Observations on the New Zealand Glow-worm *Arachnocampa luminosa* (Skuse) 1890

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Abstract

A brief resume is given of previous literature on the New Zealand glow-worm, *Arachnocampa luminosa* (Skuse). Most observations recorded in this paper are confined to tunnel and cave-dwelling members of this species. An average of 130 eggs are laid by each female fly, the incubation period being around 22 days. The larval, pupal and adult forms of both sexes are all luminous. In the larva the light attracts prey, while in the pupa and adult the light attracts the opposite sex. The nest and fishing-lines of the larva are formed of mucus and silk, and together with the light organ form the feeding mechanism of the larva. Sexual differentiation is evident in the pupal stage, which lasts about 13 days. There is a marked difference in size between tunnel and cave-dwelling forms. At Waitomo, the principal food of the larva is the midge *Anatopynia debilis* (Hutton) (Fam. Chironomidae). The larvae are also cannibalistic on other larvae, pupae and adult flies. In caves, two opiliones, *Megalopsalis tumida* Forster and *Hendea myersi cavernicola* Forster, are the main predators on *A. luminosa*. Several species of fungi attack the larval and pupal stages. No hymenopterous parasites have been found. The segregation of rhaphidophorids and hunting spiders from glow-worms on the walls of caves is explained. Indications are that in caves the life cycle was once seasonal, but with adaptation to cave conditions this has gradually been lost.

Introduction

The New Zealand glow-worm, *Arachnocampa luminosa* (Skuse) is one of the most interesting of our native insects, and yet very little is known about it. Glow-worms occur throughout New Zealand in limestone caves, unused mining tunnels, along stream banks, in damp bush-clad ravines, in damp, shady crevices and under tree fern fronds in rain forest, often forming quite impressive displays with their myriad twinkling bluish-green lights. The Glow-worm Grotto in Waitomo Cave has become world famous because of the tens of thousands of *A. luminosa* larvae which live on the walls, ceiling and stalactites of the Grotto. (Plate 27.)

When these insects were first observed, it was thought that they were related to the European glow-worm *Lampyris noctiluca* (Coleoptera, Lampyridae). An early record of them occurs in a Report of the Auckland Institute. Section 7, from the first meeting on May 29, 1871, states: "The Rev. A. G. Purchas exhibited the female insect and larvae of one or two species of Lampyridae which he had obtained from some of the drives on the Thames goldfields. He stated that their luminosity in some cases was most remarkable." (Anon. 1872.)

In 1886, Mr. E. Meyrick published a note on some Auckland specimens of the glow-worm, which he considered to be predaceous coleopterous larvae belonging

* Part of this study was carried out during the tenure of a New Zealand University Research Fund Fellowship.

to the Staphylinidae. However the editors of *Ent. mon. Mag.* added as a footnote: " There is distinct necessity for further information (with examples in fluid) respecting the animal noticed above. The larvae of Staphylinidae are ordinarily so like the perfect insect in form (allowing for absence of elytra, etc.) that we venture to doubt the connection of the animal with that family."

In 1886, as the result of an examination of adult flies submitted to him by G. V. Hudson, Baron Osten-Sacken stated that the glow-worm belonged to the Mycetophilidae or fungous gnats. In 1890, it was described by Skuse as *Bolitophila luminosa.* In 1885, Hudson commenced studying the glow-worm, and from then till the time of his death in 1946, he was the main contributor of information concerning the habits of this insect. His material was obtained from the banks of a stream in the Botanical Gardens, Wellington.

On the basis of a number of important differences in the wing venation of the adult fly, and also the form and habits of the larva, Edwards (1924) erected a new genus for the species *luminosa* choosing the name *Arachnocampa* because of the " spider-like habit of the larva, forming webs and using them for the capture of insect prey." In this respect Edwards claimed " the insect differs not only from all other Mycetophilidae, but from all other known dipterous larvae ". In 1927, Tonnoir and Edwards studied the Mycetophilidae of New Zealand and found *Arachnocampa luminosa* to be the only luminous species in the family.

In 1959, Gatenby referred *luminosa* back to the genus *Bolitophila.* Harrison (in press) however, is of the opinion that the genus *Arachnocampa* is valid. Further, he has examined numerous specimens from caves, tunnels and bush throughout New Zealand, and considers that in spite of the variation in size, they all belong to the species *A. luminosa* (Skuse).

The main study area for this paper has been the Glow-worm Grotto of Waitomo Cave, where the insects were under daily observation for most of 1955. Since then several short trips have been made to this cave. A Waitakere waterworks tunnel and the Parnell tunnel, Auckland, have been used as subsidiary study areas. Trips have been made to the limestone caves at Waipu, North Auckland; Ruakokopatuna, Wairarapa; and Rockville, Nelson, and to the Thames gold mines, as well as to Hudson's original site in the Botanical Gardens, Wellington, in order to study *A. luminosa* under natural conditions.

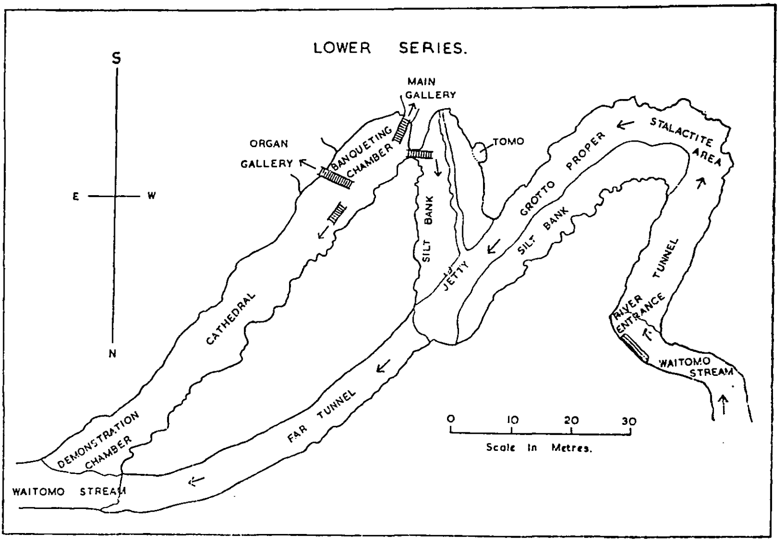
The Environment in and Around Waitomo Cave

Waitomo Cave is a large limestone cave situated in the King Country. It is estimated that its formation began about a million years ago (J. H. Richards, 1958). It consists of four separate caverns, each with its own system of corridors. Some 12 metres below the main entrance is the river entrance, where the Waitomo Stream enters the cave.

The Grotto of Waitomo Cave can be conveniently divided into four separate areas: the Far Tunnel, the Grotto Proper, the Stalactite Area and the Tunnel (Text-fig. 1). Light from the exterior penetrates into the Grotto for about 21.7 metres along the Tunnel. On a sunny morning, the light intensity* along the west wall of the Tunnel ranges from 0.5 to 1 f.c.; along the east wall or on the stalactites of that side it varies from 1 to 1.5 f.c.; behind the stalactites it is 0.5 f.c.

In 1955, the mean temperature in Waitomo Cave was 60.2′ F. (15.6′ C.) for summer, 57.4′ F. (13.7′ C.) for winter and 57.1′ F. (13.7′ C.) for autumn and spring. As diurnal variation is almost absent, these results show that conditions are

* Light intensity was measured with a Weston Photometer.



TEXT-FIG. 1.—Map of Lower Series of Corridors in Waitomo Cave

relatively stable throughout the year. The relative humidity ranges from 94% to 100%, but is usually 97% (Table 1).† (Richards, 1956).

Temperature and relative humidity readings were also taken in the bush and along the banks of the Waitomo Stream (Table II). These show that although the temperature fluctuated, the relative humidity was always fairly high. During the long, hot summer of 1955, the banks often appeared arid, yet the relative humidity was always fairly high.

TABLE I.—*Mean Temperature and Relative Humidity Recordings in Grotto, Waitomo Cave, During 1955.*

	Mid-day			Midnight		
	Temperature °F.		% Relative Humidity	Temperature °F.		% Relative Humidity
	Wet	Dry		Wet	Dry	
Summer	60	60	100	59	60	97
Autumn and Spring	57	58	97	56	57	97
Winter	55	56	97	55	56	94

† Temperature and relative humidity were measured with an Assmann Psychrometer.

TABLE II.—*Mean Temperature and Relative Humidity Recordings in the Bush at Waitomo Caves During 1955.*

	Banks Round Waitomo Cave.						Banks Round Aranui and Ruakuri Cave.		
	Day			Night			Day		
	Temperature °F.		% Relative Humidity	Temperature °F.		% Relative Humidity	Temperature °F.		% Relative Humidity
	Wet	Dry		Dry	Wet		Wet	Dry	
Summer, 1955	64	70	74	61	64	82	63	68	75
Autumn and Spring, 1955	54	56	88	52	54	91	54	55	91
Winter, 1955	50	52	87	47	49	83	49	53	79

EFFECT OF THE ENVIRONMENT ON *Arachnocampa luminosa*

In Waitomo Cave, the largest aggregaiton of glow-worms are associated with the stream, but small groups may be found scattered throughout the whole cave.

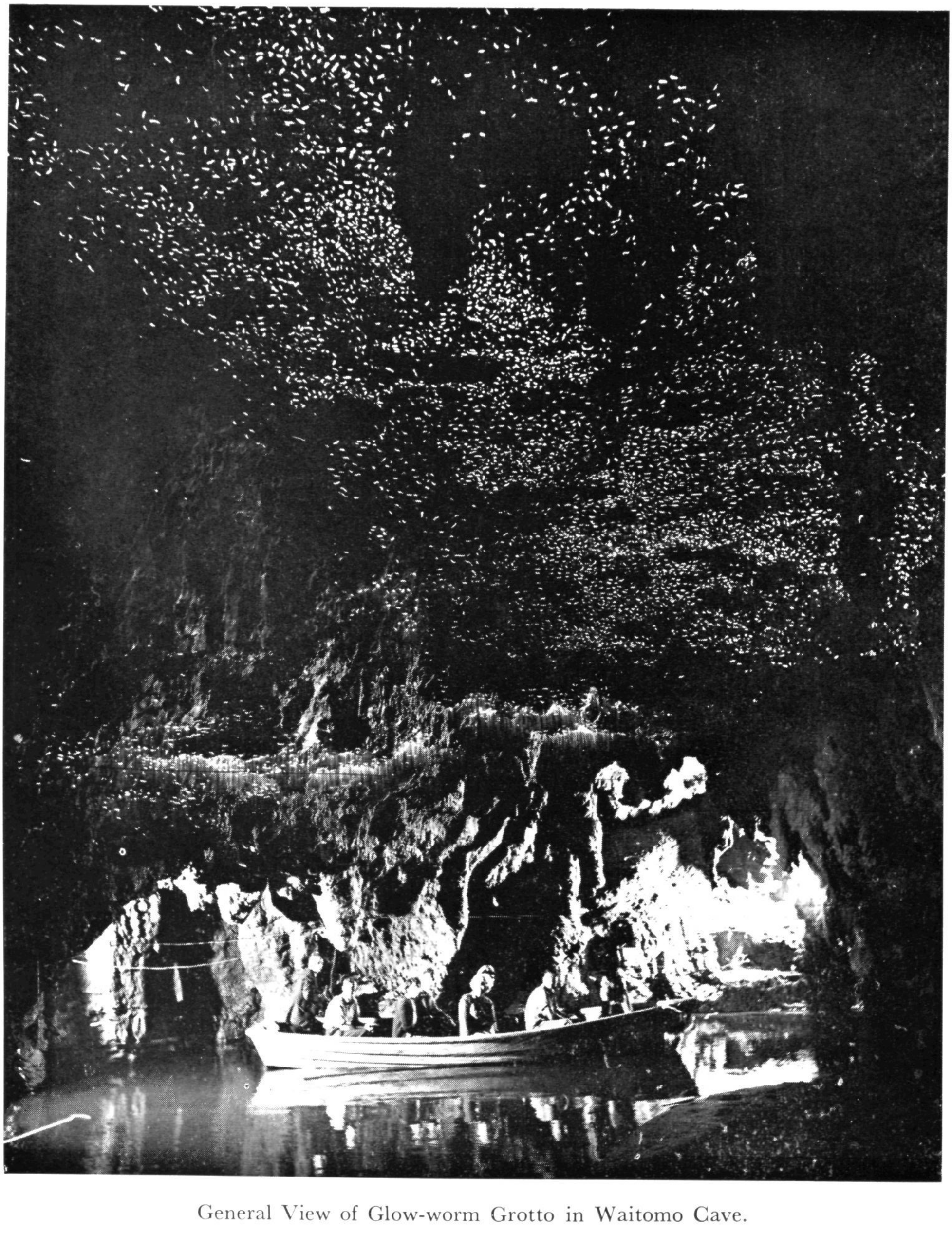
In *A. luminosa* luminescence and the intensity of light produced can be controlled by the insect. The larvae are capable of glowing 24 hours of the day when in the dark, but usually they do not glow in daylight. They will glow in a dim light, but usually not above a light intensity of 0.5 f.c. In the Tunnel area of the Grotto very few glow-worms turn their lights on in the daytime, the few observed to do so being restricted to the areas with a light intensity of 0.5 f.c. or less.

In the open, glow-worms always occur in damp, shady ravines or along the banks of streams. At Waitomo, they are common in the bush and along the banks of the Waitomo Stream. Most of them shelter in holes in the banks during the day and emerge at night to feed. Cave-dwelling glow-worms are very sensitive to moisture requirements. If the immature stages are removed to dry conditions they shrivel rapidly and die within a few hours.

LIFE HISTORY

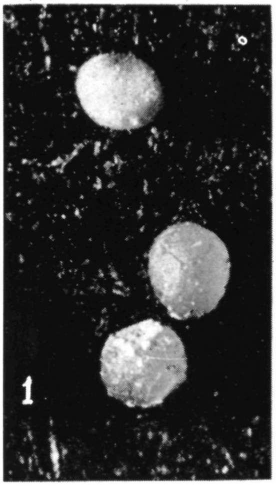
Egg. No difference was observed in size or colour of eggs laid by bush, tunnel or cave female flies. The egg is spherical in shape and 0.75 mm in diameter (Plate 28, fig. 1). When deposited it is cream in colour, but within a few hours it changes to either a light brown or an orange-red colour. Larvae hatch from both types. After hatching, the empty chorion is usually a reddish-brown colour. The eggs are slightly sticky and adhere to the substratum. They are usually deposited directly onto the limestone walls of caves, where thousands have been observed. A few may be deposited on empty pupae. According to Gatenby (1960), " they may be stuck to the substratum by an orange-coloured cement ". Although several thousand eggs have been examined by the author both in the field and in the laboratory, no trace of this cement has been observed. Many of the eggs are eaten by opiliones and isopods.

Eggs deposited on the ceiling in the Demonstration Chamber, Waitomo Cave, in early July, 1955, were segregated under a glass lid; they commenced hatching 22 days later. Another series of eggs in a box in another part of the cave took 24 days to hatch. Eggs laid on damp cotton wool in the laboratory took 20 days to



General View of Glow-worm Grotto in Waitomo Cave.

Photo by courtesy of National Publicity Studios.



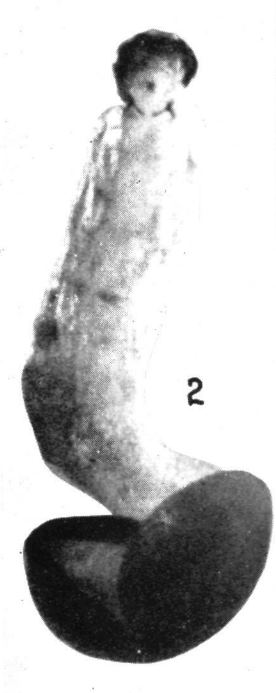


FIG. 1.—Eggs of *A. luminosa*. Natural size 0.75 mm in diameter.
Photo: J. W. Endt.

FIG. 2.—Larva of *A. luminosa* emerging from the egg.
Photo: S. A. Rumsey.

FIG. 3.—First instar larva of *A. luminosa* suspended from the ceiling in Waipu Cave.
Photo: S. A. Rumsey.

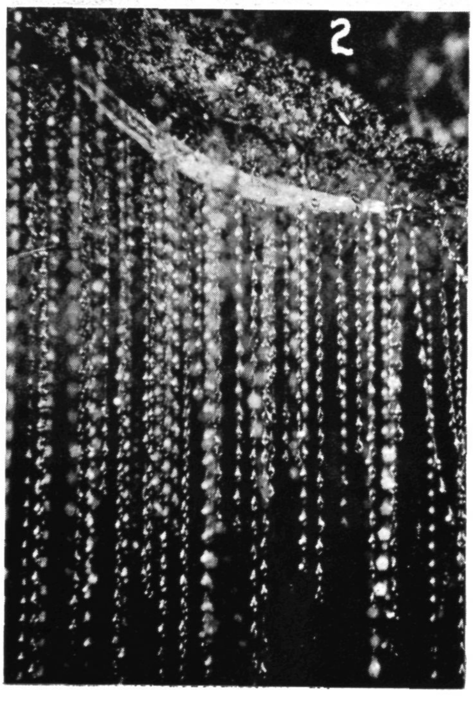


FIG. 1.—Larva of bush glow-worm near Aranui Cave, Waitomo.

Photo: S. A. Rumsey.

FIG. 2.—Larva of cave glow-worm on wall of Grotto in Waitomo Cave.

Photo: J. Pybus.

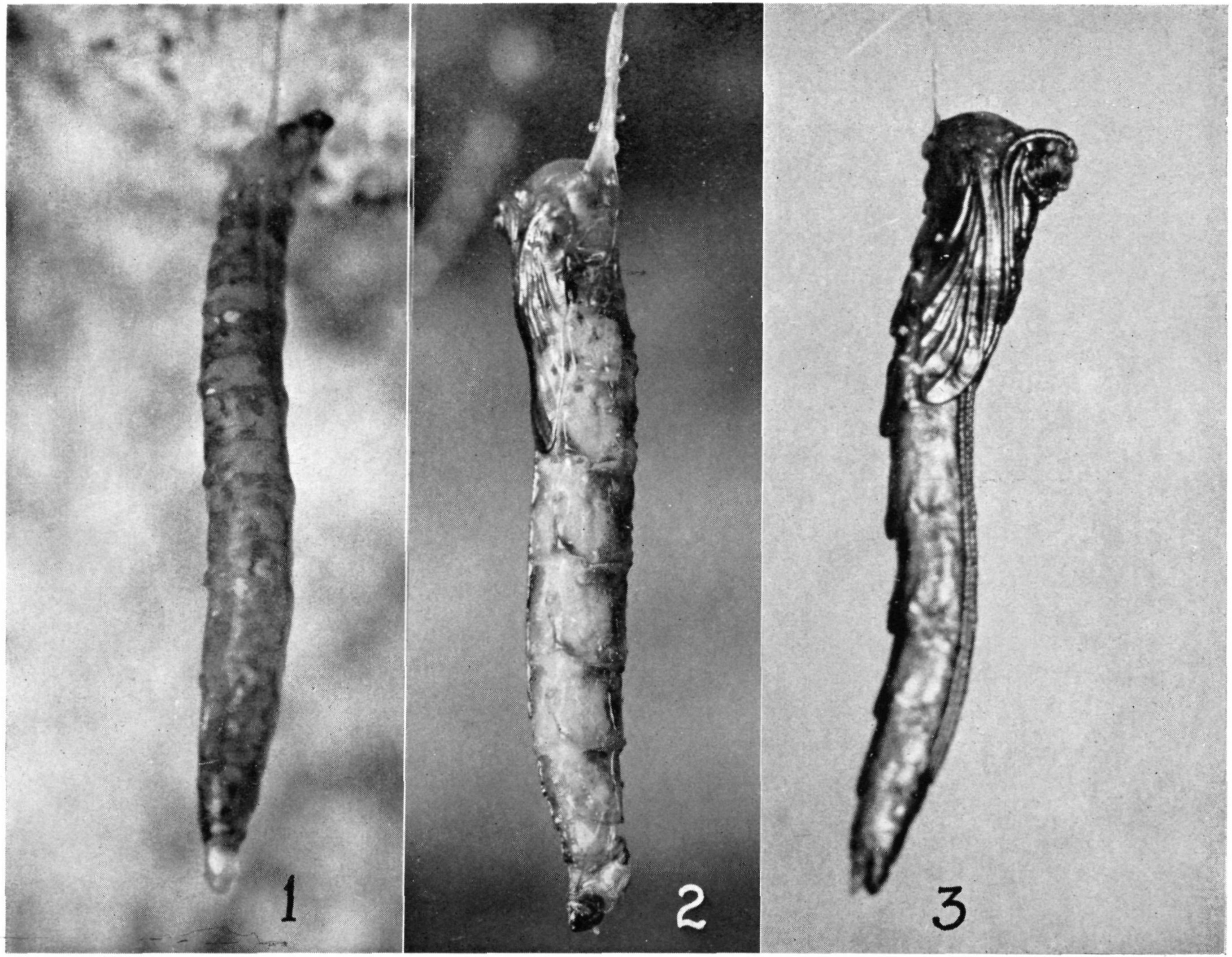


FIG. 1.—Larva of *A. luminosa* suspended vertically from the ceiling in the Swanson Tunnel, Auckland, just prior to pupation.
Photo: S. A. Rumsey.

FIG. 2.—Female pupa of *A. luminosa* showing attachment of suspensory cord to the dorsal surface of the thorax.
Photo: S. A. Rumsey.

FIG. 3.—Male pupa of *A. luminosa.*
Photo: S. A. Rumsey.

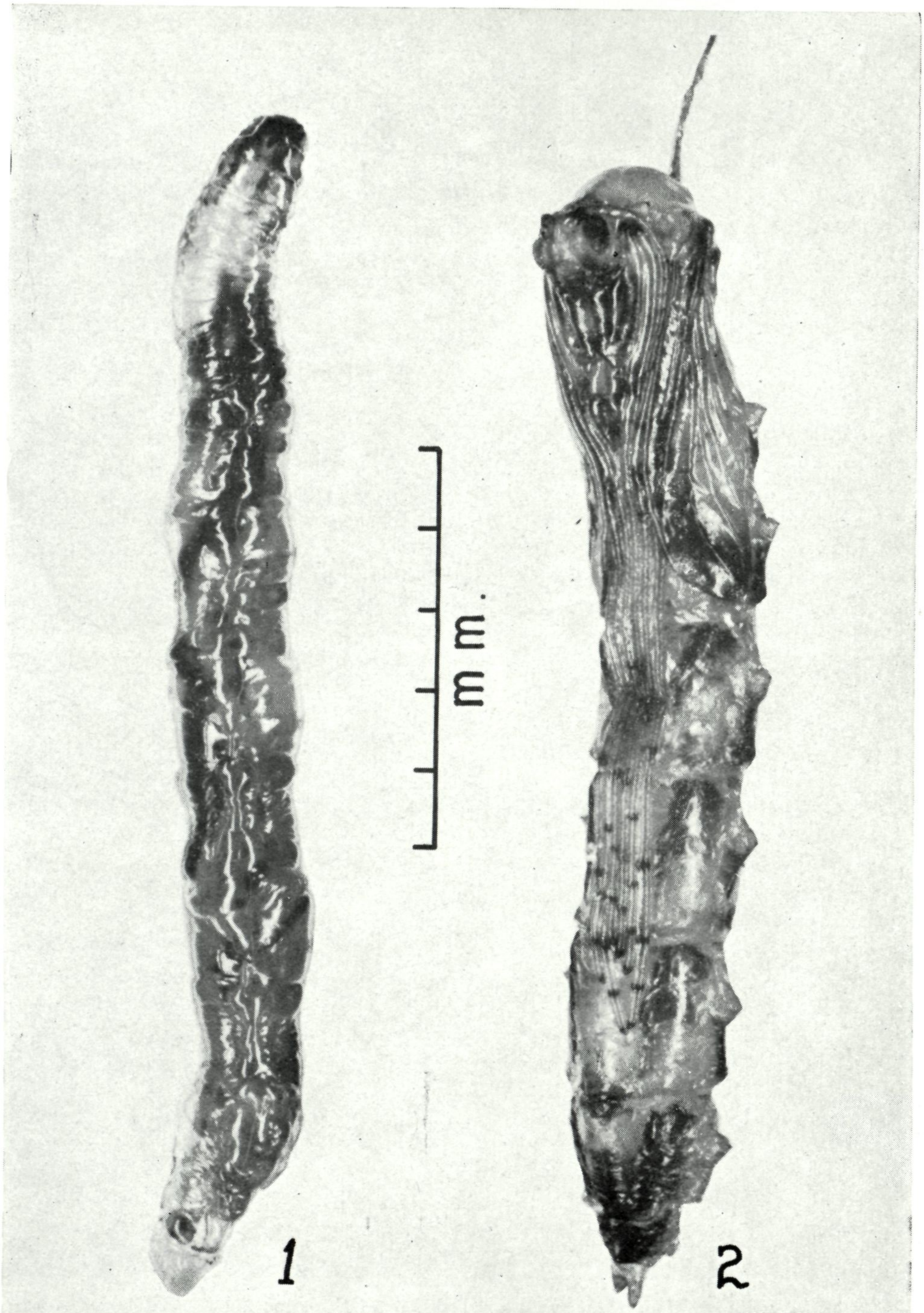


FIG. 1.—Larva of *A. luminosa* removed from its nest.
Photo: S. A. Rumsey.

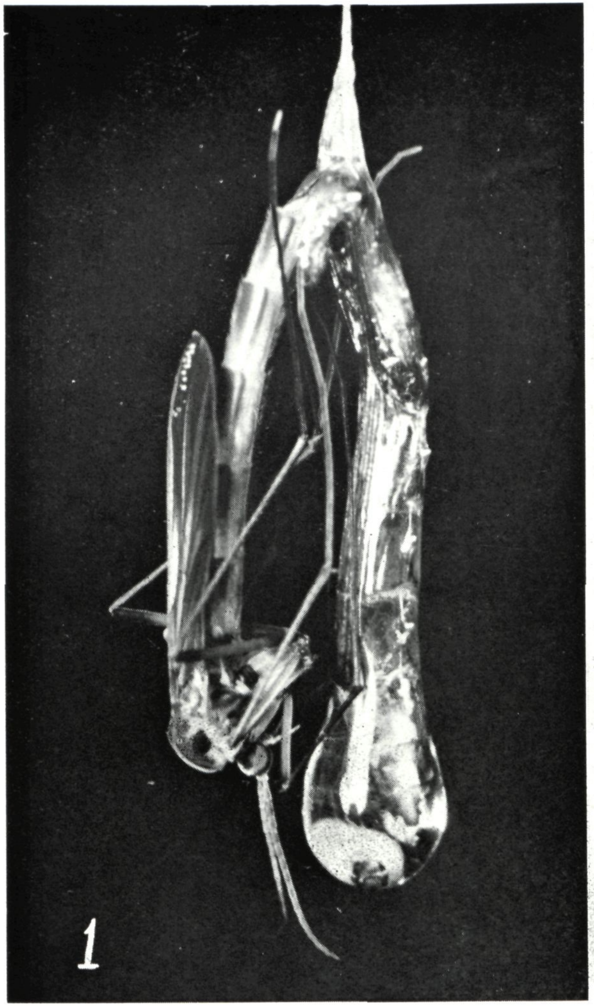
FIG. 2—Ventral aspect of female pupa of *A. luminosa*.
Photo: S. A. Rumsey.

FIG. 1.—Pupa of *A. luminosa* suspended from ceiling in Waitomo Cave. All larval fishing-lines have been removed.

Photo: J. Pybus.

FIG. 2.—Pupa of *A. luminosa* hanging amongst a dense mass of larval fishing-lines in Waitomo Cave.

Photo: J. Pybus.



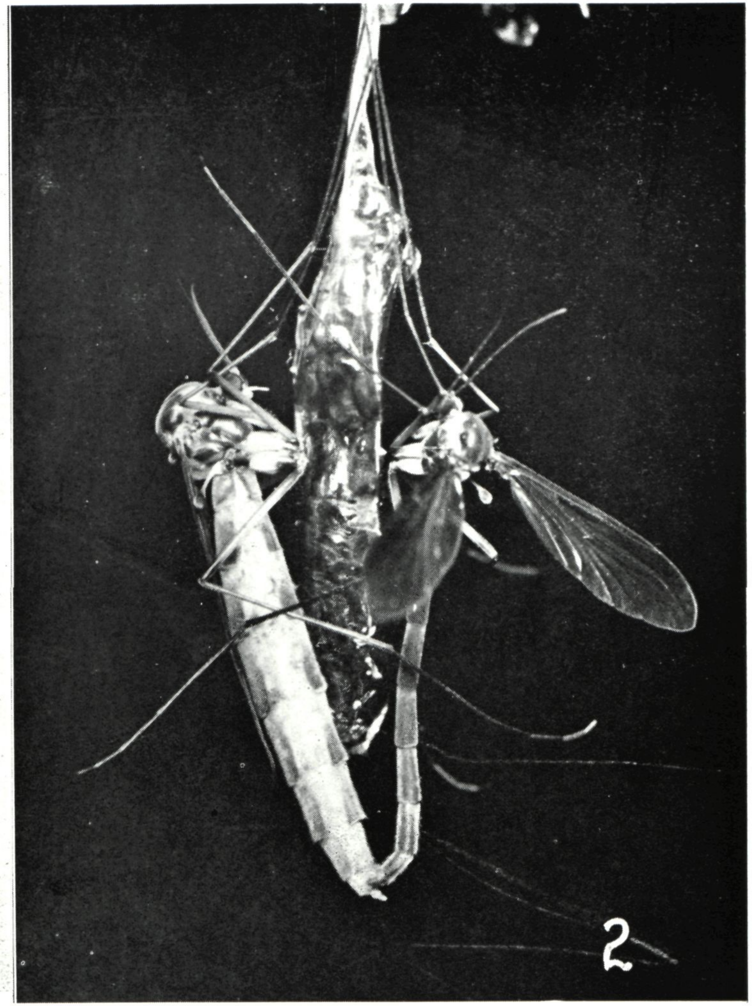


FIG. 1.—Male fly of *A. luminosa* emerging from a pupa on the ceiling of Waitomo Cave.

Photo: S. A. Rumsey.

FIG. 2.—Male and female flies of *A. luminosa* in copula. Both flies are clinging to the empty female pupal case in the centre. The female fly is on the left and the male fly on the right. The eggs are visible through the body wall of the female.

Photo: S. A. Rumsey.

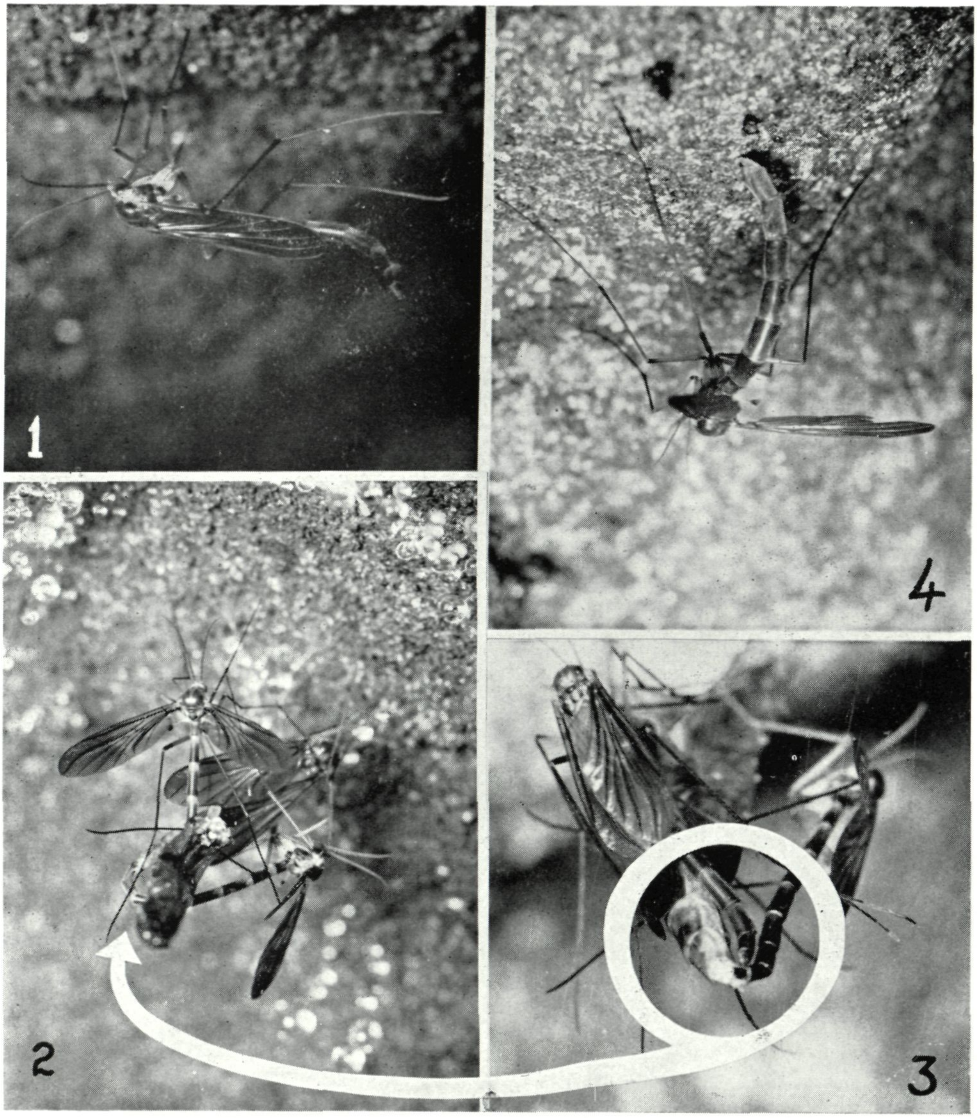


FIG. 1.—Male fly of *A. luminosa* on ceiling in Grotto of Waitomo Cave. The tip of the abdomen is characteristically raised above the rest of the body, and the wings are folded over the thorax and anterior part of the abdomen.

Photo: S. A. Rumsey.

FIG. 2.—Two male flies of *A. luminosa* attempting to copulate with a female fly which has just emerged from a pupa. They are suspended from the ceiling in the Grotto of Waitomo Cave.

Photo: S. A. Rumsey.

FIG. 3.—View of same three flies from opposite side, showing male and female in copula, while other male fly attempts to separate them.

Photo: S. A. Rumsey.

FIG. 4.—Female fly of *A. luminosa* ovipositing on the ceiling in the Grotto of Waitomo Cave.

Photo: S. A. Rumsey.

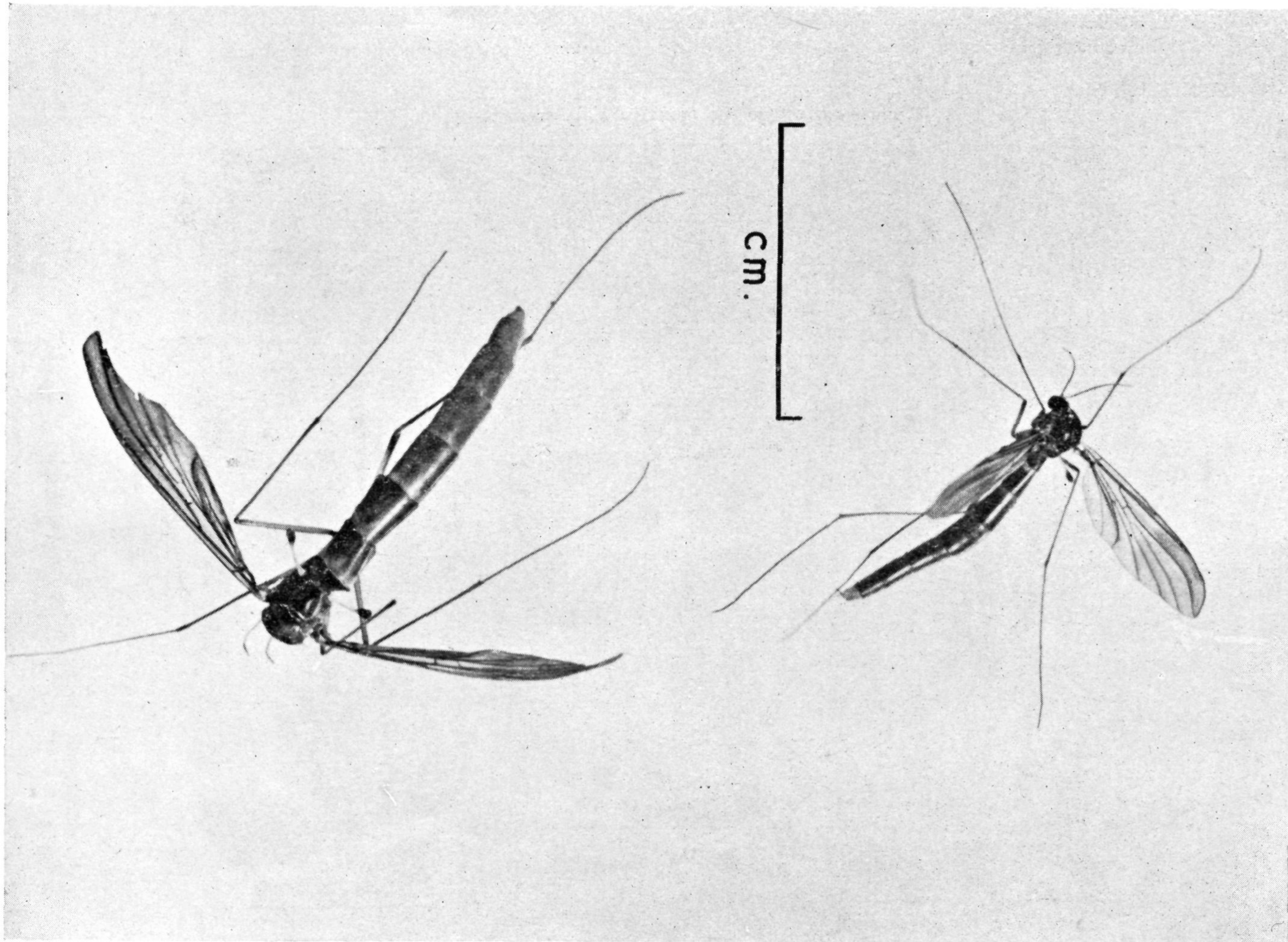


FIG. 1.—Female *A. luminosa* bush fly on left and cave fly on right. Both are photographed to the same scale.

Photo: S. A. Rumsey.

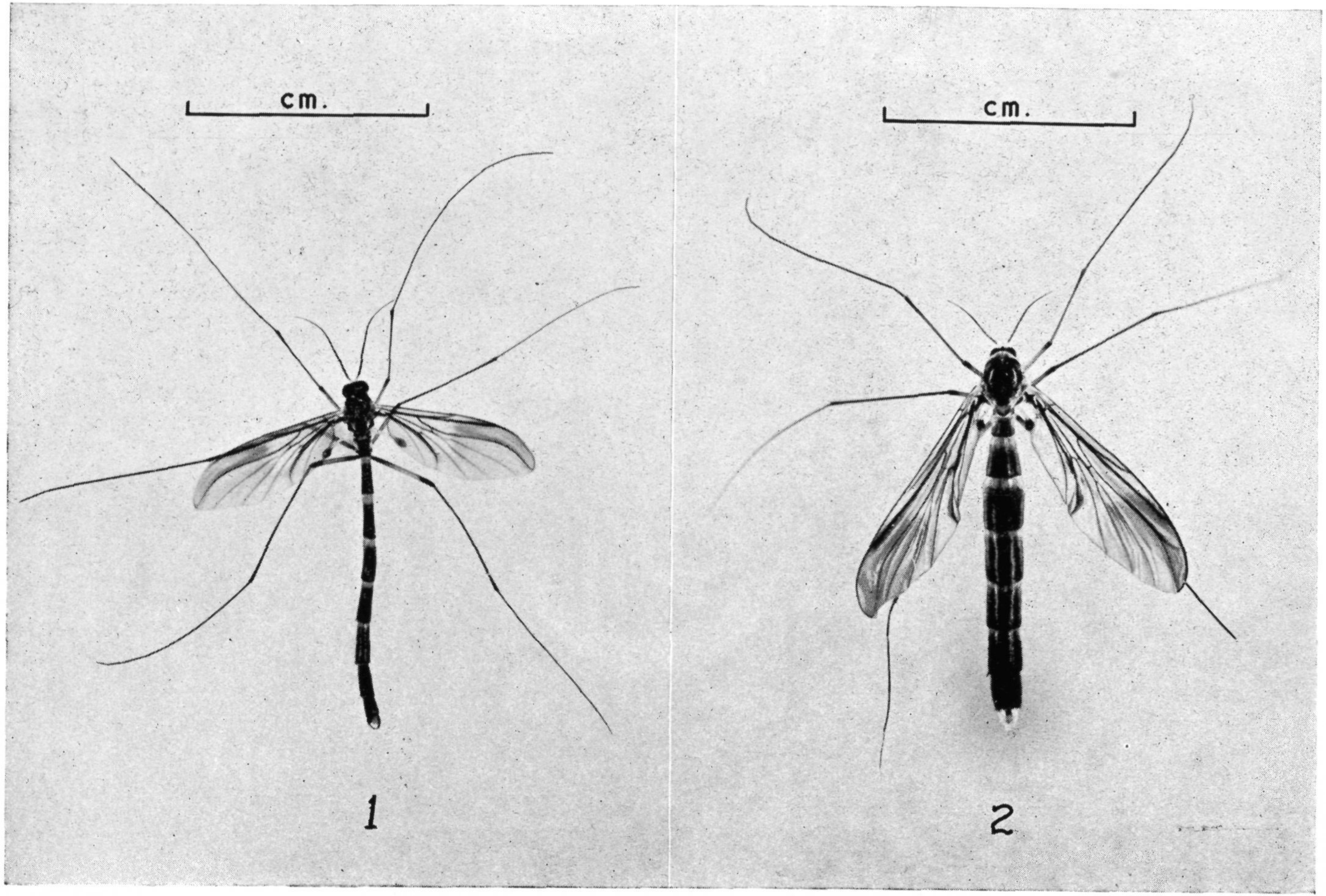


Fig. 1.—Dorsal view of male fly of *A. luminosa*.

Photo: S. A. Rumsey.

Fig. 2.—Dorsal view of female fly of *A. luminosa*. The light organ is glowing in the anal segment.

Photo: S. A. Rumsey.

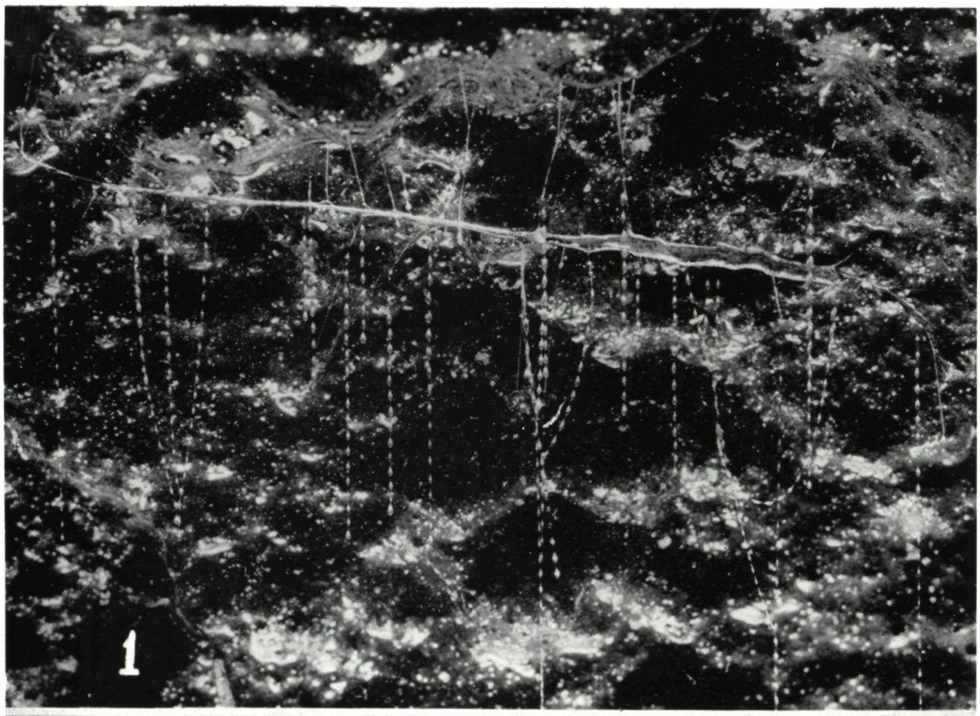


FIG. 1.—Larva of *A. luminosa* on wall of old Railway Tunnel, Parnell, Auckland, showing long braces for attachment of nest to the tunnel wall. The larva is inside the right half of the nest. Scale × 2.25.

Photo: S. A. Rumsey.

FIG. 2.—Larvae of *A. luminosa* in Demonstration Chamber, Waitomo Cave, showing very long fishing-lines.

Photo by courtesy of National Publicity Studios.

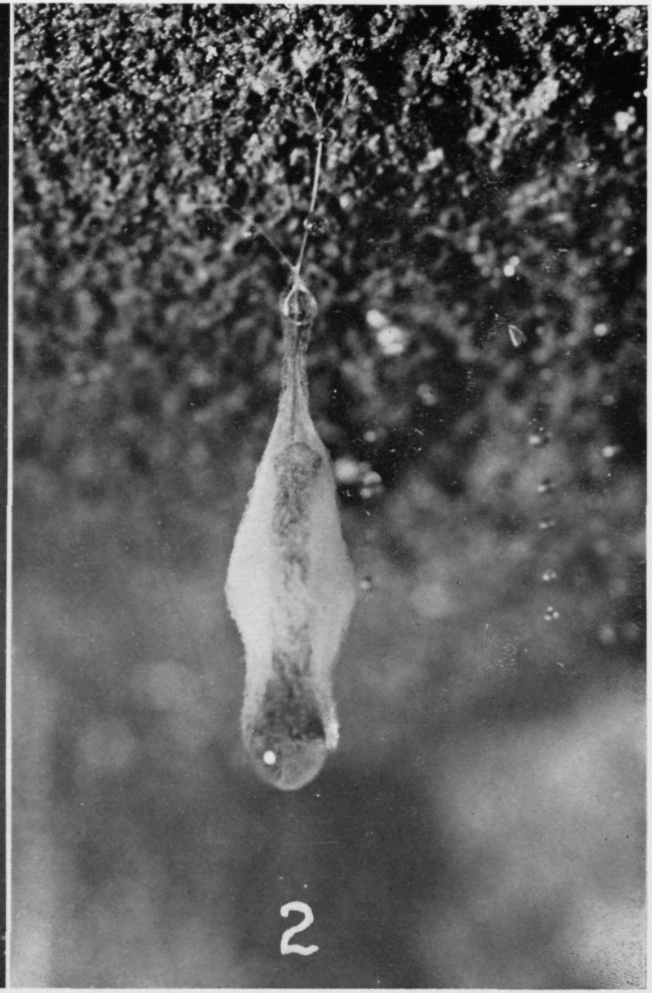


FIG. 1.—Larvae of *A. luminosa* removed from the Grotto, Waitomo Cave, after having been attacked by the fungus *Beauveria* sp.
Photo: J. W. Endt.

FIG. 2.—Pupa of *A. luminosa* which has been attacked by fungi, hanging from the ceiling in Waitomo Cave.
Photo by courtesy of National Publicity Studios.

hatch at room temperature. These results indicate that the incubation time for the egg is between 20–24 days.

In the later stages of development, a dark spot, the heavily chitinised head of the embryo, is visible through the chorion. At hatching, the chorion splits open at the anterior pole, and the split continues laterally threequarters of the way down each side of the egg (Plate 28, fig. 2). Eggs have not been observed to luminesce during any stage of their development.

Larva. A newly hatched larva is cylindrical in shape. It varies in length from 3–5 mm and is about 0.33 mm in width. The larvae grow over a period of several months till they reach a length of about 30 mm in the bush variety, and 40 mm in the cave variety (Plate 29, figs. 1, 2).

Immediately on hatching the larva emits a bright light. Were it not for its light, its transparency and size would make it very difficult to find. The larvae spread out over the ceiling of the cave or tunnel and commence building nests and letting down long sticky threads or fishing-lines. At the end of three weeks a cave larva is about 6 mm in length and 0.5 mm in width, with fishing lines about 50 mm long (Plate 28, fig. 3). These observations differ from those of Gatenby (1960) who states that very young larvae have " no vertical lines, only a runway, and on banks, always a hiding place as well ".

Larvae are not necessarily confined to their nests, but often move about for considerable distances over the substratum seeking a site for a new nest. Because of this, it is very difficult to study them unless they are caged, and consequently the complete time for larval development has not so far been recorded. It is probably about eight or nine months.

Pupa. At pupation the larva shrinks in size and becomes translucent. It removes the fishing-lines and braces of its nest and suspends itself vertically by a long thread, approximately the same length as the pupa (Plate 30, fig. 1). Then it pupates (Plate 30, figs. 2, 3; Plate 31, figs. 1, 2). This is a gradual process, which may take up to 24 hours. It has been observed by the author in Waitomo Cave, in Waipu Cave and in the Waitakere tunnel, Auckland. In captivity one larva pupated at a 45′ angle, being still partly suspended by braces from the old larval nest.

The suspensory cord of the pupa extends from the ceiling to the region of the thorax. When Hudson described the pupa in 1886, he considered this cord to be part of the pupa itself. Edwards (1933) however, considered the cord to be part of the larval web. This, he thought, on drying gave the appearance of being part of the pupa. Gatenby (1959) believed the cord to be the runway of the snare. The author believes that the thread is formed from the larval nest and its supports. In Plate 6, figs. 1 and 2 show that the thread is made up by the fusing together of a number of branching threads.

There are two different arrangements for pupation. Occasionally the pupa hangs suspended among a surrounding curtain of fishing-lines (Plate 32, fig. 2). More commonly the pupa is isolated or suspended in the centre of a circle 7–10 cm in diameter (Plate 32, fig. 1). The periphery of the circle consists of a row of fishing-lines approximately 5 cm in length. The significance of this circle is not known, but it may act as a protective shield to the pupa, the clear space preventing the fly from becoming entangled in long fishing-lines of other larvae after it emerges.

In July, 1959, 9 male and 13 female pupae were collected from Waitomo Cave, one female pupa was collected from the bush at Waitomo, and 12 male and 13 female pupae from the Waitakere tunnel. The cave forms were all larger than the bush and tunnel forms (Table III). No other differences were noticed.

Table III.—*Variability in Length of Pupae of* Arachnocampa luminosa (*Skuse*).

		Male	Female
Cave Type	Number	14	21
	Mean	13.25 mm	16 mm
	Range	12–14 mm.	15–17.5 mm
	Standard Deviation	1.3	0.74
Tunnel and Bush Type	Number	12	14
	Mean	10.8 mm	12.5 mm
	Range	10–11.5 mm	12–14 mm
	Standard Deviation	0.54	0.62
Significance of difference		All 0.001	

Sexual differentiation is evident in the pupal stage. The female pupa is larger and stouter than the male. It possesses two prominent papillae (Plate 31, fig. 2) at the distal end of the abdomen. In the male these papillae are noticeably smaller in size.

According to Norris (1894), who observed *A. luminosa* in the Botanical Gardens, Wellington, the male and female pupae are both luminous. He says, "The male is luminous in the pupa until the last two or three days before it hatches." Until the present author commenced studying *A. luminosa,* no other worker on this insect since Norris had observed a luminous male pupa. On many occasions, at Waitomo, Waipu and the Waitakeres, male and female pupae have been observed to glow throughout all stages of their development. The pupal light is very intermittent. As in the larva, the luminous organ is situated in the last abdominal segment. Hudson (1886) considered that the light from the pupa was much fainter than in the larva, but on this point the author disagrees. While shining much less frequently than in the larva, the light can be fully as brilliant. One female pupa collected in the bush at Waitomo first attracted attention because the brilliance of its light was far greater than that of any of the surrounding larvae.

Luminescence of the female pupa is particularly noticeable during the latter period of its development. When the pupa is gently touched or rocked, the light flashes on immediately for a few seconds and then goes out again. Thus, when a male fly alights on a female pupa, the light goes on. Male flies have often been observed clinging to female pupae, but female flies have never been observed clinging to male pupae. When a female fly is about to emerge it is common to find one, two, or even three male flies clinging to the pupa. The length of the pupal period is twelve to thirteen days. During the last two or three days before emergence of female flies, eggs become visible through the transparent pupal skin.

Imago. The imago emerges head-first, pulling its wings and legs after it. This may occur at any time of the day, and has been observed by the author on several occasions. It is a fairly slow process taking up to an hour or longer, the fly often glowing brilliantly the whole time.

The anterior end of the pupa is split open by the dilated thorax of the imago, and the thorax emerges followed by the head and anterior segments of the abdomen. The three pairs of legs lie against the abdominal sternites, and the antennae are directed posteriorly towards the legs. The fly emerges by muscular contraction and expansion of the body and wriggling of the legs. In the female the body is distended by eggs which are visible through the body wall (Plate 33, fig. 2). The body of the male is smaller and much narrower. The tip of the abdomen is the final part to be withdrawn from the pupal case. (Plate 33, fig. 1.) The imago hangs head-down from the pupal case till it is dry; then it turns through 180° and hangs from the pupal case till its wings are strong enough for it to fly.

At emergence, the thorax of the imago is a creamy pink colour with a number of black setae on it arranged in rows. The abdomen is pale fawn and transparent. Over a period of several hours, the colour gradually intensified to dark brown with a dorsal, median fawn stripe on the thorax and lateral fawn stripes at the anterior end of each abdominal segment. The colouring is more strongly marked in the male than in the female.

Both male and female flies (Plate 36, figs. 1, 2) are very sluggish in flight. Male flies, however, are the more active of the two. They move only comparatively short distances, and consequently are easily caught. Both flies make a buzzing noise, that of the female being louder than that of the male. When at rest, the wings are folded over the thorax and abdomen (Plate 34, fig. 1).

There is a marked difference in size between *A. luminosa* flies living in caves and those living in tunnels or in the bush (Plate 35, fig. 1). This may be attributable to the greater food supply for larvae in caves (Table IV). The size ratio between the sexes remains stable.

Table IV.—*Variability in Length of Flies of* Arachnocampa luminosa (*Skuse*).

		Male Body	Male Wing	Female Body	Female Wing
Cave Type	Number	17	17	16	15
	Mean	13.3 mm	7.9 mm	14 mm	10.2 mm
	Range	12–15 mm	7–8.5 mm	13–16 mm	9–12 mm
	S.D.	0.97	0.46	0.85	0.84
Tunnel & Bush Type	Number	9	9	12	12
	Mean	10.6 mm	6.5 mm	11.4 mm	8.2 mm
	Range	9–11 mm	6–7 mm	10–13 mm	7.5–9 mm
	S.D.	0.73	0.50	1.08	0.78
Significance of Difference		All 0.001			

At Waitomo Cave, male flies were always far more numerous than females; while in the Waitakere tunnel the reverse appeared to be the case. On June 30, 1959, a count of pupae and flies in the Waitakere tunnel showed 37.5% of the population of about 100 were males and the rest females. On July 16, 1959, a population of approximately 500 individuals in the Tunnel of Waitomo Cave consisted of 13.3% females and the rest males. The sex ratio of flies in the bush has not so far been determined.

Both male and female flies are intermittently luminescent at the distal tip of their abdomens. The light from the female is larger and brighter than that from the male. Hudson and Norris both observed luminous female flies. Hudson never saw a male fly. Norris (1894), however, saw several. He stated, "I have three males, and none of them was luminous in the imago." Hudson suspected that the female's light was used to attract male flies, but he was unable to prove this. Gatenby (1960) collected one male and two female flies from Waitomo and observed that none of them glowed. He sectioned the abdomen of the male and stated, "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." Gatenby illustrated his paper with a sketch of the posterior part of the abdomen of a male fly and a section through the abdomen. His sketch does not resemble the posterior abdominal segments and genitalia of the male *Arachnocampa luminosa* fly described and figured by Harrison (in press), so that he could not have collected the male fly of *A. luminosa*. This would explain his statement, "The adult male has degenerate light organs in which collapse of the tubules and some aggregation of the nuclei has taken place." The adult male fly is definitely luminous. This phenomenon has been observed by the author on numerous occasions. Luminous male flies have been collected from Waitomo Cave, Waipu Cave, and the Waitakere tunnel and also reared in the laboratory.

In February, 1955, luminous male flies were observed for the first time by the author and Mr. D. K. Turner. About 8 p.m. a male and female fly were removed from Waitomo Cave and placed in a glass container in the dark. An hour and a-half later, a faint light was observed through the glass. This proved to be coming from the male fly, which suddenly produced a bright light. This lasted for a few seconds and then dimmed again. About midnight the male was again faintly and continuously luminescent. No light was observed from the female. At 9 a.m. the next morning the female was shining brilliantly. No further luminosity was observed till midnight, when the male fly was once more brilliantly luminescent. The light soon faded when electric light was switched on, but reappeared faintly when the light was turned off. After that neither fly showed any further signs of luminescence. Several other male flies observed to glow in the cave were not removed for further observation. A male fly, removed as a pupa from the Waitakere tunnel and placed in a glass container, glowed intermittently in a darkened room from 5.30 p.m. to midnight.

On several occasions in Waitomo Cave luminous female flies have been observed on the wing. This does not appear to have been previously recorded. It was thought by earlier workers that *A. luminosa* flies never luminesced in flight.

It has been suggested by Gatenby (1959) that in *A. luminosa* "both male and female adults may be negatively phototropic, which would keep them clear of snares," but Gatenby admits that he has never seen *A. luminosa* flies on the wing. If he had, he could not have failed to observe that they are both positively phototaxic, and are often caught in the fishing lines of larvae. In most cases this is not a serious problem, as they are usually powerful enough to break free.

Mating. During 1955, *A. luminosa* flies in Waitomo Cave exhibited two different types of mating positions. In the first, which was the more usual, the two flies hung from the pupal case. The abdomen of the male lay to the side of the female's and the tip was turned to effect coitus. (Plate 33, fig. 2.) The wings of the female were folded while those of the male were widespread.

In the second the two flies mated vertically, tail to tail. The male hung head down clinging to the empty pupal case from which the female had just emerged, while the female clung to the limestone wall. This was observed on two occasions.

In July, 1959, a male and female fly were put together in a glass container in the laboratory, and the whole process of mating observed. The female immediately settled on the side of a piece of paper, while the male flew round excitedly for several minutes till he found her. Copulation lasted for one hour thirteen minutes. For the first forty minutes their position was as described for the first mating position.

Then the male tried to break free. While still remaining attached, they became extended end to end as described for the second mating position. Over a period of almost twenty minutes the male made numerous attempts to break free before he finally succeeded. The female was passive throughout. Thus the two mating positions observed in Waitomo were part of the one process.

The female usually mates as soon as she emerges, but copulation may not occur till several hours later. She often glows brilliantly when the male attempts to mate with her. Occasionally the male also has been observed to glow. Only one mating takes place.

Two or more male flies often hang from the female pupa waiting for the fly to emerge. Each attempts to fertilise her the moment the tip of her abdomen becomes free from the pupal case. The successful male has to fight off the attempts of the other males to separate him from the female. In Plate 8, figs. 2, 3, taken in Waitomo Cave, the unsuccessful male fly is shown clinging to the body of the female as it strives to separate the mating pair. In this particular case mating continued for seven hours. Fighting among several male flies over a female has been observed to continue for several hours.

To show that female flies can attract male flies from a distance, a newly emerged unfertilised female fly was placed on a stalactite in a part of Waitomo Cave where no flies had been seen for several days. Five hours later, the female fly was observed in the same position as when left, but she had now mated with a male fly.

Observations were also kept on another female fly that was not fertilised immediately she emerged. She used her light to attract a male fly, flashing it on and off till one arrived. Then she extinguished it and flew a short distance away. Having settled, she exhibited her light till she had succeeded in attracting him again. This pattern was repeated several times till mating was finally accomplished. Throughout the whole period the male fly did not glow.

The light in the female is used as a mating device to attract the opposite sex, while that from the male does not appear to be used in this connection. The light from the female is larger and brighter than that from the male, so that it would be possible for flies on the wing to distinguish between the sexes. This may help to explain why several male flies become attracted to the same female. It is possible that tactile and olfactory organs may also play important parts in the attraction of male flies to females in darkness.

After copulation the female fly can still turn her light on and off at will, but females seldom glow once egg laying has commenced. The length of life of the female fly can range from less than 24 hours up to 76 hours. Male flies usually live longer than females, and are capable of fertilising more than one female. They can survive up to four days.

Discussing the ability of the female fly to luminesce, Gatenby (1960) wrote, " 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." Later in the same paper he wrote, " The female remains quiescent and shows her light till she has paired, and then the light fades away." The second statement is correct.

Oviposition. Egg laying may commence almost immediately after fertilisation, or it may be delayed for several hours. During this time, the female flies about looking for a suitable spot to lay her eggs. Usually over 100 eggs are laid. Actual counts of eggs laid by single female flies isolated immediately after mating were 84, 93, 107, 112, 118, 130, 160, 160, 170, 170; an average of 130. Gatenby's (1960) statement that " the female can lay up to about eighty eggs," was based on two female flies taken from Waitomo Cave. Both specimens were killed, and the eggs inside them counted. From these counts of 65 and 75, he deduced that " about 75 eggs " were laid. However, he appears to have overlooked that egg laying may have commenced before the flies were collected.

When about to lay an egg, the female feels with the tip of her abdomen for a suitable spot. Having located it, she brings the tip of her abdomen back under the body. This is followed by violent contractions and flexing movements of the body. Then the abdomen is brought back to a normal position, and the tip gently touches the substratum depositing an egg. (Plate 8, fig. 4.) Each egg is deposited singly. Occasionally groups of up to six may be deposited in quick succession and adhere together. Egg laying is either continuous or sporadic over a period of from one to 24 hours until all eggs are laid. The female usually dies immediately afterwards. The eggs are laid in large numbers close together on the substratum. Over 30 eggs have been laid by a female fly in the seven minutes required to carry the caged fly the 300 yards from Waitomo Cave to the Hotel. As can be seen from Plate 8, fig. 4, the actual posture of oviposition in *A. luminosa* is quite different from Gatenby's (1960) drawing of how he imagined it might occur.

When kept in captivity in a test-tube, female flies usually laid their eggs on the cork, while those kept in a trough laid them on damp cotton wool in preference to glass.

In June, 1955, Mr. C. Voerman set up an observation box in one of the unfrequented corridors in Waitomo Cave. He placed male and female pupae in the box, and watched the flies emerge, mate and the females lay their eggs. Eggs were laid on the wooden frame of the box, on limestone slabs inside it, on wire suspending the limestone and on wire gauze at the back of the box. The wire gauze was covered with verdigris, yet the female clung to the wire with her legs, thrust the tip of her abdomen through one of the holes, twisted it round, and deposited eggs on the outside of the wire. Thus the female fly is apparently not selective in her choice of sites for egg-laying.

In the laboratory, unfertilised female *A. luminosa* flies have been observed to lay eggs. This was first recorded from a female fly that emerged from a pupa collected from the Waitakere tunnel. She was placed in a glass container with a male fly, but mating did not take place, and after about an hour she laid 16 eggs in quick succession. A short time later she died. The eggs were kept, but did not hatch.

Later, a female fly that had emerged from a pupa collected in the bush at Waitomo, was placed in a container with two male flies from Waitomo Cave. Mating did not take place, but over a period of an hour she laid 15 eggs. These were kept, but did not develop. No further eggs were laid, and four hours later she was dead.

It is possible, that unfertilised eggs are also laid under natural conditions, although this has not been observed. This suggests that although virgin females are capable of laying eggs, parthenogenesis does not occur.

Although spending all their time in total darkness, *A. luminosa* flies are diurnal rather than nocturnal in their behaviour. Mating and oviposition may occur at any time, but oviposition appears to be more common during daylight hours. Light itself does not stimulate this activity, as in all observed cases the flies were kept in total darkness.

Structure of Nest and Fishing-lines of Larva

The larva builds itself a hollow, tubular nest of mucus and silk, in which it suspends itself from the shelf or ceiling above by a number of fine silk threads. Norris (1894) considered that the mucus was secreted from the skin of the larva. However, the author's observations show that silk and most of the mucus axe exuded from the mouth after the head has been withdrawn into the prothorax and then thrust forward again. When a larva is ready to begin nest building, the anterior half of the body is raised in the air and a suitable spot selected. Then it bends forward with a sudden darting movement, and very gently and deliberately deposits a drop of silk from its mouth onto the rock, thus forming a fine thread which acts as a brace. Then it repeats the process, moving forward into a droplet of silk and mucus. This process is repeated till the mucus and silk have passed down the whole length of the body and the nest is complete and hollow. It is approximately 2.5 times the length of the larva, or about 10 cm. for a fully grown larva (Plate 11, fig. 1). The nest is very plastic and enables the larva to glide rapidly backwards and forwards at will. When at rest the larva lies on its upper side, and even when moving about backwards and forwards it keeps its venter turned upwards.

From the nest a larva lets down up to 70 strings of sticky droplets. Depending on the size of the larva, the fishing-lines formed in this manner vary in length from under 1 cm to 50 cm. They are remarkable for their great tensile strength (Plate 3, fig. 2). Fishing-lines are formed in a peculiar manner. Each consists of a long thread of silk which bears at regular intervals a series of mucus droplets giving the appearance of a string of beads. Droplets vary in size according to the size of the larva, but average 1 mm in diameter and 1.5 mm in length. To form each droplet the larva thrusts its head forward three times, and then, with five short jerks, withdraws it into the thorax, when a drop of mucus and silk is ejected after much movement of the jaws. During this process, the anterior half of the larva's body hangs vertically from the nest. The larva is able to break through the nest at any point along its length to let down or haul up fishing-lines.

A nest can be built in as short a time as ten minutes. One larva in Waitomo Cave, after having its nest destroyed, was observed to crawl up the wall a few inches to another niche. Within twenty minutes it had built a new nest and let down two fishing-lines, each 3 cm in length.

Formation of fishing-lines is a continuous process in which the larva moves along the nest gradually increasing the length of each fishing-line. It does not complete the full length of one before commencing the next. These fishing-lines are very delicate and so close together that even the slightest air current may cause the sticky threads to become entangled so that the larva is constantly repairing its snare. In the bush and along stream banks glow-worm fishing-lines are usually only a few millimetres long (Plate 29, fig. 1). At Waitomo, their great length is probably made possible by calm conditions present in the cave (Plate 37, fig. 2).

FEEDING BEHAVIOUR AND CANNIBALISM

One of the most peculiar features of *A. luminosa* is the feeding habits of the larva. In darkness, midges fly upwards attracted by the light of *A. luminosa* larvae and become ensnared in the long, sticky fishing-lines.

In caves at Waitomo glow-worms feed chiefly on the midge *Anatopynia debilis* (Hutton) (Chironomidae), formerly known as *Tanypus debilis* Hutton, which breeds in the mud beneath. *A. debilis* has a body length of 4 mm with a wing span of 3.5 mm. It is the only recorded member of the genus found in caves. Gatenby (1959), however, states, "The *Tanypus* (Chironomidae) from Waipu which formed the main food were 8 mm body length." This would appear to be a mistaken identification. The author visited Waipu Cave in September, 1959, and collected three species of Chironomidae. The commonest species was *A. debilis*. A species of another genus, *Chironomus zealandicus* Hudson, has a body length of 8 mm and a wing span of 5 mm. It was probably the insect observed by Gatenby.

Cave dwelling *A. luminosa* have also been observed to eat mosquitoes, psychodids, caddis flies, mayflies, stoneflies, sand flies, tipulids, anisopods and immature isopods. They are cannibalistic on other larvae, pupae and adult flies. In the Waitakeres water-works tunnel, Auckland, insects most commonly observed in *A. luminosa* fishing-lines were adult flies and large tipulids. A few chironomids and one beetle, *Necrophilus prolongatus* Sharp (Silphidae) were also observed.

The author has observed *A. luminosa* larvae feeding on numerous occasions. One midge caught at the end of a fishing-line 30 cm long was observed to cease struggling almost immediately. Following the tug on the line, the larva moved along its nest to the appropriate fishing-line, and, with the anterior half of its body hanging down vertically out of the nest, it hauled up the midge in a little over one minute. When the midge was within reach the larva immediately bit into the thorax with its mandibles and commenced eating. Within two minutes the midge was reduced to a small, shapeless mass tangled among the sticky threads of the nest. On another occasion, where the fishing-line was 8 cm long, the midge appeared to be still alive when brought to the jaws of the larva. It continued to spin around on the fishing-line while being hauled up, as if struggling to escape, and movement continued until its thorax was bitten.

It has been suggested by Edwards (1933) that the thread is wrapped round the larva's body as it is pulled in, but during the author's observations the thread appeared to be swallowed. Gatenby (1960) states that, "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." As far as the author has been able to observe, glow-worms never leave their nests to capture prey.

After eating, the larva always removes the remains of its meal from the nest, so that the fishing-lines are kept clean and in good repair for catching further prey. Lack of food makes a glow-worm glow more brilliantly, but the intensity of the light produced can apparently be controlled by the insect.

The carnivorous habits of *A. luminosa* larvae were first recorded by Norris (1892), who observed a larva feeding on a crustacean. He says, "The larva's head was thrust inside the shell of the crustacean. I . . . . could plainly see the mandibles working, and that the larva was eating the animal." In 1933, Edwards commented, "The prey is actually eaten (not merely sucked dry) by the larva." However, according to Gatenby (1960) the larva "sucks out the body contents of its prey. But afterwards it carefully chops up the whole insect into suitable sizes for swallowing. Perhaps this is why it is so rare to see entangled insects in the snares." Later in the same paper he says, "There must be few other insects which chop up their prey and swallow it entirely. Nothing is wasted." The author's observations support Norris and Edwards, but are at variance with Gatenby's statements.

Cannibalism is of fairly common occurrence, and often occurs when two larvae have nests close together. When fighting, they lean partly out of their nests and snap at each other's heads, each trying to pull the other out of its nest. While fighting continues, each larva glows brilliantly, and it is comparatively easy to pick out a pair of fighting larvae in the darkness because of the intensity of colour and brightness of their lights. Occasionally, a larva may fall out of its nest onto the mud bank beneath, where it will continue to glow. Sometimes, when a larva is eaten, its light organ is discarded, and this also will continue to glow for some considerable time. Occasionally the adult fly is caught in larval fishing-lines, drawn up and eaten by the larva, but most of the flies caught manage to break free. Those caught in the fishing-lines of small larvae may dislodge them when pulling to free themselves. This also explains why some small larvae are found out of their nests on the mud banks below.

Periodically the Waitomo Stream becomes silted up and the mud banks in the Grotto have to be removed by motor-driven pumps. The noise from this operation causes glow-worms to turn off their lights. After the first hour or so however, they turn them on again to feed. Removal of mud has a marked effect on the *A. luminosa* population. The chironomid larvae live in the mud, and when this is removed the glow-worms' food supply is considerably reduced, with the result that the *A. luminosa* population becomes greatly reduced also. Oil finding its way onto the surface of the stream from road works also depletes the food supply by killing chironomids.

PREDATORS

In Waitomo Cave, the main predators of *A. luminosa* are two species of opiliones. A number of different species live in caves as carnivorous scavengers; but only *Megalopsalis tumida* Forster and *Hendea myersi cavernicola* Forster have been observed to attack glow-worms. *H. myersi cavernicola* eats the larvae. It avoids the sticky fishing-lines, and pulls the larvae out of their nests. *M. tumida* eats the adult flies, which are very easily caught because of their slow movements. It is not uncommon to observe an opilion running along the wall of the cave with a fly in its chelicerae.

According to Hudson (1892), several pupae of *A. luminosa* observed in the Botanical Gardens, Wellington, had been parasitised by the proctotrupid wasp *Betyla fulva* Cameron. This parasite has not been recorded elsewhere.

The moist conditions inside caves and tunnels are suitable for fungous growth, and several species of fungi attack the larval and pupal stages of *A. luminosa.* (Plate 38, figs. 1, 2). The fungus attacking larvae in Waitomo Cave was found to be a species of *Beauveria* (Fam. Moniliaceae) belonging to the Fungi Imperfecta.

However, neither opiliones nor fungi are real hazards to the glow-worm population. Floods and shortage of food supply at certain times of the year are a more serious problem. During dry periods glow-worms come further down the walls of the Grotto in Waitomo Cave in search of food, but winter floods usually wash away these larvae, so that the main population is confined to the upper regions of the cave. It is claimed by Mr. D. K. Turner, who was a guide at Waitomo for several years, that *A. luminosa* larvae can survive being submerged under water during floods for a period of up to eleven hours.

SEGREGATION OF RHAPHIDOPHORIDS AND GLOW-WORMS IN WAITOMO CAVE

On the walls of the Grotto, the rhaphidophorid *Pallidoplectron turneri* Richards rarely occurs higher than 1.5 metres above the level of the water. Thus it is always out of range of any *A. luminosa* larvae. While seeking an explanation for the rigid segregation of cave-wetas and glow-worms, two cave-wetas were caught in the Grotto and released one metre from each other on the limestone ceiling above the mud bank in the Demonstration Chamber. (Plate 37, fig. 2.)

When a bright light was directed on one weta it immediately waved its antennae entangling them in the long fishing-lines. In endeavouring to free itself, the weta tugged at the threads, pulling one glow-worm out of its nest. Eventually it disentangled itself without breaking either of its antennae. After cleaning them, it slowly extended them again. When, five minutes later, light was again directed on the weta, it ran from the light blundering into one glow-worm nest after another and entangling both legs and antennae, till three *A. luminosa* larvae had their nests completely destroyed. The following afternoon, the weta was observed in the centre of a circle 25 cm in diameter surrounded by glow-worm threads.

The other weta was released near an area of 1st instar *A. luminosa* larvae with short fishing-lines about 2.5 cm long. It also became entangled in the fishing-lines of a fully grown larva, but after cleaning itself, ran into the area of young larvae and smaller threads.

Two days after the commencement of the experiment the positions of the two wetas were unchanged, except that they now sat with their antennae directed vertically downwards to avoid the fishing-lines. They still reacted to the light and the cleaning process was repeated. By the third day, they refused to react to light. On the fifth day, one weta managed to escape from the area of small fishing-lines.

The other weta remained trapped without food for sixteen days. These results, indicating that glow-worm fishing-lines and not their lights prevent rhaphidophorids from living in closer proximity to *A. luminosa* larvae, explain the complete segregation of the two species in the Grotto of Waitomo Cave.

Hunting spiders and the opilion *Megalopsalis tumida* Forster, are found in association with cave-wetas on the lower walls of the cave to a height of 1.5–2 metres above the river level, but are never found on the upper parts of the cave among the glow-worm larvae. They probably avoid glow-worms for the same reason as the wetas.

Seasonal Periodicity

The life cycle of *A. luminosa* in the caves at Waitomo and the Waitakere Tunnel, Auckland, is continuous throughout the year. However, there are definite times of the year when certain stages of the cycle are more common than others. On the whole, the period from October to February is the time of greatest larval abundance. Then the larvae are reaching their full size and shining most brilliantly. From April to July, large larvae are not very numerous, but pupae, adult flies, eggs and newly hatched larvae are common. Consequently the display of luminescence during the winter months is poor. This is often further diminished by the periodic floods in the caves.

On July 15, 1959, between two and three hundred pupae were counted in the Stalactite Area and Tunnel of the Waitomo Grotto. Fifteen male flies were seen, but only two females (one of which was ovipositing and the other mating). Female pupae were correspondingly fewer in number than male ones. First instar larvae were very common, as were the eggs.

In early November, 1955, pupae and flies were still very common in Waitomo Cave, with numerous half-grown larvae. On November 2, five male flies were seen, nine female flies were observed ovipositing, and one pair of flies were seen mating. On November 4, several dozen adult flies were seen, some laying eggs and others mating. One female fly had been caught in the fishing-lines of a larva and was being eaten. Other flies were becoming entangled but managing to escape. In one area three feet square on the ceiling near the jetty, 30 pupae were counted, as well as numerous larvae and 10 adult flies. From then on the numbers of pupae and adults rapidly diminished.

Further observations are required on bush and tunnel forms of *A. luminosa* to determine whether they have a definite seasonal cycle.

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