Notes on the New Zealand Glow-worm, *Bolitophila (Arachnocampa) luminosa*

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Abstract

Information is given on the morphology, anatomy, physiology and life history of the New Zealand glow-worm *Bolitophila luminosa*. Histological investigations into the structure of the luminous organ are described.

Introduction

In his last published work (1950), the distinguished entomologist, G. V. Hudson, stated, "the investigation of the habits and life-history of the New Zealand glow-worm has proved by far the most difficult problem I have had to face during the many years I have been privileged to work at the Entomology of New Zealand". Nocturnal visits to caves and holes in banks where *Bolitophila luminosa* lives, do not provide the opportunity for quiet observation necessary for accuracy: the cave roof is often dripping with water, and the banks slippery. In 1888, the glow-worms in the Wellington Botanical Gardens were only obtained by Hudson and Norris by walking up the bed of a stream in the big ravine there. These glow-worms must have increased greatly, because they may now be seen along many paths above the ravine mentioned by Hudson, but are usually out of reach.

Hudson, whose great ability for breeding insects was well known, used a glass tank, the bottom of which was filled with a layer of damp gravel, in which a "cave" of suitable stones was built. He appears to have found that the glow-worms sometimes wandered and ate their weaker brethren or, worse, ate the precious pupae from which the unknown adults were expected to emerge. When, indeed, Hudson did breed an adult, in 1888, he sent drawings to the two specialists in the Mycetophilidae, Osten-Sacken (at Heidelberg), and Skuse (at Sydney), and both refused to believe that it was the adult of the glow-worm larva of which Hudson had already sent them specimens!

In 1956 fixed larvae were sent to the writer’s laboratory at Dublin. Fairly complete serial sections, and whole mounts were made, and these were used by the writer and Gouri Ganguly for anatomical study. No live specimens had been examined, nor were the pupae or imagines available. It was not possible to dissect the fixed larvae properly. Enough cytological preparations were made to show that satisfactory study of the light organs would need electron microscopy. Recently three adult specimens of this insect were discovered at the Waitomo Caves, and parts of the male and female were sectioned in order to ascertain the condition of the luminescent organs, said to be present in the female by G. V. Hudson and A. Norris. At Waitomo and elsewhere, a search for pupae proved abortive, though

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what appeared to be pupae hanging from the roof of the cave were seen. These could not be reached. A somewhat similar cave at Waipu, North Auckland, was visited, and two complete pupa cases and several incomplete parts were found. In addition, the region at Arapuni, near Putaruru, where the original specimens for study at Dublin were collected, was visited several times, and some experiments were carried out on the larvae.

Some of the gaps in our knowledge of these peculiar insects were thus filled, but more work is necessary.

**Nomenclature**

F. W. Edwards (1933) agreed with Osten-Sacken that the New Zealand glowworm belongs to the family Mycetophilidae, but its precise relationships have been the subject of much doubt. It was first described by Skuse as *Bolitophila luminosa*, on the usual evidence of the venation of the wings. Edwards altered the name to *Arachnocampa* on evidence of the form and habits of the larva, noting, however, that the classification of the Mycetophilidae had hitherto been based mainly on the venation of the wings. In 1926, Tonnoir and Edwards placed *Arachnocampa* in the Bolitophilinae in spite of what they stated was the known divergence in its larval structure and habits. By 1933, Edwards had studied the head of the larva, and on this evidence, concluded that *Arachnocampa* and *Bolitophila* are only distantly related, and that *Arachnocampa* closely resembled *Ceroplatus*. In fact, if larval characters and habits are to be the criterion, it seems that Edwards has made a strong case for transferring *Arachnocampa* to the Ceroplatinae. But there appears no good reason for basing the classification of the glow-worm on its larval characters, by which Edwards must have meant the externals of the head. Hudson disliked such a classification based on the characters of a larva with peculiar habits, and was not satisfied with the erection of a new genus *Arachnocampa*: he preferred Skuse's original term *Bolitophila*, based on wing venation, which is usual. In standard books dealing with various aspects of entomology and biological luminescence, such as those of Inms, Harvey, Tillyard and Wigglesworth, the name is *Bolitophila luminosa*, and it is felt that this usage should be followed. In order to avoid confusion, the name *Arachnocampa* has been placed in brackets in the title of these notes.

**Previous Work**

In 1915, Wheeler and Williams, of the Bussey Institute, Harvard, established the fact that the light organ of the New Zealand glow-worm consists of the enlarged ends of the malpighian tubes. Up to 1958—that is, for nearly a half century, no further information on the internal anatomy of any stage in the life cycle was available. In that year, owing to his interest in the matter, Mr. Eric C. Colbeck, of the Tourist Hotel Corporation of N.Z., published for Waitomo the present author's popularly written short pamphlet, based on work done for a year in Dublin by the present writer, and the post-graduate student Gouri Ganguly. This pamphlet described the light organ and general anatomy, but contains at least one small inaccuracy, the chordotonal sense organs should be closer within the anal papillae.

Believing at the time the various accounts claiming that the glow-worm can douse its light suddenly, Gatenby and Ganguly (1958) brought forward an explanation based on anatomical structure, as to how this might be effected. There is now serious doubt, amounting to disbelief in the writer's view, about the ability of the glow-worm to douse its light quickly when alarmed. When startled, it retreats—usually backwards—rapidly into its hiding place, and thus covers its light. It can, however, fade out its light slowly, which is something different. Neither Ganguly nor the present writer had live specimens to work on, and the material forwarded
to Dublin by Dr. Simon Cotton, of Putaruru, suffered from the fact that fixatives sent to him did not easily penetrate the cuticle of the larvae, and when instead they were teased, the parts tended to get out of position or break in transit.

Ganguly had worked for a year in Dublin, and after the present writer went abroad, she continued her study under Dr. Hinton, of the Entomology Department of Bristol University. Ganguly has given a detailed description of the histology of the larva mainly based on Bouin or Gilson fixed material. At Dublin she found the peculiar scolophores or chordotonal organs in the anal papillae of the larva, and proposed that the hydroscopic mucous droplets on the snare of this larva might be produced by the diverticula of the mesenteron. Ganguly's finding may be summarized as follows:

There is no crop. The oesophageal valve is in the first abdominal segment. The mid-gut has a peri-trophic membrane, and is histologically differentiated into three regions—the anterior secretory, the middle absorptive region and the posterior secretory region. There are two gastric diverticula or caeca arising from the base of the oesophageal valve, and these produce the mucus. The hind gut extends from the 6th abdominal segment to the vent on the 8th segment. There is a pair of silk glands which run back to the 6th abdominal segment, then fold back to the 4th abdominal segment. Scolophore or chordotonal organs occur in the anal papillae. There are four such organs, two dorsal, two simpler and lateral. A minute thickened disc exists where the organ terminates at the cuticle. There are no cap or envelope cells in the scolophore organs. Sensory nerves pass to the last abdominal ganglion.

The malpighian tube consists of four parts, the fourth being the light organ. There are two types of fatty tissue; one pigmented, one non-pigmented. No intracellular penetrating tracheoles exist. The larva is apneustic.

It is not proposed to review the somewhat scanty previous anatomical work on related Mycetophilidae. Two forms, Ceroplatus testaceus and Platypura fultoni make webs with sticky droplets, both species being luminous. Their luminescent organs are not malpighian. Platypura is said to secrete mucus containing N/30 oxalic acid (Mansbridge). In this larva the ends of the malpighian tubules are bound to the intestinal region as in Bolitophila. In no other dipterous larva are scolophore organs yet known from the region of the anal papillae or "gills".

In the Waitomo pamphlet, the present writer supplied a diagram of the side of the head of the larva. There are two small eyes on each side, one simple (below), the other probably partly compound (above). The antenna is quite reduced, but the circular base remains. The mouth parts have been described by F. W. Edwards (see Hudson, 1950).

As natural historians, G. V. Hudson, to whom we owe so much, and his disciple Albert Norris, were actively interested in B. luminosa. They bred adult specimens. Hudson sent many larvae, a pupal exuvia, and adults to F. W. Edwards, of the British Museum, for investigation by a skilled microscopist, whose anatomical researches, Hudson hoped, would shortly be published (Hudson, 1946). Enquiry at the British Museum by the present writer elicited the response that his successor was unable to find anything about this in the notes, etc., left by Edwards. On the interesting question of the method by which the pupa is slung from the roof, Edwards (1933) states that it hangs "by a few strong threads which, though merely a part of the larval web, may on drying appear part of the pupa itself (as was thought by Hudson)." Hudson also sent larvae to Osten-Sacken, but so far as is known, nothing was published on their anatomy. Hudson did not at first appear to know of the work of Wheeler and Williams (1915), who examined the gut contents of the larva and recognized it as chopped up insects. But in 1892, A. Norris had proved that the glow-worm lived on other insects. Indeed, it was Mey-
rick, in 1886, who first suggested this. So far as the writer knows, Wheeler and Williams were unaware that this question had been answered by Norris.

The larvae used in Wheeler and Williams' investigation had been fixed in methylated spirit, and the correct explanation which they gave of the anatomical nature of the light organs, was not therefore made under easy conditions. Unfortunately their paper was published in a journal not well known.

Richard B. Goldschmidt (1948) discussed the adaptations of the New Zealand glow-worm for its *modus vivendi*. He considered that it was impossible to explain major adaptations, such as are found in *Bolitophilia*, as having originated by slow accumulation of minute mutants through selection along Darwinian lines. Goldschmidt favoured the view that such adaptations could have selective advantage only when they were complete or almost complete. Goldschmidt misspells *Arachnocampa* throughout his article and attributes this generic name to Skuse. He does not add anything to our knowledge of the anatomy or habits of the glow-worm, but mentions the interesting fact that O. F. Cook found in the caves of Guatemala a larva which makes webs with hanging slimy threads.

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Dr. and Mrs. Simon Cotton provided hospitality and transport at Putaruru, and assisted with some experiments. Mr. Kenneth Carey helped with his local knowledge of the Putaruru district. At Waipu, Dr. E. McInerney and Messrs. Bassett and Gerrity acted as guides. A week-end visit was made to Waitomo (due to the kindness of Mr. Eric C. Colbeck), where Mr. H. R. Sear, Chief Guide at Waitomo, discussed the natural history of the glow-worms. At Wellington, Mr. Graeme Ramsay, of Victoria University, helped the writer in various ways.

The sections of the adults were made in the laboratory of Dr. Owen Thomas, of Napier. Through the courtesy of Dr. John Sullivan, the photomicrographs were taken by Mr. John Sloan, Chief Bacteriologist at the Pathology Department of the Auckland Women's Hospital. Many preparations were made at the Zoology Department of Victoria University with the permission of Professor L. R. Richardson. Microscopical observations near the field were made possible by the loan of a microscope by Professor H. D. Gordon, of the Botany Department of Victoria University. The photograph in Pl. 28, Fig. 14, was kindly given to the author by Dr. J. T. Salmon. The writer is greatly obliged by the kindness of these friends.

TECHNIQUE

The presence of extensive fat bodies in *B. luminosa* shields the viscera and makes observation difficult (Pl. 23, Fig. 4). This fat can be dissolved out by Carnoy's fixative, which alone penetrates the thick cuticle rapidly. It is quite difficult to make good whole mounts. Holes cut in the cuticle usually cause anaesthetized larvae to eviscerate partly.

LOCATION OF LARVAE STUDIED

Caves. Waitomo, in the midlands of the North Island. Waipu, 80 miles north of Auckland, in the North Island.

Banks. Arapuni, near Putaruru, in the midlands of the North Island. Botanical Gardens at Wellington, at the southern point of the North Island. There are many accessible larvae at Khandallah Reserve, Wellington, but these were not studied.
Results

The Larva.

In Plate 23, Fig. 4, is a sketch of the full grown living larva indicating the zones of colouring. The head and front thoracic region appears black, and forms the front dark stippled zone (BZ). This is due to the presence of blue and black pigment in what appear to be special cells below the integument. Reddish or grey flattened cells also are found here. The upper middle of the larva is chocolate colour (GZ), due to the presence of food in the mesenteron (ME), and especially to the two long brown gastric diverticula (D, D) which stretch down, often below the mid section of the animal. In the full grown larva these chocolate brown tubes are partially masked by four long bands of grey fat cells (GF). In the lower mid region of the body there is a pink zone (PZ), due to the pink granules in the much coiled malpighian tubules. The end section of the body is mainly hyaline and yellowish, and forms a clearly marked region (CZ).

Imaginal discs and gonads were found in one Waipu specimen only 19 mm in length. In this larva the granules in the malpighian tubes had already been cleared out, and this part of the animal was hyaline. There are no imaginal discs in connection with the luminescent organs. The silk glands appeared empty, but were full length. Their fate in the adult has not yet been worked out, but will be studied if material is available.

On Pl. 25, Fig. 7, is a ventral view of the last segment. At (CO) is a ventral band of short, sharp comb-like setae arranged in groups. This band does not spread quite up to the dorsal surface and is the largest of several such bands which are indicated diagrammatically in Fig. 4A on Pl. 23. These more anterior bands of setae which are double, are not easy to see, but Fig. 4A gives the plan in one larva in which they were clearest. Above the posterior band shown in Pl. 25, Fig. 7, passing forwards, there is another band, then five areas still further forwards. These bands enable the larva to grip the silk and mucus runway in which it normally rests. The undersurface of the thorax is thrown into narrow cross bands which help the larva to pull its body forwards.

As is shown in Pl. 25, Fig. 7, there are longitudinal muscles arranged in three groups (LM) by the contraction of which the larva is able to pull forwards the entire segment in which the light organ lies. When pulled forward into this position, this segment lies within the seventh segment—that is, the one in front, and this telescoping tends to bring together blue pigmented cells and fat, which form a dense area. It might be assumed that the larva uses this power to douse its light. Observation of living larvae does not support this idea, though anatomically it seems quite possible. The normal position of the eighth segment in both luminescent and non-luminescent larvae is extended.

The Head.

In Pl. 25, Fig. 7B, is the upper surface of the head of a larva killed in Carnoy’s fluid. The mandibles (J) are large and sharply toothed. Below at (ML) are what may be the bluntly toothed maxillae. In between, the basket-like structure (BB) becomes everted in penetrating fluids like Carnoy, but is not normally seen in dead specimens. This basket has an aperture in front, and it appears to be an epipharynx, but its nature is not properly understood. Apparently the food is gripped by the mandibles and sawed into suitable lengths by the maxillary teeth (see Pl. 24; Fig. 6B). At each side of the head is the base of the antenna (A), and behind this is an eye (E2) which appears to be made up of a single facet but more than one ommatidium, and is therefore strictly an ocellus. Below this eye, in line with the bottom of the antenna, at (E) is another peculiar pigmented sense organ which more closely resembles a true lateral ocellus. Like most startled nocturnal
insects, the larvae do not move at first when a flashlight is directed at them: this does not say they lack light perception; but their eyes probably only function as sense organs suitable to let them know when night has fallen, and dawn has come. The glow-worms do not see as well as the larvae of the tiger beetle, which live in holes in clay banks. The glow-worm depends on its snare, the tiger beetle larva on its sight and quickness.

The Gut of the Larva.

In Pl. 24, Figs. 5 and 6, are the parts of the gut, as seen when the last segment is cut off and the viscera pulled out by the head. The oesophagus (O) is markedly contractile. The chocolate coloured diverticula (D) show muscular movements, not apparently peristaltic, but such as would be produced by contraction of scanty circular muscles. No doubt it is by such contractions that the mucous droplets are expelled at intervals from the mouth, as the snare is being constructed. Owing to the position of emergence of the diverticula from the oesophageal valve, the latter probably controls the issue of mucus. The oesophageal valve is yellow in colour.

The mesenteron was never found quite empty in newly caught specimens, but if the larvae are starved for several days, the gut contents move down leaving the upper part empty. Food was never found in the intestine (IN) except on one occasion when the digested material was observed in the lower part of the mesenteron; it quickly passed through into the intestine and was immediately voided. The food contents seen in the mesenteron always appeared brownish. Recently a larva was seen to regurgitate a drop of food. In Pl. 24, Fig. 5, the four parts of the malpighian tubes (1-4) are shown. The first part (1) is yellowish and hyaline, the second and longest part (2) is of a larger bore, very opaque, and has a pink colour in direct light. The third part (3) very gradually passes into a thinner and more transparent region of part (4); this region is usually disposed in a zigzag fashion, covered with thin connective tissue, and provides the necessary extensiile region needed as the animal contracts and lengthens quickly as it moves along; part (4) is the swollen luminescent organ, which, like the lowest part of part (3), is transparent and yellowish. The reflector is glistening white, and when cleared of attachments rapidly floats to the top of the water in the dissecting dish, resembling a tiny boat. These regions of the gut are depicted at a higher magnification in Pl. 24, Fig. 6. When the tubule is pulled out from the living animal, one occasionally sees some of the granules from part (2) passing into the lumen of part (1). It is this process which, before pupation, leads to the adult malpighian tubes being cleared of all the excretion granules collected during larval life. The adult's malpighian tubes are like part (1) of the larval tubes. Part (1), of course, leads into the gut proper. The urine (?) granules in part (2) gradually become less and less towards the distal end, until the cells become hyaline. Cross sections of the region (3) reveal that the cells do not always occupy the complete area of the tubule, one side here and there showing a gap, as in Pl. 24, Fig. 6A. This is also shown in Pl. 1, Fig. 5 (C), of the paper by Gatenby & Ganguly (1958). The significance of this method of packing the cells is not known. At the region at part (3A) in Pl. 24, Fig. 6, the lumen is still patent, but it appears to be shut off at (LN) by an area of about three cells in length. No granules were ever seen inside the lumen of the living luminescent organ.

In Pl. 24, Figs. 5 and 6, at CT, the connective tissue binding of part (3) and (3A) is drawn in diagrammatically to show that this region is so completely bound that the intestine and the four lower parts of part (3) cannot usually be separated without breaking. In Pl. 24, Fig. 5, the proportionate length of the meanderings of part (3) are not fully shown. A less diagrammatic drawing of this region in an extended animal is shown in Pl. 25, Fig. 7 (CT and M).
The silk glands extend far down to the mid region, and then each one turns up at its lower part (SI) in Pl. 24, Fig. 5. Fat cells (F) are closely bound to the silk glands.

**Tracheal System.**

In Pl. 23, Fig. 1, is a semi-diagrammatic plan of the tracheal trunks. There are two main tubes (L, L) passing from a fork which goes to head and brain, right down to the reflector and luminescent organ (LO). On the way down these give off branches (T, T) to the viscera. The main trunk leaving the reflector (LO) branches forward (lower T). At intervals the main trunk receives tubules (B) which have branched under the integument at each site. There are no tracheal openings to the exterior, the system being apneustic.

In the pupa, Pl. 23, Fig. 2, there are at least six tracheal openings, each in the mid region of the segment. A higher power drawing of one of those is given in Pl. 23, Fig. 3, the opening at TA, longitudinal trunk at L.

The tracheal system of the imago has not been studied but is probably normal for the family.

**The Luminescent Organ.**

In Pl. 27, Fig. 12, is a good photograph of the light organ (LO). There are four tubes seen in transverse section in Pl. 26, Fig. 9. In this region the reflector (R) lies underneath, and the tubes are not bound to this, but lie in depressions in the reflector. The intestine and rectum (IN) also lie free, but as far as can be ascertained, the light organ itself is not free to move up or down according to the position of the connectives (CT), and the contraction and relaxation of the longitudinal muscles (LM). The light organ is shown well at (U) in Pl. 27, Fig. 10, the lumen more clearly at (LO) in Pl. 27, Fig. 12. Although the light given by small larvae appears to be bright, their luminescent organ is comparatively small. In Text-fig. 4 (A), is an outline of the adult larval organ, in (B) that of a larva 5 mm in length.

The living cells of the light organ are hyaline and free from granulation except for mitochondria packed in the cytoplasm of the cell.

**Lengths of Parts of the Viscus of the Larvae, Etc.**

Oesophageal valve, 1.25 mm; silk glands, 22 mm; mesenteron, 10 mm; gut diverticulum, 12 mm; malpighian tube, yellow region (part 1), 2.5 mm; pink region (part 2), 9 mm; (part 3A, difficult to measure); luminescent organ, 0.9 mm; altogether about 15 or 16 mm. This, from typical larvae, but the lengths in some cases obviously depend on the amount of stretching and size of larvae.

The writer’s drawings had to be made mostly freehand, as no camera lucida was available at the time. The average larva was about one inch (25 mm) long. One from Waipu, apparently a male, nearly ready to pupate, that is with imaginal discs and visible gonads, was only ¾ inch (19 mm), yet another from the same cave was 1¼ inches (about 30 mm) long, and it had no visible imaginal discs in whole mount.

**Nervous System.**

The nervous system consists of the larger cerebral ganglia (brain), para-oesophageal commissures and sub-oesophageal ganglia, the usual double ventral cord, three ganglia in the three thoracic segments, and a ganglion just behind each abdominal segment, except in that segment containing the light organs. The brain lies just behind the head capsule, not inside it (Pl. 25, Fig. 7B, BR). In Pl. 25, Fig. 7A, are the last three segments, and the supply to the region containing the light organs (LO) comes from the ganglion (NA) in the penultimate segment. This ganglion sends down a nerve which soon branches, one part to the muscles, the other continuing down to the region of the light organs and anal papillae. One
branch (N) certainly comes from the scolophore organs, but it is difficult to follow the paths of the other small branches, some of which go to muscles. This means that it is not presently possible to say whether the central and the sympathetic visceral systems are brought down into the posterior part of the malpighian tubules which are the light organs, and to the reflector. In any case a cut anywhere below the letters (NA) in Pl. 25, Fig. 7A, will isolate the central nervous system and its anterior sense organs, from the light organs. Such a cut will also isolate the posterior part of the haemocoele from any possible hormonic influence arising in front parts of the nervous system, but it will shut off the oxygen supply arising from the segmental tracheole branches beneath the integument. The long tubular heart passes back to just near the border of the last segment. Thus the cut will also interrupt the heart, but will leave a portion of variable length according to the level of the cut below the ganglion (NA) in Fig. 7A. With these difficulties in view a few experiments were made.

EXPERIMENTS ON THE CONTROL OF LUMINESCENCE.

On Pl. 23, Fig. 4, the arrows X, Y and Z show where a cut was made or a nylon thread was tied. The thread was Size A, white, Coats and Clark's, was fine enough for the experiments, and is very strong. Three main types of experiments were tried:

1. A tie or cut behind the head, isolating the head from the rest of the body. Head cut off in all cases.

2. A tie or cut between X and Y, usually in front of Y, body cut off.

3. A tie or cut at Z, isolating any nerve ganglia from the light organ, the body being removed.

It was very difficult to get a thread on to a struggling lighted up larva, before it doused. In (1) and (2), the larva could douse. In (3) the piece below Z, could not douse, and if the experiment was carried out on a doused larva, the luminescent organ lighted up immediately. If (2) was tried on a doused larva, it did not light up, but if (3) was then carried out, it lighted up. If the lighted up piece (teased or not) from experiment (3) be covered with blood from a doused larva, it still continues to light up.

From these experiments it appears that the light is kept doused by the posterior ganglion in segment 7. In all cases the light does not turn off or come on suddenly, from which it may be concluded that some other organ is implicated, but not a humoral effect or hormone in the haemocoele fluid. It is likely, but there is no evidence, that the ganglion in segment 7, in some way prevents air from the tracheal reflector from diffusing to the light organ.

Before any conclusion can be drawn, the nerve supply to the light organs and tracheal basket must be examined, but suitable gold or silver preparations have not been made.

In the case of those glow-worms living outside on banks, at present it seems likely that the approach of evening is registered by the eyes of the larva, and a stimulus is sent down from the brain via the ventral nerve cord to the posterior ganglion, which then lifts the block which hitherto has kept air from diffusing across the small gap between the reflector and the light organs. The blood containing air from the reflector could be removed by contraction of the last segment, the swelling or contraction of which is entirely under the control of the larva. Note that in Pl. 23, Fig. 4, this segment is largely contracted, while in Pl. 25, Fig. 7, it is suffused with blood. The writer feels that this is in some way concerned with dousing.

Many attempts were made to dissect the posterior ganglion so that the nerve fibres could be followed to their end organs, but the cuticle was so tough that the task was beyond the skill and patience of the writer. The question of the use of the eyes for the perception of night and therefore of lighting-up, was not solved.
Fig. 1—Plan of the larval tracheal system. Fig. 2—Exuvia of male pupa, ventral surface. Fig. 2A—Head and thorax, ditto, from side. Fig. 3—Tracheal trunk and opening (spiracle) of pupa. Fig. 4—Nearly full-grown larva, showing zones of colouration. The spread of lines between (CO) and (LO) represents light. Fig. 4A—Plan of banded rough areas for adhesion by combs.
Fig. 5—Appearance of viscus when pulled out. The parts marked (3) and (4) lie around the intestine (IN, lower). Fig. 6—As above, higher power, light organ slightly flattened. Fig. 6A—Part of (3a), in transverse section. Fig. 6B—Chopped up lengths of chironomid legs, from gut of larva.
Fig. 7—Last segment of larva from below. The reflector is black. Compare with Fig. 9.
Fig. 7A—The three posterior segments of the larva showing position of the last abdominal ganglion (NA). Fig. 7B—Head of larva from above showing toothed mandibles (J) and serrated maxillae (ML) with everted basket (B) lying in between. Antenna base (A) and two pigmented eyes (E, E2).
Fig. 8—Left and right, anal papillae from below showing chordotonal (scolopale) organs during life. Fig 8A—Penultimate and ultimate dorsal shields (terga) of adult abdomen. Fig. 8B—Female in position of oviposition. Fig. 9—Oblique transverse section of larval reflector and luminescent tubes.
Figs. 10 and 11—Female and male adult luminescent organs in longitudinal oblique section. Fig. 12—Photograph of whole mount of larval luminescent organ (LO). Fig. 13—Longitudinal section of egg in lower oviduct of female adult.
Fig. 14—Photograph of snare, showing horizontal runway, and up to forty vertical silk lines, with mucus droplets.
Larvae are easily anaesthetized by being immersed in water containing the anaesthetic, but chloroform-water eventually killed them. It should be possible to find a more suitable anaesthetic, to dry the larvae, and then to paint over their eyes. It is to be expected that larvae so blinded will luminesce continually.

THE POSTERIOR SCOLOPHORE (SENSE) ORGANS OF B. LUMINOSA

These organs lying within the anal palps (P in Pl. 23, Fig. 4; Pl. 25, Fig. 7) can be seen clearly in the living larva. They are the integumental type (Pl. 26, Fig. 8). In all cases on the outside of the terminal papilla are two hair-like projections or setae, one curved (No. 4), one short and straight (No. 3 in Fig. 10, No. 1 in Fig. 8). The curved seta is always at the position of No. 4, and is ventrally placed. The straight seta is more dorsal. These setae almost always become detached, as in the Dublin material, during routine sectioning and whole-mounting for microscopical preparations. In the living larva they were never absent in specimens examined. Since the curved hair protrudes, presumably it is in touch with the silken fibres and mucus of the snare, and is therefore the chief means of telling the larva that prey has been caught. Now at the numeral (2) in all cases examined, there is the largest sense organ, but it never has an external seta, and it lies towards the dorsal side of the papilla. In addition, there is another somewhat dorsally placed sense organ, which may or may not be the site of emergence of the straight short seta.

It will now be clear that we can recognize three types of sense organs, one with a curved hair, one with a short straight hair, and always two without hairs, one of these being the largest sense organ of the four. Granted that the sense organs with setae function to register vibrations made by ensnared prey, it is inviting to assume that the more dorsally placed sense organs without setae function for the recording of other types of vibration. As will be mentioned below, however, there is no evidence for such an assumption. Between No. 2 and No. 3 there is always a connective (OR), a variation in its position being shown in Fig. 8.

There is connection between the cavity of the anal papilla and the general haemocoele cavity. In the former cavity what appears to be spherical, broken-down blood cells, or fat globules, commonly occur, and are shown in Fig. 8 at (Q). Pressing the cover-slip gently may cause these bodies to disappear from the papilla cavity, so it is assumed that they have passed into the general body cavity. Other mycetophilid larvae are known to have anal projections, and more careful search should establish that these contain sense organs, especially in the cases when such larvae spin snares.

The anal papillae of B. luminosa can be moved about by the larva, and in Pl. 26, Fig. 8, at (2) (upper) and (4) (lower), what are assumed to be muscles stretch upwards; but it is probable that alterations in the pressure in the cavity of the 8th segment play a part in the bulging of the papillae.

The anal papillary sense organs are definitely known to send a nerve to the last abdominal ganglion. The intimate structure of the chordotonal organs has been worked out by Ganguly, the present drawings being made from living larvae.

THE SNARE. (Plate 28, Fig. 14.)

This is well known to consist of a crack or a boring in the bank, a mainly horizontal runway leading towards this hole, and about 40 millimetres in length, and usually straight. The larva is able to traverse this runway into its hiding place in about three or four quick contractions and elongations of its body. In some cases the hiding place is more than 30 millimetres deep. From this runway hang down a varying number of vertical silk threads from about 10 mm to 60 mm in length in some cases, according to the height of the roof or ceiling. These vertical threads are usually hung 2–5 mm apart, and each one has a chain of mucus sticky beads on it, which are evenly spaced at most 1 mm apart, and do not run together. The
beads are about 0.5 mm in diameter. Wind will tangle up the vertical lines. It has already been pointed out that the larva has anal scolophore tactile organs, with external short setae (Pl. 26, Fig. 8). The question arises as to what is the relation between the horizontal runway upon which the larva normally rests, and the vertical lines, some connection presumably being necessary if the larva is to sense the struggles of captured insects. If the larval snare is destroyed, or a larva is put on a suitable rock, it first constructs the horizontal runway, the vertical lines being lowered afterwards. This account only applies to the snare made by larger glow-worms. The very young larvae show a bright light, which alone helps the observer to see their location, but there are no vertical lines, only a runway, and on banks, always a hiding place as well. Presumably newly hatched larvae are able to luminesce and to produce some sort of tiny sticky platform.

In Arapuni, many small larvae rested on steep banks, where the hanging of vertical lines would be quite impossible. These larvae must depend for food on the mucus smears on or along their runways, and when more mature, would have to move to a more favourable place to hang a curtain of fishing lines. It is remarkable that such small larvae can produce a light apparently as bright as that of larvae which are larger, because only by examining the site of the light can one discover whether the owner is large or small. The presence of a light, together with a small sticky area, in the case of small larvae, appears to provide further evidence that the light is designed to attract prey, and is not merely for the dissipation of unwanted energy, as has been suggested.

In one case an isolated larva and snare were seen partly under a rotten log. The aperture leading to its snare was gently widened by cutting with a knife, so that the larva could be used for experiments under natural conditions. On returning in two days to begin the experiments, it was found that the dissatisfied larva had cleared its old site of threads, and had constructed a new snare deeper in. This time the hole was widened so thoroughly that the larva could not get out of reach. On returning again in three days, the larva was found outside the area of the

**DESCRIPTION OF TEXT-FIGURES.**

Text-Figs. 1 and 2.—Snare made in about three hours in a glass dish by a larva; there are six evenly spaced vertical fishing lines, four in the position shown in section in Fig. 2. The runway from left (LO) to right (HO), looks like a pulled out glass rod, but is really a thick walled tube, the lumen of which opens as the larva moves forward. The larva lies ventral surface upwards; (LO) light organ, (H) head. The stretchers are silk, but may have mucus at their angles (A). At P, is water or air giving the possible patency of the tube where such droplets lie. There are about a dozen mucus droplets on each vertical line. Four lines are suspended from side lines (S) from the runway, and are seen towards the observer, two lines hang from the opposite side of the runway; (L) is the lid of the dish (D). Under normal conditions a hiding place exists at one or the other end of the runway. The scale on the left refers only to Text-fig. 1.

Text-Fig. 3.—Plan of new snare made by the same glow-worm (W) after removal from the glass dish the same evening. This took two nights to complete; the problem before the larva was how to utilize the suitable hiding place (O), and yet hang fishing lines. This was solved by the larva lying at an angle, the main horizontal line being stretched higher up, so as to allow longer lines to be let down.

Text-Fig. 4.—(A), the light organ of a larva 24 mm in length; (B), that of a larva 5 mm in length. The organ in (A) measured 0.93 mm. It is not possible with the human eye to judge the size of a larva by means of the brightness of the light.

Text-Fig. 5.—Plan of a further modification of the snare made by the larva in Fig. 3. For some unknown reason it dismantled most of the vertical lines in Fig. 3, and then spun a thick, somewhat sigmoid shaped line, from which short vertical lines were suspended. It rested higher up, still at an angle, almost hanging from where the two boughs were fastened together. In daylight it had by now snared and eaten the head and most of the abdomen of an active housefly. The remains of the carcass did not appear to be smeared with mucus, and were deposited on the bough away from the snare lines. The main sigmoid suspensory line did not now seem to be a tube, the larva moving along it as if unassisted by mucus. It was not possible to see whether the larva was then lying on its back.
previously widened hole. It had moved nearly 18 inches away from its original site.

Considerable light can be shed on the relationships of the snare and glow-worm by putting some larvae into a deep glass dish, as in Text-fig. 2. To make a nest the larva uses the angle between the glass lid (L) and the side of the dish (D). Provided the lid of the dish does not haze over with water vapour, it is possible to examine the snare with a binocular microscope.

The snare drawn in Text-fig. 1 was constructed in less than four hours, when the glass dish with larvae was put in a darkroom at midday and examined about 4.30 p.m. The larva was known to have spent about one hour examining the confines of the dish before it chose a place. In Text-fig. 2, the snare is shown in cross section, the black dot in the middle representing the section of the larva. The main runway in which it lies is mainly horizontal as in Text-fig. 1, which is drawn from the side by looking through the side of the dish. The larva lies with its ventral surface upwards, but it does move about so that the front of its body twists in any direction. Examination by the binocular microscope showed that Albert Norris was correct when he stated that the larva lived in a tube. From the left of (HO) to (LO) in Text-fig. 1, the larva is seen to occupy the centre of a glassy mucus runway, which at such places as at (P) seems to be hollow. As the larva moves backwards or forwards it does not push this glassy mucus in front of it, but just stretches it. The anal palps at (LO) where the light organ is situated, lie expanded within transparent mucus in which movements of the palps can take place. If it wishes, the larva can poke its head out of the tube anywhere, the contour of the latter being restored when the larva passes back into it.

The exact relation of the silk lines to the mucus is not understood, but outside the runway, some of the stretchers have mucus droplets held in their angles as at (A). Here the silk and the mucus appear clearly separate, but there seems to be some evidence that the animal is able simultaneously to secrete mucus and silk mixed. The stretchers holding the runway are undoubtedly silk, but where they touch the runway, they pull the mucus out into a cone. The vertical lines (V) were usually not immediately attached to the runway, but were fixed a little off it by side lines (S). The larva which made the snare in Text-fig. 1 was removed that evening to an inverted beaker or a tray on which two rotten branches were set up. During that night it constructed most of another snare (Text-fig. 3) in the only favourable place where vertical lines could be made. Another smaller larva put on the branches at the same time had no place, and stayed in the moss near the ground. It disappeared, probably eaten.

The manner in which the droplets appeared on the silk vertical lines could not at first be observed. They may at first be a continuous outer layer which, by some form of surface tension, resolves into droplets, or they may be secreted one by one. On apriori grounds the former possibility would seem the more likely, but recent observation shows that the latter is correct. Not all the beads were spherical, some being ovoid or pendant droplets. Larvae at Arapuni from a very dry bank, when placed in a very damp atmosphere, produced vertical lines on which the mucus droplets had run together into larger disorderly droplets which usually sank down to the bottom of the silk thread.

Conditions of Pupation and Possible Phototropism of Adults.

In the few cases where pupae or pupal exuviae have been found, it has been stated that the area around at least two inches in diameter is clear of other larvae and their sticky snares. Moreover, the pupa hangs suspended on a long support (Pl. 23, Fig. 2, SU). This would give the imago the opportunity of emerging without being caught by its own, and the sticky snares of neighbouring glow-worms. The larva possibly clears away parts of its own web before pupating. It has been
stated by Hudson, and has been shown by anatomical study in this present paper, that the female adult is able to luminesce for a time at least. The Chief Guide at Waitomo informed the writer that he believed that the female paired during emergence. Though her light shines at this period, there is reasonable doubt if this is done to attract the male, for if he is positively phototropic, he is then in danger of being snared by the lights of the larvae, which are said by Hudson to glow more brightly. The two females caught at Waitomo did not show a light, and were only seen after a flash-lamp had been directed on to dark walls where they reposed. One of these females, microscopically examined, had paired. It seems possible that both male and female adults may be negatively phototropic, which would keep them clear of snares. Nowhere has the writer seen it reported that moving lights have been observed inside or outside caves where the glow-worms are found. If the female really flies when she is luminiscent, this phenomenon would be likely to have been noted. It is possible that the female remains quiescent and shows her light till she has paired, and then the light fades away. The females caught at Waitomo remained quiet when the light was shone on them, and were easily bottled. They were found on parts of the cave not occupied by larvae. At Waipu several broken pieces of adult male Bolitophila were found stuck on snares. It is possible, of course, that the male is positively phototropic, but generally manages to evade the danger of being snared.

The Suspension of the Pupa.

From Hudson's illustrations, and the flashlight photograph of E. P. Christensen, it is known that the pupa appears to be fixed at the roof by a series of silken threads, which converge to a more solid single cord, which then widens as it reaches the head. From the drawing made by G. V. Hudson's daughter (Mrs. S. Gibbs) in September, 1925, we know that during emergence of the adult from the pupa, the head of the imago is directed downwards, the tail of the pupa pointing slightly upwards, the pupal suspensory cord occupying an intermediate position. When finally clear, the imago stands on the pupal skin with the extremity of its abdomen still within the exuvia, the pupal skin resuming its original vertical position.

In 1886, Hudson drew the pupa with a suspensory cord which he then considered to be a part or extension of the pupal body. His original figure will be found in his “Manual of N.Z. Entomology”, West, Newman & Co., London; this book was written when Hudson was 19 years old, and the Government of the day under Sir Robert Stout directed the purchase of 1,000 copies, both noteworthy events. Hudson, because of the opinions of other entomologists, changed his view, and in his last published “Fragments of N.Z. Entomology”, drew the cord as a silken support, not a part of the pupal body. The cord has also been stated to be the drawn-out mucus platform or tube on which the larva rests.

This question has puzzled the present writer very much. Inspection of Pl. 23, Figs. 2 and 2A, apparently shows that the pupal exuvia is suspended by a cord (SU) which is attached to the front thoracic region at (R) and (RS). In three exuviae found, at Waipu, mounted and examined microscopically, it is impossible to distinguish between the cord (R) and the chitin of the thorax. They are the same colour and merge into each other. It would therefore be natural to assume that Hudson's first view was correct. Against this, however, is the disturbing fact that there is no special area of cells in the correct region of the thorax, in large larvae with imaginal discs. There should be a large stainable area of cells here if such a long cord of chitin were to be produced suddenly as the larva pupates.

Mr. Sear sent the writer a pupa which, unfortunately, had become broken. It was, however, immersed for several days in 5% formalin, and the cord and thorax examined fairly successfully. This specimen shows the cord as formed of separate
threads gummed together, and supports the interpretation that the suspensory cord is actually the runway of the snare.

Since this paper was written a 9 mm body length pupa was discovered at Arapuni on March 6. It was glowing as brightly as the neighbouring larvae. As it was watched it doused its light, which came on again at intervals of a-half to one minute. From time to time its light went out for about 15 minutes, and at other times its light, though perceptible, was faint. When the surrounding larvae had doused, as the flashlight was being used in the area, the pupa also doused. It was suspended by a brownish stiff thread, and was dry when touched with a grass stem. It was able to move its abdomen slightly. Next day when touched, the pupa lit up for a short time.

The dark material in the posterior segments of the pupal exuvia in Pl. 23, Fig. 2, is probably partly meconium.

The Female. (Pl. 26, Fig. 8b.)

Two females were found at Waitomo by Mr. H. R. Sear. The end of the body of one was cut off immediately and fixed for study of the luminescent organs. This portion contained about twenty eggs. The other part contained 45 eggs. The other specimen was slit up slightly to help fixation. Her abdomen contained seventy-five eggs. The eggs were 0.75 mm, which is very large (see Pl. 27, Fig. 13). The eggs were spherical and very light yellowish white. The females were not luminescent when found, and did not show light when put in a bottle. The condition of the luminescent organs is shown on Pl. 27, Fig. 10 (lo). They are well developed and each contained a lumen. An attempt was made to dissect and mount whole the gut, the malpighian tubes, and the genitalia of the other specimen. This was successful, and it was found that the malpighian tubes were clear of excretion granules, resembled closely that part of the larval organ marked (1) in Pl. 24, Figs. 5 and 6, and tapered as they joined the luminescent organ behind. It appears that in these insects, the whole gut does not break down during metamorphosis, except that the mass of granules in part (2) of the malpighian tubes of Pl. 24, Figs. 5 and 6, is cleared out, leaving the cells hyaline. The sizes of larval and female adult luminescent organs are approximately the same, perhaps those of the latter being a little smaller, but this was a comparison of sections with whole mounts.

The female genitalia consists of the two ovaries; the oviducts; and two pairs of tubular sacs, one of which (Pl. 27, Fig. 13 (cn)), contains what may be a cementitious material. It is bright orange. The other pair of tubules is the receptacula seminales. The mesonenteron of the adult females contained no food.

Closely aggregated groups of glow-worms have never been seen, from which it is concluded that during oviposition the female flies or walks from place to place in a small area, but does not lay the eggs all in one place. But, judging from the positions of many small larvae at Arapuni, the female is not able to choose sites suitable for hanging vertical fishing lines.

The Male

On page 24 of the publication "The Waitomo Caves", by J. H. Richards, is a remarkable flashlight photograph of the adult male Bolitophila, taken by Mr. E. P. Christensen. One male was found at Waitomo by the writer. The end of its body was snipped off and fixed, and sectioned. On Pl. 27, Fig. 11, is an oblique longitudinal section of its body showing the luminescent organs (lo). These are much shrunken, not due to bad fixation or to poor technique, because the more delicate parts close by are well shown; neighbouring luminescent cells have here and there become confluent (LOD) and their nuclei tend to lie together. The malpighian tubule connectives are present as usual, but are shrunken. This would appear to support the findings of those naturalists who have stated that the male is not
luminescent. The fact that the female is known to be luminescent points to the view that this is connected with sexual attraction by the female. But no evidence for this has been forthcoming. Hudson mentions that one of his female specimens was taken to the Botanical Gardens at Wellington, where it lighted up, but after 45 minutes had not attracted a male. Perhaps the trial was not long enough. According to Mr. Sear, the female pairs at, or soon after emergence, and one of Hudson's specimens lighted up for two days. The pupae which were luminescent, not always, but from time to time, were probably females. It should be mentioned that the writer and his assistants, who spent many hours examining banks at night, never found a pupa. Since it was understood that pupae lighted up faintly, special care was taken to find such examples, without success.

In the photograph on Pl. 27, Fig. 11, the sacs (rc) are the vesiculae seminales, and those marked (ac) probably accessory organs. The organ (te) is one of the testes, seen to be passing down to (rc), the vesiculae.*

On Pl. 26, Fig. 8a, is a sketch of the posterior end of the body of a dead adult found at Waipu. The last segment is clear of pigment, and it is here that the luminescent organ repose.

**Measurements of Adult Insects, Etc.**

These were made with a ruler and magnifying glass, and can only be regarded as approximate.

Waitomo specimens: Female, entire length, 17 mm; individual wing, 9 mm; wing span, 20 mm; antenna, 4 mm. Male, entire length, 9 mm; single wing, 8.5 mm. The Tanypus (Chironomidae) from Waipu which formed the main food were 8 mm body length.

Hudson gives the wing span of the female (from Wellington) as 17 mm; length of larva, 25 mm; pupa, 7 mm. The present author's Waipu specimens of pupal exuviae measured 14 mm, suspensory cord 16 mm. On January 1, the larvae in the Wellington Botanical Gardens measured 10–12 mm. Large specimens appeared to be absent, but in some cases imaginal discs were present in larvae examined.

**The Fate of the Reflector During Pupation.**

In Pl. 26, Fig. 9, R, is the reflector and luminescent organs (LO) of the larva in dorso-ventrally oblique cross section. The reflector is supplied with two large tracheal tubes shown at (T) in Pl. 25, Fig. 7, and is itself formed by a dense tangle of tracheoles. It will be seen that each light organ tube lies in a reception groove in the reflector. Probably the sharp points at the anterior and posterior ends of the reflector (shown in black in Pl. 25, Fig. 7) are forward and backward continuations of the edges of such grooves. The reflector is partly divided in front.

Now in the adult, both in the male and especially in the female, there is an organ (r) shown in Pl. 27, Fig. 10, which is believed to be the remains of the reflector. It is so intimately connected to the luminescent tubes that it is almost certainly a reflector, as no other organ exists near this in the larva. But the organ marked (R) in Fig. 10 is a hollow structure, which may or may not have contained air. So far as can be ascertained, this sacculated structure is related to tubules, which are tracheal.

**The Food.**

As was stated by Wheeler and Williams, the food within the mesenteron consists of insects. In Pl. 24, Fig. 6B, obtained from a larval gut, are chopped portions of the legs of a chironomid or similar insect. The larva may, as has been claimed by Norris, suck out the body contents of its prey. But afterwards it carefully chops

* Since this paper went to press the author has received information which doubts the identification of this specimen, and this will need further study.
up the whole insect into suitable sizes for swallowing. Perhaps this is why it is so rare to see entangled insects in the snares. Apart from insects, Norris mentions that the larvae will attack crustaceans, by which he presumably meant wood-lice (Isopoda). It is difficult to believe that an adult wood-louse would not be able to plough its way through the short fishing lines seen in holes on banks where such lice abound. It is not known whether the mucus droplets of Bolitophila contain some substance which immobilizes snared arthropods, but this mucus is non-toxic to freshwater Protozoa. Experiments with weak oxalic acid made at Dublin by Ganguly did not appear to support this. The droplets from glow-worms' mucus glands have not yet been analysed. It seems likely that the sticky mucus, covering the body of struggling snared insects, gradually smotheres them. Small larvae from Arapuni are much larger than 5 mm all had food in their mesenteron.

The main food of cave dwelling Bolitophila is midges (chironomids, said to be a Tanypus). A requisite for the existence of glow-worms inside the darkness of caves is a river or pools in which the various aquatic larvae are carried. Larvae of Bolitophila may be seen in dry caves, but only near the entrance. In larvae examined after capture, food can be seen in the mesenteron, during the months when these observations were made (September to January). Compared with the light of the North American firefly, the intensity of luminescence in the New Zealand glow-worm is very much less, so far as the human eye and memory can be relied on. In the case of the North American insect, the flashes can be seen clearly from within a brightly lighted room, as the insects fly past outside. There seems no doubt that under the same circumstances the light of the New Zealand insect could not be noticed.

It is therefore a matter for surprise that the modest light of Bolitophila is sufficient to attract various flying Diptera. The light of the New Zealand glow-worm is distinctly green, and how far some sort of relation between the positive phototropism of the midges and the nature of the light has been built up to the advantage of the predatory glow-worm larva, is a matter of speculation; the present writer did not have the time or facilities for exploring this point in a scientific manner.

It has been stated by J. H. Richards that the light of B. luminosa contains no ultra-violet. In the case of the beetles Photinus, Pyrophorus and Lampyris, there is a continuous spectrum over a very narrow range of wave lengths (about 486\(\mu\) to 720\(\mu\) in Pyrophorus, the most luminescent of insects). It is known (Wigglesworth) that within this range, the human eye is most sensitive. So far as the present writer knows, the light of B. luminosa has not been analysed spectroscopically, and its exact range is unknown at present. This may be different from the light produced by Coleoptera.

The Problem of the Supposed Dousing of the Light

In the North American firefly, which is a coleopterous imago, the light flashes at intervals. This is to suggest that the light is either under the control of the insect, which is supported by experiments, or that the energy is built up and becomes released in waves. In the case of the cave dwelling dipterous Bolitophila, the light is continuous so far as the present writer has been able to ascertain. In those glow-worms living outside in the open air, the light seems to be shut off during the day. Certainly when artificial light is put on or near glow-worms at night, they all gradually shut off their lights. Hudson has stated that the glow-worm's light is brightest before dawn, when presumably most prey would be snared.

It has been widely believed that noises of various kinds cause the New Zealand glow-worm to douse its light. This appears to be believed by the guides at Waitomo; when there, the writer shouted in ordinary and falsetto voice, and clapped hands,
but no noticeable effect was apparent in the great number of specks of light seen
on the roof of the cave.

On the alleged evidence of dousing, and of the presence of screens of pigmented
cells and fat, just in front of the light source in Bolitophila, Gatenby and Ganguly
(1958) suggested a possible mechanism for the supposed sudden dousing. This
hypothesis is now abandoned by the present writer. No sudden dousing of the light
occurs when various noises are made; nevertheless the withdrawal forwards of the
segment containing reflector and light organs has been noted in living larvae
observed under a coverslip. Larvae dislodged with a knife fall down the bank but
still light up. Some then put in the box did douse. Radio music and clapping to-
gether pieces of iron (tire levers) had no effect; and (supersonic) dog whistle was
also tried without effect on glow-worms at Arapuni—that is on individuals living
outside on banks, where the ability to douse rapidly could be expected to be most
useful. But lighted larvae on a table in a darkroom soon douse if the table is
accidentally shaken during experiments. In the case of larvae living on or under
banks in the forest where retreat tunnels are available, the supposed sudden dousing
is caused by the alarmed larvae moving quickly into their hiding place. They do
this in about three seconds, especially when near their tunnel, so their light has the
appearance of being turned off. On the other hand, it is true that among a number
of larvae carried home in a tin box, some will be found luminescent on arrival,
some not. The reason for this is not known, but it is certain that the larvae can
fade out their light more slowly (in about a minute); but this is quite different
from what has been written about sudden dousing, on alarm.

It is not known whether the larva itself excavates its hiding place—but this is
likely. Since the larva usually backs into this tunnel, its position brings about the
quicker covering of its light, and presents its hard head and jaws towards any
enemy which might try to enter the larva's hiding place. In hard-walled caves,
few larvae possess a hiding tunnel, and when disturbed they move along to the
end of their horizontal web and stop, uncertain what to do.

DISCUSSION

The downward course of malpighian tubes in the abdomen, and the association
of their distal ends with the intestine, exists in other non-luminous mycetophilids.
Its significance is not understood. In Ceroptilinae, the ends of the malpighian
tubes are not known to be luminescent, the light originating in cells of the fat body.
It is remarkable that two closely related predaceous insects with similar habits of
snare building should have developed different light organs. This seems to show
that the light is really used to attract phototropic prey.

The appearance of only a few predaceous snare building insects among the
Mycetophilidae, of which about two thousand species are known to be mostly
fungivorous, is in itself remarkable. In its snare building, B. luminosa shows con-
siderable enterprise in adapting its work to the difficulties of the terrain. Under
banks it sometimes spins its vertical lines so that they touch the ground, and often it
blocks further ingress to the hole by spinning vertical stopping webs across. It has
been suggested that the light of B. luminosa is merely the outward manifestation
of metabolic breakdown, and is not a snaring device. If this is so, it is curious that
luminescence has been developed from the static fat bodies in Ceroptilus testaceus,
which has similar predaceous and snare building habits. It is usually believed that
the arthropods which crawl at night on banks—e.g., wood-lice and small centipedes,
are negatively phototropic. It is curious if these arthropods are attracted by the
light produced by the glow-worms, but night lights are often used by entomologists
to snare nocturnal insects. It is possible that the damp mucus of Bolitophila is
attractive to small arthropods in arid places. Many wood-lice must get snared by
the sticky web even if they are not attracted by the light.
The following modifications in form and habits occur in *B. luminosa*: in the larva, the transformation of the distal ends of the malpighian tubes into light organs; the transformation of posterior tracheal lines into a hollow shell of tracheoles to form a reflector; elongation and further development of the gastric diverticula which, however, occur in other Mycetophilidae. The predaceous habit is known in several other members of this family. The vertical fishing lines appear to be unique to this species of *Bolitophilia* (see back, Goldschmidt), the snares of other predaceous species resembling horizontal spider webs. In *B. luminosa*, the mucus droplets are placed on the vertical lines; in other species they are found where the web lines cross one another. Scolophore organs will probably be found in the other predaceous species with anal papillae (or gills) when they are examined more carefully. The pupal suspensory cord may be unique in *B. luminosa*. The adult insect appears outwardly normal for the Mycetophilidae, luminosity being an extra modification of those malpighian tubules which possibly exist in the same position in other nearly related mycetophilid adults. The reduction of the bolitophilid larval antennae occurs in other forms such as *Ceroplatus*. The mouthparts closely resemble those of the latter genus (see Edwards).

It is interesting to note that there are at least 100 species of Mycetophilidae already recorded in New Zealand, of which *B. luminosa* alone has been studied in detail.

Some fungivorous mycetophilids have a silken net on the pabulum. The predaceous habit thereby probably developed, and after that the ability to produce light to attract more food. *Ceroplatus testaceus* glows from its fat body, *Bolitophilia* from its malpighian tubes. On any theory of Organic Evolution it is difficult to see how these different steps took place; but in any case no new organ has been developed for the production of luminescence, silk, or mucus in addition to what other Mycetophilidae are known already to possess.

The writer agrees with Goldschmidt that the Darwinian theory of small selected variations does not explain this or similar situations in animal life. The carnivorous habit, the snare building, luminosity, and the ability to cope instinctively with various situations are all remarkable developments in an insect whose ancestral types were all fungivorous, or spent their lives boring through and eating decayed vegetable matter. But it is equally difficult to understand how all the psychological and anatomical peculiarities of this animal came together at the right moment and at the right degree of development to make it what we know it to be today.

Probably the most remarkable anatomical development in *B. luminosa* is the tracheal boat which forms the reflector. This device could have been derived from fat bodies as it is supposed to be in coleopterous fireflies, but the New Zealand glow-worm combines in one modification both reflector and air supply. In the coleopterous fireflies there are separate modifications for this. The other noteworthy modification in the New Zealand insect is psychological. The capacity for instinctive reactions has developed in a remarkable way, yet anatomically it has a conventional hexapod nervous system. How far the size of its brain compares with that of a mycetophilid larva which spends its life boring in a mushroom is not known to the present writer. Psychologically, the coleopterous firefly's behaviour is uninteresting compared with the complicated nervous reactions found in *B. luminosa*. It is this combination of anatomical and psychological developments in the New Zealand glow-worm which are of importance to those interested in Organic Evolution. There is yet no satisfactory answer to the problem.

Regarding experiments on control of luminescence, the lighting up of the cut and separated last segment containing the light organs is interesting. The isolated segment will light up continually for two days and nights if kept damp. The individual tubes of the light organ continue luminescent when teased and separated.
Not all cells luminesce, a patchwork of lighted and unlighted parts sometimes being noted.

There is a definite lag during the fade-out of the dousing light, likewise in the evening, the light comes on slowly. Glow-worms placed in the dark during the day light up after an hour or so. A flash lamp light turned on luminescent larvae at night causes slow dousing, the light starting again in the dark after about a-half hour or less according to how long the flash was on them.

The experiments reported earlier in this paper appear to show that the ganglion in the seventh segment controls the light, but not directly. It seems possible that nerves going to the tracheal reflector in some way cut off the supply of air, but neither such nerves nor valves in the reflector are known for certain. These larvae do not possess a biological clock, perception of light and darkness being usually the ultimate controlling factor. But the larvae do not always turn on their light, all larvae remaining doused on certain nights. There appear to be no careful observations on weather conditions and dousing, except for a few remarks by Hudson who did not go into this systematically. The experiments on the possibility of a "dousing hormone" failed; the lighted up pieces of the organ remaining luminescent when bathed in blood from a doused larva.

In the beetle *Luciola*, the flashing of the light at intervals ceases if the animal's head is cut off, but it can be induced to flash again if the cut end of the nerve cord is stimulated. This is the reverse of what happens in *Bolitophora*, where separation of the light organ from the body and therefore from the central nervous system, allows glowing to continue.

The nature of the pink granules in the longest region of the malpighian tubes is not known. They are probably urates, not lime. *B. luminosa* is the only insect known in which the malpighian tubes produce light, but in various other insects, silk has been described as arising from modified parts of these tubes. It is true to say, however, that the malpighian tubes throughout the orders of Insecta remain remarkably unmodified physiologically.

It has been noted that the light flashes brilliantly when larvae are dropped into Carnoy's fluid (absolute alcohol, chloroform and glacial acetic acid). This has not been followed up.

The snare presents some interesting problems. The vertical fishing lines depicted in Text-fig 1 could obviously be made by the larva fastening one end to the side threads ($) and pulling out a silk thread covered with mucus. But the vertical lines in cave glow-worms' snares are up to two feet in length, and it is not known if these are let down from the runway and subsequently fixed at one time. Regarding the question of the manner of spinning of the vertical threads of the snare, various larvae have been observed holding the thread in their mouth as it is spun and lowered. Later, the thread, when long enough, was fixed in position by the larva.

The following are the known facts about the life cycle of *B. luminosa*: Pupae have been found on banks in late September and early March. Many larvae from November to March have imaginal discs. Larvae of all sizes were found from September to March, small ones predominating at Arapuni from February to March. At Waitomo, a pupa was found in February; it contained a number of ripe eggs. From these observations it appears that adults can emerge at any time during the summer.

A larva has been kept for six weeks, and fed on houseflies. It has recently pupated and the suspensory thread was not the original runway of the snare, but was specially spun after the runway and neighbouring sticky vertical lines had been cleared away by the larva. This silken thread began to darken within two days of pupation. It is possible that existent shorter lines are cut and a new piece added and the new end fixed to the runway. How the larva recovers prey from such long
fishing lines is not known, but recently a captive glow-worm was seen to climb down the vertical lines to suck out the contents of a fly put out of reach of its runway. The larva seems such a master in the manipulation of silk and mucus that it might be able to climb down and pull up the prey. It has been suggested that the larva pulls up the relevant fishing lines and so recovers the prey.

It has been mentioned by past observers, and it has been noted by the writer, that in many cases the larvae living in holes in banks have their snares almost completely screened by spider webs. It seems that in such cases the glow-worms must live on crawling prey which can get under the spider webs.

The success of the larva in living in different situations, especially in arid banks, is due to its ability for water conservation. The cuticle is extremely tough and impermeable, and the mouth and anal openings small. The animal needs to conserve water to produce the mucus droplets. There must be few other insects which chop up their prey and swallow it entirely. Nothing is wasted. In many situations the capture of prey must be a longed-for event, upon which the growth and life of the larva depends.

On January 23, a new visit was made to Arapuni. The glow-worms tended to be in groups up to fifty in number, twenty being common, all of the same stage of development, as if the eggs had been laid by one female. Many of the groups were formed of very small larvae, their bodies being difficult to see, but the light they showed was bright. None of these young specimens had vertical fishing lines; all had an elongate runway like a narrow silk and mucus smear in the bank. In cases where this could be tested, these small larvae had a hiding place. Judging from the Arapuni larvae, the elaborate curtain of fishing lines is only produced by larger larvae, and the newly hatched larvae must begin life by either finding or boring a suitable hiding place, then secreting a runway ending in the hole.

Once again observations were made on the possibility of noises affecting the larvae. These experiments showed that ordinary noises did not alarm the larvae. But the Arapuni larvae appeared more sensitive to the light from the flash-lamp than those in Wellington. When one approached a group, the light of the lamp caused many of them soon to fade out their lights. Some of the larvae also began to move towards their hiding places. However, return to the spot in about a quarter of an hour showed that confidence had been restored, and the lights were on again.

Some of the larvae were very small, and care had to be taken in removing them. If they became broken at their end, the light continued, and if gently crushed on the back of the hand, the luminescent organs appeared as a glowing smear. Mr. K. Carey, who had often visited this locality, informed the writer that on some nights no glow-worms showed their lights. No explanation of this was forthcoming. In the Wellington Botanical Gardens some larvae turn on their light sooner than others.

Since we now know that the female can lay up to about 80 eggs, the potential increase in population of the caves could be tremendous, unless kept down by predators or cannibalism—probably by the latter and starvation. But it is well to mention that of many larvae examined, not one was found with an empty mesenteron. They may, however, retain chitinous fragments in their gut till the next meal comes along and so give a false idea of prosperity. The beginning of life of the newly hatched larvae must be a difficult period. At this time they do not seem to exist in a non-predaceous manner. In any case, the eggs are large and yolky, and this must give them a start.

The impression gained is that according to food supply, the larvae may or may not grow slowly, that they can survive during winter, that they often wander from their territory as a result of which cannibalism takes place, and that they have no
enemies except themselves. They are vigorous and strong animals, the chitinous cuticular covering is tough, the head capsule hard, and in habit they are bold, predaceous and enterprising. On the other hand, the adults are delicate and die quickly when uncomfortable.

Hudson and Norris found that a proctotrupid wasp attacks pupae of Bolitophila, but it has yet to be shown whether this is common, and whether the proctotrupid is a specific parasite of these pupae. While parasitic Hymenoptera are among the most resourceful of insects, it seems doubtful if they could oviposit in the larvae. No hymenopterous larvae were found by the writer in glow-worms. Hudson noted that some of his dead pupae had become mouldy, and moulds were found by the present writer on all pupal exuviae in Waipu. It is possible that moulds destroy many of the pupae in damp caves. At Waipu, the largest of all glow-worms were found. Until enough adults are collected and their externals and genitalia carefully examined, it will not be possible to say whether more than one species exists in New Zealand.

In the future there are many problems which can be solved by observant, but not necessarily trained, entomologists in this field. It is evident that precise information on the life cycle of the glow-worm will only be forthcoming from someone who takes the trouble to mark and watch the sites of individual larvae. We need to know how attractive their light is to flying insects. A flash-lamp, covered with cardboard, with a suitable pin hole and colour screen to give a light similar to that emitted by the glow-worm, could be used. A sticky material, not attractive to insects, could be used to smear the cardboard. But we need information on the spectroscopic nature of the light and the attractiveness of light from various parts of the spectrum, to chironomids and other food insects. Study of other New Zealand Mycetophilidae in larval stages should be very worth while. Chemical analysis of the mucus droplets, and the pink granules in the malpighian tubes needs to be carried out. Good histological preparations of the course of nerves to and from the ganglion in the 7th segment are required. Some method of removing or screening the eyes of the larvae would be helpful. Adults from various localities are wanted to ascertain whether one or more species exist in New Zealand. The effects of weather and electric storms on larvae need long-term observation. The manner by which long vertical fishing lines come to be made is unknown, as also is the method the larva uses to hoist the captured insects. In captivity, larvae could be provided with a constant supply of food, by placing fermented banana culture-tubes of Drosophila (fruit flies) in their cages.

It is hoped that these notes, often inadequate, which have been given in this paper, will encourage other entomologists to investigate some of the problems outlined above, and thus add to our knowledge of this wonderful insect.

Summary

(1) The adult female lays about 75 eggs, which are whitish, spherical, and 0.75 mm in diameter. They may be stuck to the substratum by an orange-coloured cement. The female curves down her abdomen as she oviposits. (Pl. 26, Fig. 8b).

(2) The eggs are yolky, and their large size probably means that the newly hatched larvae are provided with food until they become established. (Pl. 27, Fig. 13.)

(3) The adult female possesses four well-developed light organs, which are the distal ends of the four malpighian tubes. (Pl. 27, Fig. 10.) The reflector is lobulated, and contains a cavity, which may be filled with air. The female is known to be luminescent for up to two weeks. (Pl. 27, Fig. 10r.)

(4) The adult male has degenerate light organs in which collapse of the tubules and some aggregation of the nuclei has taken place. A reflector like that of the
female exists in the male. The male is not known to be luminescent. (Pl. 27, Fig. 11.)

(5) The larva is oblivious to various types of noises, and is not alarmed until its snare is touched, when it retreats within two or three seconds, usually backwards, into a prepared hiding place, which action quickly covers its light.

(6) Larvae at night can be dislodged by a quick thrust of a knife, fall down the bank, and continue lighted up. They may, but generally do not, douse their light under these circumstances, for some hours, and can be found lighted up wandering on leaves on the same and on the following evening. Larvae tend to douse their light shortly when a flash-lamp is turned on to them.

(7) Of a number of larvae placed on moss in a box, some continue luminescent, some douse. The larva has the power slowly to fade out its light in about a minute.

(8) No imaginal discs develop in connection with the light organs, but the larva clears out the pink excretion granules in its malpighian tubes before pupation. (Pl. 24, Fig. 6.)

(9) In direct light the full grown larva (Pl. 23, Fig. 4) is brownish black in front, brown further down, pink in the mid lower region, and mainly hyaline towards its posterior end. Larvae about to metamorphose have lost their pink colour through evacuation of excretion granules.

(10) Silk and mucous glands of the larva are separate and large (Pl. 24, Fig. 5). The mucous glands are chocolate brown in colour. The mucus droplets are not coloured.

(11) The nervous system of the larva is not known to be peculiar in any way. The ganglia are large, and the last segment is served by a ganglion lying in the segment in front (Pl. 25, Fig. 7A).

(12) There are larval integumental scolophore tactile sense organs (Pl. 26, Fig. 8) in the two terminal anal papillae. Two of the four scolopale organs are provided with an external seta, one curved, one shorter and straight. Two others have no setae. A nerve from these sense organs passes to the ganglion in the segment in front.

(13) The head has a dorsal pair of aggregate eyes with a single facet, and a more ventral sense organ of the lateral ocellus type. The antenna is reduced to a drum-like base. The jaws are powerful and sharply toothed; below are powerful maxillae, also serrated, but not so sharply. In between is an eversile basket-like bristled sac which may be an epipharynx (Pl. 25, Fig. 7B).

(14) The brain lies almost completely behind the head. The innervation of the reflector and light organs is not understood.

(15) The light organs of the larva (Pl. 27, Fig. 12), as in the adult insect, are the swollen distal ends of the four malpighian tubules. These latter are divided into four regions; where they originate from the posterior end of the mesenteron the tubes are free of excretion granules, then there is a large, much longer, wider pink region of granules, then a tapered region with fewer granules, which is bound to the intestine, then a short similar area free of granules, then finally the light organs. There appears to be a close physical, but no tracheal connection between the boat-shaped reflector and the light organs (Pl. 24, Fig. 5). The whole segment containing the light organs and reflector can be telescoped within the segment in front by the contraction of longitudinal muscles (Pl. 25, Fig. 7).

(16) Optical microscopy shows that the light organ cells have increased numbers of mitochondria.

(17) Control of luminescence is not properly understood. When the last segment containing the light organ is cut off, the light continues for as long as two
days if the piece is kept damp. If the cut is made so that the ganglion in segment 7 retains its connection with the last segment, dousing takes place. If the light organ is then cut off this piece, it lights up. Control of light does not appear to be hormonal.

(18) The tubular heart stretches from the front end of the last segment to the head capsule. It beats about 60 times a minute.

(19) The larval tracheal system is apneustic. At the posterior end it enlarges to form a boat-shaped tracheal basket, in which lie the light organs (Pl. 25, Fig. 7).

(20) The pupa (Pl. 23, Figs. 2, 2A) is suspended by a combination of silk threads and mucus. It is holopneustic. The female pupa is from time to time luminescent.

(21) The snare consists of a silken and mucus runway lying horizontally. From the sides of this are suspended vertical fishing lines, provided with mucus beads. The latter are secreted one at a time as the silk line and chain of beads is held and lowered by the larva. The snares of very young larvae have no vertical lines, but they spin a runway and have a hiding place in the bank. The light of very young larvae is bright. Protozoa and aquatic larval nematodes are not killed by being immersed in the mucus droplets from the vertical lines.

LETTERING.

A—antenna; AC—accessory gland of male ducts; AE—gonapophyses; B—tracheal trees under cuticle; BB—everted basket between jaws and maxillae; BR—brain; BZ—dark head and thorax zone containing brain and oesophagus; C—circumferential muscles; CA—haemocoelomic coagulum; CN—probable cement organ; CO—combed rough area for adhesion; CT—connective tissue; CZ—clear zone containing intestine and, below, the luminescent organ (LO); D—gastric (mucus) diverticulum; DF—pigmented fatty cells; F—fat body; G—gut; GF—grey fat body; GR—excretion granules in lumen; G2—chocolate zone, containing gastric diverticula and mesenteron; H—head; IN—intestine; L—longitudinal tracheal channel; LG—leg; LM—longitudinal muscles; LN—end of lumen; LO—light organ; LOD—collapsed part of light organ; M—pink region of malpighian tubule containing excretion granules; ME—mesenteron; MU—muscle; N—nerve; NA—last abdominal ganglion, and in Fig. 4, its position; O—oesophagus; OR—connective; OV—ripe oocyte (ovum); P—anal palps; PZ—pink zone of malpighian tube; Q—broken down material in palp cavity; R—reflector; RC—vesicula seminalis; RR—fat cells (pigmented) under cuticle of head and thorax; RS—chitinous side plates supporting suspensory card; S—pigmented flat cells associated with cuticle; SI—silk glands; SU—chitinous prolongation from head and front thoracic region, forming suspensory cords; T—side tracheal ramifications of viscus (in Fig. 1) on main tracheal trunk; TA—tracheal opening; TE—testis; U—lumen in luminescent organ; V—oesophageal valve; VE—vent; W—wing; X—cell clear of excretion granules.

MAGNIFICATION OF FIGURES.

The larva in Fig. 4 was about 1½ inches (28 mm) long. The pupal exuvia in Pl. 23, Fig. 2 measured 14 mm; the cord (SU) 16 mm. When the line below Fig. 13 measures 50 mm, the adult female in Fig. 8B will be about 2½ X. On Pl. 27, when the line below Fig. 13 measures 58 mm, Figs. 10 and 11 will be at 90 X, Figs. 12 and 13 at 60 X. Fig. 7, similarly, will be at about 130 X. For other measurements of adults and their parts, see back.

LITERATURE


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