THE BIOLOGY OF <u>MICROBRACON CEPHI</u> GAHAN, AN IMPORTANT NATIVE PARASITE OF THE WHEAT STEM SAWFLY, <u>CEPHUS CINCTUS</u> NORT.

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I. INTRODUCTION

During the past twenty-five years the wheat stem sawfly, Cephus cinctus Nort., has become one of the worst pests of wheat in the prairie provinces. Annual losses in the wheat-growing area of Saskatchewan have been estimated at up to seventeen million bushels (Farstad, 1945). This would seem to indicate inadequate natural control. There are, however, several native parasites of this pest, and of these Microbracon cephi Gahan is the most important. In some areas this parasite has been very effective in reducing severe sawfly infestations.

A study of the bionomics of Microbracon cephi has been under way for the past five seasons. Concentrated study was conducted at Rockyford, Alberta, during the seasons 1943-1944 and at Aylesbury, Saskatchewan, in 1946-1947. Previous to 1943 no special project had been undertaken, although a considerable quantity of pertinent data had been accumulated over a period of about fifteen years as a result of research in connection with the cultural control of the wheat stem sawfly.

The taxonomic position of Microbracon cephi Gahan is as follows: Order - Hymenoptera; Super-family - Ichneumonoidea; Family - Braconidae; Sub-family - Vipiinae Gahan; Genus - Microbracon Viereck; Species - cephi Gahan.

<u>Microbracon</u> <u>cephi</u> was described by A. B. Gahan in 1918 (Proc. Ent. Soc. Wash., 20:18), and it is worthwhile here to cite his original description in its entirety:-

"<u>Microbracon</u> <u>cephi</u>, new species

"This species resembles <u>M. lixi</u> Ashmead and <u>M. furtivus</u> Fyles but may be distinguished by the shorter ovipositor. The male is very similar to <u>M. rhyssemati</u> Ashmead but may be separated by the longer antennae and smoother propodeum. The cocoons of <u>rhyssemati</u> are dark brown with thicker walls than in this new species which has pale parchment-like cocoons, squarely truncate at each end and placed singly in the burrows of its host.

"<u>Female</u>.--Length 4.1 mm. Antennae 38-jointed in the type; frons and face very delicately and faintly shagreened, remainder of head and thorax polished; propodeum faintly sculptured at posterior middle on each side of the incomplete median carina; abdominal tergites all granularly opaque; suturiform articulation deep, crenulate, and scarcely at all angled at the middle but curving forward slightly at the margins of segment; ovipositor exserted not over half the length of the abdomen. Color reddish testaceous; antennae, eyes, ocelli, ovipositor sheaths, apex of hind tibiae, their tarsi, and the apical joint of the fore and medium tarsi black or blackish; wings subhyaline, the stigma blackish, venation brownish.

"<u>Male</u>.--Length 3.5 mm. Antennae 40-jointed in the allotype, and distinctly longer than the body; posterior tibiae and their tarsi only slightly infuscated; otherwise like the female.

"*Type locality*.--Bottineau, North Dakota.

"*Type*.--Cat. No. 21772, U. S. National Museum.

"*Host*.--Larvae of *Cephus cinctus* Norton.

"Type and one female paratype reared by Mr. Ainslee from *Cephus cinctus* infesting stems of *Agropyron* and recorded under Webster No. 14788. Allotype and a male paratype bear Webster Number 13734 and were reared by the same collector at Minot, North Dakota from the same host in stems of *Elymus*. Two female paratypes are from the same host in stems of *Bromus* from Rugby, North Dakota, and are recorded under Webster No. 14786. One female paratype was reared by Mr. Norman Criddle at Treesbank, Manitoba, from *Cephus cinctus* in stems of *Elymus canadensis* and is recorded under Webster No. 14788.

"The last named paratype has the head above the mesoscutum for the most part and the propodeum blackish, showing that the species is variable in color."

A. HOST DISTRIBUTION AND LIFE HISTORY

The distribution of *Cephus cinctus* Nort. may be noted on the accompanying map (Fig. II). Adults of the sawfly emerge about the middle of June to lay their eggs inside the stems of wheat. At this time of the year the wheat is in the stage of development commonly known as the "boot", and stems contain an inch or two of hollowness. During July and part of August the larvae which hatch from the eggs feed up and down the stem on the inner layers of plant tissue, completely hollowing out the stem. As the wheat begins to ripen, the larva retires to the base of the stem and girdles it with a V-shaped notch about ground level. This so weakens the stem that it breaks off at that point. The larva in the stub thus formed plugs the open end with frass and spins a transparent hibernaculum, which lines the inside of the stub. The mature larva spends the winter in the stub and pupates in the latter part of May and early June.

B. MATERIALS AND METHODS USED

1. REARING METHODS

a. Laboratory

Laboratory studies of M. cephi consisted in rearing larvae from the overwintering stage to the adult. Observations on sex ratio and on relative lengths of stadia were also made. For the latter study, larvae were dissected from cocoons and reared in groups of twenty-five in the lids of one-ounce salve tins lined with sealing wax in which twenty-five individual depressions were made. A larva was placed in each of these depressions. The larvae were reared at constant temperature and relative humidity by placing the containers in desiccators over standard sulphuric acid solutions and maintaining these in constant temperature cabinets.

Rearing for the sex ratio studies was done for the most part by placing stubble collected from the field in a constant temperature cabinet and allowing emergence to take place.

b. Field

Considerable difficulty was encountered in rearing the egg and larval stage of the parasite on its host. No satisfactory technique was developed. In the case of the more mature larvae it was relatively easy to rear them to pupation by placing them in 3/8-inch shell vials which were kept in the car for daily observation. No difficulty was experienced in emerging second-generation individuals from cocoons placed in these vials.

2. DISSECTION

a. Larvae

Larvae were dissected in the laboratory under a binocular microscope with the usual dissection equipment. In addition, fine needles manufactured from drawn glass tubing were found to be of assistance in detailed work.

Sketches of mouthparts and the tracheal system of larvae were made from individuals placed in 10% KOH for periods of from twelve to forty-eight hours, depending on the size of the larva. The integument was punctured to allow easier penetration by the KOH. Specimens were then thoroughly washed in a fifty-fifty glycerine and water mixture for examination and drawing under the microscope. This heavier medium kept the specimen steadier in the field of the microscope.

b. Adult females

Females were dissected under water in the laboratory by pulling off the ovipositor and terminal segments of the abdomen with forceps. Occasionally the entire reproductive system could be removed, but more often the remaining segments of the abdomen had to be pulled away one by one to expose the ovaries. Egg measurements were made with a vernier ocular micrometer.

A similar procedure was adopted in the field, as a binocular microscope was carried at all times. The term "mature egg" used in the text was an arbitrary term arrived at in the following manner. It was noted year by year that oviposition commenced shortly after the more mature eggs in the ovary took on a faint yellowish tinge. These eggs were termed mature for this reason.

c. Sawfly-infested stems

Detailed examinations of stems were made by splitting them longitudinally with a pen knife. Considerable deftness and speed were acquired as experience was gained. The absence of "frass" indicated no infestation, and a healthy active host larva in late July was evidence of absence of parasitism. In either case the stem could be immediately discarded.

3. SURVEY

Parasite surveys were usually undertaken in conjunction with spring and fall sawfly surveys. Regular stops every eight or ten miles over the area to be covered were the recognized procedure. Sawfly damage and initial infestation were noted in the fall, and it required very little extra work to record the mortality attributable to parasitism. Spring sawfly surveys consisted of flight and emergence observations carried out in much the same manner in June, except that the stops were often

ten to fifteen miles apart. In this case the number of C. cinctus and M. cephi recovered in a standard number of sweeps with an insect net were recorded. These records were taken by many different workers in various parts of the sawfly-infested area.

4. CAGE EXPERIMENTS

In most cases cage experiments were rather unsuccessful, mainly because of lack of the necessary time for observation. However, several small field-cage experiments were set up for the purpose of observing oviposition. Cylindrical cotton cages, 8 inches in diameter, 2 feet high, with glass fronts, were set up over wheat in the field, parasites were introduced, and activity noted.

5. FIELD OBSERVATIONS

a. Sweeps

All sweeps in wheat and grass were made with a net having an opening 12 inches in diameter, and a standard 5-foot sweep was adopted. This has been the standard method of recording C. cinctus populations and was used for M. cephi because of the similarity in flight habits of the two insects. In certain cases stands of grasses were patchy and uneven, and an attempt was made to equalize the linear footage of vegetation covered.

b. Activity

Activity of M. cephi was observed in fields with a large population by lying in the field and recording the movement.

Where the population was small, standard sweeps taken under a variety of field conditions provided a fairly accurate index of activity.

c. Oviposition

Oviposition studies were carried out (i) on individuals in the field, (ii) by enclosing females in field cages, described above, and (iii) by enclosing single females with individual mature sawfly grubs in their hibernacula in 3/4-inch vials. In this latter case, the stem wall of the stub was carefully removed so that the hibernaculum was not disturbed. This "windowed" side of the stub was placed against the inside of the vial so that the interior of the transparent hibernaculum could be examined from without by means of a binocular microscope. The stub was held in place by anchoring the base in soil in the bottom of the vial.

II. LIFE HISTORY OF MICROBRACON CEPHI

Microbracon cephi is an external larval parasite. The larval period is spent on the integument of the host and, when development is complete, the parasite spins a cocoon for itself.

Adults of *M. cephi* begin to emerge about the third week in June, males appearing first and females approximately a week later. There is a preoviposition period of about three weeks before any egg laying is noted in the field. A partial second generation occurs as well as the main flight, or first generation. In 1943 at Rockyford, Alberta, males of the second generation appeared about August 10, and females about August 19. Females were still active at Rockyford on September 28. At Aylesbury, Saskatchewan, in 1946, males appeared on August 6 and females on August 15. Females could not be recovered at Aylesbury after September 14. The length of the preoviposition period in the second generation is not definitely known.

A. EGG

The egg is very pale yellow, elongate in shape, being enlarged at the anterior end. The average length is 0.86 mm. The eggs are laid on or near the host, the ovipositor being thrust through the wall of the stem containing the host larva. Only one egg is laid on each host, and only one individual develops from each egg. The incubation period varies from one to two days. The developing embryo is clearly visible through the chorion.

B. LARVA

The newly hatched larva is about one millimetre in length (Fig. I). The general shape in all stages is vermiform, and there appear to be five instars. In the first three instars the larva has a definite, measurable head-capsule, while in the last two the head becomes merely a button-like disc. The newly hatched larva is very delicate and quite translucent, retaining the general form of the egg. In later instars the color changes to a dull brownish shade. The head of the first-instar larva is very prominent, being proportionately larger in relation to the body than in any of the succeeding instars. In the later instars, white irregular bodies close to the skin are very conspicuous and resemble the urate granules described by Cherian and Narayanaswami (1944).

There are thirteen body segments. The first-instar larva has a band of setae encircling each segment except the last two. It also shows two transverse ventral folds per segment on all but the first, twelfth, and thirteenth segments. It is quite possible that these, along with the bands of setae, have some function in locomotion, since upon hatching from the egg locomotion is sometimes required in locating its host. No other appendages, except a pair of non-segmented antennae, are conspicuous at any larval stage. These antennae are proportionately longer in the first three instars than in the last two, when they appear much reduced in size. The mouthparts are strongly sclerotized; the mandibles are well developed, being used for attachment to the host larva. The structure of the tentorium and facial rods in the first three instars varies considerably from that of the last two. The main differences are shown in Figure I. The tracheal system is present and undoubtedly functions from the first instar on. The ramifications of the tracheae have not been found in the first instar, but spiracles are absent on the second, third, twelfth, and thirteenth segments.

The newly hatched larva, upon location of its host, attaches itself by means of its mandibles and immediately begins to feed. The process of feeding is accompanied by a writhing motion of the body. Moulting has not been observed. Judging by the appearance of urate granules (Cherian and Narayanaswami, 1944) beneath the skin in the later instars, excretion is not a periodic process but is performed in one act after larval development has been completed. This probably occurs inside the cocoon. When feeding has been completed, little is left of the host in most cases but the integument. The fully grown larva spins a cocoon inside the stem, a process which takes a day or two to complete. The cocoon is a cylindrical structure, held firmly in place in the stem by two disc-like plates at either end (Fig. I). These plates are spun first in the construction of the cocoon and determine its length. Cocoons vary in color from pure white to a light brown. Early first-generation cocoons are often very flimsy in structure and are not always cylindrical in shape. They often amount to a mere covering securing the larva to one side of the stem wall. Adults emerging from these cocoons are small and atypical. It is suggested that the eggs may have been laid on small hosts and that the larvae hatching therefrom had insufficient food to complete their development in the normal manner, the resulting adults being abnormal in size and coloration. The length of the larval stage from hatching to spin-up is about ten days.

Larvae removed from cocoons are somewhat smaller than last-instar larvae prior to spin-up. This reduction in size may be attributed to two things: the utilization of stored material in the construction of the cocoon, and the excretion of the larval meconium. The larva at this stage becomes somewhat flattened dorso-ventrally and develops prominent hypopleural swellings. It becomes a pale yellow in color and the urate granules become less conspicuous.

C. PREPUPA

The prepupal stage is readily recognizable by the constriction in the body behind the third thoracic segment. Immediately prior to this change the larva becomes more active in the cocoon. Its body again becomes rounded out and begins to take on the appearance of thorax and abdomen. The developing appendages are clearly visible through the cuticle, and toward the end of the stage eye coloration is evident before the final ecdysis. The length of this stage in the laboratory at 25° C. and 70% R. H. was about two days.

D. PUPA

The newly formed pupa is delicate, white in color, with eyes generally turning pink. Coloring occurs gradually, starting with the eyes, progressing through thorax, legs, antennae and abdomen until adult coloration is attained. Pupation takes place within the cocoon, but individuals will pupate normally if removed from the cocoon. The pupa is free but is incapable of any movement. The duration of this stage in the laboratory at 25° C. and 70% R. H. was about six days.

E. ADULT

The description of this stage by Gahan (1918), quoted on page 2, needs no amplification.

1. EMERGENCE

Transformation from pupa to adult requires but a few hours, and individuals rest as adults in the cocoon until the cuticle has hardened. Escape from the cocoon and wheat stem has never been completely observed. The most common method is by chewing a neat circular hole through the walls of cocoon and stem, such that escape is directly from the cocoon to the exterior. Less commonly, however, the adult may escape from the end of the cocoon into the lumen of the stem. In such cases escape from the stem is made at another point, also by chewing a circular hole in the stem wall. Occasionally, small individuals escaping by this latter method become trapped in the stem and die.

The sex ratio of first-generation adults as determined from emergence in life history studies in the laboratory was taken from 110 individuals. Of these, 47 were male and 63 female, or a ratio of 1:1.34. Of 31 second-generation adults, 21 were male and 10 female, or a ratio of 1:0.48.

2. FEEDING

Adults have been observed in the field feeding on the nectar of small flowers growing on the headlands and roadsides. It seems most likely that they also feed on external moisture present on leaves, as they appear to be attracted to moisture. Adults kept dry in a flask for a number of days quickly approached moistened cotton and appeared to imbibe the water. They also fed upon sugar solution provided in the same manner.

3. HABITS OF LOCOMOTION

Adult M. cephi traverse stems and leaves by walking, but this activity is confined to this range. In searching for a host larva, a female may traverse the length of a stem many times. Flight of the adult is quite strong, although within a restricted area. The flight resembes that of the wheat stem sawfly in that it flits from stem to stem, by which means progress is made through the field. It is capable of sustained flight for considerable periods and, on a very calm day, may be observed flying above the crop, but with no specific directional tendency. Wind velocity has a decided effect on flight. Light breezes have little effect but to bring the adults below the top of the crop. As the wind velocity increases, the degree of activity decreases. In strong winds it is almost impossible to recover adults by sweeping because they seek shelter near the ground, clinging to the undersides of leaves.

4. RESPONSE TO LIGHT AND TEMPERATURE

Adult M. cephi are positively phototactic. Liberated in a room, individuals will fly to the window. Enclosed in a tube, they will congregate at the end of the tube nearest the light source and will move to the opposite end if the tube is reversed. In the field, only small recoveries can be made on cloudy days or toward dusk of a normal day, whether warm or cool.

During cool weather activity is greatly reduced; adults become sluggish and cannot be recovered by sweeping. Hot, dry weather, common on the prairies, also reduces activity, and it is suspected that if such conditions continue for many days, considerable mortality of adults results. Activity, especially oviposition, seems to be more pronounced in bright sunshine following a shower than in a hot, dry atmosphere. In one instance at Rockyford, Alberta, in 1943, within three days after a rain parasitism increased from twenty to fifty per cent. Maximum activity seems to occur within the temperature range of 70° to 80° F.

5. OVIPOSITION

Like many braconids, Microbracon cephi must locate its host, paralyze it, and deposit its egg. The antennae of the female appears to be equipped with sensory organs or mechanisms by which she is able to locate the host inside the stem. When the general position is found the ovipositor is inserted into the stem, and when the host passes by it is stung and paralysis follows. Before withdrawing the ovipositor, the female lays usually one egg near each host. In all studies conducted by the writer, only one case has been observed in which there were two eggs close to a single host.

Because of the cannibalistic habits of the host larva and because of the sluggishness of the parasite larva, the host must be paralyzed in order that the parasite may survive. Paralysis of the host is achieved by means of a sudden plunge of the ovipositor through its cuticle and apparently by the injection of some toxic material. If the tip of the ovipositor fails to obtain firm contact with the cuticle, it will slide off and the host will immediately move away. The parasite will often keep its ovipositor inserted in the same place, awaiting the chance return of the host. She may, however, change her relative position on the stem and make a new insertion. The material injected by the parasite seems to act in the nature of a preservative, for a paralyzed host larva harboring no parasite will remain in a turgid condition for a long time. Desiccation may eventually kill it.

The oviposition process has been only partly observed, since in the case under observation no egg was laid. Observations were made with the binocular microscope in the laboratory. The interior of the stem was examined while movements of the host were watched in relation to the parasite's ovipositor, which was inserted through the wall of the stem.

The egg is not attached to, and not necessarily laid on, the host and may be found anywhere within 5 centimetres of the host larva. If the onset of paralysis of the host is slow, it may have some chance to move a little distance before paralysis is complete. Thus, even if the egg is laid at the same point in the stem where the ovipositor was inserted to paralyze the host, the parasite larva upon hatching will in many instances have to search for its host. Considering the amount of frass present in the stem, it is easily seen why many paralyzed hosts are found without evidence of a parasite egg nearby. However, the great majority of parasite larvae succeed in reaching their hosts.

The mechanism of the adult's antennae in locating the presence of healthy host larvae is not clearly understood. It is possible that the function is olfactory but seems more probably auditory. Hrishna Ayyar (1943), describing oviposition in _Xoridescopus_, an Ichneumonid parasite of the _Amaranthus_ stem weevil in India, states that the female is guided in the location of the host apparently by the vibrations resulting from the movements of the grub within the stem.

Although discussed in more detail elsewhere in the text, it is worthwhile here to mention the relation of the texture of the stem containing the host to oviposition. It was mentioned previously that activity increases following a shower. It has also been definitely observed that the percentage parasitism increases under the same conditions. This may be attributed to the increase in adult activity as well as to the softening of the stem, permitting easier insertion of the ovipositor. However, oviposition has been observed under hot, dry conditions in the fall of the year, when the wheat was almost ripe and the stems were dry and hard.

In view of the fact that the observed oviposition required considerable time and that suitable temperature conditions for oviposition are of limited duration each day, it seems likely that no more than two to four eggs are laid daily by one female. The egg capacity of the female has not been determined, since adults do not develop a full complement of eggs at one time. The maturation is a gradual process, eggs becoming mature in batches, generally of six but sometimes of eight or ten, according to observations on gravid females. The number of mature eggs is generally divided evenly among the ovarioles.

6. LONGEVITY

Females always outlive the males. In the laboratory males kept in the same flask with females died first. Males were all dead from ten to fourteen days after they emerged, females at the end of four weeks. However, conditions were very poor in the laboratory, where the humidity was low, the temperature high, and little effort was made to provide the individuals with food or moisture.

Since the first males emerge in the field during the third week of June and are recoverable up to the end of July, it may be surmised that the normal length of life of the male is approximately three weeks. Emergence of females starts in the last week of June, and they are still present when the second-generation females appear about the middle of August. It is therefore seen that the flight of first-generation females lasts from six to seven weeks and that the average life of the female must be from four to five weeks. The life-span of adults of the second generation appears to be similar to that of the first, with the exception that second-generation females are subject to possible adverse weather conditions occurring in some districts near the end of September. In 1944 at Rockyford, Alberta, females which began to appear the middle of August were still present on September 28. At that time a frost halted their activities and was assumed to have caused their death, since none could be found under ideal conditions prevailing four days later. Figure VI shows a chart of the life history of this parasite.

III. BIONOMICS

A. DISTRIBUTION OF *M. CEPHI*

Prior to 1918, and also in 1920, this insect was recorded by Ainslie as an important parasite of the wheat stem sawfly in native grasses. Criddle (1922) reported considerable parasitism by this insect in grasses in Manitoba. Ainslie (1923) drew attention to parasitism by this species in North Dakota, while Criddle (1924) reported considerable parasitism in Manitoba. This parasite was recorded in the same numbers in the years following, and its existence has been established over a considerable area, as illustrated in the accompanying map (Fig.

II). The distribution of this species follows quite closely that of the wheat stem sawfly, but in the drier areas it may be relatively rare. It is present to a limited extent where the native grasses are the only hosts of C. cinctus.

From observations made during the past five years, populations of Microbracon are definitely influenced by rainfall and evaporation. In southern Alberta, where rainfall is low and evaporation high, the population has remained at a very low level. It has been recovered from only a few points in this area. At the northern limit of this dry area sporadic cases of parasitism occur. A definite increase in the population was noted at Arrowwood, Alberta, in 1944, while it was distinctly reduced again the following year. Generally speaking, in the area north of the Bow River up to and including the park belt, parasitism by M. cephi has been an important factor in reducing sawfly damage, in some cases, to non-economic level (Figs. III, IV). In certain districts parasitism approached 100 per cent. The northern region has a heavier rainfall, and the drying winds are not as prevalent as they are in the south. Similar conditions obtain in Saskatchewan in the northern portion of the sawfly-infested area. From observations on the effects of moisture on parasite activity (presented earlier in this paper), it appears that the amount and distribution of the rainfall is the main factor involved in the build-up and maintenance of parasite populations in a sawfly-infested area (cf. Fig. V). In the northern regions, however, there are still a very few isolated cases of severe sawfly infestation, and unless conditions for parasitism remain at the optimum these localities may well serve as focal points for the reinfestation of the entire area.

Observations at Aylesbury, Saskatchewan, in 1946 will further illustrate the effect of moisture on the parasitism of *C. cinctus* by *M. cephi*. Table 1 shows a comparison of conditions of parasitism and adult distribution in wheat in two localities in the same field. From the data in Table 1 it seems probable that moisture was the determining factor in the relative amount of parasitism which occurred. The wheat adjacent to the slough was much greener throughout the period during which the first three observations were made, while that further removed was ripening much faster. Wheat in both localities was dead ripe on September 10. The adults were attracted to, and oviposited more heavily in, the greener wheat. This might be attributed to several factors. Firstly, it is obvious that the humidity was higher in the green than in the ripe wheat, although no figures for relative humidity were recorded. It appears logical from what has gone before that this higher humidity might attract the adult parasites. Secondly, the softer texture of the stems in the greener wheat may have permitted easier insertion of the female's ovipositor into the stem. Thirdly, the delay in ripening of the greener wheat caused a corresponding delay in the maturation of the host larvae and thus exposed them to parasitism for a longer period than was the case in the riper wheat.

A set of curves (Fig. VII), prepared by P. J. G. Rock (unpublished data), shows the trends of sawfly infestations, percentage cutting, and parasitism of sawfly by _M. cephi_ through fourteen years in a single field. He states that the termination of damage in 1931 was due entirely to drought conditions, which prevented the host plants from reaching the boot stage early enough for sawfly oviposition. The reduction of sawfly damage from 1937-40 was largely the result of parasitism by _M. cephi_.

B. HOST PLANTS AND HOST PLANT RESISTANCE

Different species of grains and grasses vary in their susceptibility to wheat stem sawfly attack. This results from a variety of conditions, the most important of which are solidness of stem, size of stem, and possibly chemical constitution of the stem. Thus, it is believed that oats are immune because the stem tissue lacks some essential metabolite in the nutrition of the insect or contains some harmful substance. Certain varieties of barley appear to be immune because of exceptionally large stems, which discourage oviposition, while some grasses are immune because of extreme slenderness of stem. Certain grasses and wheat varieties are immune because of the solid pithy interior of the stem, which prevents adequate feeding progress of the sawfly larva (Farstad, 1940).

Effective parasitism by _M. cephi_ is dependent to a considerable extent on the availability of hosts. When the stems are girdled by the sawfly larvae in the fall of the year, most of these hibernating larvae become unavailable for parasitism due to the fact that the stubs are beneath the ground level. It has been demonstrated experimentally that when for any reason the stem is girdled above the soil surface, the percentage parasitism is relatively high. Table 2 illustrates this point very clearly. The availability of hosts forms a basis for explaining differences in parasitism in different wheat varieties. In such varieties as Golden Ball, a solid-stemmed wheat, the sawfly larva has considerable difficulty in reaching the base of the stem because of the mass of pith within the stem. With the resulting delay in reaching the base of the stem, the larva is exposed to parasitism for a much longer period. Stems are often girdled above the ground in such wheats. Table 3 illustrates this point.

The relation of the host plant to the effectiveness of *M. cephi* as a parasite of *C. cinctus* is more obscure and is not clear at present, but certain relevant observations are worth noting. The natural host of *C. cinctus* was native grass until wheat came to be grown extensively. So, also, native grass must have been the plant in which *M. cephi* sought out and parasitized its host. It appears that when *C. cinctus* increased in wheat, their parasites were slow in following them, possibly because of the larger stem diameter of wheat, which made oviposition more difficult. Seamans (1929), however, cites an experiment in which he forced the parasites to oviposit in wheat by cutting the grass surrounding it during the peak of adult parasite abundance. Certain observations tend to show the preference of the parasite for hosts in native grasses. In certain areas where the sawfly has never been recorded from wheat, *M. cephi* has been taken quite often from sawfly in *Agropyron smithii*, a common native grass. Table 4 shows further evidence of the preference of *M. cephi* for hosts in the introduced grass, *Bromus inermis*. Records of sweeps made at Huxley, Alberta, showed that the parasites tended to concentrate in the *Bromus*, which was adjacent to the wheat. This seems especially true in the case of the minor parasite, *Pleurotropis* sp., which was recorded in large numbers. The higher percentage parasitism in *Bromus* would indicate, on the whole, the preference of the parasite for hosts in that plant.

Table 5, published by Farstad and Platt (1946), shows the variation in susceptibility of varieties of barley to sawfly attack as well as the varying percentage parasitism in the different varieties. No explanation of this variation can be given at present.

The efficiency of a parasite in eliminating its host depends to a great extent on the time required for oviposition (Flanders, 1947). The factor of oviposition time would appear to be very important in the case of *M. cephi*. It has been noted previously in this paper that a host larva may manage to escape parasitism for a long time, with the result that a female parasite may spend a considerable length of time on a stem, thus reducing her rate of oviposition. It has further been estimated that the average number of eggs laid per female is no more than from two to four per day. It seems therefore hard to visualize this parasite overcoming its host where extremely heavy infestations occur, particularly under the extremes of climate obtaining throughout most of the prairie provinces. This is, in fact, the case. Throughout the largest part of the sawfly-infested area this parasite has never achieved a high degree of control. It has been either absent or sporadic in its outbreaks, or has maintained a more or less even balance with its host, such as has occurred during the past few years at Aylesbury, Saskatchewan. There is, however, a fairly large northern area (Fig. IV) in which the host has been almost entirely eliminated or reduced to non-economic numbers. Some factor must have been present in this area which caused a tremendous increase in parasite population. Such an increase would undoubtedly reduce the importance of the factor of long oviposition time mentioned above.

In the area outlined on the map (Fig. V) there is considerably more rainfall, but this in itself cannot be the entire explanation of such phenomenal reductions in host populations as occurred during 1942 to 1944 at Rockyford, Alberta. It has been found, however, that brome grass, *Bromus inermis*, which supports *C. cinctus* very well, is also a big factor in the build-up of M. cephi. *Bromus* was long advocated as a permanent trap-crop for sawfly control, and much of it was seeded on headlands and in roadsides throughout the sawfly-infested area. It is a late-maturing grass and, as such, contains anywhere up to four or five C. cinctus larvae per stem at the time the flight of first-generation M. cephi females is at its height. It was the general rule at Rockyford in 1940 (Farstad, unpublished) to find that in the majority of cases all of these larvae were parasitized. It appears that the parasite prefers the Bromus in which to search out its host, but it can be easily seen that with such a tremendous increase in population an overflow into the host-infested wheat occurred. Such conditions explain the high populations shown in Figure V. It appears then that it was in such a manner that infestations in the northern area were so phenomenally reduced. Moisture was certainly a contributing factor in many ways, but its most important contribution was in the maintenance of stands of Bromus on the headlands.

C. SYNCHRONIZATION OF LIFE HISTORIES OF PARASITE, INSECT HOST AND PLANT HOST

A variety of interdependent factors is involved in a study of the relation of M. cephi to its host. The rate of spring development of the overwintering host and parasite larvae, the rate of development of the host plant and its effect on the development of the C. cinctus larvae, and the activity of the adult parasites, all depend on weather conditions. An attempt will be made in the following pages to analyze these factors with the help of the figures presented.

The period of spring development from larva to adult is considerably shorter in _M. cephi_ than in its host, _C. cinctus_, as shown in Table 6. Development of _M. cephi_ commences about five days later than in _C. cinctus_ and is completed about two days earlier. The period of development, of course, varies with the season and may be several days earlier or later than that which is usually considered normal. For example, in many parts of Saskatchewan in 1947, development was one or two weeks late because of a cold, wet spring. For a period of about ten days to two weeks following the completion of emergence of _M. cephi_, there is no oviposition by this parasite. Activity is pronounced at times but seems to be confined to feeding and mating. During this time oocytes are developing within the ovaries of the female. Figure VIII shows the progressive egg development at Rockyford in 1943 and at Aylesbury, Saskatchewan, in 1946. Figures were arrived at by dissection of lots of ten females at regular intervals throughout the season and counting the number of eggs which appeared to be mature.

It was shown earlier in this paper that there is a complete first generation as well as a partial second generation of _M. cephi_ each year. Figure IX gives a fairly accurate picture of the flight of _M. cephi_ in relation to that of _C. cinctus_, while Table 7 sets out the dates of appearance of certain relevant stages at Aylesbury in 1946. Figure X shows a similar, though somewhat incomplete, set of curves for M. cephi at Rockyford in 1943. It will be noted that populations at Rockyford were considerably higher. The normal curves of the flight of C. cinctus are shown in Figure IX. The first part of the curves for M. cephi show that the males were more active than the females at that time. During this period mating occurred, which is somewhat difficult to observe in the field, as contacts between males and females are of momentary duration only. On July 18 the male population was on the decline, while the activity of females became gradually more pronounced, and the first observed oviposition took place on July 20. During the following week egg-laying was general, and by August 4 parasitism had reached about 60 per cent.

The flight of first-generation females was beginning to drop off by August 4, and on August 9 sawfly damage began to show up in the field. All those hosts which had not been parasitized by first-generation females had for the most part completed girdling of stems by August 15. On this date second-generation females were just becoming common in the field and had not yet matured their eggs. Therefore, the large majority of healthy hosts (then all at or below ground level) escaped parasitism, and the second-generation females were of little economic importance. It will also be noted from Figure IX that males of the second generation were much less active than the females. This is likely accountable for by the fact that a large number of second-generation males are small, fragile and inactive, as explained previously. Again, it may be simply a function of the sex ratio, which has already been noted.

The percentage emergence in the second generation appears to vary according to the location. In certain districts emergence is as high as 35 per cent, while in others it may be less than 5 per cent. The factors responsible for this variation are not known. It has not been possible in all cases to correlate high emergence with abundance of host larvae. A high percentage of emergence has been noted in seasons when weather has been such that the host larvae have completed their development and retired to the base of the stem before the adult parasites were ready to lay eggs. In some districts the two generations overlap considerably, while in others there is a distinct reduction in numbers of the first generation prior to emergence of the second. There is also a distinct reduction in the numbers of eggs found in females, as shown in Figure VIII. Complete figures for Rockyford are lacking, but the reduction is shown graphically for Aylesbury.

In certain cases the second generation may be extremely useful in reducing the potential sawfly population. It has already been noted that under certain weather conditions or in some wheat varieties, there is a delay in the maturation of the host larvae and a consequent delay in the girdling of stems. Where such conditions exist, the host larvae are exposed to parasitism for a much longer period and may be still exposed to oviposition by second-generation females. Oviposition in cut stubs has never been known to achieve any effective control except under the conditions already noted.

The net parasitism in a season is dependent primarily on weather conditions. In other words, weather is the most important factor governing effective parasitism. In western Canada, July rains are very important in producing a good crop of wheat, and it also appears that July rains are important in the maintenance of adequate parasite populations. In many seasons, however, very little rain falls during the month of July. Such conditions affect parasitism in several ways. First, the wheat crops may be dried up or prematurely ripened, in which case the length of time that the larval stage of *C. cinctus* spends in the above-ground portion of the stem is materially shortened and larvae may be found in the bases of stems well before the end of July. These larvae then are not exposed to parasitism. Second, there is ample reason to suppose that continued hot, dry weather causes considerable mortality among adult parasites. Figure XI shows the drastic reduction in female parasite populations at Aylesbury, Saskatchewan, after July 15 under such conditions. Third, it appears from Figure VIII that fecundity is affected in the drier climates, such as at Aylesbury. It will be noted that fecundity of the first generation remained high at Rockyford long after oviposition had commenced, whereas it dropped rapidly at Aylesbury shortly after oviposition had started. Fourth, it has been stated by Flanders (1947) that the ability of a parasite to use its ovipositor may be adversely affected by low humidity. Evidence that this is the case with

M. cephi is not directly at hand, but the possibility is worth considering.

D. IMPORTANCE OF HYPERPARASITISM

The following species of parasites have been taken by the author from C. cinctus in the past five years: Microbracon cephi Gahan, Eupelmella vesicularis Retz., Eurytoma sp., and Pleurotropis utahensis Crwfd. Another species has been recorded in the literature, Eupelmus allynii French (Criddle, 1922), but it has not been taken by the author.

From M. cephi have been taken Eupelmella vesicularis, Eurytoma sp., Pleurotropis sp. and Merisus febriculosis Gir. Of these, the latter two are of no importance as hyperparasites. However, in 1946 at Holdfast, Saskatchewan, a wheat field was found in which Eupelmella and Eurytoma combined had parasitized 30 per cent of the M. cephi larvae in their hibernacula. It has been established that there are three and possibly four generations of Eupelmella in a season. In the spring the first generation attacks the first generation of hibernating M. cephi larvae. The second generation attacks C. cinctus larvae, the third both C. cinctus and second-generation M. cephi larvae, and the fourth C. cinctus larvae only. Both Eupelmella and Eurytoma are external larval parasites. This hyperparasitism is not general, having shown up so far in only a few districts.

E. DISCUSSION

Microbracon cephi Gahan is the most important of several parasites of Cephus cinctus Nort. It has reduced the sawfly population in many districts to non-economic levels. The present study was undertaken, first, to obtain a more complete knowledge of the life history and habits of *M. cephi* and, second, to determine if possible the factors responsible for the lack of effective parasitization of *C. cinctus* in the drier portions of the hard-spring-wheat belt of the Canadian prairies.

In many years throughout the greater part of the prairies, rapid ripening of the wheat crop is accelerated by dry, hot weather throughout the month of July. This rapid ripening of the crop, although on occasion detrimental to the sawfly, appears to be a serious handicap to the parasite, *M. cephi*, by increasing its difficulty in finding and attacking its normal host.

Under favorable conditions the parasite population appears to build up very rapidly. These conditions are mainly associated with those crop conditions which delay the final movement of the host larva to the base of the wheat plant. In 1942, which was one of the wettest years on record throughout the prairies, *M. cephi* increased in areas where previously it had been very scarce. This study has shown that for perfect synchronization of the parasite with its host, the host larvae must be above ground level during a portion of the time when the partial second generation is in flight. There is also evidence that the first flight period is greatly extended under cool, moist conditions.

The lack of effective control by parasites throughout the drier portions of the prairies is primarily due to the escape of the host brought about by early rapid ripening of the wheat crop. Under such conditions the larvae of C. cinctus retire into the stubs.

The following field observations clarify some of the conditions which influence an effective host-parasite relationship:-

1) In many years general cutting of the wheat stems by the host larvae is under way before the second parasite flight begins.
2) Parasites are unable to attack the host in the stub except when a portion of the stub extends aboveground or when the stem is adjacent to a crack in the soil where the parasite can gain access to the stub.
3) Solid-stemmed wheats are more readily attacked because of the inability of the host larva to tunnel rapidly to the base of the stem. Recently paralyzed C. cinctus larvae have been found in late September with minute parasite larvae clinging to them, indicating second-flight parasitization.
4) Bromus inermis readily harbors parasites because of the nature of the ripening process. Even in dry years the base of the brome stem remains green, thus delaying the retreat of the host larva to a point where it is protected from attack by the parasite.

The future of natural control of sawfly populations by this parasite is difficult to estimate. It is quite possible that a series of years unfavorable to the parasite will allow the pest to build up again in the areas where it has now been reduced. Whether or not a strain of parasites will develop which will be effective under conditions now known to limit their effectiveness would be an interesting problem for future study. If such a strain should develop, it may well build up sufficiently in the dry areas of Alberta and Saskatchewan to eventually reduce the severity of these existing sawfly infestations.

Brome grass, seeded on the headlands and in the roadsides, has for some time been advocated as a permanent trap crop for the control of sawflies (Seamans, 1929). It appears that the presence of this grass has been instrumental in bringing about an increase in parasite numbers in the northern limits of the sawfly infestation. Whether or not this is the final solution, it is difficult to ascertain. It must be realized, however, that *Bromus* does not thrive in the drier areas, and it appears that this problem constitutes a challenge to the plant breeder to develop a late-maturing, drought-resistant variety of grass to be used as a permanent trap. As long as wheat continues to be grown intensively on the prairies, it is the opinion of the writer that *Cephus cinctus* will remain a problem in spite of all other control methods with the possible exception of sawfly-resistant wheats.

IV. SUMMARY

Microbracon cephi Gahan (Hymenoptera: Braconidae) occurs coincident with its host, *Cephus cinctus* Nort., in Canada

but varies greatly in population density from area to area. Limited laboratory and field rearing, dissection of larvae and adult females, and extensive field observations and surveys reveal the occurrence of two generations of adults. An external feeder, it hatches from an egg laid in the plant stem near the previously paralyzed host larva, develops in about ten days, spins a cylindrical cocoon and later emerges through a circular hole cut by the adult in the stem. The winter is passed as a mature larva near the base of the stem. All stages are described.

Adult males have a life span of approximately three weeks, while females live for about four weeks. The maturation of eggs requires a considerable period of time, and the act of oviposition is also slow. The adults, which are positively phototactic, are most active during periods of sunshine following rain and at temperatures of 70° to 80° F.

M. cephi adults appear to be attracted to plants grown where soil moisture is adequate. They are more numerous and more effective in the northern areas where rainfall is heavier and evaporation lower, and scarce or absent in the south where rainfall is lighter, evaporation higher, and plant maturation generally more rapid. Observations at Aylesbury, Saskatchewan, in 1946 and 1947 tend to show that adequate July rains render the stems softer and more suitable for oviposition and also expose host larvae to parasitism for a longer period due to delayed ripening of the stems. Most hibernating host larvae are below ground level and thus immune to parasitism. Hot, dry weather during July may upset the synchronization of life histories of host and parasite by drying out the wheat crop, shortening the larval feeding period of _C. cinctus_, and leaving the second-generation parasites without available hosts. Such weather may also affect fecundity, kill adults, and render stems unfit for oviposition.

Since the advocation of brome grass as a sawfly trap crop it has been found that _M. cephi_ appears to prefer hosts in this plant. The result has been a marked build-up of parasites in areas where _Bromus_ thrives. Unfortunately _Bromus_ is not well adapted to drier areas.

M. cephi seems likely to continue as an effective parasite in moister areas only, unless new strains arise. Even in those areas, unusual weather could temporarily favor the host.

Hyperparasitism does not appear important, although several species are recorded.

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TABLE 1

Comparison of Two Locations in a Wheat Field at Aylesbury, Sask., with Respect to Degree of Parasitism and Number of Adult Parasites

Date	Wheat adjacent to slough (Infestation 90%)			Wheat on higher ground (Infestation 80%)		
	No. of adults in 100 sweeps	Percentage parasitized hosts	Percentage cutting by sawfly	No. of adults in 100 sweeps	Percentage parasitized hosts	Percentage cutting by sawfly
Jul 30	13	-	-	0	-	-
Aug 2	-	42	-	-	10	-
9	-	64	-	-	10	-
Sep 10	-	-	8	-	-	47

TABLE 2

Incidence of Parasitism by *M. cephi* in Long and Short Stubs

Wheat variety	Number of larvae			
	In long stubs		In short stubs	
	Non-parasitized	Parasitized	Non-parasitized	Parasitized
Not known .	1	10	16	0
Cross 7 ...	0	3	7	0
Apex	1	6	27	0

TABLE 3

Comparison of the Incidence of Parasitism by *M. cephi* in Golden Ball (A Solid-stemmed Wheat) and Apex (A Hollow-stemmed Wheat), at Davidson, Sask., in 1943

Wheat variety	Number of infested stems		
	Parasitized	Non-parasitized	Total
Golden Ball .	24	26	50
Apex	13	37	50

TABLE 4

Comparison of the Incidence of Parasitism
by *M. cephi* in *Bromus inermis* and Wheat

Date	Place	Percentage parasitism	
		In *Bromus*	In wheat
Jul 17, 1944	Huxley, Alta.	-	-
Aug 10, 1943	Delia, Alta.	81	2
Aug 10, 1943	Craigmyle, Alta.	96	98
Sep , 1942	Swift Current, Sask.	20	2
Aug 5, 1943	Rockyford, Alta.	80	50

TABLE 5

Percentage Culms of Barley Varieties Infested with *C. cinctus*, and Percentage Larvae Parasitized by *M. cephi* in These Varieties, at Swift Current and Shaunavon, Sask., in 1944

Variety	Percentage infested			Percentage parasitized		
	Swift Current	Shaunavon	Average	Swift Current	Shaunavon	Average
Trebi	58.3	46.6	57.5	0	13	6
Plush	55.0	86.6	70.8	33	13	23
Prospect	76.6	50.0	63.3	14	12	13
Newal	78.0	76.6	77.3	28	10	19
Titan	60.0	60.0	60.0	8	18	13
O. A. C. 21 ..	65.0	60.0	62.5	26	20	23
Regal	56.6	86.6	71.6	17	18	18
Rex	90.0	73.3	81.7	49	35	42
Hannchen	95.0	100.0	97.5	51	52	51

TABLE 6

Comparative Spring Metamorphosis of *C. cinctus* and *M. cephi*, at Aylesbury, Saskatchewan, 1946

Date	*C. cinctus*							*M. cephi*						
	Percentage							Percentage						
	L	PP	P	PC	AM	AF	Em	L	PP	P	PC	AM	AF	Em
May 21	-	-	-	-	-	-	-	100	-	-	-	-	-	-
23	60	40	-	-	-	-	-	100	-	-	-	-	-	-
29	12	52	36	-	-	-	-	74	20	6	-	-	-	-
Jun 4	8	34	58	-	-	-	-	32	38	30	-	-	-	-
6	4	40	50	6	-	-	-	28	40	32	-	-	-	-
8	2	43	55	-	-	-	-	14	42	44	-	-	-	-
11	-	47	51	2	-	-	-	14	20	61	5	-	-	-
13	-	12	84	4	-	-	-	6	8	62	20	2	-	2
15	2	6	70	17	5	-	-	2	6	49	32	11	-	-
18	-	4	60	20	10	-	6	2	10	31	33	17	-	7
20	-	4	48	14	28	-	6	-	-	24	30	24	4	18
22	-	5	29	16	18	-	32	2	2	12	36	4	8	36
25	-	-	16	33	29	-	22	-	-	17	36	9	9	29
27	-	-	11	17	27	14	31	-	-	16	14	10	21	39
30	-	-	-	19	39	11	31	-	-	8	16	-	18	58
Jul 2	-	-	3	5	36	8	48	-	-	8	10	-	8	74
4	-	-	-	-	7	9	84	-	-	-	2	-	-	98
6	-	-	-	-	5	2	93	-	-	-	-	-	-	100
8	-	-	-	-	-	-	100	-	-	-	-	-	-	100

L - larvae. PP - prepupae. P - pupae. PC - colored pupae. AM - adult male. AF - adult female. Em - emerged.

TABLE 7

Dates of Occurrence of Events in Studies of Life History of M. cephi in Relation to Its Host during 1946 Season, at Aylesbury, Saskatchewan (cf. Fig. IV)

July	6	- First observed mature M. cephi found.
	18	- First observed tunnelling of nodes by C. cinctus larvae. Maximum observed number of eggs per female M. cephi.
	20	- First observed oviposition by M. cephi.
	30	- First observed M. cephi cocoon.
August	6	- First observed male of second generation of M. cephi recovered.
	9	- First observed cutting of wheat by C. cinctus larvae. First observed female of second generation of M. cephi recovered.
	15	- Cutting of wheat by C. cinctus general.
	27	- First recovery of parasitized stub.