

## THE BIONOMICS OF *DINOCAMPUS COCCINELLÆ* SCHRANK.

W. V. BALDUF\*

Many entomologists are acquainted with the spectacle of our common adult ladybeetles secured to the cocoon of their parasite and exposed on the trunks of trees, on weeds, grasses and other objects. Although this parasite has been studied by various men from the days of Dr. C. V. Riley to date, many phases of its cycle and habits have been unknown heretofore in this country. Its bionomics were therefore deserving of some attention and inasmuch as this same species is now believed to occur in some European countries, a comparison of its life history and habits here and there is of more than passing interest.

### SYSTEMATIC POSITION AND SYNONYMY.

This parasite of ladybeetles is a hymenopterous insect of the family Braconidæ, subfamily Euphorinæ, and known scientifically as *Dinocampus coccinellæ*. Probably because of its wide distribution in several countries on both sides of the Atlantic, the parasite had long been treated as several species, whose identity, however, was established by Mr. R. A. Cushman in 1922 (1). The original description was written by a German naturalist, Franz von Paula Schrank in 1802. The following data on the synonymy are quoted from Cushman:

"In 1811 Nees (von Esenbeck) described his *Bracon terminatus*, later (1834) erecting for it and one other species the genus *Perilitus*. Nees' species was subsequently transferred by Wesmæl (1885) to his genus *Microctonus*, and Foerster (1862) erected for it the genus *Dinocampus*. In 1872 Cresson described his *Euphorus sculptus* and in 1889 Riley his *Perilitus americanus*." Riley (4) had however previously assigned it the provisional name *Centistes americana*, which was adopted by Weed and Hart (9) in their paper on the habits of this parasite.

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“The synonymy is therefore as follows:

*Dinocampus coccinellæ* (Schrank)

*Ichneumon coccinellæ* Schrank, Fauna Boica, vol. 2, 1802, p. 310, ♀.

*Bracon terminatus* Nees, Mag. Ges. Naturf. Fr. Berlin, vol. 5, 1811, p. 26, ♀.

*Perilitus terminatus* Nees, Ichn. Affin. Monog., vol. 1, 1834, p. 30, ♀ ♂.

*Microctonus terminatus* Wesmael, Nouv. Mem. Acad. Sc. Bruxelles, vol. 9, 1835, p. 63, ♀.

*Dinocampus terminatus* Foerster, Verh. Naturh. Ver. Preuss. Rheinl., vol. 19, 1862, p. 252.

*Euphorus sculptus* Cresson, Can. Ent., vol. 4, 1872, p. 227, ♀.

*Perilitus americanus* Riley, Insect Life, vol. 1, 1889, p. 338, ♀.

*Perilitus terminatus* Dalla Torre, Cat. Hym., vol. 4, Braconidæ, 1898, p. 122.

*Ichneumon coccinellæ* Dalla Torre, loc. cit., vol. 3, part 2, 1902, p. 875.

*Dinocampus terminatus* Timberlake, Proc. Hawaiian Ent. Soc., vol. 3, 1918, p. 401.

DISTRIBUTION AND HISTORY.

*Dinocampus coccinellæ* has been reported to date from New Zealand, Europe, North America, and Hawaii. Timberlake (2) says it was probably introduced into Hawaii from North America with the coccinellid *Olla abdominalis* which is known from Indiana, Southern California and Texas. Further records for the parasite from North America are given in the literature as follows: Glover (3), Maryland; Chittenden (10) and Riley (4), Washington, D. C.; Riley (4), North Bend, Ohio; Missouri; Oxford, Indiana; Sheldrake, New York; Cutright (7), Ohio; Cresson (5) and Folsom (10), Illinois; Weed and Hart (9), and the following records from the Illinois State Natural History Survey: Mahomet, Seymour, May 21, 1891, Urbana, May 13 and 22, 1891, and Normal, May 12, 1884; Cushman (6) Vienna, Virginia; Timberlake (8) Salt Lake City, Utah; Agawam, Mass.; Brownsville, Texas, and Humboldt Canyon, California; Girault (11), Paris, and Will's Point, Texas. Professor R. C. Smith, Manhattan, Kansas in a letter to the writer states that the parasite was rather plentiful during 1919 at Charlottesville, Virginia, and he has seen them since in Kansas.

Records of its occurrence in Europe indicate a wide distribution there. Ratzeburg (4) found them in Neustadt, Germany; Tullgren (12) gives an account of its activity at Stockholm, Sweden; while in Russia its presence in Riazan (13), Petrograd (14), and St. Petersburg (15) was made known by Goriainov, Bogdanov-Katkov, and Oglobin, respectively. Riley (4) gives indications that it also occurs in France and Great Britain. According to a privately published paper (1925) by A. A. Girault, it may occur also in New Zealand. It may therefore be deduced that *D. coccinellæ* occurs in many countries of at least the north temperate zone, and is perhaps generally distributed in most of this area.

Whether it was brought to America from Europe is not known, but that such introduction is possible is suggested by its transposition into Hawaii from western United States. Schrank's original description of the parasite was written in 1802, or a hundred and twenty-four years ago, whereas Cresson first named it from Illinois fifty-four years

ago, in 1872. Its known occurrence in foreign countries that have long had commercial relations with the United States favors the theory that it may have been carried to us from abroad. However, it may be a native species.

#### HOSTS.

All information accumulated to date indicates that *D. coccinellæ* parasitizes only adult beetles of the family Coccinellidæ. Within this group some species, as far as known at present, are never attacked, while a considerable number become infested with it to a moderate extent, and a few are evidently strongly favored by the parasite. Cushman (6) placed the following species in a cage with the parasite: *Adalia bipunctata*, *Anatis 15-punctata*, *Hippodamia glacialis*, *H. convergens*, *Coccinella 9-notata*, *Ceratomegilla fuscilabris* (*Megilla maculata*), *Cycloneda sanguinea* (*munda*), and *Hyperaspis* species. All the species were attacked except *Hyperaspis* sp. Larvæ of various ladybeetles were also caged in this way, and were likewise pursued by the parasite. However, the parasite was obtained in these tests only from a single specimen of adult, a *C. fuscilabris*. From beetles brought from nature, Cushman invariably reared the parasite from *C. fuscilabris* adults, with the exception of a single specimen from *H. convergens*. Riley (4) indicates that it was obtained most frequently from *C. fuscilabris*, but "one specimen of *C. 9-punctata* was also found which had evidently been infested by the same parasite." Folsom (10) reported the same two species parasitized. Weed and Hart (9) bred it from cocoons in connection with *C. fuscilabris*, while Glover (3) makes brief mention of the same common ladybeetle being attacked by a "parasitic insect." Timberlake (2) indicates that it develops also on *Olla abdominalis* Say, a ladybeetle introduced into Hawaii from California, but since its introduction the parasite usually attacks *Colephora inaequalis* F. Later (18), the same writer reports rearing the parasite repeatedly from *O. abdominalis*. In his paper on the bionomics of *Hippodamia tridecim-punctata* L., Cutright (7) states that very rarely an adult of this species may be found parasitized by *D. coccinellæ*. Hubbard (3) increased the host list by adding *Hippodamia convergens*, which Timberlake (8) also found to be a fairly common subject.

The above records are for coccinellids native to the United States. The range of species reported attacked in Europe is more limited. Ratzburg (4) obtained it from *Coccinella 5-punctata* and *C. 7-punctata*. Tullgren (12) bred it from *C. 7-punctata*. Goriainov (13) also found cocoons of the parasite among the latter host, while Oglobin (15), who has made the most extensive study of the parasite up to the present, took it commonly from *C. 7-punctata*, and less frequently from *Adonia variegata*, and only once was *Halysia 14-punctata* found attached to the cocoon of its enemy. From a review of the published papers on the two common species of phytophagous ladybeetles in the United States (*Epilachna corrupta* and *E. borealis*) it was learned that these pests are not known to be attacked by this parasite.

During the present study at Urbana in 1924 and 1925, some of the old host records were confirmed and several new ones established. *Ceratomegilla fuscilabris*, as reported by former workers, was found to be the host most commonly parasitized. Other species already reported and here again shown to be hosts, were *Hippodamia convergens*, *Coccinella 9-notata*, and *H. 18-punctata*, while *C. sanguinea*, *H. parenthesis*, and *Adalia bipunctata* were added to the host list. In most cases these species have been found quite commonly, in proportion to their numbers, with the parasite cocoon, excepting *C. 9-notata*. Here only the eggs or the first instar larvæ of the parasite were obtained from two individuals exposed to the adult parasite in cages. These seven species of ladybeetles are the larger ones most commonly taken here.

#### METHOD OF ATTACKING THE HOST.

When individuals of *D. coccinellæ* were released in a tall chimney cage containing ladybeetles, the parasite usually recognized its prospective host promptly. Several factors influence the promptness of the discovery: (1) age affected the responsiveness of the parasite, which, under cage conditions, lived on the average of four days, and was most active in parasitizing the coccinellids when two and three days old; (2) distance between the parasite and the ladybeetle, the latter being most easily discerned at a distance of three inches or less away, although the parasite can recognize an active beetle at greater distances; and (3) the degree of activity and perhaps the conspicuousness of the colors of the beetle. It was demonstrated again that insects spy objects in motion much more readily than when the same body is at rest.

Having centered its attention upon a beetle, the parasite responds in one of two ways, depending on whether the beetle is at rest or moving. When the ladybeetle is quiet, the braconid approaches it with antennæ vibrating in the brisk manner characteristic of parasitic Hymenoptera, and strikes the beetle with the antennæ, the first legs, or even brings the head in contact, or runs over the back of the beetle. In so doing, the parasite sometimes waltzes clear round the beetle, striking it on all sides. In some instances the ovipositor is brought into use, punching the beetle here and there, which conduct must perhaps be interpreted as an effort to oviposit. However, the vulnerable parts of the body being covered by the elytra when the beetle is at rest, these thrusts do not often end in oviposition, hence only have the effect of prodding the beetle into travel, if any response at all is obtained. The parasite has been seen repeatedly thrusting the ovipositor at the head, sides and posterior of a *Coccinella novem-notata* without penetrating the integument or causing the stolid beetle to move. However, most often the ovipositor is carried ensheathed until the beetle is made to run by tapping it with the anterior appendages.

When the parasite succeeds in inducing locomotion, it quickly darts after the beetle from behind. Usually, during the first part of the brief interval of pursuit, the ovipositor is promptly and quickly drawn from the sheaths in which it is carried directed caudo-ventrad; it is brought forward by turning the abdomen ventrad and cephalad

between the three pairs of legs and produced almost or quite against the venter of the thorax. In changing its position, the ovipositor thus describes an angle of almost one hundred eighty degrees made possible by the movement of the base of the ovipositor from the back to the front of the ventral orifice of the abdomen, and by the hinging of the abdomen at the petiole. The ovipositor is then exerted and produced forward to such an extent that its apex reaches slightly beyond the face.

The parasite quickly arrives within striking distance of the fleeing beetle, and when conditions are favorable makes an extra effort and suddenly thrusts the ovipositor still further forward, and in successful instances penetrates the body wall. The majority of the thrusts are directed at the posterior aspect of the abdomen when it is slightly elevated during locomotion. When at rest, the elytra of some species of Coccinellidæ, notably *Coccinella sanguinea* and *C. novem-notata*, fold so far over the tip and sides of the abdomen that but a small unprotected surface or none at all remains exposed at which the parasite can aim its ovipositor. When the beetle is in motion its sides are beyond the reach of the parasite. The ovipositor is so small and sharp, and the act performed so quickly that the details regarding the exact point of insertion could not be determined. However, it seems that the tip of the ovipositor slides along the external surface of the abdomen until it strikes a coria. Here the force behind the needle-like rods would seem to push them through quite readily due to the greater flexibility and lesser thickness of the conjunctivæ. But the transverse slit-like terminal aperture of the abdomen of these beetles also seems to offer good possibilities because it is least obstructive and most favorably situated. The fact that a large percent of the parasite eggs or newly hatched larvæ found in the beetles examined occurred in the posterior extremity of the body cavity confirms the latter view.

Although it seems that most beetles are running or crawling when attacked, some may rest in such a position or place as to expose vulnerable points in their body armor,—perhaps chiefly the sides of the abdomen. This state obtains especially when the beetle has had an abundance of food, or females are very gravid, with the result that the abdomen becomes much distended, exposing the terga and coriæ of several of the terminal abdominal segments beyond the tips of the wing covers, much as when the beetle contains a full grown parasite. Many thrusts at the cephalo-lateral surfaces of the thorax have been noted, but subsequent dissection revealed that no eggs were injected. Numerous beetles direct from nature were also examined, and less than one percent had been punctured anterior to the abdomen, as determined by the position of the parasite egg or small larva in the host. Hence, the most effective parasitizing is accomplished when the parasite finds the beetle active or succeeds in getting it excited. Then the parasite is most enthusiastic and alert, and moves most quickly, whereas the beetle, in its efforts to elude the pursuer, is least able to defend itself and carries the abdomen raised up in an attitude favorable to attack.

However, the beetle is not entirely defenseless. In several cases, caged beetles were noticed to drive away, or snap at, the parasites. In other instances, while the parasite was pursuing beetles closely, the latter quickly raised their abdomens and actually kicked their hind legs at the parasite. But that act was at the same time utilized by the ingenious enemy which thrust at the venter of the abdomen when it was thus elevated. The beetles, if congregated, may gain some respite by what resembles a game of cross-tag played with a parasite. The latter pursues the original prospect, and when another beetle chances to intervene, the parasite follows the interloper. The attention of the pursuer has been seen to be diverted in this way several times without a stop.

The mode of attack by *Dinocampus coccinellæ* has been briefly described before by Ratzeburg (4) and Cushman (6), who state that it performs in the same manner as *Aphidius*, while Oglobin (15) and Glover (3) refer to the similarity of this procedure with that of *Meteorus*, both of these genera being braconid relatives of *D. coccinellæ*.

#### STRUCTURE OF THE OVIPOSITOR.

The ovipositor of *D. coccinellæ* consists of three long, slender, needle-like parts, each slightly more than 1.5 mm. long, tapering distinctly at the tips. Two of them are in a ventral position, their inner faces contiguous, and the third rests upon them, fitting into the dorsal furrow formed by the convex surfaces of the other two parts. When examined in cross-section, the latter were found to be of equal size and solid, and if their detail structure could be discerned a tongue and groove device might be found uniting them. Their position and structure suggests that they are supporting rods for the superimposed element. The single upper needle is hollow, and seems therefore to be the tube for conducting the eggs from the oviduct of the parasite to the body cavity of the host. It is 0.104 mm. in outside diameter at the base, and the terminal third tapers gradually, reaching a thickness of about 0.016 mm. at the apex. Each of the two solid rods is about two-thirds the diameter of the egg tube.

The means of joining the single tube to the pair of supporting rods could not be seen satisfactorily, but inasmuch as the three needles can be separated only by persistent manipulation it is obvious that they are quite intimately united by a definite mechanism. All of them are sharp distad, hence seem to play some part in making a way through the hard body wall of the host. One parasite penetrated so far that the ovipositor stuck, the beetle drawing its offender along a short distance before the connection could be broken. Hence, whatever the detail method of functioning is, the ovipositor penetrates one third its total length. The basal two-thirds of the ovipositor forms a very obtuse angle with the distal one-third, the latter portion being bent upward when this instrument is set to make an attack. This bend facilitates reaching and penetrating the host inasmuch as the point of the prospective host struck by the tip of the ovipositor is generally on a slightly higher level than the proximal portion of the ovipositor.

## RATE OF OVIPOSITION.

The oviposition habits were determined from observations when the parasite was caged with beetles, and by dissections of the parasite and its usual hosts, the latter brought from nature in most cases. Eggs were not sought at length in coccinellids from outofdoors, but such as had been exposed to the parasite in cages were examined carefully. The number of parasite larvæ together with the isolated head capsules found is taken as just as accurate an index of the rate and manner of the egg laying as the number of eggs themselves found on several occasions.

The ovaries are yellow and spindle-shaped. Not less than ten, and perhaps twelve ovarian tubes compose each ovary. Eggs bearing the characteristic attenuated cephalic appendage are recognizable in the caudal half of the tube. It was possible to make out at least 100 eggs more or less matured in both ovaries at one time in two-day individuals. If, as generally believed, the adult *D. coccinellæ* lives two weeks or more in nature, it is probable that a single parasite is potentially able to lay from two to four hundred eggs during its lifetime.

Beetles parasitized in natural situations generally contain from one to three parasites each. Three were rarely found, and two per host did not occur in more than two beetles in each hundred dissected. In the majority only one larva and no extra head capsules were found, indicating that usually not more than one egg is delivered in a single attack. All of the larvæ found in one host were usually of the same size and age, which may be taken to signify that these numbers of eggs are deposited simultaneously by one parasite at one thrust. A few exceptions, all arising under cage conditions, should be mentioned.

In one instance, an embryo and two larvæ of distinctly different sizes were discovered. In another, two living larvæ of different ages occurred. In a third case a beetle was found killed by the emergence of a mature larva. An examination of this beetle revealed the presence of 31 very small larvæ in the abdomen of the beetle. One *C. fuscilabris* exposed to fresh parasites in cages for 24 hours was taken dead 10 days later. The abdomen of the host contained 30 small parasite larvæ of the first instar. Another individual contained evidence that seven eggs had been injected, perhaps simultaneously. Oglobin (15) reports finding as many as 60 eggs and first stadium larvæ in a single *Coccinella 7-punctata* found dead in captivity. Even though these are abnormal examples they possess the value of showing that the parasite is not able to ascertain whether or not its prospective host has already been infested, either by itself or another of its kind.

These instances of caged parasites illustrate more strikingly than do the parasitized beetles direct from nature what are the conditions affecting the number of eggs injected at one time. In case of extreme superparasitism the eggs are probably not all inserted at once. Such are the result of close and protracted confinement of a few beetles with a proportionately larger number of parasites than occur out of doors. In all probability the development of eggs in the ovaries of

the parasite continues whether or not beetles are available. If circumstances compel the parasite to search for hours or days to locate a ladybeetle, thus permitting mature eggs to accumulate in the oviduct, a relatively large number of eggs is probably delivered at the first opportunity. Whether or not all the mature eggs can be discharged into this one beetle also hinges much on the favorableness of the chance to attack. A more or less deliberate assault may possibly be made on some species not easily made to move, e. g. *Hippodamia convergens*, as compared with a high strung species like *Ceratomegilla fuscilabris*. At the same time it is realized that the greater activity of the latter appears to induce the parasite to pursue more vigorously and perhaps with more success in injecting an unusual number of eggs. The abundance of the beetles is also probably a factor in determining the number of eggs the parasite injects. When one parasite per host is common it seems to signify that numbers of beetles were at hand opportunely so as to prevent an accumulation of eggs in the oviduct.

At the usual rate of egg laying, a single parasite has the potentiality to parasitize several hundred beetles. If this capacity were realized, ladybeetles attached to the cocoons of their enemy would be much more plentiful than they are. It is first quite improbable that one *D. coccinella* can find two or three hundred ladybeetles in its adult lifetime, which has been found to be at most two to three weeks in cages. Observations on caged parasites show that oftentimes several thrusts are necessary to accomplish the act of oviposition. Even when a prospective host is sighted, much time is consumed by the parasite in its necessary attempts to get a favorable chance at it. After pursuing beetles as long as an hour continuously, the parasite sometimes stood apart and preened itself for varying lengths of time before reassuming its efforts. Three successive charges and thrusts were made on one occasion by a single parasite in one minute. Such persistent and vigorous efforts consume much energy, and it raises the question whether the vitality of the parasite is sufficient to support the infestation of two hundred beetles or more at the rate of one egg per beetle.

Inasmuch as the great majority of attacks are directed at the pygidium of the beetles, it is to be expected that most of the eggs are located just within the body wall near the tip of the abdomen of the host. All eggs ever located in dissecting beetles, and not less than 98% of the first instar larvæ found, occupied this terminal position.

#### THE EGG AND THE INCUBATION PERIOD.

Eggs from the oviduct and newly deposited specimens from the hosts, (Fig. 1) possessed the same general form. The egg is composed of (1) a bulbous part which bears a short and sharp point at the posterior end, and (2) an elongate, slightly curved petiole broadly fused to the egg proper, and tapers off gradually toward the apex. Hence, the egg may be described as flask-shaped. Embryonic development shows that the petiolate end is cephalic.

The dimensions and shape of the egg vary greatly. Oglobin (15) found fully grown eggs in the parent that were 0.08 mm. long and

0.02 mm. in maximum width. The writer obtained eggs from the same source that were much larger, or 0.29 mm. in length and 0.06 mm. in greatest diameter. The caudal point measured 0.04 mm. in length, the petiole 0.10 mm. and the bulb about 0.14 mm. This difference in size of the eggs is possibly to be explained by their age, the larger having perhaps been retained longer in the oviduct. Growth of the eggs in the host cavity, and possibly also in the parent, seems to result

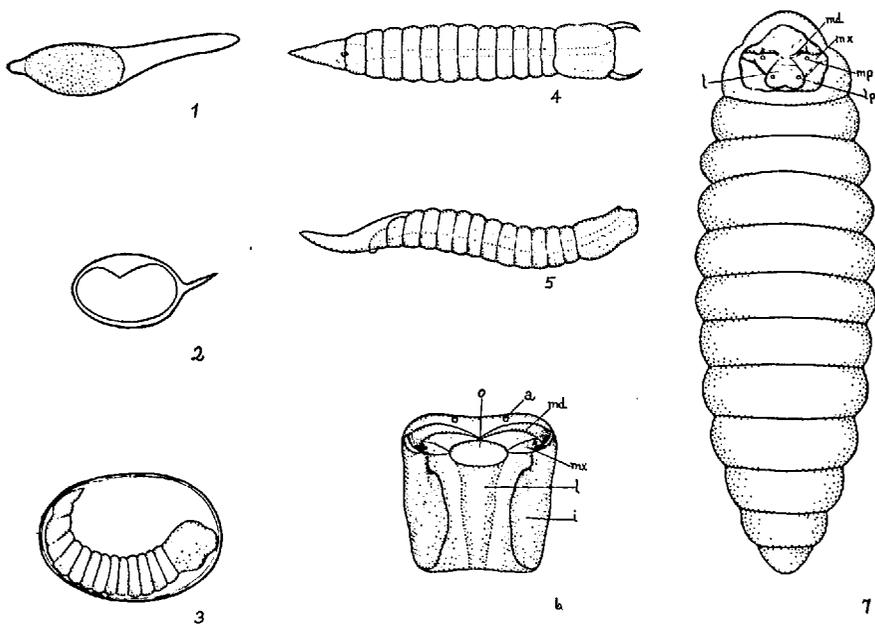


Fig. 1. Egg from oviduct, or newly deposited in host. X 100.

Fig. 2. Same egg aged about four days. X 40.

Fig. 3. Egg shortly before hatching. X 40.

Fig. 4. First instar larva, dorsal view, showing mandibles extended, squarish head, tail-like appendage, and alimentary tract in outline. X 25.

Fig. 5. First instar larva, lateral view. X 25.

Fig. 6. Head capsule of first instar larva, ventral view; a, antennæ; md, mandibles; mx, maxillæ; o, oral cavity; l, labium; i, inflexed portion of tergum of head. X 69.

Fig. 7.—Mature larva, ventral view, showing mouthparts: md, mandibles; mx, maxillæ; m. p., maxillary palpus; l, labium; l. p., labial palpus. X 17.5.

(All figures drawn by Mrs. W. V. Balduf.)

from assimilation of liquids from the surroundings. From the date of deposition to the time the larva hatches, the egg enlarges noticeably in diameter, shortens greatly, and assumes a different shape. In the first day or two the short caudal point is resorbed, and at the age of about five days the egg bears only a very short slender, curved appendage (Fig. 2), the shrunken petiole, which is now 0.06 mm. or less in length, and the egg proper is robust oval. The petiole disap-

pears entirely before the larva leaves the egg (Fig. 3). At this age, one lot of five eggs from one caged beetle ranged between 0.31 mm. long by 0.16 mm. thick, and 0.43 mm. by 0.21 mm., with these dimensions averaging 0.37 mm. by 0.19 mm. Six eggs four days old from another beetle exposed to a single parasite for one continuous period of 17 hours measured between 0.37 mm. by 0.22 mm. and 0.22 mm. by 0.14 mm., the average dimensions being 0.29 mm. in length by 0.19 mm. in width, and their petioles having an average length of 0.08 mm. The disparities in the length of the petiole are correlated with the ages or individual differences of the eggs.

When four or five day eggs removed from beetles were left in a 0.5% saline solution the chorion was pulled away from the vitelline membrane by the liquid absorbed and stored between the layers. In this condition the structures of these membranes could be noted. The chorion is unsculptured, smooth and transparent, but the vitelline membrane is marked off into quadrangular, pentagonal, and hexagonal patches, and is slightly less transparent than the chorion.

The transparency of the egg shell permits the study of the embryo in position. The four day egg contains an embryo that suggests the newly hatched larva by its moderately blocky head and general body shape. The body then lies doubled upon itself and remains thus till hatching time. At five days the segments are quite readily discerned and the head has the appearance of becoming quite heavily chitinized.

To determine the duration of the egg stage, caged beetles were exposed to the adult parasite from 17 to 24 hours at a time. Careful subsequent dissections revealed the state of growth of the embryo on successive days and showed that the larva comes from the egg in 6 or 7 days in the laboratory where day and night temperatures were similar and the average was between 70 and 75 degrees Fahr.

Only one larva was discovered that seemed to be in the process of hatching. The egg had become attenuated and sharpened along the ventral edge due to the tendency of the pointed-tailed body of the larva to extend itself from its doubled state. The dorsal edge was rounded and broad in conformity to the width of the insect's body which at that time assumed a curved state. Presumably, therefore, hatching consists simply of breaking the egg shell incident to the extension of the body. The pointed tail possibly punctures the shell, or produces leverage for the mandibles, which may in that case, force an opening by reason of their pointed construction.

#### THE STRUCTURE OF THE LARVA.

Oglobin (15) implies that the larva has four instars, but states that he did not examine the third and fourth. This is the only reference made heretofore to the instars. The writer distinguished only three instars, but four are probably present as in some other species of braconid parasites whose larval development was studied intensely. The first and second have plain external distinguishing features, and if the two further instars exist they bear close superficial resemblance to one another.

## THE FIRST INSTAR.

The first instar larva (Fig. 4) has a flat squarish, heavily chitinized, light-brown head, and a subcylindrical or somewhat depressed whitish thorax and abdomen, the latter tapering, first slightly to the anal region, then sharply the rest of the way, terminating in a conspicuous pointed, post-anal process or tail. In lateral view, the body of a normal specimen undulates considerably in outline as shown in Figure 5. In dorsal view the head is plain and smooth, but the surface is somewhat uneven, but of uniform color and texture. It continues around the sides of the head to the ventral surface. There it terminates on each side in a longitudinal curve beginning at the base of the mandibles, bending toward the median line and receding to the lateral margin at the posterior edge of the head.

The dorsal margin extends forward shelflike. On its under surface one finds structures that might be interpreted as antennæ (Fig. 6). The most conspicuously retained elements of the mouthparts are the mandibles. They are thick at their bases and curve gradually backward so that their sharp-pointed apices usually rest slightly overlapped and directed into the oral cavity. The mouth opening is readily seen and circular. Arising just posterior to the base of each mandible, and extending mediad to the lateral margins of the mouth one seems to discern a pair of wedge-shaped sclerites which the writer interprets as the maxillæ. They are probably no longer functional, perhaps being fused to the head. The sclerites of the labium do not remain, but the depressed region between the ventral productions of the heavily chitinized tergum appear to be the labium.

The thorax and abdomen together consist of twelve somites of uniform length and the unsegmented tail which is perhaps to be interpreted as another, or thirteenth segment. These regions are semi-opaque, hence the fat contents and the outline of the alimentary tract are recognizable. The latter may be traced through its entire length. It begins as a wide opening in the anterior third of the head, and narrows funnel-like to about one half the diameter of the mouth at the hind margin of the head. Posterior to the head it continues with a uniform diameter and unspecialized structure until it reaches the tail segment. At that point it broadens conspicuously bulblike, and makes a turn dorsad, terminating blindly in the body wall at the base of the tail. There it is indicated on the outside by a squat circular elevation with a shallow central concavity. This depression may possibly represent the remains of the former anus.

The presence of a pointed tail and the pre-dorsal termination of the hind gut recalls similar conditions in the rotifers, the leeches, and other animals including a few arthropods. Superficially this similarity suggests a common ancestry among these animals, but the dorsal position of the anus is a secondary development originating incident to the rise of a post-anal appendage in each case. These appendages are simply specialized portions of the body that serve for locomotion, adherence to objects, or similar functions. This condition furthermore obtains in scattered groups of animals and seems therefore to be purely adaptive without phylogenetic value.

## THE SECOND INSTAR.

When the first instar larva moults the heavily chitinized head is lost, but this region still remains somewhat blocky and differentiated from the rest of the body. The tail becomes proportionately much abbreviated and assumes a ventro-terminal position almost or quite at right angles to the long axis of the larva. The digestive tube becomes more sack-like, yet retains some tendency to open dorsad, but in the mature larva loses even this semblance to opening behind. It is of such large vertical and transverse diameter that it occupies almost the entire body-cavity excepting the posterior portion.

## THE THIRD AND FOURTH INSTARS.

In the last instar the larva is still further reduced than in the earlier stadia in the process of becoming adapted to the parasitic life. The form of the body is grub-like, and the head loses the distinctive shape present in the second instar, whereas the tail is very rudimentary or lost entirely. However, the mouthparts are still traceable, and the elements present can be quite definitely identified (Fig. 7). The mandibles are slender, sharp-pointed and wedge-shaped; the maxillæ are broader, subquadragular and separated by a heart-shaped labium. Both the maxillary and labial palpi are visible although inconspicuous. All these parts are flattened against the face and appear to be capable of but little usefulness in feeding. The openings of the silk glands are on the middle of the labium, according to Oglobin (15). The same writer found nine pairs of spiracles, the first located between the first and second segments behind the head, and the rest on segments four to eleven. Each of the latter pairs is situated in the front corner of the fleshy lateral projections of the segment.

## DEVELOPMENT OF THE LARVA.

The smallest larvæ removed from ladybeetles were 1.2 mm. long. Considering that five day old embryos were 1.14 mm. long and that seven days is the incubation period, it may be assumed that the above larvæ had hatched only a short time before they were found. Oglobin (15) gives the same measurements for larvæ of that age. Their width is approximately 0.25 mm. at that time. However, the body in this instar grows greatly in length, width and thickness. The maximum length discovered was 2.52 mm.; the other dimensions reached two or three times the original size. The head capsule enlarges only to a small extent compared with the body. The changes in its size take place in the extension of the width and thickness of the hind portion due to the swelling of the body. Seventy head capsules measured 0.31 mm. in length and 0.29 mm. in width, with variations of only one or two hundredths millimeters above or below these figures.

Most ladybeetles contain but one parasite. This fact connected with the failure to discover more than one moulted heavily-chitinized head capsule in such instances indicates that all larvæ having these head characteristics are of the first instar. In the course of rearing

larvæ of known ages the maximum size of this instar was reached in a few cases in approximately nine days.

Several larvæ of the second instar were measured. One had a length of 2.36 mm., which is less than the maximum size of the first instar. This indicates overlapping in the size of individuals of the two instars. Another second instar specimen was 2.61 mm., whereas the largest perhaps reaches about 3.0 mm. in length and 0.9 mm. in thickness.

The duration of this and each of the succeeding instars was not determined separately. However, the entire larval stage requires fifteen to twenty days for its development, so that the last three instars are passed relatively rapidly in from six to ten days. The largest larvæ of the species ranged from 3.25 mm. to 4.5 mm. in length, and 1.13 mm. to 1.46 mm. in maximum diameter. Oglobin gives the length of the last instar larvæ as 5.6 mm. with a width of 1.5 mm.

#### HABITS OF THE LARVA.

The newly hatched larva begins its existence within the body cavity of the host and near the body wall. In a high percentage of the cases, the incipient location is in the caudal extremity of the cavity, while a very few begin their life in other parts of the abdomen or even possibly of the thorax. However, their position is not fixed because they have been found in all quarters of the body cavity. They migrate probably with the aid of their caudal appendage which is perhaps manipulated in lateral or dorso-ventral directions, prying against the internal parts of the host. Locomotion is apparently rather limited, because with a small number of exceptions, these larvæ occur within the limits of the abdomen. Even here their distribution is confined to the space between the viscera and the dorsal wall. Rarely are larvæ to be found among the vital organs of the host, excepting the dorsal blood spaces and the fat body which constitute their abode. Here the larvæ of all instars are found, and the amount of locomotion necessarily decreases as the parasite approaches the state of maturity. The young larva lies in a longitudinal-diagonal position for most part, but also transversely, or one end of the body on a lower level than the other. The larger individuals generally lie in the long axis of the host, pressing the viscera down, and extending gradually further forward into the lumen of the thorax as they grow. Thus they eventually occupy all available space, and in addition create more needed room by distending the body wall of the host along the transverse and the pleural coriæ of the abdomen. Larvæ of the second instar and others large enough to be at least third instar individuals are known to turn end for end within the host. The facts that some are headed cephalad in the beetle and that the parasite, when mature, issues head foremost from a point near the cauda indicates that even the mature larvæ need to double upon themselves in order to acquire an attitude favorable to emergence. Presumably these movements cause great discomfort to the host.

## CANNIBALISM.

In instances where two or more larvæ hatch quite simultaneously in the same host, the first act of these individuals seems to be an attack upon one another. In all cases specifically noted, one larva survived the conflict, its body being plump and entire, whereas its victims are left in various physical states. In all cases they are represented by at least the chitinous head to which is attached the more or less depleted thorax and abdomen. Such specimens not uncommonly have the body walls broken or constricted, indicating the points at which the mandibles of the assailant were applied. Often the punctured spots had turned black, and seemed to be disintegrating. This condition probably signified the work of the phagocytic cells of the host subsequent to the death of the larva by cannibalism. Again the victims may be clear-bodied and only collapsed, having had their body fluids extracted. The relative position of certain two larvæ noted led to the conclusion that mutual and simultaneous attacks may occur, and perhaps with fatal results to both individuals. When many larvæ of the same age occur in a single host, as for instance in some beetles exposed to the adult parasite for a day or two in cages, it is probable that several larvæ are attacking others at the same time. For a time, several survive, but eventually even these successful individuals are probably killed in turn by their more aggressive or more favorably situated fellows, and at last only one remains.

Two living first instar larvæ in more advanced states of growth were found on only two occasions. Here, one occupied the abdominal cavity while the other occurred in the thorax, their remote situations being their mutual safeguard. If two larvæ in this state should moult at the same time no further cannibalism could presumably take place on account of the condition of the mandibles, but death of both would probably result from ultimate overcrowding and starvation, or the premature death of the host. When, as in the two instances above, one larva moults one or two days before the other, the helpless second instar individual might possibly be destroyed by its better equipped first instar cohabitant. Sometimes eggs are injected into ladybeetles that already contain a large parasite. In these cases it was found that the newcomer larva failed to develop beyond the first instar.

## FOOD OF THE LARVA.

Thus, in instances of superparasitism, the first food of the incipient instar larva is the body liquids of its fellows. However, in the majority of cases only one larva occurs per host. In most instances then their food is quite obviously derived from the immediate situation occupied by them. Inasmuch as the larvæ lie in the upper spaces of the host's body lumen which are the seat of adipose tissue and the blood, the chief food of the larvæ in all instars is derived from the fat body and the circulatory system. Unparasitized beetles generally contain an abundant store of fat in the dorsum of the abdomen and, in parasitized individuals, the smaller larvæ frequently lie within its mass. It seems

conclusive that the falciform mandibles of the first instar serve only to puncture the host tissue and to secure the larva to it, and not to tear off and transfer particles of solids to the mouth. It would seem then that the victim is pressed close to the mouth opening so the body juices can be imbibed directly. That chiefly liquid rather than solid substance is taken as food is also demonstrated by the absence of liquids in the host's body cavity, while the musculature, reproductive organs, nervous system and alimentary tract remain intact although relatively dry and collapsed. In all instars after the first, the larva lacks the grasping mandibles, and having no functional mouthparts, is under necessity of sucking up primarily liquid substances.

#### EMERGENCE OF THE LARVA.

The entire process of emergence of a mature larva from its host and the reactions of the beetle were observed in a single instance. Thirty-five minutes before it came forth, its host was capable of running about but did so only when prodded. Otherwise it remained stationary, the body and appendages quivering, and exhibiting nervous convulsions at intervals. At this time the abdomen had become much distended both sidewise and longitudinally, so that several of the caudal segments extended beyond the tips of the elytra. The degree of distention is naturally greatest in the smaller species of lady-beetles. This expanded state of the body, however, is not peculiar only to parasitized beetles. When plenty of food is available the alimentary tract is sometimes so engorged that the abdomen is enlarged, and females in an advanced state of gravidity also bear a general resemblance to infested beetles. However, this specimen of parasitized beetle, in addition to having the body greatly distended, was humped up at the juncture of the pronotum and the elytra.

The point of emergence of the parasite was for years a matter of conjecture. Riley (4) in 1888, said it "seemed probable that the ventral portion of the thoracico-abdominal suture was used for this purpose." He dissected a beetle and found "an apparently fullgrown" larva with "its head directed towards the suture between the abdomen and the metathorax, thus strengthening the probability that this is the point of exit." Webster, collaborating in this study, concurred with him in this opinion, but Patton believed the "larva had apparently emerged from a perforation in the last segment of the abdomen." Folsom (10), in 1909 acknowledged that "some mystery exists as to where the larva makes its exit, for the shell of the beetle appears to be unbroken." It remained for Cushman (12) to settle this point. He discovered a *Ceratomegilla* "from which the parasite larva was just emerging. It was protruding from beneath the elytra of the host and had forced the tip of the abdomen downward. The exact point from which the parasite was coming—I found to be the suture between the fifth and sixth abdominal segments slightly to the right of the median dorsal line."

In the present study, beetles from which the parasites had gone were examined and the exit was always found to be at the place de-

scribed by Cushman, although varying slightly to the right or left of the median line. The distended state of the abdomen previous to the emergence of the larva brings the juncture of the fifth and sixth segments near to the apex of the wing covers, hence the exit is accomplished without much hindrance except from the body wall itself. This thin flexible dorsal wall is the least resistant part of the beetle's anatomy, and when stretched to its limit the still thinner coriæ are forced to unfold. This condition, together with the abnormal humped posture of the body, makes a most favorable condition for the exit of the parasite. During emergence, the body wall is also rent slightly lengthwise, involving only the two segments immediately concerned, thus affecting four small right-angled flaps which are folded back during the pushing out of the larva.

The larva first slowly extruded the first head segment and after a few minutes the second. This condition obtained for fifteen minutes, and in the following five minutes the greater part of the body emerged rapidly. However, the parasite did not become separated entirely from the host, the caudal three or four abdominal segments serving to anchor the footless grub during its initial period of helplessness in the new environment. This position was maintained during the next thirty-five minutes, but the parasite gradually pulled out further during this period. No sooner had the larva emerged, as far as stated, than it began spinning its cocoon, relinquishing its hold on the host only when the network of silk was so far constructed as to insure itself against falling off the host's support.

#### COCOON FORMATION.

When spinning began the anchored larva was headed caudad from the beetle, but soon bent its anterior third dorso-cephalad, excreting two parallel strands drawn out in the direction of the middle of its body. This act was repeated several times, forming a loose maze of threads entirely unattached to the larva. In a few moments the head was turned ventro-cephalad under the abdomen of the host, drawing out strands of silk by the characteristic vibrations of the anterior part of the body. Now it laid down a loose springy jumbled mass of continuous silk threads on the host's support and about its hind legs. Gradually the larva extended its telescopic body, meanwhile building a similar jumble of silk all over the space under the beetle and between its legs, until it reached the venter of the beetle's head. During this process the larva enmeshed first the hind legs, then the middle and front legs in succession in the same manner. This act of enmeshing the legs must be regarded as entirely incidental to the formation of the cocoon and determined by the nature of the environment, and not for securing the host against escape as is sometimes implied in the literature. The above procedure required thirty-five minutes. At this time the head of the parasite had reached that of the host, and the anchoring segments were completely withdrawn from their attachment. The final medium that connected the parasite to the host was a few threads of viscous material, probably a substance from the host and toughened from exposure to the air.

The parasite has now completed its preliminary covering and is safely hemmed in against the possibility of dropping from its support. At this stage its head is approximately under the head of the host. In order to continue cocoon building henceforth, it is necessary that all the space under the beetle be within reach of the parasite's head. Consequently the parasite shifts its body in two ways, (1) longitudinally, and (2) laterally. First, the whole body is turned end for end at intervals. In this act the anterior part is turned back upon the rest of the body, the hind portion first remaining stationary. But when the front portion has overlapped the posterior, the latter is pulled in the opposite direction and assumes the place formerly occupied by the head. Just before this shift the larva may be lying on its back, venter, or one of the sides, hence, the direction in which the head is turned depends on the previous position of the body. The period of time consumed between these shifts varies greatly, as was determined by watching several larvæ perform in various stages of cocoon formation. Just after the larva releases its hold on the host, they occurred at intervals of about five minutes. After having spun approximately four hours, one individual was observed continuously for nine hours and ten minutes. During this period the larva turned end for end thirty-two times. The duration of the stay between turns varied gradually from a minimum of six minutes at first to a maximum interval of twenty minutes one hour and forty minutes later. Thereafter the extent of the intervals vacillated between eighteen and nineteen minutes for two and a half hours longer. During the final seven hours the periods were on the average about seventeen minutes, with the minimum interval occurring near the end of the whole period. The cocoon was not yet finished when observations ceased.

In the last two hours of another instance, the larva turned end for end five times. The intervals in minutes were from first to last, 18, 22, 22, 31, and 17 respectively. From these and similar observations, it is estimated that any given larva makes about 110 longitudinal changes. Early in the process, the act of shifting requires five to ten seconds, but in the last hour over a half minute was needed, presumably due to the proximity of the larva to the pupa condition.

The second kind of change in position is a lateral shift. One end of the body is braced against the inner wall of the cocoon, furnishing leverage for accomplishing the act. The lateral turns take place during the intervals between the longitudinal shifts. After each lengthwise turn, the act of spinning is resumed in whatever attitude the larva happens to be. After applying the silk to the space within reach in the original position, it turns sidewise to reach the other areas of the inner wall. In one instance observed in detail two and a half complete lateral rotations were made between two successive longitudinal shifts. A complete lateral rotation was found to consist of six or seven separate sidewise shifts, in which the larva lies successively upon its back, shoulders, side and venter, and intermediate aspects of the body. The direction in which the shifts are begun is perhaps determined by the original position of the larva just after its longitudinal

change. Some larvæ shifted at times from right to left, and at other times from left to right, but each appears to continue throughout a given interval in the direction in which the lateral shift began.

#### THE WALLS OF THE COCOON.

As a result of the two types of shifts, a cocoon is made that has all parts uniform in thickness and structure. When the process of emergence of the larva from the host was depicted, it was stated that the parasite spins a loose jumble of threadwork under the host in the first thirty-five minutes of its external existence. When the connection with the host is severed, the larva continues to form a loose meshwork within the original covering, but now the longitudinal and lateral shifts are involved. The meshes appear gradually to decrease in size, and eventually form a continuous layer, which, when the cocoon is complete, shows its shiny gold brown color through the loose silk strands of the outer layer. At this time the larva seems to cease to draw the threads from its silk pores. Instead of placing them loosely as before, they are now applied directly to the inner wall before they harden from exposure, the hardening taking place on the wall itself. The anterior part of the body still vibrates hither and thither as before, but the direct contact of the face with the cocoon wall suggests the term 'painting' rather than 'spinning' for description of this act. The cocoon therefore consists of two layers, (1) the outer, loose, meshwork and loops of silk, which is directly attached to (2) the inner, solid and continuous layer.

The inner layer is itself a composite structure. In each interval between the longitudinal shifts, the larva applies silk with its face, seeming to spread it thinly over all the area in reach in each of its positions. The silk thus applied hardens quickly, and as a result of the two types of shifts, the application made in each successive position of the larva would seem to be discontinuous with the next, resulting in the deposition of numerous very thin sheets. If each lateral rotation involves six separate shifts, and two and a half rotations are made between each two consecutive longitudinal shifts, the estimated one hundred ten longitudinal turns would imply the formation of approximately sixteen hundred fifty such thin sheets of silk by one larva in the process of constructing its cocoon. If so, each sheet or plate was observed to require not less than twenty-five complete vibrations of the body of the larva, which works almost incessantly at its task for a period of twenty-seven and a half hours as noted in two instances. A cross-section of a completed cocoon was examined with four hundred magnifications, but the separate laminae could not be isolated. However, the laminate character of the inner layer was made known by teasing a cocoon apart by the use of dissecting needles. Numerous very thin plates resembling mica-sheets in transparency and texture, and overlapped much as the outer layers of an onion, were found to compose the cocoon beneath the loose mixture of silk on the outside.

Superficially the sides of the finished cocoon appear to be slightly convex, but actually a broad shallow constriction extends clear around

the cocoon at the middle at right angles to the long axis. This condition results from the alternate spinning process. In each longitudinal position the larva in painting the inner face of the cocoon describes an arc of about forty-five degrees, being able therefore to reach the wall space intermediate between the ends of the cocoon as effectually as that nearer the ends. This shape is not very obvious until the fluffy outer layer of silk is removed.

The ends of the finished cocoon are also well differentiated. The caudal end is broadly rounded, whereas the cephalic end is pointed. The pointed tip is hard and thick, somewhat button-like, with a concavity on its inner face. This tip, like other parts of the inner layer of the inner portion of the cocoon, consists of numerous laminæ of silk which can be peeled off. The larva appears to spend more time and effort at that place than at any other of equal size. One is sometimes led to think that the larva is resting with its head inserted into this end, but it is perhaps really making a heavy deposit of silk without the usual body vibrations. This button structure is begun when the loose outer layer is completed. The larva pokes its head repeatedly into the maze of strands, shaping this end dome-like and simultaneously making it rigid by laying down a proportionately greater quantity of silk. The caudal end is similar to the sides of the cocoon in respect to thickness.

#### THE SPINNING CAPACITY OF THE LARVA.

To determine the spinning capacity of the larva, an individual that had finished the outer layer of its cocoon was removed from it. The outer layer is completed in approximately one hour. This larva promptly began the construction of another case, and was allowed to continue until the inner layer was well under way. Being again deprived of its case, it proceeded again to make a third, and was permitted to make it more nearly complete than in the second instance, and was again taken out. The next day the exhausted, emaciated larva was found dead. The total spinning time here was only six hours and forty-two minutes, as compared with twenty-seven hours normally required to finish a cocoon. The death, and no doubt also the cessation of spinning, was premature, the chief contributing factor being the expenditure of much energy resulting from depriving the larva of the usual anchorage derived from its place under the host. Two factors may be involved that determine the duration of the spinning. First, if the silk glands are exhausted of their productive capacity in the normal period of twenty-seven hours, the act of cocoon formation is automatically checked by this exhaustion. It is unlikely that the continuous addition of laminæ of silk on the inside so far reduces the space that it acts as a check on spinning. The lumen of the cocoon is maintained much larger than the diameter of the larva by the frequent doubling of the insect upon itself incident to the longitudinal shifts. Besides, the extrusion of much silk from the body reduces the size of the larva at the same time that the lumen slowly becomes less spacious. However, the relentless and irrevocable processes of histolysis and histogenesis leading to the pupa condition would seem to be the main forces that fix the temporal limits of the spinning period.

## LOCATION OF THE COCOONS.

Most of the cocoons found either out-of-doors or in the cages were formed under the host and fit snugly there in respect to both their length and diameter. The beetle stands astride the cocoon, the right legs and the left legs of the beetle being on opposite sides, and the head and posterior of the host extending somewhat beyond its ends. As seen from a limited number of instances, the cephalic end of the cocoon may be directed either toward the head or the cauda of the host, regardless of whether the host is headed up or down the support it occupies when the parasite emerges. In a few instances the cocoons were constructed very near but not under the host. This seems to result from a change in the position of the beetle while the cocoon is being formed, which in turn disturbs the parasite. For example, one larva observed had made the usual loose outer layer of the cocoon under the host, but due to the movements of the beetle, the final cocoon was established a few millimeters away from the original spot.

In the springtime in the university forest, the cocoons were common on dandelion leaves, stems, bracts, and flowers, and upon the upper surface of the foliage of broad-leaved plantain. Trunks of apple trees and the under side of bark flakes on the trunks of these trees near whose bases the beetles may winter, were common locations of cocoons in late April and during May. In the fall they occurred attached to corn foliage, ears and stalks. Other writers have taken them from under boards, by sweeping grain, from clover, and other plants. In fact there is no type of situation exclusively occupied by them, their exact location being determined by the place the beetle host happens to occupy when it becomes incapacitated for locomotion by the emergence of the parasite. Hence, the situation inhabited by the largest number of ladybeetles, especially of those species apparently preferred by the parasite, yields the largest number of cocoons. Again, these situations are those near which the beetles winter, or which are richest in aphids, pollen, fungi, and other foods of ladybeetles.

## THE PUPA STAGE.

A series of beetles collected in the university forest on May 9, 1925, gave rise to a number of parasites the date of whose emergence from their hosts was determined. The time of appearance of the adults from the cocoons was likewise known. These parasites were in their cocoons in cages indoors from eight to ten days. Oglobin states that the adult comes out in ten or eleven days after the insect is in the cocoon. Some larvæ have required about twenty-seven hours to make a complete cocoon, and some adults are known to have needed over a day to effect their escape from the same, hence the pupa stage involves six to eight days, according to local data.

## ESCAPE FROM THE COCOON.

The mature parasite escapes from the pointed or cephalic end of the case. The chief means of effecting an exit are the mandibles,

elongate rectangular in form, and each bearing a terminal tooth, and another post-terminal on the median margin. Its antennæ lie parallel with each other on the back, the face is inserted into the concavity at this end of the cocoon, and the legs, braced against the inner surfaces, serve to hold the body forward. Assuming this position, the parasite applies its cutting mandibles to the solid inner layer of silk composed of numerous mica-like laminae. By alternately separating the mandibles and bringing them together on the wall of its prison these plates are gradually cut off at one place until the mandibles penetrate to the outside of the cocoon. By repeatedly exerting them and drawing them in knife-like, first the median tooth, then the terminal one is pulled across the obstruction at the edge of the aperture. The neck of the parasite enables it to turn its mandibles to all points in the circular incision it needs to make to escape, except to a point directly over its head. The latter sometimes remains unsevered and becomes a hinge attaching the cap to the rest of the cocoon. However, this end of the case is not uncommonly entirely cut off, which implies that the parasite shifts to its side or back in order to perform this act. This was furthermore observed when a parasite, in the act of cutting out, was subjected to favorable light and magnification, and deliberately turned over sidewise from time to time. It seemed to make little difference whether it worked dorsum up or down or upon its side. In fact, leverage was obtained by pushing against the inner wall with its legs, and with its head against the cap end, so that the body did not seem to rest down fully upon any side, being partially suspended in the lumen of the cocoon.

The process of cutting out is continued almost without cessation for hours, the intervals of rest usually being only a few seconds. The labor is so protracted and energetic that one marvels at the endurance of the insect. While observing one specimen almost continuously for three and a half hours it punctured the wall and enlarged the incision but had not yet done more than one-fifth of the necessary work to effect its exit. It was left at 9:30 P. M., and in a total of fifteen and three-quarters hours had completed only one-half of its task. It may have ceased work in the dark, but the lumen is normally not well lighted. At the end of that period the intervals of rest were of longer duration, seeming to indicate fatigue. At this rate, the act of escape could not be accomplished in less than two days. This cocoon was dry, and as compared with those in nature that are moistened nightly by dew or saturated by an occasional shower, was probably tough and resistant to cutting. However, getting out is no mean task, which with the twenty-seven hours required to construct the cocoon, consumes almost three days of the life of the parasite, a heavy price, not uncommonly paid with complete futility, to the instinct of cocoon building.

#### DESCRIPTION OF THE ADULT.

As a result of Cushman's conclusions on the identity of this parasite it happens that we have three original descriptions of *D. coccinellæ* in American entomological literature. The earliest is by Cresson (5)

and is therefore reproduced in full below. The others are by Riley (16) and Weed and Hart (9), the latter also giving our only description of the male which they claim to have reared from a cocoon under "*Megilla maculata*."

"Female black; head shining, pale yellow-ferruginous; spot enclosing ocelli, and occiput black; palpi fuscous; antennæ long, slender, entirely black; mesothorax finely punctured, somewhat shining; scutellum, metathorax and first abdominal segment densely rugose, opaque; metathorax broad, abruptly truncate behind; tegulæ rufo-piceous; wings faintly dusky, nervures and stigma fuscous, the latter broad; legs dull ferruginous, coxæ black, four posterior trochanters, femora at base, and more or less of their tibiæ and tarsi blackish; abdomen beyond first segment sub-ovate, flattened, smooth and polished; first segment broadly dilated at tip; ovipositor pale, nearly as long as abdomen, sheaths black and thickened at tips. Length, .15 inch. Habitat, Illinois, one specimen."

#### LIFE TIME OF THE ADULT.

All the adults reared during the season of 1925 failed to live longer than four or five days. They were kept in small vials when at rest or in large chimneys when given access to beetles, and fed drops of diluted honey which they ate readily. When caged with ladybeetles, they were intensely active a good part of the time, which was obviously energy-exhausting work and probably contributed materially toward the reduction of their life time. Ratzeburg (4) indicates that one individual lived only about three days. The life of the adult, however, is apparently distinctly longer than five days, for Oglobin reports that his parasites lived about twenty days in captivity, the exact conditions not being described. The writer kept one individual almost altogether in darkness and fed with honey for eighteen days, September 12 to 30, 1925, which shows that the short lifetime of the others above was probably the result of close confinement in daylight. Under these latter conditions, the parasite makes constant and futile efforts to escape, tiring itself greatly in so doing. The low moisture content of the laboratory atmosphere was doubtlessly another factor contributing to their early death.

#### PARTHENOGENESIS.

In general, the articles published by various workers with *Dinocampus coccinellæ* indicate or state that only the female sex was taken. Ratzeburg (4) observed a female attack a *Coccinella 7-punctata*, but concluded that since the parasite "was not impregnated" he "could not expect to get any progeny." Riley (4) states that "The adult insect was bred in some numbers \* \* Only females, however, were reared." In Russia, Oglobin (15) did not find a single male during two years. In 1912 his females laid unfecundated eggs and these yielded only females. Nees (17) reports having obtained one male in 1834. Weed and Hart (9), referring to the statement quoted above from Riley, state that "he had obtained only female specimens, \* \* while both sexes are represented in the Laboratory (Illinois State Laboratory of

Natural History) collection," and descriptions of both sexes, from three females and one male, are given.

In the present studies, the adult parasite was obtained in the spring, summer and fall seasons of 1925 and a few in 1924. Altogether not less than sixty individuals came to the writer's attention and without exception all were females. It is not possible to verify or disprove the accuracy of Nees' determination of the male he reported. In the instance of the single male described by Weed and Hart we are more fortunate. These writers state in their paper that one male specimen occurs in the collection of the Illinois State Laboratory of Natural History. Their paper was published in 1889, and in it refer to one specimen, collected in 1884. The name they applied to the parasite was the synonym *Centistes americana*, the provisional name suggested by Riley (4), and published only once thereafter, by Weed and Hart. In consultation with Doctor T. H. Frison, systematist of the Illinois State Laboratory of Natural History insect collection, a headless specimen was found bearing a label with the name *Centistes americana*, the male sign, and the date 1884, in Hart's handwriting. The specimen agrees with the description which Weed and Hart published. The evidence, therefore, indicates that this is the male which Weed and Hart had. It was sent to Mr. R. A. Cushman, of the U. S. Bureau of Entomology, who found it not to be a male of *Dinocampus coccinellæ* (*Centistes americana*) "but apparently *Euphorus mellipes* Cresson." Riley (16) cast doubt upon the correctness of the determination by Weed and Hart, saying it seemed they may have had another species.

From the above circumstances it rather appears that Weed and Hart were mistaken in their male, even though they state that it was reared along with three females on which their descriptions were based. The writer recognizes that some species of ichneumonoid parasites produce chiefly females, and that males sometimes occur. However, *D. coccinellæ* seems to be one species in which the males do not appear, or if so, very rarely. Beetles in which the unfertilized females oviposited in cages gave rise to other females in four instances. In a few other cases, the hosts were dissected and found to contain a goodly number of embryos in an advanced state of growth and some newly hatched larvæ. It is thereby conclusively shown that coition is not essential to reproduction and that the species reproduces at least for most part parthenogenetically.

Further evidence tending to demonstrate that the species is strictly parthenogenetic is furnished by the kindness of Mr. A. B. Gahan, of the U. S. Bureau of Entomology, who states that of the hundreds of specimens in the collection of the Bureau from many sources all are females.

#### HIBERNATION.

Hundreds of adult *Ceratomegilla fuscilabris* were gathered from their typical winter quarters under foliage beneath shrubs and trees on March 14 and 17, and April 13, 1925. Even on the latter date, the beetles had scarcely moved from their places of shelter, although at that time they seem to have been active for brief periods on the warmer

days preceding. These beetles were preserved in alcohol and later dissected. The rate of parasitism was generally high, which made it possible to establish the fact that on the dates above, all the parasites were in the larval stage in various grades of development within the first instar. No recognizable increase in size was made from March 17 to April 13, hence it is safe to assume that no growth took place previous to March 17 as far back as the cessation of the activities of the beetles in late autumn. The winter is therefore spent in the first larval instar, or possibly as eggs in a few cases, within the host, at Urbana. The exact places of the parasites in the beetle are no different than at other seasons, but the hosts, being conditioned for cold weather, contain relatively larger amounts of fat especially in the dorsal portion of the abdominal cavity. In this wealth of fatty tissue the parasitic larvæ lie embedded and effectively insulated against injurious low temperatures. Their own bodies likewise contain a larger amount of oil and fat than usual, which serves to save them further from the effects of the frigid season.

#### GENERATIONS IN A YEAR.

A few cocoons formed by larvæ that had hibernated in the first instar were found on April 24, 1925, in the woods, and had become common there by May 9. The adult insects emerged from this lot of cases from May 5 to June 9. The second largest number of the season came from cocoons from various sources about Urbana from the 24th to the 28th of June. These later comers probably represent the second generation of adults. Most of these developed in the *Ceratomygilla fuscilabris* beetles that did not harbor hibernating larvæ, but other common species also contributed a good percentage. During the singularly dry months of July and August, 1925, parasites were difficult to get, perhaps on account of the scarcity of beetles incident to meager food supply. From September 4 to 8, six adults were reared from the common spotted ladybeetle at West Lafayette, Ohio, in the latitude of Urbana. Cocoons were not found after that date in Illinois, which may mean that most parasites were in the wintering larva stage. However, a few were dissected out that were in the advanced instars, indicating that some adults develop as late as September 20, and probably infest beetles thereafter, possibly as late as October 1. These eggs would presumably hatch about the first or second week of October, and the larvæ hibernate in that state.

The limits of development as known now are therefore April 24 to approximately September 20. Each generation requires about four weeks in the most favorable weather. Hence, it is possible that four or five generations occur in the five months between these known extreme dates. Oglobin (15) made a similar estimate for St. Petersburg, Russia.

#### SUMMARY OF THE LIFE HISTORY AND HABITS.

Adults of *Dinocampus coccinellæ* have been found attacking lady beetles of our common species from May to September. The ovipositor is thrust through the exoskeleton, usually of the abdomen, of the prospective host, and one or more eggs placed in the body cavity just inside

the body wall. The embryonic stages are known to be passed in six to seven days, at the termination of which there hatches a square-headed and tail-bearing larva. The larval stage probably comprises four instars. The mature state of the larva is reached in fifteen to twenty days after hatching.

When mature, the larva emerges through a rift in the dorsum of the abdomen, and promptly spins a cocoon under the host, which is completed in about twenty-seven hours. Transformation to adult requires approximately six days, and in somewhat more than a day the fully matured imago succeeds in chewing off the cap of the cocoon in order to emerge. Only females of the species were found. The adult parasite lives four days to two weeks. In this time the unfertilized females parasitize an unknown number of various species of common ladybeetles, the ovary contents indicating a potentiality for infesting perhaps several hundred individuals.

The life cycle is passed in approximately four weeks. Because mating is not necessary, and feeding is not absolutely prerequisite to oviposition, there is no delay in reproduction. It is believed, therefore, that from April to October, four and possibly five generations of the parasite develop annually in the latitude of Urbana, Illinois.

#### EFFECT OF PARASITISM ON THE HOST.

Parasitism of ladybeetles by *D. coccinella* gives evidence of itself both before and after the maturity and emergence of the larva. In only one instance out of numerous parasitized beetles examined did infested female ladybirds contain ovaries in a state of development. The parasite concerned was small and would probably soon have robbed its host of that store of excess energy out of which the eggs are formed. When larvæ occur in advanced gravid females they naturally disrupt the ovaries because the dorsal cavity of the abdomen normally occupied by the parasite is then filled with eggs.

At least some cases of superparasitism resulted in the death of the host a few days after the larvæ hatched. In the first place the vital fluids were probably absorbed by the eight to thirty eggs during their incubation, and the vitality of the host was further reduced by the feeding of a number of larvæ, not to mention the result of the irritation caused by them. In another instance, an individual of *Coccinella sanguinea* was found dead and infested with a second instar parasite. The premature death in this case is probably to be attributed to the severe drain of the parasite on a beetle of such small size. Some individuals of this species are known to have reared the larva, while others fail to do so. This instance seems to show conclusively that *Psyllobora* and *Brachyacantha* species and other ladybirds smaller than *C. sanguinea* are incapable of sustaining a parasite larva until it is ready to emerge, if indeed, they are ever parasitized at all.

The consequence of parasitism after the parasite has left its host ranges from death soon after emergence to complete recovery. Timberlake (8) describes instances in which a few individuals of *Hippodamia convergens* and *Olla abdominalis* not only survived their parasites, but recovered, resumed feeding, and were subsequently reparasitized,

one individual giving issue to a second mature larva. "The beetles of *Olla abdominalis* in five out of nine cases were observed fully recovered within a few days after the larva of the parasite had made its escape. Such beetles failed to become palsied and wandered away from the cocoon, even before the construction of the latter was fairly under way. It is only the exceptionally vigorous beetles which recover." On the other extreme, according to the writer's records and others from the literature, the beetles frequently live only two to five days after the emergence of the larva, although Folsom (10) states that "The beetle (*Ceratomegilla fuscilabris*) may remain alive two weeks and doubtless a little longer." Death within a week is probably the fate of most of our averaged sized ladybeetles.

The parasitized beetles seem to move about normally until a few hours before emergence. Definite observations on this matter can scarcely be made due to the difficulty attending the recognition of infested beetles. The abdomen is generally greatly distended, but a closely similar state exists incident to the ingestion of an excess quantity of food or to an advanced condition of gravidity in some females. A few beetles harboring large larvæ were seen crawling about of their own accord, and when stimulated, even one hour before the parasite issued. Oglobin stated also that the presence of the parasite inside *Coccinella 7-punctata* cannot be discovered from its appearance. This writer observed that the insects act and feed like normal ones, gradually losing the power of motion before the exit of the parasites. In the case of *Adonia variegata*, a smaller species, he continues that the presence of the parasite is visible in the last stages of its development, as the abdomen of the host becomes swollen, though without affecting its activity.

From the time the parasite begins to break through the dorsum of the host, the latter does not travel, but its appendages shake nervously. This reaction continues while the larva emerges, and after it has come out is prolonged as long as the beetle lives. The entire body trembles intermittently, and more constantly the antennæ, palpi, and legs twitch quickly. When prodded with a needle, when the support was jolted, or the beetle otherwise stimulated, it quavered still more, drawing its legs toward the body and turning the antennæ under the head. The host is therefore made extremely irritable.

Beetles, even of the same age, when disentangled from the cocoons for observation, exhibited some differences in their ability to travel. This, in general, seemed to be correlated with size and temperament, the larger species seeming to be less seriously affected, while the nervously disposed *C. fuscilabris* sometimes ran away several inches. Complete recovery was not observed, but in a few instances beetles in nature had deserted the cocoons, hence their fate was not known, although their absence indicated a fair degree of vitality subsequent to emergence of the larva. But in the usual instances the host is found in connection with the cocoon because emergence leaves the beetle in a seriously paralysed state. In this condition the legs can only be drawn toward the middle of the body and the extensor muscles are

obviously affected. A slight amount of forward action of the legs is possible, some liberated beetles traveling awkwardly and tilting up on the end of their straightened and stiffened tarsi and legs. Consequently the beetle clutches firmly to large objects that are placed, or normally occur, between its legs. Inasmuch as the parasite constructs its cocoon beneath the host, this clutching ability only serves to make certain the permanent detention of the beetle, because every struggle serves to enslave it the more fatally. Hence, even though the beetles may sometimes have the necessary reserve power to feed and possibly recover, they usually can not become free to do so, and starvation is perhaps one cause of their death.

#### PERCENTAGE OF BEETLES PARASITIZED.

In 1924, only thirty-six miscellaneous ladybeetles were studied. This was done from June 26 to August 24. Eight of these were parasitized. In 1925, sixteen hundred and fifty beetles of eight species of ladybeetles were collected and dissected to determine the rate of infestation. These records are tabulated by species below. In addition to these, several hundred beetles were used in cage work, making the total number examined approximately two thousand. The normal rate of parasitism of the latter is for most part not known because they were exposed to the parasites in cages, which raised the percentage above normal. However, fifty-six parasites were reared chiefly from *Ceratomegilla fuscilabris* and for most part between May 5 and 30. In the cage work it was demonstrated that *Adalia bipunctata* is also subject to oviposition by the parasite, but only the immature larvæ were obtained from this species.

The data applies to Urbana, Illinois, except where stated otherwise. The average percentage given at the foot of each table is based on the total number of beetles found parasitized during the year, and does not apply to the average percentages for each of the several lots of beetles examined.

One hundred ninety-eight of the sixteen hundred sixty-one beetles dissected contained one or more parasites. This gives an average parasitism of all species concerned of 11.92 percent for the year. Four beetles harbored more than one larva each,—two having two each, the third had three, and the fourth four larvæ. The total number of parasites found in the hundred ninety-eight beetles taken from nature directly was therefore two hundred five, or an average parasitism of 1.035 larvæ per infested beetle.

Two facts should be considered here as affecting the percentage. First, the parasite was always found in the larval stage, with exception of one instance in which an egg was discovered. Due to the small size of the eggs, this stage was doubtlessly overlooked in a good number of instances. Usually only the larva was sought in dissecting beetles direct from nature. Hence, the percentage of parasitism was actually higher than the presence of larvæ indicated. The other fact is that the Mexican bean beetle was included in determining the rate of infestation. This species does not occur in Illinois (March, 1926), and has

never been found infested by this parasite, whereas all other lady-beetles tabulated are known hosts in this state. Hence the degree of parasitism is higher than stated above. The annual rate for Urbana in 1925, for all species from which the parasite has been taken, is therefore estimated to be near fifteen percent.

In the majority of infested beetles, the parasite was found to be in the first instar. Inasmuch as only living beetles were collected, the predominance of this instar may perhaps signify that the beetles bear-

TABLE I.  
*Ceratomegilla fuscilabris* (*Megilla maculata*).

When Collected	Sources	Number Dissected	Number Parasitized	Percent Parasitized	Instars of the Parasite
3-14	Wintering.....	100	11	11.0	All first instar.
3-17	Wintering.....	200	37	13.5	All first instar.
4-13	Wintering.....	100	11	11.0	All first instar.
4-19	Dandelions....	51	19	36.0	18 first instar; 1 second instar.
4-24	Active near winter site..	104	26	23.0	1 first instar; 25 larger.
5-13 to 6-30	Various.....	17	8	47.04	3 first instar; rest emerged full-grown in cages.
July 8-4	.....	None in	the usual	places.	
9-4, 9-5	Sewage Disposal Plant.. Corn; West Lafayette, O.	84 138	1 7	1.2 5.06	Almost mature. 1 egg; 2 first instar; 1 second, and 3 larger.
9-5	Corn; West Lafayette, O.	211	2	0.94	1 first instar; 1 almost mature.
9-16	Corn.....	7	0	0.00	.....
9-19	Sewage Disposal Plant..	73	1	1.36	1 first instar.
	Totals.....	1,085	123	Average 11.33	

ing larger larvæ or several smaller ones are more retiring in their activities or also that some of them are prematurely killed as a result of the levy the enemy makes on their energy resources. Furthermore, the majority of beetles found infested contained but one larva. Especially among the smaller species, the presence of two or more parasites even in an early state of larval growth may cause an untimely death. These suggested explanations for the dominance of first instar larvæ found are in some measure supported by observations upon caged specimens. These considerations tend furthermore to indicate that the above estimated rate of parasitism is below that which may actually occur.

## SEASONAL AND LOCAL DISTRIBUTION OF THE BEETLES AND THE PERCENTAGE OF PARASITISM.

Table I shows that the percentage of parasitism of the common spotted ladybeetle is not uniform throughout the year and in specimens obtained from various local and interstate situations. Fifty-one beetles that hibernated along a fence in town were thirty-six percent parasitized as compared with a percentage of about twelve per-

TABLE II.  
*Hippodamia convergens.*

When Collected	Sources	Number Dissected	Number Parasitized	Percent Parasitized	Instars of the Parasite
6-16	Clover.....	15 (not dissected)	2	13.30	Adults reared.
6-18	Clover.....	1	0	00.00	.....
6-23	Vacant lots...	9	2	22.00	First instar.
6-23	Alfalfa field...	10	1	10.00	First instar.
6-30	Various.....	12	3	25.00	First instar.
7-2	Plantain.....	2	0	00.00	.....
7-6	.....	3	1	33.33	4 first instar.
7-23	Clover.....	7	1	14.30	First instar.
8-4	General sweeping....	3	2	66.66	3 first instar in one beetle; one mature.
8-13	Clover and alfalfa.....	4	0	00.00	.....
9-5	Corn; West Lafayette, O.	4	0	00.00	.....
9-16, 9-17	Corn.....	81	4	3.24	3 first instar; one beetle with a first and a fourth instar.
9-28	Clover and alfalfa.....	15	0	00.00	.....
	Totals.....	166	16	Average 9.63	

cent for four hundred beetles from winter quarters in a woods margin. Again, only one of eighty-four beetles from an isolated situation—the Champaign-Urbana sewage disposal plant, was infested on August 4, and the same rate held in seventy-three beetles from the same source on September 19. During July in miscellaneous situations this beetle species was rare. On September 16, it was scarce as compared with other Coccinellidæ, and seven specimens yielded no parasites. Earlier in September, three hundred forty-nine individuals collected at West Lafayette, Ohio, also contained parasites at a low rate, or 2.5 percent. The species of ladybeetle present in largest numbers during June, July and August was *Hippodamia parenthesis*, taken usually on legumes

chiefly red clover and alfalfa. Three lots collected in these months totaled two hundred sixty-two, with an infestation of 10.3 percent.

These records and similar ones for other species, indicate a slump in the population of *Ceratomegilla fuscilabris* during the hot dry season in July, with the result that the rate of parasitism in this species is so reduced that it does not again reach the maximum point until September and October. On the other hand, *H. parenthesis*, aided by *H. convergens* and *Coccinella sanguinea*, carried the parasite over the summer when the preferred host, *C. fuscilabris*, was not very common.

TABLE III.  
*Hippodamia parenthesis.*

When Collected	Sources	Number Dissected	Number Parasitized	Percent Parasitized	Instars of the Parasite
6-16	Clover.....	18 (not dissected)	3	16.60	Reared
6-18	Clover.....	6	3	50.00	First instar.
6-23	Vacant lots...	2	0	00.00	.....
6-23	Alfalfa.....	62	4	6.44	3 first instar; one mature.
6-30	Various.....	16	4	25.00	First instar.
7-6	Buck plantain.	5	0	00.00	.....
7-28	Alfalfa and red clover..	106	12	11.66	First instar.
8-4	General sweeping....	1	0	00.00	.....
8-13	Alfalfa and red clover..	94	11	11.70	First instar.
9-5	Corn; West Lafayette, O.	3	2	66.66	First instar.
9-28	Alfalfa.....	18	0	00.00	.....
	Totals.....	331	39	Average 11.78	

It seems, therefore, that the rate of parasitism of ladybeetles differs during a year due to several factors. First, the life cycles of the Coccinellidæ are not all parallel in time of appearance, thus insuring a continuous supply of prospects for the parasite in all months and seasons of the year. Second, the several species of ladybeetles appear to exhibit a preference for certain types of habitats, resulting in a local distribution that may not always be most favorable to the propagation of the parasite to the same degree in each species. Associated with the seasonal and local distribution of the beetles is the rise and decrease of their numbers. *C. fuscilabris* dominated in the spring and fall, whereas *H. parenthesis* exceeded all species numerically in the summer months. The fact that the latter was present in open fields and the former in woodland, implies a considerable hazard to the parasite in getting from one situation, in which the ladybeetles have become decimated, to another more or less distant and harboring

a relatively larger number of ladybeetles. The weather appears also to have been operative although indirectly in determining the rate of infestation. The very dry summer of 1925 affected the succulency of vegetation, which in turn limited the supply of aphids, particularly *Macrosiphum pisi*. In latter August and in September the growth of plants was much stimulated by rains, the small, soft-bodied bugs feeding on legumes increased greatly in numbers, and the added food supply soon made itself felt in the larger numbers of ladybeetles, with the probable final outcome that the parasite became more plentiful.

TABLE IV.  
*Coccinella sanguinea.*

When Collected	Sources	Number Dissected	Number Parasitized	Percent Parasitized	Instars of the Parasite
6-16	Clover.....	9 (not dissected)	3	33.33	Reared.
6-20	Plantain.....	.....	1	100.00	Taken as cocoon.
6-23	Vacant lots...	1	0	00.00	.....
6-23	Alfalfa.....	5	0	00.00	.....
6-30	Various.....	5	1	20.00	One first and one second instar.
7-2	Plantain.....	7	3	43.00	First instar.
8-4	Sewage disposal Plant..	4	0	00.00	.....
9-5	Corn; West Lafayette, O.	4	1	25.00	Large larva.
9-16	Corn.....	3	0	00.00	.....
9-28	Alfalfa.....	1	0	00.00	.....
	Totals.....	39	9	Average 23.07	

These are presumably the chief agencies that affected the varying rate of parasitism in 1925 at Urbana, Illinois, and perhaps operate in a similar manner in other years and places.

FACTORS AFFECTING HOST SELECTION.

While the percentage of ladybeetles found parasitized at different dates during the seasons is dependent on their relative abundance and locations, these factors do not account for all the disparities in the proportionate numbers infested. These differences seem also to be in part inherent in the structure and behavior of the several species of ladybeetles themselves. In other words such differences are in part attributable to what may be appropriately termed the personality of these beetle species. Although the writer is not ready to single out the specific properties operative in this preferred selection, some that may be significant here are: size, the small *Psyllobora* and *Brachycantha* being unknown as hosts; structure, particularly the extent to

which the body is shielded by the elytra; the degree of conspicuousness of the colors, this determining in part the distance at which the beetle may be sighted; the irritability of the species, which affects its response to the thrusts of the parasite; speed in travel, a rapid runner being more readily discerned by its enemy than a similarly colored species of slower gait; perhaps the intensity of the odors peculiar to the ladybeetles; and its tropisms, notably whether it feeds chiefly in exposed places or under cover.

TABLE V.  
*Other Species.*

Name of Beetle	Date beetles were Collected	Number Dissected	Number Parasitized	Percent Parasitized	Instars of the Parasite Represented
<i>Coccinella</i> <i>9-notata</i> .....	6-16	6	0	00.00	.....
	6-23	2	0	00.00	.....
	7-16	2	0	00.00	.....
<i>Adalia</i> <i>bi-punctata</i> ....	6-16	7	0	00.00	.....
	6-30	2	0	00.00	.....
	7-2	1	0	00.00	.....
	9-5	1	0	00.00	.....
	9-16	1	0	00.00	.....
<i>Hippodamia</i> <i>13-punctata</i> ...	6-30	1	0	00.00	.....
	7-23	2	1	50.00	Four first instar.
	7-28	1	0	00.00	.....
<i>Epilachna</i> <i>corrupta</i> ..... (Taken at West Lafayette, O.)	9-9	14	0	00.00	.....
	Totals..	40	1	Average 4.00	.....

ECONOMIC IMPORTANCE OF THE PARASITE.

As far as known, *D. coccinellæ* does not attack our species of phytophagous ladybeetles, *Epilachna corrupta* and *E. borealis*. Inasmuch as its hosts are most of the common carnivorous species, it is injurious from the human standpoint. Ladybeetles, together with *Chrysopa* and *Aphidius*, are the primary enemies of aphids, and their most timely aid is given in the spring months. At this time the parasite of the ladybeetles seems to prevail in largest numbers and therefore reduces the extent of their usefulness when it is most needed. The scarcity of *C. fuscilabris* during July, 1925, may be in part explained by the reduction of their numbers by two generations of the parasite that developed through May and June. The other species of ladybeetles were in all probability decimated to somewhat the same extent in the same season. Expressed in a positive manner, the efficiency of the ladybeetles, on the basis of the records for 1925, at Urbana, Illinois, would be greater by at least one-eighth than it now is if the untoward influence of the parasite could be removed.

## NATURAL ENEMIES OF THE PARASITE.

When the fullgrown larvæ emerge from their hosts in cages containing a number of ladybeetles, they are sometimes destroyed by the other beetles. Some such larvæ were represented by merely a few tangled strands of silk, while others which had formed a larger part of their cocoons were killed by having some of their bodies torn away. Presumably such fatalities are much less common in nature where the beetles are less apt to occur in numbers within a very limited space. The beetles appear to have an innate hatred for the parasite which is sometimes demonstrated by the coccinellids pursuing the adult parasite in a vicious manner.

On April 28, 1925, several cocoons of *D. coccinellæ* in connection with *C. fuscilabris* were taken from the trunks of apple trees. One of these yielded five minute chalcids on May 12, and from another the same number of this chalcid emerged on May 13. Through the courtesy of the Bureau of Entomology, these insects were determined as *Dibrachys boucheanus* Ratzeburg. In as much as *D. coccinellæ* winters in its host, its parasite passed through all its life stages probably in April and May. An emergence hole was made on the side of each host cocoon. In one instance it was near the head end, in the other midway between the ends. The secondary parasites were permitted to live several days, during which time they took water and honey, but were not observed to copulate. When admitted to the presence of a newly emerged *D. coccinellæ* larva, some of them paused on the larva but did not oviposit. Even after confining them in this way a whole day no progeny resulted. They exhibited a marked tendency to crawl into small holes in the cork stopper of their cage, during the night, and seemed to sleep so soundly that only a succession of sharp jolts in artificial light could bring them out again.

Failure to get *Dibrachys boucheanus* on other occasions during the year rather indicates that it was not a very strong factor in reducing the number of *Dinocampus coccinellæ* in 1925. However, its many other hosts would seem to assure its perpetuation in good numbers at all times of the season and in most situations. Doctor L. O. Howard (18), in giving a general report on the species in 1897, indicated it to be a "widespread and very abundant hyperparasite" in Europe, and was then also known from this country. Up to the present time it has been recorded from Asia, and in North America from such far separated places as Ontario, Canada; Connecticut, West Virginia, Missouri and Oregon, but from many other places also. Its hosts are a long series of primary hymenopterous parasites, notably of the common bagworm (*Thyridopteryx ephemeraeformis*), the tent caterpillar (*Clisiocampa americana*), the tussock moth (*Hemerocampa leucostigma*), the fall webworm (*Hyphantria cunea*), the brown-tailed moth (*Euproctis chrysorrhoea*), the gipsy moth (*Porthetria dispar*), the oriental peach moth (*Lespyrczia molesta*), the codling moth (*Carpocapsa pomonella*), and the alfalfa weevil (*Phylonomus posticus*). It is generally conceded to be a very potent force in checking the beneficial work of

usually Ichneumonoid parasites, but in its attack upon *Dinocampus coccinellæ* it becomes a benefactor. No previous record of *D. boucheanus* as a parasite of *D. coccinellæ* seems to have been made.

♂: *D. boucheanus* has been mentioned in past writings under several synonyms. Those encountered in reviewing the literature in the present connection are *Pteromalus boucheanus* Ratze, (19), *P. gelechiæ* Webster (20), and *Cleonymus clisiocampæ* Fitch (18). Webster (21) reared it from the Angoumois Grain-moth (*Sitotroga cerealella*), and mistakenly regarded it as a new species.

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LIST OF FIGURES OF *D. coccinellæ* IN THE LITERATURE

- Riley, C. V. (4), Fig. 14, *Megilla maculata*, beetle astride the cocoon of its parasite. Fig. 15, *Centistes americana*, imago enlarged, wings spread.
- Cushman, R. A. (6). One figure. Shows the mature parasite larva in the process of issuing from the host (*Ceratomegilla fuscilabris*).
- Oglobin, A. A. (15), Fig. 1, Embryo of *D. terminatus* in its natural position within the egg. Fig. 2, *Adonia variegata*, its abdomen much distended caudad due to parasitism. Fig. 3, first instar larva, dorsal view. Fig. 4, head of the first instar larva, enlarged, ventral view, showing mouthparts in detail. Fig. 5, second instar larva enlarged, lateral view. Fig. 6, advanced instar larva, enlarged, lateral view. Fig. 7, face view of last instar larva, showing mouthparts in detail.
- Tullgren, Albert (12), p. 96, *Coccinella 7-punctata*, caught in the cocoon strands of *Perilitus terminalus*.