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ZOOTAXA



Thirteen new species of Agromyzidae (Diptera) from the United States, with new host and distribution records for 32 additional species

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Table of Contents

Abstract	4
Introduction	4
Materials and methods	4
Results and discussion	5
Subfamily Agromyzinae	5
Agromyza aristata Malloch	5
Agromyza parca Spencer	6
Agromyza pseudoreptans Nowakowski	6
Agromyza reptans Fallén	7
Melanagromyza arnoglossi Eiseman & Lonsdale, spec. nov.	7
Melanagromyza gentianivora Eiseman & Lonsdale, spec. nov.	8
Melanagromyza hieracii Eiseman & Lonsdale, spec. nov.	9
	10
8 V-	11
3 · · · · · · · · · · · · · · · · · · ·	12
8 7	13
8 7- 1	15
8 V- 1	15
8 7- 1	15
8 7- 1	16
	16
	16
	17
Ophiomyia cf. frosti Spencer	
	18
Ophiomyia rugula Eiseman & Lonsdale, spec. nov. Subfamily Phytomyzinae	19
3 · 3 · 3 · C · 7	20
	20
	21
Cerodontha (Dizygomyza) morosa (Meigen)	21
Haplopeodes loprestii Eiseman & Lonsdale, spec. nov.	22
	22
	23
Liriomyza of cracentis Lonsdale	
Liriomyza ci. craceniis Lonsdaie Liriomyza eupatorii (Kaltenbach)	
	23
Updated key to the species of <i>Liriomyza</i> feeding on <i>Euphorbia</i> .	
Liriomyza hypopolymnia Eiseman & Lonsdale, spec. nov.	
Liriomyza nypopotymnia Eiseman & Lonsdane, spec. nov.	
Liriomyza taraxaci Hering	
Liriomyza taraxact Hernig Liriomyza trifolii (Burgess)	
Phytomyza cf. aesculi Eiseman & Lonsdale	
Phytomyza astotinensis Griffiths	
Phytomyza confusa Eiseman & Lonsdale	
Phytomyza doellingeriae Eiseman & Lonsdale	
Phytomyza flavicornis Fallén	
Phytomyza flavilonicera Eiseman & Lonsdale, spec. nov.	
Phytomyza flexuosa Spencer	
Phytomyza krygeri Hering	
Phytomyza notopleuralis Spencer	
Phytomyza palmeri Eiseman & Lonsdale	
Phytomyza solidaginophaga Sehgal	
Phytomyza thermarum (Griffiths)	
Phytomyza tiarellae Griffiths	
Phytomyza triostevena Eiseman & Lonsdale, spec. nov.	
Acknowledgments	
Literature cited	
Index of agromyzid genera and species	
Index of host plant genera	
- -	

Abstract

We present novel rearing records of Agromyzidae (Diptera) from throughout the United States. We describe leaf mines or other larval habits for 27 species, plus five others whose identification is tentative, and another five that are identified only to genus due to the absence of male specimens. We review host and distribution data for the known species, reporting 26 new host species records (including the first rearing records for *Phytomyza flexuosa* Spencer, *P. notopleuralis* Spencer, and (tentatively identified) *Ophiomyia frosti* Spencer) and 25 new state records (including the first USA records for *P. krygeri* Hering, *P. thermarum* (Griffiths), and (tentatively identified) *Liriomyza cracentis* Lonsdale). We also describe and provide natural history information for the following 13 new species: *Haplopeodes loprestii* Eiseman & Lonsdale, *Liriomyza euphorbivora* Eiseman & Lonsdale, *L. hypopolymnia* Eiseman & Lonsdale, *M. leanagromyza arnoglossi* Eiseman & Lonsdale, *M. gentianivora* Eiseman & Lonsdale, *M. hieracii* Eiseman & Lonsdale, *M. rudbeckiae* Eiseman & Lonsdale, *M. urticae* Eiseman & Lonsdale, *M. verbenivora* Eiseman & Lonsdale, *Ophiomyia nabali* Eiseman & Lonsdale, *O. rugula* Eiseman & Lonsdale, *Phytomyza flavilonicera* Eiseman & Lonsdale, and *P. triostevena* Eiseman & Lonsdale.

Key words: leafminer, plant-insect interactions, rearing

Introduction

This is the fourth in a series of papers presenting records of Agromyzidae reared in the United States by CSE and colleagues and examined by OL (Eiseman & Lonsdale 2018, 2019; Eiseman *et al.* 2019). Although host plants are unknown for hundreds of the 850+ species recorded from the USA and Canada, we continue to find new species at a substantially faster rate than the discovery of immature states of previously described species. Here we present the first rearing records for three species, new observations (including host and distribution records) for over 20 others, and descriptions of another 13 new species.

Materials and methods

Methodology for collecting, rearing, and photographing specimens was as described in Eiseman & Lonsdale (2018). For most stem-boring *Melanagromyza* species, there was no external evidence of larval feeding, and puparia were discovered by splitting open stems at random. Overwintering puparia were mostly stored in a refrigerator at 1–3 °C from 20 October 2017 to 1 April 2018, but refrigeration dates (if any) were not recorded for specimens collected by JvdL, MWP, and E. Stansbury.

All specimens (including holotypes and paratypes) were preserved in 95% ethanol and later critical point dried, glued to pins or paper points, and deposited in the Canadian National Collection of Insects, Arachnids & Nematodes (CNC). The prefix "#CSE" in the Material examined sections refers to collection events; alphanumeric codes with the prefix "CNC" are unique identifiers assigned to individual specimens. The first date listed for each collection event indicates when the larvae or puparia were collected, and "em." precedes the date(s) of adult emergence; "ex" before a plant name indicates that the specimens were reared from this plant and not merely collected on it as adults.

The abdomens of dissected males were prepared by maceration in hot lactic acid followed by washing in ethanol; these are stored in glycerin in genitalia vials pinned with the specimens. Terminology follows that in Lonsdale (2011), with updates to wing terminology as in Cumming & Wood (2017), including the following abbreviations: ori refers to the inclinate fronto-orbital setae; ors refers to the reclinate posterior fronto-orbital setae. The sizes of illustrated structures are shown in correct proportion to each other, with the epandrium reduced due to space constraints; some structures were not illustrated if they were damaged, could not be found (ejaculatory apodeme), or were uninformative for diagnosis within the genus. Holotypes are illustrated unless otherwise indicated. Due to the importance of male genitalic features in species-level diagnosis of agromyzids, several specimens listed below for which these structures were unavailable are only tentatively assigned to species, or are only identified to genus level groups; in these cases, specimens examined are listed under separate headings for species, or are treated as "sp. 1" or "sp. 2" under their respective genus group headings. Classification of *Phytomyza* follows Winkler *et al.* (2009).

An asterisk (*) before a country or state or a plant family, genus, or species name indicates a new distribution

or host record confirmed by rearing. Host records from outside North America (Benavent-Corai *et al.* 2005; Ellis 2020) are not included here, but were considered when determining whether our records were new. Square brackets ([]) enclosing host and distribution records indicate that they are based only on observations of leaf mines or rearing of tentatively identified females; these records are drawn either from the cited literature or from photographed leaf mines listed after the Material examined sections. These photographed mines all contained larvae or puparia unless otherwise indicated. Records annotated with "BG" followed by a number can be found online by adding that number to the end of this URL: https://bugguide.net/node/view/. For those annotated with "iNat", the number is added to the end of https://www.inaturalist.org/observations/.

Plant taxonomy generally follows POWO (2019), but we follow Roskov *et al.* (2019) (among others) in recognizing the genus *Fagonia* Tourn. ex L. and the families Hydrophyllaceae and Turneraceae.

Results and discussion

Subfamily Agromyzinae

Agromyza aristata Malloch (Fig. 59)

Material examined. NORTH CAROLINA: Scotland Co., Laurinburg, St. Andrews University, 18.iv.2017, em. ~17.iv.2018, T.S. Feldman, ex *Celtis laevigata*, #CSE4418, CNC1144090 (1 \updownarrow); 19.iv.2017, em. ~17.iv.2018, T.S. Feldman, ex *Celtis laevigata*, #CSE4417, CNC1135675 (1 \updownarrow); **OKLAHOMA**: Payne Co., Mehan, 36.013839°, -96.998103°, 7.v.2017, em. 24.iv.2018, M.W. Palmer, ex *Celtis occidentalis*, #CSE4435, CNC1135641 (1 \circlearrowleft).

Photographed mines. ALABAMA: Madison Co., Owens Cross Roads, 2.v.2020, kidneymoth, *Ulmus alata* [vacated mines], iNat 44595725; Redstone Arsenal, 18.iv.2020, kidneymoth, *Ulmus americana* [vacated mine], iNat 42532868; 19.v.2020, kidneymoth, *Ulmus rubra* [vacated mine], iNat 46547423; **COLORADO:** Boulder Co., Boulder, S 45th St., 14.vii.2019, J. Shorma, *Ulmus* [vacated mine], iNat 32754344; **CONNECTICUT:** Hartford Co., Windsor, 41.893658, -72.634136, 29.v.2020, M. Apgar, *Ulmus*, iNat 47765803; **GEORGIA:** Fulton Co., Atlanta, Simmons Lake, 2.v.2020, E. Summerbell, *Ulmus americana* [vacated mine], iNat 44678255; KANSAS: Brown Co., Horton, 25.v.2020, ksgardener1, *Ulmus* [vacated mine], iNat 47359824; MASSACHUSETTS: Franklin Co., Gill, Pisgah Mountain Rd., 29.iv.2012, C.S. Eiseman, *Ulmus*; **MARYLAND**: Baltimore City County, Herring Run Park, 6.v.2015, T. Wilson, Ulmus, BG 1067957; MICHIGAN: Marquette Co., Ives Lake, 20.vi.2019, C.S. Eiseman, Ulmus [vacated mine]; MINNESOTA: Scott Co., Prior Lake, Cleary Lake Regional Park, 44.690462, -93.391813, 16.vii.2019, A. Manning, *Ulmus rubra* [vacated mines], iNat 27098197; NEW JERSEY: Somerset Co., Warren Twp., 10.v.2011, S. Rall, Ulmus, BG 514546; NORTH CAROLINA: Durham Co., Durham, Stagecoach Road Eagle Spur Trail, 10.vii.2017, T.S. Feldman, *Ulmus alata* [vacated/predated mine], BG 1401462; Wake Co., Lake Crabtree County Park, 27.vi.2018, T.S. Feldman, *Ulmus alata* [vacated/predated mine], BG 1763158; **NORTH** DAKOTA: Burleigh Co., Bismarck, 804 N Third St., 20.vi.2020, megnd, Ulmus [vacated mines], iNat 50350205; TENNESSEE: Chester Co., Henderson, 27.iv.2015, K. Childs, *Ulmus* [mine with dead larva], BG 1179873; WIS-CONSIN: Dane Co., Cross Plains, 28.v.2011, I. Loser, Ulmus [aborted mine], BG 614335; TEXAS: Harris Co., Houston, Wedgehill Ln., 24.iv.2020, D. Johnson, Celtis pallida [vacated/aborted mine], iNat 43187133; Tarrant Co., Keller, 10.iv.2020, K. Sasan, Ulmus americana, iNat 42888081; Tarrant, 7.iv.2020, K. Sasan, Ulmus americana, iNat 41740783; NEW BRUNSWICK: Sunbury Co., Maugerville, 17.vi.2015, C. Adam, Ulmus [mine with dead larva], BG 1162296; QUÉBEC: Communauté-Urbaine-de-Québec, Neufchâtel Est-Lebourgneuf, 5.vi.2020, C. Grenier, *Ulmus* [vacated/aborted mine], iNat 48760929.

Hosts. *Cannabaceae: [*Celtis laevigata* Willd.], *C. occidentalis* L., [*C. pallida* Torr.]; Ulmaceae: [*Ulmus alata* Michx.], *U. americana* L., *U. rubra* Muhl. (Eiseman & Lonsdale 2018).

Leaf mine. (Fig. 59) On *Ulmus*, the mine is formed on the upper surface, usually beginning near the leaf margin; initially green and linear, later widening into a brown, elongate blotch. Frass is indistinct in the narrow, green portion, but later present in blackish particles that often form two rows, becoming more randomly scattered toward the end. Concentric feeding lines are evident in the blotch (Eiseman & Lonsdale 2018). Mines on *Celtis* (Fig. 59) are more often formed on the lower leaf surface, may begin well away from the leaf margin, and tend to remain essentially linear throughout their length, though sometimes contorted so that this is not obvious.

Puparium. Yellowish-brown to reddish-brown; formed outside the mine.

Phenology and voltinism. This species is univoltine, with larvae feeding in April and May; pupae overwinter. **Distribution.** USA: [AL, AR, CO, CT, FL, GA], IL, IN, IA, [KS, MA, MD, MI, MN, *NC, ND, NJ], NY, OH, OK, PA, [TN], VA, VT, [WI, TX]; Canada: AB, [NB], ON, [QC] (Eiseman & Lonsdale 2018).

Comments. *Liriomyza* adults were reportedly reared from the mines on *Ulmus americana* in Keller, TX that are cited above (Sasan 2020). The mines were collected on 10 April, puparia appeared on 13 April and were transferred to glass jars, and adults emerged on 21 April. Repetition of this rearing would be desirable; we suspect that a mixup of puparia with some from another rearing occurred, since the photographed mines are identical with those of *Agromyza aristata*.

Five closely related *Agromyza* species are now known to feed on *Celtis*. The entirely yellow legs easily distinguish *A. aristata* from the others—*A. fission* Eiseman & Lonsdale, *A. varifrons* Coquillett, the gall inducer *A. deserta* (Patton), and the European *A. trebinjensis* Strobl—which all have mostly dark legs (Strobl 1900; Spencer & Steyskal 1986; von Tschirnhaus 2017; Eiseman & Lonsdale 2018). Whereas in *A. fission*, *A. trebinjensis*, and *A. varifrons* the posterior spiracles of the larva each have three bulbs as is typical of the genus, those of *A. aristata* have 8–10, and those of *A. deserta* over 20.

Agromyza parca Spencer

Material examined. IOWA: Allamakee Co., Footbridge Farm, 22.vii.2018, em. by 14.viii.2018, J. van der Linden, ex Poaceae, #CSE4946, CNC1643675–1643677 (23); **NORTH CAROLINA:** Durham Co., Durham, 17-Acre Wood Preserve, 8.v.2017, em. 4.v.2018, T.S. Feldman, ex *Dichanthelium*, #CSE4482, CNC1135677–1135678 (13); Scotland Co., Laurinburg, St. Andrews University, 10.v.2017, em. 6–14.v.2018, T.S. Feldman, ex *Dichanthelium*, #CSE4502, CNC1144099–1144100 (13); Wake Co., Morrisville, Lake Crabtree County Park, 6.vi.2018, em. 25.vi.2018, T.S. Feldman, ex *Dichanthelium scoparium*, #CSE4695, CNC1135686 (13).

Tentatively identified material. NORTH CAROLINA: Scotland Co., Laurinburg, St. Andrews University, 3.v.2017, em. 6.v.2018, T.S. Feldman, ex *Dichanthelium*, #CSE4503, CNC1144101–1144102 (2°).

Hosts. Poaceae: *Dichanthelium clandestinum* (L.) Gould, *D. *scoparium* (Lam.) Gould, *Glyceria canadensis* (Michx.) Trin., *G. striata* (Lam.) Hitchc. (Eiseman & Lonsdale 2018).

Leaf mine. On *Dichanthelium*, eggs are inserted near the leaf margin, associated with a cluster of feeding punctures. The usually gregarious larvae initially mine along the margin toward the apex, then turn around and form a large, dirty whitish upper surface blotch with generally distributed, liquidy, greenish to brown frass. Concentric feeding lines are present in some mines. Mines on *Glyceria* may be on the lower leaf surface and the photographed examples do not have associated feeding punctures.

Puparium. Yellowish-brown to reddish-brown; formed outside the mine.

Phenology and voltinism. In Massachusetts, larvae feeding from late June to mid-July emerge as adults from mid-July to early August; larvae collected in mid-August yielded some adults in early September, with some females emerging the following spring (Eiseman & Lonsdale 2018). In Iowa, a larva found feeding in late July emerged as an adult about three weeks later. In North Carolina, larvae collected in early May did not emerge as adults until the following spring, whereas a larva collected in early June yielded an adult later that month.

Distribution. USA: *IA, MA, NC, TN.

Agromyza pseudoreptans Nowakowski

Material examined. MASSACHUSETTS: Franklin Co., Northfield, 276 Old Wendell Rd., 26.x-1.xi.2017, em. 2-8.v.2018, C.S. Eiseman, ex *Urtica dioica*, #CSE4463, CNC1135695–1135702 (3359).

Photographed mines. IOWA: Linn Co., Cedar Rapids/ICNC, 6.xi.2011, J. Zito, *Urtica dioica* [vacated mine], BG 592789; **MARYLAND:** Harford Co., Susquehanna State Park, 28.v.2018, J. Emm, *Urtica dioica*, BG 1527598.

Host. Urticaceae: Urtica dioica L.

Leaf mine. A dark greenish linear-blotch, turning brown; following the leaf margin for several serrations and

then expanding away from it. The egg is often laid near the leaf margin but may be laid along a lateral vein away from the margin, in which case the initial linear portion meanders until reaching the margin. Frass is deposited in numerous irregular, dark lumps.

Puparium. Brown; formed outside the mine.

Phenology and voltinism. This species is bivoltine, with a summer pupal diapause and an exceptionally late-feeding fall generation. A photograph taken in Maryland shows an occupied mine on 28 May. A larva collected in Vermont in late June emerged as an adult in mid-October (Eiseman & Lonsdale 2018). Larvae of our new reared series were active in Massachusetts from late October into early November, and in Washington we found larvae feeding as late as 3 December 2018.

Distribution. USA: AK, CA, [IA], ID, *MA, [MD], MN, OR, VT, WA; Canada: AB, BC, MB, NT, ON, QC; Europe; Georgia, Kazakhstan; Russian Far East (Nartshuk & von Tschirnhaus 2017; Eiseman & Lonsdale 2018).

Agromyza reptans Fallén

Material examined. MASSACHUSETTS: Franklin Co., Northfield, 276 Old Wendell Rd., 22.x.2017, em. 30.iv.2018, C.S. Eiseman, ex *Urtica dioica*, #CSE4459, CNC1144082 (1♀).

Host. Urticaceae: Urtica dioica L.

Leaf mine. Blackish, with paler greenish-brown patches only in the newest portions where the larvae are actively feeding; initially narrow and following the leaf margin, later expanding to a broad blotch. Frass is partly diffuse and partly in irregular lumps.

Puparium. Reddish-brown; formed outside the mine.

Phenology and voltinism. This species has at least two generations per year; it has not been observed to have a summer pupal diapause as observed in *A. pseudoreptans*, but there is evidently some variation in length of the pupal stage. Spencer (1969) listed a specimen emerging on 14 August from a larva collected on 5 June in Ontario, whereas Eiseman & Lonsdale (2018) listed specimens emerging on 21 July from larvae collected on 28 June in New York. The larvae from which our Massachusetts specimen was reared were found on 22 October, a few days before larvae of *A. pseudoreptans* appeared several meters away.

Distribution. USA: CA, *MA, NY, WA; Canada: ON, QC, SK; Europe; Kazakhstan; Turkmenistan (Nartshuk & von Tschirnhaus 2017; Eiseman & Lonsdale 2018).

Melanagromyza arnoglossi Eiseman & Lonsdale, spec. nov.

(Figs. 1-4, 60, 87-92)

Holotype. USA. IOWA: Winneshiek Co., Chattahoochie Park, 6.xi.2017, em. spring 2018, J. van der Linden, ex *Arnoglossum*, #CSE4643, CNC1144035 (1♂).

Etymology. The specific epithet refers to the host plant genus, *Arnoglossum* Raf.

Host. Asteraceae: Arnoglossum Raf.

Larval biology. (Fig. 60) The larva forms a narrow linear gallery (not externally visible) in the thin layer of pith lining the inside of the hollow stem.

Puparium. (Fig. 4) Straw-colored; formed within the stem, at the end of the larval gallery.

Phenology and voltinism. Pupae overwinter; further details unknown.

Distribution. USA: IA.

Adult description. Wing length approximately 2.8 mm (\circlearrowleft). Female unknown. Length of ultimate section of vein M_4 divided by penultimate section: 0.7. Eye height divided by gena height: 4.0. First flagellomere small, rounded. Orbital plate and dorsal half of parafacial strongly projecting and broadly rounded. Ocellar triangle ill-defined apically where it takes on texture of more rugose vitta, but it likely ends short of lunule. Lunule with medial groove, extending almost to level of second fronto-orbital. Gena somewhat straight with slight upwards curve on anterior half. Cheek wide, not well-defined. Clypeus narrowly rounded anteriorly. Eye and head longest above midpoint. Thorax subshining. Specimen in relatively poor condition, with body partially collapsed, and aristae, fore tarsi, right mid leg and most setae missing.

Chaetotaxy: Fronto-orbital setae mostly broken or missing; five setae evident from sockets or remaining bases of setae, possibly becoming shorter and more slender anteriorly, evenly spaced with anterior seta slightly displaced forward. Orbital setulae in several scattered rows; short, appearing erect and lateroclinate. Postvertical seta subequal to ocellar seta. Eye with relatively narrow patch of hairs dorsomedially that are longer than orbital setulae. Most thoracic setae missing dorsally, including dorsocentrals, but two large sockets evident. Acrostichal setulae in ten irregular rows. Katepisternum with two additional subdominant setae. Mid tibia with one posteromedial seta.

Coloration: (Figs. 1–3) Setae dark brown. Color dark brown, including halter; gena and anteroventral region of parafacial paler brown; abdomen and thorax green metallic, with color less evident on thorax below notum; wing veins brown. Calypter margin and hairs yellow.

Genitalia: (Figs. 87–92) Epandrium with small anteroventral spine. Surstylus fused to anteroventral margin of epandrium, wide and shallow, with two irregular rows of tubercle-like setae along inner surface. Cercus large, well-developed. Hypandrium subtriangular, broad basally with thick arms, with narrow tapered apex; inner lobe split, sinuate. Phallophorus cylindrical, base narrow, venter bulging. Basiphallus U-shaped, adjacent to phallophorus, dorsal surface long; distance between it and distiphallus+mesophallus as long as phallophorus. Mesophallus small, cylindrical, fused to ventromedial surface of distiphallus; base of mesophallus and distiphallus level. Distiphallus with one pair of tubules flanking mesophallus; long dorsomedial process enclosed ventrally by narrow plate; dorsal chamber relatively shallow, flat, with one pair of spinulose pads on inner surface; subovate in ventral view, length twice width. Ejaculatory apodeme with narrow base and stem; blade large, pale and ovate with sclerotized medial rib; stem with globose lateral process; sperm pump with transverse sclerotized bar curved up at ends and with long faint tubule emerging from end opposite duct.

Comments. This is the first rearing record of any agromyzid from *Arnoglossum*. The host was a hollow-stemmed woodland species; in Iowa we have also found stems of the prairie species *A. plantagineum* Raf. with the solid pith riddled with galleries of an unknown *Melanagromyza* species (the empty puparia were similarly straw-colored). In Wisconsin, Klein (2013) photographed what appears to be a vacated *Liriomyza* mine (with frass in alternating strips) on the lower surface of a leaf of *A. atriplicifolium* (L.) H.Rob.

This dark metallic green species has a frons that strongly projects above the eye, a modestly well-developed ocellar triangle and five fronto-orbitals. This list of features will key it to *Melanagromyza cirsiophila* in Spencer & Steyskal (1986), which is known on *Cirsium* and *Carduus* (Asteraceae) in California and Costa Rica (Shi & Gaimari 2015). The distiphallus of *M. cirsiophila* differs, however, in being adjacent to the basiphallus, and it is much longer with a broad base and medial constriction. The species *M. angelicae* (Frost), known from *Angelica* (Apiaceae) in New York and Ohio, has an additional sixth fronto-orbital and is otherwise quite similar externally. The phallus is also similar, but the length of the distiphallus is equal to the length between it and the basiphallus (not the phallophorus), the distiphallus does not have a pronounced tubule emerging anterodorsally, the dorsal chamber of the distiphallus is highest apically (not basally), and the basiphallus is narrower. Illustrations in Steyskal (1980b) also show the surstylus to be more pronounced and the distiphallus (ventral view) to be shorter compared to its width and more sharply pointed.

Melanagromyza gentianivora Eiseman & Lonsdale, spec. nov. (Figs. 5–8, 93–98)

Holotype. USA. IOWA: Winneshiek Co., Upper Iowa River Wildlife Management Area, 29.xi.2017, em. spring 2018, J. van der Linden, ex *Gentiana andrewsii*, #CSE4647, CNC1144037 (1♂).

Paratypes. IOWA: Winneshiek Co., i.2018, em. spring 2018, J. van der Linden, ex *Gentiana andrewsii*, #CSE4666, CNC1144033 (1\operation is same collection as holotype, CNC1144037 (1\operation is WISCONSIN: Grant Co., Thomas Wet. Prairie, A.H. Williams, stems of *Gentiana andrewsii*, T7N R1W Sect. 7, [host stem] stripped of inflorescences and leaves, put in sterile containers over sterile soil and netted with hosiery on 30.ix.1997, outdoors until 2.iii.1998, when tightly caged in lab, em. 12–14.iii.1998, CNC934513–934524 (3\operation 7\operation, WIRC; 1\operation 1\operation, CNC).

Etymology. The specific epithet refers to the host plant genus, *Gentiana* Tourn. ex L.

Host. Gentianaceae: Gentiana andrewsii Griseb.

Larval biology. The larva bores in the pith of the stem.

Puparium. (Fig. 8) Pale brown, formed within the stem. Most puparia were found in the upper half or upper third of the stem.

Phenology and voltinism. Pupae overwinter, with adults emerging within two weeks of exposure to warm temperatures in spring.

Distribution. USA: IA, WI.

Adult description. Wing length 2.6 mm (\circlearrowleft), 2.8–3.0 mm (\circlearrowleft). Length of ultimate section of vein M₄ divided by penultimate section: 0.7–0.9. Eye height divided by gena height: 4.6–5.7. First flagellomere small, rounded. Orbital plate and parafacial relatively pronounced, continuing as strong cheek under eye. Lunule high, extending to level of posterior ori, with shallow medial groove. Ocellar triangle reaching level of anterior ors. Facial ridge present, with broad sloping sides. Venter of gena relatively straight to modestly angled behind middle. Clypeus rounded with anterior margin somewhat straighter. Head longest above midpoint. Thorax subshining.

Chaetotaxy: Three ori (sometimes two on one side), two or three ors (sometimes two on one side and three on the other), with ori and ors sometimes difficult to differentiate due to gradual change in orientation; setae long and overlapping, subequal to ocellar and postvertical setae, almost evenly spaced. Eye hairs subequal to orbital setulae in male, relatively dense dorsomedially; female eye hairs very short and inconspicuous, slightly denser dorsomedially, nearly extending to eye midpoint. Orbital setulae relatively short, in two to three scattered rows, orientation lateroclinate or reclinate to slightly erect. Two strong dorsocentral setae, second slightly more than $\frac{2}{3}$ length of first. Acrostichal setulae in ten rows. Two strong katepisternal setae. Mid tibia with two posteromedial setae (three in one male).

Coloration: (Figs. 5–7) Setae dark brown. Color dark brown, including halter; abdomen with metallic green shine that is also present but less evident on thorax, and faintly visible on legs; wing veins brown. Calypter margin and hairs yellow.

Genitalia: (Figs. 93–98) Epandrium with small distoventral spine. Surstylus shallow, wide and slightly rounded, fused to anteroventral margin of epandrium, with cluster of tubercle-like setae along distal margin. Hypandrium very broad and rounded basally, contrasting long apical apodeme; inner lobe arched, setose. Phallophorus narrow with base constricted, venter strongly bulging. Basiphallus U-shaped with base almost straight; slightly overlapping mesophallus. Mesophallus cylindrical, slightly curved, ventromedially fused to distiphallus; base slightly exceeding that of distiphallus. Distiphallus with basal third consisting of paired tubules flanking mesophallus; remainder very narrow in ventral view, with one pair of dark swollen pads past mesophallus followed by one pair of lateral wingshaped, internally spinulose extensions beneath a long, narrow distal process; laterally compressed dorsal chamber evident in lateral view. Ejaculatory apodeme large, dark, well-developed; base narrow, stem with lateromedial process; sperm pump with dark transverse bar upcurved at ends.

Comments. The only previous record of a North American agromyzid from *Gentiana* refers to this species; the specimens of an undetermined *Melanagromyza* that Williams (1999) reared from overwintering stems of *Gentiana* andrewsii in Wisconsin are included here as paratypes. The only other Agromyzinae species known from the host family Gentianaceae is *Ophiomyia akbari* (Singh & Ipe), a leafminer of *Enicostema verticillatum* (L.) Engl. in India (Singh & Ipe 1971).

Melanagromyza gentianivora is a relatively large, greenish species with a slightly projecting orbit (less so than the strongly pronounced state seen in M. arnoglossi). Depending on how pronounced the orbit is interpreted to be, this species will key either to M. cirsiophila Spencer or M. longensis Spencer in Spencer & Steyskal (1986), but the first species has the gena deepest medially (not posteriorly), and the second has a shallower orbit, fewer rows of acrostical setulae and a shining ocellar triangle and orbital plate. Both of these other species also have only two ors and an unmistakably different phallus. The unusual distiphallus of M. gentianivora sets it far apart from all congeners, and its closest relative cannot be confidently guessed at present.

Melanagromyza hieracii Eiseman & Lonsdale, spec. nov. (Figs. 9–12, 61, 99–104)

Holotype. USA. IOWA: Allamakee Co., Fish Farm Mounds WMA, 30.ix.2017, em. spring 2018, J. van der Linden, ex *Hieracium scabrum*, #CSE4669, CNC1144040 (1♂).

Etymology. The specific epithet refers to the host plant genus, *Hieracium* L.

Host. Asteraceae: Hieracium scabrum Michx.

Larval biology. (Fig. 61) The larva bores in the pith of the stem, forming a linear gallery.

Puparium. (Fig. 12) Straw-colored, formed at the end of the larval gallery; rear spiracular horns pronounced, blackish, curved and pointed.

Phenology and voltinism. The holotype emerged after overwintering from a puparium collected on 30 September. All other puparia found at that time in stems of *H. scabrum* were already empty. Assuming these represented the same species, this suggests either that *Melanagromyza hieracii* has more than one generation or that adults may be capable of overwintering.

Distribution. USA: IA.

Adult description. Wing length 2.7 mm (\circlearrowleft). Female unknown. Length of ultimate section of vein M_4 divided by penultimate section: 0.7. Eye height divided by gena height: 4.5. First flagellomere small, rounded. Ocellar triangle largely obscured by detritus, appearing to reach past posterior ori. Anterior half of gena slightly angled upwards. Cheek not evident. Clypeus rounded. Eye and head longest above midpoint. Thorax subshining. Body in relatively poor condition; partially collapsed, some setae missing.

Chaetotaxy: Four gracile ori strongly incurved (nearly flat on frons), two strong ors; setae long. Several rows of scattered orbital setulae, as long as eye hairs, erect (inner setulae) to reclinate (outer). Ocellar setae possibly missing, bases obscured. Eye hairs sparse and scattered on dorsal half with dense dorsomedial patch. Anterior of two dorsocentral setae missing, sockets large. Acrostichal setulae in ten irregular rows. Katepisternum with one additional subdominant seta. Mid tibia with two posteromedial setae.

Coloration: (Figs. 9–11) Setae dark brown. Body dark brown, including halter; notum faintly green metallic; abdomen green metallic with blue tint; wing veins brown. Calypter margin and hairs yellow.

Genitalia: (Figs. 99–104) Epandrium with posteroventral spine. Surstylus fused to anteroventral margin of epandrium, relatively narrow and produced with slight posterodistal extension; distal margin with irregular rows of tubercle-like setae. Cercus large and well-developed. Hypandrium broadly rounded basally, with long narrow apical apodeme; inner lobe U-shaped with minute setulae. Phallophorus swollen ventrally, base much narrowed. Basiphallus U-shaped (right side irregularly sclerotized in dissected male), with short gap between apex and mesophallus. Mesophallus swollen cylindrical, narrowest at point of insertion to distiphallus, which is relatively posterobasal. Distiphallus short, globular, with short ventromedial swelling into which mesophallus inserts; basal section mostly made up of posteriorly convergent tubules flanking mesophallus; ventral plate subquadrate, distal margin slightly flared laterally; dorsal chamber shifted distally, widest subapically, with one pair of minutely spinulose internal pads; tubular process narrow, distal half exposed, sinuate when viewed laterally. Ejaculatory apodeme with short dark stem with long lateromedial process; blade narrow with medial rib, margin along one side narrow and irregular (broken?), other side wider and rounded with margin clear; sperm pump with dark transverse bar upcurved at ends.

Comments. This is the first record of a North American *Melanagromyza* from *Hieracium*. The European *M. oligophaga* Spencer includes *H. umbellatum* L. among its hosts (Spencer 1990).

Externally, *Melanagromyza hieracii* is not unlike many other congeners with a metallic green shine (weak on the thorax and with a blue tint on the abdomen), a white calypter, two dorsocentrals and a shallow orbital plate. The key in Spencer & Steyskal (1986) will bring the species to *M. longensis* Spencer / *M. virginiensis* Spencer, but unlike these species, it has four ori. The phallus is unlike those of these two species in that the dorsal chamber of the distiphallus is parallel-sided, the lateral margins of the distiphallus are very strongly flared apically, the medial tubule is pronounced and long, far exceeding the apex of the short dorsal chamber, and the mesophallus is strongly shifted basally on the distiphallus. The combination of these phallic features, especially the flared distolateral margins of the distiphallus and the basally shifted mesophallus, is quite unusual for the genus.

Also see comments for Melanagromyza urticae.

Melanagromyza minimoides Spencer

(Figs. 62-63)

Material examined. IOWA: Winneshiek Co., Decorah, Will Baker Park, 10–13.viii.2017, em. by 16.viii.2017, J. van der Linden, ex *Rudbeckia laciniata*, #CSE4945, CNC1643663–1643667 (2♂3♀).

Hosts. Asteraceae: Borrichia frutescens (L.) DC., Helenium flexuosum Raf., Helianthus annuus L., Heliopsis

helianthoides Sweet, Melanthera nivea (L.) Small, Rudbeckia laciniata L., Symphyotrichum simmondsii (Small) G.L.Nesom, Verbesina encelioides (Cav.) Benth. & Hook.f. ex A.Gray, V. virginica L.; Cucurbitaceae: Cucurbita foetidissima Kunth; Urticaceae: Urtica dioica L., U. gracilis subsp. holosericea (Nutt.) W.A.Weber (Spencer & Stegmaier 1973; Steyskal 1980b; Spencer & Steyskal 1986; Shi & Gaimari 2015).

Larval biology. (Figs. 62–63) On asteraceous hosts, larvae have been consistently reported as feeding in the seedhead. We noted individual disc florets of *Rudbeckia laciniata* turning brown before the other disc or ray florets had begun to wilt, and opening the affected florets revealed feeding damage to the developing achenes as well as excavations in the receptable.

Puparium. (Fig. 63) Whitish-yellow, with black, strongly chitinized posterior spiracular processes, appreciably projecting beyond anal segment (Spencer & Stegmaier 1973); formed in the seedhead.

Phenology and voltinism. This species is evidently multivoltine. The Iowa specimens emerged in mid-August, a few days after the puparia were collected. Adults have been reared in Ohio in mid-September (Spencer & Stegmaier 1973), and in Maryland Steyskal (1980b) reported an adult emerging in December (indoors) from host material collected in November. Emergence dates of Florida specimens (reared under unknown conditions) include every month from November to March (Spencer & Stegmaier 1973), and in southern California and Texas adults have been collected in May, with a reared specimen emerging on 1 July (Shi & Gaimari 2015).

Distribution. USA: AR, CA, FL, *IA, MD, OH, TX; Mexico; Caribbean; South America (Shi & Gaimari 2015).

Comments. Details are lacking for all of the purported rearing records of this species from non-asteraceous hosts. Steyskal (1980b) indicated that a single male (as *Melanagromyza radicicola* Steyskal) had "emerged indoors from [a] root presumed to be of nettle, *Urtica dioica* L." collected in Maryland. According to Spencer (1990), this specimen was found dead in a rearing container and "[n]o puparium from which it might have emerged could be located. Earlier, specimens of *M. minimoides* had been reared in the same container from *Heliopsis* and *Rudbeckia*." He thus concluded that the *Urtica* record was erroneous. Shi & Gaimari (2015) stated that *M. minimoides* has been reared from *U. dioica* subsp. *holosericea* in California, although this is not reflected in their listed label data. Their record from *Cucurbita foetidissima* is based on a single male labeled "ex. *Cucurbita foetidissima* (host plant), 1.VII.1963"; there is no indication of the larval feeding site or whether a puparium was found.

Melanagromyza rudbeckiae Eiseman & Lonsdale, spec. nov.

(Figs. 13–15, 105–110)

Holotype. USA. IOWA: Winneshiek Co., Meadow Farm, 20.viii.2017, em. ?, J. van der Linden, ex *Rudbeckia laciniata*, #CSE4664, CNC1135655 (1♂).

Paratypes. USA. WISCONSIN: Grant Co., Thomas Wet. Prairie, 23.ix.1997, A.H. Williams, stems of *Rudbeckia lacinata*, T7N R1W Sect. 7, [host stem] stripped of leaves and inflorescences, put into sterile containers over sterile soil and netted w/hosiery, outdoors until 2.iii.1998 when tightly caged in lab, em. 15–24.iv.1998, CNC934510–934512 (2Å, WIRC; 1Å, CNC).

Etymology. The specific epithet refers to the host plant genus, Rudbeckia L.

Host. Asteraceae: Rudbeckia laciniata L.

Larval biology. Internal stem borer.

Puparium. Formed within the stem.

Phenology and voltinism. Pupae overwinter, with adults emerging after six to eight weeks of exposure to warm temperatures in spring. The holotype was reared from a larva or pupa collected in mid-August, but unfortunately its emergence date was not recorded.

Distribution. USA: IA, WI.

Adult description. Wing length approximately 2.3-2.5 mm (\circlearrowleft). Female unknown. Length of ultimate section of vein M_4 divided by penultimate section: 0.7-0.8. Eye height divided by gena height: 3.6-4.8. First flagellomere small, rounded. Orbital plate slightly projecting. Gena horizontal on posterior half, angled upwards on anterior half. Face with very shallow ridge. Clypeus rounded. Head distinctly higher than long, not as developed anteriorly as in most congeners; many fibers trapped under setae on head, obscuring much of frons. Thorax subshining. Right foreleg and left hindleg missing.

Chaetotaxy: Three ori (anterior seta nearly flat on frons), two ors. Orbital setulae in several rows, mostly erect to proclinate on outer row, mostly reclinate on inner. Eye setose dorsomedially, relatively dense in paratypes, sparse in holotype. Postvertical seta slightly longer than ocellar. Two strong dorsocentral setae. Acrostichal setulae in eight rows. One smaller additional seta on katepisternum. Mid tibia with two posteromedial setae, only one on left leg of holotype.

Coloration: (Figs. 13–15) Setae dark brown. Color dark brown, including halter; slight metallic green shine on dorsum of thorax that is also evident and slightly more pronounced on abdomen. Calypter margin and hairs yellow.

Genitalia: (Figs. 105–110) Epandrium with minute posteroventral spine. Surstylus shallow, wide, curved, fused to anteroventral surface of epandrium; inner distal margin with scattered tubercle-like setulae. Cercus large, well-developed. Hypandrium relatively wide, sides slightly converging apically to narrower apical apodeme; inner lobe Y-shaped with sockets on anterior process. Phallophorus with base abruptly constricted, short and with sides flared; swollen distoventrally. Basiphallus U-shaped, long dorsally, pointed at ends; distant from basiphallus+mesophallus, with intervening gap nearly as long as phallophorus. Mesophallus short, cylindrical, tapering to ventromedial point of fusion on distiphallus; base slightly exceeding that of distiphallus. Distiphallus relatively short compared to congeners, subovate in ventral view with length twice width; one pair of ventrolateral tubules flanking mesophallus; dark, thick ventromedial plate greatly swollen immediately past mesophallus; dorsal chamber small, short, widest apically with margin flared laterally, internally with one pair of spinulose pads; tubular process arising from dorsal chamber short and straight. Ejaculatory apodeme with narrow, pale blade with medial rib, short stem with long lateromedial process, and long weak tube arising from base on side opposite duct; sperm pump with wide basal sclerotization, including transverse bar that is upcurved at ends.

Comments. Another Nearctic species, *Melanagromyza minimoides* Spencer, has been reared from *Rudbeckia laciniata*, but the larvae feed in the seedhead rather than boring in the stem (Spencer & Steyskal 1986; this paper), and the calypter hairs are dark brown, not yellow. *Melanagromyza rudbeckiae* is the undetermined species Williams (1999) reported rearing from overwintering stems of *R. laciniata* in Wisconsin, and his specimens are included here as paratypes.

Melanagromyza rudbeckiae is a relatively small, faintly greenish species with a characteristic phallus that has the distiphallus and basiphallus widely separated, the mesophallus base slightly exceeds that of the distiphallus, and the distiphallus is relatively short with the medial tubule well exposed apically, the venter is thickly sclerotized, and in ventral view the outline is narrowly egg-shaped with the sides slightly flared distolaterally. Unlike similar Melanagromyza identifiable from couplet 36 in Spencer & Steyskal (1986), M. rudbeckiae has a relatively long space between the basiphallus and the distiphallus. Melanagromyza longensis is slightly larger (wing length 2.6 mm) but otherwise externally similar (including three ori), but the distiphallus is approximate to the basiphallus. Other similar but slightly larger Nearctic species are either bluish in color (M. hicksi Steyskal) or have a projecting frons (M. angelicae).

Melanagromyza urticae Eiseman & Lonsdale, spec. nov.

(Figs. 16-19, 111-116)

Holotype. USA. IOWA: Winneshiek Co., Will Baker Park & Roslien Woods, 7.i.2018 & 1.ii.2018, em. spring 2018, J. van der Linden, ex *Urtica dioica*, #CSE4661, CNC1144052 (1♂).

Paratypes: same data as holotype, CNC1144049–1144051, CNC1144053 (4°)

Etymology. The specific epithet refers to the host plant genus, *Urtica* L.

Host. Urticaceae: *Urtica dioica* L. **Larval biology.** Internal stem borer.

Puparium. (Fig. 19) Straw-colored; formed within the stem.

Phenology and voltinism. Pupae overwinter, with adults emerging in spring.

Distribution. USA: IA.

Adult description. Wing length 2.4 mm (\circlearrowleft), 2.5–2.6 mm (\circlearrowleft). Length of ultimate section of vein M₄ divided by penultimate section: 0.6–0.7. Eye height divided by gena height: 2.7–3.1. First flagellomere rounded. Orbital plate (seen laterally) projecting, continuing as ring under eye and ending at point behind midpoint of eye. Eye and head

(seen laterally) longest at dorsal ½. Ocellar triangle ending at posterior ori, nearly meeting high lunule. Gena angled upwards on anterior half. Clypeus rounded. Thorax subshining. Specimens in fair to poor condition, females with light to thick coating of white powdery to crustose foreign substance.

Chaetotaxy: Two ori, three ors; setae long, incurved and overlapping, orientation of ori and ors not strongly dissimilar; setae somewhat evenly spaced with ors sometimes more tightly clustered; posterior ori reduced on left side in one female. Eye with hairs dorsomedially (more numerous in male) that are sparse and difficult to observe in most angles; shorter than orbital setulae. Orbital setulae in few scattered rows; erect to mostly proclinate medially, lateroclinate laterally. Approximately 10 irregular rows of acrostichal setulae. Two strong dorsocentrals. Katepisternum with two strong dorsocentral setae. Mid tibia with two posteromedial setae in male, and one or two setae in female.

Coloration: (Figs. 16–18) Setae dark brown. Color dark brown, including halter; faint metallic green shine on notum, and strong metallic green shine on abdomen that may be blue or golden tinted; wing veins brown. Calypter margin and hairs yellow.

Genitalia: (Figs. 111–116) Epandrium with small posteroventral spine. Surstylus relatively narrow and rounded, fused to anteroventral margin of epandrium, with irregular rows of tubercle-like setae on distal margin. Cercus large and well-developed. Epandrium long and narrow, with very long, narrow apical apodeme; inner lobe small and U-shaped with several sockets. Phallophorus relatively small, base wide and short. Basiphallus U-shaped with ends slightly convergent, with short gap between apex and mesophallus. Mesophallus bulging basally, tapered apically; fused ventrobasally (not ventromedially) to distiphallus. Distiphallus with one pair of ventrolateral tubules flanking base of mesophallus; relatively short, distal half dominated by long, thick medial tubule enclosed ventrally and laterally by lightly sclerotized and laterally flared membrane; distiphallus with narrow ventromedial plates followed by short, shallow row of subspherical bulges; dorsal chamber simple, slightly constricted subapically, mostly filled by medial tubule, with one pair of shallowly tuberculate dorsal pads on inner surface. Ejaculatory apodeme large, well-developed, with long sinuate medial rib, spade-shaped blade with clear margins, mediolateral process on stem, and long narrow clear tubule emerging from base on side opposite from duct; sperm pump sclerotized basally, including dark transverse bar with ends upcurved.

Comments. This is the fifth *Melanagromyza* species to be reared from *Urtica* stems, and the third in North America. *Melanagromyza aenea* (Meigen) is known from Europe; *M. urticivora* Spencer from Pakistan; *M. urticella* Spencer from California; and *M. martini* Spencer is widespread in Canada, and recently discovered in California and Iowa (Spencer 1990; Eiseman & Lonsdale 2019). As discussed above, *M. minimoides*, which normally feeds in seedheads of Asteraceae, has twice been reported from *Urtica*, purportedly feeding in the roots in one instance and with no details recorded in the other.

Melanagromyza urticae keys with some difficulty to M. vectabilis Spencer / M. verbesinae Spencer in Spencer & Steyskal (1986), but the phallus cleanly differentiates it from all congeners: the mesophallus is inserted almost basally on the distiphallus (not ventromedially), the distiphallus is short and flared laterally on the distal margin, and the tubular process emerging from the dorsal chamber is quite long compared to the remainder of the segment.

Also described in this paper is *Melanagromyza hieracii*, which is similar in that the distiphallus is flared apically and has a long tubular process, but in this species, the distiphallus is stouter, it has a broad ventral plate that is much flatter and without the complex series of medial swellings, the ventrolateral tubules are pronounced and loop far away from the remainder of the segment, the mesophallus is inserted ventromedially on the distiphallus on an unusual swelling, and the tubular process is more sinuate and much narrower. Additionally, the orbital plate is not projecting, there are four ori and two ors (not two ori and three ors), the male eye is densely pilose dorsally and the surstylus is longer.

Melanagromyza verbenivora Eiseman & Lonsdale, spec. nov.

(Figs. 20–23, 66–67, 117–121)

Holotype. USA. IOWA: Winneshiek Co., Beard Farm, 12.vii.2017, em. summer 2017, J. van der Linden, ex *Verbena stricta*, #CSE4648, CNC1144043 (1♂).

Paratypes. IOWA: same data as holotype, #CSE4649, CNC1135656 (1♀); same data as holotype, em. 14.vii.2017, #CSE4653, CNC1144047 (1♂ [illustrated]); Winneshiek Co., Beard Farm, vi–vii.2017, em. summer

2017, J. van der Linden, ex *Verbena stricta*, #CSE4657, CNC1144042 (1 $\stackrel{\frown}{}$); Decorah, Trout Run Trail, 43°18'5.04''N 91°48'6.60''W, 12–22.vii.2017, em. late vii—early viii.2017, J. van der Linden, ex *Verbena stricta*, #CSE4942, CNC1643670–1643672 (1 $\stackrel{\frown}{}$ 2 $\stackrel{\frown}{}$).

Etymology. The specific epithet refers to the host plant genus, *Verbena* L.

Host. Verbenaceae: Verbena stricta Vent.

Larval biology. (Figs. 66–67) Some larvae bore in the stem, forming a spiral gallery that is partly visible externally. This causes some stunting of the growing shoot and wilting of the terminal portion (Fig. 66). Others bore in the rachis of more developed shoots, resulting in a somewhat thickened seedhead with a shriveled, blackened tip (Fig. 67). The interior of the stem or rachis is filled with granular frass.

Puparium. (Fig. 23) Whitish; formed within the larval feeding site.

Phenology and voltinism. Larvae feed in early summer, with adults emerging beginning in mid-July. Later generations have not been observed.

Distribution. USA: IA.

Adult description. Wing length 2.4–2.6 mm (\circlearrowleft), 2.7–2.9 mm (\circlearrowleft). Length of ultimate section of vein M₄ divided by penultimate section: 0.7. Eye height divided by gena height: 4.8–5.3. First flagellomere small, rounded. Lunule extending to level of middle ori. Ocellar triangle slightly shinier than vitta, extending to level of middle or posterior ori. Facial carina shallow, sharp. Gena shallowly upcurved anteriorly. Cheek narrow, only evident on anterior half. Clypeus rounded. Head (seen laterally) longest at midpoint. Eye tapering to a point posterodorsally. Thorax subshining.

Chaetotaxy: Three ori, two ors; spacing subequal with anterior ori sometimes slightly distant; setae becoming slightly more slender and short anteriorly. Ocellar and postvertical setae subequal to posterior ori. Eye sparsely short setose on dorsal half; female with hairs slightly denser dorsally, male with longer, denser patch of hairs dorsomedially. Orbital setulae in several scattered rows; erect to slightly reclinate. Two strong dorsocentral setae. Acrostichal setulae in ten irregular rows. Katepisternum with two additional smaller, closely spaced setae dorsomedially. Mid tibia with two posteromedial setae.

Coloration: (Figs. 20–22) Setae dark brown. Body dark brown, including halter; thorax and abdomen metallic green with blue tint that is stronger on abdomen; blue color dominant in one female. Calypter margin and hairs yellow.

Genitalia: (Figs. 117–121) Epandrium with small posteroventral spine. Surstylus fused to anteroventral margin of epandrium, very short and wide with 1–3 irregular rows of tubercle-like setae along inner surface. Cercus large, well-developed. Hypandrium subtriangular with apex slightly narrowed; inner lobe U-shaped and irregular with several sockets. Phallophorus (damaged in dissected male) tapering basally, venter bulging. Basiphallus U-shaped, nearly reaching mesophallus. Mesophallus cylindrical, slightly curved, narrowed to ventromedial point of fusion on distiphallus; base of mesophallus and distiphallus level. Distiphallus pear-shaped in ventral view, with narrow ventromedial plate swollen immediately past mesophallus; ventrolateral tubules narrow, largely hidden behind mesophallus along midline; dorsal chamber widest dorsally, broadly opened apically, with one pair of thick spinulose dorsal pads on inner surface; tubular inner process relatively wide, not far exceeding ventral plate. Ejaculatory apodeme not found.

Comments. The only previous record of a North American *Melanagromyza* from *Verbena* was that of an unemerged male of an apparently undescribed species that was said to be entirely black, extracted from a stem of *V. scabra* Vahl in Florida (Spencer & Stegmaier 1973). It was noted that "The posterior spiracles of the puparium each bear ten bulbs, without a central horn; the two processes are separated by twice their own diameter." Unfortunately no puparia of *M. verbenivora* have been preserved for comparison. *Melanagromyza verbenae* Spencer was described from adults caught on *V. litoralis* Kunth in Chile, and due to the general similarity of the male genitalia with those of the Florida specimen, Spencer (1982) considered it certain that this plant was the larval host and presumed that the Chilean species is likewise an internal stem borer. Spencer (1990) referred to the two species as "related or possibly identical".

Using Spencer & Steyskal (1986), some specimens of *Melanagromyza verbenivora* key to *M. longensis*, which also has three ori and a similar phallus, but in that species, the arista appears bare (not minutely pubescent), there are about eight rows of acrostichal setulae, the basiphallus nearly forms a complete ring, and the dorsal chamber of the distiphallus is more rounded dorsally (not flat) and constricted apically (not broadly open). Other specimens will key to *M. verbesinae*, but in this species there are two ori, the ocellar triangle does not reach the posterior ori, and the

distiphallus is widest apically. The gena is slightly angled forward as in *M. buccalis* Spencer, but not as prominent; *M. buccalis* is slightly smaller (wing length 1.9–2.5mm), there are two to four ori (widely spaced if only two), there are only eight rows of acrostichal setulae and the phallus is narrower.

Melanagromyza sp. 1

Material examined. IOWA: Winneshiek Co., Lake Meyer Park, 28.xi.2017, em. spring 2018, J. van der Linden, ex *Cryptotaenia canadensis*, #CSE4651, CNC1135658 (1 \bigcirc).

Host. Apiaceae: Cryptotaenia canadensis (L.) DC.

Larval biology. Internal stem borer. **Puparium.** Formed within the stem.

Phenology and voltinism. Pupae overwinter, with adults emerging in spring.

Distribution. USA: IA.

Comments. The only previous record of an agromyzid from this host is a leaf mine of an unidentified *Phytomyza* species collected in Montreal, QC, listed by Spencer (1969), who did not describe the mine in any way. The only dipteran leafminer that has been reared from *Cryptotaenia* is *Euleia fratria* (Loew) (Tephritidae), and it does not seem impossible that its mine could have been mistaken for that of a *Phytomyza*.

Melanagromyza sp. 2

Material examined. OKLAHOMA: Payne Co., Mehan, 36.013839°, -96.998103°, 12.vii.2017, em. ~10.iv.2018, M.W. Palmer, ex *Lactuca canadensis*, #CSE4452, CNC1135642 (1♀).

Host. Asteraceae: Lactuca canadensis L.

Larval biology. Probably an internal stem borer (see Comments).

Puparium. Formed within the stem.

Phenology and voltinism. This species is evidently univoltine, given that the adult emerged in spring from a stem collected the previous July.

Comments. The only previous record of a *Melanagromyza* from *Lactuca* is that of several *M. splendida* Frick paratypes from Hawaii, listed as "reared from larvae mining lettuce leaves" (Frick 1953)—which should not be construed as representing true leafmining since as far as is known *M. splendida* feeds as a borer in the stem or in the midrib of large leaves (Spencer 1973). Unlike *M. splendida*, the Oklahoma female has closely spaced fronto-orbitals (the anterior pair is not anteriorly displaced) and the wing is approximately 3.2 mm (not 1.9–2.6 mm). The female emerged from a bulk sample of mined stems, with the mines terminating in conspicuous gall-like "scabs" of stem tissue and dried latex, inside which the puparia were formed. We are reasonably sure that these external symptoms were in fact caused by an undetermined *Ophiomyia* species, and we presume that the *Melanagromyza* larva fed and pupated in the pith of a stem.

Melanagromyza sp. 3

Material examined. IOWA: Winneshiek Co., Decorah, Twin Springs Park, 31.i–1.ii.2017, em. by ix.2017, J. van der Linden, ex *Prenanthes alba*, #CSE4660, CNC1144026–1144027 (2°); 10.ix.2017, em. spring 2018, J. van der Linden, ex *Prenanthes alba*, #CSE4662, CNC1135654 (1°).

Host. Asteraceae: Nabalus albus (L.) Hook.

Larval biology. Internal stem borer. Lower in the stem, where it is hollow, larvae feed as described above for *Melanagromyza arnoglossi*.

Puparium. Straw-colored; formed within the larval feeding site.

Phenology and voltinism. Pupae overwinter, with adults emerging in spring or perhaps summer.

Comments. This is the first record of any *Melanagromyza* from *Nabalus* (nor is any known from *Prenanthes* L., the European genus from which *Nabalus* was recently separated).

Melanagromyza sp. 4

Material examined. IOWA: Winneshiek Co., Upper Iowa River Wildlife Management Area, 8.ii.2018, em. spring 2018, J. van der Linden, ex *Xanthium strumarium*, #CSE4665, CNC1144063 (1 \bigcirc).

Host. Asteraceae: *Xanthium strumarium* L.

Larval biology. Internal stem borer.

Puparium. Formed within the stem.

Phenology and voltinism. Pupae overwinter, with adults emerging in spring.

Comments. This unidentifiable female belongs to the *Melanagromyza virens* group. Spencer (1973) listed *Xanthium* among the known hosts of *M. splendida*, and this was repeated by Shi & Gaimari (2015), but the origin of this record is unclear and it does not appear in Spencer's later works. The only other record we have found of a *Melanagromyza* from *Xanthium* is that of an undetermined species Hilgendorf & Goeden (1983) reported as common in stems of *X. strumarium* in southern California.

Ophiomyia abutilivora Spencer

(Figs. 64–65)

Material examined. IOWA: Winneshiek Co., Decorah, Trout Run Trail, vii.2017, em. by 26.vii.2017, J. van der Linden, ex *Abutilon theophrasti*, #CSE4940, CNC1643668–1643669 (1♂ 1♀).

Hosts. Malvaceae: *Abutilon theophrasti* Medik.; adults have been collected on flowers of *Sida cordifolia* L. (Spencer & Steyskal 1986).

Larval mine. (Figs. 64–65) The larva mines up and down the stem, forming an irregular, gall-like "welt" and associated scarring.

Puparium. Whitish to yellowish; formed within the stem, with the anterior spiracles projecting through the epidermis.

Phenology and voltinism. The only reared specimens in the type series are from Mississippi with a date of 22 October; whether this was the collection or emergence date was not stated, but either way they would seem to represent a different generation from our Iowa specimens, which emerged from green stems in late July. Adults have been collected in August and September in Minnesota, and in March in Florida (Spencer & Steyskal 1986).

Distribution. USA: FL, *IA, [IL], MN, MS, [WI] (Spencer & Steyskal 1986).

Ophiomyia carolinensis Spencer

(Fig. 68)

Material examined. NORTH CAROLINA: Durham Co., Durham, Leigh Farm Park, 4.v.2018, em. 25.v.2018, T.S. Feldman, ex *Symphyotrichum patens*, #CSE4558, CNC1144104 (1♀); 10.v.2018, em. 25.v.2018, T.S. Feldman, ex *Symphyotrichum patens*, #CSE4563, CNC1144103 (1♂).

Hosts. Asteraceae: *Symphyotrichum *patens* (Aiton) G.L.Nesom. We have seen similar leaf mines on *S. cordifolium* (L.) G.L.Nesom, *S. georgianum* (Alexander) G.L.Nesom, *S. laeve* (L.) Á.Löve & D.Löve, *S. lateriflorum* (L.) Á.Löve & D.Löve, *S. novae-angliae* (L.) G.L.Nesom, and *S. novi-belgii* (L.) G.L.Nesom.

Leaf mine. (Fig. 68) Mostly greenish and interparenchymal, with portions sometimes becoming discolored reddish or brownish; initially long, narrow, and linear, later becoming an elongate, poorly defined blotch running along both sides of the midrib. The linear portion is sometimes only intermittently visible on the upper surface.

Puparium. Whitish; formed within the leaf, with the anterior spiracles projecting through the lower epidermis. On *Symphyotrichum patens*, each puparium was found at the tip of one of the basal leaf lobes, which in one instance was 6 cm away from the apparent end of the mine.

Phenology and voltinism. Our North Carolina specimens were collected as larvae in early May, with adults emerging later that month. In New York, larvae are present in June and July (Scheffer & Lonsdale 2018).

Distribution. USA: NC, NY (Scheffer & Lonsdale 2018). We have seen similar leaf mines in GA, IA, MA, MD, NH, NJ, VT, and ON.

Comments. The only previous host record for this species is that of "possibly *Symphyotrichum* sp." from Scheffer & Lonsdale (2018); the host genus is now confirmed.

Ophiomyia cf. chondrillae Spencer

Material examined. IOWA: Allamakee Co., 5.ix.2017, em. spring 2018, J. van der Linden, ex *Lactuca*, #CSE4671, CNC1135659–1135660 ($1 \stackrel{\wedge}{\bigcirc} 1 \stackrel{\vee}{\bigcirc}$).

Hosts. Asteraceae: Chondrilla juncea L. (Spencer & Steyskal 1986), *Lactuca L.

Larval mine. An externally visible stem mine.

Puparium. Details not recorded by either Spencer & Steyskal (1986) or us, but we believe the puparium was not covered by a "scab" as described in the Comments under *Melanagromyza* sp. 2.

Phenology and voltinism. The holotype of *O. chondrillae*, from Washington, is labeled with a date of 11 July; whether this was the collection or emergence date was not stated, but there are evidently at least two generations since our Iowa specimens emerged in spring from stems collected in early September.

Distribution. USA: *IA, WA (Spencer & Steyskal 1986).

Comments. Ophiomyia chondrillae was described from a single specimen in poor condition (Spencer & Steyskal 1986), which we have not examined, but our specimens key readily to this species in Spencer & Steyskal (1986). The morphology of the flies reared from *Lactuca* seems to fit this species, and we suspect that slight differences in genitalic morphology compared to the original illustrations are due to error or a difference in the angle in which the phallus was illustrated. Given this, and the fact that the host is in the same tribe (Cichorieae) as that of the holotype, we choose to regard them as conspecific until we can examine specimens reared from *Chondrilla*.

Ophiomyia cf. frosti Spencer (Fig. 69)

Material examined. OKLAHOMA: Payne Co., Meham, 36.014339° N, -96.996744° W, 16− 21.iii.2018, em. 29.iii.2018, M.W. Palmer, ex *Lactuca*, #CSE4412, CNC1135643 (1♀); 23.iii.2018, em. 8.iv.2018, #CSE4413, CNC1135644−1135646 (3♂); 1.iv.2018, em. 8.iv.2018, #CSE4414, CNC1144112−1144113 (2♀); 4.iv.2018, em. 15.iv.2018, #CSE4453, CNC1135650 (1♂).

Host. *Asteraceae: Lactuca L.

Leaf mine. (Fig. 69) Whitish, upper-surface (nearly full-depth), extending along the midrib from the base of the petiole to the blade, where irregular lobes or branches extend to either side (these may be partially green and interparenchymal); ~5 cm long in total. Frass is deposited densely along the midrib.

Puparium. Black, formed within a leaf (not necessarily the one with the conspicuous mine), on the lower surface near the base of the petiole, with the anterior spiracles projecting through the lower epidermis.

Phenology and voltinism. In Oklahoma, larvae and puparia (some already empty) have been found beginning in mid-March, with adults emerging from late March to mid-April. The holotype of *O. frosti* was collected in New York on 16 May (Spencer & Steyskal 1986).

Distribution. USA: NY (Spencer & Steyskal 1986), *OK.

Comments. Ophiomyia frosti was described from a single caught adult. Spencer & Steyskal (1986) noted that it closely resembles O. pulicaria (Meigen), known from western Canada and common in Europe, where it feeds on various genera of Cichorieae including Lactuca, forming midrib-based mines that are apparently indistinguishable from those from which our Oklahoma specimens were reared.

The new specimens differ from the type in usually having two ori (not three), but there is sometimes one on one side, and one male has three on one side. The specimens are slightly larger, with a wing length of 2.8–3.0 mm (not 2.3 mm); the male genitalia appear to match those of the holotype (Spencer & Steyskal 1986: Figs. 187, 188). *Ophiomyia pulicaria* differs in being smaller (wing length 1.9–2.2 mm), and in having a very broad and apically flattened distiphallus and an H-shaped basiphallus (ventral view—see Spencer (1976: Fig. 97)).

Ophiomyia nabali Eiseman & Lonsdale, spec. nov.

(Figs. 24–28, 122–126)

Holotype. USA. IOWA: Winneshiek Co., Decorah, Twin Springs Park, 24.viii.2017, em. ?, J. van der Linden, ex *Prenanthes alba*, #CSE4667, CNC1135652 (1♂).

Paratype. IOWA: Winneshiek Co., Decorah, Twin Springs Park, 19.x.2017, em. spring 2018, J. van der Linden, ex *Prenanthes alba*, #CSE4641, CNC1144031 (13).

Other material examined. IOWA: Winneshiek Co., Decorah, Twin Springs Park, 10&13.ix.2017, em. spring 2018, J. van der Linden, ex *Prenanthes alba*, #CSE4668, CNC1144030 (1 empty puparium), same data as paratype, #CSE4641, CNC1144032 (1 partial puparium).

Etymology. The specific epithet refers to the host plant genus, *Nabalus* Cass.

Host. Asteraceae: Nabalus albus (L.) Hook.

Larval biology. The larva mines in the stem (CSE4641) or bores in the petiole (CSE4667, CSE4668). In the latter case, slight discoloration is evident externally, and in one instance (which first alerted us to this species' existence), the petiole was partially severed and scabbed over. One petiole gallery was observed to begin as a narrow mine extending ~2.5 cm into the leaf midrib. After opening the petiole to inspect this larva, it was successfully transferred to the midrib of a dandelion leaf (*Taraxacum officinale* F.H.Wigg.), where it fed for over a week before perishing. At one point its linear mine wandered into the leaf blade and then back into the midrib, but this species has otherwise been observed only to feed in the midrib, petiole, and stem of *Nabalus*.

Puparium. (Figs. 27–28) Black; formed just beneath the petiole or stem epidermis, through which the anterior spiracles protrude.

Phenology and voltinism. Larvae have been found beginning in late August. Pupae overwinter, with adults emerging in spring.

Distribution. USA: IA.

Adult description. Female unknown, wings of male not expanded; specimens died soon after emergence and are undeveloped, with one in poor condition; one specimen represented by partial puparium in preserved host stem; costa presumably extending to M_1 , wing length likely to be approximately 2.3–2.7 mm based on body size. Eye height divided by gena height: 5.3. First flagellomere small, rounded. Ocellar triangle reaching level of posterior ori. Face with pronounced ridge with medial bulb; bulb narrow, with very thin medial groove that continues onto lunule where it is bordered by shallow ridges. Gena produced, forming nearly 60° angle; apex narrower and slightly pronounced. Cheek developed. Clypeus very narrow and apically truncated with arms bowed. Thorax subshining.

Chaetotaxy: Two ori, two ors. Fasciculus developed, strongly upcurved on apical ½ where hairs separate and appear frayed. Ocellar and postvertical setae subequal to ors. Two strong dorsocentral setae. Approximately ten rows of acrostichal setulae. Mid tibia with one small posteromedial seta.

Coloration: (Figs. 24–26) Setae dark brown. Body dark brown, including halter. Calypter margin and hairs dark brown.

Genitalia: (Figs. 122–126) Surstylus short, rounded, fused to distoventral margin of epandrium, with several irregular rows of tubercle-like setae on inner-distal surface. Hypandrium with long, laterally bulging arms; distal region subtriangular with pointed apex; inner lobe twisted, U-shaped with several sockets. Phallophorus narrow with swollen venter and strongly constricted base. Basiphallus mostly consisting of strong right-lateral band that reaches level of distiphallus; very short, weak, ill-defined left lateral band present; base truncated along margin of phallophorus. Mesophallus small, cylindrical, fused to ventromedial surface of distiphallus. Distal half of distiphallus relatively long and well-sclerotized with lateral texturing, narrowing apically to broadly rounded apex that is slightly upcurved; with thick ventral ridge along midline; with slightly swollen medial chamber at level of mesophallus that extends posterodorsally and is flared behind dorsal opening; widest at base, which is mostly clear except for scattering of minute sclerotized patches that concentrate ventrally. Ejaculatory apodeme not found.

Comments. We have found similar *Ophiomyia* mines and puparia in stems and peduncles of *Nabalus trifoliolatus* Cass. in MA, NH, and NY, possibly representing *O. nabali*. The only other *Ophiomyia* known from *Nabalus* is *O. congregata* (Malloch), which has a fringe of peristomal hairs in the male and no fasciculus. Whereas *O. nabali* feeds exclusively in the stem, petiole, and leaf midrib, overwintering as a black puparium, *O. congregata* feeds partly as a leafminer, overwintering as an immature larva in the crown of the plant and forming a whitish puparium in the spring (Eiseman & Lonsdale 2018).

The unfortunate state of preservation of known specimens of *Ophiomyia nabali* prevents the confident use of existing keys for identification, but the genal angle (60°), presumed wing length and groove along the facial keel key the holotype to *O. lacertosa* Spencer using Spencer & Steyskal (1986). The strongly bent fasciculus and unusual phallic morphology would eliminate this as a possibility, as they exclude the possibility of including the type in any other known species. The mesophallus is somewhat small and inserted far forward on the distiphallus, but it is the distiphallus itself that is most characteristic.

Ophiomyia rugula Eiseman & Lonsdale, spec. nov.

(Figs. 29–31, 70–72, 127–132)

Holotype. USA. NORTH CAROLINA: Durham Co., Durham, Leigh Farm Park, 29.iv.2018, em. 17.v.2018, T.S. Feldman, ex *Baccharis halimifolia*, #CSE4553, CNC1135680 (1♂).

Paratype. Same data as holotype, CNC1135681 (13); Wake Co., Morrisville, Lake Crabtree County Park, 12.vii.2018, em. 13.vii.2018, T.S. Feldman, ex *Baccharis halimifolia*, #CSE4951, CNC934530 (13).

Etymology. The specific epithet (L. *rugula*—a small wrinkle) refers to the appearance of the larval feeding site as a small wrinkle in the leaf.

Host. Asteraceae: Baccharis halimifolia L.

Leaf mine. (Figs. 70–72) Mostly green and interparenchymal, consisting of a short, narrow wrinkle along the midrib. In some examples the mine is confined to the basal portion of the midrib, and in others the basal portion appears to have been mined but the mine is only conspicuously wide or wrinkled at or somewhat beyond the middle of the leaf.

Puparium. (Fig. 72) White; centered on the midrib in the distal end of the mine.

Phenology and voltinism. This species is evidently at least bivoltine, with larvae feeding in April emerging as adults in mid-May, and with adults of another generation emerging in mid-July.

Distribution. USA: NC.

Adult description. Wing length 2.3–2.4 mm (\circlearrowleft). Female unknown. Length of ultimate section of vein M₄ divided by penultimate section: 0.8. Eye height divided by gena height: 6.2–6.5. First flagellomere subcircular with slightly longer hairs on anterodorsal margin. Orbital plate very narrow. Ocellar triangle slightly shinier, ending near level of anterior ors. Face with shallow, rounded ridge. Gena rounded anteriorly, only slightly extending past anterior margin of eye; neither pointed nor projecting. Lunule somewhat semicircular with wide medial groove. Palpus narrowed basally. Clypeus with narrow, truncated apical margin with sharp corners. Thorax subshining.

Chaetotaxy: One ori, three ors; anterior ors slightly shorter than other fronto-orbitals; paired setae not equally positioned on both sides. Single row of orbital setulae. Ocellar and postvertical setae subequal to posterior ors. Two strong dorsocentral setae. Eight rows of acrostichal setulae. Katepisternum with several enlarged dorsal setae, including one nearly as long as dominant seta. Mid tibia with two posteromedial setae.

Coloration: (Figs. 29–31) Setae dark brown. Body dark brown with halter stem light brown with dark patches. Calypter margin and hairs dark brown.

Genitalia: (Figs. 127–132) Surstylus broad, rounded, fused to epandrium, with short, pointed tubercle-like setae along inner-distal margin. Cercus large, well-developed. Hypandrium stout medially; inner lobe V-shaped, nearly smooth. Phallophorus cylindrical, weakly connected dorsally to basiphallus; phallus past phallophorus angled ventrally. Basiphallus with short, wide, thin dorsal sclerite, laterally produced into one pair of long sinuate ventral bands and one pair of more dorsally positioned pockets. Mesophallus lightly sclerotized, straight, resembling slightly thickened terminal section of ejaculatory duct. Distiphallus band-like, dorsoventrally compressed, slightly wider than mesophallus (both weakly differentiated in ventral view), which is inserted medially on ventral surface. Additional small U-shaped sclerite suspended in membrane ventral to apex of mesophallus of uncertain homology.

Comments. Ophiomyia rugula is clearly related to O. similata (Malloch) based on genitalic structure, and is indistinguishable from it externally, although O. similata has one or two mid tibial setae and most of the type series has smaller fronto-orbitals that are less than half the width of the frons (not slightly more). The genitalia of O. similata differ in lacking the ventrolateral bands of the basiphallus, the distiphallus is wider and higher, and the suspended ventrodistal sclerite of uncertain origin is thicker and more distally positioned.

The immature stages of *Ophiomyia similata* are unknown, but *O. abutilivora* (discussed above) belongs to a related lineage, and it forms a characteristic gall-like raised mine or "welt" in the stem of *Abutilon theophrasti*

(Malvaceae). *Ophiomyia tiliae* (Couden) also belongs to this lineage, and it forms galls in twigs of *Tilia americana* L. (Malvaceae) (Spencer & Steyskal 1986). The feeding damage of *O. rugula* is also gall-like, and it may be that *O. similata* and allied species of the California *O. jacintensis* group (see Spencer & Steyskal (1986: 37)) will prove to have similar larval biology.

The only *Ophiomyia* previously associated with *Baccharis* is *O. spicatae* Spencer, known from a single female reared from a stem mine on *B. spicata* (Lam.) Baill. in Brazil (Spencer 1963).

Subfamily Phytomyzinae

Amauromyza flavifrons (Meigen)

Material examined. ILLINOIS: Mason Co., Forest City, Sand Ridge State Forest, 28.vi.2019, em. 15–23.vii.2019, C.S. Eiseman & J.A. Blyth, ex *Silene stellata*, #CSE5621, CNC1722676–1722680 (3♂ 2♀); **MASSACHUSETTS:** Franklin Co., Northfield, 42.647239, -72.425369, 20.vi.2018, em. 9.vii.2018, C.S. Eiseman, ex *Stellaria media*, #CSE4732, CNC1135720 (1♂).

Photographed mines. CONNECTICUT: Litchfield Co., Falls Village, 24.vi.2015, C. Vispo, Silene latifolia, BG 1093955; IDAHO: Kootenai Co., Hayden Lake, English Point, 30.ix.2012, C.S. Eiseman, Dianthus armeria; IOWA: Winneshiek Co., 100 Acre Wood, 4.x.2017, MJ Hatfield, Silene, BG 1450731; KENTUCKY: Edmonson Co., Mammoth Cave National Park, 37.224793, -86.221129, 23.vi.2020, T. Hulsey, Stellaria pubera, iNat 51138728; MARYLAND: Baltimore City Co., Herring Run Park, 22.v.2015, T. Wilson, Silene sp., BG 1072111; Herring Run Watershed, 15.vii.2013, T. Wilson, Stellaria ?media, BG 809049; NEW YORK: Delaware Co., 42.041286, -75.0233, 23.vii.2020, astrobirder, Stellaria aquatica, iNat 54593139; NORTH CAROLINA: Buncombe Co., Blue Ridge Parkway, 35.656365, -82.484747, 7.vii.2020, E. Raskin, Stellaria pubera, iNat 52357035; 35.658185, -82.485474, 7.vii.2020, E. Raskin, Silene virginica, iNat 52357053; Watauga Co., Boone, 3.ix.2016, T.S. Feldman, Saponaria officinalis [vacated mines], BG 1286592; VERMONT: Washington Co., Calais, 44.383117, -72.399941, 4.vii.2020, N. Sharp, Silene vulgaris, iNat 52070937; NOVA SCOTIA: Colchester Co., Truro, Center, St., 45.363787, -63.265562, 4.viii.2020, P. Manning, Silene coronaria, iNat 55434578.

Hosts. Amaranthaceae: *Beta vulgaris* L.; Caryophyllaceae: *Atocion armeria* (L.) Raf. (Craves 2018), [*Dianthus armeria* L.], *D. barbatus* L., *D. chinensis* L. (Adam 2019), *Saponaria officinalis* L., [*Silene chalcedonica* (L.) E.H.L.Krause], *S. coronaria* (L.) Clairv., [*S. flos-cuculi* (L.) Greuter & Burdet], *S. latifolia* Poir., *S. rotundifolia* Nutt., *S. stellata* (L.) W.T.Aiton, [*S. virginica* L., *S. vulgaris* (Moench) Garcke], [*Stellaria aquatica* (L.) Scop.], *S. media* (L.) Vill., [*S. pubera* Michx.] (Eiseman & Lonsdale 2018).

Leaf mine. A white linear-blotch; the completed blotch may obliterate the linear portion. Frass is in sparsely scattered black grains.

Puparium. Brown; formed outside the mine.

Phenology and voltinism. This species is multivoltine, with larvae present from June to November in New York (Scheffer & Lonsdale 2018). The earliest record we have seen is a photograph of a mine taken in Maryland on 22 May. Adults have emerged within three or four weeks of our larval collections, except for a series collected in October that overwintered as pupae, emerging as adults a month after removal from refrigeration (Eiseman & Lonsdale 2018).

Distribution. USA: [CT], DE, [IA, ID] *IL, [KY], *MA, [MD], MI, MN, [NC], NY, OH, OR, PA, VT, WA, [WI]; Canada: BC, NB (Adam 2019), [NS], ON, QC; Europe (Eiseman & Lonsdale 2018).

Aulagromyza luteoscutellata (de Meijere)

Material examined. MASSACHUSETTS: Nantucket Co., Nantucket, Dead Horse Valley, 6.xi.2017, em. 26–30.iv.2018, C.S. Eiseman, ex *Lonicera morrowii*, #CSE4440, CNC1135691–1135692 (1♂1♀).

Hosts. Caprifoliaceae: [Lonicera canadensis J.Bartram & W.Bartram ex Marshall], L. morrowii A.Gray, L. tatarica L., [Symphoricarpos albus (L.) S.F.Blake] (Eiseman & Lonsdale 2018).

Leaf mine. Widening, linear, sometimes becoming contorted; filled centrally with diffuse green frass. In some

cases the egg is inserted near the leaf margin and the larva at first follows the margin toward the apex, but mines are frequently formed away from the leaf margin.

Puparium. Yellow to yellowish-brown; formed outside the mine.

Phenology and voltinism. Previous North American records of this species have documented larvae feeding in May and June in New York and Massachusetts (Eiseman & Lonsdale 2018; Scheffer & Lonsdale 2018), and early July in Ontario (Spencer 1969), with adults emerging within a month in each case. Spencer & Steyskal (1986) gave a date of 13 September for specimens reared in Wisconsin, but it is unclear whether this was the collection or emergence date. Our new specimens from Massachusetts were collected as larvae in early November, overwintered as pupae, and emerged as adults about a month after removal from refrigeration.

Distribution. USA: MA, [MN], NY, WI; Canada: AB?, ON, QC; Europe (Eiseman & Lonsdale 2018).

Comments. Although the new specimens do not represent a new host or distribution record, the presence of larvae actively feeding in early November is noteworthy. *Agromyza pseudoreptans* (discussed above) is the only other agromyzid we can recall actively mining leaves in New England as late as November.

The only hosts of *Aulagromyza luteoscutellata* confirmed by rearing in North America are invasive honey-suckles (*Lonicera* spp.) introduced from the Palearctic. Further rearing from native Caprifoliaceae will be needed to clarify the host ranges and leaf mine characteristics of *Aulagromyza* known or suspected to feed on these plants, which include seven described species and two undescribed (known only from females).

Aulagromyza orbitalis (Melander)

Material examined. OKLAHOMA: Payne Co., Mehan, 36.013839°, -96.998103°, 24.iv.2017, em. 22.iv.2018, M.W. Palmer, ex *Symphoricarpos orbiculatus*, #CSE4424, CNC1144117 (1♀); WASHINGTON: Thurston Co., Olympia, Centralia Western Trail at 45th Ave., 29.ix.2017, em. 19.ii.2018, E. Stansbury, ex *Symphoricarpos albus*, #CSE4606, CNC1135596 (1♂).

Hosts. Caprifoliaceae: *Diervilla lonicera* Mill., *Lonicera dioica* L., *L. sempervirens* L., *Symphoricarpos albus* (L.) S.F.Blake, *S. mollis* Nutt., *S. *orbiculatus* Moench, *S. rotundifolius* A.Gray., *Triosteum aurantiacum* E.P.Bicknell; a mine possibly of this species found on *T. perfoliatum* L. (Eiseman & Lonsdale 2018).

Leaf mine. Variously placed on the upper surface; green to yellowish-green or whitish; in some cases linear throughout, in others widening to a more or less distinct blotch (Eiseman & Lonsdale 2018). On some hosts the frass tends to be regularly deposited in alternating, closely spaced particles or streaks in the narrow linear portion, but on *Symphoricarpos orbiculatus* it is indistinct or diffuse throughout.

Puparium. Yellowish-brown to brown; formed outside the mine.

Phenology and voltinism. Our Oklahoma females were collected as larvae in late April and emerged as adults the following spring; a full-year diapause was also reported by Spencer (1969) for a female collected as a larva in Alberta in early June. Otherwise, adults have emerged within a few weeks from larvae collected in North Carolina in April, and from Alberta, Iowa, and Massachusetts in June (Eiseman & Lonsdale 2018). Our new Washington specimens were collected as larvae in late September, emerging after overwintering.

Distribution. USA: CA, IA, ID, KS, MA, MI, NC, *OK, WA; Canada: AB, MB (Eiseman & Lonsdale 2018).

Cerodontha (Butomomyza) angulata (Loew)

Material examined. IOWA: Winneshiek Co., Freeport Marsh, 18.vi.2017, em. vii.2017, J. van der Linden, ex sedge, #CSE4658, CNC1144048 (1♂); **MASSACHUSETTS:** Nantucket Co., Nantucket, Squam Swamp, 27.vii.2017, em. 26.iv–1.v.2018, C.S. Eiseman, ex *Juncus tenuis*, #CSE4444, CNC1135688–1135689 (1♂ 1♀).

Hosts. Cyperaceae: *Carex crinita* Lam., *C. stipata* Muhl. ex Willd., *Scirpus hattorianus* Makino; Juncaceae: **Juncus tenuis* Willd., *Luzula* DC.; Poaceae: *Dichanthelium acuminatum* (Sw.) Gould & C.A.Clark, *D. clandestinum* (L.) Gould (Eiseman & Lonsdale 2018).

Leaf mine. Whitish, occupying the full width of the narrow leaves of *Juncus tenuis*, and not distinguished in the field from a mine that produced a female tentatively identified as *Cerodontha (Poemyza) incisa* (Meigen); see Eiseman & Lonsdale (2018) for a discussion of mines on other hosts.

Puparium. Oval, typically reddish-brown but ranging from yellowish-brown to blackish-brown; formed within or outside the mine. See Eiseman & Lonsdale (2018) for further details.

Phenology and voltinism. This species is multivoltine in Massachusetts. We have exceptionally found larvae in mid-April (adult emerging in early May), and they are common beginning in June. Many of our collections have been of puparia, but we have observed larvae in late July and in October. Reared adults have emerged in July, August, and September, always within a few weeks of collecting larvae or pupae, with 25 September being the latest emergence date. The new specimens from Nantucket are unusual in having overwintered as pupae from larvae collected as early as 27 July. In North Carolina we have found feeding larvae as early as 10 January.

Distribution. Probably present in most states; Canada: AB, ON; Europe (Eiseman & Lonsdale 2018).

Cerodontha (Dizygomyza) morosa (Meigen)

Material examined. OKLAHOMA: Payne Co., Mehan, 36.013839°, -96.998103°, 20.xii.2017, em. 12.ii.2018, M.W. Palmer, ex *Carex amphibola*, #CSE4377, CNC1135648 (1♀)

Hosts. Cyperaceae: [Carex *amphibola Steud., C. festucacea Willd.], C. gracillima Schwein., C. hitchcockiana Dewey, C. leptonervia (Fernald) Fernald (Eiseman & Lonsdale 2018).

Leaf mine. A long, whitish corridor, changing direction a few times, with frass in a single blackish lump toward the leaf apex.

Puparium. Yellowish or reddish to blackish-brown; formed within the mine, glued to the floor toward the base of the leaf.

Phenology and voltinism. In Massachusetts, *Cerodontha morosa* has been reared in late June and early July from leaf mines collected in June. In Oklahoma, tentatively identified females have been reared from overwintering pupae, and from mines collected in early and late May with adults emerging in early May and early June (Eiseman & Lonsdale 2018).

Distribution. USA: CA, MA, MO (Spencer 1981), [OK]; records from IL, IN, MD, MI (Priest *et al.* 2020), and SD require verification; Europe (Eiseman & Lonsdale 2018). The Montana record given by Spencer & Steyskal (1986) and repeated by Eiseman & Lonsdale (2018) was evidently an erroneous substitution for the Missouri record given by Spencer (1981).

Comments. This is the first record of an agromyzid from Carex amphibola.

Haplopeodes loprestii Eiseman & Lonsdale, spec. nov.

(Figs. 32–39, 133–139)

Holotype. USA. CALIFORNIA: San Diego Co., Coyote Canyon, 14.iii.2018, em. 18.v−3.vi.2018, E. LoPresti, ex *Fagonia laevis*, #CSE4545, CNC1135597 (1♂).

Paratype. Same data as holotype, CNC1135598 (1 \mathfrak{P}).

Etymology. This species is named for Eric F. LoPresti, ecologist and evolutionary biologist, who collected the host material from which it was reared.

Host. Zygophyllaceae: Fagonia laevis Standl.

Larval biology. Apparently a leafminer. The host material was collected to rear leaf-mining larvae of a gelechiid moth, and the presence of the flies only became evident when the puparia appeared. The rearing vial also contained fruits and stems, so the possibility of these as feeding sites cannot be entirely excluded, but as far as is known all *Haplopeodes* species are leafminers.

Puparium. (Fig. 34) Pale, straw-colored; formed externally.

Phenology and voltinism. The two known specimens were reared from larvae that fed in March, pupating by the 20th and emerging as adults four to six weeks later.

Distribution. USA: CA.

Adult description. Wing length 1.2 mm (\circlearrowleft), 1.4 mm (\looparrowright). Vein dm-m absent. Eye height divided by gena height: 3.2–3.5. First flagellomere slightly longer than high, apically rounded. Arista short, only 1.5 times length of first flagellomere. Orbital plate shallow but distinctly projecting when viewed laterally, especially anteriorly on

head; continuing as modestly developed ring around eye. Seen dorsally, frons wider than eye, slightly broader anteriorly. Anterior ocellus slightly displaced anteriorly. Epistoma large, broad, subrectangular, resulting in correspondingly shorter face; face with shallow medial carina. Palpus small, narrow, length approximately three times width. Thorax subshining. Wing veins costalized (closely spaced anteriorly), with width of cell r_{4+5} subequal to that of cell sc; length of costal cell subequal to length of cell r_1 past insertion of vein R_1 .

Chaetotaxy: Setae short. Three ori, very gracile; ors absent. Few orbital setulae, slightly inclinate and erect, partially proclinate. Ocellar seta straight, approximately \(^2\)_3 length of ori. Postvertical seta absent. Five dorsocentral setae, strongly decreasing in length anteriorly; female with additional small setula in dorsocentral row anteriorly. Only one notopleural seta, medially positioned. Notal setulae mostly absent; female with 1 anteromedial acrostichal setula and with few setulae in intra-alar region. One pair of lateral scutellar setae and two pairs of apical scutellar setae (left anterior seta absent in male). Katepisternal seta not visible in male.

Coloration: (Figs. 32–33, 35–39) Setae brown to dark brown with pale brown shine. Base color light yellow with head paler. First flagellomere brown with inner surface (not including margins) yellow; ocellar triangle dark brown; vertex light yellow; posterolateral corner of frons with brown patch fading to base of inner vertical seta; face deeper yellow with slight orange tint; venter of gena with brownish line; back of head dark brown with dorsomedial region paler and venter yellow. Notum dark brown to brown; center of scutellum and mediotergite slightly paler brown; postpronotum light brown, becoming yellower anteriorly and laterally; notopleuron and supra-alar spot light brown to yellow, with notopleuron yellower medially; katatergite light brown. Proepisternum light brown; ane-pisternum with anteroventral corner paler yellow, bordered posteriorly by oblique brown stripe; katepisternum with brown spot below level of seta; anepimeron irregularly brown; meron mostly dark brown. Legs light yellow; base of coxae narrowly brown; femora with indistinct brownish tint on apical ½–½; tibiae brown with mediolateral and medioventral regions broadly yellow; tarsi brown. Abdomen brown with lateral margin of tergites narrowly yellow; epandrium darker brown. Calypter margin and hairs yellow.

Variation. Female: Darker than male. Setae darker brown to blackish. Only inner-basal surface of first flagel-lomere yellow; scape and pedicel yellow. Posterolateral corner of frons darker. Paler parts of scutum brown tinted. Anepisternum, anepimeron and meron brown; base color of katepisternum brownish-orange. Femora extensively brown mottled. Abdominal tergites entirely brown.

Genitalia: (Figs. 133–139) Epandrium shallow. Surstylus short, incurved, apical margin irregular but essentially straight, without tubercle-like setae or narrow protrusions referred to as "teeth" in Steyskal (1980a); base (concealed within epandrium) incurved. Cerci weakly sclerotized, much thicker laterally, closely spaced. Hypandrium with short, semicircular arch; inner lobe weakly sclerotized, more so on distal margin bearing single seta; arm long, well-defined. Postgonite dark, narrow, with single subapical seta. Phallus small and weakly sclerotized, but comparatively large and dark for *Haplopeodes*; phallophorus cylindrical, fused to curved basiphallus, which is represented by short ventral sclerotization that is slightly elongated on left side. Ejaculatory duct strongly upcurved past basiphallus, with exposed portion approximately as long as basiphallus; apex rounded, dorsoventrally flattened and lightly sclerotized. Ejaculatory apodeme narrow but well-developed, darker stem grading into blade.

Comments. This is the first record of any agromyzid from *Fagonia*, and the only agromyzids previously recorded from Zygophyllaceae are extremely polyphagous *Liriomyza* spp. Known hosts of *Haplopeodes* are otherwise restricted to Amaranthaceae, Portulacaceae, and Solanaceae (Benavent-Corai *et al.* 2005).

While minor color differences between the sexes are evident in some *Haplopeodes*, the sexual dimorphism observed here is pronounced and unique, with the female being much darker than the male. Both sexes are considerably darker than other *Haplopeodes*, with the scutellum entirely dark brown (unique among Nearctic *Haplopeodes*), the first flagellomere and scutellum brown, the pale grey pruinosity usually observed on the thorax is absent (the scutum is subshining), the tibiae are brown with yellow medial regions and the femora are brown mottled. Furthermore, the acrostichal setulae are virtually absent, the orbital plate and parafacial are produced, an epistoma is present, the radial veins are crowded anteriorly, the phallus is pigmented apically and surstylus spines are absent.

Liriomyza arctii Spencer

Material examined. MASSACHUSETTS: Hampshire Co., Northampton, 42.318438, -72.643259, 1.vi.2018, em. 19–21.vi.2018, C.S. Eiseman, ex *Silphium perfoliatum*, #CSE4637, CNC1144085–1144088 ($3\ensuremath{\lozenge}$ 1\overline{\Pi}).

Hosts. Asteraceae: *Arctium lappa* L., *A. minus* (Hill) Bernh., *Bidens cernua* L., *Heliopsis helianthoides* (L.) Sweet, **Silphium perfoliatum* L., *Verbesina alternifolia* (L.) Britton ex Kearney (Eiseman & Lonsdale 2018).

Leaf mine. Greenish, entirely linear; on *Heliopsis* and *Verbesina*, frass is diffuse throughout, whereas on the other hosts, there are more or less distinct, black, alternating strips in the later portion (Eiseman & Lonsdale 2018).

Puparium. Yellow to brown (dark brown according to Spencer 1969), formed outside the mine.

Phenology and voltinism. This species is multivoltine in the northeastern USA. We have collected larvae in early June, mid-July, early August, and late September, with adults emerging in 12–23 days in all cases except the last, when the pupae overwintered (Eiseman & Lonsdale 2018).

Distribution. Distribution. USA: CT, MA, MN, NY, OH, WI; Canada: ON (Eiseman & Lonsdale 2018).

Comments. This is the second *Liriomyza* species to be reared from *Silphium*, after *L. ivorcutleri* Eiseman & Lonsdale, which is known from a single Iowa specimen (Eiseman & Lonsdale 2018).

Liriomyza blechi Spencer (Fig. 73)

Material examined. MASSACHUSETTS: Hampshire Co., Florence, Mill River (42.336164, -72.679353), 20.viii.2020, em. 3.ix.2020, C.S. Eiseman, ex *Mimulus ringens*, #CSE6562, BG 1891588 (2\(\text{\Pi}\); **NEW YORK:** Orange Co., Cornwall, Black Rock Forest, 29.viii.2019, em. 10–12.ix.2019, C.S. Eiseman & J.A. Blyth, ex *Plantago major*, #CSE5898, BG 1881415 (1\(\text{\Pi}\); **NORTH CAROLINA:** Wake Co., Morrisville, Lake Crabtree County Park, 12.vi.2018, em. 30.vi.2018, T.S. Feldman, ex *Ruellia caroliniensis*, #CSE4709, CNC1144110–1144111 (2\(\text{\OMA}\); **OKLAHOMA:** Payne Co., Mehan, 36.013839\(^{\text{\OM}}\), -96.998103\(^{\text{\OM}}\), 13.vii.2018, em. by 29.vii.2018, M.W. Palmer, ex *Ruellia strepens*, #CSE4966, CNC1643660 (1\(^{\text{\OM}}\)); same collection, em. 16.vii.2018, #CSE4965, CNC934531 (1\(^{\text{\OM}}\)).

Photographed mines. KANSAS: Riley Co., Konza Prairie Biological Station, 3.vii.2015, C.S. Eiseman, *Ruellia humilis*; **MASSACHUSETTS:** Middlesex Co., Lincoln Co., Drumlin Farm, 6.vii.2019, C.S. Eiseman, *Plantago major*; **NORTH CAROLINA:** Durham Co., Durham, Bobbitt Hole trail, 28.vi.2015, T.S. Feldman, *Plantago rugelii*, BG 1093459; **WISCONSIN:** Buffalo Co., Alma, S1287 State Road 88, 18.vii.2015, C.S. Eiseman, *Plantago rugelii* [vacated mines].

Hosts. Acanthaceae: Ruellia blechum L., R. *caroliniensis (J.F.Gmel.) Steud., [R. humilis Nutt.], R. *strepens L.; Boraginaceae: Heliotropium curassavicum L.; Loganiaceae: Spigelia anthelmia L.; *Phrymaceae: Mimulus ringens L.; Plantaginaceae: Plantago *major L., P. media L. (Lonsdale 2017a), [P. rugelii Decne.], P. virginica L.; Poaceae: Digitaria sanguinalis (L.) Scop. (Lonsdale 2017a); Verbenaceae: Phyla nodiflora (L.) Greene (Eiseman & Lonsdale 2018).

Leaf mine. (Fig. 73) According to Spencer & Stegmaier (1973), a number of larvae feed together on *Ruellia blechum*, "forming a mine primarily along the mid rib with irregular extensions into the leaf blade." Spencer & Steyskal (1986) described the mine on the same host as "an irregular blotch, normally but not exclusively associated with the midrib or one of the lateral veins." Eiseman & Lonsdale (2018) described mines on *Plantago virginica* as irregular whitish blotches with frass in discrete black grains and occasional small lumps. All mines we have seen on *Ruellia* spp. have distinct primary and secondary feeding lines and present a brainlike or intestinelike appearance (Fig. 73). They likewise have frass in discrete black grains. Mines on *Plantago* spp. sometimes have similar feeding lines, but much fainter. The two mines found on *Mimulus ringens* were both entirely linear, with frass at first in closely spaced grains or beaded strips, and later in series of discrete, roundish particles interspersed with squiggly masses. The presumed *L. blechi* mines we have seen on *Spigelia anthelmia* begin as compact spirals and then open into irregularly contorted linear mines, in some cases compact enough to resemble the mines on *Ruellia*, but with frass in an almost continuous line of closely spaced grains or beaded strips.

Puparium. Yellowish-brown to brown, formed within the leaf, with the anterior spiracles projecting through the lower epidermis.

Phenology and voltinism. We have collected leaf mines in late March (Florida), mid-June (North Carolina), mid-July (Oklahoma), and mid- to late August (Massachusetts and New York), with adults emerging within a few weeks in each case (Eiseman & Lonsdale 2018).

Distribution. USA: DE, FL, GA, IA, ID, IL, [KS], *MA, MD, MI, MS, *NC, NY, OH, *OK, PA, SC, SD, TX, VA, [WI], WV; Canada: AB, NL, ON, QC; Bermuda; Bolivia; Brazil; Dominica; Dominican Republic; Guadeloupe; Martinique.

Comments. Lonsdale (2017a) noted that the specimens he examined from "elm leaves" in Illinois and from *Digitaria* in Florida "would be unusual rearing records, and are possibly incidental adult associations." The label data for the latter specimens reads "Miami, 24.ix.1963, ex. *Digitaria sanguinalis*, K.A. Spencer." These would seem to be the same specimens Spencer & Steyskal (1973) discussed under *L. marginalis* (Malloch): "Specimens bred from *Digitaria sanguinalis* and from *Panicum miliaceum* have the mesonotum shining black, but the genitalia do not entirely agree with those of *marginalis*." They unfortunately did not provide more specific data for these specimens, but this publication on Florida Agromyzidae makes no other reference to *Liriomyza* on *Digitaria*. Monteiro *et al.* (2019) reported rearing *L. blechi* from Poaceae in Brazil (*Digitaria* sp., *Panicum miliaceum* L., *Paspalum* spp.), and noted that on these hosts the mines are linear with widely spaced frass, in contrast with mines on *Dicliptera sericea* (=*D. squarrosa* Nees, Acanthaceae) and *Spigelia anthelmia*, which they stated "are similar to *L. blechi* mines." They also noted that in specimens reared from Poaceae "the central area of the mesonotum is predominantly paler, almost orange, similar to description of *L. marginalis*. However, the shape of aedeagus resemble which illustrated by Eiseman & Lonsdale (2018) to *L. blechi*." The genitalia of *L. blechi* were not illustrated by Eiseman & Lonsdale (2018), and Lonsdale (2017a) was presumably the intended citation.

Liriomyza cf. *cracentis* Lonsdale (Fig. 74)

Material examined. ILLINOIS: Cook Co., Glencoe, Chicago Botanic Gardens, McDonald Woods, 42°8′56.66″N 87°47′21.99″W, 12.vi.2018, em. by 27.vi.2018, J.F. Steffen, ex *Eupatorium rugosum*, CNC1135572 (1a/2).

Hosts. The label of the *Liriomyza cracentis* holotype indicates a host of "*Euperomum maculata*", possibly referring to *Eupatorium maculatum*, a synonym of *Eutrochium maculatum* (L.) E.E.Lamont (Asteraceae) (Lonsdale 2017a). The Illinois specimens were reared from *Ageratina altissima* (L.) R.M.King & H.Rob., which like *Eutrochium* is in the tribe Eupatorieae.

Leaf mine. (Fig. 74) Upper-surface, greenish to whitish, entirely narrow and linear; the photographs provided by J. Steffen do not show the entire mines, but no frass is evident in the portions photographed.

Puparium. Details not recorded, but presumably formed outside the mine.

Phenology and voltinism. All known specimens tentatively identified as *Liriomyza cracentis* have been reared or captured between late June and mid-July. Larvae are present in June.

Distribution. The *Liriomyza cracentis* holotype was collected in Canada: QC, and a tentatively identified male was collected in ON. The new material is from USA: IL; also see Comments below.

Comments. Based on the host, leaf mine, and adult characters, this fly is possibly conspecific with the Massachusetts female discussed by Eiseman & Lonsdale (2018) as *Liriomyza* sp. 2; the mines in both cases seem consistent with Spencer & Steyskal's (1986) unidentified leaf mine #4 (known from DC, MN, and WI). We should note, however, that the photographed mines are not the exact ones from which the Illinois specimen was reared; no host material was preserved, and after the adult emerged, J. Steffen returned to the group of plants from which the mines had been collected and photographed old, vacated mines that at least superficially resembled them.

Liriomyza eupatorii (Kaltenbach)

Material examined. ILLINOIS: Cook Co., Glencoe, Chicago Botanic Gardens, 42°8′56.66″N 87°47′21.99″W, oak woodland, 21.vi.2018, em. by 25.vi.2018, J.F. Steffen, ex *Symphyotrichum shortii*, CNC1135573−1135575 (2♂1♀); **ONTARIO:** Nipissing, Algonquin Provincial Park, Basin Depot, 6.vii.2018, em. 16.vii.2018, C.S. Eiseman & J.A. Blyth, ex *Symphyotrichum ?cordifolium*, #CSE4778, CNC1643629 (1♂).

Hosts. Apocynaceae: Asclepias L.; Asteraceae: Baccharis halimifolia L., Mikania micrantha Kunth, M. scandens (L.) Willd., Solidago altissima L., S. canadensis L., S. latissimifolia Mill., Symphyotrichum chilense (Nees) G.L.Nesom, S. cordifolium (L.) G.L.Nesom, [S. lateriflorum (L.) Á.Löve & D.Löve, S. novae-angliae (L.) G.L.Nesom], S. praealtum (Poir.) G.L.Nesom, S. puniceum (L.) Á.Löve & D.Löve, S. *shortii (Lindl.) G.L.Nesom, Xanthium strumarium L. (Eiseman & Lonsdale 2018). California specimens apparently reared from Callistephus Cass. (Asteraceae) have been tentatively identified as L. eupatorii (Lonsdale 2011); see Comments for other likely hosts.

Leaf mine. Whitish, upper surface; long, narrow and linear; often beginning with a distinctive spiral, but this is sometimes reduced to a minute contorted area, and sometimes there is no hint of it whatsoever. The black frass is mostly in distinct, alternating strips, sometimes devolving into irregular, squiggly fragments toward the end (Eiseman & Lonsdale 2018).

Puparium. Yellow to orange to dark brown; formed outside the mine (Eiseman & Lonsdale 2018).

Phenology and voltinism. This species is evidently multivoltine in the USA, although all of our rearing records involve larval collections and adult emergences prior to midsummer. We have reared adults of *Liriomyza eupatorii* from larvae found in Oklahoma as early as 23 March, and from larvae found in Massachusetts on 11 May, 11–13 June, and 24–28 June. In New York, Scheffer & Lonsdale (2018) similarly recorded larvae only in May and June. Later dates have been observed in Canada, including an Alberta specimen emerging on 19 August from a larva collected on 4 August (Lonsdale 2017a). In all of our rearings, adults have emerged 10–22 days after the larvae were collected.

Distribution. USA: CA, DE, GA, *IL, MA, MI, MS, MT, NC, NY, OK, PA, SC, TN, VA, WA, WV; Canada: AB, BC, MB, NB, NS, ON, QC, SK; Europe (Eiseman & Lonsdale 2018).

Comments. We have found *Liriomyza* mines beginning with distinct spirals, and thus likely representing *L. eupatorii*, on the following additional asteraceous hosts: *Ambrosia artemisiifolia* L. (MA), *Erigeron canadensis* L. (MA, NC), *Euthamia graminifolia* (L.) Nutt. (MA), *Senecio triangularis* Hook. (ID), *Solidago rigida* L. (MA), *S. sempervirens* L. (NY), *S. simplex* var. *randii* (Porter) Kartesz & Gandhi (NH), *Symphyotrichum firmum* (Nees) G.L.Nesom (IL), *S. lanceolatum* (Willd.) G.L.Nesom (MA), *S. pilosum* (Willd.) G.L.Nesom (NC), *S. ulmifolia* Muhl. ex Willd. (OK), and *Zinnia elegans* Jacq. (NC). *Liriomyza* mines without spirals, but nonetheless probably representing *L. eupatorii*, have been found on *Solidago patula* Muhl. ex Willd. (MA).

Papp & Černý (2017) considered *Liriomyza eupatorii* to be synonymous with the senior *L. pusilla* (Meigen), which is supported by close overall external and genitalic morphological similarity, notably including general phallic morphology, a large ejaculatory apodeme with a narrowed stem, and the occasional presence of a third ori. Liriomyza pusilla is known from Arctium L., Aster L., Bellis L., Bidens L., Callistephus Cass., Crassocephalum Moench, Epaltes Cass., Hypochaeris L., Synedrella Gaertn., Tithonia Desf. ex Juss., Vernonia Schreb., Solidago L., and Xanthium L. (Asteraceae) (Benavent-Corai et al. 2005; von Tschirnhaus & Karimpour 2006; Ellis 2020), the last two of which are also host genera of L. eupatorii. Beyond its Nearctic hosts, L. eupatorii has been reported from Aster, Eupatorium L., Helianthus L., Lapsana L. (Asteraceae), and Galeopsis L. (Lamiaceae) (Spencer 1976; Benavent-Corai et al. 2005). This synonymy follows notes of similarity by previous authors including Spencer (1971), who stated that adult morphology appeared identical, both external and genitalic, but that the form of the leaf mines was distinct. Mines of L. eupatorii typically start with a characteristic spiral, but we have observed some to lack this spiral (Eiseman & Lonsdale 2018), as seen in L. pusilla. Spencer (1976) further differentiated the two by L. pusilla having the "mesonotum brilliantly shining black" and L. eupatorii having the "mesonotum deep black but less shining". While these two species are clearly closely related, their synonymy may be unwarranted on the basis of minimal overlap in host genera, a relatively (but not entirely) consistent difference in larval mine pattern, and slight differences in the phallus. While no specimens of L. pusilla were available to us, descriptions and illustrations were examined from Spencer (1971) and Papp & Černý (2017). Lonsdale (2017a) noted variation in the shape of the phallus of L. eupatorii, but in all cases, the mesophallus is quite small, being narrow, stem-like, and no more than half the length of the larger distiphallus, while it is slightly longer in L. pusilla and much thicker in lateral view. Regarding the distiphallus itself, it is longer and usually widest at or past the midpoint of the segment in L. eupatorii, and shorter, rounder, and either parallel-sided or widest on the basal half in L. pusilla (also one atypical male of L. eupatorii from Alberta (Lonsdale 2017a: Fig. 267)). Based on all of the above evidence, the two species are here considered separate (with L. eupatorii being Holarctic and L. pusilla known only from the Palearctic and Oriental regions), but because of their strong similarities, further scrutiny is certainly warranted, ideally including molecular data sets.

Liriomyza euphorbivora Eiseman & Lonsdale, spec. nov.

(Figs. 40–43, 75, 140–143)

Holotype. USA. OKLAHOMA: Payne Co., Marena, 36.072618°, -97.247242°, 29.v.2018, em. 14.vi.2018, M.W. Palmer, ex *Euphorbia marginata*, #CSE4617, CNC1144138 (1♂).

Etymology. The specific epithet refers to the host plant genus, Euphorbia L.

Host. Euphorbiaceae: Euphorbia marginata Pursh.

Leaf mine. (Fig. 75) The single collected mine was a whitish (partially greenish), roughly circular blotch on the upper leaf surface, centered on the midrib, 7 mm across when complete, with frass in a few small, dark grains and lumps. A photo taken of the lower leaf surface at the time of collection shows what appears to be a 0.2-mm wide, epidermal linear mine, but this does not appear to be contiguous with the mine that contained the fly larva and we believe it is unrelated. It is not discernible in the preserved leaf.

Puparium. Yellow; formed outside the mine.

Phenology and voltinism. The only known specimen was collected as a larva in late May, emerging as an adult in mid-June.

Distribution. USA: OK.

Adult description. Wing length 1.5 mm (\circlearrowleft). Female unknown. Length of ultimate section of vein M_4 divided by penultimate section: 2.8. Eye height divided by gena height: 3.0. First flagellomere small, rounded. Thorax subshining.

Chaetotaxy: Two ori, two ors; subequal to ocellar and postvertical setae. Four dorsocentral setae, only first seta long, with second seta % length. Five rows of acrostichal setulae.

Coloration: (Figs. 40–43) Setae dark brownish-black. Head yellow with ocellar spot dark brown; posterolateral corner of frons dark brown nearly to base of outer vertical, paler brown to base of inner vertical; back of head and clypeus brown. Scutum dark brown with wide, complete lateral yellow stripe on scutum (reaching base of posterior supra-alar and intra-alar) that continues along posterior margin as narrow line along scutellum. Mediotergite dark brown; anatergite brown with posterodorsal corner yellow; katatergite yellow with posteroventral corner brown. Pleuron yellow in base color; anepisternum with wide clavate anteroventral stripe (wider anteriorly) and narrow posteromedial line along suture; anepimeron mottled brown; katepisternum brown below level of seta; meron mostly brown. Scutellum dark anterolaterally. Legs yellow with basal half of fore coxa dark brown, mid coxa basally brownish and hind coxa mottled brown; base of femora narrowly brown (reduced ventrally); tibiae brown with base of fore and mid tibiae yellow, fore tibia yellower and hind tibia darker; tarsi brown. Abdomen brown dorsally, stripe narrowing posteriorly to tergite 5; epandrium brown. Calypter margin yellow with grey tint, hairs greyish-brown.

Genitalia: (Figs. 140–143) Epandrium not fused to surstylus, with one spine. Surstylus with two apical spines. Phallophorus with venter much reduced, short. Basiphallus sclerotized along dorsal and left lateral surface with extension on left distal margin below paraphallus. Paraphallus simple, narrow. Hypophallus with small rod-shaped sclerite with apical hairs. Ejaculatory duct swollen and pigmented apically. Mesophallus slightly shorter than distiphallus, subcylindrical, fused to distiphallus dorsally, with slight ventral carina along suture. Distiphallus slightly wider than mesophallus, distal half shallow and cup-shaped, enclosing one pair of short processes, angled dorsally; basal half slightly narrower, sides parallel in ventral view, tapering basally in lateral view. Ejaculatory apodeme large and well-developed with broad blade; sperm pump with broad sclerotized cup-like venter.

Comments. This is the second *Liriomyza* to be reared from *Euphorbia* in North America, after *L. euphorbiella* Eiseman & Lonsdale. That species is likewise known only from Payne Co., Oklahoma, but it was reared from *E. heterophylla* var. *cyathophora* (Murray) Griseb. rather than *E. marginata*, and its mine begins with a distinct linear portion and does not cross the midrib. Mines on *E. marginata* similar to that of *L. euphorbivora* have been photographed in Ontario (Mews 2019b), and the aborted mine on *E. cf. brachycera* Engelm. in Colorado noted by Eiseman & Lonsdale (2019) could conceivably have represented this species. TSF has found largely linear *Liriomyza* mines on *E. curtisii* Engelm. in North Carolina, but so far adults have not been reared from these.

Worldwide, 12 *Liriomyza* species have now been reported from *Euphorbia*, including three listed by Benavent-Corai *et al.* (2005) that were omitted without explanation from the review of *Euphorbia*-feeding Agromyzidae by Martinez & Sobhian (2000). Of these three, *L. congesta* (Becker) normally feeds on Fabaceae, and *L. sonchi* Hendel on Asteraceae, so these records seem likely to be erroneous (both are derived from a paper on parasitoids of Agromyzidae in Valencia, published in 1987). The record of the highly polyphagous *L. sativae* Blanchard appears plausible, however, apart from its being poorly documented (the cited source, Martinez (1993), is apparently a simple

list of host genera, and is a publication we have been unable to obtain after multiple attempts; Martinez & Sobhian (2000) explicitly stated that *L. sativae* is "not yet recorded on *Euphorbia*"). Possibly this record refers to McClanahan (1975), who caged a population of *L. sativae* with *E. pulcherrima* Willd. ex Klotzsch and observed light mining but no puparium formation. Whether the unidentified Nearctic mines noted above represent any of these 12 species remains to be seen, but to aid in the identification of *Liriomyza* specimens reared from *Euphorbia*, a modified version of the key by Martinez & Sobhian (2000) is presented below with *L. euphorbiella*, *L. euphorbivora*, and *L. sativae* added, and supplemented with data from Ellis (2020).

Updated key to the species of Liriomyza feeding on Euphorbia

1.

1'. 2.	Mesonotum largely black, without distinct yellow longitudinal bands
	rows
	[mine initially narrow and serpentine, developing into an irregular blotch; on <i>E. kotschyana</i> Fenzl and <i>E. macroclada</i> Boiss.; Turkey]
2′.	Back of head, at level of vertical bristles, partly brown. Acrostichal setulae more numerous, arranged in four almost regular
	rows
	nia, Romania, former Soviet Union]
3.	Wings without vein dm-cu
3'.	Wings with vein dm-cu. 5
4.	Orbits between upper ors and vti completely yellow. Abdominal tergites without yellow lateral band. Penultimate section of M ₄ 2.5 to 3 times longer than last section
	[mine broadly linear or a linear-blotch; on <i>E. cyparissias</i> L., <i>E. esula</i> , <i>E. myrsinites</i> L., and possibly <i>E. amygdaloides</i> ; Germany and Poland to Turkey]
4'.	Upper part of orbits black. At least the basal part of abdominal tergite with yellow border. Penultimate section of M ₄ maximum 2 times longer than last section
	[mine a blotch preceded by a short linear portion; on E. myrsinites; Bulgaria, Spain]
5.	Orbits between upper ors and vti completely yellow. Mesophallus long, narrow, fused to distiphallus with broad, bilobed cup-
	like base from which one pair of short weakly scleritized tubules emerge
	[mine a primary blotch, generally containing several larvae; on E. amygdaloides, E. characias L., E. dulcis L., E. esula, E.
- .	glareosa Pall. ex M.Bieb., E. palustris, and E. pithyusa L.; throughout Europe]
5'.	Upper part of orbits black. Phallus not as above
6.	Frons yellow at base of inner vertical seta. Distiphallus entirely split, short, with minute basal stem contrasting rounded apical chamber
	[branching mine centered on the midrib; a polyphagous species, uncommonly reported from unspecified <i>Euphorbia</i> ; throughout Europe]
6'.	Frons brown at base of inner vertical seta. If distiphallus entirely split and short (<i>L. huidobrensis</i>), then apical chamber narrow, not much wider than stem
7.	Surstylus with two apical spines. Distiphallus angled dorsally, with very short apical chamber
7′.	Surstylus with one apical spine. Distiphallus various, but not as above
8.	Eye 4.8–5.9 times higher than gena. Posterior margin of scutum along scutellum black. Ventral 2/3 of anepisternum brown.
	Femora entirely yellow. Left distal margin of basiphallus long, extending to apex of paraphallus. Basal stem-like half of distiphallus (fused to mesophallus) gradually narrowing to point of fusion with mesophallus
	[mine initially narrow and linear with the frass in alternating strips, expanding to an elongate blotch with irregular and more or less diffuse frass; on <i>E. heterophylla</i> var. <i>cyathophora</i> ; USA]
8'.	Eye 3.0 times higher than gena. Posterior margin of scutum narrowly yellow. Anepisternum yellow with brown clavate spot.
	Femora brown basally (paler on venter). Left distal margin of basiphallus shorter, not reaching apex of paraphallus. Basal stem-
	like half of distiphallus parallel-sided and abruptly wider than mesophallus Liriomyza euphorbivora Eiseman & Lonsdale
	[mine a roughly circular blotch on upper leaf surface, centered on the midrib, with frass in a few small, dark grains and lumps; on <i>E. marginata</i> ; USA]
9.	Femora usually only brown basally, but sometimes more heavily mottled. Abdominal tergites narrowly yellow laterally. Acros-
	tichal setulae (acr) between second and fourth pairs of dorsocentral setae in four more or less regular rows. Distiphallus simple,
	cup-shaped
	[mine linear; a polyphagous species, with one questionable record from unspecified <i>Euphorbia</i> (light mining of <i>E. pulcherrima</i> observed in a laboratory setting, but no puparia were formed); North and South America; introduced in Europe, Asia, Africa,
	Australia, and several Pacific islands]
9′.	Femora brown basally and with additional light to heavy dorsal mottling. Lateral margin of abdominal tergites brown. Acrostichal setulae (acr) between second and fourth pairs of dorsocentral setae in two to three more or less regular rows. Distiphallus

divided into one pair of short tubules. Liriomyza huidobrensis (Blanchard)

[mine linear, often following the midrib and lateral veins; a polyphagous species, uncommonly reported from unspecified *Euphorbia* according to Martinez & Sobhian (2000); the only record listed by Weintraub *et al.* (2017) is one of *E. marginata* from China; this South American fly is introduced in North America, Europe, Asia, and Africa]

Characters of the thorax of *Liriomyza euphorbivora* best differentiate it from other *Liriomyza* externally, as four rows of acrostichal setulae and a very narrow yellow posterior margin on the scutellum is not found in many species. In the United States, it occurs in *L. eupatoriella* Spencer, but this species has both vertical setae on yellow, the femora are entirely yellow (not basally brown) and the distiphallus is of a different structure, being more cup-shaped with the base strongly narrowed in lateral view. In Canada, the new species keys most readily to *L. cracentis* Lonsdale and *L. agrios* Lonsdale, although the spot on the anepisternum of these two species is much larger, their femora are entirely yellow, and the distiphallus is more cup-shaped, without a short apical chamber. The phallus instead shows more similarity to species without the posteriorly yellow scutum. These include *L. conclavis* Lonsdale (host unknown), *L. asclepiadis* Spencer and *L. peleensis* Spencer (both on *Asclepias*), which have a medially constricted mesophallus and a very sharply upturned distiphallus, and *L. subasclepiadis* Spencer (also on *Asclepias*), which also has a more strongly angled distiphallus.

Liriomyza hypopolymnia Eiseman & Lonsdale, spec. nov.

(Figs. 44–47, 76–77, 144–147)

Holotype. USA: IOWA: Winneshiek Co., Craggy Rocks, 43°25′58.82″N, 92° 0′29.92″W, 20.x.2017, em. 18.iv.2018, MJ Hatfield, ex *Polymnia canadensis*, CNC1144061 (1♂).

Paratypes. USA: IOWA: same data as holotype, CNC1144055, CNC1144058, CNC1144062 ($2 \stackrel{\wedge}{\circ} 1 \stackrel{\hookrightarrow}{\circ}$), Decorah, Dug Road, 30.vi.2017, em. by 21.vii.2017, J. van der Linden, ex *Polymnia canadensis*, #CSE4654, CNC1144029 ($1 \stackrel{\hookrightarrow}{\circ}$).

Additional material examined. same data as holotype, CNC1144054, CNC1144056–1144057, CNC1144065–1144073 (13 puparia).

Etymology. The specific epithet refers to the position of the larval mines (Gr. *hypo*—"under, beneath") on the lower surface of leaves of *Polymnia* Kalm.

Host. Asteraceae: Polymnia canadensis L.

Leaf mine. (Figs. 76–77) A long, rather indistinct, linear mine on the lower leaf surface, with frass in grains and beaded strips along the sides; the mine may be evident from above as a faint green line or mottling. Some mines intermittently switch to the upper surface, where they are much more distinct and appear whitish.

Puparium. (Fig. 47) Yellow; formed outside the mine.

Phenology and voltinism. This species is at least bivoltine in Iowa. Larvae have been found in late June, with an adult emerging within a few weeks; larvae of the overwintering generation have been found from mid-October to mid-November, emerging as adults in spring.

Distribution. USA: IA; leaf mines have also been found in PA (Woods 2018) and TN.

Adult description. Wing length 1.9–2.0 mm (\circlearrowleft), 1.9 mm (\circlearrowleft). Length of ultimate section of vein M_4 divided by penultimate section: 2.5–3.1. Eye height divided by gena height: 5.3–7.0. First flagellomere rounded and slightly enlarged, being higher than long; distal margin with longer hairs subequal to width of base of arista. Thorax subshining. Vein dm-m slightly angled.

Chaetotaxy: Two ors, two ori; anterior ori slightly shorter. Four dorsocentral setae, decreasing in length anteriorly, only posterior two pairs strong. Six rows of acrostichal setulae; reduced in number posteriorly, typical of Liriomyza, but posterior-most pairs between first pair of dorsocentrals atypical in being widely spaced and incurved. Eye bare and mid tibia without medial setae (eye often minutely haired and mid tibia with posteromedial seta in Liriomyza with convergent posteromedial acrostichal setulae).

Coloration: (Figs. 44–46) Overall color of most specimens relatively pale yellow compared to congeners, perhaps because specimens were preserved while still slightly teneral; base color of most whitish-yellow with pigmented patches brown to orange-brown, but female specimen CSE4654 with color typical of most other *Liriomyza* with pigment dark brown. Setae brown with yellowish shine (shine not pronounced on major setae of thorax and head). Ocellar tubercle light brown; posterolateral corner of frons with light brown spot reaching margin of eye, but not base of vertical setae; back of head brown with venter yellow. Scutum brown with complete lateral yellow stripe

that is relatively wide and encompasses base of posterior inter-alar and supra-alar setae; posterior margin of scutum yellow with quadrate spot between dorsocentral rows that has anterior corners extending as one pair of small short points approaching bases of second dorsocentrals; spot on postpronotum and anterolateral spot on scutellum faded, small. Mediotergite dark brown; anatergite with small brown anteroventral spot extending onto posteroventral corner of katatergite. Anepisternum with very small faded anteroventral spot; anepimeron entirely pale; katepisternum brown ventrally, far from base of seta; meron brown on ventral half. Hind tarsus sometimes brownish apically. Abdomen paler brown dorsally with wide yellow lateral margin; stripe narrows to medial spot on tergite 5; epandrium light brown with dorsomedial region light yellow. Calypter margin slightly greyish, hairs yellow.

Genitalia: (Figs. 144–147) Epandrium separate from surstylus, with one pair of small ventral spines. Surstylus with one pair of large spines (apical and basal). Phallophorus with venter reduced, short. Basiphallus sclerotized along dorsal and left lateral surfaces, with narrow process extending from left apical margin. Hypophallus small, narrow, with short apical hairs. Paraphallus very small, narrow. Ejaculatory duct swollen and pigmented apically. Mesophallus subcylindrical, tapered at base and apex, very lightly fused to distiphallus; venter flared along suture. Distiphallus wider and longer than mesophallus, cup-shaped with base tapered (abruptly constricted in ventral view), widest before apex, enclosing small internal processes. Ejaculatory apodeme very pale, narrow; sperm pump with small ventral sclerotization.

Comments. The only previous record of an agromyzid from *Polymnia* is that of an undetermined stem-boring *Melanagromyza* species we reared from *P. canadensis* in Iowa (Eiseman & Lonsdale 2019). The host of the Venezuelan *M. polymniae* Spencer is *Smallanthus riparius* (Kunth) H.Rob. (Spencer 1990).

Liriomyza hypopolymnia is distinct in being quite pale with the vertical setae on yellow, the abdomen largely yellow and the scutum posteriorly yellow with a subquadrate yellow spot in front of the scutellum between the dorsocentral rows. This subquadrate spot has small points anterolaterally along the dorsocentral rows, and the few acrostichal setulae within the spot are incurved. These characters are also seen in some *L. blechi*, except this species usually has the brown scutal spot divided into bands, the third dorsocentral is most reduced (not with anterior two pairs of dorsocentrals reduced with the fourth smallest), and the mid tibia has two posteromedial setae. The male genitalia of this species are also drastically different (see Lonsdale 2017a: Figs. 29–32). The genitalia of *L. hypopolymnia* more closely resemble those of other species with a large, pale cup-shaped distiphallus such as *L. eupatorii*, but the new species differs from most of these in having a lateromedially constricted distiphallus and a surstylus with two spines (one apical and one basal); both of these features are shared by *L. sabaziae* Spencer, but this is a much darker species with a slightly smaller distiphallus that is dorsoventrally compressed on the basal half (see Lonsdale 2011: Figs. 202, 203).

Liriomyza orilliensis Spencer (Fig. 78)

Material examined. IOWA: Winneshiek Co., Decorah, Twin Springs Park, 24.viii.2017, em. ?, J. van der Linden, ex *Prenanthes alba*, #CSE4644, CNC1144028 (1♀).

Photographed mines. MASSACHUSETTS: Franklin Co., Northfield, 276 Old Wendell Rd., 7.x.2015, C.S. Eiseman, *Nabalus altissimus* [aborted/predated mines]; Nantucket Co., Squam Swamp, 8.ix.2019, C.S. Eiseman, *Nabalus trifoliolatus*; **MICHIGAN:** Ingham Co., Okemos, Ted Black Woods, 19.vi.2019, C.S. Eiseman, *Nabalus*; **NORTH CAROLINA:** Guilford Co., Browns Summit, Haw River State Park, 29.v.2015, T.S. Feldman, *Prenanthes alba* [vacated mine], BG 1075103; **VERMONT:** Chittenden Co., Williston, Mud Pond, 28.viii.2016, C.S. Eiseman, *Nabalus* [vacated mines].

Hosts. Asteraceae: *Nabalus *albus* (L.) Hook., [*N. altissimus* (L.) Hook., *N. trifoliolatus* Cass.], *Taraxacum* F.H.Wigg. (Eiseman & Lonsdale 2018).

Leaf mine. (Fig. 78) Pale greenish to whitish, turning brownish; in some cases beginning as an irregular track, gradually expanding to an elongate blotch, with frass mostly in squiggly strips; in others, forming a more or less compact blotch with distinct secondary feeding lines, and with frass mostly in fine grains. Two or three larvae may feed together.

Puparium. Yellow to brown; formed outside the mine.

Phenology and voltinism. Data from the few known specimens of this species indicate it is at least bivoltine. Larvae collected in Massachusetts in mid-June emerged as adults in early July (Eiseman & Lonsdale 2018); a larva

collected in Alberta in early August emerged as an adult the following spring (Lonsdale 2017a); and the Iowa specimen emerged on an unknown date from a larva collected in late August.

Distribution. USA: *IA, MA, [MI, NC, VT]; Canada: AB, ON (Eiseman & Lonsdale 2018).

Liriomyza taraxaci Hering (Fig. 79)

Material examined. VERMONT: Washington Co., Montpelier, North Branch River Park (44.283214, -72.571026), 21.vii.2018, em. 9.viii.2018, C.S. Eiseman & J.A. Blyth, ex *Taraxacum officinale*, #CSE4914, CNC1643637 (1♀); **ONTARIO:** Renfrew Co., Pembroke, Pansy Patch Park, 45.821464, -77.112117, 7.vii.2018, em. 20.vii.2018, C.S. Eiseman & J.A. Blyth, ex *Taraxacum officinale*, #CSE4811, CNC1643630 (1♂).

Tentatively identified material. NORTH CAROLINA: Scotland Co., Laurinburg, St. Andrews University, 10.iv.2017, em. 6.v.2018, T.S. Feldman, ex *Krigia virginica*, #CSE4499, CNC1144028 (1♀).

Photographed mines. MARYLAND: Baltimore City Co., Herring Run Watershed, 19.vi.2017, T. Wilson, *Taraxacum ?officinale*, BG 1228804; **MINNESOTA:** Fillmore Co., Rushford, Magelssen Bluff Park, 24.vi.2019, C.S. Eiseman, *Lactuca canadensis* [vacated mines]; **NORTH CAROLINA:** Wake Co., Lake Crabtree County Park, 9.v.2019, T.S. Feldman, *Krigia dandelion* [vacated mines], BG 1660443.

Hosts. Asteraceae: [Cichorium intybus L., Krigia dandelion Nutt., K. *virginica (L.) Willd.], Lactuca biennis (Moench) Fernald, L. canadensis L., L. sativa L., [L. serriola L.], Taraxacum officinale F.H.Wigg. (Eiseman & Lonsdale 2019).

Leaf mine. (Fig. 79) The mines on *Krigia* are linear throughout, necessarily contorted in the small leaves, with frass in grains, irregular particles, and short strips along the sides. Mines of *L. taraxaci* s.l. on *Lactuca* and *Taraxacum* rapidly widen to form blotches, and larvae are frequently gregarious on *Lactuca* (Eiseman & Lonsdale 2018, 2019).

Puparium. Yellow to yellow-orange; formed outside the mine.

Phenology and voltinism. The tentatively identified female was collected as a larva in early April and the adult emerged the following spring. Otherwise, adults we have reared of *Liriomyza taraxaci* s.l. have emerged 11–25 days after the larval collection dates, indicating the species is at least bivoltine. These have included larvae collected in North Carolina on 28 April and 10 June, and in Massachusetts on 6 July, 12 July, and 21 August (Eiseman & Lonsdale 2018, 2019). In Alberta, a larva collected in August apparently emerged as an adult the following spring, unless the error in the reported emergence date was in the month rather than the year (collected 18.viii.1974, emerged 5.v.1974, according to Lonsdale (2017a)).

Distribution. USA: AK, IL, MA, [MD, MN], NC, NY, *VT, WA, [WI]; Canada: AB, BC, MB, NB, ON, QC, SK, YT; Europe (Eiseman & Lonsdale 2019).

Comments. The only previous record of an agromyzid from *Krigia* is that of *Ophiomyia beckeri* (Hendel), also in North Carolina (Eiseman *et al.* 2019). The year-long diapause observed in this rearing of *Liriomyza* cf. *taraxaci* from *Krigia* is highly unusual for *Liriomyza* in our experience. Due to this, along with the entirely linear leaf mines, the rearing of males to confirm the identity of the *Krigia* feeders is desirable.

The *Taraxacum officinale*-reared specimens in collections CSE4811 and CSE4914 reveal previously unappreciated variation in *Liriomyza taraxaci*, as both have a very narrow yellow line along the posterior margin of the scutum. This character will key it to *L. cracentis* in Lonsdale (2017a), but they differ in that the posterior yellow margin is much narrower (almost indistinguishable) and doesn't narrowly extend anteriorly at two points to touch the bases of the posterior pair of dorsocentrals. Furthermore, the bases of the femora are brown dorsally and the fore femur has brownish streaking, as seen in *L. taraxaci*. We have stated that *L. taraxaci* is a relatively variable species, so this additional small variation is not entirely surprising if it is conspecific. Material discussed in Lonsdale (2017a) was re-examined, and this line is present in some specimens collected in Ottawa.

(Fig. 80)

Material examined. NORTH CAROLINA: Scotland Co., Laurinburg, St. Andrews University, 20.v.2018, em. 4.vi.2018, T.S. Feldman, ex *Mecardonia acuminata*, #CSE4579, CNC1135666–1135670, CNC1144089 (3♂3♀).

Hosts. (Note: underlined hosts are from a greenhouse experiment.) Amaranthaceae: Amaranthus palmeri S.Watson, Beta vulgaris L., Chenopodium album L., Spinacia oleracea L.; Amaryllidaceae: Allium cepa L.; Apiaceae: Apium graveolens L., Daucus carota L.; Araliaceae: Hydrocotyle umbellata L., H. verticillata Thunb.; Asteraceae: Ageratum L. (Heinz & Parrella 1990), [Ambrosia artemisiifolia L.], "Aster" (cultivated), Baccharis halimifolia L., Bidens alba (L.) DC., B. pilosa L., Callistephus chinensis (L.) Nees, Chrysanthemum × morifolium (Ramat.) Hemsl., Conoclinium coelestinum DC., [Cosmos bipinnatus Cav.], Dahlia Cav., Erechtites hieraciifolius (L.) Raf. ex DC., Eupatorium capillifolium (Lam.) Small ex Porter & Britton, E. serotinum Michx., Flaveria trinervia (Spreng.) C.Mohr, Gaillardia aristata Pursh, Galinsoga quadriradiata Ruiz & Pav., Gamochaeta pensylvanica (Willd.) Cabrera, Gerbera jamesonii Bolus, Helianthus annuus L., Hymenopappus scabiosaeus L'Hér., Lactuca canadensis L., L. sativa L., [Leucanthemum vulgare Lam.], Melanthera nivea (L.) Small, Mikania scandens (L.) Willd., Packera glabella (Poir.) C.Jeffrey, Parthenium hysterophorus L., "Senecio", Sonchus asper (L.) Hill, S. oleraceus L., Symphyotrichum cordifolium (L.) G.L.Nesom, Synedrella nodiflora (L.) Gaertn., Tagetes erecta L., Taraxacum officinale F.H.Wigg., Tridax procumbens L., [Vernonia gigantea (Walter) Trel.], Xanthium L., Zinnia L.; Caryophyllaceae: Gypsophila L.; Cucurbitaceae: Cucumis melo L., C. sativus L., Cucurbita pepo L., Melothria pendula L.; Fabaceae: Crotalaria incana L., [Lathyrus japonicus Willd.], Medicago lupulina L., M. sativa L., Phaseolus lunatus L., P. vulgaris L., Pisum sativum L., Trifolium repens L., <u>Vicia sativa L.</u>, Vigna luteola (Jacq.) Benth., V. radiata (L.) R. Wilczek, V. unguiculata (L.) Walp.; [Lamiaceae: Glechoma hederacea L.]; Malvaceae: Abelmoschus esculentus (L.) Moench, "Hibiscus", Malva moschata L.; Nyctaginaceae: Abronia villosa S. Watson; Plantaginaceae: *Mecardonia acuminata (Walter) Small, <u>Plantago major L.</u>; [Poaceae: Avena sativa L.; <u>Polygonaceae:</u> Fallopia convolvulus (L.) Á.Löve, Persicaria maculosa Gray.]; Ranunculaceae: Ranunculus repens L.; Solanaceae: Capsicum annuum L., Petunia Juss., Physalis angulata L., P. philadelphica Lam. (Pérez-Alquicira et al. 2019), P. pubescens L., Solanum americanum Mill., S. dulcamara L., S. lycopersicum L., S. melongena L., S. nigrum L., S. tuberosum L.; [Turneraceae: Piriqueta cistoides subsp. caroliniana (Walter) Arbo]; Verbenaceae: Verbena L.; Zygophyllaceae: Kallstroemia maxima (L.) Hook. & Arn., Tribulus terrestris L. (Eiseman & Lonsdale 2018 and references therein; see Lonsdale (2011) for additional host genera recorded outside of North America).

Leaf mine. (Fig. 80) Narrow and linear throughout; greenish to whitish, with dark green to black frass, typically in alternating strips or closely spaced grains, but in some cases partially forming a squiggly line. Mines are generally confined to the upper leaf surface, but some mines on *Mecardonia* were partly formed on the lower surface.

Puparium. Yellowish; formed outside the mine.

Phenology and voltinism. This species is multivoltine. We have collected larvae on 7 March in southern California, 26 March in Florida, and 20 May and 2 June in North Carolina, with adults emerging in 12–25 days in each case.

Distribution. Widespread in North, Central, and South America; introduced in the Old World. Largely restricted to greenhouses in colder temperate regions (Lonsdale 2011).

Comments. This is the first record of any agromyzid from *Mecardonia* Ruiz & Pav.

Phytomyza cf. *aesculi* Eiseman & Lonsdale (Fig. 81)

Material examined. VIRGINIA: Radford, Wildwood Park, 3.v.2017, em. 8–11.iv.2018, N.V. Kent, ex *Aesculus flava*, #CSE4400, CNC1135662–1135664 (3♀).

Hosts. The type series of *Phytomyza aesculi* was reared from Sapindaceae: *Aesculus glabra* Willd. (Eiseman & Lonsdale 2018). The Virginia specimens were reared from *A. flava* Sol., and mines have also been found on *A. pavia* L. and *A. sylvatica* W.Bartram.

Leaf mine. (Fig. 81) Upper-surface; mines associated with the type series were described as "linear, gradually widening from 0.3 mm to 2–3 mm; whitish, with liquidy frass forming a broad, green central band, and with black-

ish particles scattered within this." The mines on *Aesculus flava* are initially narrowly linear with frass in closely spaced grains along the sides, but then rather quickly widen to an elongate blotch ~4.5 mm wide, in which the frass is scattered at random. The completed mine is thus shorter and more compact than the mines on *A. glabra*. On both hosts, there are often multiple mines per leaflet.

Puparium. Yellowish-brown to reddish-brown; on *A. flava*, frequently formed in the exit slit at the end of the mine, or adhering to the upper leaf surface nearby.

Phenology and voltinism. *Phytomyza aesculi* is univoltine, with larvae feeding in spring and adults emerging the following spring. The type series was collected as larvae in central Ohio between 6 and 11 May. A photo on iNaturalist shows larvae in St. Louis, Missouri on 24 April; photos on BugGuide.net show puparia in Radford, Virginia as early as 1 May, and we have found mines as early as 26 March in North Carolina.

Distribution. USA: OH; see Comments.

Comments. Confirmed specimens of *Phytomyza aesculi* are only known from USA: OH; leaf mines on *Aesculus glabra* and undetermined *Aesculus* spp. matching those of the type series have been found in IA, KS, MN, MO, and Canada: ON. Some mines on *A. pavia* and *A. sylvatica* from AL, AR, GA, NC, and SC are long and narrow like those from OH, while others become blotchy like those from which the VA specimens were reared, as do those found on *A. glabra* in PA. It is possible that there is a single *Phytomyza* species on *Aesculus* with somewhat variable leaf mine morphology, but the VA females differ from the type series of *P. aesculi* in having the face darker, the venter of the lunule and the region around the antennal bases blackish, and the apices of the mid and hind femora are dark. More reared males will be needed to clarify the situation.

Phytomyza astotinensis Griffiths

Material examined. MASSACHUSETTS: Worcester Co., Rutland, 42.381206, -71.964980, 9.vi.2018, em. 24.vi.2018, J.A. Blyth, ex *Solidago rugosa*, #CSE4689, CNC1135714 (1♂).

Hosts. Asteraceae: *Solidago canadensis* L., *S. flexicaulis* L. (tentatively identified specimens), *S. gigantea* Aiton, *S. latissimifolia* Mill., *S. *rugosa* Mill. (Eiseman & Lonsdale 2018). We have seen leaf mines likely referable to this species on *S. altissima* L. and *S. macrophylla* Banks ex Pursh.

Leaf mine. Whitish, on the upper surface, narrow and linear throughout; frass typically in fine particles, mostly forming short beaded strips, but in some cases mostly deposited in an erratic jumble of squiggly fragments, rarely appearing as straight strips for a very short stretch (Eiseman & Lonsdale 2018).

Puparium. Black; formed outside the mine.

Phenology and voltinism. As discussed by Eiseman & Lonsdale (2018), this species is thought to be univoltine in Alberta, where larvae collected in early August and late September emerged as adults the following spring, but it is at least bivoltine in Massachusetts, where larvae collected between 9 and 12 June emerge as adults by the end of the month, larvae collected in late July have yielded tentatively identified females in mid-August, and larvae of the overwintering generation have been collected in early October.

Distribution. USA: MA, WI?; Canada: AB (Eiseman & Lonsdale 2018). We have found leaf mines likely referable to this species in IA and MI.

Phytomyza confusa Eiseman & Lonsdale

Material examined. IOWA: Winneshiek Co., Beard Farm, 23.v.2017, em. ?, J. van der Linden, ex *Hydrophyllum virginianum*, #CSE4645, CNC1135657 (13).

Host. Hydrophyllaceae: Hydrophyllum virginianum L.

Leaf mine. Irregular in shape, sometimes with a distinct linear portion and sometimes seeming to form a primary blotch, even when very small. Mines are whitish with brownish patches and discrete, dark frass grains (Eiseman & Lonsdale 2018).

Puparium. Pale brown; apparently formed externally, but this requires confirmation (Eiseman & Lonsdale 2018).

Phenology and voltinism. Larvae have now been found in May and September (the latter overwintering as pupae), indicating *Phytomyza confusa* is at least bivoltine.

Distribution. USA: IA.

Comments. Although no details of the leaf mine characteristics or pupation site were recorded for this new rearing, it confirms the tentative identification of the host plant that was given in the original description.

Phytomyza doellingeriae Eiseman & Lonsdale

Material examined. MASSACHUSETTS: Worcester Co., Rutland, 42.381206, -71.964980, 9.vi.2018, em. ~29. vi.2018, C.S. Eiseman, ex *Doellingeria umbellata*, #CSE4705, CNC1135713 (1♂).

Host. Asteraceae: Doellingeria umbellata (Mill.) Nees.

Leaf mine. Whitish, upper surface, narrow, entirely linear; frass in closely spaced grains or beaded strips along the sides (Eiseman & Lonsdale 2018).

Puparium. Blackish; formed outside the mine.

Phenology and voltinism. This species is at least bivoltine, with larvae feeding in early June in Massachusetts emerging as adults within a few weeks; in Maine, larvae have been found in late August, with adults emerging the following spring.

Distribution. USA: *MA, ME.

Comments. *Phytomyza solidaginivora* Spencer has been reared from larvae forming similar mines on *Doellingeria umbellata* in mid-June in Maine (Eiseman & Lonsdale 2018); it therefore appears that phenology is not useful in distinguishing mines of the two species.

Phytomyza flavicornis Fallén

(Fig. 57)

Material examined. IOWA: Winneshiek Co., Roslien Woods, 1.ii.2018, em. 18.ii.2018, J. van der Linden, ex *Urtica dioica*, #CSE4943, CNC1643673–1643674 ($1 \circlearrowleft 1 \circlearrowleft$).

Hosts. Urticaceae: Urtica dioica L.; adults have been caught on U. gracilis Aiton (Spencer 1969).

Larval biology. The larva bores in the pith of the stem and roots.

Puparium. (Fig. 57) Slender and yellowish, with deep intersegmental grooves; formed within the stem.

Phenology and voltinism. Pupae overwinter, with adults emerging in spring. Collection dates for adults range from 23 April in Oregon to 7 July in Manitoba (Spencer 1969; Spencer & Steyskal 1986).

Distribution. USA: *IA, IN, MI, OR; Canada: AB, MB, ON; Europe (Spencer 1969; Spencer & Steyskal 1986).

Phytomyza flavilonicera Eiseman & Lonsdale, spec. nov.

(Figs. 48–52, 82–83, 148–153)

Holotype. USA. OKLAHOMA: Payne Co., Stillwater, Bustani Plant Farm, 22.iv.2018, em. 4–14.v.2018, M.W. Palmer, ex *Lonicera sempervirens*, #CSE4480, CNC1144151 (13).

Paratypes. OKLAHOMA: same data as holotype, CNC1144152–1144157 (3♂ 3♀); Payne Co., Stillwater, Bustani Plant Farm, 22.iv.2018, em. 29.iv.2018, M.W. Palmer, ex *Lonicera flava*, #CSE4614, CNC1135622–1135624 (3♀); same data, #CSE4621, CNC1135639–1135640 (2♀); em. 5.v.2018, #CSE4623, CNC1144147–1144150 (1♂ 3♀); Bustani Plant Farm, 22.iv.2018, em. 22–25.iv.2018, M.W. Palmer, ex *Lonicera sempervirens*, #CSE4450, CNC1144144, CNC1144146 (1♂ 1♀); em. 29.iv.2018, #CSE4616, CNC1135618–1135621 (1♂ 3♀); em. 6.v.2018, #CSE4618, CNC1135610–1135618 (5♂ 4♀); Sanborn Lake, 9.vi.2017, em. 18.vi.2017, M.W. Palmer, ex *Lonicera sempervirens*, #CSE3940, CNC939928 (1♀).

Etymology. The specific epithet is a noun in apposition, a portmanteau referring to the yellow head of the adult (L. *flavus*—yellow) and the host plant genus, *Lonicera* L.

Hosts. Caprifoliaceae: Lonicera flava Sims, L. sempervirens L.

Leaf mine. (Figs. 82–83) Whitish, on the upper leaf surface; initially stellate, and in some cases remaining a small, digitate blotch throughout development; in other cases one or a few linear branches emanate from the stellate beginning. Frass forms a dark central patch in the stellate portion and is otherwise deposited in closely spaced grains or beaded strips.

Puparium. (Fig. 52) Whitish to pale brown, with a broad, dark, elongate central band on the ventral surface; formed within the mine, with the ventral surface against the upper epidermis.

Phenology and voltinism. This species is probably multivoltine. Leaf mines have been collected in April with adults emerging from late April to mid-May, as well as in early June with an adult emerging in mid-June.

Distribution. USA: OK.

Adult description. Wing length 1.5–1.6 mm (\circlearrowleft), 1.7–1.8 mm (\circlearrowleft). Vein dm-m absent. Eye height divided by gena height: 3.7–4.2. First flagellomere slightly longer than high, stout and appearing somewhat enlarged with dorsal and ventral margins parallel for short distance medially. Orbital plate projecting along anterodorsal eye margin (seen laterally). Cheek distinct. Posterior ocelli slightly displaced. Thorax pruinose (see below).

Chaetotaxy: Two ors, two ori, decreasing in length anteriorly; anterior ori sometimes setula-like; sometimes smaller third ori present on one side posteriorly; one ors sometimes missing. Postvertical seta subequal to posterior ors. Ocellar seta slightly shorter than postvertical. Four dorsocentral setae, decreasing in length anteriorly. Approximately six scattered rows of acrostichal setulae. Setulae on pleuron nearly absent.

Coloration: (Figs. 48–51) Setae dark brown. Head mostly light yellow; first flagellomere dark brown, scape and pedicel deep yellow; back of head, vertex (slightly paler), broad spot around ocellar tubercle and posterolateral corner of frons past base of inner vertical seta dark brown; orbital plate dark brown posteriorly with stripe extending to surround base of posterior ors and paler stripe with slight silvery pruinosity extending to meet base of anterior ors; slight mottling at base of posterior ori; remainder of orbital plate and frontal vitta dirty yellow; clypeus greyish-brown, very narrow and pale medially; palpus brown. Thorax dark brown dorsally, paler on pleuron; with bluish-grey pruinosity that is dense on notum and with a coppery tint posteriorly on scutum and scutellum; yellow mottling along notopleural sutures and postalar wall; anterior spiracle and vertical line dorsal to it yellow; anepisternum sometimes with margins irregularly yellow; yellow above coxopleural streak; halter yellow. Wing veins light brownish-yellow. Legs brown; apices of fore and mid coxae yellow; apices of femora yellow for distance equal to width of femur apex; bases of tibiae yellow (spot narrower on posterior legs) and dorsal apex of fore tibia yellow; fore tarsus brownish-yellow. Abdomen brown with lateral margin of tergites yellow; epandrium paler brown with anterior and posterior margins yellow. Calypter yellow with hairs light brown to golden.

Variation. Female: Pigmented line along vertex paler, usually at least at base of postvertical setae. Apex of fore tibia faintly yellow; fore tarsus light brown. Abdominal tergites entirely brown or with very narrow yellow margin restricted to tergites 1–3. Calypter hairs light brown to brown.

Genitalia: (Figs. 148–153) Surstylus small, rounded, incurved, short setose; fused to epandrium. Hypandrium subtriangular with broad, rounded apex; inner lobe narrow, V-shaped with two apical setae. Postgonite narrow with one seta. Phallophorus simple, cylindrical, with one pair of narrow band-like lateral lobes. Basiphallus consisting of one pair of long narrow plates with irregular margins and tapered apices; right plate with base positioned dorsally, left plate with base wrapping around venter. Hypophallus (one pair of lateral sclerites) small, irregular in outline, longer than wide; some dissected males with sclerite atrophied to entirely absent. Mesophallus not evident. Distiphallus short, sharply angled dorsally, narrow; when viewed ventrally, with wider, rounded base that splits into one pair of narrow subparallel bands that slightly diverge apically and appear slightly bifid with outer arm weaker and shorter. Ejaculatory apodeme very small, weakly sclerotized, with long weak tubule emerging from base opposite duct; sperm pump clear.

Comments. The leaf mine of *Phytomyza flavilonicera* is similar to that of *P. sempervirentis* Eiseman & Lonsdale, which also occurs on *Lonicera sempervirens*, but the latter species usually moves to the lower leaf surface before pupating, and the dark ventral area on its puparium is usually a narrow stripe rather than a broad band (Eiseman & Lonsdale 2018). However, a pair of mines photographed in Missouri (Hartley 2017) seems to be within the range of variation of both species. The two are not known to be sympatric, with *P. flavilonicera* found only in Oklahoma and *P. sempervirentis* recorded from Oregon, Massachusetts, North Carolina, and Alabama, but more collecting of these mines from Midwestern states will be needed to clarify the extents of their distributions.

Twelve parasitoids reared from *Phytomyza flavilonicera* were identified by J.T. Huber as *Diglyphus websteri* (Crawford) (Eulophidae), a specialist on Agromyzidae but with a wide host range within this family.

Phytomyza flavilonicera is a relatively pale Caprifoliaceae-mining Phytomyza, being yellowish laterally on the scutum (the central disc is bluish-grey pruinose), and paler on the pleuron and legs with the knees yellowish. The head is also mostly pale, having a yellow face, a dirty yellow frontal vitta and anteriorly yellowish orbital plate. It is further characterized by having numerous rows of acrostichals, a small to absent subovate sclerite on the hypophallus, and a relatively small, simple, upturned distiphallus. In ventral view, the outline of the distiphallus differs from that of similar species such as P. nigrilineata in being very narrow with a broader lobate base, and it is medially split past the insertion point of the duct, with the points slightly diverging, fading and appearing partially bifurcated apically. This distiphallus structure is similar to some P. sempervirentis Eiseman & Lonsdale (see Eiseman & Lonsdale 2018: Figs. 358, 359), but this is a darker species with a brown head, the distiphallus is much more wedge-shaped in appearance laterally and in ventral view a dark V-shape predominates.

Phytomyza flexuosa Spencer

Material examined. IOWA: Winneshiek Co., Beard Farm, 27.v.2018, em. spring 2018, J. van der Linden, ex *Ranunculus abortivus*, #CSE4646, CNC1144044–1144046 ($1 \stackrel{>}{\circ} 2 \stackrel{\frown}{\circ}$).

Host. *Ranunculaceae: Ranunculus abortivus L.

Leaf mine. A blotch formed at the apex of a leaf lobe.

Puparium. Formed outside the mine.

Phenology and voltinism. Our specimens were collected as larvae on 27 May and emerged as adults within a few weeks. The holotype was collected as an adult on 27 August (Spencer & Steyskal 1986).

Distribution. USA: *IA, WA (Spencer & Steyskal 1986).

Comments. This species was described from a single specimen caught while sweeping *Erigeron canadensis*, but its host was presumed to be in Ranunculaceae due to the close similarity of the genitalia to those of *Phytomyza davisii* (Walton). The latter species also feeds on *Ranunculus abortivus*, forming blotch mines and pupating externally (Eiseman & Lonsdale 2019).

Phytomyza krygeri Hering

Material examined. MASSACHUSETTS: Franklin Co., Northfield, 42.647283, -72.424726, 20.vi.2017, em. 26.iv–6.v.2018, C.S. Eiseman, ex *Aquilegia canadensis* seedpods, #CSE4441, CNC1135721–1135728 ($5\marringle$ 3); **WISCONSIN:** Vernon Co., Battle Bluff Prairie State Natural Area, 43°18′5.04″N 91°48′6.60″W, 13.vi.2017, em. spring 2018, J. van der Linden, ex *Aquilegia canadensis*, #CSE4947, CNC1288661–1288662 ($2\marringle$).

Hosts. Ranunculaceae: Aquilegia *canadensis L., A. vulgaris L. (Lonsdale 2017b).

Larval biology. Larvae feed in developing seed pods, which become distorted and discolored brown.

Puparium. Formed within the seed pod; subshining and dark brown, almost black; similar in size and appearance to the remains of the slightly paler brown seeds damaged by larval feeding (Lonsdale 2017b).

Phenology and voltinism. This species is univoltine, overwintering as pupae. In Ottawa, adults are present in May and puparia are formed by the end of June (Lonsdale 2017b).

Distribution. *USA: [IA], MA, WI; Canada: ON; Europe (Lonsdale 2017b).

Comments. This European species was discovered ovipositing in flowers of cultivated European columbine in Ottawa, Ontario in the spring of 2015 (Lonsdale 2017b). The new rearing records, along with larvae and puparia we observed in northeastern Iowa in June 2018, indicate that it is already widespread in the USA and utilizing native columbines.

Phytomyza notopleuralis Spencer

(Figs. 58, 84)

Material examined. MASSACHUSETTS: Berkshire Co., Great Barrington, 42.197870, -73.335897, 17.ix.2017, em. ~16.iv.2018, C.S. Eiseman, ex *Cornus sericea*, #CSE4416, CNC1144083–1144084 (1♂1♀).

Host. *Cornaceae: Cornus sericea L.

Leaf mine. (Fig. 84) Entirely linear, on the upper leaf surface; frass in somewhat liquidy strips along the sides.

Puparium. Shining dark brown with paler brown intersegmental boundaries; formed outside the mine.

Phenology and voltinism. Our specimens were collected as larvae in mid-September and emerged as adults the following spring. There is presumably at least one earlier generation; the only other known specimens were collected as adults on 3 June (Ontario) and 9 July (Michigan) (Spencer 1969; Spencer & Steyskal 1986).

Distribution. USA: *MA, MI; Canada: ON (Spencer & Steyskal 1986).

Comments. Neither Spencer (1969) nor Spencer & Steyskal (1986) made any statements about the possible relationships of *Phytomyza notopleuralis* to other *Phytomyza*. Winkler *et al.* (2009) indicated that it is near *P. spinaciae* Hendel, a Palearctic species mining leaves of Cynareae (Asteraceae) and forming a white puparium within the leaf, and placed it in the *syngenesiae* group. However, the leaf mine is identical with that of *P. agromyzina* Meigen, which feeds on various dogwoods including *Cornus sericea*, and the younger *P. notopleuralis* may eventually prove to be its junior synonym. External morphology is nearly identical, excluding the presence of a strongly pale yellow notopleuron in *P. notopleuralis* (Fig. 58) (yellowish tint with margins yellower in *P. agromyzina*), and the genitalia (Spencer 1969: Fig. 470) only differ in that the distiphallus of *P. agromyzina* is basally straight (not shallowly curved) and sometimes slightly abbreviated; the apex of the distiphallus is also sometimes a bit straighter. The phallus of *P. agromyzina* illustrated in Spencer (1969: Fig. 395) shows the distiphallus as a simple membranous lobe without the narrow, apically forked and medially deviated sclerotized band; this is apparently an artifact of illustration, as this structure is present in all dissected material examined at the CNC.

Phytomyza palmeri Eiseman & Lonsdale

Material examined. OKLAHOMA: Payne Co., Mehan, 36.013839°, -96.998103°, 15.xi.2017, em. 22.xi.2017, M.W. Palmer, ex *Symphoricarpos orbiculatus*, #CSE4380, CNC1135649 (1♂); 30.xii.2017, em. 30.xii.2017, M.W. Palmer, ex *Symphoricarpos orbiculatus*, #CSE4375, CNC1144114–1144115 (1♂ 1♀).

Host. Caprifoliaceae: *Symphoricarpos orbiculatus* Moench.

Leaf mine. Upper surface, gradually widening, at least sometimes linear throughout, but often contorted to form a secondary blotch. The black frass is in closely spaced grains or beaded strips, allowing the larva's path to be traced even when the mine forms a nearly continuous blotch (Eiseman & Lonsdale 2018).

Puparium. Brown; formed within the mine, its anterior spiracles projecting ventrally through the upper epidermis (Eiseman & Lonsdale 2018). A broad, dark ventral stripe is at least sometimes present, as in *Phytomyza flavilonicera*, but this is not evident in all photographed mines, perhaps due to the rest of the puparium being fairly dark and not providing sufficient contrast to show through the epidermis.

Phenology and voltinism. 25 October is the earliest date we have found probable mines of this species, with some mines recently initiated and some already complete. Specimens have been reared from mines collected between 7 November and 30 December, with adults emerging indoors without a pupal diapause (17 November to 30 December).

Distribution. USA: OK.

Comments. These additional rearings do not provide new host or distribution records for *Phytomyza palmeri*, but it is worth noting that the genitalia of these specimens differ slightly from those of the type series, representing new intraspecific variation. While agreeing in overall external and genitalic morphology, the apex of the ill-defined and slightly annulated distiphallus of the new specimens is slightly larger, in some cases up to ½ longer, and one male has a slight medial constriction in the segment (seen ventrally).

Phytomyza solidaginophaga Sehgal

Material examined. IOWA: Winneshiek Co., Decorah, Twin Springs Park, 24.v.2017, em. ?, J. van der Linden, ex *Solidago flexicaulis*, #CSE4670, CNC1144022 (13).

Hosts. Asteraceae: *Solidago caesia* L., *S. canadensis* L., *S. *flexicaulis* L., *S. patula* Muhl. ex Willd., *S. rugosa* Mill., *S. simplex* Kunth (Eiseman & Lonsdale 2018); see Comments for other likely hosts.

Leaf mine. Greenish-white to greenish-brown, entirely linear, with frass in closely spaced grains, partly forming short beaded strips (Eiseman & Lonsdale 2018).

Puparium. Black; formed outside the mine.

Phenology and voltinism. This species is univoltine, overwintering as pupae, with larvae present only in spring. Although Alberta collection dates range from 7 to 13 June (Griffiths 1976), larvae have only been found from 11 to 24 May in the USA (Eiseman & Lonsdale 2018).

Distribution. USA: CO (Winkler et al. 2009), *IA, MA; Canada: AB, [YT] (Eiseman & Lonsdale 2018).

Comments. Given that the latest recorded date for larvae of *Phytomyza solidaginophaga* in the USA (24 May) is more than two weeks before the earliest recorded date for *P. astotinensis* (9 June; this paper), we believe mines found in Massachusetts on two additional hosts likely represent *P. solidaginophaga*: occupied mines on *Solidago gigantea* Aiton between 18 and 22 May, and a mine on *S. arguta* Aiton containing a dead larva on 25 May. An occupied mine on *S. speciosa* Nutt. photographed on 31 May in Wisconsin (Klein 2019) may also represent *P. solidaginophaga*.

Phytomyza thermarum (Griffiths)

(Fig. 85)

Material examined. VERMONT: Windham Co., Marlboro, Hogback Mountain, 42.852158, -72.797828, 21.vi.2018, em. 4.vii.2018, C.S. Eiseman, ex *Erigeron pulchellus*, #CSE4720, CNC1135661 (13).

Hosts. Asteraceae: Erigeron philadelphicus L. (Griffiths 1976), E. *pulchellus Michx.

Larval mine. (Fig. 85) Partly in the stem, petiole, and basal part of the leaf midrib, with whitish linear channels radiating into the blade. These channels are mostly more or less full-depth but may be on the upper or lower surface. Frass is mostly in discrete grains (partly forming beaded strips in most mines according to Griffiths (1976)).

Puparium. White or yellowish-white, formed within the mine, either in the petiole or on the lower surface of the blade, with its anterior spiracles projecting ventrally through the epidermis (Griffiths 1976).

Phenology and voltinism. This species is evidently multivoltine in western Canada, with larvae collected in early June emerging as adults within two weeks, larvae and puparia collected in mid-July emerging as adults in late July and early August, and those collected in early September emerging as adults within a month (Griffiths 1976).

Distribution. *USA: VT; Canada: AB, BC (Griffiths 1976). Mines possibly representing this species have been found on *Erigeron philadelphicus* in PA (Schultz 2020).

Phytomyza tiarellae Griffiths

Material examined. WASHINGTON: Thurston Co., Lacey, Chehalis Western Trail / S. 45th Ave., 11.iii.2018, em. ?, E. Stansbury, ex *Tolmiea menziesii*, #CSE4608, CNC1135594–1135595 (1 \circlearrowleft 1 \circlearrowleft); Olympia, Watershed Park, 15.iii.2018, em. ?, E. Stansbury, ex *Tolmiea menziesii*, #CSE4607, CNC1135586 (1 \circlearrowleft); Olympia, Watershed Park, 11.v.2018, em. 29.v.2018, ex *Tellima grandiflora*, E. Stansbury, #CSE5038, CNC934532–934534 (2 \circlearrowleft 1 \circlearrowleft); Tolmie State Park, 23.v.2018, em. 8.vi.2018, E. Stansbury, ex *Tiarella trifoliata*, #CSE4610, CNC1144078 (1 \circlearrowleft); same but em. 11.vi.2018, #CSE4609, CNC1135583 (1 \circlearrowleft).

Photographed mine. BRITISH COLUMBIA: Vancouver Island, Sooke, 10.viii.2019, Mews, *Tiarella trifoliata*, iNat 30890584.

Hosts. Saxifragaceae: *Heuchera micrantha* Douglas, *Tellima grandiflora* (Pursh) Douglas ex Lindl. (Spencer 1981), *Tiarella trifoliata* L., *Tolmiea menziesii* (Pursh) Torr. & A.Gray (Griffiths 1972).

Leaf mine. Upper-surface; entirely linear, "appearing white in incident light, up to 20-25 cm long, about 2 mm wide terminally; faeces scattered as discrete particles (mostly separated by over 1 mm), or forming short "threads" (Fadenstucke) in terminal part of mine" (Griffiths 1972).

Puparium. Brown or white, with darker strip on ventral surface; formed within the leaf, on the lower surface, with its anterior spiracles projecting ventrally through the lower epidermis (Griffiths 1972).

Phenology and voltinism. In Alaska, larvae and puparia collected in late August yielded one adult in early September and one the following spring. From this, Griffiths (1972) concluded that this species is at least partly

multivoltine. The Washington material collected in March likely involved puparia that had overwintered, with the next generation represented by the mines collected in late May, which yielded adults in early to mid-June.

Distribution. USA: AK (Griffiths 1972), CA (Spencer 1981), [OR] (see below), WA; [Canada: BC].

Comments. This species was reported from Washington previously, but based only on a female specimen (Winkler et al. 2009). The California records of Spencer (1981) are based on a male and female reared from Heuchera micrantha in Santa Cruz Co., along with leaf mines found on Tellima grandiflora in Marin Co. Griffiths (1972) also reported the latter host based only on leaf mines, and the CSE5038 specimens are the first actually to be reared from Tellima. Eiseman & Lonsdale (2018) reported as "Phytomyza sp. 7" a female reared from Tiarella trifoliata in Oregon that could not be confidently identified as P. tiarellae, but this specimen does fit within the known range of P. tiarellae and we thus have not seen evidence that there is another species west of the Rocky Mountains whose leaf mine could be mistaken for that of P. tiarellae.

Phytomyza triostevena Eiseman & Lonsdale, spec. nov.

(Figs. 53-56, 86, 154-158)

Holotype. USA. IOWA: Allamakee Co., 5.ix.2017, puparium removed from midrib 26.ix.2017, adult em. by spring 2018, J. van der Linden, ex *Triosteum*, #CSE4663, CNC1144064 (13).

Etymology. The specific epithet is a noun in apposition, a portmanteau referring to the position of the larval mines in the veins and midribs of leaves of *Triosteum* L. (L. *vena*—a vein).

Host. Caprifoliaceae: *Triosteum* L.; similar leaf mines have been found on *T. aurantiacum* E.P.Bicknell (Mews 2019a).

Leaf mine. (Fig. 86) The larva initially forms a narrow, serpentine mine in the leaf blade. It soon enters a lateral vein and follows this to the midrib, in which it feeds until mature.

Puparium. (Fig. 56) Brown; formed within the midrib, near the base of the leaf.

Phenology and voltinism. Leaf mines have been observed beginning in early September, with adults probably not emerging until the following spring.

Distribution. USA: IA; similar leaf mines have been found in Canada: ON (Mews 2019a).

Adult description. Wing length 1.8 mm (3). Female unknown. Vein dm-m absent. Eye height divided by gena height: 3.5. First flagellomere rounded, as long as high. Orbital plate well-defined, pruinose, narrowing anteriorly. Frontal vitta minutely pitted, appearing darker. Cheek well-developed. Thorax subshining.

Chaetotaxy: Two ori (anterior seta slightly shorter and positioned closer to eye margin); one ors. Ocellar seta subequal to anterior ori; postvertical subequal to ors. Four dorsocentral setae, decreasing in length anteriorly, with anterior two much shorter (less than half length of first seta). Approximately four to five irregular rows of acrostichal setulae.

Coloration: (Figs. 53–55) Setae dark brown. Body dark brown to black; with thick greyish pruinosity on thorax that is more distinct on scutum; gena, parafacial and lunule brown; inner margin of orbital plate beige; halter whitish-yellow. Calypter yellow, hairs light brown.

Genitalia: (Figs. 154–158) Surstylus small, rounded, fused to venter of epandrium, curved posteriorly with dense apical cluster of short setae. Cercus small. Hypandrium broadly rounded; inner lobe V-shaped with two medial setae. Postgonite simple and narrow with one seta. Phallophorus cylindrical with anterodorsal margin lengthened to reach base of basiphallus; lateral lobe simple, narrow. Basiphallus consisting of one pair of long, narrow plates with irregular margins and narrower apices; right plate with base positioned dorsally, left plate with base wrapping around venter. Hypophallus (one pair of lateral sclerites) small, irregular-ovate in outline. Mesophallus not evident. Paraphallus very small, with irregular subovate outline. Distiphallus sharply angled dorsally, thick with apex narrower and slightly curved; seen "ventrally", outline X-shaped with short arms and long middle section, with apical arms shorter, irregular and less well-defined, each ending in its own small membranous lobe. Ejaculatory apodeme not found.

Comments. This is the second agromyzid to be reared from *Triosteum*, after *Aulagromyza orbitalis*. Also in Iowa, we have found mines representing two other *Phytomyza* species, presumably likewise in the *periclymeni* superspecies. One is an entirely linear mine in the leaf blade, with frass in closely spaced grains and with a brown puparium formed at the end; the other is digitate and centered on the midrib, similar to those of *P. chamaemetabola* (Griffiths) and *P. gregaria* Frick on *Lonicera involucrata* (Richardson) Banks ex Spreng. (Griffiths 1974).

Phytomyza triostevena is a modestly sized and almost entirely dark species with one ors and pale greyish-blue pruinosity on the thorax. Among the Caprifoliaceae mining Phytomyza, it can be differentiated by having numerous rows of acrostichal setulae, and a small pair of lateral sclerites on the hypophallus that are irregularly ovate in outline and positioned distal to the end of the basiphallus; this combination of characters will key it approximately to P. nigrilineata (Griffiths) in Griffiths (1974). The small, upturned distiphallus must be examined for confident diagnosis; in lateral view, it is relatively stout with the apex narrowed and curved, and in ventral view, is more than twice as long as wide with shallow bifurcations at either end, appearing somewhat X-shaped; the distal points are shallower, somewhat ill-defined and annulated.

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FIGURES 1–12. Figures 1–4: *Melanagromyza arnoglossi* Eiseman & Lonsdale, **spec. nov.**; 1: holotype, dorsal; 2: same, head; 3: same, lateral; 4: puparium. Figures 5–8: *M. gentianivora* Eiseman & Lonsdale, **spec. nov.**; 5: paratype, dorsal; 6: same, head; 7: same, lateral; 8: puparium. Figures 9–12: *M. hieracii* Eiseman & Lonsdale, **spec. nov.**; 9: holotype, dorsal; 10: same, head; 11: same, lateral; 12: puparium.



FIGURES 13–23. Figures 13–15: *Melanagromyza rudbeckiae* Eiseman & Lonsdale, spec. nov.; 13: paratype, dorsal; 14: same, head; 15: same, lateral. Figures 16–19: *M. urticae* Eiseman & Lonsdale, spec. nov.; 16: holotype, dorsal; 17: same, head; 18: same, lateral; 19: puparia. Figures 20–23: *M. verbenivora* Eiseman & Lonsdale, spec. nov.; 20: holotype, dorsal; 21: same, head; 22: same, lateral; 23: puparium.



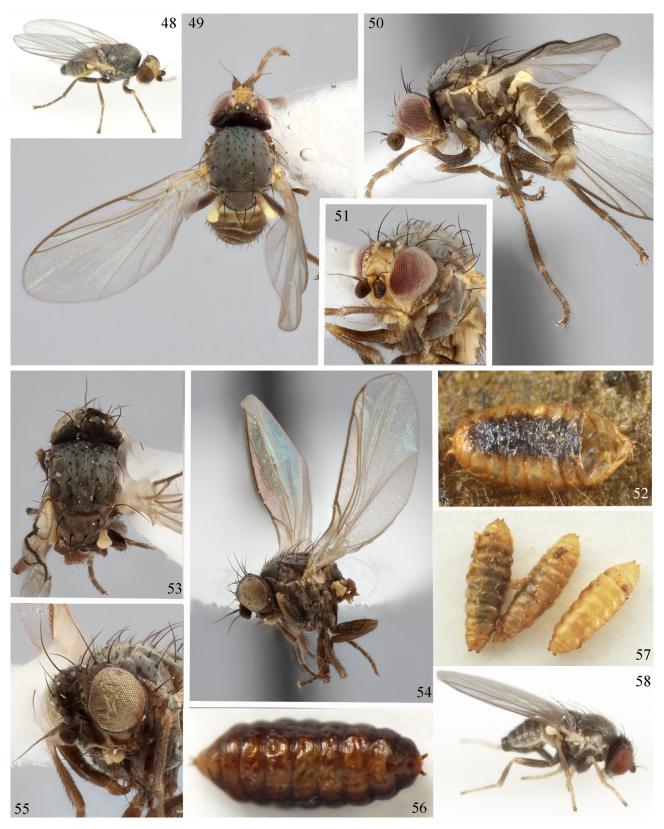
FIGURES 24–31. Figures 24–28: *Ophiomyia nabali* Eiseman & Lonsdale, **spec. nov.**; **24:** holotype, dorsal; **25:** same, head; **26:** same, lateral; **27:** puparium within host; **28:** same, host epidermis peeled back. **Figures 29–31:** *O. rugula* Eiseman & Lonsdale, **spec. nov.**; **29:** holotype, dorsal; **30:** same, head; **31:** same, lateral.



FIGURES 32–39. *Haplopeodes loprestii* Eiseman & Lonsdale, **spec. nov.**; **32:** holotype male; **33:** paratype female; **34:** puparia; **35:** holotype male, dorsal; **36:** same, lateral; **37:** same, head; **38:** paratype female, dorsal; **39:** same, lateral.



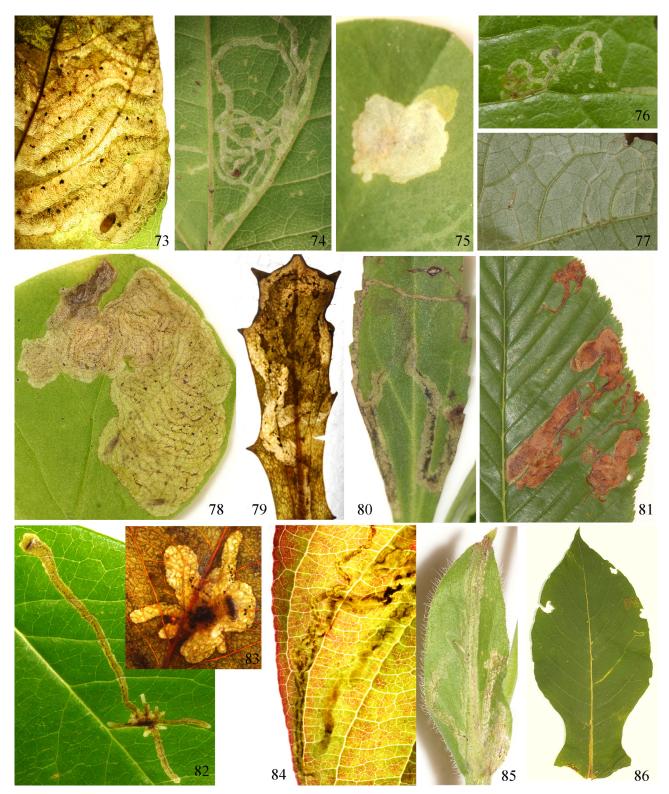
FIGURES 40–47. Figures 40–43: *Liriomyza euphorbivora* Eiseman & Lonsdale, spec. nov., holotype; 40: dorsal; 41: head; 42: lateral; 43: habitus. Figures 44–47: *L. hypopolymnia* Eiseman & Lonsdale, spec. nov.; 44: paratype, dorsal; 45: same, head; 46: same, lateral; 47: puparia.



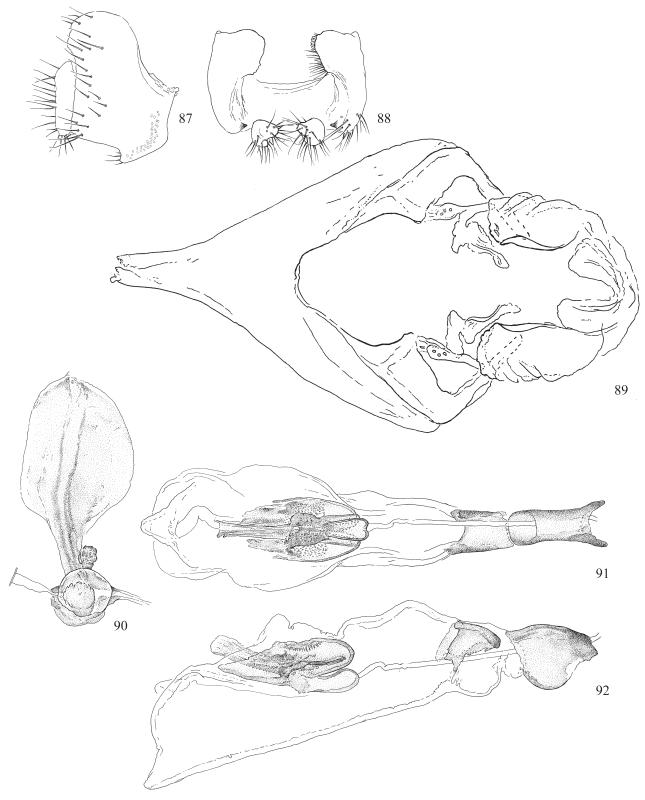
FIGURES 48–58. Figures 48–52: *Phytomyza flavilonicera* Eiseman & Lonsdale, spec. nov.; 48: paratype female habitus; 49: paratype male dorsal; 50: same, lateral; 51: same, head; 52: puparium. Figures 53–56: *P. triostevena* Eiseman & Lonsdale, spec. nov., holotype; 53: dorsal; 54: lateral; 55: head; 56: puparium. Figure 57: *P. flavicornis* Fallén, puparia. Figure 58: *P. notopleuralis* Spencer, female.



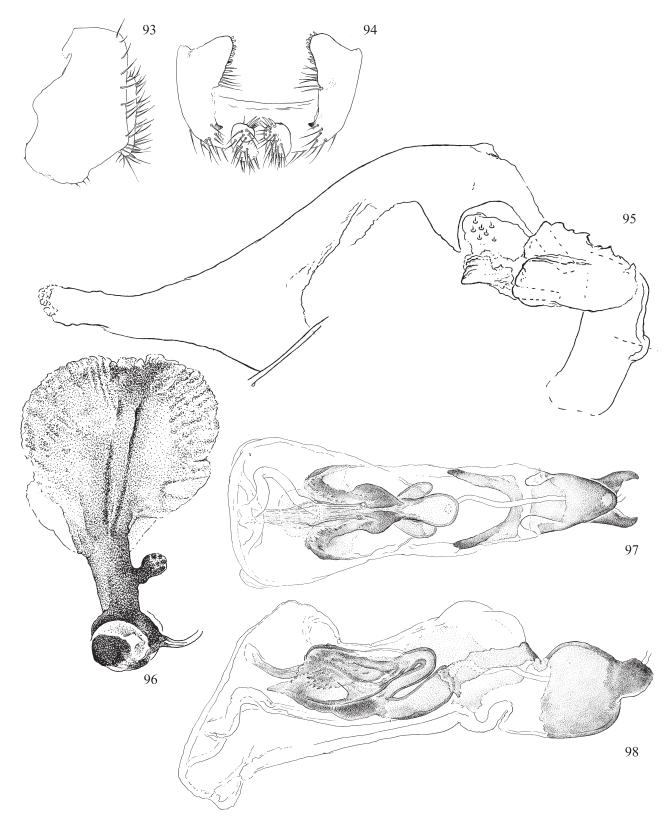
FIGURES 59–72. Mines and other feeding damage of Agromyzinae on host plants: 59: Agromyza aristata Malloch on Celtis laevigata; 60: Melanagromyza arnoglossi Eiseman & Lonsdale, spec. nov. on Arnoglossum sp.; 61: M. hieracii Eiseman & Lonsdale, spec. nov. on Hieracium scabrum; 62: M. minimoides Spencer on Rudbeckia lacinata; 63: same, section of flower head with puparia inside; 64: Ophiomyia abutilivora Spencer on Abutilon theophrasti; 65: same; 66: Melanagromyza verbenivora Eiseman & Lonsdale, spec. nov. on Verbena stricta, spiral gallery in stem with resulting leaf wilting; 67: same, affected seedhead; 68: Ophiomyia carolinensis Spencer on Symphyotrichum patens; 69: O. cf. frosti Spencer on Lactuca (puparium at upper right); 70: O. rugula Eiseman & Lonsdale, spec. nov. on Baccharis halimifolia; 71: same; 72: same, backlit, showing empty puparium.



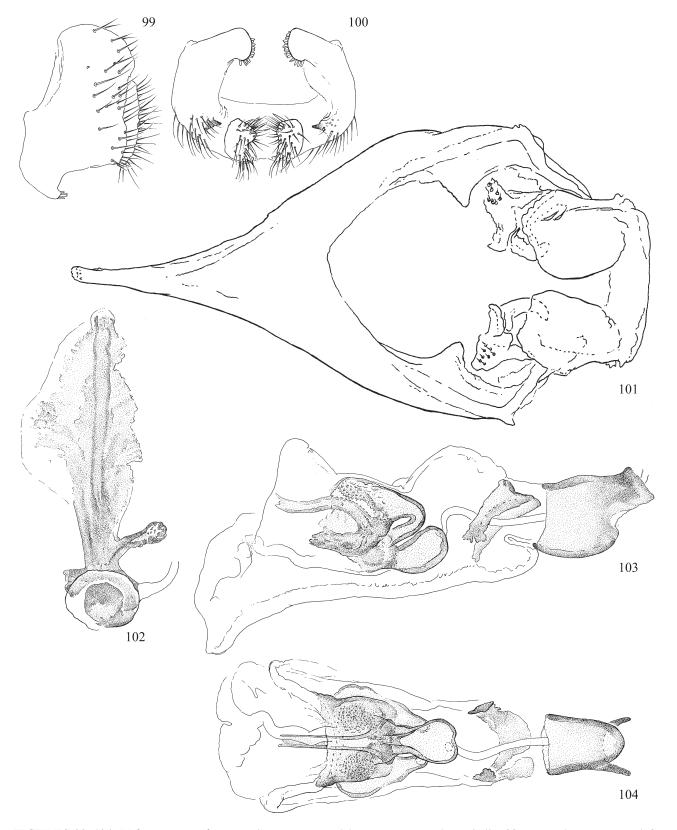
FIGURES 73–86. Mines of Phytomyzinae on host plants: 73: Liriomyza blechi Spencer on Ruellia carolinensis; 74: Liriomyza cf. cracentis Lonsdale on Ageratina altissima; 75: L. euphorbivora Eiseman & Lonsdale, spec. nov. on Euphorbia marginata; 76: L. hypopolymnia Eiseman & Lonsdale, spec. nov. on Polymnia canadensis, upper surface; 77: same, lower surface; 78: L. orilliensis on Nabalus sp.; 79: L. cf. taraxaci Hering on Krigia virginica; 80: L. trifolii (Burgess) on Mecardonia acuminata; 81: Phytomyza cf. aesculi Eiseman & Lonsdale on Aesculus flava; 82: P. flavilonicera Eiseman & Lonsdale, spec. nov. on Lonicera sempervirens; 83: same; 84: P. notopleuralis Spencer on Cornus sericea; 85: P. thermarum (Griffiths) on Erigeron pulchellus; 86: P. triostevena Eiseman & Lonsdale, spec. nov. on Triosteum sp.



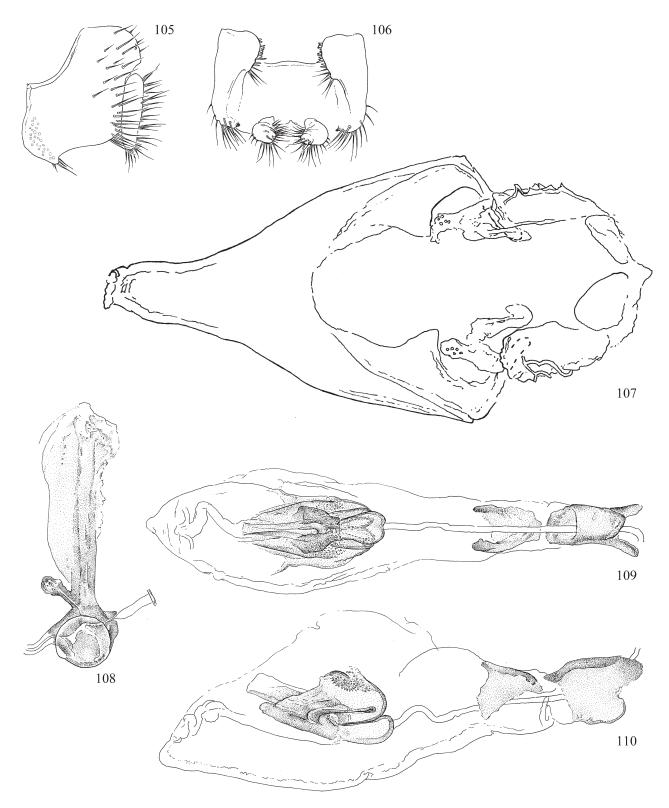
FIGURES 87–92. *Melanagromyza arnoglossi* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **87:** external components, right lateral; **88:** same, ventral; **89:** hypandrium to epiphallus, ventral; **90:** ejaculatory apodeme; **91:** phallus, ventral; **92:** same, left lateral.



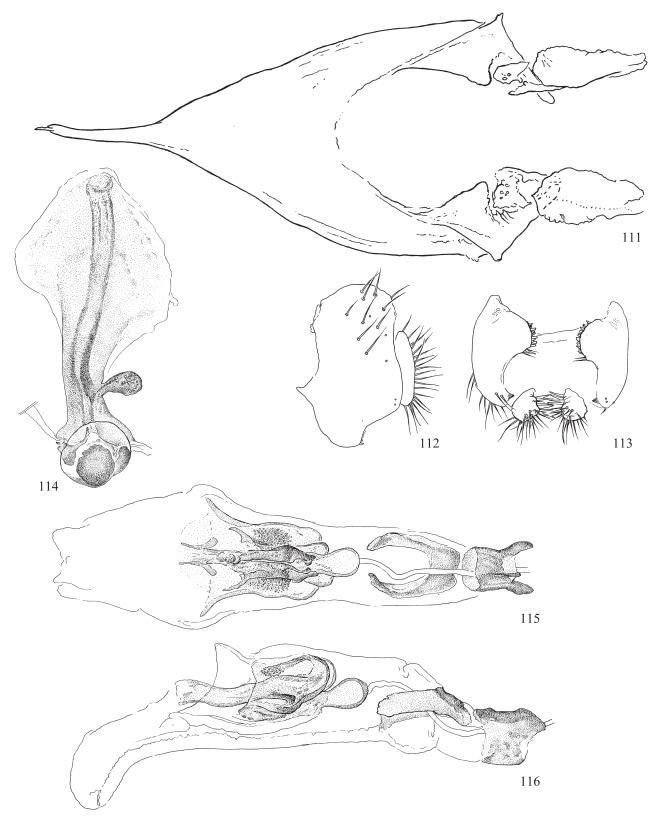
FIGURES 93–98. *Melanagromyza gentianivora* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **93:** external components, left lateral; **94:** same, ventral; **95:** hypandrium to epiphallus, ventral; **96:** ejaculatory apodeme; **97:** phallus, ventral; **98:** same, left lateral.



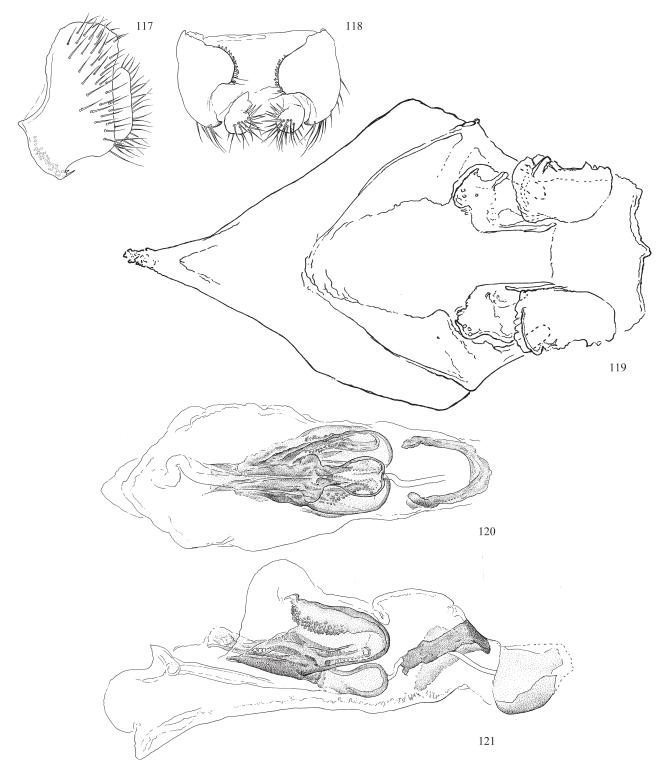
FIGURES 99–104. *Melanagromyza hieracii* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **99:** external components, left lateral; **100:** same, ventral; **101:** hypandrium to epiphallus, ventral; **102:** ejaculatory apodeme; **103:** phallus, left lateral; **104:** same, ventral.



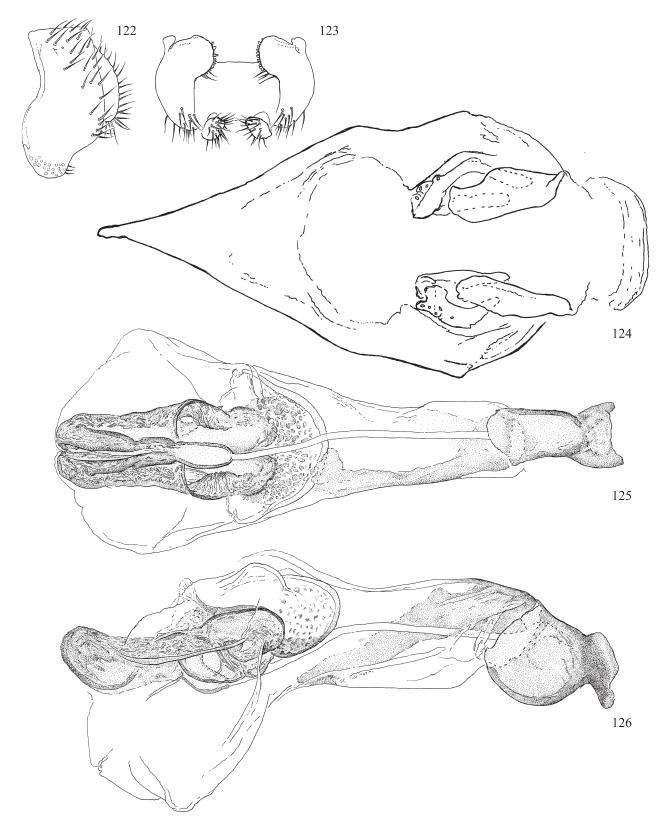
FIGURES 105–110. *Melanagromyza rudbeckiae* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **105:** external components, left lateral; **106:** same, ventral; **107:** hypandrium to epiphallus, ventral; **108:** ejaculatory apodeme; **109:** phallus, ventral; **110:** same, left lateral.



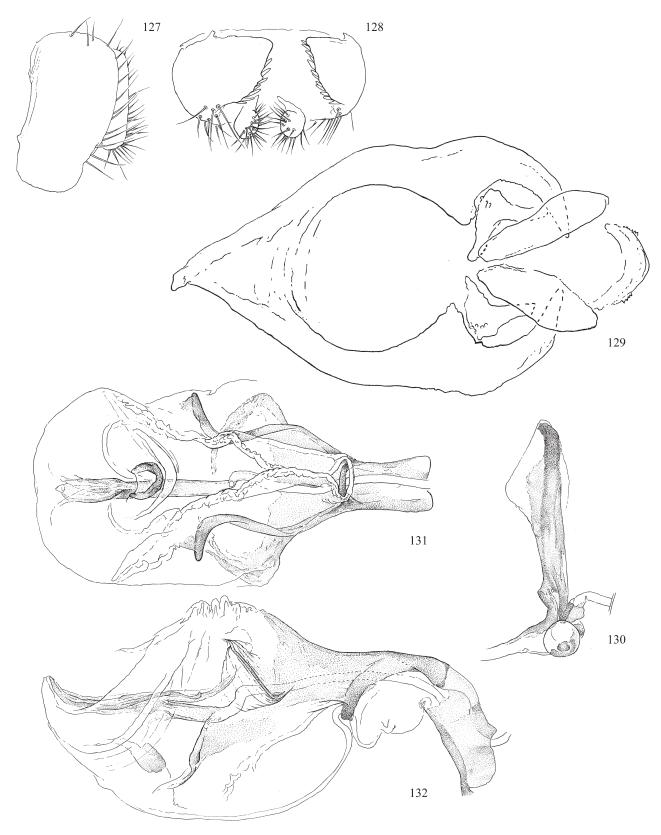
FIGURES 111–116. *Melanagromyza urticae* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **111:** hypandrium to epiphallus, ventral; **112:** external components, left lateral; **113:** same, ventral; **114:** ejaculatory apodeme; **115:** phallus, ventral; **116:** same, left lateral.



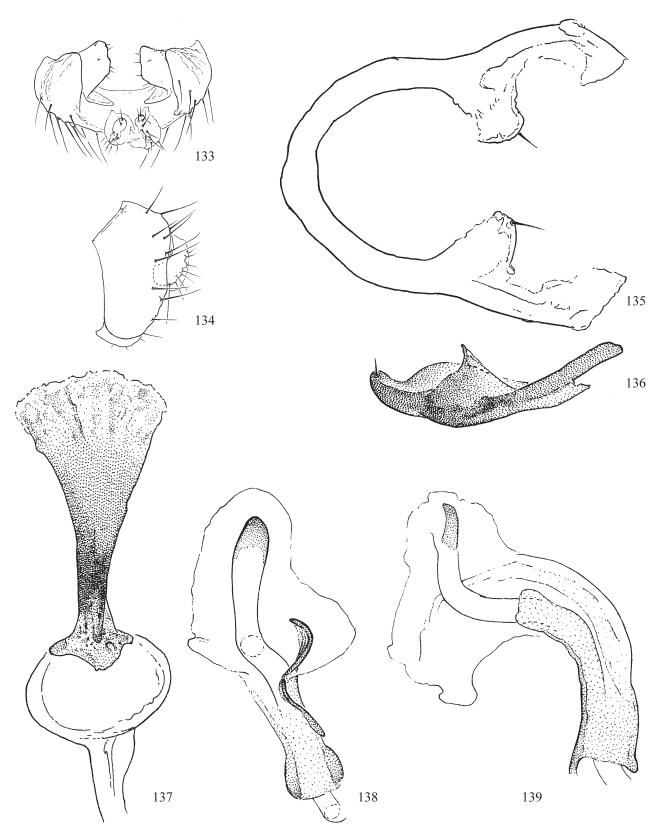
FIGURES 117–121. *Melanagromyza verbenivora* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **117:** external components, left lateral; **118:** same, ventral; **119:** hypandrium to epiphallus, ventral; **120:** phallus, ventral; **121:** same, left lateral.



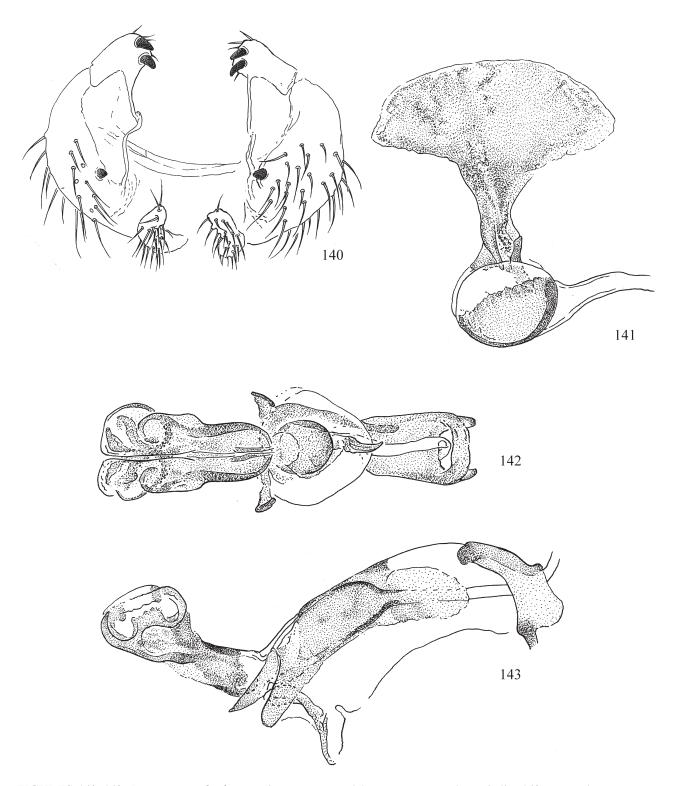
FIGURES 122–126. *Ophiomyia nabali* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **122:** external components, left lateral; **123:** same, ventral; **124:** hypandrium to epiphallus, ventral; **125:** phallus, ventral; **126:** same, left lateral.



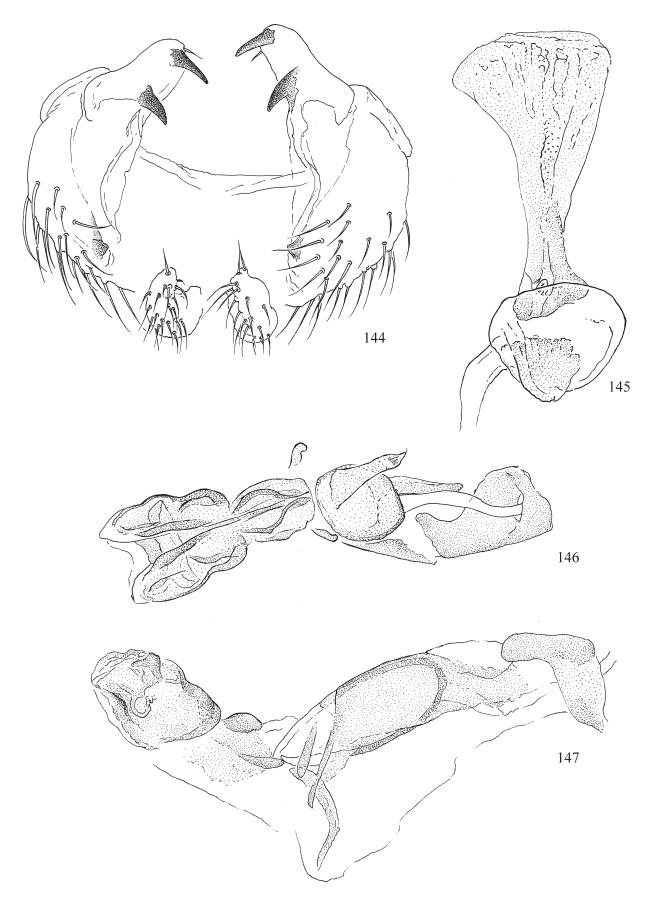
FIGURES 127–132. *Ophiomyia rugula* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **127:** external components, left lateral; **128:** same, ventral; **129:** hypandrium to epiphallus, ventral; **130:** ejaculatory apodeme; **131:** phallus, ventral; **132:** same, left lateral.



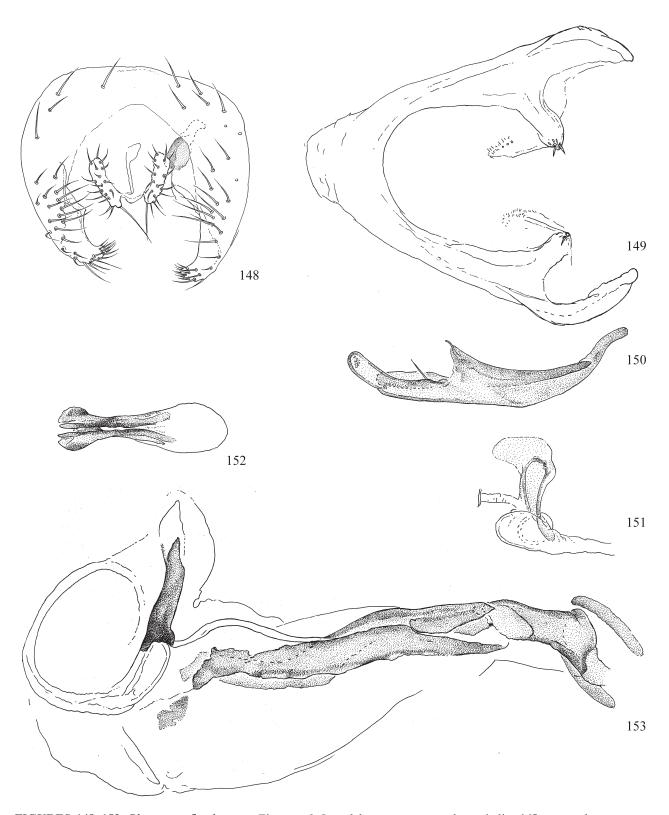
FIGURES 133–139. *Haplopeodes loprestii* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **133:** external components, ventral; **134:** same, left lateral; **135:** hypandrium, ventral; **136:** postgonite; **137:** ejaculatory apodeme; **138:** phallus, ventral; **139:** same, left lateral.



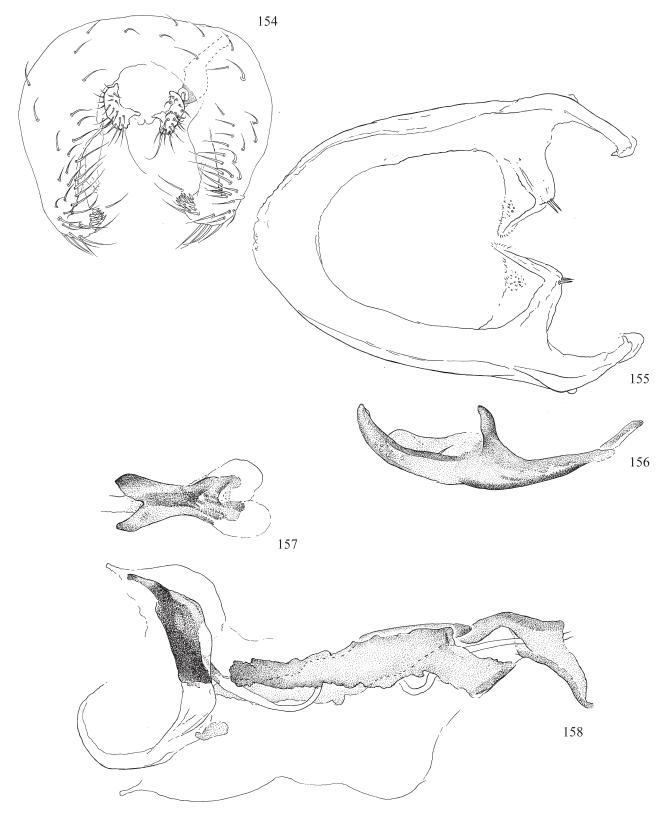
FIGURES 140–143. *Liriomyza euphorbivora* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **140:** external components, ventral; **141:** ejaculatory apodeme; **142:** phallus, ventral; **143:** same, left lateral.



FIGURES 144–147. *Liriomyza hypopolymnia* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **144:** external components, ventral; **145:** ejaculatory apodeme; **146:** phallus, ventral; **147:** same, left lateral.



FIGURES 148–153. *Phytomyza flavilonicera* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **148:** external components, posterior; **149:** hypandrium, ventral; **150:** postgonite; **151:** ejaculatory apodeme; **152:** distiphallus, ventral; **153:** phallus, left lateral.



FIGURES 154–158. *Phytomyza triostevena* Eiseman & Lonsdale, **spec. nov.**, male genitalia; **154:** external components, posterior; **155:** hypandrium, ventral; **156:** postgonite; **157:** distiphallus, ventral; **158:** phallus, left lateral.

Index of agromyzid genera and species

aenea (Melanagromyza)	13
abutilivora (Ophiomyia)	
aesculi (Phytomyza)	
agrios (Liriomyza)	29
Agromyza	
agromyzina (Phytomyza)	
akbari (Ophiomyia).	
angelicae (Melanagromyza)	
angulata (Cerodontha).	
arctii (Liriomyza) aristata (Agromyza)	
arnoglossi (Melanagromyza) 7-9.	
asclepiadis (Liriomyza).	
astotinensis (Phytomyza)	
Aulagromyza.	
balcanica (Liriomyza)	
blechi (Liriomyza)	
buccalis (Melanagromyza)	
Butomomyza	
carolinensis (Ophiomyia)	
Cerodontha	
chamaemetabola (Phytomyza)	
cirsiophila (Melanagromyza)	
conclavis (Liriomyza).	
confusa (Phytomyza)	
congesta (Liriomyza)	
congregata (Ophiomyia)	
cracentis (Liriomyza)	
davisii (Phytomyza)	
Dizygomyza	
doellingeriae (Phytomyza)	
eupatoriella (Liriomyza)	
eupatorii (Liriomyza)	
euphorbiella (Liriomyza)	
euphorbivora (Liriomyza). 27-29,	
flavicornis (Phytomyza)	
flavifrons (Amauromyza)	
flavilonicera (Phytomyza)	
flexuosa (Phytomyza)	36
frosti (Ophiomyia)	
gentianivora (Melanagromyza)	
gregaria (Phytomyza).	
Haplopeodes	
hicksi (Melanagromyza)	
hieracii (Melanagromyza). 9-10, 13,	
huidobrensis (Liriomyza)	
hypopolymnia (Liriomyza)	
incisa (Cerodontha)	21
ivorcutleri (Liriomyza)	
jacintensis group (Ophiomyia)	
krygeri (Phytomyza)	
lacertosa (Ophiomyia)	
Liriomyza 6, 8, 23-32, 47 longensis (Melanagromyza) 9	
loprestii (Haplopeodes)	
luteoscutellata (Aulagromyza).	
marginalis (Liriomyza).	
martini (Melanagromyza)	
<i>Melanagromyza</i>	, 49, 51-56

minimoides (Melanagromyza).	
morosa (Cerodontha)	
myrsinitae (Liriomyza)	
nigrilineata (Phytomyza).	
notopleuralis (Phytomyza)	
oligophaga (Melanagromyza).	
Ophiomyia	49, 57-58
orbitalis (Aulagromyza)	
orilliensis (Liriomyza)	
palmeri (Phytomyza).	
parca (Agromyza)	
pascuum (Liriomyza)	
peleensis (Liriomyza)	
periclymeni superspecies (Phytomyza). Phytomyza	
Poemyza	
pseudoreptans (Agromyza)	
pulicaria (Ophiomyia)	
pusilla (Liriomyza)	
radicicola (Melanagromyza)	11
reptans (Agromyza)	7
rudbeckiae (Melanagromyza)	
rugula (Ophiomyia)	
sabaziae (Liriomyza)	
sativae (Liriomyza)	
sempervirentis (Phytomyza)	
solidaginivora (Phytomyza)	
solidaginophaga (Phytomyza).	
sonchi (Liriomyza)	
spicatae (Ophiomyia)	
spinaciae (Phytomyza)	37
splendida (Melanagromyza)	
strigata (Liriomyza)	
subasclepiadis (Liriomyza)	
syngenesiae group (Phytomyza)	
taraxaci (Liriomyza)thermarum (Phytomyza)	
tiarellae (Phytomyza)	
tiliae (Ophiomyia)	
trifolii (Liriomyza)	
triostevena (Phytomyza)	18, 50, 63
urticae (Melanagromyza)	
urticella (Melanagromyza)	
urticivora (Melanagromyza)	
vectabilis (Melanagromyza)	
verbenae (Melanagromyza) 13-14, 4 verbenivora (Melanagromyza) 13-14, 4	
verbesinae (Melanagromyza).	
virginiensis (Melanagromyza).	
Index of host plant genera	
Abelmoschus (Malvaceae)	32
Abronia (Nyctaginaceae)	
Abutilon (Malvaceae)	
Aesculus (Sapindaceae).	
Ageratina (Asteraceae).	
Allium (Amaryllidaceae).	
Amaranthus (Amaranthaceae)	
Angelica (Apiaceae)	
Apium (Apiaceae)	
Aquilegia (Ranunculaceae).	

Arctium (Asteraceae).	
Arnoglossum (Asteraceae)	
Asclepias (Apocynaceae)	
Aster (Asteraceae).	
Atocion (Caryophyllaceae)	
Avena (Poaceae)	
Baccharis (Asteraceae)	
Bellis (Asteraceae)	
Beta (Amaranthaceae)	20, 32
Bidens (Asteraceae)	24, 26, 32
Borrichia (Asteraceae)	
Callistephus (Asteraceae)	
Capsicum (Solanaceae)	32
Carduus (Asteraceae)	8
Carex (Cyperaceae)	21-22
Celtis (Cannabaceae)	
Chenopodium (Amaranthaceae)	32
Chondrilla (Asteraceae)	17
Chrysanthemum (Asteraceae)	32
Cichorium (Asteraceae)	
Cirsium (Asteraceae)	8
Conoclinium (Asteraceae)	32
Cornus (Cornaceae)	36-37, 50
Cosmos (Asteraceae).	32
Crassocephalum (Asteraceae)	
Crotalaria (Fabaceae)	
Cryptotaenia (Apiaceae)	
Cucumis (Cucurbitaceae)	
Cucurbita (Cucurbitaceae)	
Dahlia (Asteraceae)	
Daucus (Apiaceae)	
Dianthus (Caryophyllaceae).	
Dichanthelium (Poaceae)	
Dicliptera (Acanthaceae)	
Diervilla (Caprifoliaceae).	
Digitaria (Poaceae).	
Doellingeria (Asteraceae)	
Enicostema (Gentianaceae).	
Epaltes (Asteraceae)	
Erechtites (Asteraceae)	
Erigeron (Asteraceae)	
Eupatorium (Asteraceae)	
Euphorbia (Euphorbiaceae)	
Euthamia (Asteraceae)	
Fagonia (Zygophyllaceae)	
Fallopia (Polygonaceae)	
Flaveria (Asteraceae)	
Gaillardia (Asteraceae).	
Galeopsis (Lamiaceae)	
Galinsoga (Asteraceae).	
Gamochaeta (Asteraceae).	
Gentiana (Gentianaceae)	
Gerbera (Asteraceae)	
Glechoma (Lamiaceae).	
Glyceria (Poaceae)	
Gypsophila (Caryophyllaceae)	
Helenium (Asteraceae)	
Helianthus (Asteraceae).	
Heliopsis (Asteraceae).	
Heliotropium (Boraginaceae).	
Heuchera (Saxifragaceae).	
Hibiscus (Malvaceae)	
Hieracium (Asteraceae)	
Hydrocotyle (Araliaceae).	
<i>y</i>	

<i>Hydrophyllum</i> (Hydrophyllaceae)
Hymenopappus (Asteraceae).
Hypochaeris (Asteraceae)
Juncus (Juncaceae)
Kallstroemia (Zygophyllaceae)
<i>Krigia</i> (Asteraceae)
<i>Lactuca</i> (Asteraceae). 15, 17, 31-32, 49
Lapsana (Asteraceae)
Lathyrus (Fabaceae)
Leucanthemum (Asteraceae). 32
Lonicera (Caprifoliaceae)
Malva (Malvaceae)
Mecardonia (Plantaginaceae)
Medicago (Fabaceae) 32
Melanthera (Asteraceae). 11, 32
Melothria (Cucurbitaceae)
<i>Mikania</i> (Asteraceae)
Mimulus (Phrymaceae)
Nabalus (Asteraceae)
Packera (Asteraceae)
Panicum (Poaceae)
Parthenium (Asteraceae)
Paspalum (Poaceae)
Persicaria (Polygonaceae)
Petunia (Solanaceae)
Phaseolus (Fabaceae) 32
Phyla (Verbenaceae)
Physalis (Solanaceae)
Piriqueta (Turneraceae)
Pisum (Fabaceae). 32
Plantago (Plantaginaceae)
Polymnia (Asteraceae) 29-30, 50
Prenanthes (Asteraceae)
Ranunculus (Ranunculaceae)
Rudbeckia (Asteraceae)
Ruellia (Acanthaceae)
Saponaria (Caryophyllaceae)
Scirpus (Cyperaceae). 21
Senecio (Asteraceae). 26, 32
Sida (Malvaceae)
Silene (Caryophyllaceae)
Silphium (Asteraceae)
Smallanthus (Asteraceae)
Solanum (Solanaceae).
Solidago (Asteraceae)
Sonchus (Asteraceae)
Spigelia (Loganiaceae)
Spinacia (Amaranthaceae)
Stellaria (Caryophyllaceae)
Symphoricarpos (Caprifoliaceae)
Symphyotrichum (Asteraceae) 11, 16-17, 25-26, 32, 49
Synedrella (Asteraceae)
Tagetes (Asteraceae) 32
<i>Taraxacum</i> (Asteraceae)
Tellima (Saxifragaceae)
Tiarella (Saxifragaceae)
Tilia (Malvaceae)
Tithonia (Asteraceae)
Tolmiea (Saxifragaceae)
Tribulus (Zygophyllaceae)
Tridax (Asteraceae)
Trifolium (Fabaceae)
Triosteum (Caprifoliaceae)
Ulmus (Ulmaceae)

Urtica (Urticaceae).	6-7, 11-13	5, 34
Verbesina (Asteraceae)	11	, 24
Verbena (Verbenaceae)	13-14, 32	2, 49
Vernonia (Asteraceae)	26	5, 32
Vicia (Fabaceae)		. 32
Vigna (Fabaceae)		. 32
Xanthium (Asteraceae)	16, 25, 26	5, 32
Zinnia (Asteraceae)	26	32