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Fine structure of the primary eyes in *Heterochthonius gibbus* (Oribatida, Heterochthoniidae) with some general remarks on photosensitive structures in oribatid and other actinotrichid mites.

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Abstract

Heterochthonius gibbus is an oribatid mite which has three eyes located on the prodorsum: an externally unpaired median eye, and a pair of posterolateral eyes. The fine structure of these eyes shows that they consist of a few retinula cells bearing rhabdomeric microvilli. The median eye has two small retinas that are inverted with respect to the cuticular cornea (lens) and each lateral eye has a single retina that is everted. In both types, a thin corneagen layer is located underneath the cornea. The receptor cells are partly surrounded by pigment cells, which are derived from epidermal cells. The location and structure of the eyes, representing typical arachnid ocelli, suggest that they are plesiomorphic structures in contrast to the clear spots and lenticuli occurring on the notogaster of some so-called higher Oribatida (Brachypylina). A scenario which could describe the evolution of photosensitivity or photosensitive structures in oribatid mites is presented. Since clear spots and the spectacular lenticuli evidently are apomorphic features, their potential value for phylogenetic systematics is stressed.

Keywords: evolution, lenticulus, naso, secondary eyes, ultrastructure

1. Introduction

Oribatida is a rather large mite taxon comprising more than 10,000 named species (Oribatida in its traditional sense, i.e., Astigmata not included, see Schatz et al. 2011), which mostly live in the soil-litter system playing an important role as decomposers (e.g., Schuster 1956, Dunger 1983, Norton 1986, 1990, Beck 1993, Alberti et al. 1996, Behan-Pelletier & Kanashiro 2010). Exceptions are arboreal and few aquatic oribatids (Norton & Behan-Pelletier 2009).

Reports on eyes in oribatid mites are rather scarce, but early details were included in Vitzthum's (1940/43) rather complete overview of light receptor organs in Acari. In particular, he wrote of clear spots and lenticuli occurring in the highly derived oribatid taxon Brachypylina, which are structures occurring dorsally just behind the dorsosejugal furrrow. The clear spot is simply a region which is not as dark as other parts of the cuticle. It is, as Vitzthum (1940/43) stated, a region where the cuticle is more transparent allowing access of light to the underlying synganglion. The neurons constituting the synganglion are thought to be light-sensitive. The lenticulus is a more or less distinct lens-like elevation found in the same region in certain oribatid mites and it was thought that this structure would improve photoreception.

The main problem of interpreting these structures is their peculiar location in the mite body plan (Grandjean 1961). They are located behind the dorsosejugal furrow, which coincides with the anterior border of the opisthosoma in the interpretation of the actinotrichid body plan that is most widely accepted (e.g., Grandjean 1969, Coineau 1974, Hammen 1989, but see also Weigmann 2001). By contrast, well-formed eyes in other actinotrichid mites are restricted to the prodorsum, a region located in front of the dorsosejugal furrow (Alberti & Coons 1999), hence, Grandjean (1961) concluded that the lenticulus is a secondary structure.

Alberti & Fernandez (1988, 1990) studied the fine structure of the lenticulus of the aquatic species *Hydrozetes lemnae* in detail. This structure was well known already from light microscopic investigations by Richard Piersig who provided an excellent description and figure that was published by Oudemans (1916). After this convincing description, it is hard to understand why the role of this structure as an eye was apparently doubted, but perhaps it was due to the strange location (Grandjean 1961). Thus in the very comprehensive overview on Acari given by Moritz (1993), the lenticulus and the clear spot were not mentioned at all. The studies by Alberti & Fernandez (1988, 1990) have changed this situation and the function of these structures as photoreceptors is generally accepted (see Evans 1992, Alberti & Coons 1999, Krantz 2009, Norton & Behan-Pelletier 2009).

These fine-structural studies have shown the very unusual structure of the lenticulus being composed of two receptor cells with long dorsally directed dendrites ending with lamellar bodies (no rhabdoms) underneath a dome-shaped cornea (lens). The perikarya of these cells are located in the synganglion (not in the periphery as usual in arthropod eyes). The lamellar bodies are bordered by two pigment cells. In investigated species with a clear spot, lamellated bodies are directly and laterally attached to the synganglion. Based on these peculiarities (location posterior of the dorsosejugal furrow, lamellar bodies instead of rhabdoms, perikarya of receptor cells located in the synganglion) Alberti & Fernandez (1988, 1990) concluded that these structures represent secondarily evolved photoreceptors. Thus the interpretations of Piersig and Oudemans (Oudemans 1916) and Vitzthum (1940/43) about their function and the statement of Grandjean (1961) about their secondary nature were corroborated.

However, the lenticuli and clear spots are not the only photoreceptor organs in oribatid mites. In 1927 Grandjean collected a number of oribatid mites belonging to the species *Heterochthonius gibbus* (Berlese, 1910) which he found to be 'diffèrent par un caractère insolite dont il n'existe pas d'autre exemple, à ma connaissance, chez les Oribatidés: ils ont, en effet, trois yeux bien visibles, dont l'un est impair et frontal, tandis que les deux autres, symétriques, sont placés près des pseudostigmates' (pseudostigma = bothridium of the bothridial seta or trichobothrium). In fact, he was apparently so impressed by this finding that he published it as his first paper on Acari (Grandjean 1928).

In the following years he and other authors found in certain early derivative oribatid taxa (e.g. some Palaeosomata, Enarthronota) an anterior, unpaired eye located on the underside of a short protuberance of the prodorsum called a 'naso' in the acarological literature (Grandjean 1958, Moritz 1993, Norton & Behan-Pelletier 2009), which was considered 'probably of acronal origin' (Hammen 1980). Grandjean's (1958) detailed account on this structure includes the observation that the unpaired eye underneath the naso in fact is a paired structure, which became fused in certain species. In comparing these eyes with those of other actinotrichid mites, i. e. certain Endeostigmata and many Prostigmata, he stated that this 'naso eye' and two pairs of lateral eyes are frequently found in these groups. He thus concluded that (at least) 3 pairs of eyes is the plesiomorphic number in Acari.

All prodorsal eyes have been lost in oribatid mites, with few exceptions. Some oribatid mites retained the naso eye(s) only, e.g. certain Palaeosomata, some Brachychthoniidae (Grandjean 1958). A peculiar brachychthoniid mite, *Eobrachychthonius* sp., has in addition to a paired anterior naso eye a pair of lateral eyes close to the bothridia. All the eyes of that species are devoid of pigment (Travé 1968). In *Heterochthonius gibbus*, as mentioned already, and another species, *H. caucasicus* Krivolutsky, 1977 a pair of lateral eyes and an unpaired anterior eye located on the prodorsum are present (Grandjean 1928, Ryabinin & Krivolutsky 1977). Another heterochthoniid species, *Ovochthonius rossicus* Ryabinin, 1977, has instead of one anterior eye two eyes in a similar position, but lacks the lateral eyes (Ryabinin & Krivolutsky 1977). Finally, a circular spot in the middle of the prodorsum was observed in *Galapagacarus schatzi* Balogh, 1985 (Hermanniidae).

Since the anterior eye of *Heterochthonius gibbus* is located dorsally on the prodorsum, Grandjean (1958) apparently concluded that this eye 'diffère totalement' from the naso eye. He thought that the latter was completely lost in *Heterochthonius* and that the anterior eye in this species is a fusion product of the anterior pair of lateral eyes found in Endeostigmata and Prostigmata. He cautiously stated that 'ces homologies ne sont pas sûres' and further studies are needed.

Coineau (1970) suggested that the naso eye might be homologous with the median eyes of other Arachnida and this view was shared by Wachmann et al. (1974), Mischke (1981), Alberti & Coons (1999) and Haupt & Coineau (2002), and is further supported in the present study. We hence term the anterior eye (naso eye) of *H. gibbus* 'median eye' in the following text, in accordance with these authors.

The present study thus aims to clarify the fine structure of the prodorsal eyes of *H. gibbus.* In this way we hope to understand the peculiar anterior eye of *H. gibbus* and its possible relationship to the median eye of other early derivative oribatid mites. By comparing these findings with the structure of the lenticulus and clear spot, we can further clarify their status as secondarily evolved, apomorphic structures.

2. Materials and methods

Heterochthonius gibbus (Berlese, 1910) seems to be rather rare. Our first specimens were obtained by the second author mostly by chance while collecting in summer 1994 near Grindelwald (Switzerland), a second trip was made to the same location a few days afterwards, where substrate was collected close to and from a rotten tree-stump at about 1500 m above s.l. The samples were brought to the Zoological Institute, University of Heidelberg (Germany) (the former working place of G.A.), and about 20 specimens were extracted using Berlese-funnels. They were further processed as follows: Living specimens were observed under an Olympus stereomicroscope connected with a Sony video-camera at the University of Vechta (Germany) (LM).

Subsequently, 10 specimens were transferred to 70% ethanol to be used for scanning electron microscopy (SEM). These were dehydrated using graded ethanols, transferred into dichlor-difluormethan, critical point dried using liquid CO_2 as final medium. The specimens were mounted on Al-stubs, coated with gold and examined with a Philips SEM 505.

For transmission electron microscopy (TEM), 10 specimens were transversely cut into halves and fixed in ice-cold 3.5% glutaraldehyde (pH 7.4, phosphate buffer 0.1M) for two hours. After rinsing with buffer solution, the tissues were postfixed with 2% OsO_4 aqueous solution. After rinsing again, specimens were dehydrated with graded ethanols and embedded in Araldite using propylenoxide as intermedium. Transverse, sagittal and horizontal sections of three specimens were made with a Leica UCT using a Diatome diamond knife, then stained with uranylacetate and lead citrate and studied with a JEOL JEM-1011 TEM, these procedures were done at the Zoological Institute and Museum in Greifswald.

3. Results

3.1. External aspects

In *Heterochthonius gibbus* the gnathosoma is dorsally overhung by a projection of the prodorsum, the rostral tectum, forming a (secondary) camerostome, a situation called stegasimy (Grandjean 1932, 1954a, Weigmann 2006, Norton & Behan-Pelletier 2009, Alberti et al. 2011).

The three eyes of *H. gibbus* are located on the prodorsum, one anterior median eye and two lateral eyes close to the dorsosejugal furrow and ventral to bothridial setae *bo*. In living animals the eyes are distinct because of a dark pigmentation which lies under a transparent cuticular cornea (lens) (Fig. 1). Under the SEM the eyes are indicated by their lens-like elevated cuticles (Fig. 2).

The median eye is located slightly anterior of an imaginary line connecting setal pair *le.* Its cornea is a simple dome-shaped elevation, with a small posterior indentation (Fig. 2b, arrowhead). In front of the anterior eye a pair of tiny setae ro is present almost immediately at the anterior border of the rostral tectum.

The paired lateral eyes have corneae with rather sharp edges at their dorsal, ventral and posterior borders (Figs 2c, 6a, b).Two tiny exobothridial setae (exa, exp) are situated in front of each of these lateral eyes (Fig. 2b, c).

Fig. 1 LM-figure of live specimen of *Heterochthonius gibbus*. Arrows point to pigmented eyes.

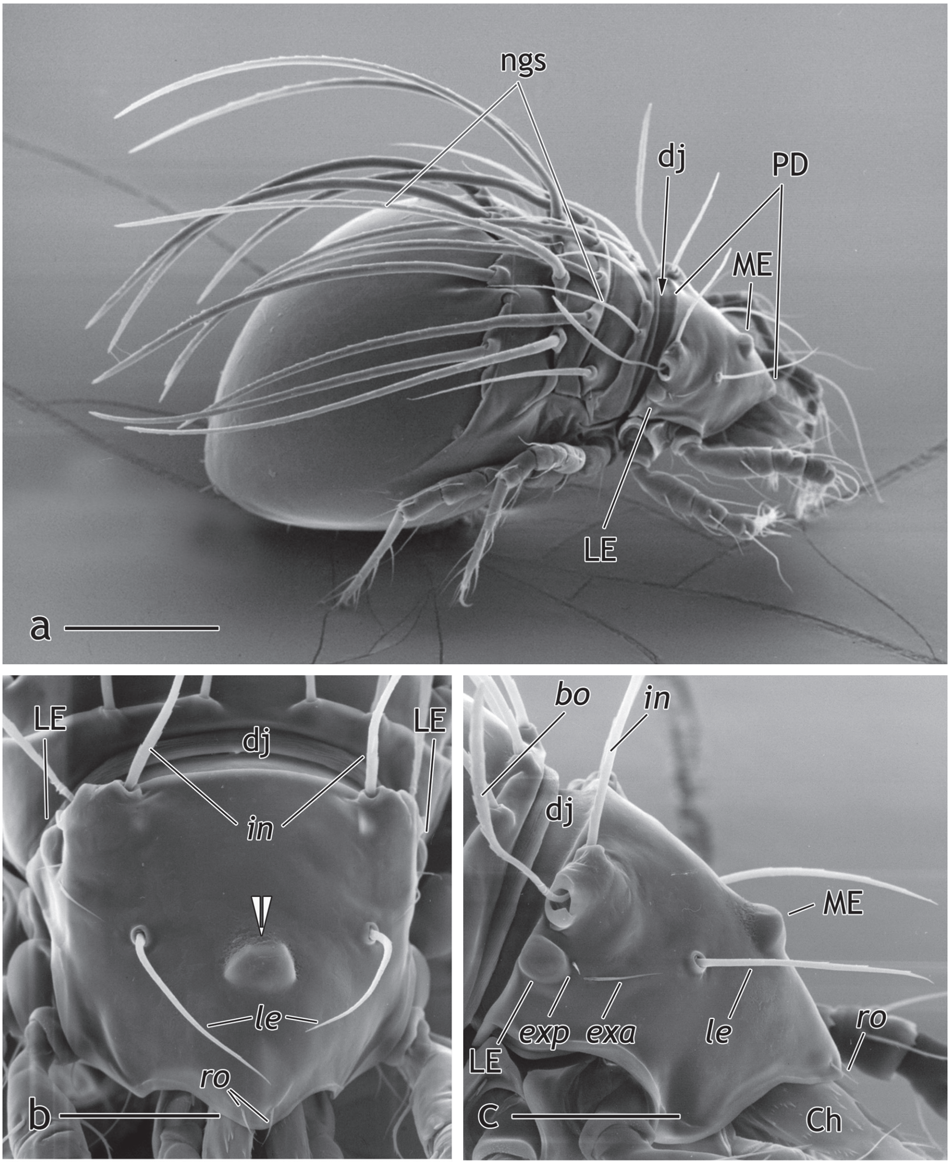


Fig. 2 SEM-figures of *Heterochthonius gibbus*. **a**: Lateral view. Note eyes located on prodorsum which is projecting forming a rostral tectum. The notogaster is subdivided by several transverse scissures (typical for Enarthronota). Note position of lateral eyes immediately in front of dorsosejugal furrow. The long notogastral setae may be erected upon disturbance. Scale bar: 100 µm. **b**: Dorsofrontal view on prodorsum. Arrowhead points to small posterior indentation of cornea of anterior eye. Scale bar: 50 µm. **c**: Lateral view of prodorsum. Note tiny rostral and exobothridial setae. Scale bar: 50 µm.

Abbr.: bo - bothridial seta, Ch - chelicera, dj - dorsosejugal furrow, exa - anterior exobothridial seta, exp - posterior exobothridial seta, in - interlamellar setae, LE - lateral eye, le - lamellar setae, ME - median eye, ngs - notogastral setae, ro - rostral setae.

3.2. Internal aspects

Median eye: The sections reveal that the eye is located in the rostral tectum (Fig. 3a). The uniconvex cornea is a simple thickening of the cuticle of the rostrum (the dorsal layer of the rostral tectum) which is multilayered (Figs 3a, 4a). It is underlain by a very thin corneagen layer, which is continuous with the epidermis (Fig. 4a). Immediately underneath this layer, the retinula (receptor) cells are located with their cell bodies containing nuclei with rather electron-lucent nucleoplasm (Figs 4a, b; 5b). These cell bodies are rather flat and bear densely interdigitating rhabdomeric microvilli which are arranged horizontally, i.e. parallel to the cuticle, and thus at right angle to the incident light. The cell bodies of the retinula cells contain large and elongated crista-mitochondria and many vesicles (not shown). They are apically connected by zonula adhaerens-like cell junctions (Fig. 4c). Underneath the rhabdomeric microvilli several pigment cells form a cup (Figs 3a, b; 4a–c; 5). These cells are filled with dense granules, which frequently break off during sectioning and thus may be rather solid at least after fixation. The nuclei of the pigment cells are squeezed between the pigment granules and thus show a deformed outline (Figs 4c, 5c). They appear rather electron-dense, containing much heterochromatin. The pigment cells are modified epidermal cells since they directly border the ventral cuticle of the rostral tectum, i.e. the rostrophragma (Figs 4b, c; 5c). The cuticle of the rostrophragma underneath the posterior parts of the eye and further back to the base of the tectum is much thinner than that of the rostrum, but its thickness increases anteriorly (Figs 3a, 4b). The anterior and lateral borders of the rostral tectum are made of cuticle only and thus represent a conspicuous rostral limb (Fig. 3a, terms acc. to Hammen 1989, Alberti et al. 2011).

Cross and horizontal (frontal) sections reveal that two rhabdoms are formed which are medially separated, thus indicating a fundamentally paired nature of the median eye (Fig. 5). However, externally this is indicated only by the slight posterior indentation of the cornea, mentioned above (Fig. 2b).

The arrangement of components indicates that the median eye contains an inverted retina, the receptor poles (rhabdoms) pointing away from the cornea.

We were not able to determine the exact numbers and arrangement of cells forming the median eye. Nuclei could rarely be identified with certainty as belonging to the retinula cells, these are located underneath the cornea and corneagen layer as described above. We found a tiny median nerve running back from the median eye which consisted of four (or five) axons (Fig. 7a, b). Hence it is likely that four (or five) retinula cells are involved in forming the median eye and consequently each rhabdom may be formed by at least two cells. Nuclei of pigment cells were more frequently seen.

A thin fold of the integument projects from the posterior of the camerostome and parallels the region of the rostral tectum in which the anterior eye is located. This fold thus forms a shallow, frontal cavity ventral to the median eye (Figs 3a; 4a, b). This arrangement may protect the eye from mechanical stresses caused by movements of the gnathosoma, in particular the chelicerae.

The rostral setae are each connected to two receptor cells terminating with tubular bodies indicating their mechanosensitivity (Fig. 7c).

Lateral eyes: The lateral eyes are smaller than the anterior eye and have a more pronounced cornea, as indicated above (Figs 2c; 6a, b). Each lateral eye also forms a uniconvex cuticular lens underlain by a thin corneagen layer. The rhabdoms of the retinula cells lie immediately below this layer. Each eye contains only one rhabdom. The rhabdomeric microvilli again are oriented parallel to the cuticle and thus at right angle towards the incident light. A cup formed by pigment cells is also conspicuous. All these components are rather similar to those

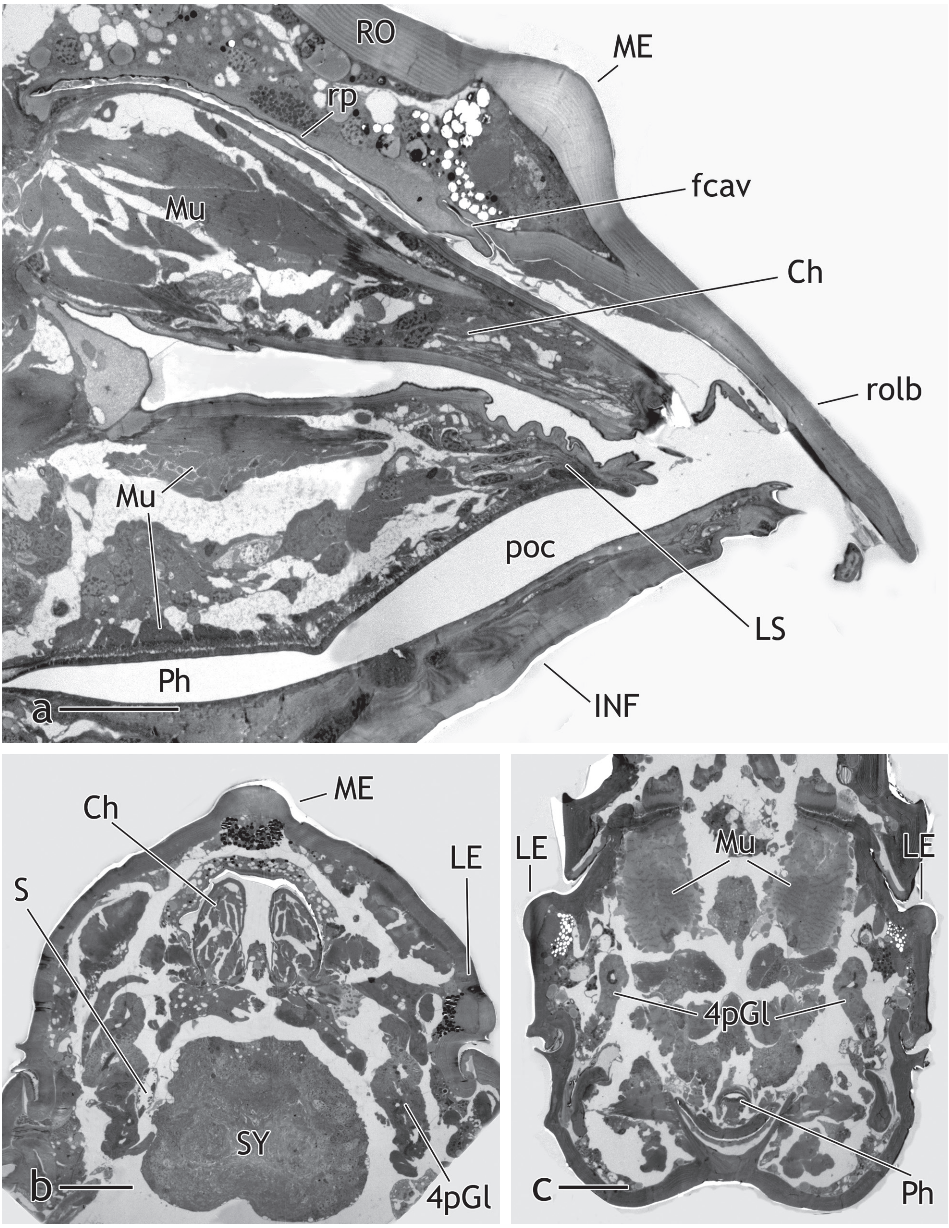


Fig. 3 TEM-figures of *Heterochthonius gibbus*, overviews. **a**: Sagittal section through gnathosoma and rostral tectum. Scale bar: 10 µm. **b**: Slightly oblique horizotal (frontal) section slightly above frontal cavity showing median eye and one lateral eye. Scale bar: 20 µm. **c**: Transverse section through both lateral eyes and posterior part of pharynx. Scale bar: 20 µm.

Abbr.: Ch - chelicera, fcav - frontal cavity, INF - infracapitulum, LS - labrum, ME - median eye, Mu - muscles, 4pGL - fourth podocephalic gland (coxal gland), Ph - pharynx, rolb - rostral limb, rp - rostrophragma, s - sacculus of coxal gland, SY - synganglion.

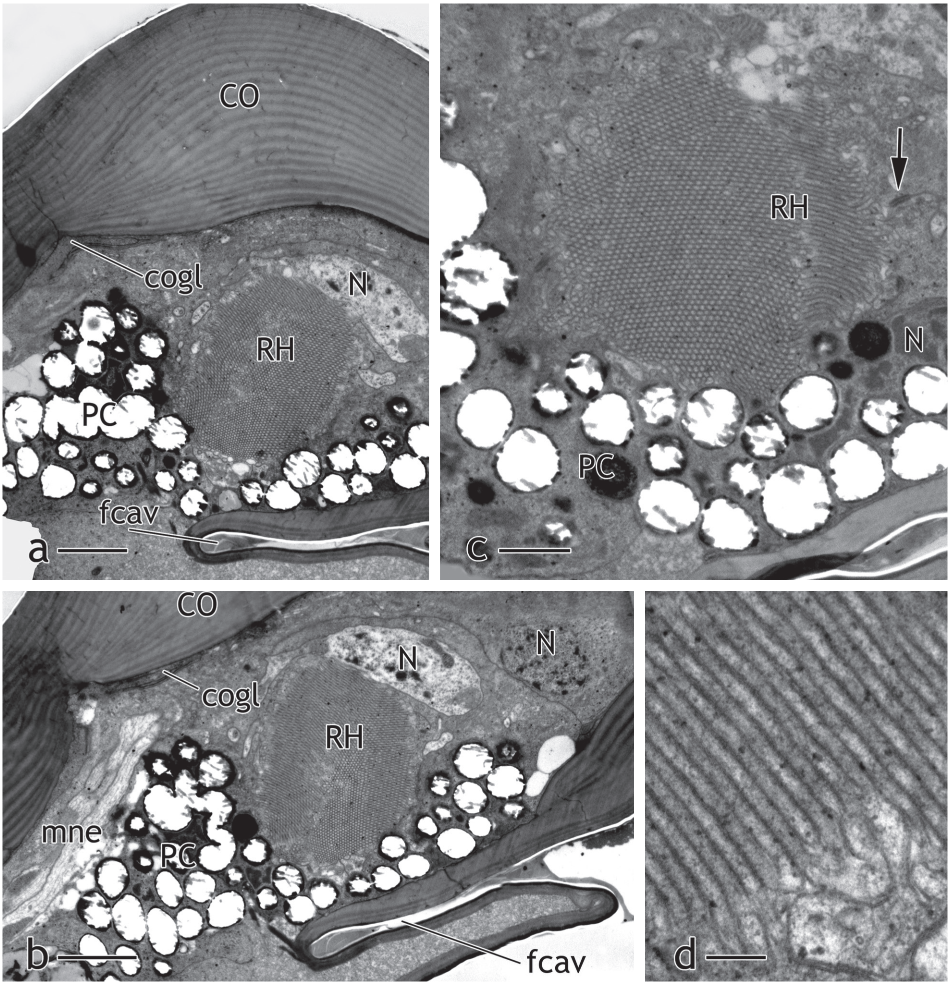
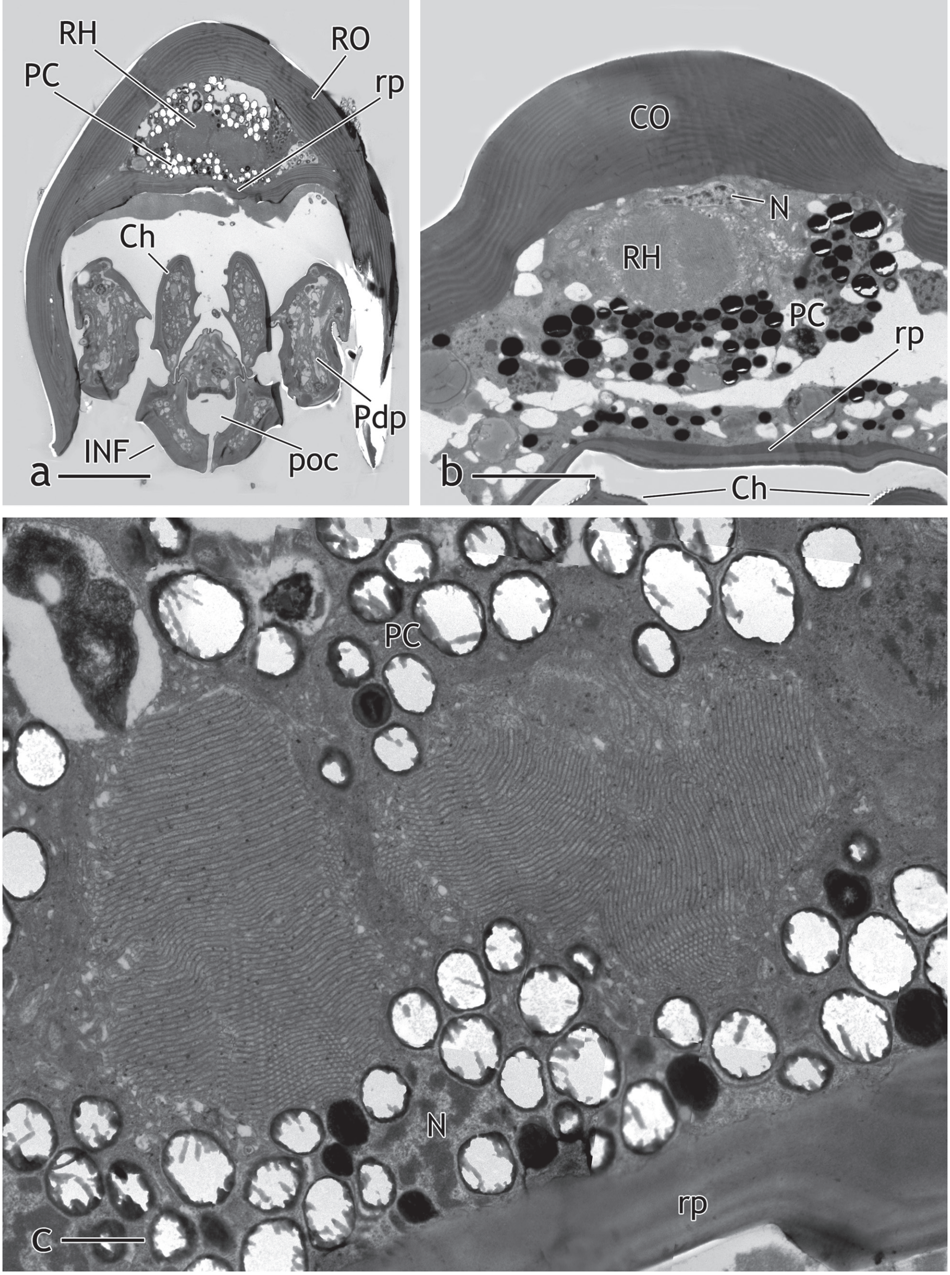


Fig. 4 TEM-figures of sagittal sections through median eye of *Heterochthonius gibbus*. **a**: Parasagittal section showing rhabdom partly covered ventrally by pigment cells (pigment granules mostly broken away during sectioning). A prominent uniconvex cuticular cornea (lens) is obvious. It is underlain by a very inconspicuous thin corneagen layer. Note cell body of one retinula cell containing nucleus located between rhabdom and cornea. Scale bar: 2 µm. **b**: Similar aspect showing median eye nerve and frontal cavity. Scale bar: 2 µm. **c**: Detail of rhabdom showing rhabdomeric microvilli close together (closed rhabdom). The microvilli, though arranged in different directions are mostly oriented parallel to the cornea, thus at right angle to the incident light. Scale bar: 1 µm. **d**: Detail of rhabdomeric microvilli. Scale bar: 0.2 µm.

Abbr.: CO - cornea, cogl - corneagen layer, fcav, frontal cavity, mne - median eye nerve, N - nucleus, PC - pigment cell, RH - rhabdom.

Fig. 5 (page 399) TEM-figures through gnathosoma and rostral tectum of *Heterochthonius gibbus* (**a**, **c** = cross sections, **b** = horizontal section). **a**: Overview slightly posterior of frontal cavity showing location of median eye and its composition of two subunits. Scale bar: 10 µm. **b**: The paired nature of the median eye is not as evident as in Fig. 5a, c but again a nuclear region of a retinula cell is visible located between rhabdom and cornea. Note thin, unmodified...



...rostrophragma. Scale bar: 5 µm. **c**: The paired nature of the median eye is evident from this figure. Note electron-dense nucleus of pigment cell squeezed between pigment granules. Scale bar: 1 µm.

Abbr.: Ch - chelicera, INF - infracapitulum, N - nucleus, PC - pigment cell, poc - preoral cavity, Pdp - pedipalp, RH - rhabdom, RO - rostrum, rp - rostrophragma.

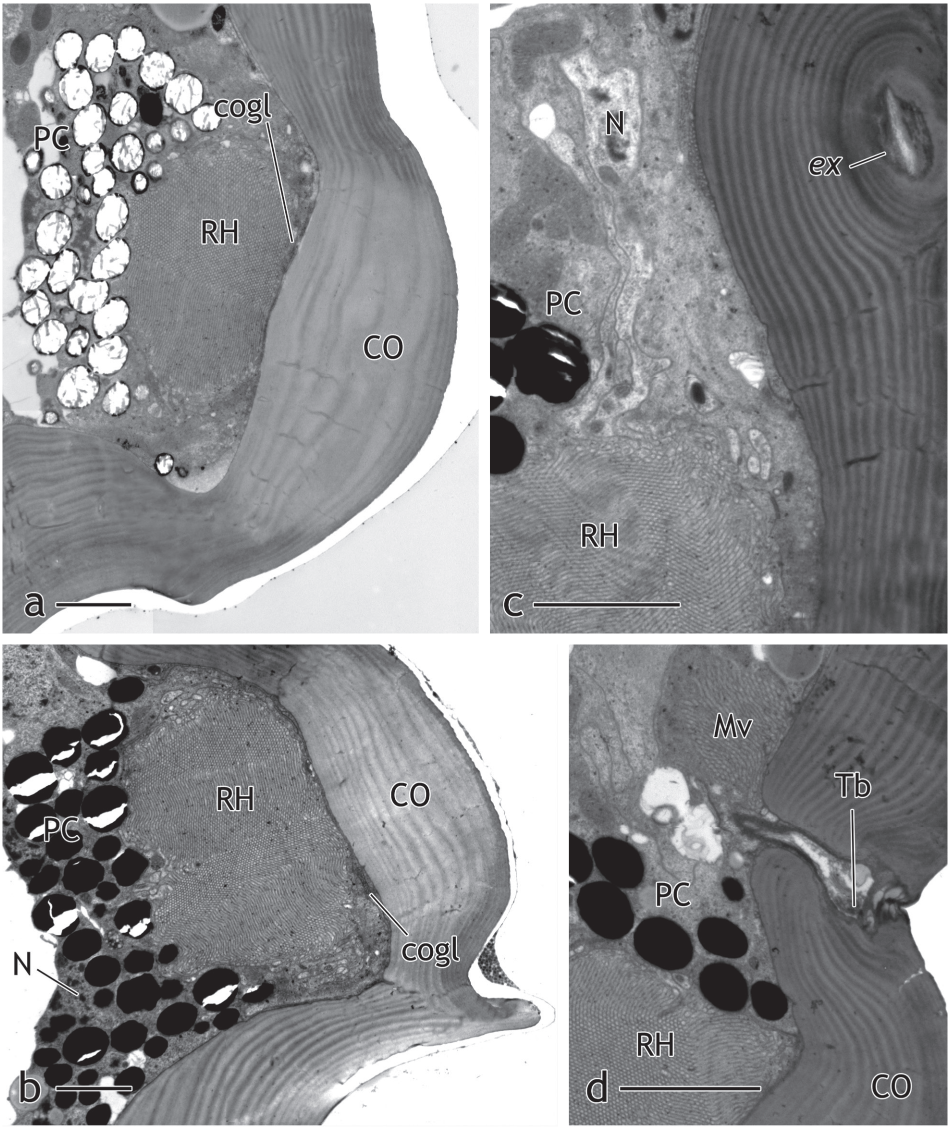


Fig. 6 TEM-figures showing details of lateral eyes of *Heterochthonius gibbus* (**a** = cross section, **b–d** = horizontal sections). **a**: The lateral eye is largely similar to the median eye, but no cell bodies with nuclei are located between rhabdom and cornea. Scale bar: 2 µm. **b**: Rhabdomeric microvilli again are mostly oriented parallel to the cornea. Note sharp and pronounced posterior border of the cornea. Scale bar: 2 µm. **c**: Anterior part of the eye with slender processes which connect cell body containing the nucleus of a retinula cell with the rhabdom. The socket of one of the exobothridial setae (exa) is visible. Scale bar: 2 µm. **d**: Anterior part of lateral eye with the nearby base of an exobothridial seta (exp) showing tubular body. The field of microvilli belongs to a sheath cell of this seta. Scale bar: 2 µm.

Abbr.: CO - cornea, cogl - corneagen layer, ex - exobothridial seta, Mv - microvilli, N - nucleus, PC - pigment cell, RH - rhabdom, Tb - tubular body.

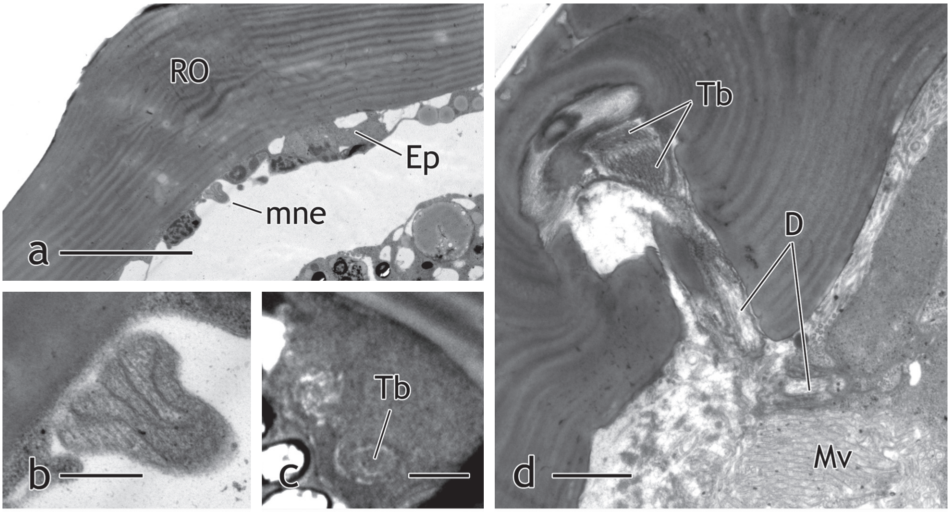


Fig. 7 TEM-figures showing details from prodorsum of *Heterochthonius gibbus* (**a**, **b** = horizontal sections, **c**, **d** = cross sections). **a**: Shortly behind the median eye, its small nerve is visible (arrow). Scale bar: 5 µm. **b**: Same nerve and section enlarged showing 4 (or 5) axons. Scale bar: 0.5 µm. **c**: Two dendrites belonging to one rostral seta. One dendrite shows a tubular body surrounded by a sheath cell with hemicircular thickenings typical of mechanosensitive setae. Scale bar: 1 µm. **d**: Innervation of an exobothridal seta by two dendrites ending with tubular bodies (compare Fig. 6c, d). Scale bar: 1 µm.

Abbr.: D - dendrite, Ep - epidermis, mne - median eye nerve, Mv - microvilli, RO - rostrum, Tb - tubular body.

of the median eye. Again, we rarely found nuclei of retinula cells, so perhaps only two such cells form the rhabdom. Contrary to the median eye, we never found nuclei underneath the corneagen layer (Figs 6a, b), so we interpret these eyes as everted. The perikarya (cell bodies) of the retinula cells are located laterally and are connected to the receptor poles by slender cell processes (Fig. 6c). The exobothridial setae (exa, exp) are innervated by two dendrites ending with tubular bodies and thus are mechanosensitive (Figs 6c, d; 7d). We saw several small nerves devoid of glia cells close to the eyes. But since other sensory structures (bothridial and exobothridial setae) are in the vicinity of the eyes, and because of the limited amount of material to study, we could not determine which would belong to the eyes.

4. Discussion

The eyes of *Heterochthonius gibbus* show the general structures of arachnid (or even euarthropod) ocelli (Paulus 1979): a cuticular cornea (lens) overlying a corneagen (lentigen) layer, retinula (receptor) cells with rhabdomeric microvilli, perikarya of the retinula cells located peripherally, close to the rhabdomeres, a cup of pigment cells underlying the receptor cells.

These eyes are thus of a plesiomorphic morphology and are located in front of the dorsosejugal furrow and thus in a position which is plesiomorphic for actinotrichid mites (or even for all Arachnida) (see, e.g., Paulus 1979, Alberti & Fernandez 1988, 1990, Moritz

1993, Alberti & Coons 1999). This further supports, on the other hand, the conclusion that the lenticulus (and clear spots) of certain oribatid mites are secondarily evolved structures.

The median eye is of particular interest. It very likely represents the homologon of the median eyes of other Arachnida or even of all Chelicerata (Coineau 1970) and has hence been frequently termed this way. Such an eye apparently does not occur in anactinotrichid mites (Alberti & Coons 1999, Alberti 2006). In early derivative Actinotrichida it is associated with a dorsomedian protuberance named naso. In fact the eye is located on the ventral side of this protuberance and plesiomorphically consists of two eyes which are close together and more or less fused (Grandjean 1958). Such a position is found in the early derivative oribatid groups, Palaeosomata and some Enarthronota (Brachychthoniidae), but also in some Endeostigmata and Prostigmata (e.g., Grandjean 1939, 1943, 1954b, 1958, Coineau 1970, Alberti & Coons 1999, Norton & Behan-Pelletier 2009). In those species that have been investigated in detail, the retina of the eye (or the pair of eyes) is directed ventrally and is covered by a ventral (lower) cornea pointing into a small frontal cavity (e.g., Oribatida: Brachychthoniidae, Prostigmata: Caeculidae) established by an integumental fold projecting from the posterior (Grandjean 1958, Coineau 1970, Wachmann et al. 1974, Haupt & Coineau 2002). Frequently, the dorsal cuticle overlying the median eye(s) may form a (secondary) dorsal (upper) cornea, which may become morphologically and functionally dominant (e.g., Caeculidae, Penthalodidae, Wachmann et al. 1974, Haupt & Coineau 2002). Finally, the naso may become regressive and the median eye may be moved posteriorly being finally located closely behind the anterior border of the idiosoma. An example of this posterodorsal movement having occurred within the same family may be found in the snout mites (Bdellidae, Prostigmata), in which *Spinibdella cronini* and *Biscirus silvaticus* have an eye in the plesiomorphic location and orientation, whereas *Cyta latirostis* has a dorsomedian eye (Alberti 1975, Alberti & Coons 1999) like that of certain freshwater mites (Hydrachnidia: e.g., *Hydryphantes ruber*, Mischke 1981). By this movement, the retina comes into an everted orientation with regard to the (secondary) cornea (and incident light) (Mischke 1981, Alberti et al. 1991, Alberti & Coons 1999).

With respect to *H. gibbus*, our few observations indicate that the anterior eye is the homologue of the median eyes mentioned above. It is composed of two eyes (almost fused), and its retina points ventrally into a small frontal cavity. The dorsal cornea located opposite the retina (and making it appearing inverted) is likely a secondary feature, as in the other examples mentioned above. Interestingly, a frontal cavity appears in the development of the median eyes of certain non-mite Arachnida (e.g., Schimkewitsch 1906, Dawydoff 1949, Moritz 1957, Coineau 1970, Homann 1971). We think that the two anterior eyes of *Ovochthonius rossicus* are homologous to the median eyes of *H. gibbus* and *H. caucasicus* being simply more separated and thus demonstrating the paired nature of the median eye evidently. The lateral eyes of this species apparently were reduced.

This interpretation contrasts with that published by Grandjean (1928) with respect to the median eye of *H. gibbus* (see Introduction). But it corroborates the suggestions of Grandjean (1958) concerning the evolution of the rostral tectum in Oribatida which integrates the naso and makes it more or less disappear. *Heterochthonius gibbus* may represent an intermediate stage conforming to Fig. 2J in Grandjean (1958).

Grandjean (1958) defined the small rostral setae as belonging to the naso ('Les poils rostraux sont poils du naso'). Since they are positioned at the anterior border of the body – and originally close to the anterior eye – and since they are mechanoreceptors they likely function as short-distance touch receptors. Their original function might be preventing mechanical damage of the eye.

The few TEM-observations on the median eyes of actinotrichid mites revealed some differences in components. In both caeculid and hydrachnid eyes, no specific pigment cells have been seen (Wachmann et al. 1974, Mischke 1981). In contrast, pigment cells were found in median eyes of *Cyta latirostris* (Alberti et al. 1991), Penthalodidae (Haupt & Coineau 2002) and *H. gibbus* (this study). *C. latirostris* was the only species possessing receptor cells which contain probably crystalline particles (Alberti et al. 1991). The number of receptor cells may differ. In *Microcaeculus* six retinula cells were reported for each of the two retinas, while in *Hydryphantes* the single retina likely consists of five retinula cells. The numbers in penthalodid and bdellid median eyes was not reported and that of *H. gibbus* probably is 4 (or 5). The nerve of the median eye of *Microcaeculus* is enveloped by a sheath (glia) cell (Wachmann et al. 1974) in contrast to that of *Hydryphantes* and *Heterochthonius* (Mischke 1981, this study). This feature was mentioned neither for the bdellids (Alberti et al. 1991) nor penthalodids (Haupt & Coineau 2002).

The lateral eyes of *H. gibbus* are smaller than the median eye and have a more pronounced cornea. Otherwise their fine structure is similar, but the components are arranged in a different way. The small retina is everted and the cell bodies of the receptor cells containing the nuclei are laterally located. Apparently, the rhabdomeres are connected with the perikarya via slender processes. Such a situation was also observed in the lateral eyes of the spider mite *Tetranychus urticae* (Tetranychidae, Prostigmata) (Mills 1974), but not in *Microcaeculus* (Wachmann 1975) or *Hydryphantes* (Mischke 1981). In contrast to the median eyes of *Hydryphantes* and *Heterochthonius*, but similar to the median eye of *Microcaeculus*, the lateral eye nerves of *Hydryphantes, Tetranychus* and *Microcaeculus* are provided with glia cells (Mills 1974, Wachmann 1975, Mischke 1981). This is uncertain in *H. gibbus,* but all the nerves seen in the vicinity of the lateral eyes lacked a glia sheath. As mentioned already, one or two pairs of lateral eyes may occur in Endeostigmata and Prostigmata. These are located in front of the dorsosejugal furrow, like the single pair of *H. gibbus*. In taxa having two pairs, the eyes may show different morphologies and functions (see Alberti & Coons 1999 with further ref.). Presently it seems difficult to decide whether one pair or two pairs is the plesiomorphic condition in Actinotrichida.

A vitreous cone (also called vitreous body), a prominent transparent refractive structure located between cuticular lens and receptor cells, was reported in the anterior lateral eye of *Tetranychus urticae* (Mills 1974). However, this structure has not been found in other mites studied fine structurally, including *H. gibbus* (Alberti & Coons 1999).

The exobothridial setae of *H. gibbus* likely serve primarily the same function as the rostral setae, i.e. as mechanoreceptors preventing damage to eyes by nearby substrate particles, etc. According to Norton & Behan-Pelletier (2009), the exobothridials are the prodorsal setae most susceptible to loss, which may be understandable since most oribatid mites lost the lateral eyes. In contrast the rostral setae insert close to the anterior border of the rostral tectum in stegasime oribatid mites and thus detecting obstacles close to the gnathosoma may remain important and they are thus very stable setae.

Regarding the function of the eyes of *H. gibbus* nothing more can be said than that they are most likely capable of detecting the intensity and direction of incident light (concluding by analogy with ocelli of *Tetranychus urticae* or other ocelli of Invertebrates, e.g., Mc Enroe 1969, Penzlin 1996).

Considering the evolution of photosensitivity in oribatid mites, the following scenario may be suggested (for discussions on phylogenetic hypotheses on Oribatida see, e.g., Hauman 1991, Norton 1998, Woas 2002, Norton & Behan-Pelletier 2009):

After having invaded the dark and damp soils the early oribatid mites, like many cave-dwelling animals, lost the primary eyes completely with few exceptions (some Palaeosomata, some Enarthronota including *H. gibbus*, perhaps *Galapagacarus schatzi*). The reasons, why only these few taxa retained the eyes are not yet known.

Probably all oribatid mites, whether they have distinct eyes or something similar or not, are photosensitive and many avoid exposure to light (Vitzthum 1940/43, Grandjean 1961, but see, e.g., Riha 1951, Pauly 1959). Having lost the eyes, photosensitivity depends on sensitivity of neurons, likely of the synganglion.

Middle-derivative oribatid mites (such as *Archegozetes longisetosus*, Alberti et al. 2003, see also Norton 1998) evolved preventricular glands, i.e. small anterior diverticles of the ventriculus paralleling the synganglion and containing dense granules (so-called 'organes racémiformes'). These granules, spherites, primarily serve as mineral deposits ($CaCO_3$), which may be used to buffer the hemolymph under certain conditions (compare calciferous glands of Lumbricidae, Peters & Walldorf 1986, Jamieson 1992). They furthermore may serve for detoxification in storing, e.g., heavy metals which might become bioavailable in acid soils. Note that oribatid mites predominate in acid soils as a faunal element (see Ludwig et al. 1992, Kratzmann et al. 1993, Alberti et al. 1996). As a side-effect the granules may have influenced photosensitivity by providing a shading effect that could give information about the direction of light incidence.

Making the cuticle above the synganglion transparent (clear spot) and evolving lamellated bodies as specific photoreceptor sites may have further improved this capacity.

Elevating the lamellated body dorsally underneath a cuticle forming a uni- or biconvex lens (lenticulus), and providing these with specific pigment cells (likely) evolved from the fat body, increased the effectiveness of this system (Alberti & Fernandez 1988, 1990). The lenticulus of, e.g., *Hydrozetes lemnae* is morphologically one of the most peculiar and – relative to body length (1:10) – one of the largest eyes in the animal kingdom (compare <without arms/legs>: *Sepia officinalis* 1:12, *Homo sapiens* 1:65). If we would have an eye as spectacular as *Hydrozetes* it would have the size of our fist. Presently, the selective advantage of having such a huge eye, such as positive effects on behavior or autecology, are unknown.

Whether this scenario reflects the true history or not, the lenticulus is a secondarily evolved, apomorphic feature and thus certainly should be of value for phylogenetic systematics. Both structures (clear spots and lenticuli) have only been found in the so-called 'higher oribatid mites', the Brachypylina. However, as judged from the external aspect, such structures are not known from many other brachypyline taxa. Brachypyline species of Cymbaeremaeidae, Scutoverticidae, Hydrozetidae, Oripodidae, Chamobatidae, Euzetidae, Oribatellidae, Achipteriidae and Galumnidae showing lenticuli or clear spots were more or less intensively studied with TEM and all showed lamellated bodies as receptor processes (Alberti & Fernandez 1988, 1990, Alberti & Coons 1999, pers. observ.). Do species with very dense, deeply black cuticles lacking these external structures, e.g. species of Damaeidae or Carabodidae, have lamellated bodies? It seems likely that the lamellated bodies represent a synapomorphy, whereas lenticuli may have evolved several times independently from ancestors with lamellated bodies. Hence, future investigations should try to find out the occurrence of lamellated bodies within (higher) oribatid mites testing the hypothesis that this feature may define a monophyletic group of brachypyline mites.

The only exception presenting a structure also called lenticulus outside the Brachypylina is *Malacoangelia remiger* Berlese 1913, a middle-derivative mite (Hypochthonioidea, Enarthronota) (Grandjean 1935). However, Grandjean (1935) was not sure about the homology of this structure with the lenticuli of Brachypylina discussed above. The preliminary study of this structure by Alberti et al. (2001) indeed revealed that it is much unlikely to be a 'true' lenticulus.

Similarly enigmatic and exceptional is the occurrence of a light spot (unfortunately also termed lenticulus) in the middle of the prodorsum in one hermanniid species, *Galapagacarus schatzi* (Balogh 1985). The systematic position of Hermanniidae is different according to authors. However, all agree that they are close to the base of Brachypylina (see, e.g., Haumann, 1991, Woas 2002, Norton & Behan-Pelletier 2009). Norton & Behan-Pelletier (2009) speculate on the basis of its position that this structure 'may represent a transitional organ linking prodorsal eyes and the light-receptive notogastral lenticulus … of many Brachypylina'. According to our interpretations, this seems unlikely. A fine structural study certainly would be very interesting.

A further aspect concerns the astigmatid mites (Astigmata, Astigmatina = Acaridida). Since astigmatid mites likely have evolved from middle-derivative oribatid mites (e.g., Norton 1998, Norton & Behan-Pelletier 2009, Lindquist et al. 2009, O'Connor 2009, Dabert et al. 2010) and since eyes evidently occur in some astigmatid mites (e.g., Evans 1992, O'Connor 2009), it would be very interesting to clarify their structure.

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