DESCRIPTION OF A NEW SPECIES OF PHYTOSEIID MITE FROM NORTHEASTERN BRAZIL AND REDESCRIPTION OF NEOSEIULUS GRACILIS (ACARI: PHYTOSEIIDAE)

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ABSTRACT
A new species of phytoseiid mite, Phyllodromus trisetatus n.sp., collected in northeastern Brazil is described. Phyllodromus DeLeon, 1959 has been a monotypic genus known only from Florida, U.S.A. Neoseiulus gracilis (Muma, 1962) is redescribed based on the holotype and specimens from northeastern Brazil.

Key Words: predaceous mites, biological control, taxonomy, Gamasida

RESUMEN
Es descrita una nueva especie de ácaro fitoseido, Phyllodromus trisetatus n.sp., colectado en el noreste de Brasil. Phyllodromus DeLeon, 1959 fue un género monotípico conocido solamente de la Florida, U.S.A. Neoseiulus gracilis (Muma, 1962) es redescrito basado en el holotipo y en especímenes del noreste de Brasil.

Phytoseiid mites (Acari: Phytoseiidae) have received considerable attention worldwide because of their potential as natural enemies of phytophagous mites (McMurtry 1984). Few papers have reported on species of phytoseiid mites from Brazil (Moraes et al. 1986), and only 4 papers on phytoseiid mites from northeastern Brazil (Farias et al. 1981; Moraes & Oliveira 1982; Moraes & McMurtry 1983; Moraes et al. 1989).

The present paper provides a description of a new species of phytoseiid mite from northeastern Brazil, and a redescriptions of Neoseiulus gracilis (Muma) based on the holotype as well as specimens collected in northeastern Brazil.

All measurements are given in micrometers. Setal nomenclature is that of Rowell et al. (1978) and Chant & Hansell (1971) for dorsal and ventral surfaces, respectively. Dorsal and ventral idiosomal setal patterns are determined according to Chant & Yoshida-Shaul (1989, 1991).

GENUS PHYLLODROMUS
Phyllodromus DeLeon, 1959: 260; Muma, 1961: 290; Muma et al., 1970: 114

Phyllodromus trisetatus Moraes & Melo, n. sp.
(Figs. 1-5)

Diagnosis. This species is similar to the only other species in the genus, Phyllodromus leiodis DeLeon, 1959, but differs from it mainly by having JV1 on the ventrianal plate and S2 and S4 setiform.
Female (3 specimens measured). Dorsum - Dorsal plate faintly striate anterolaterally, smooth or with faint circular pattern in the center, especially near J 2; setal pattern 10A:9B; 388 (386-390) long, 223 (219-226) wide at s4 level, j1 18 (17-19), j3 37, j4 12 (11-14), j5 10 (10-11), j6 18 (17-19), J 2 12 (11-14), J 5 7 (6-8), z2 38 (37-40), z4 44 (43-45), z5 11 (9-13), z1 14, z4 63 (62-65), Z5 61 (59-65), s4 56 (56-57), s2 52 (50-54), S4 13 (13-14), S5 11 (10-13), R3 38 (37-39), R1 16 (15-17). Setae j3, z2, z4, s4, s2, Z4, Z5 and r3 flattened and oblanceolate, with a small knob at the tips; other setae setiform. Peritreme - Extending anteriorly to level slightly anterior to z2. Venter - Sternal and genital plates smooth; ventrianal plate with a few transversal striae anterior to JV2 and reticulate posteriorly; metasternal plates smooth; metapodal plates punctuated. All ventral setae setiform, except for JV5 which are flattened and oblanceolate. Distances between setae ST1-ST3 44 (43-45), ST2-ST2 64 (63-66), ST5-ST5 62 (60-65). Posterior margin of sternal plate expanded into a differentiated flap; sternal plate with ST3 on hook-shaped posterior extensions. Ventrianal plate vase-shaped, 124 (122-128) long, 74 (73-76) wide at ZV2 level and 78 (76-80) wide at anus level; JV1 on anterior margin of the plate; 2 small pores postero-laterad of JV2, in line with JV4. Chelicera - Fixed digit 25 (22-28) long, with 7 teeth; movable digit 25 (24-26) long, with 2 teeth. Spermatheca - Cervix deep bell-shaped, 18 (15-22) long; atrium encrusted at the proximal portion of the cervix. Legs - Macrosetae absent on legs; chaetotaxy of GeII 2-2/1,2/1-1 and GeII 1-2/1,2/0-1.

Male Unknown.

Figs. 1-5. Phyllodromus trisetatus n. sp.: 1. female dorsal plate; 2. female ventral surface; 3. female chelicera; 4. spermatheca; 5. female genu, tibia and tarsus of leg IV.
Locality and Type Material. Holotype female collected from Solanum erianthum, Piritiba, State of Bahia, Brazil, on 25-VII-94, by A. R. de Luna; 2 paratype females collected from Waltheria indica, at Goiana, State of Pernambuco, Brazil, on 7-III-91, by M. G. C. Gondim Jr. All types deposited at Depto. de Zoologia, ESALQ/USP.

Remarks. Phyllodromus trisetatus fits the description of the genus Phyllodromus, except for having JV1 on the ventrianal shield; however, it seems that this should not preclude the placement of the species in this genus, considering that it is not uncommon to observe variations even at the species level in relation to the location of preanal setae on or off the ventrianal plate. Phyllodromus leiodes is known only from Florida, where it was collected from W. indica, one of the plant substrates on which P. trisetatus was found in this study.

The trivial name of the new species refer to the presence of 3 preanal setae (JV1, Jv2 and Zv2) on the ventrianal plate.

GENUS NEOSEIULUS


Amblyseius (Neoseiulus), Karg, 1983: 313

Neoseiulus gracilis (Muma) (Figs. 6-12)

Cydnodromus gracilis Muma, 1962: 9
Neoseiulus gracilis, Muma et al., 1970: 104
Amblyseius (Neoseiulus) atri Karg, 1989: (new synonymy)

Material Examined: - Sebring, Florida State, USA, from citrus litter, 11-IV-60, J. A. Murrell (holotype female); Saint Lucia, Lesser Antilles, host?, 1980, S. Mahunka & L. Mahunka-Papp (holotype female of Amblyseius (Neoseiulus) atri Karg, 1989); Goiana, Pernambuco State, Brazil, from soil, 22-XI-90, M. G. C. Gondim Jr. (8 females, 9 males); Goiana, Pernambuco State, Brazil, from soil, 17-IV-91, M. G. C. Gondim Jr. (12 females, 6 males).

Female (Figs. 6-10). Dorsum - Dorsal plate with a few striae anterolaterally; setal pattern 10A:9B. The average measurements of 8 specimens collected in Brazil followed by the respective ranges and the measurements of the holotype are given subsequently: dorsal plate 329 (312-350) 342 long, 170 (155-179) 157 wide at s4 level, j1 12 (11-13) 15, j3 18 (17-19) 20, j4 15 (13-16) 18, j5 16 (16-17) 18, j6 16 (14-19) broken, j2 19 (19-21) 20, j5 10 (9-11) 13, z2 16 (16-19) 18, z4 16 (16-17) 20, z5 17 (16-19) 18, z1 18 (17-19) broken, z4 23 (22-25) 30, z5 27 (24-30) 33, s4 17 (17-19) 23, s2 21 (19-22) 23, s4 20 (19-21) 23, s5 20 (17-22) 25, r3 12 (9-14) 17, R1 15 (14-16) 15. All setae smooth. Peritreme extending anteriorly to level of j1. Venter - Sternal plate with a few striae anteriorly and laterally; genital plate smooth; ventrianal plate with a few transversal striae anterior to Jv2 and reticulate posteriorly; metapodal plates smooth; metastral plates punctate. All ventral setae setiform. Distances between setae ST1-ST3 59 (54-62) 58, ST2-ST2 60 (54-65) 63, ST5-ST5 55 (51-59) 63. Ventrianal plate shield-shaped, 114 (110-128) 121 long, 91 (88-101) 101 wide at Zv2 level and 76 (73-81) 76 wide at anus level; 2 small pores posteromesad of Jv2. Chelicera - Fixed digit 31 (29-33) 28 long, with 4-5 teeth and a pilus dentilis; movable digit 31 (30-32) 30 long, with 1 tooth. Spermatheca - Cervix cup-shaped, 20 (19-22) 18 long; atrium nodular. Legs - Macrosetae absent on legs of Brazilian specimens; macroseta found...
only on basi-tarsus of leg IV of holotype, 30 long. Chaetotaxy of GeII 22/0,2/0-1; GeIII 1-2/1,2/0-1.

Male (Figs. 11-12) (5 Brazilian specimens measured). Dorsum - Dorsal plate striate along the margins, 264 (254-276) long, 156 (151-166) wide at s4 level, j1 12 (10-12), j3, j4, j6, j2, z2 and x4 16 (14-17), j5 and z5 15 (14-17), j5 10, z1 18 (17-19), z4 20 (19-22), z5 19 (17-22), s4 and r3 14 (12-17), S2, S4 and S5 18 (17-19), R1 11 (10-12). All setae smooth. Peritreme - Extending anteriorly almost to level of j1. Venter - Sterno-genital plate faintly striate. Ventrianal plate reticulate, sub-triangular, 109 (101-113) long, 121 (120-125) wide at anterior corners, with 5 pairs of pores. Chelicera - Shaft of spermatodactyl 13 (12-14) long. Legs - Macrosetae absent on legs; chaetotaxy as in female.

Remarks. The measurements of the holotype female of A. (N.) atrii agrees well with the measurements mentioned previously. Similarly to the holotype of N. gracilis, it also has a single macroseta, on basi-tarsus IV. It is here considered a junior synonym of N. gracilis. Hirschmann (1962) considered N. gracilis a junior synonym of Neoseiulus marinellus (Muma, 1962); Tuttle & Muma (1973) suspected that N. gracilis could be a senior synonym of Neoseiulus mckenziei (Schuster & Pritchard, 1963). We have not seen the types of N. marinellus or N. mckenziei. However, based on the original descriptions of the latter two, we consider them distinct from N. gracilis and from each other because of the different spermathecae. Apparently correctly, Ragusa & Athias-Henriot (1983) synonymized N. mckenziei under Neoseiulus barkeri Hughes, 1948, a species distinct from N. gracilis.
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MORTALITY OF MEXICAN FRUIT FLY (DIPTERA: TEPHRITIDAE) IMMATURES IN COATED GRAPEFRUITS

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ABSTRACT

Coatings applied to fruits have been shown to kill tephritid fruit fly immatures inside of the fruits. The present research investigated the efficacy of coatings against distinct life stages of Mexican fruit fly, Anastrepha ludens (Loew), and results showed high levels of disinfestation of grapefruits of up to the early third instar (95%) for one commonly used grapefruit coating, Citrus Lustr 402. Emergence was reduced significantly even for late third instars. Leaving one-third of each grapefruit uncoated reduced efficacy considerably. Mixing Citrus Lustr 402 into the diet used to rear Mexican fruit fly did not affect survival indicating that this coating is not toxic to larvae. This research supports the hypothesis that coatings act primarily to modify atmospheres inside the fruits and kill larvae by restricting gaseous exchange. Fruit coating could be incorporated as a component of an integrated systems approach to quarantine security where a series of pest infestation-reducing steps decreases risk to insignificant levels.

Key Words: Fruit wax, quarantine security, systems approach, Anastrepha ludens

RESUMEN

Ha sido demostrado que ciertas cubiertas aplicadas a las frutas matan a los inmaduros de las moscas tefrítidas en el interior de las mismas. En la presente investigación se estudió la eficacia de las cubiertas contra diferentes estadios de la mosca mexicana de las frutas, Anastrepha ludens (Loew). Los resultados mostraron que la desinfección de toronjas tratadas con la cubierta comúnmente usada alcanza el 95% en el tercer estadio temprano de la mosca. La eficacia se redujo considerablemente al dejar un tercio de cada fruta sin cubrir. La mezcla de Citrus Lustr 402 con la dieta usada para criar la mosca mexicana no afectó la supervivencia, indicando que esa cubierta no es tóxica a las larvas. Esa investigación sostiene la hipótesis de que las cu-
biertas actuan primariamente modificando la atmósfera dentro de las frutas y matan las larvas mediante la restricción del intercambio de gases. La cubierta de las frutas podría ser incorporada a los sistemas integrales de seguridad cuarentenaria donde una serie de pasos para la reducción de la infestación de plagas disminuya el riesgo a niveles insignificantes.

Tephritid fruit flies are major horticultural pests and probably the chief group of quarantined pests worldwide. To prevent inadvertent introduction of fruit fly species into areas of the world where they do not exist but could become established, fruits are subjected to quarantine treatments, shipped from areas certified to be free of the pests, or packed under systems which reduce the risk of infestation to negligible levels (Sharp & Hallman 1994).

Fruit fly larvac have been shown to kill Caribbean fruit fly, Anastrepha suspensa (Loew), immatures in various fruits (Hallman 1996, Hallman & Foos 1996, Hallman et al. 1994, 1995). One-hundred percent Caribbean fruit fly mortality was observed in grapefruits coated with Sta-Fresh 600, a non-drying coating commercially applied to melons in transit and washed off after arrival (Hallman et al. 1994). Apparently, coatings also killed Mediterranean fruit fly, Ceratitis capitata (Wiedemann), immatures in fruits (Saul et al. 1985, 1987). Coatings probably kill fruit fly immatures inside of fruits largely by creating a modified atmosphere (Hallman 1994).

None of the previous research addressed the effect of coating fruit on different fruit fly stadia. The goals of the research reported herein were to determine if coating grapefruit would kill Mexican fruit fly, Anastrepha ludens (Loew), and to determine the mortality levels at different insect life stages. An experiment was also conducted to determine if coatings would kill Mexican fruit fly larvae when mixed in their diet.

**Materials and Methods**

Mexican fruit flies were from a colony reared on a semi-artificial diet at the U.S. Department of Agriculture, Subtropical Agricultural Research Laboratory in Weslaco, Texas (Spishakoff & Hernandez-Davila 1968). Grapefruit cultivars 'Ruby Red' and 'Rio Red' (mean weight about 450 g) were placed 180-200 fruits at a time in an aluminum screen cage (228 x 81 x 46 cm) with about 10,000 Mexican fruit fly adults for 24 hours. About half of the flies were females, and all were fed water, sugar, and yeast hydrolysate. After exposure to oviposition, the grapefruits were cleaned with water and light hand scrubbing and held at about 24°C until the Mexican fruit fly immatures reached the desired stage: early egg (1 day), second instar (7-8 days), early third instar (11-14 days), and late third instar (15-18 days). Several grapefruits were cut open and the stage of fruit fly development verified before grapefruits were coated. The experimental design was a randomized complete block with three replicates and 20 grapefruits per replicate-treatment combination, including uncoated controls.

The following coatings were used: Sta-Fresh 590 HS (FMC Corp., Lakeland, FL), Citrus Lustr 402 (ELF Atochem North America, Inc., Monrovia, CA), and Nature Seal 2020 (EcoScience, Orlando, FL). Sta-Fresh 590 HS and Citrus Lustr 402 are commercially-used, high-gloss citrus coatings which contain alkali soluble resins, propylene glycol, fatty vegetable acid soaps, and silicone antifoam. Nature Seal 2020 is a cellulose-based coating which is used on limes. Each grapefruit was hand coated with 0.9-1.0 ml, which is approximately the rate used commercially on grapefruits in southern Texas, and allowed to dry in ambient air.
To determine if complete coating of fruit was necessary to achieve fruit fly mortality, in one test one-third of the surface area of the grapefruits was covered with a single piece of 5.15-cm wide tape before coating and then removed about one-half hour after coating, leaving about one-third of the fruit uncoated in a single patch. This test was conducted on fruits 10-13 days after infestation when most larvae had developed to early third instar. The experimental design was randomized complete block with three replicates and 20 fruits per replicate including the uncoated controls.

All grapefruits were placed individually in 2-liter plastic containers containing about 250 cm$^3$ of sand which provided a burrowing and pupation site for emerging larvae. About two weeks after larvae began emerging, the fruits were dissected, and all puparia and live and dead larvae were counted.

To test if the coatings were actually toxic to Mexican fruit fly larvae, 1 ml of coating was mixed with 150 ml of diet, placed in 275-ml plastic containers, and infested with 100 early third instars. When the larvae completed feeding they were removed from the diet and placed in 0.5-liter heavy paper containers with 100 cm$^3$ of vermiculite and held for pupation and adult emergence. This experiment was a randomized complete block with four replicates, including the controls without coating.

All data were analyzed by the SAS ANOVA procedure after normality was tested with the UNIVARIATE procedure (SAS Institute, Inc. 1988). Data which were not normal were transformed by log($n + 1$) and then tested again.

RESULTS AND DISCUSSION

Analysis of variance [log($n + 1$)] showed significant differences among numbers of Mexican fruit fly larvae emerging from grapefruits coated at different life stages of the insect ($F = 5.14; df = 3, 6; P \leq 5\%$) and between the different coatings used ($F = 20.3; df = 3, 6; P \leq 1\%$) (Table 1). The least number of larvae emerged from grapefruits coated with Citrus Lustr 402. Standard errors of the mean overlapped only in the case of third instars in grapefruits coated with Citrus Lustr 402 and Sta-Fresh 590, indicating no difference between these two coatings for third instars. Survival remained low through the early third instar, but increased greatly among late third instars. The life stage by coating interaction was not significant ($F = 1.74, df = 9, 18$), indicating that the relative effectiveness of the three coatings was similar among the various Mexican fruit fly life stages.

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<thead>
<tr>
<th>Stage</th>
<th>Coating</th>
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<tr>
<td></td>
<td>Citrus Lustr 402</td>
<td>Sta-Fresh 590</td>
<td>Nature Seal 2020</td>
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<tr>
<td>1-day old egg</td>
<td>0.03 ± 0.03</td>
<td>2.6 ± 1.3</td>
<td>9.0 ± 0.9</td>
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<tr>
<td>2nd instar</td>
<td>0.02 ± 0.02</td>
<td>1.8 ± 1.5</td>
<td>10.7 ± 4.2</td>
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<tr>
<td>Early 3rd instar</td>
<td>1.1 ± 1.1</td>
<td>3.1 ± 2.0</td>
<td>14.7 ± 3.6</td>
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<tr>
<td>Late 3rd instar</td>
<td>6.6 ± 2.6</td>
<td>4.5 ± 2.2</td>
<td>14.9 ± 3.7</td>
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$^1$Mean number of larvae from uncoated control = 19.0 ± 4.0.
Mixing Citrus Lustr 402 into the diet did not affect survival of early third instar Mexican fruit fly to the adult stage (mean of 81% survival for control versus 80% for diet plus coating) demonstrating that the coating was not directly toxic to the insect.

Mortality of Mexican fruit fly in grapefruits that had about two-thirds of the surface area coated leaving a single, uncoated 5.15 cm wide strip was greatly reduced compared with totally coated fruits. Mean number of insects per grapefruit (± SEM) was 21.1 ± 4.6, 7.8 ± 1.5, and 8.5 ± 0.9 for the control, Citrus Lustr 402, and Sta-Fresh 590, respectively. Grapefruits infested with early third instars and that were two-thirds coated yielded 37-40% of the total Mexican fruit fly larvae emerging from uncoated grapefruits compared with 5.8-16% for completely coated grapefruits. Nevertheless, analysis of variance indicated significant differences between the control and the two partially coated treatments (F = 7.09; df = 2,4; P ≤ 5%).

CONCLUSIONS

Application of citrus coatings at commercial rates provided high levels of disinfection of Mexican fruit fly immatures from grapefruits. Although the level of reduction was inadequate to provide quarantine security, which requires virtually 100% mortality, the data suggest that coatings could be easily incorporated as a component of a quarantine security system consisting of a series of pest mitigating steps to reduce the risk of infestation to a negligible level (Hallman 1995). Partial coating reduced the effect greatly, but still provided some abatement. The coating even provided significant mortality of late third instars, many of which probably could have avoided mortality simply by emerging from the fruit. In this study, Citrus Lustr 402 was markedly better than the other two coatings used in reducing Mexican fruit fly survival in grapefruits. It is arguable that the effect of coatings on fruit fly disinfection would be more pronounced than these studies indicated because most of the grapefruits that were coated would have been culled due to their substandard condition caused by remaining at room temperature for 7-18 days after infestation while waiting for the insects to reach the desired stage of development before coating. Commercially, fruits would be coated very soon after harvest.

Because the coating itself was not directly toxic to the larvae it seems likely that the mode of action of coatings is simply a modified atmosphere where lowered oxygen and raised carbon dioxide levels kill insects inside of fruits (Hallman et al. 1994).

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REFERENCES CITED


PARASITOIDS OF COMSTOCKIELLA SABALIS (HOMOPTERA: DIASPIDIDAE) IN FLORIDA AND DESCRIPTION OF A NEW SPECIES OF THE GENUS COCCOBIIUS (HYMENOPTERA: APHELINIDAE)

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ABSTRACT

Coccobius donatellae Pedata and Evans, spec. nov. is described and illustrated from specimens reared from Comstockielia sabalis (Comstock) on palmetto palm (Sabal palmetto) in Florida. Coccobius donatellae is the most common parasitoid that attacks this host in Florida and is believed to be the same species reported in the literature as “Physcus sp.” that was introduced into Bermuda from Florida in the 1920’s. Evidence suggests that earlier reports of Encarsia portoricensis (Howard) as a parasitoid of the palmetto scale are based on erroneous identifications of what were probably Coccobius donatellae males. Recent collections in Florida confirm Aphytis diaspidis (Howard), reported previously as Aphytis fuscipennis, and Encarsia citrina
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(Craw) as parasitoids of C. sabalis. Intraspecific variation occurring in C. donatellae and in Coccobius testaceus (Masi), is discussed.

Key Words: Coccobius, Aphelinidae, Diaspididae, Comstockiella, armored scale, biological control, parasitoid

RESUMEN

Se describe y se ilustra Coccobius donatellae Pedata and Evans, spec. nov., criado de Comstockiella sabalis (Comstock) sobre la palma palmetto (Sabal palmetto) en Florida. Coccobius donatellae es el parasito más común que ataca este hospedero en Florida y se cree que es la misma especie reportada en la literatura como "Physcus sp. que fue introducida a Bermuda de Florida en los años 1920. Se presenta evidencia que indica que los informes anteriores de Encarsia portoricensis (Howard) como parasito de C. sabalis son basados sobre identificaciones erróneas de los machos de Coccobius donatellae. Se confirma Aphytis diaspidis (Howard), reportado anteriormente como, Aphytis fuscipennis, y Encarsia citrina (Craw) como parásitos de C. sabalis basado en las recolecciones recién hechas en Florida. Se incluye información sobre la variación intraespecifica que ocurre en C. donatellae y en Coccobius testaceus (Masi).

Comstockiella sabalis (Comstock) is an armored scale insect (Homoptera: Diaspididae) known from the southern United States, Mexico, several of the Caribbean Islands, and from greenhouses in Germany (Nakahara, 1982). Although it is commonly found on palm species, it rarely causes economic damage due to the severe attack of parasitoids on this species throughout its geographic range. However, this has not always been the case. C. sabalis invaded Bermuda in 1921 and quickly spread throughout the islands, severely damaging or killing Sabal bermudana Bailey trees (Russell 1934a). Parasitized C. sabalis specimens were collected in Florida and sent to Bermuda in 1926 and 1929. No mention was made of the specific identity of parasitoids introduced into Bermuda from Florida at that time; however, in a survey of the natural enemies of the palmetto scale in Bermuda conducted in 1933, Physcus sp., Encarsia portoricensis Howard, Aphytis fuscipennis Howard and two undetermined Hymenoptera were reported as being reared from this host (Russell, 1934b). The parasitoid referred to in the survey as "Physcus sp.,” now placed in the genus Coccobius, was particularly effective against the scale. Russell (1934b) reported that “the palmettos on which this species was placed that were once badly infested, were later free from scale”. Bennett and Hughes (1959) reared Physcus sp. and Aphytis fuscipennis from C. sabalis collected in Bermuda in 1956 and stated that “it would seem that E. portoricensis is no longer of importance as a control for this scale”.

Recent collections of C. sabalis in Florida have helped to clarify our knowledge of the natural enemies of C. sabalis in Florida and provided insight as to the identity of the parasitoid species introduced into Bermuda from Florida in the 1920’s. We suggest that specimens identified in the Bermuda survey as “Physcus sp.” and Encarsia portoricensis, represent the female and male of Coccobius donatellae, respectively. This species is the most common parasitoid reared from C. sabalis in Florida, and undoubtedly plays a key role in its control. Evidence supporting our hypothesis that specimens reared from C. sabalis in the Bermuda survey that were identified as Encarsia portoricensis were actually males of Coccobius donatellae consists of: Encarsia portoricensis is a whitefly parasitoid that is not known to occur in Florida, males of Coccobius donatellae are similar to females of E. portoricensis in color, and in the number
of and relative lengths of antennal segments (6-segmented); and specimens deposited in the Museum of Natural History, London from the 1933 Bermuda survey, identified by Ferriere as Encarsia sp., were later identified as Coccobius males (A. Polaszek, personal communication).

The third species mentioned in the survey, Aphytis fuscipennis Howard, was synonymized with Aphytis diaspidis (Howard) by Rosen and DeBach (1979), who did not list C. sabalis as one of its hosts. We confirm the identity of A. diaspidis based on three specimens of Aphytis diaspidis reared from C. sabalis from the 1933 Bermuda survey and deposited in the Florida State Collection of Arthropods, Gainesville, Florida. Our collections in Florida confirm Aphytis diaspidis and Encarsia citrina (Craw) as parasitoids of C. sabalis; it appears that both of these species play minor roles in controlling populations of the scale.

The majority of the 79 described species of the genus Coccobius are parasitoids of diapine scales; 10 species have been reported as parasitoids of soft scales (Coccidae), 1 species from a mealybug (Pseudococcidae), and 1 species from a lac scale (Kerridae). Hayat (1984) reviewed the 58 Coccobius species known worldwide at that time and provided a taxonomic key to 48 of those species. Since then, twenty-one species have been described; of these are, 7 from South Africa (Prinsloo, 1995), 10 from China (Huang, 1990), 1 from Japan (Tachikawa, 1988), 2 from Turkmenia (Myartseva, 1995) and 1 from Azerbaijan (Jasnosh and Mustafeva, 1992). Only 6 species are known to occur in the continental United States; of these, 2 species (howardi, stanfordi) were described from California, 1 species (varicornis) from Washington, DC, and 3 (flaviventris, fulvus, testaceus) are introduced species. Coccobius donatellae is the fourth species of this genus to be described from the continental United States.

Terminology follows that used by Hayat (1984). Figure 1 shows the mesosoma divided medially with the surface sculpturing on the left side and the setation on the right side. The metasoma is divided medially showing the dorsum on the left side and the venter on the right side.

Coccobius donatellae Pedata and Evans, **NEW SPECIES**
(Figs. 1-6)

**Female** (Figs. 1-4)

Length: 0.70-0.90 mm, mean of 5 specimens = 0.82 mm. Coloration: Body (Fig. 1) yellowish; basal half of head dark brown; pronotum, metanotum, metasomal tergites I-VI, fuscous; legs white with central portion of femora and basal two-thirds of tibiae, faintly fuscous; antennae yellowish, basal half of scape, dorsal margin of pedicel, F1 and club, grayish; fore wing hyaline. Structure: **Head** slightly wider than mesosoma. Antenna (Fig. 3) consists of radicle (R), scape (S), pedicel (P), 3 funicle segments (F1-F3) and 2 club segments (F4-F5), length:width ratio for each segment as follows: R:3.2, S:3.5, P:1.4, F1:1.5, F2: 1.7, F3:1.6, F4:1.4, F5:2.5; relative length of each segment to length of F1 segment: R:1.1, S:2.8, P:1.1, F1:1.0, F2:1.3, F3:3.1, F4:1.3, F5:2.2; flagellar segments F1-F6 with 2, 2, 2, 2 and 5-6 linear sensilla, respectively. **Mesosoma** with broad mesocutum, 1.8× as wide as long with approximately 40 setae and small, reticulate cells each with internal striations; scutellum with 3 pairs of setae, and sculpturing similar to that of mesocutum; mesophragma reaching base of metasomal tergite II. **Fore wing** 2.6× as long as wide, discal setation uniformly distributed with narrow setose area basally near posterior margin; marginal vein as long as costal cell with 10-12 marginal setae; submarginal vein with 6-7 setae; longest marginal cilia 0.2× as long as the maximum width of fore wing. **Metasoma** slender, 1.7× as long
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as mesosoma, tergites I-VI with reticulate lateral margins, tergites V-VI with stipules, centrally; tergites I-VII with 1,4,4,4,3,6,6 pairs of setae, respectively; ovipositor arises at level of tergite II, slightly protruding from apex, 1.7-1.9× as long as tibia II (Fig. 2) and 4.1× as long as valvular III.

Male (Figs. 5-6)

Coloration: Head with occiput yellow and basal half, dark brown; mesoscutum, scutellum and axillae, light brown; pronotum, metanotum, metasoma and coxae, dark brown; femora, except for pale apices, and proximal two thirds of tibiae, brownish; tarsi yellow; antennae fuscous, fore wing hyaline. Differs structurally from the female primarily by the 6-segmented flagellum (Fig. 5) and by the scape which has a ventral, circular glandular area (Viggiani et. al., 1986) separated from the 6 medial pores. Length:width ratios of antennal segments R-F6 as follows: R:2.1, S:2.8, P:1.3, F1:1.4, F2:1.5, F3:1.5, F4:1.5, F5:1.6, F6:1.8; relative length of each segment to length of F1: R:0.8, S:2.1, P:0.9, F1:1.0, F2:1.1, F3:1.1, F4:1.1, F5:1.2, F6:1.2.

Morphological variation

Individuals of Coccobius donatellae vary primarily in body size, number of mesoscutal setae, number and size of reticulated cells of the mesoscutum, relative lengths of the flagellar segments, and the relative length of the marginal fringe of the fore wing to its maximum width. In general, smaller individuals have fewer mesoscutal setae (30-36), larger and fewer reticulate cells on the mesoscutum, and longer marginal fringes (0.22-0.26× maximum width of fore wing) than do larger individuals (40-46 mesoscutal setae, marginal fringe = 0.12-0.16× maximum width of fore wing). The F1 antennal segment tends to be shorter (Figs. 4, 6) in smaller individuals, at times, almost quadrate, 1.1-1.4× as long as wide, and 0.8× as long as the F2; whereas in larger individuals, the F1 is usually more elongate, 1.5-1.7× as long as wide and approximately as long as the F2.

Relationships

The female of Coccobius donatellae can easily be distinguished from females of the other 3 species described from the continental United States by the coloration of its body which is almost entirely yellow; whereas the head, mesosoma and at least part of the metasoma of the other species are dark brown. Coccobius donatellae is most similar in coloration and structure to Coccobius testaceus (Masi), a European species introduced into California for the control of Lepidosaphes ulmi L. and L. conchiformis (Gmelin) (Flanders 1942). Females of C. testaceus can be distinguished from females of C. donatellae by the grayish F2 segment (Fig. 7), reported in the past as being pale, and the pale apical half of F5 segment and relative length of the ovipositor:tibia II (1.4-1.5:1). Males of C. testaceus differ from C. donatellae males by having the head completely dark brown, the length of the pedicel only about one half as long as the F1 segment, and by the larger, contiguous glandular area on the scape. Most C. testaceus males have 2 rows of linear sensilla on the F1 (Fig. 8); however in smaller individuals there may be a single row (Fig. 9).

Material examined

Female holotype (in Canada Balsam), 12♀, 6♂ paratypes (in Modified Hoyer’s Mounting Medium), 7♀, 5♂ paratypes (in Canada Balsam), 10♀, 3♂ paratypes (card

Figures 1-9. (1-6) Coccobius donatellae 1♀ habitus 2♀ tibia II 3♀ antenna (normal) 4♀ antenna (small individual) 5♂ antenna (normal) 6♂ antennal segments R-F1 (small individual); (7-9) Coccobius testaceus 7♀ antenna 8♂ antennal segments R-F2 (normal) 9♂ antennal segments R-F2 (small individual).
Deposition

Female holotype and 5♀, 5♂ paratypes are deposited in the United States National Museum of Natural History, Washington, D.C.; remaining paratype specimens are deposited in Florida State Collection of Arthropods, Gainesville, Florida; the Natural History Museum, London, England; and the Dipartimento di Entomologia e Zoolgia Agraria, Università di Napoli "Federico II", Portici, Italy.

Etymology

*Coccobius donatellae* is named in memory of Donatella Pedata.

ACKNOWLEDGMENTS

We thank Fred D. Bennett who collected the majority of the specimens used in this study. Avas Hamon for identification of specimens of Comstockella sabalis. Andrew Polaszek for his assistance and Gennaro Viggiani for his advice and support. Funding for the senior author provided, in part, by the National Biological Control Institute, USDA/APHIS, Postdoctoral Fellowship in Systematics. Florida Agricultural Series No. R-05675.

REFERENCES CITED


FEEDING RECORDS OF COSTA RICAN LEAF BEETLES  
(COLEOPTERA: CHRYSOMELIDAE)

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ABSTRACT

Host plant associations are given for 137 species representing 7 subfamilies and  
92 genera of Costa Rican Chrysomelidae. A numeric score is introduced to objectively  
describe confidence that a field observation of an interaction between a chrysomelid  
and a plant represents true herbivory. Literature host plant records, if they exist, are  
given for included chrysomelid taxa.

Key Words: herbivory, Criocerinae, Chrysomelinae, Cryptocephalinae, Eumolpinae,  
Galerucinae, Hispinae, Lamparosominae, host plants

RESUMEN

Se presentan asociaciones de plantas hospederas para 137 especies de Chrysome-  
elidae de Costa Rica, representando 7 subfamilias y 92 géneros de escarabajos. Se in-  
troduce una calificación numérica para describir objetivamente la confianza en que  
una observación de campo de una interacción entre un escarabajo y una planta repre-  
senta un caso verdadero de herbivoría. Se presentan datos de plantas hospederas de  
la literatura, si existen, para los taxa de escarabajos incluidos.

In recent years, there has been a surge of interest in relationships between tropi-  
cal plants and insects. The interest is driven by the related agendas of studying them  
for their intrinsic scientific interest, and protecting tropical biodiversity through find-  
ing practical and non-destructive ways to use it. The latter agenda is exemplified by  
the biochemical prospecting programs recently started in several areas of the world  
(Reid et al. 1993).  

Most plant-insect research begins with a basic event: an observation that a specific  
plant is somehow important in the life cycle of a specific insect. Unfortunately, huge
sections of the tropical insect fauna are still unusable as subjects of insect-plant re-
search because that first step of linking plant and insect taxa has been largely ne-
glected. In-depth studies of plant-insect interactions have focused on temperate zone
insects and on a few relatively well known tropical groups (e.g., Lepidoptera). Only a
small percentage of the fauna of tropical herbivores has been similarly studied.

The family Chrysomelidae (Coleoptera), or leaf beetles, is a natural subject for
studying plant-insect and inter-herbivore interactions (Strauss 1988). Of the esti-
imated 37,000 species, world-wide, in this family, almost all, as far as we know, are
herbivores or seed predators. However, for about 70% of the described species, we do
not have records of host plants. Most of the known host plant records are Holartic
(Jolivet 1988b). For Neotropical Chrysomelidae other than Bruchinae, the most spe-
cific information treats economically important species (e.g., King & Saunders 1984,
Ostmark 1975, Jolivet 1979, Hilje et al. 1991). However, a review of known host plants
of the tortoise beetles (Cassidinae) of Panama was recently published by Windsor et
al. (1992); Moldenke (1971) listed host plants for some Mexican Chrysomelidae, and
Anaya (1989) reviewed the known host plants of North and Central American Chry-
Jolivet et al. 1986) and in a recent book (Jolivet & Hawkeswood 1995) summarized
current host plant data on a world level for the Chrysomelidae. However, in much of
this literature, beetle species are usually identified only to genus and their plant hosts
only to family. A few field studies have documented significant attacks by chry-
somelids on plants in Central American ecosystems (e.g., Rockwood 1974, Memmott
et al. 1993), and some detailed field and laboratory studies have been undertaken for
several Neotropical species (Bach 1986, Begossi & Benson 1988, Buzzi & Winder
1986, Hsiao 1988, Strong 1977a,b). Apart from these ecological studies of specific chrysomelids, many of the published host plant records are of dubious value, stating
merely that beetle X was taken on plant Y (or, all too often, “genus X feeds on plant
genus Y”). A further problem, also noted by Furth (1985), is that a large proportion of
such records are buried in taxonomic monographs and regional studies (e.g., Bechyné
& Bechyné 1975) and accessible only by reading these studies in their entirety. Much
more data on a much broader spectrum of chrysomelid taxa will have to be accumu-
lated and made available before any credible generalizations about the nature of leaf
beetle-plant interactions can be made.

In this paper, we present feeding records of adults and larvae for 137 species of
Costa Rican Chrysomelidae, representing 7 subfamilies and 92 genera. The majority
of these observations were made by the senior author during a six-month sabbatical
at Costa Rica’s Instituto Nacional de Biodiversidad (INBio) in 1991, and by the junior
author during the years 1978 to 1995 as a byproduct of an on-going intensive study of
the caterpillars of the dry forests of Sector Santa Rosa of the Guanacaste Conserva-
tion Area (Janzen 1993, Janzen & Gauld 1996). Our records include results from di-
rect observations of free-living feeding, feeding tests, and field associations. We have
omitted many records where a single beetle was seen or collected on a plant, except for
a few cases where the beetle was seen actively feeding.

Beetles were identified by the senior author (Criocerinae, Cryptocephalinae, Lam-
prosomiinae, Eumolpinae) and the following specialists: Catherine N. Duckett (Uni-
versity of Puerto Rico, Alticini), Vilma Savini P. (Universidad Central de Venezuela,
Alticini), David G. Furth (U.S. Natural History Museum, Alticini), Shawn M. Clark
(West Virginia Department of Agriculture, Galerucini), Charles L. Staines (Maryland
Department of Plant Protection, Hispini), and Edward G. Riley (Texas A&M Univer-
sity, Cassidini). Plants were identified by the authors and Quirico Jiménez (INBio),
Nelson Zamora (INBio), and Pablo Sanchez (Museo Nacional de Costa Rica).
Our data are organized into a table with three supplementary appendices. Table 1 lists observations by chrysomelid taxon, gives field data in summary form, and lists voucher specimens. Appendix 1 is a key to plant family name abbreviations. Appendix 2 gives the full localities for locality codes used in Table 1. Appendix 3 gives miscellaneous field observations, as well as relevant literature citations for many of the chrysomelid taxa. In Table 1 we have followed the higher classification of Reid (1995) which reduces several well-known subfamilies to tribal status and confirms earlier opinions (eg. Crowson 1955, Lawrence 1982) that Bruchidae, or seed weevils, are a subfamily of Chrysomelidae. Bruchinae are not included in this report; for information on their host associations, see Janzen (1980a), Johnson (1990), and literature citations therein. While not all workers fully agree with all aspects of Reid's classification, it represents the latest and most comprehensive phylogenetic arrangement of the Chrysomelidae. For differing views, see Kingsolver (1995), Verma & Saxena (1996), and Reid (1996).

Explanation of Table 1

Leaf Beetle

Scientific names follow Wilcox (1983) and Flowers (1996). In a few cases, approximate species identifications are indicated by “nr.” before the species name: e.g., Plagiodera nr. uniformis. In some cases only generic identifications were possible, and distinct morphospecies are numbered as such.

Plant

Names follow current usage in the Costa Rica National Herbarium and in the botany department at INBio. In cases where species identification is approximate, the term “cf.” is used (e.g., Solanum cf. torvum).

Plant Family

Classification follows the listings of the Flora of Costa Rica by the Missouri Botanical Garden and INBio, viewable on the World Wide Web at http://cissus.mobot.org/manual/plantas/lista.html. Families are coded by initial letters of their family names. See Appendix 1 for full listing.

Stage

A, adult; L, larva; P, pupa

Locality

See Appendix 2 for full locality data.

Date

Date of initial collection is given in cases where beetles were reared from larvae or held for testing.
Flowers & Janzen: Chrysomelid Feeding Records

Collectors

DHJ & WH: Daniel H. Janzen & Winnie Hallwachs
RWF: R. W. Flowers
Names of other collectors are given as they appear on voucher data labels.

Score

This is an attempt to objectively communicate our level of confidence that an observed association involved actual feeding by the chrysomelid.

6 Chrysomelids were observed in the field actually eating plant material.
5 Chrysomelids fed on plant when confined.
4 10 or more chrysomelids were collected from a plant and feeding damage that could reasonably be attributed to the beetles was present.
3 Five to nine chrysomelids were collected from a plant and feeding damage that could reasonably be attributed to the beetles was present, or 10 or more chrysomelids were collected from a plant but obvious feeding damage attributable to the beetles was not present.
2 Two to four chrysomelids were collected from a plant and feeding damage that could reasonably be attributed to the beetles was present, or five to nine chrysomelids were collected from a plant but obvious feeding damage attributable to the beetles was not present.
1 Two to four chrysomelids were collected from a plant but no noticeable feeding damage was observed.

Number (No.)

Number of vouchered specimens. In general, one feeding record equals one voucher; the few exceptions are mentioned in the Note column.

Voucher

Specimens collected by the senior author have voucher codes in the form “(Collection No.)-RWF(Year)” and are deposited in INBio. Those collected by the junior author have codes in the form “(Year)-SRNP-(Number)” and are nominally specimens of INBio but are on temporary loan to the University of Pennsylvania.

Note

These are numbered consecutively and appear in Appendix 3.

Appendix 2. Localities

Localities cited in Table 1 are listed on an approximate north-south gradient. The first letter of each locality code corresponds to the first letter of its province. Localities in the Área de Conservación Guanacaste also include Lambert Coordinates in parentheses. Lambert Coordinates are used in Costa Rica in preference to latitude-longitude because the 1:50,000 topo sheets are gridded with Lambert Coordinates and, being metric, Lambert positions are easier to use.
The data presented in these tables represent only the beginnings of the task of working out host plant relationships for the Central American Chrysomelidae. Our data cover less than 7% of the estimated 2000 chrysomelid species present in Costa Rica alone (Flowers, unpublished data). In some cases, our data confirmed previously published relationships between chrysomelid genera and host plant families (summarized in Jolivet & Hawkeswood 1995); 30 of our records represent host plant family range extensions, and 19 records are for chrysomelid genera in which, apparently, no host plants have been recorded previously.

Most previously published host plant studies for the Neotropical Chrysomelidae (aside from focused studies on specific taxonomic groups, e.g., Bach 1986; Begossi & Benson 1988; Windsor 1986) make no distinctions between accidental or casual associations of plant and beetle and true host relationships. The dangers in not making these distinctions have been demonstrated to us on several occasions when we found chrysomelid species that move off their food plants for resting or defecating. An example is Ommophoa simulans (Alticini, see Table 1), a group of which was first observed sitting on leaves of a Luehea sapling (Tiliaceae). Although large numbers of beetles were on the Luehea, and their frass was also evident on these leaves, closer inspection revealed that no feeding was taking place on the Luehea and that the true food plant (Evolvulus nummularis; Convolvulaceae) was growing beneath the shrub. Similar warnings about possible confusion of Alticini food plants due to the beetle's mobility have been given by Hawkeswood and Furth (1994). Nevertheless, collection records can still provide useful information—for many taxa opportunistic collecting has provided the only information we have on possible host plants—if their limitations are clearly acknowledged. For our data we have included a “reliability scale” to roughly measure the confidence that a given association represents a true chrysomelid-host plant relationship. While ecological studies of narrow groups of chrysomelids or plants will always provide the most unambiguous data on feeding requirements, recent emphasis on and support for inventory collecting can rapidly increase knowledge of the feeding habits of a broad range of chrysomelids, if observations are qualified in some manner.

We intend to continue expanding on the present work, and we encourage other collectors of Chrysomelidae to record, categorize and publish the plant associations they observe. Rapidly expanding our knowledge of chrysomelid-plant interactions is important for two reasons. On the practical side, knowing host plants for more chrysomelid species will facilitate programs in chemical prospecting which are currently focused on plants. When a family of plants is being surveyed for active chemicals, the insects feeding on those plants represent another level of chemical derivatives available for screening. The phytophagous insect may produce novel chemical varieties which cannot be synthesized directly from the host plant.

A second area where more host plant data are needed is in the testing of hypotheses of the evolution of host plant selection. At present there are two competing theories of what chiefly influences this evolution: phylogenetic and ecological mediation. Phylogenetic mediation (cospeciation) postulates that most cases of herbivory arise from cospeciation or parallel descent. This theory has become a popular explanation of host plant selection, under the name “coevolution” (though we caution the reader that this is not the original meaning of the word, see Janzen 1980b). Phylogenetic mediation has been demonstrated in the Chrysomelidae for Phyllotreta species (Galerucinae) and their hosts in the Lamiales (Farrell and Mitter 1990). However, their study represents one of the few documented examples of coevolution (Anderson 1993).
### Table 1. Feeding records of Costa Rican leaf beetles. See text for explanation of columns.

<table>
<thead>
<tr>
<th>Leaf Beetle</th>
<th>Plant Family</th>
<th>Plant</th>
<th>Stage</th>
<th>Locality</th>
<th>Date</th>
<th>Collectors</th>
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<th>Voucher</th>
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<td>G10</td>
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### Table 1. (Continued) Feeding records of Costa Rican leaf beetles. See text for explanation of columns.

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Table 1. (Continued) Feeding records of Costa Rican leaf beetles. See text for explanation of columns.

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### TABLE 1. (CONTINUED) FEEDING RECORDS OF COSTA RICAN LEAF BEETLES. SEE TEXT FOR EXPLANATION OF COLUMNS.

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**TABLE 1. (CONTINUED) FEEDING RECORDS OF COSTA RICAN LEAF BEETLES. SEE TEXT FOR EXPLANATION OF COLUMNS.**

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Table 1. (Continued) Feeding records of Costa Rican leaf beetles. See text for explanation of columns.

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<td>Xenochalepus omogera (Crotch)</td>
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| **HISPINAE: CASSIDINI**         |              |              |       |          |           |            |       |     |             |      |
| Akantaka insidiosa Boh.         | Tabebuia ochracea | BIG | A | G10          | 5/VI/1982 | DHJ &WH  | 6    | 1   | 82-SRNP-169 | 55   |
|                                 | Tabebuia ochracea | BIG | L, A | G9         | 30/VI/1989 | DHJ &WH  | 6    | 2   | 89-SRNP-448 |      |

Table 1. (Continued) Feeding records of Costa Rican leaf beetles. See text for explanation of columns.
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<td>Coptocycla leprosa</td>
<td>Cordia alliodora</td>
<td>BOR A G13 16/VI/1989 DHJ &amp; WH 6 3 89-SRNP-218</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
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</tr>
<tr>
<td>Cydista diversifolia</td>
<td>BIG L, A G11 18/VI/1991 RWF 1 2 66-RWF91</td>
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</table>

**TABLE 1. (CONTINUED) FEEDING RECORDS OF COSTA RICAN LEAF BEETLES. SEE TEXT FOR EXPLANATION OF COLUMNS.**

*Note: Missing data or notes not provided.*
Table 1. (Continued) Feeding records of Costa Rican leaf beetles. See text for explanation of columns.

<table>
<thead>
<tr>
<th>Leaf Beetle</th>
<th>Plant Family</th>
<th>Plant</th>
<th>Stage</th>
<th>Locality</th>
<th>Date</th>
<th>Collectors</th>
<th>Score</th>
<th>No.</th>
<th>Voucher</th>
<th>Note</th>
</tr>
</thead>
<tbody>
<tr>
<td>Dorynota aurita (Boh.)</td>
<td>Tabebuia impetiginosa (Mart. ex DC.) Standl.</td>
<td>B1 G</td>
<td>L, P</td>
<td>G25</td>
<td>16/V/1979</td>
<td>DHJ &amp; WH</td>
<td>1</td>
<td>2</td>
<td>79-SRNP-16B</td>
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<tr>
<td>Ischnocodia annulis (Fab.)</td>
<td>Ocotea veraguensis</td>
<td>LAU</td>
<td>A</td>
<td>G10</td>
<td>5/XI/1979</td>
<td>DHJ &amp; WH</td>
<td>1</td>
<td>4</td>
<td>79-SRNP-311</td>
<td></td>
</tr>
<tr>
<td>Omocerus caeruleopunctata (Boh.)</td>
<td>Cordia spinescens L.</td>
<td>BOR</td>
<td>A</td>
<td>C1</td>
<td>5/IX/1991</td>
<td>RWF, D. Coto, J. Saunders</td>
<td>4</td>
<td>7</td>
<td>47-RWF91</td>
<td></td>
</tr>
<tr>
<td>Orexta wagneri (Boh.)</td>
<td>Cordia panamensis Riley</td>
<td>BOR</td>
<td>L, A</td>
<td>G8</td>
<td>23/VI/1980</td>
<td>DHJ &amp; WH</td>
<td>6</td>
<td>1</td>
<td>80-SRNP-218</td>
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Flowers & Janzen: Chrysomelid Feeding Records
Table 1. (Continued) Feeding records of Costa Rican leaf beetles. See text for explanation of columns.

<table>
<thead>
<tr>
<th>Leaf Beetle</th>
<th>Plant</th>
<th>Plant Family</th>
<th>Stage</th>
<th>Locality</th>
<th>Date</th>
<th>Collectors</th>
<th>Score</th>
<th>No.</th>
<th>Voucher</th>
<th>Note</th>
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</thead>
<tbody>
<tr>
<td>Plagiometrina crucipennis (Boh.)</td>
<td>Asteraceae</td>
<td>AST</td>
<td>A</td>
<td>G10</td>
<td>11/VI/1982</td>
<td>DHJ &amp; WH</td>
<td>6</td>
<td>2</td>
<td>82-SRN-P-545</td>
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<tr>
<td>Plagiometrina testudinaria (Boh.)</td>
<td>Lycopersicon esculentum Mill.</td>
<td>SOL</td>
<td>L, A</td>
<td>G14</td>
<td>30/VI/1986</td>
<td>DHJ &amp; WH</td>
<td>6</td>
<td>7</td>
<td>86-SRN-P-477</td>
<td>65</td>
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<tr>
<td>Xenocassis ambita (Champ.)</td>
<td>Ipomoea sp.</td>
<td>CNV</td>
<td>A</td>
<td>A1</td>
<td>21/V/1991</td>
<td>RWF</td>
<td>3</td>
<td>5</td>
<td>46-RWF91</td>
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</table>
The alternative hypothesis is that ecological mediation (colonization and host transfer) is the primary explanation for current host associations. In cases of ecological mediation, phylogenies of herbivores and host plants are not congruent, and host shifts are not necessarily between sister taxa of plants Anderson (1993). In a survey of the Curculioninae (Curculionidae), Anderson (1993) found that in taxa where systematics and plant associations were reasonably well known, evidence for cospeciation of plant and insect taxa is lacking, and ecological mediation appeared to be the rule. However, like the Chrysomelidae, the majority of curculionine taxa lack any host plant data. Until host plants are known for a much larger proportion of phytophagous insect taxa, speculations on the evolution of host plant selection by insects will continue to be based on small subsets of the phytophagous insect universe.

ACKNOWLEDGMENTS

We sincerely thank the staffs of the Area de Conservación Guanacaste (ACG), and the Instituto Nacional de Biodiversidad (INBio) for their assistance and many kindnesses during the course of this study. This research was funded in part by a grant (FLAX 91005) from the CSRS, USDA, to Florida A&M University, a National Science Foundation Mid-Career Fellowship (BSR-9003898) to the senior author, and NSF DEB-9400829 to the junior author.

REFERENCES CITED


APPENDIX 1—ABBREVIATIONS OF PLANT FAMILY NAMES IN TABLE 1.

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<tr>
<th>Abbreviation</th>
<th>Family Name</th>
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<tr>
<td>ACA</td>
<td>Acanthaceae</td>
<td>CNV</td>
<td>Convolvulaceae</td>
</tr>
<tr>
<td>AMA</td>
<td>Amarantaceae</td>
<td>DIO</td>
<td>Dioscoreaceae</td>
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<tr>
<td>APO</td>
<td>Apocynaceae</td>
<td>ERY</td>
<td>Erythroxylaceae</td>
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<tr>
<td>ASC</td>
<td>Asclepiadaceae</td>
<td>ERI</td>
<td>Ericaceae</td>
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<tr>
<td>AST</td>
<td>Asteraceae</td>
<td>EUP</td>
<td>Euphorbiaceae</td>
</tr>
<tr>
<td>BIG</td>
<td>Bignoniaceae</td>
<td>FAB</td>
<td>Fabaceae:</td>
</tr>
<tr>
<td>BOR</td>
<td>Boraginaceae</td>
<td>PAPO</td>
<td>Papilionoidea</td>
</tr>
<tr>
<td>BUR</td>
<td>Burseraceae</td>
<td>FLA</td>
<td>Flacourtiaceae</td>
</tr>
<tr>
<td>CAE</td>
<td>Fabaceae:</td>
<td>HIP</td>
<td>Hippocrateaceae</td>
</tr>
<tr>
<td></td>
<td>Caesalpinoidea</td>
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<td>Lauraceae</td>
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<td>CAP</td>
<td>Capparidaceae</td>
<td>LOG</td>
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<td>CLU</td>
<td>Clusiaceae</td>
<td>MLP</td>
<td>Malpighiaceae</td>
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<td>Cecropiaceae</td>
<td>MLV</td>
<td>Malvaceae</td>
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## Appendix 2—Localities from Table 1.

<table>
<thead>
<tr>
<th>Locality Code</th>
<th>Description</th>
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<tbody>
<tr>
<td>G1</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Pitilla, Estacion Pitilla, 8 km S Santa Cecilia, 700 m (N330000, E380400)</td>
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<td>G2</td>
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<td>G3</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Area Recreativa Junquillal, 3 km N Cuajiniquil, 0 m (N328000, E351700)</td>
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<tr>
<td>G4</td>
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<tr>
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<tr>
<td>G6</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Orosi, Estacion Maritza, sendero Casa Fran, 21 km SE La Cruz, 600 m (N326000, E373300)</td>
</tr>
<tr>
<td>G7</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Estacion Santa Rosa, 28 km NNW Liberia, 250 m (N313700, E359000)</td>
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<tr>
<td>G8</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Santa Rosa, Bosque Humedo, 30 km NNW Liberia, 300 m (N314800, E360500)</td>
</tr>
<tr>
<td>G9</td>
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<tr>
<td>G10</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Santa Rosa, Bosque San Emilio, 29 km NNW Liberia, 300 m (N313800, E359800)</td>
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<tr>
<td>G11</td>
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<tr>
<td>G12</td>
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<td>G13</td>
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<td>G14</td>
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<td>G15</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Santa Rosa, Cliff Top Light, 31 km NNW Liberia, 300 m (N315200, E360200)</td>
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<td>G16</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Santa Rosa, Casetilla Entrada, 33 km NNW Liberia, 300 m (N317800, E362600)</td>
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<td>G17</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Santa Rosa, Laguna Escondida, 30 km NNW Liberia, 250 m (N314500, E357900)</td>
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<tr>
<td>G18</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Santa Rosa, Llano Guacimil, 32 km NNW Liberia, 300 m (N317000, E361600)</td>
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<td>G19</td>
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<tr>
<td>G22</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Santa Rosa, Cruz de Piedra, 33 km NNW Liberia, 300 m (N317200, E360900)</td>
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<tr>
<td>G23</td>
<td>Guanacaste Prov., Area de Conservacion Guanacaste, Sector Cacao, Estacion Cacao, 9 km N Quebrada Grande, 1000 m (N323100, E375500)</td>
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APPENDIX 2—(CONTINUED) LOCALITIES FROM TABLE 1.

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<td>G29</td>
<td>Guanacaste Prov., Finca La Pacífica, 5 km NW Canas.</td>
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<tr>
<td>G30</td>
<td>Guanacaste Prov., 12 km NW of Bebedero, Hacienda Horizontes.</td>
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<tr>
<td>G31</td>
<td>Guanacaste Prov., Bebedero, Ingenio Taboga.</td>
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<td>A1</td>
<td>Alajuela Prov., Finca San Gabriel, 2 km SW Dos Ríos, 600 m</td>
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<td>A2</td>
<td>Alajuela Prov., Reserva Forestal San Ramon, 900 m</td>
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<td>A3</td>
<td>Alajuela Prov., Bijagua, 20 km S Upala, 500 m</td>
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<td>A4</td>
<td>Alajuela Prov., Canton Guacima, Río Segundo, 780 m</td>
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<td>Alajuela Prov., Canton Ciruelas, Río Ciruelas, 800 m</td>
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<td>Heredia Prov., Estac. Biol. La Selva, 50 m</td>
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<td>San José Prov., San Pedro, Univ. Costa Rica</td>
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<tr>
<td>S2</td>
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<td>C1</td>
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<td>Cartago Prov., Madreselva, nr. Empalme</td>
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<td>P3</td>
<td>Puntarenas Prov., Peninsula de Osa, Cerro de Oro</td>
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</tr>
</tbody>
</table>
Appendix 3—Notes to Table 1.

1. These beetles were sitting on heavily eaten leaves, 1.5 m above ground.
2. Additional specimens were observed at time of collection, and C. Chavez reported seeing this species frequently on the same host plant.
3. This species was tested on the host plant. J olivet (1978) gave Asteraceae, Mimosaceae, Ericaceae and Fagaceae as other host plant families of this genus.
4. This species was found feeding at shoot tips of its host plant.
5. The host plant is an abundant roadside weed on the entrance road in Sector Santa Rosa and elsewhere in this sector. Beetles have been collected both in the rainy and dry seasons. The larvae make cone-shaped cases, apparently utilizing hairs of the host's leaves. Moldenke (1971) listed both Malvaceae and Convolvulaceae as host plant families for this species.
6. The vouchers were collected from a swarm of this species feeding on the low bush in dense dry forest. The intense feeding and mating activity was similar to that observed in other Clytrinae (Flowers et al. 1994, Moldenke 1971). J olivet (1978) lists Mimosaceae as the predominant host for this genus.
7. The beetle was seen eating bark of new stems. Monróes (1949) and J olivet (1978) described bark feeding by other members of this genus.
8. This species was very abundant on the leaves of its host at several regenerating pasture sites in 1991. This cosmopolitan genus has been recorded from Araliaceae from the Paleartic and from Myrtaceae from Puerto Rico (J olivet 1978).
9. In 1991 this species was very abundant in the pastures and open areas after the onset of the summer rains. Individuals were also collected on other pasture shrubs. The collection of J an Bechyné in Maracay Venezuela contains several specimens of this species collected in El Salvador and bearing the (apparently) manuscript name "saltator". The only other host record for this genus is Theobroma cacao L. (Sterculiaceae) for an unidentified species (J olivet 1987b).
10. J olivet (1987b) stated that all host observations of the genus Chalcophana have been Asteraceae.
11. Although only one voucher was preserved, numerous adults were observed, and several were tested on the leaves of the plant host. J olivet (1987b) noted that this genus is both cosmopolitan and polyphagous.
12. Adults were feeding at night on very new expanding leaves of a 1.5 m shoot at base of tree. J olivet (1987b) stated that the only reliable feeding records for this genus are from Fabaceae.
13. The only host records in the literature for Percolaspis are from Poaceae and Theobroma cacao (J olivet 1987b).
14. This species has been found feeding on several species of Rubiaceae. Adults are agile leapers when disturbed. J olivet (1987b) gave a single record for this genus: Persea (Lauraceae) for a Cuban Phanaeta.
15. Adults of this genus were found on new foliage and in some years defoliated their hosts.
16. This species was very common feeding on various species of Melastomataceae. J olivet (1987b) described Typophorus as polyphagous but does not list any Melastomataceae among its host plants.
17. The voucher is one of many collected, seen and reared at Estación Pitilla and San Gabriel on various species of Solanum.
18. Larvae skeletonize host plant leaves. This species extensively defoliates its host during some years. Literature records for New World Plagiodera are limited to Salix, Populus (Salicaceae), Croton (Euphorbiaceae), and Lueha (Tiliaceae); how-
ever, species in the Philippines and India have been reported on Xylosoma and Flacourtia (Flacourtiaecae) (Jolivet & Hawkeswood 1995).

19. This is the most commonly collected of the Costa Rican species of Platyphora. During one feeding test, two very small larvae were observed in the plastic bag which up till then held a single female, suggesting that Platyphora bicolor is viviparous. Schroder et al. (1994) described the biology of the viviparous Platyphora quadrisignata (Germar) from southern Brazil.

20. Adults and larvae were frequently found feeding on host plant throughout the 1991 rainy season. Apparently, our observations represent the only known host plant data for Stilodes.

21. A group was followed from egg to adult. Larvae feed and rest on underside of leaves. Pupation takes place in leaf litter.

22. Larvae are sooty black, covered with branched hair-like projections, and with red heads. Pupae are yellow. This chrysomelid was parasitized by Myopharous (Tachinidae: Diptera).

23. In 1991 this beetle caused a major defoliation of its host plant, a pioneer species in cleared pastures.

24. The host plant of this galerucine was found growing along the edge of a small patch of forest.

25. The host plant was a low understory tree in tropical dry forest.

26. This galerucine was seen on several occasions feeding on young leaves of its host plant. This genus has been recorded from Acacia (Fabaceae) in the USA (Jolivet 1987a).

27. A large group of these Masurius (which may represent more than one species) was found feeding on the two host plants growing within a few yards or each other along a trail in montane forest.

28. This and the following species were reared to adult.

29. In addition to the voucher specimens, other specimens were collected two years earlier on the same host plant.

30. RWF observed adults of this species every year since 1989 defoliating basal shoots of a tree growing in front of the main administration building at the University of Costa Rica. Jolivet (1987a) listed Cordia and Lantana (Verbenaceae) as hosts of this genus.

31. In both cases, beetles were observed feeding on the host plant. Jolivet (1991) listed Labiaceae and Verbenaceae as probable hosts for this genus and noted other citations of Lauraceae, Buddlejaceae, Asteraceae, Umbelliferae, Sterculiaceae, and Fabaceae.

32. In addition to the vouchered specimen from Byrsonima crassifolia, this species was abundant on this host plant at Estacion Maritza (G4) in 1991.

33. Unlike many other chrysomelids which were found associated only with young foliage, A. salvadorense was found actively feeding late in the rainy season on older leaves.

34. A large group of these beetles was found on a broken stalk of the host plant, feeding on sap and milky latex. The host plant was growing in the shaded understory of montane forest.

35. RWF observed individual at night eating a hole in the middle of a leaf of the Ipomoea host plant.

36. Adults were reared from larvae feeding on the host plant.

37. Jolivet (1991) listed Samanea (Fabaceae/pap.) as a host of this genus.

38. Jolivet (1991) cited Theobroma and Tecoma (Bignoniaceae) as other known host plants of this alticine genus.
39. Both this and the following host plant were growing close together in a mixed stand next to a road.
40. The host plant, growing in a wet depression in a cleared area, sustained heavy feeding damage from this alticine in 1991. J olivet (1991) listed Cleome, Solanum, Beta (Chenopodiaceae), Labiaceae, Cordia, and Adiantum (Adiantaceae) as host plants of Leptophysa.
41. These beetles were swept from a tree that showed heavy feeding damage to the leaves. No active feeding was observed, but this collection was made during an abnormal dry spell during what was supposed to be the wet season.
42. This Longitarsus is a flightless species.
43. Field observations by DHJ indicate that the adult appears on the host plant to oviposit; larvae are free living and cut islands out of leaf margin.
44. The host plant is a small prostrate weed. The beetles were first observed resting and defecating on a shrub of Luehea (Tiliaceae) which grew over the Evolvulus. When no feeding damage on the Luehea was seen, despite the beetle activity, a wider search revealed the true host plant.
45. These small pinkish-orange flea beetles were observed feeding on newly expanding leaves (which are also reddish to pinkish orange) of their ericaceous hosts.
46. This alticine was collected abundantly from a very dense stand of its host plant. In 1994 it was found equally abundantly in the same stand of plants.
47. RWF has observed this species over several years, actively feeding on Euphorbiaceae even during the dry season in quite arid habitats.
48. These represent five different morphospecies of Syphrea collected on various plants.
49. This species feeds by scraping pits in the expanding leaves of this host plant. The following plant record may be an alternate dry season food source.
50. Huge numbers of this species were found defoliating the host plant during the voucher year. In 1991, on the other hand, no specimens were found and no damage to the host was apparent. This is the species called Oedionychis sp. in Rockwood (1974). Bechyné (1955) restricted the definition of true Oedionychis to a small group of flightless Mediterranean flea beetles. New World species formerly in Oedionychis are now placed in Walterianella, Alagoasa and other genera.
51. J olivet (1991) listed Venezuelan records of Gardinia (Rubiaceae) and Tabebuia (Bignoniaceae) for this genus.
52. The genus Cephaloleia is well known from various species of Heliconia and other Zingiberales (Strong 1977a,b). This species was regularly encountered in rolled-up terminal leaves of Costus at this and other localities.
53. This hispine was very abundant in a dense stand of grass growing on a river sand bar.
54. A large number of these hispines were feeding on and heavily damaging leaves of a shrub of its host growing along the bank of a river in deep shade.
55. These cassids have black larvae with long black caudal brushes; the pupae have a creamy white thorax. Adults were reared.
56. Windsor et al. (1992) gave Ipomoea lindenii Mart. & Gal. as host plant for true C. egregia.
57. This species periodically defoliates its host.
58. Feeding on young leaves of Alibertia was seen; some feeding damage was also seen on the two bignoniaceous plants as well.
59. The cassid caused a major defoliation in 1979, but has been rare since. The 1991 record was from a single tree growing by the seashore and heavily damaged by a group of the cassids. J olivet (1988a) also listed Tabebuia and other Bignoniaceae as hosts for this genus.
60. These records are of beetles aestivating in the dry season; see Flowers (1991) for more details on this behavior. Windsor et al. (1992) listed several species of Cordia as the true host plants of this species.

61. The host plant was an understory plant in a pine plantation. Jolivet (1988a) also listed Hyptis (Labiaceae) as a host plant for this genus.

62. The record from Bursara simaruba is for beetles hiding under bark plates during the dry season. Jolivet (1988a) listed Phaseolus (Fabaceae) and Passiflora (Passifloraceae) for this genus.

63. In 1991 this species was common during the rainy season. A colony at the Administration Area in Sector Santa Rosa (G14) was followed for several months, during which time predatory pentatomids were observed resting on foliage above the cassids, and occasionally descending to feed on them.

64. Windsor et al. (1992) listed Cordia spinescens for a P. nr. alutacea from Panama.

65. Windsor et al. (1992) also list Solanum seaforthianum Andr. and Physalis cor-data Mill (Solanaceae).
EFFECT OF THE MICROSPORIDIUM THELOHANIA SOLENOPSÆ (MICROSPORIDA: THELOHANIIDAE) ON THE LONGEVITY AND SURVIVAL OF SOLENOPSIS RICHTERI (HYMENOPTERA: FORMICIDAE) IN THE LABORATORY

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ABSTRACT

The longevity of colonies of the black imported fire ant, Solenopsis richteri Forel, and the survival of starved workers and sexual females was compared between healthy colonies and colonies infected with the microsporidium Thelohania solenopsae Knell, Allen, & Hazard. The colonies were collected in the field and reared for approximately four mo. Individual workers and sexuals were held without food until death. The body weight of infected and healthy workers was compared. After 3 mo of laboratory rearing, longevity of infected colonies was significantly shorter than that of healthy ones; mortality of infected colonies was 92% and mortality of healthy colonies was 49%. At 27°C, mortality rate of workers from infected colonies was higher than in healthy workers. Workers from infected colonies lived between 8.8 and 29.2% less than healthy workers. At 22°C, no statistical significance was observed. At 21°C, only the initial mortality of sexual females was higher in infected than in healthy individuals. The weight of infected workers was very similar to that of healthy workers. T. solenopsae should be considered for the biological control of the imported fire ants in the United States.

Key Words: Solenopsis invicta, imported fire ants, microsporidium, ant longevity
Resumen

La longevidad de colonias de la "hormiga colorada" (u "hormiga brava") Solenopsis richteri Forel y la supervivencia de obreras y hembras sexuadas en inanición fueron comparadas entre colonias sanas y colonias infectadas con el microsporidio Thelohania solenopsae Knell, Allen y Hazard. Las colonias fueron colectadas en el campo y criadas durante aproximadamente cuatro meses. Las obreras y sexuadas fueron mantenidas sin alimento hasta su muerte. Se comparó el peso corporal de obreras enfermas y sanas. Después de 3 meses de círculo en laboratorio, la longevidad de las colonias infectadas fue significativamente menor que la de las colonias sanas; la mortalidad de las colonias infectadas fue del 92% y la mortalidad de las sanas fue 49%. A 27°C, la tasa de mortalidad de obreras de colonias enfermas fue mayor que la de obreras sanas. Obreras de colonias enfermas sobrevivieron entre 8.8 y 29.2% menos que las obreras sanas. A 22°C, no se observó significancia estadística. A 21°C, sólo la mortalidad inicial de las hembras sexuadas fue mayor en los individuos enfermos que en los sanos. El peso de las obreras enfermas fue muy similar al de las obreras sanas. Thelohania solenopsae debería ser considerado para el control biológico de la "hormiga colorada" en los Estados Unidos.

The presence of a microsporidian pathogen in the red imported fire ant, Solenopsis invicta Buren, was first reported by Allen & Buren (1974) from Brazil, and was later described as Thelohania solenopsae Knell, Allen, & Hazard (1977) (Microsporida: Thelohaniidae). A similar microsporidium was discovered in the black imported fire ant, Solenopsis richteri Forel, and other Solenopsis species, in Argentina and Uruguay (Allen & Silveira Guido 1974). The presence of microsporidia was later reported in surveys of fire ant natural enemies conducted in South America (Jouvenaz 1983, 1986; Jouvenaz et al. 1980, 1981; Wojcik et al. 1987; Briano et al. 1995). A comparative study conducted by Moser (1995) confirmed that these microsporidia were conspecific.

Thelohania solenopsae is the most common microorganism of fire ants in Buenos Aires Province, Argentina (Briano et al. 1995). Recently, it was discovered infecting colonies of S. invicta in the United States (Williams et al. 1997). Briano et al. (1995a, 1995b, 1996) reported for Argentina a high intracolonial prevalence of the infection and a detrimental effect on native fire ant field colonies and populations. They suggested that T. solenopsae may be a suitable candidate for the biological control of the red and black imported fire ant in the United States.

Although Knell et al. (1977) reported that field-collected colonies of S. invicta infected with this microsporidium cannot be maintained under laboratory conditions as long as healthy colonies, this detrimental effect was never quantified. We speculated that a similar effect of T. solenopsae could be expected in S. richteri. Our primary objective was to compare the longevity of field-collected healthy fire ant colonies, and the survival of individual workers and female sexuals, with those infected with T. solenopsae. This work reports the results of laboratory tests conducted since 1992.

Materiales y Métodos

Longevity of Colonies

In January 1992, 38 colonies of S. richteri were collected along the roadsides of Rt. 12, km 104, Isla Talavera, Buenos Aires Province, Argentina. This sampling site was selected based on previous surveys that revealed high prevalence of T. solenopsae (Briano et al. 1995).
This microsporidium was detected in 16 colonies, being the other 22 colonies healthy. The colonies were separated from the soil by flotation according to the techniques described by Banks et al. (1981). Colonies with no queen were removed from the study, consequently, only 14 infected colonies were considered. Fifteen of the 22 healthy colonies collected at the same site were used as controls.

Because all colonies were polygyne, each one was fragmented into separate, equal subcolonies comprised of one queen selected at random, 50 small and 50 large workers. The fragmented colonies were kept in plastic rearing trays (40 x 30 x 15 cm) dusted with talc to prevent escape. The test was conducted in a walk-in rearing chamber (28.6 ± 1.3°C and 60-90% RH). The colonies were fed twice a week with approximately 100 adult house flies and ½ egg yolk; a water source and honey-agar cubes were always present in the rearing trays.

The egg laying of the queens was checked daily only to confirm their fertility. Mortality of the colonies was recorded and compared between infected and healthy colonies. A colony was considered dead when its queen was found dead. Growth of colonies and mortality rate of individual workers was not quantified.

Survival of Workers. Test I

In December 1995, 4 colonies of S. richteri (2 Thelohania-infected and 2 healthy) were excavated from Rt. 205, km 180, Saladillo, Buenos Aires Province. They were separated from the soil by flotation (Banks et al. 1981). Although the exact percentage of infected workers present in the infected colonies was not determined, based on previous work (Briano et al. 1996), we estimated that it was, on average, 88%. A total of 160 workers was selected from the colonies. Twenty small (head width: 0.67 ± 0.06 mm) and 20 large workers (head width: 1.08 ± 0.17 mm) were separated at random from each of the 4 colonies. The selected workers were put in groups of 10 in individual cells (4 x 4 x 2 cm) of plastic rearing trays (40 x 20 x 2 cm). A plastic lid covered each cell preventing escape. The workers were held without food until death. A small piece of moistened cotton was present in the cells as a source of moisture. The test was conducted in a walk-in rearing chamber (27.3 ± 1.6°C; 70-90% RH). Mortality was recorded daily and survival of small and large workers was compared.

Survival of Workers and Sexuals. Test II

In April 1996, 3 colonies of S. richteri (2 Thelohania-infected and a healthy one) were excavated in Moreno, Buenos Aires Province, and separated from the soil by flotation (Banks et al. 1981). Sixty-four workers of different sizes separated at random from each infected colony along with 13 female sexuals were put individually in cells of plastic rearing trays with moistened cotton as above. The trays were kept at room temperature (21.8 ± 1.4°C for workers and 20.7 ± 1.6°C for sexuals). The workers and sexuals were held without food until death. Only a small piece of moistened cotton was present in the cells as above. Workers of different sizes (n = 32) and sexuals (n = 18) separated from the healthy colony were used as controls. Once dead, the head width of each worker was measured under an ocular micrometer. To confirm infected and healthy individuals, the workers and sexuals were crushed individually in a drop of water placed on a microscope slide and checked under a phase-contrast microscope. Mortality was recorded daily and survival was compared between confirmed infected and healthy individuals. Arbitrarily, we considered minor workers those with head widths from 0.6 to 0.8 mm, medium workers those with head widths from 0.9 to 1.1 mm, and major workers those with head widths from 1.2 to 1.5 mm.
Weight of Workers

Sixty-seven infected and 65 healthy workers (not starved) of different sizes were selected at random from the colonies used in Test II. They were weighed (live weight) on an electronic balance (Precisa 120 A, PAG Oerlikon AG, Zurich, Switzerland), killed in 70% ethyl alcohol and their head widths measured under an ocular micrometer. Each worker was crushed on a microscope slide and examined under a phase-contrast microscope to confirm the presence or absence of T. solenopsae. The live weights of infected and healthy workers were compared and correlated with worker size.

Statistical Analysis

Mortality rate was analyzed with the logrank method, an application of the Mantel-Haenszel method (Mantel & Haenszel 1959). Longevity of colonies and survival of individual ants was analyzed with 2-sample test. The simple linear regression model was used to correlate survival of workers with their size, and the curvilinear (cubic) model was used to correlate the live weight of workers with their size. Minitab Statistical Software (1991) was used for t tests and regressions. Means are reported ± 1 SD.

RESULTS AND DISCUSSION

Longevity of Colonies

Longevity of infected colonies was significantly shorter than in healthy colonies (Fig. 1). The cumulative mortality during the first 21 d was 64% for infected colonies and 24% for healthy colonies. After 3 mo, mortality was 92% for infected colonies and 49% for healthy colonies (Logrank method; $\chi^2 = 6.0; df = 1; P < 0.025$). In most colonies the queens died after the workers.

The different mortality rate between infected and healthy colonies suggests that T. solenopsae is lethal to stressed laboratory colonies of the black imported fire ant. Although mortality of healthy colonies is usually high under laboratory conditions, as this test showed, clearly this pathogen exerted additional stress and increased mortality. This is consistent with results of field work that showed a detrimental effect of this microsporidium on native fire ant populations and individual colonies of S. richteri (Briano et al. 1995a; 1995b). These results also agree with Knell et al. (1977) who reported that colonies of S. invicta infected with this microsporidium cannot be maintained under laboratory conditions as long as healthy colonies.

In this experiment we actually compared residual longevity because queens and workers were not newly eclosed when the test started. Comparisons are still valid because this also happened for healthy colonies. The actual life span of infected colonies compared to healthy colonies in the laboratory remains unknown and should be investigated.

Egg-laying started at day 11 in 2 healthy colonies and at day 14 in one infected colony. At day 21, 72% of the surviving healthy colonies and 80% of the surviving infected colonies showed worker brood production. The egg-laying rate of infected and healthy queens was not compared and deserves further investigation.

Survival of Workers. Test I

Mortality rate of workers from infected colonies was higher than that of workers from healthy colonies (Fig. 2). For small workers, after 3 d of starvation, mortality of
individuals from infected colonies was 75% and mortality of healthy ones was 43%. At day 4, when all workers from infected colonies had died, 8% of healthy workers were still alive (Logrank method; \( \chi^2 = 4.5; df = 1; P < 0.05 \)). On average, the survival of small workers from infected colonies was 8.8% shorter than that of healthy ones. The mean survival time was 3.1 ± 0.2 d for workers from infected colonies and 3.4 ± 0.7 d for healthy ones (\( t = 2.691; df = 78; P = 0.0087 \)).

For large workers, after 4 d of starvation, mortality of individuals from infected colonies was 95% and mortality of healthy ones was 33% (Fig. 2). At day 6, when all workers from infected colonies had died, 8% of the healthy workers were still alive (Logrank method; \( \chi^2 = 16.45; df = 1; P < 0.001 \)). On average, large workers from infected colonies lived 29.2% less than healthy workers. The mean survival time was 3.4 ± 0.7 d for workers from infected colonies and 4.8 ± 1.3 d for healthy ones (\( t = 5.633; df = 78; P < 0.0001 \)).

The difference in survival time both in small and large workers was underestimated because some workers from infected colonies could have been actually healthy. The difference was larger in large than in small workers (Fig. 2). It seems that \emph{T. solenopsae} affected large workers more than small workers. This is consistent with the assumption that \emph{T. solenopsae}, being a chronic disease, would affect more severely those individuals with longer life span such as large workers. The tasks performed by large workers in the colony (mound construction, foraging, territory defense, and transport of sexual broods) would be affected more severely than the tasks performed primarily by small workers. The actual impact that the high prevalence of infected
Survival of Workers and Sexuals. Test II

The mortality rate of healthy workers was similar to that of infected workers (Fig. 3; logrank method; $\chi^2 = 0.256; df = 1; P > 0.5$). Although the mean survival time of infected workers was shorter than that of healthy workers, no statistically significant differences were found. Infected minor workers survived $5.9 \pm 5.3$ d and healthy minor workers survived $6.5 \pm 5.0$ d ($t = -0.457; df = 76; P = 0.648$). Infected medium workers survived $9.0 \pm 9.3$ d and healthy medium workers $10.0 \pm 8.8$ d ($t = -0.278; df = 44; P = 0.782$). Infected major workers survived $11.5 \pm 9.1$ d and healthy major workers $12.9 \pm 13.9$ d ($t = -0.313; df = 22; P = 0.756$).

The regression of survival on worker size showed very low coefficients of determination for both healthy workers ($r^2 = 0.07$) and infected ones ($r^2 = 0.05$). The main reason for this was the high individual variability. Calabi & Porter (1989) also reported a high scatter in regression of longevity on worker size for S. invicta in the United States ($r^2 = 0.02$). They speculated that the scatter was due to the absence of queens,
brood and/or intercolony differences. In our experiment, an extra source of variability would be the undetermined age of the workers when the test started.

Considering the tests reported in this article, worker survival decreased about 60% when temperature increased from 22 to 27°C. The validity of this comparison may be questionable because the tests were conducted separately, the ants were collected in different locations and in different seasons. However, the information reported is consistent with studies conducted in the United States by Calabi & Porter (1989) showing that workers of S. invicta had an 80% reduction in longevity when the temperature increased from 17 to 30°C. It seems that at lower temperatures, the reduced activity and metabolic rate of the workers can reduce the debilitating effects of the infection. This should be investigated. We speculate that the detrimental effect of T. solenopsae could be more important in areas with warmer temperatures. According to Tanada & Kaya (1993), temperatures higher than 30°C can limit the infectivity of pathogens, but moderately high field temperatures accelerate the infectious process and result in quicker mortality.

The mortality rate of infected female sexuals was not significantly different from that of healthy ones (Fig. 4; logrank method: $\chi^2 = 0.45; df = 1; P > 0.5$). However, the mortality during the first 10 d was much higher for infected individuals ($\chi^2 = 6.36; df = 1; P < 0.025$). This means that infected sexual females (future queens) died quicker than healthy ones and might represent a negative effect of T. solenopsae on the colony.

Fig. 3. Mortality of starved infected and healthy workers of S. richteri kept at 21.8°C.
founding within infested areas. Again, this is consistent with field work showing a detrimental effect of this pathogen on *S. richteri* (Briano et al. 1995a, 1995b).

On average, infected sexuals survived 23.0 ± 21.0 d and healthy ones survived 32.2 ± 15.5 d, but this difference was not statistically significant (*t* = -1.413; df = 29; *P* = 0.168). This was probably due to the small sample size and high individual variability. Unfortunately, no more sexuals were available when the test started. This test should be replicated with larger sample size and at several temperatures.

As expected, mean survival time of sexuals was longer than that of major workers. This can be attributed in part to the fact that the ambient temperature was slightly lower in the test with sexuals, but the longer survival should be primarily attributed to their larger body size and their extra energy source provided by the histolysis of wing muscles. After 2-3 wk of starvation, all sexuals lost their wings.

**Weight of Workers**

The live weight of infected workers was very similar to that of healthy workers. Infected minor workers weighed 0.656 ± 0.225 mg (range 0.3-1) and healthy minor workers 0.653 ± 0.246 mg (range 0.3-1.3). Infected medium workers weighed 1.636 ± 0.362 mg (range 0.9-2.4) and healthy medium workers 1.628 ± 0.386 (range 1-2.7). Infected major workers weighed 3.665 ± 0.824 (range 2.2-5.4) and healthy workers 3.311 ± 0.747 (range 2.3-5).
As expected, the weight of workers was highly-positive correlated (cubic function) with their size (Fig. 5). The regression equation for infected workers was $y = 0.091 + 1.480x^3$ ($r^2 = 0.93; F = 857.1; df = 1, 67; P < 0.0001$) and for healthy workers was $y = 0.225 + 1.447x^3$ ($r^2 = 0.93; F = 847.5; df = 1, 65; P < 0.0001$). This agrees with Porter & Tschinkel (1985) who reported a similar relationship for workers of *S. invicta* in the United States. There was not any evidence that the presence of *T. solenopsae* affected the weight of the workers. As suggested by Knell et al. (1977) for *S. invicta*, we had speculated that the progressive destruction of the fat body produced by *T. solenopsae*, would have an impact on body weight in workers of *S. richteri*. However, a hypothetical loss of weight in infected workers could be balanced, at least in part, by the weight of the cysts totally filled with masses of Thelohania spores. This deserves further investigation.

We conclude that the microsporidium *T. solenopsae* affected the mortality rate and shortened the longevity of colonies of *S. richteri* reared under laboratory conditions. Survival of starved workers, mainly large workers, and initial mortality of sexual females was also affected. Temperature could be a regulating factor of this effect. These laboratory findings are consistent with results of field work reported by Briano et al. (1995a, 1995b), showing reduced mound volumes of infected colonies, less frequent presence of sexual brood in infected colonies and decreased mound densities in a Thelohania-infested area of Argentina.

The introduction of a complex of natural enemies into the United States has been the ultimate goal of the imported fire ant control project. Among the several potential
candidates, T. solenopsae has been the first microorganism evaluated in South America as a potential biological control agent. Still, important aspects of its life cycle, such as the horizontal transmission and field propagation, remain unknown. After those studies are completed, T. solenopsae should be considered for the biological control of the imported fire ants in the United States.

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PHYTOSEIID MITES (ACARI: PHYTOSEIIDAE) FROM GUADELOUPE AND MARTINIQUE

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ABSTRACT

Nine species of mites of the family Phytoseiidae are reported for the first time from Guadeloupe and Martinique. Measurements of the specimens of each species collected are given.

Key Words: French Caribbean Islands, predatory mites, Thrips palmi, Solanum melongena

RESUMEN

Nueve especies de acaros de la familia Phytoseiidae están señaladas por primera vez en Guadeloupe y Martinique. Medidas de los individuos de las especies recolectadas son presentadas.

This paper reports on phytoseiid mites from plants in Guadeloupe and Martinique, in collections made sporadically between 1985 and 1989. This is the first report of phytoseiid mites from those Caribbean islands. Setal nomenclature is that of Row-
ell et al. (1978) and Chant & Hansell (1971) for dorsal and ventral surfaces, respectively. All measurements are in micrometers. Except where indicated, the collector of the specimens was J. Etienne, and information on world distribution of each species was based on Moraes et al. (1986, 1991). The following abbreviations are used in this paper: I.N.R.A. (Institut National de la Recherche Agronomique; Antilles-Guyane); E.N.S.A.-M. (Ecole Nationale Supérieure Agronomique de Montpellier).

**Amblyseius aerialis** (Muma)

Amblyseius aerialis Muma 1955: 264; Garman 1958: 75.


Previous Records: Algeria, Bermuda, Brazil, Colombia, Cuba, Galapagos, Guyana, Honduras, India, Jamaica, Mexico and USA.

Remarks: The measurements of the specimens collected agree well with those of specimens from British Guyana (DeLeon 1966). The average measurements of 4 adult females followed by the respective ranges (in brackets) are: dorsal shield length 374 (367-382), width 262 (245-284), j1 26 (24-29), j3 49 (46-53), j4 4 (2-5), j5 3 (2-5), j6 5, j 2 5 (5-6), j 5 6 (5-6), z2 7 (5-9), z4 9 (6-10), z5 5, Z1 7 (6-7), Z4 145 (133-163), Z5 281 (257-318), s4 106 (94-118), S2 5, S4 10 (9-12), S5 10 (10-11), r3 10 (9-12), R1 10 (7-13), Sge 44 (43-46), Sgel I 38 (36-38), Sgel II 62 (58-70), St 1 43 (38-48), Sgel V 136 (118-152), StIV 94 (89-97), StIV 82 (72-89), ST1-ST3 71 (64-79), ST2-ST2 80 (77-82), ST5-ST5 84 (81-86), length of ventrianal shield 120 (118-121), width at ZV2 level 85 (77-89), width at anus level 83 (74-89), length of sclerotized proximal portion of cervix of spermatheca 14 (12-17), length of unsclerotized distal portion of cervix of spermatheca 20 (17-22), length of fixed digit 37 (36-38) with 12-14 teeth, length of movable digit 41 (41-42) with 4 teeth.

**Iphiseiodes zuluagai** Denmark & Muma

Iphiseiodes zuluagai Denmark & Muma 1972: 23.
Amblyseius zuluagai Moraes et al. 1991: 125.


Previous Records: Brazil, Colombia, Cuba, Panama and Puerto Rico.

Remarks: The measurements of the female specimens collected are very similar to those of the holotype. The average measurements of 5 adult females followed by the respective ranges (in brackets) are: dorsal shield length 357 (334-394), width 330 (312-356), j1 15 (13-19), j3 24 (23-28), j4 2 (1-3), j5 1 (1-3), j6 3 (1-3), j 2 3 , j 5 4 (3-4), z2 2 (1-3), z4 1 (1-3), z5 1, Z1 3 (3-4), Z4 4, Z5 90 (84-95), s4 97, S2 3 (3-4), S4 3, S5 3 (3-4), r3 4, R1 4, Sgel 51 (47-55), Sgel I 31 (29-33), Sgel II 46 (41-51), StI 25 (24-27), Sgel V 80 (77-85), StIV 49 (44-51), StIV 33 (29-36), ST1-ST3 47 (44-51), ST2-ST2 72 (66-76), ST5-ST5 111 (104-118), length of ventrianal shield 108 (102-117), width at ZV2 level 130 (126-140), width at anus level 117 (114-122), length of cervix of spermatheca 14 (13-15), length of fixed digit 31 (29-34) with 11 teeth, length of movable digit 35 (34-36) with 3 teeth.

The measurements of one of the 2 adult males collected are: dorsal shield length 287, width 217, j1 13, j3 27, j4, j5, j6 and J 2 1 , J 5 4 , z2, z4, z5 5, Z1 and Z4 1, Z5 62,
Neoseiulus anonymus (Chant & Baker)


**Neoseiulus anonymus** Denmark & Muma 1973: 265.

Specimens Examined: GUADELOUPE - Matouba, VI-1988, on Fragaria sp., S. Simon leg.

Previous Records: Brazil, Colombia, Cuba, Guatemala, Honduras, Mexico and Peru.

Remarks: The measurements of a single adult female collected are: dorsal shield length 312, width 144, \( j_1 \) 19, \( j_3 \) 38, \( j_4 \) 36, \( j_5 \) 41, \( j_6 \) 51, \( j_2 \) 53, \( j_5 \) 10, \( z_2 \) 46, \( z_4 \) 46, \( z_5 \) 42, \( Z_1 \) 55, \( Z_4 \) 71, \( Z_5 \) 72, \( s_4 \) 58, \( S_2 \) 61, \( S_4 \) 51, \( S_5 \) 39, \( r_3 \) 36, \( R_1 \) 36, \( S_1 \) 62, \( S_1 \) 63, \( S_2 \) 69, \( S_T \) 60, \( S_T \) 62 and \( S_T \) 5 58, length of ventrianal shield 101, width at ZV2 level 77, width at anus level 72, length of cervix of spermatheca 12, length of fixed digit 22, length of movable digit 24.

**Fundiseius urquharti** (Yoshida-Shaul & Chant), Comb. nov.


Previous Records: Antigua (Type material - Yoshida-Shaul & Chant 1988).

Remarks: The measurements of the female specimens collected are similar to those of the holotype (only known female specimen of this species to date), except for the shorter \( j_3 \) and longer \( Z_4 \) and \( s_4 \). The average measurements of 5 adult females followed by the respective ranges (in brackets) are: dorsal shield length 376 (344-423), width 301 (286-324), \( j_1 \) 16 (13-18), \( j_2 \) 22 (19-25), \( j_4 \) 3 (1-6), \( j_5 \) 2 (1-5), \( j_6 \) 7 (6-9), \( z_2 \) 6 (5-6), \( z_5 \) 10 (8-11), \( z_4 \) 15 (14-17), \( Z_1 \) 7 (6-10), \( Z_5 \) 89, \( Z_4 \) 86 (86-89), \( s_4 \) 82 (80-86), \( S_2 \) 14 (11-17), \( S_4 \) 11 (10-11), \( S_5 \) 9 (6-10), \( r_3 \) 17 (13-18), \( R_1 \) 13 (11-14), \( S_T \) 39 (37-42), \( S_T \) 44 (42-46), \( S_T \) 71 (69-76), \( S_T \) 5 126 (121-130), length of ventrianal shield 145 (140-152), width at ZV2 level 206 (184-225), width at anus level 161 (130-178), length of cervix of spermatheca 11 (8-19), length of fixed digit 34 (33-34) with 10-12 teeth, length of movable digit 38 (37-38) with 2 teeth. The wide amplitude for the measured length of the cervix of the spermatheca relates to the difficulty in determining its distal end, because the sclerotization of this structure diminishes very slowly toward this portion.

**Phytoseiulus macropilis** (Banks)

**Laelaps macropilis** Banks 1905: 139.


Previous Records: Angola, Barbados, Brazil, Canary Islands, Cook Islands, Colombia, Cuba, Fiji, Guatemala, Hawaii, Jamaica, Mexico, New Caledonia, Panama, Peru, Puerto Rico and USA.
Remarks: The measurements of the adult females collected are similar to those provided by Denmark & Schicha (1983), except for the longer j5, j6, z4, s4 and r3. The average measurements of 3 adult females followed by the respective ranges (in brackets) are: dorsal shield length 328 (310-344), width 213 (199-230), j1 24 (23-25), j3 41 (38-46), j4 52 (48-56), j5 75 (72-77), j6 154 (145-165), j5 5, z2 9 (8-9), z4 57 (55-60), z5 9 (6-13), Z1 107 (98-114), Z4 126 (118-135), Z5 109 (98-114), s4 174 (163-185), s5 28 (27-28), r3 and R1 24 (23-25), SgeI 47 (44-52), SgeII 31 (28-32), SgeIII 31 (30-32), StI-II 28 (25-29), SgelV 77 (72-79), StIV 37 (34-41), StIV 109 (104-114), ST1-ST3 65 (64-67), ST2-ST2 74 (70-76), ST5-ST5 72 (70-75), length of ventrianal shield 91 (89-93), width at JV2 level 67 (61-75), width at anus level 66 (64-70), length of proximal, inflated portion of the cervix of spermatheca, 13 (11-14), length of remaining sclerotized, distal portion of cervix 19 (18-22), length of fixed digit 22 (20-23) with 9 teeth, length of movable digit 24 (23-24) with 3 teeth.

The measurements of 2 adult males collected are: dorsal shield length 241-267, width 127 (201-226), j1 19-20, j3 29-42, j4 38-50, j5 56-60, j6 116-121, j5 4-5, z2 8-10, z4 52-61, z5 10-11, Z1 75-83, Z4 89-95, Z5 80, s4 121-133, S5 28-29, r3 15-17, R1 18-20, SgelII 25, StI-II 24, SgelV 52, StIV 27, StIV 74-79, length of ventrianal shield 105-116, width at anterior corners 152-163, length of shaft of spermatodactyl 15-17.

Proprioseiopsis cannaensis (Muma)

Previous Records: Brazil, Colombia, Cuba, Ecuador, El Salvador, Guyana, New Caledonia, Paraguay and USA.
Remarks: The measurements of the adult females collected agree well with those of the holotype; however, similarly to specimens from Brazil (Moraes & McMurtry 1983), Colombia (Moraes & Mesa 1988) and Cuba (Moraes et al. 1991), S4 is shorter than in the holotype. The average measurements of 5 adult females collected followed by the respective ranges (in brackets) are: dorsal shield length 334 (316-343), width 264 (250-279), j1 25 (23-27), j3 67 (64-72), j4 5 (4-5), j5 5 (4-6), j6 10 (9-12), j5 9 (8-12), z2 38 (36-42), z4 24 (19-26), z5 5 (4-6), Z1 23 (19-25), Z4 110 (95-114), Z5 88 (77-101), s4 100 (95-112), S2 20 (13-23), S4 14 (14-15), S5 14 (13-17), r3 20 (18-24), R1 15 (13-17), SgelII 27 (22-32), StI-II 25 (19-24), SgelV 53 (46-60), StIV 35 (28-41), StIV 76 (70-83), ST1-ST3 52 (51-55), ST2-ST2 74 (70-76), ST5-ST5 95 (90-97), length of ventrianal shield 107 (91-117), width at ZV2 level 116 (113-121), width at anus level 101 (104-110), length of cervix of spermatheca 17 (12-19), length of fixed digit 31 (28-33), length of movable digit 32 (30-34).

Proprioseiopsis mexicanus (Garman)

Amblyseiopsis mexicanus Garman 1958: 75.
Specimens Examined: Saint François, XI-1987, on S. melongena infested with T. palmi; Matouba, VI-1988, on Fragaria sp., S. Simon leg.
Previous Records: Australia, Brazil, Colombia, Cuba, Hawaii, Mexico, New Zealand, Panama and USA.
Remarks: The measurements of the adult females collected are very similar to those of the holotype, provided by Moraes & McMurtry (1983). The average measurements of 5 adult females collected followed by the respective ranges (in brackets) are: dorsal shield length 335 (331-339), width 224 (212-241), j1 19 (15-22), j3 30 (24-34), j4 and j5 5 (4-7), j6 5 (5-6), J 5 9 (9-10), z2 12 (11-14), z4 10, z5 4 (4-5), Z1 6 (5-7), Z4 74 (72-76), Z5 103 (97-110), s4 59 (56-65), s2 and s4 9 (8-10), s5 9 (9-12), r3 11 (9-14), R1 9 (8-10), SgeI 23 (20-24), SgeII 24 (23-25), StI 22 (20-24), SgeV 49 (48-51), StIV 32 (27-36), StV 56 (51-60), ST1-ST3 60 (58-62), ST2-ST2 68 (65-74), ST5-ST5 66 (64-72), length of ventrianal shield 108 (103-114), width at ZV2 level 92 (86-97), width at anus level 85 (80-89), length of cervix of spermatheca 9 (6-10), length of fixed digit 33 (29-38), length of movable digit 31 (29-32). Fixed digit with 8 teeth; movable digit with 1 tooth.

The measurements of a single adult male collected are: dorsal shield length 279, width 194, j1 17, j3 24, j4 5, j5 4, j6 5, J 5 9, z2 and z4 11, z5 10, z1 8, z4 56, z5 74, s4 13, S2, S4 and S5 9, r3 10, R1 8, SgeI 19, SgeV 32, StIV 23, StIV 48, length of ventrianal shield 103, width at anterior corners 121, length of shaft of spermatodactyl 18.

Phytoseius (Phytoseius) rex DeLeon

Phytoseius rex DeLeon 1967: 12.
Phytoseius (Phytoseius) rex Denmark & Muma 1975: 295.
Previous Records: Guyana, Puerto Rico and Trinidad.
Remarks: The measurements of the specimens collected are very similar to those of the holotype, except for the slightly longer StIV. The average measurements of 5 adult females collected followed by the respective ranges (in brackets) are: dorsal shield length 285 (276-290), width 153 (149-156), j1 27 (26-29), j3 44 (41-48), j4 5 (5-7), j5, j6 and J 5 6 (5-7), z2 11 (7-12), z3 24 (22-29), z4 8 (7-10), z5 6 (5-7), Z4 73 (70-77), Z5 68 (62-72), s4 108 (101-110), s6 76 (72-79), r3 42 (41-46), SgeV 21 (19-22), StIV 48 (43-50), StV 30 (29-31), ST1-ST3 60 (58-60), ST2-ST2 72, ST5-ST5 68 (62-70), length of ventrianal shield 89 (84-96), width at ZV2 level 54 (50-58), width at anus level 53 (50-58), length of cervix of spermatheca 29 (24-36), length of inflated region of major duct adjacent to atrium 13 (17-17), length of fixed digit 25 (24-26), length of movable digit 26. Fixed digit with 3 teeth; movable digit with 1 tooth.
The measurements of 2 adult males collected are: dorsal shield length 214, width 127 (120-134), j1 19, j3 24-29, j4, j5 and j6 5, J 5 5-7, z2 7-10, z3 17, z4 and z5 5, Z4 38-41, Z5 34, s4 62-67, s6 43-48, r3 29-31, SgeV 12, StIV and StV 19-22, length of ventrianal shield 79-91, width at anterior corners 127, length of shaft of spermatodactyl 12-14.

Phytoseius (Phytoseius) woodburyi DeLeon

Phytoseius (Phytoseius) woodburyi DeLeon 1965: 130.
Phytoseius (Dubininellus) woodburyi Denmark 1966: 64.
Phytoseius (Phytoseius) woodbury Muma and Denmark 1968: 236.
Specimens Examined: MARTINIQUE - Fort-de-France, I-1987, on Hibiscus sp., B. Hostachy leg.
Previous Records: Colombia, Hawaii, India, Jamaica, Puerto Rico and Trinidad.
Remarks: The measurements of the specimens collected are similar to those of the holotype. The average measurements of 6 adult females collected followed by the respective ranges (in brackets) are: dorsal shield length 286 (283-293), width 160 (156-163), j1 29 (26-31), j3 31 (29-31), j4 and j5 5 (5-7), j6 6 (5-7), j5 7, z2 12 (7-14), z3 31 (29-34), z4 11 (10-14), z5 5 (5-7), Z4 89 (82-94), Z5 69 (65-72), s4 121 (115-130), s6 81 (77-86), r3 44 (43-48), StiIV 49 (48-50), Stiv 25 (22-29), ST1-3 53 (48-55), ST2-ST2 61 (60-62), ST5-ST5 61 (58-65), length of ventrianal shield 87 (84-91), width at ZV2 level 35 (34-36), width at anus level 48 (46-50), length of cervix of spermatheca 4 (2-5), length of fixed digit 23 (22-24), length of movable digit 21 (19-22).

Fixed digit with 3 teeth; movable digit with 1 tooth.

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CHEMICALLY-MEDIATED ATTRACTION OF THREE PARASITOID SPECIES TO MEALYBUG-INFESTED CASSAVA LEAVES

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ABSTRACT

We investigated whether cassava plants that are infested by the cassava mealybug, Phenacoccus herreni (Pseudococcidae, Sternorrhyncha), emit attractants for the encyrtid parasitoids Aenasius vexans Kerrich, Apoanagyrus (Epidinocarsis) diversicornis Howard, and Acerophagus cocois Smith. Bioassays with a Y-tube olfactometer showed for all three species that female wasps were most responsive and selective when they were 1.5 to 2.5 days old. Females of these age groups were used to test their ability to distinguish between the odor of plants with and without mealybugs. The wasps were offered choices between infested cassava leaves vs. healthy ones, infested leaves vs. clean air, and healthy leaves vs. clean air. A. vexans and A. diversicornis were strongly attracted to infested leaves and preferred these over healthy ones. In contrast, A. cocois was significantly attracted to either healthy or infested leaves, and did not distinguish between the two. The results suggest that A. cocois, which has the broadest known host range of the three, may be responsive only to general plant odors, while A. vexans and A. diversicornis respond more specifically to odors associated with mealybug infestation.

Key Words: Aenasius vexans, Apoanagyrus (Epidinocarsis) diversicornis, Acerophagus cocois, cassava (Manihot esculenta), host location, semiochemicals

RESUMEN

Se investigó si las plantas de yuca que son infestadas por el piojo harinoso, Phenacoccus herreni (STERNORRHYNCHA: Pseudococcidae), emiten sustancias atractivas para los parasitoides Encyrtidae Aenasius vexans, Apoanagyrus (Epidinocarsis) diversicornis y Acerophagus cocois. Ensayos con un tubo olfactómetro en Y mostraron que las tres especies tienden a responder y seleccionar más frecuentemente cuando tienen de 1.5 a 2.5 días de edad. Las hembras de esta edad fueron usadas para determinar su capacidad de distinguir entre el olor de plantas con y sin piñones. Se ofreció a las hembras olores de yuca infestadas o limpias, hojas infestadas o aire puro y hojas limpias o aire puro. A. vexans y A. diversicornis fueron atraídas fuertemente por las hojas infestadas y presentaron preferencia por estas hojas contra las hojas limpias. En contraste, A. cocois fue atraída de manera significante por hojas limpias u hojas infestadas contra aire, y no pudo distinguir entre ambos olores. Los resultados sugieren que A. cocois, que tiene el más alto rango de huéspedes de los tres, puede responder sólo a los olores generales de las plantas, mientras A. vexans y A. diversicornis responden más específicamente a los olores asociados con la presencia de los piojos harinosos.
Cassava mealybugs are among the most damaging pests of cassava in South America and Africa (Vargas & Bellotti, 1984). The two most important species are *Phenacoccus herreni* Cox & Williams and *P. manihoti* Matile-Ferrero (Sternorrhyncha: Pseudococcidae), which both originate from South America (Cox & Williams, 1981; Bellotti et al., 1984). *P. herreni* appeared as a problem rather suddenly in Northeast Brazil in the mid-1970s and was then reported from Colombia, Venezuela and Guyana (CIAT, 1984; 1987; 1988; 1990); it can cause root yield losses up to 80% (Bellotti et al., 1984; Bellotti, 1983). In Africa, the closely related *P. manihoti* became a serious pest in most of the cassava growing regions after its accidental introduction in the 1970s (Matile-Ferrero, 1977; Herren & Neuenschwander, 1991). For both pest species biological control programs have been developed. The encyrtid parasitoid *Apoanagyrus* (*Epidinocarsis*) *lopezi* (De Santis) was successfully released in Africa in the 1980s. It established and now maintains the mealybug population at an acceptable low-density in most regions (Herren & Neuenschwander, 1991; CIAT, 1992). For the 5% of the African cassava fields where the parasitoid has not been effective in controlling the mealybug (Neuenschwander et al., 1991), alternative control agents were investigated such as two strains of the coccinellid predator *Hyperaspis notata* Mul-sant (Stäubli Dreyer et al., 1997a; 1997b; 1997c).

Natural enemies of *P. herreni* have been systematically collected for the control of the mealybug in South America, and laboratory colonies of three encyrtid parasitoids were established at CIAT (Centro Internacional de Agricultura Tropical), in Cali, Colombia. These parasitoids are *Aenasius vexans* Kerrich, *Apoanagyrus* (*Epidinocarsis*) *diversicornis* Howard (asexual strain) and *Acerophagus coccois* Smith (CIAT, 1982; 1983; 1990). Knowledge on the biology of these insects is limited. Published information is mostly restricted to CIAT reports (1982-1992).

At the beginning of this century, studies showed that parasitic wasps use olfaction to locate hosts and that they may first be attracted to the food that their hosts feed on (Picard & Rabaud, 1914; Thorpe & Jones, 1937; Thorpe & Caudle, 1938). More recently, it was demonstrated that herbivore-damaged plants can play a key role in attracting enemies of insect herbivores (Dicke et al., 1990; Turlings et al., 1990; 1995; Vet & Dicke, 1992). For example, lima bean plants under spider mite attack release specific volatiles that are attractive to predatory mites (Dicke et al., 1990) and similar volatile compounds released by caterpillar-infested maize plants are used by parasitoids to locate caterpillars (Turlings et al., 1990).

Volatiles emitted by mealybug-infested plants are also suspected to attract natural enemies of the mealybug (Nadel & van Alphen, 1987). Changes in chemicals produced by the cassava plant due to *P. manihoti* infestation have been reported by Calatayud et al. (1994). Such changes could result in the emission of volatiles and explain why *A. lopezi* and *A. diversicornis* (sexual strain) are attracted by *P. manihoti*-infested cassava plants (Nadel & van Alphen, 1987; van Alphen et al., 1990). The feeding behavior of *P. herreni* is very similar to that of *P. manihoti* (Castillo & Bellotti, 1990), and it can be expected that they evoke similar reactions in the cassava plant. However, studies with the asexual strain of *A. diversicornis* of South America by Hofstee et al. (1993) showed no response by this parasitoid to the odor of *P. herreni*-infested cassava plants (var. Odungbo). A better understanding of the interactions between cassava plants, mealybugs, and parasitoids requires more behavioral as well as chemical studies.

In this paper, we report on olfactometer studies with the three encyrtid parasitoids reared at CIAT, *A. vexans*, *A. diversicornis* (asexual strain), and *A. coccois*. The studies were conducted to determine whether these parasitoids are attracted to odors that may emanate from cassava plants infested by *P. herreni*.
Plants
CMC40 cassava stakes (20 cm long) were planted every week in pots and kept in a screened compartment, where they were subjected to natural weather conditions at Palmira, Colombia, though protected from rain. The plants were used in experiments when they carried 10-30 leaves (approximately 6 weeks after planting).

Insects
The cassava mealybug, *P. herreni* was reared at CIAT on potted cassava plants (var. CMC40). Every week 30-40 cm high plants were infested with 15 mealybug ovisacs, as described by van Driesche et al. (1987). The plants were separated in different cages based on the age of the mealybugs they carried.

The parasitoids, *A. vexans*, *A. diversicornis* and *A. coccis* were continuously reared at CIAT on mealybug-infested cassava plants (var. Mcol 1505). The colonies of *A. vexans* and *A. coccis* were initiated with insects collected in Venezuela in 1990 and the colony of *A. diversicornis* with insects from Colombia (1984). The colonies were maintained in a greenhouse at 35°C and under natural light conditions.

The Olfactometer
A Y-tube olfactometer similar to the one first described by Sabelis & van de Baan (1983) was used in our experiments (Fig. 1). Two arms of a glass Y-shaped tube were connected to glass chambers (6.5 cm diam.) in which odor sources could be placed. Activated charcoal filtered air at a rate of 400 ml/min was pushed into each glass chamber. To avoid visual distractions and to diffuse the light, a wooden frame covered with white cloth was placed around the Y-tube. A lamp (100 watt) was placed outside this visual barrier opposite from the entrance where the insects were introduced. As these parasitoids are attracted by light, the lamp helped to induce the insects to walk upwind in the direction of the odor sources. When a female reached the center of the Y-tube, where the three arms met, she could choose one of the offered odors.

Odor Sources
Every week ovisac-infested cassava plants were transferred into a greenhouse, where they were kept in nylon cages for three weeks before being used for the Y-tube experiments. Control (healthy) plants were transferred weekly from the screened compartment and enclosed in a nylon screen cage in the same greenhouse as the infested plants. Care was taken that no mealybugs came in contact with healthy plants. To serve as an odor source, two leaves of either infested or healthy plants were cut off and the cut ends were wrapped in wet cotton wool. The leaves were carefully placed in one of the odor chambers. The infested leaves that were selected carried honeydew and sooty mold, as well as mealybugs and exuviae.

Experimental Procedure
On the day of each experiment, parasitoid females were removed from their cage and kept in a glass jar (400 ml) with some honey. The jar was placed in the air-conditioned chamber (28-30°C) where the experiments would take place. The insects were left one or two hours in their new environment to become adjusted. Before each olfactometer test, female parasitoids were allowed to parasitize a mealybug on a cassava leaf. An infested cassava leaf was placed upside down in a petri dish and several fe-
males were introduced and observed until they had parasitized, or at least stung a mealybug. The parasitoids were given this experience as it may increase their responsiveness to host-related odors (Turlings et al., 1993; Vet et al., 1995, Steinberg et al., 1992). The parasitoids were then captured in a gelatin capsule and kept there for 10 to more than 60 minutes. Before each Y-tube test, the gelatin capsule was opened and inserted at the base of the Y-tube. Females were introduced and were observed indi-
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vidually in the olfactometer and used only once. The odor sources were reversed each time three wasps had been tested.

Evaluation of Choices

A stopwatch was started when the insect left the gelatin capsule. The female was allowed 5 minutes to walk up the no-choice-area (Fig. 1) to reach the center of the olfactometer, which is the area where the three arms meet. If a female did not reach this center within 5 minutes, she was counted as a "no-choice". For the other females, the observation was stopped 5 minutes after they had made it to the center, or after they had reached the end of one of the arms. Each arm, was divided into four zones (Fig. 1), which measured 8, 6, 6, and 3 cm, respectively.

A female had to enter at least zone 2 (Fig. 1) to be considered to have made a choice. A few females switched arms after reaching zone 2. In those cases, females were considered to choose the arm which they entered the furthest. For statistical analyses, a chi-square test was applied, using the total number of females that made a choice for a particular odor ($\alpha = 0.05$).

PROCEDURES AND RESULTS

The Effect of Wasp Age

It has been shown that the responsiveness to odors may change when parasitoids get older (e.g. Thorpe & Caudle, 1938; Steinberg et al., 1992). To determine the optimal age of our parasitoids for olfactometer bioassays, parasitoid females of different ages were tested. Newly emerged wasps were isolated daily at about noon and transferred to Plexiglas® cages in which they were provided honey and water. The insects remained in the cage until they had reached a certain age. Six different age classes were tested, varying from 0.5 to 6.5 days after emergence. Each wasp was given an oviposition experience, and then introduced into the olfactometer, in which they had a choice between the odors of infested and healthy cassava leaves.

Responsiveness, i.e. proportion of females that made a choice, did not decrease with increasing age of females. Overall it was high for A. diversicornis with an average of 73% and medium to low for both A. vexans and A. coccois with an average of respectively 49 and 48% of the responding females.

Preference for an odor source changed in two of the three species (Fig. 1-3). In A. vexans and A. diversicornis, the preference for the odor of infested leaves over odor of healthy leaves was age dependent and significant for young females only. Of the younger (1.5-2.5d old) A. vexans females, 80% preferred infested cassava leaf odors ($\chi^2 = 7.2, P < 0.01$). The youngest A. diversicornis (0.5-1.5d) showed the clearest preference (82.6%) for the odor of infested leaves over the odor of healthy leaves ($\chi^2 = 9.78, P < 0.005$), but 17.4% of the females that made a choice switched between arms before making a final decision. The 1.5 to 2.5-day-old A. diversicornis switched arms much less (3.8%), but exhibited a weaker preference for odors of infested leaves (69.2%, $\chi^2 = 3.85, P < 0.05$). The older wasps showed no significant preference. All age classes of A. coccois did not differentiate between infested and healthy plant odors. Like A. diversicornis, A. coccois walked a lot in the olfactometer, often switching between arms (26.3% of the choosing females).

The Role of Plant Odors

In a subsequent series of experiments we more specifically determined the relative attractiveness of healthy and infested cassava leaves. Based on the results of the pre-
Fig. 2. Age dependency of response. Choices by A. vexans females of different age classes between the odors of mealybug-infested and healthy cassava leaves in a Y-tube olfactometer. In each bar the actual number wasps that made a particular choice is given, while the x-axis indicates the percentages of choosing wasps that the numbers represent. To the right of the bars is the proportion of females that made a choice for one of the two odors, as well as the total number of females that were tested per age class.
Fig. 3. Age dependency of response. Choices by A. diversicornis females of different age classes between the odors of mealybug-infested and healthy cassava leaves in a Y-tube olfactometer. In each bar the actual number wasps that made a particular choice is given, while the x-axis indicates the percentages of choosing wasps that the numbers represent. To the right of the bars is the proportion of females that made a choice for one of the two odors, as well as the total number of females that were tested per age class.
vious experiments, only females that were 1.5 to 2.5 days old were used. On a given day
three different pairs of odor sources were tested, namely "Infested vs. Healthy", "Infested vs. Blank", and "Healthy vs. Blank". In the case of "Blank", one arm introduced clean air that had passed through an odor chamber with just a piece of wet cotton wool. For each pair of odor sources, 4 to 6 insects per day were individually tested in the Y-tube. Occasionally, another series of 6 insects per odor source was tested the same day.

A. vexans females were significantly attracted to infested cassava leaves compared to healthy ones or a blank (Fig. 5a). Healthy leaf odors were less attractive, since only 64.5% of the females responded in the "Healthy vs. Blank" test without showing a significant preference for one of the two odor sources ($\chi^2 = 2.5$, $P > 0.05$).

A. diversicornis females were significantly attracted to infested and healthy cassava leaves when offered against a blank. They also showed a significant preference for infested cassava plant odors over healthy ones ($\chi^2 = 6.08$, $P < 0.025$).

Only 51.7 to 58.3% of A. coccois females made a choice, but these were significantly attracted by healthy and infested plant odors when offered against a blank ($\chi^2 = 7.53$, $P < 0.01$ and $\chi^2 = 11.65$, $P < 0.001$). In the "Infested vs. Healthy" test, the choosing females very often switched sides before going up one arm, and they showed no significant preference for either odor source ($\chi^2 = 0.26$, $P > 0.05$) (Fig. 5c).

**DISCUSSION**

The preference of female wasps to plant odors in the olfactometer was age dependent for A. vexans and A. diversicornis. The younger age classes of both these species significantly preferred the odor of infested leaves, while older females showed no particular preference. The preferences exhibited by young A. vexans and A. diversicornis may have been due to the experience that the wasps received with an infested leaf just before their introduction into the olfactometer. During such an experience the females may learn to respond to the odors that they encounter through a process of association (Turlings et al., 1993; Vet et al., 1995), which may be age dependent. Some parasitoids only learn as young adults (Kester & Barbosa, 1991), which could explain why older wasps did not make a distinction in our tests. It is possible that if these older wasps had been given an experience at a younger age, they would have shown a preference as well. In the subsequent experiments only younger females were used.

For A. coccois, the lack of preference of females of any age class may be due to the particular choice offered. This species obviously did not distinguish between infested and healthy cassava leaves. An alternative choice, such as between plants and a blank might have revealed a similar age dependency of the response as found for the two other species.

All three species distinguished between plant material and clean air (blank). A. vexans showed only a marginal attraction to healthy leaves, but was strongly attracted to infested leaves. A. diversicornis was attracted to healthy leaves, but preferred the odor of infested leaves. A. coccois was also attracted to both healthy and infested leaves, but did not distinguish between these two odor sources. These differences in response of the three encyrtid parasitoids suggest that they may employ different foraging strategies. A. vexans and A. diversicornis recognized odors that are specifically associated with mealybug infestation. A. coccois, on the other hand, appeared to respond only to general cassava plant odors. It remains unknown if A. vexans and A. diversicornis are attracted to odors emanating directly from the mealybugs or if the infested plants emit the attractive odors.

In the petri dish, where females were experienced by giving them the opportunity to walk over a cassava leaf and sting a mealybug, A. vexans walked slower, but showed a more direct orientation towards mealybugs. This slower, but directed searching be-
Fig. 4. Age dependency of response. Choices by A. cocois females of different age classes between the odors of mealybug-infested and healthy cassava leaves in a Y-tube olfactometer. In each bar the actual number wasps that made a particular choice is given, while the x-axis indicates the percentages of choosing wasps that the numbers represent. To the right of the bars is the proportion of females that made a choice for one of the two odors, as well as the total number of females that were tested per age class.
Fig. 5. Responses of the three parasitoid species. (A) *A. vexans*, (B) *A. diversicornis* and (C) *A. coccois* in a Y-tube olfactometer. The wasps were offered choices between the odors of clean air vs. healthy leaves, clean air vs. infested leaves, and healthy leaves vs. infested leaves. In each bar the actual number wasps that made a particular choice is given, while the x-axis indicates the percentages of choosing wasps that the numbers represent. Next to the bars the proportion is given of the females that made a choice for one of the two odors, as well as the total number of females that were tested per choice.
behavior was also observed in the olfactometer. *A. vexans* was clearly attracted to the infested cassava plants, but not to the odors of healthy plants. After it found a mealybug, this solitary parasitoid needed only a few seconds to parasitize it. *A. coccoides* is gregarious and took up to an hour to parasitize a host. It spent a lot of time walking rapidly around the petri dish and had fewer encounters with mealybugs. Also in the olfactometer, this species walked much faster and in more different directions than the other species, particularly when the females were given the choice between infested and healthy plant odors. This fast moving species did not readily distinguish between the odors of infested and healthy leaves.

The reported host preference of these parasitoids may explain their behavior in the olfactometer to some extent. *A. vexans* prefers *P. herreni* over a related species, *Phenacoccus gossypi* (= madeirensis) (CIAT, 1990). It has been most frequently recovered from *P. herreni* on cassava, but its host range does include other *Phenacoccus* species on different plants (Noyes & Ren, 1995). Pijls & van Alphen (1996) studied the specificity of a sexual strain of *A. diversicornis* on cassava. It appears to be specific to *P. herreni* and *P. manihoti*. An asexual strain from Venezuela has been shown to prefer *P. herreni* over *P. gossypi* (= madeirensis) (Van Driesche et al., 1987). *A. coccoides* seems to be the most polyphagous of the three. It parasitizes *Pseudococcidae* species of different genus such as *Oraclia acuta* (Hemiptera: Pseudococcidae) on loblolly pine (*Pinus taeda* L.) (Clarke et al., 1990). On cassava plants, it parasitizes *P. herreni* and *P. madeirensis* more or less equally (CIAT, 1990). As a generalist, *A. coccoides* may be more responsive to general plant odors, while the more specialized wasps, *A. vexans* and *A. diversicornis*, may have adapted to exploit odors that are specifically associated with the presence of mealybugs on cassava.

It remains to be determined if cassava volatiles play an important role in the specific attraction to infested plants, or if the mealybug and its by-products emit odors that are attractive. It is known that some herbivores induce reactions in plants that make them highly attractive to some parasitic wasps (Turlings et al., 1995). Nadel & van Alphen (1987) found evidence that mealybug-infested cassava plants also release odors that are attractive to the parasitoid *A. lopesi*. The odors probably come from the plant itself, as the parasitoid was not attracted by the mealybug and its by-products. Van Alphen et al. (1990) also found an attraction to *P. manihoti*-infested cassava plants by *A. diversicornis*. Unlike our results, the females were not attracted by healthy cassava plants but showed a clear attraction to uninfested leaves taken from a partially infested plant, which suggests that the infested plant emits attractants. Little is known about the exact source and identity of parasitoid attractants. Our ongoing experiments aim to determine the exact role of the cassava plant in the foraging success of the parasitoids in order to consider and exploit this role in further control measures against the cassava mealybug.

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EFFICACY OF BACILLUS THURINGIENSIS AND CABBAGE CULTIVAR RESISTANCE TO DIAMONDBACK MOTH (LEPIDOPTERA: YPONOMEUTIDAE)

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ABSTRACT

Population density estimates were used to determine the effectiveness of a commercial formulation of Bacillus thuringiensis Berliner subsp. kurstaki and aizawai (Agree 50 WP®) and host plant resistance in three cabbage cultivars against the diamondback moth, Plutella xylostella (L.). Cabbage plots treated with Agree 50 WP® had significantly fewer larvae per plant compared with untreated ones. The ranking from most to least susceptible of the three main cabbage cultivars grown in Jamaica was ‘KY Cross’ > ‘Early Jersey’ > ‘Tropicana’. These findings provide evidence that a new cabbage hybrid, ‘Tropicana’, and products containing effective strains of B. thuringiensis may be successfully used for P. xylostella management in Jamaica.

Key Words: P. xylostella, Agree 50 WP®, plant resistance, Jamaica

RESUMEN

Fueron usados estimados de la densidad poblacional para determinar la efectividad de una formulación comercial de Bacillus thuringiensis Berliner subsp. kurstaki y aizawai (Agree 50 WP®) y la resistencia de tres cultivares de col a la polilla Plutella xylostella (L.). Las parcelas de col tratadas con Agree 50 WP® tuvieron significativamente menos larvas por planta que las no tratadas. El rango de susceptibilidad en orden decreciente de los tres cultivares más usados en Jamaica fue ‘KY Cross’ > ‘Early Jersey’ > ‘Tropicana’. Estos hallazgos muestran que un nuevo híbrido de col, ‘Tropicana’, y productos conteniendo cepas efectivas de B. thuringiensis podrían ser exitosamente usados para el manejo de P. xylostella en Jamaica.

Cruciferous vegetables grown in Jamaica and other Caribbean islands are susceptible to damage by many insect pests: armyworms, Spodoptera spp., cabbage looper, Trichoplusia ni (Hubner), cabbage white butterfly, Pieris rapae L., and diamondback moth, Plutella xylostella (L.). A complex of these pests occurs whenever these crops are grown for commerce, and their control is a prerequisite for meeting quality standards for damage- and pest-free produce. Populations of P. xylostella frequently account for 75% of the insect pest population and cause crop loss of up to 90%, making it the key insect pest from an economic standpoint (Salinas 1986, Alam 1992).

Historically, farmers have relied primarily on multiple applications of broad-spectrum insecticides for control of P. xylostella in Jamaica. Alam et al. (1987) recommended an action threshold of six larvae per plant at the post-transplanting stage of cabbage. Over 18 different insecticides have been used since 1972 (Walton 1989), and between 20-22 insecticide applications over a growing season are not uncommon. As a result, many insecticides from the organophosphate, carbamate, and pyrethroid groups are now ineffective because of insecticide resistance (Alam 1992, Robinson et
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al. 1995). Reports of low efficacy of Biotrol® and Thuricide® (products containing the kurstaki strain of Bacillus thuringiensis Berliner) in controlling P. xylostella, presumably due to insecticide resistance, led Alam (1992) to question their reliability. Because of pest management problems, environmental degradation, and occupational and public health risks associated with insecticides, it is imperative to find an integrated pest management (IPM) approach for P. xylostella management which utilizes tactics such as host plant resistance and microbial control.

The utility of host plant resistance as an insect pest management tactic is well established (Painter 1951, Lim 1992). Dickson et al. (1984, 1986) reported the release of four cabbage breeding lines possessing resistance to P. xylostella. Results of genetic and other studies indicated that the host plant resistance exhibited by these cabbage breeding lines was associated with the glossy dark-green leaf found in the cauliflower Plant Introduction (PI) 234599 (Dickson et al. 1990, Stoner 1990, Eigenbrode & Shelton 1992). However, P. xylostella-resistant cabbage cultivars are not generally commercially available. Use of microbial agents for controlling P. xylostella has been most successful with B. thuringiensis; certain strains of this bacteria are highly effective against early instars (Hofte & Whiteley 1989). Furthermore, B. thuringiensis is environmentally benign and non-toxic to beneficial organisms, many of which are natural enemies of P. xylostella. Because the kurstaki strain of B. thuringiensis is already of questionable reliability in Jamaica (Alam 1992), and field resistance in P. xylostella has been reported in the Philippines (Kirsch & Schmutterer 1988), Hawaii (Tabashnik et al. 1990), Malaysia (Syed 1992), mainland USA (Shelton et al. 1993), and in Central America (Perez & Shelton 1997), it is unwise for farmers to rely solely on this microbial insecticide. To thwart the development of resistance to this insecticide and preserve its longevity and effectiveness, a more integrated approach should be developed. Combining the use of B. thuringiensis and host plant resistance for P. xylostella control is plausible. A new product, Agree 50 WP® (wettable powder), containing both kurstaki and aizawai strains of B. thuringiensis and a new cabbage cultivar, 'Tropicana', reputed resistant to P. xylostella, has recently become available to farmers. Before the advent of this new cultivar, two hybrids ('KY Cross' and 'KK Cross') and an open-pollinated cultivar ('Early Jersey') were available to growers in Jamaica. In 1995, marketing of 'Tropicana' began by the leading distributor of agricultural inputs with claims of resistance to P. xylostella. However, the relative resistance of these cultivars to P. xylostella, under local conditions, has not been empirically studied. Therefore, toward achieving our long range goal of IPM of P. xylostella, the objective of this study was to determine the efficacy of Agree 50 WP® and evaluate the relative resistance of cabbage cultivars grown in Jamaica to P. xylostella.

Materials and Methods

In September 1995, a field experiment was initiated on the farm of the College of Agriculture, Science, and Education, Port Antonio, Portland, Jamaica. Three cabbage cultivars, 'Tropicana', 'Early Jersey' (Petoseed, Saticoy, CA), and 'KY Cross' (Takii Seed, Kyota, Japan), were subjected to two different treatment regimes: Agree 50 WP® (Ciba-Geigy, Greensboro, NC) applied weekly and untreated controls. Cultivars and treatments were replicated four times in a completely randomized experimental design with a split-plot treatment arrangement. Main plots were cultivar and sub-plots were Agree 50 WP® and untreated controls. Individual plots were 2.73 m × 4.45 m and were separated by a distance of 1.52 m. Four-week-old seedlings of the three cabbage cultivars, raised in outdoor seedbeds, were planted 0.45 m apart on raised beds spaced 0.91 m apart. Standard cultivation practices for cabbage production were employed. Plots were sampled for P. xylostella once per week for seven weeks, between 18 No-
vember and 30 December, by counting larvae on the leaves of 10 plants in each plot. Agree 50 WP® (3.8% (AI) (25,000 IU per ml) (B. thuringiensis subsp. kurstaki and aizawai)), was applied to the appropriate plots once per week, at the rate of 83 g in 15 liters of water using a Solo 475 Knapsack Sprayer (Solo Incorporated, Newport News, VA). The data were subjected to analysis of variance using PROC GLM (SAS Institute 1989).

RESULTS

P. xylostella larval population density per plant was significantly affected by cabbage cultivar \( (F = 20.94; \text{df} = 2, 18; P = 0.0001) \) and insecticide treatment \( (F = 52; \text{df} = 1, 18; P = 0.00001) \). The ranking of cultivars from most to least susceptible to P. xylostella was ‘KY Cross’ > ‘Early Jersey’ > ‘Tropicana’. Plots treated weekly with Agree 50 WP® had significantly \( (F = 52; \text{df} = 1, 18; P = 0.00001) \) fewer larvae per plant compared with untreated plots (Table 1).

The interaction between cabbage cultivar and insecticide treatment was marginally significant \( (F = 3.38; \text{df} = 2, 18; P = 0.0567) \). Further examination of this interaction was done using PROC PLOT (SAS Institute 1989). The cell means for the levels of the two factors, insecticide treatment and cabbage cultivar, as shown in Table 1, indicated that the ‘Tropicana’ cultivar supported fewer larvae per plant across insecticide treatments compared with the other two cultivars.

DISCUSSION

Based on larval population density estimates, the ‘Tropicana’ cultivar was superior to the other two cultivars in resisting attack from P. xylostella. To our knowledge, before this study, cabbage cultivars available to growers in Jamaica had never been evaluated under local conditions regarding their relative susceptibility to P. xylostella. The existence of host plant resistance to P. xylostella in a commercially cultivated cabbage cultivar, such as ‘Tropicana’, is significant because of the economic importance of this insect pest related to the intractable problem of its widespread development of resistance to conventional insecticides. Several authors have reported on breeding and the potential for using resistant cabbage cultivars for P. xylostella management (Dickson et al. 1984, 1986, 1990, Stoner 1990, Eigenbrode & Shelton 1992), but host plant resistance in a commercially available cabbage cultivar has hitherto not been reported.

It appears that the ability of the ‘Tropicana’ cabbage cultivar to resist P. xylostella is based on leaf texture; the epidermis of its leaves is relatively thicker, especially as plants approach the heading stage, compared with those of the other two cultivars. Importantly, there have not been any reports of complaints from consumers regarding the texture of ‘Tropicana’. Because first instars of P. xylostella are leafminers and must tunnel into the leaf to feed, the thicker epidermis of ‘Tropicana’ may have been too great a challenge for the mandibles of neonate larvae. These neonates may starve to death, desiccate, drown or be washed from leaves, and be vulnerable to predators. Eigenbrode and Shelton (1992) found that neonate P. xylostella larvae had greater movement on resistant cabbage breeding lines than on susceptible ones. Also, Tanton (1962) found that leaf texture affects the number of nibbles and subsequent leaf area of Brassica rapa L. consumed by Phaedon cocklelae F. In addition, Iheagwam (1981) reported that penetrability of the leaf tissue of Brassica oleracea L. influences the degree of exploitation by Aleyrodes brassicae Walker. And, Martin et al. (1975) found a negative correlation between internode hardness of Saccharum officinarum L. and susceptibility to attack by neonate Diatraea saccharalis (F.) larvae.
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Agree 50 WP® proved to be effective in controlling P. xylostella. This was probably due primarily to the presence of the aizawai strain of B. thuringiensis. There are differences in the crystal protein toxin profiles of B. thuringiensis subsp. kurstaki and subsp. aizawai; the former produces Cry IA (a), Cry IA(b), Cry IA(c), Cry IIA, and Cry IIB, whereas the latter produces Cry IA (a), Cry IA(b), Cry IC, Cry ID, and Cry IIB (Hofte & Whiteley 1989). Shelton et al. (1993) found differential responses between P. xylostella populations treated with two formulations containing B. thuringiensis subsp. kurstaki (Javelin WG® and Dipel 2X®) and populations treated with B. thuringiensis subsp. aizawai (ZenTari®). Commercial formulations of B. thuringiensis subsp. kurstaki, for example, Biotrol® and Thuricide®, have been used in Jamaica for many years to control P. xylostella but their reliability is now questionable (Alam 1992). However, formulations of B. thuringiensis subsp. aizawai have only recently begun to be more widely used. So, P. xylostella populations have no prior exposure to this strain of B. thuringiensis. In fact, B. thuringiensis subsp. aizawai was first used against P. xylostella in Jamaica in 1995.

The existence of a significant interaction makes it necessary to exercise caution when making statements about the main effects (cabbage cultivar and insecticide treatments), even though both were statistically significant with \( P \) values of 0.0001 (Freund & Wilson 1993). The consistently lower numbers of larvae on the ‘Tropicana’ cultivar, compared with ‘Early Jersey’ and ‘KY Cross’, across plots treated with Agree 50 WP® and in untreated plots, clearly show that the ‘Tropicana’ cultivar was superior to the other two cultivars in resisting P. xylostella. Also, from the interaction between cabbage cultivar and insecticide treatment, it can be inferred that the ‘Tropicana’ cultivar may be compatibly combined with use of Agree 50 WP® for successful management of P. xylostella.

Regarding the effect of these two control tactics on armyworms and cabbage looper, past experience has shown that tactics which are successful in controlling P. xylostella simultaneously also controlled armyworm and cabbage looper populations. Usually, insecticides are more effective against other insects in the crucifer pest complex than P. xylostella. In fact, for the duration of the study, armyworms and cabbage loopers were not encountered.

Considering the low efficacy and tenuous reliability of commercial formulations of B. thuringiensis subsp. kurstaki against P. xylostella in Jamaica (Alam 1992), the effectiveness of Agree 50 WP® (B. thuringiensis subsp. kurstaki and aizawai) seen in this study makes continued use of toxins of B. thuringiensis for controlling this insect a viable option, especially when combined with the ‘Tropicana’ cabbage cultivar. How

<table>
<thead>
<tr>
<th>Cultivar</th>
<th>No. larvae per plant</th>
<th>Overall cultivar means ± SEM²</th>
<th>Tropicana</th>
<th>Early Jersey</th>
<th>KY Cross</th>
<th>Overall treatment means ± SEM¹</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Agree 50 WP®</td>
<td>Untreated</td>
<td>0.30 ± 0.21</td>
<td>1.55 ± 0.39</td>
<td>0.93 ± 0.31</td>
<td></td>
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<tr>
<td>Tropicana</td>
<td></td>
<td></td>
<td>0.30 ± 0.21</td>
<td>1.55 ± 0.39</td>
<td>0.93 ± 0.31</td>
<td></td>
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<tr>
<td>Early Jersey</td>
<td></td>
<td></td>
<td>0.88 ± 0.25</td>
<td>4.23 ± 0.33</td>
<td>2.55 ± 0.66</td>
<td></td>
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<tr>
<td>KY Cross</td>
<td></td>
<td></td>
<td>2.23 ± 0.70</td>
<td>4.95 ± 0.40</td>
<td>3.59 ± 0.64</td>
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<tr>
<td>Overall</td>
<td></td>
<td></td>
<td>1.13 ± 0.34</td>
<td>3.58 ± 0.48</td>
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</tr>
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</table>

¹Treatment means significantly different (ANOVA F test; \( a = 0.05 \)); ²Cultivar means significantly different (Waller-Duncan K-ratio t test; \( a = 0.05 \)).
ever, we do not recommend that formulations containing both the kurstaki and aizawai strains of B. thuringiensis, such as Agree 50 WP®, be used extensively as this may allow for the development of resistance in P. xylostella to the aizawai strain without losing its resistance to the kurstaki strain. It might be a better strategy to alternate both strains.

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ATTRACTION OF TOBACCO BUDWORM MOTHS 
(LEPIDOPTERA: NOCTUIDAE) TO JAGGERY, A PALM SUGAR 
EXTRACT

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ABSTRACT

Male tobacco budworm, Heliothis virescens Fab., moths released into a field cage were recaptured in traps baited with aged 10% jaggery, a palm sugar extract. Both male and female tobacco budworm moths were attracted to aged 10% jaggery in a flight tunnel, exhibiting oriented flights ending in contact with the bait. Although the bait was initially not attractive either to females in a flight tunnel or to males in a field cage, it subsequently became attractive after one week and increased in attractiveness for up to 24 days after it was made.

Key Words: attractant, feeding, Heliothis virescens, trap, behavior, sugar

RESUMEN

Machos adultos del gusano del tabaco, Heliothis virescens Fab., liberados en una jaula de campo fueron recapturados en trampas cebadas con 10% de jaggery envejecido, un extracto de azúcar de palma. Tanto hembras como machos adultos fueron atraídos por el cebo en un túnel de vuelo, y ambos mostraron vuelos orientados terminando en el contacto con el cebo. A pesar de que el cebo inicialmente no fue atractivo a las hembras en el túnel de vuelo, o a los machos en la jaula de campo, éste se tornó atractivo después de una semana e incrementó su atractividad hasta los 24 días de haber sido preparado.

The tobacco budworm, Heliothis virescens (Fab.), is a pest of several agricultural crops in North America, including tobacco and cotton. The principal means of monitoring the presence of tobacco budworm is a female sex pheromone blend that is attractive to males (Sparks et al. 1979, Ramaswamy et al. 1985). However, such a method is ineffectual in fields treated with female sex pheromone as a mating disruptant. Also, the relationship between numbers of males captured in pheromone traps and either population levels or crop damage is not clear. Additional attractants, particularly if effective for females, would be useful under such circumstances.

A variety of moths are attracted to sweet materials, presumably as a source of adult nutrition. Sugar-rich concoctions often are used by moth and butterfly collectors (Holland 1903, Sargent 1976). Molasses solutions have been used to trap oriental fruit moth, Grapholita molesta (Busck), (Frost 1926) and codling moth, Cydia pomonella (L), (Eyer 1931) in tree fruit orchards. Many noctuid moths are attracted to sugar
baits (Norris 1936), although documentation of which species are attracted is lacking. Frost (1928) captured 23,574 noctuid moths in 300 pails containing sugar baits set out for oriental fruit moth, but did not identify them below the family level. Poisoned sweet baits were used for control of corn earworm, Helicoverpa zea (Boddie), during the 19th century (Ditman & Cory 1933 and references therein). The grass looper, Mocis latipes Guenee, can be captured in traps baited with solutions of molasses or jaggery (Landolt 1995). Jaggery is an unrefined sugar made from palm sap, used as a cooking sweetener in some areas of subtropical and tropical Asia. Landolt (1995) also reported the capture of 13 additional species of Noctuidae in glass traps baited with jaggery or molasses solutions in Florida.

There are no reports of captures of tobacco budworm moths in traps with baits containing sugars or sugar-based materials. However, a great number of species of Noctuidae likely are attracted to sugar baits (Norris 1936), and most Noctuidae captured in traps baited with sugar-rich materials have not been identified (e.g., Frost 1928). The tobacco budworm moth feeds at flowers, extrafloral nectaries, artificial sugar sources, and grass heads (Lingren et al. 1977, Ramaswamy 1990) and may be attracted to sugar baits.

We report here the attraction of male and female tobacco budworm moths to solutions of jaggery, and we also determined the optimum age of the bait for attractiveness to moths in a flight tunnel. This work demonstrates the upwind orientation of tobacco budworm in response to food baits and provides a convenient assay system for pursuing the isolation and identification of attractive volatile chemicals emanating from sugar baits. It is hoped that such compounds may be useful as attractants for tobacco budworm as well as other pestiferous species of moths.

**Materials and Methods**

**Insect Rearing and Handling**

Tobacco budworm pupae were obtained from the laboratory colony maintained at the Gainesville, Florida, United States Department of Agriculture, Agricultural Research Service laboratory. Pupae were sorted by sex and were held in screened cages (25 x 25 x 25 cm) for adult emergence. Pupae were moved to new cages daily to provide moths of discrete age groups. A water jar was placed on the top of each cage, and each cage was provisioned with a 60 ml paper cup containing water-soaked cotton balls. Males and females were held in separate environmentally-controlled rooms at 24°C, 60-80% RH and a 14:10 (L:D) photoperiod with lights off at 0800 and on at 1800 hours (E.S.T).

**Field Cage Bioassay**

An initial test of tobacco budworm moth response to jaggery (Indian Kolhapur Jaggery, House of Spices Inc., Jackson Heights, NJ) was conducted in 2 large cylindrical cages, each 2.2 m in height and 2.7 m in diameter (Calkins & Webb 1983), which were set up in an area of lawn largely beneath the shade of a live oak tree. Pairs of glass McPhail traps (Newell 1936) were hung from the ceiling of each cage, about 0.5 m north and 0.5 m south of the center of the field cage. Traps were hung by a wire with the trap opening 20 cm below the cage ceiling. One of each pair of traps in a cage was baited with 200 ml of 10% jaggery in deionized water (5 to 16 days old) and the other trap was baited with 200 ml of deionized water. From 20 to 30 male tobacco budworm moths (3 to 5 days of age) were released into a field cage in late afternoon, and the numbers of moths captured in traps were counted the following morning. Jaggery bait...
was 5 to 16 days old when placed in the field cages. This assay was conducted 20 times, with jaggery bait reused for replicates. Jaggery-baited and control traps were alternated in position with each assay replicate for both field cages. Mean trap catch data, combined for all bait ages, were analyzed by Students t-test to determine if the catches of moths in treatment and control traps were significantly different. Catch data for jaggery-baited traps were also evaluated in comparison to bait age by regression analysis.

**Flight-Tunnel Bioassays**

Two experiments were conducted using a flight tunnel to evaluate tobacco budworm moth responses to jaggery. The flight tunnel and room were described by Landolt and Heath (1987). Moths were tested during the 3rd through 5th hours of the 10 h scotophase, and they were placed in the flight tunnel room 30 min before the bioassays. Moths were tested individually. They were released from a plastic vial near the center of the downwind end of the flight tunnel and were given 2 min to respond to test materials placed at the upwind end of the flight tunnel. Moths were scored for upwind oriented flights within the odor plume and for proximity or contact with the odor source following plume tracking. The baits tested were 10% solutions of jaggery made up as 400 ml batches and placed in open glass jars in a laboratory fume hood until used. For flight tunnel assays, 200 ml of solution were poured into a 9 cm plastic petri dish supported by a ring and ring stand. A paper towel was hung into the middle of the dish to act as a wick, increasing the surface area of the solution.

The first flight tunnel experiment was a demonstration of male and female tobacco budworm attraction to aged jaggery. Three to four-day old unfed females were tested to either a 200 ml batch of aged (12 to 28 days) 10% jaggery in water or to 200 ml of water alone. Ten female moths were sequentially tested for a response to water, followed by ten females sequentially tested for response to jaggery. This experiment was conducted on five different days, with water presented first in 2 trials, and jaggery presented first in 3 trials. This experiment was repeated with males, but on 7 different days. The treatment sequence (water and jaggery) was also alternated between replicates in this experiment. Attraction response data (attraction is upwind oriented flight and contact with the bait) were analyzed by Student's t-test, after transformation to percentages of moths tested within each data set.

Because microbial fermentation may be a determining factor in the attractiveness of food baits to many lepidopterans (Norris 1936), a second flight tunnel experiment was conducted to evaluate the effect of the age of the jaggery bait on its attractiveness to female tobacco budworm. It is expected that colonization and growth of microbes in baits, and resultant changes in odorants released from baits, occur over time. Attractiveness to bait may then increase with time, as microbes and their metabolic byproducts increase in abundance. This experiment was conducted as two separate series of bait ages: a short series and a long series. The short series consisted of baits held for 0, 3, 6, 9, and 12 days in a fume hood in the laboratory. Baits were made every 3 days and bioassays were conducted on 6 different days when baits of all age cohorts were available simultaneously. The long series consisted of baits held for 0, 6, 12, 18, and 24 days. Similarly, these were made every 6 days and bioassays were conducted on 6 different days when baits of all age cohorts were available simultaneously. Every time a series of bait ages was tested in the flight tunnel, five females were tested per treatment (bait age). Thirty females were tested per treatment over the course of the replicates. The treatment sequence was altered daily over the 6 days that the test was replicated. Response data for the long series was subjected to regression analysis for relationship between bait age and moth response.
Male tobacco budworm moths were captured only in traps baited with 10% jaggery placed in field cages. Mean numbers of released males captured in glass McPhail traps baited with 10% aged jaggery (4.45 ± 1.5 moths per trap per day) were significantly greater than those captured in traps baited only with water (no moths captured) (t = 3.0, df = 19, p = 0.008). There was a significant linear regression of bait age versus numbers of male tobacco budworm captured in traps baited with jaggery ($r^2 = 0.65$, t = 2.58, df = 18, p = 0.03, $Y = -9.26 + 1.42X$) (Fig. 1).

Both sexes of tobacco budworm were attracted to 10% solutions of jaggery presented in the flight tunnel. Twenty-four percent of females flew upwind and contacted the jaggery bait, compared to no females responding to the control (water only) (t = 4.71, df = 4, p = 0.009). Twenty-seven percent of males tested flew upwind and contacted the jaggery bait compared to no males responding to the control (t = 3.14, df = 6, p = 0.022).

In a direct comparison of the attractiveness of jaggery bait of different ages, no female tobacco budworm moths were attracted to bait that was freshly made or was 3 or 6 days old. Nine-day old jaggery was essentially non-attractive as well. Female response to jaggery increased with bait age from 12 through 24 days old (Fig. 2), with the highest response (40%) obtained with 24 day old bait. The relationship between bait age and moth response for the long series was significant by regression analysis ($r^2 = 0.948$, t = 5.14, df = 4, p = 0.014, $Y = -6.3 + 1.72X$).

**Fig. 1.** Numbers of male tobacco budworm moths released into a field cage and captured in traps baited with 10% jaggery of different ages. February-March 1996.
DISCUSSION

These results demonstrate that both sexes of tobacco budworm are attracted to fermented bait made from 10% jaggery. Both females and males were attracted to jaggery (exhibited upwind oriented flights from the release dispenser and contacted the bait) in the flight tunnel. The recapturing of male tobacco budworms in baited traps in a field cage also indicates an ability to orient to the source of odors from such baits. This is the first report of orientation responses to food baits by *H. virescens*. Adult tobacco budworms feed at materials that are sugar rich, including flowers, extrafloral plant nectaries, and grass florets (Lingren et al. 1977, Ramaswamy 1990). There are also reports of corn earworm moths feeding at sweet baits (Ditman and Cory 1933) and at fungal-infected grass florets (Beerwinkle et al 1993), with the assumption that they are attracted to such materials. Tobacco budworm attraction to odors emanating from fermenting sugar solutions is likely a mechanism to locate the sources of such odors in order to feed.

The significant regressions of bait age versus males captured in traps in a field cage and bait age versus female response in a flight tunnel support the assumption of Norris (1936) that microbial activity is a critical factor in moth attraction to sweet baits. The grass looper, *M. latipes*, also responds optimally to sweet baits that are aged (Landolt 1995). However, 3-day old jaggery or 3-day old molasses was most effective as a trap bait for the grass looper, compared with 16 or 24 day old jaggery for the tobacco budworm. Perhaps the grass looper moths and tobacco budworm moths respond to different sets of odorants emanating from baits of different ages.

![Graph showing the percentage of female tobacco budworms attracted to contact a pan containing 200 ml of 10% jaggery in a flight tunnel for different ages of jaggery.](image)

Fig. 2. Percentages (± SEM) of female tobacco budworm moths attracted to contact a pan containing 200 ml of 10% jaggery in a flight tunnel, for different ages of jaggery. The short series (solid bars) included 0, 3, 6, 9, and 12-day old baits. The long series (cross hatched bars) included 0, 6, 12, 18, and 24-day old baits.
The positive results using the flight tunnel provide a convenient bioassay technique for pursuing the isolation and identification of odorants from solutions of jaggery that are attractive to tobacco budworm. The liquid bait and trap used in these experiments are too limited and inconvenient to use as a monitoring method for female tobacco budworms. The trap is heavy and fragile, and trap maintenance is time-consuming. The trap also holds a limited number of captured moths, and captured specimens may be difficult to identify if allowed to remain and decompose. For these reasons, it is considered that a formulated blend of synthetic chemicals that are attractive to tobacco budworm can be adapted to a cheaper and easier trap design for field use.

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A NEW INTRODUCTION OF A SUBTERRANEAN TERMITE, COPTOTERMES HAVILANDI HOLMGREN (ISOPTERA: RHINOTERMITIDAE) IN MIAMI, FLORIDA

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During April 1996, we were informed by the Department of Agriculture and Consumer Services of a possible new infestation of the Formosan subterranean termite, Coptotermes formosanus Shiraki, in a commercial building at the northwest corner of Highway 1 and State Road 836 in Miami, Florida (Fig. 1). This infestation, which is 2 blocks west of the Port of Miami, is about 10 km south of the currently known distribution of C. formosanus in southeastern Florida, and about 1.5 km south of the site of another introduced subterranean termite, Heterotermes species (Scheffrahn & Su 1995). A large number of alates swarmed in the front office of this building, and numerous foraging tubes similar to those of C. formosanus were found on the garage walls. Workers and soldiers were also collected from a nearby tree. A close examina-
tion of alates revealed that the infestation belonged to another destructive species of subterranean termite, Coptotermes havilandi Holmgren. This is the first record of this species in the continental United States. Voucher specimens were deposited at the University of Florida termite collection in Ft. Lauderdale.

Alates of C. havilandi are readily distinguishable from C. formosanus by the differential dorsal and ventral coloration. Head and abdominal dorsal tergites of C. havilandi alates are dark brown, and the ventral surfaces of their heads and abdomens are light yellowish brown. Alates of C. formosanus are entirely light yellowish brown. The presence of white, halfmoon-shaped “antennal spots” in front of each ocellus (Fig. 2) is also characteristic of C. havilandi alates (Ahmad 1965). Alates of C. formosanus lack such antennal spots. A consistent diagnostic characteristic that distinguishes soldiers of C. havilandi from C. formosanus is the single pair of setae projecting dorso-laterally from the base of the fontanelle. Soldiers of C. formosanus have two pairs of such setae (Scheffrahn et al. 1990).

Coptotermes havilandi is a destructive pest of structural wood and agricultural crops in Thailand, Malaysia, and Indonesia (Ahmad 1965, Gay 1967, Roonwal 1979). Like C. formosanus, C. havilandi is considered native to the Orient (Araujo 1970, Grassé 1984) and has been widely exported. First introduced to Brazil in 1923, C. havilandi is currently considered the major structural pest in the city of Sao Paulo (Lelis 1995). This termite species was first found in the West Indies on Barbados (Adamson 1938). Current distribution of C. havilandi in the West Indies also includes Antigua, Cayman Islands, Cuba, Isla de la Juventud, Jamaica, Montserrat, and Turks and Caicos Islands (Scheffrahn et al. 1994). Other regions of known C. havilandi distribution are Madagascar and Mauritius (Edwards & Mill 1986).

Coptotermes havilandi is mostly found in the tropics whereas C. formosanus is distributed primarily in subtropical and temperate regions (Su & Tamashiro 1987). Both C. havilandi and C. formosanus cause devastating damage to structures wherever they occur. Records showed that C. havilandi in southeast Asia attacks dead and dying trees of various species, construction timber, furniture, structural wood, plastics, and synthetic fibers (Roonwal 1979). Like C. formosanus, C. havilandi in Sao Paulo, Brazil also construct aerial nests in high rise buildings (Lelis 1995). No data are available for the overall economic impact by C. havilandi in the Caribbean, but it is a serious pest of structures in Little Cayman, and Providenciales and Turk (Su & Scheffrahn, unpublished data).

Numerous timbers in the one-story concrete building infested by C. havilandi in Miami were so severely damaged that they had to be replaced. The infestation was noticed by the occupants 5 years ago, but commercial pest control firms contracted for treatment have mistaken the infestation for native subterranean termites, Reticulitermes species. Soil termiticides have been applied annually for the last 5 years. The most recent soil termiticide treatment was done in April 1996. Despite the annual application of soil termiticide, infestation by this C. havilandi colony continues.

According to the occupant, alate swarming was observed 3 years ago. Because it generally takes 3-5 years for a colony to be mature enough for alate production, and because of the treatment history, C. havilandi was probably introduced to Miami about 10 years ago. Leisure-crafts infested by C. havilandi have been found in Caribbean and Florida waters (Scheffrahn et al. 1990). The close proximity of this infestation to the Port of Miami suggests a maritime introduction. Our suspicion that C. havilandi is not limited to this site was confirmed when, in August, another infestation was found in a church at the northeast corner of I-95 and State Road 836; about 1 km west of the first find (Fig. 1). Damage potential and behavior of C. havilandi is similar to that of C. formosanus, but these two pest species are geographically separated because of their different climatic adaptations. This is an unprecedented inci-
dent in which both C. havilandi and C. formosanus are found within such a short distance, and their interaction will be closely monitored.

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**SUMMARY**

The first introduction record of the subterranean termite, Coptotermes havilandi Holmgren, into the continental United States is reported. Thus far, two infestations
have been recorded in Miami, Florida. The infestation history suggests that C. havi-
lardi was probably introduced to Miami about 10 years ago through maritime trans-
portation. Coptotermes havilandi is found primarily in tropical regions such as
southeast Asia, Brazil, and the Caribbean, and its damage potential is similar to that
of the Formosan subterranean termite, C. formosanus Shiraki.

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The English word beetle means a member of the order Coleoptera, and the word scarab means a member of the family Scarabaeidae. The Spanish word escarabajo does double duty, meaning in its broadest sense beetle, but in its most restricted sense scarab. The authors of this book use the word escarabajo to mean a member of the evocatively-named superfamily Lamellicornia (having laminate antennae). The name Lamellicornia in most modern works has been replaced by Scarabaeoidea, following recommendation 29G of the International Code of Zoological Nomenclature.

This is one of two books, the other still in preparation, which deal with the scarabaeoid fauna of Mexico. This one deals with the family Melolonthidae, and the forthcoming one will deal with the families Trogidae, Scarabaeidae, Lucanidae, and Passalidae. Most readers in America north of Mexico will not be familiar with the family name Melolonthidae, because the retrograde classification used in the USA recognizes only 3 families of Scarabaeoidea (Lucanidae, Passalidae and Scarabaeidae) and thus includes Melolonthidae and Trogidae as subfamilies of Scarabaeidae. In the classification used in this book, the family Melolonthidae includes subfamilies Rutelinae, Dynastinae, Trichiinae, Valginae, Cetoniinae, and Melolonthinae.

In English, some of the vernacular names for members of this family Melolonthidae are chafer, May beetle, or June beetle. The name chafer conjures up an image of a chunky, thumb-nail sized beetle with bright pattern or metallic coloration seen feeding on flowers of the family Umbelliferae, whereas the name May beetle or June beetle evokes a picture of a cylindrical brown beetle about the size of the last segment of a little finger, and sometimes attracted to electric lights in surprising numbers. Those names do not do justice to the magnificent Mexican beetles described and illustrated in this book. If you have not seen Dynastes hercules (70-130 mm) or Megasoma elephas (51-120 mm) alive you have missed something.

It is unfortunate that the name dung beetle is promoted in the USA for members of the Scarabaeidae. These Melolonthidae are not dung beetles: their larvae feed on roots of plants or in decaying wood, and their adults feed on flowers or foliage of plants.

This book has a diagnosis of each of the 110 genera of Melolonthidae known from Mexico. It includes a brief description and notes on habitat, distribution, and in some instances behavior, for 253 of the 1,040 known species. The distribution (by Mexican state) of the remaining 787 species is given in tables. There are 61 black and white illustrations of adults: most of them are drawings and many of them are of superb quality. Remarkably, there are 32 plates containing 253 color photographs, some showing living larvae or pupae, some showing adults in nature, most showing pinned specimens. A preface by Gonzalo Halffter, and prologue and introduction by Miguel Morón set the background (and show that the states with by far the highest recorded diversity of species are Chiapas, Oaxaca, and Veracruz). A bibliography, and systematic and thematic indices complete the book which is well-printed on glossy paper.
I look forward to seeing Volume II of this ground-breaking work. Volume I should serve as an inspiration and challenge to entomologists in Mexico (and elsewhere) to match its quality in publications on other families of insects in their country. Entomologists north of the border should note the event of its publication and buy a copy while supplies last. The next generation of the work must include keys to adults and genitalic illustrations to allow identification to the species level, but this will require a great increase in number of pages and will drive the price much higher.

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Here is a great book bargain! If you want to know what terms such as 'gene targeting', 'horizontal transmission', 'pseudogene', 'punctuated equilibrium', or 'telomerase' mean, this is the book for you. There are 6,600 definitions of genetic, evolutionary, and molecular biology terms, with 250 of them illustrated by drawings or tables. You get more than a dictionary in this volume, because it includes a series of appendices with an abundance of useful information, including a classification of organisms. You will be able to completely identify particular species referred to in the dictionary using this classification. A second appendix includes the common and scientific names of various domesticated species of plants and animals. The third appendix includes a chronology of important events in the history of genetics, cytology, and evolutionary biology from 1590 to 1996. There is an index to the scientists mentioned in the chronology, a bibliography containing approximately 100 important books on genetics and evolution, and a list of about 500 periodicals cited in the genetics, cytology, and molecular biology literature. Foreign words commonly found in scientific journal titles are translated into English. A list of genetic databases is included where you can locate data on specific genes, their products, and details on the genetics of species that are studied as genetic models, including humans, the mouse Mus musculus, the nematode Caenorhabditis elegans, the bacterium Escherichia coli, and the fruitfly Drosophila melanogaster.

You will discover that insects have played a very important role in the history of genetics, evolution, and molecular genetics. Many of the milestones listed by King and Stansfield are based on studies conducted with insects, and especially the fruitfly Drosophila melanogaster. The following examples illustrate the role insects have played in advancing our understanding of genetics and evolution.

The theory of spontaneous generation was disproved in 1669 by Redi using fly maggots. Dzierzon initiated studies on sex determination in 1845 when he reported that drone bees hatch from unfertilized eggs while worker and queen bees hatch from fertilized eggs. Montgomery (1901) studied spermatogenesis in hemipteran species and concluded that maternal chromosomes only pair with paternal chromosomes during meiosis. In 1902, McClung found that equal numbers of two types of spermatozoa were produced in many insect species; one type had an "accessory chromosome" and the other did not. He suggested that the extra chromosome was a sex determinant and argued that sex was determined at the time of fertilization in both insects and humans.
Insects became a particularly valuable tool in studying evolution and genetics during the 1930s. Hashimoto (1933) described the chromosomal control of sex determination in *Bombyx mori*. L'Heritier and Teissier (1934) demonstrated that a deleterious gene disappeared from populations of *D. melanogaster* maintained in population cages for many generations, providing an example of natural selection in a laboratory setting. In the same year Bauer discovered that the giant chromosomes of the salivary gland cells of fly larvae are polytene, which allowed the banding patterns to be mapped. In 1935, Beadle, Ephrussi, Kuhn and Butenandt worked out the biochemical genetics of eye color synthesis in *Drosophila* and the flour moth *Ephestia*, and illustrated that series of genes were required to synthesize the final product. Also in 1935, Bridges published detailed maps for *D. melanogaster* salivary gland chromosomes that have been used to this day to locate specific gene locations. In 1936, Stern discovered somatic crossing over in *Drosophila* and Schultz noted that gene expression in *Drosophila* was affected by its position in the chromosome, with genes located next to heterochromatin often having a mosaic pattern of expression. In 1937, L'Heritier and Teissier demonstrated that mutants of *D. melanogaster* were selected in a frequency-dependent manner in laboratory populations.

Extensive work during the 1940s on *Drosophila* continued to provide advances in our understanding of evolution and fundamental genetics. Auerbach and Robson (1941) discovered that mustard gas induced mutations in *Drosophila*, although they could not publish their results until 1946 because of censorship during World War II. Their discovery opened the field of chemical mutagenesis. In 1944, Dobzhansky described the phylogeny of gene arrangements in the third chromosome of *Drosophila pseudoobscura* and *D. persimilis* and showed that field selection influenced the frequency of these chromosome types. White published his book *Animal Cytology and Evolution* in 1945, in which the cytogenetics of insects (and other animals) were analyzed from an evolutionary point of view. His work illustrated that genomes evolved and highlighted the incredible diversity of insect genetic systems. In 1948, Muller coined the term ‘dosage compensation’ to describe a phenomenon in which the expression of genes located on the sex chromosomes is made equal in males and females despite the fact that most males have one X chromosome and females have two. Evolutionary studies remained important during the 1950s. Patterson and Stone (1952) published *Evolution in the Genus Drosophila*, which summarized an encyclopedic body of information on the evolution of chromosomes in the genus. In 1956, Kettlewell reported that the peppered moth exhibited industrial melanism and demonstrated that moths that are conspicuous are eaten more often by birds than the inconspicuous moths. This study provided a classic example of natural selection in progress.

In the 1960s gene regulation, the genetic basis of development, and population genetics were investigated using insects. Clever and Karlson (1960) were able to induce specific puffing patterns in the polytene chromosomes of *Chironomus* larvae by injecting the flies with ecdysone, thus demonstrating that hormones were important in gene regulation. In 1961, Beermann showed that the puffing patterns on *Chironomus* polytene chromosomes are inherited in a Mendelian fashion, and Tokunaga demonstrated that the *engrailed* gene of *D. melanogaster* causes a shift from one developmental prepattern to a different, but related, prepattern. In 1962, Ritossa reported that salivary gland chromosomes of *D. buskii* responded to heat shocks by puffing, indicating that environmental stresses could induce puffing (and thus a specific type of gene activity). In 1965, Karlson et al. determined the complete structural configuration of ecdysone and Ritossa and Spiegelman demonstrated that ribosomal RNAs of *Drosophila* are produced in the nucleolus organizer regions of the X and Y chromosomes. Roller et al. (1966) determined the structural formula for the juvenile hormone of *Hyalophora cecropia*. Lewontin and Hubby (1966) revolutionized population stud-
ies when they used electrophoretic methods to survey protein variants in natural populations of Drosophila pseudoobscura. They demonstrated the presence of high levels of variation within populations and opened the field of molecular ecology and evolution. In 1969, Hotta and Benzer and Pak and Grossfield independently induced and characterized neurological mutants in Drosophila, providing a new tool for studying neurobiology.

In the 1970s, insects provided answers to various questions. Konopka and Benzer reported the first mutants in Drosophila that affected the circadian 'clock', opening a new field in behavior genetics and neurobiology. In 1972, Suzuki and Brown isolated and identified the messenger RNA for silk fibroin from Bombyx mori. Kavenoff and Zimm measured the molecular weights of DNA molecules isolated from cells of different Drosophila species and concluded that a chromosome contains one long uninterrupted molecule of DNA. Garcia-Bellido and colleagues dissected the development of imaginal wing discs in Drosophila. Tissieres et al. (1974) found that heat shocks result in the synthesis of six new proteins in Drosophila, even in tissues that do not have polytene chromosomes. This work on heat shock proteins led to a thriving investigation into the cellular responses to stress that remains active today. In 1975, McKenzie et al. isolated messenger RNAs for heat shock proteins and showed that they hybridized to specific puff sites on the Drosophila polytene chromosomes.

The 1970s also were significant because genetic engineering began. It is remarkable that in 1975 a group of molecular biologists from around the world met at Asilomar, California to write a historic set of rules to guide research in recombinant DNA experiments. That same year, the National Institutes of Health Recombinant DNA Committee issued guidelines aimed at eliminating or minimizing the potential risks of recombinant DNA research. The first genetic engineering company (Genentech) was formed in 1976. In 1978, Finnegan et al. analyzed dispersed repetitive DNA in Drosophila, which was the beginning of extensive studies to understand mutability, transposition, transformation, hybrid dysgenesis, and retroviruses in multicellular organisms. In 1978, Lewis concluded that the component genes in the bithorax complex have related functions in Drosophila segmentation and that they evolved from a smaller number of ancestral genes by duplication.

During the 1980s, studies on Drosophila melanogaster contributed to fundamental advances in understanding the processes of development and gene regulation. The studies initiated by Nusslein-Volhard and Wieschaus in the 1980s are especially notable and their work culminated in a Nobel Prize in Medicine in 1995 for their analyses of the genetic mechanisms that control cell differentiation during embryogenesis and metamorphosis. In 1987, Nusslein-Volhard and colleagues showed that a small group of genes exist in Drosophila that determine the anterior—posterior and dorsal—ventral patterns of development of the embryo. These “maternal effect genes” direct the very earliest development of the zygote. In a series of ensuing papers, Nusslein-Volhard and her colleagues provided additional details on the genetics of early embryonic development.

Recombinant DNA research initially was limited to the manipulation of genomes of microorganisms, but that changed in the 1980s when genetic engineering of Drosophila melanogaster became possible. Once D. melanogaster could be genetically engineered, large numbers of genes could be cloned and details of development studied. This revolution in Drosophila genetics was initiated by the discovery in 1982 by Spradling and Rubin that P element vectors could be used to introduce foreign genes into D. melanogaster in a repeatable and reliable manner. That breakthrough has led to an explosion of studies on development and gene regulation.

Other revolutionary changes took place in the 1980s. Saiki, Mullis and five colleagues described the use of the polymerase chain reaction (PCR) to allow the ampli-
fication of a specific gene. The PCR technique revolutionized molecular biology and ecology and has become one of the most important tools in a biologist's tool kit. Mullis and Smith received the Nobel Prize in Chemistry in 1993 for inventing the polymerase chain reaction and site-directed mutagenesis, respectively.

In the 1990s we learned that many of the genes in Drosophila were highly conserved and provided a method to identify genes and developmental processes in other organisms, including mammals. For example, Milicki et al. introduced a homeobox gene from the mouse into Drosophila embryos and found that the mouse gene could induce developmental changes in the fly. This implies that genes from animals that have been evolving independently for hundreds of millions of years may generate gene products that function interchangeably. Bargiello and Young had cloned and sequenced the period gene in Drosophila in 1984, which is the first gene known to control a biological clock. Work on this system continued during the 1990s, and Wheeler et al. were able to introduce the cloned Drosophila simulans period gene into the genome of a strain of D. melanogaster lacking active period genes. The newly-transformed D. melanogaster males subsequently could “sing” the simulans mating song, which represented an interesting example of a single gene affecting a complex behavior. In 1994, Orr and Sohal constructed transgenic lines of Drosophila that have extra copies of the catalase and superoxide dismutase genes. The new strains aged more slowly, leading to hopes that genetic studies on insects may lead to insights into the fundamental processes involved in aging. Also in 1994, Tully and eight colleagues isolated genes that control the formation of memory in Drosophila and opened new avenues to investigate learning. In 1995, Hader et al. demonstrated that the eyeless gene in D. melanogaster is a master control gene for eye morphogenesis.

Genetic terms are added to the literature on a regular basis. This is the fifth edition of a highly regarded and popular dictionary of genetics. The fourth edition was published in 1990, the third in 1985, the second in 1972, and the first in 1968. The need for new editions has been determined by the rapidity with which the fields of genetics, evolution, and molecular biology change. Even though this dictionary was published in 1997, I was unable to find definitions for the term ‘RAPD-PCR’ and other variations upon the basic PCR technique. Perhaps these will be found in the sixth edition.

Molecular genetic tools are important to an increasingly broad array of scientific disciplines. This volume will be of interest to anthropologists, chemists, computer specialists, engineers, geneticists, mathematicians, molecular biologists, paleontologists, physicians, physicists, zoologists, and ENTOMOLOGISTS, all of whom are using genetic tools to solve interesting basic and applied problems.

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This incomparable volume is the product of presentations and subsequent research on the Monarch Butterfly, Danaus plexippus initiated at international meetings during the 1980s. The Symposium on the Biology and the Conservation of Monarch Butterflies ("Moncon-1"), held in Cocoyoc, Morelos, Mexico, in 1981, focused
on the development of a scientific rationale for the protection of the overwintering sites in Mexico and the immediate urgency to provide objective supportive documentation for conservation efforts. The Second International Conference on the Monarch Butterfly ("Moncon-2"), convened 2-5 September 1986 in honor of Fred A. Urquhart, was organized by Julian P. Donahue and hosted by the Natural History Museum of Los Angeles County. This symposium had a strong emphasis on research on every aspect of the biology and conservation of the Monarch butterfly. The presentations were subsequently divided into eight major subheadings: (1) systematics, (2) chemical communication, (3) mating behavior, (4) hostplant use, cardenolide sequestration, and defense against natural enemies, (5) physiological ecology and the annual cycle, (6) migration, (7) overwintering biology, and (8) conservation. Long in gestation, this volume has been updated and revised to include detailed research findings following the symposium. Separate black and white and color photographs introduce and provide convenient interludes between each major section. A list and current addresses of the contributors and a lengthy index complete this excellently produced volume.

Stephen Malcolm and Myron Zalucki provide a brief introduction and present an updated overview of the current status of the research and conservation on the Monarch butterfly in comparison with other well-known organisms as research models. Kitching, Ackery and Vane-Wright summarize the systematic relationships and evolution of the nymphalid subfamily Danainae in light of recent analyses derived from immatures and allozyme studies and present a historical perspective on the possible origins.

The second section features chemical ecology and reviews the systematic complexity of Danainae with the characteristic cardiac glycosides and other toxic secondary compounds such as the pyrrolizidine alkaloids, long known in other Lepidoptera but more recently detected in many of the danaines. Courtship behavior is summarized through detailed studies on the chemical mediation of male secondary sexual characters and the physiology of pheromone-sensitive receptor neurons.

Mating behavior is examined with a review of sexual selection and reproductive fitness in overwintering populations of Monarch butterflies in Mexico. Comparative studies on both Mexican and Californian populations investigate multiple mating, male fitness, survival rates and male vs. female vs. hostplant distributions.

Under host plant use and chemical defense against natural enemies, the mechanisms for cardenolide sequestration and resource partitioning are postulated and discussed. The final two papers in this section reinforce the need to critically reexamine previous information in the literature. Borkin reappraises and refutes the earlier accounts of Apocynum androsaemifolium and A. sibiricum as possible larval hostplants for D. plexippus. Similarly, Ritland and Brower present evidence that the mimicry relationships among Viceroy, Queens, and Monarchs are not as well defined as once believed. This mimicry complex may be a more dynamic one shifting along a continuum from Batesian to Mullerian mimicry due to variation in spatial, temporal and seasonal factors.

The next section reviews the interrelationship of physiological ecology and the annual cycle. This research encompasses a particularly diverse set of topics from juvenile hormone in the reproductive cycle, neuropeptide control of diuresis and diglyceride levels for flight metabolism, to thermoregulation through behavioral plasticity, morphological adaptations, and physiological acclimation.

Migration and overwintering biology are the interrelated themes for the last two sections. Dick Vane-Wright's erudite discussion on the Columbus Hypothesis proposes a possible explanation for the dramatic range expansion of the Monarch butterfly in the 19th century. Other authors examine the ecology (including plant interactions), physiology, social interaction, and migratory patterns in Australia,
Costa Rica, and several sites in the U.S. There are comprehensive studies focused on predator/prey relationships in respect to chemical defenses and the cyclic nature of reproductive cycles in several danaines at one site.

The final section discusses the question of preservation and conservation of the Monarch butterfly, especially in North America. The fragmentation and loss of available habitat combined with the potential loss of overwintering roosting areas could certainly have severe deleterious effects on the butterfly populations in future years. The implementation of conservation initiatives versus the “anthropocentric considerations of sociology, politics, and economics” underlie the major problems involved in protection and preservation of species at multiple sites, and these issues are examined in detail.

With a multi-authored volume such as this, it is sometimes difficult to organize sections appropriately and have similar scientific breadth. This compilation succeeds admirably, is remarkably well written and edited, and is an invaluable compendium of the knowledge available on this unique butterfly species until approximately 1991. In a few cases, the reviews of previous and present research are perhaps too abbreviated, but each paper has a separate bibliography for additional reading which is an invaluable asset. With an organism such as Danaus plexippus that has been studied in such depth, it is remarkable to note how much information investigators have been able to amass and how much more knowledge is still required, for example on factors affecting behavior during migration.

Despite your particular area of research or endeavor, this volume is a must for any avid, working lepidopterist, and definitely sets a higher standard for future research on the Lepidoptera.

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The author’s stated objectives are “to define and analyze our current knowledge of the functioning of the brain of one animal, the locust, and to show how this contributes to our understanding of brains in general.” In accomplishing these objectives Burrows emphasizes how the brain and other central nervous system components function to produce and control behavior, rather than giving descriptions of how the sensory system functions. The author has a long career in insect neurobiology research and writes with the authority of that experience.

It should be said at the outset that there is a great deal of comparative insect neurophysiology in the book. It seems to me that the title is misleading, because the book covers far more than the brain, and more than neurobiology of locusts.

The book is divided into 12 chapters. Chapter 1 gives a brief introduction to locust anatomy and biology, and Chapter 2 has a thorough description of the anatomy of the locust brain, ventral ganglia, and major nerves. Chapter 3 is a very comprehensive (about 70 pages) description of the cellular components of the nervous system. Beginning in this chapter and for much of the remaining chapters the book contains much that is comparative insect neurophysiology and it is sometimes difficult to determine from the text if the author is describing something known to occur in locusts or in
some other insect. Fortunately many citations to the literature have been given, and
by looking at the titles of these citations included at the back of the book one can some-
times see the name of the insect for the cited work.

Chapter 4 is an excellent discussion of the embryological development of the ner-
vous system. Chapters 5 and 6 (about 85 pages in the two chapters) contain a thor-
ough description of neurotransmitters, neuromodulators, neurohormones, and their
physiological actions. Research in this particular arena of neurobiology, in both verte-
brates and invertebrates, is perhaps the most rapidly expanding area of neurobiology.
One of the fascinating aspects of the emerging research is the often high degree of
similarity between vertebrate and insect neuropeptide structures, suggesting ancient
molecules that have been adapted many times to perform different functions.

About 60% of the book is given to Chapters 7 (control of the legs), chapter 8 (walk-
ing), chapter 9 (jumping), chapter 10 (escape), chapter 11 (flying), and chapter 12
(breathing) which fulfill the author's promise to relate the nervous system to behavior.
Of necessity these discussions require some reference to peripheral sensory struc-
tures, but as the author admits in the preface, the book is not about sensory physiol-
ogy, and few details are given.

An outstanding feature of the book is a very thorough and excellent glossary
(a bout 20 pages) at the end. Although every discipline has to have its own language
to some extent, neurobiology, perhaps more than most areas of physiology, is loaded
with jargon. The glossary will be especially helpful to nonspecialists and noninsect bi-
dologists who may use the book. The book is well illustrated with line drawings and
printed on high quality paper.

This book will be useful to vertebrate neurobiologists, especially in a comparative
sense, but they need to be cautioned that insects are a very diverse group of animals
and there is considerable variability from one group to another. Thus, to assume that
everything described in the book is characteristic of a locust, or of any other insect, is
a grave error.

The book will be valuable to anyone teaching a course in insect physiology, insect
behavior, or comparative neurobiology.

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ERRATA


The specific name rotundus was incorrectly misspelled as roten-dus.