THE UNIVERSITY OF MANITOBA

BIOLOGY AND OVARIAN DEVELOPMENT OF THE CABBAGE MAGGOT *Hylemya brassicae* (BOUCHÉ) (DIPTERA: ANTHOMYIIDAE)

by

MANOCHAI KEERATIKASIKORN

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ABSTRACT

by

Manochai Keeratikasikorn

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CABBAGE MAGGOT *Hylemya brassicae* (BOUCHÉ)

(DIPTERA : ANTHOMYIIDAE)

Field and laboratory experiments were conducted in 1970 and 1971 to study the biology and ovarian development of *H. brassicae*, an important pest of cruciferous crops.

Infestation on host plants was light in 1970 and heavy in 1971. Studies showed that two generations and a partial third generations occurred in Manitoba. The first generation population was much lower than the subsequent ones. Longevity and fecundity of a single pair of cabbage maggot were observed in the laboratory.

Ovarian development of cabbage maggots was correlated with their age using ovarian dissecting techniques. The earliest ovipositions were found on the fourth day following emergence. Few water-fed flies developed into the stage V and most of the wild flies laid at least one batch of eggs. The earliest mating of females occurred on the fourth day after eclosion.

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TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

FIGURE PAGE

APPENDIX

CHAPTER I

INTRODUCTION

The cabbage maggot is the common name of *Hylemya brassicae* (Bouché) used in North America (Muesebeck, 1942) and the cabbage root fly in the United Kingdom. This insect was first described by Bouché in 1833 as *Anthomyia brassicae*. Since then it was described under several generic names although the specific name, *brassicae*, has been generally accepted. Coaker and Finch (1971) reported *Hylemya* was used by workers in Canada and the United States and some French, German and Russian authors used *Chortophila* while others used *Phorbia*, *Hylemyia* or *Delia*, and *Delia* has been superseded by *Erioischia* in the United Kingdom.

In Manitoba, the cabbage maggot was first found on the roots of rape in 1958 (Allen, 1964). This insect has long been a pest of economic importance in cruciferous crops particularly in cabbages, cauliflowers, radishes, turnips and rape throughout Canada (Harris and Svec, 1966).

Importance of the study

Under suitable weather conditions, as many as 90% of the plants in some brassicae crops may be killed in North America (Forbes and King, 1957). The maggots feed mostly on the cortex and make grooves and passages with their hookshaped mouthparts. When damaged plants are pulled up the maggots can be seen embedded in the tap root and lateral roots. The symptoms of light damage are wilting of the outer leaves with ready recovery, and those of moderate damage, wilting is followed by the leaves turning bluish or reddish, with recovery possible only under favourable weather conditions. Severely damaged plants die owing to the combination of larval feeding and subsequent rotting.

Problem

Considerable information is available concerning insecticidal control of this insect in North America and the United Kingdom. However, little is known about its biology in Manitoba.

The purpose of this research was: (1) to study the development of the life history and generations in the field (2) to study the ovarian development in the laboratory. Ovarian development was used as a marker of physiological age and was correlated with mating.

Organization of the thesis

The studies comprising this thesis are organized into two parts. In the first part, biological field studies are described. The second part consists of ovarian development studies of cyclodiene susceptible strain in the laboratory.

PART I

BIOLOGY OF THE CABBAGE MAGGOT

Hylemya brassicae (Bouché) IN MANITOBA

CHAPTER II

REVIEW OF THE LITERATURE

The number of generations of cabbage maggots in a year depends on the climatic conditions and varies from one in Northern U.S.S.R. (Semenov, 1953) to five in parts of the United States (Carlson, Breakey and Webster, 1947) and Canada (Brooks, 1951). Probably two generations a year occur in Manitoba (Allen, 1964). There are three generations annually in South Western Ontario and two generations in Eastern Ontario (Mukerji and Harcourt, 1970) as well as in Southern Alberta (Swailes, 1958). One generation in this study describes the cycle starting from the egg and ending with the adult based on Miles' (1954) description.

Adults are active, greyish brown flies resembling small slender house flies. The male is smaller, darker and more bristly than the female with the tip of the abdomen more broadly rounded (Brittain, 1927). Several other Anthomyiids are very similar to *Hylemya brassicae* and small variable characters are all that can be used to separate the species. *H. brassicae* is characterized by the third and fourth wing veins being parallel at their apices and by the pre-alar bristle being more than half as long as the following bristles (Brooks, 1951). In the male, the eyes meet at the front of the head (holoptic) and the basal half of the hind femur is exceptionally hairy (Schoene, 1916). Females are distinguished by having well-separated (dichoptic) eyes and a strong antero-ventral bristle near the base of the middle femur and two posterior bristles on each front tibia (Brooks, 1951).

Hylemya brassicae overwinters in the soil in the puparium. Abu Yaman (1960) in Holland reported no third instar larva or pupa were found beyond a distance of 8 centimetres from the plant, but Smith (1927) found puparia as deep as 20-23 centimetres particularly of the later generations.

Pupation usually takes place in the soil near the roots of the host plant. The majority of puparia are found at a depth of 8-12 centimetres (Coaker and Finch, 1971).

At Wellesbourne, England, adults of first generation emerge in late April and May from the overwintering pupae. After a preoviposition period of 6-8 days the females begin to lay eggs (Hughes and Salter, 1959). Allen (1964) stated that adults emerged and were in flight by the end of June and the maggots appeared on the roots of rape during the first week in July in Manitoba. The eggs are white and elongate with one side convex and the other slightly concave. The average length of the eggs is 0.93 millimetres (Miles, 1952). The eggs are laid singly in the soil within 5.0 centimetres of the stem of the host plant.

Under both field and laboratory conditions, the average viability of the egg is 89-96% (Hughes and Salter, 1959; Finch and Coaker, 1969). Maximum hatch is obtained when eggs are kept on a wet surface or at relative humidities of 90% or more (Goaker and Finch 1971). Under dry conditions between 10^{o} and $30^{o}C$, eggs did not hatch (Swailes, 1963). Eggs incubated at constant temperatures on moist filter paper required the following accumulation of day-degree (D^{o}) above a threshold of $7.2^{o}C$

to complete development and hatch: 30 D° when incubated at 10°C, 39 D° at 15°C, 51 D° at 20°C, 53 D° at 25°C and 85 D° at 30°C (Finch and Coaker, 1969; Swailes, 1963).

The larvae enter the roots and develop through three instars before re-emerging to form their puparia in the soil about the base of the plant (Mukerji and Harcourt, 1970). Most larvae reach the host plant but only a few become established on the host plants (Abu Yaman, 1960). The highest mortality between egg and pupal stages was 97.5%. The larval stage usually lasts 19-32 days (Schoene, 1916; Smith, 1927) but it may be shortened in the absence of food or water (Schoene, 1916) or extended if the temperatures are low (Smith, 1927). Under field conditions at Wellesbourne, England, the first instars usually feed for about 4 days before moulting, the second for about 6 days, and the third for 10-20 days until pupation (Hughes and Salter, 1959).

In the field at Geneva, New York, the pupal stages of the early generations last about 12-18 days (Schoene, 1916) whereas those of later generations, which overwinter in the soil, last 5-10.5 months.

The optimum temperature for 80% of the adults to emerge ranges between 16.1° and 21.7°C (Harris and Svec, 1966).

CHAPTER III

MATERIALS AND METHODS

1. Field collection

To determine the seasonal development of the cabbage maggot, an experiment was carried out at the Plant Science Experimental Field, University of Manitoba, during the growing season of 1970 and 1971. The experimental plots contained spring cabbages, radishes and rape in 1970 and spring and summer cabbages and radishes in 1971. The cabbage rows were spaced 90 centimetres apart, with plants at 45 centimetres apart in the row. Radishes and rape were sown to have 12 to 15 plants per foot of row, with rows 30 centimetres apart. Data were recorded from the beginning of June until the first week of September.

The infestation of plants in 1970 was measured by the number of larvae and pupae on or near cabbage roots and number of larvae and pupae per foot of radishes and rape.

Ten conical fly traps were used on radishes and rape to determine the number of adults emerging in the field. Each trap was placed over a randomly chosen plant and emerging adults in each cage were counted daily.

In 1971, field samplings were made twice a week. Ten cabbages and one hundred radishes were used for each sample. Later, adult trapping was abandoned and infestation was determined by pupal counts which were more reliable. Adults were collected by a sweeping net from broccoli, cabbage, cauliflower, radish, rape and turnip plots (Results shown in Chapter VIII).

Cabbage samples

For egg counts, the volume of soil was approximately 94.3 cubic centimetres with cover 12.0 centimetres in diameter and 5.0 centimetres in depth. For larval and pupal counts, the plant roots were dug out and the soil around their roots was collected, the volume of soil was approximately 2,650.7 cubic centimetres, it covered 15.0 centimetres in diameter and 15.0 centimetres in depth.

Radish and rape samples

For egg counts, the volume of soil examined was collected along the row 81 square centimetres from centre of the plant and 5 centimetres deep. For larval and pupal counts, the plant roots were dug out and the soil around their roots was collected. The volume of soil collected was 225 square centimetres from the centre of the plant and 15 centimetres deep.

The plant roots and soil samples were collected and stored in a cold room at 4.4°C during the interval required for the examination in the laboratory.

2. Laboratory examination of field materials

Recovery of eggs

The eggs were floated from the soil with tap water and recovered by filtration. This procedure was repeated several times to ensure that all the eggs were recovered. The eggs were counted directly on the seive.

Recovery of larvae

To obtain the larvae from the samples, the soil was spread out on a tray and searched for the larvae. The plant roots were dissected and searched.

Recovery of pupae and empty pupae

Pupae and empty pupae were collected by flotation. The soil samples were immersed in tap water and pupae and empty pupae were skimmed from the surface or picked from the residue.

Measurement of the size of mouthhooks

In 1970, larval samples collected from the rape field were used for determination of the numbers of each larval instar. The anterior part of larval mouthhooks was dissected with forceps on a slide. The distance between the tip of the mandible and the posterior end of the dorsal process of the pharyngeal sclerite was measured by a binocular dissecting microscope.

Measurement of the diameter of cabbage core

The plant roots collected from the field for larval counts, were brought into the laboratory. Before they were dissected, the diameter of cabbage cores was measured and recorded for the study of the relationship between the diameter of the core and the number of eggs deposited.

3. Laboratory studies

Longevity and fecundity

In the beginning of 1971 studies were started. Cabbage maggots utilized in this study were a cyclodiene-susceptible strain sent by Dr. G. E. Swailes from Lethbridge, Alberta. Adults that emerged from the pupae, were identified and kept as a pair in the plastic cages, size 17.8 x 17.8 x 17.8 cubic centimetres. The cage consisted of five sides of plastic; a cloth front provided easy access to the cage. The flies were provided with water, honey, a 70:15:15 mixture of soya flour, brewers' yeast and yeast hydrolysate. The cage of adult flies was held in the laboratory at a relative humidity 60 $\pm$ 5% and constant temperature cabinet maintained at 21.1^{o} $\pm$ 1^{o}C with a 16-hour photoperiod (6:00 a.m. - 10:00 p.m.). A petri-dish of moist soil containing a slice of turnip was provided for oviposition. The honey and mixture diet was changed three times a week and the oviposition sites were examined daily.

Hatching studies

For hatching studies, eggs were collected from laboratory reared adults which were held at 21.1^{o}C and 60% relative humidity. Eggs were placed on moistened plotting paper in small petri plates (Millipore Limited - Catalogue No. PD 10-047-00). The plates were covered to prevent drying and placed in the rearing cabinet. Fifty eggs were used in each plate. The plates were examined for larvae after 48, 72, 96 and 120 hours of incubation. The results are summarized in Table IX.

CHAPTER IV

RESULTS AND DISCUSSION

Field collection

Data from larval, pupal and adult collection during 1970 in radish plots were insufficient to determine life history of insects. There were some results in cabbage and rape. The first batch of eggs was found in cabbage on June 9th. The percentage of the cabbage maggot infestation on cabbages is summarized in Table I. The highest infestation occurred on June 15th. In rape, the number of larvae and pupae per linear foot were tabulated in Table II. There are two peaks in the larval counts, the first peak on July 10th and the second peak on August 14th. On the pupal counts, there are two peaks also, the first peak on July 10th and the second peak on August 21st. The number of adult flies per 10 conical traps was tabulated in Table III. Population of adult flies varied. From these data, probably three generations occurred in the year of 1970. The first generation was in early cabbage and the second and third generations were found in the later rape crop in 1970.

TABLE I

PERCENTAGE OF INFESTED CABBAGES IN 1970

Date	Percentage of infestation
June 9th	36.2
15th	77.6
22nd	37.3
July 2nd	28.4
7th	25.4

TABLE II

THE NUMBER OF CABBAGE MAGGOTS PER LINEAR FOOT

IN RAPE DURING THE GROWING SEASON OF 1970

Date	Number of cabbage maggots per linear foot	
	Maggots	Pupae
July 10th	1.7*	12.7*
13th	1.4	4.2
17th	1.0	1.3
22nd	0.6	0.7
27th	0.3	0.8
August 3rd	2.2	0.2
13th	11.9	1.6
14th	15.0**	3.2
17th	8.3	4.0
19th	7.7	5.9
21st	3.2	6.6**
28th	0.4	1.0

*The highest number of cabbage maggots in the first peak
**The highest number of cabbage maggots in the second peak

TABLE III

THE NUMBER OF ADULT CABBAGE MAGGOT FLIES CAPTURED IN 10 CONICAL TRAPS ON RAPE DURING THE SUMMER OF 1970

Date		Number of adults per 10 conical traps
July	16th	14
	17th	3
	20th	8
	21st	1
	22nd	1
	27th	0
	29th	7
August	4th	1
	10th	1
	14th	2
	19th	1

The results obtained during the growing season of 1971 are summarized in Table IV and Figure I for cabbage and Table V and Figure 2 for radish. The first batch of eggs was found in both cabbages and radishes on June 8th. The first larvae were found in cabbages on June 17th and in radishes on June 14th. Pupae were first found in cabbages on June 24th and in radishes on June 21st. Empty pupae were first found on July 12th in cabbages and June 24th in radishes.

Table IV and Figure I show that there are three peaks on egg counts and larval counts and two peaks on pupal counts. The first, second and third peaks of egg counts were on June 24th, August 3rd and August 23rd and the number of eggs were 439, 1,446 and 1,030 respectively. The first, second and third peaks of larval counts were on July 2nd, August 12th and September 2nd and the number of larvae were 204, 1,149 and 340 respectively. The first and second peaks of pupal counts were on July 12th and August 25th and the number of pupae were 63 and 583 respectively.

These data show that two generations and a partial third generation occur in Manitoba. There is a small population in the first generation when host plants are still small. The second generation is a very large population because there is an abundance of food source and host plants are large. Coaker and Finch (1967) reported that under laboratory conditions the female flies laid their first batches of eggs when provided with only a source of nutritive carbohydrate. To develop the second and subsequent batches of eggs, females must imbibe protein as well as carbohydrates.

Some of the second generation eggs complete development and the emerging adults lay their eggs which give rise to a partial third generation, the others develop into the diapause pupae. Read (1969) demonstrated that induction of pupal diapause in the cabbage maggot involved a relationship between photoperiodic, temperature, and light intensity conditions provided for the flies, eggs and larvae.

TABLE IV

THE NUMBER OF CABBAGE MAGGOTS AND PERCENTAGE OF INFESTED PLANTS ON TEN CABBAGES DURING THE GROWING SEASON OF 1971

Date		Eggs	Maggots	Pupae	Empty pupae	Infested plant %
June	14th	199	none	none	none	none
	17	293	90	none	none	90
	21	196	102	none	none	100
	24	439*	159	3	none	100
	28	117	181	11	none	100
July	2	141	204*	17	none	100
	5	71	85	15	none	100
	8	101	57	14	none	100
	12	82	55	63*	12	100
	15	74	99	46	3	100
	20	567	106	8	none	100
	23	881	166	13	none	100
	27	872	287	7	none	100
	30	442	244	14	none	100
August	3	1446*	337	37	1	100
	6	1305	605	50	4	100
	9	1382	669	46	3	100
	12	1090	1149*	82	12	100
	16	897	862	191	15	100
	20	852	290	495	49	100
	23	1046*	73	524	55	100
	26	1001	54	584*	76	100
	30	860	61	379	69	100
September	2	816	342	518	211*	100
	9	707	149	599	149	100

*The peak of different stages of cabbage maggots

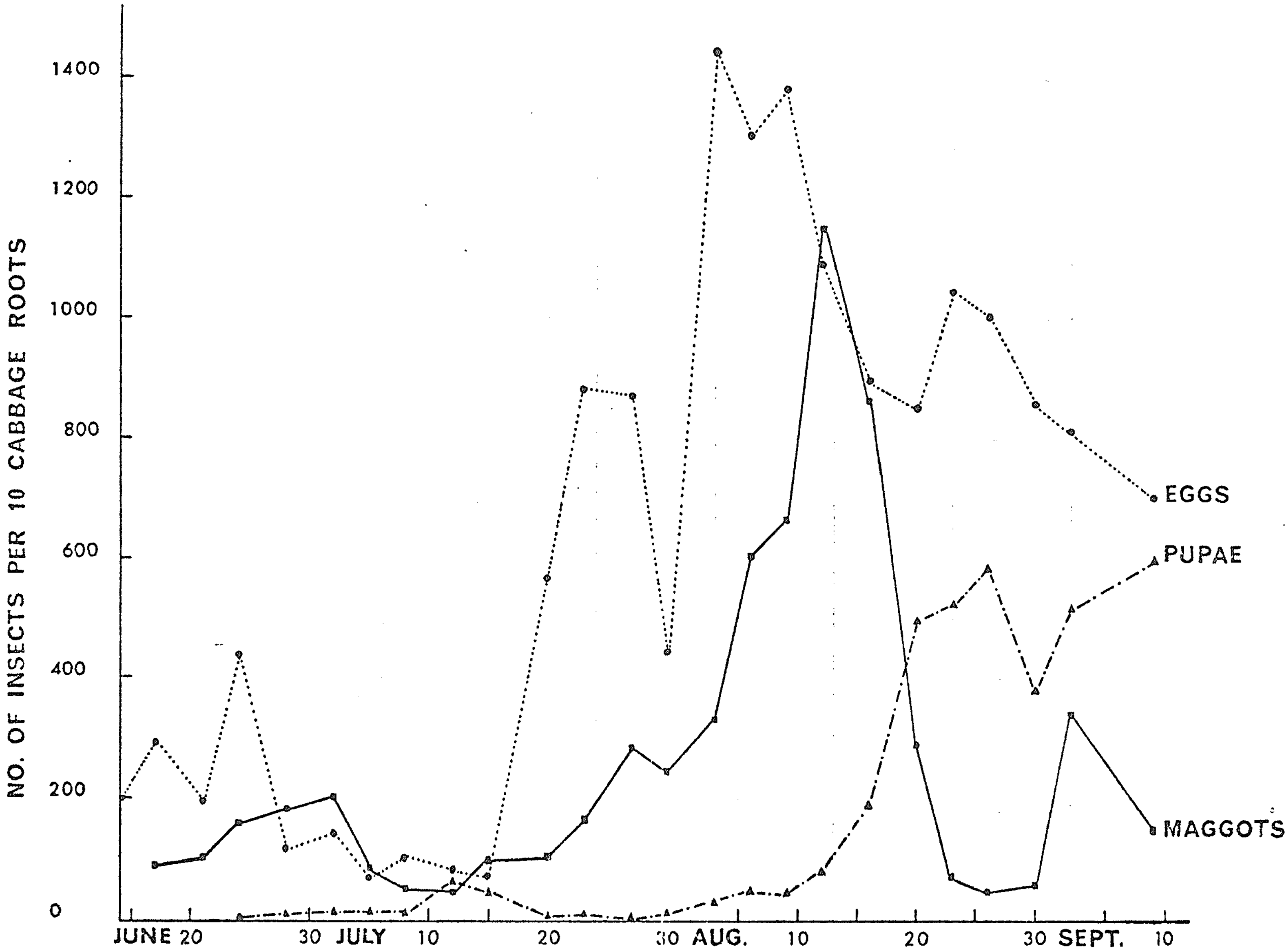


FIGURE 1. SEASONAL DEVELOPMENT OF Hylemya brassica (Bouché) IN MANITOBA DURING SUMMER 1971

Table V and Figure 2 show that between 51 to 95% of the plants were infested by the first generation and 27 to 100% in subsequent generations. The peak of egg counts were on June 24th and August 19th and the number of eggs 189 and 1,388 respectively. The peak of larval counts were on June 28th, August 9th, August 26th and September 9th and the number of larvae were 340, 854, 514 and 390 respectively. The peak of pupal counts were on July 5th, August 12th and September 2nd and the number of pupae were 20, 174 and 590 respectively. Empty pupal counts were insufficient in the first crop and there was one peak in the second crop on September 2nd; the number of empty pupae was 166. There was a small population in the first generation and a large population in the second generation on radishes which was the same situation as on cabbages.

The reasons are described in the cabbage section. This study showed that egg density in the first generation was lower than that in the second. Opposite observations were made by Hughes and Mitchell (1960) in England; Abu Yaman (1960) in Holland and Mukerji (1971) in Ontario, Canada.

TABLE V

THE NUMBER OF CABBAGE MAGGOTS AND PERCENTAGE OF INFESTED PLANTS ON ONE HUNDRED RADISHES DURING THE GROWING SEASON OF 1971

Date		Eggs	Maggots	Pupae	Empty pupae	Infested plants %
			First Planting			
June	14	150	163	none	none	51
	17	58	131	none	none	45
	21	136	126	4	none	64
	24	189*	211	7	2	63
	28	118	340*	2	none	88
July	2	180	264	5	none	89
	5	119	246	20*	none	95
	8	79	171	13	none	88
			Second Planting			
July	20	94	27	none	none	27
	28	167	112	none	none	39
August	3	326	195	6	none	67
	6	786	694	24	none	98
	9	516	854*	104	none	98
	12	746	572	174	none	100
	16	922	702	94	none	100
	19	1388*	258	84	6	100
	23	366	136	160	74	98
	26	106	514*	112	82	96
	30	202	194	352	66	98
September	2	422	308	590*	166*	98
	9	72	390*	194	110	96
	13	38	326	140	50	98
	16	132	304	261	69	95

*The peak of different stages of cabbage maggots

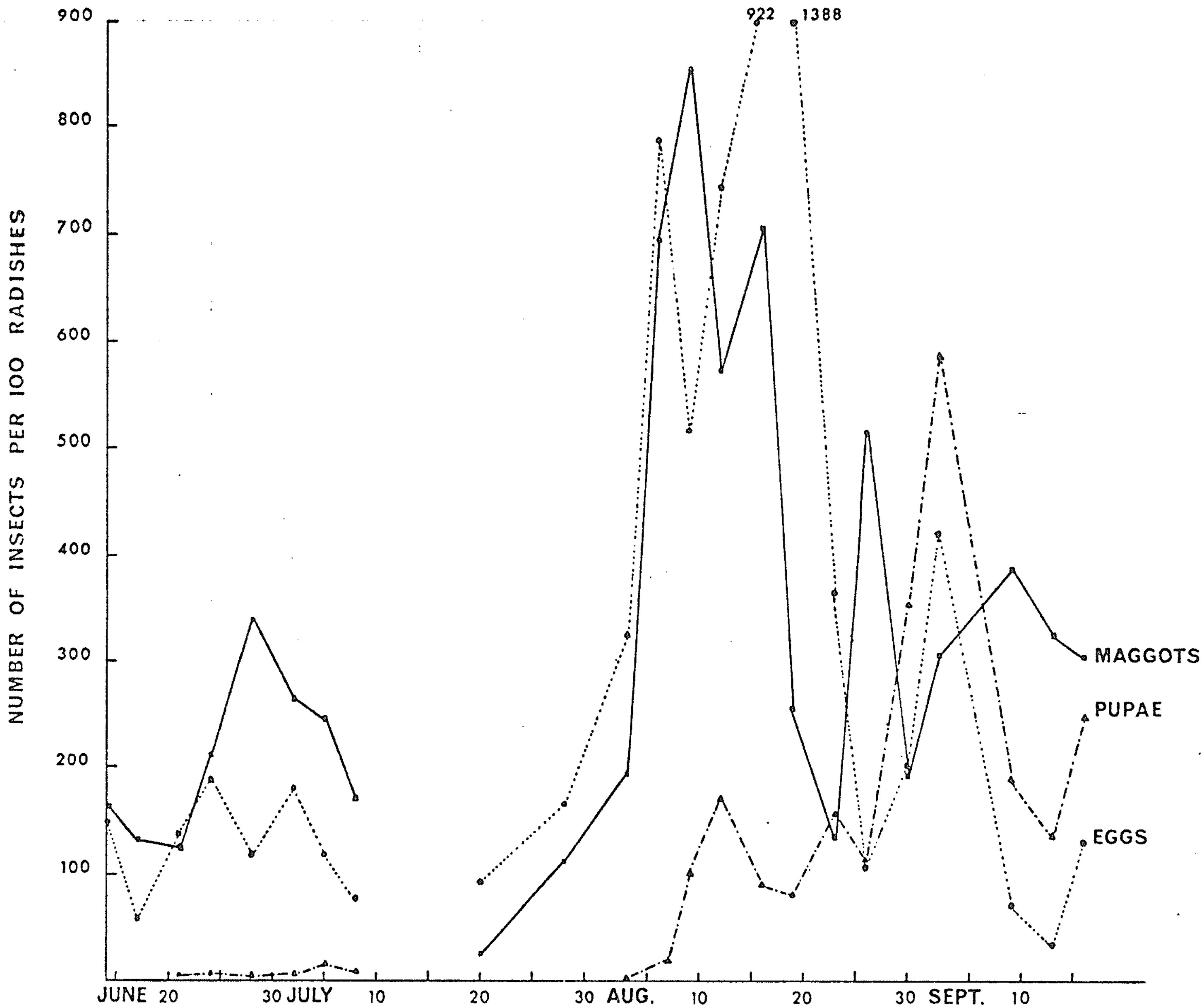


FIGURE 2. SEASONAL DEVELOPMENT OF *Hylemya brassicae* (Bouché) IN MANITOBA DURING SUMMER 1971

Measurement of the size of mouthhooks

In Table VI and Figure 3 the number of larvae in each instar is shown. The measurement can be divided into three groups. The first group ranges between 0.64 to 0.69 millimetres (mm) the second group is 0.74 to 0.84 mm. and the third group is 0.86 to 1.02 mm. which belong to the first, second and third instar larvae respectively. Hughes and Salter (1959) measured the distance between the tip of mandible and the posterior end of the ventral process of the pharyngeal sclerite. They found that the mouthhooks of the first, second and third instar larvae were a mean of 0.29, 0.53 and 0.88 mm. respectively.

TABLE VI

THE NUMBER OF MAGGOTS IN DIFFERENT INSTARS OCCURRING ON RAPE IN MANITOBA DURING JULY AND AUGUST 1970

Size of mouthhooks (mm.)	Date of collecting													Total
	July						August							
	7	10	13	16	17	27	3	14	17	19	21	28	31	
.64		1	1						1					3
.66	1													1
.69	1													1
.71														0
.74		1		1		1								3
.76		1	1			1						1		4
.79				1										1
.82		1					2					1		4
.84				1		1			1		2			5
.86				1	1	1		3		1	1	2		10
.89			1	3	1	3	1	1		1	1	1	1	14
.92	2		1	1		1		1	4	1	3	1	2	17
.94		1	2	2	2			2	4	4	2	2	1	22
.97	1	1			1	2	2	1		2		2	4	16
.99	2		1		3			2	1				1	10
1.02			3		1		4						1	9
Total	7	6	10	10	9	10	9	10	11	9	9	10	10	120

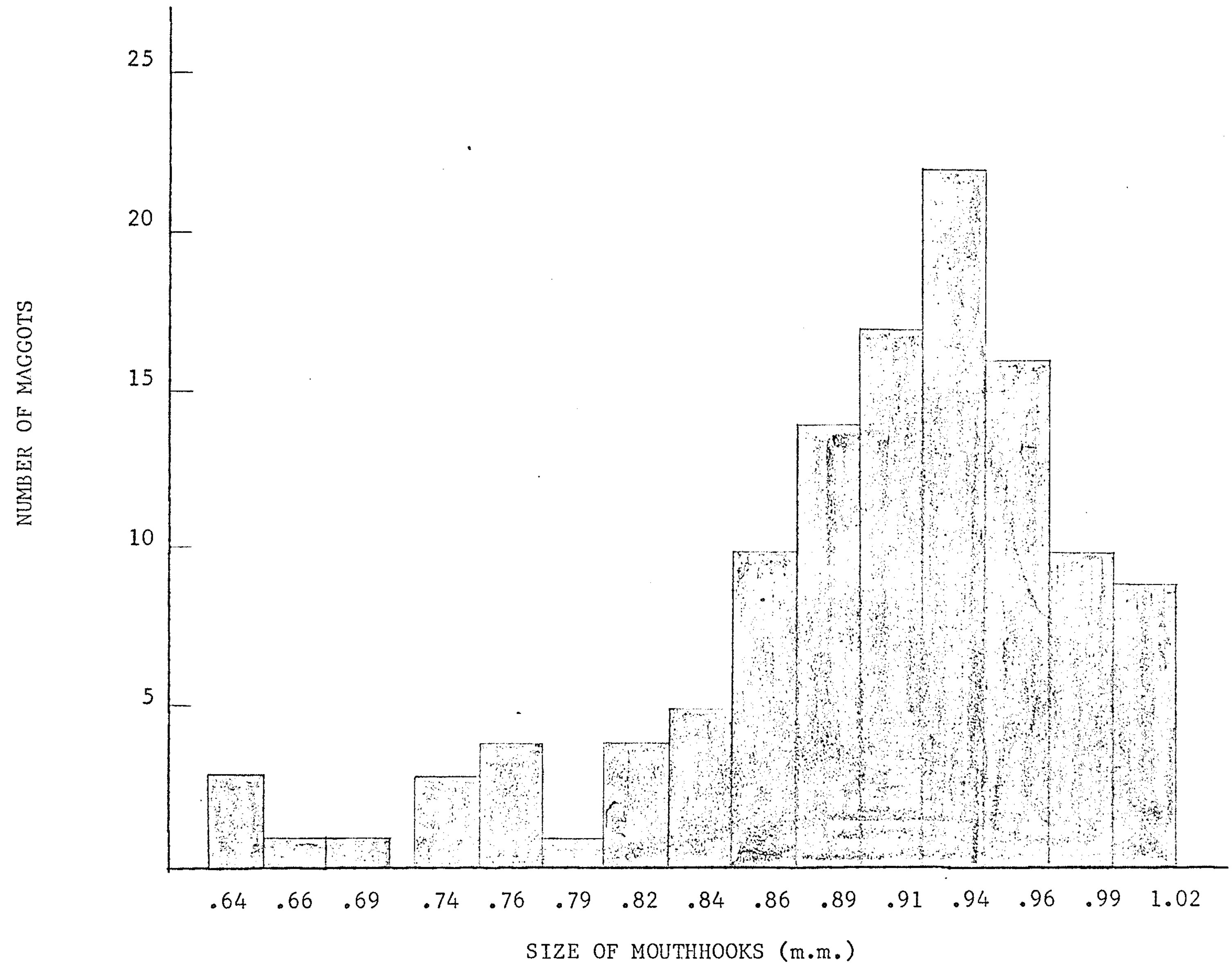


FIGURE 3. SIZE OF MOUTHHOOKS OF THE LARVAE OF THE CABBAGE MAGGOTS IN RELATION TO INSTARS

Relation between the diameter of the cabbage core and the number of eggs deposited in 1971

There is a direct relation between the diameter of the cabbage core and the number of eggs deposited, which is shown in Table VII. From 10 to 14 centimetres diameter the number of eggs are considerably lower than that laid on roots 15 to 20 centimetres. This may not be due to any physical attraction of the thicker roots but because at this time of the year the fly population is much greater than during early summer. Abu Yaman (1960) concluded that there was a positive correlation between plant diameter but not plant age and the number of eggs deposited.

TABLE VII

RELATION BETWEEN THE DIAMETER OF THE CABBAGE CORE AND THE NUMBER OF EGGS DEPOSITED IN 1971 IN THE FIELD

Diameter of the cabbage core (cm.)	Number of eggs counted	Total	Average	No. of plants scored
10	10, 16, 16, 8, 3, 8, 7, 10, 3.	81	9.0	9
11	8, 4, 3, 0, 12, 8, 7, 19, 5,	66	7.3	9
12	29, 5, 5, 9, 12, 15, 11, 13, 3, 23, 17, 20, 17, 18, 39, 2, 3.	241	14.2	17
13	18, 1, 31, 10, 7, 9, 5, 4, 5, 21, 8, 7, 38, 27, 33, 6, 34, 6, 34, 22, 11.	297	15.6	19
14	10, 0, 16, 6, 7, 19, 27, 42, 57, 12, 10, 34, 6, 1, 1.	248	16.5	15
15	69, 5, 12, 0, 5, 25, 41, 30 7, 26, 49, 30, 18, 40, 41, 114, 98, 84, 74, 63, 91, 4, 2, 3, 8, 3.	942	36.2	26
16	10, 6, 3, 1, 0, 11, 18, 5, 4, 8, 20, 15, 10, 35, 40, 10, 31, 48, 37, 42, 154, 2, 4	514	22.4	23
17	2, 4, 10, 50, 44, 61, 80, 64, 94, 126, 24, 2, 40.	601	46.2	13
18	12, 115, 58, 32, 35, 6, 49, 285, 151, 75, 44, 78, 45, 19, 21, 19, 1, 12, 2, 4, 3, 26.	1092		22
19	22, 110, 81, 43, 58, 11, 32.	357	51.0	7
20	17, 7, 73, 10, 31, 0, 12, 9, 157, 125, 125, 142, 53, 2, 19, 22.	804	50.3	16

Longevity

The results from Table VIII show that male flies live 8 to 36 days, the average being 24.0 days. Females live 11 to 54 days, the average being 29.8 days. In this study one female lived for 54 days.

Foot (1954) reported that longevity of males was 19 days and 22 days for female, some females living as long as 63 days (Schoene, 1916; Miles, 1951). Swailes (1961) described the average age at death of the mated females was 22.2 days when fed a 10% honey solution and some dry yeast. Studies on adult flies by Harris and Svec (1966) indicated that cyclodiene resistant females lived longer than susceptible strain. Adult longevity was reduced more by mutual disturbance than by any other factor (Finch and Coaker, 1969).

Fecundity

The results from Table VIII show that a single female lays from 14 - 353 eggs. The average of egg production per female is 171.8. The highest daily egg production for a single female was 84 eggs in a 24-hour period. Harris and Svec (1966) found that the female of the cyclodiene susceptible strain produced an average of 348.7 eggs and the resistant strain 393.5 eggs; the highest daily egg production for a single female was 51 and 50 eggs respectively. During an average life span of 22.2 days one female laid an average of 78 eggs when held at 18.3° - 23.9°C (Swailes, 1961). Vereecke and Hertveldt (1971), using a different diet, reported the best result was 13.7 eggs per female per day when fed on water, sucrose and brewer yeast extract (5:3:2).

Swailes (1961) noted that oviposition occurred in cycles for the susceptible strain, but oviposition cycle did not show clearly in the resistant strain (Harris and Svec, 1966). Fecundity under culture conditions depends on the size of the adults (Finch and Coaker, 1969) and also on the diet (Finch, 1971; Vereecke and Hertveldt, 1971). Vereecke and Hertveldt (1971) also described that factors other than food may influence fecundity and if mated females were caged separately, their fecundity was irregular and much lower than normal, indicating a certain "grouping" effect. However, Finch and Coaker (1969) reported that flies laid an average of 220 eggs per female when caged together in large numbers and 376 eggs per female when caged singly.

TABLE VIII

LONGEVITY AND FECUNDITY OF FEMALE *H. brassicae* IN SINGLE PAIR EXPERIMENTS AT 21.1° ± 1°C

Fly No.	Oviposition cycle for single pairs — Date of eggs laid																																																				Total
	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	52	53	54	
1	-	41	-	10	-	♂	-	-	♀																																												51
2	-	-	-	-	-	-	-	-	3	12	11	-	7	7	2	-	-	-	-	-	-	♀	-	-	-	-	-	-	-	♂																							42
3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	6	-	-	-	2	13	26	-	-	-	-	41	3	-	-	-	-	♂	-	-	-	-	-	-	-	-	-	-	-	-	-	34	♀				127
4	-	-	-	-	6	-	-	-	2	1	1	1	2	-	1	♂	-	-	-	-	-	-	♀																														14
5	-	-	-	-	-	-	-	-	-	20	♂31	-	56	-	♀48																																						155
6	-	-	-	-	37	-	-	44	-	7	-	-	49	-	-	7	1	-	2	-	-	-	-	-	3	-	-	♀																									155
7	-	-	-	38	40	1	39	-	14	32	45	-	♂7	9	23	18	-	4	-	-	-	7	6	-	3	-	-	-	♀																								286
8	37	-	15	42	38	8	41	4	48	-	50	5	20	26	-	♀	-	-	♂																																		334
9	-	-	-	-	-	-	-	-	-	-	-	-	5	11	-	2	-	-	-	♀	-	-	-	-	-	-	-	♂																									18
10	-	-	-	-	-	-	-	-	-	-	-	10	-	-	-	-	6	84	9	3	-	59	-	46	1	1	4	2	1	3	9	-	♂	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	♀	241
11	-	-	-	27	13	11	19	2	2	19	19	-	-	1	31	2	4	14	3	9	8	21	-	5	6	-	14	3	-	♂	28	-	3	-	1	-	-	21	-	-	♀												286
12	-	-	40	-	42	-	19	22	10	8	21	35	-	45	1	-	28	-	24	10	23	2	4	11	♂5	-	3	-	♀																								353

♂ Indicates the date when male died
♀ Indicates the date when female died

Hatching studies

The results from Table IX show that the average hatch was 88.8% and varied from 64-100%. The minimum time required for the newly-laid eggs to hatch was between 24 and 48 hours and the hatch was complete after 120 hours. Finch and Coaker (1969) found that the viability of the eggs laid in the culture varied from 60 to 100% and averaged 86%. Swailes (1963) reported that the average hatch per female was 79% and varied from 18 to 100%. Finch and Coaker (1969) also examined the eggs that failed to hatch and they revealed that the embryos were well developed with many larval characteristics, and this suggested that exposure to dry conditions had affected hatching rather than development.

TABLE IX

PERCENTAGE OF HATCHING AFTER INCUBATION

PERIOD FOR 5 DAYS AT $21.1^{o} \pm 1^{o}C$

FROM LABORATORY CULTURE

No.	No. of eggs	No. of eggs hatched	Percentage of hatching
1	50	37	74
2	50	50	100
3	50	45	90
4	50	48	96
5	50	50	100
6	50	43	86
7	50	50	100
8	50	44	88
9	50	32	64
10	50	45	90
Total	500	444	888
Average	50	444	88.80

PART II

OVARIAN DEVELOPMENT OF THE CABBAGE MAGGOT, *Hylemya brassicae* (Bouché)

CHAPTER V

INTRODUCTION

Ovarian development has been used as an indicator of the physiological age in insects since the beginning of this century. Most of the work was done on insects of medical and veterinary importance. Among the calyptrate Diptera, species of *Musca* (Smith, 1968), *Fannia* (Anderson, 1964), *Phortophormia* (Harlow, 1956) and *Sarcophaga* (Abasa, 1972) have been studied. Most examinations of follicular development have been limited to the species of *Musca* due to the large size of adults, availability and the ease of culture. Few detailed studies have been done on the Anthomyiidae. This study was undertaken with the objectives

a. To determine the correlation between mating and the female age.

b. To determine the correlation between ovarian development and the female age in females fed a normal diet and in water fed females.

CHAPTER VI

REVIEW OF THE LITERATURE

The process of oögenesis was reviewed for the Insecta in general by Bonhag (1958). Many workers devised a basic scheme of ovarian development for each specific insect. Christophers (1911) studied the development of the follicles in *Anopheles*. Mer (1936) based on Christophers' studies divided oögenesis in *Anopheles elatus* into 5 stages and this was applied to *Hippelates pusio* by Schwartz (1965) and to *Musca domestica* by Smith (1968). Oögenesis in *Drosphila melanogaster* was divided into 14 stages by King *et.al*. (1956). Adam and Mulla (1967) described the ovarian development in *Hippelates collusor* in 10 stages which Adam and Hintz (1969) adapted for studies on *Musca domestica*.

Correlation between mating and ovarian development have been studied. Adam and Hintz (1969) reported that male house flies (*Musca domestica*) preferred mating with females with ovaries in stage 6 to 10. Swailes (1971) indicated that most male cabbage maggots (*Hylemya brassicae*) mated for the first time within 5 days of emergence and the peak number of mating at the age of 3 days.

The role of nutrition in the reproduction and egg development of insects was reviewed by Johansson (1964). The cabbage maggot must feed on carbohydrate but not on protein to mature its initial batch of eggs (Finch and Coaker, 1969). It had to imbibe suitable sources of proteinaceous materials or free amino acids before it could lay its second and subsequent batches of eggs (Finch, 1971). Monroe and Lamb (1968) reported that the effect of only egg albumen, yeast hydrolysate and defatted milk on ovarian development in house flies produced repeated good results at 91%, 100% and 100% respectively.

Temperature is another factor that influenced ovarian development. Adam and Mulla (1968) showed with the eye gnat *Hippelates collusor* that no ovarian development occured at 15.6°C or at 41.1°C but optimal temperatures ranged between 21.1° to 32.2°C.

Studies on the effects of alkylating and non-alkylating agents on ovarian development have been reported by many workers. Morgan and LaBrecque (1962, 1964) described the cytological effects of 1.0% concentration of 3 alkylating agents - apholate, tepa and metepa and non-alkylating - hempa (Morgan, 1967) on ovarian development of the house fly. They inhibited but did not eliminate ovarian development. This was verified by Abasa (1968) from the two strains of the house fly, insecticide-resistant flies and apholate-resistant flies.

CHAPTER VII

MATERIALS AND METHODS

1. Normally fed flies

Larvae were reared at 21.1°C until they reached the pupal stage. Adult flies were allowed to emerge from the pupae. Female adults of known age (1 to 25 days) were removed daily and dissected for ovarian development (Table X). The spermathecae in the females were examined if mating had occurred.

The flies were maintained in plastic cages size 15.2 x 22.8 x 48.2 cubic centimetres. The cage consisted of two sides of screen and the third side of plastic. A cloth sleeve provided easy access to the cage. Several emergence groups were used, the data for all emergence groups were combined to produce the tables. Samples were taken at a rate of 10 to 20 specimens at a time until no more flies were left in a cage. Adult flies taken in the sample were anesthetized with CO_2 and sexed. The female abdomens were dissected with forceps in a drop of saline solution using a binocular dissecting microscope. The internal ovarian structure of the fly was noted and the fly classed into the appropriate category. Characteristics used for the classification were: the presence of pupal fat balls, the stage maturation of follicles described by Christophers (1911) with modifications suggested by Clements (1963), the presence of follicular relics and the presence of ovariole dilatations.

2. Water fed flies

The flies were maintained and treated like the normally fed flies except that water only was provided. Samples were collected from the dead flies from the first day to the seventh day. The female abdomens were dissected by the same method and the same classification of the normally fed flies were followed.

3. Classification of ovarian development

Christophers' (1911) method was used with the modifications suggested by Clements (1963).

The scheme used in the present study to classify ovarian development was as follows:

Stage 1 a	The follicle is spherical and fully separated from the germinal epithelium of the ovariole.
Stage 1 b	The definitive oocyte is distinguishable in the terminal portion of the follicle.
Stage II a	Very small quantities of yolk, visible only with phase contrast at high power are present in a sphere around the oocyte nucleus.
Stage II b	Sufficient yolk is present in the oocyte so that the yolk can be seen as a small plaque at magnifications of about 35x. The yolk occupies less (usually much less) than one-half the follicle.
Stage III a	The yolk occupies between one-half and two-thirds of the follicle.

Stage III b	The yolk occupies between two-thirds and three-quarters of the follicle.
Stage IV a	The follicle begins to elongate; the yolk occupies about nine-tenths of the follicle.
Stage IV b	The follicle assumes the shape of the mature egg.
Stage V	The mature egg, complete with chorion.

Stages earlier than Ia were observed in the cabbage maggots. These are recognized by ovaries embedded in the fat body and firmly held to the cuticula by tracheae.

4. Mating

Mating was determined by examination of the spermathecal ducts for the presence of sperm. Spermathecae were placed on a slide in a drop of saline solution and covered by a cover slide. By pressing the cover slide, the spermathecae were broken and the presence of sperm was checked by using a high-powered microscope.

CHAPTER VIII

RESULTS AND DISCUSSION

1. Ovarian development in normally fed flies

The results are summarized in Table X and show that females require 4 days to complete the first cycle of egg maturity and 9 days to reach the second cycle. Newly emerged flies are in stage N (Figure 4). Ovarioles of a nulliparous female could be distinguished from parous females by the presence of tracheal skeins (Figure 5) and by the absence of the "yellow bodies" or follicular relics in the ovariole pedicels and lateral oviducts (Figure 6). Follicular relics are clearly visible at the base of the ovariole, they consist mainly of remnants of nurse cells and are surrounded by the contracted portion of the intima in which the egg developed. In females which have completed a different number of ovipositions the distribution and number of yellow bodies differ. These characteristics were reported by Lineva (1953 cited in Destinova, 1962) on the house fly, *Musca domestica* and in the paper described by Anderson (1964) on *Fannia cannicularis* and some other cyclorraphous Diptera.

The abundant fat bodies in adult females at the time of emergence are depleted as follicular development proceeds to maturity. By the time the first follicles reach stage V, most of the fat bodies have been used and the second follicles are at stage I b to III a. In a few cases, the development of second follicles may reach stage V.

By the fourth day some females have deposited eggs. A recent oviposition is determined by a stretched ovariole and the presence of immature ovarioles only (Figure 7) or retained mature eggs in developed ovary (Figure 8). As maturation proceeds in the second cycle, the ovarioles again contract and a dilatation which the previous follicle has developed inside, can be seen at the posterior end of the developing eggs (Figure 9). However, the dissection of the ovaries of cabbage maggots to count the number of dilatations, is technically difficult.

The stage of ovarian development of the cabbage maggot, Hylemya brassicae is shown in Figure 10 to 20. Figure 21 illustrates accumulation of follicular relics in a 14-day old female.

TABLE X

THE OVARIAN APPEARANCE OF A POPULATION OF *Hylemya brassicae* AT VARIOUS DAYS SUBSEQUENT TO EMERGENCE, EXPRESSED AS THE PROPORTION IN AN OVARIAN STAGE ON A GIVEN DAY

Day	Nulliparous stage										Parous stage										No. of female
	N	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb	V	N	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb	V	
0	1.00																				16
1	.72	.28																			18
2	.06	.45	.27	.09	.06	.03	.03														33
3	.025	.375	.25	.05	.15	.125	-	.025													40
4	-	.04	.02	.02	.10	.32	.08	.02	.08	.30	-	-	.02								50
5	-	-	.04	-	.01	.09	.01	.06	.01	.46	-	.05	.14	.01	.10						70
6	-	.03	.15	-	.03	-	.03	-	.03	.53	-	.03	.09	.03	.03						32
7	-	-	.04	-	.09	.04	-	.04	-	.54	-	-	.14	-	-	.09					22
8										.46	-	-	-	.08	.08	.15	-	.23			13
9										.54	-	-	.13	-	.08	.08	-	-	.04	.13	24
10									.03	.81	-	-	.03	-	-	.05	-	-	-	.08	38
11									.09	.36	-	-	-	.18	.09	.18	-	-	-	.09	11
12										.20	-	.05	.03	.10	.10	.20	.13	.08	.03	.08	39
13										.18	-	.03	-	.06	.27	.15	.12	-	.06	.12	33
14						.03			.06	.40	-	-	.11	.09	.06	.17	.06	.03			35
15										.41	-	-	-	-	.09	.32	.045	.09	-	.045	22
16										.41	-	.04	.04	.07	.11	.22	.04	-	-	.07	27
17										.33	-	.20	-	.07	.20	.07	-	-	-	.13	15
18										.31	-	-	-	-	-	.06	-	.13	-	.50	16
19										.35	-	-	-	.06		.12	-	-	.12	.35	17
20										.31	-	-	.06	-	.31	.19	.06	-	-	.06	16
21										.27	-	.14	.18	.14	.05	.05	-	-	-	.18	22
22										.64	-	-	.09	.09	-	.18					11
23										.18	-	-	-	-	.24	.35	.06	.06	.06	.06	17
24										.41	-	-	-	-	.06	.06	.06	-	.18	.24	17
25										.42	-	-	.11	-	.05	.11	-	-	.16	.16	19
																					673

2. Ovarian development in water fed flies

The results from Table XI show that females can complete the first cycle on the fourth day as normally fed flies can. Female flies died before they developed the second cycle. In this study, there are two female flies that lived until thirteen days old. From these data it may be concluded that water fed female flies can develop their first batch of eggs.

Development of the follicles generally progresses uniformly but in some cases there is evidence of follicle reabsorption.

TABLE XI

PROPORTIONS OF WATER FED FEMALE *Hylemya brassicae*, IN VARIOUS OVARIAN STAGES AT THE AGE OF DEATH

Age of death (day)	Nulliparous stage										Parous stage			No. of females dissected
	N	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb	V	Ia	Ib	IIb	
1		.66	.17		.17									6
1½	.25	.63		.12										8
2		.37	.73											11
2½		.40	.50		.10									10
3		.25	.34	.13	.06	.09	.03		.09					32
3½		.30	.50	.10					.10					10
4	.02	.19	.18	.08	.07	.20	.02		.07	.14				83
5	.01	.22	.19	.03	.16	.10	.03	.03	.10	.07	.01	.01		67
6			.25	.06					.06	.06	.19	.38		16
7		.33			.17						.33		.17	6

3. Ovarian development in adults caught from the field

The results from Table XII to XVII show that ovaries from female adult flies caught in the field, developed into the second batches of eggs. Most of the flies laid the first batches of eggs from the end of June until the middle of August. The number of flies caught from turnip, cabbage, cauliflower, radish, broccoli and rape were 79, 46, 44, 35, 25 and 10 respectively. The figures in the nulliparous stage of ovarian development stand for the number of fully developed eggs which were found unlaid in the ovaries. The stage of ovarian development shows in nulliparous and parous flies indicating ovaries developed into those stages (Table XII - XVIII).

TABLE XII

THE STAGE OF OVARIAN DEVELOPMENT OF ADULT FEMALE

CABBAGE MAGGOTS CAUGHT IN BROCCOLI PLOTS DURING 1971

Date		Stage of ovarian development		No. of Flies caught		
		Nulliparous	Parous	Male	Female	Total
June	29	-	-	1	-	1
July	2	-	-	-	-	-
	6	-	Ib**	1	3	4
	9	-	-	2	-	2
	13	-	-	2	-	2
	16	N	Ib	2	2	4
	20	53,* IIIb	Ib, 2IIb, III b	3	5	8
August	3	-	-	-	-	-
	6	-	-	-	-	-
	10	4	IIIa	2	1	3
	.12	IIIa	-	-	1	1
				13	12	25

* The number of eggs found unlaid in the ovaries
** The stage of ovarian development found in the ovaries
(* and ** comment applies to Tables XII - XVII)

TABLE XIII

THE STAGE OF OVARIAN DEVELOPMENT OF ADULT FEMALE CABBAGE MAGGOTS CAUGHT IN CAULIFLOWER PLOTS DURING 1971

Date	Stage of ovarian development		No. of flies caught		
	Nulliparous	Parous	Male	Female	Total
July 6	39, 50, 16	2 IIb, 2IIIa	3	4	7
9	-	-	-	-	-
13	6	IIa	3	1	4
16	32	2IIb	1	2	3
18	N, IIIa,38,29, 22,7,19,27,12	N,Ia,3IIb,3IIa	3	10	13
20	35, 9	2Ib	1	3	4
August 3	IIIa, 28,44,25	3IIb	1	4	5
6	-	Ia	1	1	2
10	59	IIIa	1	1	2
12	13,48,17	2IIb, IIIa, IVa	0	4	4
			14	39	44

TABLE XIV

THE STAGE OF OVARIAN DEVELOPMENT OF ADULT FEMALE CABBAGE MAGGOTS CAUGHT IN CABBAGE PLOTS DURING 1971

Date		Stage of ovarian development		No. of flies caught		
		Nulliparous	Parous	Male	Female	Total
June	25	N, 38	IIIa	-	2	2
	29	-	-	-	-	-
July	2	30	IIIa	1	1	2
	6	N,29,25,38	3IIa, IIIa	2	4	6
	9	-	-	2	0	2
	13	19	2IIa, IIIa	4	3	7
	16	N, IIb	IIb	1	3	4
	18	IIIb	-	1	1	2
	20	28	Ib, IIb	5	2	7
August	3	9, 7, 3	2Ib, IIIa	0	3	3
	6	-	-	-	-	-
	10	17,28,29,29	4IIb, IIIa	2	5	7
	12	IVb	Ia, IIIa	1	3	4
				19	27	46

TABLE XV

THE STAGE OF OVARIAN DEVELOPMENT OF ADULT FEMALE

CABBAGE MAGGOTS CAUGHT IN RADISH PLOTS DURING 1971

Date		Stage of ovarian development		No. of flies caught		
		Nulliparous	Parous	Male	Female	Total
June	25	IIIa,22,22,1	IIa,IVb	1	5	6
	29	N, IIIa, 1	2IIb, IIIa	3	5	8
July	2	IVa	-	3	1	4
	6	IV b, 28, 33	2IIb, IIIa	1	4	5
	9	IIa	-	6	1	7
	13	-	-	-	-	-
	16	-	-	1	0	1
	18	-	-	3	0	3
	20	-	-	-	-	-
August	6	-	-	1	0	1
	10	-	-	-	-	-
				19	16	35

TABLE XVI

THE STAGE OF OVARIAN DEVELOPMENT OF ADULT FEMALE CABBAGE MAGGOTS CAUGHT IN RAPE PLOTS DURING 1971

Date		Stage of ovarian development		No. of flies caught		
		Nulliparous	Parous	Male	Female	Total
June	25	-	III a	1	1	2
	29	15	III a	2	1	3
July	2	-	-	0	0	0
	6	-	-	4	0	4
	13	V	-	0	1	1
				7	3	10

TABLE XVII

THE STAGE OF OVARIAN DEVELOPMENT OF ADULT FEMALE CABBAGE MAGGOTS CAUGHT IN TURNIP PLOTS DURING 1971

Date		Stage of ovarian development		No. of flies caught		
		Nulliparous	Parous	Male	Female	Total
June	29	N, IIb	-	1	2	3
July	2	-	-	1	0	1
	6	29,46,38,25 21,5	4IIb, 3 IIIa	2	7	9
	9	-	-	0	0	0
	13	-	-	1	0	1
	16	9	IIb	2	0	3
	18	34,19,39,18 33,26,52,36 7,20,IVb,V	Ia,2Ib,2IIb	6	14	20
	20	14,37	2Ib	1	2	3
August	3	IIIa,V,40,47 19,14,18,20 25,13	Ia,4lb,4IIb	4	11	15
	6	2IV,19,18,8 4,34,9,3,21	6IIb, 7IIIa	6	18	24
				24	55	79

4. Mating

The results from Table XVIII show that in the samples taken from the mixed population, no sperm was observed at spermathecae in one, two or three day old females. The earliest mating occurred in the four-day old females and it reached 100% when females were eight days old. Swailes (1961) and Coaker and Finch (1967) reported that females required three days post-emergence maturation. Most females mated only once (Swailes, 1961) and males mated up to four times from two days after they emerged until they died. Adam and Mulla (1968) found the relationship between ovarian development and mating in the eye gnat *Hippelates collusor* when males were given a choice of females in five different stages of ovarian development. They mated only with females in stage 6 to 9 and not with females in stage 2 to 5 or stage 10.

Spermathecae of a virgin female are shown in Figure 22. The presence of sperm cells in spermathecae of mated females is illustrated in Figure 23 a, b and c.

TABLE XVIII

RELATIONSHIP BETWEEN AGE AND MATING

IN CABBAGE MAGGOT, *Hylemya brassicae*

Age (day)	Number observed	Number mated	Percentage
1	10	0	0
2	10	0	0
3	10	0	0
4	15	3	20.0
5	17	10	58.8
6	15	10	66.6
7	18	11	61.1
8	10	10	100.0
9	19	19	100.0
10	10	9	90.0

CHAPTER IX

SUMMARY

The biology and ovarian development of *H. brassicae* were studied under both field and laboratory conditions in 1970 and 1971. Population density and the infestation of the host plant were investigated in the field. Ovarian development studies were made on flies cultured in the laboratory and wild flies caught in the field.

1. Infestation on cabbages was 25.4 to 77.7% in 1970 and 90 to 100% in 1971; on radishes 27 to 100% in 1971.
2. Two generations and a partial third generation occurred in Manitoba and the population of the first generation was lower than those in the subsequent ones. The first batch of eggs was found on or near the host plants on June 9th in 1970 and June 8th in 1971.
3. Larvae undergo three instar before they pupate. This was determined by measurements of the size of mouthhooks.
4. The average life span of males and females was 24 days and 29.8 days respectively. Females laid from 14 to 353 eggs or an average of 171.8 eggs.
5. Hatchability of cultured eggs at $21.1^{o} \pm 1^{o}C$ was 64 to 100% or an average of 88.8%.
6. There was a direct correlation between the diameter of the core and the number of eggs deposited.
7. Studies were undertaken to rear the cyclodiene-susceptible strain in the laboratory in order to determine ovarian development with females of known age.

8. The time required for completing the first cycle of ovarian development was four days and the second cycle was nine days in normally fed flies.

9. A few water fed flies developed into the stage V within four days but they died before starting the second cycle.

10. Most of wild flies laid at least one batch of eggs.

11. The earliest mating of females was on the fourth day after eclosion.

Figure 4

Follicular development of *Hylemya brassicae*,

Stage N. 63x

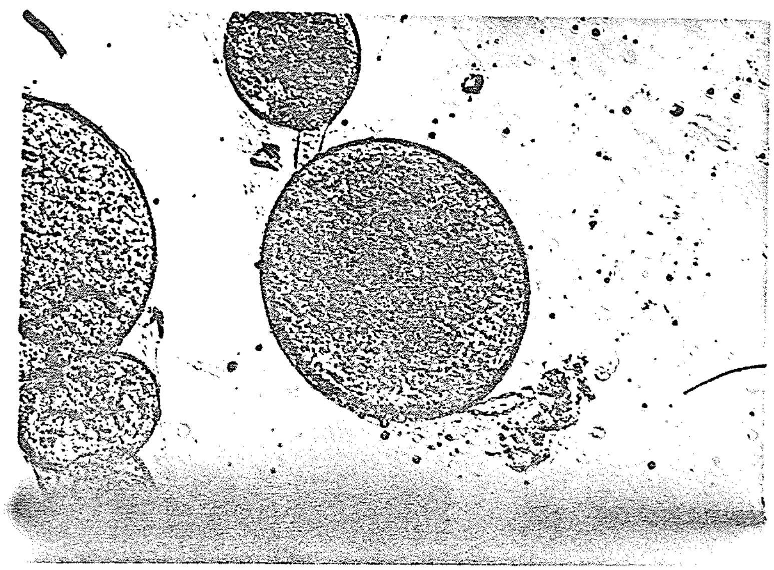


Figure 5a (Top right)

Follicle of nulliparous female of *Hylemya brassicae* showing the presence of tracheal skeins. 40x

Figure 5b (Bottom right)

Follicle of nulliparous female of *Hylemya brassicae* showing the presence of tracheal skeins. 63x

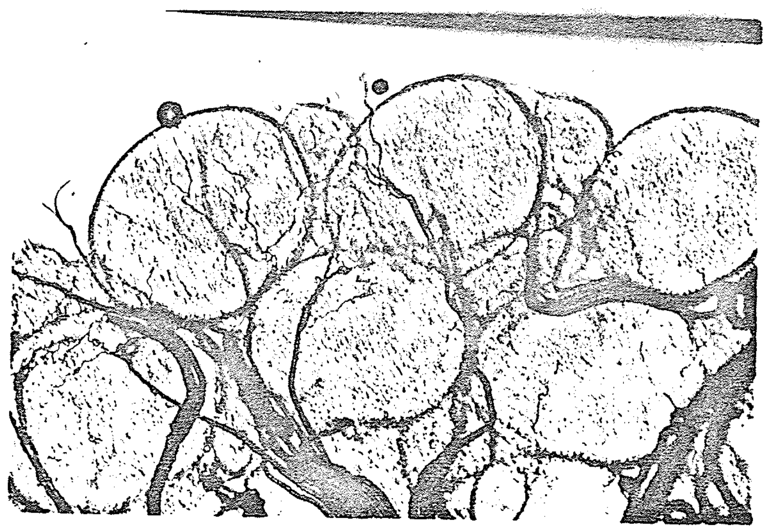
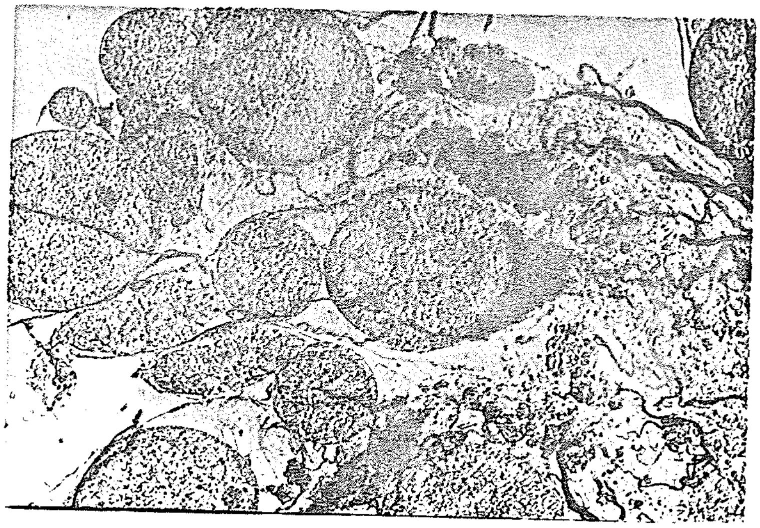


Figure 6 (Top right)

Follicular development of a 13 day old female of Hylemya brassicae after laying 52 eggs. Illustrates follicular relics. 40x

Figure 7 (Bottom right)

Ovary of a thirteen day old fly of Hylemya brassicae laying 52 eggs, showing follicular relics. 10x



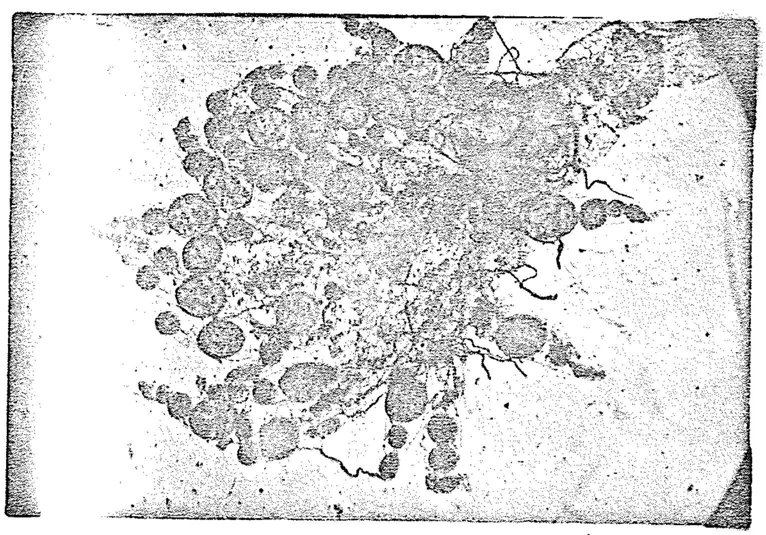


Figure 8

Retained mature eggs of *Hylemya brassicae* in developed ovary. 10x

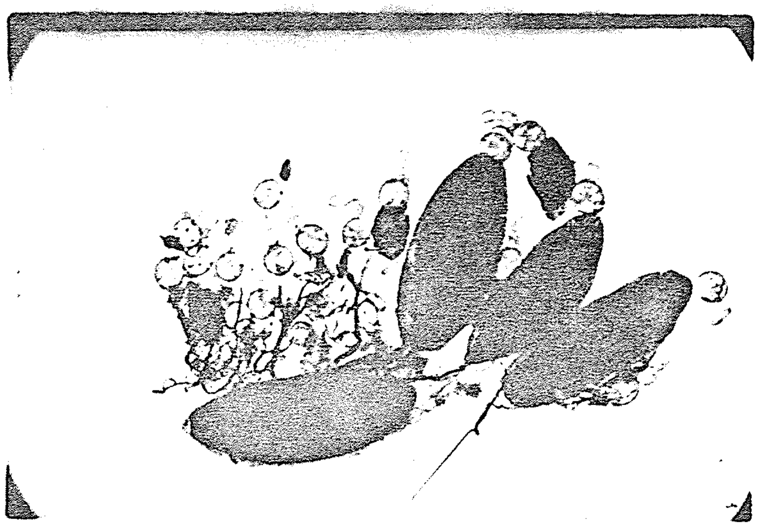


Figure 9

Ovariole pedicels of a 19 day-old fly of *Hylemya brassicae*. Illustrated accumulation of follicular relics in ovariole pedicels at base of follicles. 40x

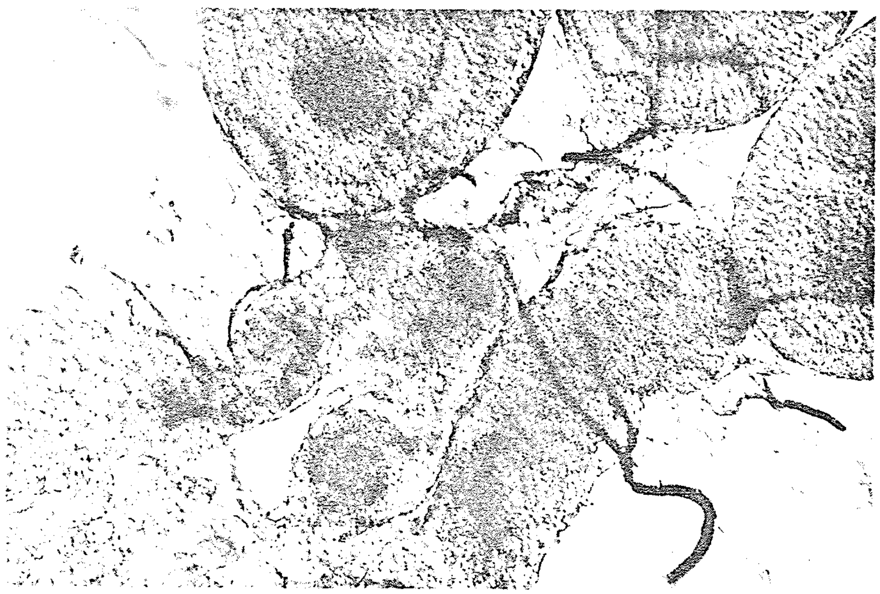


Figure 10

Ovaries of *Hylemya brassicae*,

Stage Ib : one day old. 10x

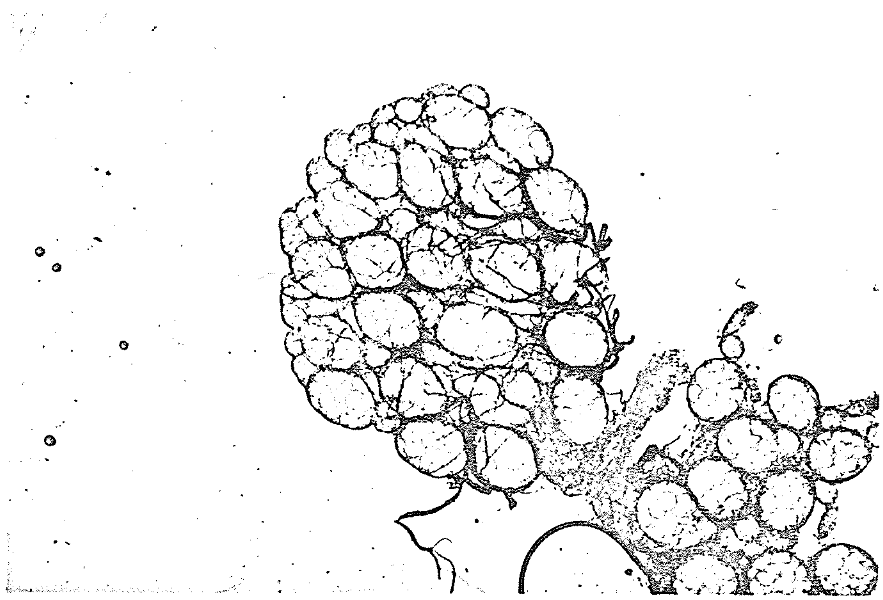


Figure 11 (Top right)

Follicular development of *Hylemya brassicae*,

Stage Ia. 40x

Figure 12 (Bottom right)

Follicular development of *Hylemya brassicae*,

Stage Ib. 40x

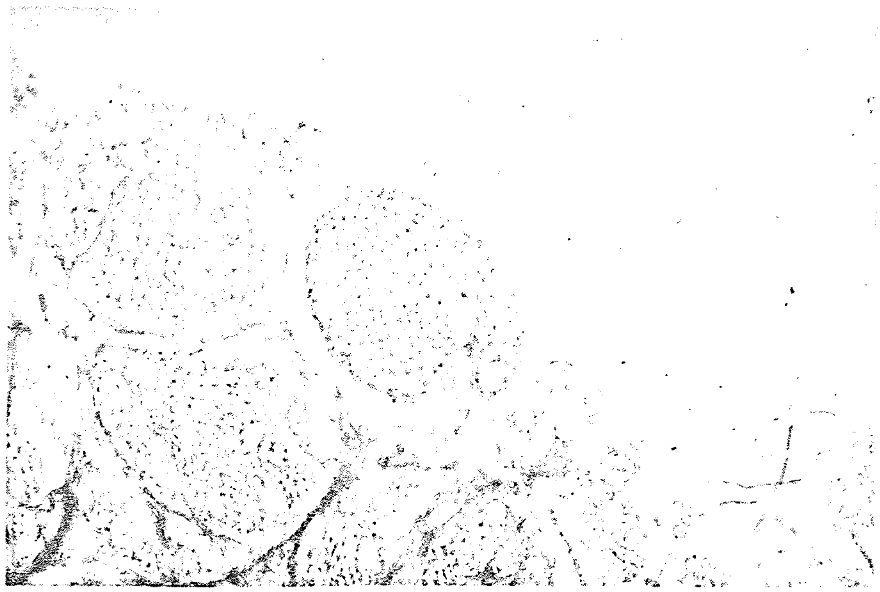


Figure 13

Follicular development of *Hylemya brassicae*,

Stage IIa. 40x

Figure 14 (Top right)

Follicular development of *Hylemya brassicae*,

Stage IIa. 40x

Figure 15 (Bottom right)

Follicular development of *Hylemya brassicae*.

Stage IIb. 40x

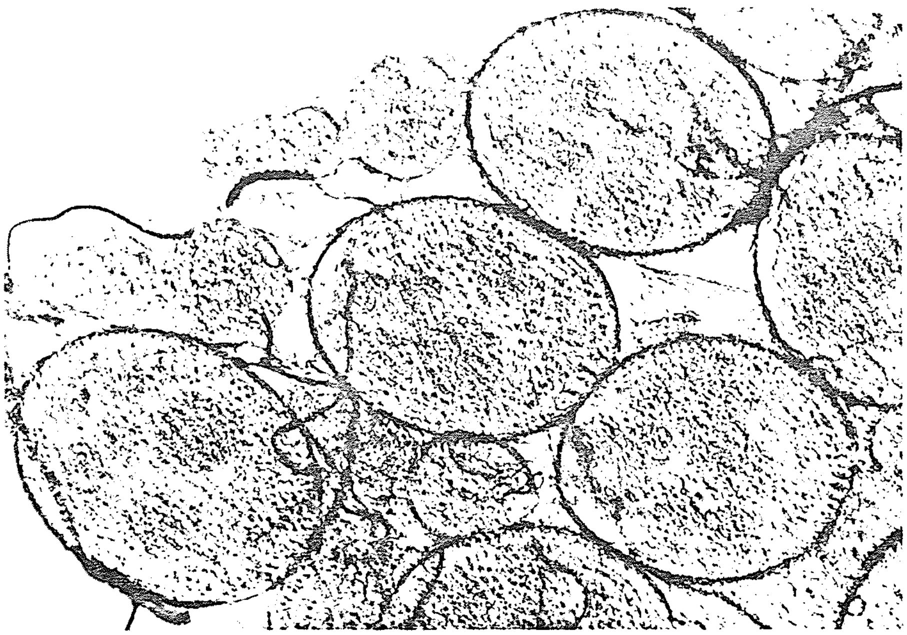


Figure 16 (Top right)

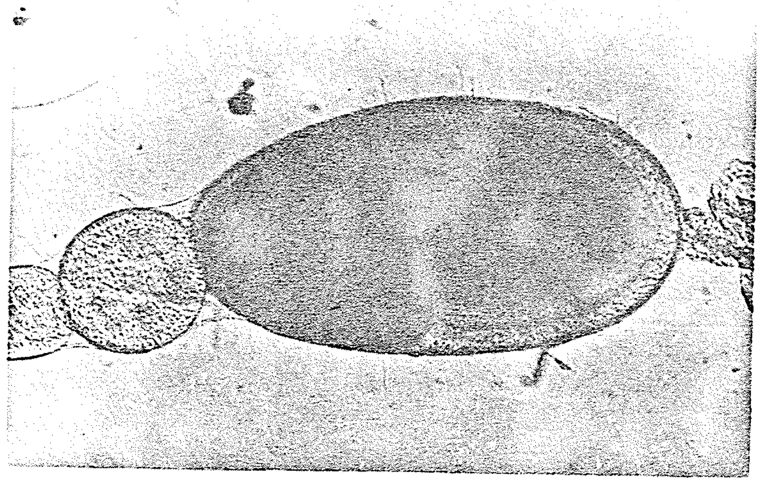
Follicular development of _Hylemya brassicae_.

Stage IIIa. 40x

Figure 17 (Bottom right)

Follicular development of parous female of

Hylemya brassicae Stage IIIa. 10x



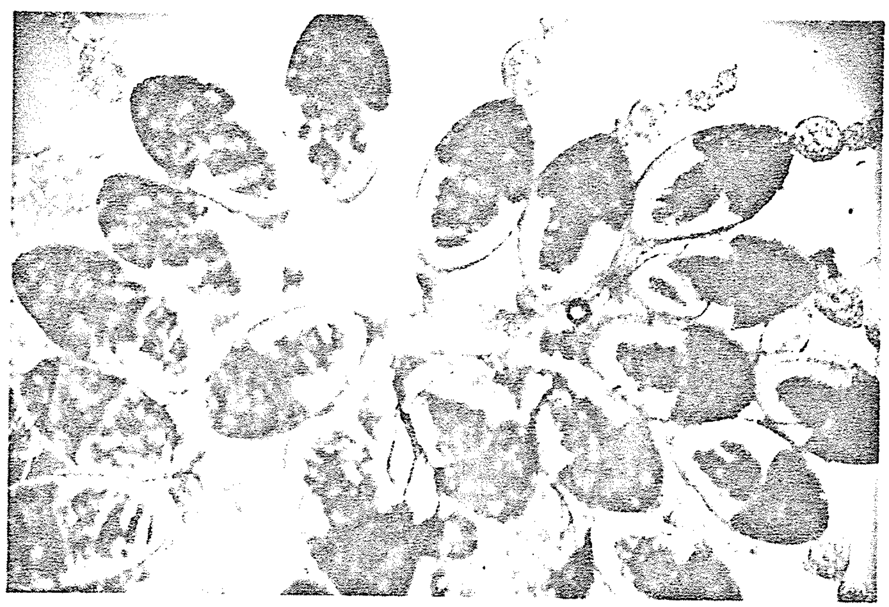


Figure 18 (Top right)

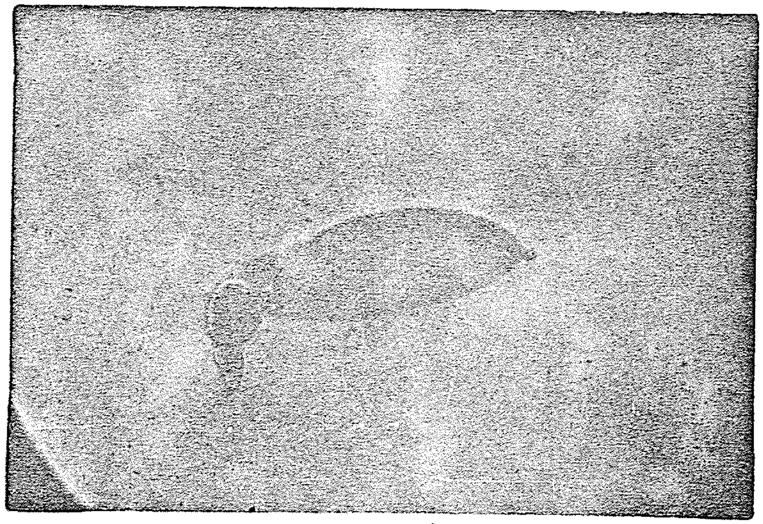
One fully-developed follicle of

Hylemya brassicae, Stage V. 10x

Figure 19 (Bottom right)

Follicular development of *Hylemya brassicae*,

Stage V. 10x



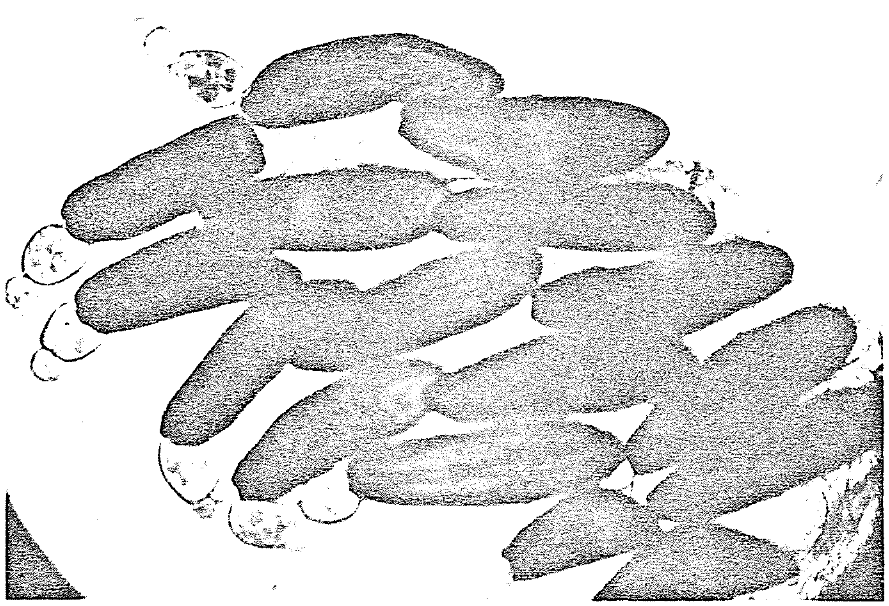


Figure 20 (Top right)

Follicular development of *Hylemya brassicae*

Stage V.

The picture shows three spermathecae also. 10x

Figure 21 (Bottom right)

Ovaries of a 14 day-old fly of *Hylemya brassicae*. Illustrates accumulation of follicular relics in ovariole pedicels at the base of follicles. 10x

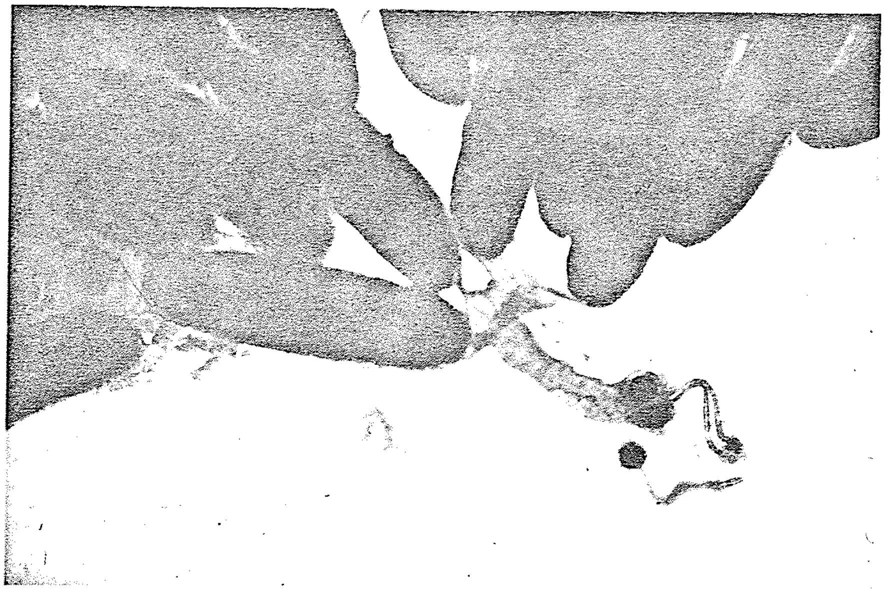


Figure 22 (Top right)

Spermatheca of a virgin female of

Hylemya brassicae. 63x

Figure 23a (Bottom right)

Sperm cells from spermatheca of

mated female of *Hylemya brassicae*. 160x

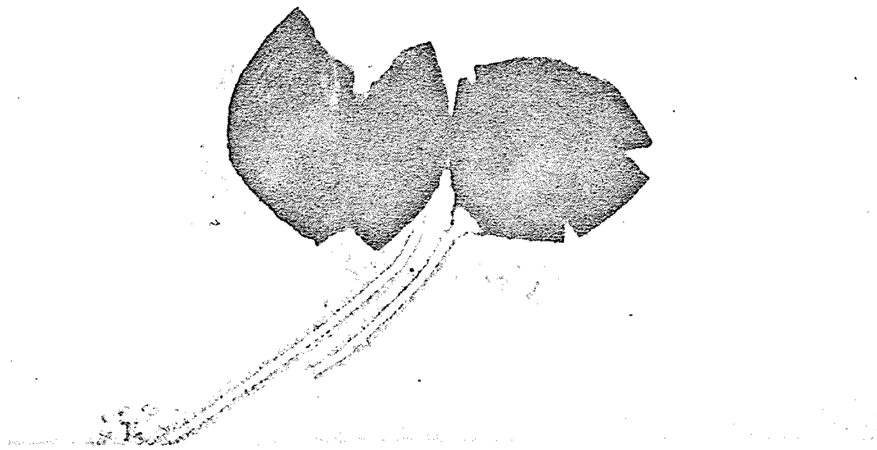


Figure 23b (Top right)

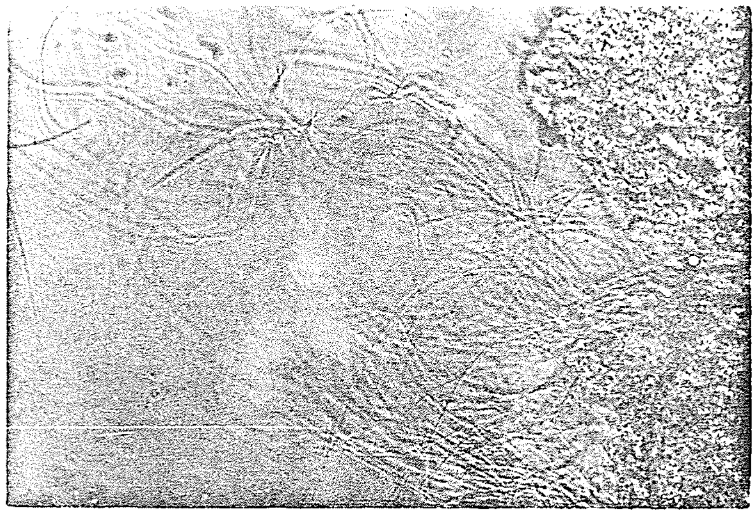
Sperm cells from spermatheca

of mated female of _Hylemya brassicae_. 160x

Figure 23c (Bottom right)

Sperm cells from spermathecae of

mated female of Hylemya brassicae. 63x



LITERATURE CITED

Abasa, R. O. 1968. An apholate-resistant strain of the house fly, Musca domestica. Ann. ent. Soc. Am. 61:1351-1354.

Abu Yaman, I. K. 1960. Natural control in cabbage root fly populations and influence of chemicals. Meded. Landb. Wageningen 60:1-57.

Adams, T. S. and A. M. Hintz. 1969. Relationship of age, ovarian development and the corpus allatum to mating in the house fly, Musca domestica. J. Insect Physiol. 15:201-215.

Adams, T. S. and M. S. Mulla. 1967. The reproductive biology of Hippelates collusor (Diptera : Chloropidae) II. Gametogenesis. Ann. ent. Soc. Am. 60:1177-1182.

Adams, T. S. and M. S. Mulla. 1968. Ovarian development, pheromone production and mating in the eye gnat, Hippelates collusor. J. Insect Physiol. 14:627-635.

Allen, W. R. 1964. The occurrence of cabbage maggot on rape in Manitoba and evaluation of insecticides for control. Proc. ent. Soc. Manitoba 20:54-58.

Anderson, J. R. 1964. Methods for distinguishing nulliparous from parous flies and for estimating the ages of Fannia canicularis and some other cyclorrhaphous Diptera. Ann. ent. Soc. Am. 57:226-236.

Bonhag, P. E. 1958. Ovarian structure and vitellogenesis in insects. Ann. Rev. Ent. 3:137-160.

Brittain, W. H. 1927. The cabbage maggot, Hylemya brassicae (Bouche) and its control in Nova Scotia. Bull. Nova Scotia Dep. nat. Resour. No. 11.

Brooks, A. R. 1951. Identification of the root maggots (Diptera : Anthomyiidae) attacking cruciferous garden crops in Canada, with notes on biology and control. Can. Ent. 83:109-120.

Carlson, E. C., E. P. Breakey and R. L. Webster. 1964. The cabbage maggot in North West Washington. J. econ. Ent. 40:57-64.

Christophers, S. R. 1911. Development of the egg follicle in Anopheles. Paludism 2:73-88.

Clements, A. N. 1963. The physiology of mosquitoes. Pergamon Press, London. 393 pp.

Coaker, T. H. and S. Finch. 1967. The behavior of the cabbage root fly. Rep. natn. Veg. Res. Stn. 1967:61-62.

Coaker, T. H. and S. Finch. 1971. The cabbage root fly, Erioischia brassicae (Bouche). Rep. natn. Veg. Res. Stn. 1971:23-42.

Destinova, T. S. 1962. Age-grouping methods in Diptera of medical importance with special reference to some vectors of malaria. WHO. Monograph series No. 47 Geneva, Switzerland.

Finch, S. 1971. Comparison of the nutritive values of proteins and related compounds to adult cabbage root fly, Erioischia brassicae (Bouche). Ent. exp. & Appl. 14 (in press).

Finch, S. and T. H. Coaker. 1969. A method for the continuous rearing of the cabbage root fly, Erioischia brassicae (Bouche) and some observations on its biology. Bull. ent. Res. 58:619-627.

Foot, W. H. 1964. The biology of the adults of Hylemya brassicae (Bouche) (Diptera : Anthomyiidae). Eighty fifth Ann. Rept. ent. Soc. Ont. 42-53.

Forbes, A. R. and K. M. King. 1957. Control of the cabbage maggot in British Columbia. Can. Agric. 1027 pp.

Harlow, P. M. 1956. A study of ovarial development and its relation to adult nutrition in the blowfly, Protophormia ferae-novae (R.D.) J. Expt. Biol. 33:777-797.

Harris, C. R. and H. J. Svec. 1966. Mass rearing of the cabbage maggot, Hylemya brassicae under controlled environmental conditions with observations on the biology of cyclodiene-susceptible and resistant strains. J. econ. Ent. 59:569-573.

Hughes, R. D. and B. Mitchell. 1960. The natural mortality of Erioischia brassicae (Bouche) (Diptera : Anthomyiidae) : life tables and their interpretation. J. anim. Ecol. 29:359-374.

Hughes, R. D. and D. D. Salter. 1959. Natural mortality of Erioischia (i.e. Hylemya) brassicae (Diptera : Anthomyiidae) during the immature stages of the first generation. J. anim. Ecol. 28:231-241.

Johansson, A. S. 1964. Feeding and nutrition in reproductive process in insects. In symposium No. 2, Royal ent. Soc. London. (K. C. Highman ed.) pp. 43-55.

King, R. C., A. C. Rubison, and R. F. Smith. 1956. Oögenesis in adult Drosophila melanogaster. Growth 20:121-157.

Mer, G. G. 1936. Experimental study on the development of the ovary in Anopheles elatus Edw. (Diptera : Culicidae). Bull. ent. Res. 27:351-359.

Miles, M. 1951. Factors affecting the behaviour and activity of the cabbage root fly, Erioischia brassicae (Bouche). Ann. appl. Biol. 38:425-432.

Miles, M. 1952. Studies of British Anthomyiid flies. III. Immature stages of Delia cilicrura (Rond.), D. trichondactyla (Rond.), Erioischia brassicae (Bouche), E. floralis (Fall.) and Pegohylemyia fugax (Meig.). Bull. ent. Res. 43:84-90.

Miles, M. 1954. Field studies on the influence of weather on egg laying by the cabbage root fly, Erioischia brassicae (Bouche) II. Ann. appl. Biol. 41:586-590.

Monroe, R. E. and N. J. Lamb. 1968. Effect of commercial proteins on house fly reproduction. Ann. ent. Soc. Am. 61:456-459.

Morgan, P. B. 1967. Effects of hempa on the ovarian development of the house fly, Musca domestica (Diptera : Muscidae). Ann. ent. Soc. Am. 60:812-818.

Morgan, P. B. and G. C. LaBrecque. 1962. The effect of apholate on the ovarian development of house flies. J. econ. Ent. 55:626-628.

Morgan, P. B. and G. C. LaBrecque. 1964. Effect of tepa and metepa on the ovarian development of house flies. J. econ. Ent. 57:896-899.

Muesebeck, C. R. W. 1942. Common names of insects approved by the American Association of economic Entomologists. J. econ. Ent. 35:83-101.

Mukerji, M. K. 1971. Major factors in survival of immature stages of Hylemya brassicae (Diptera : Anthomyiidae) on cabbage. Can. Ent. 103:717-728.

Mukerji, M. K. and D. G. Harcourt. 1970. Design of a sampling plan for studies on the population dynamics of the cabbage maggot, Hylemya brassicae (Diptera : Anthomyiidae) Can. Ent. 102:1513-1518.

Read, D. C. 1969. Rearing the cabbage maggot with and without dispause. Can. Ent. 101:725-737.

Schoene, W. J. 1916. The cabbage maggot: its biology and control. New York Agr. Expt. Sta. Bull. 419:99-147.

Smith, K. M. 1927. A study of Hylemyia (Chortophila) brassicae (Bouche) the cabbage root fly and its parasites, with notes on some other Dipterous pests of cruciferous plants. Ann. appl. Biol. 14:312-329.

Smith, T. A. 1968. Comparison of known age with physiological aging in the adult female house fly, Musca domestica L. J. Med. Ent. 5:1-4.

Swailes, G. E. 1958. Periods of flight and oviposition of the cabbage maggot, Hylemya brassicae (Bouche) (Diptera : Anthomyiidae) in Southern Alberta. Can. Ent. 90:434-435.

Swailes, G. E. 1961. Laboratory studies on mating and oviposition of Hylemya brassicae (Bouche) (Diptera : Anthomyiidae). Can. Ent. 93:942-943.

Swailes, G. E. 1963. Effects of temperature on hatching and on longevity of starved first instar larvae of Hylemya brassicae (Bouche) (Diptera : Anthomyiidae). Can. Ent. 95:878-881.

Swailes, G. E. 1971. Reproductive behaviour and effects of the male accessory gland substance in the cabbage maggot, Hylemya brassicae. Ann. ent. Soc. Am. 64:176-179.

Vereecke, A. and L. Hertveldt. 1971. Laboratory rearing of the cabbage maggot. J. econ. Ent. 64:670-673.

APPENDIX A

DAILY TEMPERATURES AND PRECIPITATION AT WINNIPEG, MANITOBA, JUNE, JULY, AUGUST AND SEPTEMBER 1970 AND 1971

Tables I - VIII give daily maximum (Max. Temp.) and minimum (Min. Temp.) air temperatures in degrees fahrenheit (°F); precipitation (Ppt.) as the sum of rainfall and one-tenth of snowfall in inches and the monthly sum of precipitation for the months of June, July, August and September of 1970 and 1971.

All data were recorded at the Winnipeg Internation Airport, Winnipeg, Manitoba.

APPENDIX A

TABLE I

DAILY TEMPERATURES AND PRECIPITATION

JUNE 1970

Day	Max. Temp. °F	Min. Temp. °F	Ppt. (inches)
1	68	46	0
2	73	52	.01
3	83	50	0
4	85	53	0
5	88	55	0
6	86	50	0
7	84	42	0
8	97	63	.21
9	78	58	.17
10	79	55	.40
11	68	61	.07
12	77	61	.11
13	78	60	Tr.
14	72	56	0
15	74	57	Tr.
16	77	59	.18
17	73	48	Tr.
18	64	47	0
19	69	40	Tr.
20	74	45	0
21	76	50	0
22	84	51	0
23	75	55	.12
24	69	44	0
25	68	53	.36
26	74	54	0
27	77	59	.08
28	90	63	Tr.
29	90	65	0
30	90	65	.28
		Total =	1.99

APPENDIX A

TABLE II

DAILY TEMPERATURES AND PRECIPITATION

JULY 1970

Day	Max. Temp. °F	Min. Temp. °F	Ppt. (inches)
1	81	56	0
2	72	55	.17
3	64	51	.02
4	73	46	0
5	85	53	.08
6	82	61	.09
7	76	56	Tr.
8	84	50	0
9	92	62	Tr.
10	90	66	0
11	93	67	.04
12	86	65	.21
13	83	59	.01
14	71	59	1.28
15	82	55	0
16	87	61	0
17	71	55	Tr.
18	64	53	.18
19	72	47	0
20	77	48	0
21	82	57	0
22	78	64	.06
23	79	62	.15
24	74	62	.17
25	85	56	.12
26	81	62	Tr.
27	79	56	0
28	87	60	Tr.
29	85	69	.16
30	85	64	0
31	73	57	0
		Total =	2.74

APPENDIX A

TABLE III

DAILY TEMPERATURES AND PRECIPITATION

AUGUST 1970

Day	Max. Temp. ^{o}F	Min. Temp. ^{o}F	Ppt. (inches)
1	86	55	0
2	67	49	0
3	72	48	0
4	81	54	0
5	86	56	0
6	90	60	0
7	90	68	0
8	88	66	0
9	82	55	02
10	86	48	0
11	92	61	0
12	92	58	0
13	96	59	0
14	80	63	0
15	73	54	.08
16	71	48	0
17	93	53	.02
18	80	62	Tr.
19	70	49	0
20	73	46	0
21	69	51	.65
22	73	52	0
23	81	49	0
24	78	47	0
25	75	47	0
26	80	46	Tr.
27	72	47	0
28	74	40	0
29	74	54	2.20
30	67	45	0
31	71	39	0
		Total =	2.95

APPENDIX A

TABLE IV

DAILY TEMPERATURES AND PRECIPITATION

SEPTEMBER 1970

Day	Max. Temp. ^{o}F	Min. Temp. ^{o}F	Ppt. (inches)
1	83	57	Tr.
2	76	59	.16
3	78	55	Tr.
4	74	50	0
5	90	59	.20
6	85	63	0
7	66	49	.28
8	64	45	.06
9	61	41	.22
10	62	37	Tr.
11	53	39	.44
12	48	37	.08
13	49	30	Tr.
14	54	29	0
15	48	38	.31
16	72	35	0
17	65	48	0
18	79	42	0
19	82	53	0
20	71	53	2.01
21	62	43	.53
22	53	43	.01
23	70	42	Tr.
24	60	45	Tr.
25	55	39	.06
26	52	32	.05
27	57	29	0
28	69	35	0
29	72	44	0
30	79	42	0
		Total =	4.41

APPENDIX A

TABLE V

DAILY TEMPERATURE AND PRECIPITATION

JUNE 1971

Day	Max. Temp. °F	Min. Temp. °F	Ppt. (inches)
1	75	35	0
2	81	45	0
3	89	54	0
4	82	59	.28
5	74	61	.86
6	65	55	Tr.
7	60	42	Tr.
8	69	40	0
9	74	51	.02
10	71	59	.22
11	84	56	.08
12	78	57	.05
13	78	51	0
14	82	53	0
15	81	62	Tr.
16	78	57	.10
17	79	61	Tr.
18	76	54	0
19	66	55	.52
20	70	50	0
21	76	51	0
22	80	54	.03
23	66	46	.01
24	68	47	0
25	76	52	0
26	70	62	.24
27	72	55	.13
28	74	50	0
29	76	57	.10
30	64	48	.35
			Total = 2.99

APPENDIX A

TABLE VI

DAILY TEMPERATURES AND PRECIPITATION

JULY 1971

Day	Max. Temp. °F	Min. Temp. °F	Ppt. (inches)
1	75	48	0
2	78	54	Tr.
3	79	56	.31
4	70	53	Tr.
5	75	52	0
6	74	46	Tr.
7	74	56	.96
8	71	51	0
9	71	49	Tr.
10	70	54	.32
11	75	52	Tr.
12	78	56	.14
13	78	52	0
14	74	56	Tr.
15	80	56	.22
16	68	46	0
17	74	40	.72
18	74	55	.09
19	71	52	.21
20	79	46	.11
21	73	48	0
22	73	50	.08
23	71	46	.08
24	87	60	.17
25	63	50	.40
26	68	48	Tr.
27	61	48	.26
28	59	45	.32
29	65	40	.02
30	75	45	0
31	67	53	.12
		Total =	4.53

APPENDIX A

TABLE VII

DAILY TEMPERATURES AND PRECIPITATION

AUGUST 1971

Day	Max. Temp. °F	Min. Temp. °F	Ppt. (inches)
1	65	43	Tr.
2	68	38	0
3	73	41	0
4	76	49	0
5	80	53	0
6	84	54	0
7	88	57	0
8	90	64	Tr.
9	79	60	0
10	71	55	0
11	75	50	0
12	73	53	0
13	66	50	.01
14	76	52	0
15	93	62	Tr.
16	75	63	.45
17	86	62	Tr.
18	78	55	0
19	73	56	.13
20	81	52	0
21	90	60	0
22	80	60	0
23	79	55	.07
24	66	52	.01
25	72	53	Tr.
26	82	53	0
27	88	55	0
28	92	53	0
29	76	52	Tr.
30	77	42	0
31	69	52	Tr.
		Total =	.67

APPENDIX A

TABLE VIII

DAILY TEMPERATURES AND PRECIPITATION

SEPTEMBER 1971

Day	Max. Temp. °F	Min. Temp. °F	Ppt. (inches)
1	74	60	.03
2	87	48	0
3	83	62	Tr.
4	68	61	Tr.
5	76	56	.75
6	66	53	.06
7	81	50	.01
8	75	45	0
9	78	46	0
10	74	40	0
11	76	38	0
12	75	54	Tr.
13	76	45	Tr.
14	65	43	Tr.
15	57	41	.06
16	58	36	.10
17	54	31	0
18	59	33	0
19	67	42	0
20	58	35	Tr.
21	49	28	.07
22	61	30	.01
23	61	29	0
24	72	37	0
25	68	49	Tr.
26	62	54	.14
27	66	49	0
28	63	39	0
29	65	35	Tr.
30	61	53	.73
		Total =	1.96