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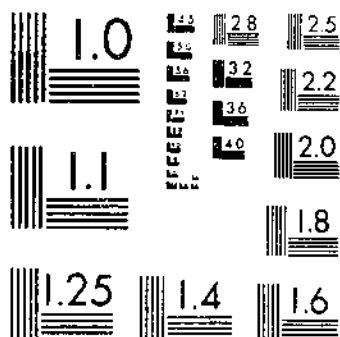
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APANTELES THOMPSONI LYLE: A BRACONID PARASITE OF THE EUROPEAN CORN BORER

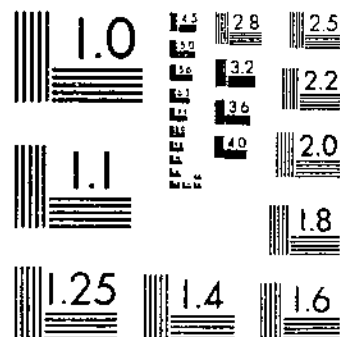
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UNITED STATES DEPARTMENT OF AGRICULTURE
WASHINGTON, D. C.

APANTELES THOMPSONI LYLE,
A BRACONID PARASITE
OF THE EUROPEAN CORN BORER

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INTRODUCTION

The gregarious braconid parasite *Apanteles thompsoni* Lyle² was first mentioned in literature in 1927, when it was described by Lyle (11)³ as a new species from specimens collected in northern France. W. R. Thompson and H. L. Parker, of the United States Bureau of Entomology at the European parasite laboratory, Hyères, Var, France, first found it in larvae of *Pyrausta nubilalis* Hübn., in *Artemisia*, near Brussels, Belgium, in 1920. In their bulletin on this insect and its controlling factors in Europe (25) they give a brief discussion of the biology, limiting factors, and extent of parasitism by this species.

¹ The writer expresses his appreciation to H. L. Parker, under whose direction these studies were carried on, for his inspiration and willing advice which have been of invaluable aid; to H. D. Smith, a laboratory associate, for his many helpful suggestions; to Esther Hart for her drawing of the adult; to Jean Boitchenko for his field collection of parasite material; and to Theodore Malama for his clerical assistance.

² Order Hymenoptera, family Braconidae.

³ Italic numbers in parenthesis refer to Literature Cited, p. 26.

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A single colony of what is thought to have been *A. thompsoni* was found by Thompson and Parker in corn in the Jura district of eastern France in 1921. In 1924 a more extended search for the parasite resulted in the discovery of several points in northern France, notably in the region of Lille, Nord, where it occurred as a parasite of the borer in *Artemisia* in sufficient abundance to permit its collection for shipment to the United States.

The first shipment in quantity was made in 1926 and has been followed by further shipments each year since that time. To date 159,355 individuals of *A. thompsoni* have been collected in northern

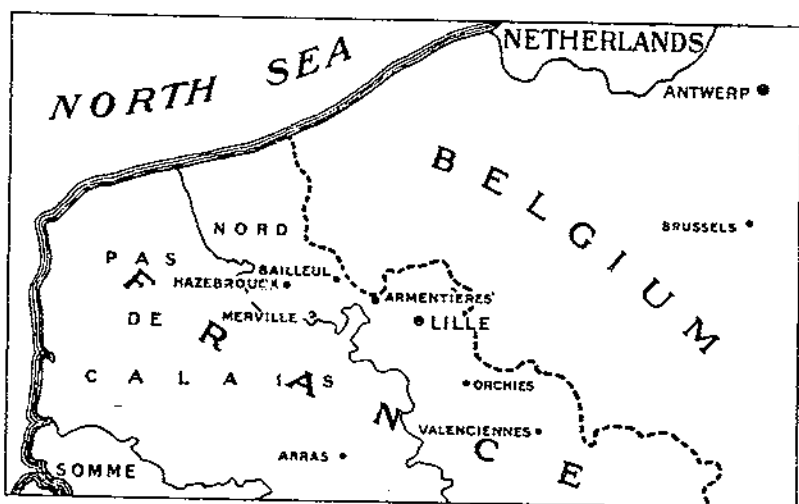


FIGURE 1.—Map of area in which *Apanteles thompsoni* occurs in greatest abundance, including the district in northern France from which collections of this parasite are sent to the United States. Colonies have been found in all towns indicated.

France and shipped to the United States. Of this number 5,935 were sent in 1926, 33,175 in 1927, 96,789 in 1928, and 23,456 in 1929.

DISTRIBUTION AND HOST RELATIONS

The favored habitat of *A. thompsoni*, so far as it is known, appears to be the Sequanian (north) zone,⁴ covering an area that extends, roughly, from Arras (fig. 1), in the upper part of France, north to the coast and east toward Antwerp and Brussels in Belgium. Practically no corn is grown in this area, but within a radius of a few miles of the city of Lille about 50 per cent of the plants of *Artemisia vulgaris* L. are commonly infested by *P. nubilalis*.

⁴The arrangement of the biogeographical zones used in the discussion of *A. thompsoni* corresponds to that followed by Thompson and Parker (25) and Parker, Vance, Smith, and Gamkrelidze (16). Physical and climatic characteristics form the basis for the separation of these areas. Briefly, the zones here mentioned are: The Sequanian (north), comprised of the lowlands of north-central France, including the region of Flanders; the Sequanian (south), in the basin of the Seine, with the exception of its more eastern parts, including the city of Paris and its environs; the Rhodanian, the region east of the upper Rhône in France and the valley itself as far south as Privas, Valence, and Digne; the Aquitainian, covering the southwestern corner of France, bounded on the south by the Pyrenees, on the north and northeast by the foothills of the central plateau, and extending westward to the Atlantic Ocean; and the Danaprisian, the mixed forest and steppe region of the Dnieper River in Russia.

A. thompsoni has been found, however, in several other districts where corn is the chief food of the borer. In 1921 a few specimens were collected in the Jura area of eastern France known as the Rhodanian zone; its presence in very limited quantities was discovered near Bayonne, France, in the maritime part of the Aquitainian zone in 1928. Borer larvae collected in 1928 from the Danaprisian zone in Russia were parasitized by a gregarious braconid which was probably *A. thompsoni*; and Kotlán (10) has recorded a borer parasite from Hungary which may be the same species.

Although at present *P. nubilalis* is the only known host of this species of *Apanteles*, there is no reason to suppose that under proper conditions it would not attack larvae of related species.

CLIMATE AND AGRICULTURE OF FAVORED HABITAT

The Sequanian (north) zone, considered the favored habitat of *A. thompsoni*, as pointed out by Thompson and Parker (25), has a transitional type of climate. The mean yearly temperature is about 50° F., and that of the winter is 35° to 37°. There is an average absolute minimum temperature of about 12° and an average absolute maximum of about 93°. The five months, December to April, inclusive, constitute the drier part of the year, whereas the period from May to October has a higher precipitation. June and October are the rainiest months, and February is the driest. The average annual rainfall for Lille is about 27 inches.

For the most part the area is one of mixed agriculture. The successful culture of corn is prevented by the low summer temperatures, and *Artemisia*, a weed common in waste areas and along the railway lines, provides the chief food supply of the larvae of *P. nubilalis*.

ECONOMIC IMPORTANCE OF APANTELES THOMPSONI

The average parasitism of *Pyrausta* larvae by *A. thompsoni* for different years from 1920 to 1929, inclusive, in its various zones of known distribution, is shown in Table 1. The parasitism in the Sequanian (north) zone, where the most extensive investigations have been made, dropped decidedly, from 22.9 per cent in 1924 to 2.9 per cent in 1925, and has since remained rather low.

TABLE 1.—Parasitism of larvae of *Pyrausta nubilalis* by *Apanteles thompsoni*, by years, in different zones

Zone	Year	Average parasitism	Host plant	Zone	Year	Average parasitism	Host plant
		Per cent				Per cent	
Sequanian (north)	1920	(1)	Artemisia.	Sequanian (south)	1924	-0.01	Artemisia.
	1924	22.9	Do.		1921	-.01	Corn.
	1925	2.9	Do.	Rhodanian	1925	1.1	Artemisia.
	1926	3.2	Do.		1925	.08	Corn.
	1927	6.6	Do.	Aquitainian	1927	-0.01	Do.
	1928	2.5	Do.	Danaprisian	1928	6.3	Do.
	1929	.5	Do.				

¹ First found.

In the year of heaviest parasitism, i. e., 1924, a maximum of 42.6 per cent was found in a collection of 513 specimens of host larvae from Lille, and in the same year 16.3 per cent of a collection of 276 borers was parasitized in the vicinity of Brussels.

The degree of parasitism by *Apanteles* varies at different points in the Sequanian (north) zone, as shown by a survey made during the winter of 1928-29 and presented in Table 2. These data show that as high parasitism as 15 per cent occurred that year at Merville, but that the average for Lille, obtained from the examination of a large number of specimens, was only 2.8 per cent.

TABLE 2.—Local variation in degree of parasitism of *Pyrausta nubilalis* larvae by *Apanteles thompsoni* in northern France, 1928

Locality	Host specimens examined	Parasitism	Locality	Host specimens examined	Parasitism
	Number	Per cent		Number	Per cent
Lille.....	3,803	2.8	Armentières.....	188	3.7
Arras.....	261	2.5	Orchies.....	159	2.6
Hazebrouck.....	118	8.5	Valenciennes.....	258	1.6
Merville.....	100	15.0	Total.....	5,144	
Bailleul.....	320	2.5	Average.....		3.1

With the exception of the 6.3 per cent parasitism found in a lot of larvae from Russia in 1928, the parasitism by *Apanteles* in borers infesting corn has been very slight, and the greater supply of this parasite has been obtained from *Pyrausta* larvae inhabiting *Artemisia*. In central Europe the species is so rarely encountered as a parasite of the corn borer that it is a negligible factor of control.

Superficially *A. thompsoni* does not appear to have great importance as a factor in the control of the corn borer, but it is undoubtedly true that it plays a certain rôle in the preservation of a natural balance which, if upset by its elimination, might allow the reproductive rate of the borer to increase and permit it to become a more severe pest of marketable crops than it is now.

DESCRIPTIONS

ADULT

(Fig. 2)

The original description of the species by Lyle (11), based on a study of 11 females collected in Lille, Nord, France, is as follows:

♀. Black, shining; palpi pale; antennae beneath fusco-testaceous; clypeus and mandibles rufo-testaceous; belly at base testaceous; sides of abdominal segments 1 and 2 fusco-testaceous; legs testaceous, with hind coxae black or blackish, hind femora and tibiae slightly infuscated at tips, and hind tarsi more or less infuscated. Wings subhyaline, stigma pale fuscous, nervures paler but usually visible to the extreme margin of the wing.

Thorax: Mesothorax smooth, shining, feebly punctate; scutellum and metathorax smooth and shining. Legs with spurs on hind tibiae half as long as the metatarsus. Abdomen with first segment rather more than twice as long as its medial breadth, with sides parallel for half its length then narrowed to the almost truncate apex, smooth with some faint lateral striation; second

segment rather more than half as long as third with two oblique impressed lines converging forward and enclosing a triangular space, smooth and shining like the remaining segments. Terebra briefly exerted, barely surpassing the anus.

Length, 3 mm.; expanse, 5-6 mm.

The male is at present unknown.

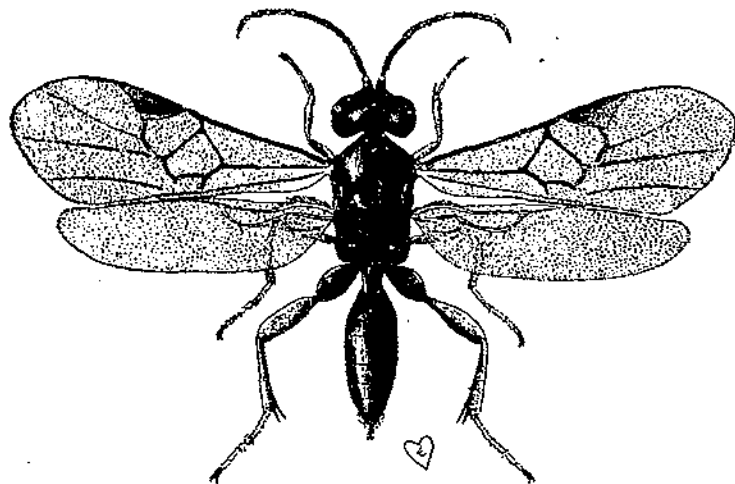


FIGURE 2.—Adult female of *Apanteles thompsoni*. X 16

EGG

Length at oviposition, 0.17625 mm.; greatest width, 0.05625 mm.

The ovarian or newly laid egg (fig. 3, A) of *A. thompsoni* is translucent white, quasicylindrical in form, broadly rounded at its

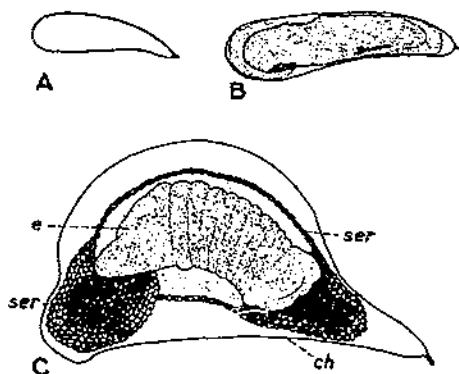


FIGURE 3.—Eggs of *Apanteles thompsoni*; A, Well-developed ovarian egg; B, egg 3 days old; C, egg 5 days old and just prior to hatching.

cephalic end, and of nearly the same width for half of its length, after which it gently narrows to a smaller rounded caudal extremity which possesses a short blunt petiole. The surface is smooth.

Symbols used in Figures 3, 4, 5, 6, and 7

<i>ac</i> , anterior commissure.	<i>mi</i> , mid-intestine.
<i>av</i> , anal vesicle.	<i>mt</i> , Malpighian tube.
<i>br</i> , brain.	<i>mtb</i> , mouth.
<i>ch</i> , chorion.	<i>mx</i> , maxilla.
<i>cin</i> , chitinous intima.	<i>mcp</i> , maxillary palpus.
<i>e</i> , embryo.	<i>mase</i> , maxillary seta.
<i>epth</i> , epithelium.	<i>r</i> , rectum.
<i>es</i> , esophagus.	<i>rov</i> , rudimentary ovary.
<i>h</i> , head.	<i>s8</i> , eighth abdominal segment.
<i>hbg</i> , histoblasts of external genital appendages.	<i>s9</i> , ninth abdominal segment.
<i>hi</i> , hind-intestine.	<i>ser</i> , serosa.
<i>hrt</i> , heart.	<i>sesgn</i> , subesophageal ganglion.
<i>int</i> , intestine.	<i>sikd</i> , common duct of silk glands.
<i>lb</i> , labium.	<i>sikdo</i> , external opening of common duct of silk glands.
<i>lbp</i> , labial palpus.	<i>sikgl</i> , silk glands.
<i>lbr</i> , labrum.	<i>sp</i> , spiracle.
<i>lbrpr</i> , labral process.	<i>spo</i> , spiracular opening.
<i>lbse</i> , labial seta.	<i>vnc</i> , ventral nerve cord.
<i>md</i> , mandible.	

FIRST-STAGE LARVA

Length on hatching, 0.64 mm.; near end of stage, 2 mm.; head width, 0.16 mm.; length of mandible, 0.0763 mm.

The larva (fig. 4, A) of *A. thompsoni*, upon hatching from the egg, has a translucent white body, fairly uniform in width but tapering very slightly from the head to the anal segment. The rather square head (*h*) is followed by three thoracic and seven distinct abdominal segments. The last abdominal segment is three times the length of any of the other segments, and might, perhaps, better be regarded as a division, since it, no doubt, represents several true but as yet undifferentiated segments. It carries at its extremity a slight cap-like swelling (*av*), which later further evaginates to form the anal vesicle.

Each of the last two thoracic and the seven abdominal segments bears dorsally a single transverse row of sharp, translucent spines directed posteriorly. These spines are nearly half as long as a segment, and the first eight rows are arranged across the middle of the segment; on the last and largest segment they are placed more anteriorly. Their number on any or all segments is variable, but commonly there are more present and they are less widely separated on the last three abdominal than on the other segments.

After a period of feeding and growth the larva (fig. 4, E), although still in the first stage, has changed considerably in appearance from that of its earliest condition just described. The body is now rather transparent, somewhat narrowed toward the head, and has at the anal extremity a large vesicle. In addition to the head there are now three thoracic and nine distinct abdominal segments, and an anal vesicle (*av*) which consists of an evagination of the hind-intestine. At this time the spines are so small in comparison with the increased size of the larva that they are seen with difficulty. The transparency of the cuticle and hypodermis, however, more easily permits a study of the internal anatomy of the larva.

The head (fig. 4, B, C) has a mouth opening (*mtb*), located somewhat ventrally, with two sharp, slightly curved mandibles (C, *md*;

D). Both labrum (*lbr*) and labium (*lb*) are present, and from the top of the head a protuberance carrying two labral processes (B, C, *lbrpr*) projects over the mouth opening.

The 2-lobed brain (fig. 4, E, *br*) and subesophageal ganglion (*sesgn*) fill a large part of the head. The ventral nervous system (*vnc*) is continued by a chain of 13 ganglia, consisting of 1 ganglion in each of the three thoracic segments, 1 in each of the first seven abdominal segments, and 3, more or less fused, in the eighth and ninth abdominal segments. Main branches pass from the ganglia

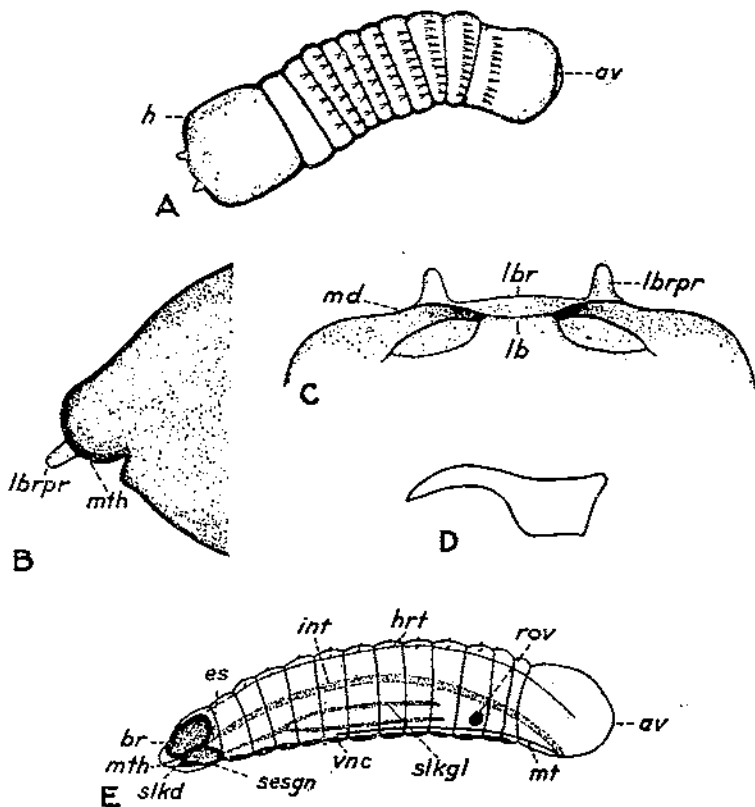


FIGURE 4.—First-stage larva of *Apanteles thompsoni*: A, Early first-stage larva, dorsal view; B, head of first-stage larva, lateral view; C, head of first-stage larva, viewed somewhat ventrally; D, mandible of first-stage larva; E, gross internal anatomy of late first-stage larva, lateral view, showing digestive tract, left Malpighian tube, ventral nervous system, heart, one of the silk glands, and one of the rudimentary ovaries

into the various segments and further distribute themselves to supply the entire body, with the exception of the anal vesicle, into which the nervous system does not extend.

Two fairly straight silk glands (*slkgl*) extend posteriorly and lateroventrally from the head region. These become bifurcated in the third thoracic segment—the branches of each ending abruptly in the region of the sixth abdominal segment. Just back of the mouth the two glands empty into a short common duct (*slkd*) which leads to the upper border of the labium.

From the mouth opening (*mt*) the digestive tract is continued by a slender esophagus (*es*) into the first thoracic segment, where it enlarges into the mid-intestine (*int*). This is a long, slightly curved tube lying near the center of the body and entering the anal vesicle, which it partially traverses. It ends on the ventral wall of this vesicle. At this point, and arising at the very apex of the mid-intestine, are attached two straight, slender Malpighian tubes (*mt*) which extend forward ventrally to the region of the second abdominal segment.

The heart (*hrt*) runs dorsally from the anterior segments to the anal vesicle; the posterior end situated within the vesicle is somewhat enlarged. The flow of blood, as usual, is controlled by a series of valves.

The tracheal system is present, but the very small tubes are not yet inflated with air. Situated in the region of the seventh abdominal segment and rather latero-ventrally are two rudimentary ovaries (*rov*).

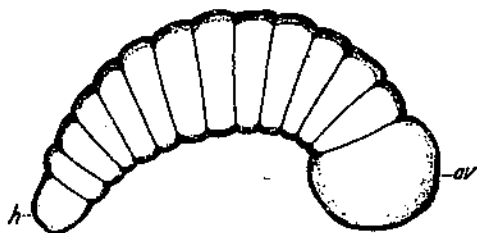


FIGURE 5.—Second-stage larva, lateral view

SECOND-STAGE LARVA

Length near end of stage, 4 mm.; width, 0.84 mm.; head width, 0.28 mm.

The larva (fig. 5) of this stage is somewhat club-shaped, being larger posteriorly and tapering toward the oblong head (*h*). The anal vesicle (*av*) is now as large or slightly larger in diameter than the widest abdominal segment, and the body segmentation is the same as in the fed larva of the previous stage. The larva has become more opaque and is of a creamy or yellowish color. Both mandibles and buccal armature are very slightly chitinized.

The tracheal system consists of two lateral longitudinal trunks, each of which gives rise to 10 principal branches; it appears to be filled with air but is still apneustic.

The mid-intestine is larger because of the feeding of the larva and the consequent accumulation of undigested material within the peritrophic membrane. Otherwise it differs little from that of the first-stage larva. The Malpighian tubes have increased in size and now extend to the first abdominal segment.

The silk glands, which have become larger and very much convoluted, fill the greater portion of the body cavity as far back as the seventh abdominal segment, and scattered fat cells are visible. The pear-shaped rudimentary ovaries are in the seventh abdominal segment, and the histoblasts of the external genital appendages (fig. 6, A) appear on the ventral floor of the eighth and ninth abdominal segments. The six imaginal buds of the legs show on the ventral surface of the three thoracic segments; laterally on the second and third thoracic segments are the developing wing pads.

LAST-STAGE LARVA

Length at end of feeding, 4.5 mm.; width, 1 mm.; head width, 0.48 mm.; length of mandibles, 0.08438 mm.; diameter of thoracic spiracular opening, 0.02437 mm.

In the earlier part of the last stage the shape of the *Apanteles* larva resembles that of the second stage; the anal vesicle persists and segmentation is the same. Later, at about the time of its issu-

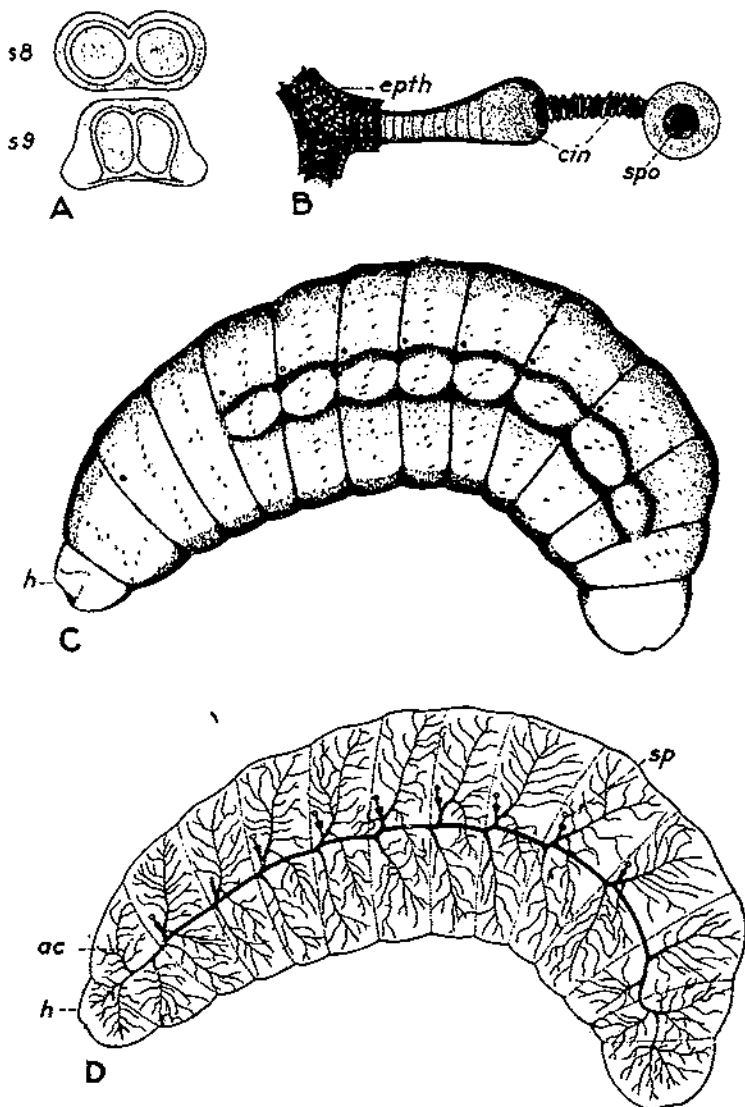


FIGURE 6.—Last-stage larva of *Apanteles thompsoni*: A, Histoblasts of external genital appendages located ventrally on the eighth and ninth abdominal segments of second-stage and last-stage larvae; B, thoracic spiracle and portion of trachea of last-stage larva, with part of epithelial layer cut away to show the chitinous intima; C, last-stage larva, lateral view; D, main tracheal system of last-stage larva, lateral view. (Only left half shown)

ance from the host, the parasite larva (fig. 6, C) assumes a more rounded and plump form, and the anal vesicle by invagination becomes the hind-intestine. The head and thoracic segments are now

supplemented by 10 well-differentiated abdominal segments, on the first 8 of which are rather large lateral lobes produced by the arrangement of the muscles in that part of the body. The larva is quite opaque, and urate cells are visibly distributed among the fat cells.

The tracheal system (fig. 6, D) is well developed and consists of two longitudinal trunks, one on each side of the body, united in the first thoracic segment by a transverse dorsal commissure (*ac*), but not joined posteriorly as in the case of certain ichneumonids, chalcids, and some other braconids. The head is supplied by two anterior branches from each longitudinal trunk, while the last abdominal segment is entered by the posterior end of the trunk, which there branches in all directions. From each main trunk a dorsal and a ventral branch are given off in each of the thoracic and first nine abdominal segments; these branches terminate in a network of fine ramifications. In addition, from near the base of these dorsal branches in the last two thoracic and first seven abdominal segments, a smaller branch leads inward in a ventral direction.

Open spiracles (fig. 6, D, *sp*) are present, one pair being located laterally and slightly dorsally in the second thoracic segment and in each of the first to seventh abdominal segments, inclusive. Each spiracular opening (fig. 6, B, *spo*) is surrounded by a light-brown chitinous ring. The chitinous intima (*cin*), surrounded by its single layer of epithelial cells (*epth*), runs inward for a short distance as a rather small spiral tube, but soon enlarges into a bulblike structure which gradually narrows to the general diameter of the main tracheal trunk.

The ventral nervous system, typical in general arrangement of that of the Hymenoptera, is composed of a brain (fig. 7, A, *br*), subesophageal ganglion (*esgn*), and 11 other ganglia (*vnc*), the last of which occurs in the eighth abdominal segment. The two cords which connect the various ganglia, while not fused, are not very widely separated.

The digestive system consists of the mouth (fig. 7, A, *mtb*), the slender esophagus (*es*), the mid-intestine (*mi*) distended with the contents of the peritrophic membrane and closed at its posterior end, the rather bulb shaped hind-intestine (*hi*), and the rectum (*r*) opening at the extremity of the last segment. From the anterior extremity of the hind-intestine two Malpighian tubes (*mt*) emerge, make a sharp downward curve, and continue rather straight along the ventral floor to the third abdominal segment.

The two large silk glands (fig. 7, A, *slkgl*) occupy much of the body cavity; their general arrangement is similar to that of the previous stages. The short common duct coming from the opening (*slkdo*) on the labium quickly branches into the two lateral glands, each of which subdivides in the third thoracic segment, after which the branches convolute for the remainder of their length in the abdominal segments.

The dorsal heart (fig. 7, A, *hrt*) is the chief organ of circulation, and by its valvular action causes the blood to flow and bathe the various internal organs.

The head (fig. 7, C) of the last-stage larva, with its well-chitinized and more distinctly outlined buccal parts, differs considerably in appearance from that of either previous stage. The lower edge of

the wide and somewhat raised labrum (*lbr*) extends back into the mouth opening (*mth*) in the form of a wide inverted V, in the apex of which are located four very minute, round, sensorial structures.

On each half of the upper lip are four short, closely placed, spinous sensory organs lying within a light-brown area, and immediately above are three short spines placed in a triangular form. Two more

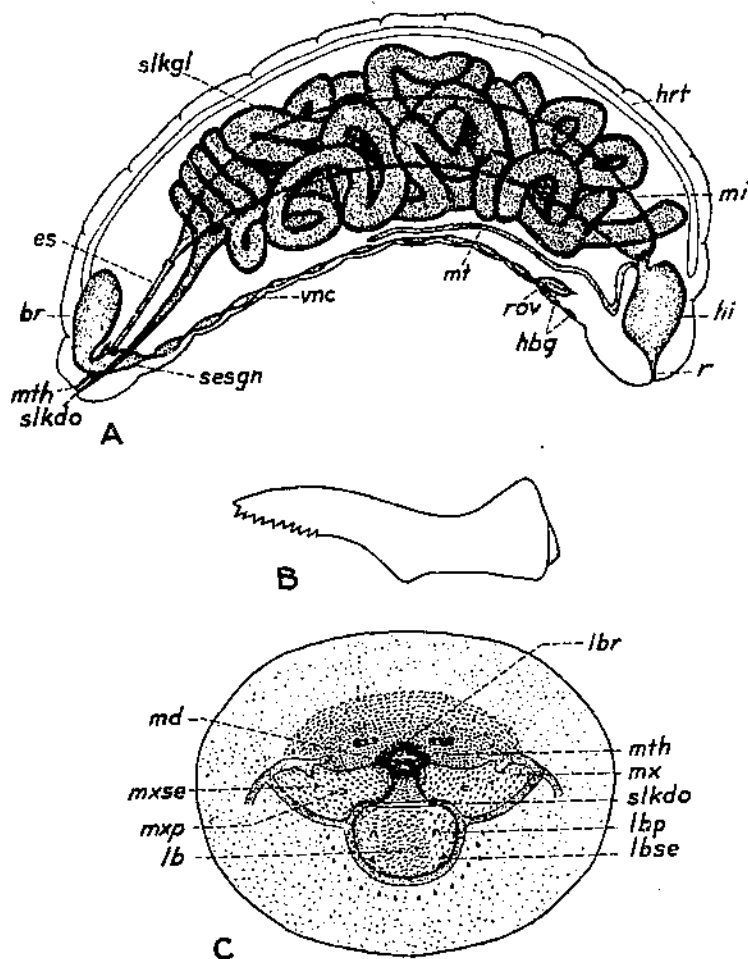


FIGURE 7.—Parts and organs of last-stage larva of *Apanteles thompsoni*: A, Gross internal anatomy of last-stage larva, lateral view, showing digestive system with left Malpighian tube, ventral nervous system, heart, one of the silk glands, and one of the rudimentary ovaries with histoblasts of external genital appendages; B, mandible of last-stage larva; C, head of last-stage larva, front view

such spines occur near the base of each mandible, and a row of five others extends from that region, but slightly nearer the mouth opening, in a direction upward and mediad.

Rather round in shape and slightly elevated, the labium (fig. 7, C, *lb*) bears near its lower edge a pair of widely separated setae (*lbse*), above which are situated the two labial palpi (*lbp*). Near its upper

margin occurs the slitlike opening (*skdo*) of the common silk duct, beyond which the lip slopes into the mouth cavity.

The raised maxillae (fig. 7, C, *mx*) lie one on each side of the lower lip. Each bears a palpus (*mxp*) and a short seta (*mxse*), while about the lower edge of the labium on what may be termed the mentum 16 short spines are arranged in a semicircle.

Each of the two brownish and strongly chitinized mandibles (fig. 7, B and C, *md*) has a wide base, a short sharp point, and 10 saw-like teeth. The mandibles articulate on two short processes of the thickened epicranial suture, and the maxillae and labium are bounded by thickened chitinous borders.

The labrum, labium, and maxillae are covered with tiny round tubercles. These are most numerous on the labrum and on those parts of both labrum and labium bordering the mouth opening.

PUPA

Length, 3 mm.

The pupa of *A. thompsoni* is motionless and of the free or exarate type common to the Hymenoptera. At first it has a light-yellowish color, except for the blackish eyes and dark-brown ocelli. Within a few days the head and both ventral and dorsal parts of the thorax become smoky colored, and the entire pupa gradually darkens to the black of the adult.

COCOON

Length, 4 mm.; width, 1.5 mm.

The cocoon is woven with delicate white threads secreted by the silk glands of the full-grown larva after its issuance from the host. Its surface is dull. Both ends of the cocoon are rounded. All of the cocoons of a colony are loosely bound together in an irregular manner by similar threads and are also fastened to the inside of the plant tunnel or other surface upon which the host was resting when the parasite larvae issued. Occasionally the dead or dying host itself is included in the webwork.

BIOLOGY

BEHAVIOR UNDER LABORATORY CONDITIONS

For the writer's purpose, a box 2 feet square and 6 inches deep, covered at one end with cheesecloth and closed at the other end by a sliding glass plate, provided a satisfactory cage for handling the adults. Such a cage was placed with the cheesecloth toward a window and the opposite side partly opened. Young borer larvae (stages 1 to 4) to be parasitized were placed on the cage floor, and each one was removed after having been stung by the female. Quantitative handling and breeding of *Apanteles*, however, call for the use of a modification of such a cage to reduce the possibility of escape of the lively adults and so facilitate manipulation by the worker.

Immediately after being parasitized, the young borer larvae, in lots of 20 or 25, were put into small round tin boxes and supplied with leaves of dock for food. They were kept under such conditions at various temperatures until about their fourth instar, when each

was put into a glass vial and fed with stems of dock until the issuance and spinning of the mature parasite larvae. The colonies of parasite cocoons were then kept in similar vials and provided with slight moisture until the adults emerged.

Water and drops of sugar solution were constantly kept before the caged females, which fed on both fluids. Prolongation of the life of *A. thompsoni* seems to be best accomplished by the method used by Jones (9), i. e., keeping the adults in a box cage (similar to that just described) in a cool, dark closet and bringing them out into light and warmth for only a short time each day to allow them to feed and oviposit. Adults so treated lived as long as one month, whereas females placed in small glass globe cages, even when given food and moisture, lived only a few days.

Colonies of cocoons, if put in dry glass vials and kept at a constant temperature of either 68° or 77° F., almost invariably failed to produce adults, and subsequent dissection showed that death occurred at various points in the transformation of the pupa into the adult. The placing of moist blotting paper or a bit of green vegetable matter within the tube, as a rule, insured a satisfactory emergence. If too much moisture was provided, however, the results were sometimes unfavorable.

Temperature alone, during the development within the cocoon, seemed to be a less important factor, as equally high percentages of emergence were obtained under conditions of a constant temperature of either 68° or 77° F., and of ordinary room temperatures with a fluctuation from about 68° in the daytime to around 61° at night.

OVIPOSITION

Only a few seconds are required for the actual deposition of the eggs. Upon sensing the presence of a host larva the female quickly approaches and with one thrust of her ovipositor deposits a number of eggs in it.

She may oviposit two or three times in the same larva before leaving it to go through the more or less usual postoviposition motions of preening herself. The host larva is not paralyzed by the ovipositor of the female and continues to squirm constantly until the completion of oviposition. Oviposition may occur at any time of day.

The female assumes no characteristic position during the act of oviposition. At times the wings are held upright over the back and remain motionless, and often the clinging female is rolled completely over several times by the wriggling host larva. It was observed that the apparent inclination of the parasite to oviposit in a certain larva was sometimes more pronounced when two or more females were attacking it than when only one was present, and it was not uncommon to see several females in close contact and thrusting their ovipositors sharply at one another. In this connection it was noted that not all of the larvae punctured by the ovipositor of the female parasite actually contained eggs.

The number of eggs deposited at a single thrust of the ovipositor was variable. From 20 to 25 seems to be a normal number, although often more or fewer were found. Large numbers of eggs within a host, however, are usually the result of several depositions by one or several females. At one time the writer made an attempt to

"saturate" a large third-stage borer larva with *Apanteles* eggs. The larva was placed for 15 minutes in a cage containing many females, and according to close observation received 45 ovipositor thrusts. Upon dissection a total of 868 eggs were counted, or an average of 19 eggs per thrust, and no doubt the actual number of eggs deposited was even greater than could be determined by this count. The average capacity of the female ovaries seems to be about 230 eggs, although as many as 262 fairly well developed eggs were dissected from the ovaries of a female which had no opportunity to oviposit for several weeks.

The female will deposit eggs immediately after emergence, although the oviposition activities are considerably more pronounced after several days of feeding. It may be that in nature she first feeds and allows some time to pass before she begins a search for borer larvae.

There seems to be no decided preference on the part of the female as between second, third, and fourth stage larvae, and for oviposition purposes all three stages probably serve equally well. First and fifth stage larvae are not immune from attack, but the former are too small and weak in themselves to withstand parasitism effectively and soon die either from the shock of the sting or the presence of the parasite eggs, while the skin of the latter is too thick easily to permit the penetration of the ovipositor.

DEVELOPMENT OF THE EGG

At a constant temperature of 68° or 77° F. eggs within second, third, or fourth stage host larvae hatch in about five days. Under field conditions the incubation period is perhaps slightly longer.

Soon after deposition the egg begins to increase in size, and a steady growth, accompanied by slight changes in shape, is maintained until the time of hatching. The individual eggs from a single lot deposited at one time differ in the degree of development attained within the oviducts of the female, and a certain variation in the embryonic growth also occurs. The average daily development, however, as based upon a study of numerous entire and sectioned specimens, takes place about as described in the paragraphs that follow.

Cell differentiation soon commences, and on the first day after oviposition the entire preembryonic mass gradually pulls slightly away from the chorion at the posterior end of the egg.

The egg when 2 days old contains an outer layer of long columnar cells or blastoderm, within which lies a narrow longitudinal region filled with yolk matter and containing a number of yolk cells.

In the 3-day-old egg (fig. 3, B) are to be found the early embryonic layers in the process of formation and differentiation, surrounded by a cellular membrane. This envelope, the writer believes, is the serosa. A few cells are grouped at the two ends of the embryonic mass while the remaining cells form a narrow layer along its sides.

By the fourth day the embryo has formed, and the segments and larval organs are becoming defined. This embryo, composed of a large head and 10 other segments, lies in the center of the egg entirely surrounded by the cells of the serosa. The anterior half is

inclosed by a great mass of these round-shaped cells which extends out to the chorion, and a smaller quantity of the same type of cells is segregated at the posterior end. A single layer of the cells (more oval in form) extends lengthwise on both sides of the embryo to join the masses segregated at the anterior and posterior ends. Certain instances, however, have been observed in which a smaller quantity of serosal cells was present at either extremity of the embryo and more than one layer extended partly down the sides. Except where the serosal cells touch the very anterior inside of the chorion, the embryo inclosed within its cellular envelope lies free within the chorion of the egg, which is now considerably swollen but still retains more or less of its original shape.

The appearance of the egg (fig. 3, C) when 5 days old and just prior to hatching (bursting of the chorion) resembles in most respects that of the previous day as just described. It is greatly swollen dorsally and anteriorly, while the posterior portion of the chorion with its petiole is empty. Both the embryo (*e*) and the cells of the surrounding serosal envelope (*ser*) have increased in size, and the entire mass lies free in the expanded chorion. In fact the entire egg has so developed in size since its deposition that it is now three times the length of a fresh egg and eight times as wide through its middle. The embryo has attained its full growth, and shortly the chorion (*ch*) bursts, liberating a first-stage larva nearly surrounded by the clinging masses of serosal cells. The head parts, especially the labral processes, are the first to emerge from the cellular envelope. It is, however, several weeks before the first-stage larva has freed itself from these cells, and in some cases a few serosal cells have been found clinging to *Apanteles* larvae 1 month old. These cells distribute themselves throughout the body cavity of the host larva and are quite conspicuous when parasitized host larvae are dissected.

DISCUSSION OF THE EMBRYONIC ENVELOPE

Numerous references to the presence of a cellular envelope about the embryo of monembryonic entomophagous parasites have been published. Some authors, in speaking of the embryology of the parasitic Hymenoptera, term this envelope the amnion; others speak of it as the serosa; while those of a third group consider that both the amniotic and serosal layers are present. Recorded instances of the existence of very large quantities of serosal cells at the time of hatching of the egg, however, are less numerous, and many of these records, if not the larger part, appear to be confined to the Braconidae.

Tower (27) has figured diagrammatically the embryo of *Apanteles militaris* Walsh as surrounded first by the fused amniotic and serosal envelopes, later by these fused envelopes dividing into two parts, with the serosal cells grouped at each pole, and finally, at the time of hatching, by an amniotic layer inclosing the entire embryo and all within a thick layer of serosal cells extending out to the very chorion of the egg. He believed that there occurred a separation of the cells into one portion which is cast out at the poles of the egg and becomes a body of loose cells (of serosal origin) lying between the chorion and the embryo, and another portion which becomes a layer of broad flattened cells (amnion) inclosing the embryo.

Pemberton and Willard (17), in treating of the biology of several braconid fruit-fly parasites in Hawaii, speak of a "gelatinous mass of large cells" extending along the ventral surface of the body of the first-stage larva of *Diachasma tryoni* Cameron, from the back of the head to the tip of the abdomen, and state that these are the serosal cells which adhere to the larva until it molts for the first time. In making a comparison of *Opius humilis* Silv. with *D. tryoni*, these authors say that the ventral mass of serosal cells retained by *O. humilis* after the hatching of the larva is much smaller in volume, less conspicuous, and is often broken away from the larva before the molt to the second instar. The same authors also figure serosal cells still clinging to a cast skin of a first-instar larva of *Diachasma fullawayi* Silv. According to Willard (28), the larva of the braconid *Opius fletcheri* Silv. (a parasite of the melon fly), when first hatched, is surrounded by a mass of serosal cells which cling to it until it is almost ready to molt to the second instar. Willard states that these cells of *O. fletcheri*, however, were never observed clinging to the first larval molt as in the case of the three parasites of the Mediterranean fruit fly (*D. tryoni*, *O. humilis*, and *D. fullawayi*).

The egg of another braconid, *Daemusa arcularis* Nees, is illustrated by Haviland (6) as containing a well-developed embryo surrounded by a "trophic membrane" which apparently consists of a large quantity of cells of serosal origin, polygonal in surface view, and resembling those present in the egg of *A. thompsoni*. This author states that toward the end of embryonic development the nuclei of these cells appear in various stages of degeneration. In an earlier paper Haviland (5) briefly considered the embryonic membrane in Charips, a member of the Cynipidae, and at the same time discussed the interpretations of Silvestri and Gatenby relative to such a membrane in certain of the Chalcididae.

Zorin (30), in a paper on *Apanteles gabrielis* Gaut. and Riel, has figured both the early and late stages of the egg of that species, showing the changes which take place in shape and size as the larval embryo develops. The egg of the later embryonic stages, as drawn by Zorin, appears to contain quantities of cells which are undoubtedly of serosal origin, although no explanation to this effect is offered. In fact the egg of *A. gabrielis* in all stages resembles very much that of *A. thompsoni*.

Grandori (3) mentions only the amnion as present in the egg of *Apanteles glomeratus* (L.) Reinh., and discusses the persistence of the cells of this envelope until the issuing of the internal-feeding parasite larvae from their host.

In a study of the parasites and hyperparasites of aphids Spencer (24) has given some interesting data on the serosa as it occurs in certain species of the Aphidiinae, a subfamily of the Braconidae. This author states that only a single embryonic membrane is formed by these species and that in the case of *Diaeretus rapae* Curt. it is derived from a delamination or extrusion of cells from the ectoderm of the early embryo. During embryonic development these cells increase in size and number, become polyhedral in shape with oval nuclei, and fit rather loosely around the embryo. There exists the probability, according to this writer, that the serosal membrane is broken up by a cytolytic enzyme secreted by the larva. At any rate, with the hatching of the larva the serosa divides into various-sized

fragments which undergo a strange process of vacuolization and growth and are finally devoured with the various tissues of the aphid.

More recently Jackson (8) has thrown new light on the serosal membrane and the way in which it functions in the braconid *Dinocampus* (*Perilitus*) *rutilus* Nees, and has summarized much of the previous work on this subject. Miss Jackson discovered that the cells of the embryonic membrane in *D. rutilus* increased in size with the development of the embryo until the hatching of the egg. They then became dissociated and dispersed throughout the body cavity of the host, where they grew in size by the absorption of fatty matters from the host until they became quite stretched out with fat globules, and in this condition they constituted the principal food of the parasite larva in its later stages. Death of the parasite larva did not affect the dissociation and subsequent development of the cells of the embryonic membrane. This writer believes that many workers have considered similar cells in parasitized larvae only as disorganized fat bodies of the host and have overlooked their true nature.

Among the Chalcididae the embryonic envelope has received the attention of several authors. Henneguy (7, p. 337), in speaking of the group of insects having a single embryonic envelope, illustrates the egg of *Smicra clavipes* and says that the cells of the membrane, after the hatching of the egg, become somewhat spherical in shape, absorb fat globules, and then degenerate in the body cavity of the host, where it is possible that they are later eaten by the parasite larva.

An account of the embryonic membrane found in the Platygaster has been given by Marchal (12). Following the eclosion of the larva of *Trichacis remulus* Walker, the amnion breaks up into round or oval bodies to which this author has given the name "pseudogermes." The bodies grow and multiply for some time after they are free and floating about in the blood of the host larva. The dissociation of the embryonic envelope in *Platygaster lineatus* Kieffer and *P. marchali* Kieffer was found to be similar, but in the species *P. ornatus* Kieffer a "trophamnion" is present and a paranucleus undergoes multiple division to form a body which finally divides into irregular masses, some of which remain attached to the larva while others float free in the body cavity of the host as "pseudogermes."

In a new and interesting paper on the *Sirex* parasites Chrystal (9) speaks of the embryonic envelope in *Ibalia* as the trophic membrane or trophamnion and says that it is composed of various-sized cells possessing large nuclei. This writer found that the larva of *Ibalia leucospoides* Hochew. issued head-first from one end of the trophamnion and the ruptured cuticular envelope remained unchanged in appearance up until the third stage of the parasite. Up to that time no dissociation of the cells was observed and it seemed unlikely that any difference would be noted in the fourth or last stage larva. It, therefore, appeared probable that the cells either degenerated or disappeared just previous to the final destruction of the host larva or that they were devoured by the parasite.

The cellular envelope present in the egg of *Encyrtus aphidivorus* Mayr, and of *Oophthora semblidis* Aur., two species of Chalcididae,

is called the "pseudoserosa" by Silvestri (22), who considers it as differing in origin from the serosa of other insects.

LARVAL GROWTH AND PUPATION

The larva of *A. thompsoni*, so far as observed, is strictly an endoparasite which spends practically all of its life free within the body cavity of the host larva from whose substance its nourishment is derived.

According to the writer's observations the parasite passes through three distinct and well-defined larval stages, molting twice in the body of the host and a third time within the newly spun cocoon. The cast skins of the first and second molts are pushed back toward the posterior end of the larva, where they sometimes remain attached for a short time before being entirely shed.

The writer at one time observed the movements of several *Apanteles* in their efforts to issue from the host larva. Through the integument of the host could be seen the head of the parasite larva as it moved back and forth over a small area on the inside of the host's skin, and the chitinous head armature, aided by the sharp-toothed mandibles, scraped away the intervening hypodermis and other tissues. Finally the tip of one of the mandibles pierced the skin, and after several minutes of the same to-and-fro motion the mandibles gradually enlarged the hole until the head of the parasite larva could be pushed through. Forward muscular movements of the larva continued until it issued free from the host about 45 minutes later. There is a tendency for the parasite larvae to issue along the lateral line of the host larva.

An *Apanteles* larva often starts spinning while issuing from the host, and the threads are first attached near the middle of its own body. In about 8 hours it has inclosed itself within a fine network of white threads through which the head may be seen still moving about as more threads are spun and attached. Nearly 24 hours are required for the whole spinning process and another period of like duration elapses before the casting of the meconium and voiding of waste matter within the cocoon just prior to pupation. A few days after spinning it is easy to distinguish through the white texture of the cocoon the dark-colored cast meconium at the posterior end and the brown eyes of the developing pupa near the other end.

Observations made on *Apanteles* colonies kept under outdoor insectary conditions during the middle of May at Hyères, where the temperature averages higher than at Lille during the same period, showed the pupal period to vary between a minimum of 9 days and a maximum of 15, with 14 as an average. At a constant temperature of either 68° or 77° F. the pupal period was only 8 days, and at ordinary room temperature approaching those just mentioned, but fluctuating, little difference in length of time was noted.

In emerging from its cocoon the adult cuts a neat cap almost off from the cephalic end of the cocoon and emerges head first. The average colony of *Apanteles* consists of from 15 to 20 individuals. In one count of 37 colonies containing 864 individuals, based on dissections of host larvae, the average size of a colony was 23, with a maximum of 61 and a minimum of 9. Thompson and Parker (25) have recorded an average of 15 individuals per colony.

LIFE OF THE ADULT

The adult of *A. thompsoni* is a delicate insect and rather susceptible to meteorological conditions. It dies quickly if provided with too little or no food or if kept constantly at a temperature that is too high or where the relative humidity is too low. Regardless of temperature, death usually occurs within 24 hours after emergence unless the female is able to ingest moisture. Provided only with such moisture, the maximum longevity of females at a constant temperature of 77° F., or at a fluctuating room temperature, was only 2 days. At 64.4° the life of one individual given only water was prolonged for a period of 4 days. All of the above females were confined separately in small glass globe cages. One female remaining from a lot put into a large square box cage lived for 26 days at 64.4° when given moisture and sugar water, and others placed in box cages at the same temperature, similarly fed, and subjected to light and warmth for only a short time each day, lived several weeks.

Usually all of the adults of a single colony emerged within a few hours, and it was seldom that living adults remained in their cocoons longer than 24 hours after the start of emergence. In controlled experiments, at both a constant temperature of 77° F. and under ordinary heated-room conditions, the emergence was 83.7 per cent, at 68° it was 78.1 per cent, and in an outdoor insectary it was 76.5 per cent.

The adult of *A. thompsoni* is positively phototropic, but not as decidedly so as are many other hymenopterous parasites. When handled, the adults will often attempt to escape from the cage by flying or walking directly away from a source of strong light, and in this action they are sometimes very persistent.

EFFECT OF PARASITE ON HOST

Parasitized larvae of *P. nubilalis*, regardless of the stage in which they are attacked by *A. thompsoni*, grow and approach maturity. Within such borers the *Apanteles* larvae feed upon the substance of the host and at times possibly attack the vital organs. Such feeding has a weakening effect upon the host, and parasitized larvae containing nearly mature *Apanteles* larvae can often be distinguished from healthy specimens by their somewhat drawn appearance and the slowness of their movements. In the earliest stages of parasitism by *Apanteles*, however, such distinction is more difficult.

Death is the fate of any larva of *P. nubilalis* from which *Apanteles* have issued, and in no known instance has pupation of the host followed. The wounds caused by the exit of the parasite larvae soon close, and the *Pyrausta* larva may continue to move about sluggishly for days before death takes place. It is probable that the longevity of such a larva from which parasites have issued is dependent upon the number of parasite larvae which it has nourished and the severity of direct injury which has occurred to the more vital organs.

The average length of life of six host larvae after parasite issuance was 9 days at 77° F., with a maximum of 14 and a minimum of 4 days, while for six other larvae kept at a room temperature of about 68° the average longevity was 11 days, with a maximum of 19 and a

minimum of 4. One larva of *P. nubilalis*, at 68°, lived 25 days after the issuance of the parasite larvae.

SEASONAL HISTORY

A. thompsoni, after overwintering as a partly grown first-stage larva within the body of its host, continues development into the second and third stages in early spring, and issues to spin its cocoon from the middle of April to the end of the third week in May. The period of maximum spinning varies somewhat from year to year according to weather conditions, but in general this may be said to occur between May 7 and 21. Adults usually start emerging about May 15, and by June 4 nearly all have left their cocoons.

In the spring of 1925, in the vicinity of Brussels, Belgium, spun colonies were found in the field on May 2, and near Antwerp the first colony was observed on May 7. In 1926 a colony of *Apanteles* cocoons was found on April 22 in the region of Lille, France, and from 21 borer larvae (out of a collection of 323) parasite colonies had issued and spun on May 1. Records for 1928 indicate a somewhat earlier spinning and pupation of the parasite larvae, and in shipments from Lille to Hyères colonies had spun as early as April 16. Fresh colonies of cocoons were found from that date on until May 24.

The first colony of cocoons in 1929 was collected in the field in the Lille region on May 8, when approximately 10 per cent of the *Apanteles* colonies had issued from their hosts. On May 13 about 25 per cent had issued, and by May 23 practically 100 per cent had spun. Issuance from daily collections of *Pyrausta* larvae sent to Hyères and kept under outdoor insectary conditions covered a nearly parallel period from May 14 to 24.

Although the first empty *Apanteles* cocoons were not found in the field in 1929 until May 31, the emergence of adults, from the first colony of cocoons collected, had started by May 20. Laboratory data taken on the colonies under observation showed an emergence period lasting from May 22 to June 1, and it seems quite certain from later field collections that the majority of the adults had emerged by June 7.

All of the writer's data indicate the occurrence annually of only one full generation of *A. thompsoni* in northern France and Belgium. The females which emerge in late May and early June probably wait several weeks for the occurrence of *Pyrausta* larvae large enough to serve for oviposition. Just when egg laying by *Apanteles* commences or when the peak of oviposition is reached has not been determined.

Thompson and Parker (25) were of the opinion that *Apanteles* had two generations a year in the Lille region, from the fact that empty cocoons were found about the middle of August, 1925, in green *Artemisia* plants. However, several times in June and July, 1929, *Apanteles* cocoons from which the adults had emerged were collected from *Artemisia* of that year's growth, indicating that the overwintering host larvae sometimes migrate into the fresh *Artemisia* stems in the spring before the time for the parasite larvae to issue. It seems probable, therefore, that the first record was of this nature and that *A. thompsoni* really has but one generation a year.

Field collections of young borer larvae were made at frequent intervals during the summers of 1927 and 1929 in the region of Lille, and such larvae were later dissected. The data are summarized in Table 3. It should be mentioned that the collections, 611 larvae in 1927 and 767 in 1929, contained second, third, fourth, and fifth stage borers, but that only those which were found parasitized by *A. thompsoni* are listed in the table.

TABLE 3.—Parasitism by *Apanteles thompsoni* in summer field collections of *Pyrausta nubilalis* at Lille, France, 1927 and 1929

Year	Number of larvae collected	Period of collection	Apanteles found			Percentage of parasitism
			Date	Stage of host larva	Stage of parasite larva	
1927	611	Aug. 10 to 30	Aug. 27	Fourth	First	3.9
			Aug. 29	do	do	3.3
			Aug. 30	do	do	2.4
1929	767	July 16 to Sept. 10	Sept. 6	Fifth	do	1.7

¹ Collections contained larvae of various stages as found in the field.

It seems peculiar that *Apanteles*, either in the egg or first larval stage, was not found in these collections of early-stage host larvae earlier than August 27 in 1927 or September 6 in 1929. Two possible explanations of this condition may be offered; (1) that the collections were too small and that borer larvae in the field contained early stages of *Apanteles* but by chance were not included in the collections; and (2) that *Apanteles* has a summer generation in an alternate host and does not attack *Pyrausta* larvae before the latter part of August. To the writer the first explanation seems the more plausible.

LIMITING FACTORS

It is difficult to explain why this parasite is not more widely dispersed in other similar and apparently favorable regions inhabited by the corn borer. In this respect the writer can only say that perhaps the various climatic factors operating to produce a certain synchronization between the seasonal rhythm of the host and parasite do not operate to produce the same results in other zones.

Drought and excessive heat would appear to be two factors which prevent a continuance of the species in the more southerly regions of western Europe. Its confinement to the Sequanian (north) zone and apparent absence in the Paris district are less easy to explain, however. It may be that the somewhat warmer climate of the latter with its less abundant rainfall is the responsible factor.

The foregoing explanation, while it may account for the geographical limits of this species, does not explain its numerical limits within the zone where it is found. Although the writer has never reared any hyperparasite from *A. thompsoni*, the fact that other members of this genus are often so attacked would indicate that this species is not immune. It does not seem probable, from dissections and observations, that superparasitism is a factor limiting the abundance of the species (although it does limit its efficiency).

On the other hand, counts made on colonies of cocoons sent in from the field during the summer of 1929 and after the period of normal emergence have shown that a certain mortality occurred among the parasites in the pupal or adult stages within the cocoons. As high as 25 per cent mortality has been found, and it may be that some factor, operating in the field to prevent a normal emergence of adults from the cocoons, limits the abundance of the insect in the zone considered as its optimum.

THELYTOKY

Parthenogenesis, or the ability of a female to produce offspring without actual fertilization by a male of the species, is not uncommon in many groups of the animal kingdom and has often been mentioned in literature upon various hymenopterous parasites.

Many careful observers have shown that fertilized females of the Hymenoptera normally produce both males and females while unfertilized females are generally arrhenotokous and leave only male descendants or more rarely exhibit deuterotoky and give rise to progeny of both sexes. In every such case, however, so far as the writer has been able to learn, both sexes of the species in question are known to occur in reasonable abundance.

On the other hand, thelytoky, in which only females are constantly produced and the opposite sex is either unknown or only rarely encountered, is much more unusual among the parasitic Hymenoptera. *A. thompsoni* is an example of this class in which the male is unknown, and parthenogenesis of the thelytokous type may be regarded as a normal procedure in this species.

It is interesting to review different examples of thelytoky already discovered among the three best-known families of the parasitic Hymenoptera. At the present time the family Chalcididae lead both the Ichneumonidae and Braconidae in the number of species recorded as reproducing in this manner, owing possibly to the more extended studies made upon the biology of the members of this group.

The offspring of *Thripoctenus russelli* Crawford, an internal chalcid parasite of Thysanoptera, according to the observations of Russell (21), were always females.

McConnell (13) has stated that unfertilized females of the chalcid *Eupelmianus saltator* Lindm. are thelytokous and that rearings from unmated females for as many as six generations always give female progeny. This characteristic of the species has been further corroborated by Phillips and Poos (18), as well as by Muesebeck and Dohanian (14).

Timberlake and Clausen (26) have reported *Achrysocephalus modestus* Timberlake as producing generation after generation of females without the intervention of the male, and add that reproduction of the species *Pseudoleptomastix squamulata* Girault and *Anagyris subalbicornis* (Girault) is "generally parthenogenetic," the male being found only occasionally and not in sufficient numbers to permit the general fertilization of the females.

Smith and Compere (23) believe that *Coccophagus modestus* Silv. is thelytokous, the males only occasionally being found, and state

that such a condition is true in the case of certain other species of *Coccophagus*.

In a recent paper, part of which is devoted to the biology of *Aphelinus jucundus* Gahan, a primary parasite of the geranium aphid, Griswold (4) states that the male of this insect has never been described and concludes from various studies that the species is thelytokous.

This form of parthenogenesis has been noted only a few times among the Ichneumonidae. Picard (19) mentions it in the case of *Hemiteles longicauda* Thoms. and remarks that "Les mâles doivent être très rares car je n'en ai pas obtenu en élevage et n'en ai pas rencontré dans la nature." He further observes that such parthenogenesis is very remarkable in the Ichneumonidae.

In their study of hyperparasitism Muesebeck and Dohanian (14) also found a species of *Hemiteles* which proved to be thelytokous, the male being unknown, and they have employed this characteristic of *Hemiteles tenellus* Say to distinguish it from the European species *H. areator* (Panz.) which exhibits no difference in morphological characters.

The only other example of thelytoky in the Ichneumonidae seems to be that of *Nemeritis canescens* Grav., mentioned by Picard (20) and later corroborated by Wojnovskaja-Krieger (29). Only females are produced by this species, and the male is unknown.

An even lesser number of references to agamogenesis in which only female progeny result is to be found in literature upon the Braconidae. Ogloblin (15), in speaking of *Dinocampus terminatus* Nees, says that "jusqu'à présent c'est le seul exemple connu de parthénogénèse thélytoque dans la famille des Braconides"; and Balduf (1), in writing on the same species under the name of *D. coccinellae* Schrank, expresses the belief that the reproduction of this parasite is purely thelytokous. No other instance seems to have been recorded until the present writing.

Thelytoky is probably more common among the parasitic Hymenoptera than it is now supposed to be, and future investigations will no doubt reveal much interesting evidence upon the subject. Time may reveal the existence of the male, at least in rare occurrence, among those species in which it is now entirely unknown.

ECONOMIC IMPORTANCE OF THELYTOKY IN THE HYMENOPTEROUS PARASITES

Certain authors, more notably Clausen (26), have discussed the economic value of thelytoky among the parasitic Hymenoptera, and Clausen has attempted to show that frequent or general reproduction in this way results in a much greater rate of increase than would be the case if a portion of the progeny were males. To bear out this idea he has calculated that the possible increase for one year, allowing five generations of 50 each and no mortality, of *Achrysocephalus modestus* Timberlake, producing only females, would be at least four times as great as if fertilization had taken place and progeny of both sexes in the ratio of one to three had been produced.

As this writer states, no evidence has been given to show that the continued absence of the male contributes to a weakening of

the race, although in certain cases a reduction in the average number of the progeny because of lack of fertilization might offset any advantage otherwise obtained.

It is possible that a thelytokous species of parasite has an economic advantage over an arrhenotokous or even a deuterotokous species, and by mathematical calculation, considering other factors as constant, one may readily reach this conclusion. However, in the case of *A. thompsoni* at least, it would seem that any such advantage, if not offset by other disadvantageous factors in the zone it inhabits, would manifest itself in a proportionately greater economic importance of the species in its particular habitat as compared with that of other coexistent species of parasites. But this does not seem to be the case, and it is necessary to conclude that if any such advantage really exists, it is utilized in maintaining the species at its present quantitative level; and conversely, without this advantage the species would be numerically less abundant. It therefore appears unlikely that any essential advantage of thelytoky, unless of value in the native home of a parasite, would develop following its importation into a new environment.

It is true, of course, that in the breeding of a thelytokous parasite in the laboratory for liberation in the field, much time and labor are saved because matings are unnecessary and the actual rearing and handling of the males is dispensed with. There is also one other point which may be favorable to a thelytokous species, namely, that after liberation in a new environment, there will be no hindrance to, or even slowing up of, the reproduction of the parasite because of nonfertilization of the surviving females, which for some time may be limited in numbers and rather widely distributed.

METHODS OF QUANTITY COLLECTION AND SHIPMENT

Owing to the fact that *A. thompsoni* overwinters as a larva within the body of its host, it was found that the most feasible method of handling was to collect and ship the host borers during the winter months and allow the adult parasites to emerge the following spring.

Hired collectors of larvae of *P. nubilalis* usually work in the field in the vicinity of Lille from the middle of October until the end of March. Each worker carries a round tin screen container in which pieces of folded paper have been placed. He dissects stems of dry standing *Artemisia* plants as he finds them in the field or by the wayside and places all *Pyrausta* larvae in the container where they soon crawl into the folds of the paper.

As the climate in northern France during the winter months is cold, the larvae when collected are very inactive. It is therefore necessary to put them in a warm place to increase activity so that they will crawl more readily into the holes in the strips of corrugated paper provided for them in the metal shipping can. The shipping can used, together with its contents of narrow upright strips of corrugated paper, is of the type designed by D. W. Jones, of the European corn-borer laboratory of the United States Bureau of Entomology at Arlington, Mass.

The larvae when placed in such a can readily enter the paper corrugations and inclose themselves by a compact silk web spun across

the openings, until the bundle of paper sections looks more or less like a honeycomb. Approximately 400 larvae are put into each can, and the cans of larvae so prepared are packed tightly in a wooden box for shipment to the United States.

SUMMARY

Apanteles thompsoni Lyle is a gregarious braconid found most abundantly in Europe in the environs of the city of Lille, France, where it occurs as an internal parasite of the larva of the European corn borer, *Pyrausta nubilalis* Hübn. In this area the parasite attacks *Pyrausta* larvae infesting the weed *Artemisia vulgaris* L. It has also been recorded from *Artemisia* in the Sequanian (south) zone, from both *Artemisia* and corn in the Rhodanian zone, and from corn in the Aquitainian and Danaprisian zones.

From the Sequanian (north) zone, in which the city of Lille is situated, winter shipments of the host larvae have been made to the United States by the Bureau of Entomology from 1926 to 1929, inclusive, and a total of 159,355 individuals of *A. thompsoni* have been reared from this material.

Collectors of the host larvae usually work in the field from the middle of October until the end of March. The larvae are cut out of dry *Artemisia* stems, packed in specially designed tin cans, and shipped in large lots to the United States, where emergence of the parasite is obtained the following spring.

The economic importance of this parasite of the corn borer in its natural habitat has varied from year to year, and its prevalence within restricted areas has differed considerably. The maximum parasitism recorded for the species is 42.6 per cent, found in a lot of borer larvae from Lille in 1924, with an average of 22.9 per cent for all collections made that year. Parasitism since that time has been much lower, the highest annual average in the 5-year period, 1925 to 1929, having been only 6.6 per cent.

The species, first described by G. T. Lyle in 1927, is thelytokous, the male being entirely unknown. The female, with a single thrust of her ovipositor, usually deposits 20 to 25 eggs within the body cavity of the young *Pyrausta* larva. After about five days these eggs hatch into larvae which pass two full stages and the greater part of a third stage within the host, from whose substance nourishment is derived. When nearly full grown, the parasite larvae issue from the host and spin their cocoons. Emergence of the adults occurs about 14 days later.

The female is capable of depositing several hundred eggs and may oviposit more than once within the same host larva. The normal colony of *Apanteles* consists of from 15 to 20 individuals; a colony of 61 is the largest found in the course of dissections.

The host larva, from which *Apanteles* have issued, dies. Actual death, however, may not occur for a number of days or even several weeks after the issuance of the parasite larvae.

The developing embryo within the egg of *Apanteles* is surrounded by an envelope of serosal cells which often remains partly attached to the hatched larvae for several weeks. Other workers have noted similar embryonic envelopes among certain species of hymenopterous parasites.

Apanteles adults, if provided with proper moisture and food conditions, may be kept alive in the laboratory for several weeks, and oviposition in young *Pyrausta* larvae is easily obtained.

A. thompsoni overwinters as a partly grown first-stage larva within the body of the host. Development into the second and third stages begins in early spring, and the larva issues from the host to spin its cocoon from the middle of April to the middle of May. Adult emergence starts by the end of the second week in May and continues into early June. Present available data indicate the occurrence of only one generation annually in the Lille region.

Examples of thelytoky among the Chalcididae have been recorded by numerous writers and more rarely mentioned by observers of the Ichneumonidae. The present bulletin records what is thought to be the second example of this form of parthenogenesis among braconid parasites.

LITERATURE CITED

- (1) BALDUE, W. V.
1926. THE BIONOMICS OF *DINOCAMPUS COCCINELLÆ* SCHRANK. *Ann. Ent. Soc. Amer.* 19: 465-498, illus.
- (2) CHRYSTAL, R. N.
1930. STUDIES OF THE STREX PARASITES. *Oxford Forestry Mem.* 11, 63 p.
- (3) GRANDORI, R.
1911. CONTRIBUTO ALL' EMBRIOLOGIA E ALLA BIOLOGIA DELL' *APANTELES GLOMERATUS* (L.) REINH. (IMENOTTEMO PARASSITA DEL BRUCO DI *PIERIS BRASSICÆ* L.). *Redia* 7 (fasc. 2): [363]-428, illus.
- (4) GRISWOLD, G. H.
1929. ON THE BIONOMICS OF A PRIMARY PARASITE AND OF TWO HYPERPARASITES OF THE GERANIUM APHID. *Ann. Ent. Soc. Amer.* 22: 438-458, illus.
- (5) HAVILAND, M. D.
1921. ON THE BIONOMICS AND POST-EMBRYONIC DEVELOPMENT OF CERTAIN CYNIPID HYPERPARASITES OF APHIDES. *Quart. Jour. Micros. Sci.* [London] 65 (pt. 3): [451]-478, illus.
- (6) ———
1922. ON THE LARVAL DEVELOPMENT OF *DACNUSA AREOLARIS* NEES (BRACONIDAE), A PARASITE OF PHYTOMYZINAE (DIPTERA), WITH A NOTE ON CERTAIN CHALCID PARASITES OF PHYTOMYZIDS. *Parasitology* 14: 167-173, illus.
- (7) HENNEGUY, L. F.
1904. LES INSECTES, MORPHOLOGIE—REPRODUCTION—EMBRYOGÉNIE. 804 p., illus. Paris.
- (8) JACKSON, D. J.
1928. THE BIOLOGY OF *DINOCAMPUS (PERILITUS) RUTILUS* NEES, A BRACONID PARASITE OF *SITONA LINEATA* L.—PART I. *Zool. Soc. London Proc.* 1928 (pt. 2): 597-630.
- (9) JONES, D. W.
1929. IMPORTED PARASITES OF THE EUROPEAN CORN BORER IN AMERICA. *U. S. Dept. Agr. Tech. Bul.* 98, 28 p., illus.
- (10) KOTLÁN, A.
1928. A DOUBLE PARASITIC INFECTION OF A LARVA OF *PYRAUSTA NUDILALIS* HB. *Internat. Corn Borer Invest. Sci. Rpts.* 1927-28: 174-178, illus.
- (11) LYLE, G. T.
1927. TWO NEW SPECIES OF *APANTELES* (HYM., BRACONIDAE). *Bul. Ent. Research* 17 (pt. 4): 415-416.

- (12) MARCHAL, P.
1906. RECHERCHES SUR LA BIOLOGIE ET LE DÉVELOPPEMENT DES HYMÉNOPTÈRES PARASITES. LES PLATYGASTERS. Arch. Zool. Expt. et Gen. (4) 4: [485]-640, illus.
- (13) McCONNELL, W. R.
1918. EUPHEMINUS SALTATOR LINDM. AS A PARASITE OF THE HESSIAN FLY. Jour. Econ. Ent. 11: 168-175, illus.
- (14) MUESEBECK, C. F. W., and DOHANIAN, S. M.
1927. A STUDY IN HYPERPARASITISM, WITH PARTICULAR REFERENCE TO THE PARASITES OF APANTELES MELANORCELUS (RATZBURG). U. S. Dept. Agr. Bul. 1487, 35 p., illus.
- (15) OGLOBLIN, A.
1924. LE RÔLE DU BLASTODERME EXTRAEMBRYONNAIRE DU DINOCAMPUS TERMINATUS NEES PENDANT L'ÉTAT LARVAIRE. Pub. Inst. Zool. Univ. Charles de Prague, v. 2: 1-27, illus.
- (16) PARKER, H. L., VANCE, A. M., SMITH, H. D., and GAMKRELIDZE, W.
1929. PYRAUSTA NUBILALIS HÜRN. IN EUROPE; NOTES ON INFESTATION AND PARASITISM FROM 1926 TO 1928. Jour. Econ. Ent. 22: 688-693.
- (17) PEMBERTON, C. E., and WILLARD, H. F.
1918. A CONTRIBUTION TO THE BIOLOGY OF FRUIT-FLY PARASITES IN HAWAII. Jour. Agr. Research 15: 419-466, illus.
- (18) PHILLIPS, W. J., and POOS, F. W.
1927. TWO HYMENOPTEROUS PARASITES OF AMERICAN JOINTWORMS. Jour. Agr. Research 34: 473-488, illus.
- (19) PICARD, F.
1922. CONTRIBUTION À L'ÉTUDE DES PARASITES DE "PIERIS BRASSICÆ" L. Bul. Biol. France et Belg. 56 (fasc. 1): [54]-130.
- (20) ———
1923. RECHERCHES BIOLOGIQUES ET ANATOMIQUES SUR "MELITTOBIA AC-ASTA" WALK. (HYMÉNOPTÈRE CHALCIDIEN.) Bul. Biol. France et Belg. 57 (fasc. 4): [409]-508, illus.
- (21) RUSSELL, H. M.
1912. AN INTERNAL PARASITE OF THYSANOPTERA. U. S. Dept. Agr., Bur. Ent. Tech. Ser. 23 (pt. 2): 25-52, illus.
- (22) SILVESTRI, F.
1909. CONTRIBUZIONI ALLA CONOSCENZA BIOLOGICA DEGLI IMMENOTTERI PARASSITI. II. SVILUPPO DELL' AGENIAJPRIS FUSCICOLLIS (DALM.) E NOTE BIOGRAFICHE. Bol. Lab. Zool. Gen. e Agr. R. Scuola Super. Agr. Portici 3: 29-85, illus.
- (23) SMITH, H. S., and COMPERE, H.
1920. THE ESTABLISHMENT IN CALIFORNIA OF COCCOPHAGUS MODESTUS SILV. (APHELINIDAE, HYMENOPTERA), WITH NOTES ON ITS LIFE HISTORY. Calif. Univ. Pubs., Ent. 4(3): [51]-61, illus.
- (24) SPENCER, H.
1926. BIOLOGY OF THE PARASITES AND HYPERPARASITES OF APHIDS. ANN. Ent. Soc. Amer. 19: 119-157, illus.
- (25) THOMPSON, W. R., and PARKER, H. L.
1928. THE EUROPEAN CORN BORER AND ITS CONTROLLING FACTORS IN EUROPE. U. S. Dept. Agr. Tech. Bul. 59, 63 p., illus.
- (26) TIMBERLAKE, P. H., and CLAUSEN, C. P.
1924. THE PARASITES OF PSEUDOCOCCUS MARITIMUS (EHRHORN) IN CALIFORNIA (HYMENOPTERA, CHALCIDOIDEA). PART I. TAXONOMIC STUDIES. (By P. H. Timberlake.) PART II. BIOLOGICAL STUDIES AND LIFE HISTORIES. (By C. P. Clausen.) Calif. Univ. Pubs. Ent. Tech. Bul., v. 3, no. 2, p. 223-292, illus.
- (27) TOWER, D. G.
1915. BIOLOGY OF APANTELES MILITARIS. Jour. Agr. Research 5: 495-508, illus.

- (28) WILLARD, H. F.
1920. OPIUS FLETCHERI AS A PARASITE OF THE MELON FLY IN HAWAII.
Jour. Agr. Research 20: 423-438, illus.
- (29) WOJNOVSKAJA-KRIEGER, T.
1927. ZUR BIOLOGIE VON NEMERITIS CANESCENS GRAY.—DES PARASITEN DER
MEHLMOTTE EPHESTIA KÜHNIELLA ZELLER. Bur. Appl. Ent. Rpts.
[Leningrad] 3: 24-35, illus. [In Russian. Summary in German,
p. 34.]
- (30) ZORIN, P.
1925. CONTRIBUTIONS À LA BIOLOGIE DE L'APANTELES GABRIELIS GAUT. ET
RIEL. [In Russian.] La Défense des Plantes. Bul. Bur. Perm.
Cong. Entomo-Phytopath. Russie 2 (3): 138-147, illus.

END