ON THE BIONOMICS AND POST-EMBRYONIC DEVELOPMENT OF *EURYTOMA SALICIPERDAE* MAYR, A SUPPOSED CHALCIDOID PARASITE OF THE CECIDOMYIID OR GALL MIDGE *RHABDOPHAGA SALICIPERDA* (DUF.).*

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CONTENTS.

I.—INTRODUCTION.

Eurytoma saliciperdae† along with four other species (*E. aciculata*, *E. salicis*, *E. nobbei* and *E. dentata*) was first described from the Cecidomyiid galls by Mayr (1878). Of these *E. salicis* only appears in Morley's (1910) list of 23 Eurytoma as indigenous to British Isles. *E. saliciperdae* and *E. aciculata* have since been recorded from England as emerging from

*The work reported here was completed a few years back at the laboratories of the Imperial College of Science, London, but its publication had to be withheld owing to the outbreak of war and certain other unforeseen difficulties.

† The species was very kindly identified by late Dr. Waterston.

galls on willow plants (*Salix fragilis*, *Salix alba*) formed by the midges *Rhabdophaga saliciperda* and *R. triandraperda* respectively (Barnes, 1935 ; Sen, 1938 ; Callan, 1940).

The mere fact that *E. saliciperdae* lives in the same gall inhabited by the midge *R. saliciperda* led Sen (*loc. cit.*) to suggest that the species might be a parasite of the midge as did a few others in reporting on the Eurytoma species they studied (Lichtenstein, 1919 ; Urbahns, 1920 ; Barnes, *loc. cit.*). Recently, however, in pursuing the life-history of this insect more critically, its parasitic role could not be established and it transpired from all evidences that the species was primarily phytophagous.

II.—Methods.

The galled stems of the willow *Salix fragilis* were opened up at frequent intervals and the developmental phases in the life-history of the insect noted.

Experiments were also conducted for studying the general behaviour and habits of the Eurytoma in captivity within glass cells similar to those designed by Balfour-Browne (1922) in his studies on the life-history of *Melittobia acasta*. The glass cells, about 8 mm in diameter and 3 to 4 inches in length, were closed at both ends with pieces of muslin. These cells contained different stages of the gall midge and into each was liberated a fertilised female Eurytoma to note its parasitic propensity, if any.

Microscopic preparations also were studied. For whole mounts the specimens were deeply stained in Carbol Fuchsin and treated in warm caustic potash solution (8 %) until sufficiently clear, dehydrated and then mounted in the usual way. Borax carmine was found unsuitable for mass staining. The earlier stages were mounted unstained in Berlese medium.

III.—Bionomics.

Eurytoma saliciperdae emerges as adults from the galled parts of the willow twigs sometime in May and June depending on temperature. In an incubator set at 26°C, the insects would emerge from the galled twigs even during the winter as discussed elsewhere. They are positively phototrophic on emergence and are poor fliers, often making peculiar leaping movements. The males appear to emerge earlier in the month and they constituted 43 per cent. of the emergences in a total of 223, in other words the sexes are represented in the proportion of two males to every three females. In captivity they do not live for more than 9 or 10 days.

The females lay eggs up to 12 in number in a chain soon after emergence with or without mating, but the eggs from the virgin females never hatch. The eggs with long distorted pedicels are laid on the cambium and can be seen on striping the bark of the twig floating freely within the cell sap. The eggs hatch out into the minute larvae which persist till the last week of August. These undergo three moults growing in size after each moult and the maximum size is attained in March or April at the close of winter.

The larvae cause some amount of damage to the willow plants by tunnelling the woody tissue and usually lie separately, one in each burrow, almost next to the galleries inhabited by the gall midge larvae ; very rarely two or three such burrows may become continuous. The number of Eurytoma larvae present in a gall and their proportion to the midge larvae are highly variable and largely depend on the size of the gall and the intensity of infestation as will be seen from the accompanying table (Table I).

TABLE I.

(*Relative abundance of Eurytoma and Rhabdophaga larvae in willow galls.*)

Sample No.	Total Rhabdophaga larvae. (1)	Total Eurytoma larvae. (2)	Ratio (1) : (2.) Per cent.
A	104	35	33·6
B	40	4	10·0
C	39	7	18·0
D	37	7	19·0
E	21	3	14·3
F	20	1	5·0
G	13	8	61·5

The larvae pupate towards the end of April or in May and the pupal period is short occupying 10 to 15 days only. The pupae are highly sensitive to the atmospheric changes and will not grow as a rule if they are exposed. The mature larvae however, are not so affected by this change since the full-grown larvae on being exposed may transform into the pupae.

The insects thus appear to possess one generation a year.

IV.—DESCRIPTION OF THE DIFFERENT STAGES.

(*a*) The Egg.

The eggs when newly laid are cylindrical in shape with the distal end tapering but with age they increase in size and assume a globular shape (Fig. 1,*a*) like that of the Braconid *Dacnusa areolaris* (Haviland, 1922). The egg is about 0·4 mm long and 0·3 mm broad. It has a long distorted pedicel with the tip slightly swollen at one pole. The pedicel which is used for attachment of the egg to the plant tissue shortens as the egg advances in age. At the other pole—the anterior end, the egg has a short slender stalk narrowed almost to a point apically. This structure sticking out of the cell-sap obviously assists respiration.

The chorion is smooth and blackish in an advanced egg. The embryos hatch out at a comparatively early stage owing to poor yolk contents of the eggs in this group of insects as already suggested by Imms (1919) for *Blastothrix britannica.*

(*b*) The Larva.

There are four larval instars in this species.

(i) *The First Instar.*

The newly hatched larva is transparent and cylindrical, the thoracic region being the widest part of the body (Fig. 1,*b*). The larva measures about 0·9 mm to 1·1 mm in length with a maximum width of 0·5 mm. The head is glabrous and the abdominal segments are undifferentiated without any appendages. Such incomplete segmentation of the abdominal region has also been noted in various other groups of Chalcid, Cynipid and Proctotrypidae (Clausen, 1923; Parker, 1924; Marchal, 1906; Keilin and Pluvinel, 1913; Eastham, 1929).

A pair of papillae, the antennae, and four to six stiff bristles dorsally can be made out on the head. The bidentate mandibles are prominent but the maxillary and the labial areas are not well-differentiated. The labrum is hood-like covering the mandibles partially.

The respiratory system consists of a pair of spiracles situated nearer the posterior margin of the mesothorax; the tracheal trunks are ill-defined.

This stage is prevalent from the middle of July to late August.

(ii) *The Second Instar.*

In this stage the larva measures about 1·5 mm in length and 0·6 mm in width. The body-segments of the larva become distinct and it has a well-defined head slightly bent downwards.

The larva now possesses eight pairs of spiracles, one mesothoracic and seven abdominal, one in each of the first seven abdominal segments.

This stage is of short duration and prevails towards the end of August and the first week of September.

(iii) *The Third Instar.*

The third stage larva measures about 2·0 mm to 2·3 mm in length and 0·9 mm in width. These larvae differ from those of the preceding stage mainly in the respiratory system which now becomes typically holopneustic bearing nine pairs of spiracles, one pair each in the mesothorax and metathorax and the first seven abdominal segments. The head is more sharply differentiated and the larva appears somewhat brownish and opaque owing to greater development of the fat-body. The abdominal segments are distinct and the larva is arched ventrally. The mouth-parts are more strongly chitinised, and as the general pattern is the same, these have been described in the final stage.

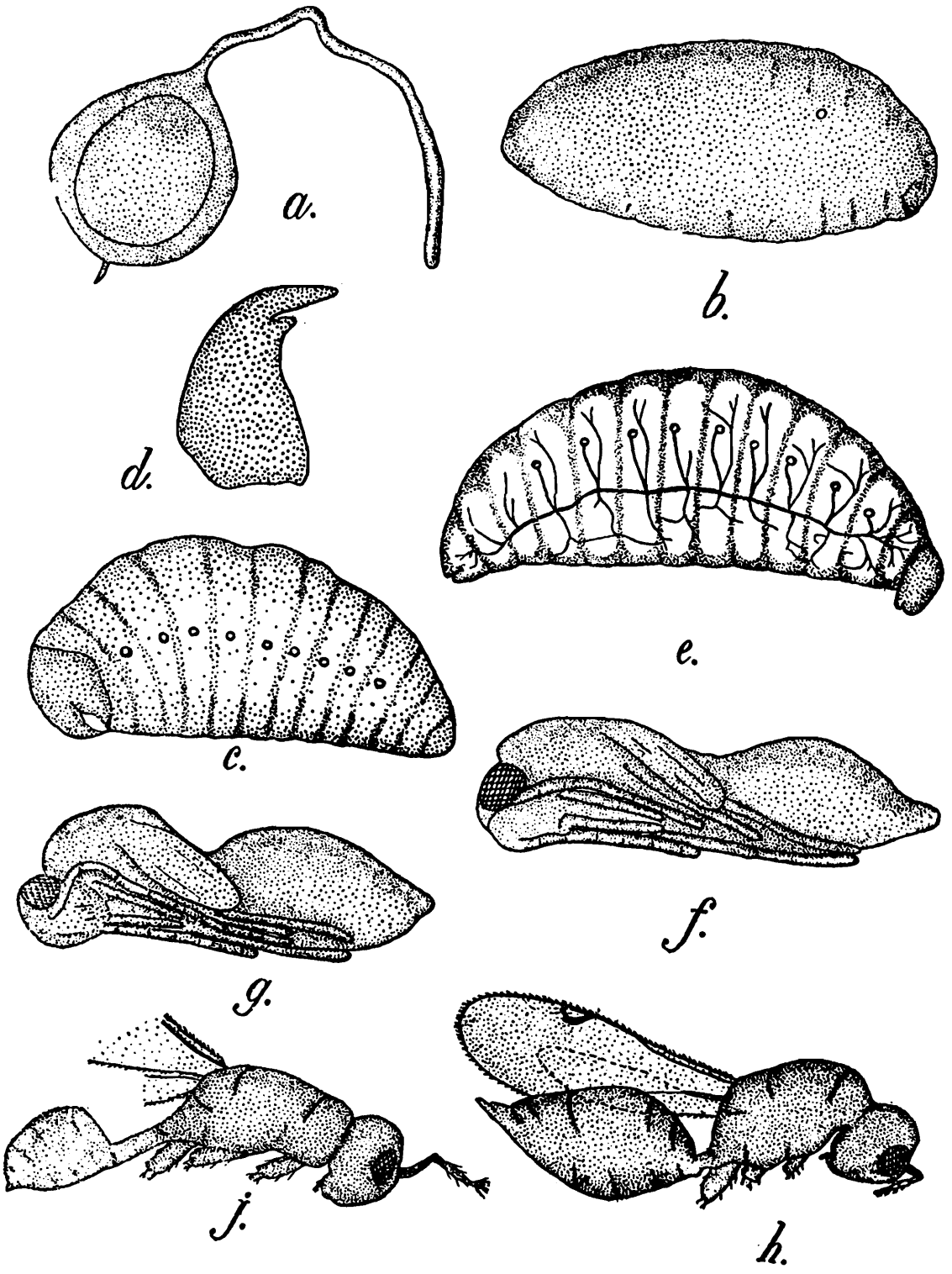
The third instar larvae are met with till late September.

(iv) *The Fourth Instar.*

The full grown larva (Fig. 1,*c*) varies considerably in size, the smallest measuring about 2·8 mm and the largest 3·7 mm in length with a width of 1·3 mm and 1·5 mm respectively. It is dark brown and highly opaque at this stage.

The bidentate mandibles have their dentition sharply edged (Fig. 1,*d*). Bordering the mandibles lie a pair of maxillary prominences, but the labium is imperfectly developed. The labrum becomes strongly chitinised.

The tracheal branches are highly developed with extensive ramifications which are best seen in a freshly killed specimen, otherwise the respiratory system resembles to that of the third instar larva (Fig. 1,*e*). The main longitudinal tracheae running laterally one on each side of the larva give off two cross branches on either side one going inwardly



TEXT. FIG. I. (*a*). Egg of *Eurytoma saliciperdae.* (*b*) First instar larva. (*c*) Final stage larva. (*d*) Mandible of larva. (*e*) Final stage larva showing tracheae of one siep. (*f*) Female pupa. (*g*) Male pupa. (*h*) Female *Eurytoma saliciperdae.* (*j*) Male *Eurytoma saliciperdae.*

and the other outwardly; these ultimately break up into the minute tracheoles in the different parts of the viscera. There is also another short tracheal transverse branch in each of the spiracle-bearing segments connecting the main trachea with the spiracle of its side.

The species normally winters in this stage.

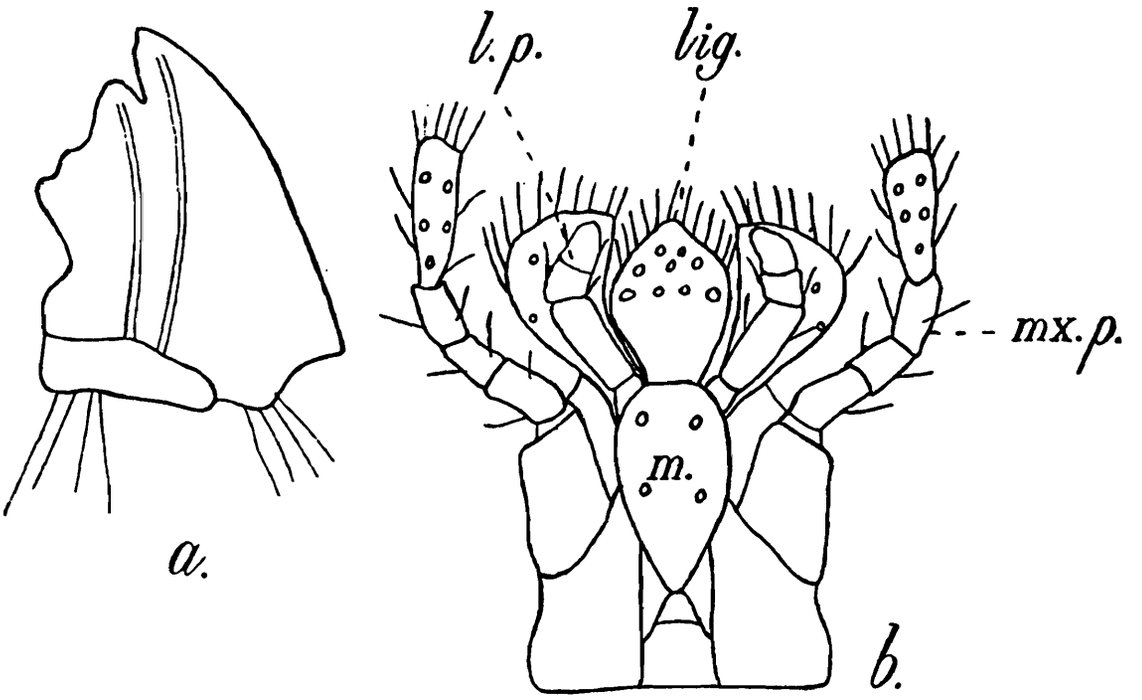
(*c*) The Pupa.

The pupae (Fig. 1, *f* and *g*) when newly formed are whitish but soon turn blackish and measure 2·2 mm to 3·0 mm in length. The pupae of both the sexes may be of equal size, but usually the male is smaller than the female. There are other characters also to differentiate the sexes. The antennal sheath in the male extends beyond the posterior extremity of the wing sheath; in the female it stops short of the wing sheath. The eyes of the male are usually pinkish and the male claspers are visible through the pupal sheath.

(*d*) The Imago.

The imagines (Fig. 1, *h* and *j*) are dark non-metallic in colour. The head is compressed antero-posteriorly and bears a pair of typical chalcidoid antennae provided with grooved sensillae and a few stiff hairs.

In the mouth-parts the mandible (Fig. 2,*a*) is roughly quadridentate of which the anterior pair is sharp and prominent. The maxilla bears

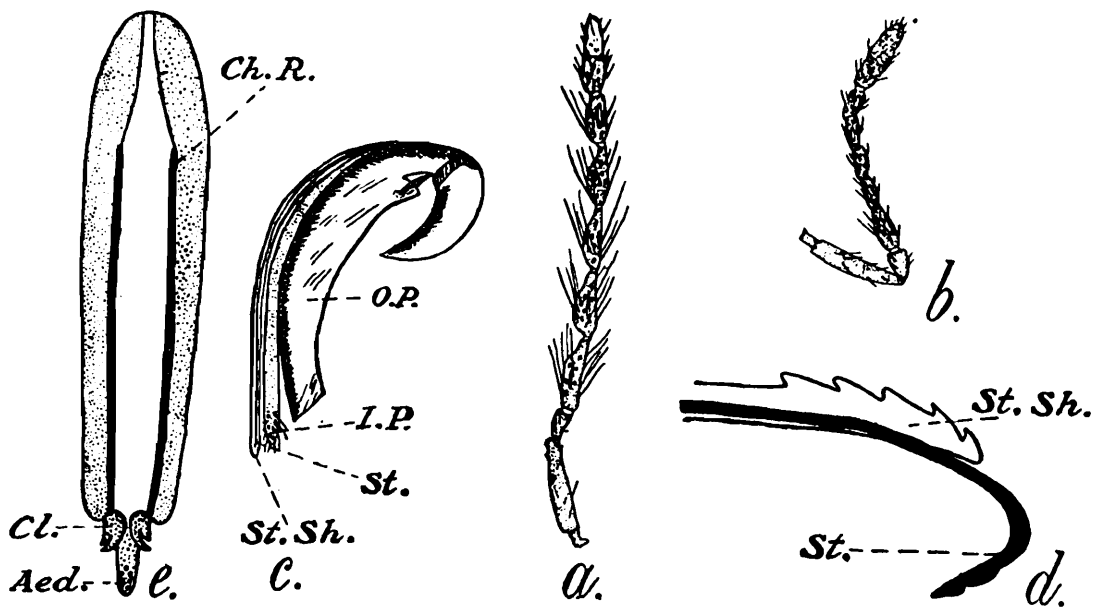


Text Fig. 2. (*a*). Quadridentate mandible of *Eurytoma salaciperdae*. (*b*) Maxillae and Labium of *E. saliciperdae*. (Abbreviations explained under Fig 3.)

a four-segmented palp of which the distal segment is usually the longest (Fig. 2,*b*). The labium is composed of a strongly chitinous basal piece, the mentum, and a distal portion the ligula provided with rows of strong setae. The submentum is rudimentary. The labium bears on either side a three-segmented palp of which the basal segment is the longest. The small labrum has a few minute setae.

(i) *The Female Characters.*

The female (Fig. 1,*h*) is distinctly larger than the male and measures about 3·2 mm in length. The head is nearly as broad as the thorax. The conspicuously elbowed antenna has the club composed of three segments (Fig. 3,*b*). The petiole is short and the abdomen is the widest part in the body which terminates in a pointed ovipositor.



TEXT-FIG. 3. (*a*). Antenna of male *E. saliciperdae.* (*b*) Antenna of female *E. saliciperdae.* (*c*) Female genitalia from side. (*d*). Tip of ovipositor showing the serrated nature of the stylet and the sheath. (*e*). Male genitalia.

Abbreviations used :

Aed, Aedeagus ; *Ch. R.*, Chitinous rod ; *Cl,* Clasper ; *I. P.*, Inner plate ; *l. p.*, Labial palpi ; *lig.*, Ligula ; *m, Mentum* ; *mx. p.*, Maxillary palpi ; *O. P.*, Outer plate ; *St.*, Stylet ; *St. Sh.*, Stylet sheath.

The ovipositor consists of a pair of slender tubular stylets which when expanded surpass in length the sheath enclosing the stylets (Fig. 3,*c*). The tips of the sheath and the stylets are serrated, the sheath having five teeth and the stylets two each (Fig. 3,*d*). Basally, the sheath and along with it the stylets diverge into a pair of arms, one on each side. The two pairs of chitinous plates, the inner and outer plates of Hymenoptera, are well developed. The inner plates are much narrower and lie closely apposed to the stylet sheath ; the apical ends of these plates are provided with certain sensory hairs. The outer plates are much wider and shorter and they terminate bluntly at the apex.

(ii) *The Male Characters.*

The male (Fig. 1,*j*) measures about 2·8 mm in length. The head is broader than the thorax and this constitutes the widest region of the insect. The antenna is larger than that of the female and is darker. The antennal hairs are larger and denser. The flagellar segments are separated by deep constrictions and the club is composed of two segments, (Fig. 3,*a*).

The petiole is long and slender and the abdomen short and thin. In the external genitalia the cylindrical aedeagus is enclosed in a saccular

sheath and supported by a pair of chitinous rods one on each side at its base. Its tip is provided with a few genital papillae, and a pair of claspers lie ventral to the structure (Fig. 3,*e*).

V.—The Habits of the imagines.

(*a*) *Emergence.*

The imago cuts a hole by means of its sharp mandibles on the bark of the tree in the act of emergence with characteristic side to side revolving movements of the head. In this process the antennae come out first through the hole, then the head is pushed out and thus the insect gradually frees itself from the burrow. The whole process takes about 35 to 40 minutes.

The newly emerged insect is very weak and does not move from the site of emergence for sometime. The wings remain closely apposed to the body of the insect at this time. They are soon released by working the hind legs in between the wings and the body. The wings are then brushed clean by the sweeping movement of the spurs in the hind legs. All the rubbish is then passed on to the mid-legs and from there to the front legs which also help to clean the antennae by alternately grasping them within the front tarsi and releasing with slow pulls. The waste matter thus accumulated on the front legs is eventually passsed to the mouth to be devoured by the insect. This cleaning process takes about 15 to 20 minutes.

(*b*) *Courting.*

The male soon after emergence finds out his mate and brings his antennae close to the female. The female usually responds by moving towards the male and her antennae then become interlocked with those of the male. The male mounts on the back of the female while mating and remains in this position for nearly an hour.

(*c*) *Oviposition.*

The female *Eurytoma* when ready to lay her eggs first moves about the host plant for a short while in search of a suitable spot which is almost always in the vicinity of the previous years' attack. When the spot is found her ovipositor is brought in contact with the bark. The ovipositor can now be seen to be slowly expanding and contracting in the act of penetrating the bark; when sufficiently penetrated she starts to deposit the eggs usually laying one at a time. The number of eggs laid by a female under natural conditions is difficult to determine as the eggs are not laid at one place.

VI.—Experimental.

Since evidence of parasitisation by *E. saliciperdae* was not noticed under natural conditions a number of experiments was set up to induce these insects to parasitise the gall midges in artificial cells. The fertilised females of the chalcid were introduced to the special glass cells one in each containing either (i) the living larvae of *R. saliciperda* or (ii) their

pupae or (iii) the eggs. The result of five sets of experiments under each head is given below (Table II) :—

TABLE II.

(Experiments to study parasitisation of *E. saliciperdae.*)

Series.	Date Eurytoma introduced.	No. of Eggs laid.	Date Eurytoma died.	Remarks.
		(With larvae of *R. saliciperda*).		
(1)	11-5-29	1	16-5-29	Larvae of *saliciperda* unattacked. Eurytoma eggs laid on glass surface.
(2)	11-5-29	12	16-5-29	
(3)	14-5-29	2	19-5-29	
(4)	14-5-29	4	19-5-29	
(5)	1-6-29	7	4-6-29	
		(With pupae of *R. saliciperda*).		
(1)	21-5-29	6	23-5-29	Pupae of *saliciperda* unattacked. Eurytoma eggs laid on glass surface.
(2)	21-5-29	1	23-5-29	
(3)	1-6-29	3	3-6-29	
(4)	3-6-29	2	7-6-29	
(5)	3-6-29	4	8-6-29	
		(With eggs of *R. saliciperda*).		
(1)	26-6-29	3	2-7-29	Midge eggs unattacked. Eurytoma eggs laid on glass surface.
(2)	26-6-29	2	2-7-29	
(3)	26-6-29	6	4-7-29	
(4)	28-6-29	4	3-7-29	
(5)	28-6-29	1	4-7-29	

The result obtained from the above table may be summarised as follows : (*a*) *Eurytoma saliciperdae* females did not attack the eggs, larvae or pupae of the gall m dge *Rhabdophaga saliciperda*, (*b*) Eurytoma laid 1 to 12 eggs in captivity and (*c*) *Eurytoma saliciperdae* females lived for 3 to 9 days.

VII.—Incubation.

Series A.

With larvae inside galled twigs.

21-3-29.—A galled twig of *Salix fragilis* infested with the larvae of both *R. saliciperda* and *E. saliciperdae* was placed in an incubator at about 26°C.

12-4-29.—Pupation of Eurytoma was noticed a week after that of the Rhabdophaga.

19-4-29.—Four Eurytoma males were obtained twelve days after Rhabdophaga started emerging.

20-4-29.—Another lot of Eurytoma of which only one was female was obtained.

25-4-29.—Last emergence of Eurytoma recorded ; females prepondered.

Conclusion.—The Eurytoma larvae were ready to pupate after three weeks' stay at summer temperature within the incubator. The pupal duration lasted about a week. The males emerged first and then the females ; the emergence continued for a week.

Series B.

With larvae removed from the galls.

12-11-30.—Mature larvae of *E. saliciperdae* were placed in a petri-dish with moistened sterilised sand and kept in an incubator at about 22°C. The sand was kept moist throughout the experiment.

24-11-30.—The larvae started pupating, the early pupae being whitish.

4-12-30.—The imagines began to emerge.

Conclusion.—The larvae started pupating after twelve days' stay inside the incubator at 22°C and the pupation lasted for ten days. This difference in the number of days from that observed under *Series A* where the larvae were incubated at 26°C while still inside the galls depended on two factors—the absence of food, the larvae being removed from the galls, and the altered temperature condition. While the absence of food in the present series and a comparatively lower temperature hastened the pupation of the insect, the pupal life on the other hand lengthened at this lower temperature.

VIII.—Discussion.

The Eurytomidae are of variable habits, some among them may be parasitic but there are others which are not only phytophagous living either as guests in galls of other insects or as pests but may even be gall-producers themselves like *Eurytoma fellis* (Noble 1933). From the present study *E. saliciperdae* appears to be strictly phytophagous living in the same gall with *R. saliciperda* as an inquiline. The species has not been observed to parasitise the gall midge *R. saliciperda* at any stage of its development.

Many Eurytoma which were considered as parasitic on Cecidomyiidae at one time proved false on closer observation ; *E. tylodermatis* is a recent example (Berry, 1947). On the contrary, they constituted in most such instances, pests to the plants themselves as in the present instance (Westwood, 1882 ; Urbahns, *loc. cit.*). And many among those which are parasitic in habit have been known to attack not only certain pests injurious to a plant but other insects as well equally important as parasites of the pests concerned. The Eurytoma sp. attacking both the clover stem-borer *Languria mozardi* and its parasite *Habrocytus languriae* affords an instance for illustration (Wildermuth and Gates, 1920). The importance of Eurytoma at least in instances where it is a parasite of the nature cited above is therefore of a low order.

Besides, the parasitic role played by many Eurytomid is greatly overshadowed by the subsequent damage they cause to the plant owing to many of them taking up a simultaneous liking for the phytophagous mode of feeding. *Eurytoma parva* for example, a parasite of *Harmolita* (*Isosoma*) *tritici* infesting wheat plants has been reported to cause more damage than the recognised pest by continued feeding inside the plant tissue when the primary pest Harmolita was inactivated (Phillips, 1927). Similar digression into the phytophagous mode of feeding among Chalcidoidea is taken as a secondarily acquired character evolved as a result of severe struggle for existence. (Brues, 1921).

Many earlier workers consider the pedicel in the eggs of Eurytomidae as respiratory in function (Adler, 1881 ; Cameron, 1890 ; Imms, *loc. cit.*); accordingly the length of the structure is greater in eggs laid deeper in the plant tissue than those laid superficially (Cameron, *loc. cit*). Riley (quoted by Sharp, 1910), on the other hand, took this as an organ of attachment as confirmed by the present study in *E. saliciperdae.* The respiration in the egg is carried out by the stalk-like prominence at the anterior end. The pedicel in *E. saliciperdae* eggs has been noticed to reduce in size with the egg advancing in age, and the view that its length is proportional to the depth of the site of deposition of the eggs cannot therefore be supported. With regard to this organ Haviland (1921), however, pursues a middle course ; she observes pedicel to function for both the respiration and attachment in certain eggs.

Parker (*loc. cit.*) mentions of three instars only in the several Eurytoma he studied as opposed to four instars noted in *E. saliciperdae* in the present study, a condition corroborated in *Eurytoma fellis* by Noble (1936). Parker must have missed one of the stages and possibly the first, since the stage described as first by him showing four pairs of spiracles or even five pairs according to Phillips (*loc. cit.*), in fact corresponds more closely to the multi-spiracular second instar larva in *E. saliciperdae* where the first instar larva as mentioned above shows one pair of spiracles only, a condition not detected before in the Eurytoma.

The reason for missing one of the stages in the larval development of Eurytoma is not difficult to understand. It is extremely difficult to follow the moultings in the same individual larva inside the gall, and once exposed it will not grow well. This difficulty was mitigated in the present study by observing many individuals of the same age

often as possible through several years, a method indicated by Eastham (*loc. cit.*). The changes in the respiratory system of the Eurytoma larvae following each instar also afforded a reliable guide to differentiate the various instars.

Summary.

1. *Eurytoma saliciperdae* is not a parasite of the gall midge *Rhabdophaga saliciperda* as has been hitherto believed but a phytophagous inquilinous chalcidoid insect damaging the willows (*Salix fragilis*) to a certain extent along with the midge whose galls it inhabits.

2. The life-history of the insect has been fully dealt with ; it has one generation a year, and the imagines emerge during May and June in nature. The males comprised 43 per cent. of the total emergence. The female in captivity lays not more than 12 eggs and she may live upto 9 days. The insect normally winters in the last larval stage.

3. The eggs are laid inside the bark, each being attached to the tree by a long pedicel which shortens with age. The different interpretations on the function of the pedicel have been discussed.

4. Four larval instars have been detected in the Eurytoma described here. The first instar larva possesses a pair of spiracles on the mesothorax. In the second instar, the number increases to eight pairs, one mesothoracic and seven abdominal ; the last two instars are typically holopneustic possessing nine pairs of spiracles including the two pairs in meso-and metathorax.

5. The pupal and imaginal features with special reference to the male and female characters are given.

6. Experimental evidence to show the non-parasitic habit of the species towards the different stages of the gall midge has been detailed.

7. Results of incubating the larvae of *Eurytoma saliciperdae* while both inside and outside the galls and at altered temperature conditions show that the time required to be ready to pupate and the period of pupation which is normally 10 to 15 days may somewhat vary with the temperature.

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