Systematics and Biology of Caloptilia triadicae (Lepidoptera: Gracillariidae), A New Species of Leaf-Mining Moth of the Invasive Chinese Tallow Tree(Triadica sebifera (L.) Euphorbiaceae)

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SYSTEMATICS AND BIOLOGY OF *CALOPTILIA TRIADICAE* (LEPIDOPTERA: GRACILLARIIDAE), A NEW SPECIES OF LEAF-MINING MOTH OF THE INVASIVE CHINESE TALLOW TREE(*TRIADICA SEBIFERA* (L.) EUPHORBIACEAE)

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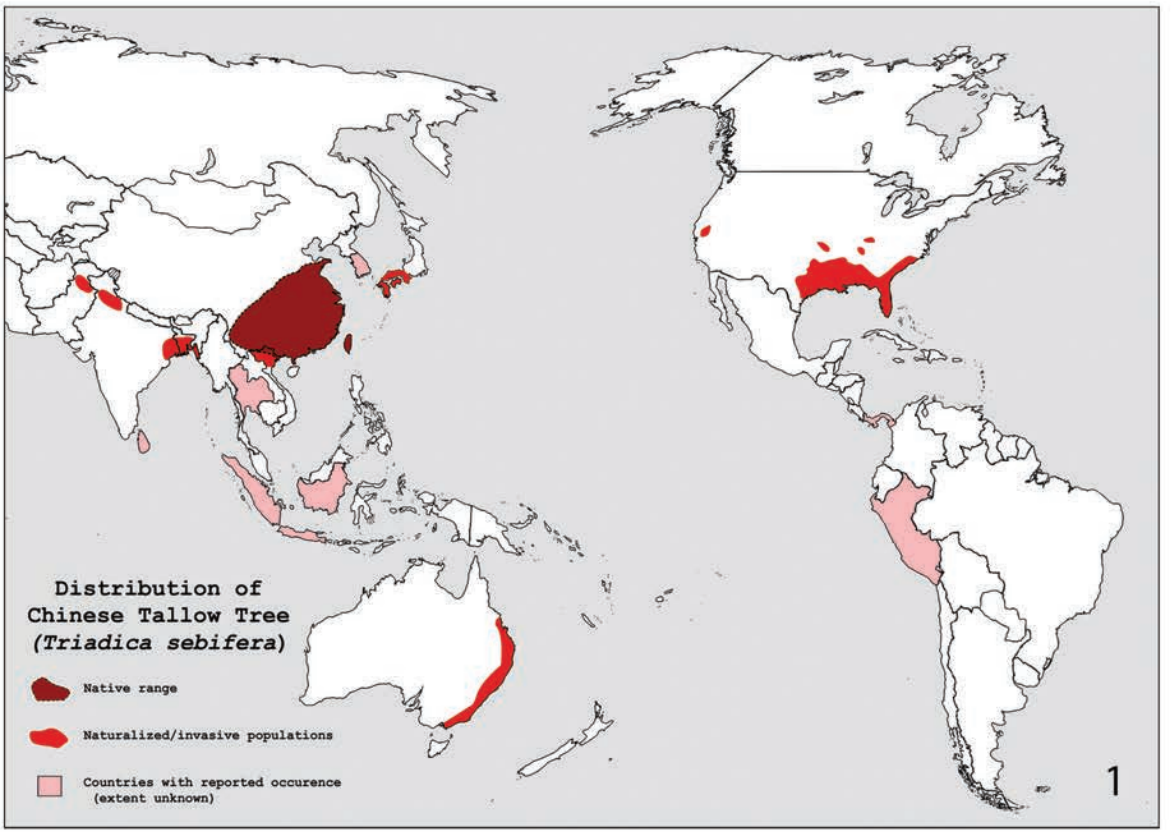
ABSTRACT. A new species of leaf-mining moth, *Caloptilia triadicae*, is described from the southern United States from Florida to eastern Texas. Larvae of this moth are known to feed preferentially and at high densities on the Chinese Tallow tree, *Triadica* (= *Sapium*) *sebifera* (L.) Roxb. (Euphorbiaceae), a tree first introduced into Georgia in 1772 from Asia, which has since become an invasive plant species of grave concern over much of the southeastern United States and California. *Caloptilia triadicae* is also known to feed rarely on *Gymnanthes lucida* Sw. (Euphorbiaceae), a tree not known to occur in the Old World but native to Florida, the Bahamas, the Caribbean, and Central America. Because of the origin of the preferred host and the morphological affinities of the moth to the Chinese species, *Caloptilia hamulifera* Liu and Yuan, it appears likely that *C. triadicae* also originated from Asia. The larvae of *Caloptilia* are hypometamorphic and possess two distinct larval body forms and feeding behaviors—an early stage sap-feeding form with a flattened body and prognathous mouthparts and a later stage tissue-feeding form with a more cylindrical body and possessing hypognathous mouthparts. The sap-feeding larvae initially construct long, serpentine, subepidermal mines on the upper (adaxial) leaf surface. After developing to the tissue-feeding form, the larva of *C. triadicae* leaves the mine and crawls to the edge of the leaf and cuts a narrow strip of leaf which is rolled into a tight coil. It continues feeding externally on the leaf inside the roll in which it eventually forms a silken cocoon for pupation.

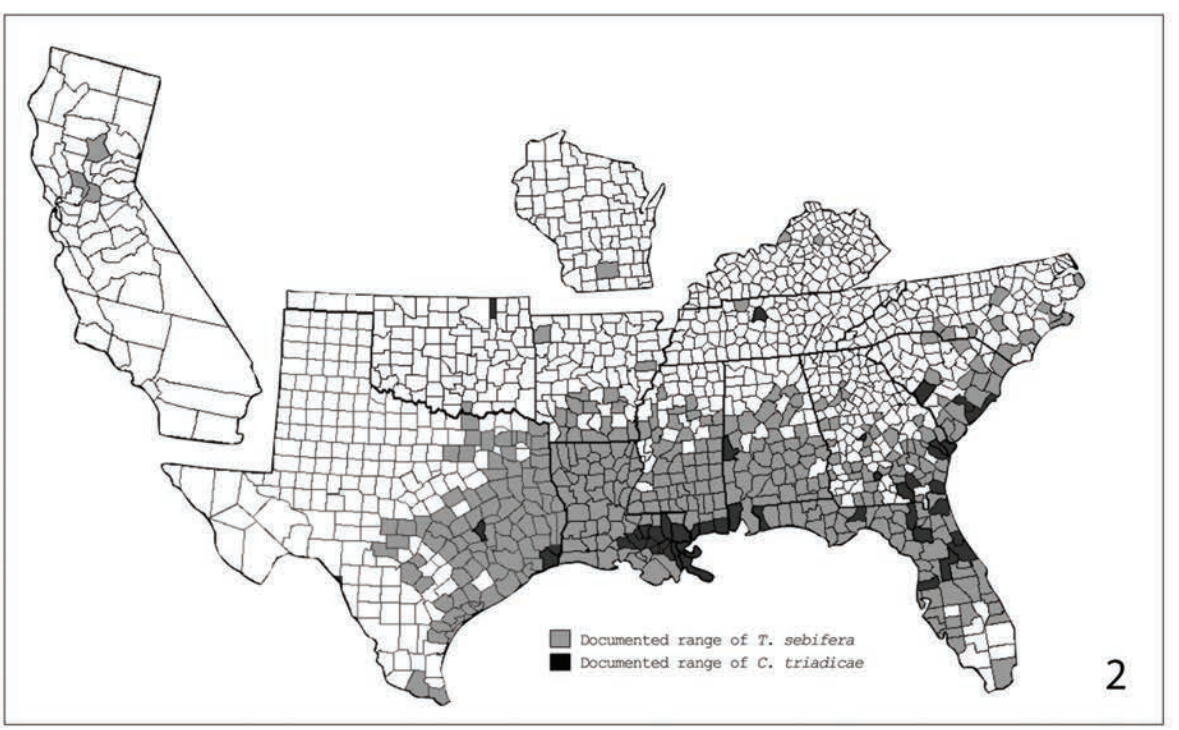
Additional key words: Biocontrol, biogeography, genital morphology, hypermetamorphic larva, invasive plant species, larval biology.

Chinese tallow tree (*Triadica sebifera* (L.) Roxb., Euphorbiaceae) is native to south-southeastern China, Taiwan, and northern Vietnam (Pattison & Mack 2008), is cultivated in Japan and may have naturalized there (Huang et al. 2010), and is either naturalized or invasive in northern India, northern Pakistan, Bangladesh, Java, Indonesia, and southeastern Australia (Figure 1). Tallow tree is reported from Thailand (Sangsawang et al. 2009), and from Panama and Peru (Pattison & Mack, 2008), though the status of the tree populations in these countries is unknown. The species is presently cultivated in South Korea, where there is interest in its capacity to support honey production (Ryu et al. 2008).

In the United States, *Triadica sebifera* is a noxious and highly invasive species that reportedly was introduced into Georgia in 1772, by Benjamin Franklin (Bell 1966). Recent studies on the genetic variation of *T. sebifera* (DeWalt, et al 2011; Boyd 2011) have revealed that the genetic strain that Franklin imported (and now confined to coastal areas of southern South Carolina and northern Georgia) is genetically distinct from the more invasive, widespread strain which was introduced by federal biologists around 1905 and has since spread primarily from Florida to East Texas. DeWalt et al, (2011) also concluded that the different phenotypic traits and relative invasiveness evident between the different strains of *T. sebifera* probably resulted from their different origins within the native range in Asia as well as geographic differences in selective pressures within their introduced ranges. The tree generally is chemically well-defended (although this varies between the different genetic strains), and few native herbivores consume Chinese tallow, though the species has been in the United States for more than 240 years (Siemann & Rogers, 2001). *T. sebifera* has been documented in 12 states in the southeastern United States, as well as three counties in California and one county in Wisconsin (Figure 2). Tallow tree grows well in riparian or swampy areas where soil is consistently damp or frequently inundated. It is also highly successful in disturbed habitats and open fields where sunlight is plentiful, and thrives in urban areas including Baton Rouge and New Orleans, LA, and Houston, TX.

The earliest known records of the proposed new species, *Caloptilia triadicae*, are from Baton Rouge, Louisiana and Sumter County, Alabama, both based on diagnostic leaf mine damage from July (photograph) and October (herbarium specimen) of 2004, respectively (Fox et al. 2012). One year later, June 7, 2005, a single male was collected by G. T. Austin in Gainesville, Florida. Larvae of *C. triadicae* were first discovered on September 16, 2008 and reared by Jason





FIGS. 1–2. Distributions of Chinese Tallow tree (*Triadica sebifera*) and *Caloptilia triadicae*. **1.** World distribution of *Triadica sebifera*. **2.** Distributions of *Caloptilia triadicae* and its host, *Triadica sebifera*, in the United States.

Sharp from *Triadica sebifera* at Branchton Park in Tampa, Hillsborough County, Florida and from Gainesville, Florida on September 20, 2008 by Susan Wright and James Lollis (Heppner 2008). These adults were sent eventually to DRD who identified them as a probably undescribed species of *Caloptilia*, not closely allied to any known North American *Caloptilia*.

Because of the morphological characteristics observed, as well as the origin of its host, DRD suspected that *C. triadicae* may have originated from Asia. A search for all *Caloptilia* known to feed on *Triadica* (= *Sapium*) revealed three Old World species: *Caloptilia octopunctata* Turner (= *C. cirrhocrotala* (Meyrick), *C. tetratype* (Meyrick)), reported from Australia and India; *C. sapina* Vári, from South Africa; and *C. sapiivora* Kumata, from Japan (De Prins & De Prins 2012). *Caloptilia sapina* resembles *C. octopunctata* in morphology and the two may be conspecific (Kumata 1981). The male genitalia of all three species are distinct from that of *C. triadicae*, and none possess the relatively large spine from the ventral angle of the cucullus which partally characterizes *triadicae*. Images of *C. triadicae* also were sent to colleagues T. Kumata (Japan) and D. Yuan (China), as well as to the late G. Robinson at the Natural History Museum, London, for comparison with other possibly similar Old World species. Nothing identical was reported.

The biology, morphology, and synonymy of *Caloptilia* (*Sphyrophora*) *octopunctata* (Turner) were treated in detail by Kumata (1981). Kumata followed Vári (1961) in recognizing *Sphyrophora* as a valid subgenus, characterized primarily by the strongly constricted valvae and presence of only a single, short pair of coremata on the male abdomen. Although these characters clearly distinguish *C. triadicae* (without constricted valvae and with two pairs of long coremata) from this subgenus, it is interesting to note that the late instar larval biology of *C. triadicae* resembles that of *octopunctata* with the larva cutting a strip from the leaf margin of its host and rolling this to form a cone on the abaxial (underside) of the leaf, within which it eventually pupates. *Caloptilia triadicae* closely agrees in wing venation with *C. octopunctata*, particularly with regard to their extremely narrow hindwings and separation of M_2 and M_3 in the forewing (Fig. 9). The forewing pattern of *C. octopunctata* also is similar to that of *C. triadicae* in possessing four evenly spaced, whitish strigulae along the wing margins, compared to three pairs in the latter. All subgenera previously recognized in *Caloptilia* were treated as synonyms of *Caloptilia* by W. and J. De Prins (2005). Adults of the four species of *Caloptilia* currently known to feed on *Triadica sebifera* can be distinguished using the following key.

1. Forewing with four white marginal spots, two on the costa and two on the hind margin; male valva constricted at apical third to form relatively large, lobate cucullus.....2
   Forewing either lacking spots or with only 3 white spots; male valva not constricted; cucullus connected smoothly to base of valva.....3
2. Male valva with sacculus bearing prominent lobe (ampulla) arising near base of cucullus; dorsal margin of cucullus rounded; distribution Australia, India..... *octopunctata*
   Ampulla indistinct; dorsal margin of cucullus angulate; distribution South Africa..... *sapina*
3. Forewing with 3 large white spots, two on costa and one on hind margin; fascia absent; male valva with short spine present from lower apical margin of cucullus (Fig.); distribution United States.....*triadicae*
   Forewing without large white spots, instead with 3 narrow, oblique, lemon-yellow fascia; spine absent from lower apical margin of cucullus; distribution Japan..... *sapiivora*

MATERIALS AND METHODS

Specimens examined in this study are deposited in the following institutions:

FSCA Florida State Collections of Arthropods, Gainesville, FL, USA.

USNM Collections of the former United States National Museum, now deposited in the National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA.

Specimen preparation. Genitalic dissections were cleared by heating in hot 10% KOH for ~30 minutes, and subsequently cleaned and stained with either 2% chlorazol black E or mercurochrome solutions. All genitalic illustrations were drawn from dissections temporarily stored in glycerine, which were later permanently embedded in Canada balsam. Genitalic terminology follows Klots (1970) and Kristensen (1984b).

The COI mitochondrial gene region was sequenced for *C. triadicae* recovered from Florida (n = 18) and Louisiana (n = 20) (Table 1). Specimens were field collected in 2008, curated in 95% EtOH, and were destructively sampled using whole larvae. DNA extraction was performed on each specimen using a Chelex extraction protocol. Each mtDNA PCR was carried out with Stratagene © Paq polymerase (0.1 µl), with primers LCOI-2198 and HCOI-1490 (Folmer et al. 1994) (1.5 µl) and additional MgCl2 (0.5 µl). Samples were thermocycled on MBS Satellite 0.2 G © units at an annealing temperature of 49° C for 35 cycles. PCR products were cleaned using Exo-SAP IT (Affymetrix) and then prepared in separate forward and reverse PCR reactions with Dyenamic dye-terminator chemistry (GE Health Care) for sequencing. Resulting

TABLE 1. Sample information for specimens submitted for COI barcoding.

Sequence ID	Locality	GenBank Accession number
F_1	USA: FL: Gainesville	KF061052
F_2	USA: FL: Gainesville	KF061061
F_3	USA: FL: Gainesville	KF061048
F_4	USA: FL: Gainesville	KF061047
F_5	USA: FL: Gainesville	KF061046
F_6	USA: FL: Gainesville	KF061060
F_7	USA: FL: Gainesville	KF061045
F_8	USA: FL: Gainesville	KF061059
F_9	USA: FL: Gainesville	KF061053
F_10	USA: FL: Gainesville	KF061054
F_11	USA: FL: Gainesville	KF061055
F_12	USA: FL: Gainesville	KF061062
F_13	USA: FL: Gainesville	KF061051
F_14	USA: FL: Gainesville	KF061056
F_15	USA: FL: Gainesville	KF061057
F_16	USA: FL: Gainesville	KF061050
F_17	USA: FL: Gainesville	KF061049
F_18	USA: FL: Gainesville	KF061058
h1	USA: LA: Honey Island Swamp	KF061067
h2	USA: LA: Honey Island Swamp	KF061073
h4	USA: LA: Honey Island Swamp	KF061074
h5	USA: LA: Honey Island Swamp	KF061066
h7	USA: LA: Honey Island Swamp	KF061078
h8	USA: LA: Honey Island Swamp	KF061079
h9	USA: LA: Honey Island Swamp	KF061076
h10	USA: LA: Honey Island Swamp	KF061063
h11	USA: LA: Honey Island Swamp	KF061075
h12	USA: LA: Honey Island Swamp	KF061072
h13	USA: LA: Honey Island Swamp	KF061065
h14	USA: LA: Honey Island Swamp	KF061064
h15	USA: LA: Honey Island Swamp	KF061080
h16	USA: LA: Honey Island Swamp	KF061071
h17	USA: LA: Honey Island Swamp	KF061070
h18	USA: LA: Honey Island Swamp	KF061068
h19	USA: LA: Honey Island Swamp	KF061069
h20	USA: LA: Honey Island Swamp	KF061077

products were cleaned with Sephadex columns. Sequences were then electrophoresed on an ABI 3730xl Genetic Analyzer ©.

RESULTS

Caloptilia triadicae Davis, **new species**
(Figs. 3 – 15)

Diagnosis. The forewing pattern of *Caloptilia triadicae*, consisting of two, white, slightly oblique, costal stigulae and a single white dorsal strigula, is distinct among the North American species of *Caloptilia*. In addition, the presence of a relatively large, curved spine from the ventral angle of the male cucullus is not known to occur in any other American species. A similar spine is present on the cucullus of *Caloptilia hamulifera* Liu and Yuan, an unreared species described from two males from Hunan and Sichuan Provinces, China. The distal half of the valva of *C. hamulifera* differs significantly from that of *triadicae* in being curved more sharply dorsad. The forewing pattern of *hamulifera* also differs from that of *triadicae* in being "brown and scattered with yellow spots."

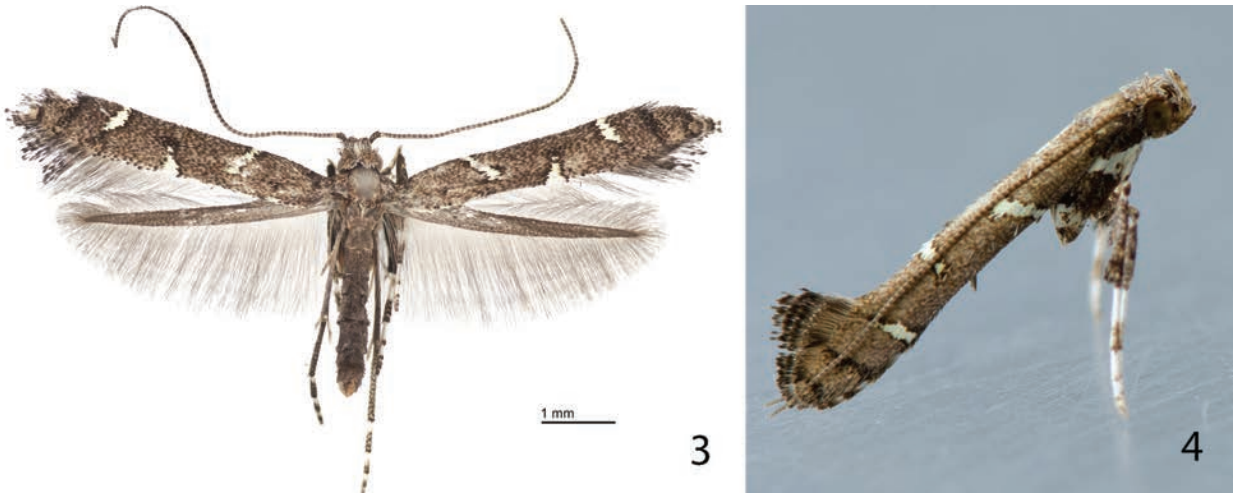
Description. Adult (Figs. 3 – 4). Forewing length 4.3 –4.7 mm.

Head: Vestiture mostly smooth, covered with moderately broad, round-tipped scales; a pair of raised, broad scale tufts from either side of occiput; all scales with pale grayish-white apices, dark fuscous subapically, and with more slender bases pale grayish white. Antenna ~ equal to forewing in length; scape mostly fuscous dorsally, minutely irrorated with pale cream; mostly pale cream ventrally; pedicel mostly pale cream with dark fuscous base; flagellomeres with single annulus of slender, dark fuscous-tipped scales with pale brownish bases. Maxillary and labial palpi mostly dark fuscous laterally and ventrally, pale cream mesally.

Thorax: Smoothly scaled, concolorous with head and base of forewings; scales moderately broad with pale grayish-white apices, dark fuscous subapically, with more slender bases pale grayish white. Vestiture along caudal margin of mesothorax white on lateral-ventral surfaces. Forewing mostly dark fuscous (fuscous scales with pale gray bases), with two white, slightly diagonal strigulae located at basal ¼ and distal ¾ of costa; a single median strigula near middle of dorsal (hind) margin; margins of strigulae irregular, lined with black scales; a small white spot often present along anal hind margin; cilia fuscous, with a subterminal row of pale gray scales. Hindwing immaculate, with similar ground color as forewing. Foreleg mostly dark fuscous, white at base of coxa; tarsomeres mostly white, banded with dark fuscous. Midleg similar in color to foreleg but with less white at base of coxa. Hindleg similar to other legs in color but with white annuli on tarsomeres more reduced in width.

Abdomen: Dark fuscous dorsally, mostly pale cream irorrated with fuscous scales ventrally. Seventh abdominal segment of male mostly membranous, with a narrow, transverse sternum and a pair of large, dense coremata with piliform scales as long as segment VI; eighth segment also membranous with a much smaller, slender "T"-shaped sternum and a pair of slightly shorter coremata ~ 2/3 the length of previous pair. Female abdomen unspecialized.

Male genitalia (Figs. 7–8): Tegumen simple, smoothly rounded, weakly sclerotized, sparsely setose. Vinculum U-shaped, slightly narrowing anteriorly. Valva becoming gradually broader from base to nearly truncate apex of cucullus; subapical region of cucullus densely covered with long setae with apical margin of cucullus nearly devoid of setae; costal margin of valva smoothly curved ventrally; subapical margin below apex of valva curved inwards (dorsally); a short, slightly



FIGS. 3–4. *Caloptilia triadicae*, adults. **3.** Holotype ♂, Gainesville, Florida. **4.** Adult in resting posture, Bartlesville, Oklahoma.

curved spine present at lower angle of cucullus. Transtilla with a slender process directed anteriorly. Aedeagus ~ 1.5 x length of valva, consisting of a slender, subacute cylinder, without cornuti; hood of phallobase relatively slender, elongate, ~ 1.3 x length of aedeagus.

Female genitalia (Figs. 5– 6): Anterior apophyses short, ~ 0.8 x length of posterior apophyses. Eighth abdominal segment ~ equal in length to papilla analis. Ostium bursae a small opening in membrane between abdominal sterna VII and VIII; ventral rim of ostium (antrum) with more sclerotization than dorsal rim; ductus bursae slender, walls of anterior 2/3 finely wrinkled; corpus bursae pyriform, walls minutely wrinkled, with a pair of cresentic signa; one signum ~ ¼ x larger than other; arms of both signa minutely serrated, but more densely serrated along inner margins

Types. Holotype - ♂; UNITED STATES: FLORIDA: Alachua Co: Gainesville, 29 Oct 2008, S. Wright & J. Lollis 08-6506, ex. *Triadica* (= *Sapium*) *sebifera*, digital image captured. (FSCA). Paratypes. UNITED STATES: FLORIDA: Alachua Co: Gainesville: 2004 SE 41st Avenue: 29°36.95'N, 82°17.91'W: 1 ♂, 7 Jun 2005, G. T. Austin. Gainesville: 5 ♂, 7 ♀, 25 Aug – 2 Sep 2008, S. Wright & J. Lollis 08-6506, Host: *Triadica sebifera*, slide USNM 34067, (USNM). Gainesville: lot 0811971, 2 ♂, 2 ♀, 2 Sep 2008, J. A. Wright, Host: *Triadica sebifera*, slide USNM 34065, (USNM). Gainesville: 1 ♂, 1 ♀, 29 Oct 2008, S. Wright & J. Lollis 08-6506, Host: *Triadica sebifera*, slide USNM 34066, (USNM). Gainesville: N 29° 38.114' W 082° 22.245': 1 ♂, 1 ♀, 23 Sep 2011, em. 6, 17, and 31 October 2011, J. G. Duncan, Host: *Gymnanthes lucida*, collected from live plant cage, (USNM). Broward Co: USDA ARS PRL: 1 ♀, 27 Jun 2012, Wheeler and Dyer, reared from *Triadica sebifera*; 2 ♂, 2 ♀, 27 Jun 2012, Wheeler and Dyer, reared from leaves *Triadica sebifera*, (USNM). Miami/Dade Co: Alice Wainwrite Park: 1 ♂, 27 Jun 2012, Wheeler and Duncan, reared from leaves *Gymnanthes lucida*, slide USNM 34520, (USNM). LOUISIANA: St. Tammany Par: near Pearl River, PRWMA, Honey Island Swamp: 6 ♂, 4 ♀, 22 May 2009, R. Hazen & M. Fox. PRWMA 30'23.442"N/89'43.297"W Plot 240: 8 ♂, 4 ♀, 22 May 2009, Rebecca Hazen, Host: *Triadica sebifera*. (Paratypes deposited in FSCA, USNM).

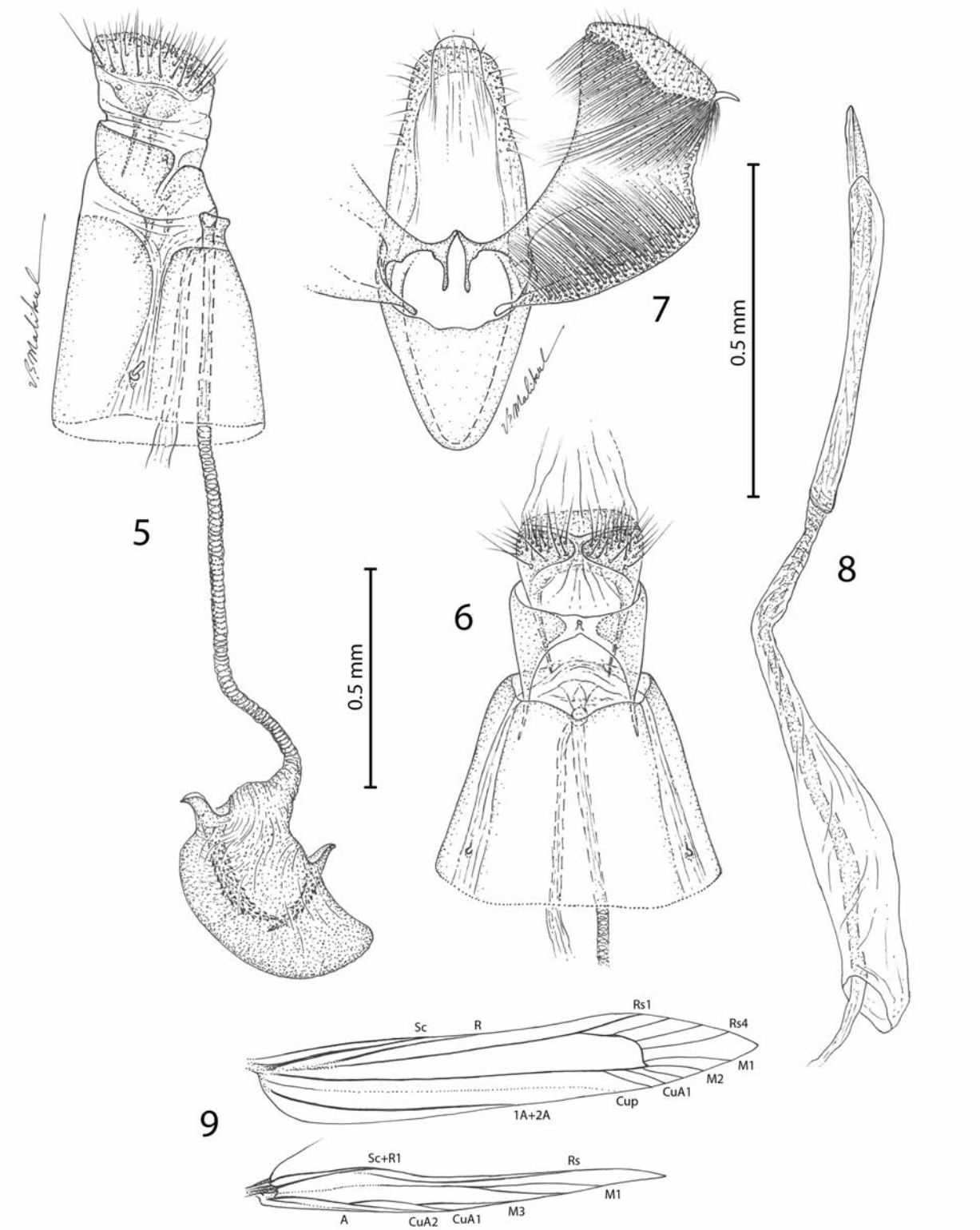
Distribution (Fig. 2). Though it has not yet been collected from any other country, *Caloptilia triadicae* is presumed to be adventitious to the United States. This presumption is partly based on the close association with its host plant, the Chinese tallow tree (*Triadica sebifera*), which is native to southeastern China (Fig. 1). *Caloptilia triadicae* has only been collected on or in the vicinity of its host plant, accordingly the known distribution of the moth is entirely encompassed by the distribution of the Chinese tallow tree (Fig. 2). The earliest U.S. records of *C. triadicae* are from 2004, in coastal Louisiana and Alabama. The species has since been found in Texas, Oklahoma, Mississippi, Florida, Georgia, South Carolina and Tennessee. In the U.S. it appears that *C. triadicae* is an effective disperser and that there may be little or no temporal lag between the invasion of new territory by the host tree and by the moth. The first photographic records of the moth in Davidson County, TN (S. Bren, 2009) and Washington County, OK (Fig. 4; M. Dreiling, 2012) actually preceded the first documentation of Chinese tallow tree in those counties.

Etymology. The species name is derived from the generic name of its primary plant host, *Triadica*, and is considered an adjective in the nominative singular.

Hosts. Euphorbiaceae: *Triadica* (= *Sapium*) *sebifera* (L.) Roxb.; *Gymnanthes lucida* Sw.

DISCUSSION

Biology. Eggs are laid on either the lower or upper leaf surface of young, tender leaves (Hazen and Fox 2011), often adjacent to a major vein or at the junction of two veins (Fig. 12). The eggs are flat and ~ 0.3 mm in diameter with a white, reflective surface; they are pressed to the leaf surface, resembling a small blemish on the leaf epidermis. First instar larvae emerge from the egg and immediately chew into the cuticle of the leaf. The initial subepidermal, serpentine mine is ~ the same width as the diameter of the egg (~ 0.3 mm). The sapfeeding larva tends to form a rather meandering mine, except upon encountering a vein or the margin of the leaf it typically follows that boundary (Figs. 10, 13). The mine is often enlarged two- or threefold into a chamber at two or three locations along its course. If such a chamber occurs at the leaf margin, the entire leaf may be slightly folded over giving the superficial appearance of an external shelter, but the epidermis of the leaf is not broken and the larva continues to feed internally. Sapfeeding larvae do not consume all the tissue between the upper and lower leaf surfaces and on heavily infested trees there may be distinct mines on



FIGS. 5–9. *Caloptilia triadicae*, adult morphology. **5.** Female genitalia, lateral view, USNM 34067. **6.** Female genitalia, ventral view. **7.** Male genitalia, ventral view, USNM 34065. **8.** Male aedeagus. **9.** Wing venation, USNM 34065, male.

FIGS. 10–15. *Triadica sebifera*, biology and larval feeding by *Caloptilia triadicae*. **10.** Foliage with initial evidence of larval feeding (New Orleans, Orleans Parish, Louisiana. 22 June 2012). **11.** Infested tree with detail insets showing various stages of larval feeding (along Hwy 90, Lake St. Catherine, Orleans Parish, Louisiana. 14 May 2012.) **12.** Oviposition sites of *Caloptilia triadicae* (indicated by arrows) (same collection site as 11). **13.** Serpentine mines of early stage sapfeeding larvae (New Orleans, Orleans Parish, Louisiana. 10 October 2012). **14.** Characteristic leaf cones rolled by later stage tissue feeding larva (same collection site as 13). **15.** Larval predation within cones by ant, Pseudomyrmex gracilis (Bell Chasse, Plaquemines Parish, Louisiana. 19 August 2011).

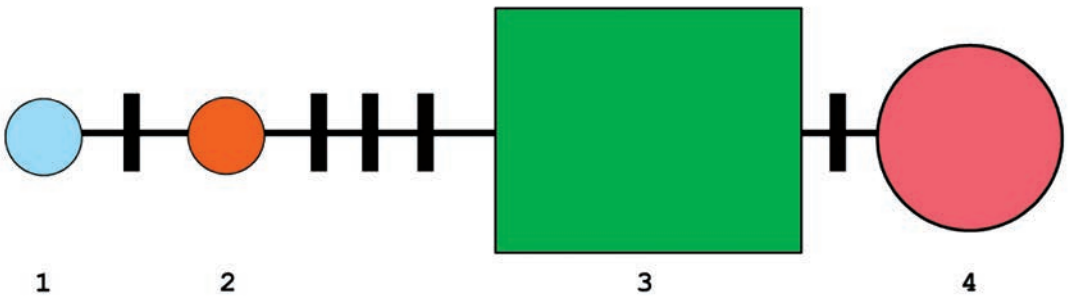


FIG. 16. *C. triadicae* haplotype tree generated for four haplotypes exhibited by study populations in North America. Bars on connecting lines indicate single basepair changes that differentiate lineages. The size of the numbered shapes, representing different haplotypes, corresponds with the abundance of each haplotype relative to the overall sample size for North America. The colors of the numbered shapes correspond to the pie charts in Figure 17, illustrating haplotype distribution by geography).

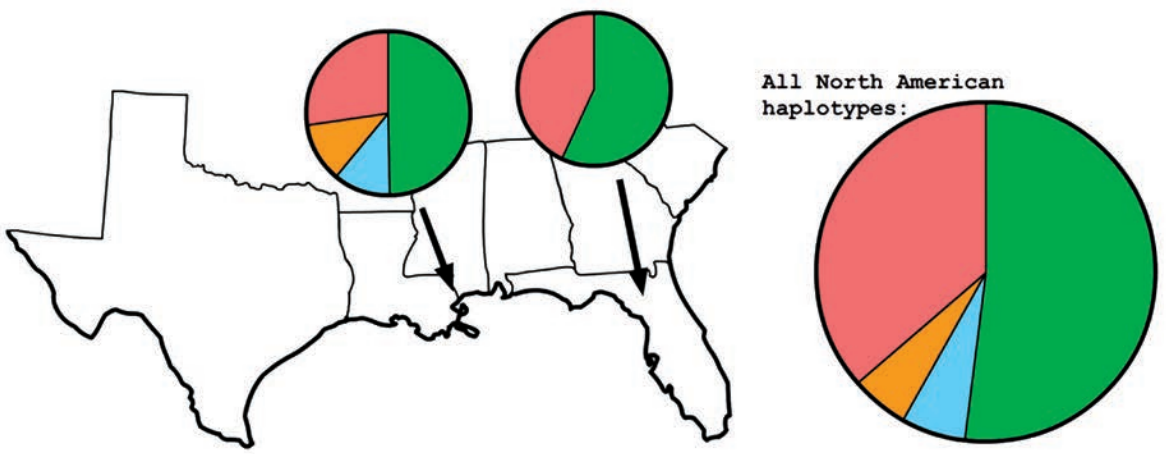


FIG. 17. Distribution of North American *C.triadicae* haplotype diversity from initial collections in the southeastern U.S. in Louisiana and Florida.

both upper and lower leaf surfaces which overlap without interfering with each other. The later externally feeding larval stages (tissue-feeding instars) construct a coiled, rosette-shaped leaf shelter (Figs. 10, 11, 14, 15). An incision is chewed across the leaf, perpendicular to the leaf margin, and the larva uses silk to coil the resulting flap of leaf (usually the flap closer to the apex of the leaf) into the shape of a cone. The dimensions of the coiled leaf shelter vary with the size of the larva and the size of the leaf, but it is always approximately cone-shaped, with the smaller base of the cone (diameter 4–9 mm) toward the midline of the leaf, and the apex of the cone (diameter 7–16 mm, or typically ~1.75 × diameter of base) at the leaf margin. Pupation takes place within the same shelter, and following the emergence of the adult moth the empty pupal exuvium remains protruding from the center of the leaf coil.

In New Orleans, LA, both pupae and external feeding larvae of *C. triadicae* were collected in February, 2012 by RH and MF; adults were photographed by R. L. Zimlich in Mobile, AL, in January, November, and December of 2012. These observations suggest that there is no extended overwintering stage for *C. triadicae*, at least for the populations in the southeastern United States. In the vicinity of New Orleans, in a typical year, the authors

commonly begin observing damaged leaves of *T. sebifera* in April or May, with adult *C. triadicae* emerging shortly thereafter. A complete generation takes only a few weeks, and abundance increases through the growing season, typically reaching a nearly total infestation of host trees by July or August. However, it seems that abundance of the moth early in the growing season and its subsequent rate of population growth are associated with the severity of the preceding winter: following several sustained hard freezes in winter of 2009-10, MF did not observe any evidence of *C. triadicae* in New Orleans until August, 2010. The population of *C. triadicae* plummets in winter when the temperature first approaches freezing and the host trees shed their leaves. Winter temperatures may determine the eventual northern boundary of the Chinese tallow tree's distribution, and therefore should present a similar boundary for *C. triadicae*.

Three species of *Triadica*, all native to Eastern and southeastern Asia, are currently recognized (Esser 2002). All are trees growing to maximum heights between 10–25 meters. *Triadica cochinchinensis* Lour. ranges widely from India to China and the Philippines. *Triadica rotundifolia* (Hemsl.) Esser is the least widespread of the species and occurs from southern China into Vietnam. The native range of *Triadica sebifera* (L.) Small includes the more southern provinces of Japan and China and is widespread in Taiwan. Because this species can grow within a wide range of dry or wet conditions and is frost hardy, its potential as an invasive species is the greatest. It is likely that larvae of *Caloptilia triadicae* are capable of feeding on all three species of *Triadica*.

Adults of *Caloptilia triadicae* have also been reared in Florida from a secondary host, *Gymnanthes lucida* Sw. (Euphorbiaceae). The genital morphology of males from this host was found to be identical with those reared from *T. sebifera*. *Gymnanthes lucida* is native to Florida, the Bahamas, the Caribbean, and Central America, and is not known to occur in the Old World (Miroslav 2005). Although possessing dissimilar native distributions and are not considered sister taxa, *Gymnanthes* and *Triadica* are closely related and belong to the same subclade within the tribe Hippomaneae of the Euphoriaceae (Wurdack et al 2005). Both genera have latex and appear relatively pest free except for specialist herbivores. Consequently, host switching between these two genera by certain herbivores may be possible. Because *Caloptilia triadicae* is most similar mophologically to other Asian species of *Caloptilia*, particularly *Caloptilia hamulifera* Liu and Yuan, and not to any North American *Caloptilia*, its utililization of New World *Gymnanthes* as a host is believed to be a later, secondary adaptation.

Natural enemies. The authors (RH & MF) have commonly seen polistine wasps investigating leaf rolls on tallow trees heavily infested with *C. triadicae*, though actual predation by these wasps has not been observed. Ants, most commonly *Pseudomyrmex gracilis* (Fabricius 1804), have been observed marauding leaf rolls and removing larvae of *C. triadicae* (Figure 15). Arachnids are often found residing in leaf rolls formerly inhabited by *C. triadicae*, but it is unclear whether the spiders consumed the resident larva or pupa or were opportunistically using empty shelters. Several species of parasitoid wasp have also been reared from *C. triadicae* in the U.S., but have not yet been identified (Hazen and Fox, unpublished data, Greg Wheeler, personal communication).

COI Sequence data. To date, sequence data for the mtDNA COI gene region of *C. triadicae* from two North American locations (Florida and Louisiana), suggest that populations exhibit multiple mtDNA haplotypes (Fig. 16) and appear to comprise a single species. Analysis of mtDNA sequences yielded four total haplotypes, all of which were found in Louisiana while only two were found in Florida (Fig. 17). This degree of genetic diversity is consistent with field observations (by MF and RH) of outbreak-level infestations of *C. triadicae* larvae on *T. sebifera* trees.

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