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# PHAEOGENES NIGRIDENS WESMAEL, AN IMPORTANT ICHNEUMONID PARASITE OF THE PUPA OF THE EUROPEAN CORN BORER<sup>1</sup>

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## INTRODUCTION

*Phaegenes nigridens* Wesm.<sup>3</sup> is an internal solitary parasite which attacks the pupal stage of *Pyrausta nubilalis* Hbn. and, so far as is known at present, is the only one of any importance attacking this stage. During the years 1922 to 1928 much miscellaneous informa-

<sup>1</sup>The work upon which this bulletin is based was begun in the fall of 1928 at the European parasite laboratory at Hyères, Var, France, and continued with a few minor interruptions until the end of 1930.

<sup>2</sup>The writer gratefully acknowledges his indebtedness to H. L. Parker, under whose supervision this work was done, for valuable counsel and criticisms; to A. M. Vance, a laboratory associate, for many helpful suggestions; to Esther H. Hart for the drawing of the adult; to R. A. Cushman for the description of the species; and to W. R. Walton for assistance with the manuscript.

<sup>3</sup>Order Hymenoptera, superfamily Ichneumonidae, family Ichneumonidae, subfamily Joppinae, group Joppinae cyclopeustici, tribe Phaegenini.

tion concerning the abundance, economic importance, and biology of *Phaeogenes nigridens* was gathered by the staff of the European parasite laboratory. In the fall of 1928 the writer assumed the task of bringing to completion a detailed account of its morphology and biology and of endeavoring to breed it in large numbers in the laboratory. After completing the first part of this program and experiencing two years of only moderate success with the second phase, the results are published herein. The ultimate solution of quantity breeding may take several additional years. As shipments to the United States have been made in varying numbers since 1924, the information published herewith may prove valuable to those engaged in manipulating this parasite.

Except for numerous systematic records and a few brief biological notes, very little has been published on any species of the subfamily Joppinae. Chewyrev (8)<sup>4</sup> published some notes on *Amblyteles vadatorius* Illiger, belonging to the stenopneustic group of the Joppinae, in which he included some morphological data on the immature stages, according to Cushman (10). Meier (16) also published various biological data on the same species. Strickland, in his paper on the parasites of the prairie cutworm (26), recorded a few notes on *A. subfuscus* Cress., but he did not completely follow out its life history. Nothing has been written on the immature stages of the division Joppinae cyclopneustici, to which *Phaeogenes nigridens* belongs.

## GEOGRAPHICAL DISTRIBUTION

Originally described from Belgium, this species has since been found in Sweden, Germany, and France, as cited by Dalla Torre (11). Recently Italy and Hungary have been added to the list. Little is known about the distribution of this parasite in Belgium, Sweden, and Germany, but in France, where a more or less intensive survey has been conducted for a number of years, it has been recovered from the following zones:<sup>5</sup> Aquitanian, Armorican, Rhodanian, and the Mediterranean (south). Several large collections of *Pyrausta nubilalis* have been made from the north of France in localities around Paris and Lille, but no specimens of *Phaeogenes nigridens* have ever been reared from such material. In Italy it has been found in practically all of the northern Provinces where corn or hemp is grown. In 1930 three specimens were reared by Sachtleben (22) from *Pyrausta* pupae collected at Békéscsaba, Békcs County, Hungary.

Since the first shipment of this parasite to the United States in 1924, it has been recovered in satisfactory numbers from the liberation areas of Massachusetts by Jones (15), of the Arlington (Mass.) laboratory.

## HISTORY

The earliest definite reference to this species in literature appeared in 1844, when Wesmael (32, p. 192) first described it as *Phaeogenes nigridens*. In 1848 (33, p. 322) the same writer made a more complete description of both sexes in order to correct an error previously made in his description of the male. Since then it has been redescribed by various writers.

<sup>4</sup> Italic numbers in parentheses refer to literature cited, p. 44.

<sup>5</sup> The names used in this bulletin are those established by Thompson and Parker (27).

When first reared from *Pyrausta nubilalis*, in 1922, the species was erroneously determined as *Phaeogenes planifrons* Wesm. and as such was recorded in practically all the literature until 1929, when Cushman and Roman identified it as *P. nigridentis* Wesm.

It was first mentioned as a parasite of the corn borer by Caffrey and Worthley (5) in 1927, under the name of *Phaeogenes planifrons* Wesm. Mention was here made of its introduction and liberation in the United States in 1924. The stage of host attacked and its value as a parasite of the corn borer in Italy were also noted. Later in 1927 Poutiers (20) recorded it, under its correct name, as a parasite of *Tortrix pronubana* Hbn. In October of the same year Parker (1) listed the number of *P. nigridentis* shipped to the United States during the previous fiscal year, and Jones (14) and Caffrey and Worthley (6) made short notes showing that liberations had been made in the corn borer infested areas of the United States.

In 1928 Thompson and Parker (27) gave a brief account of its distribution, limiting factors, extent of parasitism of the European corn borer, and life history in so far as it was known at that time. Goidanich (13) mentioned *P. nigridentis* as parasitic on *Pyrausta nubilalis* infesting hemp in Italy, and included a few biological notes.

In 1929 Jones (15) published a brief résumé of the life history of the species, its recovery in the United States, and the total numbers of individuals shipped each year up to that time. Later in the year Parker and collaborators (19) recorded the extent of parasitism on *Pyrausta* for the years 1926 to 1928, inclusive, and gave *Phaeogenes nigridentis* as the correct determination.

### SYSTEMATIC POSITION

In 1894 Berthoumieu (3, p. 505) revised the Ichneumonidae and divided the tribe Ichneumonini into two subtribes, the stenopneustici and the cyclopneustici, based on the shape of the metathoracic spiracles. *Phaeogenes nigridentis* was included in the second group, which is characterized by having round or broadly oval spiracles.

Ashmead (2), in 1900, gave the tribes of Berthoumieu a subfamily classification and elevated *Phaeogenes* to tribal rank. The subtribes of Berthoumieu were not used.

Morley (17), in 1903, observed the same classification as Ashmead in so far as *Phaeogenes* was concerned.

Schmiedeknecht (23, p. 551), in 1907, used a classification similar to that of Berthoumieu except that the tribes and subtribes were raised to the next higher ranks.

In 1925 Ceballos (7, p. 60) revised the subfamily further, giving it the name Joppinae. The two tribes used by Schmiedeknecht were no longer considered as such, being changed to groups Joppinae stenopneustici and Joppinae cyclopneustici. *Phaeogenes nigridentis* remained in the latter group.

### HOST RELATIONS

In addition to the corn borer the only other host from which *Phaeogenes nigridentis* has been reared is *Tortrix pronubana* Hbn., a serious pest of carnations on the French and Italian Rivas. One specimen was bred from a pupa of this species collected by Poutiers (20) near Antibes, France.

A closely allied species, *P. stimulator* (Grav.), has been reared from pupae of *Tortrix viridana* L. by Silvestri (25) in Italy, where in one year it attacked 57 per cent of its host. This species has also been reported by various authors as a primary parasite of *Hyponomeuta padella* L. and *Ellopija fasciaria* L. It is possible that *P. nigridens* may attack any one of these hosts.

*P. nigridens* has been found associated with the corn borer regardless of the species of plant in which the latter was living. In the Armoric zone, where no corn is grown and *Artemisia* is the chief food plant, the parasite is found in about the same abundance as in some of the strictly corn-growing regions. In the hemp regions of the Padovian (south) zone, where both hemp and corn are found, the parasite attacks the pupae in hemp much more severely than those in corn.

### METHODS OF INVESTIGATION

In the course of many experiments, conducted in an effort to develop a suitable technic for quantity production of the parasite, the females could not be induced to oviposit with any regularity. The breeding that was accomplished, however, sufficed for a detailed study of the biology and morphology of the species.

In order to obtain *Phaeogenes* adults for the various breeding, longevity, and other experiments, *Pyrausta* pupae were collected both in the spring and in the summer. In the spring they were taken from the old cornstalks in the field, placed between layers of mulberry leaves in small cardboard boxes, and mailed to the laboratory. Upon arrival at the laboratory they were placed between fresh leaves in metal boxes with screen-wire tops. As the parasites emerged they were removed to cylindrical wire-screen cages 11 cm in diameter and 25 cm in height. Suitable hiding places were supplied by adding crumpled and corrugated paper. As food for the emerged adults sugar solution saturating a wad of cotton was attached to the side of the cage; it was renewed each week. The *Pyrausta* adults from unparasitized pupae were removed from the metal boxes as soon as they emerged. In the summer the parasitized pupae were placed in special small, flat boxes, which will be described later under methods of shipping. The pupae were held at about 8° C. (46.4° F.) until they reached the laboratory, when they were immediately removed and left to complete their development at room temperature. As the quantity at this time was always large, the emergence of the adults was allowed to take place in a wire-screen cage 35 by 60 by 90 cm.

Mating was accomplished either in the cylindrical cages or in vials, the latter being preferable for small-scale breeding as the female could be easily manipulated into a small space by use of the cotton stopper, thus bringing the two sexes into contact more easily and quickly. The larger the cage the longer was the time required to induce mating.

To obtain the fresh, white host pupae necessary for oviposition of the female *Phaeogenes*, larvae of *Pyrausta nubilalis* were collected in the fall, placed in shipping cans,<sup>6</sup> and allowed to spin up in the tun-

<sup>6</sup> These are round tin cans having two wire-screen windows and containing strips of corrugated paper tied together, like those used for the gross shipment of larvae to the Arlington (Mass.) laboratory.

nels of the corrugated-paper core. These cans were held at temperatures ranging from 5° to 10° C. (41° to 50° F.) until the following March, when the larvae were removed and occasionally wet and then dried at 25° C. (77° F.) At the end of two or three weeks prepupae appeared. These prepupae were removed, placed on moist blotting paper on the bottom of the cardboard box, and examined hourly for fresh pupae. The fresh pupae were then placed in old, half-exposed *Pyrausta* tunnels which had been taken from the corrugated paper cores and in which there still remained some of the larval web and the cast skin. Several of these pupae were put with a *Phaeogenes* female in a vial 3 by 9 cm in size. After a female had oviposited in a pupa, the latter was removed and reared in another similar vial. The humidity of the rearing cage was maintained at from 50 to 70 per cent.

In experiments with large-scale breeding, paper cores containing the overwintering larvae were placed in the cage and given the wetting and drying treatment, but the subsequent collection of the prepupae was omitted. This gave the female a more natural condition in which to work, as the hosts and their tunnels were not disturbed.

In experiments on the length of life of the adult, empty shipping cans having two wire-screen windows on each side were usually used as cages. The food consisted of weak sugar solution supplied by means of cotton plugs tied to the sides of the cage.

## EXPLANATION OF SYMBOLS USED IN THE ILLUSTRATIONS

<i>acgl</i> , acid gland.	<i>fnmx</i> , flexor muscle of maxilla.
<i>algl</i> , alkaline gland.	<i>fr</i> , frons.
<i>am</i> , anal muscles.	<i>fsu</i> , frontal suture.
<i>an</i> , anus.	<i>gc</i> , germ cells.
<i>antr</i> , antennal rudiment.	<i>glfo</i> , glenoid fossa or cavity in which
<i>ap</i> , apodeme or vestiges of tentorium.	mandibular condyle articulates.
<i>aptra</i> , anterior pleurostomal ramus or	<i>hbpf</i> , histoblasts of female genitalia.
superior mandibular support.	<i>hbpm</i> , histoblasts of male genitalia.
<i>atp</i> , location of anterior tentorial pit.	<i>hint</i> , hind-intestine.
<i>atrac</i> , anterior tracheal commissure.	<i>ht</i> , heart.
<i>br</i> , brain.	<i>htra</i> , host tracheae.
<i>cc</i> , cephalic end.	<i>hy</i> , hypostoma.
<i>cl</i> , clypeus.	<i>hypb</i> , hypodermal branches.
<i>co</i> , condyle.	1 l, 2 l, 3 l, histoblasts of legs.
<i>csor</i> , circular sensory organs.	<i>lafd</i> , lateral folds.
<i>ctrab</i> , cephalic tracheal branches.	<i>laphm</i> , lateroanterior pharyngeal mus-
<i>daphm</i> , dorsoanterior pharyngeal mus-	cle.
cle.	<i>lb</i> , labium.
<i>dln</i> , dorsal longitudinal muscles.	<i>lbpl</i> , labial palpus.
<i>dom</i> , dorsal oblique muscles.	<i>lm</i> , labrum.
<i>dpphm</i> , dorsoposterior pharyngeal	<i>lea</i> , lateral epicranial angle.
muscle.	<i>lom</i> , lateral oblique muscles.
<i>dvm</i> , dorsoventral muscles.	<i>mal</i> , Malpighian tubes.
<i>dvom</i> , dorsoventral oblique muscles.	<i>maladr</i> , rudiments of adult Malpighian
<i>emd</i> , extensor muscle of mandible.	tubes.
<i>ep</i> , epistoma.	<i>maoo</i> , mature oöcyte.
<i>epla</i> , epithelial layer.	<i>md</i> , mandible.
<i>fac</i> , fat cell.	<i>mesu</i> , metopic suture.
<i>fld</i> , folds in skin representing weakly	<i>mint</i> , mid-intestine.
defined sutures.	<i>mintb</i> , branch to mid-intestine.
<i>fmd</i> , flexor muscle of mandible.	<i>mth</i> , mouth.
<i>fmlb</i> , flexor muscle of labium.	<i>mtratr</i> , main tracheal trunk.
<i>fmlm</i> , flexor muscle of labrum.	<i>mx</i> , maxilla.

*mæpl*, maxillary palpus.

*neqa*, nerve ganglion.

*nu*, nucleus.

*nc*, nutritive cells.

*oc*, esophagus.

*oo*, oöcyte.

*os*, ostium.

*ovd*, oviduct.

*ovl*, ovariole.

*ph*, pharynx.

*pl*, pleurostoma.

*poc*, postocclput.

*pplra*, posterior pleurostomal ramus or Inferior mandibular support.

*psa*, polson sac.

*ptrac*, posterior tracheal commissure.

*rc*, rectum.

*rte*, rudiments of testes.

*rov*, rudiments of ovaries.

*ru*, rugosities.

*se*, seta.

*skld*, common duct of silk glands.

*skldo*, silk duct opening.

*skgl*, silk gland.

*slt*, secondary lateral trunk.

*socng*, subesophageal ganglion.

*sp*, spiracle.

*splm*, sensory protuberances of labrum.

*spm*, spermatheca.

*spn*, spines.

*svm*, subventral muscle.

*tac*, taenidium.

*tefl*, terminal filament.

*tefo*, temporal fossa.

*tegn*, terminal ganglion.

*trac*, tracheal commissure.

*u*, urate cell.

*vade*, vas deferens.

*vaphm*, ventroanterior pharyngeal muscle.

*vlm*, ventral longitudinal muscle.

*vne*, ventral nerve cord.

*vpphm*, ventroposterior pharyngeal muscle.

*vpro*, ventral protuberance.

*wng*, histoblasts of wings.

## DESCRIPTION

### ADULT

#### EXTERNAL ANATOMY

*Phaeogenes nigridens* (fig. 1) is readily distinguished from the other ichneumonid parasites of the corn borer by its general robust appearance, its rusty red-brown abdomen with black anal portion, and, in the female, the white band around the middle of the antennae (fig. 1, C) and the short, slightly exserted ovipositor. The male is usually somewhat larger than the female and is easily distinguished from the latter by the absence of the white band around the antennae. (Fig. 1, B.)

As all descriptions of the adult heretofore published have been too meager and generally unsatisfactory, a new and more comprehensive description has been drawn up by R. A. Cushman, of the taxonomic unit of the Bureau of Entomology, as follows:

*Female*.—Length, 7 to 9 mm. Black with basal four segments of abdomen, except base of petiole, ferruginous; antennae largely ferruginous at base and black at apex with a white annulus near the middle; coxae black, legs otherwise largely ferruginous; wings hyaline, faintly stained with yellow, veins brown.

Head and thorax polished, coarsely, evenly, but not densely, punctate, the punctation becoming denser and somewhat confused on metapleura and posterior face of propodeum. Head deeply concave posteriorly, the temples strongly convex; face short, medially elevated; clypeus broad, polished, with few punctures; mandibles long, stout, nearly twice as broad at base as their distance from eyes; antennae short, stout, involute, thickened beyond middle, basal joint of flagellum little longer than thick and shorter than second.

Thorax depressed, mesoscutum and scutellum flattened; propodeum with fine but distinct carinae, the median area distinctly longer than broad; legs stout, coxae and femora distinctly punctate, hind coxae with a short, stout tooth on the under side toward apex.

Abdomen narrowly ovate, first segment polished, otherwise opaque coriaceous, segments 2 to 4 distinctly punctate, second with transverse impression near base; ovipositor extending a little beyond apex of abdomen.

*Male*.—Much like the female but with abdomen more slender and thorax less distinctly depressed; antennae longer, more slender, tapering toward apex, and without a white annulus; legs more largely black, the hind femur especially so, hind coxae not toothed below.

## REPRODUCTIVE ORGANS OF FEMALE

The reproductive organs of the female (fig. 2) are similar to those of other ichneumonids, being composed of two long, slender ovaries, their respective genital ducts, the spermatheca, and the colleterial or accessory glands. Each ovary is about half as long as the abdomen and is composed of three polytrophic ovarioles, in the lower portion of which nutritive cells contained in distinct chambers alternate with

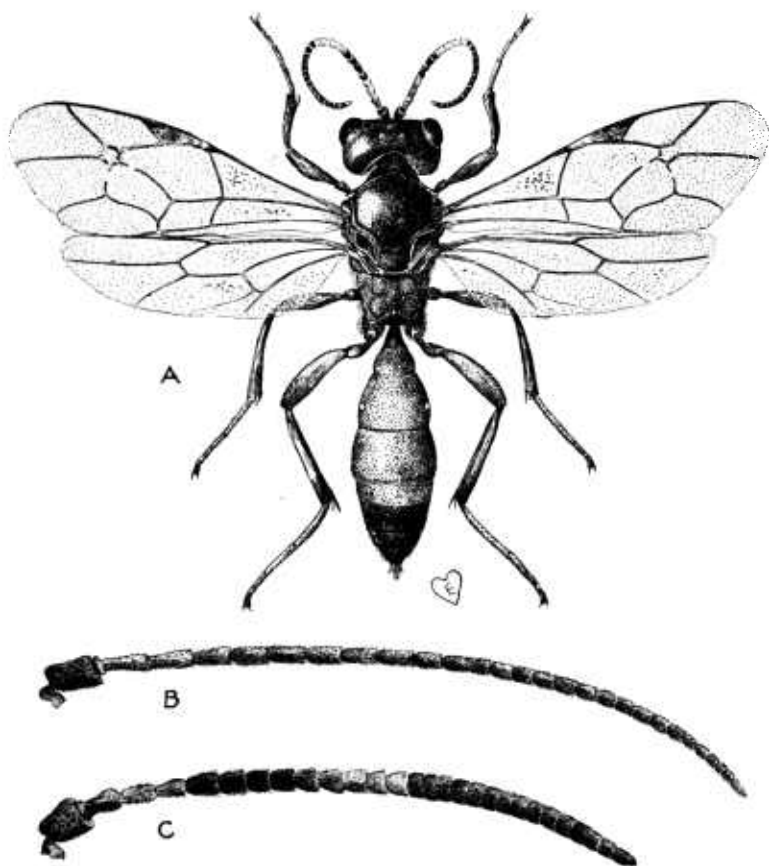


FIGURE 1.—*Phaeogenes nigridens*: A, Adult female; B, male antenna; C, female antenna

the developing oöcyte. Farther up in the ovarioles the nutritive cells and oöcytes become smaller until they are indistinguishable from the germ cells. The ovarioles of each ovary are joined together at the upper end by their terminal filaments, which in turn unite with those of the opposite ovary to encircle the posterior part of the ventriculus. The lower end of each ovariole opens by a very short oviduct into the common duct and vagina. The spermatheca is a round, flat pouch of light-brown color located on the dorsal side of the common oviduct, to which it is attached by a short duct along its upper circumference. It lies flat against the oviduct. The col-



leterial glands include an acid gland with its poison sac, which is connected with the base of the ovipositor by a long canal. The shorter alkaline gland narrows at its lower end to discharge alongside the opening of the acid-gland canal.

Pampel (18), in 1913, published a detailed account of the female reproductive organs of the ichneumonids, which he separated into four types according to their form. On the basis of the anatomical characters of these organs, *Phaeogenes nigridens* falls in his Type I, containing one member of the Joppinae and several of the Ichneumonidae (new sense).

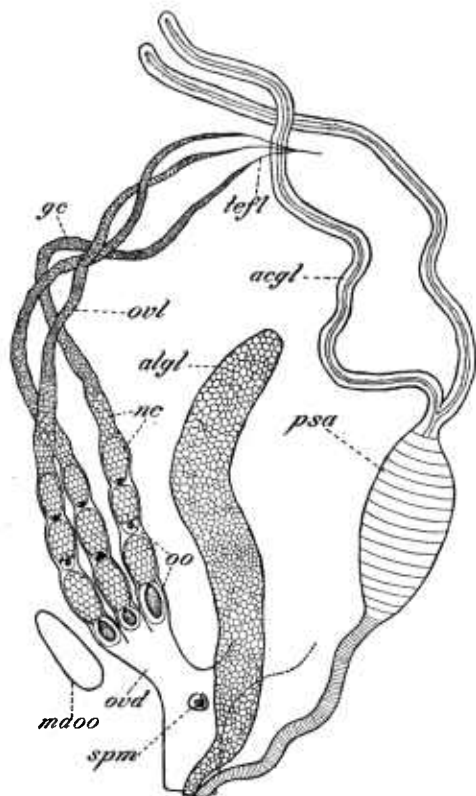


FIGURE 2.—Reproductive organs of a typical female of *Phaeogenes nigridens* 5 days old, showing the comparative size of the eggs and the associated cells and organs

based are given below, but whatever the actual number of molted skins cast by the larva, the latter in its development assumes four distinct, easily recognizable forms. These forms will be known as primary, secondary, tertiary, and last instars.

The primary larva is easily recognized by its long, brown, heavily sclerotized head, the slender mandibles, and the absence of spiracles. The secondary larva is recognized by a protuberance of the labiobase or ventral neck region<sup>7</sup> of the head. The tertiary larva is recognized

### EGG

Average length, 1 mm; average width, 0.29 mm.

The ovarian or newly laid egg (fig. 3, A) is hyaline, oblong-ovate, slightly arched, and entirely devoid of spines, sculpturing, or processes of any sort. It tapers gradually from the cephalic to the caudal extremity.

### LARVA

#### PRELIMINARY REMARKS ON THE LARVAL INSTARS

It has been impossible in the case of *Phaeogenes* to determine exactly the number of larval instars. After dissecting a large number of the host and examining a greater number of exuviae, the writer is of the opinion that there are at least four instars, and possibly five. The data upon which this opinion is

<sup>7</sup> The ventral neck region is that part of the head skeleton between the labium and the posterior ventral border of the head.

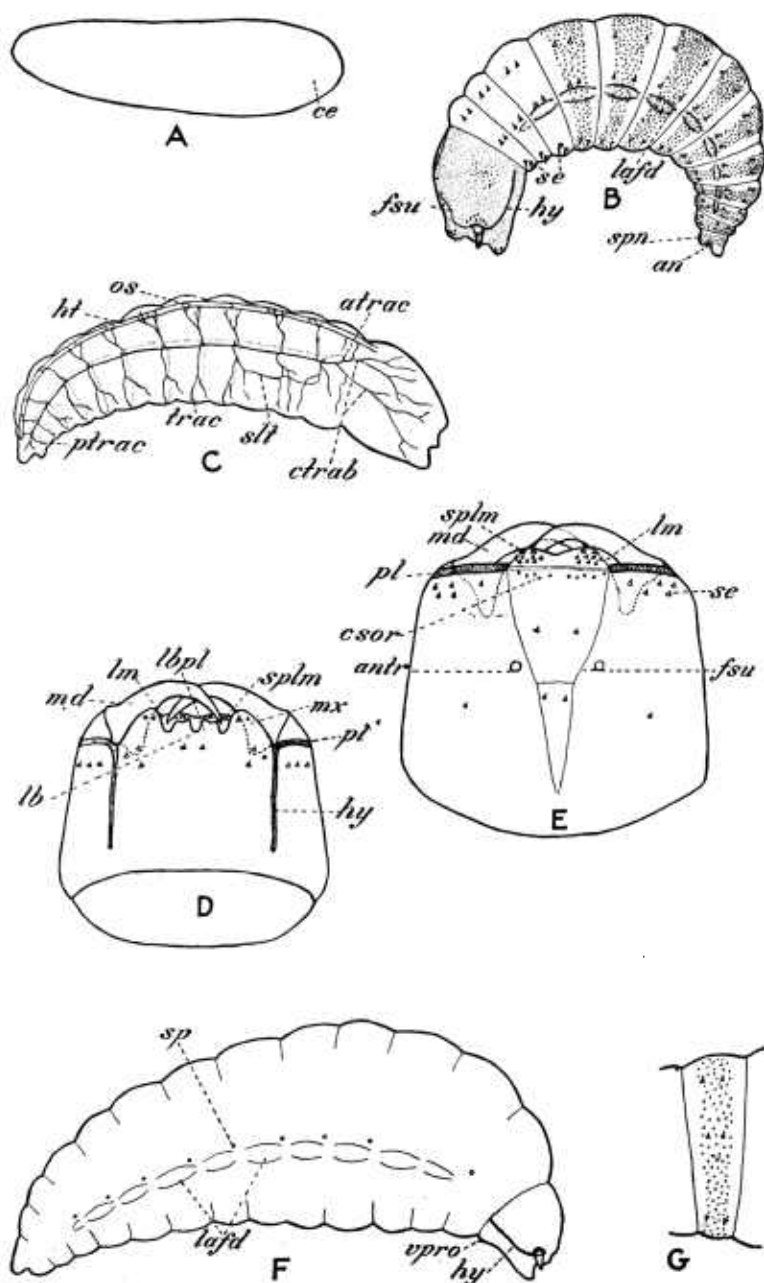


FIGURE 3.—*Phaeogenes nigrident*: A, Newly laid egg; B, unfed primary larva; C, same larva showing tracheal system and heart; D, ventral aspect of primary larval head; E, dorsal aspect of the same head; F, secondary larva; G, abdominal segment of secondary larva showing arrangement of setae and spines

by the mandibular and spiracular measurements and the absence of the ventral protuberance. The last instar is readily distinguished by its size, the mandibular and spiracular measurements, the head characters, and the dorsal hump.

It would seem from exuvial examinations that there are five larval molts. In nearly all cases three, and occasionally four and five, molted skins or pairs of mandibles were found. Absolute reliance can not be placed on these results, however, for superparasitism sometimes occurs. Sometimes *Pyrausta* pupae fresh from the field yield, after dissection, two or three eggs or young larvae of *Phaenogenes*, although never does more than one reach maturity in a single host. If there are five larval instars, they might be separated in the manner indicated in Table 1, and in this case the third instar would certainly fit in between the secondary and tertiary stages.

TABLE 1.—Measurements and characters of the various larval forms of *Phacogenes nigridens*

Probable larval instar <sup>1</sup>	Length of mandible <sup>2</sup>	Width of base of mandible <sup>3</sup>	Spiracles	Diameter of thoracic spiracles	Ventral protuberance	Dorsal hump	Author's classification
	<i>Mm</i>	<i>Mm</i>		<i>Mm</i>			
1.....	0.1504	0.1080	None.....		Absent.....	Absent.....	Primary.
2.....	.1530	.1440	9, all closed.....	0.0090	Present.....	do.....	Secondary.
3.....	.1620	.1530	do.....	.0144	do.....	do.....	
4.....	.1980	.1620	do.....	.0198	Absent.....	do.....	Tertiary.
5.....	.2340	.2070	7 open during most of instar, later all 9 open.	.0469	do.....	Present.....	Last instar.

<sup>1</sup> Instars 1, 4, and 5 are readily determined.

<sup>2</sup> Measured from the lower base to the tip.

<sup>3</sup> Measured from the upper to the lower base of the mandible mounted on its side.

#### PRIMARY LARVA

##### EXTERNAL ANATOMY

The newly hatched larva (fig. 3, B) averages 1.25 by 0.30 mm, or slightly larger than the egg. The head averages 0.3035 mm in width.

The body, exclusive of the head, has 13 segments. When newly hatched, it is widest in the head and thorax and tapers gradually to the caudal end. It is cylindrical, white, and transparent when first hatched, becoming opaque later as the larva ingests food.

The large, heavily sclerotized head (fig. 3, D, E) is thimble shaped, light brown in color, and bears a pair of large, strongly arched mandibles. The hypostoma and pleurostoma are readily identified, being much darker and more heavily sclerotized than the rest of the head cuticle. The labrum is bilobed and has on the upper and lower surfaces, near the apex of each lobe, a pair of dome-shaped sensorial organs; posterior to these on the upper surface are 14 small setae; and farther back, near the posterior margin of the labrum, from 8 to 12 brown circular sensorial organs. The maxillae project beyond both the labrum and labium and have two small setae near the apex and three near the base. The labium has two small palpi and a pair of setae at its base. Each labial palpus has two small prolongations, the median ones bearing a short seta at the tip. The other setae on the head are located as follows:

Eight arranged in a semicircle just caudad of the pleurostoma and six widely separated on the dorsal area. The antennal rudiments are small and circular in outline and are located near the median dorsal region. The cuticle covering them is less sclerotized and more transparent than that of the rest of the head.

Dorsally from near the posterior border two faintly sclerotized sutures, probably the frontal sutures, extend forward to each pleurostoma. At the end of the instar the head splits along these sutures and back to the posterior border, thereby allowing the succeeding larva to emerge and cast its skin.

The body of the larva (fig. 3, B) has a series of lateral folds along each side extending from the second thoracic to the eighth abdominal segment, inclusive.

There are six pairs of small setae on each segment located sub-dorsally, laterally, and subventrally. Around the middle of each abdominal segment is a wide, compact band of minute, triangular, integumentary spines. These are apparently nonsensorial and are about one-fourth the size of the setae. The anal segment is bilobed and has two short prolongations, one inclining dorsad and the other, much shorter, ventrad. Between these is the anal opening.

#### INTERNAL ANATOMY

The digestive system is well developed at hatching. The fore-, mid-, and hind-intestines are easily distinguished, as are also the Malpighian tubes and salivary glands. The stomach begins in the fore part of the first thoracic segment and extends into the seventh abdominal segment. The hind-intestine is very narrow and entirely transparent.

The salivary glands arise from an almost imperceptible opening on the floor of the mouth and, branching in two near the mid-ventral portion of the head, run to the third thoracic segment on each side, where they divide into two ducts, one considerably above the other. They end in the sixth abdominal segment.

Each of the two pairs of Malpighian tubes arises from a common duct at the base of the hind-intestine in the seventh abdominal segment, and runs anteriorly along the side of the stomach and between the salivary glands to the first abdominal segment, where it turns posteriorly and stops in the next segment.

The brain and ventral nerve cord are distinct, and the latter extends to the eighth abdominal segment.

The heart (fig. 3, C) extends from the posterior border of the ninth abdominal segment into the head. It has 10 ostia, one in the middle of each segment from the second thoracic to the eighth abdominal, inclusive. It is best seen in a living specimen. There is no ostium in the ninth abdominal segment.

The tracheal system (fig. 3, C) is as follows: A main lateral trunk runs along each side of the body from the first thoracic to the ninth abdominal segment. These trunks are joined anteriorly by a dorsal transverse commissure in the first thoracic segment; from each side of this commissure run two branches to the upper regions of the head. The two larger branches, aerating the middle and lower regions of the head, arise at the point on the main trunk where it turns to cross over the stomach. Posteriorly the lateral trunks are

united by a ventral transverse commissure in the ninth abdominal segment. The lateral trunks are also united in each segment from the first to the ninth abdominal, inclusive, by a transverse ventral commissure which runs external to the nerve cord in the middle of each segment.

A secondary lateral trunk, typical of all ichneumonids thus far studied by Seurat (24), Thompson and Parker (28), and others, runs from the posterior margin of the first thoracic segment to the anterior margin of the first abdominal segment and is connected with the main trunk by three branches, one arising just caudad of the first spiracular branch, another from the anterior part of segment 2, and the third from just posterior to the second spiracular branch.

Strickland's drawing (26, p. 13) of the tracheal system of the second-instar larva of *Amblyteles subfuscus* Cress. does not show the secondary lateral trunk, but as a discussion of the tracheal system of the larva is not taken up in the text, further confirmation is needed before it can be classed as differing in this respect.

The main lateral trunk gives off two main branches in each segment, which in turn are much ramified. The two branches in the anal segment arise from the main trunk in the ninth abdominal segment. The secondary lateral trunk gives off branches to the lower part of the thorax and first segment of the abdomen. There are no spiracles.

#### SECONDARY LARVA

Length of larva near the middle of this stage, 1.91 mm; width, 0.77 mm; average width of head, 0.5816 mm.

The color and shape of the secondary larva (fig. 3, F) remain about the same as in the first instar. The head is lighter brown, less sclerotized, and much shorter. The mandibles are of approximately the same length as in the first instar, less hooked at the tip, and more robust in appearance. The other head appendages and structures, the various setae, and the sensorial organs are the same as in the previous instar. The most characteristic feature of the head is the large protuberance of the ventral neck region. The type and arrangement of setae and spines (fig. 3, G) on the body are the same as in the first instar, but the spines are not so large. The lateral folds are the same as in the first instar.

There are nine pairs of spiracles in this stage, one near the posterior border of the first thoracic segment and the remaining eight near the anterior border of the first eight abdominal segments. All are slightly dorsad of the lateral folds. In this stage they are closed and do not function.

#### TERTIARY LARVA

Average length, 4.80 mm; average width, 1.80 mm; average width of head, 0.83 mm.

The larva of this stage differs from that of the secondary stage by its larger size and the absence of the ventral protuberance on the head. The general characters of the head resemble more those of the last instar, except that the cuticle of the ventral neck region and base of the maxillae is much more heavily sclerotized and pigmented, the mandibles are longer and less arched on the inner side, and the spiracles are slightly larger but still closed. The setae on each segment are the same except for their smaller size. Each of the last

three abdominal segments has a wide band of minute rugosities extending around the middle of the segment. There are no spines such as are found in the primary stage.

#### LAST-INSTAR LARVA

##### EXTERNAL ANATOMY

Average length of newly molted larva, 5.90 mm; average width, 2.05 mm; average width of head, 0.96 mm; average length of fully fed larva, 10.05 mm; average width, 3.10 mm; average width of head, 1.21 mm; largest larva found, 15.50 by 3.12 mm.

The newly molted last-instar larva is cylindrical, usually light pink or tan in color owing to the material in the stomach, and opaque except in the last three abdominal segments. It is uniform in width except in the much narrower head and the last three abdominal segments, where it tapers sharply to the caudal end.

Shortly after molting a small dorsal hump begins to form in the third thoracic and first abdominal segments. (Fig. 4, A.) This gradually increases in size as the larvae grows, reaching its greatest proportions at the end of the instar. Its rigidity is preserved by the stomach, which is forced into the enlargement. The causes of this hump will be explained later under Larval Development.

The setae and rugosities on the body are the same as in the previous stage. Lateral folds are present and arranged as in the other stages. The anal segment has the same characteristic shape as in the first instar. There are nine open spiracles, but the last two do not function until the last part of the instar.

The head<sup>8</sup> (fig. 5), described from specimens treated with caustic potash, is transparent and composed of the usual epicranial, oral, and ventral neck regions common to hymenopterous larvae. The ventral border of the epicranium (hypostoma, pleurostoma, and epistoma)<sup>9</sup> is a distinctly thickened band extending from one side of the head to the other. It is brownish in color along the hypostoma and pleurostoma, but the epistoma is colorless. The clypeus is pigmented, however, and gives the impression of a continuous transverse brown band across the head, which separates the epicranium from the mouth and ventral regions. The postociput is distinctly differentiated only near the lateral epicranial angles and at the apex; metopic suture distinct, not continuous with frontal sutures; frons triangular-shaped and lightly pigmented, frontal sutures indistinct; temporal fossae (apparently the external markings of imaginal eyes) narrow, shallow grooves; antennal rudiments large, oval, located just laterad of the frons; transverse bridge of tentorium absent, this structure probably represented by two long sclerotic spurs or apodemes extending inside the head from the lateral epicranial angles; posterior pleurostomal ramus bearing a distinct glenoid fossa in which the condyle of the mandible articulates; anterior pleurostomal ramus (superior mandibular support) reduced to a

<sup>8</sup>To describe the various characters of the head, the author has used well-known and accepted terms found in general entomological literature, more especially in the numerous publications of Berlese, Snodgrass, and Nelson.

<sup>9</sup>Thorpe (29), in an article on the parasites of the pine shoot moth (*Rhyacionia buoliana* Schiff.), separates several species of Ichneumonidae and Braconidae by means of the sclerotized head characters of the last-instar larva. In this paper he calls the hypostoma the mandibular strut and the combined pleurostoma and epistoma the labial strut.

slight bulge. One short sclerotic spur or apodeme extends internally from each anterior tentorial pit. This is probably the upper end of the undeveloped anterior tentorial arm or ramus. The apo-

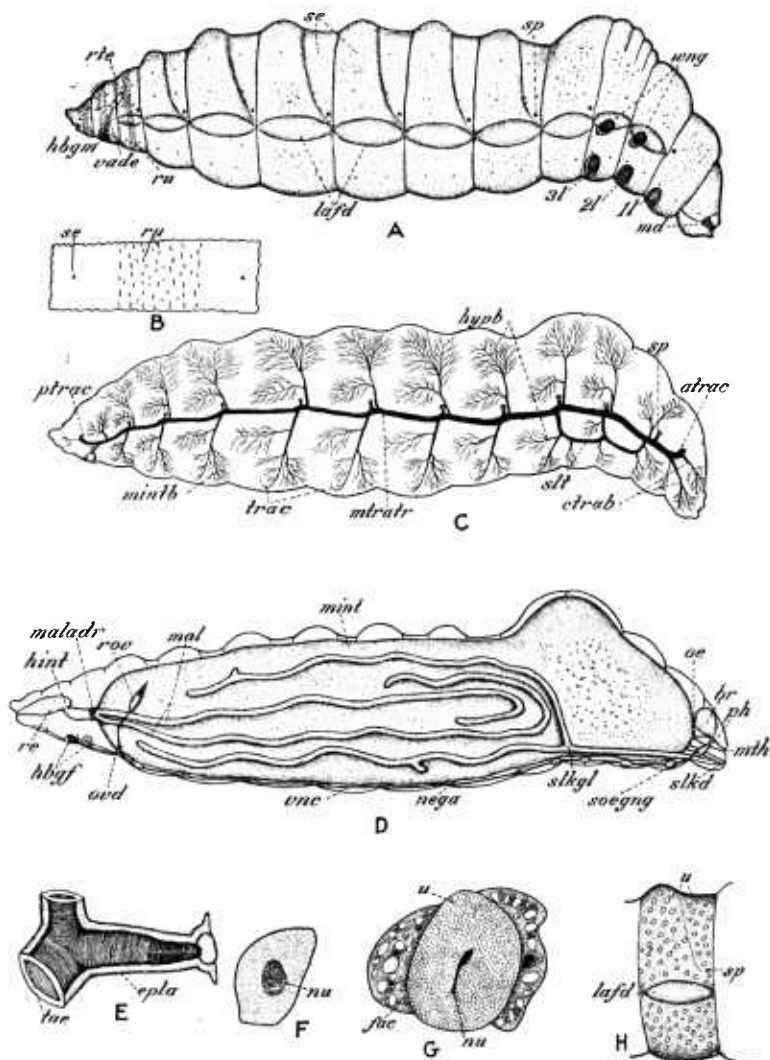


FIGURE 4.—Mature larval anatomy of *Phaeogenes nigridens*: A, Lateral aspect; B, portion of anal segment showing setae and rugosities, highly magnified; C, tracheal system; D, internal anatomy; E, spiracle of last-instar larva; F, oenocyte; G, urate cell; H, segment of abdomen showing urate cells in situ

demes extending from the anterior tentorial pits support the latero-anterior pharyngeal muscles and the apodemes of the incomplete transverse bridge of the tentorium support the ventroposterior pharyngeal muscles.

The mandibles are simple and broadly oval at base; clypeus with 4 to 6 pairs of circular sensory organs or papillae; labrum with 7 pairs of short spines arranged in 2 distinct groups, around which the cuticle is pigmented; maxillae prominent, projecting beyond the mouth and bearing 3 setae in addition to the maxillary palpus, which has 5 slightly elevated sensory organs, one of which has the form of a blunt spine; maxillary suture (the line separating the maxilla from

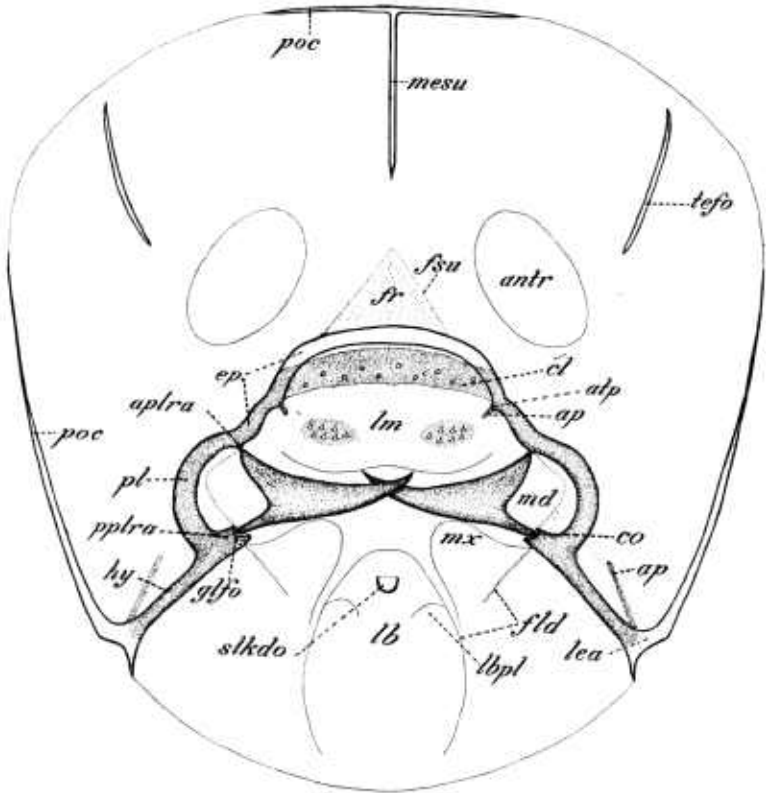


FIGURE 5.—Anatomical details of the head capsule of a mature larva of *Phaeogenes nigridentis*. Stippled areas represent brown epidermal thickenings; unstippled areas (outlined by heavy lines) represent unpigmented epidermal thickenings.

the ventral neck region) indistinguishable; labium distinct, bearing 3 pairs of short setae and a pair of palpi in each of which are 4 slightly elevated sensory organs, one of which has the form of a blunt spine; base of labium not sclerotized or pigmented but identified as a slight fold; ventral neck membrane or labiobase provided with 5 pairs of short setae. The U-shaped salivary-gland opening, located on the upper part of the labium, is heavily sclerotized on its sides and base. The miscellaneous setae on the epicranium are approximately the same in arrangement and number as those of the first instar.

The principal characters of the mature larval head of *Phaeogenes nigridentis* may be summarized as follows: The heavily sclerotized



ventral epicranial border, the absence of the tentorial bridge, and the indistinct sutures of the maxillary and labial regions. When the larvae of this group have been more extensively studied, it will be interesting to see whether or not these characters will be found generally applicable to the Joppinae.

#### INTERNAL ANATOMY

The alimentary canal (fig. 4, D) consists of a short and slender fore-intestine, a voluminous mid-intestine, and a relatively short hind-intestine.

The fore-intestine comprises the mouth, pharynx, and esophagus. The mouth is a narrow, transverse slit that opens into the pharynx. The latter is spindle shaped and extends almost to the posterior border of the head, where it passes into the narrower esophagus. This is a short tube extending into the mid-intestine in the anterior part of the first thoracic segment.

The mid-intestine, or stomach, extends from the first thoracic to the eighth abdominal segment and almost fills the intervening space. It is pink or light tan in color owing to the ingested food.

The hind-intestine is a narrow tube leading from the closed posterior end of the mid-intestine to the anus. It curves upward near the middle to form the spindle-shaped rectum.

The salivary glands have the same general form and disposition as described in the first stage. They consist of four undulating longitudinal tubes, two on each side of the mid-intestine, extending from near the posterior extremity of this organ to the third thoracic segment. Here they unite on each side to form a straight single tube, which continues forward ventrally into the head and joins the one from the opposite side. The common duct is very short and opens on the upper part of the labium in a U-shaped opening.

There are two pairs of Malpighian tubes, each arising from a common duct at the fore part of the hind-intestine in the eighth abdominal segment. They are similar to the salivary glands in size and general appearance. They run anteriorly and laterally between the branches of the salivary glands to the first abdominal segment, where they turn and stop in the second and third abdominal segments.

The nervous system (fig. 4, D) of the larva consists of the brain, the subesophageal ganglion, and the ventral cord. The brain occupies the upper part of the head and extends slightly into the thorax. It is connected to the succeeding ganglia by two cords which encircle the middle portion of the pharynx. The subesophageal ganglia are elongated and fused. They are located just below the pharynx in the posterior part of the head.

The ventral nerve chain includes 11 double ganglia, the terminal one being in the seventh abdominal segment. The thoracic and terminal ganglia are the largest except those in the head. The first abdominal segment has two ganglia, and the others have one in each. The ganglia give off nerves which control the various muscles, sensory organs, and histoblasts of the locomotive and reproductive organs.

The nerves in the thorax and the first abdominal segment arise from the ganglia in the same segment, whereas those in the other

segments originate from ganglia in the preceding segment. The terminal ganglion (fig. 6, F) is evidently a fusion of the ganglia of the last three segments, as it sends out three pairs of nerves, one pair for each segment.

The tracheal system (fig. 4, C) is essentially the same as in the preceding instars, but the branches are much larger and more ramified. Two pairs of branches extend from the anterior transverse commissure to the upper and lower regions of the head. The first seven spiracles function during the entire stage, but the eighth and the ninth are not open to the exterior until the larva has nearly finished feeding.

The oenocytes (fig. 4, F) are visible only in sectioned material, where they are very conspicuous on account of their great affinity for stains. They are usually found in small groups of contiguous cells along the laterad portion of the abdomen. They are much smaller than the urate cells.

The urate cells (fig. 4, G, H) are white and irregularly shaped and easily seen through the body of the larva. They are found only between the first and ninth abdominal segments and are arranged in 4 large longitudinal groups, 2 subdorsally and 2 subventrally. In sections they are usually found closely surrounded by slightly smaller fat cells. The cytoplasm of the urate cells has slight affinity for stains.

The histoblasts or imaginal buds (fig. 4, A, D; fig. 6, A, F) of the various external organs are most easily distinguished in this stage. The most conspicuous ones are the antennal histoblasts situated in the antennal rudiments, the wing buds found laterally in the second and third thoracic segments, the leg buds located ventrally on each segment of the thorax, and the histoblasts of the genitalia located ventrally in the eighth and ninth abdominal segments in the female and in the ninth abdominal segment in the male. All the histoblasts of the external organs, being semiopaque and lying just underneath the cuticle, are very easily distinguished.

The rudiments of the ovaries (fig. 4, D; fig. 6, F) consist of two spindle-shaped bodies with long, narrow stalks, both located in the seventh abdominal segment. The ovaries are attached to the ventral wall of the heart in the anterior part of the segment. Their oviducts run posteriorly under the ventrolongitudinal muscles to two points on the integument in the posterior part of the segment.

The rudiments of the testes (fig. 4, A) are found in the eighth and ninth abdominal segments. They are peanut shaped and lie above the union of the hind-intestine and mid-intestine. Each has a short, narrow stalk with a deep slanting constriction just before it enters the histoblast of the genitalia.

The imaginal buds or rudiments of the Malpighian tubes (fig. 4, D) become very prominent at the end of this stage. They arise from the anterior end of the hind-intestine just back of the larval Malpighian tubes.

#### MUSCULAR SYSTEM

The muscles of the head (fig. 6, B) can be divided into five groups, according to their location and function. The first and most powerful group is that operating the mandibles, comprising the extensor

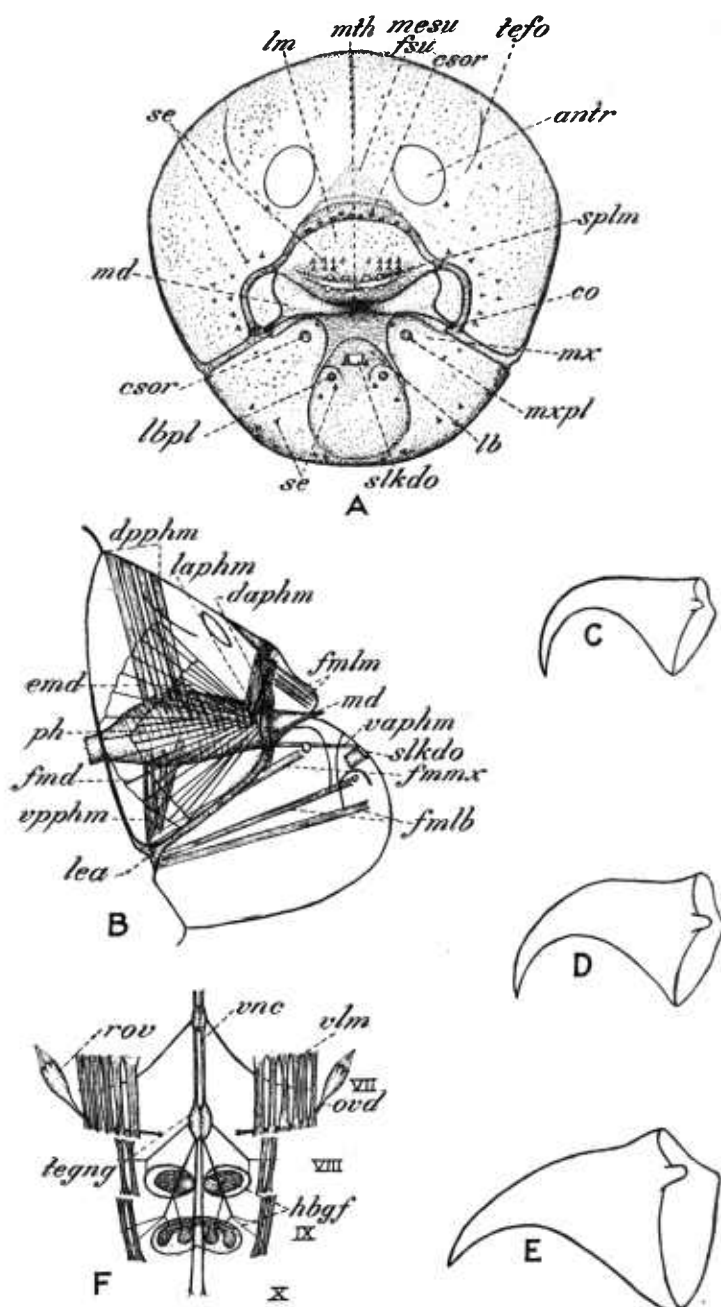


FIGURE 6.—Anatomical details of *Phacogenes nigridens* larva: A, Anterior aspect of mature larval head; B, lateral aspect of mature larval head, showing muscular system; C, D, and E, mandibles of primary, secondary, and last-stage larvae; F, rudiments of female reproductive organs viewed from inside the mature larva. VII, VIII, IX, and X refer to respective abdominal segments

and flexor muscles. The flexor muscle is twice as large as the extensor and occupies more than one-half the width of the head. The second group is that of the pharynx, from which arise five pairs of muscles varying greatly in size. Two muscles of four strands each run from the upper posterior part of the pharynx to the dorsal part of the head directly above. Two more muscles of four strands each extend from the lower posterior part of the pharynx to the two sclerotic spurs or apodemes projecting inward on each side of the head from the bifurcations of the hypostoma. The fore part of the pharynx has three pairs of smaller muscles, two pairs running from the upper part to the epicranial suture supporting the labrum and a very light pair running from the lower surface to the salivary-duct opening. The third group, operating the labrum, is composed of

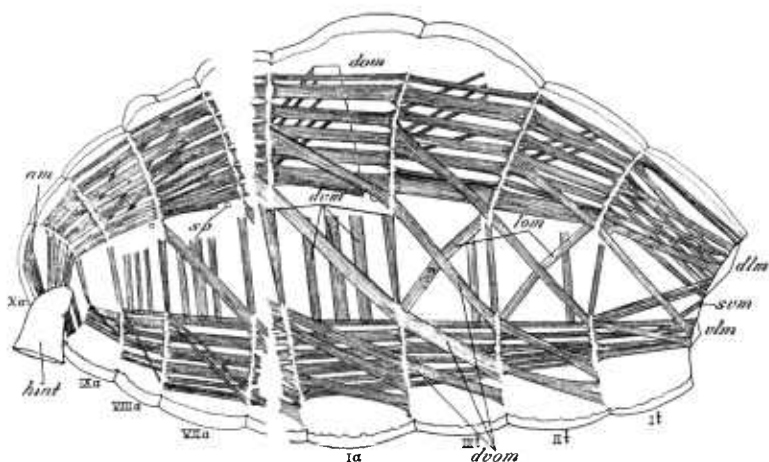


FIGURE 7.—Integumentary muscles of mature *Phacogenes nigridentis* larva (left side) located in the three thoracic (*t*) and the first, seventh, eighth, ninth, and tenth abdominal (*a*) segments. Roman numerals refer to segments

two pairs of narrow muscles, the medial pair having one strand and the other having two strands each. The medial pair runs from the area between the antennae to the extreme anterior part of the labrum. The other pair runs from just anterior to the epicranial suture to the mouth opening. The fourth group is composed of one pair of muscles of one strand each and extends from just dorsad of each apodeme to the maxillae. The fifth group has one pair of two strands each, which extend from just ventrad of each apodeme to the labium.

The muscles of the thorax and abdomen (fig. 7) have a more or less uniform arrangement throughout and can be separated into a series of distinct groups, as was the case with those of the head.

### VENTRAL LONGITUDINAL MUSCLES

The ventral longitudinal muscles (fig. 7, *vlm*) consist of from 4 to 6 strands in each segment except the last abdominal, where there are only 2, running from the posterior border of the ninth abdominal segment to the anal opening.

## DORSOVENTRAL OBLIQUE MUSCLES

The dorsoventral oblique muscles (fig. 7, *dvom*) overlie all the other integumentary muscles and extend anteriorly in a dorsoventral direction. Between the head and the fourth abdominal segment the muscles begin at the posterior line of attachment of the dorsal longitudinal muscles in each segment, and cross four segments to end just ventrad of the ventral longitudinal muscles. Each of these muscles is attached to the hypodermis where it crosses the intersegmentary line. In the first and second thoracic segments one muscle extends from the middle posterior portion of the dorsal longitudinal group to the head at the middle of the ventral longitudinal muscles. In the fourth to seventh abdominal segments, inclusive, the oblique muscles cross only three segments, originating just laterad of the dorsal longitudinal group. In the ninth and tenth abdominal segments these oblique muscles also cross three segments, but are a continuation of a part of the dorsoventral muscles. In the first to seventh abdominal segments, inclusive, each muscle splits into two strands as it crosses the ventral longitudinal muscles. The upper strand continues to the anterior border of the preceding segment and the lower strand to the anterior border of the same segment.

## DORSAL LONGITUDINAL MUSCLES

These dorsal longitudinal muscles (fig. 7, *dlm*) comprise a set of mostly wide bands of from 5 to 11 strands on each side of the median line. The first thoracic segment is the only one having 11 strands, and these are in 2 groups, 1 above the other and crossing each other at a slight angle. The sixth and seventh abdominal segments have 6 and 5 strands, respectively, while the others have either 6 or 7.

## DORSAL OBLIQUE MUSCLES

The dorsal oblique muscles (fig. 7, *dom*) are found in every segment but the first and last two. They vary from three slender bands in the second segment to eight in the seventh abdominal on each side. Their number varies with different individuals. Their posterior ends are attached to the posterior margin of each segment, and they run slightly dorsad to attach themselves near the middle of each segment. They lie exterior to the dorsal longitudinal muscles. All are in a compact parallel series, except one which runs to just posterior to the spiracle in the first to seventh abdominal segments, inclusive.

## DORSOVENTRAL MUSCLES

In each segment but the first thoracic and last two abdominal segments there are from 1 to 3 muscles (fig. 7, *dvm*) on each side, which extend from ventrad of the lowest dorsal longitudinal muscle to underneath the upper strand of the ventral longitudinal muscles. The second and third thoracic segments have 1 muscle each, near the anterior border. Each of the first eight segments of the abdomen has three placed evenly throughout. Besides the muscles in the segments there is 1 strand which is located along each intersegmental line, making 12 in all. This muscle has its attachment and direction similar to the others.

## MISCELLANEOUS MUSCLES

In the first segment there is one small subventral muscle (fig. 7, *svm*) running from the head on each side to a point midway in the segment. The second and third thoracic segments have two lateral oblique muscles (fig. 7, *lom*) running cephalad from a point just under the upper ventral longitudinal muscle at its posterior attachment to a point near the attachment of the lower dorsal longitudinal muscle. In the anal segment there are four light bands (fig. 7, *am*) running from near the posterior end of the heart to the anal opening.

The most powerful muscles of the trunk are the ones in the dorsal longitudinal group, and especially those in the thorax, where they are brought into frequent action by the constant bending of this part of the body to permit the larva to secure the food lying along the wall of the host. The dorsal oblique muscles, when contracted, are responsible for the deep constrictions found dorsally in their respective segments. The muscles of the eighth, ninth, and tenth abdominal segments are much thinner and weaker than the corresponding muscles of the other segments.

## PREPUPA

The prepupa is of the usual hymenopterous type. It is of about the same length as and more slender than the mature larva and has a constriction in the first abdominal segment. Most of the appendages of the adult head appear in the larval head; the eyes show up in the first thoracic segment, and the stomach now completely fills the caudal end.

## PUPA

Length, 10 mm; width, 2.5 mm.

The pupa is inclosed in a thin, closely fitting, transparent case. It almost completely fills the host pupa and is usually oriented in the same direction as the host.

There is a loose network of silk attached to the inside of the host pupa, but it can hardly be called a cocoon.

## BIOLOGY

## EMERGENCE

When ready to emerge, the adult splits its pupal skin at the head end and by its contortions slowly works it off the body in one piece. Just before this skin leaves the abdomen, that part of the adult meconium inclosed in a peritrophic membrane is discharged. This is an oval-shaped sac 1 by 2.5 mm closed at one end and containing a white granular substance. The adult then goes through a resting period of about 24 hours, during which the wings and other organs become adjusted to the changed conditions. Also during this time more white meconial matter is cast in a soft mass, but devoid of any peritrophic membrane. Finally the adult chews an irregularly shaped hole near the head of the host and pushes itself out.

In only one instance has the writer observed an emergence hole in the caudal end of a host pupa. Often the opening is made so large

that the host head is broken off when the adult emerges. The hole is usually made on the ventral side.

Emergence takes place at any time during the day or night, in this respect differing from that of *Theronia atalantae* Poda, a rare pupal parasite of *P. nubilalis*, which, according to Constantineanu (9, p. 423), emerges only during the night.

### BEHAVIOR ON THE FIRST DAY AFTER EMERGENCE

During the first 24 hours after emergence the adult remains in a lethargic condition and moves about only when disturbed. The abdomen in the early part of this period contains numerous large white cells closely resembling the urate cells of the larva, and within the first few hours these disappear coincidentally with evacuation of the remaining meconium. This meconium is often in the shape of small white pellets. Whether the disappearance of the white bodies in the abdomen has any direct relation to the discharged meconium it was impossible to determine, but the writer believes that these groups of cells are eliminated by way of the hind-intestine or Malpighian tubes.

In all cases where adults died within two or three days after emergence it was noted, by external view as well as by dissection, that these cells were still intact. The average time required for the complete discharge of the meconium was three hours. Adults which showed none of these cells on the second day always had normal longevity.

Mating was not usually attempted before this adult meconium was cast. Temperatures below 10° C. (50° F.) were often fatal to adults that had not completed this evacuation.

### LIGHT REACTION

Immediately after emergence both sexes appear positively phototropic to a slight degree. After a few hours the female loses this reaction, and during the remainder of her life exhibits only a strong negative phototropism. The male retains the positive phototropic reaction, although it is somewhat diminished later in life. This tendency of the female to conceal herself in a dark corner adds difficulties to the handling in laboratory breeding work. When the female is suddenly exposed to an ordinary electric light, she will fly directly into it and flutter there for several minutes before becoming adjusted to her surroundings and seeking the dark.

### FOOD

Both sexes feed readily on honey, raisins, and other fruits, but the best results in survival were obtained by feeding the adults sugar solution. Dry sugars attract the adults only slightly. The parasite does not normally take any nourishment from the host. Only in one instance, when the host was broken and exuding part of its blood, did the writer notice a female feeding from this source. This is somewhat different from the feeding of another pupal parasite of the borer, *Itoplectis ephippium* Brullé, which punctures the fresh white pupae and greedily laps up the blood, often causing the death of the host.

## MATING

Mating may take place, as to both sexes, within a few hours after emergence. Apparently one mating is sufficient for the proper fertilization of the eggs, and one male is able to fertilize many females. The male parasite will not mate before voiding the meconium, but the female will permit mating prior to such voidance. For breeding purposes, however, it is deemed advisable to isolate the female until the end of this period, as otherwise some die shortly after mating. The female attracts the male whether or not she has already been fertilized, but if this has taken place the male usually turns away after a quick examination with his antennae. The average length of time spent in mating is one minute.

Mating can be secured under a great variety of conditions, but the writer's best results have been obtained by placing a male 1 or more weeks old in a 2-mm vial with a female less than 1 day old and forcing them by means of the cotton plug to occupy as small a space as possible.

Mating will take place at any temperature between 18° and 30° C. (64.4° and 86° F.), but the preferred range is from 20° to 25° C. (68° to 77° F.). A female more than a week old is very difficult to mate, the males being only mildly attracted to her, if at all; but when some of the larval meconium and cast skins in the old host pupa were brushed lightly over her body with a fine camel's-hair brush, mating took place immediately. It would seem, therefore, that the odor of this material plays an important rôle in inducing mating.

These details of mating have importance in connection with the artificial or controlled breeding of the parasite.

## OÖGENESIS

At emergence there is usually only one extremely miniature egg at the base of each follicle. Females fed on sugar solution and kept at 25° C. (77° F.) developed their first mature eggs in from one to two weeks, the average being 11 days. At the end of this period there were from 1 to 6 fully developed eggs and from 9 to 12 partly developed ones. At the end of three weeks there were from 6 to 12 fully developed eggs, and if none was laid the lowest ones disintegrated and passed out through the oviduct. No eggs were ever found in the oviduct—a strong contrast with the condition obtaining in many other ichneumonids and braconids. Table 2 shows the development of the ovarian eggs of various females when exposed to different temperatures. The females used in the experiment were held more or less closely at their respective temperatures, being kept only for a half hour twice a week at room temperature to permit better feeding conditions.

TABLE 2.—Approximate time required to develop mature eggs in the ovaries of females of *Phaeogenes nigridens* exposed to different temperatures

Number of individuals	Temperature of cage		Time required to develop mature eggs	Number of individuals	Temperature of cage		Time required to develop mature eggs
	°C.	°F.			°C.	°F.	
10.....	25	77.0	11 days.	4.....	8	46.4	7 weeks.
3.....	18	64.4	4 weeks.	5.....	5	41.0	12 weeks.



## OVIPOSITION

The female prefers freshly formed white or light-brown pupae in which to oviposit, seldom paying any attention to pupae that are more than 2 days old. This may be due to the difficulty of piercing the hard pupal shell. She will oviposit in pupae lying loose or concealed in artificial or natural tunnels, but prefers those lying in their cocoons, the restricted space therein appearing to aid her in ovipositing.

Oviposition takes place at any temperature between 18° and 30° C. (64.4° and 86° F.), with a slight preference for temperature midway between these extremes.

When supplied with a pupa in a cornstalk tunnel, the female is first attracted to the tunnel itself. She enters this, feeling with her antennae as she goes, until she reaches the host cocoon. After examining this slightly, she forces an opening in it by cutting some of the silk with her mandibles. If she finds that the host is newly pupated, she quickly crawls inside with her head near that of the host, grips the struggling pupa with her legs, arches her abdomen, and thrusts in her ovipositor. Perforation of the pupa is usually made at the base of the wing pads or in its proximity. The entire length of the ovipositor is pushed inside and held there from 30 to 60 seconds. Occasionally she moves this organ up and down slowly in the host before depositing the eggs. Only one egg is deposited at a time, and ordinarily only one is deposited in a given host.

While the ovipositor remains inside, the pupa usually ceases its movements but resumes them as soon as the ovipositor is withdrawn, often continuing them for several minutes after the parasite has left. This struggling, instead of discouraging the female, seems to accentuate her desire to oviposit.

When a brown pupa—viz, one 3 days or more old—is encountered in the corn-borer tunnel, the female usually leaves without entering the cocoon. If she does enter and attempt oviposition, her efforts are often unsuccessful owing to her inability to pierce the hard sclerotic case during the violent struggles of the host. When she is successful, it is usually because the ovipositor has struck the softer part located between the telescoping segments.

The hole made by the ovipositor in the host integument usually permits some of the host blood to exude, which seals the opening. When dry, this blood turns black and leaves a characteristic spot by which parasitized pupae can be recognized in many instances.

In the field, as well as in the laboratory breeding, more than one egg is occasionally found in a host. Where two are placed in the same host, one of the resulting larvae kills the other with its long hooked mandibles as soon as they come in contact, usually in the first stage.

Occasionally the writer has seen a female thrust her ovipositor into the host without depositing an egg. It is possible that, although stimulated to oviposit by the presence of the host, she has not an egg sufficiently developed for deposition, especially as her ovaries can hold but very few mature eggs, three being the average and six the maximum found in a laying female. One female, dissected after she had punctured the host in this manner, contained no developed eggs.

When given loose pupae, the female shows a keen interest in the cast-off skin of the larva, especially the head capsule, and examines this very carefully before hunting for the pupa. Corrugated paper strips which contain or have contained pupae always excite her, and even corrugated paper which has never been exposed to *Pyrausta* larvae arouses her interest. She is apparently attracted by its rough surface, as smooth paper does not produce the same reaction.

Females are most active in the sunlight or at high temperature. When exposed to direct sunlight, they become more active under its influence, but they soon move away to a shady place. Semidarkness appears to stimulate oviposition to its greatest extent.

Females are never interested in *Pyrausta* larvae or prepupae.

In the laboratory breeding experiments three has been the maximum number of eggs laid in any one day, showing that the female has a prolonged oviposition period.

Pupae of *Sesamia (nigralis rubra)* Stoll, a pest of corn in southwestern France, were exposed to different females, but in these they showed no interest whatever. This species of Lepidoptera occurs in company with *Pyrausta* in corn and has habits and a life somewhat similar to it.

### INCUBATION

The egg of *Phaeogenes* floats freely in the body of the pupa, but it is always found where laid. In eggs nearly ready to hatch, the forming larva may easily be detected with the aid of a binocular microscope. The abdomen is not folded on itself, as is the case with many ichneumonid larvae, but is straight and extends to the caudal extremity of the egg. As it completely fills the posterior portion of the egg, a slight movement of the inclosed larva causes the large head to come into close contact with the cephalic end, which is then easily broken open by the long, sharp mandibles, and the larva emerges. The eggshell remains where the egg was laid unless moved or eaten by the larva and is never attacked by phagocytes as are eggshells of *Eulimneria crassifemur* Thom., *Campoplex multicinctus* Grav.,<sup>10</sup> and *C. pyraustae* Smith,<sup>10</sup> also parasitic on the borer.

The incubation period at 25° C. (77° F.) was approximately two days and at 18° C. (64.4° F.) about twice as long. This was determined by dissecting the host near the end of each period, when practically all the eggs were found to contain fully developed larvae. The eggs were then placed in normal salt solution, and the larvae emerged a few hours later.

Tothill (31, p. 95), in describing *Therion morio* Fab., an ophonine parasite attacking the larva and emerging from the pupa of the fall webworm (*Hyphantria cunea* Drury), states that "an unattached egg in a pupa undergoing histolysis would be at a disadvantage in the matters of oxygenation and phagocytic attack compared with an egg attached to the inner side of the wall of the pupa." He also states that the phagocytic action taking place in the pupa during formation of the adult organs is fatal to unprotected eggs or larvae of parasites attacking this stage of the host. The writer can not agree with these statements, as his study of *Phaeogenes* has shown

<sup>10</sup> From unpublished notes of the writer.

that neither eggs nor larvae have ever been found dead from any cause originating from the host.

Cushman (10) treats of various types of parasitism among the Ichneumonidae, with particular reference to the egg, larval form, and habits. *P. nigridens*, on account of its habits and more especially its larval anatomy, appears to fit into Cushman's second type of internal parasites along with *Amblyteles vadatorius* Illiger and *Ichneumon sarcitorius* L. and probably others of the subfamily Jopinae. Both of the last two species, however, lay their eggs in the last-stage larvae, and the adults emerge from the pupae of the lepidopterous host, whereas *Phaeogenes* passes its entire life cycle in the pupa. The egg is identical with that of *I. sarcitorius*, according to the drawing of Chewyrev (8). The general form of the *Phaeogenes* first-stage larva is also very similar to Chewyrev's drawings of the same stage of *I. sarcitorius* and *A. vadatorius*, particularly in respect to the head. On the basis of the appearance of the egg and the characters of the first-stage larva, *Phaeogenes* is more closely allied with this group than with any of the others.

## LARVAL DEVELOPMENT

### FEEDING

The generally accepted theory on the feeding habits of internal parasitic larvae is that advanced by Ratzeburg (21, p. 13). He believed that such larvae feed upon the lymph and blood of the host rather than on the solid tissues. Later Timberlake (30, p. 88), as a result of his study of *Limnerium validium* Cress., contended that the small larvae of this species "institute pathological changes" which break down the solid tissues to a size which can be readily swallowed by the larva. The last-stage larva, having in addition "chitinized, supporting, or possibly rasping ridges" around the mouth, was believed to be able to ingest solid tissues even before they had been entirely disintegrated.

With *Phaeogenes*, however, the writer believes that the larva, no matter in what instar, always breaks down the large fat bodies, chiefly by its mandibles. In the first stage particularly the mandibles seem to be larger in comparison with the size of the head.

The writer has noticed in dissections that, when a first or second instar larva is encountered in the host, the fat bodies are always broken up into small pieces, whereas a normal host has its fat distributed in comparatively large masses. When the last instar is reached, there is very little liquid food left, and thus the larva has to depend on the solid matter. Most of these older larvae, when dissected, have parts of some host organ projecting from the mouth.

During the process of feeding, the labrum, the maxillae, and to a lesser extent the labium are continually pushed in and out while the mandibles tear and direct the food into the mouth.

The food of the first and second instar larvae is mainly the blood and fat of the host. In the third stage, however, the larva attacks the vital organs and some of the integumentary muscles—in fact, almost everything except the large tracheal branches.

## GROWTH

With *P. nigridentis*, as with many parasites whose larvae live internally, it was difficult to follow the larval development closely. However, by completing numerous dissections and making a study of the various body, head, and mandibular measurements and the number of molted skins, a fairly accurate estimation of the larval development was obtained.

At various intervals dissections were made of parasitized pupae reared at a constant temperature of 25° C. (77° F.), and the results showed the length of each larval stage to be approximately as follows:

	Days
Primary stage-----	1
Secondary stage-----	1¼
Tertiary stage-----	1
Last stage-----	2¾
Total-----	6

These figures are somewhat low for the actual larval period under field conditions in the spring, as the mean temperature at this time is from 16° to 20° C. (60.8° to 68° F.), depending on the zones. In the second generation, however, which develops during the latter part of July and the first part of August in the 2-generation host zones, the larval development follows very closely the above rates, and the parasite has in normal years a total larval period of from 6 to 10 days.

No notes were made on the length of the larval stages at 18° C. (64.4° F.), but as the total time from egg to adult at 25° C. (77° F.) was just one-half what it was at 18° C., it may not be far wrong to estimate each instar on this basis. This would give for the entire larval stage a period of about 15 days. At constant temperatures below 14° C. (57.2° F.) the larvae did not seem to develop well, and most of them died without pupating.

## ACTIVITY IN THE HOST

The activity of the larva within the host could be followed only within certain limits. Hence, the data were obtained by making a large number of dissections and noting the position, food, etc., of the larva found therein.

After hatching from the egg, the larva makes its way, feeding as it goes, toward the posterior end of the abdomen, where it remains throughout the short first and second stages. Its activity during these two stages is much greater than during the last instar, but in all its migrations it rarely enters the anterior half of the host. It moves about by bending and straightening out its body, the numerous spines and finlike shape of its caudal extremity aiding it in these movements.

During the early part of the last instar the larva is almost as active as in the previous instar; but as it becomes larger and its width approaches that of the host pupa it takes a permanent position with its head facing the anterior end of the host. It now almost fills the posterior half of the pupa. At this point the development of the

dorsal hump begins. This is a gradual process, and the hump attains its largest proportions at the end of the stage. A possible explanation of the cause of this character is as follows:

As most of the food lying in the middle of the host has already been devoured, the larva has to feed on those tissues clinging to the body wall. To do this in such close quarters, the width of the larva being practically the same as that of the host, requires the thorax to be bent at a right angle with the body, thus forcing the dorsal part of the third thoracic and first abdominal segments to bulge out into the open space in front. This characteristic larval hump has never, to the writer's knowledge, been recorded as occurring in any other ichneumonid.

As the larva grows, it pushes against the posterior end of the pupa, causing the abdomen to extend. The undevoured muscles controlling this region of the host body have already been rendered functionless by the destruction of the nervous system; so the segments are no longer able to retract, therefore remaining in this position permanently. If the pupa is disturbed at this time, the imprisoned larva moves its body and the host abdomen is moved along with it. Hitherto the activity of the host has remained entirely unaffected by any movements of the larva. When completely fed, the larva fills all that part of the host posterior to the head and first two thoracic segments.

Many species of ichneumon larvae which pupate within the pupae of their hosts spin a thin film of silk across the inside of the host's head, as with *Ichneumon rubens* Fons. (3, v. 63, p. 258), or around themselves, as with *Amblyteles subfuscus* Cress. (26). *Itoplectis conquisitor* (Say), according to Fiske (12, p. 196), often spins a little brownish silk "over the interior surface of the pupa shell. Any accidental opening if not too large in the anterior portion will be repaired by a thin membrane of this substance." The larva of *Phaeogenes nigridens* is similar to the last species in this respect.

### PREPUPAL DEVELOPMENT

Intervening between the larval and pupal stages there is a short period during which the parasite prepares itself for transformation into the pupa. Although this may not represent a true instar as judged by ecdysis, it is so entirely different from any other instar that it can be considered as a distinct stage of ontogenesis.

To determine the prepupal period, records were made of eight parasitized *Pyrausta* pupae kept constantly at 25° C. (77° F.), and these showed the average length of the prepupal stage to be one and one-half days. At 18° C. (64.4° F.) it was correspondingly longer.

In an effort to determine this period more accurately, many fully fed larvae were removed from the host, but all died without completing this stage. In addition, a number of host pupae were opened slightly in order to see the mature larva or prepupa within, but the parasite so treated rarely reached the pupal stage.

The exact starting point of the prepupal stage is always difficult to fix, but the writer has arbitrarily placed it as the time when the

eyes first appear as small reddish spots. At about the same time the larval organs in the head break down and make way for the adult mouth parts and antennae, the dorsal hump disappears, and the larva becomes slightly longer and narrower. The adult head forms in the first thoracic segment of the larva. The histoblasts of the legs, wings, and genitalia are also well developed and approach closely the form of their respective adult organs. A few hours later the stomach opens into the hind-intestine, and its contents are voided in one long, narrow mass. This larval meconium is brown and inclosed in a transparent peritrophic membrane. It is about 1 mm wide and 4 cm long and lies in a convoluted mass at the extreme end of the host abdomen.

Simultaneously with the casting of the meconium a constriction forms in the first abdominal segment. Shortly after the meconium is voided, the last larval skin is cast, thus revealing the pupa.

### PUPATION

The newly formed pupa is cream colored. After two days the thorax and later the head turn black, and the adult emerges from its pupal skin. When disturbed, the pupa sways its abdomen slowly back and forth, and if the host case is not too stiff it succeeds in moving that also. The pupal period at a constant temperature of 25° C. (77° F.) averaged four and one-half days.

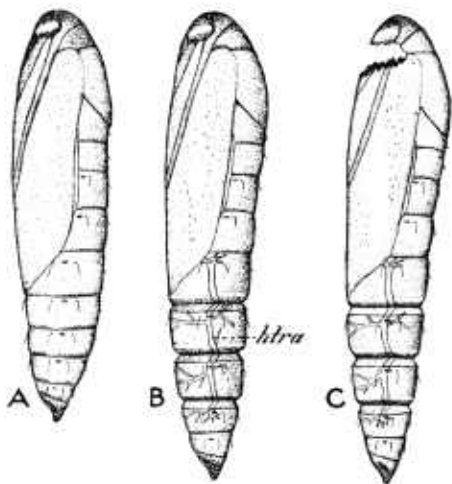


FIGURE 8.—*Pyrausta nubilalis* pupae; A, Either unparasitized or containing a *Phaeogenes nigridens* egg or young larva; B, containing a mature parasite larva; C, pupa from which the parasite has emerged

### EFFECT OF PARASITE ON HOST

The first external indication that the *Pyrausta* pupa has been parasitized occurs when the collapsed host tracheae show through the body wall (fig. 8, B) in the fourth to the sixth abdominal segments. The host is then dead. At the same time these segments become extended by the pressure of the growing larva within, and the sutures between these segments become deeply constricted. Previous to this, when the host was disturbed, the abdomen moved in its normal rapid twisting manner. Now, however, its movements are actuated entirely by the inclosed parasitic larva, which gives it a slow swaying movement that continues long after the external stimulus has stopped. When the parasite reaches the pupal stage, the host case has often dried to such an extent that it can no longer be moved by the parasite.

## LENGTH OF LIFE OF ADULT

Both male and female *Phaeogenes nigridens* are very hardy and when placed in an optimum environment live for a long time. In order to determine the longevity of each sex, 124 males and 65 females were subjected, immediately after emergence, to various food, temperature, and humidity conditions. Each individual was confined in a separate cage, of the type already described, and given daily attention until it died. Table 3 summarizes the results of these observations.

TABLE 3.—Length of life of *Phaeogenes nigridens* under various conditions of food, temperature, and humidity

Temperature	Approximate humidity	Males						Females					
		No food			Fed sugar solution			No food			Fed sugar solution		
		Longevity		Individuals	Longevity		Individuals	Longevity		Individuals	Longevity		Individuals
		Maximum	Average		Maximum	Average		Maximum	Average		Maximum	Average	
		Num-ber	Days	Days	Num-ber	Days	Days	Num-ber	Days	Days	Num-ber	Days	Days
°C.	Per cent												
1 27 (80.6° F.)	30-50	10	7	4	11	21	14	4	8	4	4	47	34
25 (77.0° F.)	40-60	13	13	5	11	45	19	8	13	7	5	68	43
18 (64.4° F.)	60-80	8	30	18	15	58	31.5	9	26	14	9	110	70
8 (46.4° F.)	40-60	18	25	12	17	130	83	7	41	22	9	110	76
5 (41.0° F.)	60-80	7	22	10	14	152	108	7	39	28	3	9	16½

<sup>1</sup> Average temperature of screened insectary, in which this set of experiments was conducted.

<sup>2</sup> Months.

The insectary was screened and subject to all the fluctuations of temperature and humidity prevailing in the Hyères locality. The experiments in the insectary were conducted during July and August, when the average maximum temperature was 33° C. (91.4° F.) and the mean about 27° C. (80.6° F.). The cages having temperatures of 25° C. (77° F.) and 18° C. (64.4° F.) were electrically heated and held at their respective temperatures by an electrothermostat. To obtain the temperatures of 8° and 5° C. (46.4° and 41° F.) the electric refrigerator was used. The temperatures of this cold chamber had a variation at times of 1° C. (1.8° F.) either way. Those adults which were not given food were given no water.

## HIBERNATION

*P. nigridens* passes the winter only as an adult female. The writer has arrived at this conclusion through a series of laboratory and field observations which may be summed up as follows:

It was first definitely proved that neither eggs nor larvae could survive long exposures to temperatures below 12° C. (53.6° F.). Periods of from one to four weeks at these temperatures always resulted fatally to the parasite. When exposed to higher temperatures, development progressed in direct ratio to the temperature, but it was never sufficiently slow to enable either of these stages to bridge the long gap between the fall and spring.

The pupae were able to withstand a longer period of exposure to the temperatures below 12° C. (53.6° F.), but could not survive long enough to pass the winter in this stage. In some cases a slight development took place. At higher temperatures the pupae developed in the same manner as the larvae.

Adult females, on the other hand, have been easily kept on sugar solution in the laboratory at temperatures of from 5° to 8° C. (41° to 46.4° F.) from August to May of the following year, and a few have lived until the middle of June. Males kept under identical conditions always died during the winter.

The hibernation experiment, made under conditions more or less similar to those in the field, was conducted as follows: On August 16, 1930, newly emerged adults (80 males and 70 females) were placed in an outdoor cage measuring 4 by 6 by 5 feet and screened on all sides and the top. The cage was placed in the laboratory yard at Hyères. Mature cornstalks, previously placed within, were sprinkled with water every few days, depending on the rainfall. Sugar solution was also poured over some of the stalks once a week to maintain a constant supply of food. When the cage was examined for the first time, on September 26, all the males and 19 females were dead. The next examination was made March 24, 1931, at which time there were 13 living females. These females died during May, the last one on May 26.

In view of these facts it is believed that *P. nigridens* hibernates only as an adult female.

Of the ichneumonids hibernating as adults, by far the greater number belong to the subfamily Joppinae, according to the records thus far published. Constantineanu (9, p. 418), in his study of the ichneumonids in Rumania, found only one species outside of this group hibernating as an adult. Morley (17, p. xxviii) states that hibernating females belong "almost, or quite, exclusively to the Ichneumoninae [now Joppinae] and Cryptinae." Thus far males have never been known to hibernate.

Constantineanu captured hibernating females of each of the following: 40 species of *Ichneumon*, 4 of *Hoplismenus*, 4 of *Amblyteles*, 2 of *Chasmias* (*Chasmodes*), and 1 each of *Herpestomus*, *Heterischus*, *Stenodontus*, and *Ischnus*. All belong to the same subfamily as *Phaeogenes*. The specimens were found hidden in the bark or moss of dead trees as well as in the tunnels of xylophagous insects. In the latter part of February, 1927, Constantineanu collected in the field 22 species of females belonging to the foregoing genera. They were placed in cages and fed. Most of them lived until the middle of July of that year, and a few even lived until the middle of August. *P. nigridens* probably hibernates and lives as long as any of the closely allied genera mentioned above.

#### RATIO OF SEXES

Adults were reared from two summer collections made in northern Italy, and in general the number of females was slightly greater than that of the males. The record of emergence is found in Table 4.

Data on emergence from the second-generation hosts obtained in the spring were too meager to make it possible to determine ac-



curately the proportion of the sexes, but they seem to be about equal at this time also. In the Aquitanian zone, which has usually one generation of the corn borer each year, the males and females also appear to be about equal in number.

TABLE 4.—Ratio of sexes of *Phaeogenes nigridens* obtained from summer emergences in Italy

Year	Locality	Males	Females
		Number	Number
1929.....	Bergamo.....	36	59
1930.....	Sernide.....	79	95
1930.....	Bergamo.....	86	79
Total.....		201	233

### PARTHENOGENESIS

Unfertilized females of *P. nigridens* oviposited readily and their eggs developed in the normal manner. The progeny, however, were always males.

### SEASONAL HISTORY

With *Phaeogenes nigridens*, which spends the greater part of its life in the adult stage, it is difficult to follow accurately the seasonal history. There apparently is no actual diapause or resting stage in any of the immature stages. As a new generation may be produced every 26 days at 25° C. (77° F.) and every 50 days at 18° C. (64.4° F.), the problem becomes more complicated, particularly when one considers the annual 1- and 2-generation cycle of the host. Since it has been shown to have at least one other host, its true life cycle can not be solved by studying merely the seasonal history of *Pyrausta nubilalis*. It is known, however, that the seasonal history of *Phaeogenes* follows more or less closely that of *Pyrausta* in all the zones in which both occur. One parasite generation may extend over at least 11 months, judging by the combination of the maximum length of the immature stages and the maximum life of the female, under conditions more or less comparable with those in the field. Therefore, the parasite is able to reproduce itself with only one generation annually. This would apply to the regions with a low mean summer temperature, such as the Armorican, Rhodanian, and Aquitanian zones. On hosts other than *Pyrausta*, however, there may be one, and possibly two, additional generations in each of these zones, as fully developed females are always present during July and August.

In each zone *Phaeogenes nigridens* passes the winter as an adult female, the males dying before or during the winter.

As the other known host, *Tortrix pronubana* Hbn., occurs in practically all the zones where *Phaeogenes* is found, it could serve as an intermediate host in those regions where the parasite has more generations than *Pyrausta*.

The seasonal history of *Phaeogenes* for the various zones in which it has been studied (fig. 9) is summarized as follows:

## ARMORICAN ZONE (TOURS, ANGERS)

In the Armorican zone there is one generation of the host and probably two of the parasite. The overwintering females oviposit in the *Pyrausta* pupae which appear during May and June. Females of this generation emerge during the latter part of June and the early part of July and, after an oögenetic period of three weeks, lay their first eggs either in the current summer or the following May or June. They may also lay part of their eggs in one summer and the remainder the following spring. As there are no *Pyrausta* pupae present after the middle of July, the parasite must have an intermediate host in which to lay these summer eggs. The plant in which *Pyrausta* develops in this zone is *Artemisia vulgaris* L.

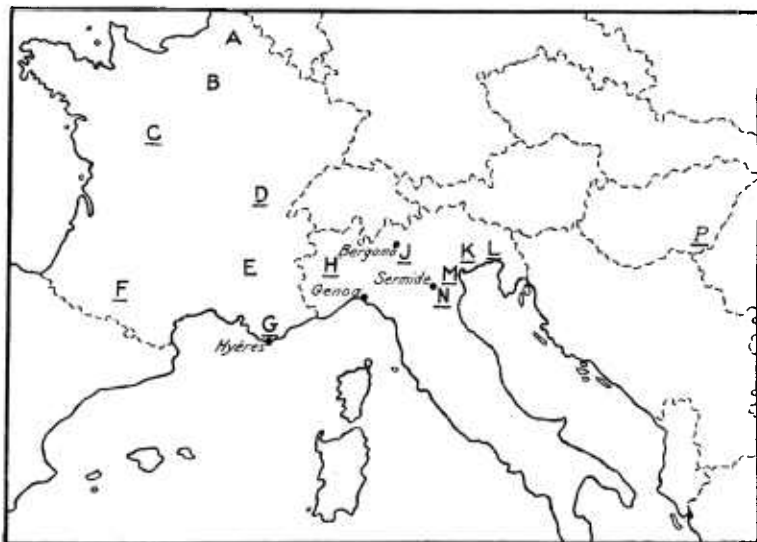


FIGURE 9.—Map showing the zones in Europe in which *Phaeogenes nigridens* has been studied: A, Sequanian (north); B, Sequanian (south); C, Armorican; D, Rhodanian; E, Mediterranean (north); F, Aquitanian; G, Mediterranean (south); H, Padovian (Piedmont); J, Padovian (north); K, Venetian (high); L, Plavisian; M, Venetian (low); N, Padovian (south); and P, Hungarian. Underlined letters represent zones in which the parasite occurs; letters not underlined represent zones from which large host collections have been made but no *P. nigridens* found

## RHODANIAN ZONE (JURA)

In the Rhodanian zone the seasonal history is about the same as in the Armorican zone. There is probably a much smaller second generation here, however, as the first adults appear a month later, thus having a much shorter period in which to find suitable hosts. Both corn and *Artemisia* serve as host plants of *Pyrausta* in this zone.

## AQUITANIAN ZONE (SOUTHWESTERN FRANCE)

In the Aquitanian zone the seasonal history of the parasite is also similar to that in the Armorican zone. The only difference is that in some years there is a partial second generation of the host, and in that

case there will be two generations on *Pyrausta*. No investigations were made definitely to prove this conclusion, but as laying females are present all summer it seems quite probable. The adults emerge in the latter part of June or early part of July and lay their eggs either in the following month or in the succeeding May or June, at which time *Pyrausta* pupae are available. Corn is the chief food plant of *Pyrausta* in this zone.

#### MEDITERRANEAN (SOUTH) ZONE (HYÈRES)

In the Mediterranean zone there are regularly two full generations of the host and two of the parasite. The females from the previous year lay eggs in the first *Pyrausta* pupae that appear in the latter part of April and the first part of May. Adults of this generation appear a month later, and the eggs are laid in the first-generation *Pyrausta* pupae during the latter half of July. Adults from this brood appear early in August and hibernate until the following spring. As *Phaeogenes* females of the first generation are in condition to oviposit during June, there is a possibility of a second generation at this time either on late *Pyrausta* pupae or on some intermediate host. Adults from this generation would appear about three weeks later and the eggs laid in pupae of the second host generation present, during the latter half of July. Females emerging from these pupae could have a fourth brood during the latter part of August or first part of September, but it would have to be on an intermediate host as there are usually no *Pyrausta* pupae present at this time. Females of this possible fourth generation would then hibernate until the following spring before laying their eggs. Corn is the chief host plant of *Pyrausta* in this zone, but it is not extensively cultivated.

#### PADOVIAN (PIEDMONT) ZONE (TURIN)

In the Padovian (Piedmont) zone there are normally two generations of the host and two of the parasite. Overwintering females lay eggs the first part of June. The second generation begins late in July, and females from this generation lay eggs the following spring. There may be a partial third generation on another host late in August. Corn is the chief host plant of *Pyrausta* in this zone.

#### PADOVIAN (NORTH) ZONE (BERGAMO, PAVIA, MANTOVA)

The Padovian (north) is also a 2-generation zone for both host and parasite, although in some years there is a possibility of a partial third parasite generation on an intermediate host at the end of the summer. The adults lay their eggs in the latter part of May. The second generation begins in the middle of July, and the resulting adults oviposit the following spring. The most detailed studies of the seasonal history of *Phaeogenes* have been made in this zone, particularly around Bergamo, and all the data show that the parasite has only two generations on *Pyrausta*. The notes were all based on field observations. By comparing the knowledge of the time of first emergence, length of life, habits, etc., of *Phaeogenes* with the seasonal history of the host, it will be readily seen that there can occur a

partial third generation on the *Pyrausta* pupae present in the late summer. As field observations did not bear this out, it does not enter into the data used in Figure 10, which shows the seasonal history of *Pyrausta* and *Phaeogenes* as determined from field observations and laboratory rearings. Corn is the principal host of *Pyrausta* in this zone and is cultivated extensively. Of all the *Pyrausta*-infested regions of Europe this zone most closely approaches the climatic conditions of the corn-borer-infested districts in New England. It is characterized by rather long, cold winters

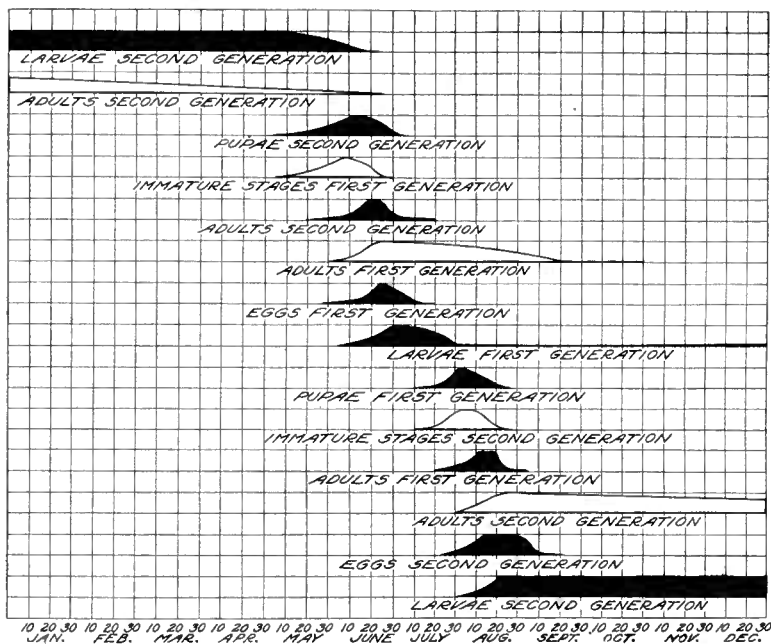


FIGURE 10.—Seasonal history of *Pyrausta nubilalis* and its parasite, *Phaeogenes nigridentis*, based on field observations and laboratory rearings. Black areas represent *P. nubilalis*, and the clear areas represent *P. nigridentis*.

with abundant snowfall, and short, hot summers with occasional heavy rainfall. All the important parasites of this zone have also been recovered from the New England area.

#### PADOVIAN (SOUTH) ZONE (PIACENZA, FERRARA, SERMIDE)

The Padovian (south) zone is similar to the Padovian (north) zone. Both *Pyrausta* and its parasite have two generations. Pupation of the host begins about two weeks earlier in the spring and summer than in the Padovian (north) zone, and the development of the parasite is synchronized with it. Both corn and hemp serve as host plants of *Pyrausta* in this zone, but the latter plant supports only the first generation of the borer, as it is cut before the second generation can attack it.

**VENETIAN (LOW) ZONE (PADUA)**

The data for the Venetian (low) zone are somewhat meager, but it is known that there are at least two generations. The climate and agriculture are practically identical with those of the Padovian (south) zone. The seasonal history is also the same as in the Padovian (south) zone. Corn is the chief host plant.

**VENETIAN (HIGH) ZONE (TREVISO)**

The data for the Venetian (high) zone are only sufficient to show that there are two generations of host and parasite. The seasonal history is identical with the Venetian (low) zone.

**PLAVISIAN ZONE (UDINE)**

The studies in the Plavisian zone have also been incomplete, but they are sufficient to put it in the 2-generation class for both host and parasite. There appears to be very little difference between this zone and the Venetian zone.

**HUNGARIAN ZONE**

In the Hungarian zone there is one generation of the host and probably two of the parasite. No studies have been made on the seasonal history of the *Phaeogenes* in this zone, but it is probably similar to that in the Armorican, Rhodanian, and Aquitanian zones. Corn is the chief host plant of *Pyrausta* and is extensively cultivated.

**HYPERPARASITES**

*Phaeogenes nigridentis* is practically free from attacks by other parasites. During the course of the work more than 65,000 *Pyrausta* pupae parasitized by *Phaeogenes* have been reared, and only one doubtful hyperparasite has been found. This is *Haltichella maculipennis* Destefani, and it was reared at the Arlington laboratory from *Pyrausta* pupae collected in Italy and supposedly parasitized by *Phaeogenes*.

Goidanich (13) recorded rearing a gregarious pteromalid species from *Pyrausta* pupae, but he could not confirm it as a parasite on *Phaeogenes*. It is probably not parasitic on *Phaeogenes*, however, as the writer has reared from healthy pupae a number of specimens of a gregarious pteromalid identified as *Dibrachys* sp. This species was later bred in the laboratory on unparasitized *Pyrausta* pupae.

**PHAEOGENES NIGRIDENS AS A CONTROLLING FACTOR OF PYRAUSTA NUBILALIS**

*Phaeogenes nigridentis* is widely distributed in Europe, but its degree of effectiveness on *Pyrausta nubilalis* appears relatively low in all the regions outside of northern Italy. In the Padovian (north) zone of this area, where the most consistent studies of this parasite have been made, the records show that from 1924 to 1927, inclusive, and

in 1930 *Phaeogenes nigridens* had annually the highest percentage of parasitism of all the *Pyrausta nubilalis* parasites. In 1928 the total parasitism by all species was about the same as its average for other years, but the parasitism by *Phaeogenes nigridens* fell much below its yearly average. It was even surpassed in this year by two other species, *Angitia (Inareolata) punctoria* Roman and *Microgaster tibialis* Nees. In 1929 the total parasitism dropped to almost half what it usually was, but only *A. punctoria* exceeded *P. nigridens* in parasitism.

In the other European zones the degree of parasitism remains more or less constant, although occasionally it goes to zero for some years, as has been the case in the Mediterranean (south) zone.

Table 5 shows the relative importance of *P. nigridens* in the various zones.

TABLE 5.—Average and maximum parasitism by *Phaeogenes nigridens* in Europe for the period of investigations

Zone	Average parasitism	Maximum parasitism <sup>1</sup>	Year in which maximum parasitism occurred	Host plant
	<i>Per cent</i>	<i>Per cent</i>		
Padovian (Piedmont) <sup>1</sup>	12.89	12.89	1930	Corn.
Padovian (north)	7.73	17.50	1927	Do.
Padovian (south)	6.23	7.34	1930	Hemp.
Plavisan	1.85	4.60	1928	Corn.
Armorican <sup>2</sup>	1.43	1.43	1929	Artemisia.
Padovian (south)	1.33	2.70	1925	Corn.
Venetian (high) <sup>2</sup>	1.20	1.20	1928	Do.
Aquitanian	.79	3.15	1930	Do.
Venetian (low)	.70	1.90	1928	Do.
Rhodanian	.35	.70	1925	Artemisia.
Mediterranean (coast)	.14	.84	1921	Corn.
Rhodanian	.12	.25	1925	Do.

<sup>1</sup> The maximum parasitism was always in the first generation.

<sup>2</sup> Only one year's observation available.

<sup>3</sup> Computed from additional data obtained since the publication of earlier records of Thompson and Parker (27).

Table 6 shows in detail, by year and generation, the percentage of parasitism of *Pyrausta* by *Phaeogenes nigridens* as observed in corn, Artemisia, and hemp in the various zones during the years in which it has been studied. It should be borne in mind that, although the figure for the average parasitism in the Padovian (Piedmont) zone for 1930 is slightly higher than that in the Padovian (north) zone for the same year, the figure was based on only 450 individuals as against 2,200 for the latter zone.

The highest percentage of parasitism of the first generation of *Pyrausta* is found in the earliest sown fields, which also have usually the heaviest corn-borer infestation. In determining this point, observations were made in three adjacent cornfields near Bergamo in the summer of 1930, after the *Pyrausta* pupation was practically complete. The results are summarized in Table 7. Observations made at Turin in the same summer gave similar results, and these are also given in Table 7. In this latter case, however, the dates of planting were not known, and the cornfields were several miles apart.

TABLE 6.—Percentage of parasitism of *Pyrausta nubilalis* by *Phaeogenes nigridens* in corn, *Artemisia*, and hemp in the various zones of Europe for 1921–1930<sup>1</sup>

Year	Gen-eration	Medi-terran-ean coast, corn	Aqui-tanian, corn	Rhodanian		Ar-mori-can, corn	Padovian				Venetian		Pia-vi-sian, corn
				Corn	Arte-misia		Pied-mont, corn	North, corn	South		High, corn	Low, corn	
									Corn	Hemp			
1921	1	<i>P. ct.</i> 0.84	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>	<i>P. ct.</i>
1922	1	.48											
1923	1	.09											
1924	1			0	0			6.70					
1925	1	.40	0.01	.25	.70			14.00	2.70				
1926	1	0	0					8.10					
	2	0											
	0												
1927	1	0	0					17.50					
1928	1	0				1.43							
	2	0						4.30			1.20	1.90	4.60
	0							1.25					
1929	1	0	3.15					2.49	1.29	5.13		.21	.33
	2	0						2.78					.68
	0												
1930	1	0					12.89	12.44	0	7.34		0	

<sup>1</sup> Spaces in which no figures are found indicate that no studies were made.TABLE 7.—Parasitism by *Phaeogenes nigridens* in early and late planted corn-fields near Bergamo and Turin, Italy, 1930

Locality	Field No.	Date planted	Date ex- amined	Degree of maturity of corn		Infesta- tion by <i>Pyrausta</i> <i>nubilalis</i> <sup>1</sup>	Hosts studied	Parasit- ism by <i>Phaeo- genes ni- gridens</i>
				Tassels	Silk			
Bergamo	1	Apr. 3	Aug. 1	Dry	Dry	Per cent 70	Number 842	Per cent 21.49
	2	Apr. 7	do	In flower	Not dry	53	266	8.27
	3	Apr. 9	Aug. 2	do	do	25	429	3.49
Turin	1	Unknown	Aug. 11	do	do	15	104	2.89
	2	do	do	Dry	Dry	44	60	16.66
	3	do	do	do	do	81	124	19.03
	4	do	do	do	do	62	162	12.96

<sup>1</sup> The number of plants examined in each instance was 200.

With the second generation of *Pyrausta*, where both *Pyrausta* and *Phaeogenes* occur, the highest percentage of parasitism is found among those cornstalks lying outside the barns.

## LIMITING FACTORS IN EFFECTIVENESS OF PHAEOGENES NIGRIDENS

An important limiting factor is probably the very low reproductive rate of *Phaeogenes nigridens* as compared with that of *Pyrausta nubilalis*. It was not possible to determine the potential number of eggs in the female ovaries, but the average number deposited in the laboratory was 6; the maximum number was 11. These figures are probably much lower than they would be in the field, but at the most it appears that a *Phaeogenes nigridens* female does not lay more than 50 eggs.

Experiments have shown conclusively that, when the eggs have become mature in the ovaries of the *Phaeogenes nigridens* female and

remain undeposited after a week or so, the eggs will die, disintegrate, and pass out through the oviduct. In the summer there is probably sufficient host material so that this destruction of the eggs takes place only occasionally. In the long hibernating period of the female from August until the following spring, however, the eggs continue to develop slowly, and before the spring oviposition period arrives many eggs will have matured and died, the number varying in direct ratio to the temperature.

The *Phaeogenes* female possesses a very short ovipositor, projecting only slightly beyond the tip of the abdomen, and therefore can attack only those individuals into whose tunnels she is able to penetrate. As the female requires from 11 days to 4 weeks to get into condition to oviposit, this further reduces her effectiveness. The long hibernation period of the females, with its consequent mortality, must also greatly lower the importance of this species as a controlling factor of *Pyrausta*.

Another limiting factor, operating particularly in northern Italy, is the practice of storing the cornstalks in a shed. All experiments have shown that *Pyrausta* pupae in stalks kept under these conditions are comparatively free from attack by *Phaeogenes*. The only breeding places that the parasite can find are infested stalks used around the buildings for protection against the cold, the few corn stacks that happen to be left outside, and the odd pieces of infested stalks lying around outside of barns and on the fields.

Hyperparasitism does not constitute a limiting factor, as there is only one record of such occurrence among the thousands of parasitized pupae reared, and that record is doubtful.

*Phaeogenes*, a parasite of the corn-borer pupa, is not subjected to competition, as are the parasites of the egg and larva. The other parasites attacking the pupal stage of *Pyrausta* have been reared only at rare intervals and in negligible numbers, and can not, therefore, be considered as serious factors in controlling *Pyrausta*. For the same reason they can not be considered as detrimental to *Phaeogenes*.

## COLLECTION AND SHIPMENT OF THE PARASITE

Although *P. nigridens* was found to occur near Hyères in 1922, no gross collecting operations were possible until it was discovered by H. L. Parker in large numbers near Bergamo, Italy, in the summer of 1924. In that year the first collection of larval parasites of the corn borer was begun in this district, and along with them were collected several thousand pupae which were brought back to the Hyères laboratory. From these pupae 1,683 adult parasites issued, and 1,601 were sent to the United States. Since then shipments have been made annually from this district, the average percentage of emergence after arrival in the United States being 38.5.

The first shipment was made with freshly emerged adults in small glass lantern globes. They were fed just previous to shipment, and no food was supplied en route. The globes were securely packed and carried to Cherbourg in refrigerator valises identical with those originated by the gipsy moth laboratory (4, p. 101). Arriving at the port, they were placed in the refrigerator room of the first passenger ship sailing to New York. From there they were re-



shipped to the Arlington laboratory, located just outside of Boston. The entire trip from Hyères to Arlington consumed from 9 to 10 days. Only a few of the adults died en route, and these were practically all males.

The following year collections of all parasites were made as in the previous year, but the parasitized pupae were separated from the unparasitized ones in the field laboratory at the base of operations. The entire procedure was as follows: The date on which to begin work was first established by making field collections in the latter part of July to determine when most of the other parasites of the corn borer had formed their cocoons and puparia. The time when host pupation had reached about 60 per cent was fixed as the correct date. On August 3 about 150 peasants were assembled, and to each was issued a small can, having a hole in the cover through which to drop the pupae, and a box for the other parasites. The workers scattered over the district and made collections in any field they chose. At the end of each day the pupae were brought in, counted, placed in shallow trays covered on the bottom with wire netting, and stored in a cool cellar. The next day women separated the parasitized pupae from the others and placed them in flat cardboard boxes 5.5 by 0.9 cm. The boxes were then packed in larger wooden ones and taken to Genoa in the refrigerator valises. At Genoa they were placed in the cheese or vegetable room of the first passenger boat sailing for New York or Boston. From the time of collection of the parasites till their arrival at Arlington, a period of 15 to 23 days, the temperature ranged from 4° to 10° C. (39.2° to 50° F.), most of the time being near the lower temperature.

The percentage of adult emergence<sup>11</sup> from the 1925 shipment was 44.7. In 1926, 1927, and 1928 the methods of collecting and shipping were the same as in 1925. The percentage of emergence at Arlington for these shipments was 36.6 in 1926, 37.2 in 1927, and 37.2 in 1928.

In 1929 several different methods of packing the parasitized pupae were tried, but the results did not warrant the use of any of them. The technic was in other respects the same as in the previous years. The emergence for this year was 37 per cent.

In 1930 the collection of the other parasites from the Bergamo district was discontinued and only *Phaenogenes nigridentis* collected. This permitted collections to be made under optimum conditions. Therefore it had become necessary to begin the work while many individuals of *Phaenogenes nigridentis* were in the larval stage. This resulted in high mortality when they were exposed to the cold temperature necessary for shipment. Many others also died because of drying out in the trays.

To fix the date on which to begin work under these changed conditions, several hundred pupae were collected during the last week of July and dissected to determine the stage in which most of the *Phaenogenes* were. When the majority were found to be in the late mature larval or young pupal stage, collecting on a large scale was begun. This date coincided approximately with a host pupation of 80 per cent and a moth emergence of 20 per cent. The entire work was confined to a relatively short period in order to keep as many of the parasites as possible from emerging before being placed in cold

<sup>11</sup> The notes on adult emergence were supplied by D. W. Jones, of the Arlington (Mass.) laboratory.

storage. Males preceded females in emergence by three or four days and continued to predominate until the end of a week, so collections could be made several days after the appearance of the first adult without undue loss. Collections for this year began on July 29 and ended August 6.

The methods of packing used in the summer of 1930 differed from any previously used in that they provided for the feeding of the parasites that emerged en route. This embodied the principle of the nondripping feeding tube as developed at the European branch of the gipsy moth laboratory (4, p. 93) in Budapest, Hungary. The wooden box used in other years was arranged inside so as to accommodate five flat wooden partitions, placed equidistant from each other, which could be moved in or out. Two feeding tubes were nailed to the inside of each box cover. The design of the flat cardboard boxes was changed somewhat in order to give the emerged parasites a more nearly ideal environment. A large square opening was cut in the cover of each box and a piece of mosquito netting glued across this opening on the inside. The holes in the netting were just large enough to allow the parasite to push itself through.

In preparing the boxes for shipment, the nicked-brass feeding tubes, containing a wick slightly longer than the tube, were filled with saturated sugar solution and tightly plugged with cotton. In the meantime the cardboard boxes were filled with the parasitized pupae and tied to each side of the partitions. The latter were then slid into place and the cover nailed down.

By this means not only are food and ample resting places supplied for any adult parasites which may emerge en route, but since there is always a certain small percentage of nonparasitized pupae in the boxes, the resulting moths are also prevented from filling the air with their fine scales.

The percentage of emergence en route for this shipment was 6.6 and the mortality 3.1. The percentage of emergence for the entire shipment was 38.4. The number of days from collection to arrival at Arlington was from 13 to 21. In every case the feeding tubes were still moist at the end of the trip.

A small shipment of parasitized pupae collected in hemp was also made from Scrinide, in the Padovian (south) zone, by H. L. Parker. This collection, however, was merely incidental to the main project, which was to collect and ship the chalcid *Eulophus viridulus* Thoms., an external parasite of *Pyrausta nubilalis* larvae.

After several seasons of experiments with different shipping methods, the writer concludes that the optimum conditions for the parasitized pupae are a temperature range of from 14° to 18° C. (57.2° to 64.4° F.) and a humidity of from 50 to 70 per cent, which allows the immature stages to develop slowly and at the same time prolongs the life of the adults. This procedure will be put into practice in making future shipments.<sup>12</sup>

<sup>12</sup>As it was impossible to obtain the optimum temperature of 14° to 18° C. (57.2° to 64.4° F.) on board any ship from Genoa, the collecting and shipping technic used in 1930 was changed in 1931 to allow the parasites to develop normally until they were placed (at sailing time) in the ship's refrigerator room at a temperature of from 4° to 10° C. (39.2° to 50° F.) To feed the greatly increased number of adults, two 150 c c bottles containing sugar solution were stoppered with large plugs of cotton and secured to a rack nailed to the inside of the usual shipping box. A total of 7,300 parasitized *P. nubilalis* pupae and 1,074 adults were shipped under these conditions. The percentage of emergence for this shipment at the Arlington (Mass.) laboratory was 62.5, an increase of 24 per cent over the average emergence of other years.

As the Bergamo district is an industrial center with correspondingly high wage scales, other areas have been scouted at various times to locate, if possible, additional sources having a lower cost per parasite for collection, but thus far none has been found. Practically the whole of northern Italy and the Aquitanian and Rhodanian zones in France have been surveyed and, although the parasite has been found occasionally in sufficient quantities, other factors have always entered which made the cost of collection higher than at Bergamo.

## SUMMARY

The ichneumonid *Phaeogenes nigridens* Wesm. is the most important parasite of the pupal stage of the European corn borer in Europe. It occurs in Sweden, Germany, Belgium, France, Italy, and Hungary.

The adult is distinguished from the other parasites of the corn borer by its robust appearance, its rusty red-brown abdomen with black terminal portion and, in the female, the white band around the middle of the antennae. The female reproductive organs have three polytrophic ovarioles in each ovary, a spermatheca, and two accessory glands. The egg is hyaline, oblong-ovate, slightly arched, and entirely smooth.

The larva has at least four distinct instars. There is a possibility of a fifth instar, but the evidence is insufficient. The primary larva is robust, segmented, and has a large, heavily sclerotized head with long, hooked mandibles. The cuticle of the body is covered with many definitely arranged setae and spines. There are no spiracles in this instar. The head of the secondary larva is much shorter, less sclerotized, and has a large ventral protuberance. There are nine pairs of functionless spiracles. The tertiary larva is distinguished from the previous stages by its larger mandibles and spiracles, the absence of the ventral protuberance on the head, and the disappearance of the integumentary spines. Each of the last three abdominal segments has a band of minute rugosities extending around the middle of the segment.

The mature larva is light pink or tan and has a prominent hump dorsally in the third thoracic and first abdominal segments. The ventral region of the head is unpigmented and only lightly sclerotized. There are numerous epidermal thickenings and structures of the head skeleton with a definite arrangement and function which may serve the purpose of future larval determinations. The first seven pairs of spiracles function during the entire instar, but the eighth and ninth pairs are not open until the larva is nearly mature. The muscles of the head are divided into five distinct groups and the integumentary ones of the trunk into eight. The latter are somewhat complicated.

Pupation takes place within the host pupa, the abdomen of which has been extended by the growing larva within. The latter character serves to identify the pupae.

The adults feed on honey, raisins, dry sugar, or weak sugar solution, and occasionally on the blood of the host. Mating is easily secured with young adults. Females kept at 25° C. (77° F.) require an oögenetic period of from one to two weeks.

The female oviposits only in the pupal stage of *Pyrausta* and shows a preference for the freshly formed pupae. Usually only one egg is deposited in a host. Both egg and larva float freely within the body of the host, entirely unaffected by the phagocytes of the latter. At first the larva feeds on the blood and fat of the host, later attacking the vital organs. The entire period from egg to adult at a temperature of 25° C. (77° F.) is about 15 days.

The adults are very long lived, some females having been kept alive at low temperature for about 10 months. Hibernation occurs in the adult stage.

The seasonal history of *Phaogenes nigridens* synchronizes closely with that of *Pyrausta* in all the European zones. It can survive with only one generation a year, as may be necessary in the 1-generation host zones, but as it is known to have at least one other host (one specimen having been reared from *Tortrix pronubana* Hbn.), it may have two or more generations in any of these zones, the additional ones being on the intermediate host. In the 1-generation areas the overwintering female lays its eggs in the *Pyrausta* pupae formed in the spring and emerges three or four weeks later, depending on the temperature. These females either hibernate or lay eggs in an intermediate host in the same summer. In the 2-generation host zones the hibernating females oviposit in the host pupae and the resulting females attack the summer pupae formed in July and August. The females of this brood then hibernate until the following spring. In these regions there is also a possibility of one or two extra generations on an intermediate host owing to the presence of laying females in the field at all times.

Of all the regions in Europe, the area in which the parasite is most effective is the Padovian (north) zone in northern Italy, where the climatic conditions approach most closely those of the corn-borer area of New England. In this zone *Phaogenes nigridens* had annually from 1924 to 1927, inclusive, and in 1930, the highest percentage of parasitism of any *Pyrausta* parasite. The maximum parasitism of the host that has thus far been recorded is 17.5 per cent. The parasite has been found in *Pyrausta* pupae in corn, *Artemisia*, and hemp.

Factors that may limit the effectiveness of this species are the small number of eggs produced by each female; the mortality of some ovarian eggs, especially among hibernating females; the rather long oögenetic period; and the generally unsuitable oviposition conditions in the spring.

Shipments of the parasite have been made annually since 1924. The first shipment was made in the adult stage and the others in the pupal stage inside the host pupa. All shipments were kept at from 4° to 10° C. (39.2° to 50° F.) during the period between their collection and their receipt at Arlington. The average percentage of emergence after arrival in the United States was 38.5.

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