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THE LIFE HISTORY AND IMMATURE STAGES OF THE WEEVIL *ANTHONOMUS MONOSTIGMA* CHAMPION (COLEOPTERA: CURCULIONIDAE) ON *MICONIA CALVESCENS* DC (MELASTOMATACEAE)

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Abstract.—We describe and illustrate the life history and immature stages of *Anthonomus monostigma* Champion (Curculionidae: Curculioninae: Anthonomini). This weevil is a fruit borer in *Miconia calvescens* DC (Melastomataceae), a Neotropical tree that is invasive in Pacific islands. The larva has three instars, and development from egg to adult requires approximately two months. In Costa Rica, *A. monostigma* larvae were found in three *Miconia* species, and adults fed only on *Miconia* species. Host relationships of the *A. monostigma* group suggest that this group could be related to the *A. partiarius* and *A. albocivitensis* groups (sensu Clark 1992, 1993b). The potential of *A. monostigma* as a biological control agent is discussed.

Key Words: biological control, fruit-borer, invasive species, host plants, Costa Rica, Hawaii

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The velvet tree, *Miconia calvescens* DC (Melastomataceae), is native to the Neotropics and is invasive in Hawaii, Tahiti and other Pacific islands where it poses a serious threat to natural ecosystems because of its ability to displace native plants (Meyer 1996, 1998; Medeiros et al. 1997). Classical biological control via the introduction of natural enemies from the native (Neotropical) habitat is probably the best long-term means of managing this invasive plant (Badenes-Perez et al. 2008). For this reason researchers at the University of Costa Rica have been studying potential biocontrol agents of *M. calvescens* in its native habitat; examples of species that have been studied include a psyllid (Hemiptera) (Burckhardt et al. 2005) and riodinid (Lepidoptera) (Allen 2010, Nishida 2010). Several weevil (Curculionidae) species have also been found feeding on this plant, including *Cryptorhynchus melastomae* Champion (Reichert et al. 2010) and *Copturus tricolor* Champion in stems, and *Pedetinus halticoides* (Champion) and *Anthonomus monostigma* Champion in fruits. The latter species is the focus of the current investigation.

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The curculionid genus *Anthonomus* Germar, with over 500 species worldwide, includes about 400 Neotropical species (Clark 2008). It is the largest genus in the tribe Anthonomini and contains many species that are still undescribed. Several species are of economic importance as crop pests (Burke and Cross 1966, Dieckmann 1968, Burke 1976), while others have been proposed as biological control agents (Pedrosa-Macedo et al. 2000, Medal et al. 2002, Caxambu 2003).

Because of their host specificity and ability to damage flowers and fruits, *Anthonomus* weevils have been studied as potential biological control agents for three weeds of South American origin. These include *Anthonomus tenebrosus* Bozeman for control of *Solanum viarum* Dunal (Solanaceae) in the southeastern United States (Medal et al. 2002), *Anthonomus santacruzi* Hustache for control of *Solanum mauritianum* Scopoli (Solanaceae) in South Africa (Pedrosa-Macedo et al. 2000) and *Anthonomus partiarius* Boheman for control of *Tibouchina herbacea* Cogniaux (Melastomataceae) in Hawaii (Pedrosa-Macedo et al. 2000, Caxambu 2003).

Anthonomus monostigma, described by Champion in 1903, has been collected from Mexico to Panama (Champion 1903, O'Brien and Wibmer 1982). In Costa Rica, adults were collected on *Miconia nervosa* Triana (Melastomataceae) at the La Selva Biological Station, Heredia (Clark 1993a), but the specific nature of its host plant associations was otherwise previously unknown. Clark (1993a) classified *A. monostigma* in the *A. monostigma* species group; however, the phylogenetic relationships between this and other species groups of *Anthonomus* are unresolved (Clark 1993a). Here we describe the life history and illustrate the immature stages of *A. monostigma* and discuss its host relationships and potential as a biocontrol agent for *Miconia calvescens* DC.

Materials and Methods

This study was conducted in Costa Rica from June 2005 to December 2006 at three locations: Vereh (Cartago Province, Turrialba; 09°47′00″ N, 83°31′40″ W; 1200 m elevation), located on the Caribbean slope of the Cordillera de Talamanca with annual rainfall of 3000 mm (unpubl. data, Centro Agronómico Tropical de Investigación y Enseñanza, Turrialba); La Selva Biological Station (Heredia Province, Sarapiquí; 10°25′27″ N, 84°00′05″ W; 50 m elevation), located in the Caribbean lowlands, with an annual rainfall of ca. 4000 mm, peaking from May to December, and a mean annual temperature of 25.8 °C (Sanford et al. 1994); and the campus of the University of Costa Rica (San José Province, Montes de Oca; 09°56′16″ N, 84°03′00″ W; 1200 m elevation), located in the Valle Central, with mean annual rainfall of ca. 1800 mm, concentrated between May and November (unpubl. data 2004–2005, University of Costa Rica Meteorological Station) and a mean annual temperature of ca. 20 °C (Stiles 1990).

Larvae of *A. monostigma* were collected at Vereh from dissected fruits of *M. calvescens* and were preserved in 70% ethanol. Additional fruits were held in plastic containers (7 × 21 × 28 cm) to rear larvae to the adult stage. Adults were identified by Robert S. Anderson (Canadian Museum of Nature). Ten third instar larvae were selected for description; these were macerated and boiled in a 10% KOH solution and washed in distilled water and 95% ethanol (May 1979). These larvae, their mouthparts and four pupae were mounted in euparal on glass slides for microscopic observation and illustration. The terminology for larval and pupal descriptions follows Burke (1968) and Ahmad and Burke (1972).

To determine the number of instars, 176 preserved larvae were digitally photographed at a fixed magnification under a microscope, and widths of head capsules were measured using Imagetool 3.0 software (UTHSCSA 2002). The duration of immature stages was determined by rearing *A. monostigma* in bagged infructescences of *M. calvescens* trees cultivated on the campus of the University of Costa Rica. Groups of six adult *A. monostigma* were enclosed in seven mesh bags (10 × 15 cm), each bag covering a portion of a developing infructescence, for a period of 5–6 days to allow oviposition. After removal of adults from the bags, samples of 20–30 fruits per infructescence were dissected every five days. Ages of dissected larvae were determined by days elapsed after the removal of adults. The larval instar was determined based on head capsule width. The longevity of adults was determined by maintaining 5–20 adults in each of five petri dishes with mature and immature *M. calvescens* fruits given as food. Fresh food was supplied weekly.

The host range of *A. monostigma* was evaluated by searching selected melastome species at the La Selva Biological Station and Vereh, Turrialba. A voucher of each melastome species was deposited in the Herbarium of the University of Costa Rica. At each locality 1–15 plants of each potential host species were searched at 1–2 month intervals for one year. Plant phenology was recorded during each visit. Particular attention was given to flowers and fruits because the weevils use these structures for their development. When fruits were present, samples of approximately 20–400 fruits per melastome species were collected and taken back to the laboratory where they were dissected or kept in plastic containers for rearing.

Results

Larval development.—The frequency distribution of head capsule widths showed three separate peaks, indicating three larval instars (Fig. 1). Larvae hatched from eggs within 5–9 days of oviposition. The first, second and third stadia lasted approximately five, 10 and 20 days, respectively (Table 1). After 45 days from oviposition, when specimens were in the prepupal stage, we ran out of fruits for dissection, so it was not possible to determine the duration of the pupal stage. Adults lived up to nine weeks in the laboratory. Ten specimens of one parasitoid species, *Bracon* sp. (Braconidae), emerged from approximately 600 *M. calvescens* fruits which contained *Anthonomus* larvae. No weevil species other than *A. monostigma* were reared from *M. calvescens* fruits.

Immature stages of *A. monostigma* were monitored at Vereh during the *M. calvescens* fruiting period in 2005–2006. First instars were observed in late November 2005 and early January 2006 in small- and medium-sized immature fruits. Second instars were present between December 2005 and March 2006 in immature fruits. Third instars were observed between December and April in immature and nearly mature fruits. A few pupae were observed in March and April in mature fruits.

Host range.—At the La Selva Biological Station, 13 melastome species (Fig. 2) were surveyed for the presence of *A. monostigma*. Adults were found feeding on fruits of *Miconia affinis* DC., *Miconia impetiolaris* (Sw.) D. Don ex DC., *Miconia longifolia* (Aubl.) DC. and *Miconia nervosa* (Sm.) Triana, but larval development was detected only in fruits of *M. longifolia*. This host plant produced fruits during almost the entire year, and adult weevils were observed on *M. longifolia* during every visit (Fig. 2).

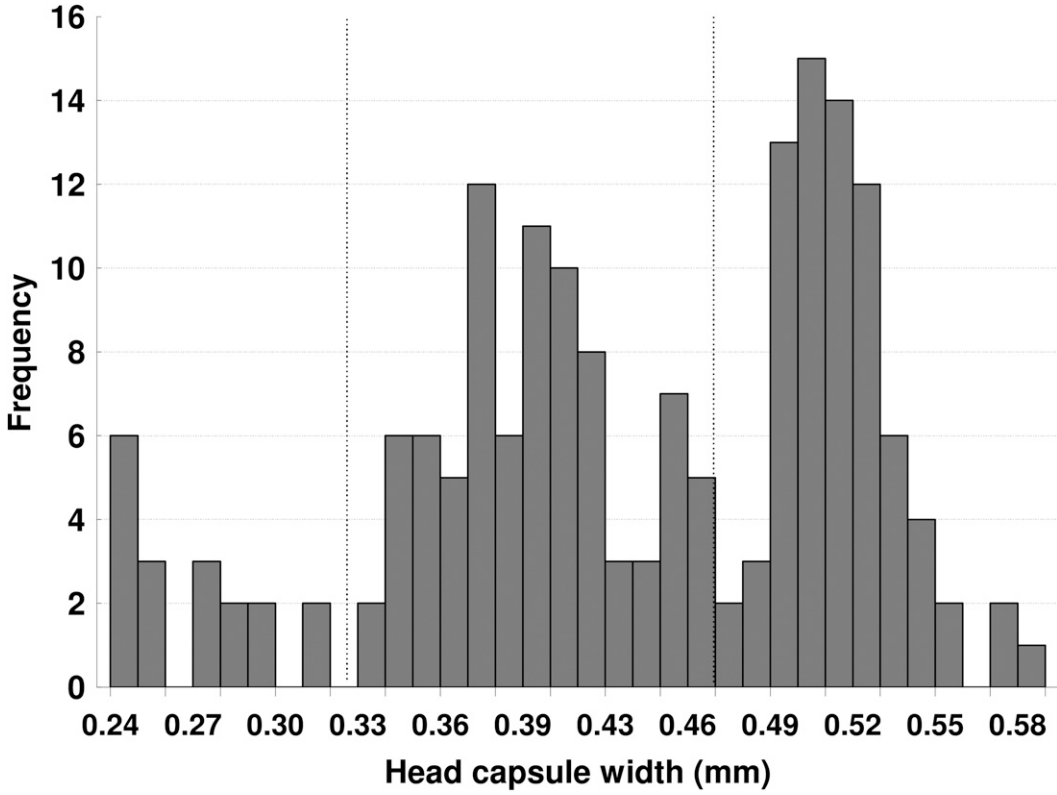

Fig. 1. Frequency distribution of head capsule widths of *A. monostigma* larvae. Vertical dotted lines indicate probable limit of each instar (n = 176).

At Vereh, 12 melastome species were surveyed (Fig. 3), and *A. monostigma* adults were found feeding on fruits of *M. affinis*, *M. calvescens* and *Miconia nutans* Donn. Sm. Larval development was detected only in fruits of *M. affinis* and *M. calvescens*. Neither *M. affinis* nor *M. calvescens* fruited year-round, but fruits of one or the other of these species were present throughout the year (Fig. 3).

Description of last instar larva (Fig. 4).—Body moderately convexly curved dorsoventrally, white, length 2.42 ± 0.03 mm (mean ± SD; n = 6).

Head: 0.51 ± 0.02 mm wide (n = 33), hypognathous, semicircular, sclerotized, yellow orange, slightly retracted in prothorax. Epicranial suture nearly half of head length, frontal suture forming "V" and reaching antennal base. Mandibles, setae and sensilla reddish. Antenna 1-segmented, with sensorium encircled by sensorial papillae on basal membrane. Frontal seta 4 long; setae 1, 3, and 5 very reduced and inconspicuous; frontal seta 2 absent. Four pairs of dorsal epicranial setae present; seta 1 slightly shorter than others; setae 2 and 4 similar in length; seta 3 absent or not evident; and seta 5 nearly twice the length of setae 2 and 4. Four short and obscure posterior epicranial setae present. Two lateral epicranial setae present and equal in length. One pair of stemmata apparent, each positioned anterior to epicranial seta 5 and near frontal suture. Clypeus with two inconspicuous setae on each side with one sensillum between them. Labrum with three pairs

Table 1. Frequency of *A. monostigma* larvae in *M. calvescens* fruit exposed to adults for 5–6 days. Fruits were dissected at several time periods after removal of adults to estimate time of development.

Days since removal of adults	Number of larvae per instar			Number of fruits dissected
	1st instar	2nd instar	3rd instar	
5	-	-	-	150
10	7	-	-	132
11	-	-	-	20
15	12	4	-	119
16	-	-	-	19
20	-	14	-	143
21	-	2	-	10
25	-	2	12	67
30	-	-	16	66
35	-	-	14	72
38	-	-	3	16
40	-	-	11	55
45	-	-	15	49
Totals	19	22	71	918

of setae and one pair of sensilla. Epipharynx bearing six anterolateral and four anteromedial setae; labral rods moderately long, converging posteriorly; four epipharyngeal sensory pores arranged in two clusters with two pores in each. Mandibles robust and pyramidal, dark orange, with two apical brown teeth, two mandibular setae equal in length, and two sensilla. Maxillary palpus with two segments; basal segment longer and wider than apical segment. Two sensilla and one short bristle on basal segment; apical segment with at least two tiny palpal setae. Mala with six dorsal malar setae equal in length, five ventral malar setae and a sensillum. Four stipital setae: 1 slightly longer than or equal to seta 4, 3 slightly shorter than 4, and 2 reduced. Labial palpus consisting of two articles, each with one sensillum; premental sclerite with long posteromedial extension; premental setae equal to stipital seta 3; glossa bearing four minute setae; postmental setae 1 and 3 short, 2 slightly longer than stipital seta 1.

Thorax and abdomen (description of left lateral aspect of body, Fig. 4): Thoracic spiracle bicameral, its air tubes with 6–8 annuli. Pronotum with three long setae and one minute seta near spiracle. Mesothorax and metathorax segments with two folds. Prodorsum of mesothorax and metathorax with one moderately long seta. Postdorsum of mesothorax and metathorax without evident setae. Epipleural lobe of mesothorax and metathorax with one long and one minute seta. Pedal area of each thoracic segment with five setae, two long and three minute. One pair of sternal setae evident only on segment I. Abdominal segments with eight pairs of lateral bicameral spiracles, their air tubes with 4–9 annuli, spiracle 8 generally with more annuli and larger than others. Segments I–VIII each with one minute prodorsal seta and five postdorsal setae, setae 1, 2 and 4 minute, setae 3 and 5 long. Spiracular area with two minute or inconspicuous setae. Epipleurum of segments I–VIII with one seta as long as postdorsal long setae and one very short seta. Pleuron with one long and one minute seta. Pedal area with one minute or inconspicuous seta. Anus subterminal.

Description of pupa (Fig. 5).—Length 2.27 ± 0.05 mm (n = 11). Body yellow white; eyes creamy white in color, brown when mature. Rostrum with one pair of short distirostral setae located on conical tubercle. One pair of basirostral setae, like distirostral setae in shape and length, also located on small conical tubercles. Head with one pair of small frontal setae. Supraorbital setae absent. Prothorax with slender and slightly curved pronotal setae, all similar in length; each located on conical tubercle. Two pairs of anterolateral setae. One pair of anteromedial setae slightly more widely separated than one pair of dorsomedial setae located posteriorly. One pair of posteriomedial and three pairs of posterolateral

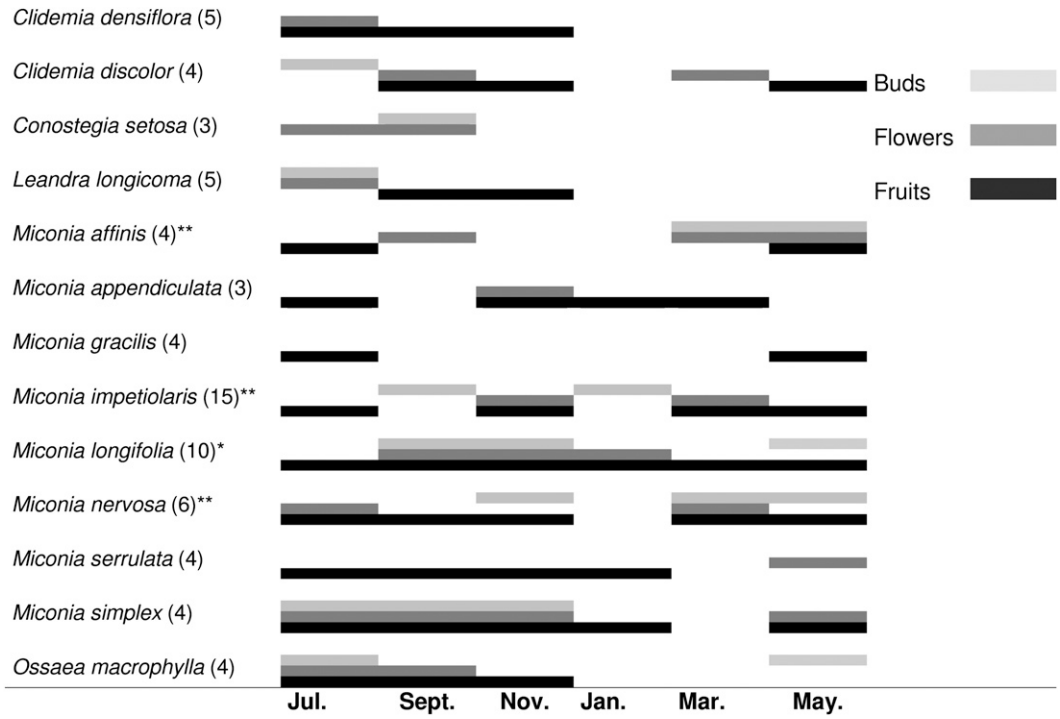

Fig. 2. Bimonthly reproductive phenology of melastome species surveyed as potential *A. monostigma* hosts between July 2005 and May 2006 in La Selva. Numbers of trees sampled in parentheses; * = host fruit utilized by *A. monostigma* larvae and adults; ** = fruits eaten by adults.

setae, all set on tubercles, arranged in strongly curved row on each side. Mesonotum with two pairs of setae, similar in length and borne on tubercles. Metanotum with three pairs of setae, similar in length, two inner setae closer to each other than to outer seta. Abdomen with five pairs of discotergal setae on terga I–VI, three of these slender, curved and borne on small tubercles, other two small, not evident or absent in some cases. Three pairs of discotergal setae on terga VII and VIII, setae slender, curved and borne on tubercles. Laterotergal seta 1 minute and laterotergal seta 2 long, slender and borne on spinelike tubercle. Spiracles evident only on first five segments. Abdominal sternal setae absent. Segment IX without setae and prolonged into sclerotized median process terminating in double hook (like inverted T).

Discussion

This is the first formal description of immature stages for any species in the *A. monostigma* species group. Keys for the immature stages of *Anthonomus* are only available for a few species principally belonging to the *Anthonomus grandis* Boheman species group (Ahmad and Burke 1972). Three dorsal folds in abdominal segments, the subterminal anus and the absence of frontal seta 2 in *A. monostigma* larvae are diagnostic characters found in all Anthonomini species (Ahmad and Burke 1972). Compared with described larvae of other *Anthonomus* species, *A. monostigma* larvae differ by having frontal setae 1, 3 and 5 very short and only frontal seta 4 long (Burke and Gates 1974, Clark and Burke 1986, Caxambu 2003). The pupa of *A. monostigma* differs considerably

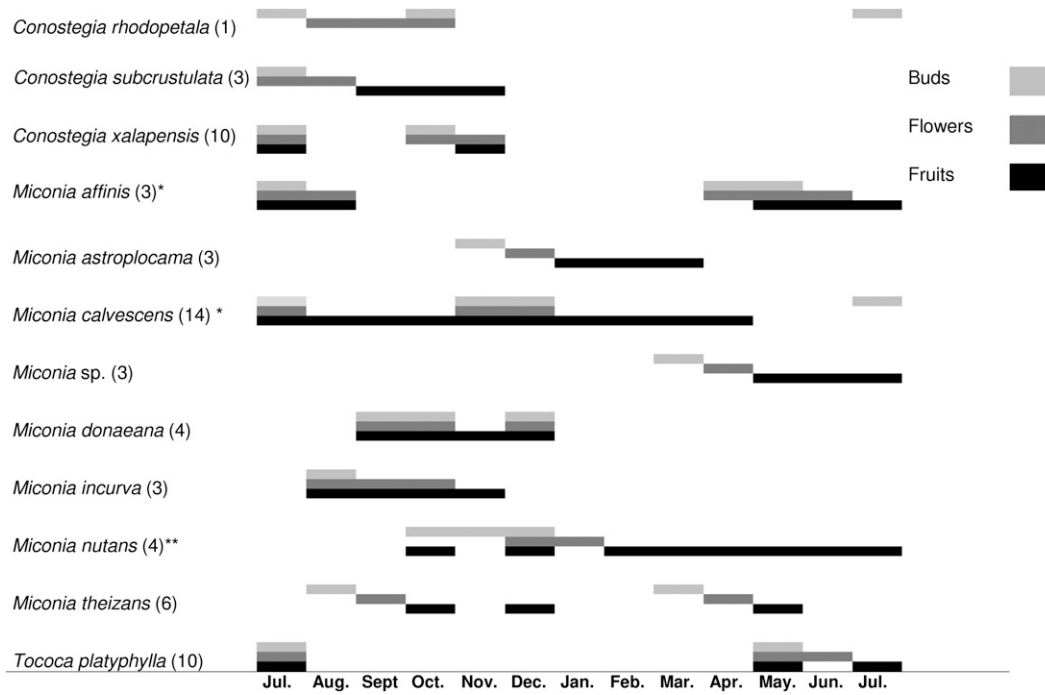

Fig. 3. Monthly reproductive phenology of melastome species surveyed as potential *A. monostigma* hosts between July 2005 and May 2006 in Vereh, Turrialba. Numbers of trees sampled in parentheses; * = host fruit utilized by *A. monostigma* larvae and adults; ** = fruits eaten by adults.

from pupae of other *Anthonomus* described by Burke (1968) in that *A. monostigma* has a single posterior process on segment IX, similar to *Pseudanthonomus validus* Dietz (Burke 1968). Other *Anthonomus* species and *Pseudanthonomus krameriae* Pierce have a paired process on segment IX (Burke 1968, 1972).

Three is the most common number of larval instars in the Anthonomini (Ahmad and Burke 1972, Burke 1976), and *A. monostigma* shares this trait with *A. grandis* (Parrott et al. 1970), *Anthonomus eugenii* Cano (Patrock and Schuster 1992) and *A. partiarius* (Caxambu 2003). Although this character may seem of little importance, it is highly conserved (Burke 1976). The development from egg to adult required approximately two months in *A. monostigma*, substantially longer than some *Anthonomus* species that can complete their development in less than a month (Burke and Woodruff 1980). However, several temperate species feed over a period of several months during the winter (e.g., *Anthonomus piri* Kollar in the buds of pear and, rarely, apple trees (Dieckmann 1968)). The period of larval development time is likely tied to time for fruit development and maturation in hosts of *A. monostigma*. As in other anthonomine species, pupation occurs within the same plant part where the larva develops (Burke 1976).

The phylogenetic relationships between the *A. monostigma* group and other groups are unresolved (Clark 1993a). Host plant associations in species of *Anthonomus* seem to be useful for establishing phylogenetic relationships between and within groups (Clark and Burke 1996, W. Clark pers. comm.). The only other *Anthonomus*

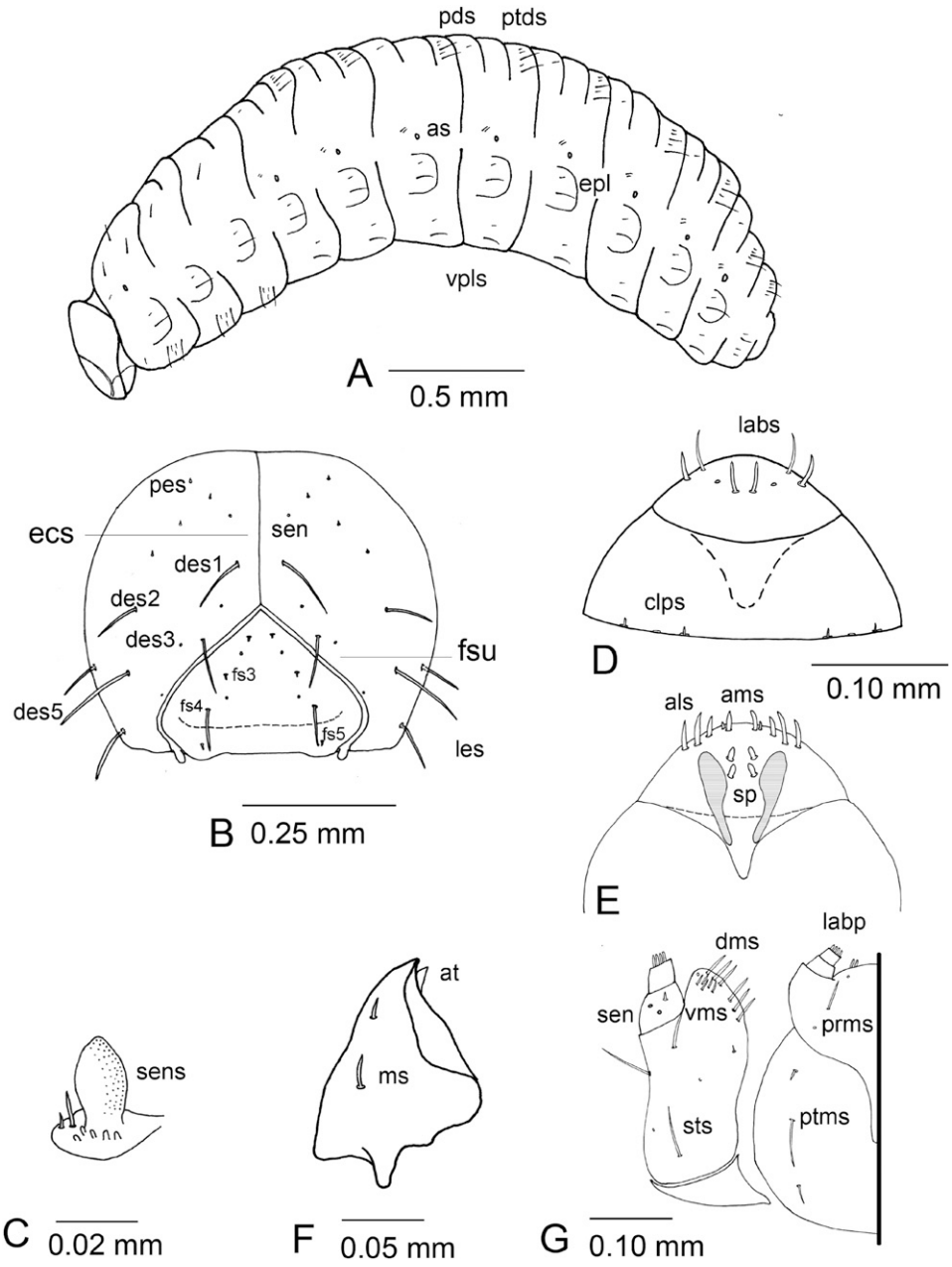

Fig. 4. Last instar larva of *Anthonomus monostigma*. A, Entire larva, lateral view: as = abdominal spiracle, epl = epipleurum, pds = prodorsal seta, ptds = postdorsal setae, vpls = ventropleural seta; B, Head capsule: des = dorsoepicranial seta, ecs = epicranial suture, fs = frontal seta, fsu = frontal suture, les = lateral epicranial setae, pes = posteroepicranial setae, sen = sensilla; C, Antenna: sens = sensorium; D, Clypeus and labrum: clps = clypeal setae, labs = labral setae; E, Epipharynx: als = anterolateral setae, ams = anteromedial setae, sp = sensorial pores; F, Mandible: at = apical tooth, ms = mandibular seta; G, Maxilla and labium: dms = dorsal malar setae, labp = labial palpi, prms = premental seta, ptms = postmental setae, sen = sensilla, sts = stipital seta, vms = ventral malar setae.

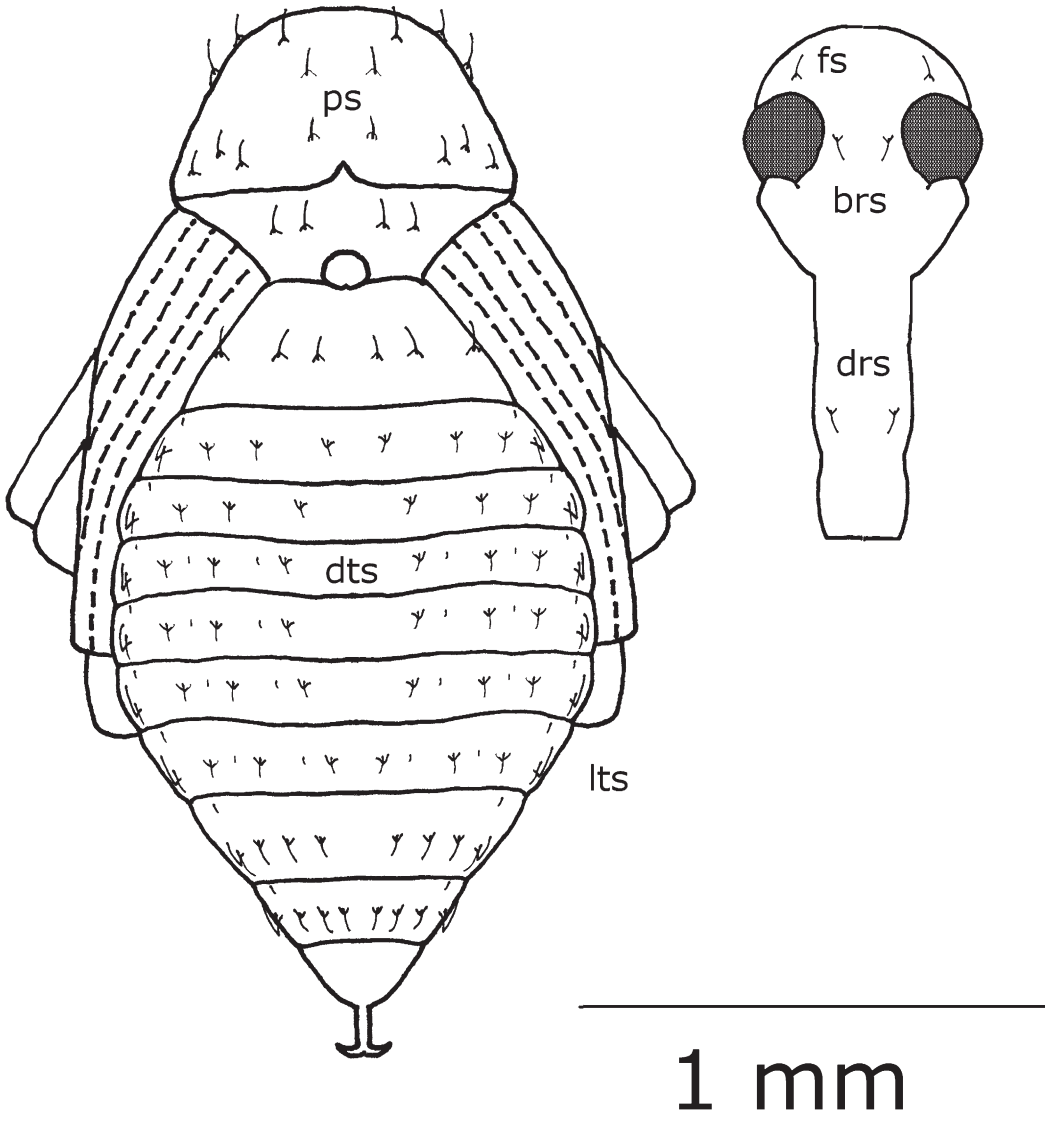

Fig. 5. Pupa of *Anthonomus monostigma*. A, Dorsal view: dts = discotergal setae, lts = laterotergal setae, ps = pronotal setae; B, Frontal view of head and rostrum: brs = basirostral setae, drs = distirostral setae, fs = frontal setae.

species previously known to utilize host plants in the family Melastomataceae are *Anthonomus coactus* Clark, *A. partiarius* and *Anthonomus opis* Clark, all in the *A. partiarius* group (Clark 1992, Caxambu 2003). According to Clark (1993b), the *A. partiarius* group could be related to the *Anthonomus albocivitensis* Clark group because both groups have sclerotized enlargements of the ejaculatory duct. Recently *Anthonomus stellatus* Clark, belonging to the *A. albocivitensis* group, was reared from fruits of *Conostegia oerstediana* O. Berg ex Triana (Melastomataceae) (E. Chacón unpubl.), supporting the link with the *A. partiarius*

group suggested by Clark (1993b). Given that the known host plants of *A. monostigma* are Melastomataceae, the *A. monostigma* species group also appears to be related to the *A. partiarius* and *A. albocivitensis* groups. However, in addition to this host range, morphological or molecular studies are needed to definitively discern the phylogenetic relationships among these species groups (W. Clark pers. comm).

Anthonomus species are associated with a broad range of flowering plants, with larvae occurring in 22 plant families across 13 orders. However, individual species appear to be narrowly specialized without exception. Each of the 113 species with recorded larval host plants has been reported from just a single plant family and may be restricted to a few closely related plant species within the same genus (Anderson 1993, Jones 2001). *Anthonomus* larvae commonly develop in floral buds or fruits, but some species induce galls or are inquilines in galls induced by other organisms (Burke 1976). There is little information about adult diet, but *Anthonomus* adults may be less specific than their larvae. For example, adults of *A. grandis* are known to feed on pollen of five different plant families (Cuadrado 2002).

Although we did not search for *A. monostigma* weevils in plant families other than Melastomataceae, finding this species only in a few *Miconia* species and no other genera suggests it is very narrowly host specific. Physiological and ecological factors governing host use by *A. monostigma* will require additional study. Reproduction in just one host at La Selva versus two hosts at Vereh may have been a function of fruit production at each site given that *M. longifolia* fruits were available year-round at La Selva (Fig. 2), whereas each of the two larval hosts at Vereh produced fruits for only part of the year (Fig. 3). Preference for *M. longifolia* over *M. affinis* for reproduction was notable at La Selva, suggesting that the use of *M. affinis* at Vereh may have resulted from seasonal absence of *M. calvescens* fruit. Elevated levels of feeding by weevils on the few *M. calvescens* fruiting structures that matured out of season at Vereh provide additional circumstantial evidence that *A. monostigma* is highly host specific and has a strong preference for *M. calvescens* fruit at this site (Chacón-Madrigal 2007).

To adapt to seasonal scarcity of host fruit, *A. monostigma* may need to survive for long periods as adults. Adults lived for nine weeks in the laboratory, but we have no knowledge of how long or where this weevil might remain concealed away from host plants in the field. Some *Anthonomus* species are known to overwinter for almost a year as adults, waiting for fruit in which to lay eggs (Burke 1976).

Classical biological control has been identified as an essential tool for long term management of *M. calvescens* in Pacific islands (Smith 2002). The potential for *A. monostigma* as a biological control agent appears high given its host specificity and possible impacts on seed production (E. Chacón unpubl.). Restriction to the genus *Miconia* would be a suitable level of specificity in Tahiti where there are only a few native melastome species, and family-level specificity likely would be suitable in Hawaii, where there are no native Melastomataceae (Wagner et al. 1990). Although the reproductive phenology of *M. calvescens* may limit its suitability as a year-round host for *A. monostigma* in Costa Rica (Chacón-Madrigal 2007), this does not appear to be a barrier in Pacific islands, where there are multiple reproductive events per year, and fruits can be present all year (Meyer 1998). Because the success of *M. calvescens* as an invasive plant

is largely due to its prolific production of bird-dispersed seeds (Medeiros et al. 1997, Meyer 1998), fruit-feeding specialists such as *A. monostigma* merit consideration for their potential to slow the spread of *M. calvescens* into new areas (Badenes-Perez et al. 2008).

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