THE OHIO JOURNAL OF SCIENCE

Vol. XXII JUNE, 1922 No. 8

SOME BIONOMICS OF ALPHELINUS SEMIFLAVUS (HOWARD)*

Chalcid Parasite of Aphids

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CONTENTS.

GENERAL CONSIDERATIONS.

Aphelinus semiflavus How. is one of a few species from the genus *Aphelinus*, of the Chalcidoid family Eulophidæ, known to attack aphids. The others are scale parasites. At present there are but seven described species for North America, recorded as aphid feeders; namely, *Aphelinus mali* Hald., *A. nigritus* How., *A. Semiflavus* How., *A. Flaviceps* How., *A. Lapisligni* How., *A. varicornis* Gir., and *A. automatus* Gir. In addition to this number, the writer has recently taken two new species: one from an aphid on potato sprouts in the State Insectary at Whittier, California, and the other from *Sanbornia juniperi* Perg., an aphid on juniper in Pennsylvania. Both are being described by Dr. L. O. Howard.

* Contribution from the Department of Zoology and Entomology, Ohio State University, No. 70.

These parasites, so far as known, are limited to the aphids as hosts, and most, if not all of them, are confined to a few species. *Aphelinus mali* was long considered an exception, appearing many times in the records as a scale parasite, also. However, Dr. Howard,* authority on the group, now believes these records to be in error, and further states that it is probably not only confined to aphids, but is likely restricted to the woolly forms, especially the common *Eriosoma lanigera* Hausm., of the apple, a species often associated with scale insects; a fact which may account for the confusion in the records.

The group, on the whole, are extremely minute and inconspicuous insects, not often met with by the average entomologist. Many of the species are quite rare, even to the specialist on the alert for them. At best they rank secondary to the Braconid subfamily Aphidinini as a factor in the control of aphids; although they have been known (Prof. T. H. Parks†) to play a considerable part in some outbreaks (Toxoptera in Kansas during 1909). For these reasons, they have practically escaped attention from a biological standpoint, and most of them have been known systematically but a few years (since 1908).

With the hope of contributing something to the knowledge of the bionomics, life-history, economic importance, and relationship to the aphid complex in general, work was begun on *Aphelinus semiflavus* in the greenhouse insectary of the Ohio State University, Department of Zoology and Entomology, in the fall of 1920, as part of a thesis for the degree of Master of Science in Entomology. This was continued throughout the winter to the middle of May, 1921; when the thesis was written. After graduation in June, part of a series of parthenogenetic generations of the parasite was taken to Oak Lane, Philadelphia, Pennsylvania, where rearing and study was continued at intervals until the time of this writing, February, 1922.

ACKNOWLEDGMENTS.

The writer here wishes to express appreciation for the kind assistance of Dr. Herbert Osborn, who directed the work with many valuable suggestions and criticisms, and to Dr. R. C.

* Private communication.
† Private communication.

Osburn for suggestions and corrections in manuscript. Many thanks are given to Prof. T. H. Parks for useful suggestions on rearing methods and recording of data; to Dr. C. H. Kennedy for aid in microtechnique and drawing; and to the entire staff of the Department for aid in advice and equipment.

Among those outside the University to whom the writer is especially grateful, are Dr. L. O. Howard, authority on aphis-feeding Aphelinids, who very generously gave of his valuable advice, and assisted greatly in the confirmation of records and determinations; Mr. A. B. Gahan, of the National Museum, for determining the parasites; Mr. T. L. Guyton, of the Pennsylvania Department of Agriculture, for determining the aphids; and Dr. Paul Marchal, director of the Entomological Station, Department of Agriculture, Paris, France, for giving first hand his experience in colonizing *Aphelinus mali* How. in France.

METHODS AND APPARATUS.

Practically all the data included in this paper are from indoor rearing, either in a greenhouse or room. Most of it was carried on in the greenhouse insectary of the Ohio State University, and near a window in room 107 of the Botany and Zoology building. The observations made in Pennsylvania were taken on material grown before an open window in the writer's private room in Oak Lane. That the results thus obtained should vary with outdoor conditions is a fact which must not be overlooked; especially since experience has shown *Aphelinus* to be quite sensitive to slight temperature changes below a certain point.

The temperature in the greenhouse insectary varied from 50 degrees Fahr. on cold winter days, to 100 degrees on warm, sunny days of early fall and late spring. For the greater portion of the time, it remained between 70 and 80 degrees Fahr. The room in the Botany and Zoology Building stayed very close to 70 degrees all the time. No temperature readings were taken for Oak Lane, but here it was very near outdoor temperature during the summer and warm room temperature (70 degrees and above) for the winter.

Light and humidity were not measured.

Those cages which gave the most satisfaction in the matters of light, ventilation, security, and accessibility, were the

standard lantern globe cage used in rearing aphids, and a specially designed celluloid cage. The celluloid cage was found to be far superior to the lantern globe in ventilation and its equal in all the other factors. However, both were used with success throughout the work.

Myzus persicæ Sulz., a common aphid on dock and crucifers, was used for a host in practically all the experiments, although several other species were carried along for the purpose of testing the parasite in other hosts. This aphid proved to be quite satisfactory in every way; since it was the natural preferred host of *Aphelinus semiflavus*, reproduced readily throughout the winter on a number of common plants, and was attacked by practically every other aphid parasite. Dock (*Rumex cripus*, and *R. obtusifolius*) was found to be the best host plant for this aphid, and was also very satisfactory from an experimental standpoint; being easily grown, and having large smooth foliage which greatly facilitated observation and handling.

Parasite-free material was obtained by rearing in tight cages.

In all experiments, a few specimens confined in a small, neat cage gave better and more accurate results than many in a large cage. Too many aphids to start with would multiply so rapidly that they would kill the plant before the experiment could be closed, making it necessary to transfer them, which always resulted in loss of material.

For development studies, a number of parasites were confined with parasite-free aphids for a few hours and then removed. A number of these aphids were dissected at intervals to determine the stages reached by the parasite in a given time. These dissections were made in normal salt solution held in a hollow ground slide under a binocular microscope. Very fine sewing needles mounted in matches served as excellent instruments. When the parasites had killed the aphids, they were removed to gelatin capsules marked with the number of the cage and date of removal. These were then filed in small cardboard boxes, by the month, for further reference, in watching their development from then on. These developments in the capsules were checked by cage rearing and found to coincide. Gelatin capsules were made use of as containers for all the material that was retained for future reference.

IDENTITY AND DESCRIPTION.

Aphelinus semiflavus was first described by Howard ('07) as follows:

Female.—Length 1.08 mm.; expanse 1.87 mm.; greatest width of fore wing 0.3 mm. Antennæ short, excluding scape about the length of face; pedicel long, more than three times as long as wide; funicle joints 1 and 2 in length and width and each slightly less than one-third length of pedicel; joint 3 two-thirds length of pedicel and about as wide as its tip; club slightly swollen, ellipsoidal, and about twice the length of pedicel. Eyes faintly hairy. General color black; thorax smooth, shining, scape and pedicel dusky, flagellum pallid, club becoming somewhat dusky at tip; front and middle femora and all tibiæ somewhat dusky; hind femora straw yellow. Abdomen light yellow shaded around margin with brownish. Wings rather short, otherwise normal.

Male.—Length 0.85 mm.; expanse 1.58 mm.; greatest width of fore wing 0.204 mm. Differs from female in having antennæ nearly uniform brown, scape slightly darker, and in the proportion of third funicle joint and club. Third joint cylindrical, twice as long as pedicel and six times as long as broad; club one-quarter longer than third funicle joint, elongate ovate in shape.

Described from 14 male and female specimens reared by C. P. Gillette, Fort Collins, Colorado, July 15, 19, 1908, from Myzus persicæ, and reared at Washington from the same host sent in by Professor Gillette. The parasitized host turns black.

U. S. N. M. type No. 12,931.

DISTRIBUTION.

Geographical.

There are very few available records on the distribution of *Aphelinus semiflavus*, but these seem to indicate that it is rather wide for the United States, at least. Dr. Howard has kindly furnished the writer with the United States Bureau of Entomology records that he had available, which follow:

Reared from Myzus persicæ Sulz., Fort Collins, Colorado, by C. P. Gillette, July 15, 1908.

Reared from Myzus (new species) on Aguilegia, at Lafayette, Ind., by J. J. Davis.

In addition to these, Webster and Phillips ('12) have published records from St. Anthony Park, Minn., and Mesilla Park, N. Mex. The present work will add Ohio to the States in which *Aphelinus* occurs. So far it has not been found about Philadelphia, Pa., after a summer season of diligent search.

Seasonal.

The data on this point are likewise very scant. Practically all records show that *Aphelinus* appears rather late in the summer and fall. The writer did not find it about Columbus until the first of November, in spite of the fact that he was collecting aphid parasites there from the middle of September on. Mr. T. H. Parks*, who was with Webster and Phillips in Kansas during the work with the "green bug" parasites, is of the openion that *Aphelinus* does not become numerous until late fall.

Winter is probably passed in the pupal stage within the blackened remains of the host, according to the observations of Kurdjumov ('13) working with a similar species in Russia. A few attempts were made to carry it through the winter in hybernation cages outdoors in Columbus, but all failed, even though *Aphidius* confined with them emerged on the first warm days of spring. These attempts were repeated the following fall and winter in Philadelphia with no better success.

As soon as the weather began to moderate in the spring an outdoor wire-screen cage was established over some dock plants (*Rumex obtusifolius*) in which was placed a colony of parasite-free *Myzus persicæ*, together with ten or fifteen *Aphelinus semiflavus*, to note the behavior of the parasite out of doors at this season. Observations began on April 11th and continued every other day until May 13th, and then every few days until May 24th, when the experiment was closed.

On the first night after the cage was established there occurred a slight frost which numbed the parasites for a time, but they became active again as soon as the sun came out. Several warm days followed, with rather cool nights, and then about a week of cool rains followed by more warm days.

Several parasites were observed in the cage among the aphids for three or four days, when they disappeared. On the 25th of April, one live *Aphelinus* was again observed in the cage ovipositing in the aphids. Observations were made on this one intermittently until May 20th. The aphids multiplied rather slowly for the first ten days in the cage and then gradually recovered their normal rate, producing a good supply of young.

* Private communication.

In spite of the fact that live parasites were confined with these aphids for over a month during a period of rather moderate weather conditions, none of them showed the characteristic blackened appearance of parasitism.

On May 5th, fifteen aphids were dissected and one parasite egg found, which appeared just ready to hatch. Later observations, however, showed no sign of parasitism. On May 20th, more aphids were dissected in which were found three or four well grown larvæ, apparently normal. On the twenty-second, one aphid had turned black. This was the only one of the lot turning by May 24th when the experiment was closed.

While the above observations are rough and incomplete, they more than suggest a considerable influence of weather conditions on the activity and development of *Aphelinus*.

Where conditions are favorable, *Aphelinus* will multiply throughout the year; the generations following each other in cycles of 20 to 30 days, depending largely on temperature.

BIONOMICS OF ADULT.

Emergence.

Emergence takes place through an irregular rounded hole cut on the posterior-dorsal side of the blackened host remains. The fact that the emergence hole is always cut in this one particular spot, is due to the peculiar orientation of the parasite in respect to the host; the main axes of the latter being exactly vice versa to those of the former, which always bring the mouthparts of the parasite in this one position.

Locomotion.

Movement is rather sluggish in Aphelinus compared with other aphid parasites. Unless disturbed, it usually crawls deliberately about among the aphids. At times, however, it was observed to hop from one leaf to another, or from the side of the cage over onto a plant. When stimulated with a needle, it will hop away much like a flea; taking short jumps of two or three inches. Many attempts were made to goad it into sustained flight, but all were unsuccessful. In every case, it would slant downward, even when held several feet above a piece of white paper before a window. The wings are slightly reduced,

and probably are not capable of sustaining it in flight at all. On the other hand, the legs are well developed.

The above evidence would tend to discredit *Aphelinus* where rapidity of dispersion was a prerequisite for efficiency, but Mr. H. S. Smith and Harold Compere ('20) have pointed out in their work with *Aphycus lounsburyi*, an imported parasite of the black scale in California, that this is a trait in the parasite's favor where it is for local distribution by man.

Reaction to Light.

The adult *Aphelinus* is slightly positive to light, but it does not become quiescent in darkness, as shown by several experiments to determine the effect of light on oviposition, which will be taken up in detail under that heading.

Oviposition.

When the attention of *Aphelinus* is directed toward an aphid for oviposition, it moves with extreme precaution and deliberation; approaching very slowly and steadily, swaying from side to side and feeling forward with the antennæ. Just before the antennæ touch (in some cases they do touch), it halts its forward progress, sizes the situation up carefully from short range, obliques slightly, turning the head toward the aphid with a last parting look as if to make sure of the aim, position, etc., and then suddenly faces about, rising well up on the legs, thrusts the ovipositor out and downward with three or four quick backward strokes toward the victim. In the majority of cases, these miss the mark, either by the aphid moving or through poor aim. Usually they fall short and the point of the ovipositor is brought down on the substratum on which the aphid rests. If the host is in an advanced stage, the parasite may have difficulty in piercing the integument. In either case after about three or four thrusts, it will turn and repeat the act, or crawl away in search of a more favorable victim. However, if successful, it remains in position, standing well up on the legs, the ovipositor thrusts out and downward, with just the tip inserted in the host. (Plate I, Fig. 2). This position is often maintained for several minutes. In fact, some were observed to last as long as fifteen minutes, and repeated twice in succession for a like period without depositing a single egg.

In the majority of instances, the aphid appears undisturbed while oviposition is going on. This is especially true of the younger stages. However, there are times when the slightest touch with the antennæ or a prick with the ovipositor will cause them to kick up and make off. If this happens when the ovipositor is fastened in one of the larger stages, it drags the parasite with it. If the host is smaller, however, the parasite is able to master it and keep it in place in spite of its struggles. This is done by the parasite standing well up on its legs and holding up the victim slightly so that it cannot get a firm foothold on the substratum. The ovipositor is held in place during the struggle by the presence of three retractile barbs near the tip. These function so efficiently that the parasite itself often has difficulty in getting free, often having to brace the hind legs against the aphid and give several vigorous pulls before it is withdrawn. At times, the ovipositor may be fixed so firmly in place that it permits a larger host to drag the parasite about so violently that injury results. Several times *Aphelinus* has been observed in a crippled condition after getting free from one of these encounters. In this condition, the ovipositor remains extruded, the parasite not having the power to retract the abdominal segments that bring it back in position, and the individual goes stumbling off with head down and abdomen elevated until it topples over apparently dead.

The ovipositor is usually inserted on the dorsal surface of the host's abdomen, but almost any other part of the body may be chosen, depending on the point of approach. Many times it has been observed on the head between the antennæ, and among *Macrosiphum pisi* on clover, a large species that stands at a considerable angle from the plant, well up on its long legs, the parasite was observed to attack it from beneath, elevating the ovipositor well up and making contact with the ventral surface of the abdomen.

Stage of Host Preferred.—A distinct preference was early shown for the younger stages of aphids. In order to determine this more exactly, several experiments were planned and carried out. Some difficulty, however, was encountered in eliminating a number of factors that might alter a true expression of this preference. These factors were the variation in numbers of the different stages available for oviposition; the high mortality of

the first and second stage nymphs after being parasitized; and the difficulty of handling large numbers of the various stages of aphids necessary to obtain accurate results.

At first a large number of parasites were placed with a greater number of aphids, in the different stages, for a short time and then removed. An equal number of aphids, representing the different stages, were then isolated and the parasites allowed to develop in these until they showed externally. These parasitized individuals were then counted and the percentage taken to indicate the preference of the parasite for a given stage. (See Table I.).

TABLE I.

Showing the Percent of Parasitism in the Various Instars of the Aphid Host, Reared Through Until It Appeared.

No. Aphids Used	Instars	No. Parasitized	Percent.
100	1–2	26	26
100	2–3	16	16
75	4–adult	5	6.6

This method was unsatisfactory, as it did not account for the death of a large number of the smaller stages, which would lower the percentage considerably for that group. It also did not necessarily provide an equal number of the various stages, either at the beginning or the end, to eliminate chance. Then finally the separating and keeping the aphids in different cages for any length of time always made possible the death and escape of many specimens that could not be accounted for.

To get around these difficulties, the following modifications were introduced: As nearly equal and smaller numbers of the different stages were placed together with a number of parasites for a day or so and then all were dissected. The percent parasitized in the various groups, as indicated by the presence of the parasite's egg, showed fairly accurately the preference for that particular stage. Three separate lots were thus treated with the results shown in Table II.

The extreme rarity of parasitism in the adult aphids was clearly demonstrated in the experiments to determine the effect of parasitism on the production of young, in which it was neces-

sary to bring about a parasitized condition in the adult after she had started to produce young. Out of many trials to bring this about, but three were successful; notwithstanding the fact that several parasites were confined for days with the adult aphids time and again.

It is believed that several factors operate here to determine this preference for the younger stages of the host; namely (1) size, it being easier to ovipost in a small aphid than a large one, due to position alone; (2) irritability, the large aphids are

TABLE II.

Showing the Percent of Parasitism in the Various Instars, Dissected Immediately After the Parasites Were Removed.

Approx. Instar	No. Dissected			No. Parasitized			Percent Parasitized		
	Lot 1	Lot 2	Lot 3	Lot 1	Lot 2	Lot 3	Lot 1	Lot 2	Lot 3
1-2	90	105	42	54	58	19	60	55.7	45.2
3-4	161	84	57	66	26	20	41	31	35
4-5	62	61	19	10	4	1	16	6.9	5.2

more irritable than the small nymphs, which often renders oviposition impossible; and (3) toughness of the integument which makes it difficult for the ovipositor to penetrate.

Number of Eggs per Host.—In more than 3,000 separate dissections for egg counts, etc., there were only two or three cases where more than one egg was deposited in a single host. These few exceptions occurred only where a number of parasites were confined with a few aphids for several days, and even then no more than two eggs were ever found in a single host. In some of these trials a parasitism of 100 percent was obtained for 20 first to third instar nymphs confined with one parasite for a single day of twelve hours. Instances were observed several times where parasites apparently oviposited in hosts already parasitized, even to the blackened condition; but in no case did subsequent dissection show that an egg was deposited. *Aphelinus* has also been observed to return several times to a single host, but here, likewise, only a single egg is left, or in many cases none at all.

The above observations seem to indicate that *Aphelinus* places but one egg in a host, but that it is incapable of determining whether a given host harbors a parasite already until the ovipositor is inserted. The above habit is decidedly in its favor when its efficiency as a parasite is considered in contrast to some of the more wasteful species like *Aphidius*, which generally places a number of eggs in a single host, but only one of the resulting larvæ matures.

Number of Eggs Laid per Day and Night.—To determine the number of eggs laid per day and night over the period of egg production, experiments were carried out with a single *Aphelinus* confined with a given number of nymphs from the first to the third instar. Dissections were made on these both in the evening and morning, and a fresh supply of parasite-free aphids placed in the cage for the parasite to oviposit in for the succeeding period. During the night, the cages were kept in a dark chamber so that practically absolute darkness prevailed until the time came to change to light. As nearly equal periods of light and darkness were obtained as was possible; likewise, other factors, such as temperature and humidity, were fairly uniform. All experiments were carried out in room 107 of the Botany and Zoology Building, in a temperature of from 70 to 75 degrees.

Owing to the extreme minuteness of the specimens dealt with, considerable difficulty was experienced in carrying a single parasite through its total life without its escaping or being accidently killed in handling. This was so great that only one specimen went through its total period of egg production to a natural death. Two others were carried for seventeen and eighteen days respectively before they escaped or were accidentally killed. The results of these experiments appear graphically in Figure 1.

Feeding.

It is quite evident from observations made that the commonest means of sustaining life in the adult *Aphelinus* is by its habit of feeding at the puncture holes made by the ovipositor in the young aphids.

This habit is not restricted to *Aphelinus* alone, but seems to be rather common among chalcid parasites in general. The

records with which the writer is familiar date from Howard ('08), where he quotes Dr. Marchal's observations on this habit in the parasite *Tetrastichus xanthomelænæ* Rond, on the eggs of the elm leaf beetle *Galerucella luteola*. Later Howard ('10) in a more general article on this habit among the Chalcidoidea, again refers to Marchal's observations on *Tetrastichus*, in addition to some similar observations on *Aphelinus mytilaspidis* in *Aspidiotus ostreæformis*, along with several others; namely, Dr. H. T. Fernald on *Tetrastichus asparagi*, feeding on the eggs

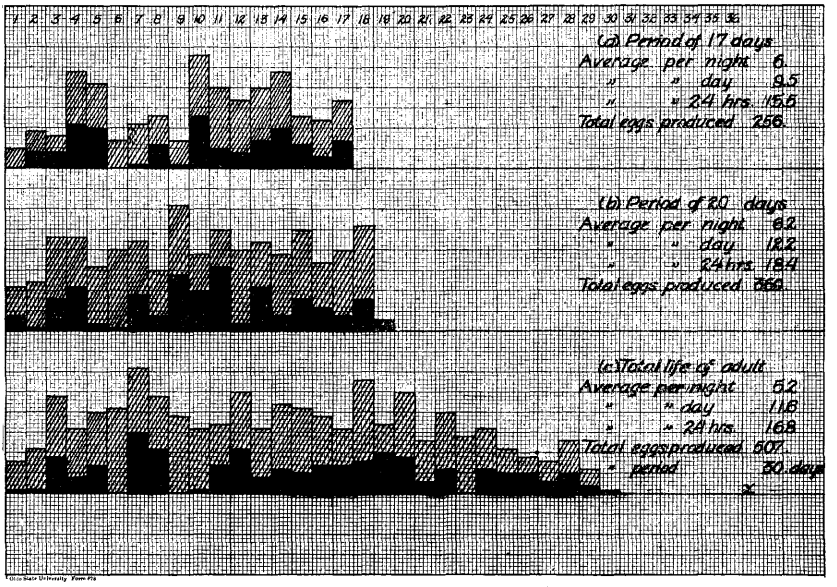

Fig. 1. *Number of eggs deposited by a single Aphelinus semiflavus per day and night for a given period.* Black equals night, cross lines equals day; large squares on abscissa equal 24 hours; small squares on ordinate equals one egg; "x" equals point where natural death occurred.

of the asparagus beetle (*Crioceris asparagi*), and Mr. J. G. Sanders concerning *Aphelinus fuscipennis* on *Aspidiotus* rapax. Mr. H. J. Quayle ('10) also refers to a similar habit as occurring rarely in *Aphelinus diaspidis*, parasite of the red or orange scale (*Chrysomphalus aurantii*) in California. He also observed this species to feed on honey dew, plant juices, and fruit. Mr. L. P. Rockwood ('17) published for the first time observations on this habit in *Aphelinus lapisligni* How., feeding at the

puncture holes in *Aphis bakeri*, in which the actions are described in some detail.

A number of the above cited observations have been verified, by the writer, on *Aphelinus semiflavus*, and additional data have been secured on this interesting feeding habit.

These parasites confined in glass vials or other receptacles without food or water were noticed to live but two or three days at most; while those among aphids lived a much longer time (two weeks or more). This species had also been observed feeding at the puncture holes made by the ovipositor in aphids. In addition to this aphid-feeding habit, the writer was interested to know whether they fed on any other substance, and if so, how long they would live on the various kinds of food that might be available. This point was thought to have considerable bearing on methods of handling and transporting species to be used in an economic way for the suppression of injurious forms.

Several experiments were undertaken to test out the effect of various foods on the length of life of adult Aphelini. Specimens emerging at the same time were placed in cages as follows: One lot on dock (*Rumex obtusifolius*) only, in a lantern globe cage; another with four or five large aphids not yet producing young; still another on a dock plant to which leaves covered with honey-dew were added every other day; and lastly, a lot on a plant with honey solution added every day. All were confined in lantern globe cages with growing dock plants in room 107 of the Botany and Zoology Building. The results appear in Table III.

Some careful observations were made on *Aphelinus semiflavus* in the act of feeding at the puncture holes made by its ovipositor in aphid nymphs. To confine the specimens so that they could be easily observed under a binocular microscope, two hollow ground slides were used with the aphids and parasite in the space between them on a bit of leaf. Four or five 2-instar nymphs were thus enclosed with one female *Aphelinus*. Oviposition began immediately after they were placed together, and was repeated several times in the same aphid, after which the victim was noticed to droop down in a sickly condition. In this state the parasite approached and carefully examined the aphid with its antennæ. Being apparently satisfied, it placed its forefeet on the victim's back and its mouthparts to the puncture.

This position was then held for several minutes without moving, during which the body of the aphid was noticed to slowly collapse. After it was apparently sucked dry, *Aphelinus* would withdraw and search out another victim where the same maneuvers were repeated. Three small nymphs were thus fed upon in half an hour, after which the parasite's abdomen appeared quite distended with their contents.

These dead aphids were later dissected, and it was found that *Aphelinus* had deposited an egg in each. This would seem to indicate that oviposition was the primary object in puncturing a host, and that feeding was a secondary, acquired habit.

TABLE III.

Effect of Different Food, Accessible, on Length of Life in the Adult Parasites.

Food	Number of Parasites	Length of Life
Dock plant	3	3 days
4th instar aphids	3	4 days
Honey-dew (on leaves)	3	11–12 days
Honey solution (fresh)	1	39 days

However, with this habit of feeding, the parasite defeats its primary purpose by killing the host and preventing the development of the egg immediately after it is deposited.

Observations made in the course of other experiments show that a single parasite ordinarily kills, in the above manner, from three to five of the smaller instars per day. The very young stages are almost always preferred, although it has been noticed to feed on a third or fourth instar nymph. That the older stages are seldom if ever attacked, has been demonstrated in a number of instances where *Aphelinus* was confined with adult aphids for various purposes. The parasite not only failed to oviposit in these adults, but actually died with them for want of food when the adult aphids did not produce young for it to feed on. In all cases the aphid is very much weakened so as to offer practically no resistance, before the parasite will attempt to feed. While the feeding is going on, the aphid

remains slumped down apparently oblivious to the slow ebbing away of its life blood, the only movement being a slight wave of a leg or antenna.

Length of Adult Stage.

The length of life in the adult has been observed to vary according to the kind of food available. Temperature also is undoubtedly an important factor, but no accurate experiments have been attempted to show how it operates.

The effect of the different kinds of food on the length of life is shown in Table III, and may be briefly summarized as follows: Confined without food, on plants alone, among older aphids on plants, or in small receptacles, death ensues in less than four days; on honey dew they live for twelve days; and one specimen was kept alive for thirty-nine days on honey solution in distilled water, given fresh every day until it finally escaped. There is reason to believe that they will live much longer on this. The only one carried through to normal death on aphids, lived thirty-six days; producing eggs for thirty of these days.

REPRODUCTION AND DEVELOPMENT.

Method.

The prevailing method of reproduction in *Aphelinus semiflavus*, as well as in a number of other chalcid parasites, is by parthenogenesis. Seventeen successive generations have thus far been reared parthenogenetically, and there is every reason to expect many more to follow indefinitely; since the last offspring appear as vigorous as the first.

Proportion of Sexes.

Males are quite rare in this species. Out of more than 900 individuals examined from the different generations throughout the series of parthenogenetic generations, but seven males were found. These were scattered more or less irregularly through the series as shown in Table IV. It is quite possible that males might have appeared from time to time in other rearings and passed unnoticed, due to the difficulty of distinguishing the sexes without a microscope. However, throughout all the observations, of either living or dead material, males

were encountered but one other time, when three were taken from Cage 48a3 on March 2, 1921. One of these was confined with females among some aphids on a dock leaf in a small vial, and copulation was observed. No observations were made on mated females to determine whether mating had any effect on the proportion of sexes and number of offspring produced. This must be left for later investigation.

TABLE IV.

Sample Counts from a Series of Parthenogenetic Generations Showing Proportion of Sexes.

Generation.....	a_1	b_1	c_1	d_2	e_1	f_1	g_2	h_1	i_2	j_2	k_1	l_1	m_2	n_1	o_1	p_1	q_2
Date.....	3-6 1921	3-22 1921	4-3 1921	5-4 1921	5-23 1921	6-7 1921	6-23 1921	6-29 1921	8-11 1921	9-1 1921	9-24 1921	9-20 1921	10-30 1921	11-19 1921	11-27 1921	12-13 1921	1-30 1922
No. Females...	66	38	61	135	55	59	15	8	132	113	81	6	74	57	1	12	8
No. Males.....	0	0	0	3	0	0	0	0	0	1	3	0	0	0	0	0	0

Some of the Encyrtidæ, a family of scale parasites, closely related to the Eulophidæ, produce but few males or none at all. In other species of the genus *Aphelinus*, feeding on aphids, the males are not known.

The production of females parthenogentically that are capable of producing more females in the same manner, for an indefinite number of generations, is a very valuable asset to a parasite when it is to be established in new territory. By this method of reproduction the chances of its increase are greatly enhanced. Likewise, it is less liable to die out through reduction in numbers and consequent scattering of individuals that would reduce the chances of mating where this was important for the perpetuation of the race.

The Egg.

Description.—The egg is elongate ovate, and slightly bent in the middle, with dimensions of .21 x .05 mm. The anterior end is slightly more rounded than the posterior, which tapers bluntly to a point. At the anterior end, there also appears a small nipple-like micropyle that projects just far enough from the surface to be seen with a high power compound microscope. The color, in reflected light, is a very light cream-white; darker

in transmitted light. The corion is very thin and transparent; showing the finely granular structure of the contents, which is homogeneous throughout for a few hours after the egg is laid. Soon development begins to appear by the characteristic form of the growing embryo. At the end of twenty-four hours the egg clears up slightly, except for certain parts of the embryo, which show darker in the form of two blotches; the one in the anterior portion of the egg having a long and wavy form which bends around like a hook near the end of the egg; the other in the posterior portion is more rounded. Both of these blotches finally join together by the growth of the mesenteron, shown by two faint lines. When the egg is forty-six to forty-eight hours old, it becomes still more transparent, and only one elliptical dark spot appears near the center. It is now almost ready to hatch. (See Figs. 3, 4, and 5, Plate I.).

Position in Host.—The egg floats loose in the hæmocœl of the host, where it may be seen on dissection under the high-power of a binocular microscope. It is quite large in size compared with the size of the adult.

Length of Stage.—The period of time spent in the egg stage is very near three days (72 hours) for all the observations.

Number Laid.—The only actual count made of the number of eggs laid by a single individual in the course of its life, gave 507. (Fig. 1). Other partial counts would lead one to believe that this is a good high average. The conditions under which the eggs were deposited may be considered almost optimum, since the parasite was closely confined with a number of parasite-free aphids of the most desirable stage. It is difficult to make an estimate of what the total number would be under more natural conditions out of doors, but it is probably much less than the actual counts indicate for caged material. From the number of blackened aphids obtained from the different cages, one might estimate the total number parasitized by one adult female to be around 200.

Like many other parasitic Hymenoptera, there are only a few mature eggs in the ovarian tubes at a time; about ten for *Aphelinus*. The other eggs mature from day to day in such numbers as required, which is probably regulated by some external stimulus, like the presence of a large number of hosts.

Larva.

Description.—The larva when first hatched has practically the same size and form as the egg, but slightly shorter and broader. As growth proceeds the anterior and middle segments enlarge to accommodate the increasing mesenteron, giving it at first a spindle form and later a distinct top shape; the head forming a knob on the broad rounded anterior end, and the posterior tapering to a rounded point. When the larva reaches maturity it is contracted more in a longitudinal direction, becoming almost globular in general shape. (Fig. 7, Plate I).

In the younger stages the color is almost absent, except the dark mesenteron which stands out against the general transparency. Later on the accumulating fat body lends a light yellow color to the larva.

The segmentation of the larva is rather obscure, but with careful search thirteen may be counted. The head is distinct, supported by a visible tentorium, and bearing a mouth opening in the anterior ventral portion. This mouth is armed with two sharp dark mandibles which are situated well back in the cavity, but are capable of protrusion sufficient for grasping purposes. A peculiar botryoidal structure may be also observed covering the front and vertex. (Fig. 8, Plate I). This is probably a group of sensory organs. The entire digestive tract may be traced from mouth to anus in transmitted light; though the fore and hind guts-are indistinct. Several other internal organs were slightly visible, but no attempt was made to identify them. Spiracles are observable on segments five to nine inclusive, but could not be seen on any of the others. Small tracheæ lead off from these, but it was not determined whether they function or not.

Position in Host.—During most of the growing period the larva occupies no definite position in the host, but moves freely about in the fluid of the body cavity. However, when it has devoured most of the internal organs of the host and has become large enough to fill the abdominal cavity it assumes a position with its primary axes similar to those of the host. Just before pupation this position is exactly reversed, so that the primary axes of the parasite are opposite to those of the host, both anterior-posteriorly and dorso-ventrally.

Length of Stage.—The larval period varies from about six to eleven days, or even longer in some cases where the temperature is low. The usual time from egg deposition until the aphid host turned black, was nine to ten days. Pupation began within one or two days after the host turned black, and by the end of three days the last larval skin was cast and the full pupal form assumed.

It was found that it took two days longer for the larva to kill and turn black an adult aphid than it did for a third instar nymph, and one day longer for a first instar nymph than for a third instar. This would seem to indicate that the medium instars furnished optimum conditions for the development of the larva, where other factors were equal.

Pupa.

Description.—The pupa is characteristic of the Hymenoptera in general, *i. e.*, of a form similar to the adult, with rudimentary wings, and large turgid legs and antennæ lying near the body on the ventral side, and enclosed in transparent sheaths. When first formed the pupa is almost transparent or very light yellow throughout. Soon the eyes turn to a reddish brown and the light yellow deepens with age until the colors of the adult are reached at maturity.

Meconia.—As soon as the pupa begins to take form, or just before it sheds the last larval skin, it voids several brown bodies of an oval shape. These are the characteristic meconia of the parasitic Hymenoptera, and represent the total, larval excrement that has accumulated throughout the period and discharged at this time.

Position.—The position of the pupa with reference to the host is exactly opposite to the primary axes of the latter, the same as described for the mature larva. This places the mouth parts of the adult *Aphelinus* in a position to gnaw out the emergence hole on the posterior-dorsal surface of the blackened host remains.

Length of Stage.—The average length of the pupal stage is seven to eight days, but it may vary between five and fifteen days, or even longer under adverse conditions. There is every reason to believe that it passes the winter in this stage.

Effect of Parasite on Host.

On Internal Structures.—As soon as the young *Aphelinus* larva hatches, it begins feeding on the fat body and developing young of the host. Within three or four days after hatching nearly all the young aphids within the mother are destroyed. The feeding continues on the other structures, until nothing is left, when the parasite larva approaches maturity, but the digestive tract. This is in common with the habits of other parasitic Hymenoptera larva which spare the vital organs of the host until the very last.

The larva of Aphelinus is armed with well developed mandibles, which, however, do not project out of the mouth as in the larva of the Braconid parasite, *Aphidius;* but seem situated back in the mouth cavity where they are less effective in tearing up host tissue. There is no gathering of bunches of fat globules in a host parasitized by *Aphelinus*, as in one harboring *Aphidius*, which would indicate that the fat cells are not broken down. However, many bits of tissue and separate cells may be observed floating promiscuously around in the body fluids of a host parasitized by *Aphelinus.*

On External Appearance.—The first external appearance of parasitism is a change in color of the host from green to light cream. Then a honey-colored spot appears in the abdomen, which is the darker mesenteron of the larval parasite within. This light color of the host deepens into a yellow or light amber in another day, and by the following day begins to turn gray. Within a very few hours after graying begins, the aphid is coal-black, except for the head and appendages, which are transparent. Death occurs during this last darkening. Just before death the aphid spreads out its legs in symmetrical form and firmly grasps the plant on which it rests. This tends to make them adhere to the plant after death; still, they are further secured by some form of silk secretion through the ventral wall. No detailed observations were made on this act, but it is evident that no hole is cut through, as in *Aphidius.* Perhaps only a very small puncture is made and the silk forced through it. The amount is very small, at most, and in some cases there is not enough to detect; nevertheless, the black aphid remains adhere quite firmly to the substratum.

On Production of Young.—Several experiments were undertaken to determine the effect of parasitism in the various instars on their subsequent maturity and production of young. An equal number of parasites were confined with separate lots of different ages and instars of aphids for a day and then removed. The aphids were observed until they showed parasitism and died. One nymph, parasitized on the day it was born, carried the parasite through to maturity, but did not mature itself, or produce any young. Three nymphs, parasitized in the second instar, produced but one young, which was doubtfully from one of these nymphs, since another unparasitized one occurred in the same cage. Nine second instar nymphs matured and produced but two young at the end of eleven days from birth. Seven nymphs, parasitized in the third instar, matured and produced sixteen young before succumbing to the parasite. With the larger stages, parasitism was so rare that no data were obtained.

It appears from these experiments that those aphids parasitized in the second instar seldom mature and produce young; while those parasitized in the third instar may mature and produce several young before they are killed.

In the few cases where adult aphids were parasitized after they had begun to produce young, the production continued for six days from the time the parasite's egg was deposited. During this time two females produced twenty-five young. Allowing three days for the egg of *Aphelinus* to hatch, it will be seen (Fig. 2, curve "d") that the decline in production of young began shortly after the egg hatched. Production ceased altogether two days before the death of the host.

Aphelinus may also disturb the production of young in aphids by worrying or exciting the viviparous females. This is shown in Figure 2, curves a, b, and d, between the points x and x_1 where the parasites were introduced and removed. In every case a marked drop occurs in the production. However, as soon as a few young are born, the parasite's attention is directed to them so that the adults may go on producing others unmolested. Here is where the preference of *Aphelinus* for the younger stages of the host is of marked significance as a factor in their control, since it does not attack at the source of production, the adult female. This may account for the fact that *Aphelinus* is much slower than *Aphidius* in exterminating a colony of aphids with which they are confined.

Effect of Host on Parasite.

As in common with most parasitic Hymenoptera, there is a great variation in size of adults according to food supply or size of host. This was more than double in *Aphelinus*, or from .35 mm. to .75 mm. in length. The extremely small specimens were apparently sterile, for several trials on parasite-free nymphs failed to get them to reproduce, or even lay eggs. An attempt at oviposition was noticed in one case, but the parasite was unable to extrude the ovipositor its full length.

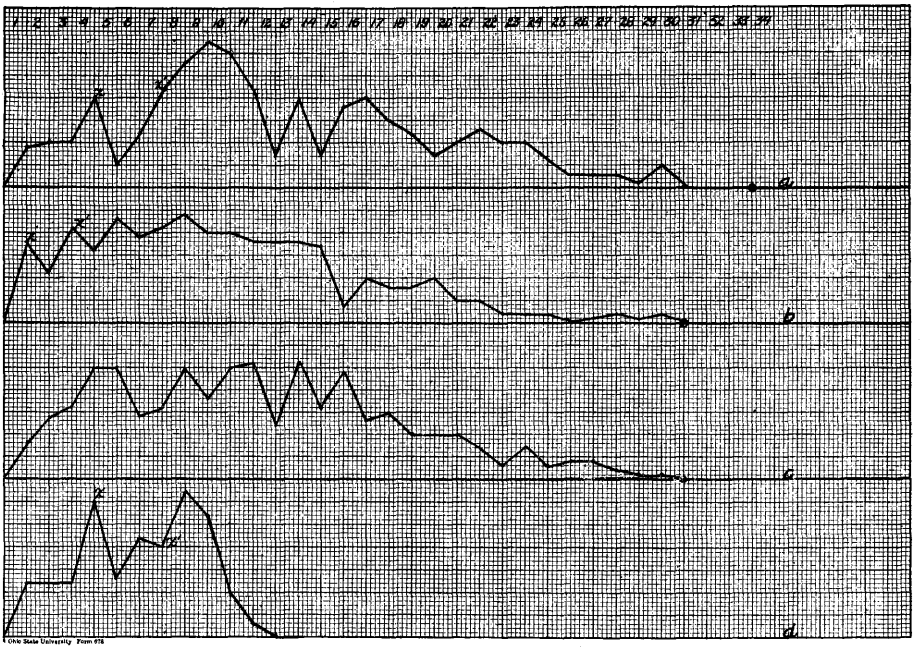

Fig. 2. *A series of curves showing the effect of the parasite Aphelinus semiflavus on the production of young in adult viviparous Myzus persicæ. a.* Average daily production of young in six females for the average total period of production, with *Aphelinus* but unparasitized (note drop in curve between x and x_1 when parasites were introduced, showing effect of the presence of *Aphelinus* on production of young); *b.* average daily production of young in ten females for the average total period of production with *Aphelinus* but unparasitized. (note drop between x and x_1 as in *a*); c. average daily production of young in ten females free from parasites; d. average daily production of young in two females for the average total period of production before and after parasitism. The parasites were introduced at the point x and removed at x_1. Death from parasitism occurred at the end of he curve.

COHOSTS.

Previous records give *Myzus persicæ* Sulz., *Aphis gossypii*(?) Glover, *Aphis maidis* Fitch, and *Chaitophorus viminalis* Mon., as hosts for *Aphelinus semiflavus*. The writer can add to this list from his own rearings, the following: *Macrosiphum pisi* Kalt., *M. granarium* Kirby, *M. Sanborni* Gillett, rarely, and *Anuraphis viburnicola* Gillett.

Myzus persicæ, from which most of the field records come, seems to be the preferred host, although it took to *Macrosiphum granarium* and *Anuraphis viburnicola* quite as readily in captivity. *Macrosiphum pisi* was not parasitized very heavily, due, perhaps to its long legs and large size, and irritability. *Macrosiphum sanborni* escaped almost entirely for no apparent reason. They were only rarely attacked even when confined in a cage with a number of parasites, and a colony went through the winter in the greenhouse among many parasites with but a scarce eight or ten being parasitized.

Several attempts were made to rear *Aphelinus* in *Aphis rumicis*, another common dock aphid, but all were unsuccessful. The parasite would oviposit in them freely, and subsequent dissection showed that the eggs would hatch and the larva become nearly half grown, in some cases; but they would always die before reaching maturity. In most cases death occurred shortly after the egg hatched.

INTERRELATIONS WITH APHIDIUS.

Considerable importance has been attached to the interrelations of primary parasites in a single host, since the discovery by Pemberton and Willard (18) of the disastrous results of the interrelations of two primary fruit fly parasites imported to the Hawaiian Islands.

From what is known of the two groups of primary aphid parasites, there seems to be no question about the superiority of *Aphidius* over *Aphelinus* as a controlling factor for aphids. It not only appears earlier in the season, but lays more eggs in a shorter time, is more vigorous in its actions, is not confined so closely to the younger aphids, and has a much greater dispersal than *Aphelinus*. It was, therefore, both interesting and important to determine to what extent these two occurred in the same host, and the ultimate outcome of such occurrence.

Observations on colonies of aphids in the open greenhouse among both *Aphidius* and *Aphelinus* showed that parasitism of a single host by both parasites was rare at best, if not entierly absent. In fact, it was often difficult to bring this about when they were confined in a small cage. However, when they were put in and taken out separately, the one before the other, results were different. *Aphidius* would parasitize practically every aphid in a small colony, and all the eggs that *Aphelinus* would deposit later, which was always considerably less than *Aphidius* for a given period, would be in the same host with one or more *Aphidius* eggs or larvæ.

When *Aphidius* was placed with a colony of aphids a day ahead of *Aphelinus* and removed before *Aphelinus* was introduced, a heavy parasitism by both resulted. But in practically every case, the *Aphelinus* eggs failed to hatch. The conditions were then reversed, and *Aphelinus* was given a day's start. In this case *Aphelinus* hatched and began development in the usual way, but they did not interfere in the least with *Aphidius* which came along later. This very efficient parasite emerged from its membraneous cover in the normal manner and within a day or two the small *Aphelinus* larva would die. This happened even when the *Aphelinus* larva was allowed several days the advantage over *Aphidius* and was quite large when the latter hatched.

It was, therefore, practically established that for the younger instars, at least, *Aphidius* would always dominate, regardless of whether it came before or after *Aphelinus* in the same host; and that *Aphelinus*, coming after *Aphidius* for a day, would never hatch. In fact, the egg would never begin development as shown in the characteristic change in appearance (Plate I, Fig. 3, 4 and 5.)

Possible Ways by Which Aphidius May Cause the Death of Aphelinus.

Just how the death of *Aphelinus* is brought about still remains a mystery that will only be solved by more careful investigation. Several theories are suggested to explain it, but all of them require refined methods to prove. They are given here for what they are worth.

Cannibalism.—*Aphidius* is much better armed with mandibles and a spiny body, than *Aphelinus*, and is also more active. It might, therefore, be expected to kill *Aphelinus* by feeding directly on it or injuring it fatally by striking against it in the host. Yet, in the many cases that were examined, *Aphidius* was never found feeding on *Aphelinus*, nor did there ever appear evidence of mutilation in the dead larvæ. In each case, *Aphelinus* simply stopped movement and turned darker in color, in which condition it remained until it finally shriveled up and disintegrated.

Starvation.—This theory does not carry much weight when we consider the abundant supply of food present at the time of death.

Toxic Substance.—It is quite possible that something of this nature may be thrown off by *Aphidius* that has an injurious effect on *Aphelinus*, but it is difficult to prove.

Lack of Oxygen.—Our knowledge of respiration in this group of parasites is still very meager, so it is scarcely possible to say just how the above condition might effect the parasites. It appears that both derive their oxygen from the blood of the host, in which they float, and it is also possible that *Aphidius*, being the more active of the two and better adapted for breathing might get around and monopolize it; though it is doubtful if this could be reduced low enough to kill *Aphelinus* and not work permanent injury on *Aphidius*.

Economic Importance.

While the above theories are of considerable importance from a biological standpoint, it is sufficient for economic purposes simply to know which of the two parasites will dominate when the two come together. This the writer has shown. Since *Aphidius* is the more efficient one in every respect, there need be little fear over the fact that it will kill *Aphelinus*, since this efficiency will in no way be lessened where they accidentally come together. The aphids that *Aphelinus* parasitized would not interfere with *Aphidius*, and would be so many more dead aphids in addition to those killed by *Aphidius*.

SECONDARY PARASITES.

Throughout most of the winter of 1921–22, at Columbus, Ohio, very few secondary parasites appeared to infest *Aphelinus* in the greenhouse insectary. But by February, two species began to appear in from ten to twenty percent of the specimens taken in the open greenhouse. One was determined by Mr. Gahan of the United States National Museum, as *Asaphes* (*Megorismus*) *americana* Gir., and the other by Mr. Rowher, also of the Museum, as *Alloxysta* sp., a Figitid resembling *Charips* (*Allottria*).

In the fall of 1921, another secondary was reared from a new species of *Aphelinus* on a juniper aphid near Philadelphia, Pennsylvania, which likewise proved to be a secondary of *Aphelinus semiflavus*. This was determined by Mr. Gahan as *Aphidencyrtus aphidiphagus* Ashm.

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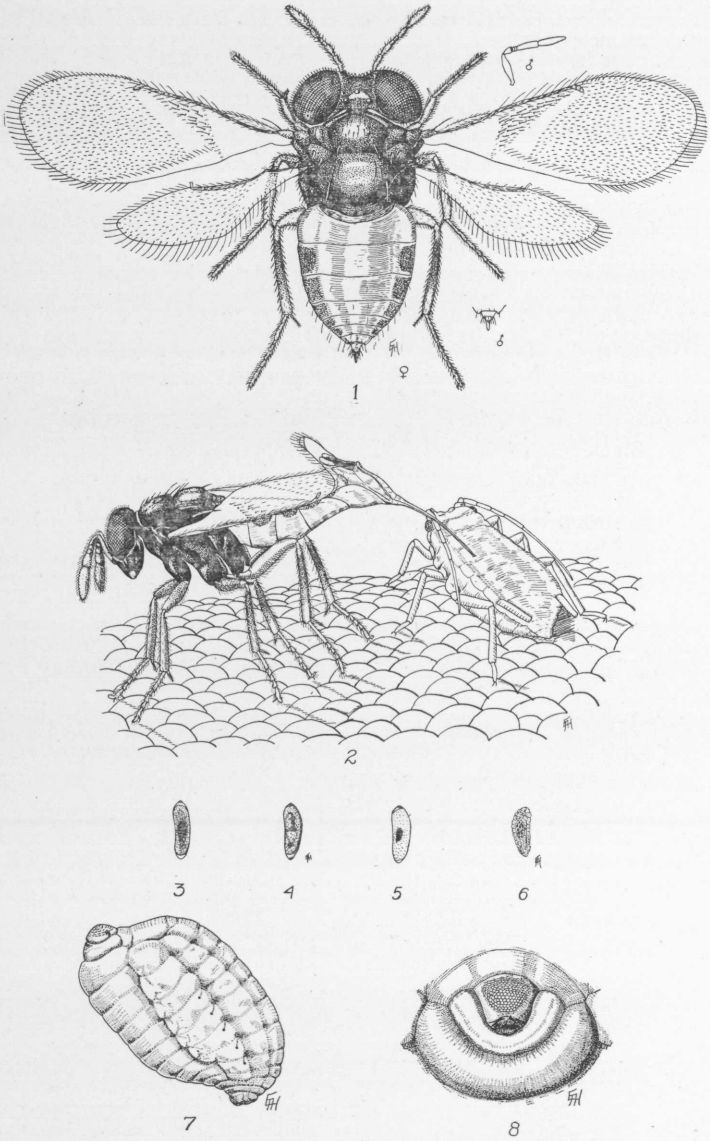
EXPLANATION OF PLATE.

Fig. 1. Adult female *Aphelinus semiflavus* with male antenna and genitalia in insert.
Fig. 2. Female *Aphelinus* ovipositing in aphid nymph.
Fig. 3. Egg less than five hours old.
Fig. 4. Egg twenty-four to twenty-eight hours old.
Fig. 5. Egg forty-six to forty-eight hours old.
Fig. 6. Small larva just hatched.
Fig. 7. Lateral view of full grown larva, just before pupation.
Fig. 8. Front view of larval head, greatly enlarged.

All figures, except Figure 8, are drawn approximately to the same scale, enlarged thirty-three and a third times.



E. A. Hartley.

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