Snare Building and Pupation in *Bolitophila luminosa*

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Abstract

Details are given of snare building, mucus secretion, pupation and emergence of the New Zealand glow-worm, *B. luminosa.*

In a previous paper (Gatenby, 1959), it had not been possible to report on pupae or pupation, and on certain aspects of snare building. Three pupae were subsequently examined in early March, 1959, and the junior author, who helped to watch captive specimens, was able to take some interesting electronic flash photographs of the feeding, pupation and emergence, but these came too late to include in the previous communication.†

The externals of three pupae have now been studied. One of these, the Waitomo specimen, a female, had been crushed in transit, but it proved useful. The other pupae were intact and have been drawn in Text-fig. 2, Figs. 5 and 6.

Observation of glow-worms is somewhat difficult owing to the fact that they are nocturnal, and disturbed by the light of the flashlamp. The reactions of glow-worms to light passing through various coloured screens is not yet known; the best that could be done was to flash on the light quickly for the time only necessary to ascertain what they were doing, and then to move up the necessary apparatus for the electronic flash photograph.

These notes were brought together in Sydney, Australia, and the senior author thanks Professor P. D. F. Murray for facilities in his laboratory. The photographs were developed and printed by Mr. John Sloan, Chief Bacteriologist of the Auckland Women's Hospital, New Zealand. Dr. Salmon, of Victoria University, Wellington, was ever ready to discuss various points in connection with this work, and kindly corrected and saw this paper to press, during the absence of the senior author. Dr. A. R. Woodhill, of the Entomology Department of Sydney University, kindly discussed the segmentation of the dipteran pupa, and helped to get specimens of the unnamed New South Wales species, which is now being studied. The authors once again have to thank Mr. H. R. Sear, Chief Guide at Waitomo, for help.

The Construction of the Vertical Lines

These are usually no longer than an inch in the case of glow-worms living on banks outside, but may be much longer as in caves like Waitomo and Waipu. It has been stated that in Waitomo the lines may be 24 inches in length, but this is said to be exaggerated, 16 or 17 inches being the longest. We have seen vertical lines 3 inches in length within a hole in an outside bank. The problem is how the glow-worm constructs such long lines. Those even a foot long must be comparatively weighty and perhaps could be difficult for the glow-worm to manage. However, it must be remembered that the glow-worm is surprisingly strong, and can push aside and escape from a 1-inch square coverslip with water between it and the slide.

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† The Editors of the Journal of the Royal Microscopical Society of London state that they are publishing a paper on the histology of the larva of *B. luminosa*, by Dr. Gouri Ganguly, in Vol. 79, part 2, about June 30, 1960.

On the banks at Arapuni, at night, it is possible to find some glow-worms in the act of producing new vertical lines. In Text-fig 1, Fig. 1, the new line, the sixth, is seen to be held in the mouth of the glow-worm. The worm presumably first produces a mucus droplet, in the centre of which runs the silk thread: this is lowered, and the silk thread is lengthened and another droplet is produced. During the secretion of the mucus droplet, the worm makes slow, convulsive movements at its anterior end which appear to be peristaltic, and the mucus collects around the head as in Text-fig. 1, Fig. 2, M. The worm pulls its head out of the droplet, which remains on the silk thread. Something like this observation was previously made by Albert Norris. So far as can be judged from quick examination by flashing on the light at intervals so as to alarm the worm as little as possible, the production of the mucus droplet is not rapid. From the anatomy of the parts concerned, we know that the musculature of the mucus glands is scanty, and the mucus has a considerable distance to pass along the oesophageal valve and oesophagus. In the previous paper it was shown that about 60 mucus droplets had been produced by a captive glow-worm in the space of three hours, but not all this time had been devoted to mucus secretion. There is no evidence that the worm cuts and adds lengths to an already constructed and fixed vertical line, and the only possible conclusion is that very long lines have been secreted at one sitting by one glow-worm, and have been lowered from above. If a vertical line is removed by fine forceps and laid on a glass slide for examination by the microscope, the droplets are seen to contain a small number of short, opaque inclusions as depicted in Text-fig. 2, Fig. 5A. The nature of these stick-like bodies is unknown; they may assist in keeping the mucus droplets *in situ*. So far as could be ascertained, each droplet is nearly spherical when secreted, but certainly in snares outside on banks, becomes somewhat irregular, presumably by evaporation. It will be seen in Text-fig. 2, Fig. 5A, that the droplets tend to pull down to a pyriform shape, and the silk thread in the initial droplet (the lowermost of the three) may be turned up. In some cases it is frayed at the end. Good preparations of the snare were made by holding a cover slip vertically and wiping the snare on it. When dried these smears stain well in Leishmann's blood stain, the silk being deep blue, the mucus reddish. The droplets are not so sticky as those on the snare of the British Epeira, nor is the silk so strong as in this spider. The multiple silk line (or lines) which forms the horizontal runway is very strong.

The Condition of the Snares in the Morning

At Arapuni, places occupied by glow-worms on a bank were examined during the daytime. It is not easy to find the snares, except those well within marked holes in the bank. The majority of the snares found were tattered, and needed repair. There had not been a storm during the previous night, but there had been a slight breeze. It is believed that after dark the glow-worm living outside on banks, works for some hours mending its net and producing new mucus droplets; most of the prey is probably captured after midnight, when the lights seem to be brightest. The snares built in caves, or in particularly deep holes in banks, would not need repairs unless partially destroyed by struggling prey.

The Method of Feeding by the Larvae

As has been mentioned, a captive glow-worm which has lowered vertical fishing lines can be fed on flies. The house fly (*Musca domestica*) is somewhat too large, and it must be stunned or else it will tear away the whole snare. In nature the food consists mainly of midges and Microlepidoptera. The stunned fly was placed at the bottom of the vertical lines, usually two lines being necessary to suspend the fly. After dark, or about an hour after the worm had been offered the fly, the former climbed down the vertical lines, punctured the fly (Pl. 9, Fig. 10), and began to

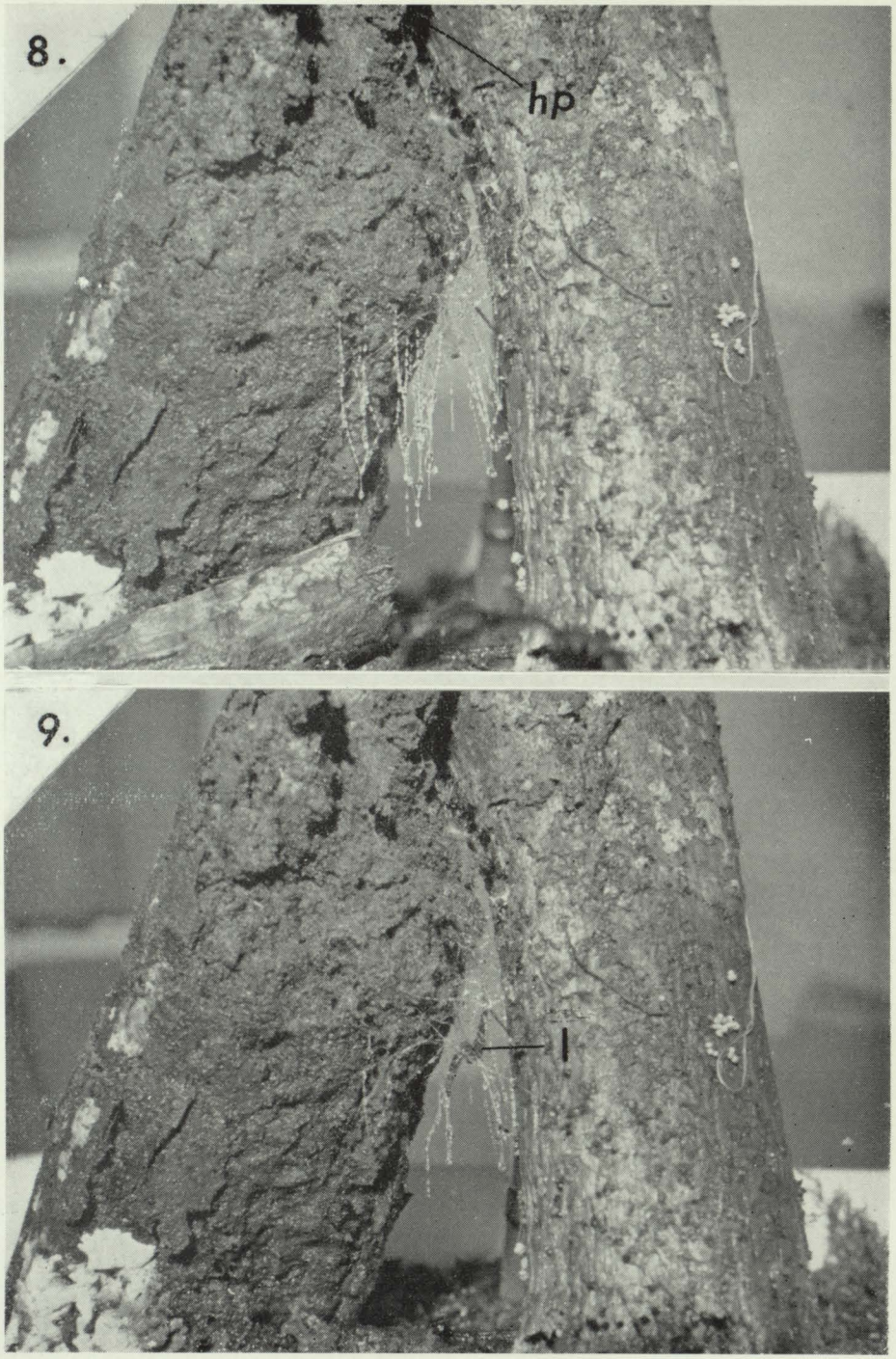


Fig. 8—Two small rotten boughs pinned together leaving space for hanging snare lines which have been partly tangled owing to the tray not being carefully enough carried from table to the place for photographing (8 p.m.). Fig. 9—The larva descends from its hiding place above to inspect and mend the damage (10 p.m.).

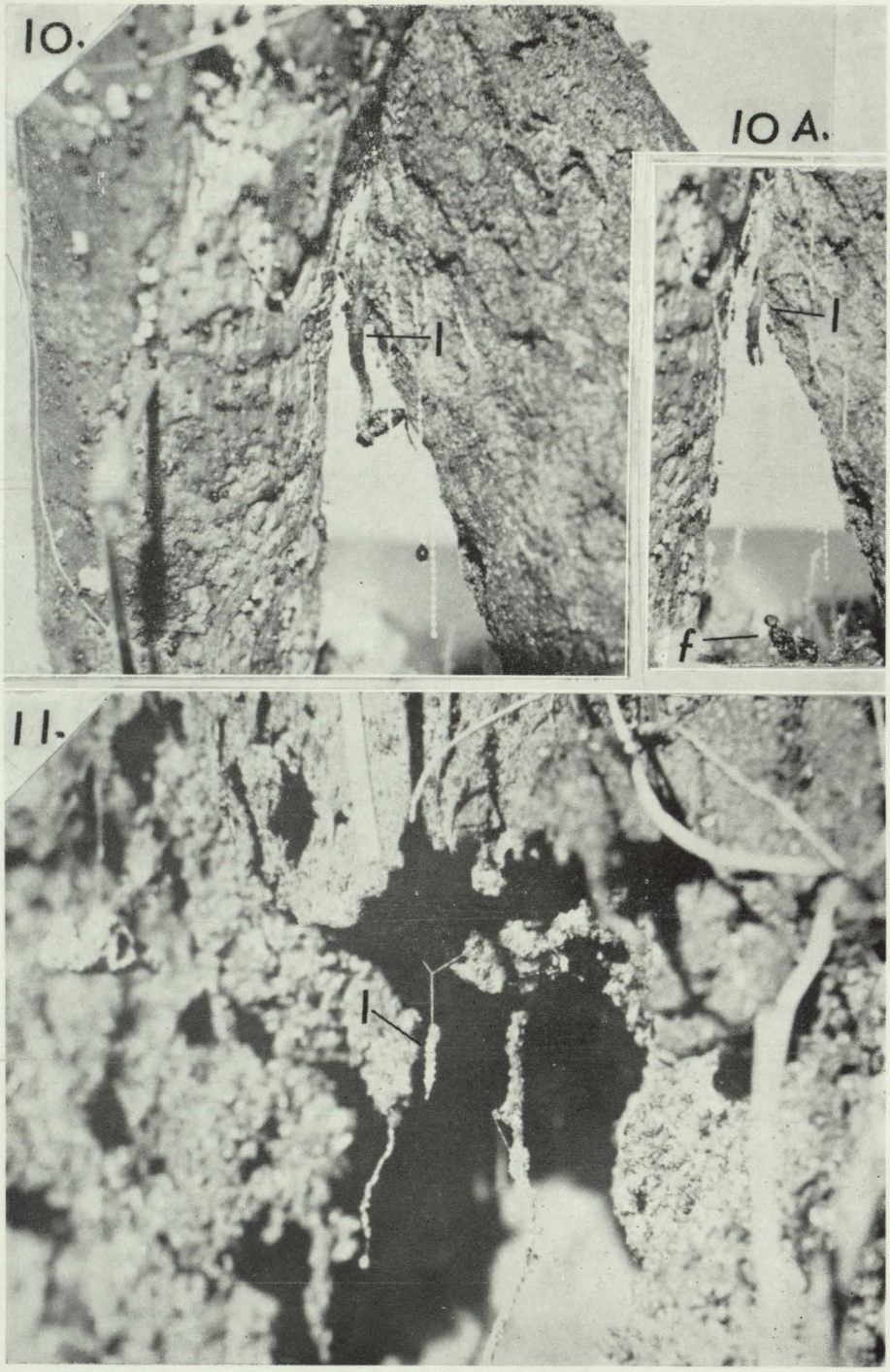


Fig. 10—The larva has pulled up a house fly and is sucking out its juices. The snare has been mostly demolished by struggles of prey, and the dragging up. Inset on right, disturbed by a flashlamp, the larva drops the fly and retreats to its hiding place. Note mucus on carcase of fly. Fig. 11—The suspended pupa in a cavity in a bank at Arapuni. The soil around was crumbling sandy gravel. This was the only pupa found during six months search.

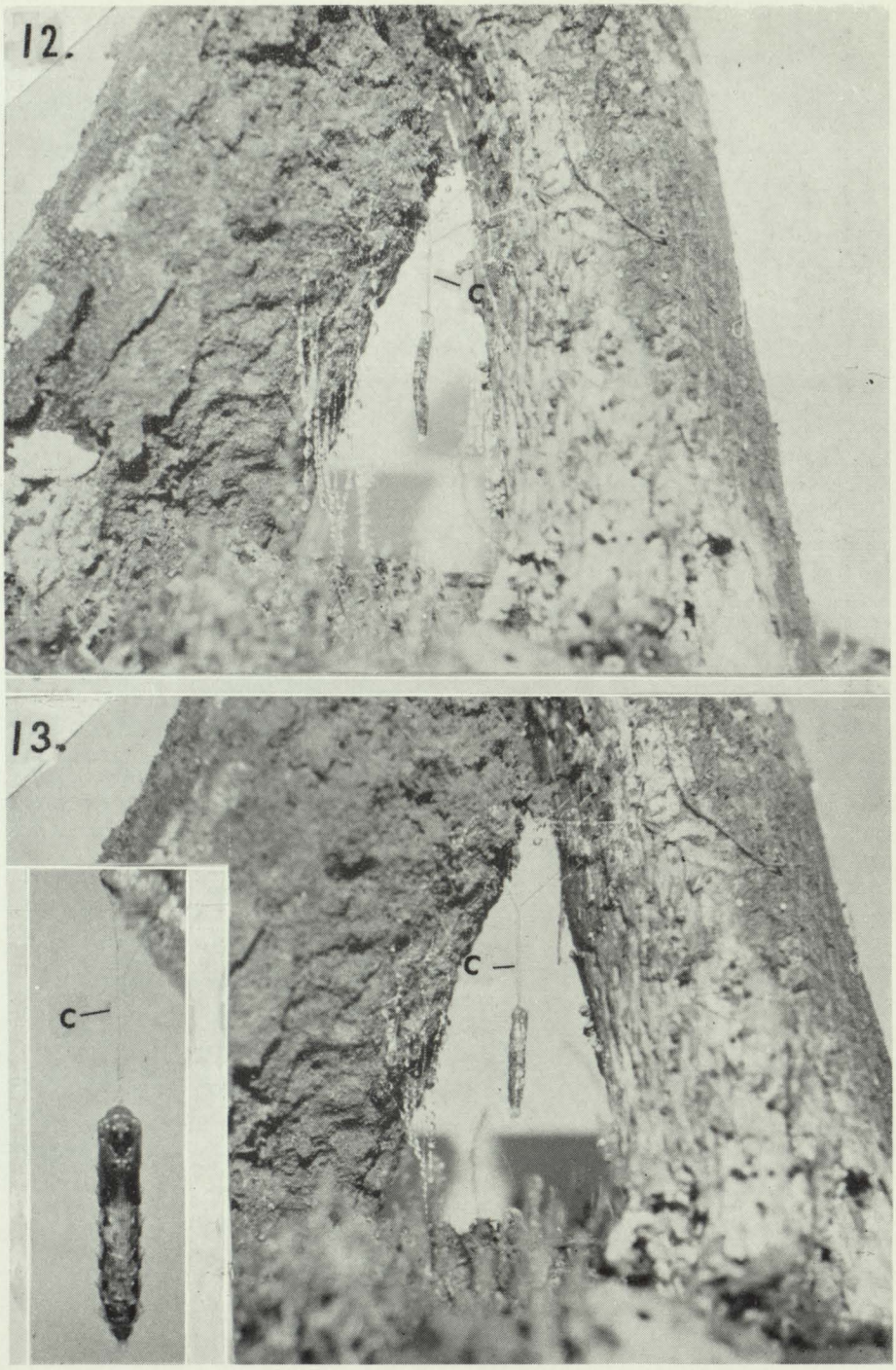
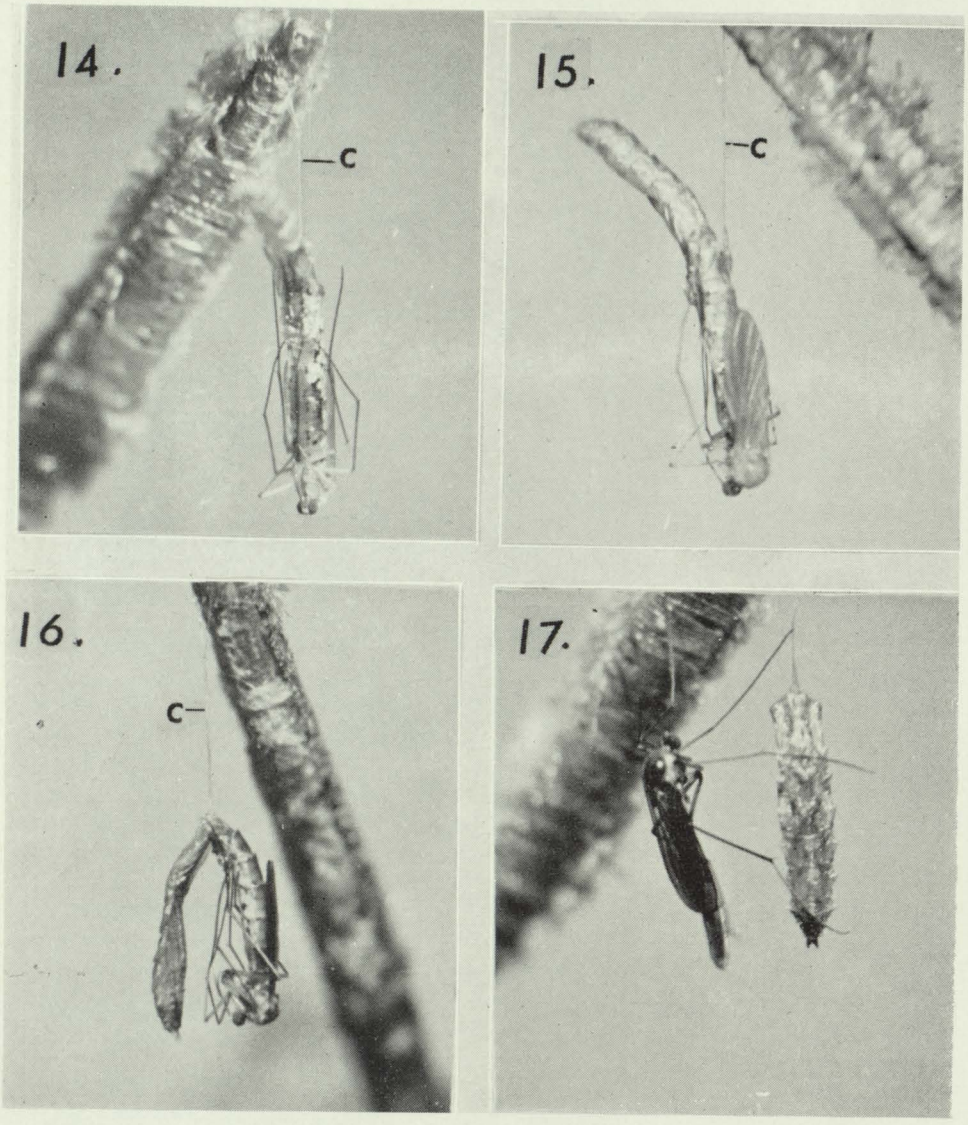
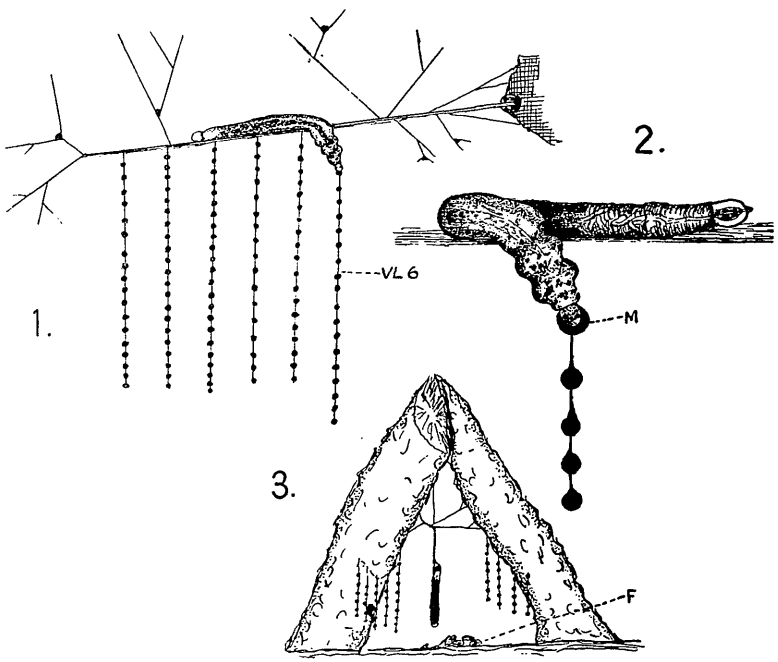


Fig. 12—The larva in Fig. 10 has now suspended itself after clearing away the sticky vertical lines around it. Clearance 20 mm on each side. Fig. 13—Next day it had pupated. The clear ultimate segment, also seen in the previous figure, is, in this photograph, partly covered by the larval exuvia. On the left inset, is a lateral view of another pupa which shows tapered suspensory cord (C) as depicted in Pl. 10, Fig. 13.



Figs. 14-17—Stages in the emergence of the female imago from the pupa shown on the left of Pl. 10, Fig. 13.

turned out. Either by the struggles of the fly, or by the dragging upwards of the fly by the glow-worm, the major local part of the snare is destroyed as in Pl. 9, Fig. 10. Sometimes the fly is found to have been dropped subsequently by the glow-worm beneath the snare as in Pl. 9, Fig. 10A, the carcase is shiny, being covered with mucus from the tangled web; eventually over a period of weeks, sucked-out bodies of flies collect beneath the snare. In other cases, if the insect offered had been small enough, the remains of the carcase were found adherent to an outer part of the snare. Before morning the satiated worm had mended the broken snare. The worms were never seen to come down suddenly when the fly was placed on the snare, as happens with spiders, but this may be due to the fact that captive worms were over fed, or were merely cautious. It has been concluded that the larva neither pulls up the lines which have snared the prey by turning its body, nor does it use its mouth parts for this purpose. In all cases observed, the worm stretched down, holding on to various lines undoubtedly by means of the roughened segmental bands on its body, and proceeded to feed. Only after that did it attempt to haul up the snared prey, holding it by its jaws, and as has been pointed out, in doing



TEXT-FIG. 1.—Fig. 1—Diagram of production of a vertical line. Five lines have already been made, and the larva is holding a sixth just prior to attaching it near the horizontal runway. Fig. 2—The mucus droplet just before inclusion on the vertical line surrounds the larval head, which is then pulled out of the mucus, and the silk line then continued until the next droplet should be placed. Fig. 3—Diagram of suspension of larva prior to pupation. The vertical lines have been cleared away, so as to leave a free area for the eventual emergence of the adult. The suspensory thread is a new production, not the converted runway. Carcases of flies at F.

suck out its juices. If alarmed by the shaking of the table or by the flashlight, the worm retreated (Pl. 9, Fig. 10A) but re-engaged shortly after the light had been so dragged up the tangled local vertical lines as well as the carcase. These remarks refer to well fed worms in captivity. Undoubtedly the worms in caves consume most of the small midges they live on.

Disposal of Faecal Matter

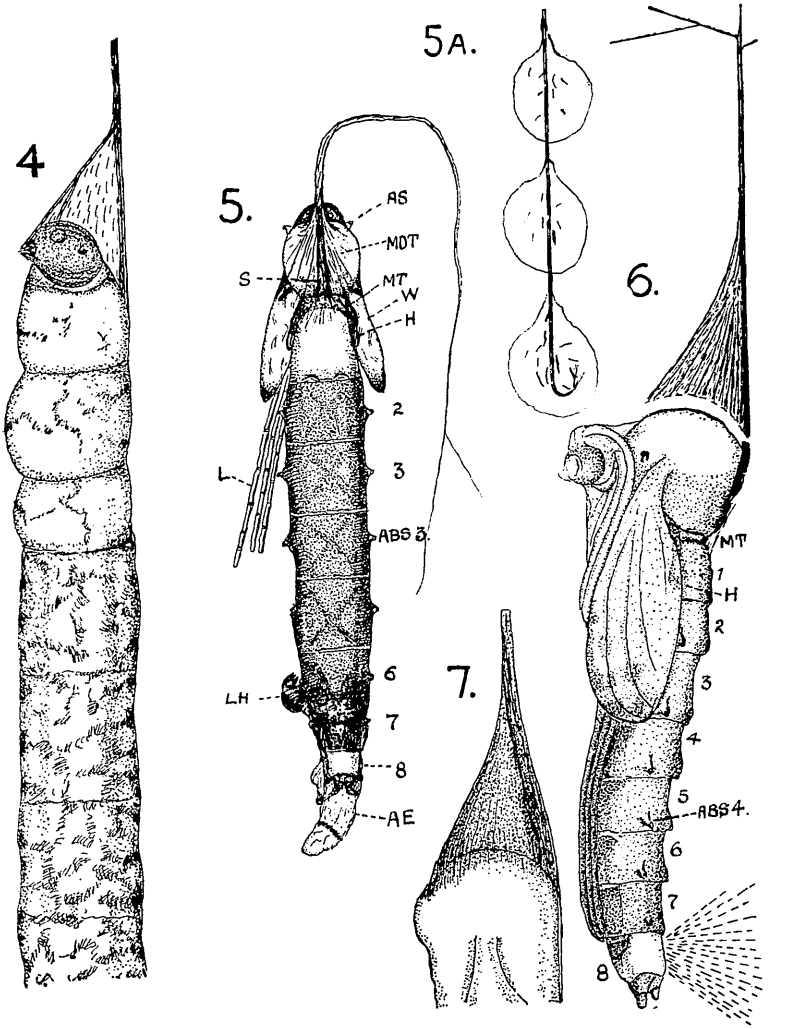
Perhaps one of the peculiarities in the anatomy of *Bolitophila luminosa,* which has not been stressed as much as desirable, is the absence of digested food in the intestine. Digestion takes place entirely in the mesenteron, and a portion of its liquid contents passes quickly through the intestine and is immediately voided. It seems likely that this is in some way connected with the proximity of the intestine to light organs; presumably a mass of collected undigested matter lying upon the luminescent organs would interfere with their control and functioning. The captive glow-worms which were fed often on house flies were seen at times to regurgitate a yellow drop of food which fell down below the snare. In other instances, liquid faecal matter was voided on to, and ran down one of the vertical lines. It is certain that an anal opening is present and functional.

Pupation

In the previous account no pupae suitable for examination could be described. Two pupae were seen in March. The first, a male, was discovered at Arapuni, amidst a group of glow-worms, and a photograph of it is given in Pl. 9, Fig. 11, and a sketch in Text-fig. 2, Fig. 6. It was glowing as brightly as the glow-worms nearby, and it doused its light at the same time as did the neighbouring glow-worms when the flash-light was turned on the area. This pupa was only 9 mm in length, and was not sticky. It was suspended by a dry stiff thread 6 mm in length, which forked unevenly where it became attached to the bank. The pupa was detached from its position with a grass stem wetted at the end. Before it was touched, however, its reactions were observed for some time. It occasionally doused completely for as long as 15 minutes, and often glowed faintly. While it appeared to sense the presence of the observer, its behaviour was not quite the same as that of the glow-worms, for these soon lighted up again when the flashlight was put out, whereas the behaviour of the pupa was unpredictable. On arrival home, the pupa was examined with dissecting spectacles, and owing to accidental touching, the suspensory thread parted from the thorax as depicted in Text-fig. 2, Fig. 6. The region of parting (mainly meso-thoracic) was clear of pigment, and of a dome-like nature. The pupa itself was not injured, and was placed on a leaf in a tin box. When this was opened in the morning, the pupa glowed brightly for about half a minute. It turned on the light certainly within three seconds, the light becoming gradually visible like the hot wire on an electric radiator just switched on. It was concluded that the pupa was aware of the flashlight turned on it, and that it was able to light up more quickly than had previously been expected. The pupa was able to move its abdomen slightly but not so actively as the pupae of some other holometabolous insects. This pupa was fixed in Carnoy for sectioning.

The second pupa observed, a female, had undergone pupation during captivity. It metamorphosed from a large larva taken in the Botanical Gardens at Wellington during late January, and immediately adopted as suitable the arrangement of rotten boughs shown in Pls. 8, 9 and 10, Figs. 8–13. The larva (Pl. 8, Fig. 9) was fed on small house flies, whose wings were snipped off, and their head slightly squeezed so as to stun but not to kill them. The boughs were enclosed by an inverted chemical beaker 7in in diameter resting on wet earth. This larva, then 25 mm in length, was fed for more than six weeks, and it was therefore at first assumed that

it was not going to metamorphose during summer; but on the night of March 9, it was seen to be working away at the vertical lines of its snare. No special significance was attached to this, but on the morning of March 10, it was found suspended as in Pl. 10, Fig. 12, all vertical lines around it having been cleared away. The clearance was 20 mm on each side. Next morning it had pupated as in Pl. 10, Fig. 13.



TEXT-FIG. 2.—Fig. 4—Newly suspended larva before pupation. Same specimen as in Pl. 5, Fig. 12. Fig. 5—Pupa 24 hours later, as in Pl. 5, Fig. 13. Fig. 5A—Three bottom droplets in vertical snare line, showing inclusions in mucus. Fig. 6—Pupa, as in Pl. 4, Fig. 11. Fig. 7—Thorax and suspensory region of newly metamorphosed pupa.

This pupa, a female, was 12½ mm in length, and the suspensory thread was 10 mm before it forked. At this time the silken support was distinctly yellow. This pupa was fixed in Carnoy on March 13 during late morning. It will be noted that the larva was shrunken in length after pupation.

An attempt was made to examine closely the suspensory thread. By removing a microscope tube from its base, and holding this by hand, the appearance shown in Text-fig. 2, Fig. 4 was noted. There seemed to be a triangle of threads, one to the dorsum of the thorax, and two passing to the mouth region. A flat membrane appeared to stretch to each front line, from the thread attached to the dorsum of the thorax. Next morning the space between the threads appeared to be filled out with fluid as in Text-fig. 2, Fig. 7. Owing to the rarity of the specimen, it was not possible to risk touching it, but it did seem that mucus or liquid silk was passed upwards just before pupation, and when the larval skin split, this fluid presumably touched the emerging pupae skin and anchored it as the larval skin was discarded. In Text-fig. 2, Fig. 5, the larval skin has been sloughed down, the head capsule at (LH) and the remains of the body cuticle at (AE). The pupa then three days old, was fixed in Carnoy, the legs (L) and developing wings (W) becoming loosened from the body. This pupa has been drawn from the dorsal surface and may be compared with the obviously more mature pupa got at Arapuni (Text-fig. 2, Fig. 6).

It is interesting that this larva from the Wellington Botanical Gardens, which appears in the series of drawings and photographs, Text-fig. 2, Figs. 4 and 5, and Pls. 3, 4 and 5, Figs. 8–13, never showed its light after it had adopted the site for its snare shown in the figures. The reason for this is unknown—but it might have been injured during capture. Nevertheless it led an active life during the weeks it was observed, and successfully pupated.

It could not be claimed that a satisfactory explanation of the fixation and origin of the suspensory line has been given. This will need close observance of more pupating larvae, and perhaps more satisfactorily, the killing of metamorphosing larvae at different stages so that the attachment of the line to the pupa can be examined properly under high powers of the microscope. But it is now clear that the suspensory cord is not a part of the thorax, that it is specially secreted, and that it is not the horizontal runway; the colour of the cord was yellowish after three days, and it becomes brown in the maturer pupa. If the cord is silk, as we believe, it appears that the silk must be mixed with some substance which goes yellowish brown on exposure to the air. This material might come from the mucus glands, but as has previously been reported, the mucus droplets of the larval phase are colourless. In older pupae and pupal exuviae, the main part of the suspensory cord is light chitin-brown in colour.

It should be mentioned that only one pupa was found in the field after six months searching at frequent intervals from late September to early March.

The Externals of the Pupa

In Text-fig. 2, Fig. 4, is the larva just before metamorphosis, also shown in a photograph on Pl. 5, Fig. 12. This changed into a pupa during the following night, and is shown in Text-fig. 2, Fig. 5, and in photograph on Pl. 5, Fig. 13. This early pupa is three days old, and is drawn in Text-fig. 2, Fig. 5, from the dorsal surface. At (MOT), is the mesothorax, and the suspensory cord (S) is spread over this extending down below the metathorax (MT). The haltere is at (H), and there are seven spiracular openings, the first at (AS) in the front of the mesothorax, the others abdominal, the third at (ABS 3). The wings (W), and legs (L), are shorter than in the older pupa shown in Text-fig. 2, Fig. 6.

In the latter figure, the pupa photographed in Pl. 9, Fig. 11, is seen from the side. The anterior spiracle is seen between the antenna and the base of the wing. In this pupa, the wings and legs have attained their full size.

EMERGENCE OF THE IMAGO

Before leaving New Zealand, the senior author placed several larvae from Arapuni on the two rotten boughs seen in the photographs. One specimen took up residence and made a complete snare, and was luminescent at night. It was fed on house flies and was watched by the junior author. It pupated on April 5, taking 24 hours to slough its larval integument. On April 13 emergence of the female adult began, which took 24 hours. It did not fly for 48 hours, and was still flying actively up to about April 19, when it appeared weaker, and was fixed in Carnoy. Several electron flash photographs were taken and appear on Plates 3–6.

The actual pupa is shown in the inset on the left of Pl. 10, Fig. 13. Before the photographic apparatus could be collected, the imago had pulled itself out of its pupa case as shown in Figs. 15 and 14, the former photograph being a little earlier. It will be noticed that the emergent adult over-balances so as to reverse the direction of the pupal body. When the imago is nearly free, the pupa case (Pl. 11, Figs. 16 and 17) resumes its former position. This was first recorded by Mrs. S. Gibbs, in 1925. In Pl. 11, Fig. 17, the imago, a female, is free of the pupal integument.

LUMINESCENCE OF PUPA AND IMAGO

There are now a number of careful observations which show that the pupa can luminesce. Three adult females and a male have been seen by us and did not luminesce. So far as we have been able to ascertain, Hudson alone has noted that the female adult can luminesce, and in a previous paper it was shown that both sexes have luminescent organs in the adult, those of the male being somewhat shrunken. It has been mentioned, too, that flying lights have not been recorded in caves or gullies where glow-worms live. One of us (S. C.) watched a female adult during emergence, and for about a week never saw it light up. These observations appear to indicate that the luminescent organs of the female are not used to attract the male; confirmation of Hudson's observation must be awaited, but it should be mentioned that his account of luminescence in the female is categorical.

DEVELOPMENT OF EGGS IN THE PUPA

In the two female pupae examined, large eggs were present, and it is presumed that these are ready to be laid after emergence and pairing of the adult female.

SUMMARY

1. A single hanging vertical line of the snare appears to be secreted at one time, and there is no evidence that a pre-existing line is cut and a new piece joined, so as to make a combined line. In all cases the lines are lowered from near the main runway, and there is no evidence that a line is first fixed and then secreted and hung from the side or from below.
2. In cases where the snare lines are about an inch in length, it is certain that the worm climbs down the necessary distance to reach the snared prey. The latter is not recovered from the runway by the worm rolling the lines around its head end, or by gathering relevant lines in its jaws.
3. The mucus droplets as secreted first flow around the head, and the droplets are placed *in situ*, by the worm pulling its head out of the mucus.

4. What appeared to be an adult worm was caught and fed for six weeks before it pupated. It seems obvious that glow-worms mature slowly at this period.
5. The glow-worm about to pupate clears away the nearby sticky lines, leaving a clearance of at least 20 mm on each side. It then becomes suspended on a silken thread usually about the length of its body. The clearance of sticky droplets, and the suspension of the pupa, provide a certain degree of safety for the pupa, and for the adult at the time of emergence.
6. After three days, the suspensory cord is seen to be yellowish in colour. It finally becomes chitin-brown in older pupae. The cord appears to be formed of silk threads gummed by mucus.
7. The suspensory thread is not the converted runway. It is a new formation which has a main dorsal thread attached to the meso- and meta-thoracic regions, and appears to form a part of the pupa. However, it separates from the thorax if roughly handled, the dorsal thread breaking at its junction with the thorax.
8. The single male pupa observed glowed as brightly as neighbouring larvae. It doused at the same time as the latter, but did not light up when they did. Unlike the larvae it glowed faintly for periods. It lighted up in a few seconds when the tin container was opened in the morning.

Literature

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Lettering. ABS, abdominal spiracle; AE, larval exuvia; AS, anterior spiracle; C, suspension cord; F, carcase of house fly; H, haltere; HP, hiding place; L, larva; LH, head capsule of larva; M, mucus; MOT, mesothorax; MT, metathorax; S, suspensory thread; VL, vertical snare line; W, wing.