A journal of world insect systematics

INSECTA MUNDI

1220

Review of the North American species of *Rhopobota* Lederer (Lepidoptera: Tortricidae: Olethreutinae: Eucosmini), with the description of a new species and a new subspecies mining leaves of hollies (Aquifoliaceae: *Ilex* Tourn. ex L.)

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Date of issue: October 30, 2026

Center for Systematic Entomology, Inc., Gainesville, FL

Eiseman CS, Feldman TS, Moparthi S, Bertone MA. 2026. Review of the North American species of *Rhopobota* Lederer (Lepidoptera: Tortricidae: Olethreutinae: Eucosmini), with the description of a new species and a new subspecies mining leaves of hollies (Aquifoliaceae: *Ilex* Tourn. ex L.). Insecta Mundi 1220: 1–37.

Published on October 30, 2026 by
Center for Systematic Entomology, Inc.
P.O. Box 141874
Gainesville, FL 32614-1874 USA
https://centerforsystematicentomology.org/

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October 30, 2026 **INSECTA MUNDI** 1220: 1–37

Review of the North American species of *Rhopobota* Lederer (Lepidoptera: Tortricidae: Olethreutinae: Eucosmini), with the description of a new species and a new subspecies mining leaves of hollies (Aquifoliaceae: *Ilex* Tourn. ex L.)

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Abstract. The North American species of *Rhopobota* Lederer (Lepidoptera: Tortricidae: Olethreutinae: Eucosmini) are reviewed. All feed as larvae on hollies (Aquifoliaceae: *Ilex* Tourn. ex L.). The Holarctic species *R. naevana* (Hübner), which feeds on evergreen and deciduous hollies as well as ericaceous and other plants, overwinters as eggs and apparently never feeds as a leafminer. *Rhopobota dietziana* (Kearfott) s. str. is an external leaf feeder on various deciduous and evergreen hollies, overwintering as pupae, while *R. dietziana glabricola* Eiseman, **new subspecies**, was reared from larvae found mining leaves of inkberry (*I. glabra* (L.) A. Gray) in late March. *Rhopobota finitimana* (Heinrich) feeds initially as a leafminer, and later as a leaftier, on deciduous and evergreen hollies; it mostly overwinters as pupae, but on North Carolina's coastal plain it overwinters as leaf-tying larvae on yaupon (*I. vomitoria* Aiton). *Rhopobota opacae* Eiseman, **new species**, has a larval biology similar to that of *R. finitimana* but is a specialist on American holly (*I. opaca* Aiton) and overwinters as leaf-mining larvae. This species previously has been confused with *R. finitimana* but differs substantially in its DNA barcode and female genitalia; the male differs more subtly in its genitalia, but can be distinguished externally by the location of the androconial scales. DNA barcodes of the other species are also discussed.

Key words. DNA barcoding, rearing, leafminer, holly, cryptic species.

ZooBank registration. urn:lsid:zoobank.org:pub:E5394FB7-7B62-431B-AE8B-C80AA7627AE2

DOI. https://doi.org/10.64338/im.1220.tcuit

Introduction

The genus *Rhopobota* Lederer (Lepidoptera: Tortricidae: Olethreutinae: Eucosmini) is characterized by the presence in the male genitalia of paired, widely separated projections of the tegumen (generally referred to as a bifurcate uncus, but not necessarily homologous with the uncus of other Tortricidae), and in the female genitalia a posterior sclerotized band extending along both sides of the corpus bursae (Brown 1979, 1983; Zhang 2017). It includes 85 described species distributed in the Holarctic, Oriental, Australian, and Neotropical regions (Zhang 2017; Clayton 2017; Gilligan et al. 2018; Nasu 2021). Just three of these are known from North America, all with

a similar forewing pattern including more or less well-defined basal and subbasal fasciae (usually coalescing into a basal patch), a weakly expressed "median" fascia (actually postmedial in position), and a dark spot at the apex (Gilligan et al. 2008). In all three species the forewing has a pointed apex and a deeply concave termen (Brown 1983).

Rhopobota naevana (Hübner), the "blackheaded fireworm," is thought to be native to eastern North America, Europe, and Asia. It also occurs in northwestern North America, apparently having been introduced when cranberry plants were imported to Washington from Massachusetts in the early 1890s (Smith 1893). It is a polyphagous species with hosts in Aquifoliaceae, Ericaceae, Oleaceae, Rhamnaceae, and Rosaceae, feeding on buds and as a leaftier (Bradley et al. 1979; Brown 1983; Johnson and Lyon 1994; Ganai et al. 2018; Pathania et al. 2020). *Rhopobota dietziana* (Kearfott) and *R. finitimana* (Heinrich) both occur only in the eastern USA and adjacent Canada, and the larvae of both are specialists on *Ilex* Tourn. ex L. (Aquifoliaceae). These two species have been reported to mine leaves initially before completing development as leaftiers (Eiseman 2014; Eiseman et al. 2020).

The biology of *R. naevana* is well studied due to its economic importance as a pest of cranberry crops (Labarre et al. 2024), and we have seen no indication that it ever feeds as a leafminer. The other three *Rhopobota* species that occur in Europe—*R. myrtillana* (Humphreys and Westwood), *R. stagnana* (Denis and Schiffermüller), and *R. ustomaculana* (Curtis)—have all been reported to mine leaves in early instars (Hering 1957; Ellis 2025). To our knowledge, the first published reference to leafmining by North American *Rhopobota* is that of Eiseman and Charney (2010: 163), who briefly discussed an unspecified species feeding on winterberry (*Ilex verticillata* (L.) A. Gray) and mountain holly (*I. mucronata* (L.) M. Powell, Savol. and S. Andrews). Eiseman (2014) reported rearing *R. dietziana* from leaf mines on inkberry (*I. glabra* (L.) A. Gray) and winterberry and finding similar mines on American holly (*I. opaca* Aiton) and mountain holly. Eiseman et al. (2020) reported rearing *R. finitimana* from mines on American holly and possumhaw (*I. decidua* Walter) and noted that mines of an unknown species had been found on yaupon (*I. vomitoria* Aiton).

We succeeded in rearing adults resembling *R. finitimana* from yaupon in 2021. In 2023, J. Petranka (in litt.) obtained larvae from American holly and sent them to J.W. Brown for DNA barcoding, and the resulting sequences differed from those of *R. finitimana* by nearly 5%. This prompted a discussion with J.B. Sullivan (in litt.), who noted substantial variation in male genitalia among his and our own "*R. finitimana*" specimens. After obtaining additional specimens reared from various *Ilex* spp., we are convinced that the form feeding on American holly is distinct, and it is described herein as *R. opacae* Eiseman, **new species**. We also describe a new subspecies of *R. dietziana* from the series that Eiseman (2014) reared from inkberry. New rearing records are provided for *R. dietziana* and *R. finitimana*, and we now believe that all *Rhopobota* leaf mines on deciduous hollies are attributable to *R. finitimana*. Based on our recent observations, *R. dietziana* s. str. feeds externally throughout its larval development, and we believe the single specimen that Eiseman (2014) reared from winterberry was a contaminant in a collection of *R. finitimana* mines.

Materials and Methods

Leaves with tortricid larvae were collected in airtight vials, jars, or resealable plastic bags. If deemed necessary, a crumpled piece of toilet paper was added to the container—either a dry one to absorb excess moisture, or moistened with several drops of water to prevent desiccation. These containers were stored away from direct sunlight and checked daily, and as needed, fresh leaves were added and paper was replaced. Overwintering larvae were kept at room temperature; pupae were stored in a refrigerator at 1–3°C from 17 October 2022 to 21 February 2023, 1 November 2023 to 1 March 2024, and 1 November 2025 to 1 March 2026. Adult moths reared by the first author (CSE) were placed in a killing jar with ammonium carbonate and then pinned, spread, and double-mounted. Moths reared by others were killed by freezing, allowed to dry, and later placed in a humid airtight chamber overnight before pinning. Parasitoids were preserved in 95% ethanol.

The following abbreviations are used for depositories of our specimens and other material examined or listed: CBG = Centre for Biodiversity Genomics, University of Guelph, ON, Canada; CNC = Canadian National Collection of Insects, Arachnids & Nematodes, Ottawa, ON, Canada; CSEC = personal collection of C.S. Eiseman, Northfield, MA, USA; CUIC = Cornell University Insect Collection, Ithaca, NY, USA; MEM = Mississippi Entomological Museum, Mississippi State University, MS, USA; MSC = personal collection of M. Sabourin,

Marshfield, VT, USA; USNM = United States National Museum, Washington, DC, USA. This study focused on our own reared material, but because we had no specimens of *R. naevana*, we borrowed those held by CUIC, and while doing so we took the opportunity to borrow the rest of that institution's Nearctic *Rhopobota* holdings. We also borrowed many specimens of *R. dietziana* from MSC to further assess variation in that species. Some specimens are annotated with "BG," "iNat," or "BOLD," followed by a hyperlinked number or code; these refer, respectively, to the BugGuide, iNaturalist, and Barcode of Life Data System (BOLD) websites. The full URL for each of these records can be obtained by adding the number or code to the end of https://bugguide.net/node/view/ (for "BG" records), https://www.inaturalist.org/observations/ (for "iNat" records), or https://portal.boldsystems.org/record/ (for "BOLD" records). Some of these are specimens at CUIC that we physically examined, and for the others only photographs were examined.

Wing measurements were made using a Bausch & Lomb StereoZoom Microscope (0.7×–3×, set to 1×) with an ocular micrometer, except for wingspans greater than 10 mm, which were measured with a handheld ruler with 1 mm increments. All other external examination and dissection of specimens was conducted using a Nikon SMZ18 stereo microscope. To examine genitalia, abdomens were removed and placed in a ~20% KOH solution at room temperature overnight. After initial cleaning with fine-tipped paintbrushes in 30% ethanol, each abdomen was placed in a small dish of 88% lactic acid with a few drops of OG-6 solution for 4.0–8.5 hours for staining and to neutralize the KOH. After final cleaning, the genitalia were placed under a small piece of a broken microscope slide in 99.9% isopropanol for 4–56 hours. The genitalia were then transferred to 100% clove oil, in which they were left for 3.5–28.0 hours. They were then slide-mounted in Canada balsam (thinned with 100% orange oil). This procedure was not followed for the preparation shown in Fig. 73; in this case the genitalia were never placed in lactic acid, were stained in 1% Eosin Y for a few hours, and were then mounted in Euparal immediately after final cleaning. The procedures followed for preparations without "CE-" slide numbers are unknown.

Genitalia slides with "CE-" slide numbers were photographed with a View4K digital camera mounted on an Accu-Scope EXC-350 compound microscope, usually using the InFocus software's "Extended Depth of Focus" feature. The photograph in Fig. 88 was taken by TSF using a Sharper Image Portable Digital LCD Microscope. Other uncredited photographs were taken by CSE, using either a Nikon D50 digital camera with a Nikon AF Micro Nikkor 105mm lens (Fig. 45, 48–58, 86, 91, 92, 94) or a Canon EOS Rebel XSi SLR digital camera with MP-E 65 mm macro lens and Macro Twin Lite MT-24EX flash unit (all others).

Molecular methods and analyses followed the methodology detailed in Eiseman et al. (2024). Legs were used for each extraction, or if this failed, a second attempt was made using the thorax. Existing COI sequences from other *Rhopobota* specimens were provided by A.E. Timm and J.-F. Landry or were accessed and downloaded from BOLD: The Barcode of Life Data System (Ratnasingham and Hebert 2007; https://www.boldsystems.org). New sequences are deposited in GenBank under accession numbers PZ687437–PZ687442. Numbers preceded by "BIN BOLD:" are DNA Barcode Index Numbers registered in BOLD (Ratnasingham and Hebert 2013).

In the lists of material examined, each number with the prefix "#CSE" refers to one or more specimens resulting from the same collection event and emerging on the same day. The first date listed for each collection event indicates when the larva (or pupa, in one instance) was collected. An "em." preceding a date indicates the date of adult emergence. The prefix "ex" before a plant name indicates that the specimens were reared from this plant.

Terminology follows Gilligan et al. (2008). Plant taxonomy follows POWO (2026). The synonymies listed under each species heading are not intended to be complete, and include only the references consulted for this study.

Results

Adults of the North American *Rhopobota* species differ markedly in the color of the head (labial palpi, upper frons, vertex, and antennal scapes). In general, *R. finitimana* and *R. opacae* have entirely brown heads, including the inner surfaces of the labial palpi. The remaining species have at least the inner surfaces of the labial palpi white; other structures are variable in color, especially in *R. naevana*, but in *R. dietziana* s. str. the upper frons and lower vertex are normally bright white. The short, closely appressed, upwardly directed scales of the lower frons

are sometimes difficult to observe, but they appear to be consistently white/pale in all species. Therefore, in badly rubbed specimens that are missing the long, anteriorly directed scales of the upper frons and vertex, it should not be assumed that the remaining scales are indicative of the overall head color.

The forewings of all four species have the same basic pattern (Fig. 1–4, 11–16, 20–27, 59–64). The ground color varies from white to gray or brown. There is a dark basal patch with a typically angulated or rounded outer margin, whose maximum extent varies from $^{3}/_{10}$ to ½ the distance from the base of the wing to the apex (including the fringe). The patch is solid in *R. finitimana* and *R. opacae*, but in *R. dietziana* and sometimes *R. naevana* it is interrupted by ground color, resulting in more or less distinct subbasal and sometimes basal fasciae. Following the median interfascial area is a median fascia, which is always in actuality in a postmedial position. It is often well-developed in *R. naevana* but in the other species tends to be reduced to scattered dark mottling, with a small medial black spot or patch typically being most prominent. A narrow postmedian fascia may be distinct or weakly expressed. The gray interfascial areas surrounding the postmedian fascia are typically mottled with white-tipped scales, but rarely so in *R. naevana*. Along the costa are white, brown, and black strigulae, which may be weakly expressed in the basal patch when the latter is distinct. The black apical spot is usually within a larger brown spot.

In the genitalia, males differ in features of the valvae, as noted in the key below, and females differ in the form of the sterigma and in the pattern of posterior sclerotization of the corpus bursae. Females of all North American species possess a pair of hornlike or thornlike signa; we have observed substantial intraspecific variation in their shape and microsculpture, and have concluded that they are not useful in distinguishing among the species.

Key to North American *Rhopobota*

1. Forewing (Fig. 1–4) often with reduced pale interfascial area, the basal patch extending to 40–51% of the total wing length; male hindwing with large patch of dark androconial scales on lower surface (Fig. 5, 6); valva lacking long spines on the cucullus, with fingerlike clasper on proximal margin of medial surface and a line of stout setae along the ventral margin of the neck (Fig. 7); female sterigma funnel-shaped, appearing as a simple posteriorly concave opening in ventral view (Fig. 9, 10); posterior sclerotization of corpus bursae consisting of two narrow lateral patches that project posteriorly well beyond the narrow arch that joins them (Fig. 8); polyphagous and transcontinental ..... ***Rhopobota naevana* (Hübner)**

— Forewing with extensive pale interfascial area, the basal patch extending to 29–41% of the total wing length; male hindwing without a patch of dark androconial scales on lower surface; valva with long spines on cucullus, with neither a fingerlike clasper nor stout setae on the ventral margin of the neck; female sterigma appearing flask-shaped or posteriorly domed in ventral view; posterior sclerotization of corpus bursae with lateral patches projecting posteriorly only slightly beyond their junction, if at all; *Ilex* specialists, east of the Rocky Mountains **2**

2. Head and basal patch of forewing dark (Fig. 13–16, 59–64); male valva with 1–3 spines on cucullus that greatly exceed the adjacent dense setae, and lacking dense setae on sacculus (Fig. 67–76); female sterigma in ventral view appearing either flask-shaped, with the neck longer than the length and width of the bulb (Fig. 80–82), or posteriorly domed (Fig. 83, 84); posterior sclerotization of corpus bursae with lateral patches joined by a narrow ventral portion (Fig. 77–79) (*R. finitimana* complex) **3**

— Head and basal patch of forewing partly pale (often not markedly so in the southeastern *R. dietziana glabricola*) (Fig. 11, 12, 20–27); male valva with multiple spines on base of cucullus that do not exceed the longest setae, and with dense setae on the sacculus (Fig. 28–31); female sterigma appearing flask-shaped in ventral view, with the neck shorter than the width of the bulb (Fig. 33–35, 38–40); posterior sclerotization of corpus bursae broadly contiguous dorsally, with a ventral gap that widens anteriorly (Fig. 32, 36, 37, 41) (*R. dietziana*) **4**

3. Male with hair pencil on medial surface of hind tibia (Fig. 66); valva with long marginal setae that largely cover the neck and cucullus, and with 2–3 spines on the cucullus that are much longer than the setae (Fig. 74–76); female sterigma appearing posteriorly domed in ventral view (Fig. 83, 84); larva on *Ilex opaca* ..... ***Rhopobota opacae* Eiseman, new species**

— Male with hair pencil at base of anal margin of hindwing (Fig. 65); valva with shorter marginal setae that do not overlap large areas of the neck and cucullus, and with 1–2 spines on the cucullus that are much longer than the setae (Fig. 67–73); female sterigma appearing flask-shaped in ventral view, the neck open at the posterior end (Fig. 80–82); larva on various *Ilex* spp. (not known from *I. opaca*) . . . . . ***Rhopobota finitimana* (Heinrich)**

4. Scape brown, vertex partly brown (Fig. 19); pale areas on forewing gray (Fig. 12, 24–27); forewing length up to 5.6 mm; larva on *Ilex glabra*, initially a leafminer; southeastern USA . . . . . ***Rhopobota dietziana glabricola* Eiseman, new subspecies**

— Scape and vertex bright white (Fig. 17); pale areas on forewing white (Fig. 11, 20–23); forewing length up to 8.1 mm; larva on various *Ilex* spp., always feeding externally; widespread . . . . . ***Rhopobota dietziana dietziana* (Kearfott)**

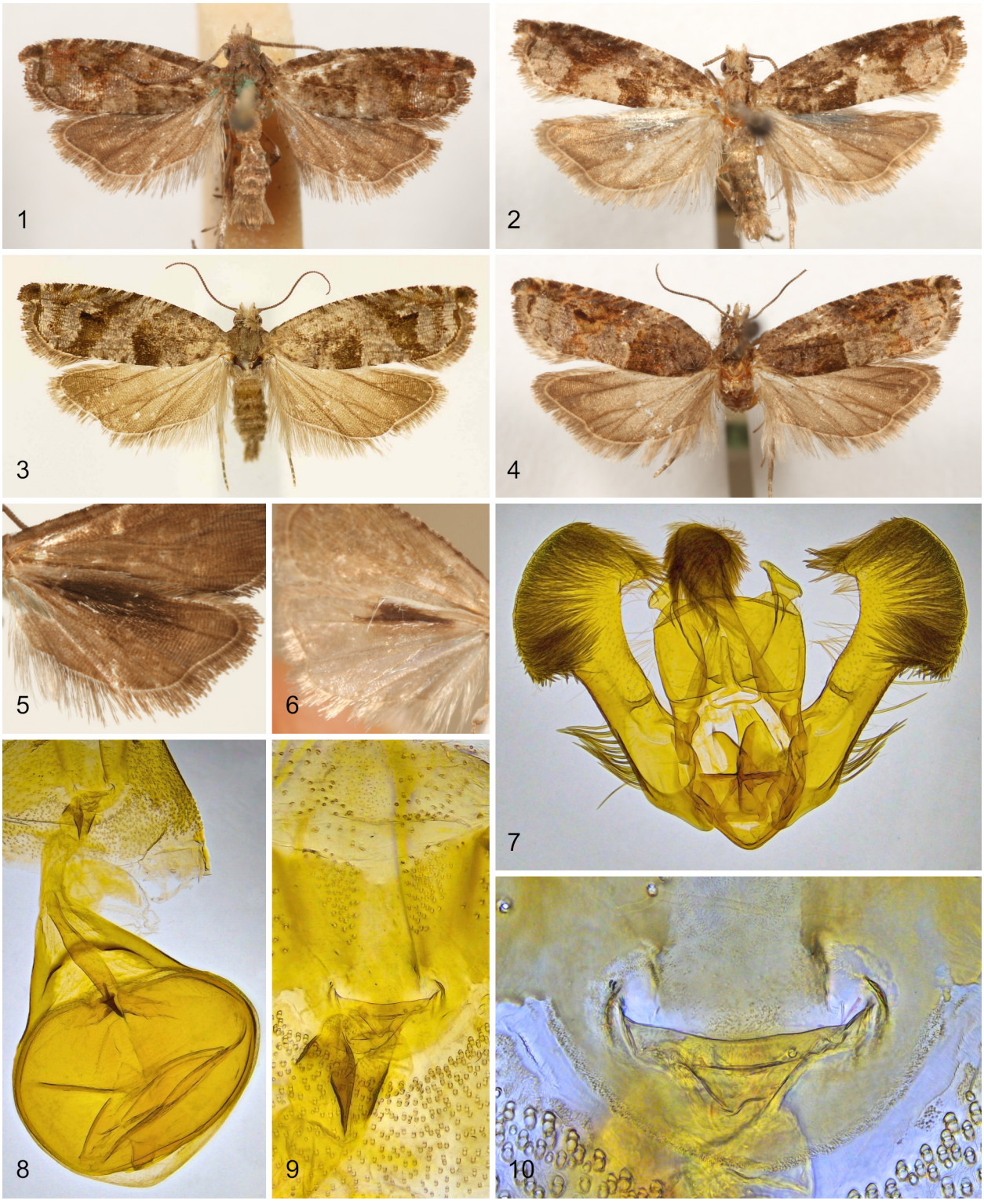
Rhopobota naevana (Hübner)

(Fig. 1–10)

Anchylopera vacciniana Packard. Packard 1869: 338–340.
Epinotia ilicifoliana Kearfott. Kearfott 1907a: 158–159, 1907b: 52, 53.
Rhopobota naevana. Disque 1908: 54; Heinrich 1923: 193–194, Fig. 6, 37, 416; Forbes 1923: 411; Jones and Kimball 1943: 157; Ferguson 1975: 34; Bradley et al. 1979: 137–138; Brower 1983: 37; Brown 1983: 98, 99, 103; Johnson and Lyon 1994: 206–208; Landry et al. 2002: 37–39; Robinson et al. 2002: 386–387; Spitzer et al. 2003: 49, 51; Gilligan et al. 2008: 150, 233, 282; Ganai et al. 2018: 77–81; Pohl et al. 2018: 154; Shaw et al. 2018: 11; Gilligan et al. 2020: 39, 50; Pathania et al. 2020: 55; Labarre et al. 2024: 351–356.
Rhopobota geminana (Stephens). Disque 1908: 73, 139.
Rhopobota ilicifoliana. Heinrich 1923: 191.
Rhopobota naevana ilicifoliana. Heinrich 1923: 194; MacKay 1959: 125, 126, 128.
Rhopobota ilicifolana [misspelling]. Forbes 1923: 412.
Rhopobota vacciniana. MacKay 1959: 125–127; Brower 1983: 37.
Rhopobota naevana geminana. MacKay 1959: 127–128.
Rhopobota sp. (*R. ilicifoliana* (Kft.) or *R. naevana* (Hbn.)?). Ferguson 1975: 34–35.
Rhopobota unipunctana (Haworth). Brown 1979: 21–25; Robinson et al. 2002: 387.
Rhopobota unipunctana geminana. Robinson et al. 2002: 387.

Diagnosis. The forewing pattern is variable but typically has a narrower pale interfascial area than in the other species (Fig. 1–4). The basal patch extends to 40.0–50.9% of the total wing length in *R. naevana*, whereas in other species it is usually substantially shorter (up to 40.7% observed in *R. dietziana*). Males differ from those of all other Nearctic *Rhopobota* species in possessing a large patch of blackish androconial scales on the underside of the hindwing (Fig. 5, 6). The male valvae are unique in lacking long spines on the cucullus, and in possessing a fingerlike clasper on the proximal margin of the medial surface and a line of stout setae along the ventral margin of the neck (Fig. 7). The female genitalia are unique in having a simple funnel-shaped sterigma (Fig. 9, 10). The posterior sclerotization of the corpus bursae is broken into two distinct, narrow lateral patches that are joined by a distinct, narrow arch (Fig. 8); the pattern of sclerotization is somewhat similar in species of the *R. finitimana* complex, but the lateral patches do not extend as far posteriorly beyond the band of sclerotization that joins them, which is broader than in *R. naevana* (Fig. 77–79).

Specimens examined. Canada. ALBERTA: Kootenay Plains Ecol. Res., Siffleur Falls St. Area, 52.051, −116.412, 7.viii.2007, J.J. Dombroskie & A. Rose, UV trap, JD4182 (1♂, genitalia in microvial pinned with specimen, CUIC 0000069314); Kootenay Plains, near Whirlpool Point, 51.999, −116.496, 6.viii.2007, J.J. Dombroskie & A. Rose, at MV light, JD3612 (1♂, genitalia in microvial pinned with specimen, CUIC 000153535); Swan Hills, 54.746, −115.396, 16.viii.2009, J.J. Dombroskie & A. Rose, 1273m, JD6791 (1♂, CUIC 000069311); **BRITISH COLUMBIA:** Vancouver Island, Vernon Lake, 50.057, −126.447, 2.ix.2013, J.J. Dombroskie, MV light, JD11933 (1♂, genitalia in microvial pinned with specimen, CUIC 000069319); **ONTARIO:** Prince Edward Co., Skyline Ridge, 44.148, −77.085, 3.viii.2014, J.J. Dombroskie et al., UV trap, JD16517 (1♂, CUIC 000069308). **USA. MAINE:** Washington Co., Eagle Hill, Orchid Tr, 44.458, −67.930, 24.vii.2018, J.J. Dombroskie et al., UV trap, JD38350 (1♂,



Figures 1–10. *Rhopobota naevana*. **1)** New Jersey ♂ (CUIC 000153519). **2)** Washington ♂ (CUIC 000069316). **3)** Quebec ♀ (CNCLEP00027603; © Jean-François Landry, CreativeCommons – Attribution Non-Commercial Share-Alike). **4)** Washington ♀ (CUIC 000069318). **5)** Underside of hindwing, New Jersey ♂ (CUIC 000153519). **6)** Same, Maine ♂ (CUIC 000069297). **7)** Genitalia, New York ♂ (CUIC 000153427, slide CE-2026-48). **8)** Vermont ♀ (MSC, slide CE-2026-50), corpus bursae. **9)** Same, sterigma at 100×. **10)** Same, sterigma at 400×.

CUIC 000069297); **NEW JERSEY:** "N.J.", 20.viii.1891, "Murtfeldt Coll., Cornell Univ., Lot 451, Sub. 954" (1♂, CUIC 000153565); same but 24.viii.1891 (1♂, CUIC 000153519); same but no location, 24.viii.1890, "Cranberry Tortrix" (1♀, CUIC 000069306) [the preceding three dates are written in the format, "8/24.90", and given that they appear to be from the same rearing lot, they are perhaps all from 1890, but the first two appear to say "91"]; same but no location/date label, instead "*Rhopobota vacciniana* Pack." (1♀, CUIC 000069302); no location/date label, "Murtfeldt Coll., Cornell Univ., Lot 451, Sub. 1025" (1♀, CUIC 000069317); **NEW YORK:** Chautauqua Co., Kabob WMA, 42.279, −79.324, 22.vii.2017, J.J. Dombroskie, G. Erdosh & J. Gorneau, UV trap, JD33574 (1♂, genitalia slide CE-2026-48, CUIC 000153427); same but JD33613 (1♂, CUIC 000153205); **OREGON:** Lane Co., Blue R., 44.141, −122.324, 15.v.2018, em. 8.vi.2018, M. Palmer, ex *Vaccinium parviflorum*, 4126.1 (1♂, CUIC 000153704; 1♀, CUIC 000153107); **VERMONT:** Chittenden Co., Colchester, railway by bog, 5.viii.1992, M. Sabourin (2♀, genitalia slide CE-2026-50, MSC); **WASHINGTON:** Whatcom Co., Bellingham, 3.vii.1928, J.F. Clarke (1♂, CUIC 000069316; 1♀, CUIC 000069318).

Adult description. Forewing length 4.6–7.0 mm; wingspan 10.5–15.0 mm (10 mm reported by Heinrich (1923)).

Head: Labial palpus brown with purple reflections; 2nd segment with inner and dorsal surface whitish to white, outer surface sometimes mottled dark brown or black; 3rd segment sometimes white. Upper frons brown, sometimes mixed with whitish, or entirely whitish to white. Vertex brown with purple reflections, sometimes partially whitish to white. Scape brown, sometimes partially whitish, or white mottled with black, or entirely gray. Pedicel and flagellomeres brown to black, sometimes paler proximally.

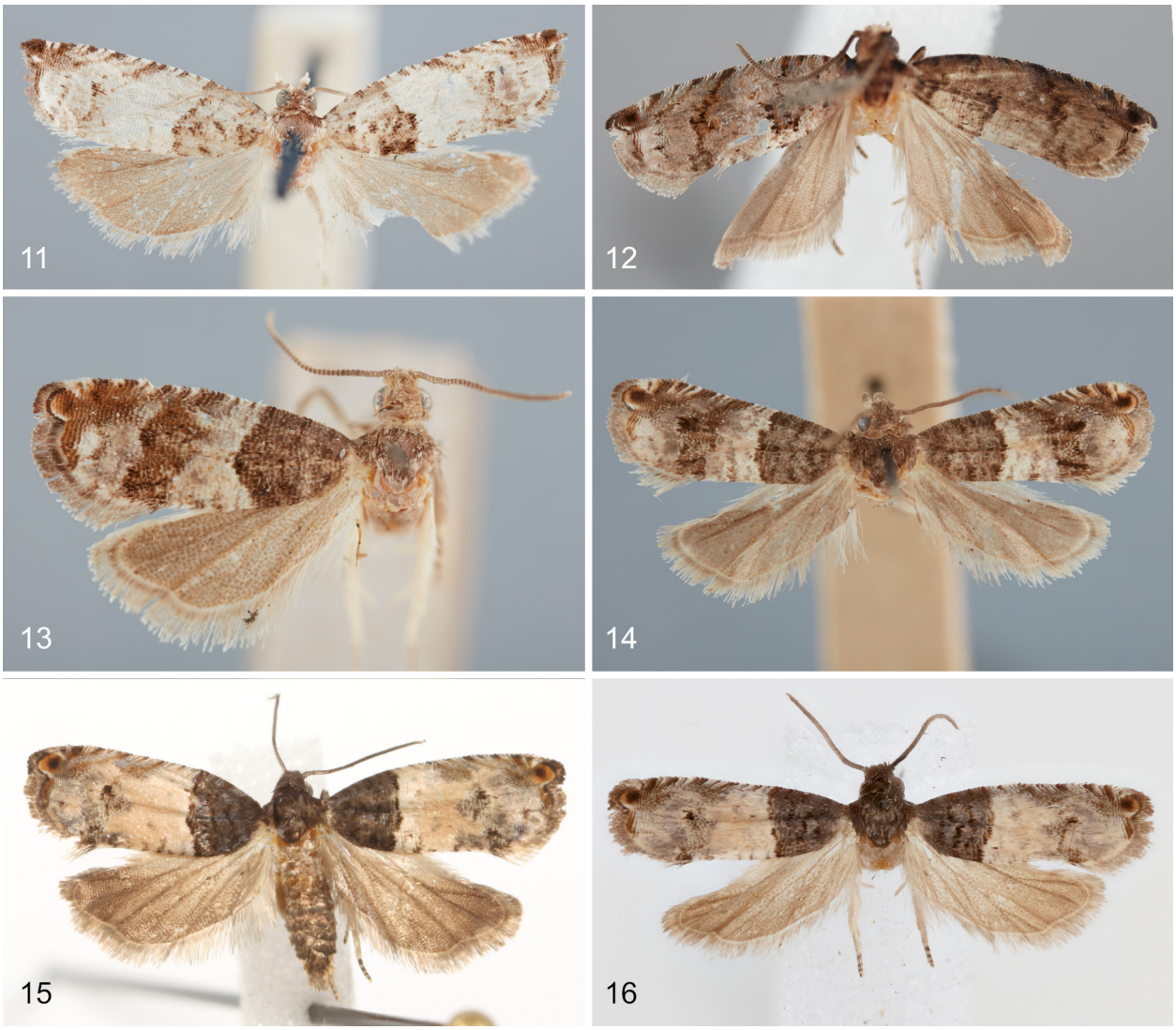
Thorax: Dorsally brown with some purple reflections; sometimes partly (banded) white or silver. Forewing (Fig. 1–6) with white, brown, and black costal strigulae (these minute/obscure in the basal patch when the latter is well-defined); basal patch well-defined or patchy (e.g., with a distinct partial subbasal fascia), usually distinctly angulated, asymmetrical, variously mottled with brown, light brown, dark brown, gray, and blackish, the different colors partly forming striae; interfascial area light brown mottled with gray and sometimes brown or dark brown, or mostly gray with blackish intrusion from median fascia, relatively narrow due to longer basal patch; median fascia relatively broad, more or less well-defined, brown with variable dark brown to blackish mottling (or light brown with brown mottling and a black ~medial spot; rarely some white-tipped scales); next interfascial area with similar coloring to previous, but more heavily gray than light brown, or entirely gray; postmedian fascia more or less distinct, brown, sometimes very pale, sometimes with blackish mottling, and sometimes with white-tipped scales; gray patch beyond the postmedian fascia usually without white-tipped scales; a narrow brown to blackish patch along middle of termen; black apical spot within a larger brown spot (sometimes ~entirely black, or brown with an indistinct black smudge); fringe gray, generally darkening from tornus to apex (black adjacent to apical spot), sometimes with distinct dark line near base, sometimes with light brown mottling. A cream color is sometimes present in the interfascial areas and fringe mottling, and sometimes there is a broad brown swath from the middle of the median fascia to the apex. Hindwing light brown to dark gray-brown, sometimes dark gray at apex; fringe gray to light brown or brown with more or less distinct darker band at base. Underside of forewing and hindwing uniformly brown to pale gray in female; male with elongate black patch along middle of costa of hindwing (Fig. 5, 6). Legs white to light brown with brown and black banding/mottling.

Abdomen: Dorsally mottled with blackish, dark brown, brown, and silver mottling; ventrally light brown and brown, sometimes mottled with black. Male genitalia with valva bearing a fingerlike clasper on the proximal margin of the medial surface and a line of stout setae along the ventral margin of the neck; cucullus without spines (Fig. 7). Female genitalia with funnel-shaped sterigma (Fig. 9, 10); posterior sclerotization of corpus bursae broken into two distinct, narrow lateral patches joined by a distinct, narrow arch (Fig. 8).

Hosts. English holly (Aquifoliaceae: *Ilex aquifolium* L.) is a common host in the Pacific Northwest and in Europe (MacKay 1959; Bradley et al. 1979; Johnson and Lyon 1994). In eastern North America, *R. naevana* has been reared from winterberry (*I. verticillata*) (Kearfott 1907a; Heinrich 1923; Ferguson 1975) and mountain holly (*I. mucronata*) (Ferguson 1975). In Asia, it is also reported from Japanese holly (*I. crenata* Thunb.) and mochi tree (*I. integra* Thunb.) (Pathania et al. 2020). Non-holly hosts reported worldwide include Ericaceae: *Arctostaphylos* Adans., *Calluna* Salisb., *Erica* Tourn. ex L., *Gaultheria* Kalm ex L., *Vaccinium* L. (Disque 1908; Ferguson 1975; Brown 1983); Oleaceae: *Fraxinus* Tourn. ex L., *Ligustrum* L., *Syringa* L. (Shaw et al. 2018, Pathania et al. 2020); Rhamnaceae: *Rhamnus* L.; and Rosaceae: *Crataegus* L., *Malus* Mill., *Prunus* L., *Pyrus* L., *Sorbus* L. (Brown 1983;

Pathania et al. 2020). The Oregon specimens labeled "*Vaccinium parviflorum*" were in fact reared from *V. parvifolium* Sm., which appears to be a new host record; previous *Vaccinium* hosts include *V. macrocarpon* Aiton (Packard 1869; Labarre et al. 2024), *V. myrtillus* L. (Bradley et al. 1979), *V. uliginosum* L. (Spitzer et al. 2003), *V. vitis-idaea* L. (Pathania et al. 2020), and "blueberry" (MacKay 1959).

Biology. Eggs are laid singly on the undersides of leaves or on bark of the current season's growth (Johnson and Lyon 1994; Ganai et al. 2018). Larvae hatching from overwintered eggs initially feed on opening buds (or on old leaves of cranberry), later within shelters of folded, crumpled, rolled, or tied leaves. They have also been reported to feed on flowers and fruits of cranberry (Landry et al. 2002). When finished feeding, they may pupate among the tied leaves or drop to pupate among the leaf litter and duff; frequently the cocoon is spun under a small flap that is cut out of a leaf and folded (Packard 1869; Kearfott 1907a; Johnson and Lyon 1994). In the Himalayas, Ganai et al. (2018) reported a larval period of 19–22 days and a pupal period of 7–10 days. The pupal stage lasts



Figures 11–16. *Rhopobota* type specimens. **11)** *R. dietziana* paratype ♂, Pennsylvania (USNM). **12)** *R. dietziana glabricola* holotype ♂, ex *Ilex glabra*, Florida (CSE509, USNM). **13)** *R. finitimana* holotype ♂, New Hampshire (USNM). **14)** *R. finitimana* paratype ♂, ex *I. verticillata*, Virginia (USNM). **15)** *R. opacae* holotype ♀, ex *I. opaca*, North Carolina (CSE9498, CUIC). **16)** *R. opacae* paratype ♂, ex *I. opaca*, North Carolina (CSE5261, CUIC). Photos in Fig. 11–14 by John W. Brown; Fig. 16 by Loren Jones.

about 10–13 days in Massachusetts according to Packard (1869); Kearfott (1907a) reported 14–24 days in North Carolina.

Without reference to a specific region, Johnson and Lyon (1994) stated that there are one or two generations per year, with larvae of the second generation (when present) appearing by late July. Records from primary literature suggest this species is at least bivoltine throughout its range in North America, with a third generation possible under favorable climatic conditions (Labarre et al. 2024); three generations per year have also been documented in the Himalayas (Ganai et al. 2018). Kearfott (1907a) reported that larvae are active on winterberry in May in North Carolina and New Jersey, pupating by the end of the month and emerging as adults in mid-June. Packard (1869) stated that larvae from eggs overwintering on cranberry in Massachusetts emerged as adults in late June or early July, giving rise to a second generation of larvae that pupated in mid- to late July—although three paragraphs earlier, he stated that larvae of the first generation become fully grown in July. In any case, according to Packard (1869), a few eggs laid in August may hatch in September, but most overwinter. In Nova Scotia, larvae have similarly been collected in May, with adults emerging from late June to late July, and larvae collected in July have emerged as adults from early to mid-August (Ferguson 1975).

Distribution. Alaska to Newfoundland and Labrador (Pohl et al. 2018), south to Oregon in the western USA, and south to Mississippi and South Carolina in the east; also Europe and Asia (Gilligan et al. 2008, 2020; MPG 2025).

DNA barcoding. The over 800 *R. naevana* sequences from Canada, the USA, Europe, and Asia are all assigned to BIN BOLD:AAA9812, and there is no evidence of any cryptic taxa (Gilligan et al. 2020). The nearest neighbor, differing by 3.41%, is BOLD:ABA0121, represented by a single undetermined *Rhopobota* specimen from Australia (BOLD ANICW716-11) (Fig. 105).

Notes. Gilligan et al. (2008) state that the solid basal patch on the forewing distinguishes *R. naevana* and *R. finitimana* from *R. dietziana*. However, we have seen a specimen of *R. naevana* dissected by J. Vargo (in litt.) with pale scaling in the basal patch that is as extensive as in typical specimens of *R. dietziana*. In the UK, according to Bradley et al. (1979), "In lightly suffused specimens the ground colour is shining white, sometimes tinged with pinkish ochreous, the markings contrasting strongly. Almost unicolorous red-brown and melanistic black-brown specimens are not uncommon."

Rhopobota dietziana dietziana (Kearfott)

(Fig. 11, 17, 18, 20–23, 28, 29, 32–36, 42–47, 99)

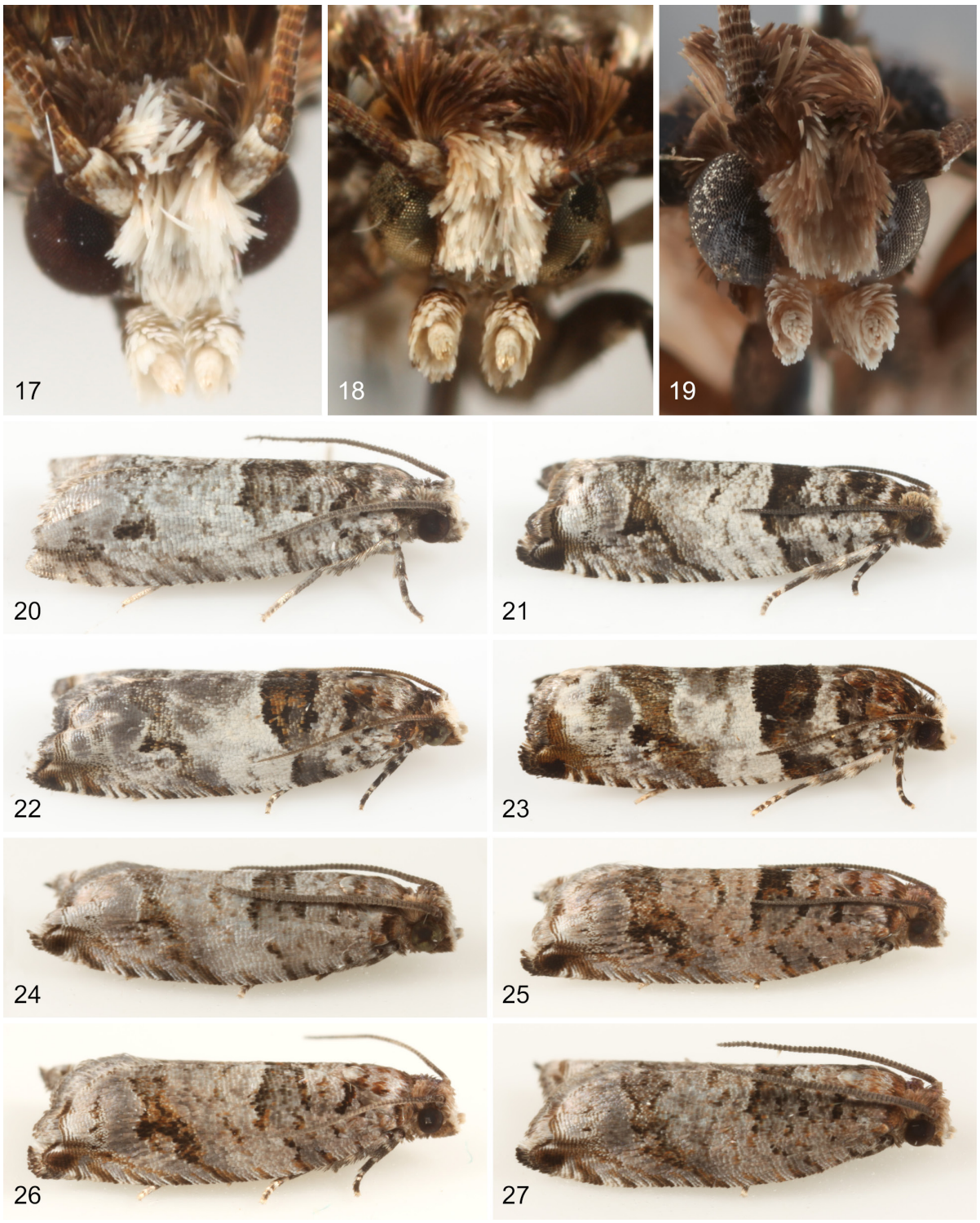
Epinotia dietziana. Kearfott 1907b: 92–93.

Norma dietziana. Heinrich 1923: 191, fig. 33, 414; Forbes 1923: 411; Jones and Kimball 1943: 157; MacKay 1959: 125, 128–129; Ferguson 1975: 34; Brower 1983: 36.

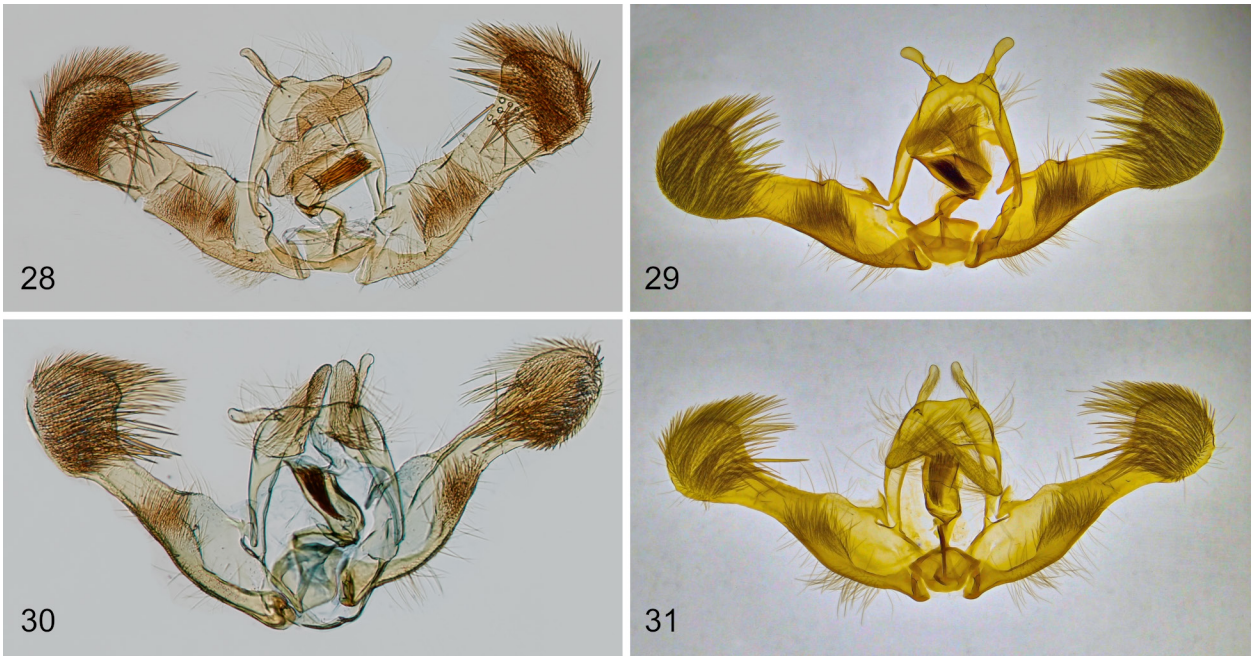
Rhopobota dietziana. Brown 1979: 21–25; 1983: 98–100; Robinson et al. 2002: 386; Gilligan et al. 2008: 150, 233, 282; Eiseman 2014: 218–219 [excluding specimens reared from *Ilex glabra*]; Pohl et al. 2018: 154.

Diagnosis. Externally, *Rhopobota dietziana* s. str. is distinctive in having the upper frons, scape, and third segment of the labial palpus bright white (Fig. 17). The basal patch is interrupted by extensive white scaling, resulting in a usually well-defined subbasal fascia and sometimes a partial subbasal fascia (Fig. 11, 20–23), in contrast with the *R. finitimana* complex and some *R. naevana*. The basal patch extends to 31.7–40.7% of the total wing length in *R. dietziana*, compared with 40.0–50.9% in *R. naevana*, and the male lacks the patch of blackish androconial scales that is present on the underside of the hindwing in *R. naevana*. The southeastern subspecies *R. dietziana glabricola* is small and dark; see its diagnosis below for details. In the male genitalia of *R. dietziana*, the sacculus is densely clothed in long setae, and multiple long spines arise from the base of the cucullus and distal portion of the neck, similar in length to the dense setae on the cucullus (Fig. 28–31). In the female (Fig. 32–41), the sterigma appears flask- or pear-shaped in ventral view, with the narrower posterior portion being shorter than the width of the wider anterior portion. On the corpus bursae, the posterior sclerotization is continuous dorsally, with an anteriorly widening gap on the ventral surface.

Specimens examined. CANADA. ONTARIO: Niagra R. M., Marcy's Woods, 42.859, –79.112, 7.vi.2014, J.J. Dombroskie, B.C. Schmidt, MV light, JD14650 (1♂, CUIC 000069304); Renfrew Co., Pembroke, Pansy Patch Pk, 45.820, –77.112, 7.vii.2018, J.J. Dombroskie et al., JD37930 (1♂, CUIC 000152997). **USA. LOUISIANA:** Caddo

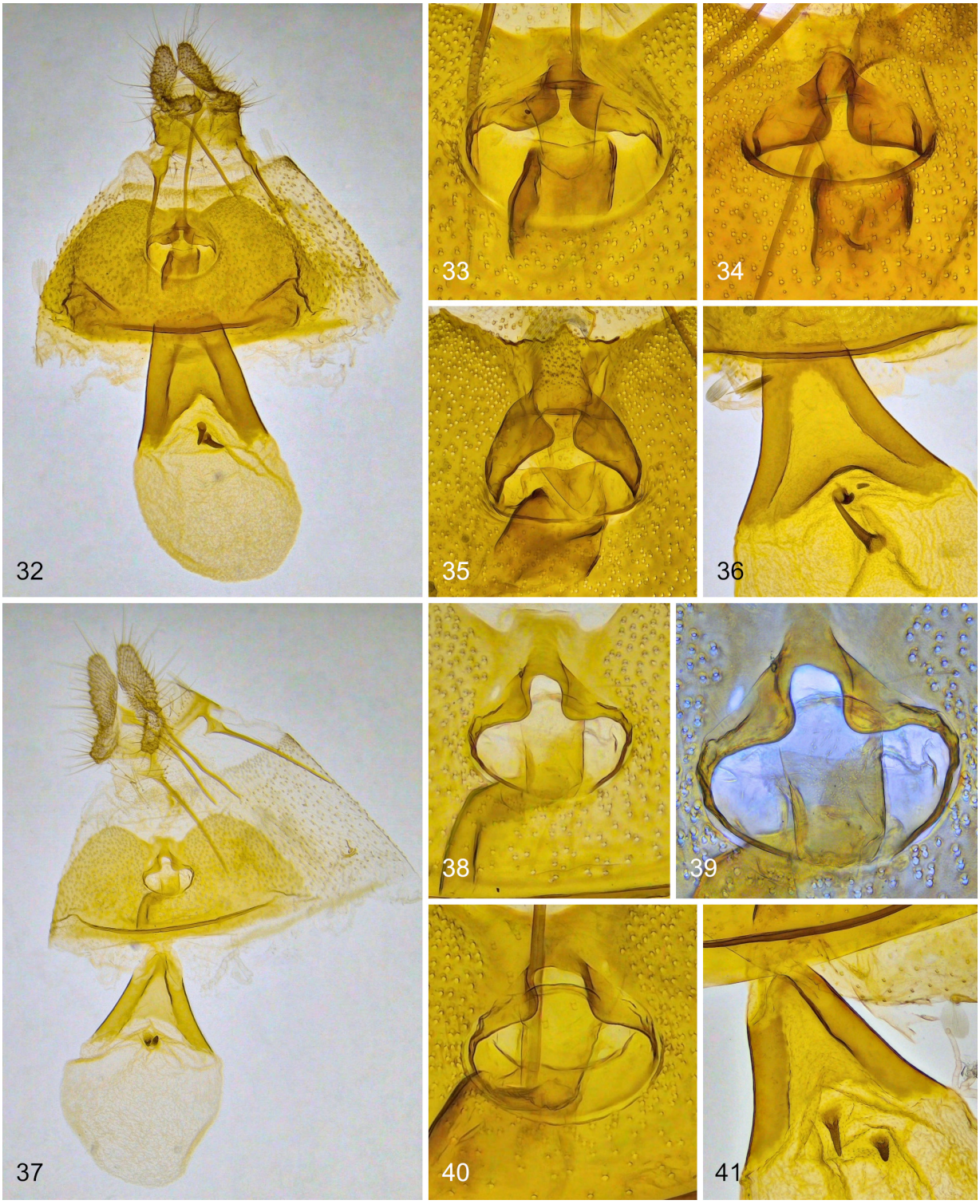


Figures 17–27. *Rhopobota dietziana* adults. **17)** Typical head of *R. dietziana dietziana*, ♀ ex *Ilex montana*, North Carolina (CSE9972). **18)** Unusually dark head of *R. dietziana dietziana*, ♀ ex *I. montana*, North Carolina (CSE9725). **19)** Head of *R. dietziana glabricola* holotype, ♂ ex *I. glabra*, Florida (CSE509). **20)** *R. dietziana dietziana* ♂ ex *I. mucronata*, Maine (CSE8026). **21)** *R. dietziana dietziana* ♀ ex *I. mucronata*, Maine (CSE8028). **22)** *R. dietziana dietziana* ♀ ex *I. montana*, North Carolina (CSE9725). **23)** *R. dietziana dietziana* ♀ ex *Ilex montana*, North Carolina (CSE9972). **24)** *R. dietziana glabricola* paratype ex *I. glabra*, Florida. **25)** Same. **26)** Same. **27)** Same.

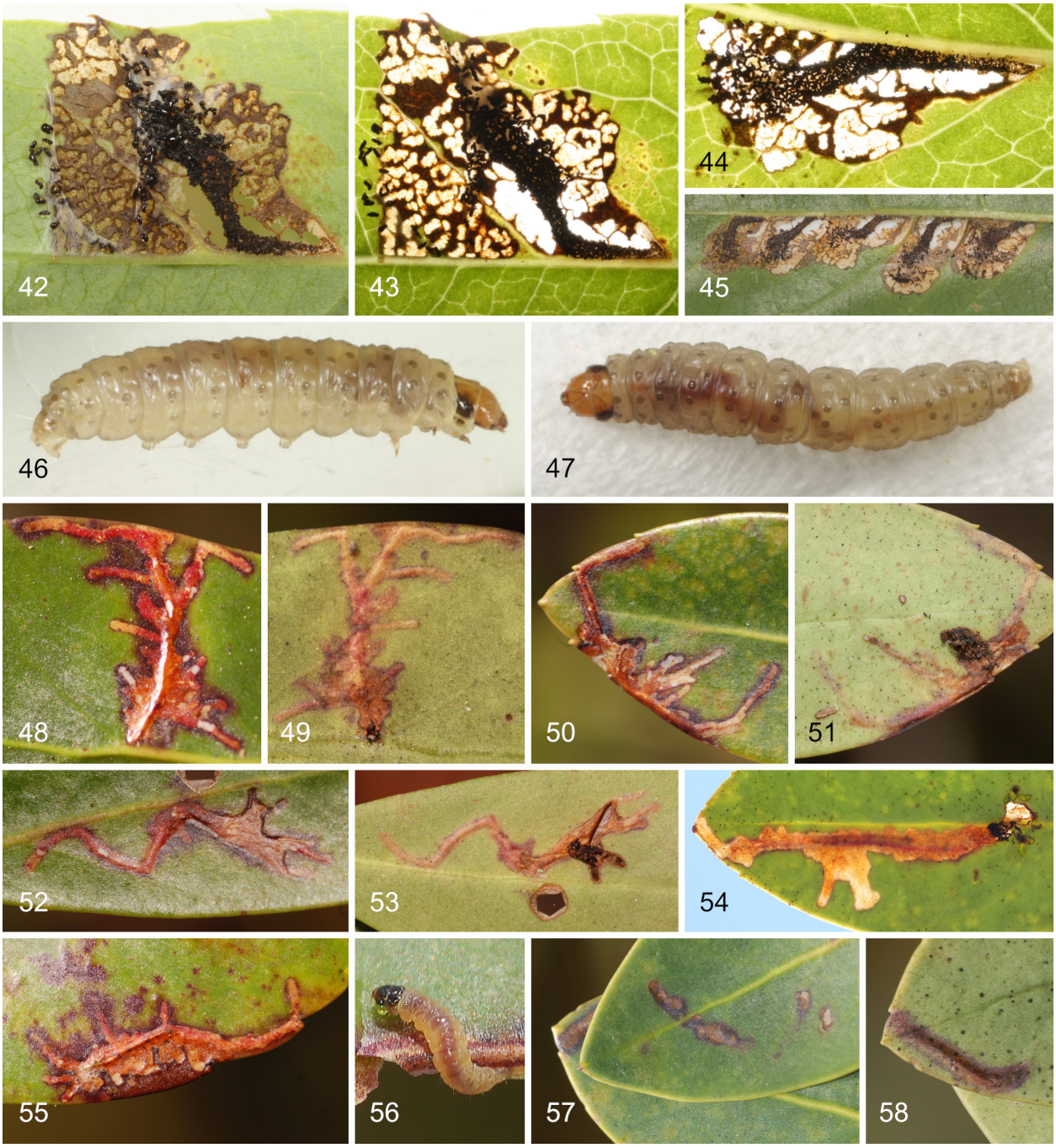


Figures 28–31. *Rhopobota dietziana* male genitalia. **28)** *R. dietziana dietziana* paratype, Pennsylvania (USNM). **29)** *R. dietziana dietziana* ex *Ilex opaca*, North Carolina (CSE9515, slide CE-2025-44, CUIC). **30)** *R. dietziana glabricola* holotype, ex *I. glabra*, Florida (CSE509, USNM). **31)** *R. dietziana glabricola* paratype, ex *I. glabra*, Florida (CSE516, slide CE-2025-45, CUIC). Photos in Fig. 28 and 30 by John W. Brown.

Parish, 32.84, -93.92, 6.viii.2020, em. 31.viii.2020, R. Tyler, ex bush, iNat 58236908 (1♂, genitalia in microvial pinned with specimen, MSC); 7.viii.2020, em. 27.viii.2020, R. Tyler, ex wild plum, iNat 55800464 (1♀, genitalia in microvial pinned with specimen, MSC); Royal Hills Farm, 32.838, −93.915, 29.ii.2023, 7:35pm, R. Tyler, iNat 149979718 (1♀, MSC); Iberville Parish, St. Gabriel, 545 Pecan Drive, 30.310698, −91.096158, bottomland forest drainage canal, 4.v.2023, J.V. Remsen, LED, MV, UV, white lts., iNat 159942649 (1♀, CUIC 000143960); **MAINE:** Hancock Co., Deer Isle, 44.174, −68.719, 11.vii.2015, J.J. Dombroskie, M. Crowell, K. Crowell, MV light, JD20356 (1♀, CUIC 000153610); same but JD20379 (1♀, CUIC 000153583); 44.175, −68.716, 14.vii.2015, J.J. Dombroskie, M. Crowell, K. Crowell, UV trap, JD28688 (1♂, CUIC 000069305); Washington Co., Steuben, Eagle Hill, 44.460, −67.933, 4.viii.2019, J.J. Dombroskie et al., UV/MV light, JD43587 (1♀, CUIC 000143963); Eagle Hill Institute, 44.459629, −67.932211, 2.viii.2022, em. 15.iii.2023, S. Rall & C.S. Eiseman, ex *Ilex mucronata*, #CSE8004 (1♂, genitalia slide CE-2023-35, CNCLEP00309473); same but em. 16.iii.2023, #CSE8005 (2♂, CUIC); same but em. 18–19.iii.2023, #CSE8026 (2♂, CUIC); same but em. 20.iii.2023, #CSE8028 (1♀, genitalia slide CE-2025-47, CUIC); same but em. 28.iii.2023, #CSE8046 (1♂ 1♀, CUIC); same but em. 22–23.iii.2023, ex *Ilex verticillata*, #CSE8039 (1♂, CUIC); **MASSACHUSETTS:** Bristol Co., Fall River, Powerline cut, St. B1, 41.71944, −71.08722, M. Mello, 15.vii.2024, UV trap (2♀, 1 with genitalia in microvial pinned with specimen, MSC); Plymouth Co., Bridgewater, 15.viii.2013, em. 24.ix.2013, C.S. Eiseman, ex *Ilex verticillata*, #CSE917 (1♀, CUIC 000143954); **MISSISSIPPI:** Clay Co., 2200 Old West Point Rd., 33.515, −88.496, 23.vi.2008, J.J. Dombroskie et al., MV light, JD4689 (1♂, CUIC 000153443); Oktibbeha Co., Echols Rd., 33.380, −88.828, 27.vi.2008, J.J. Dombroskie et al., MV light, JD14401 (1♂ [badly rubbed; identification uncertain], CUIC 000153520); **NEW YORK:** Cattaraugus Co., Rock City, 5.vi.1915 (1 adult, CUIC 000143944); 10.vi.1915 (1♂, CUIC 000143943); Suffolk Co., E. Marion, 3.viii.1966, R. Latham (1♀, CUIC 000143953); Montauk, 1.viii.1956, R. Latham (1 adult, CUIC 000143952); Napeague, 9.viii.1956, R. Latham (1♀, CUIC 000143951); Orient, 1.vii.1948, R. Latham (1♀, CUIC 000143950); 12.vii.1951, R. Latham (1♂, CUIC 000143949); Tompkins Co., Ithaca, 42.451, −76.465, 14.vii.2012, J.J. Dombroskie, MV light, JD9563 (1♀, CUIC 000153529); Westchester Co., Ward Pound Ridge Res, 41.258, −73.602, 29.vii.2022, J.J. Dombroskie et al., MV light, JD60091 (1♂, CUIC 000143962); **NORTH CAROLINA:** Wake



Figures 32–41. *Rhopobota dietziana* female genitalia. **32)** *R. dietziana dietziana* ex *Ilex mucronata*, Maine (CSE8028, slide CE-2025-47, CUIC). **33)** Same, sterigma. **34)** *R. dietziana dietziana* ex *I. montana*, North Carolina, sterigma (CSE9725, slide CE-2025-48, CUIC). **35)** *R. dietziana dietziana* ex *I. opaca*, North Carolina, sterigma (CSE9514, slide CE-2025-43, CUIC). **36)** Same, posterior portion of corpus bursae. **37)** *R. dietziana glabricola* paratype, ex *I. glabra*, Florida (CSE460, slide CE-2025-46, CUIC). **38)** Same, sterigma, 100×. **39)** Same, 400×. **40)** *R. dietziana glabricola* paratype, ex *I. glabra*, Florida, sterigma (CSE538, slide CE-2025-41, CUIC). **41)** Same, posterior portion of corpus bursae.



Figures 42–58. *Rhopobota dietziana* larvae and their feeding evidence. **42)** *R. dietziana dietziana* window feeding and frass tube on lower surface of *Ilex mucronata* leaf, Maine. **43)** Same, transmitted light. **44)** Another example of same. **45)** Same but on *I. verticillata*, adjacent feeding areas of five different larvae. **46)** Late instar from same collection of *I. mucronata* leaves, lateral view. **47)** Late instar from same collection of *I. verticillata* leaves, dorsal view. **48)** Leaf mine of *R. dietziana glabricola* on *I. glabra*, Florida, upper surface. **49)** Same leaf, lower surface. **50)** Second example of same, upper surface. **51)** Same leaf, lower surface. **52)** Third example of same, upper surface. **53)** Same leaf, lower surface. **54)** Fourth example of same, lower surface in transmitted light, larva in center. **55)** Fifth example of same, upper surface. **56)** Same collection of leaves, larva removed from mine. **57)** Same collection, two leaves tied together with some mining and some window feeding. **58)** Same, lower surface of mined leaf.

Co., Raleigh, Durant Nature Preserve, 22.iv.2025, em. 15–23.v.2025, T.S. Feldman, ex *Ilex opaca*, #CSE9511 (1♂, CUIC); Horseshoe Farm Nature Preserve, 25.iv.2025, em. 13.v.2025, T.S. Feldman, ex *Ilex opaca*, #CSE9514 (1♀, genitalia slide CE-2025-43, CUIC); same but em. 17–19.v.2025, #CSE9515 (1♂, genitalia slide CE-2025-44, 1♀, CUIC); Watauga Co., near Moses H. Cone Memorial Park, 15.vii.2025, em. 13–14.ix.2025, T.S. Feldman, ex *Ilex montana*, #CSE9725 (1♀, genitalia slide CE-2025-48, CUIC); same but em. 26.iii.2026, #CSE9972 (1♀, CUIC); **RHODE ISLAND:** Washington Co., Block Island, 41.1615, −71.6050, 14.vi.2018, N.D.F. Grindley, MV light (1♂, CUIC 000143961); 41.1950, −71.5652, 28.vi.2017, A.S. Hunt, MV light, 1396815 (1♂, CUIC 000143956); **TENNESSEE:** Chester Co., near Henderson, 35.541, −88.594, 6.iv.2015, K. Childs, MV light, JD22276 (1♂, CUIC 000153475); same but JD22278 (1♂, CUIC 000153521); same but 13.iv.2015, JD21675 (1♂, CUIC 000069303); Sevier Co., Pigeon Forge, 17–20.vii.2006, J. Vargo (1♂, genitalia in microvial pinned with specimen, MSC); **TEXAS:** Harrison Co., Karnack, 26.v.2023, em. 15.vi.2023, G. Smiley, ex *Ilex decidua* (1♂, BG 2256557); **VERMONT:** Jericho, Ethan Allen Firing Range, Site#1, 7.vi.1999, M.S. Griggs (1♀, genitalia in microvial pinned with specimen, MSC); **WEST VIRGINIA:** Pendleton Co., Spruce Knob, el. 4800', 6 miles SW, Riverton, 30.v.2010, S. Johnson (2♀, 1 with genitalia in microvial pinned with specimen, MSC); **WISCONSIN:** Burnett Co., 27.v.199[1 or 8], M. Sabourin (1♀, MSC); vic. Gov. Knowles SF, T38N R19W, Sec. 18, 29.v.2001, diurnal (1♂, genitalia in microvial pinned with specimen, MSC); vic. Kohler Peet area, T40N R18W, Sec. 23, 3.vii.2000, M. Sabourin, light trap (1♂, genitalia in microvial pinned with specimen, MSC); same but 30.vi.2001 (2♂ 2♀, MSC); same but 28.vi.2002 (3♂, MSC); same but 8.ix.2002 (1♂, MSC); Grantsburg, Johnson Rd., 19.vi.2001, M. Sabourin, at light (1♀, MSC); same but 22.vi.2002 (1♀, MSC).

Adult description. Forewing length 4.3–8.1 mm; wingspan 9.6–16.5 mm.

Head (Fig. 17, 18): Labial palpus blackish on outer surface, but bright white on inner surface and at apex of 2nd segment (partially cream-colored or mottled with pale brown in two North Carolina specimens) and entire 3rd segment (rarely cream-colored or mottled with pale brown and blackish—two North Carolina specimens and one from Tennessee). Frons bright white (pale brown laterally in one North Carolina and one Tennessee specimen). Vertex bright white between antennae (cream-colored in two Tennessee specimens), rarely with scattered dark brown scales; head posterior to antennae varying from white to gray with white-tipped scales, or entirely gray-brown or dark brown (sometimes with blue/purple reflections). Scape white (rarely cream-colored or pale brown—one North Carolina, one Tennessee, and one Wisconsin specimen; brown in one Mississippi and two Tennessee specimens) mottled with dark brown and black (mostly ventrally and laterally). Pedicel and flagellomeres dark brown to black, more or less shining white proximally.

Thorax: Dorsally variously mottled or banded with white, gray-brown, and dark brown. Forewing (Fig. 11, 20–23) with white ground (very reduced in one Tennessee specimen, which has mostly fuscous-based scales, and extensive gray in dorsal half of interfascial area) and dark gray-brown markings; basal patch usually distinctly angulated, white with scattered dark brown to black scales, forming a more or less well-defined subbasal fascia, and sometimes a partial basal fascia; interfascial area with sparser and paler dark scales, sometimes forming striae, especially dorsally; median fascia indistinct to well-defined, brown to blackish, with a more or less distinct medial black patch; this is followed by a mottled white and pale gray band, followed by an apical area of white-tipped scales with some patches of dark scales (rarely forming a complete narrow postmedian fascia) in the proximal portion; apical spot black, only rarely surrounded by a larger brown spot, though a brown area sometimes extends from middle of termen to the apical spot and along the costal strigulae to the median fascia; fringe variably patterned with gray, dark gray, blackish, and pale brown scales, sometimes with a well-defined dark line at base; fringe black adjacent to apical spot; scales on underside of forewing gray-brown with white bases. Hindwing pale brown to gray-brown, sometimes with a distinct darker line at base of fringe.

Abdomen: White to pale golden brown or pale gray-brown, variably mottled with dark brown. Male genitalia with sacculus densely clothed in long setae, and multiple long spines arising from base of cucullus and distal portion of neck, similar in length to the dense setae on the cucullus (Fig. 28, 29). Female genitalia with ostium appearing flask- or pear-shaped in ventral view, with the narrower posterior portion being shorter than the width of the wider anterior portion; corpus bursae with the posterior sclerotization continuous dorsally, and with an anteriorly widening gap on the ventral surface (Fig. 32–36).

Hosts. Apart from one record from an unspecified holly (MacKay 1959), all previously published rearing records are from winterberry (Aquifoliaceae: *Ilex verticillata*) (Heinrich 1923; Ferguson 1975; Eiseman 2014), and we have reared one additional specimen from this host. The specimens Eiseman (2014) reared from inkberry (*I. glabra*) are here considered to represent a distinct subspecies, *R. dietziana glabricola*. We newly report the nominate subspecies from possumhaw (*I. decidua*), big-leaved holly (*I. montana* Torr. and A. Gray), mountain holly (*I. mucronata*), and American holly (*I. opaca*). A Louisiana specimen is labeled as having been reared from "wild plum," suggesting a species of *Prunus* L. (Rosaceae). We note that on the day this larva was collected (Tyler 2020b), the same person collected a caterpillar on Georgia holly (*I. longipes* Chapm. ex Trel.) (Tyler 2020a), and we suspect the host plants were mixed up.

Forbes (1923) gave *Crataegus* L. (Rosaceae) as the only larval host for *R. dietziana*, and this was repeated by Robinson et al. (2002). The source of this record is unclear, but it is surely erroneous. Forbes was familiar with Heinrich (1923), since he used the combination *Norma dietziana* that was introduced in that publication, but he did not mention Heinrich's rearing record from *Ilex verticillata*. It is clear from Forbes' (1923) distribution data (see below) that some of his records refer to a different species.

Biology. Heinrich (1923) reported rearing this species from winterberry along with specimens of *R. finitimana* and *R. naevana*, but he gave no indication of the larval habits. MacKay (1959) described a final-instar larva labelled "holly berries." Eiseman (2014) reared one specimen from a large collection of mined winterberry leaves that otherwise produced only parasitoids, as well as 18 specimens from leaf mines on inkberry. Based on our subsequent observations and rearing results, we believe that *R. dietziana* s. str. is not a leafminer, and that the parasitized winterberry leafminers discussed by Eiseman (2014) were in fact *R. finitimana*, while the inkberry leafminer represents a distinct subspecies, *R. dietziana glabricola*.

Our rearings of *R. dietziana* from winterberry and mountain holly in Maine involved larvae collected as early instars. Each larva skeletonized a small patch of leaf tissue surrounding a short tube of frass and silk that began at the leaf midrib; as many as five larvae were found on a single leaf (Fig. 42–45). Each tube soon widened to an irregular sheet of silk with fecal pellets scattered over it, and the larva window-fed beneath this sheet (i.e., consumed the lower epidermis and mesophyll, leaving the upper epidermis intact as a transparent "window"). Some leaf mines, presumably those of *R. finitimana*, were observed on the same plants, but these were carefully excluded from the rearing vials. In the vials, the larvae (Fig. 46, 47) transitioned to feeding between tied leaves. The larvae feeding on American holly in North Carolina were collected in spring, when they were feeding on tender new leaves (in one case adjacent to old leaves on which larvae of *R. opacae* were beginning to window-feed, having recently abandoned their mines (Feldman 2025a)). Photographs taken at the time of collection show a larval shelter formed by curling/folding the leaf margin downward, with frass deposited around the periphery, and with lower-surface window feeding and holes eaten into the surrounding leaf tissue. The larvae on big-leaved holly in North Carolina were found feeding in a similar fashion within shelters consisting of crumpled, rolled, or tied leaves. No leaf mines were observed in connection with either of the North Carolina rearings (apart from the *R. opacae* mines on American holly, confirmed as such by rearing), nor did we see any frass tubes like those collected in Maine, but since the North Carolina larvae were collected as later instars we presume that these initial tubes were concealed within the subsequent leaf shelters. In rearing containers, many of the larvae pupated in simple silk-lined leaf folds, or between two leaves tied together, but at least some of those on big-leaved holly constructed pupation shelters by folding together one or two excised leaf flaps, as has been observed in *R. naevana* (Kearfott 1907a) and *R. finitimana* (Eiseman et al. 2020).

Our Maine specimens all were collected as early instars in early August and emerged as adults the following spring. The time of pupation was not observed. The reared specimen that Ferguson (1975) reported emerging in early May in Nova Scotia clearly also had overwintered in the same way. In Massachusetts, Eiseman (2014) reported an adult emerging in late September from leaves collected in mid-August. This probably would not have occurred under natural conditions; Whitebread et al. (2026) report that the flight period of *R. dietziana* in Massachusetts is 11 May to 29 August. Gilligan et al. (2008) similarly indicate a flight period of April to mid-August in the Midwestern USA. Our mid-July collection of larvae feeding on big-leaved holly in North Carolina yielded one adult in mid-September, and the remaining pupae appeared viable but had not eclosed by the end of October. Following four months of refrigeration, an adult emerged from one of these pupae 25 days after being returned

to room temperature. This confirms that at least some individuals overwinter as pupae and suggests that the first adult emerged prematurely. The same would seem to be the case for the Virginia specimen MacKay (1959) reported emerging on 24 November from a berry-feeding larva collected in October. Whether there is more than one generation per year in the north is not entirely clear, but there are at least two in North Carolina, where we collected larvae on American holly in late April and adults emerged in mid-May. Recorded flight dates in North Carolina's Piedmont region (where these larvae were collected) are from early March to early September; on the coastal plain, small numbers of adults have also been observed throughout February as well as in late October and early November (Hall et al. 2025), which leaves open the possibility that some adults overwinter in this area. The Texas specimen listed above was collected as a final instar in late May and emerged as an adult in mid-June (Smiley 2023).

Distribution. Ontario to Newfoundland (Pohl et al. 2018; BOLD), south to Florida and west to Colorado and Texas (Gilligan et al. 2008). If the Colorado record is accurate, it must be based on an introduced population on planted hollies, because no native *Ilex* species occur in the western USA. The basis for Forbes' (1923) record from Arizona is unclear, but we presume it is erroneous.

DNA barcoding. All 25 previously sequenced specimens of *R. dietziana* in the BOLD database, distributed from Newfoundland to Florida, are assigned to BIN BOLD:AAB8879. One of our specimens reared from mountain holly in Maine (CSE8004; BOLD process ID: MNAS5451-25) was sequenced and is likewise assigned to this BIN (99.69% match to previous barcodes). The nearest neighbor of BIN BOLD:AAB8879, differing by 5.52%, is BOLD:AEY8134, which comprises a single specimen of an undetermined *Rhopobota* sp. from Puerto Rico. A BOLD TaxonID Tree generated from our sequence does not show this Puerto Rican sequence, and based on that tree, the closest barcodes to those of *R. dietziana* are two from specimens of *Lobesia semosa* Diakonoff (Tortricidae) collected in Kenya, plus one from an undetermined tortricid collected in Guatemala (the latter is apparently a private barcode, as we have been unable to locate its source). We included the Puerto Rican sequence as well as one of the Kenyan sequences in our neighbor-joining tree (Fig. 105), and as one would expect, the latter appears on a branch separate from all of the *Rhopobota* sequences.

Rhopobota dietziana glabricola Eiseman, new subspecies

(Fig. 12, 19, 24–27, 30, 31, 37–41, 48–58, 100)

Rhopobota dietziana. Eiseman 2014: 218–219 [specimens reared from *Ilex glabra*]; Eiseman and Hansson 2026: 69.

Diagnosis. This form is at the small end of the size range for *R. dietziana* (forewing and wingspan up to 5.6 mm and 12 mm, respectively, vs. up to 8.1 mm and 16.5 mm for *R. dietziana dietziana*). The coloration is darker than in *R. dietziana dietziana* (Fig. 12, 19, 24–27): the third segment of the labial palpus is at least partly pale brown or darker (almost always entirely bright white in *R. dietziana dietziana*); the upper frons and vertex are pale brown to creamy white (vs. bright white); the scape is pale brown or darker (vs. usually bright white dorsally); on the forewing, the paler areas of the basal patch and adjacent interfascial area are silvery-gray to brown (vs. white), with the only white being in the costal strigulae and the white-tipped scales in the apical area. The basal patch is poorly defined, except for sometimes a dorsal fragment of the subbasal fascia (well defined in *R. dietziana dietziana*, with a complete subbasal fascia and often a partial basal fascia).

Specimens examined. Holotype: **USA. FLORIDA:** Indian River Co., Fellsmere, St. Sebastian River Preserve State Park, 28.iii.2013, em. 13.v.2013, C.S. Eiseman & J.A. Blyth, ex *Ilex glabra*, #CSE509 (1♂, USNM).

Paratypes: Same data as holotype but em. 4.v.2013, #CSE418 (1♂, genitalia in microvial pinned with specimen, CUIC000143955); same but em. 6.v.2013, #CSE460 (1♀, genitalia slide CE-2025-46, CUIC); same but em. 11.v.2013, #CSE493 (1♂, CUIC000144128; 2♀, CUIC000144127, CUIC000144129; 2 pupal skins in gel capsule, CUIC000144126); same but em. 16.v.2013, #CSE516 (1♂, genitalia slide CE-2025-45, CUIC); same but em. 19.v.2013, #CSE525 (1♂, genitalia slide CE-2022-22, CUIC); same but em. 21.v.2013, #CSE534 (1♂ [thorax removed in failed DNA extraction; hindwings in gel capsule], genitalia slide CE-2022-23, CUIC; 1♂, USNM); same but em. 23.v.2013, #CSE537 (1♂, CUIC), #CSE538 (1♀, genitalia slide CE-2025-41, CUIC); same but em. 29.v.2013, #CSE548 (2♂ [1 with genitalia in microvial pinned with specimen; thorax removed in failed DNA extraction], CUIC).

Non-type material: **USA. FLORIDA:** Alachua Co., Austin Cary Forest, 29.749, −82.200, 10.v.2014, J.J Dombroskie et al., MV/UV light, JD14205 (1♂, CUIC 000153489); Columbia Co., ONF, 7.v.2002, Vargo (1♂, MSC); Escambia Co., Tarkiln Bayou SP, 30.36699, −87.40714, 30.iii.2010, Biobus 2010, UV light trap (2 adults, 10BBLEP-00888, 10BBLEP-00889, CBG; BOLD USLEP888-10, USLEP889-10); Highlands Co., Lake Placid, Archbold Biological Station, 24–26.ix.2007, B. Patterson, J. Vargo, S. Johnson & M. Sabourin (1♀, genitalia in microvial pinned with specimen, MSC); Archbold Biological Station, Lake Annie, 27.21044, −81.34904, 21.vi.2006, P.D.N. Hebert, K. Pickthorn, J.F. Landry, J. deWaard, UV sheet (1 adult, HLC-16804, CBG; BOLD LOFLD229-07); **MISSISSIPPI:** George Co., Pascagoula River Wildlife Management Area, 16 km SW Lucedale, 30 52 40N, 88 46 05W, 10.iii.1995, R. Davidson, R. Acciavatti, D. Koenig & W. Zanol (1♂, genitalia in microvial pinned with specimen, MSC); Harrison Co., Biloxi, 13.vi.1917 (4♂, CUIC 000143945–48).

Adult description. Forewing length 4.7–5.6 mm; wingspan 10.5–12 mm.

Head (Fig. 19): Labial palpus with 1st segment dark brown to black; 2nd segment dark brown or mottled brown and black on outer surface, white to creamy white at apex and on inner surface; 3rd segment white to pale brown with pale brown to dark brown or blackish outer surface. Upper frons pale brown or rarely creamy white, the lower margin sometimes white or creamy white. Vertex pale brown to brown (rarely creamy white), variably mottled with dark brown to black, scales reflecting blue and purple at some angles of light. Scape variably mottled with pale to medium brown, dark brown, and black; pedicel and flagellomeres distally dark brown to black, basally light to medium brown.

Thorax: Dorsally brown or gray, mottled with dark brown and black. Forewing (Fig. 19, 24–27) with dark brown and white strigulae along entire costa; basal patch extending to 33–38% of the total wing length, predominately silvery-gray to brown, with scattered clusters or broken striae of brown to black scales; a broad interfascial area in the middle of the wing, generally concolorous with ground color of basal patch, with scattered scales of darker gray, brown, and black; median fascia irregular, typically brown mottled with black scales, sometimes with the black scales coalescing into a medial blotch; beyond this is a broad, more uniformly brown or silvery-gray band, followed by a terminal area of white-tipped scales (sometimes clearly organized into continuations of the costal striae) that may include a broken dark brown postmedian fascia, or only a few dark scales, near its proximal margin; at apex a black spot within an elongate brown patch; fringe gray to gray-brown with a more or less distinct blackish line at base, the two shades separated by a narrow white line; apart from this white line, the fringe scales adjacent to the apical spot are entirely black; lower surface of forewing with scales dark brown with pale brown bases. Hindwing light brown to gray-brown; fringe light brown to gray with a more or less distinct darker line at base. Legs banded and mottled with whitish, blackish, and brown.

Abdomen: Creamy white to pale brown, variably mottled with brown to dark brown. Male (Fig. 30, 31) and female (Fig. 37–41) genitalia as in the nominate subspecies.

Etymology. The subspecies epithet refers to the host plant, *Ilex glabra* (L.) A. Gray (combined with the Latin *colo*, to inhabit). It is borrowed from the name of the leaf-mining insect most commonly found on this plant, *Phytomyza glabricola* Kulp (Diptera: Agromyzidae).

Host. Inkberry (Aquifoliaceae: *Ilex glabra*). This mostly coastal plant occurs from Florida to Nova Scotia and Texas (POWO 2026).

Biology. Larvae initially feed in full-depth leaf mines (Fig. 48–55). Each mine includes a small irregular blotch with a hole in the lower surface, where frass is expelled and accumulates in an irregular mass. The hole may be located anywhere from the midrib to the leaf margin. From the blotch several linear tracks emanate, and these in turn may have linear branches. The larva at this stage is whitish with a black head and prothoracic shield (Fig. 56). Upon exiting their mines, larvae may establish new ones or tie together two overlapping leaves and feed externally on the concealed surfaces (Fig. 57, 58). When multiple mined leaves were placed together in rearing vials, the leaves all became bound together in a frass-filled mass, preventing observation of the larvae (Eiseman 2014). Larvae were collected in Florida on 28 March, and adults emerged from 4 to 29 May. Adults have been collected in Florida in late March, early May, late June, and late September, and in Mississippi in early March and mid-June. These data suggest there are at least two generations per year, but are insufficient to determine what stage(s) overwinter. An early, but not necessarily occupied, *Rhopobota* leaf mine on inkberry has been photographed

in Florida in mid-December (Frade 2022), and one that appears to contain a larva has been photographed in South Carolina in late December (Zappa 2024), but these cannot be said with certainty to represent *R. dietziana glabricola*.

A male and female of the parasitoid wasp *Zagrammosoma* cf. *velerii* Yefremova (Eulophidae) were reared along with the type series (Eiseman 2014; Eiseman and Hansson 2026).

Distribution. Florida, Mississippi; an adult possibly representing this subspecies has been photographed in Virginia (Gilbert 2026).

DNA barcoding. Our attempts to sequence two paratypes were unsuccessful. However, three Florida specimens in BOLD (listed above under non-type material) are consistent with this subspecies, and they are assigned to BIN BOLD:AAB8879 as with all other *R. dietziana* that have been sequenced. They are labeled as *R. dietziana glabricola* in Fig. 105; sequences not identified to subspecies in our tree are those for which no images have been uploaded in BOLD.

Notes. We have chosen to treat this form as conspecific with *R. dietziana* due to the matching genitalia and DNA barcodes. We feel that it warrants recognition as a subspecies due to its distinct (leaf-mining) larval biology and restricted geographic distribution. With the exceptions of badly worn or poorly photographed specimens, we have been able to confidently assign each individual we have examined to one subspecies or the other. As noted in the description of *R. dietziana dietziana*, occasional individuals of that subspecies have reduced white on the head (Fig. 18), and one Tennessee specimen has reduced white on the forewing, but these otherwise fit the diagnosis of *R. dietziana dietziana* and in most cases are substantially larger than any known individual of *R. dietziana glabricola*.

More rearing of *Rhopobota* from inkberry throughout the distribution of this plant would be desirable to better assess the extent of the distribution of *R. dietziana glabricola*. A review of iNaturalist observations with *Ilex glabra* in the "Host Plant ID" field (https://www.inaturalist.org/observations?verifiable=any&field:Host%20Plant%20ID=129347) yielded 187 records from Louisiana and Florida to Nova Scotia, nearly all showing leaf mines of *Phytomyza glabricola*. Just five show *Rhopobota* leaf mines; two from Nova Scotia (Klymko 2021a, b), and one each from Florida (Frade 2022), South Carolina (Zappa 2024), and New Jersey (Mollenhauer 2024). Another observation from Nova Scotia shows leaf tying that could conceivably be from any of the *Rhopobota* species or even another tortricid (Blaney 2021). The leaf mines cannot be assigned to species without rearing, because *R. finitimana* (whose known distribution includes these localities except for Florida) has been reared from *I. glabra* in Nova Scotia.

Rhopobota finitimana (Heinrich)

(Fig. 13, 14, 59–62, 65, 67–73, 77, 78, 80–82, 85–90, 101, 102)

Kundrya finitimana. Heinrich 1923: 192–193, Fig. 8, 34, 415; Forbes 1923: 412; Jones and Kimball 1943: 157; Prentice 1966: 635; Brower 1983: 36.

Kundryia finitimana [misspelling]. Ferguson 1975: 34.

Rhopobota finitimana. Brown 1979: 21, 23–24; 1983: 98–101; Robinson et al. 2002: 386; Gilligan et al. 2008: 151, 233, 282–283; Austin 2010: 42; Scholtens 2012: 150; 2014: 163; Pohl et al. 2018: 154; Eiseman et al. 2020: 517 [excluding specimen reared from *Ilex opaca*], 519.

Rhopobota sp. Eiseman and Charney 2010: 163.

Rhopobota dietziana [misidentification]. Eiseman 2014: 219, Fig. 1.

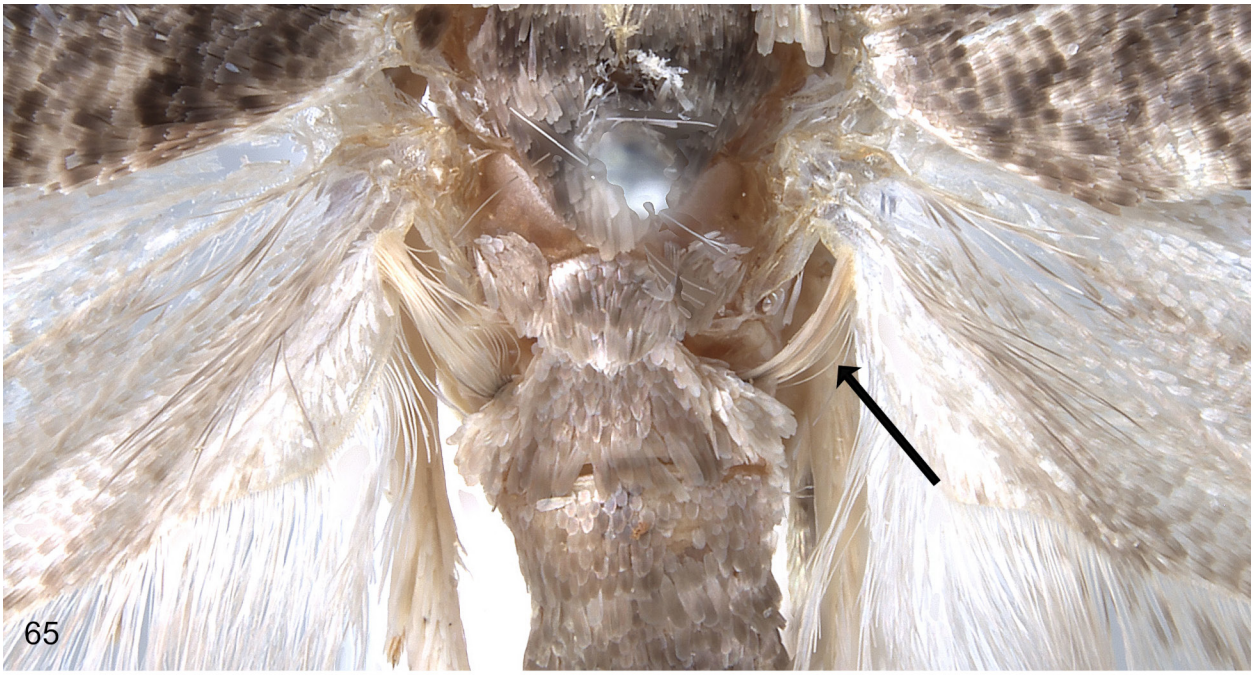
Diagnosis. Adults of the *R. finitimana* complex (*R. finitimana* and *R. opacae*) are distinguished from *R. dietziana* and *R. naevana* by the combination of small size (wingspan 8.5–10.5 mm, rarely up to 12.5 mm; forewing length 3.8–5.5 mm), brown head (including labial palpi, frons, vertex, and scapes), and solid basal patch that extends to 29–39% of the total forewing length. The basal patch also tends to be less angulated than in the other species, with the difference between its maximum and minimum lengths being 0.0–0.5 mm in the *R. finitimana* complex, 0.3–0.9 mm in *R. dietziana*, and 0.4–1.1 mm in *R. naevana*. The two species of the *R. finitimana* complex differ from one another most conspicuously in the female genitalia, with the sterigma of *R. finitimana* appearing flask-shaped in ventral view (Fig. 80–82), vs. posteriorly domed in *R. opacae* (Fig. 83, 84). The two have similar male



Figures 59–64. Adults of the *Rhopobota finitimana* complex. **59)** *R. finitimana* ♀ ex *Ilex decidua*, North Carolina (CSE3965). **60)** *R. finitimana* ♀ ex *I. mucronata*, New York (CSE8101). **61)** *R. finitimana* ♀ ex *I. verticillata*, Connecticut (CSE8745). **62)** *R. finitimana* ♂ ex *I. vomitoria*, North Carolina (CSE9873). **63)** *R. opacae* paratype ♂ ex *I. opaca*, North Carolina (CSE5261). **64)** *R. opacae* holotype ♀ ex *I. opaca*, North Carolina (CSE9498).

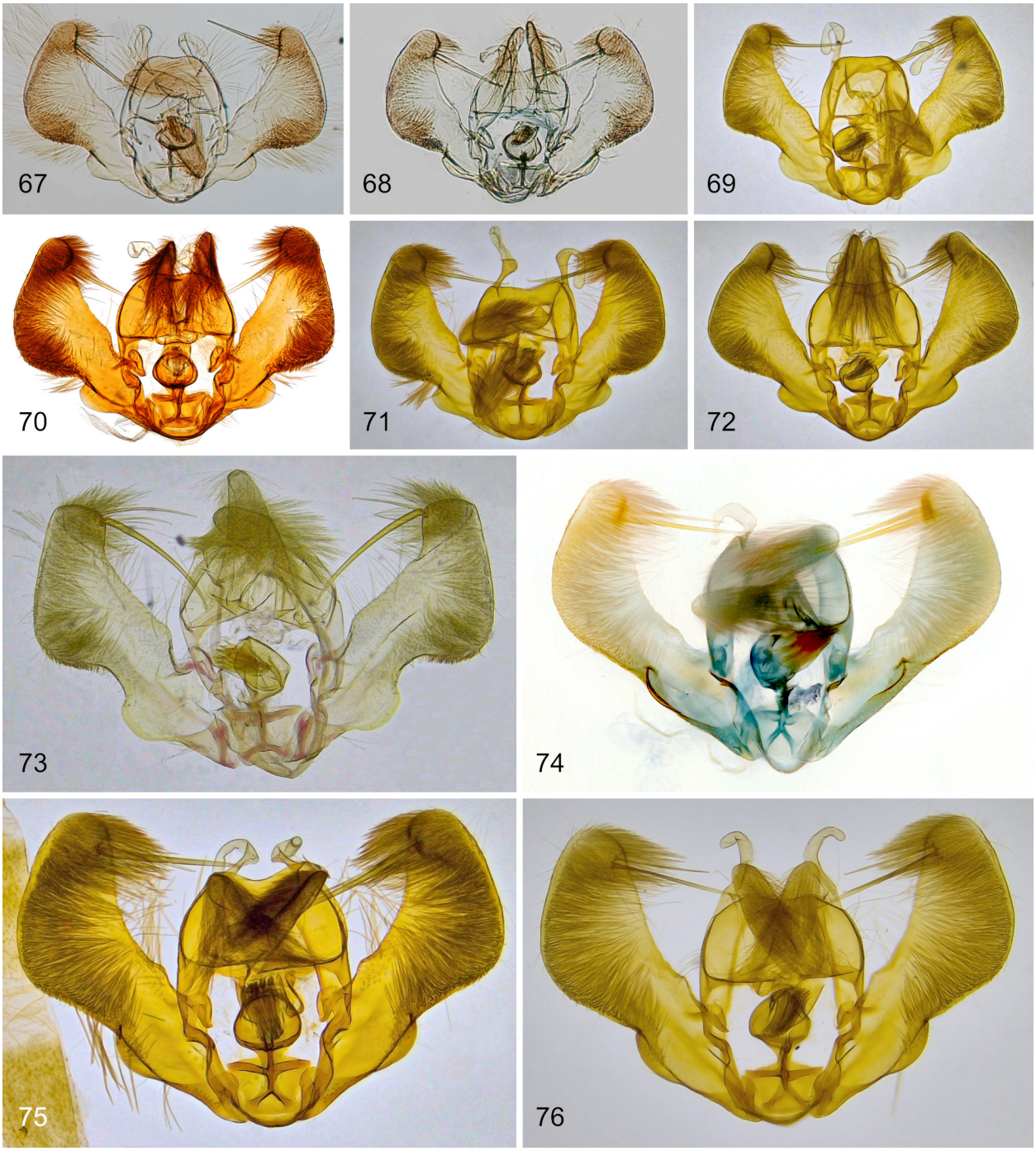
genitalia, but in the valva of *R. finitimana* large areas of the neck and cucullus are not overlapped by the marginal setae, and there are 1–2 spines on the cucullus that are much longer than the setae (Fig. 67–73), whereas *R. opacae* has longer marginal setae that largely cover the neck and cucullus, and there are 2–3 spines on the cucullus that are much longer than the setae (Fig. 74–76). Externally, the forewing of *R. finitimana* (Fig. 13, 14, 59–62) frequently has extensive gray or brown coloring in the distal portion of the median interfascial area, whereas this area is almost entirely cream and white in the known specimens of *R. opacae* (Fig. 15, 16, 63, 64). Well spread male specimens of *R. finitimana* can be recognized by the hair pencil at the base of the anal margin of the hindwing (Fig. 65); this is absent in *R. opacae*, which instead has a hair pencil at the base of the hind tibia (Fig. 66).

Specimens examined. [Data also included from some CNC specimens not examined by us, as indicated.] **Canada. NOVA SCOTIA:** Barrington, 1973, em. 14.i.1974, G.G. Lewis, ex *Nemopanthus mucronata*, 73-15 (1 adult [not examined], CNC); Lake Annis, 1960, em. 22.i–8.ii.1961, Freeman & Lewis, ex *Ilex glabra*, 60-195 (1♂, CNCLEP00309492, genitalia slide TOR 5324; 1♀, CNCLEP00309493, genitalia slide TOR 5325; 19 other adults [not examined], CNC); **ONTARIO:** Ottawa, Constance Bay, 30.viii.1956, em. 11–22.iii.1957, G.G. Lewis, ex *Ilex verticillata*, 56-205 (6 adults [not examined], 3 mined leaves, CNC); Manotick Station, 45.242, –75.600, 27.vii.2012, J.J. Dombroskie, JD9637 (1♀, CUIC 000144125); South March, 16.viii.1955, em. 14–26.vi.1956, G.G. Lewis, ex *Nemopanthus mucronata*, 55-169 (5 adults [not examined], 4 mined leaves + 2 pairs of tied leaves, CNC); Renfrew Co., Richard's Twp., 45.606, –77.593, 4.vii.2017, J.J. & L.M. Dombroskie, UV trap, JD32399 (1♂, CUIC 000069309); same but JD41031 (1♂, CUIC 000143966). **USA. CONNECTICUT:** Litchfield Co., Norfolk,

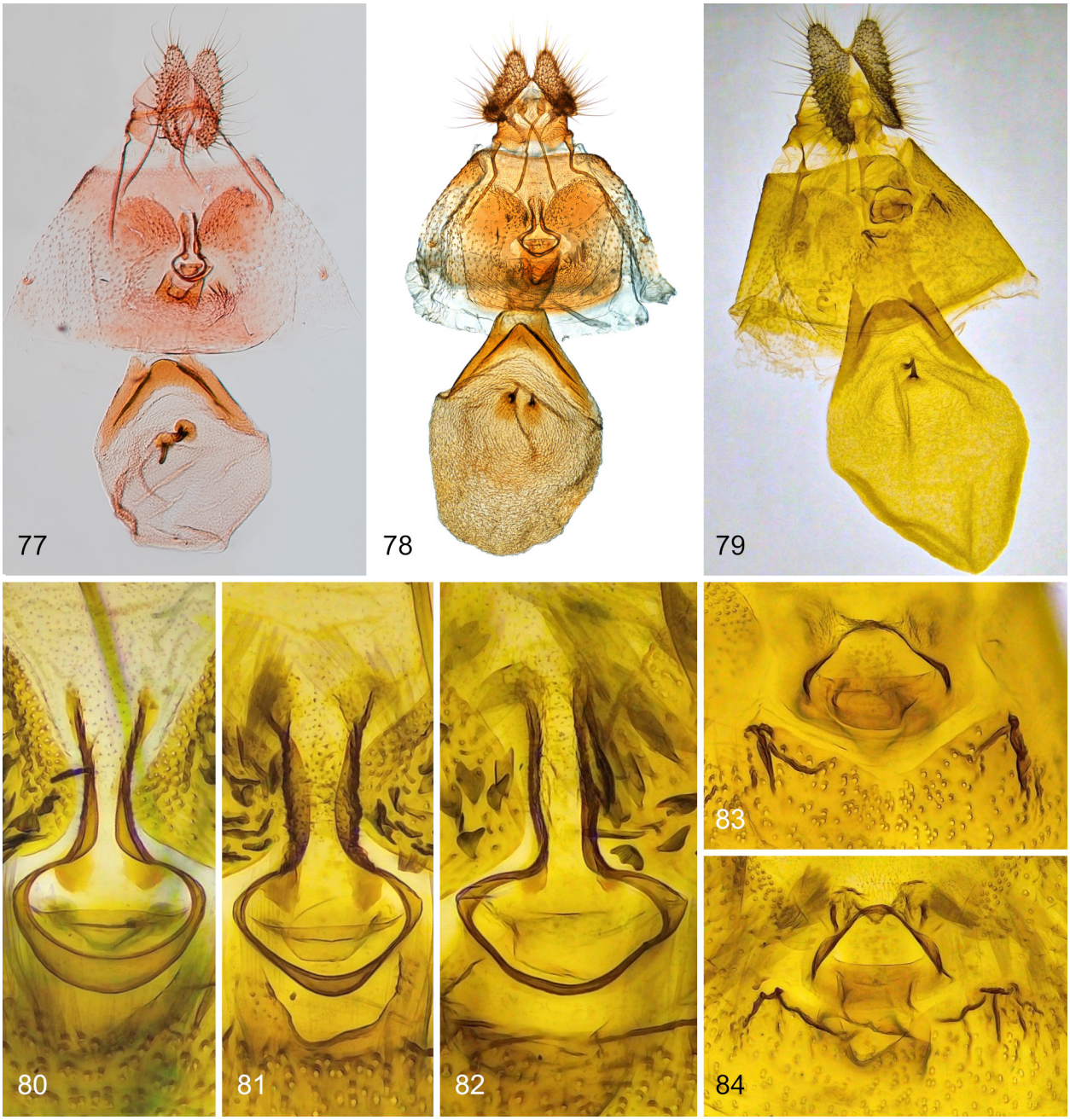




Figures 65–66. Hair pencils (androconial scales) on males of the *Rhopobota finitimana* complex. **65)** *R. finitimana*, bases of hindwings (Louisiana, MEM). **66)** *R. opacae*, base of hind tibia (Georgia, MEM). Photos by Joe A. MacGown.



Figures 67–76. Male genitalia of the *Rhopobota finitimana* complex. **67)** *R. finitimana* holotype, New Hampshire (USNM). **68)** *R. finitimana* paratype ex *I. verticillata*, Virginia (USNM). **69)** *R. finitimana* ex *I. decidua*, North Carolina (CSE9208, slide CE-2025-31, CUIC). **70)** *R. finitimana* ex *I. glabra*, Nova Scotia (CNCLEP00309492, slide TOR 5324, CNC). **71)** *R. finitimana* ex *I. verticillata*, Illinois; two long spines on right valva (slide CE-2025-38, CUIC). **72)** *R. finitimana* ex *I. vomitoria*, North Carolina; two long spines on each valva (CSE9873, slide CE-2026-49, CUIC). **73)** *R. finitimana* ex *I. vomitoria*, North Carolina; decurved spines at valva apices (CSE7290, slide CE-2022-24, CUIC). **74)** *R. opacae* paratype ex *I. opaca*, North Carolina (CSE5261, CUIC000058822). **75)** *R. opacae* paratype ex *I. opaca*, North Carolina (CSE9207, slide CE-2025-29, CUIC). **76)** *R. opacae* paratype ex *I. opaca*, Maryland (CSE9494, slide CE-2025-39, CUIC). Photos in Fig. 67 and 68 by John W. Brown; Fig. 70 by Jean-François Landry; Fig. 74 by Loren Jones.

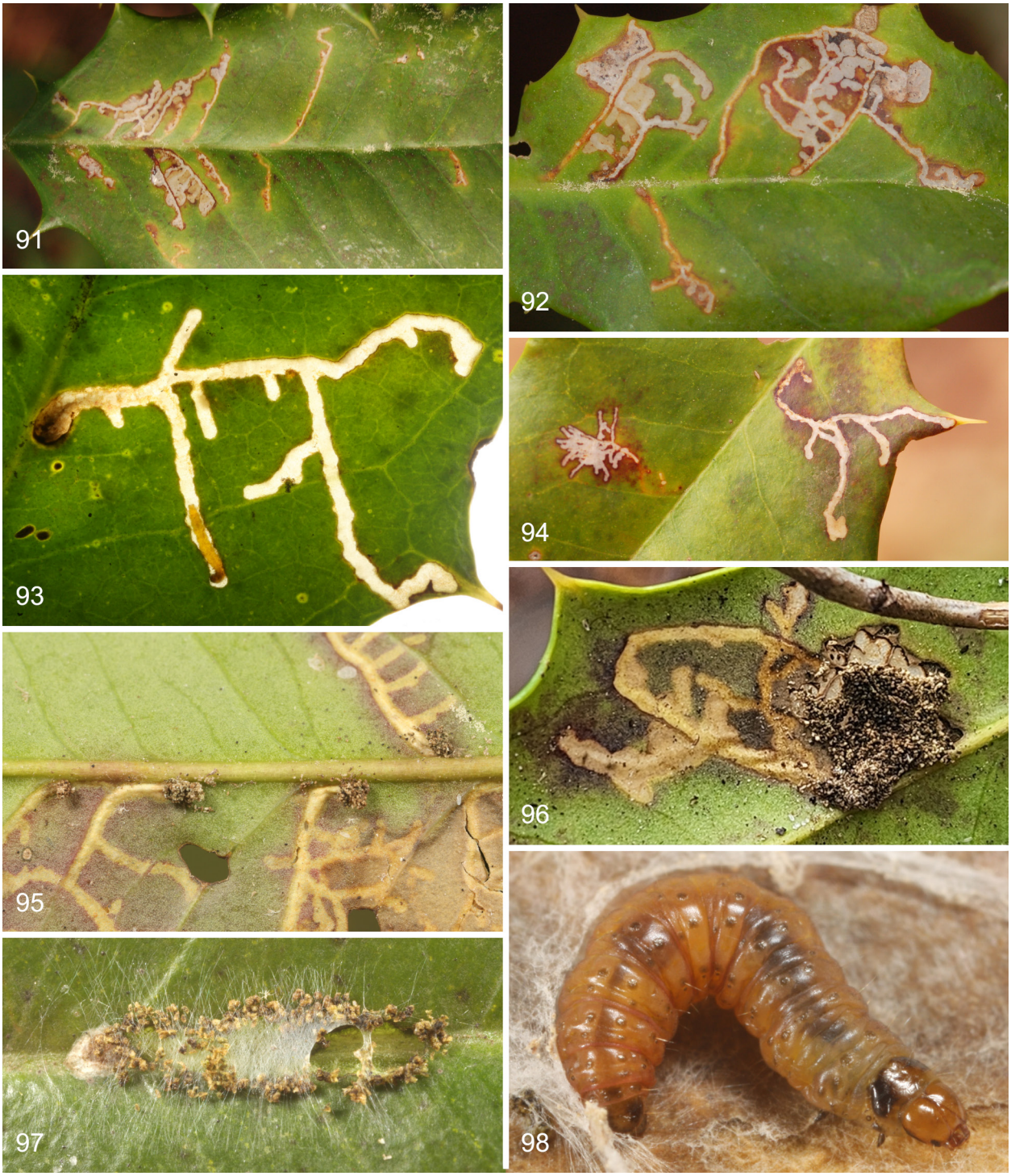


Figures 77–84. Female genitalia of the *Rhopobota finitimana* complex. **77)** *R. finitimana* paratype ex *Ilex verticillata*, Virginia (USNM). **78)** *R. finitimana* ex *I. glabra*, Nova Scotia (CNCLEP00309493, slide TOR 5325, CNC). **79)** *R. opacae* paratype ex *I. opaca*, North Carolina (CSE9511, slide CE-2025-42, CUIC). **80)** Sterigma, *R. finitimana* ex *I. decidua*, North Carolina (CSE9208, slide CE-2025-30, CUIC). **81)** Sterigma, *R. finitimana* ex *I. mucronata*, New York (CSE8019, slide CE-2025-32, CUIC). **82)** Sterigma, *R. finitimana* ex *I. vomitoria*, North Carolina (CSE7290, slide CE-2025-24, CUIC). **83)** Sterigma, *R. opacae* paratype (same as Fig. 79). **84)** Sterigma, *R. opacae* paratype ex *I. opaca*, New Jersey (CSE9487, slide CE-2025-40, CUIC). Photo in Fig. 77 by John W. Brown; Fig. 78 by Jean-François Landry.



Figures 85–90. *Rhopobota finitimana* larvae and their feeding evidence (Fig. 85–88 all show the lower leaf surface). **85)** Leaf mine on *Ilex decidua*, North Carolina. **86)** Mines of three larvae on *I. verticillata*, Massachusetts. **87)** Mine on *I. verticillata*, Massachusetts. **88)** Mine on *I. vomitoria*, North Carolina (CSE7290). **89)** Late instar ex *I. vomitoria*, North Carolina (CSE9910). **90)** Pupal shelter on *I. mucronata*, New York.

Aton Forest, 42.033994, −73.14245, 27.viii.2023, em. 10–11.iii.2024, C.S. Eiseman, ex *Ilex verticillata*, #CSE8658 (1♂, genitalia slide CE-2025-20, CUIC); same but em. 12–13.iv.2024, #CSE8745 (1♀, genitalia slide CE-2025-22, CUIC); **ILLINOIS:** Lake Co., Zion, Hosah Park, 14.vii.2024, em. 31.viii.2024, J. Steffen, ex *Ilex verticillata* (1♂, genitalia slide CE-2025-38, CUIC); same but em. 1.ix.2024 (1♀, CUIC); **LOUISIANA:** Bossier Parish, Barksdale A.F.B., 32.52028, −93.59611, 11.iv.1996, D.M. Pollock (1♂, MEM [photos examined]); **MAINE:** Hancock Co., Bar Harbor, em. 26.vi.1935, A.E. Brower, ex *Ilex verticillata*, Lot #246 (2♂, CUIC 000143958; 1♀, CUIC 000143959); same but em. 28.vi.1935 (1♂ 1♀, CUIC 000143957); **MISSISSIPPI:** *Ilex decidua*, G.G. Lewis, 63-13 M. (4 mined leaves, CNC); **NEW YORK:** Dutchess Co., South Brace Mountain, 30.viii.2022, em. 18–19.iii.2023, C.S. Eiseman, ex *Ilex mucronata*, #CSE8019 (2♀, genitalia slide CE-2025-32); same but em. ~30.iv.2023, #CSE8101 (1♀, CUIC); **NORTH CAROLINA:** Carteret Co., Fort Macon State Park, 12.xii.2025, em. 30.i.2026, T.S. Feldman, ex *Ilex vomitoria*, #CSE9873 (1♂, genitalia slide CE-2026-49, CUIC); same but em. 8.ii.2026, #CSE9889 (1♀, CUIC); same but em. 13.ii.2026, #CSE9910 (1♀, CUIC); Durham Co., Durham, 3800 Farmgate Ave., 31.iii.2015, em. ~19.iv.2015, C. Sheffield (Croasdaile CC), ex *Ilex vomitoria*, PDIC #20736 (1 photographed adult, https://flic.kr/p/rgyHn8; specimen reared by MAB and possibly now at CUIC, but not among those seen by CSE); Leigh Farm Park, 14.vi.2017, em. 16.vii.2017, T.S. Feldman, ex *Ilex decidua*, #CSE3965 (2♀, CUIC 000058795, CUIC 000058939 [genitalia in microvial pinned with specimen]); New Hope Creek Bottomlands, 30.v.2023, em. 2–6.vii.2023, T.S. Feldman, ex *Ilex decidua*, #CSE9208 (3♂, genitalia slide CE-2025-31, 2♀, genitalia slide CE-2025-30, CUIC); Iredell Co., Davidson College Ecological Preserve, 35.510, −80.835, 14.iv.2017, K.A. Austin & J.A. Dadul, powerline cut through mixed pine-hardwood forest, UV light (1♂, CUIC 000143964); Scotland Co., Laurinburg, St. Andrews University, 13.xii.2020, em. 22–25.iii.2021, T.S. Feldman, ex *Ilex vomitoria*, #CSE7290 (1♂, genitalia slide CE-2022-24, 3♀, genitalia slide CE-2025-24, CUIC); same but 11.xii.2025, em. 29.i.2026, #CSE9871 (1♀,



Figures 91–98. *Rhopobota opacae* larvae and their feeding evidence on *Ilex opaca*. **91)** Mines of at least ten different larvae, South Carolina. **92)** Mines of five larvae, South Carolina. **93)** Backlit mine with feeding larva at bottom center, New Jersey. **94)** Mines of two larvae, Georgia. **95)** Lower surface showing expelled frass of four larvae, New Jersey. **96)** Lower surface showing external "window feeding" adjacent to mine, the feeding area mostly covered by frass and silk, New Jersey (© Jeff Mollenhauer, CreativeCommons – Attribution Non-Commercial Share-Alike). **97)** Silk- and frass-covered "window feeding" patch on upper surface of midrib, New Jersey. **98)** Late instar, New Jersey.



Figures 99–104. Pupal exuviae of *Ilex*-feeding *Rhopobota* spp. **99)** *R. dietziana dietziana* ex *I. verticillata* (CSE917, Massachusetts). **100)** *R. dietziana glabricola* ex *I. glabra* (CSE493, Florida). **101)** *R. finitimana* ex *I. decidua* (CSE3965, North Carolina). **102)** *R. finitimana* ex *I. vomitoria* (CSE9910, North Carolina). **103)** *R. opacae* ex *I. opaca* (CSE5261, North Carolina). **104)** *R. opacae* ex *I. opaca* (CSE9498, North Carolina).

CUIC); Wake Co., Raleigh, Horseshoe Farm Nature Preserve, 9.vii.2025, em. 4.viii.2025, T.S. Feldman, ex *Ilex decidua*, #CSE9772 (1♂, CUIC); 26.vii.2025, em. 18–20.viii.2025, T.S. Feldman, ex *Ilex decidua*, #CSE9689 (1♀, 1 partially emerged adult in gel capsule [pinned together], CUIC); **OKLAHOMA:** McCurtain Co., Red Slough, 33.732, –94.634, 29.iv.2019, em. by 9.vi.2019, M. Palmer, ex *Ilex decidua*, 5141.4 [collected as leafminers: BG 1660810] (1♂, CUIC 000143967); **TEXAS:** Harrison Co., Karnack, 26.v.2023 [pupa], em. 1.vi.2023, G. Smiley, ex *Ilex decidua* (1 adult, BG 2250739).

Adult description. Forewing length 3.7–5.1 mm; wingspan 9.0–10.5 mm.

Head: Labial palpus light brown to brown with some blue/purple reflections, and sometimes with black mottling on outer and dorsal surface; sometimes also gray mottling on outer and dorsal surface. Smooth scales of lower frons silvery whitish; frons and vertex otherwise light brown to brown with some blue/purple reflections, sometimes with black or gray mottling. Scape light brown to brown or gray, usually with black mottling; pedicel and flagellomeres brown or gray proximally, distally dark brown to black. One old female specimen from Maine has the palpi, frons, and vertex creamy white, and scapes creamy white with some brown mottling, but it was reared along with typical *R. finitimana* specimens and its forewing pattern and length (3.9 mm) are consistent with this species.

Thorax: Dorsally variably mottled or banded with dark brown, brown, pale brown, black, and gray, sometimes with purple reflections. Forewing (Fig. 13, 14, 59–62) with white, black, and brown strigulae along costa

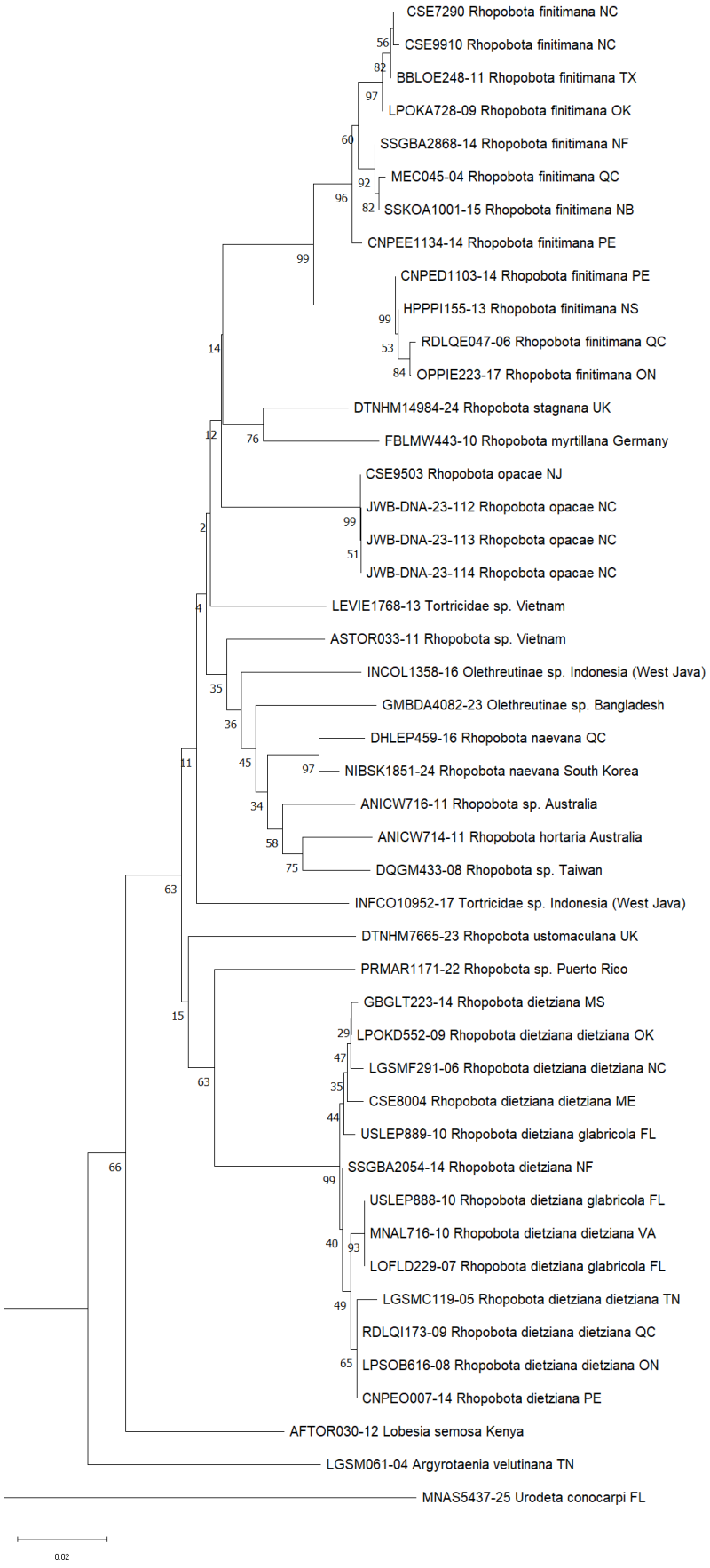


Figure 105. *Rhopobota* tree generated using neighbor-joining method based on COI sequences amplified from specimens in this study and those downloaded from BOLD (Ratnasingham and Hebert 2007), with each taxon name preceded by our specimen ID or the BOLD Process ID and followed by the geographic location. Three other moths are included as outgroups: *Lobesia semosa* Diakonoff (Tortricidae: Olethreutinae), *Argyrotaenia velutinana* (Walker) (Tortricidae: Tortricinae), and *Urodeta conocarpi* Eiseman (Elachistidae). Support values on nodes were generated from 10,000 bootstrap replicates.

(obscure in basal patch); basal patch extending to 29–39% of total forewing length, varying from distinctly angulate (symmetrical) to rounded, undulate, or nearly straight, gray to brown with black and sometimes brown mottling, partly forming striae; interfascial area a variable mix of cream and white, with more or less extensive distal gray and brown mottling or solid patches, such that the whitish area sometimes appears much narrower; median fascia broad, brown with black mottling (a medial spot usually being the largest, as in other species) and only a few cream-tipped scales, or narrow/indistinct with more cream to white-tipped scales and otherwise not always clearly differentiated from the interfascial gray patches that precede and follow it; a sinuous gray patch immediately following the median fascia; white-tipped scales mostly restricted to the median ⅓ of the area between this gray patch and the narrow brown patch along the termen, or extending onto the postmedian fascia; the dorsal half of this apical area may be mostly cream-colored, or it may be mostly white with a gray patch; black apical dot within a brown patch that is usually separated from the oblique, brown, postmedian fascia by a parallel narrow gray patch, but sometimes incompletely; fringe pale to dark gray, sometimes with black, brown, and/or white mottling, sometimes with a fairly distinct dark line at base; fringe black adjacent to apical dot, except for a medial or sometimes basal whitish line; underside of forewing mostly gray to dark gray, usually whitish near dorsal margin. Hindwing light brown to gray, whitish along costa toward base, rarely blackish at apex; fringe light brown to gray, sometimes with a distinct darker line at base; male hindwing with a light brown hair pencil at base of anal margin, extending into a pocket in the basal segment of the abdomen (Fig. 65); underside of hindwing mostly gray to dark gray, usually whitish along costa (Illinois male and non-reared North Carolina male instead whitish in dorsal half). Legs light brown to brown, variably mottled and banded with brown, black, and gray; hind legs largely white except for black mottling on tibial spurs and tarsi.

Abdomen: Dorsally variably banded and mottled with light brown, brown, gray-brown, silver, and black; ventrally white to light brown variably mottled with black. Valva of male genitalia with large areas of the neck and cucullus not overlapped by the marginal setae; typically with one long, straight spine that arises before the apex and far exceeds the surrounding setae (Fig. 67–70); occasionally a second, somewhat shorter and weaker spine is present, along with others that are not obviously longer/stronger than the setae (Fig. 71, 72); one specimen (CSE7290) with a decurved spine arising from the valva apex (Fig. 73). Female genitalia with sterigma appearing flask-shaped in ventral view, with a narrow, open posterior neck (Fig. 80–82); posterior sclerotization of corpus bursae with lateral patches joined by a narrow ventral portion (Fig. 77, 78).

Hosts. Several paratypes were reared from winterberry (Aquifoliaceae: *Ilex verticillata*) (Heinrich 1923), and *R. finitimana* has been repeatedly reared from this host subsequently (Jones and Kimball 1943; Ferguson 1975; Brower 1983). Other prior host records include mountain holly (*I. mucronata*) (Ferguson 1975, as *Nemopanthus mucronata*) and possumhaw (*I. decidua*) (Eiseman et al. 2020). In addition to further rearing records from all three plants, the present study adds inkberry (*I. glabra*) and yaupon (*I. vomitoria*) as confirmed hosts. The previous record of American holly (*I. opaca*) (Eiseman et al. 2020) was based on a specimen that is here included as a paratype of the new species *R. opacae*, and we have seen no evidence that true *R. finitimana* uses this host.

Prentice (1966) listed a single record of *R. finitimana* being reared from balsam poplar (Salicaceae: *Populus balsamifera* L.). That publication is a source of many highly suspect host records based on specimens that are difficult to locate, if they exist at all (J.-F. Landry and G.R. Pohl in litt. to CSE, May 2026), and we believe this record is based on a misidentified moth. Prentice characterized this species as a "Solitary leaf roller," with larvae collected in Ontario in early June. This is much earlier than any other records of *R. finitimana* larvae from Canada. We have reared the very similar tortricid *Gypsonoma substitutionis* Heinrich from balsam poplar in Vermont (CSE1366, USNM; Eiseman 2015), and we suspect Prentice's record refers to this species.

In addition to repeating Prentice's (1966) record, Robinson et al. (2002) listed three ericaceous plants as hosts for *R. finitimana*, all based on Ferguson (1975): bearberry (*Arctostaphylos uva-ursi* (L.) Spreng.), large cranberry (*Vaccinium macrocarpon* Aiton), and small cranberry (*V. oxycoccos* L.). The *Vaccinium* records were actually listed by Ferguson (1975) under *R. naevana*, directly below his entry for *Kundryia finitimana*, and what Ferguson's record stated was "cranberry (*Vaccinium oxycoccos* or *V. macrocarpon*)," so *V. oxycoccos* is not a confirmed host for *R. naevana* either. Ferguson (1975) did, in fact, list one specimen reared from *Arctostaphylos uva-ursi* under *K. finitimana*, but annotated with "doubtfully the same species." This specimen surely was actually

R. naevana, like the other Nova Scotia specimens he reported from the same host. It emerged in mid-July, again contrary to the phenology of *R. finitimana* in Canada.

Biology. Heinrich (1923) gave no details of the larval biology beyond "feeding on leaves of *Ilex verticillata*." Jones and Kimball (1943) reported, "Larvae abundant between webbed leaves of *Ilex verticillata*." Although Eiseman and Charney (2010) provided the first published description and illustration of the leaf mine (attributed to an undetermined *Rhopobota* sp.), which was further discussed by Eiseman (2014) and attributed to *R. dietziana*, and finally correctly attributed to *R. finitimana* by Eiseman et al. (2020), we now know that G.G. Lewis had reared *R. finitimana* from leaf mines decades earlier. This is documented by preserved mines at the CNC and by Lewis' unpublished manuscript, "Microlepidoptera recorded as leaf miners in America north of Mexico with notes on immature stages and illustrations of mines and cases" (copies at CNC and USNM). His entry under *Kundrya finitimana* reads, "The mine is a transparent blotch. The frass is ejected through a hole and is built into a pistol-shaped tube on the lower side of the leaf. The larva may make more than one mine; in some cases these become almost digitate. Later the larva leaves the mines and skeletonizes between two leaves." The frass tube is used as a retreat when the larva is not feeding. On deciduous hosts (Fig. 85–87), it is narrow and curved, up to about 4 mm long, and consistently adjacent to the leaf midrib. On yaupon (Fig. 88) the frass is instead deposited in a loose, amorphous mass, which may be well away from the midrib—as is the case for *R. dietziana glabricola* on inkberry. Lewis reared *R. finitimana* from inkberry, and we presume the mines of the two species on this host are indistinguishable. Older larvae (Fig. 89) may either feed between two leaves tied together, as noted by Lewis, or crumple a single leaf (Eiseman et al. 2020). On yaupon, we have often found the larva in between a newer leaf on which it is currently feeding and an older, brown, severed leaf on which it has fed previously. The cocoon may be spun between two leaves but is frequently within a folded section of a single leaf, made by cutting one or two small arcs (Fig. 90).

In the northern part of its range, *R. finitimana* appears to be univoltine, with pupae overwintering. Our examined material from Canada includes specimens collected as adults in early and late July; all reared specimens emerged after overwintering, with the recorded larval collection dates being in mid- to late August. The reared Nova Scotia specimens listed by Ferguson (1975) likewise all emerged after overwintering; collection dates were not recorded, but some larvae were preserved in mid-September. Whitebread et al. (2026) report records of adults in Massachusetts from 31 May to 31 July, and Gilligan et al. (2008) indicate a flight period of June and July in the Midwestern USA. We have not observed larval mines before mid-July in the northeastern USA. Larvae collected in New York and Connecticut in late August emerged as adults the following spring; Brower (1983) also reported larvae in late August in Maine, and his reared specimens at CUIC emerged in June. In Massachusetts, Jones and Kimball (1943) reported an adult collected on Nantucket in mid-July, and on Martha's Vineyard, "Larvae abundant between webbed leaves of *Ilex verticillata*; emergences, late July, Aug." If the latter refers to adult emergences, this is at odds with all other data from the Northeast.

In northern Illinois, Steffen (2024 and in litt.) collected small leaf mines on winterberry on 10 June. After these larvae failed to thrive, he returned to the same site on 14 July and found well-developed mines. Larvae from these mines began to exit and window-feed in late July, and adults emerged in late August and early September. Whether this indicates a partial second generation can occur in the Midwest is unclear, since the larval development period of any offspring from these adults would need to be greatly accelerated in order to be complete before the senescence of leaves in October and early November. Clearly there are at least two generations per year farther south: adults have been reared in early June from leaf mines collected in Oklahoma in late April, and from a pupa collected in Texas in late May. The specimens Heinrich (1923) reared from winterberry in Virginia in April were certainly overwintered, but he did not indicate the collection date. In North Carolina's piedmont region, one adult was collected in mid-April, and another was reared in mid-April from a larva found tying leaves of yaupon in late March; collections of leaf mines on possumhaw in late May and mid-June have produced adults in early and mid-July, and mines collected on this host in early and late July produced adults in early and mid-August. On North Carolina's coastal plain, larvae have been found feeding on the evergreen leaves of yaupon in mid-December. Although they were found in association with mines, at least some, and we suspect all, had transitioned to feeding externally by this time (Feldman 2020, 2025c, 2025d). Adults were reared from these in late

January and late March (those emerging earlier had been kept at room temperature from the time of collection; the rearing details were not recorded for the others, but they were likely kept in an outdoor shed over the winter).

The series of 17 specimens of the "*Bassus*" *annulipes* (Cresson) complex (Braconidae) that Eiseman (2014) reported rearing from *R. dietziana* in Massachusetts, emerging from mid-September to early October, were in fact parasitoids of leaf-mining larvae of *R. finitimana*. According to Sharkey and Chapman (2017), this complex represents an as yet undescribed genus of Mesocoelini, but for now it is best considered as belonging to the genus *Therophilus* Wesmael (M.J. Sharkey in litt., 5 June 2026). Adults of undetermined Eulophini (CSE9800 and CSE9821, CNC; Eiseman 2026a, b) emerged from both of our 2025 collections of yaupon leaves that later produced adults of *R. finitimana*, and although we were unable to determine their exact sources, we checked all the collected leaves and found no possible sources other than *Rhopobota* mines.

Distribution. Ontario to Prince Edward Island and Nova Scotia (Pohl et al. 2018), south to Texas and Georgia. Previous records from Alabama (Gilligan et al. 2008), Georgia (Scholtens 2014), South Carolina (Scholtens 2012), and Florida (Austin 2010) may refer to *R. opacae*, but leaf mines of *R. finitimana* have been found on possumhaw in Alabama (Kimmerling 2022a, b) and on yaupon in Georgia (Feldman 2024).

DNA barcoding. We sequenced two specimens reared from yaupon in North Carolina, and both matched BIN BOLD:AAB9898 (the CSE7290 male showed a 99.84% match to the most similar previous barcode, and the CSE9910 female showed a 99.69% match). This BIN includes all barcodes of *Rhopobota finitimana* from the USA (Oklahoma and Texas), as well as some from Canada (Quebec, Newfoundland, New Brunswick, Prince Edward Island, and Nova Scotia). Its nearest neighbor, differing by 2.85%, is BIN BOLD:AAB9899, which comprises 20 Canadian specimens likewise identified as *R. finitimana*: Ontario, Quebec, Nova Scotia, Prince Edward Island (Fig. 105). All specimens from the latter BIN were collected at lights or from Malaise traps. It would be of interest to examine their genitalia, and to determine the host plants and larval biology associated with this BIN, but for now we accept it as representing *R. finitimana*.

Notes. The genitalia of males and females reared from *Ilex decidua, I. glabra, I. verticillata*, and *I. vomitoria*, and of a female reared from *I. mucronata* (no male available), are all consistent with *R. finitimana* (Fig. 67–72, 77, 78, 80–82). One male reared from *I. vomitoria* has unusual genitalia, with curved spines arising from the valva apices instead of straight spines arising before the apices (Fig. 73), and we considered the possibility that it represents a distinct species. However, its DNA barcode matches BIN BOLD:AAB9898, and the dissected female from the same series has typical *R. finitimana* genitalia (Fig. 82). We have therefore concluded that this male represents an aberrant individual of *R. finitimana*.

Heinrich (1923) wrote of this species, "The pupa is quite characteristic with large, protruding orange yellow spiracles." The spiracles of most *R. finitimana* pupal exuviae we have photographed (Fig. 101) are indeed orange and much larger than those of *R. opacae* (Fig. 103, 104) and *R. dietziana* (Fig. 99, 100); those of the sequenced female from *Ilex vomitoria* are somewhat smaller and are brown (Fig. 102), but still larger than in the other species.

Rhopobota opacae Eiseman, new species

(Fig. 15, 16, 63, 64, 66, 74–76, 79, 83, 84, 91–98, 103, 104)

Rhopobota finitimana [misidentification]. Eiseman et al. 2020: 517 [specimen reared from *Ilex opaca*].

Diagnosis. This species is externally essentially indistinguishable from *R. finitimana*, although the known specimens all have the median interfascial area almost entirely white and cream (Fig. 15, 16, 63, 64) (frequently with extensive distal brown and gray in *R. finitimana*; Fig. 59–62), and the undersides of the wings are often paler. Males lack the hair pencil that is present on the hindwing of *R. finitimana* (Fig. 65), and instead have one on the medial surface of the hind tibia (Fig. 66); in most specimens this is difficult to observe unless the leg is removed. In the male genitalia of *R. opacae*, the neck and cucullus are largely covered by the marginal setae, and there are 2–3 spines on the cucullus that are much longer than the setae (Fig. 74–76), whereas in *R. finitimana* large areas of the neck and cucullus are not overlapped by the marginal setae, and there are only 1–2 spines on the cucullus that are much longer than the setae (Fig. 67–73). The clearest difference is in the female genitalia; the sterigma

of *R. opacae* appears posteriorly domed in ventral view (Fig. 83, 84), whereas that of *R. finitimana* appears flask-shaped, with a narrow, open posterior neck (Fig. 80–82).

Specimens examined. Holotype: **USA. NORTH CAROLINA:** Wake Co., Raleigh, Durant Nature Preserve, 31.iii.2025, em. 20.v.2025, T.S. Feldman, ex *Ilex opaca*, #CSE9498 (1♀, CUIC).

Paratypes: **USA. MARYLAND:** Queen Anne's Co., Kent Island, 38.985536, −76.327144, 2.ii.2025, em. 29.iv.2025, A. van den Beemt, ex *Ilex opaca*, #CSE9494 (1♂, genitalia slide CE-2025-39, CUIC); same but em. 4.v.2025, #CSE9495 (1♂, CUIC); **NEW JERSEY:** Cumberland Co., Stow Creek State Park, 39.443035, −75.405191, 15.ii.2025, em. 11.v.2025, J. Mollenhauer, ex *Ilex opaca*, #CSE9484 (1♂, CUIC); same but em. 13.v.2025, #CSE9487 (1♀, genitalia slide CE-2025-40, CUIC); same but em. 16.v.2025, #CSE9490 (1♀, CUIC); same but em. 27.v.2025, #CSE9503 (1♀, CUIC); Gloucester Co., Mantua Township, Ceres Park, 39.748072, −75.158351, 15.ii.2025, em. 1.vi.2025, J. Mollenhauer, ex *Ilex opaca*, #CSE9517 (1♂, CUIC); **NORTH CAROLINA:** Chatham Co., White Pines Nature Preserve, 24.iii.2024, em. ~19.v.2024, D. George, ex *Ilex opaca*, #CSE9207 (1♂, genitalia slide CE-2025-29, CUIC); Mecklenburg Co., 35.381189, −80.949797, 22.xii.2021, em. 9.v.2022, K. Kneidel, ex *Ilex opaca*, #CSE7412 (1♀, genitalia slide CE-2022-29, CUIC); Scotland Co., Laurinburg, St. Andrews University, 27.ii.2019, em. 13.v.2019, T.S. Feldman, ex *Ilex opaca*, #CSE5261 (1♂, genitalia in microvial pinned with specimen, CUIC 000058822); Wake Co., Raleigh, Durant Nature Preserve, 22.iv.2025, em. 15–23.v.2025, T.S. Feldman, ex *Ilex opaca*, #CSE9511 (1♂, 1♀, genitalia slide CE-2025-42, CUIC); **SOUTH CAROLINA:** Greenville, Congaree Preserve, 34.78002, −82.35335, 20.iii.2026, em. 8.v.2026, G. Merkert, ex *Ilex opaca*, #CSE10089 (1♀, CUIC); same but em. 10.v.2026, #CSE10087 (1♀, CUIC); same but em. 12.v.2026, #CSE10088 (1♂, CUIC); Paris Mountain State Park, Sassafras Trailhead, 34.931, −82.384, 28.ii.2026, em. 10–13.v.2026, G. Merkert, ex *Ilex opaca*, #CSE10084 (1♂ 1♀, CUIC); same but em. 12.v.2026, #CSE10081 (1♀, CUIC); same but em. 15.v.2026, #CSE10082 (1♂, CUIC); same but em. 16.v.2026, #CSE10080 (1♂, CUIC); same but em. 17.v.2026, #CSE10083 (1♀, CUIC).

Non-type material: **USA. GEORGIA:** Rabun Co., Clayton, L.E.S. [Lillian E. Smith] Center, 34.865, −83.389, 3–9.vi.2016, M. Baquero & K. Austin, pine-hardwood forest (1♂, MEM [photos examined]); **NORTH CAROLINA:** Madison Co., Mars Hill, 782 River Bend Drive, 26.xii.2021, em. from mines on or shortly before 15.i.2022, J. Petranka, ex *Ilex opaca* (3 larvae, JWB-DNA-23-112, JWB-DNA-23-113, JWB-DNA-23-114, USNM).

Adult description. Forewing length 3.8–5.5 mm; wingspan 8.5–12.5 mm.

Head: Labial palpus brown, reflecting blue/purple, outer surface mottled with or entirely black; 3rd segment and sometimes inner and dorsal surface of 2nd segment mottled with or entirely light gray. Upper frons and vertex uniformly brown, reflecting blue/purple, or with some black or rarely light gray mottling (one North Carolina specimen entirely black anterior to antennae, except for the light gray scales of the smooth lower frons, and mostly light gray dorsally/posteriorly; another North Carolina specimen with entire lower edge of upper frons light gray). Scape normally brown, sometimes partly or entirely black and light gray; pedicel and flagellomeres normally brown proximally and dark brown distally, sometimes with broad black central band or entirely black.

Thorax: Dorsally variably banded or mottled with brown, gray, black, creamy white, and silver. Forewing (Fig. 15, 16, 63, 64) with silvery-white, brown, and black strigulae on costa, obscure in basal patch; basal patch extending to 29–34% of total forewing length, the distal margin varying from rounded-convex to undulate or nearly straight, dark gray with black mottling, partly forming striae; interfascial area broad, a variable mix of white and cream, with variable, mostly indistinct, gray, black and dark spots and dorsal striae; the cream color tends to permeate the remainder of the wing, including between the brown and black spots of the median fascia (and with cream-tipped, or rarely pure white, scales within these spots), and surrounding the adjacent sinuous gray patch; the brown component of the median fascia may be nearly complete, or nearly obsolete, but the black portion is always limited to a few spots or scattered scales; a well-defined black spot at apex, surrounded by a brown spot, which is more or less contiguous with an oblique, cream- or white-speckled brown (rarely black) area that extends from several of the costal strigulae to (or nearly to) a narrow brown patch along middle of termen (sometimes the oblique brown area is only connected to the strigulae level with the medial black spot of the median fascia, and separated from the other strigulae by a narrow gray patch, which may be speckled with white); fringe generally darkening from pale gray at tornus to black at apex, more or less mottled with white or light gray along its length, always black adjacent to apical spot; underside of forewing dorsally whitish and otherwise light

to dark gray. Hindwing white to creamy white at base, distally darkening to gray, gray-brown, or pale brown; fringe gray with a more or less distinct dark band near base, sometimes dark gray or black at apex; underside of hindwing entirely whitish, or light to rarely dark gray except near costa. Legs partly white (hind legs mostly white except for dark banding on tarsi), partly brown mottled with black; male hind tibia with a light brown hair pencil arising from the base on the medial surface (Fig. 66).

Abdomen: Dorsally banded or mottled with silvery-white, silver, gray, brown, light brown, and black; ventrally pale brown mottled with black. Male genitalia (Fig. 74–76) as in *R. finitimana* except the neck and cucullus are largely covered by the marginal setae, and there are 2–3 spines on the cucullus that are much longer than the setae. Female genitalia (Fig. 79, 83, 84) with sterigma appearing posteriorly domed in ventral view; corpus bursae as in *R. finitimana*.

Etymology. The species epithet refers to the host plant, *Ilex opaca* Ait., and is borrowed from the name of another leaf-mining insect commonly found on this plant, *Phytomyza opacae* Kulp (Diptera: Agromyzidae).

Host. American holly (Aquifoliaceae: *Ilex opaca*). This plant occurs from Florida to Massachusetts, west to Texas, Oklahoma, Missouri, and Illinois (POWO 2026).

Biology. The yellowish larvae feed initially as leafminers, forming narrow, branching, full-depth tracks (Fig. 91–96). All of the frass is expelled through a hole in the lower epidermis next to the midrib, where it accumulates in a compact mass. This mass appears to be used as a retreat as in *R. finitimana*. It is unknown when oviposition and hatching take place, but larvae are in leaf mines at least from December to late March. Captive larvae kept at room temperature exit their mines within a few weeks. When the mined leaf is not overlapping another leaf, the larva (Fig. 98) begins window-feeding on the lower leaf surface adjacent to its abandoned mine, expanding the initial pile of expelled frass into a mat that is held together with silk and covers most of the feeding area (beneath which the larva is concealed) (Fig. 96). This occurs outdoors in North Carolina by 8 April (Russ 2025) and in New Jersey by 20 April (Mollenhauer 2025a). After beginning to feed externally, the larva may still use the mine as a retreat, and perhaps intermittently feed within it (Mollenhauer 2025b). One captive larva spun a small sheet of silk over the midrib on the upper surface of a leaf and began to window-feed beneath this, depositing frass around the margins and on the surface (Fig. 97). Most captive larvae tied two leaves together and window-fed on the concealed surfaces. Some established new, blotchy mines in conjunction with leaf tying (G. Merkert in litt., 14 March 2026). Pupation was typically between tied leaves. The earliest recorded adult emergence is 29 April, from a larva collected in Maryland on 2 February. All other adults have been reared in May, except for one that emerged on 1 June from a larva collected in New Jersey on 15 February. What this species does between June and December remains to be confirmed, but we suspect it is univoltine, with larvae developing slowly through the summer. The earliest date a fresh mine has been documented is 5 August, in South Carolina (Merkert 2026). We found a single occupied *Rhopobota* mine on American holly in North Carolina on 8 September 2025, and upon being brought indoors, the larva began feeding externally as a leaftier by 21 September. A week or so later it abandoned the leaves and died (Feldman 2025b).

Distribution. Specimens are known from New Jersey, Maryland, North Carolina, South Carolina, and Georgia. Leaf mines have also been found in Pennsylvania (Dennehy 2024), West Virginia (Frey 2021), Delaware (Brighton 2020), the District of Columbia (Pearson 2015), Kentucky (Raskin 2022), Virginia (Abugattas 2018), Tennessee (Carpenter 2017), Alabama (Kimmerling 2023), and Florida (Eiseman 2014, 2026c). The mines are commonly documented by iNaturalist contributors, and their absence northeast of southern New Jersey is conspicuous.

DNA barcoding. Sequences were obtained from three larvae collected in North Carolina and one adult reared in New Jersey. These closely match one another, but while the closest matches in BOLD to the North Carolina sequences are 95.06–95.09% similar to sequences of *R. finitimana* from Quebec (BOLD:AAB9898), the closest match to the New Jersey sequence is 94.75% to one of *R. naevana* from South Korea (BIN BOLD:AAA9812). The second closest match to the New Jersey sequence is 94.72% to one of *R. finitimana* from Newfoundland (BOLD:AAB9898). Our neighbor-joining tree (Fig. 105) includes the South Korean sequence but shows *R. opacae* clustering with *R. finitimana* and the European species *R. myrtillana* and *R. stagnana*, while *R. naevana* clusters with several species from Australia and Asia. Based on external appearance and genitalia, it is clear that *R. finitimana* is the closest relative of *R. opacae*.

Discussion

Rhopobota is one of two insect genera responsible for leaf mines on *Ilex* spp. in North America. As noted in the etymology sections, the names of *R. dietziana glabricola* and *R. opacae* refer, in addition to their host plants, to agromyzid flies that occur on the same plants. *Phytomyza glabricola* and *P. opacae* belong to the *P. ilicis* group, which comprises 13 closely related species (one as yet undescribed), each of whose hosts are restricted to one or several *Ilex* spp. (Kulp 1968; Lonsdale and Scheffer 2011; Scheffer et al. 2021). These agromyzids feed as leafminers throughout their development, pupating within the leaf, and their mines are confined to one leaf surface, with all frass deposited inside. *Phytomyza* mines are thus easily distinguished from *Rhopobota* mines, which are full-depth, have all of the frass expelled on the lower surface, and have larvae that ultimately abandon the mines to feed on leaves externally.

The first literature reference to lepidopteran mines on *Ilex* is this statement by Chambers (1878): "In Washington, D. C., in January, I have found empty mines of two species of *Tineina*, both of which are undescribed. They were found in leaves of different species of Holly. One mine is probably that of a *Lithocolletis* larva, of the flat group [i.e., *Cameraria* Chapman (Gracillariidae) or a close relative], in leaves of *I. opaca*. The other is probably that of a *Nepticula* [i.e., *Stigmella* Schrank or another nepticulid], and was in leaves of another species." Having examined thousands of examples of leaf mines on *Ilex* spp., including hundreds of iNaturalist observations from the Mid-Atlantic USA, we are confident that Chambers was referring to *Phytomyza* mines, with the species on *I. opaca* being *P. ilicicola* Loew (since it makes a blotchy mine like *Cameraria*); it would not be the first time he incorrectly assumed that mines were lepidopteran (Chambers 1872).

Bucculatrix ilecella Busck (Lepidoptera: Bucculatricidae) is so named because the type specimens were supposedly reared from an *Ilex* sp. collected in Victoria, Texas (Busck 1915). Braun (1963) stated that the host is deciduous. According to NRCS (2026), *I. vomitoria*, an evergreen species, is the only *Ilex* occurring in Victoria County. Statewide, four deciduous species are known, and based on their distributions as shown by NRCS (2026), only *I. decidua* could possibly be found in Victoria, which is well south and west of the mapped ranges of *I. ambigua* (Michx.) Torr., *I. longipes*, and *I. verticillata*. We have examined photographs of the leaf fragments pinned with a cotype of *B. illecella* at the USNM, and based on their texture, venation, and margins, it is evident that they do not represent these or any other *Ilex* species, and that the host plant was misidentified.

Based on our own rearings and those of G.G. Lewis, we are satisfied that all lepidopteran leaf mines on deciduous *Ilex* spp. are attributable to *Rhopobota finitimana*. On evergreen hosts, *R. finitimana* is so far the only leaf-mining moth to be reared from *I. vomitoria*. Mines on *I. glabra* may be the work of either *R. finitimana* or *R. dietziana glabricola*, although *R. finitimana* has not been confirmed south of Georgia, and it is unclear how far north of Florida *R. dietziana glabricola* may occur. Only *R. opacae* has been reared from leaf mines on *I. opaca*. Given the broad host range of *R. finitimana*, it seems possible that it could occasionally feed on *I. opaca*, but if it were to do so, occupied mines could be distinguished by phenology. Whereas larvae of *R. opacae* are present in mines from December to late March, *R. finitimana* mostly overwinters as pupae. On North Carolina's coastal plain, *R. finitimana* larvae overwinter as leaf-tying larvae, after exiting their mines. Also, the mines of *R. finitimana* are quite different in appearance from the long, narrow, branching mines of *R. opacae*; they are much more compact, being smaller, wider, and with only a few short branches/lobes if any.

Leaf-tying tortricid larvae on *Ilex* cannot be assumed to represent *Rhopobota*, unless they have emerged from leaf mines. Our collections of *I. vomitoria* in North Carolina yielded one adult of *Argyrotaenia velutinana* (Walker) (Wake Co., Raleigh, Durant Nature Preserve, 2.xii.2025, em. 16.ii.2026, #CSE9913, CSEC) and one of *Platynota rostrana* (Walker) (Carteret Co., Fort Macon State Park, 12.xii.2025, em. 8.ii.2026, #CSE9890, CSEC). Both of these were collected together with *R. finitimana*. There appear to be no prior rearing records of any Tortricidae from *I. vomitoria*. *Argyrotaenia velutinana* is highly polyphagous and has been reared previously from *I. decidua* (Brown and Allen 1974). Among the many hosts for *P. rostrana*, Heppner (2007) lists *I. cassine* L., *I. cornuta* Lindl. and Paxton, and *I. opaca*. Other North American Tortricidae recorded from *Ilex* spp. include *Archips fuscocupreanus* Walsingham, *Argyrotaenia franciscana* (Walsingham), *Cenopis daphnana* (McDunnough), *C. reticulatana* (Clemens), *Choristoneura rosaceana* (Harris), *Clepsis spectrana* (Treitschke), *Ditula angustiorana*

(Haworth), *Episimus tyrius* Heinrich, and *Larisa subsolana* Miller (Shropshire and Tallamy 2025; Brown et al. 2026).

Acknowledgments

We thank Julia Blyth for assistance in specimen preparation and curation, as well as in collecting leaf mines of *R. dietziana glabricola*. We are also grateful to Jim Petranka for providing information about the *R. opacae* larvae he collected, which were the catalyst for this study, and to John Brown and Alicia Timm for providing the DNA barcodes of those larvae. Adrienne van den Beemt, David George, Ken Kneidel, Grace Merkert, and Jeff Mollenhauer all provided additional material of *R. opacae*. Sara Rall brought to CSE's attention the feeding evidence of early instars of *R. dietziana* s. str., and Jim Steffen provided specimens and rearing details of *R. finitimana*. For the loan of specimens, and/or for providing dissections, images, and information about museum specimens, we thank John Brown (USNM), Richard Brown (MEM), Jason Dombroskie (CUIC), Loren Jones (CUIC), Jean-François Landry (CNC), Michael Sabourin (MSC), and Jack Whisenant (CUIC). We also thank Jim Vargo and the late Bo Sullivan for sharing images and for helpful discussion, Rob Edmunds and Rod Page for pointing us to relevant literature, and Jim Young (USNM) for providing images of the leaves associated with *Bucculatrix ilecella*. CSE thanks the Florida Division of Recreation and Parks (permit #02031310) for permission to collect at St. Sebastian River Preserve State Park, and Aton Forest, Inc. and the Aton Forest Fellowship trustees for supporting his research at Aton Forest. TSF thanks the City of Raleigh for access to Durant Nature Preserve and Horseshoe Farm Nature Preserve; Scotland Development, owners of the former site of St. Andrews University, for access to their property; David Bradley, the Durham County Open Space Program, and the North Carolina Biodiversity Project (NCBP) for access to New Hope Bottomlands; the NCBP, Randy Newman, and Ed Corey for access to Fort Macon State Park; the NCBP and the Triangle Land Conservancy for access to White Pines Nature Preserve; and Sara Marschhauser and the City of Durham for access to Leigh Farm Park. TSF's trips to Fort Macon were funded by a grant from the NCBP. Finally, we thank John W. Brown and Richard L. Brown for their reviews of the manuscript.

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Received July 5, 2026; accepted October 2, 2026.
Review editor David Plotkin.