

PHOTOTROPISM, BIOLUMINESCENCE, AND THE DIPTERA

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ABSTRACT

Many arthropods move toward or away from lights. Larvae of certain luminescent mycetophilid fungus gnats exploit this response to obtain prey. They produce mucus webs, sometimes festooned with poisonous droplets, to snare a variety of small arthropods. Their lights may also protect them from their own negatively phototropic predators and/or be used as aposematic signals. On the other hand, lights may aid hymenopterous parasitoids to locate fungus gnat hosts. The luminescence of mushrooms can attract small Diptera, and might have evolved to aid mechanical spore dispersal. Among Diptera, bioluminescence is found only in the Mycetophilidae, but the variety of light organs in fungus gnats suggests multiple evolutions of the trait. This concentration of bioluminescence may be due to the unusual, sedentary nature of prey capture (i.e., use of webs) that allows the "mimicry" of a stationary abiotic light cue, or the atypically potent defenses webs and associated chemicals might provide (i.e., an aposematic display of unpalatability).

Key Words: Mycetophyllidae, *Orfelia*, fungi, prey-attraction, aposematism

RESUMEN

Muchos artrópodos se mueven hacia o lejos de una fuente de luz. Larvas de ciertos moscos micetofílicos luminiscentes aprovechan este comportamiento para obtener sus presas. Estos moscos producen redes con una mucosidad, en ocasiones adornadas con gotitas venenosas, para atrapar a una variedad de artrópodos pequeños. Es posible que al mismo tiempo las luces los protejan de sus depredadores fototrópicos negativos y/o que las usen como señales aposemáticas. Por otra parte, las luces pueden ayudar a himenópteros parasitoides a localizar a los moscos micetofílicos. La luminiscencia de los hongos puede atraer a dípteros pequeños, pudiendo haber evolucionado para facilitar la dispersión mecánica de sus esporas. Entre los dípteros, la bioluminiscencia sólo se encuentra en los Mycetophilidae, pero la variedad de órganos luminiscentes que existe en esta familia de moscos sugiere una evolución múltiple de esta característica. Esta concentración de bioluminiscencia quizá se deba a la forma, fuera de lo común, sedentaria de la captura de la presas (por ejemplo, el uso de redes) que permite el "mimetismo" de una señal luminiscente abiótica estacionaria, o a las atípicamente potentes defensas que sus redes y los productos químicos asociados pueden proveer (por ejemplo, una exhibición aposemática de ser desabridos).

Much of life, including flies, moves toward or away from light, an attribute that has interested both scientists and poets ("Ah sun-flower! Weary of time, / Who countest the steps of the sun," William Blake). In general, the mechanics of orientation to light have attracted more study than their functions; the functions often seeming self-evident. Mast (1911) provided an early list of plausible reasons for phototropisms, and included examples drawn from the Diptera: "Negative responses to light tends to keep these creatures (*fly larvae*) buried in the cadavers where they find food. . . . When . . . a bee in a flower or a pomace fly in a wormhole of a decaying apple is excited it flies directly to the light and ordinarily escapes."

In addition to simply moving towards shelter and darkness or freedom and light, arthropods also use light sources to navigate toward specific locations (the "light-compass reaction"). Bees use relative sun position to communicate food locations to their sisters (e.g., von Frisch 1967). Ants navigate with the aid of the sun in order to return along a "bee-line" to their nests (Santschi 1911). By keeping a constant angle to the sun (or to a pattern of polarized light in the sky generated by the sun) and taking into account the passage of time, certain ants can steer a straight course across even such complex and changing terrains as windswept desert sand. More interesting to the nocturnal student of bioluminescence, the moon is the light source used by at least two genera of navigating ants (Santschi 1923, Jander 1957). A beach dwelling amphipod, *Talitrus saltator* (Montague), also uses the moon, in this case to determine the direction towards optimum habitats (Papi 1960). On moonless nights the large yellow underwing moth, *Noctua pronuba* L., uses stars about 95 degrees from Polaris for navigation (Sotthibandhu & Baker 1979). When such an insect ". . . starts to fly across an area of 'unsuitable' habitat as part of a search for 'suitable' habitat it orients in it's individual-specific preferred compass direction." By avoiding 'wandering' it can cover the greatest possible territory with the least expense of time and energy (see also Baker 1978).

There can be dangerous consequences to positive phototropism and celestial navigation. A light, man-made or bioluminescent, can be mistaken for the greater illumination in a more open habitat. When a navigating insect confuses a small, nearby light source for a heavenly one, an attempt to keep the light at a constant angle rela-

tive to the body results in a spiraling flight into the source (e.g., Frankel & Gunn 1967). Flies can be both the victims and the beneficiaries of these mistakes.

BIOLUMINESCENT ADAPTATIONS IN FLIES

Luminous flies and prey attraction: Whatever the reasons for the orientation and movement of insects towards light, some bioluminescent Diptera have exploited the behavior for their own ends. All are fungus gnats (Mycetophilidae: Keroplatinae); Nematocera with vermiform larvae that resemble small crane flies as adults (Fig. 1a, d). Just a dozen or so of the more than 3000 species in the family are luminous, always as larvae, and often as pupae and adults; e.g., only the egg-stage of the New Zealand species *Arachnocampa luminosa* (Skuse) is nonluminous (Richards 1960), but adults and young larvae of the Swedish *Keroplatus sesiodes* Wahlerg bear no lights (Harvey 1952).

Most luminescent fungus gnats are poorly studied and some specimens remain officially undescribed. The latter include a single larva found on a New Guinea rain forest floor (Bassot & Hanson 1969, Lloyd 1978), an assembly of larvae once observed on the ceiling of a Nicaraguan cave (Gissele Mora, pers. comm.), a suspected new form of *Arachnocampa* collected in Fiji (Harvey 1952), and a spelunker's report of luminous "glow-worms" in an unidentified gypsum cave in the southwestern United States (Davis 1966: for a discussion of light organ placement and morphology see the section "Conclusion: the distribution of bioluminescence in flies").

The majority of mycetophilids develop in fleshy or woody fungi. Even those found in dead wood, under bark, or in the nests of squirrels and birds are probably mycetophagous (Vockeroth 1981). However, the larvae of luminous species are typically carnivorous. A possible exception to be addressed later is the Japanese *Keroplatus nipponicus* Okada (Kato 1953; in addition, see feeding habits of the German species *K. testaceus* Dalman [Pfeiffer & Stammer 1930, Stammer 1933]).

Luminescent species produce webs of mucous and silk. Web building is frequently encountered in both luminous and nonluminous carnivorous fungus gnats, (e.g., Mansbridge & Buston 1933). The strands of the web are often scattered with adhesive or poisonous droplets (i.e., the oxalic acid found in *Platyura* and *Orfelia* species). Generally, the larva has some sort of shelter associated with its web, either a connected crevice or a mucous tube. It ventures out to subdue small arthropod prey with a venomous oral secretion, and then retreats to the shelter with its meal. Larvae, acting in a manner reminiscent of spiders, restrain insects larger than themselves with mucous and later wrap them in silk. Rather than descend along the hanging strands of their webs, the larvae of *A. luminosa* swallow the line and pull their prey toward themselves (Richards 1960).

The forms of the webs vary substantially. That of *Orfelia fultoni* (Fisher) is a spray of strands suspended in a flat plane over hollow places on the surface (Fulton 1941; Fig. 1c). Spindle shaped deposits of adhesive anchor the side strands of the web, which may measure up to 5 cm across. The web of *A. luminosa* is suspended from the ceilings of caves and hollows, and consists of a horizontal thread from which are hung multiple "fishing lines" that can be more than 50 cm long in still, subterranean air, but are much shorter in more exposed situations (Gatenby & Cotton 1960; Fig. 1b). The lines are studded with adhesive droplets. A similar web is produced by a nonluminous species of *Orfelia*, *O. aeropiscator* Jackson, in the jungles and caves of Costa Rica (Jackson 1974), thus demonstrating that the very different plane-surface and suspended fishing-line designs can be generated by species within a single genus (see a discussion of the historical relationship of mycetophilid phylogeny and adaptation to saltation in evolutionary theory in Gould 1986, Goldschmidt 1948).

The prey of luminous fungus gnats consists of small arthropods, some of which presumably have been attracted by the predator's lights. *Arachnocampa luminosa* glows more brightly when hungry (Richards 1960). Larvae of this species in New Zealand's famous Waitomo Cave feed mainly on the chironomid midge, *Anatopynia debilis* (Hutton), that breeds in the waters beneath the glow-worm colony (Richards 1960). In other locations trogophytic tipulids, moths, stone flies, caddis flies, sand flies, red ants (apparently falling from the ceiling), spiders, millipedes, isopods, and even small snails are also captured (Stringer 1957). Cannibalism is common. Fulton (1941) found the remains of a cockroach and an ant in webs of *O. fultoni*, but noted that smaller insects were completely consumed and supposed that Collembola were its normal fare.

Transparent and blackened petri dishes covered with an adhesive have been placed over and near *O. fultoni* larvae in order to a) substantiate the hypothesis that larvae glow to attract prey and, b) to sample the insects attracted (Sivinski 1982). Collembola were commonly collected in both dark and illuminated traps, but only small Diptera, particularly cecidomyiids and phorids, were significantly more numerous in traps baited with larval lights. The attraction of flying (i.e., mobile), but not of nonflying (i.e., relatively sedentary) arthropods, is consistent with the phototropic behaviors of the victims serving as a means of orientation during travel.

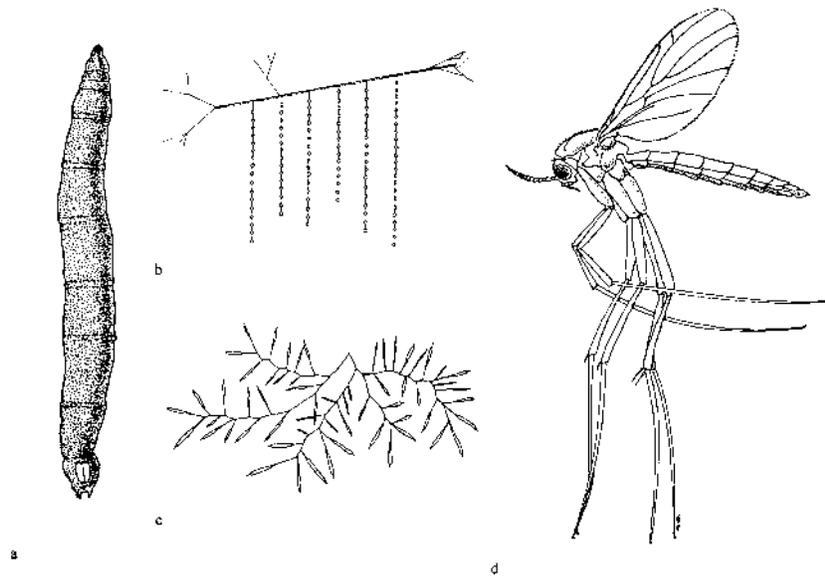


Fig. 1. a—The vermiform larva of *Arachnocampa luminosa* bears a single light organ on the terminal segment. Other species have lights on the head and tail (*Orphelia fultoni*), or glow along most of their bodies (e.g., *Keroplatus* spp.). b—Mycetophilids use various forms of webs to capture prey. In *Arachnocampa luminosa*, "fishing lines" are suspended from a major horizontal line connected to a larval retreat. c—The web of *Orphelia fultoni* is a flat spray of lines, typically spread over fissures in mossy soil. The lines are anchored to the substrate by adhesive droplets. d—An adult male of *Orphelia fultoni*.

The colors of mycetophilid luminescence differ from the usual greens and yellows of other insect lights (Sivinski 1981a). *Keroplatus sesiodes* and *japonicus* larvae emit a bluish-white light (Wahlberg 1849). *Orphelia fultoni* larvae, locally abundant in the damp ravines of the southern Appalachian Mountains where they are known as "dismal-lights," produce a vivid blue luminescence (Fulton 1939). *Arachnocampa luminosa* glows blue-green, with a peak emission at 487 nm (Shimura et al. 1966). Adult males, who seek out luminous female pupae and adults, have a corresponding peak in their visual sensitivity (Meyer-Rochow & Eguchi 1984; see section on luminous sexual signals). These unusual colors might contribute to prey attraction. Insect eyes tend to be more sensitive to the short wavelength colors, and Tyndall scattering may give a bluish cast to the celestially lite night sky, (unnoticed by human observers except "once in a blue moon"). If so, insect prey might perceive attractive, open, areas in foliage as being blueish.

Luminescence as a defense against predators: In addition to luring prey, bioluminescence may serve other roles. For instance, one Japanese fungus gnat, *K. nipponicus*, is both luminous and a web builder, yet it appears to eat only fungal spores (Kato 1953). Presumably, its light performs a function other than prey attraction, perhaps repelling negatively phototropic enemies (see Sivinski & Forrest 1983), or serving as an aposematic signal.

Mycetophilid larvae may not be defenseless. A web festooned with poisons and adhesives might alert a resident of a predator's approach or restrain it from reaching the larva. Fulton (1939) noted that webs woven by gregarious and nonluminous fungus gnats in decaying wood seemed to serve chiefly to block predatory or parasitic enemies (the luminous *K. sesiodes* is also gregarious, living in groups under a common glutinous web on the lower surface of mushrooms [Wahlberg 1848]; see also *K. tipuloides* Bosc [Santini 1982]). Cave wetas (Rhopidophorids) in New Zealand caverns avoid the webs of *A. luminosa*, which tangle in their legs and antennae (Richards 1960). One unfortunate weta placed among webs remained corralled without food for sixteen days. A number of mycetophilid pupae are luminous (e.g., Gattenby & Cotton 1960, Sivinski 1982), and while these are unlikely to be engaged in prey attraction they might be emitting a warning signal. Attraction of food with light could be a secondarily evolved elaboration of what was initially an aposematic display and a fortress.

The luminescence of a number of fungus gnats, larvae and pupae, changes following disturbance (e.g., Gatenby 1959). This is consistent with lights repelling/startling negatively phototropic intruders, or acting as a warning signal. *Keroplatus testaceus* larvae brighten their lights when stimulated (Wahlberg 1849), although the glow of *K. nipponicus* remains constant despite "pressing, puncturing, and cutting" (Haneda 1957). *Orphelia fultoni* also continues to glow while its' container is handled (Fulton 1941). Tapping on the vial containing the unidentified New Guinean specimen increased the frequency of its' light emissions, but not its' intensity (Bassot & Hanson 1969). On the other hand, disturbances cause *A. luminosa* larvae to "gleam very brilliantly" for a brief time and then douse their lights (Hudson 1886, Gatenby & Ganguly 1956).

Miscellaneous luminous social signals: Manipulation of the phototropic responses of arthropods, including flies, is presumably responsible for the evolution of lights in mycetophilids. However, once evolved, lights could be used as displays in aggressive and sexual interactions.

i—Luminescence in larval conflicts: Light may communicate size and strength among conspecific larvae. Neighboring *A. luminosa* larvae commonly fight, the loser sometimes being eaten; "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 the color and the brightness of their lights" (Richards 1960).

ii—Luminous sexual signals: Males of certain mycetophilid species orient towards adult-female and pupal lights to locate mates. While male pupae of *A. luminosa* are luminous (Gatenby & Cotton 1960), those of nearly mature females are particularly bright and likely to glow in response to touch (Richards 1960). An adult male landing upon a female pupa will cause it to luminesce. Males (up to 3 at a time) cling to such pupae, fighting to dislodge competitors and waiting for the female to eclose. If no male is attached at the time of eclosion, adult females employ light to “. . . attract a male fly, flashing it on and off till one arrived.” Females usually lose their luminescence with the commencement of oviposition, though males continue to glow throughout their lives. The function of their continued luminescence is mysterious. Lloyd (1978) discusses the sexual selection of *A. luminosa*'s luminescent signaling system, and suggests that females, both as pupae and adults, may attempt to attract multiple suitors before copulating. The resulting competition among the males might result in inseminations by particularly fit mates. *O. fultoni* pupae are luminescent and adult males have been captured in traps baited with glowing larvae (Sivinski 1982). These larval lights may resemble luminous pupae to searching males.

THE DANGERS OF BIOLUMINESCENCE AND FUNGAL EXPLOITATION OF PHOTOTROPISM IN FLIES

Fly luminescence attracting predators and parasitoids: Luminous mycetophilids are attacked by hymenopterous parasitoids. An ichneumonid, *Eusterinx* (= *Dallosia*) sp. emerged from a larva of *O. fultoni* (Fulton 1941), and a diapriid, *Betyla fulva* Cameron, was reared from the pupae of *A. luminosa* (Marshall 1882). Small unidentified Hymenoptera were most abundant in traps where *O. fultoni*'s larval lights were used as bait (Sivinski 1982). Two species of phalangids prey on the larvae of *A. luminosa* (Richards 1960). All 4 of the phalangids trapped in an *O. fultoni* habitat occurred in the ~1/4 of the traps where larval lights were visible, as did 10 of 18 spiders (Sivinski 1982).

Luminescent bacteria infect Diptera and other arthropods. For example, luminous, diseased chironomid midges have been observed across Europe, and in the New World, mosquito pupae in Brazilian epiphytes sometimes have glowing purple patches on their cuticles (cit. in Harvey 1952). Many infections appear to be benign, although some are fatal to their hosts. It is possible that bacterial lights attract new hosts, alternative hosts (e.g., fish) or agents of dispersal (Hastings 1978). For example, after entering an insect, one entomopathogenic nematode releases luminescent bacterial symbionts into the hemocoel. The microbes first kill the victim, and then luminesce (Nealson 1991). The light attracts other nematodes, which presumably carry the bacteria to another insect.

From a different perspective, nonluminous dipteran predators and parasitoids might locate luminous nondipteran prey by their lights. Adult North American fireflies (Lampyridae) of several genera are attacked by the parasitic phorid fly *Apocephalus antennatus* Malloch (Lloyd 1973), and to a lesser extent by a tachinid, *Hyalomyodes triangulifer* (Loew) (Sabrosky & Braun 1970, Lewis & Monchamp 1994). It is not known if the flies exploit bioluminescence to hunt down their hosts. However, host beetles occur in both luminescent and nonluminous genera (Brown 1994), and male and female *Photinus marginellus* LeConte, whose light displays differ considerably in frequency and duration, have similar rates of parasitism (Lewis and Monchamp 1994).

Luminous fungi and the exploitation of flies: A relationship based on positive phototropism may exist between luminous mushrooms and certain flies. Some fungi emit light. Luminescence can be present in mycelia (e.g., a number of *Mycena* species, Wasink 1978) or in both the mycelia and the fruiting body (e.g., North American populations of *Panellus stypticus* (Bull. Ex Fr.) Karst. (Cf. Singer), Buller 1924). Mushroom

(fruiting body) lights have been described as blue, white, or green depending on the species (Buller 1924, Wassink 1979). Emission intensities vary considerably. In the forests of Borneo *Mycena manipularis* (Berk.) Metrod are visible at 40 meters (Zahl 1971). One Australian species "pours forth its emerald green light" with sufficient intensity to read by (Lauterer 1900 in Buller 1924). An American journalist wrote his wife from a World War II battle field in New Guinea; "I'm writing to you tonight by the light of five mushrooms." (Zahl 1965). Others, such as the common Floridian species *Dictyopannus pusillus* (Lev.), are dimmer and the eye often requires several minutes of dark adaptation before their glows can be perceived.

There have been a number of speculations on the function (if any) of fungal bioluminescence. For example, it has been suggested that the lights of mushrooms repel negatively phototropic fungivores, attract arthropods that then excrete in the vicinity of the fungus and so nurture it, and act as an aposematic display of distastefulness (at least one luminous species, the Japanese *Pleurotis japonicus* Kawam, is a common cause of human poisoning; cit. in Sivinski 1981b).

Perhaps the oldest of these hypotheses is that the lights attract spore-dispersers, i.e., insects that either contact and mechanically distribute spores, or feed upon and then defecate spores (Ewart 1906). The odor and colors of nonluminous stinkhorn fungi (Phallales) serve this role (e.g., Ramsbottom 1953). What rewards, similar to the stinkhorn's odoriferous, spore-laden "gleba," that luminous fungi might provide are unknown. If insects bear spores, it may be that they are simply manipulated by lights into contacting spore-bearing surfaces. Certain insects, particularly Collembola and small Diptera such as Phoridae, are more likely to be captured in glass traps baited with live, glowing *D. pusillus* than in traps containing freshly killed and dark specimens (Sivinski 1981b). Increased interactions with insects diminishes the plausibility of the argument that luminescence is a functionless, and by implication consequence less, by-product of metabolism and is consistent with the attraction of spore dispersers.

The topography and timing of lights in fruiting bodies are suggestive of guiding dispersers. In *Mycena pruinosa-visida* Corner and *M. rorida* (Fr.) Quel. from the Far Eastern tropics only the spores glow (Haneda 1955). Most fruiting body lights are restricted to, or brightest, in the spore-bearing hymenium, i.e., "gills" (Wassink 1979), and *P. stypticus* glows most strongly at the time of spore maturation (Buller 1924). Interestingly, a number of fungal mycelia have a daily luminous rhythm, with minima around 9 o'clock in the morning and maxima around 9 o'clock at night (Berliner 1961a,b). Although spore dispersal is unlikely to be the function of these lights, their increased intensity during times when they can be best perceived suggests they play some communicative role in the biology of their emitters.

CONCLUSION: THE DISTRIBUTION OF LUMINESCENCE IN FLIES

E. Newton Harvey, a giant in the study of bioluminescence, regarded the phyletic distribution of living light as its most puzzling aspect. He noted that while the number of luminous species is "vanishingly small," their diversity is surprisingly great; "... as if a handful of damp sand has been cast over the names of various groups written on a blackboard, with luminous species appearing wherever a mass of sand struck." (1952). In the Diptera the "sand" only struck the Mycetophilidae.

The distribution of bioluminescence among flies presents a similar peculiar pattern. While luminescence is unique to single subfamily of fungus gnats, there is an extraordinary variety of light organ morphologies within the taxon. Lights are present in the anterior 5 segments and the small posterior segment of *O. fultoni* larvae, and consist of binucleate-giant-black, secretory cells (Bassot 1978). Species of *Keroplatus* tend to be luminous throughout their bodies, as was an unidentified New Guinean

larva whose glows traveled in waves along its length (J. M. Bassot & F. E. Hanson 1969). In *Keroplatus* larvae the light originates from fat cells found around the gut (Kato 1953, Baccetti et al. 1987). The source of light in the New Guinean insect is unknown, although giant black cells were not present in the specimen (Bassot & Hanson 1969). The single light organ on the terminal segment of the abdomen of *A. luminosa* consists of modified Malpighian tube tissue and includes a concave mat of tracheoles on its ventral side that acts as a reflector (Wheeler & Williams 1915). The various morphologies of fungus gnat light organs suggest several independent evolutions of bioluminescence within the family.

Why among flies did selection favor lights only in mycetophilids, but then so often? First, the step from nonluminescence to luminescence may not be particularly complicated, hence the potential for evolution to produce the great variety of luminous species (and fungus gnat light organs). In addition to the luminous Mycetophilidae, there are numerous instances of bioluminescent arthropods isolated from a phyletic history of bioluminescence; i.e., luminescence arising without sharing the genetic heritage of a recent luminous ancestor. For example, luminescent species of millipedes occur in only 2 genera, one Asian and the other restricted to certain mountain valleys in California (Haneda 1955, Causey & Tiemann 1969; see an odd case of luminous-milliped phobia in Yuswasdi [1950]). In the Coleoptera, hundreds of luminous species occur in families rich in bioluminescence such as the Lampyridae and Phengodidae. Yet only a single throcid (i.e., trixagid) species, *Balgus schnusei* Heller from French Guiana, is known to be luminescent. It emits green light from 2 swollen spots on the prothorax (Costa 1984; note that the Throcididae are related to the Elateridae, which contains a number of luminous species with similar prothorasic light organs [e.g., Lloyd 1978]). More surprising is the recent discovery of a luminous staphylinid! Costa et al. (1986) collected larvae of a Brazilian *Xantholinus* sp. with a light organ in the 8th abdominal segment. This is the only known case of luminescence in the entire Staphyliniformia, a clade of 28 families.

If bioluminescence can arise without extensive "preadaptation," why is it so rare or absent in many taxa? Or to turn the question around, what unusual set of circumstances favor its evolution in the fungus gnats, and not in other Diptera? Carnivorous mycetophilids are peculiar in that the larvae are nocturnal predators that employ webs to capture prey. Perhaps, such a stationary nature is both a requirement for duping phototropic victims and rarely encountered in flies (the pit-trap digging larvae of Vermilionidae are stationary, but underground and not visible to potential prey, e.g., Wheeler 1930). A slightly facetious critic of this argument might wonder why there are no bioluminescent spiders (although Brown 1925, 1926 reports a luminous spider in Myanmar [Burma] that glowed more brightly "when approached or shaken"). Alternatively, perhaps webs and their associated chemicals are one of the few potent defenses raised by relatively exposed dipteran larvae. If so, fungus gnat larvae may have rare opportunities to advertise their unpalatability to predators with light.

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