LIFE HISTORY AND HABITS OF *Pachygonatopus minimus* Fenton AND *Tomosvaryella sylvatica* Meig., PARASITES OF THE SIX-SPOTTED LEAFHOPPER, *Macrosteles fascifrons* (Stal) IN MANITOBA

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by

Clifford Francis Barrett

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ABSTRACT

by

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LIFE HISTORY AND HABITS OF *Pachygonatopus minimus* Fenton AND *Tomosvaryella sylvatica* Meig., PARASITES OF THE SIX-SPOTTED LEAFHOPPER, *Macrosteles fascifrons* (Stal) IN MANITOBA

The aim of this study was to determine the biology of *Pachygonatopus minimus* Fenton and *Tomosvaryella sylvatica* Meig. and their importance in the control of the six-spotted leafhopper, *Macrosteles fascifrons* (Stal). The six-spotted leafhopper, which occurs throughout the United States of America and across Canada, is the chief vector of aster yellows, a virus disease of plants. The disease has become a major limiting factor in the production of several commercial crops.

The information in this study was obtained from observations and tests in the field and in the laboratory.

The six-spotted leafhopper is the only known host of *P. minimus*. Parasitized leafhoppers were collected in the northern Great Plains area of North America. The parasite increased in abundance from less than one per cent in spring to 37 per cent in fall. The female adult is also a predator of leafhoppers and in cages consumed an average of one and one-half nymphs per day.

In the adult stage the sexes differ in form, color and habits. The male is winged and the female wingless. Males lived an average of 2.15 days and females 12.14 days. The sex ratio was near 1:1. Mating was of short duration. In ovipositing the female grasped its prey with its chelate fore limbs or mandibles.

The egg is laid in the abdomen of the host and hatches in less than three hours. As the larva develops it protrudes through an intersegmental membrane. There are five larval instars. The first four are sedentary, attached to the host and are contained within their successive cast skins. The duration of the first instar was about 100 hours and that of the second, third and fourth about 50 to 75 hours each. The fifth instar is an active feeding stage and at the time of emergence from the host consumes the contents of the leafhopper. The larva spins a cocoon within which are spent most of the fifth larval stadium, all of the pupal period and the preimaginal period. The mean duration of these stages was 16.4 days.

Oviposition and parasitism was noted only on third, fourth and fifth instar nymphs and adults. Parasitized nymphs did not generally molt. Multiple parasitism was frequent but normally only one parasite developed. Parasitized leafhoppers were as active as non-parasitized leafhoppers. The use of insecticides to control the leafhopper did not affect the rate of parasitism of the leafhopper by P. minimus.

T. sylvatica is a small black fly with a large head characterized by very large eyes. It has parasitized up to twenty per cent of the leafhopper population in fall. Eggs of T. sylvatica, which hatch in 6 to 7.5 days, were dissected from the head, thorax and abdomen of leafhoppers. Only very small larvae were found in the head and thorax of the host whereas large larvae were found only in the abdomen. There appeared to be two larval instars. The larva pupated in the soil.

ACKNOWLEDGMENTS

This study was carried out as part of a project on the life history, behavior and control of the six-spotted leafhopper under the leadership of Mr. P. H. Westdal. It has involved use of facilities of the Canada Agriculture Research Station, Winnipeg, Manitoba, by permission of Dr. R. D. Bird, Head of the Entomology Section. Professor A. G. Robinson, Department of Entomology, University of Manitoba has acted as my advisor. Grateful appreciation is extended to these men for their guidance, encouragement and helpful criticisms.

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CHAPTER I

INTRODUCTION

The problem

The purpose of this study was to determine the life history, habits and distribution of *Pachygonatopus minimus* Fenton (Hymenoptera : Dryinidae) and *Tomosvaryella sylvatica* Meig. (Diptera : Pipunculidae) and their importance in the control of the six-spotted leafhopper, *Macrosteles fascifrons* (Stal) (Homoptera : Cicadellidae) in Manitoba. The work was organized as part of an integrated program of study on the life history, behavior, ecology and control of the six-spotted leafhopper, conducted at the Research Station, Research Branch, Canada Department of Agriculture, Winnipeg, Manitoba.

Importance of the study

Aster yellows, a virus disease of plants, has become a major limiting factor in the production of several commercial crops in North America. The disease is transmitted almost exclusively by the six-spotted leafhopper which, according to Beirne (1956), occurs throughout the United States and across Canada and Alaska to the tree line. The tendency for this insect to feed on a very wide range of host plants probably accounts for its abundance and widespread

occurrence. The aster yellows virus, like its insect vector, also has a very wide host range. However, for many groups of plants the two host ranges of the vector and the virus do not coincide. The six-spotted leafhopper feeds and breeds on many plant species immune to aster yellows but can transmit aster yellows to some plants toxic to the insect and on which it cannot live for more than a few days (Kunkel, 1931).

In Canada the six-spotted leafhopper is common throughout all the provinces and the Northwest Territories. It is of greatest economic importance from Nova Scotia to Saskatchewan. In Manitoba and Saskatchewan it transmits aster yellows to various vegetables and ornamentals and to flax and sunflowers, whereas, in the other provinces mentioned its greatest economic importance is because it transmits the disease to vegetables and ornamentals.

Each year, in Manitoba, there is a considerable crop loss due to aster yellows and occasionally the loss may be very substantial (Lee and Robinson, 1958; Sackston, 1957, 1958). In 1957, 3,485,600 acres of flax were grown in Canada of which 865,000 were grown in Manitoba.[1] Because of hot dry weather, aster yellows and wilt, yield dropped to an average of 5.7 bushels per acre from 11.3 bushels per acre

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[1]Current Review Agric. Cond. in Canada Nov. 1957 and Jan. 1958.

in 1956. On the basis of a 15 per cent drop in yield, due to aster yellows alone (Sackston, 1957), from the 1956 average, the loss in 1957 would be 1,466,175 bushels. At an average price of $2.66 per bushel, the loss to Manitoba producers would be $3,900,000.00. In 1957, 450 acres of carrots and 460 acres of onions were grown on the prairies. These crops were severely damaged with a loss of many thousands of dollars. Lettuce has not been an economical crop to grow in Manitoba since 1954 because of aster yellows. Because of the past history of aster yellows, the Manitoba product is no longer acceptable to the consumer. Were it not for aster yellows, annual crops of lettuce, having a market value of approximately $3,000.00 per acre would otherwise be possible in Manitoba.

Control measures of various kinds in the United States and Canada have not proven entirely satisfactory. In order to obtain a more enlightened approach to the ultimate control of the leafhopper and aster yellows it is essential to learn something of the biology of parasites and predators of the six-spotted leafhopper and their importance as control agents.

Location of the study

The work was conducted chiefly in the Winnipeg area with most of the work being carried out in the laboratory and greenhouse at the Canada Agriculture Research Station,

Winnipeg, Manitoba. Leafhopper collections were made at many points in Manitoba, including Winnipeg, Elm Creek, Portage la Prairie, Fisher Branch, Altona, Neepawa, The Pas and Oak Lake. Collections were made near Moosomin and Regina in Saskatchewan, at Lethbridge in Alberta and in Montana and North Dakota in the United States of America.

Organization of the thesis

The thesis is divided into nine chapters. Chapter I is the introduction. In Chapter II a review of the literature pertaining to the subject is presented. Chapter III deals with the materials and methods used in conducting the study. Chapter IV deals with hosts, distribution and abundance of P. minimus. A description of the life stages of the insect is presented in Chapter V. Chapter VI covers the life history and behavior of P. minimus and constitutes the major part of the work. Chapter VII deals with the effect of insecticides on population of P. minimus. Notes on T. sylvatica are presented in Chapter VIII. Chapter IX is a summary of the thesis and is followed by a bibliography.

CHAPTER II

REVIEW OF THE LITERATURE

The six-spotted leafhopper and its relationship to the aster yellows virus, Chlorogenus callistephi H., has been studied extensively in North America. The history of this relationship has been thoroughly reviewed by Chapman (1949) and Chiykowski (1958). Lee and Robinson (1958) and Sackston (1957, 1958) have reviewed the importance of the insect and the disease in Manitoba.

When the present study on parasites of the six-spotted leafhopper was begun, specimens of the dryinid were sent to Dr. W. R. M. Mason, Entomology Research Institute, Canada Department of Agriculture, Ottawa, Ontario and to Dr. K. V. Krombein, U.S. National Museum, Washington, D.C. The specimens were identified as Gonatopus n. sp. Subsequently, they were identified by Dr. Mason as Pachygonatopus minimus Fenton (Barrett and Westdal, 1961). Since that time Dr. Mason[1] has stated that "the North American dryinids are badly in need of revision." and "...that Pachygonatopus is not the correct genus ...". Fenton's placement of minimus in the genus Pachygonatopus was apparently incorrect since "...it is actually an Australian genus and has nothing to do with the Nearctic fauna" (Mason[1]).

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[1]personal communication

Despite the taxonomic confusion of this group, for the purpose of this work the dryinid parasite will be referred to as Pachygonatopus minimus Fenton.

Because P. minimus is obviously closely related to the genus Gonatopus and as Mason[1] further stated that "The closest relatives will be found under the genus Epigonatopus...", all three genera are discussed in the review of literature.

The genus Pachygonatopus was originally described by Perkins (1905) from the type species P. melanias from Australia. The species P. minimus was described by Fenton (1927) from a single female reared from a cicadellid collected in the United States of America on September 13, 1914. Fenton stated, "This minute species answers to the description of this genus by Perkins, but the maxillary palpi are invisible or broken." According to Richards (1939) the genus does not occur in Britain. Barrett and Westdal (1961) reported the occurrence of P. minimus as a parasite of the six-spotted leafhopper in Manitoba. No other references to this species have been noted in the literature.

The genus Epigonatopus was originally described by Perkins (1905) from the type species E. solitarius. Fenton (1927) described several new dryinid species including E. plesius.

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[1]personal communication

According to Muesebeck et al (1951) the genus Gonatopus was first described by Ljungh in 1810. He described G. formicarius as the type species. Ashmead (1893), in a monograph of the Proctotrypidae (Proctotrupidae), included the group Dryininae. He described the genus Gonatopus using G. pedestris Dalm. as the type species. He listed two other species and described three new species of Gonatopus. Perkins (1905) compiled an important general account of the Dryinidae. He discussed their habits, economic value, life stages and made a comparative study of their generic characters. He described the distinguishing features of Gonatopus as a 5-jointed maxillary palpus and a 2-jointed labial palpus. He discussed also the use of the chela in differentiating genera in this family. Perkins (1905, 1906) referred to Lichtenstein (1874) who reported Gonatopus ptinorum as being parasitic on the beetle Ptinus fur. Perkins (1906) stated that Kieffer (1905) considered the parasite involved to be probably of the genus Cephalonomia in the Bethylidae. It was not so placed by Muesebeck et al (1951).

Perkins (1912) considered Gonatopus to be made up of groups entirely distinct from each other phylogenetically and was convinced of this from his examination of Dryinopsis simplicipes Brues, a Gonatopus-like species with a 12-jointed antenna and a simple front tarsus.

Keilin and Thompson (1915a) in a treatise on the life history of dryinids, reviewed some of the literature on the family. They stated that Curtis, in 1836, first reported the dryinid type of parasitism and that Mik, in 1882, found Gonatopus pilosus to be a parasite of nymphs of Deltocephalus xanthoneurus. Fenton (1918) reviewed the parasites of leafhoppers, especially the biology of the Anteoninae (Dryinidae).

The findings of Perkins (1905, 1906, 1907) and of Fenton (1918) constitute most of the literature on the family Dryinidae. Fenton (1918) compiled an extensive host list. He dealt also with the phylogeny and taxonomy of the group and with the life histories of species, including some species of Gonatopus. Fenton (1918) also described the histological effects of the parasite-host relationship. Fenton (1921) described three dryinids, two in the genus Gonatopus.

Haupt (1932) described the mouthparts and some other features of dryinids and referred especially to Gonatopus and to Ophelopus. Clausen (1940) synthesized the findings of several of the above authors. Muesebeck et al (1951) reviewed the dryinid species of North America and listed fourteen species in the genus Gonatopus. Kieffer (1907) divided the Dryinidae into the subfamilies Dryininae, Gonatopinae and Anteoninae. For other references see the bibliographies of Fenton (1918), Clausen (1940), Mik (1882) and Swezey (1903).

Perkins (1905) stated that leafhopper nymphs and adults are parasitized by Anteoninae (Dryinidae), Pipunculidae, Strepsiptera, Epipyropidae and Encyrtidae. Misra (1917) added Chalcididae to this group. Perkins (1907) stressed the importance of parasites and predators, particularly the importance of egg parasites, in controlling leafhoppers.

In 1954, Barrett and Westdal (1961) noted the parasite sacs of a species of dryinid on the abdomens of the six-spotted leafhoppers collected on rapeseed crops in the interlake area of Manitoba. This may have been P. minimus. An undetermined species of dryinid parasite was reported by Robinson and Lee (unpublished) on six-spotted leafhoppers in 1958. Barrett and Westdal (1961) in 1958 reared both sexes of P. minimus from six-spotted leafhoppers collected at Elm Creek and Winnipeg in Manitoba. Another species, E. americanus Fenton was collected at Fisher Branch, Manitoba, in an alfalfa-sweet clover-medic grass field and at Wanless, Manitoba, in an alfalfa field. The latter species is very similar to E. plesius (Fenton). The host of E. americanus is unknown.

Miller and DeLyzer (1960) in studies on the six-spotted leafhopper in southwestern Ontario observed only one parasite, the dryinid E. plesius.

There are no taxonomic keys by which to separate and identify the larvae of species of Dryinidae. However, there are at least three and perhaps four species that attack the six-

spotted leafhopper in North America. These are P. minimus, Neagonatopus ombrodes Perkins, E. plesius, and an undetermined species collected at Portage la Prairie, Manitoba. N. ombrodes has been listed by Muesebeck et al (1951) from Ohio, Colorado, California, Connecticut and South Dakota in the United States of America. E. plesius has been listed in Ontario, by George (1959) and by Miller and DeLyzer (1960). Both state that the percentage of parasitism was very low. Miller and DeLyzer (1960) reported two per cent parasitism by E. plesius. An illustration of the larva of E. plesius by Miller and DeLyzer (1960), differs markedly from the appearance of the larva of P. minimus. The dryinid collected at Portage la Prairie differed markedly from P. minimus in that each segment of the larval sac showed light areas alternating with dark bands. This is similar in appearance, but not identical, to larval sacs of E. plesius from Ontario, which I have examined. This undetermined species could possibly be N. ombrodes but I have not had an opportunity to compare them.

Perkins (1905), Fenton (1918) and Richards (1939) have given general accounts of the life history and habits typical of dryinids. The following is a summary of their findings.

The adult parasites are found wherever their hosts are found. Adult females are much more active than males.

In species where the female is wingless the habits of the sexes are very different. Males are rarely seen in fields and live from one to a few days, often dying after copulation. Females are more commonly seen and live as long as 17 days in captivity. The parasites feed on honey dew or any sweet liquid and, according to Perkins (1905), "without liquid food, in a hot locality the parasites die very quickly." Mating is of short duration. The prey is sought on foot. The attack is deliberate and the capturing stroke is "marvellously rapid" (Perkins, 1905). The host is captured with the parasite's modified fore-leg and stung to insensibility before oviposition. The leafhopper soon recovers and runs about normally again. Occasionally the prey is released without any attempt at oviposition. The host is often killed and to some extent devoured. The egg is inserted into the body of the host and the act may take 2 or more minutes. The egg hatches within two days and the larval sac, composed of cast skins, becomes visible within four to seven days. The larva becomes mature within a few days or a week after the larval sac becomes visible. There are normally five instars. Some species attack only nymphs, others attack only adults and others attack both nymphs and adults. Parasitized nymphs do not become adult. A single host may sustain one or more parasites. The number is dependent on the amount of food available and is related to the size of

the host. The leafhopper becomes sluggish, shortly before the mature parasite larva emerges, and dies as the larva ingests the contents of the host. The larva spins a cocoon, usually within the first day after emergence, and the adult emerges in three to five weeks. There are one or more generations a year depending on the species of parasite and the species of host attacked.

CHAPTER III

MATERIALS AND METHODS

Collecting and rearing

Most parasites were collected as larvae in the leafhopper host. Leafhoppers were collected by sweeping host plants with an insect collecting net, 15 inches in diameter, with an 80 mesh dacron bag. Sweeps were made with a lateral motion of the net while the collector moved forward through the crop. In tall crops the net was dipped at least its full diameter into the crop while in short crops the net was swept just above the soil surface. Material collected was placed in a cage 14 x 14 x 16 inches covered with 54 mesh nylon cloth (Figure 1) or caged in lamp chimney cages (Figure 2) or was removed directly from the net with an aspirator (Figure 3) and preserved in 70 per cent ethyl alcohol. All rearing was conducted in cages or lamp chimneys in the laboratory at ordinary fluctuating room temperatures.

Description of life stages

The egg and the first four larval stages were obtained by dissecting parasitized leafhoppers in 70 per cent ethyl alcohol under a low power microscope. The leafhoppers were held with number 5 jeweller's forceps and dissected with a small probe. Gravid parasites were dissected, and eggs obtained from the ovary, by the same technique. Fifth instar

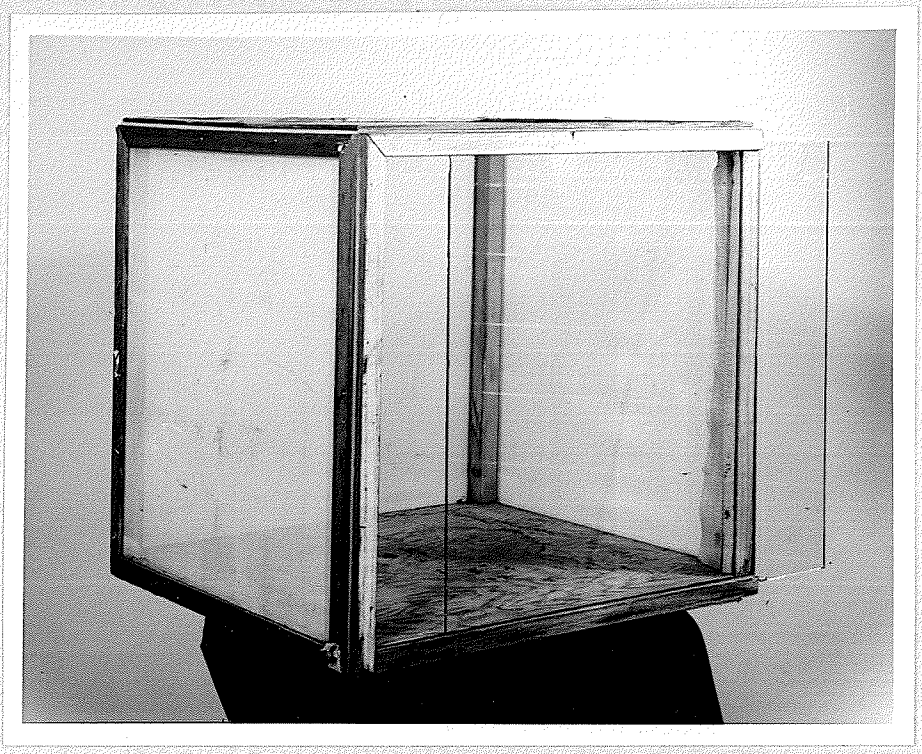

FIGURE 1

REARING CAGE (14 x 14 x 16 inches)
FOR LEAFHOPPERS

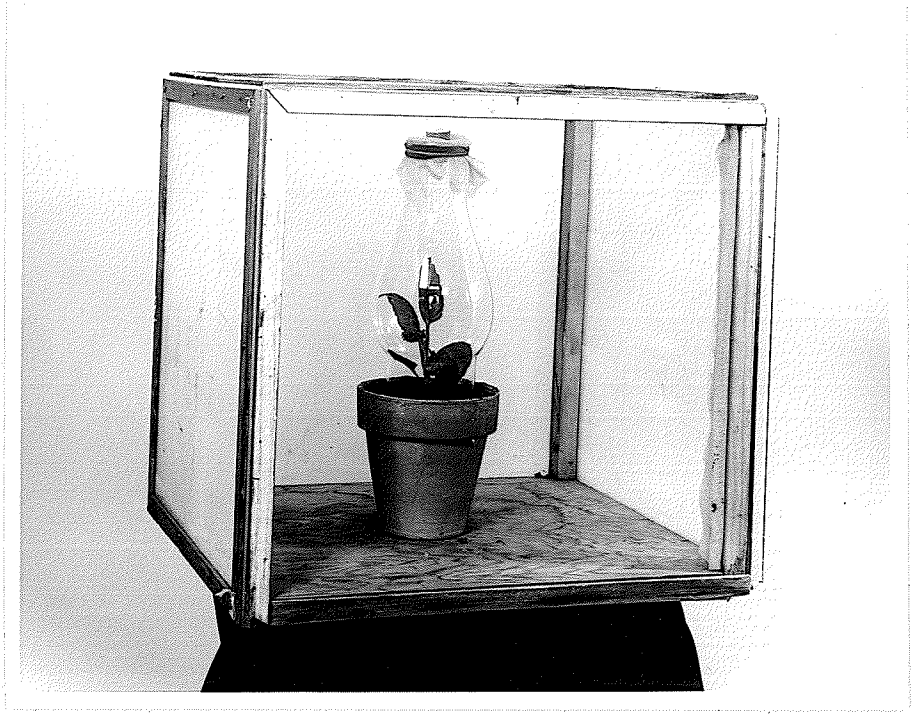

FIGURE 2

LAMP CHIMNEY REARING CAGE
FOR LEAFHOPPERS

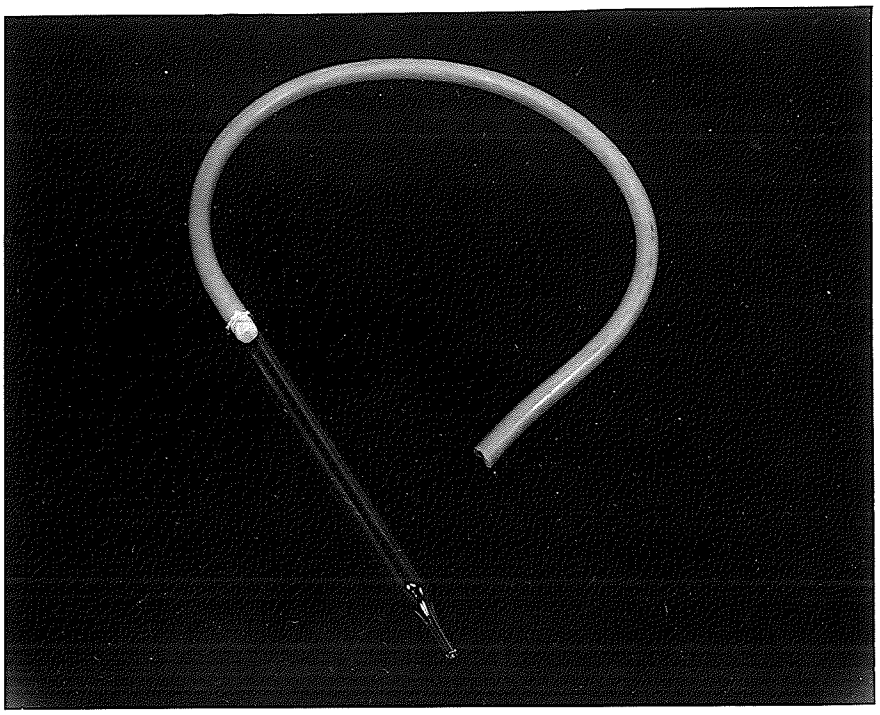

FIGURE 3

ASPIRATOR FOR COLLECTING
LEAFHOPPERS

larvae were preserved after emergence from the host, for subsequent observation. All stages were measured on a Zeiss Opton stereomicroscope with a filar micrometer calibrated against a graduated stage scale. Because the late second and the third and fourth instar larvae are curved they were measured from the foremost tip of the cephalic lobes through their longest dimension. This was not their full length but provided a relative measure of size. They were measured also in depth, from the dorsal aspect to the ventral, at right angles to the longitudinal measurement.

Sex ratio

Several thousand leafhoppers collected at Fisher Branch on barley, July 1, 1960, yielded 175 parasitized adults. These were placed in large groups in lamp chimney cages and examined frequently for emerging parasite larvae. The larvae were caged individually in one-half dram screw cap vials in order of emergence from their respective hosts. The time of emergence from the cocoons and the sex of each individual were recorded.

Predation

Predation was determined by caging an adult female of P. minimus with a known number of leafhopper nymphs for various periods of time in lamp chimney cages and examining dead and living prey for predation scars.

Longevity

Longevity of P. minimus adult males and females was determined by caging them in lamp chimney cages with leafhopper nymphs supplied as food for the female, and observing them daily for date of death.

Larval instars

To determine the number and duration of larval instars of the parasite, groups of leafhoppers were caged serially with adult females of P. minimus for known periods of time (usually 24 hours or less). When fifth instar parasite larvae began to emerge from the first group of leafhoppers exposed, the entire series was preserved in 70 per cent ethyl alcohol. This provided material of known age, ranging from newly deposited eggs to emerged fifth instar larvae. The series was subsequently examined and the finding of a cast skin was regarded as evidence of a molt.

Pupal stage

The pupal stage is herein defined as that stage in the life cycle of the parasite spent within the cocoon. This is chiefly the pupal stage but also includes part of the last larval stadium and the pre-imaginal stage. Duration of the pupal stage was determined by observing when a cocoon was spun and when the adult emerged.

Mobility of parasitized leafhoppers

The mobility of leafhoppers was checked by three different methods to determine whether parasitized leafhoppers were more or less mobile than non-parasitized leafhoppers.

In the first test a collection was made by a sweep net in an oat field until it was estimated visually that 600 or more leafhoppers had been collected. These were taken from the net with an aspirator, as they crawled upward, in samples estimated at fifty to one hundred leafhoppers. Twelve samples were made from the whole collection and were numbered in order of selection. The samples were preserved in 70 per cent ethyl alcohol. These were later examined to determine if the percentage parasitism differed between samples.

A second test was conducted by collecting leafhoppers in a 10-acre field of wild oats and mustard by sweeping in the direction of the four cardinal points of the compass. Collections were made during the early afternoon of September 23, 1959. The wind was from the west at 15 m.p.h. Each collection consisted of 250 sweeps made by sweeping briskly and laterally in a short arc while the collector walked quickly forward. Several hundred leafhoppers were taken in each collection. Sweeps were duplicated and consisted of six methods as follows:

1. Sweeps to the east, above the crop, to collect only flying leafhoppers.
2. Sweeps to the east, in the crop, to collect downwind where leafhoppers should accumulate.
3. Sweeps to the west, in the crop, to collect upwind and avoid accumulation.
4. Sweeps to the north across the middle of the crop where the collector's shadow would fall on the area to be swept.
5. Sweeps to the north at the border of the crop.
6. Sweeps to the south where leafhoppers were undisturbed by a shadow and not accumulated by wind.

The leafhoppers collected were preserved and subsequently examined for parasites.

A third test to check for mobility of parasitized leafhoppers was conducted on head lettuce. Leafhoppers from lettuce heads were shaken into a net so that they had little chance to escape. Samples were also made by sweeping, wherein only the more mobile leafhoppers would be collected. There were three replicates. Collections were examined for parasitism in each nymphal instar and for parasitism of male and female adult leafhoppers.

Effect of insecticides on parasitism of the six-spotted leafhopper by P. minimus

Head lettuce was seeded in plots in a randomized split

plot design, replicated three times. The whole plot was the insecticide treatment and the split plots were the intervals between applications. Each plot was 50 by 50 feet. Plots were separated from one another by seven feet of cultivated soil. There were five schedules of treatment and a check. Malathion at the rate of 2 lb. actual per acre was applied at 2 and 4 day intervals. The first schedule of treatment was started when the plants emerged. Subsequent treatment schedules were started at approximately two week intervals.

Collections of leafhoppers were made, usually at eight-day intervals, and consisted of one hundred sweeps from each plot swept. Since malathion was very effective in controlling leafhoppers with a four-day interval of treatment, sweeps were early discontinued on the plots with a two-day interval of treatment. It should be noted that the last application of malathion was made on July 15.

Carrots were grown in plots arranged in the same manner as described for the lettuce. DDT at the rate of 2 lb. actual per acre and Sevin at the rate of 2 lb. actual per acre were applied at six-day intervals on the split plots. Collections of leafhoppers were made at approximately six-day intervals.

CHAPTER IV

HOSTS, DISTRIBUTION AND ABUNDANCE OF *Pachygonatopus minimus*

Hosts

The six-spotted leafhopper is the only known host of *P. minimus*. In early spring of 1959 a parasitized nymph of an unknown species of Homoptera was collected near Rosenfeld, Manitoba. This appeared to be the same species of parasite but the specimen was preserved and could not be reared for identification.

Distribution

Female adults of *P. minimus* have been collected in Manitoba at Winnipeg, Elm Creek, Portage la Prairie, Fisher Branch, Altona, Neepawa and Oak Lake. A female adult was collected near Moosomin, Saskatchewan. Adults of both sexes have been reared from material collected at Moosomin and Regina in Saskatchewan and from most of the above mentioned locations in Manitoba. Collections of leafhoppers preserved in alcohol and containing dryinid larvae believed to be *P. minimus*, were made at Warner, Alberta, on September 23, 1959; at Cummings, North Dakota, and at Breckenridge, Minnesota, on May 16, 1959; in Montana at Billings, at a point one hundred miles east of Billings, at Glendive, and at a point fifteen miles south of Sidney; and at Ray, North

Dakota, on August 27, 1959. Although it has not been possible to positively identify preserved larval material, there is strong circumstantial evidence to indicate that these are of the same species as that under consideration in Manitoba.

The reasons for believing the larval dryinids collected in Alberta, Montana, North Dakots and Minnesota to be P. minimus are that they occur on the same host, they have the same appearance, they are similarly located on the host, their distribution is contiguous to that known for P. minimus and they occur on the same path of migration as the host of P. minimus.

Abundance

The abundance of P. minimus varies greatly with the season. In the spring migration, probably less than one per cent of the leafhoppers are parasitized. By fall, parasitism may rise to 37 per cent.

CHAPTER V

DESCRIPTIONS OF LIFE STAGES OF *Pachygonatopus minimus*

P. minimus has a complete metamorphosis with egg, five larval instars, pupa in a cocoon, preimaginal stage and adult. The life stages were studied in considerable detail and are described and illustrated with photographs.

Adult

The species is strongly dimorphic. The sexes differ not only in form but also in color and habits.

The female (Figure 4) is wingless and ant-like but has long slender legs. It is from 2.7 to 3.0 mm. long, depending partly on the extent of ovarial expansion of the abdomen. The color of females may vary from bright red to testaceous.

The male (Figure 5) is winged and capable of flight. It is black and from 1.75 to 2.0 mm. long.

Ovary

The mature ovary is large and with the other internal reproductive organs nearly fills the abdominal cavity of the female. A section of the ovary is shown in Figure 6. Eggs are not completely developed by the time the parasite emerges from its cocoon. Development of the ovaries appears to

FIGURE 4

ADULT FEMALE OF P. minimus (x 40)

FIGURE 5

ADULT MALE OF P. minimus (x 40)

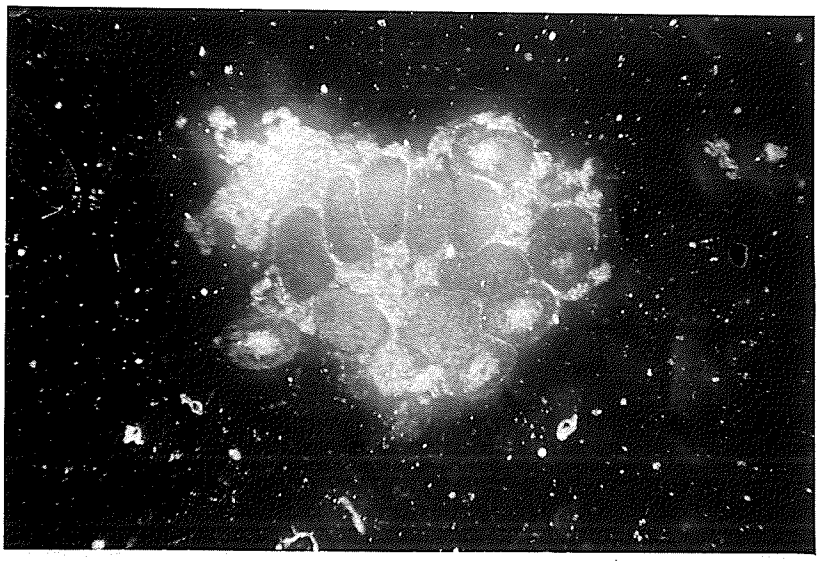

FIGURE 6

SECTION OF MATURE OVARY

OF P. minimus

depend upon how much protein food is available to the female. Full oviposition depends on an adequate supply of leafhoppers. Further, since the degree of feeding by the fifth instar larva before leaving its host appears to influence the chances of survival of that larva, it seems probable that this also influences ovarial development.

Egg

The egg of P. minimus is almost always laid on the inner aspect laterally of the intersegmental membrane of the abdomen (Figure 7). Very rarely does a parasite develop deep within the host and no instance was found of an egg being deposited externally on the host. Usually the egg is laid and the larva protrudes through the intersegmental membrane between segments 3 and 4, 4 and 5, or 5 and 6, and as often on the right side as on the left (Table I). Perkins (1905) stated that Echthrodelphax usually oviposits beneath the wing lobes of its host but that "The position of insertion of the sting is apparently not always the same, this being sometimes inserted beneath the wing-lobe, and sometimes in the ventral side of the body, but the larval sac in either case appears beneath the wing-lobe."

Dissections showed that the egg is creamy white when laid. In eggs near hatching the chorion is light tan. This color change may be due to the action of the ethyl alcohol used as a preservative. The egg (Figure 8) is

FIGURE 7

OVIPOSITION SCAR AND PLACEMENT
OF EGG OF *P. minimus*

TABLE I

LOCATION OF LARVAL STAGE OF *P. minimus* ON THE ABDOMEN OF ADULT SIX-SPOTTED LEAFHOPPERS COLLECTED IN THE FIELD

Intersegmental membrane	Number of parasites	
	Left	Right
Between segments		
1 - 2	0	0
2 - 3	6	0
3 - 4	48	43
4 - 5	83	81
5 - 6	27	14
6 - 7	3	1
7 - 8	0	0
Total	167	139
Per cent	54.6	45.4

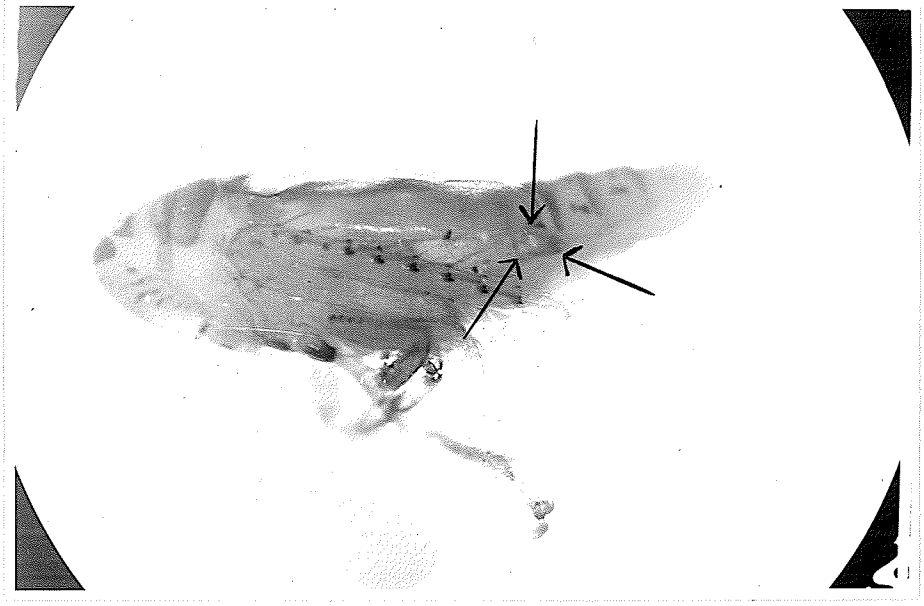

FIGURE 8

EGG (BETWEEN ARROWS)
OF P. minimus

about 0.19 mm. long by 0.10 mm. wide, oval to reniform. There is no sculpturing on the chorion. Eggs dissected from the parasite oviduct measured 0.164 mm. long to 0.070 mm. wide. They were subreniform and white.

Fenton (1918) found that the eggs of the species of Gonatopus that he studied were either oval or kidney-shaped, varying from light yellow to dark grey or dark brown. They ranged from 0.15 to 0.211 mm. in length and from 0.08 to 0.095 mm. in width. There was "no sculpturing on the chorion of any studied" and "no surface structures" on those laid within the body of the host. The position of an oviposition scar in relation to the egg is shown in Figure 7. Usually the oviposition scar is not visible due to non-formation of scar tissue or to protrusion of the larva through the puncture. The larva protrudes through the oviposition scar because of the pressure set up by its development. Fenton (1918) found the oviposition puncture to be the point of rupture by the larva when protruding from its host. He stated that, "It also pushes its way along the path previously made by the ovipositor toward the external point of insertion of the latter."

The empty chorion has not been detected due to its translucence and minute size.

Larva

There are five larval instars. The first four are sedentary and parasitic in the host and the fifth is an active, voracious stage. The exuviae of the first, second, third and fourth ecdyses are permanently fastened into the body wall of the host. Oral lobes (Figure 9) are present in the second, third and fourth instars. These lobes resemble somewhat a greatly expanded and fleshy mandible. Each lobe is supported at its base by four hard, dark, rod-like structures. These lobes have been described by Fenton (1918) as homologues of the mandibles of the fifth instar larva. A ventral process (Figures 10 and 11) is present in the mature second instar and the third and fourth instars. It is located about midway between the cephalic and caudal extremities and serves to anchor the parasite to the host. Table II shows the measurements of the five larval instars in relation to period of development.

First instar. The first instar larva (Figure 13) is sacciform, subreniform, white, and when it hatches is about the size and shape of the egg. It is 0.156 mm. long and 0.086 mm. deep when eclosed and 0.216 mm. long and 0.149 mm. deep just prior to the first ecdysis (Table II).

This stage is similar to the embryonic stage which Keilin and Thompson (1915a) reported to occur between the egg stage and first instar in the polyembryonic Aphelopus

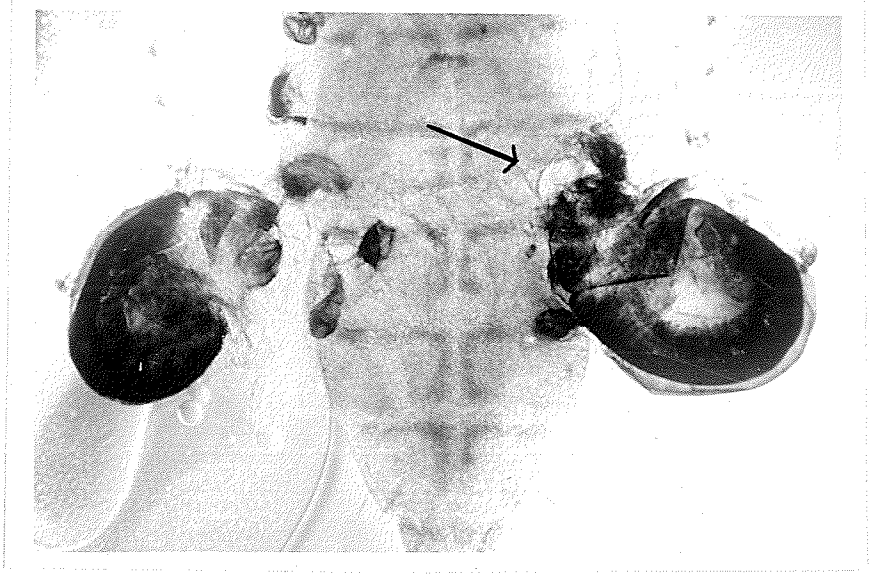

FIGURE 9

ORAL LOBES OF THE FOURTH INSTAR
LARVA OF P. minimus

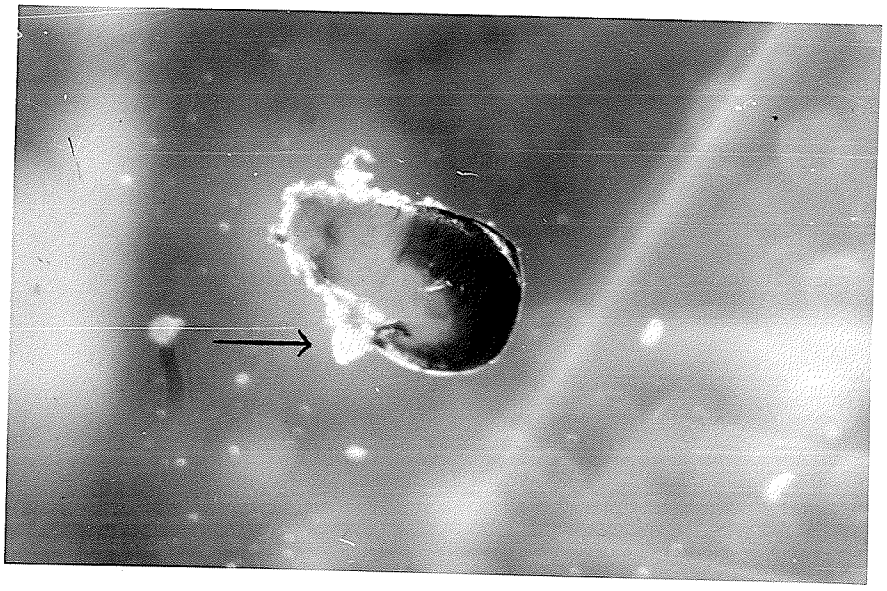

FIGURE 10

THIRD INSTAR LARVA OF *P. minimus*
SHOWING VENTRAL PROCESS

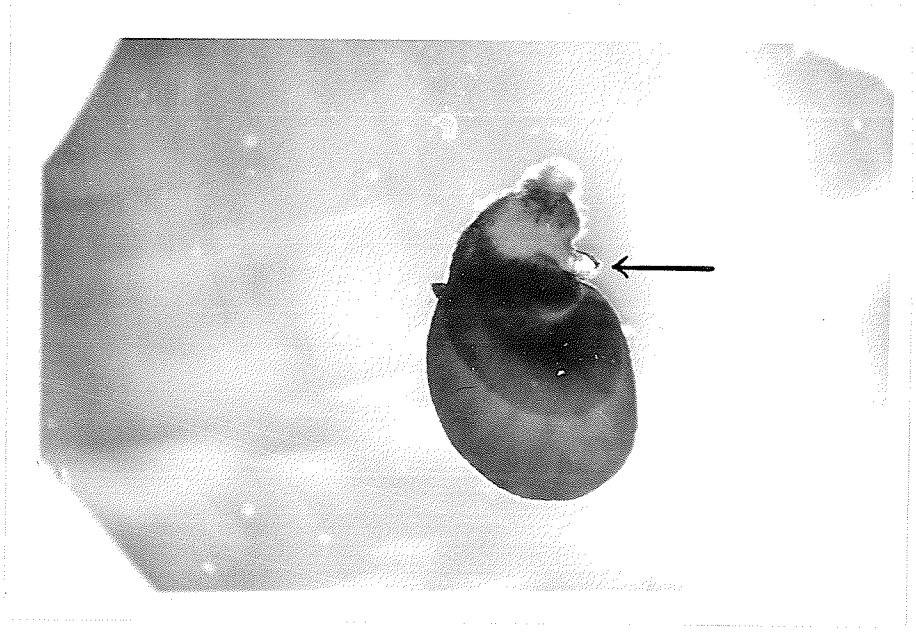

FIGURE 11

FOURTH INSTAR LARVA OF P. minimus
SHOWING VENTRAL PROCESS

TABLE II

MEAN LENGTH AND DEPTH[A] (MM.) OF LARVAL INSTARS OF
P. minimus IN RELATION TO PERIOD OF DEVELOPMENT

Period of development (hours)	Instar									
	FIRST		SECOND		THIRD		FOURTH		FIFTH	
	Length	Depth	Length	Depth	Length	Depth	Length	Depth	Length	Depth
0 - 24	0.181	0.115								
24 - 33	0.194	0.119								
33 - 46	0.185	0.120								
46 - 58	0.184	0.123								
58 - 71	0.203	0.117								
71 - 95	0.200	0.119								
95 - 100	0.216	0.149								
100 - 107			0.294	0.164						
107 - 119			0.367	0.197						
119 - 125			0.427	0.236						
125 - 144			0.443	0.229						

TABLE II (continued)

Period of development (hours)	Instar									
	FIRST		SECOND		THIRD		FOURTH		FIFTH	
	Length	Depth	Length	Depth	Length	Depth	Length	Depth	Length	Depth
144 - 150			0.464	0.233						
150 - 159			0.518	0.324						
159 - 165					0.581	0.359	0.816	0.454		
165 - 183					0.630	0.354	0.818	0.456		
183 - 221					0.556	0.349	0.883	0.527		
221 - 232							1.121	0.793	2.390	0.890

*Definition of the term "depth" is illustrated in Figure 12.

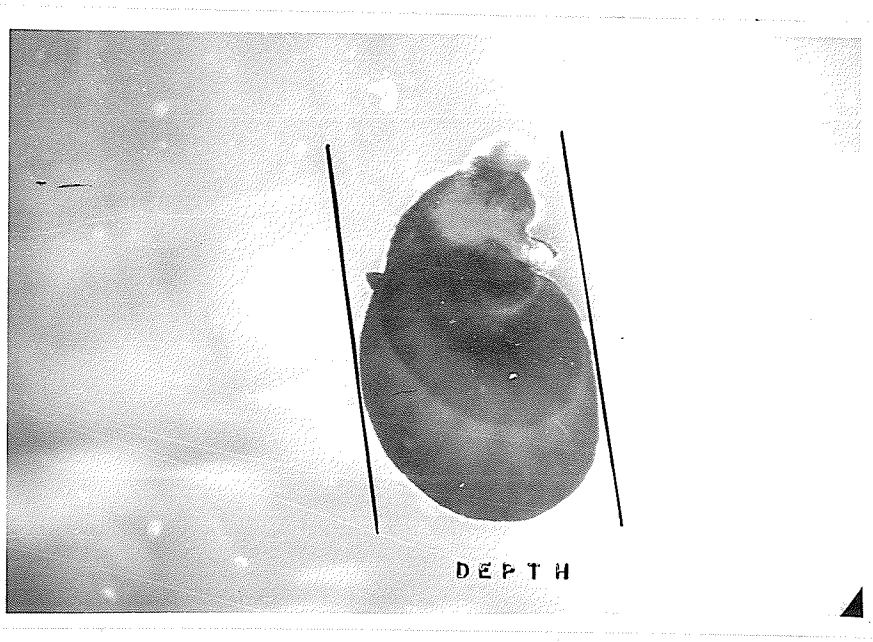

FIGURE 12

ILLUSTRATION OF THE TERM "DEPTH" USED
IN MEASUREMENTS OF LARVAE

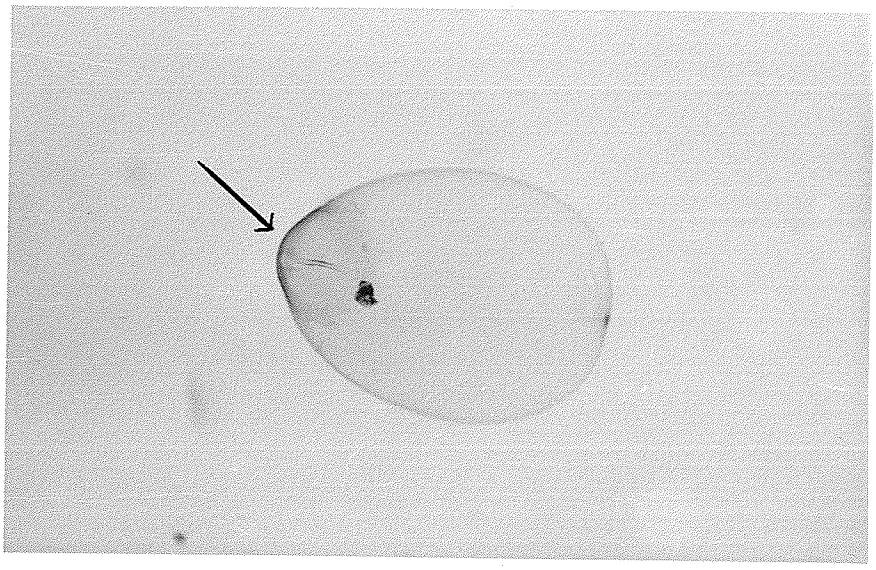

FIGURE 13

FIRST INSTAR LARVA OF *P. minimus*
SHOWING BREATHING PORE

melaleucus, a parasite of Erythroneura hippocastani. Fenton (1918) stated that he did not know the relationship of this "embryo" to the first instar larva.

The first instar larva becomes blunt ovate as it completes its development. Anteriorly there is a dark rod-like spot in the cuticle at which position the mouth parts of the second and successive instars develop. Possibly this rod anchors the parasite to its host. Caudad, this stage exhibits a pigmented disk-like area possibly darkened by action of the atmosphere. This darkened area is split forming a breathing pore which late in the first instar is extruded from the intersegmental membrane of the host (Figure 13). The larva is visible under a low power microscope within three hours of oviposition in either nymphs or adults. The larval sac is visible externally on the host in the late first or early second instar, approximately four to five days after oviposition. The transition from first to second instar is marked by a splitting of the first instar cuticle. The split begins at the anterior end and continues back for about two-thirds of the body length.

Second instar. The early second instar larva is white, straight, 0.294 mm. long and 0.164 mm. deep. Late second instar larvae are "U-shaped" and have measured up to 0.518 mm. long and 0.324 mm. deep. The relationship of length to depth (Table II) is a good indication of the curl-

ing tendency which late in the second instar produces the "U-shaped" larva. Oral lobes are present.

The early second instar is covered toward the posterior end by the exuviae of the first instar larva. This cast skin is noticeably darker in that portion which protruded from the host in the last part of the first instar. As the second instar larva enlarges, this darker portion splits (Figure 14), remaining just outside the host at the point of attachment of the parasite. The cast skin becomes a portion of a collar-like attachment of the larva into the integument of its host. Two oral lobes are visible at this early stage.

A small remnant of the first exuviae is present on each side of the parasite larva at the point of juncture with the host. Fenton (1918) appears to have overlooked this small exuviae, a fact inferred by Clausen (1940) who stated "on the basis of the illustrations given, there would seem to be some doubt that the first exuviae of the sac is the actual first exuviae of the larva."

Third instar. The third instar larva (Figures 15 and 16) is white and much more curved than the second instar. The early third instar is 0.581 mm. long and 0.359 mm. deep. Although the mean length for the late third instar was 0.556 mm. long and 0.349 mm. deep (Table II), the greatest length for any specimen measured was 0.652. Oral lobes are present.

FIGURE 14

EARLY SECOND INSTAR LARVA OF P. minimus
SHOWING SPLIT OF FIRST EXUVIAE

FIGURE 15

THIRD INSTAR LARVA OF *P. minimus*

FIGURE 16

CAST SKIN OF THIRD INSTAR LARVA OF
P. minimus SHOWING SPIRACLES

The third instar larva may be recognized by the two exuviae which surround it. The second exuviae is much larger than the first and is located inside of and protruding from the first. The first exuviae is minute and scale-like and is easily overlooked.

Fenton (1918) stated: "The second molt occurs from five to ten days after the emergence of the sac, and is indicated by the rupturing of the first exuvium along a median-dorsal line." If this unlikely finding is correct, then the third instar larva is contained within the unsplit second and the first exuviae at the start of its molt and thereafter in the second exuviae. The fourth stage would be contained within the third and second exuviae at the beginning of the molt and thereafter within the third exuviae. Similarly the fifth instar would finally split the third when it molts and would remain within the fourth exuviae until it emerged from the host. This would mean that the fifth stage in reality breaks out of two exuviae. Fenton (1918) stated, however, that the fourth instar sheds only the head capsule. Clausen (1940) stated that it appears that Fenton's first is in reality a later (second) exuviae. In P. minimus the first exuviae is much smaller than that reported by Fenton (1918). It is split by the second instar larva, just as the third is split by the fourth instar and the fourth by the fifth instar. There is a complete molt of the fourth instar larva in P. minimus.

Fourth instar. The fourth instar larva is white and U-shaped. The early fourth instar is 0.816 mm. long and 0.454 mm. deep. The late fourth instar is 1.121 mm. long and 0.793 mm. deep (Table II). This stage is encased by the fourth exuviae and the split third, second and first exuviae (Figure 17). Oral lobes are present in the fourth instar. They are easily broken off when the parasite is removed from the host. Care must be exercised in dissecting out the parasite if the lobes are to remain attached to the parasite head. Fenton (1918) shows what he considered to be a mandible, not an oral lobe, in the fourth instar of Anteon sp. His diagram, however, resembles the head of P. minimus with the oral lobes removed and with their supporting basal structures remaining in position. Fenton (1918) stated that the fourth instar is not comparable to the first three and: "It is characterized by the development of the mandible, beneath which are formed those of the fifth stage. There is no complete fourth molt, so far as is revealed by dissections, other than a shedding of the head capsule." He speculates: "It is possible that this instar is entirely eliminated in some of the more highly specialized species." There are no incomplete or suppressed molts in P. minimus.

The transition of fourth to fifth instar is shown in Figures 18 and 19 where the fourth exuviae shows splitting by a parasite near the time of emergence from the host. The

FIGURE 17

FOURTH INSTAR LARVA OF P. minimus ATTACHED TO FIFTH INSTAR NYMPH OF THE SIX-SPOTTED LEAFHOPPER

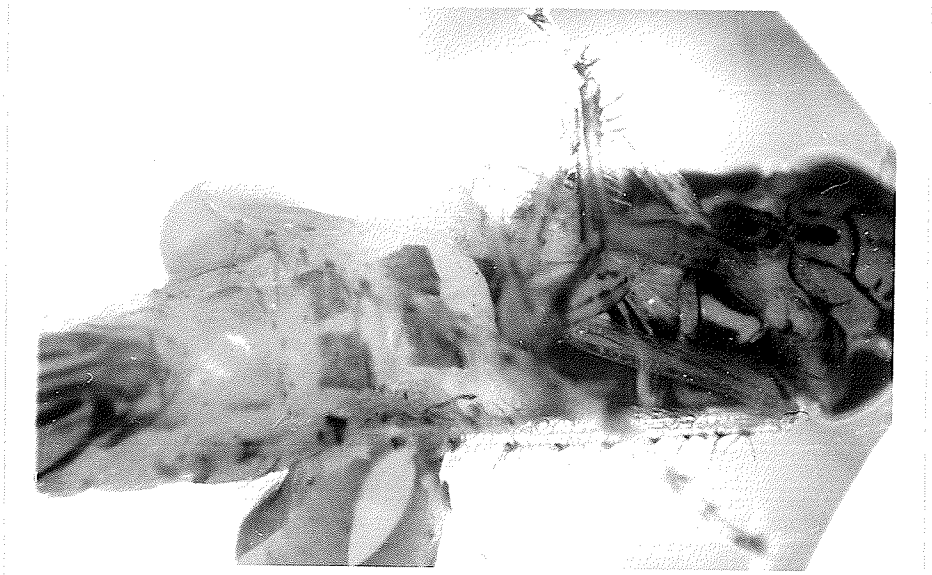

FIGURE 18

TRANSITION OF FOURTH TO FIFTH INSTAR OF P. minimus SHOWING SPLITTING OF FOURTH EXUVIAE BY A PARASITE NEAR EMERGENCE FROM HOST

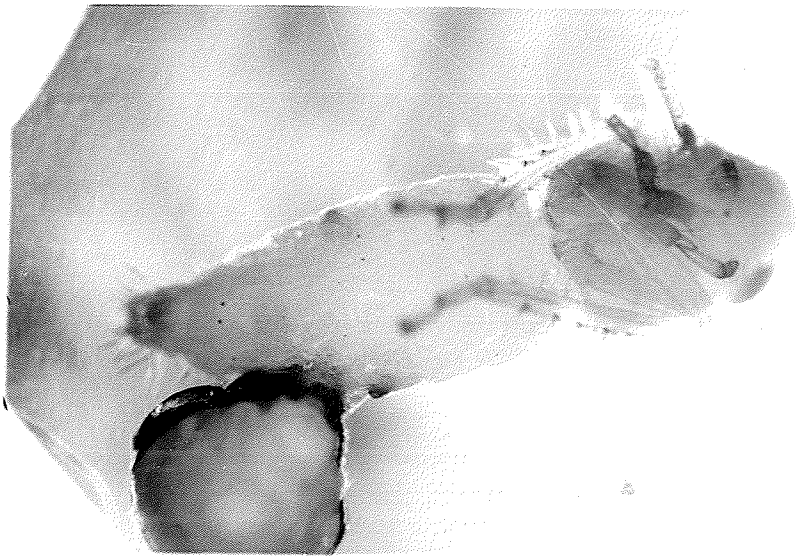

FIGURE 19

TRANSITION OF FOURTH TO FIFTH INSTAR OF P. minimus SHOWING EXUVIAE COMPLETELY SPLIT AND FIFTH INSTAR LARVA BEGINNING TO EMERGE

fourth instar is surrounded by the third exuviae as well as the second and first. The fifth instar larva, therefore, emerges from a rosette of four exuviae.

Fifth instar. The fifth instar larva (Figures 20 and 21) is an active feeding stage free from the host. It is straight, 2.39 mm. long and 0.89 mm. in diameter. It varies from milky white, at time of molting to fifth instar, to yellowish or pinkish white after eating out the host. Perkins (1905) noted a change in color of fifth instar dryinid larvae which he attributed to ingestion of the contents of the host. The fifth instar larva further differs from the first four instars in that strong sclerotized mandibles have replaced the oral lobes (Figure 22). The fifth exuviae is split anteriorly and shed along with the head capsule. It resembles a pad and is located at the caudal extremity of the cocoon. The fifth is the only conventional larval molt. All the other larval exuviae are split at both ends and retained as a cylinder about the larva.

Cocoon

The cocoon (Figures 23 and 24) is constructed of a silken outer framework much like a tent, and an inner ovate receptacle. The outer cocoon traps a layer of air about the inner cocoon at least along the lateral and ventral surfaces. This layer of air may act as insulation and aid overwintering, especially in those instances where the cocoon is spun on stems and leaves of plants and may remain above the surface

FIGURE 20

FIFTH INSTAR LARVA OF *P. minimus*
EMERGING FROM HOST

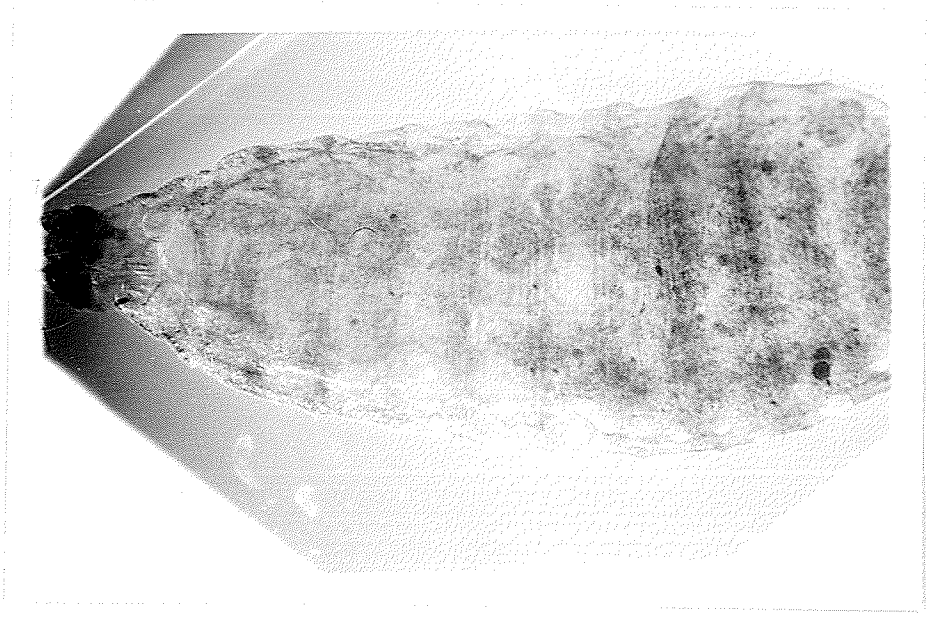

FIGURE 21

FIFTH INSTAR LARVA OF P. minimus
SHOWING SEGMENTATION

FIGURE 22

FIFTH INSTAR LARVA OF *P. minimus*
SHOWING WELL DEVELOPED MANDIBLES

FIGURE 23

COCOON AND PUPA OF P. minimus

FIGURE 24

COCOON OF P. minimus WITH
SAND PARTICLES ADHERING

of the snow cover. Cocoons of P. minimus have been found only in cages, in or on sand, and also on the stems and leaves of caged plants. Fenton (1918) stated: "The cocoon is completed in from one to two days, although larvae that are to pass the winter may be seen lining their cocoons for days after they are apparently finished."

Preimaginal stage

The preimaginal stage (Figure 25) is herein defined as that stage, within the cocoon, in which external development of the adult appears to be complete. The development of pigmentation of the preimaginal insect was observed in 93 specimens (Table III). No darkening was noted before 150 hours had elapsed from time of larval emergence from the host. At 150 hours there was a trace of darkening, involving partial coloration of the compound eyes and some show of color in the region of the rectum, perhaps indicating accumulation of fecal matter. Light coloration involving darkening of all of the compound eye, the ocelli and a further accumulation of fecal mass began at 175 hours but several specimens were still only lightly pigmented after 250 hours of development. Medium darkening was reached at 225 hours but was not general before 250 hours and involved a considerable degree of darkening of the body. Some specimens remained with only medium darkening after as many as 300 hours had elapsed. Some specimens showed

FIGURE 25

PREIMAGINAL STAGE OF *P. minimus*

TABLE III

PIGMENTATION OF PREIMAGINAL STAGE OF *P. minimus*

Hours of development from larval emergence	Degree of pigmentation							
	Trace		Light		Medium		Full	
	No. of specimens		No. of specimens		No. of specimens		No. of specimens	
	Male	Female	Male	Female	Male	Female	Male	Female
125	0	0	0	0	0	0	0	0
150	0	2	0	0	0	0	0	0
175	1	3	0	1	0	0	0	0
200	0	0	0	3	0	0	0	0
225	1	0	0	3	0	1	0	0
250	0	0	3	3	11	7	13	5
275	0	0	0	0	0	0	0	0
300	0	0	0	0	3	0	18	6
325	0	0	0	0	0	0	3	5
350	0	0	0	0	0	0	0	1

complete pigmentation when 250 hours of development had elapsed. All specimens with 325 hours of development after larval emergence showed complete body pigmentation.

CHAPTER VI

LIFE HISTORY AND HABITS OF *Pachygonatopus minimus*

The life cycle of *P. minimus* consists of egg, larva, pupa and adult. The female adult is unusual in that it is a predator as well as a parasite. The first four larval stages are also unusual in that they are contained within their successive cast skins.

Adult

Seasonal occurrence. The earliest date of collection was for a female taken on June 25, 1959. The latest date of collection was also for a female taken on October 3, 1959. No males were collected in the field. The adult female is not readily collected by sweep net because it is wingless and clings to the plant in contrast to the leafhopper which jumps or flies when disturbed. Also, the female of *P. minimus* spends some time on the soil surface moving from plant to plant. Males are short lived and emerge before the females. Observations in the laboratory have shown that they tend to remain near emerging females and probably do not leave the site after mating (Perkins, 1905). It was not possible to determine any seasonal population trend because only a few specimens were collected.

Time of emergence. Observations on caged material showed that adults emerged from their cocoons mainly from about 10:00 a.m. until 3:00 p.m.

Sex ratio. Observations on sex ratio of caged material showed that of 110 adults that emerged, 46 were females and 64 were males, a ratio of 41.8 females to 58.2 males.

Male and female parasites have been reared from both sexes of the host. From 13 parasitized male leafhoppers, 11 male and 2 female parasites emerged and from 19 parasitized female leafhoppers, 7 males and 12 female parasites emerged. In another instance where an adult parasite was known to have emerged from a doubly-parasitized host, the sex of the parasite was male.

Development rate of sexes. Of the several thousand leafhoppers collected on barley at Fisher Branch, July 1, 1960, 175 adults were parasitized. The time interval from emergence of the fifth instar larva from the host, to the emergence of the adult from its cocoon was determined by observation in the laboratory. Records were obtained for 55 males and 38 females. Some of the remainder of the 175 specimens died in rearing and some were used for other studies.

The sexes had a comparable rate of development through the fifth larval instar and the remainder of the cocoon stage. For 55 males the duration of these stages ranged from 16.0 to 18.8 days and averaged 16.3. For 38 females the range was 14.5 to 20.0 days and the average 16.6. Since it has been observed that males emerge about two days earlier than females

it may be deduced that the developmental period of the male on the host is less than that of the female.

Mating habits. Mating was observed on two occasions in the laboratory. In one instance, mating occurred in a glass tube 9 mm. in inside diameter and 20 mm. long. In the other instance, mating took place in a vial 9 mm. in inside diameter and 38 mm. in length. The mating period was perhaps one-half minute in the first and a few seconds in the second. Mating may possibly not have been completed in the second instance. On one occasion, an emerging female was noted to be highly attractive to males, which were flying about rapidly in small circles and striking their bodies against the female and the cocoon. No mating occurred on this occasion. Newly emerged and mature adults in various combinations were caged together on numerous occasions in cages of various types with sugar solution supplied. Subsequent rearings from these females resulted in only two female progeny, indicating that either very little mating occurred or that the caged females under these conditions laid chiefly male-producing eggs. George (in litt.)[1] has found that E. plesius produces only males by parthenogenesis. This is contrary to Fenton (1918) who stated: "Adults from unfertilized eggs of Gonatopus contortulus Patton were all females, and were normal and active in every way."

---

[1]George, J. A. Entomologist, Canada Agriculture Research Laboratory, St. Catharines, Ontario.

Perkins (1905) stated that Dryinidae can reproduce parthenogenetically and probably frequently do so. He stated: "In one case that was noticed, that of a species of Pseudogonatopus, of the offspring thus produced only one in forty was of the male sex."

Oviposition. The female has large compound eyes and the ability to run and climb rapidly. This may aid in location and capture of leafhopper nymphs and adults. She has chelate fore tarsi with which she can strike rapidly and accurately and grip her prey securely. The chelate limb of the dryinid female has been well described by Mik (1882), Perkins (1906, 1912), Fenton (1927) and others. The female can sometimes intercept her prey while running, but when this fails she will slowly stalk her prey or will remain stationary in which case nymphs often approach her. The capturing stroke is too rapid to see by eye. Once captured the nymph is grasped in the chela which is applied to one of the basal segments of the leg, often to the femur, of the host. The host is often grasped also by the mandible of the parasite which usually is clamped on the wing pad but which may be clamped on a coxa of the metathoracic leg. This often leaves scars, especially on the wings and coxae of nymphs. When it has clasped the host securely, the parasite curls its abdomen beneath the abdomen of the host. The parasite rests upon the four rear legs while it inserts the ovipositor (Figure 26), in or just below

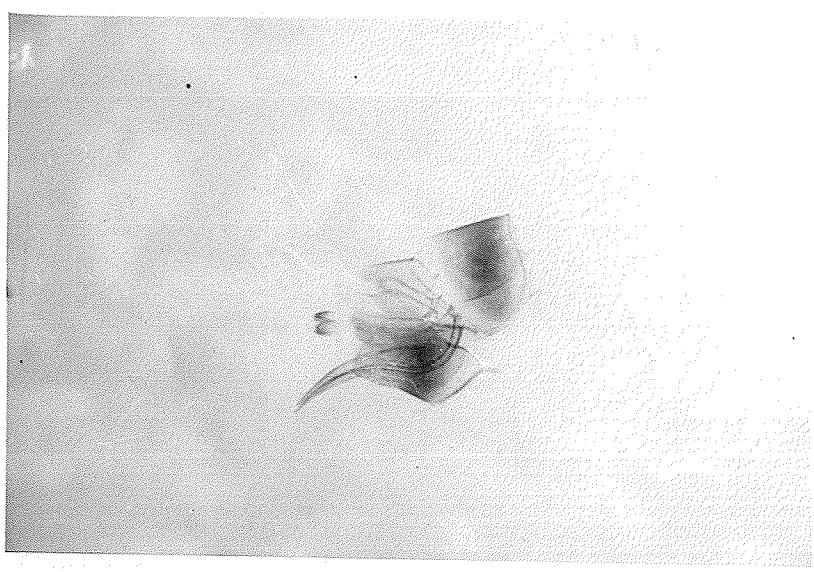

FIGURE 26

OVIPOSITOR OF *P. minimus*

the pleural area of the abdomen on the side opposite to that grasped by the parasite. Fenton (1918) noted that in the case of nymphs with opaque bodies, the sting of the dryinid could be seen "working this way and that with extreme rapidity, just beneath the cuticle." The sting is probably useful in subduing the host and in weakening the integument for subsequent oviposition. In P. minimus oviposition usually does not result in loss of consciousness by the host although it does seem dazed, and is inactive for a period of perhaps thirty seconds. During oviposition a parasite was noted to tap rapidly with one antenna upon the middle third of the leafhopper antenna while holding the other antenna at rest over its dorsum. The second antenna was used occasionally to tap the host body. This tapping was continuous during the whole of the act of oviposition and appeared to be used for its subduing or hypnotic effect. One parasite was noted to hold the host with the mandibles until the ovipositor had been completely freed.

No oviposition or parasitism of first or second instar nymphs was noted but oviposition and parasitism were noted on third, fourth and fifth instar nymphs and adult leafhoppers. Once oviposition has occurred the nymph does not generally molt. In one instance molting occurred a few minutes after oviposition and in another instance a cast skin was found

with a parasite attached indicating that the nymph had molted. Parasitized nymphs remain in the instar in which they are parasitized for a period longer than normal and die upon emergence of the parasite.

Predation. In a preliminary study, eight females were found to kill an average of one and one-half nymphs per day over a period of ten days. In a later test (Table IV) a very low level of predation was recorded. Three parasites in a total of 57.6 predator-days drained the body fluids from 24 nymphs. During this period 445 eggs were laid. On the basis of the preliminary study this ratio of nymphs killed by feeding, to the number of eggs laid, is estimated to be far too low. It may possibly be due to examining dead nymphs too long after predation.

The predatory habits of female dryinids have been considered by several authors to be of greater control value than their parasitism (Clausen, 1940). If one allows one and one-half nymphal predations per day for the 57.6 predation-days shown in Table IV, one might expect about eighty-five nymphs to be destroyed. The laying of 445 eggs might be expected to parasitize and destroy about 400 leafhoppers which, although continuing to feed, would produce no progeny.

Feeding. The predatory female captures and holds her prey with the chelae. In feeding, the female bites actively through the cuticle. The jaws may be seen to move rapidly

TABLE IV

OVIPOSITION AND FEEDING RECORD OF CAGED FEMALES OF *Pachygonatopus minimus* ON SIX-SPOTTED LEAFHOPPER NYMPHS

No. of parasites*	Date and time of exposure	Duration of exposure (hours)	No. of nymphs exposed	No. of eggs laid	No. of nymphs chewed
3	12:30 p.m., July 4 to 12:30 a.m., July 5	12.00	not recorded	3	
	12:30 a.m., July 5 to 2:30 p.m., July 5	14.00	25	8	
	2:30 p.m., July 5 to 10:30 p.m., July 5	8.00	25	21	
	10:30 p.m., July 5 to 8:30 p.m., July 6	22.00	25	15	
	8:30 p.m., July 6 to 9:15 a.m., July 7	12.75	30	12	
	9:15 a.m., July 7 to 11:30 p.m., July 8	38.25	30	37	
	11:30 p.m., July 8 to 6:15 p.m., July 9	18.75	30	44	1
	6:15 p.m., July 9 to 12:15 a.m., July 10	6.00	20	18	
	12:20 a.m., July 10 to 4:15 p.m., July 10	16.00	25	47	1
	4:15 p.m., July 10 to 10:30 p.m., July 10	6.25	30	27	2
	10:30 p.m., July 10 to 5:30 p.m., July 11	19.00	30	36	1
	5:30 p.m., July 11 to 11:15 p.m., July 11	5.75	25	21	1
	11:15 p.m., July 11 to 11:15 a.m., July 12	12.00	not recorded	25	1
	11:10 a.m., July 12 to 5:30 p.m., July 12	6.25	25	27	

TABLE IV (continued)

No. of parasites*	Date and time of exposure	Duration of exposure (hours)	No. of nymphs exposed	No. of eggs laid	No. of nymphs chewed
3	5:30 p.m., July 12 to 10:45 p.m., July 12	5.25	25	3	1
	10:45 p.m., July 12 to 11:00 p.m., July 13	24.25	15	15	4
2	11:00 p.m., July 13 to 11:45 a.m., July 14	12.75	26	14	1
	11:45 a.m., July 14 to 12:10 a.m., July 15	12.50	20	18	3
	12:10 a.m., July 15 to 1:30 p.m., July 15	13.25	20	10	
	1:30 p.m., July 15 to 11:00 p.m., July 15	9.50	25	24	3
	11:00 p.m., July 15 to 11:00 p.m., July 16	24.00	25	31	2
	11:00 p.m., July 16 to 1:30 p.m., July 18	38.50	36	6	
	1:30 p.m., July 18 to 2:30 p.m., July 20	49.00	25	4	
1	2:30 p.m., July 20 to 4:45 p.m., July 21	26.25	20	9	1
	4:45 p.m., July 21 to 11:00 a.m., July 28	162.25	20	50	
	11:00 a.m., July 28 to 10:10 p.m., Aug. 1	107.25	20	9	1
	10:10 p.m., Aug. 1 to 10:40 p.m., Aug. 3	48.50	30	8	
	10:40 p.m., Aug. 3 to 3:00 p.m., Aug. 5	40.25	25	3	1
	No. of predation days	57.60			
	Ave. no. of eggs per predation day			7.9	
	Ave. no. of nymphs chewed per predation day				0.4

*Parasites collected in field July 1, 1960

within the cuticle. There is a sucking action which in one instance observed, was so strong as to cause a heaving of the body wall of the host. One nymph, fed upon for four minutes, appeared healthy. One hour after the parasite attack, the nymph still appeared well, but twenty minutes later it appeared to be in poor condition. Two hours after being fed upon the nymph was on its back and only a few spasmodic movements of the limbs were noticeable. It is thus obvious that field samples may show some live nymphs which have been fed upon, and indeed some injured nymphs have been found in collections. These nymphs would in all likelihood soon die without becoming adults.

On one occasion, two parasites were observed to attack a nymph, one from each side, the second attacking during the disturbance caused by the first attack. The host later died, possibly due to a poor rearing technique or to predation, and it is not known if this was simultaneous feeding or oviposition or a combination of the two.

Parasites in cages have been noted to feed upon parasitized hosts.

Longevity. The longest life span noted was that of a female, reared in the laboratory, which lived from January 9, 1960 to February 24, 1960, a period of 46 days. A female collected in the field on July 1 lived in the laboratory until August 5, 1960, a period of 35 days. The lifespan of 36 females

reared in the laboratory ranged from 5 to 46 days and averaged 12.14 ± 1.57* days (Table V).

The life span of 40 males, reared in the laboratory, ranged from zero to four days and averaged 2.15 ± 0.17* days (Table VI). Some males held at 45°F lived up to 14 days.

Both in males and females longevity depends to a great extent on environmental conditions. They were not seen feeding on sugar solution supplied to them nor on moisture on leaves nor on the excretions of leafhoppers. However, they may have fed when they were not under observation. Perkins (1905) stated that: "When the hoppers (sugar cane leafhoppers) were excreting an abundance of honey-dew, the parasites (Ecthrodelphax) fed freely upon this, but if not, some sweet liquid was supplied in place of it. Without this liquid food, in a hot locality the parasites die very quickly, and the cage was freely sprinkled with water each day to advantage." Perkins (1905) further stated that a dryinid of the genus Paranteon attacks a sluggish, honey-dew secreting, ant-attended species of leafhopper. He stated that numbers of the parasites, bred together, stand suberect, ". . . stroking one another, licking each other's mouth, soliciting food . . . ." Fenton (1918) stated that both sexes of Paranteon fed readily on sugar solution. It should be noted here that the six-spotted leafhopper, at least in the nymphal stage, apparently has a high moisture requirement, particularly when deprived of food plants. Leafhopper nymphs collected and trans-

*Standard error

TABLE V

LONGEVITY OF FEMALES OF Pachygonatopus minimus REARED IN THE LABORATORY, 1960

Number of parasites	Longevity (days)	Number of parasite days
1	5	5
6	7	42
4	8	32
8	9	72
5	11	55
2	12	24
4	14	56
3	17	51
1	19	19
1	35	35
1	46	46
Total 36		437
Average		12.14 ± 1.57*

*Standard error

TABLE VI

LONGEVITY OF MALES OF *Pachygonatopus minimus* REARED IN THE LABORATORY, 1960

Number of parasites	Longevity (days)	Number of parasite days
10	1	10
18	2	36
8	3	24
4	4	16
Total 40		86
Average		2.15 ± 0.17*

*Standard error

ported in moist soil to the laboratory remained alive, active, and apparently completely unaffected after 36 hours of fasting. Nymphs held in cages without host plants or other sources of moisture died within six hours. Where the six-spotted leafhopper is found reproducing abundantly, environmental conditions may also be suitable for dryinids.

Time of adult activity. Adult females were active in the field from early morning until dusk provided that the temperature was sufficiently high for activity. They are active in the laboratory continuously provided that there is sufficient light and a suitable temperature. A comparatively low level of light is required for activity.

Males in the presence of an emerging female are very active and aggressive and even fly against the female.

Mobility of parasitized leafhoppers. Three tests were designed to check whether the mobility of leafhoppers was affected by parasitism.

In the first test, twelve lots of leafhoppers were taken from a sweep net collection, with an aspirator, as they crawled upward in the net toward light. It was thought that parasitized leafhoppers might be slower in reaching the top of the net. There was no apparent difference (Table VII) in mobility between parasitized and non-parasitized leafhoppers for adult males or females or nymphs.

TABLE VII

MOBILITY OF PARASITIZED LEAFHOPPERS

Lot No.*	Number of leafhoppers								Percent parasitism			
	Parasitized				Non-parasitized							
	Male	Female	Nymphs	Total	Male	Female	Nymphs	Total	Male	Female	Nymphs	Total
1	1	4	0	5	19	14	0	33	5.0	22.2	0.0	13.2
2	0	4	0	4	25	24	3	52	0.0	14.3	0.0	6.8
3	8	5	4	17	21	26	6	53	27.6	16.1	40.0	24.3
4	4	18	4	26	24	34	12	70	14.3	34.6	25.0	27.1
5	1	11	1	13	25	42	20	87	3.8	20.8	4.8	13.0
6	7	11	1	19	24	23	28	75	22.6	32.4	34.5	20.2
7	6	7	5	18	29	30	25	84	17.1	18.9	16.7	17.6
8	5	14	4	23	48	37	46	131	9.4	27.5	8.0	14.9
9	2	15	3	20	48	34	37	119	4.0	30.6	7.5	14.4
10	5	7	0	12	37	34	12	83	11.9	17.1	0.0	12.6
11	3	10	0	13	19	22	24	65	13.6	31.3	0.0	16.7
12	8	16	7	31	36	31	31	98	18.2	34.0	18.4	24.0
Total	50	122	29	201	344	331	244	950				
Ave.	4.2	10.2	2.4	16.8	29.6	27.6	20.3	79.2	12.3	26.9	10.6	17.5

*Leafhoppers aspirated off in lots of about 50-100 as they came to the top of the net

In the second test, collections of leafhoppers were made in an oat crop in the direction of each of the cardinal points of the compass in the crop and to the east above the crop. Two sets of sweeps were made to the north, one in the margin of the crop to check for marginal effect as compared to the other set of sweeps to the north made in the center of the crop.

The leafhopper collections were examined for parasites and showed about 11 to 17 per cent parasitism with one exception of 29 per cent. The high percentage of parasitism in this latter collection caused subsequent re-examination of the other samples. Percentage parasitism was found to be two to three times as high as had been previously found. It is believed that this discrepancy was due mainly to improved techniques in examination and to more skill in recognizing minute parasites. It was found that leafhoppers must be squeezed to create a pressure to lengthen the abdomen and expose small parasites in the intersegmental membrane. It is possible that some first instar parasites may have darkened from impurities in the alcohol or the corks. It was noted that suitable magnification and very good lighting were critical factors in detecting a high proportion of the parasites present. The results are shown in Table VIII.

Leafhoppers fly when disturbed by a shadow or movement of an object near to them. In the process of sweeping, para-

TABLE VIII

EFFECT OF DIRECTION OF SWEEPING, IN RELATION TO WIND AND SUN, UPON THE PERCENTAGE OF PARASITIZED LEAFHOPPERS COLLECTED

Direction and location of sweep	Shadow cast on swept area	Sweep direction as related to wind	Per cent parasitism in sweep
East above crop	No	Downwind	35.5
East above crop	No	Downwind	32.0
West in crop	No	Upwind	34.0
West in crop	No	Upwind	26.3
East in crop	No	Downwind	31.8
East in crop	No	Downwind	27.4
North across middle in crop	Yes	Crosswind	27.5
North across middle in crop	Yes	Crosswind	29.0
South in crop	No	Crosswind	22.0
South in crop	No	Crosswind	21.6
North at border in crop	Yes	Crosswind	27.2
North at border in crop	Yes	Crosswind	22.0

sitized leafhoppers, if sluggish, would tend to remain in the crop whereas non-parasitized leafhoppers would fly up. Therefore, in this test more parasitized leafhoppers should have been taken in the crop than above the crop, especially where a shadow was cast on the sweeping area. No differences were obtained (Table VIII). Leafhopper collections tend to be larger when made downwind. It was postulated that if parasitized leafhoppers are sluggish, they should tend to remain in the area being swept while the active leafhoppers would tend to move downwind and be swept over repeatedly. No difference was obtained as may be noted by comparing the east and west collections (Table VIII). It was further postulated that collections made to the south should show more parasitism than those made to the north, if parasitized leafhoppers are more sluggish. This is because with a shadow cast in the collections to the north the west wind would carry away flying non-parasitized leafhoppers from the path of the sweep. This effect was not obtained. It is evident that parasitized leafhoppers are at least as active as are non-parasitized leafhoppers.

In the third test collections were made either by sweeping head lettuce with a net or by shaking lettuce heads into a net. By sweeping, the more active leafhoppers should be collected in a higher proportion than in the shaken collections. The results are shown in Table IX. There was no

TABLE IX

EFFECT OF METHOD OF COLLECTION ON THE PERCENTAGE OF PARASITIZED LEAFHOPPERS COLLECTED

Method of collection	Number of nymphs and adults collected	Per cent parasitism							
		Nymphal instar					Adult		Total collection
		1	2	3	4	5	Male	Female	
Shaken	911	0	0	19.6	14.9	5.8	2.2	0.0	8.6
Swept	383	0	0	8.7	10.8	8.6	11.1	0.0	8.6
Shaken	1553	0	0	9.5	16.0	13.9	5.8	10.5	12.6
Swept	537	0	0	3.0	8.0	11.8	8.7	7.6	9.1
Shaken	1453	0	0	7.2	14.6	5.6	1.5	0.0	6.9
Swept	361	0	0	7.1	18.0	9.8	11.4	3.8	10.0

significant difference in percentage parasitism of leafhoppers collected by either method.

The finding that parasitism by P. minimus does not reduce mobility of the six-spotted leafhopper does not agree with the findings of Fenton (1918) who stated: "The host /an unstated species of leafhopper/ becomes very evidently affected by now, /by the fourth instar parasite/ being sluggish and easily caught." Knowlton[1] believes that ". . . severely parasitized ones /beet leafhoppers/ do less hopping . . . ." than non-parasitized leafhoppers.

Multiple parasitism and suppression by P. minimus. In tests devised to check egg production and larval development of the parasite, host nymphs were exposed to parasites for periods ranging from six to thirty-eight hours and were then held on asters free from parasites. Multiple parasitism was frequent and from one to eleven ovipositions (Table X) in a single host were noted. After several days it was noted that some of the parasites were not developing. When some larvae had begun to emerge from their hosts it was noted that other parasites on the same host had not developed beyond the first instar and had instead shrunk. In three instances of double parasitism (Table XI) both parasites failed to develop due either to no embryogenesis

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[1]Knowlton, G.F., Extension Entomologist, Utah State University (personal correspondence), 1959.

TABLE X

MULTIPLE PARASITISM BY 3 FEMALES OF *Pachygonatopus minimus* ON A SUCCESSION OF HOST POPULATIONS IN A SINGLE CAGE

No. of female parasites in cage	No. of hosts exposed in cage*	Duration of exposure (hours)	No. hosts recovered not parasitized*	No. of ovipositions	No. of hosts parasitized*	Average no. ovipositions per host parasitized	Range in no. ovipositions in a single host
3	30	38:25	2	30	5	6.0	1 - 11
3	15	24:25	2	15	6	2.5	1 - 5
3	30	19:00	7	36	12	3.0	1 - 7
3	30	18:75	7	35	13	2.7	1 - 7
3	25	16:00	2	47	15	3.1	1 - 9
3	30	12:75	--	7	4	1.8	1 - 2
3	Not recorded	12:00	--	25	15	1.7	1 - 3
3	30	6:25	1	27	14	1.9	1 - 5
3	25	6:25	6	27	14	1.9	1 - 5
3	20	6:00	2	16	6	2.7	1 - 5
3	25	5:75	7	16	11	1.4	1 - 2
3	25	5:25	15	3	2	1.5	1 - 2
2	25	24:00	9	31	13	2.4	1 - 6
2	20	13:25	9	10	6	1.7	1 - 4
2	26	12:75	14	14	12	1.2	1 - 2
2	20	12:50	10	18	13	1.4	1 - 3
2	25	9:50	11	24	13	1.8	1 - 5

*Totals do not correspond because of mortality caused by feeding

TABLE XI

SELF SUPPRESSION IN MULTIPLE PARASITISM
BY Pachygonatopus minimus ON THE
SIX-SPOTTED LEAFHOPPER

Number of host individuals	Number per host		
	Ovipositions	Parasites developing	Parasites suppressed
3	2	0	2
75	1	1	0
22	2	1	1
15	3	1	2
3	4	1	3
4	5	1	4
2	7	1	6
20	2	2	0
8	3	2	1
1	4	2	2
4	5	2	3
1	6	2	4
1	7	2	5
1	11	2	9
4	3	3	0
1	9	3	6

or to mutual suppression or some other parasiticidal action. Figures 27, 28, 29 and 30 show one parasite suppressing another, one parasite suppressing six others, two parasites suppressing nine others and three parasites suppressing two others, respectively. Table XI shows the number of suppressed parasites as compared to the number of parasites developing. It may be seen that 121 individuals have a single parasite developing as compared to 41 with multiple parasites developing. In the field double parasitism is rare, triple parasitism is very rare and only one instance of quadruple parasitism was noted. However, where multiple parasitism occurs, suppression may still reduce the parasitism to one per host. Normally only one parasite survives in multiple parasitism as usually the entire remaining body contents of the leafhopper are needed for the final feeding of one fifth instar larva. In a few instances two larvae have emerged from a single host and cocooned and in at least one instance an adult male was obtained.

Egg

Incubation period. Leafhopper nymphs were exposed for twenty-four hours to parasites and then preserved immediately. Upon examination of this group of nymphs there was only one egg but thirty first instar larvae. Although this test limited the incubation period to twenty-four hours or less (Table XII), a subsequent test showed that eclosion occurs within two hours

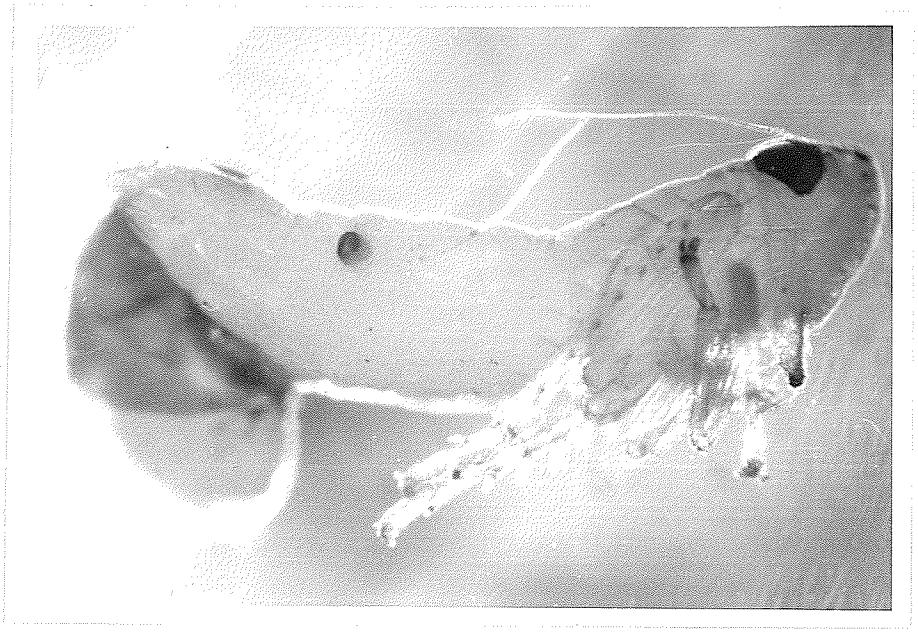

FIGURE 27

MULTIPLE PARASITISM - ONE PARASITE
FULLY DEVELOPED AND ONE SUPPRESSED

FIGURE 28

MULTIPLE PARASITISM - ONE PARASITE
FULLY DEVELOPED AND SIX SUPPRESSED

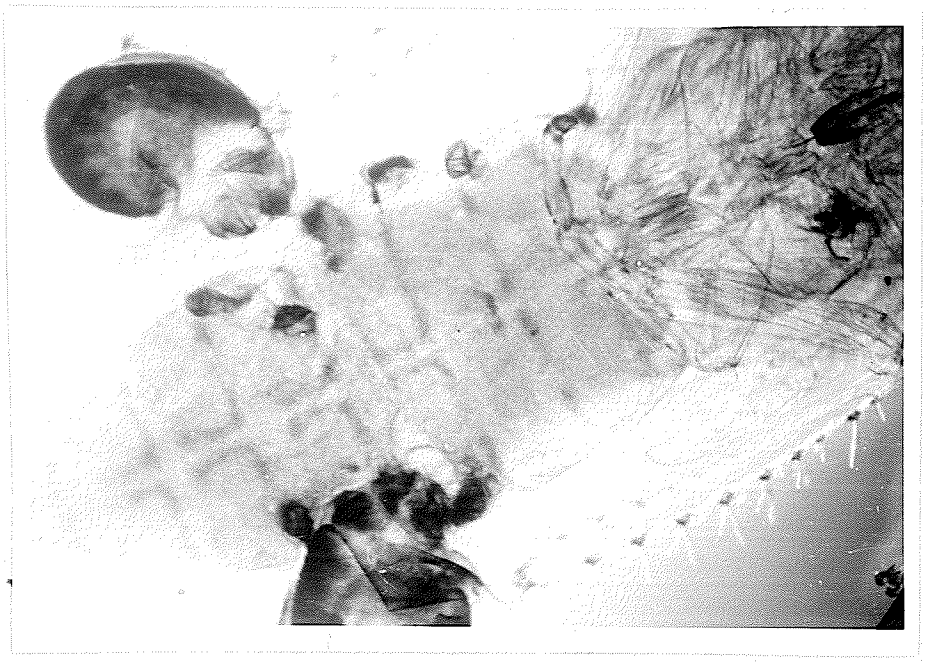

FIGURE 29

MULTIPLE PARASITISM - TWO PARASITES
DEVELOPING AND NINE SUPPRESSED

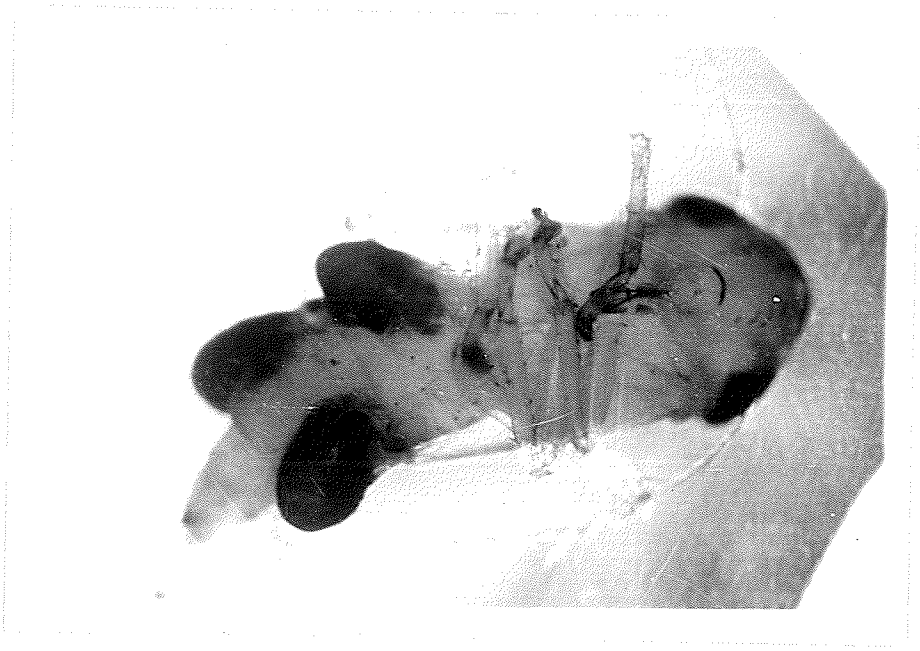

FIGURE 30

MULTIPLE PARASITISM - THREE PARASITES
DEVELOPING AND TWO SUPPRESSED

TABLE XII

DURATION OF THE FIRST FOUR LARVAL INSTARS OF Pachygonatopus minimus IN THE LABORATORY, JULY, 1960.

Length of time leafhoppers exposed to parasites (hrs.)	Period of larval development* (hours)	Number of specimens in each instar when examined				
		I	II	III	IV	V
24	0 - 24	31**				
10	23 - 33	21				
14	32 - 46	10				
12	46 - 58	18				
12	59 - 71	14				
24	71 - 95	9				
4	96 - 100	2				
6	101 - 107	1	16			
12	107 - 119		10			
6	118 - 124		11			
18	124 - 142		12			
6	137 - 143		16			
16	143 - 159		19			
6	159 - 165		2	4		
18	165 - 183		6	8		
38	183 - 221			7	2	
12	219 - 231				5	2
22	232 - 254				4	1
8	253 - 261				2	3
14	261 - 275					4

*The incubation period of the egg is about 3 hours. This time interval has been included in the period of larval development.

**One egg in this group.

and forty minutes of oviposition.

Fenton (1918) stated that: "Since the egg is very minute and often is thrust down deeply into the body, it is practically impossible to locate it either by dissection or by sectioning the host. For this reason the date of hatching is still in doubt and the incubation period can only be estimated from the time the egg is laid to the appearance of the sac outside the body wall of the hopper. In Gonatopus erythrodes (Perk.) a blackish discoloration precedes the appearance of the sac by several days and is noticed five days after oviposition. Since in this case the discoloration is due to the black sac beneath the cuticle, the egg must have hatched within two or three days after being laid."

Larva

Number and duration of larval instars. For the study on the number and duration of larval instars parasites were caged with hosts to obtain material of known oviposition date. The duration of caging varied from four to thirty-eight hours thus creating a time variation of $\pm$ 2 to $\pm$ 19 hours. However, the period caged was usually less than twenty-four hours. In order to determine the stage of development of the parasite it was necessary to kill and dissect the host thus making it impossible to follow through the entire development of any individual.

There are five larval instars. The first four are attached to the host within a sac composed of their cast skins. The fifth instar emerges from the host and moves freely about for a few minutes to a few hours until it spins a cocoon in which it pupates.

The durations of the first four larval instars are shown in Table XII. The duration of the first instar is about 100 hours or four days. This agrees in general with the observations of Fenton (1918) who stated: "In case the egg is internal, just previous to emerging from the host, the larva is seen to be curved in the form of a U, the apex of which appears first between the segments. This is the second larval stage and it is covered almost entirely and protected by the exuviae of the first instar. The appearance of the sac externally on the host takes place in from five to seven days after oviposition. During this time the egg has hatched, the "embryonic" stage has been passed, and a molt has taken place." The second, third and fourth instars are completed in fifty to seventy-five hours or two to three days. However, observation showed that there were some fully developed fourth instar larvae forty-eight hours after third ecdysis. The fifth instar forms a cocoon almost immediately after emerging from the host. The combined duration of the stages within the cocoon are discussed in a subsequent section.

Larval behavior. The first four larval instars complete their entire development attached to the host and within the larval sac formed by the remnants of the shed skins.

Emergence of the fifth instar larva from the host was only observed to occur between mid morning and late afternoon. For example, on July 10 and 11, 1960, among 176 parasitized leafhoppers caged for parasite emergence, seven emerged between 3:00 and 3:30 p.m., July 10. No emergence took place between 4:00 p.m., July 10 and 10:00 a.m., July 11. However, by 4:00 p.m., July 11, an additional eight larvae had emerged.

At 12:30 p.m., July 16, a slight split was noted in the fourth exuviae of a parasite sac. Examination showed the head of the fifth instar larva protruding from the sac. The larva next returned its head into the host. The leafhopper exhibited much activity and moved about quickly. By 1:30 p.m., the leafhopper had been sucked dry and was just a shrunken hollow shell (Figure 31). The larva now overflowed its sac. By 1:35 p.m., the larval head was seen chewing within the head of the leafhopper and trimming off vestiges of tissue from the eyes, the bases of the antennae and other areas of the head. The parasite showed great ability to stretch in reaching in through the narrow collar (Figure 32) into the host body and into the head capsule. It next withdrew slowly and chewed at the bases of the prothoracic legs to complete the removal of tissues. The head of the parasite was out of the host again

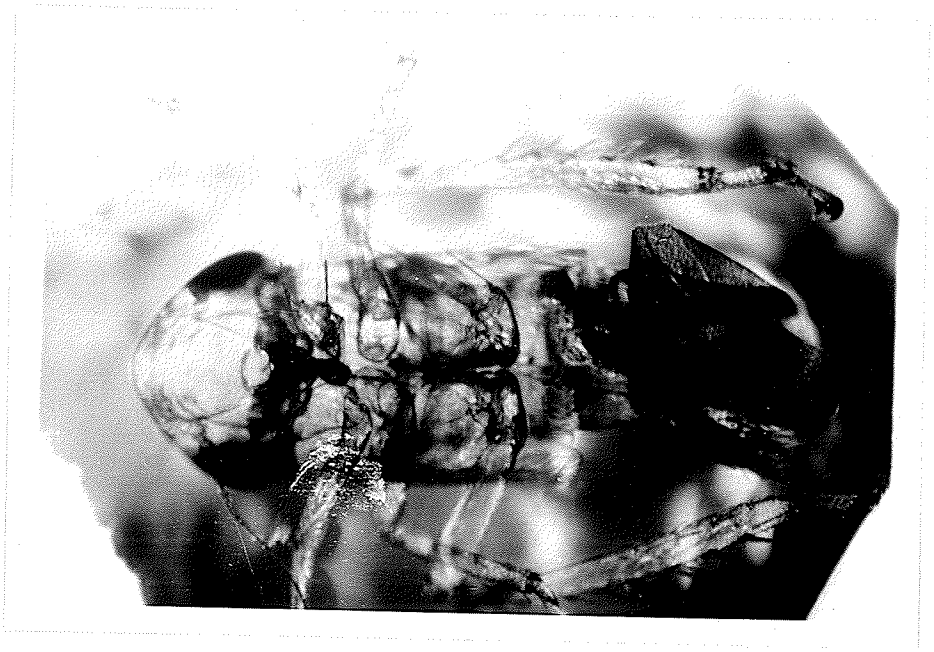

FIGURE 31

HOLLOW SHELL OF SIX-SPOTTED LEAFHOPPER EATEN OUT BY FIFTH INSTAR LARVA OF P. minimus

FIGURE 32

COLLAR-LIKE RING OF EXUVIAE AT POINT OF ATTACHMENT
OF PARASITE INTO BODY WALL OF HOST

at 1:45 p.m. The parasite cleaned its mouthparts while resting upright with only its caudal region within the parasite sac. The parasite was completely free and away from its host at 1:55 p.m. at which time it was placed in a vial. It was spinning a cocoon at 2:15 p.m.

Perkins (1905) stated that the larva both chews and dissolves the contents of the leafhopper. He noted that: "Generally early in the proceedings the soft contents of one or both eyes and of the head are seen to be in rapid motion, like a boiling fluid; suddenly all the pigment is removed from one eye (usually the one on the opposite side to the parasite) and it becomes an opaque white spot, then the other is often similarly destroyed, or sometimes both more or less simultaneously."

The larva moves on its back by a series of peristaltic movements which commence caudad and move forward. These follow as a response to the compression set up by forcing the posterior forward; the ripple serves to lift the moving body surface from the surface over which it moves. As the parasite moves on its dorsal surface, each peristaltic movement results in a slow lashing of the head, first ventrally (upward) then dorsally (downward) and either slightly left or right and vice versa, after which the whole sequence is repeated. Movement can be reversed by cephalad to caudad peristaltic movements as was observed in a larva spinning a cocoon.

After it reaches the fifth instar the larva varies in size with the degree of feeding upon its host. When two or more parasites are present often little or no emptying of the host is accomplished (Figure 33). Often a parasite has been found not to go beyond another parasite to eat out the host. On the rare occasion when two parasites emerge from the same host they are both undersized and usually fail to develop to the adult stage.

Larvae of P. minimus may begin to spin up as soon as they emerge from the host or they may crawl about for a period of up to twenty-four hours before cocooning. A similar observation was made by Fenton (1918) on Gonatopus spp. and according to Mik (1882) the period may extend to 48 hours.

Observations were made on a newly emerged larva as it spun its cocoon. Examination under the microscope showed it to protrude its spinneret and to touch this organ to the glass wall of a vial on each side of its body. It next touched the spinneret to its "neck" region. The rippling caudad-cephalad movement tended to pull the larva beneath the silken strands which it had spun. When it had moved too far forward, reverse ripples (cephalad-caudad) served to pull it back. Completion of a caudad-cephalad movement took six to eleven seconds with about seven seconds being most common. In one-half hour two silken frameworks had been constructed and vacated.

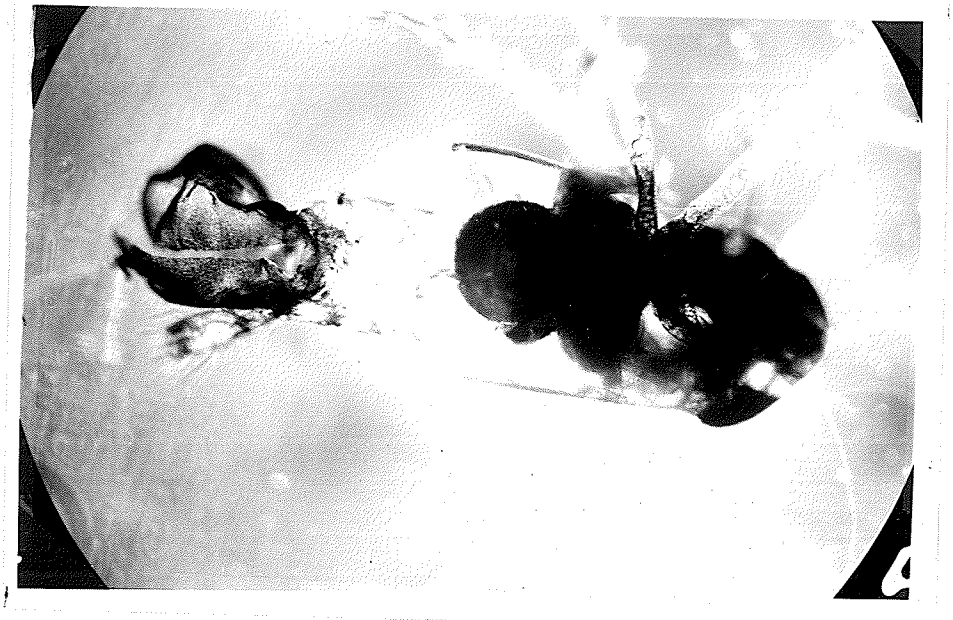

FIGURE 33

DOUBLE PARASITISM RESULTING IN ONLY THE ABDOMEN AND PART OF THORAX OF THE HOST BEING EMPTIED

Many larvae chewed through the corks of lamp chimney cages and spun up outside on the corks.

A visible change in the spun-up larva results from the accumulation of fecal matter. Larvae showed a darkening of the intestine, perhaps indicating accumulation of fecal matter, four to five days after spinning up.

Pupa

Most of the fifth larval stadium, all of the pupal period and the preimaginal period are spent within the cocoon.

Duration of last instar larva and pupa. The mean duration of these stages for 93 specimens (Table XIII) was 16.4 days with a range of 14.5 to 20 days.

TABLE XIII

DURATION OF LAST INSTAR LARVA AND PUPA OF *Pachygonatopus minimus*

Duration of stages (days)	Number of specimens	Total days
14.5	1	14.5
15.5	2	31.0
16.0	45	720.0
16.5	27	445.5
17.0	5	85.0
17.5	6	105.0
18.0	4	72.0
18.5	2	37.0
20.0	1	20.0
Total	93	1530.0
Average 16.4		

CHAPTER VII

EFFECT OF INSECTICIDES ON PARASITISM OF THE SIX-SPOTTED LEAFHOPPER BY *Pachygonatopus minimus*

The application of insecticides for the control of the six-spotted leafhopper on lettuce and carrots had no significant effect on the rate of parasitism of the leafhopper by *P. minimus* (Table XIV).

In the lettuce plots malathion gave very effective leafhopper control, reducing the population to a very low level. Sweeps were made three days after treatment and the population sampled was that which had reinvaded the plots from the untreated plots and surrounding vegetation. This would account for the similarity in percentage parasitism.

Sevin and DDT were used for the control of leafhoppers on carrots. These insecticides were less effective in controlling the leafhopper than was malathion on lettuce. However, it should be noted that the total number of leafhoppers collected in the treated plots (Table XIV) is not directly comparable to the total number of leafhoppers collected in the checks since there were up to five times as many plots sampled in the treated as in the untreated group.

Observations made during this study showed that leafhoppers rarely occur as nymphs in pure stands of carrots. The leafhoppers in the carrots were migrant adults. In treated

TABLE XIV

EFFECT OF INSECTICIDES ON PARASITISM OF THE SIX-SPOTTED LEAFHOPPER BY Pachygonatopus minimus, 1960

Dates leafhoppers collected *	Treated			Untreated		
	No. of leafhoppers		Per cent leafhoppers parasitized	No. of leafhoppers		Per cent leafhoppers parasitized
	Total	Parasitized		Total	Parasitized	
Lettuce						
June 13	0	0	0.0	68	0	0.0
" 16	4	1	25.0	89	2	2.2
" 24	9	1	11.1	86	3	3.5
July 2	30	1	3.3	90	7	7.8
" 10	0	0	0.0	15	1	6.7
" 14	0	0	0.0	579	22	3.8
" 22	2	0	0.0	1141	3	0.3
August 5	205	10	4.9	516	19	3.7
" 11	875	47	5.4	743	9	1.2
Sept. 6	266	30	11.3	434	52	12.0
Total	1391	90		3761	118	
Average			6.5 ± 3.3**			3.1 ± 1.9**

TABLE XIV (continued)

Dates leafhoppers collected *	Treated			Untreated		
	No. of leafhoppers		Per cent leafhoppers parasitized	No. of leafhoppers		Per cent leafhoppers parasitized
	Total	Parasitized		Total	Parasitized	
Carrots						
July 22	31	1	3.2	212	3	1.4
" 30	273	67	24.4	262	32	12.2
August 5	416	36	8.7	372	32	8.6
" 11	1464	142	9.7	1814	136	7.5
" 18	2085	57	2.7	4657	108	2.3
" 24	735	17	2.3	917	28	3.1
" 30	2384	83	3.5	1644	92	5.6
Sept. 6	786	133	16.9	817	80	9.8
Total	8174	536		10695	511	
Average			6.6			4.8
Grand Total	9565	626		14456	629	
G rand Average			6.5 ± 2.2**			4.4 ± 1.3**

*Leafhoppers collected on lettuce 3 days after treatment and on carrots 6 days after treatment.

**Standard error (For calculation of S.E. percentages were transformed according to the tables of Bliss).

lettuce, reinfestations were also largely the result of migrations of adult leafhoppers. There was always a residual population in the untreated lettuce and in the surrounding areas. Leafhoppers, especially in the adult stage, move about freely and disperse from untreated to treated areas. Further, it has been shown (Tables VII, VIII and IX, pages 76, 78 and 80) that parasitized leafhoppers move equally as freely as do non-parasitized leafhoppers.

Since leafhopper populations are not static and since parasitized leafhoppers move as freely as do non-parasitized leafhoppers, collections from treated or untreated plots would be essentially from the same population. This would account for the similarity in percentage of parasitism.

CHAPTER VIII

NOTES ON *Tomosvaryella sylvatica* Meig.

Tomosvaryella sylvatica was originally described by Meigen (1824). Cresson (1910) described some North American species of the genus *Pipunculus*. Further work on pipunculids was done by Rapp (1943) in which he described *T. sylvatica* as *Pipunculus nudus* var. *tangomus*. Hardy (1947) showed that *P. nudus* var. *tangomus* was in synonomy with *T. sylvatica*. Perkins (1906) described *P. eutrichodes* from cicadellids from Queensland, Australia and Perkins (1907) reported the occurrence of *Pipunculus* spp.on cicadellids from Arizona and Germany. Comstock (1947) briefly described the flies of the family Pipunculidae as big-eyed, generally small, long-winged and quick moving. He thought them to be parasitic entirely on Homoptera.

Kielin and Thompson (1915) studied the external and internal morphology of the larvae of Pipunculidae and discussed the life cycle briefly. They reported that Boheman in 1854 discovered the type of parasitic life of the larvae of this group on the family Cicadellidae. They stated that the adult oviposits in the host; that there are two larval instars which develop in the coelomic cavity; and that when mature the larva ruptures the abdomen of the host between two abdominal segments and exits from the living host. It then enters the soil where it transforms to a pupa.

Williamson (1938) worked out the biology and post-embryonic development of Pipunculus subvirescens and P. unguiculatus in Saskatchewan. He stated that the egg is laid in the host and described first and second stage larvae and the puparium and the unique manner of adult emergence therefrom. This had been previously done by Keilin and Thompson (1915b). Williamson (1938) also discussed in some detail the behavior of the adult.

Williamson (1938) showed that in 1935, P. subvirescens and P. unguiculatus parasitized 32 per cent of leafhoppers collected in the fall in Saskatchewan. The parasitism in individual sweeps was as high as 82 per cent. In 1936 and 1937 he found that ten and three per cent, respectively, of the leafhopper population was parasitized by these two species. The percentage parasitism is not given specifically for the six-spotted leafhopper, although he lists it as one of the hosts. George[1] found 18.5 per cent of six-spotted leafhoppers collected on August 11, 1959 in the Niagara Peninsula, were parasitized by T. sylvatica.

Westdal and Barrett (unpublished) reared T. sylvatica from six-spotted leafhoppers in 1958. In 1959, adult parasites were swept from the field in numbers up to five per 250 sweeps. Dissection of six-spotted leafhoppers swept from

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[1]George, J.A., Entomologist, Canada Agriculture Research Laboratory, St. Catharines, Ontario, (personal correspondence), 1960.

various crops showed that the fly parasitized up to 20 per cent of the population. The actual percentage parasitism especially in permanent or semi-permanent fields, such as alfalfa and untouched weed stands is probably higher.

Life Stages

The adult is a small black fly. The body and the wings are each about 2 mm. long and give an overall length of about 3 mm. The fly has a large head characterized by very large eyes.

In 1960 adult T. sylvatica were first taken in the field on June 15. Occasional specimens were collected in sweeps from June 15 to about July 15. For the remainder of July, during August and to September 4, specimens were collected regularly at the rate of up to 1 per 50 sweeps. There was no evident peak of population although there appeared to be an increase in numbers toward the end of the season.

Observations in the field showed that the flies were more abundant following rainfall. It was also observed in the laboratory that flies emerged from puparia after the soil in the cages was watered.

On August 24, 1960, observations in lettuce plots at Portage la Prairie showed that the fly was very active near the soil, flight varying from ten to twelve inches above the soil when the wind slacked and from one to two inches above the soil when the wind increased. The wind averaged about

15 m.p.h. and varied from 10 to 20 m.p.h. Eighteen flies were collected with a small aspirator but none was taken in the sweep net. This high activity occurred the day after a heavy rain. Flying near the ground may have been either to avoid the velocity of the wind or its drying effect which appears to be lethal to these flies.

In the greenhouse, adult T. sylvatica were noted feeding on the surface of aster leaves on a gummy residue resulting from presence of six-spotted leafhoppers and the greenhouse whitefly, Trialeurodes vaporariorum (Westw.). Williamson (1938) did not observe pipunculids near flowers, nor did he observe them to feed on sugar solution or honey dew. However, he quotes Williams (1919) who stated that males and females feed on honey dew or dew on sugar cane leaves. Williamson (1938) also quotes Heiss who saw pipunculids hovering over aphid colonies and alighting among the aphids.

Mating of T. sylvatica was observed only in cages. Mating occurred at 7:00 p.m. in two instances in one of which it lasted 13 minutes and in the other at least 36 minutes. Williamson (1938) was unable to obtain mating with Pipunculus spp. in cages measuring two feet in each dimension. He thought that both copulation and oviposition might occur early in the morning while the temperature, sunlight and humidity were favorable. At Winnipeg, caged T. sylvatica were observed to have short active periods during most of the day. Pairs in

copula were noted frequently in cages 14 by 14 by 16 inches in the laboratory as well as in cages 4 by 4 by 6 feet in the greenhouse.

Williamson (1938) stated that a pipunculid, Cryptochaetum iceryae contained a total of 90 to 110 eggs in the ovaries, and that four to twelve of the eggs were ready for oviposition.

Observations were made on flies and leafhoppers in cages 14 by 14 by 16 inches. At 9:00 p.m. on February 1, 1960, a female was observed attacking leafhopper nymphs. She averaged from one to one and one-half attacks per minute but was successful in grasping the nymph only about one time in six. Hovering of the fly stimulated the nymph to recurve its abdomen. The fly can attack successfully from the side but when it attacks from above or below, the nymph in recurved position is ready and frequently able to whip off the parasite after which the nymph often jumps to a new location. Of about thirty-five attacks observed on leafhoppers only one was attempted on an adult. The fly hovered and darted about in hunting, for periods of a few seconds to half a minute between flights. When the searching of the fly became too persistent the nymph jumped away even without the contact of attempted parasitism. The fly occasionally attacked cast skins which remained in position on the plant. One nymph was noted to arch its abdomen several times after the parasite attacked.

Sometimes the fly picked up the nymph, held it and oviposited in it while hovering. At times they fell to the earth while the fly maintained its hold. At other times the fly appeared to jab while in flight with its ovipositor, without coming to rest or grasping the host. At still other times the fly came to rest briefly upon the nymph while ovipositing in it. At times the fly would fly past several nymphs in a group, all with recurved abdomens but attempted no parasitism, while at other times it hovered and made several "runs" at a single nymph.

No attacks were noted by non-flying females and it seemed probable that they do not attack unless in flight.

Eggs of T. sylvatica have been dissected from the head, thorax and abdomen of leafhoppers. The egg chorion is translucent and the white embryo shows clearly through. Five eggs ranged in size from 0.31 mm. by 0.15 mm. to 0.37 mm. by 0.19 mm. and averaged 0.34 mm. by 0.17 mm. Embryos in two of these eggs measured 0.29 mm. by 0.14 mm. and 0.29 mm. by 0.15 mm. Two eggs were found in the eye capsule of a leafhopper indicating that multiple parasitism does occur. Williamson (1938) quoting Keilin indicated that double parasitism does occur but that in one instance at least only one larva survived. Williamson (1938) in thousands of dissections found no pipunculid eggs in cicadellids but states that McKay found one egg of Pipunculidae.

Eggs hatched in 6 to 7.5 days. The newly emerged larva was 0.41 mm. long and 0.16 mm. wide and was white and segmented. Two larvae 6 days and 18 hours ± 1 hour from oviposition measured 0.50 mm. by 0.18 mm. and 0.52 mm. by 0.18 mm.

Only very small larvae have been found in the head and in the thorax. Large larvae were found only in the abdomen where they sometimes protruded into the thorax. Williamson (1938) reported that small larvae are generally found in half grown nymphs, large first instar larvae are found in nearly mature and mature leafhoppers, while the last instar is always found in fully grown leafhoppers. This may be because growth and moulting of the host is not inhibited by this group of parasites in contrast to the dryinid, P. minimus, where development and moulting of the host is inhibited by the parasite. The mature larva is readily detected through the abdominal wall of the leafhopper whose yellowish white fat body has been absorbed by the parasite.

The puparium is oval, brown, about 1.5 to 2.0 mm. long by 1.0 mm. wide. As described by Williamson (1938) for Pipunculus spp. the puparium has at the anterior end three dehiscent plates which separate, allowing the fly to emerge. In cages the puparia were located within about one-quarter inch of the soil surface.

CHAPTER IX

SUMMARY

The aim of this study was to determine the biology of Pachygonatopus minimus Fenton and Tomosvaryella sylvatica Meig. and their importance in the control of the six-spotted leafhopper, Macrosteles fascifrons (Stal). The six-spotted leafhopper, which occurs throughout the United States of America and across Canada, is the chief vector of aster yellows, a virus disease of plants. The disease has become a major limiting factor in the production of several commercial crops.

The study was conducted chiefly in the Winnipeg area although parasites and parasitized leafhoppers were collected in other locations in the province. Leafhoppers, collected by sweeping host plants with an insect net, were placed in holding cages or in lamp chimney rearing cages or were preserved directly in 70 per cent ethyl alcohol. All rearing was conducted in the laboratory at ordinary fluctuating room temperatures.

The egg and larval instars were described from material preserved in alcohol. All stages were measured on a Ziess Opton stereomicroscope with a filar micrometer calibrated against a graduated stage scale. Observations on the biology of the parasite were made chiefly on caged material. Determination of the mobility of parasitized leafhoppers and the

effect of insecticides on parasitism of the leafhopper were made by collecting leafhoppers under appropriate test conditions in the field.

The six-spotted leafhopper is the only known host of P. minimus. The parasite was collected in Manitoba and Saskatchewan and leafhoppers containing larvae, believed to be P. minimus, were taken in Alberta, North Dakota, Minnesota and Montana. The abundance of the parasite varied with the season. In spring, probably less than one per cent of leafhoppers were parasitized but by fall parasitism rose to 37 per cent.

The life stages of P. minimus were studied in detail and are described and illustrated by photographs. In the adult stage the sexes differ in form, color and habits. The female is wingless and ant-like whereas, the male is winged and capable of flight. The egg is usually laid on the inner aspect laterally of an intersegmental membrane of the abdomen of the host. As the larva develops it protrudes through the intersegmental membrane. There are five larval instars. The larval sac is visible externally on the host in the late first or early second instar, about four to five days after oviposition. The first instar larva and early second are straight but the late second and the third and fourth instars are "U-shaped." At the time of transition from one instar to the next the portion of the larval sac or exuviae which protrudes

from the abdominal wall of the host, splits but remains attached to the host to form part of the larval sac of the new instar. Thus, the second instar is surrounded by a collar-like ring formed by the first exuviae; the third instar is surrounded by the second and first exuviae; and the fourth instar is surrounded by the third exuviae as well as the second and first. The fifth instar larva, therefore, emerges from a rosette of four exuviae. The fifth instar larva is straight and has sclerotized mandibles. It spins a cocoon of a silken outer framework with an inner ovate receptacle within which it pupates. Some time before the adult emerges, a preimaginal stage is formed within the cocoon. In this stage external development of the adult appears complete except for pigmentation.

The life cycle of P. minimus consists of egg, larva, pupa and adult. The female adult is unusual in that it is a predator as well as a parasite. The first four larval stages are also unusual in that they are contained within their successive cast skins.

Female adults were taken in the field from June to October. No males were collected in the field. In cages adults emerged mainly from mid morning to mid afternoon and the sex ratio of emerging adults was near 1:1. The developmental period on the host was about two days shorter for the male than the female but the developmental period after leaving the

host was the same for both sexes. Mating was of short duration and there were indications that only males were produced by parthenogenesis. In ovipositing the female grasped its prey with its chelate fore limbs or the mandibles which often left scars on the host. When it had captured the host the parasite curled its abdomen beneath that of the host and inserted the ovipositor. The host was usually inactive for a period of about 30 seconds after oviposition by the parasite. Oviposition and parasitism were noted only on third, fourth and fifth instar nymphs and adults. Parasitized nymphs did not generally molt and remained in that instar for a period longer than normal. Multiple parasitism was frequent and from one to eleven ovipositions in a single host were noted. Normally only one parasite developed and the remainder were suppressed. In cages the female consumed an average of one and one-half nymphs per day. The average life span of males and females was 2.15 and 12.14 days, respectively. Parasitized leafhoppers were as active as non-parasitized leafhoppers.

The incubation period of the egg was less than three hours. The duration of the first instar was about 100 hours or four days. The second, third and fourth instars were each completed in fifty to seventy-five hours or two to three days. The first four instars are sedentary and parasitic in the host and the fifth is an active feeding stage. At the time of emergence from the host the fifth instar larva consumes the

contents of the leafhopper. The larva spins a cocoon within twenty-four hours of emergence. Most of the fifth larval stadium, all of the pupal period and the preimaginal period are spent within the cocoon. The mean duration of these stages was 16.4 days.

The application of insecticides for the control of the six-spotted leafhopper on lettuce and carrots had no significant effect on the rate of parasitism of the leafhopper by P. minimus.

Tomosvaryella sylvatica is a small black fly with a large head characterized by very large eyes. It was first reared from six-spotted leafhoppers in Manitoba in 1958 and has parasitized up to twenty per cent of the leafhopper population. It has been taken in the field from June to September. The population tended to increase toward the end of the season. The parasite was more abundant after rainfall and there were indications that moisture influenced adult emergence. Mating lasted about one-half hour and was observed frequently in cages. Oviposition in the host was observed only when the parasite was in flight. Eggs of T. sylvatica were dissected from the head, thorax and abdomen of leafhoppers. Eggs hatched in 6 to 7.5 days. Only very small larvae were found in the head and the thorax of the host. Large larvae were found only in the abdomen where they sometimes protruded into the thorax. There appeared to be two larval instars. The larva pupates in the soil.

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