
The Interrelationships of
Three Gall Makers and Their
Natural Enemies, on Hackberry
(*Celtis Occidentalis* L.) John Conrad Moser

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*The University
of the State
of New York*

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The Interrelationships of Three Gall Makers and Their Natural Enemies, on Hackberry (*Celtis Occidentalis* L.)

by John Conrad Moser
Graduate Student Honorarium Program*

ABSTRACT

This bulletin describes three hackberry galls, the insects which make them, and 19 of their natural enemies in the Cayuga Valley near Ithaca, N.Y. Two galls were caused by psyllids and the third by a cecidomyiid. The taxonomy, biology, morphology, and distribution of the species are discussed.

Fourteen natural enemies attacked the psyllid gall makers, and five fed on the cecidomyiid gall maker. However, no cecidomyiid parasites were found in psyllid galls, nor were natural enemies of psyllids located in cecidomyiid galls. Whereas most natural enemies attacked only gall makers, three were normally parasites of lepidopterous leaf miners of hackberry, and two fed on a wide range of insects other than those associated with hackberry.

At least three parasites of the psyllid complex were secondary; two were specific to a single primary parasite, and the other fed on all primary parasites as well as the gall makers. Two natural enemies

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fed only on psyllid galls, but always killed the gall makers while feeding. Some parasites of psyllids fed on the gall after consuming the insects.

One of the psyllid gall makers often incorporated itself in the larger gall of the other psyllid, a condition termed marginal gall. Parasites found in marginal galls were always the same as those found in the large galls, which is considered to be evidence that certain parasites were attracted not by host nymphs, but by the gall.

Some primary parasites were more abundant than the others. Those whose larvae immediately fed on gall makers were more successful than other primary parasites, whose larvae began feeding after a period of time.

One new genus and four new species are described and methods of statistical separation are given for two closely related parasites.

Introduction

This bulletin is a study of three ecologically associated gall makers and their natural enemies on hackberry (*Celtis occidentalis* Linnaeus). Most published studies of galls have been limited to a single gall maker and its parasites. However, when three gall makers such as those which formed the basis of this study comprise such a close ecological association in the leaves of a single tree, a thorough study of all of them must be made in order to understand the biology of any one of them.

The background afforded by such an approach is particularly needed when biological control is being considered, as in the case of forest pests where chemical control is undesirable or unfeasible. Especially in view of this consideration, the work was supported by a grant of an honorarium from the New York State Museum and Science Service.

The three gall makers involved in this study represent two taxonomic groups. The psyllid group is composed of *Pachypsylla celtidis-mamma* (Riley), which causes the formation of a nipple gall on the underside of the leaf, and *Pachypsylla celtidisvesicula* (Riley), which causes the formation of a blister gall that is equally developed on both sides of the leaf.¹ The other taxonomic group is composed of one dipterous species of the family Cecidomyiidae. This species, a member of the genus *Phytophaga*, causes the formation of a thorn gall by the downward growth of the leaf tissue on the lower side of the leaf.

The problem is simplified somewhat by limiting it to the Cayuga Valley in the vicinity of Ithaca, N.Y. This reduces the number of

¹ A third psyllid, *Pachypsylla celtidisgemma* (Riley), which makes a bud gall, also occurs in the Cayuga Valley. However, it is very rare and was not discovered until after the first draft of this bulletin was written.

insects involved, since in other parts of the country other galls and different parasites occur.

To facilitate identification, references, and comparisons, the bulletin is divided into three parts. Part I contains three subsections, one for each gall maker. Part II consists of subsections on the natural enemies of the three gall makers described in part 1, including keys, descriptions of one new genus, and four new species. Part III contains a discussion of the host specificity of the natural enemies and the abundance of gall makers and parasites, a statistical analysis to assist in the separation of two species, taxonomic notes, and notes on distribution of hackberry in the Cayuga Valley.

Part I - The Gall Makers

Pachypsylla celtidisvesicula (RILEY) 1890 (Hemiptera: Psyllidae)

Pachypsylla celtidisvesicula is the most common gall maker on hackberry in the Ithaca area, and is widely distributed throughout the Cayuga Valley. Over 600 galls have been found on a single leaf, although the average is about 25–50. The gall (figure 6A) is a small, blisterlike formation, about 1/100 the volume of nipple gall made by its sibling species, *P. celtidismamma*. However, the nymph of *P. celtidisvesicula* (figure 10) is about one third the size of *P. celtidismamma*.

P. celtidisvesicula often becomes a pest in the fall by gathering in tremendous numbers on window screens. There are numerous references to it in the literature after 1890. Smith and Taylor, 1953, summarize the known biology and add many observations of their own. Important aspects of the biology not covered in Smith and Taylor, 1953, are discussed in the following paragraphs.

The egg (figure 1) is glistening white with no superficial markings, and ovate with the widest portion nearer the stalked end. The end attached to the ovary bears a protuberance before the egg is laid, but after the egg is laid the opposite end also acquires a stalk that attaches the egg to the leaf. The young nymph emerges from the top of the egg, a process requiring about 5 minutes.

In spring, adult psyllids persist about as long as the leaf buds (figure 26). In early spring, at anthesis when the buds are just opening, they are covered with psyllids. There are up to 50 adults on buds at anthesis, whereas in late June, when buds become scarce, only one or two psyllids may be found on a bud. By early July, the few remaining buds outnumber the psyllids, and by the middle of July the psyllids are gone. The adults feed actively on leaves in spring, and die within 24 hours if removed from the leaves. They apparently do not feed in the fall.

Mating took place only when insects were in direct sunlight. In the laboratory, adults on leaves in glass vials were placed in skylight, sunlight, and darkness, but mating was observed only in bottles exposed to sunlight. Oviposition in the laboratory occurred from 18 to 36 hours after mating, and the adults died shortly thereafter.

Eggs were usually laid on lower surfaces of exposed leaves, or on both sides of leaves in expanding buds. Egg-laying activity was greatest at anthesis when large numbers of psyllids clustered on hackberry flowers and swelling leaf buds. At this time numerous eggs were found even on flowers and outside surfaces of buds. Eggs laid on leaves in the laboratory required 6 days to hatch. The eyes of the embryo turned red 1 day prior to emergence.

After hatching, first-instar nymphs crawled from the lower surface, where most of the eggs were laid, to the upper surface of the leaf. After a time they settled down and fed. This feeding caused leaf tissue to proliferate and gradually close over the nymph. As the nymph became larger, its cavity gradually increased in size.

Blister galls were about 0.4 mm. in diameter immediately after the nymphs were covered by leaf tissue, and about 2.0 mm. when the adult was ready to emerge.

Emergence of fifth-instar nymphs began about September 1, but the peak emergence was at leaf fall on about October 1. Premature emergence was induced by removing the leaf from the tree.

Nymphs escaped by cutting a longitudinal slit through the gall on the top of the leaf with the anal spines, and came out tail first. Ecdysis occurred immediately after the adult emerged.

In contrast, parasites become adults before leaving the gall, and used their mouthparts to cut a small circular hole in the gall. Adults usually made their exit through the top of the leaf, rarely from the bottom.

Table 1. Measurements of the stages of *Pachypsylla celtidisvesicula*

Stage	Egg	1	2	3	4	5	5-mar- ginal*	Male **	Female **
<i>Statistic</i>									
Mean (mm.)	0.30	0.30	0.54	0.63	1.11	1.44	2.38	2.15	2.38
Minimum	0.25	0.25	0.45	0.50	0.70	0.70	1.40	1.50	1.80
Maximum	0.35	0.40	0.70	0.90	1.70	2.00	3.00	2.50	2.70
s	0.02	0.04	0.05	0.09	0.19	0.26	0.57	0.22	0.23
n	50	30	30	30	30	30	24	30	30

* Marginal galls are made by *P. celtidisvesicula* nymphs that have been incorporated into nipple galls. They are discussed later in this section.

** Only reared adults used for measurements; about 3 percent of the adults of *P. celtidis-mamma* and *P. celtidisvesicula* collected in the field cannot be determined satisfactorily to species.

Nymphal instars of *P. celtidisvesicula* (figure 1) were easily separated by size, shape or body, areas of pigmentation, anal spines, number of antennal segments, size of wing-buds, number of segments in legs, and relative length of certain setae on the head and tarsi.

Greatest growth of nymphs occurred after the third and fifth instars (table 1).

Blister galls are abundant on *Celtis occidentalis*, but less common on *C. laevigata*, *C. tenuifolia*, and *C. reticulata*; they apparently occur throughout the range of these trees in America north of Mexico.

Pachypsylla celtidismamma (RILEY) 1876 (Hemiptera: Psyllidae)

Pachypsylla celtidismamma (Riley) forms a nipplelike growth (figure 3) on the underside of hackberry leaves. Under favorable conditions as many as 30 galls may be found on one leaf, but the average number of galls on infested leaves is about three. At Ithaca, the gall is more numerous at higher elevations around the Cayuga Valley. The nipple gall is not the most common leaf gall, but is the most conspicuous. For this reason there is more literature on this gall than on any other found on hackberry. The best summary of its biology is by Smith and Taylor (1953). Details not covered by them are discussed in the following paragraphs.

The literature on *P. celtidismamma* is extensive, and numerous combinations have been used for the name. A nearly complete list of citations is given by Tuthill, 1943. Riley (1876) described the species. His description contains a figure of the nymph and gall that is reproduced in Comstock's *Introduction to Entomology*.

The period of greatest growth of the nymph of *P. celtidismamma* (figure 2) occurs between the fourth- and fifth-instars (table 2), but the gall enlarges most rapidly when nymph is in the first instar (figure 28). Nymphs of *P. celtidismamma* hatched from eggs earlier, but development was slower than nymphs of *P. celtidisvesicula* (figures 26 and 27).

Nipple galls are recorded from *Celtis occidentalis*, *C. laevigata*, and *C. reticulata*; apparently the species is distributed throughout the range of these trees in America north of Mexico.

Table 2. Measurement of the stages of *Pachypsylla celtidismamma*

Stage	Egg	1	2	3	4	5	Male	Female
<i>Statistic</i>								
Mean (mm.)	0.38	0.36	0.66	1.06	1.54	3.38	3.54	3.50
Minimum	0.37	0.25	0.30	0.80	1.00	1.80	2.90	2.80
Maximum	0.40	0.45	0.86	1.20	2.00	4.00	3.90	4.10
s	0.11	0.06	0.12	0.09	0.26	0.49	0.33	0.41
n	9	30	30	30	30	30	14	18

The marginal gall

A marginal gall is a blister gall that has become incorporated into a nipple gall. Figure 3A shows what may be the formation of this type of gall where nymphs of *P. celtidisvesicula* sink into nipple galls during their early growth. Figure 3B shows a cross section of a mature nipple gall with a marginal gall on its side. Nymphs in marginal galls have significantly larger mean lengths ($F = 34.14$) than nymphs of normal blister galls. Nymphs in marginal galls may have a greater food supply, and are of special interest because their parasites are the same as those that attack *P. celtidismamma* (figure 32).

Marginal galls are common. Examination of 162 nipple galls from four localities in the Cayuga Valley gave results shown in table 3. Over half contained one or more marginal galls, but the number of marginal galls per nipple gall varied widely between localities. Previous workers explained the phenomenon by stating that nipple galls are polythalamous, which is a freak occurrence, if it occurs at all. This may account in part for the failure of previous workers to find satisfactory morphological differences between adults of the two species, since all specimens reared from nipple galls were called *P. celtidismamma*.

Table 3. Number of marginal galls per nipple gall

Number of marginal galls per nipple gall	0	1	2	3	4	5	6	7
Percent	43.8	20.4	22.8	6.2	2.5	2.5	0.6	1.2

Phytophaga sp. nr. *spiniformis* (Patton)

(Diptera: Cecidomyiidae)

About 18 species of Cecidomyiidae (all probably *Phytophaga*) attack the genus *Celtis* in North America. Felt (1940) lists eight,

but many of his other names may be synonyms. Most species in the United States occur in the southern States. This is shown in table 4, which includes three localities extensively collected. Only the thorn gall occurs in all three localities.

Table 4. Number of species of cecidomyiid galls for three localities in the United States

Locality	Species occurring at locality	Number of species which do not occur in the other two areas
Ithaca, N.Y.	1	0
Columbus, Ohio	9	3
Austin, Tex.*	14	9

* Data from John Riemann (personal communication)

Unlike pachypsyllid galls, which occur only in North America, cecidomyiid galls on *Celtis spp.* are found in most parts of the world, and some may be closely related to the North American species. Specimens of these galls are often found in many herbaria. Professor K. Yasumatsu sent the writer galls from *Celtis siniensis* on the island of Honshu. One of these galls is identical in external appearance and position of attachment on the leaf to the spine gall at Columbus, Ohio. The other gall is similar in appearance and position of attachment to the winged gall which is found at Columbus, Ohio, and Austin, Tex. For a discussion of cecidomyiid galls on *Celtis occidentalis* at Columbus, Ohio, see Moser, 1954.

The thorn gall (figure 10F) is the most widespread gall on the North American hackberries. It has been collected on *C. occidentalis*, *C. laevigata*, and *C. reticulata*; further collections may extend its geographic distribution to the western States and its host range to *C. tenuifolia*. Although galls appear the same throughout the country, the species may be separated into three populations on the basis of the larval spatulas (figure 4D). H. F. Barnes and R. H. Foote (personal communications) think the differences may be enough to call the populations separate species. Galls of the Ithaca population were found at Ithaca, N.Y., and McKees Half Falls, Pa.; those of the Columbus population were collected at Columbus, Ohio, and Alexandria, La., and the third population is known only from the vicinity of Austin, Tex.

The nomenclature of the thorn gall is complex. C. V. Riley in Packard, 1890, described the gall (not the insect), but gave the description a number, not a name. Patton, 1897, gave the name *Cecidomyiaceltis spiniformis* to Riley's description, but failed to designate a type or type locality. Riley's material is in the U.S. National Museum.

The material is in six lots, each lot on a pin, and composed of several leaves with galls on each leaf. Most of the pins contain little or no data, but one pin has a label which reads 107L. This number refers to a Hopkins-number card that contains the following data: "Columbus, Texas; July 79. Mostly lower side but occasionally upper. Box 11/60." The author designates 107L to be lectotype of *Phytophaga spiniformis* (Patton).

From the foregoing discussion, the synonymy is as follows:

Phytophaga Spiniformis (Patton)

"No. 34" Riley, in Packard, 1890:614.

Cecidomyia-celtis spiniformis Patton, 1807: 248.

Cecidomyia unguicola Beutenmuller, 1907: 388; Felt, 1911: 457; Wells, 1916: 269, XVII, Fig. 8, 8a; Felt, 1918: 124; 1925: 64; 1940: 231.

Cecidomyia spiniformis (Patton), Felt, 1911: 458; 1918: 124; 1925: 62; 1940: 231; Smith, 1953: 110.

In summary, the name of the Texas population is *P. spiniformis*, but populations from other areas of the country may be different species. Male genitalia of specimens from other locations must be compared with the Texas population before their taxonomic status is known.

Pitcher, 1955, working with *Thomasiniana* found that Dyar's law held good for the head-capsule width of that genus, and also that differences in the respiratory system, epidermal texture, and development of the sternal spatula enabled one clearly to distinguish the instars. The writer repeated his measurements as closely as possible for the larva of *Phytophaga* sp. (figure 4). When instars are compared, it is found that head-capsule and sternal spatula lengths overlap, but that body length does not. As in *Thomasiniana*, qualitative characters are the best taxonomic characters for quick identification. The results are summarized in table 5.

The thorn gall is attached to the leaf longer than any other cecidomyiid gall on hackberry with which the writer is familiar. Other species were not observed to last on the leaf more than 1 month. The thorn gall grows more slowly, and is present for at least 3 months. This presumably allows the gall to be attacked by more parasites (figure 30). The gall is almost always present on the lower surface of the leaf, although rarely it is on the upper surface. This is true for most cecidomyiid galls of hackberry.

Most growth of the thorn gall occurs when the larva is in its second instar (figure 30), as compared to the first instar for *Pachypsylla*

celtidismamma. Galls reach a mean height of 2.7 mm. in the second larval instar, and gradually grow to 3.3 mm. as the larva reaches third instar. After feeding, the larva forms a cocoon, and the gall begins to dry. This drying causes the gall to shrink slightly, to about 3.1 mm., and drop from the leaf almost a month before leaf fall (figure 29). The galls of *Pachysylla* are not detachable and fall with the leaf.

Table 5. Comparative morphology of the larval instars of *Phytophaga* sp.

Character	Statistic	Instar		
		I	II	III
Length of body (extended)	Mean	0.36	0.72	1.71
	Minimum	0.30	0.50	1.30
	Maximum	0.40	1.10	2.00
	s	0.05	0.17	0.22
	n	7	30	30
Diameter of head-capsule (mm.)	Mean	0.039	0.048	0.063
	Minimum	0.036	0.038	0.552
	Maximum	0.041	0.065	0.792
	s	0.002	0.005	0.006
	n	7	30	30
Length of sternal spatula (mm.)	Mean		0.064	0.072
	Minimum		0.050	0.060
	Maximum		0.072	0.089
	s		0.005	0.008
	n	7	30	30
Respiratory system		Meta-pneustic	Peri-pneustic	Peri-pneustic
Sternal spatula		Absent	Present	Present
Epidermis	Texture	Smooth	Smooth	Papillate
	Microspines	Present	Present	Absent
	Setae	None	Strong	Weak
Color of body		Translucent white	Translucent white	Milk white

Part II

Natural Enemies - Keys, Descriptions, and Biologies

This part is divided into two sections: A. natural enemies of the psyllid galls, and B. natural enemies of the cecidomyiid gall. Each section begins with a key to adults reared from, and larvae found inside the galls. Discussions of individual species follow the keys.

A difficulty that appeared early in the study was that 10 of the 19 natural enemies were undescribed species. Four of these species are here described for the first time. However, adults of some species were not reared, making descriptions impossible, and in other cases no specialist could be found to describe them.

A. Natural Enemies of Psyllid Gall Makers

The 14 natural enemies of psyllid gall makers were of four types: primary parasites, secondary parasites, parasites from the hackberry leaf miners complex, and gall feeders.

Primary parasites were most abundant and contributed greatly to mortality of psyllids. Abundance of the other three categories were infrequent to rare.

Keys to insects associated with galls of *Pachypsylla*

I. KEY TO THE ADULTS

- | | |
|--|---|
| 1. Mouthparts piercing-sucking (<i>Pachypsylla</i>)..... | 2 |
| 1'. Mouthparts chewing or lapping..... | 3 |

2. Length of body seldom more than 2.5 mm.; aedeagus of male with blunt apex; ventral valve of female genital segment suddenly narrowed ventrally for apical third

Pachypsylla celtidisvesicula

- 2'. Length of body seldom less than 3.0 mm.; aedeagus of male with a ventral hook; ventral valve of female genital segment evenly narrowed to apex

Pachypsylla celtidismamma

3. Two wings *Parallelodiplosis acernea*
- 3'. Four wings 4
4. Front wings horny (weevil)..... *Conotrachelus buehneri*
- 4'. Front wings membranous (wasps)..... 5
5. Ovipositor-sheaths longer than thorax (*Torymus*)..... 6
- 5'. Ovipositor-sheaths shorter than thorax..... 7
6. Ovipositor-sheaths less than twice the length of thorax ($\bar{x} = 1.557$); hind tibia black (figure 15A)

Torymus vesiculus

- 6'. Ovipositor-sheaths more than twice the length of thorax ($\bar{x} = 2.20$); hind tibia the same color as femur

Torymus pachyphyllae

7. Tarsi four segmented..... 8
- 7'. Tarsi five segmented..... 10
8. Body black *Hypertetrastichus ithacus*
- 8'. Body yellow and/or green..... 9
9. Body yellow with metallic-green stripes... *Moserina maculata*
- 9'. Body metallic-green *Achrysocharis vesiculis*
10. Body shining black..... *Eurytoma semivenae*
- 10'. Body metallic-green *Psyllaephagus pachyphyllae*

II. KEY TO MOST DISTINCTIVE IMMATURE STAGES

1. Pupa; inside fourth-instar "puparium" of *Pachypsylla* (figure 10C) *Psyllaephagus pachyphyllae*
- 1'. Larva, external 2
2. Body yellow *Parallelodiplosis acernea*
- 2'. Body white 3
3. Body glabrous 4
- 3'. Body hairy 6
4. Body terete, much longer than wide; conspicuous "humps" present on dorsal surface (figure 10A)
Hypertetrastichus ithacus
- 4'. Body oval; dorsal surface smooth, no more irregular than lower surface 5
5. Mandibles prominent; the remains of *P. celtidisvesicula* fifth-instar nymph in gall; cavity of gall full of whitish

brown pellets; blister gall only (figure 10D)

Achrysocharis vesiculis

- 5'. Mandibles difficult to see; first-, second-, or third-instar remains of *Pachyipsylla* nymph inside gall; gall clean (figure 10A) *Moserina maculata*
6. Head distinctly sclerotized and separate from body; mouthparts somewhat reduced but present; eyes present; nipple gall only *Conotrachelus buehanani*
- 6'. Head ill defined and about the same color as the body; mouthparts reduced to two sharp opposable mandibles; eyes absent 7
7. Head not sunken into body; dorsal aspect when viewed from the front appearing flat with a V-shaped notch, thus presenting a heart-shaped appearance; only one row of sensory setae per segment; humps on back prominent when body extended (figure 22D) *Eurytoma semivivae*
- 7'. Posterior part of head sunken into body, ill defined, dorsal aspect when viewed from the front is round; at least on the prothoracic segment several rows of sensory setae of various lengths; humps on back never prominent 8
8. Body never more than 1.5 mm. in length; at least abdominal segments 6, 7, 8, and 9 with one ill-defined row of setae (best seen when larva is cleared and mounted on slide); blister galls only (figures 14, 15B) *Torymus vesiculus*
- 8'. Body never less than 2.0 mm. in length; at least abdominal segments 6, 7, 8, and 9 with two ill-defined rows of setae; nipple galls only (figures 16, 22E) *Torymus pachyipsyllae*

Moserina maculata Delucchi 1962

(Hymenoptera: Eulophidae, Entedontinae)

= *Chrysochariodes* Moser 1956; Jensen 1957

Moserina maculata is a primary internal parasite of the first-, second-, and third-instar nymphs of *Pachyipsylla celtidisvesicula* and *Pachyipsylla celtidismamma*. It is the most common parasite, and attacks 60 percent of the nymphs of *P. celtidisvesicula*. Adults of the first generation emerge in spring from the previous year's fallen leaves about the time that leaf tissue starts to form around the first-instar nymphs. *Moserina* oviposits into nymphs in galls from the top of the leaf.

After feeding, larvae escaped from inside the nymphs. These larvae were small, shrunken, translucent, with large yellow guts. However, they soon increased about four times in volume and appeared turgid,

fat, white opaque, and the gut could not be seen (figures 5, 6B). The two forms looked very different superficially, but when mounted on a slide and examined microscopically they appeared the same, except for size. This final growth was probably caused by the larva consuming gall tissue. Feeding was most evident in young nipple galls (figure 6B).

Only the large forms pupated. The prepupal stage lasted about 24 hours, and the pupal stage lasted about 9 days. Pupae turned black about 3 hours after pupation, except for the abdomen, which remained white and turned yellow about 2 days before emergence.

There was one complete generation during the summer, making a total of two generations per year (figure 31). After August 1, few adults were seen in the field and none by mid-August. Last instar larvae in galls went into an obligatory diapause, and did not pupate until refrigerated. Only large forms of larvae overwintered. These were almost twice as big as similar mature larvae from the preceding summer generation, probably because host nymphs and galls were larger.

Adults of both sexes walked in a dancelike motion, apparently moving farther sideways than forward. Adults of other chalcidoids in this study walked more or less in a straight line.

Nipple-gall forms (figure 6C) were much larger, but less common. Nipple galls are thicker and harder than blister galls, and *Moserina* may not have been able to penetrate them as easily with its ovipositor. A few larvae overwintered in nipple galls, especially in cavities of marginal galls which had thinner walls. Marginal galls were more accessible to *Moserina* than the more centrally located cavities of *Pachypsylla celtidismamma*.

M. maculata is a widespread species, collected from South Dakota, Minnesota, Kansas, Oklahoma, Texas, Arkansas, Tennessee, Ohio, West Virginia, Pennsylvania, New York, North Carolina, Georgia, and Louisiana.

Hypertetrastichus New Genus **(Hymenoptera: Eulophidae, Tetrastichinae)**

Diagnosis: The best character distinguishing the genus *Hypertetrastichus* from all other members of the subfamily Tetrastichinae of the family Eulophidae is the four-segmented funicle of the female antenna.

Type Species. Hypertetrastichus ithacus **Hypertetrastichus ithacus n. sp.**

Quadrastichodella sp. Moser, 1956, J. Kans. Ent. Soc. 29(2) : 57-62.
Quadrastichodella sp. Jensen, 1957, Hilgardia 27(2) : 71-99.

Female. Figure 7. Length of body (tip of abdomen, not including ovipositor, to head inclusive) 0.8 to 1.50 mm.. ($\bar{x} = 1.15$ mm., $s = 0.16$ mm., $n = 55$), all specimens measured in alcohol. Head and body black, shining; antennal scape black on basal half and yellow on apical half, pedicel and flagellum yellow; coxae and femora black, trochanter brown, tibiae and tarsi white with apical segment of each foretarsus brown.

Antennae inserted at ventral level of compound eyes, apices of scapes reaching two-thirds of the way from insertion to ventral margin of anterior ocellus; length of malar space five-ninths as great as height of compound eye; ocellocular line half as long as postocellar line. Mesoscutum four-fifths as long as wide and bearing two rows of bristles, each row with two bristles each of which are equidistant between the midline and lateral margin. Submarginal vein of forewing bearing two dorsal bristles; marginal vein four times as long as stigmal; median lengths of propodeum and postscutellum equal. Surface of propodeum smooth, median carina prominent, diameter of propodeal spiracle twice as great as width of space separating it from anterior propodeal margin; gaster 1.4 times larger than thorax and head combined; apex of ovipositor sheaths usually slightly exceeding apex of gaster.

Male. Unknown; the author believes it does not exist.

Type locality. Ithaca, N.Y.

Type depository. Female type deposited in the U.S. National Museum.

Range. Ithaca, N.Y., Columbus, Ohio, and Morgantown, W. Va.

Material examined. 55 female specimens from Ithaca, N.Y.

Biology. *H. ithacus* is an external obligatory parasite that parasitizes 9 percent of the *Moserina* population. No males have been found. It attacks the last-instar larva and pupa of the host. The first adult females apparently emerge about the same time as the *Moserina* adults, although in much fewer numbers. The larva (figures 8, 10A) does not enter diapause in midsummer like its host, but continues to attack *Moserina* until late fall. Length of a generation is about 1 month, but the exact number is obscure because the generations overlap in late summer and fall. It overwinters as a last instar larva inside blister galls and nipple galls. *H. ithacus* is much less common than its host, but there is a large emergence of adults about the first or second week in August. Adults can be easily collected at that time on the underside of the leaves where most of the oviposition takes place. Occasionally, adult females oviposit through to top of the leaf. The pupa remains white until about 36 hours before emergence, when

it turns partially black. The pupa of *Moserina* turns black almost immediately after pupation; this affords a good character for the separation of the pupae of the two species.

Parallelodiplosis acernea Felt 1907²
(Diptera: Cecidomyiidae)

This species is a fatal inquiline of both psyllids, and infests about 1 percent of galls. Oviposition begins by June 16, and continues until at least August 1. Eggs are laid parallel to leaf veins or perpendicular to side of gall (figure 10E). They usually occur singly, but three or four may be found together. First-instar larvae bore into galls and enter cavities with psyllid nymphs. As many as three young larvae were found in blister galls, and as many as 10 in nipple galls. However, never more than one survives to the final (third) instar.

Psyllid nymphs always die after larvae of *Parallelodiplosis* reach the third instar. Nymphs do not appear injured, and may die of starvation caused by competition for food. Apparently the larvae feed by sucking juices from galls. Most nymphs die in the fourth instar, but some in the third and fifth instars. Blister galls turn brown and dry soon after nymphs die. It appears then, that the inquiline must allow gall maker to remain alive until larva ceases feeding. Otherwise gall would die and cut off food supply of inquiline. Larvae overwinter inside galls.

Similar larvae were collected from psyllid and cecidomyiid galls at Columbus, Ohio, Raleigh, N.C., and St. Paul, Minn. They probably represent several species, and some form cocoons inside galls in the fall.

The three instars (figure 9) can be easily separated by qualitative and quantitative characters summarized in table 6. Due to scarcity of material, figures are not based on large numbers.

Leptacis sp.
(Hymenoptera: Platygasteridae)

One female was observed June 16, 1957, ovipositing in eggs of *Parallelodiplosis acernea*. Specimen is deposited at U.S. National Museum.

² G. Steyskal and A. Stone (U.S. Nat. Mus.) report that reared adults agree with types of *P. acernea* Felt 1907, N.Y. State Mus. Bull. 110 (22d Rep. State Ent. for 1906): 143. Felt's types are from soft maple, but other specimens at the Museum were collected from deformed chokeberry fruit at Stow, Mass.

Table 6. Comparative morphology of the larval instars of
Parallelodiplosis acernea

Character	Statistic	Egg	I	II	III
Body length extended (mm.)	Mean	0.39	0.54	1.09	2.09
	Minimum	0.35	0.35	0.90	1.60
	Maximum	0.40	0.60	1.40	2.50
	s	0.02	0.09	0.19	0.29
	n	8	7	5	13
Head capsule (mm.)	Mean		0.027	0.037	0.050
	Minimum		0.024	0.036	—
	Maximum		0.031	0.038	—
	s		0.003	0.001	—
	n		7	5	1
Sternal spatula length (mm.)	Mean		None	None	0.137
	n		7	5	1
Respiratory system			Meta- pneustic	Peri- pneustic	Peri- pneustic
Sternal spatula			Pseudo- spatula	Absent	Present
Epidermis	Texture		Smooth	Smooth	Papillate
	Microspines		None	None	None
	Setae		Weak	Strong	Strong
Body color			Yellow	Yellow	Yellow

Psyllaephagus pachypsyllae (Howard) 1885

The genus *Psyllaephagus* contains 11 described species; four from North America and two from Europe. All are parasites of family Psyllidae. *P. pachypsyllae* was designated as type of genus by Ashmead in 1900. Walton (1960) noted abundance of *P. pachypsyllae* around New York City, and established that it attacks the fourth-instar nymph. Moser (1956) states that it attacks all hackberry psyllids north of Mexico.

At Ithaca, *P. pachypsyllae* was the first parasite adult seen in field (May 9, 1957), and attacked first-instar nymphs of both psyllids before they formed galls. During oviposition, psyllid nymphs were often lifted off the leaf with sting, moved about, and otherwise roughly handled — but with no ill effects. Nymphs live normal life until the fourth instar (sometimes fifth) when the parasite larvae suddenly mushrooms in size (figure 10C). Nymphs swell to about three times their normal size, but remain alive until the larva reaches full size; only the essential organs remain unconsumed inside nymph. The parasite then defecates and pupates inside nymph which dies, and

turns from a milk-white to a dark-brown color. The pupa soon turns black and overwinters inside host skin in gall. Diapause is obligatory, but adult will emerge in 14 days if pupa is refrigerated for 90 days at 6° C. Other parasites attack psyllids before they reach the fourth-instar, and many dormant larvae of *P. pachypsyllae* inside nymphs may be killed. Pupae of *P. pachypsyllae* were collected from 4 percent of nymphs in fall.

Specimens of *P. pachypsyllae* are recorded from Idaho, Colorado, New Mexico, Utah, Texas, Kansas, Minnesota, Arkansas, Louisiana, Tennessee, Ohio, New York, Pennsylvania, North and South Carolina.

***Achrysocharis vesiculis* n. sp.**
(Hymenoptera: Eulophidae)

(All measurements made from dried specimens)

Female. (figures 11, 13). Length of body (tip of abdomen, not including ovipositor sheathes, to head, inclusive) 1.0 — 1.6 mm., $\bar{x} = 1.4$ mm., $s = 0.18$ mm., $n = 14$. Antennae inserted dorsal of ventral margins of compound eyes but ventral of center of frons, apex of scape reaching dorsal margin of anterior ocellus, scape white on side next to head but dark on outside surface, giving antennae dark appearance; antennal formula 11123, basal part of first funicular segment broken; height of compound eye three times as long as malar space, lower half of eyes clothed with *very* short hairs; postocellar line twice as long as ocellocular line; mandibles with two teeth; maximum width of mesopraescutum 1.3 times wider than long, one bristle present at each lateral margin halfway between cephalic and caudal ends of sclerite, surface of mesopraescutum, scutellum, metanotum and *propodeum* heavily reticulated; submarginal vein of forewing with two dorsal bristles, marginal vein six times as long as stigmal, infuscation of front wing light, heaviest around stigma and becoming obscure about midway to lower edge of wing; apex of hind wing pointed; fringe at posterior margin one-third as wide as wing at hamuli; mesoscutellum bearing one bristle on each side; proximal one-fourth of hind tibia dark; propodeum as heavily reticulated as scutellum, paraspicular carinae absent, medial length of propodeum one-third as long as median length of mesoscutellum; gaster boat-shaped, slightly longer than head and alitrunk combined, maximum width of abdomen slightly wider than thorax, gaster clothed

with short pubescence except on dorsum of first, second, and third segments, dorsum alternately shagreened and polished at each segment except first, second, and third segments; gaster pointed at apex and sheaths of ovipositor slightly produced.

Six specimens examined from Austin, Tex., appear the same as those from Ithaca, N.Y. Length of five specimens = 1.6 mm., and one = 1.9 mm.

Male. (figures 12, 13). Characters same as female except: length of two specimens 0.9 and 1.3 mm. Height of compound eye six times as long as malar space, no hairs on lower half of compound eyes; marginal vein five times as long as stigmal, infuscation of front wing very light, not heavy around stigma and extending at most to an imaginary line halfway to lower edge of wing; fringe at posterior margin of hind wing one-half as wide as wing at hamuli; proximal one-fourth of hind tibia dark on some specimens but light in others; gaster flat and almost as long as head and alitrunk combined; maximum widths of gaster and thorax about equal; white spot on gaster rather obscure and on caudal one-sixth of the first segment and cephalic half of second segment, remainder of gaster shagreened.

Two specimens examined from Austin, Tex., appear the same except for larger size (1.2 and 1.3 mm.); bodies not distorted upon drying like specimens from Ithaca, N.Y., proximal one-fourth of hind tibia white.

Type locality. Ithaca, N.Y.

Type depository. Female type deposited in the U.S. National Museum, Washington, D.C.

Range. Ithaca, N.Y.; Austin, Tex.

Material examined. 24 females and 7 males from Ithaca, N.Y.; 6 females and 2 males from Austin, Tex.

Part III contains a discussion of the taxonomic status of the species.

Biology. *Achrysocharis vesiculis* is a common, primary, internal parasite of fifth-instar (rarely fourth) nymphs of *Pachypsylla celtidisvesicula*. It parasitized 12 percent of nymphs in the Cayuga Valley, but only 1 to 7 percent on slopes of valley.

A few immature larvae were found inside nymphs of *P. celtidisvesicula* and large numbers of adults were observed ovipositing in galls by August 26; oviposition always was under leaf. No adults were observed in the field after September 14. Wings of the female were not held erect during oviposition like those of *Achrysocharis spiniformis*.

The larva of this species is similar to *Achrysocharis spiniformis* (figure 23). The last-instar larva (figure 10D) emerges from the

nymph, eats all of the host skin except the tail, and overwinters as a larva in gall. The pupa of *A. vesiculis* darkens within 1 day after pupation.

A. vesiculis and *A. spiniformis* adults are similar in appearance, and Part III contains a key for their separation.

***Torymus vesiculus* Moser 1956**

(Hymenoptera: Torymidae)

Torymus vesiculis is a common, external parasite of the fourth- and fifth-instar (rarely the third) nymphs of *Pachypsylla celtidis-vesicula*. It parasitizes 16 — 24 percent of nymphs at lower elevations, but practically none on slopes of Cayuga Valley, although host is abundant at both locations.

Oviposition takes about $\frac{1}{2}$ hour. Nymph is stung and paralyzed and egg is laid beside the host. *T. vesiculus* almost always oviposits on the underside of the leaf, but the author observed it ovipositing once on top of the leaf. During oviposition the female is attached firmly to the gall. If the body is pulled, the thorax will separate from abdomen before the ovipositor detaches.

The immature larva sucks contents from nymph and then eats the skin except the tail. Nymphal instar attacked can be determined by counting number of spines on tail.

The pupal period lasts about 2 weeks, and adult emerges inside the gall. The adult (figure 15A) cuts a circular hole in the top of the leaf and escapes. Emergence holes of *T. vesiculus* can be readily distinguished from the more numerous holes of *Moserina*. *T. vesiculus* holes average 0.5 mm. in diameter, whereas those of *Moserina* average 0.3 mm.

Males and females emerge at the same time and in about the same numbers. Males are rarely seen on leaves as are females. Instead, they usually "flit" in groups at tips of the leaves. Mating was not observed.

There are two generations per year at Ithaca. The first (summer) generation attacks the third-, fourth-, and possibly the early fifth-instar nymph. Second generation adults attack fifth-instar nymphs starting about September 5. Some of the first generation and all of the second generation overwinter as mature larvae in galls. The larva (figures 14B, 15B) will pupate without refrigeration.

Apparently *T. vesiculus* will attack *Pachypsylla celtidismamma* in special instances, although none was observed at Ithaca. The writer has one such record for Columbus, Ohio, and one for Nyack, N.Y.

Moser (1956) gives an account of the biology of this species at Columbus, Ohio. *T. vesiculus* is widespread, and has been collected in Idaho, Colorado, Texas, Minnesota, Ohio, New York, Massachusetts, West Virginia, North Carolina, and Georgia.

***Torymus pachypsyllae* (Ashmead) 1888** **(Hymenoptera: Torymidae)**

Although the name of this species is almost 70 years old, nothing has been published on its biology, and the name is often missing from taxonomic works (e.g. Huber, 1927).

Torymus pachypsyllae is closely related to *Torymus vesiculus* and the biology of their immature stages is similar. Unlike *T. vesiculus*, which is rarely found above the floor of the Cayuga Valley, *T. pachypsyllae* is common at all elevations, and was present in 25 percent of the nipple galls. Morphological differences between *T. vesiculus* and *T. pachypsyllae* are discussed in the appendix.

Fifth-instar larvae of *T. vesiculus* are less susceptible to disease in the laboratory. When larvae of both species are placed in stender dishes containing wet peat moss at room temperature, larvae of *T. vesiculus* are unaffected, while those of *T. pachypsyllae* (figures 16, 22E) are attacked by fungus. However, larvae of *T. pachypsyllae* survive (figure 17) if only a trace of water is added to the peat moss.

T. pachypsyllae is recorded from Colorado, New Mexico, Ohio, New York, West Virginia, Pennsylvania, and North Carolina.

***Eurytoma semivenae* Bugbee 1957** **(Hymenoptera: Eurytomidae)**

Eurytoma semivenae was one of four new species described by Bugbee, 1957, from galls on hackberry. At Ithaca, it was usually found in nipple galls, although Bugbee, 1957, showed that it was common in blister galls on *Celtis laevigata* and *C. reticulata*. *E. semivenae* apparently fed on any inhabitant of galls, but occurred in less than 1 percent of galls.

Hosts were stung and paralyzed. Eggs were distinguished from those of other chalcidoid larvae by their black color (figures 18A,

22C). Usually one, but as many as three eggs were found in galls, but never more than one larva. Presence of several hatched eggs with larva indicated cannibalism.

The larva is similar in shape, color, and size to *Torymus pachypsylae*, but distinguished by the heart-shaped head, sparse setae, and "humps" on dorsal surface. The larva feeds similar to that of *T. pachypsylae*, first sucking contents of host, and then eating skin. The skin is not eaten until the larva reaches the fourth- or fifth-instar. After consuming the host, the larva feeds on the inner wall of gall, a phytophagous habit fairly common for the genus. Larvae occasionally break into marginal galls and consume inhabitants. Larvae were usually found feeding on paralyzed, fifth-instar larvae of *Torymus pachypsylae*. In one instance a larva in a blister gall was seen feeding on an immature larva of *Achrysocharis vesiculis*, which was still inside the host nymph. Larvae occasionally break into marginal galls inside the host nymph. Larvae in rearing dishes commonly consumed other parasite larvae, indicating that although hosts are stung in nature, larvae may be able to feed on hosts that somehow escape stinging.

A whitish-brown material (figure 22D) is always found in the gall with the larva. A murexide test made on the material by Dr. R. L. Patton gave a red color, which showed a purine base, probably uric acid. The material may be excreted through the integument when the larva molts. Similar substances are recorded for other species of *Eurytoma*, and were also seen with *Achrysocharis vesiculis* (figure 10D).

E. semivivae has a summer and a winter generation at Ithaca, N.Y. Larvae of the latter overwinter in galls, but eggs of summer generation do not appear in galls until July. Specimens are known from Idaho, Colorado, New Mexico, Texas, Oklahoma, Kansas, South Carolina, North Carolina, West Virginia, Ohio, and New York.

Conotrachelus buchanani Schoof 1942

(Coleoptera: Curculionidae)

Conotrachelus buchanani is an uncommon phytophagous weevil that feeds solely on tissue of nipple galls at Ithaca, but always kills the gall maker in the process. Larvae were found in 3 percent of the galls at most collecting localities.

According to Schoof (1942), *C. buchanani* is closely related to the plum curculio, *Conotrachelus nenuphar* (Herbst). He further states that the weevil is apparently restricted to *Celtis*.

The larva consumes the inside of the nipple gall and leaves a characteristic black frass. It kills the nymph in the gall, and soon the outside of the gall turns brown. After feeding, the mature larva drops to the ground, forms a cell in the soil, and pupates. Mature larvae formed cells and pupated in the laboratory when put on damp peat moss in a stender dish. Pupal period for one male was 19 days. Teneral adults require 3 days to color and 2 weeks for the scales on body to reach mature form. Recently emerged adults feed readily on the outside of nipple galls, making small deep circular pits with beak, but will die soon after food is removed. Dr. Donald Anderson compared genitalia of reared male with drawing of the type and found that they were alike.

There is one generation per year at Ithaca, the adult overwintering. Specimens of *C. buchanani* are recorded from Texas, Kansas, Iowa, Ohio, New York, and Pennsylvania.

Other parasites of *Pachypsylla* (Hymenoptera: Eulophidae)

Last instar larvae of *Sympiesis massasoit* Crawford 1913, *Sympiesis lexingtonensis* Girault 1917, and *Euderus* sp. were each found once in nipple galls. All were reared to adults. They are parasites of the two *Lithocolletis* leaf miners that commonly occur on hackberry in late summer and fall.

An internal parasite of *Torymus vesiculus* was collected twice, once from a fifth-instar larva and once from a pupa. Both collections were made on September 7, 1957. Attempts at rearing failed, but the larva appeared to belong to the family Eulophidae.

B. Natural enemies of cecidomyiid gall maker

Natural enemies of *Phytophaga* sp. were less diverse in habits and fewer in number than those of psyllids. A species of *Achrysocharis* was the only parasite closely related to a parasite of psyllids.

Keys to insects associated with *Phytophaga* sp.

I. KEY TO THE ADULTS

1. Wings vestigial *Eupelmella vesicularis*
- 1'. Wings present 2

2. Two wings *Phytophaga* sp.
- 2'. Four wings 3
3. Wing veins completely absent *Trichacis* sp.
- 3'. Wing veins present along upper margin of wings 4
4. Ovipositor exerted, as long as thorax *Torymus diabolus*
- 4'. Ovipositor not exerted 5
5. Thorax dull brown or black *Tetrastichus nebraskensis*
- 5'. Thorax metallic green *Achrysocharis spiniformis*

II. KEY TO THE MOST DISTINCTIVE IMMATURE STAGES

1. Mouthparts styletlike, parallel; spatula present on body;
the gall maker. Figure 4 *Phytophaga* sp.
- 1'. Mouthparts biting, with definite mandibles that cross;
spatula absent 2
2. Body with numerous setae 3
- 2'. Body without setae, glabrous 4
3. Remains of egg as shown in figure 22B present
Torymus diabolus
- 3'. Remains of egg not as shown in figure 22B
Eupelmella vesicularis
4. Larva inside host 5
- 4'. Larva outside host 6
5. Body of unusual form, mostly composed of a "cephalo-
thorax"; "tail" deeply forked; mandibles one third as long
as body. Figure 19A First-instar *Trichacis* sp.
- 5'. Head and mandibles normal, composing less than one tenth
of body length Immature *Achrysocharis spiniformis*
6. Body oval, more than half as wide as long; prominent "col-
lar" on prothorax; body when put on slide and cleared has
spiracles reduced. Figure 23A, B
Last-instar *Achrysocharis spiniformis*
- 6'. Body cigar-shaped, less than half as wide as long; collar
absent; spiracles large and prominent when larvae put on
slide and examined under the compound microscope
Tetrastichus nebraskensis

Trichacis sp.

(Hymenoptera: Platygasteridae)

Trichacis sp. is a primary, internal parasite of the larva of *Phyto-
phaga* sp. It has one generation per year. First-instar larvae (fig-
ure 19) were found inside second- and third-instar larvae of *Phyto-*

phaga sp. by June 18. One mature *Trichacis* larva and three white pupae were collected August 5, 1957. By August 5, 1957, 90 percent of the *Phytophaga* larvae had stopped feeding and had formed cocoons, and larvae and pupae of *Trichacis* suddenly appeared. This suggests that termination of feeding by the host may cause *Trichacis* to begin larval development. By mid-September, diapausing, winged adults were found within host skins where they overwintered. Adults became active only after refrigeration at 6° C. for 90 days. Some first-instar larvae were also found in fall.

The only extensive study of *Trichacis* is by Marchal, 1906, who reported the following facts about *Trichacis remulus* Walker: (1) it is monembryonic (*Platygaster* and other closely related genera are often polyembryonic); (2) it oviposits in egg or first-instar larva; (3) the first-instar larva encysts in the posterior part of the nerve cord of the host until resumption of development.

Specimens of *Trichacis* were collected from Texas, Ohio, New York, and Pennsylvania.

***Torymus diabolus* n. sp.** **(Hymenoptera: Torymidae)**

This description is based on a single specimen reared from *Phytophaga* sp. at Ithaca, N.Y., collected August 20, 1957. The larva was extracted from the thorn gall, and refrigerated at 4° C. for 140 days. It transformed into a pupa after being warmed to room temperature; pupal period lasted 13 days. Adult emerged February 5, 1958, and lived 3 days in a vial with sugar water. Measurements are from a dried specimen.

Female (figure 20). Length of body 1.4 mm. (tip of abdomen, not including ovipositor, to head, inclusive), length of ovipositor sheathes 0.8 mm.; head metallic green, slightly longer than wide and clothed with suberect white hairs, carina around eyes extended at upper lateral corners into points giving distinct "horned" appearance; antennal formula 11173, antennae inserted just above level of ventral margin of compound eyes, apex of scape just reaching anterior ocellus, scape yellow except for apical one-fourth which is dark brown like remainder of the antennae, first funicle segment smallest and funicle segments gradually increasing in size to last segment (next to club) which is largest, pedicel slightly longer than last funicle segment; height of compound eyes three times as high as malar space; ocellocular line four-sevenths as long as postocellar line; maximum width of mesoprae-

scutum 1.1 times wider than long, parapsidal grooves weak; maximum width of scutellum 1.1 times wider than long, cross-furrow absent; propodeum shagreened like rest of alitrunk, paraspiracular carinae absent, propodeum one-third as long as scutellum; submarginal vein of forewing with 11 bristles, marginal vein five times as long as submarginal, apex of hind wing rounded, fringe at posterior margin one-seventh as wide as wing at hamuli; tarsi of all legs white with last segment dark, coxae, femora and tibia of front legs tan, middle legs brownish-tan and hind legs brown; abdomen as long as alitrunk, maximum width of abdomen shorter than thorax, length of ovipositor longer than thorax but shorter than head and thorax combined.

Male. Not reared

Biology. This external primary parasite has only one generation per year. The author has never observed oviposition at Ithaca, N.Y., but a female was seen ovipositing at the base of a thorn gall on May 31, 1954, at Columbus, Ohio.

Unlike the torymid parasites of psyllids, which sting host and lay egg free in galls, *T. diabolus* does not sting host and suspends egg (figure 22B). About a week later, larva hatches (figure 21A) and usually fastens to the host larva. However, feeding does not begin until host larva reaches third-instar, and is sufficiently large to support the parasite. Many parasite larvae started to develop by late July, but some first-instar larvae were still seen in galls by late August. Once the first-instar larva starts feeding, it develops to a mature larva in about 1 week.

The last-instar larva (figure 21C, D) overwinters inside the gall on the ground. One adult female reared at Columbus, Ohio, lived 53 days in captivity in a vial with sugar water as food.

First-instar larvae were found in about 23 percent of the galls, but last-instar larvae were found in only 1 percent or less, probably because of competition from *Achrysocharis spiniformis*. Occasionally, *Torymus* attacked *A. spiniformis*.

Type Depository - USNM

Material examined - 1 ♀ from Ithaca, NY

Achrysocharis spiniformis n. sp.

(Hymenoptera: Eulophidae)

All measurements made from dried specimens. Appendix 2 gives a discussion of the taxonomic status of this species.

Female (figure 24). Length of body (tip of abdomen, not including ovipositor sheaths, to head inclusive) 1.3 — 1.8 mm., $\bar{x}$ — 1.5 mm., s — 0.20 mm., n = 5. Antennae inserted dorsal of ventral margins

of compound eyes but ventrad of center of frons, apex of scape reaching dorsal margin of anterior ocellus, scape white on basal half and dark on anterior half; antennal formula 11123, basal part of first funicular segment broken; height of compound eye four and one-half times as long as malar space, lower one-half of eyes clothed with *very* short hairs; postocellar line twice as long as ocellocular line; mandibles with two teeth; maximum width of mesopraescutum 1.3 times wider than long, one bristle present at each lateral margin halfway between cephalic and caudal ends of sclerite, surface of mesopraescutum, scutellum and metanotum heavily reticulated; submarginal vein of forewing with two dorsal bristles, marginal vein seven times as long as stigmal, infuscation of front wing dark, heaviest around stigma and extending down to lower edges of wing; apex of hind wing pointed, fringe at posterior margin one-sixth as wide as wing at hamuli; mesoscutellum bearing one bristle on each side; hind femora white; surface of propodeum much more lightly reticulated than scutellum, appearing almost smooth, paraspicular carinae absent, median length of propodeum one-fourth as long as median length of mesoscutellum; gaster boat-shaped, slightly longer than head and alitrunk combined, maximum widths of thorax and gaster equal, gaster clothed with short silvery pubescence, dorsum alternately shagreened and polished at each segment, the shagreened parts becoming more polished at the cephalic end, gaster pointed at apex and sheaths of ovipositor slightly produced.

Four specimens from Columbus, Ohio, appear the same except that average size is larger ($\bar{x} = 1.7$ mm.), and bodies do not distort upon drying like specimens from Ithaca, N.Y.

Male (figure 25). Characters the same as female except: length 0.7 — 1.1 mm., $\bar{x} = 0.89$ mm., $s = 0.13$ mm., $n = 9$. Antenna with scape darkened entire length except for white strip on inside basal one-half, basal part of first funicle segment not broken; lower one-half of eyes without short hairs; marginal vein of front wing six times as long as stigmal vein, infuscation heaviest around stigma but extending slightly past an imaginary line one-half way to lower edge of wing; fringe at lower margin of hind wing one-half as wide as wing at hamuli; gaster flat, almost as long, or as long, as head and alitrunk combined, thorax slightly wider than gaster, cephalic one-third of gaster with an almost transparent white spot, caudal two-thirds of gaster shagreened.

Three specimens from Columbus, Ohio, appear the same except for larger average body size $\bar{x} = 1.2$ mm.

Type locality. Ithaca, N.Y.

Type depository. Female type deposited in the U.S. National Museum, Washington, D.C.

Range. Ithaca, N.Y.; McKees Half Falls, Pa.; Columbus, Ohio; and Austin, Tex.

Material examined. 16 females and 61 males from Ithaca, N.Y.; four females and three males from Columbus, Ohio.

Biology. *Achrysocharis spiniformis* is a primary internal parasite that feeds on second- and third-instar larvae of *Phytophaga* sp. It is the most common parasite found in thorn galls, and exhibits 88 to 100 percent parasitism under favorable conditions.

On July 16, 1957, two ovipositing females were seen on the lower surface of a leaf on which 15 galls were present. Their search for galls was slow and deliberate, during which they frequently held their wings vertically. In this position the characteristic strips on the wings could easily be seen. When a gall was found, she mounted and examined it carefully with her antennae as she circled the gall repeatedly. Oviposition time lasted from 3 to 5 minutes, after which she either rested or began searching for more galls.

The host larva was always stung and paralyzed and remained fresh for about 10 days. Then the body contents rapidly began to dissolve into a liquescent mass, and were entirely consumed after 3 to 4 days. The larva then egressed and ate the skin. Second-instar larvae of *Phytophaga* that were stung always had a conspicuous oviposition-puncture, and usually an immature *A. spiniformis* larva inside. However, active, second-instar larvae were sometimes found with an oviposition-puncture, but without a larva of *A. spiniformis* inside, indicating that stinging alone may not cause paralysis. Many paralyzed, third-instar *Phytophaga* larvae with larvae of *A. spiniformis* inside were found without oviposition-punctures. This may mean that stung, second-instar, host larvae were able to moult into the third instar, after which the larva of the parasite developed. Active second- or third-instar larvae of *Phytophaga* without punctures never contained larvae of *A. spiniformis*, although frequently first-instar larvae of *Trichacis* were seen.

Achrysocharis will sting and lay eggs in host larvae even though other parasites are already present. Stung, liquescent larvae of *Phytophaga* were frequently found inside galls alongside a first-instar larva of *Torymus*, leaving the latter without a host.

Adults of *A. spiniformis* from overwintering galls were seen by July 16 when *Phytophaga* larvae were mostly in the second instar. A month or more may be required to complete the cycle from egg to adult in the summer. The pupal period lasts 14 to 15 days. The first (summer) generation began to escape from galls by August 3, in the laboratory. Parasite larvae extracted from galls after September 1

were presumably of the second summer generation. Larvae and pupae in the laboratory did not enter diapause.

Adults of both species of *Achrysocharis* may be found on the same hackberry leaf, and are separated by the key in Part III.

***Tetrastichus nebraskensis* (Girault) 1916** **(Hymenoptera: Eulophidae)**

T. nebraskensis attacks chiefly gall midges. Burks, 1943, and Guppy, 1956, reported it from the clover-seed midge and Judd, 1958, collected it at London, Ontario, from *Rhabdophaga* nr. *rhodoides* Walsh that makes galls on the sandbar willow. The writer has records of it from the thorn gall at Ithaca, N.Y.; McKees Half Falls, Pa.; and Columbus, Ohio; also from *Pachypsylla* ~~?~~^{*umbilicus*} Riley (large blister gall) at Dallas, Tex.

T. nebraskensis was rare in thorn galls at Ithaca, N.Y., but appeared to be much more common at McKees Half Falls, Pa., about 50 miles south of Ithaca.

One immature larva collected at Ithaca (July 16, 1956) was feeding on a larva of *Achrysocharis spiniformis*, but four immature larvae collected at McKees Half Falls August 15, 1957, were feeding on larvae of *Phytophaga* sp. Another larva of *Tetrastichus*, which had fed on a pupa of *A. spiniformis*, was also found at the latter locality. In summary, it seems that *T. nebraskensis*, like *Eurytoma semivenae*, feeds upon whatever happens to be in the gall. The largest emergence of *T. nebraskensis* appears to be at gall fall.

***Eupelmella vesicularis* (Retzius) 1783** **(Hymenoptera: Eulophidae)**

This species was seen only once, and may be classed as an "accidental" parasite. It was collected August 21, 1957, as an adult female still inside the gall, but active and ready to emerge. The specimen was very small (1.0 mm. in length), but Burks, 1957, (personal communication), was satisfied that it was *E. vesicularis*, although he stated that it must have been greatly undernourished. A normal specimen (2.5 mm. in length) was collected sweeping by Edward Menhinick September 1, 1957, at Beebe Lake on the Cornell campus.

E. vesicularis is one of the most versatile chalcidoid species known. It is recorded as a primary and secondary parasite of Diptera, Coleoptera, Hymenoptera, Lepidoptera, Homoptera, and Orthoptera.

Part III

Miscellaneous Notes on Life Histories and Interrelationships

Discussion

Host specificity of the natural enemies (figure 32). Although cecidomyiid and psyllid galls often occurred on the same leaf, no parasites of psyllid nymphs attacked cecidomyiid larvae or vice versa.

Natural enemies of psyllid nymphs were of four types: primary parasites, secondary parasites, parasites from the hackberry leaf miner complex, and gall feeders. Habits of the primary parasites were diverse. *Moserina maculata* and *Psyllaephagus pachyphsyllae* were internal parasites. They attacked early-instar nymphs of both psyllids. *Torymus pachyphsyllae*, *T. vesiculus*, and *Achrysocharis vesiculis* were external parasites of late-instar nymphs, and with one exception, fed only on one species of psyllid. Primary parasites of early-instar nymphs were either attracted to exposed nymphs, or attacked both psyllid galls indiscriminately. There is evidence that at least one primary parasite of late-instar was attracted by the gall. *Torymus pachyphsyllae*, normally a parasite of late-instar nymphs, of *P. celtidis-mamma*, also attacked late-instar nymphs of *P. celtidisvesicula* when the latter produced marginal galls on nipple galls. Although *T. pachyphsyllae* was never found in blister galls, its presence in marginal galls showed that its larvae were capable of developing on nymphs of *P. celtidisvesicula*. From this it is concluded that ovipositing females of *T. pachyphsyllae* were attracted not by the host nymph, but by the gall. Other primary parasites of late-instar nymphs may be attracted in a similar manner. Four species of secondary parasites were found in psyllid galls. *Eurytoma semivenae* usually attacked primary parasites, but occasionally fed on psyllid nymphs. The other three apparently attacked only primary parasites.

Conotrachelus buchanani and *Parallelodiplosis acernea* fed only on galls, but always killed the psyllid nymph in the process. The former ate only nipple galls, but the latter was found inside both psyllid galls. Certain primary and secondary parasites consumed tissue inside galls after devouring the host. In fact, *Moserina* larvae apparently would not pupate until they had fed on gall tissue. *Eurytoma* larvae usually ate gall tissue, and it was suspected that larvae of *Torymus pachypsylae* and *Achrysocharis vesiculis* fed similarly.

Three parasites of the hackberry lepidopterous leaf miner complex were found once each in nipple galls.

Three primary parasites, two external and one internal, attacked *Phytophaga* larvae in thorn galls. Two secondary parasites were found in galls, but both were general feeders, and not specific to the thorn gall complex.

Relative abundance of gall makers and parasites. It was obvious at the beginning of the study that some gall makers and parasites were more common than others. One objective of the study was to learn reasons for this. Blister galls outnumbered nipple and thorn galls 100:1 or more in the Cayuga Valley, although numbers of the three galls fluctuated greatly between localities. Parasite populations also differed between localities, and in some instances, the absence of a parasite in an area resulted in a high population of the gall maker. This was most apparent for the thorn gall. For instance, in one locality *Achrysocharis spiniformis* was never found. Correspondingly, thorn galls were abundant. Although the occurrence of low numbers of a parasite in an area was sometimes a reason for the abundance of a certain gall, it was not determined why blister galls outnumbered the other two galls. Parasites do not seem to be the answer, because blister gall nymphs were as heavily parasitized as the other two gall makers. Perhaps *P. celtidisvesicula* had a greater biological potential, or was better adapted to *Celtis occidentalis* than the other two species. At Alexandria, La., however, thorn galls on *Celtis laevigata* number about the same as at Ithaca, N.Y., but seem to outnumber blister galls which are uncommon. It appears, then, that *P. celtidisvesicula* does not thrive as well on *C. laevigata* as on *C. occidentalis*, and the abundance of a gall in any particular area of the country may depend greatly on how well it is adapted to the host tree.

Only certain of the primary parasites were common in galls. Other primary parasites, secondary parasites, parasites from lepidopterous leaf miner complexes, general parasites, and gall feeders were uncommon or rare.

Ability of the young larva to develop quickly seemed to favor the abundance of some primary parasites over others. For instance,

Achrysocharis spiniformis was usually able to compete favorably with *Torymus diabolus* and *Trichacis* sp. because young larvae of *A. spiniformis* consumed the cecidomyiid larvae before the latter two came out of diapause (figure 29). Likewise, many young larvae of *Psyllaephagus* may not have been able to develop inside psyllid nymphs because other parasites ate the host first (figures 26 and 27).

The three parasites with delayed larval development, *Psyllaephagus*, *Torymus diabolus*, and *Trichacis* sp., were relatively large but, unlike other large parasites, they laid their eggs on or in very young host larvae or nymphs. Thus the young larvae had to delay feeding until the host was large enough to consume. In the meantime, however, the host was often eaten by another parasite.

Elevation affected the abundance and distribution of at least one parasite, *Torymus vesiculus*. This species was abundant in the bottom of the Cayuga Valley, but became rare above 50 feet on the sides of the valley, even though abundant host material was available. The closely related species, *T. pachypsyllae*, was common at all elevations.

Miscellaneous parasites such as those from leaf miner complexes and general parasites were probably not abundant because their life cycles were not synchronized with those of the gall makers. Although numerous secondary parasites were present, none greatly reduced numbers of the primary parasites.

In summary, primary parasites were the most abundant natural enemies, and competition between them seemed to affect numbers of individual species more than any other factor.

A method of separating *Torymus vesiculus* and *Torymus pachypsyllae* by means of the analysis of covariance

Specimens of *Torymus vesiculus* reared from blister galls differed from specimens of *Torymus pachypsyllae* reared from nipple galls in the following respects: (1) specimens reared from nipple galls were larger than those reared from blister galls, but the host of the nipple gall *Torymus* was correspondingly larger, (2) the relative length of the ovipositor when compared to the thorax was greater for *T. pachypsyllae* than for *T. vesiculus*.

The first observation is difficult to test, but the second was tested by the analysis of covariance according to Snedecor, 1956, (p. 395). The regression coefficient for *T. vesiculus* was 1.713 and for *T. pachypsyllae* was 1.940, but they were not found to be significant ($F = 0.5377$) when a test for the homogeneity of regression coefficients was made. When variances were pooled and compared, how-

ever, the difference was highly significant ($F = 42.38^{**}$). The common mean for length of thorax was 0.896 mm., and the adjusted means for the length of the ovipositors were 1.48 mm. for *T. vesiculus* and 2.11 mm. for *T. pachypsylae*.

Since F for the pooled variances was highly significant and the F value obtained from the test for the homogeneity of regression coefficients was not, the conclusion is that the regression lines do not explain the differences among the ovipositor lengths. After the ovipositor lengths were adjusted to a common thorax length, they still differed significantly. Evidently the degree of change of ovipositor length to thorax length between the two species is not the same.

It might be thought that the reason for the difference between the relative size of ovipositors of the two species is that the hosts are different species. This was ruled out because specimens of *T. pachypsylae* reared from marginal galls had ovipositor lengths the same as those reared from nipple galls. It seems, therefore, that the species of host is not the primary cause of these differences in the morphology of the parasites.

Notes on the taxonomic status of *Achrysocharis vesiculus* and *A. spiniformis*

Before these two species were described, it had to be ascertained whether or not they actually belonged in the genus *Achrysocharis* which is a poorly known and difficult genus. B. D. Burks, U.S. Department of Agriculture (personal communication), stated that they belonged to the genus *Achrysocharis*. However, the European species *formosa* Westwood has been placed in *Achrysocharis*, and it was deemed best to see if the two proposed species were congeneric with the European representative. Consequently, a male and a female of *A. vesiculis* and *A. spiniformis* were sent to Dr. M. W. de V. Graham, Hope Department of Entomology, University Museum, Oxford, England. Dr. de V. Graham made a study of the problem and sent the following reply: "I was never quite satisfied about the identity of *Achrysocharis* Gir. and *Achrysocharella* Gir., so as your question was important, I took the opportunity of obtaining Girault's types of loan. These are *Achrysocharis bifasciata* and *Achrysocharella dubia*, the two type-species. Having seen these, I would say that both your species would best be placed in *Achrysocharis*. The only European species I know which fits into this genus is *lanassa* Walker (*Entedon lanassa* Walker, 1839, mon. Chalciditum 1); this is remarkably like your species, but has much finer sculpture on the

mesoscutum and scutellum, and differs in other details. I would place *formosus* Westwood, and possibly *ruforum* Krausse (*Wolffiella ruforum*) in *Achrysocharella* Gir. *Achrysocharis* and *Achrysocharella* are usually distinguished by the number of anelli (one in the former, two in the latter), but these are very hard to see well and one is not always sure of the number. I find a difference in the forewing which may be useful:

Achrysocharis Gir. — Bare strip in front of stigma just below margin of wing which is more or less delimited below a line of hairs (this character can be seen in figures 11B, 12B, 24D, 25D).
Achrysocharella Gir. — No bare strip or line of hairs (i.e., hairy throughout). Your two species have the bare strip; *Achrysocharella dubia*, and *formosus* Westwood have not."

Achrysocharis vesiculis and *A. spiniformis* are separated by the following key:

1. Ovipositor present; last abdominal sternite divided.
 Females 2
- 1'. Ovipositor absent; white spot on second abdominal segment.
 Males 3
2. Upper part of propodeum reticulated, resembling the scutellum; proximal one-fourth of hind tibia black; scutellum usually convex; wing infuscation (figure 11) extending not more than one-half across wing from stigma... *A. vesiculis* Moser
- 2'. Upper part of propodeum smooth, not resembling reticulation of the scutellum; proximal one-fourth of hind tibia white; infuscation of wing (figure 24A) extending across wing from stigma..... *A. spiniformis* Moser
3. Middle of propodeum flat or slightly rounded, not forming a ridge, sculpturing at middle resembling the scutellum; white spot on dorsum of abdomen small, nontransparent, located on the caudal one-sixth of the first segment and the cephalic one-half of the second segment..... *A. vesiculis* Moser
- 3'. Middle of propodeum forming a ridge, not flat, sculpture weak, especially on the upper part giving a smooth and shiny appearance when compared to the deeply reticulated scutellum; white spot on dorsum of abdomen large, transparent enough to allow one to see completely through the abdomen; spot completely divides the second segment, caudal one-half of the first segment of cephalic one-half of the third segment *A. spiniformis* Moser

Distribution of *Celtis occidentalis* in the drainage of the Cayuga Lake Inlet

This species inhabits banks and streams along the sides of the Inlet valley, and the bases of the surrounding hills; isolated specimens are occasionally found in the areas between streams. It is rarely found in the valley proper below the 122-meter (400-foot) level, and rarely above the 155-meter (500-foot) level on the sides of the hills. The southern limit of its distribution in the Inlet valley is 3.2 kilometers southwest of bench mark 387 at the junction of Route 13 and Seven Mile Drive. Apparently the species is not found again in great numbers until one reaches the Susquehanna River in the vicinity of Williamsport, Pa. The author has not studied the region north of the south end of Cayuga Lake, but Wiegand and Eames, 1925, state that the species is found north along the Cayuga Lake shore.

Survey of Literature

Only general papers on galls of the hackberry are considered under this heading; papers pertaining to specific subjects are discussed at appropriate points. There is an extensive literature, consisting mostly of short notes, but it can be divided into several broad categories.

The descriptive literature is mostly by Riley, and most of it is contained in Riley, 1890. Patton, 1897, gave names to many cecidomyiid galls, described by Riley, and erected a genus for them (*Cecidomyia-celtis*).

A large category of literature consists of locality lists. It is extensive and typified by Beutenmuller's paper, 1892, entitled *Catalog of gall-producing insects found within fifty miles of New York City*. Other works include Mally, 1894; Cook, 1904; Jarvis, 1907; Smith, 1909; and Felt, 1940.

There are several good papers on the anatomy of the galls and gall makers. Cook, 1903, was the first to describe the anatomy of galls of the hackberry, and used the gall of *Pachypsylla celtidismamma*. However, he did not compare it with other galls on hackberry because he was primarily interested in comparing certain structures of galls made by the genus *Pachypsylla* to galls made by other genera occurring on other plants. Wells, 1916 and 1920, published two papers on the anatomy of galls. Detailed drawings of all the galls then known on hackberry are given, together with notes on their development. Stough, 1910, exhaustively dealt with the external morphology of the adult of *Pachypsylla celtidismamma*.

There are two catalogs and three revisionary works which deal with the North American Psyllidae. The catalogs are by Van Duzee (1917) and Aulmann (1913); the revisions are studies by Crawford (1914), Caldwell (1938), and Tuthill (1943).

Some information on the biology of the gall makers is found in almost every paper, but a great deal is repetitious. The best paper is the study of *Pachypsylla celtidisgemma* by Walton, 1960. There are no extensive works on the biology of hackberry Cecidomyiidae.

Literature on natural enemies has progressed little beyond the descriptive and listing stage, although two of the chalcid parasites were described over 70 years ago.

The best paper on the chemical control of gall makers on hackberry is by Smith and Taylor, 1953. *Pachypsylla celtidisvesicula* sometimes reaches the level of economic importance because it occurs in large numbers on window screens in the fall. *Pachypsylla venusta* and the hackberry "witches-broom" mite (*Eriophyes celtis*) are at times considered economic pests because they make hackberry trees unsightly. Smith used several types of the newer organic insecticides combined with various oils, but found that none was particularly successful. He also found that time of application was very important, and that the nymphs were almost impossible to kill after the galls had formed. Regarding biological control, Moser, 1956, states "the fact that the psyllids emerge in the fall and overwinter as adults, whereas their parasites overwinter as larvae or pupae in the galls, makes it a poor practice to rake and burn the leaves of this tree because this destroys the parasitoids."

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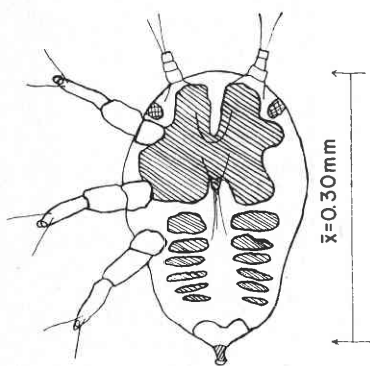
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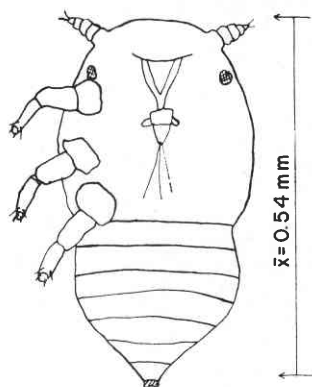
FIGURE 1

Pachypsylla celtidisvesicula, immature stages

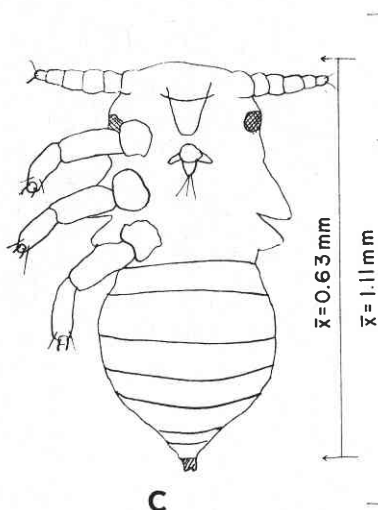
- A. First instar. Coloration of dorsal aspect. *P. celtidismamma* has no dorsal coloration.
- B. Second instar
- C. Third instar
- D. Fourth instar
- E. Fifth instar. Spines on tail are on dorsal aspect.
- F. Shape of egg in ovary.
- G. Shape of egg after it has been laid and attached to the leaf. Stalk at upper end is point of attachment to leaf. Stalk on lower end is point of attachment to ovary. Nymph emerges headfirst at lower end.



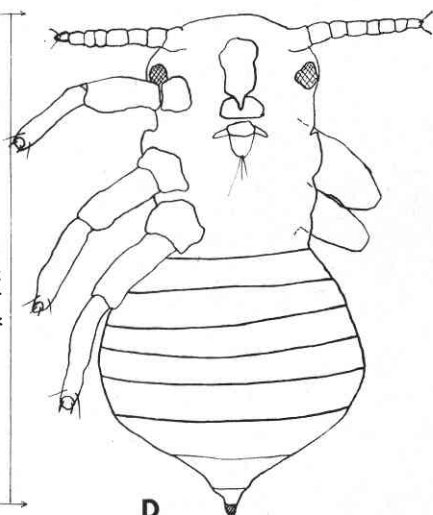
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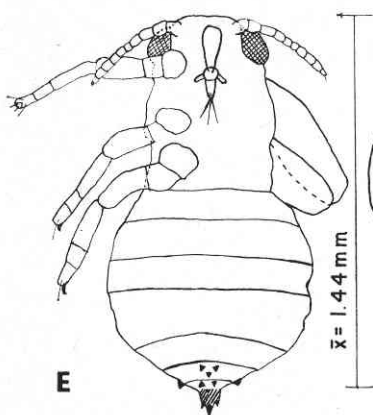
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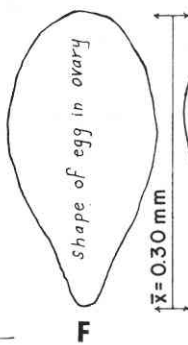
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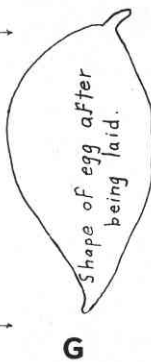
D



E



F

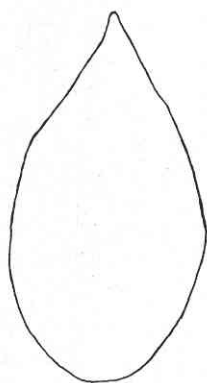


G

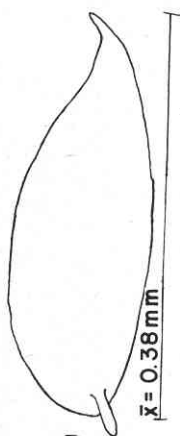
FIGURE 2

Pachypsylla celtidismamma, immature stages

- A. Shape of egg in ovary
- B. Shape of egg after it has been laid
- C. First-instar nymph
- D. Second-instar nymph
- E. Third-instar nymph
- F. Fourth-instar nymph
- G. Fifth-instar nymph

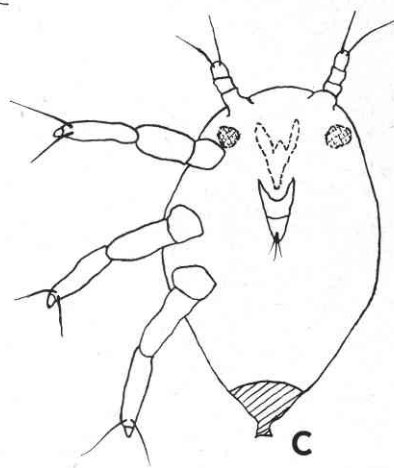


A



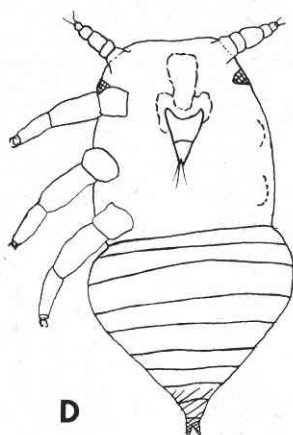
B

$\bar{x} = 0.38 \text{ mm}$



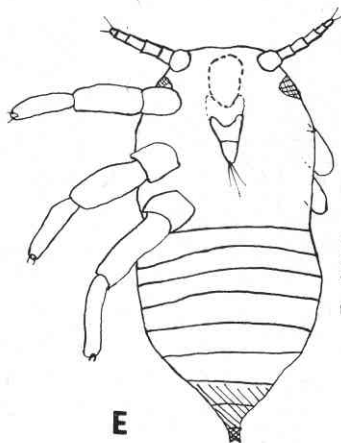
C

$\bar{x} = 0.56 \text{ mm}$



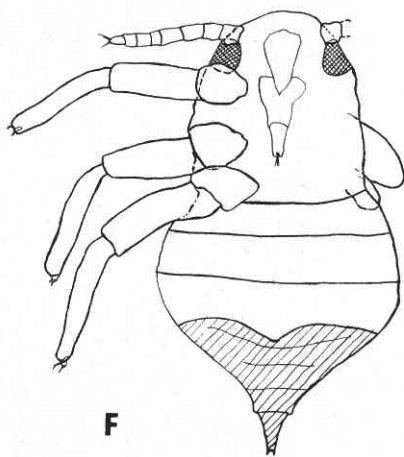
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$\bar{x} = 0.66 \text{ mm}$



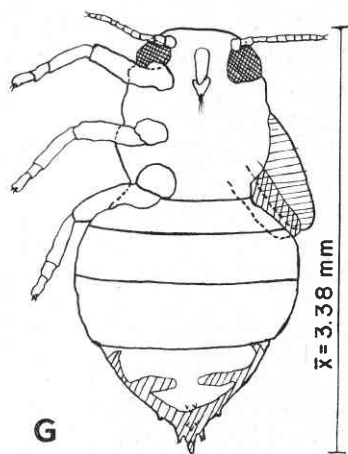
E

$\bar{x} = 1.06 \text{ mm}$



F

$\bar{x} = 1.54 \text{ mm}$



G

$\bar{x} = 3.38 \text{ mm}$

FIGURE 3

Nipple galls

- A. First-instar nymph of *Pachypsylla celtidisvesicula* on young nipple gall.
Nymph may produce marginal gall.
- B. Nipple gall with marginal cavity at left.
- C. Nipple gall containing second-instar nymph. Gall almost of mature height,
but cavity still very small. Columbus, Ohio, population.
- D. Nipple gall containing fifth-instar nymph.

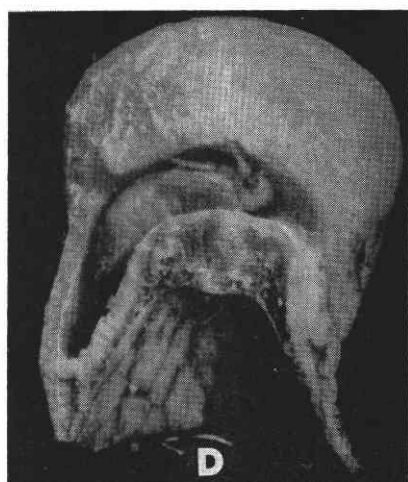
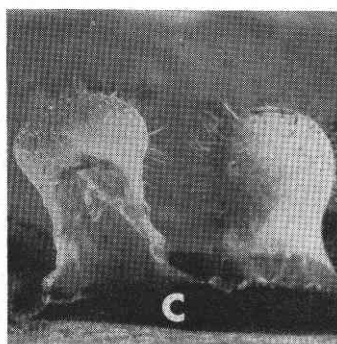
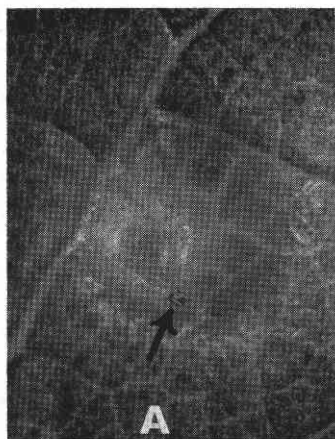


FIGURE 4

Phytophaga sp., larva

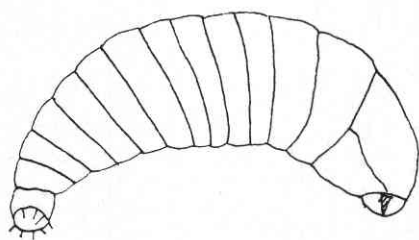
- A. First-instar larva, side view with dorsal aspect at bottom. Microspines shown only on first abdominal segment. Head shows antenna and stylets.
- B. Second instar, dorsal view (spatula on ventral aspect). Microspines shown only on third abdominal segment. Spiracle on third thoracic segment is vestigial.
- C. Second instar, side view with dorsal aspect at bottom
- D. Spatulas of third instar showing variations between Ithaca, N.Y.; Columbus, Ohio; and Austin, Tex.
- E. Third instar. Dorsal view (spatula on ventral aspect). Papillate surface shown only on third abdominal segment. Spiracle on third thoracic segment poorly developed.
- F. Third instar. Larva unextended as normally seen in gall.
- G. Third instar. Side view with dorsal aspect down. Microspines not shown, setae shown only on first thoracic segment.
- H. Third instar, ventral aspect showing details of spatula and head. Mean length = 0.20 mm., A — antenna, S — stylets.



FIGURE 5

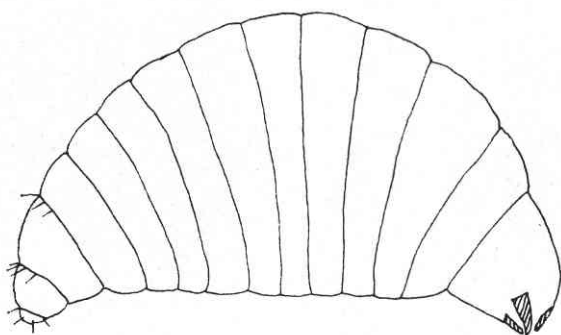
Moserina maculata, larva

- A. First instar. Lateral view. This specimen, still inside egg, was taken from inside second-instar nymph of *Pachypsylla celtidisvesicula*. The ventral portion of the head is excavated (not shown). Note disc on the 10th abdominal segment.
- B. Third instar? Lateral view. Specimen taken from inside nymph of *Pachypsylla*. Note setae on caudal segments.
- C. Last instar. Dorsal view, external.



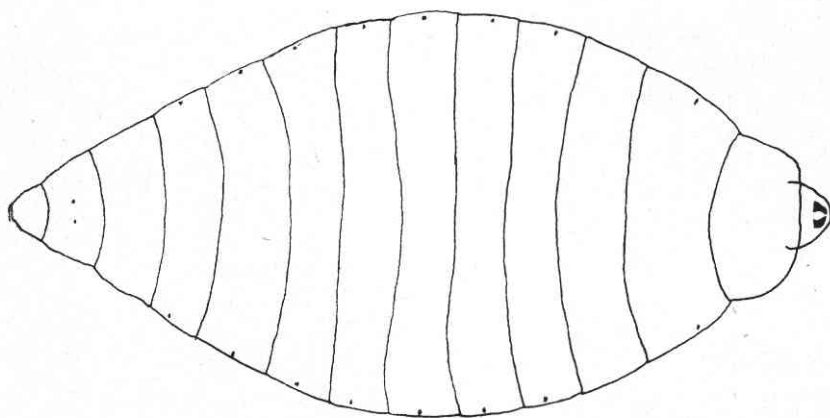
0.2 mm.

A



0.5 mm.

B



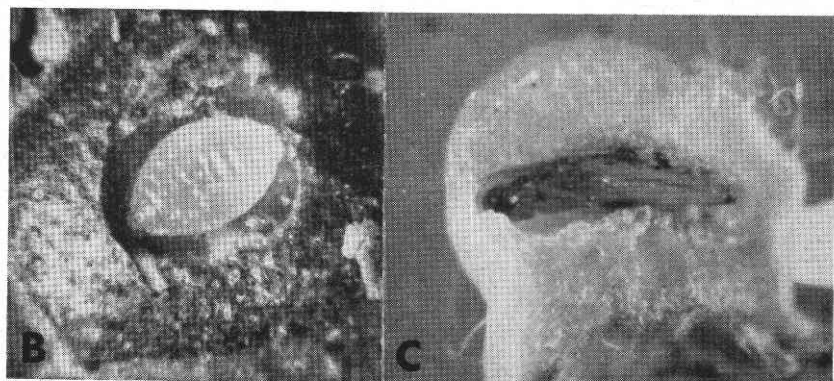
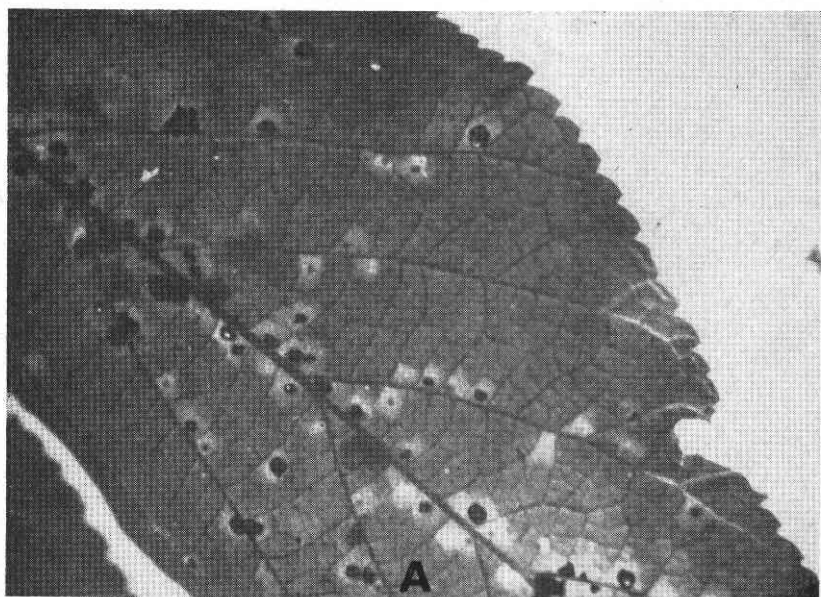
0.8 to 1.5 mm

C

FIGURE 6

Blister galls (*Pachypsylla celtidisvesicula*) infested with
Moserina maculata

- A. Lower surface of leaf showing large numbers of dead blister galls. After nymph dies, tissues of gall soon die and turn brown. Black spots indicate dead galls, lighter spots are galls that may be alive. Photograph made August 21, 1954, at Columbus, Ohio. Most parasitism of galls was by *Moserina*.
- B. Last instar larva in blister gall.
- C. Female pupa in young nipple gall. Before pupating, larva fed on gall and enlarged original cavity about five times.



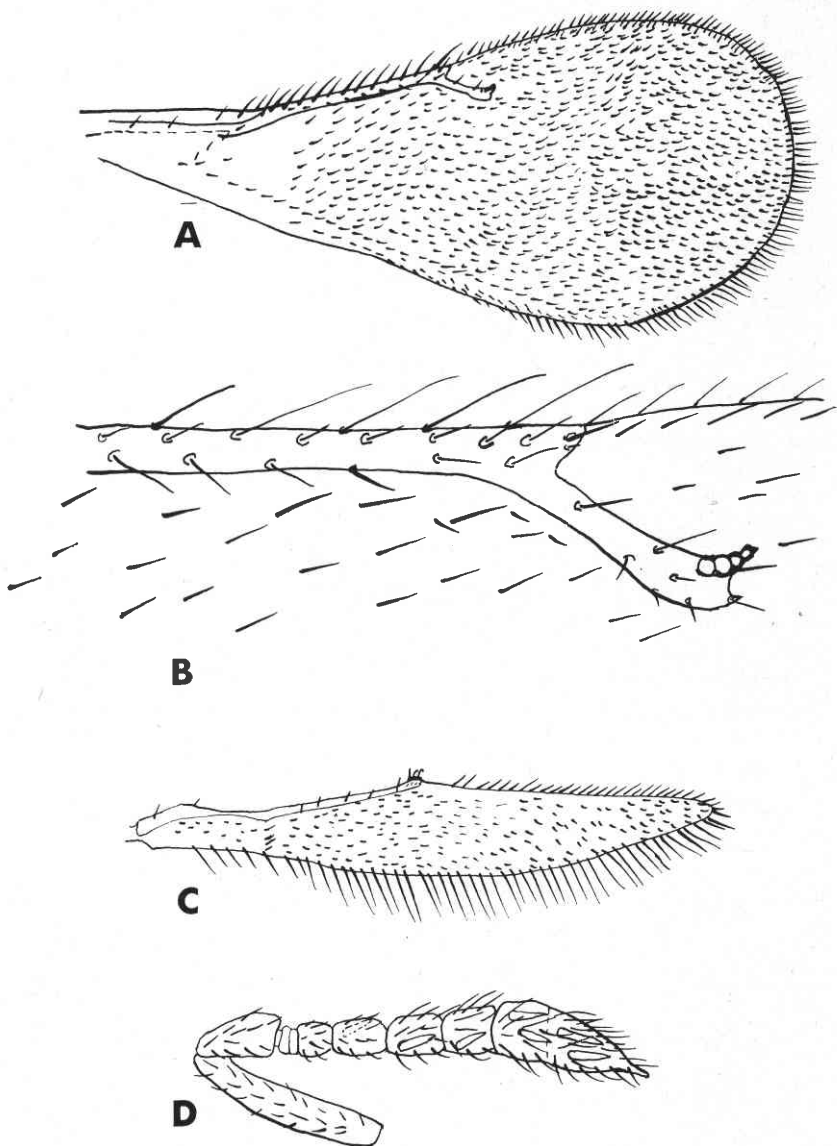


FIGURE 7

Hypertetrastichus ithacus, female

- A. Front wing
- B. Stigmal vein of front wing
- C. Hind wing
- D. Antenna

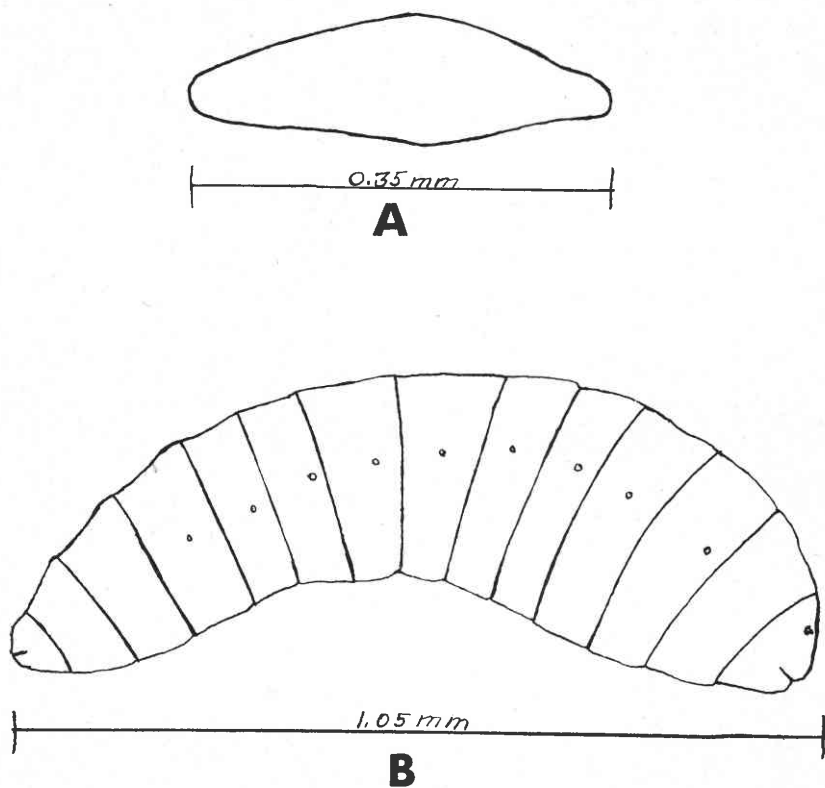


FIGURE 8

Hypertetrastichus ithacus, egg and last instar larva

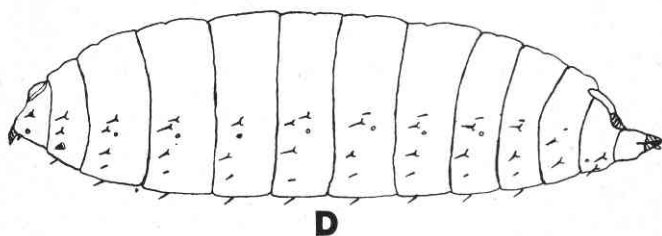
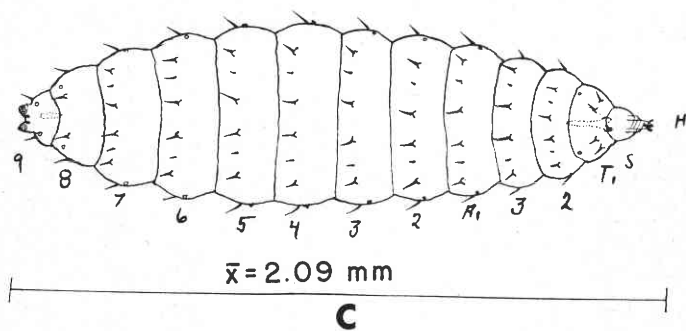
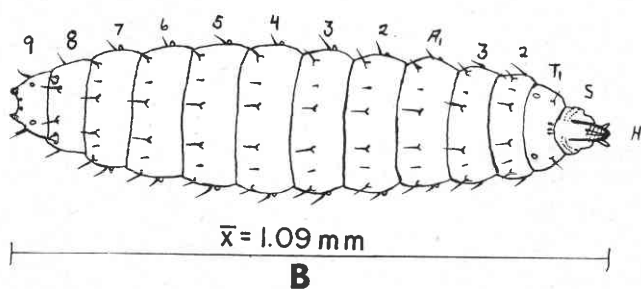
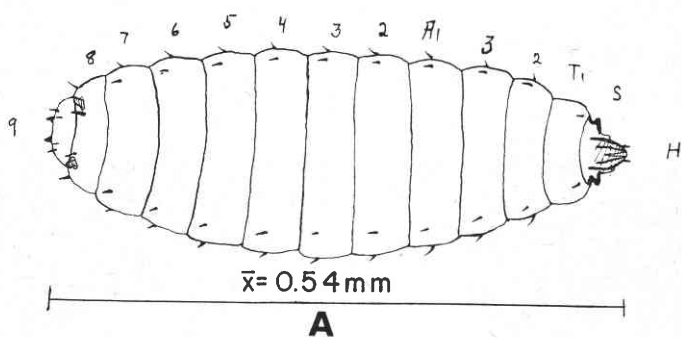
A. Egg

B. Last instar larva

FIGURE 9

Parallelodiplosis acernea, larval stages

- A. First instar, dorsal view
- B. Second instar, dorsal view
- C. Third instar, dorsal view
- D. Third instar, lateral view, dorsal aspect down



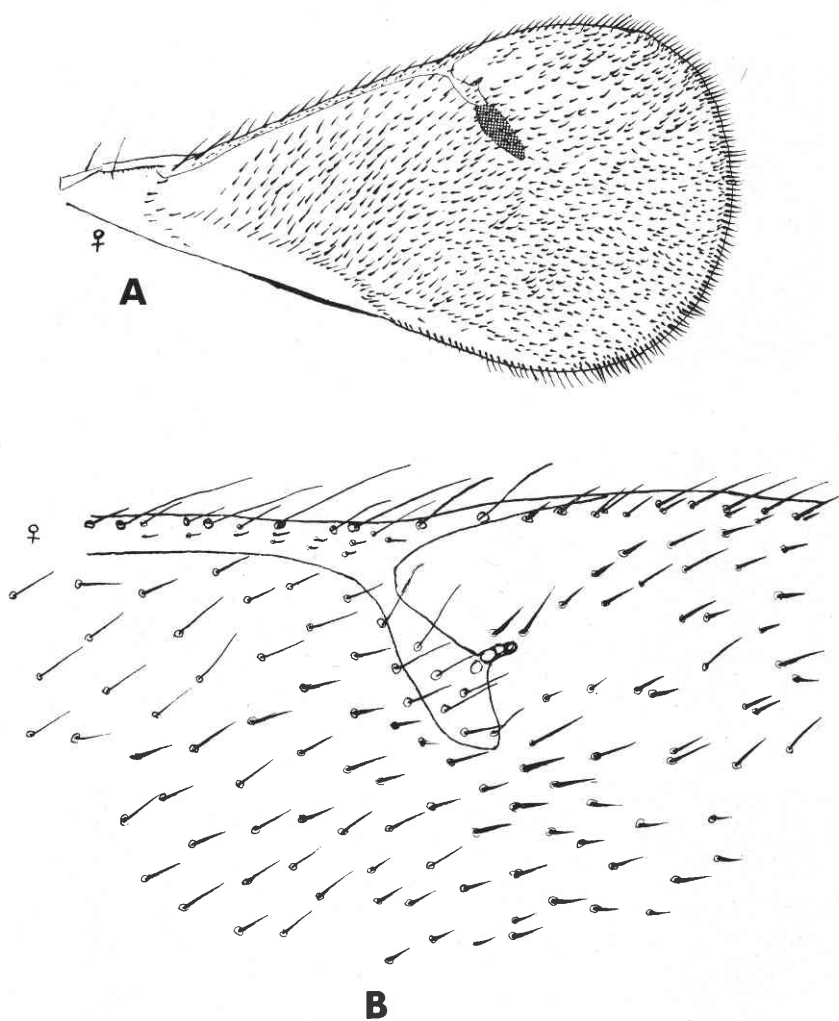


FIGURE 11

Achrysocharis vesiculis, female

- A. Front wing
- B. Stigma of front wing

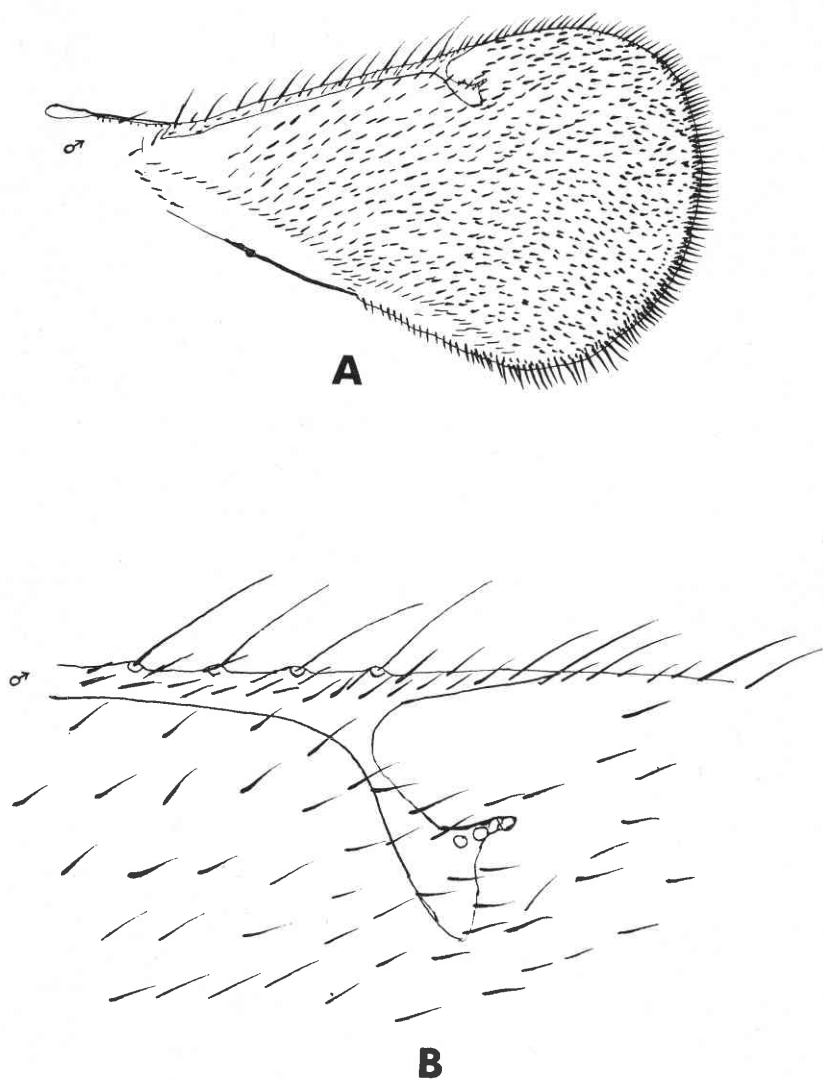


FIGURE 12

Achrysocharis vesiculis, male

- A. Front wing
- B. Stigma of front wing

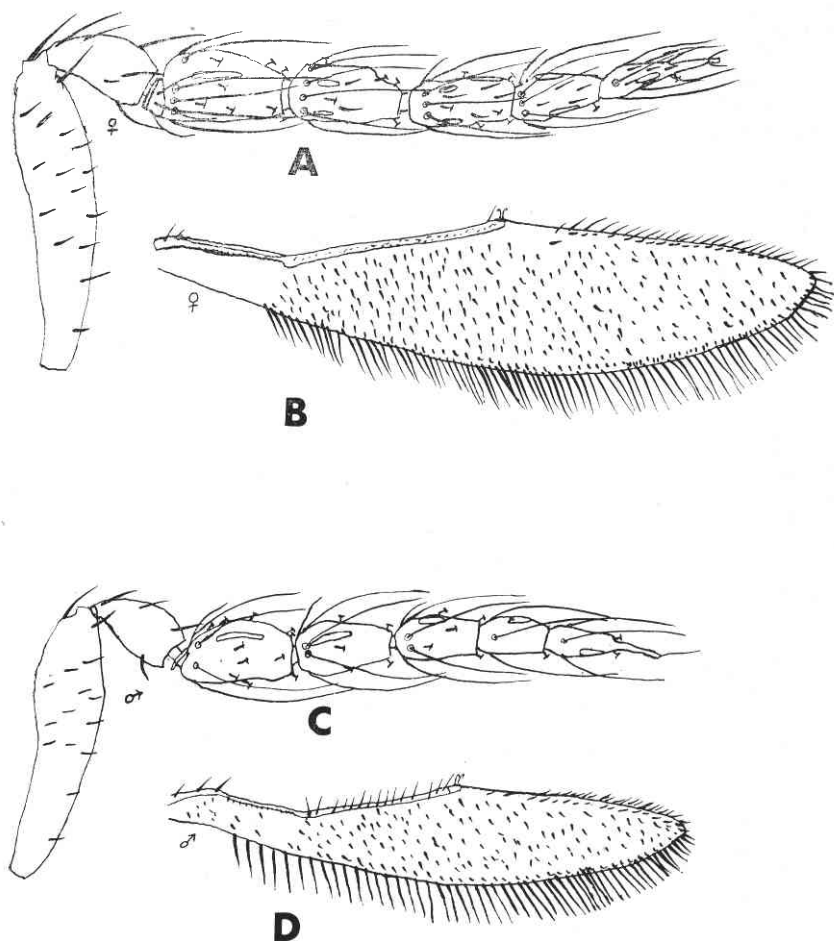


FIGURE 13

Achrysocharis vesiculis, male and female

- A. Female, antenna
- B. Female, hind wing
- C. Male, antenna
- D. Male, hind wing

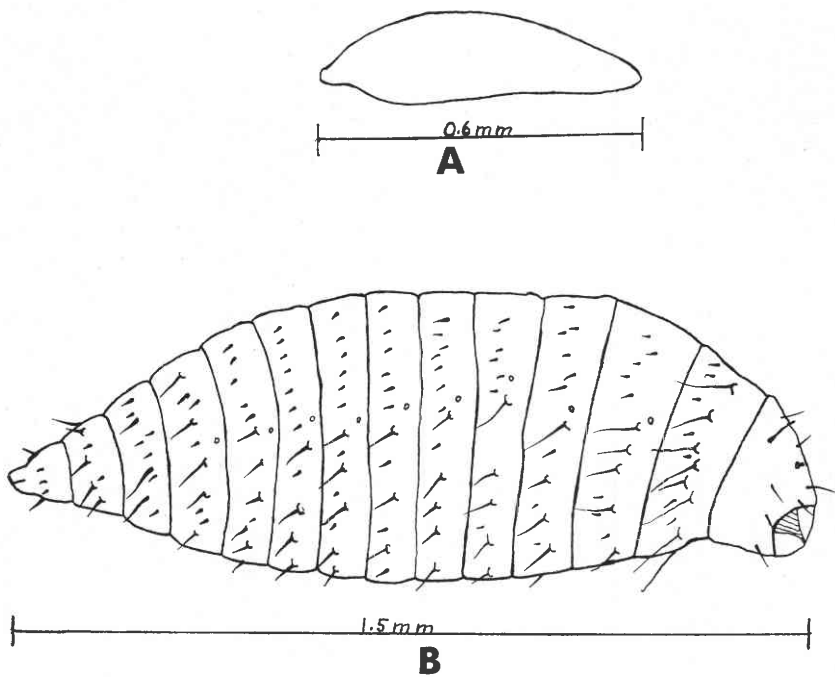


FIGURE 14

Torymus vesiculus, egg and last instar larva

A. Egg

B. Last instar larva

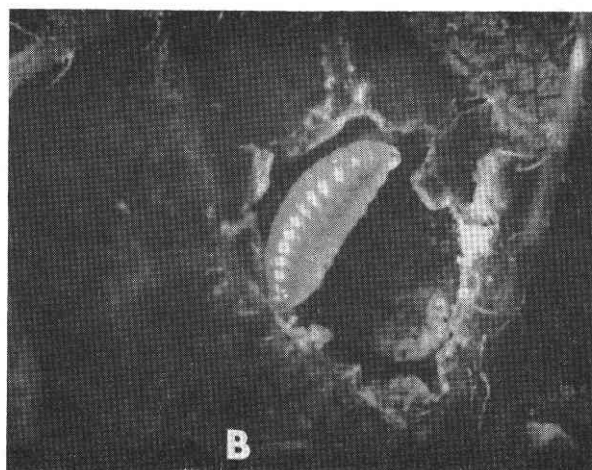
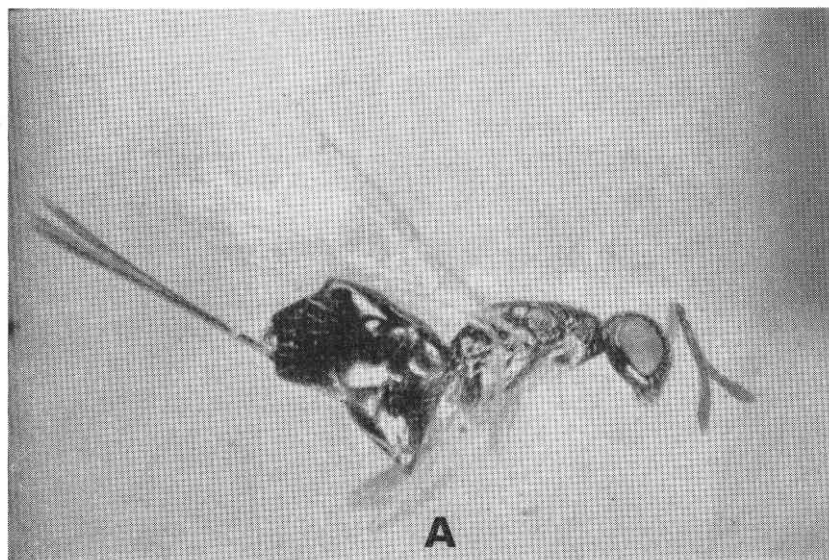


FIGURE 15

Torymus vesiculus, female and last instar larva

- A. Adult female, holotype specimen. Columbus, Ohio, population. Photo by Leland Brown.
- B. Mature, last instar larva inside blister gall. Host has been entirely consumed.

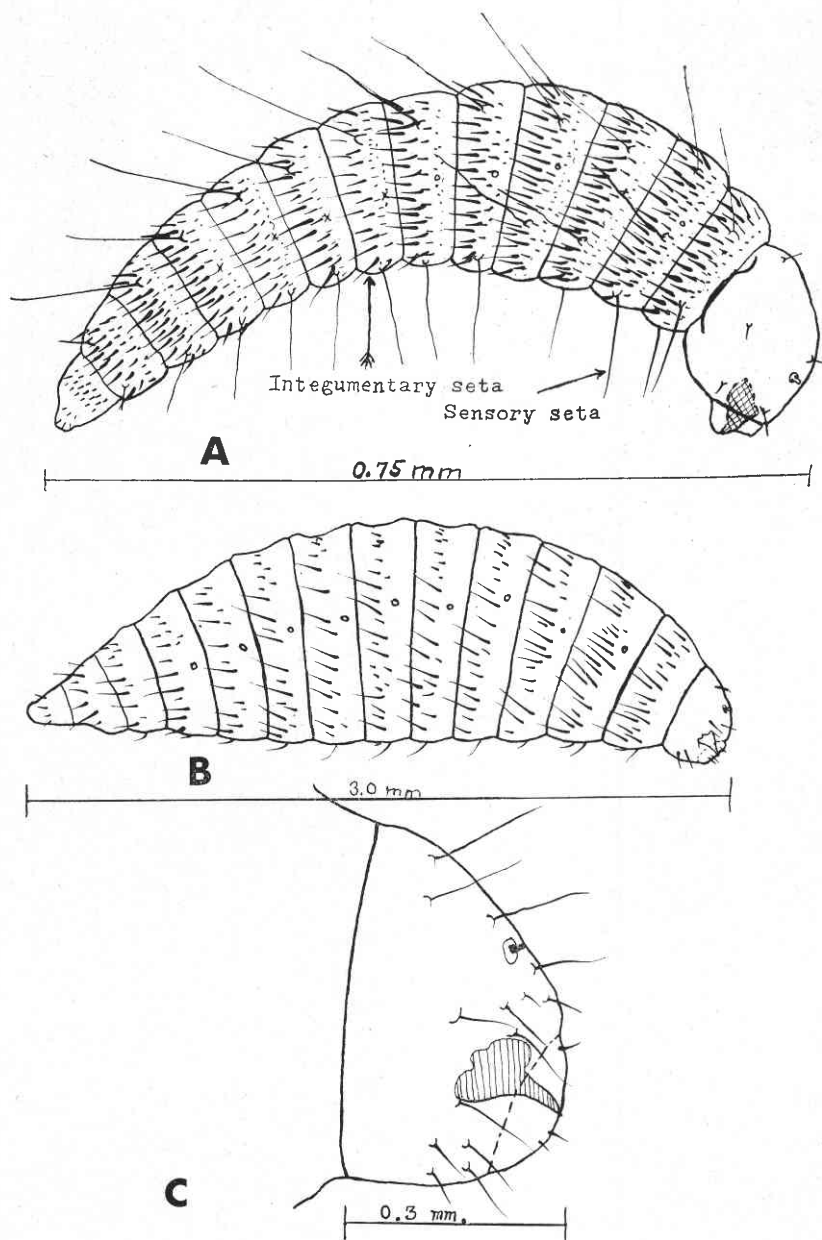


FIGURE 16

Torymus pachyphsyllae, larval stages

- A. First-instar larva
- B. Last instar larva
- C. Head of last instar larva

FIGURE 17

Torymus pachyphyllae, developmental stages of young female pupa

- A. Newly emerged pupa a few minutes after pupation
- B. Same specimen 15 minutes later
- C. Same specimen 24 minutes later
- D. Same specimen 18 hours later

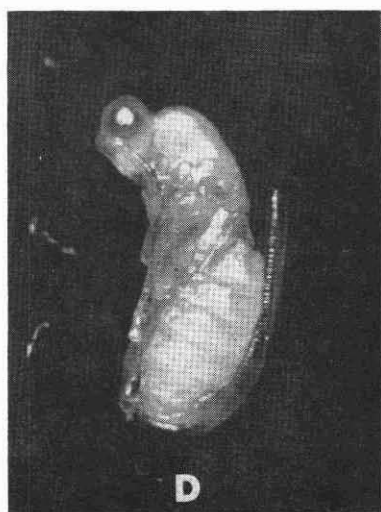
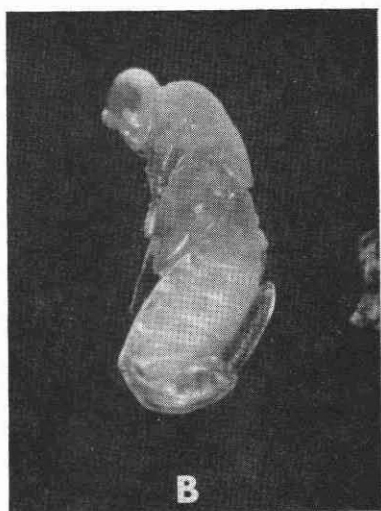
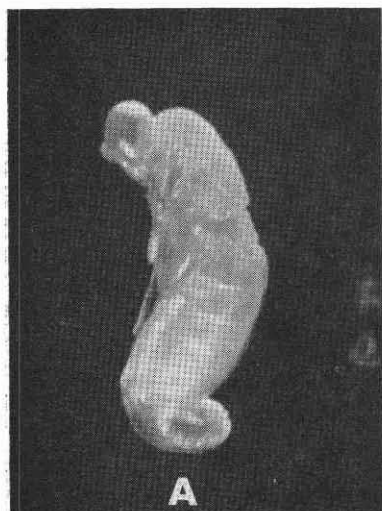
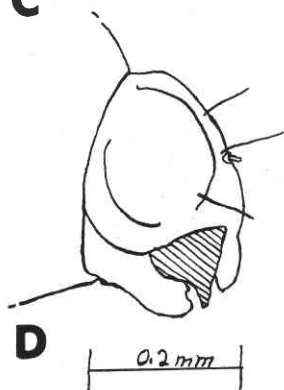
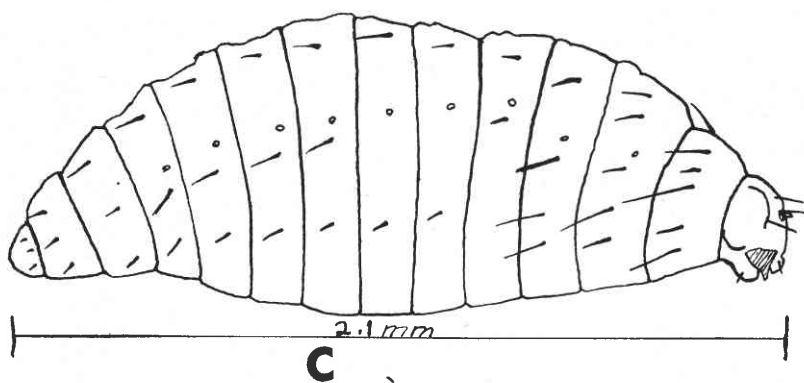
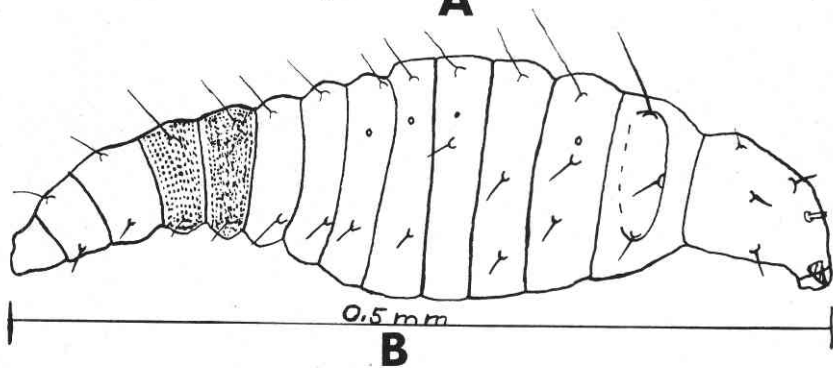
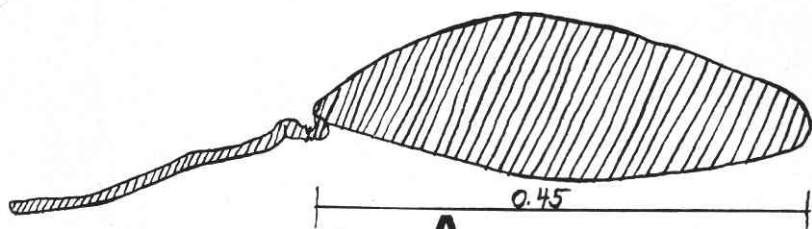


FIGURE 18

Eurytoma semivenae, egg and larval stages

- A. Egg
- B. First-instar larva, slightly flattened at middle. Microspines shown only on abdominal segments 6 and 7.
- C. Last instar larva, slightly flattened at middle
- D. Detail of head of last instar larva



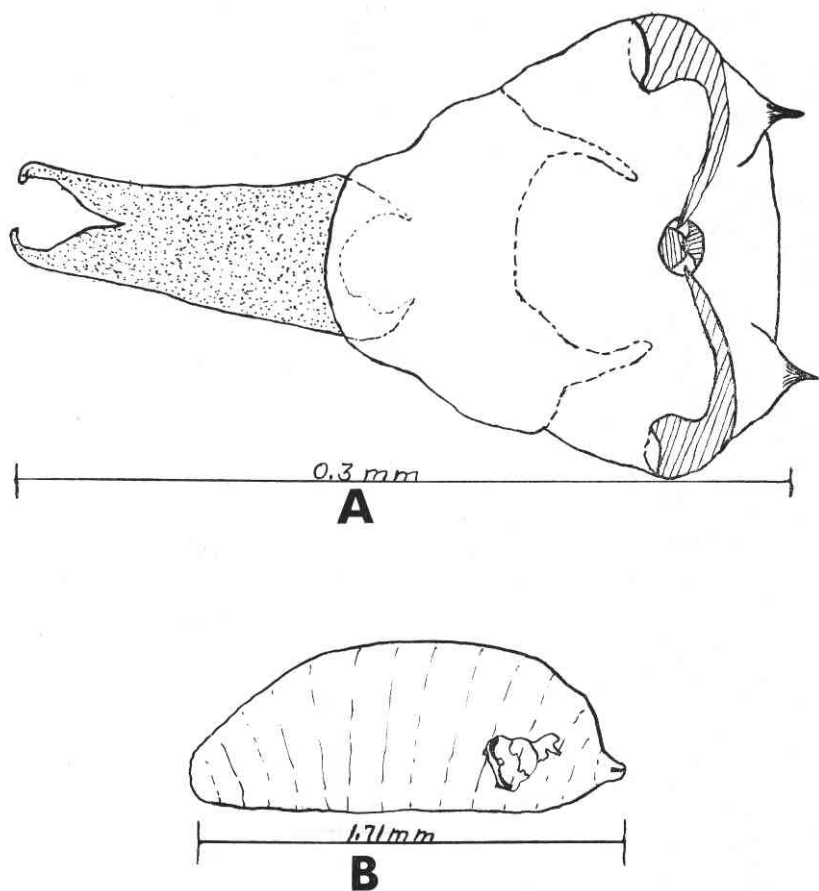


FIGURE 19

Trichacis sp., first-instar larva

- A. First-instar extracted from host. Note unorthodox shape of antennae and mandibles. Membranous part of "tail" represented by stippling.
- B. First-instar larva "in situ" inside third-instar larva of *Phytophaga* sp. after clearing with lactic acid

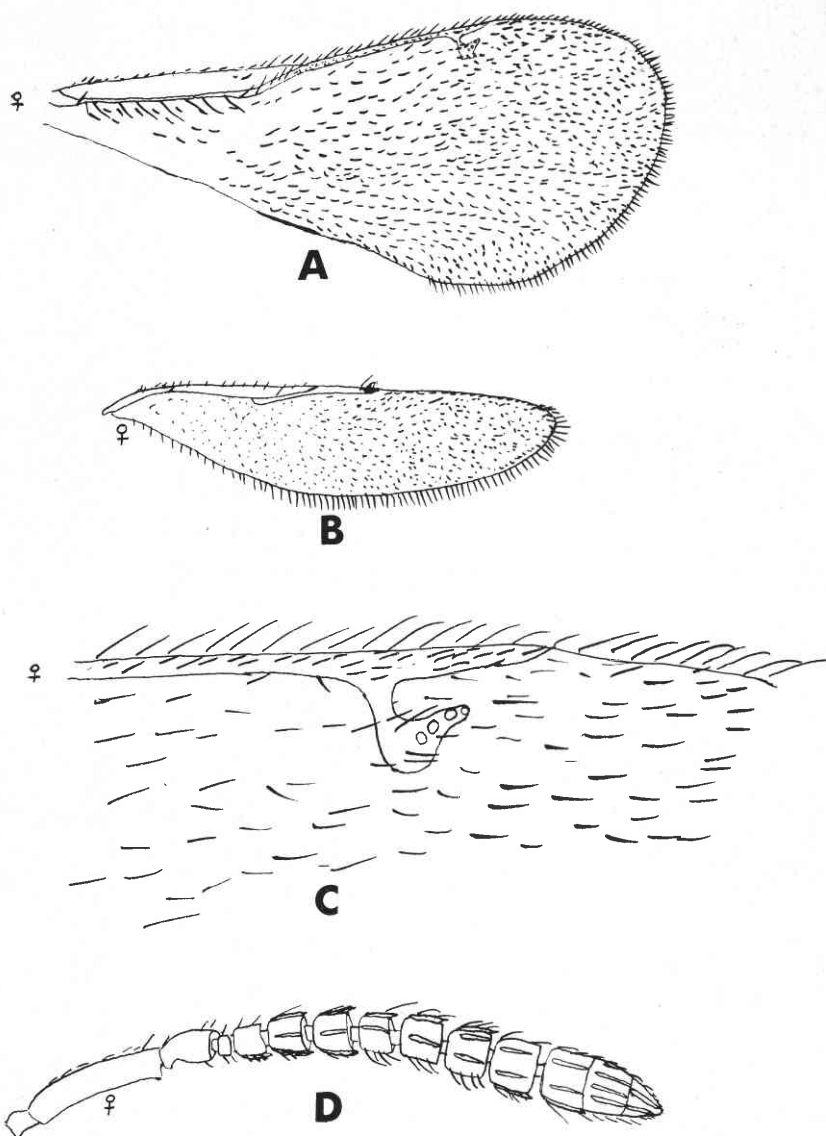


FIGURE 20

Torymus diabolus, female

- A. Front wing
- B. Hind wing
- C. Stigma of front wing
- D. Antenna

FIGURE 21

Torymus diabolus, larval stages

- A. First-instar larva, dorsal view
- B. First-instar larva, side view (microspines not shown)
- C. First-instar larva, ventral view of head
- D. Last instar larva. Note difference in anatomy between *T. diabolus* and the two species of *Torymus* that attack psyllids.

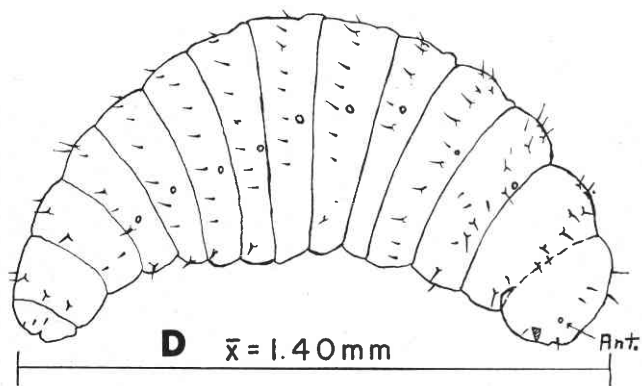
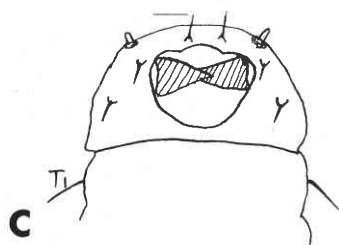
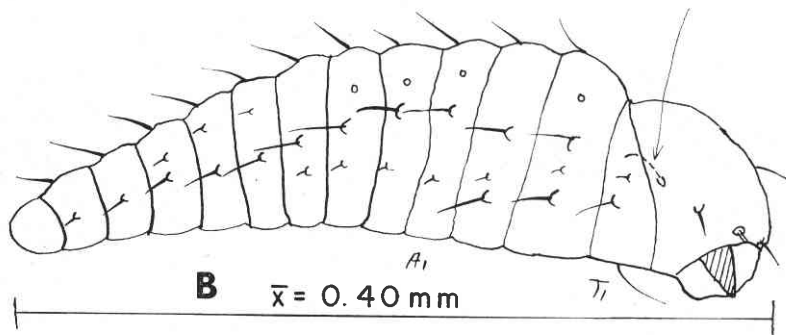
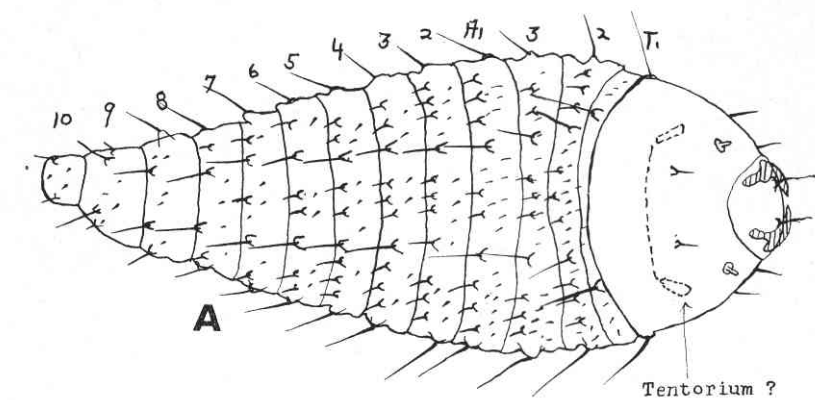


FIGURE 22

Parasites of gall makers

- A. Egg of *Torymus pachyphyllae*. Egg of *T. vesiculus* is almost identical in shape, but smaller. Egg is not attached to gall.
- B. Egg of *Torymus diabolus*. Egg is suspended inside gall.
- C. Egg of *Eurytoma semivenae* on abdomen of fifth-instar nymph of *Pachyphylla celtidismamma*. Arrow points to black area left of egg where nymph was stung.
- D. Last instar of *E. semivenae*. Note whitish-brown crystals of uric acid on and around larva.
- E. Fourth-instar larva of *Torymus pachyphyllae* beside partially sucked nymph of *P. celtidismamma*. Head of larva is facing camera.

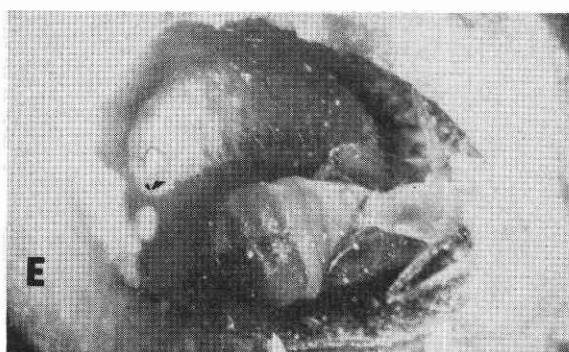
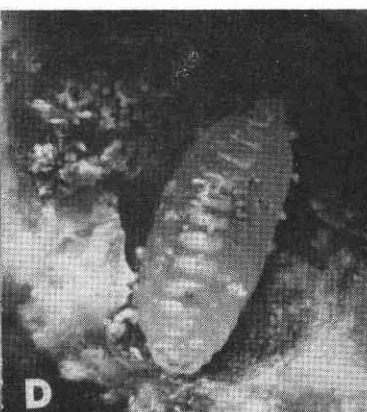
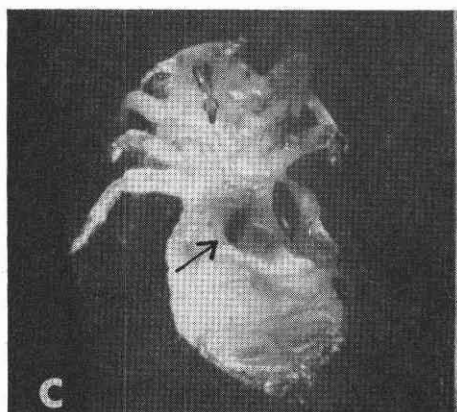
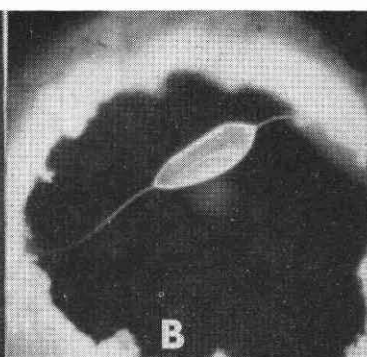
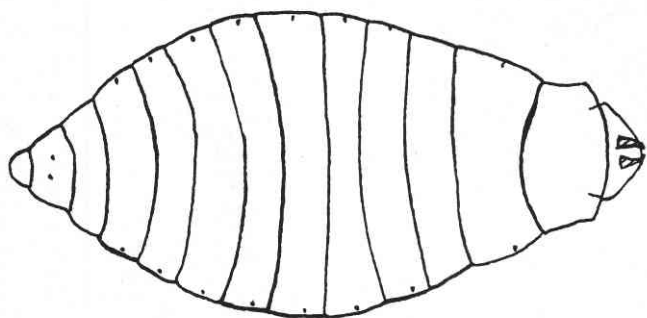


FIGURE 23

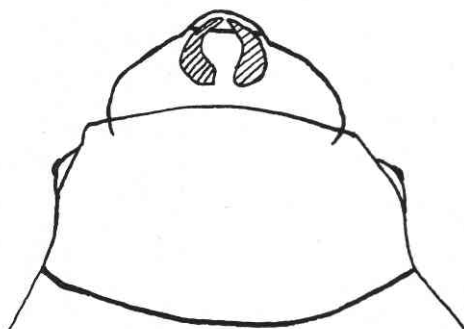
Achrysocharis spiniformis and *Psyllaephagus pachyphsyllae*, larvae

- A. Last instar larva of *A. spiniformis*. The larva of *A. vesiculis* is nearly identical.
- B. Detail of head and first thoracic segment of *A. spiniformis*
- C. Last instar larva of *Psyllaephagus pachyphsyllae*. Larva is nondescript, reduced, glabrous, and milk white in color. The spiracles, mandibles, and antennae are reduced.



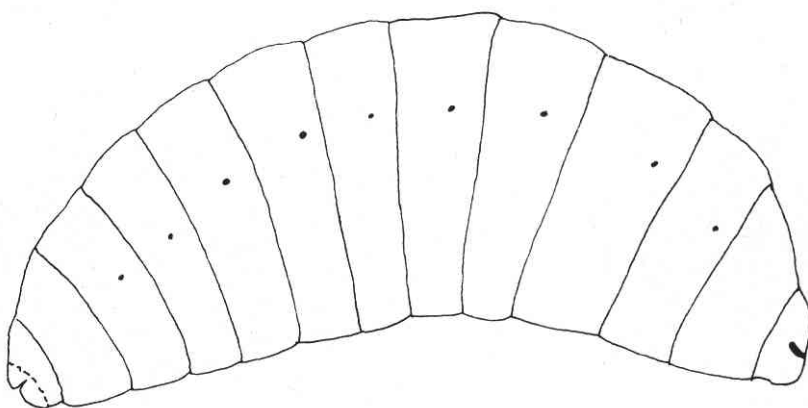
1.4 mm

A



0.2 mm

B



2.1 mm.

C

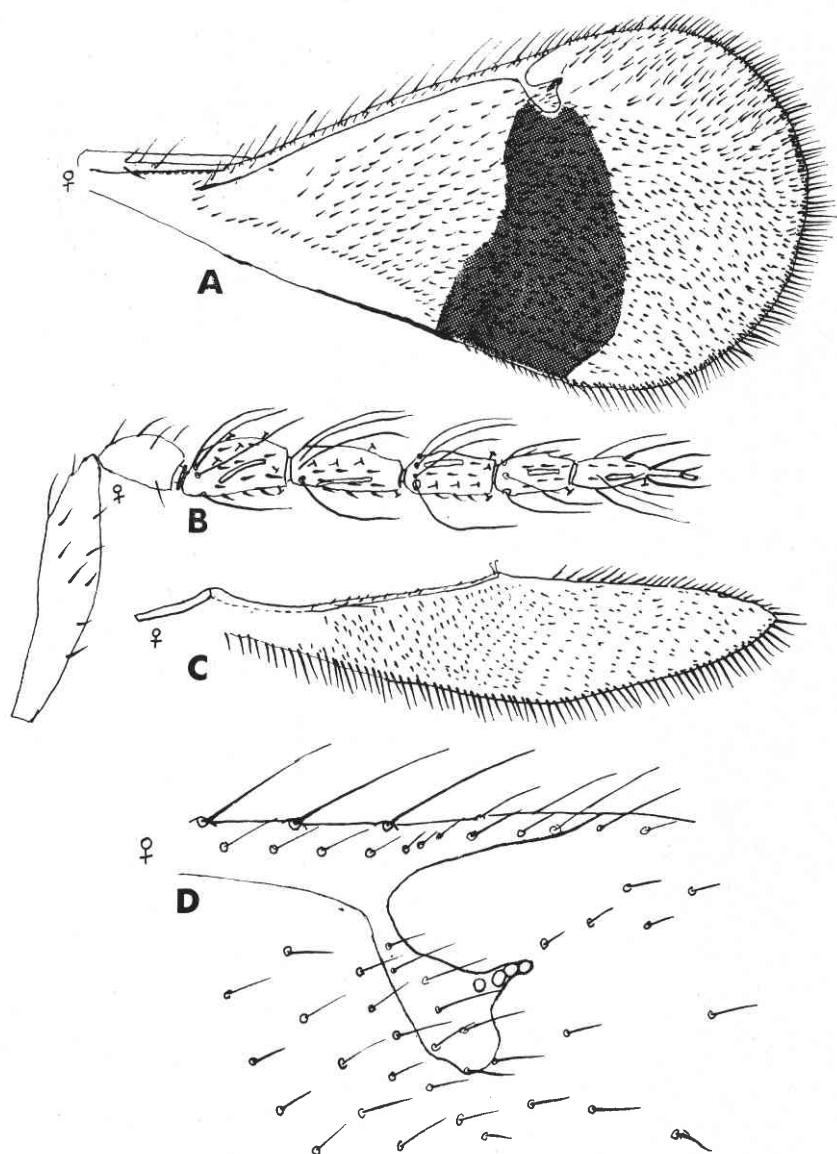


FIGURE 24

Achrysocharis spiniformis, female

- A. Front wing
- B. Antenna
- C. Hind wing
- D. Stigma of front wing

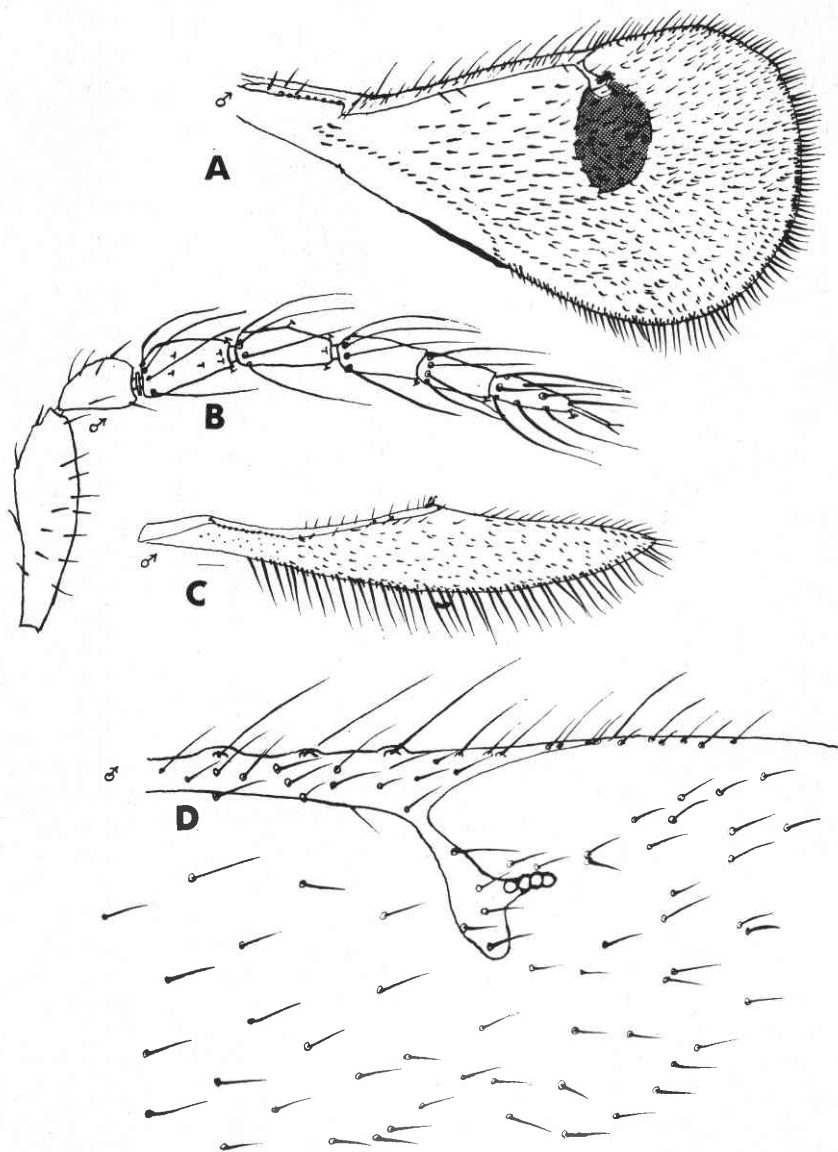


FIGURE 25

Achrysocharis spiniformis, male

- A. Front wing
- B. Antenna
- C. Hind wing
- D. Stigma of front wing

FIGURE 26

Pachypsylla celtidisvesicula and parasites, life history charts

Explanation of terms

E. Egg

1, 2, 3, 4, 5. First-, second-, third-, fourth-, and fifth-instar nymphs

S. Psyllid nymph stung by *Achrysocharis vesiculis*. Presumably egg is inside nymph.

I. Immature larva

P. Pupa

A. Adult

Solid circles represent observations in field; solid lines through circles are periods of greatest abundance of each stage. Arrows in last column show stage that overwinters. Dotted lines indicate probable occurrence of stage when no observations were made.

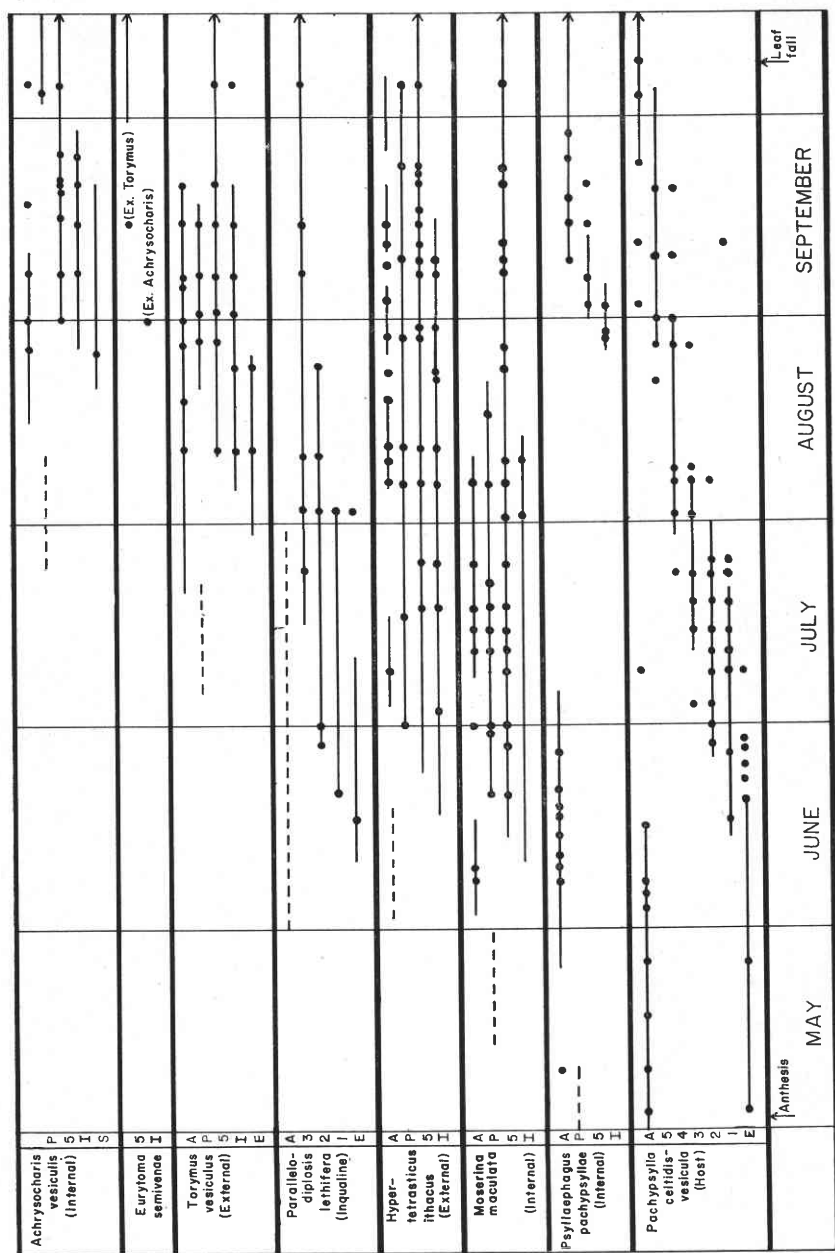


FIGURE 27

Pachypsylla celtidismamma and parasites, life history charts

Explanation of terms

E. Egg

1, 2, 3, 4, 5. First-, second-, third-, fourth-, and fifth-instar nymphs.

I. Imature larva

D. Excavated galls eaten by larvae of *Conotrachelus buchanani*

P. Pupa

A. Adult

Solid circles represent observations in field; solid lines through circle are periods of greatest abundance of each stage. Arrows in last column show stage that overwinters. Dotted lines indicate probable occurrence of stage when no observations were made.

FIGURE 28

Height of nipple gall and instar of nymph of *Pachypsylla celtidismamma*

Explanation of terms

E. Egg

1, 2, 3, 4, 5. First-, second-, third-, fourth-, and fifth-instar nymphs of *P. celtidismamma*.

A. Adult

Large circles connected by solid line are mean heights for 30 nipple galls each at selected dates. Small circles show height extremes of samples.

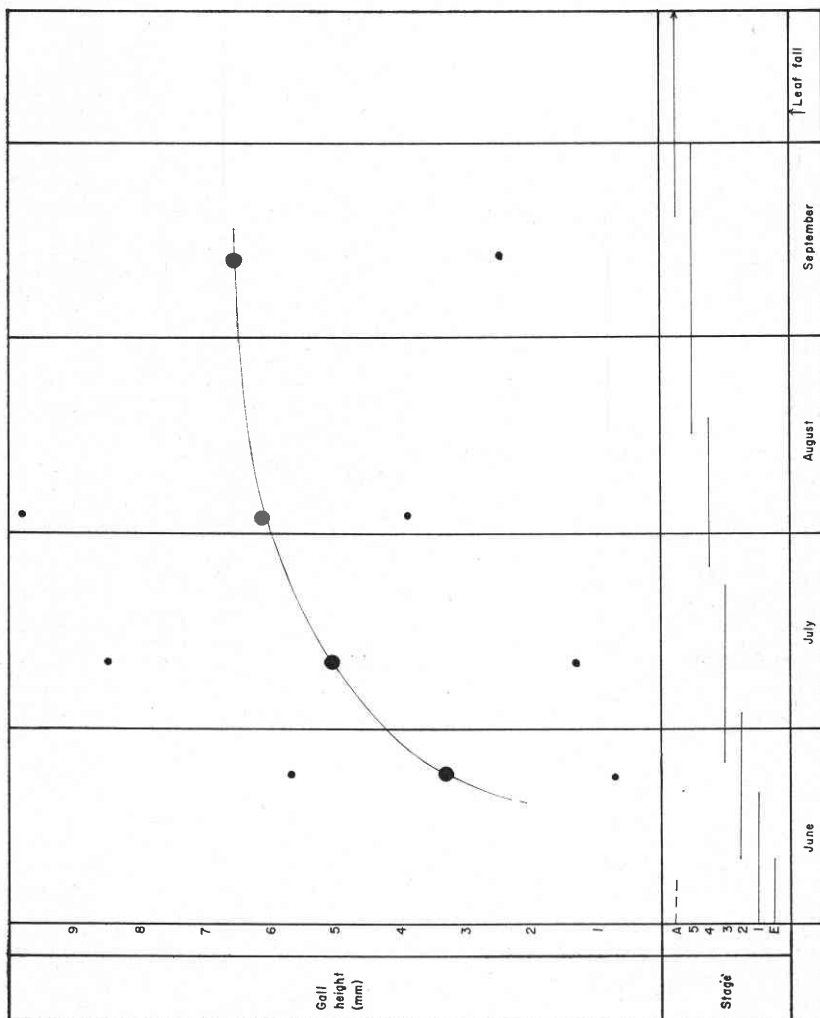


FIGURE 29

Phytophaga sp. and parasites, life history charts

Explanation of terms

E. Egg

1, 2, 3. First-, second-, and third-instar larvae.

3c. Third-instar larva in cocoon

P. Pupa

A. Adult

(A). Adult in diapause, still inside host skin in gall (*Trichacis*)

I. Immature larva

5. Mature larva

Solid circles represent observations in field; solid lines through circles are periods of greatest abundance of each stage. Arrows in last column show stage that overwinters. Dotted lines indicate probable occurrence of stage when no observations were made.

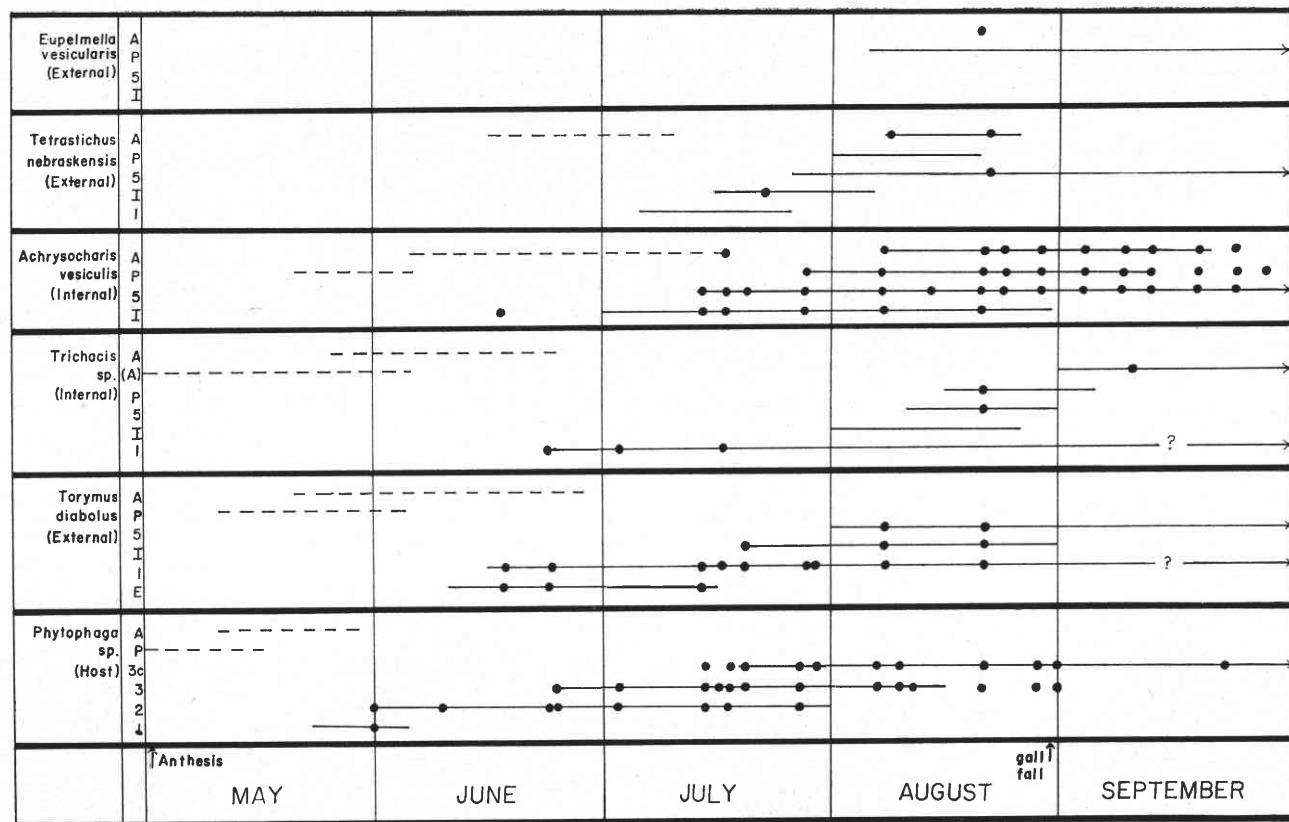


FIGURE 30

Height of thorn gall and instar of larvae of *Phytophaga* sp.

Explanation of terms

E. Egg

1, 2, 3. First-, second-, and third-instar larvae of *Phytophaga* sp.

C. Third-instar larva that formed cocoon.

Large circles connected by solid lines are mean heights for 30 thorn galls at selected dates. Small circles show height extremes of samples.

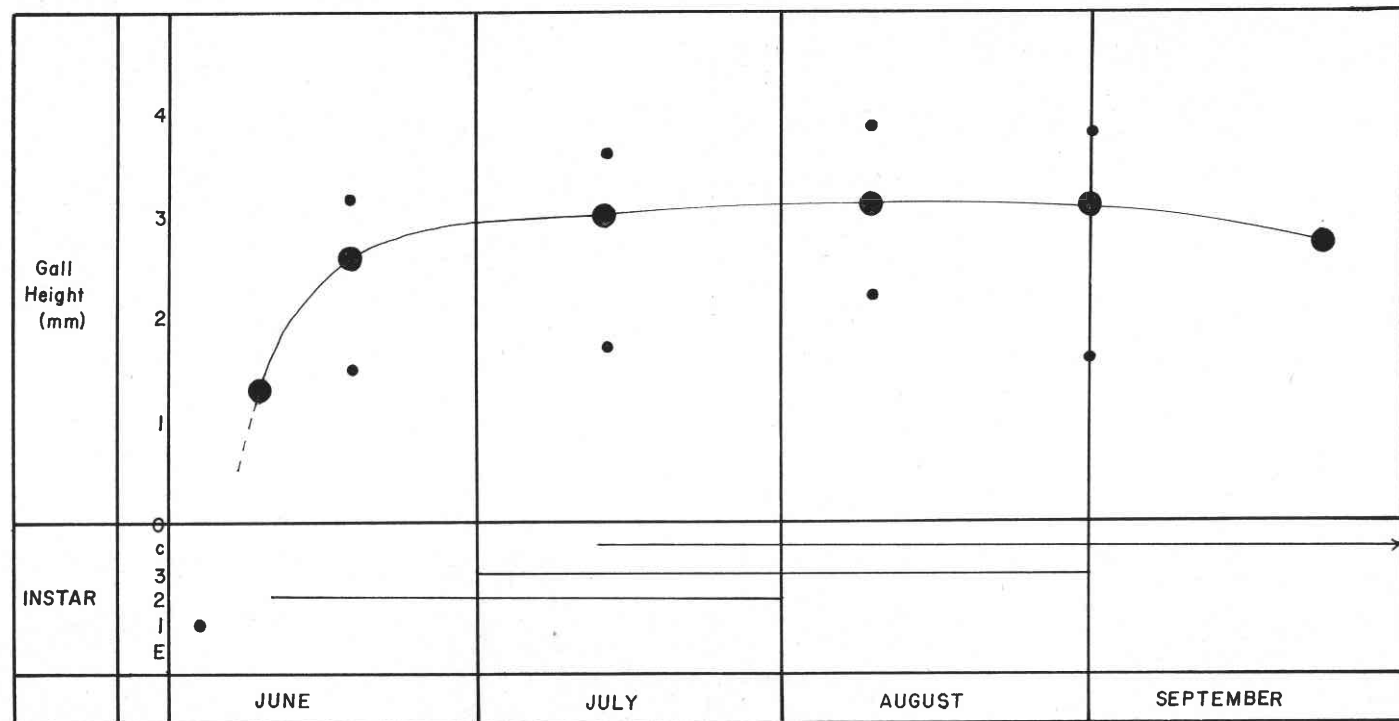


FIGURE 31

Moserina maculata, stage histogram

Relative abundance of last-instar larvae, pupae, and adults of parasite at various dates when psyllid nymphs occupied galls. The egg and early instars are not shown because they occurred inside nymphs and could not be located in numbers.

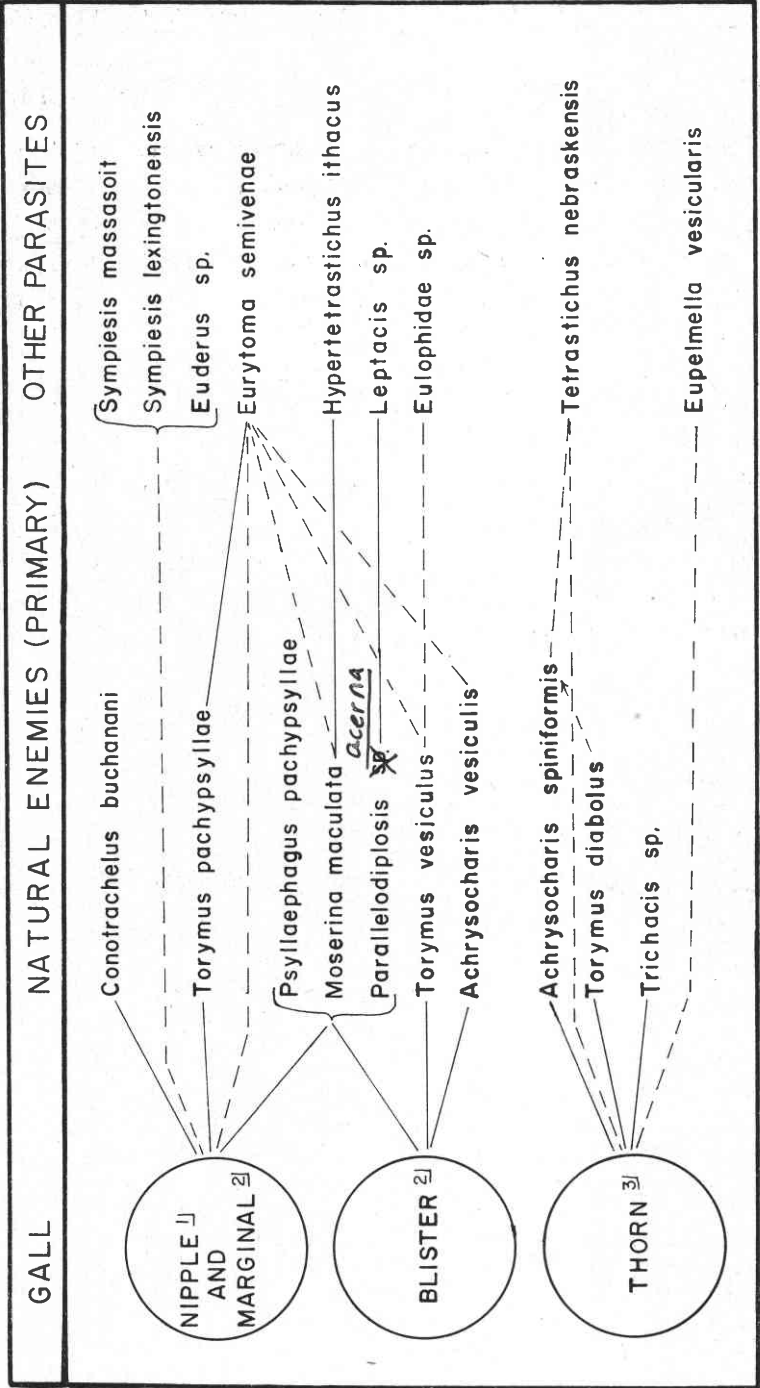
FIGURE 32

Interrelationships of natural enemies of hackberry galls in the vicinity of Ithaca, N.Y.

This figure shows the complex of parasites that theoretically can be found on a single leaf of the hackberry. The galls are illustrated in the left column by the circles, and the natural enemies are in columns to the right of the circles. Lines connecting the natural enemies and galls read from right to left. Solid lines connect the natural enemies with the host they usually attack, whereas broken lines lead to hosts occasionally attacked.

The middle column is termed "natural enemies (primary)" instead of "primary parasites" because of the weevil *Conotrachelus bucanani* and of the midge *Parallelodiposis acernea*, which are not true parasites. They feed on gall tissue and only accidentally kill the gall makers. All other species listed under the column are hymenopterous parasites.

The heading "other parasites" contains miscellaneous ecological groups of hymenopterous parasites. *Sympiesis massasoit*, *S. lexingtonensis*, and *Euderus* sp. are normally found in mines of *Lithocolletis* spp. that are common on leaves of hackberry. *Hypertetrastichus ithacus* and *Leptacis* sp. are true secondary parasites, whereas *Eurytoma semivenae* is usually secondary but occasionally attacks the gall maker. *Eulophidae* sp., *Tetrastichus nebraskensis*, and *Eupelmella vesicularis* are general parasites that are occasionally found in hackberry galls.



¹ *Pachypsylla cellidismamma*, ² *Pachypsylla cellidisreticula*, ³ *Phytophaga* sp. near *spiniformis*.

