

A taxonomic review of *Poblicia* Stål, 1866 (Hemiptera: Fulgoromorpha: Fulgoridae), with special reference to species north of Mexico

CHARLES R. BARTLETT^{1,2}, TYLER HAGERTY^{1,3}, DOUGLAS YANEGA^{4,5}, MARK S. HODDLE^{4,6}, MARCO GEBIOLA^{4,7} & FRANCESC GÓMEZ-MARCO⁸

¹Department of Entomology and Wildlife Ecology, University of Delaware, 250 Townsend Hall, Newark, DE 19716-2160, USA

² bartlett@udel.edu;  <https://orcid.org/0000-0001-9428-7337>

³ hagertyt@udel.edu;  <https://orcid.org/0009-0006-5835-4444>

⁴Department of Entomology, Entomology Research Museum, University of California Riverside, Riverside, CA, USA

⁵ dyanega@gmail.com;  <https://orcid.org/0000-0002-7294-8189>

⁶ mark.hoddle@ucr.edu;  <https://orcid.org/0000-0002-8423-5530>

⁷Department of Agricultural Sciences, University of Naples Federico II: Naples, Italy

 marco.gebiola@unina.it;  <https://orcid.org/0000-0002-4644-2934>

⁸IRTA, Sustainable Plant Protection, 08348 Cabrils, Catalonia, Spain

 francesc.gomez@irta.cat;  <https://orcid.org/0000-0002-2881-1396>

Abstract

The species of *Poblicia* Stål, 1866, here given the appellation speckled lanternflies, are reviewed with particular attention to species found north of Mexico. The genus *Poblicia* at this time consists of four species: the type species *P. misella* (Stål, 1863) (from Mexico), *P. fuliginosa* (Olivier, 1791) (from eastern USA), and two species removed from synonymy—*P. thanatophana* Kirkaldy, 1907 (western USA) and *P. cribrata* Gerstaecker, 1860 (locality uncertain). Amended diagnoses are provided for these *Poblicia* species. Life history and molecular sequence data (28S, ITS2 and CO1) are discussed to support the designation of *P. fuliginosa* and *P. thanatophana* as separate species. *Poblicia texana* is established as the type species for the new genus *Angulapteryx* **gen. nov.** as *Angulapteryx texana* **comb. nov.**

Key words: Poiocerini, Poiocerinae, Fulgoroidea, lanternflies, planthoppers

Introduction

Efforts to develop a classical biological control program targeting the invasive spotted lanternfly (SLF, *Lycorma delicatula* (White, 1845) (e.g., Broadley *et al.* 2023, Gómez-Marco *et al.* 2023, Bao *et al.* 2023, Wu *et al.* 2023, Gould *et al.* 2024, West *et al.* 2025), native to China, have generated interest in Fulgoridae native to the United States. Field studies into the biology of native Fulgoridae, in the context of developing non-target host suitability model systems, the study of efficacy and specificity of potential SLF biocontrol agents, led to the wider recognition that the underlying taxonomy of some native Fulgoridae required reassessment. Yanega *et al.* (2024) addressed one of those gaps for the US Fulgoridae placed variously in the genera *Crepusia* Stål, 1866, *Alphina* Stål, 1863, and *Calyptoproctus* Spinola, 1869 (Bartlett *et al.* 2014, Bartlett & Wilson 2023) by describing the new genus *Scaralina* Yanega, 2024, to house five US and ten Mesoamerican taxa, 14 of which were described as new (Yanega *et al.* 2024).

Both the studies Broadley *et al.* (2023) and Gómez-Marco *et al.* (2023) found that the candidate biological control agent, the egg parasitoid *Anastatus orientalis* Yang & Choi, 2015 (in Yang *et al.* 2015—Hymenoptera, Eupelmidae), which is native to China, was able to parasitize eggs of *Poblicia fuliginosa* auct. collected in eastern (North Carolina) and western (Arizona) US. After some preliminary observations, we recognized that eastern and western US *P. fuliginosa* populations may be different species. Therefore, here we review the taxonomy of the genus *Poblicia* Stål, 1866 (Poiocerinae, Poiocerini) with particular reference to the US species to address another taxonomic gap in US Fulgoridae that has come to light in the context of proactive biological control for SLF.

Poblicia is a widespread genus in the southern United States and Central America, for which we apply the common name appellation of speckled lanternflies. *Poblicia* is a small genus, but the species composition is not settled. Stål (1866) initially did not explicitly place any species into *Poblicia* but implied the placement of *Poblicia misella* (Stål, 1863) (e.g., Metcalf 1947), from Oaxaca, Mexico, which later was explicitly affirmed as the type species by Van Duzee (1916, 1917). Aside from the type species, the other species included in *Poblicia* are *P. texana* Oman, 1936, and *P. fuliginosa* (Olivier, 1791) (e.g., Porion 1994, Bartlett *et al.* 2014). However, Bourgoïn (2025) includes *Poblicia spectabilis* (Walker, 1858) (from Brazil), apparently following Metcalf (1938, 1947), but this species was returned to *Scaralis* Stål, 1863, by Porion (1994) following Distant (1887) and da Costa Lima (1935). This species was recently treated as *Scaralis (Alphinoides) spectabilis* (Walker, 1858) by Yanega *et al.* (2024). Additionally, Bourgoïn (2025) excludes *P. fuliginosa* from *Poblicia*, but instead places this species in *Crepusia* Stål, 1866, following Nast (1951), a nomenclatural issue not addressed in Bartlett *et al.* (2014), who retained the species in *Poblicia*. Ostensibly then, *Poblicia* is currently composed of *P. misella*, *P. texana* and probably *P. fuliginosa*.

Poblicia fuliginosa (described from Georgia) has two subjective synonyms—*Poblicia thanatophana* Kirkaldy, 1907 (described from Arizona) and *Poiocera cribrata* Gerstaecker, 1860 (a replacement name for *Poiocera venosa* Walker, 1851 (nec Germar, from an unknown locality) (e.g., Metcalf 1947, Nast 1951, Bartlett *et al.* 2014)). If the eastern and western US populations of *Poblicia fuliginosa* represent different species, the name *Poblicia thanatophana* is available and has nomenclatural priority for the western segregate of *Poblicia fuliginosa*.

The main objective of this study is to review the taxonomic standing of *Poblicia fuliginosa*, both from the context of generic placement and from the standpoint of whether eastern and western US populations represent distinct species. As part of this review, we will present an amended genus description, review the composition of the genus, and provide amended descriptions of the treated species. The genetic loci 28S, ITS2, and CO1 were sequenced for eastern and western US populations of *P. fuliginosa auct.* to test the species-level status of these populations.

Methods

Taxonomy and morphology. Morphological terminology generally follows that of Bartlett *et al.* (2014), except for forewing venation following Bourgoïn *et al.* (2015) and male terminalia nomenclature modified after Bourgoïn (1988) and Bourgoïn & Huang (1990) as updated for Fulgoridae by Seidel & Wessel (2013). Descriptive details specified in the genus description are not duplicated in the species descriptions, except for clarity. Distribution maps were created using SimpleMappr (Shorthouse 2010). Distribution records are compiled from published sources, specimens, and the community science forums iNaturalist (<https://www.inaturalist.org/>) and Bugguide (<https://bugguide.net/>). Label information from primary types is quoted, with “/” indicating a new line on a label and “//” indicating a new label, with comments in square brackets. Data for other material examined is arranged geographically, with the data presented in a common format and data sequence (locality data, collection date, collector, and other data followed by the number of specimens, gender, and institution); localities with many specimens were summarized to county; iNaturalist records were reported by observation number for state records (i.e., those not in Bartlett *et al.* (2014) and without cited specimen records). The catalog of citations following the synonymy list for each taxon includes the original description, the Metcalf catalog (Metcalf, 1947), and references published since Metcalf (1947). New taxa are intended to be attributed to Bartlett.

Primary types (and *Crepusia*) were photographed at their host institution. Exemplar *P. fuliginosa* were photographed using a Canon EOS 80D and Canon EOS R6 with Canon MP-E 65mm f/2.8 1–5× Macro Photo, Laowa 25mm f/2.8 2.5–5× Ultra Macro, and Laowa 100mm f/2.8 2× Ultra Macro APO lenses. Extended depth of field stacking was done using ZereneStacker software (Version 1.04 Build T2022-04-21-0715). Photograph processing was conducted using Adobe Lightroom Classic and Adobe Photoshop. Wings were photographed by detaching a wing from a specimen that had been hydrated overnight; the wing was washed in alcohol, placed on a microscope slide with a drop of hand sanitizer, and covered with a microscope slide cover. The preparation was then photographed using an OMAX 18.0MP USB3.0 camera attached to a Nikon SMZ1500 microscope. The wing images were stacked and processed using the same software as habitus images. Male terminalia were examined through the removal of the abdomen (after overnight hydration) and treatment with 15 or 20% hot KOH until flexible and soft tissues could be removed. Cleared terminalia (phallus in ‘inactive state’ *sensu* Seidel & Wessel 2013) were washed in water and moved to glycerine for study and disarticulated as necessary. Male terminalia (or

their constituent parts) were photographed similarly to the forewings and subsequently transferred to micro-vials for permanent storage with the specimen.

Specimens are referenced from the following collections:

BMNH—The Natural History Museum, London, U.K.;

BPBM—Bernice P. Bishop Museum, Honolulu, HI, USA;

CASC—California Academy of Science, San Francisco, CA, USA;

DZUP—Universidade Federal do Paraná, Departamento de Zoologia, Parana, Brazil;

MFNB—Museum für Naturkunde Berlin, Germany;

NCSU—North Carolina State University, Department of Entomology, Raleigh, NC, USA;

NHRS—Swedish Museum of Natural History (Naturhistoriska riksmuseet), Stockholm, Sweden;

RBINS—Royal Belgian Institute of Natural Sciences, Brussels, Belgium;

UDCC—University of Delaware Insect Research Collection, Newark, DE, USA;

UCRC—University of California Riverside, CA, USA.

Specimen collections and DNA Extraction. Specimens of *Poblicia* from the western population were collected from Cochise County in southeast Arizona (near Portal, 31.881971°, -109.208338°, Duquesne Road), between the 15th of August and the 15th of September of 2020. Fulgorid nymphs presumed to be *Poblicia* were collected at the Southwestern Research Station Forest, Portal, AZ, by fogging the canopy of *Juniperus deppeana* Steud. (Cupressales: Cupressaceae) with a 20% dilution of pyrethrin product in July of 2019. One adult specimen of *Poblicia texana* was from a 2016 blacklight collection by Patrick Sullivan from the Patrick Sullivan property (Ramsey Canyon, Sierra Vista, AZ). The eastern *Poblicia* were from the Bladen Lakes State Forest in Bladen County in North Carolina. The specimen of *Scaralina marmorata* (Spinola, 1839) (Hemiptera: Fulgoridae) used as an outgroup on the molecular analyses was collected from South Carolina, Pickens Co., Clemson Township, Clemson experimental forest, Wildcat Creek, at light, 20 June 2018, by A.M. Deczynski.

We produced a genetic characterization of the specimens collected to test hypotheses of species relationships. DNA was extracted from the middle leg of each specimen. The leg was mixed with 5 µL of Protease K and 80 µL of 5% Chelex solution. This mixture was incubated first at 55°C for one hour, followed by 10 minutes at 92°C.

PCR Parameters, Sequence Data, and Phylogenetic Analysis. Sequence data were generated from three loci: ITS2, 28S-D2 and cytochrome oxidase I (COI). These loci were chosen because they are a combination of nuclear ribosomal genes (ITS2 and 28S-D2) and a mitochondrial protein-coding gene (COI). ITS2 was amplified using a new primer pair designed starting from those of Campbell *et al.* (1993) to remove mismatches with the genome of *L. delicatula* (GenBank accession JX556802): FUL_ITS_F (5'TGTGAACTGCAGGACACACG 3') and FUL_ITS_R (5'TATGCTTAAATTCAGCGGGTA 3'). 28S-D2 was amplified using 28S EE paired with 28S MM (Cryan *et al.* 2000), and COI was amplified using COI-BCI and COI-BCIII, which are a degenerated version designed by Cho *et al.* (2008) of the standard COI barcoding primers LCO1490/HCO2198 (Former *et al.* 1994). All PCR were performed in 20 µL reactions containing 1 µL of DNA template (concentration not determined). The reaction components for ITS2 and 28S-D2 were 2 µL Standard PCR Buffer (New England BioLabs (NEB), Ipswich, MA), 2 µL of dNTPs (2mM), 0.1 µL Taq polymerase (NEB), and 0.5 µL each PCR primer (10 µM). For COI, PCR components were 2 µL Standard PCR Buffer (NEB), 0.4 µL of dNTP (10mM), 0.8 µL of MgCl (50 mM), 0.1 µL Taq polymerase (NEB), and 1 µL each primer (10 µM). Reactions were performed in a BioRad thermocycler. For ITS2 was programed for an initial denaturing at 95°C for 3 min, followed by 28 cycles of 94°C for 45 seconds, 55°C for 45 seconds, 72°C for 1 min and a final extension of 7 min at 72°C. For 28S PCR was programed for an initial denaturing at 94°C for 3 min, followed by 39 cycles of 94°C for 1 min, 52°C for 1min, 72°C for 2 min and a final extension of 7 min at 72°C. For COI PCR was programed for an initial denaturing at 94°C for 2 min, followed by 39 cycles of 94°C for 30 seconds, 50°C for 1 min, 72°C for 1 min and a final extension of 7 min at 72°C. Amplification was confirmed by standard gel electrophoresis and PCR products were purified using Mag-Bind Total Pure NGS beads (Promega, Madison, WI) following the manufacturer instructions. In case of double bands, the band of the target size were recovered and cleaned using Zymoclean Gel DNA Recovery Kit (Zymo Research, Irvine, California, USA) following manufacturer instructions. All amplified products were sequenced in both directions with their respective primers at Retrogen Inc. (San Diego, CA, USA). Chromatograms were assembled using BioEdit version 7.2.0 (Hall 1999) and mismatches between chromatograms were manually solved by visual inspection. Sequences

were concatenated with BioEdit, aligned with MAFFT (online version) using the ‘Auto’ strategy and analyzed by maximum likelihood using raxmlGUI2.0 (Edler *et al.* 2021), with GTRCAT substitution model and 1,000 rapid bootstrap replicates. *Scaralina marmorata* was used as an outgroup.

TABLE 1. Specimens used for molecular analyses.

Species	Specimen code	Life stage	Location	Year	Molecular marker	GenBank accession
<i>Poblicia thanatophana</i>	PW	Adult	Duquense Road, AZ, USA	2020	ITS2	PQ881593
					28S	PQ881599
					COI	PQ878476
<i>Poblicia fuliginosa</i>	PE	Adult	Bladen Co., NC, USA	2021	ITS2	PQ881592
					28S	PQ881598
					COI	PQ878475
<i>Angulapteryx texana</i>	museum	Adult	Ramsey Canyon, AZ, USA	2016	COI	PQ878477
					ITS2	PQ881594-96
					28S	PQ881600-02
					COI	PQ878478-80
<i>Scaralina marmorata</i>	CM	Adult	Clemson Township, SC, USA	2018	COI	PQ878481-83
					ITS2	PQ881591
					28S	PQ881597

Results

Phylogenetic analyses of the concatenated ITS2, 28S-D2 and COI dataset support the hypotheses that eastern and western US populations of *Poblicia fuliginosa* auct. are different species (Fig. 1). Genetic distances between the two populations are 2.9% (ITS2), 0.17% (28S-D2) and 9.2% (COI) (Tables 2–4). Fulgorid nymphs collected by fogging *Juniperus deppeana* at the Southwestern Research Station were found to be *Poblicia texana*.

Differences in host plant associations between the eastern and western populations of *Poblicia fuliginosa* auct. further support the hypothesis that they are different species. Eastern populations are consistently found on winged sumac (*Rhus copallinum* L., Anacardiaceae), and western populations were found on various Asteraceae, especially desertbroom (*Baccharis sarothroides* A. Gray). Diagnostic differences between the species are discussed below.

TABLE 2. Pairwise comparison showing evolutionary distances between sequences based on the cytochrome oxidase I (COI) mitochondrial protein-coding gene.

		1	2	3	4	5	6	7	8	9
1	<i>Poblicia fuliginosa</i>	0	-	-	-	-	-	-	-	-
2	<i>Poblicia thanatophana</i>	0.092	0	-	-	-	-	-	-	-
3	<i>Angulapteryx texana</i> _museum	0.154	0.184	0	-	-	-	-	-	-
4	N1_ <i>Angulapteryx texana</i>	0.151	0.181	0.0102	0	-	-	-	-	-
5	N2_ <i>Angulapteryx texana</i>	0.151	0.181	0.0102	0	0	-	-	-	-
6	N3_ <i>Angulapteryx texana</i>	0.151	0.181	0.0102	0	0	0	-	-	-
7	N4_ <i>Angulapteryx texana</i>	0.151	0.181	0.0102	0	0	0	0	-	-
8	N5_ <i>Angulapteryx texana</i>	0.151	0.181	0.0102	0	0	0	0	0	-
9	N8_ <i>Angulapteryx texana</i>	0.151	0.181	0.0102	0	0	0	0	0	0

TABLE 3. Pairwise comparison showing evolutionary distances between sequences based on the nuclear ribosomal gene ITS2.

		1	2	3	4	5	6
1	<i>Scaralina marmorata</i>	0	-	-	-	-	-
2	<i>Poblicia fuliginosa</i>	0.0285	0	-	-	-	-
3	<i>Poblicia thanatophana</i>	0.0268	0.0017	0	-	-	-
4	N1_ <i>Angulapteryx texana</i>	0.0268	0.0151	0.0134	0	-	-
5	N2_ <i>Angulapteryx texana</i>	0.0268	0.0151	0.0134	0	0	-
6	N3_ <i>Angulapteryx texana</i>	0.0251	0.0134	0.0117	0.0017	0.0017	0

TABLE 4. Pairwise comparison showing evolutionary distances between sequences based on the nuclear ribosomal gene 28S-D2.

		1	2	3	4	5	6
1	<i>Scaralina marmorata</i>	0	-	-	-	-	-
2	<i>Poblicia fuliginosa</i>	0.0285	0	-	-	-	-
3	<i>Poblicia thanatophana</i>	0.0268	0.0017	0	-	-	-
4	N1_ <i>Angulapteryx texana</i>	0.0268	0.0151	0.0134	0	-	-
5	N2_ <i>Angulapteryx texana</i>	0.0268	0.0151	0.0134	0	0	-
6	N3_ <i>Angulapteryx texana</i>	0.0251	0.0134	0.0117	0.0017	0.0017	0

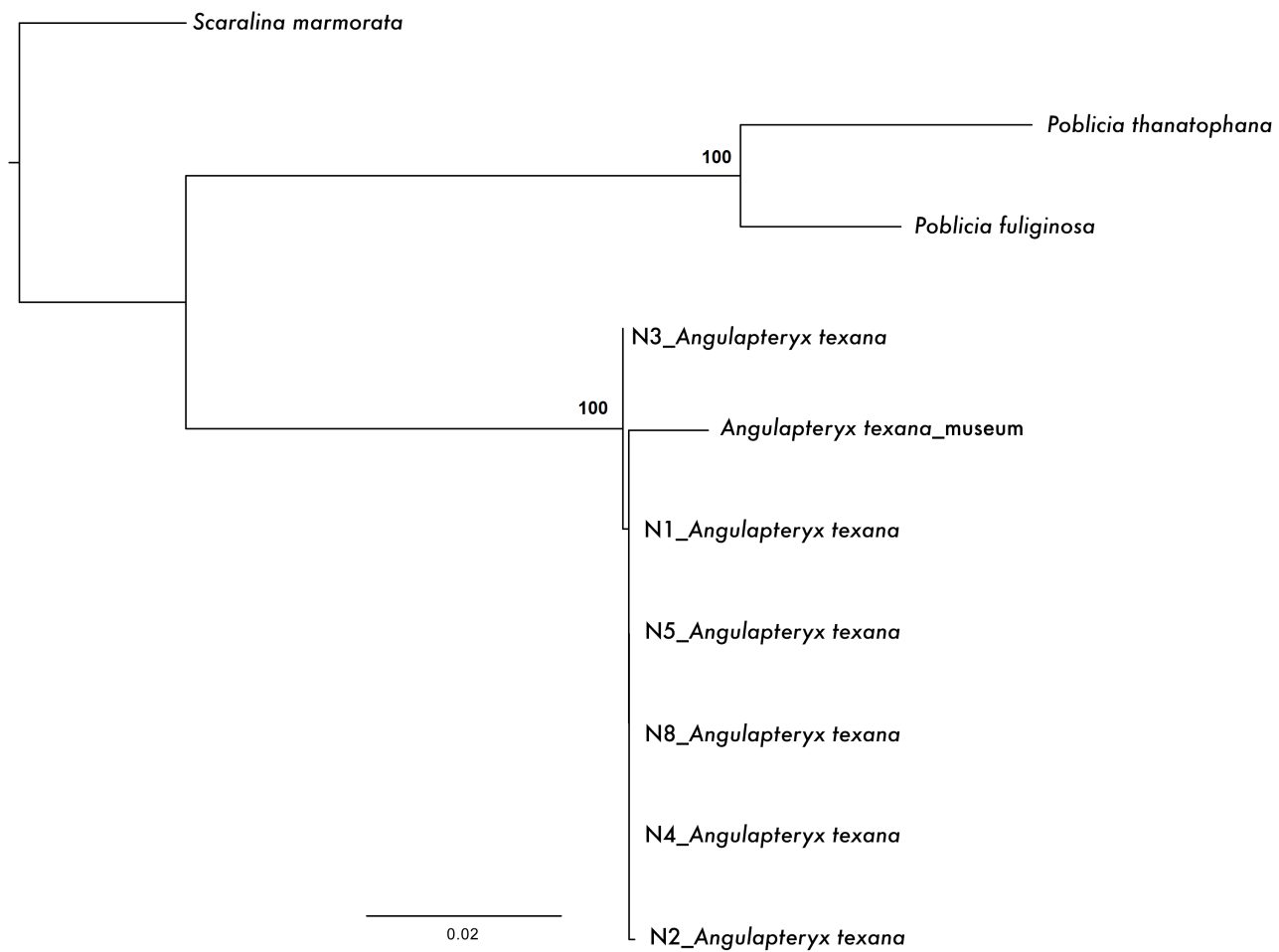


FIGURE 1. Maximum likelihood tree based on a concatenated ITS2, 28S and cytochrome c oxidase subunit I dataset. Bootstrap values ≥ 70 shown above branches.

Systematics

Family Fulgoridae Latreille, 1807

Subfamily Poiocerinae Haupt, 1929

Tribe Poiocerini Haupt, 1929

Genus *Poblicia* Stål, 1866—The Speckled Lanternflies

Type species. *Poeocera misella* Stål, 1863, by monotypy, first specified by Van Duzee (1916: 78).

Stål, 1866: 138 [genus described].—Metcalf 1947: 61 [cataloged, full synonymy list].—Nast 1951: 270, 274 [erroneous combination, comparative notes].—Wilson & McPherson 1980a: 16, 48 [key, illustrated].—Wilson & McPherson 1980b: 29 [listed].—Wilson & McPherson 1980c: 15 [listed].—Porion 1994: 21 [cataloged, illustrated].—Moran *et al.* 2005: 8803 [endosymbionts].—Urban & Cryan 2009 [phylogenetics].—Bartlett *et al.* 2011 [listed, key, illustrated].—Urban & Cryan 2012 [endosymbionts].—Bartlett *et al.* 2014: 31–32, 169 [key, illustrated, notes].—Broadley *et al.* 2023 [parasites].—Gómez-Marco *et al.* 2023 [parasites].

Diagnosis. Relatively small taxa (~10–16 mm including wings), nearly black. Body broad and parallel-sided. Head strongly transverse (lacking a projection), just wider than pronotum. Vertex strongly transverse, much wider than long, carinate on all sides. Frons quadrate, approximately twice as wide as tall. Forewings entirely opaque with pale (often bluish) maculations. Hindwings broad, anal lobe well-developed, smoky, mostly translucent, proximally deep grey, often with 1–2 large pale (pale blue or white) markings. Fore and middle legs with femora and tibiae flattened. Dorsum of abdomen broadly orange or red.

Description. *Color.* Overall coloration is nearly black (dry specimens often paler). Head with anterior margin distinctly paler; body usually with minute pale dots. Forewings opaque, differing slightly in color and texture past nodal line, bearing pale (blue or white) maculations; forewings with pale irregular reticulate lines in cells from base to nodal line; distad of nodal line forewings bearing white dashes. Hindwings mostly smoky-transparent, apex darker gray, proximal portion near black, often with two pale large irregular spots (often blue or transparent). Legs black with irregular white spots, front and middle tibiae with 1–2 white bands (may be incomplete). Abdomen ventrally near black, dorsally bright red or orange.

Structure. Body length (including wings) usually 16 mm or less. Body in dorsal view broad and parallel-sided, in lateral view, head and thorax in similar plane (not appearing hump-backed). Head in dorsal view broad (including eyes just wider than pronotum) and strongly transverse (head projection lacking), anteriorly weakly convex, and posteriorly concave. Vertex much wider than long, carinate on all margins (carina appearing thicker anteriorly), disc depressed, surface roughened; anterior margin of head (dorsal view) appearing to have second anterior carina (i.e., with “double carina between forehead and crown”, viz. Metcalf 1938). Head in lateral view with face receding ventrally, inflection between vertex and frons sharp. Frons (frontal view) broad, roughly quadrate, much broader than high, lateral margins sinuate, laterally foliate; face surface rugulose bearing faint transverse grooves, with median carina and diagonally oriented lateral carinae (approximated at base, giving a V-shaped appearance). Frontoclypeal suture arched (weakly in *P. misella*), clypeus, median third longitudinally carinate. Antennae short, scape smooth, about as tall as wide (hidden behind lateral foliations of frons from frontal view), pedicel somewhat bulbous, longer than wide, bearing numerous conspicuous sensory plaques, flagellum bristle-like with bulbous base. Eyes bulbous, laterally projecting, subcircular (in lateral view), with callus behind ventrocaudal margin (not an expanded flange), lacking a vertical carina or spine in front of eye. Lateral ocelli conspicuous at anterior ventral margin of eye. Rostrum reaching or exceeding hind coxae.

In lateral view, mesonotum and pronotum flat and on same plane. In dorsal view, pronotum broad, about 1.5–2× broader than vertex along midline, anterior margin arched and carinate, posterior margin nearly truncate (or weakly concave), surface irregularly rugulose bearing distinct median carina and a transverse carina (sometimes obscure) just anterior to pronotum midlength. Mesonotum triangular, a little exceeding length of pronotum + head at midline, bearing a distinct median carina, with lateral carinae obscure. Tegulae conspicuous. Front and middle legs with femora and tibiae expanded and flattened, hind tibiae with 4–6 lateral teeth, apical ornamentation 7(2+5)-(8–9)-(6–9) (with conspicuous setae interspersed), with teeth at the apex of tibia large and those on the basitarsus and 2nd

tarsomere in uniform row with lateral teeth largest. Forewings broad, opaque and relatively short, costal and trailing margin subparallel, apex (at apical branches of RP and MP) broadly rounding, claval apex distad of midlength. Hindwings broad, maximum breadth near base, anal lobe well-developed.

Male terminalia. Pygofer in lateral view narrowly trapezoidal (narrower posteriorly), anterior margin concave, caudal margin convex, ventral margin diagonally linear, dorsal margin sinuate; in ventral view posterior pygofer margin concave (medioventral lobe absent). Gonostyli broadly spatulate, bearing a conspicuous laterally projected hook around proximal third. Phallus stout, bilaterally symmetrical, in lateral view horizontally bisected into a dorsal and ventral lobe, each subtended by a sclerotized element; dorsal region membranous and subtended by a slender pair of rods; ventral sclerotized rods broader and cupped, enclosing a ventral pair of inflatable elements (variably everted by the macerating process) with weakly sclerotized apices. Anal tube (lateral view) broad, apex rounded; in dorsal view broad, apex exceeded by bluntly conical paraproct (epiproct hidden).

Remarks. The fulgorid genera in the United States are few (i.e., eight, with five in the Poiocerini) and *Poblicia* is distinctive and easily recognized among them. The generally dark coloration, the relatively short and blunt forewings (bearing irregularly placed pale blue to white spots often combined with fine pale reticulations or dashes), with the hindwings fuscous proximally (with 1–2 irregular pale spots), and the dorsum of abdomen red or orange, help separate *Poblicia* from other similar genera.

Providing definitive diagnostic features that separate genera of American Poiocerini is complicated by the fact that most included genera are incompletely defined and may be heterogeneous with the included species poorly known. Also, the quantitative phylogenetic study of Urban & Cryan (2009) did not recover the Poiocerini as a monophyletic taxon, suggesting that the main tribal feature (the lack of a projected head) may be a convergent feature found in distantly related lineages. The most similar genera found in Central America may be the genera *Acraephia* Stål, 1866, and *Alaruasa* Distant, 1906.

Members of *Acraephia* tend to be much larger (the type species, *A. perspicillata* (Fabricius, 1781) is approximately 45 mm [n=2]), with entirely dark forewings (lacking the fine pale reticulations or dashes) or with a bold pattern, and the hindwings are broadly fuscous, often with a large subapical transparent spot (e.g., Porion 1994, figs 20, 23). The color of the abdominal terga varies, but may be dark, yellow or pink (sometimes including the sternum).

Alaruasa is varied in its appearance with some species with boldly marked wings (often including a transverse bar near the nodal line), and sometimes with copious flocculent wax on the abdomen (e.g., Porion 1994, figs 6, 9). The hindwings of *Alaruasa* vary from uniformly fuscous (e.g., *A. anceps* (Stål, 1869), Porion 1994, fig. 5), to largely transparent with a dark distal border (e.g., *A. aerata* (Distant, 1887), Porion 1994, fig. 6). The species of *Alaruasa* that appears to be most similar to *Poblicia* is *A. pallidoconspersa* (Distant, 1905) (see Porion 1994 fig. 8; Distant 1905, Tab. 14, fig. 26) which has the forewings minutely spotted (“apical area immaculate” Distant 1905: 145), with the dorsum of the abdomen mostly dark (“lateral margins sanguineous” Distant 1905: 145); the hindwings are described and illustrated as a uniform color by Distant (1905), but shown as dark proximally, clear distally by Porion (1994, fig. 8).

We have not seen any definitive records (specimens or iNaturalist) of *Poblicia* from south of Mexico (but see comments under *P. cribrata*). On iNaturalist there are several records similar to *Poblicia*, although the individual appears relatively large with more elongate forewings (e.g., observation 38856037) that resemble *Poblicia* but are possibly *Alaruasa pallidoconspersa*. It is not clear whether the US species are distributed widely in Mexico or if there is one or more undescribed species (e.g., Figs 18C, D) of *Poblicia* in the Mexican fauna.

Etymology. Named after ‘gens Publicia’, a plebeian family in ancient Rome, and is feminine in gender (Dmitriev 2022).

Distribution. Southern USA and Mexico.

Species composition

Poblicia cribrata (Gerstaecker, 1860), **revised status** (replacement name for preoccupied *Poiocera venosa* Walker, 1851)—

Obscure speckled lanternfly

Poblicia fuliginosa (Olivier, 1791)—Sumac speckled lanternfly

Poblicia misella (Stål, 1863)—Broad-headed speckled lanternfly

Poblicia thanatophana Kirkaldy, 1907, **revised status**—Orange-tailed speckled lanternfly

***Poblicia fuliginosa* (Olivier, 1791)—The sumac speckled lanternfly**

(Figures 2–4A–C, 5–7, 12A–B, 18A)

= *Fulgora fuliginosa* Olivier, 1791: 574 (original combination).

= *Poblicia fuliginosa* (Olivier, 1791), comb. by Van Duzee (1917: 719).

= *Poblicia thanatophana* Kirkaldy, 1907; synonym by Ball (1933: 146) (error).

= *Crepusia fuliginosa* (Olivier, 1791), comb. by Nast (1951: 270) (error).

Olivier 1791: 574 [described].—Metcalf 1947: 62 [cataloged, full synonymy list].—Nast 1951: 270 [erroneous combination].—Wilson & McPherson 1980a: 16, 48 [key, illustrated].—Wilson & McPherson 1980b: 29 [listed].—Wilson & McPherson 1980c: 15 [listed].—Porion 1994: 21 [cataloged, illustrated].—Moran *et al.* 2005: 8803 [endosymbionts].—Urban & Cryan 2009 [phylogenetics].—Bartlett *et al.* 2011 [listed, key, illustrated].—Urban & Cryan 2012 [endosymbionts].—Bartlett *et al.* 2014: 31–32, 169 [illustrated, notes].—Broadley *et al.* 2023 [parasites].



FIGURE 2. Habitus views of *Poblicia fuliginosa* (male, Virginia, UDCC), A) dorsal view, B) lateral view, C) frontal view, D) labels.

Diagnosis. Body length between about 11.0–15.5 mm, nearly black with minute pale spotting on the body, and larger bluish to white maculations on the forewing, area past nodal line bearing many pale dashes between longitudinal veins. Vertex very narrow (vs. *P. misella*), in frontal view dorsum of head truncate. Fore- and middle tibiae with 2 pale bands. Hindwings smoky-transparent washed with fuscous in proximal half (enclosing two large irregular clear windows) and along wing apex. Rostrum reaching hind coxa. Abdominal dorsum red.

Amended description. *Color.* Overall coloration is nearly black (Fig. 2, darker in vivo, Fig. 18A, dry specimens notably browner in appearance) with faint brown to bluish wash; head with anterior margin distinctly paler; body with fine pale speckles everywhere, except forewings (Fig. 3A) with larger pale maculations especially following costa (forewing spots pale blue proximally, whitish past nodal line), forewings uniformly darkened (differing in hue past nodal line, before nodal line bearing many fine, irregular contrasting pale reticulate lines in cells, mostly connecting veins; beyond nodal line more distinct white dashes between veins) usually with short whitish transverse bar at apex of clavus (often obscure in vivo, more evident in dry specimens, especially if washed with alcohol), and a matching marking from costa; hindwings (Fig. 3B) mostly smoky-transparent, apex fuscous-gray, proximal portion near black with two large irregular pale spots (may fade to whitish or translucent in preserved specimens), veins dark except proximal portion of MA pale. Legs black with irregular white spots, front and middle tibiae (Fig. 4C) with two white bands (proximal one close to tibial femoral joint, distal band before tibial apex). Abdomen ventrally near black, dorsally bright red (evident on lateral portion of abdomen in repose).

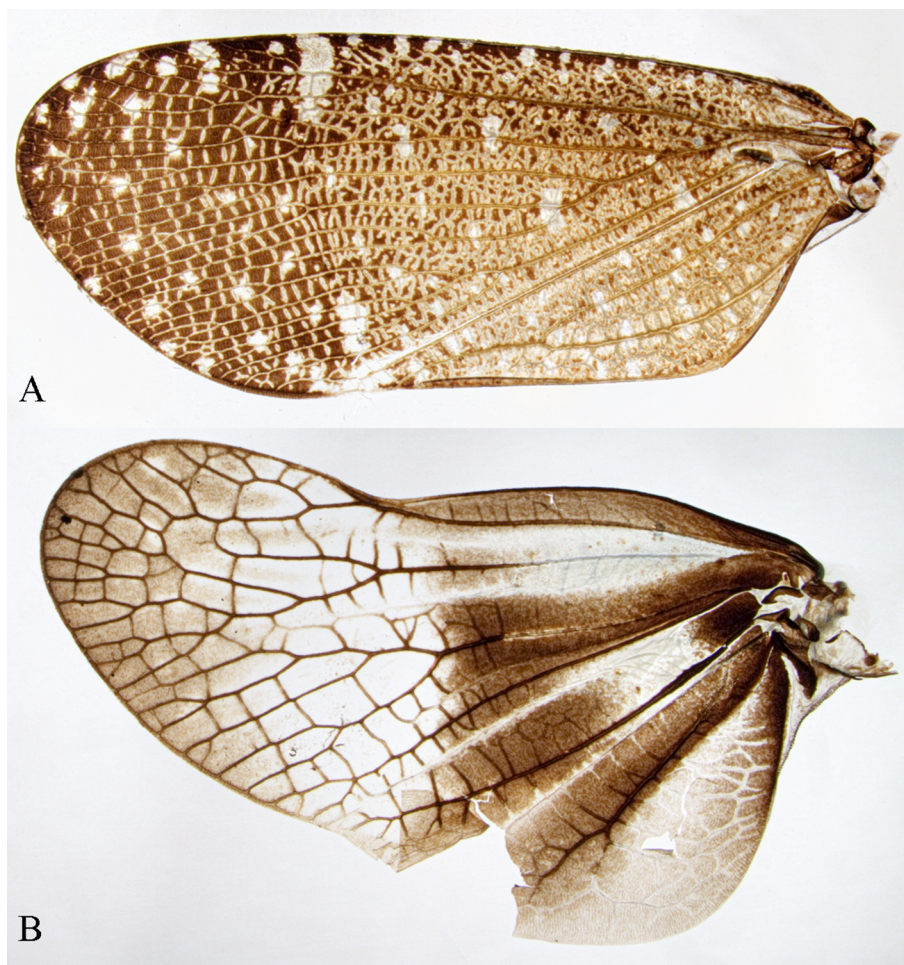


FIGURE 3. Wings of *Poblizia fuliginosa* (Male, North Carolina, UDCC), A) forewing, B) hindwing.

Structure. Body size (including wings) males $\bar{x}$ = 12.8 mm (11.0–13.5, $n=5$), females $\bar{x}$ = 15.0 mm (14.0–15.5, $n=5$). Body in dorsal view (Fig. 2A) broad and parallel-sided, in lateral view (Fig. 2B), head and thorax in similar plane (not appearing hump-backed). Head (dorsal view, Fig. 2A) broad and strongly transverse, just narrower than prothorax, anteriorly weakly convex and posteriorly concave. Vertex much wider than long (about 4.5 $\times$ wider than midlength), carinate on all margins (carina appearing thicker anteriorly), disc depressed, bearing weak median longitudinal carina, surface roughened; anterior margin of head (dorsal view) appearing to have second anterior carina. Head (lateral view, Fig. 2B) with face receding ventrally, inflection between vertex and frons sharp. Frons (frontal view, Fig. 2C) broad, roughly quadrate, much broader than high (midlength about 0.56 $\times$ width at dorsal margin), dorsal margin truncate, lateral margins sinuate, laterally foliate, somewhat narrowing ventrad; face surface rugulose bearing faint transverse grooves, with median carina (not reaching fastigium) and diagonally oriented lateral (approximated at base, giving a V-shaped appearance, becoming obsolete ventrad). Frontoclypeal suture arched, clypeus triangular with rounding dorsal margin, median third longitudinally carinate. Antennae short, scape smooth, barely as tall as wide (hidden behind lateral foliations of frons from frontal view), pedicel somewhat bulbous, longer than wide bearing numerous sensory plaques, flagellum bristle-like with bulbous base. Eyes bulbous, laterally projecting, subcircular (in lateral view), with small callus behind ventrocaudal margin, lacking a vertical carina or spine in front of eye. Lateral ocelli conspicuous at anterior ventral margin of eye. Rostrum reaching hind coxae.

In dorsal view, pronotum broad, about 2 $\times$ broader than vertex along midline (length at midline about 1/3 width), anterior margin arched and carinate, posterior margin nearly (roundly) truncate, surface irregularly rugulose bearing distinct median carina and obscure irregular tracings on disc. Mesonotum triangular, a little longer than pronotum + head at midline, bearing a distinct median carina, with lateral carinae obscure. Tegulae conspicuous. Front and middle legs (Fig. 4C) with femora and tibiae expanded and flattened, hind tibia (Fig. 4A) with 5–6 lateral teeth,

apical ornamentation (Fig. 11B) 7(2+5)-(8-9)-(6-9), with teeth at the apex of tibia large and those on the tarsi much smaller in uniform row (lateral teeth largest), interspersed with conspicuous setae. Forewings broad (Fig. 3A, length about 2.3× width), opaque and relatively short, costal and trailing margins subparallel (costal margin weakly convex, trailing margin inflected slightly at costal apex), apex (at apical branches of RP and MP) broadly rounding, claval apex just distad of midlength; venation dense with numerous secondary veinlets, veinlets in form of pale dashed in apical third, densely reticulate in proximal 2/3; apex of clavus near nodal line (at apical 1/3 of wing); ScP+R forked from MP at basal cell; PCu and A1 fused at about ¾ of clavus length. Hindwings (Fig. 3B) broad, maximum breadth near base, apex broadly rounded, trailing margin indented at claval fold; anal lobe well-developed.



FIGURE 4. Legs of *Poblicia* species, A) hind tibia of *P. fuliginosa* lateral view, B) hind tarsi of *P. fuliginosa*, ventral view, C) front legs of *P. fuliginosa* (tibiae with two white bands), D) hind tibia of *P. thanatophana* lateral view, E) hind tarsi of *P. thanatophana*, ventral view, F) front legs of *P. thanatophana* (tibiae with one white band).

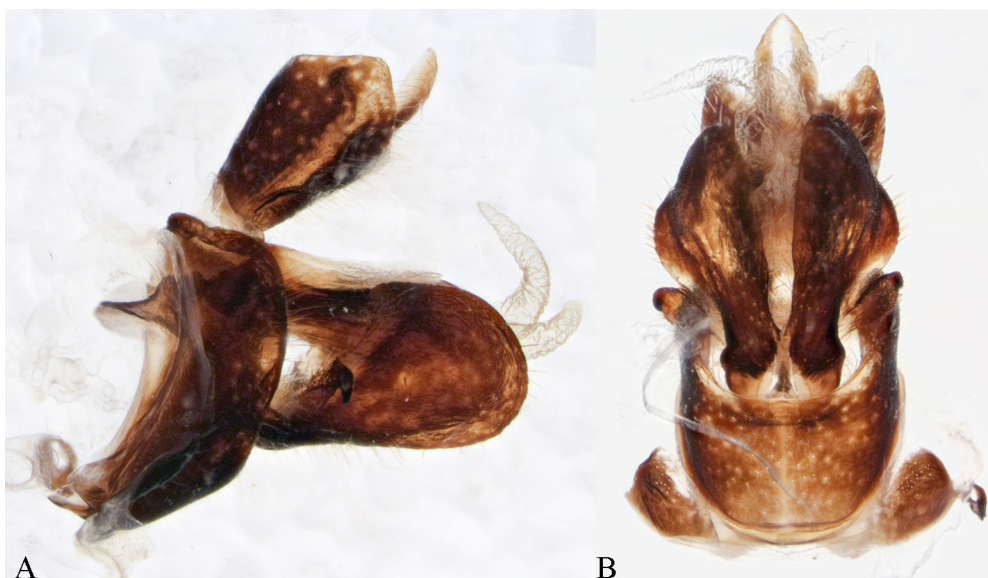


FIGURE 5. Male terminalia of *Poblicia fuliginosa* (Texas, TAMU-ENTO X1260894), A) right lateral view, B) caudoventral view.

Male terminalia. Pygofer in lateral view (Fig. 5A) narrowly trapezoidal (narrower posteriorly), anterior margin concave, caudal margin convex, ventral margin diagonally linear, dorsal margin sinuate; in ventral view, posterior pygofer margin concave (medioventral lobe absent). Gonostyli spatulate (Fig. 12B), proximal portion bearing a conspicuous laterally projected hook around basal third; distal portion roughly quadrate; dorsal surface bearing a large dentate process a little distad of midlength, distal dorsal margin truncate then angled to a second truncate portion before reaching rounded dorsoventral margin. Anal tube (lateral view) broad and elongately triangular, dorsal and ventral margins weakly sinuate, distally expanded in proximal $\frac{3}{4}$, then strongly narrowed into blunt median lobe (apex of anal tube below midpoint); in dorsal view (Fig. 6E), apex deeply concave with lateral margins expanded to blunt lobes; epiproct hidden, paraproct elongated, exceeding caudal margin of anal tube.

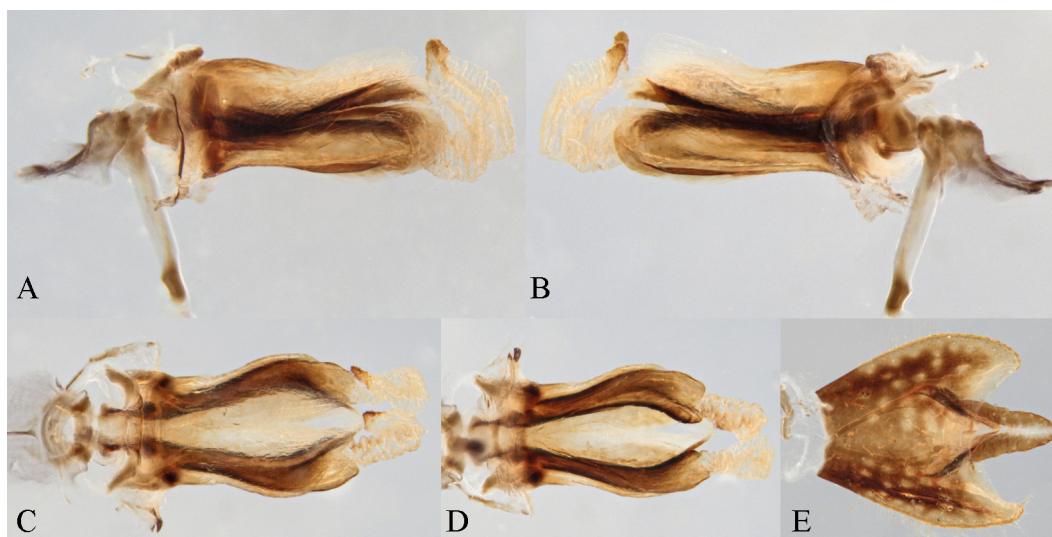


FIGURE 6. Male terminalia of *Poblizia fuliginosa*, A) aedeagus, right lateral view, B) aedeagus, left lateral view, C) aedeagus, dorsal view, D) aedeagus ventral view, E) anal tube, dorsal view.



FIGURE 7. Eggs and nymph of *Poblizia fuliginosa* on *Rhus copallinum* L., A) eggs mass, B) 5th instar nymph (Bladen Co., North Carolina); photos by Tyler Hagerty.

Plant associations. *Rhus copallinum* L. (Anacardiaceae, winged sumac). Also reported (specimen records) *Ambrosia trifida* L. (Asteraceae), and *Acer rubrum* L. (Sapindaceae).

Biology. *Poblizia fuliginosa* is a univoltine species found on *Rhus copallinum*. They have five nymphal instars with adults starting to appear in July (in North Carolina). Females lay eggs in rows and cover them with a waxy covering (Fig. 7A). Egg masses range in number of eggs (6 to 38) with an average of 25 eggs per mass (n=40 egg

masses; Hagerty 2024). Nymphs (Fig. 7B) and adults are messy feeders and often leave seeping wounds on trees, which turn into nodules in subsequent years. Favored tree behavior has been observed with this species, where certain trees will have several individuals while none will be on other nearby trees. Nymphs appear to prefer hiding in foliage in the lower portions of the host plant. This species has been reared in association with spotted lanternfly biocontrol non-target host suitability studies and we intend to describe details of its biology in a separate publication.

Distribution. USA: AL, AR, GA, IL, KS, LA, MD, MO, MS, NC, OK, SC, TN, TX (except upper Rio Grande region), VA; Mexico: Coahuila (Fig. 24).

Remarks. We have found that the eastern and western populations of *Poblicia* differ morphologically, biologically, and molecularly and therefore deserve status as separate species. *Poblicia thanatophana* was described from Nogales, Arizona (Kirkaldy 1907, Fig. 8) and is an available name for the western species, so we restore *P. thanatophana* out of synonymy with *P. fuliginosa*. The diagnostic differences between *P. fuliginosa* and *P. thanatophana* are that the former species is slightly larger, with the abdominal terga red (orange in *P. thanatophana*, at least laterally) and that *P. fuliginosa* usually bears two white bands on the front and middle legs (Fig. 4C, one band in *P. thanatophana*, Fig. 4F). The proximal forewing reticulations are more strongly contrasting in *P. fuliginosa* (Fig. 3A) than in *P. thanatophana* (Fig. 9A). The terminalia of the two species are quite similar, but can be distinguished by several subtle differences in the shape of the gonostyli (Fig. 12), and that the anal tube in *P. fuliginosa* (Fig. 6E) appears more deeply bilobed apically than *P. thanatophana* (Fig. 11E). *Poblicia fuliginosa* primarily utilizes winged sumac (*Rhus copallinum* L.) as a host species, whereas *P. thanatophana* is mainly on Asteraceae, in particular desertbroom (*Baccharis sarothroides* A. Gray).

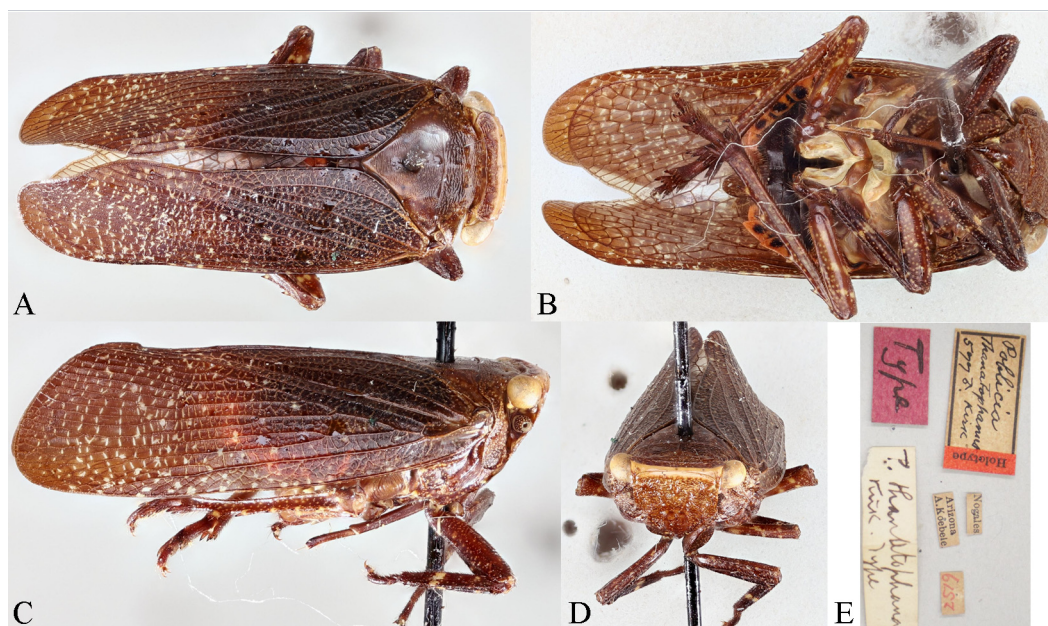


FIGURE 8. Habitus *Poblicia thanatophana* holotype male (BPBM); A) dorsal view, B) lateral view, C) ventral view, D) frontal view, E) Labels (photos courtesy of Jeremy Frank, B. P. Bishop Museum).

Nast (1951: 270), in his remarks concerning the genus *Poiocera* De Laporte, 1832, synonymized *Poiocera venosa* Walker, 1851 under *Crepusia fuliginosa* (Olivier, 1791) (which was a new combination for *fuliginosa*). This combination was missed in Bartlett *et al.* (2014) and is currently followed by Bourgoïn (2025) because the issue had not been formally addressed in prior work. Nast (1951) described his reasons for excluding a series of taxa from *Poiocera*, but not his basis for placing *fuliginosa* under the South American genus *Crepusia* Stål, 1866 (type species *Lystra miniacea* Germar, 1830 from Brazil; Costa Lima 1935, Metcalf 1947). While early authors seemed uncertain about the diagnosis of *Crepusia* (e.g., Metcalf 1923, 1938; Ball 1933), the genus (Fig. 23) appears to be robust forms with the apex of the forewing transparent and the base of the hindwings usually colored red or orange (e.g., Porion 1994, figs 36, 42). An underlying issue is that the limits of many of the genera in the Poiocerini deserve reassessment, and many species are doubtfully placed to genus. We feel the placement of *fuliginosa* in the South

American genus *Crepusia* by Nast (1951) was likely a result of a misunderstanding of the latter genus, and we here reaffirm the traditional placement of *fuliginosa* under *Poblicia* as it has been considered by all authorities since Nast (1951).

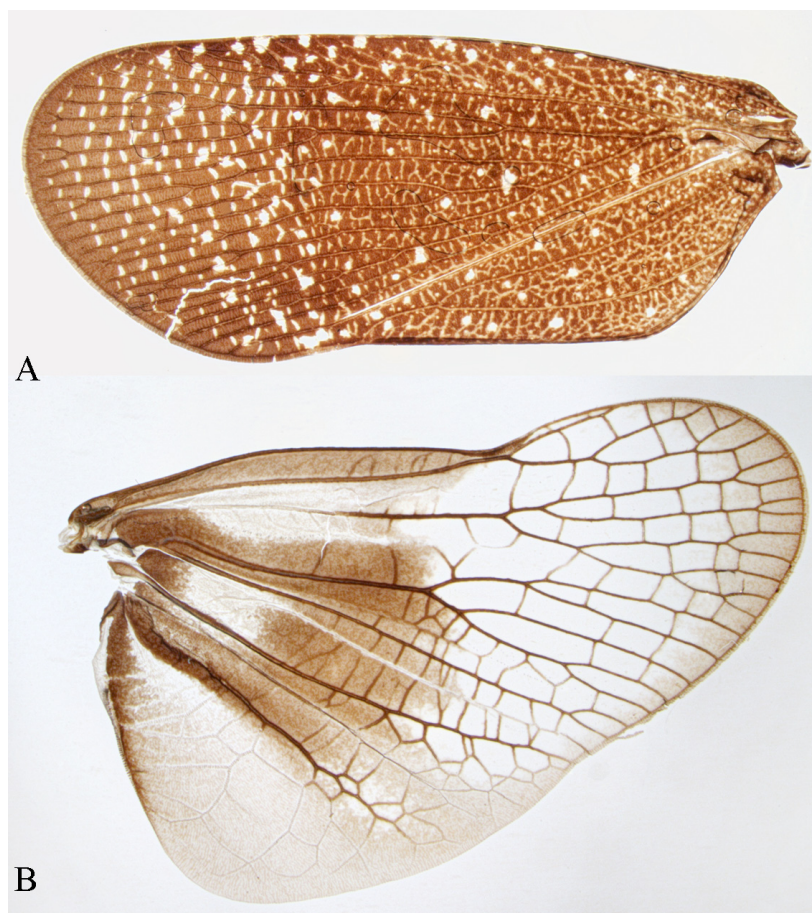


FIGURE 9. Wings of *Poblicia thanatophana* (Arizona), A) forewing, B) hindwing.

The type specimen of *Poblicia fuliginosa* could not be located. The collection of G.A. Olivier is reported to be primarily in Paris, with a portion in Scotland (Horn & Kahle 1937, Osborn 1952). The location of the type specimen of this species was not reported in Porion (1994).

Records on iNaturalist from Mexico (e.g., observation 16700436 from Coahuila State) appear quite similar to *P. fuliginosa* and may represent valid records of this species, but *P. fuliginosa* and *P. thanatophana* can not always be definitively diagnosed based on the views presented.

Material examined. **LOUISIANA:** Natchitoches parish, Kisatchie National Forest, 22–23 Sep 1995, M.J. Travitz (1 male, UDCC); same, Sep 2002, R. M. Krause (1 female, UDCC); same, 14 Sep 2002, W. Burnside (1 male, UDCC); Kisatchie Ranger District, 09 Oct 2002, M. Kleinhenz (1 female, UDCC); Tangipahoa parish, Arcola, Sandy Hollow Wildlife Management Area, 7 Sep 2002, S. T. Dash & M. Seymour, *Rhus copallina* (1 male, 1 female, UDCC); Same, 7 Sep 2002, P. L. Vasseur (1 male, UDCC). **MARYLAND:** Dorchester Co.: Linkwood Wildlife Management Area, 31 Aug 1994, M. J. Rothschild, *Ambrosia trifida* L. (1 male, UDCC). **NORTH CAROLINA:** Bladen Co., 2.5km N of Jones Lake Co. Rd. 1509, 17 Sep 1994, G. V. Fodor (1 male, NCSU); Bladen Lakes St Forest Co. Rd 1509, 6km NE Hwy 242, 7 Sep 1990, H. Zhong (1 male, 1 female, NCSU); same, 07 Sep 1990, M. A. Wolff (1 male, NCSU); same, 7 Sep 1990, R.J. Kopanic Jr. (1 male, 2 female, NCSU); Bladen Lakes State Forest, 22–27 Aug 2020, T. J. Hagerty, *Rhus copallinum* (5 males, UDCC; 3 male, 2 female, RBINS); Bladen Lakes State Forest, 5.5 km S of Ammon, SR-1508 [Lulu Long Rd] at Turnbull Creek, 8 Sep 2001, M. A. Bertone (1 male, NCSU); near Bladen Lakes State Forest, 17 Sep 1994, C. R. Bartlett, *Acer rubrum* L. (2 female, NCSU); same, 18 Sep 1994, C. R. Bartlett, *Rhus copallina* (1 male, 1 female, NCSU, 1 female UDCC); Cumberland Co., Fayetteville, 6 Sep 1945, D. L. Wray (1 female, NCSU); Durham Co., 20 Km N. of Durham, on Hill Forest, 3 Sep

1999, J. R. Carlson (1 female, NCSU); same, 3 Sep 1999, C. M. Newman (1 female, (NCSU); Durham, 21 Sep 1995, H. A. King, *Rhus copallinum* (1 male, UDCC); Moore Co., Southern Pines, 6 Oct 1908 (2 female, NCSU); same, 7 Oct 1908, A. H. Manee (1 female, NCSU); same, 26 Jun 1919 (4 male, NCSU); Southern Pines, Sep 1906, R. Woglum (2 sex undetermined, UCRC); same, 27 Sep 1906, R. Woglum (2 sex undetermined, UCRC); same, 7 Sep 1908, A. H. Manee (1 sex undetermined, UCRC); Pasquotank Co.: Elizabeth City, Late Aug 1919, F. Sherman (1 female, NCSU); Richmond Co., Hoffman, 26 Sep 1981, R. Webster (1 sex undetermined, UCRC), Wake Co., (13 specimens, NCSU). **OKLAHOMA**: Payne Co., Stillwater, 7 Oct 1993, M. Gates (2 sex undetermined, UCRC). **SOUTH CAROLINA**: Oconee Co., Seneca, 3 Sep 1989, Debbie Oliver (1 male, UDCC). **TEXAS**: Tyler Co.: Tyler County, 7 Oct 1989, C. Bordelon (1 female, UDCC). **VIRGINIA**: Northampton Co.: Kiptopeke State Park, 3.7km SW Townsend, 4 Oct 2014, S. T. Dash, *Rhus copallina* (1 male, UDCC).

iNaturalist State Records: **ALABAMA**: Chilton Co. (137657115), Colbert Co. (97167950). **ARKANSAS**: Pulaski Co. (59383343), Faulkner Co. (125299876); Cleburne Co. (136038966).

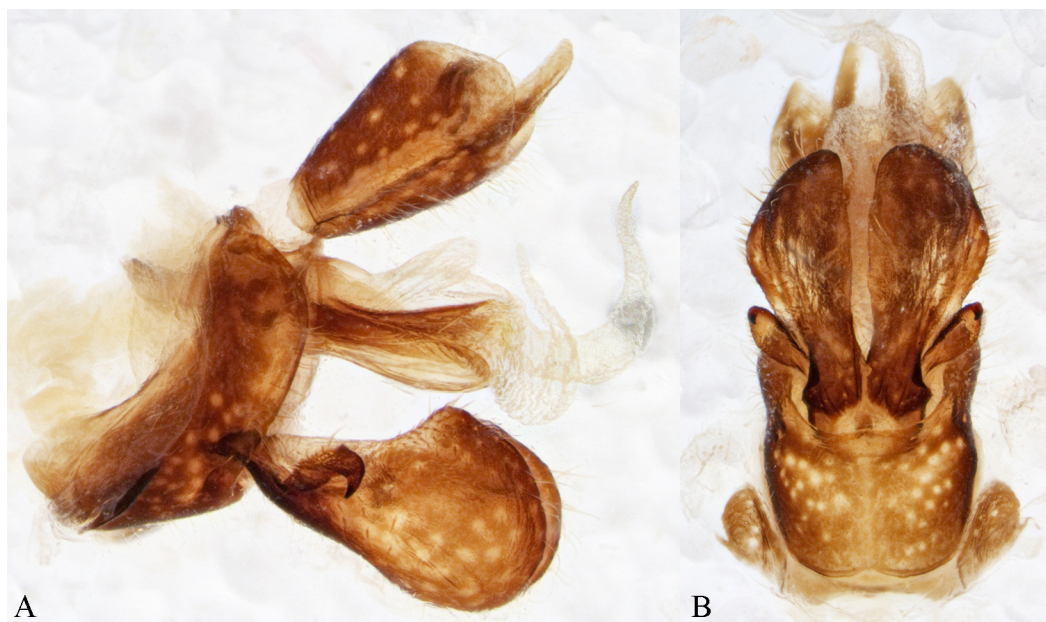


FIGURE 10. Male terminalia of *Poblicia thanatophana* (Arizona, TAMU X0630285), A) right lateral view, B) caudoventral view.

***Poblicia thanatophana* Kirkaldy, 1907, revised status.—The orange-tailed speckled lanternfly**
(Figures 4D–F, 8–11, 12C, D, 18B)

Kirkaldy 1907: 61 [described].—Metcalf 1947: 63 [cataloged as synonym of *Poblicia fuliginosa*].—Gómez-Marco *et al.* 2023 [parasites as *Poblicia fuliginosa*].

Diagnosis. Body length between about 10.5–13.5 mm, nearly black usually with minute pale spotting on body, and larger bluish to white maculations on forewing, area past nodal line with many pale dashes between longitudinal veins, proximal to nodal line with reticulate veinlets (less dense than *P. fuliginosa*). Vertex very narrow (vs. *P. misella*), in frontal view dorsum of head truncate. Abdominal dorsum orange, fore- and middle tibiae with one pale band. Rostrum reaching hind coxae.

Amended description. *Color.* Overall coloration (Fig. 8) deep blackish-brown to nearly black (darker in vivo) with faint bluish wash; head anterior margin paler; body usually with fine minute spots (may be obscure or absent), except forewings (Fig. 9A) with larger pale bluish maculations especially along costa and apically, forewings uniformly darkened and opaque (differing in hue past nodal line, before nodal line bearing many fine, irregular reticulate lines in cells, mostly connecting veins; beyond nodal line more distinct white dashes between veins); hindwings (Fig. 9B) mostly smoky-transparent, apex darker gray, proximal portion near black with two large irregular spots (may fade to whitish or translucent in preserved specimens) and pale portion of clavus; veins dark except pale in proximal irregular pale spots. Legs black with irregular white markings, front and middle tibiae (Fig.

4F) with one white band in distal third. Abdomen ventrally near black, dorsally bright orange (evident on lateral portion of abdomen in repose).

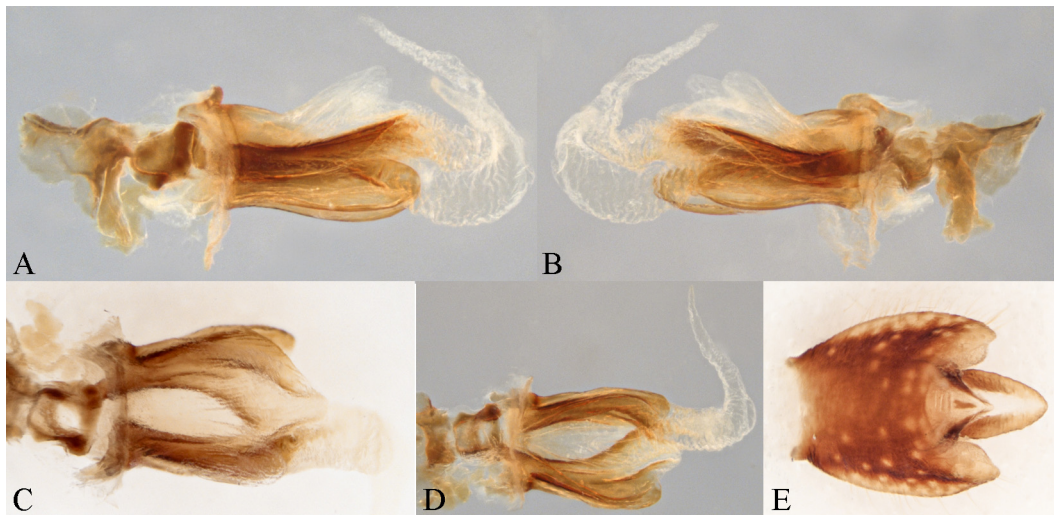


FIGURE 11. Male terminalia of *Poblizia thanatophana*, A) aedeagus, right lateral view, B) aedeagus, left lateral view, C) aedeagus, dorsal view, D) aedeagus ventral view, E) anal tube, dorsal view.

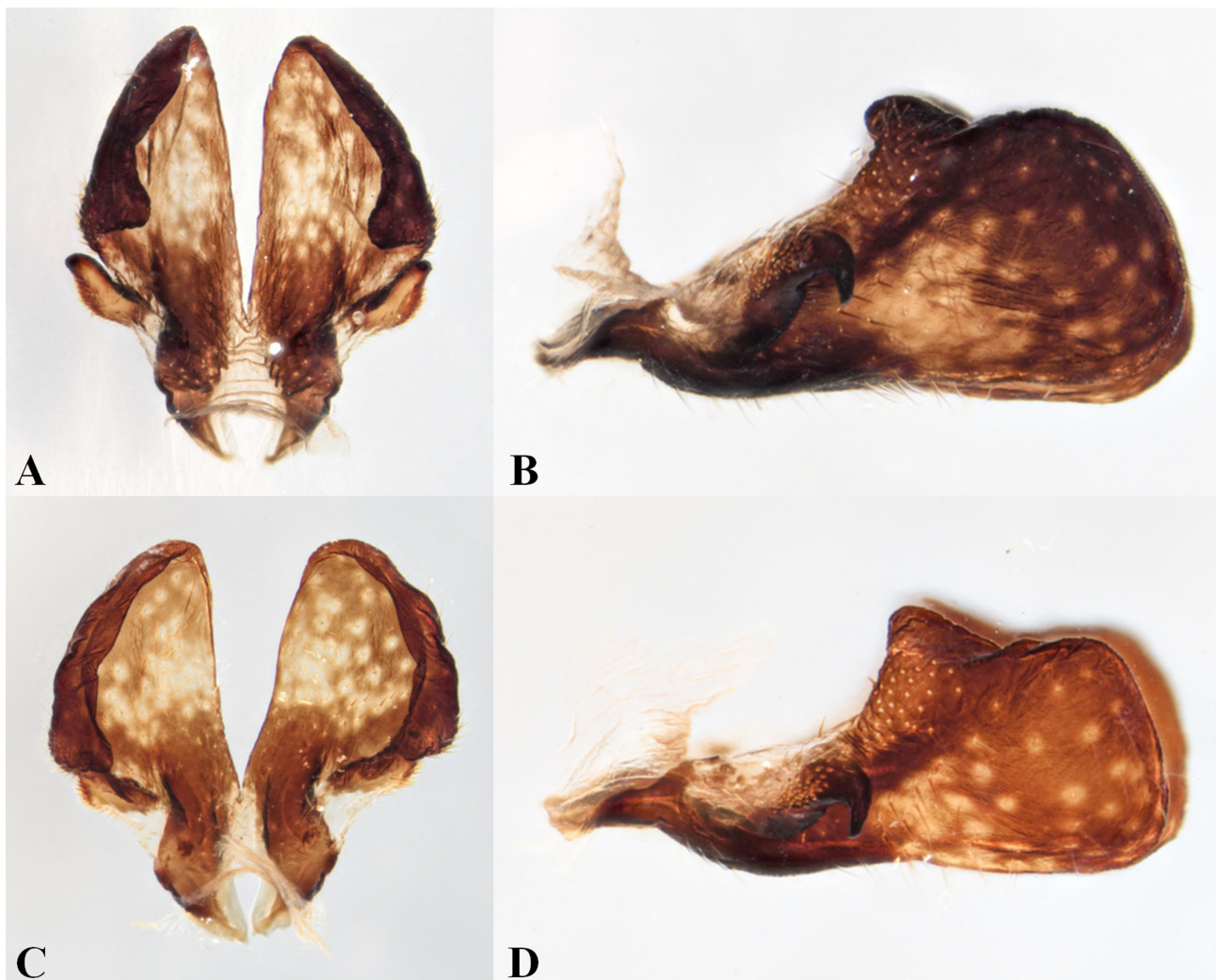


FIGURE 12. Gonostyli of *Poblizia* species, A) *P. fuliginosa*, dorsal view, B) *P. fuliginosa*, lateral view, C) *P. thanatophana*, dorsal view, D) *P. thanatophana*, lateral view.

Structure. Body size (including wings) males $\bar{x}$ = 10.9 mm (10.5–11.5, $n=5$), females $\bar{x}$ = 13.1 mm (12.5–13.5, $n=5$). Body in dorsal view (Fig. 8A) broad and parallel-sided, in lateral view (Fig. 8C), head and thorax in similar plane (not appearing hump-backed). Head in dorsal view broad and strongly transverse, just narrower than prothorax, anteriorly weakly convex and posteriorly concave. Vertex much wider than long (about 5× wider than midlength), carinate on all margins (carina appearing thicker anteriorly), disc depressed bearing weak median longitudinal carina (sometimes obscure), surface roughened; anterior margin of head (dorsal view) appearing to have second anterior carina. Head in lateral view with face receding ventrad, inflection between vertex and frons abrupt. Frons (frontal view, Fig. 8D) broad, roughly quadrate, much broader than high (midlength about 0.62× width at dorsal margin), dorsal margin truncate, lateral margins sinuate, laterally foliate, somewhat narrowing ventrad; face surface rugulose bearing faint transverse grooves, with weak median carina (not reaching fastigium) and obscure diagonally oriented lateral carinae (approximated at base, giving a V-shaped appearance, becoming obsolete ventrad). Frontoclypeal suture arched, clypeus triangular with rounding dorsal margin, median portion longitudinally carinate. Antennae short, scape smooth, as tall as wide (hidden behind lateral foliations of frons from frontal view), pedicel bulbous, about as long as wide bearing numerous sensory plaques, flagellum bristle-like with bulbous base. Eyes bulbous, laterally projecting, subcircular (in lateral view), lacking a vertical carina or spine in front of eye. Lateral ocelli conspicuous at anterior ventral margin of eye. Rostrum reaching hind coxae (Fig. 8B).

In dorsal view, pronotum broad, about 2× broader than vertex along midline (length at midline about 1/4 width), anterior margin arched and carinate, posterior margin nearly truncate, surface rugulose bearing median carina and obscure disc bearing two pits on each side of median line (median pit distinct, more laterad somewhat obscure); transverse carina of pronotum absent. Mesonotum triangular, a little longer than pronotum + head at midline, bearing a distinct median carina (becoming obsolete at scutellum), with lateral carinae obscure. Tegulae conspicuous. Front and middle legs (Fig. 4F) with femora and tibiae expanded and flattened, hind tibiae (Fig. 4D) with 4 lateral spines, apical spinulation (Fig. 4E) 7(2+5)-(9–10)-(6–7), with spinules at the apex of tibia large and those on the basitarsus and 2nd tarsomere in uniform row with lateral spinules largest, bearing conspicuous setae intersperse among apical teeth. Forewings (Fig. 9A) broad, opaque, and relatively short (length ~2.3× width at widest point), costal and trailing margin subparallel (costal margin weakly convex, trailing margin inflected at costal apex), apex (at apical branches of RP and MP) broadly rounding, claval apex just distad of midlength; venation dense with numerous secondary veinlets, veinlets in form of pale dashed in apical third, dull reticulate in proximal 2/3; apex of clavus near nodal line (in apical 1/3 of wing); ScP+R forked from MP at basal cell; PCu and A1 fused near claval apex. Hindwings (Fig. 9B) broad, maximum breadth near base, apex broadly rounded, trailing margin indentate at claval fold; anal lobe well-developed.

Male terminalia. Pygofer in lateral view (Fig. 10A) narrowly trapezoidal (narrower posteriorly), anterior margin concave, caudal margin convex, ventral margin diagonally linear, dorsal margin sinuate; in ventral view deeply concave (medioventral lobe absent). Gonostyli (Figs 12C, D) spatulate, proximal lateral portion bearing a conspicuous laterally projected hook before midlength; distal portion spatulate; dorsal surface bearing a large dentate process a little distad of midlength, posterior margin smoothly rounded. Anal tube (lateral view, Fig. 10A) broad and elongate, dorsal and ventral margins weakly sinuate, distally expanded to midline, then narrowed into blunt median lobe (apex of anal tube near midpoint); in dorsal view (Fig. 11E) apex shallowly concave, lateral margins expanded to blunt lobes; epiproct hidden, paraproct stout, exceeding caudal margin of anal tube.

Plant associations. *Baccharis sarothroides* A. Gray (desertbroom), *Baccharis salicina* Torr. & A. Gray (willow baccharis), *Baccharis* sp., *Brickellia* sp. (brickellbush), *Helianthus* sp. (sunflower) (all Asteraceae). The California record of this species at the flowers of *Opuntia basilaris* Engelm. & J.M. Bigelow (Cactaceae) is likely a dispersing individual.

Biology. *Poblicia thanatophana* adults were always collected on *Baccharis sarothroides* from 2020 to 2022 (July–August). After collection, adults were able to feed on *B. sarothroides* potted plants (~60cm high) for around 20 days inside a walk-in chamber (25 ± 1°C; 50% R.H.; 8:16 D:L) at the Insectary and Quarantine building at the University of California, Riverside. Seven *Poblicia thanatophana* egg masses were found on potted *B. sarothroides* with an average number of eggs of 29.86 ± 2.69 (SE) (Gómez-Marco *et al.* 2023).

Distribution. USA: CA, AZ, CO (Pueblo Co.), NM, TX (upper Rio Grande region); Mexico: Sonora (Fig. 25).

Remarks. The diagnostic features that separate this species from *P. fuliginosa* are described in the remarks under the latter species. It is possible that the easternmost populations of this species may be peripatric with *P. fuliginosa*.



FIGURE 13. Dorsal view of holotype of *Poiocera venosa* Walker, 1851 (photo courtesy of Mick Webb, BMNH).

Material examined. Type material (BPBM, holotype, male) “Nogales // Arizona / A. Koebele // 2519 [?] // Type [red paper] // *Poblicia* / *thanatophana* / 577 ♂ Kirk [handwritten] / Holotype [red paper, stuck perpendicular on label right side // *P. thanatophana* / Kirk Type [handwritten].

Other material examined. **ARIZONA:** Cochise Co. (46 specimens, UCRC, 1 specimen TAMU); Gila Co., 22 mi. NE of Globe, 12 Sep 1957, Timberlake, *Baccharis* sp., (5 sex undetermined, UCRC); Miami, 29 Aug 1958, M. W. Nielson, *Baccharis* sp. (1 sex undetermined, UCRC); Graham Co., Graham Mountain, 15 Sep 1940, Bryant (1 sex undetermined, UCRC); Santa Cruz Co.: 5 mi S of Patagonia, 15 Sep 1985, W. F. Barr (1 male, UDCC); AZ 82 at road to Patagonia Lake, 3.5 mi S of Patagonia, 26 Sep 1997, C. L. and S. L. Staines (1 female, UDCC); Florida Canyon, 25 Sep 1997, C. L. and S. L. Staines (1 female, UDCC); Santa Rita Mountains, 19 Sep 1964, W. F. Barr (1 female, UDCC); Yavapai Co., S Hillside, 1 Oct 1980, Art Strong (1 sex undetermined, UCRC). **CALIFORNIA:** Inyo Co., 2 Miles East of Darwin, P. H. & M. Arnaud, 4700 ft. alt., 12 Jun 1971, at flowers *Opuntia basilaris* (CASENT8139059) (1 sex undetermined, CASC). **NEW MEXICO:** Dona Ana Co.: 12 Sep 1976, J. Calderon (1 female, UDCC); Organ Mountains, Long Canyon, 30 Sep 2007, P. A. Lenhart (2 males, 4 females, UDCC); Vado, 16 Sep 1976, A. Stephens (1 male 1 female, UDCC); Eddy Co.: 4 mi. E Loving, 7 Nov 1989, T. O. Robbins, *Baccharis salicina* (1 male, USNM). **TEXAS:** Donley Co.: 4 mi. N. Clarendon, Greenbelt Reservoir, 06 Oct 1988, P.E. Boldt & T.O. Robbins, *Baccharis salicina* (1 male, USNM); El Paso Co.: McKelligon Canyon, El Paso, 08 Sep 2007, M. J. Lara (1 female, UDCC); Red sand dunes along Highway 62, 09 Sep 2007, M. Dominguez (2 female, UDCC); same, 13 Oct 2007, O.G. Uranga (1 male, UDCC); Socorro, 25 Oct 1973, G. Strong (1 female, UDCC); West El Paso, 16 Apr 2007, J. Bautista (1 male, 3 females, UDCC); same 6 May 2007, J. Bautista (1 female, UDCC); same, 21 May 2007, J. Bautista (1 female, UDCC).

***Poblicia misella* (Stål, 1863)—The broad-headed speckled Lanternfly**
(Figures 14, 15)

= *Poecocera misella* Stål, 1863 (original combination).

= *Poblicia misella* (Stål, 1863), combination by implication Stål (1866: 390), made explicit by Distant (1887: 31).

Stål 1863: 239 [described].—Metcalf 1947: 64 [cataloged, full synonymy list].—Porion 1994: 21 [listed].

Diagnosis. Vertex distinctly elongate (relative to *P. fuliginosa* and *P. thanatophana*), each lateral compartment with a distinct pit; in frontal view, frons nearly square (just wider than tall), with dorsal margin convex. Forewings generously maculated with irregularly arranged bluish spots (with similar spotting on both sides of nodal line). Abdominal terga broadly red. Legs with two pale bands on both femora and tibiae of front and middle legs. Rostrum far exceeding hind coxae.

Amended description. *Color.* Overall coloration near blackish (Fig. 14), irregularly mottled paler. Forewings opaque, generously maculated with irregularly arranged pale blue spots (including distad of nodus, irregular reticulate lines obscure in cells). Hindwings smokey in apical third and most of claval lobe, deep gray proximally. Legs black with irregular white markings (hind legs with more extensive pale markings), front and middle femora and tibiae with two white bands. Abdomen (Figs 14A, B) with apparent tergites 3–4 reddish with a pair of black spots each side of midline.

Structure. Body size (excluding wings—type with wings spread) male 7.5 mm, forewing 8.3 mm, estimated body length with wings 10.5 mm. Head in dorsal view (Fig. 15A) broad and transverse (but midline distinctly more elongate than *P. fuliginosa* or *P. thanatophana*), narrower than prothorax, anteriorly convex and posteriorly concave. Vertex much wider than long (about 4× wider than midlength), carinate on all margins, disc depressed bearing median longitudinal carina and a distinct pit near center of disc each side of midline, surface roughened; anterior margin of head (dorsal view) appearing to have second anterior carina. Head in lateral view (Fig. 15A) with face receding ventrad, inflection between vertex and frons abrupt. Frons (frontal view, Fig. 15C) broad, quadrate, about 1.1× broader than high, dorsal margin convex, lateral margins sinuate, laterally foliate, laterally flared into a low lobe near ventral margins; face surface bearing irregular grooves, with weak median carina (appearing to come to a “T” with a transverse carina before dorsal margin), and diagonally oriented lateral carinae (approximated at base, giving a V-shaped appearance). Frontoclypeal suture nearly transverse (downwardly inflected laterally), clypeus triangular median portion longitudinally carinate. Antennae short, scape hidden behind lateral foliations of frons in frontal view, pedicel bulbous, bearing numerous sensory plaques, flagellum bristle-like with bulbous base. Eyes bulbous, laterally projecting, subcircular (in lateral view). Lateral ocelli conspicuous at anterior ventral margin of eye. Rostrum (Fig. 14C) exceeding hind coxae by full segment.



FIGURE 14. Habitus *Poblicia misella* holotype male, A) dorsal view, B) right lateral view, C) ventral view, D) ventral view, male terminalia, E) labels (Photographed by Gunvi Lindberg; ©2023 Naturhistoriskarsmuseum; made available by the Swedish Museum of Natural History under Creative Commons Attribution 4.0 International Public License, CC-BY 4.0).

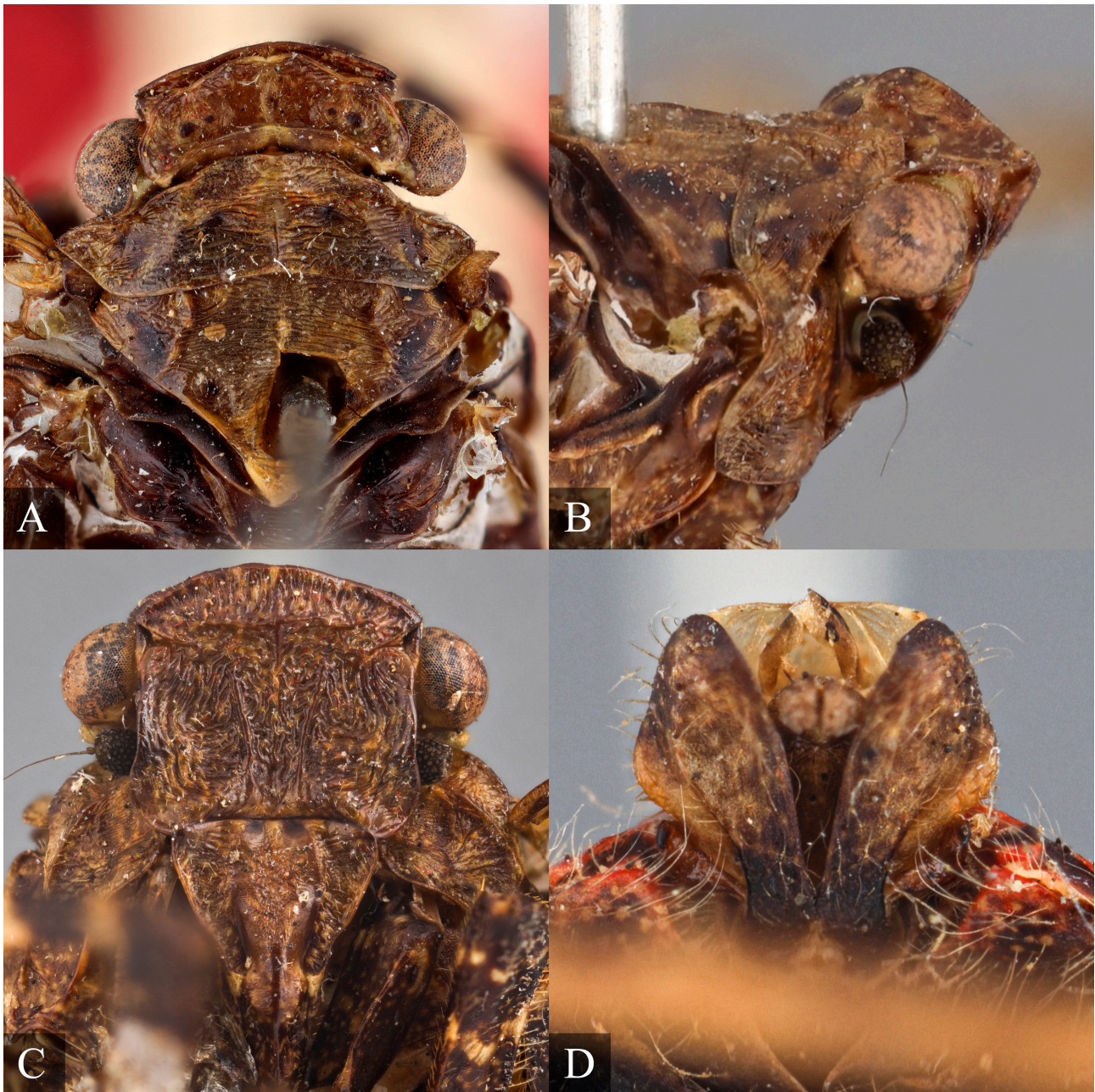


FIGURE 15. *Poblicia misella* holotype male (NHRS), A) dorsal view, head and thorax, B) right lateral view, head and prothorax; C) frontal view, D) male terminalia; Photographed by Gunvi Lindberg (©2023 Naturhistoriska riksmuseet; made available by the Swedish Museum of Natural History under Creative Commons Attribution 4.0 International Public License, CC-BY 4.0).

In lateral view, mesonotum and pronotum nearly flat and on same plane (Fig. 14B). In dorsal view (Fig. 15A), pronotum nearly $2\times$ length of vertex at midline, (length at midline about $1/3$ width), anterior margin arched and carinate, posterior margin weakly concave, surface bearing longitudinal striae. Mesonotum triangular, just longer than pronotum + head at midline. Tegulae conspicuous. Front and middle legs (Fig. 14E) with femora and tibiae expanded and flattened, hind tibia with 5 lateral spines, apical spinulation appearing $7(2+5)-9-6$. Forewings broad (Fig. 14A), opaque and relatively short, costal and trailing margin subparallel, apex (at apical branches of RP and MP) broadly rounding, claval apex distad of midlength. Hindwings broad, maximum breadth near base, anal lobe well-developed.

Remarks. Among species of *Poblicia*, *P. misella* is most readily recognized by the more elongate vertex from dorsal view (with distinct pits in each lateral compartment), and from frontal view the frons being only a little wider

than tall, with the dorsal margin of the face convex, rather than truncate as in *P. fuliginosa* and *P. thanatophana*. Also, the speckling patterns of the forewings are different with *P. misella* being more densely supplied with bluish maculations and lacking the many fine, irregular pale reticulate lines in cells before the nodal line and the white dashes between veins distad of the nodal line. Also, in the type specimen of *P. misella*, the apex of the hindwing is transparent (usually smoky in other *Poblicia*) and the hindwing base lacks the large bluish markings.

We have not yet found any additional records of this species (either specimens or iNaturalist), although iNaturalist observation 94771776 from Nayarit State, Mexico, may represent this species.

Plant associations. None reported.

Distribution. Mexico (Oaxaca).

Material examined. Type material (NHRS, holotype, male) “Oaxaca // Sallé // Typus [red paper] // 458 / 63 // *Poblicia* / *misella* Stal / V. Lallemand det., 1953 // NHRS-GULI / 00009853”.

***Poblicia cribrata* (Gerstaecker, 1860), restored name, new combination—The obscure speckled lanternfly (Figure 13)**

= *Poiocera venosa* Walker, 1851: 298 (nec Germar) (original description).

= *Poiocera cribrata* Gerstaecker, 1860 (replacement name for preoccupied *Poiocera venosa* Walker (nec Germar)).

Gerstaecker 1860: 227 [described].—Metcalf 1947: 43 [cataloged as synonym of *Poiocera venosa*].—Nast 1951: 270 [As *P. venosa*, synonym of *Crepusia fuliginosa*].—Porion 1994: 21 [cataloged as *venosa*].

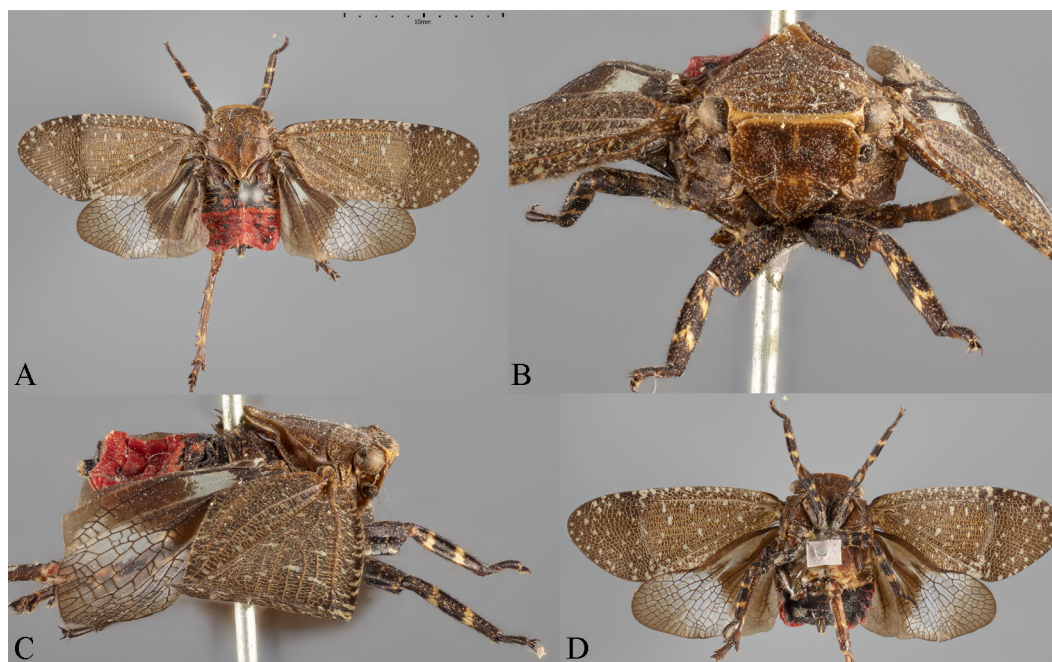


FIGURE 16. Habitus *Poiocera cribrata* Gerstaecker, 1860 (Gerstaecker reference specimen in MFNB), A) dorsal view, B) frontal view, C) right lateral view, D) ventral view.

Amended diagnosis. Vertex not elongate (vertex shorter than *P. misella*, similar to *P. fuliginosa* and *P. thanatophana*), lateral compartments without distinct pits. Forewings maculated with irregularly arranged bluish spots (with similar spotting on both sides of nodal line), forewings lacking fine, irregular pale reticulate lines in cells proximad to the nodal line, distal white dashes between veins distal to nodal line also absent. Hindwings broad, apex and proximal portion washed with fuscous, basal portion with two large, irregular, bluish spots (similar to *P. fuliginosa*). Abdominal terga broadly red.

Remarks. *Poiocera cribrata* was proposed as a replacement name for *Poiocera venosa* Walker (nec Germar) in Gerstaecker, 1860. Walker’s type specimen (Fig. 13) in the BPBM collection does not have locality information and was reported as being from an uncertain locality (Walker 1851: 298–299). As noted under remarks of *P. fuliginosa*, Nast (1951: 270) synonymized *Poiocera venosa* under ‘*Crepusia*’ *fuliginosa* (Olivier, 1791). Based on the type of

Poiocera venosa, this synonymy is in error. The pattern of spotting in the forewing differs in that the many fine, irregular pale reticulate lines in cells proximad to the nodal line and distal white dashes between veins present in both *P. fuliginosa* and *P. thanatophana* are absent. The maculations on the forewings of *P. cribrata* may be comparable to those on the forewing of *P. misella* (although fewer), but *P. misella* has a conspicuously more elongate vertex, and so we conclude that *P. cribrata* is not a synonym of any of these three *Poblicia* species. Unfortunately, we only have a dorsal view of the type and were unable to locate any additional specimens of *P. cribrata*, nor definitive observations of this species on iNaturalist. Since the intended scope of this work was to reconsider the US species of *Poblicia*, we considered further diagnostic reevaluation of *P. cribrata* to be outside of our scope, but we here restore *Poblicia cribrata* as a **new combination** and a valid species of *Poblicia*.

Gerstaecker's reference specimen (Figs 16–17, erroneously labeled as a type specimen) at the MFNB is reported as being from Brazil, based on the specimen labels). Unfortunately, this specimen does not appear to represent the same species of *Poblicia* as Walker's type specimen of *Poiocera venosa*. While the Gerstaecker specimen is labeled as being from Brazil, the specimen appears quite similar to *P. fuliginosa* in that it has a red abdomen and forewing markings similar to *P. fuliginosa*. While it appears reasonable that *P. fuliginosa* may be present in Mexico, we have no records (specimens or iNaturalist records) of *Poblicia* south of Mexico, and so we are unclear whether Gerstaecker's specimen is a mislabeled *P. fuliginosa*, or that otherwise undetected *Poblicia* species are present in southern Mesoamerica into South America.



FIGURE 17. Habitus *Poiocera cribrata* Gerstaecker, 1860 (Gerstaecker reference specimen in MFNB), A) frontal view, B) head and thorax, right lateral view, C) labels, D) left hind leg, ventral view, E) front leg, frontal view (photos courtesy of Birgit Jaenicke, Museum für Naturkunde Berlin (© Museum für Naturkunde Berlin).

Plant associations. None reported.

Distribution. Not reported, probably Central America.

Material examined. Type material (BMNH, holotype, female) “Type [circular label, green border] / *Poiocera* / *venosa* Walk / ≠ *Poblicia fuliginosa* [handwritten, possibly by Lois O’Brien]”

Other material examined (MFNB, female) “4681 // *cribrata* / gerst.* / *venosa* Walker / Brasil N. Olfers [green paper] // Typus [red paper] // MfN URI / <http://coll.mfn-berlin.de/u/de65d0> [2D barcode label]”.

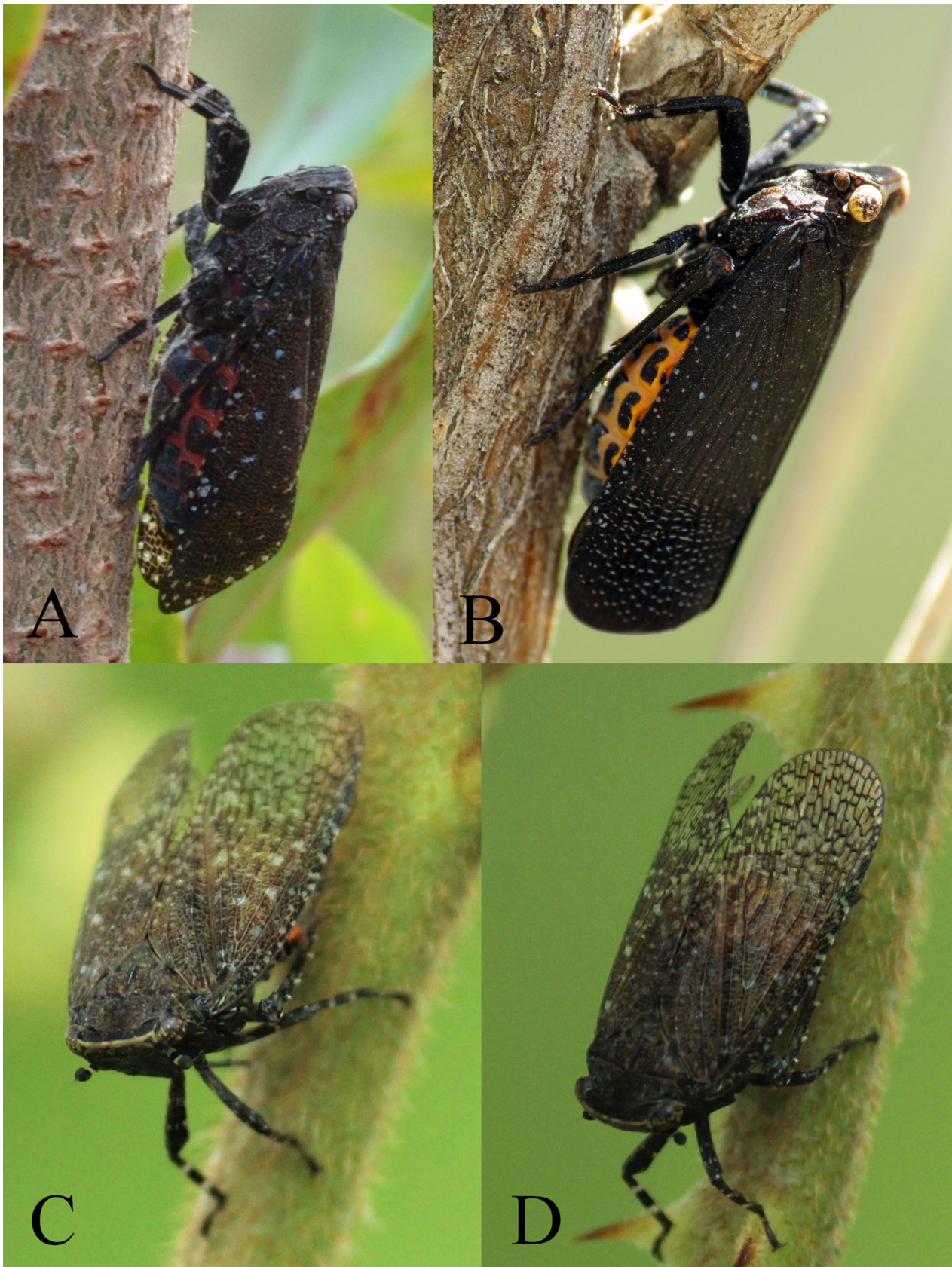


FIGURE 18. *Poblizia* species in vivo, A) *Poblizia fuliginosa* (Bladen Co., North Carolina, on *Rhus copallinum*, photo by Tyler Hagerty), B) *Poblizia thanatophana* (Pima County, Arizona, photo by Katja Schulz, iNaturalist observation 134314, used by permission), C–D) *Poblizia* sp. (Tepic, Nayarit, Mexico, photos by David Molina, iNaturalist observation 94771776, used by permission).

Genus *Angulapteryx* Bartlett, gen. nov.

The Striated lanternflies

Type species. *Poblicia texana* Oman, 1936.

Diagnosis. General color mottled grey, with a dark median vitta from head apex to apex of mesonotum. Face bearing strongly developed carinae in dorsal part and a transverse carina just above frontoclypeal suture. Vertex much broader than long. Face broad, dorsal margin convex. Forewings elongated and opaque. Hindwing broadly washed with fuscous except irregular transparent patches proximally.

Description. *Color.* Overall coloration (Fig. 19) mottled brown-grey, with a dark vitta from head to apex of mesonotum (intensity and extent varying), with the median carina of nota pale. Forewing opaque, mainly grey marked variously with irregular patches of charcoal, pale spotting and sometimes with reddish wash. Hindwing greyish to blackish, usually with 1–2 irregular hyaline windows near base. Fore and middle legs often with two pale bands on the tibiae. Dorsum of abdomen near black proximally paler or reddish distally.

Structure. Body length (including wings) ~18–22 mm. Body in dorsal view broad and parallel-sided, in lateral view dorsoventrally compressed, head and thorax in similar plane (mesonotum weakly raised relative to inclined pronotum). Head in dorsal view (Fig. 19A) broad and strongly transverse (head projection lacking), anteriorly broadly convex, posterior margin concave. Vertex much wider than long, carinate on all margins, median carina present, disc depressed often bearing one or more pits near middle, surface irregular; anterior margin of head (dorsal view) appearing to have second anterior carina (i.e., with “double carina between forehead and crown”, viz. Metcalf 1938). Head in lateral view with face distinctly receding ventrally, inflection between vertex and frons (i.e., fastigium) sharp. Frons (frontal view, Fig. 19C) broad, roughly quadrate, broader than high, dorsal margin convex, laterally foliate; median carina present (may be incomplete), dorsal portion bearing strongly developed carina partially enclosing dorsal portion of face; a sinuate transverse carina just above frontoclypeal suture. Frontoclypeal suture arched, clypeus bearing median and sublateral carinae. Antennae short, scape short (hidden behind lateral foliations of frons from frontal view), pedicel bulbous, longer than wide, bearing sensory plaques, flagellum bristle-like with bulbous base. Eyes bulbous, laterally projecting, subcircular (in lateral view), with weakly expanded callus behind ventrocaudal margin (not an expanded flange), lacking a vertical carina or spine in front of eye. Lateral ocelli conspicuous at anterior ventral margin of eye. Rostrum exceeds hind coxae.

In dorsal view, pronotum broader than vertex along midline, anterior margin truncate and carinate with lateral portions diagonally sloped; posterior margin weakly angulate, median carina distinct. Mesonotum triangular, subequal in length at midline to pronotum + head combined, median carina distinct, lateral carinae obscure. Tegulae conspicuous. Front and middle legs with femora and tibiae not expanded. Forewings elongated and opaque, costal and trailing margin subparallel, apex narrowing to rounded apex (near apical branches of RP and MP), claval apex distad of midlength. Hindwings broad, maximum width near base, anal lobe well-developed.

Male terminalia. Pygofer in lateral view (Fig. 20A), broadest near ventral margin, narrowed dorsad; in ventral view, ventral pygofer margin (Fig. 20B) concave (medioventral margin weakly convex). Gonostyli broad and spatulate, proximal lateral portion bearing a conspicuous laterally projected hook; apex rounded. Phallus stout, bilaterally symmetrical; horizontally bisected into dorsal and ventral lobes; dorsal lobe with a bifurcated inflatable process. Anal tube (lateral view, Fig. 20A) thick, broadened distally; from ventral or dorsal view (Fig. 21E), apex deeply concave, lateral margins projected; epiproct visible from above, paraproct conical, exceeding posterior margin.

Etymology. Formed from the Greek words “*angula*” (corner, bent) combined with “*pteryx*” (wing), a reference to the narrowed apex of the forewing. The genus is feminine in gender.

Remarks. Superficially, *Angulapteryx* gen. nov. is easily separated from other US Poiocerini by the mottled grey color bearing a dark median vitta. *Angulapteryx* gen. nov. has a broader vertex than all *Poblicia* species except *P. misella*. *Poblicia*, as defined here, is uniformly near black. *Angulapteryx* gen. nov. is similar in general proportions to *Scaralina* Yanega, 2024, but differs most conspicuously in having opaque instead of partially transparent forewings.

Two other genera in the Poiocerini that reach the United States in extreme southern Texas are *Alaruasa* Distant, 1906 (e.g., Bartlett *et al.* 2014, fig. 83A, D) and *Itzalana* Distant, 1905 (e.g., Bartlett *et al.* 2014, fig. 83B, E). Both are Central American genera. *Itzalana* is highly distinctive—species are short and broad with a head wider than the

thorax. *Alaruasa* as a genus is probably heterogeneous, but *Alaruasa lepida* (Spinola, 1839), the type species, is similar to *Angulapteryx* **gen. nov.** from dorsal perspective of the head and thorax, but does not have the strongly developed carinae of the face, and the transverse carina above the frontoclypeus of *Angulapteryx* **gen. nov.** is absent in *Alaruasa lepida*. The more dorsal carinae enclosing the triangular area is not fully developed. *Alaruasa* also appears to be less dorsoventrally compressed and the hindwings are of variable color but usually not uniformly fuscous (possibly excepting *A. anceps* (Stål, 1869), *A. pallidoconspersa* (Distant, 1905)). *Angulapteryx* **gen. nov.** also lacks the copious wax production found in some members of *Alaruasa* (viz. *A. aerata* (Distant, 1887), *A. anceps*, and *A. violacea* (Distant, 1887)).

Distribution. Southern USA (especially East) and Mexico.

Species composition

Angulapteryx texana (Oman, 1936), **comb. nov.**—The striated lanternfly

Angulapteryx texana (Oman, 1936), **comb. nov.**

The striated lanternfly
(Figures 19–22A)

= *Poblicia texana* Oman, 1936: 105 (original combination).

Diagnosis. Color mottled grey with a median vitta from head apex to apex of mesonotum (median carina pale). Face bearing strongly developed carinae dorsally enclosing a nearly triangular region and a transverse carina just above frontoclypeal suture. Vertex broad, width about $2.8\times$ midlength. Face broad (width at eyes about $1.4\times$ midlength), dorsal margin convex. Forewings elongate (length about $2.7\times$ width), opaque, irregularly washed with charcoal bearing irregularly placed rounded pale spots. Hindwing fuscous except irregular transparent patches proximally.



FIGURE 19. Holotype of *Poblicia texana* (male, USNM), A) habitus, dorsal view, B) habitus, ventral view, C) face, D) male terminalia, E) labels.

Description. *Color.* Overall coloration (Fig. 19) mottled olive-grey, with darker and paler markings on forewings and body. A dark vitta extends from apex of head to apex of mesonotum (intensity and extent varying), with the median carina of pro- and mesonotum pale. Forewing mainly grey with broad, irregular patches of charcoal (in claval area and irregular wash along the middle of remigium) and bearing many pale, rounded maculations of varying intensity; some specimens also with pale reddish wash. Hindwing greyish to blackish, with 1–2 irregular pale windows near base (sometimes also in claval region). Fore and middle legs olive-grey washed with blackish

with extensive pale markings; fore- and middle legs with three dark bands; hind legs paler. Dorsum of abdomen near black proximally, apically reddish.

Structure. Body length (including wings) usually less than 21 mm (males $n=1$, 18.4 mm; females $n=6$, 20.3–21.6 mm, average 20.8 mm). Body in dorsal view (Fig. 19A) broad and parallel-sided (weakly laterally convex). Head in dorsal view (Fig. 19A) broad and strongly transverse, anteriorly broadly (but weakly) convex, posterior margin concave. Vertex width about $2.8\times$ midlength, carinate on all margins, median carina weaker, disc bearing a conspicuous elongate-oval pit near middle (and a smaller, inconspicuous round pit just anterior and mesad of oval pit). Head in lateral view with face distinctly receding ventrally, inflection at fastigium sharp. Frons (frontal view, Fig. 19C) broad, roughly quadrate with width at eyes about $1.4\times$ midlength, dorsal margin convex, lateral margins sinuate; face surface bearing fine spots and diagonal striations; median carina on frons upper half, dorsally terminating in transverse carina, all enclosed within strongly developed carina enclosing a nearly triangular area (triangle apex, directed ventrad, not quite closed); a sinuate transverse carina in median third of face above frontoclypeal suture. Clypeus subtriangular, with median carina and arched lateral carinae.

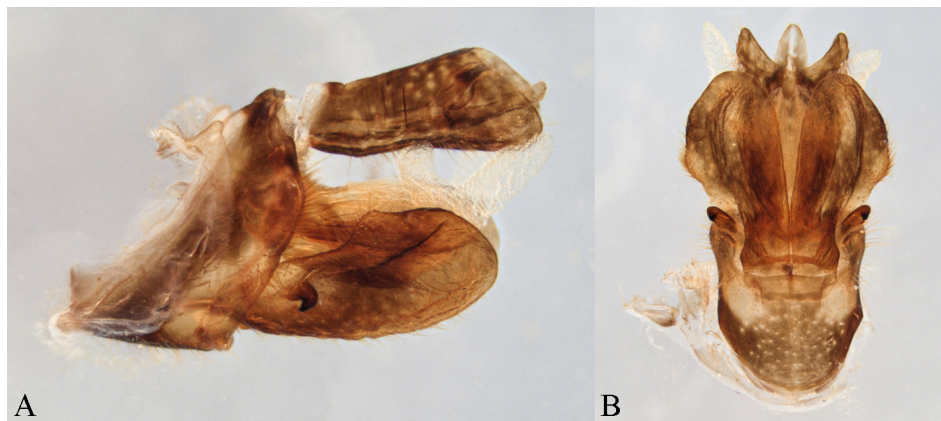


FIGURE 20. Male terminalia of *Angulapteryx texana* **comb. nov.** (Texas, Lamar Co., Paris, paratype), A) right lateral view, B) caudoventral view.

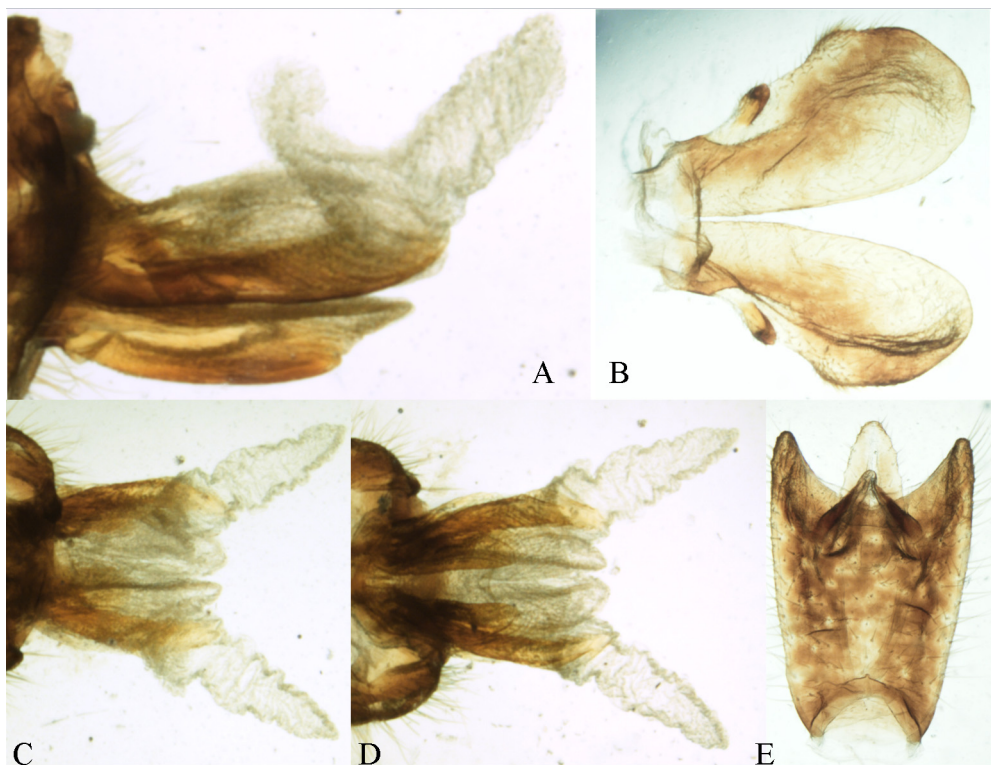


FIGURE 21. Male terminalia of *Angulapteryx texana* **comb. nov.**, A) aedeagus, right lateral view, B) gonostyli, ventral view, C) aedeagus, dorsal view, D) aedeagus ventral view, E) anal tube, dorsal view.

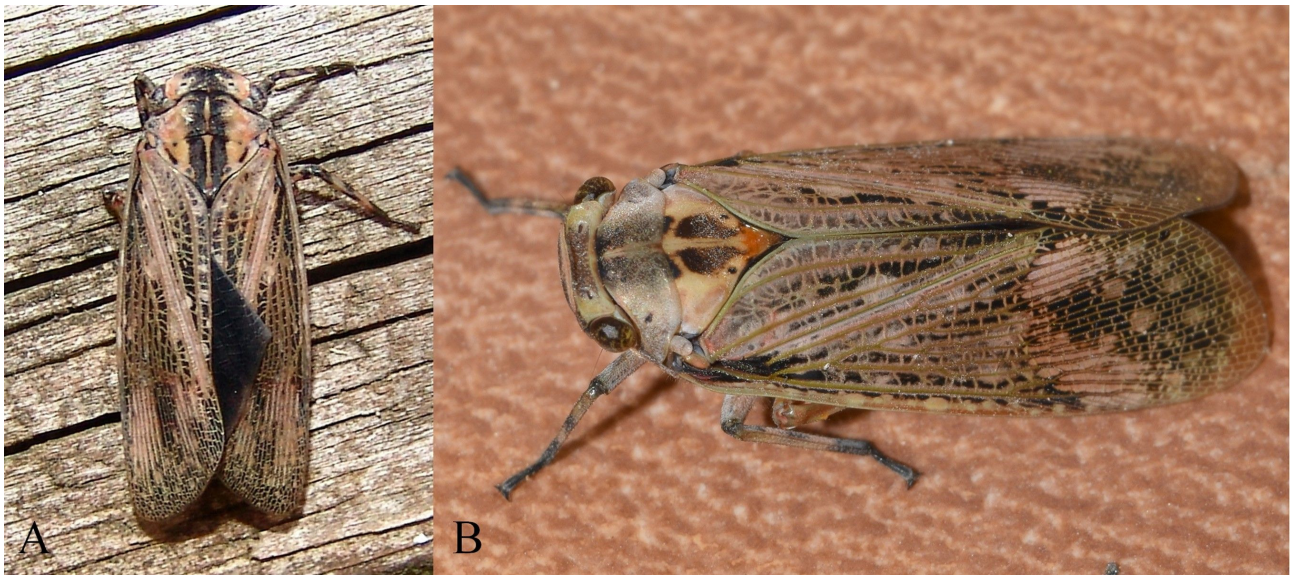


FIGURE 22. *Angulapteryx* species in vivo, A) *Angulapteryx texana* **comb. nov.** (Craighead Co., Arkansas photo by Gordon Snelling, iNaturalist observation 17113846, used by permission), B) *Angulapteryx* sp. (Irapuato, Guanajuato, Mexico, photo by Francisco Acosta, iNaturalist observation 61228128, used by permission).

In dorsal view (Fig. 19A), pronotum about $2.25\times$ broader than vertex along midline, anterior margin truncate and carinate with lateral portions diagonally sloped (giving anterior margin a broadly trapezoidal appearance); posterior margin weakly angulate, surface weakly striate bearing distinct median carina. Mesonotum triangular, length at midline about equal to combined pronotum + head length, median carina distinct, lateral carinae obscure (laterally curved). Front and middle legs not expanded, hind tibiae with 5 lateral spines, spinulation $7(2+5)-(8-9)-(7-9)$, with teeth at the apex of tibia large and those on the basitarsus and 2nd tarsomere in uniform row with lateral teeth largest. Forewing length about $2.7\times$ width, opaque, costal and trailing margin subparallel (costal margin weakly convex, trailing margin weakly concave inflected near apex of clavus), apex narrowing to rounded apex. Hindwings broad, maximum breadth near base, anal lobe well-developed.



FIGURE 23. *Crepusia nuptialis* (DZUP, Matelândia, Paraná, Brazil), A) dorsal habitus, B) lateral habitus, C) face and ventral view of thorax, D) label; photos courtesy of Andressa Paladini (Universidade Federal do Paraná, Curitiba, Paraguay).

Male terminalia. Pygofer in lateral view (Fig. 20A) irregular in shape, broadest ventrally, irregularly narrowed dorsad, leading anterior margin concave, caudal margin sinuate, nearly linear for $\frac{3}{4}$ length (narrowed dorsad); in ventral view, ventral pygofer margin (Fig. 20B) concave (medioventral margin weakly convex). Gonostyli very broad and spatulate, proximal lateral portion bearing a conspicuous laterally projected hook before midlength (Fig. 21B); apex broadly and sinuately rounded. Phallus stout, bilaterally symmetrical; in lateral view (Fig. 21A) horizontally bisected into dorsal and ventral lobes, each subtended by a sclerotized element; dorsal lobe with pair of stout elongate sclerotized rods, each subtending a bifurcated inflatable process; ventral lobe with pair of shorter and slenderer sclerotized rods subtending a membranous element. Anal tube (lateral view, Fig. 20A) thick, broadened distally, dorsal margin nearly linear, ventral margin sinuate, apical margin smoothly rounded (distal-most point below midline); from ventral or dorsal view (Fig. 21E), apex deeply concave, lateral margin projected.

Plant associations. Reported collected from the trunk of *Juniperus virginiana* L., and on ‘Cedar’ (label data given below). In this study, nymphs were collected from *Juniperus deppeana* Steud. by fogging.

Remarks. *Angulapteryx texana* **comb. nov.** is easily separated from other US Poiocerini by general color pattern including the broad median dark vitta. *Angulapteryx texana* **comb. nov.** is similar in general proportions to *Scaralina marmorata* (Spinola), but has opaque (not partially transparent forewings) which are held partially overlapping in repose (*Scaralina marmorata* wings are held weakly diverging).

Angulapteryx texana **comb. nov.** appears to have undergone a recent eastern expansion in distribution. In Bartlett *et al.* (2014), the species was known only from Arkansas and Texas, but now iNaturalist records it throughout the eastern United States (Fig. 26). This species seems poorly represented in institutional collections.

There are several disjunct records (Fig. 26) attributed to *Angulapteryx texana* **comb. nov.** from Central Mexico (Fig. 22B, e.g., states of Jalisco, iNaturalist observation 64748274, Guanajuato, observations 61228128, 35147587, Querétaro, observation 31627477, and Michoacán, observation 32386639). We believe these will likely prove to be undescribed species allied to *Angulapteryx texana* **comb. nov.**, but we do not have specimens to make this determination. Also, we note that the Arizona population appears to be disjunct relative to the eastern population. It is possible that the eastern and western US populations of *Angulapteryx* **gen. nov.** may represent different species, but we lacked the needed data and specimens to adequately address this question, although we hope to return to the problem in the future.

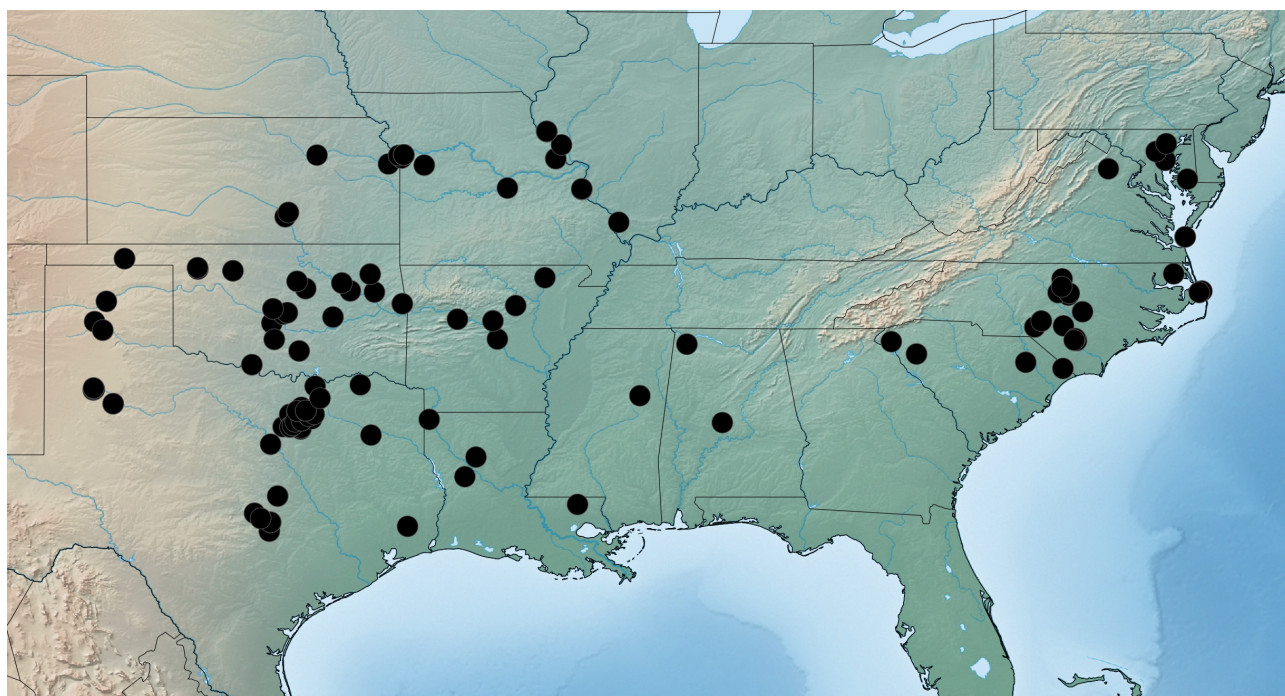


FIGURE 24. Distribution of *Poblicia fuliginosa* (data compiled from available specimens, iDigBio, GBIF, Tri—Trophic Thematic Collection Network, and iNaturalist).

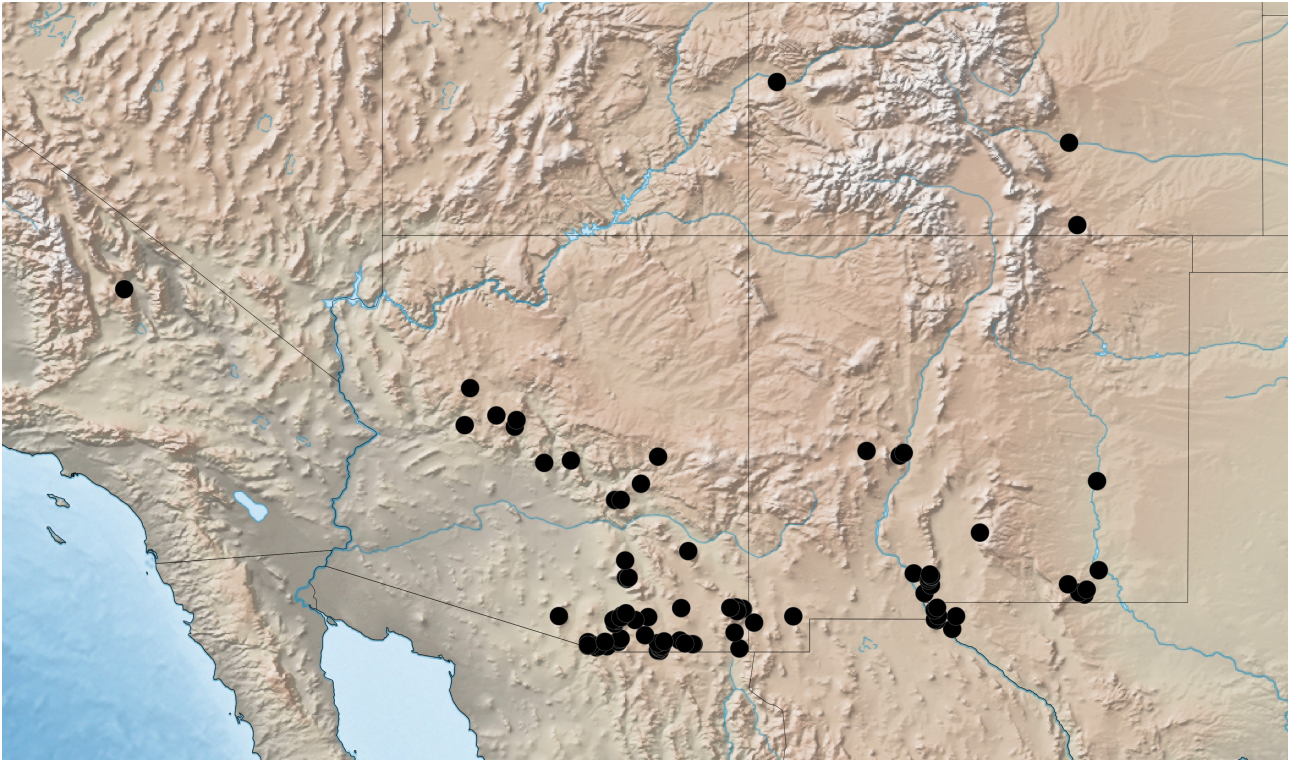


FIGURE 25. Distribution of *Poblicia thanatophana* (data compiled from available specimens, iDigBio, GBIF, Tri-Trophic Thematic Collection Network, and iNaturalist).

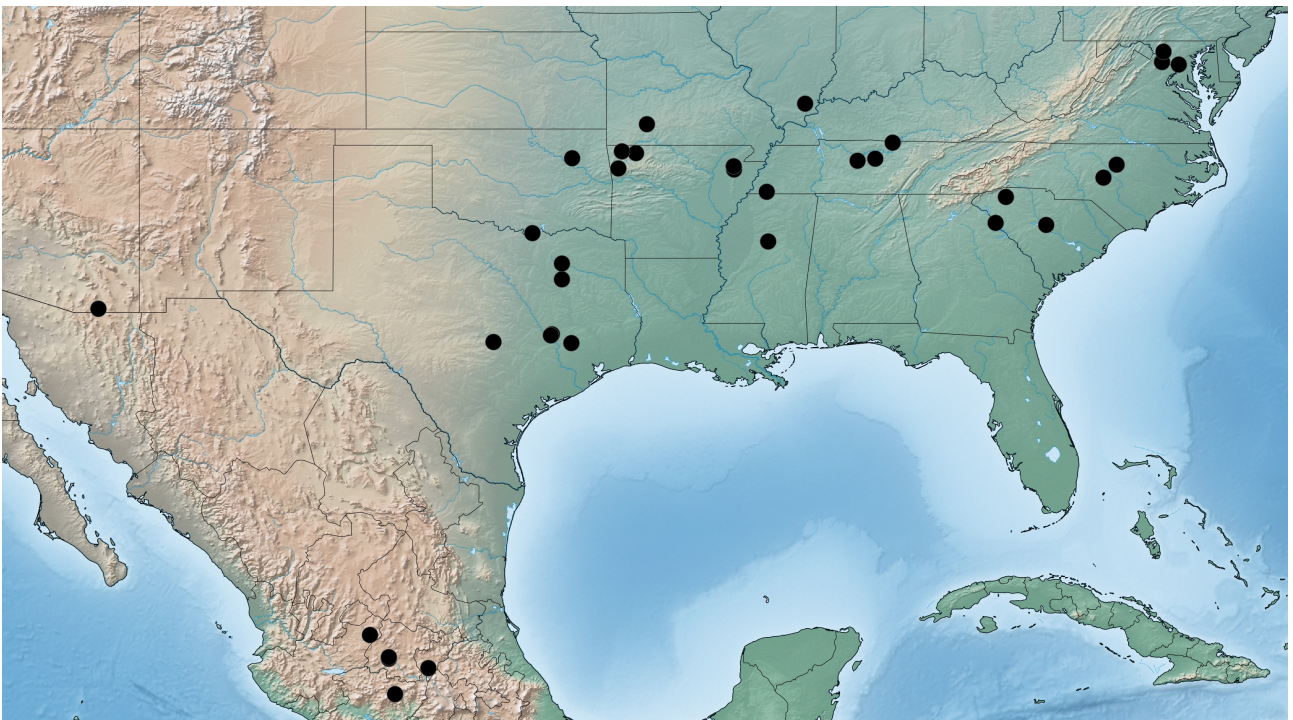


FIGURE 26. Distribution of *Angulapteryx* species; *A. texana* **comb. nov.** in the eastern United States, records from Arizona and Mexico probably represent undescribed species (data compiled from available specimens, iDigBio, GBIF, Tri-Trophic Thematic Collection Network, and iNaturalist).

Plant Associations. *Juniperus virginiana* L. and ‘Cedar’ (from label data). A specimen from Arizona (at UCRC) is from an area with abundant *Juniperus deppeana*, and nymphs tentatively associated with this taxon were found on this host plant (pers. obs., DY).

Distribution. USA: AR, AZ, DC, IL, MD, MO, NC, OK, SC, TN, TX, VA; also reported Mexico (Guanajuato, Michoacán, Querétaro, Jalisco) (Fig. 26, see Remarks).

Material examined. Type material (USNM, holotype, male) “Dallas/IX.21 Tex // GeoMGreene/Collection// Poblícia / Texana / Oman // Type No./ 51616 / U.S.N.M. [red paper]”, Paratype “ParisTx / 10.8 1904 // on cedar // CRJones / Collector // Paratype No. 51616 / U.S.N.M. [red paper] // Poblícia / texana / Oman / Det. PWoman // UDCC_TCN 00102586 [2d barcode label]”.

Other material examined. **USA: TEXAS:** Brazos Co., 12.X.1955 (1 female, TAMU); same, 12.X.1936, H.C. Johnston Collector (1 female, TAMU); College Station, H.J. Reinhard collector (1 female, TAMU); College Station, University Campus, Student collection, 28.X.2008, Thomas Hutto (1 female, TAMU); Montgomery Co., Montgomery City Park [understood as Cedar Brake Park], 25.X.2007, B.M. Drees, on trunk of *Juniperus virginiana* (2 females, TAMU).

iNaturalist State Records: **USA: ARIZONA:** Yavapai Co. (244701702, 244701537). **ARKANSAS:** Benton Co. (961517504), Craighead Co. (200134382), Madison Co. (8713829), Washington Co. (189796259). **DISTRICT OF COLOMBIA** (250917457). **ILLINOIS:** Saline Co. (134628978). **KENTUCKY:** Warren Co. (249827214). **MARYLAND:** Frederick Co. (100811485), Prince George’s Co. (98730473). **MISSISSIPPI:** Montgomery Co. (58804582). **MISSOURI:** Greene Co. (135123900, 246707994). **NORTH CAROLINA:** Durham Co. (16997853), Lee Co. (17313973), Randolph Co. (246249220), Wake Co. (248112245). **OKLAHOMA:** Tulsa Co. (185502284). **SOUTH CAROLINA:** Abbeville Co. (95028199), Greenville Co. (35073002), Richland Co. (140315009). **TENNESSEE:** Clay Co. (185838447), Shelby Co. (138403100), Williamson Co. (95290833), Wilson Co. (148971077). **VIRGINIA:** Chesapeake Co. (245654726), Loudoun Co. (191225500).

Angulapteryx sp. iNaturalist Records: **MEXICO:** Aguascalientes (250695724), Querétaro, (31627477), Distrito Federal (252306883), Durango (240838706), Guanajuato (61228128, 35147587), Jalisco (64748274), Michoacán (32386639).

Discussion

Here we restore *Poblícia thanatophana* and *P. cribrata* out of synonymy with *P. fuliginosa* and establish *Angulapteryx* **gen. nov.** for the allied taxon *A. texana* **new comb.** Our scope was intended as a review of *Poblícia* north of Mexico, in particular, to revise the status of *Poblícia thanatophana*, which we had found to be a species separate from *P. fuliginosa*, differing geographically, in plant associations, molecular markers, and bearing definitive diagnostic features. It remains uncertain if *P. fuliginosa* and *P. thanatophana* coexist in some middle geographical point (i.e., Oklahoma, Texas, New Mexico, etc.). A review of collections from Mexico is also needed to determine the distribution of known Mexican species and to ascertain whether there are undescribed species (which seems likely). It appears that the genera *Poblícia* and *Angulapteryx* **gen. nov.** are both from the southern Nearctic region and are not present south of Mexico.

The finding of an *Angulapteryx texana* **comb. nov.** specimen in Ramsey Canyon and later identification by DNA analyses confirms the existence of another fulgorid in the “Sky Island” mountain regions in southeastern Arizona. We also found nymphs of *A. texana* **comb. nov.** feeding on *Juniperus deppeana* near Portal, probably not exclusively, but the nymphs collected from fogging *J. deppeana* trees with an insecticide were all identified by molecular analyses as *A. texana* **comb. nov.** Other tree species (*Quercus arizonica* Sarg. and *Quercus emoryi* Torr. [Fagales: Fagaceae]) were also fogged with the same methodology and during the same period on the SWRS forest (results not reported in this manuscript). However, no nymphs of *A. texana* **comb. nov.** were collected.

The separation of *Poblícia fuliginosa* and *P. thanatophana* as different species also confirms the non-specificity of the parasitoid candidate as biocontrol agent *Anastatus orientalis* against *Lycorma delicatula*. Gómez-Marco *et al.* (2023) found that *A. orientalis* was able to parasitize *P. fuliginosa*, now *P. thanatophana*, which adds one more species to the large list of species that this parasitoid can use as a host.

Acknowledgments

For specimens, photographs of types, and helpful correspondence, we thank Birgit Jaenicke (Museum für Naturkunde Berlin, Berlin), Jeremy Frank, (Bernice P. Bishop Museum, HI), Gunvi Lindberg (Swedish Museum of Natural History, Naturhistoriska riksmuseet, Stockholm, Sweden), Mick Webb and Diana Isabel Rendón Mera (The Natural History Museum, London), Stuart McKamey and James Zahsiner (Smithsonian National Museum of Natural History), Adeline Soulier (Museum National d'Histoire Naturelle), Ashleigh Whiffin (National Museums Collection Centre, Edinburgh, Scotland), Harold Labrique (Museum of Confluences, Lyon, France), and Ed Riley (Texas A&M University). We thank Andressa Paladini (Universidade Federal do Paraná, Curitiba, Paraguay) for photographs of *Crepusia* specimens. We thank Christopher Grinter (California Academy of Sciences) for certifying the California *Poblicia* record. We thank Solomon Hendrix (University of Delaware) for invaluable help with specimen photography and subsequent photo processing, and Kimberley Shropshire for photography and specimen measurements. We thank the following iNaturalist users for permission to use their photos Katja Schulz (@treegrow) (iNaturalist observation 134314), David Molina (@davidmt83) (iNaturalist observation 94771776), Gordon C. Snelling (@gcsnelling) (iNaturalist observation 17113846), and Francisco Acosta (@franciscoacos) (iNaturalist observation 61228128).

Support for this project is USDA SCRI (award number 2019-51181-30014 Biology, Management and Reducing the Impact of the Spotted Lanternfly on Specialty Crops in the Eastern USA); Farm bill project 'Development of biological control methods for the management of spotted lanternflies'; from Hatch project DEL00854 (Promoting global health and sustainable food systems through integrative research in entomology and wildlife ecology); Mark Hoddle provided support and assistance for field work in Arizona, funded by the California Department of Agriculture Office of Environmental Farming and Innovation's Proactive Integrated Pest Management Solutions Grant Program, award number 18-0632-000-SG.

References

- Ball, E.D. (1933) Notes on the Fulgoridae with some new species. *Psyche*, 40, 145–150.
<https://doi.org/10.1155/1933/37563>
- Bao, K.-X., Wang, X.-Y., Cao, L.-M., Xin, B., Broadley, H.J. & Gould, R.R. (2023) Effects of transgenerational photoperiod experience on the reproduction and development of *Anastatus orientalis*, an egg parasitoid of the spotted lanternfly. *Frontiers in Insect Science*, 3 (Article 1153723), 1–10.
<https://doi.org/10.3389/finsc.2023.1153723>
- Bartlett, C.R., Adams, E.R. & Gonzon, A.T. (2011) Planthoppers of Delaware (Hemiptera, Fulgoroidea), excluding Delphacidae, with species incidence from adjacent States. *ZooKeys*, 83, 1–42.
<https://doi.org/10.3897/zookeys.83.1176>
- Bartlett, C.R., O'Brien, L.B. & Wilson, S.W. (2014) A review of the planthoppers (Hemiptera: Fulgoroidea) of the United States. *Memoirs of the American Entomological Society*, 50, 1–287.
- Bourgoin, T. (1988) A new interpretation of the homologies of the Hemiptera male genitalia illustrated by the Tettigometridae (Hemiptera, Fulgoromorpha). In: Vidano, C. & Arzone, A. (Eds.), *Proceedings of the 6th Auchenorrhyncha Meeting, Turin, Italy, 7–11 September 1987. Consiglio Nazionale delle Ricerche*. IPRA Rome, pp. 113–120.
- Bourgoin, T. (2025) FLOW (Fulgoromorpha Lists on The Web): a world knowledge base dedicated to Fulgoromorpha. Version 8. Updated 2 January 2025. Available from: <https://flow.hemiptera-databases.org/flow/> (accessed 17 January 2025)
- Bourgoin, T. & Huang, J. (1990) Morphologie comparée des genitalia mâles des Trypetimorphini et remarques phylogénétiques (Hemiptera: Fulgoromorpha: Tropiduchidae). *Annales de la Société entomologique de France*, 26, 555–564.
<https://doi.org/10.1080/21686351.1990.12277614>
- Bourgoin, T., Wang, R.R., Asche, M., Hoch, H., Soulier-Perkins, A., Stroinski, A., Yap, S. & Szewdo, J. (2015) From micropterism to hyperpterism: recognition strategy and standardized homology-driven terminology of the forewing venation patterns in planthoppers (Hemiptera: Fulgoromorpha). *Zoomorphology*, 134 (1), 63–77.
<https://doi.org/10.1007/s00435-014-0243-6>
- Broadley, H.J., Sipolski, S.J., Pitt, D.B., Hoelmer, K.A., Wang, X.-y., Cao, L.-m., Tewksbury, L.A., Hagerty, T.J., Bartlett, C.R., Russell, A.D., Wu, Y., Davis, S.C., Kaser, J.M. & Elkinton, J.S. & Gould, J.R. (2023) Assessing the host range of *Anastatus orientalis*, an egg parasitoid of spotted lanternfly (*Lycorma delicatula*) using Eastern U.S. non-target species. *Frontiers in Insect Science*, 2023 (3), 154697, 1–14.
<https://doi.org/10.3389/finsc.2023.1154697>
- Campbell, B.C., Steffen-Campbell, J.D. & Werren, J.H. (1993) Phylogeny of the *Nasonia* species complex (Hymenoptera: Pteromalidae) inferred from an internal transcribed spacer (ITS2) and 28S rDNA sequences. *Insect Molecular Biology*, 2

- (4), 225–237.
<https://doi.org/10.1111/j.1365-2583.1994.tb00142.x>
- Cho, S., Mitchell, A., Mitter, C., Regier, J., Matthews, M. & Robertson, R. (2008) Molecular phylogenetics of heliothine moths (Lepidoptera: Noctuidae: Heliothinae), with comments on the evolution of host range and pest status. *Systematic Entomology*, 33, 581–594.
<https://doi.org/10.1111/j.1365-3113.2008.00427.x>
- Cryan, J.R., Wiegmann, B.M., Deitz, L.L. & Dietrich, C.H. (2000) Phylogeny of the treehoppers (Insecta: Hemiptera: Membracidae): evidence from two nuclear genes. *Molecular Phylogenetics and Evolution*, 17, 317–334.
<https://doi.org/10.1006/mpev.2000.0832>
- Da Costa Lima, A.M. (1935) Catalogo das especies americanas de Laternaridae (Homoptera: Fulgoroidea). *Memorias do Instituto Oswaldo Cruz*, 30, 481–517.
<https://doi.org/10.1590/S0074-02761935000900010>
- Distant, W.L. (1887) Rhynchota: Homoptera. *Biologia Centrali-Americana*, 1, 33–40.
- Distant, W.L. (1905) Cicadidae and Fulgoridae. *Biologia Centrali-Americana*, 1, 140–146.
- Distant, W.L. (1906) Rhynchotal notes xxxix. *Annals and Magazine of Natural History*, Series 7, 18, 191–208.
<https://doi.org/10.1080/00222930608562600>
- Dmitriev, D.A. (2022) Etymology and grammatical gender of generic names in Auchenorrhyncha (Hemiptera). *Illinois Natural History Survey Bulletin*, 43 (2022001), 1–224.
<https://doi.org/10.21900/j.inhs.v43.837>
- Edler, D., Klein, J., Antonelli, A. & Silvestro, D. (2021) RaxmlGUI 2.0: A graphical interface and toolkit for phylogenetic analyses using RAxML. *Methods in Ecology and Evolution*, 12, 373–377.
<https://doi.org/10.1111/2041-210X.13512>
- Fabricius, J.C. (1781) *Species insectorum exhibentes eorum differentias specificas, synonyma auctorum, loca natalia, metamorphosin adiectis observationibus, descriptionibus. Vol. 2.* Impensis C. E. Bohni, Hamburgi et Kilonii [Hamburg & Kiel, Germany], 19 pp. [pp. 313–331]
<https://doi.org/10.5962/bhl.title.36509>
- Germar, E.F. (1830) Species Cicadarium enumeratae et sub genera distributae. *Thon's Entomologisches Archiv*, 2 (2), 1–57.
- Gerstaecker, C.E.A. (1860) Uebersicht der bis jetzt bekannten Arten der Fulgoriden-Gattung *Poiocera* Lap. *Archiv für Naturgeschichte*, 26, 210–244.
- Gómez-Marco, F., Yanega, D., Ruiz, M. & Hoddle, M.S. (2023) Proactive classical biological control of *Lycorma delicatula* (Hemiptera: Fulgoridae) in California (U.S.): Host range testing of *Anastatus orientalis* (Hymenoptera: Eupelmidae). *Frontiers in Insect Science*, 3 (1134889), 1–19.
<https://doi.org/10.3389/finsc.2023.1134889>
- Gould, J.R., Losch, C., Sullivan, L., Wu, Y., Wang, X.-Y., Cao, L.-M. & Broadley, H.J. (2024) Lifecycle of *Anastatus orientalis* (Hymenoptera: Eupelmidae) and synchrony with its host, the spotted lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae). *Environmental Entomology*, 53 (6), 954–965.
<https://doi.org/10.1093/ee/nvae091>
- Kirkaldy, G.W. (1907) Leafhoppers. Hemiptera Homoptera. *Bulletin. Hawaiian Sugar Planters' Association Experiment Station. Division of Entomology*, 4, 60–66.
- De Laporte, F.L. (1832) Mémoire sur quelques nouveaux genres de l'ordre des Homoptères. *Annales de la Société Entomologique de France*, 1, 221–231.
- Hagerty, T. (2024) *Developing biological control methods for spotted lanternfly (Lycorma delicatula): an investigation into non-targets and potential control agents.* Dissertation, University of Delaware, Department of Entomology and Wildlife Ecology, Newark, Delaware, xx + 200 pp.
- Hall, T.A. (1999) BioEdit: A User-Friendly Biological Sequence Alignment Editor and Analysis Program for Windows 95/98/NT/2000/XP/78/10. *Nucleic Acids Symposium Series*, 41, 95–98. [<https://thalljiscience.github.io/>]
- Haupt, H. (1929) Neueinteilung der Homoptera-Cicadina nach phylogenetisch zu wertenden Merkmalen. *Zoologische Jahrbücher. Abteilung für Systemetik, Ökologie und Geographie der Tiere*, 58, 173–286.
- Horn, W. & Kahle, I. (1937) Über entomologische Sammlungen, Entomologen & Entomo-Museologie (Ein Beitrag zur Geschichte der Entomologie). *Entomologische Beihefte aus Berlin-Dahlem*, 2–4, 1–536.
- Kirkaldy, G.W. (1907) Leafhoppers supplement. (Hemiptera). *Report of work of the Experiment Station of the Hawaiian Sugar Planters' Association. Division of Entomology bulletin*, 3, 1–186.
- Latreille, P.A. (1807) Sectio secunda. Familia quarta. Cicadariae. Cicadares. *Genera Crustaceorum et Insectorum secundum ordinem naturalem in familias disposita, iconibus exemplisque plurimis explicata.* Amand Koenig, Paris, 3, 1–258.
<https://doi.org/10.5962/bhl.title.65741>
- Metcalf, Z.P. (1923) A key to the Fulgoridae of Eastern North America with descriptions of new species. *Journal of the Elisha Mitchell Scientific Society*, 38 (3), 139–230, pl. 32.
<https://doi.org/10.5962/bhl.part.7606>
- Metcalf, Z.P. (1938) The Fulgorina of Barro Colorado and other parts of Panama. *Bulletin of the Museum of Comparative Zoology, Harvard College*, 82, 277–423.
- Metcalf, Z.P. (1947) *General Catalogue of the Homoptera. Fascicle IV Fulgoroidea. Part 9 Fulgoridae.* Smith College,

- Northhampton, Massachusetts, 276 pp.
- Moran, N.A., Tran, P. & Gerardo, N.M. (2005) Symbiosis and insect diversification: an ancient symbiont of sap-feeding insects from the bacterial phylum Bacteroidetes. *Applied and Environmental Microbiology*, 71 (12), 8802–8810.
<https://doi.org/10.1128/AEM.71.12.8802-8810.2005>
- Nast, J. (1951) Some remarks on neotropical Fulgoridae with descriptions of new genera and species (Homoptera). *Annales Musei Zoologici Polonici*, 14, 267–279.
- Olivier, G.A. (1791) Fulgore, Fulgora. Encyclopedie methodique. *Histoire naturelle des animaux. Insectes*, 6, 561–577.
- Oman, P.W. (1936) A new *Poblicia* from Texas. *Journal of the Kansas Entomological Society*, 9, 105–107.
Available from: <http://www.jstor.org/stable/25081459>
- Osborn, H. (1952) *A brief history of entomology, including time of Demosthenes and Aristotle to modern times, with over five hundred portraits*. Spahr & Glenn, Columbus, Ohio, iii + 303 pp.
- Porion, T. (1994) *Fulgoridae I: catalogue illustre de la faune americaine*. Sciences Nat, Venette, 72 pp.
- Seidel, S. & Wessel, A. (2013) On the morphology and preparation of male genitalia in the Fulgoridae - The Southeast Asian genus *Penthicodes* (Hemiptera, Fulgoromorpha, Fulgoridae). *Deutsche Entomologische Zeitschrift*, 60 (2), 193–207.
<https://doi.org/10.1002/mmnd.201300025>
- Shorthouse, D.P. (2010) SimpleMappr, an online tool to produce publication-quality point maps. Available from: <https://www.simplemappr.net> (accessed 30 January 2024)
- Spinola, M. (1839) Essai sur les Fulgorelles, sous-tribu de la tribu des Cicadaïres, ordre des Rhyngotes. *Annales de la Société Entomologique de France*, 8, 133–337.
- Stål, C. (1863) Beitrag zur Kenntnis der Fulgoriden. *Entomologische Zeitung. Herausgegeben von dem entomologischen Vereine zu Stettin*, 24, 230–251.
- Stål, C. (1866) Hemiptera Homoptera Latr. *Hemiptera Africana*, 4, 1–276.
- Stål, C. (1869) *Analecta Hemipterologica*. *Berliner Entomologische Zeitschrift*, 13, 225–242.
- Urban, J.M. & Cryan, J.R. (2007) Evolution of the planthoppers (Insecta: Hemiptera: Fulgoroidea). *Molecular Phylogenetics and Evolution*, 42 (2), 556–572.
<https://doi.org/10.1016/j.ympev.2006.08.009>
- Urban, J.M. & Cryan, J.R. (2009) Entomologically famous, evolutionarily unexplored: The first phylogeny of the lanternfly family Fulgoridae (Insecta: Hemiptera: Fulgoroidea). *Molecular Phylogenetics and Evolution*, 50, 471–484.
<https://doi.org/10.1016/j.ympev.2008.12.004>
- Urban, J.M. & Cryan, J.R. (2012) Two ancient bacterial endosymbionts have coevolved with the planthoppers (Insecta: Hemiptera: Fulgoroidea). *BMC Evolutionary Biology*, 12 (87), 1–19.
<https://doi.org/10.1186/1471-2148-12-87>
- Van Duzee, E.P. (1916) *Check list of Hemiptera (excepting the Aphididae, Aleurodidae and Coccidae) of America North of Mexico*. New York Entomological Society, New York, New York, 111 pp.
<https://doi.org/10.5962/bhl.title.7967>
- Van Duzee, E.P. (1917) Catalogue of the Hemiptera of America North of Mexico excepting the Aphididae, Coccidae and Aleurodidae. *Technical Bulletin. University of California, College of Agriculture, Agricultural Experiment Station. Entomology*, 2, 1–902.
<https://doi.org/10.5962/bhl.title.29381>
- Walker, F. (1851) *List of the specimens of Homopterous insects in the collection of the British Museum. Part II*. Edward Newman, London, 376 pp. [pp. 261–636]
- Walker, F. (1858) *Supplement. List of the specimens of Homopterous insects in the collection of the British Museum*. Edward Newman, London, 307 pp.
- West, M., Molfini, M. & Hoddle, M.S. (2025) Proactive assessment of a native North American egg parasitoid, *Anastatus redivivus* (Hymenoptera: Eupelmidae), as a potential biological control agent of *Lycorma delicatula* (Hemiptera: Fulgoridae), in California. *Biological Control*, 200 (article 105687), 1–11. [2024]
<https://doi.org/10.1016/j.biocontrol.2024.105687>
- White, A. (1845) Descriptions of a new genus and some new species of Homopterous Insects from the East in the collection of the British Museum. *Annals and Magazine of Natural History*, 15, 34–37.
<https://doi.org/10.1080/037454809495244>
- Wilson, S.W. & McPherson, J.E. (1980a) Keys to the planthoppers, or Fulgoroidea of Illinois (Homoptera). *Transactions of the Illinois State Academy of Science*, 73 (2), 1–61.
- Wilson, S.W. & McPherson, J.E. (1980b) A list of the Fulgoroidea (Homoptera) of southern Illinois. *Great Lakes Entomologist*, 13 (1), 25–30.
<https://doi.org/10.22543/0090-0222.2564>
- Wilson, S.W. & McPherson, J.E. (1980c) The distribution of the Fulgoroidea of the Eastern United States (Homoptera). *Transactions of the Illinois State Academy of Science*, 73 (4), 7–20.
- Wu, Y., Broadley, H.J., Vieira, K.A., McCormack, J.J., Losch, C.A., Namgung, H., Kim, Y., Kim, H., McGraw, A.R., Palmeri, M.Z., Lee, S., Cao, L. & Wang, X. & Gould, J.R. (2023) Cryptic genetic diversity and associated ecological differences of *Anastatus orientalis*, an egg parasitoid of the spotted lanternfly. *Frontiers in Insect Science*, 3 (article 1154651), 1–11.
<https://doi.org/10.3389/finsc.2023.1154651>

- Yanega, D., Goemans, G., Van Dam, M.W., Gómez-Marco, F.C. & Hoddle, M. (2024) Description of a new genus of North and Central American planthoppers (Hemiptera: Fulgoridae) with fourteen new species. *Zootaxa*, 5443 (1), 1–53.
<https://doi.org/10.11646/zootaxa.5443.1.1>
- Yang, Z.Q., Choi, M.Y., Cao, L.M., Wang, X.Y. & Hou, Z.R. (2015) A new species of *Anastatus* (Hymenoptera: Eulpeimidae) from China, parasitizing eggs of *Lycorma delicatula* (Homoptera: Fulgoridae). *Zoological Systematics*, 40 (3), 290–302.
<https://doi.org/10.11865/zs.20150305>