

Eyes of two Keroplatid Dipterans: the Luminescent *Arachnocampa luminosa* and the Non-luminescent *Neoditomyia farri* plus Comments on Luminescent and Non-luminescent Beetles and Gastropods

Augen zweier keroplatider Diptera: der lumineszierenden *Arachnocampa luminosa* und der nicht-lumineszierenden *Neoditomyia farri* sowie Bemerkungen zu lumineszierenden und nicht-lumineszierenden Käfern und Schnecken

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Summary: The non-luminescent *Neoditomyia farri* has eyes with more but smaller facets (1,000-1,250; 23-25 μm) than the luminescent *Arachnocampa luminosa* (approx. 750; 27-28 μm). The latter, however, has wider interommatidial angles (5.5° versus ca. 4°) and somewhat more voluminous rhabdoms, indicative of a higher sensitivity to light than *N. farri*. Corneal nipples, screening pigment granules and gross anatomical organization of the retina are virtually identical in the two species, suggesting that the bright larval luminescence in *A. luminosa* has had no or only a minimal effect on the organization of the eye of the adult unlike the situation in, for example, fireflies and luminescent and non-luminescent limpets, in which the luminescent partner of the comparison had larger eyes, a more extensive dioptric apparatus and a more voluminous retina. The significantly more numerous and longer interommatidial hairs in *A. luminosa* could be related to a more strictly cavernicolous life and need to deal with tactile stimuli.

Keywords: Bioluminescence, compound eyes, vision, insects, troglophile mycetophilids

Zusammenfassung: Die Augen der nicht-lumineszierenden *Neoditomyia farri* besitzen zwar mehr kleinere Facetten (1.000-1.250; 23-25 μm) als jene der lumineszenten Art *Arachnocampa luminosa*, doch besitzt letztere grössere Interommatidialwinkel (5,5° gegenüber ca. 4°) und etwas voluminösere Rhabdome, was auf höhere Lichtempfindlichkeit schließen lässt. Corneale Oberflächenstrukturen, Schirmpigmentgrana und allgemeine anatomische Organisation der Retinae sind nahezu identisch bei beiden Arten, so dass die helle larvale Biolumineszenz von *A. luminosa* wohl keinen oder nur einen minimalen Effekt auf die Augenausbildung der Adulten hat, anders als es der Fall bei Leuchtkäfern und lumineszierenden und nicht-lumineszierenden Wässerschnecken ist, bei denen die lichterzeugenden Arten größere Augen, einen besser entwickelten dioptrischen Apparat und eine massivere Retina aufweisen. Die signifikant zahlreicheren und längeren Interommatidialhaare von *A. luminosa* sind möglicherweise eine Anpassung an das Höhlenleben der Art und der Notwendigkeit, taktile Reize wahrzunehmen.

Schlüsselwörter: Biolumineszenz, Facettenaugen, Sehvermögen, Insekten, troglophile Pilzmücken

1. Introduction

The dipteran family Keroplatidae of the superfamily Mycetophiloidea contains species

of an astonishingly variety of dietary specialists and feeding methods. Termed 'fungus gnats' in English, the majority of the species is indeed feeding on fungi and their spores

and is not known to be bioluminescent. However, there are some species like the weakly luminescent *Keroplatus nipponicus* that in order to collect the spores construct slime webs on the underside of the fungal body (OSAWA et al. 2014). Yet others like the somewhat brighter *Orfelia fultoni*, which also secretes spore-catching webs, will, however, not hesitate to accept trapped collembolans or other small arthropods as food in addition to their main diet of fungal spores (SIVINSKI 1998). An unidentified keroplatid species has been reported to be a myrmecophile, preying on workers of *Catantopus mckeyi* ants and having a sizeable impact on the ant colony (TRIVEDI et al. 2004), but whether it, too, produces light has not been reported.

Perhaps the most amazing keroplatids are those of the genus *Arachnocampa*. Members of this keroplatid genus possess larvae that are more brightly luminescent than all of the other light emitting keroplatids and use their lights as photic lures to attract small flying insects into their up to 30 cm long, vertical silk threads (BROADLEY & STRINGER 2001). The latter are coated with tiny blobs of glue produced by the larval salivary glands to ensnare prey that touches the vertical 'fishing lines' and to make sure that the trapped prey cannot get away (see review by MEYER-ROCHOW 2007 and more recent publications on glowworm behaviour by MERRITT & CLARKE 2011; MERRITT et al. 2012; MILLS et al. 2016).

Fishing lines of an almost totally identical design and origin are also used by the larvae of neotropical *Neoditomyia* species (STURM 1973). These insects occur in habitats that are very similar (although about 15 °C warmer) to those of *Arachnocampa* in New Zealand and Australia, but *Neoditomyia* species do not employ luminescence to attract their prey. They appear to be successful predators without the use of photic lures. One question is obviously why they might not require luminescence when *Arachnocampa* larvae apparently need their lights to attract prey insects (STRINGER

& MEYER-ROCHOW 1994, 1996; BROADLEY & STRINGER 2001) and it has been suggested that the amount of potential prey available for these insectivorous larvae to feed on is simply so much greater in the neotropical forests and warmer caves than it is in the New Zealand or Australian environment in which *Arachnocampa* species occur (STRINGER & MEYER-ROCHOW 1994).

Another question, not yet answered for the luminescent and non-luminescent *Arachnocampa* and *Neoditomyia* species, is whether the fact that *Arachnocampa* larvae produce bright lights and those of *Neoditomyia* do not is reflected in the size, organization and function of the photoreceptors of their adults.

That closely related luminescent and non-luminescent invertebrate animals can possess quite different eyes in terms of their dioptric apparatus and overall morphology (Tab. 1) has been shown for the luminescent pulmonate gastropod *Latia neritoides* and the non-luminescent pulmonate *Ancylus fluviatilis* (MEYER-ROCHOW & BOBKOVA 2001), two species that share very similar lotic habitats, but in which the retina and dioptric structures of the luminescent species are vastly enlarged. Observations on eye sizes, facet diameters and facet numbers in diurnally active and nocturnal fireflies have also shown a significant difference between the weakly luminescent former and brightly luminescent latter species (Tab. 1 and EGUCHI, pers. comm.). It was these earlier findings which led to the question as to whether a similar trend might not also be observable in luminescent and non-luminescent keroplatids. Thus the investigation of the eyes of the luminescent keroplatid *Arachnocampa luminosa* and the non-luminescent species *Neoditomyia farri*, reported in this note, was initiated.

Members of the two species *Arachnocampa lumino*a and *Neoditomyia farri* are mosquito-like in appearance, but belong to the family of fungus gnats (Keroplatidae; Mycetophiloidea). The adults of both species in contrast

Tab. 1: Comparison of eye parameters in nearly identically sized luminescent and non-luminescent closely related species of fireflies and limpets.

Tab. 1: Vergleich verschiedener Augenparameter von nahezu gleich großen lumineszierenden und nicht-lumineszierenden, eng verwandten Leuchtkäferarten und Napfschnecken.

(a) Luminescent (b) Non-luminescent	Body lengths of male and female beetles	Cornea/lens diameter and thickness	Crystalline cone diameter and length	Total extent of optical apparatus	Distance cornea – basal membrane
Fireflies: EGUCHI (pers. comm. 2002)					
(a) <i>Luciola lateralis</i>	♂9; ♀10 mm	24; 10 µm	17; 51 µm	61 µm	340 µm
(b) <i>Lucidina biplagiata</i>	♂10; ♀12 mm	18; 9 µm	13; 39 µm	48 µm	141 µm
Limpets: MEYER- ROCHOW & BOBKOVA 2001					
(a) <i>Latia neritoides</i>	4-6 mm	90; 3 µm	63 (aperture)	175 µm	50 µm retinal thickness
(b) <i>Ancylus fluviatilis</i>	5 mm	60; 5 µm	43 (aperture)	100 µm	30 µm retinal thickness

to the long duration of the larval period are short-lived and usually die within two or three days and are therefore not abundant. Although we had several *A. luminosa* adults, procured in New Zealand's "Waitomo Cave", to work with, we had only very few adult individuals of *N. farri* from Jamaica's "Dromilly Cave" to study. Although intra-specific variation and sexual dimorphism in eye sizes is possible (MEYER-ROCHOW 2008, 2015), it is unlikely to occur in the two species examined since such major irregularities have not been reported from the eyes of any mosquito and secondly an adult life span of only a couple of days spent non-feeding by both genders in the same habitat does not expose individuals to separate selective pressures. Nevertheless, our results must be regarded as preliminary and as an incentive to carry out additional studies on the eyes of these and other pairs of luminescent and non-luminescent closely related species.

2. Material and methods

For the ultra structural examination several adult individuals of both species were decapitated and had their heads placed in cold 3% phosphate-buffered glutaraldehyde for 14 h (*Arachnocampa luminosa*) or

3.5% Sörenson-buffered glutaraldehyde for 12 h (*Neoditomya farri*). Rinsing in buffer three times was followed by fixation for 2 h in 1% or 2% Osmiumtetroxide (*A. luminosa* and *N. farri*, respectively). After rinsing and dehydration in a graded series of acetone, the preparations were embedded in resin and sectioned for light and electron microscopy. Ultrathin sections picked up on copper grids were first stained with uranyl acetate for 10 min, briefly washed, then stained for 3 min in lead citrate and observed under a transmission electron microscope (TEM).

For scanning electron microscopy (SEM) whole heads of air-dried specimens were critical point dried and coated with a 500 Å thick layer of gold/palladium before examination.

3. Results and discussion

Comparisons between the nocturnal and luminescent *Luciola lateralis* and the similarly-sized diurnal but almost non-luminescent *Lucidina biplagiata* show that the eyes of the former are three times as large as those of the latter, but that the latter has the larger antennae. This suggests that the luminescent signals, which *L. lateralis* males and females communicate with, has had an effect on the

evolution of their eyes and that the smaller eye but larger antennae in *L. biplagiata* are a reflection of the fact that this species does not use light signals but pheromones for communication. Regarding the eyes of two species of freshwater limpets of identical sizes, those of the luminescent species *Latia neritoides* also have a larger optical apparatus and retina than the non-luminescent *Ancylus fluviatilis* (Tab. 1).

Obviously the extent to which an eye and its photoreceptors are developed in invertebrates depends on the presence of light and the need to see. In insects the numbers and sizes of the facets of a compound eye can provide some clues on the insect's likely sensitivity to light and, in combination with the inter-ommatidial angle, the eye's resolving power (HORRIDGE 1977). The total number of facets in both *Neoditomya farri* and *Arachnomorpha luminosa* is difficult to determine as the eyes are large and bulging and no single electron micrograph allows one to see and count all the constituent facets. It is obvious, however, that the eyes are large and that a very considerable portion of the head in both species is occupied by them. Approximately 1,000-1,250 ommatidia have been counted in *N. farri* by CLARKE (2002) and a figure of 750 has been given by MEYER-ROCHOW & WALDVOGEL (1979) for *A. luminosa*.

Facet diameters, on the other hand, are easier to measure (Fig. 1A, B) and corner-to-corner distances, herewith referred to as diameters, in *N. farri* ranged from of approx. 23-25 μm , while in *A. luminosa* they averaged 27-28 μm . Inter-ommatidial angles in *A. luminosa* are known to be 5.5° (MEYER-ROCHOW & WALDVOGEL 1979), but appear to be somewhat narrower in *N. farri* (4° are stated by CLARKE 2002). It appears that *A. luminosa* facets are more bulging than those of *N. farri*, although detailed measurements were not taken and regional variations across the ommatidial array of the compound eyes cannot be ruled out. Larger facet diameters, greater

corneal convexity and wider acceptance angles would favour better overall sensitivity to light at the expense of resolving power (HORRIDGE 1977).

So-called corneal nipples, probably acting as anti-reflectants (YAMADA et al. 2011; DEWAN et al. 2012), were present on the facet surfaces in both species (Fig. 2A, B insets), but they seemed smaller, less uniform and regular in *A. luminosa* (Fig. 2B) than those seen in *N. farri* (Fig. 2C), suggesting that perhaps in the former they have become less important as anti-reflectants since precise shapes, height and arrangement of the corneal nipples are determinants of their efficiency (DEWAN et al. 2012).

Interommatidial hairs (Figs 1B, 2A) are very numerous and long in *A. luminosa* reaching up to 30 μm in length, but they are short, sparse and widely-spaced in *N. farri*. The role of interommatidial hairs in insects is far from clear and numerous suggestions as to their function have been advanced summarized by MEYER-ROCHOW (2015). They often occur on the eyes of species that live in dark environments and a tactile function is most likely. Since troglaphiles often exhibit elongated limbs, long appendages and sensory trichia, the interommatidial hairs in *A. luminosa* could be an indication of that species' greater (or longer) adaptation than *N. farri* to a life in confined and very dark places.

Retinula cell screening pigment grains measuring 0.3-0.5 μm in diameter in both species are numerous and known to migrate upon dark/light adaptation away and towards the rhabdom in *A. luminosa* (MEYER-ROCHOW & WALDVOGEL 1979) and almost certainly so also in *N. farri*. The rhabdom, made up by the contributions of 8 ommatidial retinula cells, is generally of a more open kind with less voluminous rhabdomeres in *N. farri* (Fig. 3A) than in *A. luminosa* (Fig. 3B). In the former the six outer rhabdomeres surrounding the two inner ones (the latter in tandem as is characteristics not just

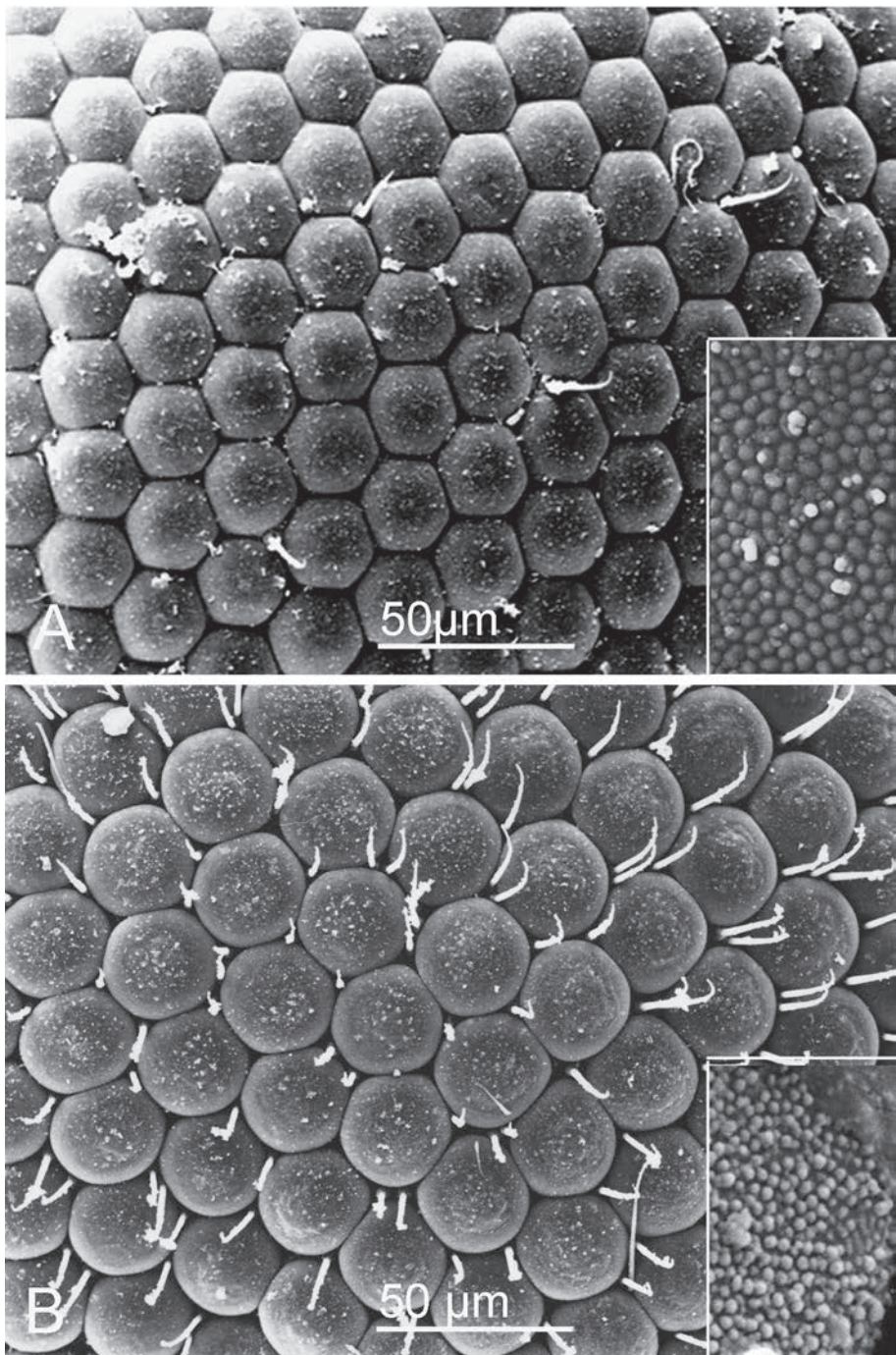


Fig. 1: SEM-micrographs of the eye of *Neoditomyia farri* (A) and *Arachnocampa luminosa* (B). The insets show corneal nipples at high magnification.

Abb. 1: REM-Aufnahmen der Augenoberflächen von *Neoditomyia farri* (A) und *Arachnocampa luminosa* (B). Rechts unten jeweils die Corneanippel bei stärkerer Vergrößerung.

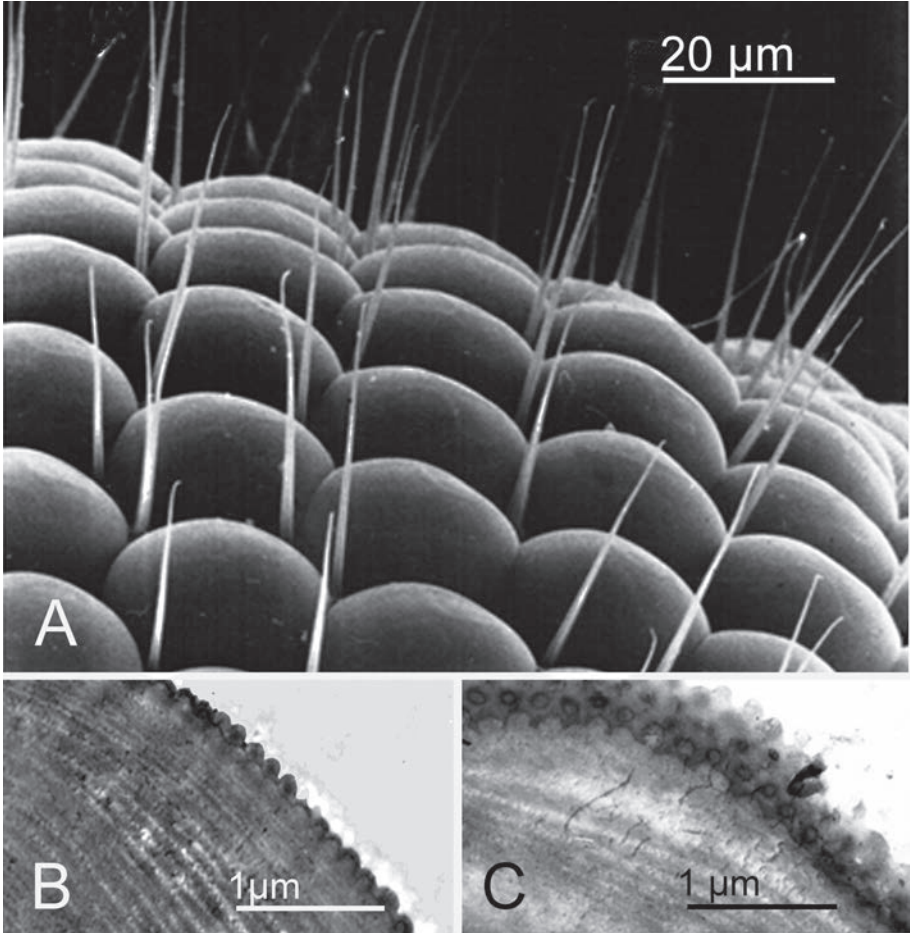


Fig. 2: SEM-micrograph of surface detail with long and protruding interommatidial hairs (A) and longitudinally sectioned corneal nipples (TEM micrograph) (B) in *Arachnocampa luminosa*. Transversely sectioned corneal nipples in *Neoditomyia farri* (TEM micrograph) (C).

Abb. 2: REM-Aufnahme der Augenoberfläche mit „Haaren“ zwischen den Ommatidien (A) und Corneanippel, längs (TEM-Aufnahme) (B) bei *Arachnocampa luminosa*. Corneanippel, transversal bei *Neoditomyia farri* (TEM-Aufnahme) (C).

of nematoceran Diptera, but members of the order Diptera generally) are not fused to the same large extent as in *A. luminosa*. In *A. luminosa*, where over a considerable length from distal to mid-rhabdom level the outer 6 rhabdomeres fuse to form a ring, the organization resembles that of crepuscular or nocturnally active mosquitoes as reported by LAND & HORWOOD (2005); furthermore the two inner rhabdomeres are noticeably more massive in *A. luminosa* than in *N. farri*.

Considerable attention has earlier been paid to the “spongy” and rather loose membranous material occupying the open inter-rhabdomeral space in the centre between the rhabdomeres of only *N. farri* but not *A. luminosa* (Figs. 3A, B) (MEYER-ROCHOW & YANG 2004). One suggestion had been that an incomplete morphogenesis had led to the situation whereby the development of the rhabdom in *N. farri* had not reached the stage in which a truly open

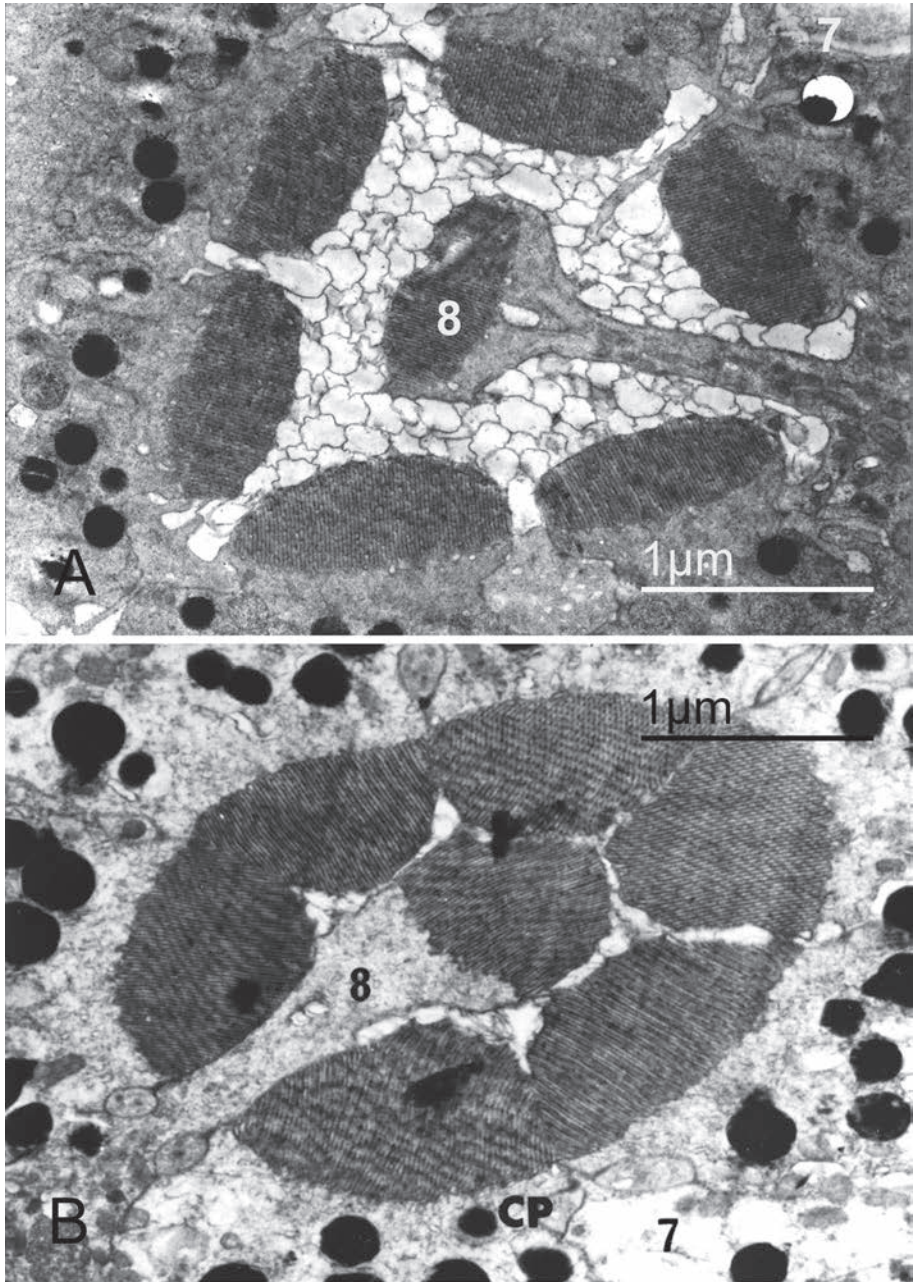


Fig. 3: TEM micrographs of rhabdom cross section in *Neoditomyia farri* (A) and in *Arachnocampa luminosa* (B) at a level where the proximal rhabdomere nr 8, surrounded by the six peripheral rhabdomeres, dominates the centre and the distal retinula cell nr 7 has already acquired a peripheral position. CP indicates the cytoplasmic projection from retinula cell nr 7 to the rhabdom centre.

Abb. 3: TEM-Aufnahmen eines Rhabdoms (quer) bei *Neoditomyia farri* (A) und bei *Arachnocampa luminosa* (B) in einer Ebene, in der das proximale Rhabdomer Nr. 8, umgeben von sechs peripheren Rhabdomeren, im Zentrum liegt und die distale Retinulazelle Nr. 7 schon eine periphere Position einnimmt; zytoplasmatische Verbindung der Retinulazelle Nr. 7 zum Rhabdomzentrum (CP).

rhabdom with rhabdomeres embedded in an extracellular matrix was present and that the loose vacuoles of the spongy material were therefore indicative of a kind of “leftover” of the ontogenetic origin of the inter-rhabdomeral space. In open rhabdoms, well studied in flies, the outer six rhabdomeres are thought to be involved especially in movement perception (SRINIVASAN & GUY 1990) while the inner two rhabdomeres assist in positive phototactic reactions (HU & STARK 1977). Fused rhabdoms in Diptera, however, will have an advantage when it comes to an improvement of general sensitivity, which is why there is reason to believe that *A. luminosa* adults are less active and possibly even shorter-lived than *N. farri* and/or represent the more darkness-loving species of the two. Optokinetic responses with screening pigment granules responding to ambient light intensities by radial movements to or away from the rhabdom edge indicate that these eyes are sensitive to light and in need of protecting their visual membranes from an over-exposure to bright stimuli (AUTRUM 1981).

Microvillus diameters are not different from those of other insect rhabdoms and measure around 60 nm in diameter. Their diameters do not change upon dark/light adaptation, but the amount of the photopigment in their membranes is likely to be negatively affected by an exposure to bright light as has been reported from other insect eyes (MEYER-ROCHOW 1999). 20% wider microvilli reported by MEYER-ROCHOW & WALDVOGEL (1979) for the distalmost rhabdomere of the two central ones in *A. luminosa* were not noticed in *N. farri*.

Based on the evidence gathered from this preliminary investigation we can draw the cautious conclusion that *A. luminosa* adults possess a compound eye that is not only sensitive to the light produced by its larvae (known from studies by MEYER-ROCHOW & EGUCHI 1984), but actually exhibits features that demonstrate high absolute sensitivity

to light and adaptations to a troglomorphic existence. The eye of *N. farri* also shows adaptations to function under very dim conditions, but lacking the dense coverage of interommatidial hairs, possessing more ommatidia, a narrower interommatidial angle and exhibiting a distinctly more “open kind” of rhabdom arrangement, the eye appears to serve an insect species, which has colonized the cave environment more recently than *A. luminosa*. It entered tropical caves possibly because of the abundant prey combined with the stable climatic conditions in them. An obvious effect of the emitted light similar to that reported from photoreceptors of luminescent and non-luminescent limpets and fireflies was not apparent with regard to the morphology and ultrastructure of the eye in the adults of the bioluminescent species *A. luminosa* when compared with that on corresponding structures of the closely related non-luminescent keroplastid *N. farri*. It must be remembered, however, that it is the larvae, which are the brightly luminescent stage in *A. luminosa*: pupae only emit their bluegreen light for a few seconds when touched and the light of the adults is so weak and short-lived that it cannot possibly play a major role in sexual recognition and communication in *A. luminosa*, in which pheromones appear to be involved (BROADLEY 2012). And yet, we cannot totally rule out that the larval light might not have had some minor influence on the organization of the adult glowworm fly’s eye. All we can say at this moment is that there is simply not sufficient information available to give a definitive answer and genetic, electrophysiological, optical, and additional behavioural and ultrastructural studies are being called for. For the time being, the described differences between the eyes of the two keroplastid species all fit the conclusion that cavernicolous individuals of *A. luminosa* possess photoreceptors of poorer resolution but higher absolute sensitivity than those of *N. farri* and that they have not regressed (as

in other cave inhabiting insects) possibly, because there is some light in their cave environment stemming from their luminescent larvae. Photoreception and a peak visual sensitivity in the blue green spectral range (MEYER-ROCHOW & EGUCHI 1984) might even help the adults of *A. luminosa* to keep away from the predaceous larvae, as the latter would not hesitate to consume one of their own adults.

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