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GENERAL MEETINGS FOR SCIENTIFIC BUSINESS

OF THE

ZOOLOGICAL SOCIETY OF LONDON

PAPERS.

15. The Life-History and Habits of two Parasites of Blow-flies. By A. M. ALTSON. With an Introduction by Prof. H. MAXWELL LEFROY, F.Z.S.*

[Received March 29, 1920: Read April 13, 1920.]

(Text-figures 1–20.)

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INTRODUCTION.

This paper deals with part of the work initiated after a visit to Australia, where the lack of any means of control of the Sheep Blow-flies is painfully evident. As some of these probably came from England, it seemed desirable to study the natural checks

* Communicated by Prof. LEFROY.

that keep down the pest here: and the accidental discovery at the Society's Gardens of three important checks gave the work a start. In this communication two Hymenopterous parasites are discussed: other parasites are under investigation.

Acknowledgments are due to the Australian Commonwealth Government for a small grant to assist the work.

H. M. Lefroy.

A Short Account of the Start of the Work.

About the last week in June Prof. Maxwell Lefroy gave the writer a tin containing approximately 1500 Dipterous puparia to breed out. These had been forwarded by Miss Cheesman, the Society's Assistant Curator of Insects.

The contents of the tin were divided into five lots, and put into an equal number of jars containing damped soil. The jars were covered with muslin. (At the outset, it should be explained that occasional damping of soil was necessitated by the fact that the soil was kept in sacks in the laboratory, and consequently any moisture originally in it soon evaporated.)

Adult flies began to emerge a week later, and continued to do so for a period of six or seven days. They were identified as *Calliphora erythrocephala* Meig.

The jars containing the empty puparia and a large number of intact puparia were then put aside. They were occasionally examined, and on 14th July the first jar inspected was found to contain an active Hymenopteron, which upon closer observation appeared to be a female Braconid; the examination of the other four jars showed that three of them also contained specimens of the Braconid. As the remaining jar did not contain any Braconid, the contents were emptied and carefully examined; all empty puparia were separated from those which were still intact, and six of the latter were opened, with the result that two were found to contain fully-formed flies which had failed to emerge, another a shapeless, smelling, moist mass—an atrophied fly-nymph—and the other three contained Braconids, one in an early pupal state, the others fully-formed adults apparently ready for emergence, free of the pupal skin, and wings fully expanded *.

With the appearance of this parasite, breeding experiments were commenced. The Braconids were released in a muslin-covered glass cylinder, which was placed in a large tray containing soil. Food was put in.

Blow-fly larvæ and eggs were obtained by exposing meat at the Zoological Gardens and on the balcony of the Imperial College of Science, South Kensington, and a test made to ascertain if the Braconids would parasitize the larvæ. The test was satisfactory, and one female began ovipositing one minute after the admission of the larvæ, and in 25 minutes five females were at work.

* Both insects crawled out of their opened puparium ; one at once passed the meconium and discharge, the other did not : both were males. The former lived a normal period, the latter was dead on the second day.

Numbers of the parasite were emerging from the jars at this time, and a large cage was brought into use to contain them. As it was desirable to obtain as many adults as possible, a search was made at the Society's Gardens at the spot where the original material was found, and a further supply of puparia obtained. Whilst sorting out this material preparatory to putting the intact puparia into jars, a number of Chalcids were observed crawling about on the soil. Most of these were captured. A closer scrutiny of the puparia disclosed minute holes in several and Chalcids emerging from some of them; it was also noticed that a few puparia showed that Braconids had emerged from them. In view of the appearance of this Chalcid, each puparium—they were of a *Calliphora* species and presumably *erythrocephala*, the same species as the flies—was placed in a separate tube. Both parasites continued to emerge from this material daily for a period of twelve days.

As no Chalcids appeared from the original material, which had been in the jars for nearly a month, it was evident that they had carried out their attack after the original material had been removed; and as this consisted entirely of puparia, it seemed reasonable to assume that this Chalcid parasitized the pupal stage. This supposition proved correct, and will be referred to later.

A constant supply of blow-fly material for parasitization was maintained by putting small receptacles containing meat out in the open and placing it under control as soon as eggs had been deposited on it. No opportunity occurred at this time to obtain meat blown by flies of definite species under control; but with this object in view, small quantities of the larvæ from each lot of blown material were segregated and allowed to develop into adults, when their species were determined, and they were then placed under control in separate cages.

In the hope that the Braconid was still about, and in order to obtain large numbers of them, receptacles containing soil and meat were put out in the vicinity of the spot from which the original material was obtained; this, Miss Cheesman kindly undertook to do, and the receptacles were left in the open until the blow-fly larvæ had commenced pupation, when the material was removed to the laboratory to be bred out. It was at once observed that the large parasite was still about. It was seen to come to the receptacles and to attack the larvæ. Whilst this was being done, Prof. Lefroy put receptacles out at Heston to see if the parasites could be obtained in this locality. Only the Braconid parasite appeared from the latter place.

All lots of material obtained from Regent's Park and Heston were bred out to observe if any parasites other than the Braconid and Chalcid made their appearance: none did.

By the end of August large numbers of the parasites were in the cages in the laboratories and extensive breeding operations in progress, and every effort was made to maintain a constant supply of active parasites so that by the end of the year there would exist a large stock of hibernating material.

It was not until October that the writer took specimens of the parasites to Mr. J. Waterston at the Natural History Museum for identification. The Braconid was identified as *Alysia manducator* Panz. and the Chalcid as *Nasonia brevicornis* Ashm. Mr. Waterston kindly brought to the writer's notice a paper by Graham-Smith (1) in which these parasites were referred to. Up to this time no reference to the Braconid was known, and that the Chalcid should prove to be *Nasonia brevicornis* was not anticipated, especially as the illustrations in Australian publications in the writer's possession depicted a female of this species walking with an extruded ovipositor, a position which it only assumes in death.

Breeding Methods.

After the first lots of the parasites had completed their work, the several species of blowflies, which had been obtained from the meat exposed in different localities, were segregated.

The species obtained were :—

Blue Bottle......................	*Calliphora erythrocephala* Meig.
,, ...	,, *vomitoria* Linn.
British Sheep Maggot-fly ...	*Lucilia sericata* Meig.
Green Bottle	,, *cæsar* Linn.
Green Bottle	*Phormia grœnlandica* Ztt.

In addition to these, the Common House-fly, *Musca domestica* Linn., which is constantly bred at the College, was available.

Upon Prof. Lefroy's advice as to the best medium in which to breed the larvæ, ox liver was used, and found very satisfactory. A somewhat important point in this connection was that liver could be procured easily as it did not fall within the scope of the "Meat Rationing Order."

The liver was cut into small pieces, placed in glass receptacles and put into the cages containing the different species of "blow-flies." As soon as it had been blown—that is, eggs deposited on it—the receptacle was withdrawn and emptied into a glass dish, in which additional pieces of liver were put when the eggs hatched. The receptacles were refilled and put back into the cages when more eggs were required; this method was continued as long as larvæ or puparia have been required. The glass dishes with the newly-hatched larvæ were placed in large trays of 18 inches diameter and 4 inches height, and which contained finely sifted sand or soil to a depth of 2 to 3 inches. It was found that the full-grown larvæ invariably crawled out of the glass dishes, and after roaming about on the sand, proceeded to disappear and pupate.

This method of breeding the blow-flies was successful with all species except *Lucilia sericata*; the original lot of these were obtained from the fleece of a "struck" sheep. A piece of sheep's skin was obtained consisting of the tail and the whole of the anal area with a quantity of fæces adhering to it, and was placed on a piece of liver on fine damped soil in a tray; artificial heating was applied, and the species was successfully reared by this means.

Several methods of presenting the larvæ for parasitization were tried, the original object being the attainment of those conditions in which they would be an easy prey for the Braconid's attack. It was found that free larvæ severely damaged the females, so that it became necessary to reproduce conditions as nearly natural as possible.

In the case of the Chalcid, host puparia—in a proportion of 20 per female—were placed in small receptacles in the cages and left there for ten days for parasitization. The puparia were obtained from the trays by sifting; this rough handling did no appreciable damage.

The breeding operations were in progress from July to the end of December; from July to the middle of September all lots of parasitized material were reared to maintain supplies of parent generations for the cages; after this period the parasitized material was exposed on the balcony of the College to hibernate and form the necessary stock for shipment.

Life-History and Habits of *Alysia manducator* Panz., and Hosts.

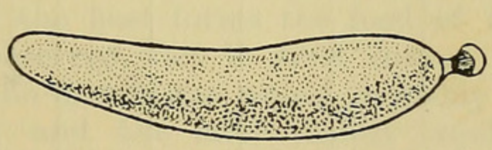
Introductory.—*Alysia manducator* Panz. was selected by Latreille as the type of his genus *Alysia*, and belongs to the group *Exodontes* of the family Braconidæ.

It should be noted that the following account is mainly based upon observations of this insect in captivity; opportunities to observe it under natural conditions were very limited.

The Length of the Life-cycle.—The length of the life-cycle from egg to adult is, under suitable conditions of temperature, from 33 days and upwards, with a mean average of 52 days, but varies considerably for some reason even amongst those of the same parent and under the same conditions. Table I. shows this extraordinary variation, and refers to nine lots of material parasitized in the laboratory. Graham-Smith (**1**) records an instance in which the life-cycle took only 25 days.

The Egg.—The egg (text-fig. 1) is very small, cylindrical, tapering, and broadly rounded at one extremity, broadest at the

Text-figure 1.



Egg of *A. manducator*, from ovary. Size ·675×·150 mm. ×61. Original.

other, with the micropyle narrowly attached and having the appearance of a large protuberance. It is just visible to the

Table I.—Showing variations in length of life-cycle.

Alysia manducator.

Dates of first and last emergence of adults.	Nos. of Jars containing parasitized material and dates when parasitized. No. 1. 17/7/19	No. 2. 18/7/19	No. 3. 18/7/19	No. 4. 19/7/19	No. 5. 21/7/19	No. 6. 21/7/19	No. 7. 31/7/19	No. 8. 31/7/19	No. 9. 6/8/19	Daily Temp. to nearest degree Cent.
Aug. 18	↑									25
19										24
20										22
21										22
22										19
23										22
24										19
25										18
26										18·5
27										17·5
28										16
29										19
30										17·5
31										19
Sept. 1										17
2										18·5
3										19
4										21·25
5			↑							24
6		↑								22·5
7				↑		↑				21
8										22·5
9										24
10										25
11		↓								27
12	↓		↓	↓	↑					27
13							↑			19
14					↓	↓		↑		18
15									↑	17
16										17
17										20
18										21
19										18
20										18
21										18
22										18·5
23										19 *
24										20
25								↓		21
26										20
27										20
28										20
29										19·5
30										19·5
Oct. 1										20
2										20
3										20
4										19·5
5										20
6							↓			20
7										20
8										19
9										20
10										20
11										19·5
12									↓	20

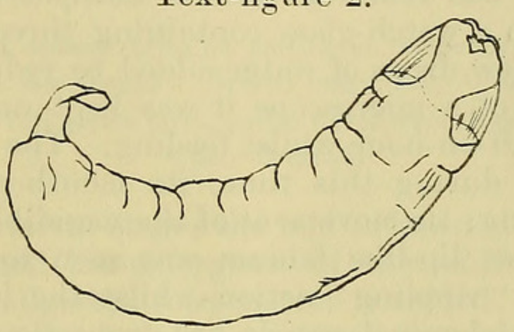
* Artificial heating from 23rd Sept.

Thus, contents of No. 1 Jar took to complete cycle 33–58 days; No. 2, 51–56 days; No. 3, 50–57 days; No. 4, 51–56 days; No. 5, 53–55 days; No. 6, 49–55 days; No. 7, 44–68 days; No. 8, 45–57 days; No. 9, 40–69 days: giving a general average of 46⅝–59 days with a mean average of 52.

naked eye. It is translucent white, with a smooth glossy surface. The time required for the egg to hatch varies, and in an investigation into this point active first instar larvæ were found in the hosts, which had pupated 66 hours after the eggs were deposited, the temperature during this time being 20° C. But, that the egg hatches in from 30 to 50 hours generally is obvious from the condition of the host pupa, which is either in a state of histolysis or an early stage of histogenesis; and also by the occasional distorted appearance of the host puparium. The egg is deposited in any part of the larval host, and this lack of discrimination accounts for the non-appearance of the parasite on occasions. If, for instance, the egg was lodged amongst muscles, it would be crushed by the movements of the host larva; this point is mentioned again under *Oviposition.*

The Larva.—The first instar larva (text-fig. 2) differs in appearance from the later instars, particularly in the shape and appearance of its head, which is a thickly chitinized brownish capsule fitted with a stout pair of mandibles, and has a pair of small protuberances on the dorsal surface, the antennæ. It

Text-figure 2.



First instar larva of *A. manducator.* Camera-lucida drawing, partly reconstructed. ×41. Original.

consists, apparently, of 14 segments including the head; the abdomen terminates in a "tail"-like appendage, the abdominal vesicle. A similar organ in *Microgaster*, and other endo-parasitic Hymenoptera, Gatenby (5) concludes is respiratory in function. That this is the function of this organ in *A. manducator* appears very probable, and it presumably functions by means of osmosis.

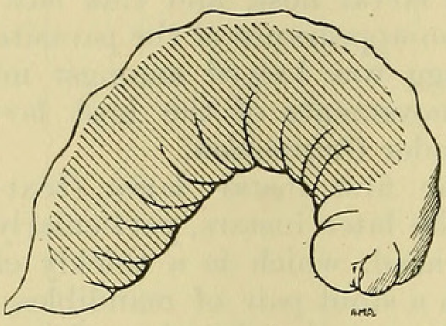
Since the larva sometimes hatches in the body of its larval host before histolysis has begun, its head seems well adapted to enable it to move in the host pupa if it hatches—as it usually does—during the process of histolysis or that of histogenesis.

What part of the host forms the food of the various instars has not been observed, but it must consist of liquid or semi-liquid, and in the first instar would probably be the body-fluid and fat-bodies; and the later instars would feed on those systems which have ceased breaking down or building up after the original attack of the first instar larva. That the larva sometimes hatches before the host pupates is evidenced by the fact that a puparium containing the parasite occasionally bears a distorted appearance—indicating the severance of a muscle—or is shrivelled and excessively wrinkled (text-fig. 8).

The first instar larva, with the exception of its brownish head, is translucent white and glabrous throughout; the integument is very soft and easily damaged.

Text-fig. 3 illustrates a larva of the second instar, in which the capsule head has disappeared and has given place to one the type of which remains constant in the later instars. The particular

Text-figure 3.

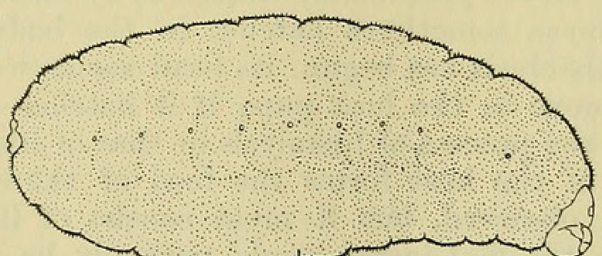


Second instar larva of *A. manducator*. Greatly magnified. Original.

larva illustrated was removed from a *Calliphora* sp. puparium, and was placed in a watch-glass containing three macerated fly-nymphs with a few drops of water added to reduce the density, and with the aid of a microscope it was kept under observation for more than half-an-hour whilst feeding. The larva remained quite motionless during this time, its mouth-parts alone were constantly working; no movement of the mandibles was observed, but the extensive lip-like labium was seen to be continually moving with a "rippling" action whilst the liquid was being absorbed. The abdominal vesicle has proportionately shortened. The mid-intestine now shows up clearly, swollen with food and giving a pale yellow colour to the larva.

The intermediate instars show no superficial difference from the second, beyond the shortening of the "tail"-like abdominal vesicle and the increase in the size of the larva and corresponding swelling of the mid-intestine.

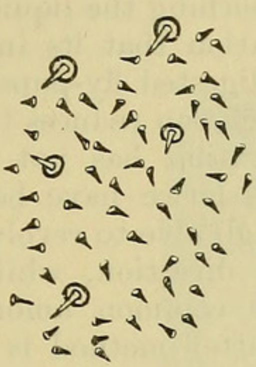
Text-figure 4.



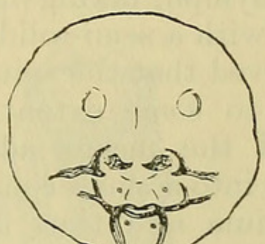
Full-grown larva of *A. manducator*. Greatly magnified. Length 4·25 mm. Original.

The last instar larva (text-fig 4) differs from the preceding instars in that --with the exception of the cephalic and posterior segments—the integument is covered with fine setæ and scattered sensory hairs (text-fig. 5). The mouth-parts of this stage are well defined (text-fig. 6). The posterior appendage has almost disappeared; easily visible just under the integument and scattered about in the abdominal region are large white particles. The spiracles, which are of a very simple structure, number nine pairs, and appear on the second thoracic and first eight abdominal segments. There appears, on either side, a small main trachea with segmental branches.

Text-figure 5.



Text-figure 6.



Text-fig. 5.—Setæ and sensory hairs on portion of integument of full-grown larva of *A. manducator*. Greatly magnified. Original.

Text-fig. 6.—Head of full-grown larva, partly reconstructed, camera-lucida drawing. × 25. Original.

During all the larval stages the mid-intestine is closed caudally, and it is not until the emergence of the adult insect that the residuary and undigested food-matter is voided.

The last instar larva has, on several occasions, been observed feeding upon the liquid remnants of its host, having at some stage pushed the tracheæ of the host to the sides of the puparium; the latter being lined with the fly-nymph's pupal skin. It seems only reasonable to assume that chitin, represented by the integument of the fly pupa, and the main tracheal trunks of the blow-fly larva which remain constant in histolysis do not form part of the larval diet. This postulation, if correct, would exempt the Braconid larva from the necessity of eating its own cast larval skins.

Before the pro-pupal stage, the final instar larva—which by this time completely occupies the puparium of its host—spins a silken cocoon, which either adheres (*a*) to the thick chitinized walls of the puparium, or (*b*) to the stretched integument of the fly pupa, and which generally is caused to adhere to the walls of the puparium. In (*a*) the absence of the fly-pupal skin would be accounted for by the first instar larva having started its attack before the host larva had settled down to pupate or before histogenesis had started, and (*b*) after histogenesis had started. So that the texture of this cocoon or lining to the puparium is not always the same, the external portion of it—that which is in contact with the fly puparium—may be silk or pupal integument, and in those cases examined the tracheal system was visible either outside the silk or between the silk and pupal integument; no cast skins however were detected, the search was not very thorough. Sometimes the cocoon with the fly-pupal integument shows the outline of the fly-nymph's legs etc., indicating late hatching of the egg and after histogenesis had proceeded some time.

The spinning of this cocoon raises an interesting point as to the means whereby the larva, which appears to fill the puparium, is able to move about within it, to accomplish the task of covering every part of the inside, and also of absorbing the liquid remains of the fly-nymph, taking into consideration that its intestine is now filled with a semi-solid mass of undigested fly-pupa. It has been observed that the spinning of the cocoon reduces the size of the larva to some extent, but observation has not definitely established the means adopted; some larvæ have been found contracted into a small compass as though able to revolve within the puparium and thus change their direction, whilst others appear to be working in the manner common amongst silk-spinning Lepidopterous larvæ. The latter method is the most probable, and is supported by the appearance of the larva.

The lining strengthens the puparium considerably, and is a sure indication of the presence of the parasite in its last stages. It is weakest at the anterior end of the host puparium, where the chitinized mouth-parts of the blow-fly larva form an obstruction.

The length of larval life in the different instars appears to vary considerably, but no details were obtained; in one instance, however, a full-grown larva was found in a puparium 18 days after the egg was deposited. This is the shortest period recorded. On the other hand, some intact puparia, which were from a lot parasitized on 6th August, were opened on 26th November, and 13 were found to contain full-grown healthy larvæ, 112 days after the eggs were deposited. The final instar larva is the stage where the great variations in the life-cycle occurs. The time taken to pass from this stage to that of the pupa varies from a few days to many months. This point has been observed by Graham-Smith (1), who also observed in 1915 that from material parasitized in 1914, "the individuals emerging in the spring were much larger than those which emerged in the autumn." This and the observations made during the course of this work have caused the writer to form the opinion that among the factors responsible—beyond the question of food-supply—is that of the size of the host puparium. The integument of the puparium of an undersized blow-fly larva is much thinner than that of the full-grown larva, consequently the parasite within the former is more susceptible to the variations of the temperature, which alone would retard development.

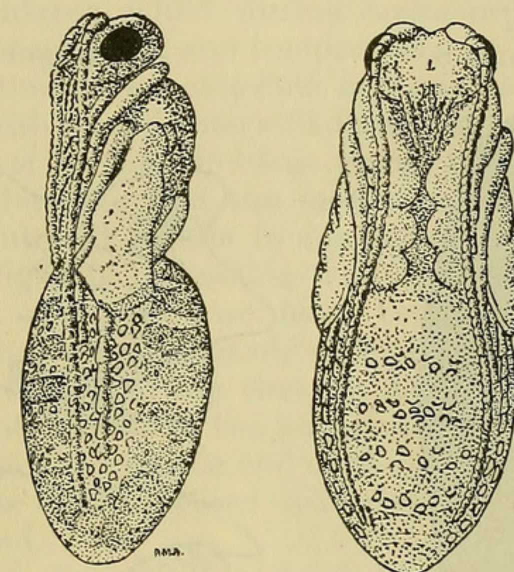
In size the full-grown larvæ vary considerably, but this is naturally dependent upon the size of the host.

The pro-pupal stage, *i. e.* after spinning the cocoon, may last a few days or several months. In two specific instances observed the pro-pupa changed to the pupa, the one 2 days after it was exposed in the puparium, the other 5 days after.

Some hibernating larvæ from the stock have been observed in puparium which they had not yet lined, although four months had elapsed since the date of oviposition.

The Pupa.—The pupa (text-fig. 7) is loose within the cocoon, and is capable of slight movement. The meconium now appears to become slightly compressed, due to the process of metamorphosis.

Text-figure 7.



Lateral and ventral aspect of pupæ of *A. manducator*. Greatly magnified. The figure on left a few days older than that on right. Original.

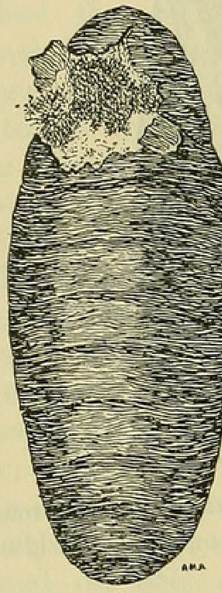
During the whole pupal stage the afore-mentioned large white particles are visible, at first scattered about in the abdomen and later can be seen between the tergites and sternites.

The pupa, which is glabrous throughout, is, at first, creamy white with reddish-brown eyes and ocelli, in a few days the head and thorax turn grey, gradually becoming black; meanwhile, the sternites and tergites—widely separated over the distended abdomen—begin to turn grey, and the eyes and ocelli darken; the legs and antennæ similarly begin to show the coloration of the adult, likewise the mouth-parts. The last larval skin splits across the head dorso-ventrally backwards, and then apparently slips back to the apex of the abdomen, from which it is disengaged by movements of the abdomen and antennæ of the male or the ovipositor of the female. In no instance has the larval exuvium been found attached to the pupa, but lying in a crumpled mass beyond the apex of its abdomen.

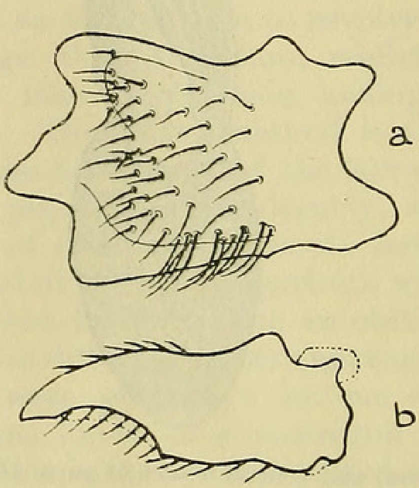
The length of the pupal stage was, in two specific instances, found to be 7 and 10 days respectively with a mean temperature of 21° C., but lengthens considerably in a low temperature; although this will not delay indefinitely the emergence of the adult, which either emerges upon the slightest increase in the temperature, or, in the event of a steady and prolonged decrease, dies within the puparium.

The Adult.—The adult emerges from the host puparium and its cocoon by breaking away that part directly in contact with the head (text-fig. 8). It is furnished with a very powerful pair of mandibles (text-fig. 9, *a*) beautifully adapted for the work in hand. It breaks away the cocoon and puparium by an outward movement, and does not bite the obstruction. Text-fig. 9, *b* illustrates the outline of a section through the centre of a mandible, and shows its scoop-like appearance ventro-dorsally. In

Text-figure 8.



Text-figure 9.



Text-fig. 8.—Shrivelled and wrinkled puparium from which *A. manducator* has emerged. Greatly magnified. Original.

Text-fig. 9.—(a) Left mandible of adult. (b) Section through centre of mandible of adult. × 41. Original.

the outward movement of the mandibles a small fracture appears on the puparium, generally between the second and fourth segment, gradually increasing in size until the perfect insect has created an aperture large enough to enable it to escape. Observation has failed to disclose any use for the mandibles other than breaking out of the host puparium, which operation, when in progress by several insects, has been distinctly audible by putting the ear over the mouth of the jar in which they were confined. It is worthy of note that the mechanism of the mandibles must be diametrically opposed to that of most insects, but upon consideration it seems obvious that by no other means could so large a parasite escape from the puparium, which presents to it a concave surface.

The aperture made in the puparium is usually just large enough to allow the insect to extricate its head and antennæ, thorax and legs, and part of the wings and the base of the abdomen, when by the pressure exerted against the distended abdomen, the voiding of the meconium is assisted, and is either accompanied or followed by a white discharge—the white particles previously referred to,—which instantly dries and has a cement-like appearance. This substance, upon analysis, has been found to contain sodium hydroxide, but whether some of this is used to soften the silk has not been established. The compressed meconium, which is a deep black-brown rod, is completely enclosed in a sac of integument, which resists boiling in caustic potash, giving the impression that it is chitinized and probably the larval mesenteron, which during metamorphosis has become closed at the anterior end and compressed.

In some instances the exit-hole is made too large, and the adult appears with its abdomen still distended ; then by constantly passing the tarsi of the hind-legs along it, it exerts sufficient pressure to enable it to void the meconium : this method is not always successful, and results in one or two days in the death of the insect. Flight is impossible with the meconium unvoided, although vain efforts to rise have been observed. In some instances the transverse cut made with the mandibles is extended so far around the puparium that, on emerging, the insect completely breaks off the top of the puparium. Emergence generally takes place from the cephalic end of the puparium, but in several instances it has been observed that this was accomplished from the posterior end.

The wings are always fully extended before the adult attempts to break out of the puparium. Only in a very few cases has it been observed that the wings have become damaged and torn by the jagged edges of the emergence hole; this condition is generally accompanied by injuries to the soft integument between the abdominal plates, resulting in the death of the insect in one to two days.

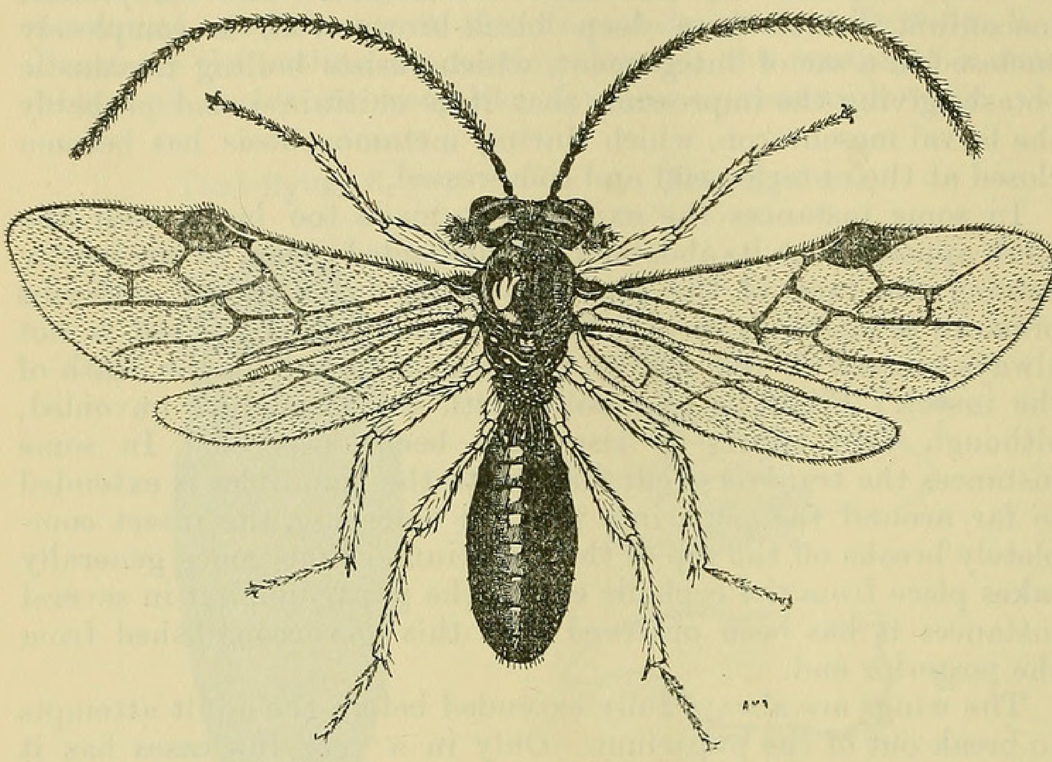
Examination of intact puparia some time after the emergence of the parasites has shown that for some reason unascertained—not due to temperature—a small number never succeed in escaping, whilst a few have been found with the cocoon-lining too thick to extricate themselves.

Nothing of the pupal exuvium of those insects, which void the meconium whilst escaping, can as a rule be seen ; it is generally buried under it, whereas the others are usually found with it attached to the apex of the distended abdomen. Males emerge before the females. The greatest emergence of males is from 3 to 4 days earlier than the females.

The Sexes.—*Size* :—The size of the adults varies considerably, but is, of course, relative to the size of the host. The measurement of several discloses a range of from $2\frac{1}{2}$ mm. to $6\frac{1}{2}$ mm. in length.

General appearance.—The males (text-fig. 10) are easily distinguished from the females by their long antennæ, which are approximately equal to the over-all length of the insect from the frons to the apex of the wings when in repose, and which extend beyond the apex of the abdomen. The ovipositor is barely visible when the insect is looked at from above, but can be seen when in a lateral aspect. Both sexes are shining black, with rufous legs.

Text-figure 10.



Male *A. manducator*. Greatly magnified. Original.

Courting and Mating.—This takes place very shortly after emergence, but never occurs unless the meconium has been voided some time. When seeking a mate (in the cage) the male moves rapidly along, violently swaying the antennæ and vibrating the wings, which are opened as in flight. Mating lasts about 8 minutes, but was not frequently observed. The sex attraction is only evident in the male, and when newly-emerged females were admitted to the cage, males eagerly sought them. The female evinces little interest in the male and can easily repel it. The males make no distinction between virgin and fertilized females.

Flight.—Both sexes are capable of sustained flight. This has been observed in the cage, and on fine days it appeared as if all were "on the wing." Any which escaped from the cages or when handling were generally instantly out of reach and through the open skylights. Those observed around baited receptacles in the open appeared to come from all directions; this is confirmed by Marshall (quoted under *Oviposition*).

Oviposition.—Females do not begin ovipositing until a day or so after emergence, and irrespective of whether they have mated or not; a few have been observed trying to oviposit before voiding the meconium.

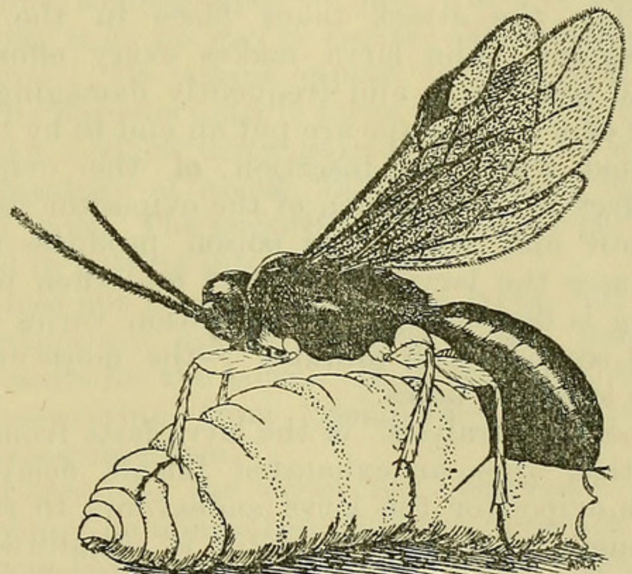
The ovaries are large and well filled with eggs. A dissection of the ovaries of 12 females gave an average of 366 eggs per female. The greatest number counted in a single female was 416. Graham-Smith (4) records a female with ovaries containing "at least 549 eggs." Table II. gives the details of the count of the contents of individual ovaries:—

TABLE II.—Contents of Ovaries of 12 females.

Females.	No. 1.	No. 2.	No. 3.	No. 4.	No. 5.	No. 6.	No. 7.	No. 8.	No. 9.	No. 10.	No. 11.	No. 12.	Total.	Average.
No. of eggs.	412	375	408	368	352	328	363	416	362	325	338	347	4394	366·16

Oviposition takes place in the larva of the blow-fly (text-fig. 11); half- to full-grown larvæ are usually selected. In the cage the

Text-figure 11.



Female *A. manducator* ovipositing in larva of *Phormia grœnlandica*. Greatly magnified. Original.

chemotropic effect of carrion was—when the atmosphere was not charged with the odour—almost instantaneous upon the females; they became violently agitated, swaying their antennæ, and then might proceed to clean themselves, particularly the antennæ and the abdomen ventrally in the region of the ovipositor, and fly to the carrion, or reverse the procedure and fly over and around the receptacle containing it and the larvæ, and then alighting near by, go through the cleaning process. It is, of course, obvious that the sense-organs in the antennæ and the palps of the ovipositor had suddenly received the odour of the carrion and stimulated the insect to oviposit. The males are also attracted by carrion—apparently a sexual tropism to enable them to locate the females. Marshall (3) observes:—"They" (both sexes) "scent the aroma of carrion at a surprising distance, as I once had occasion to observe in watching the remains of a dead rook, upon which they descended in constant succession, apparently from the sky, like vultures. The males generally alighted on blades of grass close to the attractive object, as if to wait for their partners, without interrupting them in their unsavoury occupation."

As soon as the females have alighted, they begin their search for the larvæ, and if the initial effort to insert the ovipositor is successful, they remain depositing eggs until they die, either from exhaustion or because their task is completed. A few have been observed to leave the larvæ and go in search of food and not return the same day.

Only one egg is deposited in each larva by an individual female, at least, under conditions which are approximately natural—*i. e.*, where the larva has means of escape by disappearing into the meat or earth.

The ovipositor is inserted diagonally under the integument of the larva when the attack takes place in the thoracic or abdominal regions. The larva makes every effort to escape, wriggling and squirming, and frequently damaging the female. These frantic efforts to escape are put an end to by the effect of a poison injected with the insertion of the ovipositor. The immediate effect of the insertion of the ovipositor is to cause the larva to vomit and void. The poison produces a paralyzing effect, and causes the larva to contract and then lie motionless whilst the egg is deposited. This operation varies in time, and may take 30 seconds to 5 minutes*—the more exhausted the female is, the longer it takes.

The "temporary paralysis" of the larva lasts from one to two minutes, so that when an exhausted female delays the withdrawal of the ovipositor the larva endeavours to release itself; normally though, when the ovipositor is withdrawn, it is still motionless, and remains so for some seconds. The female then moves off in search of another victim. The first movements of a larva recovering from the "temporary paralysis" are to extend itself to its full length, and then, still slightly under the influence of the poison and the unpleasant ovipositor, it goes through a series of extraordinary convulsive and constrictive movements, which ripple the integument either from the cephalic to the anal end or vice versa, as though it was endowed with intelligence

* One female, which had not oviposited in more than a dozen larvæ, was observed to retain the ovipositor within a larva for 21 minutes, and as the initial dose of poison did not suffice to keep it motionless, further doses were apparently administered each time it moved. Needless to say, this larva died.

and was trying to squeeze and crush the egg*. As soon as this ceases it hastily disappears into the soil or carrion, apparently stimulated by its experience to pupate. The foregoing observation, naturally, only refers to larvæ free of the carrion or on top of it (otherwise they could not have been observed), but those attacked which are partially buried in it do not appear to behave in the same manner; they are surrounded by food and hidden from the light.

The first 20–30 larvæ attacked will be "paralyzed" instantly, and then the poison apparently becomes less rapid in its effect; whilst it has been noticed that a female which rests for some time and feeds, seems to renew the effectiveness of its poison.

An individual female—as has been already noted—does not normally attack the same larva twice. In this connection a series of experiments were carried out under conditions as nearly natural as was possible, and by employing one female at a time it was observed that each larva parasitized, either free of the carrion or partially embedded in it, made every endeavour to get into the soil after it had recovered from its "temporary paralysis" either directly or through the carrion. It appears to be definite that effective oviposition stimulates the larva to pupate. However, in cases in which two or more females inject the same larva—the second one coming upon it just when it begins to move or encountering it on its way to escape,—its death ensues within 24 to 48 hours. Its organs appear to disintegrate, the dead larva gradually darkens until it turns black; dissections disclosed little else than a thick dirty putrid liquid. In warm weather, with a temperature of about 22° C., the dead larva dries up within 6 or 7 days. The majority of these over-parasitized larvæ never succeed in getting into the soil.

A female does not attack a motionless larva, but may prod it with the ovipositor, usually causing some movement with unpleasant results for the larva. It is also in this way that a larva just recovering from "temporary paralysis" becomes a victim to over-parasitism.

On several occasions the writer has observed a moving larva stop suddenly and lie motionless upon the approach of a female, although it may have been touched by no more than one leg of the latter. This behaviour is obviously due to the larva having been previously attacked by a female, but whether it was attributable to chemotropism, which is most probable, has not been established. The predominant odour was that of carrion.

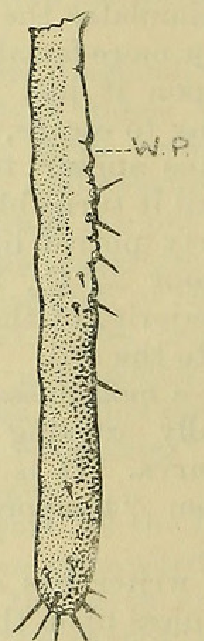
Females which have been ovipositing for some time and are in a filthy condition from the carrion and putrefactive juices, will endeavour to insert their ovipositor into any object which they happen to feel moving, with the result that frequently two or more can be seen together, "jabbing" their ovipositors amongst each other's legs in a vain effort to get it firmly fixed.

* The writer, as previously stated, is of the opinion that many of the eggs are damaged by this movement, particularly if located in or amongst muscles.

The ovipositor, which is extruded, is inserted in different parts of the larva's anatomy. Generally, when the larva is free—*i.e.*, on the surface of the carrion, under it, or on the surface of the soil,—it is inserted about the 1st to 3rd abdominal segments; very small females attack the cephalic end or the anal plate, particularly in the case of full-grown larvæ, probably owing to their inability to get astride the victim, as is usual with the larger females. When the larva is moving in the carrion and the movement is perceptible, the female endeavours to insert the ovipositor through it into any part of the larva, whilst a female coming upon a larva disappearing into the soil or carrion will attack the apex of the abdomen or anal plate, and sometimes is unable to bring the victim to a standstill before the ovipositor has disappeared into the cavity; whilst, on the other hand, a larva emerging from the carrion is attacked in the anterior region.

Whilst the insect is ovipositing, the palpi or "feelers" (text-fig. 12), which in repose form lateral sheaths to the poison and

Text-figure 12.



Palp of ovipositor of *A. manducator*. W.P., wiping-pad. × 61. Original.

piercing-blades, are constantly in use for locating the moving larva. The ovipositor is withdrawn from a victim with a distinct jerk in order to disengage the barbs of the piercing-blades, and by means of the powerful muscles attached to the hinge-like continuation of the blades, it instantly springs back between the palpi, the apex of the former alighting at the base of the latter, so that whilst the sternites are assuming their normal position of repose, the point of the ovipositor is cleaned by the "wiping-pads" (text-fig. 12, W.P.) of the receding palpi. These "wiping-pads" are on the inside of the basal portion of the palpi, extending approximately half of the length, and consist of soft dirty white integument roughly in folds.

Length of Period of Oviposition.—Females, whether freshly emerged or otherwise, and which had or had not mated, once allowed to oviposit, were dead the next day if they had been constantly ovipositing, or when resting and feeding occasionally lasted three to four days; in one instance a female lived five days ovipositing in about 50 larvæ daily.

Progeny of Single Females.—No extensive data were obtained on this point, but in the laboratory the average was 33·74 per female. (See *Percentage of Parasitization.*)

Parthenogenesis.—Unmated females reproduced males; whether the latter were fertile was not investigated.

Proportion of the Sexes.—This appears to be about equal on the whole in individual lots of material parasitized in the laboratory, although one sex may considerably predominate. The figures given under this heading are details of emergence from three lots of material which were parasitized by free Braconids in Regent's Park, and give the following result: 199 ♂ and 294 ♀. No other details of emergence from outside material were compiled. Graham-Smith (4) gives, substantially, the following details for "Spring" and "Autumn" batches which emerged in 1916 from material parasitized in the autumn of 1915. The sum total for both batches are 2891 ♂ and 749 ♀, clearly indicating arrhenotokie, a proportion, which the writer ventures to suggest may, in this instance, be due to the immediate proximity of host-infested carcases when the females of the autumn batch of 1915 emerged.

Length of Life of Adult.—In the laboratory the length of the life of adults was not very long. Observations showed that, in the case of two freshly-emerged males which were not permitted to mate, one lived 25 days, the other 31 days; two unfertilized females not allowed to mate or oviposit lived 33 and 38 days; two females and two males confined together, the former not being allowed to oviposit, the males lived, the one 18 days, the other 23 days; the females, one 25 days, the other 33 days. And as stated oviposition rapidly ends the female's life. In each of the foregoing tests ample supplies of food were given, but the insects were confined in glass jars, which did not give much opportunity for flight and the atmosphere was permeated with the odour of carrion. The length of life in the open or in unpolluted air would doubtless be longer.

The length of life within the main cage appeared to be much shorter during the months of November, December, and January in spite of a mean temperature of 20° C. Activity was always greatest on fine days, and particularly when the sunshine was directly upon the cage.

Food.—When the breeding operations began, the adults were fed on sugar diluted with water in a ratio of 1 to 5, but owing to the "Rationing Restrictions," honey had to be substituted, and diluted in the same proportion proved to be the better food, and was occasionally varied with water only. Observation in the open failed to discover any of this species feeding, and in this connection Marshall (3) only observes "both sexes likewise frequent flowers for the purpose of feeding." It is probable that "honeydew" constitutes a source of food, as is the case with many Hymenopterons, but was not tested with this species.

Seasonal Abundance.—From 14th July, 1919, to the end of January 1920, with a few days' exception, there have been active adults in the main cage; the breeding, which, to begin with, was almost a daily occurrence, caused such an overlapping of generations as to bring about this result. Graham-Smith (4) observes:—"The parasite, however, is abundant throughout the season, for it was observed attacking fly larvā from 30th May to 1st November, 1916." From the observations of the writer, these insects were present in large numbers from July to October 1919 in Regent's Park; and as the original stock bred in the laboratory appeared on 14th July, and taking the average period of the life-cycle as 52 days (see Table I.), this gives 24th May as the date upon which the parents of this generation were depositing eggs; this therefore confirms the above observation.

Details of Emergence.—Accurate sex details of the daily emergence from certain lots were kept from 18th August to 20th September, after which date these had to be abandoned, the breeding operations at this date occupying all available time. Details of daily emergence for the period 3rd to 12th September, corresponding to the period of greatest activity shown in Table I. and affecting laboratory-bred material from the jars No. 1, No. 2, No. 3, No. 4, No. 5, & No. 6 and from No. 7 for one day shown in Table I., are given below in Table III.:—

TABLE III.—Details of Daily Emergence.

Jars Nos. 1, 2, 3, 4, 5, & 6 and 7 for one day.	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	♂ ♀	Totals.
	3 —	3 2	11 3	13 9	17 13	16 38	14 42	17 34	27 31	37 42	*Males.* 158
Dates. Sept.	3rd	4th	5th	6th	7th	8th	9th	10th	11th	12th	*Females.* 214

These figures merely indicate the early appearance of the males. During the period covered by Table III. the average daily contents of the main cage was over 300 individuals of both sexes; this figure allows for the withdrawal of ovipositing females and admission of daily emergences from all sources.

Percentage of Parasitization.—Graham-Smith (1), referring to two lots of material attacked by "free" *A. manducator* in 1914 and bred out in 1915, states:—"In the former it is 60 per cent., in the latter nearly 90 per cent. That the latter figure is a true index of the extent of Braconid infection in the original stock of pupæ is shown by the fact that 9 per cent. of the pupæ in the sun tin were not parasitised." Of two lots of puparia from which— the parasite emerged during 1916, this observer found (**4**):— "At least 25 per cent. of the puparia" from one lot "and 57 per cent. of those" from the other "were infected with *A. manducator*." Summarizing his observations on emergence of this parasite in 1915–16–17, he says (**4**):—"Of the 16,028 puparia collected in the autumn of 1914–15–16 from sunny and shady situations 7041 or 43 per cent. were infected with *A. manducator*, while of the 4787 puparia collected during the summer months of 1916–17 only 508 or 10 per cent. were infected."

From two lots of material collected from Regent's Park on 27th July, and where parasitization by "free" Braconids occurred under conditions similar to those above, the writer found the percentage of parasitism to be 23·12 per cent. and 52·32 per cent. respectively. These lots were both brought in at a time when the larvæ had begun to pupate, they were examined in November, previous to this time emergence had ceased. The figures given are derived from the number of puparia from which *A. manducator* had emerged, and from those intact puparia in which dead adults, dead pupæ, and active and dead larvæ of the parasite were found, as against the total number of puparia in the receptacles, including those from which flies had emerged, or failed to emerge, and those containing atrophied fly-nymphs. It would be of interest to know the number of females responsible for these figures. Dead females were always found in the receptacle, but no reliance can be placed on their number.

In laboratory-bred material, in ten lots, it was found that the percentage of parasitization ranged from 15·04 per cent. to 48·99 per cent., the latter figure being due to nine females. But the outstanding feature of this examination was, that it took a total of 39 females to reproduce definitely 1306 individuals exclusive of over-parasitized larvæ—an average of 33·74 each, or only 9·89 per cent. of their average egg-capacity. This result can but be attributed to confinement and to the bad ventilation of the cage, also to the fact that the parasite's sense-organs, which are normally stimulated to bring about the inclination to oviposit, would have been dulled and deadened by the ever-present odour of carrion in the laboratory. Under better caging conditions and when living in an atmosphere unpolluted with the stench of the putrefactive juices of the carrion, better results would certainly be obtained.

Hibernation.—*A. manducator* hibernates as a full-grown larva. This was observed under natural conditions by Graham-Smith (**1** and **4**), and is supported by the condition of the stock material and by the Refrigerating Experiment.

Attraction to Light.—Artificial light is very attractive, and caused the insects to crowd on that side of the cage nearest to it.

Hosts.—The species of larvæ used in this work and from which *A. manducator* Panz. was successfully bred, are as follows:—

Lucilia sericata Meig.
,, *cæsar* Linn.
Phormia grœnlandica Ztt.
Calliphora erythrocephala Meig.
,, *vomitoria* Linn.

No preference was shown for any individual species, the odour of the putrefactive juices being the chemotropic stimulation to oviposit; and therefore it is probable that other carrion-feeding cyclorhaphous larvæ would be found to be suitable hosts. In this connection Marshall (**3**) states:—"They have been reared from various maggots, as *Lucilia cæsar* L., *Cyrtoneura stabulans* Fall., *Hydrotea dentipes* Fab."

Life-History and Habits of *Nasonia brevicornis* Ashm., and Hosts.

Historical.—*Nasonia brevicornis* Ashm. was first described by Girault and Saunders, 1909 (**6**). They bred it from the puparia of the Common House-fly (*Musca domestica* Linn.) at the Illinois Entomological Station at Urbana in 1908. It has since been reported from Chili and India, and was bred in 1911 from the puparia of *C. erythrocephala* Mg. by Graham-Smith (**1**) at Cambridge, England. In November 1913 it was bred from the puparia of *Pycnosoma rufifacies* by McCarthy (**2**) at the Government Sheep-fly Experiment Station at Yarrawin in New South Wales, and a few days later discovered at Longreach, Central Queensland (**7**). As already stated, page 197, it was first bred by the writer from the puparia of *C. erythrocephala* collected from Regent's Park, London, in July 1919.

Introductory.—In the following account of the life-history and habits of this insect, the writer freely quotes from the writings of the previous observers, adding here and there observations of his own. In doing this the writer desires to put forward as general and collected an account of this important insect as possible; further, it may be observed that the writer had already made an independent study of this subject before specimens were identified and the original description of Girault and Saunders (**6**) brought to his notice. Full acknowledgment is made to these references, which for the sake of the continuity of the account are mostly signified by reference numbers only.

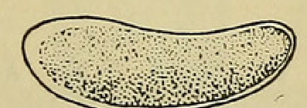
The Length of the Life-cycle.—This is entirely dependent upon the temperature, and its influence affects the full-grown larval stage the most.

The various observers differ as to the period of the life-cycle, but this can be accounted for by the probable differences in temperature when the observations were made. Girault and Saunders (**6**) give $22\frac{1}{2}$ days as the average in the spring and 15 days in autumn; McCarthy (**2**) 11 days in summer; Froggatt

(7) 11 to 14 days; Froggatt (8) 15 days. Under laboratory conditions with a mean temperature of 20° C. it was found to average 21 days.

The Egg.—The egg is translucent white, with a smooth glossy surface, cylindrical, slightly tapering to one extremity and broadly rounded at both ends (text-fig. 13). The newly-deposited egg measures from ·30 to ·35 mm. in length and ·11 to ·14 mm. wide at broadest part (8). The eggs are placed in clusters under the shell of the puparium and upon the surface of the pupal integument of the developing fly, the latter occasionally being punctured by the ovipositor. They are found in clusters of

Text-figure 13.



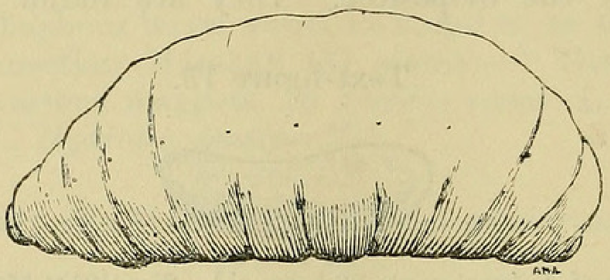
Egg of *N. brevicornis*, 26 hours old. Size ·125 × ·350 mm. ×41. Original.

2 to 12 or more or singly, and are situated on any part of the fly-nymph, but are commonly found in the depression of the junction of head and thorax, or thorax and abdomen. "The eggs appear to be coated with a trace of some sticky substance, which causes them to adhere together, and to the covering integument of the fly-pupæ" (8). The egg undergoes a slight increase in size as the development of the embryo progresses. The duration of the egg-stage varies considerably; those observed ranged from 30 to 74 hours.

The Larva.—Immediately upon hatching, the young larvæ start feeding. They puncture the pupal skin of the host with their mandibles, and with these firmly attached to the enveloping skin of the pupa, proceed to absorb the body-fluids of their host. They remain about the same position until full-grown. As the larvæ develop, the host is gradually absorbed, and consequently shrinks inversely to the growth of larvæ. "As a rule, the remains of a parasitised host—the fully-formed pupa—is a flat, scale-like mass, apparently consisting of the ventral shell of the pupa and that of the head; for example, the thecæ of the eyes, legs, and wings are discernible, and the remains are not much shrunken so far as the original length is concerned. In the case of *Cynomyia cadavernia*, in one puparium infested with 21 larvæ of the first spring generation the parasites were all attached to the dorsal surface of the host from the pronotum to the tip of the abdomen; these parasitic larvæ were nearly full-grown. But in another puparium of the same host, in which 13 larvæ were found, their attachment to the host appeared to be haphazard, and the host-pupa was considerably shrunken, especially in width" (6). No evidence of larval predaceousness is forthcoming, although dead larvæ are frequently found; these are sometimes found with living ones, but usually all are dead. The dead larva is always discoloured and appears to have shrunk to the size of the meconium, so that they are then quite hard.

The number of larval instars have not been worked out, but the general appearance of the larvæ is constant. The larva (text-figure 14) is a typical vermiform hymenopteron, broadest in the centre and tapering towards the extremities. It consists of apparently 14 segments. It has nine consecutive pairs of

Text-figure 14.



Full-grown larva of *N. brevicornis*. ×25. Original.

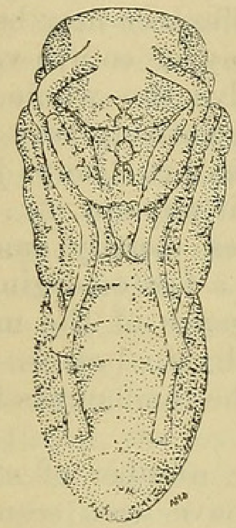
spiracles, of a very simple structure, on 2nd and 3rd thoracic and 1st to 7th abdominal segments. The integument is smooth, glabrous, very thin and easily damaged; it appears to secrete some sticky fluid which entirely bathes the integument, and which enables it to " grip " the surface over which it is moving. An examination of the larval integument discloses minute pores scattered about the surface and presumably the source of this "sticky" fluid. Larvæ have been frequently found in a puparium from which a number of adults have emerged with portions of pupal exuvia attached, sometimes completely covered with it. The mid-intestine is closed caudally during the entire larval development, and the waste matter within it is brown. This gives the larva a dirty white appearance. The slightest puncture made in an active larva about the centre of its body will cause the contents of the intestine to exude instantly, leaving the larva white. The period of development of the larvæ occupies about 7–10 days from the time of hatching, with a pro-pupal stage of 1–3 days.

A few hours before casting its last larval exuvium, the contents of the mid-intestine is voided. This appears to indicate that the mesenteron and proctodeum become connected before the pupa is formed. "The meconial discharges of this parasite, found scattered through the host puparium, are brownish yellow or dark olive-green in colour, and consist of small conglomerations of round pellets, or are sometimes in irregular chains, like some bacteria, but are never single, solid pieces. . . . . " (**6**).

The length of larval life is very variable.

The Pupa.—After voiding the meconium the larva remains motionless—unless disturbed by a fellow-occupant of the host puparium—with its posterior segments surrounded by the meconial discharge, which dries rapidly. So that when the larval skin bursts and recedes, the pupa (text-fig. 15), which does not entirely free itself from the larval exuvium, consequently becomes anchored to the meconium. This has been observed by emptying the larval contents of a puparium into a small glass tube.

Text-figure 15.



Pupa of *N. brevicornis*. Greatly magnified. Original.

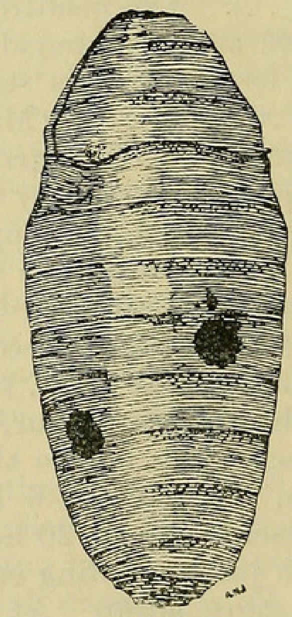
The duration of the pupal stage is variable. "This was obtained in one case only. A larva pupated during the night of Sept.17–18, 1908, ... The resulting adult female emerged at 10 A.M. Sept. 23, 1908, making a pupal stage of approximately 5½ days. The average length of this stage for the first spring generation (17 cases) was 9 days (May 14–23, 1909)" (**6**). Another observer states:—"The pupal stage occupies about five days" (**8**). Those pupæ observed by the writer ranged from 8–12 days. "When first formed, the pupæ are yellowish white, the eyes garnet, with some duskiness at the caudal edges of the abdominal segments soon afterwards; the mandibles, legs, antennæ, and wing-pads gradually become dusky, and about 48 hours previous to eclosion, the head, thorax, and abdomen, in succession, begin to show dark colour, the head and thorax together becoming a deep black before the abdomen shows very much colour, and then, after about 6 hours, the latter turns gradually but rapidly black. About 20 hours before eclosion the colour is jet-black, which just preceding emergence changes nearly to the colour of the mature adult. At eclosion the adults are fully coloured." (**6**.)

The pupal exuvium, which is very stiff, is a golden brown, and does not recede as in the Braconid, but appears to be broken up in parts; pieces which retain the outline of the antennæ are frequently found loose; similarly, pieces from the head and legs can be found; the abdominal portion seems thinner, and is usually attached to the apex of it when the insect emerges.

The Adult.—Emergence of the Adult.—"In general, it may be stated that the adult parasites emerge from the host puparium through from 1 to 3 circular holes, situated variously, usually in the dorsal or dorso-lateral aspect; and when more than one exit-hole, the two or three are usually scattered or widely separated. The manner of emergence does not differ for sex. The exit-hole varies in diameter from 0·75 to 1·50 mm.; it is usually larger and single when the host is *Musca* or *Chrysomyia* and smaller when *Phormia*, though this difference may be more apparent than real. Individual exit-holes may of course vary considerably in shape; for rarely it may involve the whole of one end of the host puparium, and is then relatively very large and irregular. The margins of the exit-holes are always jagged or serrate, showing that the adults gnaw their way out. . . . . . . In regard to the time of emergence, the males usually emerge from 2 to 20 hours earlier than the females, a few emerging some hours previous to the simultaneous emergence of the majority, but there is considerable variation in individual cases. Thus some males may be the last to emerge, but the tendency is for them to emerge earlier than females." (6.)

In the laboratory the number of exit-holes was not limited to three, four and five have been seen, and the exit-holes, consequently, dorsal, ventral, or lateral (text-fig. 16).

Text-figure 16.



Puparium with two exit-holes latero-ventrally. *N. brevicornis*. Greatly magnified. Original.

Both sexes emerge with the wings fully expanded.

Larvæ have been found in puparia from which—several weeks or months previously—adults had emerged. If this takes place under natural conditions, it would appear that these have very little chance of completing their development, and would probably be killed by mites or some other enemy.

Many attempts were made to observe the initial process of making the exit-hole, but without success. However, on one occasion a female was observed enlarging an exit-hole. A few days previously this particular puparium had been enclosed in a glass tube stopped with a cork. The tube was under observation with the aid of table binoculars to watch the movements of some adults of both sexes which had emerged. There were two exit-holes in the puparium, dorsally, with centres about 3 mm. apart, one being much larger than the other, and through the former all the large females in the tube must necessarily have escaped. Suddenly a female's antennæ were noticed to issue from the small exit-hole, and were violently agitated. The upper part of the epicranium could be seen against the inside of the puparium; the head was then moved, as was evident by the changing positions of the waving antennæ; eventually, after the scapes had several times come into contact with the serrated edges of the exit-hole, they were withdrawn; the female could then be seen changing its position. This accomplished, the head began to appear latero-ventrally through the hole, the right eye coming up first; gradually more and more of the head appeared still maintaining its latero-ventral aspect, until the edge of puparium was slightly oblique to the junction of the mandibles. The right eye and gena were then above the surface of the puparium, the antennæ still inside. The female now began to bite the puparium, the right mandible coming down on it from the outside, the left working up on it from inside. This process continued in a leaf-eating-caterpillar-like movement—semicircular forwards and backwards—until the hole was made large enough to enable the female to escape. No effort was made to test the size of the hole; the insect continued to bite until, suddenly ceasing, it began changing its position again until it was ventral side up inside the puparium, then, moving forward and bending upwards, the antennæ, head, anterior legs, thorax, middle and posterior legs, and abdomen appeared successively, until the female was on the surface of the puparium, erect. It immediately began cleaning itself: the apex of the abdomen bore a portion of the pupal exuvia, which came away with a minute white meconial discharge. A few seconds later the female was found by a male.

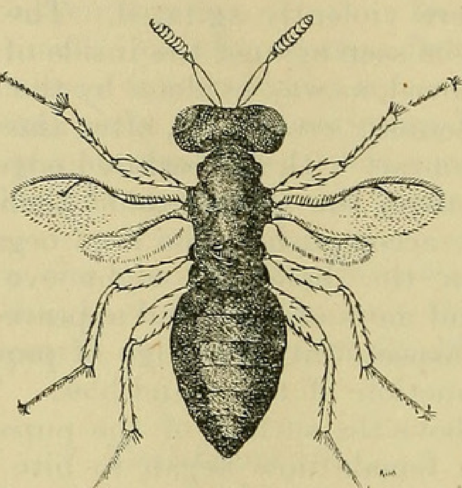
In the laboratory, when the puparia are unburied in soil, these discharges can be seen scattered all over them, and appear as minute white strings.

The Sexes.—*Size*:—The females vary from 1·0 mm. to 2·30 mm., the males from 0·60 mm. to 2·0 mm. (**6**).

General appearance.—Both sexes are distinguishable to the naked eye. The females have large wings extending beyond the apex of the abdomen, whereas the males (text-fig. 17) are semi-apterous; their rudimentary wings do not extend farther than the third abdominal segment.

"... the female is a rich dark green, the abdomen nearly black, the head and thorax dorsad, reflecting brassy scintillations, in some lights entirely brassy; in the ventral aspect and also the lateral, the thorax appears bluish; the antennæ dark, the scape and pedicel a rich brown, the legs mostly brown with darker femora. On the contrary, the males appear a brilliant bright metallic green, reflecting brassiness, the antennæ and legs light yellowish brown, the wings small, clouded, with a soiled appearance; the ventral aspect is the same, but with slight traces of metallic bluish. The male is noticeably more brilliant and bright than the female, which is somewhat sombre." (6.)

Text-figure 17.



Male *N. brevicornis.* Greatly magnified. Original.

Variations of the foregoing description of the type species were observed in the females; with light brown or yellowish brown femora, not dark or clouded; general colour deep metallic blue; fore-wings not naked in the basal triangle of wings below the submarginal vein, the costal margin with more bristles. Of six such specimens mounted for microscopical examination, no uniformity was found in the venation. The number of setæ in basal area of fore-wing varied from 2–5, position also varied. Bristles on costal margin also varied, as many as 14 were observed.

Courting and Mating.—"Courting in this insect is not a complex habit. It follows almost immediately after emergence, at least in confinement. Where a number of both sexes are gathered together, all recently emerged, the males and females are constantly in motion, the former active, seeking the females; the antennæ of both sexes also constantly in motion, held inclined upward in the natural position, giving quick, jerky, wavy movements. When one individual meets another, the antennæ simply touch whichever portion of the body presents itself first, and the two turn aside and pass on; or if they happen to be individuals of opposite sex and (apparently) the occasion is suitable—which is most often the case immediately following emergence—the male hastily climbs upon the back of the female, runs forward, and grasps her head with the fore-feet, usually at the lateral aspect of the eyes or sometimes at the cheeks; the intermediate feet grasp some portion of the thoracic pleura, usually at the mesothorax, and the hind-feet take hold along the sides of the abdomen or the edges of the flat wings. The legs are not stretched out or used for embracing the body of the female, but the hold is taken by the feet alone, and the position of the male is not strained, but rather that of the natural position of rest. His body is parallel with and above the body of the female and projects beyond (cephalad) it, so that the head is between the upturned antennæ of the female and stretched over hers, his abdomen reaching to a point above the third abdominal segment or to a point opposite to the distal end of the marginal vein of the fore-wings, upon which it actually rests. Having quickly attained this position, the male senses the antennæ of the female with his own, and immediately begins suit in earnest by rubbing his head up and down against the inner (mesal) surfaces of the flagella of the female, which are held up in a V-shaped position, at the same time holding the scapes erect and apart and the flagella back, pointing laterad at right angles to the scape and at every downward movement bringing the scapes together; this movement of the head is accompanied by a corresponding "petting" movement of the female flagella against the cheeks of the male. The up and downward movements of the head are regular and continued for from 5 to 10 seconds, each completed movement occupying slightly less than a second of time; and they are alternated with a period during which the head of the male is motionless and his antennæ sensing those of his mate, either by touching both of their tips to the tips of her antennæ, or else by stroking them up and down; the mandibles, maxillæ, and labium with both pairs of palpi are themselves in almost constant motion, but, so far as observed, they play no part as organs of sensation, with the possible exception of the maxillary palpi. Sometimes the male rubs but one of the flagella of the female, turning the head to one side. No other movements than these are observable, but there is some variation in the occurrence of either of the two movements described, and also in the number of times they are repeated before sexual union is permitted by the female. The male may be received coldly; he may make the movements without attempting union, or after alternating them three or four times, he may attempt union without success, and then run forward to repeat the actions, and this may continue as long as the female permits, either resulting successfully or unsuccessfully. In the presence of other females, if received coldly, the male soon tires, leaves and seeks another mate. In order to attempt union, the male has to reverse his position, and run back to the tip of the abdomen of the female, where he usually reaches over the tips of the wings and senses with the antennæ, quickly turning and reaching around again with the tip of his abdomen to gain entrance into the vaginal orifice. Or, on the other hand, he may simply back quickly to the caudal end of the female and attempt union. In one case, ... coition lasted for fourteen seconds, in another for ten seconds. Mating is promiscuous for both sexes." (6.)

During the breeding operations, when females were scarce—being occupied with host puparia,—the writer has frequently observed an unresponsive female crawling about with several males upon her, the lower ones holding on dorsally and laterally, and those above holding on to each other. Sometimes the female with this load on her would try to climb the side of the cage. This effort always ended in the whole party falling to the bottom. On three specific occasions the number of males thus congregated numbered 10, 7, and 11.

The males have some curious habits. When the puparia from which adults have commenced to emerge are lying unburied on soil, a male can be observed to take possession of one, and either stand on it waiting for a newly-emerged female to appear, or he will enter it and periodically make an appearance to seek a mate. Generally the males remain in the immediate vicinity of the puparia from which emergence is taking place, and running over and around these in search of females, they are continually meeting each other; then they start to fight. This usually takes place by means of the antennæ and fore-legs, resulting frequently in the loss of a few joints of the flagella by one or both antagonists. During these scuffles there were sometimes three or four participants, and then it frequently happened that a puparium became dislodged, with comical results if it was occupied by a "domesticated" male: he would sally forth and attack the first within reach; generally one in no way responsible for his discomfort. From a short distance the whole area occupied by the males seemed to consist of combatants.

Females only resorted to fighting when disturbed during oviposition; seldom did males venture into the dishes containing host puparia for parasitization.

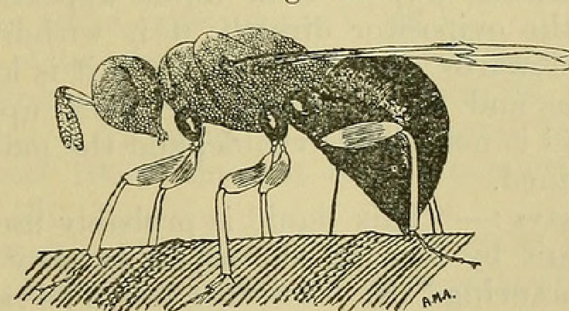
Flight.—The females, in spite of their large wings, are only capable of flying short distances, in a very jerky manner, about 6 feet at a time at most. Before starting on a flight, they usually indulge in a few preliminary movements of their wings. Their most customary method of progress is to crawl.

The males are quite incapable of flight, and the only occasions on which they have been observed to use their wings are when courting and fighting.

Oviposition.—This takes place within a host puparium, preference being shown for those between 24 to 72 hours old—that is to say, after histogenesis has started and the developing fly-nymph is covered in its pupal skin and free of the puparium except where attached anteriorly and posteriorly by the tracheæ. A female will not oviposit in a puparium containing an atrophied fly-nymph, neither one containing a fully-formed fly which for some reason has died or failed to emerge, nor will it oviposit in an empty puparium from which the occupant or occupants have emerged, although efforts to induce some to do so were made by burying that portion from which emergence took place; its behaviour with such puparia is initially the same as with a healthy puparium, but after examination and possibly an attempt to insert the ovipositor, it crawls off in search of others. To enable it to distinguish between those puparia which contain sustenance for its progeny and those which do not, the female must not only possess very delicate sense-organs, but apparently uses the point of the ovipositor, as will be shown later.

Before attempting to insert the ovipositor, a female spends some time critically examining the puparium, crawling over and around it, with her head inclined towards it, constantly waving the antennæ, with which she frequently touches it. Having, apparently, satisfied herself that it is a fit object for attack, she bends the abdomen so that the apex touches the puparium, and then with the tactile hairs upon the palpi and abdomen, and with the point of the ovipositor, she proceeds to prod it until a position is located—such as a groove in the contracted integument of the puparium—through which to make a puncture. The ovipositor is then held in the minute groove, and the apex of the abdomen springs back to a position in which it assumes almost its natural shape, although diagonally opposed to the puparium, and in doing this the full length of the ovipositor is exposed (text-fig. 18);

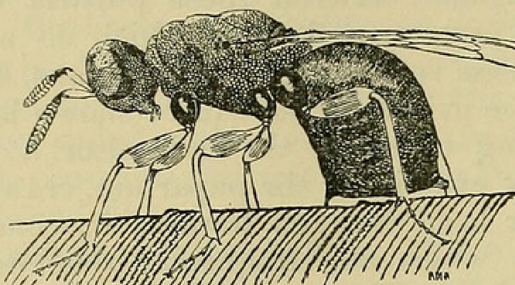
Text-figure 18.



Female *N. brevicornis* ovipositing; 1st position. Greatly magnified. Original.

this has hitherto been hidden in its recess along the ventral plates of the abdomen. The female now endeavours to pierce the puparium—not always with success, in which case she moves off to another spot and repeats the process,—which she appears to do with a slight rotatory and up-and-down movement of the ovipositor, accompanied with frequent twitching of the antennæ, a constant movement of the trophi, a slight twitching of the apex of the abdomen, and a general appearance of slight movements as if her entire strength was being exerted upon the task. As the ovipositor gradually disappears into the puparium, the position of the hind-legs is sometimes changed, and they are placed further apart so as to lower the body in rhythm. During this movement the abdomen gradually assumes an extraordinary lateral aspect until, when the ovipositor is completely inserted, its appearance is similar to that depicted in text-fig. 19. The flexibility of the sternites is remarkable. Sometimes, after the ovipositor has

Text-figure 19.



Female *N. brevicornis* ovipositing; 2nd position. Greatly magnified. Original.

been inserted its full length, it is partly withdrawn, and appears to be moving slowly in a circle, giving the impression that at this time the eggs are being discharged so as to lie together in a cluster but not on top of each other. Eventually, by lifting the abdomen till it recovers its position as shown in text-fig. 18, and then lifting the thorax with the hind-legs, it disengages the ovipositor, which instantly springs back to its normal hidden position.

Generally a minute drop of clear liquid appears at the point of insertion of the ovipositor directly it is withdrawn, but the female moves backwards over the hole until it is located by her palpi or antennæ, and then appears to "suck up" the liquid The drop of liquid is not always visible, and the nature of it has not been determined.

One observer says :—" This liquid is probably used in the first case as a lubricant by bathing the styles as they work on the sheath while puncturing " (**8**). Another :—" The liquid is either a fluid resembling in its nature a synovial fluid, or else it had been acting as a lubricant for the styles ; the former is the more probable " (**7**). Another observer says :—" In many cases it (the hole) became covered with a white mycelium-like growth the nature of which we have not determined " (**6**). That the function of the liquid is to seal the hole seems probable. Only in three instances amongst material parasitized in the open have mites (undetermined) been found inside intact puparia inhabited by developing Chalcids, and in one case a pupa had been partially devoured.

The time occupied in ovipositing is variable, ranging from a few seconds to half-an-hour. A few specific instances are quoted :—
" The deposition of an egg observed at 9.45 P.M., Sept. 14, required 16 minutes; the host was *Phormia regina*. Another

observation made at 10.15 A.M. the same day showed that the act required 8 minutes; the host puparium was that of *Musca domestica*; . . . . A female confined at 9.20 A.M., Sept. 10, deposited into puparia of the *Phormia* at 9.32 A.M. and 1.20 P.M. the same day. One confined at 10 A.M. the same date with two puparia of the same host oviposited at once." (**6**.)

The position of insertion of the ovipositor is very variable. Any segment laterally, dorsally, or ventrally is attacked, in captivity.

One female may insert her ovipositor more than once in the same puparium. One puparium may be attacked by several females in turn; sometimes two will be seen at work at the same time.

Length of Period of Oviposition.—When amply supplied with host puparia, the females appear to live from 3-4 weeks. The first generation from material obtained from Regent's Park were still actively at work, whilst their own progeny were emerging and had begun attacking hosts.

Time elapsing between Emergence and Production.—When host puparia are available, oviposition takes place within a few hours. In three specific instances observed by Girault and Saunders oviposition took place in 24, 10½, and 3 hours after emergence.

Progeny of Single Females.—The number of eggs deposited by a female varies. "In three instances one female placed in a tube with fifteen pupæ parasitized the whole, with the exception of two pupæ which had decayed. The total number developing from the one parasite in the first case was 140, in the second 148, and the third 96. (The numbers emerging from each pupa varied from 15 to 1 in these experiments.)" (**8**.)

In the case of two females each confined separately with host puparia, the first with 130, the second with 86, their respective progeny numbered 21 males, 57 females, total 78, and 38 males, 65 females, total 103. The first female parasitized 17 puparia, the second 22 (**6**).

Parthenogenesis.—"On September 27th, 1908, 12 virgin females of *brevicornis*, reared separately from puparia of *Phormia regina* and in no instance accessible to males, were confined separately, each in a small gelatine capsule with a single known healthy puparium of *Phormia*; on September 29th at 11.30 A.M., in three cases females were observed ovipositing; on October 15th, 1908, the progeny of two of the virgin females emerged as follows:— 17 males . . . . and 15 males. . . . . Other emergences did not occur, but in three instances the larvæ of the parasites were found in the host puparia, all dying, however. Hence this parasite is parthenogenetic." (**6**.)

Proportion of the Sexes.—Under this heading Girault and Saunders tabulate the numbers and sexes of 7369 specimens dealt with by them. In lot No. 3 (of this table) they bred 710 males and 786 females; these were from puparia collected "from a single host lot from a decomposed cadaver, city dumpinggrounds." In lot No. 5 they bred 228 males and 116 females from "host puparia in fæcal matter, miscellaneous." These lots represent the most complete figures for material parasitized under natural conditions, and clearly indicate parthenogenetic reproduction.

Length of Life of Adult.—As previously stated, females kept amply supplied with host puparia and a little food lived from 3–4 weeks. The males confined with these females only live 7 or 8 days.

In Australia, under similar conditions and in the cooler weather, they are stated to live from 4 to 6 weeks (7).

When confined in glass cylinders without food or host puparia, they were found to live from 4 to 6 days, the males dying first (6 and 7), and when confined in glass cylinders with food and no host puparia, they were found to live from 18 to 20 days (7).

"The difference in the length of the life of the wasps kept in a confined space, and of those actively at work in the cages, may be due partly to the direct effects of confinement; but in the writer's opinion, it is due more to over-copulation of the females in the confined spaces" (7). This may be partly accountable, but the females appear to be quite capable of resisting the advances of the males, and the writer suggests that the undetermined drop of liquid which sometimes exudes from the punctured puparium, and which all observers agree is generally "sucked up" by the female, may contain nutriment. This would explain why those confined with food and host puparia to deposit eggs in, live longer than those with food and no opportunity to deposit eggs. This view is further supported by the fact that (under breeding conditions) the females seldom left the dishes containing host puparia for food.

It has, however, been ascertained that individuals of both sexes can live for some time with very little food. In the case of three females (presumed to have mated) each was confined separately in tubes within 14 hours of emergence; and into each tube a minute drop of food was placed on the glass by the aid of a needle; no further supply was given. The first female was dead on 15th day, the second on 19th day, the third on the 21st day. Of three males confined separately in tubes (none of them had had an opportunity to mate) and given a similar initial drop of food, one managed to escape on the 7th day through a fissure in the cork, another died on 14th day, and the last on 22nd day. No test was made with virgin females.

Food.—In the laboratory the same food as was used for the braconids and flies was given to these, but very infrequently and only a very little at a time, otherwise they would get stuck in it; and if their wings came in contact with it, they seemed quite incapable of extricating themselves. How the semi-apterous males obtain food under natural conditions is not known; and taking into consideration their habit of remaining in the immediate vicinity whence they emerge, it is very probable that most never obtain any. The females have a better chance with their short jerky flight.

Effective Parasitism.—Under this term Girault and Saunders refer to an interesting phenomenon, and one which was also observed by the writer. It is, that the attack of *Nasonia* can be effective upon the host pupa within 15 to 24 hours prior to the moment when the adult fly would have emerged, the length of the period being approximately such time as is required for the depositing, development, and hatching of the egg, and which in the instances observed by the writer would be from 30 to 74 hours. In a specific instance, and one which must be about the extreme limit of effectiveness, a puparium was noticed to be cracked along the crease at the anterior end, but not sufficiently to have allowed a fly to emerge; it was opened, and found to contain seven larvæ feeding upon a perfect pupal fly which had cracked its enveloping skin anteriorly and the puparium, but which had failed to get any further, its organ of locomotion—the ptilinum—apparently having lost its efficiency gradually as the larvæ fed.

Percentage of Parasitization.—The writer has no figures relative to the percentage of parasitization under natural conditions, and the data relative to laboratory conditions cannot be taken as a true index of the capacity of *Nasonia*, as the number of host puparia presented for attack were worked out on the basis of 20 per female, and the numbers of the latter in the breeding-jars or main cage were only approximately ascertained.

Upon reference to Girault and Saunders the following is found:—" Further, the local abundance of this parasite is indicated by the fact that in at least a portion of the experiment just mentioned, a portion selected at random, the percentage of parasitism was as high as 90 per cent. We have evidence to show, on the other hand, that this percentage of mortality of the host was by no means general, but was considerably lower on the average for this season of the year." (6.)

Hibernation.—This parasite hibernates as full-grown larvæ within the puparia of its various hosts. It emerges in the spring, the earliest recorded emergence, in England, being the end of April (4).

Attraction to Light.—The females are freely attracted to artificial light, the males very slightly.

Hosts.—The different species of puparia given to *Nasonia brevicornis* to parasitize, and from which it was successfully bred are as follows:—

Musca domestica Linn.
Calliphora erythrocephala Meig.
,, *vomitoria* Linn.
Phormia grœnlandica Ztt.
Lucilia cæsar Linn.
,, *sericata* Meig.

The hosts reported from America by Girault and Saunders (6) are:—

Musca domestica Linn.
Calliphora erythrocephala Meig.
Phormia regina Linn.
Lucilia cæsar Linn.
,, *sericata* Meig.
Chrysomia macellaria Fabr.
Cynomyia cadaverinia Desv.
Sarcophaga species "K" (Spec. nova).

The hosts reported from Australia by Froggatt, jun. (7) are as follows:—

Pycnosoma rufifacies. "Mostly in the field."
,, *varipes.* "To a lesser extent in the field."
Anastellorhina augur.
Pollenia stygia.
Lucilia sericata. "In the laboratory."
Calliphora erythrocephala.
Sarcophaga aurifrons.

Super-parasitism, or Accidental Secondary Parasitism.

That *Nasonia brevicornis* might be a "Hyperparasite" upon *Alysia manducator* originally occurred to the writer, when the second lot of puparia were collected from the spot at Regent's Park whence the original Braconid parasitized material was obtained, and when it was found that this Chalcid was emerging from it. However, no Braconid lining to the puparia was observed, at the time, in any from which the Chalcids had emerged; and as the initial breeding operations showed that the latter—then undetermined—bred freely from healthy host puparium, it was assumed that "hyperparasitism" was not the *rôle* of *N. brevicornis*; although it appeared reasonable to suppose that the Chalcid might act accidentally as a secondary parasite in the early stages of development of the Braconid—that is, during the first or second instar—and when the greater part of the fly-nymph still existed. That secondary parasitism in this early stage could take place appears probable; and it does not require a great stretch of imagination to conceive the race for life within a puparium, in the fly-nymph of which an early instar larva of the Braconid is slowly feeding, when suddenly one by one a dozen, more or less, Chalcid larvæ commence feeding operations from the outside of, and through the enveloping integument of the fly-nymph. That the result of such an unequal contest would be against the Braconid, it seems only reasonable to assume; and that the latter would eventually be killed by the Chalcids biting into it. No efforts were made to investigate this point; it appeared too obvious a potentiality, and to search the remnants of a fly-nymph for evidence of the existence of the Braconid of which the chitinized head-capsule of the first instar or mandibles of the second would be the sole initial evidence of its existence, would require time, which the writer at that time could not spare.

Later—in October—a reference was found to this subject, Graham-Smith (1) on pp. 532–4 and on p. 537, in which another Chalcid, *Melittobia acasta* Wlk. (9), is definitely stated to act as a hyper-parasite * on *A. manducator*, and a passing reference to *N. brevicornis* occurs and to the existence of numbers of then undetermined Chalcid larvæ in Braconid-lined puparia. Again, in November, further reference (Graham-Smith) (4) was found to this subject, and this time referring to the presence of *N. brevicornis reared* from puparia with the silk lining of *A. manducator*. This observer states :—" Puparia collected in the autumn of 1916 and kept outside yielded in May 1917 38 males and 36 females. Some of these autumn puparia had been parasitized by *A. manducator*. . . . . Some of these autumn puparia remained intact, and were dissected in March 1918. Of these, 28 were found to contain living Chalcid larvæ, and were kept in tubes in a warm room. Nineteen of these 28 showed infection with *A. manducator*. Adult *N. brevicornis*, 11 males and 48 females, emerged in May 1918, a year and a half after the puparia were collected."

The writer therefore decided to carry out an investigation into this important matter ; and as the subject is of considerable interest, the various experiments are given in detail.

To begin with, it might be mentioned that the point previously referred to—*i. e.*, secondary parasitism in the early stages of the Braconid larvæ—was not investigated, for the reason stated.

The following two experiments were made to verify the above quoted statement :—

Experiment No. 1.—A large tube 6 inches × 1 inch was used. Into this was placed—on 25th November—one normal size *Calliphora* puparium, in which a small fracture of the pupal case was made so as to disclose the Braconid lining, and therefore denoting the presence of either a full-grown larva, pro-pupa, or pupa. Three fertilized and recently-emerged females of *N. brevicornis* were then released in the tube, and on the inside of it a small quantity of food was smeared. The tube was kept under occasional observation for four days, during which time none of the females were seen to oviposit, but could be seen crawling over the puparium, carrying out the usual critical examination. After 29th November no further observations were made. On 17th December—21 days later—the tube was opened ; the three females were dead, and the puparium was then carefully opened under binoculars. In it was found one active full-grown Chalcid larva, two dead and dried-up larvæ apparently nearly full-grown, and two small shrivelled masses of newly emerged larvæ. The

* There appears to have been nothing else in the tins where this occurred except puparia containing individuals of *A. manducator*.

Braconid was found to be in the full-grown larval stage, and was only partially dried up. In endeavouring to move the active larva, the integument was punctured by the needle, and its unvoided waste instantly exuded. This caused the writer to form the opinion that the four dead larvæ of the Chalcid might possibly have met their death by a similar agency—the setæ and sensory hairs (text-fig. 5) on the integument of the full-grown Braconid larva.

Experiment No. 2.—Another examination into this point was therefore carried out. On 30th December four normal-sized puparia, which when fractured disclosed the Braconid lining, were placed separately in glass tubes Nos. 1–4, and into each two fertilized *Nasonia* females were admitted, and a smear of food made on the inside of each tube. They were then corked. On 31st December—the next day—tube No. 3 was found to contain an active *A. manducator* male. The male was released in the Braconid cage, the *Nasonia* females were replaced by new ones, and another puparium—a small one—obtained and put into tube 3. Occasional examination of the tubes was maintained, and, when necessary, fresh smears of food made. On 9th January both females in tube No. 2 were dead. On 10th January, tube No. 1 was found to contain an active *A. manducator* female; the *Nasonia* females were still active. A new puparium was put into the tube, and that from which the Braconid female had emerged was examined. Nothing bearing any resemblance to Chalcid larvæ or eggs was found; the puparium contained the Braconid larval exuvium, pupal exuvium, the meconium, and white cement-like discharge. On 11th February tube No. 4 was found to contain an active female Braconid; both *Nasonia* females were dead. The puparium was examined, and besides its normal contents, two small masses were found adhering to the lining but which were not distinguished. The *Nasonia* females in tubes Nos. 1 and 3 were observed to be dead. On 10th March the contents of tubes 1, 2, and 3 were examined. No. 1 puparium was opened, and found to contain a dead and shrivelled larva of *A. manducator*, and attached to it was a dead Chalcid larva, and loose in the puparium two living Chalcid larvæ. No. 2 puparium contained a dead and shrivelled larva of *A. manducator* with four dried and shrivelled Chalcid larvæ—very small ones—and all adhering to their host. The puparium in No. 3 tube was examined, and towards the cephalic ventral end of it a slit was observed, through which part of the head of an adult Braconid could be seen, as though it had tried to emerge. It was then observed whilst opening the puparium that, at the point where the writer had made a fracture mid-dorsally in the first place, this had either been carelessly done, or the female—for such it was—had extended it in her efforts to emerge when bringing the necessary pressure to bear upon the cephalic end in order to get her mandibles into it, as she would cause the anterior half to bend with her, so that it acted as if hinged, and thus frustrating her efforts to emerge.

No signs of Chalcid infestation was observed. The female may have died within a few days of the start of the experiment.

The foregoing experiments show that, under certain conditions —and with fractured puparia—*Nasonia* can super-parasitize *A. manducator* lined and inhabited puparia, and in two instances three larvæ reached full growth.

Whilst experiment No. 2 was developing, experiments into other directions were undertaken.

It has been previously stated that blow-fly larvæ upon recovering from "temporary paralysis" are stimulated to pupate and to escape from the females of *A. manducator*. It was therefore decided to ascertain to what depth such larvæ worked their way into the soil.

Experiment No. 3.—A wooden box with a sliding lid was requisitioned. One end was removed, and the sliding lid sawn across into strips an inch wide. Thus when placed upright with the remaining end as the base of the box, the original base formed one side and the sliding lid in strips the other, with the original sides as ends.

This box was then gradually filled with soil which, during the building up of the requisite depth, was twice subjected to running water to damp it. Seven inches of soil were eventually put in. On the same day—9th January, 1920—pieces of liver upon which fly-larvæ had been feeding were placed on the surface of the soil in a compact mass. One female *A. manducator* was then caught in a tube from the main cage. The mouth of the tube was then held over the liver until the female was stimulated to descend upon it. As soon as she got on to it, she started examining it for larvæ. 25 of these, about three-quarters to full grown, were at hand; they were placed near the female, one at a time, so soon as she had oviposited into each of them. In three instances she attacked twice, having failed to come in contact with the substitutes, and in each case the latter were withdrawn and given to her a second time. It took 57 minutes to get the 25 larvæ parasitized. The female was moved back into the tube and given a smear of food on the cork. She was allowed to rest in the tube for 20 minutes. In the meanwhile another 25 larvæ had been collected. The female was now released again, and the same process started, but she only attacked one of these larvæ; and although others were placed near her, she could not be induced to attack any more, and after 26 minutes the experiment was given up for the day. The remaining 24 larvæ of the second lot were returned to their breeding dish, and the female caught and left in the tube with food.

No further action was taken for the next two days. On 12th January, 1920, the experiment was continued. The above female was found dying; another was therefore removed from the cage, and at 2.30 P.M. it was set to work on 25 larvæ as before, but at 3.25 P.M. it suddenly became dark, and the female refused to oviposit any more. In this time—55 minutes—she had dealt with

20 larvæ. The remainder, five, were returned to their dish, and the female placed in a tube. The surface of soil was on this date quite dry.

On 14th January the contents of the box were examined, but in removing the first inch strip of the "side," some of the dry soil fell out and the dead larva with it (this is recorded as $\frac{1}{2}''$ in the table); greater care was then exercised in removing the other strips. The result is shown for convenience in Table IV.

TABLE IV.—Depth of Soil penetrated by parasitized larvæ.

Depths	$\frac{1}{4}''$	$\frac{1}{2}''$	1''	$1\frac{1}{4}''$	$1\frac{1}{2}''$	$1\frac{3}{4}''$	2''	$2\frac{1}{4}''$	$2\frac{1}{2}''$	$2\frac{3}{4}''$	3''	Totals.
Larvæ	—	1*	—	—	3†	—	1	2	—	—	—	7
Puparia	—	—	1	1	3	4	6	7	10	3	4	39
Totals	—	1	1	1	6	4	7	9	10	3	4	46

* Dead. † 1 dead.

When removing the soil, which was done by gradually scraping it off with the edge of a steel rule, it was found that at $2\frac{3}{4}$ inches down the soil was caked and still damp. This coagulation was no doubt due to running the water into the box on very dry soil. Seven of the puparia were broken in scraping the soil off.

Experiment No. 4.—Another experiment of the above description was carried out, but in this instance the soil was spread out into a tray and damped before putting it into the box. The same wooden box was used, and filled with this soil to a depth of 7 inches. The experiment was started in the morning of 22nd January, 1920. Pieces of liver were placed on the soil, and one female *A. manducator* allowed to emerge from a tube on to it; 25 larvæ were then given separately for oviposition. The female effectively dealt with these in 45 minutes; she was then removed and another female taken from the cage. The second female was also given 25 larvæ, and disposed of these in an hour and a quarter. Over-parasitization was observed to take place in one larva in this experiment.

On 27th January, 1920, five days later, the contents of the box were examined by the same process of scraping the soil off; it had not coagulated in this case, and only two puparia were broken. The result of the experiment is given in Table V.

Table V. shows that 19 larvæ went deeper than any in No. 3 experiment, there being an absence of caked soil.

Both experiments Nos. 3 and 4 showed that the majority of Braconid parasitized larvæ reached 2 inches or more under the surface of the soil.

Three experiments were made to ascertain the burrowing capacity of *N. brevicornis*. Nos. 5 and 6 were started before the

TABLE V.—Depth of Soil penetrated by parasitized larvæ.

Depth ...	$\frac{1}{4}''$	$\frac{1}{2}''$	$\frac{3}{4}''$	1″	$1\frac{1}{4}''$	$1\frac{1}{2}''$	$1\frac{3}{4}''$	2″	$2\frac{1}{4}''$	$2\frac{1}{2}''$	$2\frac{3}{4}''$	3″	$3\frac{1}{4}''$	$3\frac{1}{2}''$	$3\frac{3}{4}''$	4″	$4\frac{1}{4}''$	Totals.
Larvæ	—	—	3*	3†	—	1	—	1	—	—	1	1	—	1	—	—	—	11
Puparia ...	—	—	—	—	—	—	3	2	4	5	4	3	4	7	4	2	1	39
Totals	—	—	3	3	—	1	3	3	4	5	5	4	4	8	4	2	1	50

* 2 dead. † 2 dead.

writer was in possession of the information gained in experiments Nos. 3 and 4.

Experiment No. 5.—A cylindrical glass jar was used. It was filled with 5 inches of damped soil; on this was placed a piece of liver with some larvæ feeding upon it. They were mostly full grown. This experiment was started on 20th December, 1919. On 22nd December it appeared that the larvæ had ceased feeding and had gone into the soil to pupate. The liver was therefore removed, and under it two puparia were found; no others were visible. The liver was replaced. 18 fertilized females of *Nasonia brevicornis* were then released in the jar, which was at once covered with bolting silk, and this smeared with food. On 1st January, 1920, adult *C. erythrocephala* were emerging; no Chalcids could be seen, so no further supplies of food were given. The flies were left to die, so that nothing should be disturbed. Adults continued to emerge up to 5th January; a few days later they were all dead. On 10th January, as no living adults could be seen, neither flies nor parasites, the two puparia on the surface were removed, and the contents of the jar emptied and sorted. No attempt was made to gauge the depth to which the larvæ had crawled. The jar was found to contain 47 empty puparia and an equal number of dead flies. 14 intact puparia were found; these were opened, and yielded four puparia containing Chalcid larvæ; the remainder consisted of dead fully-formed flies or atrophied fly-nymphs with no sign of Chalcids. The two puparia from the surface were filled with Chalcid larvæ. Of the Chalcid females, only 15 were collected; the other three were not searched for a second time in the soil.

Experiment No. 6.—This was another burrowing test, in which 20 puparia were placed at various depths ranging from two at 5 inches to seven on the surface, and were situated near the glass side so as to be visible to the observer. The soil used was very dry and lumpy, with a certain amount of fine dust due to the crumpling of the lumps. Four females and one male were released in the jar. Mating was observed. The experiment started on 1st January 1920; and on 20th February, when the contents were emptied and the intact puparia opened—there were only four of these, flies had emerged from the rest,—none bore any signs of Chalcids. This experiment, therefore, was a complete failure. The only point of interest was that the two flies placed at a depth of 5 inches reached the surface.

Experiment No. 7.—This was also a burrowing test. It was started on 30th January, 1920. The same jar was used as in No. 4. It was filled with 2 inches of damped soil, and on this 93 newly formed puparia were placed; above the puparia 2 inches of damped soil was run in. (The writer was now in possession of details of tests 1 and 2.) On the surface of the soil 12 more puparia were scattered, and a piece of liver upon which larvæ had been feeding was also put in. The liver covered five of the surface puparia. The liver was used to reproduce, on a small scale, natural conditions. 20 fertilized females were released in the jar on the same day; it was covered with bolting silk and smeared with food. The jar was kept under observation. From 31st January to 9th February some of the females could be seen at work on the surface puparia. From 10th February to 13th they appeared to be dying. On the latter date *C. erythrocephala* began to emerge, and continued to do so for several days. On 18th February all flies were dead. On 19th February the contents were examined. The 12 surface puparia were opened, and all found to contain Chalcids in advanced or early pupal stage, and a few as larvæ. 72 dead *Calliphora* were found on the surface. The 93 puparia at a depth of 2 inches below surface were then turned out, and 72 empty puparia were found; the remainder, 21, were still intact, and were opened and examined. No signs of the Chalcids were found; the contents of these intact puparia were dead flies in various stages and atrophied nymphs.

Experiments Nos. 4 and 6 indicate that female *Nasonia*, even when confined in a small space with host puparia covered with soil loosely run in, are incapable of burrowing to any extent; and in this connection the following observation of Froggatt (7) is quoted:—"It is generally amongst the pupæ of *Pycnosoma rufifacies*, and to a lesser extent *P. varipes*, that this species of Chalcid wasp is found actually at work in the field. This is largely due to the habits of the larvæ of these two species, which do not crawl away from a carcase to pupate unless the remains have been much disturbed, but pupate either just under the edge of the remains or else affix themselves to the bones, wool, or other portions of the carcase, and thus they are more easily found than the other species, all of which generally crawl a considerable distance from the carcase, and scatter . . . . . . No definite reason can yet be assigned to the apparent distaste of the wasps for the pupæ of *Ophyra nigra* and *Pycnosoma varipes* in the laboratory. In the field the pupæ of the latter species are practically always found to be parasitized."

Further, *Nasonia* does not bear the appearance of a burrowing insect; its head, viewed dorsally, is wider than any other part of its body, whereas *Melittobia acasta* females (specimens of which Mr. Waterston kindly gave the writer) have a narrow head sloping backwards ventrally, and which is attached to a tapering thorax, narrowest at the back of the head, and certainly better adapted for burrowing in loose soil.

The last point investigated was an examination of all the puparia contained in two jars, of parasitized material obtained in the open. The contents of these jars, it should be explained, were the result of exposing meat on soil in a glass receptacle at the Society's Gardens, with the object of obtaining additional supplies of the Braconid. The collection of the contents of this receptacle was delayed until 14th August, and when sorting out the intact puparia from those from which blow-flies had emerged, the writer came across a few dead female *Nasonia* as well as dead female *A. manducator*. It was therefore assumed that a double infestation had taken place. At the time, an attempt was made to differentiate between the puparium of one or other of the parasites, but both were in too early a stage to disclose any difference when subjected to transmitted light. The material was consequently left unsorted, and emptied into two jars to await developments. *Nasonia* began to emerge on 31st August, and in order to give these an opportunity of escaping as they emerged, the linen covers of the jars were replaced by pieces of mosquito netting, through the mesh of which the females were able to escape. Both jars were placed inside a large glass cylinder. This was used as the cage, and in it were put dishes with supplies of blow-fly puparia for the Chalcids. On 3rd September *A. manducator* began to emerge; the Chalcids were still doing so. This continued until 29th September. This state of affairs necessitated constant handling of the jars to release the Braconids, so that the contents became disturbed; and although it was not observed at the time, it now transpires that some of the *Nasonia* females never left the jars, but proceeded to super-parasitize the Braconids in their puparia, and, further, some of those—the progenitors of the above—found dead in the receptacle when the material was collected probably did the same.

When all the puparia had been collected from the jars, they were sorted under three headings:—(A) Those from which *A. manducator* had emerged, (B) those from which *Nasonia* had emerged, and (C) those which were intact. Those from which blowflies had emerged had already been removed, and the number is not known. The numbers under the three headings were:—(A) 195, (B) 50, (C) 506. Those under (A) were put aside, those under (B) were dissected for evidence of successful super-parasitism, and those under (C) were dissected and classified under several headings as follows:—

(1) Atrophied fly-nymphs. (2) Dead fully-formed flies. (3) „ Braconid larvæ. (4) „ „ pupæ. (5) „ „ adults. (6) Active „ larvæ.	No signs of Chalcid attack.

(7) Unlined puparia, with active Chalcid larvæ. (These had, superficially, fly-remains.)
(8) Braconid lined puparia, with dead Chalcid larvæ. (The Braconids were in all stages, pupæ predominating.)
(9) Braconid lined puparia, with active Chalcid larvæ. (These Braconids were in all stages, pupæ predominating.)
(10) Braconid lined puparia, with some dead Chalcid imagines and larvæ. (These consisted, with one exception, of at least one male.)

The examination of these puparia showed that where super-parasitism had taken place, with the exception of a very few instances—the numbers were not noted,—the puparium concerned was a very small one, about the size of *M. domestica*, and consequently, in the case of a blow-fly, a puparium with an exceptionally thin integument. And, further, that the attack of the Chalcid larvæ had taken place in the abdomen of the Braconid where this was an advanced pupa, the only part where soft integument exists, due to the distention of the abdomen consequent upon the presence of the meconium (text-fig. 7): it, therefore, seems conclusive that a *Nasonia* female is able to distinguish between a hard surface and one yielding to pressure, by means of the apex of her ovipositor. It is worthy to note that *Nasonia* appeared to be most effective when the Braconid was a pupa—that is to say, in the identical stage of development to that of its normal dipterous hosts.

The numbers under the heading (B) were (1) 33 puparia, with Chalcid exit-holes and unlined by the Braconid, presumed primary parasitism; and (2) 17 with Chalcid exit-holes and definite super-parasitism. In each instance the puparium had been lined by the Braconid. A feature of these 17 puparia was the position of the exit-hole: in 3 it was made in or about the middle of the puparium, in 6 at the apex of the anterior end, and in 8 at the apex of the posterior end. In only one instance had two efforts been made to escape. This occurred in one of the 3; a small somewhat elongated aperture had been made in a position diametrically opposed to the exit-hole used. A point of great interest in the writer's opinion, with regard to the position of the exit-hole in the above, is that in 6 the Chalcid got out at a point where the Braconid lining is weakest—that is, where it is run over the protruding chitinized mouth-parts of the late blow-fly larva; and in 8 the Chalcid got out at the next weakest point—that is, where the lining is run over the blow-fly larva's posterior spiracles.

The figures under heading (C) are not given in detail; those for sub-headings (1) to (7) do not materially bear on the subject of the investigation, but for 1 and 2 they were very high, and mainly due, in the writer's opinion, to the unshaded position of the glass receptacle and consequent evaporation of any moisture in the soil, which was aided by the delay in removing the contents. Whereas the figures for (8), (9), and (10) do bear on the subject; they are as follows :—

(8)	69	Braconid	lined	puparia,	with dead Chalcid larvæ.
(9)	15	,,	,,	,,	with active* Chalcid larvæ.
(10)	23	,,	,,	,,	with some dead Chalcid imagines and larvæ.

The outstanding point in this instance of super-parasitism is that most of it did not take place in the open, so far as (B) (2) and (C) (8), (9), and (10) are concerned ; it actually took place in the jars in the laboratory, and in proof of this postulation, the puparia could not have been lined by the full-grown larvæ by 14th August, or the adults would have emerged before the 3rd September, and further super-parasitized Braconids would have been in the larval stage if it had taken place in the open, whereas the contrary was the case.

To conclude : it has been shown in experiments Nos. 1 and 2 that under certain circumstances *Nasonia* is capable of super-parasitizing a Braconid larva within its lined puparium ; and in experiments Nos. 3 and 4 that blow-fly larvæ attacked by the Braconid are stimulated to escape and pupate, and that the majority of them—76 per cent.—reached 2 inches and more below the surface of the soil; and in experiment No. 5 *Nasonia* was unable to burrow to the depths reached by the majority, 93 per cent. of the unparasitized blow-fly larvæ; and in experiment No. 7 definitely failed to reach any one of 93 puparia 2 inches under the surface, which is consistent with their behaviour in the field.

And, it must be pointed out, that in each instance of super-parasitism reported by Graham-Smith (1 and 4) it appears that the puparia—subsequently ascertained to contain the Braconid primarily—were collected and moved from a "sun" tin to a "shade" tin or vice versa ; and in the case reported by the writer, emerging *Nasonia* remained in the jars containing Braconid parasitized puparia, which were no doubt dislodged by the frequent handling of the jars when releasing Braconids. So that in none of these instances were the conditions even approaching natural.

It therefore appears that if super-parasitism takes place in nature, it is not very frequent and then only accidental, and that where it does take place in a puparium of a full-grown blow-fly larva which has been reinforced by a normal Braconid lining, it is doubtful whether the small, short, and rectangular mandibles (text-fig. 20, *a*, *b*, *c*) of *Nasonia* will enable it to escape ; whilst in the case of the female *Melittobia acasta*, this is aided by the distinctly acute mandible (text-fig. 20, *d*) with its one large outer tooth.

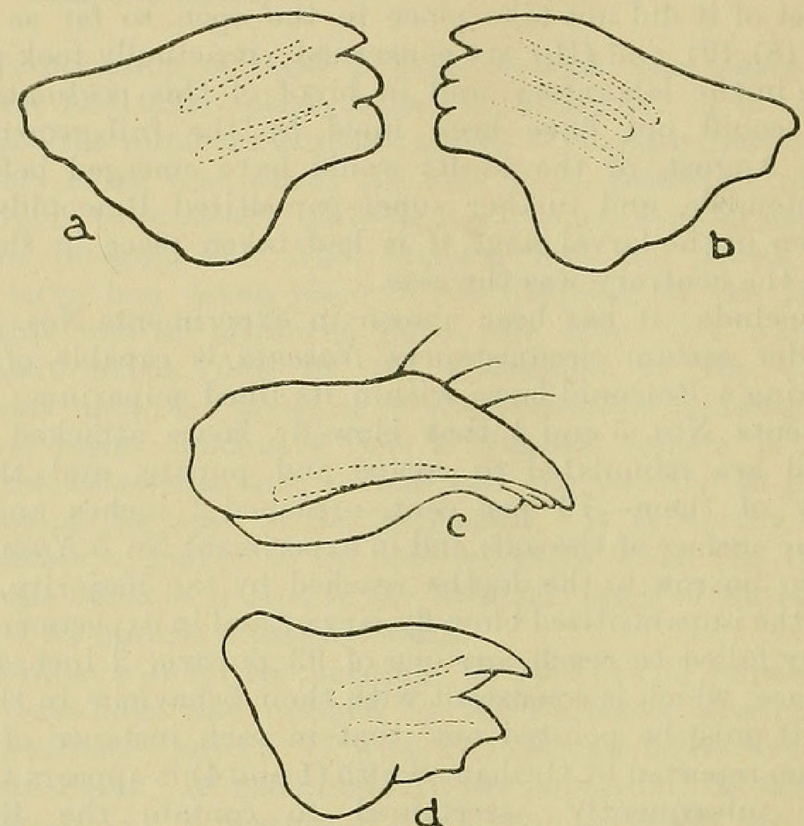
* A few of these were found singly in the puparia, and are the largest *Nasonia* larvæ seen by the writer.

Refrigerating Experiment.

In order to ascertain if the parasites would be able to undergo six weeks—the length of sea voyage to Melbourne—in the refrigerator of a ship, a few of the parasites etc. were given a test.

Prof. Blackman was approached, and kindly gave the writer permission to use a small cupboard in a refrigerating machine in his department.

Text-figure 20.



Mandibles of *Nasonia brevicornis* male: (a) left; (b) right; (c) right, in profile, outer tooth on top. × 160. Original. (d) Mandible of female *Melittobia acasta*; only females of this species emerge. After Waterston. (d) is not proportionate with (a), (b), and (c).

As other experiments were going on at the time, it was necessary to use a burying medium in which no insect life existed, and clean sand was therefore used.

A large glass jar was used as the receptacle, and sand to a depth of 3 inches was run into it as a foundation. A few puparia containing *A. manducator*, *N. brevicornis*, *Calliphora erythrocephala*, and a few larvæ of the latter species were each buried in sand in separate glass tubes left open; these were then pushed into the 3-inch foundation of sand to keep them vertical.

The jar and contents were put into the chamber on 28th November. The constant temperature was reputed to be 2° C. On 15th January—6 weeks and 6 days later—the jar was removed to the laboratory and the contents examined.

One Braconid, a male, had emerged, on what date is unknown;

another Braconid puparium was found with a dead adult half-way out of it, the remainder were intact; one of these was opened and found to contain a living Braconid larva. The Chalcid-infested puparia were all intact; one was opened and contained living larvæ. The *Calliphora* puparia were intact, and as the outline of advanced fly-pupa could be seen in each, they were left so; the *Calliphora* larvæ were all dead. The contents, except the latter, were returned to the jar in their respective tubes, and it was placed about 3 feet from a Bunsen burner. On 16th January one female *Calliphora* emerged, and in the next four days all had emerged. The Chalcids commenced emerging on 30th January, and continued to do so for some days. The balance of the Braconids began to emerge on 12th February.

To summarize: both parasites were able to stand the test when put into the refrigerator in their respective full-grown larval stage—that is, the customary hibernating condition.

Conclusions upon the Economic Importance of *Alysia manducator* Panz. and *Nasonia brevicornis* Ashm.

It is obvious that, in discussing this subject, the writer is only able to treat of it from a theoretical standpoint. But in doing so he is influenced by a desire to place on record some opinions which have been formed during the course of this work, and some of which gain considerable support from the observations and writings of those who have dealt with these parasites before him.

It would appear that both parasites working in conjunction would form an excellent combination, the one attacking the larval stage, the other the pupal. And between them—it may be assumed—a beneficial influence would be exerted in the control of the Blow-fly.

The occasional and accidental super-parasitism on the part of *N. brevicornis* is but an assurance of the maintenance of the "Wave Law"*. It is actually a twofold assurance, because although *Nasonia* may kill the Braconid, it may itself die in the course of development or become entrapped—upon reaching the imaginal stage—within the silk-lined puparium of the blow-fly larva.

Individually, *Alysia manducator* is considerably superior to *Nasonia brevicornis* as an enemy of the Blow-fly. The former is vastly superior in flight—in both sexes—a most important factor where artificial distribution is concerned; and it is also so from the greater number of hosts it can injure and eliminate in the course of breeding; the ratio is approximately 40 : 1. Its egg capacity is nearly four times greater than the Chalcid, and equal to and in some cases greater than that of several species of blow-flies. In length of imaginal life it is about equal to the Chalcid; the period of development from egg to imago is longer, and in individuals of the same parent a considerable variation takes

* Pointed out to the writer by Prof. Lefroy.

place, but where artificially propagated, this would be a great advantage in ensuring a continual overlapping of generations, and so obtain the benefit of its activity throughout its season.

On the other hand, the females only of *N. brevicornis* are capable of flight, and which—so far as has been observed—consists of long jumps of 6 feet or so at a time, its commonest method of progression being to crawl. The males are semi-apterous and quite incapable of flight, and although they are of a domesticated "temperament," remaining in the vicinity whence they emerge, they are very liable to overlook their natural functions whilst endeavouring to obtain mastery over rivals, and consequently the unfertilized females would, parthenogenetically, produce a colony of males, possibly isolated and incapable of finding mates or doing any damage to blow-flies. For these reasons, it seems obvious that *Nasonia* cannot prove to be a decisive factor in blow-fly control unless they are constantly distributed in large numbers over small areas. Whereas, if they were artificially propagated and distributed on these constant refuse-heaps found in and around populous areas, and near dung-heaps in town and country stables—whence to be farther, unwittingly, distributed,—*Nasonia* would, on account of its semi-social and "domesticated" habits, prove a most important factor in the control of "The Common House-or Typhoid-fly and its allies," which are constantly breeding in such stercoraceous places and where host puparia would be within crawling distance of the Chalcid.

Summary.

(1) The breeding operations and accumulation of supplies of *Alysia manducator* Panz. and *Nasonia brevicornis* Ashm. commenced in July and ceased in December 1919.

(2) *Alysia manducator* oviposits in the larvæ of several carrion-feeding Diptera. Only one parasite emerges from each host puparia. Over-parasitism kills the larva. The mean average of the life-cycle is 52 days, and as short as 25. Both sexes are capable of sustained flight, and lived over a month in captivity. Average percentage of parasitism over three years was 43 per cent., observed by Graham-Smith (4). Average contents of ovaries 366 eggs for 12 females.

(3) *Nasonia brevicornis* oviposits in the puparia of several species of stercoral and carrion-feeding Dipterous larvæ. From one to 62 individuals have been found in single puparia parasitized in captivity. The length of the life-cycle ranges from 11 to $22\frac{1}{2}$ days in different countries. Only the female can fly, and then only very short distances, and can live, whilst ovipositing, from 4 to 6 weeks, but for a considerably less period without host puparia. The male remains near the vicinity of emergence, where its life is spent in fighting and mating. Average progeny in the case of five females—observed by Girault & Saunders and McCarthy—was 113 per female, and affecting on the average only 16·4 hosts,

(4) *Nasonia* can act as an accidental secondary parasite upon *A. manducator* if and when puparia containing the latter are within its limited reach.

(5) Both parasites in their hibernating stage—*i. e.*, full-grown larvæ—can successfully withstand over 6 weeks at 2° C.

(6) *Alysia manducator* appears to be a more important parasite as a natural control for the Blow-fly than *Nasonia brevicornis*, which appears to be more effective as a natural control of Diptera which constantly breed in permanent refuse- and garbage-heaps, and where hosts would be within crawling distance, such as primarily the Common House-fly, *Musca domestica*.

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To Miss Cheesman, Curator of the Insect House of the Society's Gardens, Regent's Park, the writer is indebted for the original lots of material from which the parasites emerged, and for her assistance in procuring additional supplies of both blowflies and parasites.

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