Insects That Feed On *Miconia calvescens* in Costa Rica

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Abstract

Research at the University of Costa Rica on potential biological control agents of *Miconia calvescens* was initiated in 2000. Although *M. calvescens* can be fairly common at certain sites, it is generally uncommon in Costa Rica and appears to be incapable of becoming established in forests with a closed canopy. Over fifty insect species have been identified as feeding on this plant, but most of these were excluded from further research because they are probably not sufficiently host-specific. Thus far we have focused our attention on six species that appear to be promising biological control agents: *Diclidophlebia lucens* (Hemiptera: Psyllidae), a wax-producing sap-sucker on young shoots; *Euselasia chrysippe* (Lepidoptera: Riodinidae), whose caterpillars feed gregariously on the leaves; *Cryptorhynchus melastomae* (Coleoptera: Curculionidae), a stem borer; *Anthonomus monostigma* (Curculionidae), which feeds in the fruits; *Ategumia dilecticolor* (Lepidoptera: Pyralidae), a leaf-roller; and *Mompha* sp. (Lepidoptera: Momphidae), which feeds in fruits. The first three species have been sent to quarantine facilities in Hawai'i for further study, but a major problem that remains to be resolved is to find a way to breed *Euselasia* in captivity.

Introduction

Miconia calvescens is relatively scarce in Costa Rica, occurring in isolated locations, mostly (but not exclusively) on the Caribbean slope between 500-1000 m in elevation. Before we began our study there was only one specimen in just one of the three major herbaria in the country. We have found it growing in sites receiving partial sunlight, often on steep slopes, and it appears to be incapable of becoming established in forests with a closed canopy. Field sites included: La Selva (50 m), Hitoy Cerere (100 m), Lago Arenal (550 m), Laguna Hule (750 m), El Angel (750 m), Jabillos (750 m), Jicotea (900m), Cariblanco (986 m), Cerro Nara (1,000 m), Las Cruces (1095 m), and Vereh (1200m). In addition, we propagated *M. calvescens* at the University of Costa Rica in San Pedro (both in the greenhouse and on campus, 1200 m) and at various field sites. Over fifty insect species have been identified as feeding on *M. calvescens*, but most of these were excluded from further research because they appeared to lack host specificity or were very uncommon. We have focused our attention on six species that appear to be promising biological control agents.

The Six Principal Insect Species Studied

Diclidophlebia lucens (Hemiptera: Psyllidae). This is a pantropical genus that includes 14 described species in the New World, seven of which feed on Melastomataceae (Table 1) and probably constitute a monophyletic group within the genus. Of the remaining New World species, hosts are known for four, and these are associated with Sterculiaceae, Tiliaceae and Ulmaceae (Burckhardt *et al*. 2005).

Table 1. Species of *Diclidophlebia* on New World melastomes.

***Diclidophlebia* species**	**Host plant**	**Locality**
D. fava	*Miconia argentea*	Panama
D. longitarsata	*Miconia argentea*	Panama
D. lucens	*Miconia calvescens*	Costa Rica
D. paucipunctata	*Conostegia xalapensis*	Panama
D. tuxtlaensis	*Conostegia xalapensis*	Mexico
D. heterotrichi	*Heterotrichum cymosum*	Puerto Rico
D. smithi	*Miconia calvescens*	Brazil

Although *D. lucens* is a very small psyllid (2–3 mm), it can be detected readily in the field by its waxy secretions. All five larval instars produce waxy filaments, and when populations are high, these cottony masses of wax can become quite extensive. Adults are generally inactive except when disturbed. Males are smaller, brighter red and have enlarged genitalia (Burckhardt *et al*. 2005). We have found this species on *M. calvescens* in six of eight sites sampled. Species of *Diclidophlebia*, like most psyllids, are probably highly host specific; indeed there are probably numerous undescribed species on other melastomes. All life stages are found on the host plant, primarily on the terminal buds (including both leaf and flower buds) and expanding young leaves. On fruiting mature trees, they were also commonly found on flower/fruit peduncles.

Females lay eggs on the youngest leaves or buds, often in the small space between a vein and the leaf lamina. Upon hatching, the first instar larvae begin to feed on buds and barely expanded leaves, and almost immediately begin to produce long waxy filaments under which they become concealed. The larvae also produce globules of liquid excrement about one mm diameter, which are apparently coated with wax, since the globules are whitish in color and maintain their spherical shape (Burckhardt *et al*. 2005). The time from oviposition to emergence of new adults appears to be similar to that of other melastome-feeders in this genus, ranging from one to two months, depending on the temperature; adult female longevity ranges from 15-30 days (Conconi 1972, Burckhardt *et al*. 2006). In *D. smithi* each female is reported to lay 25-45 eggs during its lifetime (Burckhardt *et al*. 2006), but an African species feeding on Euphorbiaceae is reported to have a lifetime fecundity of over 500 eggs (Alene *et al*. 2005). *D. lucens* does not appear to be regularly tended by ants. No parasitoids have been reared from this species, nor are there any records of parasitoids from other New World members of this genus.

As a potential biological control agent, *D. lucens* has a number of desirable characteristics: high host specificity, the ease with which it can be reared on potted plants in the greenhouse, and the apparent lack of parasitoids. The major question remaining is whether it has a sufficient impact on the growth and/or reproduction of the host plant. Other species of *Diclidophlebia* are known to seriously affect young seedlings and are considered to be major

pests (Alene *et al*. 2005). High populations of *D. lucens* appear to result in early dehiscence of infested leaves, but more studies are needed of its impact on the host plant.

Euselasia chrysippe (Lepidoptera: Riodinidae). Members of the subfamily Euselasiinae perch with their wings held vertically above their body, like most other butterflies but unlike most members of the other major subfamily, Riodininae. As far as known, the larvae of Euselasiinae are gregarious in all instars, i.e. they feed, move, rest, and molt synchronously. The largest genus of Euselasiinae, and of all Riodinidae, is *Euselasia*, which comprises 170 described species, including about 30 in Costa Rica. Larval host plants of this genus include Clusiaceae, Euphorbiaceae, Melastomataceae, Myrtaceae, Sapotaceae, and Vochysiaceae. Where the biology is known, individual species have a narrow host range.

At least three Costa Rican species of *Euselasia* feed exclusively on Melastomataceae: *E. aurantia*, *E. bettina*, and *E. chrysippe*. Although all three species feed on *M. calvescens*, we have focused primarily on *E. chrysippe* because its eggs and larvae were more commonly found on this plant than those of the other two species. It ranges from southeastern Mexico to northern Colombia and occurs from sea level to about 1500 m. Besides *M. calvescens*, its larvae have been recorded feeding on seven other species of Melastomataceae: *M. appendiculata*, *M. donaeana*, *M. elata*, *M. impetiolaris*, *M. longifolia*, *M. trinervia*, and *Conostegia rufescens* (Allen 2007, Nishida 2007 & 2010). On the other hand, *E. chrysippe* does not feed on all species of *Miconia*; for example, eggs and larvae were not found on *Miconia affinis* and *M. paleacea* that were growing contiguously with *M. calvescens*.

Larvae of *E. chrysippe* feed gregariously, side by side. First and second instars scrape the undersides of leaves, but beginning as third instars the larvae feed on the entire leaf. The larvae move from leaf to leaf in a linear procession, which is accomplished by means of tactile stimuli (setal contact), a trail pheromone, and possibly by silk that is laid down while moving (Nishida 2007 & 2010). They also rest and molt synchronously. In the laboratory, the larvae pupated gregariously or singly on the underside of surrounding objects, but pupation sites in the field remain unknown. Adults emerge synchronously by sex, males typically 24 hours after females. Adults can be maintained on a diet of rotting fruit. In the field males maintain territories by perching on the tops of leaves situated more than two meters above the ground, and most activity occurs under sunny conditions between 6:30 a.m. and 7:30 a.m. Mating appears to occur on the undersides of leaves, also more than two meters above the ground. Due to this territorial behavior, mating does not occur in standard laboratory cages, although some success was achieved by confining males and females to very large cages ($3 \times 3 \times 4.5$ m).

Females begin laying eggs about a week after emerging from the pupa and maximum adult lifespan appears to be slightly more than a month. Eggs are deposited on the undersurface of leaves, generally on large (7-8 m tall) plants. In the field the mean number of eggs per clutch was 62.7 (range = 13-134). Approximately 160 developed eggs and 15 undeveloped eggs were found in the abdomen of three unmated, 10-15 day-old females, which suggests that each female can lay about three egg masses during its lifetime. The egg stage lasts from 3-6 weeks and larval development about 5-7 weeks, depending on temperature. The prepupal stage lasts about one day, and the pupal stage lasts seven days for females and eight days for males (Allen 2007).

Because of their gregarious behavior, detailed observations were made of the effects of larval group size on survival and adult size (Allen 2007). Clutch size did not affect hatching rates and therefore the benefits of gregarious behavior apparently arise after the egg stage. In the field there was a positive relation between larval group size and larval survival. However, in

the laboratory, group size did not affect individual larval survival until the sixth (final) instar. When sixth instar larvae were placed individually on plants in the laboratory, 37% died, whereas mortality was very low in group treatments (6% with 5 larvae per plant, 0% with 10 per plant, and 8% with 20 per plant). In the laboratory, larger groups of larvae also yielded larger-sized adults. Thus larval aggregation promotes greater fitness in *E. chrysippe*, perhaps by facilitating feeding. Non-sibling larvae in different instars sometimes joined to form larger groups, both in the field and in the laboratory. On one occasion in the laboratory, larvae formed a larger group consisting of two different species, *E. chrysippe* and *E. bettina*.

Our research corroborates previous observations by parasitoid systematists that riodinids and lycaenids lack the usual lepidopteran parasitoids. The only egg parasitoid reared from *E. chrysippe* was *Encarsia porteri* (Aphelinidae), a species that is unusual because of its heteronomous development, males being parasitoids of lepidopteran eggs and females of whitefly nymphs. Fewer than 20% of field-collected egg masses were parasitized, but among the parasitized egg masses more than 90% of the eggs were affected. Another cause of egg mortality was predation by ants. The only larval parasitoid encountered was *Calolydella* sp. (Tachinidae), which was reared from each individual in a group of five recently molted last instar larvae collected at one locality (Jicotea, Turrialba). In the field we observed larval predation by salticid spiders and vespid wasps, and in the laboratory a reduviid was observed attacking a recently hatched larva (Allen 2007).

Characteristics of *Euselasia chrysippe* desirable for biological control are its host specificity, potential impact on the plant via defoliation, wide environmental range, and potential avoidance of the usual lepidopteran parasitoids. Presently, the major challenge for additional work with this species is to reproduce natural conditions required for mating (large spaces with suitable light conditions) in a contained area.

Cryptorhynchus melastomae **(**Coleoptera: Curculionidae). Larvae of the subfamily Cryptorhynchinae feed either on dead plant material (e.g. dead stems), or on living stems, roots, or reproductive structures. One of the largest genera in the subfamily is *Cryptorhynchus*, which has become a repository for cryptorhynchines with uncertain relationships (i.e. the genus is probably not a monophyletic group). It currently comprises approximately 80 species occurring in Costa Rica. Among those species associated with living plant tissue, the larval host plants are known for very few and the only species whose biology has been studied in detail is *C. lepathi*, a Eurasian invader which feeds on poplars and willows in North America (Broberg *et al*. 2002). *Cryptorhynchus melastomae*, as the name suggests, feeds on Melastomataceae, including *M. calvescens*, and its larvae are stem borers. This species ranges from southern Mexico to Ecuador and occurs in moist forests (>2000 mm annual precipitation) from sea level to 1,500 m.

We collected adults and stem-mining larvae on host plants at three field sites. All *C. melastomae* from El Angel and Turrialba were found on *M. calvescens,* whereas all adult weevils from Reserva San Ramon were found on *M. theizans* and *Conostegia micrantha* (larvae at this site were only recovered from *M. theizans*). In no-choice host specificity tests the adults fed mainly on melastomes, and females laid eggs on *Clidemia hirta, C. setosa*, *Miconia astroplocama*, *M. calvescens*, and *Tococa platyphylla*. Although in this experiment females (which came from El Angel) did not lay eggs on *M. theizans*, adults at the San Ramon readily fed and laid eggs on this plant in the field and the lab (Reichert 2007).

The adult weevils are nocturnal (as are most Cryptorhynchinae) and feed on new stems and leaf lamina, veins, and petioles. In the field no fresh adult feeding damage was found on plants taller than 2-3 m. Females generally laid eggs in the main stem of smaller plants, and

on plants taller than two meters, larvae were usually found in side branches rather than in the main stem. Females chew a cavity, deposit an egg, and then use the abdomen to cover the egg with frass and exudate. The entire oviposition process requires about 30 minutes (Reichert 2007).

The larvae are stem-borers and usually burrow downward and sometimes reach the roots, although they often go back up, thereby enlarging the tunnel. Larval excrement protrudes out through the egg hole and later through other holes made by the larva along the stem. A large hole about 5 mm diameter is chewed in the stem in preparation for pupation and eventual adult emergence; above this exit hole the larva creates a pupation chamber that is lined with shredded plant tissue. In potted greenhouse plants, beetles developed from eggs to adults in approximately 180 days. Newly emerged females mated and began laying eggs after 32 days. One female laid 59 eggs over her seven-month lifespan (Reichert 2007). We found *C. melastomae* at field sites year-round, which suggests that there may be two overlapping generations per year.

Out of 22 field-collected larvae and pupae, three were parasitized by an undescribed species of *Capitonius* (Braconidae: Cenocoeliinae). All three were from *Miconia theizans* stems collected in July 2005 in San Ramon (Reichert 2007). The fact that these stems all had an emergence hole made by the weevil larva, suggests that the parasitoid attacks *Cryptorhynchus* as a mature larva, prepupa, or pupa. The genus *Capitonius* is restricted to the New World and members of the subfamily Cenocoeliinae are known to be endoparasitic koinobionts of beetle larvae. The only previous host record for this genus is for *Capitonius andirae*, from *Cleogonus* (Curculionidae) in seeds of *Andira inermis* (Fabaceae) (Hanson and Gauld 2006).

Desirable characteristics of *C. melastomae* as a biological control agent are its apparent host specificity, the severe damage it causes to saplings (sometimes killing them), broad environmental range, occurrence in life zones similar to miconia-infested areas in the Hawaiian Islands, and feasibility of laboratory rearing. Mating and reproduction readily occur on potted plants in small cages, and plants as small as 50 cm in height can be used to rear one insect all the way to adulthood. The principal limitation in using this species is its relatively long lifecycle and consequently slow population growth.

Anthonomus monostigma (Coleoptera: Curculionidae). *Anthonomus* is the largest genus in the tribe Anthonomini and comprises about 400 neotropical species. Some are crop pests while others have been proposed as biological control agents. *Anthonomus monostigma* occurs from Mexico to Panama, and the only biological information previously available on this species is that adults were collected on *Miconia nervosa*. We found that eggs are laid in fruits of *M. calvescens* and that the larvae feed on seeds inside the fruit. Eggs hatched in 5-9 days. The first, second and third instars lasted approximately 5, 10, and 20 days, respectively. As in other Anthonomini, pupation occurred within the substrate in which the larva developed, but we were not able to determine the duration of the pupal stage. Adults lived up to nine weeks in the laboratory (Chacon 2007).

Although adult anthonomine weevils typically feed on a greater range of host plants than do the larvae, *A. monostigma* adults were found on just a few species of *Miconia* out of a variety of melastomes searched (Chacon 2007). At La Selva, where 13 melastome species were searched, adults were found feeding on fruits of *M. affinis, M. impetiolaris*, *M. longifolia*, and *M. nervosa*, and larvae were found only in *M. longifolia*. The latter host plant produced fruits almost all year, and adult weevils were observed year-round. At Vereh, where 16 melastome species were searched, *A. monostigma* adults were found feeding on fruits of *M. affinis, M.*

calvescens, and *M. nutans*, and larvae were found in the first two. Neither *M. affinis* nor *M. calvescens* fruited year-round, but together these two species provided fruits throughout the year. Use of just one host for larval development at La Selva, but two hosts at Vereh, may be a function of host preference and temporal patterns in fruit production by *Miconia* species at the two sites. At Vereh *A. monostigma* used *M. affinis* when *M. calvescens* was fruitless, whereas at La Selva, where *M. affinis* also occurs, the weevil did not use this host, possibly because *M. longifolia* is preferred and produces fruits all year.

Additional evidence supporting the hypothesis that *M. calvescens* fruit availability is a limiting factor at Vereh is that the few fruit of *M. calvescens* that occur out of synchrony with the rest of the population are more heavily damaged by adults and larvae (Chacon 2007). Our failure to find *A. monostigma* in other more abundant *Miconia* species during seasons when there are few or no fruits in the host species is another good indication of weevil specificity for certain *Miconia* species.

To adapt to fruit scarcity, it is possible that these weevils can survive for long periods as adults, which would permit them to find trees with fruits, even when these are available for only a few months during the year. Adults of *A. monostigma* in the laboratory lived for about two months, but we have not determined longevity in the field or whether this weevil can remain dormant in concealed sites as occurs in other species. Another aspect of *A. monostigma* biology that remains unknown is its dispersal ability.

Desirable characteristics of *A. monostigma* as a biological control agent include its host specificity and ability to reduce seed production. Only one parasitoid, *Bracon* sp. (Hymenoptera: Braconidae), was reared from fruits with *Anthonomus* larvae, and vulnerability of larvae and pupae within fruit to natural enemies appears to be low. The major limitations in using this species are the difficulty in rearing it in the laboratory (the requirement of plants with fruits) and the possibility for weevils to decline in the field during periods when fruits are not available. However, in Tahiti and Hawai‘i the phenology of *M. calvescens* seems to be suitable for maintaining the life cycle of *A. monostigma* since plants reproduce several times per year (Meyer 1998).

Salbia lotanalis (Lepidoptera: Crambidae). In the near future this species will probably be placed in *Ategumia* (A. Solis, pers. comm.), a genus that occurs in Southeast Asia and the Neotropics; all species appear to be leaf rollers of Melastomataceae. Two Costa Rican species, *A. ebulealis* and *A. matutinalis*, are already present in Hawai‘i. These and two Asian *Ategumia* species were introduced to Hawai‘i between 1958 and 1970 to control *Clidemia hirta* and *Melastoma candidum*, but these leaf rollers have been ineffective, probably due to interference from generalist parasitoids (Nakahara *et al*. 1992, Conant 2002). The species most commonly found on *M. calvescens* in Costa Rica is *S. lotanalis*, which also feeds on other Melastomataceae (*Conostegia, Clidemia, Graffenrieda, Leandra, Miconia, Ossaea*) and occurs from sea level to 1800 m.

The eggs are laid alone or in small groups on the underside of a leaf and sometimes in abandoned or occupied leaf rolls. Eggs hatch after about seven days. There are five larval instars, the first through third lasting 5-6 days each and fourth and fifth lasting 8-9 days each. Young larvae aggregate and feed on the lower surface of the leaf beneath a thin shelter of silk. Beginning as third instars, they roll leaves using silk attachments and continue to feed on the lower surface. First through third instars also often move into unoccupied leaf rolls left by late instars. As fourth instars they begin chewing all the way through the leaf. While leaf rolls can be formed and occupied by more than one larva, with later instars there is typically just one larva per leaf roll. Prepupal larvae, which are recognizable by their pale orange color, cut

a section of leaf and construct a pupal chamber thinly lined with silk. The pupal stage lasts 13-14 days (Castillo 2009).

Adults emerge between 7:00 p.m. and midnight. They are usually inactive during the day and spend most of their time perched on the underside of the leaf. Mating and oviposition occur at night. The females possess eight ovarioles and about 400 eggs in total. Adult longevity is about two weeks. In the laboratory, development from egg to adult took an average of 71 days for females and 66 days for males (Castillo 2009).

Six parasitoids were reared from *S. lotanalis*. *Bracon* sp. (Braconidae: Braconinae) and *Meteorus* sp. (Braconidae: Meteorinae) emerged from prepupae, although the latter probably laid its egg in an earlier instar since it is a koinobiont. *Hyphantrophaga virilis* (Tachinidae), *Leurus caeruliventris* (Ichneumonidae: Metopiinae), an unidentified species of Cryptinae (Ichneumonidae), and *Brachymeria* sp. (Chalcididae) emerged from pupae; the first two are koinobionts and the last two are probably idiobionts.

Positive attributes of *S. lotanalis* as a potential biocontrol agent include a host range apparently restricted to Melastomataceae, ease of laboratory rearing, and high levels of defoliation seen during seasonal outbreaks at one site in Costa Rica. However, this species is attacked by numerous parasitoids in its native range, and it appears likely that it would be similarly vulnerable to a variety of parasitoids already present in Hawai‘i. For example, the closely related species *A. matutinalis* experiences 43% mortality due to parasitoids including *Brachymeria obscurata* and *Meteorus laphygmae*, generalist biocontrol agents introduced in 1895 and 1942 respectively, and *Trathala flavoorbitalis* and *Casinaria infesta*, both accidentally introduced (Nakahara *et al*. 1992).

***Mompha* sp.** (Lepidoptera: Momphidae). Host plants of *Mompha* species include Onagraceae, Lythraceae, Melastomataceae, and Rubiaceae. Larvae of *M. trithalama* feed in stems, flowers, and fruits of *Clidemia* spp., *Henrietta multiflora*, and *Miconia* spp. (*M. acinodendrum, M. lanata, M. racemosa*, and *M. nervosa*). We found a new species of *Mompha* belonging to the *M. trithalama* complex (to be described by Sjaak Koster) feeding in fruits of *M. calvescens*. Females lay eggs on floral buds and fruit, and larvae penetrate and feed on the internal structures. Unlike several other species of *Mompha*, this species does not induce gall formation. Only one larva was found per fruit. When the larvae reach the last instar they turn from white to red (as occurs in other members of the genus) and eventually leave the fruit to construct a silken cocoon. The complete life cycle from egg to adult requires from 30 to 100 days. Three parasitoid species have been reared from this microlepidopteran: an undetermined Campopleginae (Ichneumonidae), *Bracon* sp. (Braconidae), and *Chelonus* sp. (Braconidae). The percentage of fruits attacked varied between 3 and 50%, depending on the season and site. Continuous rearing of *Mompha* is a remaining challenge, but the phenological breadth of structures attacked – from early floral buds to young fruit – may make this insect somewhat easier to rear than other fruit-feeders.

Other Insects

Hemiptera. Very few Heteroptera were ever observed on *M. calvescens*. A few Auchenorrhyncha were found: Acanalonidae (adults only), *Bolbonata* sp. (Membracidae) on young leaves, and *Micrutalis* sp. (Membracidae) on peduncles. The latter two appear to complete their life cycle on *M. calvescens*, but their degree of host specificity is unknown. Among Sternorrhyncha found, only Psyllidae (see above) is host specific; the others (Aleyrodidae, Coccoidea) are unlikely to be host specific.

Chrysomelidae. Two undescribed species of *Margaridisa* (Alticini) have been found all along the Pacific side of Costa Rica and in Tortuguero National Park. They have been collected from *Conostegia xalapensis*, *Miconia schlimii* (Flowers and Janzen 1997), and *M. calvescens* that we planted. Adults of these species feed on the undersides of the leaves, causing pin-holes typical of flea beetles in general. It is not uncommon to see plants with leaves riddled with these pin-holes. Larvae are unknown but are presumed to be root feeders.

Typophorus variabilis (Eumolpinae) is a very small beetle, although slightly larger than *Margaridisa*. Like *Margaridisa*, adults of this beetle feed on leaf surfaces, leaving a small hole. The two species often co-occur on the same plant, and their combined activities can remove the majority of leaf tissue of a melastome. The larval stages are unknown, but it is likely that they feed on roots of Melastomataceae (W. Flowers, pers. comm.).

Percolaspis sp. (Eumolpinae) is larger than the other two chrysomelids mentioned here. It has been collected at night on young leaves of melastomes. The damage consists of a short irregular trench in the expanding leaves. This is a taxonomically confusing group and the identity of the species taken on melastomes has not been worked out. It is possible that these are generalist feeders on young vegetation, as is the case with some other Eumolpinae (e.g. *Rhabdopterus*) (W. Flowers, pers. comm.)

Curculionoidea. *Penestes* sp. (*P. brevitarsis* is the only species reported from Costa Rica) (Erirhinidae) is a tiny weevil that occurs on the undersides of leaves of *Clidemia*, *Conostegia,* and *Miconia*. It is found along the midvein of the leaf or along the edges, and damage usually consists of a network of small holes along the margins of the leaves. The larvae breed in succulent petioles of *M. mirabilis* in Trinidad, although adults also feed on some non-melastomes such as *Begonia* (Nakahara *et al*. 1992). It is not known whether the larvae are capable of feeding in petioles of *M. calvescens*.

Copturus tricolor (Conoderinae) larvae are stem borers and the adults appear to be fly mimics. It was collected by Burkhart (1995), and has been recovered in more recent sampling, but only from a single tree near Lake Arenal. Boring by individual larvae appeared to originate in senescing inflorescences and then continued down through the center of a green stem. Larvae bored small holes to the exterior every few centimeters. Pupae were found inside stems at branch nodes. Numbers collected so far have been very low, and the level of damage does not appear to justify the effort that would be required to collect and rear large numbers.

Pedetinus halticoides (Curculioninae: Eugnomini) occurs at altitudes varying from 200 to 1,500 m. The larvae feed in fruits and seeds, but the host range of this species has not been studied. *Exophthalmus* sp. (Entiminae) adults feed on leaves, and larvae in this group of weevils feed on roots, but the larval host plants are unknown.

Lepidoptera. Larvae of an undetermined species of Gracillariidae are leaf miners on the upper surface, and those of an undetermined species of Pterophoridae feed on leaves. Larvae of two unidentified species of Oecophoridae have also been found feeding on leaves. Among Limacodidae, four species have been observed feeding on leaves of *M. calvescens*: *Epiperola paida, Isa diana, Natada* sp., and *Vipsophobetron marisa*. Most of these are probably polyphagous. *Natada* sp. was collected on mature leaves of a melastome at Guayabo and transferred to *M. calvescens*, on which it fed, but it died before completing development.

Among Lycaenidae, *Erora* (=*Thecla) opisena* and *Temecla paron* were found feeding on developing inflorescences, flower buds and immature fruits of *M. calvescens.* Ours are the

first host plant records for these rarely collected butterflies. The larvae are highly cryptic on inflorescences of *M. calvescens*, suggesting a close host relationship, although most relatives of these species are thought to be polyphagous. Another more common thecline, *Parrhasius polibetes*, which is known to be polyphagous, was also collected on *M. calvescens*. *Theritas mavors* was collected from *M. calvescens* by Burkhart (1995); we found it on *Graffenrieda* sp. (Melastomataceae) and reared it on *M. calvescens* in captivity.

In the closely related family Riodinidae, three additional species have been reported feeding on leaves of *M. calvescens* (unlike the three species of *Euselasia* mentioned above, these belong to the subfamily Riodininae). They include: *Anteros formosus micon*, *Ancyluris inca,* and *Symmachia tricolor* (in Burkhart's collection). In general these butterfly species were either rarely found or of doubtful specificity.

At least two species of inchworms (Geometridae) were found feeding on leaves of *M. calvescens*: a species close to *Isochromodes fraterna* and an unidentified species. The latter were commonly parasitized by *Euplectrus* (Eulophidae).

Larvae of three species of Notodontidae have been observed feeding on leaves of *M. calvescens*: *Meragisa* sp. (on mature leaves), *Naprepa houla* (reared in captivity), and *Rhuda difficilis.* We have found the larvae of an undetermined species of *Antiblemma* (Noctuidae: Catocalinae) feeding on young to mature leaves of *M. calvescens*. In Brazil *A. leucocyma* feeds on this plant and is very host specific, but its potential usefulness in biological control appears to be limited by its susceptibility to parasitoids (Badenes-Perez and Johnson 2008). Larvae of *Melese* sp. (Arctiidae: Arctiinae) fed on leaves of *M. calvescens*, but only two individuals have been found so far.

Hymenoptera. Larvae of *Atomacera petroa* (Argidae) rasp the surface of leaves of *M. calvescens* and *M. astroplocama* at our wettest field sites in Costa Rica. More detailed studies of this species have been carried out in Brazil (Badenes-Perez and Johnson 2007b).

Preliminary evidence suggests that several undescribed species of *Allorhogas* (Braconidae: Doryctinae) induce galls in fruits of various species of *Miconia* and *Conostegia*, and individual species appear to be highly host specific (although this requires confirmation). An undetermined (probably undescribed) species of *Allorhogas* has been found in fruits of *M. calvescens* in Brazil (Badenes-Perez and Johnson 2007a), but we have failed to find it on this plant in Costa Rica, despite intensive searching. However, we have found *Allorhogas* in fruits of other *Miconia* species and in those of *Conostegia xalapensis*. Detailed studies have been carried out on the species found on the latter plant (Chavarría *et al*. 2009).

Conclusion

Most of the herbivorous insects found in association with *M. calvescens* have little or no potential for biological control, but several species that appear host-specific and damaging to the plant have warranted careful evaluation. Although additional species may yet be discovered, we are confident that many of the natural enemies of *M. calvescens* are now known. Gaps in our knowledge of certain species remain. For example, methods for rearing *Euselasia* butterflies and *Allorhogas* gall wasps through their complete life cycles would facilitate evaluation of their host specificity and potential effectiveness. We expect that one or more of the insects studied so far in Costa Rica is likely to contribute to future control of *M. calvescens* in Hawai'i.

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Literature Cited

Alene, D.C., J. Messi, and S. Quilici. 2005. Quelques aspects de la biologie de *Diclidophlebia xuani* Messi *et al*. (Hemiptera: Psyllidae), ravageur de *Ricinodendron heudelotii* Baill. (Euphorbiaceae) au Cameroun. *Fruits* 60:279-287.

Allen, P. 2007. Demografía, patrón de supervivencia y efectos de tamaño de grupo en larvas gregarias de *Euselasia chrysippe* (Lepidoptera: Riodinidae), un potencial agente de control biológico de *Miconia calvescens* (Melastomataceae) en Hawai. MS Thesis, Escuela de Biología, Universidad de Costa Rica, San Pedro.

Badenes-Perez, F., and M.T. Johnson. 2007a. Ecology and impact of *Allorhogas* sp. (Hymenoptera: Braconidae) and *Apion* sp. (Coleoptera: Curculionoidea) on fruits of Miconia calvescens DC (Melastomataceae) in Brazil. *Biological Control* 43:317-322.

Badenes-Perez, F., and M.T. Johnson. 2007b. Ecology, host specificity and impact of *Atomacera petroa* Smith (Hymenoptera: Argidae) on *Miconia calvescens* DC (Melastomataceae). *Biological Control* 43:95-101.

Badenes-Perez, F., and M.T. Johnson. 2008. Biology, herbivory, and host specificity of *Antiblemma leucocyma* (Lepidoptera: Noctuidae) on *Miconia calvescens* DC (Melastomataceae) in Brazil. *Biocontrol Science and Technology* 18:183-192.

Broberg, C.L., J.H. Borden, and L.M. Humble. 2002. Distribution and abundance of *Cryptorhynchus lapathi* on *Salix* spp. in British Columbia. *Canadian Journal of Forest Research* 32:561-568.

Burckhardt, D., P. Hanson, and L. Madrigal. 2005. *Diclidophlebia lucens* n.sp. (Hemiptera: Psyllidae) from Costa Rica, a potential control agent of *Miconia calvescens* (Melastomataceae) in Hawai'i. *Proceedings of the Entomological Society of Washington* 107:741-749.

Burckhardt, D., E.G.F. Morais, and M.C. Picanço. 2006. *Diclidophlebia smithi* sp. n., a new species of jumping plant-lice (Hemiptera, Psylloidea) from Brazil associated with *Miconia calvescens* (Melastomataceae). *Mitteilungen der Schwiezerischn Entomologischen Gesellschaft* 79:241-250.

Burkhart, R.M. 1995. *Natural Enemies of* Miconia calvescens. Hawai‘i Department of Agriculture, Honolulu.

Chacón, M.E.J. 2007. Historia natural de *Anthonomus monostigma* (Coleoptera: Curcuilionidae) y su potencial como agente de control biológico de *Miconia calvescens* (Melastomataceae). MS Thesis, Escuela de Biología, Universidad de Costa Rica, San Pedro.

Castillo, A. 2009. Biología y comportamiento de *Ategumia lotanalis* Druce (Lepidoptera: Crambidae) como posible agente de control biológico de *Miconia calvescens* DC. (Melastomataceae), en Hawai. Tesis de Licensatura, Escuela de Biología, Universidad de Costa Rica, San Pedro.

Chavarría, L., P. Hanson, P. Marsh, and S. Shaw. 2009. A phytophagous braconid, *Allorhogas conostegia* n.sp. (Hymenoptera: Braconidae), in the fruits of *Conostegia xalapensis* (Bonpl.) D. Don (Melastomataceae). *Journal of Natural History* 43:2677-2689.

Conant, P. 2002. Classical biological control of *Clidemia hirta* (Melastomataceae) in Hawai‘i using multiple strategies. In: C.W. Smith, J.S. Denslow and S. Hight (eds.). *Workshop on Biological Control of Invasive Plants in Native Hawaiian Ecosystems.* Technical Report 129, Pacific Cooperative Studies Unit, University of Hawai‘i at Mānoa, Honolulu, HI, pp. 13-20.

Conconi, J.R.E. 1972. Descripción y biología de *Paurocephala tuxtlaensis* sp. nov. (Homoptera Psyllidae) de la región de Los Tuxtlas en Veracruz, México. *Anale del Instituto de Biología, Universidad Nacional Autónoma de México* 43:51-66.

Flowers, R.W., and D.H. Janzen. 1997. Feeding records of Costa Rican leaf beetles (Coleoptera: Chrysomelidae). *Florida Entomologist* 80:334-366.

Hanson, P.E., and I.D. Gauld (eds.). 2006. Hymenoptera de la Región Neotropical. *Memoirs of the American Entomological Institute* 77:1-997.

Meyer, J.–Y. 1998. Observations on reproductive biology of *Miconia calvescens* DC (Melastomataceae), an alien invasive tree on the island of Tahiti (South Pacific Ocean). *Biotropica* 30:609-624.

Nakahara, L.M., R.M. Burkhart, and G.Y. Funasaki. 1992. Review and status of biological control of *Clidemia* in Hawai‘i. In: Stone, C.P., C.W. Smith, and J.T. Tunison (eds.). *Alien Plant Invasions in Native Ecosystems of Hawaii, Management and Research*. Cooperative National Park Resources Studies Unit, University of Hawai‘i-Manoa, Honolulu, HI, pp. 452-465.

Nishida, K. 2007. Historia natural de dos especies de *Allograpta* (Diptera: Syrphidae) y de dos especies de *Euselasia* (Lepidoptera: Riodinidae). MS Thesis, Escuela de Biología, Universidad de Costa Rica, San Jose, Costa Rica.

Nishida, K. 2010. Life history and description of the immature stages of *Euselasia chrysippe* and *E. bettina* (Lepidoptera: Riodinidae) on *Miconia calvescens* (Melastomataceae) in Costa Rica. Submitted to *Zootaxa*.

Reichert, E. 2007. *Cryptorhynchus melastomae* (Coleoptera: Curculionidae) as a potential biocontrol agent for *Miconia calvescens* (Melastomataceae) in Hawai‘i. MS Thesis, Department of Natural Resource Sciences, McGill University, Montreal, Canada.