EUPTEROMALUS NIDULANS, A PARASITE OF THE BROWN-TAIL AND SATIN MOTHS

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INTRODUCTION

_Eupteromalus nidulans_ (Thomson) (fig. 1) is a rather small external parasite belonging to the chalcidoid family Pteromalidae. It was introduced into Massachusetts from Europe in 1905 by the Bureau of Entomology to aid in the control of the brown-tail moth (_Nygmia phaeorrhoea_ Don.). Since it has been reared both as a primary and as a secondary parasite, the following study was undertaken to provide the basis for an understanding of its greater importance as one or the other. Although general observations upon it have been made by several workers at the gipsy-moth laboratory, no detailed study of its life history has been previously attempted. For the information presented under the head of Importation and Colonization the writer has freely used notes made during a series of years by laboratory workers.

SYNONYMY

In literature the specific name _nidulans_ has been quite generally attributed to Foerster, but the first published description seems to...
be that of Thomson (7, p. 155) in 1878, who lists the species as "P. nidulans (Foerster)." As a result of a misidentification in the Jardin des Plantes in Paris (2, p. 19), Howard and Fiske (1) in 1911 referred to the species as *Pteromalus egregius* Först., and this name has been used by several workers subsequently. In 1913 Kurdjumov (2) erected the genus Eupteromalus, designating *Pteromalus nidulans* (Förster) Thomson as genotype. Neither he nor Thomson gives any reference to a description of the species by Foerster. Kurdjumov (2, p. 13) says, however: "This species [P. nidulans Förster] was simply named by Förster, but described by C. G. Thomson." In 1927 Muesebeck and Dohanian (4) discuss the species briefly under the name of *Eupteromalus nidulans* (Foerst.)

The synonymy is as follows:

**Eupteromalus nidulans** (Thomson) Kurdjumov,

- *Pteromalus nidulans* Thomson (7, p. 155).
- *Pteromalus egregius* Howard and Fiske (1, p. 268). (Not egregius Förster.)
- *Pteromalus (Eupteromalus) nidulans* Viereck (8, p. 773).

**IMPORTATION AND COLONIZATION**

As a result of a visit of L. O. Howard to Europe in 1905, the first importation of *Eupteromalus nidulans* was effected through the shipment of hibernation webs of its host, the brown-tail moth. Only a few individuals were received and none colonized. During succeeding years Eupteromalus was reared from the hibernation webs of the brown-tail moth imported from Austria, Czechoslovakia, France, Germany, Holland, Italy, Russia, and Switzerland. During the winter of 1905–6 Eupteromalus was imported in large numbers, and a total of 50,000 individuals was distributed at nine points in the vicinity of Boston, Mass. These specimens were colonized as adults early in the spring of 1906, but collections made in the following fall yielded no recoveries. Again, in the winter of 1906–7 large numbers of webs were sent to this country and from these Eupteromalus was colonized in eight additional towns, somewhat more widely separated but well within the area infested with the brown-tail moth. In the fall and early winter of 1907–8 several thousand webs of the brown-tail moth were collected from the colonization points. No specimens of Eupteromalus were reared.

In checking up the possible causes for the nonestablishment of the species, it was thought that the numbers liberated might have been insufficient and that the time of colonization might have been too early. Accordingly, in the spring of 1908 only a part of the 116,000 adults available were liberated, in six towns. On September 5 the remaining material, which had been held during the summer at a temperature of about 0°C, was colonized. Fall collections of webs from colonization points were found to contain a few specimens of Eupteromalus, but the numbers were not promising.

At this juncture it was observed early in 1909 that Eupteromalus was capable of acting as a secondary parasite, attacking the braconid *Apanteles lacteicolor* Vier., a larval parasite of the brown-tail moth. In view of the fact that this Apanteles appeared to be by far the more valuable of the two, it was decided to abandon further importations of Eupteromalus. However, 57,600 were colonized in one huge colony in the fall of 1909.
Large collections of hibernation webs of the brown-tail moth were made during the winter of 1909–10, but only a few specimens of Eupteromalus were secured from webs taken in the vicinity of the colonization points, and none at all from the points colonized in 1908. It was therefore with more or less surprise that in the following year Eupteromalus was recovered from many widely separated points. Apparently it soon spread until it became distributed over most of the area infested by the brown-tail moth. But extensive collections have indicated that until recently an average of less than 1 per cent of the larvae of the brown-tail moth have in any one year been killed in their hibernation webs by Eupteromalus.

In 1920 the satin moth (Stilpnotia salicis L.) was discovered near Boston, Mass., and in a comparatively short time had spread over a considerable area. In the course of a study of the control of this insect by parasites Eupteromalus was discovered in 1926 to be actively attacking it in its hibernation webs. In succeeding years the percentage of this parasitism has been increasing.

**BIOLOGY AND HABITS**

**SEASONAL HISTORY**

The following description of the seasonal activities of *Eupteromalus nidulans* is based largely upon studies of its parasitism of the satin moth. This parasite spends the winter as a full-fed larva within the hibernation web of its host. Rather early in the spring the parasite larva moves somewhat away from its host, although still remaining within the web. Here the meconium is cast and the larva pupates. In the season of 1929 pupation was first observed on April 9. By the middle of April the finding of pupae under field conditions had become general, although larvae could still be found for some time thereafter. Emergence of unparasitized larvae of *Stilpnotia salicis* from their hibernation quarters began on April 27 and continued for some two or three weeks. Adults of Eupteromalus were first observed on May 8, but were not generally abundant until the middle of May. Thus it would seem that the pupal period extended over nearly a month at this season of the year. As may be seen from the above dates, some larvae of the satin moth were still to be found in their hibernation webs for some time after adults of Eupteromalus were first found in the field. Yet general observations indicate that they are not attacked by Eupteromalus at this time.

These adults of the hibernating generation, issuing during a period of perhaps two or three weeks at about the middle of May, soon find available the cocoons of certain ichneumonid parasites which the females of Eupteromalus may attack. Collections of the cocoons of two larval parasites of the brown-tail moth were made in order to determine whether or not they might serve as hosts for a spring generation. Cocoons of *Apanteles lacteicolor* were obtained between May 23 and May 30, and those of the first generation of *Meteorus versicolor* Wesm. were secured during the early part of June. The adult Eupteromalus reared from these collections issued between June 1 and June 15. By the beginning of July the second-generation cocoons of Meteorus were found generally present, giving these first-generation adults a fresh source of host material to attack. The

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1 Reference is made by number (italic) to Literature Cited, p. 56.
adults of Eupteromalus obtained from collections of this material issued near the end of July. Comparatively few individuals of Eupteromalus were reared from these primary parasites, however, and none were reared from later collections of any known hosts until August.

A study of the longevity of Eupteromalus indicates that 9 of the 20 females with which the experiment was begun were still alive and capable of laying eggs after four months had elapsed. Although the experiment was conducted under laboratory conditions, it seems possible that this might also occur in the field. Accordingly, adults of the hibernating generation might well be alive and able to oviposit until the early part of September. Hibernation webs of the satin moth were formed in the laboratory as early as July 24, 1929, by larvae hatching from the first egg masses collected in the field. While this is perhaps a little earlier than first web formation under natural conditions, observations showed webs to have been formed in the field in two localities in the first two weeks of August. These early webs would give any females of the hibernating generation remaining alive at this time an opportunity for oviposition before death. Adults of any generation reproducing on ichneumonoid parasites would have a longer period in which to attack the satin moth.

Eupteromalus eggs laid in these early formed webs of the satin moth produced adults in the third week of August. These adults in turn began ovipositing within a week, and the ensuing generation issued in the last week of September. Adults given access to webs in outdoor cages from September 18 to late in the fall continued to oviposit until November 15. No larvae hatching from these eggs, however, developed beyond the fifth larval instar, which is the hibernating stage. Thus it may be seen that there is a possibility of two generations of Eupteromalus upon primary parasites in the spring, and of three generations upon the satin moth in the fall, the third generation hibernating and becoming adult the following spring. There is also a possibility that there may be no reproduction upon the primary parasites, and that there may be but one or, at most, two generations upon the satin moth. In the field, however, all the generations overlap so completely that all stages of Eupteromalus may frequently be observed at one infestation at the same time. It seems probable that under field conditions Eupteromalus may more often have two rather than one or three generations in the fall upon the satin moth. It also seems possible that adults of three generations might well be ovipositing at the same time.

Eggs laid in webs held in an outdoor cage were isolated every second day and records were kept of the last date of hatching, as well as of the last date of deposition of an egg from which the larva developed to maturity. An egg laid between November 2 and November 4 was the last egg deposited to hatch, while no larvae hatching from those laid after November 1, and only a few from eggs deposited after October 25, developed to maturity.

**MATING**

Eupteromalus mates readily in confinement, apparently requiring no special set of conditions for the process. A newly issued male of Eupteromalus does not immediately become interested when confined with a female, but more readily seeks to mate when 24 or more
hours old. A female, on the other hand, will mate as soon as she has freed herself of the pupal skin. Since the developmental period of the male averages a day or two less than that of the female, males are usually present and active by the time the first female is ready to issue. When a male finds a female he sometimes first evinces interest by taking up a position near her and swaying his body from side to side for perhaps 5 to 10 seconds. At other times this preliminary is not engaged in, but, whether it is or not, the male approaches the female and quickly takes up a position upon her dorsum. Here he moves well forward, so that his head is directly above or a little in front of that of the female. Now the male alternately beats his wings and brings them to rest, and at the same time attempts to fold the female's antennae close to her face by tapping them with his own. When the female is ready to mate she raises her abdomen slightly and distends the ventral portion so that certain sclerites which normally are partially concealed become exposed. This movement approximately doubles the dorso-ventral diameter of the abdomen at the fourth tergite. The male now moves backward, and by grasping the female with his front legs near the posterior end of her body, he slides his abdomen, venter upward, beneath that of the female. In this position, with the head and thorax of the male at right angles to the abdomen of the female, coition takes place. This is completed in about 15 seconds, whereupon the male often returns to his original position upon the dorsum of the female. The female usually remains quiescent for a period of 20 to 25 seconds, then occupies herself for an equal length of time in cleaning her antennae and legs, and in brushing her wings. The male leaves the female as she resumes activity. When the sexes are confined together males are frequently observed to climb upon mated females and to beat their wings as if seeking to mate. However, a female has never been observed to mate a second time.

OVIPOSITION

About three days after mating the females are ready to oviposit. Occasionally the female may attempt to oviposit earlier, but no eggs are known to have been laid in such cases. Unmated females produce only males.

Oviposition has been most closely studied when the satin moth was the host, but observations have shown that the habits of the female are essentially the same when other hosts are attacked. When acting as a secondary parasite it is possible that the female does not puncture the host, since the latter is usually rather inactive. But in parasitizing the satin moth this puncturing of the host has always preceded oviposition. In an experiment in which eggs of Eupteromalus were placed upon larvae of the satin moth which had not been paralyzed by the female, the Eupteromalus larvae were unable to develop.

The satin moth spends the winter as a third-instar larva within a hibernaculum made up partly of silk and partly of the substance on which the hibernaculum is formed. The majority of these hibernacula are found on the bark of willows and poplars. Here the full-fed, second-instar larvae either cut out a hollow cell or find a crevice already present which they may or may not enlarge. This is lined with silk and a silken cover is spun for the top, into which bits of bark are often incorporated. In this hibernaculum or web the larva molts in the early fall and here it is attacked by Eupteromalus.
When the Eupteromalus female is seeking to oviposit she moves rather slowly over the surface of the bark, tapping continually with the ends of her antennae. As soon as a web is encountered she feels about on the surface with her antennae, perhaps to ascertain the position of the larva within. Then, bending her abdomen downward till the tip touches the web, she inserts her ovipositor and brings her abdomen back to a horizontal position. The ovipositor is then forced into the web by a squatting action of the female. Now she turns the ovipositor this way and that, by moving her body from side to side, the web acting as a fulcrum. If nothing is encountered, she withdraws the ovipositor and tries again in a new position. Apparently the female uses the tip of the ovipositor to learn the condition of the host within the web. If the host is dead or dried, she discovers it very soon and moves away to another web. If the host is alive, and the ovipositor touches it, the female is equally quick to perceive this. She moves the tip of the ovipositor over the surface of the larva very lightly, tapping here and there, as if to find a suitable place at which to force in the ovipositor. If she is not careful, the larva is stimulated by the prodding and moves quickly to another position in the web. When the female is satisfied as to the condition and position of the host, she suddenly thrusts the ovipositor into the larva. This produces a violent reaction, so that, in the laboratory, when the web is open in any way the larva often leaves it. Usually the female partially withdraws the ovipositor from the web, and waits about three minutes before attempting to puncture the larva again. Sometimes the egg is laid immediately after this first puncturing of the host, and one or two cases have been observed when an egg was found on a larva which was still able to react to the stimulation of the touch of a dissecting needle. But more often the female punctures the larva two or three times before an egg is laid, the host larva reacting less and less to each succeeding thrust.

This puncturing of the host by the female, preliminary to oviposition, always seems to produce a state of permanent paralysis. In the cases where an egg was found immediately after its deposition upon a larva which was still capable of movement, it has followed that the larva developed paralysis in a short time. It has been observed that hibernating larvae of the satin moth when pricked once with a micro pin show no such state of paralysis. Instead, they quickly die and become dry and much shortened. Larvae punctured by the female Eupteromalus and kept under the same conditions became dry and hard only after a considerable time had elapsed; of 48 larvae so treated that were held more than two months at room temperature, at least one was as soft as a larva newly punctured. Furthermore, these larvae punctured by the female did not shorten up as did those punctured with a micro pin. It would therefore seem that the state of paralysis produced in the larva by the female parasite is not the result of a mechanical puncture alone. No data were obtained on the cause of the paralysis, but it is suggested that possibly a substance is injected by the female. It has also been suggested that this paralysis of the host might be the result of the puncturing by the female of certain areas, such as those containing ganglia, for example. General observations indicate that the host may be punctured in nearly any part of the body, with the exception of the head, and from nearly any angle.
When the female parasite finds that the host larva will no longer react to prodding with the ovipositor, she proceeds to deposit an egg. First, she feels about over the surface of the larva with the end of her ovipositor; and then, with the ovipositor directed at the spot where the egg is to be laid, she quivers slightly. If the observer watches closely, the egg is seen to be exserted from the ovipositor at a point distant from the tip by about the length of an egg. As the egg appears, the small end issues first. Then, as more of it is exserted, it curves toward the base of the ovipositor until the entire egg lies on the outside of the ovipositor and parallel with it, the large end of the egg being toward the apex of the ovipositor. Then it is slid along the ovipositor and is usually attached to the host by the large end, which contains the cephalic end of the embryo. Under ordinary conditions all this procedure requires only about three seconds. The ovipositor does not visibly become enlarged during the passage of the egg from the body to its lower part. General observations indicate that no particular part of the host is preferred for the location of the egg.

Under laboratory conditions the female does not always oviposit upon the larva which she has punctured. Very often she leaves the web when she has succeeded in puncturing the larva, and walks about more or less. Many times she encounters another web and repeats the process of puncturing the larva, so that under laboratory conditions more paralyzed larvae without eggs are found than paralyzed larvae with eggs. Of 72 larvae which females were observed to have paralyzed, 24 were subsequently found to bear one or more eggs, and 48 had no eggs. If the female revisits a web in which the larva has become paralyzed, an egg is usually deposited without the preliminary puncturing of the host. This is believed to hold true even when another female is responsible for the paralyzing of the host larva. Because of this habit many eggs are wasted as a result of superparasitism. In the laboratory as many as 12 eggs have been deposited upon one host, while at the same time larvae in many adjacent webs were not attacked. However, the following experiment would indicate that the females prefer to oviposit upon a host which they themselves have just paralyzed. Three females were given access during a period of several days to a total of 144 webs, of which 62 contained active larvae and 82 contained previously paralyzed larvae. When the webs were examined, 56 eggs were found to have been laid in those which had contained living larvae, and 22 eggs were laid upon the paralyzed larvae.

An experiment was carried on to determine whether or not Eupteromalus would attack webs of the satin moth which contained material unsuitable for the development of the Eupteromalus larva. A total of 318 webs in each of which the host larva was dead and dried were kept with six females for a month. The webs were examined every second day, but no eggs were observed to have been laid in any web containing material of this nature. Each female regularly oviposited in adjacent webs containing live host larvae.

It has been observed that when a female is engaged in the process of oviposition she will not permit, at times at least, any interference from males or other females. If one approaches she quickly sheaths the ovipositor and darts at the intruder. Males seeking to court the female seem to be regarded with particular aversion.
FECUNDITY

To find the reproductive capacity of the female Eupteromalus, a series of experiments was carried on with 16 females. Each female was given access both to cocoons of Apanteles melanoscelus (Ratz.) and to webs of Stilpnotia salicis. Every second day these webs and cocoons were examined and the number of eggs recorded. One female laid no eggs. The largest number laid by any one individual was 583 and the average for the 16 females was 251. In general, the smallest individuals laid the fewest eggs, and the largest laid the most.

FEEDING HABITS OF THE FEMALE

Close observation of the female, while she had access to webs of the satin moth for oviposition, has shown that she feeds upon the body fluids of the host. Feeding by the female has been observed when other hosts were concerned, but no observations have been made as to how this was effected.

When the female wishes to feed she first forces the ovipositor well into the host. When the cavity is deep and the host is not near the surface of the web, she moves the host nearer by inclining the ovipositor and using it as a lever. Then the ovipositor is very slowly withdrawn from the host. As the tip of the ovipositor leaves the host, what seems to be a silvery sheen appears upon perhaps the distal third of the ovipositor itself. This sheen seems to appear a half dozen times, rhythmically. Meanwhile, the ovipositor is being gradually withdrawn from the web, and as it is lifted above the host a small white translucent tube is seen to connect it with the body of the host. When the ovipositor has been completely withdrawn from the web this feeding tube is seen to extend from the surface covering of the web to the point where the ovipositor punctured the host. This is the usual position of the feeding tube, but it was observed on one occasion that when the host was resting against the web covering, the feeding tube extended above the surface of the web. Again, when the web surface upon which the female stood while forming the tube was lifted, the tube was seen to be connected to the web at one end but failed to reach to the larva at the other. This observation would indicate that the tube originates from the parasite rather than from the host. The feeding tube is somewhat variable in length, but the tubes observed were between 0.3 and 0.5 millimeter long. Attempts at mounting these feeding tubes upon slides were unsuccessful, partly because the material of which the tube is composed seemed to become very brittle as soon as the feeding process ceased.

As soon as she completes the formation of the tube, the female turns about and applies her mouth parts to the free end of it. The tube is then seen to fill with liquid. The female feeds thus for from five to seven minutes, moving her mouth parts as she does so. On a few occasions the female has been observed to cut an opening in the web covering and to enter the web. Here she punctured the host and, waiting till it would no longer react to prodding, turned and fed at the point of insertion of the ovipositor without forming a visible feeding tube.

LONGEVITY

Studies made with a small number of females indicate that those which were fed a mixture of honey and water in the proportion of
about 1 to 5 lived longer and laid more eggs than those which had access to host material only. Females held in confinement and fed this mixture of honey and water, but allowed to oviposit only infrequently, lived longer than those kept under the same conditions but allowed to lay as many eggs as they were able. Females of the former group are known to have lived for 4 months or more, one female living for 150 days. This female laid fertile eggs at intervals until the one hundred and thirty-seventh day. Of the latter group, free to oviposit, one female lived for about 60 days, although ovipositing continually till the day of death.

Without food of any kind, the adult Eupteromalus does not live nearly so long. An experiment involving 32 adults of both sexes was conducted under laboratory conditions and at room temperature. The length of life of these individuals ranged from 5 to 19 days, both limits being represented by males. The average for the 32 individuals was about 12 days.

COMPETITION

Little is known of the results of competition between Eupteromalus nidulans and other secondary parasites when various primary parasites are hosts. A few preliminary observations indicate that when eggs of Eupteromalus and of Dibrachys boucheanus (Ratz.) of approximately the same age are placed upon the mature larva of Apanteles melanoscelus, Eupteromalus is the more likely to attain maturity. In the same way, competition with an undetermined species of Dibrachys for this host has in most instances resulted in the development of Eupteromalus.

When acting as a primary parasite, Eupteromalus, so far as is known, has no insect competitors. Recent observations of field conditions in a woodland infestation of the satin moth have shown that Eupteromalus may be attacked and killed by certain fungi which are attacking the hibernating larvae of the satin moth. Eupteromalus is usually killed in the larval stage.

By far the keenest competition with which Eupteromalus has to contend when acting either as a primary or as a secondary parasite is experienced with other individuals of its own kind. As has been mentioned under the discussion of the oviposition habits of the female, so many eggs are often deposited upon a single host that all the larvae issuing from them can not possibly develop to maturity. In most cases the actual cause of death of the nonmaturing individuals is probably starvation, the oldest and most rapidly developing members succeeding in obtaining most of the food material and thereby being able to complete development before the food supply is exhausted. In one or two instances a larva of Eupteromalus has been seen apparently feeding upon another larva of its own species. But the fact that two individuals may often be reared from one larva of the satin moth, even when there is not food enough for both to attain any considerable size, would suggest that cannibalism is not a general characteristic of Eupteromalus larvae.

As many as three adults of Eupteromalus have been reared from one larva of Stilpnotia salicis, but this condition is rare, two being the greatest number usually completing development upon one host. Seven individuals, six females and one male, constituted the largest number of adults reared from one cocoon of Apanteles melanoscelus.
Silvestri (6) noted that 29 puparia of Voria ruralis Fall. gave 383 individuals of "Pteromalus nidulans Thoms.", and that 43 cocoons of Plusia gamma containing larvae parasitized by Voria showed 11 to contain a female of the same hyperparasite. It seems possible, however, that this P. nidulans Thoms. of Silvestri may be the P. nidulans of Masi (3) which Kurdjumov (2, p. 13) says "does not agree well with nidulans Förster" (=P. nidulans Thomson, 7, p. 155).

Attempts to induce the larva of Eupteromalus to migrate to hosts in other webs when competition reduced the food supply were unsuccessful. Experiments were carried on in which a paralyzed larva of the satin moth with from one to six eggs upon it was placed in a web closely surrounded by from 5 to 12 webs containing live larvae of the satin moth. Only one Eupteromalus developed in any case, and this was always on the paralyzed larva. The surrounding larvae were unaffected by any activities of the Eupteromalus larvae, so far as could be determined.

SEX RATIO

Three trees of Populus grandidentata Mich. were selected as samples from a fairly heavy woodland infestation of the satin moth in Kingston, N. H. These trees were cut down, divided into sections, and carefully examined in the laboratory. All the Eupteromalus larvae found hibernating in the webs of the satin moth upon these three trees were removed and held for future development. Of the number reaching maturity, 104 were males and 72 were females. A few individuals dried up when confined under laboratory conditions.

HYPERPARASITISM

Howard and Fiske (1, p. 263, 269) record (Entedon) Pleurotropis albitarsis (Ashm.), reared from European material, as an internal parasite of Eupteromalus. From collections made in this country Pleurotropis nawaiii (Ashm.) has been reared in small numbers. On one occasion another member of this genus, P. tarsalis (Ashm.), was reared from Eupteromalus.

DESCRIPTION OF STAGES

EGG

The egg of Eupteromalus is pearly white, slightly curved, and considerably larger at one end than at the other. It bears on most of its surface many small blunt tubercles which are rather irregularly spaced. The concave surface and the ends of the egg are without tubercles. A single egg is just visible to the naked eye when upon a dark surface. Its greatest length may range from 0.33 to 0.41 millimeter, the average for 25 eggs being about 0.38 millimeter. At its greatest width it may be from 0.12 to 0.16 millimeter wide, with 0.14 millimeter as the average. The longest egg measured was the narrowest, though the shortest was not the widest. In general the larger eggs are both longer and wider than the averages. There is considerable variation in the size and shape of the eggs laid by a single female. Because of the sticky nature of the eggshell, the eggs of this species are rather easily transferred from one host to another. Considerable handling does not seem to prevent the hatching of the eggs.
In outdoor cages the egg stage may range in duration from between 1 and 2 days to as many as 14, the average length in July being about 4 days. As the egg nears the time of hatching the embryo may be seen inside. Owing to the activities of the contained larva, the eggshell is ruptured at the larger end, and the larva squirms out. Frequently the eggshell remains attached to the larva for a short time after feeding has begun.

FIRST INSTAR

The first-instar larva (fig. 2) consists of a head and 13 body segments. The head of the newly hatched larva is wider than the body, but as growth continues and the larva becomes ready to molt the body tapers toward both ends. In color the entire larva is white and opaque, although the contents of the alimentary tract are dark, and show through the body wall.

The head bears four pairs of stout, somewhat curved spines, one pair just dorsad of the labrum, one pair between and somewhat below the antennae, and the other two pairs placed ventrally and to the sides of the mouth opening. The antennae are short and rather conical, apparently consisting of one segment, and are placed well up on the head. The bases of the antennae are elevated above the surface of the head itself, giving to the larva something of a horned aspect. Upon the labrum are about five pairs of very minute structures which Parker (5, p. 317-318) has called “sensorial organs.” These structures appear under high magnification (530 diameters) as more or less circular divisions of the integument, somewhat comparable to the circular base of a spine as ordinarily observed. These organs upon the labrum have not been observed to bear spines, nor has any specific function been assigned to them. Posterior to the mouth opening and upon the ventral side of the head are about seven additional pairs of organs similar to those upon the labrum. At least two pairs have been noted as bearing each a short, slightly curved spine. Upon various other areas of the head there seem to be groups of small structures of circular outline, but these have not been given close study. The mandibles of the first instar (fig. 3, A) are long, narrow, and sharply pointed. They are rather uniformly testaceous and are strongly curved. Of 27 mandibles mounted in a similar position the minimum length was found to be about 0.016 millimeter, the maximum nearly 0.21 millimeter, and the average 0.019 millimeter. The length of a mandible in this stage was considered to be the distance from the tip to the most distant point of the base. However, the mandibles articulate with the chitinous parts of the head in such a way as to render difficult the determination of the basal limits of the mandible proper.

Each segment of the body except the last bears two pairs of small, slightly raised tubercles, from each of which arises a spine, one pair upon the dorsolateral surface and one pair upon the latero-ventral. In addition to these, each thoracic segment bears on its ventral surface a pair of spines. The thirteenth, or last, body segment appears to possess only a pair of knoblike structures laterally, which in this stage
have not been observed to have spines. The spiracles open upon the mesothoracic and first three abdominal segments, and are connected by short branches with the paired longitudinal tracheae. At the anterior margin of each of the 13 body segments are one or more rows of very small spines. These rows encircle the body, but are more or less irregular, so the number of rows is indefinite. There seems to be but one row on the anterior and posterior body segments of the larva, but perhaps three such rows on the second and third abdominal segments.

The first-instar larva, like the succeeding instars, is capable of considerable movement, which it effects by retraction and extension of the body segments. However, observations indicate that most larvae seldom leave the point of attachment to the host except during ecdysis. Even then the larva apparently resumes feeding at approximately the same spot, for the first four molt skins have frequently been removed from the area occupied by a fifth-instar larva. Frequently throughout larval life there may be observed rather rhythmic contractions of the alimentary tract. These contractions begin in the region of the junction of the mid-gut and hind-gut, and slowly move forward to the head. After a slight pause this action is repeated.

It has been observed that the first stadium may range in length from 24 to 48 hours.

SECOND INSTAR

The second-instar larva does not greatly differ from the first in color, habits, or general appearance. In proportion to the body the head is somewhat smaller than in the first instar. The mandibles, however, have become larger and less sharply pointed, and have a much broader base, so their outline is quite different from that of the previous instar. They are now more or less triangular in shape. (Fig. 3, B.) Measurements of nine mandibles indicate that the minimum length of a mandible in this instar is about 0.002 millimeter, the maximum about 0.024 millimeter, and the average 0.022 millimeter. In this description the length of a mandible is considered to be the distance from the tip to the middle of the base, not including the basal tubercle, the basal limits being more plainly indicated in this and the following instars. The sensorial organs of the head have not been observed to differ in either number or position from those of the first instar. The antennae and spines, likewise, appear to be much the same.

On the body the rows of tubercles and spines are very similar, but the spiracles have increased in diameter and in number. The four

Figure 3.—Mandibles of *Eupteromalus nidulans*: A, First instar; B, second instar; C, third instar; D, fourth instar; E, fifth instar. All magnified 338 diameters
pairs of spiracles of the first instar have now been replaced by nine pairs, there being one pair each upon the mesothoracic, metathoracic, and first seven abdominal segments. This number and arrangement of the spiracles are constant for this and the following instars. The very fine spines bordering the anterior margin of the body segments have not been observed in this or in the succeeding instars.

This stadium is shorter in duration than the first, probably occupying less than 24 hours on an average.

THIRD INSTAR

The third-instar larva differs little from that of the second instar except in size. The bases of the mandibles (fig. 3, C) have become broader, and the tips more pigmented. Of 10 mandibles of this stage the minimum length was found to be 0.026 millimeter, the maximum 0.036 millimeter, and the average 0.032 millimeter. The sensorial organs and the spines of the head appear about the same in number and in position as in the previous instars, except for an additional pair of sensorial organs upon the labrum.

The duration of the third stadium is much the same as that of the second, occupying from perhaps 12 to 24 hours.

FOURTH INSTAR

The larva of this instar is very hard to distinguish from that of the third. So far as has been observed, the only appreciable difference, aside from the general increase in size, is in the greater length of the mandibles. (Fig. 3, D.) Of 14 mandibles the minimum length was about 0.035 millimeter, the maximum 0.046 millimeter, and the average 0.040 millimeter.

The duration of the fourth stadium has been observed to be about the same as that of the third, i.e., from about 12 to 24 hours.

FIFTH INSTAR

In the fifth instar the larva increases much in size, but resembles the fourth instar in many respects. The head, however, is smaller in proportion to the rest of the body, so the full-fed larva (fig. 4) tapers almost equally toward either end, the fore part being a bit more blunt than the hind part. The larva may vary considerably in size, depending upon conditions obtaining during its development, one of the most important of which is the character and the quantity of food material available. Measurements of 102 larvae placed the limits of variation in the length of the body at 0.96 millimeter as a minimum and 2.6 millimeters as a maximum, the average length being 1.5 millimeters. The antennae (fig. 5) still appear to be 1-segmented,
although they are somewhat longer in proportion to their width than in the earlier instars. They are light yellowish to light brown in color. The spines of the head seem to coincide in number and in position with those of the previous instars. The labrum in the mature larva appears to have six pairs of sensorial organs, as in the preceding two instars. But the number of pairs of these organs upon the ventral side of the head seems now to be eight, of which at least four pairs bear spines. The mandibles (fig. 3, E) are considerably larger than in the fourth instar, measurements of 24 indicating that the minimum length is about 0.045 millimeter, the maximum length 0.057 millimeter, and the average 0.050 millimeter.

The rows of tubercles upon the body segments are much as described for the first-instar larva, except that now they are smaller in proportion to the size of the larva.

When the larva is full-fed it moves away from the host somewhat, within the confines of the web or cocoon, and remains inactive. It is at this time that the mid-gut opens posteriorly, so that the waste material which has accumulated during larval life may be voided. This material, the so-called meconium, is black and rather characteristically molded so that it resembles a string of closely strung beads. Soon after the meconium is voided the larva takes on pupal characters and the larval skin is cast off.

Except in the case of the hibernating generation, the fifth stadium, including the period of rest sometimes called the prepupal period, may be as short as 7 days and often as long as 8 to 10 days. The period of growth of this stadium is about two days, or similar to that of the first stadium. In the hibernating generation the time spent in the fifth stadium may be as much as seven or eight months.

**PUPA**

When first formed the pupa is almost white, later darkening through yellow and brown to black. Being somewhat sticky, it adheres to the host or to the walls surrounding it. It is naked and incapable of movement. To the posterior end of the body there is usually attached the exuvium of the fifth-instar larva.

The pupa seems to be rather tolerant of the winter temperatures at Melrose Highlands, Mass., for of 20 pupae removed from the laboratory at room temperature to an outdoor cage on December 27, 1928, eight completed their development the following spring. The pupal period normally ranges in length from 9 to 12 days under favorable conditions, but in the case just mentioned the adults issued after four months in the pupal stage. In the field, however, hibernation in the pupal stage has never been observed.

**HOST RELATIONS**

**EXPERIMENTAL EVIDENCE AS TO SELECTION OF HOST**

Since Eupteromalus is known to be both a primary parasite upon *Stilpnotia salicis* and a secondary parasite upon *Apanteles melanoscelus*, an experiment was undertaken to determine in which rôle it played the more important part. The number of eggs deposited upon one or the other host when both were equally available was taken to be a fair criterion of the parasite's response. Since an equal number
of cocoons and webs were not available, a known number of hibernation webs of *S. salicis* and of second-generation cocoons of *A. melanoscelus* were submitted together to each of 15 female Eupteromalus. The results are shown in Table 1.

### Table 1.—Comparison of oviposition by *Eupteromalus nidulans* upon *Stilpnotia salicis* and *Apanteles melanoscelus*

<table>
<thead>
<tr>
<th>Female No.</th>
<th>Period of oviposition</th>
<th>Webs of <em>S. salicis</em> exposed</th>
<th>Eggs laid in webs</th>
<th>Cocoons of <em>A. melanoscelus</em> exposed</th>
<th>Eggs laid in cocoons</th>
<th>Total eggs laid</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Days</td>
<td>Number</td>
<td>Number</td>
<td>Number</td>
<td>Number</td>
<td>Number</td>
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<td>1.</td>
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<td>38</td>
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<tr>
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<td>43</td>
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<td>4.</td>
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<td>148</td>
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<tr>
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<td>0</td>
<td>127</td>
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<tr>
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<td>101</td>
<td>25</td>
<td>14</td>
<td>119</td>
</tr>
<tr>
<td>8.</td>
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<td>140</td>
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<td>171</td>
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<tr>
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<td>178</td>
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<td>154</td>
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<td>32</td>
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<tr>
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<tr>
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<td>32</td>
<td>1</td>
<td>119</td>
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<tr>
<td>13.</td>
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<td>139</td>
<td>108</td>
<td>29</td>
<td>0</td>
<td>108</td>
</tr>
<tr>
<td>14.</td>
<td>44</td>
<td>185</td>
<td>140</td>
<td>51</td>
<td>216</td>
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<tr>
<td>15.</td>
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<td>81</td>
<td>53</td>
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<td>53</td>
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<tr>
<td>Total</td>
<td></td>
<td>441</td>
<td>2,075</td>
<td>1,706</td>
<td>501</td>
<td>2,367</td>
</tr>
</tbody>
</table>

* Females numbered 1, 2, 3, 4, and 14 were reared upon *A. melanoscelus*, the others upon *S. salicis*. Females numbered 1, 2, 3, 4, 5, and 7 had oviposited in webs of *S. salicis* before the beginning of this experiment.

It is found that in the case of 13 of the 15 females more eggs were laid in webs than in cocoons, while in the case of 2 females more eggs were laid in cocoons. In all, 1,706 eggs were laid in webs and 661 in cocoons. But in this experiment equal numbers of webs and cocoons were not available, consequently 2,075 webs and 501 cocoons were supplied to the 15 females. Now, if egg deposition upon one or the other host were dependent upon chance alone, there should be 4.1 times as many eggs laid in webs as in cocoons \( \frac{2,075}{501} = 4.1 \), while as a matter of fact there proved to be but 2.6 times as many \( \frac{1,706}{661} = 2.6 \). Viewed in the light of this result, the experiment indicates that these females showed a slight preference for the cocoons of *Apanteles melanoscelus*. But of the 661 eggs laid in cocoons by the 15 females, 450 (or about 68 per cent) were laid by the 2 females numbered 9 and 14. The results obtained from these two females, differing so much from those of the other 13, indicate that further experiments, even if conducted in exactly the same manner, might yield a very different ratio between the average number of eggs laid in webs as compared with eggs laid in cocoons. It seems plain, therefore, that a satisfactory test of "preference" would require the employment of a much larger number of females.

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As another phase of this experiment (summarized above under the discussion of fecundity), it was desired to learn the greatest number of eggs which each female was capable of depositing. In this connection it was thought well to provide each female with more host material than it was possible for her to utilize. Because of the limited number of cocoons of *A. melanoscelus*, this excess of host material was represented by webs of *S. salicis*, hence the larger number of webs over cocoons used in this experiment.
Conditions were not similar for the various females in the following three respects: (1) Not all of the 15 females were reared from the same host, for Nos. 1, 2, 3, 4, and 14 were bred from Apanteles melanoscelus while the other 10 were bred from Stilpnotia salicis. (2) In regard to mating, all of the females were observed in coition except No. 15, which reproduced parthenogenetically. (3) Females Nos. 1, 2, 3, 4, 5, and 7 had oviposited in webs of S. salicis previous to this experiment, while the other 9 females had not. Also, it should be observed that no cocoons of A. melanoscelus were provided for the former group of 6 females before the beginning of this experiment, so that a habit of ovipositing in webs might have been formed.

Attention is called to the close similarity between the records for females 3 and 4, and between those for females 5 and 14. It will be seen that the length of the oviposition period, the number of webs submitted, the number of eggs laid in webs, and the number of cocoons given the female are much the same for each member of the respective pairs. No. 3 differs from No. 4, and No. 5 from No. 14, however, in the number of eggs laid in cocoons, and, of course, in the resulting total of eggs laid. It would seem from these examples that the variability of the females in regard to ovipositing upon one or the other host is so great, even between females similar in other respects, that the results of this experiment can not be regarded as in any way conclusive.

Laboratory conditions under which experiments are carried on, no matter how well conceived these experiments may be, are seldom true reproductions of field conditions. In general, then, field experiments offer more reliable sources of data. The rest of this paper deals with information obtained from field observations, at least some of which were on a sufficiently large scale to be conclusive.

THE IMPORTANCE OF EUPTEROMALUS AS A SECONDARY PARASITE

In connection with various phases of experimental work at the gipsy-moth laboratory, the collections mentioned in the following paragraphs were made by members of the laboratory personnel at various points within the areas in New England infested with the gipsy and brown-tail moths.

Collections of the first-generation cocoons of Apanteles melanoscelus, a common parasite of the gipsy moth, have been made during a period of several years. Of a total number of 1,488, from at least nine localities, none has given Eupteromalus as a secondary parasite. These were collected as near the time of issuance of the Apanteles adults as was practicable, so that the cocoons might be subject to the greatest amount of secondary parasitism.

Large collections of the second-generation cocoons of Apanteles melanoscelus have also been made, and during a longer series of years. A total of 98,700 has been isolated and held for observation, representing collections from 30 localities. Only a single cocoon is recorded as having given Eupteromalus. Records indicate, however, that a large part of this total number collected represents material which was brought in from the field very soon after the cocoons were formed, leaving little opportunity for the secondary parasites to attack.

From collections of hibernation webs of the brown-tail moth, a total of 443 cocoons of Apanteles lacteicolor was removed. These had been
subject to secondary parasitism until nearly time for the Apanteles adults to issue. After being held until the secondary parasites had ceased issuing, these isolated cocoons showed Eupteromalus to have issued from six, or from a little more than 1 per cent of the total.

A total of 304 cocoons of the first and second generations of *Meteorus versicolor* gave two Eupteromalus, or about two-thirds of 1 per cent secondary parasitism.

Still another known host was collected at infestations of the brown-tail moth in the form of 80 puparia of the tachinid *Compsilura concinnata* Meig. These puparia, although heavily parasitized by other secondaries, yielded no Eupteromalus.

Six collections of another tachinid parasite of the brown-tail moth, *Sturmia nidicola* Town., yielded 473 puparia, none giving Eupteromalus.

Among these species are included the hosts upon which Eupteromalus has been recorded as a secondary parasite. From the information obtained from these collections, however, it seems that Eupteromalus is not an important secondary parasite of any of these hosts.

**IMPORTANCE OF EUPTEROMALUS AS A PRIMARY PARASITE**

Although Eupteromalus larvae have been found in the hibernation webs of the brown-tail moth from localities rather well distributed over the infested areas each year during a period of some 20 years, the extent of such parasitism seems to be of small importance. Some webs will show very many more of the parasites present than will others, the number ranging from none to several hundred per web. But the number of host larvae in these webs is large, ranging from 5 to 2,800 or 2,900, the average being well over 300. The records show that the percentage of parasitism of this host by Eupteromalus is seldom more than 1 per cent over the whole area. Since 1926, when Eupteromalus was found attacking the satin moth, the percentage of its parasitism of the brown-tail moth has been increasing.

Upon the satin moth the percentage of parasitism seems to be increasing over the New England area as a whole. Early in the spring of 1927, before development of either parasite or host had begun, examination of 6,429 hibernation webs of the host showed 154 to contain Eupteromalus, a result indicating about 2.4 per cent parasitism by the hibernating generation. Included in this total number of webs examined were many containing dead host larvae, which observations have indicated may have died soon after the formation of the web. Since experiments have shown that Eupteromalus does not attack these webs, it would seem that the real effectiveness of Eupteromalus was much greater than the percentage 2.4 would indicate. Again, this figure relates only to the hibernating generation of Eupteromalus, and observations show that many of the host larvae are killed by a generation previous to the hibernating generation. Besides, we do not know the amount of control exercised upon the host by the female in her habits of puncturing the larva and then leaving the web without ovipositing, or by feeding upon the host larva. These conditions obtain also in the three cases about to be considered, unless otherwise indicated.

In 1928 examinations of the hibernation webs were made in 10 townships scattered over the infested area. The method was to open
the first 100 webs encountered and to record the contents, only live host larvae and parasite larvae being included in this count. There were 1,067 webs examined in this way, of which 126 were found to contain Eupteromalus of the hibernating generation. This attempt to approximate more nearly the true percentage of parasitism by Eupteromalus gives a figure of 11.8 for the entire infested area. The examinations in some localities showed Eupteromalus to be absent, while those in others indicated a percentage of parasitism as high as 58.

In 1929 webs were examined in 21 townships, some of which were upon the border of the infested area. A total of 1,674 were examined in the same way as in the preceding year, and 153 (or about 9 per cent) of these were found to contain hibernating Eupteromalus. The parasitism in individual localities ranged from none at all to as much as 52 per cent. Of the 21 townships, Eupteromalus was found in 12.

In connection with another experiment, a rather thorough examination of all the hibernation webs to be found upon an entire tree was made at a woodland infestation of the satin moth. The infestation was upon a group of about 500 trees of Populus grandidentata which were from 40 to 60 feet in height. Three trees were chosen as samples, cut down, and brought into the laboratory in sections. Here they were carefully examined by members of the laboratory staff and the contents of all webs found were noted. From the results so obtained, it was found that there was upon each tree an average of 1,695 webs of the present year. Death of the host larva could be definitely attributed to Eupteromalus in an average of 666 webs per tree. This average gives about 39 per cent parasitism by Eupteromalus under these conditions.

CONCLUSIONS

From the foregoing figures one would conclude that Eupteromalus is of slight importance as a parasite of the brown-tail moth. As a parasite of the satin moth, however, it seems to show some promise. Although the percentage of parasitism over the entire area has not had a constant or marked increase during the years in which this parasitism has been studied, there undoubtedly was an increase between 1926 and 1929. It seems reasonable to expect that the parasite will follow the host as the latter spreads to its climatic limits, and that as the parasite catches up with the host the average percentage of parasitism will increase. Consequently, if the present rate of increase continues, the percentage of parasitism of the hibernating stage of Stilpnottia salicis by Eupteromalus will become of greater economic importance.

SUMMARY

Eupteromalus nidulans (Thomson) was first introduced into this country in 1905 to assist in controlling the brown-tail moth (Nygmia phaeorrhoea Don.). As a result of a misidentification (2), this parasite has been referred to by various workers as Pteromalus egregius Föerst. Although rather large numbers of imported material were colonized during the years 1906 to 1909, establishment of the species was not proved until more than four years after the first colonization. Records of wide dispersion were obtained very soon thereafter. In 1909 it was discovered acting as a secondary parasite upon Apanteles
lacteicolor Vier., and further colonization was stopped. In 1926 Eupteromalus was found attacking the satin moth (Stilpnotia salicis L.), which had been known to occur in Massachusetts since 1920.

Eupteromalus hibernates as a mature larva within the web or cocoon of its host. There may be as many as two generations each year upon primary parasites in the spring, and as many as three generations, the third hibernating in the fifth larval instar, upon the satin moth in the fall. Again, there may be no reproduction upon primary parasites, and but one or two generations on the satin moth in the fall. The adults mate readily in confinement. The females oviposit only upon host material which is suitable for food for the larvae. The female will oviposit readily whether mated or not, parthenogenetic reproduction producing only males. The oviposition habits of the female show that the host seems always to be punctured before eggs are laid, and that this puncturing produces a paralysis in the host which does not seem to be the result of a mechanical injury alone. The eggs are deposited upon the surface of the host, no definite part of the body being preferred for the location of the egg. Superparasitism is common, while hosts are frequently paralyzed but no eggs are laid. The paralysis of the hibernating larvae of the satin moth is permanent. The average number of eggs laid by 16 females was 251.

The females form a feeding tube through which the body fluid of the host is obtained. Unfed adults lived an average of 12 days, while some of those fed upon a mixture of honey and water lived as long as 150 days, the average being considerably less.

Little is known regarding competition with other parasites, but Eupteromalus was the successful species in the cases observed. One Eupteromalus is usually reared from a single larva of Stilpnotia salicis, although as many as three have been noted. Seven is the largest number of individuals observed to develop to maturity on one larva of Apanteles melanoscelus (Ratz.). The larva of Eupteromalus nidulans does not migrate from one web of the satin moth to another. A field observation showed 104 males and 72 females to be the sex ratio present.

The eggs of Eupteromalus nidulans average 0.38 millimeter in length, and adhere readily to nearly any surface. There are five larval instars, the first possessing four pairs of spiracles and sickle-shaped mandibles which combine to separate it from the following instars. These latter instars are alike in having nine pairs of spiracles, and mandibles much less strongly curved. The naked pupa adheres to the host or to the surrounding walls of the web or cocoon.

In a laboratory experiment to determine whether Eupteromalus laid more eggs in webs of Stilpnotia salicis or in cocoons of Apanteles melanoscelus, the variation between the results obtained from individual females was so great and the number of females in the experiment was so small that the results are inconclusive. From field collections of primary parasites recorded as, or likely to be, hosts of Eupteromalus, it was found that Eupteromalus was not an important secondary parasite of any of them. Upon the brown-tail moth, Eupteromalus has rarely exceeded a parasitism of 1 per cent over the infested area as a whole. As a parasite of the satin moth, it shows considerable promise. During the years 1926 to 1929 the average
percentage of parasitism over the entire infested area increased from about 2.4 to about 9. In a field experiment in the case of a woodland infestation Eupteromalus was found to have killed 39 per cent of the hibernating larvae of the satin moth.

LITERATURE CITED


