

Goldschmidt's Dilemma Resolved: Notes on the Larval Behavior of a  
New Neotropical Web-spinning Mycetophilid (Diptera)

ABSTRACT: A new species of *Orfelia* is described that is linked morphologically with the mycetophilid subfamily Keroplatinae and through larval behavior with *Arachnocampa*. Envisioning gradual evolution of the complex larval predatory behavior of *Arachnocampa* is thus facilitated by its existence.

INTRODUCTION

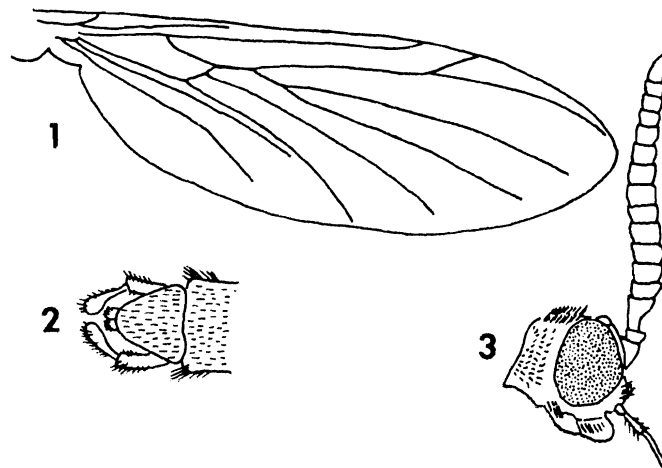
Web-building by the larvae of the mycetophilid flies, *Arachnocampa*, of New Zealand and Australia constitutes one of the more unusual feeding niches among the Diptera. Consequently, larval predatory behavior and the biology of the imago have received considerable study (Gatenby, 1959, 1960; Gatenby and Cotton, 1960; Harrison, 1966; Richards, 1960; Stringer, 1967). *Arachnocampa* became the subject of theoretical attention when Goldschmidt (1948) suggested that the larval habits probably arose through macromutation. This report describes a new species of *Orfelia* with similar larval behavior and discusses its implications for the evolution of *Arachnocampa*. Cook (1913) described a web similar to that of the present species, but he did not secure imagos of the larva responsible for it.

TAXONOMIC ACCOUNT

*Orfelia aeropiscator*, n. sp.

(Figs. 1-3)

**Diagnosis.** Head: vertex, frons, face and mouthparts cream to pale tan, except for oval black spot around ocelli; frons with dense tuft of black hairs; eyes dark reddish black. Antennae 16-segmented, flattened (Fig. 3); antennae pale tan, segments 4-14 wider than long; segment 16 twice as long as wide. Palp 3-segmented. Thorax: mesonotum pale tan, with black setae that are short and fine on central area but longer and larger laterally and in the prescutellar region; anterior pronotum cream with black setae; pleura cream with setae on pleurotergite, anepisternum of mesothorax, and postnotum (mediotergite). Halteres with pale tan knob and cream stem. Legs: coxae cream, other seg-



Figs. 1-3.—*Orfelia aeropiscator*. 1, Wing. 2, Dorsal view of unprepared male terminalia. 3, Lateral view of head

ments increasingly darker; setulae on tibiae arranged in longitudinal rows which differ in the size of the setulae. Wing: as illustrated in Figure 1; length 6 mm; membrane sepia; veins brown, but M1, M2, M1+2 and Rs paler; costa extends slightly less than halfway from apex of R5 to apex of M1; Sc indistinct; apex of R4 nearer apex of R1 than apex of R5; M1+2 very short, fork considerably proximal to R1 apex; M1 and M2 parallel apically. Abdomen: pale tan with moderately dense black hairs; terminalia darker grey tan; those of male as in Figure 2; dististyli are long and blunt; basistyli rectangular in dorsal view. Larvae: length up to 30 mm; body white; head light brown.

*Etymology.*—*aero*, Latin = air; *piscator*, Latin = fisher. Refers to the larval prey capture behavior.

*Disposition of types.*—The holotype and three paratypes were deposited in the United States National Museum. These specimens emerged from pupae that were collected from webs like those described below.

*Type locality.*—Blancaneaux Cave (17° 03' N, 88° 59' W) 9 km N of Augustine and 4 km W of Blancaneaux Lodge, in Cayo District, British Honduras. The cave is several hundred yards W of Little Vaqueros Creek where it is crossed by the Little Vaqueros Bypass Road (off the Chiquibul Road) and is reached by a trail running SW from the bypass road.

*Distribution.*—In Northern Central America this species is known definitely only from the type locality, but it is probably the form encountered by Cook (1913) and may be found throughout the karst regions of Yucatan and Guatemala. Specimens tentatively allocated to this species were collected in primary forest near the Tropical Science Center field station 3 km NW of Rincon de Osa, Puntarenas Province, Costa Rica.

*Affinities.*—Subgeneric relationships were not investigated.

#### LARVAL BEHAVIOR

Larvae were observed at two localities. At the type locality in June and December 1972, the first room of Blancaneaux Cave, which received some light and had considerable air movement in it, lacked larvae. The totally dark second room, reached via a short crawlway, was very humid with still air; there the larvae were abundant in webs attached to the underside of horizontal surfaces. No larvae were found outside the cave in the surrounding semideciduous tropical forest, probably because the open character of the forest permits stronger air movement than the delicate webs can tolerate. Larvae were also observed in early August 1970, in primary wet tropical forest 3 km NW of Rincon de Osa, Puntarenas Province, Costa Rica. Here webs were attached to the underside of large leaves of understory plants, both dicots and palms (*Asterogyne*, *Cryosophila*). Humidity was high here and wind was virtually absent in the understory. In late June 1972, *O. aeropiscator* larvae could not be found in this locality.

No attempt to observe bioluminescence was made in Costa Rica, but Belizean larvae were not luminescent, either at night in laboratory captives or in Blancaneaux Cave when it was entered quietly without lights. Tentatively, *O. aeropiscator* is assumed to be nonbioluminescent, in contrast to *Arachnocampa*. Because larvae could be observed without artificial illumination in Costa Rica, most of the observations of larval behavior were made there unless noted otherwise.

In Costa Rica the webs were constructed under large leaves from 45-245 cm above the ground. Three types of structural components form the web (Fig. 4): a single horizontal strand; support lines, usually 2-5 in number, that run at various diagonal angles from the horizontal strand to the structure from which it is suspended; and vertical "fishing lines" that hang from the horizontal

strand, or occasionally from a support line. The web, particularly the fishing lines, is covered with sticky mucus. The lower 5 mm of a fishing line appear slightly thicker than the rest and sometimes hold a sticky bead 5 mm from the free end. The size and exact structure of a web depends on the size of the larva and on its recent activity. The largest web was 66 cm long but the mean was 38 cm ( $N = 15$ ). The fishing lines ranged from 5-7 cm long. The number of lines ranged from 7-30 with a mean of 18 ( $N = 15$ ). The web is generally similar to that of *Arachnocampa*, but differences exist. The horizontal strand of *Arachnocampa* is usually only 2.5 times the length of the larva whereas in *O. aeropiscator* the strand is proportionately longer, eight times or more the length of the larva. Another difference is that the fishing lines of *Arachnocampa* are beaded with mucus droplets throughout their length, but in *O. aeropiscator* beading is only occasional and then always a single bead. Forest-dwelling *Arachnocampa* extend the horizontal strand into a crevice where they remain concealed during daylight, but *O. aeropiscator* incorporates no retreat into its web. Instead it rests fully exposed along the horizontal strand or support lines during the day. The horizontal strand of *Arachnocampa* is actually a tube within which the larva moves back and forth along the web. My optics were not adequate to determine whether such is the case for *O. aeropiscator*, but it probably is since larval gliding locomotion along the horizontal and support strands is like that of *Arachnocampa*.

Construction of horizontal and support lines was not observed, but clearing and construction of fishing lines were often seen. Destruction of fishing lines is required not only to secure prey caught on them but also to clear away lines tangled by breezes. When a fishing line is cleared most of the larva is found lying along the horizontal strand, but the anterior portion is turned perpendicularly down to parallel the fishing line. It appeared that the fishing line is hauled up by the mandibles and swallowed; but because of poor visibility the possibility cannot be excluded that, as reported for *Arachnocampa* (Stringer, 1967), the line accumulates on the exterior of the larva as a mucus droplet. For producing fishing lines, the larva hangs the anterior 5-10 mm of its body free below the horizontal strand. The suspended portion performs a "pumping" action that involves expansion and contraction with sliding movement of the internal organs: this lasts from 45-78 sec ( $\bar{X} = 53$ ,  $N = 12$ ). Then the larva arches this portion up to contact the horizontal strand with the head. The head is slowly lowered and a very thin line, 1-mm long and attached to the horizontal, is extruded from it. As the head lowers farther and extrudes more line, the line abruptly thickens and sometimes a droplet is produced 4-5 mm from

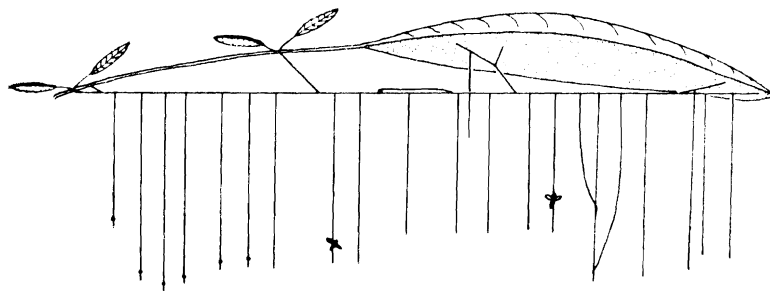


Fig. 4. Larval web of *Orfelia aeropiscator* suspended below leaf. The larva is at the center of the horizontal strand. The nonvertical fishing lines near the right end were tangled by breezes. Two prey items are shown

the attachment to the horizontal strand. As the thick portion is extruded, the thin portion stretches and finally breaks, so that the attached upper end of the line falls plumb and becomes the free lower end. The line continues to be extruded from the head until it reaches full length. Then the head of the larva rises to the horizontal strand and attaches the fishing line to it. The time required for extrusion of the line ranged from 71-123 sec ( $\bar{X} = 106$ ,  $N = 12$ ). Production of fishing lines by *Arachnocampa* differs in lacking the initial temporary attachment to the horizontal strand. There are insufficient data to determine if temporal peaks of fishing line construction exist, but construction was observed throughout daylight hours (0620-1600).

All prey observed on fishing lines were nematoceran flies, ranging from minute ceratopogonids to large culicids. They were most numerous on fishing lines in early morning but were also caught during later daylight hours. The fishing line is hauled up as previously described, and the prey on it is rapidly consumed. Gnats were ingested in less than a minute. When a large prey item struck a fishing line and began struggling, the larva would rapidly approach the line and haul it in. However, small gnats did not elicit immediate attention and sometimes remained uneaten for hours. Frequently, the larva hauls up fishing lines without prey on them, sometimes those constructed only an hour or 2 earlier. Such "random" clearing of lines may be necessary to secure prey so small that its presence on a line is undetectable.

Defecation takes place without fouling the web. The posterior 5-7 mm is held free below the horizontal strand, and the scat is extruded followed by a line of mucus. When the posterior body is returned to the horizontal strand, this fecal line attaches to the horizontal. The larva then turns around and drops the scat from the web by cutting the fecal line with its mandibles.

Like *Arachnocampa*, *O. aeropiscator* pupates in the web. Pupation behavior was not observed, but six larvae that had been watched pupated. The pupal web is the same as the larval web except that fishing lines are apparently cleared before pupation. The pupa lies dorsum up along the horizontal strand near its middle. The horizontal strand and the support lines are studded with sticky droplets. Each support line has 1-9 droplets ( $\bar{X} = 2.5$ ). Within 20 mm on each side of the pupa are 4-10 closely spaced droplets ( $\bar{X} = 6.3$ ) on the horizontal strand. Near each end of the horizontal strand are 2-9 more widely spaced droplets ( $\bar{X} = 4.4$ ). The droplets are presumably secreted by the larva immediately before pupation. They probably function as a barrier that prevents cursorial predators, particularly ants, from reaching the pupa. Such droplets were not present on pupal webs in Blancaneaux Cave, suggesting that ants are less a threat to pupae there than in primary wet forest. The Costa Rican pupae are light brown in color while those from the type locality are pallid except for the eyes. Two of the pupae collected in Costa Rica produced parasitic wasps, one an ichneumonid and one a torymid.

#### DISCUSSION

When first described by Skuse (1890), the New Zealand glowworm was assigned to the genus *Bolitophila* based on wing venation. Edwards (1924) later felt it was distinct enough to warrant a separate genus, *Arachnocampa*, and noted that the larval morphology was nearer that of the subfamily Kero-platinae than to the Bolitophilinae, but Tonnoir and Edwards (1927) retained *Arachnocampa* in the Bolitophilinae. Gatenby (1959, 1960) did not accept *Arachnocampa* and retained the combination *Bolitophila luminosa* Skuse.

When Goldschmidt (1948) considered the evolution of the larval behavior of *A. luminosa*, he was forced by the taxonomic allocation to derive it from

species of *Bolitophila*, which have larvae that feed by burrowing into soft mushrooms (Madwar, 1937). He felt that neither web-building behavior, bioluminescence nor carnivory would have been advantageous unless all three were well-developed simultaneously, and he suggested macromutation had produced the required simultaneous presence of the three traits. His dilemma was to accept hypothetical intermediate stages of larval behavior as advantageous or to embrace evolution by saltation. However, he acknowledged the observation by Cook (1913) of similar webs built by a mycetophilid larva and stated that more complete knowledge of this fly might modify his interpretation. Later, Goldschmidt (1951) did change his position and suggested that the complex predatory adaptations of *A. luminosa* probably could be understood through comparison with related forms when information became available. This second paper was largely ignored when Mayr (1960), in a criticism of evolution by saltation, pointed out that invocation of macromutation was unnecessary since all three crucial traits of larval *Arachnocampa* exist in at least rudimentary form in several mycetophilids.

Harrison (1961) moved *Arachnocampa* tentatively from the Bolitophilinae to the Keroplatinae. The present observations on *Orfelia aeropiscator* strongly support this transfer, since this species of undoubted keroplatinine affinities displays larval behavior very like that of *Arachnocampa*. Evolution of *Arachnocampa* larval behavior from other Keroplatinae is much less a problem than it is from Bolitophilinae. Larval Bolitophilinae feed only within mushrooms, but keroplatinine larval behavior can be arranged in a plausible hypothetical sequence leading to the complex predatory behavior of *Arachnocampa*. The mycetophiline *Leptomorphus* constructs and maintains a sheet web below sporulating fungi and periodically ingests parts of the web and the fungal spores caught on it; *Leptomorphus* builds a horizontal line on which to pupate that is essentially like the horizontal portion of the webs of *O. aeropiscator* and *Arachnocampa* (Eberhard, 1970). *Macrocera* (Macrocerinae) and *Keroplatus* (Keroplatinae) also build webs beneath fungi, but they eat not only spores but also minute arthropods caught in the webs (Mansbridge, 1933). The keroplatinine genera *Apemon*, *Platyura* and *Orfelia* build webs, not associated with fungi, of varying complexity and subsist entirely on arthropods caught in them (Mansbridge, 1933). For the species in these predatory genera investigated, a main horizontal strand, supported by anchor lines, is always the basic feature of the web (Fulton, 1939), but only in *O. aeropiscator* does the web have free-hanging vertical strands for intercepting flying prey. *Orfelia aeropiscator* thus provides a link between *Arachnocampa* and other Keroplatinae that build less complex webs.

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JAMES F. JACKSON, Department of Zoology, University of Florida, Gainesville 32611.<sup>1</sup> Submitted 23 July 1973; accepted 22 October 1973.

<sup>1</sup>Present address: Mello-Leitão Museu de Biologia, Santa Tereza, Espírito Santo, Brasil.

### Biology of Young Belted Kingfishers

**ABSTRACT:** Raising three young captive belted kingfishers (*Megasceryle alcyon*) from nestlings until they were able to catch their own prey brought out points regarding their biology. These, in terms of their natural history, were: (1) that nestlings eject liquid excreta forcefully up against nest walls in all directions, then bury them by a constant habit of rapping that knocks down sand and dirt; (2) young kingfishers can dive and catch prey under water within a week of fledging without being taught by parents; (3) kingfishers, when about to dive, appear to be using the two white spots in front of the eyes as sighting devices along the line of the bill to fix their prey and, by doing so, possibly to correct for the refraction of water.

On 28 June 1973 I acquired three young belted kingfishers (*Megasceryle alcyon*) when their nest was exposed by road workers. The young were well feathered but, to judge by the numbers of pinfeathers, appeared to be of different ages. They fed readily when my wife and I gave them minnows, commercial smelt and strips of raw fish, as well as suckling rats and mice. Observations of the behavior of these birds were made in three stages: first, when they were in a "nest" consisting of a plastic wash basin with straw in the bottom, placed in a large carton that could be darkened; second, when, after fledging on 9 July, they were kept in an aviary for 10 days; and finally, when, following liberation on 19 July, they remained in the yard for varying times up to a week. The