BESSA SELECTA (MEIGEN) AS A PARASITE OF GILPINIA HERCYNIAE (HARTIG).

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INTRODUCTION

This project arose out of studies of the European spruce sawfly, *Gilpinia hercyniae* (Htg.) in connection with the Canadian Forest Insect Survey at the Dominion Entomological Laboratories, Fredericton, N.B. As an introduction to the subject a brief account is here presented of the outbreak of the European spruce sawfly.

Gilpinia hercyniae was first discovered in America in the fall of 1930 in the Gaspe Peninsula. How long it had been active in this country has not been determined, but at that time it had already severely defoliated spruce over some 2,500 square miles in the interior of the Gaspe Peninsula. The spruce sawfly is presumed to have been introduced at least several decades ago (6). Like many organisms introduced without their native enemies, it increased rapidly in population and by 1939 had spread eastward throughout the Maritime Provinces, westward through the Province of Quebec into eastern Ontario. By this time it was also present in the New England States, as far south as Connecticut and west as New York. In 1941 the first sample of the species was received from Newfoundland(6).

The peak of the infestation was reached about 1938 when an estimated 12,000 square miles were heavily infested (9). Tallies in 1942 in the Gaspe Peninsula showed about 75% by volume of the white spruce dead, and about 45% of the black (8).

The decline of the outbreak coincided with the appearance of diseased larvae. Although insignificant evidence of disease appeared earlier (9), it was not until late 1938 that diseased larvae occurred in Survey samples from the field. In 1939 disease symptoms appeared among the larvae early in the season and it became very difficult to rear European spruce sawfly larvae in the laboratory. By 1942 the disease had spread among the population of sawfly throughout the greater part of its range, and by the following year the sawfly population was reduced to insignificant numbers.

Bessa selecta (Mg.) had been observed as a parasite of the larch sawfly, *Pristiphora erichsoni* (Htg). Particular interest was aroused in it as a parasite occurring on the European spruce sawfly. The latter host was frequently found to bear the eggs and integumental funnels of *B. selecta*. The object was to study its complete life history and habits and its effectiveness as a possible control factor of the spruce sawfly. However, great difficulty was experienced in rearing the host due to high mortality caused by disease. Hence the original aims were not attained to the entire satisfaction of the author.

Bessa selecta generally is referred to as a parasite of sawflies and considerable evidence of its presence is found among them. It is now known, however, that so many mishaps befall it during development from the egg to the adult that it is not considered by the author to have exerted any great amount of control on the spruce sawfly. Undoubtedly it did play a part, along with other controls, and possibly is a more important factor in the environmental resistance of such forms as the larch sawfly and the mountain ash sawfly, *Pristiphora geniculata* (Htg).

Only brief notes were found in the literature on *Bessa selecta*. Early accounts were mostly of occurrence and taxonomy. The latter is reviewed below. Other than occasional notes nothing was found regarding the biology of this species.

Nielsen (31) refers to the method used by the last instar maggot in leaving the host. Dobrodeiev (15), in connection with his studies of *Priophorus padi* L., referred to the method by which the host becomes parasitized. Baer (3) makes the generalization that 'if parasitism begins early enough the host is unable to progress to a further stage', which rule he applies to *Bessa* (*Ptychomyia*) *selecta*. The most lengthy account of *B. selecta* encountered was by Baird (10), who briefly recorded a few observations on oviposition, overwintering stage, place of pupation, and the fact that there are two generations a year.

A summary of the distribution of *Bessa selecta* as recorded by various authors appears in Table 1, along with a list of hosts from which the parasite was reared, and pertinent remarks made by the author in each instance.

The author wishes to express his gratitude for the cooperation and advice accorded him by Messrs. R. E. Balch, W. A. Reeks, and M. L. Prebble, of the Dominion Entomological Laboratories, and particularly for the suggestions offered by Mr. Reeks, while engaged on this project.

DISTRIBUTION

Some doubt exists as to whether *Bessa selecta* is native to North America or is a European species. It is generally referred to as a Tachinid parasite of sawflies and records of its occurrence have been noted in many parts of Europe and America.

Considerable of the difficulty as to its nativity appears to have arisen out of taxonomic discussions. There is little doubt that the European and American *Bessa selecta* are the same species. Aldrich (1) in this connection says, "That this European species (*Ptychomyia* (*Bessa*) *selecta*)[i] occurs in North America has now been ascertained."

There is little to indicate whether this species originated in Europe and was introduced into America on some of the introduced sawflies or whether it is an international species.

It occurs commonly as a parasite of the larch sawfly, *Pristiphora erichsoni*, both in Europe and America. In American literature it is particularly associated with this pest of larch, apparently occurring whereever *P. erichsoni* is found. There is, in the author's opinion, good reason for believing that *B. selecta* was introduced into the western world, possibly with *P. erichsoni*.

It is recorded in the literature as occurring in the British Isles, France, Germany, Russia, Finland, Austria, Italy, Montana and Great Lakes District, Maine, and British Columbia.

Records obtained in connection with this project indicate it occurs in New Brunswick and Nova Scotia, wherever *P. erichsoni* is found, and it has also been reared from *P. erichsoni* larvae received from Newfoundland.

Table 1 gives a list of points of distribution.

[i] Author's parentheses.

IDENTIFICATION

Bessa selecta (Meigen) belongs to the family Tachinidae, of the order Diptera. The genus *Bessa* was erected by Robineau-Desvoidy in 1863. The synonymy of the genus is as follows:

1863 *Bessa* Robineau-Desvoidy, Hist. Nat. Dipt. de Paris 2:64

1863 *Ephyra* Robineau-Desvoidy (preocc.), Ibid p. 156

1863 *Lilaea* Robineau-Desvoidy (preocc.), Ibid p. 160

1863 *Myrsina* Robineau-Desvoidy, (preocc.), Ibid p. 158

1863 *Osmina* Robineau-Desvoidy, Ibid p. 166

1889 *Ptychomyia* Brauer and Von Bergenstamm, Musc. Schiz. 1:21

1931 *Ptychomyia* Brauer and Von Bergenstamm = *Myrsina* Robineau-Desvoidy. Villeneuve, Konowia 10:56

1936 *Myrsina* Robineau-Desvoidy = *Bessa* Robineau-Desvoidy. Townsend, Man. Myiol. pt.IV p. 278

The synonymy of Meigen's species *selecta*, 1824, is as follows:

1824 *Tachina selecta* Meigen, Syst. Beschr. 4:377 (237)

1863 *Bessa secutrix* Robineau-Desvoidy, Hist. Nat. Dipt. de Paris 2:64 = *Tachina selecta* Meigen

1863 *Phorinia micromera* Robineau-Desvoidy, Ibid p. 156 = *Tachina selecta* Meigen.

1863 *Lilaea aurozonata* Robineau-Desvoidy, Ibid p. 160 = *Tachina selecta* Meigen

1863 *Myrsina ambulatrix* Robineau-Desvoidy, Ibid p. 158 = *Tachina selecta* Meigen

1863 *Osmina lubrica* Robineau-Desvoidy, Ibid p. 166

1892 *Daeochaeta harveyi* Townsend, Trans. Am. Ent. Soc. 19:98

1892 *Masicera tenthredinidarum* Townsend, Ibid p. 285

1900 *Tachina parallela* Meigen. Stein, Ent. Nach. 26:145 = *Tachina selecta* Meigen

1907 *Roeselia convexifrons* Pandelle. Villeneuve, Ann. Soc. Ent. Fr. 76:388 = *Tachina selecta* Meigen

1915 *Frontina* (*Masicera*) *tenthredinidarum* Townsend. Britton, Rept. Conn. Agr. Exp. Sta. pp. 125-134

1922 *Frontina tenthredinidarum* Townsend. Baird, Proc. Acad. Ent. Soc. no. 8, pp. 158-171

1927 *Tachina tincta* Meigen. Lundbeck, Dipt. Danica 7:345 = *Tachina selecta* Meigen

1930 *Daeochaeta harveyi* Townsend. Aldrich, Proc. Ent. Soc. Wash. 32:25 = *Ptychomyia selecta* Meigen

1930 *Masicera tenthredinidarum* Townsend. Aldrich, Ibid = *Ptychomyia selecta* Meigen

1931 *Prosopodes fugax* Rondani. Villeneuve, Konowia 10:56 = *Tachina selecta* Meigen

1936 *Bessa harveyi* Townsend, Man. Myiol. pt. IV p. 236 = *Daeochaeta harveyi* Townsend and *Masicera tenthredinidarum* Townsend

1936 *Bessa selecta* (Meigen). Townsend, Ibid

There appears to be some confusion regarding the species *Daeochaeta harveyi* Towns., *Masicera tenthredinidarum* Towns., *Bessa harveyi* Towns., and *Bessa selecta* Mg. In 1892 Townsend (44) described *D. harveyi* from one specimen, the female sex of which he queried. At the same time he also described a single male specimen of *M. tenthredinidarum*. In 1936 he made the following correction, "*D. harveyi* is the male and *M. tenthredinidarum* is the female of an American species of *Bessa*, to be known as *Bessa harveyi* Townsend, the European *Bessa selecta* Meigen not occurring in America." (46)

Previously Aldrich in 1930 examined the types of *harveyi* and *tenthredinidarum* and suspecting that the European *selecta* was the same, sent several specimens of the American material to Dr. J. Villeneuve, who confirmed the identity (1).

Whether Townsend was aware of this comparison he does not say. In the author's opinion, based on the facts as presented, D. harveyi, M. tenthredinidarum and B. harveyi are all identical with Bessa selecta, which from the facts occurs in America as well as Europe.

METHODS OF STUDY

The data for this thesis were collected during the summer and fall of 1939 and the spring, summer and fall of 1940. The material used was obtained both from field collections, culture rearings of both the European spruce sawfly and Bessa selecta, and from Forest Insect Survey samples.

During the summer of 1939 larvae of G. hercyniae were collected in the field and obtained from Forest Insect Survey samples. These were divided into four groups:-

1. Those bearing unhatched eggs.
2. Those bearing hatched eggs.
3. Those bearing integumental funnels.
4. Those bearing doubtful scars.

Records were kept of the host larval stages and the material was all reared in lots

1. Individually to determine:-

    (a) Where the egg was deposited, and the relationship of its position to the eventual location of the integumental funnel.

    (b) Whether the integumental funnel occurred at any regular location.

    (c) The method of egg hatch.

    (d) How the maggot became established.

    (e) In what stage of the host the maggot matured and where it pupated.

2. Individually and in groups as series for dissections to determine:-

    (a) The number of maggot stadia.

    (b) The length of each stadium.

(c) The length of the maggot stage.

(d) How soon after maggot maturity the puparium was formed.

(e) The length of the puparial stage.

(f) How and when the adult emerged.

It was originally planned to dissect lots every three or four days, but the mortality of host larvae due to disease interrupted the schedule. Instead, dying or dead larvae occurred frequently enough for these dissections.

At all times records were made of occurrences during development from egg to adult which would impair efficiency of the parasite.

Cocoons were obtained in the fall and put up in lots for immediate and subsequent dissections to determine the overwintering stage and spring development. From this material and other sources adults were obtained.

These were kept in cotton cages and notes obtained on habits. These cages were also stocked with G. hercyniae for oviposition, to supply large numbers of parasitized larvae with which to continue the work of the previous summer. In addition, material was obtained from the same sources as previously mentioned.

DESCRIPTION

Egg. (Figs. 1 and 2)

The egg of Bessa selecta has a heavy, opaque dorsal chorion. The general color is white. The ventral surface is flexible conforming in shape to the surface upon which it is deposited. This ventral chorion is thin and transparent. The general form is oblong, being broad at the posterior end, narrowing slightly toward the anterior end to give a blunt taper. In lateral view the dorsum is markedly arched with the ventral surface flattened or concave, depending on the surface of the host. The reticulate markings, formed by the impression of the ends of the ovarian follicular cells, are very indistinct.

The egg is of the dehiscent macrotype, with a distinct fracture over the anterior end, commencing at the antero-ventral edge, extending dorsally and somewhat posteriorly, completely marking off a distinct operculum. On some occasions hatching is accomplished by forcing this operculum backward, and eventually, as the eggshell ages the operculum drops off, leaving a circular aperture in the anterior end of the eggshell. Regardless of the method of hatching the operculum nearly always drops off eventually.

The egg is attached to the host integument apparently by a mucilaginous substance, which results in a darkening of the host integument at the point of deposition.

Bessa selecta eggs measure from 0.566 mms. to 0.610 mms. in length with an average length of 0.588 mms., and at the broadest part from 0.272 mms. to 0.305 mms. in width, with an average of 0.285 mms.

First Instar Maggot. (Figs. 3, 4, 5, 6, 9 and 10)

The first stage maggot is tachiniform, hatching from a macrotype egg. The body is somewhat robust, tapering toward the cephalic end and truncate at the caudal end (Fig. 3). The average length is 0.993 mms., with a range of 0.415 mms. to 1.353 mms. The body consists of eleven segments and a small retractile, conical pseudocephalon. The cuticle is colorless and transparent, so that the internal organs are visible. The cuticle of each segment bears armature in the form of bands of spinules, particularly at the segmental margins. Heavily sclerotized hooks (Fig. 3) with their points directed anteriorly for attachment to the integumental funnel (Fig. 4) occur on the posterior segments. The eleventh or terminal segment bears the posterior spiracles (Fig. 9). The anal end is elevated dorsally where it fits into the funnel.

The pseudocephalon is equipped with the buccopharyngeal armature and bears a pair of sensory papillae on its antero-lateral margins. These papillae bear short rod-like sensory organs (Fig. 10).

The buccopharyngeal apparatus is a simple unjointed sclerotized structure (Figs. 5 and 6). The median tooth has a rounded dorsal edge, the anterior part of which is equipped with teeth for making entry into the host, and a sharp dorso-ventral point. Posteriorly the apparatus divides into two lateral arms. Each of these arms continues posteriorly as a lightly sclerotized wing and each also bears a lightly sclerotized ventral wing. On either side the median tooth lies a lateral anterior plate, and ventrally there is a salivary gland plate. The entire buccopharyngeal apparatus varies in length from 0.132 mms. to 0.248 mms., with an average length of 0.186 mms.

The rows of spinules which compose the bands of armature on each segment are not easily differentiated, but adhere closely to the following description.

The prothoracic segment has a band consisting of six rows of spinules encircling the anterior edge of the segment. There are also a few scattered spinules on the posterior edge. Eight rows occur ventrally. The spinules are directed posteriorly.

The mesothoracic segment has a band on the anterior margin composed of six rows of spinules across the dorsum and pleura, increasing to eight rows midventrally. There are two rows encircling the segment on the posterior margin.

On the anterior margin of the metathoracic dorsum there is a five-row band of spinules, lessening to four rows on the pleura. There are seven and nine rows ventrally. Spinules on the venter of the thoracic segments are more closely arranged than on any of the other segments.

There are five rows in the anterior band of the first abdominal dorsum; across the antero-venter there are seven, decreasing to four laterally until on the pleura the spinules are very scattered.

The second abdominal segment has five rows of spinules on the anterior dorsal margin, six closely arranged rows across the venter, decreasing to three or four rows of more scattered spinules laterally. Located on each pleuron of this segment are two large spines directed anteriorly, which assist in maintaining the maggot's attachment in the funnel.

The third abdominal segment has a four or five row band antero-dorsally with two rows of very scattered spinules posteriorly. There is a row of four to seven large spines, directed anteriorly, on each pleuron. Ventrally there are four or five rows anteriorly and three scattered rows posteriorly.

The fourth abdominal segment has five rows dorsally on the anterior margin and three scattered rows on the posterior margin. There are seven large spines anteriorly on each pleuron. On the anterior margin of the venter there are five or six rows, while the posterior band has three or four more scattered rows.

The fifth abdominal segment has a five-row band on the antero-dorsum and a four-row band on the postero-dorsum. The large anteriorly directed spines occur in a cluster of seven on each pleuron. Ventrally there are five rows of spinules anteriorly and three rows posteriorly.

The sixth abdominal segment has four rows of spinules anteriorly and five scattered rows posteriorly on the dorsum. This is the last segment on which occur the large attachment spines, there being four on each pleuron. On the antero-venter there are four rows of spinules and three and four on the postero-venter.

Spinules occur in short very scattered rows on the anterior and posterior margins of the seventh abdominal segment.

The eighth and terminal segment has very small spinules scattered in short rows anteriorly. The posterior spinules are the larger and are located in two scattered rows encircling the segment.

Second Instar Maggot. (Figs. 7, 8, 11, 13 and 19)

The second stage maggot somewhat resembles the first in color and form. It has a thin, transparent integument. Although anterior spiracles were not observed in the first stage, they were in the second (Fig. 13). They are minute, with two elliptical openings and are situated pleurally, close to the inter-segmental space between the first and second thoracic segments. The posterior spiracles are widely spaced on the anal segment and each consists of two openings (Fig. 11). The average length of the body is 3.122 mms., with a range in length from 1.801 to 3.892 mms. The cuticular armature consists of bands of spinules arranged in rows on each segment. The armature is heavier than in the preceding stage, and although the spinules are arranged in rows, these rows are short and confused, so much so that it is difficult to accurately determine the number. Pseudopodia are discernable.

The buccopharyngeal apparatus is larger and more highly developed (Figs. 7 and 8). The length averages 0.442 mms. with variations from 0.385 to 0.539 mms. Instead of the single median hook there is a pair of curved mandibular hooks. As near as could be determined the entire structure is fused into a single unit, there being no division between an anterior region and an intermediate region. The dorsal and ventral wings are present and more highly sclerotized, as is the case with the entire structure. Lateral plates were not observed, but the ventral salivary gland plate is present.

The anterior margin of the prothorax has eight or nine rows of spinules dorsally, the rows occurring in not too distinct lineal groups of three to seven. Ventrally there is an eleven-row band of heavy spinules on the anterior margin. There is no posterior band.

The mesothorax has nine or ten rows on the dorsal anterior margin in groups of three to nine spinules, increasing to twelve and thirteen rows ventrally, while the posterior band is lacking.

There are seven rows on the anterior margin of the metathoracic dorsum. These rows consist of groups of four to twenty spinules. Ventrally there are eight and nine rows. There is no posterior band.

The spinules on the dorsum of the first abdominal segment occur in lineal groups of four to twenty-one to make up four and five anterior rows. On the venter there are six and seven anterior rows.

Ventrally the spinules on the first four body segments are considerably heavier in structure than those which occur on the dorsum.

The anterior band of the second abdominal segment consists of four or five rows in groups of four to nineteen. The groups become more scattered laterally, but are denser, and the band is wider ventrally than dorsally. Again the posterior band is absent.

On the third abdominal segment the anterior band has four or five rows of spinules in groups of five to twenty-one. The anterior ventral band of this segment is similar to that on the second segment. Dorsally the posterior band consists of two and three rows of spinules, some of which are directed anteriorly, others posteriorly. This band encircles the segment and ventrally the spines point anteriorly.

There are four rows in the anterior dorsal band of the fourth segment. Most of these spinules are directed posteriorly, while some are directed anteriorly. This band ventrally has six and eight rows. The rows become less in number, and the groups are more scattered laterally. Ventrally the posterior band is as wide as the anterior one, and it continues so laterally, diminishing dorsally to three and four rows of anteriorly directed spinules in groups of five to sixteen.

The anterior band of the fifth segment has three and four rows of posteriorly directed spinules in groups of three to twelve. Ventrally this band is similar to that of the preceding segment, but becomes narrower with widely scattered groups laterally. The posterior band encircles the segment with four rows of anteriorly pointed spinules in groups of eight to sixteen.

On the sixth abdominal segment there is an anterior band of three and four rows of small, scattered spinules directed backward. This band continues laterally as an occasional group, increasing ventrally, where it is located midventrally and consists of four and five rows. The posterior band is like that of the preceding segment.

The anterior band of the seventh segment has practically disappeared, only a few scattered posteriorly directed spinules occur dorsally and midventrally. The posterior band consists of five and seven rows of spinules directed forward.

Dorsally the terminal segment has spinules scattered all over it in groups of three to fourteen. Anteriorly on both dorsum and venter there are scattered groups of small spinules directed posteriorly, while the rest of the segment, particularly the venter, is strongly covered with anteriorly directed spinules.

Third Instar Maggot. (Figs. 12, 14, 20, 21, 22, 23 and 24)

The mature larva is more robust in general appearance than the preceding stages (Fig. 20). It has increased considerably in size, being on the average 5.84 mms. long and ranging in length from 4.669 mms. to 7.470 mms. There is an appreciable tapering cephalad and caudad. Distinct median pseudopodia occur between the abdominal segments. The anal opening occurs mid-ventrally on the seventh abdominal segment (Figs. 20 and 22).

The anterior spiracles are situated laterally, just dorsad of the pleural line, near the posterior margin of the prothorax. The spiracles are fan-shaped and consist of four lobes each bearing an oval opening to the spiracular chamber (Fig. 14).

The posterior spiracles are somewhat triangular in shape and are surrounded by highly sclerotized black peritremes. They are located in a shallow depression on the eighth abdominal segment, slightly dorsad of the transverse axis. This segment curves dorsally to fit into the integumental funnel. The spiracular plates or peritremes are separated by about one-half their width. Their inner margins are irregular with three processes projecting into the spiracle toward the spiracular scar, thus forming four lobes at the periphery of each respiratory area. Situated in three of these lobes are the spiracular slits (Fig. 12).

The buccopharyngeal apparatus is a comparatively heavy structure with two distinct articulations separating the anterior intermediate and basal regions (Figs. 23 and 24). The anterior region consists of the paired oral hooks. There is a fossa on the external lateral surface of each mouth hook, the purpose of which is not known. The intermediate region or hypostomal arch is articulated dorsally on each side with a dorsal process on each hook. Its lateral arms are connected by a ventral transverse bridge. A ventral plate occurs between the anterior and intermediate regions. The posterior or basal region consists of a lightly sclerotized ventral trough uniting the more heavily sclerotized lateral arms.

The larval head bears two pairs of circular sensory structures, which occur on distinct protuberances, situated antero-laterally (Fig. 21).

The anterior pair bear a number of small papillae. The posterior pair bear a circular sclerite with clear central areas.

Armature occurs on each segment in the form of curved lineal groups of spinules and except for those on the terminal segment which are directed anteriorly, all point posteriorly.

Dorsally on the anterior margin of the prothorax there is a wide heavy twelve-row band, which tapers to nothing laterally and consists of only a single row ventrally.

The mesothorax bears a twelve and thirteen-row band of spinules dorsally on the anterior margin diminishing to eight and nine rows laterally and to two and three ventrally.

On the anterior margin of the metathoracic dorsum there is an eleven and twelve-row band, which reduces to five and six rows laterally and three and four ventrally. There is a row of scattered groups encircling the segment posteriorly.

The first five abdominal segments have anterior bands dorsally consisting of three and four scattered rows of spinules. The first segment has the same laterally and ventrally.

The second abdominal segment, where the first pseudopodia occur, has three or four rows of spinules laterally and four and five across the pseudopodia.

The third segment has two and three scattered rows laterally while ventrally there are five and six. Five and six rows occur ventrally on each of the next three segments.

There are three rows antero-laterally and one postero-laterally on segment four; two and one respectively on segment five.

The sixth segment has two and three rows antero-dorsally, and only one antero-laterally and one postero-laterally.

On abdominal segment seven there is a band consisting of three rows postero-dorsally, one laterally, three ventrally and a four-row band antero-ventrally.

The eighth abdominal segment is heavily armed with spines that, as mentioned above, are directed anteriorly. There are intermingling groups of spinules over the entire segment, except for a small bare area mid-ventrally.

The Puparium. (Figs. 15, 28, 29 and 30).

The puparium is subelliptical and is slightly wider in the mid-region (Fig. 28). Both ends are smoothly rounded, and the segmentation is distinct. The longitudinal axis is straight. When first formed the puparium is yellowish, changing to brown in a few days. The larval spinules are visible throughout its entirety, as are the areas of the pseudopodia. The puparium ranges from 4.03 mms. to 5.6 mms. in length, and from 1.9 mm. to 2.6 mm. in width. Eleven segments are distinguishable, the first being the prothorax. Apparently the pseudocephalon is invaginated.

The mouth opening may be seen slightly ventral of the transverse axis (Fig. 30). The buccopharyngeal apparatus is seen adhering to the inner surface of the puparium. Slightly dorsad of the transverse axis, at the posterior margin of the prothoracic segment may be seen the anterior spiracles which are fan-shaped and consist of a stalk surmounted by three papillae each with a terminal pore (Fig. 15).

There are two lines of cleavage through which the two halves of the puparial cap are separated from the remainder of the puparium at the time of adult emergence. The horizontal line extends across the front, dorsad of the mouth opening, and thence posteriorly to a point almost midway on the first abdominal segment. The vertical line of cleavage does not appear in entirety but exists as partial creases on either side extending slightly dorsad and ventrad of the junction with the horizontal crease.

The external prothoracic cornicles protrude through openings located on each side of the first abdominal segment, near the posterior margin and dorsad of the horizontal axis.

The anal opening is represented by a circular scar at the posterior margin of the seventh abdominal segment.

The posterior spiracles are those of the third instar maggot and are recognizable. They are located dorsad of the transverse axis. The peritremes are slightly raised above the surrounding surface of the terminal segment.

The Pupa. (Figs. 16, 17, 18, 25, 26 and 27)

All those puparia dissected contained pupae developed to the stage illustrated in Figs. 25, 26 and 27. Within each of these puparia, which contained well-developed pupae, was found a thin transparent membranous sheath. This sheath adhered closely to the puparial wall but was not attached. It was apparently structureless and could not be related to any particular stage of the developing fly. The buccopharyngeal apparatus was always found attached to the inner wall of the puparium itself and not to this sheath. Prebble (33) found a structure, similar in some respects, in Actia diffidens which after a review of Snodgrass's description of Rhagoletis pomonella he concludes is the cast prepupal skin. The author is unable to conclude what this membrane represents in Bessa selecta. It may represent evidence of the existence of a prepupal stage, but if it does this stage apparently does not have the larval structures of the third instar which apparently is the case in above mentioned species.

The pupae found were in a stage of development where many of the adult structures were recognizable. The specimens were entirely white. The compound eyes were distinguished, as were the complete antennae. The proboscis is plainly visible, consisting of a pair of labellar lobes, a spear-shaped labrum and bearing the maxillary palpi. The legs are well-developed. Wing pads are distinct and the points of articulation with the thorax are becoming evident. Posteriorly, on the laterads of the thorax may be seen the calypteres. The thoracic dorsum is beginning to show the regions of the adult dorsum. The abdominal segmentation, or the abdominal spiracles are not in evidence.

The internal prothoracic spiracles (Figs. 15, 16 and 17) are situated laterally on the prothorax beneath the pupal integument. The spiracles have their opening through the single orifice of the prothoracic cornicles, which protrude through the puparial wall. The cornicles are each borne on a protuberance of the body wall. Each surmounts a chamber connected by a trunk to another chamber, the latter bearing the inner spiracles. The spiracles have an irregular outline and each bears fifty-seven papillae.

SEASONAL HISTORY

Hibernation.

Bessa selecta overwinters as first instar maggots within the hibernating host. Dissections of Gilpinia hercyniae cocoons collected in the field revealed the inactive first instar maggots from August 29 throughout the late fall and early winter until May 8 of the following spring when the first second stage maggots occurred (Table2). When activity was first resumed in the spring was not determined, but it was apparently between the middle and the last week of April.

First Generation.

The first generation starts with the hibernating first instar maggot. Development continues through the three instars and puparial stage to the adults which appear around the first part of July.

(a) First Instar Maggot. Unfortunately the spring dissections were not commenced early enough to determine how soon activity was resumed. The first dissections were on May 6 when only first instar maggots occurred. They continued until June 14 and later, but those still present after May 25 are presumed to have ceased development (Table 3). This is discussed below.

(b) Second Instar Maggot. The first appearance of second instar maggots was on May 8 and they continued until June 7, a period of thirty days. The mean date of development of this stadium is calculated as being May 21, (Table 3).

(c) Third Instar Maggot. This stadium is a rapid feeder and develops more quickly than the first two. The mean date of development is June 8, while the average number of days spent in this stage is eighteen. It was found within host prepupal stages from May 31 until June 14 (Table 3).

(d) Puparial Stage. Upon maturing the third instar maggot forms the puparium within twenty-four hours. Those of the first generation which were reared were formed between June 5 and 14, the mean date being June 9. The first adults emerged on July 5 and continued to emerge until July 18. The mean date of emergence was July 10. This gives a mean period in the puparial stage of thirty-two days with a range of thirty to thirty-four days (Table 4).

Adults removed from emergence boxes in the field mated as soon as they were put in a warm, sunny place. Oviposition took place shortly after copulation, eggs appearing on larvae about three days after mating.

Second Generation. (Tables 6 and 7)

(a) First instar maggots of the second generation were first observed to be established on July 16. Some were probably established as early as July 12. Dissections of second generation material were commenced on July 17. The first stage was present from July 22 to August 11, the mean date being July 28, which was about nine days after the mean hatching date of eggs. First stage maggots present after August 11 are considered to have had their development arrested. This retardation of development is discussed below.

(b) Second Instar Maggots. These were found present from July 23 to August 11, the mean date being August 1, four days after that of the first instar.

(c) Third Instar Maggots occurred between July 17 and August 25 with an average date of August 4 or three days after the second stadium.

(d) Puparial Stage. The puparia were formed within twenty-four hours after the maggots matured and emerged from their hosts. The mean date of formation of the puparia was August 5. The period of adult emergence was from July 31 to September 16, the mean date being August 21, which gives an average length of the puparial stage of sixteen days.

These adults mated and deposited their eggs about six days later, and from those eggs hatched the overwintering first instar maggots.

BEHAVIOUR

Adult Activity.

As with the great majority of Tachinidae adults, emergence takes place mainly during the early morning hours. The adult makes its exit from the puparium by exerting pressure with the ptilinum against the anterior end of the puparium thus forcing off the operculum. Having forced off this cap, emergence from the puparium is completed by a process of protrusion and retraction of the ptilinum. By a similar use of the ptilinum, aided by the posteriorly directed macrochaetae on the head and thorax and by the use of the legs, the adult forces its way upward through the soil.

Within a very short time after emergence the body has changed from the soft form of the emerging adult to the sclerotized form of the mature adult. The general body color is darker, the wings have spread, and the ptilinum is retracted permanently into the cranium.

Adults taken from emergence boxes, which were kept under moss in the woods, became very active as soon as they were placed in a warm, sunny location, Activity was always greatest during the noon hours.

Mating occurs soon after emergence from the puparia, but was observed mainly between the hours of 11 A.M. and 1 P.M., when the cages were in a warm, sunny location. Coition lasts for varying lengths of time, ranging between fifteen and fifty minutes, with the average time being between twenty-five and thirty minutes. The males of Bessa selecta will fertilize more than one female, but how many more was not determined.

Among first generation adults, oviposition takes place within three days of mating, while in those cases observed of second generation adults, six days elapsed between mating and oviposition. It is highly probable that the period of gestation has a considerable range, from approximately three to six days.

Following Townsend's (45) distinction of reproductive habits among Tachinidae, B. selecta belongs to the "host ovipositing" type and deposits its eggs supracutaneously. Nothing was observed to support the statement of Dobrodeiev (15) that "it is probable infestation of Priophorus padi L. by Bessa (Ptychomyia) selecta does not take place through actual oviposition on the skin of the host, but by the host swallowing eggs of the parasite deposited on its food plants." It might be stated here that no evidence of parthenogenesis has been observed.

There are five larval feeding instars in Gilpinia hercyniae and a sixth non-feeding instar, which spins the cocoon. Development within the cocoon proceeds through three phases, the eonymph, the pronymph, and the pupa, to the adult.

As in the case of perhaps most Tachinidae the larval stage of the host is the one attacked, and the eggs are deposited mainly on the fifth stage larvae of G. hercyniae. Eggs have been noted on younger stages, not uncommonly on fourth instars, and rarely on third and second instars (Table 8). The youngest host larva found bearing an integumental funnel was a fourth stage, from which a mature maggot emerged. Either the egg was dislodged from this larva or it was deposited on the third instar.

According to Clausen (13), most of those species of Tachinidae which deposit their eggs directly upon the body of the host do so on a particular part of the body rather than place them indiscriminately. B. selecta does not conform to this general rule, but is found to deposit eggs at random on the host. Eggs have been found on each of the thoracic segments, and segments one, two, three, five and eight of the abdomen, as well as on the head capsule. Never has it been observed that a maggot entered the host through the head capsule. Eggs have also been noted on the dorsal, lateral and ventral regions of the host's body. Baird (10) also found that Bessa selecta oviposited on any part of larch sawfly larvae.

The females of Tachinidae which deposit macrotype eggs apparently exercise little discrimination in their choice of host individuals for parasitization. This frequently results in an individual host receiving an excessive number of eggs. This habit applies equally to B. selecta. As many as twenty-nine eggs have been observed on one host from which twenty-seven maggots hatched and became established. The host larva, of course, died before any of the maggots progressed beyond the first instar. One other instance of twenty-two eggs on an individual host was noted, and not infrequently two to five eggs are found on one host.

Females of B. selecta deposit their eggs quickly and easily. They light on a larva and with a quick downward thrust of the abdomen seem to wipe the egg onto the host. Then they usually hop a short distance from the host and may return to deposit another egg or go in search of a second victim.

Under caged conditions the period of egg production extended over about two weeks among the first generation adults. Oviposition was first noticed on July 15. From this date until July 20, parasitization of larvae was 100 percent, dropping off until July 29, when only fifty percent of the larvae were parasitized by eggs.

The reproductive capacity of B. selecta females was not definitely determined. It is believed that the capacity is somewhere in the neighbourhood of one hundred eggs per female. Clausen (13) states that the productive capacity among the macrotype Tachinidae is generally between one and two hundred.

Adults lived in the insectary on sugar and water for a maximum period of thirty-five days and an average period of fifteen days.

Few definite data are available on sex ratios of Tachinidae, undoubtedly due to the difficulty in distinguishing sexes superficially. This same difficulty applies to Bessa selecta but it is possible to distinguish sexes and based on a number of reared adults the percentage of females is 46.4.

Incubation of Egg, Hatching, and Entry into Host.

In general macrotype eggs undergo the entire embryonic development outside the body of the parent (13). There are exceptions to this, an example being in the case of Ptychomyia remota (43), in which there occurs a partial and variable degree of uterine development. The normal period of incubation for macrotype eggs is thirty-six to fifty hours, with minimum and maximum periods of thirty minutes and four days respectively. Among other species it most frequently requires two to three days with a minimum of one day in a few instances.

Because of the habits of Bessa selecta it is difficult to determine when hatching has taken place. However, distinct evidence of eclosion occurring within twenty-four hours of deposition has been noted. The author suspects hatching may be delayed for two or three days, but that in general the incubation period lasts about twenty-four hours (Table 5). Baird (10) records that B. selecta eggs do not "apparently hatch" until the host has spun its cocoon. This could happen only if the eggs were deposited on the cocoon spinning stage, after the last moult.

There are two distinct ways in which Tachinidae maggots exit from macrotype eggs and enter the host. Among those many genera which have the indehiscent type of egg, the maggot bores directly downward through the thin chorion on the venter of the egg and through the host integument. In such cases there is no external evidence to indicate the egg has hatched. An exception to this method occurs in the case of

Eubiomyia calosomae (14), in which the young maggot escapes through the thin venter, but then emerges from beneath the egg to enter the host at some other point. In the other form, or dehiscent type of egg, hatching is effected by lifting a definite lid or operculum, at the cephalic end of the egg. The maggot then emerges through the resultant exit hole.

Bessa selecta has the dehiscent macrotype egg, but eclosion has been observed to take place in two ways with variations. The maggot may hatch from the egg by boring down through the thin ventral chorion and thence through the host integument. This may be accomplished near the center of the ventral surface or it may take place at the extreme cephalic end of the egg.

The young maggots may also force the operculum back sufficiently to permit exit. Regardless of the method, the operculum usually drops off with age, leaving a hole in the cephalic end of the egg. In this latter method the maggot may enter the host directly in front of the egg before it emerges entirely. With the caudal segments still enclosed within the egg, the maggot arches its body sufficiently to bring the buccopharyngeal apparatus into action against the host integument. After much scratching, the saw-like edge of the mouth-hook effects an entrance hole in the integument through which the maggot enters the body of the host. As a variation of this method the maggot may abandon the eggshell entirely and make its entry into the host at some distant point. A successful venture of this sort is infrequently found because the maggot is dislodged but occasionally a funnel is located a short distance from the eggshell.

After leaving the egg the maggot enters the host integument through the slit-like aperture formed by the mouthhook. The young maggot does not disappear entirely within the host. A small portion of the caudal end protrudes above the surface of the integument, the maggot being held in this position by the anteriorly directed spines on the posterior segments. The slit in the host integument serves as the distal opening of the subsequently formed integumental funnel eventually becoming more rounded as the funnel is formed. It is through this opening that the maggot maintains constant contact between the posterior spiracles and the outside atmosphere for respiratory requirements. As the funnel forms the maggot sinks more deeply below the surface of the integument, but still maintains direct contact with the external atmosphere.

Several interesting but unexplainable occurrences have been observed with respect to the location of the maggots. One instance occurred of two integumental funnels in one host, which bore only one egg and contained only one maggot. One funnel was located on the first thoracic segment adjacent to the head capsule, the other occurred on the second abdominal segment and this contained the maggot. On one other occasion the maggot was not found in its funnel, which was on the thorax, but after carefully dissecting the entire host, it was located near the anal segment, but not within a funnel.

On two other occasions young maggots apparently relocated themselves when the integumental openings to their respiratory funnels became sealed over. In each case the smaller funnels were unoccupied by maggots, but alongside these funnels larger funnels were present containing the maggots.

These occurrences suggest that because of some undesirable condition or another, the young maggot is capable of leaving its first point of establishment and relocating itself at another point. Whether under such circumstances the maggot effects the new opening by means of the buccopharyngeal apparatus or by some other means was not determined.

Formation of Integumental or Respiratory Funnel.

The respiratory requirements of Tachinidae maggots within the host are met by two general methods. There may occur a temporary tapping of an air sac or tracheal branch of the host; or respiration may be by means of a fixed source of exchange with the external atmosphere through the host tracheal system or directly through the integument. The latter involves the formation of a respiratory funnel within which is enclosed the caudal end of the maggot. This seems to be a very general occurrence among the Tachinidae (13).

The development of an integumental funnel outside of the Tachinidae is found only in a very few of the more highly specialized species of the Sarcophagidae. Their formation has not been found associated with any other families of parasitic Diptera (13).

These funnels are of two types (32), those developing at the point of entry of the maggot and designated as primary, which are always integumentary; and those arising as a result of activities of the maggot from within the host and termed secondary. The latter may be integumentary or tracheal in origin. An example of the secondary integumentary type occurs in Actia diffidens, a parasite of Peronea variana (33).

Funnels often begin to form immediately entry is effected into the host and may be consistent in position for a given species, as is the case with Actia diffidens (33). The position of the funnel of species that deposit macrotype eggs is governed by location of the egg on the host body.

The initial phase of the integumentary or respiratory funnel in Bessa selecta is the slit-like aperture made by the first instar maggot in entering the host. This opening widens to an elliptical shape and eventually becomes more or less round. The funnel proper is of host origin and is considered to arise as a result of a healing process to seal the injury.

The inward direction of this wound tissue, which forms the funnel is effected by the securing of the maggot to the edges of the opening by the spines of its posterior segments, thus preventing the tissue growing across the opening. The invaginating funnel usually bends to follow close to the inner body wall of the host. It has a segmented or annular appearance possibly due to irregular formation. The main part of the funnel is darkened and somewhat sclerotized, particularly near the integumentary opening. It ends abruptly as a sclerotized structure of cuticula and hypodermis and continues as a soft, membranous sleeve. The maggot rests within this sleeve with its caudal segments curved dorsally into the cone-shaped basal funnel and its spiracles applied to the aperture.

This membranous sheath is also believed to be of host origin. It is soft, flexible and opaque. Apparently it is the result of a defensive reaction on the part of the host, as is the funnel proper, similar to such structures formed where a foreign body is attacked by phagocytes. In this respect it differs in formation from the funnel. Muesebeck (29) considers the sheath of _Sturmia_ to be composed of hypodermal cells, leucocytes, and compressed fat cells, and that it envelopes only the funnel and the posterior portion of the body. In _Siphona cristata_ and other species the young overwintering maggots are entirely enclosed in the sheath or sleeve, but in older individuals the sheath is open at the anterior end (13). It is uncertain whether the sleeve is closed at the free end in the case of _Actia diffidens_. It has been observed beyond the tip of the maggot (33). If it does enclose the maggot it would have to be permeable to the host body fluids in order that the maggot obtain nourishment.

Dissections in the fall have revealed the overwintering maggots of _B. selecta_ to be encased in this sheath. Whether the opening exists at the anterior end of this sheath is uncertain. Normally it is believed to be present in the case of summer maggots. However, fall dissections of maggots which continued through the summer without developing, and spring dissections of overwintering maggots have revealed some maggots to be enclosed in a hard sclerotic shell. This shell was hard enough to greatly resist efforts to break it open with dissecting needles.

When opened many of these shells contained only decomposed remains of the maggots, while others contained dead or living maggots. It is believed that the young maggot is incapable of breaking through this shell to resume feeding in the spring. Although a number of living maggots have been taken from these shells, by far the majority have been dead at the time of later dissections, when other individuals had developed to more mature stages.

The cause of this hardened shell is undetermined. It is suspected to be a successful defensive reaction on the host's part to segregate this "foreign body" through a process which results in the hardening or sclerotization of the sheath. Since it completely envelopes the maggot, it is possible that the sheath does the same, at least in the case of the overwintering maggot. Certainly the later stages are not entirely encased by the sheath.

By the time the maggot reaches the third instar the funnel is a large, heavily sclerotized structure, with a large, shaggy membranous sheath at its anterior end. Incorporated in it are the exuviae of the first and second instars, usually attached to the sheath. These exuviae may be found at varying distances between the cephalic and caudal ends of the third stage maggot.

Development of the Maggot Instars:

The method of entering the host and establishment of the first instar maggot has been discussed. From this stage until the final engorgement by the mature maggot all functions of the maggot stage are carried on from within the funnel.

The first instar maggot feeds slowly and apparently makes its diet chiefly of the body fluids and fat bodies of the host, in the muscle layer. This stadium does not exert any apparent inhibitions on the development of the host. First instar maggots have become established in fourth stage larvae of the host and continued developing while the host advanced to the prepupal stage, from which the mature maggot emerged.

Living first stage maggots have been found within the bodies of dead, diseased host larvae. They appear capable of living within this state of decomposition until the contents have become too dry to longer serve as food. One instance of cannibalism was observed within a host which contained twenty-seven first instar maggots. One of these maggots had made its way into the body of another, and was found encased by the integument of the disposed-of maggot. Undoubtedly this occurred only because of the large number of maggots within the same host larva.

Moulting to the second instar is a gradual and relatively slow process. The first instar cuticula becomes loosened from the new epidermis. The posterior spiracles and the buccopharyngeal apparatus transform to those of the second instar, and for a time both sets of spiracles and both sets of mouth-hooks are present. The exuviae of the first instar splits at the cephalic end over the pseudocephalon, and is gradually forced backward until it becomes invested in the sheath of the integumental funnel, and perhaps eventually on the inner wall of the funnel.

The second instar maggot is larger and with its more efficient mouth-hooks is better equipped to attack the tissue of its host. It feeds more deeply in the host but apparently does not attack vital tissues since it has not been found to arrest development of the host. It probably subsists on body fluids, adipose, and perhaps other tissue. This stadium develops more rapidly, being a heavier feeder, reaching its maximum size in about four days.

Ecdysis occurs in the same manner as described above for the first instar. The second stage exuviae also eventually reach the sleeves of the integumental funnels.

The third instar maggot is armed with very heavy mouth-hooks, capable of attacking any part of the host contents. At first it feeds slowly until almost mature, and then leaving the funnel it lives freely within the body cavity of the host. Host contents at this time often appear very watery, as though some induced process of liquefaction had occurred. The maggot completely guts the host, leaving little more than the integument.

The manner of emergence of mature Tachinidae maggots from the host has several variations. The mature maggot usually makes an incision in the abdominal venter of the host. Some authors consider this is done by the mouth-hooks, while others are of the opinion it is accomplished by a pressure of the caudal end, aided by solvent action of body secretions. Nielsen (31) describes the caudal end foremost emergence of mature *Bessa selecta* maggots from the host, apparently using the latter method described above. The author has not found this to be the case, but rather that mature *Bessa* maggots leave the host cephalic end first, apparently having used the buccopharyngeal apparatus with which to incise the integument. This method has been observed to be the most normal habit (13).

Pupation.

The place of pupation of Tachinidae is variable. Most species form their puparia outside the bodies of their hosts in the soil. *Bessa selecta* forms its puparium in two places. The usual place is outside the host in the soil; but the puparium may be formed inside the cocoon. It has never been found in the larval skin.

The stage of the host from which mature maggots emerge is not consistent. Maggots have matured and left the fourth stage larva of *B. hercyniae*. Most often they emerge from the fifth stage larvae and drop to the forest floor. After entering the soil and finding a suitable location, they reverse their position so that the puparium is formed cephalic end uppermost. The maggot contracts along the antero-posterior axis until it takes on a squat sub-elliptical form. At first the forming puparium is white, gradually changing from yellowish to brown, and finally to a dark brown. The puparium thus formed consists of the third instar exuvium.

It frequently happens that the second generation maggot has not completed its development before the host larva has matured and dropped to the forest floor where it spins a cocoon. When this occurs the maggot emerges from the eonymphal or pronymphal stage of the host. Maggots may emerge from the pupal stage but this has never been observed.

Before pupating the maggot under these circumstances must prepare for its immediate or later exit from the cocoon. Robbins(35) determined that the maggot of Diplostichus janitrix cuts a circular groove with its mouth-hooks around the inner wall at one end of the Diprion pini cocoon. This cap is left only lightly attached and the fly in emerging forces it off to effect its exit from the cocoon. Other workers have found a similar occurrence with other species.

Bessa selecta does one of two things. The maggot upon leaving the host prepupal stage makes a hole in the end of the cocoon by what appears to be the combined use of the mouth-hooks and a secretion by the maggot, resulting in an aperture with a ragged protruded edge. The maggot may then leave the cocoon and pupate in the soil outside, or remain inside the cocoon to pupate. It is not uncommon in dissecting entire D. hercyniae cocoons to find B. selecta puparia, and perhaps emerged adults, inside. In such cases the maggots failed to provide a means of exit and the adults perished inside the host cocoon. The exit holes prepared by the maggots are sometimes too small to permit emergence of the adults and they may be found dead with only their heads protruding through the cocoons.

All maggots of the first generation mature inside the cocoon and either form their puparia inside the cocoon or in the soil.

Diapause.

The question of whether Bessa selecta exhibits a tendency toward diapause has come up in the past in connection with parasite studies of G. hercyniae. The problem was insufficiently covered by the author to offer any definite conclusions.

The term "diapause" as referred to here, is intended to be synonymous with dormancy, and to include in its inference the definition of the term as given by Shelford (38), "A condition in which no further activity or progress can be induced until certain physiological changes of a physico-chemical character have taken place."

Sometimes a lack of progress was observed among first instar maggots; development appeared to be suspended. Table 3 shows the extended period over which first generation first instar maggots occurred. Some of these were not dissected, but permitted to continue within the host until fall. In the meantime the hosts spun their cocoons, and some in pupating sloughed the maggots with the prepupal integument, while other host prepupae remained in their recognized diapause(34) until the maggots were dissected. Table 6 indicates the same occurrence in the first instar maggots of the second generation.

Those first generation first instar maggots which continued through the summer in a state of inactivation were found at the time of fall dissections to be enclosed in the dark, sclerotic shell referred to above. Spring dissections revealed some of the overwintering maggots were similarly encased.

The occurrence of this inactivity on the part of first instar maggots was so closely associated with the formation of a hardened sheath that it remains uncertain whether diapause exists.

If we assume that normal development of the parasite is sufficiently rapid to make unsuccessful any attempt on the part of the host to segregate the maggot, then it is difficult to understand how these maggots were trapped, unless development was suspended.

On the other hand the physiology involved in the formation of the sheath is so little understood, that no conclusions can be drawn as to whether or not the maggot, even when development is normal, may on occasion be successfully segregated. A healthy, vigorous host may be successful in its efforts, whereas a weaker individual might fail to offset the maggot.

Diapause among first instar maggots of <u>Bessa selecta</u> remains an open question, although the author doubts that it exists, believing that failure on the part of first instar maggots to develop is due to sclerotization of the sheath.

EFFICIENCY AS A PARASITE
(See Tables 9 and 10)

A number of occurrences threaten the ultimate success of Bessa selecta developing to the adult stage. If it were not for such happenings the efficiency of this Tachinid as a parasite of G. hercyniae might be greatly enhanced.

The following is a list of occurrences reducing efficiency on which data were recorded in rearings:

(a) Eggs sloughed.

(b) Maggots dead in the eggs.

(c) Maggots dislodged.

(d) Maggots sloughed.

(e) Unknown.

(a) Eggs sloughed. When the eggs are deposited on the host as it is ready to moult, they are subject to sloughing with the host exuviae. Since so little time elapses between deposition of the egg and the exit of the maggot, it seems improbable that this would happen very frequently. The difficulty of determining exactly when the maggot does leave the egg may have resulted in some error of deciding the egg had been sloughed before hatching, when actually it had died within the egg. From field collected material it was determined that 4.1 percent of the eggs had been sloughed, while 3.8 percent of the insectary deposited eggs were cast before hatching.

(b) Maggots dead in the eggs. Frequently maggots were found dead from unknown causes inside the eggs. These maggots had developed embryologically but failed to leave the eggs for some reason. This occurrence appeared to be somewhat more prevalent among field collected material than among insectary reared material. Of the total eggs collected in the field 24.8 percent contained dead maggots, while 16.9 percent of those eggs deposited under insectary conditions contained dead maggots.

(c) Maggots dislodged. When the young maggots leave the egg altogether to enter the host integument they are in a position to be dislodged rather easily. Empty eggs were found and since no integumental funnel was present on the host, the habits of the young maggots suggest they left the egg and were dislodged before entering the host. This was found to be the case with 15.9 percent of the field collected material while only 6.2 percent met a similar fate in the insectary.

(d) Maggots sloughed. Occasionally the first instar maggots have been sloughed with the host exuviae. This is understandable when the establishment of the maggot occurs just prior to or simultaneously with the moulting of the host. Under such circumstances the young maggot would not be sufficiently secured to withstand the ecdysis. On one occasion this happened when an overwintering maggot which was firmly established in its funnel was sloughed with the prepual exuvium at the time of host pupation. The adult G. hercyniae was not injured in any way, other than that it bore a scar on the abdominal dorsum. Observations have revealed only 0.4 percent of the total material handled was in this category.

(e) Unknown. Mention is made of this group, consisting of 5.9 percent of the total, as unknown. Actually they probably all belong in the two categories "died in the egg" and "maggots dislodged." It so happens that the records were not completed for several lots - the cast exuviae of the hosts were not analysed.

In addition to the above occurrences which react on the efficiency of B. selecta several other things happen on which no complete data was kept.

(f) Wasted oviposition. Occasionally a host larva is found with more than one B. selecta egg attached to it. Considering the things which may happen to a single individual before it reaches the adult stage, two or three eggs on one host larva may assure successful parasitism of the host. However, an individual host larva will apparently support only one maggot to maturity. If others are present they will succumb to the strongest. On one occasion a mature maggot emerged from the host and examination revealed two first instar and one third instar maggots remaining. None of these would have survived in a dead host depleted of food material. Of a total of 503 parasitized larvae reared, there were 590 eggs present or an average of 1.2 per larva.

(g) Emergence of Maggots from Cocoons. Frequently the mature maggots do not emerge from the cocoons but merely puncture one end and then form their puparia within the host cocoon. If this hole has not been made large enough the adult is unable to emerge, and often the adults are found dead with only their heads protruding through the punctures made by the maggots.

Dissections of cocoons bearing no punctures have revealed puparia and dead adults inside. In such cases the maggots failed to make arrangement for the subsequent emergence of the adult stage.

Field Records of Parasitism.

Before entering a discussion on records of parasitism it is felt that mention should be made regarding expression of parasitism.

While observing the activity of parasites in connection with the rearing of forest insects a number of degrees of parasitism have been noted. Larvae may be obtained from the field which contain parasite eggs or established maggots, but development of such parasites to the adult is often interrupted at various stages with the result that the adults do not emerge.

When we speak of "percent parasitism" what exactly do we mean? Do we mean that a particular percent of larvae were parasitized to the extent that they bore eggs? Do we mean a certain percentage of larvae were parasitized because they contained parasitic maggots? Do we mean that from a known number of individuals a certain number of parasite maggots emerged and hence the percent parasitism was so much? Do we mean that from that known number of parasitized individuals a certain number of parasitic adults emerged to carry on the work of their species?

Each instance definitely represents parasitism but it is no indication of the efficiency of a parasite to state that a certain percentage parasitism was observed if we are referring merely to the number of host larvae bearing eggs; or containing maggots; or from which maggots emerged but died before the adult stage; or from which adults emerged while also there were cases of each of the others.

In expressing percent parasitism some indication of the parasite's success should be given in order that at a glance one may estimate the actual efficient work done by the parasite. The following definitions are suggested as doing this. For the purpose of these definitions it is considered that the success of a parasite depends upon destruction of the host, achievement of maturity, and the production of a new generation.

(a) Unsuccessful Parasitism is that form of parasitism when the host insect has been subjected to attacks of a parasite but survived, while the parasite died as a result of being sloughed, etc., before reaching the adult stage.

(b) Partially Successful Parasitism is that form of parasitism occurring when the host insect is killed by the activities of the parasite, and the parasite dies as well before reaching the adult stage.

(c) Successful Parasitism is that form of parasitism occurring when the host insect is killed by the activities of the parasite, and the adult parasite emerges to produce progeny.

(d) Total Parasitism is an expression of the summation of all three. It is that form of expression which includes all evidence of parasitism in a given sample, whether it be successful, partially successful or unsuccessful.

In this particular paper reference is made to "potentially successful parasitism." This is merely considered a convenient term to express what might have been successful parasitism if the development of the maggots had not been stopped by dissections. It is not intended to be adopted as an expression of parasitism. In the usual studies of parasite efficiency the term would be unnecessary, although occasions might arise when it would conveniently express what might otherwise have been successful parasitism if wilful mechanical interference had not prevented it.

Another expression of parasitism which should be redefined here is that of superparasitism, which is "that form of parasitism occurring when there is a superabundance (more eggs laid than can survive) of parasites of a single species attacking an individual host insect."

Of 3,151 G. hercyniae larvae collected in the field the total parasitized was only 169 or 5.4 percent total parasitism (Table 11). When broken down this represents only 0.2 percent successful parasitism, 0.3 percent partially successful parasitism. Those potentially successfully parasitized, that is 2.5 percent, can mostly be included in the last two categories, since the percentage lost after the maggots become established is comparatively low. However this would yield at the most 3 percent successful and partially successful parasitism. Unsuccessful parasitism was 2.4 percent.

These were the only data collected on field parasitism of G. hercyniae by Bessa selecta, but they are considered to be representative of what was found in the past. Of course some areas when taken individually would yield a higher rate of parasitism. The material used for these data was collected in various parts of New Brunswick and represents the average conditions. Table 11 also shows the percentages of parasitism for the different categories in the individual lots. This reveals that the total percent parasitism varied between 0.9 and 25.0, while the successful and partially successful parasitism ranged from 0.6 percent to 10.7 percent.

Occasionally fairly high percentages of parasitism occurred. From casual observations these appeared to occur most noticeably in spruce stands adjacent to larch or mixed with larch in which the larch sawfly was present in greater than normal numbers. This is taken as indicating that *Bessa selecta* being more numerous under such conditions, was attracted to *Gilpinia hercyniae* from *Pristiphora erichsoni*, and that probably the parasite does make a better showing on *P. erichsoni* than it does on *G. hercyniae*. In some localities *B. selecta* is considered to be an important control factor.

Samples of cocoons from the field give an incomplete picture of the activity of *Bessa selecta* because of its habit of sometimes leaving the host larva before the cocoon is spun.

HOST RECORDS

The host preferences of Tachinidae are chiefly among the Lepidoptera and Coleoptera, Clausen (13). Bessa selecta is one of the relatively few species which attack sawfly larvae, the Tenthredinoidea. One frequently finds reference to Bessa selecta as "a parasite of sawflies." Rearings of this Tachinid indicate how apt a description this is.

Bessa selecta is considered by the author as primarily a parasite of Pristiphora erichsoni in Nova Scotia and New Brunswick at least. It is believed that heavy parasitism of other species of sawflies, including Gilpinia hercyniae, occurs only adjacent to or among larch stands where P. erichsoni is present in fairly large numbers.

Among those Tenthredinoidea from which the author reared B. selecta are Pristiphora erichsoni (Htg.), Gilpinia hercyniae (Htg.), Pristiphora geniculata (Htg.), Pikonema alaskensis Roh., P. dimmockii Cress., and Neodiprion abietis Harr. Only seldom was it taken from Lepidopterous hosts among which were Nymphalis antiopa, and Nepytia canosaria Wlk.

Attempts were made in the insectary to rear B. selecta on other Lepidoptera but without success. Among these were Eupithecia spp. (from spruce), Ellopia fiscellaria Gn., and Elaphria versicolor Grt. Eggs were deposited but the maggots did not become established.

Table 1 lists the hosts from which Bessa selecta has been reared as recorded in the literature.

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Table 1 Host and Distribution Records of *Bessa selecta* Meigen

Host	Locality	Remarks on *B. selecta*	Authority
Trichiocampus viminalis Fall.	Kew, Scotland	"effectively prevents pest appearing in large numbers"	Fisher (1922)
Pteronus ribesii Scop.	Kirton, Great Britain		Miles (1924)
Pteronus salicis L.	Charante-Inferieure and Deux-Sevres, France	"found in numerous rearings"	Lacroix (1928)
Lygaeonematus laricis Htg.	Mecklenburg, Germany		Hsin (1935)
L. wesmaeli Tischb.	Mecklenburg, Germany		Hsin (1935)
Hyponomeuta euonymellus Clysia ambiguella Hb. Polychrosis botrana Schiff.	Germany	"important parasite of these web-moths"	Stehli (1921)
Pristiphora alnivora Htg.	Upper Silesia		Torka (1934)
Pristiphora wesmaeli Tischb.	Bavaria		Thielmann (1938)
Priophorus padi L.	Kiev, Russia		Dobrodeiev (1916)
Pteronus ribesii Scop.	Kiev, Russia		Dobrovliansky (1915)
Pristiphora pallipes Lep.	Kiev, Russia		Dobrovliansky (1915)
Lygaeonematus moestus Zadd.	Kiev, Russia	"heavily parasitized, reduced population of host on apple trees to nil"	Lebedev (1926)
Pteronus ribesii Scop.	North Russia	"about 84% of fifth stage larvae parasitized"	Korsakova (1927)
Pristiphora pallipes Lep.	Luga District-Russia	"about 15% of larvae were parasitized"	Kazyakina-Vinogradova (1931)
Diprion polytomum Htg.	West of Finnish Lapland	"6% larvae collected were parasitized"	Lovaszy (1939)
Tortrix murinana Hb.	Lower Austria	"of minor importance in natural control"	Schimitschek (1936)
Hyponomeuta malinellus Zell.	Serbia		Vukasovic (1931)

Table 2 Dissections to Show Overwintering Stage

Lot Number	Date Dissected	Number of Maggots	Maggot Instar
1	Aug. 29	4	I
2	Sept. 8	3	I
3	" 16	6	I
4	" 23	2	I
5	Oct. 4	4	I
6	" 8	2	I
7	" 27	2	I
8	Nov. 9	6	I
9	Dec. 9	15	I
10	" 12	3	I
11	May 6	2	I
12	" 8	18	9-I and 9-II

Table 3 Development of Maggots-First Generation

Lot Number	Date Dissected	Number of Maggots	Maggot Stadia		
			I	II	III
12	May 8	18	9	9	
13	" 11	4	4		
14	" 13	8	6	2	
15	" 17	4	1	3	
16	" 18	6	6		
17	" 20	3	2	1	
18	" 24	3	1	2	
19	" 25	7	7		
20	" 27	2		2	
21	" 30	8		8	
22	" 31	2		1	1
23	June 1	6		2	4
24	" 3	2		1	1
25	" 7	7		1	6
26	" 8	5			5
27	" 10	1			1
28	" 12	6			6
29	" 14	5			5

Mean Development Dates:-

I Instar, prior to May 15

II Instar, May 21

III Instar, June 8

Table 4 Development of Puparia and Adult Emergence - First Generation

Maggots Emerged	Puparia Formed	Number of Individuals	Adults Emerged	Number of Individuals
June 4	June 5	11	July 5	3
" 5	" 6	22	" 6	16
" 6	" 7	11	" 7	10
" 7	" 8	9	" 8	6
" 8	" 9	1	" 9	17
" 9	" 10	47	" 10	21
" 10	" 11	23	" 11	10
" 11	" 12	7	" 12	4
" 13	" 14	2	" 15	1
			" 16	9
			" 17	2
			" 18	1

Range:- June 5 to 14	Range:- July5 to 18
Mean Date:- June 9	Mean Date:- July 10

Table 5 Development of Eggs

Date Deposited	Number of Individuals	Date of Hatching	Number of Individuals	
July 15	16	July 16	14	
" 16	25	" 17	21	
" 17	25	" 18	24	
" 18	120	" 19	93	First Generation
" 24	24	" 25	19	
" 25	51	" 26	35	
" 27	16	" 28	14	
" 28	21	" 29	18	
Aug. 6	?	-	-	
" 7	?	-	-	
" 9	5	-	-	Second Generation
" 26	4	Aug. 27	4	
" 27	3	-	-	
" 28	5	-	-	
" 29	11	-	-	

Table 6 Development of Maggots - Second Generation

Instar I		Instar II		Instar III	
Date Dissected	Number of Individuals	Date Dissected	Number of Individuals	Date Dissected	Number of Individuals
July 22	20	July 23	1	July 17	1
" 23	3	" 24	1	" 21	2
" 24	4	" 25	1	" 24	1
" 25	109	" 29	3	" 25	2
" 27	13	" 30	4	" 26	1
" 29	18	" 31	2	" 27	2
" 30	10	Aug. 2	1	" 29	1
" 31	7	" 5	2	" 30	2
Aug. 2	13	" 10	2	" 31	7
" 4	4	" 11	2	" 1	2
" 5	6			" 2	1
" 7	1			" 3	3
" 8	2			" 4	2
" 10	5			" 5	9
" 11	9			" 6	1
" 27	1			" 7	1
Sept.29	13			" 8	2
				" 9	1
				" 10	2
				" 11	1
				" 12	1
				" 14	1
				" 25	5

Instar I	Instar II	Instar III
Range: July 22 to Aug. 11	Range: July 23 to Aug. 11	Range: July 17 to Aug. 25
Mean Date: July 28	Mean Date: Aug. 1	Mean Date: Aug. 4

Table 7 Development of Puparia and Adult Emergence - Second Generation

Puparia Formed	Number of Individuals	Adults Emerged	Number of Individuals
July 19	1	July 31	1
" 22	2	Aug. 2	1
" 25	1	" 5	1
" 26	2	" 7	1
" 27	1	" 9	1
" 30	1	" 11	3
" 31	2	" 12	3
Aug. 1	6	" 13	2
" 2	2	" 14	1
" 3	1	" 15	1
" 4	3	" 17	1
" 5	4	" 18	2
" 6	4	" 19	3
" 7	1	" 20	4
" 8	2	" 23	5
" 9	2	" 25	1
" 10	1	" 26	1
" 11	1	" 27	1
" 12	1	" 30	1
" 13	1	Sept. 1	1
" 15	1	" 2	1
" 26	5	" 4	2
		" 6	2
		" 14	1
		" 16	1

Range: July 19 to Aug. 26
Mean Date: Aug. 5

Range: July 31 to Sept.16
Mean Date: Aug. 21

Table 8 Frequency of Host Larval Instars Parasitized

		Instars									
	Total	II		III		IV		V		VI	
Series	Larvae	No.	%	No.	%	No.	%	No.	%	No.	%
A	150	1	0.6	4	2.7	2	1.3	133	88.7	10	6.7
B	262	-	-	10	3.7	5	1.9	237	90.7	10	3.7
Totals:	412	1	0.2	14	3.4	7	1.7	370	89.9	20	4.8

Table 9 Parasitism of Field Collected <u>Gilpinia hercyniae</u> Larvae

Showing What Happened to <u>Bessa selecta</u>. Series A.

Lot Number	Number Larvae	Number Parasitized	Total Eggs & Maggots	Eggs Sloughed No.	Eggs Sloughed %	Maggots Died in Eggs No.	Maggots Died in Eggs %	Maggots Dislodged No.	Maggots Dislodged %	Maggots Sloughed No.	Maggots Sloughed %	* Maggots Established No.	* Maggots Established %	Maggots Matured No.	Maggots Matured %	Maggots Pupated No.	Maggots Pupated %	Adults Emerged No.	Adults Emerged %
1	12	3	3	2	66.6	1	33.3	-	-	-	-	-	-	-	-	-	-	-	-
2	16	1	2	2	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	88	1	1	-	-	-	-	1	100.0	-	-	-	-	-	-	-	-	-	-
4	95	1	1	-	-	1	100.0	-	-	-	-	-	-	-	-	-	-	-	-
5	135	2	2	1	50.0	-	-	-	-	-	-	1	50.0	-	-	-	-	-	-
6	105	1	1	1	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	490	6	6	-	-	1	16.7	-	-	-	-	4	66.6	1	16.7	-	-	-	-
8	367	39	40	1	2.5	12	30.0	6	15.0	-	-	19	47.5	-	-	1	2.5	1	2.5
9	290	1	1	-	-	-	-	1	100.0	-	-	-	-	-	-	-	-	-	-
10	249	3	3	-	-	1	33.3	2	66.6	-	-	-	-	-	-	-	-	-	-
11	350	11	11	-	-	3	27.3	2	18.2	1	9.1	5	45.4	-	-	-	-	-	-
12	223	36	40	-	-	11	27.5	9	22.5	-	-	15	37.5	2	5.0	-	-	3	7.5
13	176	29	29	-	-	5	17.2	5	17.2	-	-	13	44.8	3	10.4	1	3.5	2	6.9
14	50	3	3	-	-	3	100.0	-	-	-	-	-	-	-	-	-	-	-	-
15	221	12	12	-	-	3'	25.0	-	-	-	-	9	75.0	-	-	-	-	-	-
16	46	2	2	-	-	-	-	-	-	-	-	2	100.0	-	-	-	-	-	-
17	86	10	10	-	-	-	-	1	10.0	-	-	9	90.0	-	-	-	-	-	-
18	152	2	2	-	-	1	50.0	-	-	-	-	1	50.0	-	-	-	-	-	-
Totals:	3151	163	169	7	4.1	42	24.8	27	15.9	1	0.6	78	46.2	6	3.6	2	1.2	6	3.6

* Dissected before development completed

+
tain
%
20.0
-
-
-
-
-
-
-
-
29.3
-
10.8
-
20.8
9.1
11.9
gots

Table 10 Insectary Induced Parasitism of Gilpinia hercyniae

Showing What Happened to Bessa selecta Series B

Lot Number	Number Parasitized	Total Eggs and Maggots	Eggs Sloughed No.	Eggs Sloughed %	Maggots Died in Eggs No.	Maggots Died in Eggs %	Maggots Dislodged No.	Maggots Dislodged %	Maggots Sloughed No.	Maggots Sloughed %	* Maggots Established No.	* Maggots Established %	Maggots Matured No.	Maggots Matured %	Maggots Pupated No.	Maggots Pupated %	Adults Emerged No.	Adults Emerged %	† Uncertain No.	† Uncertain %
19	75	75	1	1.3	31	41.4	14	18.6	-	-	12	16.0	-	-	-	-	2	2.7	15	20.0
20	15	15	-	-	6	40.0	7	46.7	-	-	2	13.3	-	-	-	-	-	-	-	-
21	9	11	-	-	4	36.4	-	-	-	-	7	63.6	-	-	-	-	-	-	-	-
22	2	2	-	-	2	100.0	-	-	-	-	-	-	-	-	-	-	-	-	-	-
23	11	11	-	-	-	-	1	9.1	1	9.1	8	72.7	-	-	-	-	1	9.1	-	-
24	5	7	1	14.3	-	-	-	-	-	-	6	85.7	-	-	-	-	-	-	-	-
25	6	25	-	-	2	8.0	-	-	-	-	22	88.0	-	-	-	-	1	4.0	-	-
26	2	3	-	-	2	66.6	-	-	-	-	-	-	-	-	-	-	1	33.3	-	-
27	20	20	1	5.0	1	5.0	-	-	-	-	18	90.0	-	-	-	-	-	-	-	-
28	37	41	7	17.2	1	2.4	-	-	-	-	16	39.1	1	2.4	2	4.8	2	4.8	12	29.3
29	5	5	-	-	2	40.0	-	-	-	-	3	60.0	-	-	-	-	-	-	-	-
30	71	121	-	-	8	6.6	-	-	-	-	95	78.7	-	-	1	0.8	4	3.1	13	10.8
31	6	6	-	-	1	16.7	-	-	-	-	4	66.6	-	-	1	16.7	-	-	-	-
32	24	24	-	-	3	12.5	1	4.2	-	-	15	62.5	-	-	-	-	-	-	5	20.8
33	52	55	6	10.9	8	14.6	3	5.5	-	-	32	58.1	-	-	1	1.8	-	-	5	9.1
Totals:	340	421	16	3.8	71	16.9	26	6.2	1	0.2	240	57.0	1	0.2	5	1.2	11	2.6	50	11.9

* Dissected before development completed

† Belong under "Maggots died in eggs" and "Maggots dislodged"

Table 11 Parasitism of *Gilpinia hercyniae* by *Bessa selecta*

Series A

Lot Number	Total Larvae	Total Parasitism No.	%	Unsuccessful Parasitism No.	%	Partially Successful Parasitism No.	%	Potentially Successful Parasitism No.	%	Successful Parasitism No.	%
1	12	3	25.0	3	25.0	-	-	-	-	-	-
2	16	2	12.5	2	12.5	-	-	-	-	-	-
3	88	1	1.1	1	1.1	-	-	-	-	-	-
4	95	1	1.0	1	1.0	-	-	-	-	-	-
5	135	2	1.4	1	0.7	-	-	1	0.7	-	-
6	105	1	0.9	1	0.9	-	-	-	-	-	-
7	490	6	1.2	1	0.2	1	0.2	4	0.8	-	-
8	367	40	10.9	19	5.2	1	0.2	19	5.2	1	0.2
9	290	1	0.3	1	0.3	-	-	-	-	-	-
10	249	3	1.2	3	1.2	-	-	-	-	-	-
11	350	11	3.1	6	1.7	-	-	5	1.4	-	-
12	223	40	17.9	20	8.9	2	1.0	15	6.7	3	1.3
13	176	29	16.4	10	5.7	4	2.3	13	7.2	2	1.2
14	50	3	6.0	3	6.0	-	-	-	-	-	-
15	221	12	5.4	3	1.4	-	-	9	4.0	-	-
16	46	2	4.3	-	-	-	-	2	4.3	-	-
17	86	10	11.6	1	1.2	-	-	9	10.4	-	-
18	152	2	1.3	1	0.6	-	-	1	0.6	-	-
Totals:	3151	169	5.4	77	2.4	8	0.3	78	2.5	6	0.2

Fig. 1 Dorsal view of egg.

Fig. 2 Lateral view of egg.

Fig. 3 Lateral view of first-instar maggot.

Fig. 4 First-instar maggot showing position in integumentary funnel, sleeve, and sheath.

Fig. 5 Lateral view of buccopharyngeal apparatus of first-instar maggot.

Fig. 6 Dorsal view of same.

Fig. 7 Lateral view of buccopharyngeal apparatus of second-instar maggot.

Fig. 8 Dorsal view of same.

Fig. 9 Posterior spiracle and stigmatic chamber of first-instar maggot.

Fig.10 Ventral view of pseudocephalon of first-instar larva.

Fig.11 Posterior spiracles of second-instar maggot.

Fig.12 Posterior spiracles of third-instar maggot.

Fig.13 Anterior spiracle and stigmatic chamber of second-instar maggot.

Fig.14 Anterior spiracle and stigmatic chamber of third-instar maggot.

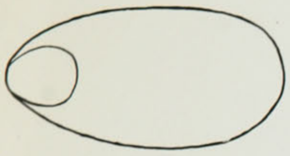
Fig.15 Anterior larval (third-instar) spiracle remaining on puparium.

Fig. 16 Lateral view of prothoracic spiracular apparatus of pupa.

Fig.17 Lateral view of prothoracic cornicle of the prothoracic spiracular apparatus.

Fig.18 Enlarged view of the prothoracic spiracle of pupa.

Fig.19 Lateral view of second-instar maggot.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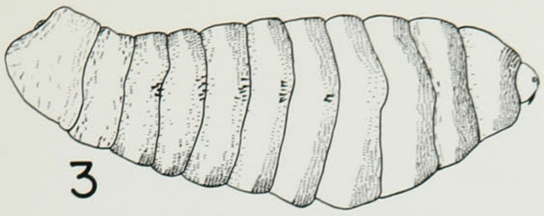
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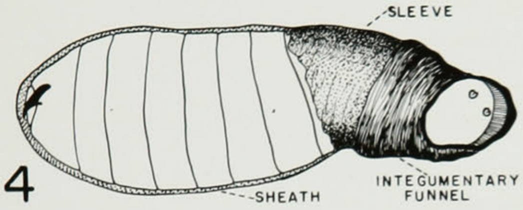
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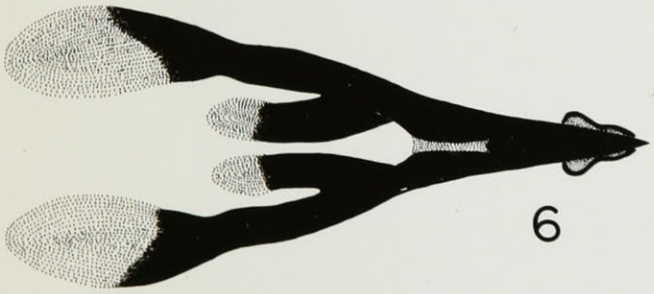
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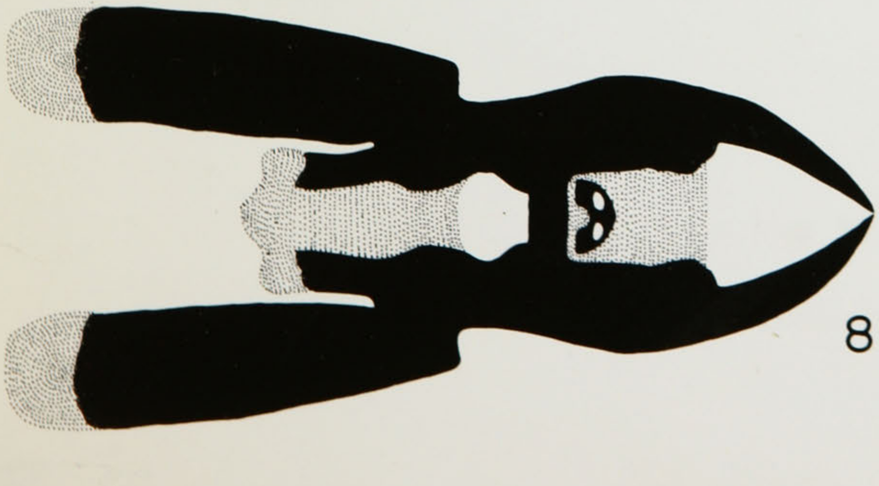
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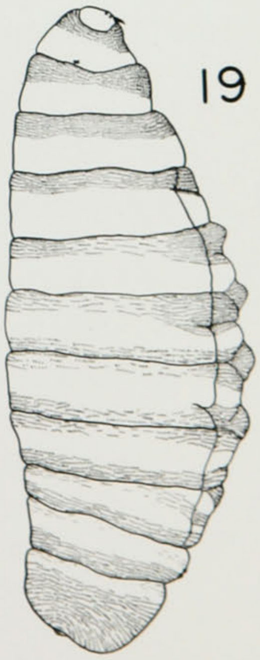
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Fig.20 Lateral view of third instar maggot.

Fig.21 Ventral view of pseudocephalon of third-instar larva, showing enlarged views of sensoria.

Fig.22 Ventral view of abdominal segments seven and eight of third-instar maggot to show position of anal opening.

Fig.23 Lateral view of buccopharyngeal apparatus of third-instar larva.

Fig.24 Dorsal view of same.

Fig.25 Ventral view of pupa showing development of appendages, mouthparts, eye regions and antennae.

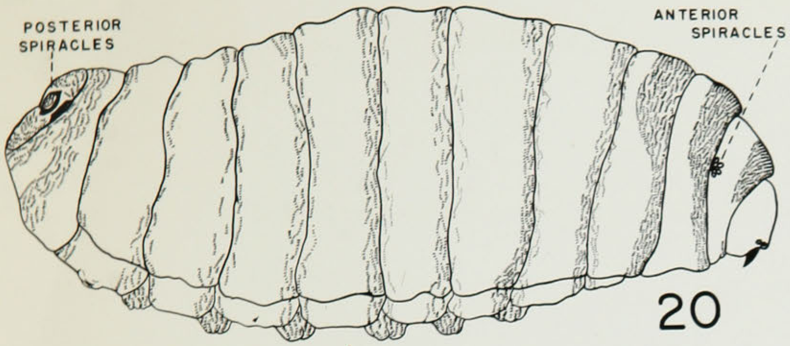
Fig.26 Dorsal view of pupa.

Fig.27 Lateral view of pupa, showing position of prothoracic spiracular apparatus.

Fig.28 Lateral view of puparium, showing position of lines of cleavage, position of prothoracic cornicle, remains of third-instar larval armature and ambulatory organs.

Fig.29 Posterior view of puparium, showing remains of third-instar larval posterior spiracles, and anal opening.

Fig.30 Anterior view of puparium, showing prothorax, mesothorax, and region of invaginated pseudocephalon.



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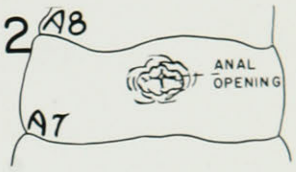

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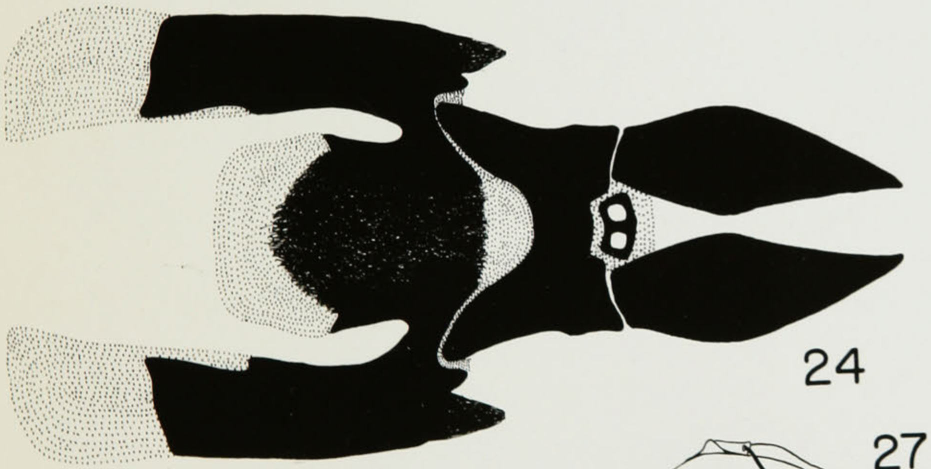

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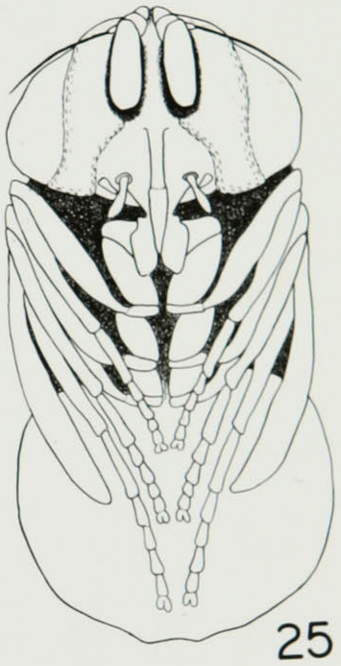

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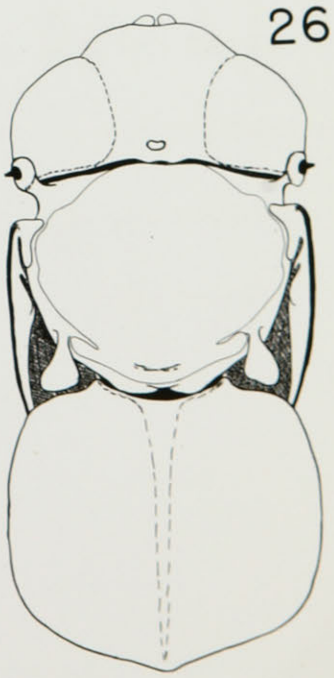

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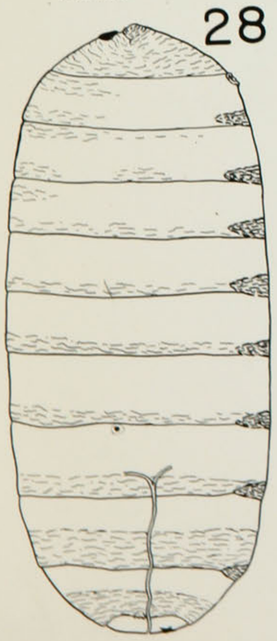

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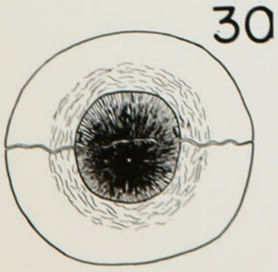

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