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Revision of the goldenrod-galling *Rhopalomyia* species (Diptera: Cecidomyiidae) in North America

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Abstract

Goldenrods (*Solidago* and *Euthamia* species) are common herbs in the eastern United States that support a large and diverse community of highly specific gall-inducing insects. The majority of these insects are gall midges, of which 16 described species are bud, leaf, stem, rhizome, or flower-head gallers belonging to the large genus *Rhopalomyia* Rübsaamen. The present work is a taxonomic revision of the goldenrod-associated *Rhopalomyia* species, which includes a key to the identification of species based on their galls and host plants and descriptions of diagnostic characters for all species. *Rhopalomyia lanceolata* Felt is designated as a new synonym for *R. lobata* Felt, and *R. albipennis* Felt and *R. carolina* Felt are designated as new synonyms for *R. solidaginis* Loew. Neotypes are designated for *R. hirtipes* Osten Sacken and *R. solidaginis*, and two new species are described—*R. gina* Dorchin n.sp. and *R. guttata* Dorchin n.sp. Descriptions include illustrations of galls, male and female morphological characters, and the first description of pupae, where available. New or additional detailed information is also provided on gall structure, phenology, and life history of the gall midges.

Key words: Gall midges, *Euthamia*, *Solidago*, Neotype, Taxonomy

Introduction

Goldenrods (*Solidago* and *Euthamia* species) are common herbs throughout the eastern United States, which have been studied extensively due to their economic importance as ornamentals, weeds, or sources of pollinators and biological control agents. Hosting a great diversity of herbivorous insects from different feeding guilds (Gagné 1968, McEvoy 1988; Maddox & Root 1990; Root & Cappuccino 1992; Fontes *et al.* 1994), goldenrods have also served as model systems for numerous studies that focused on evolutionary and ecological aspects of speciation, resistance, and tritrophic interactions (*e.g.*, Abrahamson & Weis 1997; Heard *et al.* 2006; Stireman *et al.* 2005, 2006; Wise & Abrahamson 2008, Crutsinger *et al.* 2009).

About 50 species of gall-inducing insects have been recorded from goldenrods, two thirds of which are gall midges (Diptera: Cecidomyiidae) (McEvoy 1988). Many of these species were described by Felt (1907a,b,c, 1908, 1909, 1915, 1916; see also Gagné 1989) and some of their galls were later illustrated in his book on galls and gall insects in North America (Felt 1940). Despite the good quality of his type series, Felt's treatment of the goldenrod Cecidomyiidae, as his work on gall-midge taxonomy in general, was mostly superficial. His species descriptions often lack illustrations and are based on characters of little diagnostic value. Many species were described without an association to host or from hosts that were misidentified, and some species were described several times under different names (see Gagné 1968). The dominant group of gall midges on goldenrods consists of 16 described species in the genus *Rhopalomyia* Rübsaamen, the description of which had mostly been based on body color and number of antennal flagellomeres.

Rhopalomyia is one of the largest genera of Cecidomyiidae, with over 250 species worldwide (Gagné 2004). With very few exceptions, species of this genus are restricted to plants of the family Asteraceae, on which they induce mostly complex galls in roots, stems, buds, leaves or flower heads. About 70% of the species are known from plants of the tribe Anthemidae (mainly *Artemisia* and *Chrysanthemum* species). Species life history is directly related to the phenology of the host plant and to the plant organ in which the gall develops. The number of generations per year and the larval instar that goes into diapause varies among species, but all species pupate inside their galls.

Rhopalomyia species are relatively uniform morphologically and show great reduction in taxonomically useful characters. Adults of the Holarctic species have 1–3 segmented palpi, reduced number of antennal flagellomeres, which vary within species and sometimes even in the same individual, and overall reduced setation. Larvae of most species have lost the spatula, and their remaining terminal papillae are barely visible. Pupae, on the other hand, can exhibit useful taxonomic characters (Jones *et al.* 1983), even in species whose adults are morphologically indistinguishable (*e.g.*, Russo 2007). While different combinations of the above-mentioned characters can be helpful in separating species or species groups, they do not justify erection of

separate genera (Gagné 2004) nor were they considered to reflect phylogenetic relationships within the genus (Jones *et al.* 1983). The best means for distinguishing among species remains the morphology and structure of their galls together with the identity of the host plant.

The present study is a taxonomic revision of the *Rhopalomyia* species from goldenrods, which constitute the most abundant and species-rich group of gall-inducing insects on these plants. In addition to clarifying the taxonomic status of the 16 described species, we describe their pupae for the first time, provide useful morphological characters for identification of both sexes, describe two new species, and offer new and detailed data about galls and life histories of most species.

Materials and methods

Collecting and rearing of insects

In the present study, the name "goldenrods" refers to the historically congeneric *Solidago* and *Euthamia*, which were recently shown to be more distantly related than previously thought (Zhang 1996; Semple & Cook 2006). Six species of goldenrods (*Solidago altissima, S. gigantea, S. juncea, S. rugosa, S. nemoralis,* and *Euthamia graminifolia*) were surveyed for galls at least once a week from mid May to mid October 1987 in the following localities in the Cayuga Lake Basin, western NY: Freese Rd. (N42º 27.4' W76º 26.5'), Etna (N42º 29.1' W76º 29.1'), West Dryden (N42º 30.6' W76º 24.5'), Hector Backbone (N421º 31.6' W76º 47'), and Eldride Wilderness (N42º 23.3' W76º 28.1'), and from late April to mid October in 2005–2007 in the following localities in central Pennsylvania: Route 487 (N41º 21.2' W76º 17.8'), Lairdsville (N41º 14.1' W76º 36.4'), Hughesville (N41º 14', W76º 43'), Montour Environmental Preserve (N41º 06', W76º 40'), the Bucknell University Chillisquaque Creek Natural Area (N41º 1.3', W76º 44.6'), Mauses Creek (N40º 59.2', W76º 40.9'), Mifflinburg (N40º 55', W77º 02'), Lewisburg (N40º 55' W76º 54.3' and N40º 54.4', W76º 54.4'), and Selinsgrove (N40º 49', W76º 53').

Additional surveys in central PA were done occasionally in R.B. Winter State Park (N40º 59', W77º 11'), Shikellamy State Park (N40º 52', W76º 48'), Black Moshannon State Park (N40º 54', W78º 03'), Millersburg (N40º 32', W76º 55'), and Wildwood Lake Sanctuary, Harrisburg (N40º 18', W76º 53'). Specific supplementary collecting was done in 2008 in Mauses Creek, PA and in the Blandy Experimental Farm, Boyce, VA (N39º 03', W78º 04'). Additional goldenrod species that were surveyed intermittently were *S. macrophyla* in the Adirondack Mts, NY, *S. fistulosa, S. puberula, S. sempervirens,* and *E. tenuifolia* in southern New Jersey, *S. arguta, S. bicolor, S. caesia, S. flexicaulis, S. patula,* and *S. ulmifolia* in the Cayuga Lake Basin, NY, and *S. bicolor, S. canadensis, S. caesia, S. flexicaulis,* and *S. ulmifolia* in central Pennsylvania.

Galls were either bagged in the field or collected and brought to the laboratory in plastic bags. In some cases we used small (ca. 8x6 or 10x8 cm) white mesh bags to cover galls individually in the field, after which the bags were monitored every 24–48 hours for adult emergence. Some galls brought to the laboratory were kept at room temperature in carton boxes, plastic ventilated rearing cages, Petri dishes, or small vials (depending on the type of gall) until adult emergence. Others were dissected under a stereomicroscope, their attributes and contents were recorded, and immature stages of the gall midges they contained were retained for morphological study.

Taxonomy

Immature stages and emerging adults of the gall midges were preserved in 70% ethyl alcohol for morphological study and were later mounted on permanent microscopic slides in euparal according to the method outlined in Gagné (1989). Additional pupae and larvae were studied under a Philips Quanta 400 environmental scanning electron microscope. The identity of the gall inducers was verified via comparison to type material. Types that are part of the Felt Collection are the property of the New York State Museum in Albany (NYSM), but are currently under the care of the Systematic Entomology Laboratory, USDA, at the

National Museum of Natural History (USNM), Smithsonian Institution, Washington, DC. Terminology for adult morphology follows McAlpine *et al.* (1981) and for immature morphology that of Gagné (1989). Taxonomy and nomenclature of the host plants follows Semple and Cook (2006), hence the name *Solidago canadensis* used by Felt is referred to here as *S. altissima*. All taxonomic decisions were made by the first author. Neotypes and holotypes of new species are deposited in the USNM. Other material that was collected in this study is deposited in the USNM, in the Zoological Research Museum Alexander Koenig (ZFMK), Bonn, Germany, and in the National Collection of Insects, Zoological Museum, Tel Aviv University (TAUI), Israel.

Results and discussion

Morphology

As in other groups in the genus *Rhopalomyia* (*e.g.*, Jones *et al.* 1983), larvae of the goldenrod-feeding species are very uniform and do not offer good diagnostic characters. They are white to very pale orange, have a smooth integument, no spatula, and barely perceptible papillae. Larvae were therefore not treated further in this work. Pupae are very light orange when young, and turn dark orange (almost red in *R. hirtipes* (Osten Sacken 1862)) as they mature. They, too, exhibit reductions in diagnostic characters but are more informative than the larvae, despite showing much less morphological variation than that among species from *Artemisia* (Jones *et al.* 1983). In the goldenrod-feeding species whose pupae we studied, the antennal bases are usually not developed into conspicuous horns, and the frons lacks any structures other than a tiny mid-frontal projection in some species. This reduction in the size and form of cephalic structures is probably related to the fact that all species from goldenrods develop in thin-walled or spongy galls, which do not require much force to break out from. The cephalic seta is short in all species except for *R. anthophila* (Osten Sacken 1869), and the shape of the prothoracic spiracle is similar in all species but *R. capitata* Felt 1908 and *R. solidaginis* (Loew 1862), in which it is divided apically into 2–3 lobes. Abdominal segments are covered by minute, pointed spicules. Despite the overall morphological uniformity, the shape of the frons and the antennal bases can sometimes offer good taxonomic characters, and size differences among certain species are striking – from the very large pupae of *R. hirtipes* (up to 5 mm) to the tiny ones of *R. clarkei* Felt 1907 and *R. gina* Dorchin n.sp. (1.7–2 mm).

Adults of different species can vary considerably in size and some of them offer useful taxonomic characters. This is also true for females, which were found to be uninformative elsewhere in the genus (Jones *et al.* 1983). Such characters include the length of flagellomere necks relative to their nodes in males, presence or absence of flagellomere necks in females, number of palpal segments (one or two), the shape of the gonopods, cerci, and hypoproct in males, and the shape of abdominal tergites 7 and 8 and the relative length of the ovipositor in females. The number of antennal flagellomeres varies within species and cannot serve as a diagnostic character. The last two flagellomeres in both sexes are often fused or partially fused. All species have simple (untoothed) claws with empodia longer than claws, and all have two anterior trichoid sensilla on abdominal tergites and sternites. As in all *Rhopalomyia* species, tergite 8 of the female abdomen is entire rather than divided longitudinally (as in *Dasineura* Rondani, for example), and resembles the letter Y, with two anterior arms merging into a single posterior shaft. The shape of this tergite varies considerably among the goldenrod-galling species, in particular with regard to the orientation and length of the arms relative to the shaft. The length of the ovipositor relative to tergite 7 of the abdomen is another useful character that can vary greatly among species. In the following species descriptions, the length of tergite 7 was measured from the trichoid sensilla to the most posterior seta, and the ovipositor was measured from the posterior margin of tergite 8 to the tip of the cercus. The male gonopods are robust in some species (e.g., *R. hirtipes*, *R. solidaginis*) and slender in others (e.g., *R. lobata* Felt 1908, *R. pedicellata* Felt 1908), but gonocoxites of all species have prominent and strongly setose mediobasal lobes that sheath the aedeagus, and completely

setulose gonostyli with a relatively small, brush-like tooth. In about a third of the species, including all those from *Euthamia*, the gonocoxal apodeme is divided anteriorly into two arms, whereas in the remainder of species this apodeme is entire. In the following species descriptions, characters that are common to all species are not mentioned again except in the descriptions of new species.

Life history

The *Rhopalomyia* species from goldenrods are diverse both in terms of their life histories and the types of galls they induce. Galls are found in or on rhizomes, stems, leaves, vegetative buds, and flower heads (capitula); some are conspicuous fleshy, spongy, or leafy galls that contain many larval chambers, whereas others form inconspicuous, single-chambered structures. Species that gall capitula are assumed to have one generation per year, as do some of the bud and rhizome gallers. The bud gallers *R. capitata* and *R. solidaginis*, which induce the most conspicuous and common galls in this group, go through a fast-developing spring generation and then a slow-developing summer generation. Each of these generations has its typical gall but both are induced in vegetative buds. Species inducing small, single-chambered galls on leaves, stems, or inflorescences (*e.g., R. clarkei*, *R. pedicellata*) complete multiple generations between spring and fall. Except for *R. hirtipes*, all species appear to overwinter as first-instar larvae inside tissues of the host plant, although this has been directly verified only for *R. capitata* and *R. solidaginis*, whose larvae overwinter in rhizomes (as recorded in the present study for the first time). Larvae of *R. hirtipes* were reported to overwinter in the soil, close to the rhizomes of their host plant (Spence 1969). It is possible that bud and capitulum-galling species that are currently considered univoltine actually have an early spring generation that has not been discovered so far; otherwise, it would be difficult to explain how their larvae end up developing in shoot-tip or capitulum galls high above the ground during summer and fall (e.g., in *R. lobata* and *R. anthophila*, respectively). As in all *Rhopalomyia* species, pupation takes place inside the gall.

Some of the *Rhopalomyia* galls resemble galls of other cecidomyiids or other insects on goldenrods, but this resemblance is mostly superficial. In particular, the rosette bud galls of *R. capitata* and *R. solidaginis* may appear somewhat similar to those of the gall midges *Dasineura folliculi* Felt 1908 (see Dorchin *et al.* 2007) and *Asphondylia monacha* Osten Sacken 1869, or to those of the tephritid fly *Procecidochares atra* (Loew 1862). However, galls of *P. atra* are usually much smaller, more compact, and contain a single, large chamber, and the galls of *A. monacha* are found on *Solidago juncea*, a host not used by *Rhopalomyia* rosette-gallers. All leafy bud galls induced by *Rhopalomyia* species contain white, conical larval chambers of very thin walls, which are absent in galls of the other insects mentioned above. Additional structural differences are given below under the relevant species. Following is a key to *Rhopalomyia* galls on goldenrods, including one undescribed species from galls on *Solidago fistulosa* in Florida, whose taxonomic status is yet to be established. *Rhopalomyia cruziana* Felt 1908 is not included in the key due to insufficient information about its gall. The key is followed by a detailed account on the morphology and biology of the species, in alphabetical order.

Key to *Rhopalomyia* galls on North American goldenrods

1. Vegetative bud gall, fleshy or leafy, just above the ground or high above it 2
- Galls on other plant parts 7
2. Fleshy gall on shoot tip or at the base of the plant, surrounded by few leaves. Larval chambers embedded in the fleshy tissue 3
-. Not fleshy; composed of many short leaves that form a rosette on apical or sometimes lateral shoot tips 4
3. Smooth, bare gall on *Solidago juncea* either at the base of the plant, just above the ground, or on a growing shoot tip up to 60 cm above the ground; up to 4 cm in diameter (Figs. 58–61) ..... *R. hirtipes* (Osten Sacken)
- Spongy, spherical gall tightly surrounded by leaves, on growing shoot-tips of *Euthamia graminifolia*. Up to 6 cm in

diameter (Figs. 78–81) ..... *R. lobata* Felt

4. Galls found in spring (April–early June); cryptic 5
- Galls found in summer and fall (late July–early October); large and conspicuous 6
5. Gall found very close to the ground on *S. gigantea* sprouts and therefore cryptic despite its large size; usually containing 3–20 larval chambers; composed of many short and narrow leaves surrounded by 5–10 much longer leaves (Fig. 74) ..... *R. capitata* Felt, spring generation
- Gall found at least 20 cm above the ground on young *S. altissima*, *S. rugosa*, or *S. canadensis* plants; usually containing 1–3 larval chambers; composed of 5–10 short leaves surrounded by several longer leaves. Hardly distinguishable from normal growing shoot tips (Figs. 70, 72) ..... *R. solidaginis* (Loew), spring generation
6. Gall on *S. gigantea*, containing 5–30 larval chambers situated among uniformly distributed short leaves (Fig. 75) ..... *R. capitata* Felt, summer generation
- Gall on *S. altissima* or *S. rugosa*, containing 3–10 larval chambers, each individually surrounded by a set of narrow leaves (Figs. 71, 73) ..... *R. solidaginis* (Loew), summer generation
7. Galls in rhizomes 8
- Galls in or on leaves, inflorescences or stems 9
8. Tapered, bud-like, single-chambered galls in clusters on rhizomes of *S. juncea* ..... *R. bulbula* Felt
- Cylindrical, multi-chambered galls in rhizomes of *S. altissima* ..... *R. thompsoni* Felt
9. Galls inside flower heads (capitula) 10
- Galls on leaves or stems. If associated with inflorescence, then gall not developing inside a capitulum but situated on or among capitula 12
10. Galls smooth, on *S. bicolor* ..... *R. guttata* Dorchin n.sp.
- Galls densely covered by bristles, on other goldenrods 11
11. Cylindrical galls on *S. altissima*; slightly wider at base (Figs. 56–57) ..... *R. anthophila* (Osten Sacken)
- Bulb-shaped galls, tapered at tip, on *S. altissima* and *S. fistulosa* ..... *R. racemicola* Felt
12. Bulb-shaped, grayish galls with tapered apices, forming rosette-like aggregations on stems of *S. fistulosa* .... *R.* n. sp.
- Different galls on other goldenrod species 13
13. Slender and elongate, green to purple galls with longitudinal stripes on *Euthamia* spp. 14
- Conical, mostly green galls, sometimes with purple longitudinal stripes, on *Solidago* spp. 15
14. Gall carried on long stalk on leaves, stems, or inflorescences (Figs. 84–85) ..... *R. pedicellata* Felt
- Gall sessile, without long stalk, on leaves, stems, or inflorescences (Figs. 82–83) ..... *R. fusiformae* Felt
15. Hairy galls on *S. rugosa* and *S. altissima* (Figs. 62–65) ..... *R. clarkei* Felt
- Smooth galls on *S. gigantea* or *S. juncea* 16
16. On leaves of *S. juncea;* sometimes with a tail-like extension on other side of leaf. May be found on leaves composing rosette galls of *Asphondylia monacha* on this host (Figs. 68–69) ..... *R. gina* Dorchin n.sp.
- On leaves or rarely stems of *S. gigantea*; without extension on other side of leaf. May be found on leaves composing rosette galls of *R. capitata* and *Dasineura folliculi* on this host (Figs. 66–67) ..... *R. inquisitor* Felt?

Treatment of species

Rhopalomyia anthophila (Osten Sacken 1869)

Cecidomyia anthophila Osten Sacken 1869: 302; Felt 1908: 364 (*Rhopalomyia*).

Adult: Antenna with 16–19 flagellomeres in male, 15–19 in female; necks of male flagellomeres III–VII 0.60–0.86 times as long as nodes; female flagellomeres without necks. Palpus 2-segmented; second segment thinner, 1.5 times as long as first in female, more than twice as long as first in male (Fig. 4). Wing length 2.2–2.8 mm in male, 2.2–2.7 mm in female. Legs densely covered by dark scales. Male abdomen: covered by dark, hair-like scales. Sternites 2–8 with a posterior row of setae, a band of setae mesally, and pair of adjacent trichoid sensilla; weakly sclerotized between two bands of setae. Male terminalia (Figs. 9–10): gonocoxite cylindrical, with apicoventral projection, setose and setulose, with setose mediobasal lobe; gonocoxal apodeme truncate to broad, undivided; gonostylus stout, only slightly narrowed toward apex, setulose throughout, with small brush-like tooth; aedeagus conical, rounded apically; hypoproct M-shaped, setose and setulose; cerci wide, separated by a deep notch, setose and setulose. Female abdomen (Fig. 26): scales and setation as in male; tergite 8 Y-shaped, with two trichoid sensilla anteriorly and a group of setae posteriorly; ovipositor 8.2 times as long as tergite 7.

Pupa (Figs. 40–41): Antennal bases developed into small horns, rounded posteriorly, tapering abruptly toward tip, pointed anteriorly. Posterior margins of antenna bases V-shaped in frontal view. Frons without projections. Cephalic seta long, originating from inflated base.

Type material: *Cecidomyia anthophila* Osten Sacken. Syntypes: 2 males (pinned), collected by Osten Sacken near Brooklyn, NY, IX/1867, ex. capitulum galls on *S. altissima*, deposited in the Museum of Comparative Zoology, Cambridge, Massachusetts (MCZC).

Other material examined: 1 male, 1 female, undisclosed locality and collector, 13/IX/1885, ex. *S. altissima* (*S. canadensis* of Felt), Felt # C1039 deposited in Felt Collection; 1 male, Canada, Ontario, Toronto, W.M. Brodie, deposited in USNM; 11 males, 12 females, USA, , Freese Rd. & Fall Creek, NY, 6/IX/1986, M.V. McEvoy; 8 pupae, USA, Etna, NY, 7/IX/2007, N. Dorchin and M. Wise. Felt (1915) mentioned galls that were collected in three other localities: Asheville, NC on 16/IX/1906; near Albany, NY in September; and Bushburg, MO on 11/IX/1876 by C.V. Riley.

Host: *Solidago altissima*

Gall and biology: Osten Sacken (1869) included an exemplary account of the galls and their phenology in the original description of this species. The gall (Figs. 56–57) constitutes a modified capitulum. It is cylindrical, 5–10 mm long and 2–3.5 mm wide, usually slightly wider at base than at the tip. The gall is green but densely covered by short, white hairs that give it a whitish, fuzzy appearance. Galls are almost always situated among normal capitula, and are accompanied by tiny leaves and/or ray florets at their base. Each gall contains a single smooth, thick-walled chamber. Inside this chamber is an inner, conical chamber with very thin walls, containing a single larva, facing downwards. Larvae turn to face upwards inside the gall before pupation. The gall's wall is much thinner apically than laterally, and galls that contain pupae sometimes have slits at their tips (Fig. 56). Galls become apparent in mid August and pupation takes place in late August to mid September. This is a relatively rare species that has a very patchy distribution; in 1987 it was found in only two localities and in 2007 in only one locality in the Ithaca, NY area, despite screening thousands of plants in several field sites in New York and Pennsylvania. Galls are found singly or in aggregations on the same inflorescence. Larvae and pupae of this species are attacked by ectoparasitic wasps. Oviposition and overwintering sites are unknown.

Remarks: This species is generally similar to the other capitulum gallers on goldenrods (*R. cruziana*, *R. guttata*, and *R. racemicola*), but is distinct for the apicoventral projection of the gonocoxite (Fig. 10). The pupa has well-developed antennal bases and a much longer cephalic seta than that of other *Rhopalomyia* species from goldenrods whose pupae we studied, although the pupae of the other capitulum gallers from goldenrods are unknown. The shape and structure of the gall are the best characters by which *R. anthophila* can be distinguished from similar species.

Males we examined had 16–17 antennal flagellomeres, although in his original description, Osten Sacken (1869) states that the few males he reared had 19 flagellomeres. Other aspects of the male description match the specimens we examined.

Rhopalomyia bulbula Felt 1908

Rhopalomyia bulbula Felt 1908: 365.

Adult: Antenna with 16 flagellomeres in male, 15–16 in female; necks of male flagellomeres III–VII 0.61–0.65 times as long as nodes, female flagellomeres without necks. Palpus 1-segmented, fusiform, tapered, more than twice as long as wide, setulose with few long setae. Wing length 3.2 mm in male, 2.9 mm in female. Empodia as long as claws. Male abdomen covered by dark scales. Male Terminalia (Fig. 11): gonocoxite robust, setose, with strongly setose mediobasal lobe; gonocoxal apodeme broad and truncate, undivided; gonostylus short and bulky, anterior margin straight, posterior margin evenly curved, setulose throughout, with small, brush-like tooth; aedeagus conical, rounded apically; hypoproct entire, wide, truncate, setose and

setulose; cerci separated by a shallow notch, setose and setulose. Female abdomen (Fig. 27): covered by dark, fusiform scales; tergites 1–6 rectangular; tergite 7 X-shaped, setose on most of surface; tergite 8 very narrowly Y-shaped, with two anterior trichoid sensilla and few setae on proximal half; ovipositor 11.1 times as long as tergite 7.

Pupa: unknown.

Type material: *Rhopalomyia bulbula* Felt. Syntypes: 1 male, 1 female, USA, Worcester, MA, unspecified date, M.T. Thompson, ex. *S. juncea*, Felt # 1115, deposited in Felt Collection.

Host: *Solidago juncea*

Gall and biology: Galls are found in clusters of 3–15 on rhizomes, at the base of spring shoots. The gall is single-chambered, resembles a bud, with acute apex and base, 4.5–6.0 mm long and 1.5–2.5 wide. The surface of the gall is smooth and white, with green stripes where it is exposed to light. Adults emerge in late May (Thompson 1915). No second generation has been found during summer and fall.

Remarks: Both *R. bulbula* and *R. hirtipes* develop at the base of shoots on *S. juncea*. Given that *R. bulbula* is known only from a spring generation whereas *R. hirtipes* is known only from a fall generation, the idea that these may represent the spring and summer generations of the same species is appealing (Felt 1915). However, numerous morphological differences in both males and females render this option less plausible: *Rhopalomyia bulbula* is a smaller species, and has 15–16 antennal flagellomeres and neckless female flagellomeres as opposed to the 20–22 flagellomeres and relatively long necks of the female flagellomeres in *R. hirtipes*. Furthermore, *R. bulbula* has 1 rather than 2 palpal segments, its male gonocoxite lacks the apical mesoventral lobe that is present in *R. hirtipes*, its gonopods are not as robust and spherical as those of *R. hirtipes*, and its ovipositor is much longer. Although all these differences are based on the single available couple of *R. bulbula*, originally described by Felt in 1908, it seems unlikely that a larger sample size will diminish them. We therefore assume that *R. bulbula* induces a second generation gall that is yet to be found.

Rhopalomyia capitata Felt 1908

Rhopalomyia capitata Felt 1908: 363

Adult: Antenna with 18 flagellomeres in male, 17–18 or 18–19 flagellomeres in female (spring and summer generations, respectively); necks of male flagellomeres III–VII 0.78–0.89 times as long as nodes, female flagellomeres without necks. Palpus 2-segmented, second segment at least 1.5 times longer than first, setose and setulose. Wing length 2.9–3.5 mm in male, 3.2–3.4 mm in female. Legs densely covered by brownish scales; empodia considerably longer than claws. Male terminalia (Fig. 13): gonocoxite cylindrical, setose and setulose, with prominent, setose mediobasal lobe as long as aedeagus; gonocoxal apodeme narrow, undivided; gonostylus evenly curved in posterior margin, straight in anterior margin, setose and setulose throughout, with relatively large, brush-like tooth; aedeagus very wide, truncate; hypoproct M-shaped, with shallow notch, setulose; cerci deeply separated by a triangular notch, strongly setose and setulose. Female abdomen (Fig. 29): tergite 7 trapezoid, less sclerotized along lateral and anterior margins, with two anterior trichoid sensilla, several rows of setae posteriorly, and groups of setae mesolaterally; tergite 8 wide Y-shaped, with two anterior trichoid sensilla; ovipositor 5.0–5.6 times as long as tergite 7.

Pupa (Figs. 42–43): Light orange. Antennal bases tapering into tiny pointed tips, their bases wide V-shaped in frontal view. Frons with tiny pointed projection at mid width, which is absent in pupae of spring generation, and with tapered posterolateral projections; posterior edge widely rounded. Prothoracic spiracle divided apically into two lobes. Abdominal segments with tiny barbs throughout.

Type material: *Rhopalomyia capitata* Felt. Syntypes: 1 female, 1 male, USA, W. Nyack, NY, 23/IX/1907, E.P. Felt, ex. *S. gigantea* (as *S. serotina*), Felt # a1750, deposited in Felt Collection.

Other material examined (all from *S. gigantea*): 2 males, 2 females, USA, NY, West Dryden, 15/IX/1987, M.V. McEvoy; 3 exuviae, USA, PA, Bucknell University Chillisquaque Creek Natural Area,

15/V/2005, N. Dorchin; 3 males, 3 females, USA, PA, Lewisburg, Furnace Rd., 22/V/2005, N. Dorchin; 7 pupae, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 9/IX/2006, C. Blair; 1 male, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 12/IX/2006, N. Dorchin;1 pupa, USA, PA, Lewisburg, Furnace Rd., 23/V/2007, N. Dorchin; 2 pupae, USA, PA, Montour Environmental Preserve, 25/V/2007, M. Wise.

Host: *Solidago gigantea* and occasionally *S. canadensis* and *S. leavenworthii*. Felt (1915) mentioned *S. serotina* and *S. canadensis* as the host plants of *R. capitata*. *Solidago canadensis* was the name used by Felt for *S. altissima* and is an erroneous record for *R. capitata*, whereas *S. serotina* was synonymized under *S. gigantea* (Semple and Cook 2006).

Gall and biology: The species is bivoltine and galls of the two generations are overall similar in structure. The spring-generation galls, described here for the first time, appear in early to mid May in young *S. gigantea* sprouts, and are therefore found very close to the ground (Fig. 74). The larvae that induce these galls hatch in the fall of the previous year and overwinter as first instars in rhizomes without causing any deformation. This was discovered when several rhizome sections that were dug, cut and planted in our research greenhouse in very early spring developed galled sprouts without having been exposed to any adults. The galls are composed of many short and narrow leaves among which 1–8 white, conical chambers are situated (Fig. 77), each containing a single orange larva. The white chambers appear in the gall only when larvae are second instars. The central complex of short leaves is about 3 cm in diameter and surrounded by 5–10 much longer and wider leaves, giving the gall a star-like shape and an overall diameter of up to 10 cm (Fig. 74). At young stages of development, the longer, surrounding leaves may sheath tightly the center of the gall and these loosen at a later stage. The spring generation galls of *R. capitata* can easily be mistaken for *Dasineura folliculi* galls that develop on the same host at the same time (Dorchin *et al.* 2007). However, *D. folliculi* galls never contain multiple short leaves at their center, and instead are composed of several similar-sized leaves that are wider and thicker at their base, and are accompanied by yellowish spots on leaves below and around the gall.

Pupae developing in the spring generation galls emerge from mid to late May and induce the much slower-developing summer-generation galls (Fig. 75), which become apparent around mid June and vary considerably in size. These galls are composed of several wide leaves that surround dozens of densely packed, smaller and shorter leaves, giving the gall a shape of a little sunflower that appears flatter than the similar gall of *R. solidaginis* on *S. altissima* (see Fig. 71). Occasionally, the outer leaves merge to form a continuous sheath around the central part of the gall. Summer galls reach their final size when the larvae are still tiny first instars that are found at the base of the rosette leaves. Six to twenty white, conical chambers, similar to those found in the spring galls, appear in the gall only when the larvae molt into third instars. Larvae are usually found deep at the bottom of the chamber, facing down. The chambers are 4–6 mm high and 1–2 mm wide, and are situated among the short leaves in the center of the gall rather than being individually surrounded by a group of longer leaves, as in the rosette gall of *R. solidaginis*. Pupation takes place in late August to mid September and adults emerge in September and early October.

During summer, some shoot tips can support both *R. capitata* and *D. folliculi* larvae at the same time, and the resulting gall shows morphological attributes of both species, namely, feeding spots on outer leaves (*Dasineura*) and a group of many shortened leaves at its center (*Rhopalomyia*). Larvae of *R. capitata* are heavily attacked by polyembryonic endoparasitoids, and parasitism levels can reach 90% in certain localities and dates. Ectoparasitoids are also found in the galls and feed both on larvae and on pupae of the gall inducer.

Remarks: *Rhopalomyia capitata* and its close relative *R. solidaginis* are two of several species that have been described from similar rosette galls on goldenrods, a fact that caused confusion with regard to the identity and validity of these species (Felt 1915, Gagné 1989). Although their summer-generation galls are superficially similar, *R. capitata* and *R. solidaginis* are consistently found on different hosts (the former on *S. gigantea*, the latter on *S. altissima*), their adults show clear morphological differences, and recent molecular analyses confirm that they constitute distinct species (Stireman *et al.* 2005, Dorchin *et al.*, in prep.). Fontes *et al.* (1994) recorded the galls of *R. capitata* from *S. leavenworthii* and *S. gigantea*, but attributed them

erroneously to *S. solidaginis*. Stireman *et al.* (2005) later showed that specimens recovered from galls on *S. leavenworthii* nested within the *R. capitata* clade. Both *R. capitata* and *R. solidaginis* are relatively large but *R. solidaginis* is usually larger and adults of its summer generation have more numerous antennal flagellomeres. Females of both species have short ovipositors relative to other *Rhopalomyia* species from goldenrods, but can be distinguished from each other by the typical shape of the 8th tergite in *R. solidaginis*, whose arms are narrow at their bases and widen anteriorly (Fig. 38). The male gonocoxite in *R. capitata* is much more slender and less robust than the unmistakably inflated gonocoxite of *R. solidaginis*; the gonocoxal apodeme is longer and more slender in *R. capitata*, and its gonostylus is not as stout.

Lastly, despite the superficial similarity of their summer galls, the spring generation galls of *R. capitata* and *R. solidaginis* are strikingly different morphologically: those of *R. solidaginis* contain 1–2 chambers in barely modified shoot tips (Figs. 70, 72), whereas those of *R. capitata* form complex multi-chambered rosettes (Fig. 74).

***Rhopalomyia clarkei* Felt 1907**

Rhopalomyia clarkei Felt 1907c: 18.

Adult: Antenna with 17–19 flagellomeres in male, 15–17 in female; necks of male flagellomeres III–VII 0.57–0.77 times as long as nodes, necks of female flagellomeres 0.19–0.23 times as long as nodes. Palpus 1-segmented, fusiform to triangular, tapered, setose and setulose. Wing length 2.4–2.6 mm in male, 2.2–2.5 mm in female. Male terminalia (Fig. 14): gonocoxite bulbous, setose and setulose, with setose mediobasal lobe; gonocoxal apodeme anteriorly divided into two very short lobes; gonostylus wide, hardly narrowed toward apex, setose and setulose, with small, brush-like tooth; aedeagus narrow, truncate; hypoproct entire, truncate, setose and setulose; cerci separated by a triangular notch, setose and setulose. Female abdomen (Fig. 30): tergite 7 rectangular, weakly sclerotized along anterior and posterior margins, with two anterior trichoid sensilla, a group of setae posteriorly, and groups of setae mesolaterally; tergite 8 wide Y-shaped, arms about third length of shaft, each with anterior trichoid sensillum; ovipositor 6.3 times as long as tergite 7.

Pupa (Figs. 44–45): Antennal bases developed into abruptly tapering horns, pointed anteriorly. Posterior margins of antennal bases rounded V-shaped in frontal view. Frons without projections, ridges or lateral projections, posterior edge widely rounded.

Type material: *Rhopalomyia clarkei* Felt. Holotype: female, USA, NH, Tamworth, 6/X/1907, C.H. Clarke, ex *S. rugosa*, Felt # a1634, deposited in Felt Collection.

Other material examined: 1 male, USA, MA, Magnolia, unspecified date, C.H. Clarke, ex. *S. rugosa*, Felt # a1634, deposited in Felt Collection; 2 males, 2 females, 2 pupae, USA, NY, Fall Creek and Freese Rd., 8–19/VIII/1987, M.V. McEvoy, ex *S. rugosa*; 3 pupae, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 16/VI/2005, N. Dorchin, ex. *S. rugosa*; 2 females, USA, VA, Boyce, 8/X/2008, M. Wise, ex. *S. altissima*. Felt (1915) mentioned that galls of this species were also collected by him from *Solidago canadensis* (the name he used for *S. altissima*) in Asheville, NC on 29/IX/1906, as well as by T.D. Jarvis in Ontario, Canada on 20/IX/1907.

Hosts: *Solidago rugosa*, *S. altissima*.

Gall and biology: The galls are small, conical and single-chambered, usually occurring on the lower side of leaves but occasionally on the upper side of leaves and on stems (Figs.62–65). When on leaves, the gall is always attached to either a major or minor vein (Figs. 62–64). Each gall contains a single white larva. Galls on *S. rugosa* are 2.5–6.0 mm long and 0.7–1.2 mm wide at widest part, tapering toward apex, green to yellowish green, and covered by short, whitish hairs. Very young galls are sometimes accompanied by a tuft of hair at their base, almost as long as the gall itself. The species is multivoltine and galls can be found from late May to early October. It is heavily parasitized and adults are extremely difficult to rear. In September and October 2008, similar galls were found on *Solidago altissima* in Boyce, Virginia by M. Wise (Fig. 65). Only two

females were reared from these galls, but based on their morphology and that of the galls, we concluded they belong to *R. clarkei*, confirming Felt's report (1915) of this species from *S. altissima*.

Remarks: The tiny, inconspicuous galls of *R. clarkei* were originally described only from *Solidago rugosa*, but we found very similar galls on three other hosts: *R. altissima* (Fig. 65), *R. gigantea* (Fig. 67), and *R. juncea* (Fig. 68). We initially assumed that galls from all these hosts belong to *R. clarkei*, but a recent molecular analysis (Dorchin *et al.*, in prep.) indicate that the populations from *S. gigantea* and *S. juncea* represent distinct species, with the former being the closest relative of *R. clarkei*. Samples from *S. altissima* were not analyzed. The population from *S. gigantea* is discussed below under *R. inquisitor* and *R. sp*., whereas the population from *S. juncea* is described here as a new species – *R. gina*. *Rhopalomyia clarkei* is morphologically very similar to *R. inquisitor*, but differs from *R. gina* in having stouter male gonopods and in lacking a longitudinal groove along the antennal horns and lateral projections of the eyes in the pupa.

Rhopalomyia cruziana Felt 1908

Rhopalomyia cruziana Felt 1908: 366.

Adult: Antenna with 15 flagellomeres in male, 14 in female; necks of male flagellomeres III–VII 0.62–1.00 times as long as nodes, female flagellomeres without necks. Palpus appears to be 2-segmented although the mounting orientation of the type specimens makes this difficult to establish. Wing length 1.7–1.8 mm in male, 1.5 mm in female. Male terminalia (Fig. 15): gonocoxite cylindrical, setose and setulose, with setose mediobasal lobe; gonocoxal apodeme undivided, somewhat narrowed anteriorly; gonostylus short and stout, setose and setulose throughout, with brush-like tooth; aedeagus conical, rounded distally; hypoproct with small notch, setulose; cerci separated by triangular notch, setose and setulose. Female abdomen (Fig. 31): tergite 7 rectangular, with weak sclerotization in mid-anterior part, with two anterior trichoid sensilla, a row of setae posteriorly, and few setae mesally; tergite 8 narrow Y-shaped, proximal arms considerably shorter than shaft, with two anterior trichoid sensilla; ovipositor 5.4 times as long as tergite 7.

Pupa: unknown.

Type material: *Rhopalomyia cruziana* Felt. Syntypes: 1 male, 1 female, USA, CA, Santa Cruz Mts., VIII/1890, ex. *Solidago* sp., unspecified collector, Felt # C942, deposited in Felt Collection.

Host: *Solidago* sp.

Gall and biology: The floret/capitulum galls of this species have not been described in detail and the host plant is unknown, hence it is impossible to determine whether this species is distinct and who its relatives among the *Rhopalomyia* spp. on goldenrods are. According to the information given by Felt (1915), the galls were collected in Santa Cruz Mts. in California in August 1889 and adults emerged from them "before May 1890".

Remarks: This is the smallest *Rhopalomyia* species from goldenrods. It generally resembles the other *Rhopalomyia* species that develop in goldenrod capitula but has fewer antennal flagellomeres (the smallest number among goldenrod *Rhopalomyia* spp.), a considerably shorter ovipositor, and the shortest arms of the Y-shaped 8th tergite in the female. The species appears to have 2 palpal segments, as do the other 3 species from goldenrod capitula, although the mounting orientation of the only two known individuals makes this difficult to ascertain. The very long necks of the male flagellomeres resemble those of *R. racemicola* but the male terminalia are most similar to those of *R. guttata*, from which it differs in having notched rather than entire hypoproct. The general similarity of this species to the other species from goldenrod capitula supports the assumption that it was indeed reared from capitula, but establishing the nature of the galls and the identity of the host plant requires additional collecting on goldenrods in the relevant area.

Rhopalomyia fusiformae Felt 1907

Rhopalomyia fusiformae Felt 1907a: 24
Rhopalomyia fusiformis Felt 1907b: 120, unjustified emendation of *fusiformae*

Adult: Antenna with 17–18 flagellomeres in male, 16–17 in female; necks of male flagellomeres III–VII 0.47–0.75 times as long as nodes, necks of female flagellomeres 0.08–0.23 times as long as nodes. Palpus 1-segmented, at least 1.5 times as long as wide, slightly tapered, setose and setulose. Wing length 2.6–3.2 mm in male, 2.3–2.9 mm in female. Legs densely covered by brownish scales. Male terminalia (Fig. 16): gonocoxite slender and angular at base, almost same width throughout length, setose, with strongly setose mediobasal lobe; gonocoxal apodeme wide, proximally divided into two short, strongly sclerotized arms; gonostylus curved in both posterior and anterior margins, setose and setulose throughout, with relatively large, brush-like tooth; aedeagus wide, rectangular, truncate, slightly widened distally; hypoproct with shallow notch, strongly setulose; cerci rounded, separated by a small notch, strongly setose and setulose. Female abdomen (Fig. 32): covered by dark, hair-like setae; tergite 7 rectangular, less sclerotized along mesolateral and anterior margins, with two anterior trichoid sensilla, a row of setae posteriorly, and several setae on posterior half; tergite 8 Y-shaped, proximal arms widely splayed, each with anterior trichoid sensillum; ovipositor 5.0–5.6 times as long as tergite 7. Adults are morphologically indistinguishable from those of *R. pedicellata*, but a recent molecular analysis suggests these are distinct species (Dorchin *et al.*, in prep.).

Pupa: unknown.

Type material: *Rhopalomyia fusiformae* Felt. Holotype: male, USA, Albany, NY, 16/VII/1906, E.P. Felt, ex. *E. graminifolia* Felt # a1150, deposited in Felt Collection.

Other material examined (all from *E. graminifolia*): 1 female, USA, Albany, NY, 16/VII/1906, E.P. Felt, Felt # a1150, deposited in Felt Collection; 1 male, USA, Albany, NY, 19/VII/1906, E.P. Felt, Felt # a1150, deposited in Felt Collection; 2 males, 1 female, USA, Albany, NY, 20–22/VII/1907, E.P. Felt, Felt # a1150, deposited in Felt Collection; 1 male, 1 female, USA, Hector Backbone, NY, 7/IX/1987, M.V. McEvoy.

Host: *Euthamia graminifolia, E. tenuifolia*

Gall: the galls of this species (Figs. 82–83) are identical to those of *R. pedicellata* (Figs. 84–85) except for the lack of a pedicel. This difference is consistent and no intermediate forms were found. The galls are found on leaves, stems and inflorescences, are 6–12 mm long, 1–2 mm wide at the base, and tapered towards apex. Galls are often found in aggregations (Fig. 82). They are smooth, green to purplish-green with longitudinal darker lines, contain a single chamber, and are smooth and shiny on the inside. Each gall contains a single larva and reaches its final size when the larva is still a first instar. Old galls remain on the plant and become brown and hardened. Although galls were abundant in western NY in the Ithaca area, they were completely absent from other localities, and were never found in central PA during a three-year study that involved many field sites. In western NY, this species completes at least two generations per year, with adults emerging in early to mid July and again in late August and early September. Galls were also found on *E. tenuifolia* in NJ but no adults were reared from them and they are attributed here to *R. fusiformae* based on their galls alone. This species is heavily attacked both by ectoparasitoids and by polyembryonic endoparasitoids. In a sample that included hundreds of galls in September 2007, parasitism rates reached virtually 100%, as only a single gall was found to contain a viable gall inducer.

Remarks: Adults of *R. fusiformae* are morphologically indistinguishable from those of *R. pedicellata* and their galls differ only in lacking the long pedicel that is present in galls of *R. pedicellata*. However, galls of intermediate morphology were never found and a recent molecular analysis (Dorchin *et al.*, in prep.) suggests that the two species are distinct. Males of all three species from *Euthamia* have elongate and slender gonopods and a two-armed gonocoxal apodeme, whereas females have a strongly posteriorly setose tergite 7 and widely splayed arms of the Y-shaped tergite 8. Species from *Solidago* hosts with morphologically similar males are *R. clarkei*, *R. inquisitor* and *R. gina*, which all have one-segmented palpi, two-armed gonocoxal apodemes, and all develop in single-chambered, inconspicuous leaf and stem galls.

***Rhopalomyia gina* Dorchin n.sp.**

Adult: Antenna with 16–17 flagellomeres in both sexes; last two flagellomeres often partially fused or the apical flagellomere "budding" from the subapical one; necks of male flagellomeres III–VII 0.75–0.82 times as long as nodes (Fig. 6), necks of female flagellomeres III–VII 0.20–0.22 times as long as nodes (Fig. 7). Palpus 1-segmented, tapering toward apex, with several long setae. Wing length 2.5–3.2 mm in male, 2.2–2.6 mm in female, covered by dark, hair-like scales. Claws untoothed, empodia longer than claws (Fig. 5). Male abdomen: tergites 1–7 with posterior row of setae, band of setae mesally, a pair of anterior trichoid sensilla, and evenly covered by dark, hair-like scales. Tergite 8 with fewer long setae. Sternites weakly sclerotized, with posterior and mesal groups of setae and pair of adjacent trichoid sensilla anteriorly. Male terminalia (Figs. 18–19): gonocoxite cylindrical, setose and setulose, with prominent, strongly setose and sclerotized mediobasal lobe bearing several setose apical papillae; gonocoxal apodeme bilobed; gonostylus cylindrical, setose and setulose throughout, with small brush-like tooth; aedeagus wide, cylindrical; hypoproct with very shallow notch, or entire in some individuals, evenly setulose; cerci separated by deep notch, setose and setulose. Female abdomen (Fig. 33): tergites 1–7 with posterior row of setae, several scattered long setae elsewhere, and evenly covered by dark scales; tergite 8 Y-shaped, wide and short, with few long setae; all tergites with two anterior trichoid sensilla. Sternites very weakly sclerotized or completely unsclerotized, with long setae mesally and a pair of adjacent trichoid sensilla anteriorly; ovipositor 4.1–5.5 times as long as tergite 7; cerci fused into single cylindrical lamella, setose and setulose (Fig. 8); hypoproct rounded apically, strongly setose and setulose.

Pupa (Figs. 46–47): Light orange. Antennal bases developed into tapering, anteriorly pointed horns with a longitudinal fold-like groove closer to lateral than to median edge of horn. Posterior margins of antennal bases rounded in frontal view. Frons without median projections or ridges, with pronounced lateral projections, posterior edge with a V-shaped extension in frontal view. Cephalic seta short. Abdominal segments dorsally and laterally with pointed spicules. Terminal abdominal segment divided longitudinally into two lobes.

Type material: *Rhopalomyia gina* Dorchin. Holotype: male, USA, Mauses Creek, PA, 30/V/2008, C. Blair, ex. leaf gall on *S. juncea*, deposited in USNM. Paratypes: All from USA, PA, Mauses Creek, collected and reared from leaf galls on *S. juncea*. 2 pupae, 7/VI/2007, G. Lee; 2 males, 20/V/2008, C. Blair; 2 females, 1 male, 23/V/2008, C. Blair; 5 females, 2 males, 26/V/2008, C. Blair; 8 females, 6 males, 30/V/2008; 2 pupae, 11/VI/2008, C. Blair.

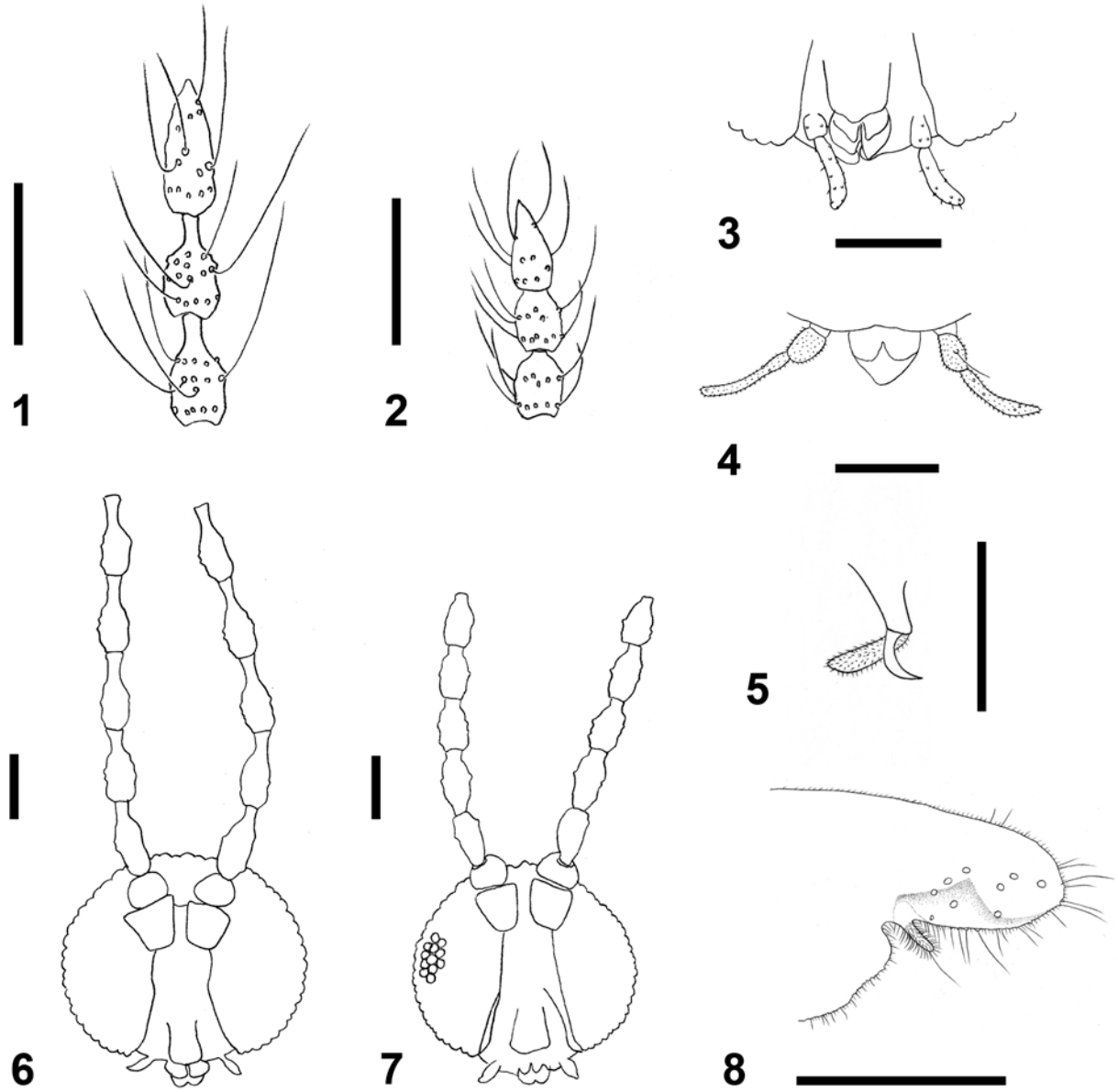
Etymology: The species is named after Gina Lee, who discovered the galls in June of 2007 during her undergraduate summer internship at Bucknell University. The name is a noun in apposition.

Host: *Solidago juncea*

Gall and biology: Galls of this species (Fig. 68) are similar in appearance to galls of *R. clarkei* on *S. rugosa* (Figs. 62–64) and of its close relative on *S. gigantea* (Fig. 67). They are 2.8–5.0 mm long and 0.6–1.3 mm wide at widest part (n=22), smooth and green, often with purplish longitudinal lines and tip, and are most often found on the upper side of leaves. The position of the gall is usually apparent on the other side of the leaf only as a small scar, but some galls had a long, curly appendage extending from that side (Fig. 69). Galls were found in mid May to mid June and adult emergence began in early June, with a sex ratio of 2:1 in favor of females. The galls were heavily attacked by ectoparasitoids (65% parasitism in 2007, n=22 galls), but in May 2008 the parasitism rate was only 12% (n= 41 galls). Further examination of the plants in early August failed to reveal any galls, but Gagné (1989 and pers. com.) found similar galls in late September on leaves subtending and composing the rosette galls of *Asphondylia monacha* on *S. juncea* in Silver Spring, MD. It therefore appears that this species completes at least two generations per year.

Remarks: This species is similar to *R. clarkei* and *R. inquisitor* in the morphology of adults and galls, but tergite 8 of the female abdomen is considerably wider and shorter in *R. gina* (Fig. 33), and the male gonopods are more slender and therefore resemble those of the three *Rhopalomyia* species from *Euthamia* (*R. fusiformae*, *R. lobata*, and *R. pedicellata*). All of these species share the one-segmented palpus, presence of necks in the female flagellomeres, and two-armed gonocoxal apodeme in the male. The pupa of *R. gina* differs

from that of *R. clarkei* in having lateral projections of the frons, which are also present in *R. lobata*, and is unique for the longitudinal groove along the antennal bases.



FIGURES 1–8. 1–3. *Rhopalomyia guttata*; 1. Male distal flagellomeres. 2. Female distal flagellomeres. 3. Mouthparts. 4. *Rhopalomyia anthophila* mouthparts. Figs. 5–8. *Rhopalomyia gina*; 5. Acropod. Scale bar = 0.05 mm. 6. Male head with 5 proximal flagellomeres. 7. Female head with 5 proximal flagellomeres. 8. Tip of female ovipositor showing fused cerci and hypoproct. Scale bars (except for Fig. 5) = 0.1 mm.

***Rhopalomyia guttata* Dorchin n.sp.**

Adult: Antenna with 16–18 flagellomeres in male, 18–19 in female; last flagellomere tapered, longer than preceding, or "budding" from it (Figs. 1–2); necks of male flagellomeres III–VII 0.36–0.67 times as long as nodes; female flagellomeres without necks. Palpus 2-segmented; first segment only slightly longer than wide, second segment at least twice as long as first, rounded apically, setulose, with several long setae and elongate, dark scales (Fig. 3). Wing length 1.9–2.3 mm in male, 2.2–2.5 in female, covered by dark, hair-like scales. Legs densely covered by brown scales. Claws untoothed; empodia longer than claws. Male abdomen: tergites

1–7 with posterior row of setae, band of setae mesally, and a pair of anterior trichoid sensilla, weakly sclerotized between mesal and posterior rows of setae; tergite 8 without setae. Sternites weakly sclerotized, with posterior row and mesal group of setae and pair of anterior trichoid sensilla. Male terminalia (Fig. 12): cylindrical, rounded proximally, with setose mediobasal lobe; gonocoxal apodeme undivided, with small, anterior projection; gonostylus short and wide, narrows only slightly toward apex, setose and setulose throughout, with brush-like tooth; aedeagus cylindrical, rounded apically; hypoproct entire or with very shallow apical notch, setose and setulose; cerci separated by deep triangular notch, setose and setulose. Female abdomen (Fig. 28): tergite 8 Y-shaped, proximal arms about third the length of shaft, each with anterior trichoid sensillum; tergite 7 rectangular, weakly sclerotized along margins, with two anterior trichoid sensilla, several rows of setae posteriorly, and groups of setae mesolaterally; sternites with two adjacent trichoid sensilla anteriorly, band of setae on proximal half and row of setae posteriorly, unsclerotized between proximal band and posterior groups of setae; ovipositor 10.7–12.6 times as long as tergite 7.

Pupa: unknown.

Type material: *Rhopalomyia guttata* Dorchin. Holotype: male, USA, Meriden, CT, Hubbard Pk., 18/IX/1998, R.J. Gagné, ex. capitulum gall on *S. bicolor*, deposited in USNM. Paratypes: 2 males, 3 females, same data as holotype.

Host: *Solidago bicolor*

Gall and biology: the galls were found by R.J. Gagné in capitula, carried on a pedicel among normal capitula but shorter and hidden by them. The gall is conical-cylindrical, smooth, white to green, or sometimes red, and apically tapering. Each gall contains a single larva. A galled capitulum is wider and harder to the touch than capitula without galls. Galls of *R. guttata* differ from the capitula galls of *R. anthophila* and *R. racemicola* in being smooth rather than bristly. The galls of *R. racemicola* further differ from those of *R. guttata* in being onion-shaped rather than cylindrical, and the galls of *R. anthophila*, although cylindrical, lack the pedicel and the tapering apex that are present in galls of *R. guttata*.

Etymology: The species is named after its droplet-shaped galls.

Remarks: This is one of the smallest species of *Rhopalomyia* on goldenrods, but females have the longest ovipositor relative to their body size. It generally resembles the other species that develop in capitula – *R. anthophila*, *R. cruziana*, and *R. racemicola*, whose females are difficult to distinguish from each other, other than the fact that *R. cruziana* has an exceptionally short ovipositor. Males of *R. guttata* and *R. anthophila* have proximally rounded gonocoxites as opposed to the proximally angular gonocoxites of *R. racemicola*, whereas, *R. anthophila* is unique for the meso-apical projection of the gonocoxite that is absent in all other capitula-galling species.

The galls of *R. guttata* were found on silverrod (*S. bicolor*) in Connecticut but not in Pennsylvania or New York. It is possible that the galls escaped our attention on silverrod and possibly on other *Solidago* species, given their small size and being hidden among normal capitula. Dry galls that appear similar to those of *R. guttata* have been recorded from *S. altissima* (Gagné 1989) but no adult gall midges were reared from them.

Rhopalomyia hirtipes (Osten Sacken 1862)

Cecidomyia hirtipes Osten Sacken 1862: 195; Felt, 1908: 363 (*Rhopalomyia*).

Adult: This is the largest of the *Rhopalomyia* species on goldenrods, which is also striking due to the bright orange-red color of the abdomen and the dark wings and legs. Most of the body is covered by dark, elongate scales. Antenna with 21 flagellomeres in male, 20–22 in female; necks of male flagellomeres III–VII 0.44–0.70 times as long as nodes, necks of female flagellomeres 0.23–0.40 times as long as nodes. Palpus 2-segmented, second segment at least 1.5 times as long as first, with numerous strong, dark setae. Wings dark and densely covered by dark, hair-like setae; wing length 4.0–4.1 mm in male, 4.0–4.2 mm in female. Legs densely covered by dark scales. Male terminalia (Fig. 17): gonocoxite massive, almost bulbous, with

prominent apicoventral projection bearing long setae, strongly setose mediobasal lobes, wide, truncate gonocoxal apodeme with strongly sclerotized arms; gonostylus cylindrical and robust, setose and setulose throughout, with small brush-like tooth; aedeagus conical, truncate; hypoproct conical, with shallow notch, setose and setulose; cerci wide and robust, bearing numerous long setae, separated by deep, rounded notch. Female abdomen (Fig. 34): tergites weakly sclerotized; tergite 7 rectangular but more sclerotized in mid- than in lateral parts, with large distal group and smaller mesolateral groups of strong setae; tergite 8 slender Y-shaped, sometimes barely sclerotized along mid part, thus appears to be divided into two longitudinal rods, each with anterior trichoid sensillum and no other perceptible setae; ovipositor 6.5–7.0 times as long as tergite 7.

Pupa (Figs. 48–49): Bright orange; sclerotized parts black. Large and robust. Antennal bases short and wide, rounded dorsally, with tiny tapering tip anteriorly. Posterior margin of antennal bases wide V-shaped in frontal view. Frons without projections or ridges, considerably wider than long, posterior margins V-shaped. Abdominal segments with tiny barbs all over.

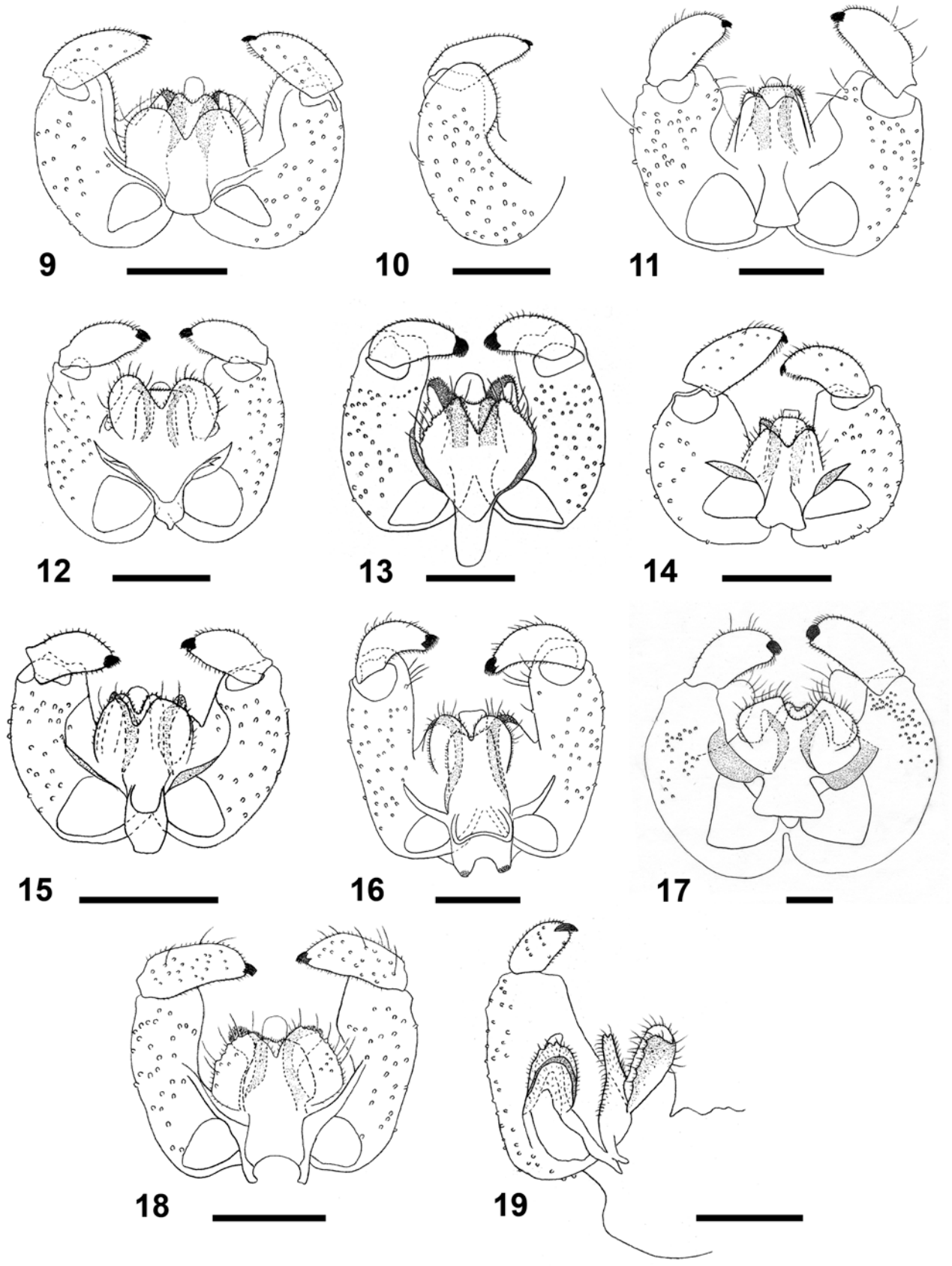
Type material: *Cecidomyia hirtipes* Osten Sacken. Neotype designated here: male, USA, Eldridge Wilderness, NY, 14/IX/1987, M.V. McEvoy, reared from *Solidago juncea*. The neotype is designated in order to clarify the taxonomic status of *R. hirtipes* (Osten Sacken), whose type series is lost. The original description of the insect and its gall match those of the specimens we reared. The neotype is so labeled and is deposited together with associated permanent microscopic slides of two females and six larvae of the same series in the USNM. This species was based on specimens collected by Osten Sacken in the environs of Washington DC, from *S. juncea*. These specimens are neither in the MCZC nor in the USNM and we consider them lost.

Other material examined (all from *S. juncea*): 1 male, 1 female, USA, NY, Glen Lake, 4/IX/1906, E.P. Felt; 1 male, 1 female, USA, Hoxie's Gorge, NY, 8/IX/1969, A. Spence; 6 larvae, USA, Hector Ridge, NY, 22/VII/1987, M.V. McEvoy; 1 male, 2 females, USA, Eldridge Wilderness, NY, 14/IX/1987, M.V. McEvoy; 2 pupae, USA, Liberty Valley Rd., PA, 29/IX/2005, T. Dowling; 1 male, 4 females, 2 pupae, 1 exuviae, USA, Liberty Valley Rd., PA, 17/IX/2006, N. Dorchin and M. Wise. Felt (1915) mentioned Elizabethtown and Albany, NY, Springfield and Magnolia, MA, and Evanston, IL as other localities in which galls of this species were collected.

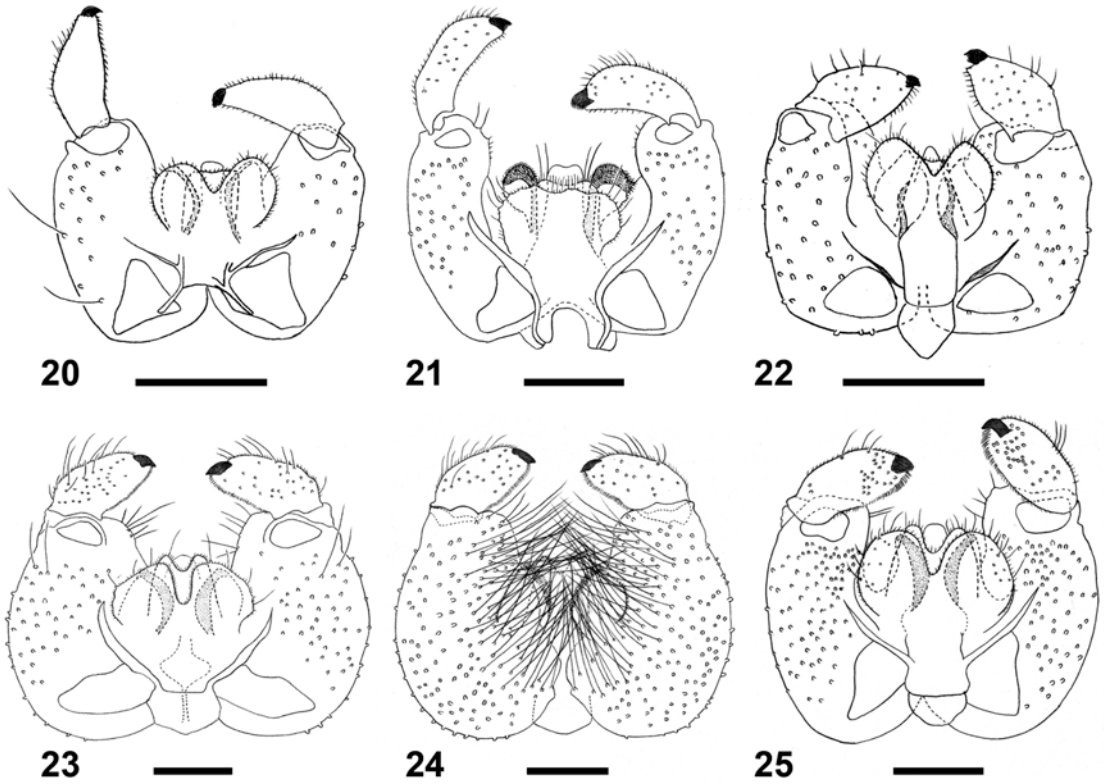
Host: *Solidago juncea*

Gall and biology: Galls of this species appear at the base of the stem in mid June to mid July (Fig. 58). They mostly occur just above the ground but are occasionally found up to 60 cm above it (Fig. 60), and are surrounded by a rosette of long leaves. It is therefore clear that the gall develops from vegetative buds rather than from rhizomes. The young gall is wide at base and has a tapered tip (Fig. 58), which disappears as the gall matures. During July and August, the gall becomes ovoid, 8–25 mm long and 6–36 mm wide and often changes its color from green to brownish, resembling a small potato (Figs. 59, 60). Galls are spongy and usually multi-chambered, containing 1–30 individual larvae in separate chambers, with an average of 8 larvae per gall (Spence 1969). As long as the larvae feed, they face downwards inside their chambers, but before the onset of pupation, in early August, they turn to face upwards. Shortly before adult emergence, the gall splits open at its apex into several lobes, similar to the shell of a hickory nut (Fig. 61). Adults emerge from early to late September, after which the gall shrivels and dries on the stem. Emergence of all adults from the same gall may continue over more than a week. Some galls fail to split, resulting in death of the pupae inside the gall.

Galls of this species can be very difficult to locate and were rare even in fields where *S. juncea* was the dominant plant. Although Spence (1969) recorded more than 1200 galls over a 2-year period in central NY, in 1987 they were found in only one field site in that area, and during 2005–2007 we found them in the same single locality out of many fields that were surveyed in central PA. The life history and behavior of *R. hirtipes* were studied in detail by Spence (1969); mating occurs on the plant a few hours after emergence and females begin to oviposit about 1.5 hours later, depositing eggs mainly under old leaf sheaths on lower parts of the stem, but also on rhizomes and among axils of leaves that surround the gall from which they emerged. Larvae hatch from the eggs about 3 weeks after oviposition and overwinter in the soil. In early spring, the larvae become active and embed themselves in small buds near leaf bases or at the bases of new shoots.



FIGURES 9–19. Male terminalia (in dorsal view unless otherwise noted). 9. *Rhopalomyia anthophila*. 10. *Rhopalomyia anthophila*, left gonopod, ventral. 11. *Rhopalomyia bulbula*. 12. *Rhopalomyia guttata*. 13. *Rhopalomyia capitata*. 14. *Rhopalomyia clarkei*. 15. *Rhopalomyia cruziana*. 16. *Rhopalomyia fusiformae*. 17. *Rhopalomyia hirtipes*. 18. *Rhopalomyia gina*. 19. *Rhopalomyia gina*, lateral. Scale bars = 0.1 mm



FIGURES 20–25. Male terminalia (in dorsal view unless otherwise noted). 20. *Rhopalomyia inquisitor*. 21. *Rhopalomyia lobata*. 22. *Rhopalomyia racemicola*. 23. *Rhopalomyia solidaginis*. 24. *Rhopalomyia solidaginis*, ventral. 25. *Rhopalomyia thompsoni*. Scale bars = 0.1 mm

Remarks: This is the largest *Rhopalomyia* species on goldenrods. It is distinct for its inflated male gonocoxites with their apicoventral projection, wide gonocoxal apodeme, and very widely splayed arms of the 8th abdominal tergite in the female (Fig. 34), which is almost T-shaped rather than Y-shaped as in other *Rhopalomyia* species on goldenrods. *Rhopalomyia hirtipes* shares a large number of over 20 antennal flagellomeres with *R. solidaginis* and *R. thompsoni*, but differs from them in having relatively short flagellomere necks in the male (very long in *R. solidaginis* and *R. thompsoni*) and relatively long flagellomere necks in the female (absent in *R. solidaginis* and *R. thompsoni*).

Rhopalomyia inquisitor Felt 1908

Rhopalomyia inquisitor Felt 1908: 364.

Adult: Antenna with 18 flagellomeres in male, 17 in female; necks of male flagellomeres III–VII 0.75–0.77 times as long as nodes, necks of female flagellomeres 0.39–0.55 times as long as nodes. Palpus 1-segmented, short, cylindrical, about 1.5 times as long as wide. Wing length 1.8 mm in male, 2.4 mm in female. Male terminalia (Fig. 20): gonocoxite wide, stout, setose, with setose mediobasal lobe; gonocoxal apodeme proximally divided into two slender arms; gonostylus curved in posterior margin, more or less straight in anterior margin, narrowed gradually toward apex, setose and setulose, with brush-like tooth; aedeagus almost rectangular, slightly widened and rounded distally; hypoproct almost rectangular, entire, setulose; cerci wide, rounded, separated by a wide notch, setose and setulose. Female abdomen (Fig. 36): tergite 7 rectangular, with two anterior trichoid sensilla and several setae posteriorly and mesolaterally; tergite 8 wide Y-shaped, proximal arms about half as long as shaft, each with anterior trichoid sensillum; ovipositor 7.4 times as long as tergite 7.

Pupa: unknown.

Type material: *Rhopalomyia inquisitor* Felt. Syntypes: 1 female, 1 male, USA, W. Nyack, NY, 25/IX/1907, E.P. Felt, ex. *S. gigantea*, Felt # a1705a, deposited in Felt Collection.

Host: *Solidago gigantea*

Gall and biology: Felt (1908) described this species from a single male and a single female and speculated (Felt 1915) that it develops as an inquiline in galls of *R. capitata*. However, we did not find any signs of its presence in galls of *R. capitata*. Given the morphological similarity of *R. inquisitor* adults to those of *R. clarkei*, it is possible that *R. inquisitor* is not an inquiline but, rather, induces inconspicuous conical galls that escaped Felt's attention. In the present study we found such galls on leaves of *S. gigantea* (Fig. 67), including on modified leaves composing the bud galls of *Dasineura folliculi*. This finding supports our hypothesis that *R. inquisitor* may well be the species responsible for these galls, but the galls were rare and we were unable to rear adults from them (see details below, under *Rhopalomyia* sp.). A comparison of such adults with the type specimens of *R. inquisitor* would be the only way to determine whether the galls we found are indeed those of *R. inquisitor.*

Remarks: The adults of *R. inquisitor* are similar to those of *R. clarkei*, but the male gonopods in *R. inquisitor* are less bulky, its ovipositor is longer, the arms of tergite 8 of the female abdomen are relatively longer, and the female flagellomeres have significantly longer necks.

***Rhopalomyia lobata* Felt 1908**

Rhopalomyia lobata Felt 1908: 366.
Rhopalomyia lanceolata Felt 1908: 367. **New synonym.**

Adult: Antenna with 16–17 flagellomeres in both sexes; necks of male flagellomeres III–VII 0.47–0.67 times as long as nodes, necks of female flagellomeres absent to 0.1 times as long as nodes. Palpus 1-segmented, usually no more than 1.6 times as long as wide, shorter in female than in male, rounded or sometimes slightly tapered at tip, setose and setulose. Wing length 2.9–3.2 mm in male, 2.7–3.2 mm in female. Legs densely covered by dark brown scales; Empodia considerably longer than claws. Male terminalia (Fig. 21): gonocoxite relatively slender and angular at base, setose, with strongly setose mediobasal lobe; gonocoxal apodeme wide, proximally divided into two short arms; gonostylus cylindrical, curved in both posterior and anterior margins, setose and setulose throughout, with brush-like tooth; aedeagus wide, rectangular, truncated and often notched apically; hypoproct wide, with very shallow notch, strongly setose and setulose; cerci completely or almost completely fused, forming a single, almost rectangular lamella, sometimes separated by very shallow notch to form a heart-shaped lamella, strongly setulose with many long setae. Female abdomen (Fig. 35) as in *R. fusiformae* and *R. pedicellata*; ovipositor 5.3–6.0 times as long as tergite 7.

Pupa (Figs. 50–51): Orange. Bases of horns undeveloped, with only tiny apical, blunt bump. Posterior margins of antennal bases V-shaped in frontal view. Frons without median projections or ridges, with pronounced lateral projections, posterior edge rounded.

Type material: *Rhopalomyia lobata* Felt. Holotype: female, USA, W. Nyack, NY, 17/VII/1907, E.P. Felt, ex. *E. graminifolia*, Felt # a1647, deposited in Felt Collection.
Rhopalomyia lanceolata Felt. Syntypes: 1 male, 1 female, USA, Lake Forest, IL, unspecified date, J.G. Needham, ex. *E. graminifolia*, Felt # c784, deposited in Felt Collection.

Other material examined (all from *E. graminifolia*): *R. lobata*: 1 female, USA, Big Moon Lake, NY, 29/VII/1985, R.J. Gagné; 9 males, 13 females, USA, Eldridge Wilderness, NY, 7/VII/1987, M.V. McEvoy; 2 pupae, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 23/VI/2005, T. Dowling; 3 males, 3 females, 2 larvae, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 27/VI/2005, N. Dorchin; 3 males, 3 females, USA, Lewisburg, PA, 28/VI/2005, N. Dorchin.

Host: *Euthamia graminifolia*

Gall and biology: The multi-chambered galls are induced in apical and lateral buds. They are first apparent in mid May, when they form about 1 cm-wide globular swellings in shoot tips (Fig. 78). Some galls occur in clusters around the shoot tip or in adjacent lateral buds (Fig. 79) At this point, several leaves surround a small spongy mass at the base of the gall, which grows gradually over the next month up to a final size of 6 cm in diameter. The small size of the gall given by Felt (1915) probably refers to a gall in a lateral bud or to one of clustered galls in a shoot tip. The leaves that are tightly wrapped around the spongy mass are much wider than the normal, thin leaves of the plant (Fig. 80). Around the second week of June, these leaves begin to loosen, revealing the whitish tissue in which 5–35 larval chambers are embedded. Adults emerge from late June to mid July, at which point the fleshy core of the gall is exposed and empty pupal skins can be seen stuck in it (Fig. 81). Soon after the gall midges emerged, the fleshy tissue turns black, and dry galls remain on the plants for several weeks. No second generation galls were observed, thus this species appears to be univoltine, with first instar larvae probably overwintering in or near the plants.

Remarks: Despite the striking differences in gall structure and morphology, adults of this species are almost identical to those of *R. fusiformae* and *R. pedicellata* – the other *Rhopalomyia* species from *Euthamia*. Females of all three species share the widely splayed arms of the Y-shaped 8th abdominal tergite, which are longer relative to the shaft in *R. lobata* than in any other *Rhopalomyia* species from goldenrods. Males of all three species share the angular and relatively slender gonocoxite, with strongly sclerotized two-armed gonocoxal apodeme, but males of *R. lobata* often have notched aedeagus and completely fused cerci, compared to the truncated aedeagus and clear notch between the cerci in *R. fusiformae* and *R. pedicellata*. The pupa of *R. lobata* has blunt antennal bases (Fig. 51), as opposed to the small, tapered projections on the antennal bases of *R. pedicellata* (Fig. 53). The pupa of *R. fusiformae* is unknown.

Felt (1908) described *R. lobata* and *R. lanceolata* in the same work from similar, spongy galls in apical buds of *E. graminifolia*. The two species are synonymized here based on their morphological similarity, the description of their galls (Felt 1915), and the fact that we never found any other type of spongy bud galls on *Euthamia*. It is noteworthy that the cerci in the single male syntype of *R. lanceolata* are atypically separated by a clear notch, thus resembling those of *R. fusiformae* and *R. pedicellata*. It is possible that this specimen represents a less common situation in *R. lobata*, in which the cerci are partially separated.

Rhopalomyia pedicellata Felt 1908

Rhopalomyia pedicellata Felt 1908: 365.
Cecidomyia euthamiae Stebbins 1910: 53; Felt 1915: 262 (*Rhopalomyia*)

Adult: Yellowish-white, with dark scales and hairs; Legs densely covered by fine, dark scales. Antenna with 16–17 flagellomeres in male, 16–18 in female; necks of male flagellomeres III–VII 0.47–0.67 times as long as nodes, necks of female flagellomeres absent to 0.25 times as long as nodes. Palpus 1-segmented. Wing length 2.4 mm in male, 2.2–2.8 mm in female. Ovipositor 4.8–5.2 times as long as tergite 7. Otherwise similar to *R. fusiformae*.

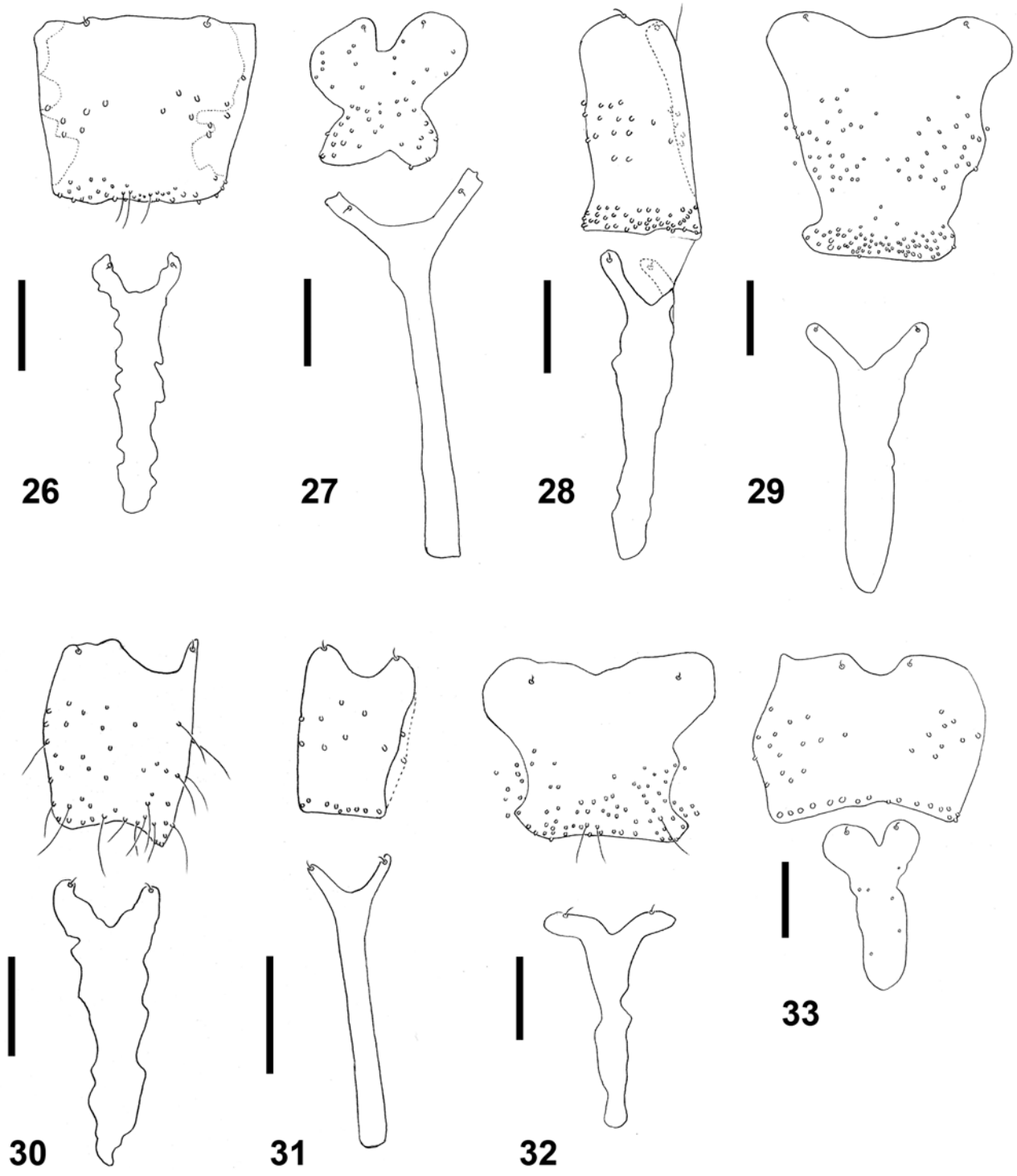
Pupa (Figs. 52–53): Orange. Antennal bases round V-shaped in frontal view, with tiny pointed tips. Frons without projections or ridges, with short lateral projections, basal edge rounded.

Type material: *Rhopalomyia pedicellata* Felt. Syntypes: 1 male, 2 females, USA, Albany, NY, 24–26/VII/1907, E.P. Felt, ex. *E. graminifolia*, Felt # a1650, deposited in Felt Collection; 1 male, USA, NY, Albany, 6/VIII/1907, E.P. Felt, ex. *E. graminifolia*, Felt # a1650, deposited in Felt Collection. Felt (1908) also mentioned a type labeled # 1311, but specimens associated with this number were not found.

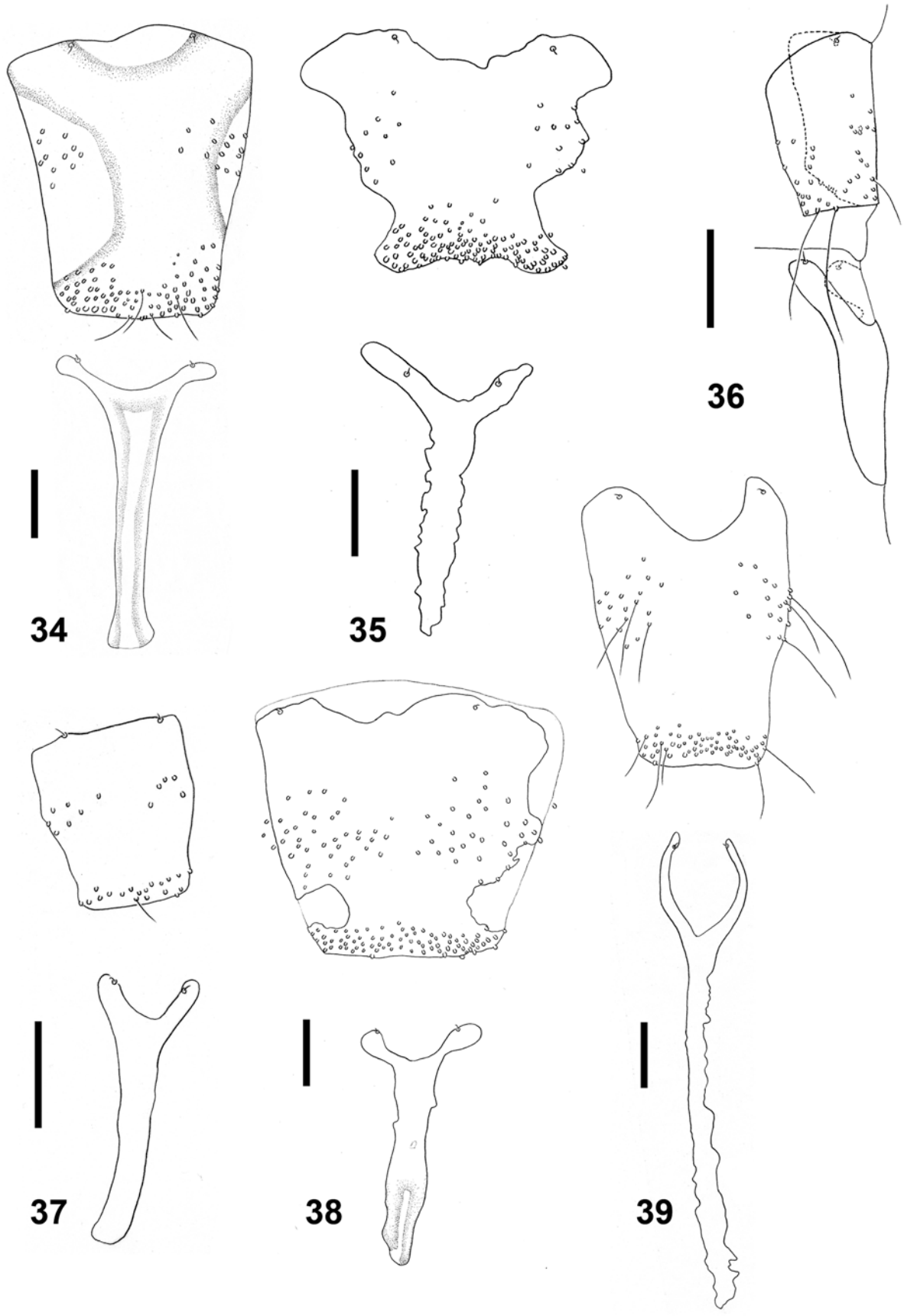
Cecidomyia euthamiae Stebbins: Holotype: 1 gall, USA, Springfield, MA, unspecified date, F.A. Stebbins, specimen # 194, deposited in the Springfield Natural History Museum, Massachusetts (NHSM).

Other material examined (all from *E. graminifolia*): 3 females, USA, Eldridge Wilderness, West Dryden, NY, 13–14/IX/1987, M.V. McEvoy; 1 male, USA, Lewisburg, PA, 15/VIII/2005, T. Dowling; 2 exuviae,

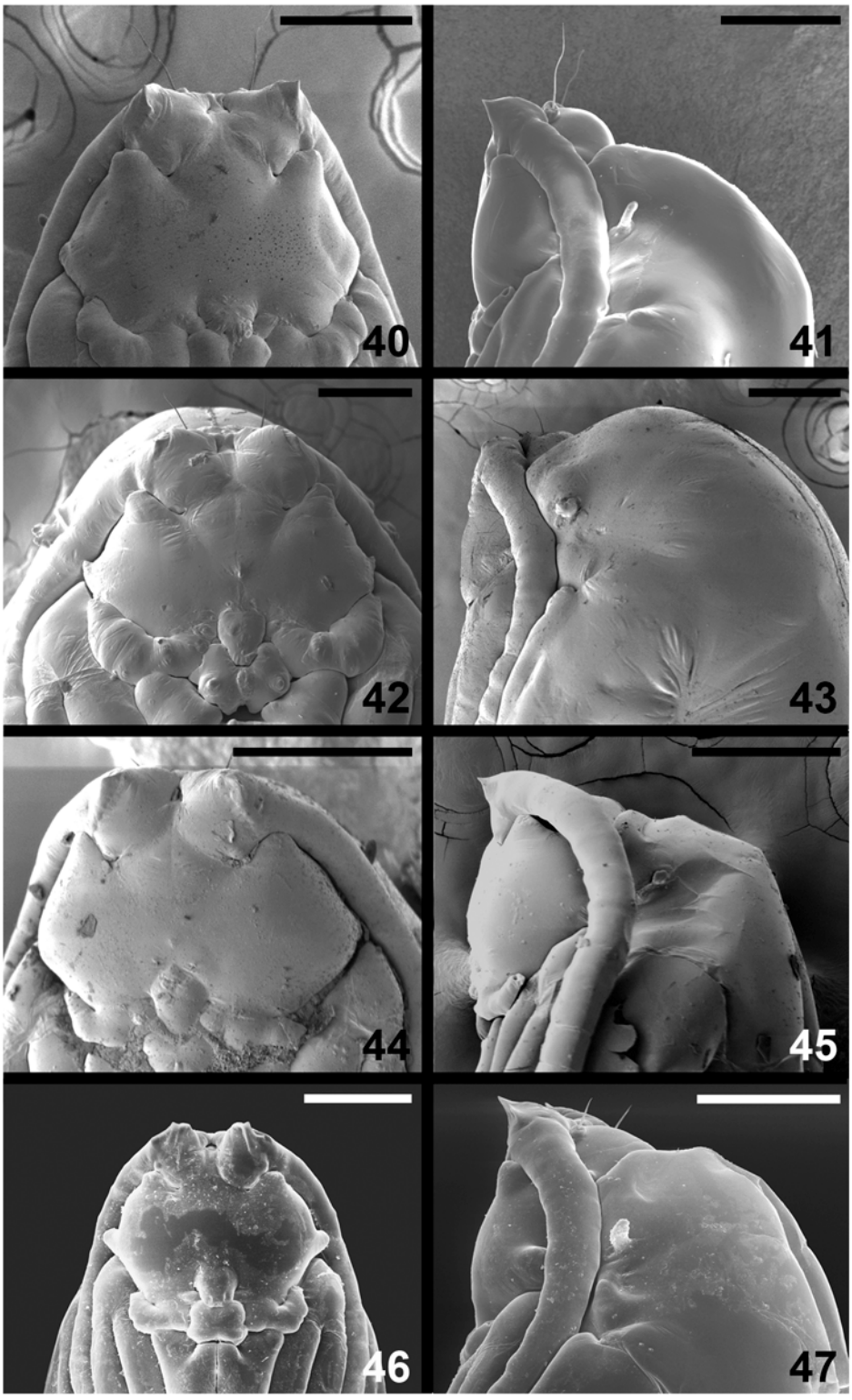
USA, Lewisburg, PA, 29/VII/2005, T. Dowling; 1 female, USA, Lewisburg, PA, Moore School Rd., 29/VII/2005, N. Dorchin; 2 pupae, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 2/IX/2005, N. Dorchin; 1 female, 1 exuviae, USA, Mauses Creek, PA, 16/IX/2005, N. Dorchin; 1 female, USA, R.B. Winter State Park, PA, 22/VII/2007, N. Dorchin.



FIGURES 26–33. Female 7th and 8th abdominal tergites, dorsal view. 26. *Rhopalomyia anthophila*. 27. *Rhopalomyia bulbula*. 28. *Rhopalomyia guttata*. 29. *Rhopalomyia capitata*. 30. *Rhopalomyia clarkei*. 31. *Rhopalomyia cruziana*. 32. *Rhopalomyia fusiformae*. 33. *Rhopalomyia gina*. Scale bars = 0.1 mm



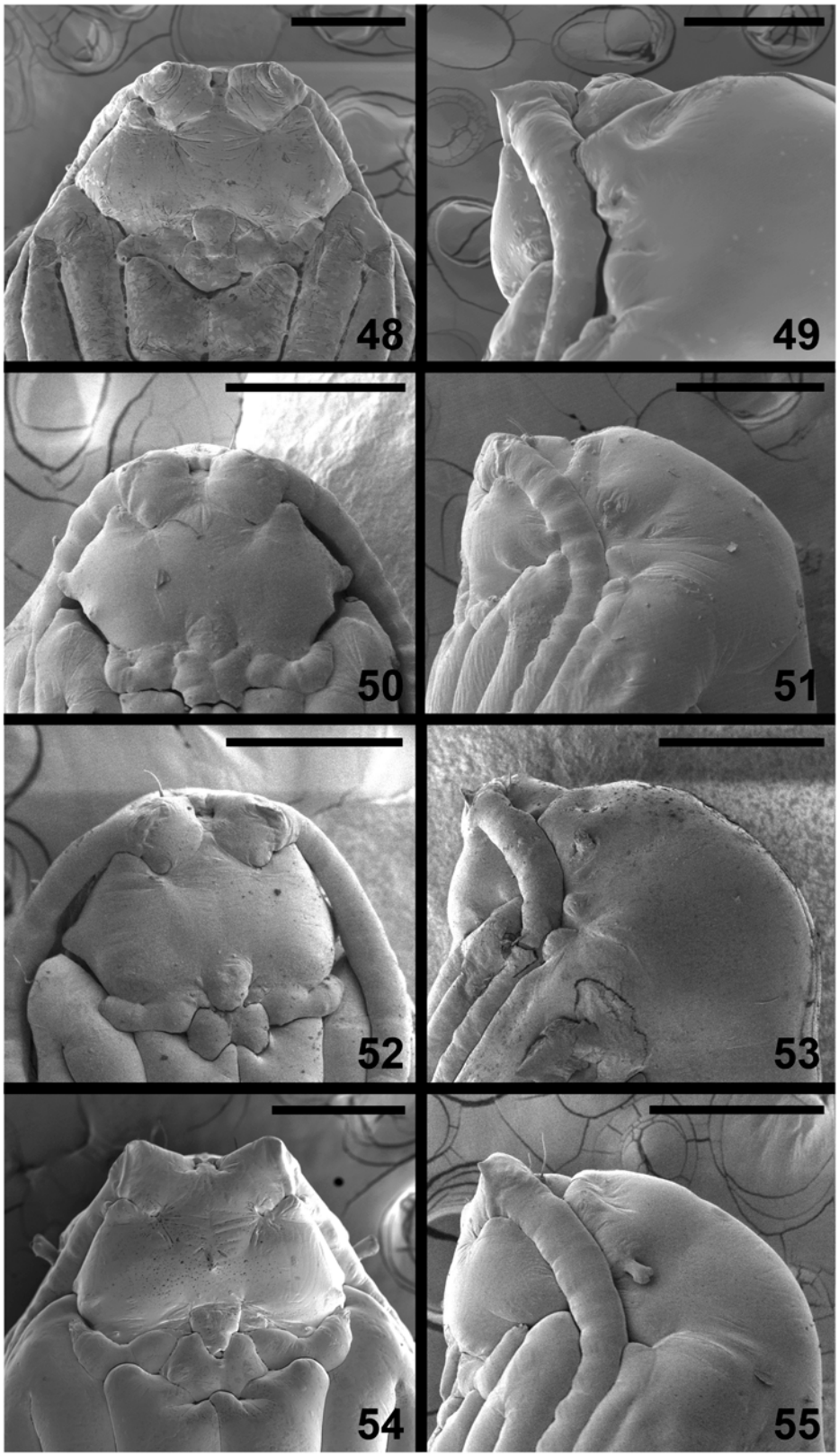
FIGURES 34–39. Female 7th and 8th abdominal tergites, dorsal view (unless otherwise noted). 34. *Rhopalomyia hirtipes*. 35. *Rhopalomyia lobata*. 36. *Rhopalomyia inquisitor*, lateral. 37. *Rhopalomyia racemicola*. 38. *Rhopalomyia solidaginis*. 39. *Rhopalomyia thompsoni*. Scale bars = 0.1 mm



FIGURES 40–47. Pupal heads. 40. *Rhopalomyia anthophila*, ventral. 41. *Rhopalomyia anthophila*, lateral. 42. *Rhopalomyia capitata*, ventral. 43. *Rhopalomyia capitata*, lateral. 44. *Rhopalomyia clarkei*, ventral. 45. *Rhopalomyia clarkei*, lateral. 46. *Rhopalomyia gina*, ventral. 47. *Rhopalomyia gina*, lateral. Scale bars = 200 μm

Host: *Euthamia graminifolia*

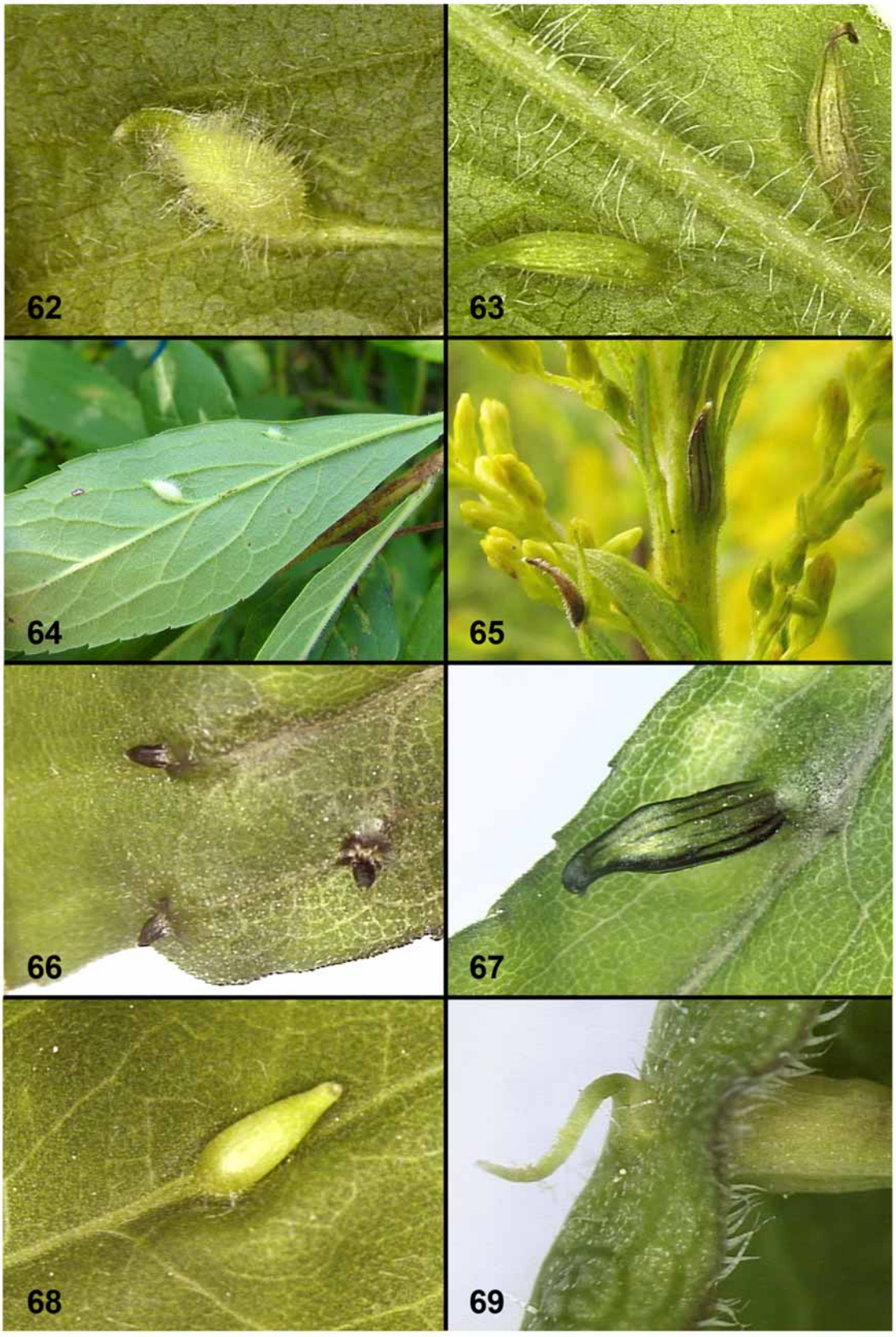
Gall and biology: The gall is found on stems, leaves, or inflorescences. This is a delicate, slender, 14–21 mm long gall, carried on a pedicel that is about half as long as the remainder of the gall (hence the species' name) (Figs. 84–85). The gall is single-chambered, green to purplish-red, with longitudinal ridges, and



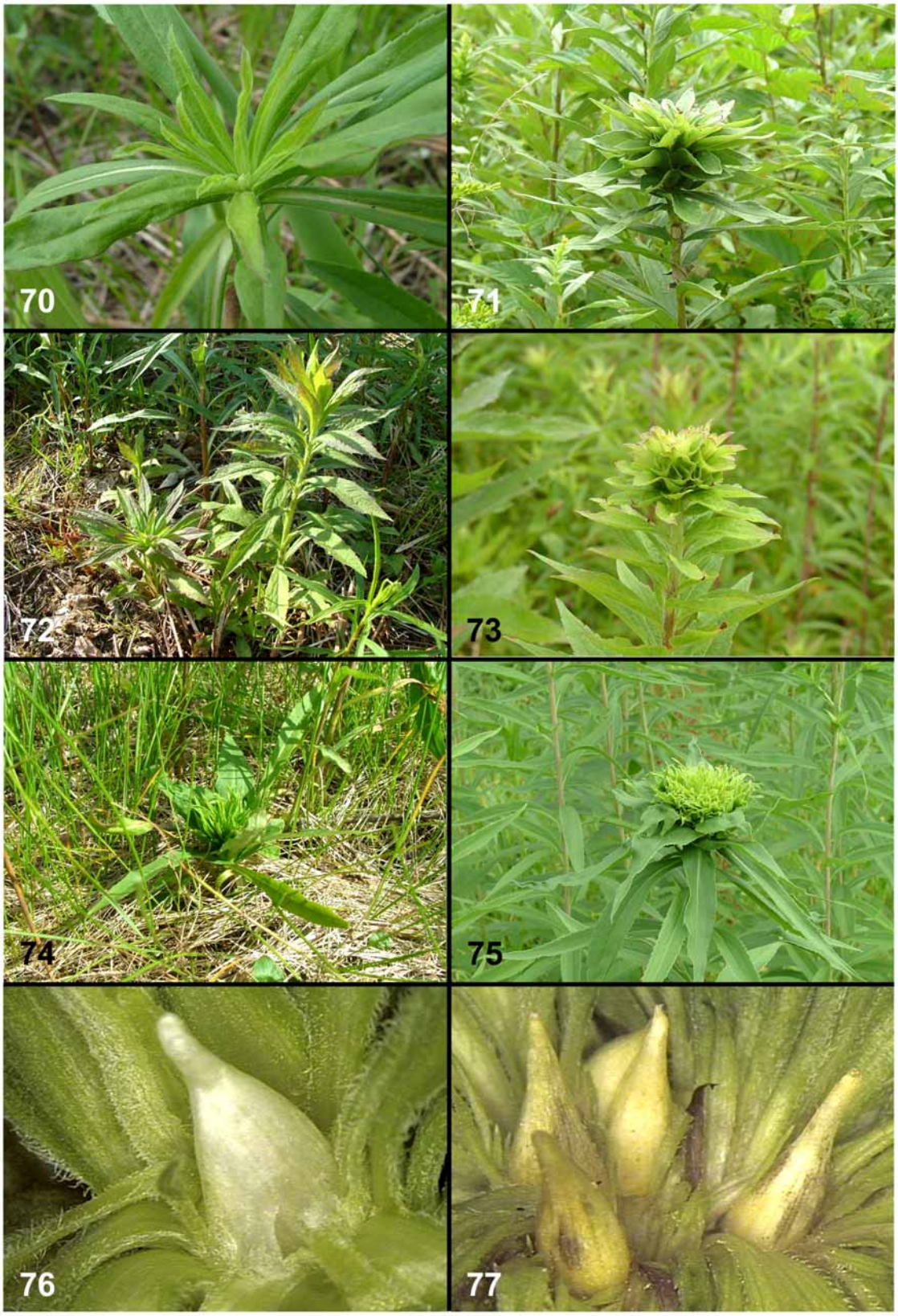
FIGURES 48–55. Pupal heads. 48. *Rhopalomyia hirtipes*, ventral. 49. *Rhopalomyia hirtipes*, lateral. 50. *Rhopalomyia lobata*, ventral. 51. *Rhopalomyia lobata*, lateral. 52. *Rhopalomyia pedicellata*, ventral. 53. *Rhopalomyia pedicellata*, lateral. 54. *Rhopalomyia solidaginis*, ventral. 55. *Rhopalomyia solidaginis*, lateral. Scale bars = 300 μm

FIGURES 56–61. *Rhopalomyia* galls. 56. A group of *Rhopalomyia anthophila* capitulum galls (arrows) among normal capitula. 57. *Rhopalomyia anthophila* gall. Figs. 58–61. *Rhopalomyia hirtipes*; 58. Young gall. 59. Mature gall at base of plant. 60. Mature gall carried on a ramet about 50 cm above the ground. 61. Mature gall that has split to allow adult emergence; the emergence bag was opened to show the gall.

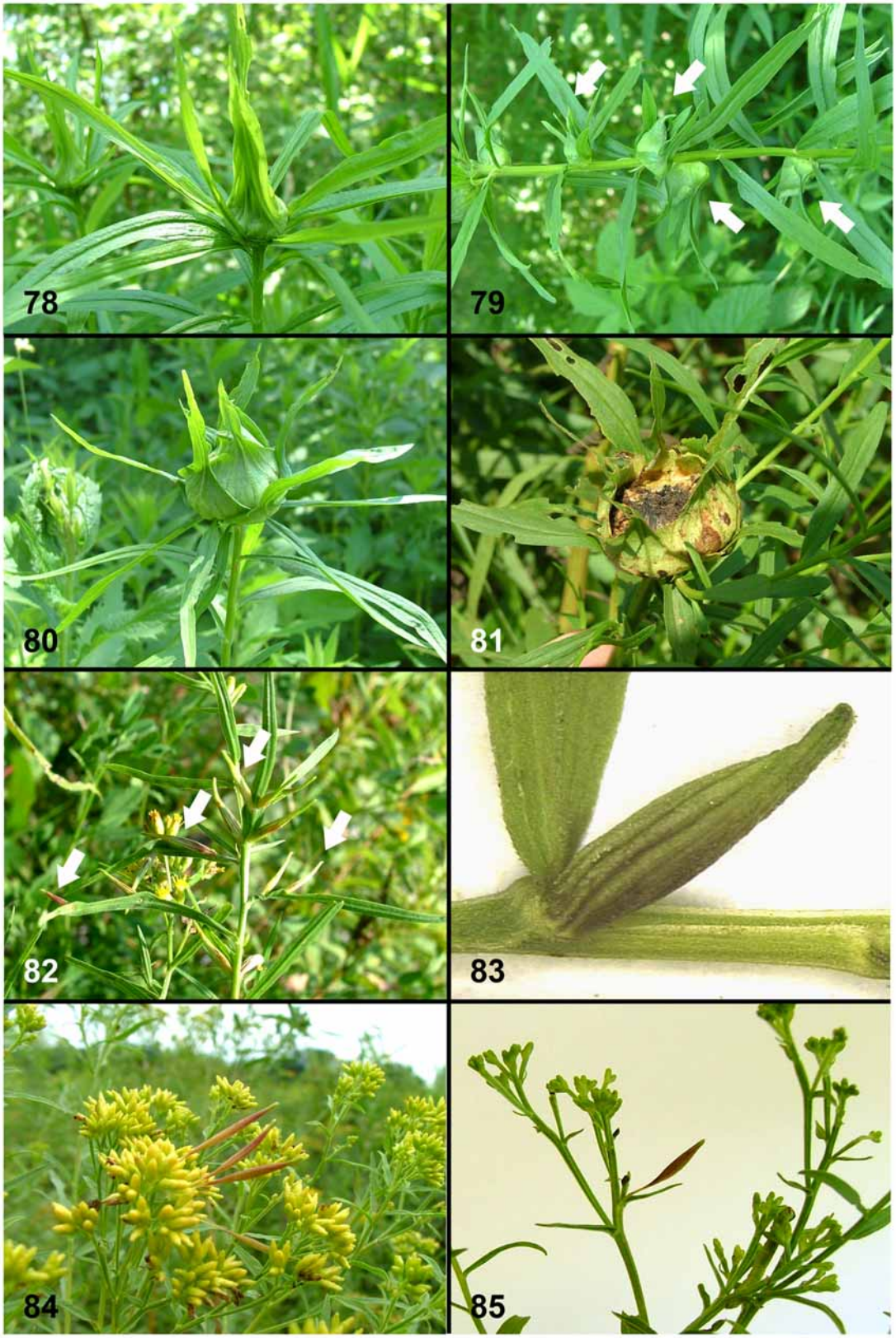
tapered at both ends. The internal walls of the gall are smooth and shiny and the larva is usually found facing downwards at the bottom of the chamber. Galls are common and found from mid June to September. The gall reaches its final size when the larva is still a first instar. The species completes at least two generations per year, with adult emergence from July to September. The structure of the gall is identical to that of *R. fusiformae* except for the presence of the pedicel.



FIGURES 62–69. *Rhopalomyia* leaf and stem galls. Figs. 62–64. *Rhopalomyia clarkei* galls on *Solidago rugosa*; 62. Young gall. 63. Mature galls. 64. Galls on underside of leaf. 65. *Rhopalomyia clarkei* galls on stem and leaf of *Solidago altissima* (photo by M. Wise). Figs. 66–67. *Rhopalomyia* sp. galls on leaves of *Solidago gigantea*; 66. Very young galls. 67. Mature gall. Figs. 68–69. *Rhopalomyia gina* galls on leaves of *Solidago juncea*. 68. Gall on upper side of leaf. 69. Tail-like appendage of gall on underside of leaf.



FIGURES 70–77. *Rhopalomyia* rosette galls. Figs. 70–73. *Rhopalomyia solidaginis*; 70. Spring gall on *Solidago altissima* showing single central larval chamber. 71. Summer gall. 72. Two ramets of *Solidago rugosa*, the left carries a spring gall, the right ungalled, demonstrating the growth-stunting effect of the gall. 73. Summer gall on *Solidago rugosa*. Figs. 74–75. *Rhopalomyia capitata*. 74. Spring gall carried close to the ground on young sprout. 75. Summer gall. 76. Larval chamber in *Rhopalomyia solidaginis* gall on *Solidago altissima*. 77. Larval chambers in *Rhopalomyia capitata* gall on *Solidago gigantea*.



FIGURES 78–85. *Rhopalomyia* galls. Figs. 78–81. *Rhopalomyia lobata*. 78. Young gall in apical meristem. 79. Young galls in lateral meristems (arrows). 80. Mature gall showing modified, broad leaves sheathing the fleshy gall center. 81. Mature gall showing exposed, fleshy center after onset of adult emergence. Figs. 82–83. *Rhopalomyia fusiformae*; 82. Aggregation of galls on stem and leaves (arrows). 28. Gall, showing longitudinal ridges and lack of pedicel. Figs. 84–85. *Rhopalomyia pedicellata*. 84. Group of galls situated on long pedicels among capitula. 85. Gall arising from stem, carried on long pedicel.

Remarks: *Rhopalomyia pedicellata* and *R. fusiformae* are similar in adult morphology but can be reliably distinguished from each other based on their pedicelled and sessile galls, respectively. No galls of intermediate morphology were found, and a recent molecular analysis suggests that the two species are valid (Dorchin *et al*., in prep.). Pupae of *R. pedicellata* differ from those of the related *R. lobata*, also on *E. graminifolia*, in having small, pointed tips on the antennal bases that are absent in *R. lobata*, and in lacking the pronounced, lateral projections of the frons. The pupae of *R. fusiformae* are unknown.

Rhopalomyia racemicola Felt 1907

Rhopalomyia racemicola Felt 1907a: 24.

Adult: Antenna with 18 flagellomeres in male, 16 in female; necks of male flagellomeres III–VII 0.75–1.00 times as long as nodes, necks of female flagellomeres absent to 0.14 times as long as nodes. Palpus 2-segmented, second segment 1.5–2.5 times as long as first, slightly tapered at tip, setose and setulose. Wing length 1.9–2.1 mm in male, 1.9 mm in female. Legs covered by brownish scales. Male terminalia (Fig. 22): gonocoxite stout, wide at base, almost square, setose, with setose mediobasal lobe; gonocoxal apodeme undivided, narrows anteriorly; gonostylus short and wide, narrows only slightly toward apex, convex along both anterior and posterior margins, setose and setulose throughout, with small brush-like tooth; aedeagus relatively narrow, conical, rounded apically; hypoproct narrows distally, with very shallow dent apically, setose and setulose; cerci separated by deep triangular notch, strongly setose and setulose. Female abdomen (Fig. 37): tergite 7 trapezoid, with two anterior trichoid sensilla and several setae posteriorly and mesolaterally; tergite 8 slender Y-shaped, proximal arms less than third the length of shaft, each with anterior trichoid sensillum; ovipositor 9.0–9.3 times as long as tergite 7.

Pupa: unknown.

Type material: *Rhopalomyia racemicola* Felt. Syntypes: 2 males, 2 females, USA, Asheville, NC, 16/IX/1906, E.P. Felt, ex. *S. altissima* (*R. canadensis* of Felt), Felt # a1605, deposited in Felt Collection.

Host: *Solidago altissima, S. fistulosa* (?)

Gall: The green, bristly, onion-shaped capitulum galls are situated among normal capitula and can sometimes be found in aggregations. They were recorded by Felt (1907a, 1915) from *S. altissima* in North Carolina, and Gagné (1989) reported similar galls on *S. fistulosa* from Florida, which he attributed tentatively to the same species. The description of the galls and the mention of previous records of this species in Felt (1915) actually refer to the galls of *Schizomyia racemicola* rather than those of *R. racemicola* (see Gagné 1971). The true nature of *R. racemicola* galls is therefore uncertain, and we tentatively adopt Gagné's assumption that the galls he received from Florida are those of *R. racemicola*. Adults emerged in mid September in North Carolina, and in December in Florida. Given that the galls develop in capitula, we assume that *R. racemicola* is univoltine, but verifying the identity of the host plant and the galls, and clarifying the life history of this species require more investigation.

Remarks: Adults of *R. racemicola* generally resemble those of the other *Rhopalomyia* species from goldenrod capitula (*R. anthophila, R. guttata*, and *R. cruziana*) but this is the only species of the four whose female flagellomeres occasionally have necks, and its male gonocoxites are angular at their bases rather than rounded as in the other species. We currently consider Gagné's record (1989) from *S. fistulosa* as representing *R. racemicola* because of the general similarity of the galls to the original description by Felt (1907a) and because the three females reared by Gagné generally resemble the *R. racemicola* types. Nevertheless, more information and additional material (particularly males) will need to be obtained before this assumption can be confirmed.

***Rhopalomyia solidaginis* (Loew 1862)**

Cecidomyia solidaginis Loew 1862: 194; Felt 1915: 246 (*Rhopalomyia*).
Rhopalomyia albipennis Felt 1908: 364. **New synonym.**
Rhopalomyia carolina Felt 1908: 363. **New synonym.**

Adult: Body densely covered by dark scales. Antenna with 17 or 19–20 flagellomeres in male (spring and summer generations, respectively), 17 or 20–23 flagellomeres in female (spring and summer generations, respectively); necks of male flagellomeres III–VII 0.63–1.00 or 0.50–0.80 times as long as nodes (spring and summer generations respectively); female flagellomeres without necks. Palpus 2-segmented; second segment at least twice as long as first, rounded or sometimes tapered apically, setose and setulose, with several elongate, dark brown scales. Wing length 3.7 or 4.0–4.2 mm in male (spring and summer generations, respectively), 3.1–3.3 or 2.8–4.1 in female (spring and summer generations, respectively). Legs densely covered by dark brown scales. Male terminalia (Figs. 23–24): gonocoxite bulbous and robust, very wide at mid length, strongly setose, with very long, mesally directed setae on ventral side (Fig. 24), with strongly setose mediobasal lobe; gonocoxal apodeme undivided, narrows anteriorly; gonostylus short and wide, narrows only slightly toward apex, setose and setulose throughout, with brush-like tooth; aedeagus rounded apically; hypoproct with apical notch, setose and setulose; cerci very wide, separated by deep notch, strongly setose and setulose. Female abdomen (Fig. 38): tergite 7 trapezoid, weakly sclerotized along anterior and lateral margins, with two anterior trichoid sensilla, several rows of setae posteriorly, and groups of setae mesolaterally; tergite 8 Y-shaped, proximal arms narrow distally and widen proximally, less than third the length of shaft, each with anterior trichoid sensillum; shaft with weakly sclerotized patches; ovipositor 4.0–4.1 or 3.6–4.6 times as long as tergite 7 (spring and summer generations, respectively).

Pupa (Figs. 54–55): Light orange. Antennal bases short and blunt; basal part wide V-shaped in frontal view. Frons sometimes with tiny projection at mid length, without pronounced lateral projections; basal edge rounded. Prothoracic spiracle divided apically into 2–3 lobes.

Type material: *Cecidomyia solidaginis* Loew. Neotype designated here: male, USA, West Dryden, NY, 28/V/1987, M.V. McEvoy, reared from rosette gall on *S. altissima*. The neotype is designated in order to clarify the taxonomic status of *R. solidaginis* (Loew), whose type series is lost. The neotype is so labeled and is deposited together with 9 associated permanent microscopic slides of 7 females and 7 males of the same series in the USNM. This species was based on 1 male and 1 female from USA, District of Columbia, collected by B. Osten Sacken in August (unspecified date), ex. *S. altissima*. These syntypes are neither in the MCZC nor in the USNM and we consider them lost.

Rhopalomyia albipennis Felt: Syntypes: 1 male, USA, Albany, NY,10–11/IX/1907, E.P. Felt, Felt # a1655, deposited in Felt Collection; 2 males (pinned), USA, Albany, NY, 14/IX/1907, E.P. Felt, Felt # a1655, deposited in Felt Collection.

Rhopalomyia carolina Felt: Holotype: 1 female, USA, Asheville, NC, 4/X/1906, E.P. Felt, Felt # a1635, deposited in Felt Collection.

Other material examined (all from *Solidago altissima* unless otherwise noted): *R. albipennis*: 1 female, USA, Bath, NY, 5/IX/1907, E.P. Felt, Felt # a1655, deposited in Felt Collection; 1 female, USA, Albany, NY, 10–11/IX/1907, E.P. Felt, Felt # a1655, deposited in Felt Collection. *R. solidaginis*: 3 males, 4 females, USA, West Dryden, NY, 28–30/V/1987, M.V. McEvoy; 4 males, 3 females, USA, West Dryden, NY, 15–18/IX/1987, M.V. McEvoy; 2 pupae USA, PA, Bucknell University Chillisquaque Creek Natural Area, 5/V/2006, N. Dorchin, ex. *Solidago rugosa*; 3 larvae, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 25/VIII/2006, N. Dorchin; 2 pupae, USA, PA, Liberty Valley Rd., 3/IX/2006, N. Dorchin; 2 pupae 3 females, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 4/IX/2006, N. Dorchin; 2 pupae, USA, PA, Bucknell University Chillisquaque Creek Natural Area, 12/IX/2006, N. Dorchin, ex. *Solidago rugosa*; 2 pupae, USA, Mifflinburg, PA, 17/V/2007, N. Dorchin & M. Wise, ex. *Solidago canadensis*.

Host: *Solidago altissima, S. canadensis*, and *S. rugosa*

Gall and biology: This species is bivoltine and induces morphologically different bud galls in spring (April–May) and summer (August–September), which are very similar on all three host plants. The spring-generation galls (Figs. 70, 72): are inconspicuous and difficult to locate due to the minor difference between galled and normal shoots, although the growth of galled ramets is sometimes stunted and they therefore appear shorter than ungalled ramets (Fig. 72). The apical leaves of a galled ramet appear splayed, and the base of the gall from which they originate is slightly thickened. Each gall usually contains only one conical, white chamber in the middle of the apical meristem (Fig. 76), ca. 3 mm long, and containing a single larva that is usually found deep at the bottom of the chamber with its head facing downwards. Occasionally 2–3 chambers are found in the same gall and may be attached to each other longitudinally. The chamber is surrounded by approximately 10 leaves that are much shorter and thinner than normal leaves (Fig. 70). On *S. altissima*, these modified leaves are lighter in color, especially along their mid vein. These are surrounded in turn by a whorl of leaves of normal shape and size. Galls contained pupae already in early May, suggesting rapid development of the spring generation soon after the plants sprout. Circumstantial evidence showed that larvae that induce the spring galls hatch from eggs in the fall of the previous year and overwinter inside the rhizomes. Rhizomes that were collected in the field, cut, and planted in our research greenhouse, yielded sprouts that developed galls without being exposed to adults (M. Wise, pers. com.).

Summer generation galls (Figs. 71, 73) become apparent around mid June and reach their final size by July, while the larvae inside them are still tiny first instars at the base of the rosette leaves. White chambers that are similar to those in the spring galls appear in the gall around mid July, when the larvae molt into third instars, and each chamber contains a single larva that is found deep in the chamber, facing downwards. Each chamber is surrounded by a group of very short and narrow leaves, which in turn are surrounded by longer and wider leaves to form a distinct subunit within the gall. Usually at least 2–5 subunits are clumped together at the shoot apex to form a conspicuous rosette that is 3–5 cm in diameter (Raman & Abrahamson 1995) (Figs. 71, 73). The rosette gall of *R. capitata* (Fig. 75) is superficially similar but does not contain distinct subunits and appears flatter than galls of *R. solidaginis*. Pupation takes place in early September, and adults emerge in September and early October. Larvae are heavily attacked by gregarious endoparasitoids.

Remarks: This is the second largest species of *Rhopalomyia* on goldenrods. Males can be recognized by their very typical large and robust gonopods, and females have the shortest ovipositors of all *Rhopalomyia* species from goldenrods (relative to the size of the 7th abdominal tergite). Adults of the spring generation are somewhat smaller and have fewer antennal flagellomeres than adults of the summer generation, but adults and pupae of the two generations are otherwise similar morphologically.

Despite the superficial similarity between the galls of *R. solidaginis* and *R. capitata* and their phylogenetic relatedness (Stireman *et al.* 2005; Dorchin *et al.*, in prep.), they can be distinguished from each other by the male genitalia, which are larger and more robust in *R. solidaginis*, and by the typical shape of the Y-shaped 8th tergite of the female abdomen, the arms of which are narrow posteriorly and widen anteriorly in *R. solidaginis* (Fig. 38) but are of the same width throughout their length in *R. capitata* (Fig. 29). The antennal bases of pupae in *R. solidaginis* form somewhat larger horns than those in *R. capitata*, but pupae of the two species are otherwise very similar.

Rhopalomyia albipennis and *R. carolina* were described by Felt (1908) from galls that are similar to those of *R. solidaginis* and from the same host plant (*S. altissima*, referred to by Felt as *S. canadensis*). The single female representing *R. carolina* has 22–23 antennal flagellomeres but is otherwise similar morphologically to females of *R. solidaginis*. Similarly, the adults of *R. albipennis* are indistinguishable from those of *R. solidaginis*, although Felt (1908) stated that the male wings are whitish in *R. albipennis* as opposed to the brownish wings of *R. solidaginis*. Examination of a slide-mounted male from Felt's type series revealed that the wing is covered by fungal mycelia which give it a very white appearance. In two other (pinned) males from that series, we found that the wings are somewhat whitish and not covered by brown microtrichia, but we consider this an accidental example which is not representative of the species. This is because the wings of all slide-mounted and pinned females in the type series of *R. albipennis*, collected at similar localities and dates, are covered by dark brown microtrichia, as are those of *R. solidaginis*. Indeed, in his later revision of

North American *Rhopalomyia*, Felt (1915) noted that the male wings are hyaline. Based on these observations, *R. albipennis* and *R. carolina* are synonymized here under *R. solidaginis*.

***Rhopalomyia thompsoni* Felt 1907**

Rhopalomyia thompsoni Felt 1907b: 159.

Adult: Antenna with 17 or 21–22 flagellomeres in male (spring and summer generations, respectively), 16–17 or 20–25 flagellomeres in female (spring and summer generations, respectively); necks of male flagellomeres III–VII 0.43–0.60 times or 0.85–1.00 times as long as nodes (spring and summer generations, respectively), female flagellomeres without necks. Palpus 2-segmented, long, setose and setulose; second segment at least 1.5 times as long as first, tapered distally. Wing length 3.3 or 3.1–3.3 mm in male (spring and summer generations, respectively), 2.8 or 2.6–3.0 mm in female (spring and summer generations, respectively). Male terminalia (Fig. 25): gonocoxite robust, with apicoventral projection, strongly setose, with setose mediobasal lobe; gonocoxal apodeme broad, undivided; gonostylus short and wide, almost same width throughout length, strongly setose and setulose, with many setae close to the apical, brush-like tooth; aedeagus cylindrical, slightly truncated and rounded apically; hypoproct M-shaped, setose and setulose; cerci very wide, separated by deep notch, setose and setulose. Female abdomen (Fig. 39): tergite 7 rectangular, weakly to unsclerotized in mid-anterior part, with two anterior trichoid sensilla, several rows of setae posteriorly, and groups of setae mesolaterally; tergite 8 Y-shaped, very long and slender, proximal arms arched mesad, slender, less than third the length of shaft, each with anterior trichoid sensillum; ovipositor 11.2 or 7.3–7.8 times as long as tergite 7 (spring and summer generations, respectively).

Pupa: unknown.

Type material: *Rhopalomyia thompsoni* Felt. Syntypes: 1 male, 1 female, USA, Worcester, MA, 3/V/1907, M.T. Thompson, Felt # 1100, deposited in Felt Collection.

Other material examined: 4 males, 4 females, USA, Freese Rd., NY, 18–25/IX/1987, M.V. McEvoy, ex. *S. altissima*.

Host: *Solidago altissima*

Gall and biology: This species has two generations per year, both of which develop in rhizome galls. The spring generation galls are solitary or clustered, bulbous, fleshy masses with 1–8 chambers each. As the galls develop, they become apparent above the ground and burst open before adult emergence in early May (Felt 1915). The second generation galls constitute brownish, globular, and usually multi-chambered swellings of the rhizomes, which were still completely subterranean in mid August, when they contained mature larvae. Pupation took place in late August to early September, at which time the galls became elongate and fleshier. Shortly before adult emergence the galls became apparent above the soil surface, and adults emerged from mid to late September. In the original description of this species, Felt (1907b) named *Solidago rugosa* and later (1915) *S. juncea* as the host, but in the present study we were unable to find similar spring galls on these plants. Given the similarity of the galls and the adults of the two generations, we conclude that they represent the same species and consider *S. altissima* to be the host plant of *R. thompsoni*. Distinguishing among different *Solidago* species in early spring can be difficult; hence it is not unlikely that the original host was misidentified. Confirmation of this conclusion will require locating spring-generation galls and verifying the identity of the host in which they are formed.

Remarks: This species resembles *R. hirtipes* both in male and gall morphology, but the two species occur on different hosts and show morphological differences in females. Males of both species have robust gonopods with wide gonocoxal apodeme and ventral, meso-apical projection of the gonocoxite. Females of *R. thompsoni* have neckless flagellomeres and very long and slender abdominal tergite 8 with mesally arched arms, as opposed to short-necked flagellomeres and thicker and widely splayed arms of abdominal tergite 8 in females of *R. hirtipes*.

The summer and spring generations of *R. thompsoni* differ in the number of flagellomeres in both sexes, in length of flagellomere nodes in the males, and in the length of the ovipositor. However, the descriptions of the spring-generation galls and the manner by which adults emerge from them (Felt 1915) are similar to what we observed in the summer-generation galls, and adults from both generations are otherwise similar morphologically. Similar differences between spring and summer generations in number of flagellomeres and length of their necks are also found in *R. solidaginis*.

Rhopalomyia sp.

Adult: unknown.

Pupa: unknown.

Host: *Solidago gigantea*

Gall and biology: Galls of this species (Figs. 66–67) are very similar in shape and size to galls of *R. clarkei* on *S. rugosa*, but are much rarer and are smooth rather than hairy. They are 2–3.3 mm long and 0.5–0.7 wide at widest part, green, sometimes with dark longitudinal lines, and most were found on the upper side of leaves. Due to the scarcity of the galls and to high parasitism rates we were unable to rear adults from them, but a molecular analysis based on larvae indicated that this species differs from *R. clarkei* (Dorchin *et al.*, in prep.). Some galls were found on leaves composing the bud galls of *Dasineura folliculi* on *S. gigantea* and there is no reason to believe they do not occur also on modified leaves of the rosette gall induced by *R. capitata* on the same host plant. If this is indeed the case, then these galls may actually be those of *R. inquisitor*, which was reported by Felt (1908) as an inquiline in *R. capitata* galls (see details under *R. inquisitor*).

Rhopalomyia n.sp.

Adult: unstudied.

Pupa: unstudied.

Material examined: 3 males, 5 females, 2 pupae, USA, Gainesville, FL, 5/V/1982, E. Fontes.

Host: *Solidago fistulosa*

Gall and biology: The galls of this species were found by E. Fontes in May and June of 1982 around Gainesville, Florida (Fontes *et al.* 1994). They developed on young stems, and seemed to have stunted the growth of the apical meristem, because galled ramets were usually only 30 cm tall and atypically branched under the galls. The galls are oval with a tapered tip, single-chambered, grayish, and are typically aggregated around a stem to form a "star-like" structure. Galls found in August were already dry except for one or two records.

Remarks: The available material was insufficient for description of this species in the present work or for determining its relations to other *Rhopalomyia* species on goldenrods. The description of the galls provided to us by E. Fontes (pers. com.) is reminiscent of *R. racemicola* galls, but the galls of *R. racemicola* develop in inflorescences in late summer whereas those of the new species develop on stems in spring and early summer. We currently consider this species as undescribed based on its galls, and intend to describe it once additional material is obtained.

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References

Abrahamson W.G., Weis AE. (1997) *Evolutionary Ecology across Three Trophic Levels: Goldenrods, Gallmakers, and Natural Enemies*. Princeton University Press, Princeton, NJ, 456 pp.

Crutsinger, G.M., Cadotte M.W. & Sanders N.J. (2009) Plant genetics shapes inquiline community structure across spatial scales. *Ecology Letters*, 12, 285–292.

Dorchin, N., Clarkin, C.E., Scott, E.R., Luongo, M.P. & Abrahamson, W.G. (2007) Taxonomy, life history, and population sex ratios of North American *Dasineura* (Diptera: Cecidomyiidae) on goldenrods (Asteraceae). *Annals of the Entomological Society of America*, 100, 539–548.

Dorchin, N., Jordan, S., & Abrahamson W. G. (in prep.). Evolution of host associations and gall types in goldenrod-galling *Rhopalomyia* (Diptera: Cecidomyiidae).

Felt, E.P. (1907a) *New species of Cecidomyiidae*. New York State Education Department, Albany, NY, 53 pp.

Felt, E.P. (1907b) New species of Cecidomyiidae. Pp. 97–165. *In*: 22nd report of the state entomologist on injurious and other insects of the state of New York 1906. *New York State Museum Bulletin*, 110, 39–186.

Felt, E.P. (1907c) *New species of Cecidomyiidae II*. New York State Education Department, Albany, NY, 23 pp.

Felt, E.P. (1908) Appendix D. pp. 286–422, 489–510. *In*: 23rd report of the state entomologist on injurious and other insects of the state of New York, 1907. *New York State Museum Bulletin*, 124, 5–541.

Felt, E.P. (1909) Additional rearings in Cecidomyiidae. *Journal of Economical Entomology*, 2, 286–293.

Felt, E.P. (1915) Appendix: A study of gall midges III. Pp. 127–288, 295–326 *In*: 30th report of the State Entomologist on injurious and other insects of the state of New York 1914. *New York State Museum Bulletin*, 180: 7–336.

Felt, E.P. (1916) A study of gall midges IV, tribe Asphondyliariae. Pp. 101–172, 199–203 *In*: 31st report of the state entomologist on injurious and other insects of the state of New York, 1915. *New York State Museum Bulletin*, 186, 7–215.

Felt, E.P. (1940) *Plant Galls and Gall Makers*. Comstock Publishing Co., Ithaca, New York, 364 pp.

Fontes, E.M.G., Habeck, D.H. & Slansky, F. Jr. (1994) Phytophagous insects associated with goldenrods (*Solidago* spp.) in Gainesville, Florida. *Florida Entomologist*, 77, 210–221.

Gagné, R.J. (1968) A taxonomic revision of the genus *Asteromyia* (Diptera: Cecidomyiidae). *Miscellaneous Publications of the Entomological Society of America*, 6, 1–40.

Gagné, R.J. (1971) Taxonomic notes on two racemicolous gall-makers on *Solidgo* spp. *Proceedings of the Entomological Society of Washington*, 73, 169.

Gagné, R.J. (1989) *The Plant Feeding Gall Midges of North America*. Cornell Univ. Press, Ithaca, New York, 356 pp.

Gagné, R.J. (2004) A Catalog of the Cecidomyiidae (Diptera) of the world. *Memoirs of the Entomological Society of Washington*, 25, 1–408.

Heard S.B., Stireman, J.O. III, Nason, J.D., Cox, G.H., Kolacz, C.R. & Brown, J.M. (2006) On the elusiveness of enemy-free space: spatial, temporal, and host-plant-related variation in parasitoid attack rates on three gallmakers of goldenrods. *Oecologia*, 150, 421–434.

Jones, R.G., Gagné, R.J. & Barr W.F. (1983) Biology and taxonomy of the *Rhopalomyia* gall midges (Diptera: Cecidomyiidae) of *Artemisia tridentata* Nuttall (Compositae) in Idaho. *Contributions of the American Entomological Institute*, 21, 1–79.

Loew, H. (1862) Monographs of the Diptera of North America. Part I. *Smithsonian Institution Miscellaneous Collections*, 6, 1–221.

McAlpine, J.F., Peterson, B.V., Shewell, G.E., Teskey, H.J., Vockeroth, J.R. & Wood, D.M. (Eds.). (1981) *Manual of Nearctic Diptera* Vol. 1. Research Branch, Agriculture Canada. Monograph No. 27.

McEvoy, M.V. (1988) *The Gall Insects of Goldenrods (Compositae:* Solidago*) with a Revision of the Species of* Rhopalomyia *(Diptera: Cecidomyiidae)*. M.S. thesis, Cornell University, Ithaca, New York.

Maddox, G.D. & Root, R.B. (1990) Structure of the encounter between goldenrod (*Solidago altissima*) and its diverse insect fauna. *Ecology*, 71, 2115–2124.

Osten Sacken, C.R. (1862) On the North American Cecidomyiidae. Pp. 173–205 *In*: Loew, H. Monographs of the

Diptera of North America. Part I. *Smithsonian Institution Miscellaneous Collections*, 6, 1–221.
Osten Sacken, C.R. (1869) Biological notes on Diptera (Galls on *Solidago*). *Transactions of the American Entomological Society*, 1, 299–303.
Raman, A. & Abrahamson, W.G. (1995) Morphometric relationships and energy allocation in the apical rosette galls of *Solidago altissima* (Asteraceae) induced by *Rhopalomyia solidaginis* (Diptera: Cecidomyiidae). *Environmental Entomology*, 24, 635–639.
Root, R.B. & Cappuccino, N. (1992) Patterns in population change and the organization of the insect community associated with goldenrod. *Ecological Monographs*, 62, 393–420.
Russo, R. (2007) First description of the stem gall of *Rhopalomyia baccharis* Felt, 1908 (Diptera: Cecidomyiidae), on *Baccharis pilularis* De Candolle (Asteraceae). *The Pan-Pacific Entomologist*, 83, 285–288.
Semple, J.C. & Cook, R.E. (2006) *Solidago*. *In*: Flora of North America Editorial Committee (Eds.), *Flora of North America North of Mexico*, Vol. 20. Oxford Univ. Press, New York and Oxford, pp. 107–166.
Spence, A.P. (1969) Biology of the gall midge *Rhopalomyia hirtipes* O.S. (Diptera: Cecidomyiidae) on *Solidago juncea* Ait. *Cornell Experiment Station Memoirs*, 409, 1–59.
Stebbins, F.A. (1910) Insect galls of Springfield, Massachusetts and vicinity. *Springfield Museum of Natural History Bulletin*, 2, 1–138.
Stireman, J.O. III, Nason, J.D. & Heard, S.B. (2005) Host-associated genetic differentiation in phytophagous insects: general phenomenon or isolated exceptions? Evidence from a goldenrod-insect community. *Evolution*, 59, 2573–2587.
Stireman, J.O. III, Nason, J.D., Heard, S.B. & Seehawer, J.M. (2006) Cascading host-associated genetic differentiation in parasitoids of phytophagous insects. *Proceedings of the Royal Society, B*, 273, 523–530.
Thompson, M.T. (1915) An Illustrated Catalogue of American Insect Galls. Nassau, NY, pp. 1–116.
Wise, M.J. & Abrahamson, W.G. (2008) Ducking as a means of resistance to herbivory in tall goldenrod, *Solidago altissima*. *Ecology*, 89, 3275–3281.
Zhang, J. (1996) *A molecular biosystematic study on North American Solidago and related genera (Asteraceae: Astereae) based on chloroplast DNA RFLP analysis*. PhD dissertation, University of Waterloo, Ontario, Canada.