

***MICRORHOPALA LAETULA* LECONTE
(COLEOPTERA: CHRYSOMELIDAE:
CASSIDINAE) ON *SILPHIUM PERFOLIATUM*
(LINNAEUS) (ASTERALES: ASTERACEAE)
IN EASTERN SOUTH DAKOTA**

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ABSTRACT

The life history of the cup plant leaf miner, *Microrhopala laetula* LeConte, in eastern South Dakota is briefly described, and the species is reported from the state for the first time. A confounding taxonomic history with *M. vittata* (Fabricius) restricted recognition of host plant specialization and beetle identity. Adult *M. laetula* overwinter and become active with mating and oviposition occurring with host plant emergence. Eggs are deposited abaxially and adaxially on leaf tips. Larvae are miners, forming a large blotch style mine, with all mesophyllic and vascular tissues consumed, resulting in most to all of a leaf dying. Pupation occurs within the leaf mine. The larva and pupa of *M. laetula* are compared to that of *M. vittata* including an ANOVA test based on morphological measurements, supporting a heuristic inference of three larval instars in *M. laetula*. The beetle's phytophagous impact on its host cup plant, *Silphium perfoliatum* (L.), can significantly reduce photosynthetic potential and biomass production through leaf loss in its first 4–6 weeks of growth.

Keywords

Natural history, taxonomy, larva, ecology, life cycle, native species, biomass, cup plant, *Microrhopala*

INTRODUCTION

Microrhopala Chevrolat, 1836 includes about 17 species of leaf beetle found in the Nearctic biogeographic realm and southward in the Neotropical realm to Colombia (Baly 1885; Blackwelder 1946). The genus, formerly in the Hispinae (Coleoptera: Chrysomelidae), is presently arranged in the Chalepini of the Cassidinae (Staines 2006, 2015). Apparently, all species with known plant hosts feed on various Asteraceae (Asterales) and most are oligophagous on species within a given plant genus, such as *M. laetula* LeConte (Figure 1) on *Silphium* Lin-

naeus species. Monophagous species are known, but this level of knowledge may be due to a lack of study. Historically, *M. laetula* LeConte was long regarded a synonym of *M. vittata* (Fabricius), but variably and most recently treated by Clark (2000, 2004), Riley et al. (2002), and Staines (2006). Here, we adopt *M. laetula* as the name for those beetles showing host association to *Silphium* species, and differences in adult and immature morphology and behavior. The first published report of a *M. vittata* host and the beetle's natural history was by Harris (1835) who reported larvae of *M. vittata* (as *Hispa vittata*) from "in the leaves of *Solidago laevigata*."

To avoid confusion between *Silphium*, the rosin weeds, and *Solidago*, the goldenrods, when abbreviated the forms "Sil." and "Sol." are used below, respectively.

Microrhopala laetula was described from Fort Riley, Kansas (LeConte 1859) and based on three specimens collected by John Xantus. There was no original indication of a host plant. LeConte separated this new species from *M. vittata* on the relatively straight pronotal margins, head and pronotum concolored red-orange, a short 3rd elytral interval red-orange vitta, a dull sheen of the lateral elytral intervals, and a smooth margin of the elytra. Crotch (1873a) treated *M. laetula* as a variety of *M. vittata*, then (Crotch 1873b) listed both *M. laetula* and *M. vittata* as species. Popenoe (1877) stated that *M. laetula* was found on stiff goldenrod, *Solidago rigida* (L.). Horn (1883) reduced *M. laetula* to a variety of *M. vittata* in a summary of the species, but did not give any host information. Henshaw (1885) listed only *M. vittata*, then Wickham (1902) followed Horn's treatment and noted that larvae mine the leaves of *Solidago*, following Popenoe (1877). Smith (1889) noted that larvae of *Microrhopala* are leaf miners, but did not specify any hosts, but stated that the "larva mines the leaves of golden rod." Beutenmuller (1890) repeated Harris' (1835) host report. Weiss (1911) and Leng (1920) treated *M. laetula* as as an aberration of *M. vittata*. Subsequently, *M. laetula* was generally treated as a synonym of *M. vittata*. Clark (2000, 2004), and Staines (2006, 2015) most recently summarized the nomenclatural and taxonomic literature for both names.

Markovitch (1916) used *M. vittata* and gave its host as cup plant, *Silphium perfoliatum* L., and noted that the larva mines leaves and gave it the name "cup plant leaf miner." Hendrickson (1928, 1930a-b) stated that *M. vittata* "Larvae are



Figure 1. *Microrhopala laetula*, adult feeding on leaf of *Silphium perfoliatum*.

leaf miners of rosin-weed [= compass plant] (*Sil. laciniatum* L.)”, were frequently seen and common, and suggested that there might be two generations per year.

The genus was taxonomically revised by McCauley (1938) who also summarized *M. vittata* reports from compass plant and five species of *Solidago*: seaside goldenrod (*Sol. sempervirens* L.), Canada goldenrod (*Sol. canadensis* L.), early goldenrod (*Sol. juncea* Aiton), Missouri goldenrod (*Sol. missouriensis* Nutt.), and slender goldentop (*Sol. graminifolia* (L.), now *Euthamia graminifolia* (L.). Then California goldenrod (*Sol. californica* Nutt. was added by Jones and Brisley 1925). Clark (1983) updated the genus for northern North America and continued regarding *M. laetula* as a synonym of *M. vittata*, while adding (Clark et al. 2004) velvety goldenrod (*Sol. mollis* Bartlett) to the host list while continuing to include compass plant and cup plant. Downie and Arnett (1996) separated *M. laetula* as a distinct species associated with *Silphium* species on relative size of elytral punctures and length of the red-orange elytral vitta; this species distinction was followed by Clark (2000).

Ford and Cavey (1985) stated that *M. vittata* prefers goldenrod species, but feed on other closely related composite plants; they listed compass plant and cited McCauley (1938) as the source, but indicated others citing the same host. Jolivet and Hawkeswood (1995) merely listed *Silphium*, without species attribution, as a host on which some *Microrhopala* are found. No species of plant or beetle was specified.

Riley et al. (2002) treated *M. laetula* and *M. vittata* as a species-pair separate from other *Microrhopala*. Clark et al. (2004) recognized *M. laetula* as distinct and noted its association with cup plant and one report of adults feeding on prairie dock (*Sil. terebinthinaceum* Jacq.) in Wisconsin. They also suggested that the report by Popenoe (1877) was probably based on a misidentification of *M. vittata*. Clark et al. (2004) listed compass plant as a host for *M. vittata*, *Sil. perfoliatum* for both *M. laetula* and *M. vittata*, and prairie dock for *M. laetula*. Stiff goldenrod was mentioned as a host for *M. laetula*. In contrast, eight species of goldenrod were given as hosts for *M. vittata*.

Staines (2006) treated *M. laetula* as a synonym of *M. vittata* and provided an apparently complete list of references for the name. Most of these references are inclusions of the name in catalogs and faunal lists. *Microrhopala laetula* and *M. vittata* are extremely similar morphologically and are geographically sympatric in the Midwestern regions of the United States, with allopatry by habitat and host. The adults of both species share similar aposematic coloration, but though *M. vittata* is transcontinental and associated with goldenrods, *M. laetula* seems to be a mid-continental species in only a portion of the cup plant range from north of the Ohio River Valley and westward from Indiana to the western extension of the host plant in the eastern Great Plains. However, given the historical confounding of these two species, a review of “*M. vittata*” specimens from throughout the range of cup plant and other rosin weed species is warranted.

Cup plant (*Sil. perfoliatum*; Asterales: Asteraceae: Heliantheae) (Figure 2), is a tall (ca. 2.5 m) and conspicuous native mesic site species that is pollinator-friendly, attractive to a broad diversity of insects, and provides extensive ecosystem goods and services. The species is readily recognized by the combination of its

size; corymbose inflorescence; flowers indeterminate, with only ray florets pistillate; leaves opposite, connate, and acropetalous; and habitat in open, mesic, well-drained areas. It is not strictly a prairie species, but in eastern South Dakota and adjacent North Dakota, Minnesota, Iowa, and Nebraska it is naturally found in mesic sites near streams, springs, and in seasonally short-term hydric meadows, areas that Weaver and Fitzpatrick (1934) regarded as “low prairie.” It has great value for biodiversity enhancement, such as a nesting and food plant for birds and small mammals. Its broad native range is the eastern United States of America (USA) from North Dakota to Oklahoma in the tallgrass prairie regions and eastward, and Ontario and Quebec in Canada (USDA Plants Database 2019). In eastern South Dakota cup plant ranges from Clay County in the southeast to Roberts County in the northeast, from



Figure 2. Well-grown (ca. 2.0m high) *Silphium perfoliatum* in late flower/early seed development during early-August at the SDSU Northeast Research Farm, Codington County, South Dakota. The opposite, connate, and acropetalous leaves are diagnostic for this species. *Microrhopala laetula* was not found on these particular plants.

which we chose to examine closely four experimental agronomic populations and seven wild and replanted populations. All known natural populations in the state occur in the Minnesota River, Big Sioux River and Vermillion River drainages and are within the Tallgrass Prairie region of the central USA.

In North America, but especially in Europe and Asia, cup plant provides numerous commodities and environmental value (e.g., Gansberger et al. 2015; Cumplido-Marin et al. 2020) such as biodiversity enhancement, oilseed, gourmet honey, biomass, biogas, human and livestock food, medicines, cosmetics, garden enhancement, groundwater nitrate filtration (reducer), heavy metal phytoremediation, wood replacement in particle board, and streambank erosion resistance (e.g., Runkel and Roosa 1989; Kowalski and Wolski 2003; Johnson and Boe 2013; Johnson et al. 2013; Assefa et al. 2015; Van Tassel et al. 2017; Boe et al. 2019a-b, Cup-Plant.com 2019; Peni et al. 2020). Weaver (1954) regarded cup plant as one of the most diagnostic and important species of prairie lowlands and noted that the species is intolerant of disturbance and unlikely to return natu-

rally when once removed; however, the seeds of cup plant are widely distributed by birds, and the plant can be an invasive weed (Ende et al. 2021). This species is favored by cattle but is intolerant of repeated grazing, trampling, herbicides, mechanized crushing, and drought; populations decrease rapidly when predated.

Here, we focus on the life history of *M. laetula* and its relationship with cup plant in eastern South Dakota. This report also provides a **new state record** for the beetle from South Dakota.

METHODS

Our study originated with the discovery of beetles attributed to *M. laetula* among experimental agronomic evaluations of cup plant in Brookings County, South Dakota. Subsequently we surveyed populations of cup plant among another 19 sites along the western-most occurrences of the plant in its natural range within the state (Figure 3), from Roberts County in the northeastern corner to Clay County in the southeastern area. These sites were a mixture of natural occurrence, conservation plantings, ornamental plantings, and presumed natural spread of seed by birds. Observations and specimen collections of each life stage of the beetle were made at each site of discovery, though the bulk of effort was spent at three agronomic populations located at experimental farms where the beetle was abundant: Brookings County, South Dakota State University Plant Pathology Farm, 44°19'13"N, 96°45'39"W, South Dakota Crop Improvement Association research farm, 2.7 km northeast of Aurora, 44°18'23"N, 96°40'16"W, and the Felt Family Farm, 5.6 km north of Brookings, 44°22'09"N, 96°47'40"W; and Codington County, South Dakota State University Northeast Research Farm, 13.2 km west of South Shore, 45°06'16"N, 97°06'01"W. Wild and conservation popu-

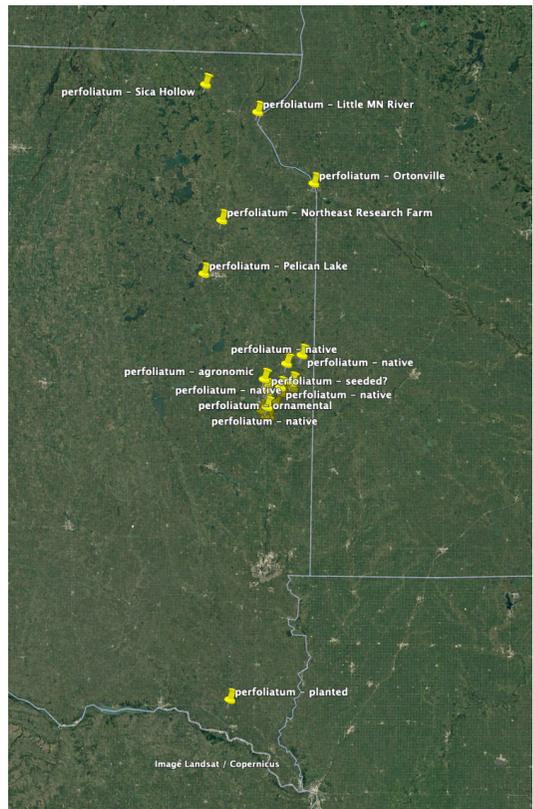


Figure 3. Google™ map of eastern South Dakota and adjacent Minnesota and Iowa showing approximate locations of *Silphium perfoliatum* study sites.

lations of cup plant of special attention were located at Brookings County, 8.0 km south of Brookings, 44°14'21"N, 96°46'19"W; 9.6 km south-southwest of Brookings, 44°13'17"N, 96°48'77"W; 2.7 km southwest of Aurora, 44°15'40"N, 96°42'25"W; 5.5 km north of Aurora, 44°19'59"N, 96°41'17"W; 2.9 km east of Bushnell, 44°19'47"N, 96°36'25"W; 1.0 km north of White, 44°26'38"N, 96°38'56"W; Codington County, Pelican Lake State Recreation Area, 11.3 km. southwest of Watertown, 44 51'20"N, 97 12'23"W; and Clay County, Spirit Mound Historic Prairie, 9.5 km north of Vermillion, 44°52'10"N, 96°57'25"W.

Seedlings of cup plant were grown from seeds produced by open-pollinated plants among natural populations in Minnesota and Illinois and in experimental plots at and near Brookings. Greenhouse grown seedlings were transplanted to spaced plant nurseries at the research farms during May 1999. Seedlings were planted in rows with 1.5 m between rows and 0.75 m intra-row spacing. A total of 800 plants were transplanted at each location. A high level of plant mortality (>50%) occurred at both locations between 1999 and 2009. The mortality at Aurora was higher than that at Brookings and Felt Farm, and this difference was attributed primarily to differences in soil texture between the locations. The sandy soil, lacking consistent subsurface moisture, at the Aurora site caused drought stress that resulted in considerable mortality (>75%) over the 10-year period.

Terminology for larval morphology is based on Stehr (1991); abdominal (= A) segments are noted alphanumerically as A1 through A9. Body lengths of larvae and pupae were measured along midlines and extending from anterior-most of frons to posterior margin of A9. Body widths were measured across A1 and A2 in dorsal aspect. Head lengths were measured from the frontal margin to the posterolateral angle of the cranium, and widths across the widest portion of the cranium. Body and head measurements are summarized in Table 1. An ANOVA analysis of variation in head capsule length, head capsule width, body length, and body width was done using Statistix 9.0. Terminology, and common and scientific names of plants, were verified from the online USDA Plants Database (2023).

RESULTS AND DISCUSSION

Clark (1983) regarded all *Microrhopala* species as oligophagous, with host associations to multiple species within a genus or closely related genera. Formerly, *M. laetula*, a cup plant specialist, was treated as a synonym of *M. vittata*, a goldenrod specialist. This resulted in host associations not only in different genera, but across different tribes of the Asteraceae, the Heliantheae and the Astereae.

Microrhopala laetula seems to be similar to other *Microrhopala* species in having a single generation each season (Clark 1983). Adults overwinter and mate and oviposit on their hosts in the spring as shoots emerge above the soil. Eggs are laid on host leaves, larvae mine the leaves, pupation occurs within the mine, and adults emerge to feed before retiring for the winter. Beyond these generalizations, each species has its own host specializations and unique adaptations separating it from other species. Curiously, *M. vittata* on goldenrods is rarely encountered in eastern South Dakota near to cup plants with *M. laetula*.

Mating and Eggs—Mating and oviposition are temperature moderated and begin soon after overwintered adults emerge from the duff and soil. If warm temperatures prevail soon after emergence of the beetles and the cup plant first leaves, then mating activity starts within 10-14 days. Mating, oviposition, and general activity slow or cease when air temperatures cool below approximately 10 °C. During the summers of 2021 and 2022 both seasonal diurnal and nocturnal temperatures were frequently 3–15 °C higher than the July climatic average of 21.7 °C for Brookings County, and these higher temperatures may have accelerated developmental periods. The general pattern is much like that observed

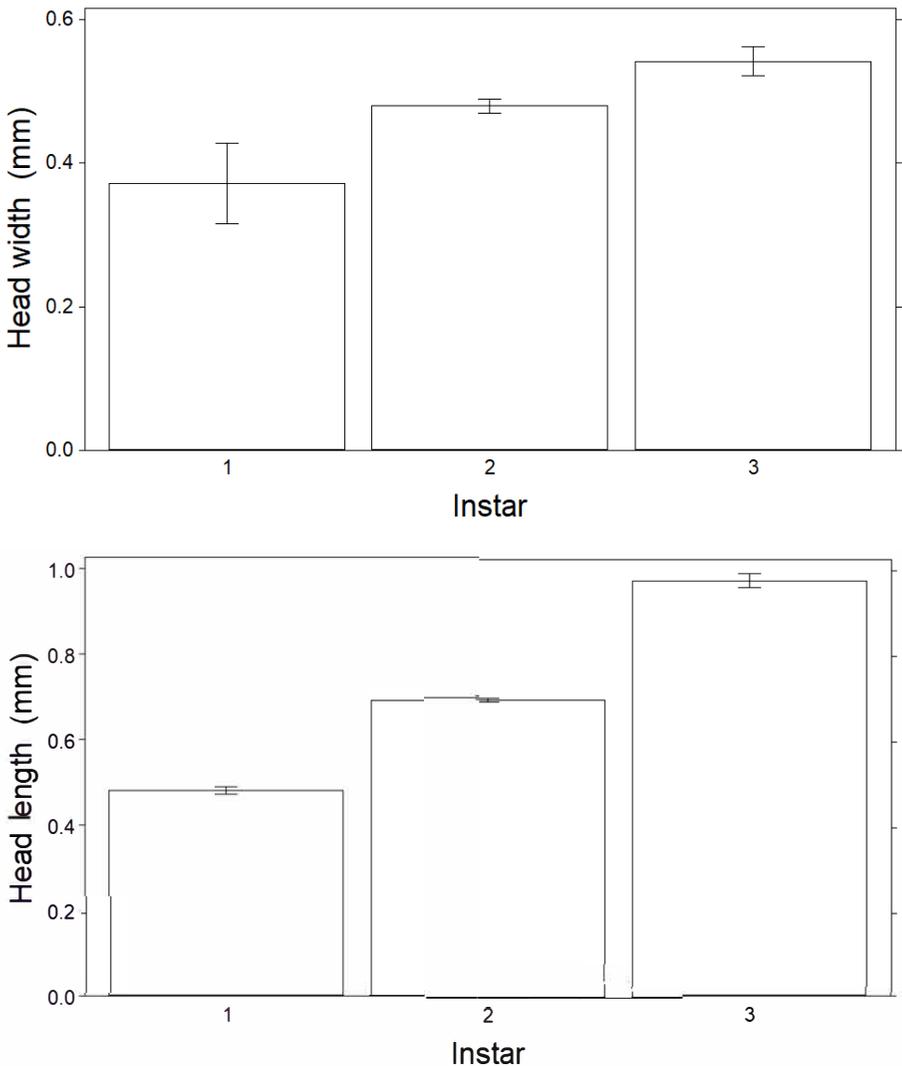


Figure 4. Histograms demonstrating mean separation of *Microrhopala laetula* larval instars; n = 87. Left, separation based on head capsule length, Pearsons correlation, 0.64. Right, separation based on head capsule width, Pearsons correlation, 0.51.

by Harris (1835) for *M. vitata* on *Sol. sempervirens* (as *Sol. laevigata*): “. . . upon the tenth of June 1834, I found it celebrating its nuptials, and discovered on the leaves of the plants, frequented by it, little black grains which, I presume, were the eggs of the insect. These granular bodies were about 7 hundredths of an inch long, somewhat elliptical, flattened on the side which was glued to the leaf, and covered upon the rest of the surface a rough, black substance. They were in clusters of four or five, placed side by side, and adhered closely together, and to the leaf on which they were fixed.” Likely, Harris was actually describing the fecal coverings of the eggs.

Oviposition occurs anytime during the day, but is more frequent and active under sunny skies when the air temperature is generally higher than about 17–19 °C. The female is in a more or less head-down position. Oviposition can occur when the male is still atop the female. Oviposition by the overwintered females continues throughout the season when late developing shoots with unmined leaves are present. On cup plant the eggs are placed at the distal adaxial area of the leaf (Figure 5), or less commonly on the apices of larger lateral lobes. On spring shoots oviposition typically ceases after the apical meristem develops past the 5th above-ground node. There is no oviposition on a shoot after the apical meristem forms flowering tissues and bolts.

Microrhopala laetula eggs are laid on all cup plant leaves from the initial apical leaves at emergence to those at the 1st through 5th above-ground nodes and can include the newest leaves at the apex of the shoot where the leaf may grow distorted due to the eggs. Individual eggs are positioned horizontally and flat against the leaf when laid. Each is 0.9–1.4 mm long, 0.5–0.7 mm wide, pale brown-yellow, oval to elongate-oval, dorsum shallowly convex, venter flat. Each egg is covered in a 1.3–2.4 mm diameter dome of fecal material, with this material often overlapping when eggs are close. They may be placed both adaxially and abaxially, most commonly adaxial, except they will be primarily abaxial on near-vertical apical new leaves. Regardless of egg placement, the tissues beneath the egg turn



Figure 5. Top: Adaxial surface of leaf apex showing blemishes from emplaced eggs. Bottom: Feces-coated eggs of *M. laetula* on abaxial surface of leaf apex.

translucent yellow-green (Figure 5) such that the eggs can be counted through the leaf. The chorion becomes light to dark brown after being covered in feces, possibly due to fecal staining.

Hendrickson (1930a) reported that oviposition by *M. vittata* on compass plant occurred on the adaxial surface of a newly emerged leaf in early May. He also noted that each of seven eggs observed was capped with feces, though closely spaced eggs of *M. laetula* can have the feces blended to form integrated caps. McCauley (1938) reported *M. vittata* eggs as being laid adjacent to each other and then covered with feces, but *M. laetula* usually places them to form an irregular arc of 5-8 eggs across the leaf, though they can also be bunched and even in 2-5 egg clusters irregularly spaced across the leaf tip. Rarely, single eggs are found. Often scattered clusters of eggs can be found slightly basad of the arc of eggs resulting in upwards of 16-20 eggs in an irregular cluster. Usually, a leaf tip has the eggs of one female, but it was occasionally observed that two females will use the same leaf tip with respective egg clutches on either side of the leaf midrib vein.

Harris (1835) reported "about a week" to eclosion for *M. vittata* on *Sol. semper-virens*. Hendrickson (1930a) reported hatching 21 days after oviposition on compass plant, while McCauley (1938) stated "probably somewhat less than three weeks" on *Sol. canadensis*. In our populations, eggs hatch 3-5 days after oviposition and are probably responsive to environmental temperatures. The fecal shell remains and eventually weathers away, though may persist until leaf-fall.

Larva—The body of *M. laetula* as a larva (Figures 6-8) is yellow-cream white throughout, except a lightly to moderately sclerotized head capsule (Figure 7-8), dorsal and ventral pronotal sclerites, small leg plates, abdominal projection apices, and an A9 dorsal sclerite. Tergites of A1-A7 with lateral angular projections. Legs of the 5-segmented polyphagan type with a single tarsungulus (Stehr 1991); moderately sclerotized ectally. Thoracic and abdominal integument variably covered with micro-asperities.

Body lengths and widths of each instar are given in Table 1, with a statistical demonstration of instar separation in Figure 1. The body is subfusiform in dorsal silhouette, broadest across the metathorax, narrowing posteriorly from the abdominal midlength. Dorsally and ventrally shallowly convex. Head prorect, dorso-ventrally compressed; lengths and widths for each instar are in Table 1. Meso- and metathoracic terga with eight widely spaced fine setae each side of ecdysial suture.



Figure 6. *Microrhopala laetula* larva in cup plant leaf mine with abaxial integument removed.



Figure 7. *Microrhopala laetula* larva. Left, dorsal habitus. Right, ventral habitus.



Figure 8. *Microrhopala laetula* larva. Left, head capsule and prothorax, dorsal aspect. Right, head capsule and prothorax, ventral aspect.

Abdomen with dorsal tergal plates not present; unsclerotized integument and intersegmental membranes. Segments A1–A7 dorsally and ventrally with undulating discal invaginations with welt-like margins. Dorsal areas of A1–A7 with micro-asperities lateral and posterior; with three widely spaced fine seta each side near anterior margin and between spiracle and ecdysial suture, and two widely spaced fine setae each side near posterior margin. A8 with two widely spaced, fine setae posteriorly. Ventrally, meso- and metathoracic segments asetose between legs; A1–7 asetose A8 with single seta each side about midwidth from midline; A9 with single seta posterolaterally and a small dorsal sclerotized plate (Figures 7 and 9). Spiracles on A1–8 subcircular, lateral, emplaced at anterior base of lateral projection.

Table 1. Body and head capsule lengths and widths of *M. laetula* larvae; total n = 87 instar 1 n = 24, instar 2 n = 57, instar 3 n = 11; R = range.

	Instar 1	Instar 2	Instar 3
Body length	R = 2.25–4.6 mm \bar{x} = 3.3 mm	R = 2.5–4.6 mm \bar{x} = 6.6 mm	R = 4.2–8.1 mm \bar{x} = 5.2 mm
Body width	R = 0.75–1.5 mm \bar{x} = 1.0 mm	R = 1.0–1.5 mm \bar{x} = 1.2 mm	R = 1.6–2.3 mm \bar{x} = 1.6 mm
Head length	R = 0.3–0.6 mm \bar{x} = 3.4 mm	R = 0.4–0.7 mm \bar{x} = 0.5	R = 0.4–0.9 mm \bar{x} = 0.5 mm
Head width	0.4–0.6 mm \bar{x} = 0.5 mm	0.6–0.8 mm \bar{x} = 0.7 mm	0.8–1.1 mm \bar{x} = 1.0 mm

There are three larval instars (Figure 4) based on means of head capsule length and head capsule width. Body length and body width supported the head capsule measurements, but with considerable variance. In general, the larva of *M. laetula* is morphologically similar to that of *M. vittata*, seeming to vary primarily in the form and paler sclerotization of the head, and thoracic and abdominal sclerites, and chaetaxy. However, head, pronotal, and A9 sclerotization varies by developmental age within an instar. Peterson (1960), Ford and Cavey (1985), and Staines (2006) described and illustrated the larva of *M. vittata*, which seems to differ in having an anterior transverse row of 4–5 setae on A1–A6, compared to two setae on each segment for *M. laetula*.

Larvae are miners in the leaves of cup plant on the basal half of a shoot, from emergent rosette leaves to those at the 5th above-ground node. During eclosion the hatchling larva chews through the chorion and the leaf integument, entering mesophyll tissues directly beneath the egg. All larvae of an egg clutch eclose within hours of each other.

Feeding seems to commence immediately with the 1st instar consuming tissues and forming a small semicircular cell from which mining begins. As the initial mining cells of each larva become larger and merge, the larval clutch forms an undulating to roughly arcuate feeding line. As larvae mature they become further

spaced across the leaf-span and progressively move the feeding line toward the base of the leaf while remaining more-or-less coordinated along the margin. All mesophylllic leaf tissues, vascular tissues and living epidermal inner cells are eaten except the thickest portions of the midrib (Figures 11–12). Markovitch (1916) described the mines as blotches and stated that upwards of 20 larvae could be found in a leaf, while 12–18 per leaf were frequent in our samples. The welted margins of the transverse invaginations on dorsal and ventral discal areas of A1–A7 appear to assist with crawling on leaf surfaces and positioning within the mine.

Cup plant in agronomic plots is most heavily impacted by *M. laetula* in our area from mid-May through early July. During this period the leaf mining by *M. laetula* larvae reduces the photosynthetically active leaf area upwards of 50–100% per leaf in the lower portions of the plant (e.g., Figures 11–12). By mid to late June, adults of the giant eucosma moth (*Eucosma giganteana* Riley; Lepidoptera: Tortricidae) begins emerging, mating, and ovipositing, and the larvae begin feeding on floral buds by the end of June (Johnson et al. 2019). This gives about 4–5 weeks of beetle activity before that of the moth larvae. Thus, by the time *E. giganteana* larvae are significantly impacting the reproductive potential of upper portions of cup plant in early and mid-July, the beetle larvae have already compromised the biomass potential of the plant. The combination of *M. laetula* and *E. giganteana* feeding can be exceptionally debilitating to the plant, particularly in drought conditions.

Pupa—The *M. laetula* pupa (Figure 10) is very similar to that of *M. vittata* (Staines 2006), being 5.4–6.6 mm, \bar{x} = 6.2 mm long, 2.2–2.6 mm, \bar{x} = 2.4 mm (n = 7) wide. Exarate. Pale yellow-white throughout, except apices of ventral abdominal asperities and T7 posterior angles. Older pupae with head, pronotal disc, and elytral areas light brown.

Head with frons arcuately concave. Pronotum transverse, broadly trapezoidal, shallowly convex. Anterior angles with three closely spaced long setae, one short seta. Three setae at midlength along lateral margin. Two long setae at posterior angles. Three long setae at midlength each side of ecdysial suture. Elytra with one strong and two weak longitudinal carinae.

Abdomen with lateral tubercles, each with 2 long, 2 short apical setae. Dorsum of T1 with single seta each side of ecdysial suture, one lateral subspiracular seta. T2–T6 with 2(–3) each side of ecdysial suture, single lateral subspiracular seta. T7 as T6 with additional single seta each side at midwidth posteriorly. T8 with pair of oblique carinae; between carinae two discal setae, two submedian setae, one midwidth seta posteriorly, one lateral seta. T8 with acutely, spiniform, extended hind angles. T9 with short, acute, subtriangular urogomphi. Ventrally S2–5 each with a posterior transverse row of six stout pale setae, 3(–4) each side of midline, one laterally. S6 with one each side of midline, two adjacent setae laterally. S7 with a row of tubercles, each sclerotized at apex, with a single thick apical seta; outer tubercle each side larger and angular ectally, with angle bearing an apical seta; second tubercle each side about half the size of the outer tubercle, with two subacute apices each bearing a seta; third, or submedian, tubercle smaller than second, with single acute apex bearing a seta.

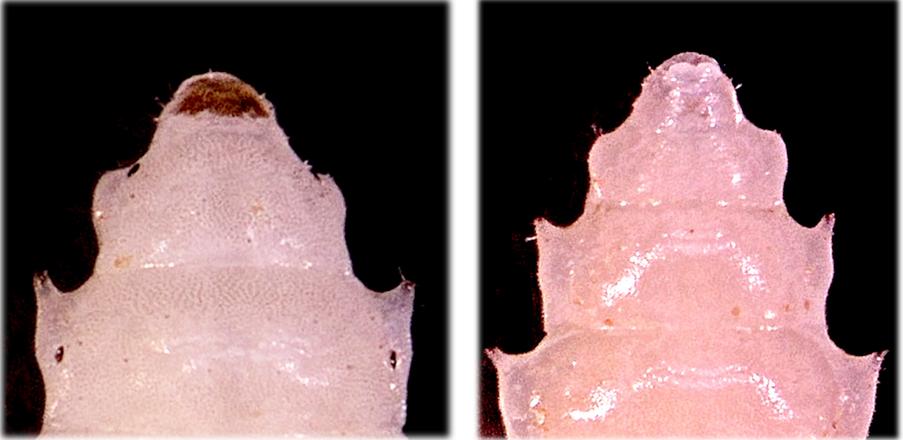


Figure 9. *Microrhopala laetula* larva. Left, dorsal aspect of A7-A9. Right, ventral aspect of A6-A9.



Figure 10. Pupa of *Microrhopala laetula*, dorsal aspect on left, ventral aspect on right.



Figure 11. *Silphium perfoliatum* leaf portion with second instar *Microrhopala laetula* larvae inside of mine in late June.



Figure 12. *Silphium perfoliatum* leaves demonstrating early leaf mining by *Microrhopala laetula* larvae (left), mid-season mining (center), and late season mining (right).

Pupation occurs within the leaf mine, with about two-thirds of a sibling clutch pupating at the basal margins of the mine while the remaining one-third pupate apically. It is unknown if this is due to spatial segregation to avoid predators and parasitoids, or for thermal associations affecting development times. Leaf bases tend to be shaded and cooler to the touch during much of the day while leaf apices are constantly exposed and may reach temperatures above atmospheric ambient.

The pupa lacks a cocoon or silk strands, and there is no organic wrap or cell formation. Pupae are motile by crawling or rotating and rolling within mine pocket of host leaf, and outside of mine, but are not significantly ambulatory. Within the mine movement is by rotating the abdomen and undulating the body with effective movement determined in part by the angles of the mine walls and friction against the walls. Abdominal rotation is clockwise when viewed posteriorly. Markovitch (1916) noted that the pupae (probably of *M. vittata*) were “motile” and that they “moved” about in his rearing cage outside of the leaf mine. We observed that pupae in an open dish rotate and undulate, but move laterally in a random action.

Parasitoids and Predators—To date, no parasitoids are confirmed for *M. laetula*, but this may be due in part to confusion with *M. vittata*. Ashmead (1896) described *Baryscapus microrhopalae* (in *Tetrastichus* Haliday) from a larva of *M. xerene*. Chittenden (1902) reported this as simply a “chalcidid” from *M. vittata*. Peck (1963) and Burks (1943, 1979) gave *M. vittata* and *M. xerene* as hosts, and LaSalle (1994) provided the genus transfer. *Microrhopala xerene* (Newman) is also reported to host *Closterocerus tricinctus* Ashmead (Hymenoptera: Eulophidae) (Peck 1963, Burks 1979). *Mesocrena microrhopalae* Ashmead (Hymenoptera: Braconidae) of McCauley (1938) is now in *Oenonogastra* Ashmead and the host record was considered an error by Marsh (1979). *Microrhopala vittata* was listed as a host of *Pnigalio uroplatae* (Howard) (Hymenoptera: Eulophidae), with the wasp reared from larvae (Ford and Cavey 1985). In sum, three species of eulophid wasp are known from species of *Microrhopala* closely related to *M. laetula*. We hypothesize that the persistent group mining within a protective single leaf of *S. perfoliatum* may dissuade parasitism, in contrast to exposed larvae of *M. vittata* in host leaf changing as noted on *Solidago altissima* L.

Although cup plant is a favorite plant for many predators and parasitoids for perching and courtship on its broad leaves, and a variety of vespid wasps visit the flowers and predate on caterpillars and aphids, none are yet associated with *M. laetula*. Shredding of dead leaf cuticle on leaves with larvae and pupae suggest bird activity, though direct predation was not observed directly. Dickcissel, red-wing blackbird, bobolink, and American goldfinch are commonly observed nesting, perching, and feeding on cup plant (Johnson et al. 2019). However, abundant specimens of single and mating adult *M. laetula* on the upper portions of plants and exposed on adaxial surfaces of leaves during daylight periods suggest that their aposematic coloration likely dissuades bird predation.

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