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ASPECTS CONCERNING THE STRUCTURE AND FUNCTION OF THE LENTICULUS AND CLEAR SPOT OF CERTAIN ORIBATIDS (ACARI, ORIBATIDA)

by Gerd ALBERTI and Nestor A. FERNANDEZ

LENTICULES TACHES CLAIRES VISION ORIBATES

SUMMAIRE : Les lenticules de Hydrozetes lemnæe et de Scutovertex sculptus ainsi que les taches claires de Oribatella quadricornuta et de Chamobates voigtsi représentent, selon les caractéristiques ultrastructurelles, des organes photosensibles. Les lenticules ont une structure nettement plus compliquée. Les deux structures émanent d’une origine secondaire.

LENTICULI CLEAR SPOTS VISION ORIBATIDS

SUMMARY : Lenticuli of Hydrozetes lemnæe and Scutovertex sculptus, together with clear spots of Oribatella quadricornuta and Chamobates voigtsi, owing to their ultrastructural properties, represent photosensitive organs. Lenticuli clearly have a more complicated structure. Both structures proceed from secondary origin.

INTRODUCTION

Within the Acari eyes are known from Opilioacarida, one species of Holothyrida, some Ixodida, many Actinedida and few Acaridida (VITZTHUM, 1943; KRANTZ, 1978; HAMMEN, 1980, 1983). Oribatida usually are devoid of eyes. However, GRANDJEAN (1928) described in Heterochthonius gibbus, representative of the early derived Heterochthoniidae, three eyes located on the prodorsum. This observation seemed to him such extraordinary that he devoted a special publication, his first in acarology (TRAVÉ and VACHON, 1975), to this discovery. In a later paper GRANDJEAN (1961) discussed also other structures which were regarded as light sensitive regions by previous authors. Since OUDEMANS (1913, 1916) a peculiar subspherical part of the cuticle located at the anterior margin of the notogaster of certain oribatids has been considered to be involved in light reception. This structure was first observed by PIERSIG (1895) as reported by OUDEMANS (1916), who published the detailed figure of the structure drawn by PIERSIG from a Hydrozetes sp. (GRANDJEAN, 1961). GRANDJEAN (1961) termed this very distinct region, which is also observable in some other species, “lenticule”. However, in contrast to earlier authors such as PIERSIG (1895), OUDEMANS (1913, 1916), VITZTHUM...
(1935, 1943), who were convinced that this region represents an eye, Grandjean (1961) expressed his opinion with caution. He recognized that the most important and outstanding characteristic of the lenticulus is its "origine secondaire". It is a structure apparently not found in "lower oribatids". If it really would represent an eye, the position at the anterior margin of the notogaster, or opisthosoma respectively (Grandjean, 1969), would in fact be extraordinary compared with the position of eyes in Heterochthonius gibbus and other Acari. In none of the Chelicerata opisthosomal eyes occur, though there may be photosensitive neurons (eg. in scorpions; Yoshida, 1979).

Besides the distinct lenticuli there are many oribatids which exhibit a clear spot (tache claire; Grandjean, 1961) in the same position (Fig. 1). Again it was Oudemans (1913, 1916) who suggested a concrete function to all these specializations. He thought that these transparent regions (lenticuli as well as clear spots) would permit the transmission of light to the brain which is located exactly under this spot.

Remarkably only one paper (Tarman, 1961) has tried to examine this interesting region histologically. However, due to the restrictions of the light microscope, the informations on the lenticulus of Hydrozetes lacustris and clear spots of Ceratozetes gracilis and Galumna nervosus are only limited. Tarman (1961) recognized receptor cells and the paired nature of the cellular components as was indicated already by the figure of Piersig (published by Oudemans, 1916).

As we have shown by electron microscopy the interpretation of the lenticulus of Hydrozetes as an eye is correct (Alberti and Fernandez, 1988). In the present study we are able to present some preliminary informations on the lenticulus of another species and to compare these organs with the clear spots.

**Material and methods**

Specimens of Hydrozetes lemnae (Coggi, 1899) (Hydrozetidae), Scutovertex sculptus Michael, 1879 (Scutoverticidae), Chamobates voigtsi (Oudemans, 1902) (Chamobatidae) and Oribatella quadricornuta (Michael, 1880) (Oribatellidae) were collected near Heidelberg and prepared as follows:

Scanning electron microscopy: Following fixation in 70% ethanol, specimens were dehydrated with graded ethanol and finally air dried. In some specimens the cerotegment was removed with fine needles after immersing the animals in chloroform before dehydration. The specimens were mounted on aluminium stubs and sputtered with gold.

Transmission electron microscopy: Specimens were cut into halves with a razor blade and fixed in ice-cold glutaraldehyde (3.5% in 0.1 ml phosphate buffer at pH 7.4). Postfixation in 2% OsO₄ occurred after rinsing in the buffer solution. The specimens were dehydrated with graded ethanol and embedded in Araldite. Ultrathin sections were stained with uranyl acetate and lead citrate. Electron microscope: Philips SEM 505.

**Results and discussion**

The lenticulus of Hydrozetes lemnae is composed of the following components: cuticular cornea (lens), epidermal layer, two cells of the fat body, two lamellated bodies, glial cells and two pigment cells. The lamellated bodies are considered to represent the photosensitive components. They are connected via two bundles of dendritic fibres to the brain where two large perikarya are located. From each perikaryon an axon arises which traverses through the brain terminating in a neuropile close to the corresponding perikaryon of the opposite side. Thus a simple chiasma opticum comprising only two axons is established. The components: lamellated body, bundle of dendritic fibres, perikaryon and axon all belong to one photoneuron, two of which are confined to the lenticulus, which thus is basically a paired structure. The photoneurons are part of the central nervous system. There are no specialized rhabdomeric receptor cells (Figs. 2, 3) (for details see Alberti and Fernandez, 1988).

Our preliminary observations on Scutovertex sculptus, a species with lenticulus (Fig. 1 a), have shown a similar arrangement. All components are
Fig. 1: a) *Scutovertex sculptus* with lenticulus (arrow). Scale bar: 250 µm. — b) *Oribatella quadricornuta* with clear spot (arrow). Scale bar: 250 µm.
Fig. 2: *Hydrozetes lemnae*: Composed figure of parasagittal sections through region of lenticulus. Note remarkable extension of lamellated body relative to central nervous system.

Abbr.: CNS = central nervous system, CO = cuticular cornea, DF = dendritic fibres, ES = endostemite, FB = Fat body cell, LB = lamellated body, PC = pigment cell, PN = perikaryon of photoneuron.
Fig. 3: a) *Hydrozetes lemnar*: Horizontal section through lenticulus showing two lamellated bodies (LB), pigment cells (PC) and fat body cells (FB). Note narrow intercellular cleft separating both fat body cells medially (arrow). Scale bar: 10 µm.

b) *Chamobates voigtsi*: Transverse section through lamellated body, which is closely apposed to the perikarya of the central nervous system (CNS). Scale bar: 5 µm.
present. Most important is apparently the occurrence of elongated dendritic fibres which connect the lamellated bodies located under the transparent cuticle with the perikarya in the brain, and of specialized pigment cells.

In Oribatella quadricornuta and Chamobates voigtsi, which possess clear spots, the lamellated bodies are also present and fine structurally very similar to those of the lenticuli. However, they are not close to the cuticle but are situated at the dorsolateral surface of the brain. There are no elongated dendrites. Furthermore, we were not able to detect pigment cells (Fig. 3 b).

Thus in all the four species investigated the structures under consideration represent basically paired organs regarding the cellular elements covered by an unpaired region of modified cuticle.

Our results evidently have demonstrated that lenticuli and clear spots are involved in light reception. In both structures a specialized receptor region (lamellated body) and a cuticular modification is present which at least in the lenticuli may serve as a lens. The lamellated bodies of Hydrozetes and Scutovertex moreover are provided with screening pigment cells. At least the lenticuli are complex enough to be referred to as eyes. Both organs are remarkable since they represent light sensitive organs which are apparently unique within the Arthropoda (compare Eakin, 1972; Paulus, 1979). They are thus deviating also from all eyes described from other Acari until now (Balashov, 1983; Mills, 1974; Mischke, 1981; Wachmann, 1975; Wachmann et al., 1974). There are no rhabdomeres (representing microvilli) instead there are lamellae. The perikarya of the receptor cells are located within the brain and not close to the receptor poles as in other arthropod eyes. Obviously the receptor cells are modified neurons of the central nervous system.

The peculiar fine structure of these organs, which are only found in "higher oribatids" apparently, confirm the suggestion of Grandjean (1961) that these organs have developed secondarily within the oribatids. Moss mites apparently have reduced their primary eyes with their primary receptor cells with the exception of only few taxa such as Heterochthonius gibbus (and few related species: see Balogh and Mahunka, 1983). These few species obviously represent the more plesiomorphic condition. In some of the Circumdehiscentiae (higher oribatids) new light sensitive organs of different complexity have been developed. Presently reasons for such a secondary development are a matter of speculation. Hydrozetidae have invaded an unusual habitat (fresh water; see Fernandez and Athias-Binche, 1986) when compared with most other oribatids, which are usually litter inhabiting "moss" mites. But lenticuli or clear spots are also found in species living in "normal" surroundings. The eyeless oribatids are also sensitive to light depending on their "sensibilité générale" (Grandjean, 1961). Probably the development of clear spots and especially lenticuli enabled the mites to react faster. At least the lenticuli should allow to recognize the direction of the incident light (screening pigments). Since exposition to light likely is combined with exposition to predators and/or desiccation the ability to react faster and directionally would reasonably be an advantage. However, the questions remain, why did reduction of primary eyes occur and why are so many oribatids apparently without such sense organs (including numerous species of "higher" oribatids). Likely the answer is related to changing selective pressures, e.g. by predators. Oribatida obviously represent a very old taxon (Norton et al., 1988). The ancestral forms were perhaps able to avoid these pressures by having invaded the soil habitat. With the increase of predators in the soil, oribatids had to develop new adaptations, one of which might have been the development of an improved light sensitive system.

Development of new light sensitive organs is also apparent in other Acari. In certain ticks lateral photoreceptors independent from eyes have been described (Binnington, 1972) and in the gamasid mite Ophionyssus natrixis light sensitive, pigmented spots are found at the pulvilli of the first pair of legs (Evans et al., 1961).

In any case, the structures described here from oribatids are certainly derived characteristics which thus are of considerable taxonomic interest. Further investigations should try to demonstrate whether all these organs are homologous and may represent
synapomorphies or they have developed by convergence. The figure by TARMAN (1961) depicting the clear spot of Galumna nervosus suggests a different conformation from that found in the species investigated in the present study. On the other hand, it might be, that the receptor cells (representing central neurons!) have evolved from "old" components of the optic system, inherited from the ancestral forms, which have been "activated" probably several times independently.

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