THE

NATURAL CONTROL OF THE FALL

WEBWORM [*Hyphantria cunea* Drury]

IN CANADA

TOGETHER WITH

AN ACCOUNT OF ITS SEVERAL PARASITES

By JOHN D. TOTHILL, D.Sc.

IN CHARGE OF NATURAL CONTROL INVESTIGATIONS
ENTOMOLOGICAL BRANCH

ENTOMOLOGICAL BRANCH

Dominion Entomologist.............Arthur Gibson

Chief, Division of Forest Insects.....................J. M. Swaine
Chief, Division of Foreign Pests Suppression..........L. S. McLaine
Chief, Division of Systematic Entomology............J. H. McDunnough
Chief, Division of Field Crop and Garden Insects......R. C. Treherne

LABORATORIES

Annapolis Royal, N.S. Headquarters for Insecticide Investigations; Arthur Kelsall, Entomologist in charge.

Fredericton, N.B. Headquarters for Natural Control Investigations; J. D. Tothill, Entomologist in charge.

Hemmingford, P.Q. Fruit Insect Investigations; C. E. Petch, Entomologist in charge.

Aylmer, P.Q. Forest and Shade Tree Insect Investigations; C. B. Hutchings, Assistant Entomologist in charge.

Vineland, Ont. Fruit Insect Investigations; W. A. Ross, Entomologist in charge.

Strathroy, Ont. Field Crop Insect Investigations; H. F. Hudson, Assistant Entomologist in charge.

Port Stanley, Ont. European Corn Borer Investigations; H. G. Crawford, Entomologist in charge.

Treesbank, Man. Field Crop Insect Investigations; Norman Criddle, Entomologist in charge.

Saskatoon, Sask. Field Crop Insect Investigations (Position vacant).

Lethbridge, Alta. Field Crop Insect Investigations; H. L. Seamans, Entomologist in charge.

Banff, Alta. Mosquito Investigations; Eric Hearle, Assistant Entomologist in charge.

Agassiz, B.C. Field Crop and Fruit Insect Investigations; R. Glendenning, Junior Entomologist in charge (Acting).

Vernon, B.C. Forest Insect Investigations; Ralph Hopping, Entomologist in charge.

   Fruit Insect Investigations; (Position vacant). E. P. Venables, Junior Entomologist in charge temporarily.

Victoria, B.C. Fruit Insect Investigations; W. Downes, Assistant Entomologist in charge.
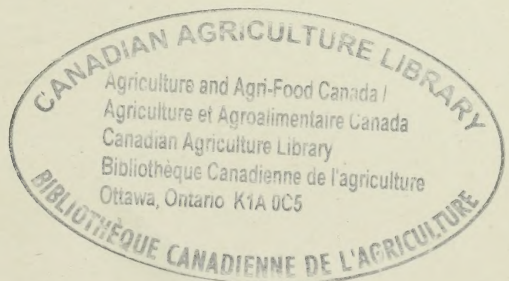
(ENTOMOLOGICAL BULLETIN No. 19)

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THE NATURAL CONTROL OF THE FALL WEBWORM

(*Hyphantria cunea* Drury)

With an account of its several parasites

By John D. Tothill, D.Sc. in charge of Natural Control Investigations, Entomological Branch

INTRODUCTION

Outbreaks of injurious insects are the cause of heavy financial losses to our agriculture and forestry and any practical means that can be devised for preventing or controlling them add stability to these two basic industries. Until recent years, little effort has been directed toward preventing outbreaks because so little has been known regarding their causes, yet it now seems probable that some of the more notorious outbreaks would have been preventable had their several causes been known in time. The recent gypsy moth (*Porthetria dispar*) outbreak in New England, the present spruce budworm (*Harmologa fumiferana*) outbreak in New Brunswick, and the outbreak of the larch sawfly (*Nematus erichsonii*) in New Brunswick of about forty years ago, are instances of this kind. The gypsy moth was free from parasites; the spruce budworm had an abnormally increased supply of the particular food that alone can nurse an outbreak, and also lacked an important parasite; and there is every reason to believe that the larch sawfly was free from important parasites.

As an outbreak is an abnormal occurrence resulting from a breaking down of the bonds or environmental pressures that normally prevent a numerical increase, it follows that it is necessary to study the environmental pressures in order to understand the causes. The present paper is an account of such a study made for the fall webworm (*Hyphantria cunea*) in Canada and shows that some of the outbreaks dealt with could probably have been greatly reduced in intensity, or even prevented, by the timely transfer of insect parasites from one part of the continent to another.

During the study, an effort has been made to examine as closely as possible the effect of the several natural barriers that govern the rapid distribution of the insect parasites met with, and to build, in so far as possible, a foundation upon which to base future practical projects for preventing outbreaks of injurious species or for reducing their severity.

There are a few men who have contributed largely toward an understanding of the particular phase of œcology called natural control. The first study of natural control seems to have been made by the English clergyman-economist, T. R. Malthus. His "Essay on the Principle of Population" is a remarkably clear and scholarly exposition of the thesis that the numerical abundance of human beings is dependent upon the food pressure. Writing in 1798, long before the time of Darwin and the development of the idea of the struggle for existence, he speaks of "the constant tendency in all animated life to increase beyond the nourishment prepared for it".

Charles Darwin clearly appreciated what he called (Origin of Species, p. 83) "the causes which check the natural tendency of each species to increase." Wallace in his various works (particularly in his "Island Life") lays the foundation of our knowledge of the ordered distribution of the productions of the earth, and explains to us the meaning of natural barriers.

Among the authors who have dealt more particularly with natural control as applied to insects, Dr. L. O. Howard has written fairly extensively upon this subject and has done more than any other man to extend its usefulness. In the gypsy moth laboratory at Melrose Highlands, Mass. a number of comprehensive papers have been written by W. F. Fiske, A. F. Burgess and C. W. Collins, and some shorter papers by W. R. Thompson, P. H. Timberlake and others. In California, H. S. Smith and colleagues have published an extensive series of valuable papers; and in Hawaii, the Sugar Planters' Association and the Government have undertaken natural control projects.

During the progress of this investigation I have received from many people assistance of various kinds, and this it is a pleasure to recall and to acknowledge. The late Dr. C. G. Hewitt, who filled the position of Dominion Entomologist with such signal success, made the investigation possible and there were many conferences during which I received much encouragement and inspiration. During his years in office his interest in the project never lagged and it was through him entirely that I was enabled to complete it. It would take too long to enumerate the innumerable ways in which my assistant, Mr. A. B. Baird, has helped along this problem and suffice it to say that he has done a large share of the actual work in New Brunswick, Nova Scotia and British Columbia. Special acknowledgments are made to him in the course of the paper. Attention should be called to his paper on the "History of the Fall Webworm in North America" (Ann. Rept. Ent. Soc. Ont., 1916), showing how the webworm tide has risen and fallen through the course of years; and showing that the modern outbreaks seem to be more severe than the older ones, owing to the increasing food supply due to the planting of apple and shade trees. Another assistant, Mr. Alan Dustan, has also contributed largely toward the preparation of this paper. He has prepared an account of three of the Hymenoptera associated with the webworm, namely; *Rogas, Hemiteles* and *Habrocytus*, which it is hoped, will be published in the near future. My various colleagues on the Branch, as well as Mr. A. W. A. Phair and Mr. Max H. Ruhmann, have helped me in many ways and particularly in making collections. I was fortunate in having the illustrations of the adult parasites prepared by Mr. A. E. Kellett, lately artist assistant of the Entomological Branch. Finally, I gratefully acknowledge indebtedness to my wife for her careful and critical revision of the text of this manuscript.

THE NATURAL CONTROL OF THE FALL WEBWORM

Scope and Methods of the Study

The study of the fall webworm was commenced in New Brunswick in 1912 and has been continued in the same province for eight successive years. From 1916 to 1918, inclusive, comparative studies were made in Nova Scotia; and from 1917 to 1919, inclusive, comparative studies were made in Southern British Columbia. It has been found convenient to relate the story for New Brunswick first and then to compare the conditions with those obtaining in Nova Scotia and British Columbia, respectively.

The province of New Brunswick is approximately a square, the sides of which are about two hundred miles in length. It was necessary at the outset to confine the study to certain representative places and nine of these were chosen, namely; Fredericton, Chipman, Salisbury, Newcastle, Campbellton, St. Leonards, Perth, St. Stephen, and Nerepis. These observation points have been adhered to during the course of the study. It has been found convenient to base the account for New Brunswick on the conditions that have obtained from year to year at Fredericton; and to close the account for this province by comparing the Fredericton conditions with those for the other places.

While the study at Fredericton has been in progress our methods have been gradually reduced to simpler terms. In 1912 there was a field trip once a week for the purpose of noting the general well-being of the webworm. On these occasions webs were examined minutely to see what was happening to the larvæ; many counts were made of caterpillars, molt skins, and hatched eggs, to find out the percentage of mortality, and as many field observations as possible were made to find out the causes of this mortality. Toward the close of the day it was our practice to gather up five typical colonies and put each into a separate box. On arrival at the laboratory, each colony was counted and put out in a 20″ by 20″ Fiske tray, where the larvæ were fed until they died or pupated. Each tray was picked over once a week and the numbers of parasites and caterpillars noted. As these field trips were made for six successive weeks, there were finally thirty trays of Fredericton caterpillars to look after, and about a hundred and twenty more from other New Brunswick points. From each tray, twenty-five typical caterpillars were picked out and dissected.

At first, difficulty was experienced in estimating parasite percentages. It was found, however, that for each parasite there was one collection that was evidently made after most of the oviposition had taken place and before any appreciable number of the parasites had emerged from the caterpillars to pupate. These "critical" collections, as they may be termed, served as a basis for securing percentage data. The percentages were established by averaging the dissection and rearing results from the five colonies collected at the proper time. If the result thus obtained did not tally with field observations, such as a series of counts of parasite cocoons in a number of webs, a further correction was made. The method has varied a little according to the particular parasite. For instance, it is very easy to determine the *Apanteles* percentage by field examinations because the cocoons are all made within the web and they can be readily seen and counted; so that for this parasite more weight has been given to results obtained from the field than to those from rearings and dissections. *Campoplex* parasitism can be readily determined either from dissections or rearings and is harder to determine from field observations; while the *Therion* percentage can be determined readily only from dissections.

In the following years, the collections for rearings and dissections were changed from weekly ones to critical ones, timed for getting accurate percentage data for particular parasites. This resulted in reducing the number of collections from six to three for larval parasites and from two to one for pupal parasites. With the late Mr. F. M. McKenzie as an assistant for making these collections, Mr. Baird was released for helping with dissections and field observations.

From 1913 on, we emphasized the re-examination of marked nests throughout the season. Five nests were selected at Fredericton and at the first visit the egg shells were counted and also the larvæ. Twenty-five of the larvæ were taken from the nest and dissected. At the time of the next collection, a count of the larvæ was again made and twenty-five more larvæ taken for dissections. This process was repeated for the third collection; and for the pupal collection, providing there were any larvæ left to pupate. In this way an accurate record was obtained for five particular nests. In 1914 there were so few webs near Fredericton that we obtained some from Nova Scotia and put them out in suitable places.

After the first year, rearing work was confined to material which would supply needed information on various life-histories or yield percentage data on the two species of *Campoplex*. Fairly extensive reproduction work was undertaken with *Hyphantria* and with several of its parasites. For the former work, Riley cages served very well, while for the latter special cages were needed in which the humidity could be easily regulated. For hymenopterous parasites, a small light tray, ten inches square and two inches deep, was used. The floor was of factory cotton and the cover of plate glass. Food was introduced either by lifting the cover or by removing a cork from a hole drilled in one of the sides. In one corner a cupful of sandy loam on a blotting paper wick connecting with a saucerful of water outside the cage effectively controlled the humidity. For tachinid flies, a wooden box about four inches square and eight inches deep was used. The floor of this was a non-corroding wire screen of fine mesh and the cover of glass. The box was filled two-thirds full of sandy loam and humidity was maintained by setting the box in a pan of water about once a month. Tachinid maggots were allowed to go to earth in this cage and when the flies emerged, they were fed, watered and supplied with material in which to deposit their young.

During 1912 and 1913 we had no satisfactory way of preserving larvæ and so had a tremendous amount of dissecting work during the season of field observation. In 1914 we developed a satisfactory method for preserving our material for examination and dissection during the winter. The larvæ were dropped into water at 80° C. and left for a minute so as to cleanse them and to coagulate the albumens. They were then drained and thrown into a liberal bath of 5 per cent chloral hydrate and set aside until the stress of the field work was over.[1]

In 1919 when the laboratory acquired a first-class microtome, parasite larvæ that had been accumulating for years were re-examined and good material all preserved by the chloral hydrate process referred to above, was embedded and sectioned. Mr. Dustan has done all the sectioning work and it is greatly to his credit that we have been able to examine splendid serial sections of almost every stage of every parasite that we have found attacking the webworm.

There is one other method that has proven indispensable for recording the changing abundance of the webworm at Fredericton from year to year. The first ten miles of each of the eight principal roads radiating out from Fredericton were traversed and every nest that could be seen from the road was counted. In 1912 the webs seen from the eighty miles of roadways totalled exactly 100. In 1913 the total was 20; next year it dropped to 3, next to

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[1] This method of preservation has now been tried out repeatedly for a number of years and has proven so satisfactory that an account of it has been published in the Annual Report of the Ent. Soc. of Nova Scotia for 1919.

2, and in 1916 only 1 web was seen. Next year the total increased to 5, the next to 24, and in 1919 the total rose to 41. This information has been plotted out and can be visualised by a glance at the accompanying chart (fig. 1).
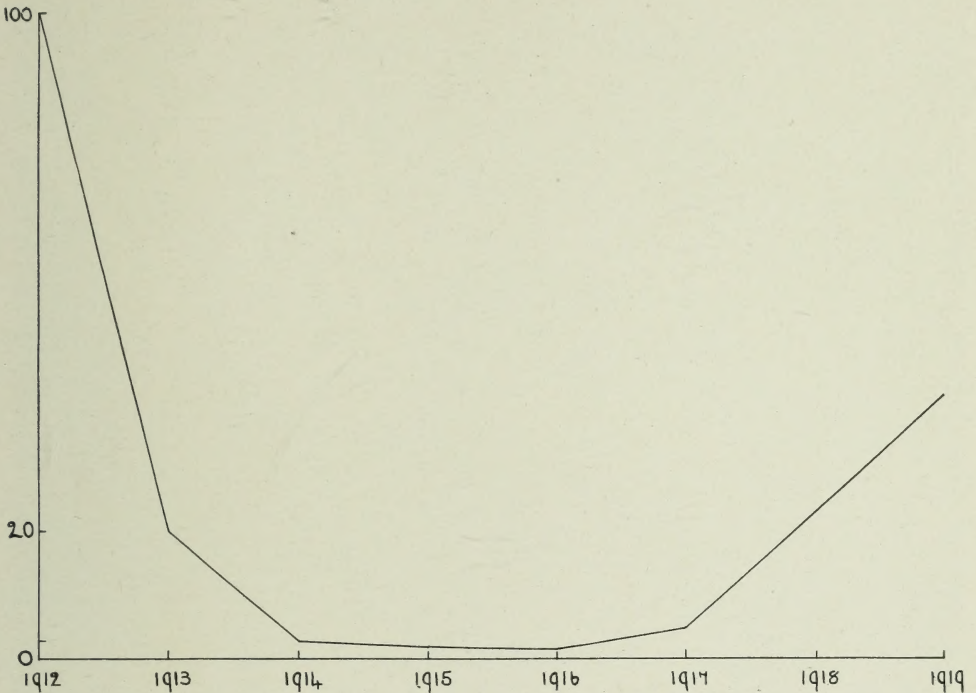

FIG. 1.   This curve shows the number of *Hyphantria* webs seen each year from 1912 to 1919 inclusive, along eighty miles of roadsides within a ten-mile radius of Fredericton.   In 1912 there were one hundred webs; in 1913 there were only twenty; and so on.

Without anticipating our story too much, it can be said that the changing numerical abundance has involved far reaching changes in the environmental pressures—or factors of control—and we shall have frequent occasion to refer back to this chart.

Such are the general methods that have been used for the Fredericton study. They have also formed the basis for the comparative studies made concurrently at eight other observation points in New Brunswick; and made in recent years at five similar points in Nova Scotia, and at five places in British Columbia. The volume of the work done can be measured in a sense by the numbers of caterpillars and pupae dissected, there being 500 such dissections from each point per annum. From 1912 until 1915 there were nine points and so 4,500 dissections; in 1916, with the five Nova Scotia points, there were 7,000 dissections; and in 1917, with some British Columbia points added, the dissections reached almost 10,000. On the whole, the work done at Fredericton has been along somewhat more intensive lines than at any of the other observation points, which is, perhaps, a natural result of our now having a splendidly equipped laboratory at this place.

Fig. 2. A full-sized web of the fall webworm collected at Ottawa by A. E. Kellett.

Natural Control of the Webworm at Fredericton in 1912

The story of control at Fredericton for 1912 will form a basis for comparing conditions at different times and places, and may be set forth very briefly as follows:—

260	eggs	less 26	or	10%	infertile		leaving
234	larvæ	less 42	,,	18%	taken by	*Apanteles*	,,
192	,,	,, 6	,,	3%	,,	,, *Meteorus*	,,
186	,,	,, 22	,,	12%	,,	,, *C. pilosulus*	,,
164	,,	,, 85	,,	52%	,,	,, *C. validus*	,,
79	,,	,, 2	,,	3%	,,	,, *C. concinnata*	,,
77	,,	,, 45	,,	59%	,,	,, *Ernesta*	,,
32	,,	,, 30·4	,,	95%	,,	,, *Birds*	,,
1·6	,,	,, ·1	,,	6%	,,	,, *Therion*	,,

1·59 moths

Of the 260 eggs in the average webworm egg mass, 26 failed to hatch owing, apparently, to their being infertile. Such eggs failed to develop a blastoderm and were not parasitized.

Fig. 3. A typical web of *Hyphantria* at Fredericton, N.B., on alder.
(Photo by Alan G. Dustan.)

When the larvæ yielded by the fertile eggs were in their first and second instars they were attacked by *Apanteles hyphantriæ*. This parasite victimized an average of 42 larvæ from each of the webs under observation. Of the 192 remaining, 6 were then attacked by *Meteorus hyphantriæ*. The remaining larvæ were then parasitized by *Campoplex pilosulus* to the average extent of 22 from each colony. Of the 164 larvæ escaping attack, 85 were parasitized by the closely related *Campoplex validus*. This reduced the larvæ in each web to 79, these now being in the fifth instar. The recently imported tachinid, *Compsilura concinnata*, victimized two of these. This attack was followed

closely by that of the native tachinid, *Ernestia ampelus*, resulting in a further reduction of 45 larvæ from the average colony. Of the remaining 32 larvæ, the chart indicates that birds carried off about 95 per cent of the remainder, thus reducing the average web content to 1·6. As a matter of fact, the 30·4 larvæ devoured by birds were not all taken after the *Ernestia* attack but were taken, for the most part, when the larvæ were in the fourth and fifth instars. To avoid repetitions, it is simpler, however, to itemize the birds only once and at the end of the chart. The birds proved to be red-eyed vireos, *Vireosylva olivacea* (Linn.) the pendant nests of which are very common in alder thickets.

Of the few larvæ left to pupate, 6 per cent were then destroyed by the large hymenopteron, *Therion morio*. An average of 1·59 were left to issue as moths from each egg mass. This estimate of 1·59, arrived at by totalling the results of each of the several factors of control, was found to err somewhat on the side of conservatism, as in 1913 there was a decrease of webs in the proportion of 10 to 2 (c.f. chart p. 7).

Ordinarily, there is very little conflict between the several parasites because each confines its attack to a particular stage of the host (c.f. discussion on page 104). There is sometimes a mild conflict between *Campoplex validus* and *Ernestia ampelus*, as they both attack medium-sized larvæ. This year, however, the conflict was very much more acute than usual on account of a period of cool, wet weather in which the hymenopterous fly could proceed with oviposition and in which the tachina fly was unable to deposit her maggots. The amount of wet weather indicated by the official meteorological report is 5·72 inches of rain for the month, as against the average 3·95 inches. This wet, cool weather naturally gave *Campoplex* a considerable advantage in the conflict with *Ernestia* because the latter had to postpone the attack until the former had completed oviposition. The result of the wet weather was that when finally we did get some warm days the larviposition of *Ernestia* was accomplished so rapidly that the leaves near *Hyphantria* webs were, in many cases, darkened in colour by the great numbers of tiny black larvæ. Most of these larvæ perished, however, either because the caterpillars they became attached to already contained a second or third stage *Campoplex* larva (this parasite was exceedingly plentiful this year) or because of supernumerary parasitism, caused by each caterpillar collecting up to a dozen of the tiny maggots.

Natural Control of the Webworm at Fredericton, from 1913 to 1918, Inclusive

In 1913 conditions were totally different from those of the previous year because the webworm, instead of being a common object along roadways, in orchards and backyards, had become a comparatively rare insect. Only 20 webs could be found in territory that had supported a hundred in 1912, so that a fivefold decrease had resulted from the combined assaults of the parasites and birds described in the preceding pages. The full significance of this decrease was not apparent in the early stages of the 1913 season, but as the work gradually progressed it became apparent that the decrease had affected all the parasites very profoundly and that it had greatly strengthened the sum total of environmental pressures operating against the webworm. The season was punctuated by a rapid procession of unexpected happenings that made it one of unusual interest.

As in the previous year, a small number of the eggs failed to hatch, seemingly as a result of infertility. About 10 per cent were accounted for in this way and thus the average egg mass was reduced to about 234.

Samples of the small caterpillars were dissected, as before, for *Apanteles* and as there had been an 18 per cent parasitism in the previous year, I anticipated a somewhat increased parasitism owing to the decreased food supply. As the dissections proceeded, however, this "reasonable expectation" proved to be unjustified. At first I was inclined to doubt the accuracy of the dissection

A. METEORUS HYPHANTRIAE, Adult female.

B. APANTELES HYPHANTRIAE, Adult female

method and waited for confirmation from the nests in the field. In time, however, the confirmation came, as none of the Fredericton webs under observation yielded a single *Apanteles* cocoon. In a single year a species of parasite had been practically eliminated as a factor in the control of the webworm.

The reason for this seemingly remarkable extermination was not at the time at all obvious. In later years, however, as evidence accumulated, it became clear that *Apanteles* had disappeared because its host had become reduced in numerical strength to such an extent that the species could no longer attack it effectively. In 1912 the webworm nests had been scattered along the roadways, often only a few hundred yards apart or less, and under these conditions the little flies had been able to find the caterpillars. This year, however, the nests were often miles apart and under these conditions the female flies are evidently unable to locate them. Like many other parasites of insects, the *Apanteles* flies are handicapped by being anchored to the immediate neighbourhood of an old pasture of the host. If the host is fairly abundant, this matters little because an old pasture will be reasonably close to a new one. When the host becomes scarce; however, the old pasture and the new may be miles apart. If the parasite be poorly equipped for flying, it is at a serious disadvantage when attacking an insect as well equipped for flying as the fall webworm.

The parasite *Meteorus* suffered a disaster similar to that of *Apanteles* and for the same reasons. The flies had emerged from their cocoons beside a 1912 *Hyphantria* web, only to find that the moths had flown and blown away to start new colonies too remote to find. It is possible, also, that this parasite is further detached from the webworm by passing an early summer generation in another host. Like *Apanteles*, this parasite is of small stature and its equipment for flying does not compare at all favourably with that possessed by the female *Hyphantria* moth.

Unlike *Apanteles* and *Meteorus*, the red-bodied *Campoplex pilosulus*, being larger of stature and stronger of flight, came to the attack in about the same numerical strength as in 1912. It parasitized 24 larvæ in each nest.

In the case of the black-bodied *Campoplex validus*, the powers of flight were demonstrated to be adequate to the needs of discovering *Hyphantria* colonies when these were far from common. The increased difficulties of finding hosts were reflected, however, in the number of victims per nest being reduced from 85 to 63.

Then came the attack of the two-winged tachina fly, *Ernestia*. As a result of the wet weather of 1912 and of the consequent struggle between this species and *Campoplex*, this parasite was almost eliminated as an important factor in the control of the webworm. In 1912 the alder leaves had been darkened in colour in some cases by the immense numbers of maggots of this fly. In 1913, however, the flies were so scarce that only about six caterpillars were parasitized by them in each nest.

As in the previous year, the attack by birds was commenced when the caterpillars reached the fourth stage and reached its height with the caterpillars in the fifth stage. Even in 1912 the vireos demolished a large number of caterpillars. In 1913, however, with the reduced number of webworm nests and approximately the same number of vireos, the destruction became greatly increased. So active were the birds that by September 4 only one larva was left in the Fredericton webs under observation, and on the next day no larvæ remained in any of the five webs under observation at St. Stephen. It was obvious, therefore, that the reduced food supply had served to increase very greatly the effectiveness of the vireos. This can be understood when it is recalled that this little bird is many times the size of a webworm moth and that it has powers of flight many times superior to those possessed by the moth.

This wholesale destruction by birds not only served to reduce the web-worms to about one-seventh of their strength, but it also brought about an even greater decrease among the parasites. The birds were so short of rations that they fed upon nearly all the larvæ parasitized by the red-bodied *Campoplex* and by the two-winged fly, *Ernestia*, and in a single season reduced these species to a condition of impotency. They also fed upon most of the larvæ victimized by the black-bodied *Campoplex* and left so few caterpillars to pupate that the pupal parasite *Therion* ceased to have any importance as a factor in control.

The net result of the season was that the already scarce webworms had been reduced in numbers to a condition of extreme rarity. From one cause or another—but depending ultimately upon the weakened numerical strength of the webworms—the parasites had practically disappeared and the vireos were left in possession with a greatly increased power of attack. The conditions obtaining in 1913 may be summarized as follows:—

SUMMARY OF EVENTS AT FREDERICTON IN 1913*

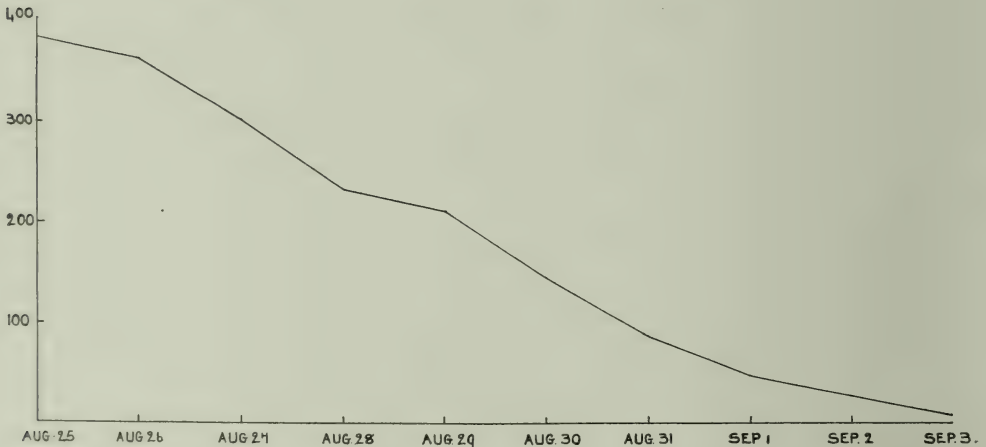|							
260 eggs...less	26	or	10%	infertile..................leaving
234 larvæ	" 0	"	0	taken by	*Apanteles*	"
234 "	" 0	"	0	"	*Meteorus*	"
234 "	" 24	"	10·5%	"	*Campoplex pilosulus*	"
210 "	" 63	"	30%	"	*Campoplex validus*	"
147 "	" 6	"	4%	"	*Ernestia*	"
141 "	" 139·5	"	99%	"	Birds	"
1·5 pupæ	" 0	"	0	"	*Therion*	"
1·5 moths						

FIG. 4. Chart illustrating the importance of birds in the natural control of the fall web-worm. On August 25, 1914, three hundred and eighty-two caterpillars were placed on a tree. The next day only three hundred and sixty-one were left; on the next, only three hundred and two; and by September 3rd, all had been taken except six that had been parasitized by *Campoplex.*

Early in the 1914 season at Fredericton it became apparent that the fall webworm had become so reduced in numbers as to be incapable of withstanding the environmental pressures that were combining to destroy it. It was so thinly distributed that any single colony fell an immediate prey to the hungry and enterprising vireos. The webs were so thinly distributed this year that only three were found in the eighty miles of roadways examined for them,

*NOTE.—The vireos destroyed nearly all the parasitized caterpillars this year because food was so scarce. The parasite percentages represent the numbers of larvæ attacked rather than the numbers actually killed. They indicate the relative abundance of the parasites.

and a few webs had to be imported from Nova Scotia and "planted out" in order to have a few available for the purpose of registering environmental pressures.

Apanteles failed to put in an appearance, as did all the other parasites except *Campoplex validus*. The small numbers of the host and the activity of the vireos were combining to exterminate all the parasites dependent for one generation upon the webworm. There was a 20 per cent parasitism by the black-bodied *Campoplex*, but even this aggressive and efficient parasite was obviously losing ground rapidly in its struggle for existence. The vireos were as energetic as they had been in 1913 and destroyed more than 98 per cent of the caterpillars. The accompanying chart (fig. 4) illustrates the important part now played by these interesting creatures.

In 1915 much the same conditions obtained, except that the examination of eighty miles of roadsides yielded two webs instead of three. As in the previous year, parasite percentages had to be obtained by importing a few webs from Nova Scotia. *Campoplex validus* was the only parasite recovered and its continued numerical decline was reflected in a further reduction of victims from 20 per cent to 10 per cent.

These conditions obtained for still another year when a climax was reached. In 1916 a most diligent search of the eighty miles of highways resulted in finding only one web and the colony was totally destroyed by birds. Parasite percentages were once again sought from imported nests planted out very early in the season and *not a single parasite was recovered*. In five short years *Hyphantria* had been reduced by a changing series of environmental pressures from a condition of mild outbreak to a condition of such great rarity that it could no longer hold its own in the struggle for existence and was in danger of local extinction. The parasites had already gone and it was obvious that unless succor were to be rendered to the webworm, it would actually become extinct locally within one or two years.*

It so happened, however, that succor was to arrive. It came in 1917 when a flight of moths from Nova Scotia distributed the species once more over a considerable area of the province of New Brunswick, including the city and district of Fredericton. Five webs were found this year in the eighty miles of roadsides examined.

One of the surprises of the year was the finding of *Apanteles*, *Meteorus* and the red-bodied *Campoplex*, none of which had been recovered since 1912. The percentages of parasitism were small but the presence of the parasites seemed to indicate that all of them had been maintaining themselves in small numbers upon hosts other than the fall webworm. Equally interesting was the absence of the two major parasites of this host, namely, the black-bodied *Campoplex* and the maggot-laying *Ernestia*. Apparently, neither of these species was able to maintain itself in New Brunswick upon hosts other than *Hyphantria*.

Another curious development of the year was an 8 per cent parasitism by an undetermined species of *Rogas*. After so many years' acquaintance with the parasites of the webworm, a new parasite seemed almost incredible. The point of chief interest in connection with this parasite is, perhaps, that it is not ordinarily a parasite of the webworm but that it will come to the attack if given an opportunity. It seems probable that *Rogas* females (plate III) are not

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*An additional reason for interest in the situation was the light it shed upon the preservation of game animals. It emphasized so strongly the damage to a species accruing from a diminished numerical strength. The last passenger pigeon and the last great auk were certainly not killed at the hand of man, but man had evidently reduced these species in numerical strength until the combination of environmental pressures became too strong for them and they disappeared in a few years, even as the webworm had done at Fredericton. The woodland caribou and the moose have now declined in numbers in New Brunswick and other places where they still exist, until the danger point has been reached and unless substantial reservations are made or other methods devised for decreasing the pressures against these animals, it seems inevitable that they must vanish from our playgrounds even as the passenger pigeon has done.

ordinarily in the field when webworm larvæ are in their fourth stage and that in 1917 something happened to bring them out at the critical time. This sychronising of the life cycles of parasite and host is, of course, one of the things that determines particular associations of parasites and hosts. In the case of *Rogas* sp., the parasite is adapted for attacking the webworm in the form of its ovipositor, in the immunity against phagocytes, and in every detail except that the females are not about at the right time for attacking the vulnerable stages of this host.

In 1918 there was a marked increase in the abundance of webworms—an increase of from 5 to 24 webs in the eighty miles of roadsides examined. This abundance was due wholly to an influx of moths from the developing outbreak along the Bay of Fundy shore, because in 1917 the vireos and other factors brought about a reduction in the Fredericton area.

It was clear that the webworm was gaining strength rapidly and that its numerical strength would soon be such as to enable it to defy the vireo attacks. It was also clear that it would have much greater freedom of action than it had in 1912 and preceding years because it was now comparatively free from its chief insect foes, the black-bodied *Campoplex* and the maggot-laying *Ernestia*. These two insects were watched for, therefore, with unusual diligence. In the case of the two-winged fly, our diligence was rewarded by finding a 2 per cent parasitism. This parasite had just managed to maintain itself during the starvation period and was now increasing in numbers. The host had an overwhelming numerical lead, however, and obviously it would be several years before a 60 per cent parasitism could be attained again. The black-bodied *Campoplex* failed to put in an appearance at all and it seemed that it had been unable to tide itself through the difficult period of caterpillar scarcity. As it failed to show up from any of the New Brunswick collecting points—at some of which the webworms were now very abundant—the likelihood of its having become locally extinct throughout the province was increased. Its extinction seemed to be proven by a repetition of these conditions in the following year. The question naturally arose as to how this useful parasite would return to New Brunswick. It was known to occur in Nova Scotia but only a chance wind at the right time could blow a few individuals across the forty miles or so of ocean separating most of Nova Scotia from New Brunswick. If it were to come from that province, the expectation would be that it would do so gradually by way of the Tantramar land bridge—a journey, for the most part, in a direction almost opposite to the prevailing winds. It was also known to occur near Montreal. Whether it was to come from the east or from the west, however, it would necessarily be some years before it could once again establish itself over the entire province of New Brunswick so as to effect an average parasitism of 50 per cent of all the caterpillars in the webs at the time of the attack.

The curious little parasite *Rogas* turned up once again but in greatly reduced numbers. This numerical decline seemed to establish its accidental relationship with *Hyphantria* and served in this way to lend a little colour to the previous years' findings.

This concludes the story of control at Fredericton from 1912 to 1918, inclusive. In the first of these years there was the culmination of what I take to have been a period of great stability that had lasted for perhaps a decade. Parasites had been gaining ground slowly, until finally in 1912 they exacted, together with birds, such a toll as to reduce the host in a single year to a condition of numerical insecurity. Then followed a period of instability during which the webworm could no longer maintain its struggle for existence. During this period the parasites became exposed to conditions they were unable to meet and one by one they dropped out of the contest. The end of this period came in 1916 when all the parasites were reduced to impotency and when the host
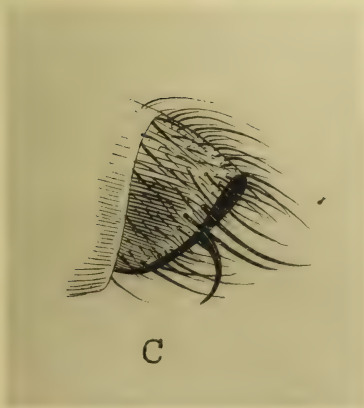
A. ROGAS SPECIES, Adult female; B. CAMPOPLEX PILOSUL - US, side view of abdomen and ovipositor; C. LYDELLA HYPHAN- TRIAE. end of female abdomen showing piercing device;

D. LYDELLA HYPHANTRIAE, end view of female abdomen.

had almost reached extinction.   Then came a flight of moths, mostly from Nova Scotia, that saved the species from local extinction and put it in a position once more to battle effectively against its several foes.   This increase of moths was coupled with a decrease of parasites, and the webworms started to increase very rapidly until in 1919 there was a mild outbreak of them.

Summary of Webworm Control at Fredericton from 1912 to 1918, Inclusive

	In 1912 host abund- ant	In 1913 host un- common	In 1914 host rare	In 1915 host very rare	In 1916 host almost extinct	In 1917 host rare	In 1918 host un- common
Infertile...........................	26	26	26	26	26	26	26
Parasitized by *Apanteles*...........	42	0	0	0	0	7	0
" *Meteorus*.............	6	0	0	0	0	2	0
" *C. pilosulus*.........	22	24	0	0	0	12	28
" *C. validus*...........	85	64	6	3	0	0	0
" *C. concinnata*........	2	0	0	0	0	0	0
" *Ernestia*.............	45	6	0	0	0	0	2
" *Rogas*...............	0	0	0	0	0	19	4
Eaten by vireos....................	30	139	227	230	233	193	190
Parasitized by *Therion*.............	1	0	0	0	0	0	0
Moths from colony.................	1	1	1	1	1	1	10
	260	260	260	260	260	260	260

The above table is based on the fact than an average egg mass contains 260 eggs.   In 1912, 26 eggs proved infertile, 42 of the larvæ were parasitized by *Apanteles*, 6 by *Meteorus*, etc., until finally the 260 were reduced to only 1 and there was a consequent numerical reduction of the host.   Notice the decrease of parasites as the host became scarce and conversely the remarkably increased activity of the vireos

Natural Control of the Webworm in New Brunswick as a whole from 1912 to 1918, Inclusive

Previous to our studies, the natural control of certain insects had been studied intensively at certain places for a number of years; for instance, the white-marked tussock moth at Washington, D.C., by Dr. L. O. Howard, and the apple-tree tent caterpillar at Durham, N.H., by W. F. Fiske.   There were, however, no data on how uniform the natural control of an insect might be over an area of any considerable size.   The opportunity was embraced, therefore, to extend the webworm study so as to make it fairly representative for the 12,000 miles or so of infested territory in New Brunswick.   Before referring to the conditions that obtained throughout the area infested, a brief comment may be made as to the more salient features of this terrain.

The whole area is made up of gently rolling, well watered, lowland country for the most part.   The shallow valleys, for the greater part, occupy continental troughs parallel with the Bay of Fundy.   The range of low hills along the Bay of Fundy has been cut through at St. John by the St. John river.   Alder bushes are distributed all through the area along the numerous streams and myriad brooks.   As the important ridges are in line with the prevailing southwesterly winds, there is no physical barrier to prevent webworm moths from spreading rapidly over the area once they have a footing in the southwestern portion. With such topographical conditions, one might expect a fair degree of uniformity in natural control conditions.   From the life zone point of view, also, one might expect the same thing.   Most of the area is strictly boreal, a large part being forest lands.   There is a small transitional element that creeps into sheltered locations along the Atlantic shore.

With this necessarily fragmentary glimpse of the area as a whole before us, we may proceed to our account of how the webworm conditions throughout this territory compared with those already related for the Fredericton observation point. The nine observation points selected (see map, fig. 5) were as

MAP OF NEW BRUNSWICK
showing
the nine observation points at
which the webworm studies were made

Legend

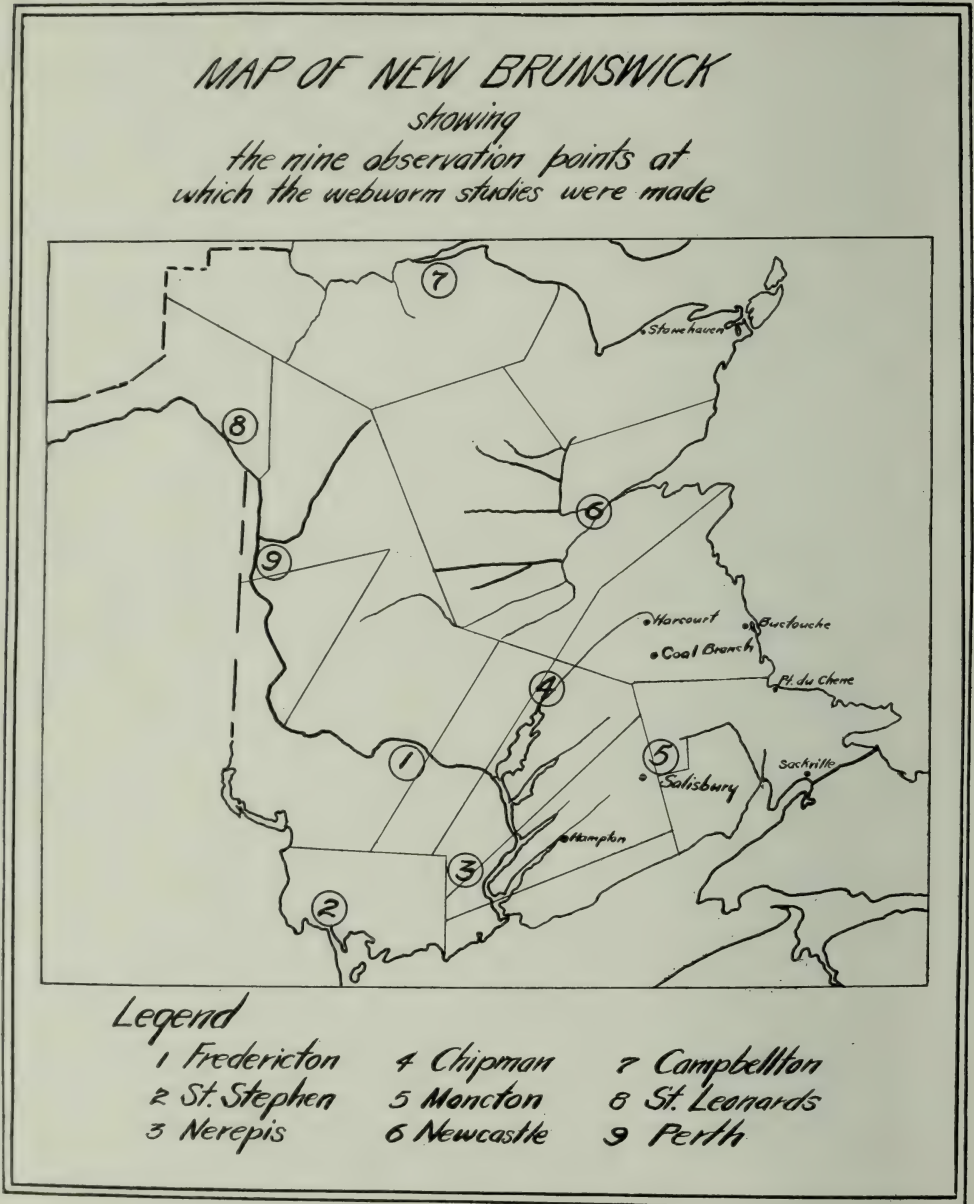| 1 Fredericton | 4 Chipman | 7 Campbellton |
| 2 St. Stephen | 5 Moncton | 8 St. Leonards |
| 3 Nerepis | 6 Newcastle | 9 Perth |

Fig. 5

well distributed over the province as travelling facilities would permit. In 1912 the fall webworm was abundant throughout the lower half of the province, including Fredericton, St. Stephen, Nerepis and Moncton. At these observation points the conditions were almost identical with those of Fredericton. There was a very heavy parasitism by a number of important parasites and there was, too, a moderate predatism by birds.

Although these points were nearly a hundred miles apart, it was remarkable how uniformly the parasites were distributed. *Apanteles* was present at all four points, although it accounted for only a small percentage of caterpillars at each place—it was thinly but evenly distributed. The little *Meteorus* was even less abundant than *Apanteles* but was present at all places except Moncton. *Campoplex pilosulus* was found at each point and in very uniform numbers. The black-bodied *Campoplex* was the most effective parasite at St. Stephen, Fredericton and Moncton, but was not found at Nerepis. The introduced *Compsilura* was only found, of course, at Fredericton where it had been liberated the year before. The maggot-laying *Ernestia* was also found at all four points in fairly uniform numbers. The curious parasite *Therion* was found in small numbers at every point but Moncton and in view of the heavy competitive parasitism by other species, it was something of a surprise to recover it at three places out of these four.

The parasite sequence and the percentages in the first years were closely comparable also to those which had been found at Melrose and Wakefield, Mass. in 1909 and 1910. From these circumstances it seems probable that such conditions were fairly uniform for the Atlantic seaboard country stretching from Moncton to Boston, during the years 1910, 1911 and 1912.

In 1913 the rapid numerical decline of the webworm noted at Fredericton obtained also at the other observation points where the insect had been found the previous year. In fact, the insects were sufficiently abundant for study only at Fredericton and St. Stephen and were not found at any of the remaining seven points. There is little doubt that had the same amount of time been spent at each point looking for webs as was spent at Fredericton, there would have been a few webs found at some of the places. A day was spent at each place on the occasion of each of the three visits.

Apanteles and *Meteorus* were found in small numbers at St. Stephen only; the red-bodied and the black-bodied *Campoplex* were found in reduced numbers at both places; the same was true for *Ernestia;* and *Therion* was not recovered at all. Wherever webs were found, they were invariably torn open by birds and most of the caterpillars, including parasitized ones, had been devoured.

In 1914 no webs were found at any place but Fredericton and at that place it will be recalled that only three webs were found in an examination of eighty miles of roadsides. In addition to the point examinations, there was corroboration of the great scarcity of webworms over the province from other sources. The provincial inspectors, including Mr. R. P. Gorham, failed to find any webs in the lower St. John valley and at Sussex when working on the army worm outbreaks at those places. Also, the late Fred McKenzie and the writer failed to find a single web during a three-week canoeing and packing trip in the north central part of the province. The webworms had disappeared everywhere, as at Fredericton, and presumably for the same reasons.

Similar conditions prevailed again in 1915 with the insect even more scarce and apparently everywhere fighting a losing battle with its arch enemy, the red-eyed vireo.

In 1916 a marked change occurred in the *Hyphantria* situation in New Brunswick in that the insect suddenly became quite abundant in the counties near, or bordering, the bay shore east of the St. John river. At Hampton, Salisbury and Moncton, webs were quite abundant; at a place between Hampton and Bloomfield, nine webs were seen within a distance of 300 yards. Webs could be seen from the train windows all the way from Hampton to Moncton and then north to Coal Branch. The peculiar bay shore distribution of the new outbreak, coupled with the fact that the insect had been conspicuous for two years in the Annapolis valley of Nova Scotia, makes it probable that a flight of moths came across the Bay of Fundy in July. As if with the stroke

of a brush, a strip of country nearly one hundred miles long had been painted thickly and suddenly with webworms. All danger of local extermination had been removed and the webworms were possessed of an unchallenged area from which to spread out once again over the province. At the other collecting points in the province not a single web could be found, except at Fredericton, where a week's search along eighty miles of roadsides yielded only a single nest. No nests whatever were found at St. Stephen, St. Leonards, Perth, Nerepis, Chipman, Newcastle or Campbellton.

The control in the sharply contrasted areas represented by Fredericton and Moncton, respectively, was found to be quite different. Vireos destroyed nearly all the caterpillars at Fredericton, but at Moncton, Salisbury and Hampton there were more caterpillars than these birds could possibly eat and the vireos made but little impression upon them. No parasites whatever were found at Fredericton, while a very few of the red-bodied *Campoplex* were found at Moncton.

This comparative absence of parasites in the newly infested area is of more than passing interest, as a principle is involved that evidently operates in the case of many insect outbreaks. The parasites, and particularly the major ones, that through the course of time have come to be highly dependent upon the webworm for an existence had been starved out of an area as large as New Brunswick. A flight of moths came from Nova Scotia and the major parasites were left behind. This can be understood when it is recalled that none of the parasites are on the wing when the moths are in flight and none of them have anything like the same ability to fly long distances.*

The fertilized female parasite seems to be chiefly concerned with reaching the nearest host in the least possible time.

Even the parasites that do manage to fly considerable distances are on the wing either before or after the moth flight and this gives them a very slight chance of following the moths to a new pasture. The moths entering New Brunswick almost certainly came across the Bay of Fundy, a distance of about fifty miles. Probably a south wind, which is rare, however, because the prevailing winds are usually up the bay, helped them across. For a similar wind to be blowing at the time of, say, the *Ernestia* flight, would be distinctly unlikely.

In 1917 the area of conspicuous webworm infestation was greatly extended. There seems to have been a flight of moths up the St. John river because an increase of webs occurred at Fredericton and a considerable number of webs were found scattered even through Carleton and Victoria counties at the upper end of the valley. The area of infestation also extended considerably in a north and northeasterly direction reaching to Point du Chene, Buctouche and Harcourt. Only one web was found at St. Stephen and none were found at Nerepis, Chipman, Campbellton and Newcastle.

In the areas of scarcity the red-eyed vireo was still the all-important factor in control, but in the areas of abundant webs the birds proved themselves to be quite incapable of devouring any considerable portion of the larvæ of each web.

Let us suppose that there are ten vireos (two families) in each square mile. In the areas and years of webworm scarcity there might be two or one or even fewer webs in a square mile and these would fall an easy prey to the ten energetic birds living in the area. There would be about 468 caterpillars to be rationed among ten birds, or approximately 50 for each during two weeks. Such a case could result in little less than complete destruction of the host. In the areas and years of abundant webworms there might be 25 or more webs for the same ten birds to share, or 580 odd caterpillars for each bird. As this would be about

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*Clouds of brown-tail moths have been seen hundreds of miles at sea, and there is evidence from many sources that moths of many kinds are carried long distances by the wind. The parasites, on the other hand, are not particularly well adapted for such a method of transportation.

42 caterpillars per bird per diem for two weeks, if they consumed them all, it is highly improbable that all would be consumed. With 50 webs per mile the daily offering per bird would be 80 caterpillars, and so on.

The parasite situation was watched with unusual interest to find out how quickly the various parasites would return to a condition of economic importance. *Apanteles* was recovered in small numbers from Fredericton and St. Leonards; *Meteorus* cocoons were recovered, but the species was too scarce to show up in dissections. *Apanteles* and *Meteorus* are undoubtedly polyvores and had been maintaining themselves on hosts other than *Hyphantria* through the lean webworm years. The red-bodied *Campoplex* was recovered from St. Leonards, Perth, Fredericton, Norton and Moncton in such numbers as to indicate that it had increased considerably during the year. This increase over a wide area seems to indicate that the species is polytrophic in New Brunswick and that it had maintained itself through the lean *Hyphantria* years upon hosts other than the webworm.

One of the most curious parasite features of the year was the parasitism by *Rogas*, already referred to in the account of the 1917 conditions at Fredericton. Although an accidental parasite of this host, it was found in measureable numbers this year, not only at Fredericton but at St. Leonards, Perth, and Moncton— generally distributed, in fact, over the webworm area of the province. The same accidental conditions that enabled it to come to the attack at Fredericton were evidently general for the province. It is, of course, a polyvore.

The maggot-laying *Ernestia* was recovered in exceedingly small numbers at Moncton, thus indicating that it had succeeded in weathering the storm and that it would probably increase in numbers rapidly now that an increased food supply was available. In New Brunswick this species is evidently monotrophic, depending for an existence upon the webworm.

The black-bodied *Campoplex* seems also to be monotrophic in New Brunswick, depending for an existence upon *Hyphantria*. No specimens of this species were recovered in 1917, indicating that it had been snuffed out during the period of reduced food supply. Its absence during 1918 confirms us in this opinion.

A single *Therion* larva was found at Moncton so that this species was at least present in the field. It is probably a polyvore in New Brunswick, as it is in other places and not solely dependent upon webworms.

The 1918 season was marked by a considerable extension of the infested area. On the north shore, webs were plentiful along the railroad from Moncton to ten miles beyond Harcourt and a few webs were found at Stonehaven, in Gloucester county. Up the St. John valley, Fredericton and Woodstock seem to have been visited by a further flight of moths from St. John county, as there was a marked increase of webs. Above Woodstock there were fewer webs than during 1917, indicating that the species was not abundant enough to withstand the attacks of vireos. A few webs were found this year at Chipman, None were found at St. Stephen, Campbellton, Newcastle and Nerepis.

In the areas of heavy infestation the insect was not held nearly down to par because there was too much food for the birds to cope with and the parasites were too few in numbers and species to be at all effective. These areas, where the webworms were increasing rapidly, served as foci from which moth flights were carried by winds in various directions. In the very lightly infested areas, such as at Perth and St. Leonards, the insect was still being reduced in strength through the agency of birds. At St. Leonards, for instance, four webs were found at the opening of the season and the first collection of 25 from each web was made with no difficulty. Ten days later it was not so easy to make the collection because nearly all the larvae had been taken from three out of the

four webs—one contained 3, one 26, and the third about 130. At the third visit made about ten days before pupation time, not a single larva remained in any of the webs.

The parasite situation in 1918 was much like that of the previous year, with one of the major parasites, *Campoplex validus*, absent at all the points; with another major parasite, *Ernestia*, gaining ground slightly; and with the remaining species widely distributed but still exceedingly scarce. *Apanteles* was so scarce that it was not turned up at all and there may have been a host shortage for its summer generation. Only a single *Therion* had been found in 1917 and none at all this year. *Rogas* was again distributed quite generally but the percentage of victims was very much smaller.

This brings us to the end of our account of the conditions for the province of New Brunswick as a whole. As at Fredericton, the period of webworm stability came to an end in 1912, when a combination of many parasites and vireos reduced its numbers suddenly to a point at which it could no longer maintain its place in the local fauna. This reduction was general over the whole of the infested area. As at Fredericton, so elsewhere in the province this reduction involved a reduction of all the parasites, no matter whether they were large or small in stature and no matter whether they were monovores or polyvores. The reduction of webworms brought about a greatly increased effectiveness of birds and in spite of the reduced importance of the parasites, the webworm became almost extinct throughout the whole area previously infested. The insect was well on the way towards a province-wide extinction in the amazingly short period of three years after its stability or "balance" was disturbed in 1912. The flight of moths presumably from Nova Scotia resulted in extensive colonization of webworms along the Bay of Fundy territory. In this area the moths were able to increase rapidly and spread out each year to adjacent territory until at the end of 1918 the infested area corresponded very closely to that of 1912. A mild outbreak had disappeared; this had been followed by a few years of great scarcity; and a mild outbreak had once again developed. Conditions were vastly different in 1918, however, from those of 1912 because in the latter the parasites of many kinds were in great numbers, while in 1918 there were not as many species of parasites and all of them had been reduced to inconsequent numbers. The period of instability had not passed in 1918 and will not have passed until the absent black-bodied *Campoplex* has again found its way into New Brunswick and until all the parasites taken together once again come to constitute an effective sequence of environmental pressures.

Perhaps the most significant thing in connection with this account of webworm events for New Burnswick is the uniformity of conditions generally throughout the area and particularly the highly uniform distribution of the parasites.

Natural Control of the Webworm in Nova Scotia from 1916 to 1918, Inclusive

One of the objects of this study in the natural control of a common insect was to compare the environmental pressures operating against the insect in New Brunswick with those operating in places as remote from New Brunswick as could be visited conveniently. The New Brunswick study had already shown that a major parasite—the black-bodied *Campoplex*—could be eliminated in a few years and it suggested that in other places there might be an incomplete assemblage of parasites. Conditions might sometimes be readjusted by transferring parasites from one part of the continent to another.

The province of Nova Scotia was a natural direction in which to extend the studies. Although close to New Brunswick as measured by mere miles, yet from the *Hyphantria* point of view, Nova Scotia is practically an island,

separated by the Bay of Fundy and the Tantramar marshes (see map, fig. 6.). Both of these are food barriers, over which the moths must fly at right angles to the prevailing winds in order to cross from one province to the other. The barrier is obviously even more of an obstacle to the parasites than to the moths. It is probable, too, that Nova Scotia receives accessions to its parasitic fauna less frequently than does New Brunswick.

MAP OF THE MARITIME PROVINCES
showing
the observation points at which
the webworm studies were made

Legend
1 Fredericton   5 Moncton   9 Perth
2 St. Stephen   6 Newcastle   10 E. Margaretville
3 Nerepis   7 Campbellton 11 Annapolis
4 Chipman   8 St. Leonards 12 Milford
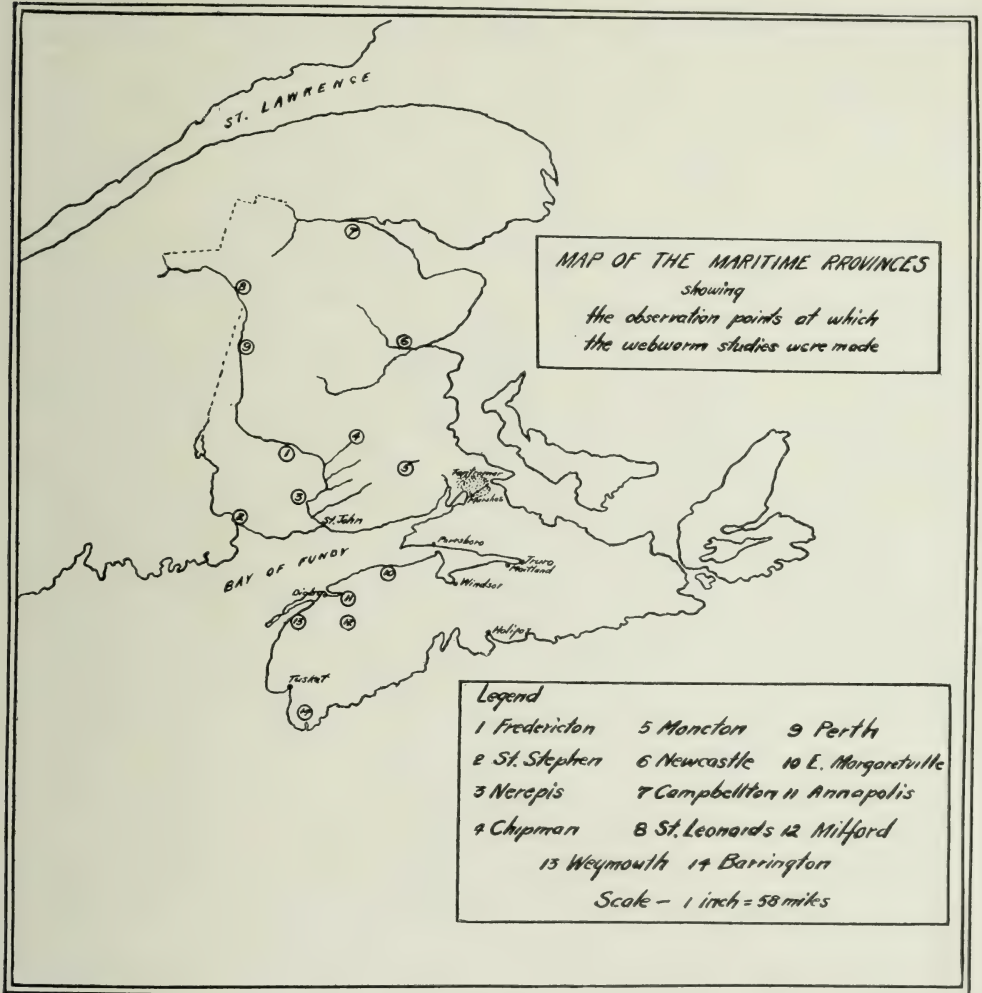   13 Weymouth 14 Barrington
     Scale — 1 inch = 58 miles

Fig. 6

In 1916 five observation points were selected in Nova Scotia and all the work was done from them. Each point was visited three times each year for collections of caterpillars and pupae, just as the New Brunswick points had been. East Margaretville, Annapolis, Milford, Weymouth and Barrington were the places selected. (See map, fig. 6.)

In 1916 the insect was quite plentiful all through the valley from Windsor to Digby; less so along the bay shore at East Margaretville, Barrington and Milford. Speaking broadly, it was scattered over the whole area between Halifax, Windsor and Yarmouth, being more abundant in the transitional zone of the valley and less abundant in the more strictly boreal highlands.

The natural control of the insect proved to be very similar to that just related for New Brunswick in 1918. It was soon obvious that the webworm was in a condition of expansion and that it would take some years for the parasites to overtake it and so to stabilize conditions.

The vireos bore the same relationship to the insect as in New Brunswick. They were everywhere present but their effectiveness depended entirely upon the abundance of the webs. In the Annapolis valley they exerted little effect, while at Barrington, Milford and East Margaretville they were much more effective than all other factors combined.

Apanteles was not found at all in 1916 and neither was *Meteorus*. *Campoplex* was found in small numbers at Annapolis, Milford and Weymouth. At the time I did not know whether both species were represented but in the next year when 130 were reared, there were 93 reds and 39 blacks (*C. validus*). Both

FIG. 7. A close view of fungous-killed caterpillars. (Photo. by S. Payne.)

species were undoubtedly present in 1916 and probably in about the proportion of 9 to 4. *Ernestia* was recovered at all the points but always in inconsiderable numbers. *Rogas* did not put in an appearance at all. Finally, the strange form, *Therion*, was found at Weymouth and Barrington in very small numbers.

From these findings and from conversations with observers in Nova Scotia, it seemed fairly certain that we were dealing in Nova Scotia with a developing outbreak of the webworm; whereas in New Brunswick from 1912 to 1916 we had been dealing with a diminishing or vanishing outbreak.

The main point, however, was that all the important parasites known to attack this insect in New Brunswick and Massachusetts were also present in Nova Scotia and no additional parasites were found. The minor parasites, *Apanteles* and *Meteorus*, failed to put in an appearance but this was rather of academic than of practical interest.

The only new agent of destruction not hitherto found was a fungous disease that utterly destroyed one colony out of ten under daily observation at Annapolis. The nest attacked was within twenty yards of ten others that were not attacked at all. The only difference in conditions noticed between this nest and its neighbours was that the diseased nest was half buried up in alder bushes while the others were exposed to winds and sunshine. The photograph taken by Mr. S. Payne (fig. 7) shows the general appearance of this nest and of its inmates. Every larva was killed and slightly whitened, the larvæ being about half grown when the attack occurred. The disease is evidently extremely uncommon and plays little or no part in the ordinary control of the webworm.

The main results, as above described, may be condensed as follows:—

NATURAL CONTROL CONDITIONS IN NOVA SCOTIA AT THE FIVE OBSERVATION POINTS IN 1916

	East Margaret-ville	Annapolis	Milford	Weymouth	Barrington
Infertile	26	26	26	26	26
Apanteles	0	0	0	0	0
Meteorus	0	0	0	0	0
Campoplex (2 sp.)	0	35	2	14	0
Rogas	0	0	0	0	0
Ernestia	2	1	11	2	9
Therion	0	0	0	11	2
Birds	230	80	198	110	210
Moths issued	2	118	23	97	13
	260	260	260	260	260

At Annapolis, for instance, about 26 eggs of each egg mass failed to hatch, owing, probably, to infertility; 35 of the caterpillars that did hatch were parasitized by the two species of *Campoplex;* of the remaining caterpillars 1 was victimized by *Ernestia;* 80 of the unparasitized larvæ were carried off by birds, and finally, 118 moths issued. These factors taken together accounted for the 260 individuals in each average egg mass.

An instructive column is the "moths issued" one. At Margaretville only 2 moths issued and *Hyphantria* was held at par; at Annapolis, where the webs were thick, 118 moths issued, representing a moth increase of 59 to 1; at Milford in the boreal zone, there was a yield of 11 pairs of moths from every egg mass; at Weymouth, where the abundance of webs was about intermediate between Annapolis and Margaretville, there was a yield of about 49 pairs of moths from each egg mass; and at Barrington, where webs were scarce, there was a yield of only about 7 pairs of moths from each mass. One sees that the area typified by Annapolis was a nursery in which were produced thousands of moths for distribution in 1917.

The parasite figures are based upon dissections of 1,325 carefully sampled caterpillars. The effect of birds (mostly, if not entirely, vireos) was measured carefully only at Annapolis, the figures for the other localities being estimates made on the occasions of the three visits to each locality.

In 1917, the webworm was quite as abundant in Nova Scotia as it had been in 1916 and moth flights from the Annapolis valley seem to have extended the area of infestation considerably in the direction of Maitland and Truro. No work was done this year in connection with bird control and the results obtained have to do entirely with the condition of the various parasites at the five observation points.

The season's results have been condensed into the following table:—

Digest of Dissection Results from Nova Scotia Points in 1917

	East Margaret-ville	Annapolis	Milford	Weymouth	Barrington
Infertile........................	26	26	26	26	26
Apanteles......................	0	0	21	0	0
Meteorus.......................	0	0	0	0	0
Campoplex......................	10	21	21	26	7
Rogas..........................	0	0	0	0	0
Ernestia.......................	2	4	6	0	0
Therion........................	0	0	0	6	0
*Birds (approx.).................	222	209	186	202	227
Moths issued.....................					
	260	260	260	260	260

As usual, a 10 per cent toll has been allowed for non-hatch; it may have been higher or lower than this and the figure simply represents a small annual loss that does not vary greatly from year to year or place to place.

Apanteles was found only at Milford but at this point it was fairly abundant; this proved at least that the species was present in Nova Scotia and indicated that it was probably increasing.

Meteorus was again not found, indicating that the species was absent from the fauna of the region studied.

There was a marked increase in the distribution and abundance of the two species of *Campoplex*. They occurred at all five points instead of at only three, and they took an average of 17 caterpillars from each web. Rearings carried on by Mr. L. S. McLaine in connection with another problem showed them to be distributed in the proportion of approximately 9 of the red-bodied species to 4 of the black ones.

Rogas was not found, although this was the year of its sudden appearance in New Brunswick.

The important tachina fly, *Ernestia*, apparently did not do as well as it had done in the previous year. It was recovered at only three places and the average parasitism was 2 instead of 5 per web. As there was a marked increase in the following year, however, it seems that the webs we happened to select for securing data may have been rather poorer in *Ernestia* maggots than the average.

The *Therion* situation scarcely differed from that of the year before; it was recovered in small numbers at the same place, namely, Weymouth.

While no work was done in connection with bird control, yet it was reasonably certain at the end of the season that although the combined environmental pressures were steadily increasing, they still fell far short of being able to hold the webworm at par. The insect was increasing both in numbers and distribution.

Our Nova Scotia studies were concluded in 1918. In this year the insect was about as abundant as it ever becomes in eastern Canada and as I drove by car to all our observation points I noticed a very general increase of the insect since my last visit to Nova Scotia in 1916. Starting from the Tantramar marshes, no nests were found until Parrsboro' was reached. At Truro they had become abundant and the same condition prevailed along the road between that point and Maitland. Here the insect was so thick that many of the late moths were seen ovipositing. From Maitland to Windsor, not so many webs were seen but the insect was by no means uncommon. Conditions in the Annapolis

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*No data were collected this year regarding the effectiveness of birds. Judging by the numerical strength of the webworm in 1918, it is probable that the bird situation was closely comparable in 1917 with that in 1916.

valley were about the same as in 1917; the webs were very conspicuous in all orchards and alder patches and were evenly and abundantly distributed from Windsor to Digby.

At East Margaretville conditions were about the same as in 1916 and 1917. The insect was not nearly as abundant as in the valley but no difficulty was experienced in finding five webs. At Milford, where the infestation had been light in 1916, the infestation was now heavy.

From Digby to Weymouth the nests were not as common, but a collection was made very easily at Weymouth. From that point to Yarmouth the food supply is very limited and no webs were found. At Tusket they reappeared and they were thinly scattered from there to Barrington. In the boreal woods just inland from Barrington the insect was found to be as abundant as at Milford, which is also situated in these boreal highlands but about seventy-five miles distant.

Once again the chief interest lay in finding out to what extent the parasites were increasing. A glance at the following table will help to make the situation clear.

DIGEST OF DISSECTION RESULTS FROM NOVA SCOTIA POINTS IN 1918.

	East Margaret-ville	Middleton	Annapolis	Milford	Weymouth	Barrington
Non-hatch	26	26	26	26	26	26
Apanteles	0	2	0	0	0	0
Meteorus	0	0	0	0	0	0
Campoplex	9	37	62	54	40	12
Ernestia	4	4	4	36	2	11
Rogas	0	0	6	0	0	0
Therion	0	0	10	0	8	6
Birds	131	191	132	144	184	205
Moths issued						
	260	260	260	260	260	260

As usual, there was a mortality due to non-hatch, and in the absence of careful estimates, 10 per cent has been allowed from the average egg mass, thus making a total of 26.

Apanteles was no more abundant than before and was, apparently, not increasing. In 1916 none were found; in 1917 a few were found at Milford; and in 1918 a few more were found at Middleton. As there are, and had been for three years, plenty of webworm nests in the area, the failure of *Apanteles* to increase is not without interest. It is a polyvore with two generations and it seems possible that there had been a shortage of food material for the first generation.

For the third time in succession *Meteorus* failed to put in an appearance, thus proving fairly conclusively its absence in this part of Nova Scotia. It seems probable that it has been eliminated from Nova Scotia in years gone by in some such fashion as has *Campoplex validus* from New Brunswick. In such case, its return would be a matter of difficulty because its powers of flight cannot compare with those of the webworm and even the webworm can pass from New Brunswick or the state of Maine to Nova Scotia only when there happens to be a favourable wind at the time of flight. It seems more likely that *Meteorus* would have to travel to Nova Scotia by way of the Tantramar marshes and even here there is the present difficulty of there being no webworms, between Sackville and Parrsboro'.

The two species of *Campoplex* showed another very marked increase this year. They were recovered from all five places and as the table shows, they had begun to take their places as major factors in control. Averaging the *Campoplex* columns in the 1916, 1917 and 1918 tables, we find that in 1916 these

parasites took an average of 10 larvæ from each web throughout the area represented by the six points; in 1917 they took 17 and in 1918 they took 43. There had been a steady and general increase during the three years.

Ernestia also showed an increase this year but was still considerably behind the two species of *Campoplex* from the point of view of numerical ascendency. The tables indicate that it was distributed throughout the whole area and was now taking a toll of 12 larvæ from each web, whereas the year previous it had taken less than 3 and the year before that about 5. It seemed to have reached the numerical strength from which it would rapidly increase to its normal position as a parasite of first-class importance. As it seldom attacks other hosts in eastern Canada and has only one generation and as there was a plentiful food supply in Nova Scotia, the conditions for its increase seemed to be fulfilled.

At Annapolis a few *Rogas* were found for the first time in Nova Scotia. It will be recalled that this species does not ordinarily attack webworms, but that it did so in New Brunswick in 1917 and again to a smaller extent in 1918.

The parasite *Therion* showed a considerable increase in numbers and in distribution. In 1916 it had been found at Weymouth and Barrington; in 1917 at Weymouth only; and in 1918 it was found at Weymouth, Barrington and Annapolis. From these fragmentary data it would appear to be increasing its distribution in a northeasterly direction. It was now taking an average (as indicated by the dissection data) of 5 caterpillars per web throughout the area, whereas in 1917 it had taken 1 and in the previous year, 2. While these figures mean very little when the numbers of victims are so small, yet they probably do mean that there was a considerable increase of *Therion* during the three years.

This brings to a close the account of the natural control of the fall webworm in Nova Scotia during the three years of our study. When the study was commenced, the webworms were quite abundant and the parasites were few and far between. During the three years the parasites, as a whole, gained so rapidly in numbers that they might be expected to attain their maximum strength in about 1920. It seemed that before our study was commenced the webworm had gone through a period of suppression so great that its major parasites had almost but not quite been exterminated. A flight of moths from the mainland then probably covered Nova Scotia in time to save all the parasites but one from extermination and to enable the webworm to increase in spite of the vireos.*

One of the things brought out in the study was the essential similarity of the environmental pressures operating against *Hyphantria* in Nova Scotia and New Brunswick. There were no additional parasites and the only real difference proved to be the absence of a minor parasite, *Meteorus*, in Nova Scotia. The vireos were active, as they had been in New Brunswick, and their effectiveness increased as the webworms decreased. They were far more effective, for instance, in the boreal highlands of Nova Scotia where the webs were at first scarce than in the Annapolis valley where they were abundant.

The absence of *Meteorus* in Nova Scotia although of little consequence in itself because of its minor character as a factor in control, was of supreme interest from a more general standpoint. It proved that a species of parasite present in New Brunswick was not necessarily present at the same time in a nearby area of greater size, separated off by a natural barrier. It happened to be *Meteorus* but might as easily have been any one, or all, of the major parasites.

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*In connection with this interesting subject of the relation of Nova Scotia to the mainland, in so far as the natural control of flying lepidoptera is concerned, there may be mentioned the case of the brown-tail moth. Flights of this insect began to arrive in Nova Scotia in 1907, and perhaps a few years before, and they have been repeated at intervals since that time. With the possible exception of an *Apanteles*, however, there is no reason for supposing that any of the several species of European parasites liberated in Massachusetts managed to follow the moth to Nova Scotia, although some of them found their way up into northern Maine. If it took a decade for these parasites to reach northern Maine, how long would it have taken them to cross over to Nova Scotia? The *Calosoma* beetle (*C. sycophanta*) at least would have been obliged to take the land route by way of the Tantramar marshes. The artificial colonization of this important assemblage of insects in Nova Scotia has undoubtedly shortened by many years the period of unstable balance of the brown-tail moth in that province.

The Natural Control of the Webworm in Southern British Columbia, 1917 to 1919, Inclusive

In 1917, there came an opportunity to extend the natural control studies to southern British Columbia. As the flora, fauna and physical features of this province are so very distinct from those of New Brunswick and Nova Scotia, the work was undertaken with a great amount of enthusiasm. We
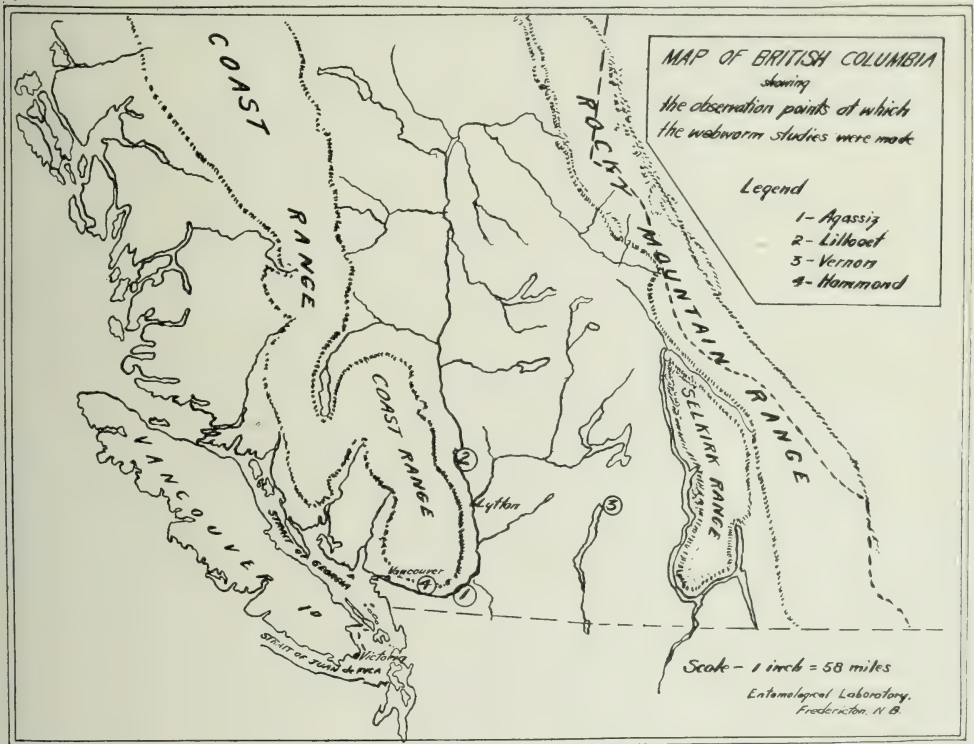

Fig 8

had already seen that the narrow barrier of water and marshes between the two Maritime Provinces had prevented the easy passage of moths and parasites from one province to the other, and it seemed that the greater barriers between New Brunswick and British Columbia might result in greater differences in natural control.

The efficiency of these barriers is reflected in the fact that the webworm of southern British Columbia is a white-winged race, while that of the Maritime Provinces is a mixture of white and spotted forms, both of which can be reared from a single egg mass. This racial difference proves that little or no inter-breeding of Pacific Coast and Atlantic Coast moths has taken place for a long period of time.

It may be well to call to mind here the great food bridge over which the webworm has travelled, either from the west to the east or vice versa, or even in both directions. I refer, of course, to the great boreal life zone that spans the continent as a belt of coniferous forest that includes practically all of New Brunswick, much of Quebec and northern Ontario; the tree belt of northern Manitoba, northern Saskatchewan, northern Alberta and northern British Columbia; and that extends down the Appalachian mountains in the east and the Cordilleras of the west into Georgia and California, respectively. This

great territory, shaped somewhat like a horseshoe, has been traversed by many species of living things, both plants and animals, including such typically boreal productions as the black bear, the bunch berry and the spruce budworm. Why is it, then, that the webworms of southern British Columbia do not commingle with those of the Maritime Provinces?

A glance at the map of British Columbia (fig. 8) shows that it is featured by a series of mountain chains and valleys running up and down the continent. This results, in a general way, in the establishment of definite paths of migration, particularly of flying animals, such as birds and moths. The general tendency of a moth flight would be up or down the continent from California to Alaska, or vice versa.

Again, the mountain ranges are so high that several life zones are represented in a journey from a valley to the top of the mountains. Insects living in the valleys are confronted with food barriers preventing free movement east and west. The webworm of southern British Columbia, for instance, depends for its existence—in any numbers—upon the numerous alder trees of the transitional valleys. Above these valleys there is a boreal belt containing a very limited number of alders of two different species and upon which I did not find webworms feeding. Above this again comes the treeless Arctic zone that, in spite of being a naturalist's paradise, contains nothing of interest for webworms. The only way, therefore, in which a flight of webworms could break through from the coast to the interior would be to travel by way of one of the few passes, such as that cut through the Coast Range by the Fraser river.

In the case of a flight developed in the interior, the only road to the east would be through one of the gaps or passes—relatively few, as the railroad engineers have discovered—through the great chain of the Rocky mountains. In the event of the moths breaking through at Lethbridge or Calgary, they would be confronted with the food barrier of the prairies and the plains, involving a further journey of anywhere from two hundred to a thousand miles before alders could be reached.

The easiest method by which a flight of southern British Columbia webworms could reach the so-called "northern forest" would be for them to fly north in the interior and then break through the Yellow Head Pass when the wind was favourable. The headwaters of the Athabasca would be the most likely meeting-ground of the two moth races. With so many 'ifs', however, it is little wonder the two races have become distinct.

From information secured from such reliable sources as the late Mr. Tom Wilson, Mr. R. C. Treherne and Mr. Max H. Ruhmann, it was certain that the webworm was in a condition of incipient outbreak in 1917 in southern British Columbia. On Vancouver island it was so scarce that I could get no records of its recent occurrence. None of the local lepidopterists knew of any recent captures and the insect has been scarce or absent for some years. As this local absence was particularly instructive, I spent three days within fifty miles of Victoria, looking for the insect, but was unable to find a single web.

In the Lower Fraser valley (only about seventy miles from the Victoria end of Vancouver island) the insects proved to be plentiful from New Westminster to Agassiz. A few nests could be seen scattered along roadside trees between Vancouver and New Westminster. About half a dozen webs were also seen between the latter place and Coquitlam. At Hammond the webs became more abundant and in one orchard of about five acres there were eight webs. Similar conditions prevailed up to about Harrison Mills, where the insect was much more abundant and where the unsightly webs were thick enough to be noticed by tourist passengers travelling over the Canadian Pacific Railway. This condition of abundance—really a mild outbreak—was equally marked at Agassiz, but less so on the opposite side of the Fraser river. The outbreak did not extend up the Fraser canyon that opens a few miles above Agassiz and that serves as one of the few passes between the coast country and the interior.

In the dry interior between the Coast Range of mountains and the Selkirks, the insect was much less abundant but two webs were finally located at Lillooet and five by Mr. Ruhmann at Vernon. Mr. Treherne wrote me that the insect was very lightly scattered through the whole of the Okanagan valley. I have no data for the Selkirks, and for the Rockies the only data is that no old webs were seen during a two-day visit in the neighbourhood of Field.

For the study of control, good collections were obtained from Lillooet (see fig. 8) through the kindness of Mr. A. W. A. Phair; and from Vernon through the kindness of Mr. Ruhmann. Agassiz and Hammond I was able to visit at frequent intervals through the caterpillar season and a fine series of collections was made for obtaining dissection data. At these two places, four collections were made throughout the season from the same nests. Altogether, 1,593 larvæ were dissected and the information obtained from both dissections and observations has been condensed in the following table:—

SUMMARY OF DISSECTION DATA FROM FOUR OBSERVATION POINTS IN BRITISH COLUMBIA IN 1917.

	Hammond	Agassiz	Lillooet	Vernon
Non-hatch..	26	26	26	26
Egg Parasites.......................................	0	0	0	0
Apanteles...	0	0	0	0
Meteorus..	0	0	0	0
C. validus..	4	5	25	88
Ernestia..	12	7	12	3
Lydella...	24	40	0	9
Therion...	9	18	2	9
Birds...	37	65	193*	123*
Moths issued (approx.)...............................	148	99	2*	2*
	260	260	260	260

* The above figures with an asterisk were not arrived at by counting caterpillars in webs of known strength. They are estimates based upon the fact that *Hyphantria* was held at par—there being no appreciable increase of webs in 1918. At both places webs were scarce and birds certainly consumed very large numbers of caterpillars.

There was a certain amount of "non-hatch", just as there had been in New Brunswick. Although no counts were made, it will be sufficiently accurate for the purposes of our table to allow a 10 per cent mortality from this cause, thus reducing each egg mass of 260 by about 26. A large number of egg masses collected at Agassiz were held for parasite rearings but no parasites appeared, thus showing that they were at least very scarce. No *Apanteles* and no *Meteorus* were obtained, thus showing that these were either very scarce or entirely absent. The first parasite recovered was *Campoplex validus* At the time I did not know the species because no rearing work was done. In 1918 and 1919, however, Mr. Baird did a lot of rearing work and this was the only species found. This parasite was recovered from all four places. It was very scarce at Hammond and Agassiz, where the host insect was so abundant, and fairly abundant at both Lillooet and Vernon where webs were few and far between.

Then came the most interesting development of the season. In the Maritime Provinces there are no parasites, except *Compsilura*, that infest the alimentary canal of the webworm. In British Columbia, however, I knew that nothing could be taken for granted and had examined all the digestive systems for parasites. The precaution was rewarded by finding, one day, the first stage maggot of a tachinid fly that had all the singular characteristics of a *Compsilura*

or *Lydella*. Its habitat was between the peritrophic membrane and the lining of the mid-intestine, and it was supplied with the three characteristic anal hooklets. It was found in material from Hammond, Agassiz and Vernon, thus proving that it had a wide distribution. It occurred in such large numbers at the first two places as to prove it to be a parasite of first importance. It turned out to be both a major parasite and a new species of the genus *Lydella*. Our dissections indicated it to be taking 24 caterpillars from each web in Hammond and 40 from each web at Agassiz.

Our old friend, *Therion*, was then recovered from all the points and at Agassiz in moderately large numbers; it was clearly more abundant than it had been in the Maritime Provinces.

It was obvious from the large number of torn webs, that birds of some kind were feeding upon the caterpillars. Counts made at Agassiz and Hammond showed that they were taking about 37 from each web at the latter place and about 65 at the former. The webs were too numerous for the birds to make much of an impression, just as they had been at certain times and places in New Brunswick and Nova Scotia. What the birds were, I do not know and unfortunately it has been impossible to determine them during the two years of subsequent work done in British Columbia. At Lillooet and Vernon, no counts for bird destruction were made but the birds were undoubtedly much more effective than in the Lower Fraser valley.

The year's work showed that there were two rather sharply contrasted areas: the Lower Fraser valley, where there was an incipient outbreak of webworms, and the great dry interior where the insects were lightly and fairly evenly distributed. In these two areas the natural control was somewhat different, as shown by the table, the chief difference being in the relative importance of birds in the two areas. It seemed also that the historical background in these two areas might be somewhat different. In the Lower Fraser valley the outbreak was obviously of recent origin, because the parasites were present in relatively few numbers and all the environmental pressures taken together were entirely inadequate to maintain control. In the dry interior, the insect seemed to be neither increasing nor decreasing, the parasites being widely distributed and reasonably effective, considering the scarcity of the host. The finding of *Campoplex validus* in effective numbers at such widely separated points as Vernon and Lillooet seems to indicate somewhat forcefully that the webworm had been in a condition of stability in the interior for a number of years.

One of the main results obtained was the finding of *Lydella*, a major parasite able to maintain an existence as a monovore upon *Hyphantria*, and known to be absent in Massachusetts, New Brunswick and Nova Scotia. Another thing of almost equal interest was the absence of *Campoplex pilosulus* that is so important a parasite in eastern Canada.

The non-appearance of *Apanteles* and *Meteorus* did not prove to have any significance, because both these species were found in later years at Agassiz by Mr. Baird.

In the following year Mr. Baird did all the webworm work in British Columbia and although his time was largely taken up with other problems, he obtained some very satisfactory data on the webworm from Agassiz and Lillooet.

There was evidently a great increase of the webs in the Lower Fraser valley. Mr. Baird says of the outbreak that it "was by far the worst I have ever seen. Its ravages extended from Vancouver and New Westminster up the Fraser river and its tributaries, some of the moths having been blown as far at least as Lillooet. City shade trees, orchards and countryside were made unsightly by the presence of thousands of webs, and most of the deciduous trees were stripped of foliage. The insect was reported rather scarce in the Okanagan

valley and this seems to have been true for the interior generally, except, perhaps for the Fraser valley from Lytton to Lillooet. On Vancouver island I was unable to find it at all, in spite of being located there for most of August and September."

Through the kindness of Mr. A. W. A. Phair, some collections were made at Lillooet, and apart from an examination of these collections, the study was confined to Agassiz where periodical collections were made in the usual way.

The net results of the season have been put into tabular form as follows:—

SUMMARY OF HYPHANTRIA DATA COLLECTED IN
BRITISH COLUMBIA IN 1918.

	Agassiz	Lillooet
Non-hatch	26	26
Egg parasites	2	0
Apanteles	2	0
Meterous	1	0
C. validus	5	36
Ernestia	7	88
Lydella	54	0
Therion	40	0
Birds	24	108*
Moths issued	99	2*
	200	200

* These figures were not arrived at by counting caterpillars in webs of known strength. They are estimates based solely upon the fact that there was no apparent increase of webs at Lillooet in 1919. Webs were scarce, and birds certainly had a great deal to do with maintaining the scarcity.

The only change of any importance at Lillooet was the increase of *Ernestia*, which species took about 88 larvæ in each of the several webs examined. It is quite likely, however, as the insect was still relatively scarce in the Lillooet district that the parasitism by *Ernestia* was somewhat erratic, being high in some webs and low in others. There was also a substantial increase of *Campoplex validus* from 25 per web in 1917 to 36. There was no marked increase of the insect and, consequently, birds seem to have continued to play an important part in their control.

At Agassiz there was, first of all, a small egg parasitism by an undetermined species resembling *Trichogramma pretiosa*. I once came across a case of webworm parasitism by that ubiquitous parasite at Melrose, Massachusetts, but it proved to be quite unimportant and there are good reasons for supposing the Agassiz parasite to be equally unimportant.

Apanteles and *Meteorus* were both found, thus demonstrating their presence in British Columbia.

Campoplex validus maintained its relative strength and so did *Ernestia*. In view of the great increase of webworms at Agassiz, this was a fairly good showing.

The new parasite, *Lydella*, made a slight gain from 40 per web in 1917 to about 54. Considering the increase of the host, this was quite a remarkable achievement.

The parasite *Therion*, however, took the honors for the year. During the study in eastern Canada it had never shown itself to be much more than of minor importance. At Agassiz this year, however, it accounted for about 40 caterpillars in each of the sample webs examined and Mr. Baird found the adults to be in such numbers that they could be taken with a net in quantities.

Birds made very little impression upon the immense numbers of caterpillars and became of less importance than either *Therion* or *Lydella*.

The work at Agassiz showed that, while the outbreak had reached its height, the major parasites had either held their own or had increased so that the sum total of the environmental pressures against the webworm was considerably greater than it had been only a year previous.

In 1919, the British Columbia work was continued by Mr. Baird, but owing to the pressure of other problems, the *Hyphantria* studies had to be confined to Agassiz where Mr. Baird was living at the time.

To use Mr. Baird's own words: "The outbreak covered practically the same territory as last year. The caterpillars were not quite so abundant at Agassiz but elsewhere in the Lower Fraser they were, if possible, even more abundant than last year. In the Lytton-Lillooet district they were quite conspicuous and also in the Okanagan. No webs were seen on Vancouver island."

Apanteles and *Meteorus* were much more abundant than last year, as shown by the cocoons in the field, but there was a considerable amount of patchiness in their distribution and for the whole area their combined efforts failed to accomplish very much.

Campoplex validus took about 12 larvæ in each web as against 5 before, thus showing a substantial increase.

The maggot-laying *Ernestia* again made a poor showing, there being a decrease in the percentage of parasitism by this species.

No special dissections were made for *Lydella* and its status for 1919 is not known. It was presumably at least as abundant as it had been the year before.

Therion was the most effective parasite, taking about 53 caterpillars in each web instead of 40, as before. This indicated a considerable increase.

Birds were no more effective than they had been in the previous year; in fact, they seem to have been less so on account of an increased supply of caterpillars.

All the factors taken together were insufficient to hold the insect at par, although they had become somewhat more effective than before. The probabilities were that it would take two more years at least before a reduction of the outbreak could be expected.

The results for the year are shown in the following table, enabling comparisons to be made with the control situation in each of the two previous years.

SUMMARY OF CONDITIONS OF NATURAL CONTROL
AT AGASSIZ, 1919

	Agassiz
Non-hatch	26
Egg Parasites	1
Apanteles	2
Meteorus	1
C. validus	12
Ernestia	2
Lydella	54*
Therion	53
Birds	21
Moths issued (approx.)	88
	260

* This figure is purely a guess, based upon last year's findings. Larval dissections showed it to be present, but as no pupal dissections were made, the figure can only be arrived at on the basis of expectations from the previous year.

Our *Hyphantria* work in British Columbia came to an end in 1919. It had been found that the barriers between the two races had also acted as barriers between the two assemblages of parasites. There was a major parasite in British Columbia, *Lydella*, not known to occur east of the Rocky mountains; and conversely, the major parasite, *Campoplex pilosulus*, found in the eastern provinces was apparently absent from southern British Columbia.

Of even greater interest, perhaps, than these differences between the factors of control in the eastern and western limits of the continent was the absence of *Hyphantria* from Vancouver island during one of the most severe outbreaks of the insect on record, only seventy miles away. The only barrier between the island and the infested area consists of the Strait of Georgia and even this is bridged to a very large extent (so far as a winged insect is concerned) by a series of small islands between Vancouver island and the mainland. Indeed, the only strip of water of any considerable width is probably less than forty miles across. This lies between the mouth of the Fraser and the first island. In spite of this seemingly trivial barrier, there has been an absence of a winged insect on one side of the barrier and an outbreak of the same insect on the other at the same time.

During the three years of the outbreak, the winds at the time of flight have been inland and moths have undoubtedly been blown up the Fraser canyon and scattered through the interior particularly through the Lytton-Lillooet area, as shown by the increase of webs in 1918 and 1919. During these years not a single cloud of moths has been able to drift to Vancouver island.

Suppose that a few moths do drift over on a favourable wind; how long is it going to take the several parasites to follow them? No one of the parasites is on the wing in numbers at the same time with another nor at the time of the moth flight. The first favourable wind for the moths will be of no use to any of the parasites. Each parasite must have a wind especially favourable for itself. None of the parasites have the power of flight developed to anything like the extent of the moths and yet the moths themselves have been unable to get across this barrier for three years.

As to the cause of the outbreak in southern British Columbia, it seems fairly certain that it was due, first of all, to a flight of moths being blown into the Lower Fraser valley; secondly, to an increased food supply in this valley, due to the advance of civilization; and thirdly, to a relaxed condition of the environmental pressures, due to the moths having flown away from their parasites.

As the webs were much more abundant at the beginning of the outbreak at the Agassiz end of the valley, it seems clear that a flight of moths came down the Fraser canyon rather than up from the coast; that it came, in other words, from the interior. Such an explanation would presuppose the insect being in the interior for some years previous to the flight and that such was actually the case is indicated very strongly by the stable condition of the insect found to obtain in 1917 at places as widely separated in this interior as Lillooet and Vernon. That the flight did not originate at the coast in 1917 is indicated by the absence of the insect on Vancouver island. That the outbreak was more likely due to a flight than to the gradual increase of a few pairs of moths is indicated by the fact that when only a few pairs of moths were left in the Fredericton district, the species fell a prey to vireos and was unable to maintain an existence.

As to the second point, namely: the increased food supply, due to the march of civilization, it may be explained that the valley was only opened up for settlement in 1885 on the completion of the Canadian Pacific Railroad. Its remoteness before that time is reflected by the fact that the surveyors from Ottawa working on the Pacific Coast link of the railroad travelled to their base of operations by way of Cape Horn. Within the last twenty years much of the primeval forest has been removed and although some of this area now supports a flourishing agriculture, yet there are also large areas reproducing to alders. There are also many alders along the roadsides and fence rows, all of which tend to consolidate the webworm food supply and so to afford an opportunity for an outbreak.

Finally, as to the relaxed tension against the webworm; this condition has already been explained in the account of natural control for Agassiz and Hammond. There were too many webworms for the birds to cope with and the parasites were entirely too scarce to be effective.

Some General Conclusions from the Studies in both Eastern and Western Canada

1. *The Value of the parasites and the birds.* One thing that seems to stand out somewhat prominently from this study in the natural control of the fall webworm is the rather peculiar position occupied by the insect parasites. In the time of an outbreak the parasites were unable to cope with the situation and some years were necessary for them to breed up to a condition of usefulness. The role of the parasites is not to check an incipient outbreak. Again, when the host became exceedingly scarce, the parasites died away and under such conditions they were largely ineffective. When the host was but moderately abundant, however, the maximum usefulness of the parasites was developed and they became largely responsible for a condition of stabilized control in which the insect neither increased nor decreased but remained for a considerable period of years as a comparatively harmless member of the fauna. During these long periods between outbreaks, the parasites seem to be essential for the maintenance of equilibrium and without the parasites such periods would evidently occur very infrequently. As no outbreaks can occur during these periods of stability, it is clear that the prevention of outbreaks is largely a matter of maintaining stability; or in other words of maintaining an adequate series of insect parasites.

The tremendously important part played by the vireos in Eastern Canada and by undetermined birds in British Columbia in the control of *Hyphantria* has also been narrated during the progress of this study. They are of least importance when the host insect is very abundant; of greatest importance when the webs are very scarce; and they share with the parasites the task of maintaining a stabilized control when the insect is just moderately abundant, Without the birds the parasites would not maintain a control, as shown, for instance by the control chart for Fredericton in 1912; and the converse is also true.

(2) *Parasites of first importance may disappear from time to time over considerable geographical areas.* Perhaps one of the most significant results of the study was the elimination by starvation of the major parasite, *Campoplex validus*, from the province of New Brunswick as a result of the near elimination of its host in 1913, 1914 and 1915. Another major parasite, *Campoplex pilosulus*, was found to be absent in southern British Columbia at the time of the study and it is probable that this species had been eliminated in some such way as had its sister species from New Brunswick. Another notable absence was that of *Meteorus* from Nova Scotia to be accounted for in a similar way. Finally, there is the absence of the webworm itself from Vancouver island and this involves the absence also of all the parasites that are dependent upon this host for a food supply, probably the two *Campoplex* species, *Ernestia*, *Lydella*, and possibly also *Therion*. These things prove that parasites necessary for the maintenance of control may disappear entirely over areas of considerable size. This means, for instance, that it is not sufficient merely to colonize parasites of, say, the brown-tail moth in Nova Scotia, but that it is also necessary to maintain a more or less constant vigil on its subsequent welfare.

(3) *Parasites once eliminated may be hindered or prevented from returning through the operation of various natural barriers.* It has been shown that the combination of the Bay of Fundy and the Tantramar marshes prevented *Campoplex validus* from crossing to New Brunswick during each of the three years from 1915 to 1918; and that it possibly prevented, also, the crossing of

Meteorus to Nova Scotia. Likewise, the narrow strait between the mainland and Vancouver island served for three successive years to keep the webworm situation entirely distinct on the mainland and on the island. Again, the direction of the mountains of British Columbia and their height has, apparently, prevented the parasite *Lydella* from wandering eastward of the Rocky mountains and has also prevented *Campoplex pilosulus* from finding its way at least recently into British Columbia. These circumstances indicate that once a parasite has been eliminated from a local fauna, its return may be prevented for an indefinite number of years by natural barriers.

(4) Opportunities presented during the progress of this study for the advantageous transfer of parasites within Canada. On account of the parasite eliminations and of the barriers preventing their return, there have been a number of opportunities uncovered during the progress of the work for transferring parasites from one part of Canada to another with a prospect of bringing about a stable condition of control more rapidly than had things been left to take their natural course. British Columbia was found to lack *Campoplex pilosulus;* New Brunswick was found to lack *Lydella*, and after 1916 *Campoplex validus;* and Nova Scotia lacked *Meteorus* and *Lydella*. In addition to these possibilities of transferring parasites to advantage, it seems clear that had some *Hyphantria* webs been introduced in numbers into New Brunswick from Nova Scotia in 1913 or 1914, the elimination of *C. validus* from New Brunswick might have been prevented. It is also clear that when the first flight of webworm moths reaches Vancouver Island there will be the best of reasons for introducing the parasites so as to stabilize the *Hyphantria* situation on the Island in the shortest possible time.

(5) The food pressure against Hyphantria. In this account a great deal has been said about environmental pressures against the webworm caused by the non-hatching of eggs, by parasites, and by birds, and little has been said about the food pressure. This food pressure, as a regulative factor in the struggle for existence of living things, has been so thoroughly appreciated, however, since the writings of Malthus, Wallace, Darwin, and of the modern evolutionists and ecologists, that it has seemed unnecessary to say very much. It is very real for *Hyphantria* and its effects are seen in numerous ways.

One effect of this pressure is that when outbreaks of this insect do occur in Canada, they are not upon the grand scale of the cutworm and grasshopper outbreaks in the Prairie Provinces; or of the spruce budworm and forest tent caterpillar in certain areas of Quebec and New Brunswick; or of the gypsy moth in the New England States. In eastern Canada this is due to the fact that although the basic food plant, *Alnus incana*, is one of the most common productions of the boreal forests, it is not massed in pure stand into vast consolidated areas. This distribution in "alder swamps" and along rivers and streams seemingly results in many a moth flight being blown by winds into foodless portions of the surrounding forest and being prevented, in consequence, from participating in the development of an outbreak. Only the alders that are exposed to the winds are found by the moths and, consequently, vast numbers of alders are never found at all.

In places like the Annapolis valley, the food pressure has been relaxed through the efforts of agricultural man. This fertile valley, nearly 100 miles in length and averaging, perhaps, five miles in width, now supports thousands of acres of apple orchards that have become justly famous. Much of the original food supply of the webworm still exists because alder land is, for the most part, too wet for agricultural purposes and there is now the additional supply of apple trees. This increased food supply seems to explain the greater severity of the outbreak studied in the Annapolis valley as compared with the New Brunswick outbreaks of 1912 and 1919.

As already mentioned, an even greater relaxing of the food pressure in the Lower Fraser valley where the basic food supply consists of *Alnus rubra* a tree of considerable size, resulted in an outbreak that seems to have been more severe than any hitherto recorded for Canada.

(6) The causes of the webworm outbreaks studied. Finally, a word may be said as to the causes of the webworm outbreaks studied. To take New Brunswick first: the insects were on the verge of local extinction in 1916 when a flight of moths probably from Nova Scotia landed along the bay shore and laid the foundation of an outbreak. So many moths arrived that the webs were too thick for the vireos to cope with and as the parasites had just been reduced by starvation, they were likewise incapable of dealing with the situation. The three features of this outbreak were (1) an abundant food supply, (2) a flight of moths that laid so many eggs that vireos were ineffective, and (3) a greatly decreased parasite pressure.

In the Lower Fraser valley of British Columbia it has been shown that the outbreak of 1917 was due (1) to an abundant food supply, (2) to a flight of moths probably down the Fraser canyon, and (3) to a greatly decreased parasite pressure.

In the Annapolis valley of Nova Scotia the outbreak of 1916 seems to have been due (1) to an abundant food supply, (2) probably to a flight of moths from Maine or New Brunswick in about the year 1910, and (3) to a greatly decreased parasite pressure.

In other words, the causes seem to have been similar in each case. The outbreaks did not develop as a result of the gradual increase of a few pairs of moths but they developed from centres of dispersion or foci created through the landing of a flight of moths. There was always an initial jump rather than a gradual deployment.

THE INDIVIDUAL PARASITES

TACHINIDÆ

Compsilura concinnata Meig.

The species now known as *Compsilura concinnata* was first described by Meigen in 1824 who placed it in the genus *Tachina*. In 1834 Bouché proposed the genus *Compsilura* for this species, which he redescribed as *C. acronyctae*. In its systematic history the fly has only been placed in three genera but it has appeared in literature under twenty-five different specific names. Eighteen of these specific names were bestowed upon the fly by Robineau Desvoidy.

Bezzi and Stein (Kat. Pal. Dipt.) give *Doria* Meig. 1838, and *Machaera* Rond. 1859, as generic synonyms. The following specific synonymy is by the same authors.

Compsilura acronyctæ Bouché	munda Meig.
antiopis R. D.	myioidea R. D.
apricans R. D.	nitens R. D.
ardeacea R. D.	noctuarum R. D.
bombycivora R. D.	pieridis R. D.
cajae R. D.	prorsae R. D.
flavifrons R. D.	pusilla R. D.
flavipennis R. D.	pygœræ R. D.
gracilis R. D.	serriventris Rond.
guerini R. D.	stupida Wulp.
iovora R. D.	taeniata Meig.
meditabunda Meig.	varia R. D.

Description of Adult.

Gray-coloured fly with clear wings. Eyes hairy. Facial ridges bristly on the lower two-thirds. Second abdominal segment with median as well as marginal macrochaetae. The venter of the female abdomen strongly carinate; the female with a curved piercing device for use in larvi-position.

Head at vibrissae shorter than at base of antennae; vibrissae on a level with the oral margin. Palpi yellow. Eyes hairy. Cheeks (genae) white pollinose, covered with black hairs. Sides of face white pollinose; bare; less than half as wide as facial depression. Facial depression white pollinose without a carina. All segments of the antennae black, the third in the female about three and a half times, in the male nearly five times as long as the second. Arista thickened on basal two-fifths; the second segment about as long as broad. Front in male about as wide as either eye; slightly wider in the female; the sides of front white pollinose; orbital bristles present in female and absent in male; frontal vitta dark-brown, opaque, about as wide as either side of front, taking measurements just in front of the ocellar triangle. Ocellar bristles present in both sexes and directed forward.

Thorax gray pollinose on a black ground with four black vittæ standing out clearly. Three sternopleural and four postsutural bristles on each side. Scutellum concolorous with rest of thorax with three pairs of strong marginal bristles and a weak apical pair. Legs black, tarsal claws of male not perceptibly longer than those of female. Wings hyaline, venation as in figure. R $4+5$ (third vein) with three to five little hairs at base. M $1+2$ without an appendage. Tegulae white.

Abdomen gray pollinose on a black ground. The second and third segments with discal as well as marginal macrochaetae. The venter of the female carinate. Female with a long curved piercer for use in larviposition.

This species ranges over the continent of Europe. It is also established on the North American continent where it has been introduced by the United States Bureau of Entomology. It is now well distributed through the New England States and is established in New Brunswick (Tothill and McLaine, Ann. Rep. Ont. Ent. Soc. 1918). There is no doubt that in the course of time the present North American range of the species will be greatly extended.

The species has not become attached to one host or even to a group of related hosts, but will attack a great many different insects. In Europe, it has been reared (Bezzi and Stein 1. c. p. 309) from no less than 57 hosts, most of which are lepidoptera and two of which are hymenoptera. In North America the species has been reared already from no less than 33 hosts (Culver, U.S.D.A. Bull. No. 766, p. 5. 1919), and as the deployment of the species progresses, this list will be greatly lengthened.

Life-history.

The following notes on life-history will apply to Fredericton unless otherwise indicated.

As a rule, mating seems to take place within a day or two after the issuance of the flies. If, however, issuance takes place on a dull, cool day, the flies become inactive as soon as the top of the soil is reached and remain so until better weather conditions obtain. In reproduction experiments carried out by Mr. A. B. Baird and the writer, it was found that mating could be delayed days, and even weeks. Unfertilized females were kept alive up to eleven days, although most of such flies died in about a week. Males that have not mated seem to live much longer than unfertilized females. Many such males were kept alive in captivity for two weeks, and three for over a month. These latter lived for thirty-two, thirty-four and thirty-seven days, respectively.

The act of mating occupies about two hours. In five cases that came under observation in August, 1915, mating took place between 10 a.m. and

1 p.m. The shortest time occupied was an hour and fifty-five minutes while the average was two hours and seven minutes.

The period of gestation is about ten days. In the case of a female fly dissected five days after mating, two ovarion eggs had just entered the uterus. In the case of a fly dissected ten days after copulation, the uterus was found to be replete with fully formed maggots. This fly issued on August 4, mated on the 7th and had maggots ready for deposition on the 17th.

The time usually needed by a female to deposit all her maggots is evidently short. This is indicated by the fact that there is no perceptible difference in the development of maggots at the two ends of the same uterus. One may find a uterus full of maggots, all of which are ready to be deposited at the same time. With favorable conditions, it is probable that larviposition can be accomplished in two or three days. Mr. A. B. Baird watched a female in captivity larvipositing on six successive days, after which the fly died. Wet or cold weather will delay operations indefinitely.

The time spent as a first stage larva is usually a few days but under certain conditions it becomes many months. Fiske (Howard and Fiske, Bur. of Ent. Bull. 91, p. 219) speaks of larvæ that are almost certainly first stage *Compsilura* being dissected from hibernating brown-tail caterpillars. J. Pantel, W. R. Thompson and J. J. Culver, each instance similar cases. I have dissected such larvæ from cabbage worm caterpillars collected in November. In these cases the species was overwintering as a first stage larva.

The number of days normally spent in each of the three larval stages is not known. Fewer days are, however, spent in the second than in the first instar and fewer again in the third. Fiske (l. c. p. 219) has called attention to the fact that the larval development can be completed in as short a period as two weeks.

The insect remains as a pupa for about fifteen days in the summer generations but this period possibly varies according to temperature, as the time given by Fiske (l. c.) is a week "or perhaps a little more". In New Brunswick it seems almost certain that the insect hibernates in the pupal stage. In Massachusetts, Mr. J. J. Culver (l. c. p. 22) has recently shown that *Compsilura* may winter over successfully as a larva in at least six different hosts.

The life-history can be put into tabular form, as follows:

From issuance to mating.........	2 days; or weeks, if weather cool or wet.
In gestation...................	10 days;
In larviposition...............	3 days; or weeks, if weather cool or wet.
In larval stages..............	14 days; first stage of one generation may hibernate.
As pupa......................	15 days; pupa of one generation may hibernate.
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Under favourable conditions, it would thus take about six weeks for a generation to be completed. Fiske came to the conclusion that only four weeks were needed (l. c. p. 219). The difference in the two conclusions can be largely accounted for by the fact that Fiske did not allow enough time for gestation, the duration of which had not been worked out at the time his account was written.

In New Brunswick, *Compsilura* has more than one generation a year, but how many it has is not known. Mr. L. S. McLaine bred out 5 flies from white-marked tussock moth larvæ, the first fly issuing on August 8, and the last on

September 13. Flies of this generation would certainly larviposit in cater-
pillars feeding contemporaneously with those of the fall webworm. First stage
larvæ have, in fact, been dissected from fall webworm caterpillars collected
in September. These maggots probably pupate and the pupæ probably hib-
ernate, though these points have not been demonstrated. Working in the other
direction from Mr. McLaine's flies and allowing forty-four days for a generation,
it would appear that the fly emerging on August 8 was a descendant (granting
good weather) of a pair of flies issuing toward the end of June. As continuously
good weather seldom prevails at this season, it is more likely that the pair of
flies would have issued during the early part of June. In this case they would
have come from hibernating pupæ and there would be two generations a year.
In especially favorable seasons one can readily understand that three generations
would be quite possible.

Habits and Behavior

Like so many other tachinid flies, *Compsilura* is a lover of warmth and sun-
shine. Indeed, the essential activities of mating, feeding and deposition of
young cease entirely on the approach of cold, wet weather.

In captivity, these flies have been kept alive for over a month on granu-
lated white sugar, dry flour, and water supplied by a strip of blotting paper.
On warm days, particularly, they drink a good deal of water and seem to prefer
drinking from damp blotting paper or earth rather than from drops sprayed upon
leaves. This preference is evidently due to a dislike of wetting the feet or
body. In nature they probably obtain most of their drinking water from
leaves dampened by dew, as drinking from a body of water as large as a rain-
drop is evidently fraught with danger.

The solid materials—the sugar and flour of captive flies—are taken up by
being first dissolved by a little bead of shining liquid regurgitated through the
proboscis. Pollen seems to be taken up in the same way, although the evidence
for pollen is not nearly as clear as for sugar. In Nature, honey dew seems to
be a chief source of food. From umbelliferous flowers of almost any species
they gather nectar. In Massachusetts the flies could be taken on such flowers
even in 1910 and 1911 long before they had become abundant.

In captivity, these flies die almost at once unless a high degree of humidity
is maintained. In fact, the unfurling of the wings is seldom achieved properly
except under humid conditions. Under cage conditions, the moisture can be
arranged for by using shallow trays, previously described, in which is kept
a little heap of dampened earth.

It is not easy to secure accurate data on the distance tachinid flies will
travel. In the case of this fly, however, a fortunate observation came to notice.
Within two weeks of liberating the first colony of *Compsilura* at Fredericton,
Mr. A. B. Baird and the writer had occasion to collect some caterpillars three
miles from the point of liberation. From these caterpillars, three first stage
maggots were obtained, thus proving that a fertilized female had flown three
miles.

The fly, as shown by Townsend (1908)) and Pantel (1909) deposits living
maggots subcutaneously The uterus, when fully distended, is a long coiled
tube that functions as an incubator. It has been described in the excellent
account of this fly by Pantel (1. c.) and needs no further description here. It
has also been figured by J. J. Culver.

The reproductive capacity of the species is limited compared with many
other tachinids In the case of a female that came under observation (a fly
that had deposited no maggots) the uterus was found to contain 119 larvæ
ready for deposition. It seems unlikely that the uterus would be filled more
than once; there is need, however, for precise information on this point.

In the fly above mentioned, the little maggots were still within their egg shells, which points to the view that eclosion normally takes place during the act of larviposition. Under special circumstances, eclosion can however be intra uterine. This was shown in the case of a fly that died without depositing her maggots; the maggots came out of their egg shells and broke into the abdominal cavity, where many found their way into the lumen of the alimentary canal.

The egg shells are probably left on the outside of the victimized caterpillars. No success has attended any attempts to search for egg shells within the bodies of such insects.

The act of larviposition has been observed by Mr. A. B. Baird and the writer in a few cases. If suitable caterpillars are placed in a cage with mature flies and the day is bright and warm, the flies usually become interested. The interest centers in the caterpillars which the flies regard with increasing excitement. If a fly is ready for larviposition, she is likely to commence operations almost immediately. She flies swiftly to a larva and stings it, leaving a little maggot in or near the mid-intestine. The whole operation is over in an instant; the caterpillar winces at the insertion of the piercer and the fly settles again on the bottom of the cage to comb her ruffled hairs and attend to her toilet generally. Mr. Baird watched one fly attack several larvæ during the course of an afternoon. In these cases the caterpillars were stung on the back in the second and third thoracic segments. From dissection results, it seems probable that the flies will attack at any point free from hardened chitin, if the hairs are not too thick.

The larvipositing device of this fly has been admirably described and figured by Pantel (1. c.). It consists essentially of a curved piercer and of a larvipositor. The piercer is the conspicuous organ one sees with the unaided eye and the top of it is grooved for the reception of the larvipositor.

The ventral part of the female abdomen is very strikingly carinate, and it seems probable that the curious shape has been developed in attacking hairy caterpillars. One can see that a wedge-shaped abdomen would fit down between the hairs of a caterpillar, whereas the more generalized, gently curved, abdomen would not.

There are backwardly directed spines on the lowest part of each segment. These groups of spines evidently enable the fly to secure the necessary purchase for inserting the piercer. Were it not for the wedge shape of the abdomen, these spines could not be brought into play for attacking hairy or pilose larvæ.

The first stage larvæ have never been found elsewhere than between the peritrophic membrane and the cellular wall of the mid-intestine and this relatively restricted part of the host is their feeding ground.

The larva resembles very closely that of *Lydella hyphantriæ*. The resemblance, is in fact, so close that the figure of *Lydella* (fig. 13 and 14) would serve as well for illustrating *Compsilura*. It is a white maggot, the integument of which is only sparingly supplied with spinules. On the caudal end are three hooklets arranged as in *Lydella*. (fig. 10).

The anal hooks are arranged like little grappling irons or anchors. Two of them have only one claw and the larger one has two claws. It seems clear that the function of these hooks is to enable the maggot to anchor itself so as to feed to better advantage. The last two segments are narrowed down and provided with a complete band of spinules and both of these features would help to make anchorage more secure. On the ventral part are five ambulatory areas, each roughened by little spinules and apparently arranged almost exactly as in *Lydella*. The first two segments are roughened by bands of spinules that evidently help the larva to migrate from one part of its feeding ground to another. On what seems to be the first segment are two little papillæ, as in *Lydella*; they probably have to do with the sense of taste.

As to the shape of the larva, I have been unable to establish either a dorsoventral flattening or a tendency to conform to the shape of the letter S. In order to demonstrate these things it is necessary either to examine living material or to kill the material in some way that will not cause it to become distorted or to shrink. My *Compsilura* material is, however, all alcoholic and in consequence not sufficiently good for the purpose.

The figure given by Fiske and Howard in their invaluable account of gypsy and brown-tail moth parasites (U.S. Bur. of Ent. Bull. 91, p. 265) is evidently from a specimen preserved in alcohol and both extremities have become invaginated toward the centre of the maggot.

The problem of breathing is evidently simple enough in the first stage larva. In this stage the spiracles seem to be closed over, as they are in many other aquatic larvæ, and breathing is accomplished by diffusion of oxygen through the skin or through the wall of the alimentary canal.

In the second stage, however, a large amount of oxygen is necessary and the maggot secures it by placing its posterior spiracles in the lumen of one of the tracheæ of its host. No particular set of tracheæ seem to be chosen as the maggots have been found attached to tracheæ in many different parts of the host.

Just how the tracheæ are entered is not known. It seems probable that a maggot enters head first and then passes partly out again, coming to rest with the posterior spiracles in the lumen of the trachea.

In an attempt to close over the wound, the tissues of the trachea grow around the larva and form a funnel, which makes a convenient home for the parasite. The base of the funnel becomes hardened and the distal part becomes a loose sleeve or sac. In structure this tracheal funnel is essentially similar to that of the integumental type illustrated in the case of *Ernestia ampelus*. In each case the basal part, or funnel proper, is an invagination of the ectoderm, and consists of an inner chitinous layer; a median hypodermal layer and an outer basement membrane. As the funnel grows, its histological structure becomes obscured on account of the fact that moult skins become pressed into the inner chitinous layer; and because fat cells and phagocytes of the host adhere to the basement membrane. The distal part of the structure, the sleeve or "sac-like layer" of Nielsen (1909 Ent. Med. 2, R. 4), has been shown by Nielsen and Pantel to consist essentially in its later stages, at least, of adipose tissue derived from the fat cells of the host.

The larva remains in its funnel until it reaches the destructive feeding stage just prior to pupation. At this stage the caterpillar is partially filled with air, and the parasite is able to secure air through both anterior and posterior spiracles without the aid of a funnel or other special device.

The problem of feeding is met in the same way as in *Lydella hyphantriœ*. The first stage larva lives and feeds between the peritrophic membrane and the epithelial layer of the mid-intestine. It seems probable that the maggot anchors by its caudal end to the epithelial layer and takes up liquid foods as they pass through the peritrophic membrane. If it anchored to the peritrophic membrane, as Pantel seems to imply, there would be danger of its passing out of the alimentary canal with the undigested food materials.

The maggot meets the problem of preserving its food supply by not voiding waste materials until just prior to emerging from the destroyed host. The fact that destructive feeding is delayed until almost the end of the larval feeding period is also of the greatest benefit in meeting the same problem. The first stage larva feeds upon juices in the mid-intestine and does not seem to inconvenience the host at all. The second stage larva feeds upon liquids that it takes up from the general body cavity; as shown by Pantel, the liquids taken up in this stage may also include tiny blood and fat cells floating therein; the second stage larva does not appear to inconvenience the host at all. The third

stage larva destroys muscular and fatty tissue and often the mid-intestine; the work of feeding is so rapid in this stage that the entire carcass is consumed before decomposition has had time to set in.

Occasionally a *Compsilura* maggot will pupate in the skin of the larva it has destroyed. The great majority, however, go to earth to pupate. In this case the maggot drops to the ground and travels until suitable conditions are found for digging in.

From an experiment carried out by Mr. Baird and the writer, it seems that under favourable conditions few flies emerge successfully from pupæ that are more than 10 or 11 inches below the surface. This indicates that the maggots rarely descend farther than a foot before pupating. In the experiment 150 pupæ were planted at different depths; 10 at 4 inches below the surface; 10 at 5 inches; 10 at 6 inches, and so on, the last 10 being planted at 18 inches below the surface. The soil used was a fine garden loam put through a quarter-inch screen; it was thoroughly dampened but not wetted and was firmed down over the pupæ but not packed. Seventy-five per cent of the flies reached the surface from the eight lots of pupæ planted from 4 to 11 inches below the surface, the remaining 26 per cent being lost in transit. From the seven lots of pupæ planted respectively from 12 to 18 inches below ground level, only 20 per cent succeeded in reaching the light of day, the remaining 80 per cent being lost in transit. Three flies actually worked their way up through 18 inches of soil.

When a maggot has achieved its descent into the soil, it changes its course and comes to rest for pupation in an oblique position, with the cephalic end directed towards the surface of the soil. This curious habit was first pointed out by W. R. Thompson, who says (Jour. Ec. Ent., Vol. III, June, 1910, p. 286) " In the experiment with the larvæ of *Blepharipa* (*scutellata*) it was noted that the larvæ which were placed upon earth, after descending for a few inches, turned about and proceeded to pupate with the anterior end directed upward. This position of the puparium has been observed at the laboratory (gipsy moth) in connection with other tachinids, and also with muscids and sarcophagids, and is very probably the usual mode of pupation among those species of calyptrate muscids which form their puparia in the soil."

The phenomenon has also been observed at this laboratory (Fredericton) for several species of tachinids and for the three species of *Lucilia* that range into the boreal zone.

The significance of the habit becomes clear when one observes the manner in which the adult fly steers itself through a number of inches of solid earth. The fact of the matter is that the adult *Compsilura* when making this journey cannot steer at all, but can only travel straight ahead; and the harder the soil is packed the straighter is the course travelled by the fly. The matter was tested out by planting a number of pupæ in earth with the cephalic end directed downwards. The bottom of the cage used was fitted with wire screening, so that any flies attempting to emerge by way of the Antipodes would be intercepted. In every case the flies came out through the bottom of the cage. In another little experiment, 12 pupæ were planted in a horizontal position. In each case the emerging fly took a horizontal course until it reached the side of the box. After coming to the side of the box the course was changed and in five cases the flies emerged through the top of the box and in seven cases through the bottom.*

These experiments seem to show that unless the maggot comes to rest for pupation with the head directed upward, it is impossible for the resulting fly to reach the light of day.

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* It seems possible that the flies which happened to be travelling on their back went downward after encountering the side of the box, and that the ones travelling right side up went upward. The point needs verification.

A. LYDELLA HYPHANTRIAE. Adult female drawn from a paratype.

B. ERNESTIA AMPELUS. Adult female.

As is shown in the case of *Ernestia ampelus* (p. 58), there is considerable evidence in support of the view that this interesting habit of tachinid larvæ is correlated with the development of the so-called macrochaetae; and that the macrochaetae serve primarily to direct the course of the fly in its dark journey from the pupal case to the surface of the soil.

Lydella hyphantriæ sp. n.

SYSTEMATIC HISTORY

The genus *Lydella* was proposed by Robineau Desvoidy in 1830. The following generic synonymy is given by Bezzi and Stein in the Katalog der Palaarctischen Dipteren:—

Lydella 1830.

Anetia R.–D..............................	1863
Aporotachina Meade........................	1894
Blondelia R.–D............................	1830
Cyrillia R.–D.............................	1863
Dexodes B.B..............................	1889
Gervasia R.–D............................	1863
Picconia R.–D............................	1863

The only reason for using *Lydella* instead of *Blondelia* is that the former has page priority over the latter. Bezzi and Stein (l.c.) place the species *nigripes* Fall. in the subgenus *Lydella*, and as the British Columbia species is closely related to Fallen's, it would fall in the same subgenus. The full name of the British Columbia species would then be *Lydella Lydella hyphantriæ*. The specific name is chosen for the sake of associating the fly with its only known host, *Hyphantriæ cunea*.

DESCRIPTION OF ADULT (Plate IV, fig. A).

Gray fly with clear wings. Eyes bare. Facial ridges bristly only on lower fifth. The female with a piercer like that of *Compsilura*, and with a well-marked ventral abdominal keel. (Plate III, figs. C and D.)

Head at vibrissæ shorter than at base of antennæ; vibrissæ on a level with the oral margin. Palpi yellow. Eyes bare. Cheeks (genæ), white pollinose and covered with black hairs. Sides of face golden pollinose, bare, about a fourth as wide as the facial depression. Facial ridges bristly on lower fifth. Facial depression golden pollinose with a shallow and not very conspicuous median carina. All segments of the antenna black, the basal one, however, tinged with rufous; the third segment in both sexes two and a half to three times as long as the second. Arista thickened on basal two fifths, the second segment as long as broad. The front in male about one-half, in female about three-fourths, as wide as either eye; the sides of front golden pollinose above the antennae, blending to black at the vertex; orbital bristles present in female, absent in male; frontal vitta dark-brown, opaque, and slightly wider than either side of front at narrowest place. Ocellar bristles present in both sexes and directed forward.

Thorax gray, subshining, thinly white pollinose. Three sternopleural bristles and three postsuturals. Scutellum concolorous with rest of thorax; with three strong pairs of marginal macrochaetæ and a weak apical cruciate pair. Legs black, the tarsal claws a little longer in the male than in the female; middle tibiæ with several bristles on the front side near the middle. Wings clear, the venation as in figure. R 4+5 (third vein) with about three little hairs at the base. M 1+2 (fourth vein) destitute of an appendage. Tegulæ white.

Fig. 9. *Lydella hyphantriæ;* first stage larva; lateral view showing typical position with head down and end bent upwards; also shows the five spinulated ambulatory areas.

Fig. 10. *Lydella hyphantriæ;* first stage larva showing in caudal view the anal hooks and the spinulated areas that enable it to anchor or attach for feeding.

Fig. 11. *Lydella hyphantriæ:* first stage larva, ventral view, showing the ambulatory areas roughened by spinules.

Fig. 12. *Lydella hyphantriæ:* diagram showing probable method of feeding of first stage larva. The caudal end of larva is anchored in the epithelial layer, and the larva is feeding on the liquid food materials passing through the peritrophic membrane.

Fig. 13. *Lydella hyphantriæ:* second stage larva. Dorsal view, showing distribution of ambulatory spines.

Fig. 14. *Lydella hyphantriæ:* second stage larva, showing distribution of ambulatory spines.

Fig. 15. *Lydella hyphantriæ:* second stage larva, dissected from *Hyphantria* pupa sent from Agassiz, B.C., March 1, 1918. It was embedded in a cyst attached to the mid-intestine of the host.

Fig. 16. *Ernestia ampelus* Walk: outline view of abdomen of male, showing the large proportions of the genitalia.

Fig. 17. *Ernestia ampelus* Walk: male genitalia. Note the large accessory plate (shown on the right), also the fused internal pair of forceps shown in two views at each end of the dotted line.

Fig. 18. *Ernestia ampelus* Walk: mouth hooks of first stage larva. In this stage they consist of a single sclerite.

Fig. 19. *Ernestia ampelus* Walk: A. first stage larva, showing the dorsal armature of imbricated scales; B. a few of the scales and three sensory pits from a larva ready to moult to 2nd stage; the larva has become distended by feeding so that the scales are no longer imbricated.

Fig. 20. *Ernestia ampelus* Walk: A. second stage larva removed from its funnel, the last segment is modified for being anchored in an integumental funnel; B. anal spiracles.

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5th sternite

Epithelium

Peritrophic membrane

Fore intestine

Hind intestine

5th sternite

A

B

A

B
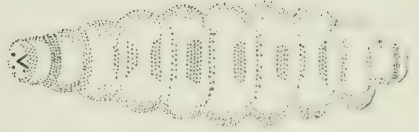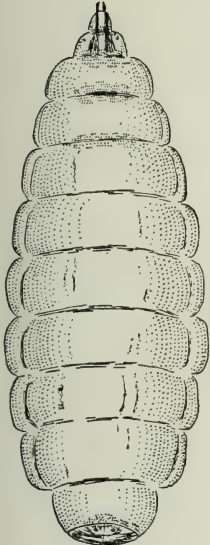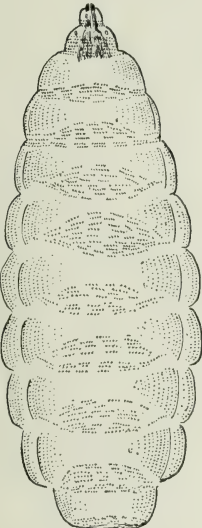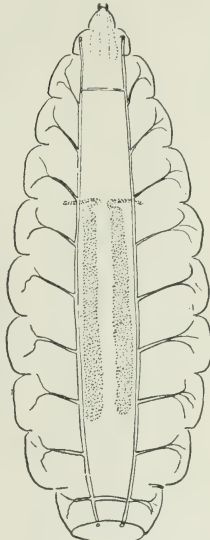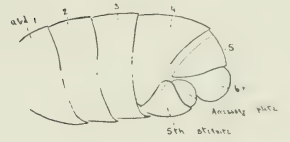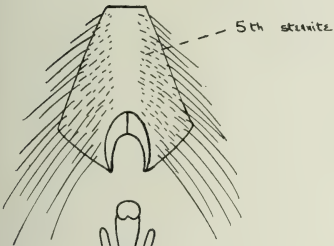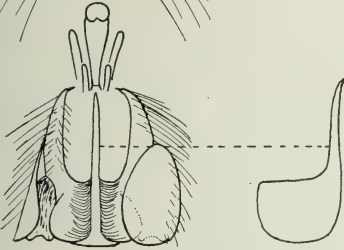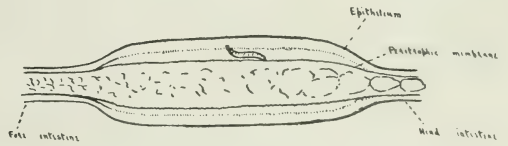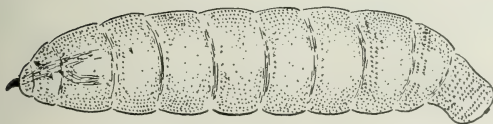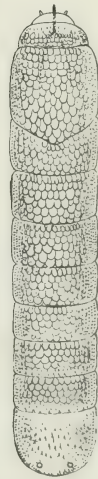
Abdomen gray, opaque, white pollinose. Second and third segments with strong discal as well as marginal bristles. The venter of the female strongly carinate; this sex with a conspicuous curved piercer (plate III, fig. C) closely resembling that of *Compsilura concinnata* Meig.

Described from one female (the type) and three paratypes of which two are males. All reared from *Hyphantria* collected at Agassiz, B.C., except one which was taken with a net at the same place.

The type and two paratypes deposited in the Canadian National Collection, Ottawa, and a partaype in the U. S. National Museum, Washington, D.C.

The larvæ of this fly have been dissected from caterpillars collected at Hammond and Agassiz in the wet coast belt of British Columbia and at Vernon in the dry belt. For the latter, I am indebted to the courtesy of Mr. Max H. Ruhmann. So far as known, the species does not occur east of the Rocky Mountains.

The only host known for the species is *Hyphantria cunea* Drury.

The fly is one of the compsilurine series, the abdomen being remarkably like that of *Compsilura concinnata* Meig. and the head characters being strongly suggestive of *Lydella nigripes* Fall. Mr. Townsend has described a Peruvian species, *meridionalis* (Proc. U.S. Nat. Mus., Vol. 43, 1912), that must be very closely related to the British Columbia species, but which, for geographical reasons, is probably distinct. I have not seen *meridionalis* Tn.

Descriptions of Early Stages

First stage larva.

The first stage larva closely resembles that of *Compsilura concinnata*. It is white in colour, and the integument is provided with spinules only in a few special areas, as shown in the figures. The first two segments are provided with complete rings of spinules. The third and fourth segments have scattered spinules on the ventral surface only. The next five segments each has its ventral area modified into a false foot (fig. 9). This is simply an elevated area provided with spinules. The anal region is narrowed down and provided with a band of spinules. These serve to anchor the larva in position for feeding. In caudal view can be seen three little hooks (fig. 10) that also serve for anchoring the larva. In shape, the larva is rather unusual, in that the anal end is elevated and the cephalic end depressed; it is also slightly flattened dorsoventrally. The modified form is, of course, to be associated with the peculiar feeding habit.

Second stage larva

Figures 13, 14 and 15 show the main features of the second stage larva. Ambulatory spines are present on both dorsum and venter in bands between the first four segments; a ring of spines is also present at the extreme caudal end of the larva; the spines reach a maximum development, however, on the venter where each patch forms a clinging foot. In walking, these patches of spines invaginate so that each makes a most efficient false foot for walking over animal tissues. In conjunction with the mouth hooks these false feet make ambulation relatively easy.

In the living larvæ examined, only 11 segments could be distinguished whereas in the house fly larva, 12 can be seen. The lost segment is between the first thoracic segment (the one carrying the anterior spiracles) and the last abdominal one. In the house fly larva the posterior spiracles are supposed to be on the eighth abdominal segment whereas in this case they "seem" to be on the seventh (Weismann '64).

The tracheal system is elaborately developed and, in the living larva, is filled with air. The two long white bodies shown in figure 16 are very conspicuous features of the living larva and probably represent the fat body, although

I have not verified this by sectioning. The alimentary canal is long and is folded upon itself many times, thus being in marked contrast to the condition met with in *Campoplex, Apanteles, Rogas*, etc.

The larva is white and transparent to such an extent that the heart beat can be easily taken (two counts gave 66 and 68 beats per minute, respectively).

The larvæ examined were all obtained from *Hyphantria* pupæ collected at Agassiz, B.C., on March 1. They were embedded in a cyst attached to the mid-intestine. All were about 3 mm. in length.

Life-history

The life-history of this species is only incompletely known, but the following notes will serve to indicate the main features.

Larviposition takes place when the webworm caterpillars are in the third to last stages. As it only takes place on fine days, larviposition begins on different dates in different localities. In 1917 it was found by dissection of host caterpillars that it began about August 22 at Hammond and Agassiz; two places subjected to very similar weather conditions. At Vernon, in the dry belt, a few maggots were deposited before August 13.

In the same year and at the same places, larviposition extended over a period of two or three weeks. At Agassiz and Hammond it extended approximately from August 22 to September 5. At Vernon it extended approximately from August 12 to September 4.

It is uncertain whether the insect hibernates as a first or second stage larva. From pupæ of *Hyphantria* dissected in March, some second stage larvæ were found. This probably indicates that the parasite hibernates as a second stage larva.

Molting to third stage probably takes place in early summer but no maggots of this stage have been seen.

The few adults reared all came out during the first two weeks of July and as larviposition on webworms begins about the middle of August, it seems that there can be only one generation a year.

Habits and Behavior

The weather exerts a very powerful influence on the adult flies as it does indeed on all tachinidæ with which I have a field acquaintance. Larvæ are not deposited when it is raining or when it is uncomfortably cool, or when there is a strong wind blowing. Larviposition will occur, however, on still dull days that are warm.

It seems likely that the other essential activities, such as feeding and mating, are also held in abeyance during unfavourable weather.

At Agassiz, an opportunity was afforded one day of watching a female fly that had been depositing larvæ. She was on an alder leaf near a webworm nest and was evidently interested in the caterpillars. A few of the caterpillars were feeding away from the silken web and it was these the fly seemed to be watching. When a larva crawled a few inches, the fly would become excited and walk around her leaf or fly to another. It was quite evident that the fly intended to attack the caterpillars and that the fly was not *Ernestia ampelus* or any other eastern parasite of this host. First of all, the desire to watch the attack was stronger than the one to capture the fly, but as the minutes passed and still the fly would only play with the caterpillars, the writer's patience became exhausted and the fly was captured.

It was seen immediately that she had a long curved piercing device (plate III, fig. C) like that of *Comps lura concinnata* and that the method of attack would have been subcutaneous.

The stray caterpillars around the web were gathered up and it was found by dissection that the fly had deposited a little maggot in almost every one.

Some data on the method of existence of the first stage larva were obtained from dissections of parasitized caterpillars. The total number of maggots obtained was 90. They were all found in the mid-intestine between the peritrophic membrane and the wall proper, so that this relatively restricted location is their normal feeding ground (vide fig. 12).

An examination of a maggot shows some interesting modifications fitting it for gaining a livelihood in such an environment. In the first place, the maggot is slightly S shaped instead of straight as in more generalized maggots (vide fig. 9). The anal end is bent up and the cephalic end bent down. The bending up of the anal end enables the maggot to attach itself caudally to the wall of the intestine; while the bending down of the cephalic end would enable the larva to feed at the level of the peritrophic membrane where liquid food materials are usually available.

The caudal end, moreover, is somewhat contracted and is fitted with spinules and hooks for securing anchorage. The spinules form a broad band at the junction of the last two abdominal segments (vide fig. 9). The last two segments of the larva are often buried in the soft tissues of the intestinal wall and seem to be anchored fairly firmly by the spinulated area and the anal hooks. If the maggots could not anchor in this way, it seems likely that they would be in danger of passing out through the hind intestine, especially when the mid-intestine was empty, as it frequently is in cold weather and at molting time.

The five prominent ambulatory ridges on the ventral surface are thickly set with spinules (figs. 9 and 11). These indicate, of course, that the maggot can travel from one part of its feeding ground to another. The slight dorso-ventral flattening would contribute considerably to the comfort of the larva if the intestine of its host became distended with food so as to press the larva against the intestinal wall.

On these maggots there are two very well marked little elevations just in front of the mouth hook. They are evidently sensory in function and their position seems to indicate that they may serve to guide the maggot to its food.

The question of how the maggots first get into the limited area between the peritrophic membrane and epithelial wall has not been answered for any of the *Compsilura* series. All recent writers agree, however, that the larvæ are placed in or near this area by means of the piercing device of the female parent. In the case of *Lydella*, the 90 maggots found were, without exception, in this localized area. As the host larvæ were killed in scalding water and the parasites all killed suddenly, this seems to indicate that there is usually no migration and that the female actually places each maggot in the feeding area. The piercer of the fly is also of such a length that if buried to the hilt in a caterpillar anywhere between the first two and last two segments, its tip would usually come to rest in the feeding ground. The question cannot, however, be regarded as settled.

This fragmentary account of the feeding habits of the first stage larva does not agree in one respect with Pantel's account for *Compsilura*.

Pantel sectioned the mid-intestine of a host from which he had dissected out a maggot and found epithelial cells distorted (Pantel l. c. 1909, figs. 58, 59, 60 and 61) as he supposed from the feeding operations of the parasite; in the case of *Lydella*, the maggot seems to feed not in the epithelial layer but at the level of the peritrophic membrane. It seems possible that the distorted cells seen by Pantel were due not to the feeding of the maggot but to its being anchored from its caudal end at that place. This point can only be verified by some one who is fortunate enough to section a maggot in situ.

Ernestia ampelus Walk.

The tachinid parasite, *Ernestia ampelus*, was described from Nova Scotia in 1849 as a *Tachina*. In 1830, however, Robineau Desvoidy had proposed the genus *Ernestia* for the reception of Fabricius' congeneric species, *radicum*, so that it should properly have been described as *Ernestia ampelus*. In 1907, Bezzi and Stein (Kat. Pal. Dipt. Vol. III, p. 210) divided the genus *Ernestia* into four subgenera, *Ernestia, Eurythia, Parerigone* and *Panzeria*, placing *radicum* Fab. in the typical subgenus *Ernestia*. As shown in the author's revision of the nearctic species in this genus (Can. Ent. 1922), *ampelus* is structurally distinct from *radicum*, with which it has been confused for many years.

The following generic synonymy is given by Bezzi and Stein (l.c. p. 210). *Ernestia* R. D. Myod. 60, 11, (1830). *Erigone* R. D. Myod. 65, VI. (1830) nec. Sav. Aracnid. *Fausta* R. D. Myod. 62, IV. (1830). *Mericia* R. D. Myod. 64, V. (1830). *Olbya* R. D. Posth. 1. 170. VI. (1863). *Platychira* Rond. Dipt. ital. Prodr. 1. 64. 15. (1856) et 111. 74. 15. (1859). *Varichœta* Speiser. Berlin. entom. Zeit. XLVIII. 69. 3. (1903).

DESCRIPTION OF ADULT.

The adult (plate IV, fig. B) has been redescribed in the above-mentioned revision (Tothill, Can. Ent., 1922).

RANGE.

The species ranges over the North American continent. I have specimens from Massachusetts, Nova Scotia, New Brunswick, Quebec, Ontario and British Columbia, where it is abundant both in the coast belt and dry interior.

HOSTS.

So far as known, the species has been bred only from *Hyphantria cunea* and *Datana ministra*.

DESCRIPTIONS OF EARLY STAGES.

First stage larva

In shape, elongate, cylindrical, truncate at the anal end and tapering somewhat at the anterior end. In length, ranging from 5 to 6 mm. when nearly hatched, to 1 or 2 mm. when ready to molt. Colour black.

The pharyngeal skeleton (fig. 18) consists of an unjointed chitinous structure that bifurcates posteriorly.

In this stage there are no anterior spiracles. There are two posterior spiracles which appear as tiny dark-coloured knobs.

There are eleven visible segments, the shape and relative size of which are shown in the figure.

The most striking thing about the larva (fig. 19) is the armature of imbricated dark-coloured scales that give it, under magnification, something the appearance of a snake. This armature extends over the back and sides from the second to tenth segments, inclusive. On the tenth and especially the eleventh segments, are a series of forwardly directed spines (*vide figure*); and on the venter are a series of ambulatory elevations bearing little spinules.

Second stage larva (fig. 20)

Very difficult to distinguish from many other second stage tachinid larvæ. It always occurs, however, in an integumental funnel. It is a colorless grub, fitted essentially for the one purpose of feeding. In size it ranges from 1 mm. to 5 mm. in length, depending upon the age.

Fig.. 21. *Ernestia ampelus* Walk: mouth hooks of second stage larva. They consist of two portions separated by a joint.

Fig. 22. *Ernestia ampelus* Walk: A. third stage larva; the last segment still somewhat modified in shape for fitting into the funnel; B. anterior spiracle; C. the place of invagination of the hind intestine; this shows in surface view as a slightly elevated pad near the base of the last segment on the ventral side; D. the posterior spiracles.

Fig. 23. *Ernestia ampelus* Walk; third stage mouth hooks ; they are composed of three distinct segments.

Fig. 24. *Ernestia ampelus* Walk: Second stage larva. Three sections showing the invagination of an anterior spiracle and the closing of the trachea leading from it. A. The opening of the trachea. The lumen is hollow and the hypodermal cells are small. B. Cut a few sections behind A. The lumen still hollow; some of the hypodermal cells becoming large and active. C. Cut ten sections behind A. The lumen closed but only a small part of it filled with chitin. Mostly filled with material that is evidently composed of broken down hypodermal cells. Note the large hypodermal cells, the nuclear figures in which indicate great activity.

Fig. 25. *Ernestia ampelus* Walk. A second stage larva in situ suspended into the body of a webworm larva. Six of the longitudinal muscle strands are shown, also some of the fat body. Note the integumental funnel at the anal end of the larva. Also note the first stage mouth hook that has molted off and passsd down toward the funnel.

Fig. 26. *Ernestia ampelus* Walk. Cross section of first stage maggot and its integumental funnel cut close to caudal end. Shows the invagination of the hind intestine, which at this stage is connected with the mid-intestine. The lumen of the canal is open at the anal end. The funnel consists of an interior chitinous layer and an exterior hypodermal layer, both invaginated around the larva by its host. The basement membrane cannot be distinguished. Cu=larval cuticle ; h=larval hypodermis ; l=lumen of hind intestine ; s.t.=tracheid ; c.=host cuticle ; h.h. host hypodermis ; t=tracheal trunks.

Fig. 27. *Ernestia ampelus* Walk. Cross section of a first stage larva in its funnel taken through the brain. Even as far forward as this the funnel is clearly integumental in structure. The funnel is not more than a few days old and shows as yet none of the fat cells characteristic of the sleeve or distal portion of older funnels. The salivary glands are filled with digestive fluid and are clearly in a condition of great activity. h=hypodermis of host caterpillar; c=cuticle of host caterpillar; cu=cuticle of parasite bearing scales; h.p.= hypodermis of parasite; p.=scales, one flattened down, the other standing out from skin and showing method of attachment: f.i.= fore intestine passing through the brain; s.g.= one of the two salivary glands, the lumen filled with saliva. It is clearly a very active gland and its secretion is perhaps the most important digestive fluid manufactured by the larva.

Fig. 28. *Ernestia ampelus* Walk. Section through the oesophageal valve of a 2nd stage larva. The funnel, even at the distal part of the sleeve here shown, consists of an outer hypodermal layer and an inner chitinous layer. The inner chitinous layer has the first stage molt skin pressed against it, as shown by the little scales. The fore intestine is cut through the oesophageal valve, which is so constructed as to prevent food materials passing from the mid to the fore intestine. The valve is arranged as in the house-fly larva, the end of the fore intestine being pushed into the lumen of the mid intestine. The outer ring has no chitinous intima and is part of the mid-intestine; the inner tube is lined with chitin and constitutes the end of the fore intestine. The narrow end of the mid-intestine is shown at m.i. Ten microns further forward in the larva it connects with the oesophageal valve. The size of the silk gland reservoirs and the large amount of finely granular secretion in them indicates the importance of these glands in the work of digestion; h=hypodermis of host caterpillar forming outer layer of funnel; c=cuticle of host caterpillar forming lining of funnel; p=scales of first stage moult skin pressed into cuticular lining of funnel; tr=one of the two main tracheæ; oe=an oenocyte; br=hind part of brain; f.i.=fore intestine cut through the oesophageal valve; s.g.=reservoir of one of the two silk glands filled with finely granular secretion; m.i.=mid intestine; it unites with the fore intestine one section (7 mm.) ahead of the one here shown.
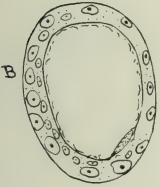
Fig. 29. *Campoplex pilosulus* Prov. An egg that was taken from a fall webworm larva; it was blackened and contained no developed embryo. The egg, which is strongly kidney-shaped in one view was attached to a fold of a silk gland.
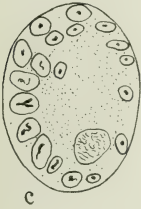
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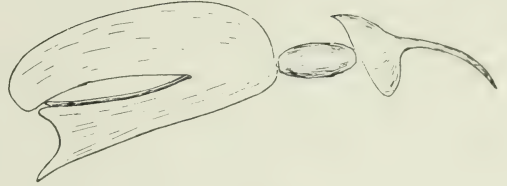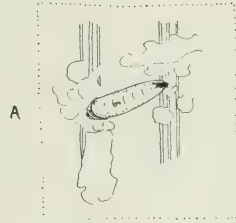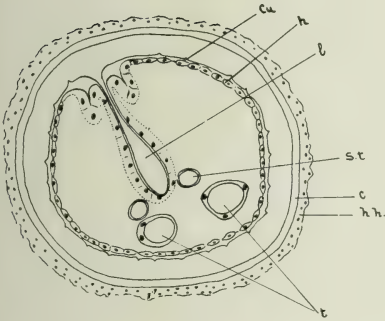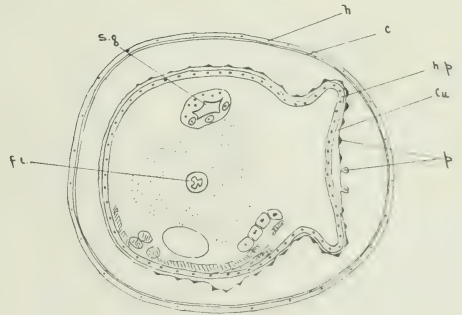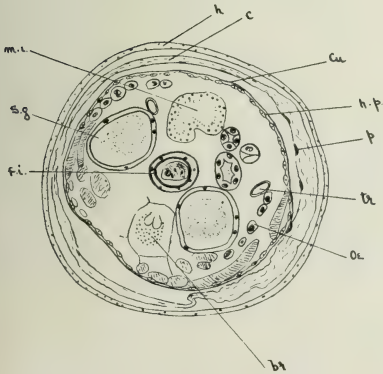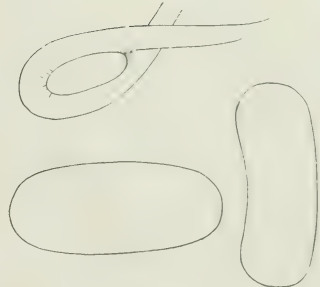23

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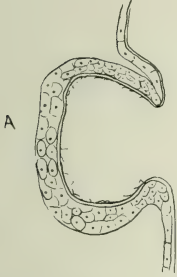
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The pharyngeal skeleton (fig. 21) shows considerably more differentiation than does that of the first stage. It is divided longitudinally almost throughout its entire length and is bilaterally symmetrical. It is divided transversely into two portions that articulate by a close fitting joint; the anterior portion consists of the two hooks characteristic for most dipterous larvæ; the posterior portion consists of a supporting framework to which are attached the muscles that control the hooks.

Anterior spiracles are present in this stage and are situated between segments two and three. The chitinized framework surrounding them consists of a short tube about one and one-half times as long as broad and with only one apparent opening. The posterior stigmata have now taken on a more differentiated form, each having two breathing pores which together with the peritremes are slightly chitinized.

The body armature is totally different from that of stage one. The lamellate scales have entirely disappeared and are replaced by inconspicuous bands of lanceolate spinules. The first segment is bare; the second has a complete band of backwardly pointed spinules; the third to eighth each possess a very few spinules that are collected into irregular bands at the segment margins and that seem to point in all directions; on the last three segments the spinules become smaller and more numerous and nearly all of them point forward.

Third stage larva (fig. 22).

In shape, similar to the preceding stage. The length is subject to great variation, depending on the individual and upon its age, but most of the variations fall within a range of from 3 mm. to 10 mm.

The larva is colourless.

The pharyngeal skeleton (fig. 23) is built on the same general plan as that of the second stage larva. An essential difference is, however, that it is divided transversely into three distinct segments articulating by true joints. The extra segment occupies a median position between the hooks and the large posterior expanding portion.

Anterior spiracles are present but are very different from those of the second stage in that the chitinous framework of each consists of a small, yellow, convex elevation perforated by a considerable number of pores.

The posterior spiracles consist of two stigmata each traversed by three converging nearly straight breathing pores.

The armature is much like that of the second stage. It consists of more or less irregular transverse bands of pointed spinules. (On the anterior end most of the spinules point backward and on the posterior end most of them point forward.) Between these extremes are bands, the rather scattered spinules of which point in various directions without conforming to any apparent system. The spinules, as a whole, are somewhat more numerous in the third stage than in the second.

Puparium

The puparium conforms to the general tachinid type. It is a highly chitinized shell with rounded ends, ranging in colour from reddish-brown to black. Under a lens it presents an unusually silky appearance. The anterior spiracles are inconspicuous and are situated on the extreme anterior end on the median axis. The posterior spiracles are situated on the extreme posterior end just dorsad of the median axis; morphologically, they are similar to those of the third stage larva.

Life-history

The following account of the life-history of *Ernestia* is based upon conditions at Fredericton, N.B., unless otherwise indicated.

The species winters over as a pupa and as it pupates towards the middle of September and as the flies do not usually emerge until the middle of June, it actually spends nine months out of the twelve in a non-feeding and mostly dormant condition. The adults are formed within the puparia before winter sets in.

When the snows have gone and the first foot of surface soil has become warm and relatively dry, the flies begin to emerge. At Fredericton, this seldom occurs until the latter part of May, and in the woods where the snows take longer to melt, it seems probable that most of the flies do not emerge until the middle of June. Flies, whose puparia happen to be in sandy soil—receiving a maximum amount of sunshine—will emerge sometimes weeks before those whose puparia lie in cold clay beneath the heavy shade of conifers like spruce and balsam.

The emergence is also more irregular in some seasons than others, owing to weather conditions, If the month of May is uniformly warm, the emergence period is short. If, however, just after the flies have emerged from favoured spots the warm weather is followed by cold, the emergence of flies from colder situations is delayed for the duration of the cold weather.

With a net, it is seldom possible to collect these flies until June is well advanced and July is the better month for them.

Mating may take place soon after the flies issue. In one case observed the flies were two days old and in two other cases in reproduction experiments, although the flies were not seen in copula, it was known that mating took place before the flies were three days old. The time occupied in mating has been noted in a very few instances and in these it varied from 15 minutes to an hour. The flies seem to remain in copula longer on cool days than on warm ones.

The period of gestation, namely; from the time of fertilization to that of depositing the little maggots, occupies from two to four weeks. In the case of six flies under observation, the period varied from 13 to 30 days; the time consumed in each case being 13, 15, 23, 24, 25 and 30 days, respectively.

With the period of gestation concluded and with weather conditions favourable, the flies begin their task of depositing offspring in the form of tiny black maggots. How long it takes for the full complement of maggots to be deposited is not known, but it seems probable that the uterus can be emptied in one or two days. At the beginning of larviposition the distended posterior chamber of the uterus is packed with maggots ready for deposition. There is, apparently, little or no difference in the development of the maggots throughout the length of the chamber. Under field conditions, when a couple of warm, sunny days followed nearly three weeks of cool, wet weather, I have seen hundreds of dozens of these little larvæ suddenly appear on the foilage near fall webworm nests. That the uterus is not always emptied as soon as it contains mature larvæ is indicated by the fact that larviposition only takes place on warm days when there is no rain. From these considerations it seems probable that larviposition may sometimes be completed in two days, or again, may not be finished for a month.

The parasites do not gain entrance to their host immediately but have to wait for a host to cross their path. A number of maggots under observation were kept alive in the free living condition on twigs for ten days; some died on the seventh day and all were dead on the eleventh.

Once in its host, the larva feeds for at least a week before molting to second stage. On August 5, some webworm caterpillars were isolated so as to be immune from further attack by parasites. Seven days later a living first stage maggot was dissected from one of these caterpillars. By other dissections it was ascertained that the larvæ molt to second stage after 7 to 10 days spent in the interior of their host.

The length of time spent in the second stage seems to be about 12 days. On August 15 a number of maggots, just molted into the second stage, were dissected from webworm larvæ. Twelve days later further dissections were made from the same web, revealing a number of *Ernestia* maggots about to molt, and one just molted, to the third stage.

The time spent in the third stage is a little less than that in either of the other larval stages, being usually from five to seven days.

Pupation takes place during the middle two weeks of September. In the case of 23 individuals, the larval issuance and pupation of which was watched in 1913, the first larva came out of its host on September 3 and the last on the 27th of the same month; most of them, however, came out between the 11th and 20th.

Resumé of Life Cycle

Issuance of adult to fertilization	2	Days;	or weeks, if cool wet weather prevails.
Fertilization to larviposition	21	"	or weeks, if cool, wet weather prevails.
In maggot stage.			
First stage.			
On twigs, etc	5	"	approximately.
In host	9	"	"
Second stage	12	"	"
Third stage	5	"	"
In pupal stage	270	"	"

From this statement it appears that there is only one generation a year at Fredericton. There is evidence for supposing, however, that under unusually favourable conditions a partial second generation may occur. In some years there is a partial fall emergence in the autumn from the pupæ that usually overwinter, and it seems at least possible that a few of the more precocious of these flies may, under favourable weather conditions, complete a second generation before the coming of winter.

There is evidence for supposing, also, that the main generation is double brooded in character. In other words, that there is an early brood attacking July caterpillars, such as *Datana*, which has only one generation a year; and that there is a late brood attacking August caterpillars, such as *Hyphantria*, which also has only one generation a year. Such an hypothesis would explain the rearing of some maggots from *Datana* larvæ collected early in July, and the non-issuance of the flies until the following May and June. It would also explain the fact that one can usually collect adult flies in the last week of May and during June, as well as in July and August. The May and June flies apparently belong to the *Datana* brood while the July and August ones belong to the *Hyphantria* brood.

Habits and Behavior

The adult flies live for several weeks and some of them, perhaps, for months. During this time they consume a considerable amount of food and water. The former is collected from flowers and the latter largely from the dew on leaves. The flowers preferred seem to be those of umbelliferæ, although the flies will visit willows early in the summer and a variety of other flowers throughout the season. Honey and pollen seem to be the principal foods and these are gathered from the flowers by being first dissolved by a little bead of liquid that is slowly regurgitated through the fleshy labella. The process can be watched conveniently by feeding some flies on loaf sugar in a cage. Shining beads of digestive fluid are repeatedly expressed through the labella and each in turn drawn rapidly into the canal as soon as some sugar has become dissolved in it. Water, of which the flies are very fond, is drawn through the labella without a preliminary regurgitation and small droplets that can be absorbed at a draft seem to be preferred to larger drops or to wet surfaces. Perhaps this is due to a cat-like distaste for getting wet.

In cool weather or wet weather, or both, the flies remain quite inactive and go into shelter on the under side of deciduous leaves or other convenient places. Under such conditions, the females will not even come out to deposit their maggots. In an instance that came under observation, larviposition was delayed for three weeks by a period of wet weather coming in the usually dry, warm month of August.

From the observations of Rambouillet and Reaumur mentioned by Pantel (Pantel J. Recherches sur les dipteres a larves entomobies, 1909, p. 67) in his most interesting account of these flies, and from an isolated observation that came to my attention, it seems likely that larviposition can be delayed too long for the health and welfare of the females. A female that had been in captivity for several weeks was noticed one morning to be quite ill; after being placed in a cyanide bottle for about half a minute, she was dissected under a binocular. It was found that she contained a number of fully developed maggots and that many of these had broken away from the posterior uterus and were burrowing actively about in the alimentary canal and fat body of their mother. The cage had not been provided with twigs or caterpillars and so there had been no stimuli to encourage larviposition.

This ability to delay for a reasonable length of time the act of parturition, while entirely foreign to most animals, is, of course, most necessary in a parasitic group like the tachinid flies, the females of which often have to wait days or weeks either for a warm day or suitable host before parturition is practicable.

The type of uterus is that described and figured by Pantel (l.c. p. 59-61) in the case of his group IV; and by Townsend for his group V of 1908 (U. S. Bureau of Ent. Tech. Ser., No. 12, pt. VI, p. 117) for his 16th series of 1911 (Townsend, C. H. T., Ann. Ent. Soc. Am., Vol. IV, p. 132) and for his fourth family *Hystriciidæ* in 1913 (Can. Ent., Feb., 1913, p. 53). The conspicuous feature of the uterus is that the posterior part expands and elongates with the development of the ovarian eggs to form a coiled chamber in which the eggs are incubated and often hatched.

As a rule, the eggs hatch at the time of larviposition and the offspring are deposited with the egg shells adhering to the forwardly directed spinules on the posterior segments (vide fig. 19). However, I have watched a female *Ernestia* fly in captivity deposit unhatched eggs in which the larvæ were still white in colour.* So that I can confirm the opinion put forward by Pantel (l.c. p. 65) that flies in this group are sometimes larviparous and sometimes oviparous.

The larvæ are deposited in the path of a host caterpillar, as described by Townsend for *Eudoromyia* (l.c. 1908) and by Pantel for *Echinomyia fera*. With the webworm (*Hyphantria*) as a host, the little maggots are deposited on the leaves and twigs near a web. On warm days, when there is little or no wind, one can often watch one of these flies at work. All that is necessary is to keep quite still and to have patience. After flying rather slowly about the alder bush where the web is, she settles on a leaf near the web. She remains motionless for perhaps a few seconds or may at once begin to explore the leaves and twigs near the nest. If in this rather measured process she encounters some feeding caterpillars, she usually moves away from them as though afraid. In a minute or so she usually begins to deposit maggots one at a time and each usually on a separate leaf, although sometimes a number will be placed on the same leaf.

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* Mr. Townsend in describing the Peruvian tachinid, *Sorochemyia oroya*, says (Insecutor Inscit. Menstr. Vol. III, p. 45): "Peru, which is noted for its unique conditions and forms of life, affords us the following unique case of perfectly white first-stage maggots in a member of the tribe Larvaevorini from the Andean altitudes." After describing his material, which included two females, he says of the one female that was not dissected, "The paratype at time of pinning showed four extended white maggots . . . . attached to larvipositor." As the related *Ernestia* will deposit white maggots under unusual circumstances, it seems likely that the white maggots deposited by Mr. Townsend's fly could be attributed to the excitement of being captured and pinned, and that under normal conditions the orthodox black larvæ would have been deposited.

All that one sees of the process is that the fly touches the tip of her abdomen to the leaf or twig once in a while and that the operation is almost instantaneous. It is rarely that a fly remains at one nest for more than five or ten minutes.

In the case of *E. magnicornis*, Townsend says (1. c. 1908) that the maggots are deposited on strands of silk spun by the host caterpillars. In the case of *E. fera*, Pantel says (1.c. p. 73) that he has never observed larvæ to be deposited on silk strands; and for *E. ampelus*, I find the case similar to that of *E. fera*.

When the little maggots are examined on the leaves, they are invariably anchored to the leaf at their caudal end by a cupule that I take to be the remains of the egg shell, including the chorion and the vitelline membrane. If a maggot is teased away from its leaf with a needle, the little white cupule usually remains on the leaf, indicating that it is fastened to the leaf by a colleterial glue. The maggot seems to be held within its cupule simply by the forwardly directed spinules on its last three segments (vide fig. 19). Mr. Townsend (1.c. 1908) reports a similar cup for *Eudoromyia;* while Pantel found no cupule in the case of *Echinomyia*.

The maggot is seen at once to be a remarkable creature, its black colour being due to the presence of imbricated scales suggestive of those occurring in snakes (vide fig. 19). These scales cover the back and sides and fit the maggot for a free living existence while waiting for a caterpillar to cross its path. In other words, the extremely important function of gaining access to the host has largely passed from the female to the larva and the larva has become especially modified into a primarily non-feeding hypermetamorphic creature, well adapted for assuming the added responsibility.

With the least excuse in the way of shock, these seemingly inanimate black specks scattered over the foliage become the most curiously animated creatures. Each maggot rises from its attached caudal region and goes through a most lively series of gyrations that become intensified as the cause of the excitement moves or is moved nearer. The least touch of a needle on the leaf or breathing upon it will bring the little maggots to activity as surely as the approach of a webworm caterpillar.

The extreme sensitiveness to shock exhibited by these little creatures may be correlated with the unusual numbers of little pits that occur particularly on the ventral or contact surface. It seems likely that these pits (fig. 19B) are of a sensory character, as supposed by Pantel.

If a luckless caterpillar crosses the lair of one of the parasites, the latter immediately attaches to a hair down which it quickly climbs to the integument. This migration is accomplished largely through a vigorous use of the mouth hook; with the aid of the backwardly directed spinules on the first few segments (fig. 19A); and with the aid of the ventral ambulatory ridges that are set with rows of spinules that 'bite' as the segments contract. Some of the more fortunate maggots attach directly, of course, to a leg or other part of the integument and do not have to make the somewhat hazardous descent down a hair.

As soon as a soft portion of the integument is reached, the maggot commences to 'dig itself in'. This is done by the aid of the mouth hook and the backwardly directed spinules of the first three segments. The process is at first quite rapid but the farther the maggot becomes embedded, the slower is the progress made. In its passage through the intergument the little larva travels head first. Progress is finally brought to a standstill on account of the forwardly directed spinules on the last segment. If it were not arrested in this way the maggot might fall into the caterpillar and drown.

In the free living muscids the problem of larval breathing is a relatively simple one. In the parasitic tachinidæ the problem is much more complex. It is met in different ways by different species, and sometimes in different ways by the successive stages of the same species. In *Ernestia ampelus* we have seen that the first stage maggot does not pass right into its host but that it remains

suspended with its anal spiracles visible from the surface of the caterpillar. Anchored so as to ensure a constant supply of air through the anal spiracles, the larva feeds and grows. During the first two instars, breathing apparently takes place through the posterior spiracles only as the anterior ones appear to be closed and functionless (fig. 24). Toward the end of the third instar, however, the anterior spiracles (fig. 22B) are open and obviously functional organs. At this time, however, the host caterpillar has been drained of most of its liquid content and it comes to be filled more and more with air as its final destruction is rapidly encompassed. So that in this last larval stage the breathing mechanism is practically the same as in the free living muscids.

The method of feeding is also considerably modified from that in the free living muscids. Although the whole larval period after the host is once invaded is in a sense the period in the life cycle of the species devoted primarily to feeding and growth, yet in the tachinids this feeding and growth is relegated chiefly to the third stage larva, as Pantel has already pointed out (1. c. p. 126). For about three weeks the animal feeds on the juices of its host without destroying any of its essential tissue systems—and the host caterpillar evinces no signs of discomfort. The larva molts to third stage, however, and almost at once enters upon what may be termed 'the destructive feeding period', after three to five days of which every tissue system of the host is destroyed and the maggot is suddenly full grown and ready to pupate. In the case of *Ernestia*, the large slender but powerful mouth hooks (vide fig. 23) are evidently of use during this period for helping to lacerate and reduce to liquid form the food materials available. During this period the maggot is very active and its movements can be watched through the skin of the dead or dying webworm caterpillar containing it.

A morphological point in connection with this destructive feeding period is that the invagination of the hind intestine seems to be delayed until the end of the second instar. There has been no opportunity to verify the point by making sections but there is certainly no visible anal opening in the first or second stage larvæ, while there is a very conspicuous one in the third instar. Also, I have never seen in host caterpillars dissected any signs of waste materials voided by these parasites; while it is a common observation to see a maggot just as it emerges from the carcass void copious quantities of dark-coloured semi-liquid excreta.

If this surmise is correct, the waste products of metabolism are stored up as they are in embryos and not voided until all danger of contaminating the food supply has passed.

The larvæ of the first two stages probably feed entirely upon liquid materials. That they are able to do so is shown by the fact that in several cases I have found these larvæ completely enclosed by the hypodermal sleeves grown by the hosts in an effort to close the wound made by the entering maggots. These sleeves (figs. 26, 27 and 28), the bases of which form the well-known integumental funnels, usually extend only for a short distance toward the cephalic end of the larvæ and when they extend farther than this they are generally open at the end.

The hypodermal origin of these sleeves is shown in figures 26, 27 and 28.

In the process of molting from one larval stage to another, the old molt skin is first loosened at the anal end, after which many hours elapse before the mouth hooks are molted away. This is indicated from the fact that a number of maggots have been obtained with third stage anal spiracles fully developed, yet having both second and third stage mouth hooks. The third stage hooks are incomplete and only represented by the first of the three segments.

Immediately after molting, the old mouth hooks can be seen attached to the maggot close to its head (fig. 25). As days go by, these hooks work down toward the anal end. One often finds, for instance, a last stage maggot with its mouth hooks properly installed showing its second stage hooks attached to

its middle and its first stage hooks well down toward, or even embedded in, the basal funnel. Such a migration of the hooks indicates, of course, the fate of the molt skins to which they are attached. These skins work down between the maggot and its integumental sleeves and finally become pressed into the sleeve or into the hardened funnel at its base.

When the maggots emerge, they go to earth almost immediately. If they drop on a hard place they will, however, travel until better conditions obtain for digging in. Sometimes they do not dig in at all but pupate under fallen leaves. Most, however, go into the soil a few inches and come to rest for pupation in an oblique position with the head directed upwards.

This habit of pupating in an oblique position with the head directed upwards has been pointed out in the account of *Compsilura* to which the reader is referred (p. 43). The significance of it becomes apparent when it is recalled that most tachinid flies, after issuing from their pupæ, have to travel through several inches of solid earth before reaching the surface; and when it is recalled that *Compsilura* adults are incapable of steering during this journey but have to take a 'head on' course, veering neither to the right nor to the left.

From an examination of the bristles or macrochætæ, as they are termed, of a freshly killed *Ernestia* fly, it seems clear that the essential function of these bristles is to help the fly to make this initial journey out of the soil. With a needle, it was found that the bristles of the abdomen and of the legs, together with the orbital and ocellar bristles of the head were arranged so as to move in one direction only, namely; backwards. With the least possible pressure of the needle, any of these bristles could be bent down so as to lie flat upon the fly and pointing backward; but they would not move forward at all. With the fly moving forward through soil, these bristles would lie appressed to the body but would prevent the fly moving backwards.

The bristles of the thorax, together with the verticals, postverticals and frontal bristles of the head, are differently arranged. Though these are so backwardly directed as to lie almost parallel with the outlines of the body, they cannot be pressed against the body. This set of bristles would keep the integument of the fly from touching the walls of its tunnel. In the case of a fly emerging through soil laden with the moisture of spring freshets, the integument would be kept dry, and breathing through the thoracic spiracles would be uninterrupted. The chief function of this second set of bristles seems to be, then, to prevent the fly being smothered in its journey through the soil.

The ptilinum seems to function in two distinct ways. First of all, it is the only tool possessed by the fly for opening the lid of its pupal box. Then as the *Ernestia* adult works its way through the soil, the ptilinum seems to be used for breaking the trail. The organ is inflated and a cavity made in the soil immediately ahead of the fly; with a vigorous use of the legs and the directive influence of the macrochætæ, the fly moves forward; it is held in its new position by the macrochætæ, the ptilinum is again inflated and so is the process continued until the fly comes to the surface.

In this account of the function of the ptilinum, I find I do not quite agree with W. R. Thompson, who says of *Blepharipa* "that the fly reaches the surface by the alternate expansion and contraction of the ptilinum, that organ being provided with many backwardly directed spines which serve to draw the fly up through the earth".

The macrochætæ of another tachinid, *Winthemia quadripustulata*, were found to be hinged in the manner just described for *Ernestia*, and the function is possibly the same throughout the family. Though empirical knowledge of the pupating habits of flies generally is not sufficiently complete to warrant any sweeping generalization, I wish to suggest that the correlation between the development of macrochætæ and the need of the fly to force its way through the soil in emergence may have a very general application in Diptera. In some

CAMPOPLEX PILOSULUS. Female.

families in which pupation takes place in the soil, this migration is performed by motile pupæ supplied with spines that are the working equivalent of the adult macrochætæ, to wit, species of *Tabanidæ, Asilidæ* and *Bombyliidæ*. In these cases, though pupation takes place in soil, the adults have not needed to develop macrochætæ. On the other hand, there are several families of diptera, many, or most, members of which are known to pupate in the soil; to have immobile pupæ; and to be characteristically bristly in the adult stage, to wit, *Muscidæ, Sarcophagidæ, Dexiidæ* and *Tachinidæ*. The *Dolichopodidæ* have developed macrochætæ but little or nothing seems to be known of their pupating habits. If our hypothesis applies, their pupæ should be looked for in the soil. The *Oestridæ*, though closely related to and presumably derived from some of the families of bristly flies, are themselves without macrochætæ. At least two species of the family *Gastrophilus intestinalis* and *G. nasalis*, according to W. E. Dove, (U.S.D.A. Bull. 597, 1918) pupate above ground. Examples of smooth flies, the larvæ of which do not go to earth to pupate, can be multiplied almost indefinitely; nematocera generally, aquatic brachycera and *Syrphidæ* come to mind as affording many familiar examples.*

HYMENOPTERA PARASITICA

Campoplex (Ameloctonus) pilosulus Prov.

The species now known as *Campoplex pilosulus* was described by Provancher in 1886 as *Limneria pilosula*. As Holmgren's genus *Limneria* has had to be abandoned in favour of Gravenhorst's earlier described *Campoplex*, the species becomes automatically *C. pilosulus*. In Viereck's Hymenoptera of Connecticut, 1916, the species is placed in Foerster's subgenus (*Ameloctonus*), an arrangement which seems to have been first suggested by Ashmead.

DESCRIPTION OF ADULT (Plate VI and Plate III, fig. B).

The following is a translation of the original description as published by the Abbé in Petite Faune Entomologique, Vol. II, p. 89.

"Female: Length three-tenths of an inch. Black, with the legs and abdomen red. The mandibles, palpi, wing attachments and also a pair of spots in front of them, and the four anterior coxæ, together with their trochanters, white. Face with short silvery pubescence, a similar but much longer pubescence showing on the sides of the metathorax. Antennæ filiform, as long as the body, the scape more or less white beneath. Thorax robust, the metathorax sloping (declive), pitted, its sides furnished with white hairs. Wings hyaline, the veins black, the areolet triangular and shortly pediculate. Legs red, including the posterior coxæ; the tibiæ (les jambes) of this last pair dark-brown and tarsi of the same pair, black. Abdomen red, black only at the base of the pedicel, the terminal segments of the abdomen forming a fusiform structure; ovipositor fully a fourth as long as the abdomen; its valves black.

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* The curious bristles or macrochætæ have been interpreted in various ways in literature. Macquart seems to have been the first to call attention to them and to attempt an explanation of them. In 1845 he said of these bristles (Ann. Soc. Ent. Fr. pp. 239–240) "They protect all the upper parts of the head against shocks and one can scarcely doubt that this method of preservation has been meted out (accordés) to this great family to the exclusion of most of the other diptera, in order to compensate for the feebleness of the integument."

Thirty-nine years later, Osten Sacken challenged the hypothesis of Macquart, which he found would not explain "how certain families can exist without any macrochætæ at all." His excellent summary of the question is the ablest that has been written, and his open-minded treatment of the issue most refreshing. After reviewing the available facts of his generation, he says (Trans. Ent. Soc., Lond., 1884, pp. 497–517) "I assume, therefore, that macrochætæ are organs of orientation, connected with the nervous system, being in their useful action not unlike the whiskers of a cat."

In the same year, Williston, in his Manual of North American Diptera (p. 43) referred to the findings of Osten Sacken and added the significant remark "Doubtless the vestiture has an intimate relation with the habits of the mature insect; just what the relations of the different kinds are is not yet well understood."

In 1910, W. R. Thompson opened the way for the pupation hypothesis when he discovered (Journ. Ec. Ent., Vol. III, p. 286) that tachinid larvæ after going to earth "turned about and proceeded to pupate with the anterior end directed upward."

Fɪɢ. 30. *Campoplex pilosulus* Prov. A first stage larva removed from its egg.

Fɪɢ. 31. *Campoplex pilosulus* Prov. First stage larva. Drawn from a chloral hydrate specimen in excellent condition; the outlines of internal structures being put in from balsam preparations.

Fɪɢ. 32. *Campoplex pilosulus* Prov. Ventral view of the head capsule of a first stage larva. Drawn from the specimen shown in fig. 31. The posterior margins of the ventral surface are elevated and strongly chitinized to form a pair of head rests. In profile these rests show as two little rounded elevations. h.r.=head rests.

Fɪɢ. 33. *Campoplex pilosulus* Prov. Mouth parts of the second stage larva shown in Fig. 34. Note that the head capsule does not extend below the head. It is delimited ventrally by two diverging lines each commencing at the base of a mandible.

Fɪɢ. 34. *Campoplex pilosulus* Prov. A young second stage larva only 2 mm. long. The head capsule has not yet darkened in colour and the caudal appendage is moderately long. Compare fig. 35.

Fɪɢ. 35. *Campoplex pilosulus* Prov. A second stage larva 4 mm. long, and older than the one shown in figure 34. Note the reduction of the caudal appendage. The lateral suture on the head marks the lower extremity of the chitinous capsule that fits on the head in the manner of a cap.

Fɪɢ. 36. *Campoplex validus* Cr. Facial plate of a third stage larva.

Fɪɢ. 37. See page 64.

Fɪɢ. 38. *Campoplex pilosulus* Prov. First stage larva. Cross section through the buccal cavity showing how the mandibles are used for setting up a current instead of for biting. Note the heavy musculature of the mandibles. Shows also the invagination of the oral cavity. Hyp.=hypodermis; Mus.=muscle; B.C.=buccal cavity; Cu.=cuticle; Md.= mandible.

Fɪɢ. 39. *Campoplex pilosulus* Prov. Second stage larva. Cross section showing the invagination of the fore intestine. The mandibles are placed well within the mouth and are well supplied with muscles. Their tips are directed toward the roof of the mouth. In action these mandibles serve to set up a current of food materials down the fore intestine. Br.= brain; Mus.=muscle; Hyp.=hypodermal cells; Cu.=chitinous cuticle; Md.=mandible; Buc. cav.=buccal cavity.

Fɪɢ. 40. *Campoplex pilosulus* Prov. Diagram of first stage mouth parts. The fore intestine bends at right angles with the result that the mouth opens ventrally. The salivary glands empty through what seems to be a recently formed duct into the oesophagus instead of into the mouth. P.P.=pump plunger; F. int.=fore intestine; M.i.=mid intestine: S.G.= salivary gland; C.O.=cut-off to oesophagus; B. cav.=buccal cavity.
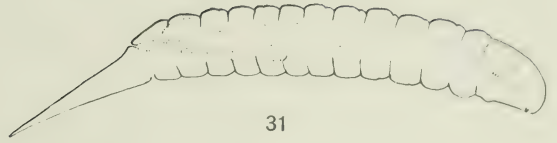
Fɪɢ. 41. *Campoplex pilosulus* Prov. Diagram of mouth parts of second and third larval stages. Note the cut-off leading from the salivary glands to the fore intestine. This cut-off becomes functionless toward the end of the third stage, when the glands secrete silk instead of saliva. PP..=pump plunger or valve; F. int.=fore intestine; Oes. Val.=oesophageal valve; M. int.=mid intestine; S.G.=silk gland; B.C.=buccal cavity.

Fɪɢ. 42. *Campoplex pilosulus* Prov. First stage larva. Cross section through portion of salivary gland, showing some actively secreting salivary cells and a few non-active silk cells. The active cells are very large, are filled with a finely granular secretion that is oozing out into the duct, and their nuclei have become shapeless and shrunken. These cells are pale in colour. The non-active silk cells are smaller, their nuclei are large and have regular out-lines, and the cells stain deeply with hematoxylin. M. int.=lumen of mid intestine; S.G.= salivary gland; Lum.=lumen of salivary gland; Gang.=ganglion.
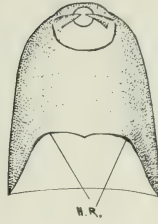
Fɪɢ. 43. *Campoplex pilosulus* Prov. First stage larva. A fragment of mid-intestine, as seen in cross section under an oil emersion lens. The food material consists of the non-cellular fluid elements of the blood and lymph with an occasional blood cell. The digestive fluid is produced by gland cells that enlarge and burst. The droplets of secretion come together into large droplets that burst through into the lumen of the intestine.
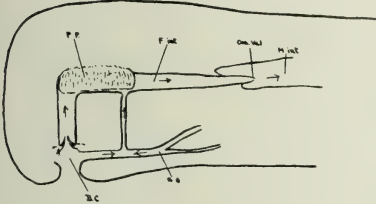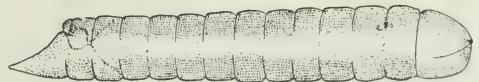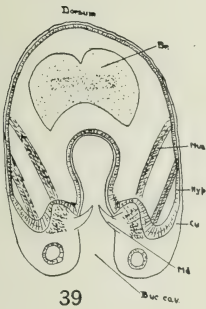
30

31

32
H.R.

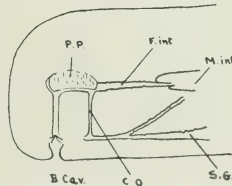33

41
P.P. F.int Oes.Val M.int
B.C

34

35

38
Roof of mouth
Hyp
Mus
B.C.
Cu
Md

39
Dorsum
Br.
Pha
Hyp
Cu
Md
Buc.cav.

40
P.P. F.int
M.int
B.Cav. C.O S.G.

36

42
M.int
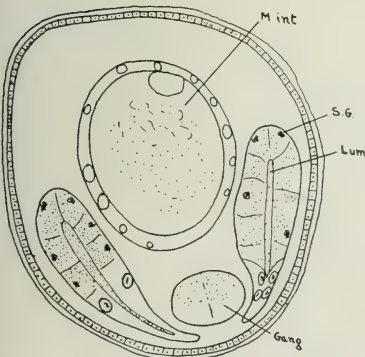S.G.
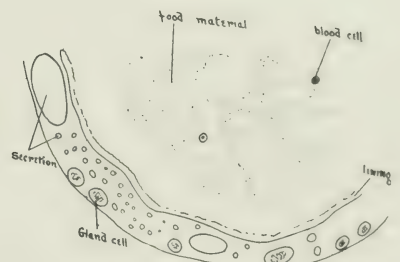Lum
Gang

43
food maternal blood cell
Secretion
Gland cell Lining
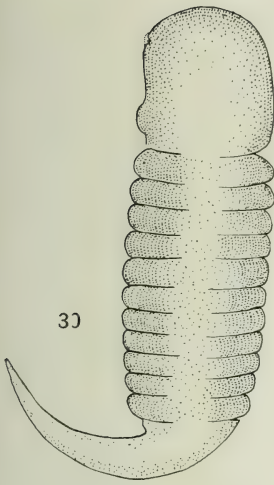
"Male: Similar to the female, with the scape white below and the anterior legs paler.

"Distinguished from *ruficoxa* by its abdomen being entirely red, and from *pallipes* by its black posterior tarsi."

New Brunswick and Nova Scotia specimens reared from *Hyphantria* agree very well with this description. The only point in the description that might possibly be misleading is in connection with the areolet. While this cell (R 5 of the Comstock-Needham system) appears to be triangular, yet under lower power of a binocular it is seen to be somewhat irregularly pentangular.

Hosts

The fall webworm (*Hyphantria*) seems to be the only host from which this species has been reared. It does not seem probable, however, that it is the only host it attacks.

Range

The Abbé Provancher described the species from material collected at Ottawa, Ont., and Cap Rouge, P.Q. I have found the species widely distributed in New Brunswick and Nova Scotia. In Massachusetts it has been bred at the gipsy moth laboratory of the United States Government, from material collected at Melrose Highlands and vicinity. Viereck in his Hymemoptera of Connecticut records a capture of this species by W. E. Britton at New Haven. From the west there are no records of this species.

Descriptions of Early Stages

For the descriptions of the early stages of this species, material was dissected from webworm larvæ collected at Fredericton. In the year in question, only this species of *Campoplex* was reared from this host and the early stages dissected out probably belong to the same species.

Egg

The egg (fig. 29) is a kidney-shaped body just large enough to see with the naked eye. It is ·3 mm. to ·4 mm. long. It is slightly convex on what is probably the ventral aspect and slightly concave on the opposite surface. Each end is rounded off rather abruptly. The surface is smooth and almost polished. Its pale-brown colour is imparted by the thick chorion.

First Stage Larva

If one dissects out a larva from its egg, the shape is that shown in figure 30; the caudal appendage being bent under the venter. Soon after eclosion, however, the shape changes to that shown in figure 31, where the caudal appendage has taken up the position characteristic for the feeding period of the first stage larva.

The larva is characterized by having a well-marked and strongly chitinized head capsule and by its long tapering caudal appendage.

The head capsule, of the colour of pale-amber, stands out in striking contrast to the milky white or colourless body of the larva. The posterior margins of the ventral part (fig. 32) are elevated on each side to form a ridge.

The mandibles (fig. 32) are strongly chitinized and gently curved, with their sharp points directed into the oral cavity.

Behind the head capsule are twelve similar body segments. The anal opening of the hind intestine which occurs on the dorsum of the twelfth segment can usually be made out under the binocular.

In the first stage the spiracles are closed.

The caudal appendage (fig. 31) is funnel-shaped, tapering very gradually to a sharp point. It is semi-transparent.

The integument of the larva is perfectly smooth and when seen removed from a fluid medium, has a shiny appearance.

The larva grows to be 1·7 mm. to 2 mm. long before it molts to second stage. During this period of growth the head capsule does not increase in size. In a newly-eclosed larva, the head capsule is a third to half as long as the entire larva, exclusive of the caudal appendage; in a full grown larva of this stage the capsule is only about a sixth as long as the larva.

Second Stage Larva

The second stage larva differs from the first stage in that the head shield is much softer in texture and lighter in colour; and in that the caudal appendage is much shorter (fig. 34).

The head shield in this stage may be likened to a cap which fits on the top of the head rather than to a capsule that fits right over it. The cap does not extend under the head at all (fig. 33).

The mandibles closely resemble those of the first stage but are, of course, of greater size (fig. 33).

Twelve segments can still be made out behind the head segment; and the spiracles are still closed.

The caudal appendage is notably shorter than in the first stage and the shrinking process continues during this stage (compare figures 34 and 35).

Third Stage Larva

The third stage larva differs from the second particularly in the condition of the facial plate and in the absence of a caudal appendage. Material of this stage is now unavailable and I cannot give a full description.

The facial plate is, however, so similar to that of the closely related species *C. validus* that in practice they are indistinguishable. The figure (fig. 36) shows how greatly the head structures differ from those of the second stage.

In this stage the spiracles can be made out under a 4 mm. objective. Although they are exceedingly minute, they appear to be open.

The Cocoon and Pupa

Campoplex pilosulus pupates within the skin of the caterpillar it has destroyed after first lining the interior of it with silk. As the parasite becomes shorter and thicker at the time of pupation, it often causes the dried caterpillar skin to crack open along its whole length. When the pupation period is completed, the adult parasite makes its exit from the pupating chamber through a hole which is usually near the cephalic end of the caterpillar skin.

LIFE-HISTORY

The following notes on life-history will apply to Fredericton unless otherwise indicated. As no reproduction experiments have been carried on with this species, many points remain to be cleared up.

Egg-laying usually commences toward the end of the first week in August while *Hyphantria* larvae are in their second stage. It progresses rapidly during the middle ten days of August during which time most of the host larvae are in stage three; and it terminates toward the end of the month when most of the host larvae are in stage five. In other words, oviposition takes place in *Hyphantria* larvae that are in stages two, three and four.

It is not known how long it takes a single fly to lay all its eggs but the structure of the female reproductive system affords a clue. Each follicle has only one egg ready for fertilization at a time and the uterus is so short that such eggs cannot

be stored up and incubated. From this it seems probable that a few eggs are laid each day and that a fortnight may be required for the completion of the process.

Fertilization takes place as the eggs pass the opening of the spermathecal duct and a spermatozoon enters the micropyle. This duct opens so close to the base of the ovipositor that fertilization probably takes place during the act of oviposition. If this is the case, almost the whole of embryonic development would take place after oviposition in the host. How long it takes for this development is not precisely known. Records show, however, that the period is a short one and that the eggs usually hatch in about a week after oviposition.

The larval period is about three weeks in length. A large share of this period is taken by the first stage larva, a smaller share by the second, while only two or three days seem to be needed by the third stage larva.

The pupal stage lasts for about nine days. To instance a single case, a larva spun its cocoon on August 30 and the fly issued on September 8. The period probably varies a little with the temperature but there seems to be no great amount of variation.

Pupation usually commences in the third week of August and the last straggler pupates a month later. Most of the larvæ pupate in the last week of August. In the case of 23 larvæ bred out in 1913, the first pupated on August 20 and the last on September 20. Mr. L. S. McLaine has very kindly furnished me with a more representative set of pupation records. In 1917, 207 pupæ were bred from webworm larvæ collected at Annapolis, N.S. The first cocoon appeared on August 20, 14 two days later, and 20 appeared three days later; after this there was a decline until the end of the month when most of the cocoons had formed. The last straggler appeared on September 20. These data have been plotted on to the accompanying chart (fig. 37).
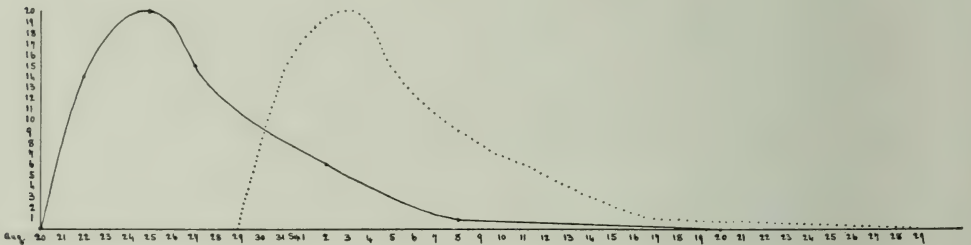

Fig. 37. Pupation record of 207 *Campoplex pilosulus* Prov. from data kindly furnished by L. S. McLaine from webworm larvæ collected near Annapolis, N.S., in 1917. The first cocoon appeared on August 20; fourteen appeared on August 22; and twenty on August 25. After this there was a decline until the end of the month, when most of the cocoons had formed. The last straggler appeared on September 20. As the pupal period is about nine days, the dotted line has been put in to represent the probable emergence of adults from the same larvæ. The height of emergence is indicated as taking place during the first week of September; and the last fly of the season as emerging on September 29.

Nothing is known as to the fate of the flies that issue from this fall generation. Owing to the lateness of the season at which they issue and the rapidly increasing number of frosty nights, it seems likely that they hibernate as do many other parasitic hymenoptera inhabiting the boreal zone.

It is extremely likely that there is a spring or early summer generation on some host other than *hyphantria* but nothing is known concerning the activities of this species until August.

Habits and Behaviour

The adults have biting mouth parts, as have all parasitic hymenoptera, and seem to feed largely upon pollen. They are flower visitors and seem to be particularly fond of a half dozen of the commoner species of goldenrod

(*Solidago*) found in New Brunswick. Males and females of a closely related species, *C. validus*, were kept alive in captivity by Mr. P. H. Timberlake (U. S. Bur. of Ent., Tech. Ser. No. 19, pt. 5, p. 73) by feeding them on sweetened water sprayed on leaves.

In marked contrast with the tachinid parasites of the webworm, *C. pilosulus* females will oviposit on comparatively dull, cool days. This is probably due to the fact that as the uterus is short and incapable of storing up ovarian eggs or embryos, only a few eggs—perhaps one from each follicle—can be deposited each day.

As the spermathecal duct empties into the posterior end of this short uterus, it seems to follow that embryological development takes place within the host.

In dissecting out several hundred of these parasites during the last eight years, it has been found that they almost invariably lie in the posterior end of the host. This seems to be due to the fact that this part of the caterpillar is the more easily attacked. When the caterpillars become excited, as they do on the approach of any hymenopterous fly, they remain anchored at the caudal end and move the fore-part of the body rapidly to and fro with rather a jerky motion. While the fore and middle parts of the caterpillars are thus protected from attack, the caudal end remains vulnerable. In the case of *C. validus*, Mr. Timberlake (1. c. p. 73) found that females instinctively laid in the caudal part of the several species of caterpillar with which he experimented.

From the presence of the parasites in this caudal region even in the second stage, it can be inferred that the first stage larva is practically non-motile. Indeed, when a larva is dissected out into a watch glass it seems almost incapable of movement; such a larva will sometimes curl up very slowly in the form of a ring or equally slowly straighten out to full length.

The little larva floats unattached in the body cavity of its victim. It may be above, below, or on either side of the alimentary canal and its head may be directed toward any part of the host. In such an environment our little larva which has lost its eyes, antennæ, palpi, and legs, and which can no longer breathe through spiracles, gains a highly satisfactory livelihood.

The problem of feeding is relatively simple, as the larva drinks the fluids which bathe it.

If a living larva immersed in a normal fluid medium, or even in water, be watched under a binocular microscope, something can usually be seen of the feeding process. When the larva is feeding the fluids in the immediate neighbourhood of the mouth are in a condition of agitation.

This agitation is effected in part by the rapid movement of two little mandibles that have been very much specialized by reduction. A study of cross-sections shows that these mandibles are seated well within the oral cavity and that their tips are directed inward (figs. 38 and 39).

In spite of the presence of these mandibles, however, the mouth parts are essentially of a sucking type and the liquid food is, apparently, sucked into the canal by means of a pharyngeal pump. An examination of cross-sections shows that the posterior part of the buccal cavity is occupied by a mass of deeply staining nucleated material that seems to consist largely of hypodermal cells. This mass is evidently under muscular control and apparently functions as the valve of a pump (figs. 40 and 41).

In the first stage larva there is evidence for supposing that a secretion from the salivary glands is also sucked into the intestine with the food material. This digestive secretion is produced only in a small localized section of the gland

situated just in front of the place where each gland bifurcates. The gland in this area is greatly distended and its individual cells are also correspondingly enlarged. In our sections these cells (fig. 42) have a very characteristic appearance as they do not stain deeply with hematoxylin. These pale cells are filled with a finely granular secretion that oozes out into the duct. Their nuclei have lost the regular outline characteristic for the silk-producing cells and have become greatly shrunken*.

The secretion passes down the lumen of each gland into the duct common to both glands. Then, instead of emptying into the buccal cavity, the secretion is apparently sucked through a newly-developed duct directly into the fore intestine and so passes to the mid intestine. In this stage there seems to be no direct connection from the common duct of these glands into the mouth, but the point is a difficult one to determine and cannot yet be regarded as established.

As will be seen from a glance at the diagram (fig. 40), the liquid food and the salivary secretions are drawn into the fore intestine separately and there mixed and passed along into the mid intestine. In this stage the so-called œsophageal valve between the fore and mid intestines is very poorly developed.

To the mixture of food and saliva is added in the mid intestine a copious secretion liberated by the gland cells in its wall. These gland cells are equally noticeable along the entire length of this intestine so that digestion evidently takes place alike throughout the length of the mid intestine.

In gross structure the mid intestine is a short straight tube, tapering somewhat toward either end. Its simplicity is not surprising for the food material must be very easy of digestion. The food consists chiefly of the non-cellular element of the blood lymphatic system. In cross-sections of the mid intestine it can be seen that the lumen, at least just after a meal, is usually almost completely filled with this food material. The material has a finely granular flocculent appearance and is almost entirely non-cellular. A few blood cells can, however, be found here and there (fig. 43); these are usually young cells with regular outlines and well-defined nuclei. The absence of fat cells in this material indicates that the parasite does not feed directly upon the fat body of its host.

In discussing the feeding of the related species *C. validus*, Mr. P. H. Timberlake concludes that though individual fat cells may sometimes be swallowed, the fat body is never directly attacked. Nevertheless, the fat body diminishes in size as the parasite grows. This was pointed out by Ratzeburg in 1844 and again by Timberlake in 1912. In the case of the first stage larva of *Campoplex*, feeding in webworm caterpillars, the disappearance of fat body cannot be directly attributable to the parasite. It seems more reasonable to suppose that this reserve food supply disappears as the lymph and blood become exhausted. In other words, that the host larva uses its own fat body to replace the loss of fluids sucked away by the parasite—a use that is comparable to that of the fat body during hibernation, and to that of yolk materials during embryonic development.

In the first stage larva, then, digestion takes place in a closed system and there is practically no elimination of waste materials either through the alimentary canal or the malpighian tubes.

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* The adaptability of these glands is not without interest. Derived, in the first place, from the pair of tracheal invaginations that occur in insect embryos on the labial segment, they evidently first functioned as tracheæ. In many insects they have come to function as silk glands; and in many others as salivary glands. In this instance of *Campoplex* part of the gland is set aside for producing a digestive fluid and part for producing silk.

In the second stage larva, the processes of feeding, digestion and elimination of wastes are closely comparable to the ones just outlined. The food consists of lymph and blood, the only cellular elements in it being a very few blood cells (fig. 43). The food is forced into the intestine; the hind part of the intestine is still closed; and there is no elimination of solid waste. There are a few minor differences, however, and to these it may be well to refer.

In this stage the efferent duct of the silk glands opens into the mouth, as shown in the diagram (fig. 41), while the short cut to the oesophagus also apparently remains open. This short cut seems to function no longer as a conduit for salivary secretion, as none of the cells in this gland seem to be in a condition of active secretion. It may be that liquid food taken into the mouth can pass into the oesophagus through either one of the channels; or in other words, that the larva may have one mouth and two throats. These suggestions are based, however, upon a study of sections of only a single larva and are in need of verification.

The œsophageal valve (fig. 45) between the fore and mid intestine is much better developed than in the first stage. It now obviously functions in preventing food materials from being regurgitated.

In the third stage larva, the processes concerned with nutrition are closely comparable with those of the second stage. The mandibles are larger and more powerful and as Mr. Timberlake says, "there is some ground for believing that even solid tissues may now be taken in, even before they have been wholly disintegrated." However, our cross-sections afford little evidence in support of this view. In these sections there are no fat cells in the mid intestine (fig. 44), the only cellular element consisting, as in the first two stages, of an occasional blood cell. Sections of an older third stage larva killed at the close of the feeding period, would probably throw further light upon the point. If these larvæ actually never ingest solid tissue, it follows that such materials would have to be digested extra intestinally.* In the case of *C. validus*, Mr. Timberlake says (l. c. p. 89): "To just what extent the tissues are broken down before being consumed has not been definitely determined, but we believe usually to a semi-liquid condition."

The silk glands show signs of activity in this stage, evidently foreshadowing the production of silk that is later to be used for building the cocoon. It is also possible, however, that they secrete a material used in extra intestinal digestion.

The œsophageal valve is well developed and the mid intestine remains short and straight. In a larva that was sectioned the food material is clearly surrounded by a membrane—presumably the peritrophic membrane.

These sections throw a little light on the process of digestion. The food material occupies less than half the entire lumen of the gut and the walls of the intestine are now in a condition of active secretion. In some first and second stage larvæ sectioned, the food occupied the entire lumen and the cell wall was in a condition of very active secretion. It seems likely that the latter represents the situation just after a full meal; and the former the situation several hours after a meal. As dragon-flies take regular meals (and Dr. Needham has shown in his admirable account of their digestive mechanism that they do) it is possible that *Campoplex* does also.

The hind intestine remains closed until the end of the feeding stage.

A problem closely associated with that of digestion has to do with the preservation of the food supply. The food with which the little parasite is surrounded must be maintained in an absolutely fresh condition. This is made

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* Possibly bacteria help.

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Fig. 44. *Campoplex pilosulus* Prov. Second stage larva. Typical cross section through mid-intestine. Ht.=heart; Mal. tub.=malpighian tube; Cu.=cuticle; Hyp.=hypodermis; Sal. Gl.=salivary gland; Tr.=trachea; Mus.=muscle; M. Int.=mid intestine with a mass of food material in its lumen; Gang.=ganglion; Tr.=bundle of tracheids; Sec.=droplet of digestive secretion in the wall of the mid intestine.

Fig. 45. *Campoplex pilosulus* Prov. Section through the oesophageal valve of a second stage larva. The hypodermal layer has shrunken away a little from the cuticle. Cu.= cuticle; Hyp.=hypodermis; M. int.=mid intestine; F. Int.=fore intestine; Tr.=trachea; F.B.=fat body; S.G.=salivary gland; Gang.=ganglion.

Fig. 46. *Campoplex pilosulus* Prov. Second stage larva, showing gonads and closed condition of alimentary canal. Ht.=heart; cu.=cuticle; Hyp.=hypodermal cells; Gon.= gonad; H. int.=hind intestine; Tr.=trachea; Tr₁=tracheids; Mus.=transverse muscle ; Gang.=ganglion; Mal. tub.=malpighian tubes.

Fig. 47. *Campoplex pilosulus* Prov. Second stage larva. This drawing shows the malpighian tubes arising from the hind intestine. 16 μ from this point the four tubes become separated from the canal. Note also that in this section the hind intestine is closed and functionless. Ht.=heart; Mal. tub.=malpighian tube; H. int.=hind intestine; Mus.= muscle; Gang.=ganglion; Tr₁=tracheids; Tr.=trachea; Hyp.=hypodermis; Cu.=cuticle.

Fig. 48. *Campoplex pilosulus* Prov. Second stage larva. Showing the invagination of the hind intestine. Cu.=cuticle.; H. int.=invagination of hind intestine; Ms.=muscle ; Tr.=tracheid; Hyp.=hypodermis.

Fig. 49. *Campoplex pilosulus* Prov. Cross section showing the valve-like structure in the hind intestine of a first stage larva. This structure is present in all three larval stages a similar one being present also in the fore intestine. It is evidently a valve and probably has to do with the passage of food materials through the alimentary canal. The one in the hind intestine does not function until the end of the feeding period. Cu.=cuticle; Hyp.= hypodermis; H. int.=hind intestine; Pump=valve of pump-like structure; Mus.=longitudinal muscles; Tr.=a bundle of tracheids.

Fig. 50. *Campoplex pilosulus* Prov. Third stage larva. Shows the valve in the hind intestine and the reproductive organs of the adult forming; Cu.=cuticle; Hyp.=hypodermis; H. int.=lumen of hind intestine; Cu₁=cuticular thickening in the valvular part of hind intestine; Tr.=trachea; F.B.=fat body; Mus.=muscle; Rep.=reproductive organs recently invaginated.

Fig. 51. *Campoplex pilosulus* Prov. First stage larva. A represents a diagrammatic figure of the caudal appendage, showing the points at which cross-section drawings were made. R represents a longitudinal section of a tracheid.

Fig. 52. *Campoplex pilosulus* Prov. First stage larva. Drawn from section cut through A–B (see diagram) near the base of the caudal appendage. Tr.=closed end of tracheid; Tr₁=tracheid entering hypodermal cell; Tr₂=tracheid; Cu.=cuticle; Hyp.=hypodermis ; Hyp₁=intracellular air space in one of the hypodermal cells; Nuc.=nucleus of one of the tracheid cells.

Fig. 53. *Campoplex pilosulus* Prov. First stage larva. Cross section through C–D or about midway between the tip and base of caudal appendage. Cu.=cuticle; Hyp.= hypodermis; Tr.=tracheid; Tr₁=tracheid opening into air chamber of a hypodermal cell; Nuc.=nucleus of a tracheid.

Fig. 54. *Campoplex pilosulus* Prov. First stage larva. Drawn from section cut through the tip of the caudal appendage or about at the point E–F (see diagram). Cu.=cuticle; Tr.=tracheid still open; Tr₁=closed termination of a tracheid; Hyp.=hypodermis.

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A.

B.

Nucleus

Lumen

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53

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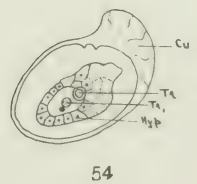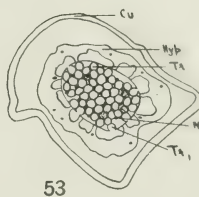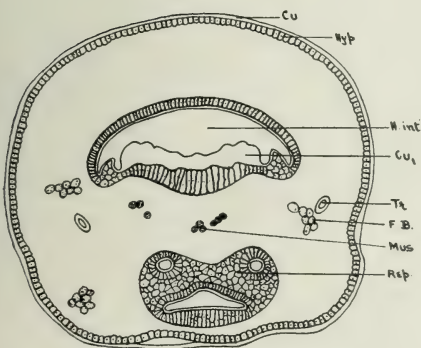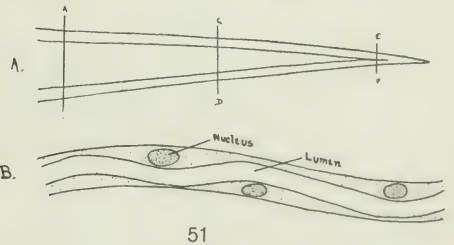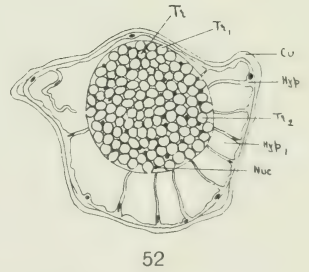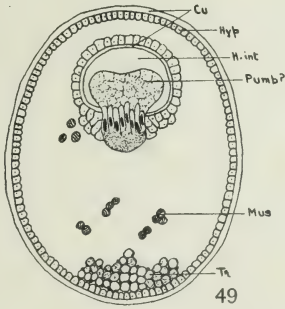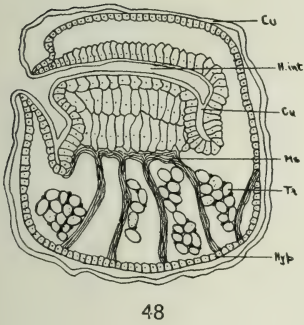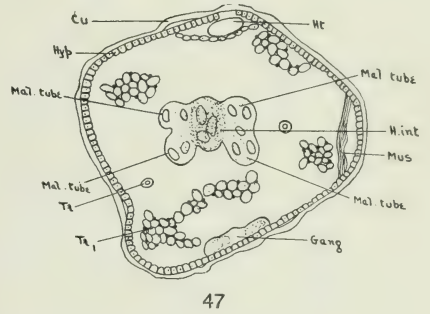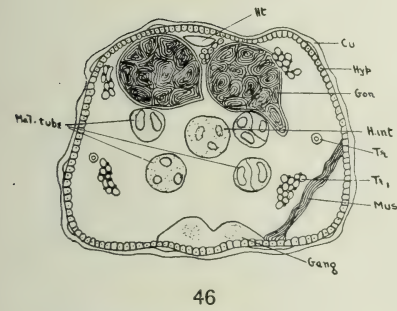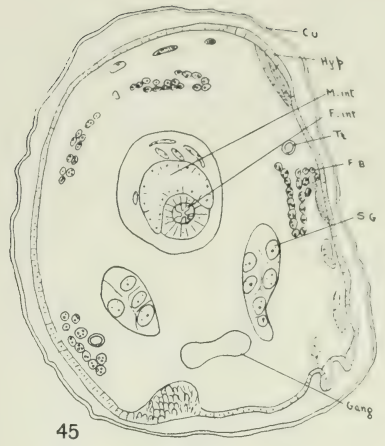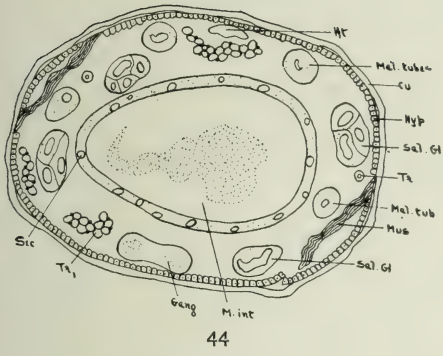
possible, even in the hottest summer, by certain biological readjustments on the part of the parasite. For one thing, the host is left alive until the last possible moment and then when death ensues or is about to ensue, the parasite enters abruptly upon a destructive feeding stage.

The host caterpillar remains alive during the first two instars of *Campoplex*, chiefly because of the feeding habits of this parasite in this part of its life. We have seen that it is only the blood serum and the lymph, with an occasional blood corpuscle that are sucked away in these stages and the main tissue systems are left intact.

This material is essentially comparable to the milk secreted by mammals for the rearing of their young; and its absorption by the parasite seems to have little more effect on the welfare of its host than does the taking of the maternal milk by a lusty infant.

Longevity of the host is also enhanced by the fact that this parasite does not eliminate solid waste during the feeding stage. As in many other hymenopterous larvæ that dare not soil the food supply, the hind intestine has become closed (fig. 46). As solid wastes cannot be voided in the ordinary way, they are stored up in the mid intestine until the feeding period has passed. It must be remembered, however, that the liquid food of this larva is so digestible that the indigestible residue to be eliminated or stored up is exceedingly small.

Moreover, there is little or no elimination of urates during the feeding stage. In the first stage the malpighian tubes are well developed (there are two of these tubes, each of which bifurcates near the point of invagination) and appear to have an open lumen. That they have fallen into at least partial disuse, however, is indicated by the fact that they empty into a part of the hind intestine that has become completely closed. It is possible that these tubes function to a slight extent by collecting wastes from the system and storing them up until the hind intestine opens again. Even this, however, seems doubtful because no urate crystals can be seen in cross-sections of the tubes and the tiny little ducts seem to be empty. In the second stage the tubes are no longer sealed up and it is now mechanically possible for urates in solution to be voided through the hind intestine. From their histological condition, it seems unlikely, however, that they actually make use of their opportunity. The lumen is still very tiny (c.f. fig. 47) and appears to be empty; and the cells have no appearance of activity. In the third stage the tubes are in the same condition as in the second stage.

So much, then, for a glance at factors tending to conserve the food supply by preserving the life of the host larva. When the host larva dies, however, the appetite of the parasite suddenly increases very greatly; the parasite becomes so ravenous, indeed, that it consumes the remainder of the food supply before putrefaction has time to set in. This phenomenon of a destructive feeding period is probably of as wide occurrence among parasitic hymenoptera as it seems to be among the tachinidæ. These two widely separated groups have met a similar problem in a similar way.

Another of the life processes that has been profoundly modified on account of the acquisition of a parasitic method of existence is that of respiration. In the generalized ancestors of *Campoplex*, the larvæ presumably breathed in the regular way by means of a set of tracheæ connected with the air supply by spiracles. The same, indeed, holds true for the adult *Campoplex* from which its larvæ are secondarily derived. In the highly specialized larva, however, such a method of breathing is out of the question because the larva is now surrounded by a fluid medium instead of air—the larva has become, in fact, an aquatic organism instead of a terrestrial one. As there are modifications in the method of breathing as we pass from the more specialized first stage larva to the more generalized third stage one, it will be convenient to outline the process for each larval stage separately.

In the first stage larva, the tracheæ are present and are filled with air. The spiracles are, however, closed. How, then, is the supply of oxygen maintained? Before speaking of ways and means, it may be pointed out that the animal has been reduced in size to microscopical proportions and that its need for oxygen has therefore become greatly lessened.

The most characteristic feature of the larva is the long tapering caudal appendage or tail (fig. 56). This structure has excited the curiosity of all those who have studied these interesting creatures and various suggestions as to its function have been put forward.*

The suggestion that the structure may be a blood gill (put forward by Timberlake, amongst others) is also open to objections. It can be seen by examining serial sections that the dorsal vessel does not enter the appendage; and that the appendage itself is completely filled with tracheids applied so closely to one another that no channel or lumen exists along which the blood stream could flow. This blood gill supposition was based on the false idea that the appendage was empty and that its lumen was, consequently, continuous with the general body cavity.

The most fruitful of these suggestions is that the structure is a breathing organ. It is not, however, as has been supposed, a blood gill but is a tracheal gill of a highly specialized type. This was partly demonstrated by Timberlake (who finally adopted the blood gill hypothesis) when he examined a living larva and saw that a trachea ran into the tail; such observations are difficult to make, as it is only in living material that the canals are filled with air and so visible in transmitted light. The demonstration can be completed, however, by reference to the minute structure as seen in serial sections. Following the course of the two main tracheæ back from the head it can be seen that they begin to branch profusely at about the junction of the mid and hind intestines. The branches branch and so each trachea becomes surrounded by a bundle of tracheids. These two bundles pass into the appendage and completely fill its entire lumen (fig. 52). Following the bundles down the narrowing tail (figs. 53 and 54), the tracheids become fewer until finally there is only a single one left. This reduction of the tracheids is due to the fact that they successively terminate in the wall of the gill.

These terminations are of unusual interest. Each tracheid passes through the basement membrane of the gill wall and so opens into an air chamber. This air chamber is the lumen of a single hypodermal cell of great size, the protoplasmic contents of which have retreated to the cell walls (fig. 52). The nuclei of these hypodermal cells can easily be seen. This modification of the

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*The suggestion put forward by Seurat and others that such appendages may have a locomotor function is now generally set aside as being highly improbable. In life, as already pointed out (p. 65), the larva scarcely moves at all and is clearly incapable of any movement comparable to swimming. Such inability to swim is also indicated by the fact that the second stage larva is nearly always found in the same part of the host as is the first stage, namely, the few last caudal segments. And finally, by the fact that a histological study of the appendage shows it to be devoid of muscles.

There are also objections to the view maintained by Weissenberg that the appendage is used to some extent for storing waste products of metabolism. Solid wastes cannot pass into it because it has no connection whatever with the lumen of the alimentary canal. Urates and other such wastes are not stored in the appendage because the collectors of these substances, namely, the fat body and malpighian tubes, do not enter the appendage.

Weissenberg's paper on the biology and morphology of some endoparasitic larvæ of hymenoptera (Weissenberg, R. '09, Sitz. Gessell. Natur. Freunde, No. 1) I have not been able to see. According to Daniel Tower, however, (Jour. Agr. Res., Vol. 5, No. 12, Dec., 1915) he speaks of pseudopod-like structures that extend into the lumen of the hind intestine; and he supposes that these structures are rudimentary proctodeal appendages. In the species I have studied, there is a structure extending into the lumen of the hind intestine (figs. 48, 49 and 50). It occurs in all three larval stages and there is a corresponding structure in the fore intestine of each stage. As the structure is flexible and controlled by powerful muscles, it seems probable that it functions as the valve of a pump and that it plays an important part in the movement of food materials through the alimentary canal. If this is the case, the structure could not be regarded as a rudimentary proctodeal appendage of the kind that finds a more complete expression in the case of *Apanteles*.

FIG. 55. *Campoplex pilosulus* Prov. Second stage larva. Cross section, through middle of caudal appendage. Cu.=cuticle; Tr$_1$=tracheid; Tr$_2$=longitudinal section of tracheid ; Nuc.=nucleus of a tracheid cell; B.M.=basement membrane; Hyp.=hypodermis.

FIG. 56. Diagram of *Campoplex pilosulus* Prov. First stage larva. Br.=brain; Ht.= heart; S.G.=salivary glands; Gon=gonad; Tr.=trachea; C. App.=caudal appendage ; H. int.=hind intestine; M. int.=mid intestine; F. int.=fore intestine; B.C.=buccal cavity.

FIG. 57. *Campoplex pilosulus* Prov. Diagram of second stage larva. Br.=brain; Ht.=heart; S.G.=silk gland; Gon.=gonad; Tr.=trachea; C. app.=caudal appendage ; H. int.=hind intestine; M. int.=mid intestine; F. int.=fore intestine; Mal. Tub.=malpighian tubes; B.C.=buccal cavity.

FIG. 58. *Campoplex validus* Cr. Diagram of third stage larva. Br.=brain; Ht.=heart; S.G.=salivary gland; G.=gonad; H. int.=hind intestine ; Mal. tub.=malpighian tubes; M. int.=mid intestine; F. int.=fore intestine; Md.=mandible; B.C.=buccal cavity.

FIG. 59. *Apanteles hyphantriæ* Riley, larva—just after hatching. In this stage the silk glands show as four straight tubes. The caudal vesicle has not yet invaginated. The mandibles are too small to be seen under a binocular, but can be made out under the high power of a microscope. The length of the larva here drawn is 2 mm.
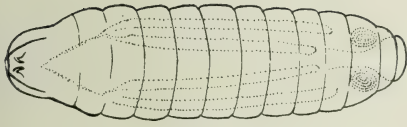
FIG. 60. *Apanteles hyphantriæ* Riley. Second stage larva. In this stage the suppressed legs show on each of the three thoracic segments as a pair of invaginal discs. The invaginal discs of the wings are also plainly visible. The silk glands still consist of four tubes. These tubes are more convoluted, however, than in the first stage larva. (For the sake of clearness only two of these tubes are represented in the drawing.) The caudal vesicle has now attained its full size and is the most conspicuous feature of the larva. The mandibles are so small that they cannot be made out under a binocular. The length of the larva here drawn is 4 mm.

FIG. 61. *Apantales hyphantriæ* Riley. Spinning stage of larva, 3d instar. This stage is passed outside the host, and its chief function is the spinning of a cocoon. The larva now breathes through spiracles; the caudal vesicle becomes completely withdrawn; and the larva is now possessed of tiny spinules arranged more or less in rows; there is also a series of lateral elevations that probably prevent the cocoon from closing the spiracles.
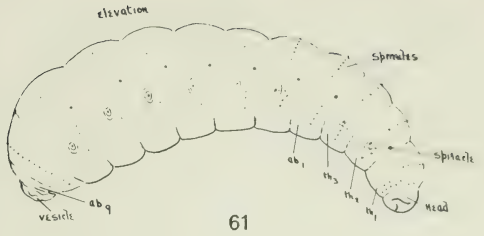
FIG. 62. See page 78.

FIG. 63. *Apanteles hyphantriæ* Riley. Female reproductive system. Ov.=ovaries ; Ac. Gl.=acid gland reservoir; Alk. Gl.=alkaline gland; Sp.=spermatheca; Ut.=uterus ; Ovip.=ovipositor.
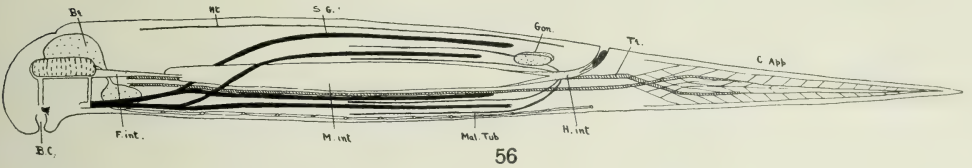
FIG. 64. *Apanteles hyphantriæ* Riley. Stage II. Cross section showing the invagination of a trachea. Cu.=cuticle; Hyp.=hypodermis; Br. lob.=brain lobe; Œs.=œsophagus; Sal. gl.=salivary gland; Sub. œs. gang.=subœsophageal ganglion; Tr.=trachea invaginating.
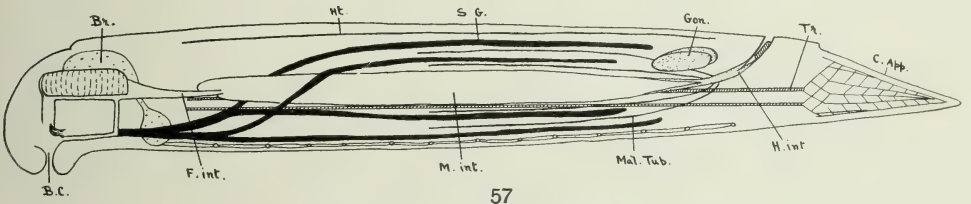
59

elevation

spinules

ab_1 th_3 th_2 th_1

spiracle

Head

vesicle

ab_9

61

Br.   Ht   S.G.   Gon.   Tr.   C.App

B.C.   F.int.   M.int   Mal.Tub   H.int

56

Br.   Ht   S.G.   Gon.   Tr.   C.App.

B.C.   F.int.   M.int.   Mal.Tub   H.int

57

Br.   Ht   S.G.   G

B.C.   Md   F.int.   M.int.   Mal.Tub.   H.int

58

th_1 th_2 th_3

60

Cu

Tr.

$Tr._2$

Nuc

B.M.

Hyp

55

Ov.

Acid Gl.

Sp.

Ut.

Alk.Gl.

Ovip.

63

Cu

Hyp

Br.lob.

Oes.

Sal.H.

Tr.

Sub.oes.gang.
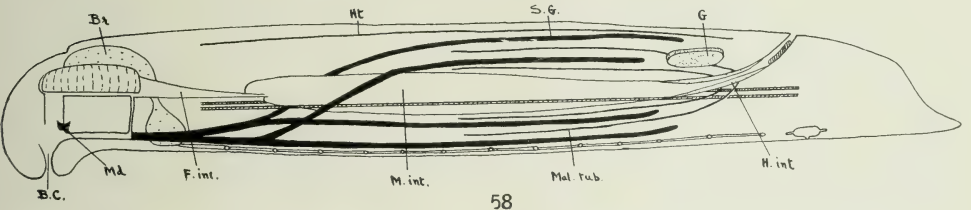
64

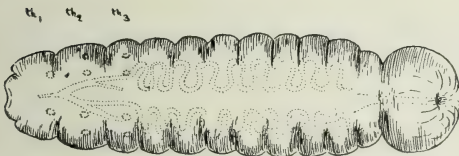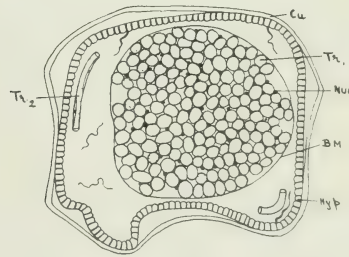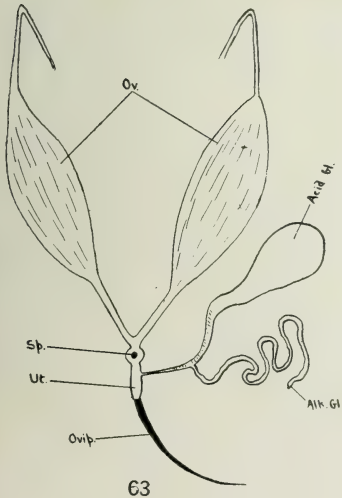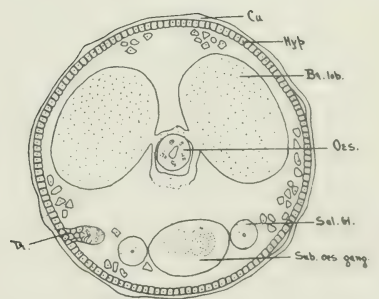gill wall cells results, of course, in an exceedingly thin wall through which oxygen can the more readily be gathered from the surrounding blood of the host. In a sense, then, each hypodermal cell of the gill wall has become modified into a breathing organ.*

In the second stage the problem of breathing is met in the same manner as in the first stage. The caudal appendage is a tracheal gill with its minute structure essentially similar to that of the previous stage. In the sections examined (fig. 55) the air spaces of the hypodermal cells that form the terminations of the tracheids do not show up as distinctly as in the sections of first stage appendages. I am inclined to think, however, that this may be due to imperfect sectioning rather than to any real difference in the structure of the wall cells. In this stage the gill is wider at the base, due to the increased larval girth, and is notably shorter than in the first stage. Although the shape is different, the structure seems to house fully as many tracheids as before.

In the third stage larva, the caudal appendage has disappeared completely. Sections through the caudal region show a mass of fat cells but no sign at all of the tracheids so conspicuous in the two earlier stages. The problem of breathing is no longer met with the aid of a tracheal gill. A study of sections shows that the spiracles are now open and from this it can be inferred that the necessary supply of oxygen is drawn into the tracheal system through them. At this time most of the liquids of the host have been transferred into the parasite and the host is becoming dry and hollow. As the process of feeding continues (and it is greatly accelerated in this instar) the spiracles come more and more in contact with air.

This account of larval habits will perhaps be made clearer by reference to the larval diagrams in figures 56, 57 and 58.

Compared with the tachinid parasites of the webworm, the method of pupation of *C. pilosulus* is exceedingly simple. Instead of going to earth, the larva simply spins a cocoon within the empty skin of its host and pupates inside the cocoon. When the adult is ready to emerge, it finds itself equipped with a powerful set of jaws or mandibles, and with these tools the task of tearing an emergence hole through the cocoon is a simple one.

It might be supposed that this method of pupation would render the pupa liable to desiccation. This danger is offset by the shortness of the pupal period which, as we have seen, is usually less than two weeks in duration.

A disadvantage of this pupation habit is that some of the pupæ are exposed to the attack of secondary parasites. The cocoons are placed wherever the host caterpillar happens to perish. If this is inside the protecting web of the *Hyphantria* colony, then all is well, for pupal parasites do not like to get beneath an entangling web. But if it is close to the surface of the web or outside it altogether, then secondary parasitism is quite likely to occur. Usually most of the cocoons are found well inside the web, for the obvious reason that as soon as the caterpillars begin to feel indisposed, they remain at home. Sometimes, however, the webs become shrunken by rain and many cocoons are brought within distance of secondary parasites.

Campoplex (Ameloctonus) validus Cress.

The species of *Campoplex* known as *validus* was described by Cresson in 1864 (Proc. Ent. Soc. Phila. III, p. 258) as *Mesoleptus? validus*. Cresson's genus *Mesoleptus* was found to be congeneric with Holmgren's *Limneria* and the species became *L. valida*. It now seems that *Limneria*, *us*, *um*, is not a valid genus. Next choice on the priority list is Gravenhorst's *Campoplex* so that the species becomes *C. validus*. In Viereck's recent and invaluable "Hymenoptera of Connecticut," the species is listed under Ashmead's subgenus *Ameloctonus*.

* Vide discussion of *Apanteles* (p. 62) to see how this organism has met the same problem of breathing by developing a blood gill by a prolapsus of the hind intestine.

The following generic synonymy is based upon that given by Dalla Torre:—

Campoplex Gravenhurst
Synon. *Limneria* Holmgren
Limnerium Ashmead
Ichneumon Gmelin
Macrus Provancher
Mesoleptus Cresson
Ophion Blanchard
Poriyon Zetterstedt

The following specific synonymy is also based upon that given by Dalla Torre:—

validum Cress. 1864.
excavata Prov., 1875.
valida Prov., 1879.
valida Ashmead, 1890.

Description of Adult

The original description given by Cresson (1.c.) is as follows:—

"Black; wings hyaline, areolet, triangular; legs pale rufous; the posterior tibiæ and tarsi annulated with black and white; basal segment of abdomen much dilated at tip.

"Female: Black, rather shining, robust, slightly pubescent; head and antennæ entirely black, the latter nearly as long as the body; tegulæ pale testaceous; metathorax sulcate behind and transversely aciculate, the elevated lines distinct, the central area not defined. Wings hyaline, nervures and stigma blackish, the former pale at base; areolet rather large, subtriangular, subpetiolated. Legs pale rufous, the four anterior tibiæ and tarsi in front yellowish-white; posterior coxæ and their trochanters above, black, their tibiæ whitish with a broad black annulus at tip and a narrow one near the base, their tarsi black with the base of the first three joints whitish. Abdomen robust, subfusiform, entirely black; first segment slender at base and much dilated at tip; apical segments broad and subcompressed; ovipositor exserted nearly the whole length of the body, piceous. Length 4 lines; expanse of wings 6 lines.

"Male: Resembles the female, except that the antennæ are longer and the abdomen subcylindric.

"Hab.: Pennsylvania. Mr. C. A. Blake.

"This may not belong to *Mesoleptus* on account of its long ovipositor and robust basal segment of the abdomen, otherwise it has the characters of the genus."

Hosts

The host favoured by *Campoplex validus* seems to be *Hyphantria* in any of its races. Dr. L. O. Howard also records it as a minor parasite of *Hemerocampa leucostigma*. Mr. Timberlake has reared the species on *Malacosoma americana* which indicates that this insect may be a normal host in the southern parts of the United States where the parasite has two generations.

Range

The range of this species is evidently as wide as that of its preferred host Dalla Torre gives it as Canada and the United States. Viereck, in the New Jersey list, says the species is of wide occurrence in the United States. In Canada I have reared it from many places in Nova Scotia, New Brunswick, Quebec and Ontario; and Mr. Baird and I have taken it from many points in British Columbia.

Descriptions of Early Stages

Excellent descriptions of the early stages of this parasite have been published by Mr. P. H. Timberlake (U.S. Bur. of Ent. Tech. Ser. No. 19, Part V, 1912) in a paper that is still available, and to this admirable account I would refer the reader for full information. Dr. L. O. Howard also has a short account of this parasite in his study of Insect Parasitism (Tech. Ser. No. 5, 1897). He includes good figures of the adult and of the cocoon.

The life-history also has been worked out by Timberlake (1. c.) for Melrose Highlands. At Fredericton, it is so closely similar that a separate account is unnecessary. There seems to be only a single generation a year.

The habits and behavior almost exactly parallel those for *C. pilosulus*. The problems of digestion, of the preservation of the food supply, and of breathing are met in identically the same manner and to the account of the preceding species the reader is referred.

The habit of pupation differs from that of *C. pilosulus* in that the host skins are not incorporated in the cocoon. The habit of hibernation is also different in that *validus* hibernates in boreal and transitional zones in the pupal stage.

Apanteles hyphantriæ Riley.

Systematic History

The species of Microgaster known as *Apanteles hyphantriæ* has been known since Riley described it in 1886. It was placed by Riley in Foerster's genus *Apanteles* and therein it has remained ever since.

The original description taken from the 1886 Report of the Entomologist for the United States Department of Agriculture is, as follows:—

"*Apanteles hyphantriæ*, n. sp. Female: Length 3 mm. Close to *Apanteles xylina* Say, with which it may be compared. Differs as follows: Mesonotum without the faint median carina or polished posterior margin; scutellum not polished; first abdominal segment about as broad as long, with a quite distinct median carina, the apex of which is polished, and its posterior margin broadly bilobed. In *A. xylina*, the first abdominal segment is rather slender and longer than wide, without distinct carina and with the apex almost straight. A quite distinct carina on the second segment, wanting in *xylina*. Third abdominal segment coarsely pitted at base, the rest quite distinctly shagreened; in *xylina* the basal punctuation is less pronounced and the rest of the segment smooth. All coxæ black (in *xylina* the apical half of lower edge of posterior coxæ is reddish); the first joint of metatarsi perceptibly stouter than the other joints (almost like the other joints in *xylina*). Cocoon white and single (in *xylina* the cocoons are enclosed in woolly masses).

"Described from two female specimens."

The adult is figured on Plate I; the cocoon on Plate II.

Host

The only host this species seems to have been reared from so far is *Hyphantria*.

Range

In the United States this species is known to occur in the District of Columbia and in Massachusetts; it probably occurs also in many other states. In Canada, it occurs in Nova Scotia, New Brunswick, Quebec, Ontario and British Columbia. From this it would seem that the distribution is probably as wide as that of the genus *Hyphantria*.

Descriptions of Early Stages

Egg:—The egg of this species of *Apanteles* has not been seen and cannot be described. The egg shells as they appear in parasitized caterpillars, are very thin and faintly yellowish.

Larva:—First Stage (endoparasitic).

The larva as it hatches from the egg is almost colourless and presents no strongly chitinized parts such as a head capsule. It is destitute of spines or hairs (fig. 59).

The head, which is, of course, a composite structure of at least six segments, appears to consist of two segments, one of which telescopes into the other. The three thoracic segments are distinct and behind them can be distinguished eight abdominal segments. The eighth is, however, a composite structure, presumably representing a fusion of segments eight to eleven.

The tiny mandibles can be seen by flattening out a larva and using a 4 mm. objective. Under a binocular they can only be made out with difficulty. Some of the internal structures may be seen through the integument of the larva. The silk glands are each bifurcated. The resulting four tubes are at first straight and then as the larva grows they become somewhat convoluted.

In the caudal region of the larva are the gonads which appear as two conspicuous masses of tissue. In fresh material these show clearly under a binocular. At the extreme caudal end is the beginning of what will later be the caudal vesicle. In this condition the vesicle can be easily mistaken for an extra abdominal segment.

Second Stage (endoparasitic).

As the larva grows, some structural changes take place and it seems probable that an actual ecdysis occurs. The process of molting has not been observed, however, and the stage here described as the second may prove to be a later part of the first.

The larva remains colorless and still has no head capsule, spines or hairs (fig. 60).

The head still appears to consist of two segments, one of which telescopes into the other. In the three thoracic segments the wing and leg buds are now visible. The paired discs of tissue representing these organs are shown in the figure as circlets of dots.

The abdomen still consists of apparently eight segments, the last of which is composite in structure.

The mandibles seem to be as inconspicuous as in the first stage larva and can scarcely be distinguished under a binocular microscope.

The caudal vesicle has now attained its full development and shows as a conspicuous bladder at the caudal end of the larva. Its diameter is as great as that of the abdominal segments.

Of internal structures, the silk glands consist of four tubes as before, but each tube has become considerably convoluted; these tubes now occupy most of the body cavity in the abdominal part of the larva. The gonads remain as before.

Third Stage (Spinning stage).

When the full fed larva leaves its host to pupate, it leaves a molt skin behind it. The resulting instar is a non-feeding one interpolated between the feeding stages and the pupal stage, and its chief function is the spinning of a cocoon.

This stage is characterized by the presence of functioning spiracles that develop serially from before backwards. There are eight pairs of these spiracles, one on the second thoracic segment and one each on the first seven abdominal segments. As the spiracles open, the caudal vesicle recedes and disappears. The larva also differs from the earlier parasitic stages in the possession of tiny

hairs or spinules. Most of these are arranged (fig. 61) in transverse rows in
the middle of the thoracic and first eight abdominal segments; a few of them are
irregularly placed. The larva is also characterized by a series of elevations
on each side of its body; these elevations are placed as indicated in figure 61.

Pupa and Cocoon (Plate II, fig. E).

The snow-white cocoon is usually found close to the caterpillar that has
served as a food supply. It is about 4 mm. long; is opaque; and is possessed
of but few attachment threads. In shape, it is almost cylindrical and is rather
bluntly rounded at each end. The adult emerges from the cephalic end of the
cocoon by pushing off a circular cap that often remains hinged to its cocoon
by a few silken cords.

LIFE-HISTORY

The following notes on life-history refer to conditions at Fredericton,
N.B., unless otherwise indicated.

The female flies usually oviposit during the first two weeks of August
when the webworm larvæ are in stages two and three.

After the eggs are laid the embryos develop very rapidly; it seems likely,
in fact, that the larvæ hatch within seven days of oviposition but the point has
not been definitely established (c.f. Tower's account of *Apanteles militaris*.)

The length of time spent as a feeding larva corresponds to the time occupied
by a host caterpillar in its development from a half-grown third stage to a fully
grown fourth stage condition. This varies a little according to the season
but would ordinarily be about two weeks. How this interval is proportioned
between the first and second stages of the larvæ of the parasite remains to be
determined.

As the second stage larva emerges from its host caterpillar it molts. Emer-
gence from the host is effected very rapidly and is completed in a few minutes.
In a case observed at this laboratory by Mr. R. P. Gorham, the larva was half
out and beginning to spin in less than a minute and was completely clear of the
host in six minutes.

The spinning stage of the insect is a comparatively short one. Mr. Gorham
found that the last larval skin is usually shed in about fifty hours after leaving
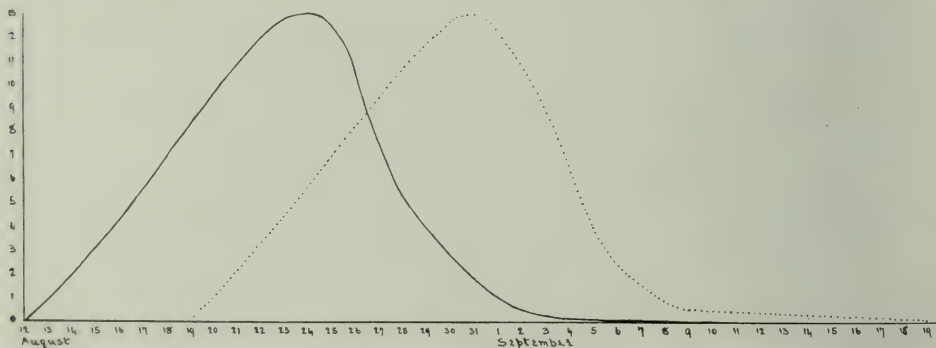the host.

FIG. 62. Pupation record of 194 *Apantales hyphantriæ* Riley, reared at Fredericton in
1912. The first cocoon appeared on August 12 and the last on September 11. Most of the
cocoons appeared during the last two weeks of August. As the pupal period lasts for about
seven days, the dotted line has been added to represent the probable emergence of adults
at Fredericton in 1912. The first fly is indicated as having emerged on August 19 and the
last on September 19.

In 1912, a pupation record was kept for the 194 *Apanteles* reared that year.
The host caterpillars were kept in open Fiske trays and the cocoons picked out
from day to day. As will be seen from the plotted curve (fig. 62), the first

cocoon appeared on August 12 and the last on September 11, while the majority of them appeared during the last two weeks of August. In 1920, Mr. Gorham kept a similar record and his results agree closely with those obtained in 1912.

The pupal stage lasts for five or six days and probably varies somewhat according to temperatures. In 1912 it lasted for about five days in the case of 13 cocoons kept under observation.

In 1920, Mr. Gorham saw a larva emerge from its host at 11.30 a.m. on August 13 and the fly emerge from its cocoon at 5.30 p.m. on August 21. In this case, 198 hours elapsed between the two operations and by deducting 50 hours for the time spent as a spinning larva, there remains a pupal period of 148 hours or approximately six days.

The season of issuance is shown approximately for 1912 by the dotted curve in figure 62.

The adults go into hibernation but nothing is known concerning their spring activities.

In New Brunswick there may be two generations a year but if so, the first must be devoted to attacking a host other than *Hyphantria*. In Washington, D.C., Riley (1886) points out that the species has two generations per year as does *Hyphantria* at the same place.

Habits and Behavior

Adults.—For several years it has been a practice to rear some flies and keep them in cages for observation. Flies so treated have nearly always lived to go into hibernation but have failed to live through until the spring. From these flies the following notes on habits and behavior have been secured.

The flies have been kept healthy and active through the autumn on a diet of sugar granules and water with an occasional addition of dry wheat flour, fresh banana peelings, and fresh goldenrod flowers yielding pollen. Under natural conditions they probably feed largely upon pollen and water.

When feeding on sugar, a granule is taken up by means of the powerful little jaws and is held firmly in the mouth. It is then apparently dissolved rather than crushed, and passes into the intestine in liquid form. The flies drink water freely from damp blotting paper by pressing the lips firmly down against the paper with the mandibles withdrawn into the mouth.

The flies are much more active on warm days than on cool ones and continue to be active at night, providing the temperature remains above 60° F. or thereabouts. The effect of rain upon them has not been noted.

No female flies have been observed depositing eggs but something of the process can be learned from a study of the reproductive system. This consists essentially (fig. 63) of a pair of ovaries, each filled with a large number of tiny tubes or follicles containing eggs; of a very small chamber or spermatheca in which the male spermatozoa are stored; of a short, and so non-incubating, uterus into which opens a large gland; and finally, of a curved, hardened and extremely sharp ovipositor. By tracing the path along which an egg must pass from one of the ovaries to the ovipositor, we shall perhaps learn something about the method of reproduction. An egg that has grown to full size must pass from the follicle in which it has been nourished into the oviduct. From here it passes—when its turn comes—into a uterus, the capacity of which is, apparently, one egg at a time. As it passes into the uterus, the egg glides past the opening of the spermatheca and in so doing receives a spermatozoan through the micropyle. In connection with the spermatheca, there is probably a pair of accessory glands that secrete a fluid in which the spermatozoa live; these glands are so tiny, however, that they cannot be seen in binocular dissections; all that one sees in this way of the spermathecal system is a slight swelling on the uterus close to the oviducts and an almost yellow dot, the spermatheca itself, in the middle of the swelling. The next thing encountered by

Fig. 65. *Apanteles hyphantriæ* Riley. Second stage larva. Longitudinal section (diagrammic). M.=mouth; Br.=brain; Ht.=heart; Mal. tub.=malpighian tubes; S.G.=silk glands.

Fig. 66. *Apanteles hyphantriæ* Riley. Stage II. This diagram shows the points at which the drawings of *Apantales* were made.

Fig. 67. *Apanteles hyphantriæ* Riley. Second stage larva. Cross section through the centre of *Apanteles* (at point M-N). This shows the normal size of the heart. Hyp.=hypodermis; Ht.=heart; Ch.=chitin; S.G.=silk gland; M. int=mid intestine; tr.=trachea; Gang.=ganglion.

Fig. 68. *Apanteles hyphantriæ* Riley. Stage II. Cross section made through point K-L, shows the heart commencing to enlarge. Hyp.=hypodermis; Cu.=cuticle.

Fig. 69. *Apanteles hyphantriæ* Riley. Stage II. Cross section through *Apanteles* at a point (I-J) just anterior to the vesicle. This shows the hind intestine beginning to close. Cu.=cuticle; Hyp.=hypodermis; Ht.=heart; H. int.=hind intestine; Bl.=blood; Mal. tub.=malpighian tubes; Gang.=ganglion.

Fig. 70. *Apanteles hyphantriæ* Riley. Stage II. Cross section through the vesicle near its anterior end (at point G-H). Cu.=cuticle; Ht.=heart; H. int.=hind intestine; Mal. tub.=malpighian tubes; Hyp.=hypodermis.

Fig. 71. *Apanteles hyphantriæ* Riley. Stage II. Cross section through vesicle of *Apanteles* (through point E-F), showing the closed condition of the hind intestine from which the malpighian tubes are taking their rise, and the enlarged condition of the heart. Ch.=chitin; Hyp.=hypodermis; Ht.=heart; Bl.=blood and lymph; H. int.=hind intestine; Mal. tub.=malpighian tubes.

Fig. 72. *Apanteles hyphantriæ* Riley. Stage II. Cross section of vesicle of *Apanteles* (through point C-D), showing the invagination of the hind intestine and the huge size of the heart; Cu.=cuticle; Ht.=heart; Bl.=blood and lymph; H. int.=invagination of hind intestine; Hyp.=hypodermis.

Fig. 73. *Apanteles hyphantriæ* Riley. Longitudinal section of cells of caudal vesicle, showing the intercellular spaces. Int. sp.=intercellular space; Cu.=cuticle; Cell=hypodermal cell; Nuc.=nucleus; B.M.=basement membrane.

Fig. 74. *Apanteles hyphantriæ* Riley. Cross section of some of the caudal vesicle wall cells in the region bathed by the impure blood of the parasite below the dorsal vessel. The intercellular spaces permit of purification of the blood by exchange of gases.

Fig. 75. *Apanteles hyphantriæ* Riley. Diagrams showing development of caudal vesicle from the proliferation of hypodermal cells near the invagination of the hind intestine. *A* shows condition in the egg just before hatching, *B*, *C* and *D* show condition in successively older larvæ.

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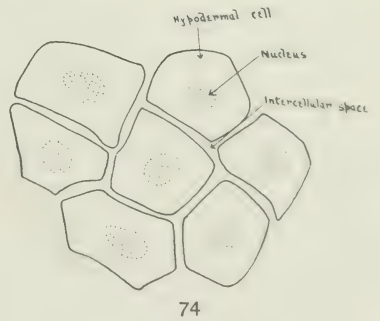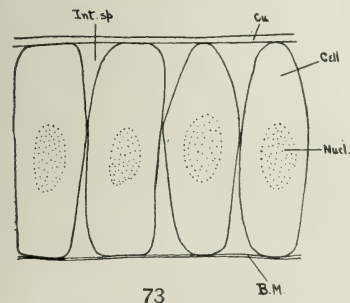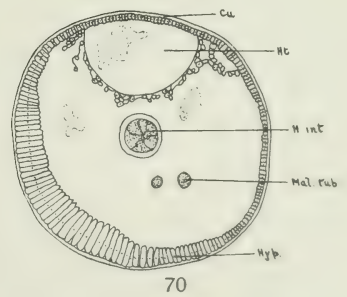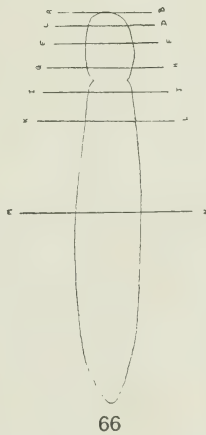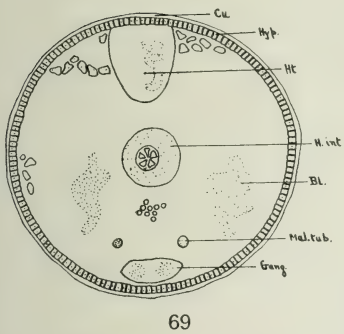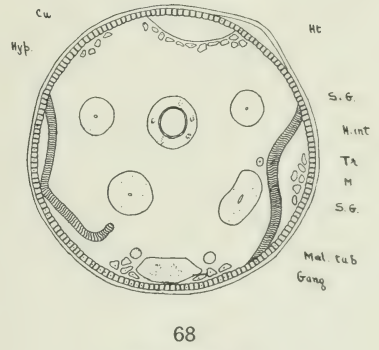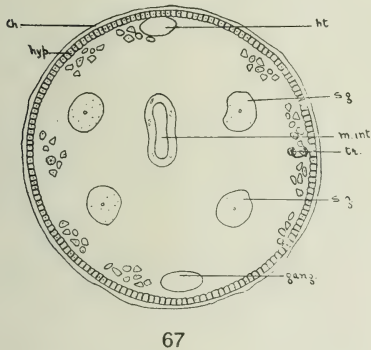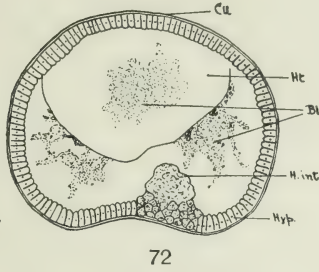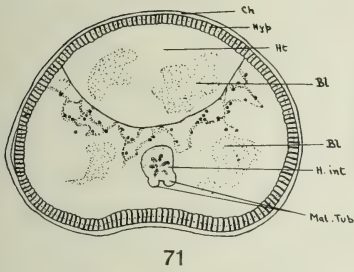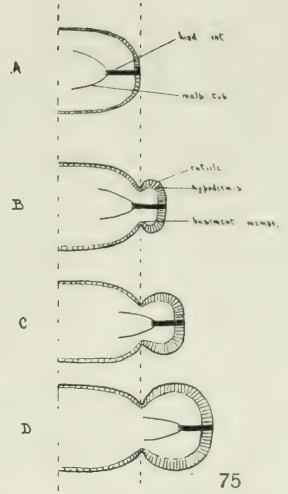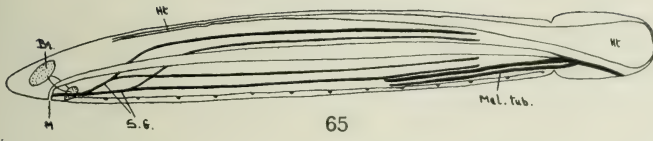
the now fertilized egg is the open duct of a large and active gland and the egg is evidently bathed at this point with a fluid. One of the functions of this fluid is probably lubrication but it is unlikely that this is the only function. The fluid is secreted by the cells of a simple but much convoluted tube (fig. 63) that is evidently homologous with the alkaline gland of ants and bees; and it is stored in a reservoir nearly half as large as an ovary that can be homologized with the reservoir of the acid gland of ants and bees. That the fluid is not in this case, a poison is clear from the fact that victimized caterpillars remain healthy for days and weeks after being attacked. The fluid may be an antiseptic that makes the ovipositor virtually a sterile needle; or may help protect the eggs from being devoured by phagocytes.

The egg, now fertilized and bathed in fluid, passes into the base of the ovipositor and in an instant becomes 'planted' in the general body cavity of a fall webworm larva.

First and Second Stage Larvæ.—As nothing is known of the embryological development of this species of *Apanteles* except that it takes place in the body cavity of its host, I will refer my readers to Tower's account for *A. militaris* (1. c.) and will pass directly to a consideration of the larva. In order to get a perspective, suppose we compare this truly remarkable creature with the generalized type of hymenopterous larva from which it has been derived.

The ancestral larva was evidently much like that of a modern sawfly; it lived in the broad light of day, in an atmosphere of purest air; and fed on vegetation. It was well fitted for such a method of existence, being caterpillar-like in general form and being possessed of eyes to see with, a whole series of spiracles to breathe with, a number of pairs of legs to walk with, and a pair of powerful mandibles to eat with. It also had an alimentary canal adapted for the assimilation of vegetable matter and for the disposal of quantities of waste materials. Our *Apanteles* larva is profoundly different from this. In the inside of a caterpillar it lives its life in total darkness; it is surrounded by the body fluids of its host instead of by air, and it feeds on the juices that bathe it. Such things as eyes, spiracles and legs are now of no use to it whatever and have become completely suppressed. Mandibles also are of little or no use and have become reduced to microscopic proportions; and as waste materials can no longer be voided on account of the resulting contamination of the food supply, the alimentary canal has become modified into a tube with only one opening, namely, the mouth.

With this brief reminder of the essential changes that have occurred in the transition from the generalized free living terrestrial larva to the highly specialized parasitic larva living in a bath of blood and lymph, we will consider some of the problems an *Apanteles* larva has to meet.

There is the problem, for instance, of breathing or blood purification. During the parasitic instars the spiracles remain closed; figure 65 shows a characteristic section taken through one of these tracheal invaginations; the tube has become plugged with hypodermal cells and the opening sealed over with a layer of chitin. Casting in other directions for a breathing organ, one's attention is drawn to the conspicuous bladder-like structure at the caudal end of the larva (fig. 60).

As the structure of the heart or dorsal vessel throws light upon the nature of this caudal vesicle, it may be referred to at this time. By studying cross-sections it can be seen that the dorsal vessel (ht in figure 65) is a long, slender tube with a backward funnel-shaped expansion that terminates in the posterior end of the caudal vesicle. This can be seen by glancing at the series of drawings of cross-sections taken at the places indicated in figure 66. At the place indicated by the line M-N, for instance, the dorsal vessel is a tiny tube (fig. 67); at K-L it is a little larger (fig. 68); and from here it expands rapidly (figs. 69-72) until C-D is reached, when it occupies about two-thirds of the entire section. As

the dorsal vessel is closed posteriorly except for the presence of lateral valves and as there are numbers of tiny muscles in connection with its posterior expansion, I gather that the part of it housed in the caudal vesicle is valvular and pulsating. From these things it seems to follow that the caudal vesicle is intimately associated with the circulatory system and that its chief, and probably only, function is the purification or oxidation of blood; or in other words, that it is a blood gill.

In support of this view there is also the fact, as revealed by a study of sections, that the lower part of the 'bladder' is largely filled with blood and lymph.

From the standpoint, also, of the wall structure of the vesicle, the organ seems to be essentially a blood gill. The wall is composed of a single layer of hypodermal cells with a thin cuticle of chitin outside and a thinner basement membrane inside. The hypodermal cells, however, are modified in a peculiar way, especially those that are below the dorsal vessel; or, in other words, those that are constantly bathed with impure blood. A close examination under high power reveals the fact that these cells are considerably shrunken so that nearly all of them are surrounded by intercellular spaces. Figure 73 shows some of these cells as they appear in a cross-section of the vesicle, and figure 74 shows some of them as seen from the surface of the vesicle. It is obvious that by an arrangement rendering the wall porous to gases, this greatly assists in an exchange of gases between the impure blood of the parasite and the comparatively purer blood of the host.

Another point that seems to favour the blood gill idea is that the caudal vesicle becomes withdrawn and ceases to function just as the larva emerges from its host and the spiracles become open. With the opening of the spiracles there would naturally be no need for a blood gill.

The caudal vesicle develops, as shown in the accompanying diagram (fig. 75) by proliferation of the hypodermal cells situated at or close to the point of invagination of the hind intestine; and as the vesicle grows, the hind intestine, with the attached malpighian tubes, is carried into it. The cells from which the structure grows are practically at the union of the hind intestine and the integument. If one regards them as belonging to the hind intestine, then the vesicle could be considered as a proctodeal structure. On the other hand, if one regards these cells as forming part of the integument, then the vesicle would be integumental rather than proctodeal.

In a paper on *Apanteles glomeratus* reviewed by Tower (Journ. Ag. Res. Vol. V, No. 12, p. 504) the author, Weissenberg, says that "the vesicle is formed by the rapid growth and elongation of the cells of the proctodeum which form the posterior end of the plug at the posterior end of the stomach, together with those adjacent cells at the anterior end of the proctodeum which surround the opening of the larval malpighian tubules and extend posteriorly a short distance to the rudiments of the adult malphighian tubules. The mass of elongated cells thus formed grows out through the anal opening of the embryo and immediately following hatching these elongated cells are compressed lengthwise so that their long axes become their short ones, resulting in broad, flat cells joined edge to edge to form the thin wall of the caudal vesicle." I am not quite sure that I understand this conception of the origin of the vesicle, but in any case, Weissenberg's conception of the wall being composed of broad, flat cells joined edge to edge to form a thin wall does not agree at all with the conditions obtaining in *A. hyphantriæ*, where the wall cells are longer and the wall thicker than anywhere else in the insect's body.

In the case of *Apanteles militaris*, which has been studied by Tower, the author comes to conclusions very similar to those of Weissenberg. Speaking of the vesicle he says, (l.c. p. 497) "when first seen, it lies inside the abdomen but can be seen gradually to grow out through the anal opening which becomes

greatly distended. The stomach becomes lengthened and extends outside the body into the vesicle, its blind end being fastened to the inside wall of the vesicle posteriorly and ventrally."

Muesebeck (Jour. Agr. Res. Vol. XIV, No. 5, July, 1918) also follows Weissenberg's interpretation very closely in his interpretation of the condition in *Apanteles lacteicolor*.

In conclusion, then it would appear that our larva has met its problem of breathing or purification of the blood through the development of an elaborate blood gill. The blood and lymphatic stream flows backward in the general body cavity into the gill, the walls of which it bathes. It is now, on account of the porous construction of the gill wall, in membraneous contact with the purer blood stream of its host and receives a new supply of oxygen. From here the stream is pumped into the large dorsal vessel and carried forward through the aorta and back again by way of the head into the body cavity. In the backward course to the gill some oxygen is probably taken up by the developing tracheal system, particularly in the second instar when this system becomes quite elaborately developed; and some is undoubtedly carried directly in the blood stream to places where metabolism is proceeding.*

The problem of feeding is another one that has to be met in a peculiar way by these endoparastic larvæ. In the case of *Apanteles*, the process is practically the same as in *Campoplex*. The larva feeds on the blood and lymph stream in which it lies; its alimentary canal is a blind tube only open at the mouth and no waste products are voided until after the larva has emerged and spun a cocoon.

If a living first stage larva be placed in a bath of caterpillar juices and watched under a binocular, one nearly always notices that the almost microscopic mandibles are moving so rapidly that the neighbouring liquid is in a condition of agitation. The mandibles are too small to serve for lacerating tissues and they probably function in directing the current of fluid food materials into the mouth. This confirms an observation of Seurat's made some twenty years ago, to the effect that in the case of *A. glomeratus* (1. c. p. 60), "the mandibles are incessantly in motion." Tower also records a similar observation for *A. militaris* (1.c. p. 498).

It is possible that a secretion from the salivary glands aids in digestion. The common duct of the glands in sections that have been examined is open and the open lumen can be traced far back into each gland. I have failed to find any region of the glands, however, that appears to be in marked activity. In the first and second stage larva these glands consist of four straight tubes, each pair of which unites, as shown in figures 76 and 65. This arrangement is similar to that recorded by Seurat for *Apanteles glomeratus* (1.c. p. 62) and differs from that recorded by Tower for *Apanteles militaris*. In the case of *A. militaris*, the glands are described as two straight tubes instead of four, but as Tower did not have an opportunity of making sections, it is possible that a branching of the tubes was overlooked.

*The problem of the function of the caudal vesicle in *Apanteles* species is an old one. Ratzeburg seems to have been the first to suggest a respiratory role, but a copy of his "Ichneumonen der Forstinsecten" is not available and I do not know whether he regarded the instrument as a tracheal gill or as a blood gill. Weissenberg (l.c.) regarded the organ as being primarily a blood gill and also an excretory organ. Kulagin, according to Seurat (Contributions à l'étude des Hyménopteres Entomophages Ann. Sci. Nat. Zool., 1899, p. 66) thought that the organ had an excretory function (Zool. Anz. 1892, p. 85). This idea is also developed by Tower, who concludes that (1.c. p.505) "the caudal vesicle is primarily an excretory organ and that the function of respiration is secondary." The chief difficulty in accepting this view is that the alimentary canal does not open into the vesicle either directly or indirectly through the malpighian tubules. The fluid seen by Tower between the two layers of the sac at the time of molting was evidently the molting fluid secreted by the molting fluid glands and not, as he thought, a discharge of waste products of digestion. Seurat (l.c. p. 67) puts forward another view when he says: "I believe that one of the essential functions of this vesicle is that of the locomotion of the larva in the interior of its host." A difficulty here is that, although these larvæ are capable of very slight motion in a lateral direction, yet they seem quite incapable of moving forwards or backwards. Another structural difficulty is that the vesicle is devoid of muscular tissue, except for the infinitely small muscles in connection with the valves of the heart.

The liquid food, with possibly some salivary secretion added, is, apparently, sucked through the fore intestine by means of a pharyngeal pump similar to that figured for *Campoplex*. It then passes through the oesophageal valve, which, as in *Campoplex*, is very poorly developed, and into the mid intestine. The food here mixes with the secretion liberated from the wall cells and becomes digested.

The mid intestine is in gross structure a short straight tube, the simplicity of which is mute testimony to the assimilable nature of the food material. As it is the most important organ in this stage of the larva's career, one would expect it to have a considerable diameter. In the few larvæ that have been sectioned, however, the diameter, as indicated in figure 68, is surprisingly small. In these particular larvæ, however, there was very little food material in the intestine and the intestine walls were not in a condition of active secretion. In a larva that has fed recently it seems likely that the mid intestine may become considerably distended.

In the case of *Apanteles glomeratus*, Seurat (1.c p. 60) evidently supposed that the fat body of the host was the chief food material; and in the case of *militaris*, Tower refers to the food (1.c. p. 498) as a mixture of fat body and blood. This idea of the fat body being the chief, or one of the chief foods of the feeding stages of parasitic hymenoptera, is an old one but I have been unable to convince myself of its truth. In the case of this *Apanteles*, one can find no fat globules in the remains of food in the mid intestine; the mandibles seem altogether too diminutive to be capable of lacerating even the softened cells of the fat body; and there is the further difficulty that as the larva seems incapable of forward or backward movement, it would be unable to crawl from one pasture to another. That the larvæ seldom or never move is indicated by the fact that nearly all of the hundreds dissected from webworm caterpillars during the past ten years have been lying in the caudal region.

As in the case of *Campoplex*, where this question is discussed at some length, it seems highly probable that the food material consists almost entirely of the blood and lymph stream and that the only fat globules ingested are the minute ones floating in this stream.

In a second stage larva that has been sectioned, the hind part of the mid intestine is empty and the walls are not in a condition of active secretion. The larva would probably have dined shortly had it not been placed without warning on the sacrificial altar table of a prying scientist. The sacrifice was not in vain, however, for the emptiness of the intestine solves for us the problem of the elimination of waste products of digestion. It is obvious that the larva cannot soil its food supply any more than a city can have a sewer system emptying into the supply of drinking water. The larva solves the question by avoiding it; it has learned to eat foods that have been already digested by its host larva (blood and lymph) and there are few waste materials to eliminate. The waste products are at least so small in volume that they can be comfortably stored until the larva has spun its cocoon. When the cocoon has been completed, the larva voids, as Tower notes for *militaris*, a little mass of waste materials "at the anal end of the cocoon". This little mass represents the sum total of waste products eliminated by an animal during the period of growth. In man, this period would be from infancy to puberty and the wastes eliminated would have to be measured in tons.

These notes on the process of digestion and the function of the alimentary canal would be incomplete without brief mention of the malpighian tubes and the hind intestine. The two malpighian tubules have their points of attachment in the closed portion of the hind intestine. From these points they pass forward, one on either side of, and almost touching, the ventral nervous system for nearly half the length of the larva, when they end blindly. In the feeding stages of the larva they are greatly reduced in size and indeed, for most of their

length, are scarcely larger than nerve commissures and are many times more slender than the salivary glands. As the closure of the hind intestine prevents egress of wastes collected from the blood stream by these tubules, their function is necessarily restricted to collecting and storing wastes. As the wall cells exhibit no histological signs of activity, however, and as the minute lumina are, apparently, devoid of content, it seems that these tubes have even lost the faculty of collecting and storing wastes and that they have become very nearly, if not entirely, functionless.

As the mid intestine passes backward, it passes imperceptibly into the hind intestine and it is difficult to say where the one begins and the other ends. So far as function is concerned, however, the essential point of interest is that the hind intestine is hermetically sealed with a plug of chitin that extends from its place of attachment to the wall of the vesicle to just in front of the place of insertion of the tubes of malpighi. Its function is to prevent the egress of both solid and liquid wastes and so to prevent the contamination of the food supply.

Third Stage Larva. The essential function of the third stage larva is the spinning of a cocoon. The larva (figure 61) is now supplied with backwardly directed spinules and little hairs and is capable of considerable movement. The spiracles have become open and in connection with these is a series of lateral elevations. These elevations (figure 61) do not occur in any other stage of the insect's development and evidently have an important mission to perform. They probably serve to prevent the cocoon from coming in contact with the spiracles and so serve to insure a free passage of air through the tracheal system.

Just why this species of *Apanteles* should construct for itself such an elaborate cocoon is not exactly clear. It lives in it for a few days only, yet the cocoon is made as carefully as that of species that hibernate in the pupal condition. The practice can, perhaps, be explained on the assumption that the wintering habits have undergone modification and the ancestral cocoon has been preserved.

One is amply repaid by spending a few hours watching a larva weave its silken shelter (plate II). On August 16, at 11 a.m., an *Apanteles* larva was found in the act of emerging. It was placed, with its host, upon a glass slide and watched by Mr. Gorham until the cocoon was completed. When found, the larva was one-third out of its host; about three minutes later it was half out and had already begun to spin a strand of silk that it attached to the glass at points as far distant as it could reach in each direction. At 11:10 the larva drew its body completely out of the host and began to spin rapidly. It now lay along the right hand side of its host and began spinning as far back toward the caudal end as it could reach, bending its body to the right for the purpose. It was weaving what was destined to be the open-mesh outerlayer of the cocoon.

The threads of this outer layer were spun transversely in a series of three or four large loops beginning at a point on the glass alongside the larva, and ending in the hairs of the host, or sometimes on the spinules of the larva itself. The larva worked from the glass up each time anchoring each loop to the already woven fabric and bringing the head back to the glass in a rapid sweep after attaching the third or fourth loop. At 11:17 the larva had made the walls and roof of this outer layer but had not closed in the ends. The larva now changed its position by taking a full turn to the left, which enabled it to fill in the front end of the cocoon by spinning as before a series of loops from the glass upwards. It took 11 minutes to fill in the front end and to strengthen the framework by adding a few loops to the inside. It then reversed its position and filled in the caudal end by spinning little rows of loops running, as before, from left to right. By half past eleven, or just half an hour after commencing its task, the larva had worked back to the position in which it

started and had finished the outer open-mesh framework of its cocoon. The work at this stage resembled a piece of crochet work, being made up of chains of loops closely resembling those made with a crochet hook.

The larva commenced immediately to weave the inner loops. Instead of spinning simple loops, as before, the larva now began to spin chains of double loops, each pair of which resembled a figure 8. These loops were made by the larva rocking its head from side to side while slowly moving forward, and each chain was attached laterally to the one previously spun. The result was a tissue of very close mesh and of very regular structure. In spinning this layer, the larva would remain in one position until it had covered all the ground it could reach, and then would shift to a new position. As a result of these shifts, it completed four end to end turns in the first hour spent on the inner layer. By half-past one the cocoon was so thick that the larva could be seen no longer by reflected light, but its movements could be followed by transmitted light. The spinning and turning went on until three o'clock, when all movements ceased. Three and a half hours had thus been consumed in completing the inner layer, which, with the half hour used for the crochet-like framework, gave a total of four hours for the making of the cocoon.

Mr. Gorham and the writer have watched other larvæ spin their cocoons, and although small variations in method occur, yet the above account seems fairly typical for the species.

The silk itself differs from that of most lepidopterous larvæ, including the silkworm, in that the two strands of which it is composed (one from each spinneret) remain distinct instead of being pressed into a single strand. Under a binocular, the two strands can be seen distinctly as the larva spins.

THE PROCESS OF MOLTING IN THE DIFFERENT STAGES

The process of molting deserves brief notice. I have been unable to observe a first stage larva in the act of molting into the second stage, but Tower has been more successful in the case of *Apanteles militaris*, and Seurat (l.c., p. 106) has observed the process for *A. glomeratus*. At this period the larva has no organs of locomotion and is incapable of energetic movement, so that the simple method of crawling out of an old molt skin is out of the question. Tower saw (l.c. p. 505) the portion of the first skin covering the vesicle become greatly swollen until it was finally ruptured and from this it appears that this ecdysis is achieved mainly through the instrumentality of the molting fluid glands which cause the old skin to be floated off.

The next molt is evidently begun inside the host caterpillar and completed as the larva emerges. With the molt skin once shed from the head and thorax, the larva finds itself in the possession of little rows and cushions of backwardly directed hairs and spinules, with the help of which it is able to crawl forwards. As it passes through the integument of its host, the entire molt skin is left in the passage and the larva becomes free to begin its new task of spinning a cocoon. Incidentally, it may be said that the old molt skins left in the host serve as landmarks that enable one to distinguish webworm larvæ killed by *Apanteles* from those killed by any other of its insect foes. Molt skins are shed in a similar way in the integument of cabbage worms killed by *Apanteles glomeratus* and in this case are easier to see because the host integument is smoother.

In the case of the next molt, Mr. R. P. Gorham found that the skin was pushed down in a little mass at one end of the cocoon. In the case of *A. militaris* Tower found (l.c. p. 501) that "the last larval skin is molted and pushed to the anal end of the cocoon and lies over the waste." As the next stage is provided with legs, the fly has no difficulty in kicking itself loose from its pupal skin as it emerges from its cocoon.

Emergence from Cocoon

As the cocoon is spun no provision whatever is made for the exit of the future fly and the fly has to cut its own doorway. This it does quite easily by shearing the silk with its mandibles. The mandibles come through the walls of the cocoon at each bite, one mandible coming through the opening made by the last cut. In this way the cut is made halfway round the cocoon. Then the fly stops, follows back along the cut with its mandibles and starts cutting in the opposite direction until the other half has been sheared. The two cuts do not quite meet and the few unsevered strands of silk serve as a hinge for the door that is now almost made. The fly now examines the cut it has made and reaches through here and there for any strands of silk missed. It then pushes the cap upward (plate II) and passes through the open door head first, stopping on the way to cut a thread here and a thread there until the door falls backward on its hinge. In a case noted by Mr. Gorham, a fly took exactly 15 minutes to cut its way out of the cocoon.

Therion morio Fabricius

(Exochilum mundum Say)

Systematic History.

The species now known as *Therion morio* was first described by Fabricius as *Ophion morio*. In 1835 it was redescribed by Thomas Say, who had not seen the type of Fabricius' species *morio*, as *Ophion mundus*. When Wesmael broke up the large genus *Ophion* he erected the genus *Exochilum* for the reception of *morio* and related species. As *mundus* was still held to be distinct from *morio*, our species became known as *Exochilum mundum* Say. Viereck finds, however, that *mundum* is the same species as *morio*, in which case the name would be *Exochilum morio* Fab., were it not that the genus *Exochilum* is found to be pre-occupied by Curtis' genus *Therion*. In Viereck's "Hymenoptera of Connecticut," the species is now listed as *Therion morio* (Fab.)

Description of Adult (Plate VI).

The original description is not available, but the following one by Say will serve to identify the species (Say, Leconte Edit. Vol. II, p. 695; and Boston Jour. Nat. Hist. 1, 239, 1835): "*Ophion mundus*—Black; antennæ, posterior tibæ and tarsi yellow. Inhabits Indiana.

"Male: body black; head with the front, nasus and anterior orbits, greenish yellow; antennæ fulvous yellow; three or four basal joints above black; the first joint beneath greenish yellow; trunk with rather dense, short hairs; wings purple-black; abdomen much compressed; basal joint cylindrical; second segment as long as the first, or a little longer, compressed towards the tip; anterior pair of the feet yellowish before; intermediate pair with a line before and base of the tibiæ yellowish; posterior pair with the tibiæ, excepting the tip, and the tarsi, excepting the terminal joint, fulvous yellow.

" Length, near one inch.

" Resembles *flavicornis* Nob. which, however, has the first segment of the abdomen considerably longer than the second. It is also allied to *morio* Fab., but that species is described to have the wings blue-tipped with brown and the legs black, the anterior ones testaceous."

A very useful key for the separation of *Therion* species will be found in the splendid work by Viereck already referred to (l.c. p. 286).

The species is well figured in half-tone by Howard in the "Insect Book," plate X, figs. 13 and 14.

THERION MORIO adult female.

Range.

A copy of Dalla Torre is not available, and I can find little information from other sources concerning the distribution of the species. It is known to occur, at least, in Washington, D.C., in New Jersey, in Massachusetts, and in Indiana. In Canada, it occurs in Nova Scotia, New Brunswick, Quebec, Ontario, and British Columbia. From this it appears that the species has a very general distribution over the entire North American continent.

Hosts.

Several hosts are known for the species. Viereck (l.c. p. 287) lists *Vanessa cardui*, *Iphidicles ajax*, and *Zerene centenaria*, and it is also a common parasite of *Hyphantria cunea*.

Descriptions of Early Stages.

Egg.—The egg, as it appears at the time of fertilization, can be distinguished very readily from those of all the other parasites of *Hyphantria* because it bears an elongation or caudal appendage. It also has a yellowish-coloured elevation in the position indicated in figure 83, which is probably the micropyle, although it is a considerable distance from the pole of the egg. The egg is almost colourless, although occasionally the chorion darkens considerably just after oviposition. The yolk not only fills the main cavity, but also fills the caudal appendage.

The feeding embryo.—The stage one finds in *Hyphantria* larvæ is what may be termed a feeding embryo. The egg has partially hatched in that the chorion has become sloughed off; it has not completely hatched, however, because an embryonic membrane is retained as a sac around the larva. The larva within the sac has completed its embryonic development, feeds through the sac, and grows in size fairly rapidly.

The larva within this sac (fig. 77) is characterized by the possession of a large, strongly chitinized head capsule, a pair of formidable-looking mandibles (fig. 78) large enough to be readily seen under the low power of a binocular microscope, and by a somewhat arcuate caudal appendage that is rounded off at the distal end. There are no spiracles; the hind intestine is closed; and the colour of the larva is milky-white, with the exception of the head capsule, which is amber-coloured, on account of its being strongly chitinized.

The Second Stage Larva.—The second stage larva (fig. 79) one can find in the spring in the pupæ of *Hyphantria*. The head capsule differs notably from that of the first stage (compare figs. 78 and 79). It is only very lightly chitinized; the mandibles, instead of being gently curved, are almost triangular in shape; and the arrangement of the facial plate is different, as shown by the figures. The caudal appendage is smaller in proportion than in the first stage. The suppressed remnants of the legs show in this stage as paired buds on the thoracic segments. There are no spiracles, hairs or setæ. The larva is milky-white, as in the preceding stage. It is, of course, larger, the specimen used for the figure being about half an inch long.

Third Stage Larva.—The third stage larva scarcely differs in general appearance from the second stage larva. It is a rather dirty-looking whitish grub about half an inch long, with a not very strongly chitinized head capsule at one end and with a caudal appendage, such as shown in figure 79, at the other. A closer inspection, however, reveals some differences. The head capsule is more of a cap than a bag, and the facial plate (fig. 80) shows clearly the position of the eyes and of the antennæ. On the thoracic segments one can make out not only the rudiments of the three pairs of legs, but also those of the two pairs

Fig. 76. *Apanteles hyphantriæ* Riley. Stage II. Showing the second branching of the salivary glands. Ht.=heart; S.G.=silk gland; F. int.=fore intestine; Tr.=trachea; Gang.=ganglion; Hyp.=hypodermis; Cu.=cuticle.

Fig. 77. *Therion morio* Fab. The feeding embryo. Note the sac of cellular tissue in which the larva is enclosed. Also note the large chitinous head capsule and the horn-shaped caudal appendage.

Fig. 78. *Therion morio* Fab. Head capsule of first stage larva or feeding embryo. *A*=dorsal view; *B*=ventral view.

Fig. 79. *Therion morio* Fab. Second stage larva and a front view of the head capsule. H. cap.=head capsule; Leg. rud.=leg rudiment; Tr.=trachea terminating in tracheids; C. App.=caudal appendage.

Fig. 80. *Therion morio* Fab. Facial plate of third stage larva.

Fig. 81. *Therion morio* Fab. Female reproductive system. In the female from which this was drawn there were about 480 eggs filled with yolk and ready for fertilization. Ov.=one of the ovaries; Fol.=one of the egg follicles; Ovid.$_1$=one of the oviducts; Ovid$_2$=the other oviduct; Ut.=uterus; Ovip.=ovipositor; Res.=reservoir of alkaline gland; Alk. gl.=alkaline gland; Ac. Gl.=acid gland; Sp.=spermatheca.

Fig. 82. *Therion morio* Fab. *A*—some eggs in one of the follicles. *B*—a single egg enlarged, showing the conspicuous micropyle and the caudal appendage. F.=follicle wall; Mic.=micropyle; Ant. Pole.=anterior pole.
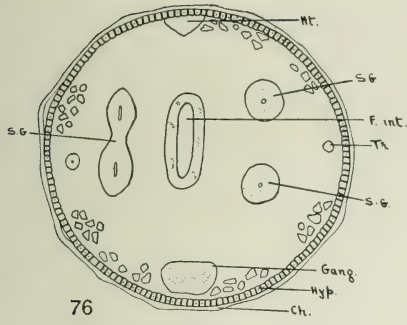
Fig. 83. *Therion morio* Fab.: Egg that has been deposited for four days.

Fig. 84. *Therion morio* Fab. Egg eight days old. C.A.=caudal appendage; Integ.=integument of host caterpillar to which the egg is attached.

Fig. 85. *Therion morio* Fab. Cross section through head of feeding embryo. The head capsule is largely filled with fan-shaped muscles that control the powerful jaws. Also note the muscular valve hanging from the roof of the mouth; the muscles of the valve are attached to the roof of the head capsule. H.C.=roof of the head capsule; Mus.=one of the muscles controlling the pump; Cu.=chitinous cuticle; Hyp.=hypodermal cells; B. Cav.=buccal cavity; Pl.=plunger of pump; Md.=mandible; Lig.=ligaments of the two chief groups of muscles controlling a mandible.

Fig. 86. *Therion morio* Fab. Stage I. Longitudinal diagrammatic drawing of a larva, showing the arrangement of the different systems and organs of the body. Sac.=embryonic sac; D.V.=dorsal vessel; S.G.=salivary glands; Br.=brain; F. int.=fore intestine; Pl.=plunger of pump; B.C.=buccal cavity; Oes. Val.=œsophageal valve; M. int.=mid intestine; Mal. tub.=malpighian tubes; H. int.=hind intestine; Tr.=bundles of tracheids in caudal appendage.

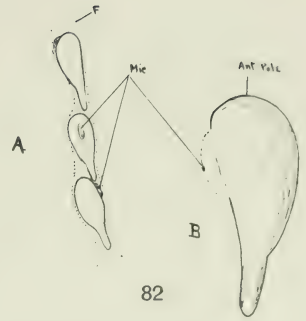Fig. 87. *Therion morio* Fab. Diagram of the pharnygeal pump of the feeding embryo. The plunger moves up and down by the alternate contracting and expanding of its controlling muscles. Mus.=muscles controlling plunger attached to roof of head capsule; H.C.=the strongly chitinized head capsule; Pl.=plunger of the pump; Md.=one of the mandibles; F. int.=fore intestine; M. int.=mid intestine; Œs. val.=œsophageal valve.
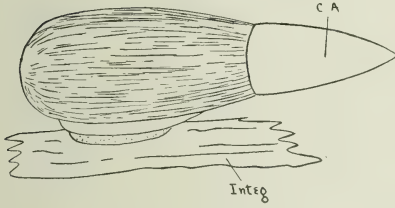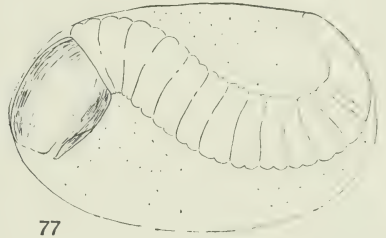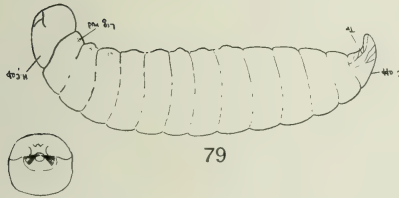
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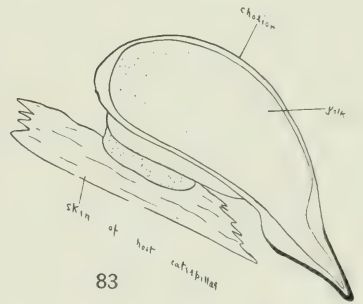of wings. By looking very closely, also, one can make out a complete set of open spiracles.

Pupa.—No material has been preserved of this stage, and a description cannot be made.

LIFE-HISTORY.

The following notes on life-history are largely the result of observations made by Mr. A. B. Baird at Agassiz, B.C. They will apply particularly to the life-history of this insect at that place.

Adults were first noted in the field about the middle of July; their maximum abundance occurred during the second week in August, and they remained fairly plentiful until late in the fall. Under laboratory conditions, the adults emerged about a month later than the *Hyphantria* moths.

The period of gestation is very short. A female issuing on August 19 mated the following day with a male that had issued on the 15th; she began to oviposit an hour and a quarter after mating. Mating took five and fifteen minutes, respectively, in two cases noted.

With favourable weather, the oviposition of the eggs can take place very rapidly. We have the performance record of an Agassiz female that oviposited in six caterpillars in fifteen minutes. From dissections of New Brunswick host caterpillars, it has been found that after a few fine days the *Therion* parasitism frequently rises from nil to the highest percentage for the season.

Embryological development takes place within a host caterpillar, but the exact time it takes is not known. An egg dissected from a caterpillar that had been oviposited in four days previously, is still completely filled with yolk and has not developed beyond the blastoderm stage. Some eggs known to be eight days old, however, are in an advanced stage of development. Judging from these eggs, it seems that from ten to fourteen days are needed for embryological development.

The insect passes the greater part of its life as a feeding embryo or first stage larva enclosed by an embryonic membrane. The chorion of the egg is usually sloughed off during the middle two weeks of August, while the host caterpillar is in its third or fourth stage and the parasite in the feeding embryo stage. In the following spring, when the host is in its pupal stage, the parasite is still a feeding embryo.

At Agassiz, no second stage larvæ were found until June 6, and no third stage until June 13. As a rule, from one to two weeks, depending on temperature, are spent in the second stage. This is in striking contrast to the very long time spent in the previous stage.

Probably not more than a week is spent in the third stage; and from two to three weeks are spent in the pupal stage.

The life-history is summarized in the accompanying table:—

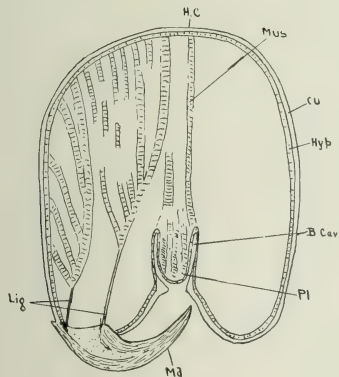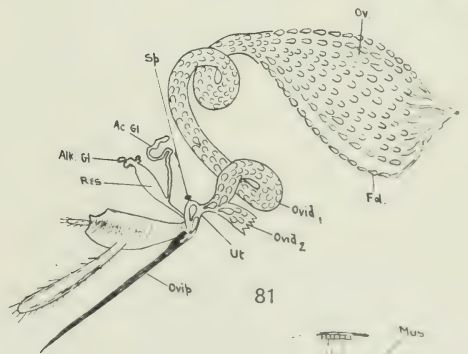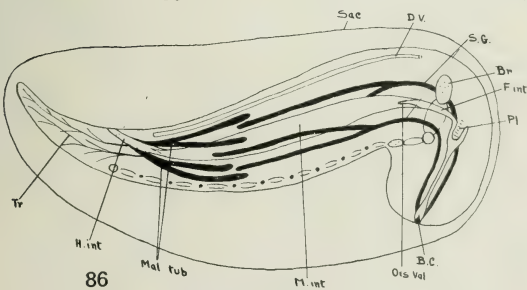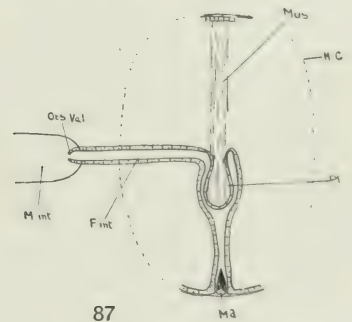|	June				July				Aug.				Sept.				Oct.				Nov. to May
	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	1	2	3	4	
Adult............																					
Egg.............																					
Feeding embryo.																					
2nd larva.......																					
3rd larva.......																					
Pupa............																					

At Fredericton, the life-history is essentially the same as at Agassiz, but it is probable that the adults do not usually emerge quite as early.

At these two places there is only one generation a year.

It is possible that there are two or more varieties of the parasite each attached more or less closely to a particular host. Our own studies have been confined to *Hyphantria*, and the life-history of the parasite synchronizes fairly well with this host. The parasite is recorded, however, from *Vanessa cardui*, the development of which does not parallel very closely that of *Hyphantria*, and it seems possible that a special race of *Therion* may have been developed, the life-history of which synchronizes with *Vanessa* rather than with *Hyphantria*.

HABITS AND BEHAVIOUR.

Adults.—The adults of *Therion* are rather docile creatures and quite amenable to laboratory discipline. They are quite sensitive to changes of temperature, becoming active on warm, sunny days and inert on dull, chilly ones. They can be kept alive on a diet of sugar and water, but will also nibble such substances as the fresh inside of a banana skin and pollen grains of goldenrod. In nature, they visit the flowers of goldenrod species and the pollen from this source is, perhaps, their chief article of food. They will mate readily in captivity; in the case of a pair of adults watched by Mr. Baird, the flies met one another on the wing and then fell to the earth to go into copula.

The thread-waisted condition of these flies is very noticeable. In the female, one can readily see that the possession of such a waist renders the fly much more facile in the use of the ovipositor. In fact, as one watches a fly walking over a *Hyphantria* web, nimbly ovipositing in a caterpillar here and there, it is obvious that her abdomen is attached to the thorax by what might be termed a "universal joint" and that in consequence she can victimize many more larvæ than she could without such a joint. In the male, however, there is a similar slender waist and a similar universal joint; in this case it is difficult to see what possible advantage there can be in such an arrangement, and one may suppose that the waist owes its existence to causes similar to those which have produced mammary glands in male human beings.

Another curious development of these flies is the lateral flattening of the abdomen. Even when the female abdomen is swollen with eggs, the lateral flattening is still very marked (Plate VI). It seems probable that this condition has been slowly evolved through a long line of ancestors that have been singling out hairy caterpillars for their hosts. So far as *Hyphantria* is concerned, at least, the fly has no difficulty in getting the abdomen in between rows or clusters of hairs and so securing good leverage for inserting the oviposior, whereas, in view of the great size of the fly, it could scarcely get in amongst the hairs to oviposit were its abdomen cylindrical instead of flattened.

This recalls the cases of the tachinid flies, *Compsilura* (p. 40) and *Lydella* (p. 46) in which there is a comparable lateral flattening of the abdomen, brought about, presumably, in the same way. It also reminds one of the more familiar case of the flea, which has not only the abdomen but also the head and thorax, strongly compressed laterally and which is thus enabled to slip through a thick forest of hairs with remarkable facility.

To what extent this explanation could be applied to other cases of lateral flattening in the parasitic hymenoptera (and there are numerous instances) I do not know. There are, at least, many cases in which flies with compressed abdomens are known to attack hairy caterpillars. There are, also, cases such as the *Labrorrhycus*, a parasite of the Ugly-nest Tortricid, where a fly with a compressed abdomen attacks a comparatively hairless larva. It is possible in such cases, however, that the ancestral stock did attack hairy caterpillars or that the parasite has other hosts which are hairy. At the moment of writing

I cannot recall a case of a hairy caterpillar acting as host for a large hymenopterous fly with a cylindrical abdomen. In the case of flies as small as *Campoplex* or smaller ones, the abdomen is slender enough to pass in between hairs and there is no need for lateral compression. Also, there is, of course, no need for lateral compression in the case of flies such as many of the Pimplas and Theronias that attack only pupæ or prepupæ.

From the structure of the female reproductive system one learns something of the reproductive habits. This system (fig. 81) consists essentially of the usual pair of ovaries, each with an oviduct leading into a common uterus; a spermatheca, two glands corresponding to the acid and alkaline gland of the bee, and lastly, of an ovipositor. Each ovary contains a number of egg follicles that empty into an oviduct. When the female is ready for oviposition, the oviduct becomes lengthened and distended and somewhat convoluted. The uterus is only large enough to hold two eggs at a time and does not, in consequence, serve as an incubator. The spermatheca is a very inconspicuous, pale-yellow, mushroom-like body in the position shown in the figure; it is remarkable that so tiny a bag can hold enough spermatozoa to fertilize all the ovules, for it is many times smaller than the spermathecæ of most tachinid flies, and in the tachinids there are usually three of them. Opening into the uterus are the ducts of two glands corresponding probably to the acid and alkaline glands, respectively, of ants and bees. The ovipositor is a very finely pointed instrument, well adapted for puncturing the skin of a webworm larva. When the female is ready for oviposition, the entire reproductive system is packed full of ovules of uniform size, each of which is ready for fertilization; each follicle contains about 12 such ovules; each oviduct is filled from end to end with ovules arranged about 4 deep; and the uterus contains 2 ovules. The capacity of the system is from 480 to 500 ovules, but, as ovules pass down the follicles they are possibly replaced to an extent from the germarium at the upper end, in which case these figures would represent only a minimum capacity.

When a fly is ovipositing, all that one can see is that she makes a sudden drive at the victim with her ovipositor and that the victim squirms. It is usually the caudal part of the larva that is pierced, for the simple reason that this is usually more stationary and so a better target than the forward part. Even when a caterpillar is alarmed the caudal part is much more likely to remain quiet than the head and thoracic segments. Just how far the ovipositor is inserted I do not know, but from the fact that the eggs are left adhering to the inside of the victim's integument, it seems to follow that the ovipositor passes either only just through the integument or that it is buried so deeply that the egg is left adhering to the wall of the caterpillar opposite to which the incision is made. As the ovipositor is just about long enough to pass right through the bodies of webworm larvæ attacked, I suspect that the usual practice is for it to be buried in the victim so that its tip comes up against the wall opposite the one in which the puncture is made.

The webworm caterpillars attacked are usually those of the third and fourth stages; sometimes, however, second stage larvæ are attacked. It is unusual in insect parasitism to find so large a fly attacking such small caterpillars.

The eggs themselves are radically different from those of any of the other parasites of this host, and for that matter, from those of any other hymenopterous parasites of caterpillars that I have seen. For one thing, the posterior pole is drawn out into a slender elongation that gives to the egg a singular and characteristic shape (fig. 82.) And again, the region of the micropyle is greatly raised above the surrounding level (fig. 82).

The tapered posterior pole of the egg seems to have arisen in connection with the caudal appendage of the first stage larva or feeding embryo. If this view is correct, we have here an unusually fine example of acceleration or tachygenesis; for we have a larval organ, the development of which is foreshadowed

before fertilization takes place; an organ that is responsible for changing the shape of the yolk mass and so of the chorion that overlies it. It is known, of course, in a general way that important organs such as the jumping legs of grasshoppers and the mandibles of predacious beetle larvæ have a tendency to develop at a very early stage of embryological development and to obscure or prevent the development of neighbouring organs. At the moment of writing I can recall no other case, however, where the development of an organ is pressed back to so early a stage as to change the shape of the yolk mass and chorion.

In this connection it may be recalled that although *Apanteles*, *Campoplex*, and *Meteorus* all have a first stage larva with a caudal appendage, yet the species in these genera retain the generalized type of egg that is rounded off at both poles.

Returning to the other peculiar feature of these eggs, namely, the raised micropyle, the explanation of the raised area is simple enough when one examines an egg that has just been laid. Figure 83 tells the story. The egg shown is attached by means of the cushion or pedestal to the inside wall of the caterpillar. As eggs are invariably found resting on these little cushions, it seems logical to suppose that the cushions are provided with a sticky substance. It is likely that the sticky substance is supplied by one of the glands, shown in figure 81, that empty into the uterus, as the pedestals of ovules that have not reached the uterus do not seem to be sticky. The ovules stick neither to each other nor to the walls of the follicles or oviducts.

Just what advantage there may be in the eggs being anchored to the inside wall of the host caterpillars during embryological development was not at first clear. Unless there were an advantage, however, it is difficult to imagine how this quite elaborate sticky pedestal could have arisen. There are reasons for supposing that the habit is a relic of ancestral days when *Therion* attacked its host in the last larval instar. One can readily see that an unattached egg in a pupa undergoing histolysis would be at a disadvantage in the matters of oxygenation and phagocytic attack compared with an egg attached to the inner side of the wall of the pupa. That *Therion* once upon a time attacked old and not young larvæ is further indicated by the fact that even to day it is much more of a pupal than a larval parasite; although the eggs are laid in small caterpillars, they do not completely hatch until the host has pupated so that most of the larval growth, and all the larval molts, occur in the pupæ of the host. Indeed, *Therion morio* may actually attack some of its hosts other than *Hyphantria* in the last larval stage. Unfortunately, its habits in these other hosts are totally unknown. The large size of *Therion* is also suggestive of its being originally a parasite of the last larval or of the pupal stage.

The embryological development of *Therion* would make a most interesting study, as it evidently differs considerably from the generalized type. It is complicated by the development of the caudal appendage and by the development of the sac of cellular tissue that surrounds the first stage larva. In some eggs that are four days old, the blastula is developed in the usual way as a cellular layer surrounding the yolk (fig. 83). And in some eggs that are eight days old, the caudal region is greatly distended by an overgrowth of cellular tissue (fig. 84). Unfortunately, no later stages are available.

The feeding embryo.—The next stage of this insect is an anomalous one that may be termed a "feeding embryo." It consists of a loose bag of cellular material, enclosing a feeding larva.

Before discussing the problem of feeding, something may be said as to the mandibles (figs. 78 and 85). Instead of being minute, as in the first stage larva of *Apanteles* and of *Campoplex*, they are exceedingly large. They are controlled by an elaborate series of powerful muscles, some of which are shown in the cross-section through the head capsule represented in figure 86. These muscles, in fact, occupy most of the head capsule, as can be seen in whole larvæ mounted in balsam; and it is obvious that the unusually large capsule has arisen in

response to the need of proper anchorage for these muscles. There is no opening in the mandibles, so that they cannot be used as sucking tubes for taking up food materials from outside the sac. In life, they can be seen to open and close very slowly, and it is evident that they are not capable of rapid agitation; it follows that the mandibles do not function, as do those of *Apanteles* and *Campoplex*, for setting up a flow of food materials into the mouth. From their location in the sac, it also follows that they cannot be used for lacerating the tissues of the host. In short, the elaborate mandibles seem to have no function whatever in connection with the feeding of this stage; it is more likely that they are ambulatory.

In a webworm caterpillar one nearly always finds the feeding embryo of *Therion* somewhere in the caudal half of its victim. In a pupa, however, if a *Therion* is present it is invariably tucked away in the extreme caudal end, perhaps with the advantage of a better air supply. This change of position may be due entirely to the shrinking of the larva during pupation, but it seems more likely that the parasite actually progresses to the caudal end of its host by the use of its mandibles as grappling hooks, getting a purchase here and there through its encumbering bag.

The feeding machinery really starts, then, with the mouth. It consists of the fore intestine and its appendages, the salivary glands; the mid intestine; and of the closed hind intestine with its appendages, the malpighian tubes. These structures are represented diagrammatically in figure 86.

The structure of the fore intestine is shown in greater detail in figure 87. Liquid food is drawn into the mouth by means of a pharyngeal pump; it passes straight upwards to the pharynx, then along a horizontal tube into the mid intestine. The most interesting feature of the fore intestine is the pharyngeal pump. The plunger of the pump is controlled by a set of muscles attached to the roof of the head capsule; as the muscles contract, the plunger is probably drawn up and the liquid food above it forced along the horizontal tube. As the muscles relax, the plunger probably drops to its first position without forcing liquid food back into the mouth, and is ready once more for the upward stroke. My interpretation of the operation of this pump is based on a study of sections, and although I have been unable to satisfy myself as to some of the structural details, yet I feel that the main features have been demonstrated. One of the difficulties of this interpretation is that it presupposes a non-chitinous lining in the plunger part of the fore intestine. It can be recalled, however, that in these parasitic insects there is a reduction of chitin in the body wall generally, and in the caudal appendages particularly, to permit of breathing; and if a reduction can take place in one place, there is really no *a priori* ground for supposing that it may not take place in another, not excepting a special region of the fore intestine.

The food passes along the short horizontal tube through the œsophageal valve into the mid intestine. This valve is a very simple device, as shown in figure 87, for preventing food being regurgitated back from the mid intestine.

Before following the food material through the mid intestine, let us return to the mouth and consider for a moment the salivary glands. As indicated in figure 86, there are two salivary glands, each of which empties into the oral cavity. In the thorax, each of these tubes bifurcates, and the resulting four tubes pass back into the abdomen, where they end blindly close to the blind ends of the malpighian tubes. These salivary glands have a well defined lumen and in the case of six feeding embryos that have been sectioned, their wall cells exhibit many little white droplets of secretion (figs. 89 and 90). From the presence of this secretion, the open condition of the canals and the length of these tubes, one must suppose that they secrete a digestive fluid that is pumped with the food into the mid intestine. In a later stage it is their function to produce the small amount of silk needed for the cocoon.

The mid intestine is a short straight tube, suggesting at once the ease with which the food material is digested. In the six feeding embryos that have been sectioned, the walls of this digestor are in an active condition of secretion and particularly the cells at the blind end (fig. 90). As all six seem to be in about the same condition, one can surmise that our diminutive Diogenes does not take regular meals and then rest during the intervals, but that he feeds more or less continuously.

The food in the mid intestine differs from that of *Apanteles* and *Campoplex* in that one cannot make out any blood cells or even an occasional fat cell. This indicates that all cellular elements of the blood and lymph stream are strained out by the embryonic membrane surrounding the larva; or, in other words, that our parasite feeds only upon the strained juices of its host that manage to percolate into the bag in which it lives. The food itself is very finely granular in appearance and is evidently coagulated by the digestive secretion. That the coagulation is not due to the processes of killing and fixing is indicated by an inability to find any coagulated material in the space between the larva and its bag.

As one follows the mid intestine backwards, it narrows down and passes gradually into the hind intestine, the canal of which is blocked with chitin. There is no accumulation anywhere of solid waste materials; in fact, there is less food material in the caudal part of the mid intestine than elsewhere. This indicates that the food is so easy of digestion that there is no unassimilated residue. Of course, one can understand this when it is recalled that the food has already been digested by the host.

The hind intestine is a short tube, the canal of which is blocked with chitin. Its point of invagination is situated dorsally just in front of the caudal appendage. It is obvious, of course, that it has lost its original function and now merely prevents the soiling of the food supply. The malpighian tubes are four in number, as shown in the diagram (fig. 86). Their function must be quite unimportant, as they are closed at both ends. Each has a well defined lumen, however, and some of the wall cells contain tiny droplets of a secretion (fig. 90) indicating that they may have a very limited function of storing up urates and other waste products of metabolism.

Before leaving the problem of digestion, a brief reference may be made to the fat body. We have seen that the food of *Therion* in this stage is really the strained liquid of the blood and lymph stream. With this food the larva manages to build up its own blood and lymph stream, a large amount of muscular tissue, a properly equipped body wall, including tracheids and other structures invaginated from it, a well-developed nervous system, and a pair of gonads. In the six larvæ that have been sectioned, however, there seems to be no fatty tissue at all. This seeming absence of the fat body is perhaps due to a straining out of the oily part of the lymph by the embryonic membrane. In support of this view it can be recalled that in insects such as *Apanteles* and *Campoplex*, where there is no embryonic membrane, there is a fairly well developed fat body.

In connection with the problem of breathing, it can be recalled that the free living ancestors of *Therion* must have been supplied with a tracheal system comparable with that now found in such generalized larvæ as the tenthredinids. The larva of *Therion*, however, has become aquatic in the sense that it lives in a fluid, and one can expect that it has developed entirely new arrangements for securing oxygenation of the blood. As it lives in a fluid, its spiracles have become closed, and as it lives in a bag, the difficulty of securing oxygen is enhanced. How does it breathe?

Fig. 88.   *Therion morio* Fab.   Diagram showing points at which cross section drawings shown in figures 89 to 96 were made.

Fig. 89.   *Therion morio* Fab.   Cross section through the feeding embryo taken just be-hind the head (number 1 of diagram).   Aort.=dorsal aorta; Tr.=tracheid; Mus.=muscle; S.G.=salivary gland; M. int.=mid intestine; Sec.=digestive secretion; mus.=longitudinal section of a transverse muscle; Gang.=ganglion.

Fig. 90.   *Therion morio* Fab.   Cross section No. 2 through the feeding embryo, taken just in front of the union of the mid and hind intestines.   D.V.=dorsal vessel; Mus.=muscle; M. int.=mid intestine; Tr.=bundle of tracheids; Gang.=ganglion; Mal. tub.=malpighian tube; Nuc.=nucleus; Lum.=lumen; Sec.=secretion.

Fig. 91.   *Therion morio* Fab. Stage I.   Drawn from cross section cut through point '3.' Shows the manner in which the malpighian tubes arise from the hind intestine.   Sac.=em-bryonic sac in which the larva lives; Cu.=chitinous cuticle; H. int.=hind intestine; Mal. tub.=malpighian tube; Bl.=blood and lymph; Hyp.=hypodermal cells; Tr.=a bundle of tracheids; Mus.=muscle; Gang.=a ganglion.

Fig. 92.   *Therion morio* Fab.   Stage I.   Drawn from cross section cut through point '4' and shows the invagination of the hind intestine.   H. int.=invaginating hind intestine ; Sac.=embryo sac; Bl.=blood and lymph; Tr.=bundle of tracheids; Mus.=muscle; Gang.= ganglion.

Fig. 93.   *Therion morio* Fab.   Stage I.   Drawn from cross section cut through point '5,' a point directly behind the spot where the hind intestine invaginates and at the cephalic end of the caudal appendage.   Sac.=embryo sac; Cu.=chitinous cuticle; Mus.=muscle; Tr.= a tracheid ending in the air chamber of a hypodermal cell; Bl.=blood; Hyp.=hypodermal cell.

Fig. 94.   *Therion morio* Fab.   Stage I.   Drawn from cross section cut through point '6,' two-thirds of the way back from the tip of the caudal appendage.   Note the transverse muscles.   Sac.=embryonic sac.; Cu.=chitinous cuticle; Hyp.=hypodermal cell; Tr.= tracheid invaginating from a hypodermal cell; Bl.=blood and lymph; Mus.=muscle.

Fig. 95.   *Therion morio* Fab.   Stage I.   Drawn from cross section cut through point '7,' and shows conditions and structures found a third of the way back from the tip of the caudal appendage.   Sac.=embryo sac; Cu.=chitinous cuticle; Tr.=tracheids; Bl.=blood and lymph; Hyp.=hypodermal cell.

Fig. 96.   *Therion morio* Fab.   Stage I.   Drawn from cross section cut through point '8,' and shows tracheids both in cross section and entering the hypodermal cells.   Sac.=embry-onic sac. Cu.=chitinous cuticle; Hyp.=hypodermal cells; Tr.=tracheids.

Fig. 97.   *Therion morio* Fab. Stage I.   This drawing shows the way in which the tracheids enter the large hypodermal cells in the caudal appendage.   Note how the cell contents has migrated to the wall of the cell and the huge air-space that has been left as a result.   Tr.=cross section through a tracheid; Bl.=blood and lymph; Cu.=chitinous cuticle; Hyp.=remains of a hypodermal cell; Tr.₁=longitudinal section through at racheid; Air sp.=air space in one of the hypodermal cells.

Fig. 98.   *Therion morio* Fab.   Surface view of the embryonic membrane surrounding the feeding embryo.   In this view the outlines of the large cells can still be distinguished and also the nuclear remnants.
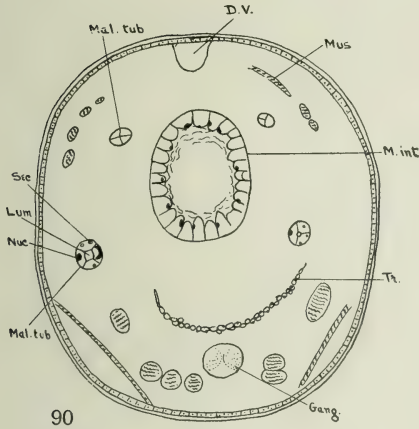
Fig. 99.   *Therion morio* Fab.   Cross section of the embryonic membrane surrounding the feeding embryo.   The membrane is clearly made up of two layers.   The outer thinner one possibly represents the degenerating serosa, and the inner one the degenerating amnion. Both layers are in a condition of degeneration because neither cells nor nuclei can be dis-tinguished.
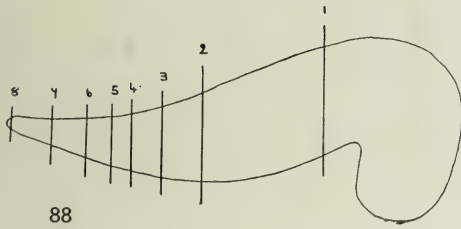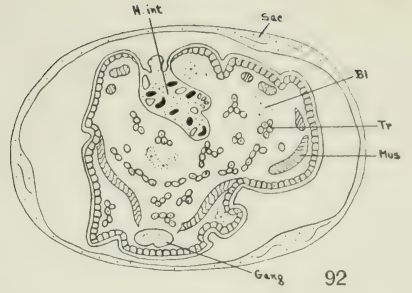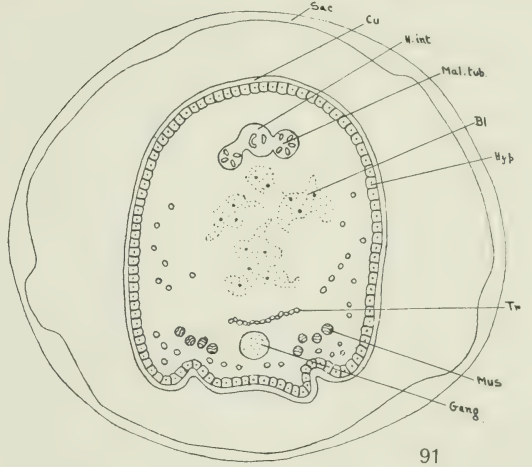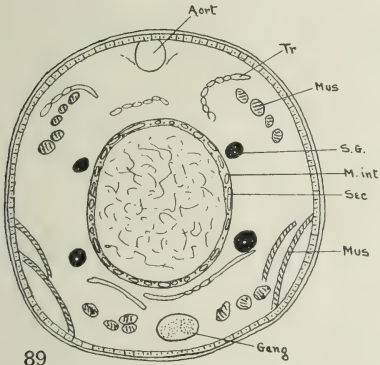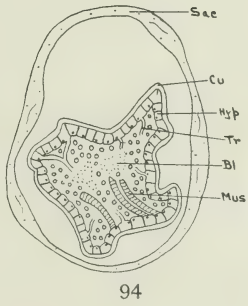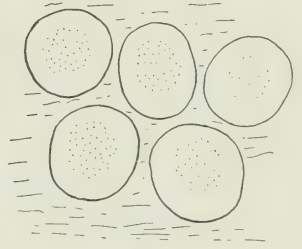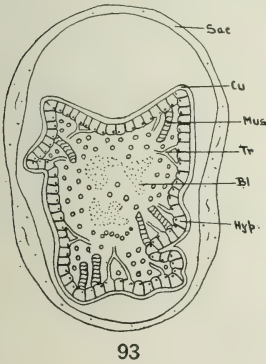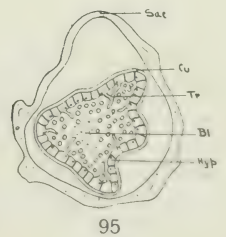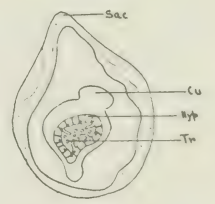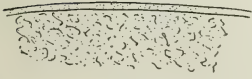
As in the case of *Apanteles* and *Campoplex*, one of the most noteworthy structures of the earliest larval stage is the caudal appendage (vide fig. 86). In life this appendage does not move perceptibly and is clearly not a locomotor organ. Furthermore, in life one can see that the appendage is literally filled with a branching system of tracheids filled with air and that it is, in consequence, a tracheal gill. The nature of this tracheal gill can be made out more clearly by examining serial sections. In section number 4 (fig. 92) taken through the point of invagination of the hind intestine, a number of longitudinal tracheids and some circular muscles can be seen. Passing back to section 5 (see diagram for position of these sections), one sees a larger number of tracheids and a smaller number of circular muscles, all immersed in a bath of blood and lymph (fig. 93). Going to the next position, the appendage has become smaller, but the structure is essentially similar. At point 7 (fig. 95), the muscles have disappeared and the entire organ is filled with tracheids and blood. Finally, at point 8 (fig. 96) one finds similar conditions, except that the diameter of the organ has become very small.

Using the ordinary 4 mm. objective, one can see that each of the many tracheids ends in the wall of the organ. By the use of an oil emersion lens, however, one sees that each tracheid ends in a hypodermal cell that has shrunken so as to become an air chamber (fig. 97). The nucleus of each hypodermal cell has receded into the cell wall and the central part of each cell has become hollow and filled with air. So that the wall of the organ has become beautifully adapted for an exchange of gases between the filtered blood in the embryo sac and the tracheids in the caudal appendage.

Following the tracheids forward from the base of the appendage, one finds that strands of them run almost into the head capsule, this being especially true in the region below the alimentary canal. So that, although the caudal appendage is the place where fresh supplies of air are received, yet these supplies are distributed to an extent through the larva by means of air tubes.

The chief distributor of the pure oxygen in these tubes is probably, however, the blood stream. This stream flows back into the caudal appendage, where many blood corpuscles can be seen and becomes purified by contact with the tracheids. It is then drawn or pumped into the dorsal vessel (fig. 96), the hind end of which is close to the base of the caudal appendage. This pumping process is partially carried on, of course, by means of the valves of the dorsal vessel. It seems, however, that the caudal appendage may also assist in this process by alternately contracting and expanding. The appendage is supplied with a number of circular muscles in its basal half and they may well have a pumping function. The purified blood now passes along the slender dorsal vessel and flows into the head. From here it flows back again into the gill, being purified to an extent in its journey by contact with the strings of tracheids encountered on the way.

With this glance at the methods by which our dimunitive parasite feeds and breathes, we may return to the question of the jaws and to that of the embryonic sac. So far, we have discovered no use whatsoever for either of these characteristic structures. We found that the jaws were not used for feeding and that the sac seems to be something of a hindrance to feeding, as it prevents the parasite securing blood cells or fat cells for its diet. If these structures are of no use to the parasite while it lives in the caterpillar stage of its host, it does not follow that they are of no use to it when that host becomes a pupa. We may remember also, that there are a number of reasons for supposing that *Therion* was originally a pupal rather than a larval parasite (vide discussion on p. 95).

When the host caterpillar pupates and turns into a seemingly inactive chrysalis, it is an outward sign that the period of greatest internal activity has been inaugurated. There is, first of all, a period of disorganization in which

most of the larval tissue systems are attacked by phagocytes and reduced to creamy liquid; and then there is a period of reconstruction in which the adult tissue systems are built from the unrecognizable ruins of the larval systems. During these processes *Therion* is exposed to the phagocytic invasion and it seems probable that the supreme function of the embryonic membrane, so carefully retained for weeks before the invasion occurs, is to ward off the phagocytic horde. The membrane is certainly immune from attack because it remains in a condition of perfect preservation all through the period of phagocytic activity and, indeed, until the following spring when the period of reconstruction is inaugurated. We have seen, also, in connection with the feeding habits of our parasite (p. 97) that ordinary blood cells do not pass through the membrane and it seems a reasonable inference that the extraordinary blood cells, called phagocytes, cannot pass through it either, in which case *Therion* would be immune from attack.

The histological structure of the sac conforms, also, to this view of its function. In surface view (fig. 98) it appears to be composed of immense cells with large degenerating nuclei and the cells seem to be embedded in a non-cellular matrix. It is probable that this appearance of large cells is due to the great stretching that the membrane has undergone due to the growth of the larva. In cross-section (fig. 99) the cellular appearance is lost and the membrane seems to be made up of two distinct layers, both non-cellular, the outer one being uniformly thin, the inner one being less thin and less uniform. From the point of view of origin, it seems likely that the two layers are the remains of the serosa and amnion, respectively, and that the individual cells have become so distorted by stretching and by degeneration that they are almost unrecognizable. This view of origin, however, cannot be regarded as established. Whatever the origin may be, the structural details of the bag accord with the view of its being functionally a blood sieve for keeping out phagocytes.

Other pupal parasites likewise guard against the invasion of phagocytes. There are a number of tachinid parasites, such as *Blepharipa*, *Blepharipeza* and *Crossocosmia* that are pupal parasites in the sense that the maggots may emerge from the pupæ instead of from the larvæ. In such cases, however, the parasites are so large by the time the host pupates that the pupa is probably killed before the phagocyte onslaught commences. Of the hymenopterous parasites, the Pimplas stand out as being characteristically pupal parasites. These, however, avoid any conflict with phagocytes by the simple expedient of feeding externally. Many other so-called pupal parasites are really secondaries and so do not come into conflict with the phagocytes of histolysis. There are other parasites, such as some of the large chalcids, that are undoubtedly true pupal parasites, but unfortunately so little seems to be known concerning their habits inside the pupa that it is impossible to draw any analogy from them. The limited information available goes to show, however, that parasites generally avoid coming in contact with the thousands of ravenous blood cells, called phagocytes, present in the early stages of a lepidopterous pupa. With this in mind, *Therion* seems justified in the possession of its bag.

Second Stage Larva. In this stage the larva comes out of its sac and evidently feeds on unfiltered blood and lymph and does not void any waste products of metabolism. The mandibles (fig. 79) are relatively much smaller than in the previous stage and are probably used in connection with feeding. The caudal appendage is still well developed (fig. 79) and breathing evidently takes place chiefly through it.

Third Stage Larva. This is the destructive feeding stage of the parasite and is of very short duration because once the host is killed, feeding has to be accomplished before the food can decompose. The mandibles (Fig. 80) are almost certainly used in connection with feeding. The caudal appendage is now almost completely withdrawn and no longer functions as a tracheal gill.

As this organ is withdrawn, however, the spiracles open and the parasite begins to resemble its free living ancestors in breathing by means of an open tracheal system.

The pupal stage has not been observed closely and I can say nothing of its habits that would be of particular interest.

Before closing this account of *Therion*, it may be said that we seem to know practically nothing about the habits and methods of existence of other parasites related to it. One of the few references I have found in literature to the early stages of *Anomalon* parasites are Ratzeburg's figures of the early stages of *Anomalon circumflexum*. This familiar figure of three larvæ, one with a small head and long tail, another with a medium-sized head and medium-sized caudal appendage, and lastly, an arcuate larva with a large head capsule and robust tail filled with tracheæ, has appeared in most of our text-books, including Sharpe, Packard and Henneguy. It is a comment on the progress of our knowledge of insect parasitism to reflect that the first figure evidently represents a first stage *Campoplex;* the next, the second stage of the same; and that the last figure, labelled the third or encysted stage (although really a stage of *Therion*), represents a first stage larva (or what I prefer to call a feeding embryo) and not the third. It is quite possible to secure all three of these larvæ in a single caterpillar and the mistake is one that even Ratzeburg could easily have made. The sad part of it is that it has taken the rest of us more than eighty years to discover the error.

SOME GENERAL REMARKS ON THE PARASITES

Certain of the highly diversified and interesting phenomena peculiar to insect parasitism have been well illustrated in our studies of the fall webworm. In the first few years of this study, the webworm was fairly abundant and the parasites extraordinarily abundant. There resulted, in consequence of the limited food supply, a life and death struggle among the parasites, which reduced their numbers by hundreds of thousands annually. Single caterpillars only large enough to supply food materials for a single parasite were attacked quite often by several females either of the same or of different species. I dissected one caterpillar that contained no less than 22 parasitic larvæ belonging to four species; all the parasites were alive but at least 21 of them were doomed to an early death.

The possibilities of this warfare among the parasites—Mr. Fiske has given it the name of superparasitism—can be seen by glancing at the accompanying chart in which the horizontal lines represent the season during which the various parasitic larvæ are found in webworm caterpillars or pupæ, as the case may be.

Sequence of Parasites of Hyphantria in N.B., 1913

Parasites	Egg Stage			Larval Stages				Pupal Stages					Adult
	Fresh	Old	1st	2nd	3rd	4th	5th	6th	7th	Pre-pup.	Fresh	Old	
Apanteles.........													
Meteorus..........													
Campoplex 1.....													
Campoplex 2.....													
Ernestia..........													
Therion..........													
Pimpla, etc.......													

By reading the columns up and down, one can see the possibilities for superparasitism in the caterpillars of different sizes. In a first stage larva, for instance, one would only expect to find *Apanteles* and a very occasional *Therion*. In a

single second stage larva one might find an *Apanteles*, a *Meteorus*, a *Campoplex*, and a *Therion.* In a third stage larva there might be an *Apanteles*, a *Meteorus*, a larva of each of the two *Campoplex* species, an *Ernestia* maggot and a feeding embryo of *Therion:* and so on. In the course of many thousands of dissections that have been made, we have not found a single case in which all the possible parasites have been harboured in one third stage caterpillar, though I have little doubt that cases of the kind occasionally occur. Four species were actually found together in one caterpillar and a number of caterpillars have been found to contain three species.

An interesting feature of this warfare is the manner in which it is waged. Under ordinary conditions there is no active combat, for the sufficient reasons that the various competitors are incapable of active movement inside their host caterpillar and are destitute of weapons of either offence or defence. It is, then, a little difficult at first to see how one of several parasites in a single caterpillar can vanquish all its opponents without itself perishing from starvation. When it is recalled, however, that all these parasites feed very slowly at first and exceedingly rapidly during their last two days, one can readily see that the first parasite to reach the *destructive feeding stage* will be victorious in the struggle. In a single day it will be able to reduce the food supply so as to starve its competitors and in two days it will have completely exhausted the food supply. The struggle, then, is simply a race for the destructive feeding stage.

Sometimes one can find the remains of a *Campoplex* larva vanquished by an *Ernestia* and sometimes the opposite. In the first case, of course, the host caterpillar was attacked by *Campoplex* first; and in the second case the host caterpillar must have stumbled over an *Ernestia* maggot before being attacked by a *Campoplex* fly. The parasite most handicapped in this struggle is *Therion* which is the last of all these parasites to reach its destructive feeding stage. A *Therion* larva that finds itself in competition with any one, or any combination, of the other parasites has no chance whatever in this contest for survival; it is absolutely at the mercy of its rivals.

Larvæ of a single species of parasite may compete in the same way. In the case of a caterpillar that was found to contain 12 *Ernestia* maggots, for instance, it was found that the maggots were not all of the same size, and it was evident that one of them—the first to enter—was destined to reach its destructive feeding stage first. If two or three competing parasites reach their destructive feeding stage within a few hours of one another, as they occasionally do, all the parasites are doomed to perish by starvation.

Though this warfare is a very real thing, which tends to offset the usefulness of parasites, our observations indicate that it is not indiscriminate and so, except under unusual circumstances, not serious. During the course of this study of *Hyphantria*, which covers a period of nearly a decade, the interparasitic warfare was confined almost entirely to 1912 and 1913, the years of extraordinary parasite abundance. Moreover, even in these years, when many webs showed 100 per cent parasitism, the cases of supernumerary parasitism were rare compared with those of single parasitism.

The reason for this is that the warfare is not an indiscriminate one. In the first place, a caterpillar that is attacked by *Apanteles* loses some of its enthusiasm after about a week and behaves a little differently from its confrères. A caterpillar of this kind can be spotted even by a human being and undoubtedly can be avoided by a *Campoplex* fly seeking a wet nurse for its offspring. And so it is with nearly all the other parasites. In the case of *Ernestia*, the maggot of which perishes unless crawled over by a caterpillar, it is obvious, of course, that there is little chance of entering a caterpillar rendered listless by a parasite already in its bowels.

THE SEQUENCE OF PARASITES

In the second place, the warfare is not indiscriminate because the parasites arrange themselves in what Mr. Fiske has aptly termed a sequence. By referring back to the chart (p. 102) it can be seen that *Apanteles* is essentially a parasite of very tiny caterpillars; that *Meteorus* confines its attacks to slightly older caterpillars, and so on through the list until we reach the Pimplas, which attack only the pupæ. The sequence is not any more precise than most of nature's phenomena and weather conditions modify it from year to year. At the same time, the effect of the sequence is very profound and in average years is sufficient to reduce the interparasitic warfare to unimportance.

There are two conspicuous gaps in this sequence. That no parasites of any consequence attack the eggs seems to be due to the fact that the egg stage is of such short duration. Parasites that did attack these eggs would need secondary hosts for their other generations and these secondary hosts would have to be almost as abundant as the webworms.*

The absence of parasites on the adult moths may likewise be associated with the extreme brevity of this stage, though adult lepidoptera in general seem to be free of them.

SECONDARY PARASITISM

These few general remarks on the webworm parasites may be concluded with a reference to secondary parasitism; that is to say, parasitism of primary parasites such as *Campoplex* and *Ernestia* by secondary parasites, such as *Hemiteles*. Throughout the whole study in New Brunswick, one of the most unexpected features has been the almost total absence of secondary or hyperparasitism. The only case of any importance at all was that of the attack on *Rogas* in 1917 by *Hemiteles*. As *Rogas* is not ordinarily a parasite of *Hyphantria* at all, it can be stated that the real primary parasites of the webworm have been practically unexploited by secondaries in New Brunswick for a period of eight years. Furthermore, the absence of secondaries has been equally pronounced in our less extensive studies in Nova Scotia and British Columbia.

When one considers the difficulties under which these secondary parasites have to work, however, their scarcity and ineffectiveness is perhaps not so remarkable. In the first place, they are under a far greater handicap (at least in the boreal zone) than most of the primaries, on account of their having two or more generations a year. *Theronia* and *Hemiteles* have at least two generations annually, and the little chalcid parasites, such as *Dibrachys* have four or five. As nearly all the webworm primaries have only one generation a year in New Brunswick, it follows that the secondaries must depend for an existence in their spring and midsummer generations on primary parasites of hosts other than the fall webworm. Moreover, they can only consume large numbers of webworm primaries if they have been able to breed upon large numbers of other primaries, and this requisite food supply for the early generations has not been available here. In the transition zone, where the webworm has two generations a year and all its primary parasites at least two generations, the secondary parasites are, of course, under much less of a handicap.

Then again, the secondaries cannot be as effective in killing the primaries as the primaries are in destroying webworms, because they lack the comparatively superior fecundity. The webworm lays about 260 eggs, *Ernestia* deposits about 500 larvæ, and *Dibrachys*—largely on account of its minute size—probably lays not more than 100 eggs. Added to this, there is the additional handicap that whereas one larva of a primary usually suffices to kill a single webworm, it often takes dozens of secondaries to bring about the destruction of a single primary parasite.

*The short-lived eggs of the spruce budworm are also seldom attacked by parasites, while the long-lived eggs of the various tent caterpillars and of the oyster-shell scale are attacked to a considerable extent by either parasites or predators.

It may be pointed out that many of the disadvantages under which the secondary parasites of the webworm labour are shared by secondary parasites of many other insects. Unfortunately, one cannot draw the inference from this that secondary parasitism is of no economic significance whatever, because there are a number of specific instances on record in which the effectiveness of primary parasites has been greatly lessened by the activities of secondaries. It seems fair to infer, however, that efficient hyperparasitism is one of nature's achievements that occurs only rarely when the many conditions necessary for it to happen be fulfilled.

SOME DEFENSIVE MEASURES OF HYPHANTRIA AGAINST ITS ENEMIES

THE ARMATURE OF THE LARVA.—The webworm is protected against enemies in various ways. In the first place, it has developed hairs on the exposed parts of its body which undoubtedly protect the species against certain kinds of birds, even though they afford no protection against the red-eyed vireo. Chiefly, however, they seem to protect the caterpillars against the attack of common polytrophic tachinids, such as *Tachina mella*, the four-spotted *Winthemia*, and *Frontina frenchii*, which flies lay large eggs on many kinds of caterpillars that are relatively destitute of hairs.

There are no hairs on the head, but that part is so protected by the hardened capsule that in thousands of dissections we have never found a parasite in the head region. The hardening of the head capsule has, of course, not been brought about in connection with protection from parasitism, but it is sometimes used directly by the webworms for the purpose of fending off parasites. The way in which they rear and flaunt this well-protected region will be presently described in connection with their communal habits. Another caterpillar *Datana ministra*, which is possessed of a hardened anal plate as well, erects both extremities for the protection of the softer body regions.

The habit of molting, too, certainly has not arisen as a defensive measure against the attack of parasites. It does, nevertheless, play such a role. There is its effect, for instance, in the case of *Ernestia*. The first stage maggot lives in an integumental funnel that grows up as a sleeve starting at the caudal end. It sometimes happens that a caterpillar molts just as one of these funnels is beginning to grow. When this occurs, the funnel is as likely as not to adhere to the old moult skin and to be pulled away. The *Ernestia* maggot involved in such a catastrophe falls into its food supply and promptly drowns. Caterpillars have been dissected on many occasions containing one or more tiny drowned maggots of this parasite, and I attribute all these cases to the molting of the host before the funnels were sufficiently developed.

THE COMMUNITY WEB AS A WEAPON OF DEFENCE.

The fact that a family of webworms continues to live in a common web undoubtedly affects their relations with parasites. It is apparent, of course, that the colonial habit gives the parasites an advantage in that each caterpillar does not have to be sought after independently. At the same time, there are reasons for supposing that the web-dwelling habit really gives much more of an advantage to the host than to the parasites; and indeed, that it has possibly arisen as a defensive measure against the enemies that have assailed it from time immemorial. The web gives almost perfect protection from parasites that have the direct method of attack during the heat of the day, during warm, rainy days, and during the long period of inertia at the time of molting. It also serves as an extra nervous system that enables any caterpillar in, or on, the web to sound the parasite alarm so effectively that the whole colony becomes instantly involved in a sort of war dance. When in virtue of the web the parasite alarm

is given, nearly every larva in the colony moves its forward half from side to side in jerks. As most of the larvæ are in massed formation, the movements of each row effectively protect the anchored, and so unprotected, caudal parts of the next row in front from attack by the parasite. This extra nervous system is not always in perfect order, its efficency varies from day to day in the same colony and varies from colony to colony. Under average conditions, however, the extra nervous system seems to be sufficiently well in tune to be of great assistance in the defence against parasites.

Phagocytosis.

The methods of defence against parasites that have been considered so far have had to do with preventing parasites from placing their eggs or larvæ on, or in, host caterpillars. They are all measures of prevention. Even when a parasite has been 'planted' within the bowels of a host, however, it is not necessarily immune from destruction, as at the eleventh hour the host is some-times able to call into play a final weapon, unseen, yet powerful enough to mete out a subtle death to its would-be assassin. The method of meting out this death has not been worked out particularly for the webworm but it is undoubtedly used by this insect on certain occasions.

This method of defence was first worked out by Mr. P. H. Timberlake for the three hosts; the brown-tail, gipsy, and rusty vaporer moths against the parasite, *Campoplex validus*. In a highly suggestive little set of experiments, Mr. Timberlake (l.c. p. 61) found that all these hosts were able to kill the eggs or tiny larvæ that were introduced into them by a captive fly. He found that the eggs introduced into these hosts would invariably die and come to be encased in a little mass of the wandering blood cells or amoebocytes.

It may be, of course, that the phagocytes are not directly responsible for the death of the parasite, but only help to dispose of it after it has been killed by protoplasmic poisoning; or they may attack it while it still lives. We know that the stage of greatest phagocyte activity in the webworm, namely, the pupal stage seems to be most studiously avoided by the various parasites. All the larval parasites except *Therion*, emerge, or at least reach their destructive feed-ing stage, before the host changes to a pupa. The parasite *Therion* lives for weeks inside an amoebocyte-proof bag in order, apparently, that it may be pro-tected from the onslaught of the blood cells during the histolysis of its host; and the characteristically pupal parasite *Pimpla* seems to avoid any dealings with the phagocytes by living on the outside of the pupal case.

Be the cause what it may, however, the important fact remains that certain caterpillars are rendered immune, either wholly or in part from the attack of certain parasites. As to how general this method of defence may be, Mr. Timber-lake came to the conclusion that it was directed by a given host against parasites that it did not ordinarily harbour. In support of this view, it may be said that in our *Hyphantria* dissections we have sometimes found a few *Campoplex* larvæ killed in this way and we have also sometimes bred a few flies of *Campoplex fugitivum*. It seems possible that the slain larvæ belonged to this unusual parasite of the webworm and that the host has a partial immunity against this parasite. On the other hand the webworm in New Brunswick was attacked in 1917 by the abnormal parasite *Rogas*, quite vigorously, especially in the Moncton district, and we failed to find a single case of so-called phagocytosis in the course of our dissections. Notwithstanding the fact that very little is known about the extent and limitations of this method of defence, it seems certain at least that it ranks second to none from the point of view of practical importance. It must often be the means of preventing an abundant parasite from becoming more abundant by limiting its food supply to a few chosen hosts.

The Habit of Flying Away From Parasites

Another method of defence is concerned with the habit of flight. The essential feature of it is that *Hyphantria* moths are sometimes carried on the prevailing wind from an area inhabited by primary parasites to an area where no parasites exist. This point has already been discussed (pp. 18, 26 and 33) and it seems unnecessary to do more than refer to it here.

These, then, are some of the defences of the webworm and the strength thereof is tacitly attested by the ingenuity with which its parasites circumvent them. The hairiness which is so effective a barricade against generalized parasites has compelled *Compsilura* and *Lydella* of the tachinidæ, and *Therion* of the ichneumons, to develop keel-shaped abdomens which slip through the hairs. *Ernestia* has surmounted the difficulties of both hairs and web by scattering its progeny on uneaten foliage immediately adjacent to the web. And it has been shown how various are the ways the parasites have of avoiding the period of most active phagocytosis.