EUCOSMA GIGANTEANA (RILEY) AND *SILPHIUM PERFOLIATUM* L., MORPHOLOGICAL VARIATION IN AN INSECT-PLANT ASSOCIATION IN EASTERN SOUTH DAKOTA

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ABSTRACT

Silphium perfoliatum L., cup plant, has potential as a new multi-purpose crop. It is pollinator-friendly and has biodiversity enhancement, conservation, economic, and medical potential. In eastern South Dakota, *S. perfoliatum* can produce more than 20 Mg (million grams) ha^{-1} of biomass and 0.09 Mg ha^{-1} of seed in agronomic plantings. The giant eucosma moth, *Eucosma giganteana* (Riley), is a major pest of agronomic *S. perfoliatum* in the region. We provide a summary of this insect and its association with its host. Our experimental objectives were to determine if the frequency of rhizome occupation by late instar larvae and if their final prepupal size were influenced by plant genetic or environmental effects. In October 2009, several individual plants from each of 32 half-sib families were removed from the field. Rhizomes, proaxes, and shoots were examined for the presence of larvae. Each larva was counted and measured for total length, width, thoracic tergite length, head length, and head width. Significant differences were found among half-sib families and between locations for frequency of shoot infestation, degree of crown and rhizome feeding, number of larvae per shoot, and larval morphometrics. The parasitoid *Bracon* cf. *mellitor* Say (Hymenoptera: Braconidae) was found parasitizing larvae feeding in floral meristems, but no parasitism was found in larvae in the crown or rhizomes.

Keywords

Biomass, cup plant, giant eucosma moth, rhizome borer, proaxis, Braconidae

INTRODUCTION

Silphium perfoliatum L., or cup plant (Asterales: Asteraceae), is a native, mesic prairie species grown for biomass production, food, medicine, and livestock feed in many countries. Its native range is the eastern United States (USA) from North Dakota to Arkansas and eastward, and Ontario and Quebec in Canada (USDA

Plants Database 2019). *Silphium perfoliatum* is pollinator-friendly and attractive to a broad diversity of insects, has great value for biodiversity enhancement, and provides commodities and environmental values, such as oilseed, gourmet honey, biomass, biogas, human and livestock food, medicines, garden enhancement, groundwater nitrate filtration, and streambank erosion resistance (e.g., Johnson and Boe 2012; Johnson et al. 2013; Assefa et al. 2015; Van Tassel et al. 2017; Cup-Plant.com 2019). The plant is used for biomass production in a number of countries, particularly for methane production (e.g., Haage et al. 2015), and in eastern South Dakota can produce more than 20 Mg (million grams) ha^{-1} of biomass and 0.09 Mg ha^{-1} of seed in agronomic plantings. Domestication may have begun when seed was sent to Russia in the 1750's. There it was planted as an ornamental and subsequently as a food crop and livestock feed, and then re-dispersed globally. Presently it is grown for all of the above reasons, at least in Argentina, Australia, Austria, Bulgaria, Chile, China, Czech Republic, France, Germany, Italy, Japan, Lithuania, New Zealand, Poland, Russia, Switzerland, and Ukraine (Stanford 1990; Gansberger et al. 2015; K. Albrecht, pers. comm.).

The common name "cup plant" comes from a water retention depression, or cup, formed by the conjoint bases of the broad opposite leaves. Beal and St. John (1887) noted that the cup of mature leaves typically held 300-600 cc of water and suggested the false notion that the presence of water prevented ants and other organisms from moving upward on the plant, but such water provides an incomplete and short-term barrier at best. In contrast, the retained water attracts a wide variety of invertebrates (e.g., ants, bees, beetles, butterflies, wasps) and vertebrates (e.g., birds, rodents, deer). Dry cups are used as nesting sites by small birds, e.g. American goldfinch (*Spinus tristis* L.), while dickcissel (*Spiza americana* Gmelin), bobolink (*Dolichonyx oryzivorus* (L.), and other birds commonly use the larger plants for perching, courtship, defensive observation, and feeding (pers. observs.). This plant also provides important architectural and food resources for bees (Assefa et al. 2015; Gansberger et al. 2015) and other wildlife. In eastern South Dakota, we observed upwards of seven species of native bee species, plus various true flies, moths, butterflies, and beetles visiting *S. perfoliatum* flowers. A wide variety of insects, including stem and petiole gall makers, stem borers, phloem feeders, leaf predators, floral predators, rhizome borers, detritus feeders, and parasitoids thereof are known from *S. perfoliatum* (e.g., Williams 1995; Lisberg and Young 2003; Henderson and Sauer 2010; Johnson and Boe 2012; Johnson et al. 2013). Weaver (1954) listed *S. perfoliatum* as one of the 38 most important species of prairie lowlands and noted that the species is intolerant of disturbance, and unlikely to return naturally when once removed.

Only a few generalist and mostly cosmopolitan non-specific minor insect and mite pests are reported from the various countries in which *S. perfoliatum* is now grown. Since the plant gained agronomic interest in the USA for purposes of biomass and oilseed production (Van Tassel et al. 2017; Boe et al. 2019a-b), we found that certain insects in eastern South Dakota can reduce per plant biomass, seed set, and general vigor. These insects were subjected to monitoring, especially those regularly feeding on the floral structures and leaves (Johnson 2011; Johnson et al. 2012; Johnson et al. 2013). Although *S. perfoliatum* is found in eastern

South Dakota from Clay County in the southeast, to Roberts County in the northeast, we chose to examine four agronomic populations and seven wild and replanted populations. All known natural populations in the state occur in the Big Sioux River and Vermillion River drainages. Insect species found to regularly prey upon the plant in both natural habitats and agronomic sites are the larva of the giant eucosma moth, *Eucosma giganteana* (Riley) (Lepidoptera: Tortricidae), the leaf beetles *Microrhopala vittata* (Fabricius) and *Rhabdopterus deceptor* Barber (Coleoptera: Chrysomelidae), and the attelabid weevil *Haplorhynchites aeneus* (Boheman) (Coleoptera: Attelabidae), and *Uroleucon* cf. *rudbeckiae* (Fitch) (Hemiptera: Aphididae). Most of these insects co-occur with *S. perfoliatum* at all of its known populations.

Here, we focus on the relationship between *S. perfoliatum* and the larva of *E. giganteana*. We also summarize the body of information now available about the moth, its larva, and the insects' association with *S. perfoliatum*, particularly the unique underground system of the plant and how the insect uses this system. We examined the morphometric data of six plant characters and eight larval characters in order to describe part of the mutualism between these two species.

METHODS

Late-instar larvae of *E. giganteana* were sampled among four agronomic populations in or near Brookings, South Dakota, and two sites in southern Wisconsin. Individual rhizomes and shoots were examined for the presence of larvae. Supplemental plant and insect samples, and observations, were taken from seven wild or conservation replanted populations in the northeastern, east-central, and southeastern areas of South Dakota.

Agronomic populations were located at three experimental farms: Brookings County, South Dakota State University Plant Pathology Farm, 44°199'13"N, 96°45'39"W, Aurora Farm Experimental Station, 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 Agricultural Experiment Station, Northeast Research Station, 13.2 km west of South Shore, 45°06'16"N, 97°06'01"W. Wild and conservation populations of *S. perfoliatum* 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; and Clay County, Spirit Mound Historic Prairie, 9.5 km north of Vermillion, 44°52'10"N, 96°57'25"W.

Seedlings of *S. perfoliatum* were grown from seeds produced by open-pollinated plants from natural populations in Minnesota and Illinois, and were transplanted to spaced plant nurseries at Brookings and Aurora, SD, 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 occurred at both locations between 1999 and 2009. The mortality at

Aurora was higher than that at Brookings, and this difference was due primarily to differences in soil texture between the two locations. The sandy soil at the Aurora site caused drought stress that resulted in considerable mortality over the 10-year period.

In October 2009, several individual plants from each of 32 half-sib families were removed by hand from the field. Individual rhizomes and shoots were examined for the presence of larvae. Shoots were collected from multiple surviving plants at each nursery to adequately represent the diversity in plant size and vigor. Ultimately, 415 shoots were collected at Brookings and 176 shoots were collected at Aurora. Shoots were excavated with a spade to an adequate depth (about 15 cm) in order to include the entire proaxis with buds and roots attached. Data collected for each shoot were: 1) length, 2) number of nodes, 3) number of roots, 4) number of crown buds, 5) number of flower heads, and 6) whether or not the proaxis was occupied by a living late instar larva of *E. giganteana*.

Larval samples of *E. giganteana* were obtained by the digging of randomly selected plants representing 40 genetic families, removing burdening soil, trimming stalks, and returning the crowns to the laboratory. Larvae were extracted from roots by carefully clipping and splitting rhizomes to remove larvae, and measure burrows and pupal chambers. Sampling was usually conducted in October and early November, with supplemental samples taken in the spring to seek pupae. Data obtained for individual larvae included: 1) body length, 2) body width, 3) head length, 4) head width, 5-7) lengths of thoracic tergites 1-3 and 8-10) widths of each of these thoracic tergites. The total numbers of larvae measured were 204 for Brookings and 114 for Aurora.

Data were analyzed using the ANOVA feature in Linear Models procedures in *Statistix* 9. The location was considered fixed. Voucher specimens of all insect species in this study are deposited in the Severin-McDaniel Insect Research Collection.

RESULTS

Differences (Table 1) were found between locations for shoot morphological traits. In general, shoots from Brookings had greater below-ground development, and shoots from Aurora had greater above-ground development, such as more nodes per shoot and more flower heads per shoot. This indicates that the early instar larval stages of the moth had a greater negative impact on shoot size and floral development at Brookings than at Aurora. Nevertheless, the high degree of floral meristem destruction by early instar larvae at both locations virtually eliminated production of viable seed during 2009.

Frequency of infested proaxes was similar between the two locations (ca. 35%) (Table 1). The frequency of multiple larvae occurring in an infested proaxis was also similar (ca. 27%) at both locations. Larvae from Brookings were generally larger than those from Aurora (Table 2). This difference corresponds with shoots from Brookings being more robust than those from Aurora (Table 1). Typically, only one larva was found in each rhizome, although there were two instances of a pair of larvae in one rhizome.

Table 1. Morphological characteristics of individual shoots of* S. perfoliatum *in 10-year-old spaced plant nurseries at Brookings and Aurora, SD in 2009.

	Location	
Trait	**Brookings (n¶=415)**	**Aurora (n¶=176)**
Shoot length (cm)	78.7	76.7
Nodes shoot^{-1}	7.6	8.2**
Roots shoot^{-1}	9.7	8.2**
Crown buds shoot^{-1}	2.7	2.4*
Flower heads shoot^{-1}	0.2	1.3**
Frequency of infested shoots$^{\phi}$	0.32	0.38*

*, ** Location means are significantly different at the 0.05 or 0.01 level, respectively.
¶ n=number of shoots examined.
$^{\phi}$ Frequency of shoots that had at least 1 living late instar larva in a hollowed-out chamber of the proaxis of the shoot.

Table 2. Location means for morphometric traits of last feeding instar larvae of* Eucosma giganteana *in crowns and rhizomes of* S. perfoliatum *in spaced-plant nurseries at Brookings and Aurora, SD in October 2009.

	Location	
Morphometric trait	**Brookings (n=204)**	**Aurora (n=114)**
Body length (mm)	24.3	21.4**
Body width (mm)	5.3	4.8**
Head length (mm)	2.0	1.9
Head width (mm)	2.9	2.7**
Tergite 1 length (mm)	1.5	1.5
Tergite 1 width (mm)	3.7	3.5**
Tergite 2 length (mm)	6.0	5.2**
Tergite 3 length (mm)	5.0	4.2**

** Difference between location means significant at the 0.01 level.

DISCUSSION

Eucosma giganteana is one of the largest species of Tortricidae (Lepidoptera) in North America with a forewing length up to 16.2 mm and has a distinctive and unique forewing color pattern (Wright and Gilligan 2015) (Figure 1). The insect is distributed from eastern North Dakota to New York and south to Florida, southeastern Colorado, and Texas. This moth is closely associated with *S. perfoliatum*, which seems to be the primary host throughout the insect's range. The species was reported from the flower of *S. gracile* A. Gray in Texas (Heinrich

1924), and the roots of *S. terebinthinaceum* Jacq. by Heitzman and Heiztman (1996) in Missouri. Metzler (1997) and Metzler et al. (2005) regarded *E. giganteana* as a tallgrass prairie dependent species. In eastern South Dakota, *S. perfoliatum* is most abundant and produces greater biomass along wetland margins and in seasonally hydric prairie or meadow sites with shallow water tables or vernal flooding. Our observations in agronomic settings in South Dakota and Wisconsin are that plants in light soils are subject to depressed growth and increased insect predation during droughty periods, and those on seasonally hydric sites experience greatly reduced rates of *E. giganteana* predation or are essentially free of predation through drowning of rhizome-feeding larvae. Plants on well-drained mesic sites can tolerate larval feeding and achieve essentially normal size and mass (Boe et al. 2019a-b).

Wright and Gilligan (2015) reported the adult *E. giganteana* activity period in Florida as from April to June, and July and August for the Midwest. In eastern South Dakota we found adult emergence as early as 7 June, although this occurred more typically in mid-June. During all years, males were observed to emerge first, with females emerging several days afterward. Eggs usually appeared within a week of adult emergence and typically laid on the adaxial surfaces of uppermost leaves. As the season progressed, eggs were also found on floral bracts, upper internodes, petioles, and peduncles. Eggs were laid individually, double, or more commonly in egg masses (Figure 2) of three to eight, though we occasionally found masses including up to 12 eggs each. Freshly laid eggs are pale yellow, turn orange-red within a few hours, and then darken over the next 3-4 days. At the end of this period the first instar larva can be seen moving within the chorion, and eclosion of all larvae with an egg mass occurs within a few hours after internal movement is observed. A freshly eclosed larva will consume the chorion before moving toward meristematic tissues at the apex of the shoot.

Larvae of instars one through four are predators of apical meristematic tissues, including floral buds and new leaves (Figures 10-11), and may cause upwards of 100% loss of seed per flower (Johnson 2011; Johnson and Boe 2012; Johnson et al. 2013). This feeding occurs when the plants have produced <50% of their potential biomass production. Larvae aggregate and feed communally, and counts of 35-60 larvae per floral head are common (Johnson et al. 2013). This larval feeding results in termination of primary and secondary floral growth (Figure 11) on each shoot and the resulting damage induces extensive secondary infections by decay organisms, including undetermined fungi and bacteria. Larval feeding usually occurs from early July until mid-August.

Eucosma giganteana larvae of instar three or four (Figure 3) leave the floral complex, enter the proaxes of plants >2 years of age, and burrow into the rhizomes. Contrary to historical reports of the larva as feeding or being a borer in roots (e.g., Forbes 1923; Heinrich 1923; Gilligan et al. 2008), the larva of *E. giganteana* is actually a stem feeder in the stout rhizomes (Johnson and Boe 2012). The larva enters the crown at the base of a shoot or the upper portion of the proaxis subtending a shoot and tunnels into the rhizome (Figure 7) forming a wide burrow, and plugs the entry hole with frass (Figures 6-7). The entry hole is enlarged to serve as an exit as the larva matures. The larva feeds until seasonal cold temperatures slow it to torpidity. In the spring, it becomes active again, returns to feeding, enlarges a burrow section into a pupation chamber in the rhizome near to the exit hole, spins a tightly woven cocoon (Figure 4), pupates, and waits for phenological emergence cues. It appears that for emergence the pupa wriggles out of the cocoon, pushes through the exit plug at the soil surface (Figure 8), where the adult ecloses and moves up the plant, but this aspect of development remains little understood.

The underground portions of *S. perfoliatum* are substantial, but the *E. giganteana* larva uses only a portion of these tissues, primarily the proaxis and the rhizome. At the beginning of the second growing season the plants produce roots from a tuber-like caudex (Figure 5) with stout and closely spaced internodes that support one or a few aerial shoots. By the end of the third growing season the internodes of this caudex extend laterally as rhizomes from buds on the proaxis, usually in multiple directions, to form a circular crown. Rhizomes grow annually from these proaxis buds, typically 10-20 cm per growing season, depending on soil and moisture conditions. Near the end of each growing season, three rhizome buds are formed per proaxis, generally one or two of which are aerial shoots (Figures 5-6), usually resulting in often overlapping bifurcating growths as shown in Figure 9. In Figure 5, two kinds of adventitious roots can be seen that emerge from internodes on the rhizomes, including at the base of each proaxial meristem. The first kind of root is a relatively long, cylindrical and fleshy structure of a yellow-brown color that somewhat resembles a thick strand of spaghetti. These function primarily to anchor the plant. The second kind of root is finer textured, is usually more heavily branched, and is presumably the primary nutrient acquisition structure. Cumulatively, the rhizomes, spaghetti roots, and fine roots form a massive organ complex that firmly anchor the plant and reduce soil erosion. The mid and late instar larvae of *E. giganteana* feed in the fibrous tissues of the rhizome and the base of the proaxis, often fully consuming the core tissues for several centimeters, as described above.

Eucosma giganteana larvae appear to be most vulnerable to parasitoids and predators during their floral meristem-feeding period, but only late instar nymphs and adults of damselbugs, *Nabis* sp. (Hemiptera: Nabidae) were observed as active predators on early instar larvae. The parasitoid *Bracon* cf. *mellitor* Say (Hymenoptera: Braconidae) (Figure 13) was reared from a wasp larva found feeding on a dead *E. giganteana* larva. Another *B.* cf. *mellitor* was observed ovipositing repeatedly into *S. perfoliatum* buds infested with *E. giganteana* larvae. No parasitism was observed for *E. giganteana* larvae located in the crown and rhizomes. An undetermined *Bracon* species was reported from *S. integrifolium* and compared with several other related species by Buffington et al. (2017), but our specimens did not key to or match descriptions of any of these reported species nor resemble the undetermined species as illustrated by these authors.

Both male and female *E. giganteana* can be found resting on the abaxial leaf surface, usually in the basal area of leaves on the upper two nodes of *S. perfoliatum.* They are consistently oriented with their head basad on the leaf and near to the petiole base, but may be at leaf midlength if there is water in the leaf cup. With this orientation, the front wing coloration is similar to that of bird droppings that are commonly found on *S. perfoliatum* leaves (Figure 12). Although adults will fly short distances during the day when disturbed, general flight activity for dispersal, mating, and oviposition is nocturnal, commencing shortly after dusk and continuing until dew point or dawn. Adult activity continues through mid-July and then rapidly tapers, with the last adults disappearing by early August.

CONCLUSIONS

Silphium perfoliatum is a native North American plant increasingly used for as a food, commodity, medicine outside of the United States, and livestock and wildlife forage and biodiversity support plant within its native range. All known serious predators of the plant remain known only from North America. Agronomic plants of *S. perfoliatum* are heavily damaged by larvae of *E. giganteana* that can completely terminate growth of shoots and inflorescences. Larvae feed extensively in the meristematic tissues of each shoot, then move to the proaxes and rhizomes to complete growth and overwinter. The frequency of infested proaxes was about 35% at the two main sites investigated, and the frequency of multiple larvae occurring in an infested proaxis was about 27% at both locations. Larvae differed in size between sites, and this variation corresponds with shoots size, which is related to consistency of available soil moisture during the primary growth period in June and July. Predation on early instar *E. giganteana* larvae was minimal and is attributed to the internal feeding behavior, but when exposed are highly vulnerable to numerous predators and parasitoids. The braconid wasp *Bracon* cf. *mellitor* is the first reported parasitoid of the early instar larvae. No parasitoids were recovered from overwintering larvae. Later instar larvae are identified as stem-borers that feed within proaxes and rhizomes, are not root feeders, and appear to be parasitoid free.

ACKNOWLEDGEMENTS

Our gratitude is extended to The Nature Conservancy for access to prairie preserves under their care, and the South Dakota Department of Game, Fish and Parks for access and collecting permission to the Spirit Mound Historic Prairie, Clay County, South Dakota. The Six Mile Creek Golf Course, White, South Dakota, is thanked for permitting access to streamside portions of their property. Kenneth Albrecht, University of Wisconsin-Madison, is thanked for his gracious hosting of our visit to the University of Wisconsin Arlington and Lancaster agricultural research stations, and the Terrace of the University Memorial Union overlooking Lake Mendota. This research was supported by the USDA-NIFA through Hatch Program projects through the South Dakota Agricultural Experiment Station, and the North Central Regional Sun Grant Center at South Dakota State University through the U.S. Department of Energy Bioenergy Technologies Office under award number DE-FG36-08G088073. This manuscript is a product of the Insect Biodiversity Lab, and the Forage and Biomass Breeding

Lab, both at South Dakota State University. Kendal Davis and Jordan Purintum are thanked for their reviews of the penultimate manuscript.

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Figures 1-4.* Eucosma giganteana, *clockwise from upper left. Figure 1, Adult, ca. 32 mm long. Figure 2, Egg mass with five eggs, each egg 1.9 mm long. Figure 3, Third instar larva removed from infested bud, ca.11.0 mm long. Figure 4, Cocoon, ca. 32 mm long, and prepupal larva, ca. 23 mm long.

Figure 5. **Silphium perfoliatum** ***crowns showing rhizomes and adventitious roots; crowns ca. 50-60 cm across.***

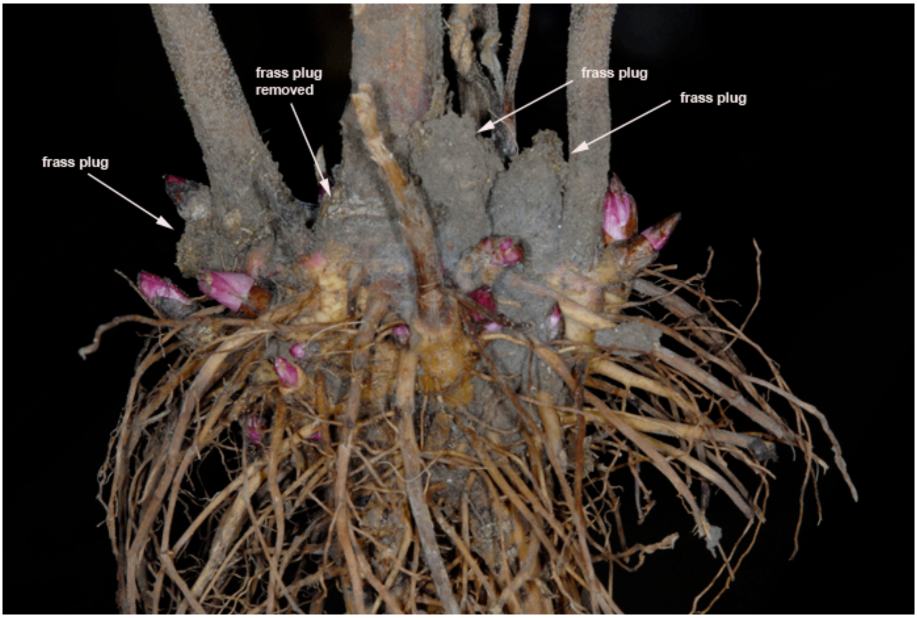

Figure 6. **Silphium perfoliatum** ***crown with*** **Eucosma giganteana** ***frass plugs and an exit hole where a frass plug was removed.***

Figures 7-10.* Eucosma giganteana *and* Silphium perfoliatum, *clockwise from upper left. Figure 7,* S. perfoliatum *rhizome beneath proxis with* E. giganteana *larva in situ. Figure 8, Pupal exuvium partially exerted from emergence hole in crown as shown in Fig. 6. Figure 9, Partial rhizome complex showing horizontal and bifurcating growth. Figure 10, Floral bud with first instar larva on disc.

Figures 11-12. Figure 11 (left)* Silphium perfoliatum *shoot apex with dead and decayed floral meristem resulting from* E. giganteana *larval feeding. Figure 12 (right)* Common *example of bird dropping on leaf midrib of* S. perfoliatum, *compare with Figure 1.

Figure 13,* Bracon *cf.* mellitor, *body length ca. 5.0 mm, collected while ovipositing into* S. perfoliatum *buds infested with* E. giganteana *larvae.