

*Perilampus*  
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BUREAU OF ENTOMOLOGY.

L. O. HOWARD, Entomologist and Chief of Bureau.

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TECHNICAL RESULTS FROM THE GIPSY MOTH  
PARASITE LABORATORY.

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IV. THE CHALCIDOID GENUS PERILAMPUS AND  
ITS RELATIONS TO THE PROBLEM OF  
PARASITE INTRODUCTION.

By HARRY S. SMITH,

*Expert.*

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## CONTENTS

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	Page.
Introductory.....	33
Biology of <i>Perilampus hyalinus</i> Say.....	34
Oviposition.....	37
Reproductive capacity.....	39
Description of planidium.....	39
Habits of planidium.....	41
Life as a parasite of <i>Varichæta</i> .....	42
As a parasite of <i>Limnerium validum</i> Cresson.....	43
As a parasite of summer-issuing Hymenoptera.....	44
As a parasite of other hosts.....	45
Later larval stages.....	45
Pupation.....	47
Food habits of the adult.....	48
Longevity and oögenesis.....	49
Length of life cycle and influence of temperature.....	49
Effect of parasitism upon host.....	51
Percentage of parasitism.....	52
Superparasitism.....	53
<i>Perilampus</i> versus <i>Perilampus</i> .....	53
<i>Perilampus</i> versus <i>Dibrachys</i> .....	55
<i>Perilampus</i> , "species A".....	55
Development of <i>Orasema</i> .....	57
Planidium of <i>Orasema viridis</i> Ashmead.....	59
Relationship of Eucharidæ and Perilampidæ.....	59
<i>Rhipiphorus</i> and other coleopterous parasites.....	60
Host relations of the genus <i>Perilampus</i> .....	61
Rearing records of <i>Perilampus hyalinus</i> at the laboratory.....	61
Other American rearing records of <i>Perilampus</i> .....	62
European rearing records of <i>Perilampus</i> .....	64
European species of <i>Perilampus</i> reared at the laboratory.....	65
Résumé of host relations of the genus.....	66
The economic aspects.....	67

## TECHNICAL RESULTS FROM THE GIPSY MOTH PARASITE LABORATORY.

### IV. The Chalcidoid Genus *Perilampus* and its Relations to the Problem of Parasite Introduction.<sup>1</sup>

By HARRY S. SMITH, *Expert.*

#### INTRODUCTORY.

Practical utilization of parasites in the control of noxious insects is becoming a more and more important means of warfare in economic entomology. For that reason accurate and detailed knowledge of the life history of the various parasitic groups is indispensable to an intelligent handling of the intricate problems which continually present themselves in work of this kind. It does not suffice merely to know that an insect is a primary parasite or a hyperparasite. Familiarity with the intimate details in its life and habits is of the utmost importance in order that it may be brought to its maximum of efficiency with the least possible delay; or, should it prove to be a hyperparasite, that an injurious insect may not thus be released unwittingly and irreparable damage be done. The great desirability of bringing this phase of economic entomology to a position of prominence has been the prime motive for a solution of some of the most perplexing problems which have confronted the student of insect parasitism; for example, the work of Marchal and Silvestri on the development of the hymenopterous, and of Townsend and Nielsen on the dipterous parasites. These men are economic workers and their discoveries of the extraordinary phenomenon of polyembryony or germi-nogony in the parasitic Hymenoptera and of the unusual habits of oviposition and larviposition in the tachinid parasites were made in connection with a study of the practical utility of these insects in the control of injurious species. Such investigations are interesting not only from the purely scientific standpoint, but are more than justifiable from that of applied entomology.

The few forms studied by these entomologists are among the most common species, which goes to show how limited the present knowledge of the biology of insect parasites really is. A fascinating field of study is open to those in a position to undertake research of this

<sup>1</sup>The writer is indebted to Mr. W. F. Fiske for valuable suggestions and criticisms throughout the course of his work on *Perilampus*.



kind, the requirements for investigating these most interesting phenomena, where the more common species are concerned, being, as stated by Dr. L. O. Howard, "simply good laboratory facilities and a skilled technique, together with trained powers of observation." These, as he points out, are to be found in many institutions and with many individuals in this country. The element of a chance discovery sometimes enters into consideration, however, even when a common insect is made the subject of study. Quite as often as not the discovery of the thread which will later lead to an unraveling of the complete life history is nothing more nor less than an accident, the clue being stumbled upon in a place and at a time altogether unlooked for. The investigations of the life history of *Perilampus hyalinus* Say received their initial impetus from just such an accidental discovery.

#### BIOLOGY OF PERILAMPUS HYALINUS SAY.

When time and opportunity have permitted, the parasites of certain among the native leaf-feeding caterpillars have been studied at the Gipsy Moth Laboratory in order to determine the part which parasitism plays in their natural control, and in an endeavor to arrive at a better understanding of the varied phases of the problem. Among others, the fall webworm (*Hyphantria textor* Harris) was selected as a promising subject, and, coming as it does at a season just after the summer's work on gipsy moth parasite importation and colonization is over, it has been possible to devote a larger share of our attention to it than to other even more interesting species which complete their transformations earlier in the season. Upon several occasions the young caterpillars have been brought in from the field, placed in insect-proof rooms and cages, and fed. In due time primary parasites, usually tachinids, species of the ichneumonid genus *Limnerium*, and occasionally *Apanteles*, emerged from these caterpillars, and the cocoons and puparia were removed to tightly stoppered vials and placed aside for the emergence of the adults. Later examination revealed the fact that adults of the species which formed the puparia or cocoons could not always be expected to emerge, for usually a certain percentage produced adults of *Perilampus* instead. How the adult female *Perilampus* obtained access to these puparia and cocoons in order to oviposit in them was a mystery inasmuch as especial pains had been taken to make the rooms and cages containing the caterpillars parasite-proof. But for a fortunate discovery during the spring of 1909 the true significance of these perplexing observations would doubtless have remained a mystery for some time to come.

While engaged in experimentation for developing a better technique in the preparation of hymenopterous larvæ for microscopical study, in which work the larvæ of the common *Limnerium validum* Cresson, an important parasite of the fall webworm, were used as subjects, a

strange little creature was discovered which was obviously the larva of an insect, but which differed very materially from any familiar form. It was impossible, from external characters, to assign it to any particular order with assurance, and consultation with several of the ablest entomologists of the country failed to throw any light upon the subject.

It was less than three-tenths of a millimeter in length, and therefore almost invisible to the unaided eye, oblong-ovate in shape and dark brown in color. Examination under the microscope showed it to be a highly organized being with well-defined mouth parts, strong, curved mandibles, conspicuous tracheal system, etc. The 13 segments were well differentiated, the first forming a distinct head, which was armed with several recurved hooks. The dorsal segments consisted of a series of heavy, chitinous, and overlapping plates, which nearly encircled the body. Most of these were furnished with one or two pairs of bristles. Ventrally the larva was furnished with several backward-projecting spines, which were evidently ambulatorial in function. An attempt to rear the adult from this larva was unsuccessful.

Among the minor projects under way at the laboratory at this time was a study of the biology of *Dimmockia incongrua* Ashmead, a rather common and important native chalcidoid parasite of tachinids. As a host for the rearing experiments with *Dimmockia* one of the most common native dipterous parasites, *Varichæta aldrichi* Townsend, also an important enemy of the fall webworm, was utilized.

In the course of an examination of the pupæ of this tachinid for the eggs and young larvæ of *Dimmockia* a second specimen of the remarkable creature referred to above, or to be more accurate one similar to it, was encountered. This second specimen, instead of being firmly attached to its host by its anterior end as was the former, was quite free and crawled about over the body of the tachinid pupa in a startlingly businesslike manner. This observation very naturally led to a further search through the abundant material at hand, and the presence of the strange parasite, for such it was now suspected of being, was found to be of not at all rare occurrence. An excellent opportunity was at once afforded for ascertaining the identity of the parasite and the subsequent rearings through the different stages were made with a great deal of eagerness. Immediately upon the completion of the first ecdysis it was seen that the larva resembled rather closely what was known to be the mature larva of *Perilampus*, and the further development of the specimens under observation confirmed that suspicion. The first-stage larva is of a very unusual type, which, with a single exception so far as known, has not been observed before. This exception is the larva of *Orasema viridis* Ashmead, described and figured by Dr. William Morton Wheeler.<sup>1</sup>

<sup>1</sup> Bulletin of the American Museum of Natural History, vol. 23, Art. I, 1907.

A comparison of the peculiar first-stage *Perilampus* larva with the *Orasema* material in Dr. Wheeler's possession indicated that while the two were very different in anatomical detail, they were of the same general character and constitute a type which, Dr. Wheeler has suggested, may be designated by the term "planidium."<sup>1</sup>

The establishment of the identity of the planidium did not assist materially in clearing up the mysterious circumstance attending the rearing of the *Perilampus* from the *Limnerium*, *Varichæta*, and *Apanteles* parasitic on the fall webworm, and with the end in view of determining if possible the manner in which *Perilampus* gained access to its host, several thousand young caterpillars of *Hyphantria* were collected during the following fall, placed in rearing trays, and reared to maturity. At frequent intervals a large series of these caterpillars was killed and preserved in order that abundant material might be had for study during the winter.

*Apanteles hyphantriæ* Riley was found to be a fairly common parasite of the younger caterpillars, and *Varichæta aldrichi* and *Limnerium validum* of the older ones, as during the preceding summer. Examination of the puparia and cocoons of the parasites disclosed the fact that the planidia of *Perilampus* were even more common than they were during the preceding year, and as large quantities of material in all stages had been preserved an excellent opportunity was afforded for working out the life history of this remarkable parasite.

As has been mentioned on a preceding page, *Perilampus* was frequently reared from puparia and cocoons formed in tight rooms or breeding cages into which it was thought impossible for an adult parasite to gain entrance. Consequently in seeking an explanation of the presence of the planidia of *Perilampus* in the puparia and cocoons of these primary parasites of *Hyphantria*, it seemed most plausible that the female oviposited in or on the caterpillar containing the parasite which was later to become the host of the young *Perilampus*. Acting upon this hypothesis, maggots of the tachinid which had emerged from the caterpillar were examined and found to contain the planidia internally. The planidium, by reason of its dark color, was easily visible through the semitransparent integument of the maggot, and even after the latter had ceased activity and had formed its puparium the *Perilampus* larva could be seen through the shell until it had changed color and had become quite opaque. Dissection of the fully developed caterpillars revealed the fact that the tachinid maggots *while still within the caterpillar* contained these planidia, and going back still further, to the younger caterpillars, the planidia were found to be present here irrespective of whether the caterpillar was infested by a primary parasite or not.

<sup>1</sup> From the Greek *πλανητης*, a wanderer, and *ιδιον*, diminutive.

Examination of a considerable number of the *Hyphantria* caterpillars showed that the planidium could be found in almost any portion of the caterpillar's anatomy, although they generally "floated about" freely in the body cavity. Occasionally specimens attached to the larval organs, such as the alimentary canal or silk glands, were encountered. Further study of still younger caterpillars revealed the most interesting and significant feature of the whole life cycle, namely, the presence of the planidia *upon the exterior* of the caterpillars. These were apparently about to make their way through the integument to the interior in a search for suitable hosts upon which to complete their development. The less heavily chitinized portions of the caterpillar's skin, that is, the portion between the different segments, offered the most vulnerable point of attack and almost invariably this was the place selected by the parasite for making an entrance. Individuals which had not yet started an opening were found quite as frequently upon the middle of the segments as between them. Just how these planidia came to be located upon the skin of the caterpillars and how, when, and where the adult female *Perilampus* places her eggs, we have been unable to ascertain up to the present time, and any statement in regard to this portion of the life cycle must take the form of mere conjecture.

#### OVIPOSITION.

There have been made, so far as published records go, at any rate, no observations upon the oviposition of members of the genus *Perilampus*. It is known, however, that oviposition does not occur in the normal way, or in the manner we are accustomed to regard as the normal method of oviposition among the parasitic Hymenoptera, and for this reason speculations on what may actually occur are rather interesting.

In the first place it is obvious from the facts recorded in the preceding pages that *Perilampus* does not oviposit directly in or upon its host. In the second place, it does not oviposit within the caterpillar of which its host is a primary parasite, which is equally obvious from observations already made. That it places its eggs *upon* the young caterpillar is improbable, the adult *Perilampus* being too slow and clumsy to be capable of accomplishing this act with any degree of certainty.

There are two plausible methods which *Perilampus* might adopt for the deposition of its eggs, and the writer is strongly inclined to the view that one of these methods is in part at least correct. As in the case of some of the parasitic beetles, it may deposit its eggs upon flower heads or upon leaves of plants not in the immediate vicinity of the caterpillar colony, the planidia hatching from these

eggs being conveyed to the caterpillars by means of some intermediate carrier. In the Coleoptera cited above the carrier is frequently a parasitic bee upon which, by means of their claws, the triungulins attach themselves and are conveyed to the nest of their host. With *Perilampus*, should this method prove to be the one which really takes place, the intermediate carrier might be any of the primary parasites which attack *Hyphantria*; that is, the hymenopterous parasites *Limnerium* or *Apanteles*, or the tachinid *Varichæta*. The planidium seems more or less fitted for this sort of a life and is apparently analogous to the triungulin of the coleopterous parasites. The chitinous plates with which it is armored are especially serviceable in preventing injury of various kinds, and the mandibles and hooks and spines would serve it very well as a means of clinging to its conveyer.

*Varichæta* as a conveyer of the planidia would expose the young *Perilampus* to one more vicissitude, as it does not oviposit upon the caterpillars, but deposits young maggots upon the leaves of the food plant of its host. These maggots, should they by good fortune happen to have been placed upon a leaf which is later crawled over by a caterpillar, fasten themselves upon their host when the opportunity offers. *Perilampus* then would twice be subjected to the same conditions as these maggots, and their success in finding a host would depend entirely upon whether or not caterpillars came within their reach.

The other method, which seems much more plausible, is that of oviposition upon the food plant *in the vicinity of a colony* of the caterpillars. This would do away with the necessity of an intermediate carrier, but would expose the delicate eggs to great danger unless they hatched immediately after deposition.

Both theories have their faults and it may easily be that neither is correct. They are offered simply as suggestions to anyone who has the opportunity to make observations upon this parasite, in the hope that they will be of assistance in completing the knowledge of this strange life cycle. The former hypothesis has the advantage of a parallel in the parasitic Coleoptera, while something similar to the latter is known to occur in certain of the tachinid parasites (notably *Varichæta*, as mentioned above) which deposit young maggots upon the leaves, the maggots attaching themselves to the caterpillar as it crawls over the leaf upon which they are located.

While the eggs of *Perilampus* have not been observed after deposition, those contained in the ovarian tubes, in one case apparently mature, have been examined. They are of the usual elongate-oval shape, not stalked, and whitish in color.

## REPRODUCTIVE CAPACITY.

It is a well-known fact that insects which are subject to very high mortality in their younger stages must have a high potential rate of reproduction in order to offset this loss and still prevent the species from becoming extinct; and conversely, we may say that insects laying a great number of eggs must of necessity experience a very high death rate or else they would in time increase beyond all bounds. We have found by the dissection of adult female *Perilampus* that the eggs are very numerous, the abdomen containing as high as 250 fully developed eggs at one time. It is therefore apparent that in some stage or stages before maturity many of the young die. As *Perilampus* is eminently well fitted to withstand the vicissitudes encountered in its later existence, the logical place to find this high death rate is during the planidium stage, while the tiny larva is wandering about either within or outside the caterpillar in search of its host. That this wandering habit of the younger, pre-eruciform stages of parasitic larvæ is accompanied by great mortality is well exemplified in the case of the Strepsiptera. Newport, in his "History and General Anatomy of Meloë and Its Affinities,"<sup>1</sup> records the production of more than 7,000 triungulins by a single female of the genus *Stylops*. *Perilampus* is apparently not only subject to a considerable mortality by reason of its wandering habit, but large numbers meet their death through a failure to find a proper host within the caterpillar and through the operations of superparasitism after they do find their host.

Whatever be the real method by which the planidium becomes affixed to the caterpillar, the life history from this point on has been worked out by actual observation in the laboratory, with an abundance of material for study.

## DESCRIPTION OF PLANIDIUM OF PERILAMPUS HYALINUS.

(Figs. 24, 25.)

Length about 0.3 mm., depending on the amount of distension; diameter at widest place about 0.06 mm. Shape obovate; composed of 13 distinct segments or rings which are dark brown and heavily chitinized, and which "telescope" into each other more or less.

Head heavily margined, both laterally and posteriorly above, the rim strongly emarginate or indented posteriorly, where it is also strongly elevated in life and darker than other portions of the head. Mandibles well developed, hook-shaped, situated in a buccal cavity, and crossing at tips; bases broad, with a rather large area for muscular attachment. Immediately back of the mandibles are two flattened, heavily chitinized organs, which are probably homologous to the

<sup>1</sup> Proceedings of the Linnean Society of London, vol. 1, pp. 317-320, 368-370.

maxillæ, but the minute character of which makes it impossible to determine their nature without considerable uncertainty. Head heavily armored with two powerful hooks or horns on the anterior margin, projecting laterally, about the size of the mandibles; above are seen two rather strong hooks at about the middle, both curved backward at tips; just back of hooks on dorsal portion of head are several semitransparent round spots, which probably bear small bristles, and may be sensory in function.

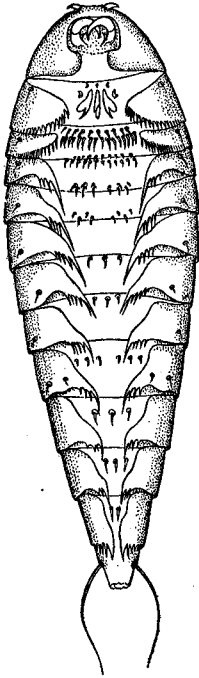


FIG. 24.—*Perilampus hyalinus*: Planidium, ventral view. Magnified about 350 diameters. (Original.)

Body segments as follows: First segment (excluding head) provided dorsally with two very minute semitransparent round spots, with dark spot in center, which is probably a minute spine, but which is rendered practically invisible by the clearing action of the balsam; ventrally the same segment is provided with two other similar spots, but which bear very distinct curved spines, one in the center of each. The heavy chitinous ring does not join beneath the body, each side ending instead with the ventro-posterior margin, which is serrated or fringed with long teeth, about 30 in number, becoming gradually shorter as they approach the lateral margin of the planidium. Between these fringed margins, situated in the center of the ventral portion of the segment, are three peculiar appendages which apparently function as ambulatory organs; these are somewhat flattened pyriform, with the broad end heavily notched somewhat at one side and attached at small end; at the bases of these are several small irregular appendages. The second segment is provided with the dorsal, backwardly curved spines, much closer together than on preceding segment and rather larger, and two ventral smaller spines; the teeth are slightly smaller. Between the serrate margins, as in preceding segment, are several hooks or motor appendages, but of quite a different type, these latter being simply plain hooks projecting backward, there being two transverse rows, about 10 in first row and about 16 in second. Between first and second segments on the

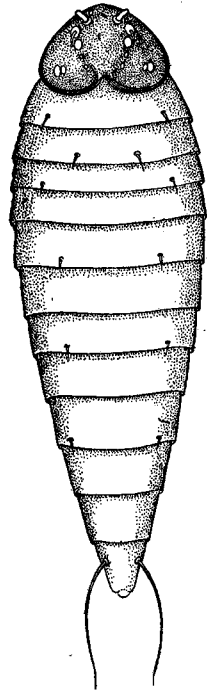


FIG. 25.—*Perilampus hyalinus*: Planidium, dorsal view. Magnified about 350 diameters. (Original.)

ventral side, situated in the elastic integument connecting the chitinized plates, are two stigmata, apparently the only spiracular openings in the whole tracheal system. Third segment similar to preceding, the two dorsal spines being considerably farther apart; the ends of the chitinous plate, however, are of quite a different type; instead of ending in a serrate margin the inner margin is smooth, but the posterior corner terminates in a long tapering projection considerably longer than the width of the chitinous sclerites; laterad of the long tapering projection referred to above are two or three much smaller ones, also situated on the apical margins of the segment; between the ends of the chitinous plates, as in preceding segments, are several hooklike motor appendages, smaller and fewer in number, however, than in the second segment; an additional series of hooks which is not provided in preceding segments is situated just laterad of these. The fourth segment seems to have no dorsal spines; there are two ventral ones, however, situated at the extreme outer margin of the ring; the chitinous plate terminates as in the third segment; motor appendages as in third segment but fewer in number. The fifth segment differs from the fourth apparently only in the possession of a pair of dorsal spines and in the smaller number of ventral motor appendages. The sixth segment does not have the dorsal spines but in other respects is similar to the fifth; the seventh segment possesses the dorsal spines; the eighth does not, nor does the tenth, eleventh, or twelfth; these latter, however, are similar in other respects, excepting that they become gradually less in size. The last segment is provided with an unjointed stylet on each side attached at about the middle of the segment, this stylet about twice the length of the segment itself.

#### HABITS OF PLANIDIUM.

Starting with the planidium upon the skin of the caterpillar, this makes its way through the thinner portion of the integument found at the junctures of the segments, this passage being effected by means of its well-developed mouth parts and specially armored head. Just how the search for the host parasite is conducted is not known excepting as it may be deduced from dissections of preserved material. The planidium has been found in almost every part of the caterpillar and it appears that its search for a host is rather thorough and extensive. The time of its attack upon the host larva has not been very definitely determined, although from the data at hand it seems most likely that this follows at once upon the finding of another parasite within the caterpillar. This supposition is substantiated by the fact that the planidium is found within the very young tachinid larvæ which have just completed their first molt. In this stage the disparity in size between the larvæ of *Perilampus* and of *Varichæta* is very much less than it is later, and it seems remarkable that the



tiny tachinid maggot can, without inconvenience apparently, continue in its development with the *Perilampus* larva boring about within its body, and sometimes with not only one but five or six.

What becomes of the planidium in case the caterpillar does not contain a primary parasite is a question which has not yet been answered, and to do so would require considerable care and patience. There are two courses open to the *Perilampus* in case it has selected an unparasitized caterpillar. It may either wander about within the body of the latter until it dies from starvation and exhaustion, or it may make its way to the outside again and continue the search for a host in another caterpillar. That it might possibly develop upon the caterpillar itself is not to be considered. Even should it remain within the caterpillar until the latter pupated,<sup>1</sup> it is not likely that it could make its way through the hard pupal shell of *Hyphantria*, and if this were possible the older *Perilampus* larva is very much too delicate a creature to be able to feed externally unprotected.

In case the former alternative is what actually takes place, there must be a great percentage of mortality due to the lack of a proper host, for relatively only a small proportion of the caterpillars hatching from the eggs ever reach an age sufficient to nourish a host for *Perilampus*. Of those that do reach that age a great many are never attacked by primary parasites and hence would not be available for *Perilampus*.

Just what is the effect upon the caterpillar itself which is infested by *Perilampus* but which contains no primary parasite is a matter for conjecture. It seems likely, however, that its presence would not prevent the caterpillar from reaching its full development and it is probably only slightly inconvenienced if affected at all.<sup>2</sup>

Having followed the *Perilampus* planidium to its host within the caterpillar it is now necessary to trace out the slightly different modes of development upon the various parasites of *Hyphantria* which are subject to its attack.

#### LIFE AS A PARASITE OF VARICHLETA.

*Varichæta aldrichi* Townsend<sup>3</sup> has been by far the most common of all of the parasites of the fall webworm in Massachusetts during the past two years. As stated on a preceding page, it belongs to that group of tachinids which deposit living maggots upon the stems and foliage in the vicinity of the caterpillars of their chosen host, a habit first discovered by Mr. C. H. T. Townsend in the course of his work

<sup>1</sup> Later dissection of *Hyphantria* pupæ, made in the spring of 1911, by Mr. H. E. Smith, discovered the planidium alive and still "waiting for something to turn up." In one instance the planidium was embedded in the gonad of the *Hyphantria*.—W. F. FISKE.

<sup>2</sup> The occurrence of the planidium in the gonad, as noted in preceding footnote, suggests that partial castration might possibly result.

<sup>3</sup> Determination furnished by Mr. W. R. Thompson.

at this laboratory and briefly described by him in an earlier bulletin of this bureau.<sup>1</sup> The maggots rarely leave their host until after it has become full fed and prepared for pupation in the fall. The tachinid maggots pupate soon after emerging from their hosts, the pupæ remain unchanged during the winter, and the subsequent transformations are accomplished quite early in the spring.

In case the planidium chooses a maggot of *Varichæta* as its host, it remains endoparasitic until the puparium is formed. During the process of histolysis the *Perilampus* either orients itself in such a manner that it will be external to the tachinid pupa when pupation is completed, or it emerges from the pupa immediately after pupation; in either case, of course, it remains within the puparium. When parasitic upon this host the planidium, so far at least as the writer has been able to learn, normally hibernates in this stage and probably without nourishment.

It is quite likely, however, that a late warm fall would start the development of the planidium on *Varichæta* at once. This would without doubt result in the death of the secondary parasite, as it would scarcely be able to pass the winter in the normal larval stage. In fact dead second-stage *Perilampus* larvæ have occasionally been found upon the pupæ during the winter, and this would seem to be evidence in corroboration of the above statement. It is probably an attempt to go through two generations per year, as this insect does, without much doubt, farther south, and the individual specimens found in the second stage during the winter in New England are probably those from the puparia which emerged as larvæ from the caterpillars earliest in the fall, although we have no absolute evidence that this is the case. The development, or rather the conduct, of the planidium up to and including its change from endoparasitism to ectoparasitism, as stated on a previous page, seems entirely dependent upon the development of its host, such are the intimate relations between the two. After the planidium has emerged from its host development takes place in the usual way.

#### AS A PARASITE OF LIMNERIUM VALIDUM CRESSON.

Of the primary hymenopterous parasites attacked by *Perilampus* probably the most common one is *Limnerium validum* Cresson, an ophionine parasite emerging from the older caterpillars in the fall and hibernating as larva in a silken cocoon. The larva of this parasite, like that of *Varichæta aldrichi*, does not reach full maturity until its host has prepared for pupation, and the cocoons are to be found in the same situations as the pupæ of *Hyphantria* and are afforded the same protection. In this respect it differs radically from the other species of *Limnerium* parasitic upon the fall webworm.

<sup>1</sup> Technical Series, No. 12, Part VI, p. 103.

*Perilampus hyalinus* in this case always remains endoparasitic throughout the winter, at least so far as our observations go, and several hundred cocoons have been examined to date. At first it seemed rather puzzling that the same species should pass the winter ectoparasitically upon tachinids and endoparasitically upon *Limnerium validum*, but dissections of hundreds of the puparia and cocoons brought to light the fact that the habit of *Perilampus* in this regard was dependent entirely upon the life cycle of the host parasite, that is to say, the planidium lives internally in its host until histolysis takes place, when it changes its mode of life from an internal parasite to an external parasite. *Varichæta* pupates in the fall, so the planidium makes its exit at this season of the year and hibernates externally. *Limnerium validum* hibernates as a larva and pupates in the spring, hence the planidium in this case remains internal until spring, when it emerges by means of its efficient mandibles and spined head, completing its development in precisely the same manner as those individuals which happen to have chosen *Varichæta* as their host. The internal disturbances which take place in the body of the host at the time of histolysis probably act as a stimulus to the activities of the planidium, and the condition of the integument is such as to make the exit of the secondary parasite especially easy at this time. The development of the host, so far as our observations have gone, invariably ceases at the time of the exit of the planidium. Whether or not it is actually killed at this time is not evident. In any case decomposition does not take place immediately, the host being left in a condition somewhat comparable to that of the prey of certain aculeate Hymenoptera.

#### AS A PARASITE OF SUMMER-ISSUING HYMENOPTERA.

The other primary parasites of *Hyphantria* from which we have reared *Perilampus* are two additional species of *Limnerium*, differing from *L. validum* in that they spin their cocoon within the skin of the caterpillar and emerge in the fall, and the braconids *Apanteles hyphantriæ* Riley and a *Meteorus* (probably *M. communis* Cresson). In all four of these species the *Perilampus* completes its development at once. Whether or not these individual specimens manage to survive the winter is open to question. It is quite possible that many of them remain within the cocoon of their host throughout the winter. This is quite strongly indicated by the result of an experiment in which a collection of old webs containing cocoons of the several parasites was made on October 20, 1908, from which several adult *Perilampus* issued between 6 and 10 days later. The material was kept in a warm room; had it remained out of doors it is very unlikely that emergence would have occurred so soon, and probable that it would have been deferred until spring.

We know that the adult of one of the European species of *Perilampus* hibernates in the puparium of certain tachinids parasitic on the gipsy moth and brown-tail moth. Most of these tachinids, like the summer-issuing hymenopterous parasites, pupate comparatively early in the fall, thus making the two cases similar. For this reason the writer feels justified in surmising that the same thing occurs in the case of *Perilampus hyalinus* parasitic on the summer-issuing Hymenoptera.

#### AS A PARASITE OF OTHER HOSTS.

There is another group of parasites of the fall webworm which hibernate either as partially grown or as full-fed larvæ within the pupæ of their host. These include certain large solitary ichneumonids, *Anomalon ambiguum* Norton, *Ichneumon cinctitarsis* Provancher, and *Melanichneumon* sp. At least one species of Tachinidæ has also been found hibernating in this manner in Massachusetts. We have not actually found *Perilampus* to be a parasite of any of the ichneumonids named above, but only a very small number of the larvæ of these parasites have been seen.<sup>1</sup> There seems to be no good reason why the secondary should not attack these hibernating hymenopterous larvæ, and it is practically certain that the examination of a considerable number would show the planidium to be present.

We have absolute proof, however, that it does attack the hibernating tachinids,<sup>2</sup> having found the planidium actually within the maggot of this species within the pupa of *Hyphantria*. Whether or not the adult *Perilampus* is able to make its way through the pupal shell of the fall webworm (presuming that the tachinid completes its larval development and pupates internally) we are unable to state definitely, as no record has been made of *Perilampus* having issued from these pupæ. There seems to be little doubt as to its ability to do this, as it has very powerful jaws. Specimens in the laboratory will eat away quite a large quantity of cork in attempting to escape from a vial in which they have been confined.

#### LATER LARVAL STAGES.

On the return of warm weather in the spring, the winter having been passed upon the various hosts in the manner indicated in the preceding pages, the planidium begins feeding by sucking the juices of its host. Growth takes place gradually and first becomes apparent through the planidium taking on a banded appearance due to the

<sup>1</sup> It has since been found by Mr. H. E. Smith within the larvæ of *Ichneumon* (which attacks the pupa of the host) and that of *Exochilum*, which hibernate in what must be considered as an embryonic state within the *Hyphantria* pupæ.—W. F. FISKE.

<sup>2</sup> Probably *Compsilura concinnata*, the recently imported parasite of the gipsy and brown-tail moths.

separation of the chitinous rings or plates by a stretching of the intersegmental membranes which are transparent. (See fig. 26, *d, d'*.) The underside of the planidium also gradually fills out until the larva has attained a bulk several times greater than that of the hibernating planidium and presents the appearance of an ovate semitransparent sack with dark median crossbars dorsally.

After a short resting period, ecdysis takes place. The skin of the planidium breaks transversely just back of the second thoracic segment, the posterior segment slips backward, and the old head and first two thoracic segments are shed at the anterior end of the larva. Just how long the planidium feeds before ecdysis has not been ascer-

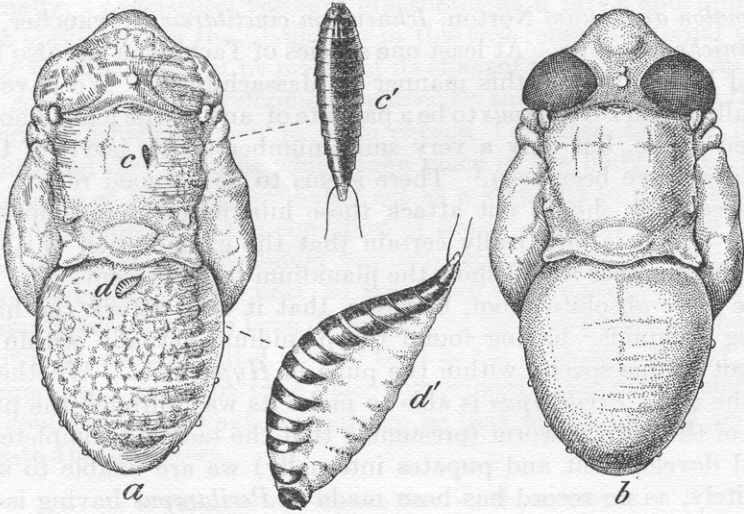


FIG. 26.—*a*, Pupa of *Varicheta aldrichi* parasitized by *Perilampus hyalinus*; *b*, unparasitized pupa of *Varicheta aldrichi*; *c*, planidium of *Perilampus hyalinus* before feeding; *c'*, same, more enlarged; *d*, planidium of *Perilampus hyalinus* after feeding; *d'*, same, more enlarged. (Original.)

tained. The period probably varies greatly in accordance with the prevailing temperature. Usually, though not always, the larva crawls away a short distance before it resumes feeding.

After settling down the second time it is likely to remain stationary for the rest of the larval and the pupal life. The larva in the second stage is of a whitish color, with the tracheal system showing through the transparent skin. The body is ovate in shape, with the head bent underneath the anterior portion. The growth during this stage is little compared to that accomplished in the third, and after feeding a short time the second ecdysis takes place.

Growth now becomes quite rapid and the larva assumes a very different appearance. (See fig. 27.) The mandibles have not increased in size to any great extent, but the mouth as a whole and the head

change quite materially. The mouth parts are in this stage situated in a triangular basinlike depression which is bounded on two sides and parts of the third by a strong chitinous carina or rim. Besides the mandibles there are two bulblike appendages just beneath, which are probably homologous to the maxillæ of the adult. Immediately above the oral opening are situated two large rounded elevations which may be called larval antennæ. The segments forming the head are now separated by a more or less distinct neck from the remaining segments and are bent beneath them with face downward, as in the second stage. The first two thoracic segments are each provided laterally with a raised tubercle at about the middle of the segment, viewed from the side, and just above this tubercle is another more or less distinct one, one also occurring on the third thoracic segment in a corresponding location. The next three segments each bear a pair of much larger tubercles or projections which give the larva a very unusual appearance. These tubercles, if they may be called such, correspond to those described and figured by Dr. Wheeler as occurring in *Orasema*, but are somewhat differently arranged. Just posterior to these there occurs an abrupt declivity, the segments becoming much smaller toward the posterior end of the larva. Beneath, the larva is smooth and free from constrictions, but the segmental sutures are visible to some extent. Dorsally through a transparent median line formed by a break in the corpus adiposum may be seen a large number of white urate masses, which pulsate slowly back and forth as the larva feeds. The tracheal system is rather conspicuous and is of the normal holoneustic type.

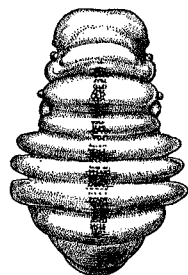


FIG. 27.—*Perilampus hyalinus*: Mature larva. Greatly enlarged. (Original.)

#### PUPATION.

(Figs. 28, 29.)

As soon as the larva is full fed, pupation takes place. The meconium is discharged, leaving the larva scarcely more than half its former bulk, and creamy white instead of translucent gray-white in color. Beneath the larval skin the imaginal appendages and the head gradually appear, and the tubercles so characteristic of the larva become less conspicuous. Finally the larval skin is discarded, and the pupa assumes its own distinctive shape.

The pupa is short and robust, corresponding very closely, of course, to the form of the adult. The abdomen bears five or six transverse carinæ or ridges, one for each segment, which are interrupted on the disk. These are very similar to those occurring on the ant parasite *Orasema viridis*, but differ in that they are not continuous dorsally

At first the pupa is white or yellowish white, but the eyes soon become pigmented with reddish, then the thorax becomes black, later changing to a metallic green. In about two days the head and abdomen assume the same metallic hue as the thorax, with the sculpture of the adult insect showing through, and soon after this the pupal skin is shed and the adult insect issues.

#### FOOD HABITS OF THE ADULT.

No observations upon the food habits of the adult *Perilampus* have been made in connection with this work, excepting that in confinement they will consume, in common with many other chalcidoid parasites, comparatively large quantities of sweetened water upon banana peelings. During June, 1905, the author found specimens of this genus in abundance upon the leaves of *Ambrosia*, *Helianthus*,



FIG. 28.—*Perilampus hyalinus*: Fresh pupa. Greatly enlarged. (Original.)

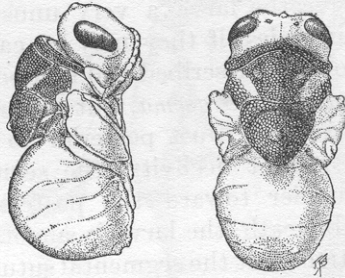


FIG. 29.—*Perilampus hyalinus*: Pupa just previous to eclosion. Greatly enlarged. (Original.)

and other vegetation at West Point, Nebr., where they were apparently feeding upon the honeydew secreted by aphides.

Dr. S. Graenicher, of the Public Museum of Milwaukee, has in the course of his extensive studies upon the pollination of Wisconsin flowers<sup>1</sup> recorded two species of *Perilampus*, *hyalinus* Say and *cyaneus* Brullé, as visitors of the following Compositæ: *Eupatorium perfoliatum*, *Solidago juncea*, *S. canadensis*, *Achillea millefolium*, *Tanacetum vulgare*, and *Erigeron canadensis*. In considering the insect visitors to the last named flower he has the following to say:

It is noteworthy that the chalcid-flies *Perilampus cyaneus* and *P. hyalinus* seem to have a certain preference for these flowers. They were regular attendants, day after day, at Cedar Lake, and were also present at Milwaukee.

Dr. Graenicher in a recent letter kindly informs me that he has also taken *P. cyaneus* at flowers of *Angelica atropurpurea*, *Pastinaca sativa*, and *Sium cicutæfolium*.

<sup>1</sup> Bulletin of the Wisconsin Natural History Society, vol. 7, Nos. 1 and 2, pp. 19-77, April, 1909.



## LONGEVITY AND OÖGENESIS.

While the *Perilampus* adults as a usual thing are very short-lived in the laboratory, there is no doubt that they live for a considerable period when out of doors under natural conditions. This is indicated by the fact that the females, when newly emerged, never contain eggs within the ovarian tubes, as do those insects which oviposit at once upon emerging.

In one instance a female was kept alive from April 6 to May 12, a period of 36 days, at the end of which time she was apparently ready to oviposit. Upon dissection approximately 250 eggs, nearly all of which seemed to be ready for deposition, were found. It is probable that many more would have developed had the individual remained alive under natural conditions.

## LENGTH OF LIFE CYCLE AND INFLUENCE OF TEMPERATURE.

The time required for *Perilampus* to develop from egg to adult is dependent upon several factors, one of the most important of which is the host. When parasitic upon *Varichæta*, the planidium begins to feed early in the spring. On *Limnerium validum*, however, the planidium must wait until its host begins pupation before it can become external, thus throwing it several days or even weeks behind the individuals infesting *Varichæta*.

There are no complete data at hand concerning the development upon *Limnerium*, owing to the failure of any individual to complete its transformations upon this host after removal from the cocoon. Its progress has been followed beyond the first ecdysis several times in the laboratory. In an apparently typical instance a larva of *Limnerium* containing two planidia was brought into the laboratory from out of doors on January 28 and placed in an incubator kept at a temperature of 78° F. On the morning of February 4 histolysis had begun, and during the evening of February 5 both planidia had made their exit. Two days later the host larva was apparently dead and the planidia were feeding. February 11 one had molted its first-stage skin, but died a short time later.

With *Varichæta* as a host it is a much simpler matter to carry the *Perilampus* through to maturity. When a single individual is watched through its development more time is required than in undisturbed puparia, owing to the fact that it is impossible to keep the host pupa from deteriorating somewhat. A typical instance of the development upon *Varichæta* under laboratory conditions follows: On January 28 a pupa of *Varichæta* with a single planidium was brought in from out of doors and placed in the incubator. On the next day the planidium had started to feed and filled up rapidly. February 1 the distance between the dorsal plates of the planidium



was rather greater than the width of the plates themselves. Three days later the first ecdysis was completed and the second-stage larva had moved some distance away from its original feeding place. The next day it had become very much distended and glistening. On February 7 it had apparently molted a second time and was very strongly tuberculate. On the 9th it was again feeding freely. Five days later it had reached full growth and ceased feeding. The next day pupation had taken place, but the pupa was still pale in color and covered with little "perspirationlike" globules. On the 19th the thorax of the pupa had begun to turn dark and the sculpture of the adult to show, and three days later it had become entirely dark colored. On February 25 the adult *Perilampus* emerged. The time required for development from start of external feeding to maturity was 28 days. The incubator was kept at a constant temperature of 78° F.

In the unopened puparia brought in at the same time *Perilampus* required about 25 days from the time they were placed in the incubator until they emerged as adults, but the period of development is dependent somewhat upon how much time they have been left out of doors, and there is some variation among the individuals themselves. From puparia brought in and placed in the incubator November 22 to 28 *Perilampus* began emerging December 27, about a month later, and continued coming out intermittently until approximately February 13, covering a period of about 48 days. Puparia brought in December 13 to 19 produced *Perilampus* first on January 17 and continued producing until February 6, a period of about 20 days. Puparia brought in January 17 to 23 produced adult *Perilampus* first on February 14 and continued until March 3, a period of about 17 days. From the above data it is seen that the later in the winter the puparia are brought in and placed under conditions favorable for the development of *Perilampus*, the shorter is the period during which the adults emerge. It is also evident that when infested puparia are brought in early in the winter a longer period of time elapses until the first adult *Perilampus* emerges than when left for a more extended period out of doors. Whether bringing the planidium in later in the winter causes it to develop more rapidly or whether it simply does not require so much time before becoming ready to begin feeding under these conditions is not known, but the latter explanation seems more reasonable.

The relative time of emergence of the adult *Perilampus* and adults of the host insect of the same lot is of considerable interest and will be given more study later. In September, 1908, a lot of *Varichæta* were placed in cold storage and kept there until January 18, when they were brought into the laboratory. From these puparia *Vari-*

*chæta* adults issued from February 2 to February 14. *Perilampus* adults issued from the same lot April 1 to April 6, approximately two months later.

In this instance the puparia were not kept at an even temperature. During the night, especially, it was frequently cool. Another lot of puparia collected at about the same time but *not* placed in cold storage or exposed to frost produced *Perilampus* adults November 30 to January 30 and adult tachinids January 22. Under these conditions the first *Perilampus* issued a month *earlier* than its host, as opposed to two months *later* when kept in cold storage until about the middle of January. It is apparent from the above that *Perilampus* adapts itself to changed conditions much more readily than does *Varichæta*. Indeed it is a necessity that it should be able to do *this*, being a parasite of other parasites which normally complete their development during either spring, summer, or fall, as the case may be.

#### EFFECT OF PARASITISM UPON HOST.

(Fig. 26.)

The *Perilampus* planidium, even before it begins to feed, exerts a very marked effect upon its host, especially in case the host is a tachinid. As mentioned on a preceding page, these planidia while living internally within the host larva do not seem to cause it the slightest inconvenience, and it is impossible to distinguish between a parasitized and an unparasitized larva before the planidium emerges, excepting, of course, where the secondary parasite itself is visible. Immediately pupation takes place in the host and the planidium becomes ectoparasitic, the effect of the parasitism becomes evident, especially after the host pupa has been subjected to warmth. Instead of responding to the increased temperature in the usual way—that is, instead of developing pigment in the imaginal eyes and bristles upon the body—it takes on a peculiar transparent appearance, principally in the cephalic and thoracic regions. The eyes and appendages develop very slightly and the imaginal head reaches scarcely one-half the size of that attained in the unparasitized pupa. These pupæ now present a very characteristic appearance (see fig. 26), and in opening a series of puparia one may recognize the parasitized individuals at a glance, even before *Perilampus* has begun to feed. This peculiar effect is noticeable to a considerably less extent where *Limmerium* acts as a host.

The pathological nature of this unusual condition of the parasitized pupæ has not been investigated as yet. It is apparently an arrested histogenesis, but in what manner this is brought about we can not say. Only a single case has come under observation where

the host pupa developed the characters of the adult to any extent. During March, 1909, a puparium of *Varichæta* was dissected and found to contain a very small pupa of *Perilampus*, only about three-fourths natural size but fully developed and apparently healthy in every way. The astonishing thing in this instance was the fact that the tachinid pupa had developed to a stage where it had taken on the characters of the adult. Even the bristles were well formed. This is the only case out of several hundred puparia examined where development had not ceased soon after the formation of the pupa and is rather difficult to explain. It is possible that for some reason the planidium did not respond to the usual stimulus, histolysis, and remained internal within the pupa, giving the tachinid an opportunity to develop considerably further than normally before the secondary parasite changed its mode of life to external feeding. There were many other puparia subject to the same conditions and they all responded in the usual way, so that the above case must be considered as abnormal.

The retardation of development in the parasitized hosts is of course brought about by the presence of the planidium, but whether indirectly or directly has not been ascertained. That it may be due to a glandular secretion is not impossible, but this hardly seems to be an adequate explanation, as nothing resembling glands of this kind have been found, although a careful study of the planidium has been made with the oil-emersion objective. In the opinion of many zoologists an insect during the process of pupation is in a very critical condition and is more susceptible to injury at this time than during any other period of its life. It does not seem improbable that in this supposition lies the explanation of the condition brought about in its host by *Perilampus*. The larva or maggot is able by reason of its great vigor to withstand the presence of the secondary parasite, but immediately histolysis and histogenesis begin to take place the weakened condition of the host makes itself apparent in the form of a cessation of development of pupal or imaginal organs and appendages and occasionally in certain instances death ensues. The development of *Limnerium* invariably ceases soon after the exit of *Perilampus*, although the latter does not emerge until the host larva has discharged its meconium and the formation of the pupa has begun. In one instance the planidium was observed located in the imaginal eye of its host, which becomes visible as a darker spot some time before the larval skin is discarded.

#### PERCENTAGE OF PARASITISM.

The percentage of parasitism of *Varichæta* and *Limnerium* by *Perilampus* in 1908 was not very high. Large numbers of the cocoons and puparia were opened, or reared through in the laboratory,

but accurate counts were kept in only a single instance, in which 35 out of a lot of 164 puparia, or 21.4 per cent, were found to be parasitized by *Perilampus*. This is known to be above the average, taking the material which was reared or studied as a whole.

The results of several counts given in Table I are indicative of parasitism in 1909.

TABLE I.—Percentage of parasitism of *Varichæta* by *Perilampus*, 1909.

Number of puparia.	Number attacked by <i>Perilampus</i> .	Per cent of parasitism.
29	16	55.0
244	58	23.3
57	28	49.1
100	54	54.0
100	23	23.0
Total.....530	179	
Average.....		41.0

The variation between the individual lots is due to their having been collected in different localities. Although it may be stated with assurance that the average was much higher than during the previous year, exact comparisons are impossible, since parasitism varies in different nests in the same locality, and in different localities. A long series of careful calculations would be required in order to secure accurate results.

As might be expected, the cocoons of *Limnerium validum* were parasitized to an approximately equal extent, and in these cocoons were found a few planidia of another species, which has been designated in the notes as "Species A." The summer-issuing *Limnerium* and *Apanteles* were not so heavily parasitized as a rule, probably because many of the planidia did not enter the caterpillars until a part of those afflicted by these parasites had died.

The percentage of healthy caterpillars of *Hyphantria* bearing the planidia, either internally or externally, ought to be, and apparently is, approximately the same as the percentage of *Varichæta* and *Limnerium* parasitized.

#### SUPERPARASITISM.

#### PERILAMPUS VERSUS PERILAMPUS.

The extent to which *Varichæta* or *Limnerium* is parasitized by *Perilampus* may be easily determined by opening the puparia or cocoons before the planidia have begun to develop, and in this manner the prevalence of superparasitism may be easily calculated. Upon several occasions as many as five planidia have been found upon one host, and four, three, and two are of frequent occurrence. In not a

single instance out of hundreds has more than one adult *Perilampus* issued from any cocoon or puparium under observation.

In a recent discussion of this phase of parasitism by Mr. W. F. Fiske<sup>1</sup> an attempt was made to classify its varied manifestations in accordance with the manner in which the parasites interested are ultimately affected. Superparasitism by *Perilampus* appears to fall in "I, b." of the scheme, i. e., one parasite lives and the other or others die, and the survivor brings about the destruction of the others by causing the premature death of the host. Several planidia may begin to feed at about the same time, but one invariably molts for the last time a little in advance of the others, and even though the difference is but a few hours it quickly devours the host, or else reduces it to such a condition as to render it unfit food for the next in succession. In no case has one larva been known to make a direct attack upon another.

In the article referred to above an attempt was made to indicate diagrammatically the probable amount of superparasitism accompanying a given amount of parasitism provided its prevalence was governed by chance alone. Whenever opportunity has permitted, the validity of the calculations which served as the basis for this diagram has been tested, and in nearly every instance, to date, the results have tended to confirm the contention at the time that "in the field \* \* \* superparasitism would be distinctly more prevalent in proportion to the percentage of total parasitism" than these calculations demanded. This has proved to be true of *Perilampus*, as will be seen by Table II, which gives the results of a series of counts to determine the point.

TABLE II.—Prevalence of superparasitism of *Perilampus* on *Varichæta*, 1909.

	Lot 1.	Lot 2.	Lot 3.
Puparia examined.....number..	100	100	57
<i>Perilampus</i> planidia found.....do...	28	87	47
Supernumerary planidia.....do...	5	33	19
Puparia parasitized.....do...	23	54	28
Parasitism.....percent..	23	54	49
Loss in efficiency through superparasitism:			
Actual.....do...	5	33	33
Theoretical <sup>1</sup> .....do...	3.3	28.8	26.6
Losses sustained by <i>Perilampus</i> through superparasitism:			
Actual.....do...	17.9	37.9	40.2
Theoretical <sup>1</sup> .....do...	11.8	33.1	32.4

<sup>1</sup> In accordance with calculations upon which the diagram published in the Journal of Economic Entomology (loc. cit.) was based.

It will be noted that in each instance the numerical loss sustained by *Perilampus*, and the decrease in its efficiency as a parasite, is greater than is theoretically called for.

## PERILAMPUS VERSUS DIBRACHYS.

Another exceedingly curious complication was observed in the winter of 1908-9 in an instance where a cocoon of *Limnerium validum* had been attacked by *Perilampus* and later by *Dibrachys boucheanus* Ratzeburg. The larvæ of the latter parasite fed externally and gregariously, and hibernated without transforming to pupæ. So soon as its original host was destroyed, the *Perilampus* planidium, not to be outwitted, calmly proceeded to take up a position internally in one of the *Dibrachys* larvæ. The particular larva bearing this planidium was killed and preserved, but in another instance a very small *Perilampus* adult issued from a puparium of *Varichæta* from which a number of *Dibrachys* adults had emerged some time before, and there is no doubt that it completed its transformations as a parasite on this host. With the exception of *Melittobia*, which from its very small size would likely prove unsuitable as an ultimate host, there is no known hymenopterous hyperparasite likely to attack the puparia of *Varichæta* or the cocoons of *Limnerium* which might not serve as well as *Dibrachys* as a host for *Perilampus*. The planidium is admirably fitted to triumph over adversity, and shows the part of wisdom in not causing the death of its host until it is ready to complete its transformations. If, for example, it had the habit of killing its host in the fall, and of hibernating as a full-fed larva, after the manner of *Dibrachys*, the latter might easily turn the tables and emerge victorious from the conflict.

## PERILAMPUS, "SPECIES A."

(Figs. 30, 31.)

In the course of the investigations upon the genus *Perilampus*, two kinds of planidia have been found parasitic upon *Limnerium validum*, which, while belonging to the same general type, are quite different in structural detail and apparently represent different species. One of these, the commoner one, is *Perilampus hyalinus*, which has been treated rather fully in the preceding pages. The other species we have never succeeded in rearing through to the adult, so are unable to give it a specific name at this time. In length it is rather shorter than *hyalinus*, measuring on the average about 0.24 mm., but is comparatively greater in diameter through the anterior segments. The color is usually somewhat darker than that of *hyalinus*. In *P. hyalinus* the head of the planidium is notched or emarginated and elevated posteriorly, but in this species the posterior margin is continuous. The mandibles are heavier and considerably less curved, and the recurved hooks on the top of the head are also considerably larger. The ambulatorial spines are very much less developed than

in *hyalinus* and the ends of the chitinous bands which surround the body are simple, not terminating in long teeth or serrate as in the other species. The dorsal and ventral bristles, however, are stronger and more numerous, and somewhat differently arranged.

Considerable difference in habit in these two species has also been noted. *P. hyalinus*, we have reared from many different hosts, but the other species has been found only upon the larva of *Limnerium validum*. Instead of remaining internal within the *Limnerium* larva until it attempts to pupate in the spring as does *P. hyalinus*,

this species, if it ever feeds endoparasitically, must emerge from its host soon after the cocoon is spun, for it is found externally upon its host during the fall and winter before the *Limnerium* has any intention of pupating, and has never been found internally. In only one instance have we succeeded in getting this species to feed, and even that did not terminate satisfactorily. During the spring of 1909 a specimen of the planidium of this species was placed on a larva of *Limnerium* in a glass cell for observation. Six days later the planidium had not fed and was noted as be-

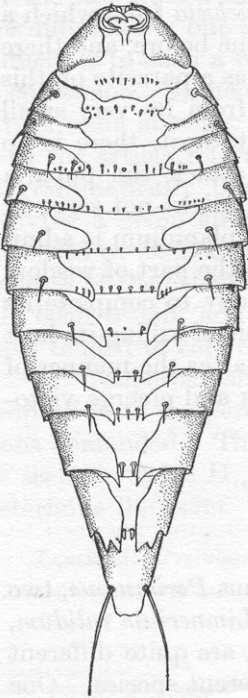


FIG. 30.—*Perilampus*, "species A." Planidium, ventral view. Magnified about 400 diameters. (Original.)

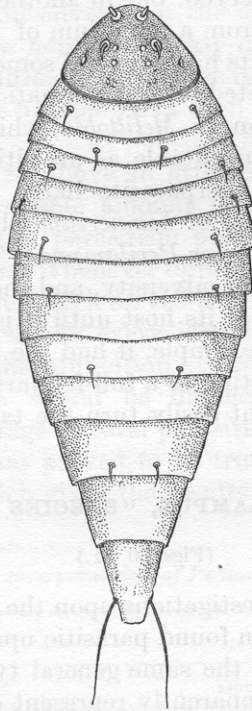


FIG. 31.—*Perilampus*, "species A." Planidium, dorsal view. Magnified about 400 diameters. (Original.)

ing apparently dead, but on the next day it was seen to have been feeding, although its host was still alive and active. Five days later the planidium had molted its skin and had taken on the globular form of the second-stage larva but was apparently not in very good condition and died two or three days later. At no other time were we able to get this species to feed. There is a possibility that it is of purely accidental occurrence upon *Limnerium*, and this may account for our inability to rear the adults. This belief is strengthened by the fact that a large percentage of the specimens of this planidium are

dead when found upon the *Limnerium* larvæ in the fall. Out of 11 specimens found during an examination of some 55 cocoons, 10 were dead and shrunken. These cocoons had been kept under perfectly natural conditions out of doors, so that it is obvious that there was something radically wrong between parasite and host. The fact that it has never been found upon *Varichæta* suggests the possibility of its being of ectoparasitic habits entirely, and that it attaches itself to the *Limnerium* larva after the latter emerges from the caterpillar, but prior to the spinning of its cocoon. This would of course preclude its being a parasite of a tachinid, as the formation of the puparium would naturally leave it outside of the hardened shell and death would inevitably result. The data on hand concerning this species, however, are too limited to warrant an attempt to draw any conclusions, and with the recording of the above facts we leave it until further investigations have thrown more light upon its habits.

#### DEVELOPMENT OF ORASEMA.

Dr. William Morton Wheeler, in the article referred to on page 35, gives an exceedingly interesting account of the life history and economy of the chalcidoid genus *Orasema*, of the family Eucharidæ. A comparison of the habits of representatives of the so-called families Eucharidæ and Perilampidæ is of unusual interest at this time and may assist in clearing up certain doubtful points in the economy of the former. *Orasema* is parasitic principally upon the harvesting ant *Pheidole instabilis* Emery, but also occurs not uncommonly upon representatives of other ant genera in the southwestern United States and Mexico. In view of the close relationship existing between the two genera and the general similarity of development so far as is known in the two forms, it would seem permissible at this time to draw certain conclusions in regard to *Orasema* which have been suggested by the investigations upon *Perilampus*. In regard to the oviposition of *Orasema* Dr. Wheeler has the following to say:

I have not seen the eggs of *O. viridis* after oviposition, but only the very young larvæ. Dissection of the female shows that, as we should expect in a parasite, the eggs are extremely numerous and minute. The mother insect, when she comes to oviposit, exercises a very careful selection among the ant brood. In the first place she has nothing to do with the *instabilis* larvæ, but directs her attention to the pupæ. In the second place she selects, as a rule, only the pupæ of the soldiers, males and females. The small worker pupæ would not furnish sufficient food for her larvæ. In the third place she selects only pupæ at the very critical moment when they have been stripped of their larval skin by the workers and are, therefore, little more than semipupæ, for obviously at this moment the cuticle is thinner and will be more easily pierced by the young *Orasema* larvæ than during the preceding or succeeding stages; and in the fourth place she does not lay her eggs at random anywhere on the body of the semipupæ, but carefully selects one of four regions near the head. Usually she places the egg on the sternal surface just beneath the very short, incurving legs of the



semipupa, but occasionally it is placed on the back of the neck between the head and the prothoracic segment or on the right or left side of the neck beneath the corresponding prothoracic leg. These regions would seem to be singularly appropriate, both because the cuticle is extremely thin and readily punctured by the parasitic larva at these points, and also because the egg or resulting larva, especially when it is covered with the overlapping appendages of the semipupa, is not so readily brushed or licked off by the *instabilis* workers.

If we may judge from the habits of *Perilampus*, the explanation of Dr. Wheeler's failure to find the eggs of *Orasema* in the ant nest is possibly that they are not deposited there. It is possible that oviposition might take place outside the nest, perhaps upon flowers or other vegetation visited by both the *Orasema* adults and the worker ants; and that from the eggs deposited upon these plants the planidia hatch, in some manner attach themselves to the worker ants, and are in that way conveyed to the nest, where they leave their carrier and attack the larvæ. Several points in the economy of *Orasema* as noted by Dr. Wheeler tend to substantiate the belief that oviposition takes place outside the nest. In the first place the large number of eggs deposited by *Orasema* (Dr. Wheeler found by dissection of the adults that they were very numerous and minute) indicates that somewhere in its early life cycle there is prevalent a very great mortality. That this mortality actually takes place was observed by Dr. Wheeler, and he thought that it might be explained in the following manner:

I believe that the danger of detaching the egg is very great, and this, together with the other special requirements enumerated above, may account for the fact that comparatively very few of the great number of *Orasema* eggs ever complete their development.

The number of eggs deposited by a single female *Orasema*, should they all become effective, would probably be sufficient to annihilate a whole colony of the *Pheidole*, and not one but many female *Orasema* are usually found in the infested nests. It would seem, therefore, that there would be little likelihood that such great mortality would occur if only the causes enumerated by Dr. Wheeler were operative. It is possible that the *Orasema* planidia attack the larvæ of *Pheidole*, not the pupæ, and that the seemingly sudden appearance of the young *Orasema* larvæ upon the pupæ of *Pheidole* immediately after the last larval ecdysis is similar to that which has been noted on a preceding page as occurring in *Perilampus*. In other words, the *Orasema* planidium may be endoparasitic within the *Pheidole* larvæ, making its exit to the exterior at the time of histolysis and feeding ectoparasitically thereafter. Dr. Wheeler's observation of the fact that the *Orasema* planidia appear upon the pupæ only at this critical time would tend to substantiate this theory.

It seems improbable that insects as highly positively phototropic as Dr. Wheeler has observed *Orasema* to be should return to the interior of an ant's nest to oviposit after having escaped and lived in the sunlight for a considerable time.

## PLANIDIUM OF ORASEMA VIRIDIS ASHMEAD.

Length about 0.16 mm. General shape like that of *Perilampus*, but comparatively broader and much more simple in structural detail. Color dark, as in *Perilampus*. Head more elongate than that of *P. hyalinus*, the recurved hooks, if present, very small; there are two pairs of organs in a location similar to that of the hooks upon the head of *Perilampus*, but their extremely minute size makes the nature of these objects difficult to define even under the oil-immersion objective. Mouth parts indefinable, considerably retracted into head. Anterior margin of head much roughened. First dorsal segment short, with a pair of distinct bristles situated along the apical margin, the base of each within a transparent spot. Second segment broader, with two apical spines farther apart than on preceding. Next segment much like second, but broader, with similar spines. Remaining segments apparently without dorsal spines. Ventral ends of the chitinous plates simple, not ending in a serrate margin or with long teeth as in *Perilampus*. Seventh segment with a pair of spines ventrally. Last segment with a pair of stylets comparatively shorter and stronger than in *Perilampus*.

Dr. Wheeler's account of the effect of parasitism by *Orasema* upon *Pheidole* tallies very well with our observations upon parasites attacked by *Perilampus*; the same microcephalic characters are present in the host pupæ in both cases, with the peculiar transparent appearance, as noted upon a previous page of this article.

Other points in the economy of *Orasema* brought up by Dr. Wheeler and which at the time seemed very puzzling are apparently rather easy of explanation in the light of our present knowledge of *Perilampus*. It is hardly within the province of this bulletin, however, to take these up in detail, and it is merely suggested here that anyone desirous of doing further work upon the development of *Orasema*, and perhaps other members of the chalcidoid family Eucharidæ, would perhaps do well to bear in mind the similarity of the life cycle, so far as known, to that of *Perilampus*.<sup>1</sup>

## RELATIONSHIP OF EUCHARIDÆ AND PERILAMPIDÆ.

The great similarity of development in the genera *Orasema* and *Perilampus* can not fail to have considerable bearing upon the taxonomic relationship of the so-called families Eucharidæ and Perilampidæ. Francis Walker, in 1846, placed the two groups together under the family name Eucharidæ. Ten years later, however, the German hymenopterist, Arnold Förster, decided that the differences

<sup>1</sup> During the winter of 1909-10 an extraordinary planidium was found on the hibernating larva of the larch sawfly (*Nematus erichsonii* Hartig), within the cocoon. This parasite was not reared, but was *Perilampus* in all probability.

were sufficient to justify him in splitting the group into two distinct families. In this move he was later supported by Dr. William H. Ashmead. It is of course impossible to come to any definite conclusions in a case of this kind until more has been learned concerning the larval development in the other genera of the two groups, and also in the related families. If it is found that this type of development is characteristic of these two groups and no others, it should certainly be an argument of considerable weight in support of Walker's views.

#### RHIPIPHORUS AND OTHER COLEOPTEROUS PARASITES.

Anyone at all familiar with the life histories of certain of the parasitic Coleoptera, *Meloë*, *Sitaris*, and more especially the hornet parasite *Rhipiphorus*, will be reminded of these genera by a perusal of the preceding pages. The similarity in development, life cycle, and habits even to certain minute details is so striking that one in reading the excellent description of the life history of *Rhipiphorus paradoxus* given by Dr. T. A. Chapman<sup>1</sup> could scarcely tell whether it belonged to that insect or to *Perilampus* were the names omitted. A brief comparison of the two may be of interest.

So far as we know, the place of oviposition of *Rhipiphorus paradoxus* has not been observed, but other members of the family, notably *Myodites*, oviposit commonly upon flowers of various kinds. From the eggs hatch the triungulins which are not only analogous to the planidium of *Perilampus* and *Orasema* but, except for the legs and antennæ, are strikingly similar in anatomical details. The dark chitinous rings which encircle the triungulin for protective purposes during its adventurous search for its host, the backward-pointing spines with which these are provided, the pair of stylets on the last segment and the "comma"-shaped mandibles retracted into the buccal cavity all forcibly remind one of the planidium of *Perilampus*. The writer is aware that the resemblance is mainly a superficial one, but it is very unusual, superficial though it be. The similarity does not end here, however, but is carried out even to the details of the life cycle. It is more comparable to *Orasema* than to *Perilampus* inasmuch as the *Perilampus* is a secondary while the others are primary parasites. The *Rhipiphorus* triungulin, after gaining entrance to the nest of its host, conducts itself almost exactly as we have reason to suspect *Orasema* does; that is, it enters the young host larva, emerges at the time the host larva attempts to pupate, and feeds ectoparasitically thereafter. It differs, however, in the fact that the *Rhipiphorus* triungulin feeds and grows to 8 or 10 times its original length while *within* the host larva, while *Orasema* and *Perilampus* apparently do

<sup>1</sup> Annals and Magazine of Natural History, 4th series, vol. 6, pp. 314-326, 1870.

not grow at all until they emerge and begin feeding outside. This resemblance is not altogether lost in the later stages. Even the large dorsal tubercles or projections of *Orasema* and *Perilampus* are reproduced in the third-stage larva of *Rhipiphorus*. There is a slight difference in the method of pupation, the *Rhipiphorus* larva leaving the host to pupate while *Orasema*, when not interfered with by the worker ants, and *Perilampus*, transform *in situ*.

We have then in *Perilampus* and *Orasema* an instance of hypermetamorphism as defined by Packard, belonging to the same type as that occurring in the Rhipiphoridae. The planidium exists as such because of the wandering and perilous life it is obliged to lead in its search for a host, but soon after that host is found, the protection of the chitinous plates or the use of the ambulatorial spines no longer being necessary, these accessory structures are discarded. As the parasite now has easy access to an abundance of rich nutritious food without the necessity of putting forth the slightest effort it becomes a mere grub—a perfect adaptation to the new mode of life.

#### HOST RELATIONS OF THE GENUS PERILAMPUS.

##### REARING RECORDS OF PERILAMPUS HYALINUS AT THE LABORATORY.

We have found the native species *Perilampus hyalinus* to attack the primary parasites of two species of Arctiidae, *Hyphantria textor* Harris and *Euchætias egle* Drury; a single notodontid, *Melalopha inclusa* Hübner; and a saturniid, *Samia cecropia* L.

The species *hyalinus* has shown an adaptability in the matter of food habits which is quite unusual in an insect with such a complicated life history. We have absolute records of this species from 10 different primary parasites belonging to 2 different orders and 6 or 7 different genera. A diversity of host relations as exhibited by *hyalinus* would not be considered at all remarkable in species of a great many chalcidoid genera, but when we consider the circumscribed method by which access to the host is gained, it seems, on first thought, to show a quite unusual versatility. When we come to analyze the habits of the parasite more closely, however, it is at once seen that the versatility is only apparent. The diversity of host relations is due more to a lack of discrimination than to any especial adaptability. Precisely the same efforts are put forth by the planidium on the occasion of its attack upon any and all of its hosts. The conditions under which it develops are somewhat variable, but even here the actual stimulus which causes the change from endoparasitism to ectoparasitism is the same, namely, that of histolysis in the host larva.

We have reared *P. hyalinus* from the following hosts:

PARASITES OF *HYPHANTRIA TEXTOR* HARRIS.

Tachinidæ:

- Varichæta aldrichi* Townsend.  
*Compsilura concinnata* Meigen.

Ichneumonidæ:

- Limnerium validum* Cresson.  
*Limnerium fugitivum* Say.  
*Limnerium pallipes* Provancher.

Braconidæ:

- Apanteles hyphantriæ* Riley.  
*Meteorus communis* Cresson.

Pteromalidæ:

- Dibrachys boucheanus* Ratzeburg (on *Varichæta*).

PARASITE OF *EUCHÆTIAS EGLE* DRURY.

Tachinidæ:

- Genus and species undetermined.

Braconidæ:

- Apanteles* sp.

PARASITE OF *MELALOPHA INCLUSA* HÜBNER.

Ichneumonidæ:

- Limnerium validum* Cresson.

PARASITE OF *SAMIA CECROPIA* LINNÆUS.

Tachinidæ:

- Frontina frenchii* Williston.

OTHER AMERICAN REARING RECORDS OF *PERILAMPUS*.

Through the courtesy of Dr. L. O. Howard the rearing records have been obtained from the collection and biological notes of the Bureau of Entomology. The species of *Perilampus* have not been determined. The hosts are all lepidopterous and are as follows:

- Dasyphyga alternosquamella* Ragonot.  
*Acrobasis caryæ* Grote.  
*Eucosma scudderiana* Clemens.  
*Eucosma desertana* Zeller.  
*Phlyctænia extricalis* Guenée.  
*Apatela haustulifera* Smith and Abbot.  
*Harrisina americana* Guerin-Méneville.  
*Retinia* sp. (?)

Prof. C. V. Riley records<sup>1</sup> *Perilampus platygaster* Say as a parasite of *Harrisina americana* in the State of Missouri.

A species of *Perilampus* was reared, according to the labels in the United States National Museum, by Mr. D. W. Coquillett from the cocoon of a *Chrysopa* at Los Angeles, Cal. Dr. Ashmead also reared

<sup>1</sup> Second Report on the Noxious and Beneficial Insects of Missouri, p. 87, 1870.

a species from *Chrysopa* at Utica, Miss., this record being the one referred to in his Monograph of the Chalcidoidea.

In a paper entitled "A list of the parasites known to attack North American Rhynchophora,"<sup>1</sup> Mr. W. D. Pierce records *Perilampus* as a parasite of the cotton boll weevil (*Anthonomus grandis* Boheman) in cotton squares in Louisiana. Mr. Pierce in a recent letter regarding this record states that it is open to question. A cotton square from which a weevil had emerged forms an excellent retreat for another insect that might be inclined to secrete itself in this manner. It may be that in this case a *Chrysopa* larva parasitized by *Perilampus* crawled into the square to pupate and from this the *Perilampus* emerged later. That *Chrysopa* is prone to do just this thing is a well-known fact. Dr. Howard described the chalcidoid parasite *Isodromus iceryæ* as a parasite of the scale *Icerya*. He later found that *Isodromus* was instead a parasite of *Chrysopa*, which in this instance had crawled beneath the *Icerya* scale, through which the *Isodromus* later emerged.

In 1897 Mr. W. F. Fiske reared a single specimen of *Perilampus hyalinus* from the cocoon of *Limnerium fugitivum* Say as a parasite of *Hyphantria*. This fact was recorded in his paper on the parasites of the American tent caterpillar,<sup>2</sup> and probably constitutes the first published record of *Perilampus* as a secondary parasite on Hymenoptera.

Quaintance and Brues in their study of the cotton bollworm<sup>3</sup> found this species to be a rather uncommon parasite of *Microplitis nigripennis* Ashmead, a braconid parasite of *Heliothis obsoleta* Fabricius in Arkansas and Texas.

Dr. L. O. Howard, in a paper entitled "The biology of the hymenopterous insects of the family Chalcididæ,"<sup>4</sup> makes the statement that *Perilampus* has been reared from Tachinidæ, but none of the details of the rearing was given. Dr. Howard, in a recent letter in regard to this, says that he is unable to find any record upon which this statement was based, but that he is of the opinion that it was reared from tachinid puparia in the office of the Entomologist at Washington prior to 1892. This is the first published record, so far as we are aware, of *Perilampus* as a parasite of Diptera.

Prof. M. H. Swenk<sup>5</sup> records having reared *Perilampus hyalinus* from a sarcophagid which in turn was reared from *Melanoplus bivittatus* Say.

<sup>1</sup> Journal of Economic Entomology, vol. 1, p. 383, 1908.

<sup>2</sup> New Hampshire College Agricultural Experiment Station, Technical Bulletin 6, p. 206, 1903.

<sup>3</sup> Bulletin 50, Bureau of Entomology, U. S. Department of Agriculture, p. 122, 1905.

<sup>4</sup> Proceedings of the U. S. National Museum, vol. 14, p. 574, 1892.

<sup>5</sup> Journal of Economic Entomology, vol. 4, p. 286, 1911.

EUROPEAN REARING RECORDS OF PERILAMPUS.<sup>1</sup>*Perilampus angustatus* Nees.

This species was reared by Rondani<sup>2</sup> from the wood-boring larva of *Anobium molle*. Gaulle<sup>3</sup> records *angustatus* as a parasite of *Dryophilus pusillus*.

*Perilampus auratus* Panzer.

According to Gaulle,<sup>3</sup> this species has been reared from the crabronid wasps *Solenius rubicola* and *S. vagus* by Lichtenstein.

*Perilampus levifrons* Dalman.

Rondani<sup>2</sup> has reared *levifrons* from the larvæ of the tortricid *Coccyx buoliana* and also from the codling moth (*Carpocapsa pomonella* L.). Gaulle<sup>3</sup> gives an additional host in *Exocentris punctipennis*. Dour<sup>4</sup> mentions the first two records, crediting the first to Gouraud.

*Perilampus micans* Dalman.

This parasite was reared by Rondani<sup>2</sup> from the larvæ of *Lyctus canaliculatus* and *Hister picipes*.

*Perilampus ruficornis* Fabricius.

Gaulle<sup>3</sup> records this insect as a parasite of *Hylophila bicolorana*. Rondani<sup>2</sup> has reared it from the lepidopterous *Halias quercena*. Dalle Torre regards *violaceus* Fabricius as a synonym of this species.

Ratzeburg<sup>5</sup> refers to a *Perilampus* which he calls *violaceus* as follows:<sup>6</sup>

Herr Reissig was so fortunate as to rear a female of this species. The host was not determined definitely, but it was without doubt a forest insect. On an oak leaf he found the dried remains of a tortricid larva. The parasitic larva had come out of this and had hung itself by a spun thread. The cocoon has the compact form of those of *Campoplex*, is two lines long, transparent (but nevertheless of close texture), dark brown, with a somewhat lighter band. The large opening through which the *Perilampus* had gnawed its way is at one end and appears as an irregularly torn circle.

There seems to be little doubt that Ratzeburg was incorrect in his surmise that this species was primary upon the tortricid. *Perilampus* of course does not spin a cocoon, or even a thread. The cocoon which he describes was almost certainly that of *Campoplex*, which he says it resembles, and with which his description agrees.

<sup>1</sup> The author is indebted to Dr. L. O. Howard for examining literature which was inaccessible.

<sup>2</sup> *Bulletino della Società Entomologica Italiana*, vol. 4, pp. 57-58, 1872; vol. 8, pp. 241-242, 1876.

<sup>3</sup> *Catalogue systématique et biologiques des Hyménoptères de France*, in *La Feuille des Jeunes Naturalistes*.

<sup>4</sup> *Catalogue synonymique des Hyménoptères de France*, in *Mémoires de Société Linnéenne du Nord de la France*.

<sup>5</sup> *Ichneumonon der Forstinsekten*, vol. 3, p. 221.

<sup>6</sup> Translation by the author.

This *Campoplex* was probably parasitic on the tortricid, and the *Perilampus* destroyed it as a secondary parasite.

There is almost certainly more than one species under the name *ruficornis*, as the records indicate that it has been reared from moths as a primary parasite, and from an ichneumonid as a secondary. That this would occur in a single species seems hardly probable in view of its highly specialized life cycle.

*Perilampus italicus* Fabricius.

Recorded by Gaulle<sup>1</sup> as a parasite of the sawfly *Athalia colibri*.

Of course there is always the possibility that the specimens recorded from Lepidoptera really came from tachinids or ichneumonids which transform within their host. It is difficult to understand how the *Perilampus* larva, being an external feeder for the greater part of its life, could feed and develop externally upon the pupa of an ectophagous lepidopteron, taking for granted that the mode of development is similar in all the species of the genus. It might, however, be able to do so upon a lepidopterous host which feeds within stems or galls, the *Perilampus* in this case being protected from injury.

EUROPEAN SPECIES OF PERILAMPUS REARED AT THE LABORATORY.

*Perilampus cuprinus* Förster.

In 1906 several individuals of *Perilampus cuprinus* were reared by Mr. Titus from puparia of imported tachinids parasitic upon the gipsy moth and brown-tail moth. Occasionally a few more were secured under similar circumstances, but never in numbers sufficient to indicate that the species was of any particular importance as a secondary parasite. Neither were there any records which indicated that any species of the genus was of more than incidental interest in connection with lepidopterous hosts.

The tachinids acting as hosts were not identified in every instance, but among those species attacking the gipsy moth are *Blepharipa scutellata* Robineau Desvoidy, *Compsilura concinnata* Meigen, and *Tricholyga grandis* Zetterstedt, and among the brown-tail moth parasites are *Pales pavidæ* Rondani and *Parexorista chelonixæ* Rondani. It is practically certain that all of the tachinids and probably some of the ichneumonids and braconids preying upon this host are liable to attack by *Perilampus*. It is also possible, but not proven, that it is at times an enemy of sarcophagids which usually and probably always attack pupæ which have died from other causes.

In no instance has the planidium of this species been seen but there is hardly a doubt that this stage exists and that in its essential

<sup>1</sup> Catalogue systematique et biologique des Hyménoptères de France, in La Feuilles des Jeunes Naturalistes.



characteristics it resembles the planidium of *P. hyalinus* and others described in the preceding pages. It is also probable that the later larval development is analogous to that of *P. hyalinus* and that the beginning of development of the pupa is the signal which stirs the planidium into activity.

*Varichæta*, as has been shown, hibernates as a pupa which has not begun to show the color or characteristics of the adult, and the *Perilampus* planidium remains dormant throughout the winter and feeds in the spring. Among the European tachinids known to act the part of host to *P. cuprinus*, *Compsilura*, *Tricholyga*, and *Pales* issue in the summer, much as do the summer-issuing hymenopterous parasites of the fall webworm, and *P. cuprinus* completes its transformations and hibernates as an adult without leaving the puparium. *Blepharipa*, unlike *Varichæta*, develops imaginal characters in the fall and is, so far as external evidences indicate, ready to emerge before winter. *Perilampus* as a parasite of *Blepharipa* acts exactly as it would had its host actually emerged in the fall, and hibernates as an adult within the puparium. *Parexorista* hibernates like *Varichæta*, and if the parallel between *P. hyalinus* and *P. cuprinus* is as close as is believed, the planidium hibernates as such and becomes active when its host begins to develop in the spring.

#### *Perilampus inimicus* Crawford.

A relatively small number of this species, recently described in Part II of this bulletin, was reared in 1908 from the cocoons of *Apanteles fulvipes* var. *japonica* Ashm., imported that year from Japan as a parasite of the gipsy moth. It has not been reared as a parasite of Japanese tachinids, but it may well be that it resembles *P. cuprinus* in habits, and that it will be reared when larger importations of tachinids from Japan have been made.

The specimens reared issued in the late summer, coincidentally with the emergence of the other more common chalcidoid parasites of the same host.

#### *Perilampus* sp.

Another species of *Perilampus*, as yet undetermined, has been reared from the cocoons of a European *Apanteles* parasitic upon the young brown-tail moth caterpillars. The circumstances are interesting and suggestive but the incident will be discussed more at length in another connection.

#### RÉSUMÉ OF HOST RELATIONS OF THE GENUS.

Species of the genus *Perilampus* have been reared<sup>1</sup> from insects belonging to five different orders, Hymenoptera, Diptera, Lepi-

<sup>1</sup> This is according to the published records, although some of them are almost certainly incorrect.

doptera, Coleoptera, and Neuroptera, in Europe, Japan, and America. Table III shows the number of each group from which *Perilampus* has been reared in those regions where the gipsy moth is found:

TABLE III.—*Classification and distribution of the known hosts of the genus Perilampus.*

	America.	Europe.	Japan.	Total.
Hymenoptera parasitica.....	8	2	1	11
Hymenoptera phytophaga.....		1		1
Hymenoptera aculeata.....		2		2
Diptera (Tachinidæ).....	4	5		9
Lepidoptera.....	8	5		13
Coleoptera.....	1 (?)	4		5
Neuroptera.....	1			1
Total.....	22	19	1	42

### THE ECONOMIC ASPECTS.

In 1906 Mr. E. S. G. Titus, at that time in charge of the Gipsy Moth Parasite Laboratory, reared a few cocoons of *Apanteles vime-netorum* Wesmæl<sup>1</sup> from caterpillars of the brown-tail moth which had been imported in the hibernating nests. From them there emerged a very few specimens of a species of *Mesochorus*, different from any known American secondary upon *Apanteles* and apparently but not certainly European. The circumstances under which the *Apanteles* were reared were not such as absolutely to protect them from the attack of the native hyperparasites, but there was good reason to believe that the *Mesochorus*, as well as the *Apanteles*, had attacked the very small caterpillars of the brown-tail moth in Europe the fall before. This was the first instance encountered in the course of the work of parasite introduction in which a secondary parasite was known or suspected to attack a primary parasite before the death of the primary host.

In 1907 this record was confirmed, and it was demonstrated beyond possibility of error that there were some secondary parasites which had this habit. The fact was of the greatest significance, since it was one of the fixed policies of the laboratory to introduce the primary parasites of the gipsy and brown-tail moths and to exclude the secondary. It had been supposed that this could be accomplished by importing the living caterpillars and pupæ of the gipsy and brown-tail moths and rearing the parasites. The fact that the primaries might be attacked before the death of their host altered the situation materially and made the strictest supervision of imported material necessary in order to meet the ideal which had been set.

That the relative importance of hyperparasitism has diminished rather than increased as a result of a better understanding of the

<sup>1</sup> As determined by Schmiedeknecht.

subject affects the matter scarcely at all. We know now that the primary parasites of the gipsy and brown-tail moths, if they become established, will be subjected to the attack of native hyperparasites to a varying degree in accordance with the closeness of their resemblance in natural affinities and habits to American species, but there are among them a few which are so different from any American species as to make it probable that they will largely escape undue parasitism in America, much as the gipsy and brown-tail moths have themselves escaped. This does not lessen the force of the original contention at all materially. It has simply served to separate the secondary parasites into bad, worse, and worst, and has left them as a group with about the same degree of odium attached as before.

The separation of the several secondary parasites into groups in accordance with their capabilities for evil has not always been easy. As with the primary parasites, the importance of which can not be inferred from the numbers which chance to be reared from the imported material, the secondary parasites, which are the least frequently encountered, may easily be the most to be feared.

*Perilampus* has never been abundant as a parasite of tachinids in any of the imported material. So far as is directly indicated by our notes and breeding records there is nothing in its life or habits which would separate it from the minor and inconsequential secondary parasites, of which there are many species.

These opinions, formerly held, have been changed as a result of the investigations into the life and habits of the native *Perilampus hyalinus*. It was not known or suspected, in spite of the considerable study which the fall webworm has received at various times and by various entomologists, that this secondary was of any more interest or importance than any other, but it is now evident that species of this genus may become of the greatest importance as hyperparasites. It is further indicated as a direct result of these studies that the different species of *Perilampus* are likely to concentrate their attack upon the parasites of some particular primary host instead of scattering their attack upon all of the very numerous species of hymenopterous and dipterous parasites suitable in other respects. Thus *Perilampus hyalinus* appears to be particularly a parasite of the parasites of the fall webworm. It is possible that it will never attack the parasites of the gipsy moth or the brown-tail moth. *Perilampus cuprinus*, for all that is positively known to the contrary, may similarly concentrate its attack upon the parasites of the gipsy moth and the brown-tail moth and might become a factor of as much importance in the natural control of these insects as *Perilampus hyalinus* undoubtedly is in the control of *Varichæta*.

It is not probable, but it is conceivable, that the establishment of *P. cuprinus* in America might make all the difference between success and failure of the whole work of parasite introduction, in so far as the gipsy moth is concerned, because, in the first place, *Blepharipa scutellata* is one of the most important parasites of the gipsy moth and the success or failure attending the attempts to introduce it into America might easily tip the scale one way or the other, and *Perilampus*, so far as known, is the most important parasite of *Blepharipa* and might in a similar manner determine whether or not its host reached the necessary state of efficiency.

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