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THE BIOLOGY OF SCHIZASPIDIA TENUICORNIS ASHM., A EUCHARID PARASITE OF CAMPONOTUS.

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Introductory.

During the summer of 1921, while engaged in the study of the parasites of *Popillia japonica* at Koiwai, Iwate-ken, Japan, the writer occasionally made miscellaneous collections of parasitic Hymenoptera by sweeping. Among those secured was found at times numbers of a large metallic green Eucharid. Realizing that the biology of this very interesting family of Chalcids had never been studied in detail, an effort was made to determine the habits of this species. In the localities where the parasite was abundant the large *Camponotus herculeanus* sub-sp. *japonicus* Mayr was very numerous, and was the only species of sufficient size to serve as host to the Eucharid. Several nests were therefore excavated, and the presence of the parasite in numbers in the cocoons was at once established.

The crucial point in this life-history was undoubtedly that of the place and manner of oviposition, as early experiments demonstrated that this did not occur in the normal manner. Sweepings of grass and weeds in the general vicinity of the nests produced a predominance of males over females in the ratio of about ten to one, an abnormal condition and one which led to the presumption that the greater proportion of the females were engaged elsewhere. Increased success resulted from sweepings on the lower branches of nearby chestnut trees, and this naturally induced a closer examination to determine the purpose of their presence in these places. A few days later, when attempting to capture a single female seen perched upon a chestnut bud, it was found that this individual had her ovipositor deeply inserted in the bud, in fact so much so as to be unable to withdraw it. An examination of the interior of this bud was then made, and there was revealed a large mass of very minute eggs closely packed within the terminal portion.

Being now in possession of what seemed to be the key to the problem, further observations were made in the same vicinity, and very soon hundreds of females were found ovipositing in an identical manner and place, and the egg-mass first seen was proved to be that of the parasite under observation. This important feature in the biology of the species thus being revealed, it remained to connect up the various stages, etc., to determine particularly the manner in which the larvæ from these eggs gain access to the *Camponotus* pupæ within cocoons in the soil. It soon became evident, however, that hatching was not to take place during that season, but that the eggs would remain in the buds throughout the winter. The investigations were thus brought to a close for the time being, to be continued and completed during 1922. The life-history as finally determined revealed a condition of affairs with hardly a parallel among the parasitic Hymenoptera.

Life-History of Schizaspidia tenuicornis Ashm.

Oviposition. As previously mentioned, the eggs are placed en masse within the buds of various trees, and pass the winter in this condition. The half-dozen or so buds at the terminal end of the young shoots were much preferred for this purpose. At Koiwai the favorite tree for oviposition was the wild mulberry (*Morus alba* L. var.), with the chestnut (*Castanea sativa* Mill.) ranking next. Occasional individuals were also seen to oviposit in white birch (*Betula* sp.). During the latter part of June, 1922, Mr. J. L. King observed egg-laying in the buds of oak (*Quercus mongolica* Fisch.) at Suigen, Korea, while Mr. K. Sato, of this station, noted the same thing in the large, fleshy buds of *Cladastis amurensis* B. et H. var. *floribunda* Maxim at Jozankai in Hokkaido, the most northern of the main islands of Japan. Further investigations in different localities will undoubtedly extend this list.

A comparison of the buds of these various trees shows that all have certain physical characters in common. They are non-resinous, and with the interior somewhat loosely packed, thus giving sufficient space for the egg-mass without undue pressure. Also, the buds of resin producing trees are usually too hard to permit of penetration by the ovipositor of *Schizaspidia*. It seems extremely probable that these physical characters alone determine whether or not a plant species is suitable as a depository for the eggs of this type of parasite.

The number of eggs deposited by a single female was found to range from 940 to 1230, with a general average of 1050 for twenty-five egg-masses taken from buds in the field, and this was verified by a count of the mature eggs in the ovaries of the adult females. This number is in excess of that known for any other parasitic hymenopteron, and is a criterion of the mortality which must occur through the difficulties to be surmounted before the planidia finally gain access to the host larvæ in the nest beneath the surface of the soil.

The female penetrates the bud scales by the use of the ovipositor and sheaths combined, these being barbed at the tips. The point of insertion is invariably on the distal half, and usually on the upper side, though occasionally through the tip. The oviposition scars on the surface scales are evident as raised blackened spots about .5 mm. in diameter. On the inner scales the point of perforation is conspicuous as a much darkened area on the light green surface. The proper penetration of these scales to the interior of the bud requires about five minutes labor on the part of the female, and after this is completed the actual deposition of eggs begins. Under normal conditions the entire quota of eggs of the female is discharged at this one time, and is completed within an average period of twenty minutes. This represents a rate of oviposition of nearly one egg per second over the entire period, a most striking and unusual phenomenon, and comparable in rapidity to that of *Termes bellicosus* (Smeathman 1781) and *Pterodontia flavipes* (King 1916), though of much shorter duration.

The stalked eggs, having passed through the ovipositor, lie free within the bud cavity, or the space normally occupied by the tips of the inner scales and the pubescence, and all are liberated at approximately the same point. As the eggs continue to issue from the ovipositor tip those first laid are forced further and further away. This force, being always from the center of the mass outwards, tends to arrange the eggs in irregular concentric circles about this point, with the stalks directed somewhat towards the center.

The completed egg-mass, comprising a thousand or more eggs, conforms in outline to the space available in the bud. Usually it approximates 1.5 mm. in length, slightly less in width, and of varying depth. Its center on the outer surface is represented by a hard, dark-brown mass, of about the volume of half a dozen eggs, which may be either a hardened fluid given off by the female at the time of oviposition or merely an exudation of sap from the lacerated tissues of the inner bud scales.

The number of these egg-masses within a single bud may be determined approximately by a count of the oviposition scars on the surface. As many as twenty-four, of normal size, have been taken from a single large mulberry bud collected in the field. In such cases the composite mass has a pronounced stratified appearance due to the difference in age of the successive individual egg-clusters. Figure 1 of Plate XV shows two egg-masses of characteristic form and position within a mulberry bud. That on the left is freshly laid, while the other is about twenty days old and consequently much darkened.

The one tree in the buds of which the greater proportion of the eggs were laid was a small mulberry bush about seven feet high, and not heavily branched, growing in a strip of waste land. In 1921, from a count of the twigs bearing buds suitable for oviposition, it was estimated that approximately six hundred buds were available for oviposition by *Schizaspidia*. Eighty-five of these were cut open and examined under the binocular. Every one was found to contain eggs, and the average was 7.2 masses per bud. Allowing one thousand eggs per mass, this being very near the general average as determined by actual count, we secure the almost unbelievable total of 4,320,000 within the buds of this single shrub. In the case of a few buds the pressure had become so great through excessive oviposition that a small number of eggs were actually forced out through one or more of the puncture holes. At times every bud on a twig would bear one, and sometimes two, females in the act of oviposition.

Oviposition on bright days occurs largely during the morning from 9:00 A. M. to 12:00 M., though a few individuals could be seen here and there during the afternoon until as late as 4:00 P. M. These late females were largely those which had been disturbed during the morning hours and had not succeeded in relieving themselves of their burden of eggs.

The Egg Stage.—When first laid the stalked eggs are white in color, but at the end of about fifteen days they show a pronounced darkening due to the development of the embryo within. After twenty days the larva is fully formed and its general characters may be readily distinguished through the transparent chorion. Under the binocular the latter is seen to give off brilliant irridescent reflections. The general color of the mass itself is a deep amber. The larva occupies less than half the volume of the egg, and the remainder is filled with a nutrient fluid of a colloidal nature, and immersed in this medium the larva remains through the winter. At this time the body segments are lightly chitinized and the large head fully formed.

During the early spring when tree growth begins (mulberry the latter part of April at Koiwai, chestnut about two weeks later) the flower buds first swell and burst through their scaly covering, being followed shortly by the leaf buds. As the heavy scales which have protected them during the dormant season fall away it is seen that the *Schizaspidia* are firmly attached to the fine, leaf-like inner scales. They are now exposed to the sun, rain, and other detrimental influences, and finally fall to the ground. In the very humid climate prevalent at Koiwai these mold very quickly, and none remain from the opened buds to reproduce the species. By May twentieth no exposed egg-masses could be found on the trees or elsewhere. The same course of events took place in the case of chestnut buds a few weeks later.

Upon the trees, however, there still remains a considerable number of buds which have failed to develop, and within these the remaining eggs are contained which serve to perpetuate the species. Being dead, these buds eventually dry out, and some open slightly, thus producing a means of egress for the imprisoned larvæ after hatching. The same result is secured in other buds by the feeding of bud-moths and other insects.

During the spring months the larva within the egg completes its development, apparently consuming the greater portion of the fluids surrounding it and leaving only the remnants of the amnion and a granular residue at the anterior end. Hatching is effected by a break in the chorion near the posterior end, this taking place during July, though live, unhatched larvæ were found in buds as late as August 28th.

First Larval Stage (Plate XV, Figs. 2–5).—The newly hatched planidia, scarcely more than one-tenth of a millimeter in length, are capable of locomotion to a limited degree. This is accomplished by a looping movement wherein the suctorial mouthparts are attached to the surface and the small attachment disk of the caudal segment brought forward into position, after which the head is again moved forward. The heavy paired spines on the four caudal segments, and particularly those of the last two, assist in bracing the body when the planidia are in a more or less upright position, as when waiting for some insect or other object to which to attach themselves. This position is not at right angles to the surface of the object, but consists merely in the elevation of the anterior two-thirds of the body to an angle of about forty-five degrees. When in this alert position the planidium extends its mouthparts much as illustrated in Figs. 2 and 3, but during cool periods, or when resting, these are retracted into the body, and the heavy dorsal "plate" of the head is brought to a position at right angles to the axis of the body, and appears as a much darkened base upon an inverted cone, as represented by the body proper.

By the looping movement above referred to the larvæ succeed in making their way out of the buds which have sheltered them for so many months. This being accomplished, they wait about for some means of transportation to the ant nest. At this time the mulberry trees are laden with ripe fruit, and chestnut trees frequently have heavy infestations of aphis. The workers of *Camponotus* visit these trees in numbers to feed upon the decaying fruit and upon honey-dew, and in their movements about the twigs and foliage give the parasite larvæ an opportunity to attach themselves to the hairs of the tarsi and other portions of the body. Figure 13 illustrates the position in which several of these were found.

Having now arrived at the nest the larvæ may eventually be brushed off during the movements of the workers about the chambers among the larvæ or they may be removed during the process of cleaning indulged in by the workers after a foray in search of food. They manage, largely by chance, to become attached to the ant larvæ and, after moving about over the body for a time settle dorsally in one of the sutures between the head and the first thoracic segment, or between the first two of the latter. The mandibles are then imbedded firmly in the derm of the host and no further movement takes place.

Second Larval Stage (Plate XV, Fig. 6).—The larva moults by a transverse dorsal split in the derm of the thoracic regions, and the posterior portion of the exuvium is sloughed off caudally, while the head of the second stage larva is lifted out of the anterior portion and reapplied to the host at a point slightly behind the previous one. A form more characteristic of the greater proportion of ectoparasitic larvæ is now assumed. The mouthparts are suctorial, with no evidence of mandibles. Attachment to the host is maintained by means of the adhesive pad made up of the cast skin of the first stage, the mandibles of which are still firmly imbedded in the derm. In dorsal view the head "plate" of the exuvium is visible on the antero-ventral margin of the first thoracic segment. With the parasite in this stage the semipupa of *Camponotus* is clearly evident within its envelope, and within a short time a rupture appears on the median dorsal line of the thorax, the exuvium then being gradually forced back over the body and finally placed at the posterior end of the cocoon. During the process of ecdysis the parasite larva struggles to free itself from the cast skin and, eventually succeeding, works its way slowly back to the desired position on the body of the newly formed pupa. With its very limited powers of movement this reattachment is possible largely because the pupa is now enclosed within its cocoon, thus retaining the parasite in close proximity to its own body. It was a rather remarkable and unexpected development to find that the second stage, rather than the first, effected this transposition from the host larva to the pupa, and it would seem that this is a further handicap imposed upon the species. It would appear more logical for the first stage to continue until the final place of development is reached.

The place of attachment to the host pupa is almost invariably on the metathorax, just underneath the wing-pads or the hind legs, though in a few cases observed the larvæ were slightly more caudad, being on the first abdominal segment. Development now takes place very rapidly, and the second moult occurs within twenty-four hours after the transformation of the host.

Third Larval Stage (Plate XV, Fig. 7).—Having now reached the final larval stage growth becomes very rapid. The position on the host pupa is identical with that of the late second stage. The mouthparts are strictly suctorial, and with no evidence of mandibles. The oral orifice is surrounded by a lightly chitinized ring, and within the buccal cavity is the sharp, stilleto-like "plunger," which serves to perforate the derm of the host and to keep the aperture open. In living individuals this can be seen moving back and forth with the regularity and almost the speed of a trip-hammer, and functioning as the piston within a cylinder. The power thus exerted is sufficient to drain from the host pupa the last drop of its fluid contents without a change in position. A semi-diagrammatic sketch of these mouthparts, showing the limits of movement of the "plunger," is shown in Fig. 10.

The above type of mouth structure is quite unique among the parasitic Hymenoptera. Normally all stages are equipped with mandibles, though among ectoparasites feeding in the first two stages is largely by suctorial action. In the third, however, the mandibles are well developed and feeding is completed by devouring the tissues remaining, this often going so far as to include the entire chitinous derm of the host. *Schizaspidia* in this stage more nearly approaches the type of mouthparts borne by certain of the parasitic Diptera rather than those typical of the Hymenoptera.

The tracheal system, which could not be distinguished in the first two stages, is now propneustic, only one pair of spiracles being present and these placed laterally on the second thoracic division.

As feeding is completed within a few days after the second moult it is evident that the host pupa is not able to progress far in its development. No appreciable effect is produced by the presence of the first and second stages on the body, and consequently the pupa is of normal size and form in every respect. The third stage parasite larva however, drains the body so rapidly and thoroughly that no parasitized pupa is ever able to advance sufficiently to exhibit any traces of pigmentation in the eyes, the first organs to exhibit coloration in normal individuals.

In the nests of *C. herculeanus* sub-sp. *japonicus* at Koiwai during August and September may be found the cocoons of queens, males and major and minor workers. With the exception of the pupæ of the queens and major workers a single parasite is capable of consuming the entire body contents, and all that remains is the perfectly transparent, collapsed pupal envelope. In the case of the larger individuals only a portion of the body fluids are withdrawn, though death is nevertheless effected. Occasionally two larvæ may be found upon a single host pupa, and in such instances their position is symmetrical with respect to the body of the host. Figure 8 shows a half-grown *Schizaspidia* larva in characteristic position upon a male pupa.

Pupal Stage (Plate XV, Fig. 9). The third and final larval ecdysis invariably takes place *in situ*, the remains of the host serving as a ventral cushion upon which the parasite pupa rests. Moulting is effected by a median dorsal split on the thorax, and the exuvium is then forced backwards over the body and is finally left between the caudal end of the pupa and the host remains. If the cocoon contains two parasite pupæ these always assume positions facing each other, and with the empty pupal skin of the host between them. In all such instances observed both individuals were of the same sex.

The pupa is at first of an opaque, whitish color, and of the form represented in the figure. The characteristic intersegmental welts extend over three sides of the abdomen, and are slightly more pronounced on the caudal segments. The males may be readily distinguished by the longer antennal sheaths. Pigmentation sets in very shortly and the coloration and surface markings of the developing adults become clearly visible through the derm.

The Adult (Plate XIV).—The final transformation having taken place the adult remains within the cocoon for one, and occasionally two, days before emerging. This is then effected by the cutting away of a perfectly regular cap from the anterior end of the cocoon, the cut representing two-thirds of the circle and the cap remaining attached by one edge. Crawling out of the cocoon the parasites wander about the nest for a time and then escape into the open air. No assistance whatever is rendered by the ants of the colony at the time of emergence, nor are the parasites disturbed or interfered with in their movements.

In the laboratory several colonies were confined in artificial nests for observation as to the relations existing between the adult parasites and the ants themselves. Having no means of egress from the nest the parasites wandered aimlessly about and exhibited not the slightest interest in the larvæ or cocoons of the host. Occasionally they would be seized by workers and carried to the refuse heap, but without injury. Later, weakening through their fruitless wanderings, they are dismembered by the worker ants in exactly the same manner as decrepit individuals of their own species. No instance was ever observed of workers feeding the parasites, and likewise repeated efforts to induce them to partake of honey or sugar solution resulted negatively. None were seen in the field visiting flowers or partaking of food in any manner, and it is therefore very probably that this species abstains wholly from feeding during its short adult life.

Dissections of adult females not yet emerged from the host cocoons revealed the fact that practically the entire quota of eggs in the ovarian tubes is already mature, and the gestative period is therefore reduced to a minimum. Counts of the fully-developed ovarian eggs yielded from slightly over nine hundred to eleven hundred, practically the number which is eventually deposited. Oviposition normally occurs on the day of emergence from the *Camponotus* nest.

Observations on emergence from several field colonies and on a considerable quantity of collected material gave the females predominance in numbers of two to one, and this is in accordance with the general ratio known to exist among the greater proportion of the Chalcidoid Hymenoptera.

Mating takes place almost immediately after the emergence of the female from the nest. On warm days, from 9:00 A. M. onwards, it was possible to observe swarms of males, numbering in some cases upwards of one hundred individuals, hovering in the air one or two feet above the entrance to the ant nests. The assembling of the males under these circumstances may be induced by the nest odor, though it is possible that the presence of the females themselves in the burrows can be detected. As the females first emerge into the light they are immediately pounced upon by the males, and mating takes place immediately and before the former are able to take to flight. Mating apparently occurs only once, as it has never been observed in places other than above mentioned, and laboratory experiments have failed to induce copulation except with newly emerged individuals.

The length of life of the adults of this species is extremely short, and under field conditions does not extend over more than three days following emergence from the nest. As oviposition occurs on the day of emergence, or the following day at the latest, the essential function of the individual is fulfilled and death takes place with little delay. In the laboratory, under conditions inhibiting oviposition, females were kept alive for a maximum of five days.

No secondary parasites have thus far been found upon *Schizaspidia tenuicornis.* A considerable number of eggs are devoured or destroyed by an undetermined bud-moth on mulberry, while numerous adults fall prey to the large Asilid, (*Promachus yesonicus* Big.). However, the greatest loss among the adults is brought about by spiders of the family *Thomisidæ*, which abound upon the foliage of trees and shrubs, and which feed upon any of the smaller insects which they are able to catch. The female *Schizaspidia*, having begun oviposition, are unable to take wing quickly and are consequently very easily captured by the spiders. However, the combined loss from these natural enemies is not great.

Life Cycle.—During the season of 1921 the first adults were collected by sweeping on August 20th, though judging from the quantity of eggs later found in the buds they must have been present for some time previously. The maximum numerical abundance was attained about August 27th, and all adults had disappeared by September 15th. An examination of *Camponotus* nests at this time revealed the fact that all pupæ had developed and emerged, and only eggs and first stage larvæ were to be found. During the following season this locality was visited frequently in order to determine the date of first emergence. Two females were found ovipositing on August 14th, and their appearance in numbers from that date onwards was rapid. The greatest numbers were present on August 21st and 22nd, and none could be found after September 7th. This, then, also represents the period over which eggs are deposited.

In Korea emergence took place much earlier in the season, as ovipositing females were taken by J. L. King at Suigen during the latter part of June, 1922, the host in this case possibly being *C. herculeanus* sub-sp. *ligniperdus* var. *obscuripes* Mayr, as *C. herculeanus* sub-sp. *japonicus* does not mature sufficiently early to permit of the development of the parasite at this date.

At Jozankai, Hokkaido, Mr. K. Sato observed adults in numbers on August 5th, but not a single one could be found by the writer when he visited the same locality on August 31st.

In order to appreciate the significance of these varying times of emergence it is necessary to know certain facts in the life-history of the host. At Koiwai *C. herculeanus* sub-sp. *japonicus* passes the winter in the egg and first larval stages, and by the middle of May all are in the second instar. In 1922 the first cocoons were found on July 11th, and a very few of these contained advanced first stage *Schizaspidia* larvæ. It is, of course, evident that no parasites can develop on this host until the pupal stage is reached, and consequently, by force of necessity, its advanced stages are limited strictly to the two months following the above mentioned date. The Korean *Camponotus* above mentioned attains the cocoon stage earlier in the season, and accordingly the development of the parasite is advanced to that extent. Jozankai, Hokkaido, being in a more northern latitude, has a much shorter summer season, and *Schizaspidia*, as well as most other insects, appears later and does not persist so long as at Koiwai.

Referring once again to the latter place, where observations were most complete, we have the eggs deposited in buds during the month following August 14th, and with the planidia within the eggs well developed twenty days later. In this condition they pass the winter and spring months. The first eggs hatch late in June and the larvæ crawl out on the twigs and foliage to await some means of transportation to the ant nest. Apparently solely by chance an occasional planidium succeeds in attaching itself to a worker ant as the latter wanders over the tree in search of food. Being transported in this way it reaches the nest and finally gains its place upon an ant larva. The first moult takes place before the host pupates, the second immediately after pupation, and the third less than one week later. Next comes the pupal stage of about six days, followed by a day of rest and finally emergence into the open air. The duration of the various stages of *S. tenuicornis* may therefore be given as follows:

Egg stage	approx. 11 months
First larval stage	20 days
Second larval stage	3 "
Third larval stage	4 "
Pupal stage	6 "
Adult, within the cocoon	1 "
Adult, outside the nest	2-3 "

This life-cycle contrasts very strikingly with that of such Chalcidoid Hymenoptera as are at present known. The egg stage in this super-family is normally of very short duration, ranging from one to four days, and extended to seven to ten days in the case of *Perilampus*.

Habitat. The necessity for oviposition within the buds of various trees and shrubs has the effect of greatly restricting the general distribution of this parasite. Nests of *Camponotus* fifty or more yards distant from such trees were entirely free from attack. At Koiwai the district within which the parasite was extremely abundant comprised an area, about one hundred yards square, of waste land overgrown with weeds and bordered on one side by a grove of chestnut trees. In the center of the plot were two small mulberry trees, one of which has been referred to as containing such a great quantity of eggs. Nearby was one large birch tree, a few pines and miscellaneous shrubs. The elevation is approximately 1200 feet, and the climatic conditions somewhat comparable to those of the north central states, though the summer season is characterized by almost daily rains and with a constantly high atmospheric humidity.

General Considerations.—There are several points in the life-history of *S. tenuicornis*, as presented in the preceding pages, which give ground for much cogitation. The first of these is the early loss of such a great proportion of the eggs through the shedding in the spring of the bud scales to which they are attached. That the bud should open and develop is a normal sequence of events and it seems illogical that this should lead to the destruction and utter loss of the larger portion of these eggs. Those remaining in dead buds are often permanently imprisoned, while the remainder, after hatching and emerging from the buds, must depend solely upon chance for a means of transportation to the nest, and even when this is attained their very limited powers of locomotion render small the likelihood of the actual attainment of the position necessary to further development. It would seem, under these combined influences, that even the five-hundred-fold potential rate of increase would hardly be sufficient to compensate for all the adverse factors present.

An interpretation which was considered at one time was that of the egg-masses, as they fell from the trees during the month of May, being occasionally gathered up by the worker ants and stored in the nest with the brood, and their care by the ants over the following period of about two months. This theory is supported by the fact that the larva is not of the true planidium type, having but limited powers of locomotion, and possibly requiring care and attention if it is to reach maturity. To test out this point a number of egg-masses were placed in an isolated corner of an artificial nest and the reactions of the ants observed. When first discovered the masses were examined carefully and finally carried into the inner chamber and placed among the larvæ. This appeared somewhat promising, but the following morning revealed them on the rubbish heap. Other egg-masses placed in the nest were discarded immediately. In the field none of these were ever found in the nests, though admittedly it would be easily possible to overlook them even were they present.

The main consideration which would seem to render the above interpretation untenable is the number of eggs in a single mass. In 1921 the average number per bud was 7200, and if only a single one of these masses were taken into a nest comprising several hundred larvæ the latter would certainly be annihilated. As a matter of fact, from the ten million or more eggs deposited that season within the limits of an area about one hundred yards square, less than one thousand adults were finally produced the following summer, a reduction in numbers of about ninety per cent as compared with the preceding season. The mortality in the early stages was therefore about 99.99 per cent. The highest degree of parasitism in any single nest observed during 1921 was 47 percent as compared with .16 percent for the following season. This result is diametrically opposed to that which we would have every right to expect were the above theory based upon fact.

It is conceivable that under different climatic conditions the egg-masses fallen from opening buds would contribute to the perpetuation of the species. As previously mentioned, the excessive humidity and daily rains prevalent at Koiwai during the summer season were conducive to extensive molding, and egg-masses placed in the open air were destroyed in a few days, the infection starting from the decaying bud-scales and quickly extending through the masses. In a dry climate it is possible that some of these egg-masses would fall in such a position as to be sheltered from direct sunlight and other detrimental influences, and be able to live and develop normally during the month or more preceding hatching. This having been accomplished, their opportunity to gain access to the ant nests would be equal to that of larvæ hatched from dead buds on the trees.

Another point in the life-history of this species which would seem to work to its disadvantage is the fact that the first larval ecdysis occurs prior to the attainment of the final position for development on the host pupa. While the planidium itself has no remarkable powers of locomotion, yet its capabilities in this respect are much greater than those of the second stage. It appears however, that the commencement of histolytic action preparatory to pupation provides the initial stimulus to development, and a moult consequently is forced prior to the transformation of the host larva to the pupal stage. Were the latter not enclosed within a cocoon it is very improbable that the parasite in its second stage would be able to regain connection with its host. For this reason it would seem necessary, in such species of ants as produce naked pupæ, for the Eucharid parasite to persist in the unfed planidium stage until attachment to the pupa is accomplished or, on the other hand, to complete its development before ecdysis actually takes place.

The remarkable habit of an insect parasitic upon the immature forms of ants in nests in the soil depositing its eggs in the buds of trees leads one to wonder as to the means by which such a habit could have been brought about. There are no parasitic groups among the Hymenoptera which are known to exhibit this marked departure from the normal, nor anything even more analogous to it, and we are thus left without a clew as to its origin. Were it suggested that the species had been originally a plant feeder and later developed its parasitic propensities, we are confronted by the fact that the entire family *Eucharidæ*, so far as known, is parasitic exclusively upon ants, and consequently parasitism must have been one of the earliest developments in the phylogeny of the race, and that the oviposition habit is a more recent departure. Any conjectures which we might make in this respect would be entirely in the realm of speculative entomology, and as such would be of little value.

Salient Features in the Biology of Schizaspidia tenuicornis.

1. The eggs are deposited en masse in the buds of various trees, and there pass approximately eleven months of the year.
2. Egg-masses in buds which develop normally in the spring are a total loss, only those in dead buds serving to perpetuate the species.

3. An average of slightly more than one thousand eggs is produced by each female, and these are all deposited within a period of not more than twenty minutes, or at the rate of about one per second.

4. The planidium, having emerged from the bud, gains access to the nest of *Camponotus* by attaching itself to a worker ant as the latter moves about the tree in search of food.

5. The second stage larva, rather than the first, effects the transfer from the cast larval skin to the pupa of the host.

Literature on the Biology of the Eucharidæ.

Considering the great extent to which ants and their associated insects have been studied in various parts of the world it seems remarkable that so very little has become known regarding the *Eucharidæ*. Host records are numerous, but further than this little is available. Forel (1890) first recorded a species of this family (*Eucharis myrmeciæ* Cameron) as parasitic upon ants, and gave a general description of the third stage larva. He reached the conclusion that *Eucharis* is parasitic upon the mature larvæ of *Myrmecia*, and this is doubtless true in the earlier stages, but it is very possible that transference to the pupa takes place just as in *Schizaspidia*.

The next, and last, contribution to our knowledge of this group was that by Dr. W. M. Wheeler (1907), wherein was presented an extended exposition of the biology of *Orasema viridis* Ashm., with notes on *O. coloradensis* Ashm., *O. wheeleri* Ashm., and *Pseudochalcura gibbosa* Provancher. As there are radical differences in the biology of *O. viridis* as presented by Dr. Wheeler, from that of *Schizaspidia*, it may be well to make a comparison of the two.

In general form the planidium of *Orasema* is very similar to that of *Schizaspidia*, though the latter is unique in having a heavy armature on the caudal segments instead of the usual unjointed stylets. The supposed banded second stage of *Orasema* is unquestionably an advanced first, and is similar to that of *Schizaspidia* and *Perilampus* (Smith 1912). The actual second stage is not mentioned or figured, unless it is his figure 16, though this has more the appearance and size of the early third, and resembles that of *Schizaspidia*. We now come to a rather surprising development in the biology of *Orasema* as compared with that of other Chalcidoid Hymenoptera, and this is the intervention of two additional instars between the third larval and the pupa, namely, the pustulate fourth and the semipupa. These are entirely absent in *Schizaspidia*.

Orasema is said by Dr. Wheeler to emerge from the nest and mate in the open fields, and then to return and oviposit directly upon the mature larvæ and semipupæ. While the egg itself was never observed by him yet the probable manner and place of oviposition were discussed at some length. The need of a high potential rate of reproduction was attributed to the great danger of the egg becoming detached from the host. Smith (loc. cit.) in reviewing this portion of the paper, questioned this interpretation, and, assuming a parallelism in habit between *Orasema* and *Perilampus*, presented the hypothesis that the eggs are not laid in the nest at all, but upon flowers or other vegetation frequented by the parasite adults and worker ants; that the eggs hatch and the planidia in some manner attach themselves to these workers and are conveyed to the nest; and finally, that these planidia are at first endoparasitic, later emerging and completing their development as ectoparasites. It is possible that Mr. Smith's interpretation of this latter point may have been modified after his finding of *Perilampus chrysopæ* var. (1921) developing externally through all its larval stages upon *Chrysopa*.

Knowing now the life-history of *S. tenuicornis* in considerable detail it is possible to draw some conclusions as to the probable true state of affairs in the biology of *Orasema viridis*. Smith's assertion that oviposition occurs outside the nest is undoubtedly correct, though the likelihood of the eggs being placed upon flowers or foliage is small. In this connection it must be borne in mind that no trace of the parasite in any stage could be found in the *Pheidole* nests during the autumn, winter and early spring months. It is therefore probable that the winter is passed in the egg stage as in *Schizaspidia*, and such being the case they must be placed in some more sheltered position than is secured by indiscriminate oviposition upon foliage. Whatever occurs, the planidia upon hatching must be carried into the nests by the worker ants, as they are of a type very similar to that of *Schizaspidia* and probably possess no greater powers of locomotion. In case more than one generation per year is produced, and the appearance of adults in May makes this quite possible, it would necessitate a modification in the manner and place of oviposition, yet this presents some difficulties. Might it be that the eggs of the spring brood of adults are placed in the seed-capsules of certain annuals rather than in the buds of trees?

In concluding this consideration of the biology of *Orasema viridis* it may be said that every known fact in its life-history points to a fundamental similarity to that of *Schizaspidia tenuicornis*.

Literature on the Biology of Perilampus.

In the family *Perilampidæ*, very closely allied taxonomically to the *Eucharidæ*, we find the only instances of oviposition entirely apart from the host that have heretofore been known to occur among the Chalcidoid Hymenoptera. Smith's contributions to the biology of the genus *Perilampus* constitute the only information available upon this extremely interesting group. One of its notable features is the great diversity shown to exist among the hosts, this being at present known to range over five different orders of insects, as contrasted with the single superfamily to which the *Eucharidæ* are apparently restricted.

The planidia of the species studied by Smith have far greater mobility than is evidenced by that of *Schizaspidia*, and this is made necessary by the habits and location of the hosts. Morphologically they are very similar, except that the former bears an extensive armature entirely lacking in *Schizaspidia*, but with a pair of unjointed stylets on the caudal segment in place of the five pairs of very heavy lanceolate spines on the four terminal segments of the latter. *Perilampus* is doubtless a more primitive form, and the greater specialization of *Schizaspidia* has rendered the above type of armature superfluous.

The habit of bud-oviposition herein recorded for *Schizaspidia* represents a considerable advance over the more or less indiscriminate leaf-oviposition of *Perilampus*. It may be asserted that certain of the *Leucospidæ* are at present in the incipient stages of development of a habit similar to that of the latter genus. According to Fabre (1886) the egg of *L. gigas* is placed within the cell of the mason-bee (*Chalicodoma muraria*) but not directly upon the host larva. The resulting first stage larva is of the planidium type and bears ventrally on each segment a pair of ambulatory setæ. The gap separating this departure from the normal from that of *Perilampus* is not great, but neither gives a clew to the manner in which bud-oviposition, with its consequent prolongation of the egg stage to approximately eleven months, could have been brought about.

Oviposition Habits in Other Parasitic Groups.

Among the *Tachinidæ* the habit of leaf-oviposition has been demonstrated in the genus *Crossocosmia* by Sasaki (1887), in *Chætogædia* by Swezey (1908) and in *Blepharipa* by Townsend (1908). In other families, such as the *Bombylidæ*, oviposition is said to take place upon blossoms, etc., frequented by the hosts. Certain of the *Dexiidæ* scatter their eggs or larvæ promiscuously upon the surface of the soil, and the planidia burrow about in search of Scarabæid larvæ within which to develop. Several writers have observed the oviposition of *Oncodes* (fam. *Cyrtidæ*) upon twigs, and more recently King (1916) presented a detailed account of the biology of *Pterodontia flavipes*, parasitic upon Lycosid spiders. Oviposition takes place upon the trunks of trees, and the resulting planidium is very similar to that of *Perilampus*, both in form and habit. Modifications of the above oviposition habits are known to occur in other orders, such as the Coleoptera, and may even extend to the little-known group of parasitic Lepidoptera (fam. *Epipyropidæ*).

Among the parasitic Hymenoptera *Perilampus* has heretofore been the only group in which leaf-oviposition was known to occur. In an as yet unpublished paper Mr. Cho Teranishi, of this station, records the same habit in the family *Trigonalidæ*, and it is quite possible that this phenomenon will eventually prove to be much less rare than has thus far been supposed.

Descriptions.

Adults. (Plate XIV).

Female (Fig. 1).—Head nearly twice wider than deep. Lateral ocelli separated by half the distance between the eyes at the vertex. Mandibles (Fig. 1a) long, sickle-shaped, the left with one large tooth near the base, the right with two, which are subequal; two long spines on the inner edge near the base. Labrum palmate, with 8–11 digits, these produced at the tips. Antennæ 12-jointed, 2.2 mm. in length; the scape one-half longer than wide; pedicel as wide as long; first flagellar joint longest, one-third as wide at the tip as long; the second two-thirds as long as the first; those remaining of decreasing length, except the eighth, which is equal to the seventh, and the last, which is longer than either of the preceding four. Ratio, 6:4:14:9:8.5:8:7.5:6.5:6:6:5.5:7.

Fore wings 4.5 mm. in length, 1.6 mm. in width; veins in the ratio of 22:11:1:4; marginal vein obscured by a fuscous cloud, which broadens below. Alar expanse 11 mm. Hind-wings 2.7 mm. in length, .6 mm. in width; the submarginal vein extends to the hooks, which are four in number; posterior margin from the tip with a fringe of fine ciliæ.

Femora of fore-legs thickened and broadest at the middle; tibial spur with a tooth near the apex, which is lacking on the spurs of the mid- and hind-legs. Tarsal joints in the ratio of 12:4.5:3:2:8.

Abdomen visibly six-segmented, the first longer than the remaining five combined; all posterior margins emarginate medially. Petiole slightly shorter than the femora of the hind legs (10:11), somewhat dilated at the middle. Ovipositor barbed at the tip.

General color of the head and thorax metallic blue-green with bronze and purple reflections. Antennal scape, pedicel and basal half of first flagellar joint yellowish-brown, the remainder dark brown. Mandibles yellowish, with the inner margins black. Legs yellowish, except the coxæ, which are of the general body color, with the distal margin brownish; the last tarsal joint dark. Petiole testaceous, and broadly ringed with fuscous at the middle. First segment of the abdomen black, the remaining five testaceous except for a fuscous band at each posterior margin. In dried specimens the segments are largely retracted into the first, and the testaceous areas largely concealed.

Head with the transverse striations on the face, these turning upwards and curving around and between the eyes; vertex longitudinally, occiput transversely striate. Thorax generally foveate-punctate except the parapsides and episternum, which are smooth, with marginal punctuations. Outer face of the middle coxæ with large, shallow punctures. Petiole slightly rugose.

Length, 5.0–6.0 mm.

Male (Fig. 2).—Head slightly wider proportionally than in the female. Antennæ 12-jointed; length, 3.2 mm.; scape one and one-half times longer than wide; pedicel as wide as long; first six flagellar joints slightly swollen at the tips; tapering somewhat distad from the middle; first flagellar joint one-fifth as wide as long; ratio 7:4:23:18.5:17.5:16:16:15:14:13:14.5.

Fore wings, length 4.0 mm., width, 1.5 mm.; alar expanse, 9.5 mm. Hind wings, length, 2.5 mm.; width, .5 mm.

Petiole longer than the hind femora (20:12). Abdomen of three visible segments, the first much the largest, and in dried specimens enclosing the second and third.

General color of the head and thorax metallic indigo-blue with bronze reflections. Petiole dark brown, with the base yellowish. First abdominal segment black, the second and third testaceous.

Punctuations of the thorax uniform with that of the female except the parapsides, which are shallowly, uniformly punctate instead of smooth. Petiole slightly rugose at the base.

Other characters as in the female.

Length, 4.5–5.5 mm.

Specimens were submitted to the U. S. National Museum for comparison with Ashmead's types of *S. tenuicornis*, and the determination verified by Mr. A. B. Gahan. The types, according to Gahan, comprise one female, lacking antennæ, and one male, the abdomen of which is missing. The original description of the female (N. Y. Ent. Soc., XII, 2, p. 151. June, 1904) apparently combines the characters of both sexes, as the antennæ described are certainly those of the male.

The species figured by Matsumura (Classification of Insects. Vol. II, p. 283, Pl. V, Tokyo, 1915) as *S. tenuicornis* is of some genus other than *Schizaspidia*.

Host.—*Camopnotus herculeanus* sub-sp. *japonicus* Mayr, and probably other members of the same genus. Such host relationships of other members of the genus *Schizaspidia* as are at present known indicate that it is restricted largely to this one group of ants.

Habitat.—Japan (northern Hondo and Hokkaido) and Korea.

Immature Forms.

(Plate XV).

The Egg (Fig. 11). Mature ovarian egg .125 mm. in length, .06 mm. in width, and with a stalk .23 mm. in length at the posterior end. This stalk is dilated at its distal end to three times the diameter at the middle.

After being laid, the main egg body is slightly increased in size, being .135 mm. in length, with the stalk measuring .21 mm. The latter is somewhat collapsed, due to a portion of the contents having been forced into the main body. Color white, and semitranslucent.

First Stage Larva (Figs. 2–5). Length fully extended, .1 mm.; width, .04 mm., and thickest at the thoracic regions, tapering sharply caudad. Segments nine in number, with no appreciable distinction between the thorax and abdomen. Head, .03 mm. in length, very deep brown in color, heavily chitinized, rounded at both ends, and tapering slightly cephalad. The heavily chitinized portion does not extend ventrad. The mouthparts comprise a membranous funnel terminating in a chitinized, transversely striate, ring. The mandibles (Fig. 12) are strong, heavily chitinized, with an excision at the base of the inner edge, and situated within the buccal cavity.

Body segments lightly, uniformly chitinized, pale amber in color, and tapering caudad, each fitting telescopically into the one preceding. The fifth (not counting the head), sixth and seventh each bear a pair of heavy spines ventrally near the lateral margin, these increasing the length on the successive segments. The terminal segment with two pairs of very heavy, lanceolate spines 10 μ in length.

The advanced first stage larva (Fig. 5) is .25 mm. in length and marked dorsally with six transverse bands, the first being widest and uniform throughout its length, the second and third slightly widened medially, and the remaining three somewhat linear. The two caudal segments show no distention. The elastic integument between the bands is uncolored.

Second Stage Larva (Fig. 6). Length, .6 mm., and with the nine segments distinct. The head is small, unchitinized, and placed ventrally beneath the first thoracic segment. The latter large and hemispherical, the second shorter, and the next five subequal, with the last longer and narrower. Mouthparts suctorial, with no evidence of mandibles. Color translucent, with the yellowish contents of the digestive tract clearly evident through the derm.

Third Stage Larva (Fig. 7). Immediately after the ecdysis 1.0 mm. in length, increasing to 6.0–7.0 mm. at the end of the stage. Possibly nine-segmented, the lines of demarcation indistinct at first and later entirely obliterated except for that between the head and thorax, between the first and second thoracic segments, the latter and the third apparently being fused, and a distinct division between the thorax and abdomen. The body therefore comprises only four main divisions; namely, the head, the first thoracic segment, the second and third combined, and the abdomen, the latter being much the largest. The caudal segment bears ventrally a conspicuous tubercle representing the anal orifice. Color opaque-white, with the derm thickly and uniformly set with minute raised dots, which produce a slightly roughened appearance.

The mouthparts (Fig. 10) are suctorial, comprising an oral opening at the base of a circular depression having a lightly chitinized rim, and within the buccal cavity a heavily chitinized and sharply pointed stylet, or "plunger." Immediately below the oral orifice are two bulbous prominences, doubtless homologous to the maxillæ, while above are two inconspicuous protuberances representing the antennæ.

Pupa (Fig. 9). Length, 5.0–8.0 mm., and 2.5–3.0 mm. in width at the posterior part of the abdomen, the widest point. Three conical protuberances are present dorsally on the head, these being superimposed over the developing ocelli. A number of similar prominences occur on the thorax. The abdomen bears five transverse intersegmental welts, which do not extend ventrally.

Color at first pure white, but later showing clearly the coloration and surface markings of the developing adult through the transparent pupal envelope.

The male is smaller and similar, but distinguished by the much longer antennal sheaths, these extending to the middle of the abdomen.

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EXPLANATION OF PLATES.

Schizaspidia tenuicornis Ashm.

Plate XIV.

Fig. 1. Adult female, dorsal view, with profile. (x 11). a. Mandibles.
Fig. 2. Adult male, dorsal view, with profile (x 11).

Plate XV.

Fig. 1. Mulberry bud with scales removed to show two egg-masses in situ. (x 20).
Fig. 2. First stage larva, lateral view. (x 500).
Fig. 3. First stage larva, dorsal view. (x 500).
Fig. 4. First stage larva, lateral view, with head retracted. (x 500).
Fig. 5. Advanced first stage larva, dorsal view. (x 200).
Fig. 6. Second stage larva, dorsal view. (x 85).
Fig. 7. Third stage larva, lateral view. (x 10).
Fig. 8. Third stage larva in situ on male pupa of *Camponotus*. (x 9).
Fig. 9. Female pupa, lateral view. (x 10).
Fig. 10. Sagittal section (diagrammatic) of the mouthparts of the third stage larva.
Fig. 11. Ovarian egg. (x 100).
Fig. 12. Mandibles of first stage larva.
Fig. 13. Three first stage larvæ adhering to the leg of a *Camponotus* worker. (x 50).

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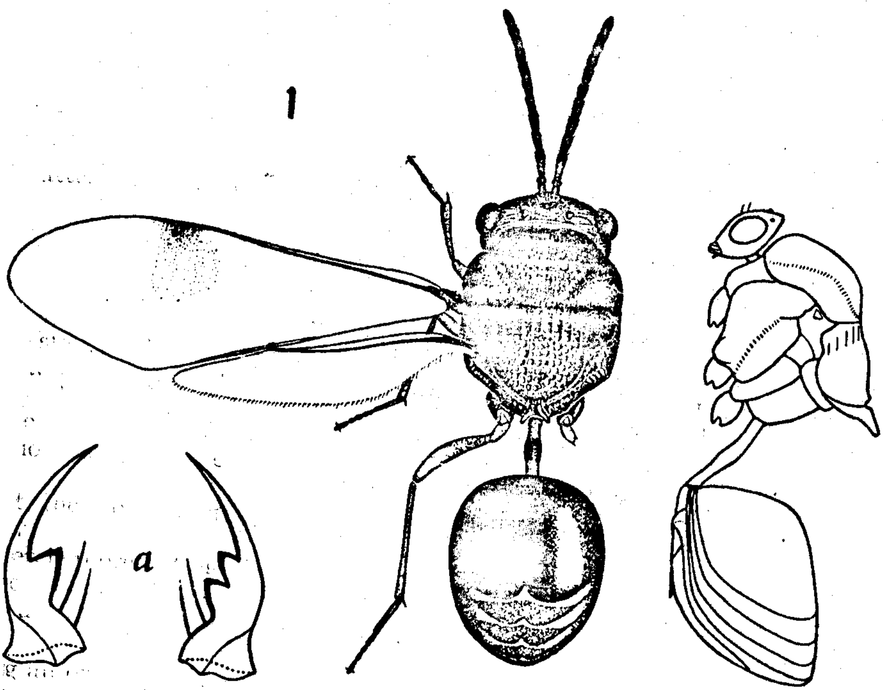

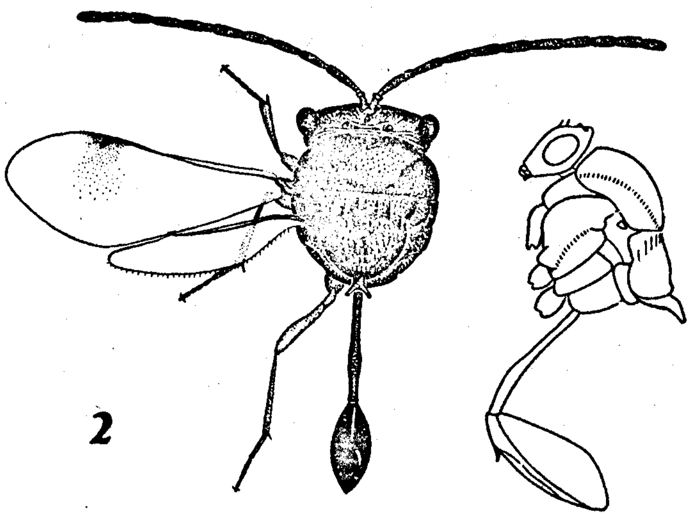

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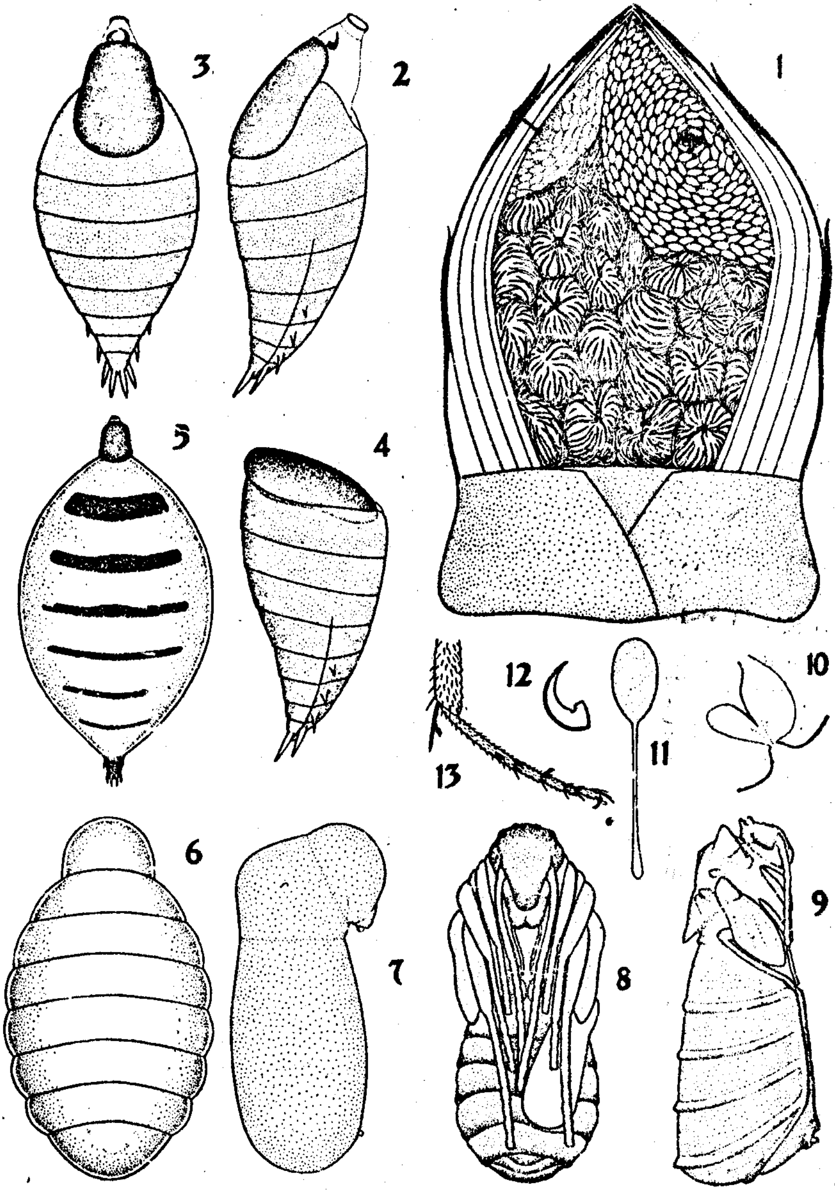

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