cow feces  
2: rotting banana and tree-tomato fruit  
3: aluminum foil and urine  
4: Naranjilla fruit  
5: dog feces  
6: sap  
7: bird droppings

_Astraptes fulgerator, Memphis morvus, Perisama vitringa_ defended low canopy or lightgap perches along the hillside switchbacks. Sorties were directed at individuals of the same species, at other perching species, at canopy-flying species such as _Gluthophrissa drusilla_ and _Anteos clorippe_ and at patrolling species such as _Oxoschistus isolda_ and _Pronophila orcus_. Finally, many species defended perches in treefall gaps and sunflecks within deep rainforest at 1700m. Perching heights of _Astraptes fulgerator_, three _Euptychia_ sp., _Pedaliodes_ sp., _Stichelia apoplecta_, _Thecla danaus_ and diurnal _Erateinamoths_ (Geometridae) were 3-7m above ground, while those of _Adelpha colada_, _Epiphile oreas_ and _Perisama opellii_ were above 10m in height.

**Discussion**

Faunal checklists for specific localities or habitats provide data bases that may be used to identify local endemism (Descimon et al. 1974, Llorente and Luis 1988, Llorente and Escalante 1992), aid in comparative studies on a regional scale (Adams 1986, DeVries 1987, DeVries, Chacon and Murray 1992, Raguso and Llorente 1991, in press), focus conservation efforts (de la Maza and de la Maza 1985, Emmel and Austin 1990, Brown 1991, Kremen 1992, 1994) and identify avenues for further research. Our preliminary checklist of the butterflies of MTR represents the first step in characterizing the butterfly fauna of an important mid-elevation forest habitat fragment in
<table>
<thead>
<tr>
<th>Species</th>
<th>Time</th>
<th>Height Above Ground</th>
<th>Elevation</th>
<th>Habitat Type*</th>
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<td>Leodonta</td>
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<td>5-7m</td>
<td>1270-1300m</td>
<td>T, C</td>
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<tr>
<td>dysoni</td>
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<td><strong>Nymphalidae</strong></td>
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</tr>
<tr>
<td>colada</td>
<td>1100-1200</td>
<td>10-15m</td>
<td>1700m</td>
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<td>R</td>
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<td>H, S</td>
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<td>oreas</td>
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<td>H, S</td>
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<td>morvus</td>
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<td>1550-1600m</td>
<td>T, S</td>
</tr>
<tr>
<td>sp. 3</td>
<td>1230-1300</td>
<td>3-4m</td>
<td>1700m</td>
<td>H, S</td>
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<td>Perisama</td>
<td>1230-1300</td>
<td>15-30m</td>
<td>1700m</td>
<td>H, T, C</td>
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<td>opellii</td>
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<td>Perisama</td>
<td>1000-1100</td>
<td>4-5m</td>
<td>1550-1600m</td>
<td>T, E</td>
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<td>vitrings</td>
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<tr>
<td>Prepona</td>
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<td>6-8m</td>
<td>1550-1600m</td>
<td>T, E, C</td>
</tr>
<tr>
<td>laertes</td>
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<td><strong>Riodinidae</strong></td>
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</tr>
<tr>
<td>Charis</td>
<td>0900-0930</td>
<td>3-4m</td>
<td>1350m</td>
<td>E, (Piper sp.)</td>
</tr>
<tr>
<td>iris</td>
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</tr>
<tr>
<td>Euselasia</td>
<td>0900-0930</td>
<td>3-4m</td>
<td>1350m</td>
<td>E, (Piper sp.)</td>
</tr>
<tr>
<td>bettina</td>
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<td>Species</td>
<td>Time</td>
<td>Range</td>
<td>Altitude</td>
<td>Habitat</td>
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<td>-------------------------</td>
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</tr>
<tr>
<td><em>Euselasia eucrates</em></td>
<td>0900-0930</td>
<td>3-4m</td>
<td>1350m</td>
<td>E, (Piper sp.)</td>
</tr>
<tr>
<td><em>Necyria zaneta</em></td>
<td>1130-1245</td>
<td>4-5m</td>
<td>1270m</td>
<td>R</td>
</tr>
<tr>
<td><em>Sarota chrysus</em></td>
<td>1440-1500</td>
<td>2m</td>
<td>1270</td>
<td>R</td>
</tr>
<tr>
<td><em>Sarota gamelia</em></td>
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<td>3-4m</td>
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<td>E, (Piper sp.)</td>
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<tr>
<td><em>Stichelia apoplecta</em></td>
<td>1300-1330</td>
<td>4-5m</td>
<td>1700</td>
<td>H, S</td>
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**Lycaenidae**

<table>
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<tr>
<td><em>Calycope xeneta</em></td>
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<td>2m</td>
<td>1270m</td>
<td>R</td>
</tr>
<tr>
<td><em>Cyanophrys pseudolongula</em></td>
<td>1400-1415</td>
<td>4-5m</td>
<td>1350-1400m</td>
<td>H, S</td>
</tr>
<tr>
<td><em>Lamprospilus nicetus</em></td>
<td>1230-1300</td>
<td>6-7m</td>
<td>1700m</td>
<td>H, S</td>
</tr>
<tr>
<td><em>Thecla balzabamba</em></td>
<td>1100-1430</td>
<td>6-8m</td>
<td>1700m</td>
<td>H, S</td>
</tr>
<tr>
<td><em>Thecla caninus</em></td>
<td>1500-1515</td>
<td>2m</td>
<td>1270m</td>
<td>R</td>
</tr>
<tr>
<td><em>Thecla danaus</em></td>
<td>1200-1350</td>
<td>6-8m</td>
<td>1550-1600m</td>
<td>T, E</td>
</tr>
<tr>
<td><em>Thecla eronos</em></td>
<td>1200-1400</td>
<td>4-5m</td>
<td>1700m</td>
<td>H, T, S</td>
</tr>
<tr>
<td><em>Thecla photismos</em></td>
<td>1130-1230</td>
<td>3-4m</td>
<td>1550-1600m</td>
<td>T, E</td>
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**Hesperiidae**

<table>
<thead>
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<th>Time</th>
<th>Range</th>
<th>Altitude</th>
<th>Habitat</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Astraptes fulgerator</em></td>
<td>1200-1300</td>
<td>6-8m</td>
<td>1550-1600m</td>
<td>T, E</td>
</tr>
<tr>
<td><em>Pyrrhopyge nr. phydias</em></td>
<td>1030-1300</td>
<td>2-5m</td>
<td>1700m</td>
<td>H, T, S</td>
</tr>
<tr>
<td><em>Urbanus proteus</em></td>
<td>0900-0930</td>
<td>3-4m</td>
<td>1350m</td>
<td>E, (Piper sp.)</td>
</tr>
<tr>
<td><em>Urbanus proteus</em></td>
<td>1230-1500</td>
<td>3-5m</td>
<td>1700m</td>
<td>H, T</td>
</tr>
</tbody>
</table>

*Habitat types (modified from Callaghan)
R. riverside gallery forest
E. forest edge, trail
C. forest canopy
S. sunfleck
T. treefall lightgap
H. hilltop
western Ecuador. Closer examination of our specimens, especially riodinids and satyrines, may lead to the identification of novel taxa endemic to western Ecuador (see Willmott and Hall 1994, Balint and Johnson 1994, 1995), as may further surveys at higher elevations within the MTR.

Altitudinal stratification of related insect species has been described for passalid beetles on Guatemalan volcanos (MacVean and Schuster 1981) and satyrine (Pronophilini) butterflies from cloud forests, bamboo thickets and páramo in the Andes of Colombia (Adams and Bernard 1977, 1979, Adams 1986) and Venezuela (Adams and Bernard 1981). The altitudinal transect found within the MTR (1270-2800m) is appropriate for such an endeavor. Our preliminary results show some interesting patterns of altitudinal distribution among related species of Taygetis, Caligo and Pteronymia, but these results should be viewed with caution, considering that species absence over such narrow elevational bands (50-200m) are likely to be an artifact of habitat heterogeneity or disturbance on a small spatial scale. One such example is the case of Leptophobia caesia, which is absent below 1400m at MTR but abundant at 670m at Tinailandia. We found a large number of pronophiline satyrines at MTR, but genera such as Lymanopoda, Pedaliodes (+ Penrosada and Stereomnia) and Pronophila may have been underrepresented in our survey due to our inability to thoroughly sample the bamboo zone from 1800-1900m and the páramo near the higher summits within MTR. Species richness and altitudinal zonation among these genera are greatest above 2000m in Colombia, Venezuela and probably in Ecuador; thus Adams and Bernard’s zonation hypothesis cannot be appropriately tested for the pronophilines of the northwest Ecuadorean Andes with our data set.

Most of the butterfly species that we collected in traps baited with rotting fruit were charaxines or satyrines, and thus were similar taxonomically to those species collected using comparable methods in Costa Rica (DeVries 1988), Brazil (Austin and Riley 1995), Malaysia (Corbet 1942, Corbet and Riley 1956), Kenya (Van Someren 1963, Larsen 1991) and Australia (Common and Waterhouse 1972). The importance of using non-floral attractants to more fully sample tropical butterfly faunas has been discussed amply by Owen (1971), DeVries (1987), Brown (1991), Larsen (1991), Raguso and Llorente (1991), Lamas et al. (1993) and many others. The variety of empirically tested attractants described by Corbet (1942), van Someren (1963), Owen (1971) and Austin and Riley (1995) and detailed in Table 3 hints at the diversity of nutrient sources utilized by tropical butterflies.

Perching behavior in butterflies has been defined by various workers (Scott 1974, Callaghan 1982, Rutowski et al. 1991) as the occupation and defense of a specific site (often by males on tree trunks or vegetation), from which passing butterflies are accosted (defensive sorties) and to which the occupant repeatedly returns. The importance of perching to reproductive isolation has been investigated for numerous nymphalid and riodinid butterflies (Callaghan 1982, Brown and Alcock 1991, Rutowski 1991, Rutowski et al. 1991). Our observations of butterfly perching suggest that the “sit and wait” strategy of mate location (Alcock 1984, Rutowski 1991) is fairly common
among many MTR butterflies, that subsets of these species show different habitat preferences (e.g. riparian vs. hilltop perch sites) and that different individuals of the same species (e.g. *Thecla danaus*) exhibit variation in perch height and microhabitat choice at different elevations.

Vertical zonation of butterflies has been discussed with reference to different “mimicry rings” (Papageorgis 1975, Llorente and Garces 1983, Burd 1994) and foraging patterns of fruit-feeding butterflies (DeVries 1988). Vertical stratification also may occur among species that engage in hilltopping behavior as a mating strategy when the hilltops are covered with forest (Turner 1990). Studies of other insects (scarab and tiger beetles) suggest that resource partitioning among related species with similar habits or trophic requirements could occur through vertical stratification of perching (and foraging; Howden and Nealis 1978, Pearson and Anderson 1985). In this context, the potential for vertical stratification among perching *Adelpha rothschildi* (4-7m), *A. colada* (6-10m) and *A. serpa* (8-15m) in low canopy sites (1500-1600m) along hillsides at MTR deserves further examination.

In conclusion, we have presented observational and distributional data for 220 species of butterfly found from 1270 to 1900m at the Maquipucuna Tropical Reserve in western Ecuador. This list of species represents a seasonally, regionally and elevationally biased subset of the true butterfly fauna that inhabits the MTR’s rainforests between Nanegal and Calacalí, a fauna comprised of both coastal (tropical) and Andean (temperate) elements. We urge Ecuadorian researchers and visiting lepidopterists to extend these surveys beyond the cloud forest into the bamboo zone, páramo and less-disturbed forests in the southern end of the Reserve and to sample throughout the year. It is our hope that this communication will serve as a point of departure for further research, observation and conservation of the butterflies of MTR.

Acknowledgements. We are most grateful to Rebeca Justicia and Rodrigo Ontaneda for their enthusiastic support during all phases of work in Ecuador and to Bernardo Castro, Luis Eduardo Pozo and Simon Uren for their assistance in the field. Dr. Grady Webster provided plant identifications and numerous helpful suggestions in the field. We thank Dr. Diego Bastidas for access to the collections of the Museo Ecuatoriano de Ciencias Naturales and Drs. Phil DeVries, Sherry Graves, Don Harvey, Gerardo Lamas, Jim Miller, Bob Robbins, Art Shapiro, Peggy Stern and Richard Vane-Wright for specimen identification, encouragement and stimulating discussions about Ecuador’s butterflies. We are grateful to Brian Harris, Ron Leushner and Don Strasburg for generously sharing their unpublished data from Tinalandia and to Greg Kareofelas and Carol Witham for sharing their observations and species list from Pululahua Crater. Finally, we thank the Diego Cordovez family for their kind hospitality in Quito.

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Appendix 1. Preliminary Checklist of the butterflies of the Maquipucuna Field Station, Pichincha Province, ECUADOR

<table>
<thead>
<tr>
<th>Butterfly Species</th>
<th>Elevation (m)</th>
<th>Habitat Types</th>
<th>Dates² Observed</th>
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<tbody>
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<td><strong>Papilionidae:</strong></td>
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<tr>
<td><em>(5)</em></td>
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<td></td>
<td></td>
</tr>
<tr>
<td><em>Eurytides protesilaus</em></td>
<td>1270</td>
<td>M,R</td>
<td>5</td>
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<tr>
<td>Linnaeus B</td>
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<td></td>
<td></td>
</tr>
<tr>
<td><em>(T) Papilio anchisiades</em> Esper</td>
<td>1270</td>
<td>R</td>
<td>8,11,12</td>
</tr>
<tr>
<td><em>(P,T) Papilio thoas nealces</em> Rothschild and Jordan</td>
<td>1270-1300</td>
<td>M,R,C</td>
<td>8,9,11,12</td>
</tr>
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<td>Parides erithalion Boisduval</td>
<td>1270</td>
<td>R,C</td>
<td>8,9</td>
</tr>
<tr>
<td><em>(T) Parides iphidamus</em> Fabricius</td>
<td>1270-1300</td>
<td>R,D</td>
<td>11,12</td>
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<td><strong>Pieridae:</strong></td>
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<tr>
<td><em>(21)</em></td>
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<tr>
<td><em>Anteos clorinde</em> Godart *</td>
<td>1700</td>
<td>C</td>
<td>12</td>
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<tr>
<td><em>(T) Archonias tereas archidona</em> Fruhstorfer</td>
<td>1270</td>
<td>R,M</td>
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<tr>
<td><em>Catasticta susiana</em> Hopffer</td>
<td>1540</td>
<td>L</td>
<td>8</td>
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<tr>
<td><em>Dismorphia lelex</em> Hewitson</td>
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<td>D</td>
<td>8,9,11,12</td>
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<td><em>Dismorphia medora</em> Doubleday</td>
<td>1450-1685</td>
<td>D,L</td>
<td>8,10,11,12</td>
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<tr>
<td><em>Dismorphia (Leienix) nemesis</em> Latreille</td>
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<td>8</td>
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<td><em>(T) Dismorphia theucarilla</em> Doubleday</td>
<td>1350-1400</td>
<td>D,M</td>
<td>12</td>
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<tr>
<td><em>Dismorphia zathoe othoe</em> Hewitson</td>
<td>1300-1450</td>
<td>D,L</td>
<td>11,12</td>
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<tr>
<td><em>Enantia melite</em> Linnaeus</td>
<td>1310</td>
<td>M,R</td>
<td>8,11,12</td>
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<td><em>(T)</em> Eurema reticulata* Butler</td>
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<td>R,D</td>
<td>8,11</td>
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<tr>
<td><em>(P,T)</em> Eurema xanthochlora* Kollar</td>
<td>1270-1600</td>
<td>M,L</td>
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<td><em>Eurema sp.</em> 3</td>
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<td><em>(T)</em> Gluthoprissa drusilla Cramer</td>
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<td><em>Leodonta dysoni</em> Doubleday</td>
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<td><em>(T)</em> Leptophobia caesia* Lucas</td>
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<td><em>(P)</em> Leptophobia eleusis* Lucas</td>
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<td><em>(T)</em> Leptophobia tovaria* Felder</td>
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<td><em>(T)</em> Phoebis argante* Fabricius</td>
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<td><em>Phoebis rurina</em> Felder *</td>
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<td><em>(T)</em> Phoebis sennae marcellina* Cramer</td>
<td>1270</td>
<td>R</td>
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Nymphalidae: (116)

Heliconiinae

Altinote alcione Hewitson 1270-1550 R,L 8,11
(P) Altinote equatoria Bates 1270-1300 M,C 10,11,12
(P,T) Altinote ozomene Godart 1270-1550 R,M,L 8,10,11,12
(T) Dione junon Cramer 1270-1300 R,M 8
(P,T) Dione moneta butleri Stichel 1270-1300 R,M 8
(T) Dryas iulia Fabricius 1270-1320 R,M,C 8,11,12
Eueides emsleyi Brown 1550 L 12
Eueides procula (= edias) 1270 R,M 8

Heliconius athis Doubleday 1270 R,C 8,10
Heliconius clysonymus 1510-1700 D,L 8-12
Latreille

Heliconius melpomene 1400 M 11
Linnaeus

Heliconius sapho eleuchia 1270-1300 R,C,L 8,10,11,12
Hewitson

Nymphalinae

(T) Anartia amathea Linnaeus 1270-1300 M 8-12
Anthanassa ardyis Hewitson 1300 M 8
(T) Anthanassa drusilla Felder 1350 M,L 12
Eresia alsina Hewitson 1540 L 8
Eresia carme Doubleday 1600 L 12
(T) Eresia casiphia Hewitson 1550 L 11,12
Hypanartia dione Latreille 1270 L 10
Hypanartia kefersteinii 1270-1550 R,L,C 8,12

Doubleday

Hypanartia thea Fabricius 1270-1600 R,L,C 8,10,11,12
(P,T) Junonia evarete Cramer 1270-1320 M 8-12
Pycina zamba Doubleday 1270 L 11
(T) Siproeta epaphus Latreille 1270-1400 M,C 8,9,11,12
(T) Tegosa anietta Hewitson 1270-1400 M,L 8,10,11,12
(P) Vanessa virginensis Drury 1450-1500 M 8,9

Limenitidinae

Adelpha colada 1400-1550 L,C 8,11,12
(T) Adelpha cytheria Linnaeus 1270-1350 R,M 8,10,11,12
Adelpha irmina Doubleday 1570-1590 L,C 8
Adelpha justina Felder 1580 L,C 10
Adelpha melanthe spruceana Bates
Adelpha sp. aff. phylaca Bates
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<td><em>Adelpha serpa</em> Boisduval</td>
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<td><em>Adelpha sp. aff. valentina</em></td>
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<tr>
<td><strong>(T) Adelpha serpa</strong> Boisduval</td>
<td>1560</td>
<td><em>L,C</em></td>
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<td><strong>(T) Adelpha sp. aff. valentina</strong></td>
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<td><em>R,C</em></td>
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<td><strong>(T) Catonephele chromis</strong></td>
<td>1500</td>
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<td><strong>(T) Diaethria marchalii</strong> Guérin</td>
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<td><em>Diaethria neglecta</em> (f. nystographa)</td>
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<td><em>Epiphile epicaste</em> Hewitson</td>
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<td><em>Epiphile orea</em></td>
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<td><em>Hamadryas amphinome</em> Linnaeus*</td>
<td>1650</td>
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<td><strong>(T) Historis odius</strong> Fabricius</td>
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<td><strong>(T) Marpesia chiron</strong> Fabricius</td>
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<td><strong>(T) Marpesia coresia</strong> Godart</td>
<td>1270-1560</td>
<td><em>R,L</em></td>
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<td><strong>(T) Marpesia corinna</strong> Latreille</td>
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<td><em>Perisama euriclia</em> Doubleday</td>
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<td><em>Perisama humboldtii</em></td>
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<td>(= <em>rhodoptera</em>) Guérin</td>
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<td><em>Perisama opellii</em> Latreille</td>
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<td><em>Perisama vaninka</em> Hewitson</td>
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<td><em>Perisama vitringa</em> Hewitson</td>
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<td><strong>(T) Smyrna blomfildia</strong> Fabricius</td>
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**Charaxinae**

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<td><em>Archaeoprepona</em> (Noreppa) chromus Guérin</td>
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<td><em>Archaeoprepona</em> demophon muson</td>
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<td><strong>(T) Archaeoprepona demophon andicola</strong></td>
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<td><em>Archaeoprepona meander</em> Cramer</td>
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<td><em>Fountainea nessus</em> Latreille</td>
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<td><em>Memphis austria</em> Comstock</td>
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<td><em>Memphis morvus</em> Fabricius</td>
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<td>Fruhstorfer *</td>
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<td><em>Siderone</em> sp. *</td>
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**Morphinae**

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<td><em>Opsiphanes quiteria</em> angostura Bristow</td>
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<td>Satyrinae</td>
<td><em>Chloreuptychia arnaea</em></td>
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<td><em>Cithaerias menander</em> Drury</td>
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<td><em>Corades enyo</em> Hewitson</td>
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<td><em>Corades pannonia</em> Hewitson</td>
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<td><em>Eretris apuleja</em> (= subrufuscens?) Felder</td>
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<td><em>Euptychia benedicta</em> Butler</td>
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<td><em>Euptychia harmonica</em> Butler</td>
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<td><em>Euptychia inornata</em> Felder</td>
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<td><em>Euptychia obscura</em> Butler</td>
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<td><em>Megeuptychia antonoe</em> Cramer</td>
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<td><em>Mygona irrina</em> Doubleday</td>
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<td><em>Oressinoma typhla</em> Doubleday</td>
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<td><em>Pedaliodes sp. 3</em></td>
<td>1550-1810</td>
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Pedaliodes sp. 4 1550-1860 D,L,B 8,10,11,12
(P) Pronophila orcus Latreille 1350-1700 L,C 8-12
(T) Taygetis andromeda Cramer 1480-1550 D,L 8,9,10,11
Taygetis lineata Godman and Salvin
Taygetis puritana Weeks 1625-1750 D,B 8,9

Danainae
(P,T) Danaus plexippus 1270-1350 R,M 8,11,12
megaliipe Hübner *

Ithomiinae
Dircenna adina Hewitson 1300-1660 D,L 8
Eutresis hyperia Doubleday and Hewitson

(T) Greta andromica Hewitson 1300-1700 D 8,11,12
Greta dirctitis Doubleday and Hewitson
Hypoleria riafarthi Haensch 1300-1400 D 11,12

(T) Ithomia cleora Hewitson 1400 D 11,12
Ithomia terra Hewitson 1450-1550 D,L 8,11,12
(T) Mechanitis menapis mantineus Hewitson
(T) Miraleria cymothoe Hewitson 1300-1500 D 11,12
Oleria victorina Guérin 1300-1700 D,L,M 8-12
Patricia dercyllidas 1640-1900 D 8-12
Hewitson
Pteronymia parva Salvin 1270-1510 D,L 8,10,11,12
Pteronymia zerlina Hewitson 1460-1900 D 8,10
Tithorea harmonica Cramer 1400 D 11,12

Lycaenidae: (17)
Arawacus leucogyna Felder 1270 R 8
Calycopis xeneta Hewitson 1270 R 11
Contrafacia marmoris Druce 1700 L 11
Cyanophrys pseudolongula
Clench
Lamprospilus nicetus Felder 1700-1890 D,L 10,12

(P) Micandra aegides Felder 1560 L 8
Strymon bazochii Godart 1270 R 11
(P) Thecla balzabamba Goodson 1700 L 12
Thecla caninius Druce 1270 R 11
(P) Thecla danaus Felder 1550-1700 L 11,12
Thecla eronos Druce 1550 L 11
Thecla monica Hewitson 1460 D 8
Thecla photismos Druce 1550 L 12
Theda upupa Druce 1540 L 8
Theda sp. (auda gr.) 1520 L 8
Theritas mavors Hubner 1620-1660 L 8
(T) Zizula sp. 1270-1300 M 8-12

Riodinidae: (21)
(T) Charis iris Staudinger 1270-1350 R,M 11,12
(T) Emesis cypria Felder 1270-1550 R,M 8,10,11,12
Emesis tenedia Felder 1270-1580 R,M 8-10
(T) Emesis ocyphore Hübner 1350-1700 R,D,L 11,12
(T) Euselasia bettina Hewitson 1270-1350 L 8,11,12
Euselasia eucrates Hewitson 1270-1350 L 8,11,12
Hermathena candidata Hewitson 1610 D 8
Leucochimona lagora
Herrich-Schaffer 1270-1570 R,L 8,11,12
Mesosemia asa Hewitson 1550-1740 D,L 10,12
Mesosemia mancia Hewitson 1550 L 12
Mesosemia mevania Hewitson 1640-1880 L 10
Mesosemia sp. 4 1600 L 12
Napaea theages Godman and Salvin 1400-1650 D,L 11,12
Napaea nr. merula Thième 1520-1660 D 8,10
Necyria zaneta Hewitson 1270 R 8
Necyria sp. 2 1270 R 8
(T) Sarota nr. chrysus Cramer 1270 R 11
Sarota nr. gamelia Godman and Salvin 1350-1560 L 8,11
Siseme aristoteles
saturata Thième 1270 R 8
Stichelia apoplecta Bates 1580-1700 L 11,12
Symmachia probator Stoll 1350-1700 M,L 12

Hesperiidae: (40)
Pyrrhopiginae
Pyrrhopyge sp. aff. phidias Linnaeus 1350 L 11

Pyrginae
(T) Achlyodes pallida Felder 1300-1530 M,L 8,10
Astraptes alardus Stoll 1610-1660 D,L 8
Astraptes fulgerator azul Reakirt
Autochton sp. aff. neis Hübner 1270-1580 R,L 8,10,12
(T) Carrhene unifasciata Felder 1270-1700 R,M,L 11,12
Cyclosaemia phidyle Godman and Salvin 1870  B  10
Dion rubrinota Druce 1400  L  12
Ebrietas badia Plötz 1270  R  8
Entheus dius Mabille 1700  L  11
Entheus matho Godman and Salvin 1600  D,L  8
Eracon sp. 1600  D,L  8
Goniurus talus Cramer 1620  L  10
(T) Heliopetes sp. 1270-1330  R,M  10-12
(T) Lento epictetus Fabricius 1350  M  12
Metrocles sp. 1890  B  10
Ouleus fredericus 1270-1500  R,D  8,11,12
hilarina Mabille
Phocides thermus Mabille 1270  R,M  8,11
(P) Pyrgus olieus Linnaeus 1270-1360  R,M  8-12
Pythonides menedemus (?) 1280-1320  M  10
Pythonides paterculus 1550  L  12
Herrich-Schaffer
Serdis sp. 1550  L  8,12
(T) Spathelepa clonius Cramer 1540  L  8
Theagenes albiplaga Felder 1360-1470  M  8,10
Thracides sp. 1510  L  10
Urbanus dorantes Stoll 1300  M  8
Urbanus sp. aff. 1270  M  10
euricles Latreille
Urbanus proteus Linnaeus 1500-1700  L  8,11,12
(T) Urbanus teleus Hübner 1270  R  8,11,12
Xeniaeides orchamus Cramer 1270  R  8
(T) Xenophasen tryxus Cramer 1270-1560  M,L  8,10,11
Zera tetrastigma Godman and Salvin 1640  D  8

Hesperiinae
(T) Apaustas gracilis Felder 1270-1600  R,L  8-12
Callimormus alsimo 1270  R  11
Möscher *
(T) Enosis sp. 1270  R  8
(P) Vettias coryna Hewitson 1540-1660  D  8,10,12
+ 4 unidentified species

Total: 220 species of butterflies

Number of species per family listed in parentheses.
1. Habitat types: R = riverside gallery forest, M = meadow or disturbed open trail, D = Deep mature forest understory, L = forest light gap, B = bamboo (Chusquea) above 1700 m.

2. Dates observed: 8 = August, 9 = September, 10 = October, 11 = November, 12 = December. Note: observations were limited due to heavy rains in late Sept./early Oct. 1989. Observations during other months are described in text.

* indicates a sight record.

B: collected by Sr. Ernesto Burriones at Maquipucuna

(T) indicates species also present at Tinalandia resort, near Santo Domingo de los Colorados, Pichincha Province (670-700m); data from B. Harris, R. Leushner, D. Strasburg (unpublished), Shaw and Shaw (1987), Emmel and Drummond (1988).

(P) indicates species also present at Pululahua Crater, between Calacalí and San Isidro, Pichincha Province (2500-3000m); unpublished data from G. Kareofelas and C. Witham.
Postembryonic study on the development of the female efferent genital system in the lemon-butterfly, *Papilio demoleus* L. (Lepidoptera)


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**Abstract.** Development of the female efferent genital system was studied during the larval-pupal transformation in the lemon-butterfly, *Papilio demoleus*. Two pairs of genital histoblasts (imaginal discs) — a pair each in the 8th and 9th abdominal segments of the 5th (ultimate) instar larva — are the precursors of this system. These histoblasts fuse to form a composite elongate structure, the parent body, which by late larval stage produces rudiments of the various components of the system: the oviduct, bursa copulatrix, spermatheca, vagina and accessory glands. These rudiments grow and differentiate into their definitive (adult) forms and sizes during the first 4 of the 6-7 day pupal life. While the external opening of the parent body on the 9th abdominal segment becomes the primary gonopore or the ovipore, the secondary (functional) gonopore or the ostium bursae develops *de novo* as an invagination on the 8th abdominal sternum that meets the bursal rudiment above, possibly by mutual growth of the two. The bursal rudiment subsequently gets detached from the parent body except in the mid-posterior region where it retains its connection with the former. This connection later elongates to give rise to the adult seminal duct. By day 4 of the pupal stage, the adult efferent genital system is fully formed.

**Key Words:** female efferent genital system, development, *Papilio demoleus*

**Introduction**

Development of the efferent genital system in female Lepidoptera has been studied by several workers (Jackson, 1889; Verson and Bisson, 1895; Du Bois, 1931; Dodson, 1937; Ammann, 1954; Brunold, 1957; Srivastava and Srivastava, 1959; Wittig, 1960; Joubert, 1964; Leclercq-Smekens, 1976; Sethi and Dhillon, 1981). However, details and timings of the development of various components of the system, particularly those of the bursa copulatrix, its detachment from the parent body and formation of two separate gonopores are largely lacking. We have attempted to throw some light on these aspects in the following paper.

**Materials and Methods**

Young larval stages of *P. demoleus* were collected from the field and raised in a BOD

Paper submitted 19 November 1993; revised manuscript accepted 23 February 1995.
incubator at 28 ± 1 °C, 75-80 per cent RH and 16 hr photophase. Newly moulted 5th (ultimate) instar larvae were sorted from culture jars with different ages of the instar under study reckoned from moult. The 5th instar lasts for 5 days inclusive of a one day prepupal stage followed by a 6-7 day pupal stage. Observations on the development of the efferent genital system were carried out from day 2 of the 5th instar larva to day 4 of the pupal stage; at which time all components of this system are fully formed. Insects of the desired ages were dissected in insect Ringer (Ephrussi and Beadle, 1935) which was then replaced by Bouin’s fluid for better visibility after clearing unwanted tissues from around the developing organs. For histological study, the tissues were routinely processed and cut at 7 and 5μm respectively and double stained in haematoxylin and eosin.

Fig. 1. Diagrams of the stages in the development of the EGS in *Papilio demoleus*. Details in the text.
RESULTS

Development during the larval stage

The development of the female efferent genital system (EGS) in *P. demoleus* begins with two pairs of rounded ectodermal invaginations, the genital histoblasts (GH = imaginal discs), a pair in each of the 8 and 9th abdominal segments close to the posterior margins of the respective sternum (Figs. 1a-c and 2). Being invaginations, each histoblast has its own lumen and external opening underlaid by the old larval cuticle (Figs. 1a-c, 3 and 4). Changes in these structures commence in day 4 larva when the intrasegmental histoblasts, which are separated in earlier instars, are drawn closer in order to fuse with each other, possibly due to shrinkage of the segments. Following fusion, the cavities and external openings of the histoblasts are reduced to one in each pair (Fig. 1b). On day 5, further fusion also occurs between the (previously) fused intersegmental histoblasts of the 8th and 9th segments, giving rise to a composite elongate structure named here as the parent body (= genital pouch of Leclercq-Smekens, 1976, Figs. 1c and 5). The parent body has a single cavity and a single external opening that constitutes the primary gonopore, the ovipore of the adult female (Fig. 1c, also Fig. 7). The parent body hereafter starts sending out rudiments of the various components of the EGS. In the middle-aged (12 hr) prepupa, rudiments of the oviduct (ODR) and bursa copulatrix (BCR) are produced from the anterior-half of the parent body while those of the vagina (VGR) and accessory glands (AGR), from the posterior-half (Fig. 1d). The rudiment of the oviduct is in the form of a tube projecting anterior to the bursal rudiment and occupying the anterior-third of the parent body, that of the bursa copulatrix, in the form of a rounded body dorsal to the former, that of the vagina, in the form of an oblong tube behind the oviduct accessory gland rudiments, in the form of two posteriorly directed and inwardly curved arms at the end of the vaginal rudiment. In the late (24 hr) prepupa, a longitudinal groove appears medially on the dorsal surface of the oviduct rudiment and a finger-like spermathecal rudiment (SPR) behind the bursal rudiment (Fig. 1). Appearance of the spermathecal rudiment completes the formation of all the precursors of the EGS.

Development during the pupal stage

In the newly emerged (0 hr) pupa, the groove on the surface of the oviduct rudiment sinks deeper to split it into two ectodermal components of the definitive lateral oviducts (LOD), as well as to demarcate the rudiment of the common oviduct (CODR) behind them (Figs. 1f and 6). The ectodermal LOD subsequently join their pre-existing mesodermal counter parts (not shown in the figures) to produce the LOD of the adult. By 12 hr pupal stage, the accessory gland rudiment produces a short duct (RDR) from its basal part (Fig. 1g). At 25 hr this structure is differentiated into three definitive parts namely, the reservoir duct (RD), reservoir (RES) and accessory glands (AG) (Fig. 1h). During the same period, an invagination occurs on the 8th
abdominal segment that grows upwards to meet the COD rudiment on its ventral aspect. The external opening of the invagination becomes the secondary (functional) gonopore, the ostium bursae (OB) and its upper passage, the ductus bursae (DB) (Figs. 1h and 7). By 36 hr pupal stage, the bursal and ductus components meet, possibly by mutual growth toward each other, at the same time retaining their connections with the COD (Fig. 8). In the same stage, a small proximal outgrowth from the spermathecal rudiment marks out the lagena (LAG) and the utriculus (UT). The anterior end of the utriculus subsequently elongates and differentiates into a considerably long (and convoluted) spermathecal gland (SPG) of the adult during the remainder of the developmental period (Figs. 1i-l). By 48 hr pupal stage, the bursa with its ductus starts detaching itself from the COD part of the parent body while leaving the middle region of the latter still connected. This connected portion represents the future seminal duct (SD) (Fig. 1j, Fig. 8). Hereafter, all rudiments grow and differentiate only to acquire their adult forms and sizes so that by day 4 of the pupal stage, the EGS of the adult is fully developed (Fig. 1k, 1l and Fig. 10).

**Discussion**

Despite development of the female EGS in Lepidoptera having been a subject of several studies, its descriptions and interpretations have differed with different workers. Jackson (1889) derived the median oviduct (or COD) component of the system in *Vanessa* from an unpaired median longitudinal groove, while Dodson (1937) derived the same in *Zygaena* in three parts: an anterior, from the fused posterior ends of the larval (mesodermal) LOD; a median, from a ventral ectodermal groove; and a posterior, from a thickened ectodermal band. All three subsequently joined to a bursal rudiment to produce the definitive COD. Srivastava and Srivastava (1959), on the other hand, derived the entire system in *Leucinodes* from two unpaired median invaginations present on the 8th and 9th abdominal segments which they called uterine and spermathecal rudiments respectively. However, what they called paired ectodermal longitudinal grooves on these segments, and interpreted as the remnants of gonapophyses, most probably represent the imaginal discs of other workers according to Matsuda (1976). Most other workers, however, derive the EGS from imaginal discs rather than from longitudinal grooves. The number of these discs has varied from two pairs present on the 8th and 9th abdominal segments (Verson and Bisson, 1896; Du Bois, 1931; Wittig, 1960; Leclercq-Smekens, 1976) and three pairs present in the 7-9 segments (Ammann, 1954; Brunold, 1957). Ammann (1954) in *Solenobia* reported that the discs of the 7th segment fuse to become an unpaired genital passage, the common oviduct (COD), while other components of the EGS namely, the bursa copulatrix and spermatheca, are produced from the 8th segment, and vagina and accessory glands by the 9th segmental discs after they formed a dorsoventrally superposed cavities. In *Papilio*, which lacks the 7th segmental discs, all components of the EGS
Fig. 2. WM (whole mount) of the genital histoblasts in the 8th and 9th abdominal segments of the 5th instar larva. x 60

Fig. 3 and 4. Sections through the anterior (Fig. 3) and posterior (Fig. 4) histoblasts showing their lumens and external openings underlaid by the old larval cuticle. x 50

Fig. 5. WM of the parent body in the process of formation by fusion of the histoblasts in the early prepupa. x 100

Fig. 6 WM of the parent body of 12 hr pupa with its rudiments and split in the LOD rudiment. x 100

Fig. 7 Sagittal section showing formation of the ostium bursae and ductus bursae with ovpore at the end of the parent body in 24 hr pupa. x 50

Fig. 8 WM of the EGS in 36 hr pupa showing union of the bursal and ductus rudiments with the attachment to the parent body still continuing. x 100

Fig. 9 WM of the EGS in 48 hr pupa showing detachment of the bursa copulatrix from the parent body (COD part) with the future seminal duct region still attached. x 25

Fig. 10 The fully developed EGS in a 4 day old pupa. x 16

Abbreviations used in the figures
AG accessory glands
AGR accessory gland rudiment
BC bursa copulatrix
BCR bursa copulatrix rudiment
COD common oviduct
CODR common oviduct rudiment
DB ductus bursae
GHA anterior genital histoblasts
GHP posterior genital histoblasts
ISM intersegmental membrane
LAG lagena
LC old larval cuticle
LPB lumen of the parent body
LOD lateral oviduct (ectodermal part)
OB ostium bursae
ODR oviduct rudiment
OVP ovipor
PB parent body
RD reservoir duct
RDR reservoir duct rudiment
RES reservoir
SD seminal duct
SDR seminal duct rudiment
SL split line
SPG spermathecal gland
SP spermathecal rudiment
UT utriculus
VG vagina
VGR vaginal rudiment
including the COD are derived from the 8th and 9th segmental discs albeit after their fusion into a parent body that does not permit identification of the specific discs of origin, as in Solenobia. Another feature in which Solenobia differs is in possessing a purely mesodermal LOD which in Papilio are partly ectodermal (basal parts) and partly mesodermal (distal parts).

More striking differences in the development of the EGS, however, were reported by Leclercq-Smekens (1976) in Euproctis chrysorhea. The imaginal discs in this insect were not only shown to differ morphologically in the 8th and 9th abdominal segments, but also in the right and left discs of the 8th segment itself. In Papilio the discs are all spherical and identical. Further, the components of the EGS in Euproctis arise from the imaginal discs themselves prior to their fusion, while in Papilio this occurs after all the discs have fused to form a common parent body. Furthermore, a thickened genital area, producing the precursor to the oviduct, and located between the 8th and 9th abdominal segments in Euproctis, is lacking in Papilio. A feature about which most workers seem to differ is the origin of the two genital pores, the ovipore and the ostium bursae. While Srivastava and Srivastava (1959) note that in Lecucinodes these structures exist from the very beginning of the larval stage, Brunold (1957) in Solenobia and Leclercq-Smekens (1976) in Euproctis describe their formation by partition of a single genital passage and opening. In Papilio, however, the external opening of the parent body constitutes the ovipore with the ostium bursae formed de novo from an invagination occurring on the 8th abdominal sternum, meeting the rudiment of the bursa copulatrix above most likely by mutual growth of the two toward each other. In the process the ductus bursae is formed (see Figs. 7 and 9). Photographic evidence of the developmental events of EGS, as presented in this paper, have not been presented heretofore.

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Literature Cited


Butterflies of the Andaman and Nicobar Islands: Conservation Concerns

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Abstract. The insular butterfly fauna of the Andaman and Nicobar Islands has a high degree of endemism (50% at the subspecies level). It shows high biogeographical affinity to both Indo-Myanmar and Indo-Malayan fauna. The endemics are generally rare taxa that inhabit specialized niches in some islands and should be regarded as vulnerable to extinction or extirpation in the near future. The complete fauna includes, with recent records, 236 taxa recorded to date. Only 50% of the total taxa have been found in recent years, since 1985. Following independence, several different development activities have come into play that have degraded the environment of these islands and caused widespread negative effects on their fauna. Several current programs put into place by the Indian Government include agriculture, agroforestry, forest-based industries and tourism. These programs pose immediate threats not only to the irreplaceable endemic butterflies, but to most other components of the endemic biota, not the least of which are forest landscapes. There is an urgent need to conserve and preserve the biodiversity in butterflies and to immediately implement monitoring schemes to both evaluate their present status and their dynamics over time. Thus far government action has included declaration of a biosphere reserve, designation of National Parks and Sanctuaries, and implementation of the Wildlife Protection Act 1972. These actions do not appear effective in checking the degradation of most butterfly species and the natural resources upon which they are dependent. Additional measures are required to counter human impacts and to conserve the critical habitats in order to circumvent mass extinction of many endemics from these biogeographically rich islands.

Key Words: Andaman and Nicobar Islands, Butterflies, Lepidoptera, Rhopalocera, Development, Deforestation, Endemcity, Biodiversity, Conservation Biology.

Introduction

The Andaman and Nicobar islands prehistorically carried one of the richest tropical humid forest areas of India. In contrast to continental India with its dense human populations extending back for millennia, the islands remained in pristine condition until 1788. More than 1500 species of flowering plants with an attendant diverse and rich habitat for butterflies were characteristic. About 301 plant species are endemic. The region should be included with the Western Ghats and Sri Lanka as one of the major biodiversity "hotspots" of the globe (Myers, 1990). With arrival of the penal settlement in 1858, the closed ecosystem experienced its first major human

Paper submitted 14 April 1994; revised manuscript accepted 23 March 1996.
Table 1. Rare (R), very rare (VR) and straggler (S) species of the Andaman and Nicobar islands.

<table>
<thead>
<tr>
<th>Family</th>
<th>Subfamily</th>
<th>Andamans</th>
<th>Nicobars</th>
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</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td>R</td>
<td>VR</td>
</tr>
<tr>
<td>Papilionidae</td>
<td></td>
<td>3</td>
<td>2</td>
</tr>
<tr>
<td>Pieridae</td>
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<td>1</td>
</tr>
<tr>
<td></td>
<td>Amathusinae</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>Satyrinae</td>
<td>2</td>
<td>-</td>
</tr>
<tr>
<td>Hesperiidae</td>
<td></td>
<td>19</td>
<td>2</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td></td>
<td>52</td>
<td>13</td>
</tr>
</tbody>
</table>

The impact with a slowly expanding population in the decades following. The magnitude of impacts gradually intensified beginning in 1941 when convicts along with repatriates from Myanmar, Sri Lanka and Bangladesh were settled in these islands. During the post-independence period from 1947 onward, ex-service men and more refugees from West Bengal, South India, and Sri Lanka brought about further habitat degeneration. The settlers were allotted land for homes and agriculture, but they illegally encroached upon surrounding land, clearing forests for revenue and growing cash crops. Environmental degradation accelerated with the implementation of development schemes on several islands. Recent plans to further expand agroforestry, agriculture, forest-based industries and tourism pose irreversible threats to the fauna and flora of these islands.

The butterfly fauna of the Andaman and Nicobar Islands is insular with its origins in the faunas of the Indo-Myanmar and Indo-Malayan regions. The Andaman elements have their closest affinities to Myanmar and mainland elements whereas the Nicobar elements appear most closely related to Malayan elements. The long isolation of these islands from the Asian continent, if the islands indeed ever had a continental connection, and their until recently undisturbed ecology provided optimal conditions for the evolution of many local and endemic taxa. Evans (1932) described 260 forms, followed by Ferrar (1951) who described 268 forms from these islands. There are 214 species and 236 subspecies in 116 genera belonging to five families and three subfamilies. More than 50% of the taxa are endemic to these islands. Many endemic taxa in each family are rare, very rare, or stragglers (Table 1). (Since these taxa are not included in Schedule I, II, or III of the Indian Wildlife Protection Act, they can not be assigned “threatened” or “endangered” status.)

Continuing development of the islands causes habitat destruction through deforestation, with correlative decreases predicted in population viability of the butterfly fauna. Because of host specificity of many butterflies, they are
unable to adapt to ecologic changes that include hostplant loss below critical levels. A number of species of the islands may already be extinct as a result of habitat destruction during the past fifty years. This paper represents an attempt to analyze factors threatening the butterfly fauna by comparing and compiling the past and recent available literature and recent observations.

**Study area**

The archipelago of the Andaman and Nicobar islands stretches over 800 km in the Bay of Bengal. It comprises 572 islands, reefs and rocks, but only 38 islands are inhabited, of which 12 are in the Nicobars. The islands lie between 6°5′–13°30′ N and 92°20′–93°56′ E with a total geographical area of 8249 sq km. The Andaman islands are separated from the Nicobars by a channel of 155 km known as Ten Degree Channel. There is active volcanism with major eruptions on Barren island in 1991 and 1994. A map of the region is given as Figures 1 and 2.

**CLIMATE**

The Andaman and Nicobar Islands have a warm, humid, tropical climate. There are two monsoons, a main one from May to October and a second shorter one in December-January. Average annual rainfall is 300 cm with June and July the months of heaviest rainfall. The temperature ranges from 16°C to 34°C and relative humidity from 60 to 99%. The climatic conditions exemplify those described by Walter (1973) for evergreen tropical rain forest. A monthly chart of rainfall and maximum/minimum temperature is given as Figure 3.

**ZOOGEOGRAPHY**

Zoogeographically the butterfly fauna of the islands can be classified into six major groups: 1) wide ranging fauna, 2) similar to Myanmar fauna, 3) similar to Malayan fauna, 4) fauna common to the Andamans and Nicobars, 5) endemic to the Andamans, and 6) endemic to the Nicobars. Wide ranging taxa which show affinities with Indian mainland elements form 10% of the total fauna and are rare in these islands. Half the taxa are endemic to these islands (Table 2) and 20% of the species are common to both groups of islands. The remaining taxa show similarities with Myanmar and Malayan elements.

**IMPACTS**

There have been direct and indirect ecological consequences of island development as a consequence of both planned and unplanned activities. Deforestation directly destroyed habitat, but indirect long term effects include establishment of monoculture forests with their attendant loss of general biodiversity and establishment of weedy species that have complex effects along the entire natural community. Replacement of native forest with cash crops have the same, but perhaps not so severe, effect since for the
Fig. 1  Map showing location of Andaman and Nicobar islands in relation to India, Malaysia and Indonesia.

Fig. 2  Map of the Andaman and Nicobar Islands
Table 2. Endemic subspecies of the Andaman and Nicobar islands.

<table>
<thead>
<tr>
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<th>Nicobars</th>
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<td>-</td>
</tr>
<tr>
<td></td>
<td>Sayrinae</td>
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<tr>
<td>Hesperiidae</td>
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<td>Total</td>
<td></td>
<td>170</td>
<td>109</td>
<td>13</td>
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</table>

Table 3. New records of butterflies during the last decade from the Andaman and Nicobar islands.

<table>
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<th>Family</th>
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<th>Andamans</th>
<th>Nicobars</th>
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<tr>
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<tr>
<td></td>
<td>Amathusiinae</td>
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<td>Hesperiidae</td>
<td></td>
<td>1</td>
<td>-</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>20</td>
<td>10</td>
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</tbody>
</table>

most part these are small landholdings with some residual diversity. Pesticide use for both insect and plant control under all human centered activity is a negative impact.

Tourism, augmented by general increase in continental traffic, provides dispersal routes for many exotic invasive plants and animals that may further alter natural communities. Effects of exotic invaders around the world has had serious consequences on natural biodiversity and the effect can be expected to only get worse without strict control.

Observations on butterfly populations

Ferrar (1951) mentioned that areas remained completely or partially unstudied to his time. No butterfly surveys had been made on Narcondam, Barren Islands, the Brothers, the Sisters and in the Nicobars, Bomboka. A partial survey was made on the Cocos, North Sentinel, Little Andaman, and in the Nicobars, Tillanchong. The statement is still true for these islands.
Fig. 3  Climate diagram (after Walter, 1973) for Port Blair, Andaman Islands. Base on ten year data. Highest and lowest mean monthly temperature records are 32.2° C and 21.4° C.

Thus we have no data on how many butterflies were incinerated on Barren Island during the 1991 and 1994 eruptions when all but about 10% of the vegetation was covered.

On the Little Andaman, distinct local races of *Euploea andamanensis* and *Parthenos sylvia* were recorded by Ferrar (1951), but these have not been sighted since, possibly a consequence of habitat destruction by the 16 sq km area of Red Oil Palm plantation.

*Appias albina darda* have declined greatly in numbers. These butterflies were recorded as abundant in 1923 by Ferrar in the Middle and South Andamans, but are now rare. Similarly, *Atella p. phanthas*warmed in uncountable numbers during 1923-1927, overcasting the sky and flying from Ross Island to Mount Harriet in a northwest direction in April-May (Ferrar, 1951), but no more than 10 butterflies can be sighted together today (Khatri 1991).

*Jamides kankena pseudepis* and *Eurema andersoni andamana*, common to Bomlungta in December from 1923-1931 (Ferrar, 1951), have become extremely rare in Middle Andaman. *Byasa sambilanga, Neptis jumba binghami,*
N. ebusa, N. nar, Artipe erylx and Doleschallia celinde continentalis never have been recorded since the type specimens. Similarly Polyura schreiber tisamenus is no longer extant. Additional taxa may have been affected over the past 60 years.

Some taxa inhabit extremely small areas, e.g., the common Heliophorus epicles and the rare Artipe erylx, were found at Bomlungta, Middle Andaman, but have not been collected during recent surveys. The Malayan Hypolimnas antilope anomala, known only from a small locality in Car Nicobar, is very rare and coconut plantations threaten its existence in the island. The status of Danaus affinis malayana, confined to central Nicobars, is unknown.

The common butterflies of the mainland such as Danaus chrysippus, Lampides boeticus and Appias libytha alferna are very rare in the Andamans, but do occur regularly.

Habitat destruction

Evans (1932) mentioned that during his visit in 1931 the best localities in the Andamans for butterflies were Webi, reached from Stewart south (Bonington) in North Andaman; Bomlungta in the Middle Andaman; Mount Harriet, Ariel Creek and Austinabad forest in the South Andaman; and Bumila and Ingoi in the Little Andaman. In the Nicobars Evans especially noted Sawi and Arug in Car Nicobar, Pulo Milo and the opposite coast in Little Nicobar, Kondul off Great Nicobar (an outstanding collecting area), and Pulo Babi, the Alexandra River and a few other localities in Great Nicobar.

These localities are presently no longer productive for butterfly collecting. Diglipur in the North Andaman has been extensively cleared for cultivating vegetables and cash crops, with active wood extraction taking place without control from the reserve forest. Bomlungta in Middle Andaman has also been impacted by agriculture. Two forest-based industries extract wood from this area with the completion of an access road having facilitated the process. Cane industries have accelerated the destruction of this area further. The second largest population settlement at Rangat and Maya Bunder in Middle Andaman consumes a substantial area of the forest every year. Regeneration of the forest is poor in these areas. Evidence to date indicates that loss of primary forest is irreversible.

The situation is much worse in South Andaman. Mount Harriet, formerly reported to be rich habitat for many lycaenids and hesperiids, no longer provides good habitat for these butterflies. Large areas are under coconut cultivation, especially the foothills at South Bay. Austinabad forest has been totally cleared for commercial gain. Brichganj is occupied by a military base. Ferrar (1951) mentioned that these two places were the best collecting localities in South Andaman. Rangachang and Maimyo have also lost their surrounding virgin forest. A large plywood factory at Port Blair consumes a major area of forest every year. Extension of the airport for tourist development is a recent development that has destroyed habitat and has indirect impacts on all natural areas by permitting massive secondary effects from
trampling and further demands for high level consumerism. The recently opened Grand Trunk Road across South Andaman, connecting to Middle Andaman, has exposed further virgin forest for extraction of wood, especially bamboo forest. The scarcity of fresh water for both local and temporary populations compelled the government to construct dams that submerged forest areas. Neil and Havelock Islands are fully under cultivation.

Little Andaman has experienced its most serious ecological degradation in the north and at Hut Bay. Among the chief factors responsible for the disaster are the Red Oil Palm Plantation (16 sq km with plans to extend up to 96 sq km), construction of a dam at R. K. Puram, and farming, including sugar cane and coffee plantations, and wood-based industries at Hut Bay.

Sawi Bay and Arug in Car Nicobar are under coconut plantations while Katchal in the Middle Nicobars has rubber and coconut plantations. Although Great Nicobar has been declared a Biosphere Reserve the environment remains under unending human population pressure. The declaration of Great Nicobar as a free port and the construction of an air base and runway has further damaged the ecology of the island. Thus biodiversity at all levels is suffering from both small piecemeal and larger scale losses with nothing being replaced or allowed to regenerate.

It is clear that if the present trend of clearing and development continues, whatever fauna now remains will either become extinct or highly localized and endangered. At present, sixty years after the first comprehensive reports, the existence of many butterfly taxa is threatened due to the destruction of habitats. During this period, no attempt has been made to study the food plants, ecology, or life history of any of the endemic butterfly taxa (Ferrar 1951). Such studies are essential aspects for even the most rudimentary planning for their conservation needs. The same state of affairs undoubtedly applies to all other invertebrate taxa for which butterflies are but an indicator species.

Recent Trend of Fauna.

Out of 236 taxa 118 have been recorded in recent years (since 1985). New records of the past ten years are presented in Table 3. These data indicate an influx of more widespread taxa as exotic intruders. In Papilionidae these include Troides helena cerberus, Papilio polytes romulus, P. d. demoleus, Pachliota a. aristolochia, P. a. ceylonica; and in Pieridae Delias hyparete indica, Eurema l. laeta and others (Arora and Nandi 1980 and 1982; Khatri and Singh 1988; Khatri and Mitra 1989 a, b; Khatri 1991, 1992).

The fauna elements of the Andamans are mixing with the Nicobar elements and vice versa; e.g., Graphium agamemnon pulo and Pachliopta aristolochia sawi, known earlier from the Nicobars, are new records for the South Andamans (Khatri and Singh 1988), and Eurema l. laeta, Cepora nerrisa depha and Gandaca harina nicobarica from the Nicobars have also spread to the Andamans (Khatri and Mitra 1989b). On the other hand Catopsilia c. crocale and Cepora nandina andamana, hitherto not recorded from the Nicobars,
have recently been found. The mixing of faunal elements most likely indicates anthrogenic effects.

**Indian Government Action**

In an attempt to conserve its formerly rich fauna, the Indian Government passed the Wildlife Protection Act of 1972, published Schedule I and II of endangered species, and imposed a total ban on international trade in Indian butterflies. About 350 species are included in the Red Data Book, but the butterflies of the Bay Islands are not included among these schedules. Specimen collection has been almost universally discredited, however, as having any other than superficial impact on insect populations and serves only to divert attention from habitat destruction that is the ultimate cause of the preponderance of the current mass extinction event.

Another step to protect the flora and fauna was the declaration of National Parks Sanctuaries and the Biosphere Reserve in the Andaman and Nicobar islands. There are five National Parks in the Andamans (Mount Harriet, Saddle Peak, Middle Button Island, North Button Island and South Button Island) and none in the Nicobars although Great Nicobar was designated as biosphere reserve in 1989. However, evaluation of the present status of endemic butterflies, demographics, bionomics and community process have not been undertaken, and there have been no monitoring schemes put in place either by government or by private organizations. There is an urgent need to assess the present fate of the butterflies with special attention to rare and very rare endemic taxa. The meager measures taken by the government are insufficient to check faunal loss from these islands.

**Acknowledgments.** Financial assistance of U. G. C., New Delhi greatly assisted this work. Suggestions of two anonymous reviewers greatly improved an original manuscript.

**Literature Cited**


Khatri, T. C. 1991. On some Nymphalidae (Rhopalocera: Lepidoptera) from the Andaman and Nicobar Islands. *Islands on March* 3: 82-94.
Table 4. A list of the butterflies (Rhopalocera: Lepidoptera) from Andaman and Nicobar islands.

<table>
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<th>Andamans</th>
<th>Nicobars</th>
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<td><em>Chilasa clyto flavolimbatus</em> Oberthur</td>
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</tr>
<tr>
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</tr>
<tr>
<td><em>decoratus</em> Rothschild</td>
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<td>+</td>
</tr>
<tr>
<td><em>pulo</em> Evans</td>
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<td>+</td>
</tr>
<tr>
<td><em>antipathes epaminondas</em> Oberthur</td>
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<tr>
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</tr>
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<tr>
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<tr>
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<td><em>lichenosa</em> Moore</td>
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**Lycaenidae**

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<td>Zeltus etolus</td>
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Zizeeria kansandra Moore 0 –
Zizina otis otis Fabricius + +
Zizula gaika Trimen + +

Riodinidae
Abisara echerius bifasciata W-M & de Niceville + –

Nymphalidae
Amathusia phidippus andamanensis Fruhs. + –
Atella alcippe andamana Fruhs. + –
fratera Moore – 0
Athyma nefte rufula de Niceville o –
Cethosia bisbis andamana Stichel + –
nicobarica F. +
Charaxes bernardus agna Moore o –
Cirrochroa fasciata F. 0 –
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Cupha erymanthis andamanica Moore + –
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Cyrestis cocles formosa F. + –
tabula de Niceville – 0
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nesippus F. – +
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bumila Evans – 0
camorta Moore – +
scherzeri F. – +
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crameri esperi F. – 0
frauenfeldii F. – 0
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midamus chloe Guerin – 0
roepstrophi Corbet 0 –
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Herona marathus andamana Moore 0 –
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<td>hylas andamansana Moore</td>
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<tr>
<td>nicobarica Moore</td>
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<tr>
<td>sambilanga Evans</td>
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<tr>
<td>jumbah amorosca Frus.</td>
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<tr>
<td>bingham Frus.</td>
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<tr>
<td>nandina clinia Moore</td>
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<tr>
<td>sankara nar de Niceville</td>
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<tr>
<td>soma mananda Moore</td>
<td>+</td>
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<tr>
<td>Orsotrioena medus medus Fabricius</td>
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<tr>
<td>nicobarica Evans</td>
<td>-</td>
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<tr>
<td>ryneka Moore</td>
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<td>Pantoporia hordonia cnacalis Hewitson</td>
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<td>Parantica aglea agleoides F.</td>
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<td>melanoleuca Moore</td>
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<td>melaneus platenistson Frus.</td>
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<tr>
<td>nilgiriensis Moore</td>
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<td>Parthenos sylvia roepstorffii Moore</td>
<td>+</td>
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<tr>
<td>nila Evans</td>
<td>-</td>
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<td>Phalanta phalanta phalanta Drury</td>
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<tr>
<td>Polyura athamas andamanicus Frus.</td>
<td>o</td>
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<tr>
<td>schreiber tisamenus Frus.</td>
<td>-</td>
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<tr>
<td>Precis almana almana L.</td>
<td>+</td>
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<tr>
<td>nicobariensis F.</td>
<td>-</td>
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<td>atlites L.</td>
<td>+</td>
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<tr>
<td>hierta magna Evans</td>
<td>+</td>
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<tr>
<td>orithya ocyle Hubner</td>
<td>-</td>
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<tr>
<td>Radena similis nicobarica W-M &amp; de Niceville</td>
<td>-</td>
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<tr>
<td>Tirumala gautama gautamoides Doherty</td>
<td>o</td>
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<tr>
<td>limniace exoticus Gmelin</td>
<td>+</td>
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<tr>
<td>septentronis septentronis Butler</td>
<td>+</td>
</tr>
<tr>
<td>Vanessa cardui cardui L.</td>
<td>+</td>
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<tr>
<td>Vindula erotica pallida Staudinger</td>
<td>+</td>
</tr>
<tr>
<td>Yoma sabina vasuki Doherty</td>
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</table>
### Hesperiidae

**Asictopterus jama permagnus** Fruhs. o -  
**Badamia exclamationis** Fabricius + 0  
**Baoris cahira cahira** Moore 0 0  
**oceia scopulifera** Moore + -  
**Bibasis amara** Moore o -  
  **sena sena** Moore o -  
**Borbo cinnara** Wallengren + 0  
**Calaeorrhinus andamanica** W-M & de Niceville o -  
  **leucocera leucocera** Kollar o -  
**Cephehes palmarum nicobarica** Evans - 0  
**Cupitha purreea** Moore o -  
**Daimio bhagava andamanica** W-M & de Niceville o +  
**Erionota thrax acroleuca** Moore + 0  
**Gangara thyasis yasodara** Fruhs. + -  
**Hasora badra badra** Moore o -  
  **chromus chromus** Fabricius (= alexis) - 0  
  **leucocpora parnia** Fruhs. - 0  
  **salanga** Moore - 0  
  **taminatus almea** Swinhoe - 0  
  **malayana** F. o -  
  **vitta vitta** Butler o -  
**Hyarotis adrastus praba** Moore + -  
**Ismene harisa harisa** Moore 0 -  
  **jaina astigmanta** Evans 0 -  
**Matapa aria aria** Moore o -  
  **druna** Moore + -  
  **shalgrama** Moore o -  
**Notocrypta curvispica** F. + -  
  **paralysos paralysos** W-M & de Niceville o -  
**Oriens gola gola** Moore + -  
**Paduka lebadea andamanica** W-M & de Niceville o -  
**Pelopidas conjuncta javana** Mabille o 0  
  **mathias mathias** Fabricius + -  
  **sp. new to Andamans** + -  
**Potanthus maesooides ottalina** Evans + -  
  **serina serina** F. o -  
  **tropica nina** Evans + -  
**Sarangesa dasahara dasahara** Moore o -  
**Suastus rama aditus** Moore o -  
**Tagiades atticus helferi** F. - +  
  **ravina** Fruhs. + 0  
  **litigiosa andamanica** Evans o -  
  **obscurus alicia** Moore + 0  
**Zographeos ogygia andamana** Evans o -  

**Legend:**  
W-M Wood-Manson  
+ Present in most recent survey  
- Absent in most recent survey  
O Present initially; not recorded after Evans (1932) and Ferrar (1951); currently believed extinct
Book Reviews

P. APOLLO - SEINE UNTERARTEN. Helmut Glassl. 1993. Published by the author: H. Glassl, Schwalbenweg 5, D-91096 Möhrendorf, Germany. 214 pages, 10 maps, paperback. 29.7 x 21.1 cm, ca. 130,-DM.

This is one of those works which are written and produced as a true one-man enterprise with enormous enthusiasm by a most dedicated author. The result is a quite beautiful and well made book devoted entirely to the most popular European, if not palaeartic, butterfly, *Parnassius apollo*, the “Apollo,” and its considerable geographic and individual variation.

The naming and classification of all the variations in “apollo” wing pattern has been the heart of many amateur and professional European lepidopterists’ activities for a long time, and this book follows well within that tradition. The largest part of Glassl’s monograph is devoted to the enumeration of 278 named subspecies and some 192 individual forms and aberrations of *P. apollo*. Each of these taxa is characterized by a brief diagnosis, and, in the case of subspecies, the bibliographic reference of the original description, the type locality, and some information about its geographic range are given. A brief general section provides an introduction to the species’ biology and its present distribution in the light of having been influenced by the ice ages. An alphabetic index of all the subspecies and forms mentioned in the text concludes the volume.

The book is entirely written in German and contains no summary in any other language. The geographic arrangement of the subspecies and 10 large, detailed color-printed maps which indicate the distribution of all the subspecies will help the reader unfamiliar with German to make good use of the book. In addition, more than 40 color photographs interspersed in the text illustrate live specimens of different taxa and some characteristic habitats from different parts of the species’ range. All the illustrations are of excellent quality, and in terms of printing, layout, and quality of reproduction, the book certainly meets very high standards.

In terms of its scientific content, however, the book could have gained much by just a little professional editing. This apparent lack of professional advice is evident in several definite shortcomings such as the omission of authors mentioned (and in one case even cited!) in the text from the literature citations (e.g., p. 13: Ackery, Sabariego & Aragones, Storace, Verity), and an apparent unfamiliarity with certain rules and principles of the International Code of Zoological Nomenclature. In the introduction (p. 8), for example, the family name is given as “Parnassiinae,” and in several instances the principle of priority has not been followed, e.g., in one case (p. 74) an older available subspecific name is synonymized with a younger one on the ground that the type locality of the former taxon had not been fully indicated in the original description, and in the case of two subspecific names published in the same year it is maintained that the rule of priority could not be applied and the taxon with the larger range is accepted as the senior name (p. 102). Further criticisms concern the many inconsistencies in the citations of the original descriptions and the bibliography, where the references are often abbreviated in an unfamiliar fashion and volume and page numbers are frequently not stated. A number of relevant publications have apparently not been considered (e.g., Dabrowski, J. S. 1986. Atala
10-12:34; Janzon, L. A. 1990. Entomologist’s Gazette 41:81-83; Rusti, D. M. & Dragomirescu, L. 1991. Travaux du Muséum d’Histoire Naturelle Grigore Antipa 31:261-218; Wagener, S. 1977. Nota lepidopterologica 1:23-37, and at least one published name has been missed (ssp. fabrei Rouget, 1980) - which is hardly a shame considering the high number of available names for this butterfly. Finally, although the book is explicitly not intended as a revision, about 60 names are listed as synonyms of other subspecies, often without any reason being given for doing so.

In short, the book stands, and will hold its own, in a long tradition of classical European “parnassiological” studies. This largely typological approach, however, might no longer be up to date at a time when already a dozen of the named Central European subspecies have become extinct and P. apollo is a prime target for conservation efforts in many European countries and states. Still, this beautifully illustrated book can and will achieve its aim to draw attention to a truly fascinating butterfly.

Christoph L. Häuser, Staatliches Museum für Naturkunde, Rosenstein 1, D-70191 Stuttgart, Germany.


Namibia (formerly Southwest Africa) is a large country in southern Africa with a coastline along the Atlantic Ocean. Despite its large size, the saturniid fauna is somewhat depauperate due to the arid climate. The author Rolf Oberprieler, an entomologist in Pretoria, was a long-term resident of Namibia and has done an outstanding job of documenting the Saturniidae of this region. There are 25 species known from that country, plus three that are likely to occur there. The text for each species covers the basics, and on the facing page are color photographs of pinned adults and, in many cases, mature caterpillars. Photographs in introductory chapters show eggs, cocoons, young larvae, and live adults. The author is an accomplished photographer and the color reproduction of his photographs is good but not excellent. I did not find misspellings or typographical errors. The book is well-organized.

Oberprieler discusses the collecting history of the region, a discussion which is entirely eurectionic by necessity. He also gives brief discussions on the ecology, biology, and conservation of these moths. He then describes the ecosystems of Namibia as they relate to the distributions of the saturniids. Another introductory chapter deals with collecting, preservation, and rearing of specimens. The ideal reader of the book would be an amateur entomologist who is a resident of southern Africa. However, considering the worldwide popularity of these big moths and the literature about them, I am sure many copies will be sold outside of Africa. There is almost nothing available that is not out-of-print on the saturniids of Africa. Use these reasons plus the abundant color photographs to justify paying the price.

Richard S. Peigler, Denver Museum of Natural History, 2001 Colorado Blvd., Denver, CO 80205-5798
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Electronic submission: The Journal is now being produced via desktop publishing, allowing much shorter publication times. Although typewritten manuscripts are acceptable, those submitted on computer disk are highly preferred. After being notified of your paper’s acceptance, submit either a Macintosh or IBM disk (3.5 inch) version. Include on your disk both the fully formatted copy from your word processing program and a text-only (ASCII) copy. The preferred format for text is Microsoft Word, although translation utilities will allow conversion from most formats. Put returns only at the ends of paragraphs, not at the end of each line. Use one tab to indent each paragraph. Even if your printer is incapable of outputting italics, please specify italics rather than underline in your disk copy. Please note in your cover letter any special characters that are used in either the body of the text or the tables (e.g. ¨, ü, °, §, µ, δ, ϕ). All figures which are prepared on the computer should also be submitted electronically. Please include these figures in a standard interchange format such as EPS or TIFF.

Title material: All papers must include the title, author’s name, author’s address, and any titular reference and institutional approval reference. A family citation must be given in parenthesis (Lepidoptera: Hesperiidae) for referencing.

Abstracts and Short Papers: All papers exceeding three typed pages must be accompanied by an abstract of no more than 300 words. Neither an additional summary nor key words are required, although key words are recommended.

Name citations and Systematic Works: The first mention of any organism should include the full scientific name with unabbreviated author and year of description. There must be conformity to the current International Code of Zoological Nomenclature. We strongly urge depositing of types in major museums, all type depositories must be cited.

References: All citations in the text must be alphabetically listed under Literature Cited in the format given in recent issues. Abbreviations should not be used; write out the entire journal name. Do not underline or italicize periodicals. If four or less references are cited, please cite in body of text not in Literature Cited. For multiple citations by the same author(s), use six hyphens rather than repeating the author’s name.

Tables: When formulating tables, keep in mind that the final table will fill a maximum space of 11.5 by 19 cm either horizontally or vertically oriented. Number tables with Arabic numerals. When submitting tables on disk, use tabs between columns rather than multiple spaces.

Illustrations: Color can be submitted as either a transparency or print, the quality of which is critical. Black and white photographs should be submitted on glossy paper, and, as with line drawings, must be mounted on stiff white cardboard. Authors must plan on illustrations for reduction to page size. Allowance should be made for legends beneath, unless many consecutive pages are used. Drawings should be in India ink. Include a metric scale. Each figure should be cited and explained as such. Each illustration must be identified by author and title on the back. Indicate whether you want the illustration returned at your expense. Retain original illustrations until paper is accepted. Legends should be separately typed on pages entitled “Explanation of Figures.” Number legends consecutively with separate paragraph for each page of illustration.

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Catalog of Parasitoids of Saturniidae of the World

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2001 Colorado Boulevard, Denver, Colorado 80205-5798 U.S.A.

Abstract. Parasitoids known to attack Saturniidae, and hyperparasitoids reared from Saturniidae, are listed in taxonomic categories; about 350 species of parasitoids are recorded from about 175 species of Saturniidae. These include 105 Ichneumonidae, 21 Braconidae, 3 Trigonalyidae, 115 Tachinidae, 4 Sarcophagidae, 2 Pyralidae, as well as about 100 records for families of Chalcidoidea (Torymidae, Eurytomidae, Perilampidae, Pteromalidae, Chalcididae, Eupelmidae, Encyrtidae, Eulophidae, Trichogrammatidae) and Proctotrupoidea (Diapriidae, Scelionidae). The worldwide phorid Megaselia scalaris is occasionally reared from pupae of Saturniidae, but is not a true parasitoid. All records are documented with citations to literature or specific records, many previously unpublished. Nomenclature of parasitoids and hosts is updated as far as possible. An index to the hosts refers back to the taxonomic list of parasitoids, so that all known parasitoids for a particular host can readily be found. The catalog includes several new unpublished records of parasitoids in southern Africa supplied by Rolf G. Oberprieler of the Plant Protection Research Institute, Pretoria.

Key Words: Anastatus, Belvosia, Braconidae, Chalcidoidea, Cotesia, Diptera, Enicospilus, Eupelmidae, Exorista, Hymenoptera, hyperparasitoids, Ichneumonidae, Lepidoptera, Lespesia, moth, parasitism, Proctotrupoidea, Pyralidae, saturniid, Tachinidae

Introduction

The primary purpose of this catalog is to contribute toward understanding the ecology of saturniid moths and to assist the identification of those parasitoids that are reared from saturniids by hundreds of amateurs and professionals around the world. Moreover, I hope that this compilation will enable ecologists to make generalizations about the parasitoid and host groups, in spite of the fact that it is only as complete as was possible by surveying literature and a few institutional collections, collecting in the field myself, and asking colleagues to send me parasitoids. More parasitoids are probably known from Saturniidae than any other family of insects, except the extensive family Noctuidae of which many are economic pests. No previous author has attempted to catalog all known parasitoids of Saturniidae of the world, except a brief preliminary list given by Packard (1914).

There are over 1500 known species of Saturniidae. This catalog gives parasitoid records for only about 175 species of Saturniidae. Specific parasitoids are recorded to attack almost all of the saturniids of Japan, North America and Europe, but comparatively few records are known for all other

Paper submitted 5 February 1996; revised manuscript accepted 15 March 1996.
regions. Yet the vast majority of Saturniidae occur in the tropics, so it is clear that we have only begun to scratch the surface of the host-parasitoid-
hyperparasitoid relationships that exist. Recent studies by Coffelt & Schultz
(1992, 1993a, b) reveal that new parasitoid records await discovery even in
the eastern United States. Therefore, this catalog must be viewed as prelimi-
nary.

If lepidopterists who use this catalog will send me their new records, and
dipterists and hymenopterists will point out to me my oversights and errors,
I will endeavor to publish a supplement consisting of additions and corrections
in this same journal in about three to five years.

When a parasitoid is reared from a host insect, there is often little hope of
getting its name (and therefore learning more about its host range, distribu-
tion, and biology), unless one can send the specimen to a specialist in the
respective group of Hymenoptera or Diptera. Unfortunately, taxonomists
who work with Ichneumonidae, Tachinidae, etc., are frequently unable to
provide this identification service to any and all who request it, because large
numbers of requests can significantly interfere with research, teaching, or
curatorial responsibilities. The alternative is to try to find published keys,
descriptions, or figures of the parasitoid. Success on this front will depend on
the persistence and training of the person seeking an answer, as well as the
availability of a good entomological library at a nearby university or museum.
Library skills may be more important here than knowledge of insect mor-
phology. At the very least, a parasitoid should be pinned and labelled
properly and deposited in an institutional collection so that eventually its
identity and record will be published. This catalog provides minimal or no
descriptions of parasitoids, no keys, and only a few figures, yet should be
useful as a first step in obtaining an identification of a parasitoid that has
been reared from a saturniid, if the host species is known.

There are hundreds of published records of host-parasitoid associations
for the Saturniidae and their parasitoids. I have endeavored to cite most
current literature containing these records, but obviously there are some in
foreign or obscure journals of which I am not aware or could not obtain.
Historical literature is either cited here, or well covered in the bibliographies
of the major works cited, as for examples Arnaud (1978), Herting (1960),
approach has been to make use of as many catalogs and revisions available
in the parasitoid groups themselves, because those authors have already
surveyed collections and compiled records from earlier literature.

The parasitoids that have been reared and labelled with their host data and
deposited into major museum or university collections will generally have
been located and found by the dipterist or hymenopterist. I urge curators to
use a system of cross reference in their collections; whether the parasitoids
are kept in the collection with the host species or in their appropriate
phylogenetic location, labels should refer to the other place in the collec-
tion. In this way, researchers looking at the hosts or the parasitoids will find
labels directing them to the other part of the collection, and identities of
hosts can be verified. I believe that there are many parasitoid specimens representing unpublished records kept in Lepidoptera collections, private and institutional, for which the dipterist or hymenopterist does not have access or is not aware, sometimes even within the same institution.

This project is more than a mere compilation of records in literature. I have reared numerous parasitoids from Saturniidae, and specimens or records have been sent to me by lepidopterist colleagues. Some of these records were already published in the papers authored or coauthored by me as cited in the bibliography. Many host-parasitoid associations included in this catalog are previously unpublished. I also include data from rearings that increase our knowledge of the geographical distribution of the host-parasitoid relationship or the parasitoid itself. For example, if a parasitoid has been known for decades to attack a certain host in the northeastern United States based on numerous rearings, that same association discovered in the South or West is well worth documenting. Comments pertaining to certain parasitoids are included where bringing together information from diverse sources has hopefully provided me with a larger perspective than could be derived from the individual publications. For example, rearings of *Enicospilus lebophagus* from *Rothschildia lebeau* in southern Texas and Costa Rica in the 1980s (Gauld 1988a) enabled me to assume with confidence that the unidentified *Enicospilus* reared from the same host in El Salvador by Quezada (1967) must be the same parasitoid. It is frustrating to have to cite records like "*Chetogena* sp. reared from *Hemileuca* sp." where the specific identity of the host and parasitoid are not known, but I include such records because they at least contribute to the overall picture.

It may be surprising that it is still relatively easy to discover new parasitoid records for common and wide ranging saturniids such as *Antheraea polyphemus* or *Saturnia pavonia*. It is true that the Saturniidae are the most commonly reared insects in the world, but let us consider the mechanics of these rearings. When eggs are obtained in captivity, and the eggs, larvae, and pupae are kept indoors (or caged outdoors) throughout the rearing, there is minimal chance to secure parasitoids. A large proportion of the known parasitoids of Saturniidae emerged from host cocoons since this is the most common stage to be collected in the field. If more field work was carried out in which one would secure wild collected eggs and larvae, more records would be available. It often requires a lot of work—hours in the field—to find larvae and particularly eggs. It is much easier to collect females at light or obtain matings in cages of reared moths and rear from the resulting eggs. Likewise, more parasitoids are known for saturniids of which the cocoons are found attached to the hostplants than for those that pupate below ground or have cocoons at ground level well hidden in leaf litter. For genera that are commonly collected as larvae but rarely as pupae, such as *Hemileuca* and *Anisota*, we have few records for those parasitoids that oviposit into the host after it pupates.

Another problem that hinders our knowledge is the fact that many amateur lepidopterists are repulsed by the sight of slimy tachinid maggots,
or wasps which can sting, issuing from a cocoon that held the hope of a beautiful moth for the collection. Killing and discarding these parasitoids, instead of rearing them through (if immature) and pinning and labelling them, may fulfill a psychological need for revenge, but does not contribute to our knowledge of the ecology of the moth which the rearer claims to admire. I advocate here a change in perspective and attitude. Many advanced entomologists begin as amateur lepidopterists, but others do not advance beyond the collection-oriented phase, and in my opinion, deprive themselves of many interesting and rewarding facets of their hobby. Thus, another intended purpose of this catalog is to stimulate interest and professionalism among these amateurs to properly deal with and learn about any parasitoids that they may be fortunate enough to rear.

In my judgment, too many authors on Lepidoptera have paid insufficient attention to the subject of parasitism. Many papers have appeared in the past 20 years on various moths giving details on the hostplants, morphology of the immature stages, and other ecological observations, but make no mention of parasitoids. One can only assume that amid all of this collecting and rearing, parasitoids must have been obtained. Another example is the very brief and superficial discussion of parasitoids in the large volume on North American butterflies by Scott (1986), a book which is otherwise excellent in its scientific approach. Scott hardly gave any specific records of butterfly parasitoids, yet the book is promoted as having a focus on the biology of butterflies. By contrast, Powell (1962) cited a very high number of parasitoid records for Tortricinae based on only four years of collecting and rearing observations. A valuable chapter on parasitoids was provided by Stehr & Cook (1968) in their classic treatise of Nearctic Malacosoma (Lasiocampidae). The Saturniidae share many of the same parasitoids with the related Lasiocampidae (see below). Among the books available that deal with rearing Saturniidae, Gardiner (1982: 23-24) outlined good instructions for proceeding if parasitoids are obtained. Pinhey (1972), Villiard (1969), and Baxter (1992) gave brief comments indicating that parasitoids are merely something to avoid, and made no suggestions to pin, label, and submit them for identification. Voelschow (1902) referred to parasitoids under several different saturniids, but apparently none were identified. Collins & Weast (1961) devoted an entire chapter on parasitoids of saturniids, which has served well to stimulate interest in many beginners (including me in 1971). Some insect pathologists may be similarly frustrated with loss of data when saturniid larvae fall to diseases, although freezing diseased larvae and preserving pathogens is less easily accomplished than pinning parasitoids.

Many parasitoids of saturniids are named and long known to science but are not included in this catalog because they have never been reared from Saturniidae, or never reared at all. These specimens have been collected at light, on flowers, in malaise traps, or by other means. On the other hand, some parasitoids reared from Saturniidae are sometimes found to be unnamed, particularly tropical species. In any case, one should not automatically assume that a parasitoid obtained from a well known saturniid probably does not represent a new record. It often does.
The word parasite was used in earlier literature exclusively for these insects, and continues to be used today in lieu of the term parasitoid by some authors. The traditional definition of a parasite includes the point that it does not kill its host, but parasitoids almost invariably do cause the death of the host (but see English-Loeb et al. 1990). I have resisted the pressure to use the term parasitoid in most of my earlier publications, preferring instead to simply have a broader definition of the term parasite. However, I use the term parasitoid in this catalog since virtually all entomologists now use it consistently, and I assume the word has acquired a permanent and concise meaning in the entomological literature, and eventually will in the English language. The word hyperparasitoid is also used in this catalog, but I do not use words like parasitoidism and parasitoidic, instead of parasitism and parasitic.

The literature citations consist of a mixture of references on Saturniidae and various groups of Hymenoptera and Diptera. Authors of Lepidoptera literature sometimes did not use the current or correct names of the parasitoids. Authors who are dipterists or hymenopterists sometimes have used incorrect names for the host moths. All these I have corrected as far as could be determined. Therefore, I cite these synonyms of moths and parasitoids, but only those that appeared in the relevant literature, no attempt being made to give full synonymies of any species.

As far as is known, some parasitoid species are host-specific to only Saturniidae, indeed to only a single species of Saturniidae. Examples include species in *Gambrus* and *Enicospilus*. Other genera of parasitoids specialize on, but are not limited to saturniids, such as *Belvosia*. The specializations appear to be more ecological than taxonomic. For example, we might say that the saturniid genus *Agapema* suffers from "Hemileucinae envy" because it is ecologically more like many sympatric Hemileucinae than the Saturniinae, *Agapema* belonging to the latter subfamily taxonomically. For this reason, we find that some parasitoids among Ichneumonidae and Braconidae which routinely attack various hemileucines like *Hemileuca* and *Coloradia*, also attack species of *Agapema*. The reverse is true for *Automeris io* which lives throughout eastern North America and is ecologically more like Saturniinae, than to Hemileucinae to which it actually belongs.

The non-Saturniidae most frequently cited as hosts for the parasitoids commonly reared from saturniids belong to the Lasiocampidae. This does not mean that the two moth families are very closely allied, although most classifications place both in the Bombycoidea. I include within the Saturniidae the two Neotropical groups formerly considered full families, i.e., Cercophanidae and Oxytenidae (see Minet 1994). The host-parasitoid relationships shared by Saturniidae and Lasiocampidae exist because the two have similar ecological characteristics, i.e. hairy larvae feeding externally on foliage of woody plants, pupation in cocoons above ground level, living in the same ecosystems, etc. That the shared ecology is more significant than the shared taxonomy is further illustrated by the fact that some parasitoids (*Enicospilus, Lespesia*, etc.) that attack Saturniidae are closely allied to, or the
same as, the ones that attack certain Noctuidae, Lymantriidae, Notodontidae, and Arctiidae.

Our knowledge is based mainly on the Northern Hemisphere fauna, so we naturally compare North American and Eurasian records. We need more data from the tropics to make broader generalizations. There are certainly relationships between the Nearctic and Neotropical regions, such as *Enicospilus americanus* attacking *Rothschildia* in Argentina and other Saturniinae in the United States. Townes & Chiu (1970: 42, 51) and Gauld (1988a: 44) pointed out that some records of a single parasitoid species attacking both saturniids and lasiocampids can now be sorted into two closely allied parasitoid species, each specializing on one family of hosts; historical records were sometimes based on misidentifications. In the present catalog, I cite specific or general host ranges for all parasitoids to indicate whether the parasitoid is narrow or broad in its suite of hosts. Family names are cited for non-saturniid hosts, which are not listed individually in the index to hosts.

It would require too much space to cite data for all material examined or records in literature. However, under the “Remarks” sections of parasitoids, I give some specific data, since many of these are previously unpublished or represent significant range extensions of the host-parasitoid association. Deposition of these specimens is also given so that future workers can locate them and verify identifications. In the 1970s and 1980s I deposited many specimens in museums where entomologists worked who provided the identifications to me. Most of my recent material is in the Denver Museum of Natural History, with duplicates sometimes distributed to other collections. The acronyms used for the collections cited are:

BMNH - The Natural History Museum, London; formerly British Museum (Natural History)
CM - Carnegie Museum of Natural History, Pittsburgh
CNC - Canadian National Collection, Agriculture Canada, Ottawa
CSU - Colorado State University, Fort Collins
CUAC - Clemson University Arthropod Collection, Clemson
CUIC - Cornell University Insect Collection, Ithaca
DMNH - Denver Museum of Natural History, Denver
LACM - Natural History Museum of Los Angeles County, Los Angeles
RMNH - Nationaal Natuurhistorisch Museum, Leiden; formerly Rijksmuseum van Natuurlijke Historie
ROM - Royal Ontario Museum, Toronto
SDNHM - San Diego Natural History Museum, San Diego
TAMU - Texas A&M University, College Station
UCB - University of California, Berkeley
UCM - University of Colorado Museum, Boulder
USNM - National Museum of Natural History, Smithsonian Institution, Washington
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**Economic Value of Saturniidae**

Saturniids are admired and enjoyed by people throughout the world. Their aesthetic value is reflected in the large number of publications that has appeared about them, as well as depictions in art. Their popularity with collectors and for use in exhibits gives many of them a consistent market value as dried specimens. Although commercial collectors and dealers are increasingly maligned among the entomological and paleontological communities, I believe that they provide a valuable service. In the case of collecting of insects, this rarely has an impact on population decline, which is instead almost always due to habitat destruction. Creating and maintaining a market for insects contributes toward the incentive to protect their habitats, as many people in tropical countries are learning as they seek to fill a demand for preserved or living specimens, the latter for educational facilities commonly called butterfly houses or insect zoos. Along with swallowtail butterflies and giant scarab beetles, Saturniidae are part of the "charismatic megafauna" of the insect world. Some saturniids are mass-

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reared in laboratories for studies of diapause, endocrinology, or other aspects of insect physiology. Field and lab studies of Saturniidae enhance our general knowledge of genetics, evolution, and ecology.

Caterpillars of many saturniids are consumed as food by indigenous peoples in New Guinea and Africa. Some of these are Cirina forda, Lobobunaea, Pseudobunaea, and several species of Imbrasia. The best known is the "mopane worm," which is the larva of Imbrasia belina. These provide significant supplements to the protein in the diet of many people, but with increased habitat loss and exploding human populations, the caterpillars can no longer be regarded as a renewable resource. Larvae and pupae of some saturniids are also eaten by certain Native Americans and by some hill tribes in the Himalayas.

Exploitation of certain Saturniidae as sources of silk dates back many centuries in Asia. The main ones, both historically and today, are tusah silk (Antheraea pernyii) in China, tensan silk (A. yamamai) in Japan, and muga (A. assamensis), tasar (A. paphia), and eri (Samia ricini) silks in India. Millions of dollars annually are earned by export of these silks from China and India. Wild silk crops are more susceptible to economic loss from parasitism than domestic silk (Bombyx mori), which is mainly raised indoors. Parasitoids that are particularly troublesome to sericulture in Asia are the chalcidoid wasps attacking eggs of the wild silk moths and certain tachinid flies that attack the caterpillars.

There are relatively few records of Saturniidae being pests, and in these cases pest status is attained as a result of human interference of the natural ecosystem. (Of course, this is true of virtually all arthropod pests.) Although never agricultural pests, saturniids may cause damage in forestry, horticulture, and range grasslands. Anisota senatoria reaches pest status in the northeastern United States for one of the same reasons that the gypsy moth does: there is now an artificial dominance of oaks in those forests that did not previously exist. The Japanese Antheraea yamamai is a pest in southeastern Europe because it is introduced, yet the related Chinese A. pernyii introduced to the Balearic Islands of Spain is uncommon (V. Sarto i Monteyes, pers. comm.). In the high plateaus of New Mexico the "range caterpillar" (Hemileuca oliviae) reaches pest levels because of overgrazing by cattle. The insect is not a pest in the disjunct part of its range in Chihuahua to the south.

Fruit trees are sometimes damaged by saturniid caterpillars. Factors contributing to pest situations are urban environments (which lack fewer natural enemies), monocultures of trees, and cultivation of non-native trees. In Israel Saturnia pyri causes damage in orchards of Prunus such as almond and apricot. Shabtili hashaked, the common name of the moth in Hebrew, means "Saturn almond." Imbrasia tyrhea is recorded to damage fruit trees occasionally in South Africa. The "pine emperor" (Imbrasia cytherea) attacks pine, which is not native to, but widely grown in, South Africa. Larvae of Hylesia strip willows in Brazil and Argentina. Tropical fruit trees like avocado, citrus, star-fruit, guava, and others are attacked by Attacus in Indonesia, the Philippines, and mainland Southeast Asia.
Where saturniids are exploited as food or silk producers, parasitoids are highly detrimental. In situations where saturniids are pests, parasitoids are desirable. Virtually all Saturniidae serve as alternate hosts for certain parasitoids with broad host ranges that are valuable in the control other lepidopterous pests.

The Mechanics of Parasitism

Classic works on the topic of parasitic insects include those by Clausen (1940), Askew (1971), and Waage & Greathead (1986), the latter cited in the bibliography under Askew & Shaw. A book by Godfray (1994) is a magnificent synthesis on the ecology of insect parasitoids. The serious student would be well advised to consult any of these books or to take a course in biocontrol to become familiar with the terms and concepts of this fascinating topic. Many active research programs are underway worldwide, but much of the best work in this field comes from entomologists in England. Insight into the origins of parasitism by insects was outlined by Eggleton & Belshaw (1992).

Although the term co-evolution is widely misapplied, there may be true cases where some Saturniidae have co-evolved with certain of their parasitoids (see Timm 1983). Godfray (1994: 244-248, 349-350) discussed co-evolution between parasitoids and hosts from the physiological and ecological aspects, but applied the term co-cladogenesis to what I am writing about when I observe that allied species of *Enicospilus* in America and Asia attack allied host saturniids. It is tempting to assume that some parasitoids in Asia migrated across Beringia into America along with their hosts, for example.

In general, an insect parasitoid locates a host in one of its immature stages, deposits one or more eggs into or onto that potential host, and the larva or larvae of the parasitoid develop in or on the host, eventually killing it. Several terms need to be defined, since some lepidopterist users of this catalog will not be familiar with them.

**Multiparasitism**: more than one species of parasitoid lives within a host. One always wins out; adults of two parasitoids of different species are never produced in a single host individual. It is also called multiple parasitism.

**Superparasitism**: too many parasitoid individuals of a single species develop in a host, resulting in reduced size or even death of the parasitoids. This may be due to a female misjudging the number of eggs to deposit, or from one or more additional females depositing eggs into the same individual (see Hofsvang 1990).

**Synovigenic parasitoid**: an adult female emerges with a full complement of eggs and deposits all of them in a short time.

**Pro-ovigenic parasitoid**: an adult parasitoid female develops eggs over an extended period.

**Ovarian parasitoid**: a parasitoid of insect eggs. The complete metamorphosis occurs within, with an adult wasp emerging from the host egg.

**Ectoparasitoid**: feeds externally on (attached to) the host.

**Endoparasitoid**: feeds internally in the host.
gregarious parasitoid: more than one parasitoid emerges from a single host individual.
solitary parasitoid: one parasitoid emerges from a single host individual.
secondary parasitism: involves a hyperparasitoid; i.e., a parasitoid of a parasitoid, both living within the primary host.
tertiary parasitism: involves a parasitoid of a secondary parasitoid.
oblige hyperparasitoid: a parasitoid that must complete its life cycle within another parasitoid.
facultative hyperparasitoid: a parasitoid that can complete its life cycle as a primary parasitoid, or as a hyperparasitoid.
polyembryonic parasitoids: a single egg is deposited into a host and the resulting divisions give rise to many, sometimes hundreds, of parasitoid larvae.
larval-larval parasitoid: the egg is laid in the larva of the host, and the adult parasitoid emerges before the host pupates.
larval-pupal parasitoid: the egg is laid in the larva of the host, but the adult parasitoid does not emerge until after the host pupates. (In parasitoids that attack Lepidoptera, the adults always emerge before the adult moth develops.)

Two attack strategies provide a model to predict host range. Idiobionts usually kill or permanently paralyze the host at the time of oviposition. This category includes virtually all parasitoids that attack eggs and pupae, and selecting hosts in protected or concealed environments is an obvious advantage in avoiding predation and hyperparasitism. Most ectoparasitoids and some endoparasitoids are idiobionts. By contrast, koinobionts include most endoparasitoids, and they permit the host to continue to feed and grow. Most hyperparasitoids, probably all Tachinidae, and many genera of Hymenoptera are koinobionts. The koinobiont benefits from the continued life of its host, until a critical surge in its own development. Koinobionts in general have a narrower host range (Askew & Shaw 1986, Godfray 1994: 9, 338, 361-363).

Defenses by saturniids against parasitism are varied but limited. Eggs may be covered with scales or even urticating scales that the female rubs off her abdomen after deposition of eggs. Eggs may be covered by a hardened coating as in Malacosoma (Lasiocampidae), but this may not deter some parasitoids (see Janzen 1984). Pupae mainly rely on being concealed in soil or cocoons; I am not aware of any saturniid pupae with gin traps (Chinery 1989: 240). For larvae, camouflage is of no benefit against parasitoids which search at night or by odor. Caterpillars may physically thrash when attacked, drop to the ground (Stamp & Bowers 1990), or release toxic fluids (Demi & Dettner 1990). The white waxy powder on larvae of saturniid larvae of the tribe Attacini has been suggested to deter parasitoids, but I disagree. This wax more likely gives the larva the appearance of a patch of mold (Peigler 1989: 90), as it is present only in the middle instars of some species. A caterpillar may escape parasitization if the eggs of a tachinid deposited on the integument are lost if the larva molts before the eggs hatch (Collins &
Weast 1961). For this reason, many tachinids probably only oviposit on mature larvae. Stinging spines, as we see on caterpillars of Ludiinae, some Saturniini, and virtually all Hemileucinae are probably not effective deterrents against parasitoids.

Many papers appear in entomological journals every month with new data and conclusions on interactions between parasitoids and their hosts (e.g., Van Driesche et al. 1991, Takabayashi et al. 1991, and English-Loeb et al. 1993). Regarding Saturniidae, a few works stand out as providing insight into the complex ecological interactions that occur between saturniids and their suites of parasitoids and hyperparasitoids. Fiske & Thompson (1909) observed an array of host-parasitoid interactions in large Saturniinae in Massachusetts. Smith (1908), Marsh (1937), and Duncan (1941) studied populations of Hyalophora. Coffelt & Schultz (1992, 1993a, b) studied the dynamics of parasitism in pest populations of Anisota senatoria in Virginia.

**How to Use this Catalog**

All data are cited under the parasitoids, which are arranged in phylogenetic order as far as possible following the *Catalog of Hymenoptera in America north of Mexico* (Krombein et al. 1979), B. Herting's (1984) *Catalogue of Palearctic Tachinidae*, Z. Boucek's (1988) Australasian Chalcidoidea, and other works. Each host is listed under every parasitoid that is known to attack it, and hosts are listed alphabetically in the index, which will refer the user to all parasitoids for each host. Host moths are also listed as hosts under hyperparasitoids, because it is not always evident when a parasitoid is reared from the host remains of a saturniid that hyperparasitism was involved. Moreover, the hyperparasitoid ultimately derives it nourishment from the saturniid, although it can be argued that it benefits the saturniid population by killing the primary parasitoid. Also, some species of parasitoids occur in Saturniidae as both primary parasitoids and as facultative hyperparasitoids. Family names are cited for hosts which are not Saturniidae. These non-saturniid hosts are included to demonstrate how broad or narrow is the host range of the parasitoid.
HYMENOPTERA

Family Ichneumonidae

This is one of the largest families of insects, with thousands of species worldwide. There are numerous subfamilies, but the classification has not reached a stable consensus. All are parasitic on or in other insects. The mode of parasitization is varied: some are solitary, others gregarious; some are koinobionts, others idiobionts; larvae of some feed as ectoparasitoids, others as endoparasitoids; some attack exposed caterpillars or other insect larvae, others attack concealed larvae (borers, miners) or spiders’ eggsacs or insect pupae in cocoons or tunnels or soil. If the ovipositor of the female is retracted or very short, the host is generally exposed; if medium in length (i.e., 1 cm), the host is internally hidden, such as in a cocoon; if very long, we may assume the host tunnels deeply in wood. Thus, the adult insect gives a clue to its host. The females of many ichneumons inject venom (i.e., sting) if handled. Stinging is used to paralyze hosts temporarily or permanently at the time of oviposition. Some kinds are attracted to light, but most are diurnal. They are easily collected in malaise traps or by sweeping with nets. Although abundant in the tropics like most insect groups, they appear to be even more common in the northern forests (Janzen 1981; Godfray 1994: 357-360).

The late Dr. Henry Townes and his wife Dr. Marjorie Townes have been the most prolific publishers on this family, cataloging most known species of the world in their monographs. They founded the American Entomological Institute containing their famous collection of parasitic insects which was moved several years ago from Ann Arbor, Michigan, to Gainesville, Florida. The monumental catalog of North American species by Dr. Robert Carlson, formerly of the USNM, has proven indispensible for successful completion of the present catalog.

Ichneumonidae are widely studied because they are important agents of biological control of many groups of insects, including some agricultural, horticultural, and forest pests. We do not know the hosts for most species, because they have never been reared; instead the adults were taken at light or collected in nets or traps.

Subfamily Pimplinae

1. Pimpla robusta Rondani
   **Hosts:** Actias isabellae
   **Distribution:** Europe

2. Acropimpla persimilis (Ashmead)
   **Hosts:** Samia cynthia, Samia pryeri, various other Lepidoptera including Lasiocampidae and Tortricidae
   **Distribution:** Japan, Korea, eastern Russia, China, Kurile Islands
   **References:** Townes et al. (1965: 23-24), Arzone (1970)

3. Iseropus himalayensis (Cameron)
   **Hosts:** Samia pryeri, Samia cynthia, Archaeoattacus edwardsii, Antheraea roylei, several Lasiocampidae, Bombycidae, and other Lepidoptera
   **Distribution:** Japan, Korea, China, India (Kashmir to Assam), probably also other southeastern Asian countries.
   **Biology:** The parasitoid larvae are gregarious, and spin their cocoons within that of the host. The host is attacked in the pupal stage. Species of hosts that are attacked have exposed cocoons.
Remarks: Townes et al. placed this species in the genus Gregopimpla, but Gupta considered Gregopimpla to be a subgenus of Iseropus. The species of *Samia* that serve as hosts cannot be decided without locality data; if the record for *Samia cynthia* comes from India instead of China, it should be referred to *Samia canningii*. This is possibly the parasitoid of which the cocoons within a cocoon of *Antheraea roylei* were shown by Cotes (1891-1893: pl. 9) (see also remarks under *Gambrus polyphemis* below). This parasitoid was cited by several authors including Arzone under the name *Pimpla attaci*.

4. *Scambus hispae* (Harris)
Hosts: *Dryocampa rubicunda*, several other lepidopterans including Tortricidae, Psychidae, Noctuidae, Lasiocampidae, and hyperparasitic on other Ichneumonidae
Distribution: Nova Scotia to Alaska to California
References: Carlson (1979: 324)

5. *Echthromorpha agrestoria variegata* (Brullé)
Hosts: *Imbrasia wahlbergii*, *Heteronymgia dissimilis* (Lymantriidae)
Distribution: most of sub-Saharan Africa
Biology: The pupa is the stage of the host from which the parasitoid emerges.
References: Thompson (1944), Townes & Townes (1973: 36-37), Gauld (1984: 64)
Remarks: The nominotypical *E. agrestoria* (Swederus) occurs in Australia.

6. *Echthromorpha nigricornis* (Smith)
Hosts: *Opodiphthera saccopoea*
Distribution: Australia
References: Gauld (1984: 63-64)

7. *Itopectis conquisor* (Say)
Hosts: *Hemileuca lucina*, *Hemileuca oliviae*, hyperparasitoid in *Enicospilus americanus* in *Callosamia securifera*; many hosts in Lepidoptera and Hymenoptera
Distribution: across North America, probably into Mexico
Biology: An idiobiont primary parasitoid or a facultative hyperparasitoid. The pupal stage of the host is attacked.
Remarks: I reared one of these from a cocoon of *Callosamia securifera*. The moth cocoon contained a cocoon of *Enicospilus americanus*, and the emergence hole of the *Itopectis* was from the side of the ophionine cocoon. The wasp then emerged through the anterior exit valve of the moth cocoon. It is possible that the single female reared by Ainslie was a hyperparasitoid of *Enicospilus texanus* in *Hemileuca oliviae*. These wasps show a wide range in size, the smaller ones developing from smaller hosts.
Specific record: *ex Callosamia securifera*: 8 km W of Awendaw, Charleston Co., South Carolina, emerged indoors 26 February 1979, R. S. Peigler (BMNH).

8. *Itopectis viduata* (Gravenhorst)
Hosts: *Hemileuca oliviae*, Noctuidae, Lasiocampidae, Lymantriidae, Nymphalidae, Pieridae, and Tortricidae, with mostly one species recorded per family
Distribution: Palaeartic; Northwest Territories and British Columbia to California and New Mexico
References: Carlson (1979: 342)
9. *Ephialtes capulifera* (Kriechebaumer)

**Hosts:** *Saturnia japonica*, several other Lepidoptera including Lasiocampidae, butterflies and *Lymantria dispar* (L.), Lymantriidae

**Distribution:** Japan; Korea; Russia; Kurile Islands; China, mostly northern states but also Sichuan and Taiwan; Germany

**References:** Thompson (1944), Townes et al. (1965: 42-44), Gupta (1987: 76-77)

**Remarks:** Cited by Thompson as *Pimpla japonica*. The saturniid host was cited by most authors as *Dictyoploca*, which is a junior objective synonym of *Caligula*, which I consider to be a junior subjective synonym of *Saturnia*.

A record cited by Marsh (1937) and repeated by Tuskes et al. (1996) of "*Ephialtes aequalis*" attacking *Hyalophora cecropia* could not be verified in Carlson (1979). Perhaps it is an error in identification of a similar-looking ichneumonid. The name may refer to *Ichneumon nubivagus* (Cresson), of which *aequalis* is a synonym (Carlson 1979: 515).

10. *Coccygomimus disparis* (Viereck)

**Hosts:** *Samia walkeri*, other Lepidoptera including butterflies and Lasiocampidae

**Distribution:** Japan, Korea, Russia, China

**References:** Townes et al. (1965: 48-50)

11. *Coccygomimus indra* (Cameron)

**Hosts:** *Saturnia pyri*, other Lepidoptera including butterflies, Lymantriidae, and Lasiocampidae

**Distribution:** China, India, westward into European Russia

**References:** Townes et al. (1965: 50-52)

12. *Coccygomimus instigator* (Fabricius)

**Hosts:** *Saturnia pyri*, *Antheraea yamamai*, other Lepidoptera including Notodontidae, Noctuidae, Lymantriidae, Geometridae, Pieridae, Lasiocampidae, and Arctiidae

**Distribution:** Germany to China, Japan, and Russia, including on Kurile Islands and Sakhalin

**References:** Townes et al. (1965: 51), Zivojinovic & Vasic (1963), Pujade & Sarto (1986: 23).

**Remarks:** Pujade & Sarto (1986: 20) figured both sexes of this wasp in color. It is black, with orange legs and has an ovipositor of moderate length. The record for the Japanese *Antheraea yamamai* is from the introduced population in southeastern Europe.

13. *Coccygomimus luctuosus* (Smith)

**Hosts:** *Samia walkeri*, *Samia pryeri*, *Bombyx mandarina*, several other Lepidoptera including Lasiocampidae, Lymantriidae, and butterflies

**Distribution:** China including Taiwan, Japan, Korea, Kurile Islands, Russia, and probably west to Poland and Germany

**Biology:** This wasp is an idiobiont. According to Uedo & Tanaka, females use different host individuals for host-feeding and for oviposition. When they host-feed, it usually kills the host. A single egg is deposited into a host. Males develop in about 17 days, females in about 19. Adult males live about 29 days, females about 38.

Remarks: The record cited by Townes et al. as "Samia cynthia walkeri" included citations by Morley from both China and Japan so these could refer to Samia walkeri, Samia cynthia, or Samia pryeri. This parasitoid was cited by Arzone and Uedo & Tanaka under the name Pimpla luctuosa.

14. Coccygomimus parnarae (Viereck)
Hosts: Samia pryeri, Bombyx mandarina, other Lepidoptera including especially Lasiocampidae
Distribution: China including Taiwan, Japan, Korea, Kurile Islands, Ryukyu Islands
References: Townes et al. (1961: 32; 1965: 56)
Remarks: The record of Samia cynthia given in Townes et al. came from Japan, so I refer it to Samia pryeri.

15. Coccygomimus sanguinipes erythopus Viereck
Hosts: Hemileuca oliviae, Hemileuca sp., Lasiocampidae, other Lepidoptera
Distribution: western Canada, Mexico, United States
Biology: Probably the pupae of the hosts are attacked by the ovipositing wasp.
Remarks: This wasp is called Pimpla sanguinipes by some earlier authors. Ainslie reported that this parasitoid (and/or Itoplectis conquistor) produced hyperparasitoids in the genus Dibrachys (Pteromalidae, see below).

16. Coccygomimus tomyris Schrottky
Hosts: Hylesta nigricans, Eudyaria venata, Papilionidae, Psychidae
Distribution: Argentina, Uruguay, Paraguay, Brazil
Biology: Probably the parasitoids lay eggs into the pupae of the hosts. The hosts listed above all pupate above ground level.
References: Townes & Townes (1966: 28-29)

Genus Xanthopimpla
This is a very large genus of several hundred species, some in Africa and South America, but most in the Indo-Australian region. Those of the latter region were revised by Townes & Chiu (1970). They are usually yellow with black markings that are usually species-specific. They are solitary idiobionts. Females locate a suitable host; in the case of Saturniidae, this is a healthy pupa in a cocoon. The ovipositor is inserted, the pupa stung, and an egg laid. Sometimes this leaves a visible mark on the abdomen of the host pupa. To emerge, the wasp eventually bores out the anterior end of the pupa, and chews or pushes its way out of the host cocoon.

17. Xanthopimpla brullei Krieger (Figure 1)
Hosts: Attacus atlas, Samia insularis, Samia luzonica, Cricula trifenestrata, Cricula trifenestrata javana, Cricula trifenestrata kransi
Distribution: Greater Sunda Islands (Java, Borneo, Sumatra) of Indonesia; Sabah, East Malaysia; West Malaysia; Sulawesi, the Moluccas (eastern Indonesia); the Ryukyus (Japan)
Remarks: The records for "Philosamia cynthia" given by Townes & Chiu and earlier
authors must be referred to *Samia insularis* based on the localities in Java for these records.

Specific records: *ex Cricula trifenestrata javana*: Sukabumi, 700m, Jawa Barat, Java, Indonesia, May 1990, U. & L. Paukstadt (DMNH); *ex Attacus atlas*: Padangpandjang, 735m, 775m, and 875m, Sumatera Barat, Sumatra, Indonesia, emergences April 1981, 1983, 10 August 1985, U. & L. Paukstadt (DMNH); Mt. Salak, 600m, Jawa Barat, Java, Indonesia, March 1981, U. & L. Paukstadt (DMNH); Gopeng, Tapah, Perak, West Malaysia, August 1979, U. & L. Paukstadt (DMNH); *ex Samia luzonica*: Boac, Marinduque, Philippines, 22 August 1987, L. & H. Paukstadt (DMNH); *ex Cricula trifenestrata kransi*: Tondano, Sulawesi Utara, Indonesia, August 1994, S. Naumann (Naumann 1995). The latter record gives a range extension for this parasitoid.

18. *Xanthopimpla konowi* Krieger

**Hosts:** *Attacus atlas, Attacus dohertyi* [possibly a record for *Archaeoattacus staudingeri*; see remarks below], *Antheraea paphia* (=*mylitta*), *Antheraea assamensis*, *Antheraea frothi*, *Saturnia pyretorum*, *Actias maenas* [see remarks under *X. lepcha* below], *Cricula trifenestrata*

**Distribution:** Orissa and Uttar Pradesh states of India to Taiwan and Ryukyu Islands, down into Sumatra


**Remarks:** Some of the records cited by Townes & Chiu (1970) under *Xanthopimpla pedator* (Fabricius) (=*pedator* Maxwell-Lefroy & Howlett; =*punctator* Vollenhoven) belong under *X. konowi* and *X. lepcha*. These authors explained that there has been much confusion in the past and many misidentifications were made. It now appears that *X. pedator* parasitizes only Lasiocampidae, whereas *X. konowi* parasitizes only Saturniidae. These parasitoids appear much alike. Indian authors cited above have reported this parasitoid as being reared from *Antheraea* under the names *X. pedator*, *X. dohertyi*, and *X. punctator* (Linnaeus). This wasp is considered a pest in India where it damages the wild silk industry. Ulrich Paukstadt sent me a specimen reared from *Attacus atlas* that Robert Wharton ran through the key in Townes & Chiu (1970). It did not key to any known species, but is near *X. pedator*; I donated the specimen to the Taiwan Agricultural Research Institute.

Records for *Xanthopimpla iaponica* Krieger parasitizing Saturniidae also belong under *X. konowi*. Other synonyms are *X. antheraea* Cameron, *X. watsoni* Cameron, *X. grandis* Cushman, and *X. princeps* Krieger.

The host record of *Attacus dohertyi* requires some interpretation, because that moth occurs only in the Lesser Sunda Islands, considerably farther east than the known range of the parasitoid. As explained by Peigler (1989), *Archaeoattacus staudingeri* was figured under the name *dohertyi* in a standard reference on tropical Asian moths, so the host record may have been based on that species or *Attacus atlas*.

Specific record: *ex Attacus atlas*, Hong Kong, emerged 17 March 1992, Stefan Naumann.

19. *Xanthopimpla lepcha* (Cameron)

**Hosts:** *Actias maenas, Antheraea frothi, Cricula, Erionota thrax* (Linnaeus) (Hesperiidae)

**Distribution:** widespread in India and mainland of southeastern Asia, Fujian Province in China, on Taiwan, and the islands of Java and Sumatra of Indonesia

Remarks: In his synonymy under this taxon, Gupta indicated that many of the older records of *X. pedator* belong under this species. It is likely that the rearings from *Antheraea frithi* and *Actias maenas* (cited by Gupta as *Sonthonnaxia leto*) belong here instead of under *X. konowi*.

The hymenopterous parasitoids that Watson (1911) referred to as emerging from *Rhodinia newara* cocoons he obtained from India probably belong to this species or an allied one.

**Genus Theronia**

These wasps are closely related to *Xanthopimpla* to which they look similar but smaller. Parasitization is the same: solitary idiobionts attacking hosts in the pupal stage. Many or most may actually be hyperparasitoids that were mistaken as primary parasitoids when reared out. A detailed revision of the Indo-Australian species was published by Gupta (1962).

20. *Theronia atalantae fulvescens* (Cresson)

**Hosts:** *Hyalophora cecropia*, *Callosamia promethea*, and several other Lepidoptera including Lymantriidae and Lasiocampidae, as well as being hyperparasitic on *Enicospilus americanus*, *Gambrus extrematis*, *Itopectis conquistator*, and *Hyposoter fugitivus*.

**Distribution:** New Brunswick to British Columbia, Virginia to California

**References:** Thompson (1944: 106), Collins & Weast (1961), Carlson (1979: 346-347)

**Remarks:** The nominotypical subspecies of this parasitoid is European according to Carlson. Thompson cited the American taxon under the name *T. fulvescens fulvescens*.


**Hosts:** *Opodiphthera astrophela*, *Anthela acuta* (Walker) (*Anthelidae*)

**Distribution:** Australia (New South Wales, Victoria, Queensland, South Australia, Tasmania)

**Biology:** Gauld indicated that this species may always be a hyperparasitoid of ichneumonids of the tribe Pimplini. Lepidoptera recorded as hosts may have been misinterpreted as primary hosts.


22. *Theronia steindachneri* Krieger

**Hosts:** *Opodiphthera astrophela*, *Teia anartoides* (Lymantriidae), *Pericyma cruegeri* (Noctuidae: Catocalinae), *Hyalarctia huebneri* (*Psychidae*)

**Distribution:** eastern Australia, and a possible record from Sulawesi, central Indonesia

**Biology:** Gauld said that species in this group (subgenus *Theronia*) may all be hyperparasitoids on Pimplini (*Ichneumonidae*)


23. *Theronia zebra diluta* Gupta

**Hosts:** *Saturnia pyretorum*, *Saturnia japonica*, some Lymantriidae, Lasiocampidae, and butterflies

**Distribution:** China (Taiwan, Fujian, Guangdong), Japan (Ryukyu Islands), Burma, India

Remarks: This species belongs to the subgenus Poecilopimpla. The synonym Theronia rufescens belongs here.

24. Theronia zebra zebra Vollenhoven

Hosts: Cricula trifenestrata, Cricula trifenestrata javana, Attacus atlas, Pieridae

Distribution: Karnataka, India; East and West Malaysia; Java, Indonesia


25. Theronia sp.

Hosts: Attacus atlas

Distribution: Java, Indonesia

Biology: One female was reared from a host cocoon, there was an exit hole in the anterior end of the host pupa.

References: Peigler (1989: 94-95)

Remarks: Specific record: ex Attacus atlas: Mt. Salak, 600 m, Java, Indonesia, Ulrich Paukstadt. Robert Wharton at Texas A&M University attempted to key the specimen using Gupta (1962), but it did not key to any known species. The specimen was subsequently given to the Taiwan Agricultural Research Institute.

26. Theronia sp.

Hosts: Imbrasia cytherea

Distribution: South Africa

Biology: A larval parasitoid of the pine emperor, according to van den Berg. However, according to Carlson, other authors, and my own observations, ichneumons of this genus are parasitoids of pupae. Perhaps van den Berg reared this wasp from a pupa and believed it had been attacked as a larva.

References: van den Berg (1974), Carlson (1979: 346)

Remarks: This parasitoid is hyperparasitized by a species of Eurytoma. The saturniid primary host was cited by van den Berg under the name Nudaurelia cytherea clarki Geertsema.

Subfamily Tryphoninae

27. Netelia sp.

Hosts: Automeris spp.

Distribution: northern Argentina

References: Townes & Townes (1966: 44), Carlson (1979: 359)

Remarks: Ichneumons in this genus are not otherwise known to parasitize Saturniidae. The adult wasps closely resemble species of nocturnal Ophioninae. It is likely that this record is based on a misidentification of a species of Enicospilus. The report was under the name Paniscus, a synonym of Netelia.

Subfamily Cryptinae

28. Isdromas lycaenae (Howard)

Hosts: Hyposoter fugitivus in Anisota pellucida and Anisota peigleri

Distribution: eastern United States, known from Pennsylvania to Alabama west to Iowa and Texas
Biology: This wasp is always a hyperparasitoid of smaller ichneumonids and braconids.


Remarks: Specific records, all hyperparasitoids in *Hyposoter fugitivus: ex Anisota peigleri*: Hendersonville, North Carolina, September 1974; D. Montross (DMNH, USNM); Clemson, South Carolina, 3 September 1976, R. S. Peigler (USNM); Greenville, South Carolina, 1 October 1982, 8 September 1984, R. S. Peigler (DMNH, DMNH); *ex Anisota pallidula*: Baton Rouge, Louisiana, May 1978, J. E. Eger and R. S. Peigler (DMNH); *ex Anisota*: Stubblefield Lake, Walker Co., Texas, October 1979, G. W. Brooks (LACM).

29. *Gelis tenellus* (Say)

Hosts: Hyperparasitoid in many Hymenoptera including *Enicosipitus americanus, Gambrus extrematis, Hyposoter fugitivus,* and *Phobocampes clisiocampae*

Distribution: Québec to Georgia, Alaska to California, also recorded from Hawaii and Argentina

Biology: A solitary diidiont. In *Hyposoter fugitivus*, the host makes its cocoon in the mummified primary host larval skin, then this cocoon is attacked by the secondary parasitoid. When *P. clisiocampae* serves as the host, the exposed cocoon is probably attacked. Cocoons of *Enicosipitus* and *Gambrus* are contained within the primary host cocoon, well hidden. Duncan indicated that the females of *G. tenellus* enter through exit holes in the walls of the moth cocoon to attack the ichneumonid cocoons. This suggests that *Gelis tenellus* is a very opportunistic, since exit holes would be made by those *Gambrus* emerging first, and the others would emerge within only a few days afterwards. This would not explain how a female of *G. tenellus* could gain access to a cocoon of *Enicosipitus americanus* within a moth cocoon. Duncan found it in only 20 cocoons of almost 5000 of *Gambrus* that he dissected. He said that only one or two *Gelis* emerge from a single cocoon of *Gambrus*, and that the ovipositing female of *Gelis* may die within the primary host cocoon before it can escape.


Remarks: Patterson reared only one of these parasitoids, which emerged in May, and did not recognize that it was a hyperparasitoid. His account of its pupation method and site should be discounted. He believed the host to have been *Coloradia pandora*.

Reports by Packard (1914: 268) and repeated by Collins & Weast (1961: 95) of *Hemeteles compactus* Cresson attacking *Callosamia promethea* probably refer to this parasitoid. Carlson (1979: 405) gave no host records for *Gelis compactus (=Pezomachus compactus)*, and so I assume the original report by Packard was a misidentification for *G. tenellus*, and was also then mistaken to be a primary parasitoid.


30. *Gelis insolens* (Gravenhorst)

Hosts: *Saturnia pavonia*

Distribution: Europe

References: Rougeot (1971: 107, as *Pezomachus insolens*), Carlson (1979: 403)

Remarks: According to Carlson, *Pezomachus* is a junior synonym of *Gelis*. 
31. *Gelis palpator* (Gravenhorst)

**Hosts:** *Saturnia pavonia*

**Distribution:** Britain

**References:** Thompson (1944: 535)

**Remarks:** A synonym is evidently *Hemiteles palpator*. Thompson listed both names. Possibly this species belongs under the latter generic name.

32. *Mastrus* sp.

**Hosts:** Hyperparasitic in *Hyalophora columbia gloveri*

**Distribution:** North America

**Biology:** This species is probably a hyperparasitoid; see Remarks below.

**References:** Duncan (1941), Carlson (1979: 410-413)

**Remarks:** *Aenoplex* is a synonym of *Mastrus* (Carlson 1979: 411). Several specimens of an unidentified species of *Mastrus* were reared in Utah by Bruce Duncan from cocoons of *Hyalophora columbia gloveri*. A pair of these was sent to David Wahl who identified them to the generic level, but gave no species determination. Carlson cited *Gambrus nuncius* as a host of *Mastrus cressoni* (Riley), *Gambrus extrematis* as a host of *M. smithii* (Packard), and *Gambrus* sp. as a host for *M. mucronatus* (Provancher). Duncan has also reared *Gambrus canadensis* from the same saturniid cocoons in the same region, so these may be the true host of this *Mastrus*. The parasitoid is gracile and mainly a coal black color, but somewhat resembling *Gambrus*.

Specific record: Utah, Utah Co., Spanish Fork, 1340 m, reared 1992 from cocoons of *Hyalophora columbia gloveri*, J. B. Duncan (DMNH, AEI).

33. *Gnotus* sp.

**Hosts:** Hyperparasitoid in *Cotesia sp. in Hyalophora cecropia*

**Distribution:** North Atlantic States and Great Lakes States

**Biology:** Reared as a hyperparasitoid from *Cotesia sp.* (reported as *Apanteles* sp. by Peigler 1985a) from half-grown larvae of *Hyalophora cecropia* in Aurora, Arapahoe Co., Colorado.

**References:** Carlson (1979: 421), Peigler (1985a)

**Remarks:** Material from Colorado sent to me by S. E. Stone was forwarded to K. van Achterberg who determined it as *Gnotus* sp., so voucher material is presumably in RMNH. Only a single species of *Gnotus* is recorded from North America, namely *G. chionops* (Gravenhorst), so this may be the species to which this record belongs. It also may be conspecific with specimens from Europe and Japan.

34. *Agrothereutes fumipennis* (Gravenhorst)

**Hosts:** *Saturnia pavonia*

**Distribution:** northern Europe, including Britain

**Biology:** It is a gregarious idiobiont. Wasps probably oviposit onto larvae as they spin their cocoons, the parasitoids feed as ectoparasitoids, then emerge from the host's cocoon the following spring. This was found to be the case by Kugler of a parasitoid in the same genus attacking a lymantriid.


**Remarks:** Nordström cited this ichneumon under the generic name *Spilocryptus*, now considered a synonym of *Agrothereutes*. This parasitism record is probably for the same species as the following one. Nordström cited his *tibialis* Thomson as a possible synonym of *zygaenarum* Thomson. Carlson indicated that *zygaenarum*, which is the
type-species of Spilocryptus, is believed to be a synonym of fumipennis. Therefore, all three names may refer to the same species of parasitoid. Rouget cited this insect under the name Cryptus fumipennis.

This may be the species of parasitoid of which pupae are shown in a color photograph of an opened cocoon of S. pavonia by Ebert. This genus is very closely related to Gambrus (Townes & Townes 1962: 70).

35. Agrothereutes incubator Strom.  
Hosts: Saturnia pavonia  
Distribution: Britain  
References: Thompson (1944: 535, as Spilocryptus incubator)

36. Agrothereutes tibialis Thomson  
Hosts: Saturnia pavonia  
Distribution: northern Europe  
Biology: Parasitoids emerged through small holes in a host cocoon found on the ground by Nordström in 1915 in Runmarö, Sweden. First 4 males emerged, and then after a week, 14 females emerged. The parasitoid cocoons were tightly packed within the host cocoon.  
References: Nordström (1916: 125), Carlson (1979: 447)  
Remarks: See remarks under Agrothereutes fumipennis above. I assume that the name A. saturniae (Boie) is a synonym of this species or the previous one.

Genus Gambrus  
For parasitism of Saturniinae in North America, this is one of the most frequently reared genera. Specimens may be easily identified using the keys of Townes & Townes (1962: 70-71). They are gregarious idiobionts. These wasps attack hosts as they spin their cocoons. The ovipositing parasitoids are probably attracted to the odor of freshly spun silk. The host is stung, and thus paralyzed, ceases spinning and does not pupate. The wasp larvae feed as ectoparasitoids. Some host cocoons are packed full of those of the parasitoid, while in others there is a dead, blackened, dried host larva, with only a few wasp cocoons clustered within the inner chamber of the host cocoon. Adult wasps do not emerge through the exit valve of the host cocoon; instead they chew one or more holes in the side of the host cocoon. Species in this genus appear in most older literature under the generic names Cryptus and Spilocryptus.

37. Gambrus canadensis (Provancher)  
Hosts: Hyalophora columbia gloveri, Orgyia (Lymaenidae), Malacosoma (Lasiocampidae), other smaller moths, and possibly a tenthredinid (Hymenoptera)  
Distribution: Most of North America, recorded from Alaska and British Columbia to Arizona, and Nova Scotia to North Carolina  
Biology: There are usually four to ten parasitoids per host in Malacosoma, and I would expect more to emerge from Hyalophora. According to Townes and Townes "the cocoon is elliptic, of moderate length, thin but dense, and with a felt of loose silk on the outside. The color ranges from white to gray-brown."  
References: Townes & Townes (1962: 80-85), Carlson (1979: 449)  
Remarks: Specific records: ex Hyalophora columbia gloveri: Spanish Fork, 1340m, Utah Co., Utah, emerged indoors April 1992, J. B. Duncan (DMNH, AEI). Specimens were identified by David Wahl.
38. *Gambrus extrematis* (Cresson) (Figure 2)

**Hosts:** *Hyalophora cecropia, Hyalophora euryalus, Hyalophora columbia columbia, Hyalophora columbia gloveri*

**Distribution:** British Columbia to Nova Scotia, south to Virginia, Kansas, Utah, and California

**Biology:** According to Marsh, more than 1000 eggs were found in a single host cocoon resulting from oviposition of several females. The maximum number of mature cocoons found in a single host cocoon was 172. Marsh wrote that the larvae move about freely over the dead host, eventually consuming all of it except the most chitinized parts in cases of heavy parasitism, and that cannibalism among the parasitoid larvae seems certain. He said that the wasp is bivoltine in Chicago, completing a life cycle in about 18 days. This should be possible where larvae of the host spin their cocoons over a period of three or more weeks. The parasitoids overwinter in their cocoons within the host’s cocoon. About 5—40 wasps of one or both sexes emerge from a single host cocoon.

In the region around Denver, Colorado, I found that this parasitoid is attacked commonly by the facultative hyperparasitoid *Monodontomerus minor*, listed elsewhere in this catalog. I also found that the moth host is usually left as a blackened larva, with only a small mass of *Gambrus* cocoons alongside.

**References:** Eliot & Soule (1902: 256), Gibson (1906), Marsh (1937), Duncan (1941), Townes & Townes (1962: 87-90), Carlson (1979: 449)


39. *Gambrus nuncius* (Say)

**Hosts:** *Samia cynthia, Callosamia angulifera, Callosamia promethea, Callosamia securifera, Antheraea polyphemus*

**Distribution:** New Brunswick to Northwest Territories, down to Alabama.

**Biology:** My observations indicate that a brood of this parasitoid almost always consumes the entire host, and form a mass of tightly packed cocoons within that of the host.


**Remarks:** Specific records: *ex Callosamia* hybrids: Greenville, South Carolina, July 1974, July/August 1976, R. S. Peigler (DMNH, USNM); *ex Callosamia angulifera:* Greenville, South Carolina, April-May 1983, May 1984, R. S. Peigler (BMNH, LACM); *ex Callosamia securifera:* Highway 6, Berkeley Co., South Carolina, emerged indoors March 1975, R. S. Peigler.

Peigler (1985a) erroneously reported material of *G. extrematis* from Colorado under the name *G. nuncius*. The record(s) for this parasitoid attacking *Antheraea polyphemus* should be verified, as it may be based on *Gambrus polyphemus*. The two species look much alike. However, no species of *Callosamia* nor *Samia* range into far northern Canada, so if the geographical records are correct for *Gambrus nuncius*, the most likely hosts would be *Antheraea polyphemus* or *Hyalophora columbia*. No saturniid is known to range into the Northwest Territories. I have not seen material reared from *Samia cynthia*, but this host is quite likely, considering that *Samia* is closely related to *Callosamia* and has a hanging cocoon of similar shape and size, found on some of the same hostplants (*Sassafras, Prunus*, etc.).
The rearings by me in central Greenville County indicate that the normal host in that area is *C. angulifera*. *Callosamia promethea* does not exist there, but does occur in northern Greenville County at higher elevations in disturbed forests and along highways. *Callosamia securifera* does not occur within 150 km of Greenville, whereas *C. angulifera* is common throughout Greenville County including some urban areas. Some of the rearings from the hybrids produced smaller wasps in larger numbers, examples of superparasitization. The hosts were parasitized through cloth bags as they spun their cocoons in folds of the bags, covering branches of *Liriodendron tulipifera* and *Magnolia virginiana*, the latter tree not native that far inland in South Carolina. The record for *C. securifera* cited by Ferguson was from northern Charleston County, South Carolina.

40. *Gambrus polyphemus* H. Townes

**Hosts:** *Antheraea polyphemus*

**Distribution:** All across southern Canada and over much of United States, corresponding to the range of the host. According to Townes and Townes, it is more common in the East than the West, like its host species. See Remarks below.

**Biology:** Townes & Townes cited host records of *Hyalophora cecropia* but expressed skepticism. Carlson did not list the doubtful host records. I agree that these records need to be verified before being perpetuated in literature. Townes & Townes wrote that the host cocoon is packed full of parasitoid cocoons, and that about 15 parasitoids, usually of both sexes, emerge from a single host. They reported that this parasitoid is moderately common along edges of deciduous forests. As with other species of *Gambrus*, the host is attacked as it spins its cocoon, and the parasitoids overwinter within. The adults are found mainly from early June through the middle of September, but sometimes into November.

**References:** Townes & Townes (1962: 90-93), Carlson (1979: 449)

**Remarks:** Specific record: *ex Antheraea polyphemus*: San Antonio, Bexar Co., Texas, August 1972, T. McGregor (TAMU).

I have never reared it from numerous wild-collected cocoons from South Carolina, Texas, and Colorado, so I suspect this wasp is more common in the Northeast than the Southeast. The map of Townes & Townes shows no records for the Ozarks, the Great Plains, the Rocky Mountains (except in New Mexico), the Great Basin, nor California and Arizona. The host is largely absent from the Great Basin. An unidentified ichneumon which makes cocoons within the host cocoon much like those of *Gambrus* was illustrated by Cotes (1891-1893: pl. 9) in a cocoon of *Antheraea roylei* from northeastern India.

41. *Lymeon orbis* (Say)

**Hosts:** A hyperparasitoid in other ichneumonids, including *Hyposoter fugitivus*, and a primary parasitoid of other insects

**Distribution:** eastern half of United States

**Biology:** Apparently a solitary idiobiont. In Louisiana Khalaf found that *L. orbis* is a hyperparasitoid on the ichneumonid *Lanugo retentor* (Brullé) which in turn is a parasitoid of the megalopygid moth *Megalopyge opercularis* (J. E. Smith).

**References:** Khalaf (1980), Carlson (1979: 474-475), Riotte & Peigler (1981: 120)

**Remarks:** Specific record: *ex Anisota fuscens*: Stubblefield Lake, Walker Co., Texas, 3 November 1976, R. S. Peigler (DMNH, USNM).

Three specimens were obtained, two males and one female, from this rearing (three separate hosts).
There is a record cited by Thompson (1944: 105) of Acrocinus stylator aequatus (Say) (=A. junceus), an ichneumon related to Lymeon, attacking Callosamia promethea. This record is erroneous, because all species in this subtribe attack only Hymenoptera such as Sphecidae (Carlson 1979: 476-477).

42. *Trachysphyrus chacorum* Porter

**Hosts:** Rothschildia sp.

**Distribution:** northern Argentina

**Biology:** Several specimens emerge from a single host cocoon. The female wasp oviposits into the host cocoon, stinging the pre-pupa or pupa. Thus species of this genus are gregarious idiobionts.

**References:** Porter (1967: 248-250)

**Remarks:** The species of Rothschildia that occur in this region of northern Argentina are *R. maurus*, *R. tucumani*, *R. condor*, and *R. schreiteriana*. Probably all of these serve as hosts.

43. *Trachysphyrus desantis* Porter

**Hosts:** unidentified saturniid

**Distribution:** from Cuzco, Peru, to central Argentina

**Biology:** Based on knowledge of other species in the genus, the parasitoid female oviposits into a host cocoon, laying several eggs. This species inhabits high montane grasslands in the northern part of its range, and lowland pampas in central Argentina.

**References:** Porter (1967: 242)

**Remarks:** Porter wrote: “The male and female from Olivos in Buenos Aires Province were reared from an unidentified saturniid moth.”

44. *Trachysphyrus horsti* (Brèthes)

**Hosts:** Cercophana frauenfeldi, Neocercophana philippi, Macromphalia dedecora (Lasiocampidae)

**Distribution:** Chile

**Biology:** The wasps are very common in forests around Temuco, where they fly slowly among trees. They particularly search on various trees which are hostplants of the two cercophanines. Eggs are laid occasionally into larvae, but most frequently into pupae in cocoons. Several adult parasitoids emerge from a single host cocoon.

**References:** Porter (1967: 227)

**Remarks:** Porter cited the above two saturniid hosts based on a literature report on *T. horsti*, and he indicated that there is a possibility that the report actually belongs under a different species of Trachysphyrus. The lectotype of *T. horsti* (designated by Porter) was reared from the laisiocampid host. The Cercophaninae are now considered to be a subfamily of Saturniidae (Minet 1994).

45. *Trachysphyrus kinbergi* Holmgren

**Hosts:** Automeris coresus, Ormisicodes amphinome lauta

**Distribution:** Peru, Chile, Argentina, Bolivia, Uruguay, from the Peruvian and Bolivian Andes all the way south to the Strait of Magellan and the Chilean province of Aisén.

**Biology:** There is some confusion as to whether larvae or pupae are attacked. Presumably oviposition is into mature host larvae and adult parasitoids emerge from host cocoons. Some of the material in collections labelled as being reared from larvae probably simply means that the hosts were collected as larvae.
References: Porter (1967: 306-309)
Remarks: Porter cited the hosts as Automeris cresus and Catocephala lauta. The latter host should probably be cited simply as O. amphinome, because the subspecies lauta is doubtfully valid (C. Lemaire, pers. comm.).

46. Trachysphyrus tucuman Porter
Hosts: Rothschildia tucumani
Distribution: northern Argentina
Biology: Oviposition is into the cocoon of the host, stinging the pupa or pre-pupa. According to Porter (1967: 33), adult wasps of this genus feed in flowers, but not commonly.
References: Schreiter (1925: 15), Porter (1967: 251-253)
Remarks: There is a series of this wasp in the USNM that was reared from the host cited above.

47. Trachysphyrus sp.
Hosts: Rothschildia arethusa
Distribution: Brazil
References: d’Araújo e Silva et al. (1968: 271)

48. Gotra octocincta (Ashmead)
Hosts: Saturniidae, Dendrolimus spp. (Lasiocampidae)
Distribution: China, including Taiwan, Korea, Japan
References: Townes et al. (1965: 193)
Remarks: No specific saturniids were cited as hosts.

Subfamily Ichneumoninae

49. Cratichneumon anisotae Heinrich
Hosts: Anisota senatoria, Dryocampa rubicunda
Distribution: southeastern Canada and northeastern United States, as far as Virginia and Wisconsin
Biology: A solitary idiobiont, attacking pupae of hosts. No saturniid pupae are recorded to possess a gin trap to counter attacks by probing ovipositors (Chinery 1989: 240).
References: Carlson (1979: 492)
Remarks: A specimen reared in Ada, Michigan, reputedly from a cocoon of Callosamia promethea was sent to me by W. Buttrick in 1993. This fragmentary specimen was identified as C. anisotae by David Wahl. Considering that Buttrick was not able to locate the host remains, and had pupae of Anisota senatoria at the same time (he sent me cocoons of C. promethea and pupae of A. senatoria in the same package), it is likely that the latter was the true host. This anecdote is given to demonstrate the importance of keeping different hosts in separate containers.

50. Cratichneumon insulae Heinrich
Hosts: Hemileuca maia
Distribution: known only from Rhode Island and New Jersey
Biology: The pupae of hosts are attacked. This parasitoid is a solitary idiobiont. These wasps are not attracted to light.
References: Carlson (1979: 494), Peigler (1985a)
Remarks: I collected a specimen of *C. insulæ insignitus* Heinrich in Greenville, South Carolina, 28 May 1977 (DMNH).

Specific record: *ex Hemileuca maia* Baton Rouge, Louisiana, 7 August 1982, J. E. Eger (BMNH, LACM). If this wasp and related species are specialists on Saturniidae, they would be able to attack pupae of *Hemileuca* in early summer and *Anisota* in late summer, overwintering in the latter.

51. *Cratichneumon unifasciatorius* (Say)
Hosts: *Coloradia pandora, Hemileuca* sp.
Distribution: southern British Columbia to Québec, south to Florida and Arizona
Biology: Less than 1% of pupae of *Coloradia* in northern Arizona were attacked, limited to those near the soil surface.
References: Schmid & Bennett (1988), Carlson (1979: 496)

52. *Cratichneumon w-album* (Cresson)
Hosts: *Anisota senatoria, Dryocampa rubicunda*
Distribution: Québec to Georgia, west to Alabama and Wisconsin
Biology: The pupae are attacked. The wasps emerge from the anterior ends of the host pupae.
References: Hitchcock (1961b), Allen (1976), (Carlson (1979: 497)
Remarks: According to Carlson, *Cratichneumon variegatus* (Provancher) is a synonym of *C. w-album*.

Specific records: Cave Run Lake, Ramey Creek, Daniel Boone National Forest, Rowan Co., Kentucky, 28 May 1993 and 25 May 1994, B. C. Kondratieff (CSU).

53. *Amblyteles armatorius* (Forster)
Hosts: *Saturnia pavonia*
Distribution: Europe, including Britain
Remarks: This wasp is black with broad yellow bands on the abdomen and legs. The scutellum and tegulae are also yellow. It was figured in color by Chinery and Pujade & Sarto.

54. *Amblyteles erythronotus* Rondani
Hosts: *Saturnia caecigena*
Distribution: southeastern Europe
References: Lederer (1952: 144), Rougeot (1971: 116)
Remarks: Lederer wrote “Von Rudow wird die Ichneumonide *Amblyteles erythronotus* Rd. (?) als Schmarotzer angegeben.” I did not find Rudow cited in his text or bibliography. The host species is usually classified in the genus *Perisomena*.

55. *Amblyteles oratorius* (Fabricius)
Hosts: *Saturnia pavonia*
Distribution: Britain
References: Thompson (1944: 535)

56. *Ichneumon microstictus* Wsm.
Hosts: *Actias isabellae*
Distribution: Europe
Remarks: I was not able to clarify the current generic placement of this taxon and the next one, because H. Townes and colleagues did not catalog the European ichneumonid fauna in their many monographs.

57. Ichneumon sulfuripes Rondani
Hosts: Actias isabella
Distribution: Europe

58. Protichneumon grandis (Brullé)
Hosts: Dryocampa rubicunda
Distribution: British Columbia to Québec, Oregon and New Mexico to Florida
Biology: Most species in this Holarctic genus attack Sphingidae. The saturniid host listed above, being a ceratocampine, is “sphingiform”.
References: Carlson (1979: 534)

59. Conocalama quebecensis (Provancher)
Hosts: Eacles imperialis
Distribution: New England, Great Lakes region, Nova Scotia to British Columbia
References: Carlson (1979: 537-538)
Remarks: No other host is recorded for this parasitoid.

60. Pedinopelte gravenstii (Guérin)
Hosts: Automeris sp., Papilio (Papilionidae)
Distribution: South America, including Surinam, Venezuela, Brazil, Boliva, Paraguay, and Argentina.
References: Townes & Townes (1966: 281), d’Araújo e Silva et al. (1968: 263)

Subfamily Metopiinae

61. Metopius dentatus (Fabricius)
Hosts: Saturnia pavonia
Distribution: Britain, Norway, Russia
References: Thompson (1944: 535), Townes et al. (1965: 347)
Remarks: This parasitoid is placed in the subgenus Peltocarus.

62. Metopius micratorius (Fabricius)
Hosts: Saturnia pyri
Distribution: Europe, including Russia
References: Thompson (1944: 535), Packard (1914: 268)

63. Metopius pollinctorius (Say)
Hosts: Actias luna, Gluphusia septentrionis (Walker) (Notodontidae), Acronicta oblinita (J. E. Smith) (Noctuidae)
Distribution: Nova Scotia to British Columbia to Florida and Illinois
References: Carlson (1979: 553)
Remarks: Carlson cited the saturniid host with a “?” and listed the parasitoid as subspecies M. pollinctorius pollinctorius.
Subfamily Banchinae

64. *Glypta erratica* Cresson

**Hosts:** Hemileuca maia, Hemileuca lucina

**Distribution:** Vermont to northern Georgia, west to eastern South Dakota

**References:** Schaffner & Griswold (1934), Thompson (1944: 293), Carlson (1979: 565)

**Remarks:** The original report by Schaffner & Griswold was as "Hemileuca maia and/or lucina." Carlson did not repeat the host record, so perhaps he believed it needs verification.

65. *Glypta* sp.

**Hosts:** Eacles imperialis magnifica

**Distribution:** Brazil

**References:** d’Araujo e Silva et al. (1968: 261) Carlson (1979: 564-567)

**Remarks:** There are numerous species of this genus in North America.

66. *Apophua simplicipes* (Cresson)

**Hosts:** Hemileuca sp., many other Lepidoptera, including Lasiocampidae, Notodontidae, Noctuidae, and Tortricidae.

**Distribution:** British Columbia to Nova Scotia south to New Mexico, Texas, and Florida. One specimen from California without further locality data.

**References:** Carlson (1979: 564), Dasch (1988: 16-20), Thompson (1944: 293, as Glypta simplicipes).

67. *Exetastes illusor* Gravenhorst

**Hosts:** Saturnia pavonia

**Distribution:** Europe

**References:** Rougeot (1971: 107), Carlson (1979: 575-578)

**Remarks:** There are numerous species in this genus in North America.

68. *Exetastes nigripes* Gravenhorst

**Hosts:** Saturnia pavonia

**Distribution:** Britain

**References:** Thompson (1944: 535)

Subfamily Anomaloninae

69. *Podogaster* sp.

**Hosts:** Hylesia lineata

**Distribution:** Colima, Mexico

**Biology:** This group of parasitoids lives in humid, lowland forests.

**References:** Ian Gauld (pers. comm.)

**Remarks:** The name Philodrymus is probably a junior synonym of Podogaster.

Specific record: *ex Hylesia lineata*: Chamela Biological Station, 120 km N of Manzanillo, Colima, June 1986 (BMNH).

70. *Anomalon signatum* Gravenhorst

**Hosts:** Saturnia pavonia

**Distribution:** Europe

**Biology:** Probably a larval-pupal solitary endoparasitoid.

**References:** Packard (1914: 268)
Remarks: The record, quite old and in need of verification, was supplied to Packard by an entomologist named Mocsary, so the record probably came from eastern Europe.

71. Habronyx australasiae (Morley)
Hosts: Opodiphthera sp.
Distribution: New South Wales and Tasmania
References: Morley (1913: 75), Gauld (1976), Gupta (1987: 628-629)
Remarks: The host record was cited as Antheraea sp., but this genus does not occur in Australia. Species of Opodiphthera and Syntherata have often been classified as Antheraea. The record is probably based on a rearing of Opodiphthera eucalypti.

72. Habronyx insidiator (Smith)
Hosts: Antheraeahamamai, Antheraea peryui, Saturnia japonica, Saturnia jonasii, Saturnia boisduvalii
Distribution: China, Taiwan, eastern Russia, Japan, Korea
Biology: Probably a larval-pupal solitary koinobiont parasitoid.
References: Thompson (1944: 50), Townes et al. (1965: 365-366), Sakamoto (1990: 150)
Remarks: Cited by Thompson under the name Acanthostoma insidiator.

73. Habronyx magniceps (Cresson)
Hosts: Anisota oslari, Anisota stigma, Anisota virginiensis, Anisota senatoria, Drycampa rubicunda, Hemaris diffinis (Boisduval) (Sphingidae)
Distribution: Maine to southern Manitoba to eastern Texas and southeastern Arizona; one record for Placer Co., California
Biology: The wasps fly from early July until mid-October, depending on locality.
Remarks: Dasch cited the specific host records for specific regions: Anisota oslari in Arizona, Anisota virginiensis in Manitoba, Anisota stigma in Michigan and New York, Anisota senatoria in Ontario, and Drycampa rubicunda in New Jersey, New York, Ontario, Quebec, and Pennsylvania. He cited with doubt a record for an unidentified species of Geometridae as a host.

74. Habronyx pyretorum (Cameron)
Hosts: Saturnia pyretorum
Distribution: known from only a few specimens from Hong Kong
Biology: Presumably a solitary koinobiont that oviposits into host larvae and emerges from host pupae.
References: Cameron (1912), Morley (1913), Packard (1914: 268), Townes et al. (1961: 312), Peigler (1985a), Gupta (1987: 629)
Remarks: The spelling of the name of the parasitoid in literature prior to Gupta was pyretorum. Two specimens were sent to me by Michael Bascombe in 1980, as follows. Ian Gauld verified the determination.
75. Therion sasacus Viereck
Hosts: Hemileuca eglanterina, other moths in Arctiidae, Geometridae, etc., and Tenthredinidae (Hymenoptera)
Distribution: British Columbia to Nova Scotia, southern California to northern Alabama, also northern New Mexico and Arizona
Biology: The adults fly mainly from mid-July to late August.
References: Dasch (1984: 376-379)

76. Agrypon illinois Dasch
Hosts: Hyalophora columbia gloveri
Distribution: known only from Livingston County, Illinois
Remarks: Dasch described this species from a single male from Fairbury, Illinois, collected by A. H. Lundt. It was reported as a probable parasite of Hyalophora gloveri. If the host record is correct, the locality is not, since gloveri (the Rocky Mountain form of Hyalophora columbia) does not occur further east than far western South Dakota. Other possibilities for the host are Hyalophora eceropia (common throughout Illinois) or Hyalophora columbia (found in some areas of southern Wisconsin). The host cocoon may have been transported from the original collecting site, or it may have been a misidentification. One other possibility is that Lundt reared gloveri in Fairbury, from eggs he received from the Rocky Mountain region. The specimen is over a century old, since it came from the collection of C. V. Riley.

77. Encardia picta Tosquinet
Hosts: Bunaee alcinoe caffra, Bunaee alcinoe, Gynanisa maja, Lobobunaee angasana, Imbrasia petiveri, Imbrasia cytherea, Imbrasia zambesina, Imbrasia thyrrhea, Imbrasia wahlbergii, Tagoropsis flavinata, Gonometa maputana (Lasiocampidae)
Distribution: central and southern Africa
Biology: All of the saturniid hosts pupate in the ground without a cocoon. The lasiocampid host forms a strong silk cocoon on its hostplant, well above ground.
References: Townes & Townes (1973: 203-204), Gauld (1980), Oberprieler (unpubl.)
Remarks: The nomenclature of the host names Lobobunaee saturnus, Nudaurelia dione (=Imbrasia petiveri), and Antheraea ringleri (=Imbrasia zambesina) as cited by Townes & Townes is corrected in the list above.

Subfamily Campopleginae
78. Campoplex quadrimaculatus Ratzeburg
Hosts: Aglia tau
Distribution: Europe
References: Packard (1914: 268).
Remarks: The record is old and thus in need of verification, especially as regards the identity of the parasitoid.

79. Phobocampe clisiocampae (Weed)
Hosts: Actias luna, several other Lepidoptera including Sphingidae, Lasiocampidae, and Notodontidae
Distribution: North America, mainly northern, from Nova Scotia to Alberta to Arkansas and upper South Carolina
Biology: The 2nd or 3rd instar larva was attacked while feeding on foliage of Liquidambar styraciflua. This larva was then kept in a jar. The wasp larva emerged (and
would have fallen to the ground in nature) from the host larva and made a hard, ovoid, dark brown cocoon. It is difficult to decide if such cases of parasitization of young larvae are koinobiontic or idiobiontic.

References: Carlson (1979: 658-659)

80. Melalophcharops sp.

Hosts: Opodiphthera eucalypti
Distribution: Australia
References: Gauld (1984: 278)

81. Hyposoter fugitivus (Say) (Figure 4)

Hosts: Anisota senatoria, Anisota finlaysoni, Anisota consularis, Anisota virginiensis, Anisota stigma, Anisota pellucida, Anisota peigleri, Anisota discolor, Anisota fuscosa, Dryocampa rubicunda, Automeris io, Hemileuca lucina, Hemileuca maia, and several other caterpillars in Arctiidae, Lasiocampidae, and Notodontidae

Distribution: Nova Scotia to Washington, south to central California, eastern Texas, and central Florida

Biology: Small caterpillars are attacked, in saturniids usually in the 2nd instar (never when more than about 10 mm in length). The egg is apparently laid into the host. It is probably an endoparasitic idiobiont. The wasp matures quickly and makes a mummy of the host skin, spinning its elongated and papery white cocoon within, the mummy affixed to the leaf or twig of the host's hostplant. The adult parasitoids emerge within a couple weeks or more. During this time their exposed cocoons are vulnerable to attack from hyperparasitoids.

Remarks: It is almost impossible to collect young larvae of Anisota in the southeastern United States without encountering this parasitoid, usually in high numbers. I have found it in populations of Anisota in Florida, North Carolina, South Carolina, Arkansas, Texas, and Louisiana. Donald Henne (pers. comm.) has also reared this parasitoid from Anisota virginiensis from Belair, on the southeastern shore of Lake Winniepeg, Manitoba.


82. Hyposoter havrylenkoi Havrelenko & Winterhalter

Hosts: Ormiscodes cinnamomea, other Saturniidae, Lasiocampidae
Distribution: Argentina
References: Townes & Townes (1966: 153)
83. Cryptophion moragai Gauld & Janzen
Hosts: Syssphinx molina
Distribution: All known specimens are from Guanacaste Province, in northwestern Costa Rica.
Biology: No specimens have ever been collected in malaise traps, probably because they fly in tree tops. The wasp oviposits into first to third instar larvae of the host, and complete their development while the host is in the second or third instar. The parasitoid ranges at 300 m in altitude and lives in seasonally dry tropical forests. No months were given for its emergence by the authors cited below.
References: Gauld & Janzen (1994)
Remarks: This parasitoid belongs to a group of species that attack Sphingidae larvae. The larvae of ceratocampine saturniids are “sphingiform”, so the switch to the saturniid host is logical. The genus Cryptophion is closely allied to Hyposoter, and Gauld & Janzen believed that it may be derived from Hyposoter (which would make the latter genus paraphyletic). See also text of Thyreodon santarosae below. The name Cryptophion may cause confusion since this genus does not belong to the Ophioninae.

Subfamily Phygaeduontinae
84. Paraphylax sp.
Hosts: Opodiphthera sp.
Distribution: Australia
Biology: Gauld reported that 37 wasps emerged from one host cocoon.
References: Gauld (1984: 128)

Subfamily Ophioninae
Considerable advances in the systematics on this subfamily have been published in recent years by Dr. Ian Gauld and his wife Pamela Mitchell. They have described hundreds of new species and worked out the generic relationships by applying modern cladistic methodology. Some of their monographs are cited in this catalog. See additional remarks below under the genus Enicospilus.

85. Ophion sp.
Hosts: Anisota senatoria
Distribution: northeastern North America
Biology: Oviposition is likely into the larva, and the parasitoid emerges from the pupa.
References: Carlson (1979: 697-698), Gauld (1988b)
Remarks: A female wasp (length 21mm) with light amber wings is in the Carnegie Museum of Natural History. The slender cocoon (8mm X 18mm) of the parasitoid is on the same pin. The labels read as follows: “Ophion emerged VI.18.1925 from pupa of Anisota senatoria, the larva of which was taken on alder at Squaw Run, Pittsburgh, Pa., September 1924, [B.] Krautwurm” “The cocoon of the Ophion was inside the pupa of Anis. senatoria when it emerged.” This specimen was identified as Ophion sp. by H. E. Evans (CSU). A trace of segmentation on the cocoon suggests that it was packed firmly inside the host pupa, of which there are no traces. Alder is not a known host of Anisota, although larvae sometimes move from oaks to other trees and begin feeding (Riotte & Peigler 1981). There is a possibility that Krautwurm misidentified the host.
**Genus Thyreon**

These are very large ichneumons because they have large hosts. They have flattened abdomens like other ophionines, but have black wings, black bodies, and yellow antennae—obvious mimics of Pompilidae. They are day active, so do not come to lights. I have observed them flying near the ground in forests in South Carolina. Most species attack Sphingidae.

86. *Thyreon santarosae* Porter

**Hosts:** *Sphinxix molina*, *Ptiloscola dargei*, *Othorene purpurascens*

**Distribution:** Guanacaste Province, Costa Rica

**Biology:** The parasitoid lives in seasonally dry tropical deciduous forests at altitudes of 250 to 350 m. All known specimens were reared from ceratocampine saturniids collected as larvae between 3 and 20 m above the ground in trees. Emergences were between April and December, coinciding with the wet season. No parasites have been collected with hand nets or in malaise traps, probably because they fly high in trees. Most species in this genus attack larvae of Sphingidae. Larvae of ceratocampine saturniids are “sphingiform” and live in tops of trees, so the switch to these hosts is understandable. The parasitoid is a koinobiont.

**References:** Porter (1986), Gauld (1988b: 61)

**Remarks:** This parasitoid was named for Santa Rosa National Park, now part of Guanacaste National Park. Porter deposited type material in BMNH, USNM, LACM, and TAMU, among other institutions. See also text of *Cryptophion moragai* above.

87. *Thyreon sp.*

**Hosts:** *Eacles imperialis*

**Distribution:** northeastern North America

**Biology:** The host larva is attacked, and the adult parasitoid emerges from the host pupa. The emergence exit is not centered on the end of the cocoon and has a ragged edge where the parasitoid chewed its way out. Adults of *Enicospilus* chew a neat circular hole at the end of their cocoons to exit.

**References:** Carlson (1979: 700), Gauld (1988b)

**Remarks:** A female is in the Carnegie Museum of Natural History with its plump cocoon (11mm X 24mm) on the same pin. It has solidly back body and legs, dark brown wings, and orange antennae; length 29 mm. The label reads: “From pupae of imperialis, Aug. 10, 1928, B. Krautwurm.” This collector apparently lived in the Pittsburgh area (see *Ophion* above). The genus was verified but the species could not be determined by H. E. Evans (CSU).

88. *Stauropoctonus bombycivorus* (Gravenhorst)

**Hosts:** *Actias artemis, Stauropus fagi* (L.) (Notodontidae)

**Distribution:** Britain, France, Germany, Switzerland, Russia, China, Japan, possibly also northern India and Nepal

**Biology:** Although in separate families, the two known hosts have large larvae that feed on beech (*Fagus* sp.). Also, both spin a fairly large cocoon.


**Remarks:** Townes et al. cited this parasitoid as the subspecies *S. bombycivorus variegatus* (Uchida). Gupta and Gauld did not use the trinomial.
89. *Dicamptus nigropictus* (Matsumura)

**Hosts:** unidentified Saturniidae, *Dendrolimus spectabilis*, *Dendrolimus punctatus* (Lasiocampidae)

**Distribution:** India (Arunachal Pradesh); Korea; China (Guangdong, Guangxi, Taiwan, Yunnan, Guizhou, Zhejiang, Shanghai, Jiangxi. Hunan, Sichuan, Shaanxi, Shanxi, Gansu), Japan including Ryukyu Islands; Laos; Brunei; and Indonesia (Borneo).


**Remarks:** Gupta cited a record of *Monodontomerus dentipes* (Torymidae) as a hyperparasitoid of this ichneumon.

**Genus Enicospilus**

Parasitoids of this genus are important enemies of Saturniidae, especially in the New World. They are probably also common enemies of Asiatic and African Saturniidae, but only a single rearing record exists! Hundreds of species are known from the tropical and temperate regions of the world, of which most specimens in collections were taken at lights. Hosts are known for relatively few species, but where known, are Lepidoptera. Because they are nocturnally active, most are colored monotonously orange brown, there being no ecological need for markings and varied coloration. They rest by day on plants, and by night mate and search for hosts. The orange ichneumons with flattened abdomens that we see commonly at lights are mostly of this genus, although some are *Netelia* (Tryphoninae), *Ophion*, or even “ophionoid” braconids. Most females of these wasps can deliver a painful sting, but it is easy to see the ovipositors (stingers) to distinguish them from males. The genera *Dicamptus* and *Stauropoctonus* are very closely related to *Enicospilus* (Gauld 1985).

For purposes of identification, it should be noted that most species look identical without magnification; although Figure 3 shows *E. americanus*, the figure would easily pass for many of the larger species like *E. lebophagus*, *E. aktipes*, *E. plicatus*, or *E. glabratrus* (Say). The latter attacks Arctiidae and Lymantriidae and is not included in this catalog, and *E. texanus* is usually smaller and darker. Amateurs rearing these wasps in North America will find the key by Gauld (1988a) to be surprisingly user-friendly. Identification of specimens from other areas can be made using keys by Gauld (1988b), Gauld & Mitchell (1978, 1981), and Tang (1990). Some of the gigantic species of these wasps described by Gauld & Mitchell (1981) from Indonesia and New Guinea are surely parasitoids of Saturniidae, but so far they have only been taken at light.

Hosts are attacked as larvae. The parasitoid remains in the host as a first-instar larva until the hormone change in the host when it is ready to pupate triggers the parasitoid larva to quickly feed and grow. By the time the host has completed its cocoon or pupal chamber it is overcome and devoured by the parasitoid larva. These ichneumons are typical koinobionts. The cocoon of the parasitoid is ovoid, dark brown, with a light tan equatorial band.

Using new rearing records from Costa Rica discovered by D. H. Janzen, Gauld (1988b: 13-14) made an interesting observation. In North America, almost all of the Saturniidae are attacked by two species in this genus; *Enicospilus americanus* hits most Saturniinae and *Automeris* (Hemileucinae), whereas *E. texanus* hits numerous Hemileucinae and *Agapema* (Saturniinae). In the tropics it appears that most species of *Enicospilus* that attack saturniids specialize on a single genus of host. Gauld hypothesized that these specialist parasitoids in the tropics may have been derived.
from generalist ancestors to the north, but it is difficult to find synapomorphies to support it.

90. Enicospilus americanus (Christ) (Figure 3)

Hosts: Samia cynthia, Rothschildia orizaba, Rothschildia maurus, Rothschildia schreiteriana, Rothschildia arethusa, Rothschildia cincta, Hyalophora cecropia, Hyalophora euryaltus, Callosamia promethea, Callosamia securifera, Antheraea polyphemus, Actias luna, Automeris io, Automeris pamena

Distribution: Nova Teutonia, Brazil; Cochabamba, Bolivia; Tucumán, Argentina; Nuevo León and Chihuahua south to Chiapas, Mexico; Québec and Ontario, Canada; New England to California, United States

Biology: Host larvae of the early to middle instars are attacked by an egg being inserted into them. The larva of the parasitoid does not begin to mature until the host makes its cocoon, and then it eats all of the host except the cast larval skin which is found in the bottom of the host cocoon. There are no remnants of the host’s pupal shell, so the parasitoid larva apparently finishes consuming the host quickly after the host pupates.


Remarks: The record for Tolyde (Lasiocampidae) in Townes & Townes (166: 174) is probably erroneous; it probably refers to E. cushmani Gauld, which attacks Lasiocampidae (Gauld 1988a). Enicospilus americanus has appeared in the literature under many names. All of the following names cited by Packard refer to this parasitoid, including the last two names which were misidentifications by Europeans who imported parasitized cocoons and then assigned names of European ophionines to what emerged: Eremotylus arctiae, Eremotylus macrurus, Ophion bilineatus, Ophion macrurum, Ophion bifoveolatus, Enicospilus purgatus, Allocamptus undulatus, Henicospilus merdarius. Several of these were repeated by Collins & Weast, Eliot & Soule, and Frank, but this problem was corrected by Tuskes et al., who listed all records only under the one correct name.

The first record listed below was determined by me using the larval head capsule extracted from the vacated cocoon of the parasitoid, sent by M. Collins. The configuration of the head is clearly that of E. americanus and not E. texanus or E. lebophagus as figured by Gauld (1988a).

I observed population fluctuations of this parasitoid and two of its hosts by collecting host cocoons for several consecutive winters. These populations were for Callosamia securifera in Berkeley Co., South Carolina, from 1972 to 1982, and Callosamia promethea in Walker Co., Texas, 1976 to 1982. It appears that the parasitoid first is not found in samples of host cocoons, then appears in small numbers, then dominates killing most hosts the following winter, and then both the host and parasitoid are rare after that. This cycle of movement of host populations followed by the parasitoid probably takes 7 to 12 years, and is complicated by the fact that other suitable host species (Automeris io, Antheraea polyphemus, etc.) are common in the same areas. Resident collectors could make valuable contributions to our understanding of the host-parasitoid interactions by collecting host cocoons in particular areas every winter and keeping records of numbers of cocoons collected, and of moths and wasps that emerge. Data for 20 or more years in habitats with moderate
alteration by human activity would be especially interesting. See similar remarks below for *E. lebophagus*.


91. *Enicospilus bozai* Gauld

**Hosts:** *Copaxa moinieri*

**Distribution:** Guanacaste and Puntarenas provinces, Costa Rica; Barro Colorado Island, Panama

**Biology:** There are two emergence peaks in lowland wet forests of Panama where many specimens have been collected at light: May to June and October to November. It is much less common in the dry forests of Santa Rosa National Park (now part of Guanacaste National Park) where adults fly from June to December.

**References:** Gauld (1988b: 123-124)

**Remarks:** Gauld (1988b) noted that *C. moinieri* does not occur at the Panama locality, so other species of *Copaxa* may serve as hosts.

92. *Enicospilus lebophagus* Gauld

**Hosts:** Rothschchildia lebeau, Rothschchildia forbesi, Rothschchildia cincta

**Distribution:** southern tip of Texas, through Mexico including Baja California, Guatemala, Costa Rica, and Panama

**References:** Peigler (1985a), Gauld (1988a, b)

**Remarks:** Taxonomists have been unable to decide if the host population in southern Texas known as *forbesi* is a full species or a subspecies of the more southerly and widespread *R. lebeau*. I list *forbesi* separately so that the host record will not be lost in future catalogs assembled by hymenopterists in the event that it is eventually demonstrated to be a full species. Note that *E. lebophagus* appears to be replaced as a parasitoid of Rothschchildia in southern Arizona (but not western Mexico) by *E. americanus*.

The species was referred to as "*Enicospilus* near, but not *americanus*" by Peigler (1985a). It was formally described by Gauld (1988a) using material from Costa Rica (type-locality: Santa Rosa National Park) collected by D. Janzen, from southern
Texas sent by me, and museum material from places between these northern and southern locales. I collected cocoons of the host moth in the lower Rio Grande Valley each winter from 1976 till 1982. The level of this parasitoid went from “absent” (not found) to abundant (killing more than half of all host pupae), back down to rare. The fluctuation of the host population is certainly related to this parasitoid, but is complicated by cold climate, the Texas populations being at the northern tip of the moth’s (and the parasitoid’s) range.

Specific records: *ex Rothschildia forbesi* Hidalgo and Cameron counties, Texas (BMNH, LACM); Bentzen-Rio Grande Valley State Park, Hidalgo Co., Texas, emerged 21 October 1981 and 6 April 1982 (overwintered twice), R. Peigler (DMNH); *ex Rothschildia sp.* (probably *cincta*) Jocotepec, Jalisco, Mexico, 1979, R. Halbert, identified from larval head capsule in cocoon of parasitoid (DMNH); *ex Rothschildia lebeau* Santa Rosa National Park, Guanacaste, Costa Rica. At light: Rancho San Bernardino, Baja California Sur, Mexico, 15 November 1961, det. H. E. Evans (SDNHM).

**93. Enicospilus plicatus** (Brullé)

**Hosts:** *Attacus atlas*, *Trabala vishnou* Lefebvre (Lasiocampidae), and an unidentified lasiocampid

**Distribution:** China (Guangdong, Guangxi, Fujian, Yunnan, Guizhou, Zhejiang, Anhui, Jiangxi, Hunan, Sichuan, Shaanxi, Xizang (=Tibet), Taiwan); Philippines; Indonesia (Greater Sunda Islands); Thailand; Vietnam; West Malaysia; India; Sri Lanka. See remarks below.

**Biology:** Tang (1990: pl. 30) showed the larval head capsule.


**Remarks:** There is some confusion regarding this species and its nearest relatives. Gauld & Mitchell (1981) and Tang (1990) cited *malayanus* Cameron as a synonym, but Nikam (1980) listed it as a separate species. Gauld & Mitchell considered *grandis* to be a separate species, giving a range for it in regions further west and north (India, Sri Lanka, and China) than they cited for *plicatus*. Tang listed 13 Chinese provinces for *plicatus*. Nikam gave India and Sri Lanka to Japan and New Guinea as the range of *malayanus*.

Specific record: *ex Attacus atlas*. West Malaysia, 1979, reared by Stefan Kager in Germany and sent to Peigler (BMNH).

**94. Enicospilus robertoi** Gauld

**Hosts:** *Hylesia lineata*

**Distribution:** Belize and the following provinces of Costa Rica: Alajuela, Guanacaste, Puntarenas.

**Biology:** This is a larval endoparasitoid. Larvae of the host collected in the fourth instar yielded the parasitoid larvae when mature, but before becoming pre-pupae. Parasitoid larvae presumably pupate in leaf litter or just below ground level. Adult parasitoids have emerged from hosts or been collected at lights in every month between January and July.

**References:** Janzen (1984), Gauld (1988b)

**95. Enicospilus texanus** (Ashmead)

**Hosts:** *Hemileuca oliviae*, *Hemileuca tricolor*, *Hemileuca maia*, *Hemileuca magnifica*, *Hemileuca slosseri*, *Hemileuca juno*, *Hemileuca griffini*, *Hemileuca peigleri*, *Hemileuca stonei*, *Hemileuca tricolor*
**Hemileuca nevadensis**, *Agapema anona*, *Agapema dyari*, *Agapema platensis*, *Olcellostera seraphica* (Dyar) (Bombycidae)

**Distribution**: Mexico (Chihuahua), United States (Arizona, California, New Mexico, Texas, Florida, Georgia, North Carolina, Virginia)

**Biology**: Specimens cited below as reared in January 1995 from cocoons in a screen cage emerged in early evening, after nightfall. I observed a mating of a pair that had emerged earlier the same evening. Mating commenced at 19:46 hours (Mountain Standard Time), and lasted 8 minutes. The female hung motionless from the top inside of the cage; the male hung motionless by his abdomen, straight down, with his legs free, his antennae forming a 90° angle to each other.

Although most of the known hosts pupate “underground”, they usually form pupae at ground level below debris, so the wasps would have minimal difficulty emerging from the pupal chamber.


**Remarks**: The records cited by Gauld (1988a) for this parasitoid attacking *Hemileuca maia* are probably based on *Hemileuca peigleri*, formerly considered to be a Texas subspecies of *H. maia*. However, it is very likely that *E. texanus* attacks *H. maia*, as the locality Gauld cited of Highlands, North Carolina, has granite outcrops that support populations of *H. maia*, and no other suitable host occurs there.

There has been confusion regarding the record of *Olcellostera seraphica* from western Texas. Larvae of this bombycid (formerly in Apatelodidae, see Minet 1994) are found on the same host plant (*Chilopsis*) as the larvae and cocoons of a geometrid *Encaterua variaria* Grote, which resulted in confusion in rearings by Kendall. A specimen of *E. texanus* reared by Kendall from *Olcellostera* in my opinion was mislabeled as being reared from *Encaterua*, and the specimen was donated to the U. S. National Museum. Gauld (1988a) doubted this record, as do I, because the host moth is too small to support this parasitoid. The report of this wasp attacking *O. seraphica* was given by Peigler & Kendall (1993), but unfortunately reported again erroneously as reared from the geometrid by Peigler (1994). The record for *Olcellostera seraphica* is entirely logical; it has a large hirsute larva that pupates in soil, and is phylogenetically related to Saturniidae (*Agapema, Hemileuca*).

The coloration of adult parasitoids ranges from normal orange brown (like Figure 3) to a dark blackish red. The wings may be clear or smoky. Specimens reared from *Agapema anona* are small, very dark, and have smoky wings. Those reared from *Hemileuca junio* are orange brown or darker, with clear or lightly smoky wings. Those reared from *Hemileuca slosseri* have orange brown bodies and smoky wings. Gauld (1988a) noted that material he saw reared from *Hemileuca tricolor* differed from typical *E. texanus*. Tuskes et al. listed the ones reared from *H. tricolor* as “*Enicospilus* near texanus.” More than one species may be involved.


96. *Enicospilus ugaldei* Gauld

**Hosts:** *Automens tridens*

**Distribution:** Guanacaste Province, Costa Rica; Chiapas, Quintana Roo, and San Luis Potosí, Mexico

**Biology:** Specimens from Costa Rica were collected in October to December, in Mexico June to September. The species is not common.

**References:** Gauld (1988b: 161-164)

97. *Enicospilus sp.*

**Hosts:** *Hemileuca sororius*

**Distribution:** Baja California Sur, Mexico

**Remarks:** Stated to be rare. Placed under the genus *Primophion* by Townes & Townes (1973)

98. *Euryophion adustus* (Townes)

**Hosts:** *Pseudobunaea paratyrrhena*

**Distribution:** West and central Africa, including Zaïre, Malawi, and Nigeria

**Remarks:** Townes & Townes (1973: 168), Gauld & Mitchell (1978: 26-27)

99. *Euryophion latipennis* (Kirby)

**Hosts:** *Bunaea alcinoe caffra*, *Imbrasia macrothyris*, *Janomima westwoodi* Aurivillius (Eupterotidae)

**Distribution:** Over much of sub-Saharan Africa, including Zaïre, Uganda, Zimbabwe, Ghana, Gabon, Namibia, Sierra Leone, Nigeria, Angola, and the Central African Republic.

**References:** Townes & Townes (1973: 169), Gauld & Mitchell (1978: 24-25)

100. *Euryophion nigripennis* Cameron

**Hosts:** *Imbrasia belina*

**Distribution:** Africa

**Biology:** The parasitoid was reared from the host larva at Ndumu, Natal, South Africa by Oberprieler.

**References:** Townes & Townes (1973: 169), Oberprieler (1990), Gauld & Mitchell (1978: 24)
101. *Euryophion ikuthana* (Kriechbaumer)

**Hosts:** *Usta terpsichore*

**Distribution:** Africa


**Remarks:** Some have referred to this parasitoid as *Rictophion ikuthana*, but Gauld (1985) synonymized that generic name under *Euryophion*. Oberprieler reared what is probably this parasitoid from the same host species.

102. Ichneumonidae, genus undetermined

**Hosts:** *Saturnia cephalariae*

**Distribution:** Turkey

**References:** Romanoff (1885: 18)

**Remarks:** Romanoff wrote "Ces chenilles sont pour-suivies par une grande espèce d'Ichneumon et une grande Tachina."

103. Ichneumonidae, genus undetermined

**Hosts:** *Opodiphthera astrophela*

**Distribution:** Australia

**Biology:** Froggatt wrote that this species is "very subject to the attacks of ichneumons."

**References:** Froggatt (1907: 259)

**Remarks:** Froggatt used the name *Antheraea simplex* for the host moth.

104. Ichneumonidae, genus undetermined

**Hosts:** *Hemileuca eglanterina*

**Distribution:** western Canada

**Biology:** The parasitoid was reared from a second instar larva and made a white, translucent ovoid cocoon that was 5 mm long.

**Remarks:** Specific record: *ex Hemileuca eglanterina:* Vasoux Lake, British Columbia, June 1988, Stephen Ife (BMNH). I sent this specimen to BMNH in 1988. It was given to me by S. E. Stone. It is a small species, about the size of *Isidromas*.

105. Ichneumonidae, genus undetermined

**Hosts:** *Hemileuca electra*

**Distribution:** southwestern United States

**Biology:** Two specimens were reared from second instar larvae. The dried larval host remains were alongside light ovoid cocoons attached lengthwise to a twig. Cocoons were 6 mm long. The host larvae were collected in the field 5 km N of Four Peaks Road, Highway 87, Maricopa Co., Arizona, on 19 February 1987 by Patrick Savage, and the two wasps emerged 28 March 1987.

**Remarks:** I sent these specimens to BMNH in 1988.

**Family Braconidae**

The braconids are closely related to ichneumons (both are in the superfamily Ichneumoidea), but are generally smaller. There are many thousands of species, all of which are parasitoids. The records below are comparatively few because most braconids that parasitize saturniids are koinobionts that attack young larvae. As pointed out in the introduction to this catalog, Saturniidae are less often collected as larvae, especially in the early instars.
Most of the species of the Microgastrinae (=Microgasterinae) listed below were formerly classified in the huge, worldwide genus *Apanteles*. The work of Mason (1981) with amendments by Walker et al. (1990) will be useful to anyone trying to key specimens. Some of those listed in that genus below will be assigned to other genera with more study. They are all tiny black wasps that look much alike to the untrained eye and without magnification. Some other Braconidae are brightly colored. Some are diurnal, others nocturnal.

**Subfamily Macrocentrinae**

106. *Macrocentrus ancyliorus* Rohwer

**Hosts:** *Eacles imperialis magnifica*

**Distribution:** Brazil

**References:** d’Araújo e Silva et al. (1968: 261)

**Subfamily Microgastrinae**

107. *Protapanteles immunis* (Haliday)

**Hosts:** *Saturnia pavonia, Orgyia antiqua* (Linnaeus) (Lymantriidae), and many other Lepidoptera including mostly Geometridae but also Lycaenidae, Noctuidae, Tortricidae, Plutellidae, and Coleophoridae

**Distribution:** Europe, including Britain

**Biology:** The larvae of the hosts are attacked, and the adult parasitoids emerge from host larvae before the latter reach maturity.


**Remarks:** This genus is very closely allied to *Glyptapanteles* and *Cotesia*.

108. *Glyptapanteles maculitarsis* (Cameron)

**Hosts:** *Imbrasia cytherea, Imbrasia zambesina, Imbrasia wahlbergii, Imbrasia tyrhrea, Aurivillius aratus, Bunaea alcinoe, Gynanisa maja, Lechriolepis basirufa* Strand (Lasiocampidae), *Pachypasa* (Lasiocampidae), *Spodoptera exempta* (Walker) (Noctuidae), *Busseola fusca* (Fuller) (Noctuidae)

**Distribution:** Sierra Leone and Nigeria across to Kenya and south to South Africa

**Biology:** The very young larvae of the host are attacked. Tooke & Hubbard wrote that eggs are laid on the host, parasitoid larvae feed externally, and the cocoons are attached to the host. There may be a large number on each host. They reported a high incidence of parasitism at the locality of Wolwekloof. According to van den Berg, this braconid caused highest mortality of the pest host among several other parasitoids. Host larvae that feed externally are preferred according to Walker; only the latter host in the above list is an internal feeder.

**References:** van den Berg (1974), Geertsema (1975), Tooke & Hubbard (1941: 51-52), Walker (1994)

**Remarks:** Van den Berg cited the host, which is a pest called the pine emperor, under the name *Nudaurelia cytherea clarki* Geertsema. This parasitoid species was not listed by Mason (1981).

109. *Apanteles anagleti* Muesebeck

**Hosts:** *Antheraea paphia, Ectomyelosis creatoninae* (Pyralidae)

**Distribution:** northeastern India

**Biology:** The second instar is the main stage attacked, although third and fourth
instars may also be attacked. The fifth (final) instar is not attacked. Larvae feed internally and then emerge to spin cocoons on the surface of the host. The whitish cocoons are formed on and alongside the host larva in a mass, and measure 3 to 4 mm long. The life cycle is completed in 10 to 15 days. Almost 200 wasps may emerge from a single host. Parasitism of the second brood (i.e., second crop) of tasar larvae in September was found to be as high as 40%.

**References**: Kole & Chatterjee (1995), Thangavelu et al. (1988)

**Remarks**: This parasitoid is harmful to the production of tasar silk by destroying larvae of the host before they spin cocoons. Earlier reports by Indian authors of "Apanteles sp." and "Apanteles glomeratus" attacking *Antheraea paphia* and *A. assamensis* may refer to this species. Probably dozens of species of Microgastrines have been reported under the name *A. glomeratus* in literature. *Antheraea paphia (=mylitta)* and *A. assamensis* produce tasar and muga silks, respectively. These parasitoids are thus detrimental to the national economy of India.

110. *Apanteles* spp.

**Hosts**: *Saturnia mendocino*, *Automeris* spp.

**Distribution**: northern California and Brazil

**Biology**: Tilden reared the Californian ones from larvae of the first cited host collected in the Santa Cruz Mountains in July 1941.

**References**: Tilden (1945), Ferguson (1972: 181), d’Araújo e Silva et al. (1968: 263)

**Remarks**: The California parasitoid could be *Cotesia electrae* which attacks the phylogenetically related *Agapema* and the ecologically related *Hemileuca* in western North America. It could also be *Cotesia teleae*, or an undescribed species of *Apanteles* or *Cotesia*. Tuskes et al. (1996) cited it as *Cotesia*. The Brazilian record is probably not for a true *Apanteles*, but for another microgastrine.

111. *Dolichogenidea aethiopica* (Wilkinson)

**Hosts**: *Holocerina angulata*, *Imbrasia tyrribe*, and several other Lepidoptera in Arctiidae, Lasiocampidae, Noctuidae, Nymphalidae, Pyralidae, and Zygaenidae

**Distribution**: widespread in sub-Saharan Africa

**References**: Walker (1994)

**Remarks**: A synonym of this parasitoid is *Apanteles procerae*.

112. *Apanteles* spp.

**Hosts**: *Antheraea assamensis*, *Loepa katinka*, *Samia walkerii*, *Antheraea yamamai*, *Attacus atlas*

**Distribution**: Eastern Asia

**Biology**: Thangavelu et al. indicated that the first to third instar larvae of *A. assamensis* are attacked.


**Remarks**: Several unidentified species of microgastrines were reported as "*Apanteles* sp." by the above authors. The report by Peigler (1989) for *A. atlas* in Taiwan was from Shui-Chen Chiu of the Taiwan Agricultural Research Institute. Mike Bascombe sent specimens reared in Hong Kong from *S. walkerii* and *L. katinkato* to me, and I submitted them to K. van Achterberg who gave these general identifications (Peigler 1985a), indicating that there are no good keys to species of the world fauna.

Specific records: *ex Loepa katinka*: Hong Kong, 1981, from mature host larva, M. J. Bascombe (DMNH); *ex Samia walkerii*: Hong Kong, 1981, from young host larva, M. J. Bascombe (DMNH).
113. *Cotesia anisotae* (Muesebeck)

**Hosts:** Anisota discolor, Anisota senatoria, Anisota fuscosa, Anisota stigma, Anisota pulluloida, Dryocampa rubicunda

**Distribution:** New Brunswick and Ontario to Florida and Texas

**Biology:** Parasitoid cocoons are generally seen on host larvae in the third and fourth instars. Larger host larvae support more parasitoids, but the number rarely exceeds ten. The cocoons are spun on and attached to the integument of the host, and are light yellowish. Hyperparasitism in Texas was by the eulophid *Horismenus floridanus* (see under that species).


**Remarks:** Surprisingly, I have not encountered this parasitoid in the Carolinas or Georgia, despite the fact that the host genus is abundant in those areas.


114. *Cotesia electrae* (Viereck)

**Hosts:** Agapema anona, Agapema dyari, Agapema platensis, Agapema homogena, Automeris io, Coloradia pandora, Coloradia doris, Hemileuca nevadensis, Hemileuca slosserii, Hemileuca electra, Hemileuca eglanterina, Hemileuca nuttalli, Hemileuca hera, Hemileuca magnifica, Hemileuca chinatiensis conwayae, Hemileuca diana, Hemileuca stonei, Hemileuca tricolor, Hemileuca oliviae, Hemileuca burnsii, Dirphia sp.

**Distribution:** western half of United States; British Columbia; Baja California Norte and probably other states in northern Mexico

**Biology:** Cocoons of the parasitoid are usually seen on the third to fifth instars, sometimes the second. Most species of *Hemileuca* have at least six larval instars.


**Remarks:** Specific records: *ex Coloradia doris:* Horsetooth Reservoir, Larimer Co., Colorado, 10 July 1985, D. Leatherman (CSU, DMNH); *ex Hemileuca electra:* El Pedregoso, 765 m, Baja California Norte, April 1989, K. L. Wolfe (DMNH, CUAC, BMNH); 6 km N of Cataviña, 23 January 1988, P. Savage (DMNH, USNM); *ex Hemileuca nevadensis:* Jacks Canyon, Navajo Co., Arizona, June 1987, M. J. Smith (DMNH, CUAC, USNM, BMNH); 10 km S of Byers, Arapahoe Co., Colorado, June 1991, R. S. Peigler (DMNH, BMNH); Pawnee Buttes, Weld Co., Colorado, 5 July 1985, D. Leatherman (DMNH); *ex Hemileuca magnifica:* Jaroso, Costilla Co., Colorado, September 1985, S. E. Stone (LACM); *ex Hemileuca slosserii:* 10 km SE of Wellman, Terry Co., Texas, May 1981, R. O. & C. A. Kendall (DMNH, BMNH, RMNH); *ex Hemileuca chinatiensis conwayae:* Culberson Co., Texas, April 1981, R. & C. Kendall (RMNH); *ex Agapema homogena:* Tucson, Pima Co., Arizona, 5 April 1988 (DMNH, BMNH); *ex Agapema dyari:* Reeves Co., Texas, April 1981, R. O. Kendall (TAMU); *ex Agapema platensis:* Kinney Co., Texas, 20-22 February 1989, R. O. Kendall (TAMU); *ex Hemileuca diana:* Schnebly Hill overlook, 8 km E of Sedona, Coconino Co., Arizona, 23 May 1987, P. Savage (USNM); Hualapai Mtn. Park, SE of Kingman,

It is clear that this parasitoid attacks virtually all species of *Agapema* and *Hemileuca* (Hemileuca, Coloradia) except *Automeris* in western North America, especially the Southwest. It lives in many diverse habitats including grassland prairies, arid deserts, oak/pine forests, and riparian zones. The saturniid hosts that are used and not used coincide exactly to those of *Enicospilus texanus*, as discussed under that species above.

115. *Cotesia hemileucae* (Riley)
**Hosts:** *Automeris io, Hemileuca maia*
**Distribution:** Massachusetts to Florida, Kansas, Missouri, Minnesota, Oregon
**Remarks:** Scott Shaw, who gave me the specimens cited below, compared these to specimens I had of *C. electra* and said the two species are very distinct from one another.

Specific record: *ex Automeris io* Keys, E9, Florida, 12-10-1967 [October or December?], D. Simberloff (DMNH).

116. *Cotesia melanoscela* (Ratzeburg)
**Hosts:** *Hemileuca maia*
**Distribution:** Europe; North Africa; introduced to North America, recorded from eastern Canada and Massachusetts to British Columbia, Washington, and Oregon
**References:** Thompson (1944: 294), P. M. Marsh (*in* Krombein et al. 1979: 250), Mason (1981: 112)
**Remarks:** This wasp was apparently introduced to North America from Europe as a control of the gypsy moth. It was cited as attacking *Hemileuca maia* by Thompson, but this record was not repeated by Marsh who probably considered it to be unreliable.

117. *Cotesia telea* (Muesebeck)
**Hosts:** *Antheraea polyphemus, Citheronia regalis*, possibly *Actias luna* (see Remarks below)
**Distribution:** Connecticut, Pennsylvania, Maryland
**References:** P. M. Marsh (*in* Krombein et al. 1979: 255), Mason (1981: 113)
**Remarks:** This may be the species which was found to attack small (1st and 2nd instar) larvae of *Actias luna* by Fiske and Thompson (1909: 460); their reference to larvae of *Antheraea polyphemus* being attacked in the same experiments probably refers to this species of parasitoid. The specific name comes from the generic name of the host, *Telea*, a synonym of *Antheraea*.

118. *Cotesia sp.* (Figure 6)
**Hosts:** *Hyalophora columbia gloveri, Hyalophora cecropia*
**Distribution:** Utah, California, Colorado
Biology: Numerous cocoons, usually over 50, are seen on the host larva.

References: Duncan (1941: 40), Peigler (1985a)

Remarks: The specimens from Utah and California look identical to me, but I am not able to say with certainty if they represent one or two species. The material from Colorado was reported as Apanteles sp. under its hyperparasitoid Gnotus by Peigler (1985a).

Specific records: ex Hyalophora columbia gloveri: 32 km east of Nevada City, 1525 m, Mono Co., California, 19 August 1995, M. M. Collins (DMNH, CUAC, BMNH) [host is not native to that locality, but Hyalophora euryalus is]; Spanish Fork, Utah, August 1991, J. B. Duncan (BMNH, DMNH); ex Hyalophora cecropia: Aurora, Colorado, 1982, S. Stone (pers. comm).

Eliot & Soule (1902: 256-257) reported a species of Cotesia or Apanteles under the name Microgaster as parasitizing Hyalophora cecropia in Massachusetts. It made white or yellow-brown cocoons on the host larvae. It is possible that all of these records from Massachusetts, Colorado, Utah, and California refer to one widespread species of Cotesia that specializes on Hyalophora.

119. Cotesia sp.

Hosts: Saturnia pavonia

Distribution: central Europe

Biology: At least 6 parasitoids were reared from a larva of the host species.

References: Mason (1981), Papp (1990)

Remarks: This material does not appear to me to be of the genus Protapanteles. Papp listed numerous European species of Cotesia, so perhaps it is one of those.

Specific record: ex Saturnia pavonia: Kopernica, Czech Republic [or Slovakia?], July 1988, Michael Klingner (DMNH). The dark yellow cocoons are included with the series of specimens.

120. Microplitis aduncus Ruthe

Hosts: Saturnia pavonia

Distribution: Germany

References: Thompson (1944: 535)

Subfamily Euphorinae

121. Meteorus eaclidis Muesebeck

Hosts: Eacles imperialis magnifica

Distribution: Brazil

Biology: Crocomo & Parra reported that 86 parasitoids emerged from the one host larva.

References: Crocomo & Parra (1979: 70), d'Araújo e Silva et al. (1968: 261)

Remarks: Crocomo & Parra erroneously cited this parasitoid as belonging to the Eulophidae. They obtained one rearing from Ouro Fino, Minas Gerais, a Brazilian state north of where the above host is known to occur. The host may have actually been another species of Eacles. As parasitoids of E. i. magnifica, d'Araújo e Silva et al. cited both Meteorus sp. and M. eaclidis.

122. Meteorus hyphantriae Riley

Hosts: Hemileuca maia, many other Lepidoptera

Distribution: Canada to Mexico

References: Thompson (1944: 294)
Remarks: The record listed below under no. 124 probably belongs under this species.

123. *Meteorus luridus* Ruthe
Hosts: *Saturnia pavonia*
Distribution: Europe
Biology: Probably a gregarious primary, larval parasitoid.
References: Rougeot (1971: 107)

124. *Meteorus* sp.
Hosts: *Hemileuca maia*, *Hemileuca lucina*
Distribution: northeastern United States
References: Schaffner & Griswold (1934), Thompson (1944: 293-294)
Remarks: The host was cited by Schaffner & Griswold as *Hemileuca maia* and/or *lucina*.

125. Subfamily Rogadinae, genus undetermined
Hosts: *Ludia delegorguei*
Distribution: southern Africa
Biology: Reared from the larva of the host.
References: R. Oberprieler (unpubl.)

Superfamily Chalcidoidea
This superfamily is a huge one, consisting of thousands of species worldwide and more than 15 families. Commonly called chalcids (pronounced KAL-sidz), they are among the most important insects in biological control. Some are mass reared in insectaries for use in agroecosystems or to combat forest pests. Some are parasitoids of larvae or pupae, particularly Lepidoptera, but most of the smaller ones attack insect eggs. These egg parasitoids are classic idiobionts. Some are hyperparasitoids. It appears that most are diurnal, and they are rarely collected at lights.

Family Torymidae
126. *Monodontomerus minor* (Ratzeburg)
Hosts: *Gambrus extrematis*
Distribution: Europe; New England to Virginia to California
Biology: This is a hyperparasitoid of *Gambrus extrematis* and possibly tachinids in cocoons of *Hyalophora*.
Remarks: Specific records: *ex Gambrus extrematis* in *Hyalophora cecropia*: Aurora, Colorado, 1980, S. Stone (USNM); Aurora, Colorado, spring 1988, R. S. Peigler (DMNH), Denver, Colorado, 1982. S. Stone (USNM);
Gupta (1987: 503) cited a record for the Holarctic *Monodontomerus dentipes* (Dalman) as a hyperparasitoid of *Dendrolimus* (Lasiocampidae) attacking the ophionine ichneumonid *Dicamptus nigropictus* in Asia.

127. *Microdontomerus fumipennis* Crawford
Hosts: *Hemileuca magnifica*, *Enicospilus texanus* (Ichneumonidae), *Malacosoma* (Lasiocampidae), *Choristoneura rosaceana* (Harris) (Tortricidae)
Distribution: southwestern United States
Biology: Apparently a facultative hyperparasitoid. It was reared as a primary parasitoid from larvae of *Hemileuca magnifica*, although this should be verified if puparia of tachinids were kept in the same rearing cage. It was also reared from a single cocoon of *Agapema anona* containing a cocoon of *Enicosiphis texanus*. The ophionine cocoon had four emergence holes in the side. I do not know if the ovipositing female of *M. fumipennis* oviposited into the larva of *Agapema* or the cocoon of *Enicosiphis*.


Hyperparasitism in cocoons of *Enicosiphis* is known in other cases. Ferrière reported an example of a eupelmid hyperparasitoid in *Enicosiphis cohacarrum* Seyrig in *Borocera* (Lasiocampidae) in Madagascar. Many moth cocoons yielded the eupelmids, all of which contained cocoons of the ophionine. The cocoons of *Borocera* are used to make landibe silk fabrics.

128. *Microdontomerus* sp.

Hosts: *Hemileuca oliviae*

Distribution: Chihuahua

Biology: A parasitoid in eggs of the host. Fritz et al. pointed out that this species may actually be a hyperparasitoid on *Anastatus*, and I agree that this is likely.

References: Fritz et al. (1986)

Remarks: Judging from the distributions of the three North American species listed by E. Grissell (in Krombein et al. 1979: 764), the record here from Chihuahua is probably *M. fumipennis*.

129. *Perissocentrus chilensis* Crawford

Hosts: *Cercophana frauenfeldi*, *Ormiscodes cinnamomea*, *Tanatopsyche chilensis* Phil. (Psychidae?)

Distribution: Chile

References: De Santis (1979: 25)

Remarks: The second host listed above was cited by De Santis as *Ormiscodes crinata*.

130. *Perissocentrus* sp.

Hosts: Hyperparasitoid in the tachinid *Zygofrontina* in *Rothschildia*

Distribution: Brazil

Biology: A hyperparasitoid, but I do not know whether facultative or obligatory.

References: d’Araújo e Silva et al. (1968: 270)

Family Eurytomidae

131. *Eurytoma* sp.

Hosts: Hyperparasitoid in *Glyptapanteles maculitarsis* and *Theronia* in *Imbrasia cytherea*

Distribution: South Africa

Biology: The eurytomid develops as a hyperparasitoid in cocoons of the braconid *Glyptapanteles maculitarsis* and the ichneumonid *Theronia*. As with the closely related perilampids (see below) it probably oviposits into the primary host, in this case the saturniid.

Remarks: Eurytomidae are a diverse family that are poorly known taxonomically. It is possible that this parasitoid belongs to a different genus in Eurytomidae. Boucek described several new genera from the Australasian region, yet listed 67 species of under *Eurytoma* from that area. The genus remains a depository for unplaced eurytomids.

**Family Perilampidae**

These small wasps have a metallic blue coloration. The thorax and propodium are robust, the gaster very small. Some species are always primary endoparasitoids, while others are obligate hyperparasitoids. Apparently all are koinobionts. There are many species in the genus *Perilampus*, including the four species below. B. D. Burks (*in* Krombein et al. 1979: 770) treated this group as a subfamily of Pteromalidae.

132. *Perilampus carolinensis* (Smulian)

**Hosts:** *Anisota senatoria*

**Distribution:** North Carolina to Vermont

**Biology:** Probably always a hyperparasitoid according to C. Darling (pers. comm.), but available rearing records are not sufficient to be certain.

**References:** Burks (*in* Krombein et al. 1979: 771), Riotte & Peigler (1981: 121)

**Remarks:** This and the following species are very closely related.

Specific records: *ex Anisota senatoria*: Patuxent Wildlife Refuge, Bowie, Maryland, 11-6-1945, R. T. Mitchell (ROM).

133. *Perilampus hyalinus* (Say)

**Hosts:** Hyperparasitoid in tachinids (*Lespesia anisotae* and *Belviosia bifasciata*) in *Anisota senatoria*, and in tachinids in *Hyalophora cecropia*

**Distribution:** Mexico, Puerto Rico, Peru, Canada (Québec to British Columbia), United States (Florida to California)

**Biology:** In coastal Virginia, Coffelt and Schultz found that this hyperparasitoid killed 2% of *Lespesia anisotae* and 23.5% of *Belviosia bifasciata*. De Santis cited two nonsaturniid hosts.


**Remarks:** The two specimens reported by Peigler (1985a) were reared as hyperparasitoids (I observed these emerging from tachinid puparia). They are likely *hyalinus*, instead of *carolinensis* as I reported there.

Specific records: *extachinid (perhaps Lespesia anisotae)* in *Anisota peigleri*: Greenville, South Carolina, May-June 1980, T. C. Boozer (LACM); collected in field: 30 km E of Denver, Arapahoe Co., Colorado, 10 July 1988, R. S. Peigler & M. J. Smith (DMNH); County 88, Iowa, 24 July 1939, 9 July 1940, County 70, Iowa, 28 July 1957, W. W. Steinmetz (DMNH). The material from Colorado and Iowa was identified by C. Darling (ROM) in 1995.

134. *Perilampus maurus* (Walker)

**Hosts:** *Imbrasia tyrrea*

**Distribution:** Africa

**Biology:** Possibly a hyperparasitoid in tachinid or ichneumonid parasitoids of the moth host, or possibly a primary endoparasitoid.

**References:** Packard (1914: 268)

**Remarks:** Packard indicated that the host record was cited by Walker, I assume in the original description. Packard cited the host under the name *Thyella tyrrea*.
135. Perilampus paraguayensis (Girault)
Hosts: Hyperparasitoid in the tachinid Zygofrontina in Rothschildia
Distribution: South America
Biology: A hyperparasitoid in tachinids. De Santis cited two non-saturniid hosts, at least one of which is a dipteran.
References: d'Araujo e Silva et al. (1968: 270), De Santis (1979: 111)

Family Pteromalidae
136. Pteromalus hemileucae Gahan
Hosts: Hemileuca oliviae
Distribution: Mexico and New Mexico
References: Peck (1963: 938), Burks (in Krombein et al. 1979: 809)
Remarks: Peck misspelled the specific name as semileucae.

137. Pteromalus communis Nees
Hosts: Saturnia pyri
Distribution: Europe
References: Rougeot (1971: 92)

138. Pteromalus sp.
Hosts: Hyperparasitoid in Hyposoter fugitivus in Anisota senatoria
Distribution: coastal Virginia
Biology: Reared as a hyperparasitoid of Hyposoter fugitivus. It is a gregarious endoparasitoid that may be a primary or secondary parasitoid. A mean number of 1.9 was reared from cocoons of H. fugitivus.
References: Goffelt & Schultz (1993b), Burks (in Krombein et al. 1979: 809-810)
Remarks: The authors stated that this parasitoid may be Pteromalus puparium, according to E. E. Grissell, but species in the group are difficult to identify pending a revision.

A note sent by T. Pergande to Packard (1914: 196) read “A. H. Mundt, of Fairbury, Ill., sent eggs of T. (Tropaea=Actias) luna which were infested with what was supposed to be a species of Pteromalus.” Considering the mass confusion of the chalcidoid groups by many entomologists, I believe this record could refer to several possible species in several families.

139. Pteromalus sp.
Hosts: Saturnia pavonia
Distribution: Europe
References: Rougeot (1971: 107)
Remarks: There is a possibility that this record belongs under the following species of European pteromalid.

140. Eupteromalus arzoneae Boucek
Hosts: Hyperparasitoid in Pales pavida (Tachinidae) in Samia cynthia
Distribution: Northern Italy
Biology: Ovipositing females of this hyperparasitoid are able to detect and parasitize larvae of the tachinid within the caterpillars of the primary host. After the tachinid maggots form their puparia, the development of E. arzoneae continues. After about 20 days, adults of E. arzoneae emerge through a small hole which they chew in the side of the puparium. Nine to 18 individuals emerge from each puparium. These then
exit through a small hole they chew in the side of the moth cocoon, or via the pre-formed exit at the top of the cocoon.

References: Arzone (1971a)
Remarks: A detailed account of this hyperparasitoid was given by Arzone, along with photographs. See also texts of *Pales pavida* and *Anastatus bifasciatus* in this catalog.

141. *Pachyneuron porteri* (Brèthes)
Hosts: *Ormiscodes rufosignata*
Distribution: Chile
Remarks: The host was cited by De Santis under the synonym *Catocephala rufosignata*.

142. *Psychophagus omnivorus* (Walker)
Hosts: *Hyalophora cecropia*, numerous other Lepidoptera, Diptera, and Hymenoptera
Distribution: Europe; introduced to North America in 1890s, now found from Québec to Delaware, west to Wisconsin and Colorado
Biology: A primary and a secondary (hyperparasitoid) parasitoid.
Remarks: It seems likely that this species of parasitoid can be reared from several Saturniidae, since it is a hyperparasitoid on several of their known primary parasitoids, such as *Compsilura concinnata* (Tachinidae).

143. *Tritneptis doris* Burks
Hosts: *Coloradia doris, Hemileuca* sp.
Distribution: Utah and Wyoming
Remarks: The host was cited by De Santis under the synonym *Catocephala rufosignata*.

144. *Dibrachys cavus* (Walker)
Hosts: *Hyalophora cecropia, Hyalophora columbia gloveri, Actias luna*, numerous other Lepidoptera, Hymenoptera, and Diptera
Distribution: worldwide, in North America including Alaska to Florida
Biology: Extremely polyphagous. It can be a primary, secondary, or tertiary parasitoid. Among the more than 100 hosts listed by Burks, there are several which are parasitoids and hyperparasitoids of Saturniidae, including ones in Tachinidae, Ichneumonidae, Braconidae, and Chalcidoidea.
Remarks: The host was cited by De Santis under the synonym *Catocephala rufosignata*.

145. *Agiommatus attaci* Ferrière
Hosts: *Attacus atlas*
Distribution: West Malaysia to western Java
Biology: Eggs of the host moth are attacked.
Remarks: Since this species was not included in the monograph of Boucek, I am not certain if it has been reassigned to a different genus since the original description.
Specific record: ex Attacus atlas Lake Toba, near Brastagi, Sumatera Utara, Sumatra, Indonesia, 8 October 1986, U. Paukstadt (DMNH).

147. Agiommatus sp.
Hosts: Antheraea spp.
Distribution: Australasia
Biology: Eggs of the host are attacked.
References: Boucek (1988: 458)
Remarks: If the host records come from the Papuan region, they may be erroneous, and actually refer to Syntherata or Opodiphthera, species of which are often misclassified as Antheraea.

148. Agiommatus sp.
Hosts: Antherina suraka
Distribution: Madagascar
Biology: Griveaud stated that the eggs of the host are strongly infested by this parasitoid and Mesocomys.
Remarks: Although the type species of the genus was described from Sumatra, the parasitoid reported by Griveaud (1962) may in fact be a true Agiommatus. In his monograph, Boucek (1988) described many new genera in the Pteromalalini, but indicated that this genus does range in Madagascar.

Family Chalcididae
These are on average the largest chalcids. The family has been spelled Chalcidae in much literature. Adults typically have enlarged hind femora which make recognition easy. Boucek (1988) downgraded the subfamily Brachymeriinae to the tribe Brachymeriini, within the Chalcidinae.

149. Ceratosmicra albifrons (Walsh)
Hosts: Hyperparasitoid in Hyposoter fugitivus in Anisota senatoria, many Lepidoptera including Microlepidoptera and Noctuidae, also several parasitic Hymenoptera
Distribution: Québec and Maine to Florida; British Columbia to Mexico
Biology: The wasp is probably a facultative hyperparasitoid. It is not known if C. albifrons would oviposit into a healthy larva of Anisota, or must find a larva that is mummified containing a cocoon of the primary parasitoid H. fugitivus. The parasitism appears to be similar to that observed for Ceratosmicra meteori in the southeastern United States.
Remarks: Specific record: ex Anisota senatoria: Patuxent Wildlife Refuge, Maryland, 8 October 1951, R. T. Mitchell (DMNH). This specimen given to me by Mitchell has a dried cocoon of Hyposoter fugitivus (in a mummified larva of Anisota senatoria) pinned below it with an exit hole in the side.
This species was classified under the genus Conura by Delvare (1992). He considered Spilochaleis, Conura, and Ceratosmicra to be three subgenera of Conura, pointing out his reasons for considering each of the three groups to be monophyletic.
Therefore, such an arrangement is subjective. I, also subjectively, choose to retain
the three groups as full genera. Subgeneric usage has been accepted much more
extensively in the classification of Hymenoptera, than in that of Lepidoptera. Several
authors have listed this species previously under the generic name *Spilochalcis*.

150. *Ceratosmicra meteori* Burks

**Hosts:** Hyperparasitoid in *Hyposoter fugitivus* in *Dryocampa rubicunda*, *Anisota fuscosa*,
*Anisota peigleri*, *Anisota senatoria*

**Distribution:** Massachusetts to Washington State, down into Mexico

**Biology:** Apparently this species is usually or always a hyperparasitoid of Braconidae
and small Ichneumonidae. It is the most abundant of all hyperparasitoids attacking
*H. fugitivus* in Virginia according to Coffelt & Schultz.

**References:** Burks (1979: 868), De Santis (1979: 54), Riotte & Peigler (1981),

**Remarks:** This species was listed by Delvare in the genus *Conura* and subgenus
*Ceratosmicra*. See remarks above pertaining to generic classification in this group.

Specific records: All hyperparasitoids in *Hyposoter fugitivus: ex Dryocampa rubicunda*,
Greenville, South Carolina, June 1980, R. S. Peigler (LACM); *ex Anisota fuscosa*,
Brazos and Walker counties, Texas, 1976, R. S. Peigler (USNM); *ex Anisota peigleri*,
Henderson Co., North Carolina, September 1974, David Montross (USNM); Clemson,
South Carolina, 10 September 1976, R. Peigler (USNM); Seneca, South Carolina, 30
September 1975, R. S. Peigler (USNM); *ex Anisota senatoria*, Patuxent Wildlife
Refuge, near Laurel, Maryland, R. T. Mitchell; Stubblefield Lake, Walker Co., Texas,
October 1979, G. W. Brooks (DMNH); collected with net: Walsenburg, Huerfano

151. *Conura maria* (Riley) (Figure 5)

**Hosts:** *Samia cynthia*, *Rothschildia cincta*, *Rothschildia forbesi*, *Callosamia angulifera*,
*Callosamia promethea*, *Hyalophora cecropia*, *Antheraea polyphemus*, *Agapema anona*,
*Hemileuca oliviae*, *Hylesia, Thyridopteryx ephemeraeformis* (Haworth) (Psychidae)

**Distribution:** North America, Central America, Trinidad, probably northern South
America

**Biology:** Emergence patterns of adults were tabulated in Packard (1914) and Peigler
(1985a). Frank stated that the percent parasitization of *Samia cynthia* in Philadelphia
was as high as 85%. This chalcid and other closely related ones are koinobionts.
This species is a larval-pupal parasitoid.

**References:** Packard (1914: 247, 268), Collins & Weast (1961), Peck (1963: 938), De
Santis (1979: 48), Burks (in Krombein et al. 1979: 866), Peigler (1977, 1985a), Frank
(1986), Fritz et al. (1986), d’Araújo e Silva et al. (1968), Young (1985), Weast (1989: 6),
Delvare (1992: 253), Tuskes et al. (1996)

**Remarks:** Although I retain the three subgenera as full genera in this group, this
species, long known in most literature under *Spilochalcis mariae*, actually belongs to
the subgenus *Conura* as defined by Delvare. The original spelling of the specific
epithet is to be preserved, *maria* instead of *mariae*, as noted by Delvare.

It is interesting to note that there are few host records for the genus *Hyalophora*.
Hosts with hanging cocoons appear to be especially attacked. Although most species
of *Hemileuca* form their pupae at ground level, that of *H. oliviae* is in a weak cocoon
among weeds, well above ground level.

Young (1985) reported “*Spilochalcis* sp.” attacking “*Rothschildia* sp.” at a site 5 km
N of Bagaces, Guanacaste, Costa Rica in 1984. The parasitoid was probably *C. maria*
or a closely allied species. The host was almost certainly *R. lebeau*. It is also likely that the report of a "black and yellow chalcidine wasp" attacking caterpillars of *Hylesia* on the Osa Peninsula, Costa Rica, by Hogue (1972) is this species.

The parasitoid reported from *Agapema anona* from Pima Co., Arizona, by Tuskes et al. under the name "Spilochalcis n. sp." is undoubtedly the same as those I received from Chris Conlan from the same host and region. Conlan's material agrees with that of *C. maria* from the eastern United States, and is conspacific in my opinion.


152. *Conura mendozaensis* (Cameron)

**Hosts:** Rothschildia arethusa

**Distribution:** known from the original locality of Mendoza, Argentina

**Biology:** The larva is the site of oviposition, the host then matures, spins a cocoon and pupates, and the adult parasitoids emerge from the cocoon of the host. The parasitoid is gregarious.

**References:** Delvare (1992: 253)

**Remarks:** According to Delvare, the lectotype female in the BMNH is all that remains of the original type material. In addition, Delvare examined a series reared from the only known host, also from Argentina.

153. *Spilochalcis* sp.

**Hosts:** Rothschildia sp., Eacles imperialis magnifica

**Distribution:** Brazil

**Biology:** The authors cited it as a hyperparasitoid under *Eacles*.

**References:** d'Araujo e Silva et al. (1968: 260-261, 270)

**Remarks:** The record for *Rothschildia* likely refers to *Conura mendozaensis*. The record for *Eacles* is probably for a species of *Conura* also, perhaps even *C. mendozaensis*.

154. *Phasgonophora bauhiniae* Girard

**Hosts:** Epiphora bauhiniae

**Distribution:** Africa

**References:** Packard (1914: 268); Burks (in Krombein et al. 1979: 869), Boucek (1988: 62-63)

**Remarks:** The current generic placement of this species is undoubtedly incorrect (J. LaSalle, personal communication). True *Phasgonophora* species parasitize larvae of wood-boring beetles. A future revision of the sub-Saharan Chalcididae will certainly result in reassignment of *P. bauhiniae* to another genus.

Peck (1963: 938) cited *Phasgonophora sulcata* Westwood as a parasitoid of *Antheraea*
polyphemus. This record is surely an error so I do not give it a full listing in this catalog. This parasitoid parasitizes only beetles of the family Buprestidae as far as known (Burks in Krombein et al. 1979: 869).

The citation by Schultz (1913: 16) of “Schlupfwespen” emerging from cocoons of Epiphora bauhiniae may refer to this parasitoid.

155. Brachymeria intermedia (Nees)

**Hosts:** Hemileuca oliviae, numerous other hosts in Lepidoptera and Diptera

**Distribution:** Native to Europe and North Africa, introduced to United States, ranging from Maine to Maryland

**Biology:** Probably attacks the pupae of hosts as an idiobiont.

**References:** Burks (in Krombein et al. 1979: 872), Sullivan (1987: 3); Boucek (1988: 68)

**Remarks:** Under the text of the range caterpillar (Hemileuca oliviae), Sullivan reported that releases of chalcid and ichneumon wasps were begun in 1977 in the vicinity of Branson, Las Animas Co., Colorado, resulting in a reduced infestation of the pest. Releases of 6,250 Brachymeria intermedia were made in 1986 in hopes of establishing the parasitoid in the field permanently for control of the range caterpillar.

Specific record: Fort Collins, Colorado, lab colony, January 1979 (CSU).

156. Brachymeria ovata (Say)

**Hosts:** Hemileuca oliviae, Hyposoter fugitivus in Anisota senatoria and Anisota peigleri; see Biology below

**Distribution:** All of continental United States into Mexico, most islands of the Caribbean, Venezuela, Colombia, Paraguay, Uruguay

**Biology:** According to Burks, this parasitoid attacks pupae of over 100 species of moths and butterflies which have a pupal size of more than 15 mm and are exposed in the open. It is a solitary idiobiont. Burks stated that it is always a primary parasitoid of Lepidoptera. However, Coffelt & Schultz observed it to be a hyperparasitoid in Virginia, as did I in South Carolina.


**Remarks:** This wasp is referred to in the older literature under the name Chalcis ovata. The wasp is coal black with white markings. Boucek stated that this coloration is useful to recognize this genus.

Specific record: Three specimens were reared as hyperparasitoids of Hyposoter fugitivus in Anisota peigleri, Greenville, South Carolina, July 1992, ex-larvae on Quercus palustris, R. S. Peigler (DMNH, BMNH); Palisade, Colorado, lab colony, 1979 (CSU); Corona, Riverside Co., California, 10 June 1939 (CSU); Urbana, Illinois, June 1934, E. M. Heiss (CSU).

157. Brachymeria sp.

**Hosts:** Maltagorea fuscicolor

**Distribution:** Madagascar

**Biology:** According to Griveaud, the larvae of the host are attacked. However, Boucek indicated that species of this large, widely distributed genus are parasitoids of pupae.

**References:** Griveaud (1962: 26), Boucek (1988: 68-69)

**Remarks:** Griveaud cited the host as Tagoropsis subcellata form madagascariensis.
158. *Brachymeria* sp.
Hosts: *Epiphora* sp.
Distribution: sub-Saharan Africa
Biology: There are 22 specimens that were reared from one host cocoon in the BMNH. The host cocoon is present, and has an exit hole chewed in the side. It is clearly of the genus *Epiphora*.
References: previously unpublished
Remarks: The series of 22 specimens bears the following data: Mt. Mzonje, Nyassaland, 24 December 1913, S. A. Neave (BMNH). The locality may also be spelled Mazonle. The former Nyassaland is now the country of Malawi. John LaSalle (personal communication) said that Lepidoptera having large conspicuous cocoons are commonly attacked by species of *Brachymeria* in many regions of the world. There is a possibility that this series represents the taxon cited above under the name *Phasgonophora bauhiniae*.

159. *Brachymeria* sp. or spp.
Hosts: *Samia走leri, Samia canningii, Cricula trifenestrata kransi*
Distribution: Guangdong Province, China; Assam, India; Sulawesi, Indonesia
Biology: The larvae of the host are probably attacked and then the wasps emerge from the cocoons of the host. In the case of the one reared from *Cricula*, they were solitary parasitoids.
Remarks: The parasitoids reared from *Cricula* by Naumann were illustrated by him in color. They were from hosts from Tondano, Sulawesi Utara, collected August 1994.

Hill & Cheung wrote “many of the pupae [of *Samia走leri*] observed locally are parasitized by large black chalcid wasps.” Robert Mayo (pers. comm.) reported to me chalcids from cocoons of *Samia canningii* from Assam in 1993. Unfortunately, no specimens were retained.

160. *Hockeria crassa* Boucek
Hosts: *Imbrasia cytherea*
Distribution: southern Africa
Biology: Reared from pupa of host.
References: Geertsema (1975)
Remarks: The record is based on material reared by H. Geertsema in 1968 in Cape Province. An unidentified species of *Hockeria* was also reared by Geertsema from the pupa of *Imbrasia belina*, which he indicated was apparently not *H. crassa* or *H. nudaureliae*.

161. *Hockeria nudaureliae* Boucek
Hosts: *Imbrasia cytherea*
Distribution: southern Africa
Biology: Reared from pupa of host.
References: Geertsema (1975)
Remarks: The record is based on specimens reared by H. Geertsema in 1968 in Cape Province. The specific name comes from the generic name *Nudaurelia*, a synonym of *Imbrasia*. 
162. *Kriechbaumerella* sp.
**Hosts:** *Bunaea alcinoe*
**Distribution:** western Africa
**Biology:** Reared from the larva of the host.
**References:** Akanbi (1973)
**Remarks:** The rearing was in Ibadan, Nigeria. Akanbi cited the genus of parasitoid as *Eucepsis*, which is a synonym of *Kriechbaumerella* according to G. Prinsloo (personal communication to R. Oberprieler).

Family Eupelmidae
163. *Eupelmus cyaniceps* (Ashmead)
**Hosts:** Hyperparasitoid in *Hyposoter fugitivus* in *Anisota senatoria*, and numerous other hosts in Lepidoptera, Coleoptera, and Hymenoptera
**Distribution:** California to Florida to Ontario
**Biology:** Recorded as a hyperparasitoid by Coffelt & Schultz.
**References:** Coffelt & Schultz (1993b), Burks (in Krombein et al. 1979: 882)

164. *Eupelmus urozonus* (Dalman)
**Hosts:** *Imbrasia belina*
**Distribution:** southern Africa
**Biology:** The eggs of hosts are attacked.
**References:** van den Berg (1971)

165. *Eupelmus* sp.
**Hosts:** *Antheraea pernyi, Antheraea yamamai*
**Distribution:** Europe, presumably Balearic Islands of Spain (see remarks below)
**Biology:** Parasitoid of the eggs of the host.
**References:** Arzone (1971b), Sonthonnax (1899: 72)
**Remarks:** Arzone cited this genus of egg parasitoid attacking *A. pernyi* in Europe. The first host is native to China, but has been introduced to the Balearics where it remains established. The second host is native to Japan but introduced into southeastern Europe more than a century ago.

Genus *Anastatus*
These tiny wasps resemble ants, and probably mimic them as they crawl on leaves and stems searching for hosts. They are all primary idiobiont parasitoids of eggs of insects. The key by Burks (1967) is only for females, and is not sufficient for me to make determinations with great confidence, so anyone revising this genus in the future should re-examine my material to verify the identifications. The host range is wide enough that alternate hosts besides Saturniidae obviously exist. For those developing from overwintering eggs (*Hemileuca*), it is clear that the eggs are routinely attacked in the autumn. In cases where only males are reared, it is likely that unmated females parasitized the host eggs. (Males of most Hymenoptera are haploid, developing from unfertilized eggs.) Males of *Anastatus* are mostly black or metallic blue-black.

Kapraly (1990) stated that three other species of *Anastatus* besides *A. pearsalli* were reared from eggs of *C. promethea* in Ohio, but that (pers. comm., 1995) no voucher specimens were deposited in The Ohio State University insect collection and he discarded all parasitoids after the study.
166. *Anastatus albitarsis* (Ashmead)

**Hosts:** *Antheraea yamamai, Saturnia japonica, Saturnia pyreorum*

**Distribution:** Japan, Taiwan, China

**Biology:** Attacks eggs of the host.


**Remarks:** Sakamoto published a photograph of the adult parasitoid. It measures 4-5 mm long. According to Boucek, the name *Pseudanastatus* is a synonym of *Anastatus*; Sakamoto used the former name. This is probably the parasitoid that Voelschow reared in Germany from eggs he imported from Japan.

167. *Anastatus bifasciatus* Fourcroy

**Hosts:** *Samia cynthia, Malacosoma neustria* L. (Lasiocampidae), *Dendrolimus pini* L. (Lasiocampidae), *Dendrolimus spectabilis* Butler, *Gonometra fasciata* (Lasiocampidae), three species of *Thaumetopoea* (Notodontidae), and Hemiptera (Coreidae and Pentatomidae)

**Distribution:** Europe, including Italy, Ukraine, Spain, Crete; Asia including Korea; Africa, including Uganda

**Biology:** Parasitizes the eggs of the host.

**References:** Arzone (1971b)

**Remarks:** This parasitoid attacks eggs of *Samia cynthia* in Italy. The saturniid host species is native to China, but introduced populations occur in northern Italy. According to Arzone, she collected a cluster of 12 eggs of *Samia cynthia* from which 4 caterpillars had hatched, but later 3 males and 4 females of the parasitoid emerged, one per egg. The preimaginal stages of the parasitoid take about two months to develop. Arzone described how the wasps chew out of the host eggs. It is possible that the host in northern Italy is *Samia Walkeri* instead of S. *cynthia*. I have not yet resolved that taxonomic problem.

168. *Anastatus colemani* Crawford

**Hosts:** *Attacus atlas*

**Distribution:** Malaysia, elsewhere in tropical Asia

**References:** Ferrière (1930b), Thompson (1944), Boucek (1988: 550-552), Peigler (1989), Arzone (1971b)

**Remarks:** I am not certain that this species is correctly placed under *Anastatus*. It is not listed in the monograph by Boucek, although he cited numerous species for the Indo-Australian region.

169. *Anastatus furnissi* Burks

**Hosts:** *Callosamia promethea, Coloradia pandora, Hylesia lineata, Hemileuca*

**Distribution:** Recorded from Oregon, upper South Carolina, and Guanacaste Province, Costa Rica

**Biology:** A primary ovarian parasitoid.


**Remarks:** The record of "Pseudohazis" given in the original description by Burks (1967) from Oregon refers to one of the following three species of *Hemileuca: hera, eglanderina, or nuttalli*. It is almost certain that all of these species serve as hosts in Oregon, even if still not recorded as such. See also possible record from Georgia below under *A. reduvii*. 
Specific records: *ex Callosamia promethea*: Greenville, Greenville Co., South Carolina, July 1984, R.S. Peigler [host is not native to locality; eggs obtained from a captive female were attached to a tree of *Quercus nigra* for a few days and then brought indoors] (USNM).

170. **Anastatus hirtus** (Ashmead)

**Hosts:** Anisota senatoria, Thyanta custator (Fabr.) (Hemiptera: Pentatomidae)

**Distribution:** New York to Florida

**Biology:** Attacks the eggs of the host. An average of almost 12% of the egg masses were attacked in coastal Virginia.

**References:** Coffelt & Schultz (1992), Burks (in Krombein et al. 1979: 887)

171. **Anastatus pearsalli** Ashmead

**Hosts:** Callosamia promethea, Antheraea polyphemus, Paonias astylus (Drury) (Sphingidae), eggs of various Pentatomidae (Heteroptera), and cocoons of Apanteles (Braconidae) [possibly Cotesia]

**Distribution:** Massachusetts to North Carolina, westward to Wisconsin and Arkansas

**Biology:** Attacks the eggs of the host as a primary parasitoid. The non-saturniid hosts were cited by Burks.

**References:** Burks (1967: 429), Burks (in Krombein et al. 1979: 887), Kapraly (1990)

**Remarks:** In the study by Kapraly, parasitism by *A. pearsalli* ranged from 51% to 74%. Egg parasitism was highest on *Sassafras albidum*, intermediate on *Fraxinus americana*, and lowest on *Prunus serotina*.

172. **Anastatus reduvii** (Howard)

**Hosts:** Eupackardia calleta, Antheraea polyphemus, Agapema platensis, Anisota consularis, Anisota pellucida, Anisota discolor, Anisota fuscosa, Anisota senatoria, other insects in orders Orthoptera, Neuroptera, and Heteroptera, and other Lepidoptera including Arctiidae

**Distribution:** Maryland to Florida, west to Kansas and Texas, West Indies, Central America, northern South America

**Biology:** I have reared this species from eggs of *Anisota* and *E. calleta*. The parasitoid from the latter host was several times larger than those from *Anisota*, although the coloration and markings were the same. Eggs of *E. calleta* are much larger than those of *Anisota*.


Some of the specimens from Georgia listed above keyed to *A. furnissi*, but I think they are probably *A. reduvii*. 
173. *Anastatus semiflavidus* Gahan

**Hosts:** *Hemileuca nevadensis, Hemileuca oliviae, Hemileuca electra, Hemileuca neumoegeni, Eupackardia calleta*

**Distribution:** Kansas and Texas to California

**Biology:** Fritz et al. verified that this parasitoid can remain dormant in the larval stage in a host egg for up to two years. Host eggs are attacked in the fall. Adult parasitoids are not active below 15°C according to studies by Mendel et al. in New Mexico. The latter authors provided a detailed account of the biology of this parasitoid.


**Remarks:** This is an important parasitoid of the range caterpillar (*H. oliviae*), which reaches pest status in New Mexico because of overgrazing by cattle in grasslands on plateaus at high elevations.

All five specimens reported by Duncan (1991) are to be this species, but the series includes both sexes.


174. *Anastatus* sp.

**Hosts:** *Imbrasia helina, Imbrasia cytherea*

**Distribution:** southern Africa

**Biology:** Parasitoid of eggs of the host species.

**References:** van den Berg (1971, 1974), Geertsema (1975)

175. *Anastatus* sp. (Figure 7)

**Hosts:** *Saturnia walterorum, Agapema anona, Hemileuca nevadensis, Hemileuca burnsi*

**Distribution:** Southern California and southern Arizona

**Biology:** Attacks the egg of the host. The eggs of *Saturnia walterorum* normally hatch within 10 days, but those containing these parasitoids did not yield adult wasps until August, suggesting that alternate hosts must be used since the host flies only in early spring (February and March). The parasitoids reared from an egg mass of *Agapema anona* emerged in March, shortly after being collected; the larvae of *A. anona* on the same tree of *Condalia globosa* (and probably from the same egg mass that produced the parasitoids) were nearly mature.

**Remarks:** This is probably one (or more) of the other species listed above, but since only males were obtained from these rearings, it was not possible to identify them to species level. The wasps are solidly metallic blue-black. The specimens from the first host listed are larger because its eggs are larger. It is not certain that the parasitoids from the four rearings represent one species.

Specific records: *ex Saturnia walterorum:* 8 km west of Escondido, 250 m, San Diego Co., California, emerged 8-13 August 1994, K. L. Wolfe (DMNH); *ex Agapema anona:* Ajo, Pima Co., Arizona, emerged March 1994, R. S. Peigler (DMNH); *ex Hemileuca nevadensis:* Chino, Los Angeles Co., California, host eggs collected January 1978, D. C. Hawks (DMNH); *ex Hemileuca burnsi:* Littlerock, Los Angeles Co., California, emerged February 1989, K. L. Wolfe (DMNH).
176. *Anastatus* sp.

**Hosts:** *Samia cynthia, Samia ricini, Dendrolimus* spp. (Lasiocampidae)

**Distribution:** China

**Biology:** Parasitoids of eggs of the moths.

**References:** United Nations (1980: 73)

**Remarks:** The United Nations report on sericulture in China stated that eggs of *Samia* were being used for mass rearing of *Anastatus* and *Trichogramma* for biological control of *Dendrolimus sibiricus* and *D. punctatus*, which are forest pests in China. *Samia* stocks were also being used to culture the pathogens *Bacillus thuringiensis* and *Beauveria* to combat the same pests. I believe that mass applications of these pathogens and parasitoids adversely affect populations of native Lepidoptera, including Saturniidae, the same sort of ecological damage we see in North America by similar attempts to control the gypsy moth (*Lymantria dispar* (Linnaeus), Lymantriidae).

177. *Anastatus* sp.

**Hosts:** *Attacus memullenii*

**Distribution:** Andaman Islands, India, in the Bay of Bengal

**Biology:** Solitary ovarian parasitoids.

**References:** Veenakumari et al. (1995: 172)

**Remarks:** This species is probably not *A. colemani*, because it was identified by A. Polaszek (International Institute of Entomology, London) who presumably had material of *A. colemani* available for comparison. It may be an undescribed species. Dammerman (1929) also reported an unidentified species of *Anastatus* attacking *Attacus atlas*; it may be this species or *A. colemani*.

178. *Mesocomyys menzeli* (Ferrière)

**Hosts:** *Attacus atlas, Samia ricini, Antheraea* sp.

**Distribution:** southeastern Asia; Sumatra, and as far east as Java

**Biology:** The female oviposits into eggs of large Saturniidae and probably also other Bombycoidea which are laid in clusters. Probably only one parasitoid egg is deposited per host egg. Menzel stated that there may be up to 80% parasitism of eggs.


**Remarks:** Reported by Menzel and van Hall as *Anastatus* sp. and by Ferrière, Thompson, Arzone, and Peigler as *Anastatus menzeli*. Boucek reassigned this species to *Mesocomyys*. Ferrière referred to “variety obscurus”, which may be a dark form of this species or a separate species.

179. *Mesocomyys pulchriceps* Cameron

**Hosts:** *Imbrasia cytherea, Imbrasia tyrhrea, Imbrasia belina, Pseudobunaea irius, Gynanisa maja, Aurivillius aratus, Bunaea alcinoe, Cirina forda, Heniocha dyops, Urota sinope, Usta terpsichore, Argema mimosae, Epiphora mythisma*

**Distribution:** southern Africa

**Biology:** Primary parasitoid of eggs of the host moth. This parasitoid probably attacks eggs of several species of Saturniidae, as Boucek indicated that wasps of this genus favor eggs of large Bombycoidea. Most of the host records above result from laboratory rearings of the parasitoid by van den Berg, who offered eggs of the various moths to attack. There is no doubt they would attack all of these hosts in nature.

Remarks: Van den Berg cited the first host under the name *Nudaurelia cytherea clarki* Geersema.

180. *Mesocomys vuilleti* Crawford
Hosts: *Bunaea aslauga, Cirina forda*
Distribution: Madagascar, Sudan
Biology: Eggs of the hosts are parasitized.
Remarks: Griveaud wrote "Les élevages effectués ont donné un Chalcidien parasite: *Mesocomys vuilleti* Crawford." Some authors have cited the host as *Cirina butyrospermi*, a synonym of *C. forda*. R. Oberprieler (pers. comm.) suspects that the name *vuilleti* could be a synonym of *pulchriceps*.

181. *Mesocomys pauliani* Ferrière
Hosts: *Antherina suraka*
Distribution: Madagascar
Biology: Eggs of the host are attacked.
References: Griveaud (1962: 51), Arzone (1971b)
Remarks: Griveaud stated that eggs of the host are strongly infested by this parasitoid (which he cited only as *Mesocomys sp.*) and a species of *Agiommatus*.

182. *Arachnophaga* sp.?
Hosts: *Hemileuca nevadensis*
Distribution: Los Angeles County, California
Biology: Parasitoids of eggs.
References: Burks (in Krombein et al. 1979: 884-885)
Remarks: Specific record: *ex Hemileuca nevadensis*: Chino, Los Angeles Co., Arizona, host eggs collected January 1978, D. C. Hawks. These specimens were sent by me to USNM and the following reply came from M. E. Schaufl: "Specimens have critical parts missing. More precise determination depends on characters found in other sex." He identified them as "probably *Arachnophaga*.”

183. Eupelmidae, genus undetermined
Hosts: *Citheronia laoocoon*
Distribution: southern Brazil
Biology: Parasitoid of eggs.
References: Dias (1978)

Family Encyrtidae

184. *Ooencyrtus cirinae* Prinsloo
Hosts: *Cirina forda*
Distribution: known only from the vicinity of Pretoria, Transvaal, South Africa
Biology: Parasitoid of eggs of the host. Wasps emerged in October.
Remarks: The original rearing was made by R. Oberprieler.

185. *Ooencyrtus kuvanae* Howard
Hosts: *Saturnia pyreorium, Hemileuca oliviae*, other Lepidoptera and Hymenoptera
Distribution: Taiwan, introduced to North America, where it occurs in New England and New Mexico at least
Biology: Parasitoid of eggs, or in the case of *Apanteles* perhaps of the exposed cocoons.
Remarks: This parasitoid has sometimes been classified in the genus *Schedius*. It has been spelled in some literature as *kuwanae*.

186. *Ooencyrtus phoebi* Huang & Noyes

*Hosts:* *Attacus atlas*

*Distribution:* Java, and probably elsewhere in tropical Asia

*Biology:* Egg parasitoids.


*Remarks:* This species was listed by the first four authors above as *Ooencyrtus major* Ferrière.

187. *Ooencyrtus sp.*

*Hosts:* *Anisota senatoria*

*Distribution:* coastal Virginia

*Biology:* Attacks the eggs of the host. Only a mean egg mass parasitism of 0.09% was recorded.

*References:* Coffelt & Schultz (1992), Askew (1971: 139)

188. *Epiencyrtus thyreodontis*? (Ashmead)

*Hosts:* *Automeris zozine, Thyreodon atricolor* (Olivier) (Ichneumonidae)

*Distribution:* eastern United States, from at least Massachusetts to upper South Carolina

*Biology:* This tiny wasp was observed on the integument of a mature larva of the host cited above, but was removed before it could oviposit. The host, native to Chiapas, Mexico, was being reared under a cloth bag on a small tree of *Quercus nigra*. It is not known if it could have successfully parasitized the host. If so, *Automeris io* would serve as a normal host in the locality.

*References:* G. Gordh (in Krombein et al. 1979: 963)

*Remarks:* Specific record: on *Automeris zozine*. Greenville, South Carolina, 24 June 1977, R. S. Peigler (DMNH). The parasitoid was identified by J. LaSalle (BMNH) with a question mark on the species name.

189. Encyrtidae, genus undetermined

*Hosts:* *Citheronia laocoon*

*Distribution:* southern Brazil

*Biology:* Parasitoid of eggs.

*References:* Dias (1978)

Family Eulophidae

LaSalle (1994) provided a monumental reclassification of the Tetrastichinae, a large group that includes several genera below beginning with *Tetrastichus*. He pointed out that the subfamily is one of the largest and most widespread of all parasitic Hymenoptera, and that "species can be solitary or gregarious, internal or external parasitoids, primary or secondary parasitoids, predatory, or phytophagous" (LaSalle 1994: 115).
190. *Eulophus* sp.

**Hosts:** *Hemileuca nevadensis*

**Distribution:** upper South Carolina

**Biology:** Attacks the mature larva of the host, the parasitoid larvae leave the host and form naked pupae on the leaf. There were 14 eulophids in this lot.

**References:** unpublished

**Remarks:** This series of sibling wasps was reared from a mass of cocoons that emerged from a mature larva of the host (not native to the area), reared on Lombardy poplar. The parasitoid was identified by J. LaSalle (BMNH).

Specific record: *ex Hemileuca nevadensis*: Greenville, South Carolina, July 1973, R. S. Peigler (DMNH).

191. *Dimmockia incongrua* (Ashmead)

**Hosts:** Hyperparasitic in *Hyalophora cecropia*, parasitic in other insects including Tachinidae and Braconidae

**Distribution:** eastern North America

**Biology:** This is almost always a secondary parasitoid.

**References:** Peck (1963: 938), Burks (in Krombein et al. 1979: 976)

**Remarks:** Although Peck cited the saturniid above as a host, Burks did not, evidently because he knew that the rearing on which the record was based resulted from hyperparasitism.

192. *Euplectrus comstockii* Howard

**Hosts:** *Rothschildia lebeau*, other Lepidoptera including mostly Noctuidae

**Distribution:** El Salvador, Puerto Rico, Trinidad; widespread in North America from Arizona to Florida to South Dakota to Connecticut; also in South America

**Biology:** Burks wrote “This is one of the very few chalcidoid genera that spin cocoons; these usually are placed under the emaciated body of the host larva.”

**References:** De Santis (1979: 254), Burks (in Krombein et al. 1979: 977)

**Remarks:** The saturniid host was cited by De Santis as *Rothschildia aroma*.

193. *Euplectrus nigroclypeatus* Ferrière

**Hosts:** *Antherina suraka*

**Distribution:** Madagascar

**Biology:** According to Boucek, the species in this genus are primary gregarious ectoparasites of lepidopterous larvae. When mature, they then spin a loose cocoon beside the dead host and pupate below the cocoon. This method of pupation is an unusual and perhaps unique characteristic for the Chalcidoidea.

**References:** Griveaud (1962: 51), Boucek (1988: 633)

**Remarks:** Griveaud misspelled the generic name as *Euplectus*.

194. *Cirrospilus inimicus* Gahan

**Hosts:** Hyperparasitic in *Gambrus extrematis* (Ichneumonidae) in *Hyalophora cecropia*

**Distribution:** Illinois, southward

**References:** Peck (1963: 938), De Santis (1979), Burks (in Krombein et al. 1979: 983-984)

**Remarks:** Although Peck cited this as a parasitoid of *H. cecropia*, Burks did not, because he knew it was a hyperparasitoid.
Hosts: *Hemileuca oliviae, Callosamia promethea*
Distribution: Ohio and New Mexico (probably two species)
Biology: Eggs are attacked. No details were given by the authors.
References: Burks (1943), Fritz et al. (1986), Kapraly (1990)
Remarks: These records probably refer to two species of *Aprostocetus*. The one from New Mexico may in fact be *A. pandora*; that from Ohio perhaps is the one cited below as "*Aprostocetus* sp. near *pandora*".

196. *Tetrastichus* sp.
Hosts: *Arsenura xanthopus*
Distribution: state of São Paulo, Brazil
Biology: One wasp emerges from each host egg. Parasitism can approach 100%. The egg is layed within 80 to 120 seconds after the ovipositor of the female wasp is inserted into a host egg. This parasitoid was considered to be valuable by Lordello & Mariconi as a control agent of the moth which is a frequent defoliator of *Luehea* trees.
References: Lordello & Mariconi (1958), d’Araújo e Silva et al. (1968: 262)
Remarks: This parasitoid is probably a species of *Aprostocetus*, as many of the species in that genus were formerly considered to be in the genus *Tetrastichus*. The report of a species of *Tetrastichus* as a hyperparasitoid in the tachinid *Zygofrontina* by d’Araújo e Silva et al. in Brazil is possibly an error.

197. *Tetrastichus* sp.
Hosts: *Attacus atlas*
Distribution: Java, Indonesia
Biology: Eggs of the host moth are attacked.
Remarks: Whatever species was being referred to by Ferrière in the original report, it probably was not a true *Tetrastichus* based on the host preferences cited by Boucek, who indicated that eggs of Lepidoptera are not hosts.

198. *Aprostocetus pandora* Burks
Hosts: *Coloradia pandora*
Distribution: western United States
Biology: Patterson reared 128 wasps from 17 eggs of *Coloradia pandora*, with as few as 3 coming out of one egg and as many as 11 from another egg, with 7.5 being the average.
References: Patterson (1929), Burks (1943; in Krombein et al. 1979: 999), Peck (1963: 938), LaSalle (1994: 148)
Remarks: This parasitoid was cited as *Tetrastichus* sp. by Patterson and Peck. The name should not be confused with *Brachymeria pandora* (Crawford) a South American species of the Chalcididae that attacks Hesperiidae (De Santis 1979: 60).

199. *Aprostocetus* sp. near *pandora*
Hosts: *Anisota senatoria, Anisota peigleri*
Distribution: eastern United States including Connecticut, Virginia, South Carolina, and Texas
Biology: This is a primary parasite of eggs of the hosts.
Remarks: This parasitoid was cited as *Tetrastichus* sp. by Hitchcock and Riotte & Peigler. Coffelt & Schultz reported this parasitoid to be a new species. J. LaSalle
(BMNH) gave me some of the specimens from Coffelt & Schultz, and identified my Texas material as being the same. The females are blackish, the males light brown.

Specific records: ex Anisota senatoria: Norfolk, Virginia, 6 August 1987, M. Coffelt (DMNH, USNM, BMNH); ex Anisota sp.: Subblefield Lake, Walker Co., Texas, 11 September 1976, R. S. Peigler (DMNH); ex Anisota peigleri: Greenville, South Carolina, August 1978, R. S. Peigler (USNM).

200. Horismenus bisulcus Ashmead

Hosts: Automeris sp.

Distribution: Brazil

Biology: This is stated to be a hyperparasitoid of Apanteles.

References: d’Araujo e Silva et al. (1968: 263)

Remarks: I am unable to verify this name in De Santis (1979) who apparently did not list it anywhere under Horismenus.

201. Horismenus cockerelli Blanchard

Hosts: Hyperparasitoid in Apanteles in Eacles imperialis magnifica

Distribution: Brazil

Biology: Stated to be a hyperparasitoid of Apanteles (Braconidae) by the authors cited below.

References: d’Araüjo e Silva et al. (1968: 260-261), De Santis (1979: 271)

Remarks: The braconid host is probably not a true Apanteles, but another microgastrine.

202. Horismenus floridanus (Ashmead)

Hosts: Apanteles, Cotesia (Braconidae) attacking Anisota and other Lepidoptera

Distribution: New Jersey to California to Florida

Biology: These tiny black wasps emerge from cocoons of microgastrine braconids. The comment by Riotte & Peigler that exposed cocoons are not attacked, but that eggs of the eulophid are laid in the lepidopterous host needs to be verified with more carefully controlled rearing conditions.

References: Burks (in Krombein et al. 1979: 1014), Riotte & Peigler (1981: 121)

Remarks: Specific record: ex Cotesia anisota in Anisota spp.: Subblefield Lake, Walker Co., Texas, 15 October 1976, R. S. Peigler (DMNH, USNM). Material from the rearing was determined by G. Gordh.

203. Horismenus sp. near lixivorous (Crawford)

Hosts: Hyperparasitoid in Hyposoter fugitivus in Anisota senatoria

Distribution: coastal Virginia

Biology: A hyperparasitoid attacking mummified larvae of Anisota senatoria containing cocoons of Hyposoter fugitivus.

References: Coffelt & Schultz (1993b)

Remarks: According to the above authors who reared two specimens, it does not match any other known Horismenus in the USNM as communicated to them by M. E. Schauff.

204. Pediobius tarsalis (Ashmead)

Hosts: Hyperparasitoid in Ichneumonidae and Tachinidae in Lepidoptera, including Hyalophora cecropia

Distribution: New Hampshire to North Carolina, west to Washington and California

Biology: Always a secondary parasitoid.

References: Peck (1963: 938), Burks (in Krombein et al. 1979: 1018)
205. *Pediobius* sp.

**Hosts:** *Imbrasia cytherea, Imbrasia belina*

**Distribution:** South Africa

**Biology:** Parasitoid of eggs.

**References:** van den Berg (1971, 1974), Geertsema (1975)

**Remarks:** The pine emperor (*Imbrasia cytherea*) is considered a pest of pines in South Africa. Van den Berg reported that host under the name *Nudaurelia cytherea clarki* Geertsema.

206. Eulophidae, genus undetermined

**Hosts:** *Citheronia laocoon*

**Distribution:** southern Brazil

**Biology:** Parasitoid of eggs.

**References:** Dias (1978)

**Family Trichogrammatidae**

These are among the tiniest Hymenoptera, most measuring much less than 1 mm in length. They are all egg parasitoids, and a few are mass-reared for biocontrol programs. Host range is based more on habitat instead of taxonomy of the host.

207. *Trichogramma australicum* Girault

**Hosts:** *Antheraea yamamai*

**Distribution:** Japan, Indo-Australian region

**Biology:** A primary parasitoid of eggs of the host.

**References:** Burks (1979: 1037), Sakamoto (1990: 150-153)

**Remarks:** Boucek (1988) did not treat this family. Burks wrote that the species of *Trichogramma* do not select their host eggs based on taxonomy of the host, but rather by environmental conditions. For example, one species of *Trichogramma* may oviposit into eggs of most insects in a moist coniferous forest, while another may attack many species of hosts in a grassland prairie.

208. *Trichogramma dendrolimi* Matsumura

**Hosts:** *Samia cynthia, Samia ricini, Saturnia japonica, Antheraea yamamai, Dendrolimus* spp. (Lasiocampidae)

**Distribution:** China, Japan

**Biology:** Parasitoids of eggs.


**Remarks:** Eggs of *Samia* are being used in China to mass rear this parasitoid to be used as a biological control agent against forest pests in the genus *Dendrolimus*. See also *Anastatus* sp. above. In Japan, where *Antheraea yamamai* is mass reared for production of tensan silk, the trichogrammatid is considered a pest when it attacks eggs of this moth.

209. *Trichogramma minutum* (Riley)

**Hosts:** *Anisota senatoria, Dryocampa rubicunda, Coloradia pandora*, and many other insects

**Distribution:** North America, including southern Canada down to central United States, but not in the Southwest and Deep South

**Biology:** Patterson reared this parasitoid from 5 eggs of *Coloradia pandora*. He
obtained 20 to 37 wasps from each host egg, the average being 29.5, and a total of 147 wasps. Burks stated that eggs of almost any arboreal insect will be parasitized.


210. *Trichogramma pretiosa* (Riley)
Hosts: *Anisota senatoria*
Distribution: same as for *T. minutum* above
Biology: Host eggs deposited on lower vegetation in rural areas will be attacked.
References: Hitchcock (1961a), Coffelt & Schultz (1992), Burks (in Krombein et al. 1979: 1039)

211. Chalcidoidea, family and genus undetermined

*Cynips* "bombycida" Rondani
Hosts: *Saturnia pyri*
Distribution: Europe
References: Packard (1914: 268)
Remarks: Packard apparently cited the generic name in quotes, as do I, because he knew that Cynipidae are Hymenoptera that make galls, i.e. are plant feeders instead of parasitoids, in general. It is not possible at this time to track this name until the type specimen can be located, unless it is lost.

Superfamily Prototruopoidea

212. Family Diapriidae, genus and species undetermined

Hosts: A hyperparasitoid of the tachinid *Carcelia evolans* reared from *Imbrasia cytherea*
Distribution: South Africa
Biology: Emerged from the puparium of the tachinid. The diapriid may be attack the tachinid larva within the caterpillar of the moth; more likely, it oviposits into the puparium of the tachinid after the latter has left the primary host, since diapriids specialize in parasitizing Diptera. It is thus not likely to be a facultative hyperparasitoid.
Remarks: Van den Berg cited the saturniid primary host as *Nudaurelia cytherea clarki* Geertsema.

Family Scelionidae

213. *Telenomus almanzori* Marelli
Hosts: *Hylesia nigricans*
Distribution: Argentina
References: d’Araújo e Silva et al. (1968: 267)

214. *Telenomus attaci* Nixon
Hosts: *Attacus atlas*
Distribution: Malaysia and Thailand
Biology: Egg parasitoid.
References: Arzone (1971b)

215. *Telenomus graptae* Howard
Hosts: *Antheraea polyphemus*, butterflies in Nymphalidae, Lycaenidae, and Hesperiidae
Distribution: Québec to Arizona
Biology: This is an idiobiont parasitoid of eggs. The wasps are usually less than 1 mm long.


Remarks: Since all known hosts listed by Muesebeck are butterflies, the record for *Antheraea polyphemus* should be verified. It may have been based on a misidentification of another species in the genus *Telenomus*.

216. *Telenomus hyelosiae* (Brèthes)
Hosts: *Hylesia nigricans*
Distribution: Brazil
References: d’Araújo e Silva et al. (1968: 267), De Santis (1967, 1980)
Remarks: This insect was listed under the name *Neonecremnus hyelosiae* by d’Araújo e Silva et al., who attempted to correct the original spelling of the specific name, which is based on the host genus.

217. *Telenomus poeta* Girault
Hosts: *Saturnia japonica*
Distribution: Japan
References: Thompson (1944: 204)

218. *Telenomus sp.*
Hosts: *Callosamia promethea*
Distribution: North America
Biology: Parasitoid of eggs.
References: Kapraly (1990)
Remarks: Kapraly (1990) indicated that a single species of *Telenomus* was reared from eggs of *C. promethea* in Ohio, but that (personal communication, 1995) no voucher specimens were kept. This record may belong under *T. graptae* above.

219. *Telenomus sp.*
Hosts: *Coloradia pandora*
Distribution: northern Arizona
Biology: Parasitism ranged from 4% to 56%. Parasitized eggs are black and easily distinguished from unparasitized ones. Some eggs in an egg mass are not attacked, alongside of ones that are.
References: Schmid & Bennett (1988)

220. *Telenomus sp.*
Hosts: *Hylesia* (probably *nigricans*)
Distribution: Parana State, Brazil
References: Janzen (1984)
Remarks: The observations cited by Janzen were made by J. A. Winder in Brazil, who cited the host under the synonym *Hylesia fulviventris*.

Superfamily Trigonalyoidea
Family Trigonalyidae
These wasps resemble small yellowjackets and are koinobiont hyperparasitoids of Tachinidae and Ichneumonidae. Carlson (1979) said that eggs are laid singly on leaves, to be injected by caterpillars. The report by Hirai & Ishii (1995) gives
additional details typical of their parasitization. In most literature the family name has been spelled Trigonidae, but Trigonalyidae is apparently correct.

221. Lycogaster pullata pullata Shuckard
Hosts: Hyperparasitoid in Enicospilus americanus in Antheraea polyphemus
Distribution: Vermont to Georgia across to North Dakota
Biology: Hyperparasitoid. Eggs are deposited on leaves and eaten by a caterpillar. Then the hyperparasitoid larvae find larvae of the primary parasitoid within the caterpillar (primary host).
References: Packard (1914: 268), Carlson (1979: 1198)
Remarks: Cockerell (in Packard) wrote that this wasp was bred in Berlin by an entomologist named Bischoff from an imported cocoon of A. polyphemus, but that it was apparently a hyperparasitoid in a cocoon of Enicospilus americanus. Cockerell used the name Erymotylus macrurus for the latter.

222. Lycogaster pullata nevadensis Cresson
Hosts: Hyperparasitoid of tachinid in Agapema dentifasciata
Distribution: Oregon, South Dakota, Colorado, New Mexico, Nevada, northeastern Mexico
Biology: One specimen was reared from a cocoon of Agapema, undoubtedly as a hyperparasitoid of a tachinid.
Remarks: Specific record: ex Agapema dentifasciata: 58 km ENE of Matehuala, Nuevo León, emerged 9 January 1981, R. O. Kendall (TAMU). The specimen was determined by A. S. Menke (USDA). This rearing gives a range extension for the parasitoid to the southeast beyond that cited by Carlson.

223. Poecilgonalos costalis (Cresson)
Hosts: Hyperparasitoid in tachinids in Automeris io, Anisota senatrix, Anisota virginiensis, and Anisota discolor
Distribution: Massachusetts to Florida to Ohio to Texas
Biology: Hyperparasitoid.
References: Carlson (1979: 1198), Riotte & Peigler (1981: 120), Tuskes et al. (1996)
Remarks: Specific records: ex Anisota senatrix: Stubblefield Lake, Walker Co., Texas, 1977, R. S. Peigler; ex Anisota discolor: Stubblefield Lake, Texas, 27 April 1977, R. S. Peigler (USNM). This rearing gives a range extension for the parasitoid to the southwest beyond that cited by Carlson.

DIPTERA
Family Tachinidae
These flies are usually black or gray, often with conspicuous stripes and prominent bristles. Many resemble large house flies and calliphorid flies. Most Tachinidae (pronounced tak-EYE-ni-dee) are endoparasitoids of larvae of insects, especially Lepidoptera. An archaic synonym is Larvaeoradae. The German name for the group is Raupenfliegen meaning “caterpillar flies.” They are, as far as I know, all koinobionts, and virtually none are hyperparasitoids. Some are gregarious, others solitary. There are various mechanisms of oviposition to get the egg onto or into a suitable host. Some females inject one or more eggs into a host, with a slender ovipositor telescoped within the abdomen. Others deposit eggs onto hosts, to which these adhere very firmly. It is not unusual to see the oval, flattened white or gray eggs on
a caterpillar. Many kinds of tachinids spread large numbers of eggs indiscriminately on leaves so that some will be consumed by appropriate hosts. Such eggs are called microtype (Salkeld 1980) and must be resistant to crushing in the mandibles of the caterpillar. Eclosion is triggered by enzymes in the digestive system of the host. A remarkable variation is known in the genus Belvosia, as described below under that genus.

Herting (1960) gave a detailed and well-illustrated account of the internal development of larvae of tachinids in their hosts. In most species the mature maggots exit the host, drop to the ground, and pupate in the soil. It is easier for a maggot than an adult fly to chew a tiny hole and squeeze through a cocoon or pupa, the fragile adult lacking chewing mouthparts. A trail of mucus which dries to a glossy, transparent streak may reveal which cocoon or cocoons in the rearing cage yielded the maggots. The mature maggot will contract, turn reddish brown, forming a puparium (plural: puparia), and pupate within the puparium, which shows segmentation since it is really the last larval skin, darkened and reshaped. Entomologists must protect puparia from desiccation or flies will die before emerging. Care should be also taken to avoid excessive moisture and lack of ventilation, which leads to mold and can also be fatal. Adult flies are often collected at flowers and in malaise traps.

A good discussion of biology of Tachinidae was given by Wood (1987: 1197-1200).

The taxonomy of the family is in disarray, because many unrelated groups look alike. The group is traditionally difficult and many misidentifications exist in literature where host records are reported. Many species have been reassigned to other genera, and many genera synonymized in recent years. Existing classifications, especially at the tribal level, include some groupings that are not natural. Newer studies based on valid synapomorphies are finally advancing our knowledge of tachinid classification. I have updated the nomenclature whenever possible. For this catalog I arranged the genera phylogenetically as far as possible using literature available to me, retaining subfamilies but omitting tribes, because of considerable disagreement among even recent authors. It would not have been possible to compile the Tachinidae section of the present catalog without access to the taxonomic catalog by Dr. Benno Herting of Germany and the host-parasitoid catalog by Dr. Paul Arnaud of the California Academy of Sciences, San Francisco. Arnaud's catalog is a monumental work that is valuable because many tachinids are important factors in biological control of other insects that are pests in forests and agro-ecosystems.

**Subfamily Phasiinae**

The tachinids in this subfamily differ considerably in appearance from all others listed below. The Phasiinae often have dark brown wings, flat orange abdomens, and dense brushes of hairs on the legs. Most of these attack adult bugs of the hemipteran families Coreidae and Pentatomidae.

**224. Cylindromyia binotata** (Bigot)

**Hosts:** Actias luna, Euschistus spp. (Hemiptera: Pentatomidae)

**Distribution:** North America

**Biology:** According to Arnaud, the pupa of A. luna and the adults of the Hemiptera were attacked. I have often observed the white eggs of various Phasiinae attached to adult bugs (Pentatomidae and Coreidae). It therefore seems possible that the rugose, brown pupa of a moth could be attacked, since it resembles the exoskeleton
of a brown stink bug. However, how would the bug enter the cocoon of the moth to oviposit on the pupa? Moreover, almost all phasines parasitize only Hemiptera.


Remarks: Pujade & Sarto gave a color illustration of a species in this genus, showing that it differs greatly in appearance from all other tachinids listed below.

Subfamily Tachininae

225. Ceromya luteicornis (Curran)
Hosts: Bunaea alcinoe, Imbrasia belina, Imbrasia cytherea, Imbrasia epimethea
Distribution: South Africa
Remarks: Crosskey listed this genus as attacking Saturniidae, Sphingidae, Lymantriidae, and Noctuidae.

226. Tachina sp.
Hosts: Antheraea yamamai
Distribution: Japan
References: Sakamoto (1990: 150), Herting (1984: 84)
Remarks: Sakamoto listed "Echinomyiasp." as a parasitoid of A. yamamai. According to Herting, that generic name is a synonym of Tachina. I do not know which species this record belongs to, because Herting listed numerous Palaearctic species in the genus.

227. Linnaemyia comta (Fallén)
Hosts: Saturnia pavonia
Distribution: Transcaucasus; Scotland to far eastern Russia
References: Thompson (1944: 535), Herting (1984: 96-97)
Remarks: The name is sometimes misspelled as L. compta.

228. Eurithia consobrina (Meigen)
Hosts: Saturnia pavonia
Distribution: Ireland and Scotland to Transcaucasus to northern Kazakhstan; northern China (Gansu); far eastern Russia (Kunashir Islands and Sakhalin)
Remarks: The name of the parasitoid was cited by Thompson as Ernestia consobrina.

Subfamily Goniinae

229. Compsilura concinnata (Meigen)
Hosts: Hemileuca lucina, Hemileuca maia, Hemileuca oliviae, Automeris io, Anisota senatoria, Anisota virginiensis, Dryocampa rubicunda, Cirina forda, Imbrasia cytherea, Callosamia promethea, Hyalophora cecropia, Actias luna, Actias isabellae, Saturnia pavonia, Antheraea polyphemus, Bombyx mori (L.) (Bombycidae), many sawflies (Hymenoptera: Symphyta), many Lepidoptera in Lasiocampidae, Lymantriidae, Arctiidae, Notodontidae, Sphingidae, Geometridae, Hesperiidae, Nymphalidae, Pieridae, Papilionidae, other families, and some Microlepidoptera
Distribution: Europe; introduced to eastern North America to control gypsy moth (Lymantria dispar (L.)), and now recorded from California and British Columbia; southern Africa; Australia; Asia
Biology: The ovipositing female fly larviposits, i.e., deposits live larvae into the host sawfly or caterpillar. Solitary host larvae are more vulnerable to attack than ones in aggregations.


Remarks: Interactions between Lepidoptera that feed on blueberry and their parasitoids were discussed by Szujecki. These associations included *Saturnia pavonia* and *Compsilura concinnata*.

230. *Oswaldia aurifrons* (Townsend)

Hosts: *Anisota senatoria, Nematus ventralis* Say (Hymenoptera: Tenthredinidae)

Distribution: eastern North America to Utah


Remarks: Records in literature prior to Arnaud appear under the name *Dexodes aurifrons*. Cole treated *Dexodes* as a subgenus of *Oswaldia*.

231. *Pilimyia, or an allied genus*

Hosts: *Opodiphthera helena*

Distribution: eastern Australia

References: Cantrell (1986)

Remarks: Cantrell cited the host under the name *Antheraea helena*.

Genus *Exorista*

The biology of a species in this genus was described by Kugler (1961). The eggs are deposited by female flies onto the integument of the host larvae. Generally, late stage larvae are attacked. Upon eclosion, the tachinid larva immediately penetrates the host integument. It feeds on fat-bodies and hemolymph at the point of internal attachment, then at maturity attacks vital organs of the host. It leaves the host to pupate in the soil.

232. *Exorista japonica* (Townsend)

Hosts: *Antheraea yamamai*

Distribution: Japan, Taiwan, and mainland China.

References: Sakamoto (1990: 150 as *Eutachina japonica*), Herting (1984: 5)

233. *Exorista larvarum* (Linnaeus)

Hosts: *Saturnia pyri*

Distribution: Europe

References: Thompson (1944: 535), Herting (1984: 5)

Remarks: This record is probably based on a misidentification of the parasitoid.

234. *Exorista mella* (Walker)

Hosts: *Hemileuca grotei, Hemileuca oliviae, Callosamia promethea*, one sawfly (Hymenoptera: Tenthredinidae), and numerous Lepidoptera in Lasiocampidae, Arctiidae, Lymantriidae, Notodontidae, Noctuidae, Nymphalidae, Danaidae, and a few others.

Distribution: North America

Biology: Larvae of the parasitoid emerge from mature host larvae. Judging from the
long host list given by Arnaud, it would appear that hairy or spiny caterpillars are preferred. There are many such hosts listed in Arctiidae, Lymantriidae, and Lasiocampidae, but very few with smooth integuments like Danaus plexippus (L.) and Callosamia promethea. The latter hosts should be verified.


Remarks: According to Watts & Everett, a synonym is E. larvarum.

235. Exorista sp. near mella
Hosts: Hemileuca oliviae, Hemileuca burnsi
Distribution: California, New Mexico

Biology: Maggots emerge from mature host larvae and pupate in the ground.
Remarks: These two records may represent one or two species. They were identified by N. E. Woodley. There were eight specimens reared from California, and one from New Mexico. A puparium is pinned with each specimen.

Specific records: ex Hemileuca burnsi: Phelan, San Bernardino Co., California, June 1986, D. C. Hawks (DMNH, USNM); ex Hemileuca oliviae. 18 km W of Grenville, Union Co., New Mexico, September 1987, R. S. Peigler (USNM).

236. Exorista rustica (Fallén)
Hosts: Saturnia pyri, sawflies (Hymenoptera), other Lepidoptera including Lasiocampidae
Distribution: Ireland, England, Scandinavia, Transcaucasus, Israel, Siberia, Mongolia

References: Rougeot (1971: 92, as Tachina festivata), Herting (1960: 39; 1984: 9-11)
Remarks: Herting (1960) pointed out that this very common tachinid may indeed use Lepidoptera as hosts occasionally, although sawflies are the normal hosts. In my opinion, there has been so much taxonomic confusion for this fly (two pages of synonymies in Herting 1984) that the record for Saturnia pyri is likely based on a misidentification.

237. Exorista sorbillans (Wiedemann) (Figure 9)
Hosts: Saturnia caecigena, Saturnia spini, Saturnia pavonia, Saturnia pyri, Antheraea yamamai, Antheraea assamensis, Antheraea paphia, Samia cynthia, Samia ricini, Attacus atlas, Attacus caesar, Attacus lorquinii, Imbrasia tyrrhea, Holocera smilax
Distribution: Mediterranean (Europe and northern Africa), eastward to Japan, tropical and temperate Asia, tropical Africa

Biology: Good details were given by Bannerjee. Aspects of the egg were given by Manjunatha & Puttaraju. Watanabe & Mitsuhashi succeeded in rearing the larvae on artificial diet.


Remarks: Gupta reported that this tachinid had been reared as a hyperparasitoid of the ichneumonid Lissoscopula javanica (Cameron) (Ichneumoninae: Gyrodonitini). The primary host was probably the lasiocampid moth Dendrolimus punctatus. I do not list this species under the Ichneumonidae as it has not been reared as a parasitoid of Saturniidae.
The record of *Samia cynthia* cited by Crosskey is apparently from West Malaysia, therefore probably refers to one of the more tropical species of *Samia* occurring on the mainland. Crosskey (pers. comm. in 1996) indicated the name *sorbillans* refers to a complex of species, and that at least 12 species are still arranged under this name in the BMNH collection.

Although Herting (1984: 6) listed virtually no synonyms, it is clear that several are being used in the sericulture literature. The main one is *Tricholyga bombycis* (Lederer, Chowdhury, Sarkar, etc.), also spelled *Thrycolyga* (Cuthbertson & Munro). Indian authors call this species the "uzzi fly," a name also applied to *Blepharipa zebina* and *B. sericariae* (see below). Probably reports of these three species and others are widely confused, especially in tropical Asia. The word uzi is apparently of Japanese origin. It would be a worthwhile project for an entomologist in Asia to make a comprehensive taxonomic study of the tachinids that damage the domestic and wild silk crops of Japan, China, India, Thailand, etc. to resolve the nomenclatural confusion. Such work would be useful in developing effective control programs.

238. *Exorista* sp.
**Hosts:** *Hemileuca magnifica*
**Distribution:** southwestern United States
**References:** Stone et al. (1988)

**Genus *Chetogena***

This genus is commonly reared from saturniids in North America, especially from *Hemileucinae* in the West. The genus needs taxonomic revision, and it has not been possible for experts to assign species names to most of the material we have reared in recent years. The generic names *Spaggosia* and *Euphorocera* are now considered to be synonyms (Herting 1984: 13; Woodley 1987: 1221), so most records in the literature under those names belong under *Chetogena*. Herting spelled the name *Chetogena*. Eggs are laid on the head or integument of the caterpillars, often easily seen. Some biological observations on a species in this genus were given by Terkanian (1995).

239. *Chetogena claripennis* (Macquart)
**Hosts:** *Hemileuca oliviae, Hemileuca maia, Hemileuca lucina, Hemileuca artemis, Hemileuca electra, Hemileuca nevadensis, Automeris io, Callosamia promethea, Hyalophora cecropia, Anisota senatoria, Dryocampa rubicunda*
**Distribution:** Throughout almost all of the continental United States, into Mexico and Canada
**References:** Ainslie (1910), Packard (1914: 269), Watts & Everett (1976), Allen (1976), Arnaud (1978: 219-229), Schaffner & Griswold (1934)
**Remarks:** This parasitoid is in most literature under the name *Euphorocera claripennis*, and in Schaffner & Griswold as *Phorocera claripennis*.

240. *Chetogena floridensis* (Townsend)
**Hosts:** *Dryocampa rubicunda*, several other families of moths and butterflies
**Distribution:** United States: Colorado to Maryland, and all through Southeast
**References:** Arnaud (1978: 231-233)

241. *Chetogena* sp. near *floridensis* (Townsend)
**Hosts:** *Agapema galbina*
**Distribution:** southern Texas
Remarks: The authors above cited this parasitoid under the generic name *Euphorocera*.

242. *Chetogena obliquata* (Fallén)

**Hosts:** *Saturnia pyri*

**Distribution:** Sweden to Israel to Tajikistan

**References:** Thompson (1944: 535), Herting (1984: 14)

**Remarks:** Thompson cited the species as *Phorocera echinura*.

243. *Chetogena spp.*

**Hosts:** *Hemileuca oliviae, Hemileuca magnifica, Hemileuca juno, Hemileuca eglanterina, Hemileuca grotei, Hemileuca slosseri, Automeris io*

**Distribution:** western North America

**Biology:** Eggs are seen on the heads or integuments of mature larvae. Mature host larvae die without pupating, and maggots emerge from them, pupating in a rearing container, or in nature, dropping to the ground and pupating in soil.


**Remarks:** As mentioned above, records cited in earlier literature (including recent) under the generic names *Spoglossia* and *Euphorocera* refer to this genus. Wood (1987) synonymized these names under *Chetogena*. Virtually all species of the *Hemileuca* of the western United States will produce flies in this genus if mature larvae are collected in the field. Among the series cited below reared from *H. grotei* and *H. magnifica*, more than one species appears to be in each lot.


**Genus Belvosia**

This genus is important in the New World as significant parasitoids of Saturniidae. They are large flies and are specialists on large hosts like Sphingidae, large Noctuidae, Arctiidae, and Saturniidae. The genus needs revision, and N. E. Woodley is currently working on that project, making particular use of copious material being reared by D. H. Janzen in Costa Rica. Woodley's revision will not be published for at least a few more years, so I am not delaying publication of this catalog in anticipation of it. For the moment, we must rely on older taxonomic works like that of Aldrich (1928), and host records as found in Arnaud (1978) and d'Aratijo e Silva et al. (1968). Some of the parasitoid names and host records listed below are undoubtedly in error. Synonyms of *Belvosia* include *Triachora*, *Willistonia*, and *Belvosiopsis*.

The eggs are microtype (Salkeld 1980) and the method of oviposition is remarkable. The female locates a suitable host caterpillar and then deposits an egg or eggs on the leaf just in front of where it is eating. This efficient method differs from microtype eggs of other tachinids in which a lot of eggs are wasted by never being injected by a suitable host. Some species like *B. bifasciata* have a fairly broad host range, attacking hosts in three or more subfamilies of Saturniidae and also Sphingidae. Other species appear to be very specific to a single genus of host.
244. Belvosia argentinfrons Aldrich

Hosts: Citheronia regalis

Distribution: Florida

References: Aldrich (1928), Arnaud (1978: 88), Peigler (1985a)

Remarks: Specific record: ex Citheronia regalis; Gainesville, Florida, 17 February 1983, C. Bennett (USNM). Specimens of the aforementioned record were sent to me by Steven Passoa and identified by N. E. Woodley.

245. Belvosia bella G. T.

Hosts: Hylesia lineata

Distribution: Guanacaste Province, Costa Rica

Biology: The adult flies emerge from the cocoons of the host.

References: Janzen (1984)

246. Belvosia bicincta (Robineau-Desvoidy)

Hosts: Eacles imperialis magnifica, large Noctuidae

Distribution: Brazil; Costa Rica; Jamaica

Biology: Crocomo & Parra reared this parasitoid from the above host in the state of São Paulo. They found generally two to four flies per host. Of 870 host pupae, they found that 16 had this parasitoid, for a 4.32 percent parasitization.

References: Aldrich (1928), d’Araujo e Silva et al. (1968: 261), Crocomo & Parra (1979), Arnaud (1978: 88)

247. Belvosia bifasciata (Fabricius) (Front Cover illustration)

Hosts: Callosamia securifera, Antheraea polyphemus, Hemileuca maia, Hemileuca lucina, Hemileuca slosseri, Hemileuca peigleri, Hemileuca nevadensis, Hemileuca juno, Citheronia regalis, Eacles imperialis, Anisota discolor, Anisota assimilis, Anisota senatoria, Dryocampa rubicunda, and a few Sphingidae

Distribution: Across much of United States from Atlantic States (Connecticut to Florida), New Mexico, Arizona, and California. According to Cole, restricted to the temperate zone.

Biology: Packard stated that the specimen he illustrated emerged from a pupa of H. nevadensis that was two years old. In small hosts such as Hemileuca and Anisota, one parasitoid develops, whereas in large hosts such as Eacles, several parasitoids emerge. Perhaps ovipositing females are able to distinguish the number of eggs to “feed” the host based on its size. Parasitoids pupate within the pupa of the host, the adult flies emerging from the anterior end of the host pupa, sometimes leaving their puparia partially exerted.


Remarks: Specific records: ex Eacles imperialis: Stubblefield Lake, Walker Co., Texas, May 1980, R. S. Peigler (DMNH); ex Anisota discolor: Stubblefield Lake, Texas, emerged indoors 2 December 1977, R. S. Peigler (DMNH); netted on oaks: Stubblefield Lake, Texas, 3 October 1993, R. S. Peigler (DMNH); on flowers of Euonymus japonica: Greenville, South Carolina, 9 August 1987, R. S. Peigler (DMNH); ex Hemileuca maia: Louisiana State University campus, Baton Rouge, Louisiana, August 1980, J. E. Eger (USNM); ex Hemileuca juno: Wickenburg, Arizona, 26 September 1938 (Comstock & Dammers 1939); ex Dryocampa rubicunda: Chafee, New York, April 1935, J. G. Franclémont (CUIC).
248. Belvosia chelsai (Blanchard)
Hosts: Eacles imperialis opaca
Distribution: Argentina

249. Belvosia ciliata Aldrich
Hosts: Copaxa, possibly lavendera, Leucanella leucane, Hesperiidae
Distribution: North America (Missouri), Central America (Mexico, Panama), South America (Brazil)
References: Aldrich (1928), Arnaud (1978: 90-91)
Remarks: Tuskes et al. (1996) cited Hyalophora cecropia erroneously as a host for this parasitoid. The confusion was apparently in reference to Lespesia ciliata as cited by Arnaud (1978: 665).

250. Belvosia esuriens (Fabricius)
Hosts: Automeris janus
Distribution: Trinidad
References: Aldrich (1928: 42-43), Thompson (1944: 89)
Remarks: The parasitoid was cited under the name Willistonia by Thompson.

251. Belvosia formosa Aldrich
Hosts: Rothschildia orizaba, Automeris sp.
Distribution: Mexico, West Indies, Costa Rica, Brazil
References: Aldrich (1928), Arnaud (1978: 91)

252. Belvosia leucopyga van der Wulp
Hosts: Rothschildia jacobaeae, Hylesia (probably nigricans)
Distribution: South America (Brazil and Venezuela), Central America (Yucatán, Mexico)
Remarks: A synonym is Belvosiopsis brasiliensis, according to Aldrich. The rearing from Hylesia cited by Janzen was done by J. A. Winder in the state of Parana, Brazil, who used the synonym Hylesia fulviventris.

253. Belvosia nigrifrons Aldrich (Figure 8)
Hosts: Rothschildia orizaba, Rothschildia lebeau, Rothschildia cincta guerreronis, Rothschildia erycina, Eupackardia calleta
Distribution: Mexico, El Salvador, Honduras, Costa Rica
References: Aldrich (1928), Thompson (1944), Quezada (1967)
Thompson (1944: 532) cited Belvosia analis Macquart as attacking Rothschildia jorulla [which only occurs in Mexico]. I consider the most likely host for a species of Rothschildia in El Salvador to be R. lebeau., but Aldrich (1928: 45) pointed out that this name cannot be identified because it is based on a type-specimen that is lost. Considering the locality and the host, it is surely a record for B. nigrifrons.
254. *Belvosia recticornis* (Macquart)
**Hosts:** *Hylesia alinda*, *Hylesia umbrata*, *Hylesia spp.*
**Distribution:** Mexico, Panama, Ecuador
**References:** Aldrich (1928), Arnaud (1978: 91-92)
**Remarks:** *Hylesia darlingi* (a name used by both Aldrich and Arnaud) is a junior synonym of *H. umbrata* (C. Lemaire, pers. comm.).

255. *Belvosia townsendi* Aldrich
**Hosts:** *Eacles imperialis*, *Eacles oslari*, *Citheronia regalis*
**Distribution:** New York, Pennsylvania, New Jersey, Virginia, Ohio, Indiana, North Carolina, South Carolina, Georgia, Kansas, Texas, Arizona
**Biology:** Material from the rearing from Austin, Texas, cited below was given to me by T. Friedlander; there were two parasitoids in this host. There were 3 or 4 or more parasitoids per host in the rearings from Arizona.
**References:** Aldrich (1928), Schaffner & Griswold (1934), Arnaud (1978: 92), Peigler (1985a)
**Remarks:** Specific records: *ex Eacles imperialis nobilis*: Austin, Texas, July 1976, H. Pianka (USNM); *ex Eacles oslari*: Sonoita Creek, Santa Cruz Co., Arizona, 1972, K. Hansen (USNM).

256. *Belvosia weyenberghiana* van der Wulp
**Hosts:** *Rothschildia jacobaeae*, *Rothschildia sp.*
**Distribution:** South America (Argentina, Brazil)
**References:** Aldrich (1928), d’Araújo e Silva et al. (1968: 270), Margheritis & Rizzo (1965: 156)

257. *Belvosia spp.*
**Hosts:** *Hylesia nanus*, *Hemileuca magnifica*, *Hemileuca stonei*
**Distribution:** southern Brazil; Arizona
**References:** d’Araújo e Silva et al. (1968: 269)
**Biology:** One parasitoid per host.

The first host was cited as *Micrattacus nanus* from Brazil.

**Genus Leschenaultia**

This genus appears to be closely related to *Belvosia*, although Cole, Arnaud, and others place it in a separate tribe. The flies are large, and resemble those of the previous genus, but are a bit more flattened. The eggs are microtype (Salkeld 1980), so are probably deposited on foliage of the hostplants of the hosts. A synonym is *Blepharipeza*.

258. *Leschenaultia adusta* (Loew)
**Hosts:** *Coloradia pandora*, *Malacosoma* (Lasiocampidae), several Arctiidae
**Distribution:** North America, Atlantic States to California
**Biology:** Apparently prefers larvae that are hairy or spiny. Patterson stated that host larvae are parasitized but fail to pupate. The maggots emerge from the pre-pupae of the hosts and form their puparia alongside in the soil cavities. He stated that as many as 41 puparia were collected in an area of ground about 1 m square where 76 pupae of *C. pandora* were found.
Remarks: This parasitoid is cited in most literature under the name *Blepharippeza adusta*.

259. Leschenaultia fulvipes (Bigot)
Hosts: *Hemileuca lucina, Hemileuca groteti, Hemileuca maia*, *Malacosoma* (Lasiocampidae)
Distribution: New England to Texas

260. Leschenaultia sp. near fulvipes (Bigot)
Hosts: *Hemileuca slosseri*
Distribution: Texas

261. Leschenaultia spp.
Hosts: *Hemileuca oliviae, Hemileuca slosseri, Hylesia sp., Automeris sp.*
Distribution: North America, South America
Biology: Fritz et al. stated that the parasitoid oviposited on ends of spines near the host's head.
Remarks: Specific records: *ex Hylesia on Pinus*: La Unión, Departamento de Olacho, Honduras, October 1981, J. Mankins, sent to Peigler by S. Passoa (USNM); *ex Automeris sp.:* Mexico City, Mexico, 10 June 1979, R. L. Halbert (DMNH). The latter record probably refers to *A. cecrops* since I have observed that host to be common in the suburban habitat of Mexico City. J. E. Slosser reported to me the records of "Leschenaultia sp. near fulvipes," and possibly another species of *Leschenaultia* from reports of parasitoids he had submitted for identification.

262. Masicera pavoniae (Robineau-Desvoidy)
Hosts: *Saturnia pavonia, Saturnia pyri, Saturnia spini, Acherontia atropos* (L.) (Sphingidae), *Eligmodonta ziczac* (L.) (Notodontidae)
Distribution: France, Germany, and Poland to Turkey and Syria, but not on British Isles
Biology: The host larvae are attacked, and the adult flies emerge after overwintering in the pupae or cocoons of the hosts. There can be a single parasitoid in a small host, or as many as 20 in a large host like *S. pyri*. There was only a single fly reared from the specific record cited below, and its puparium was in the host cocoon alongside of the host pupa. It overwintered within, but I do not know whether the maggot exited the pupa in the fall or the spring.
Remarks: Herting used the name *pratensis* in his 1960 catalog, but synonymized this name under *pavoniae* in his 1984 catalog. The true *pratensis* is a species of the closely related genus *Blepharippeza* (Herting 1984: 76). Any records in literature under the names *pratensis* and *marginalis* cited as parasitoids of Saturniidae should be referred to *pavoniae*. Claude Lemaire sent me the following specimen, identified by C. Sabrosky.
263. Masicera silvatica (Fallén)

**Hosts:** Actias isabellae, Saturnia pavonia, Saturnia spini, Macrothylacia rubi (L.) (Lasiocampidae)

**Distribution:** Sweden to Spain


**Remarks:** There has been some confusion by earlier authors of this species with Exorista sorbillans. The latter would be a logical parasitoid for A. isabellae and Saturnia, so the records of *M. silvatica* need to be verified in these hosts. However, the record of *M. rubi* is valid, and therefore it is likely that the three saturniids are also hosts.

264. Baumhaueria goniaeformis (Meigen)

**Hosts:** Saturnia pyri

**Distribution:** Europe to Israel to Transcaucusus

**References:** Thompson (1944: 535), Herting (1984: 79)

265. Pimelimyia natalensis Curran

**Hosts:** Cirina forda, Bombycomorpha bifascia Walker (Lasiocampidae)

**Distribution:** Africa

**Biology:** The larva is attacked, the mature parasitoid larvae emerge from the pupa of the host, drop to the ground, form puparia in soil, and emerge a few weeks later.

**References:** Taylor (1961), Crosskey (1984)

**Remarks:** Richard Harland-Rowe sent me specimens of *Pimelimyia semitestacea* (Villeneuve) that he reared from Gonometa rufobrunnea Aurivillius (Lasiocampidae): Francistown, Botswana, emerged October 1991 and January 1992 (DMNH). The maggots emerged from the host cocoons and pupated a few weeks prior to the emergence of the adult flies. I extrapolated these data to make comments on the biology of *P. natalensis* above. The *P. semitestacea* is a large fly with chestnut eyes, black and gray striped thorax, tan scutellum, and tan patches on the abdominal tergites. Taylor cited it under the name *Sturmia semitestacea*, and as having been reared from *Gonometa postica* Walker.

266. Sturmia sp.

**Hosts:** Automeris sp.

**Distribution:** Brazil

**Biology:** If a true *Sturmia*, oviposition is on foliage of foodplants of host caterpillars. Hosts inject eggs, tachinid larvae mature when the host pupates, then maggots leave the host to pupate in soil. These notes are based on the report of Hirai & Ishii on *Sturmia bella*.

**References:** d’Araújo e Silva et al. (1968: 263), Hirai & Ishii (1995)

**Remarks:** This vague record may not represent a true *Sturmia*.

267. Blepharipa sericariae Rondani

**Hosts:** Antheraea yamamai, Bombyx mori

**Distribution:** Japan

**Biology:** The best treatment of the biology is a well-illustrated account by Bolle.

**References:** Bolle (1898), Sakamoto (1990: 150), Herting (1984: 75-76)

**Remarks:** Sakamoto placed this fly in the genus *Sturmia*, but under that genus Herting cited only *S. bella* from the Palaearctic region. The name *sericariae* refers to the fact that species of *Bombyx (=Sericaria)* serve as hosts. Bolle called this pest the
"Ujifliege" and *Ugimyia sericaria*. The Japanese name “uzi” is also applied by Indian authors to *Exorista sorbillans* (see above) and *Blepharipa zebina* (see below). All of these tachinids kill millions of caterpillars, thus diminishing yields of cocoon crops in domestic and wild silk industries.

268. *Blepharipa tibialis* (Chao)
**Hosts:** *Antheraea pernyi, Malacosoma neustria* (L.) (Lasiocampidae),
**Distribution:** northern China, including provinces of Liaoning and Heilongjiang
**References:** Qu et al. (1990), Herting (1984: 76)

269. *Blepharipa waimurighti* (Baronov)
**Hosts:** *Archaeoattacus edwardsii, Attacus atlas*
**Distribution:** southeastern Asia
**References:** Crosskey (1976: 303), Peigler (1989: 93-94)

270. *Blepharipa zebina* (Walker)
**Hosts:** *Archaeoattacus edwardsii, Antheraea paphia, Sphingidae, and other large Lepidoptera*
**Distribution:** far eastern Russia, Japan (Kyushu and Hokkaido), Himalayas of India.
**Biology:** The female lays up to 250 eggs. About 30 to 40 are deposited on the body of a caterpillar. Eclosion is within 3 days. Mature maggots emerge within 10 to 12 days. Pupation is in the ground where they overwinter, and emergence is in the spring. Adult flies mate while in flight.
**References:** Jolly et al. (1974, 1975), Herting (1984: 76), Singh et al. (1993)
**Remarks:** In some of the sericulture literature coming out of India this species has been confused with *Exorista sorbillans* (see above). It is, along with that species, apparently a significant pest of tasar and other wild silk crops, although I find no reports of *Samia ricini* and *Antheraea assamensis* as hosts, the sources in Assam of eri and muga silks, respectively. *Exorista sorbillans, B. zebina, and B. sericariae* are all called “the uzi fly” in the sericulture industry.

271. *Drino atropivora* (Robineau-Desvoidy)
**Hosts:** *Imbrasia tyrrhea*
**Distribution:** Africa
**References:** Cuthbertson & Munro (1941), Crosskey (1984)
**Remarks:** This parasitoid has been listed under the generic names *Sturmia* (by Robineau-Desvoidy and Cuthbertson & Munro) and *Zygothria* (Crosskey). The latter is a synonym of *Drino* in the opinion of Herting (1984: 52).

272. *Drino incompta* (van der Wulp)
**Hosts:** *Eacles imperialis, Hemileuca maia*, and several Sphingidae
**Distribution:** eastern United States
**References:** Packard (1914: 269), Arnaud (1978: 190-191)
**Remarks:** Most records are in literature under the name *Sturmia inquinata*.

273. *Drino inconspicua* (Meigen)
**Hosts:** *Actias isabellae, Gynanisa maja, Holocerina smilax*, other Lepidoptera including *Arctiidae, Sphingidae, Lasiocampidae, Lymantriidae*, and *Notodontidae, and many species of Diprion* (Hymenoptera: Diprionidae)
**Distribution:** Europe, including Sweden, across to central Siberia, but not in Britain; northeastern North America; Africa
**Biology:** Females lay about 100 eggs, deposited onto larvae of the hosts. About 5 to 10 minutes after hatching, larvae bore into the hosts. In Europe, virtually all of the hosts are sawflies and caterpillars that feed on pines (*Pinus*) and other conifers. The first instar parasitoid larvae overwinter in the hosts, which in some cases are larvae themselves (i.e., *Dendrolimus pini*).


**Remarks:** For *Actias isabellae*, most European authors cited this parasitoid under the name *Argyrophylax inconspicua*. Another synonym according to Ceballos & Ajengo is *A. bimaculata* Hartig. Most American authors cited it as *Sturmia inconspicua*. The hosts cited by Arnaud in North America correspond closely to those of Europe, except for the addition of non-conifer-feeding Lasiocampidae in the genus *Malacosoma*. The parasitoid has been classified as *Carcelia* by some authors, in the genus *Palexorista* by Crosskey, and in *Sturmia* by Cuthbertson & Munro! I am grateful to R. Oberprieler for his insight in helping me clarify the tangled taxonomy of this parasitoid. He and I assume that all five generic combinations with *inconspicua* refer to a single widely ranging tachinid.

274. *Drino lota* (Meigen)

**Hosts:** *Aglia tau*, Sphingidae, and a few other Lepidoptera

**Distribution:** Scotland to southern Sweden

**Biology:** Up to 12 eggs are laid on the top of a larva, the latter instars preferred. The tachinid larvae bore into the host when they hatch. They mature and emerge from the host, dropping to the ground to pupate in soil. They overwinter in their puparia. The larva of *Aglia tau* could be considered "sphingiform" so the fact that it and certain sphingids serve as hosts is logical.

**References:** Herting (1960: 79; 1984), Cole (1969: 578)

275. *Patelloa fuscimacula* (Aldrich & Webber)

**Hosts:** *Antheraea polyphemus, Orgyia vetusta* Boisduval (Lymantriidae)

**Distribution:** California and British Columbia

**Biology:** If this species is truly congeneric with the three species of *Patelloa* studied by Salkeld, we may assume it has microtype eggs laid on leaves of hostplants.


**Remarks:** The lymantriid host was cited as *Hemerocampa vetusta*. The parasitoid is cited in virtually all literature as *Phorocera fuscimacula*.

276. *Phryxe pecosensis* (Townsend)

**Hosts:** *Hemileuca maia, Hemileuca lucina*, sawflies (Hymenoptera: Tenthredinidae), several families of Lepidoptera

**Distribution:** Québec to British Columbia south to California and New Mexico

**Biology:** Females "deposit maggots in choria [eggshells] on hosts." The eggs are whitish, small to medium macrotype.


**Remarks:** There is confusion of the relationship of this genus. Various authors have placed it in or near *Drino, Zenilla, Exorista*, and *Lydella*. The record cited by Thompson (1944: 294) of the Palearctic *Phryxe vulgaris* (Fallén) attacking *Hemileuca* surely represents a misidentification and probably belongs here.
277. *Pales blepharipus* (Brauer & Bergenstamm)

**Hosts:** *Lobobunaea angasana*

**Distribution:** Africa

**References:** Cuthbertson & Munro (1941)

**Remarks:** The parasitoid was cited under the generic name *Ctenophorocera* by Cuthbertson & Munro.

278. *Pales pavida* (Meigen)

**Hosts:** *Samia cynthia*, many Lepidoptera from several families including Nymphalidae, Noctuidae, Sphingidae, Bombycidae, Lasiocampidae, Arctiidae, Geometridae, Lymantriidae, Notodontidae, Pyralidae, and Tortricidae. (see Herting’s catalog also)

**Distribution:** Scotland to Japan; Transcaucasus

**Biology:** The microtype eggs are laid on the leaves of the hostplant, and are thus injected by the host caterpillars. Parasitoid larvae hatch in the alimentary canal and migrate to the silk glands living apneustically until the first molt. They then go to the integument (no particular region as in some parasitoids) and establish a respiratory hole. Some host larvae spin little or no silk; otherwise, the host cocoons are thin and usually lack a peduncle. The host pre-pupa does not pupate. One to 9 parasitoid larvae emerge from the pre-pupa and form their puparia in the host cocoon. Adult flies emerge about two weeks later via the pre-formed exit of the host cocoon. Larvae of this tachinid are attacked by *Eupteromalus arzoneae* (Pteromalidae).

**References:** Arzone (1970, 1971a), Herting (1984: 68)

**Remarks:** Arzone published a very detailed and well illustrated article on the biology of this tachinid in the host *Samia cynthia*, established along the western banks of Lake Maggiore in northwestern Italy. The host may actually be *Samia walkerii*, as I have not yet resolved the taxonomic question of which species (or both) occurs in Italy as introduced populations from China.

279. *Pales pumicata* (Meigen)

**Hosts:** *Samia cynthia*

**Distribution:** Europe

**References:** Arzone (1970), Herting (1984: 67-68)

**Remarks:** This tachinid has sometimes been classified in the genus *Phorocera*.

280. *Pales setigena* (Curran)

**Hosts:** *Lobobunaea angasana*

**Distribution:** Africa

**References:** Cuthbertson & Munro (1941), Crosskey (1984)

**Remarks:** The first authors cited this tachinid under the generic name *Phorocera*.

281. *Pales* sp.

**Hosts:** *Saturnia pavonia*

**Distribution:** Europe

**References:** Rougeot (1971: 107), Herting (1984: 15-16)

**Remarks:** This record is probably referable to *P. pumicata* above or to some other species of Tachinidae recorded from *S. pavonia*. 
Genus *Winthemia*

This is an important genus of tachinids that parasitizes many Lepidoptera, including Saturniidae, in many regions of the world. Eggs are laid on the integument of the host, and then maggots hatch and bore into the host. The African species which Taylor (1961) cited below were listed under the genus *Sericophoromyia*. Lester Kohalmi (pers. comm. in 1993) has reared an unidentified species of this genus from both *Hyalophora cecropia* and *H. columba columbia* in Kenora, Ontario.

282. *Winthemia amplipilosa* (Curran)
**Hosts:** Imbrasia cytherea, Urota sinope
**Distribution:** Africa
**References:** Taylor (1961), Crosskey (1984)

283. *Winthemia cecropia* (Riley)
**Hosts:** Actias luna, Antheraea polyphemus, *Hyalophora cecropia*
**Distribution:** North America, probably only in the East
**References:** Arnaud (1978: 506-507)
**Remarks:** A synonym is *Winthemia platysamiae*.

284. *Winthemia citheroniae* Sabrosky
**Hosts:** Citheronia regalis, Eacles imperialis
**Distribution:** Florida
**References:** Arnaud (1978: 507)

285. *Winthemia conformis* (Curran)
**Hosts:** Imbrasia belina, Imbrasia wahlbergii, Pseudobunaea irius
**Distribution:** Africa
**References:** Cuthbertson & Munro (1941), Crosskey (1984)

286. *Winthemia cruentata* (Rondani)
**Hosts:** Saturnia pyri
**Distribution:** Japan and Mongolia to Transcaucasia to Italy and Sweden
**References:** Thompson (1944), Herting (1984: 38)

287. *Winthemia datanae* (Townsend)
**Hosts:** Anisota senatoria, Anisota virginiensis, Dryocampa rubicunda, *Hyalophora cecropia*, several moths in Notodontidae, Arctiidae, Noctuidae, Sphingidae, Lasiocampidae, and Lymantriidae
**Distribution:** eastern North America
**References:** Schaffner & Griswold (1984), Hitchcock (1961b), Arnaud (1978: 507-510), Peigler (1985a)
**Remarks:** This parasitoid was cited by Schaffner & Griswold from *Anisota senatoria* and *Dryocampa rubicund*a as "variety B". Their record from *Samia cynthia* as "*Winthemia (?) datanae*" is surely an error, so I do not list it in the above list of hosts. Hitchcock also listed a parasitoid called "*Winthemia* sp. near *datanae*" as attacking *Anisota senatoria*.

Donald Henne (pers. comm.) has reared this parasitoid from *Anisota virginiensis* in Manitoba, near the southeastern edge of Lake Winnipeg.
288. *Winthemia lateralis* (Macquart)
Hosts: *Opodiphthera eucalypti*, several other Lepidoptera in Noctuidae, Notodontidae, Pieridae, Nymphalidae, and Geometridae
Distribution: Australia
References: Cantrell (1986)

289. *Winthemia leucaneae* (Kirkpatrick)
Hosts: *Hyalophora cecropia*, other Lepidoptera in Noctuidae, Sphingidae, and Pyralidae
Distribution: North America
References: Arnaud (1978: 512-514)
Remarks: Arnaud included *H. cecropia* as a host under both normal *W. kucanae-Mid* the form "lacking red at tip."

290. *Winthemia militaris* (Walsh)
Hosts: *Hyalophora cecropia*, other insects including butterflies (Hesperiidae), moths (Noctuidae), and grasshoppers (Acrididae)
Distribution: eastern North America
References: Arnaud (1978: 514-515)

291. *Winthemia quadrata* (Wiedemann)
Hosts: *Bunaea alcinoe, Imbrasia cytherea, Imbrasia tyrrhea, Urota sinope*
Distribution: Africa
References: Cuthbertson & Munro (1941), Crosskey (1984)

292. *Winthemia quadripustulata* (Fabricius)
Hosts: *Anisota senatoria, Antheraea polyphemus, Hyalophora cecropia, Callosamia promethea, Saturnia pavonia, Saturnia spini*, many other Lepidoptera including Noctuidae, Sphingidae, Geometridae, Arctiidae, and even Curculionidae (Coleoptera) and Diprionidae (Hymenoptera)
Distribution: North America; Scotland to Transcaucasus to Mongolia
Remarks: The record under *Saturnia pyri* cited by Thompson as "*Winthemia quadripustulata cruentata*" belongs under *W. cruentata* according to synonymies by Herting (1984).

293. *Winthemia tricolor* (van der Wulp)
Hosts: *Arsenura xanthopus, Arsenura armida, Samia cynthia*
Distribution: Central America, South America
Biology: According to Lordello & Mariconi cited below, the female fly lays 1 to 33 eggs on mature caterpillars, especially near the prolegs. The prolegs are favored because the host will thrash to resist the fly, but the prolegs remain fixed and are thus easily approached. They found that it is impossible to remove the eggs without destroying them, because they are so firmly attached. Before the host larva pupates, the parasitoid larvae crawl over the surface of the pre-pupa and try to enter the body, usually at intersegmental membranes. Some parasitoid larvae die because they are pushed off on the larval skin when it pupates. Eight days later 1 to 10 maggots emerge from the host. These pupate and produce adult flies in 15 days.
References: Lordello & Mariconi (1953), d’Araújo e Silva et al. (1968: 262), Arnaud (1978: 528)
Remarks: I do not know the source of the record for Samia cynthia cited by Arnaud. It may have been based on a laboratory rearing in Panama where the record for Arsenura armida (as A. erythrinae) was made.

294. Winthemia variegata (Meigen)
Hosts: Saturnia pavonia
Distribution: England to Germany to Russia
Remarks: Thompson cited this fly under the name Winthemia quadripustulata nigrithorax.

295. Winthemia spp.
Hosts: Hemileuca maia, Hemileuca lucina, Opodiphthera astrophela
Distribution: New England, California, Australia
Remarks: Specific record: ex Hyalophora euryalus: 32 km east of Nevada City, 1525 m, Nevada Co., California, collected 27 August 1995 ovipositing onto mature host larva, on dorsum of abdominal segment near posterior end, M. M. Collins (DMNH).

296. Huebneria affinis (Fallén)
Hosts: Saturnia pavonia, Saturnia pyri, various Arctiidae, Noctuidae, Lasiocampidae, Lymantriidae, and other Lepidoptera
Distribution: England, Scandinavia, central Europe, Transcaucasus, southern Siberia, Mongolia
Biology: Judging from the host list, large hairy or spiny caterpillars are preferred.
Remarks: Thompson cited this parasitoid as Aplomyia [Aplomyia] affinis, and Herting classified it under the genus Huebneria, although he considered Aplomyia also to be a valid genus.

297. Carcelia bimaculata (Hartig)
Hosts: Imbrasia cytherea
Distribution: Africa
Biology: Attacks the larva of the host.
Remarks: This species was placed by Crosskey in the genus Palexorista, but Cole (1969) and Herting (1984) indicated that the latter is a synonym of Carcelia. Crosskey cited the names Carcelia and Palexorista separately.

298. Carcelia evolans (Wiedemann)
Hosts: Bunaea alcinoe, Epiphora sp., Gynanisa maja, Heniocha apollonia, Holocerina smilax, Imbrasia belina, Imbrasia wahlbergii, Imbrasia tyrrea, Imbrasia cytherea
Distribution: Africa

299. Carcelia formosa (Aldrich & Webber)
Hosts: Automeris io, several Noctuidae
Distribution: eastern United States to Colorado
References: Schaffner & Griswold (1934), Arnaud (1978: 116), Peigler (1985a)
Remarks: Some records for this parasitoid in older literature are under the name Zenilia formosa.

300. *Carcelia modicella* (van der Wulp)
Hosts: *Cricula trifenestrata javana*
Distribution: Java (Indonesia)
References: Dupont & Scheepmaker (1936: 180)
Remarks: The authors cited this parasitoid under the name *Parexorista modicella*. The rearing was reported to them by K. W. Dammerman.

301. *Carcelia lucorum* (Meigen)
Hosts: *Saturnia pyri*, Lasiocampidae, Arctiidae, Noctuidae, and other Lepidoptera
Distribution: England, Finland, Italy, Israel, western Russia to Tajikistan, Altai, and Mongolia onward to Japan
References: Herting (1960: 84-85; 1984: 57)

302. *Carcelia malacosomae* Sellers
Hosts: *Hemileuca lucina*, *Hemileuca maia*, Notodontidae, Arctiidae, Lasiocampidae (*Malacosoma* spp.), sawfly (Hymenoptera: Tenthredinidae)
Distribution: eastern United States to Colorado and British Columbia
Remarks: According to Cole, a synonym is *Exorista cheloniae*.

303. *Senometopia excisa* (Fallén)
Hosts: *Saturnia pyri*
Distribution: Japan to southern England, widespread in Europe and Asia
References: Thompson (1944), Herting (1984: 59)
Remarks: The record was cited by Thompson under the name *Carcelia excisa*.

304. *Epicampocera succincta* (Meigen)
Hosts: *Saturnia pavonia*
Distribution: Europe to Japan including down into Transcaucuses
References: Thompson (1944: 535), Herting (1984: 44)

305. *Sisyropa eudryae* (Townsend)
Hosts: *Automeris io*, Noctuidae, Nymphalidae, Arctiidae
Distribution: Ontario and Vermont to North Carolina
Biology: Apparently large hairy or spiny caterpillars are preferred, judging from the host list.

306. *Eusisyropa virilis* (Aldrich & Webber)
Hosts: *Callosamia promethea*, *Hyalophora cecropia*, and numerous other Lepidoptera in Danaidae, Pieridae, Nymphalidae, Hesperiidae, Lymantriidae, Noctuidae, Arctiidae, Geometridae, Psychidae, Sphingidae, Notodontidae, and a few other families
Distribution: North America
Biology: The eggs are deposited on leaves of the hostplants of hosts.

Remarks: A synonym is *Zenillia virilis*. Monty Wood (CNC) (pers. comm.) told me that "Exorista" blanduta has been reared as a parasitoid of *Auto meris io*, but according to Arnaud (1978: 251) the name *Exorista bland a* can refer to either *Eusisyrop a virilis*, *Eusisyro p a bland a*, or *Anaporia pristis*. Records cited by Arnaud (1978: 542, 553-554) under "Zenillia sp." for the following hosts probably belong here: *Anisota senatoria*, *Anisota virgin iensis*, *Eacles imperialis*, *Actias luna*, *Antheraea polyphemus*, *Hemileuca, Automer is io, Hyaloph ora cecrop ia, Callosam ia promethea*. I do not list any hosts under *Zenillia* in this catalog.

307. *Hyphantrophaga hyphantriae* (Townsend)

Hosts: *Anisota senatoria*, *Lasiocampidae, Noctui dae, Pyralidae, Geometridae, Megalopygidae, Nymphalidae, and Arctiidae*

Distribution: Recorded throughout most of the United States

References: Arnaud (1978: 287-288)

Remarks: Some of the records in literature cite this fly under the name *Zenillia ceratomiae*.

308. *Eumasicera sternalis* (Coquillett)

Hosts: *Dryocampa rubicunda, Anisota senatoria, Anisota virgin iensis, Anisota consularis*

Distribution: eastern North America, New England to Missouri to the coastal plain of Georgia, possibly to Oregon

Biology: Judging from the host records listed in Arnaud, this species is a specialist on ceratocampines, but not if Cole’s record for Oregon is based on a correct identification. The eggs are deposited on foliage of hostplants so that host larvae will injest them.


Hosts: *Hyaloph ora euryalus, Anisota pellucida*

Distribution: North America

Biology: Eggs are laid on host larvae. Adult flies emerge from pupae of hosts.

Remarks: Specific records: *ex Hyalophora euryalus*: Nevada City, 975 m, Nevada Co., California, June 1995, M. M. Collins (DMNH); *ex Anisota pellucida*: Interstate Highway 10 at Apalachicola River, Gadsden Co., Florida, July 1992, R. S. Peigler (DMNH). Specimens from the above two records were identified by R. D. Hall using key to genera in Wood (1987).

310. *Argyrophylax* sp.

Hosts: *Hemileuca maia*

Distribution: North America

References: Arnaud (1978: 86)

311. *Pacidianus persimilis* Reinhard

Hosts: *Dryocampa rubicunda*

Distribution: Ontario
References: Arnaud (1978: 407)
Remarks: No other hosts are recorded for this fly.

312. *Pacidianus* sp.
Hosts: *Anisota pellucida*
Distribution: Florida
References: Arnaud (1978: 407)
Remarks: The record came from Florida, so the host which was quoted as *Anisota virginiensis* was probably *A. pellucida*, formerly considered a subspecies of *A. virginiensis*.

Genus *Lespesia*

Most of the Saturniidae of the eastern half of North America are parasitized by one or more species of this American genus. Synonyms of this generic name cited in much of the literature are *Frontina* and *Achaetoneura*. A detailed revision was published by Beneway (1963). Sabrosky (1980) provided an improved key to the species, and clarified some of the taxonomic problems that Beneway did not resolve. The membranous eggs are deposited on the body of the host. In general, the host then pupates, and the mature maggots emerge from the host pupa in the fall or spring.

313. *Lespesia aletiae* (Riley)
Hosts: *Hemileuca maia*, *Anisota senatoria*, numerous other Lepidoptera in several families, plus one species of Chrysomelidae (Coleoptera)
Distribution: Ontario to southern Florida to California
Biology: a larval-pupal parasitoid
Remarks: In 1978 I noted the following fly in the collection at Louisiana State University, identified by C. Sabrosky: Baton Rouge, Louisiana, May 1976, M. L. Burks, reared from *Hemileuca maia*.

314. *Lespesia anisotae* (Webber)
Hosts: *Anisota pellucida*, *Anisota peigleri*, *Anisota senatoria*, *Anisota virginiensis*, *Dryocampa rubicunda*
Distribution: eastern North America
Biology: This parasitoid is very commonly reared from host larvae collected in the eastern United States, but I have not collected it in eastern Texas despite the abundance of hosts in that region. It is a larval-pupal parasitoid. Mature maggots exit the host pupae in the autumn and adults emerge in spring or summer.
Remarks: Arnaud (1990) gave a detailed account of the identity of this species and how it came to be designated as the type-species of *Lespesia*. This parasitoid has been confused with *Lespesia datanarum* (Townsend), and tachinid taxonomists confused the two until Sabrosky (1980) solved the problem. The larvae of *Anisota* and *Datana* (Notodontidae) both live in masses on trees, and both are particularly common in the eastern United States. Apparently the two species of *Lespesia* are closely related, yet specialize on different genera of hosts.

Specific records: *ex Anisota pellucida*: Martin, Florida, 1974, R. S. Peigler; Ludowici and Statesboro, Georgia, 1974, 1975, R. S. Peigler (USNM); *ex Anisota peigleri*

315. Lespesia archippivora (Riley)
Hosts: Hemileuca oliviae, many other Lepidoptera
Distribution: widespread in North America
References: Watts & Everett (1976), Cole (1969: 583)

316. Lespesia sp., archippivora complex
Hosts: Hyalophora cecropia
Distribution: North America
Biology: As many as 90 flies have been reared from a single host of H. cecropia. In another case, 147 maggots emerged from one pupa of the same host species, but not all of them survived to reach adulthood.

317. Lespesia callosamiae Beneway
Hosts: Callosamia securifera, Callosamia promethea
Distribution: eastern United States, possibly also eastern Canada
Biology: Maggots emerge in spring from host pupa, exit the cocoon through the pre-formed emergence valve, drop to ground, pupate in soil, emerge shortly thereafter. There are usually 2 to 6 parasitoids per host.
If the specimens from Eugene, Oregon, cited by Beneway (1963: 643) were correctly identified and labeled with the correct locality, the species has alternate hosts, since Callosamia occurs only in eastern North America.

318. Lespesia dimmocki (Webber)
Hosts: Automeris io, Simyra henrici (Grote) (Noctuidae)
Distribution: Manitoba to Massachusetts south to Maryland

319. Lespesia frenchii (Williston)
Hosts: Dryocampa rubicunda, Anisota senatoria, Anisota virginiana, Syssphinx bicolor, Citheronia regalis, Eacles imperialis, Actias luna, Antherea polyphemus, Automeris io, Callosamia promethea, Hyalophora cecropia, Hyalophora columbia, Hyalophora euryalus, Samia cynthia, numerous other Lepidoptera including Lasiocampidae, Noctuidae, Lymantriidae, Sphingidae, Notodontidae, and butterflies
Distribution: North America, from coast to coast; possibly introduced into Europe
Remarks: There are many records in American literature for this species attacking various Saturniidae. These were usually cited as Frontina frenchii or Achaetoneura frenchii. Herting (1960) listed L. frenchii as introduced into Europe "mit importieren Raupen von Philosamia [Samia] cynthia?" from North America. However, in his later
catalog (Herting 1984), he did not include this species among the Palaearctic fauna, instead citing Lespesia anisotae. It is known that the latter species was once introduced into France (Sabrosky 1990), but due to lack of hosts (Anisota spp.) for this very host-specific parasitoid, it probably could not have become established in Europe. By contrast, L. frenchni could use numerous European Lepidoptera as hosts.

320. Lespesia sabroskyi Beneway

**Hosts:** Antheraea polyphemus, Hyalophora euryalus, Automeris io

**Distribution:** British Columbia to Québec, California to Florida.

**Biology:** The mature maggots chew a tiny hole in the host cocoon and squeeze through, drop to the ground, pupate in the soil, and emerge the following spring or summer. Cocoons of Antheraea are sealed, lacking a pre-formed exit valve. There are usually about 20 parasitoids per host. Interestingly, species of Lespesia that attack hosts having exit valves in their cocoons, pupate within the host cocoon. It would be interesting to see if maggots of L. sabroskyi would pupate in the cocoon of hosts like H. euryalus.

**References:** Beneway (1963: 666-668), Sabrosky (1980), Peigler (1985a)


There are several series of *Lespesia* in the UCB collection reared from *Antheraea polyphemus* and *Hyalophora euryalus* (J. A. Powell, pers. comm.). These are probably all *L. sabroskyi*.

321. Lespesia samiae (Webber)

**Hosts:** Hyalophora cecropia, Hyalophora columbia gloveri, Hyalophora columbia columbia, Hyalophora euryalus, Agapema anona, Agapema dyari, possibly Malacosoma (Lasiocampidae)

**Distribution:** North America

**References:** Sabrosky (1980), Peigler (1985a), Arnaud (1978: 318-319, as L. ciliata), Peigler & Kendall (1993)

**Remarks:** Specific records: *ex Hyalophora cecropia:* Aurora, Arapahoe Co., Colorado, indoors March 1982, S. Stone (USNM); *ex Agapema anona:* Tucson, Pima Co., Arizona, 4 December 1988, D. Mullins (DMNH); Cochise Co., Arizona, November 1984, S. E. Stone (DMNH); Sierra Vista, Cochise Co., Arizona, December 1992, R. D. Weast (DMNH); *ex Agapema dyari:* 2 km E of Hueco Inn, Hudspeth Co., Texas, 1-3 November 1994, J. Reiser (DMNH); *ex Hyalophora columbia columbia:* Kenora, Ontario, 1984, [note: *H. cecropia* at the same locality were not attacked], Lester Kohalmi (pers. comm.).

The adult flies are very difficult to identify, but this species can apparently be separated from *Lespesia* sp. near texana (see below) by the structure of the spiracles of the puparium. This is fortunate because the flies often die in puparia from desiccation before emerging, and thus an identification can sometimes still be made by comparison to puparia of flies associated with properly identified adults. In *L. samiae*, the puparium has spiracles in a deep pit with a rugose rim, whereas they are flush with the surface in *L. sp. near texana.*
The records listed by Arnaud (1978) under L. ciliata belong here, as pointed out by Sabrosky (1980), but I do not know if Arnaud's records for Malacosoma also belong here.

322. Lespesia sp. near, but not texana (Webber)

**Hosts:** Rothschildia lebeau, Rothschildia cincta, Rothschildia sp., Agapema homogena, Agapema anona, Agapema galbina

**Distribution:** southwestern United States into Central America

**Biology:** The maggots pupate within the cocoons of the hosts. The adult flies emerge from the host cocoons, or sometimes in Rothschildia die within because they are unable to escape. In the cocoon from Jalisco from 1978, numerous (more than 20) flies emerged. In the cocoon from Baja California Sur from 1995, only one puparium (which did not emerge but was identified by spiracles of puparium) was in the host cocoon, along with the shriveled host larva which did not pupate.


More than one species may be involved. These one or two species were distinguished structurally from the true L. texana by Sabrosky (1980), but there appear to be no host records for the true L. texana (Beneway 1963: 673).

323. Lespesia sp. or spp.

**Hosts:** Dryocampa rubicunda, Anisota senatoria, Citheronia regalis, Antheraea polyphemus, Hemileuca maia

**Distribution:** North America

**References:** Arnaud (1978: 335, 339)

**Remarks:** Arnaud listed the above host records from older literature, mostly from Lespesia anonya, which is not a valid taxon. All of these records belong under other species of Lespesia or other tachinids.

324. Lespesia lanei Guimarães

**Hosts:** Rothschildia sp.

**Distribution:** Brazil

**References:** d'Araújo e Silva et al. (1968: 270), N. Woodley (pers. comm.)

325. Euexorista fulitis (Osten Sacken)

**Hosts:** Antheraea polyphemus, several other medium and large Lepidoptera in Noctuidae, Nymphalidae, Lasiocampidae, Arctiidae, Geometridae, and Hesperiidae

**Distribution:** North America

**Biology:** Microtype eggs are laid on foliage. Some hosts are tree feeders, others herb feeders.

326. Gnadochaeta sp.
**Hosts:** *Anisota peigleri*
**Distribution:** upper South Carolina
**Biology:** One specimen was reared from a host pupa that was collected as a larva on *Quercus palustris*. It is apparently a solitary parasitoid, and it overwintered in the host pupa.
**References:** Wood (1987)
**Remarks:** Specific record: *ex Anisota peigleri*: Greenville, South Carolina, emerged 12 May 1993 from host pupa collected as a larva in August 1992, R. S. Peigler (DMNH). The specimen from this rearing was tentatively identified by R. D. Hall using the key to genera by Wood (1987). This fly is very tiny compared to others that I have reared from Saturniidae; it is about 3 mm long.

327. Leptostylum sp.
**Hosts:** *Automeris liberia*
**Distribution:** Peru
**Biology:** Thirty-three puparia were reared from a single host larva.
**References:** Jacobson (1991)
**Remarks:** Voucher specimens of this rearing are in the CUIC and USNM.

328. Conactiodoria aleurites Townsend
**Hosts:** *Citheronia laocoon*
**Distribution:** southern Brazil
**Biology:** According to Dias, based on material he reared in the state of São Paulo, larvae of the tachinid emerged from fifth instar larvae of the host in February and April. From one host, 21 maggots emerged, of which 12 formed perfect puparia (11 flies emerged), 5 made small puparia and never emerged, and 4 died without successfully forming puparia.
**References:** Dias (1978: 192)

329. Lydellina villeneuevi Townsend
**Hosts:** *Imbrasia belina*
**Distribution:** Africa
**References:** Cuthbertson & Munro (1941)
**Remarks:** The parasitoid was cited as *Lydellina caffra*.

330. Lydellina sp.
**Hosts:** Saturniidae, several other Lepidoptera in Notodontidae, Pyralidae, and Lasiocampidae
**Distribution:** Africa
**References:** Crosskey (1984)

331. Trixomorpha indica
**Hosts:** *Antheraea paphia*
**Distribution:** India
**References:** Crosskey (1976: 302)

332. Zygofrontina sp.
**Hosts:** *Rothschildia sp.*
**Distribution:** Brazil
References: d’Araújo e Silva et al. (1968: 270)
Remarks: The tachinid is cited by the above authors as being hyperparasitized by the perilampid *Perilampus paraguayensis* and the torymid *Perissocentrus*. They spelled the name as both *Zygofrontina* and *Zigofrontina*.

333. *Promasipoda pinguoides* Tt.
Hosts: *Arsenura armida*
Distribution: Brazil
References: d’Araújo e Silva et al. (1968: 262)

334. *Plagiotachina* sp.
Hosts: *Automeris* sp.
Distribution: Brazil
References: d’Araújo e Silva et al. (1968: 263)

335. *Tapajohoughia* sp.
Hosts: *Lonomia* sp.
Distribution: state of Rio de Janeiro, Brazil
References: d’Araújo e Silva et al. (1968: 268)

336. *Pandaromyia versatilis* Villeneuve
Hosts: *Maltagorea fusicolor*
Distribution: Madagascar
References: Griveaud (1961: 26)
Remarks: The host was cited by Griveaud as *Tagoropsis subcellata* form *madagascariensis*.

337. *Tachinidae, genera unidentified*
Hosts: *Hylesia, Saturnia cephalariae, Epiphora bauhiniae, Samia walkeri, Coloradia pandora, Antheraea yamamai*
Distribution: Respectively for hosts cited above: Costa Rica; Turkey; Africa; Hong Kong; northern Arizona; Slovenia
Remarks: Romanoff wrote “Ces chenilles sont pour-suivies par une grande espèce d’*Ichneumon* et une grande *Tachina.*” Schultzze referred to “Raupenfliegen.” Hill & Cheung wrote “large fat bristly flies belonging to the family *Tachinidae.*” The latter authors referred to unidentified tachinids reared from *A. yamamai*, a Japanese moth introduced in the 1860s to Austria and since spread down into Italy and the Balkans.

338. *Tachinidae, genera unidentified*
Hosts: *Bunaea alcinoe, Epiphora bauhiniae, Ludia delegorguei, Imbrasia wahlbergii, Usta terpsichore*
Distribution: South Africa and Namibia
References: R. Oberprieler (unpubl.)

Family Sarcophagidae

339. *Sarcophaga formosana* Senior-White
Hosts: *Samia* sp.
Distribution: West Malaysia
340. Sarcophaga lambens Wiedemann

**Hosts:** Arsenura xanthopus, Citheronia regalis, other Lepidoptera including Noctuidae and Cossidae, Hemiptera including Coreidae and Pentatomidae, Orthoptera including Acrididae

**Distribution:** North America, South America, Central America, Greater Antilles

**Biology:** Lordello & Mariconi wrote that ten flies emerged from one pupa of Arsenura xanthopus. They also gave an exhaustive list of other hosts recorded for this fly.

**References:** Thompson (1944), Lordello & Mariconi (1953)

341. Sarcophaga sp.

**Hosts:** Hemileuca maia

**Distribution:** Louisiana

**Biology:** Attacks the larva of the host.

**Remarks:** In 1978 I noted the following fly in the collection at Louisiana State University identified by R. J. Gagne (USDA-ARS), labelled as having been reared from a larva of Hemileuca maia: Baton Rouge, Louisiana, 17 April 1976, M. L. Burks. The fly had a checkered thorax and striped abdomen. The host moth is abundant on the university campus.

342. Sarcophaga sp.

**Hosts:** Bunaea alcinoe

**Distribution:** Western Africa

**Biology:** The larva is attacked.

**References:** Akanbi (1973)

**Remarks:** The rearing was done at Ibadan, Nigeria.

**Family Ceratopogonidae**

343. Forcipomyia sp.

Small biting flies have been recorded as attacking Saturniidae, but these dipterans are not parasitoids. Biting midges of the genus Forcipomyia were listed by d’Araújo e Silva et al. (1968: 270) as attacking Rothschildia in Brazil. Some ceratopogonids suck hemolymph from other insects (Scott 1986: 70). I do not know if the Brazilian record was for caterpillars or adult moths.

**Family Culicidae**

344. Genus unidentified

Mosquitoes (Culicidae) were observed by Ulrich and Laela Paukstadt in Java to suck hemolymph from wings of Attacus atlas (see Peigler 1989: 95). As with Ceratopogonidae, these are not parasitoids. They are ectoparasites.

**Family Anthomyiidae**

345. Phaonia signata Meigen

**Hosts:** Actias isabella

**Distribution:** Europe

**Biology:** Flies in this family have larvae of varied habits, but are not endoparasitoids. Some feed on plants, others on dung, and others are predaceous. It is likely that the record is based on a case where flies emerged from a dead pupa or larva of A. isabella and were assumed to be parasitic. See comments below under Phoridae.

Remarks: This record has been perpetuated repeatedly by European authors. It should be verified.

Family Phoridae
346. Megaselia scalaris (Loew)

Peterson (1987) reviewed the North American Phoridae. Adult phorids are small active flies, that run with quick, jerky movements. The larvae live in many materials including seed pods, and infect wounds of higher animals. Larvae of most species feed on dead and decaying plant or animal matter. Many kinds live in caves, rodent burrows, and ant nests; others parasitize molluscs. The records below are probably all for the genus Megaselia. See Disney (1990).

These flies are likely to be encountered occasionally by anyone who routinely rears Lepidoptera. They are not true parasitoids, but live in pupae that have already died, and thus when they emerge as adults, are mistaken for parasitoids. Therefore, I include them in this catalog. The ubiquitous M. scalaris, a grackle, light brown colored fly, is probably the species to which all or most of the records below refer, according to Brian V. Brown (personal communication) of the Natural History Museum of Los Angeles County. All were reared from moth pupae.

Specific records: ex Attacus lorquinii, Philippines, emerged in 1978 from cocoons in Germany (Peigler 1989:93); ex Eacles imperialis, College Station, Brazos Co., Texas, November 1979, T. J. Kring; ex Hemileuca maia, College Station, Texas, 15 July 1979, R. S. Peigler; ex Antheraea montezuma, 8 km west of Escondido, San Diego Co., California, 16 September 1990, K. L. Wolfe; ex Attacus atlas, Taipei, Taiwan, July 1980, Ying Min Wu (all DMNH); ex Hemileuca groete, San Antonio, Bexar Co., Texas, R. O. Kendall (TAMU) (Kendall and Peigler 1981).

R. Oberprieler (personal communication) has reared these flies occasionally in South Africa from dead pupae of various Saturniidae.

LEPIDOPTERA

Although the vast majority of larvae of Lepidoptera are phytophagous, a surprising number are predaceous or parasitic. This topic was reviewed in detail by Pierce (1995). Two moths are recorded as parasitizing Saturniidae as follows.

Family Pyralidae
347. Phycita dentilinella

Hosts: Cricula trifenestrata, Parasa lepida (Cramer) (Limacodidae), other Lepidoptera, and probably other insects

Distribution: southern and eastern India

Biology: With the saturniid and limacodid hosts, the moth apparently oviposits onto the caterpillar just before it spins its cocoon. The parasitic larvae then feed on mature host larvae and continue feeding on the host pupa within its cocoon if the host lives long enough to pupate.

References: Ayyar (1929), Clausen (1940), Pierce (1995)

348. Sthenobaea parasiticus (Jordan)

Hosts: Automeris spp., Dirphia sp.

Distribution: northern Brazil and French Guiana

Biology: The blackish adult moths of the parasitoid were taken at light. Other moths were reared from spiny larvae of one species of Dirphia and several species of
Automeris by A. M. Moss at Pará. Eggs are apparently laid on the host. The shiny black parasitic larvae spin webs among the spines between spiracles on opposite sides of the same segment, forming a tunnel. They are agile and feed on the scoli of the host. After host larvae die, the parasitic larvae will sometimes bore into it. When mature they leave the host and form a black cocoon in the ground covered with sand or soil. Adults have emerged in March and November.

**References:** Jordan (1926), Pierce (1995)

**Remarks:** I agree with Pierce that the generic name *Sthenobaea* should be used, since it has priority over *Sthenauge*, if they are indeed synonyms, based on comments by Jordan himself. The generic name *Dirphia* has been used as a repository genus for many species of Hemileucinae that are now classified in several genera; the host was probably not a true *Dirphia*. Also, several Hemileucinae formerly included in *Automeris* are now considered to belong to other genera.

**Family Noctuidae**

**349. Scotia sp.**

This is not a parasitoid of Saturniidae. The generic name belongs in the Noctuidae (Lepidoptera), proposed by J. Hübner [1821]. Rougeot (1971: 107) cited "Scotia sp." as a parasitoid of *Saturnia pavonia*, stating that it is in Diptera. He probably confused the name of a host that shares a parasitoid with *S. pavonia*, thinking it was another record. Perhaps he was attempting to extract data from literature in a language foreign to him. I hope this "record" will not be further perpetuated in literature by authors who consult Rougeot's parasitoid lists. I did not find the name *Scotia* in any catalogs of Diptera, including Herting's (1984) on Palaearctic Tachinidae.

**COLEOPTERA**

**350. Lema flavipes**

Rougeot (1971: 92) cited the beetle *Lema flavipes* as parasitizing *Saturnia pyri*, but this record is apparently an error, since the genus *Lema* belongs to the family Chrysomelidae, which are leaf-feeding beetles. Adults and larvae of these beetles are phytophagous. The Rhipiphoridae are a family of beetles that is parasitic, but all attack only wasps and bees (Hymenoptera) as far as known.

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Catalog of Parasitoids of Saturniidae of the World
Richard S. Peigler

COVER ILLUSTRATION: Belvosia bifasciata (Fabricius), a large tachinid fly that parasitizes several Saturniidae in North America. Drawn by Michael G. Kippenhan.