Literature review of the New Zealand glowworm *Arachnocampa luminosa* (Diptera: Keroplatidae) and related cave-dwelling Diptera

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Abstract

The literature on *Arachnocampa luminosa* is reviewed together with a description of its taxonomic status. Information on other cave-dwelling keroplatids and mycetophilids is also included.

Keywords: Diptera; Keroplatidae; Mycetophilidae; *Arachnocampa luminosa;* New Zealand glowworm; cave ecology; evolution.

ARACHNOCAMPA LUMINOSA

Arachnocampa luminosa (Skuse, 1890), was first reported as a species of Lampiridae, the European coleopterous glowworm, by Purchas (1871). Meyrick (1886) considered the larva to be a predacious coleopterous larva, although this was doubted by the journal editors. Osten-Sacken (1886, 1887) finally identified a larva as that of a mycetophilid. Hudson, a well known New Zealand naturalist, pioneered the study of

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A. luminosa in a series of publications, describing his observations on the habits and life cycle (Hudson 1886, 1887, 1890, 1892a, 1892b, 1926a, 1926b, 1928, 1950). Norris (1894) added further details.

Marshall (1892) described a new species of Belytidae reported by Hudson (1892a, 1892b) as being parasitic on glowworm pupae in the botanical gardens, Wellington. It has not been reported as a glowworm parasite since then.

More recently Gatenby (1959, 1960a, 1960b), Gatenby & Cotton (1960), Gatenby & Ganguly (1958), Richards (1956, 1960, 1964), and Stringer (1966, 1967) have added to the now considerable body of descriptive information on the glowworm.

The anatomy of the glowworm was first described by Wheeler & Williams (1915). Ganguly (1960) and Gatenby (1959) studied the histology and anatomy of preserved larvae. Stringer (1966, 1967), with access to fresh material, depicted the larval viscera and the adult reproductive system. The ultrastructure of the light organ (Flower 1973), malpighian tubules (Green 1978), and eyes (Meyer-Rochow & Waldvogel 1979), have since been investigated.

Bioluminescence in *Arachnocampa luminosa* has been mentioned in most standard works on the subject (Harvey 1952; Lloyd 1971; McElroy, Seliger & DeLuca 1974). Shimomura, Johnson & Haneda (1966) reported in detail on the biochemistry of light production. Lee (1976) carried out a more extensive series of experiments on bioluminescence in *A. richardsae.*

Theoretical attention was focused on *A. luminosa* by Goldschmidt (1948), who suggested that the larval habits probably arose through macromutation. But, in a later paper Goldschmidt (1951) withdrew or modified many of his earlier statements. However, Jackson (1974) described a new species of web-spinning mycetophilid which enables gradual evolution of *A. luminosa* to be envisaged. Cook (1913) found a similar larva but no adults.

Glowworms were first reported from the Glowworm Cave at Waitomo N.Z. by Humphries (1889), but it was not until Richards (1960) that information specific to the cave, as opposed to the more common bush habitat, was published.

Taxonomy

There has been considerable confusion and debate on the taxonomy of *A. luminosa* at the generic, subfamily, and family level since Skuse (1890) first described it as *Bolitophila luminosa,* Sect. Bolitophilinae, Fam. Mycetophilidae. A new genus, *Arachnocampa* was created by Edwards (1924), but he still assigned it to the subfamily Bolitophilinae. Tonnoir & Edwards (1926) kept the same classification, but Tillyard (1926) placed *Arachnocampa* in the subfamily Diadocidinae. After examining larval head capsules of related genera *Ceroplateus* and *Bolitophila,* Edwards (1933) found further justification for his new genus *Arachnocampa,* but concluded, on the basis of larval characteristics, that the genus had closer affinities with *Ceroplatus* than *Bolitophila.*

Gatenby & Ganguly (1958) refer to *A. luminosa,* but in subsequent publications (Gatenby 1959, 1960a, 1960b; Gatenby & Cotton 1960) the name *Bolitophila luminosa* was used. Harrison (1961, 1966) reaffirmed the name *Arachnocampa luminosa* by which it is now always known.

Harrison (1961) retained the classification of *A. luminosa* in the subfamily Ceroplatinae (= Keroplatinae) of the family Mycetophilidae. However, on the basis of the distinctive characteristics of the light organ and wing venation, Matile (1981) proposed to transfer the genus *Arachnocampa* to the family Keroplatidae in a new subfamily, the Arachnocampinae. Matile also moved the subfamilies Keroplatinae and Macrocerinae to the Keroplatidae, although originally they were in the Mycetophilidae. However in the past these two groups have also been referred to as separate families; also, they have on occasions been amalgamated as the Keroplatinae

or Keroplatidae, depending on the author's view of their taxonomic status. Matile's classification is used in the following section of this paper.

OTHER CAVE DWELLING KEROPLATIDS AND MYCETOPHILIDS

A. luminosa is the only species of the genus recorded in New Zealand. The other 3 species are restricted to Australia (Harrison 1966). They are all found in caves and produce spectacular bioluminescent displays (Ferguson 1925; Lee 1976; Perkins 1935). Although caves in Tasmania (Ferguson 1925) and "glowworm caves at Bundadoon", New South Wales (Perkins 1935) contain glowworms in large numbers, they have not been developed as tourist attractions to the same extent as at Waitomo. Perhaps as a consequence there is little information on the ecology of these Australian populations.

Apart from *Arachnocampa* the family Keroplatidae also contains the luminous *Platyura fultoni* (Fisher 1940) which occurs in both caves and damp areas above ground in the United States (Fulton 1939, 1941; Barr 1949a, 1949b, 1951). The light organs of *P. fultoni* differ from those of *Arachnocampa* in that they are not associated with the malpighian tubules and consist of separate cephalic and caudal structures. These are black bodies, probably closed sacs, of various shapes which are well supplied with tracheal branches but have no other connection (Fulton 1941). The web of *P. fultoni* also lacks the regular arrangement of free hanging fishing-lines characteristic of *Arachnocampa* (Fulton 1939).

An as yet unidentified, non-luminescent larva has often been seen in caves in the Mammoth Cave National Park, Kentucky (Barr 1971, personal observation). The arrangement of the fishing-lines and general appearance of the larva is very similar to that of *A. luminosa*. This larva may have affinities with *Orfelia aeropiscator*, a non-luminescent keroplatinid found in caves in British Honduras, and on the underside of large leaves in tropical forest in Costa Rica (Jackson 1974). It is probably the same species as reported from Guatemala by Cook (1913). An apparently similar larva has been photographed in Sotano de Vasquez, a cave near Ocampo, Mexico (P. Mothes, personal communication) and from caves in Jamaica (Peck 1975). *O. aeropiscator* is the only species in the predatory genera of the Keroplatinae (*Apemon, Platyura*, and *Orfelia*) in which the strands of the web form free-hanging fishing-lines, like those in *A. luminosa*.

The Macrocerinae contains at least 2 facultative cave-dwelling (troglophilic) species. *Macrocera fasciata* is found in European caves (Jeannel 1926; Matile 1970; Vandel 1965), and *M. nobilis*, previously known from mountain forest, has now been reported from caves in the United States (Vockeroth 1976; Peck & Russell 1976). Both species are predaceous, show no sign of bioluminescence, and have extensive webs, but lack the free-hanging fishing-lines present in *Arachnocampa* and *Orfelia*.

Cave dwelling mycetophilids are found in the Sciophilinae, Bolitophilinae, and Sciarinae (Madwar 1937), the latter group now being referred to as a separate family, the Sciaridae. *Speolepta leptogaster* is a troglobite (obligate cave dweller) in European caves (Jeannel 1926; Matile 1970; Vandel 1965). *Bolitophila cinerea* is a troglophile in caves in North America and throughout Europe (Jeannel 1926), and May (1963) reported *Sciara* from caves in the Waitomo district of New Zealand.

The carnivorous habit is present in all 3 subfamilies of the Keroplatidae, i.e., the Keroplatinae, Macrocerinae, and Arachnocampinae. Fluid from the larval webs of *Platyura* and *Ceroplatus*, both of which are predaceous, was found to be acidic (pH 1.8) because of the presence of oxalic acid (Buston 1933; Mansbridge 1933). The lines of *A. luminosa* were analysed as part of a recent ecological study (Pugsley, in prep.) and found to have a pH of 3.6, but the presence of oxalic acid was not confirmed. The other cave dwelling keroplatids *Orfelia aeropiscator, Macrocera nobilis, M. fasciata,* and *Platyura*

fultoni, are all carnivorous, trapping their prey on a sticky mucus web (Fulton 1939, 1941; Jackson 1974; Peck & Russell 1976). Unlike *P. fultoni* and the Arachnocampinae, *M. nobilis* has no light to attract prey, but newly hatched larvae can feed on organic matter (Fulton 1941; Peck & Russell 1976). The 3-dimensional web structure of *M. nobilis* can be more than 1 m long; the extra size and longer threads of its web may help to compensate for the lack of bioluminescence.

A. luminosa probably represents the most advanced member of the group in that it has evolved the most sophisticated feeding mechanism by combining the free-hanging larval web of *Orfelia aeropiscator* with the bioluminescence found in *Ceroplatus* and *Platyura.* However the type of light organ in *A. luminosa* is very different from that found in *Ceroplatus* and *Platyura* (Fulton 1941; Ganguly 1960; Harvey 1952; Kato 1953; Wheeler & Williams 1915).

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