

LIFE-HISTORY OF THE LEAF-EATING CRANE-FLY.

Cylindrotoma splendens, Doane.

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INTRODUCTION.

On April 28, 1917, whilst on a journey undertaken with a view to determining the distribution of the Pear Thrips, *Taeniothrips inconsequens* Uzel on Vancouver Island, the author had the good fortune to discover a curious, Tipulid larva quite unknown to him. The locality of the discovery was in the rural district of Westholme about 40 miles north of the town of Victoria. His attention was first drawn to the insect by his co-worker, Mr. E. W. White, Assistant Horticulturist of the Department of Agriculture, British Columbia, whose interest was first aroused by the feeding activities of the larva. In a rich woodland timbered by lofty cedars and spreading, large-leaved maples, there was growing in great luxuriance the false bugbane, *Trautvetteria grandis*, which affects damp and well-shaded habitats. It was on the leaves of this perennial, ranunculaceous herb that the larvæ in question were feeding in large numbers, eating out large, irregular holes. The insect was successfully reared, and the adults submitted to Mr. Chas. P. Alexander, Department of Entomology, Cornell University, who identified the species as *Cylindrotoma splendens*, Doane, in a letter dated May 25, 1917. In reply to a letter of the author, in which the finding of the larvæ was mentioned and their general appearance outlined, Mr. J. R. Malloch, of the Illinois State Laboratory of Natural History, Urbana, Illinois, under

date of May 20, 1917, suggested with admirable foresight, that the species perhaps belonged to the tribe *Cylindrotomini* of the Tipulidæ; but, as material had not then been forwarded to him, he could not naturally diagnose the species from a brief, written description. Later, however, he was able to corroborate Mr. Alexander's determination from specimens sent from the writer's collection.

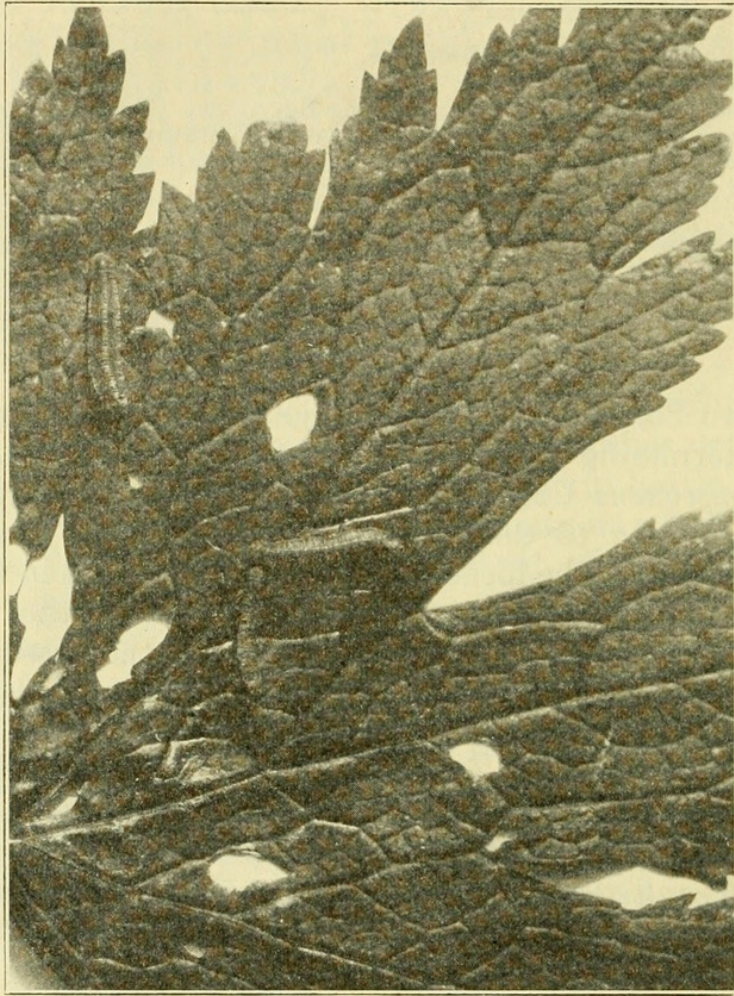


Fig. 1. Larvae of *C. splendens* feeding on a leaf of their food plant (*Trautvetteria grandis*. About natural size. (Original.)

The intrinsic value of the discovery lies in the fact that, according to Mr. Alexander, this represents the first finding of the immature stages of any species of the genus *Cylindrotoma* on the American continent, and it is hoped that the publication of this paper will stimulate other entomologists to search for these very interesting larvæ. A study of their habits will well repay one's efforts by reason of their decided contrast to those of the generality of Tipulid larvæ.

PRESENT KNOWLEDGE OF THE CYLINDROTOMINI.

The literature dealing with this very interesting tribe of the Tipulidæ has not been accessible to me, with the exception of Mr. Alexander's paper, "Biology of the North American Crane-Flies (Tipulidæ Diptera)," published in the Pomona College Journal of Entomology and Zoology, Vol. VI, No. 3, Sept., 1914. Here is presented excellent résumé of the known facts, culled from various workers, regarding this very remarkable group of species, which, according to Osten Sacken, quoted by the author (p. 105), occupies an isolated and intermediate position between the *Tipulidæ brevipalpi* and *longipalpi*. Mr. Alexander goes on to say that "the structure of the adult flies, especially as regards certain details of the venation of the wings, is quite unique, but it is in the immature stages of the different genera that the most interesting distinctions are found. The larvæ, instead of living in the mud along the banks of streams, or in rotten wood, as do the majority of the known crane-fly larvæ, are found on the leaves of various terrestrial and aquatic plants; instead of being brown or grey in color, they are bright green and usually resemble the leaves of their host plants to a very remarkable degree.

The five known larvæ of the *Cylindrotomini* are distributed among four genera as follows: *Phalacroceræ replicata*, L., which is aquatic or nearly so and feeds on *Fontinalis antipyretica*, *Hypnum elodes*, *H. exannulatum*, *Ranunculus fluitans*, etc.; *Cylindrotoma distinctissima*, Meig., terrestrial, feeds on *Viola biflora*, *Stellaria nemoralis*, *Anemone nemorosa*, etc.; *Triogma trisulcata*, Schumm., aquatic, on *Fontinalis antipyretica*; *Liogma glabrata* Meig., terrestrial, on *Hypnum squarrosum*; *Liogma nodicornis* O. S., terrestrial, on *Hypnum cupressiforme* and a related species. All with the exception of the Nearctic *Liogma nodicornis* are Palearctic. For the larvæ of these five species Mr. Alexander (*loc. cit.*, pp. 109-110,) has constructed a key wherein the distinguishing characters are the shape of the body-appendages and the number and position of the teeth on these appendages. He proceeds to state that "the larvæ of the *Cylindrotomini* may be distinguished from those of other crane-flies by the following easily determined points: color green or greenish; the body provided with filiform or leaf-like appendages; larvæ living upon various Bryophytic or Spermatophytic plants."

LIFE-HISTORY AND HABITS.

The adults first appear on the wing about the middle of May, the first specimen in the rearing-boxes emerging from the pupal skin on May 15, the great majority appearing on May 21 and 24. Without food, they do not live longer than five to six days, but in the breeding-cages when they were supplied with food in the shape of sugar solution, they lived as long as 7 to 9 days. In the field, the adults were found on the wing for a period extending over three weeks, May 17–June 7. Soon after emergence the adults begin to copulate, and one male may perform the act of coition with more than one female.

Copulation.—The first individuals were observed to be copulating in the rearing boxes on May 22. The act is undertaken by the sexes apposing their abdomens end to end, the claspers of the genitalia of both interlocking. The head of the female is oriented in the direction diametrically opposed to that of the male which remains suspended with his head towards the ground. When copulation occurs between individuals resting on a vertical surface, such as the walls of the rearing-box, the female is invariably superior in position to the male. In both cases the sexes have all their legs applied to the supporting surface. Sometimes copulation was observed to be taking place among individuals on the inside of the roof of the rearing-cage. Here, only the female at times would be resting on the roof with the male suspended head downwards, its body at an angle of 90° with that of the female and its legs unsupported. The act of copulation is not always interrupted when the sexes are disturbed, but the female may walk off dragging the male after her, or flight may be actually undertaken with the female transporting the male. Pairs in copula were frequently transferred from one rearing cage to another without the union being broken.

In the field, the behavior during copulation was similar to that observed among the sexes in the rearing-cages. Here the act was generally undertaken in the deep shade of the large leaves of the food-plant, *Trautvetteria grandis*, the sexes resting on the under-surfaces of the leaves, or on the stems. When disturbed, the females took to flight, bearing the males with them undisturbed.

No exact records were kept of the time that the sexes remain in copula. It varies considerably, however, and gen-

erally, copulation may continue for two or three hours and even longer. In some cases, the sexes remained in union only a matter of a few minutes.

Oviposition.—Eggs were first observed on the leaves of *Trautvetteria grandis* in the breeding-cages on May 25th when the first female was seen to oviposit. On the following day, a few eggs were found on the leaves in the field at Westholme and on a subsequent visit on May 31, were found to be very numerous.

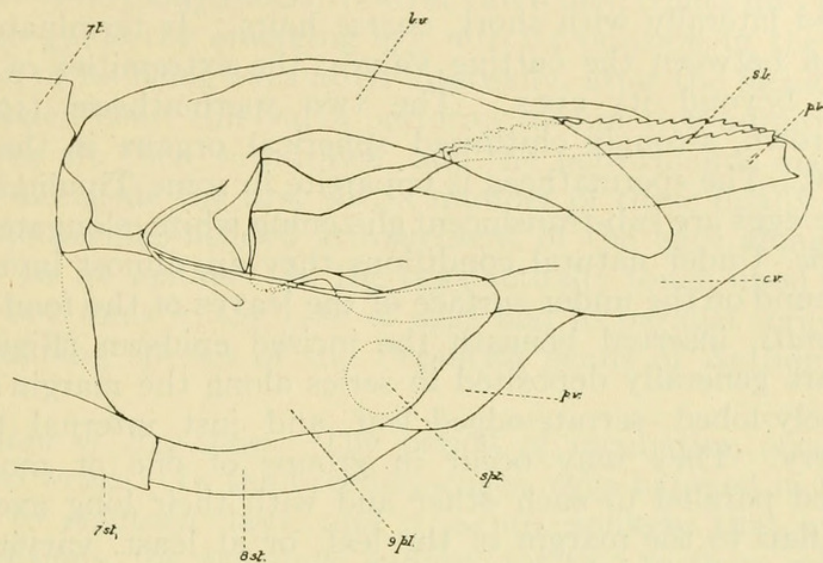


Fig. 1a. Ovipositor: 7 t., seventh tergite; 7 st., seventh sternite; 8 st., eighth sternite; 9 pl., ninth pleurite; spt., spermatheca; b. v., bifurcated valve; p. v., ploughshare valve; c. v., cutting valve bearing serrated blade (s. b.) and plain blade (p. b.). Camera lucida drawing. $\times 40$.

In order to understand the behavior of the female *Cylindrotoma* in ovipositing, it is necessary that we should recapitulate in brief the structure of the ovipositor (See Figure 1a). It consists of a pair of large double-bladed valves (c. v.), each of which is sparsely clothed with rather elongated, delicate hairs and more closely invested with short ones. The inner blade (s. b.) in each case is serrated along its upper margin which is distinctly recurved externally. The serrations of the proximal half of the blade are directed anteriorly, those of the distal half being directed posteriorly. On each of these cutting valves, external to the saw-edged blade, is a plain blade (p. b.), the upper margin of which is slightly recurved externally and overtopped by the serrated margin of the inner blade. Both blades have their attachment in the dorsal half of the valve. Dorsal to

these cutting valves is an unpaired and unarmed valve, bifurcated in its posterior third (*b. v.*), the two arms of the bifurcation each straddling the cutting valves and being continued at rest beyond the insertion of the blades of these latter valves. It is sparsely invested with long, slender hairs, more thickly disposed on the two bifurcating arms. Along its dorsal median line there runs from the point of bifurcation a narrow depression which terminates at its base. Ventrally, and arising apparently from the eighth sternite and between the paired ninth pleurites, is a ploughshare-shaped valve (*p. v.*), strongly chitinated and invested laterally with short, coarse hairs. It terminates in a position between the cutting valves, the extremities of which extend beyond its apex. The two spermathecæ (*sp.*) are dark-brown, strongly chitinated spherical organs in the ninth segment. The spermatheca is tripartite in some Tipulidæ.

The eggs are sub-translucent glistening white, elongate-ovate in shape. Under natural conditions they are almost invariably to be found on the under surface of the leaves of the food-plant, *T. grandis*, inserted beneath the incised epiderm (Figure 7). They are generally deposited in series along the margin of the palmately-lobed, serrate-edged leaf, and just internal to the periphery. They may occur in groups of one or more, all arranged parallel to each other and with their long axes perpendicular to the margin of the leaf, or at least, varying but slightly from the perpendicular. The eggs are only partly hidden beneath the incised epiderm. They are exposed dorsally, the margins of the slit made by the ovipositor overlapping the egg laterally, and to a small degree, both anteriorly and posteriorly. The arrangement of the eggs in series and their partial exposure, lends to the leaf-margin a somewhat beaded appearance. When newly laid, the eggs are not readily observed by the naked eye, unless one examines the leaves closely. Later, owing to a darkening of color of the eggs as well as of the leaf-margin which turns brown, they are more readily detected.

Not only are the eggs deposited along the leaf-margin, but often where a leaf has been eaten earlier in the season by the larva, one will find eggs deposited along the ragged edge of the damaged leaf.

In the breeding-cages, the females laid their eggs indiscriminately on both the upper and lower surfaces of the leaves, but in nature, no eggs were ever found on the upper surface.

The actual method of oviposition was frequently observed. The female rests on the under side of a leaf with the extremity of the abdomen directed towards the leaf-edge. The abdomen is slightly recurved vertically, and the margin of the leaf is grasped between the bifurcated valve of the ovipositor which is applied to the upper surface of the leaf, and the paired, cutting valves the blades of which are apposed to the under surface. These blades are then moved to and fro, and a slit is cut in the epiderm, the recurved margins of the blades serving to widen the aperture of the slit. The ploughshare, ventral valve then comes into play, serving to guide the emerging egg into its position in the slit. By reason of its being excavated internally, after the fashion of a deep-keeled boat, this valve performs its function admirably. The valves are then withdrawn, and the performance may be repeated alongside the first slit, a number of these finally producing the parallel-beaded arrangement of the eggs along the margin. In no instance do the eggs actually touch upon each other as one finds in the case of eggs laid in parallel series by the leaf-mining species of the *Pegomyia* genus of Anthomyiid diptera.*

Duration of Egg-stage.—The period of incubation occupies about two weeks. In the breeding-cages, eggs hatched in from fourteen to eighteen days, and it is not unlikely that under field conditions, the egg-stage endures for two to three weeks. Records show that under experimental conditions, the first eggs were deposited on May 22, and the date of first hatching was June 7. The first, newly-emerged larva was taken at Westholme on a leaf of *T. grandis* on May 31.

The Embryo and Emergence of Larva.—The maturing embryo is at first distinguishable within the egg by the appearance of two dull, red spots, one on each side of the anterior extremity of the egg. Presumably these indicate the position of the eyes. Later, as the embryo develops, the black head-capsule stands out quite markedly within the transparent chorion.

The actual time occupied by the larva in leaving the egg is about three hours. In its efforts to free itself, it is not at all energetic. In one particular case, on June 7, the young larva made slow movements from side to side, erecting its head and

*Cameron, A. E.—A Contribution to a Knowledge of the Belladonna Leaf-Miner, *Pegomyia hyoscyami*, Panz. its Life-History and Biology. Ann. App. Bio. Vol. I, No. 1, May 1914, London, p. 57.

straining forward in an endeavor to liberate itself. As soon as success attended its efforts, it buried its mandibles in the leaf-tissue and commenced feeding.

The anterior extremity of the egg is proximal to the leaf-margin. The chorion splits longitudinally along the mid-dorsal line, the aperture extending almost half the length of the egg. In emerging, the grayish-white larva, almost transparent, avails itself of its tubercles in disengaging itself from the egg-case. In that they are posteriorly directed, their function in assisting the larva to liberate itself from the egg, is at once apparent.

When the larva has succeeded in emerging, the aperture in the chorion has assumed an ellipsoidal shape. The empty egg-case remains in the slit originally made by the ovipositor of the adult, and on no occasion was the larva observed to devour it.

Larval Habits.—The first-stage larvæ (July 7) are semi-translucent, grayish-white, and measure 1.19 mm. long by 0.37 mm. broad. The alimentary canal by reason of its contents, is yellowish-green or sometimes reddish-brown, and the head is black. The larvæ feed on both the upper and lower surfaces of the leaf, embedding their mandibles through the epiderm and eating the parenchyma inside. Whether working on the upper or lower surfaces, the first-stage larvæ rarely disturb the epiderm of the surface other than that on which they are feeding. Their activities are later accentuated by the parts which are eaten, turning a brownish-black, shrivelling and dying.

The young larvæ are very sluggish and not readily disturbed when feeding. The mandibles are very firmly embedded in the leaf-tissue. Gentle exhortation with a camel-hair brush will not serve to induce them to loosen their hold. They assume various attitudes. Usually they lie horizontally on the surface of the leaf, but often the only part of their bodies in contact with the leaf, is the head and mandibles. In the latter case, the rest of the body is elevated at varying angles to the leaf-surface. Sometimes the larva may literally stand on its head with the abdomen erect and vertical. Again, it may assume a looped position where the abdomen is recurved dorsally, and its extremity comes to rest in close proximity with and anterior to the head, like an inverted U, the arms of which are almost closed.

Often they drop voluntarily from the leaves to the ground. It is supposed that many never regain their original positions

but perish either from starvation or are preyed upon by spiders and insect predators.

In nine days (July 16), the larvæ had increased in length to 5.84 mm. long, although a few were only 3.57 mm. Except for the green color of the alimentary canal, they were of a dirty grayish hue. Even in the young stages they display all the characteristic behavior and movements of the full-grown larva, which can be most aptly compared with those of "measuring worms" or "looper" caterpillars (Geometridæ).

The first larval moult occurs after a period of about 18 to 21 days, although in some cases it did not take place for 5 or 6 weeks. Growth is very slow and quite in accord with the sluggishness displayed by the animal. Previous to this first moult, the larvæ, in moving over the leaves, become invested with particles of their excreta which adhere readily to the skin as if it were coated with a sticky substance. The freshly-moulted larvæ are almost translucent white, and the two tracheal trunks with their ramifications are readily distinguishable by the aid of the binocular microscope.

The larvæ have the power, when young, of secreting a silken thread from the mouth, which is probably the product of the salivary glands. They frequently adhered by this thread to the camel-hair, water-color brush used in transferring them from one leaf to another. The power to produce this thread is but limited, and on no occasion was it observed to be of any great length. Usually, it measured not more than half-an-inch.

The second-stage larvæ gradually assume a leaf-green color as they continue to feed, obscured in some by a brownish pigment beneath the cuticle. Laterally, in the more mature first stage larvæ, on each side of the median, dorsal line, there runs an irregularly-defined, brownish-gray band somewhat interrupted intersegmentally. In the larvæ of the second stage, these bands may still persist or give place on each segment to two similarly colored lines representing a V, the arms of which, however, do not meet and fuse posteriorly. On each side, the band on any one segment is parallel with that on the others.

Towards the end of July, more accurately, on the 26th, coincident with the dying off of the food-plant, *T. grandis*, the larvæ which had now assumed a size of 8.32 to 9.00 mm. long, became quiescent and ceased to feed. Previously, in the middle of July, when the larvæ in the breeding-cages were transferred

to fresh food-plants they evinced a decided tendency to creep under the curled-up edges of withered leaves. Feeding and movement gradually ceased completely, and they remained clinging motionless to the leaves. When disturbed, they rolled up, like a watch-spring, moved about a little and then resumed their dormant attitude again. It was also observed that as the leaves withered, the larvæ dropped off and, if possible, attached themselves to the stems. In the breeding-cages, they adhered to the edges of the plant-pot. In the field, they fell to the ground among the dead leaves, and under these they passed the winter in a dormant condition. In color, they match exactly that of their environment of dead leaves, but a large number seemed to retain their original leaf-green tint. In the beginning of September, the larvæ had apparently contracted a little and now measured only 7.00 mm. long by 1.50 mm. broad. This apparent shrinking was probably associated with insufficient moisture under breeding conditions.

The over-wintering larvæ first begin to show signs of activity in March when the *Trautvetteria* sends up its fresh shoots. The growth of the larvæ then proceeds quite rapidly until the larvæ pupate in the middle of May.

In many respects, the details of the larval life-history agree with those of the species *glabrata* of the closely allied genus *Liogma*, as described in the admirable paper of Dr. Mueggenberg published in 1901. Mr. Alexander (*loc. cit.*, p. 106) quotes this author as having found the larva feeding on the moss *Hypnum squarrosum* Brch. and Schp. in the wet, grassy spots of woods in the environs of Berlin. According to Mueggenberg, the larva moults several times, probably at least eight, which Alexander says is the number determined for *Phalacroceras* by Bengtsson. As to the exact number of moults of the larva of *C. splendens*, the author is unable at present to make a definite statement. With tolerable certainty, it can be stated that close observation revealed only one moult as occurring before hibernation and two after, the last being the casting of the larval skin previous to pupation. In the penultimate stage, the larva measures 15.00 mm. and the full-grown larva 17.00 mm. The duration of the various larval stadia, except that of the first, cannot be stated with any degree of accuracy, but it is hoped that it will be possible to decide this, as well as the number of larval moults, later.

The behavior of the full-grown larva (Figure 1), presents much that is interesting. The larva is invariably found on the upper surface of the leaf and in the spring is actively engaged in feeding. On a fresh leaf the larva usually begins by skeletonising it, leaving the lower epiderm intact. Later, however, large holes are eaten completely through the leaf.

Reference has already been made to the extraordinary movements of the first-stage larva. These are much more accentuated in the full-grown animal. The organs used in facilitating its travel, are chiefly the mandibles and the abdominal pro-legs or *pseudopodia*,* which are merely ventral protrusions, of the body-cavity two on each of the last eight segments. They are apparently distensile, and it would appear as if they were capable of secreting some kind of fluid that assist the animals in retaining its hold on a smooth surface, especially so if the surface be inverted. On the three thoracic segments there are no definite pseudopodia, but the function of these is served by the development of a distinct, ventral fold which becomes apparent as the animal contracts. Two pairs of small tubercles or papillæ on the ventral surface of each thoracic segment, are also employed in locomotion.

In moving forward, the last segment is elevated from the leaf-surface. Simultaneously almost with this action, the middle region of the body contracts and arches so that one pair of pseudopodia after another is methodically raised from the leaf in a postero-anterior direction. The last segment comes to rest in a position about half-an-inch anterior to its original one. A series of rhythmical, muscular contractions pass wave-like along the body from segment to segment, pulling the two extremities towards each other with the result that the body assumes the shape of an inverted U involving at first only the abdominal region. The contractions pass along to the thorax and head which also become arched, whilst the pseudopodia of the last five body-segments are applied to the leaf-surface again. The inverted U is then composed of that part of the body anterior

*The author has preferred to apply the name *pseudopodia* to the unsegmented, paired tubercles of the abdominal segments because of their locomotory function as well as their acting as adhering agents. They are charged with body fluid and tracheated. The mechanism which determines their close application to a surface is apparently blood pressure, and this together with the aid of the viscid fluid which they secrete, is capable of maintaining the weight of the larva by surface-tension on an inverted glass-surface.

to the fifth last abdominal segment. All this time the mandibles of the larva have remained fixed, but when the last five segments have renewed contact with the leaf, the head is slowly raised. The anterior region of the body may be moved slowly from side to side, finally extending straight forward, eliminating the arch of the inverted U. The whole body then comes to rest on the leaf. The final result of this methodical series of movements is that the animal has now advanced in its progression just as far as the distance measured by the last body-segment in its original displacement. The whole process is marked by the extreme slowness of an orderly series of individual reflex actions which impart to the observer the notion of an apparent calculation on the part of the organism by reason of their perfect co-ordination. The persistence of the appropriate stimuli determines the continued repetition of the whole series of ambulatory reactions.

In a quiescent condition, the thoracic region of the body has a noticeably humped appearance, apparently produced by the slight ventral retraction of the head-segment.

The full-grown larvæ are very sluggish and inactive. When disturbed, they relax their hold on the leaf-surface and readily fall to the ground. This response to a disturbing factor, together with their marked resemblance to the leaf-color, appears to be their only asset of defense against predaceous species. In all, somewhat more than one hundred adults were reared from larvæ collected in the field, and in not a single instance was one found to be parasitised.

Pupation.—Previous to pupating, the larva attaches itself firmly to the surface of the leaf or leaf-petiole by means of its anal pseudopodia. The skin splits transversely posterior to the head but is only partially sloughed off. The head, thorax and first four abdominal segments of the pupa are exposed, but the remainder of the abdomen remains enclosed in the larval skin, the terminal portion of which, attached to the leaf-surface, is collapsed and wrinkled. The head-capsule of the larva which is moulted with the rest of the exuvium, lies ventrad of the fifth abdominal segment of the pupæ. On the leaf, pupation may take place on both the upper or lower surfaces, but generally on the former. On the petiole, the pupæ generally occur at the axils.

Duration of Pupal Period.—In the breeding-cages, the period of pupation varied from six to ten days. Mueggenberg, quoted by Alexander (*loc. cit.*, p. 106) states that for *Liogma glabrata* the pupal period persists for 11 to 12 days, and it will be probably found that in individual cases the period is as long for our species under natural conditions in the field.

Emergence of Adult.—The pupal skin splits in T-shaped fashion on the dorsal region of the thorax. The adult thorax and head are the first to appear followed by the wings. After a series of efforts, punctuated by periods of quiescence, in which the prevailing movement is a straining forward of the free parts of the body, the legs are unsheathed from their closely-investing cases and the adult emerges. At first, it is of a pale-green color which gradually gives place to the yellow and black of the mature animal.

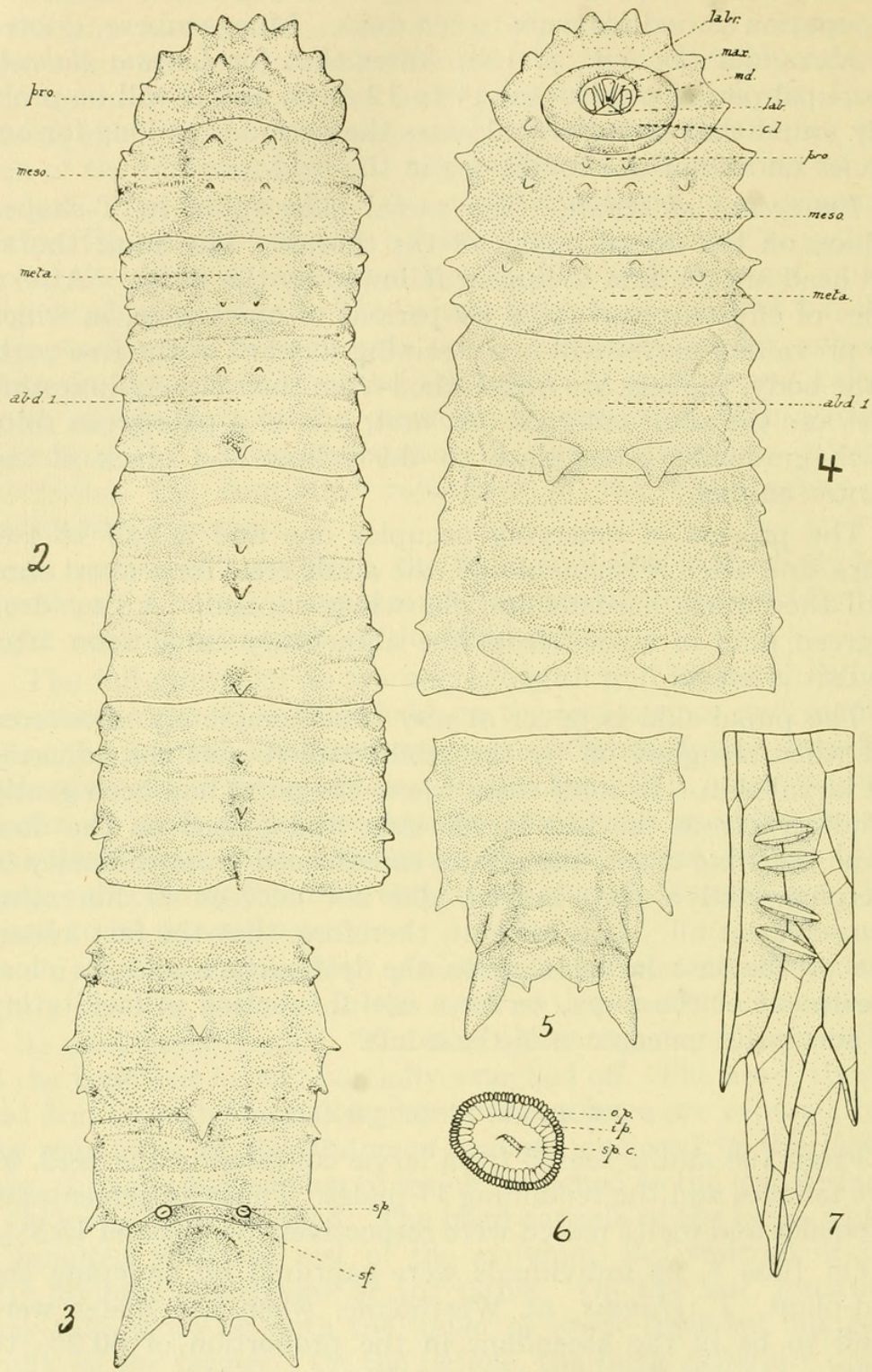
The process of emerging occupies one and a half to two hours, and after it is completed, the adult rests for a short time until the cuticle hardens and the wings expand. A tiny drop of green fluid is voided from the alimentary canal soon after the exit is made.

The pupal skin is never at any time completely uncovered and when sloughed off by the adult, still retains the adhering last larval skin. In some cases where the pupæ had been gently withdrawn from the last larval skin and placed on the floor of the breeding-cages, the adults experienced great difficulty in emerging, and a few, indeed, did not succeed in liberating themselves at all. It is evident, therefore, that the fast adherence of the last larval skin to the leaf-surface and its close investment of the pupa, serves a useful function in facilitating the successful emergence of the adult.

PROPORTION OF SEXES. •

From 108 adults reared from larvæ collected in the field, 91 were females and the remaining 17 males. Thus the percentages of females and males reared were respectively 84.2% and 15.8%.

On June 1, 96 individuals were captured by sweeping the food-plant, *T. grandis*, at Westholme, when the males were found to be in the ascendant in the proportion of 60.2% to 39.8%. On this date many were taken in copulâ.



The marked discrepancy between these two sets of figures appears at first sight to be inexplicable. It is probable, however, that the figures resulting from rearing the adults from the larvæ, represent approximately the actual superiority in total numbers of the females over the males. On the date that the collection was made at Westholme, there were comparatively few adults to be seen. When one adds to this the fact that the females emerge in larger numbers before the males and that they die off soon after laying their eggs, the greater proportion of the later-emerging males towards the end of the adult season on June 1, is readily accounted for. It has already been noted that a single male may copulate with several different females.

DESCRIPTION.

Egg (Fig. 7).—When first deposited, the egg is sub-translucent, grayish-white, spindle-shaped, partly inserted beneath the slit epiderm of the leaf. The chorion is unornamented. It measures, on an average, about 0.840 mm. in length and about 0.303 mm. in breadth at the widest part in the middle.

Just before hatching, two, dull-red spots corresponding to the eyes of the young larvæ are apparent at the anterior end. The black head-capsule of the young larva is also readily distinguishable.

Full-grown Larva (Figs. 2-6).—Length, 17 mm.; maximum breadth, 2.5 mm.; maximum depth, 1.5 mm.

The live larva (Fig. 1) chlorophyll green, closely resembling in color that of the leaves of the food plant, *Trautvetteria grandis*, except for the sclerites of the head-capsule which are black, the less heavily chitinised parts brown. In bright sunlight, the lateral tubercles and margins of the body almost transparent. Dorsally, the middle region of the body darker green because of the contents of the alimentary canal within. The two, main, tracheal trunks apparent as silvery strands, running laterally and posteriorly to their termination in the spiracles of the eighth abdominal segment. Some of the tracheal branches also evident. Two irregular, sub-parallel, fuscous, brown bands on each side of the mid-dorsal line extending from the mesothorax to the spiracles of

EXPLANATION OF FIGURES.

- Fig. 2. Larva, dorsal aspect, thoracic and first three abdominal segments; *pro.*, prothorax; *meso.*, mesothorax; *meta.*, metathorax; *abd. 1*, first abdominal segment. $\times 14$.
 Fig. 3. Larva, dorsal aspect, last two abdominal segments, *sp.*, spiracle. $\times 16$.
 Fig. 4. Larva, ventral aspect, head, thoracic and first two abdominal segments, *labr.*, labrum; *max.*, maxilla; *md.*, mandibles; *lab.*, labium; *c. l.*, circumoral lip. Other lettering as in Fig. 1. $\times 16$.
 Fig. 5. Larva, ventral aspect, last abdominal segment. $\times 20$.
 Fig. 6. Spiracle; *o. p.*, outer periphery; *i. p.*, inner periphery; *sp. c.*, spiracle cleft. Camera lucida drawing. $\times 80$.
 Fig. 7. Eggs deposited in the slit epiderm of leaf of *T. grandis*. The ruptured epiderm partly envelops the egg. $\times 7$.

the ultimate abdominal segment and indicated in Figures 2 and 3, by the darker shading; often faint and indistinct in parts on the anterior segments, but generally well-defined posteriorly. Lateral margins of the body appressed. Skin delicately reticulated and tuberculated, transversely rugose both dorsally and ventrally with the wrinkles either isolated, separate and sub-parallel, or converging and confluent.

Prothorax (Figs. 2 and 4, *pro*) with a broad, circumoral lip (Fig. 4, *c. l.*) on ventral surface, penetrated in the middle by the transverse slit through which the head-capsule may be exerted. Two pairs of ventral tubercles, the members of the inner pair small and merely papillæ. Anterior, marginal tubercles three pairs, the median pair largest. One pair of lateral tubercles. One comparatively large pair of dorsal tubercles.

Mesothorax (Figs. 2 and 4, *meso*), 2 pairs of tubercles ventrally as in the prothorax, small. Two lateral pairs, of which the members of the anterior pair are more pronounced. Two pairs of median, dorsal tubercles the members of the anterior pair the larger.

Metathorax (Figs. 2 and 4, *meta*), with the ventral and lateral tubercles similar to those of the mesothorax. Two pairs of small, median, dorsal tubercles, all of equal size, the members of each pair equally separate but not so widely separate as the median dorsals of the mesothorax.

Abdominal segments, dorsal tubercles: first segment (Figs. 2 and 4, *abd 1*) with an anterior, small pair of tubercles and a larger median, posteriorly-directed, single one behind. Segment II with three, single, posteriorly-directed median tubercles, of which the first is smaller than the second and the second than the third, the first and second not so widely separate as the second and third. Segments III–VII each with three, single, median, posteriorly-directed tubercles as in Segment II, the first equidistant from the second as the second from the third; the third tubercle largest of the median dorsals in each of these segments. *Lateral tubercles:* segments II–VII each with four pairs of tubercles of which the members of the second and third are more prominent than those of the first and fourth. *Ventral tubercles:* first segment with one pair of *pseudopodia** situated posteriorly, broad at the base, bluntly conical in shape. Segments II–VII each with a posteriorly-situated pair of pseudopodia, larger than those of segment I, more widely separate and bases broader.

Eighth segment (Figs. 3 and 5) bearing the stigmal field and the caudal appendages. Posteriorly, two pairs of processes of which the members of the outer pair are directed latero-posteriorly, larger than the members of the faintly-brownish, inner pair which are situated just posterior to the anal orifice. Lateral tubercles two pairs, of which the posterior pair is the larger, posteriorly directed. Ventrally, on each side of the two rounded, anal swellings representing the pseudopodia of other segments, is a pair of large, lateral, anal processes, directed latero-posteriorly. The stigmal field (Fig. 3, *s f.*) somewhat depressed,

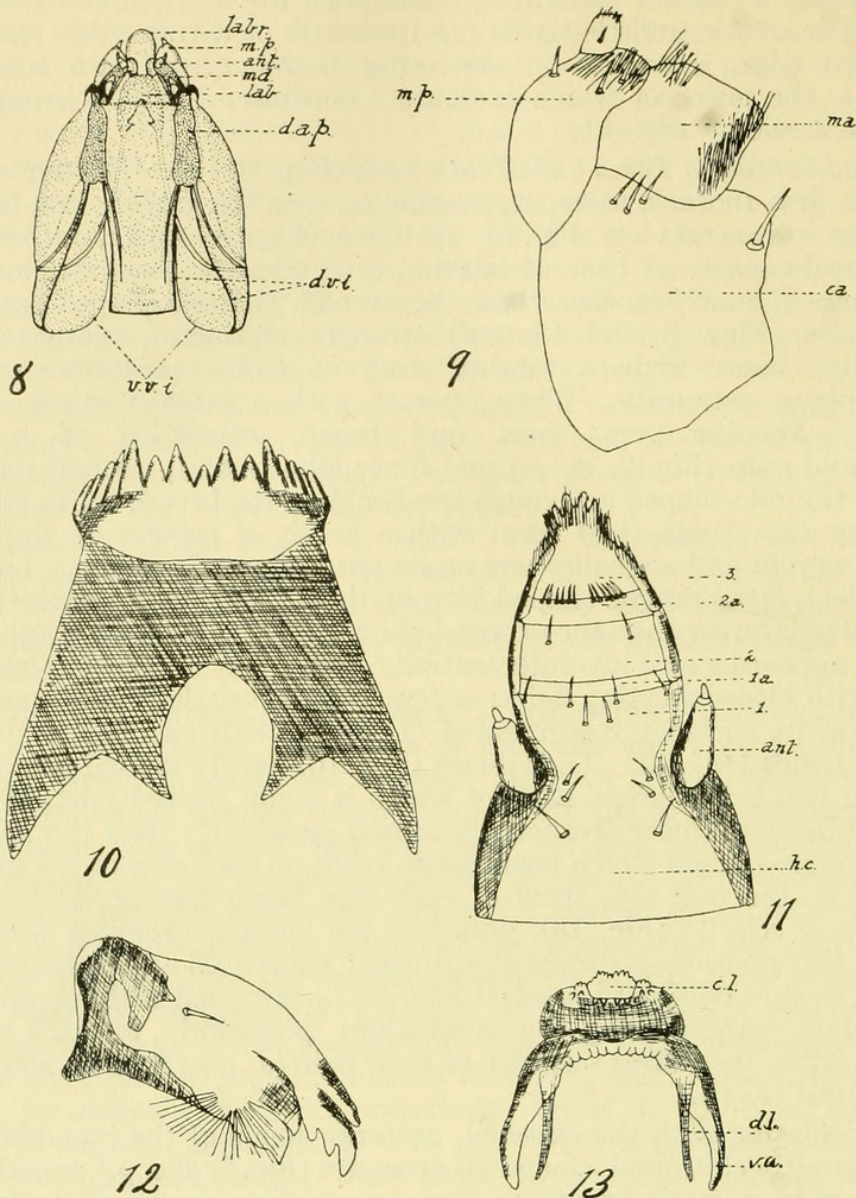
*Explanation has already been made that this term was adopted to signify the paired, ventral, locomotory tubercles of the abdominal segments.

transversely elongate, somewhat overlapped anteriorly by a cuticular fold. The oval-rounded stigma (*sp.*) consists of a transverse slit with scalloped edge, encircled on the outer periphery by two scalloped margins, the outer of which is densely chitinated. The stigmata are somewhat widely separate.

Head-capsule of Larva and Mouth-parts (Figs. 8-13).—Head retracted into the first thoracic segment, mandibles, maxillæ, labium and labrum apparent in ventral view (Fig. 8). Antennæ (Figs. 8 and 11, *ant.*) arising from head-capsule at base of labrum, 2-segmented, the first elongate, pear-shaped, much stouter than the second, thimble-shaped segment, Mandibles (Figs. 8 and 12, *md*) strongly chitinated, many-toothed ventrally, beset with a ventral tuft of hairs posterior to the odontophore extremity. They operate with a latero-vertical movement. Maxillæ very short and broad, consisting of a two-segmented palp (Fig. 9, *m. p.*) and inner lobe (*mala*); second segment of palp thimble-shaped and much smaller than the broad, splint-shaped, first segment; mala (*ma*) beset with a brush of bristles on its inner, lateral margin and a smaller one on its anterior, outer corner. Labrum (Figs. 8-11, *labr.*) tongue-shaped, terminating in four teeth anteriorly, the internal pair larger than the external pair; stoutly chitinated marginally, margin appearing as if involute ventrally, terminally and antero-laterally beset with close-investing hairs; a few, sparse, bristles distributed regularly on its surface; 3-segmented (1, 2, 3), with two paler intersegmental bands (1*a*, 2*a*). The labium (Fig. 10) deeply incised posteriorly to form two broad arms, each of which is again incised posteriorly in fish-tail fashion; more strongly chitinated posteriorly than the anterior odontophore margin which bears seven teeth on each side of the median small one, the first and third of each side being the largest. Hypopharyngeal sclerite (Fig. 13), dorsal to the labium, provided with two rows of tiny denticles; strongly chitinated; excavated anteriorly trough-wise, a weakly chitinated, central lobe (*c. l.*) provided with an anterior, denticulate margin filling the excavation; posteriorly, on each side, a pair of arms, the dorsal member of each pair (*d. a.*) more slender than the ventral (*v. a.*).

Articulating with the external, posterior angle of the mandible is a pair of stoutly chitinated, elongated processes (Fig. 8, *d. a. p.*), broadening considerably posteriorly where they are deeply incised to form two slender arms of which the outer, directed postero-laterally, is apparently continuous with an equally slender process given off ventrally from the labium; the inner tapers off gradually in the dorsal wall of the capsule. Anteriorly, from each dorsal, articulating process, there arises laterally a small process which partly encircles the ocular aperture. The slender, chitinous continuations of the various sclerites serve to support and strengthen the very delicate, transparent walls of the head-capsule.

In the walls of the capsule itself, (Fig. 8) there is dorsally on each side a deep, v-shaped incision (*d. v. i.*) separated by a tongue-process, sharply truncate posteriorly and ventrally, a similar incision situated medially and ventrally (*v. v. i.*).



EXPLANATION OF FIGURES.

- Fig. 8. Head-capsule of larva. *Labr.*, labrum; *m. p.*, maxillary palp; *ant.*, antenna; *md.*, mandible; *lab.*, labrum; *d. a. p.*, dorsal articulating process; *d. v. i.*, dorsal V-shaped incision; *v. v. i.*, ventral V-shaped incision. $\times 30$.
- Fig. 9. Maxilla of larva; *m. p.*, maxillary palp; *ma.*, mala; *ca.*, cardo. Camera lucida drawing. $\times 115$.
- Fig. 10. Labium of larva. Camera lucida drawing. $\times 160$.
- Fig. 11. Labrum of larva; 1, 2, 3, number of segments; 1a, 2a, intersegmental areas; *ant.*, antenna; *h. c.*, head-capsule. Camera lucida drawing. $\times 130$.
- Fig. 12. Mandible of larva. Camera lucida drawing. $\times 160$.
- Fig. 13. Hypopharyngeal sclerite of larva; *c. l.*, central lobe; *d. a.*, dorsal arm; *v. a.*, ventral arm. Camera lucida drawing. $\times 115$.

Pupa (Fig. 14).—Length from head to tip of abdomen, ♂, 11.7 mm.; ♀, 13.3 mm. Length from head to tip of tarsi, ♂, 5.9 mm.; ♀, 6 mm. Dextro-sinistral width at the wing-pad, ♂, 2.2 mm.; ♀, 2.8 mm. Dorso-ventral depth at the wing-pad, ♂, 1.4–1.6 mm.; ♀, 2 mm. Color leaf-green, thoracic spiracles grayish-white, margins of abdominal segments sub-translucent, eyes black in mature individuals.

Bases of antennæ arising between the cephalad half of the compound eyes, slightly divergent on either side of the mid-ventral line, more so in the male than in the female. In the *male*, the antennæ rather enlarged, bending round and closely applied to the anterior margin of the compound eye as far as the point where the palpi, reflexed antero-laterally, terminate; then directed postero-medially in the line between the fore femora and tibiæ, the extremity about on a level with the lobes of the labium. In the *female*, the antennal sheaths less stout, continuing around the anterior margin of the eye latero-posteriorly, abruptly bending posteriorly a short distance from their tips to terminate above and just beyond the proximal extremity of the second tibiæ; in mature specimens, the irregular, nodose segments of the adult antennæ apparent through the transparent sheath. Eyes large. Labium elongate, triangular. Head flat and broad dorsally, sloping back to the thorax, devoid of tubercles.

Pronotal breathing horns prominent, somewhat enlarged distally, directed antero-laterally with a distinct, ventral inclination. Mesonotum faintly wrinkled, pronouncedly arched, with two tubercles one on each side of the dorso-median line at the apex of the arch, directed cephalad and laterally; slightly anterior and external to these, a smaller tubercle at the base of wing-sheath. Metanotum devoid of tubercles, slightly wrinkled. The fore femur long, terminating on a level with the middle region of the eye, fore tarsi longest, hind tarsi shortest with a corresponding relationship in the comparative length of the segments of each tarsus. In the *female*, the tip of the hind legs just anterior to the caudal margin of the third abdominal segment, extending slightly beyond those of the first and second pair which are on a level; in the *male*, the tips of all three pairs of legs in alignment just anterior to the caudal margin of the second abdominal segment, the wing-cases completely overlapping the tibia and first tarsal segment of the hind legs.

Abdomen of eight segments, dorsally with the first segment half as long as the second; segments II–VII subequal in length, devoid of tubercles except in so far as small indistinct lateral protrusions may be so considered; segments with transverse wrinkles subparallel or curved, isolated or converging and confluent; lateral margins somewhat appressed. In the *male*, the eighth or terminal segment contains the genitalia of the adult; the ninth tergite a small, well-defined plate with posterior margin slightly concave, lying superior to but only partially covering the valve of the ninth pleurite with its recurved appendages which extend beyond, both laterally and posteriorly; the pleural appendages distinctly evident, recurving dorsally on each side of median line of the valve and terminating at the ninth tergite. From beneath, valve of hypopygium divided by a small, median notch into

two rounded lobes, the notch recurving dorsally to its termination at the posterior margin of the ninth tergite. In the *female*, the eighth segment encloses the ovipositor of the adult, tapering to a blunt, divided extremity; the dorsal valve deeply notched, completely obscuring and overlapping the smaller, ventral valve of which the notch is less than half that of the upper.

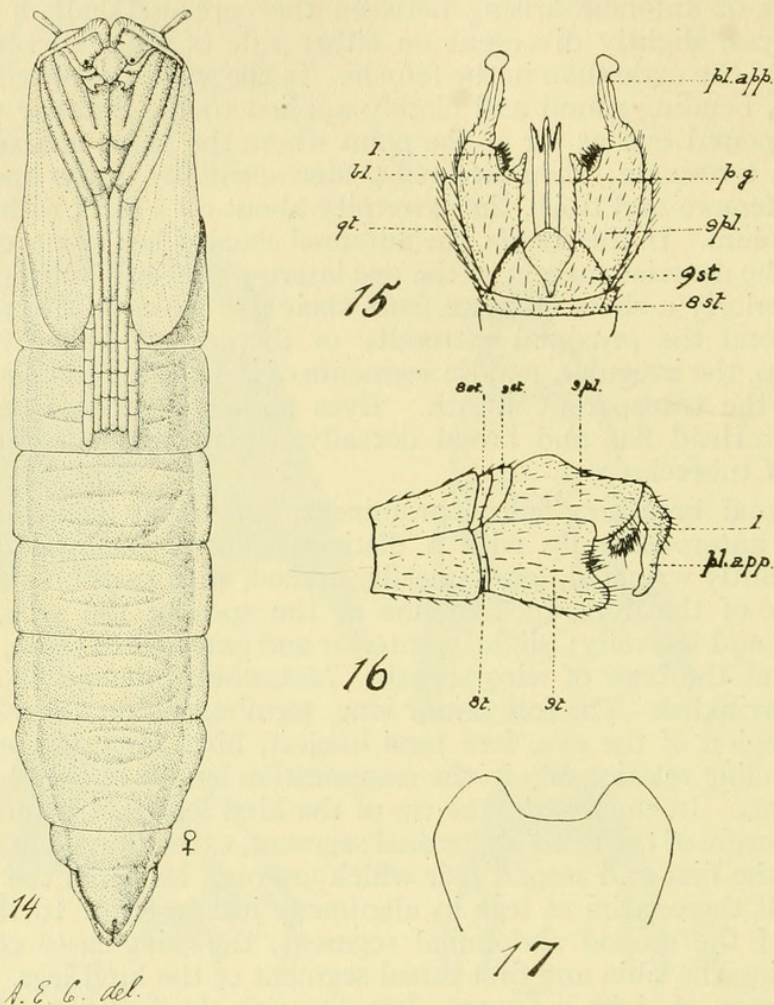


Fig. 14. Pupa (♀). × 8.

Fig. 15. Hypopygium (adult), ventral aspect; 8st., eighth sternite; 9st., ninth sternite; 9t., ninth tergite; 9 pl., ninth pleurite; l., pleural lobe; pl., pleural blade; pl. app., pleural appendage; p. g., penis guard. Camera lucida drawing. × 20.

Fig. 16. Hypopygium, lateral aspect, inverted; 8t., eighth tergite; other lettering as in Fig. 2. Camera lucida drawing. × 20.

Fig. 17. Ninth tergite. Outline of dorsal aspect. × 32.

Last larval skin invariably persistent, attached to the pupa which is only partially withdrawn; head, thorax and first four abdominal segments exposed, the remainder enclosed in the exuvium; moulted, larval head-capsule ventral to the fifth abdominal segment of pupa; posteriorly, the exuvium collapsed and wrinkled, its terminal segment adhering to the support by the anal pseudopodia.

Eggs described from numerous specimens collected from host-plant in breeding-cages at Royal Oak, Victoria, V. I., May 25, 1917, and from several found at Westholme, V. I., May 31, 1917.

Larvæ described from numerous specimens collected in rich woodland at Westholme, V. I., May 3, 1917.

Pupæ described from several specimens, ♂ and ♀ reared from larvæ at Royal Oak, Victoria, V. I., killed May 9, 1917, and from several taken at Westholme, V. I., May 15, 1917, killed on same date.

Adult.—The species was first described by Doane* in 1900, who gave it the name of *Cylindrotoma splendens*. His specimens, three males, were obtained from Unalaska. In 1901, Coquillett† redescribed the species under the name of *Cylindrotoma juncta* from a male specimen collected at Virgin Bay, Prince William Sound, Alaska.

The following is Doane's description:

"*Cylindrotoma splendens*, sp. now. (Pl. VIII, Fig. 21).

Pale yellow and black; head very pale yellow almost whitish; occiput, front, rostrum and palpi brown; first and second segments of antennæ whitish, first with a brown ring, other segments brown, cylindrical, if bent back they would reach to about the middle of the first abdominal segment; thorax very pale yellow or whitish; dorsum with three opaque black stripes, the lateral ones merge anteriorly into broader brown stripes which curve in and meet the median stripe; collar with a black band; a large, black spot on the pleura between the base of the wing and the anterior coxæ, another over the anterior coxæ, and another between the first and second pair of coxæ; a smaller one just in front of the base of the halteres, and a double one on the posterior border of the metanotum; scutellum with a median, brown stripe; halteres pale, slightly infuscated above and at the tips; legs brown, base of femora lighter; tarsi and tips of the tibia darker; abdomen black; male forceps large, brownish posteriorly; wings rather narrow, hyaline; stigma pale, veins brown; auxillary vein ends abruptly just before the stigma; the small, cross vein connecting the first longitudinal vein with the costa is very faint and situated a little beyond the middle of the stigma; submarginal cell either longer or shorter than the first posterior cell. (In two of my specimens it is longer in one wing and shorter in the other.) Thus the præfurca may either end in the submarginal cell or in the first posterior cell; five posterior cells, the second sessile; discal cell elongated, somewhat pointed ante-

*Doane, R. W. New North American Tipulidae. Jour. N. Y. Entom. Soc., Vol. VIII, Sept. 1900, p. 197. Pl. VIII, Fig. 21.

†Coquillett, D. W. Diptera Entomological Results. Papers from the Harri-man Alaska Exp. IX. Proc. Wash. Acad. Sci., Vol. II, pp. 389-464, 1900, p. 401.

riorly; posterior cross vein a little before the middle of the discal cell; fifth vein incurved at the tip. Length, male 9 mm.; wing 9 mm."

"*Habitat*: Unalaska, three males. (Kincaid) Type No. 145. Wash. Agric. Coll. and S. of S."

Hypopygium (Figs. 15-17).—Mr. Alexander has very kindly aided in interpreting the relationships and disposition of the various sclerites which compose the hypopygium. In a letter under date of Sept. 26, 1917, he gives a lucid explanation of the whole structure.

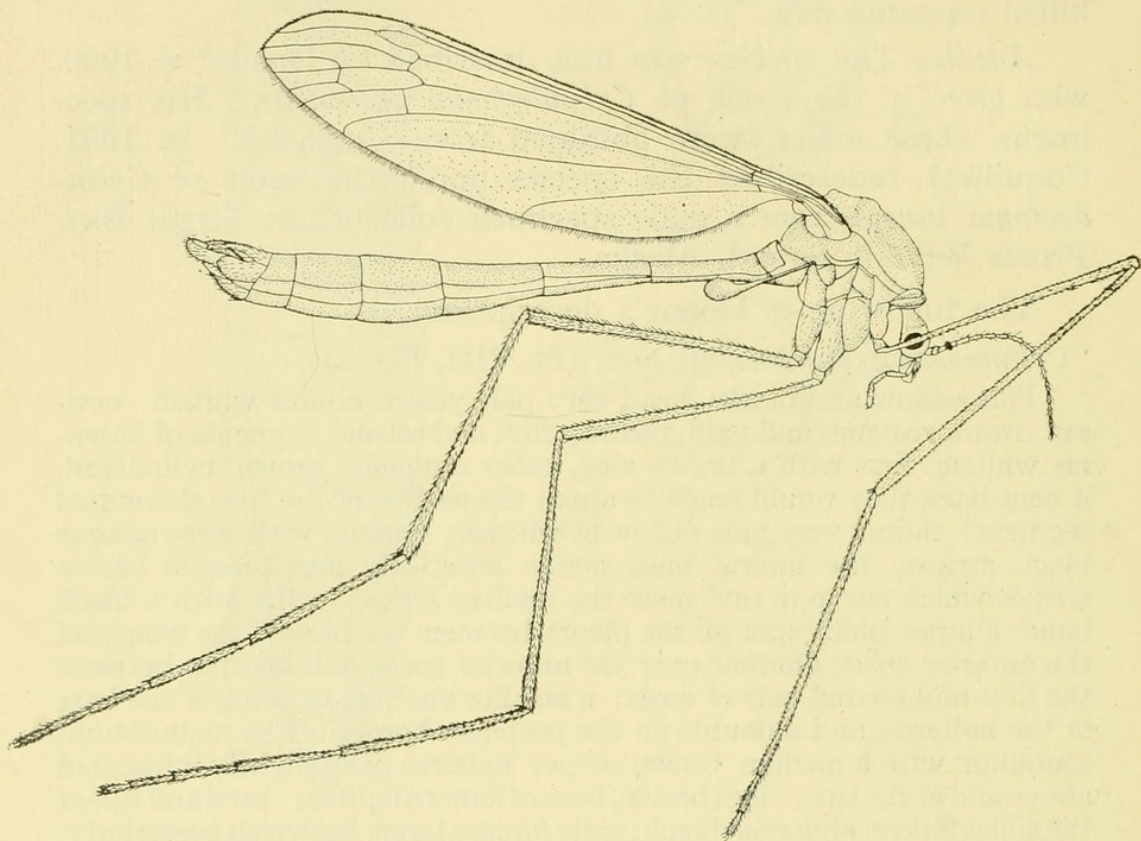


Fig. 18. Adult female. $\times 6.5$.

"The ninth tergite (Fig. 17) large, prominent, the caudal margin with a deep, broad notch, the adjacent lobes rounded at their apices. Ninth pleurite (9 *pl*) (Figs. 15 and 16, *pl*.) prominent, the inner margin at the tip produced caudad into a small flattened blade (*bl*.), a projection of the pleurite; pleural appendage (*pl. app.*) large; fleshy lobe (*l*.), on dorsal face of pleurite densely beset with fine hairs. Ninth sternite (9 *st.*) small, deeply split on the mid-ventral line by a very acute angle. Penis guard (*p. g.*) trifid with numerous appressed teeth on the inner edge of the lateral arms."

This paper would be incomplete were I not to express my gratitude to Mr. C. P. Alexander, of Cornell University, who, as a keen student of the Tipulidæ, showed extreme interest in the progress of the work. To Mr. E. W. White and Mr. W. Downes I am also grateful, the former for first bringing the larvæ to my notice and the latter for carefully attending to the immature larvæ during my absence this summer in Saskatchewan.

SUMMARY.

C. splendens belongs to the sub-family Cyindrotomini of the Tipulidæ. The species, the life-histories of which are known, are peculiar among crane-flies in that the larvæ feed openly on Bryophytic and Spermatophytic plants.

The adults first appear about the end of May on Vancouver Island. Their distribution is apparently determined by their foodplant, *Trautvetteria grandis*, which is confined to moist, rich woodlands.

In ovipositing, the female cuts a slit in the epiderm on the under surface of the leaf by means of its saw-toothed ovipositor. The sub-translucent glistening white eggs are partially concealed. They are generally deposited in series along the margin. A few eggs may be laid on the upper surface also.

The period of incubation occupies about 2 to 3 weeks.

The recently-emerged larvæ feed on both the upper and lower surfaces of the leaves and as they develop, they eat out large holes. There would appear to be at least three moults before pupation, one previous to hibernation and two after. In their movements the larvæ show a marked resemblance to "looper" caterpillars.

About the end of July, the larvæ, now in the second-stage, cease feeding and become quiescent. In this condition they hibernate among the dead leaves. Some remain leaf-green in color, whilst others assume the dirty-brown hue of decayed leaves.

In the spring they resume feeding and grow more rapidly until they pupate in the middle of May. The pupal period lasts for 6 to 10 days. The last larval skin is only partially shed and serves to attach the pupa to the leaves and petioles.



Cameron, A. E. 1918. "Life-History of the Leaf-Eating Crane-Fly. *Cylindrotoma splendens*, Doane." *Annals of the Entomological Society of America* 11, 67–89.
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