THE MALE AND THE FEMALE GENITALIA AND THE BIOLOGY OF
EUCHALCIDIA CARYOBORI HANNA (HYMENOPTERA,
CHALCIDINAE)

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WITH THIRTY-EIGHT TEXT-FIGURES.

CONTENTS.

INTRODUCTION .......................... 107
Female abdomen .......................... 108
Male abdomen .......................... 108
Female armature .......................... 111
Sting muscles .......................... 113
Sting glands .......................... 116
Male genitalia .......................... 117
LIFE-HISTORY STUDIES .......................... 118
Copulation .......................... 119
Oviposition .......................... 119
Superparasitism .......................... 120
The egg and the period of incubation .......................... 121
Number of eggs laid and the influence of age on egg laying .......................... 121
Factors influencing the choice of prey .......................... 121
STAGES OF THE LARVA .......................... 123
EXTERNAL MORPHOLOGY OF THE LARVA .......................... 126
INTERNAL MORPHOLOGY OF THE LARVA .......................... 126
THE PUPA .......................... 132
LIFE-HISTORY .......................... 134
Influence of food on the total period of life-history .......................... 134
Emergence of the imago .......................... 135
Duration of the life of the imago .......................... 135
Parthenogenesis .......................... 135
ACKNOWLEDGMENTS .......................... 135
REFERENCES .......................... 135

INTRODUCTION.

In October 1931 Mr. C. Potter and Mr. A. Smith of the Department of Entomology, Imperial College of Science and Technology, obtained samples of senna (Cassia sp.) pods from London docks which were infested by the Bruchid, Caryoborus pallidus Oliv. Amongst the Bruchids, I found also a Hymenopterous parasite which lays its eggs in the cocoons of the early pupa and late larval stages of the beetle. The larva, after hatching, lives externally on the host inside the cocoons. Dr. H. Scott of the British Museum and Dr. Ferrière of the Imperial Institute of Entomology were able to place this parasite in the genus Euchalcidia, but could not identify it specifically. They very kindly sent specimens to Dr. L. Masi, who wrote that it was not a species of Euchalcidia with which he is acquainted but it might be close to E. nebulosa Fonsc. Dr. Scott then wrote Mons. Berland of the Paris Museum, who kindly sent a male and a

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female of *E. nebulosa*. Fonsscolombe's collection seems to be lost, and these specimens were identified by Grillant of Lyons and were found in the de Gaulle collection. The female *E. nebulosa* is definitely different from the new species. The male of *nebulosa* does not differ, but there is no evidence that it really corresponds to the female. The best course appeared to be to treat the Bruchid parasite as a new species (see Hanna, 1934) until more is known about *E. nebulosa*.

When studying the oviposition, I found that very little is known about the detailed structure of the different parts of the ovipositor and the muscles that govern the stylets and their sheath. I therefore think it desirable to give a short description of them.

**The Abdomen.**

The abdomen is pear-shaped, its apex being narrower than the base which is joined to the thorax by a stalk. In the female it measures about 1·6 mm. in length and 0·1 mm. across.

(I) The female abdomen consists of nine segments with the tergites very dark metallic black. The tergites are well developed and extend ventrally so as to cover most of the sternites which are not so dark and form a sort of ventral keel.

The first segment is fused with the thorax to form the propodeum. The second is the petiole, which is very short and slender but heavily chitinised. When looked at laterally, it is triangular in outline, one side being ventral (fig. 16). In a front view it is V-shaped, and between its two arms there is a triangular foramen through which the viscera pass into the abdomen (fig. 16, r). On the upper inner sides of the arms there are two selerites which proceed upwards and inwards, meeting in the median line (fig. 16, ctr) to form an attachment for the muscles which move the abdomen. The third segment (fig. 4, 3 r and 3 s) has a very large semicircular tergite which does not extend ventrally like the other tergites. It rests in front on the internal skeleton of the petiole. Its sternite is very long and its articulation to the petiole can be seen in fig. 16. The fourth segment (fig. 4, 4 r & 4 s) is by far the largest segment of the abdomen as its tergite occupies nearly one-third of its area. Its dorsal surface is not so broad as its lateral surface, which extends forwards to reach the petiole. Its sternite is rather small and has a keel. The fifth and sixth segments (figs. 4, 5 & 6, 5 r, 5 s, 6 r & 6 s) are subequal in size. Their tergites consist of incomplete rings with their sides produced forwards. Their sternites are similar to that of the fourth segment. The seventh segment (figs. 4, 5 & 6, 7 r & 7 s) is different from the preceding ones, the tergite extends only a little distance laterally. It embraces the eighth tergite posteriorly. The sternite is longer and has a little notch in the posterior median line. Its detailed structure will be dealt with when considering the female reproductive organs. The eighth segment is incomplete owing to the apparent absence of its sternite. The tergite is semicircular and its sides are not produced laterally as in the other tergites. On its outer surface, near its anterior angles, there are two very small spiracles (fig. 4, sr) which are the only ones on the abdomen. The ninth tergite is the apparent terminal tergite. It is heavily chitinised and deeply concave on the dorsal side, where it has a median longitudinal suture dividing it into two. On each side of this suture there is a circular pit (the cercus) (fig. 4, c) which carries very long articulated hairs. The ninth tergite is keeled ventrally and extends forwards as the outer plate of the sting, which will be described later.

(II) The male abdomen is smaller than that of the female and can readily be distinguished by its rounded posterior end. There are ten tergites and ten
Figs. 1-3.—(1) Lateral view of the male abdomen. CR, cercus; T, tergite; S, sternite; PT, petiole; SP, spiracle. (2) Ventral view of the same. (3) Dorsal view of the same.

Sternites resembling in their shape those of the female except that the tergites of the sixth, seventh and eighth segments are broader dorsally and become narrow laterally. The seventh tergite is similar to the preceding ones and does
Figs. 4–6.—(4) Lateral view of the female abdomen. (5) Ventral view of the same. (6) Dorsal view of the same. CR, cercus; T, tergum; S, sternum; SP, spiracle; PT, petiole.
Genitalia and the Biology of Euchalcidia caryobori Hanna.

not embrace the eighth tergite as in the female; there is also an eighth sternite which is apparently absent in the female. The ninth tergite and sternite are heavily chitinised. This tergite also carries the cerci (fig. 1, cr) and its tip is flattened out to form an articulated anal papilla or the tenth tergite. There is a corresponding papilla ventrally which is the tenth sternite.

The Female Armature.

The ovipositor is a highly developed organ modified for stinging. It is situated in the abdomen and occupies a large space on the ventral side a little distance behind the petiole. It does not project from the apex of the abdomen. The ovipositor consists of the following parts:—

1. The *stylet-sheath* (fig. 8, serry) is formed of two very long and thin chitinous rods which fuse distally to form a groove with thicker edges. At the base it bifurcates into two diverging arms, each bent upwards in a semicircle. These are also grooved to hold and guide the stylettes (fig. 10). The tip of the fused sheaths has four projecting barbs diminishing gradually in size towards the tip (fig. 9). Near the base of the sheath, before it bifurcates, there is on each side a triangular heavily chitinised process (fig. 8, cs). Because of the function of this process, the name "rotatory process" may be suggested for it. Its structure is complex and very difficult to investigate owing to its minute size. A very powerful binocular microscope must be used as it is a thick solid process and a monocular microscope is insufficient. It is a triangular piece fused with the base of the stylet-sheath. The anterior lower part of the triangle is (figs. 13 & 15) produced forwards and then reflected upwards in a groove on the anterior upper surface to form the root of the stylet (figs. 13 & 15, rstry). There is also a process which is the continuation of the posterior part of the triangle (fig. 15, cm), fitting in between two chitinous arms in the stylet-sheath (fig. 15, sery).
This strengthens the sheath during rotation at a moment of great tension. These structures can only be clearly seen when looked at laterally.

Figs. 8–10.—(8) The ovipositor. CRB, chitinous rib; CS, chitinous rotatory process; FUL, fulcal plate; IP, inner plate; OP, outer plate; PAP, palp; PIV, pivoting process; STY, stylet; STYS, stylet-sheath; CR, cercus. (9) Teeth at the tip of the stylet-sheath. (10) The stylet in its groove in the stylet-sheath.

At the base of the stylet-sheath, just before it bifurcates into two, there are a number of transverse chitinous ribs which help to hold the two rods of the sheath together at a point of particular tension.
The stylets are also very long and slender rods held together posteriorly by a ridge on each ventral side of the sheath, which fits into a groove on the dorsal side of the stylets, so that the three pieces together form a central canal. The stylets are pointed at their free ends and are attached to the upper tip of the fulcrum at their base (fig. 8, sty).

(2) The inner plates of Imms, corresponding to the oblong plates of Snodgrass, are two long chitinous lamellae on each side of the sheath expanding in a vertical plane at their posterior end, where they carry two palp-like organs (fig. 8, pap) covered with long hairs. Anteriorly they expand dorsally in a vertical plane to form a thin chitinous plate. The outer edge is fused with the diverging arms of the stylet-sheath. The ventral anterior extremity is continuous with a triangular sclerite articulating to the centre of the rotatory process (fig. 8, rrv) and may be called the "pivot sclerite." It is twisted 180° to the plane of the inner plate (fig. 14) and has a transverse groove (fig. 14, crv) a little behind its tip where the sting is held and kept in position during stinging, relieving the muscles. A little behind this sclerite, there is a chitinous rib running posteriorly in the lamella of the inner plate for a considerable distance (fig. 8, crb). At the base of this rib the fulcral plate articulates with the inner plate. The function of the rib is to afford attachment to the muscles which work the sting and to give a firm attachment to the fulcral plate.

(3) The outer plates of Imms, the quadrate of Snodgrass, are situated on the outer side of the inner plate and are heavily chitinised (fig. 8, or). Each is articulated at its anterior end to the middle of the fulcral plate. It broadens and becomes more chitinised posteriorly where it is ornamented with punctures. Near its posterior end, it carries the circus (fig. 8, crb) which is a depression forming a sort of a cup with a membranous bottom beset with very long hairs. Like the inner plate, on its anterior surface, it has a chitinous rib bifurcating posteriorly (fig. 8, crb).

(4) The fulcral plates of Imms, triangular plates of Snodgrass, are triangular in shape (fig. 8, ful) each with its base heavily chitinised and articulated by means of a chitinous rod to the inner plate. Its apex is thinned out and is attached to the base of the stylet.

My conclusions agree with Alder's work on the structure of the ovipositor in Cynipidae, Kraepelin's on the ovipositor of the Hymenoptera, and Imms on that of a Chalcidoid.

Zander studied the embryology of these gonapophyses and, according to him, the inner plates represent the ninth sternum, the outer plate the ninth tergum and the fulcral plate the eighth sternum.

The Sting Muscles.

The muscles which govern the movement of the stylets and their sheath may be classified as indicated below. An entirely comparable description of these muscles has been given by Ferrière (1924) in another Chalcidoid.

(1) The muscles that swing the stylets and their sheath at right angles to the body just before stinging. Of these there is one on each side. They have a very long tendon inserted on the anterior end of the rotatory process (figs. 12 & 13, b) and spread partly over the lower surface of the chitinous rib running along the inner plate and partly over the latter itself.

(2) The sting is pulled back to its place after stinging by one muscle on each side. It also has a long tendon inserted on the posterior extremity of the rotatory process, spreading like a fan and finally attached to the arm of the stylet-sheath (figs. 12 & 13, a).
Figs. 11-12.—(11) Poison glands. ALG, alkaline gland; ACG, acid gland; RSV, reservoir. For other lettering see Fig. 8. (12) The muscles of the sting. B, swings the sting at right angles to the body; A, pulls the sting back into its place; C & D, protrude the stylets out; E, withdraws the stylets.
(3) The muscles that protrude the stylets are two in number.

(a) One spreads below the chitinous rib of the outer plate and is inserted by means of a long tendon to the lower chitinised edge of the fulcrum just where it articulates (fig. 12, D).

(b) The other muscle extends from above the chitinous rib of the outer plate to the posterior extremity of the lamellate expansion of the inner plate (fig. 12, C).

The contraction of these muscles pulls the outer plates forward. This movement is communicated to the fulcral plate and thus to the stylets attached to it, resulting in the protrusion. This movement is also helped by the contraction of the longitudinal muscles of the abdomen.

![Diagram of the base of the sting](image)

**Fig. 13.**—The base of the sting.

**RIB.** chitinous rib; **RL.** chitinous triangle; **RSTY.** root of the stylet; **STYS.** styletsheath; **B.** the muscle that swings the sting at right angle to the body; **A.** the muscle that pulls the sting back to its place.

(4) The muscles that withdraw the stylets to their place are one on each side. They stretch from the lower side of the rib on the outer plate to the upperside of the rib belonging to the inner plate (fig. 12, E). The contraction of these muscles pulls the outer plate backwards. This movement is communicated to the fulcral plate and thus the protruded stylets are again withdrawn. This is also helped by the relaxation of the muscles of the abdomen.

(5) The muscles that raise or lower the sting while the insect is actually stinging. When the insect is stinging, the sting moves up and down. This movement is brought about by two muscles.

(a) One is inserted on the chitinous fork of the vagina on the one hand and on the anterior edge of the seventh sternite on the other (fig. 7, μσ). The contraction of this muscle causes the sting to move downwards. James (1926)
found a similar muscle in *Harmolidae*, but he is of the opinion that it helps in the expulsion of eggs. This does not appear to be its function in *Euchalcisidae*.

(b) The other muscle stretches from the two arms of the seventh sternite and is inserted below on the outer plate behind the fulcral plate (fig. 7, Mus). The contraction of this muscle raises the sting.

(6) *The muscles that rotate the sting.* It was noticed that the sting, at the beginning of its insertion into the prey, rotates backwards and forwards. The same movement was also observed when the act of stinging is over and the insect starts to withdraw its sting from the prey. It is evident that this movement makes the penetration of the sting or its retraction much easier. There are no separate muscles to bring about this movement, but it seems that the alternate contraction of the two muscles (A & B, fig. 12) on each side causes this rotation.

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**Figs. 14-15.—(14) Pivoting process. GRV, groove; IP, inner plate; PIV, pivoting process. (15) The chitinous ring of the rotatory process. CRL, posterior process of the chitinous ring; RL, chitinous triangle; RSTY, root of the stylet; STYS, stylet-sheath.**

*The Sting Glands.*

There are two sets of glands associated with the sting.

(1) The *acid gland* (fig. 11, AC), of which there is only one, resembles in shape a Malpighian tubule, being narrow and much convoluted. It lies between the outer and the inner plate of each side. It opens directly into a very wide oval sac, the *reservoir* (fig. 11, Res), which lies in the median line with its long axis parallel to that of the body. The reservoir stretches from the base of the sting to half as far back as the inner and outer plates. Its diameter is greater anteriorly. Its walls are very thin and its contents solidify in alcohol to form a wax-like substance. The reservoir opens by a very short slender neck into the base of the ovipositor.

(2) The *alkaline gland* (fig. 11, ALG) is an unpaired tubular gland lying on the left side of the reservoir and extending a long way behind it. Its diameter is small and it opens separately into the base of the sting by means of a very long minute neck.
The Male Genitalia.

The male genitalia consists of the penis and its two sheaths. The penis (fig. 17, AD) is a cylindrical chitinous and membranous tube, tapering a little posteriorly. At its base it is strengthened on each side by a

Figs. 16-17.—(16) Lateral, front and ventral view of the petiole. CTR, chitinous arms. (17) Male genitalia. AD, penis; ADS, penis-sheath; CTR, chitinous rib; DEJ, ejaculatory duct; PAP, palpi and sensory hairs; PO, the opening of the penis; SET, claspers carrying setae.
chitinous rib thinning out at the apex. These support the penis and enable it to retract into or protrude from the sheath (fig. 17, cfr). In the centre of the penis there is a tube, the ductus ejaculatorius (fig. 17, deij), which opens at its extreme posterior end (fig. 17, po).

There are two penis-sheaths, one inside the other. The inner one is a chitinous cylinder incomplete dorsally. It envelopes the penis along its entire length (fig. 17, ad). At its apex it carries two toothed, chitinous plates. These are the claspers and there is one on each side ventral to the penis (fig. 17). Each is concave on the dorsal surface and carries about six long, sharp, curved teeth, strongly chitinised and borne on its posterior surface. On each side of the posterior outer extremity of the sheath there is a small process carrying setae (fig. 17, set). The muscles that move the penis in and out of its sheath are inserted obliquely between them.

The outer sheath is membranous and is attached at one extremity to the anterior edge of the inner sheath and the other to the dorsal and ventral anal papillae of the abdomen.

During copulation the penis is pushed out of the inner sheath, which is itself pushed out by the evagination of the outer sheath.

**Life-History Studies.**

I. *The Life-history of Caryoborus pallidus Oliv.*

Before studying the life-history of the Chalcid it was thought desirable to make a short survey of the life-history of the Bruchid. The eggs of *Caryoborus pallidus* Oliv. are dome-shaped and are laid on the surface of the senna pods. After six or seven days the egg hatches and the larva eats its way to the seed, inside which it penetrates. The larva consumes only one seed. On the average it is mature after 20 days and it then leaves the seed, after eating all its contents, and spins a cocoon, usually on the surface of the pod, where it now casts its skin and finally pupates. The whole life-cycle takes, on an average, 52 days. The minimum time taken by 43 individuals bred from egg to adult was 47 days, the maximum 57 days at 27° C.

To obtain enough Bruchid pupae to keep pace with the Chalcid, it was necessary to get a large quantity of pods as most of the seeds inside were already empty. Every effort to rear the Bruchid larvae on different seeds was unsuccessful as they died shortly after penetration. They can only live on senna seeds which were obtained with the insect material by sifting senna pods from boxes in the warehouse.

The Bruchid beetles were placed with fumigated senna in big glass jars. Moistened sultanas were added as food. The beetles laid their eggs on the pods which were changed every day. If the eggs are picked up carefully with a needle and each placed on a seed, the larva after hatching wanders about and does not penetrate the seed. If on the other hand the egg is stuck to the seed with gum, the newly hatched larva eats its way through, and although this method involved much time, yet it was the surest way of getting the pupae of the Bruchid free from mites (*Pediculoides ventricosus* Newport) which were a serious pest of the eggs of both the Bruchid and the Chalcid.

II. *Life-history of Euchalcidia caryobori* Hanna.

In the experiments carried out to investigate the life-history of the Chalcid, each pair was placed in a small glass tube with some of the Bruchid pupae with
a small piece of sultana stuck on the cork of the tube. The sultana usually dries quickly, and, to avoid this, all the tubes were placed in a large glass jar covered with an airtight stopper and a piece of wet blotting-paper to keep the atmosphere damp. Humidity in the jar was about 75–80%.

Copulation.

Copulation takes place soon after the adults emerge. At first the male and the female do not seem to take much notice of each other. Then the male starts to pursue the female, which tries to escape, and, after a great effort, manages to climb on her back, with the tip of his abdomen not reaching to the apex of the female’s and his legs holding her on both sides. His antennae are seen in constant motion on the surface of her head. Then he moves gradually backwards with his antennae still moving and at the same time lifting the front part of his body upwards to make an angle with the female. This angle increases and at the same time the female lowers the seventh sternite, and thus the male introduces his abdomen into it and the penis can already be seen far exerted. It is ultimately introduced into the copulatory pore at the base of the sting. Copulation lasts for a very short time from 5–20 seconds. Once the female is impregnated, she seems to reject all further attempts at copulation by pushing the male away with her hind legs. The eagerness of the male for copulation seems to increase in the sun or electric light.

Oviposition.

Although some individuals start to lay eggs on the day of their emergence, yet the average pre-oviposition period is three days and the maximum eight days. Before oviposition, the female wanders round the pupae in the glass tube feeling them one after the other with her antennae. Having found a suitable one, she feels with her antennae the place where she will insert her ovipositor. Finally she stands on the surface of the pupa and lowers her seventh sternite and also the stylets and their sheath, which is held in a groove on the posterior median part of the seventh sternite (fig. 7, grv). The stylets and the sheath penetrate the cocoon and the claws are seen to cling firmly to the surface. During this period the palps of the inner plate are seen to project backwards at intervals owing to the contraction of the abdomen, which indicates that the stylets are moving up and down in the host. The insect does not move, its head is reflected backwards and the antennae folded and the wings lie flat over the body. It takes the female from 4–15 minutes to deposit one egg.

The eggs are laid practically anywhere on the host, but usually on the ventral side of the pupae in the thoracic region. Only one egg is deposited at each act of stinging, very rarely two. In the latter case the two eggs are seen lying side by side stuck together.

The eggs are many times thicker than the diameter of the sting and it seems that they are subject to great pressure during their downward course. Attempts to see the egg actually in the sting by killing the female during oviposition were not successful.

After egg-laying the female usually licks the puncture hole. This habit has been noticed by various authors observing different species of Chalcids. The association of this act with oviposition seems to be due to one of the two following causes.

(1) Either the female is closing the puncture,
(2) Or it actually licks and feeds upon the liquid it draws from the hole.
To determine the possible significance of (2), 20 females were kept separately in glass tubes each with some cocoons of the host but with no food. It was found on the average that these females lived four days. Now if the female actually feeds on the punctures it might be expected that its life will be shorter when kept without either cocoons or food. For this purpose 20 females were starved and the average length of life was again four days. But it seems that the number taken was not enough to draw any certain conclusion. It should be noted that the females used in this experiment were all of the same age, eleven days old.

The attitude of the female in moving her head in only one direction suggests that it is licking. If she is producing threads to close the puncture, the head would move in all directions during interweaving. Moreover, it was noticed that the act of stinging does not necessarily correspond to an egg-laying. It seems, therefore, that the female makes a puncture for drawing the liquid from the host.

The female does not instinctively lay each egg in a separate pupa. As many as ten eggs were seen in one cocoon, and yet seldom does more than one adult emerge from a single cocoon. Occasionally, but very rarely, two emerge from one cocoon, but only when two eggs have been laid on opposite sides of the host and the larvae did not meet. To determine what usually happens when more than one egg is laid in the host, it was necessary to rear the eggs on pupae extracted from their cocoons. Under these conditions they were reared successfully when the block watch-glasses and their covers were boiled in water to disinfect them. The cocoons containing the eggs were then opened and laid in the watch-glass. The cover was greased with vaseline to keep the chamber airtight and reduce evaporation.

When the female lays an egg in a cocoon already containing another egg, the eggs may be either of nearly the same age or one older than the other. In any case, after hatching one larva attacks the other, with results which the following experiments demonstrate:—

| (1)  | Ten of the first-stage larvae each with a first-stage larva. |
| (2)  | Ten " " " " " " " second " |
| (3)  | Ten " " " " " " " third " |
| (4)  | Ten " " " " " " " fourth " |
| (5)  | Ten " " " " " " " fifth " |
| (6)  | Ten " second-stage larvae " " second " |
| (7)  | Ten " " " " " " " third " |
| (8)  | Ten " " " " " " " fourth " |
| (9)  | Ten " " " " " " " fifth " |
| (10) | Ten " third-stage larvae " " third " |
| (11) | Ten " " " " " " " fourth " |
| (12) | Ten " " " " " " " fifth " |
| (13) | Ten " fourth-stage larvae " " fourth " |
| (14) | Ten " " " " " " " fifth " |
| (15) | Ten " fifth-stage larvae " " fifth " |
| (16) | Ten " full-grown larvae " " full-grown larvae. |

The stages of the larvae were determined by the width of the head capsule. The results were as follows:—

(a) When the two larvae are of different ages, in 82%, the older larvae attacked and killed the smaller ones, in 9% smaller larvae attacked and killed the older ones, and in 9% both larvae were dead.
(b) When the two larvae are of the same age, in 35 cases out of 50 one attacked and killed the other, and in 15 cases both died.

It will be seen that the older larva attacks the younger one, inflicting a wound with the mandibles and sucking its body fluid. The opposite may also happen but more rarely, and in this case it seems probable that the attacking takes place when the older larva is quiescent before moulting for the succeeding stage. This is confirmed by the experiments in which the fifth-stage larva was accompanied by one in an earlier stage. In almost all cases the fifth-stage larva survived, probably because it has no further moults to pass through. After pupation there may be a renewal of attack. Sometimes both larvae are found dead, and this happens especially when they are of the same stage. If on the other hand one egg hatches before the other, the newly hatched larva sucks the egg if it happens to come across it, but as they are very small, the chance of attacking before the other hatches is remote.

When two fully grown larvae are placed together neither of them attacks the other as their feeding period is nearly over and there is then no competition.

The survival of one larva only is due to its being of such a comparatively large size, that the host provides only just enough food for one larva to reach maturity.

The Egg and the Period of Incubation.

The egg is sausage-shaped with one end a little broader than the other. Its colour is white and opaque owing to the yolk granules. The chorion is smooth, colourless, slimy and leathery. Its length is about 0.565 mm. and width 0.132 mm. (fig. 18).

The period of incubation at a constant temperature of 27° C. is a little less than two days. A short time before hatching, the larva can be seen through the transparent chorion to be wriggling inside. A colourless liquid appears between the chorion and the body of the larva. It moves from one pole to the other whenever the larva moves. This liquid seems to help the larva to draw its body from the integuments during eclosion. There is no special organ for eclosion, but the mandibles are used in making a slit in the chorion through which the larva escapes.

The Number of Eggs laid and the Influence of Age on Egg laying.

The average number of eggs of 55 females was 102 the maximum being 220. The usual number of eggs laid per day was 6. Sometimes none are laid, and this is due probably to the host being unsuitable for egg laying, as the number of eggs is seen to be nearly doubled the next day. Some time before the female dies, she lays an egg or two occasionally then finally stops laying altogether until she dies.

The Factors Influencing the Choice of Prey.

The behaviour of the parasite towards the host suggests that the latter possesses certain attractive qualities which exist either in the cocoon, in the pupa, or in both.

I. Testing the qualities of the enveloping membrane as an attractant.

(a) The colour of the cocoon does not seem to be of great importance as the female still lays its eggs through artificially coloured cocoons which were painted green, blue, white, black, yellow, red and light brown. Practically every colour was attacked, and although the number of eggs laid in the natural cocoons was
more than those laid in the coloured ones, yet it seems that this is because they can penetrate them more easily than the ones covered with hard paint.

(b) The texture and the form of the cocoon. Experiments showed that the texture and form of the cocoon do not possess great attractive qualities. The female was still capable of laying eggs on the pupae if the latter are taken out of the cocoons and wrapped in cigarette paper, and by doing so the normal oval shape of the cocoon is not attained and yet this change of form does not seem to prevent the parasite from laying eggs.
They refused to lay eggs in specimens wrapped in silver paper, but it seems that the sting could not penetrate it.

In other experiments the cocoons were given:—

1. Empty.
2. Filled with blotting-paper soaked in the body fluid of the host.
3. Filled with coagulated egg albumen.

Not a single egg was laid, nor were they seen to sting these cocoons. The attractive qualities must therefore be sought in the pupa itself.

II. The attractive qualities of the pupa.

Eggs were deposited in cocoons containing dead larvae or pupae, but not so freely as on live pupae. For laying they prefer live pupae to live larvae and dead pupae to dead larvae. The percentage of mortality of the newly hatched larvae of the parasite placed on the larva of the host is very great, but this percentage is much reduced if the later stages of the parasitic larvae are placed on the larva of the host.

So it seems that the pupa when it is alive and to a less extent when dead exerts an attraction on the parasite. The exact nature of this attractant is unknown. Under a little pressure of egg-laying, the parasite can be made to lay eggs on bare pupae, dead or alive, but not on live larvae, although it can lay on them if confined in a cocoon. The reason seems to be that the pupa has a limited movement which enables the parasite to sting it easily, while the rapid movement of the larva will move the sting out of its course when in action.

The factors which attract the parasite could have been better studied if different species of Bruchid pupae that can be parasitised had been available. By accurate comparison of the exact qualities of the hosts on which attack depends, we can form an idea about the relation between the host and the parasite.

The Stages of the Larva.

Since the skin of the larva is colourless and the mandibles of microscopic size, it was impossible to see them unless they adhered to the surface of the larva. The number of moultts was partly worked out by the actual observation of each moult and partly by measuring the width of the head capsule by an accurate scale having 656 divisions to one millimetre, and as the width of the head remains unaltered during each stadium, owing to the presence of the endoskeleton, it was possible to determine the number of ecdysis.

The First-stage Larva.

When the larva hatches its average width is 0.105 mm. and an average length of 0.23 mm. The width of the head is 0.109 mm. It is oblong and tapers a little posteriorly. Its colour is very pale yellow and transparent owing to the fat-body being little developed. The body is divisible into a clearly marked head (fig. 19, HED) and thirteen segments. The head is much broader than the body, relatively big, and nearly hemispherical in shape, tapering a little anteriorly. It carries on its dorso-lateral and anterior surface a pair of antennae (figs. 20 & 21, ANT) which under the microscope look like a pair of domes with a small bristle in the centre. Below the antennae there is a pair of minute hairs. A similar pair is also found on either side behind the mouth on the anterior ventral surface of the head. The mandibles are similar to those of the fully grown larva, only much more curved (fig. 22).

On each side of each of the body segments there is one hair carried on a
dome-like protuberance which under the microscope resembles that of the antennae.

The alimentary canal can hardly be seen owing to its transparency, but if the larva is fed on a mixture of the crushed pupa and solid borax carmine its outlines can be determined. The pharynx is a very narrow tube leading to the oesophagus which enlarges behind it to give rise to the stomach, which is an elongate sac ending blindly in the eleventh segment (fig. 19, sr). The salivary duct of each side joins to form a common duct (fig. 19, scd) directly after they enter the head. This duct shows taenidia along its walls and opens on the floor of the mouth.

The respiratory system consists of two lateral tracheal trunks (fig. 19, rt) one on each side, joined by a transverse commissure anteriorly in the second segment and posteriorly in the eleventh. In front, the anterior commissure gives off two branches directed forwards and the posterior gives off a pair directed backwards. Four pairs of spiracles are present on the mesothorax and the first three abdominal segments respectively. On the outer side of each lateral trunk in the metathorax and abdominal segments four, six and seven, there are outgrowths which are the developing spiracular branches.

This instar lasts (at 27° C) from two to three days, and at its conclusion the larva is about 0·45 mm. long and it becomes slightly brownish owing to the food contained in it. In other essential details, it is similar to the fully grown larva.

*The Second-stage Larva.*

The larva is darker in colour and more opaque than the preceding stage. The width of the head is 0·16 mm. and the length 0·83 mm. The spiracular branches which were budding in the metathorax, fourth, fifth, sixth and seventh abdominal segments are more complete and open into spiracles on the corresponding segments, but the calibre of these branches is much smaller than those formed in the first stage. The duration of this instar (at 27° C.) is only one day.

*The Third-stage Larva.*

The third-stage larva is 1·8 mm. in length, the width of the head is 0·229 mm. The duration of this stage is one day at the above temperature.

*The Fourth-stage Larva.*

The width of the head capsule is about 0·29 mm. and the length of the body 1·8 mm. The duration of this stage is one to two days.

*The Fifth-stage Larva.*

The fifth stage is the last stage. The width of the head capsule is 0·42 mm. and its length about 4·2 mm. The duration of this stage is from 3–4 days at 27° C.

*Coloration.*

The fully grown larva is bright brown at first and becomes white later owing to the formation of the fat body underneath the skin. The stomach can be seen occupying almost the whole interior as a large brownish bag with a greenish tint due to its contents. The last segments are whitish because the stomach does not reach so far back.
Figs. 23–26.—(23) Front view of the head. ANT, antenna; 1THS, first thoracic segment; HED, head. (24) The endoskeleton of the head. (Dorsal branch)—LA, labium; LF, lower fork; LM, lip muscle; LRM, labrum; MAND, mandible; MT, main trunk; MX, maxilla; XM, maxillary muscles; UF, upper fork. (25) Last-stage larva. HED, head; SP, spiracle. (26) Mandibles of the last stage and the muscles that move them.
The External Morphology.

The larva is fusiform (fig. 25), its greatest thickness being in the middle, and tapering gradually towards both extremities. It is divisible into the head and the body segments.

The head is much narrower than the first segment of the abdomen and is circular in outline with a sort of chin below (fig. 23). The antennae are similar to those of the first-stage larva, only bigger. No legs or leg-like processes are present. The integument of the head, though not heavily chitinised, is much thicker than that of the body.

The endoskeleton of the head consists of two heavily chitinised trunks which proceed from its outer surface below the horizontal axis and bend upwards and inwards (fig. 24, \textit{mt}). Near the centre of the head, each gives rise to two forks, a lower one proceeding in nearly a horizontal direction to meet and fuse with the corresponding forks of the other side (fig. 24, \textit{lf}). The upper fork is bent upwards and inwards to meet that of the other side (fig. 24, \textit{uf}), so it forms together with the lower fork a semicircle. The two trunks and their forks run a little below the integument.

The mouth-parts. Owing to the parasitic habit of the larva, the mouth-parts have been much modified.

The mandibles lie horizontally in the mouth in the form of half a cone, heavily chitinised, with their apex drawn into a fine point (fig. 26). The base of the cone is grooved and occupied by the muscles that move the mandibles. The apex of each mandible is directed inwards so as to touch the other in the median line. The base is directed outwards and articulated to a process on the upper fork (fig. 24, \textit{mand}). On the lower fork there is a socket which receives a process from the base of the mandible. Two muscles which move the mandibles are inserted on the head capsule in a fan-like manner.

(1) The adductor muscle is inserted by a long tendon to the base of the groove (fig. 26).

(2) The abductor muscle is inserted near the apex of the cone, and owing to the position of the fulcrum it pulls the mandible outwards.

The upper lip is a membrane stretching between the upper forks and partially covering the mandibles (fig. 24, \textit{lr}m). It has vertical muscles which are inserted on the head capsule and move the lip in a vertical plane (fig. 24, \textit{lm}). Its free edge is covered by fine sensory hairs.

The maxillae and the labium are also membranous and fused together basally. They extend transversely just below the mandibles. The maxillae (fig. 24, \textit{mx}) are triangular in shape. On both sides they embrace the labium which is simply a semicircular flap. In well-stained specimens the oblique muscles which move the maxillae (fig. 24, \textit{xm}) and the vertical muscles which move the labium can be seen (fig. 24, \textit{la}). Some sensory hairs are located on their edges.

The body segments. The body consists of 13 segments without any differentiation between the thorax and the abdomen. No legs are present. The nine spiracles lie each in a slight depression on the sides on the anterior border of the corresponding segments (fig. 25, \textit{sp}).

The Internal Morphology.

The Digestive System.

The digestive system is very simple and consists of a wide conical mouth on the antero-ventral surface of the head. This leads to the \textit{pharynx} (fig. 27), which is a wide short tube. If a larva of the first stage is placed on a slide with

A drop of water and a cover-slip on top, the muscles that move the pharynx can be seen in action, as the larva keeps alive for a considerable time. Three sets of these muscles can be recognised.
(1) A series of dorsal muscles stretching between the dorsal wall of the pharynx and the dorsal wall of the head capsule.

(2) The second set of muscles extend from the ventral surface of the pharynx to the ventral surface of the head.

(3) The third set stretches from the lateral side of the pharynx to each side of the head capsule.

It seems that these three sets of muscles widen the diameter of the pharynx considerably, which is then narrowed up again by means of circular muscles causing strong peristaltic movement. In feeding, the larva is seen to take in semi-liquid food by means of the mouth-parts and this travels in globules through the pharynx and oesophagus to the stomach.

The oesophagus is very short and opens into a very wide sac (fig. 27, oes), the stomach has a constant peristaltic movement and entirely fills the whole body-cavity. It stretches from the metathorax anteriorly to the eighth abdominal segment posteriorly where it is connected to the hind intestine, though there is no opening in the stomach to connect them together (fig. 27, st). A thin membrane separates their contents and thus the larva does not pass excreta until it stops feeding. When, however, full growth is attained the larva stops feeding, the extremity of the stomach becomes perforated and the excreta passes out in a series of pellets. In all cases where the larvae were reared exposed on the host, they left the host and lay without movement for a few hours, after which they passed all the excreta.

In the hind intestine, three regions can be recognised: an anterior narrow region, a wider one and a narrow hind region (fig. 27, hi). The salivary glands are two in number and attain an enormous size. They lie on both sides of the stomach, forming a loop in almost every segment during their course (fig. 28, sc). The two short canals of each gland unite into a common duct just after they enter the head. This common duct has taenidia on its walls and runs under the oesophagus and pharynx to open on the floor of the mouth.

The Malpighian tubes are three in number and open in the anterior part of the hind intestine. Two of them are very long (fig. 27, m.t.) and extend forwards on both sides under the salivary glands for nearly half the length of the stomach. The third one is much shorter and is directed backwards and lies below the stomach. They are constricted at intervals along their course.

The Respiratory System.

The respiratory system of the full-grown larva consists of two longitudinal trunks on both sides connected anteriorly in the prothorax and posteriorly in the ninth abdominal segment by transverse commissures, each in its turn gives two branches directed to the head and the tenth abdominal segment respectively (fig. 29, antb & pstb). Each lateral trunk is connected by spiracular branches to the nine spiracles (fig. 29, sp). Opposite the root of each spiracular branch there are a few other very fine branches directed ventrally. Other fine branches are given off from the spiracular branch and are directed dorsally. The atrium of the spiracle is funnel-shaped and opens into the trachea, which is not uniform in calibre as it has four dilations along its course (fig. 28).

The Nervous System.

The nervous system consists of the cerebral ganglion and the ventral nerve cord.

The cerebral ganglion is in the form of two compressed spheres lying one
beside the other (fig. 31) in the anterior part of the prothorax above the oesophagus. Parker also found it in a corresponding position in different Chalcids, and Miall and Hammond in a Chironomous larva. In the full-grown larva, the imaginal head is formed in relation to the cerebral ganglion; thus each antenna

![Diagram](image)

**Figs. 31–32.**—(31) The brain. (32) BRN, brain; RANT, rudiment of antenna; REYE, rudiment of the compound eye. (33) The nerve cord. SUBO, sub-oesophageal ganglion; 1TH–3TH, thoracic ganglia; 1AB–7AB, abdominal ganglia.

(fig. 32, RANT) is seen lying folded like an elbow on the front surface of the brain and the compound eyes arise on its upper surface (fig. 32, REYE).

The sub-oesophageal ganglion is oval (fig. 33, SUBO) and connected to the brain by two short connectives.

The first two thoracic ganglia are larger than the third, which is nearly equal in size to the abdominal ganglia (fig. 33, 1, 2 & 3 TH).

The abdominal ganglia are seven in number. They are also oval, but of
nearly uniform size with the exception of the last one which is a little larger. Every ganglion is connected to the one preceding by two longitudinal commissures which are very short in the thorax and longer in the abdomen, with the exception of the last which is very short.

Each ganglion gives off two principal nerves one on each side, the last abdominal gives rise to three pairs of conspicuous nerves.

*The Circulatory System.*

The dorsal vessel lies directly below the integument on the mid dorsal line and is flanked on each side by a fat body (fig. 34, FTB).
Genitalia and the Biology of Euchalcidia caryobori Hanna.

The heart consists of three chambers located in the third to the eighth abdominal segments. The first chamber (fig. 34, 1c) is tubular and oblong in outline; the second is nearly twice as long as the first (fig. 34, 2c); the third is almost as long as the first chamber.

The aorta runs dorsally and narrows till it enters the head. There is a pair of ostia between each chamber.

The best way to dissect the heart is to leave the larva for twelve hours in 70% alcohol to harden it and to prevent the shrinking of the integument when the larva is opened.

The Muscular System.

If a full-grown larva is cut longitudinally in a dorso-ventral plane, the alimentary canal and fat body is removed, and the remainder stained in borax carmine, two series of muscles, one dorsal and one ventral can be distinguished (fig. 35, ds & vs). The spiracles lie between them (fig. 35, sr). Each series consists of five longitudinal muscles. In the anterior and posterior part of the body the muscles approach one another and are reduced in number; thus in the prothorax there are four bands in each of the dorsal and ventral series, and in the mesothorax, there are only four bands in the dorsal series. In the eighth abdominal segment there are only four bands in the ventral series and two in the ninth. In the tenth segment there is only one band in each of the dorsal and ventral series. The upper band of the ventral series extends to the head, where

---

**Fig. 35.—The muscles of the larva cut vertically into two halves (the right half is shown).**

AOP, additional oblique muscles; DS, dorsal set; HM, muscle proceeding to the head; OB, oblique muscle; ODS, additional muscles; POP, branching of the posterior oblique muscles; SP, spiracle; VS, ventral set.
it is attached to the endoskeleton (fig. 35, HM). The upper series belonging to the same segment has four additional bands which are attached anteriorly to the head (fig. 35, ODS).

In addition, there are also some oblique muscles. Each one starts from the lower band of the dorsal series and runs forwards and downwards along one segment until it reaches the upper band of the ventral series and then its course differs in different segments thus: the first oblique muscle crosses two segments, the second, third, fourth and fifth bifurcate (fig. 35, OB), the anterior fork crosses two additional segments and the posterior fork crosses one segment only. The sixth, seventh, eighth, ninth and tenth oblique muscles (fig. 35, POP) also bifurcate, but each furca traverses only one segment. In the eighth abdominal segment there is only one oblique muscle which crosses the four bands of the ventral series and ends at the termination of the lower band of the same series belonging to the seventh abdominal segment.

![Fig. 36.—Ventral view of the male pupa.](image)

In the three thoracic segments, there is also an oblique muscle which is perpendicular to the other oblique muscles (fig. 35, AOP).

**The Last Stages of the Full Grown Larva.**

When a larva reaches maturity it passes its excreta and undergoes a brief period of quiescence during which it becomes whitish in colour, and in shape narrow anteriorly and broader posteriorly. This period lasts about twelve hours during which it prepares itself for pupation. The wings, the antennae, the legs and the eyes can be seen through the skin which appears to be separated from the larva by a fluid which helps the pupa to withdraw from the skin. This skin is now cast off and the pupa appears. No cocoon is spun.

**The Pupa.**

The pupa after casting the larval skin is white in colour and no black pigment is seen. It remains so for three or four days, then the black pigment starts to appear in spots usually on the pronotum first and then the mesothorax. The head is flexed downwards on to the sternum. The eyes are whitish at
first and then they get darker and darker. A rough outline of the adult segments can be seen; the petiole is marked by a slight constriction. On the frons there is a swelling on which the scape of the antennae are borne. Each funicle

![Lateral view of the male pupa.](image)

is directed inwards and backwards on the ventral surface. At first its segments are not clear. Below the swelling on the frons is the triangular labrum flanked on both sides by the rudiment of the mandibles. The tibia and the tarsi of the

![Ventral view of the female pupa.](image)

front legs are present on the inner side of the antennae. Those of the middle legs on its outer side. The coxa, femur, tibia and tarsus of the hind leg are very prominent, but the coxa is comparatively small. The divisions of the tarsi are blurred. All these structures are glued to the ventral surface of the body.
The male pupa (figs. 36, & 37) can be distinguished from the female (fig. 38) by the antennae. In the male the angle between the scape and the funicle is rounded and in the female the angle is very sharp. In later stages of the pupa there is a longitudinal chitinised streak along the ventral posterior median line which indicates the position of the sting in the female. In addition the female pupa is usually bigger than the male.

With advancing age more and more pigment is deposited until the pupa becomes metallic black and the different parts of the body are differentiated.

**THE LIFE-HISTORY AT 27° C.**

The total period of the life-history differs in the sexes.

(1) In the male, the length of the life-history of 123 males was worked out as follows:

<table>
<thead>
<tr>
<th>Stage</th>
<th>Minimum</th>
<th>Mean</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>1 day</td>
<td>2 days</td>
<td>3 days</td>
</tr>
<tr>
<td>Larva</td>
<td>7 days</td>
<td>8 &quot;</td>
<td>11 &quot;</td>
</tr>
<tr>
<td>Pupa</td>
<td>7 &quot;</td>
<td>9 &quot;</td>
<td>11 &quot;</td>
</tr>
<tr>
<td>Total life</td>
<td>18 &quot;</td>
<td>19 &quot;</td>
<td>21 &quot;</td>
</tr>
</tbody>
</table>

(2) In the female the length of the life-history of 104 females was worked out:

<table>
<thead>
<tr>
<th>Stage</th>
<th>Minimum</th>
<th>Mean</th>
<th>Maximum</th>
</tr>
</thead>
<tbody>
<tr>
<td>Egg</td>
<td>1 day</td>
<td>2 days</td>
<td>3 days</td>
</tr>
<tr>
<td>Larva</td>
<td>8 days</td>
<td>10 &quot;</td>
<td>14 &quot;</td>
</tr>
<tr>
<td>Pupa</td>
<td>7 &quot;</td>
<td>9 &quot;</td>
<td>11 &quot;</td>
</tr>
<tr>
<td>Total life</td>
<td>20 &quot;</td>
<td>21 &quot;</td>
<td>26 &quot;</td>
</tr>
</tbody>
</table>

It may be noticed that the pupal stage ends when the adult starts to walk. Under natural conditions, where the pupa is contained within the host cocoon, the latter precludes observation of the commencement of the adult stage. In the present experiments the host cocoon had been removed and this difficulty did not arise.

**The Influence of Food on the Total Period of Life-History.**

It was thought desirable to find whether the food of the larvae has any influence on the total life-history. Thus they were fed on

(1) The pupa of the host.
(2) The larva of the host.

For 90 males, the average length of life of the larva reared on the pupa was 8-6 days, the pupa 9 days and the total length of life-history 19 days.

Another 50 males were bred on the larva of the host, the average length of the larval life was 9 days, the pupa 8 days and the total life-history 19 days.

From this it seems that in the first case the life of the larvae was short and that of the pupae long, although the total life-history in the two groups was the same.
Genitalia and the Biology of Euchalcidia caryobori Hanna.

The Emergence of the Imago.

The pupae after reaching maturity are seen in exposed specimens to move their legs and antennae, and when the adult starts to move they clean their antennae and head by means of the front legs and the thorax, wings and abdomen by means of the hind legs.

Specimens that were not exposed are seen to leave the host cocoon by eating their way out with the mandibles. A circular hole is made in one of the poles of the cocoon. Through this they push their heads and then their front legs, finally they crawl out. It seems that it takes a very long time for individuals to emerge from the cocoon. This was shown by calculating the total life-history until emergence from the cocoons for 50 males and 50 females. In the latter the average was 25 days and the former 23 days. By comparing this result with those in tables 1 and 2, it seems that it takes each about 4 days from the time they start to move inside the cocoon until they emerge from it.

The Duration of the Life of the Imago.

The average length of the life of the imago worked out from 60 males was 50 days, the maximum being 75 days, and the average duration of 56 females was 51 days and the maximum 82 days.

Parthenogenesis.

To ascertain whether parthenogenesis takes place, female pupae were placed each in a separate watch-glass until emergence. They were divided into two groups each consisting of 50 females.

1. In the first group each female was placed in a tube with a male, a sultana, and five Bruchid pupae which were replaced every day, 383 individuals were produced, 195 females and 188 males or the sexes roughly in equal number.

2. In the second group each female was placed alone in a tube as above mentioned, 319 individuals were produced, all males.

Thus the fertilised female produces both sexes in equal numbers and the unfertilised female produces only males.

Acknowledgments.

In conclusion, I wish to express my indebtedness to Professor J. W. Munro and Mr. O. W. Richards for their continuous help and advice throughout the course of the work. I am also grateful to Mr. C. Potter for giving me facilities to visit London warehouses for material.

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