NOTES ON THE LIFE HISTORY OF PROSPALTELLA PERNICIOSI TOWER¹

By DANIEL G. TOWER, M. Sc., Amherst, Massachusetts

INTRODUCTION

The following notes were taken during the early spring, fall and winter of 1913, and the spring of 1914.

This parasite, a description of which, both male and female, was published in the Ann. Ent. Soc. Am., vol. VI, No. I, pp. 125-126, is a true internal parasite, the larval forms living within the body tissues of its host, the female San José scale, *Aspidiotus perniciosus* Comst., except during the last part of the second larval stage as at this time the entire contents of the host are consumed by the larva, which, after passing its waste, pupates in the empty skin of the scale.

Both male and female parasites emerge from the empty skins of second-stage and early third-stage female scales, but by far the largest number emerge from second-stage scales.

The following description of the life cycle of the parasite, which has been worked out, is that of a parasite maturing in and emerging from a second stage scale. No doubt the development of those which emerge from third stage scales is the same.

THE EGG

Developed eggs are readily seen within the abdomen of the female parasite when examined under the microscope at the time of emergence, and many are even fully developed in the late pupal stage. They can also be examined as found in the bodies of first-stage and early second-stage scales.

The egg is ovate and has a distinct micropyle at the smaller end. The chorion is smooth and hyaline and the nucleus, located at the larger end, and the opaque granules, with which the egg is filled, show through.

The egg measures .085 mm. in length and .04 mm. in width.

The number of eggs deposited by an individual is not known, but 1,364 developed eggs were obtained from twenty females selected as they emerged, giving an average of sixty-eight developed eggs apiece. Of the twenty females examined, the smallest and largest number of eggs found in a single specimen was forty-six and 102, respectively, and in most of these females there were still undeveloped eggs.

¹ Contribution from the Entomological Laboratory, Massachusetts Agricultural College.

DEVELOPMENT OF THE EGG

The egg is usually found lying about medially in the scale and slightly nearer the pygidium end of the scale than the head end, although it may be found almost anywhere in the body. Here the egg swells in embryonic development to two to three times its size when laid and the young larva may be seen forming within it. The larva is practically fully developed before hatching and lies curled within the egg. On hatching it straightens itself out in the egg and the chorion, which has become very thin, is ruptured, allowing the larva to escape into the body of its host.

FIRST LARVAL STAGE

The larva, when hatched, is large compared with its host. Its mouth-parts, which were fully formed while in the egg, now become fully chitinized and the mandibles, which are the most prominent parts, are very sharp, strongly chitinized and decidedly hook-like.

The tracheal system, which lies close to the body surface and which was only partially filled with air when the larva was in the egg, now becomes filled and the two longitudinal main trunks, which lie on either side of the body meeting anteriorly and posteriorly, forming an oval, each show ten short stub-like branches.

Apparently there are thirteen body segments, the thirteenth or posterior segment lying partly within the basal portion of the tail. A distinct head region containing the mouth-parts is marked off. This region in the newly hatched larva is of the same diameter as the body, but subsequent growth enlarges the body, while the diameter of the head increases little if any. Thus the head region becomes more definitely marked off.

The tail is about one-fifth the length of the larva. It is seen in the embryonic larva lying close to the body, while in the hatched larva it is extended and is used for propulsion inside the host. A number of pointed folds or hyaline scales, which protrude slightly from the surface and point backward, are placed irregularly on the surface of the tail and these doubtless make the tail an even more efficient organ of propulsion.

Oxygen must be obtained through the skin or from the food eaten, as the larva lives submerged in a liquid medium having no connection with the tracheal system of its host or with the exterior, also its own tracheal system does not connect with the outside of its own body.

Feeding is carried on by means of a sucking pharynx aided by the mandibles. The ventral surface of the pharynx is a rigid chitinous

plate extending from the mouth backwards to the posterior limits of the head. The membranous dorsal wall of the pharynx is raised from the ventral wall of the pharynx by muscles situated in the dorsal region of the head. These induce wave-like motions in the dorsal wall of the pharynx, which suck in and carry the food through the pharynx to the œsophagus. Here it is passed down into the stomach by the contracting action of the walls of the œsophagus.

The stomach is a blind sac in which the food is, during the early life of this stage, churned or rolled about by the movements of the larva. Later the stomach muscles become developed and constrictions, which run in waves from one end to the other, roll and turn the food content over and over, thus aiding digestion.

The posterior portion of the alimentary tract or proctodæum is scarcely developed and there is no external opening, as waste is not passed during this stage.

The larva at first feeds on the blood and smaller fat globules and avoids the vital parts as the growth of the second stage scale is not arrested until maturity has been reached. At this time usually the first larval stage of the parasite becomes full grown and apparently attacks, during its last days of growth, the vital parts of the scale, thus interfering with its normal functions and preventing the second molt of the scale from taking place. The scale, which previous to this time has been normal in its development, now becomes swollen and distended and at this time begins to turn from its normal lemon yellow to a light orange. The first molt of the parasite usually takes place at approximately the same time that the scale takes on the orange color.

The molting of this form terminates the first larval stage.

SECOND LARVAL STAGE

This larval form is tail-less and its mandibles are not at first well developed, but soon grow to full size and become chitinized. The head region is indistinct and the body segments are practically indistinguishable.

The tracheal system lies deep within the body and at first contains little or no air, but soon becomes filled and develops rapidly. The first, second and fourth to ninth inclusive short branches of each longitudinal main trunk grow rapidly and terminally at the surface of the body develop spiracles, while the third and tenth branches remain short and do not develop spiracles. The two main longitudinal trunks are joined posteriorly and anteriorly as in the first larval stage and from these and the bases of the twenty branches are given off numerous branches which ramify to all parts of the body.

Respiration during the early life of this form is carried on in the same way as that of the first larval stage, but later as the fluid contents of the scale is consumed and an air space forms in the scale, some of the spiracles which have developed no doubt open and function. Without doubt by the time all the fluid content of the scale is consumed all the spiracles are fully developed and function.

The stomach is, as in the previous stage, a blind sac well filled with food. Its contents is even more thoroughly churned by more powerful contractions of the stomach walls. These contractions may start at either end running the length of the stomach, or starting at both ends run to the middle, or again starting in the middle run to both ends. The contents are at first the same yellow color as the scale, due to the fat globules swallowed, but later they become at first, due to digestion, a light orange, changing to dark orange and previous to being excreted a deep red to black color.

Feeding is carried on in the same manner as has been described for the first stage larva except that in the last part of this stage the mandibles, which are blunter and less curved than in the first stage, are used in destroying the internal organs and in scraping clean the inside of the skin of the scale.

The proctodæum is partially developed in the early part of this stage, but does not become fully developed or open until after the larva has consumed the entire contents of the scale and has entered a short quiescent period during which the contents of the stomach completes its digestive processes and is prepared to be excreted.

Following this period the waste, which has been accumulating in the stomach during the life of the two larval forms, is passed and is usually deposited along the lateral margins of the skin of the scale or at the ends. The chitinous portions of the proctodæum are passed out with the last of the waste and no doubt the chitinous portions of the fore-gut and tracheæ are also gotten rid of at this time.

The larva, following the passing of its waste, is usually found lying on its back with its head at the head end of the swollen skin which has dried and become a hardened case in which the parasite now pupates.

PUPATION AND THE PUPA

Rapidly following the passing of the waste the larva usually begins to show differentiation into the three principal regions: namely, the head, thorax and abdomen. Following this condition, which externally marks the beginning of the pupal stage, pigmentation begins in the antennæ and its segments commence to form.

This coloration is quickly followed by that of the eyes, the dusky band of the fore-wings and a small portion of the ventral abdominal

plates. These last do not appear in any regular order. These areas continue to darken for the next few days and the surface of the pupa becomes wrinkled, indicating the formation of the legs, mouth-parts and sclerites. Following this the abdomen and other pigmented or darkened portions of the body rapidly darken and the pupa becomes nearly black.

Previous to emergence the antennæ, legs and mouth-parts become free and the last larval skin is kicked off and the now active insect soon starts cutting and gnawing its way out. There is considerable variability in the length of time it takes for the adult to emerge. Some very active ones emerge in about three hours while others take a day or more. In emerging, a hole is made through which the head is thrust and the insect then pulls and pushes itself out, working its body from side to side and forward and backward, all the time lifting and pushing with its legs.

After emerging the parasite walks a few steps and then cleans itself and straightens out its wings. The insect spends some time in this way and then starts crawling about and is ready for copulation.

DURATION OF THE LIFE CYCLE

The following data are based on rearings of parasites in the laboratory at room temperatures which averaged from 68° to 72°F.

In working out the length of the different stages of this life cycle it has been found that the variability in the length of the different stages indicates a very elastic life history, and one well suited for its life in the host. Hence, it is impossible to give more than average time lengths for the periods.

Examination of large numbers of scales, during the spring of 1914 at Amherst, shows that in general the scales survive the winter in two forms: first, that of well-grown, first-stage scales, which when parasitized contain eggs of the parasite; and, second, well-grown second-stage scales, which, when parasitized, contain well-grown first stage parasite larvæ.

It has been found by raising parasitized scales of the first stage that the parasites reached maturity in from thirty-six to thirty-nine days, while the parasites in the second stage scales matured in from nineteen to twenty-three days.

It is seen that the duration of the life cycle of those parasites raised from eggs compares favorably with that of the scale, thirty-three to forty days, as given by Marlatt. This is further supported by the observations of Dr. H. T. Fernald and the author that the scale in Massachusetts occurs in more or less distinct broods, and the examina-

tion of large numbers of parasitized scales indicates that the broods of the parasite coincide with those of the scale.

It has not been possible to work out the length of the egg and first larval stage, as while this work was in progress young scales were not available for experimentation; however, it was possible to work out the other stages, and these subtracted from the total leave an average of from fourteen to nineteen days for the egg and first larval stages combined. Again according to Marlatt the female scale molts for the second time on the average eighteen days from birth and observations made on non-parasitized and parasitized scales show that the majority of the first stage parasite larvæ molt at approximately the same time that the non-parasitized scales molt the second time.

The length of the second larval stage averages from six to eight days.

The waste passing period, which terminates the growth of the second larval stage and ends arbitrarily with the pigmentation of the antennæ, averages from one to two days.

The pupal stage averages from eleven to twelve days. Internal pupal development commences during the waste passing period.

COPULATION

Sexual reproduction seems to be the rule as copulation has been observed to take place in hundreds of cases among insects that emerged both in the spring and fall. The percentage of males to females seems to be about equal, as of 463 insects selected at random as they emerged, 235 were males and 228 were females.

Copulation was found to take place as soon as the parasites had dried off after emergence and no doubt oviposition commences at once, for as stated earlier females previous to emergence contain developed eggs.

Males and females crawling about do not seem to locate each other from a distance by any apparent sense but more by accidentally coming very close or in actual contact. In such cases the male either pays no particular attention to the female or mounts her and is then either driven off or copulation takes place.

In copulation the male stands on the head and thorax of the female and rapidly pats and rubs her antennæ with his own and endeavors to draw the antennæ of the female to an erect position. The female may resist the male and drive him away; even in cases where copulation takes place the female usually resists at first, but occasionally not at all. When the antennæ of the female are raised to an erect position by the efforts of the male, assisted by the female, they are held behind and beneath those of the male and their tips are in con-

tact with the underside of the first and second basal segments of the flagellum of the male antennæ. The act of raising the antennæ seems to be that of assent, for copulation always follows this act. The male now shifts his position backward and grasping the abdomen and wings of the female with his fore and middle tarsi he leans backward and resting partially on his wing tips bends his abdomen between his hind legs which rest on the branch, and beneath the wing tips of the female and copulation takes place. Often a number of attempts are made before copulation finally takes place and this lasts from seven to sixteen seconds, the average length of time being from eight to eleven seconds.

During the act of copulation the female may stand quietly but usually walks, dragging the male with her.

After copulation takes place, the male again mounts the female and, drawing the antennæ of the female beneath and behind him as previously, the antennæ of the female having remained erect during copulation, usually stands quietly at first, occasionally moving his feet and gently patting her antennæ with his. Later he becomes restless and flits and fans his wings and finally leaves her, having stayed on her back from three to six minutes or more.

POLYGAMY AND POLYANDRY

Emerging males and females were confined separately before copulation could take place and were then used to ascertain if the males would copulate more than once. A male and a female were confined together and copulation took place. The fertilized female was then removed and an unfertilized female substituted and the male readily copulated again, thus showing that they are polygamous.

The females that had been fertilized in the previous experiments were confined with males which had not copulated and these were under observation for two to three hours but copulation did not take place. Again often three or four males will attempt to copulate with one female and violent struggles take place among them, but in the cases observed only one male finally copulated with the female.

These last experiments indicate that polyandry is not, or is not the usual case.

OVIPOSITION

The few cases of oviposition observed took place in young scales which had just formed a scale covering. In these cases the parasite crawled over the material on which she was placed until she found a young scale. This was examined by tapping it with the antennæ. She then turned back to the scale and thrust her ovipositor downward

and backward through the scale covering and into the scale until the tip of her abdomen almost touched the scale covering. While it was not possible to see the egg deposited in the scale it is evident that this takes place for, in the examination of first-stage scales, one finds the egg lying within the body.

The examination of mature first-stage scales, which are wintering over, shows eggs in all stages of development and even live larvæ may be found in the early stages of the second-stage scales as they are forming within the skin of the first-stage scales. From the large number of observations made upon first-stage wintering scales, which were brought into the laboratory to complete their development, it seems that the majority of the eggs hatch just as the second-stage scale is forming within the first-stage scale, although many hatch after the molt previous to the feeding period of the second-stage scale. Undeveloped and partially developed eggs have also been found in second stage scales after feeding and growth have begun. These scales developed from first stage scales in the laboratory and hence it is seen that these eggs were laid late in the life of the first-stage scale. The above data indicate that oviposition takes place all through the life of the first-stage scale, after it has settled down, and that normally the majority of the eggs are laid early in the life of the young scale and these complete their development in mature second-stage scales, while those eggs which are deposited late in the life of the first-stage scale hatch so late in the life of the second-stage scale that it would not be damaged enough by the parasite to prevent it from passing into the third stage. This, it is seen, would account for the fact that some of the parasites emerge from early third-stage scales. However, there is a possibility of the parasite ovipositing in second-stage scales, but this seems unlikely as even its early life is additionally protected by the first exuvium and in its later life it seems even less likely due to its large size as compared with first-stage scales normally oviposited in.

Large numbers of the scales are oviposited in twice and possibly even more times, but twice is the most that has been observed. As a rule when two eggs are found in one scale they are widely separated in development, showing that they were laid at different times and hence by different individuals. In other cases one often finds an undeveloped or a partially developed egg and a live feeding larva in the same scale. Only two cases of like development have been observed; one was in which the two eggs found were at the same stage of development, and the other was in which the two larvæ were of approximately the same age. However, from the large number of observations made, it should not necessarily be taken that the same adult laid the two eggs in the scale, but rather that the scale in these cases was oviposited

in by a second parasite the same day that the first oviposition took place. These facts together with the fact that only one parasite matures in and emerges from a single scale certainly shows that normally this parasite is uni-oviparous.

In the cases where the hatching of the larva from the second egg deposited occurs long enough after the hatching of the first egg, so that the first larva has had time enough to nearly mature or to pass into its second stage before the second larva hatches or is able to seriously interfere with its feeding, then the second larva attacks the first and enters its body usually posteriorly and does not greatly injure the first larva at first, as the second larva has been observed many times within the body of the first, feeding on the stored granular substances of the older larva while it was still feeding on the scale. In the case of wintering over forms, which will be discussed later, and in cases which have been observed in the laboratory, the second smaller larva does not greatly injure the first larva until after it has passed its waste and then with the rapid development of the second larva (during its second larval stage) the first larva is consumed and the second then passes its waste, pupates and emerges.

Probably, in cases where the eggs laid are not separated by enough time for the above to take place, the hatching larvæ destroy each other, or, on the other extreme, the egg resulting from the second oviposition is destroyed before it hatches by the larva hatching from the first egg.

Large numbers of male second-stage scales were also examined for the eggs and larvæ of the parasite, but none were found. This seems rather strange as it does not seem possible that the parasite distinguishes between male and female first-stage scales. Owing to the comparatively small number of male second-stage scales found, it not being possible to distinguish male first-stage scales from the female scales, there being certainly far fewer males than females as compared with the statement given by C. L. Marlatt (Bull. 62, n. s., Bureau of Ent. U. S. Dept. of Agri., p. 43), that the male scales comprise 95 per cent or more of those wintering over, the only suppositions then left are that oviposition in male first-stage scales results in their death or that in the material collected here at Amherst the males are actually much fewer and are not oviposited in.

WINTERING OVER STAGES

As stated previously the parasites pass the winter as undeveloped and partially developed eggs in the bodies of first- and second-stage scales. The first larval stage also winters over in the second-stage scales and also in the bodies of second-stage larval parasites, in the

latter case usually lying centrally within its body. These second-stage larvæ are not arrested in their development by the second parasite within them in such cases, until after they have completed their growth and passed their waste. In the spring these first-stage parasites continue their growth consuming the older second-stage parasite larvæ and after passing their waste pupate and emerge.

Older forms of the parasite such as the second-stage larva, pupa and adults have not been observed to winter over.

It will be readily seen from the above that dormant or winter spraying would not only kill the scale but also the parasite.

DISTRIBUTION

This parasite has been reported from Massachusetts, Pennsylvania and the District of Columbia, and the examination of material received from Drs. E. P. Felt, P. J. Parrott and W. E. Britton, entomologists in the states of New York and Connecticut, show the parasite to be present in those states.

LENGTH OF LIFE OF THE ADULT

It was noted that the adult parasite died on the average in two days, when confined in test tubes plugged with cotton. Previous to this time adults had been observed drinking or feeding on sap and also on the bodies of crushed scales, so an experiment was tried in which the insects were supplied with water. The parasites drank readily and lived on an average four days under this treatment. Honey water was also tried, but the parasites did not live longer than those given water.

FUNGUS ENEMIES

It has been noted that the same fungi which attacks the scales as readily attacked the larval and pupal stages of the parasite, also that a number of parasites confined in test tubes died from the attacks of a species of *Empusa*.

PREDACEOUS ENEMIES

The predaceous enemies of the scale, as *Microweisia* (*Pentilia*) *missella*, are incidentally destructive to the parasite in all its stages of development except the adult stage. However, as yet predaceous enemies of the scale in nowise control it and thus there is little danger of the parasite being extensively destroyed even in newly planted colonies.

PARASITE ENEMIES

No cases of true parasitism have been observed, but a type of parasitism does occur which may be termed incidental or accidental, as such external parasites as those belonging to the genus *Aphelinus*, which lie beneath the scale covering and suck out the entire contents of the second or third-stage San José scales; pupating between the scale covering and the empty skin of the scale and at the same time destroying the internal parasite as well.

GEOTROPISM AND PHOTOTROPISM

The adult parasites show both positive geotropism and phototropism and these two reactions, together with the instinct of the parasite to search for scales, no doubt accounts for the fact that the scales on the smaller and outermost branches and twigs of infested material are well parasitized. This fact was also noted by H. E. Hodgkiss and P. J. Parrott (*Jour. Econ. Ent.*, vol. VII, 227, April, 1914).

NOTES ON THE RICE WATER-WEEVIL (*LISSORHOPTRUS SIMPLEX* SAY)

By J. L. WEBB, *Bureau of Entomology*

The amount of damage done yearly to the rice crop by the rice water-weevil is extremely hard to estimate. In most cases no rice is killed outright. On the other hand practically every rice field is infested to a greater or less degree. The effect of an attack is the pruning off of the roots near the base of the stalk. In severe attacks all the roots may be cut off, in others only a few. Where the pruning is not too severe, the rice plant promptly throws out new roots, continues to live, and will mature. Yet we do not know just how much has been lost in weight or quality of yield. The difficulty is in finding a field of rice entirely free from attack with which to compare infested fields. In extreme cases the rice plants are killed and the loss is then more easily estimated. In general, however, the loss from this source is considerable, and well worth active efforts in the way of prevention or elimination.

SEASONAL HISTORY AND HABITS

According to the writer's observations the adult passes the winter in dead grass, especially grass that is matted down upon the ground. In order to find the weevils in hibernation the grass must be lifted up and thoroughly shaken out, allowing them to fall to the ground. Close examination of the debris is then necessary in order to distin-