THE NEW ZEALAND GLOWWORM

Arachnocampa luminosa

A SUMMARY

Les Kermode

Abstract

The larval stage of the insect Arachnocampa luminosa is unique in cave fauna because it provides dispersed, living illumination for cave visitors. The small blue lights of the glowworms shine not only in the subterranean darkness of caves with streams, but are also common in damp forests. At Waitomo the glowworms are the main attraction in one of the tourist caves. The life cycle, behaviour and luminescence are described and illustrated. The less spectacular kindred Australian species are compared.

Zusammenfassung

Die Larvenstufe des Insektes Arachnocampa luminosa ist einzigartig in der Höhlenfauna, weil sie eine zerstreute, lebende Beleuchtung für die Höhlenbesucher liefert. Die kleinen, blauen Lichter der Glühwürmchen kommen nicht nur in der unterirdischen Dunkelheit der Höhlen mit Flussläufen vor, sondern auch oft in feuchten Wäldern. In Waitomo ziehen die Glüwürmchen in einer der Höhlen besonders die Aufmerksamkeit der Touristen an. Ihre Lebensfolge, ihr Betragen, und ihre Lichterregung werden beschrieben und illustriert. Man zieht einen Vergleich mit den verwandten aber wenig auffallenden australischen Spezies.

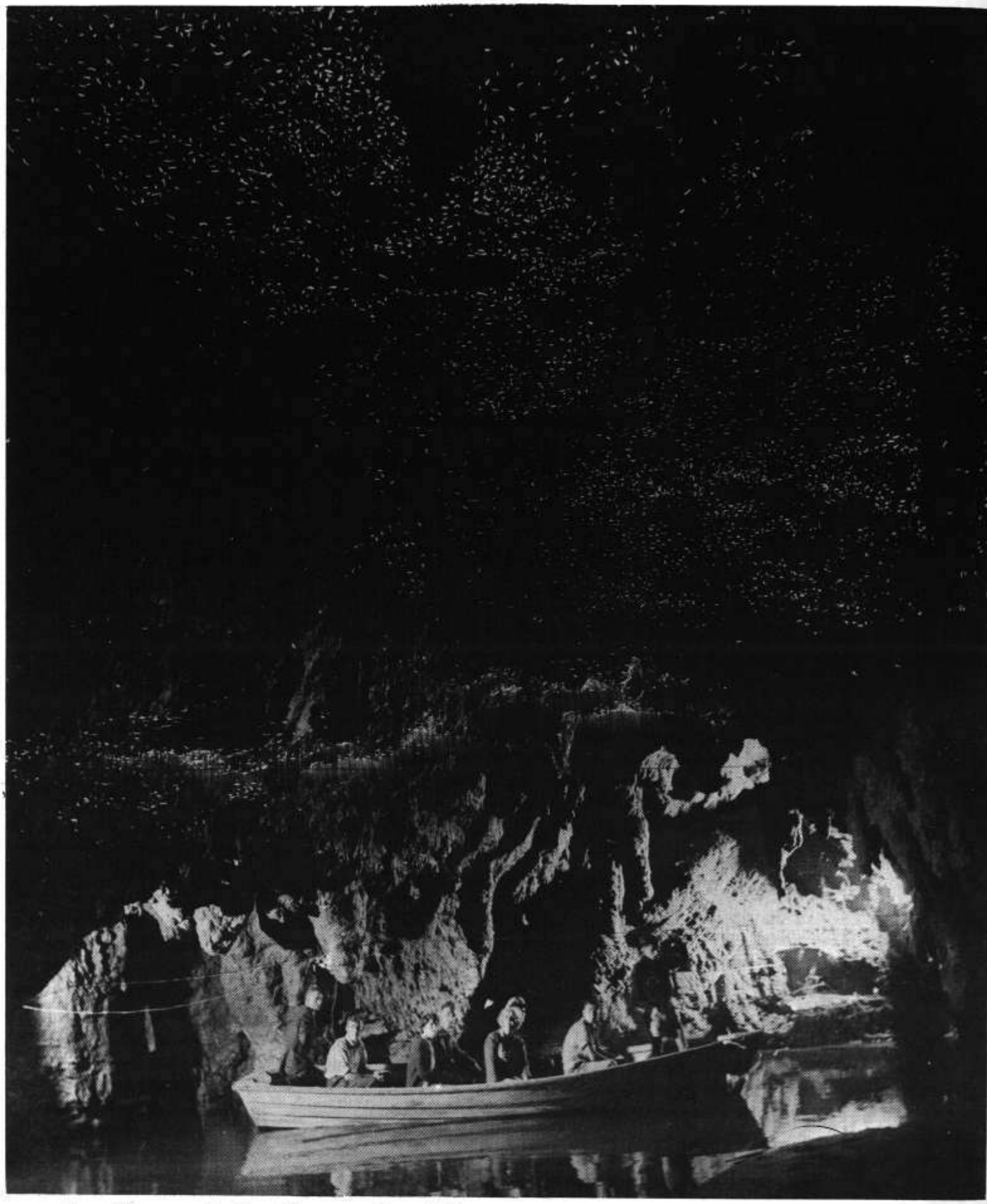
Résumé

L'état larvaire de l'Arachnocampa luminosa est unique parmi les insectes cavernicoles, qu'il offre une illumination dispersée et vivante aux visiteurs des grottes. On aperçoit les petits points de luminère bleue des vers luisants non seulement dans l'obscurité souterraine des grottes où il y des cours d'eau, mais souvent aussi au fond des forêts humides. A Waitomo les vers luisants sont la grande attraction touristique d'une des grottes. On décrit avec illustrations leur cycle d'évolution, leur comportement et leur luminescence. On établit aussi une comparaison avec les espèces australiennes analogues qui sont moins frappantes.

A brief version of this paper was prepared as a complement to two other papers — "Conservation and Cave Development" and "Tourist Caves of New Zealand", and submitted with them to the 6th International Congress of Speleology held in Olomouc, Czechoslovakia 1973.

N.Z. Speleological Bulletin 5(91): 313-28

Received by Editor, 14 August, 1974.



1. Glowworm Grotto, Glowworm Cave, Waitomo.

A remarkable photo of Glowworm Grotto taken about 25 years ago. The 3-hour exposure has made the pinpoints of glowworm light appear as bright trails that silhouette a large stalactite. The thousands of droplets on the glowworm snare lines sparkle in the cross light above the boat.

Photo: E.P. Christensen
[illegible]

INTRODUCTION

Throughout New Zealand every explorer of caves and nocturnal visitor to the forest has been impressed by the familiar, tiny, blue lights of hundreds of glowworms, and our best known tourist cave — Glowworm Cave, Waitomo — derives its most important attraction not from the geological or mineral features, but from the fascination and biological uniqueness of an insect that luminesces during most of its life cycle. However, in more than 20 years of publication our own Bulletin has had very little to say about the glowworm — its description, life cycle, behaviour, luminescence, habitat, enemies or close relations. A literature search through many confusing and some inaccurate publications has shown that the best information has been prepared by Society members or their professional colleagues, who must forgive a geospeleologist for making a summary of biospeleological matters.

NAME

The New Zealand glowworm is the larval stage of an insect troglophile with the full name of Arachnocampa (Arachnocampa) luminosa (Skuse) of the subfamily Ceroplatinae of the fungus gnat family (Diptera, Mycetophilidae). It is related to three Australian species of the genus Arachnocampa Edwards. There are two descriptive Maori names, titiwai and puratoke.

The glowworm must not be confused with luminescent earthworms, such as, unpigmented Microscolex phosphoreus (Duges) measuring 42 x 2mm, or the much larger transparent or pale brown Octochaetus thomasi Beddard measuring 140 x 5mm, or the striped (purplish red-brown and yellow) Eisenia foetida (Savigny) measuring 32 to 130 x 2 to 4mm.

HABITAT

Glowworms are found throughout New Zealand in forests, tunnels, and caves wherever there is high humidity produced by streams, pools or sodden vegetation, with suitable overhanging surfaces in deep shade or total darkness.

The best displays of glowworms are found in limestone cave chambers about 10m across and 5m high having complete darkness, a free-surface stream to bring organic matter from forest or farmland, no air currents to disturb the web-like snares, pools of calm water or thick banks of mud in which insect food supplies can breed, and only occasional minor floods. Such ideal ecological conditions are found in several North Island caves especially in Glowworm Cave, Waitomo, where, however, there are fewer large larvae luminescing during winter because of occasional higher floods and the resultant scarcity of food. In Te Ana-au Cave in southern South Island the more rigorous seasonal changes have a noticeable effect on the glowworm displays.

At Waitomo the relative humidity in the stream passage of Glowworm Cave is 94 to 100 per cent and the air temperature 13^{o} to 16^{o}C.

The relative humidity in the forest at Waitomo is always high (70 to 100 per cent) and the measured air temperatures range from 0^{o} to 21^{o}C.

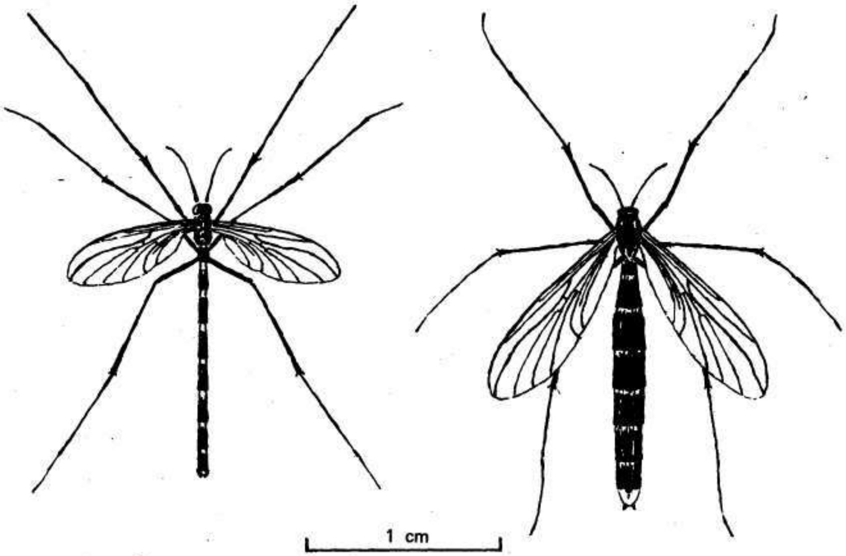
DESCRIPTION AND LIFE CYCLE

Arachnocampa luminosa is a luminescent species of fungus gnat whose light is a blue-green colour. A full taxonomic description was given in 1961 by R.A. Harrison.

The adult has a body length ranging from 9 to 16mm, and an approximate wingspan ranging from 13 to 26mm. Cave dwelling adults are generally larger than their forest dwelling kindred, and females are larger than males in both habitats.

The body colouring is a combination of areas of yellow, various browns, and black. Each abdominal segment is dark brown merging to yellow on the forward margin. The wings are transparent brown, with dark brown veins. Each slender leg is about equal in length to the body, and the antennae are about 3 to 4mm long. Both male and female flies are intermittently luminescent at the distal tip of their abdomens.

2. Adults of Arachnocampa luminosa



MALE

Wings usually folded back over body and tip of abdomen raised.
Converging genital claspers.

FEMALE

Abdomen arched downward during oviposition.
Light organ shown glowing.
Diverging genital papillae.

Drawn by L.O. Kermode from photos by S.A. Rumsey, Plant Diseases Division, D.S.I.R.

Variations in size of adults of Arachnocampa luminosa.

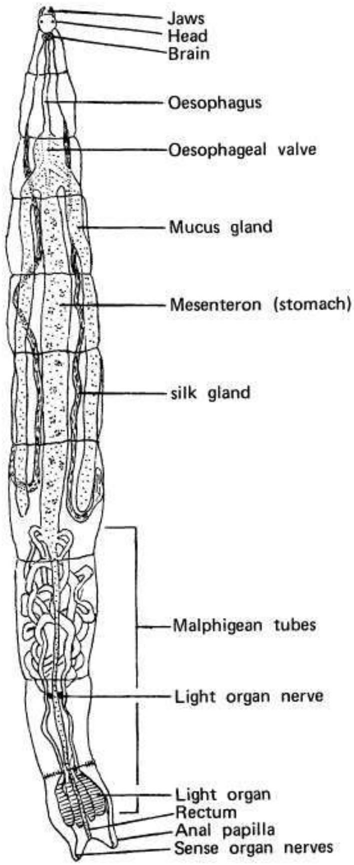
	MALE		FEMALE	
	Bush	Cave	Bush	Cave
Body length	9-11	12-15	10-13	13-16
Body width approx.	0.3	0.5	1.0	1.5
Wing length	6-7	7-8.5	7.5-9	9-12
Wing width approx.	1.4	2.0	2.2	3.0
	millimetres			

The spherical egg is 0.75mm in diameter and coloured pale yellow, changing to reddish brown before hatching. Incubation takes 20 to 24 days.

The newly hatched larva is cylindrical, 3 to 5mm long, 0.3mm wide, and segmented. It is creamy white with a brown head and a luminscent tip to its abdomen. After several months the larva has grown to 30 to 40mm long and is 1.0 to 1.5mm wide, the cave variety being the larger. The mature glowworm is partly brown and partly transparent with visible, coloured, internal organs. It becomes translucent just before pupation.

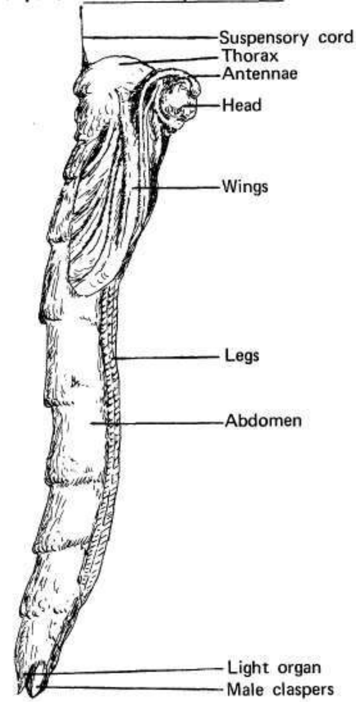
The light brown pupa glows intermittently,and sex differences can be distinguised. The adult emerges after 8 to 13 days.

3. Larva of Arachnocampa luminosa



from Gatenby 1960a

4. Pupa of Arachnocampa luminosa



Drawn by L.O.Kermode from photo by S.A.Rumsey,D.S.I.R.

Variations in length of pupae of Arachnocampa luminosa

MALE		FEMALE	
Bush	Cave	Bush	Cave
10-11.5	12-14	12-14	15-17.5
millimetres			

The variations in the size of adults, pupae, and larvae from forest and from caves are thought to be infraspecific. The constancy of the cave environment and the ample food supply could cause the cave specimens to be larger by about 20 per cent.

BEHAVIOUR

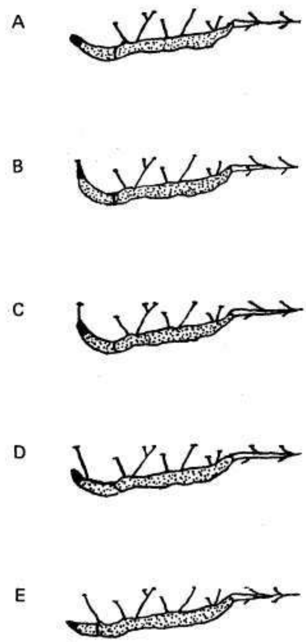
The inactive pupa is able to glow. The female often glows brilliantly but intermittently just before emerging, and thus attracts males to the pupal case. The pupa is sometimes surrounded by a circle of short larval lines.

The emerging adult female is awaited by one or more males and mating takes place immediately the abdomen is free. After a single copulation the female flies sluggishly and noisily for a short distance to an unselected site and lays between 80 and 170 single eggs within a period of about 24 hours. Unfertilised females can lay eggs, but parthenogenesis does not occur. The female dies at the completion of oviposition, 1 to 3 days after emerging. The male lives for 1 to 5 days and is more commonly seen than the female. Both adult flies can glow in flight or while resting, and they tend to be diurnal in habit, even when in total darkness.

The tiny egg adheres to the cave wall or forest bank but does not glow.

The larval stage is the longest in the life cycle. It lasts for several months and gives the common name to the species. The larva continuously secretes from its mouth an enveloping tube of clear mucus and silk which assists movement. Progress is made by the larva arching the front part of its body outside the tube, then it darts forward to a suitable anchoring point for a suspensory silk thread. After withdrawing slightly, two or three peristaltic waves that almost retract the head into the body, pass the thread backward on to the tube. The larva does not slide backward into the tube because there are minute bristles on the underside of its body between the segments.

5. Method of progression

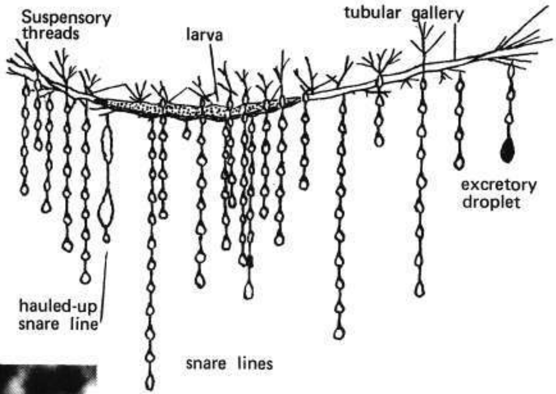


A. Larva arches forward and searches for an anchor point.
B. Larva touches ceiling and pauses for a moment.
C. Larva withdraws its head and forms a thread.
D. Contractive (peristaltic) waves pass thread back on to tube.
E. Tube attached to ceiling and larva ready to move forward.

drawings adapted from Stringer, 1967.

Within 20 minutes the glowworm can build itself a nest by renovating and strengthening the tube and its supporting web of fine silk threads to form a hollow gallery in which it suspends itself on its back from an overhanging ledge or ceiling. In the forest one end of the gallery usually leads into a crevice in which the larva hides during the day. The gallery is two or three times the length of the glowworm and is very plastic. The larva glides rapidly back and forth and is able to turn around inside the gallery by folding back on itself.

6. The Glowworm in its nest with snares



adapted from Stringer, 1967.

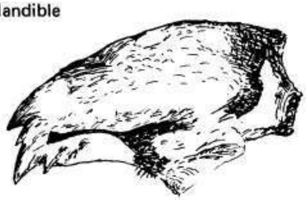
7. A Glowworm at Waitomo.

Photo: S.A. Rumsey, D.S.I.R.

From the nest hangs a curtain of closely spaced strings of sticky droplets which snare the prey. There might be as many as 70 strings ranging from 1 to 50cm in length. The droplets vary in size from 0.5 to 1.5mm in diameter and are spaced about 1mm apart along the snare line. The first droplet is the largest and succeeding ones are produced about every 15 seconds in very humid conditions. Snare formation is a continuous process in which the larva moves along the gallery gradually lengthening each string of droplets. The forest dwelling glowworms sometimes rest for a day or so after building its nest, and before commencing its nocturnal activity of building snares which are usually less than 5cm long and more widely spaced thus avoiding entanglement by the wind.

9. Powerful glowworm jaws

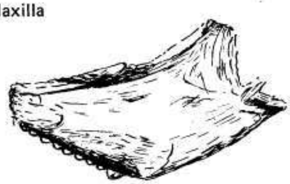
Mandible



with two strong and two weak teeth near the front point and one tooth on the inner surface

0.1 mm

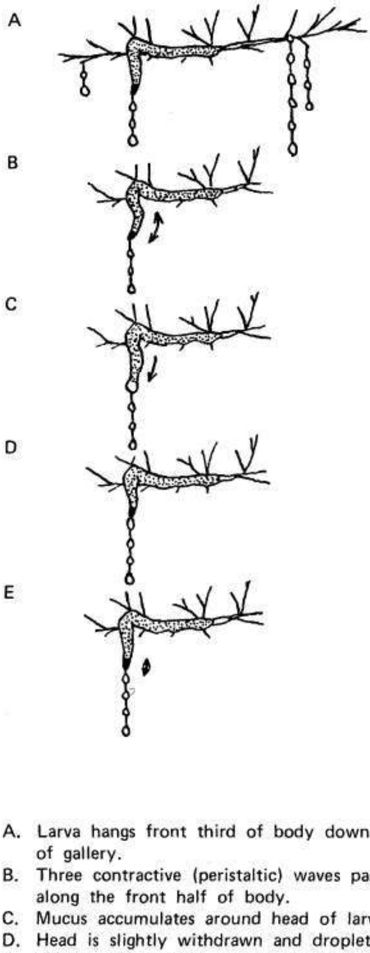
Maxilla



with approximately ten distinct teeth in a row along the outer edge

drawn by L.O. Kermode
from photo by S.A. Rumsey, D.S.I.R.

8. Snare building

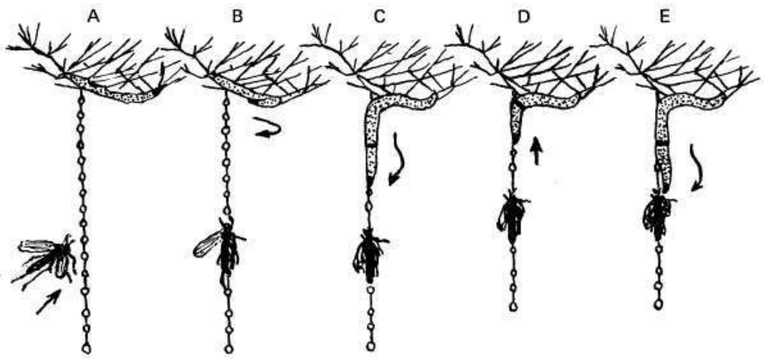


A. Larva hangs front third of body down out of gallery.
B. Three contractive (peristaltic) waves pass along the front half of body.
C. Mucus accumulates around head of larva.
D. Head is slightly withdrawn and droplet forms
E. Head moves up and down while droplet is hung from thread.

drawings adapted from Stringer, 1967.

The commonest victim of prey attracted to the larval lights in caves is the midge Anatopynia debilis (Hutton) (4 x 3.5mm) which breeds in the mudbanks and shallow water of the cave stream. The ensnaring of many different species, and the cannibalism of adult flies, pupae and larvae has been observed. In laboratory situations glowworms will feed on flies, moths, ants, millipedes and small snails. The prey snared in flight is jerkily hauled up 2 or 3mm at a time like a hand-held fishing line, and the victim is quickly bitten to prevent further struggling. The glowworm has powerful jaws and normally eats its prey, but in times of plenty merely sucks it dry, and large victims are kept suspended for several meals. The remains of meals, used snares, and execretory droplets produced while the tail hangs from the nest, are lowered on threads and then dropped.

10. Larva retrieving ensnared prey



drawings adapted from Stringer, 1967.

A. Prey attracted by light of glowworm (tail to left).
B. Prey becomes entangled in snare line. Glowworm turns around in gallery.
C. Glowworm slides partly out of nest and down snare line.
D. Glowworm contracts body to lift snare line and prey.
E. Glowworm arches down beyond 2 or 3 droplets and repeats the lifting process. Contractive (peristaltic) wave shown as dark band.

The larva rarely leaves its nest, but if two nests are close together fighting and cannibalism occur, so that nests of mature larvae tend to be spaced about 10 to 15cm apart. There are tens of thousands of glowworms in the Grotto of Waitomo Cave.

When about to pupate the larva clears away the snares around the nest and destroys the gallery. It spins a cord about 1 to 2 cm long, attaches it to its thorax, then gradually shrinks in size, sheds its skin, and becomes a translucent pupae.

BIOLUMINESCENCE

The basic bioluminescent reaction is that of an enzyme-catalysed decomposition of a peroxide to form an electronically excited product that emits photons. Although oxygen is required there is no perceptible emission of heat despite the very high efficiency of light production.

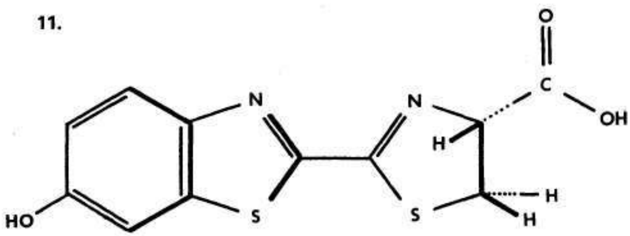
There is a possibility that the glowworm is similar to the North American firefly (Photinus pyralis) whose luminescence has been studied for more than 20 years by W.D. McElroy, M. DeLuca, and other workers. The light reaction of the firefly is between luciferin and oxygen in the presence of activiation from the enzyme luciferase, and energised by the decomposition of adenosine triphosphate complexed with magnesium

$E + LH_2 + ATP\text{-}Mg$	—	$E.LH_2\text{-}AMP + PP_i\text{-}Mg$
$E.LH_2\text{-}AMP + O_2$	—	$H\text{-}L\text{-}O\text{-}OH\text{-}AMP + E$
$H\text{-}L\text{-}O\text{-}OH\text{-}AMP$	—	$L_{O\text{-}} = O^* + H_2O + CO_2$ (+ AMP-)
	—	$L_{O\text{-}}\text{-}O^*\text{-} +$ Light + AMP

E The enzyme luciferase is a complex protein that contains some 18 animo acids in two similar monomeric units with a total molecular weight of about 92,000. Only two of the eight free sulfhydryl groups produce enzymic activation (possibily from D-cysteine). The luciferase is merely a catalyst and is not permanently altered in the reaction.

LH_2 There are several luciferins with similar molecular weights (about 400) and slightly different structures. D(-) luciferin is involved in bioluminescence.

11.



D(–) Luciferin

ATP-Mg Adenoisine triphosphate is involved in many life processes and during breakdown produces energy as heat or light. The complexing with magnesium increases fluorescence more than twofold to give 88 per cent light production.

$E.LH_2\text{-}AMP$ Enzyme-bound luciferyl adenylate.

$PP_i\text{-}Mg$ Inorganic magnesium pyrophosphate.

O_2 Oxygen is needed for all oxidation processes.

H-L-O-OH-AMP Oxidised luciferyl adenylate.

$L_{O}\text{-} = O^*$ Electronically excited oxyluciferin with one free oxygen and a double bonded oxygen.

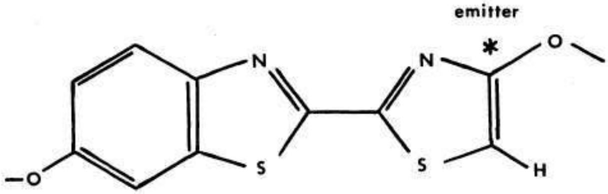
H_2O Water

CO_2 Carbon dioxide.

AMP Adenosine monophosphate (or adenylic acid) is not only a product of the reaction, but also activates light production.

L_{O}-O*- Electronically excited oxyluciferin with two free oxygens and a single bonded oxygen that emits light.

12.



L_{O}-$\overset{*}{O}$-

Light The amount of light emitted per molecule is infinitely small and lasts for less than one millionth of a second. However, the reaction is reactivated by ordinary life processes and collectively the millions of molecules make a visible light. The regularly flashing, firefly light is yellow (562nm) but the same luciferin can produce light ranging in wave-length from 485-720nm. More than 2 000 fireflies must be caught and dissected in order to produce 1mg of luciferin.

GLOWWORM LUMINESCENCE

In the forest at dusk and dawn glowing does not occur when the reflected light intensity is greater than 10 lux, and at its best when the intensity is less than 0.5 lux. In caves, luminescence is continuous.

The blue-green glowworm light, with a wave length of 487nm is produced in the distal segment of the abdomen. The light organ is formed from the dilated tips of four execretory (malphigian) tubules within a layer of respiratory tissue (tracheae) that acts as a reflector directed upward, that is, from the larva or adult towards the cave floor.

The glowworm can douse its light in about a minute. The mechanism is not clearly understood, but the luminescent chemicals are slowly dissociated. The bush glowworms appear to douse their lights very quickly because they reverse into their hideouts in a few seconds. The larvae glow brightest when they are hungry, especially when they are fighting or lifting prey. Pupae and adults glow to attract the opposite sex.

In caves air currents and the turbulence created by passing visitors entangle the snares and cave glowworms spend much time unlighted while they repair the snare lines. Glowworms do not react to noise as such because they nest close to noisy underground streams and waterfalls. Noises to which they are unaccustomed, such as a petrol engine confined in a cave or noisy traffic passing a road cutting, might cause temporary dousing. The natural increases in lighting do influence bush glowworms, and bright artificial lighting might also cause dousing. Glowworms close above the heads of talkative cave visitors will quickly douse their lights, possibly because of prolonged noise, air turbulence, or changes in carbon dioxide concentration, air temperature, or relative himidity, but radiated heat is the main suspect.

The well known publicity photograph of Glowworm Grotto, Waitomo, shows thousands of short trails of light. This is because the points of larval light have moved along the galleries during the very long time exposure of three hours. Glowworm light will register clearly on slow-speed colour film (25 ASA) in a few minutes at f8. The human eye must spend some minutes adapting to the darkness before the collective brightness of glowworms is appreciated.

PREDATORS AND NATURAL HAZARDS

In Waitomo Cave two species of opiliones attack glowworms. Megalopsalis tumida Forster eats the easily caught adult flies, and Hendea myersi cavernicola Forster attacks the larvae. Moist conditions are suitable for a species of Beauveria (Moniliacaea) of Fungi Imperfecta to attack the larvae and pupae. Flooding by the stream during any season, and the resultant food shortages are more serious hazards to the glowworm population.

The territorial segregation between Arachnocampa luminosa and the rhapidophorid (cave weta) Pallidoplectron turneri Richards at a boundary about 1.5m above water level in Waitomo Glowworm Cave is possibly the result of flood devastation. The very mobile rhaphidophorids quickly repopulate the almost vertical walls and avoid entangling their very long delicate antennae in the sticky snares of the surviving glowworm larvae that remain under the overhangs and on the cave ceiling.

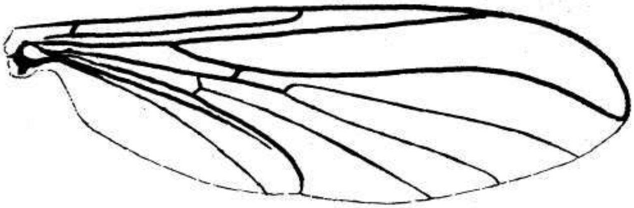
THE GLOWWORM'S NEAR RELATIONS

The first taxonomic description of the glowworm was made in 1890 by F.A.A. Skuse who considered it to belong to the sub-family Bolitophilinae of the fungus gnat family (Mycetophilidae), and named the new species luminosa in the genus Bolitophila. In 1924 F.W. Edwards erected a new genus Arachnocampa because of the spider-like habits of the larva, forming webs and using them for the capture of insect prey (Greek, arachne = spider, kampe = caterpillar). He left the genus within the subfamily Bolitophilinae because of its wing venation. In 1933, after detailed study of the structure and habits of the larva, Edwards transferred the genus Arachnocampa to the subfamily Ceroplatinae. One other troglophilic member of the genus, Arachnocampa tasmaniensis Ferguson 1925, had been described from Ida Bay, Tasmania. The naming and description of the glowworm was confused in 1959-60 by some inaccurate research by J.B. Gatenby, but clarification was soon made by R.A. Harrison and Aola M. Richards in the following year.

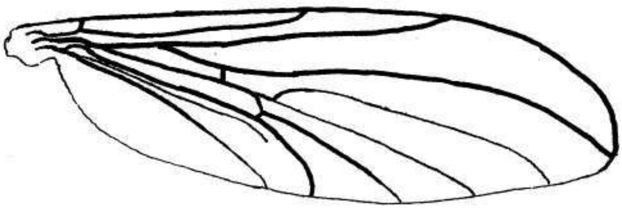
Two other smaller species of Arachnocampa are known from the Australian mainland and in 1966 R.A. Harrison erected a new subgenus Campara and described the species, richardsae from New South Wales and flava from Queensland (Latin, flavus = yellow). It is interesting to note that the Tasmanian species is more closely related to the New Zealand species than to the subgenus on the Australian mainland.

Genus:	Arachnocampa Edwards 1924
Subgenus:	Arachnocampa (Arachnocampa) Edwards m-cu cross vein before r-m cross vein wings shaded brown on apical half body length greater than 10mm Arachnocampa (Arachnocampa) luminosa (Skuse) 1890 basal segment of fore tarsus 1.0-1.3 x length of fore tibia Arachnocampa (Arachnocampa) tasmaniensis Ferguson 1925 basal segment of fore tarsus 1.75-2.0 x length of fore tibia
Subgenus:	Arachnocampa (Campara) Harrison m-cu cross vein beyond r-m cross vein wings faintly shaded brown body length less than 10mm Arachnocampa (Campara) richardsae Harrison 1966 body colours brown and dark brown Arachnocampa (Campara) flava Harrison 1966 body colours shining yellow and pale brown

13. **Wings of Arachnocampa**



Pattern of wing veins for subgenus A. (Arachnocampa)
A. luminosa, from photo by S.A. Rumsey, in Harrison, 1961.

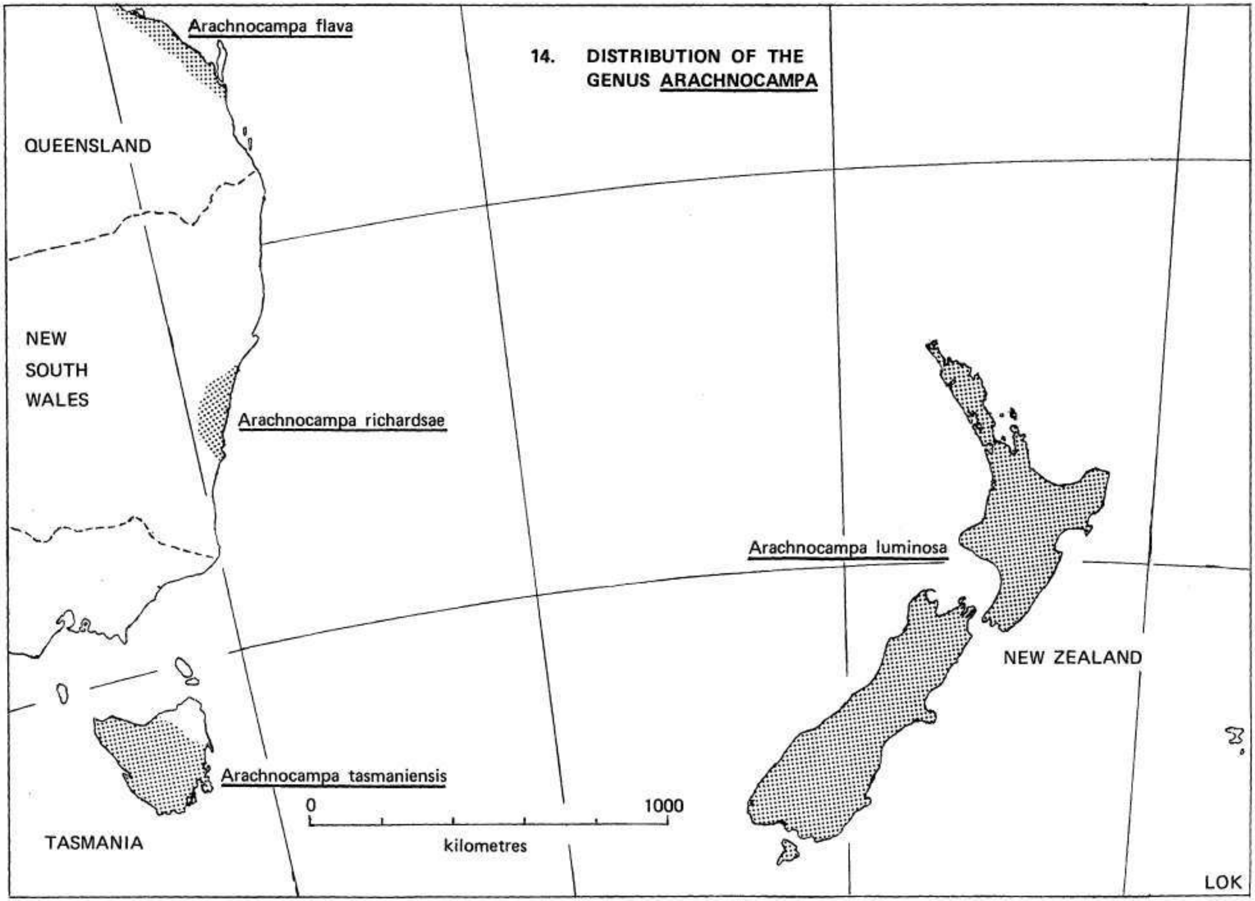


Pattern of wing veins for subgenus A. (Campara)
A. richardsae, from Harrison, 1966.

Comparison of Body and Wing Lengths of Species of the Genus Arachnocampa.

	BODY LENGTH		WING LENGTH	
	M	F	M	F
A. luminosa	9-15	10-16	6-8.5	7.5-12
A. tasmaniensis	12-14	12-15	7-9	8-10
A. richardsae	8-9	8.5-10	6-6.5	7-7.5
A. flava	8	9.5-10	5	6.5-7
	millimetres			

In New Zealand a more distant, but non-luminescent, fungus gnat relative of the glowworm is also troglophilic. A species of the genus Sciara breeds in the organic rubbish of caves, but the larva is not carnivorous, so the sticky nest gallery is only for protection.



14. DISTRIBUTION OF THE GENUS ARACHNOCAMPA

CONCLUSION

The thousands of tiny blue lights reflected in the still water of a darkened grotto and viewed by silent visitors is an experience unequalled in tourist caves of the world. Arachnocampa luminosa is a fascinating insect that deserves further study.

SELECTED BIBLIOGRAPHY

BOWIE, L.J.; HORAK, V.; DeLUCA, M. 1973: Synthesis of a new substrate analog of firefly luciferin. An active-site probe. Biochemistry 12(10): 1845-51.

BOWIE, L.J.; IRWIN, R.; LOKEN, M.; DeLUCA, M.; BRAND, L. 1973: Excited state proton transfer and the mechanism of action of firefly luciferase. Biochemistry 12(10): 1852-7.

DeLUCA, M. 1969: Hydrophobic nature of the active site of firefly luciferase. Biochemistry 8(1): 160-6.

DENBURG, J.L.; LEE, R.T.; McELROY, W.D. 1969: Substrate-binding properties of firefly luciferase. I. Archives of Biochemistry and Biophysics 134: 381-93.

EDWARDS, F.W. 1924: A note on the New Zealand glow-worm (Diptera: Mycetophilidae). Annals and Magazine of Natural History Series 9(14): 175-9.

FERGUSON, E.W. 1925: Description of a new species of Mycetophilidae (Diptera) with luminous larvae. Proceedings of the Linnean Society of New South Wales 50: 487-8.

GANGULY, G. 1960: Notes on the histology and anatomy of the larva of Bolitophila luminosa of New Zealand. Journal of the Royal Microscopical Society 79(2): 137-54.

GATENBY, J.B. 1957: The New Zealand glow-worm (Arachnocampa luminosa). Life history. N.Z. Tourist and Publicity Department. Whitcombe and Tombs Ltd, Wellington, New Zealand. 8 pp.

GATENBY, J.B. 1959: Notes on the New Zealand glow-worm Bolitophila (Arachnocampa) luminosa. Transactions of the Royal Society of New Zealand 87: 291-314.

GATENBY, J.B. 1960a: The New Zealand glow-worm. Tuatara 8: 86-92.

GATENBY, J.B. 1960b: The Australian Mycetophilid Glow-worms. Transactions of the Royal Society of New Zealand 88(3): 577-593.

GATENBY, J.B.; COTTON, S. 1960: Snare building and pupation of Bolitophila luminosa. Transactions of the Royal Society of New Zealand 88(1): 149-56.

GATENBY, J.B.; GANGULY, G. 1958: On a possible explanation of the sudden dousing of the light by A. luminosa. Journal of the Royal Microscopical Society 76: 146.

GOEDE, A. 1967: Tasmanian cave fauna: character and distribution. Helictite 5(4): 71-86.

GREEN, A.A.; McELROY, W.D. 1956: Crystalline firefly luciferase. Biochimica et Biophysica Acta 20: 170-6.

HARRISON, R.A. 1961: Notes on the taxonomy of the New Zealand glow-worm Arachnocampa luminosa (Skuse). (Dipt: Mycetophilidae). Transactions of the Royal Society of New Zealand (Zoology) 1(14): 197-201.

HARRISON, R.A. 1966: Australian glow-worms of the genus Arachnocampa Edwards. Pacific Insects 8(4): 877-83.

HUDSON, G.V. 1890: The habits and life-history of the New Zealand glow-worm. Transactions and Proceedings of the New Zealand Institute 23: 43-9.

HUDSON, G.V. 1926a: The New Zealand glow-worm Bolitophila (Arachnocampa) luminosa: Summary of observations. Annals and Magazine of Natural History Series 9(17): 228-35.

HUDSON, G.V. 1926b: Observations made on the New Zealand glow-worm (Arachnocampa luminosa) during 1926. Annals and Magazine of Natural History Series 9(18): 667-70.

HUDSON, G.V. 1928: The New Zealand glow-worm. Transactions of the New Zealand Institute 59: 426-9.

HUDSON, G.V. 1950: Natural history of the New Zealand glow-worm. Fragments of New Zealand Entomology. Ferguson and Osborne, Wellington, New Zealand. Pp. 15-37.

LEE, K.E. 1959: The earthworm fauna of New Zealand. New Zealand Department of Scientific and Industrial Research Bulletin 130. 486 pp.

LEE, R.T.; DENBURG, J.L.; McELROY, W.D. 1970: Substrate-binding properties of firefly luciferas. II. Archives of Biochemistry and Biophysics 141: 38-52.

LEE, R.T.; McELROY, W.D. 1971: Effects of 5'-adenylic acid on firefly luciferase. Archives of Biochemistry and Biophysics 145: 78-84.

MAY, B.M. 1963a: By the light of the glow-worm. New Zealand Speleological Bulletin 3(46): 169-72.

MAY, B.M. 1963b: Bibliography of New Zealand biospeleology 1811-1963. Glow-worm. New Zealand Speleological Bulletin 3(46): 185-7.

MAY, B.M. 1971: Cave fauna. New Zealand Speleological Bulletin 4(79): 571-6.

McCAPRA, F. 1973: The chemistry of bioluminescence. Endeavour 33(117): 139-45.

MEYRICK, E. 1886: A luminous insect larva in New Zealand. Entomologists Monthly Magazine 22: 266-7.

MORTON, R.A.; HOPKINS, T.A.; SELIGER, H.H. 1969: The spectroscopic properties of firefly luciferin and related compounds. An approach to product emission. Biochemistry 8(4): 1598-607.

NORRIS, A. 1894: Observations on the New Zealand glow-worm Bolitophila luminosa. Entomologists Monthly Magazine 30: 202-3.

OSTEN-SACKEN, C.R. von 1886: A luminous insect larva from New Zealand. Entomologists Monthly Magazine 22: 133-4.

RENWICK, K. 1954: Glow-worms in sea caves. New Zealand Speleological Bulletin 1(10): 17.

RICHARDS, A.M. 1960: Observations on the New Zealand glow-worm Arachnocampa luminosa (Skuse) 1890. Transactions of the Royal Society of New Zealand 88(3): 559-74.

RICHARDS, A.M. 1964: The New Zealand glow-worms. Studies in Speleology 1(1): 38-41.

ROCHE, M.J. 1967: What makes New Zealand glow-worm glow. New Zealand Speleological Bulletin 4(62): 50-2.

SHIMOMURA, O.; JOHNSON, F.H.; HENEDA, Y. 1966: Observations on the biochemistry of luminescence in the New Zealand glow-worm. Arachnocampa luminosa. Bioluminescence in Progress. Princeton University Press.

SKUSE, F.A.A. 1890: Description of Bolitophila luminosa. Transactions and Proceedings of the New Zealand Institute 23: 47.

STRINGER, I.A.N. 1967: The larval behaviour of the New Zealand glow-worm Arachnocampa luminosa. Tane 13: 107-17.

TONNOIR, A.L.; Edwards, F.W. 1927: New Zealand fungus gnats (Diptera, Mycetophilidae). Transactions of the New Zealand Institute 57: 747-878.

TRAVIS, J.; McELROY, W.D. 1966: Isolation and sequence of an essential sulfhydryl peptide at the active site of firefly luciferase. Biochemistry 5(7): 2170-6.

WHEELER, W.M.; WILLIAMS, F.X. 1915: The luminous organ of the New Zealand glow-worm. Psyche, a Journal of Entomology 22: 36-43.

ZAHL, P.A. 1971: Nature's Night Lights. National Geographic Magazine 140 (1): 45-69.

Les Kermode, Otahuhu.