# THE GOLDENROD GALL MOTH GNORIMOSCHEMA GALLAESOLIDAGINIS (RILEY) AND ITS PARASITES IN OHIO

(LEPIDOPTERA: GELECHIIDAE)

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Gnorimoschema gallaesolidaginis (Riley) forms the familiar spindle shaped galls on the stems of certain goldenrod (Solidago) species. It has been mentioned many times in faunal lists since its description in Riley's (1869) first Missouri report. The two main studies of its biology were done in North Carolina, New York, and Vermont (Leiby, 1922a) and in Virginia (Barber, 1938). Except for Riley's (1869) notes in Missouri, little or nothing on the insect's biology west of the Appalachains has been reported.

The gall maker and its parasites in Ohio were studied from 1951 through 1953 at four areas located in three counties (Fig. 1). All study areas were abandoned farm fields in which goldenrod was the dominant herbaceous vegetation. All

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were next to woodlands, and two of the northernmost three contained young, planted red pine, *Pinus resinosa* Ait., which was severely infested by the European pine shoot moth, *Rhyacionia buoliana* (Schiff.). The question whether *G. gallaesolidaginis* might be an alternate host of shoot moth parasities prompted this investigation.

G. gallaesolidaginis galls were easy to find in fence rows and abandoned fields containing goldenrod. The pattern of distribution records in the 38 counties where the writer observed the galls (fig. 1) leaves little doubt that the gall maker occurs in every county in Ohio.

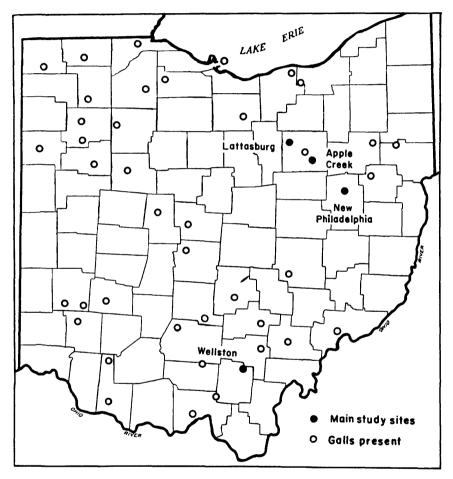


FIGURE 1. Study areas and distribution of records for *Gnorimoschema gallaesolidaginis* galls made during this study.

Only the goldenrods Solidago altissima L. and S. canadensis L. were found to contain the galls. S. altissima is perhaps the commonest goldenrod on abandoned agricultural land in Ohio. Other goldenrods frequently growing in infested fields but never found harboring G. gallaesolidaginis galls were Solidago gigantea Ait., S. juncea Ait., S. ulmifolia Muhl., S. graminifolia L. (Salisbury), and S. nemoralis Ait. Gall formation seems to cause little if any adverse effect on host plants.

The identity of G. gallaesolidaginis specimens was verified by J. F. Gates Clarke of the U. S. National Museum. The most recent taxonomic treatment of

the insect is that of Busck (1939) who illustrated male and female genitalia. Figure 2 in the present paper shows the wing pattern of the brownish colored adult.

Hymenopterous parasites were identified by specialists of the Insect Identification and Parasite Introduction Research Branch, U. S. Dept. of Agriculture, as follows: Chalcidoidea, B. D. Burks; Ichneumonidae, L. M. Walkley; Braconidae, C. F. W. Muesebeck. Nematode parasites were determined by Gotthold Steiner of the Crops Protection Research Branch, U. S. Dept. of Agriculture. Fungal

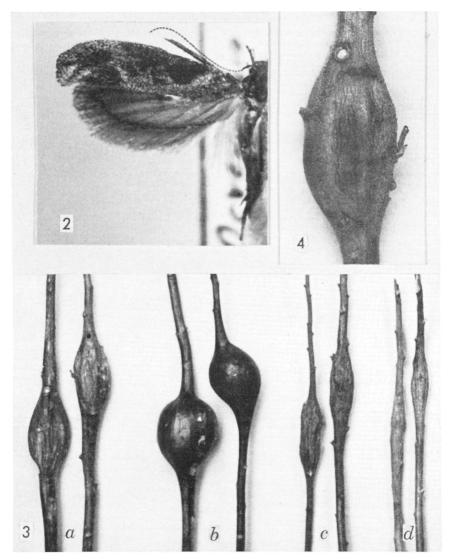


FIGURE 2. Wing pattern of an adult Gnorimoschema gallaesolidaginis from Tuscarawas Co.,

Figure 3. One-celled stem galls commonly found on goldenrods in Ohio. a, Gnorimoschema gallaesolidaginis on Solidago altissima; left, with bung; right, without bung; b, Eurosta solidaginis on Solidago gigantea; c, Epiblema scudderiana on Solidago altissima; d, Epiblema desertana on Solidago graminifolia.

FIGURE 4. Close-up view of Gnorimoschema gallaesolidaginis gall with bung.

parasites were diagnosed by E. A. Steinhaus of the Insect Pathology Laboratory,

University of California.

Goldenrods were diagnosed or their identity verified by E. C. Leonard and L. M. Smith of the U. S. National Herbarium, and S. F. Blake, New Crops Research Branch, U. S. Dept. of Agriculture. Nomenclature of goldenrods follows Fernald (1952).

#### OTHER STEM GALLS OF GOLDENROD

In Ohio, several other one-celled stem galls caused by insects other than species of Gnorimoschema also occur on goldenrod. The ubiquitous goldenrod ball gall (fig. 3b) formed by the tephritid fly Eurosta solidaginis Fitch occurs mainly on S. altissima and S. gigantea (Miller, 1959). The gall of the olethreutid moth Epiblema scudderiana (Clemens) (fig. 3c) occurs on S. altissima and at least three other goldenrod species, but the gall caused by Epiblema desertana (Zeller) (fig. 3d) is found only on the distinctive grass-leaved goldenrod, S. graminifolia. Galls of G. gallaesolidaginis (fig. 3a, 4) and related species can be easily distinguished because they possess exit bungs which the other galls lack and because they are characteristically shaped.

More often than not, Eurosta solidaginis and Epiblema scudderiana galls are present in the same stands and sometimes even on the same plants with G. gal-

laesolidaginis galls.

The other Gnorimoschema species producing stem galls on goldenrod in Ohio affect different species of goldenrod than the two which G. gallaesolidaginis affects. Indeed, finding a Gnorimoschema gall on a goldenrod other than S. altissima or S. canadensis is reliable evidence that it is not a G. gallaesolidaginis gall. Also, the whitish exit bung of the G. gallaesolidaginis gall (fig. 3a, 4) can serve in the field to separate this gall from those of its Ohio relatives, which make dark brown exit bungs.

## LIFE HISTORY

The life history of G. gallaesolidaginis as set forth by Leiby (1922a) seems to hold for Ohio also. Eggs are laid on goldenrod in late summer and fall. The fully developed embryo winters in the egg. In the spring, the newborn larva burrows into the terminal of a young goldenrod plant, then downward in the rod, through the pith. It concentrates its feeding several inches or less below the tip and there the gall forms. Pupation takes place inside galls in July. A month or so later, adults emerge and evacuate their galls through a previously prepared exit. Some of these events are depicted on a time scale in Fig. 5.

Larval Stage.—New goldenrod shoots become noticeable in early May in Ohio. Larvae have been found in them as early as May 19; the goldenrod stand was about 1 ft tall when this observation was made. The galls develop rapidly, and

by the end of May some have reached mature size.

In June, the larva begins preparing the moth exit. At some point in the upper third of the gall chamber, a passageway just large enough for the adult is eaten through the wall nearly to the outside. A thin, translucent cap of outer plant tissue is left uneaten. The larva then makes a hard, honey-colored bung which By the time the bung is completed, the cap of plant tissue seals this passageway. has deteriorated. The newly exposed bung soon weathers to become whitish in Besides constructing an exit, the mature larva also lays down a silken mat on the walls of the gall chamber. This mat seals off the chamber above the passageway and helps guide the newly emerged moth smoothly into the passageway. About 4 weeks elapsed between first signs of passageway construction and the appearance of bungs (fig. 5). It seems likely that during part of this period the passageway could serve as an easy entrance for parasites. A week or so after completing the bung, the larva pupates (fig. 5).

Pupal Stage.—Pupation takes place in late July and August (fig. 5).

actual pupation rate shown in figure 5 is retarded in relation to other life history events. This retardation is attributed to parasitization by *Dicaelotus gelechiae* (Ashmead) and *Pleurotropis sexdentata* (Girault). Although combined parasitization by these two wasps amounts to only 7 percent when considered with other mortality factors (table 1), it assumes a much larger value when related to the segment of the gall maker population still alive in late summer when these parasites exert their effect. No healthy gall maker larvae or pupae were carried over the winter because none were found at any study area when over 300 galls of the previous season were checked in early spring. The intermittent line in figure 5 probably represents pupation progress among unparasitized members of the population more accurately than the solid line. From the intermittent line, the pupal period is inferred to last about 6 weeks. Gall makers which have not pupated by about August 15 are doubtless doomed to death by parasitization even though they may remain alive till much later and eventually pupate.

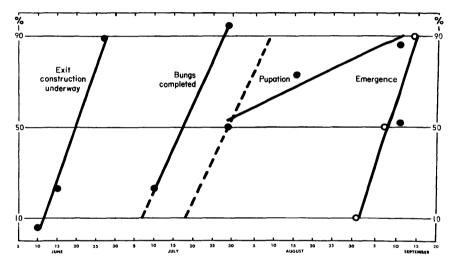


Figure 5. Seasonal occurrence of some developmental events of the gall maker and its gall in Ohio. The diagram is based on combined data obtained during 1951-53 at 4 study areas. Solid points represent field observations; hollow points, insectory observations. The trend lines were sight fitted. The intermittent line is explained in the text.

Emergence and Adult Stage.—Moth emergence during three summers was recorded separately in the insectary for a total of 9 separate collections of galls from all study areas. Each collection produced from 8 to 23 moths. The dates of initial appearance of moths in these collections ranged over a 4-day period, beginning August 30. Emergence continued for 8 to 20 days, averaging 12 days per collection. Insectary and field emergence seemed to proceed at about equal rates (fig. 5).

The total longevity of adults is uncertain. Several adults were still alive as late as the middle of October in the insectary, but these were inadvertently killed on that date. Riley (1869) stated that he captured an adult in May which had presumably overwintered.

#### MORTALITY

More than 600 galls were collected from the four study areas and examined in the laboratory to determine the fate of their makers. These galls were collected as they were spotted during searches in the study areas. All stages of

gall formation from the earliest swelling onward were represented. The interval encompassed by this range in gall development was roughly the end of May to the middle of September—from the early larval stage through the pupal stage of the gall maker. Results of these examinations (including parasite rearings) are given in table 1.

Of the gall makers getting established in the host plant, about one-fourth survived to issue as adults. Nearly half died because of parasitization, and the remaining one-fourth succumbed to unidentified causes. Some of the unaccountable deaths may have been due to undetected parasitization; generally, however, parasites left easily recognized evidence of their development. There was nothing characteristic about the galls, or, when present, the dead insects in them, to suggest the cause of the unaccountable deaths.

Table 1
Fate of the gall maker following gall formation

Fate	Percentage <sup>1</sup>				
	Apple Creek	New Philadelphia	Wellston	Lattasburg	mean
Moths issued from galls Moths emerged but failed	28	18	37	29	28
to issue from galls	<b>2</b>	1	0	<b>2</b>	1
Larvae and pupae died unaccountably	22	32	22	19	24
Larvae and pupae died because of parasitization by:					
Campoplex depressus	16	14	14	12	14
Copidosoma g. gelechiae	$\tilde{9}$	3	12	$\frac{12}{22}$	11
Eurytoma bolteri	6		9	6	7
Dicaelotus gelechiae	4	6 5 8 5	ŏ	ğ	4
Pleurotropis sexdentata	ĩ	8	$\check{\mathbf{z}}$	ŏ	$\hat{\mathbf{a}}$
Calliephialtes notandus	$ar{2}$	5	ī	ĭ	$egin{array}{c} 4 \ 3 \ 2 \ 2 \end{array}$
Bracon furtivus	4	<b>2</b>	ī	$\bar{0}$	$\bar{2}$
Beauveria bassiana	$\bar{3}$	1	ĩ	Ŏ	$\bar{1}$
Nematode	Õ	$\frac{1}{3}$	$\tilde{0}$	Õ	ī
Others	3	<b>2</b>	1	Ô	$ar{2}$
Total	48	49	$\overline{41}$	50	$4\overline{7}$

<sup>&</sup>lt;sup>1</sup>From 103 to 178 galls studied at each locality.

Chi-square was used to test for significant differences among the frequencies of any one event recorded at different study areas in table 1. Only chi-squares for parasitization by *Copidosoma g. gelechiae*, *Dicaelotus gelechiae*, and *Pleurotropis sexdentata* proved significantly larger than expected from chance variation (5-percent level). Further investigation will be necessary to elucidate the meaning of these differences. However, so few differences show that patterns of mortality and survival were very similar among the four study areas.

## PARASITIZATION

Ninety-six percent of the parasitization was caused by seven wasps, a fungus, and a nematode worm (table 1). The remaining parasitization was probably caused by the following six wasps: Spilochalcis igneoides (Kirby) (Chalcididae), Bracon hebetor Say, Bracon variabilis Prov., Schizoprymnus sp., Heterospilus languriae (Ashmead), and Rhaconotus graciliformis (Viereck) (Braconidae).

Several of the commoner parasites in this study have been reared from the same host in Virginia (Barber, 1938) and New York (Leiby, 1922a).

None of the parasites affecting European pine shoot moth (Rhyacionia buoliana) populations at two areas used in this study (Miller and Neiswander, 1955) were found to be associated with the gall maker. However, B. hebetor, a rare parasite of another pine moth, Rhyacionia rigidana (Fernald) (Miller and Neiswander, 1959), did appear to parasitize the gall maker, but as mentioned above, it was infrequent.

To test for differences in the abundance of gall maker parasites, the section of table 1 giving parasitization percentages was subjected to analysis of variance after first transforming the percentages to arcsin values (Snedecor, 1956). The analysis showed that any two mean percentages differing by roughly 10 percentage points or more were significantly different at the 5-percent level. It should be stressed that this analysis examined only abundance of parasites, not their importance in the dynamics of host populations.

Information about individual parasite species is given in the sections which follow. It was obtained partly from the material used to prepare Table 1 and partly from special supplementary collections. Parasites reared under observation were held in an insectary in 25 by 95 mm shell vials. Adults were fed by

means of a moist raisin pinned to the cork inside the vials.

Campoplex depressus Viereck (Ichneumonidae).—C. depressus was the most frequent parasite of the gall maker, being well represented at all study areas (table 1). It had a one-year life cycle which was well synchronized with the host's. G. gallaesolidaginis is the only known host (Muesebeck et al., 1951) and it seems likely that the parasite maintains itself solely on the gall maker.

C. depressus is a solitary, external feeder on the larva. The larvae passed the winter inside host galls in cocoons which they spun in the summer after completing their feeding. Based on 2 years' insectary records, representing all study areas, the emergence period of 36 adults ranged from May 2 through 17, a week or two before new galls were first noticed. Natural emergence of three adults was also witnessed in the field within the above dates. With food, 16 adults, including both sexes, lived an average of 20 days, ranging from 4 to 34 days. Without food or water, 6 adults of both sexes lived an average of 9 days, varying from 6 to 12 days. Of 43 adults, 30 percent were males and 70 percent were females.

Fourteen individuals underwent the latter part of their development under observation in the insectary. From the time meconia became visible through cocoons till adults appeared, there elapsed an average of 21 days with a range of 17 to 25 days. One of these larvae was known to pupate the day after casting its meconium.

Campoplex cocoons were vertically suspended in the center of the gall chamber by a network of silken strands. Cocoons were either white or dark brown, the two occurring in about equal numbers. Both sexes emerged from both color cocoons. Moreover, the taxonomic specialist who identified the parasite found no differences related to different cocoon color in 15 adults.

Occasionally, Campoplex itself was parasitized by Tetrastichus sp., a gregarious parasite which issued from the host cocoon in late May, but which could not be identified further from the specimens reared. The species may have been T. fumipennis (Girault), a specimen of which was found inside a gall not containing Campoplex.

Of 117 galls in which parasite larvae completed development, 85 percent had exit bungs and 15 percent did not. Campoplex thus tended to allow its host to

complete a convenient exit.

*Copidosoma* g. gelechiae Howard (Encyrtidae).—C. g. gelechiae was another relatively frequent parasite of the gall maker (table 1). It is well adapted to this host; and although known from other hosts (Muesebeck et al., 1951), it can probably maintain itself solely on G. gallaesolidaginis populations.

C. g. gelechiae is a polyembryonic, internal parasite of the larva. Based on 1952 insectary records from two study areas, adults emerged from September 3 to 25, more or less concurrently with host adults. This parasite was extensively studied by Leiby (1922b). Females oviposit in host eggs in the fall. Overwintering takes place as a polynuclear mass within the completely formed host embryo. After the host larva hatches, the parasite body develops into a polygermal mass, later becoming a mass of embryos which are set free in the host's body cavity. These parasite larvae devour everything in the host but the chitinous parts. In the present study, host larvae completed exit tunnels before dying, but never began making bungs. In 91 percent of 70 examples where the wasps emerged from galls, a tiny escape hole had been gnawed the rest of the way through the host's exit passageway. In the remaining 9 percent, escape holes were gnawed elsewhere. In 11 percent of Copidosoma aggregations completing development, the emerged wasps failed to escape from the galls and perished in them.

Eurytoma bolteri (Riley) (Eurytomidae).—E. bolteri regularly parasitized the gall maker at all study areas (table 1). Muesebeck et al. (1951) record it from several hosts feeding on goldenrod. It very likely subsists partly on G. gallae-

solidaginis and partly on other hosts.

E. bolteri is usually a solitary, external feeder on the larva. Out of a total of 94 wasps obtained, 91 issued from Gnorimoschema larvae; 1 from a Gnorimoschema pupa; and 2 from cocoons of Calliephialtes notandus (Cresson). Although the parasite had a one-year life cycle, there were two annual emergence periods: summer and spring. Of 77 individuals completing development, 59 percent emerged in summer while 41 percent remained in host galls over the winter and emerged the following spring. In the insectary, summer emergence occurred from July 10 to September 4 and spring emergence from May 18 to June 3 during 3 years' observations. The emergence of one adult was witnessed in the field on July 7. Twenty-six specimens representing both emergence periods were examined by a taxonomic specialist and all were determined as the same species. Dual emergence periods were likewise reported by Barber (1938) and Leiby (1922a) for this species and this phenomenon is also known in other species of Eurytoma (Miller, 1959). Of 15 adults whose sexes were recorded, 7 were males and 8 were females.

Of 50 galls in which Eurytoma parasites completed development, 22 percent had bungs, while 78 percent had not progressed that far. Thirteen of the galls with bungs were about equally divided between summer and spring emerging groups. Most of the parasites of both emergence periods therefore disabled the host a month or so before the end of its larval stage and consequently had to gnaw their own exit through the gall to escape. Examination of 29 galls whose makers were prevented from making exits by Eurytoma revealed that 14 percent of the parasite adults failed to escape from the galls, perishing inside them.

Several Eurytoma larvae collected in July 1951 developed to the adult stage under observation in the insectary. Three of these pupated between August 4 and 8 and their pupal periods lasted from 10 to 13 days. Three other larvae did not pupate till the following spring, although one had expelled its meconium in early August. These overwintering larvae pupated between April 29 and May 1, and their pupal periods lasted from 26 to 35 days. Except for the one larva mentioned, larvae of both groups pupated from 1 to 3 days after expelling meconia. No cocoons were spun by larvae of this species.

There is no obvious explanation for the dual emergence periods of this parasite, but one possible explanation is postulated below. The spring emerging adults appear about the same time as newborn larvae of *G. gallaesolidaginis*. If spring emerging adults attack this host promptly, their progeny could issue as adults by late summer. Such adults emerging in late summer might attack alternate hosts on which the progeny overwinter and issue as adults late the

next spring. Late spring adults might then return to *Gnorimoschema* to produce a group of progeny which would issue early the next spring to repeat the cycle.

Dicaelorus gelechiae (Ashmead) (Ichneumonidae).—D. gelechiae was detected at three of the four study areas (table 1). It probably was present at the fourth, but was missed by chance in the sampling. It is known only as a parasite of G. gallaesolidaginis (Muesebeck et al., 1951). To subsist wholly on this host, the parasite would need to either oviposit in host eggs, which seems unlikely, or overwinter as an adult and oviposit on the caterpillars. It is concluded for the present that Dicaelotus uses the gall maker as an alternate host.

*Dicaelotus* is a solitary, internal feeder whose adults issue from host pupae. In the insectary, 12 adults appeared between July 30 and September 15 from galls collected at 2 study localities. Of 15 specimens available, 9 were females and 6 were males.

Calliephialtes notandus (Cresson) (Ichneumonidae).—C. notandus parasitized the gall maker at all study areas (table 1). It also attacks other lepidopterous larvae feeding in weed stems. Adults are common not only in fall when they emerge from G. gallaesolidaginis, but also in the spring (Townes and Townes, 1960). It therefore seems likely that Gnorimoschema is an alternate host of this wasp.

Calliephialtes notandus is a solitary, external feeder on the host larva. Based on insectary records for 2 study localities and 2 years, the emergence period of 6 adults ranged from September 2 through 19. Of 11 adults, 5 were males and 6 were females. One larva (female) under observation in the insectary cocooned on July 16, cast its meconium 37 days later, pupated after 3 more days, and emerged on September 3 after 9 more days. The light brown cocoon is tough; it is ellipsoidal and is firmly attached to the gall chamber. Of 14 galls in which parasites completed larval development, 4 contained bungs, and 10 did not, indicating that this parasite tends to disable the host in early July, before exit facilities are completed. The majority of parasite adults therefore have to gnaw their way to freedom. Of 17 parasites which had reached the cocoon stage, 2 or about 12 percent were themselves parasitized. The hyperparasites were E. bolteri.

Bracon furtivus Fyles (Braconidae).—B. furtivus was obtained at three study areas (table 1), and very likely occurred at the fourth, but was missed by chance. It is well adapted to the gall maker. It is known from one other host which is also of the genus Gnorimoschema (Muesebeck et al., 1951), but it very likely can subsist solely on G. gallaesolidaginis.

Bracon is a gregarious feeder on the larva. It has a one-year life cycle which seems well synchronized with the host's. Based on 1 year's insectary records for 3 study localities, the adult emergence period of 8 aggregations ranged from May 2 to 25, the same period that G. gallaesolidaginis larvae hatch and start forming their galls. Three aggregations seen in the field within the above dates had emerged also. Five unfed males lived from 1 to 8 days, averaging 6, and 1 unfed female lived 9 days. Seven fed males lived from 7 to 15 days, averaging 10 days, and 2 fed females lived 9 and 16 days. Of 62 adults, 34 percent were females and 66 percent were males.

The larvae complete their feeding and begin cocooning in July. The earliest cocoon was found on July 14, and 2 out of 3 colonies seen on July 31 had cocooned. The larvae do not pupate till the following spring, however. They overwinter inside the host gall. The thick, light brown cocoons are cylindrical and those in one aggregation are often fused together. In 16 cocooned aggregations the number of individuals ranged from 3 to 16, averaging 8±4. Also, 87 percent exhibited moth exit bungs, indicating that most aggregations have a convenient exit from galls.

Pleurotropis sexdentata (Girault) (Eulophidae).—P. sexdentata was reared from three study areas (table 1), and, as with other less abundant parasites, probably

was present at the fourth but failed by chance to appear in the sample. It seems well adapted to the gall maker. Although known from several other hosts as well (Muesebeck et al., 1951), this wasp can probably subsist wholly on *G. gallaesolidaginis*.

Pleurotropis is a gregarious, internal feeder which emerges from host pupae. It had a one-year life cycle and wintered in the larval stage inside host galls. Adults appeared between May 10 and June 22 during 2 years' observations on material in the insectary from 2 study areas. During this period, G. gallaesolidaginis larvae are hatching, forming galls, and constructing exits (fig. 5). The parasite adults might gain access to the host at this time through the exit passageway. With food, 15 wasps lived from 8 to 14 days, averaging 11 days. Without food, 13 lived from 4 to 11 days, averaging 7 days. Two larval aggregations undergoing development under observation in the insectary both began transforming to pupae on April 21. Emergence began 23 and 25 days later, respectively. Three aggregations had 17, 32, and 44 individuals, averaging 31.

Fungal and Nematode Parasites.—Infection of gall maker larvae by the fungus Beauveria bassiana (Bals.) Vuill. was detected at three study areas (table 1), and wider searching would probably have revealed it at the fourth. The fungus probably reaches the larvae while they wander about just after hatching and before starting to feed on the goldenrod. The larvae succumbed when they were

nearly fully grown.

The nematode parasite (Family Mermithidae; genus and species undetermined) was found at one locality only (table 1). These worms were about as long as fully grown host larvae and very slender. They disabled the host just before host pupation. Infestation probably took place while the newly hatched larvae wandered about.

Other Parasites.—Several or all of the six species listed earlier as comprising this category accounted for about 2 percent of the gall makers (table 1). These wasps were probably using the gall maker as an incidental host. Because of their infrequent occurrence, little was learned about them. Five species were merely found in emergence cages, with only Spilochalcis igneoides definitely being seen to emerge from the gall maker. Two Spilochalcis adults emerged from host pupae in the insectary on May 27 and June 1 after overwintering inside galls.

### SUMMARY AND CONCLUSIONS

1. G. gallaesolidaginis (Riley) forms spindle shaped galls on the stems of the goldenrods S. altissima L. and S. canadensis L. The insect occurs throughout Ohio and the galls are common in old fields and fence rows. The natural history of the gall maker and its parasites were studied for three years at four study areas.

2. The gall of *G. gallaesolidaginis* can be differentiated from other one-celled goldenrod stem galls occurring in Ohio by its characteristic shape and its whitish

moth-exit bung.

3. The gall maker has a one-year life cycle, wintering in the egg stage. Adults appear late in the summer. Larvae hatch the following spring and galls become conspicuous in May. The pupal stage is passed in late July and August.

4. About one-fourth of the gall makers getting established in host plants survived to issue as adults. Another one-fourth died of unidentified causes, and

nearly half died because of obvious parasitization.

5. The following four parasites, because of abundance, apparent adaptation of life cycle to the host, and narrow host spectrum, probably can maintain themselves solely on G. gallaesolidaginis populations: Campoplex depressus, Copidosoma g. gelechiae, Bracon furtivus, and Pleurotropis sexdentata. Although fairly abundant as parasites of the gall maker, Calliephialtes notandus, Dicaelotus gelechiae, and Eurytoma bolteri may require alternate hosts for subsistence.

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