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New Observations on the Biology of *Keroplatus nipponicus* Okada, 1938 (Diptera: Mycetophiloidea; Keroplatidae), a Bioluminescent Fungivorous Insect

Neue Beobachtungen zur Biologie von *Keroplatus nipponicus* Okada, 1938 (Diptera: Mycetophiloidea; Keroplatidae), ein biolumineszierendes fungivores Insekt

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Summary: One of the least studied terrestrial luminescent insects is the fungus gnat *Keroplatus nipponicus* Okada, 1938. Its larvae emit a constant blue light of a λ_{max} of 460 nm from the entire body and construct a slime web underneath certain tree-fungi, e.g. *Grammothele fuligo*, whose spores can be identified in larval guts and faeces. The intensity of the light of the larvae increases when the latter are injured or electrically stimulated; a biorhythm with dimmer lights during the day seems to be related to the overall activity of the larva. Most likely specialized cells of the larval and pupal fat body are responsible for the light production. While in the larvae the head region glows brighter than the caudal region, the reverse holds true for the pupa. Larval body liquid from dissected specimens glows and dried and crushed larvae will emit a blue light when water is added. As to the biological function of the light, we only can speculate, e.g. that it may have a defensive function. The larvae avoid bright places and seem most abundant in late summer and autumn. After an about 10 day long pupal stage, non-luminescent adults appear.

Keywords: Bioluminescence, fungus gnats, glowworms, Hachijojima

Zusammenfassung: Von allen terrestrischen Insekten, die biologisches Licht erzeugen, ist die Pilzmücke *Keroplatus nipponicus* Okada, 1938 eine der am wenigsten untersuchten Arten. Der gesamte Körper der auf der Unterseite von Baumpilzen (z. B. *Grammothele fuligo*) lebenden und sich von deren Sporen ernährenden Larven sendet ein blaues Licht mit einer Wellenlänge von λ_{max} = 460 nm aus. Verletzungen oder Elektroschocks veranlassen die Larven die Lichtintensität zu erhöhen, doch während bei den Larven die Kopfgegend am hellsten leuchtet, so sind es bei den Puppen die Abdominalsegmente. Es wird angenommen dass das Licht, das bei Nacht heller ist als am Tage, von speziellen Zellen des Fettkörpers stammt und auch das Leuchten ausgeflossener Körperflüssigkeit verursacht. Licht kann auch erzeugt warden, wenn zu getrockneten, zerriebenen Larven etwas Wasser hinzugegeben wird. Hinsichtlich der biologischen Rolle des Lichts gibt es nur Vermutungen, z. B. könnte es der Abschreckung dienen. Die Larven vermeiden helle Orte und sind am häufigsten im Spätsommer und Herbst zu finden. Das Puppenstadium dauert etwa 10 Tage und adulte Tiere sind nicht lumineszent.

Schlüsselwörter: Biolumineszenz, Pilzmücken, Glühwürmer, Hachijojima

1. Introduction

Few people know that even in Germany there exists a species of fungivorous mycetophiloid that has luminescent larvae and is taxonomically related to the New Zealand glowworm *Arachnocampa luminosa* (Meyer-Rochow 2007). The species that I am referring to is *Keroplatus testaceus* (in the older literature the genus is spelled *Ceroplatus*). It

has been collected from the so-called "butt rot" tree fungus *Polyporus* (*Placodes*) *ungulatus* in the Heuscheuergebirge (today Poland) and near Breslau (today Wroclaw, Poland) by STAMMER (1932) and from *Trametes gibbosa* (the "lumpy bracket") on the Vogelsberg (Hessonia, Germany) by SCHERF (1970). In southern Norway *K. testaceus* has been found in association with the carpophores of the tinder fungus *Fomes fomentarius*, also known as "touchwood" (ØKLAND & SØLI 1992).

The fact that *Keroplatus* larvae emit a faint blue light from their entire body was discovered in 1849 by WAHLBERG (1849) in *Keroplatus sesioides* (cited in PFEIFFER & STAMMER 1930; STAMMER 1932; SCHERF 1970; SIVINSKI 1998), while aspects of the general biology and behaviour as well as detailed descriptions of the larval anatomies of *K. testaceus* and *K. nipponicus* were given by STAMMER (1932) and KATO (1953), respectively.

Since then at least seven additional species of the genus *Keroplatus* have been credited with an ability to luminesce (BACCETTI et al. 1987), so that by 1990 ten keroplatids, placed under the Mycetophiloidea, were known from the Holarctic region (MATILE 1990). Together with *Orfelia fultoni* from North America (SIVINSKI 1998) and various species of *Arachnocampa* in Australia and New Zealand (BAKER 2009) these mycetophilids are the only Diptera known to be able to produce biological light.

What is interesting with regard to the light production, however, is that these various species of luminescent mycetophiloid insects do not employ a common method to produce their lights. Species of the genus *Arachnocampa* use their Malpighian tubules to metabolize waste products in a process during which light is produced and emitted from the rear end of the abdomen (GREEN 1979). *O. fultoni* larvae apparently possess light-emitting structures only in their five anterior segments (in the form of huge cells with granules derived from mitochondria) and in a region near the abdominal tip (BASSOT 1978). In *Keroplatus tipuloides and K. reaumuri pentophthalmus* specialized proteinaceous granules of the fat body have been described as being responsible for the glow that lights up the entire larval body (BACCETTI et al. 1987).

Equally puzzling is the function of the light emission. While for the predatory *Arachnocampa* species it has clearly been established that in caves or other dark places the lights attract small arthropods, serving as prey, into the sticky, up to 30 cm long, vertical fishing lines, which the larvae secrete around their mucus shelters (BROADLEY & STRINGER 2009), the situation for *O. fultoni* and the various *Keroplatus* species is less clear. *O. fultoni* has been reported to feed on Collembola and other tiny insects that get attracted to the larval light and become caught in the larvae's horizontal "spray of lines, typically spread over fissures in mossy soil … anchored to the substrate by adhesive droplets" (SIVINSKI 1998, p. 285). But *Keroplatus* spp. larvae seem to feed only on fungal spores that they trap in their mucilaginous horizontal webs beneath the fungus, for to date no evidence has been presented that any of the luminescent species of this genus are predatory and feed on other invertebrates (KATO 1953; SCHERF 1970).

Because of the relative rarity of all *Keroplatus* species and the small amount of observations on them, several questions remain to be answered. According to MATILE (1990) ten keroplatid species occur in the Holarctic region, but most of them are regarded as vulnerable. In museum collections they are not represented well and sampling in the field frequently results in only very small numbers: for example, one male *Keroplatus tuvensis* of the *testaceus* group was reported by POLEVOI et al. (2006) from Finland; one single *K. testaceus* female was collected by ØKLAND & SØLI (1992) in southern Norway; and one male *K. testaceus* was identified by KURINA & HEDMARK (2004) from sweep netting in Latvia.

According to some researchers the larval light is continuous and constant despite pressing, puncturing and cutting the larva

(Kato 1953; Haneda 1957); others report a biorhythm or avoidance of illuminated areas (Scherf 1970) and an increase of the intensity of the light emission following physical stimulation (Stammer 1932; Scherf 1970). Sivinski (1998) expressed some doubt as to whether *Keroplatus nipponicus* (termed *K. nipponensis* by Kato 1953) was really feeding only on spores and suggested that the light in *K. nipponicus* (and possibly other spore-consuming keroplatids) could serve as an aposematic signal and "repelling negatively phototropic enemies" (Sivinski 1998, p. 286).

Another unresolved question in connection with the larval luminescence is, whether light can be obtained from dried larval specimens of *K. nipponicus* and whether the light emitted from the pupae differs from that of the larvae. Adult *K. nipponicus*, incidentally, have been reported to be non-luminescent by Kato (1953), although Stammer (1932) and Scherf (1970) stated that for a couple of days following eclosion, imagines, at least of *K. testaceus*, also glowed faintly until their fat body was used up. *K. tipuloides* and *K. reaumuri pentophthalmus* adults still maintain in the abdominal region, immobile in their cocoons, "a residue of progressively disappearing luminescence" (Baccetti et al. 1987, p. 170).

Since we had access to a number of larval *K. nipponicus* on the Japanese island of Hachijojima and were able to observe them in the wild as well as under laboratory conditions, we felt it was worth investigating some of the open question and trying to shed some light on the conflicting statements regarding *K. nipponicus*' light production.

2. Material and methods

2.1. Site location and description

Observations were carried out over a period of approx. one year (28/10/2012 – 15/09/2013) in a small grove of 23 cultured fan palms (*Livistona chinensis*) on Hachijojima, a 63 km^2 large island approximately 300 km south of Tokyo. There are two dormant volcanoes, 700 and 850 m high, on the island and the climate is subtropical with frequent rains throughout the year (yearly average 3000 mm) and temperature averages for the months of August and January of 29 °C and 13 °C, respectively. Famous for its abundant sea life (attracting divers and fishermen from around the world), the island also possesses extensive rain forest areas with at least seven species of luminescent fungi. In our study area luminescent fungi were plentiful, but in addition there were small populations of another luminescent organism: *Keroplatus nipponicus*. Larvae that could be detected by their weak and blue luminescence were found in dark places under the bases of palm fronds, where they had constructed their slimy webs beneath tree-attacking fungi like, for instance, *Grammothele fuligo*.

2.2. Experimental design

In the field abundances of *Keroplatus nipponicus* with regard to the position of the trees and time of year were recorded. However, since the insects were not marked or labelled in any way, it is possible that some may have been recorded more than once.

Photographs of luminescing larvae were taken in the field and in the laboratory with a digital camera to establish whether a biorhythm controlled the light emission. Photographic exposure times were usually of the order of one minute. For figures 1 and 2 a Nikon D3, for figures 3-11 a Nikon D3S and for figure 13 a Nikon D5100 was used.

Larval intestinal tracts were investigated and qualitative analyses of faecal pellets were carried out. Larvae were subjected to various forms of stimulation, e.g. mechanical by squeezing, prodding with pointed instruments and cutting, electrical by one minute exposures of 4, 6, and 8 Volt alternating current, repeated 2 and 3 times with a 5 mi-

nute interval for rest in between (see below). Luminescing pupae were only subjected to electrical stimulation. The intensity of the emitted light was assessed by human eye (i.e. light is absent, weak, medium, strong). Dried larvae were ground up in a mortar; a small amount of water was then added and visually examined for light emission. Information on the larval spectral emission peak was provided from Prof Yuichi Oba of Nagoya University.

3. Results

On twelve of the 23 fan palms of heights of around 2.5-3.5 m luminescent larvae were present. The trees were planted in two parallel rows with twelve trees in one and eleven in the other row, together prescribing a rectangular area of 6 x 22 m. The trees were of similar ages, shapes and conditions and 129 *Keroplatus nipponicus* larvae were found on them over the one year period of observation. However, there were clearly preferences since on only four of the occupied trees more than ten larvae were counted. The highest densities of 35 and 24 individuals were found on two trees in association with the tree fungus Aianatake (*Grammothele fuligo*). A further two trees were home to 28 and 16 larvae, but associated with a tree fungus representing a new genus and new species, known locally as Urokotake. Not once was a larva seen without a fungus and as far as we were able to ascertain only the two aforementioned tree fungi were involved. Since the larvae were detected visually with the unaided eye and counted on the basis of their light emission, it is possible that the total population of *K. nipponicus* larvae was even larger, for first instars and young larvae generally emit only extraordinarily weak light that is almost impossible to spot.

As has been described for other keroplatids (SCHERF 1970), the slime nests constructed by the larvae and attached very close to the underside of the host fungus may contain several individuals that need not necessarily be of exactly the same size (Fig. 1). The larvae are never in direct physical contact with the fungal surface as the slime nest separates the two. The larvae (and contrary to earlier reports we found that even the smallest larvae emitted a faint light) can be detected on account of their weak emission of blue light (Fig. 2), which appears stationary as the larvae seem to be resting most of the time. There is only a single emission peak of the light at λ_{max} = 460 nm (OBA et al. 2011). Slightly more active at night, the larvae (Fig. 3) can then be seen to occasionally move around on their slime nest. Prolonged exposure to the white light of a torch caused some larvae to withdraw to shady or protected parts of the nest, suggesting that photoreception is of some value to the larvae, thus confirming SCHERF (1970, p. 115), who reported the presence of "kleine pigmentierte Augen" in *Keratoplatus testaceus* larvae. Ultrastructurally, however, the only eyes of mycetophiloid larvae that have ever been studied were those of *Arachnocampa luminosa* by MEYER-ROCHOW & WALDVOGEL (1979).

The first appearance in the year of a *K. nipponicus* larva was in April, but since it took until the 22nd of June before additional larvae were noticed once more, the occurrence in April appears to have been exceptional. Throughout July on average five larvae were sighted during tree inspections at night, but the abundance of *Keroplatus* larvae increased to between 15 and 20 during weekly counts from mid August to mid October. Weekly counts in November and December showed a sharp decline in numbers and on the 9th of December the last glowing *K. nipponicus* larva for the year was seen. That only larger, light-emitting larvae were recorded and earlier instars because of their almost imperceptible light could have remained undetected has already been mentioned.

Somewhat preliminary observations with a larva taken into the dark room of the lab

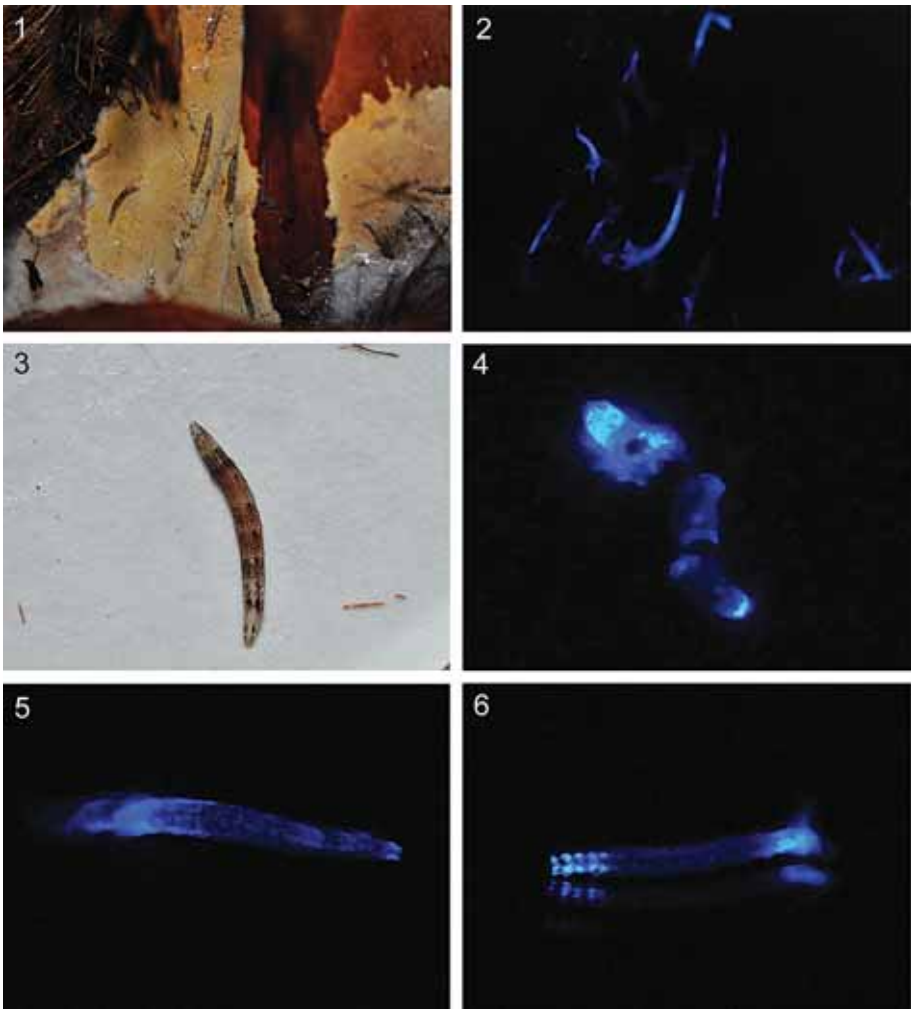

Fig. 1-6: *Keroplatus nipponicus*. **1** Several larvae of different sizes in the same mucous web on the underside of a tree fungus. The largest larva measures approx. 2 cm in length (flashlight photograph, taken at night in the field). **2** The larvae can be visually detected by their blue glow (photograph taken in the field at night with 1 min exposure). **3** Single larva, approximately 18 mm long, photographed in the light. **4** The blue light emission intensifies and becomes concentrated in the anterior and posterior ands after the larva is cut into three pieces. **5** Normally luminescing larva at night. **6** Stimulation with 6 V results in strongly luminescing head region with apparently paired foci of light emissions and almost equally bright tail region with more diffuse light emission (4-6: Head left).
Abb. 1-6: *Keroplatus nipponicus*. **1** Mehrere unterschiedlich große Larven im selben Schleimgespinst auf der Unterseite eines Baumpilzes. Die größte Larve ist etwa 2 cm lang (Blitzlichtphotographie nachts im Gelände). **2** Die Larven können durch ihr blaues Licht erkannt werden (Freilandaufnahme, nachts, Belichtungszeit 1 min). **3** Eine einzelne, ca. 18 mm große Larve, im Licht aufgenommen. **4** Das blaue Leuchten der Larve wird stärker und bildet im vorderen und hinteren Teil Schwerpunkte nachdem die Larve in drei Teile geschnitten wurde. **5** Normal lumineszierende Larve bei Nacht. **6** Reizung mit 6 V hat zur Folge, dass die Kopfregion sehr stark leuchtet und paarige Lichtemissionszentren auffallen und dass sich die Biolumineszenz auch im caudalen Bereich intensiviert (4-6: Kopf links).

indicated that the light *K. nipponicus* emitted remained constant until about 10.00, but then dimmed rapidly to imperceptible levels until the evening, when the light re-appeared. Parallel to this brighter light emission at night is an increased tendency of the larvae to move around in the nest. In a series of additional observations it was demonstrated that the light intensity of the larval light is not constant (as had been reported earlier by KATO 1953 and HANEDA 1957), but responds with an increase to physical and electrical stimulation of the larvae.

In the first series of experiments larvae were taken from their nest, placed on a piece of moist filter paper and cut in two and sometimes more than two pieces (Fig. 4). Not only did the separate pieces glow, but the liquid that was oozing out of the severed body parts and soaked up by the filter paper was glowing more intensively than the intact larva had done before (Fig. 5). The head region was the source of an especially bright blue light emission, which increased even further upon addition of a drop of cold water.

Stimulation with exposure to electrical pulses was carried out under three different conditions. In all three test conditions a larva was placed on filter paper that had been placed on agar, to which a little salt had been added. An ac-generator supplied pulses of a range of voltages and durations. An exposure to a voltage of 4 V resulted in a visible increase in emitted light intensity. The light intensity increased further with an increase of the voltage to 6 V. At 8 V the larvae usually showed some kind of distress and crawled away, besides any brighter response than to 6 V was not seen.

Sticking with 6 V exposures of one minute duration, we tested how the larvae reacted to repeated stimulations of the same kind. When a break of five minutes was used between exposures and the exposure to a one minute 6 V was repeated, light emission of the blue light not only visibly increased in intensity, it also concentrated the light emission to the caudal, but in particular the head region of the larva (Fig. 6). A third exposure, led to a further increase in the intensity of the emitted lights, highlighting paired and seemingly segmentally arranged clusters of light emission centres. Additional exposures did not result in yet further intensity increases.

In another observation larvae were allowed to die in dry air during the day in the light. When completely dry, the larvae were ground up in a mortar (Fig. 7). When a small amount of cold water was added, the dried and crushed pieces of the larval bodies emitted blue light (Fig. 8), which slowly faded, but could still be perceived 20 minutes later in the dark.

Three pupae were available for observations and they, too, emitted blue light (Fig. 9). In contrast to the larvae, however, the head region of the pupa, when freed from pupal case, was almost non-luminescent; light was concentrated in six of the most abdominal segments (Fig. 10). Exposure to repeated electrical stimulation with 6 V resulted only in very minor increases of the intensity of the emitted light. The two adults that we obtained from three pupae in close proximity to the larval web, were non-luminescent and emerged from their silk cocoons after a ten day long pupal stage at around 22 °C (Fig. 11).

Although uptake of any kind of food (fungal spores or anything else) was not observed, faecal pellets and intestinal content were examined. Both contained clearly identifiable spores and nothing else. Since spores of Aianatake and Urokotake differ from each other and can be identified, it was possible to show that they were present only in those *K. nipponicus* larvae that had occupied the respective species of tree fungus. No larva was ever seen under or in association with a luminescent fungus.

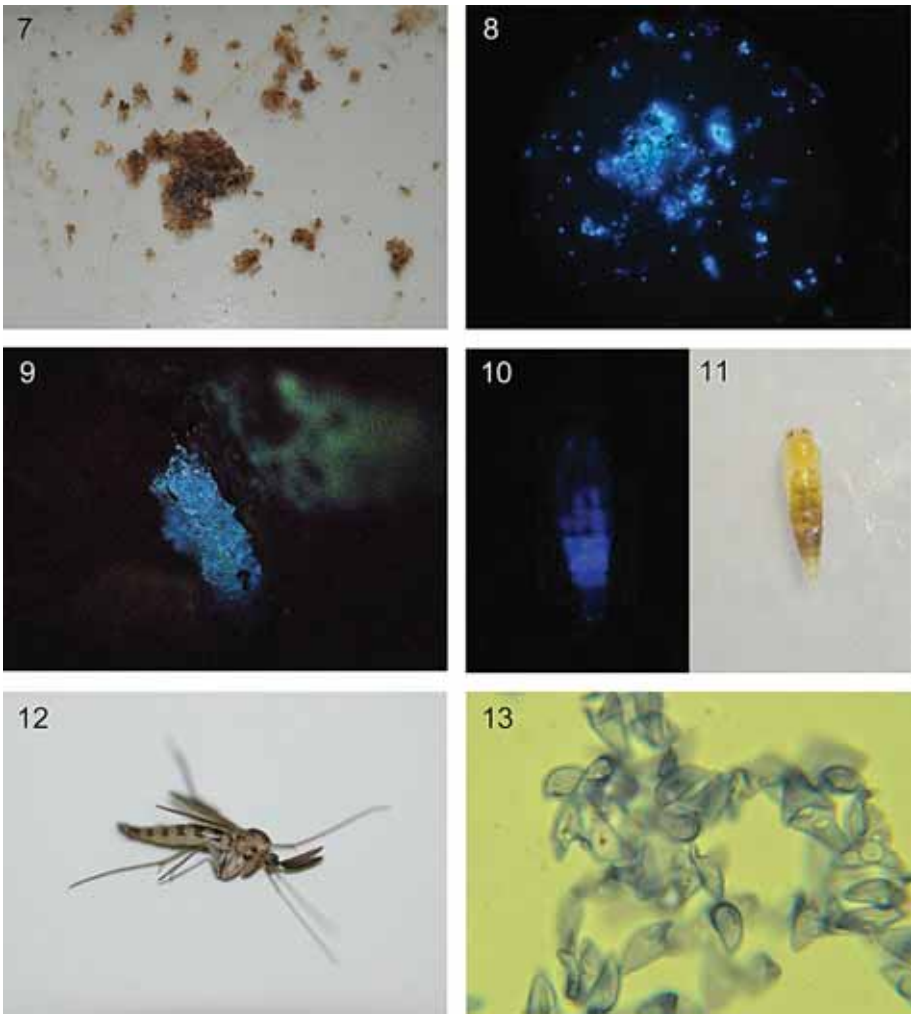

Fig. 7- 13: *Keroplatus nipponicus*. **7** Dried and ground up larvae in the light, but without water added. **8** With a bit of water added the dried larval material glows brightly. **9** The pupa, measuring approximately 15 mm in length, also produces a constant blue light. **10** Freed from its pupal case, it is obvious that the pupa emits light mainly from its posterior end (1 min exposure time). **11** Almost ready-to-eclose individual isolated from its case and observed in the light (note pigmented eyes). **12** Imago with body length of about 16 mm. **13** Spores of Urokotake tree fungus isolated from larval faeces (1000 x).

Abb. 7-13: *Keroplatus nipponicus*. **7** Getrocknete und zerriebene Larven im Licht betrachtet, aber ohne Zufuhr von Wasser. **8** Nachdem etwas Wasser hinzugegeben wird, leuchtet das trockene Larvenmaterial hell auf. **9** Die etwa 15 mm lange Puppe produziert ebenfalls ein konstantes blaues Licht. **10** Befreit von der Puppenhülle wird es klar, dass die Puppe hauptsächlich vom hinteren Teil strahlt (Belichtungszeit 1 min). **11** Fast schlupfbereites, von der Puppenhülle befreites Insekt im Licht betrachtet (man beachte die pigmentierten Augen). **12** Imago mit einer Körperlänge von ca. 16 mm. **13** Sporen des Urokotake-Baumpilzes im Larvenexkrement (1000 x).

4. Discussion

Like other keroplatids, *Keroplatus nipponicus* is rare and difficult to study. It is therefore of importance to report whatever little new information there is on this unusual bioluminescent insect. Unusual, because of mainly three reasons: (a) it emits the bluest light of all terrestrial arthropods, (b) the entire body emits light, although head and tail region are the brightest parts of the body and (c) in contrast to other light-emitting ketroplatoid Diptera, where a biological function of the light has been shown to exist (SIVINSKI 1998; MEYER-ROCHOW 2007; BROADLEY & STRINGER 2009), no clear function of the light of *K. nipponicus* (or other keroplatids) has been demonstrated to date. Although first instars (or generally speaking, young larvae) have frequently been reported to be non-luminescent (SCHERF 1970), we believe (as did KATO 1953) that this statement is only a reflection of the human observer's own visual sensitivity and that a fully dark-adapted human with light-sensitive eyes may well detect a very faint bluish glow emitted by even the smallest larva. What remains unconfirmed, however, is whether the eggs really emit no light at all as stated by STAMMER (1932) and KATO (1953) and whether peak spectral emission of the pupal light corresponds to that of the larva. What happens during larval moults and whether at that time light emission ceases (as is perhaps to be expected) also still remains to be elucidated. According to SCHERF (1970) the pupal stage in *Keroplatus testaceus* lasted approximately 14 days and the adults measured 12-15 mm in length. For *K. nipponicus*, KATO (1953) reported a one week long pupal phase at 20 °C and described the imago as being 15-20 mm long and rapidly flying 30 minutes after eclosion. Young imagos of *K. testaceus* were reported by PFEIFFER & STAMMER (1930) to continue to emit a weak light for two days following eclosion and BACCETTI et al. (1987, p. 170) reported that "the adult immotile in the cocoon, still maintains in the abdominal region a residue of progressively disappearing luminescence". However, to date none of the researchers studying *K. nipponicus* (e.g. KATO 1953; HANEDA 1957) have found any adult individual, irrespective of its age, to luminesce and we believe that specific or individual differences in combination with environmental factors may contribute to whether newly eclosed adults for a short while still retain some ability to emit light.

K. nipponicus is obviously not feeding on insects and in agreement with STAMMER (1932), KATO (1953) and SCHERF (1970) we conclude that the diet of fungivorous keroplatids consists entirely of fungal spores, which then larval insects capture in the slimy web spun by them over the fungal under-surface. Whether a single larva or several help secreting this spore trap remains unknown, but the fact that several larvae can share one web is undisputed. There are other consumers of fungal spores, but the various *Keroplatus* species appear to be the only ones emitting light. The earlier occasionally expressed idea that the larval luminescence could stem from the ingested spores of luminescent fungi dates back to WAHLBERG (1849) and is clearly wrong. However, that fungi, in which only the spores glow, do exist, was shown by HANEDA (1955).

The somewhat 'patchy' distribution of the larvae in the fan palm orchard deserves mentioning. Rather than the tree's position that determines the presence of *K. nipponicus* larvae, it is more likely the type of tree fungus and the condition of the latter that influences the occurrence and distribution of the larvae. The tree fungi in turn may prefer certain trees, so that climatic effects and the host trees' conditions combine to allow certain tree fungi, whose spores are acceptable to *K. nipponicus* larvae, to grow on them. Additionally, preference given to certain trees by *K. nipponicus* larvae could be related to the presence or absence of other insects, since *K. nipponicus* larvae, according

to observations by Yumiko Oba (pers. comm.) dislike other insects to be around and choose spots, where they can build their nests in an undisturbed fashion. As with *K. testaceus* in Germany (Scherf 1970), late summer and autumn seem to be the best seasons to find larval *K. nipponicus* on the island of Hachijojima.

The idea has been muted that the light of keroplatids could possibly function as a deterrent "repelling negatively phototropic enemies or serving as an aposematic signal" (Sivinski 1998, p. 286) and although theoretically this is possible (especially in view of the fact that injured larvae emit brighter light: Pfeiffer & Stammer 1930; Stammer 1932; Scherf 1970; this paper), the light is so faint that it is not very likely to be terribly obvious to possible predators of *Keroplatus*. Moreover, arthropod eyes usually possess sensitivity peaks in the green and UV range and not in the blue part of the spectrum (Menzel 1979), so that as a deterrent blue light would seem to be less effective than, for example, green light. However, there have not been any tests which insects or spiders might actually prey on *Keroplatus*. What has been suggested is that the faint light could perhaps lead positively phototactic parasitoid wasps to their targets (Sivinski 1998), but the same limitations expressed in connection with the idea of an aposematic role would apply. Whether the light has any effect on the host fungus (perhaps responding with greater spore production) has never been investigated.

Contrary to an earlier statement by Haneda (1957), that no light can be obtained from dried larvae, we managed to do so. This indicates that there have to be luciferin and luciferase chemicals that retain their ability to react with each other to produce blue light in the presence of water. The chemicals responsible for the light emission, according to Baccetti et al. (1987), are present in special cells of the fat bodies of mature larvae and pupae. However, there seem to be paired light-emitting centres near the head region and near the abdominal end, because these two regions emit the brightest light. This observation of paired and clearly distinguishable bright spots appears to fit the description of the light-emitting structures in *Orfelia fultoni* (Sivinski 1998) and suggests that in addition to the luminescent granules of the fat body there have to be some other light-emitting structures in the head and tail region, perhaps derived from the fat body, because lobes of the fat body accompany gut and salivary glands; Scherf (1970) believes them to be the cause of the greater light emission in the anterior and caudal regions of larvae and pupae.

What is certainly interesting (see above) and has not received the attention it may deserve is the fact, that in the larvae the intensity of the light could be increased by rough physical handling and injury, already reported by Pfeiffer & Stammer (1930), but not seen by Kato (1953) and Haneda (1957) despite physical stimulation of the larvae, and that both physical and electrical stimulation caused especially the head region to brighten up. Remarkably, in the pupa any form of stimulation only resulted in a very small intensity increase of the light, but clearly demonstrated that the light was emitted from the abdominal region and not the head region, the latter being almost completely dark. Whether the fat body, thought to be the major organ responsible for the light production, diminishes first in the anterior region of the insect and last in the abdominal tip is something a future histological study should focus on, for if this were the case it would strengthen the argument of the fat body being the major (or only) light source even for the head region. Almost certainly the presence of the anterior imaginal discs is involved in the loss of bioluminescence from that region.

Another area worth exploring would have to be the chemistry behind the light production in keroplatids generally and *K. nipponicus* in particular. For luminescent lampyrids mo-

lecular weights of various luciferases and the nature of the luciferins are well known (cf. review by DAY 2009), substrates and co-factors have been identified (VIVIANI 2002) and evolutionary genetics have been studied (OBA 2009), but for *Keroplatus* spp. no luciferase molecular weights or substrate co-factors let alone luciferin has been identified. Perhaps *Orfelia fultoni* luciferase with the highest molecular weight known for any terrestrial luminescent arthropod (i.e. 140 kDa: VIVIANI 2002) is closest to that of *Keroplatus* spp., because light emission mechanisms and certain aspects of their biologies (although *O. fultoni* does capture and consume Collembola and other tiny arthropods while *Keroplatus* spp. do not) are common to both. In any case, there is considerable work left to be done on *K. nipponicus* and the other blue light emitting keroplatids (OBA 2014), including the enigmatic *K. testaceus* in Germany.

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