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Classical Biological Control of Brazilian Peppertree (*Schinus terebinthifolia*) in Florida[1]

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Brazilian peppertree, *Schinus terebinthifolia* Raddi (Anacardiaceae), also known as Christmasberry, Florida Holly, and aroeira (Brazil), is an aggressive, rapidly colonizing invasive weed of disturbed habitats, natural communities and conservation areas in peninsular Florida (Cuda et al. 2004, Cuda et al. 2006, Manrique et al. 2013). Native to Argentina, Paraguay, and Brazil, Brazilian peppertree was introduced into Florida as a landscape ornamental in the late 19th century. The popularity of Brazilian peppertree as an ornamental plant can be attributed to the numerous bright red drupes (fruits) produced during the October to December holiday season (Figure 1). Grown as a substitute for the more traditional English holly (*Ilex aquifolium* L.), Brazilian peppertree was common in cultivation in Florida during the first half of the 20th century. However, this relative of poison ivy was a rare component of the native flora in Florida until the late 1950s when the first naturalized plants were discovered in Monroe County.

Brazilian peppertree currently dominates entire ecosystems in south-central Florida (Cuda et al. 2006). It is considered an important invader of the Everglades National Park and poses a significant threat to ongoing Everglades restoration efforts (Rodgers et al. 2014). Brazilian peppertree also is one of the costliest upland invasive plants in Florida. State agencies spend nearly $3 million each year for its control (Hiatt et al. 2019). Once established, Brazilian peppertree quickly displaces the native vegetation, often forming dense monocultures that reduce the biological diversity of plants and animals in the invaded area. Although herbicides (http://edis.ifas.ufl.edu/aa219) and mechanical or physical control practices (e.g., cutting, burning, and flooding) are routinely used often in combination for controlling existing stands (http://ipm.ifas.ufl.edu/pdfs/BPmanagPlan.pdf), these conventional methods are expensive, labor intensive, and provide only temporary control due to the plant's regenerative capacity. Furthermore, nonselective chemical and mechanical controls are unsuitable for sensitive natural areas (e.g., coastal mangrove forests) because they can have negative effects on nontarget species and increase water pollution. Minimizing the use of herbicides and other nonselective control practices is needed to maintain the integrity of Florida's fragile environment and natural resources. Biological control—the introduction of host-specific natural enemies into Florida that are capable of selectively damaging Brazilian peppertree—will accomplish this goal.

In the 1980s, Brazilian peppertree was identified as a suitable target for introductory or classical biological control (Habeck et al. 1994). Biological control is an appropriate management tactic because the invasive characteristics exhibited by Brazilian peppertree are consistent with the enemy release hypothesis (Williams 1954). The key

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elements of this hypothesis are that (a) native host-specific enemies strongly control the abundance and distribution of native plants; (b) escape from host-specific enemies is a key contributor to exotic plant success; and (c) enemy escape benefits exotic plants because they gain a competitive advantage over native plants as a result of being liberated from their herbivores. Also, because no native species in the genus *Schinus* occur in the United States, the potential for nontarget damage by approved biological control agents would be low.

Figure 1. Leaves and fruit of Brazilian peppertree.
Credits: A. Murray, University of Florida, Center for Aquatic and Invasive Plants (used with permission).

Several insects have been identified from exploratory surveys conducted in Argentina, Brazil, and Paraguay as potential biological control agents of Brazilian peppertree (Habeck et al. 1994, Hight et al. 2002, Cuda et al. 2006, McKay et al. 2009). The following insects were selected for further study because they visibly damage the plant in its native range and were collected only from Brazilian peppertree or a few closely related species during field surveys.

Brazilian Peppertree Thrips, *Pseudophilothrips ichini*

The biology and field host range of *Pseudophilothrips ichini* (Hood) (Thysanoptera: Phlaeothripidae) were studied in southeastern Brazil (Garcia 1977). *Pseudophilothrips ichini* has not been observed feeding on plants other than Brazilian peppertree in its native range (Garcia 1977, J. H. Pedrosa, personal observation). Because this thrips was found attacking only Brazilian peppertree in field surveys, Garcia (1977) suggested that *P. ichini* might be a good candidate for biological control of this invasive weed. Recently, *P. ichini* was found to be a complex of two cryptic species (Cuda et al. 2009, Mound et al. 2010).

The life cycle of *P. ichini* begins when the female deposits her eggs on the leaves of the plant. After hatching, the immature thrips undergo two larval instars that are the active feeding stages. The wingless larvae are red or orange in color (Figure 2). As soon as the larval feeding phase is completed on the host plant, the remainder of the life cycle occurs in or on the soil. Unlike other families of the Thysanoptera that have only two pupal instars (the propupa and pupa), thrips belonging to the family Phlaeothripidae that includes *P. ichini* are unique in that they undergo three nonfeeding pupal instars (the propupa, pupa I and pupa II) instead of two (Mound and Marullo 1996). Although these developmental phases are not true larvae or pupae, these terms are commonly used to describe the immature stages in a thrips life cycle.

Figure 2. *Pseudophilothrips ichini*, a thrips that kills the shoot tips of Brazilian peppertree. Adult female (left); larvae on young stem (right).
Credits: (adult) M. Vitorino, University of Blumenau; (larvae) V. Manrique, University of Florida

Adults of *P. ichini* are black, winged, and relatively small (3–6 mm) (Figure 2) but have a high reproductive rate. *Pseudophilothrips ichini* is polyvoltine; up to four generations per year have been observed in Curitiba, Brazil, and it is considered a common species in its native range (Garcia 1977). Mating is not required to produce offspring. Unmated females deposit eggs that develop only into males whereas mated females produce eggs that develop into females (Mound and Marullo 1996). This form of parthenogenetic reproduction is called arrhenotoky.

In Brazil, the adults overwinter on Brazilian peppertree. In early spring (September), females start laying eggs singly or in small groups on the leaflet pedicels and blades, or on the new tender shoot growth. The duration of the immature stages is variable, depending on climate and other factors. The larvae hatch from the eggs in 7–8 days at 24°C. The first and second instars last 6 days and 11–12 days, respectively.

The two nonfeeding prepupal and pupal stages require ~ 8 days to complete their development. After transformation to the adult stage, females undergo a 5 to 15 day preoviposition period, and can oviposit up to 220 eggs during their lifetime (45–78 days). Duration of the complete life cycle for *P. ichini* is temperature dependent. For example, the life cycle from egg to egg was completed in 76 days at 18°C, 38 days at 24°C (Garcia 1977), and 20 days at 27°C (Wheeler et al. 2016), Under laboratory conditions, adults lived on average 78 days at 23.1°C and 50 days at 27°C (Garcia 1977, Wheeler et al. 2016) when maintained in vials provided with food.

Both the larval and adult stages damage the plant. Larvae of *P. ichini* usually are found clustered around the stem of a tender shoot (Figure 2). They feed by rasping and sucking the plant sap, which frequently kills the growing tip. Adults are usually found on the new unfolding leaves where they feed, mate, and oviposit. Although they can be more randomly distributed on the plant, adults usually are found aggregated with the developing larvae. Adults also will feed on the flowers, causing them to abort. This type of feeding damage can inhibit seed production in mature plants and has been shown to reduce the growth rate of younger plants (Furmann et al. 2005). In addition, there is anecdotal evidence suggesting that feeding damage by *P. ichini* promotes infection by plant pathogens that contributes to shoot death (R. Barreto, pers. comm.).

The laboratory host range of *P. ichini* was investigated in approved Florida containment laboratories (Cuda et al. 2009, Wheeler et al. 2017). A petition to release *P. ichini* from quarantine was initially prepared and submitted to the federal interagency Technical Advisory Group for the Introduction of Biological Weed Control Agents, or TAG (http://edis.ifas.ufl.edu/in607) in November 1996. Request for field release was initially denied because the biological and host range testing data presented in the original petition did not adequately address the risk to native Caribbean plant species and to the closely related California peppertree, *Schinus molle* L., a common introduced ornamental in southern California. A new petition to release the thrips in Florida was prepared and resubmitted to the TAG in October 2002 (Cuda et al. 2002). The revised petition adequately addressed all of the concerns raised by reviewers in the earlier petition, and the TAG recommended field release of *P. ichini* in May 2007. However, because of the cryptic species issue (Mound et al. 2010), TAG withdrew the recommendation for field release until the host range of the species complex was resolved. The release of *P. ichini* from quarantine was finally recommended by TAG in May 2016, and it was released in Florida on 16 July 2019. This is the first insect released for biological control of Brazilian peppertree in the continental United States.

Brazilian Peppertree Sawfly, *Heteroperreyia hubrichi*

Heteroperreyia hubrichi Malaise (Hymenoptera: Pergidae) is a primitive nonstinging wasp native to northern Argentina and southeastern Brazil. The biology, ecology, and host range of the sawfly *H. hubrichi* were investigated in Brazil, Florida, and Hawaii (Vitorino et al. 2000, Medal et al. 1999, Hight et al. 2002, Cuda et al. 2005). The larval stage of this insect is phytophagous (plant feeding). The adults are black with yellow legs (Figure 3), and the sexes can be separated on the basis of size (females are larger), the presence of the ovipositor in females, and also antennal morphology. Field data collected in Brazil indicate this species is bivoltine (two generations per year). Sex ratio of the adults is approximately 1:1 (males to females) when reproduction is bisexual, but the sawfly also exhibits arrhenotoky; mated females produce females and unmated females produce only males. In Brazil, a pupal diapause period occurs in the summer (December to February) and winter (June to August).

Figure 3. *Heteroperreyia hubrichi*, a defoliating sawfly of Brazilian peppertree. Adult female guarding egg mass inserted into stem (left); gregarious larvae feeding on leaflet (right).
Credits: J. C. Medal, University of Florida.

Upon emergence from the pupal stage, females mate and/or oviposit in young woody branches that are adjacent to the more tender terminal shoots. This behavior enables the sawfly to avoid the toxic resin common in the Brazilian peppertree's terminal growth. The female uses her saw-like ovipositor to cut the stem tissue and insert her eggs between the thin bark and the phloem, the vascular tissue that transports nutrients from the leaves (Figure 3). The eggs are elliptical in shape and are deposited side by side in long rows of variable length and number. Females exhibit

maternal behavior by guarding the egg masses during the incubation period, but die as soon as the first larvae hatch.

The period of egg maturation is about 15 days. The number of eggs is directly linked to the size of egg mass. The average number of eggs per mass is ~ 100. Females prefer to oviposit on plants that are < 3 m in height, and select young branches with a diameter between 2.5 to 5 mm for oviposition. In Brazil, the majority of sawfly egg masses (76.5%) occurred on plants with hairy leaves (varieties *pohlianus* and *rhoifolius*). However, in laboratory and greenhouse studies, sawflies readily accepted var. *raddianus*, the smooth variety of Brazilian peppertree that commonly occurs in Florida.

The larvae are bright green with a black head capsule (Figure 3) and have red areas at the end of abdomen and adjacent to the head capsule in the last two instars. The larval stage has seven instars in the females and six in the males. The duration of the larval stage (from emergence of the neonate larvae to pupation) is 45 days. The prepupal phase is characterized by the change in the size of the last instar larvae (25% smaller), and cessation of feeding. In this phase, the larvae burrow in the soil to a depth ranging from 3 to 4 cm to pupate. The pupation chamber acquires the color of the surrounding soil, and is ~ 1 cm in length, and ~ 0.5 cm in width. The pupal stage lasts from 1 to 5 months, with an average of 4 months.

The larva of *H. hubrichi* is the damaging stage. Developing larvae are voracious leaf feeders (Figure 3) and can cause complete defoliation of Brazilian peppertrees depending on the size of the plant and quantity of larvae present. This type of feeding damage could severely injure or kill young plants and prevent older plants from reproducing, which would reduce the competitive advantage that Brazilian peppertree currently holds over native vegetation. In Brazil, it is not uncommon to find Brazilian peppertree shrubs and more rarely trees completely defoliated by the sawfly. Larvae are gregarious in the early instars and feed in groups on tender leaves, mainly on new shoots. When the larvae reach the third instar, they disperse over the plant and attack leaves of all age classes.

Because the entire life cycle from adult to adult can be completed in less than 4 months under ideal conditions, this insect may be capable of producing two or three generations per year in central and south Florida where Brazilian peppertree is a severe problem. Simulated herbivory studies conducted under field conditions in south Florida over a 2-year period have shown that growth and reproduction of Brazilian peppertrees are severely impacted when the plants are subjected to multiple defoliations within the same growing season (Treadwell and Cuda 2007).

The TAG recommended field release of the defoliating sawfly *H. hubrichi* in Florida in 1997. However, a release permit was not issued by APHIS PPQ because of concerns raised about toxins present in the larvae, which could have a negative impact on native fauna if the larvae were ingested. Nevertheless, temporary releases of the sawfly have been proposed for risk assessment purposes by taking advantage of the insect's parthenogenetic reproduction (Cuda 2016). For example, by conducting single sex releases, the negative effects of male larvae produced by unmated females on native birds and mammals could be monitored during the temporary field evaluations of the biocontrol agent. If unanticipated damage to nontarget flora or fauna from the male larvae was discovered during or soon after the unmated female sawfly releases, then no further releases would be made. Stopping the sawfly releases would effectively prevent the insect from establishing permanent, reproducing populations (Cuda 2016).

Brazilian Peppertree Leaflet Roller, *Episimus unguiculus*

Episimus unguiculus Clarke, previously known as *E. utilis* Zimmerman (Lepidoptera: Tortricidae), was introduced into Hawaii for classical biological control of Brazilian peppertree in the 1950s (Krauss 1963). Martin et al. (2004) investigated the biology of *E. unguiculus* in the process of establishing a laboratory colony for conducting host range tests in an approved Florida containment laboratory. Adults (Figure 4) are small, grayish brown moths with distinctive markings on the forewings. When at rest, the adults are cryptically colored, resembling either tree bark or bird droppings. Sexes can be readily separated without magnification by examining the wing pattern. Average life span for the adult moths is 8 to 9 days, and development from egg to adult stage occurs in about 42 days.

Females can deposit up to 172 eggs during their lives. Eggs are usually deposited singly but occasionally in groups of up to six eggs on the upper and lower surfaces of Brazilian peppertree leaflets. The eggs, which are glued to the leaflet, are compressed, ovoid, and light green in color with a smooth chorion when first deposited but darken as they develop. The thin, scalelike shape and transparency of freshly deposited eggs probably afford them some protection from predation and possibly parasitism.

The caterpillar (or larval stage) of *E. unguiculus* (Figure 4) attacks the foliage of Brazilian peppertree. Early instars

are tan to light green in color, but as they reach maturity, the larvae turn bright red before pupating and are approximately 15 mm long. The larval stage has five instars, although a sixth instar may occur on occasion.

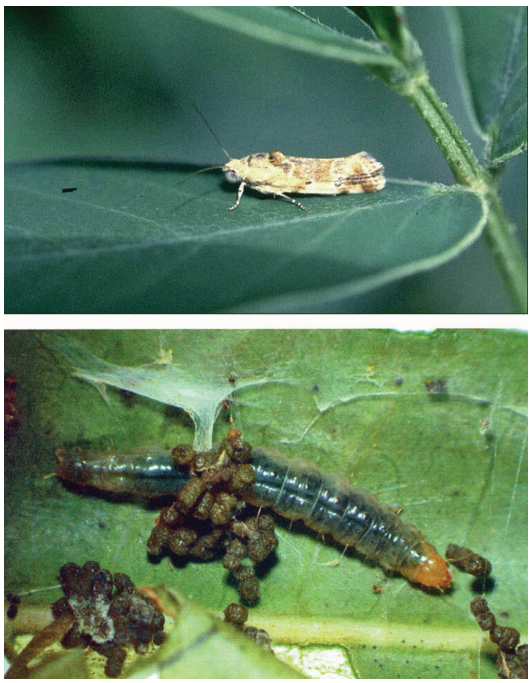

Figure 4. Adult (top) and mature larva (bottom) of *Episimus unquiculus*, a leafrolling moth introduced into Hawaii for biological control of Brazilian peppertree.
Credits: Photo of larva by M. Fukada, Hawaii Department of Agriculture (Used with permission).

Feeding habits of the larvae vary depending upon their age. Newly hatched larvae and early instars feed by scraping the surface of the leaflets. Early instars are leaflet tiers, and normally feed between young and expanding leaflets that have been tied together with silk. The first to third instars typically web together two or more adjacent leaflets flat against each other. Older larvae bind single leaflets into the characteristic cylindrical roll that is usually associated with *E. unguiculus* in nature. A cohort of approximately 35 larvae is capable of completely defoliating a 0.5 m tall Brazilian peppertree potted plant in less than three weeks (Martin et al. 2004). The results of a recent study by Manrique et al. (2009) showed that high levels of defoliation by *E. unguiculus* significantly reduced the number of leaflets, plant height, foliar biomass, relative growth rate (RGR), and shoot:root ratio of potted Brazilian peppertrees. Moreover, plants were not able to recover from the effects of the herbivory after 2 months.

Unlike the sawfly *H. hubrichi* that pupates in the soil and is vulnerable to flooding and possibly ant predation, mature larvae of *E. unguiculus* pupate in the tree canopy inside rolled leaflets attached to the plant. Pupae are brown in color with the head, appendages, and wings darker than the abdomen.

In Hawaii, where it was released in the 1950s, *E. unguiculus* is widely distributed on Brazilian peppertree, but the insect apparently is not sufficiently abundant to severely damage the plant (Yoshioka and Markin 1991; J.P. Cuda 2002, personal observation). The ineffectiveness of *E. unguiculus* as a biological control agent in the Hawaiian Islands may be due in part to biotic mortality factors unique to that environment. For example, two wasps that were introduced into Hawaii for classical biological control of the sugar cane leafroller *Hedylepta* (=*Omiodes*) *accepta* (Butler) were discovered attacking *E. unguiculus* soon after it was released against Brazilian peppertree (Krauss 1963).

Although satisfactory biological control of Brazilian peppertree by *E. unguiculus* was not achieved in the Hawaiian archipelago, this failure should not preclude the introduction of the insect into Florida. *Episimus unguiculus* could be a more effective biological control agent of Brazilian peppertree in Florida because it would be introduced into a new environment where biotic mortality from introduced and native parasitoids and predators may be less severe compared to Hawaii. Host range testing was completed, and a release petition was submitted to the TAG in September 2009, later revised and resubmitted in September 2012 (Cuda et al. 2019). However, TAG did not recommend field release in Florida because of the risk of apparent competition with native *Episimus* spp., and also the potential for the insect to attack cultivated pistachio in the unlikely event that *E. unguiculus* emigrated to southern California and Arizona. The risk to nontarget insects and plants from *E. unguiculus* could be field tested using the F1 Sterile Insect Technique (Cuda 2016). Production of F1 sterile progeny would be obtained by exposing the parental generation to low doses of gamma radiation (Moeri et al. 2009). This would facilitate observations on survival and impact of the F1 larvae on nontarget plants under actual field conditions with no risk of permanent establishment, because the adults produced from the F1 larvae are completely sterile.

Brazilian Peppertree Stem Boring Weevil, *Apocnemidophorus pipitzi*

Surveys conducted recently in northern Argentina (McKay et al. 2009), and southeastern Paraguay revealed the presence of several new natural enemies of Brazilian peppertree. Among these were two species of stem boring weevils belonging to the genus *Apocnemidophorus* Hustache. The weevils resemble bird droppings and immediately fall off

the plants when they are disturbed. Adults of *Apocnemidophorus pipitzi* (Faust) were collected in southeastern Paraguay and imported into a Florida containment laboratory in April 2006. According to Wibmer and O'Brien (1986), *A. pipitzi* is native to Argentina, Brazil, and Uruguay. An examination of weevil specimens deposited in the entomology museum of the Federal University of Parana in Curitiba, Brazil, revealed that collections of *A. pipitzi* have been made in the states of Parana, Santa Catarina, and Minas Gerais. The occurrence of *A. pipitzi* in Paraguay is a new country record for this species.

The adults range in size from 4 to 7 mm in length and are grayish brown in color, with live specimens often appearing more creamy than grayish (Figure 5). A thick patch of white scales is clearly visible on the sides of the pronotum and is less pronounced on the underside of the abdomen. Other parts of the body have just a few scattered areas with white scales. There also are several patches of black scales over the elytra, which are clearly visible under magnification, giving the elytra (forewings) a slightly mottled appearance.

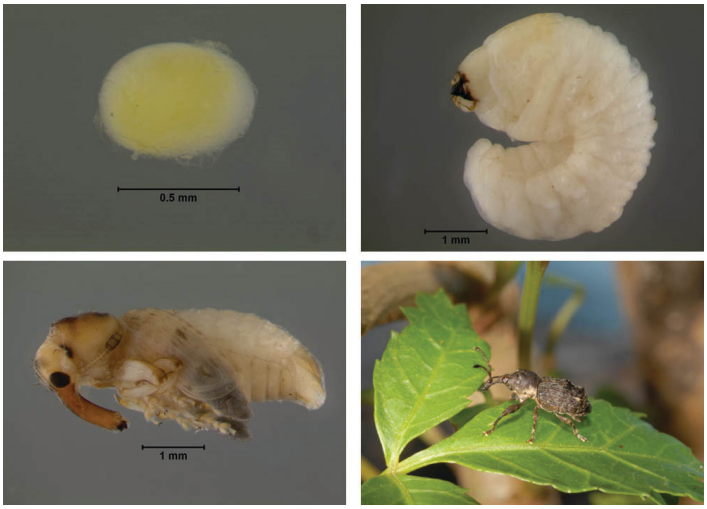

Figure 5. Egg, larva, pupa, and adult male of the weevil *Apocnemidophorus piptzi*. The larvae mine the stems, and the adults feed on the leaflets of Brazilian peppertree.
Credits: Lyle Buss, University of Florida.

The sexes of *A. pipitzi* are readily distinguishable. According to C. W. O'Brien (person. comm.), there are obvious differences in the rostrum (snout) and antennal insertion in males and females of *A. pipitzi*. The females have an evenly curved relatively uniformly cylindrical rostrum with no difference in diameter or curvature at the antennal insertion. In contrast, the males have a strong dorsal expansion at the antennal insertion, and the rostrum is narrowed beyond the insertion, strongly angled ventrally, and dorsally flattened. This is evident even in very small specimens. Other species of the genus, some very similar in appearance, do not have such obvious male differences in the rostrum.

The life stages of *A. pipitzi* are shown in Figure 5. The adults are long-lived, surviving in the laboratory for almost 2 months (Cuda et al. 2016). Females chew small holes (0.5 mm) into the stems and then insert their ovipositors into the cavities. After depositing an egg (or multiple eggs), they seal the cavities with a frass plug that initially is bright green in color but eventually turns brown. The entire process lasts approximately 45 minutes. In the laboratory, a new generation of weevils emerged from cut stems of Brazilian peppertree in 3 to 4 months (Cuda et al. 2016). The length of the life cycle suggests that multiple generations of *A. pipitzi* would be produced annually if this insect were approved for release in Florida.

Both the adults and larvae of *A. pipitzi* are capable of damaging Brazilian peppertree (Cuda et al. 2016). Adults feed preferentially on the tender, subterminal leaflets of the plant. The characteristic feeding scars produced by the adults generally do not completely perforate the leaflets, causing a thin, translucent layer of plant tissue or "window" to remain. However, leaflets that sustain heavy feeding damage eventually abscise. The larvae (Figure 5) tunnel extensively just under the bark of BP (in the vicinity of the cambium) until they reach the pupal stage. This type of feeding damage can weaken the plant because it interferes with the normal transport of water and nutrients in the xylem and phloem tissues.

Brazilian Peppertree Leaf Galling Psyllids, *Calophya* spp.

Three other promising insects that have biological control potential are the leaflet galling psyllids *Calophya terebinthifolii* Burckhardt and Basset (Figure 6) (Vitorino et al. 2011, Christ et al. 2013) and the congeners *Calophya latiforceps* Burckhardt and *Calophya lutea* Burckhardt (Hemiptera: Calophyidae) (Burckhardt et al. 2011, 2018, Diaz et al. 2014a). These three *Calophya* spp., which are native to Brazil and Paraguay, create open pit galls on the leaflets of Brazilian peppertree as they complete their development to the adult stage. Results of field and laboratory studies in Brazil indicate that these insects are *Schinus* specialists (Vitorino et al. 2011, Diaz et al. 2014b. Burchkardt et al. 2018). Females live between 9 to 11 days and deposit 55 to 86 eggs. A new generation is produced in about 44 days. At high densities, these psyllids cause leaf abscission and can stunt the growth of Brazilian peppertree (Prade et al. 2015). A petition to release *C. latiforceps* from quarantine was submitted to the TAG in April 2015, TAG recommended field release in April 2016, and a release permit was issued in June 2019.

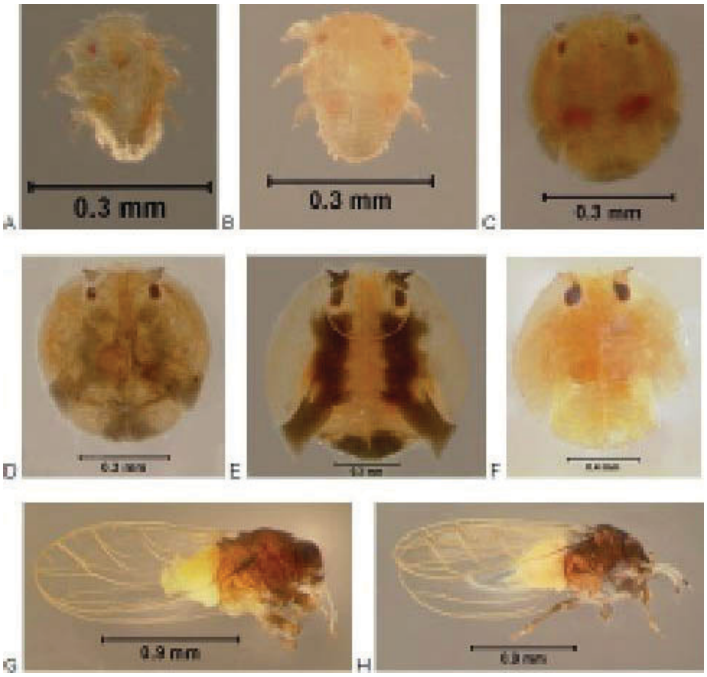

Figure 6. *Calophya terebinthifolii*. A) 1st instar, B) 2nd instar, C) 3rd instar, D) 4th instar, E) 5th instar, F) 5th instar prior to darkening, G) adult male, and H) adult female.
Credits: Lindsey R. Christ, University of Florida.

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